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

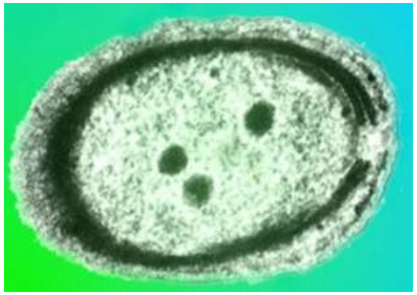
Lower nutrient requirements (Partensky, 1999)

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)

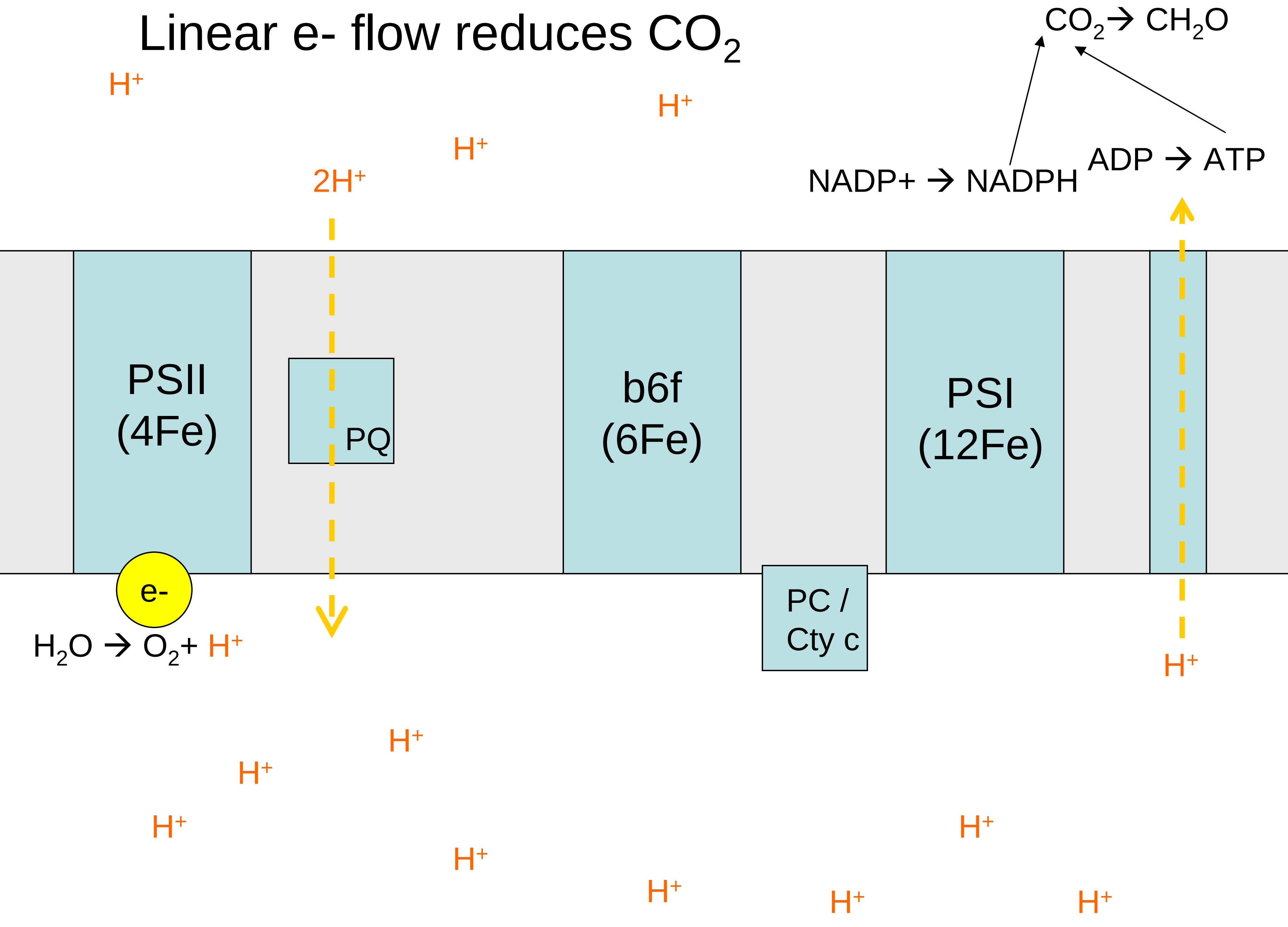
Lower Fe requirements (Strzepek, 2004; Partensky, 1999)



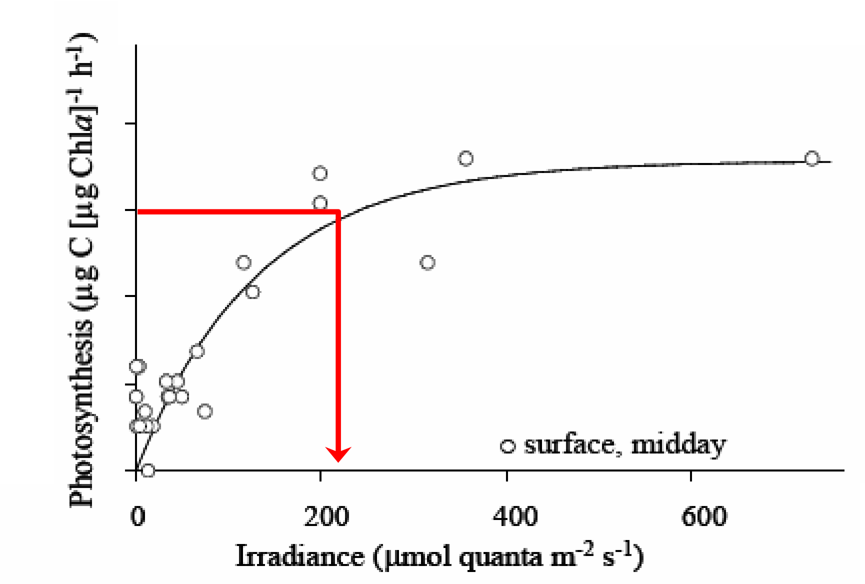
Prochlorococcus marinus
http://www.lbl.gov/Science-Articles/ Archive/assets/images/ 2003/Aug-14-2003/Prochlorococcus.jpg

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

Linear e- flow reduces CO_2



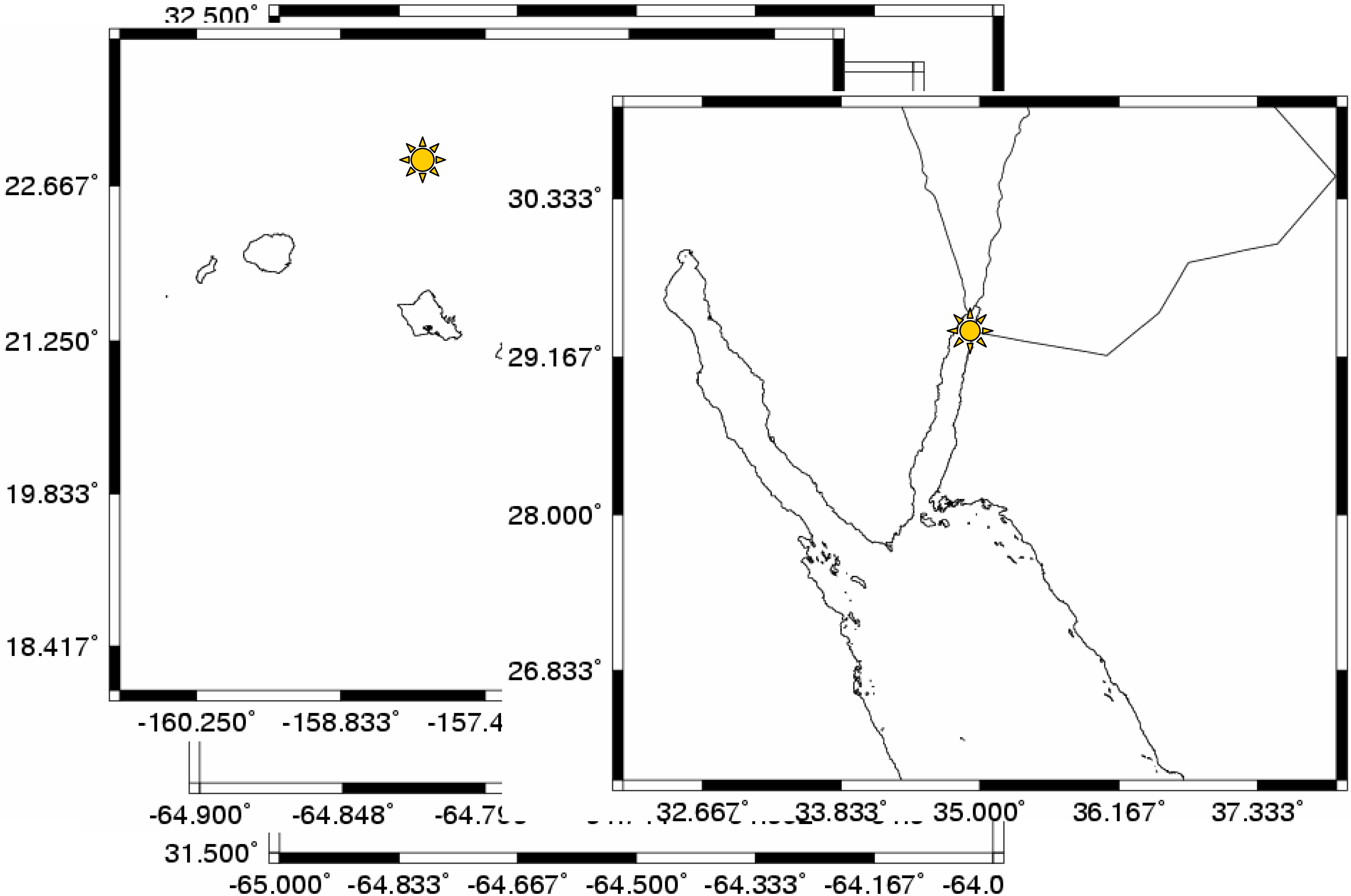
Carbon fixation saturates at relatively low irradiances



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

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

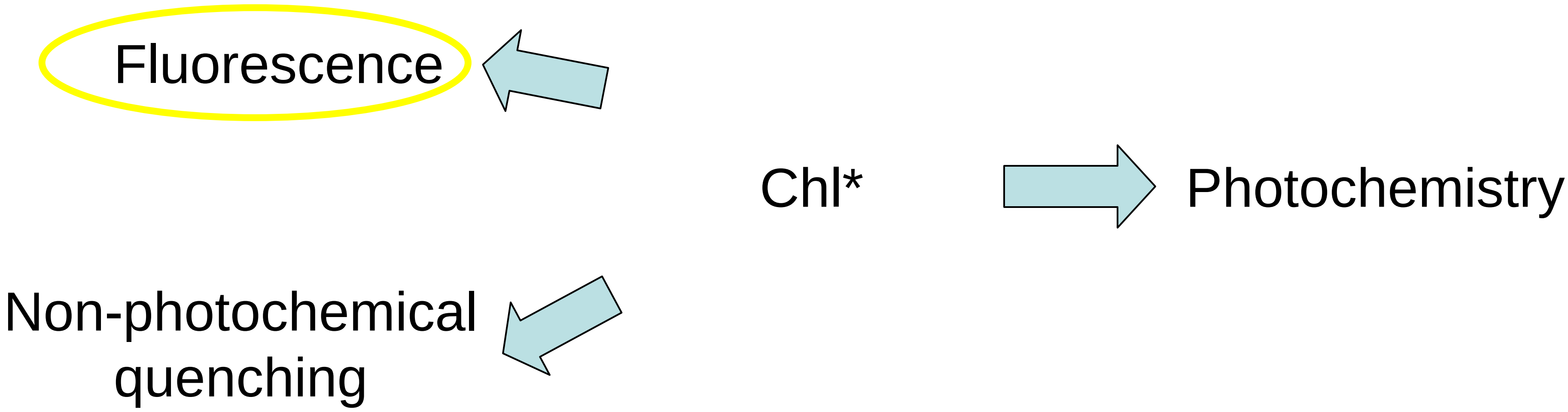
What adaptations allow picocyanobacteria to cope
with too much excitation energy?

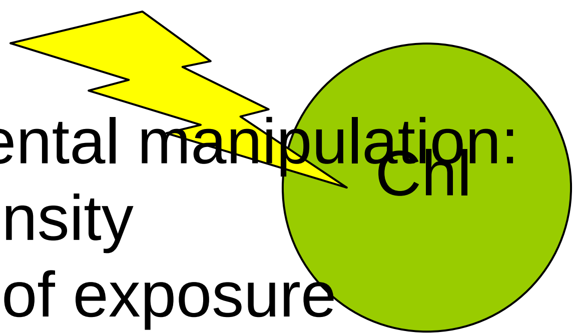


32.500°
22.667°
21.250°
19.833°
18.417°
-160.250°
-158.833°
30.333°
29.167°
28.000°
26.833°
-64.900°
-64.848°
32.667°
33.833°
35.000°
36.167°
37.333°
31.500°
-65.000°
-64.833°
-64.667°
-64.500°
-64.333°
-64.167°

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

Fluorescence measurements taken using a PAM fluorometer

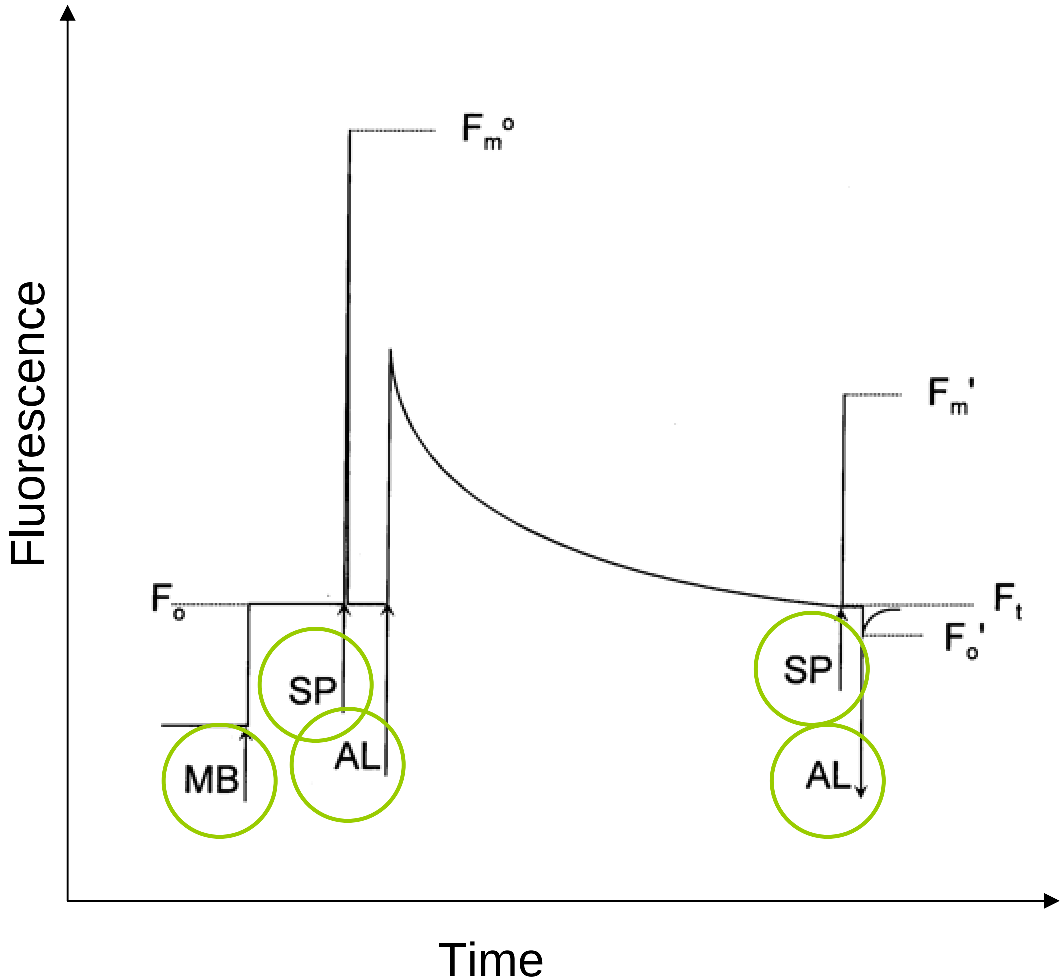




Allows experimental manipulation:

- Light intensity
- Duration of exposure
- Inhibitors of photosynthetic e- transport

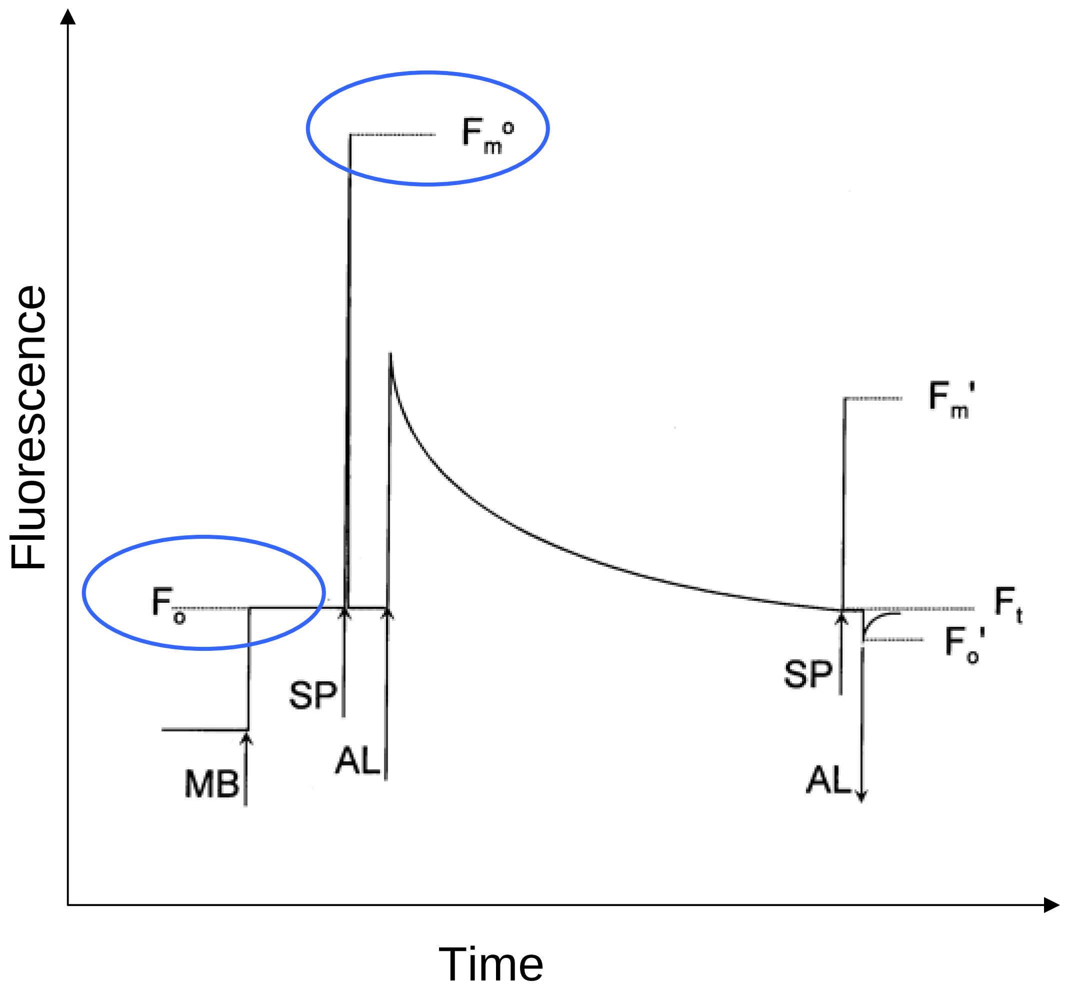
Sequence of a typical fluorescence trace



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

Maxwell and Johnson, 2000

Maximum quantum yield of PSII (Fv/Fm) gives the maximum quantum efficiency of PSII photochemistry

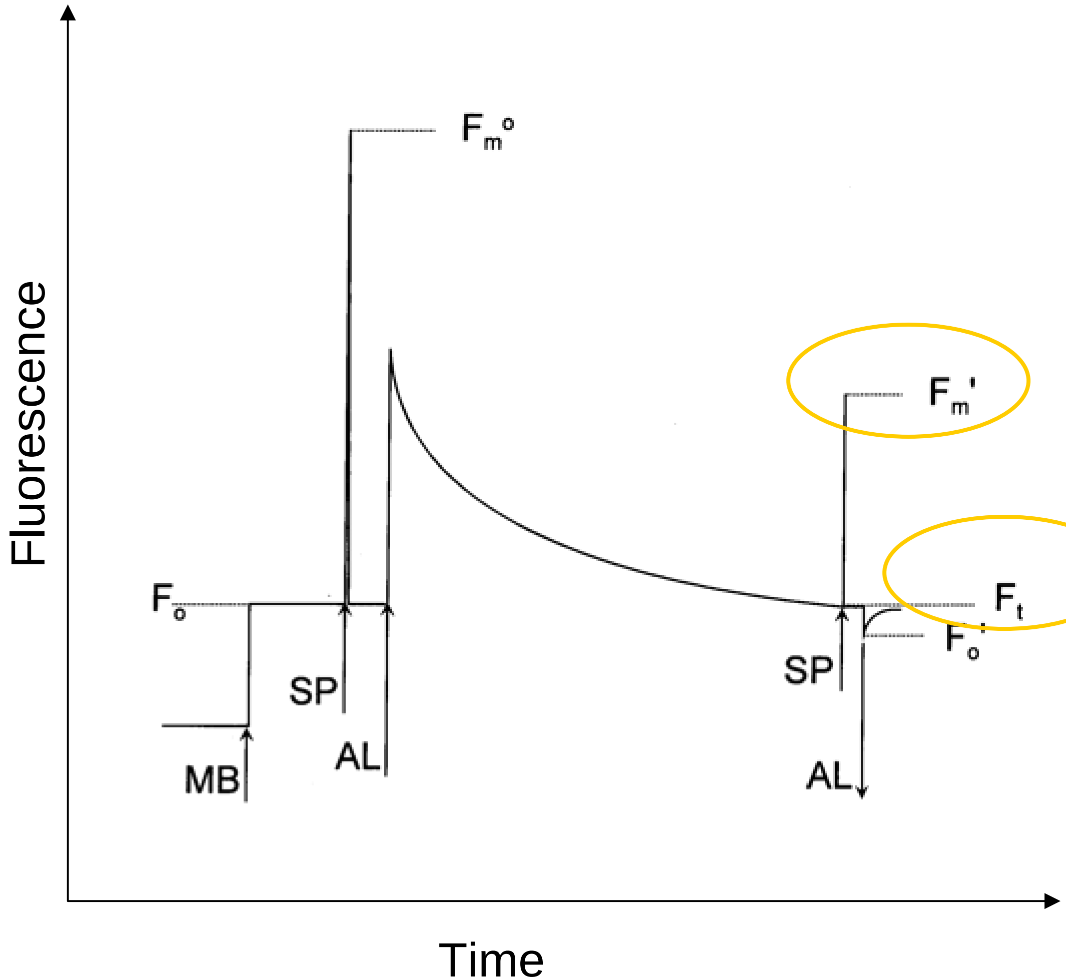


$$\frac{F_v}{F_m} = \frac{F_m - F_o}{F_m}$$

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

Maxwell and Johnson, 2000

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



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

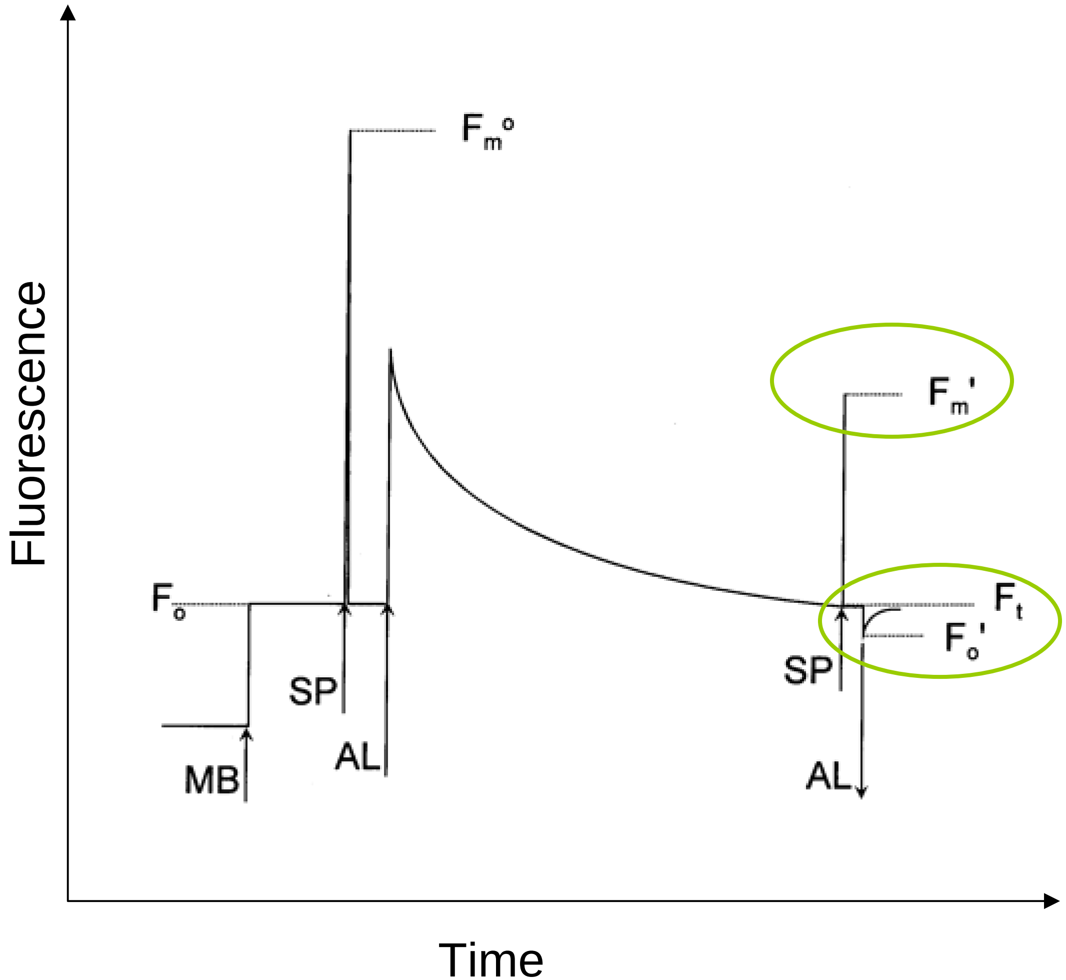
MB: Measuring beam

SP: Saturating pulse of light

AL: Actinic light

Maxwell and Johnson, 2000

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



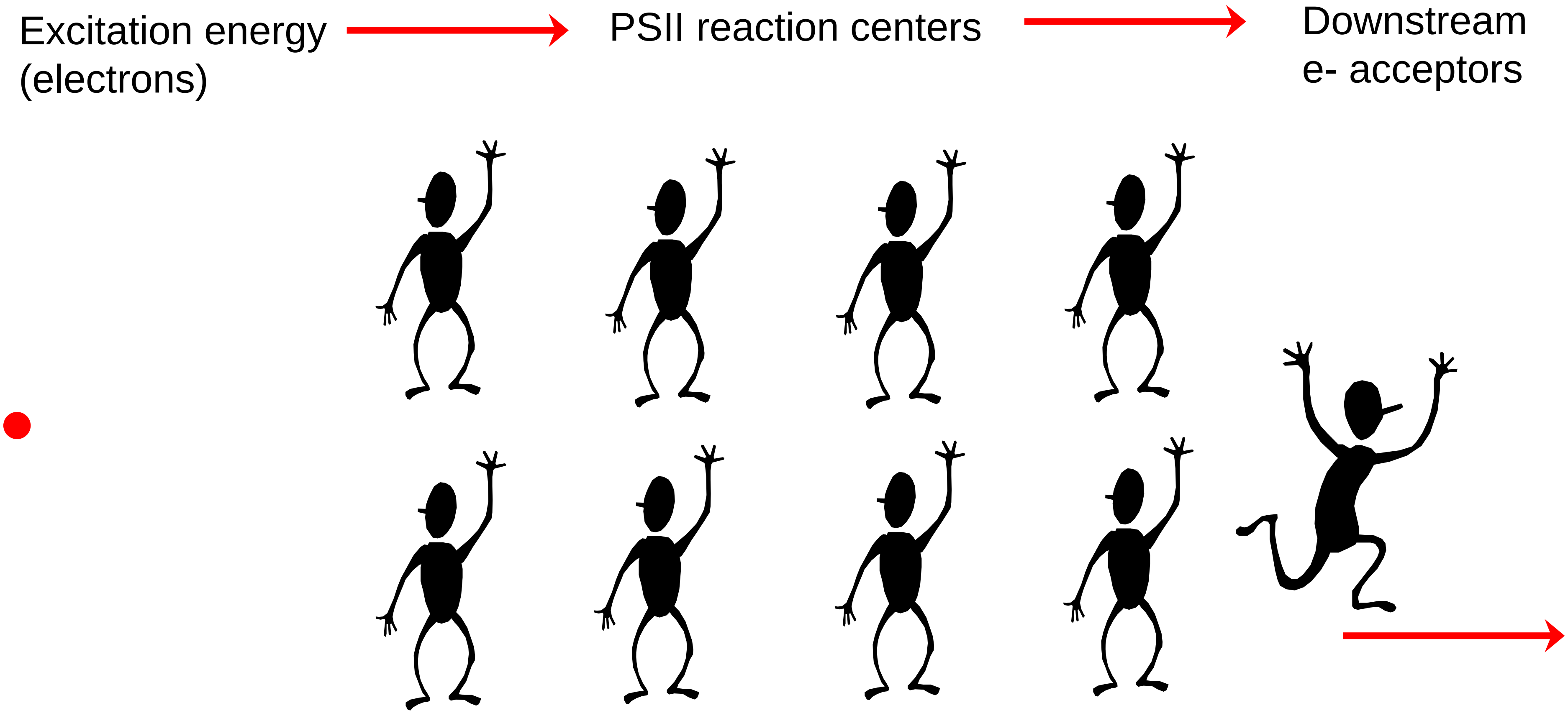
$$qP = \frac{F_m^{'} - F_t}{F_m^{'} - F_o^{'}}$$

MB: Measuring beam

SP: Saturating pulse of light

AL: Actinic light

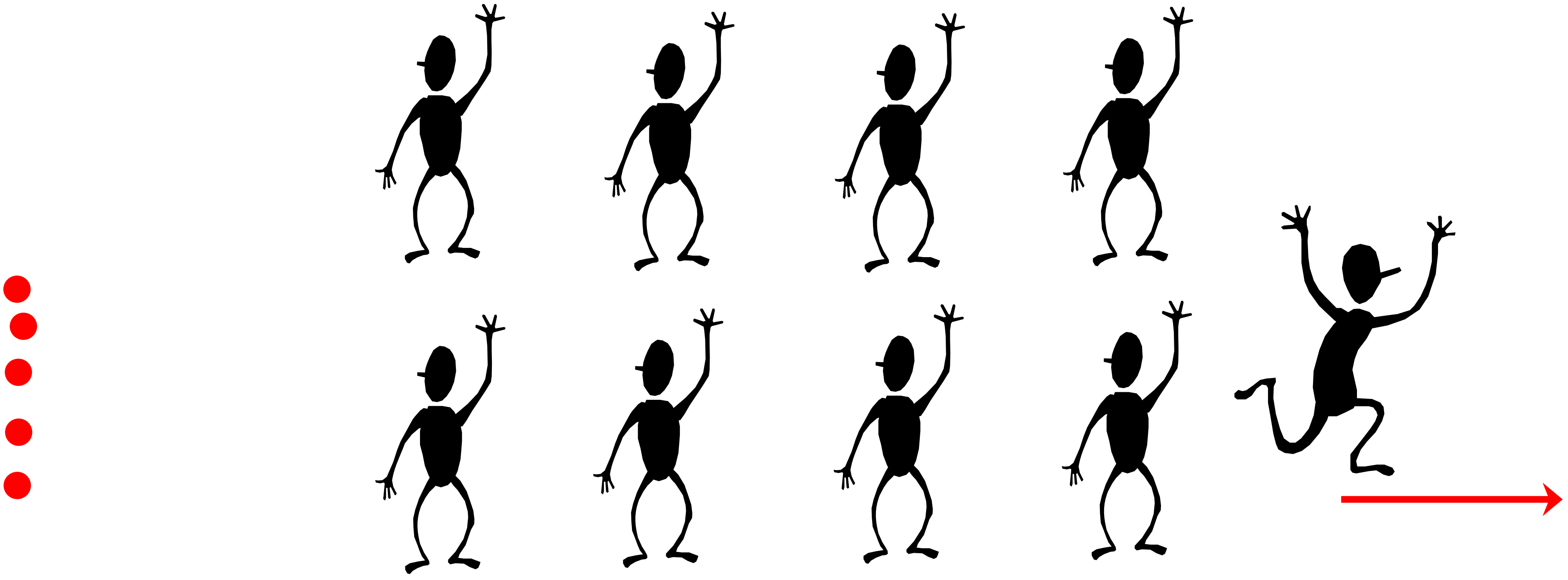
Maxwell and Johnson, 2000

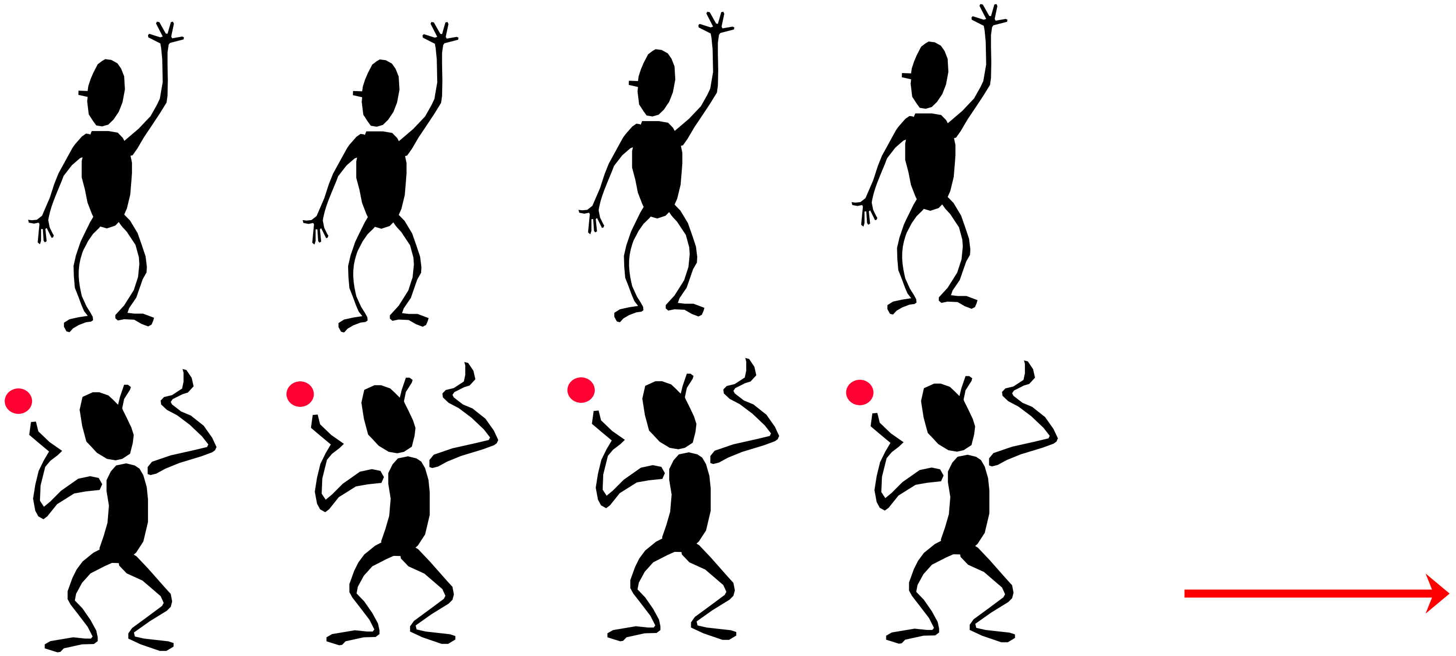


Fv/Fm represents the total number of workers able to do a job (8)

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

ΦPSII is related to the number of able workers available now (8)

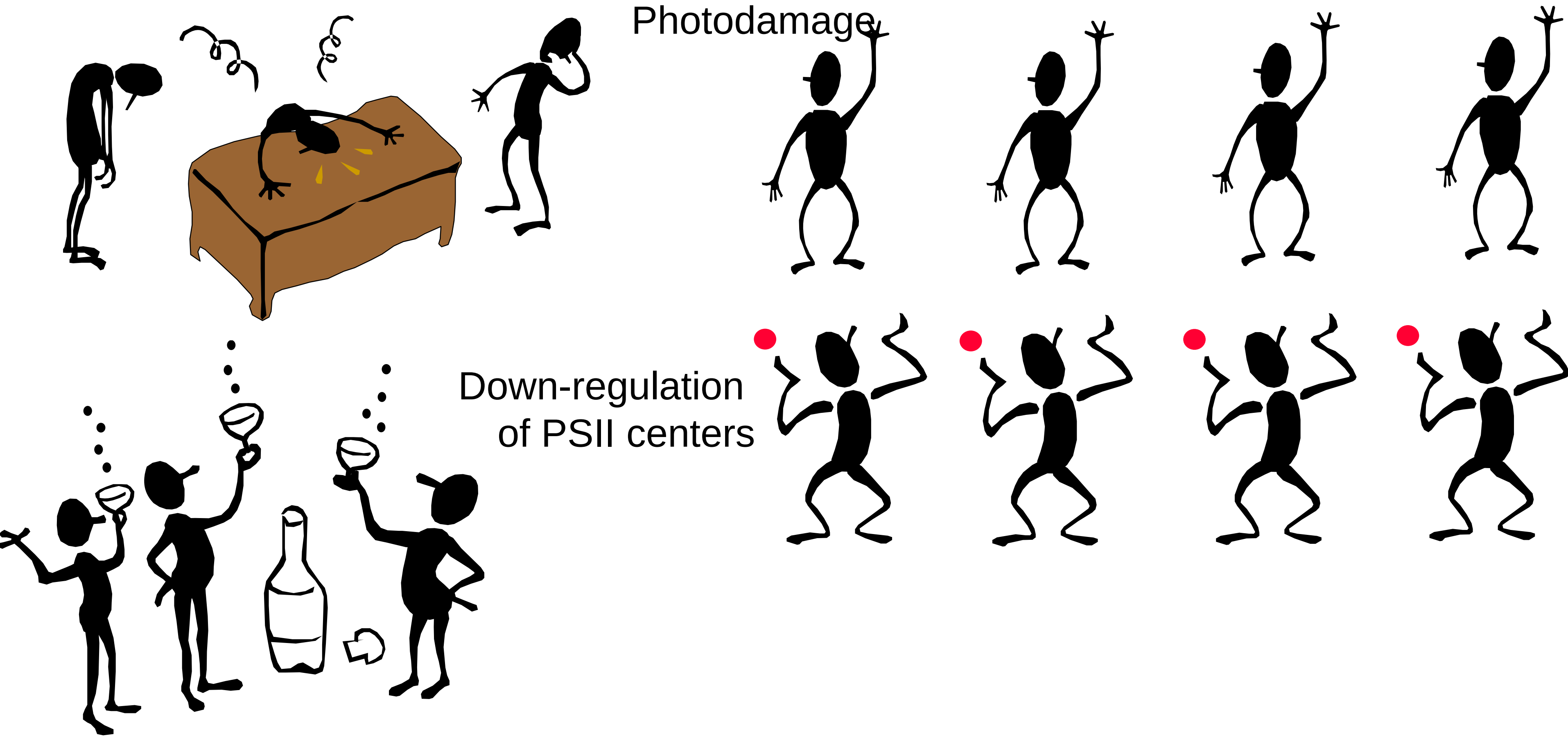




Fv/Fm represents the total number of workers able to do a job (8)

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

ΦPSII is related to the number of able workers available now (4)

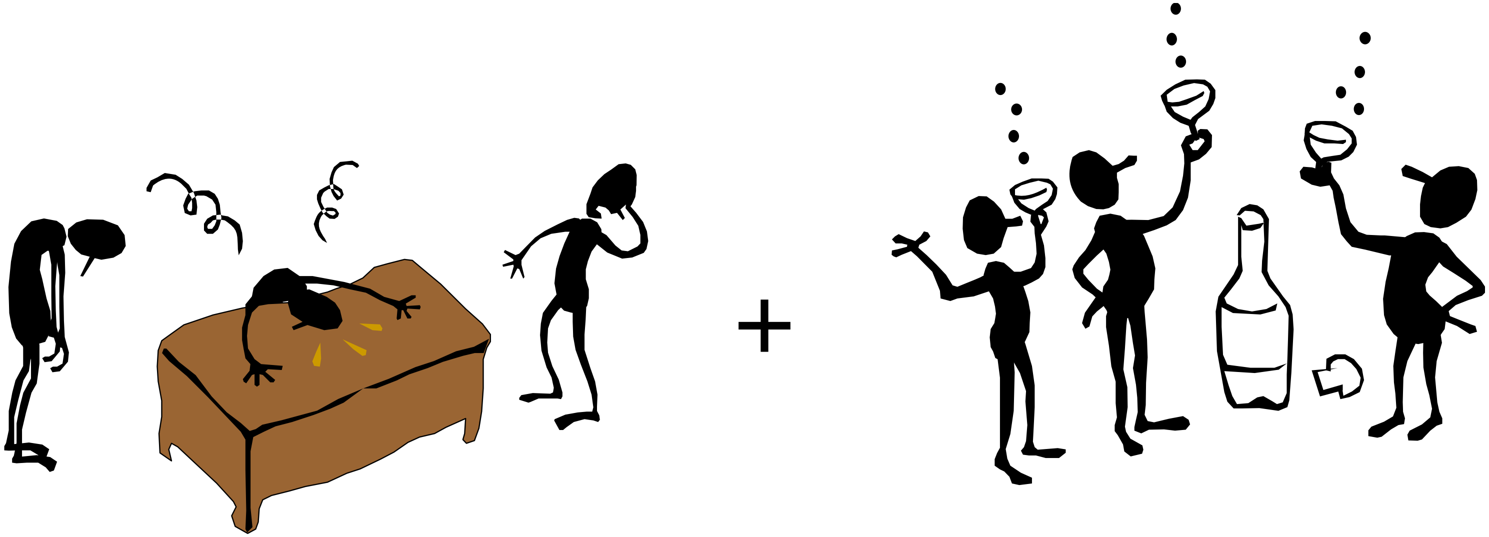


Fv/Fm represents the total number of workers able to do a job (2)

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

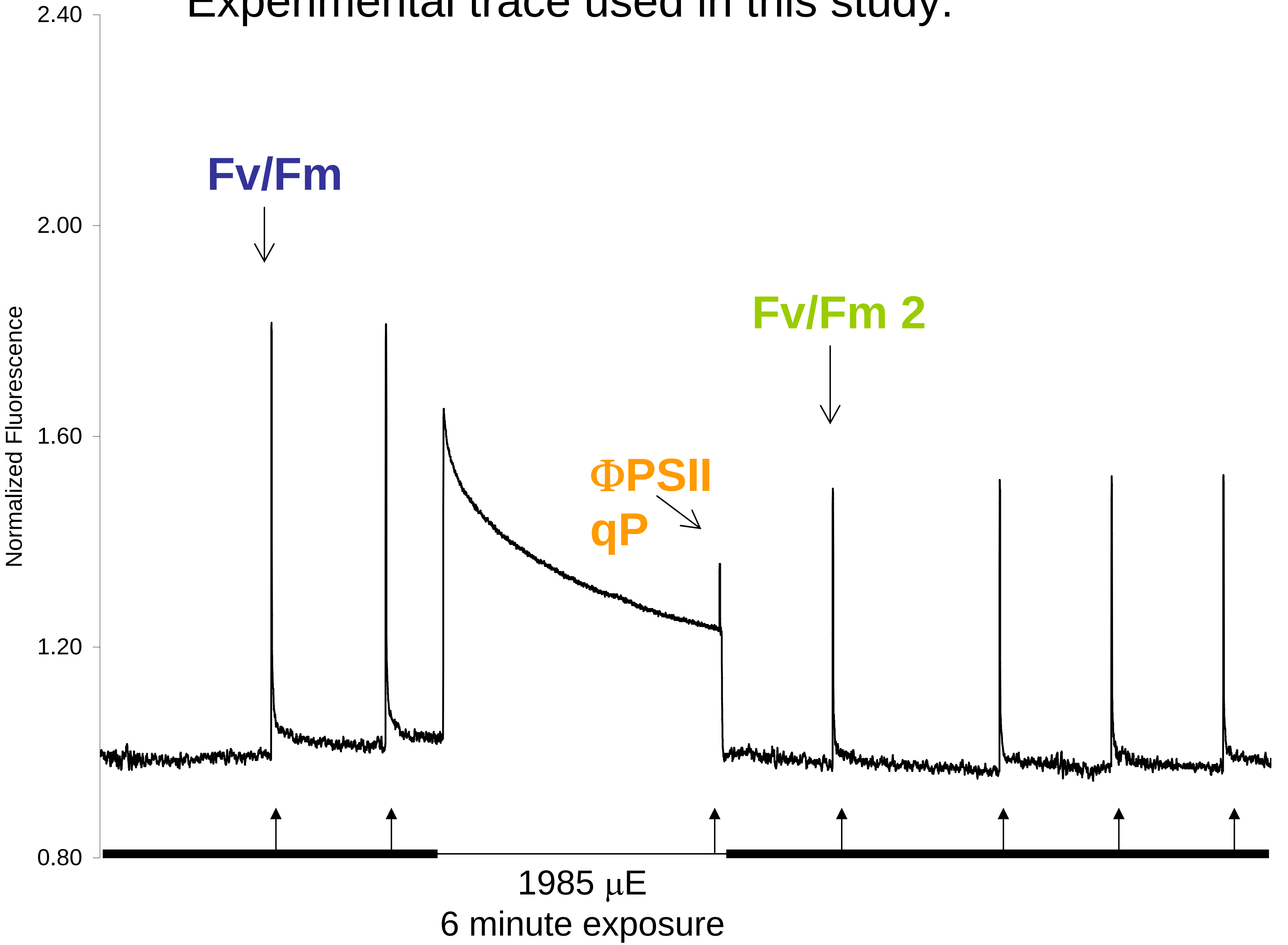
ΦPSII is related to the number of able workers available now (1)

Photoinhibition

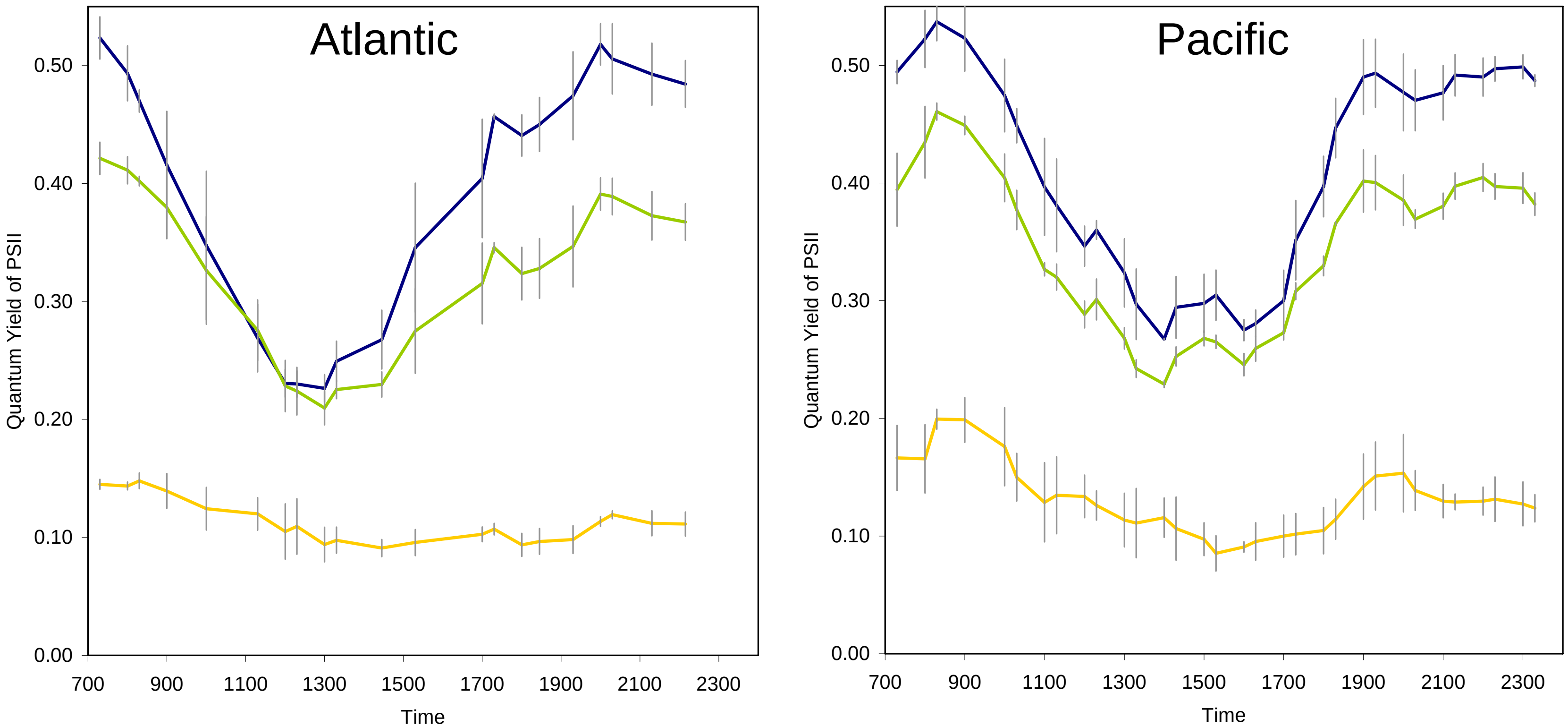


- The combination of PSII photodamage and down-regulation
- Causes a decrease in Fv/Fm

Experimental trace used in this study:

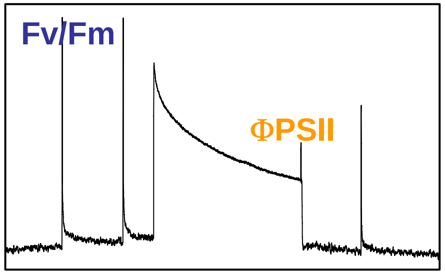


Diel quantum yields in two open ocean gyres

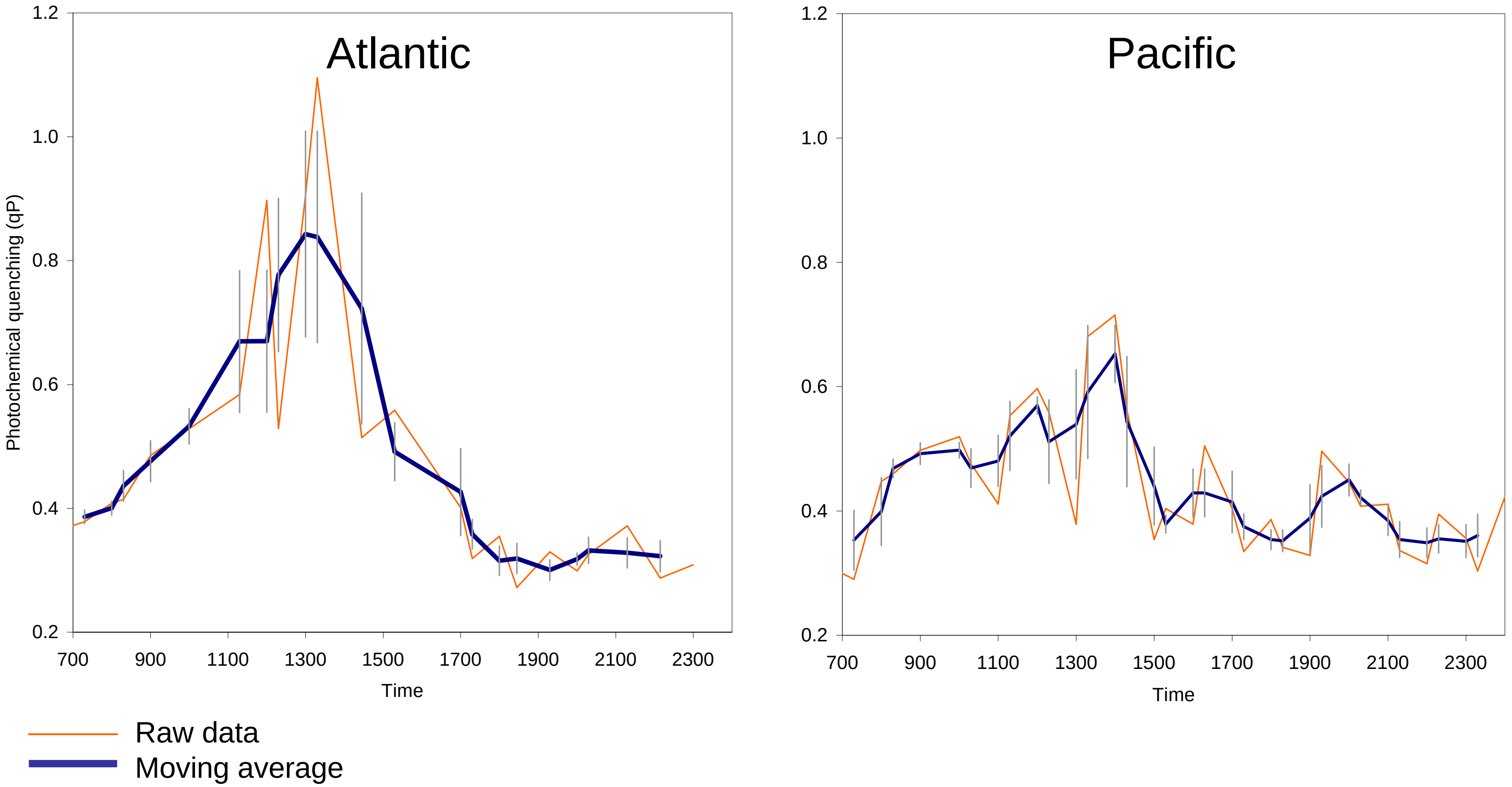


Midday photoinhibition reduces the maximum quantum yield (Fv/Fm) by 57%, with rapid recovery occurring by evening

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

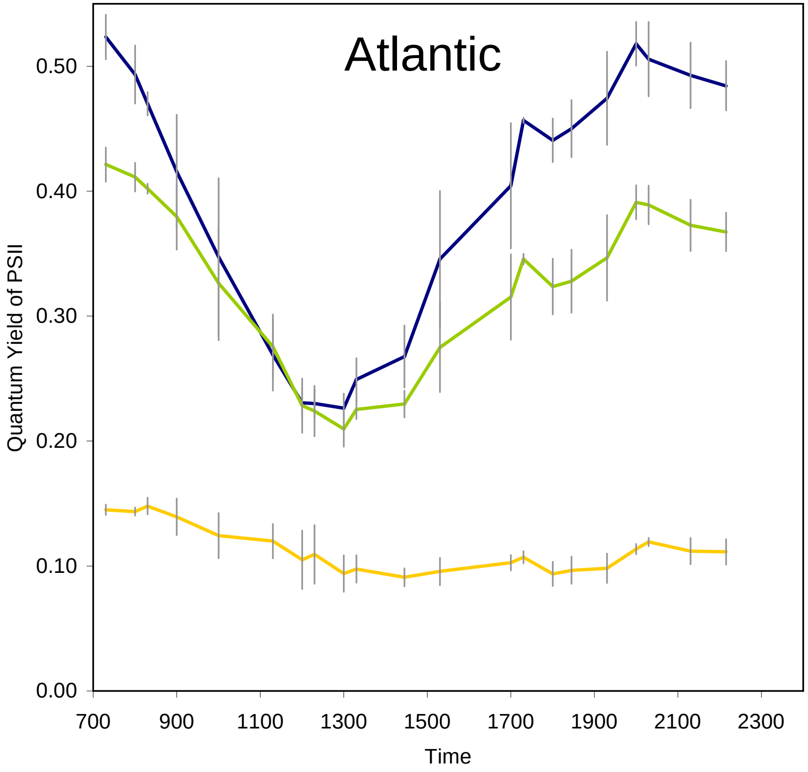


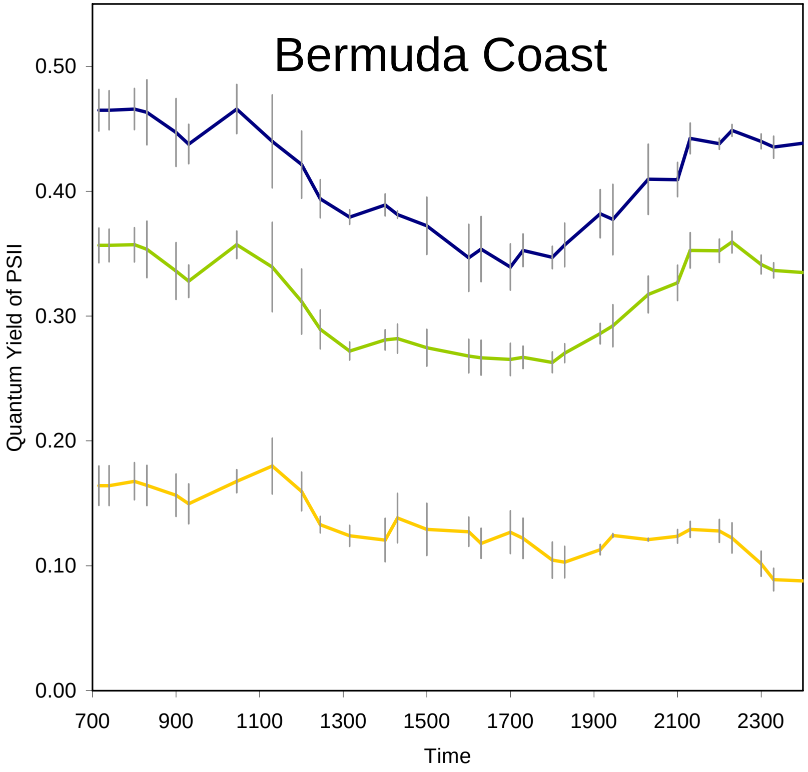
Diel photochemical quenching in two open ocean gyres



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

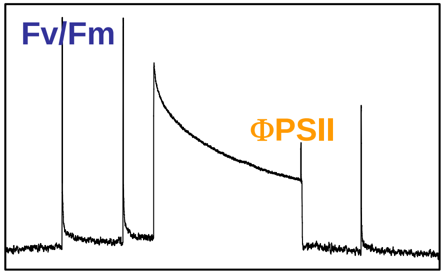
Diel quantum yields in a near-shore site (more nutrients)



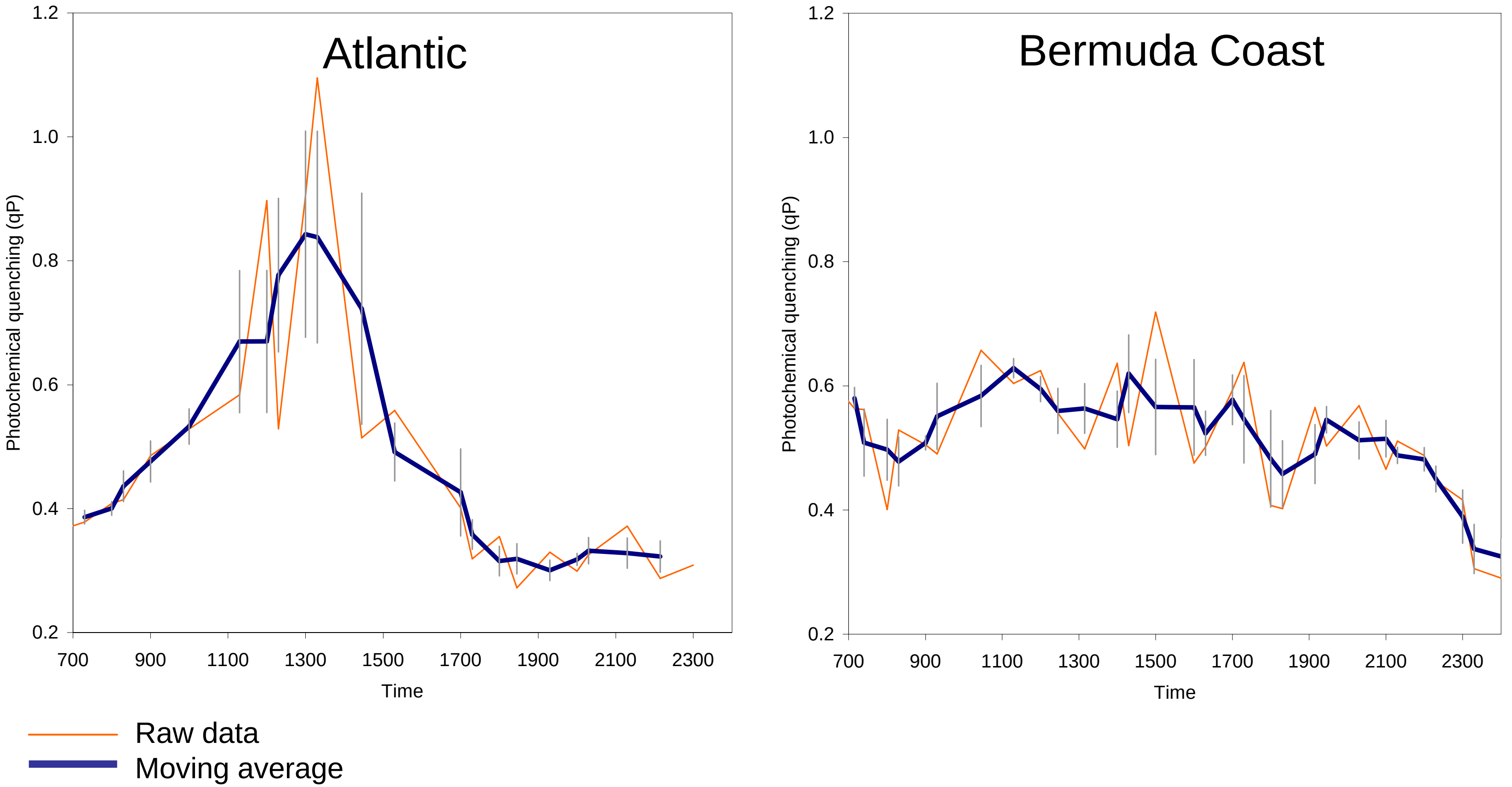


Midday photoinhibition of Fv/Fm is less pronounced

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



Diel photochemical quenching in a near-shore site

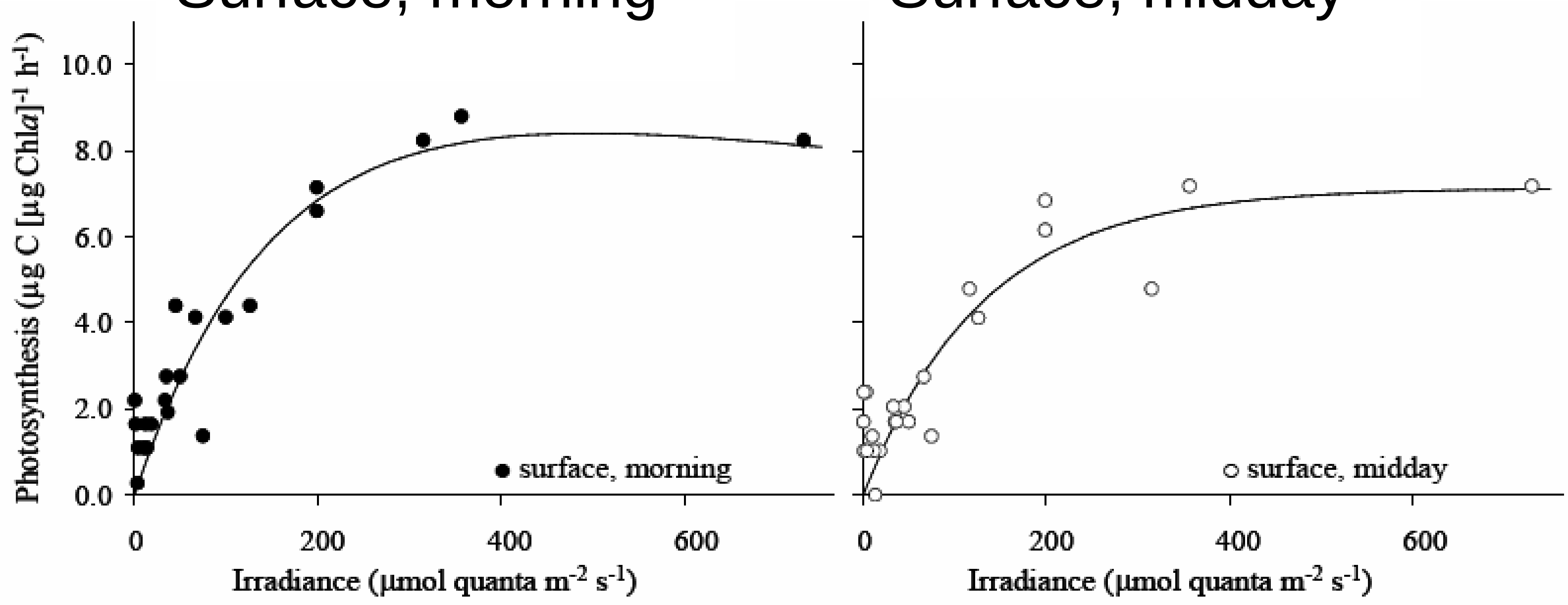


Less photoinhibition is mirrored by a less pronounced midday increase in the fraction of open reaction centers

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

Surface, morning

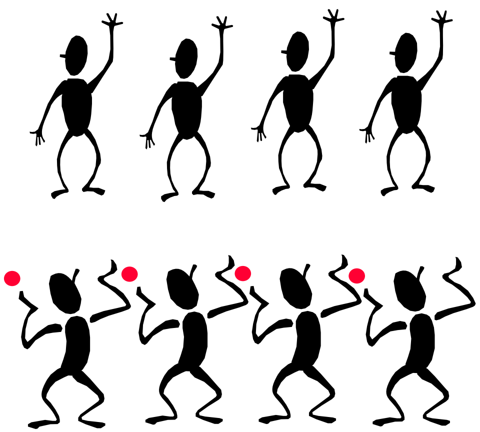
Surface, midday



In the surface open ocean…

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

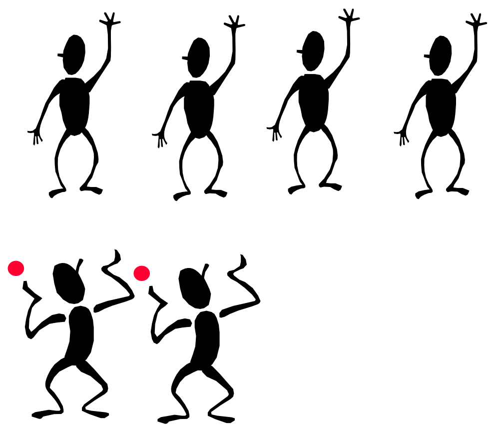
One way picocyanobacteria maintain photochemical efficiency is by increasing the portion of open reaction centers



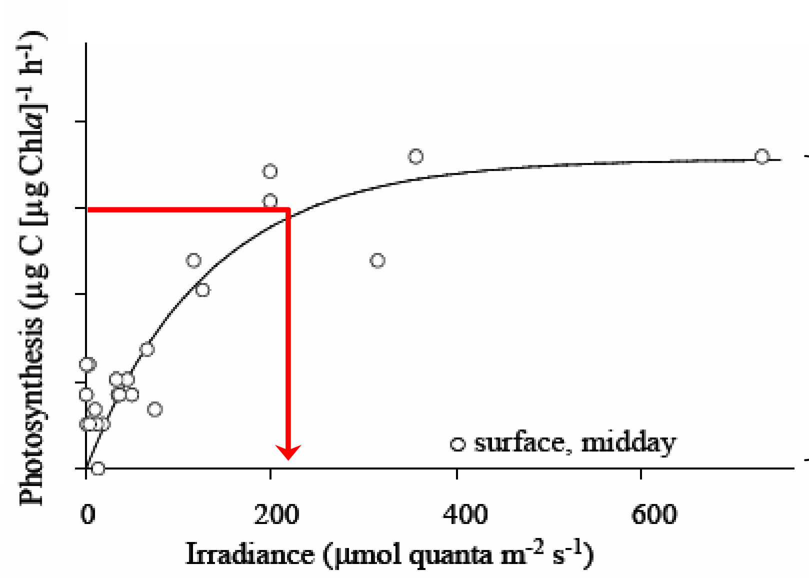
Fv/Fm (8)
qP (50%)
ΦPSII (4)

→

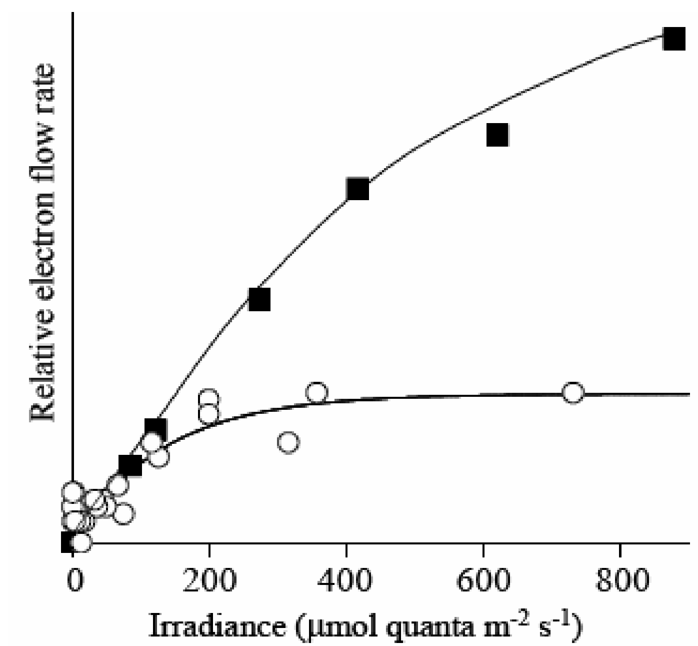
Fv/Fm (6)
qP (66%)
ΦPSII (4)



How do they do that?



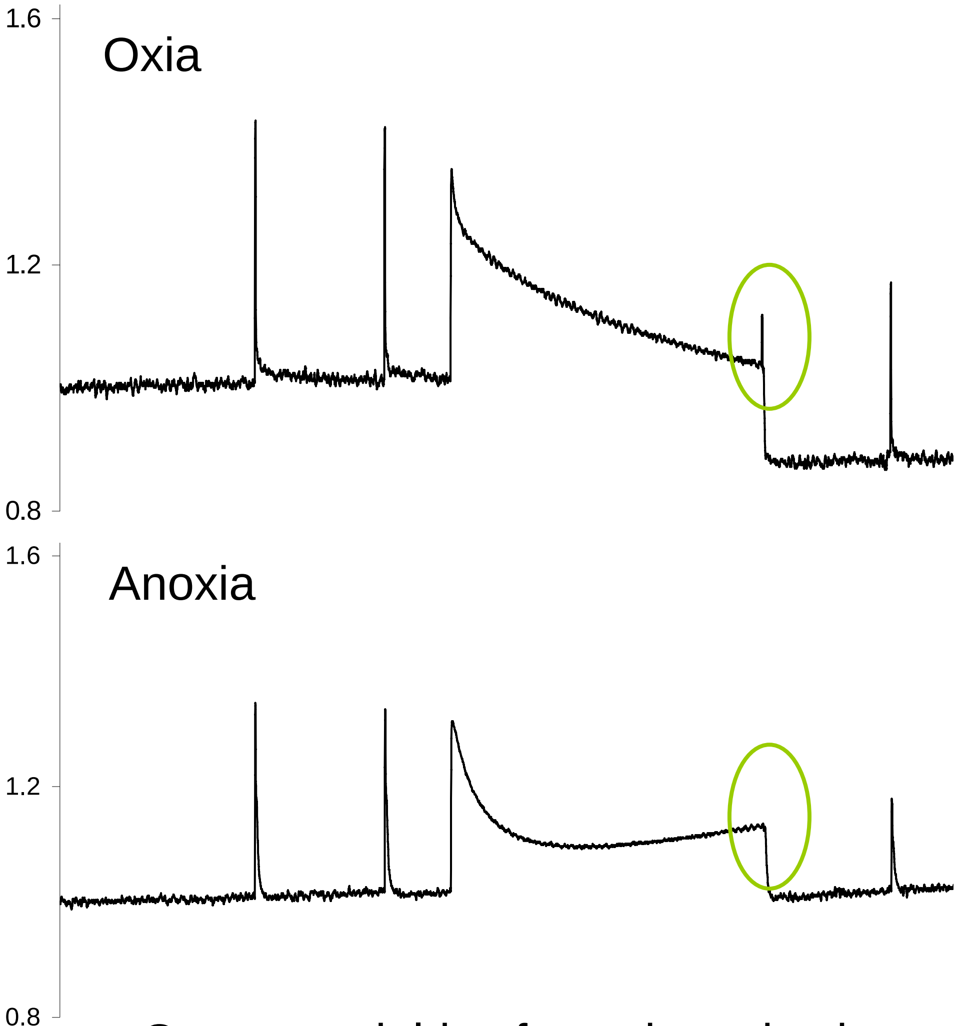
e- to CO_2

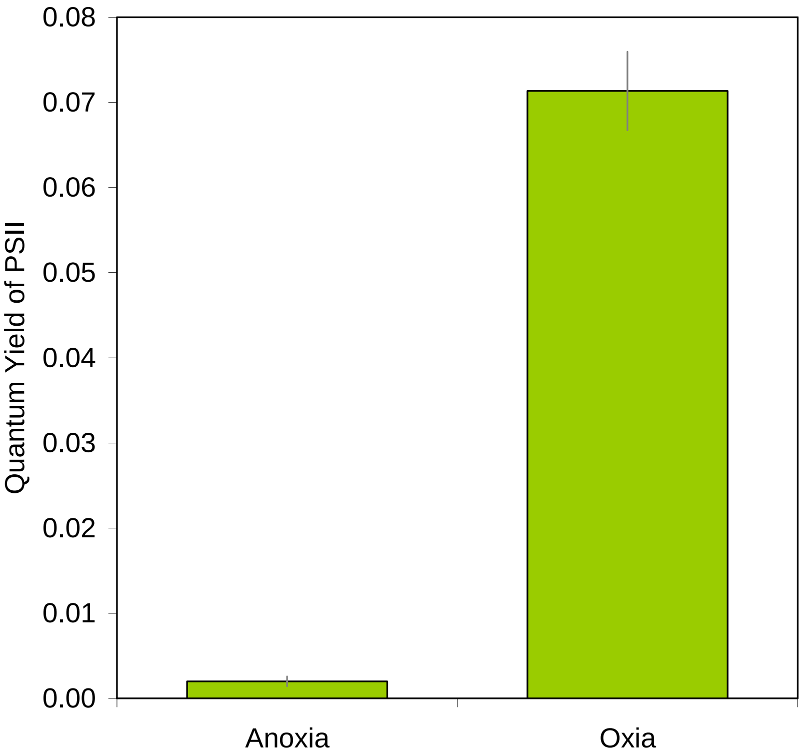


e- to all other acceptors than CO_2

e- to CO_2

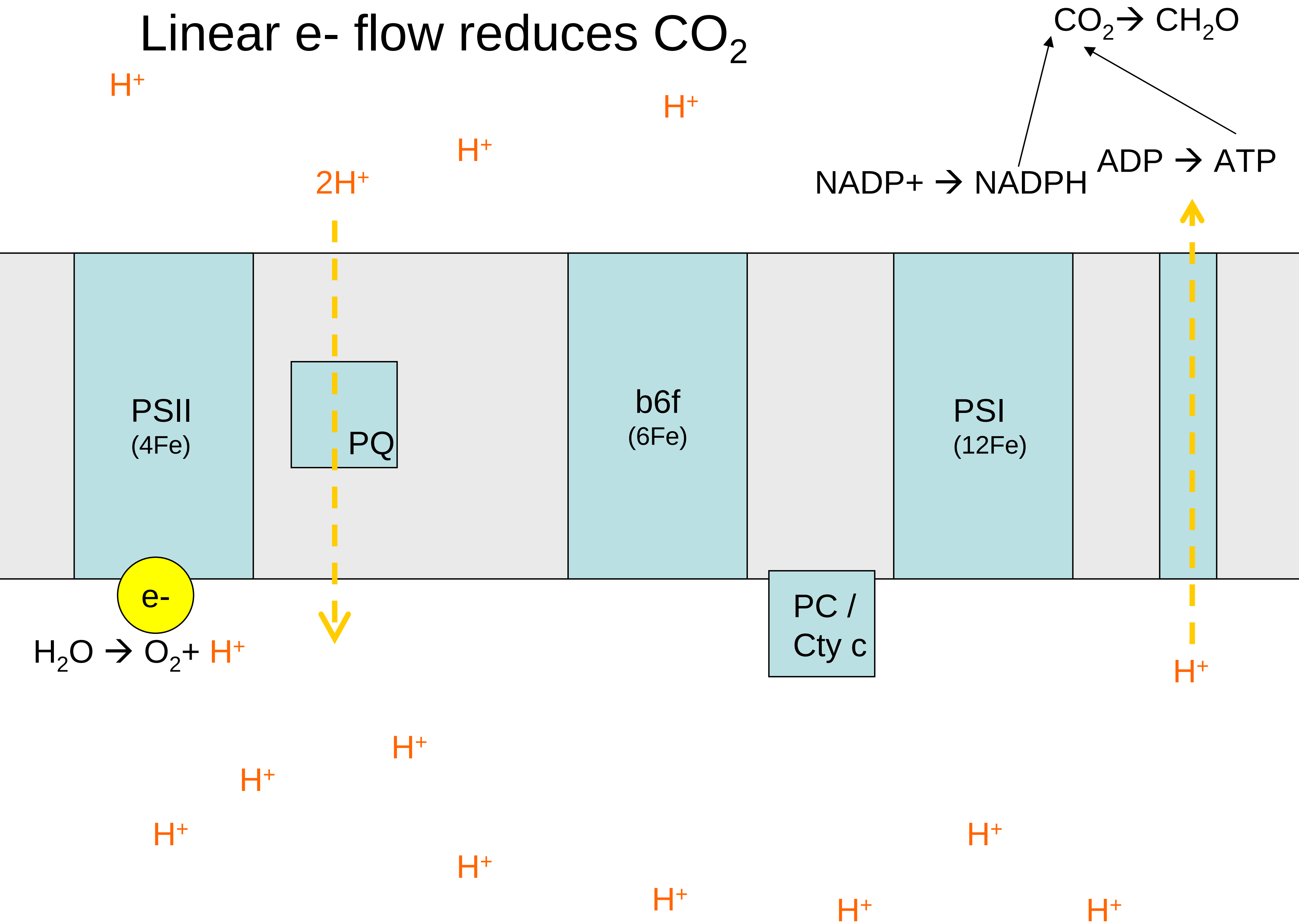
Oxygen is required to maintain open reaction centers



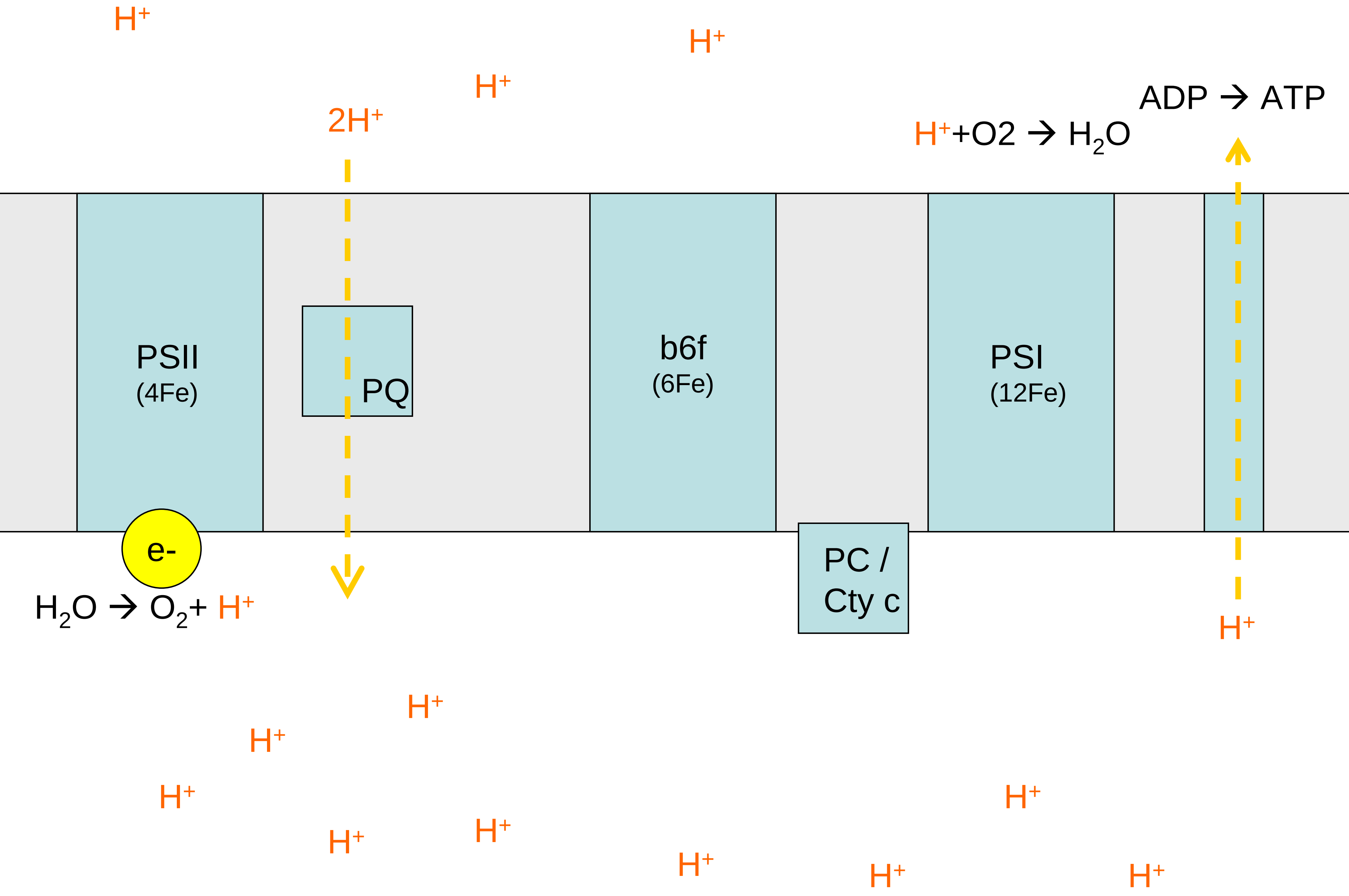


Quantum yields of anoxic and oxic samples during exposure to 1985 μE actinic light were significantly different (n=3, $p<0.0001$)

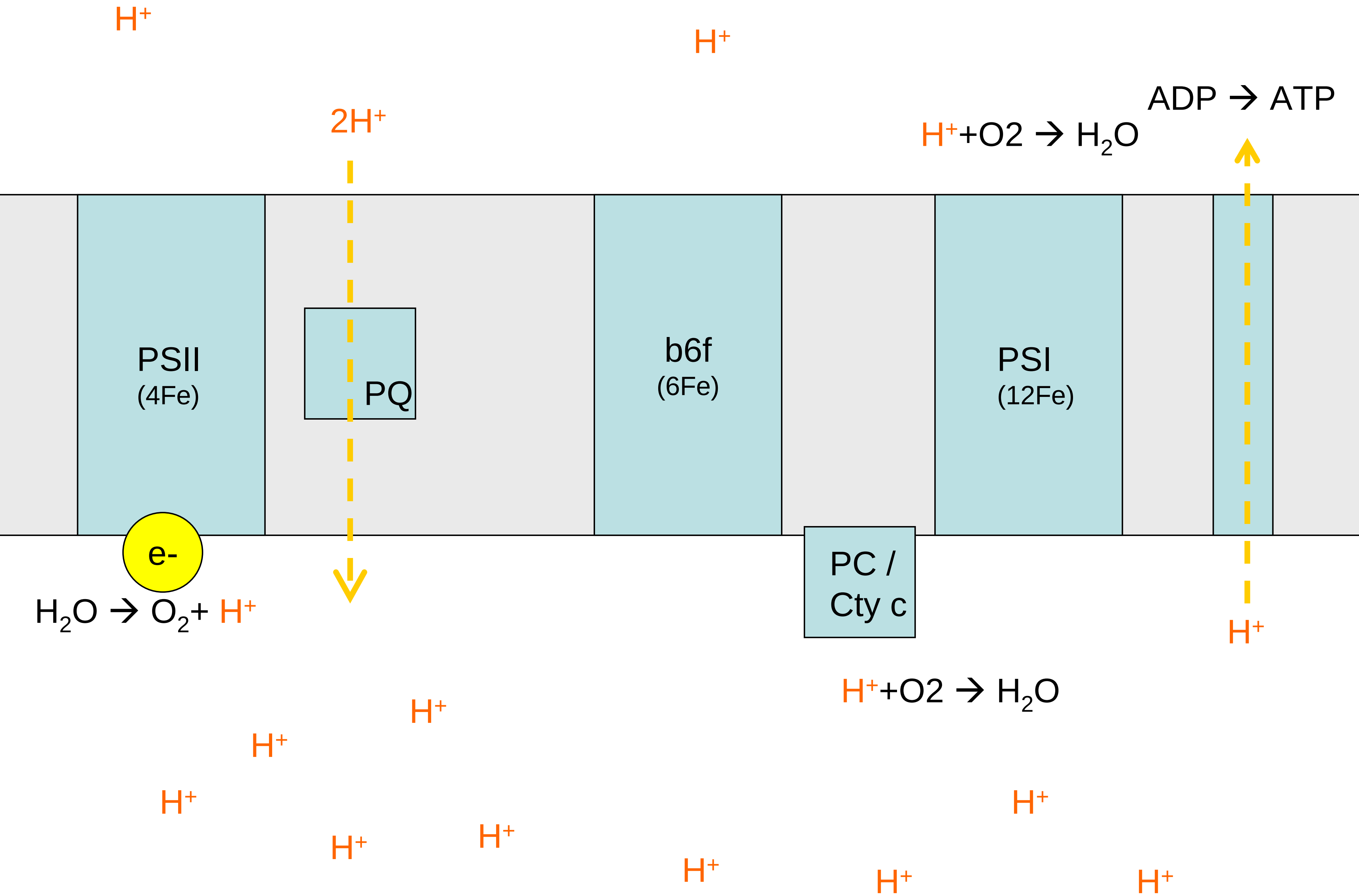
Linear e- flow reduces CO_2



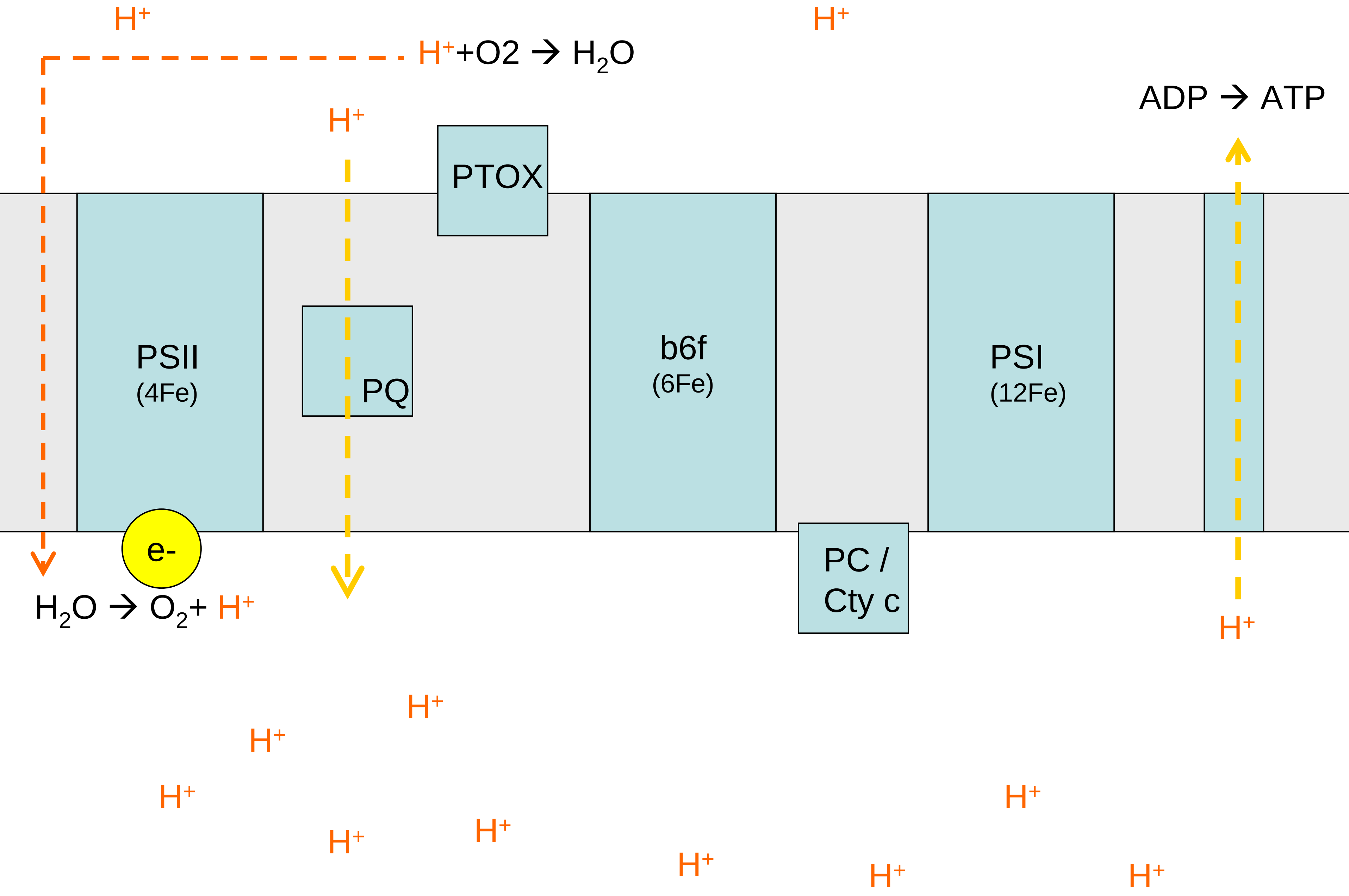
Mehler cycle reduces O_2



Cytochrome c oxidase cycle reduces O_2

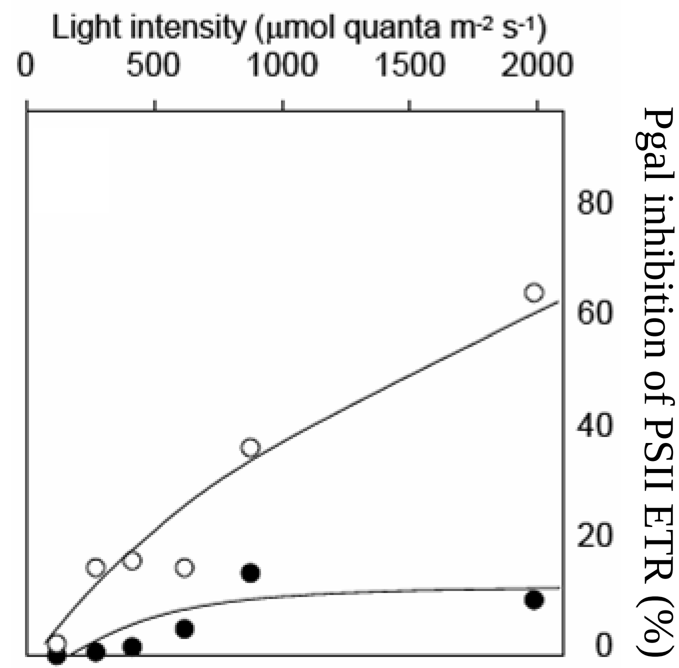


PTOX PSII pseudo cycle reduces O_2



Propyl gallate inhibits PTOX, reducing relative PSII electron transport rate

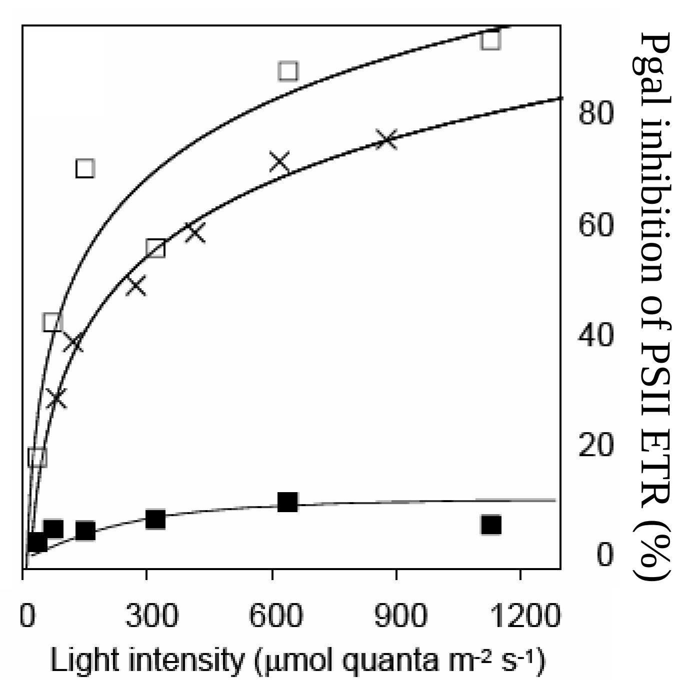
○ Open ocean
● Coastal ocean



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

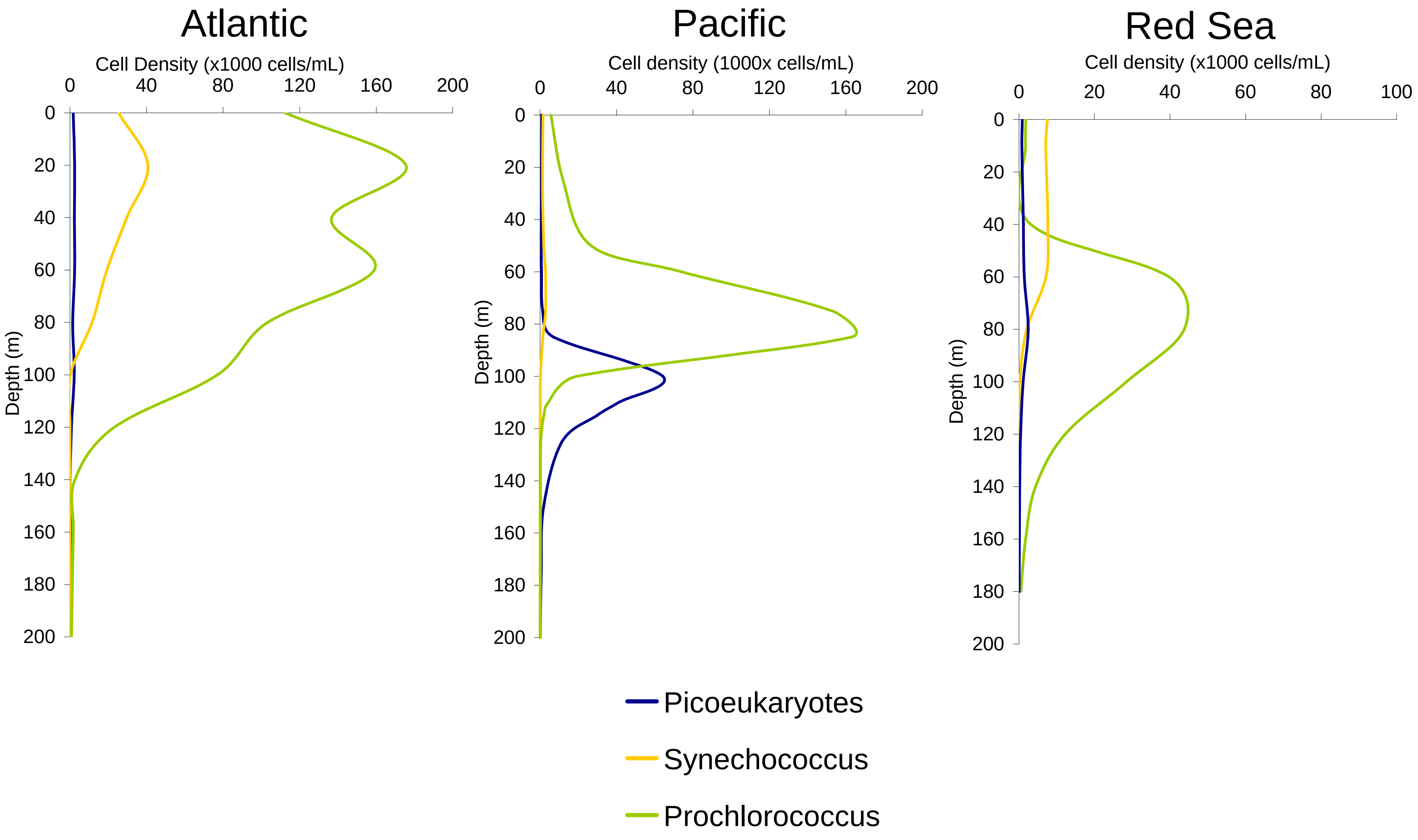
PSII protected from photodamage by traps remaining oxidized

Generates excess ATP that can be used in nutrient acquisition

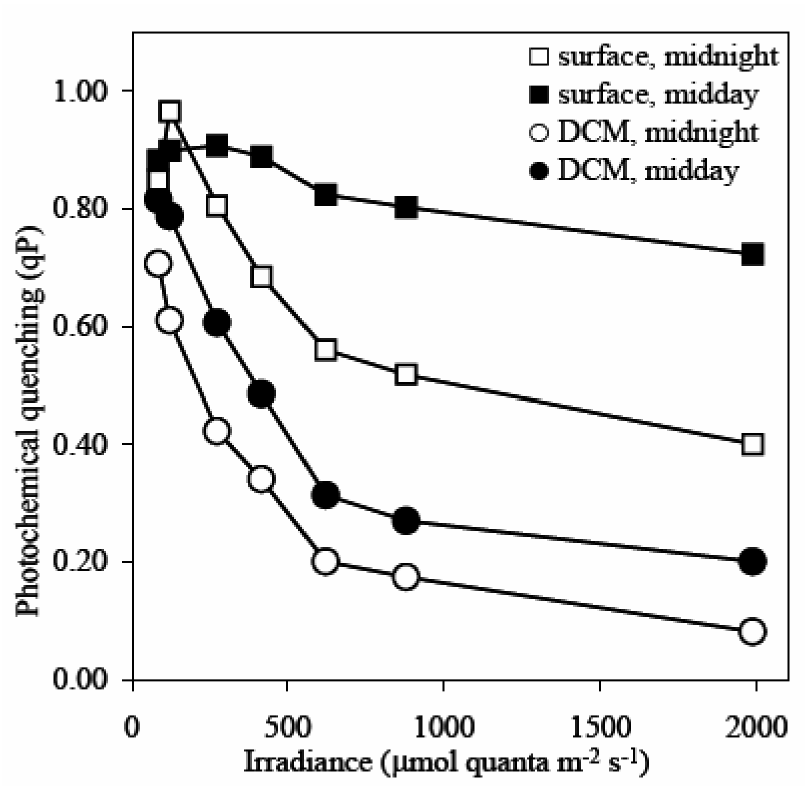
PTOX is necessary to keep traps open during high light

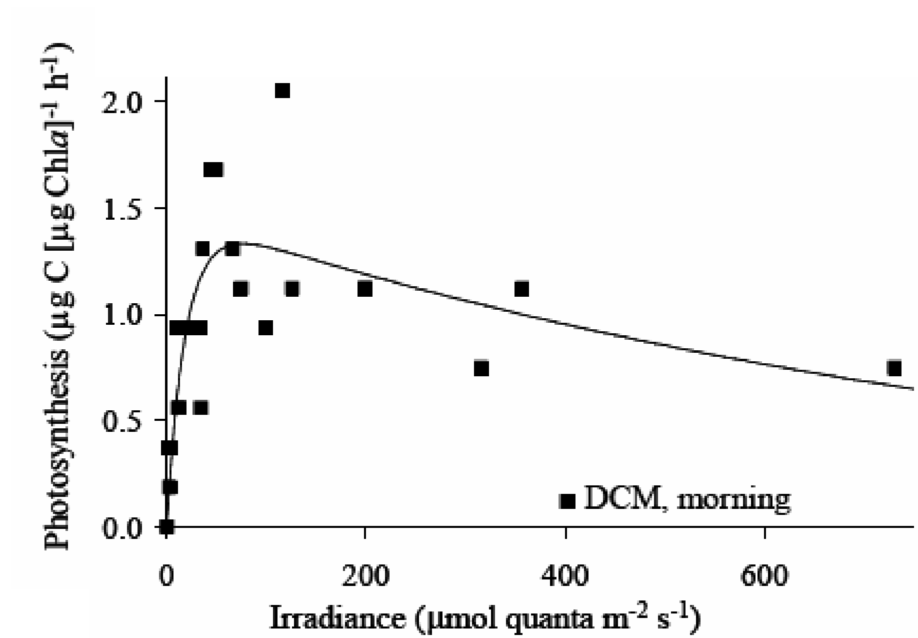
Is this phenomenon apparent throughout the euphotic zone?

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 Fv/Fm

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

DCM carbon fixation is impaired in high light

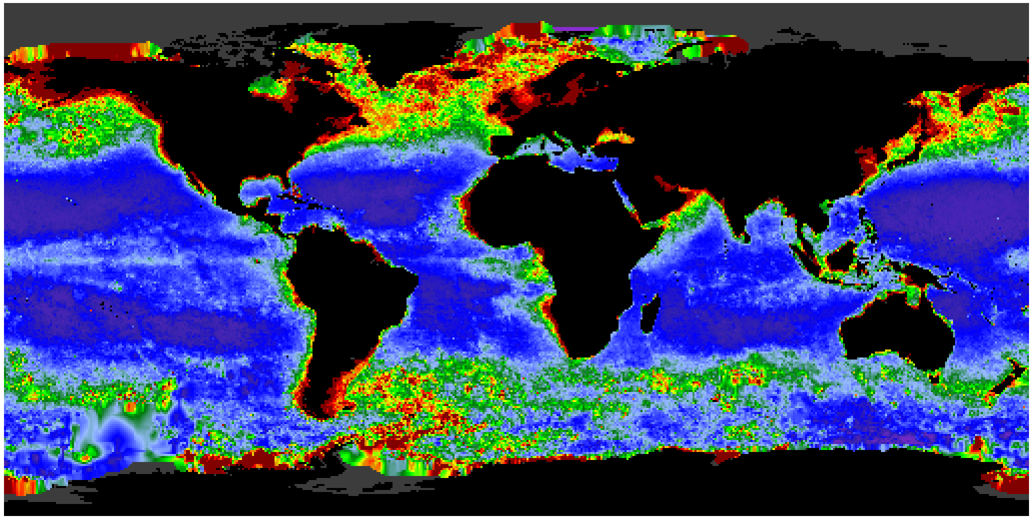
Cells did not show a decrease in the proportion of open traps under anoxic conditions

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 *Prochlorococcus* and *Synechococcus*	2/3
Global primary production attributed to *Prochlorococcus* and *Synechococcus*	1/3

(Bryant 2004)

Fluorescence in CO_2 fixation models

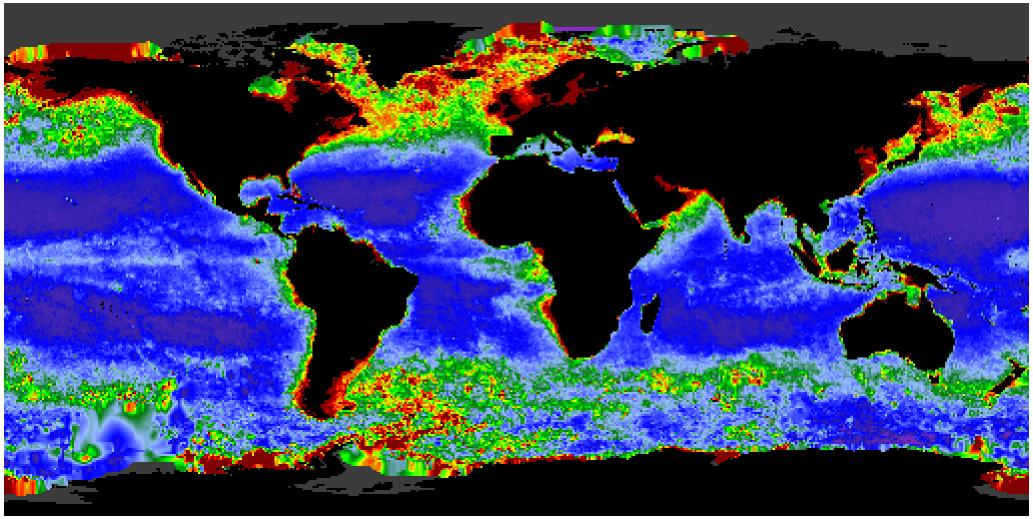


Discrepancies in actual and modeled C fixation rates have prompted the suggestion of scaling C fixation by Fv/Fm

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

Reduction of O_2 is another explanation

Fluorescence in CO_2 fixation models



Because empirical data is weighted toward coastal waters where e- flow to O_2 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

Thanks to the following groups:

Mike Lomas, Bermuda Institute for Ocean Science BATS Program

Dave Karl, University of Hawaii HOTS Program

The Interuniversity Institute for Marine Science, Eilat, Israel

Kevin Arrigo, Mine Berg, Jeff Shrager, and Gert van Dijken, Stanford

KRMM supported by:

DOE Global Change Education Program (GCEP) Fellowship (2006-200?)

NSF Graduate Research Fellowship (2004-2006)

This research was also supported by:

NASA New Investigator Program grant NAG5-12663 to AP

NSF Oceanography grant OCE-0450874 to ARG

Stanford School of Earth Sciences McGee Grant to KRMM

Phytoplankton community composition