





Aiken's 1st law:

A mixed layer, is a mixed layer, is a mixed layer

Definition: A Mixed layer is a layer of constant density, at any depth: surface; bottom; mid-depths. Other than a 'freak', this comprises a layer of constant Temperature & Salinity.

Processes are:

 Density-driven, convectional cooling: in winter, surface water overturn or at night convectional overturn (every night, if atmosphere colder than ocean). Mainly surface layers, but density driven processes operate throughout the water column and everywhere.
 Surface layers of low salinity (from precipitation) can be mixed, but are a restriction on deeper mixing.

2. Tidal mixing in shallow areas, principally the shelf seas (estuaries). Bottom-up mixing, all year in shallow layers with strong high tides, and bottom mixed layers in seasonally stratified shelf regions. (Pingree h/u³)

3. Wind-mixing of surface waters, occurs everywhere, but episodic; - no wind, no mixing - surface stratification by day, but eroded at night.





Examples of patterns of stratification at L4 in WEC: winter; spring summer; late autumn.





A 16 February, 2007
B 10 April, 2007
C 6 August, 2007
D 11 September, 2003
Red Temperature (°C)
Green Fluorescence (V).

James Fishwick Western Channel Observatory



Examples of patterns of low surface salinity at L4: 22/4/02; 27/05/02; 18/06/02; 12/08/02





Pingree: $S = log_{10} [h/C_d u^3]$; h = depth; u = ave tidal velocity; 1.5 = front; Mixed (all year); stratified (spring, summer); transitional (Mix/strat)







Depth of mixed layer in N Atlantic in winter (Woods)





TIME : 11-FEB-2008 00:00

Met Office ET: 9e1240a0de3fef65e2862de340719c9f



BOT-



CASIX BARANTER SEL MALANA

AMT profiles in gyres

deep mixed layers, > 100m in S gyre.

17 cruises: 960 CTD casts.

UOR tows 5 -65 m, vertical resolution ~0.3 m

2 km/und, ~50 undulations per tow,

at 11 knots (20 km/h), 100km in 5h tow.





AMT-05N (09/97); T, S, sig Postage stamps (all mid-day casts)

AMT-05S (09/97); T, S, sig Postage stamps





AMT-07S (09/98); T, S, sig Postage stamps







AMT-03 (09/96) Vertical Sections of T, S, Chla from UOR tow across equatorial front, 1.3° N to 1.8° S > 350 km 150 undulations 150 VPs. Tow Speed 11 knots (20 km/h)

Tow speed selected to obliterate any evidence of fine structure



Chuck & Jim with UOR in the Arctic, USNS Lynch, 1986

Below — Deployment of the UOR in the Arctic from USNS Lynch.





Above — The Undulating Oceanographic Recorder – overall length 1m, height 0.5m. The chlorophyll sensor (CHS) projects through the top hatch cover and the hemispherical light sensors are attached to the tail fins.



UOR measurements of temperature and chlorophyll fluorescence from north to south across the Arctic front on 19 August 1986.



WTP?



The point is, if there is a simple model for vertical physical structure, we can infer a simple model for vertical biological structure:

Shelf seas - Surface Mixed Layer / Thermocline / Bottom mixed layer

Ocean - SML / seasonal thermocline / permanent thermocline

Shelf or Ocean Biological structure: -SML with mixed biomass (possible maximum at surface);

- or there may be a biomass maximum in the thermocline.





Aiken's 2nd law

If you can't see it from space it is not important

No controversy – surface observations of roughness from SAR and altimeter.

Transfer of atmospheric radiatively-active and biogenic gases:

O₂, N₂, **CO**₂, etc

N₂O, CH₄, DMS, COS, SO₂, VOCs etc





Aiken's 2nd law

If you can't see it from space it is not important Biogeochemistry of the pelagia – bio-optics ocean colour

Satellite RS of OC 'sees' to 1 optical depth ($Z_{90} = 1/K_d$, m); but measures surface mixed layer, usually 20 m or more. Euphotic depth $Z_{eu} = 1\%$ surface light

Chla	Zone (mld, m)	K _d 490	1/Kd	Z _{eu}	K _d 443	Z _{eu}
(mg m ⁻³)		(m-1)	~(m)	(m)	(m-1)	
0.03	mid-gyre (100)	0.027	37.0	170	0.022	209
0.1	gyre (60-100)	0.035	28.6	131	0.032	144
0.2	gyre edge (40-60)	0.043	23.3	107	0.044	105
0.5	meso (30-50)					
1.0	meso	0.083	12.0	56	0.099	46
3.0	eutrophic (20-30)					
10.0	eutrophic (<20)	0.300	3.33	15	0.394	12



Shallow MLD in WEC, high Chla on surface



Holligan et al 1983 Western English Channel

MLD, 10m; Chla 50 mg.m⁻³ 1% PAR = ~5 m MLD, 16m; Chla 20 mg.m⁻³ 1% PAR = ~10 m









AMT T, S, σ profiles in S gyre: deep mld > 80 m; > 100m **a**) 533: 23 54 S; mld = 80 m; $PAR = 35 \ \mu E; < 2\%$ of surface b) 737: 08 02 S; mld = 85 m; $PAR = 38 \ \mu E; < 2 \%$ surface c) 15xx: 16 09 S; mld = 130 m; $PAR = 40 \ \mu E??$





WTP?



Remote sensing missions are global, daily, long-term and provide data ideal for Earth system science problems; we must exploit these.

The surface ocean (SML) is the interface between the ocean C-cycle and the global C-cycle (atmosphere) and diagnosis of the biogeochemistry of this layer is the important part of air-sea and sea-air interactions.

There can be a missing fraction below the surface layer that may be important for shallow layers, particularly in the shelf seas.

Deep sub-surface Chla layers at >100 m (< 0.1% surface PAR) are not important.

HAVE NO FEAR – SUPERMODEL IS HERE!!

We have the Taylor, Harris, Aiken (1986) model!!



Taylor, Harris, Aiken (1986) Time-dependent, 1D, 1P, 1N Model

V	is the sinking speed
K(z)	is the turbulent eddy diffusion coefficient

Devised to simulate the 'quasi steady state' vertical structures of temperature and Chlorophyll concentration measured by UOR in stable areas such as central Celtic Sea.

Taylor, Harris, Aiken (1986) model results: a. Vertical profiles in 'steady state' numerical analysis b. Steady state 'Shelf', 'Ocean' and analytical '2-layer' analysis.



Fig. 1 Vertical profiles of phytoplankton and nutrient after 100 days under shelf or oceanic turbulence conditions (see text), with v = 0.2 mM per cubic m, m = 0.078 per day and $\varepsilon = 0.2$.



Steady-state, 2-layer analysis

$$P_m/P_t = (m - \Theta_t + q3)/q2$$

$$\Theta_{t} = \alpha_{t} [N_{to}/(N_{to} - v)]$$

 α_t = light dep rate of photosynthesis
 q (and s) are transfer terms (constants)

P_m from satellite Calculate P_t from P_m/P_t





Aiken's 3rd law



Every oceanographer should be a modeller and every modeller should go to sea.

Scientific method: make observations, derive empirical relationships, look for mechanisms, processes, formulate rules and hypotheses, test with observations.

THA model was devised to show how the physical structure (in shelf seas) regulated the vertical structure of phytoplankton biomass (chlorophyll) from observations of T, Chla from UOR tows.

AMT observations provide data of diverse ecosystems (biogeochemical provinces) with different patterns of stratification, nutrient status, characteristic flora (phytoplankton assemblages) and bioenergetics.

Added observations from process studies: BOFS/JGOFS; L4 seasonal; Arctic and Antarctic studies; Benguela. Different ecosystems (different flora) function differently in different locations. What is in common? What is universal? What is distinct?

MODELS

Musings on Models, PFTs, Remote sensing of PFTs

Modelling biogeochemical cycling by phytoplankton (e.g. C, N, P, S, Ca cycles) in aquatic ecosystems is crucial to quantifying and understanding the Earth System & climate change.

Models need realistic representation of complex bio-mechanistic processes; use of **Plankton Functional Types** to describe ecosystem functioning is logical.

The functional properties of phytoplankton (ecological, photosynthetic) and their bio-optical traits, provide functional relationships for derivation of Phytoplankton Functional Types (PFTs) from remotely sensed ocean colour.

Environmental differences (light, nuts, T, S, turbulence, stratification, seasonality) between ecosystems force phytoplankton diversity and seasonal succession. **BIOMES, PROVINCES**.

Phytoplankton dynamics can only be understood by contextual correlation with environmental factors: physical (turbulence, stratification, clines), chemical 3 (nutrient availability) and radiant energy (light climate, photon flux),





Diagnosis of PFTs from remotely sensed data of Ocean Colour

The functional properties of phytoplankton (ecological, photosynthetic) and their bio-optical traits (BOT), provide functional relationships for derivation of Phytoplankton Functional Types (PFTs) from remotely sensed ocean colour.

- 1. Phytoplankton Bioenergetics (photosynthesis) BOT?
- 2. Bio-optical traits derive from Phytoplankton pigments (Chla, carotenoids) taxa-specific pigments?



CHLOROPHYLL, pigments, optical properties

Chlorophyll-a, -b, -c, the carotenoids (PSC &PPC) + phycobillins (low abundance in surface) colour the surface ocean.

Chlorophylls are cyclic tetrapyrroles, with N (C₅₅H₇₂N₄O₅Mg)

Chla has distinctive strong blue absorption 'soret' band (~400-470 nm, centre ~443 nm) and secondary absorption peak at ~675 nm.

Xanthophylls (carotenoids, Fuc, Per, Hex, Lut, Zea) are carbohydrates formed from carotenes (hydrocarbons) Carotenoids have identical chromophores and very similar blue-green absorption spectra (~400-550 nm, peak ~490 nm) – no BOT from Carotenoids!!!

Chla needs 'N'; Carotenoids do not use 'N'.

Chla has distinctive 'blue' spectra: concentration of Chla has greatest influence on phytoplankton spectra in blue-green.



Functional classification of the Phytoplankton: PFTs

Alignment of phytoplankton size classes (Pico, Nano, Micro) with environmental niches (nutrient availability and light climate) and their photosynthetic capacity or bio-energetic status:

Microplankton bloom in high nutrient environments (upwelling zones, spring and summer blooms at temperate and sub-polar latitudes).

Nanoplankton grow in regions with some inorganic nitrogen & re-cycled nuts (inorganic and organic).

Picoplankton survive in low nutrient environments (permanently stratified oligiotrophic gyres)

Pico (prok) have low Chl-a, low TChla/Tpig, low Tot-carbon, Chla-a/C & low PQE; **Nano** (flag) have med Chl-a, med TChla/Tpig, med Tot-carbon, Chl-a/C & med PQE; **Micro** (D+d) have high Chl-a, high TChla/Tpig, high Tot-carbon, Chl-a/C & hi PQE.

WEALTH OF AMT DATA SUPPORT THESE OBSERVATIONS:

Plankton: Zubkov, et al 1998, 2000; Tarran et al 2006; Heywood et al 2006.
Pigs: Gibb et al, 2000; Barlow at al, 2002, 2004; Poulton et al, 2006; Aiken et al 2008
Productivity: Maranon & Holligan, 1999; Maranon et al, 2000, Maranon, 2005.
Scaling of Photosynthesis & cell size: Maranon et al 2007, Maranon, 2008



Maranon 2008 JPR, in press

Scaling of phytoplankton photosynthesis and cell size in the ocean.



Functional classification of the Phytoplankton: PFTs



Conventionally phytoplankton classified by size:

Picoplankton (typically < 2 μ m) pico-prokaryotes (cyanobacteria) + pico-eukaryotes; Nanoplankton (~ 2-20 μ m) eukaryote flagellates (prymnisiophytes etc) Microplankton (20- >200 μ m) mostly diatoms and dinoflagellates These ranges are not Robust: diatoms range from 5 μ m 2 mm (whole nano range); some flagellates < 2 μ m (pico-eukaryotes).

ERSEM has bacteria, heterotrophs, zooplankton, 4 phytoplankton: Picoplankton, flagellates, dinoflagellates and diatoms.

DGOM (LeQuere et al., 2005) has 10 functional types: bacteria, 3 zooplankton and 6 phytoplankton arranged by size class:
PICO - (pico-autotrophs, prochlorophytes, cyanobacteria, N₂-fixers, pico-eukaryotes);
NANO - Calcifiers (coccolithophores); DMS producers (e.g. Phaeocystis spp); other nano-flagellates;
MICRO - Silicifiers (Diatoms); others (Dinoflagellates).

Currently there is no consensus, systematic definition of PFTs.

Phytoplankton size groups, taxa specific, diagnostic pigments. Diagnostic Pigment method Claustre, 1997; Vidussi, 2000; Uitz, '06.

Taxa specific pigments: Micro-plankton Diatoms: FUC; Dinos: PER; not present in all Dinos (replaced by FUC)

Nano-plankton (various flagellates) Prymnisophytes: HEX Chrysophytes: BUT Cryptophytes: ALLO Many nano-Eukaryotes also have Chlb (ambiguity with prochlorophytes)

Pico-plankton (prokaryotes + pico-eukaryotes) Prokaryotes (synechococcus & prochlorococcus): ZEA Pico-eukaryotes are flagellates with HEX, BUT pigments (anomalies) Pico-Eukaryotes prochlorophytes: Chlb

Caveats: PER not present in all Dinos (replaced by FUC) FUC is pre-cursor pigment for HEX & BUT and always co-exists. Phaeocystis (flagellate) has HEX when in single cell populations (ss Chla max) but has FUC when in colonial bloom (> 2 mg.m-3) Not definitive, many ambiguities, many exceptions!!! Functional Classification of Phytoplankton: Phytoplankton Functional Types, PFTs Or Phytoplankton Size Classes, PSCs.

EVIDENCE, RESULTS

WEC, L4 annual cycle of pigments, photosynthetic and optical properties in the Western English Channel 2001.

Benguela, 2002

Historical Evidence:

Fe Enrichment Experiments

AMT NOMAD







Chla/Tpig ratio and Chla/AP ratio are not constant But log-linear function of Chla and Tpig; CONCLUSION: Phytoplankton synthesise Chla preferentially in active growth.


L4: Linear relationship between PQE and optical ratios a674/a443, a676/a443



L4: Also Cph linear with Chla and Chla/Tpig linear with Chla/Cph Chla = 0.018 Cph + 0.2; R = 0.875; L4: Chla/Cph = 0.270 Chla/Tpig - 0.138; R = 0.725.







TChla/TP linearly related with Fv/Fm and a676/a440; a676/a440 linear with Fv/Fm

Fe Enrichment Experiments: Fv/Fm and TChla/TP both increase after Fe addition

Similarly Fv/Fm linear With TChla/TP

TChla Log-linearly With TChla/TP

Floristic shifts: Mostly Flagellates to Diatoms



PFTs, Historical Evidence:

Margalef (1967) – optical ratio D440/D670 inverse of TChla/TP or TChla/AP hi in small cells, lo in large cells and decreased with seasonal succession

Ryther & Yentsch 1957 – D665/D440 hi in cells with low Chla, lo in cells hi Chla

Yentsch et al (1958, 1962) - Chla synthesised & decomposed quicker than other pigments; Chla responded quicker to growth opportunities

Schluter et al 1997; Holmboe et al 1999 – AP/Chla hi in starved cultures

Jeffrey & Hargelef (1980) – D480/D665 lo for healthy cells, hi for older cells.

Heath et al (1990) – C/Chla, D480/D665, C/N, all co-varied and low for hi Chl/Ap, Chl/C and N/C, i.e. healthy photosynthesising cells

Flynn et al <u>Fe Enrichment Experiments</u>



Phytoplankton Community Structure from Space T. Hirata, J. Aiken, N. Hardman-Mountford, T. Smyth

NOMAD DATA ANALYSIS

An absorption model to derive phytoplankton size classes from satellite ocean colour.

Phytoplankton absorption spectra for range of Chla concentrations and size classes from Benguela and AMT

 $a_{ph}443$, δ [$a_{ph}510$ - $a_{ph}443$], or slope S = $\delta/67$ all increase with Chla and phytoplankton size.



Magnitude of a_{ph}(443) is a signature of PCS

NOMAD Quality Control: a) Chla vs DP; b) a_{ph}443 vs a_{ph}490; c) & d) Chla vs a_{ph}





NOMAD Fractional occurrence = MP/DP for:

a) Zea (MP for prok) Fuc (MP Diatom/Micro

b) Hex (MP for Prymn) Chlb (MP Chloro/Prochlo) Per (MP for Dino; some)

c) Hex/Fuc ratio

But, Lut < 0.03

Note co-incident stepchanges of key MP, indicating changes of Phytoplankton community Structure (PCS) or Size Class (PSC)

Magnitude of a_{ph}(443) is a signature of PCS



NOMAD, a_{ph}443 vs S marked with dominant size class using modified DPA: Upper, nano displaced +0.0004; P-Euk (defined as flagellates Chla < 0.025

Magnitude of Chla is a signature of PCS



NOMAD, Chla vs S marked with dominant size class using modified DPA: Upper, nano displaced +0.0004; P-Euk (defined as flagellates Chla < 0.025

Magnitude of a_{ph} & Chla are signature of PCS



NOMAD, a_{ph}443 vs S and Chla vs S marked with dominant size class using modified DPA. Which is best?

SeaWiFS data 2004 analysed, using Smyth et al (2006) for a_{ph} 443 and a_{ph} -model partitioning for PSCs.















f) 11/2004











02/2005



04/2005



06/2005













10/2005



12/2005



Verification of PSC model AMT-07: AMT PSC (in situ pigs) versus a_{ph}-model (SeaWiFS data)



AMT-05; AMT-06



NS = No SeaWiFS at end of AMT-05

NS = No SeaWiFS; Benguela too close to coast for 9 x 9 km composite

8-year time series from Sea WiFS, 1998-2006 for 6 ocean basins: Pico plankton in oligotrophic gyres – upward trend?? More biomass or larger gyres, greater area of permanent stratification



8-year time series from Sea WiFS, 1998-2006 for 6 ocean basins: Nanoplankton and microplankton (x5) - downward trend??



NOMAD, a_{ph} model: Conclusions

- a_{ph} model needs true validation vs phytoplankton species counts and AFC carbon.
- Satellite ocean colour provides a_{ph} at discrete wavelengths (443, 490, 510) that can be used for derivation of PSCs.
- The model uses only 1 variable a_{ph}443 or S so the number of error sources are minimal.
- Implementation is simple so large data sets can be processed easily and quickly, providing capability to determine trends in oceanic ecosystems.
- Refinements of the model can provide further partitioning of PSCs.

Musings on Models, PFTs, Remote sensing of PFTs



Modelling biogeochemical cycling by phytoplankton (e.g. C, N, P, S, C cycles) in aquatic ecosystems is crucial to quantifying and understanding the Earth System & climate change. NOMAD study - PSCs.

Models need realistic representation of complex bio-mechanistic processes; use of **Plankton Functional Types** to describe ecosystem functioning is logical. YES – NOMAD study

The functional properties of phytoplankton (ecological, photosynthetic) and their bio-optical traits, provide functional relationships for derivation of Phytoplankton Functional Types (PFTs) from remotely sensed ocean colour.

Environmental differences (light, nuts, T, S, turbulence, stratification, seasonality) between ecosystems force phytoplankton diversity and seasonal succession. **BIOMES, PROVINCES**. Yes – Hardman-Mountford et al

Phytoplankton dynamics can only be understood by contextual correlation with environmental factors: physical (turbulence, stratification, clines), chemical (nutrient availability) and radiant energy (light climate, photon flux). Bring it all together



from Hardman-Mountford et al (in press)

Classification of biomes from a hierarchical cluster analysis of global mean Chla (SeaWiFS 1998-2004 average): Oligotrophic cluster cyan, blue and magenta (sub-clusters); Mesotrophic cluster yellow and green (sub-clusters); Eutrophic cluster shown in red; From SeaWiFS analyses, Oligotrophic ~63%, Meso ~35%, Eutrophic ~2%



The big Earth System questions are: How is the Earth changing and what are the consequences for life on Earth?



Global Carbon cycle and the climate system are intimately linked with the ocean C-cycle through the air-sea exchange of CO₂

PAST: the carbon cycle and climate of the Earth System have been tightly coupled through the glacial-interglacial cycles and since. - but the mechanisms behind this coupling are not well understood

PRESENT: human-induced changes in the contemporary carbon cycle have great relevance to climate change policies and agreements. (e.g. Kyoto Protocol) *- but current sources and sinks of carbon are poorly quantified*

FUTURE: carbon cycle feedbacks will have a significant influence on climate change over the next 100 years - but the magnitude of these feedbacks are highly uncertain





For the Marine Environment, surface oceanlower atmosphere, the questions are:



How do marine systems vary with time? (e.g. changes of THC, etc?) How are marine ecosystems regulated by ocean processes? (physics, structure) How do marine ecosystems interact with the global carbon cycle? (CO_2 flux)

Ocean circulation, currents, stratification, surface properties and ocean biogeochemistry, all regulate the Air-Sea fluxes of CO₂ often separated in TIME and SPACE.

We can understand change in marine systems from:
1. Observations – observatories, WCO, AMT,
other time series, other seasonal cycles.
2. Remote sensing observations.
3. Modelling, coupled circulation-ecosystem models with
realistic ecosystem models, having representative PFTs





ATLANTIC MERIDIONAL TRANSECT: characterisation of Atlantic Ocean biogeochemical provinces (physics, biology, bio-optics) plus remote sensing. Twice yearly research cruise on BAS ship RRS James Clark Ross, UK to Falklands (or S. Africa) 50N to 50S (35S), southbound Sept (BFAS), northbound April (AFBS)



Aiken et al, Prog Ocean 2000; Robinson et al DSR, 2006. DSR special issue 2008 in review



AMT: twice yearly on BAS ship RRS James Clark Ross, 18 cruises, 1995-2005.



AMT-5; UK to Falklands, Sept 1997 SeaWiFS Atlantic Characterisation



AMT-6; Cape Town, Benguela to UK, May/June 1998.





Summary: Phytoplankton pigments & PQE, Fv/Fm



Conclusion: Is there a generalised relationship? Is there a functional link between PQE and Chla/Tpig? Log-linearily with Chla.



How will marine ecosystems change? Ecosystem Change Associated with Global Warming; interaction with global C-cycle.





5. BE-BOT hypothesis



The bioenergetics of photosynthesis, coupled to environmental properties (nutrients, light fluxes, etc), is the definitive phytoplankton functional process that determines phytoplankton taxa, size classes and ecosystem trophic status, and that BE status is quantitatively linked to phytoplankton bio-optical traits (BOT) that are specific properties of phytoplankton size and taxa. Specific BOT are conferred by the unique absorption spectrum of Chla (blue, 400-470 nm in vivo) that is distinct from carotenoid (PSC+PPC) absorption spectra (blue-green, 400-550 nm, peak ~490 nm).

A corollary of this hypothesis is that ocean IOPs, determined in situ or from ocean colour, are primarily a function of phytoplankton photosynthetic activity, through the instantaneous absorption of solar radiation (akin to action spectrum) and secondarily a function of the steady state biomass, (approximated by Chl-a determined in vitro from phytoplankton absorption or pigment analyses

Pigments, pigment-protein complexes, PSI, PSII and LHC are synthesised much slower, over 12-24 h and are cumulative from photosynthetic activity over the previous few days.



Oligotrophic Ocean: 63% of global ocean (Chla < 0.25 mg.m⁻³); Pico-plankton, prokaryotes (synechococcus; prochlorococcus) and pico-eukaryotes (pico-eukaryotes)

Mesotrophic ocean, 35% of global ocean (Chla > 0.25 - ~1.25) Nano-plankton, mostly flagellates (prymnesiophytes etc)

Eutrophic Ocean, ~2% ocean (Chla >~1.25) Microplankton, mostly diatoms & dinoflagellates

Chla concentrations from SeaWiFS data; agrees with the published data (e.g. Morel et al.)









SWT?



BOT-6

PHOTOSYNTHESIS, fluorescence, BIOENERGETICS

The quantum efficiency for C-fixation, φ or photosynthetic quantum efficiency (PQE) derived from Fv/Fm measured by fast repetition rate fluorometry (FRRF, Suggett *et al*, 2004; Rottgers, 2007) are closely related to bioenergetic (BE) status.

Bioenergetics is the transformation of light energy (photosynthesis) through intermediate stages to the synthesis of plants (Govindgee 1975), regulated by macro & micro nutrient quality and availability, or by photon flux if light limits.

Productivity 'P' (mols C m⁻³ d⁻¹) while dependent on BE status, is driven by light energy, E_{PAR}:

 $P = \varphi a_{ph} E_{PAR}$ (Marra et al, 2000); or comparably $P = \text{const PQE } \sigma_{PSII} E_{PAR}$ Chla (Suggett et al, 2001; 2004; Smyth et al, 2004);

Neither expression includes nutrient concentrations explicitly, inferring nutrient regulation of PQE, σ_{PSII} or ϕ , probably through the synthesis of protein-pigment complexes in the light harvesting complex (LHC) and photosystems (PSI, PSII).

The system is fuelled by N (& P, but rarely limiting).