



**HAL**  
open science

## Can the xanthophyll cycle help extract the essence of the microalgal functional response to a variable light environment?

Christophe Brunet, Johann Lavaud

### ► To cite this version:

Christophe Brunet, Johann Lavaud. Can the xanthophyll cycle help extract the essence of the microalgal functional response to a variable light environment?. *Journal of Plankton Research*, 2010, 32 (12), pp.1609. <10.1093/plankt/FBQ104>. <hal-00614854>

**HAL Id: hal-00614854**

**<https://hal.science/hal-00614854v1>**

Submitted on 17 Aug 2011

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



HAL Authorization



**Can the xanthophyll cycle help extract the essence of the  
microalgal functional response to a variable light  
environment?**

Journal:	<i>Journal of Plankton Research</i>
Manuscript ID:	JPR-2010-174.R1
Manuscript Type:	Horizons
Date Submitted by the Author:	15-Jul-2010
Complete List of Authors:	Brunet, Christophe; Stazione zoologica Anton Dohrn, Laboratory of Ecology and Evolution of plankton Lavaud, Johann; Unuversity of La Rochelle, UMR CNRS 6250 "LIENS" - Institute for coastal and environmental research
Keywords:	phytoplankton, photosynthesis, ecophysiology

SCHOLARONE™  
Manuscripts

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

# Can the xanthophyll cycle help extract the essence of the microalgal functional response to a variable light environment?

CHRISTOPHE BRUNET<sup>1,\*</sup> & JOHANN LAVAUD<sup>2,\*</sup>

<sup>1</sup>: LABORATORY OF ECOLOGY AND EVOLUTION OF PLANKTON - STAZIONE ZOOLOGICA A. DOHRN, VILLA COMUNALE, 80121 NAPOLI – ITALY.

<sup>2</sup>: UMR CNRS 6250 'LIENSS' - INSTITUTE FOR COASTAL AND ENVIRONMENTAL RESEARCH (ILE) - UNIVERSITY OF LA ROCHELLE - 2, RUE OLYMPE DE GOUGES, 17000 LA ROCHELLE CEDEX – FRANCE.

\* The 2 authors contributed equally to this work.

\* Corresponding authors: CHRISTOPHE.BRUNET@SZN.IT, JOHANN.LAVAUD@UNIV-

LR.FR

**ABSTRACT**

*How do pelagic microalgae cope with light changes in marine ecosystems? Is photosynthesis enhanced or depressed by frequent light fluctuations and how? These long-lasting questions are still under debate. A great diversity of responses has been documented relative to the spatial and temporal scale of study, the groups and species, etc. The answers to these questions probably lie in the interplay between fast photoregulation and longer term photoacclimation whose framework (amplitude, kinetics) is defined by environmental genetic adaptation. One of the main photoregulatory processes is the light-dependent operation of the so-called xanthophyll cycle (XC). XC is activated when the incident light becomes excessive with respect to its optimum necessary for maximization of photosynthesis. The present paper aims at (i) describing a short state-of-the-art on the XC functioning in microalgae with an ecophysiological point of view, (ii) discussing the relevance of the in situ XC operation and its response to the underwater light climate, (iii) addressing a series of open questions for filling the gap between XC functional features and field studies with respect to its role in the photophysiology of microalgae and its potential use for characterizing the hydrodynamics of water bodies.*

**FAST REGULATION OF PHOTOSYNTHESIS AND ‘THE PARADOX OF THE PLANKTON’**

Phytoplankton live in a three-dimensional environment characterized by strong physical and chemical driving forces and a rapid attenuation of light with depth. In contrast, the terrestrial habitat is essentially two-dimensional, although it can be argued that forests put a lot of energy in catching that third dimension by forming support tissues to lift their photosynthetic tissues up towards the light and above the competition. A second important difference is that on land, higher plants have to invest a huge part of their organic products in unproductive support and transport tissues. Nonetheless, living in the plankton poses some problems that are arguably less relevant for higher land plants. Phytoplankton has to cope with a highly variable environment that continuously requires energy for maintenance of photosynthetic productivity and growth. This is

1  
2  
3 relevant in such aquatic ecosystems where biodiversity is high and competition for  
4 resources is strong. Indeed, in a few cubic millimeters of water, many phytoplankton  
5 species can grow together, sharing and competing for the same energy resources,  
6 especially light and nutrients (Liess *et al.*, 2009). This is the ‘paradox of the plankton’ as  
7 discussed by Hutchinson (1961). How does diversity persist in such a small spatial  
8 framework is still a matter of debate (Bastow Wilson, 1990). High frequency variability  
9 of environmental cues can help in maintaining and even increasing phytoplankton  
10 biodiversity (Sommer, 1995; Flöder *et al.*, 2002). Hence to be competitive, phytoplankton  
11 must be able to respond quickly to any kind of changes occurring in its habitat. The main  
12 abiotic driving forces are temperature, nutrients and light, the latter showing the highest  
13 variations in amplitude and frequency (McIntyre *et al.*, 2000; Raven and Geider, 2003;  
14 Dubinsky and Schofield, 2010). Hence, the response of phytoplankton might be  
15 supported by at least one irradiance-dependent physiological process, which must be fast,  
16 flexible and efficient (Li *et al.*, 2009; Dubinsky and Schofield, 2010).

17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
Huisman *et al.* (2001) proposed that the diversity of life history and of  
physiological abilities might promote the high biodiversity of phytoplankton. It has been  
proposed that the variability of physiological responses to light fluctuations would allow  
competitive exclusion and thus the spatial co-existence and/or the temporal succession of  
a multitude of species in both pelagic (Meyer *et al.*, 2000; Strzepek and Harrison, 2004;  
Dimier *et al.* 2007b; 2009b; Lavaud *et al.*, 2007) and benthic (Serodio *et al.*, 2005; van  
Leeuwe *et al.*, 2008) ecosystems. Indeed, growth rate responds to fluctuating light in  
different ways as a function of groups/species of phytoplankton (Litchman, 2000; Flöder  
*et al.*, 2002; Mitrovic *et al.*, 2003; Wagner *et al.*, 2006) and of the photoacclimation  
ability and light history of the cells (Litchman and Klausmeier 2001; van Leeuwe *et al.*,  
2005; Wagner *et al.*, 2006; van de Poll *et al.* 2007; Laurion and Roy, 2009). The  
photoresponse ultimately leading to a change in growth rate is thus a matter of both  
genomic plasticity and time scale (Grobbelaar, 2006; Dubinsky and Schofield, 2010). In  
the short term (few seconds/minutes), the light fluctuations are mainly due to cloud  
movement, surface sunflecks and vertical mixing generating unpredictable changes.  
These fluctuations, and especially their extremes (darkness and excess light), can be  
harmful for the photosynthetic productivity of microalgae by promoting an imbalance

1  
2  
3  
4 between the harvesting of light energy and its use for photochemical processes and  
5 carbon fixation (Long *et al.*, 1994; Raven and Geider, 2003; Dubinsky and Schofield,  
6 2010). In order to regulate photosynthesis *versus* rapid light fluctuations, phytoplankton  
7 has evolved a number of physiological photoprotective mechanisms such as the  
8 photosystem II (PS II) and PS I electron cycles, the state-transitions, the fast repair of the  
9 D1 protein of the PS II reaction center, the scavenging of reactive oxygen species (see  
10 Falkowski and Raven, 2007; Lavaud, 2007; Ruban and Johnson, 2009). Among these  
11 processes, the XC and the dependent thermal dissipation of the excess light energy (NPQ  
12 for non-photochemical fluorescence quenching) play a central role (Lavaud, 2007; Brunet  
13 *et al.*, in press; Goss and Jakob, 2010). At longer time scales (hours to seasons),  
14 acclimation processes are supported by gene regulation which modifies the architecture  
15 of the photosynthetic apparatus as well as enzymatic reactions involved in  
16 photochemistry and metabolism (Raven and Geider, 2003; Grobbelaar, 2006; Dubinsky  
17 and Schofield, 2010). These two types of responses, regulative and acclimative, are not  
18 mutually exclusive (Lavaud *et al.*, 2007; Brunet *et al.*, in press). For instance, long-term  
19 acclimation to a prolonged light regime (low or high intensity, or intermittent light)  
20 modifies the amount of pigments involved in the XC leading to a modulation of the high  
21 light response via the kinetics and amplitude of NPQ (Lavaud *et al.*, 2003; van de Poll *et*  
22 *al.*, 2007; Gundermann and Büchel, 2008; Dimier *et al.*, 2009b).

## 37 38 39 **XANTHOPHYLL CYCLE FUNCTIONING AND VARIABILITY**

40  
41  
42 The xanthophyll cycle (XC) is one of the main processes regulating excessive  
43 photon flux in the light-harvesting complexes of photosystems since it is responsible for  
44 most of NPQ (for recent reviews, see Demmig-Adams and Adams, 2006; Lavaud, 2007;  
45 Goss and Jakob, 2010). In microalgae, two main groups can be distinguished with regard  
46 to the pigments involved in the XC (Brunet *et al.*, in press). The first group possesses the  
47 two-step de-epoxidation of violaxanthin (Vx) into zeaxanthin (Zx) via antheraxanthin  
48 (Ax) (a truncated Vx to Ax version also occurs in some primitive green algae). The  
49 second group shows a simpler conversion as the main XC, with only one step de-  
50 epoxidation of diadinoxanthin (Dd) into diatoxanthin (Dt). Many specificities of the Dd-  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

1  
2  
3 cycle relative to the Vx-cycle (Wilhelm *et al.*, 2006; Lavaud, 2007; Goss and Jakob,  
4 2010) might explain the rapid and effective synthesis of Dt in large amounts (Lavaud *et*  
5 *al.*, 2002a; Lavaud *et al.*, 2004). In other groups of phytoplankton, there is no  
6 (cyanobacteria) or a questionable (red algae) XC (Goss and Jakob, 2010) but the  
7 involvement of various de-epoxidized forms of xanthophylls (including Zx) in NPQ  
8 (Kirilovsky, 2007).  
9

10  
11  
12  
13  
14 The photoprotective NPQ process takes place into the light-harvesting complex of  
15 PS II. When irradiance exceeds the photosynthetic capacity of the cell, NPQ dissipates  
16 part of the light energy absorbed in excess, thus decreasing the excitation pressure on PS  
17 II (Demmig-Adams and Adams, 2006; Lavaud, 2007; Li *et al.*, 2009). NPQ is composed  
18 of three components (qE, qT and qI) whose respective importance varies among  
19 photosynthetic lineages, qE being essential for most of them. qE is the energy-dependent  
20 quenching which is regulated by the build-up of a transthylakoid  $\Delta$ pH and the operation  
21 of the XC. qT refers to the part of the quenching which is due to state-transitions, while  
22 qI is due to photoinhibition. qT is relevant in phycobilisome-containing organisms  
23 (cyanobacteria and red algae) and green microalgae but it is not really significant in light  
24 conditions triggering maximal qE (i.e. high light; Mullineaux and Emlyn-Jones, 2004;  
25 Ruban and Johnson, 2009). The origin of qI is not clearly defined except for some higher  
26 plants (overwintering conifers and tropical evergreen species) and it requires special  
27 conditions (prolonged environmental stress) (Demmig-Adams and Adams, 2006).  
28 Although the relationship between qE and the accumulation of de-epoxidized  
29 xanthophylls has been reported in many algal groups (Lavaud *et al.*, 2007; Brunet *et al.*,  
30 in press), there is still no clear picture of the functioning of qE in microalgae, although  
31 models have been proposed (Lavaud, 2007; Goss and Jakob, 2010), with the exception of  
32 *Chlamydomonas* (Peers *et al.*, 2009). Even though qE has been investigated down to the  
33 molecular level in higher plants (Cogdell, 2006), its level of complexity is still not fully  
34 understood in microalgae for two main reasons: 1) the joint partners of the XC for the  
35 regulation of qE and their interactions are not all identified, 2) the intricacy of qE/NPQ  
36 dependency on the light exposure (regime and duration) as well as on the light history of  
37 the cells, especially when simulated light field conditions are applied (Dimier *et al.*,  
38 2009a; Van de Poll *et al.*, 2010), has been only been partially appreciated. In  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

1  
2  
3 cyanobacteria and red algae, although there is a qE quenching which is supported by the  
4 presence of xanthophylls and a  $\Delta pH$  (for the red algae, Lavaud, 2007), the composition  
5 and organization of the antenna obviously support another type of qE mechanism (see  
6 Kirilovsky, 2007; Bailey and Grossman, 2008). Nevertheless qE in cyanobacteria is not  
7 as powerful as in other phytoplankton taxa (see Lavaud, 2007) possibly because of the  
8 lack of a finely regulated XC. When necessary, cyanobacteria favour other  
9 photoprotective processes such as qT (described above) and the rapid repair of the D1  
10 protein of the PS II reaction center (Six et al., 2007).  
11

12  
13  
14  
15  
16  
17  
18 The microalgal XC activity shows striking peculiarities with respect to higher  
19 plants. It includes a high degree of variation in its regulation among the different  
20 taxa/species (Lavaud *et al.*, 2004, Goss and Jakob, 2010; Kropuenske *et al.*, 2009; Van de  
21 Poll *et al.*, 2010), together with the growth phase (Arsalane *et al.*, 1994; Lavaud *et al.*,  
22 2002a, 2003; Dimier *et al.* 2009b), the nutrient state (Staehr *et al.*, 2002; van de Poll *et*  
23 *al.*, 2005), and the light history with both visible and UV radiation (see Lavaud, 2007;  
24 Laurion and Roy, 2009; Van de Poll and Buma, 2009). Also recent reports demonstrated  
25 how the XC activity and efficiency might be influenced by niche adaptation and *vice*  
26 *versa* in both pelagic (Meyer *et al.*, 2000; Dimier *et al.* 2007b, 2009a; Lavaud *et al.*,  
27 2004, 2007) and benthic (Serodio *et al.*, 2005; van Leeuwe *et al.*, 2008) species, and how  
28 it could influence species succession (Meyer *et al.*, 2000; Serodio *et al.*, 2005; van  
29 Leeuwe *et al.*, 2008). This functional trait is part of the overall adaptive  
30 photophysiological properties of PS II, as shown for the diatoms (Strepzeck and Harrison,  
31 2004; Wagner *et al.*, 2006; Wilhelm *et al.*, 2006). It highlights the narrow functional  
32 relationship between the niche adaptation and the capacity for photo-regulation/  
33 acclimation which leads to the above discussed proposal that the fast regulation of  
34 photosynthesis might be a crucial functional trait for microalgal ecology. In that respect,  
35 diatoms are currently the most studied group probably because they appear to be the best  
36 XC/NPQ performers among microalgae (Lavaud, 2007). Nevertheless, diatoms show a  
37 large inter-species XC/NPQ diversity (Lavaud *et al.*, 2004, 2007; Dimier *et al.*, 2007b)  
38 which might take its source in the special evolution of this group (Armbrust, 2009)  
39 leading to its successful adaptation to all aquatic habitats driven by a switch from benthic  
40 to a pelagic way of life (Kooistra *et al.*, 2006). Especially, the decrease of accessory  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

1  
2  
3 pigment diversity in diatoms compared to other microalgal groups would be an advantage  
4 for an opportunistic strategy (Dimier *et al.*, 2009b) that might be related to the high  
5 plasticity of their PS II antennae function including the XC (Lavaud, 2007).  
6  
7

8  
9 The influence of the size and shape of cells on the capacity for regulation of  
10 photosynthesis and in particular via the XC operation merits more interest (Key *et al.*,  
11 2010). We observed that the size of cells could significantly affect the XC functioning  
12 (Lavaud *et al.*, 2004; Dimier *et al.* 2007b; 2009b). Indeed, physiological acclimation to  
13 light changes is a costly process. Cell size determines the structure of the PS II antenna  
14 and therefore the pigment content which constrains the use of light resource as well as the  
15 cell energy requirement for physiological responses to light fluctuations (Finkel, 2001;  
16 Raven and Kübler, 2002; Litchman and Klausmeier, 2008; Key *et al.*, 2010). The  
17 influence of cell size/shape on metabolism coupled with the Metabolic Theory of  
18 Ecology (Brown *et al.* 2004) applied to the fast regulation of photosynthesis *versus* light  
19 would bring interesting insights for studying the photoadaptative strategies *versus* niche  
20 properties in microalgae. It would provide a background to understand how the  
21 environmental conditions affect photoregulatory capacity and efficiency and what their  
22 impact is on cell metabolism. Picoeukaryotes turned out to be interesting models to  
23 further explore this hypothesis (Dimier *et al.*, 2007a; 2009a; Six *et al.*, 2008, 2009).  
24 Dimier *et al.* (2009a) suggested that the energy cost of enhanced photoregulation due to  
25 high light fluctuation could be responsible for the decrease of growth rate in the shade-  
26 adapted picoeukaryote *Pelagomonas*. Additionally *in situ* studies (Brunet *et al.* 2006,  
27 unpublished results) showed, in agreement with laboratory experiments (Dimier *et al.*,  
28 2007a; 2009a), that picoeukaryotes have high plasticity of PS II photoregulatory  
29 responses. This is probably related to the fact that the main limiting resource for these  
30 organisms is light (Timmermans *et al.*, 2005) since nutrient availability seems not to  
31 significantly determine their rate of primary productivity (Brunet *et al.*, unpubl. results).  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50

## 51 THE XANTHOPHYLL CYCLE IN THE FIELD: A MATTER OF SCALE

52  
53  
54  
55 Several studies have explored the response of the microalgal XC to the  
56 underwater light climate in coastal areas (Brunet *et al.*, 1993, 2003, 2008; Moline, 1998;  
57  
58  
59  
60

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

Eisner *et al.*, 2003; Fujiki *et al.*, 2003; Müller and Wasmund, 2003), frontal systems (Claustre *et al.*, 1994; Brunet and Lizon, 2003) and offshore areas (Bidigare *et al.*, 1987; Olaizola *et al.*, 1992; Kashino *et al.*, 2002; Brunet *et al.*, 2006, 2007). Because the activation of the XC in reaction to the *in situ* changes in irradiance is fast, it can bring useful information on the physical properties and especially the mixing of water bodies at different time scales (Lewis *et al.*, 1984). Indeed, the XC is well adapted for studying the physical-biological coupling of photosynthesis response to hydrodynamics. This is especially true for the surface mixed layer and the coastal zone. At short time scales (below an hour), the relative amount of photoprotective pigments, mainly Dt, is closely related to the light fluctuations especially due to hydrodynamics. For instance, it is possible to relate the shape of the vertical distribution of the XC pigments with light distribution and depth to highlight the mixing velocity cells have been exposed to (Brunet *et al.*, 2003, 2008; Griffith *et al.*, 2010). At longer time scales, variations of the pool size of Dd bring information on the 'average' light climate to which the cells have been exposed in the past hours/days. The amounts of Dt versus Dd can be used as tracers for microalgal cell movement within the euphotic zone, and in some cases the past light history of the phytoplankton can be extrapolated (Welschmeyer and Hoepffner, 1986; Moline, 1998; Brunet *et al.*, 2003). Generalization from a given ecosystem/water body is impossible due the variety of biotic and abiotic driving forces acting on the XC functioning. Obviously, the impact of latitude and/or of the seasons is important, both directly through climatology and indirectly by shaping the algal community composition, structure and functioning. For instance, in coastal ecosystems, the phytoplankton community is dominated by cells of larger size whose activity is seasonally dependent thus largely modulating their photoadaptive strategy and sensitivity to light stress. Additionally, there is a clear response of the XC to the diurnal cycle, which also depends on season and latitude (Brunet *et al.*, 2007; 2008). On a daily scale, the XC is a good indicator of light stress responsible for the noon decline of photosynthesis (Long *et al.*, 1994). XC operation has also been investigated in benthic estuarine systems, where diatom dominated microphytobenthos forming a dense biofilm at the surface of intertidal mudflats during emersion (Serodio *et al.*, 2005; van Leeuwe *et al.*, 2008; Chevalier *et al.*, 2010). In this special case, the dynamics of the XC can also provide information on the

1  
2  
3 migration of motile diatoms within the sediment together with the changes in incident  
4 irradiance *versus* the tidal cycle/season/latitude (van Leeuwe *et al.*, 2008; Chevalier *et al.*,  
5 2010).  
6  
7

8  
9 On a methodological level, such observation must be considered for improving  
10 the sampling strategy of phytoplankton and the evaluation of its productivity at the  
11 mesoscale as well as for larger scale studies. Indeed, the information extracted from the  
12 XC dynamics at different time scales has been shown to be useful for regional field  
13 studies of the dynamics of phytoplankton photosynthetic productivity (e.g., Brunet *et al.*,  
14 2003). It might be as well an additional tool for larger scale studies especially in the  
15 framework of the impact of climatology on the mixed layer and its potential effect on  
16 marine primary productivity (Rost and Riebesell, 2004; D'Ortenzio *et al.*, 2005).  
17 Recently, in the context of a trans-Mediterranean sampling program, a significant  
18 relationship between mixed layer depth, the distribution of light and the variations in XC  
19 pigments as well as the related NPQ extent was determined (Brunet *et al.*, unpubl.  
20 results). Additionally, the impact of cell size on this relationship was demonstrated with a  
21 significant discrimination between picoeukaryotes and the rest of the phytoplankton  
22 community. Obviously further field investigations are needed in order to increase the  
23 available data set from marine areas with both different trophic status and hydrodynamic  
24 conditions. Also, there is a significant lack of modeling exercises on physical-biological  
25 coupling based on the XC as a marker for photoregulatory physiological processes. There  
26 are already enough data to begin such approach which would be a good alternative to *in*  
27 *situ* regional and large scale systematic investigations. It would help in answering the  
28 question of how far the XC is relevant for the fast regulation of photosynthetic  
29 productivity and carbon fluxes in the upper layer of the water column, and if so, in which  
30 context (Lavaud, 2007; Alderkamp *et al.*, 2010).  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48

## 49 **NEXT STEPS TOWARDS ILLUMINATION**

50  
51  
52  
53 In this paragraph, we report some gaps in understanding, in our opinion, on XC  
54 eco-physiology and its use for a better understanding of *in situ* microalgal ecology.  
55  
56  
57  
58  
59  
60

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

(1) At a functional level, there is a need to increase the data-set on XC characteristics in as many as possible different microalgal species/groups. Especially, it is essential to increase the diversity of biological models, taking into account different functional traits (e.g., size, shape, niche occupancy) together with investigating the feedback of the photoacclimative strategy (sigma- or n-type, Six *et al.*, 2008) of the taxa on the light-dependent XC responses. For instance, one relevant question in the productive lineage of the Heterokontophyta is the role of the secondary XC (the Vx cycle) in the photoregulatory response of cells: is it involved in fast regulation by increasing the capacity for NPQ and/or prevention of lipid peroxidation, and/or is it involved in long term acclimative response by increasing the pool size of precursors for Dt *de novo* synthesis under prolonged excess light exposure?

(2) A conceptual model of photoprotection in phytoplankton is still lacking. Through the recent highlighting of the peculiarities of diatoms (Lavaud, 2007), green microalgae (Peers *et al.*, 2009) and cyanobacteria (Kirilovsky, 2007), it appears that the fast regulation of photosynthesis and the interplay between the photoprotective processes involved is much more complex and diverse than previously thought compared to higher plants. Obviously the post-genomic era our field of research has now entered thanks to the recent publication of genomes from several eukaryotic groups in addition to the ones of photosynthetic bacteria (see <http://www.jgi.doe.gov/>) will strongly push forward the detailed examination of the photoprotective processes at the molecular level. It will help understanding their diversity and evolution among phytoplankton lineages (Lavaud, 2007). For instance, in diatoms, such functional investigations have already started focusing on the light-dependent regulation of photosynthetic genes (Nymark *et al.*, 2009) and the production of photosynthetic mutants (Materna *et al.*, 2009). Coesel *et al.* (2008) showed that the number of genes encoding the enzymes involved in the XC is different in *Phaeodactylum tricornutum* and *Thalassiosira pseudonana*. Is this feature functionally relevant? Could it have implications for the ecophysiology of these species? Also by manipulating the gene encoding the Dd de-epoxidase (which ensures the conversion of Dd into Dt under excess light exposure) we could highlight specific regulatory properties of the XC, i.e. the Dd de-epoxidase concentration appears to be finely regulated in order to provide fast and efficient photoprotection concomitant with the light intensity (Lavaud

1  
2  
3 *et al.*, unpubl. results). Our previous non-molecular physiological investigations (Lavaud  
4 *et al.*, 2002b; Lavaud and Kroth, 2006) could not achieve such a fine level of  
5 understanding.  
6  
7

8  
9 (3) At an ecophysiological level, there are many *in situ* and experimental  
10 observations raising intriguing questions. The first point concerns the effects of UV  
11 radiation on XC which is still under debate due to opposite conclusions from different  
12 studies (see Lavaud, 2007, Laurion and Roy, 2009; van de Poll and Buma, 2009; van de  
13 Poll, 2010). It is now urgent to clarify this aspect regarding the expected growing impact  
14 of UV radiation in the upper layer of the water column due its enhanced stratification by  
15 global warming (Rost and Riebesell, 2004). The influence of nutrient depletion on the  
16 synthesis of xanthophylls (Staehr *et al.*, 2002) and the XC functioning (van de Poll *et al.*,  
17 2005) will also need a deeper investigation in order to assess potential differences in the  
18 photoprotective behaviour of phytoplankton in oligo-/meso-/eutrophic waters. For  
19 instance, Dd/Dt synthesis and NPQ have been reported to dramatically increase in iron  
20 depleted coastal diatoms (Allen *et al.*, 2008) while oceanic species have adapted to low  
21 iron concentrations by sacrificing their ability for NPQ response to irradiance changes  
22 (Strzepek and Harrison, 2004; Lavaud *et al.*, 2007). In this framework, the Antarctic /  
23 Arctic habitats are of special interest to better understand the environmental driving  
24 forces of XC and NPQ (Mangoni *et al.*, 2009; Alderkamp *et al.*, 2010). Indeed, they  
25 allow investigation of special light features (increased UV radiations and/or prolonged  
26 continuous light and dark periods) in combination with other strongly influencing  
27 environmental cues such as nutrients (van de Poll *et al.*, 2005; van Leeuwe *et al.*, 2005).  
28 The role of temperature on the enzymatic regulation of XC has additionally been only  
29 scarcely explored. The synthesis and role of Dt in habitats where the cells never  
30 experience high light is obviously relevant, as for instance in the deep-chlorophyll  
31 maximum, where Dt has been reported (Brunet *et al.* 2006, 2007). Such observations  
32 support the finding that not all Dt molecules are involved in NPQ-driven photoprotection  
33 (Lavaud *et al.*, 2004; Schumann *et al.*, 2007; Dimier *et al.* 2009a); some of them might  
34 play a role as antioxidants (Casotti *et al.*, 2005; Lavaud, 2007). The deployment of  
35 mesocosms under different environmental conditions (trophic status, light quantity and  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

1  
2  
3 quality, temperature) would most probably provide strong support for future  
4 ecophysiological investigations.  
5  
6  
7

## 8 9 **ACKNOWLEDGMENTS**

10 The authors would like to thank Dr. W.H.C.F. Kooistra for critical reading of this  
11 manuscript. The two anonymous referees are kindly acknowledged for their remarks and  
12 criticisms on the previous version of the manuscript.  
13  
14  
15  
16

## 17 18 **FUNDING**

19 C.B. work is supported by the Stazione Zoologica A. Dohrn. J.L. work has been  
20 supported by the National French Institute for Scientific Research-CNRS, the French  
21 consortium CPER-Littoral and the German Research Foundation-DFG (grant LA 2368/2-  
22 1).  
23  
24  
25  
26  
27

## 28 29 **REFERENCES**

- 30 Alderkamp, A.-C., de Baar, H. J. W., Visser, R. J. W., Arrigo, K. R. (2010) Can  
31 photoinhibition control phytoplankton abundance in deeply mixed water columns  
32 of the Southern Ocean ? *Limnol. Oceanogr.*, **55**, 1248-1264.  
33  
34  
35 Allen, A. E., LaRoche, J., Maheswari, U., Lommer, M., Schauer, N., Lopez P. J., Finazzi,  
36 G., Fernie, A. R., Bowler, C. (2008) Whole-cell response of the pennate diatom  
37 *Phaeodactylum tricornutum* to iron starvation. *Proc. Natl. Acad. Sci. USA*, **105**,  
38 10438-10443.  
39  
40  
41  
42 Armbrust, E. V. (2009) The life of diatoms in the world's oceans. *Nature*, **459**, 185-192.  
43  
44 Arsalane, W., Rousseau B., Duval, J.-C. (1994) Influence of the pool size of the  
45 xanthophyll cycle on the effects of light stress in a diatom: Competition between  
46 photoprotection and photoinhibition. *Photochem. Photobiol.*, **60**, 237-243.  
47  
48  
49 Bastow Wilson, J. (1990) Mechanisms of species coexistence: twelve explanations for  
50 Hutchinson's 'paradox of the plankton': evidence from New Zealand plant  
51 communities. *New Zealand J. Ecol.*, **13**, 17-42.  
52  
53  
54  
55 Bailey, S., Grossman, A. (2008) Photoprotection in cyanobacteria: regulation of light  
56 harvesting. *Photochem. Photobiol.*, **84**, 1410-1420.  
57  
58  
59  
60

- 1  
2  
3 Bidigare, R. R., Smith, R. C., Baker, K. S., Marra, J. (1987) Oceanic primary production  
4 estimates from measurements of spectral irradiance and pigment concentrations.  
5 *Global Biogeochem. Cycles.*, **1**, 171-186.  
6  
7  
8  
9 Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., West, G. B. (2004) Toward a  
10 metabolic theory of ecology. *Ecology*, **85**, 1771-1789.  
11  
12 Brunet, C., Brylinski, J.M., Lemoine, Y. (1993) *In situ* variations of the xanthophylls  
13 diadinoxanthin and diatoxanthin: photoadaptation and relationships with an  
14 hydrodynamical system of the Eastern English Channel. *Mar. Ecol. Prog. Ser.*,  
15 **102**, 69-77.  
16  
17  
18  
19 Brunet, C., Lizon, F. (2003) Tidal and diel periodicities of size fractioned phytoplankton  
20 pigment signatures at an offshore station in South-Eastern English Channel.  
21 *Estuar. Coast. Shelf Sci.*, **56**, 835-845.  
22  
23  
24 Brunet, C., Casotti, R., Aronne, B., Vantrepotte, V. (2003) Measured photophysiological  
25 parameters used as tools to estimate vertical water movements in the coastal  
26 Mediterranean. *J. Plankton Res.*, **25**, 1413-1425.  
27  
28  
29  
30 Brunet, C., Casotti, R., Vantrepotte, V., Corato, F., Conversano, F. (2006)  
31 Picophytoplankton diversity and photophysiology in the Strait of Sicily  
32 (Mediterranean Sea) in summer. I. Mesoscale variations. *Aquatic Microb. Ecol.*,  
33 **44**, 127-141.  
34  
35  
36  
37 Brunet, C., Casotti, R., Vantrepotte, V., Corato, F., Conversano, F. (2007) Vertical  
38 variability and diel dynamics of picophytoplankton in the Strait of Sicily  
39 (Mediterranean Sea) in summer. *Mar. Ecol. Prog. Ser.*, **346**, 15-26.  
40  
41  
42  
43 Brunet, C., Casotti, R., Vantrepotte, V. (2008) Phytoplankton diel and vertical variability  
44 in photobiological responses at a coastal station in the Mediterranean Sea. *J.*  
45 *Plankton Res.*, **30**, 645-654.  
46  
47  
48 Brunet, C., Johnsen, G., Lavaud, J., Roy, S. (in press) Selected pigment applications in  
49 oceanography\_Pigments and photoacclimation processes. In Roy S, Johnsen G,  
50 Llewellyn C, Skarstad E (eds) *Phytoplankton Pigments in Oceanography:*  
51 *Guidelines to Modern Methods*, Series: Oceanographic Methodologies Vol. 2,  
52 SCOR-UNESCO Publishing, Cambridge University Press.  
53  
54  
55  
56  
57  
58  
59  
60

- 1  
2  
3 Casotti, R., Mazza, S., Brunet, C., Vantrepotte, V., Ianora, A., Miralto A. (2005) Growth  
4 inhibition and toxicity of the diatom aldehyde 2-trans-4-trans decadienal on  
5  
6 *Thalassiosira weissflogii* (Bacillariophyceae). *J. Phycol.*, **41**, 7-20.  
7  
8  
9 Chevalier, E. M., Gévaert, F., Créach, A. (2010) *In situ* photosynthetic activity and  
10 xanthophylls cycle development of undisturbed microphytobenthos in an  
11 intertidal mudflat. *J. Exp. Mar. Biol. Ecol.*, **385**, 44-49.  
12  
13  
14 Claustre, H., Kerhervé, P., Marty, J.-C., Prieur L. (1994) Phytoplankton photoadaptation  
15 related to some frontal physical processes. *J. Mar. Systems*, **5**, 251-265.  
16  
17  
18 Coesel, S., Obornik, M., Varela, J., Falciatore, A., Bowler, C. (2008) Evolutionary  
19 origins and functions of the carotenoid biosynthetic pathway in marine diatoms.  
20 *PLoS ONE*, **3**, e2896.  
21  
22  
23 Cogdell, R. J. (2006) The structural basis of non-photochemical quenching is revealed?  
24 *TRENDS Plant Sci.*, **11**, 59-60.  
25  
26  
27 Demmig-Adams, B., Adams III, W. W. (2006) Photoprotection in an ecological context:  
28 the remarkable complexity of thermal energy dissipation. *New Phytol.* **172**, 11-21.  
29  
30  
31 Dimier, C., Corato, F., Saviello, G., Brunet, C. (2007a) Photophysiological properties of  
32 the marine picoeukaryote *Picochlorum* RCC237 (Trebouxiophyceae,  
33 Chlorophyta). *J. Phycol.*, **43**, 275-283.  
34  
35  
36 Dimier, C., Corato, F., Tramontano, F., Brunet, C. (2007b) Photoprotection and  
37 xanthophyll cycle activity in three diatoms. *J. Phycol.*, **43**, 937-947.  
38  
39  
40 Dimier, C., Brunet, C., Geider, J. R., Raven, J. A. (2009a) Growth and photoregulation  
41 dynamics of the picoeukaryote *Pelagomonas calceolata* in fluctuating light.  
42 *Limnol. Oceanogr.*, **54**, 823-836.  
43  
44  
45 Dimier, C., Saviello, G., Tramontano, F., Brunet, C. (2009b) Comparative ecophysiology  
46 of the xanthophyll cycle in six marine phytoplanktonic species. *Protist*, **160**, 397-  
47 411.  
48  
49  
50 D'ortenzio, F., Iudicone, D., Boyer Montegut, C., Testor, P., Antoine, D., Marullo, S.,  
51 Santoleri, R., Madec, G. (2005) Seasonal variability of the mixed layer depth in  
52 the Mediterranean Sea as derived from *in situ* profiles. *Geophys. Res. Lett.*,  
53 32(L12605): doi:1.1029/2005GL022463.  
54  
55  
56  
57  
58  
59  
60

- 1  
2  
3 Dubinsky, Z., Schofield, O. (2010) From the light to the darkness: Thriving at the light  
4 extremes in the oceans. *Hydrobiologia*, 639: 153-171.  
5  
6  
7 Eisner, L. B., Twardowski, M. S., Cowles, T. J., Perry, M. J. (2003) Resolving  
8 phytoplankton photoprotective: photosynthetic carotenoid ratios on fine scales  
9 using *in situ* absorption measurements *Limnol. Oceanogr.*, **48**, 632-646.  
10  
11  
12 Falkowski, P. G., Raven, J. A. *Aquatic Photosynthesis*, Blackwell Science Publishers,  
13 Malden, USA, 375 pp.  
14  
15  
16 Finkel, Z. (2001) Light absorption and size scaling of light-limited metabolism in marine  
17 diatoms. *Limnol. Oceanogr.*, **46**, 86-94.  
18  
19  
20 Flöder S. U. J., Kawabata, Z.-I. (2002) The influence of fluctuating light intensities on  
21 species composition and diversity of natural phytoplankton communities.  
22 *Oecologia*, **133**, 395-401.  
23  
24  
25 Fujiki, T., Toda, T., Kikuchi, T., Taguchi, S. (2003). Photoprotective response of  
26 xanthophyll pigments during phytoplankton blooms in Sagami Bay, Japan. *J.*  
27 *Plankton Res.*, **25**, 317-322.  
28  
29  
30 Goss, R., Jakob, T. (2010) Regulation and function of xanthophyll cycle-dependent  
31 photoprotection in algae. *Photosynth. Res.*, in press.  
32  
33  
34 Grobbelaar J (2006) Photosynthetic response and acclimation of microalgae to light  
35 fluctuations. In: Subba Rao, D. V. (Ed) *Algal Cultures Analogues of Blooms and*  
36 *Applications*, Science Publishers, Enfield, USA, pp 671-683.  
37  
38  
39 Griffith, G. P., Vennell, R., Williams, M. J. M. (2010) An algal photoprotection index  
40 and vertical mixing in the Southern Ocean. *J. Plankton Res.*, **32**, 515-528.  
41  
42  
43 Gundermann K., Büchel C. (2008). The fluorescence yield of the trimeric fucoxanthin  
44 chlorophyll-protein FCPa in the diatom *Cyclotella meneghiniana* is dependent on  
45 the amount of bound diatoxanthin. *Photosynth. Res.*, **95**, 229-235.  
46  
47  
48 Huisman, J., Johansson, A. M., Folmer, E. O., Weissing, F. J. (2001) Towards a solution  
49 of the plankton paradox: the importance of physiology and life history. *Ecology*  
50 *Lett.*, **4**, 408-411.  
51  
52  
53 Hutchinson, G. E. (1961) The paradox of the plankton. *Am. Nat.*, **95**, 137-145.  
54  
55  
56  
57  
58  
59  
60

- 1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60
- Kashino, Y., Kudoh, S., Hayashi, Y., Suzuki, Y., Odate, T., Hirawake, T., Satoh, K., Fukuchi, M. (2002) Strategies of phytoplankton to perform effective photosynthesis in the North water. *Deep-Sea Res. II*, **49**, 5049-5061.
- Key, T., McCarthy, A., Campbell, D. A., Six, C., Roy, S., Finkel, Z. V. (2010) Cell size trade-off govern light exploitation strategies in marine phytoplankton. *Env Microbiol.*, **12**, 95-104.
- Kirilovsky, D. (2007) Photoprotection in cyanobacteria: the orange carotenoid protein (OCP)-related non-photochemical-quenching mechanism. *Photosynth. Res.*, **93**, 7-16.
- Kooistra, W. C. F., Gersonde, R., Medlin, L. K., Mann, D. G. (2007) The origin and evolution of the diatoms: Their adaptation to a planktonic existence. In: Evolution of planktonic photoautotrophs. Eds: Paul G. Falkowski and Andrew H. Knoll. Academic Press, Inc., pp 207-250.
- Kropuenske, L. R., Mills, M. M., van Dijken, G. L., Bailey, S., Robinson, D. H., Welschmeyer, N. A., Arrigo, K. R. (2009) Photophysiology in two major Southern Ocean phytoplankton taxa: Photoprotection in *Phaeocystis antarctica* and *Fragillariopsis cylindrus*. *Limnol. Oceanogr.*, **54**, 1176-1196.
- Laurion, I., Roy, S. (2009) Growth and photoprotection in three dinoflagellates (including two strains of *Alexandrium tamarense*) and one diatom exposed to four weeks of natural and enhanced ultraviolet-B radiation. *J. Phycol.*, **45**, 16-33.
- Lavaud, J., Rousseau, B., van Gorkom, H. J., Etienne, A.-L. (2002a). Influence of the diadinoxanthin pool size on photoprotection in the marine planktonic diatom *Phaeodactylum tricorutum*. *Plant Physiol.*, **129**, 1398-1406.
- Lavaud, J., Rousseau, B., Etienne, A.-L. (2002b) In diatoms, a transthylakoidal proton gradient alone is not sufficient for non-photochemical fluorescence quenching. *FEBS Lett.*, **523**, 163-166.
- Lavaud, J., Rousseau, B., Etienne, A.-L. (2003) Enrichment of the light-harvesting complex in diadinoxanthin and implications for the nonphotochemical quenching fluorescence quenching in diatoms. *Biochemistry*, **42**, 5802-5808.

- 1  
2  
3 Lavaud, J., Rousseau, B., Etienne, A.-L. (2004) General features of photoprotection by  
4 energy dissipation in planktonic diatoms (Bacillariophyceae). *J. Phycol.*, **40**, 130-  
5 137.  
6  
7  
8  
9 Lavaud, J., Kroth, P. G. (2006) In diatoms, the transthylakoid proton gradient regulates  
10 the photoprotective non-photochemical fluorescence quenching beyond its control  
11 on the xanthophyll cycle. *Plant Cell Physiol.*, **47**, 1010-1016.  
12  
13  
14 Lavaud, J. (2007) Fast regulation of photosynthesis in diatoms: Mechanisms, evolution  
15 and ecophysiology. *Funct. Plant Sci. Biotech.*, **1**, 267-287.  
16  
17  
18 Lavaud, J., Strzepeck, R. F., Kroth, P. G. (2007) Photoprotection capacity differs among  
19 diatoms: possible consequences on the spatial distribution of diatoms related to  
20 fluctuations in the underwater light climate. *Limnol. Oceanogr.*, **52**, 1188-1194.  
21  
22  
23 Lewis, M. R., Cullen, J. J., Platt, T. (1984) Relationships between vertical mixing and  
24 photoadaptation of phytoplankton: similarity criteria. *Mar. Ecol. Prog. Ser.*, **15**,  
25 141-149.  
26  
27  
28 Li, Z., Wakao, S. Fischer, B. B., Niyogi, K. K. (2009) Sensing and responding to excess  
29 light. *Annu. Rev. Plant Biol.*, **60**, 239-260.  
30  
31  
32 Liess, A., Lange, K., Schulz, F., Piggott, J. J., Matthaei, C. D., Townsend, C. R. (2009)  
33 Light, nutrients and grazing interact to determine diatom species richness via  
34 change to productivity, nutrient state and grazing activity. *J. Ecol.*, doi:  
35 10.1111/j.1365-2745.2008.01463.x  
36  
37  
38  
39 Litchman, E. (2000) Growth rate of phytoplankton under fluctuating light. *Freshwater*  
40 *Biol.*, **44**, 223-235.  
41  
42  
43 Litchman, E., Klausmeier, C. A. (2001) Competition of phytoplankton under fluctuating  
44 irradiance. *Am. Nat.*, **157**, 170-187.  
45  
46  
47 Litchman, E., Klausmeier, C. A.; (2008) Trait-based community ecology of  
48 phytoplankton. *Annu. Rev. Ecol. Evol. Syst.*, **39**, 615-639.  
49  
50  
51 Long, S. P., Humphries, S., Falkowski, P. G. (1994) Photoinhibition of photosynthesis in  
52 nature. *Ann. Rev. Plant Physiol. Plant Mol. Biol.*, **45**, 633-662.  
53  
54  
55 MacIntyre, H. L., Kana T. M., Geider J. R. (2000) The effect of water motion on the  
56 short-term rates of photosynthesis by marine phytoplankton. *TRENDS Plant Sci.*,  
57 **5**, 12-17.  
58  
59  
60

- 1  
2  
3 Mangoni, O., Carrada, G.C., Modigh, M., Catalano, G., Saggiomo, V. (2009)  
4 Photoacclimation in Antarctic bottom ice algae: an experimental approach. *Polar*  
5 *Biol.*, **32**, 325-335.  
6  
7  
8 Materna A. C., Sturm S., Kroth P. G., Lavaud J. (2009) First induced plastid genome  
9 mutations in an alga with secondary plastids: *psbA* mutations in the diatom  
10 *Phaeodactylum tricornutum* (Bacillariophyceae) reveal consequences on the  
11 regulation of photosynthesis. *J. Phycol.*, **45**, 838-846.  
12  
13  
14 Meyer, A. A., Tackx, M., Daro, N. (2000) Xanthophyll cycling in *Phaeocystis globosa*  
15 and *Thalassiosira* sp.: a possible mechanism for species succession. *J. Sea Res.*,  
16 **43**, 373-384.  
17  
18  
19  
20 Mitrovic S. M., Howden C. G., Bowling L. C., Buckney R. T. (2003) Unusual allometry  
21 between *in situ* growth of freshwater phytoplankton under static and fluctuating  
22 light environments: possible implications for dominance. *J. Plankton Res.*, **25**,  
23 517-526.  
24  
25  
26  
27 Moline, M. A. (1998) Photoadaptive response during the development of a coastal  
28 Antarctic diatom bloom and relationship to water column stability. *Limnol.*  
29 *Oceanogr.*, **43**, 146-153.  
30  
31  
32 Müller, A. M., Wasmund, N. (2003). Photophysiology of surface phytoplankton  
33 communities in a transect from the mouth of the Peene-strom to the Arkona Sea  
34 (Baltic). *Internat. Rev. Hydrobiol.*, **88**, 482-497.  
35  
36  
37  
38 Mullineaux, C. W., Emlyn-Jones, E. (2004) State-transitions: an example of acclimation  
39 to low-light stress. *J. Exp. Bot.*, **56**, 389-393.  
40  
41  
42 Nymark, M., Valle, K. C., Brembu, T., Hancke, K., Winge, P., Andresen, K., Johnsen,  
43 G., Bones, A. M. (2009) An integrated analysis of molecular acclimation to high  
44 light in marine diatom *Phaeodactylum tricornutum*. *PLoS ONE*, **4**, e7743.  
45  
46  
47 Olaizola, M., Bienfang, P. K., Ziemann, D. A. (1992). Pigment analysis of phytoplankton  
48 during a subarctic bloom: xanthophyll cycling. *J. Exp. Mar. Biol. Ecol.*, **158**, 59-  
49 74.  
50  
51  
52  
53 Peers, G., Truong T. B., Ostendorf, E., Busch, A., Elrad, D., Grossman, A. R., Hippler,  
54 M., Niyogi K. K. (2009) An ancient light-harvesting protein is critical for the  
55 regulation of algal photosynthesis. *Nature*, **462**, 518-521.  
56  
57  
58  
59  
60

- 1  
2  
3 Raven, J. A., Kübler, J. A. (2002) New light on the scaling of metabolic rate with the size  
4 of algae. *J. Phycol.*, **38**, 11-16.  
5  
6  
7 Raven, J. A., Geider, J. R. (2003) Adaptation, acclimation and regulation in algal  
8 photosynthesis. In Larkum W. D., Douglas S. E., Raven J. A. (Eds)  
9 *Photosynthesis in Algae*, Kluwer Academic Publishers, Dordrecht, The  
10 Netherlands, pp 385-412.  
11  
12  
13  
14 Rost, B., Riebesell, U. (2004) Coccolithophores and the biological pump: responses to  
15 environmental changes. In Thierstein, H. R., Young J. R. (Eds) *Coccolithophores:*  
16 *from molecular processes to global impact*, Springer, Berlin, Germany, pp 99-  
17 125.  
18  
19  
20  
21 Ruban, A. V., Johnson, M. P. (2009) Dynamics of higher plant photosystem cross-section  
22 associated with state-transitions. *Photosynth. Res.*, **99**, 173-183.  
23  
24  
25 Schumann, A., Goss, R., Jakob, T., Wilhelm, C. (2007) Investigations on the quenching  
26 efficiency of diatoxanthin in cells of *Phaeodactylum tricornutum*  
27 (Bacillariophyceae) with different pool sizes of xanthophylls cycle pigments.  
28 *Phycologia*, **46**, 113-117.  
29  
30  
31  
32 Serodio, J., Cruz, S. Vieira, S., Brotas, V. (2005) Non-photochemical quenching of  
33 chlorophyll fluorescence and operation of the xanthophyll cycle in estuarine  
34 microphytobenthos. *J. Exp. Mar. Biol. Ecol.*, **326**, 157-169.  
35  
36  
37 Six C., Finkel Z. V., Irwin A. J., Campbell D. A. (2007) Light variability illuminates  
38 niche partitioning among marine picocyanobacteria. *PLoS ONE* **2**, e1341.  
39  
40  
41 Six, C., Finkel, Z., Rodriguez, F., Marie, D., Partensky, F. and Campbell D. A. (2008)  
42 Contrasting photoacclimation costs in ecotypes of the marine eukaryote  
43 picoplankter *Ostreococcus*. *Limnol. Oceanogr.*, **53**, 255-265.  
44  
45  
46 Six C., Sherrard, R., Lionard M., Roy S., Campbell D. A. (2009) Photosystem II and  
47 pigment dynamics among ecotypes of the Green Alga *Ostreococcus*. *Plant*  
48 *Physiol.*, **151**, 379-390.  
49  
50  
51 Sommer, U. (1995) An experimental test of the intermediate disturbance hypothesis using  
52 cultures of marine phytoplankton. *Limnol. Oceanogr.*, **40**, 1271-1277.  
53  
54  
55  
56  
57  
58  
59  
60

- 1  
2  
3 Staehr, P. A., Henriksen, P., Markager, S. (2002) Photoacclimation of four marine  
4 phytoplankton species to irradiance and nutrient availability. *Mar. Ecol. Prog.*  
5 *Ser.*, **238**, 47-59.  
6  
7  
8 Strzepek, R. F., Harrison, P. J. (2004) Photosynthetic architecture differs in coastal and  
9 oceanic diatoms. *Nature*, **431**, 689-692.  
10  
11 Timmermans, K. R., van der Wagt, B., Veldhuis, M. J. W., Maatman, A., De Baar, H. J.  
12 W. (2005) Physiological responses of three species of marine pico-phytoplankton  
13 to ammonium, phosphate, iron and light limitation. *J. Sea Res.*, **53**, 109-120.  
14  
15 van de Poll, W. H., van Leeuwe, M. A., Roggeveld, J., Buma A. G. J. (2005) Nutrient  
16 limitation and high irradiance reduce PAR and UV-induced viability loss in the  
17 Antarctic diatom *Chaetoceros brevis* (Bacillariophyceae). *J. Phycol.*, **41**, 840-850.  
18  
19 van de Poll, W. H., Visser, R. J. W., Buma A. G. J. (2007) Acclimation to a dynamic  
20 irradiance regime changes excessive irradiance sensitivity of *Emiliana huxleyi*  
21 and *Thalassiosira weissflogii*. *Limnol. Oceanogr.*, **52**, 1430-1438.  
22  
23 van de Poll, W. H., Buma, A. G. J. (2009) Does ultraviolet radiation affect the  
24 xanthophyll cycle in marine phytoplankton? *Photochem Photobiol Sci.*, **8**, 1295-  
25 1301.  
26  
27 van de Poll, W. H., Buma, A. G. J., Visser, R. J. W., Janknegt, P. J., Villavañe, V. E.,  
28 Helbling, E. W. (2010) Xanthophyll cycle activity and photosynthesis of  
29 *Dunaliella tertiolecta* (Chlorophyceae) and *Thalassiosira weissflogii*  
30 (Bacillariophyceae) during fluctuating solar radiation. *Phycologia*, **49**, 249-259.  
31  
32 van Leeuwe, M. A., van Sikkelerus, B., Gieskes, W. W. C., Stefels, J. (2005) Taxon  
33 specific differences in photoacclimation to fluctuating irradiance in an Antarctic  
34 diatom and a green flagellate. *Limnol. Oceanogr.*, **288**, 9-19.  
35  
36 van Leeuwe, M. A., Brotas, V., Consalvey, M., Forster, R. M., Gillespie, D., Jesus, B.,  
37 Roggeveld, J., Gieskes, W. W. C. (2008) Photoacclimation in microphytobenthos  
38 and the role of the xanthophyll cycle. *Eur. J. Phycol.*, **43**, 123-132.  
39  
40 Wagner H., Jakob T., Wilhelm C. (2006) Balancing the energy flow from captured light  
41 to biomass under fluctuating light conditions. *New Phytol.*, **169**, 95-108.  
42  
43 Welschmeyer, N. A., Hoepffner, N. (1986). Rapid xanthophyll cycling: an *in situ* tracer  
44 for mixing in the upper ocean. *EOS (Trans. Am. Geophys. Union)*, **67**: 969.  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

1  
2  
3 Wilhelm, C., Büchel, C, Fisahn, J., Goss, R., Jakob, T., LaRoche, J., Lavaud, J., Lohr,  
4 M., Riebesell, U., Stehfest, K., Valentin, K., Kroth, P. G. (2006) The regulation of  
5 carbon and nutrient assimilation in diatoms is significantly different from green  
6 algae. *Protist*, **157**, 91-124.  
7  
8  
9

10 Wilson, A., Ajlani, G., Verbavatz, J.M., Vass, I., Kerfeld, C.A., Kirilovsky, D. (2006) A  
11 soluble carotenoid protein involved in phycobilisome-related energy dissipation in  
12 cyanobacteria. *Plant Cell*, **18**, 992-1007.  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

For Peer Review