

The missing P-step in red tide dinoflagellates: A productive quenching model for Form II RuBisCO bioenergetics

Christopher Hewes

chewes@ucsd.edu

University of California San Diego

Research Article

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Abstract

Photosynthetic organisms display characteristic polyphasic chlorophyll-a fluorescence transients - specifically the OJIP (Origin, J-step, I-step, and P-step) signature - under pulse amplitude modulated (PAM) fluorometry over the first second of light exposure. The P-step represents the maximum fluorescence yield (F_M) where the photosystem II (PSII) acceptor pool is fully reduced, while the Origin represents its complete oxidation. Although non-photochemical quenching (NPQ) reduces these signatures under excess irradiance, the overall OJIP profile remains highly conserved across diverse phyla. However, natural populations of the red tide dinoflagellate *Lingulodinium polyedra* sampled in La Jolla, California (2024–2025) challenge this paradigm. Dark-acclimated cells completely lack a P-step, with fluorescence peaking prematurely at the I-step (~ 30 ms), whereas a brief bright light exposure subsequently induces a prominent P-step. Consequently, standard biophysical metrics are methodologically invalid because F_M is irresolvable in the dark-acclimated state. Other laboratory studies have shown that the P-step disappears by stealing electrons away from ferredoxin-NADP⁺ reductase (FNR). A model of "productive quenching" is proposed to explain the missing P-step in natural populations. In this model, photosystem I (PSI) electrons are efficiently re-routed into alternative pathways - specifically cyclic electron flow (CEF) and the water-water cycle (WWC) - bypassing standard linear electron flow (LEF) and FNR. Massive adenosine triphosphate (ATP) pools are generated to fuel energy-expensive carbon-concentrating mechanisms (CCMs) necessitated by the inefficient Form II ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO). The trans-thylakoid proton gradient (ΔpH) serves as a metabolic switch, coordinating photoprotective dissipation, NPQ, with enhanced carboxylation via ATP generation driven CCMs – productive quenching.

Introduction

To initiate photosynthesis, photosystem (PS) II requires two quantum-derived reductions of the quencher plastoquinone A (Q_A) to double reduce a single plastoquinone B (Q_B), and $2 Q_B^{2-}$ (with help of local protons) to produce plastoquinol (PQH_2). This four-electron charge is carried as a linear electron flow (LEF) that is re-energized via ferredoxin (Fd) through a photon-charged PS I in order for carboxylation to occur in the Calvin Benson Bassham (CBB) cycle (Shevela et al. 2018). After an initial absorption of photons in the reaction center, the LEF is temperature dependent implying it is a chain of redox reactions (Govindjee 2004). When LEF has an incomplete coupling along its redox route, in-vivo chlorophyll (Chl)-a fluorescence results. At specific steps of photosynthesis along the LEF sequence (referred to as "bottlenecks"), PQH_2 cannot be oxidized fast enough to produce a sufficient Q_B pool for reduction (Johnson 2025, Levin 2025). Ultimately the Q_A^- concentration builds up under continued irradiation as a backlog that occurs for lack of Q_B to reduce; the relaxation of this charge is into antenna Chl that then fluoresces. With an intense pulse of light to a photosynthetic organism, Chl fluorescence increases additively at specific elapsed times as a result of LEF encountering different bottlenecks in this chain of redox reactions for photosynthesis. Measured over short periods (< 1 sec), a characteristic "signature" of

timing for varying fluorescence yield is found in common amongst most photosynthetic organisms (Strasser and Govindjee 1991, Papageorgiou et al. 2007).

The Pulse Amplitude Modulated (PAM) Chl fluorometer is a preeminent tool for studying LEF and its bottlenecks. Strasser and Govindjee (1991,1992) observed (with time plotted in log scale) that the initial, fast rise of Chl fluorescence that followed a burst of illumination (known as the fast transient, $t \leq \sim 1.0$ s) was polyphasic having a minimum (F_0 , measured at $\sim < 50$ μ s) and a maximum (F_M , at ~ 300 ms). The F_0 is the basic, intrinsic fluorescence as propagated from non-photochemical (e.g., background) reactions. Between F_0 and F_M , two major plateaus (F_J at ~ 3 ms and F_I at ~ 30 ms, also called F_I and F_{II} , respectively) occur, as well are (sometimes) found two minor inflections (F_K and F_G ; Strasser and Govindjee 1991, 1992). The times separating each major phase takes place approximately one order of magnitude greater than the preceding one; i.e., $F_0 \approx 0.3\text{--}0.5$ ms, $F_J \approx 3$ ms, $F_I \approx 30$ ms, and $F_M \approx 300$ ms, or there abouts. This characteristic signature was termed “OJIP” signifying the “origin” (O), the two major inflections (J and I), to the peak (P) as steps (Strasser et al. 1995). Beyond the P-step (= F_M), a period referred to as the slow transient phase ($t > \sim 1.0$ s), additional polyphasic fluorescence signal structures are observed (see Papageorgiou and Govindjee 2011, Mohammad Aslam et al. 2022, 2023), and not discussed any further.

Most emphasis by observing the fast transient has been placed upon the relationship of variable fluorescence ($F_V = F_M - F_0$) relative to F_M , i.e., F_V / F_M (Schansker et al. 2013). The ratio F_V / F_M (measured in the dark-acclimated state) is an estimate of the relative (i.e., qualitative) maximum quantum efficiency of PSII. This is under the conditions that (1) F_0 is the minimum (e.g., background) fluorescence without photosynthesis (the photosystem is “open” and fully oxidized), and (2) F_M is the maximum fluorescence during photosynthesis that results when PSII is fully reduced (i.e., “closed” to any further reduction) – hence the P-step.

Non-photochemical quenching (NPQ) occurring in the PSII antenna matrix will reduce the overall exciton flux directed to the reaction center (Lavaud 2007; Grouneva et al. 2009; Büchel 2019), thereby diminishing Chl fluorescence intensity. It is a frequently used parameter derived from the P-step (F_M ; Stirbet and Govindjee 2011; Stirbet et al. 2014, 2018). In green algae and land plants, this process is mediated through Δ pH modulation of PsbS proteins. In diatoms, Δ pH modulation occurs through Lhcx proteins, whereas in peridinin-containing dinoflagellates, it operates via conformational shifts within membrane-bound Chl-a -Chl-c -peridinin-protein complexes (acpPC) alongside the uncoupling of peripheral peridinin-Chl-protein (PCP) complexes (Goss and Lepetit 2015). Although xanthophyll-cycling profiles and active structural proteins differ significantly across these phyla, all remain fundamentally regulated by the trans-thylakoid gradient, Δ pH. This gradient exploits lumenal acidification (Δ pH < 5.5) to trigger thermal dissipation (NPQ) while utilizing stromal alkalization (Δ pH ~ 8.0) to drive upstream enzymatic rearrangements and carbon acquisition. Although xanthophyll cycling profiles and active structural proteins differ significantly across these phyla, Δ pH is central to their control. This photosynthetic reaction, NPQ, to light exposure seems “universal” and is well known; reversal to a dark-

acclimated (to a completely oxidized PS II) state takes about 20 minutes (Schansker et al. 2006), and is a primary reason that samples be dark-acclimated before OJIP analyses with PAM (Schreiber 2004).

The P-step reflects the maximum number of electrons (capacity) that PSII can store, providing the maximum fluorescence yield ($= F_M$). This, at least, is a dogma incorporating terrestrial plants and common algae. Light, temperature, nutrients, and toxins are primary ecological variables that impact algal photosynthesis and productivity; therefore, it had been anticipated that F_v/F_M could be used to appraise phytoplankton health in the field under extreme environmental conditions. In practice, it is not so simple (Parkhill et al. 2001; Kruskopf and Flynn 2006; Antal et al. 2009). As a consequence of its simplicity for measure, F_v/F_M has become an often-applied parameter in investigations that analyze algal photosynthesis and physiology, and the dynamics for microbial communities. Yet, because of its very simplicity, has this led to overlooking important details?

Challenging the green algae – terrestrial plant paradigm The polyphasic Chl-a fluorescence rise (OJIP) provides a powerful non-invasive probe into the induction kinetics of PSII, yet its application to marine phytoplankton is frequently complicated by phylum-specific deviations from the terrestrial plant paradigm. In particular, dinoflagellates exhibit several unusual biophysical features that challenge standard interpretations of the J-, I-, and P-steps (Antal et al. 2009, 2011, 2025). The phylum **Dinoflagellata** exhibit notable variability in photosynthetic induction kinetics depending on ecological niche and physiological state.

For instance, studies on the endosymbiotic *Symbiodiniaceae* (formerly *Symbiodinium* sp.) have documented polyphasic fluorescence transients that include traditional P-steps alongside distinct slow transient phases (Mohammad Aslam et al. 2022, 2023). These endosymbionts utilize active carbon-concentrating mechanisms (CCMs) and alternative electron pathways, such as the Mehler reaction (water-water cycle; WWC), to balance photosynthetic flux and satisfy the metabolic demands of their host-symbiont relationship. Taxa such as *Amphidinium carterae* and *Prorocentrum minimum* often display a pronounced "dip" immediately following the J-step and a secondary dip after the I-step, likely reflecting transient imbalances between PSII donor-side activity and the high rate of electron transport from P680 to Q_A (Antal et al. 2025). Unlike green algae and higher plants, dark-adapted photosynthetic dinoflagellates maintain a robust capacity for PSI-mediated re-oxidation of the plastoquinone (PQ) pool even under strong actinic illumination (Antal et al. 2009). This efficient intersystem throughput can prevent the complete reduction of the PQ pool, leading to a significant underestimation of the maximum fluorescence (F_M) and a markedly reduced I-P phase.

The dinoflagellate red tide A *Lingulodinium polyedra* dominated "red tide", succeeded by lesser blooms of other dinoflagellate species, occurred along the coast of La Jolla, CA, between early-fall, 2024, and late-spring, 2025. Historical records indicate that this red tide for 2024–2025 was not unusual, and similar dinoflagellate blooms do occur every few years (Allen 1923, 1941; McGowan et al. 2017; Zheng et al. 2023). The red tide observed 2024–2025 provided the opportunity to examine the relationships between the fast transients of PAM fluorescence for a phytoplankton community with concurrently measured

environmental variables and in context to microbial population dynamics. Induction kinetics studies of PAM fluorescence for the red tide event of 2024–2025 found that the fast transient signature of the phytoplankton population was different than what has been generally described for most other plants and algae in the literature, a terrestrial plant-based paradigm.

Materials and Methods

For a reference base of algal OJIP signatures, fast transits of PAM fluorescence were derived from six cultures of taxonomically different algae. Growth rates were not of paramount importance rather was the maintenance of turbid culture for analysis. Two of the cultures were SIO Pier water isolates: (1) an unknown, mat-forming filamentous cyanobacterium having a close association with a pennate diatom (unpublished). These samples were lightly processed with a hand-held cell grinder to break up chains/mats then filtered through 10 μm mesh prior to analysis; (2) a Green Algae identified as *Chloropicophyceae* sp. (Lopes dos Santos et al. 2017); (3) a mixture of different algae developed through cultured sea water from La Jolla Bay. Laboratory cultures included (4) an unclassified *Navicula* sp. pennate diatom; and both (5) *Thalassiosira pseudonana* and (6) *Chaetoceros radians*, having unknown origins as obtained from the SIO graduate student culture collection. Except for the cyanobacterium, cultures maintained uniform suspension that did not require filtration prior to analysis. The algae were cultivated using Guillard F media (Hewes 2015a; Hewes 2015b), using either a SolarStat semi-continuous culture method (Hewes and Hewes 2016; 12 hr day cycle with irradiance having Gaussian distribution; maximum incident irradiances were $\sim 600 \mu\text{mol photon m}^{-2} \text{s}^{-1}$ daylight white light;) or traditional semi-continuous batch cultivation methods (Hewes 2016; 2 dilution per week under continuous light; $\sim 300 \mu\text{mol photon m}^{-2} \text{s}^{-1}$ daylight white light). Samples were taken during light-limited linear stage growth.

Net tow microplankton samples have been obtained twice weekly as a regular procedure of current (Southern California Coastal Ocean Observing Systems, and Harmful Algal Bloom (HAB) Program Monitoring and Alert Program) SIO Pier sampling regimes since 2008 (CalHABMAP 2026). These net tows are taken by a 20 cm diameter conical Nytex net (20 μm mesh) raised 4 m-to-surface twice, representing a concentration of $\sim 250 \text{ l}$. After the tow is complete the cod-end is sealed as a 500 ml light-tight jar. Most variability of photosynthetic plankton sampled from the SIO Pier occurs within the 20–200 μm (micro-) plankton fraction (Allen 1923, 1941; Reid et al. 1970). These plankton net tows capture a phytoplankton dynamic, although not being truly quantitative (e.g., by excluding the nano-), of the phytoplankton population. Sub-samples were primarily taken for qualitative microscope analyses (see CalHABMAP 2026, data not discussed) and fluorescence induction kinetics with PAM fluorometer as described here.

Publicly available quantitative cell counts determined by microscope of HAB phytoplankton taxa were obtained through SCCOOS (2026a), as part of the Southern California Coastal Ocean Observing System (SCCOOS 2026b). These data include Chl-a concentrations as discussed. The limited phytoplankton classifications as used to obtain cell counts in this paper, and are listed in Table 1, being a subset of a

larger, more complete floristic analysis (M. Carter, pers. comm.) that is not presented. An *in-situ* Imaging Flow Cytobot (IFCB; Olson and Sosik 2007; Sosik and Olson 2007) is also deployed off the SIO pier, with publicly available data (CalOOS 2026). Average diatom and dinoflagellate biovolume of taxa calculated by IFCB (Table 1) were used to determine population biovolumes (Moberg and Sosik 2012) using the HAB species abundance data as obtained by microscope. Of these IFCB data, random selection of daily sampling times ~ 1500 GMT (approximately the same time as HAB sampling for microscope and PAM) provided 122 samples contained in ~ 3–5 ml sea water, with 132 mechanically classified particles, corresponding with 173,582 individual particle biovolumes. Mechanical classification was based on a probability of particle identification (see Moberg and Sosik 2012), with a 50% or better probability of correctness used to define a given taxon (Table 1). In addition, each of these classified data were subjected to a Z-score, whereby scores of > 2 or < -2 of a taxon's biovolume were considered outliers and eliminated. These “cleaned” IFCB biovolume data were averaged according to taxa corresponding with HAB abundance groupings as listed in Table 1. The IFCB biovolumes were provided in pixels, and converted as 3.4 pixels = 1 μm (McClane 2026). The biovolume of individual taxon as estimated with IFCB was factored with abundance numbers as determined by microscope, to obtain population biovolumes. Table 1 provides, along with the IFCB counts of “acceptable identifications”, average biovolumes and standard errors (in $\mu\text{m}^3 \text{ cell}^{-1}$) for the composition of diatoms and dinoflagellates that are used. These data are not intended for an in-depth analysis of the microbial populations, but serve as a general proxy for microplankton dynamics between diatoms and dinoflagellates of the local waters within La Jolla, California during the red tide of 2024–2025.

For measurements of fast fluorescence transients, a 50 ml net-tow water sub-sample was measured into each of two 125 ml glass Erlenmeyer flasks in a darkened room. Two procedures followed. First, a 50 ml sample (“Dark”) was placed into a light-tight desk drawer before measurements (10 minutes minimum). The other category was “Exposed”, with the sample placed under 600 $\mu\text{mol photon m}^{-2}$ daylight white light-emitting diode irradiance (10–20 minutes) and mixed via gentle bubbling. The Exposed category protocol was initiated after November 17, 2024, upon the discovery of its effect, which happened during the early middle-half of the 2024–2025 bloom study period. The entire process, from initial sample collection to analyses, took 1–1.5 hr., with care taken to avoid extreme temperatures or exposure to light of samples. Measurement for each of the fast transient of fluorescence sub-samples for the “Dark” and “Exposed” categories were replicated 10 times.

PAM measurements were carried out using a Photosynthetic System Instruments (PSI; Drásov, Czech Republic) FL-6000F. Measurements were obtained using a factory supplied program for “OJIP Kinetics”, but modified to have a 3-second duration with a continuous actinic irradiation of 2220 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ daylight white light and progressive logarithmic sampling routine. A 3 ml sub-sample was measured into a 1 cm^2 polystyrene cuvette that was placed in the fluorometer sample chamber. For the Dark samples, all processing and measurements were made in a dark room; for the Exposed samples, room lights were on at all times.

Fluorescence of the fast transient was integrated over different time segments, with each segment incorporating a 200 ns measurement of fluorescence. To reduce data file size, measurements began after 20 μ s actinic irradiation was switched on, with segment measurements taken at 10 μ s intervals apart for the first 4.9 ms, then segments at 100 μ s intervals apart until 400 ms, and finally segments at 2 ms intervals apart until the finish at 3 seconds. This provided 5740 lines of segment data over the 3 s period per sample. Averages were made of raw values over 10 segment time intervals, with every non-overlapping segment time interval having 10 measures each of 10 replicate samples (e.g., 100 measurements each per averaged segment time interval per daily sample), and used to process and analyze data (raw data in Hewes 2026).

Table 1

Biovolume estimates ($\mu\text{m}^3 \text{ cell}^{-1}$) as calculated by mechanical sorting and sizing by the Imaging Flow Cytobot (IFCB) moored off the SIO Pier, and used to obtain biovolume estimates from taxon abundances determined through microscope analysis. Harmful algal bloom (HAB) dinoflagellates, *Pseudo-nitzschia* group, and other diatoms biovolumes as used to generate Fig. 1 are shown. Vertical lines show taxa that were pooled into averaged single groups

IFCB Taxa	<i>n</i>	Average of biovolume ($\mu\text{m}^3 \text{ cell}^{-1}$)	Standard error ($\mu\text{m}^3 \text{ cell}^{-1}$)	Pooled average biovolume ($\mu\text{m}^3 \text{ cell}^{-1}$)	Pooled standard error ($\mu\text{m}^3 \text{ cell}^{-1}$)
<i>Akashiwo</i>	1,389	1,605,819	15,341		
<i>Alexandrium catenella</i>	35	777,193	41,657		
<i>Dinophyceae</i>	15,251	115,710	1,677	147,144	2,469
<i>Dinophyceae</i> TAG cyst	716	699,734	10,820		
<i>Dinophysis</i>	113	807,582	49,666		
<i>Dinophysis tripos</i>	2	4,704,039	388,151		
<i>Gymnodinium</i>	2,908	115,180	1,062		
<i>Lingulodinium polyedra</i>	1,152	966,831	6,636		
<i>Tripos</i>	2	580,351	180,861	762,813	10,460
<i>Tripos balechii</i>	15	667,566	74,764		
<i>Tripos furca</i>	531	916,994	9,879		
<i>Tripos fusus</i>	256	450,014	6,567		
<i>Prorocentrum</i>	30	305,234	21,209	514,144	2,661
<i>Prorocentrum gracile</i>	1,310	107,916	1,435		
<i>Prorocentrum micans</i>	3,245	683,856	2,434		
<i>Prorocentrum rostratum</i>	61	312,651	31,924		
<i>Prorocentrum scutellum</i>	25	992,572	84,275		
<i>Pseudo-nitzschia</i> group	1,321	27,875	1,073		

IFCB Taxa	<i>n</i>	Average of biovolume (μm^3 cell^{-1})	Standard error (μm^3 cell^{-1})	Pooled average biovolume ($\mu\text{m}^3 \text{cell}^{-1}$)	Pooled standard error (μm^3 cell^{-1})
HAB Dinoflagellates	22,459	302,589	3,241		
Other Diatoms	38,326	87,887	2,008		
Other Dinoflagellates	1,865	150,453	9,209		

AI Disclosure Statement **Google Chrome AI** (powered by **Google Gemini**; accessed March-July, 2026) was used for extensive literature searches and refinement of the “productive quenching” model. **Gemini NotebookLM** (powered by **Google Gemini**; accessed July-August, 2026) assisted in the synthesis and condensation of manuscript and to ensure the narrative's alignment with journal-specific formatting requirements, and general grammar. All scientific interpretations—specifically the formulation of the "productive quenching" model and the biophysical analysis of Form II ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) bioenergetics—were derived, reviewed, validated, and finalized by the author.

Results

Ecological Backdrop. A notable red tide dinoflagellate bloom occurred in La Jolla, CA, during the 2024-25 fall to spring season (Fig. 1). In brief, *L. polyhedra* increased concentrations of Chl-a to 3.2 $\mu\text{g l}^{-1}$ on 14 October 2024, reached a maximum of Chl-a at 25.2 $\mu\text{g l}^{-1}$ on 11 November 2024, with subsequent decline. The bloom sequence was then continued by increased *Tripos spp.* (formerly *Ceratium*) abundance, having a maximum of 9.7 $\mu\text{g Chl-a l}^{-1}$ on 23 December 2024, and finally a winter increase of *Prorocentrum micans* having two peaks at 5.3 and 6.2 $\mu\text{g Chl-a l}^{-1}$ on 13 January and 2 February, 2025, respectively (Fig. 1). In the meantime, the toxic, domoic acid-producing diatom *Pseudo-nitzschia spp.* became an increasingly dominant portion of the microbial community starting early December 2024 (see CalHABMAP 2026). Maximum total diatom biovolumes occurred late-December, 2024 through early-January, 2025, but only approximating those of bloom dinoflagellate biovolumes twice on 06 January, 2025, and 18 February, 2025 (dates encapsulated by circles in Fig. 1). Carbon biomass was not calculated for these biovolume data (an additional level of uncertainty), but note that dinoflagellates have generally higher biomass than diatoms per biovolume (Menden-Deuer and Lessard 2000). These data summarize a dynamic played between diatoms and dinoflagellates, with the wide variation of measured Chl-a concentrations and phyla biovolumes, as a good indication that there were rigorous growth and decay for each of the respective populations (diatom and dinoflagellate population dynamics) contributing to the community health at different times of year.

Fluorescence signatures. To demonstrate similarity of traditional OJIP spectra, two centric and one pennate diatom species (cultures grown under light-limiting conditions) show differences in the relative intensity for their inflections at JIP, but the timing that these inflections occurred was comparable (Fig. 2a). The sample results of dark exposure were double standardized, first with the normalization of $F_0 = 0$, and the P-step (~ 300 ms) standardized to $= 1$. The light- acclimated sample data were first normalized as $F_0 = 0$, then the P-step (at ~ 300 ms) was proportioned to its dark- acclimated P-step. These OJIP signatures were also similar with non-diatoms (a green algae, a

cyanobacterium and an alga mix; Fig. 2b), as well as that these signatures are like those found of higher plants (Papageorgiou et al. 2007; not shown). This standardization of fluorescence allowed comparison of OJIP fluorescence signatures between cultures having large differences in Chl-a concentration. NPQ quenching of fluorescence under bright light was expected to compact OJIP fluorescence signatures. When dark-adapted diatom and non-diatom cultures were exposed to 10–20 minutes of intense light (Exposed category; $600 \mu\text{mol photon m}^{-2}$), the timing for the OJIP inflections varied little from those of the Dark category, but fluorescence yield was greatly reduced.

Figure 2 OJIP signatures of (a) diatom and (b) non-diatom algal cultures that were dark-acclimated (thick lines) and after bright light exposure ($600 \mu\text{mol photon m}^{-2}$ daylight white irradiance) for 10–20 minutes (thin lines). In (a), species are indicated by color: green (triangles), *Navicula sp.*; blue (circles), *Chaetoceros radians*; and orange (squares), *Thalassiosira pseudonana*. In (b), colors represent species: green (triangles), *Chloropicophyceae sp.*; blue (circles), cyanobacterium; and orange (squares), unknown mixture. Dark data were double standardized by first normalization at F_0 , then normalized at P-step $= 1$ (note that diatoms had slightly early F_M). Exposed data were standardized by F_0 , then factored to relative height as based on their P-step dark-acclimated value. Fluorescence values expressed as arbitrary units (a.u.). For the most part, diatoms and non-diatoms had similar OJIP signature patterns before and after exposure, but the OJIP signature of Exposed groups was greatly compressed relative to the dark-adapted groups. Non-photochemical quenching (NPQ) initiated by excess light in the Exposed group quenched the OJIP fluorescent yield relative to the dark-acclimated groups. The first maximum, M_1 , of the slow transitional phase is indicated

The fast transients with PAM fluorometry from SIO Pier samples for 2024–2025 (Fig. 3) had different OJIP signatures that contrasted with those found of diatom and non-diatom cultures (Fig. 2). Since the influence of bright-light exposure was discovered Nov 18, 2024, the data are divided between pre-discovery (only Dark-acclimated) and post discovery (both Dark and Exposed categories). Importantly, dark-acclimated bloom dinoflagellates did not have a P-step of the OJIP, but instead had a maximum fluorescence ($\neq F_M$) found around the I-step (~ 30 ms; Fig. 3a, b). However, a “P-step” was generated after several minutes of exposure to bright ($600 \mu\text{mol photon m}^{-2}$) light (Exposed category, Fig. 3c); the fluorescence maximum shifted (~ 1 order of magnitude) to a longer time scale.

Differences in maximum heights for the dark-acclimated sample signatures is assumed related to Chl-a concentration (Tunzi et al. 1974). As a general observation, the JIP signature of diatoms and non-diatoms was greatly reduced in intensity upon light exposure (Fig. 2), whereas the JI signature for bloom dinoflagellates with light exposure became indistinguishable as compared with development of the P-step (Fig. 3).

OJIP in mixed assemblages. Diatoms (and non-diatoms) lose fluorescence yield upon exposure to high-intensity irradiance (Fig. 2), which contrasts with the bloom dinoflagellates that increased maximal fluorescence and extended the timing for when fluorescence begins its decay (Fig. 3). Therefore, it is of interest how the OJIP signature of a mixed dinoflagellate and diatom communities appear. From the population dynamics observed for this study (Fig. 1), two dates occurred during diatom blooming when the biovolume of diatom was similar (encircled) to that of dinoflagellates. Compared with adjacent sample dates having higher dinoflagellate biovolume, the timing for maximum fluorescence of dark acclimated cells increased with higher diatom biovolume (Fig. 4a). Upon exposure to high-intensity ($600 \mu\text{mol photon m}^{-2}$) light, the enhancement and extension of the P-step occurred with higher dinoflagellate biovolume (Fig. 4b). Diatom cultures reduced their fluorescence yield upon exposure to high-intensity light (Fig. 2), but this didn't correspond with field observations here (Fig. 4b). Diatoms in the dinoflagellate-

Figure 4 OJIP fluorescence signatures for higher diatom biovolume (thick lines, green) are compared with higher dinoflagellate biovolume (thin lines, orange) under (a) dark-acclimated and (b) bright light-exposure conditions. Dates (see encircled data in Fig. 1) are shown for samples taken, with the date of higher diatom biovolume marked with (*). (a) Samples for dark-adapted cells with higher dinoflagellate biovolumes had maximum fluorescence earlier than those with higher diatoms. Upon bright light-exposure (b), maximum fluorescence of samples with bright light lowered diatom fluorescence (Fig. 2), but this didn't correspond with all field observations here (Fig. 4b)

dominant population had only little influence upon the OJIP signature. Since diatom and dinoflagellate biovolumes were approximately similar on these dates (Fig. 1), their differences in OJI signature cancelled each other. Therefore, some of the variability for timing (covering about 1 order of magnitude) of elevated fluorescence between the I-step and P-step (Figs. 3, 4) can be accounted for by relative proportions of dinoflagellate to diatom in similar marine microbial populations (Fig. 1).

Discussion

Challenging the Terrestrial Paradigm The OJIP fluorescence signatures of the fast transient for Chl fluorescence can have relative heights and timing of peaks and plateaus that vary slightly (Papageorgiou et al. 2007; Antal et al. 2009), but there is, nonetheless, considerable coherence in the characteristic for these signatures among different photosynthetic organisms (Strasser et al. 1995; Papageorgiou and Govindjee 2011; Stirbet and Govindjee 2016), including that of diatoms and non-diatoms (Fig. 2). Non-photochemical quenching (NPQ) occurring in the PSII antenna matrix reduces the overall exciton flux

directed to the reaction center, thereby diminishing Chl fluorescence intensity (Lavaud 2007; Grouneva et al. 2009; Büchel 2019). Diatoms and non-diatoms exposed to bright light showed this clearly (Fig. 2). However, this paradigm does not hold with blooming dinoflagellates. Dark-acclimated red tide samples had no P-step (F_M), and exposure to bright light caused development from non-existent to a well-developed P-step (Fig. 3).

These data reveal that maximum fluorescence in natural plankton populations is not always the P-step ($\neq F_M$), which should represent electron-saturation of PSII for dark-acclimated cells. Without certainty as to what maximum fluorescence in dinoflagellates measures, the maximum quantum efficiency of PSII cannot be described as F_V/F_M . Furthermore, standard mathematical descriptions derived from terrestrial plant and green algal biophysical studies (see Stirbet and Govindjee 2011; Stirbet et al. 2014, 2018) as fundamentally based on F_M (such as NPQ) also come under question. These data from a natural red tide demonstrate biophysical proof that marine dinoflagellate light processing cannot be modeled using terrestrial plant paradigms. Additionally, mixed assemblages primarily of diatoms vs. of dinoflagellates can vary the timing for when the fluorescence maximum occurs (Fig. 4), which does not necessarily reflect the “health” of the ecosystem (Fig. 1).

Biochemistry leading to the I- and P-steps Both F_0 and F_M are considered the most important parameters to measure for analysis of the fast transient for Chl fluorescence (Schansker et al. 2013). The F_0 is the baseline background fluorescence “noise” under the fully oxidized state of PSII. The bottleneck producing the I-step (F_I) is associated with the cytochrome (Cyt) b_6f complex (Schansker et al. 2005, 2006; Hasan and Cramer 2012; Degen and Johnson 2024). Oxidation of PQH_2 to $2Q_B$ both replenishes the plastoquinone pool and provides electrons to the Cyt b_6f complex that transfers electrons via the plastocyanin (PC; or Cyt c_6 in diatoms and dinoflagellates; Castell et al. 2021; Slater et al. 2021) cycle into PSI. The magic of the Cyt b_6f pathway is that two extra H^+ are pumped into the lumen in addition to the four pumped with the electrons supplied. When the oxidation back to Q_B is not fast enough to oxidize the Q_A^- pool, a backlogged Q_A^- builds up, leading to its relaxation through fluorescence. This I-step is the largest bottleneck for PSII (Hasan and Cramer 2012; Tikhonov 2014; Johnson 2025), giving it a dominating presence in the OJIP signature.

After the Cyt b_6f cycle, an additional bottleneck occurs on the electron-accepting side of PSI resulting in the P-step (F_M) (Schansker et al. 2005, 2006; Antal et al. 2009). Electrons from PC reduce ferredoxin (Fd) that further reduces ferredoxin NADP⁺ reductase (FNR; Schansker et al. 2005) to protonate nicotinamide adenine dinucleotide phosphate (NADP⁺) to NADPH for the CBB cycle (Eichelmann et al. 2009). Within classical models, FNR is the terminal step for LEF with generation of NADPH that fuels carboxylation.

Carboxylation RuBisCO is among the slowest enzyme complexes known (de Pins et al. 2025). Three major forms occur (Morse et al. 1995; Shi and Bloom 2021), with Form II exclusively found in peridinin-containing dinoflagellates and certain proteobacteria. Form II RuBisCO has inferior CO_2/O_2

discrimination compared to Form I, requiring carbon-concentrating mechanisms (CCMs) to overcome this inferiority in dinoflagellates. Peridinin-containing dinoflagellates concentrate the vast majority of their Form II RuBisCO within a pyrenoid (Leggat et al. 1999; Jenks and Gibbs 2000; He et al. 2023). This phase-separated, protective micro-environment is dedicated to maximizing carboxylation efficiency while minimizing photorespiratory loss.

Alternative Electron Flow and CCM Demands The CBB cycle is inactive in the dark and rate-limited by NADPH and adenosine triphosphate (ATP) in the light. Yet, sufficient ATP relative to NADPH for carboxylation is not generated through LEF (Kramer and Evans 2011; Tikhonov 2014). Cyclic electron flow (CEF) from Fd through the Cyt b_6f complex is the primary alternate route of electron flow from PSI. This protonates the chloroplast lumen providing a ΔpH that activates ATP synthase for additional ATP generation (Degen and Johnson 2024; Emrich-Mills et al. 2025; Johnson 2025). In addition to moving protons into the lumen (during LEF in Cyt b_6f), the WWC also increases ΔpH through its consumption of H^+ in the stroma. There are two variants of WWC (Mohammad Aslam et al. 2023; Emrich-Mills et al. 2025): competing directly with $NADP^+$ for reduction by Fd (Rizhsky et al. 2003) or through consumption of NADPH (Roberty et al. 2014).

Both CEF and WWC compete with FNR for electrons from Fd, raising the photon quota of $NADP^+$ reduction. Additionally, CCMs effectively increase the total ATP demand of carbon fixation by 50–100% (Raven 1991; Hopkinson et al. 2011) to prevent RuBisCO from photo-respiring in the presence of O_2 (Roberty et al. 2014). Quigg et al. (2012) suggested that oxygen consumption by the WWC also might reduce local oxygen concentrations to enhance the effectiveness of Form II RuBisCO (see Roberty et al. 2014). While active CO_2 concentration via CCMs is targeted within the pyrenoid matrix, oxygen reduction via the WWC also operates along the flanking thylakoid membranes to shield the pyrenoid from photo-respiratory stress.

Model for Productive Quenching (refer to Fig. 5 and Online Resources 1). For dark-acclimated terrestrial plants, FNR remains inactive until light-driven LEF delivers reducing equivalents to generate NADPH. This activates the CBB cycle alongside a strict requirement for extra ATP (Schansker et al. 2006; Shimakawa and Miyake 2018; Emrich-Mills et al. 2025). The partitioning of this flux depends on whether FNR is securely docked to thylakoid anchors or freely dispersed (Joliot and Johnson 2011; Emrich-Mills et al. 2025). Because FNR is structurally restricted in these dark-acclimated systems, a saturating pulse (e.g., PAM) immediately saturates the Fd pool; this acceptor-side bottleneck backlogs to Q_A^- , resulting in a prominent P-step (Schansker et al. 2005, 2006; Antal et al. 2009; Ilík et al. 2006).

In stark contrast, dark-acclimated bloom dinoflagellates completely lack this P-step. This indicates that instead of encountering an immediate blockade, electrons are efficiently vacuumed through alternative sinks bypassing the dark-restricted FNR. Without CEF and WWC pathways, a severe intersystem bottleneck would develop, producing fluorescence as a P-step (Fig. 5).

In the alternative dark state, FNR is structurally dissociated from thylakoid anchors, allowing electrons from reduced Fd to be immediately redirected through CEF and WWC. Because the chloroplast ATP synthase is dark-locked and closed, this rapid pseudo-cyclic routing traps protons within the thylakoid lumen within the first 30–50 ms (at the I-step). This activated sink-network accelerates electron flow through the intersystem PQ pool faster than PSII can reduce it, producing ATP, which results with a sharp fluorescence quenching following the I-step. The P-step is truncated (Fig. 5).

Bioenergetic Reorganization and Ecological Significance Upon light-acclimation (Exposed category), the activation of photosynthetic dark reactions reorganizes kinetic boundaries. In exposed diatoms and non-diatoms, robust antenna-level NPQ intercepts excitation energy to compress overall fluorescence yield (Lavaud 2007; Grouneva et al. 2009; Büchel 2019). Under high light, the slow enzymatic rate and poor CO₂/O₂ specificity of Form II RuBisCO does create a bottleneck. To prevent photorespiration, the WWC operates as a localized oxygen-scavenger at the thylakoid-pyrenoid interface; local O₂ pools are drawn down while the CCM supercharges the pyrenoid with CO₂. However, because Form II RuBisCO has an inherently limited carboxylation rate, PS II reaction centers become trapped in a chronically closed, reduced state that enhances OJIP fluorescence.

This bottleneck establishes a bioenergetic equilibrium where high ΔpH executes a critical dual role: both driving photoprotection and fueling carboxylation (Fig. 5; Online Resources 1). Illumination causes FNR to migrate to the Cyt b₆f complex, accelerating CEF to work with the WWC as a powerful proton-generating engine. This massive proton influx creates a profound ΔpH that satisfies two vital demands. First, the severe lumenal ΔpH triggers the xanthophyll cycle and coordinates thermal dissipation within the intrinsic acpPC complexes, keeping the core-centered NPQ safety valve open while promoting structural uncoupling of peripheral PCP antennas. Second, this same ΔpH drives maximum ATP synthase rotation to generate the vast pools of ATP required for energy-expensive CCM pumps and lumenal carbonic anhydrases. Because the CCM acts as a continuous, high-capacity metabolic sink for ATP, a constant supply of substrate adenosine diphosphate (ADP) and inorganic phosphate (P_i) is regenerated. This keeps the ATP synthase active without collapsing the proton gradient, with the ΔpH driving the phosphorylation of ADP and P_i to power CCM pumps, while CEF pumps H⁺ into the lumen matching its loss by ATP synthase. The ΔpH controls ATP generation vs. NPQ, two diametrically opposed operations. This highly efficient system represents "productive quenching," redirecting otherwise excess photon energy from heat (NPQ) into active CO₂ concentration, under the coordination of ΔpH . Thus, ΔpH regulates NPQ to not reduce productive quenching so that ATP satisfies the needs of CCMs and RuBisCO. Such a strategy provides a competitive advantage to explain the rapid proliferation and ecological dominance of dinoflagellate red tide blooms.

Abbreviations

acpPC

chlorophyll a–chlorophyll c–peridinin-protein complex

ADP
adenosine diphosphate
ATP
adenosine triphosphate
CBB cycle
Calvin-Benson-Bassham cycle
CCM
carbon-concentrating mechanism
CEF
cyclic electron flow
Chl
chlorophyll
Cyt
cytochrome
 ΔpH
trans-thylakoid proton gradient
Fd
ferredoxin
 F_t
Fluorescence at time t
 F_0
minimal fluorescence yield
 F_M
maximum fluorescence yield
 F_V
variable fluorescence ($F_M - F_0$)
 F_V/F_M
maximum quantum efficiency of PSII
FNR
ferredoxin-NADP⁺ reductase
HAB
Harmful Algal Bloom
IFCB
Imaging Flow Cytobot
LEF
linear electron flow
NADPH
nicotinamide adenine dinucleotide phosphate (reduced)
NPQ

non-photochemical quenching
OJIP
polyphasic fluorescence transient (Origin, J-step, I-step, P-step)
PAM
pulse amplitude modulated (fluorometry)
PC
plastocyanin
PCP
peridinin-chlorophyll-protein
 P_i
inorganic phosphate
PQ
plastoquinone
 PQH_2
plastoquinol
PSI
photosystem I
PSII
photosystem II
 Q_A
primary quinone electron acceptor in PSII
 Q_B
secondary quinone electron acceptor in PSII
RuBisCO
ribulose-1,5-bisphosphate carboxylase/oxygenase
WWC
water-water cycle

Declarations

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Figures

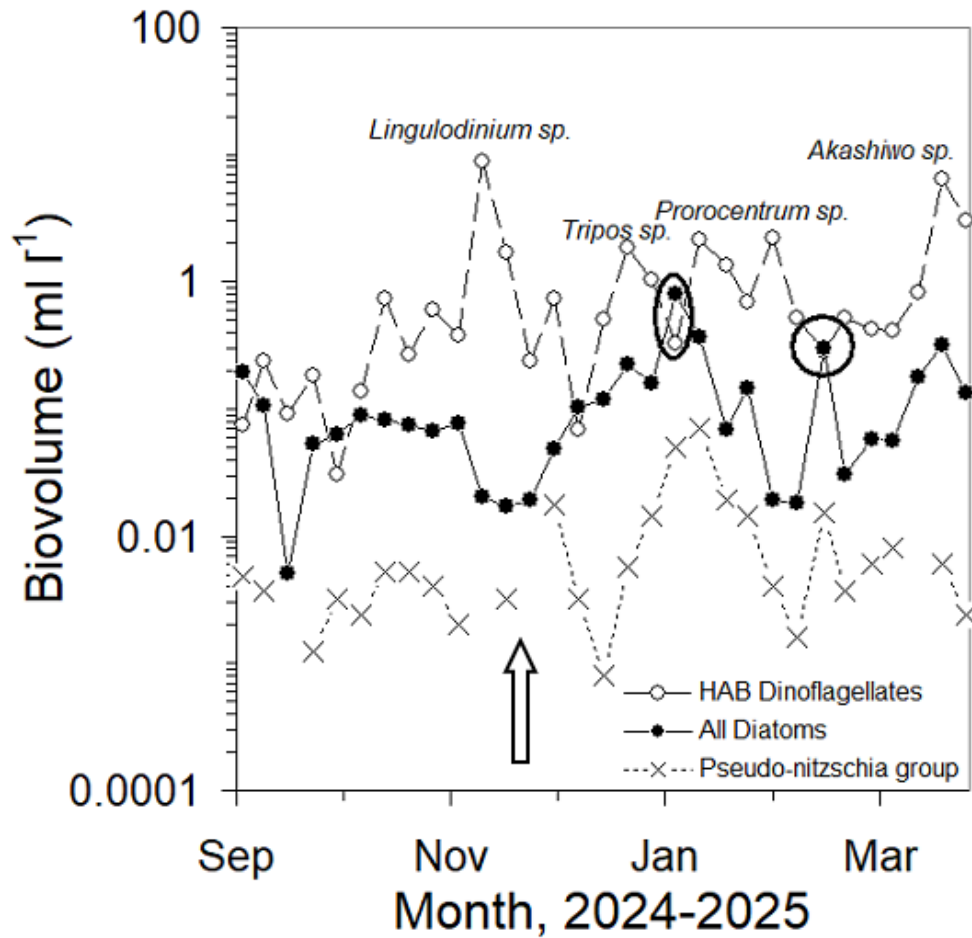


Figure 1

Development and duration of a red tide in La Jolla, 2024-2025. Biovolume of red tide dinoflagellates (open circles) relative to total diatoms (filled circles) was higher for much of the season. *Pseudo-nitzschia sp.* (x) is an important toxic diatom group for the area. Vertical arrow indicates when the effect of bright light exposure was discovered. Approximate times that dominant dinoflagellate groups appeared during the bloom are shown. Circled data indicate when dinoflagellate and diatom biovolumes were approximately the same

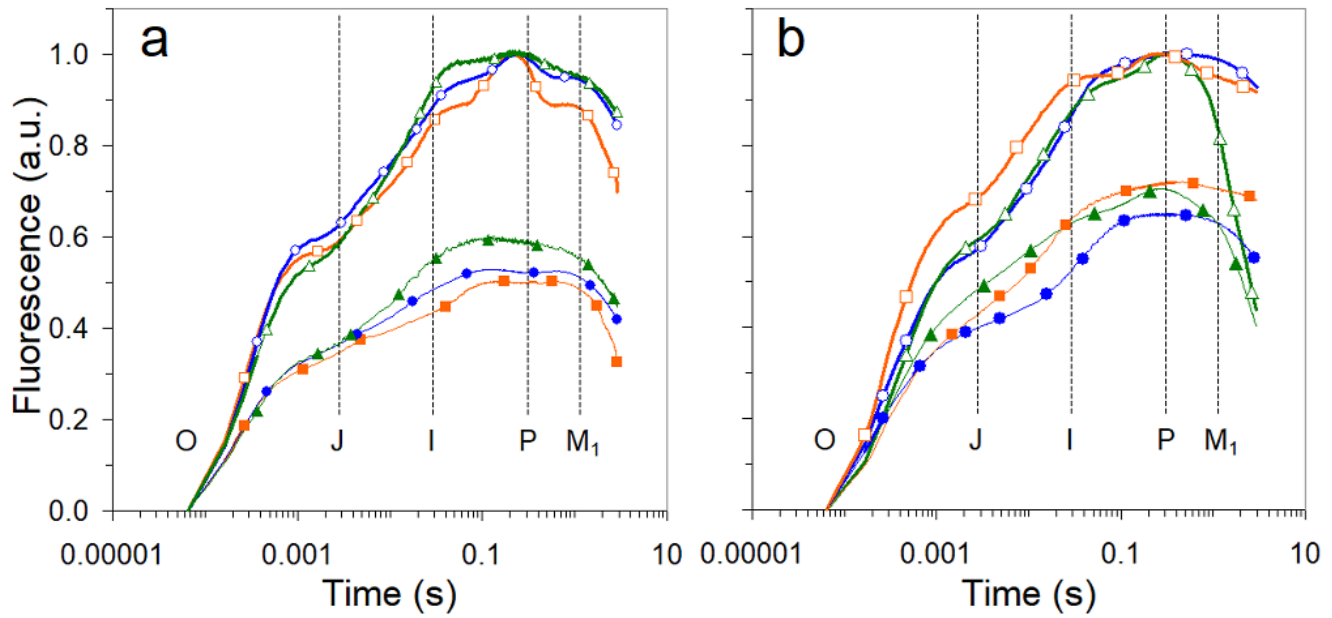


Figure 2

OJIP signatures of (a) diatom and (b) non-diatom algal cultures that were dark-acclimated (thick lines) and after bright light exposure ($600 \mu\text{mol photon m}^{-2}$ daylight white irradiance) for 10-20 minutes (thin lines). In (a), species are indicated by color: green (triangles), *Navicula sp.*; blue (circles), *Chaetoceros radians*; and orange (squares), *Thalassiosira pseudonana*. In (b), colors represent species: green (triangles), *Chloropicophyceae sp.*; blue (circles), cyanobacterium; and orange (squares), unknown mixture. Dark data were double standardized by first normalization at F_0 , then normalized at P-step = 1 (note that diatoms had slightly early F_M). Exposed data were standardized by F_0 , then factored to relative height as based on their P-step dark-acclimated value. Fluorescence values expressed as arbitrary units (a.u.). For the most part, diatoms and non-diatoms had similar OJIP signature patterns before and after exposure, but the OJIP signature of Exposed groups was greatly compressed relative to the dark-adapted groups. Non-photochemical quenching (NPQ) initiated by excess light in the Exposed group quenched the OJIP fluorescent yield relative to the dark-acclimated groups. The first maximum, M_1 , of the slow transitional phase is indicated

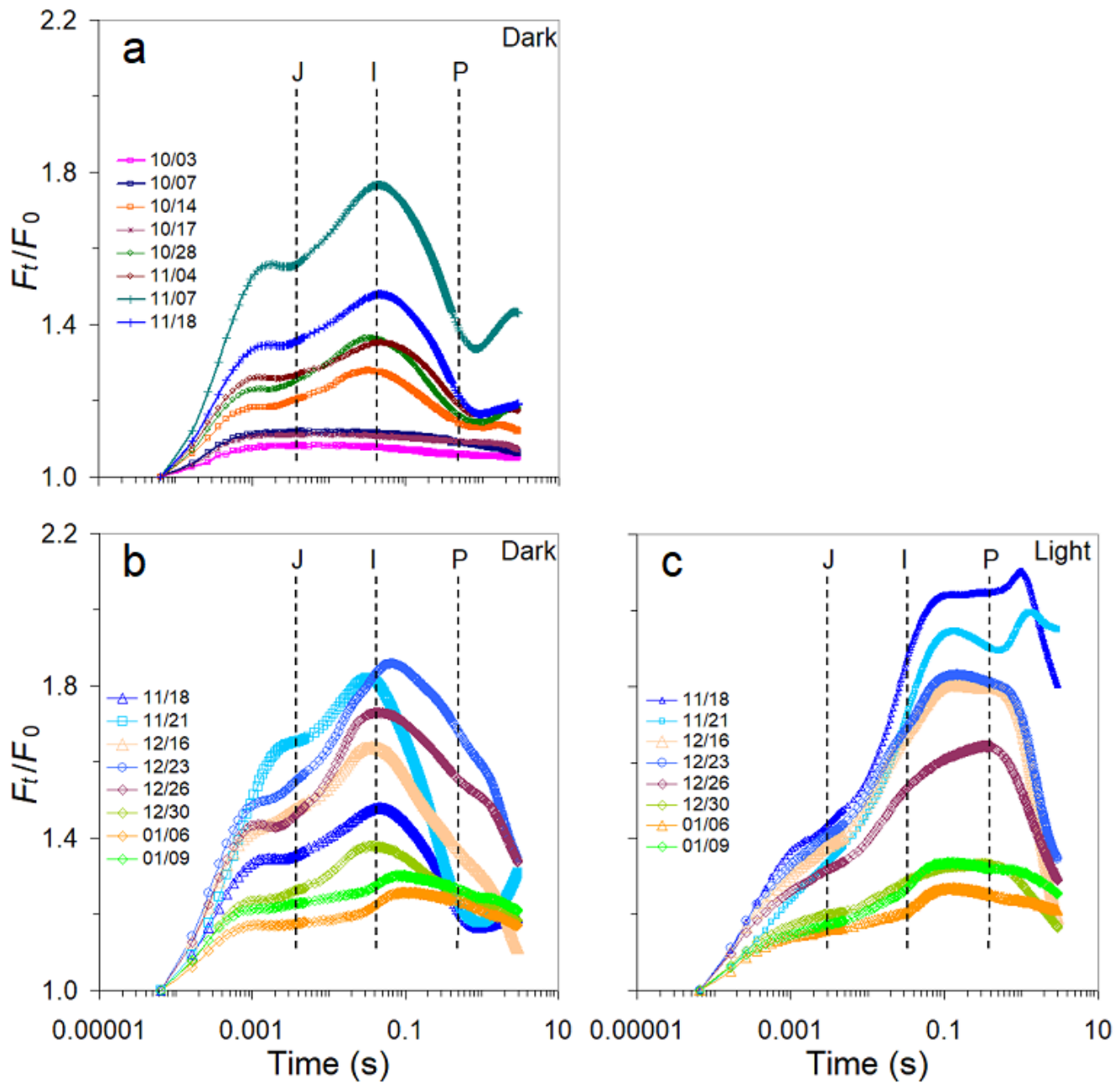


Figure 3

OJIP signature curves of red tide sample taken during 2024-2025. The effect of bright-light exposure upon dinoflagellates was made on November 18, 2024 (see Fig. 1). Consequently, data are divided into pre-discovery having only dark-adapted samples (a), and post-discovery having both (b) dark-acclimated and (c) light-exposed groups. Key to dates (mm/dd) given in each plot

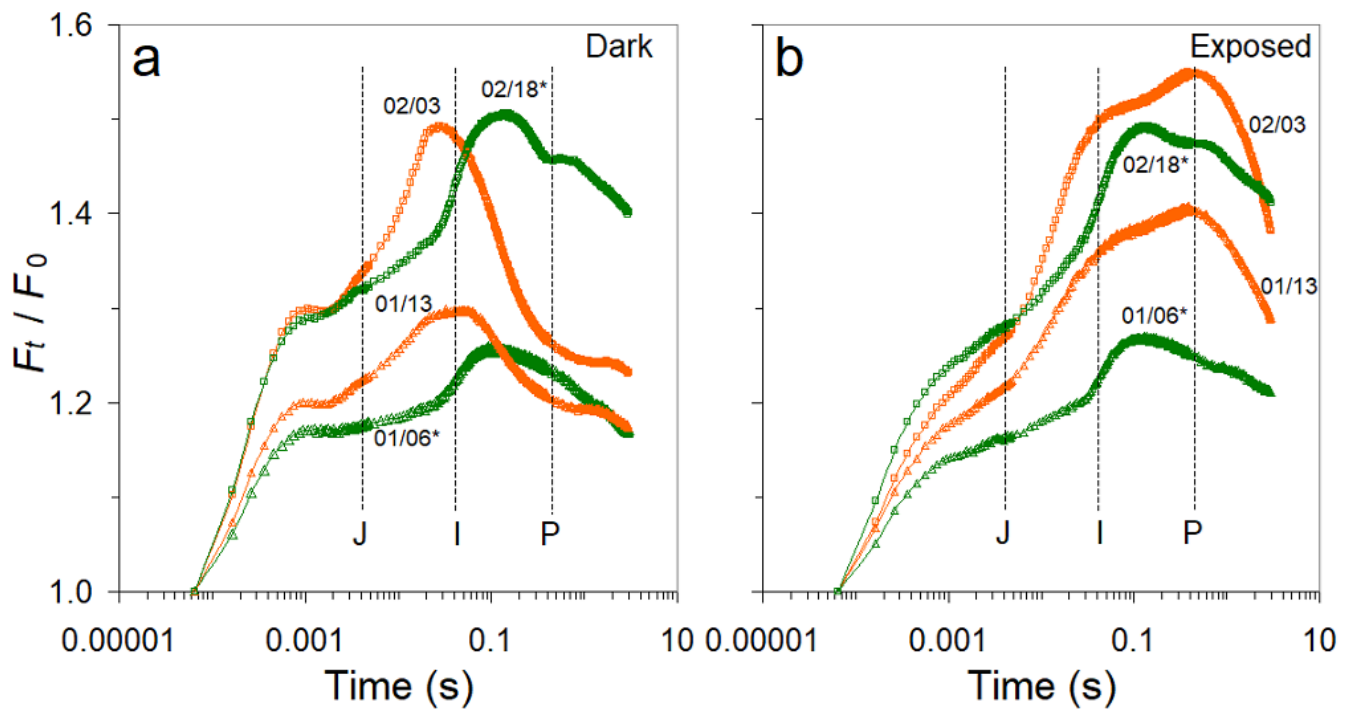


Figure 4

OJIP fluorescence signatures for higher diatom biovolume (thick lines, green) are compared with higher dinoflagellate biovolume (thin lines, orange) under (a) dark-acclimated and (b) bright light-exposure conditions. Dates (see encircled data in Fig. 1) are shown for samples taken, with the date of higher diatom biovolume marked with (*). (a) Samples for dark-adapted cells with higher dinoflagellate biovolumes had maximum fluorescence earlier than those with higher diatoms. Upon bright light-exposure (b), maximum fluorescence of samples with bright light lowered diatom fluorescence (Fig. 2), but this didn't correspond with all field observations here (Fig.4b)

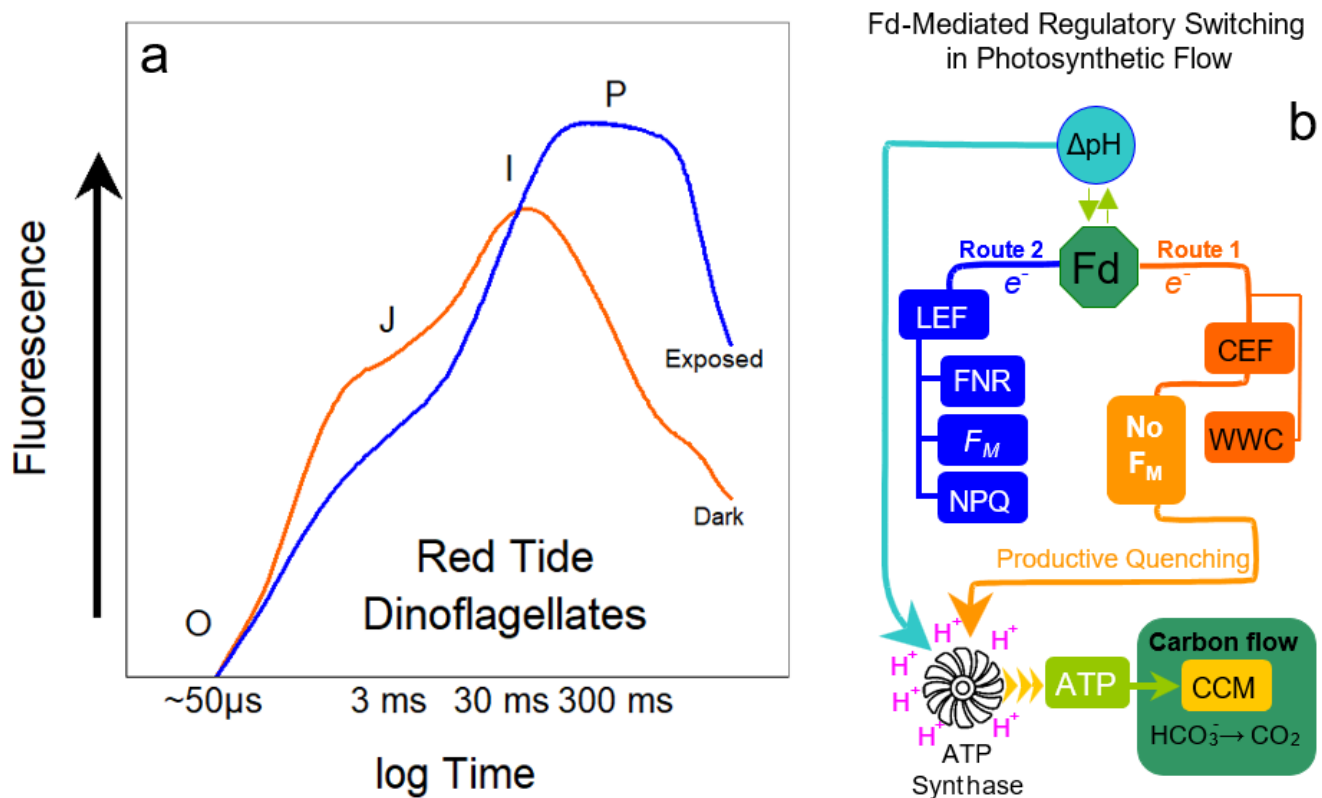


Figure 5

Bioenergetic proof of "Productive Quenching" and its simplified energy flow. (a) The absence of a dark-acclimated P-step (F_M), as red tide dinoflagellates peak prematurely at 30 ms of the OJIP (Origin, J-, I-, and P-step) signature. A F_M develops after exposure to bright light. (b) This "Missing F_M " indicates electrons are "vacuumed" into the water-water cycle (WWC), or cyclic electron flow (CEF) to increase the trans-thylakoid proton gradient (ΔpH). ΔpH switches the ferredoxin (Fd) hub, directing linear electron flow (LEF; Route 2, blue) from ferredoxin NADP⁺ reductase (FNR) and wasteful non-photochemical quenching (NPQ), to instead (Route 1, orange) generate adenosine triphosphate (ATP) by increased proton concentration (via Cyt b_6f) that drives carbon-concentrating mechanisms (CCMs) converting bicarbonate (HCO_3^-) to carbon dioxide (CO_2). More explanatory detail for (b) is found in Online Resource 1

Supplementary Files

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- [OnlineResource120260827.pdf](#)