

BREAKTHROUGH REPORT

Diatom Phytochromes Reveal the Existence of Far-Red-Light-Based Sensing in the Ocean^{OPEN}

Antonio Emidio Fortunato,^{a,1} Marianne Jaubert,^{a,1} Gen Enomoto,^b Jean-Pierre Bouly,^a Raffaella Raniello,^c Michael Thaler,^a Shruti Malviya,^{d,2} Juliana Silva Bernardes,^a Fabrice Rappaport,^{e,3} Bernard Gentili,^f Marie J.J. Huysman,^{g,h,i} Alessandra Carbone,^{a,j} Chris Bowler,^d Maurizio Ribera d'Alcalà,^{c,4} Masahiko Ikeuchi,^b and Angela Falciatore^{a,4}

^a Sorbonne Universités, UPMC, Institut de Biologie Paris-Seine, CNRS, Laboratoire de Biologie Computationnelle et Quantitative UMR 7238, 75006 Paris, France

^b Department of Life Sciences (Biology), Graduate School of Arts and Sciences, The University of Tokyo, Meguro, Tokyo 153-8902, Japan

^c Stazione Zoologica Anton Dohrn, 80121 Naples, Italy

^d Ecole Normale Supérieure, PSL Research University, Institut de Biologie de l'Ecole Normale Supérieure, CNRS UMR 8197, INSERM U1024, F-75005 Paris, France

^e Institut de Biologie Physico-Chimique, UMR 7141 CNRS-UPMC, 75005 Paris, France

^f Sorbonne Universités, UPMC Univ-Paris 6, CNRS, UMR 7093, Laboratoire d'Océanologie de Villefranche, F-06230 Villefranche/mer, France

^g Protistology and Aquatic Ecology, Department of Biology, Ghent University, B-9000 Gent, Belgium

^h Department of Plant Systems Biology, VIB, B-9052 Gent, Belgium

ⁱ Department of Plant Biotechnology and Bioinformatics, Ghent University, B-9052 Gent, Belgium

^j Institut Universitaire de France, 75005 Paris, France

ORCID IDs: 0000-0002-3173-5742 (A.E.F.); 0000-0001-5419-5796 (M.J.); 0000-0002-3680-2043 (R.R.); 0000-0002-5492-9961 (M.R.d.A.)

The absorption of visible light in aquatic environments has led to the common assumption that aquatic organisms sense and adapt to penetrative blue/green light wavelengths but show little or no response to the more attenuated red/far-red wavelengths. Here, we show that two marine diatom species, *Phaeodactylum tricornutum* and *Thalassiosira pseudonana*, possess a bona fide red/far-red light sensing phytochrome (DPH) that uses biliverdin as a chromophore and displays accentuated red-shifted absorbance peaks compared with other characterized plant and algal phytochromes. Exposure to both red and far-red light causes changes in gene expression in *P. tricornutum*, and the responses to far-red light disappear in DPH knockout cells, demonstrating that *P. tricornutum* DPH mediates far-red light signaling. The identification of DPH genes in diverse diatom species widely distributed along the water column further emphasizes the ecological significance of far-red light sensing, raising questions about the sources of far-red light. Our analyses indicate that, although far-red wavelengths from sunlight are only detectable at the ocean surface, chlorophyll fluorescence and Raman scattering can generate red/far-red photons in deeper layers. This study opens up novel perspectives on phytochrome-mediated far-red light signaling in the ocean and on the light sensing and adaptive capabilities of marine phototrophs.

INTRODUCTION

Phytochromes (PHY) represent a major class of photoreceptors first discovered in terrestrial plants as red and far-red (R-FR) light sensors controlling key adaptive and developmental processes

(Franklin and Quail, 2010). Subsequently, these photoreceptors have been identified in several prokaryotic and eukaryotic organisms, from phototrophs to heterotrophs (Rodriguez-Romero et al., 2010; Auldrige and Forest, 2011).

PHY spectral characteristics are determined by covalent interaction with a heme-derived linear tetrapyrrole chromophore in the N-terminal photosensory module (PSM) of the apoprotein. The canonical PSM typically consists of conserved consecutive PAS (Period/Arnt/Single-minded), GAF (cGMP phosphodiesterase/adenylyl cyclase/FhlA), and PHY (Phy specific) domains, which undergo reversible conformational changes upon irradiation, from a Pr to a Pfr form and vice versa. The photoswitchable PSM controls the activity of the C-terminal output module (OPM) involved in signal propagation. Compared with the PSM, larger diversification is found in the OPM, which can contain PAS, ATPase (H), histidine kinase (KD), diguanylate cyclase (GGDEF),

¹ These authors contributed equally to this work.

² Current address: CSIR-National Institute of Oceanography, Dona Paula, Goa 403 004, India.

³ Deceased.

⁴ Address correspondence to maurizio@szn.it or angela.falciatore@upmc.fr.

The author responsible for distribution of materials integral to the findings presented in this article in accordance with the policy described in the Instructions for Authors (www.plantcell.org) is: Angela Falciatore (angela.falciatore@upmc.fr).

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