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PERSPECTIVE

A PERSPECTIVE ON PHOTOSYNTHESIS IN THE OLIGOTROPHIC OCEANS: HYPOTHESES CONCERNING ALTERNATE ROUTES OF ELECTRON FLOW[1]

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Many regions of the open, oligotrophic oceans are depleted of nutrients, especially nitrogen and iron. The biogenesis and the functioning of the photosynthetic apparatus may be specialized and tailored to the various marine habitats. In this mini-review, we discuss some new findings with respect to photosynthetic processes in the oceans. We focus on findings that suggest that some cyanobacteria may route electrons derived from the splitting of H_2O to the reduction of O_2 and H^+ in a water-to-water cycle, and that other cyanobacteria that fix nitrogen during the day are likely missing PSII and enzymes involved in the fixation of inorganic carbon. Both of these proposed "variant" forms of photosynthetic electron flow provide new insights into ways in which marine phytoplankton satisfy their energetic and nutritive requirements.

Key index words: **ecosystem; iron; nitrogen fixation; oceans; oligotrophic; oxidase; photosynthesis; photosystem**

Abbreviations: **C, carbon; cyt, cytochrome; DBMIB, 2,5-dibromo-3-methyl-6-isopropyl-p-benzoquinone; DCMU, 3-(3,4-dichloro-phenyl)-l,l-dimethyl-urea; ETC, electron transport chain; Fe, iron; F_m, maximal fluorescence; FNR, ferredoxin NADP-oxido-reductase; F_v/F_m, variable fluorescence divided by the maximal fluorescence, which is a measure of the dark-adapted photochemical efficiency of PSII; F_v, variable fluorescence; Fx, ferredoxin; N, nitrogen; P700, reaction center chl of PSI; PQ, plastoquinone; PS, photosystem; PTOX, plastoquinol terminal oxidase**

The term oligotrophic comes from the Greek and literally means ''small'' or ''little food''; nutrient resources can be very scarce in oligotrophic ecosystems. Oligotrophic oceans represent ~70% of the marine environment, are generally distant from coastal areas that provide nutrient inputs, and often have highly diminished iron (Fe) and nitrogen (N) levels (Zehr and Ward 2002, Arrigo 2005, Kupper et al. 2008). In spite of a ''severe'' nutrient-deprived lifestyle, picophytoplankton (photosynthetic phytoplankton of <2 μm) thrive in the oligotrophic ocean environment and may be responsible for 50% of the earth's primary productivity (Field et al. 1998, Behrenfeld et al. 2006). Dominant picophytoplankton in oligotrophic oceans are represented by prokaryotic cyanobacteria of the genera *Prochlorococcus* and *Synechococcus*. *Prochlorococcus*, typically 0.5–1.0 μm in diameter with a divinyl chl-based light-harvesting complex, was discovered in 1988 (Chisholm et al. 1988). This organism is one of the most abundant bacteria on the planet and is detected at depths in the water column down to 200 m (Olson et al. 1990). *Synechococcus,* also small (usually 1.0–2.0 μm), has a distinctive light-harvesting complex composed mostly of pigmented phycobiliproteins. The oligotrophic environment also supports the growth of many eukaryotic algae including picoeukaryotes such as *Ostreococcus* spp. The major issue highlighted in this brief review focuses on novel, potentially critical aspects of photosynthesis performed by oceanic phytoplankton, and especially those in the oligotrophic oceans.

In oxygenic photosynthesis, energy from the sun is used to split water, extracting electrons and causing a light-driven vectorial electron flow that generates reductant and energy used for various processes, including the fixation of CO_2 into biomass. The complexes of the electron transport chain (ETC) include the water-splitting complex,

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two photosystems (PS), PSI and PSII, that are excited by light energy absorbed by light-harvesting pigment protein complexes, the cytochrome (cyt) b_6f complex and an ATP synthase. The electron carriers that connect PSII to PSI are involved in pumping protons across the photosynthetic membranes; the proton gradient generated can drive the formation of ATP. A simplified schematic of photosynthetic electron transport is depicted in Figure 1A.

Interestingly, there are a number of intriguing features of photosynthesis that have been associated with the oligotrophic marine environment (Morel and Price 2003). Cyanobacteria and some eukaryotes that reside in the open oceans appear to have low

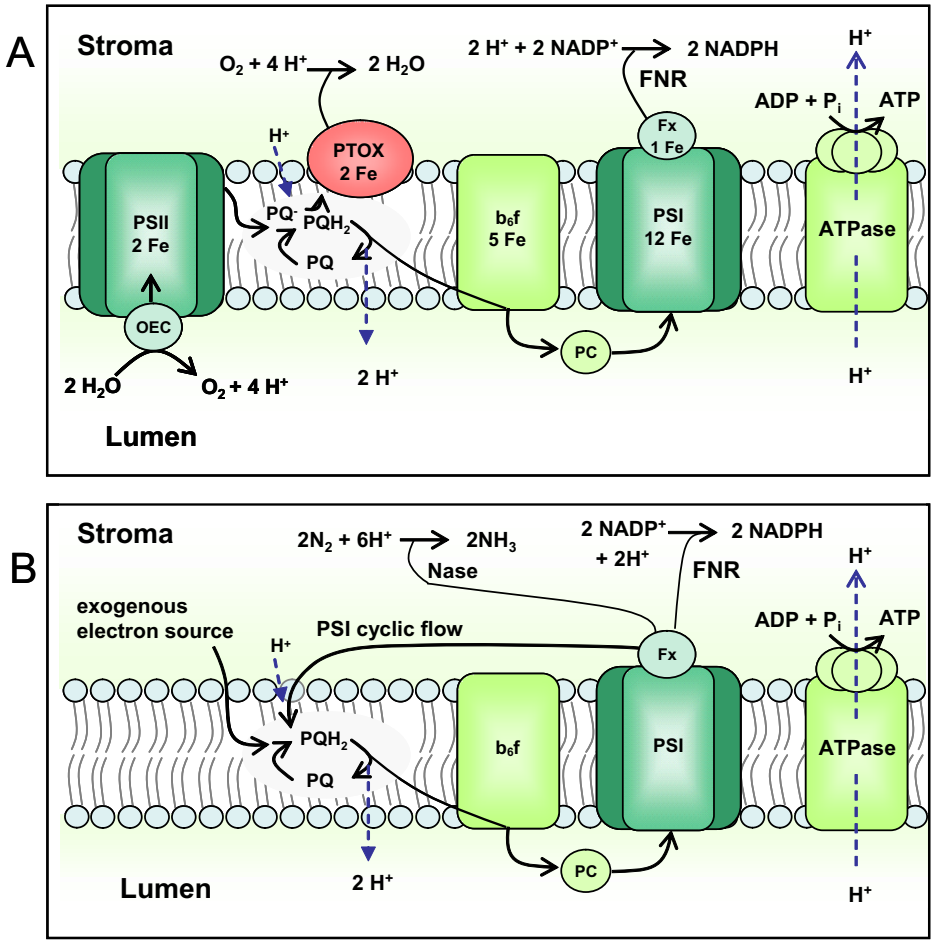

FIG. 1. (A) Photosynthetic electron transport—principle components, electron flow pathways, and iron requirements of some photosynthetic organisms in the oligotrophic oceans. This is a model proposed for the role of plastoquinol terminal oxidase (PTOX; or a similar oxidase) in photosynthetic electron flow associated with some marine phytoplankton in the oligotrophic oceans. Photosynthetic electron transport begins with excitation of the photosynthetic reaction centers, PSII and PSI, and water splitting by the oxygen-evolving complex (OEC) of PSII. Electrons are passed from PSII to the plastoquinone (PQ) pool (to generate PQ^- and then, with the entry of protons from the stromal compartment, PQH_2). The electrons from PQH_2 are then sequentially transferred to cytochrome b_6f (b_6f), with a deposition of protons into the lumen of the thylakoid membranes, the mobile carrier plastocyanin (PC), PSI, ferredoxin (Fx), and then to ferredoxin NADP-oxido-reductase (FNR). FNR reduces $NADP^+$ and H^+ to form NADPH, which can be used for CO_2 fixation. In the PSII H_2O-to-H_2O cycle, electrons are extracted from the PQ pool (e.g., from reduced, unprotonated PQ^-), upstream of the Fe-rich cytochrome *b6f* and PSI complexes, by a terminal oxidase (PTOX or another oxidase with some properties that are similar to that of PTOX) and that can reduce O_2 and H^+ to H_2O. ATP is formed by ATP synthase (ATPase) using the proton gradient (dotted blue arrow) generated either during traditional electron flow (cytochrome b_6f–mediated proton pumping) or via the H_2O-to-H_2O cycle (production of protons by the OEC in the lumen and consumption of protons by PTOX in the stroma). The number of iron atoms (Fe) associated with each of the complexes is given below the name of each of the complexes. Black arrows indicate electron flow, while blue broken arrows indicate proton translocation. (B) Putative electron flow pathway in oceanic UCYN-A cyanobacteria lacking the PSII apparatus. It has been suggested that UCYN-A cells are photoheterotrophic, using PSI to generate ATP for nitrogen fixation but not to fix C by the Calvin–Benson–Bassham cycle. Electrons could be introduced into the electron transport chain via organic substrates, although the immediate source has not been identified. Electron flow may proceed as in the traditional linear electron flow pathway, terminating with the formation of reductant (NADPH) at the level of PSI, or may form a cycle around PSI, thereby facilitating ATP synthesis by helping to establish a proton gradient. Electrons from PSI may also proceed directly from ferredoxin (Fx) to nitrogenase (Nase), where they reduce atmospheric N_2 to bioavailable NH_4^+. Black arrows indicate electron flow, while blue broken arrows indicate proton translocation.

levels of PSI and the cyt b_6f complex relative to PSII (Strzepek and Harrison 2004, Bailey et al. 2008, Cardol et al. 2008). This situation may have evolved since PSI and cyt b_6f are Fe-rich complexes with 12 and five atoms of Fe, respectively (Golbeck 2003). Since nutrient resources in oligotrophic oceans are scarce, and have been scarce for billions of years, some oligotrophic ocean organisms may not develop high levels of PSI even when supplemented with Fe (Bailey and Grossman 2008). Also, phytoplankton of oligotrophic waters show a peak value for dark-adapted photochemical efficiency of PSII (F_v/F_m) at dawn, and for photoinhibition (decreased F_v/F_m) at midday when irradiance is highest; these features are linked to low Fe and N availability (Behrenfeld et al. 2006). However, the photochemical efficiency of PSII in the light (Φ_{PSII}) remains remarkably stable at midday despite photoinhibition (Mackey et al. 2008), suggesting a mechanism to keep a population of PSII reaction centers or ''traps'' open (i.e., able to accept electrons) while electron input is high (e.g., in high light).

The observations described above may relate to the surprising finding that even when CO_2 fixation is light saturated, PSII photosynthetic electron transport can remain high; PSII traps can remain open at light intensities at which CO_2 fixation no longer increases. These findings were demonstrated in laboratory studies with the oligotrophic cyanobacterium *Synechococcus* WH8102, for which a significant proportion of PSII traps remained open at light intensities of close to 2,000 μmol photons $\cdot m^{-2} \cdot s^{-1}$, even though CO_2 fixation saturated at ~200 μmol photons $\cdot m^{-2} \cdot s^{-1}$ (Bailey et al. 2008). A similar phenomenon occurs in the open-ocean picoeukaryote *Ostreococcus taurii* (Cardol et al. 2008), as well as in mixed populations of oligotrophic picophytoplankton (Mackey et al. 2008).

Studies discussed above raise important issues with respect to the ways in which photosynthetic electrons are used in both prokaryotic and eukaryotic marine phototrophs (Behrenfeld et al. 2008). A growing body of data suggests that at least some populations of marine phytoplankton have developed a means of extracting a significant proportion of electrons from PSII (either directly or indirectly) without using them for CO_2 fixation, raising a number of important questions: (i) Where are the extracted electrons going if they are not being used to fix CO_2? (ii) What mechanism(s) are involved in removal of these electrons? (iii) Are such activities advantageous in oligotrophic oceans, and if so, how? (iv) Are these phenomena prevalent in nature? While many of these questions are still not fully answered, experimentally addressing these questions will lead to a better understanding of the energetics of photosynthesis and primary productivity in the oceans.

First, consider the relatively low PSI to PSII ratio in oligotrophic picophytoplankton. This feature can result in an imbalance in electron flow through the two photosystems and cause a serious problem since PSI-dependent reoxidation of PSII might be slow, and excited singlet chl of PSII could accumulate leading to the production of potentially toxic levels of reactive oxygen species. This situation may be partially ameliorated by developing a larger PSI light-harvesting complex, which would facilitate more efficient PSI function at low light. This does occur in some Fe-limited cyanobacteria, with the large antennae formed by the IsiA protein (Nield et al. 2003). While the *isiA* gene does not appear to be prevalent in oligotrophic oceans, it is genetically diverse in coastal and high-nutrient, low-chl marine ecosystems (Bibby et al. 2009, Rivers et al. 2009). The strategy to generate a large antenna for PSI in Fe-poor environments might be beneficial at low light. However, in high light, such a strategy would favor highly reduced PSI reaction centers (P700), especially if the rate of downstream CO_2 fixation is low (e.g., due to low nutrient availability), and the P700 anion that accumulates could cause PSI damage and dysfunction. More work is needed to determine if the synthesis of IsiA or similar strategies for maximizing PSI function are used by phytoplankton in the oligotrophic ocean.

A potentially critical feature of open-ocean picophytoplankton is their ability to efficiently extract electrons from PSII without concomitant CO_2 fixation. PSII electron flow in *Synechococcus* WH8102 and *O. taurii* can be uncoupled from CO_2 fixation (Bailey et al. 2008, Cardol et al. 2008). For *Synechococcus* WH8102 in the light, PSII traps attained an open state as PSI became starved for electrons; a significant proportion of the electrons from PSII appeared to never reach PSI. Experiments designed to determine mechanism(s) required to maintain open PSII traps in high light demonstrated the dependence of this phenomenon on O_2; the traps closed rapidly when cells were placed under anoxic conditions but gradually opened as oxic conditions were reestablished in cultures (Bailey et al. 2008). Furthermore, inclusion of propyl gallate (pgal), an inhibitor of the plastoquinol terminal oxidase (PTOX), in the assays caused greater closure of PSII traps in the light (Bailey et al. 2008). A similar oxidase-dependent activity was observed in the open-ocean ecotype of *O. taurii* based on various observations. First, the quantum yield of PSII (Φ_{PSII}) was inhibited by pgal without altering the capacity of the cells for O_2 evolution, and a light-driven ΔpH was observed even when electron flow was blocked at the level of the cyt b_6f complex (by DBMIB). This ''extra'' ΔpH could be inhibited if photosynthetic electron transport was blocked at the level of PSII by DCMU, or if pgal was added to the reaction mixture (Cardol et al. 2008). When the results presented above are considered together, they strongly suggest that in at least some of the marine phytoplankton, electrons from PSII are being used to

reduce O_2 on the stromal side of the photosynthetic membranes, at a site in the electron transport chain prior to cyt b_6f; this would result in a H_2O-to-H_2O cycle for electron flow.

Light-stimulated O_2 uptake by phytoplankton has been discussed by others (Behrenfeld et al. 2008), and early studies by Falkowski demonstrated a light-enhanced rate of respiration in the marine diatom *Thalassiosira weissflogii* (Weger et al. 1989). Recently, light-stimulated O_2 uptake was examined for a variety of eukaryotic marine phototrophs (mostly coastal) (Suggett et al. 2009). Fast repetition rate fluorometry, mass inlet membrane spectrometry (MIMS), and ^{14}C uptake were used for simultaneous evaluation of PSII electron transport, gross and net O_2 evolution, and the fixation of inorganic carbon by six microalgal species (*Dunalliella tertiolecta*, *Pycnococcus provasoli*, *Storeatula major*, *Aureococcus anophagefferens*, *T. weissflogii,* and *Prorocentrum minimum*). Importantly, the MIMS data suggested that the three algal species studied (*P. minimum*, *P. provasoli,* and *S. major*) exhibited a significant light-elicited uptake of O_2 (Suggett et al. 2009). Furthermore, light-stimulated O_2 uptake that likely occurs close to the site of photosynthetic O_2 evolution in a number of different phytoplankton was recently demonstrated by Luz and Kaplan through analyses of heavy O isotope fractionation (Eisenstadt et al. 2010). At this point, the molecular mechanisms associated with these O_2-uptake activities have not been clearly defined, although they could involve the Mehler reaction, chlororespiration, cytochrome and alternative oxidase-dependent mitochondrial respiration, or pathways for alternative electron flow (e.g., PTOX-dependent O_2 uptake).

The discussion presented above suggests that a number of photosynthetic organisms that thrive in marine environments use O_2 as an electron acceptor and that this could potentially help maintain PSII traps in an open state when CO_2 fixation is saturated. Inhibition of electron extraction by pgal, at least for *Synechococcus* WH8102 and *O. taurii*, suggests that an oxidase related to PTOX, a quinol oxidase with homology to the mitochondrial alternative oxidase (Carol et al. 1999), can function to extract electrons from the photosynthetic ETC, most likely from the plastoquinone (PQ) pool. These conclusions are also supported by the finding that genes encoding PTOX are prevalent in metagenome databases generated from open-ocean samples (e.g., Sargasso Sea samples) (McDonald and Vanlerberghe 2005). Furthermore, the *ptox* gene has been found integrated into the genomes of marine cyanomyoviruses, which are related to the bacteriophage T4 (Millard et al. 2009), where it may impact viral-host interaction and cyanobacterial evolution. While others have shown that the photoreduction of O_2 can take place on the acceptor side (downstream) of PSI through the Mehler reaction (Asada 1999), the extent to which such a reaction occurs on the donor side (upstream) of PSI in oceanic organisms such as *Synechococcus* WH8102 (Bailey et al. 2008), the picoeukaryote *O. taurii* (Cardol et al. 2008), and likely in assemblages of phytoplankton from the open ocean (Mackey et al. 2008) is surprisingly high (as much as 50%). The PSII H_2O-to-H_2O cycle, which may be a significant component of photosynthetic electron flow in marine phytoplankton, has been integrated into the photosynthetic electron transport scheme presented in Figure 1A. The potential functions of this cycle in organisms that thrive in Fe-poor oligotrophic oceans are as follows:

1. Reduce the need for high PSI levels, the most Fe-rich complex in the cell, since electrons could be extracted from the system prior to PSI. While the H_2O-to-H_2O cycle would limit CO_2 fixation, the growth potential of the cells would already be low because of low nutrient (e.g., N, Fe) levels.
2. When PSI levels are low or PSI activity is constrained, it is critical that the PSII traps be kept open to protect the system from photodamage. Creating an electron valve on the acceptor side (downstream) of PSII could allow for rapid extraction of electrons from intersystem electron transport under high-light conditions or when downstream CO_2 fixation is saturated. The redox pressure resulting from PSII activity may also be alleviated to some extent by nonphotochemical quenching (Wilson et al. 2007).
3. Providing a strong electron outlet from the PQ pool would reduce electron flow to PSI and cyt b_6f, favoring a cationic P700 that may protect PSI reaction centers from photodamage, as previously suggested (Karapetyan 2007). This function of the PSII H_2O-to-H_2O cycle may be critical since PSI repair would require energy, and it may not be as easy to reassemble this reaction center when Fe levels are low.
4. The cycle may also serve a function similar to that of PSI cyclic electron flow. It would facilitate the generation of protons in the thylakoid lumen and the reduction of protons and O_2 on the cytosolic side of the thylakoid membranes, which would create a ΔpH for ATP synthesis, augmenting the cell's ability to efficiently scavenge ions from the environment.

Photosynthesis in some organisms in the oligotrophic oceans may have also become tailored for the fixation of N_2, a process poisoned by O_2. In oligotrophic regions, biological N_2 fixation has been traditionally attributed to the cyanobacterium *Trichodesmium* and cyanobacterial symbionts. However, recently it has been shown that there is a clade of unicellular cyanobacteria, ''group A'' or UCYN-A, that fix N_2 and that are related to *Cyanothece* sp. strain ATCC 51142, a marine unicellular

cyanobacterium isolated from an intertidal habitat, and to cyanobacteria that are symbiotic with the diatom *Rhopalodia gibba* (Prechtl et al. 2004). While these organisms have been found both in the Atlantic and widely distributed in the North and South Pacific oceans (Falcon et al. 2002, Zehr et al. 2008), they have not been successfully cultivated in the laboratory. New sequence information that contains a high degree of coverage of the UCYN-A genome suggests that these unicellular cyanobacteria have genes encoding PSI and nitrogenase (the N_2-fixation enzyme) but lack genes encoding components of the carbon concentration mechanism, the Calvin–Benson–Bassham cycle and PSII (Zehr et al. 2008). These findings were supported by the inability of the researchers to amplify a PSII reaction center gene (*psb*A) and the gene encoding the LSU RUBISCO from UCYN-A–enriched DNA samples (in contrast, the genes encoding PSI components were readily amplified). These results suggest that the UCYN-A cyanobacteria perform cyclic electron flow around PSI (which would generate ATP) without evolving O_2 (depicted in Fig. 1B). Furthermore, this novel adaptation would explain how some cyanobacteria of the oligotrophic oceans can fix N_2 during the day when most diazotrophs (N_2 fixers) cannot. Rather than fixing N_2 in specialized O_2-impermeant heterocyst cells, or at night when oxygenic photosynthesis ceases (as occurs for oxygenic, diazotrophic cyanobacteria), intracellular O_2 levels in the UCYN-A organisms may remain low enough during the day to allow the functioning of nitrogenase; these organisms still consume O_2 but do not evolve it during photosynthetic electron transport. The lack of CO_2-fixation genes in these cyanobacteria suggests a photoheterotrophic mode of growth in which N_2 fixation is uncoupled from CO_2 fixation. Hence, achieving this highly specialized adaptation for N_2 fixation comes with the tradeoff that these organisms must exploit other sources of organic carbon/reductant for both growth and nitrogen fixation (indicated as ''exogenous electron source'' in Fig. 1B), and they must also efficiently scavenge Fe from the environment to produce PSI centers and Fe-rich nitrogenase enzymes. The levels, activity, and composition of PSI in these cyanobacteria need to be carefully characterized. These findings are also likely to have significant implications with respect to the N and C budgets of the oligotrophic ocean.

In conclusion, the photosynthetic ''variant processes'' discussed above suggest a diversity of photosynthetic mechanisms that have evolved in phytoplankton of the oligotrophic ocean. A PSII H_2O-to-H_2O cycle appears to be a significant alternative route of electron flow in these organisms (and potentially in some organisms that grow in coastal regions). Interestingly, while an activity involving PTOX has been known to occur in plants for over a decade, and has been attributed roles in both carotenoid biosynthesis and poising of the redox state of the PQ pool (reviewed in Rumeau et al. 2007), it has recently become clear that it can represent a more prevalent pathway in plants exposed to stress conditions (Quiles 2006), as well as in certain organisms adapted to survival in high-light, low-temperature (Streb et al. 2005), and high-salt (Stepien and Johnson 2009) environments. We still need a clearer picture of the physiological/ecological relevance of the PSII H_2O-to-H_2O cycle in open-ocean organisms, how widespread the process is among the various phytoplankton (and if it does occur to any extent in organisms from coastal habitats), and the advantages/disadvantages associated with the various alternate routes of photosynthetic electron flow. It is also critical to understand how phytoplankton that synthesize large PSI antennae under Fe-limiting conditions, and others that may fix N_2 without oxygenic photosynthesis, impact C fixation and sequestration in the oceanic environment. Clearly, these variant processes have the potential to modify our understanding of the relationship between chl levels and primary productivity in oligotrophic environments. Evolution has tailored photosynthesis in the oligotrophic oceans over the course of many millions of years in ways that we are only just beginning to understand. This understanding is critical if we are to evaluate how photosynthetic processes and C cycling in the oceans will be impacted by the very rapidly changing environment that is being shaped by humans.

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