On Saturating Response Curves from the Dual Perspectives of Photosynthesis and Nitrogen Metabolism

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Introduction

Biological processes often respond in a way that "saturates", or comes to a maximum rate despite having increasingly available resources or substrate. A saturating response separates two important phenomena—a region where the substrate influences the rate, and a region where the process is functionally at or near a maximal rate and substrate has no or little influence. A key idea is that as the substrate increases in concentration or magnitude, its influence on the process ultimately stops. Accordingly, the substrate is *controlling* at low concentrations and *noncontrolling* at high concentrations. This simple, nontrivial, and profound concept is at the heart of nearly all biological and ecological systems models and is commonly the basis for evaluating "limitation" by environmental factors, whether it is at the level of cell physiology or ecosystem response. Rao (2000) considered the saturating response curve so fundamental to biological processes that he termed it "a curve for all reasons."

Classical examples of saturation curves are the photosynthesis–irradiance curve (the PE curve) and nutrient uptake kinetics (the V *vs* S curve), typically parameterized similarly, but not identically, as

$$P = P_{\max}\left(1 - e\left(-\alpha E_{\mathrm{o}} / P_{\max}\right)\right) \tag{1}$$

$$V = V_{\max}\left[S / \left(K_s + S\right)\right] \tag{2}$$

where P is the photosynthesis rate, $P_{\max}$ is the maximal rate of photosynthesis, E_{o} is the light intensity, α is the initial slope (Jassby and Platt 1976; Smith 1936), V is the

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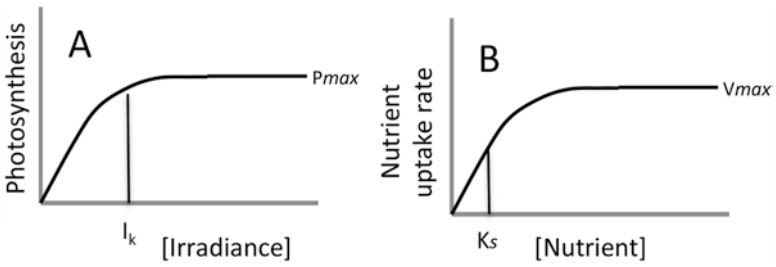

Fig. 1 Examples of saturating hyperbolic relationships and their application to (**a**) the rate of photosynthesis as a function of irradiance; (**b**) the rate of uptake of nutrients as a function of their concentration in the water column

specific uptake rate, V_{max} is the maximum uptake rate, S is the substrate concentration, and K_s is the half-saturation constant for uptake (Menten and Michaelis 1913; Fig. 1). Blackman and Tansley (1905) were the first to describe the saturating response as it relates to photosynthesis. *"…[T]hat photosynthesis in Nature is proportional to light intensity is only true up to a limit set by the amount of CO_2 that can reach the plastids by diffusion."* Blackman and Tansley recognized that photosynthesis ceded control from irradiance to CO_2 supply. Application of the saturation curve to the concept of limitation is perhaps one of the most well-known concepts in phytoplankton ecology, with the half-saturation constant as the break-point wherein nutrient limitation is considered to be overcome. For photosynthesis, the break-point for light limitation is typically evaluated using the parameter, E_k ($=P_{max}/\alpha$), the light intensity at which photosynthesis begins to saturate and has been used to characterize organisms according to their "sun" vs. "shade" response (e.g. Prézelin 1981).

For organisms, biochemical and physiological processes are generally constrained by a maximum rate of reaction and saturating responses are the basis of most models describing organism responses to the environment. At larger scales, saturation responses have been applied to ecosystem management of nutrient loading responses; there is a region of rapid response where systems are changing and a region of slow response where systems have considerable resilience to change to either increasing nutrient loading or nutrient reductions (Glibert et al. 2010). Across these scales, the processes of photosynthesis and nutrient acquisition are central to understanding environmental limitation on growth and ecology of phytoplankton and this brings together our dual perspectives on the biological regulation of saturating responses and implications for understanding ecological behavior.

Static vs. Dynamic Behavior

In classical phytoplankton physiology, the kinetics of nutrient uptake and growth (analogous to the relationship describing enzyme–substrate kinetics) utilizes a half-saturation "constant" (K_s) calculated from a curve fit, and that parameter is used to

assess the degree of limitation of that nutrient for growth. Often, this parameter is assumed to be characteristic or fixed and the literature is replete with comparisons of K_s and V_{max} for different species or different water bodies (e.g. Kudela et al. 2008). The use of "fixed kinetics" continues to persist in spite of the recognition decades ago that there is considerable variation, even within a given organism, in such relationships (e.g. Goldman and Glibert 1983 and references therein). As with nutrient kinetics, photosynthesis kinetics vis-à-vis irradiance effects also exhibit a well-characterized saturation response (we ignore photoinhibition) and curve fit equations are plentiful (Jassby and Platt 1976) and the literature is replete with species comparisons of PE parameters. The importance of those parameters that define saturating curves cannot be overstated as they are the input to mathematical models formulated to describe both cellular and ecological behavior of more complex systems.

Implicit in a saturating response curve is the notion that the cell follows the response as the independent factor changes. Photosynthesis follows a PE curve as irradiance changes. Likewise, N uptake follows an uptake curve as N concentration changes. At one level, the cell must follow the curve—it is an empirical result. At this most simple conceptual level, we can think of a cell's physiology as "running up and down" the saturation curve as substrate availability changes. But it has also been long known that saturating response curves depend on physiological state of the cell and/or the manner in which the experiment is performed (e.g. Harris 1978; Goldman and Glibert 1983 and references therein), so any specific curve has some arbitrariness related to the measurement protocol. This dynamic is nicely exemplified by "rapid light curves" (i.e. PE curves measured in short duration) using variable fluorescence methods (White and Critchley 1999). Rapid light curves are strongly dependent on the investigator-determined duration of irradiance at each step, which affects the physiological state and resulting response curve. Similarly, nitrogen uptake curves have long been known to be dependent on the length of time an experiment is performed (e.g. Wheeler et al. 1982). Therefore, it can be argued that a cell does not "run up and down the curve", but simply responds instantaneously to its environment based on its physiological state, which is dependent on its history.

The challenge is to relate measured saturating curves (implicitly static) to the activity of cells that undergo regulation during or around the process of measurement. A common approach has been to obtain "catalogs" of curves for processes, as was done for many years with PE measurements in efforts to understand species responses to environmental factors. Here we develop an alternative perspective whereby the curves are used to inform us about mechanisms of regulation and from an understanding of those mechanisms, we develop a perspective on how the organism "sees" the world and manifests saturation curves under experimentation.

Gradient Signals and Dynamics of Response Curves

Thirty years ago we conducted experiments with the recently-discovered marine cyanobacterium, *Synechococcus*, with an interest in growth and photosynthesis capability over a broad irradiance range (it had been considered a low-light adapted

organism; Kana and Glibert 1987a, b). Using cultures from eight growth irradiances spanning a saturating growth rate curve, we measured PE responses. And, relating carbon uptake rates to four different basis units (cell number, cell carbon, chlorophyll, and phycoerythrin), the data provided us with a suite of 32 unique PE curves for this one species. The *Synechococcus* experiments clearly demonstrated that under steady-state conditions rates of photosynthesis and growth were linked, but that potential short-term photosynthesis at irradiances different from the growth irradiance (i.e. across a PE response) exhibited varied, but highly regulated rates. This finding paralleled earlier observations for N uptake, which clearly demonstrated that short-term rates of N uptake and growth were uncoupled, but were also highly regulated and followed similar patterns (McCarthy and Goldman 1979; Goldman and Glibert 1983).

In both cases, only under conditions of maximal growth rate (μ_{max}) did the maximal rate of photosynthesis (P_{max}) or nutrient uptake (V_{max}) balance the growth demand. At light limitation for growth, there was an excess capacity of photosynthesis that was not utilized under the growth conditions. When comparisons were made of the rates of P_{max} relative to P_i (photosynthesis at the growth irradiance) in relation to the ambient growth rate (μ_i) relative to μ_{max} (i.e. μ_i:μ_{max}, or the relative growth rate), one finds that excess photosynthetic capacity diminishes as relative growth rate approaches 1, and similarly for nitrogen uptake, V_{max} exceeds V_i (ambient uptake rate) under nitrogen limitation and the ratio V_{max}:V_i diminishes toward μ_{max} (McCarthy and Goldman 1979; Goldman and Glibert 1982, 1983 and references therein; Kana and Glibert 1987b; Fig. 2).

The parallels between nutrient- and light-dependent responses to relative growth rate imply that the uptake *capacities* for the major resources (nutrients and photons) regulate to a balance point that satisfies μ_{max}. An alternative way of looking at this is that μ_{max} provides the rate constraints (i.e. slow steps) for regulation of light and nutrient harvesting. An important implication of this is that growth rate per se can be used as a "grand integrator" of metabolism. Growth rate links all processes related to nutrient and energy acquisition, a conclusion that would be drawn a priori from mass balance considerations (Shuter 1979).

Early work on photoacclimation (termed photoadaptation prior to the mid-1980s), which is ubiquitous among plants and algae, was generally in the context of "sun vs. shade" or "high vs. low" irradiance acclimation. In that experimental context, species appeared to sort themselves out in terms of two or more "strategies" depending on patterns of change in α and/or P_{max} (Prézelin 1981; Richardson et al. 1983). However, the *Synechococcus* light gradient study (Kana and Glibert 1987b) demonstrated that all of the strategies previously described existed in one organism when observed over a growth irradiance range that encompassed limiting and saturating irradiances. This implied that there must be a single mechanism for photoacclimation rather than multiple strategies. Subsequently, it was demonstrated that the "light meter" for photoacclimation resided in the electron transport chain and was related to the reduction state of the plastoquinone (PQ) pool (Escoubas et al. 1995; Maxwell et al. 1995) whereby a shift in reduction state

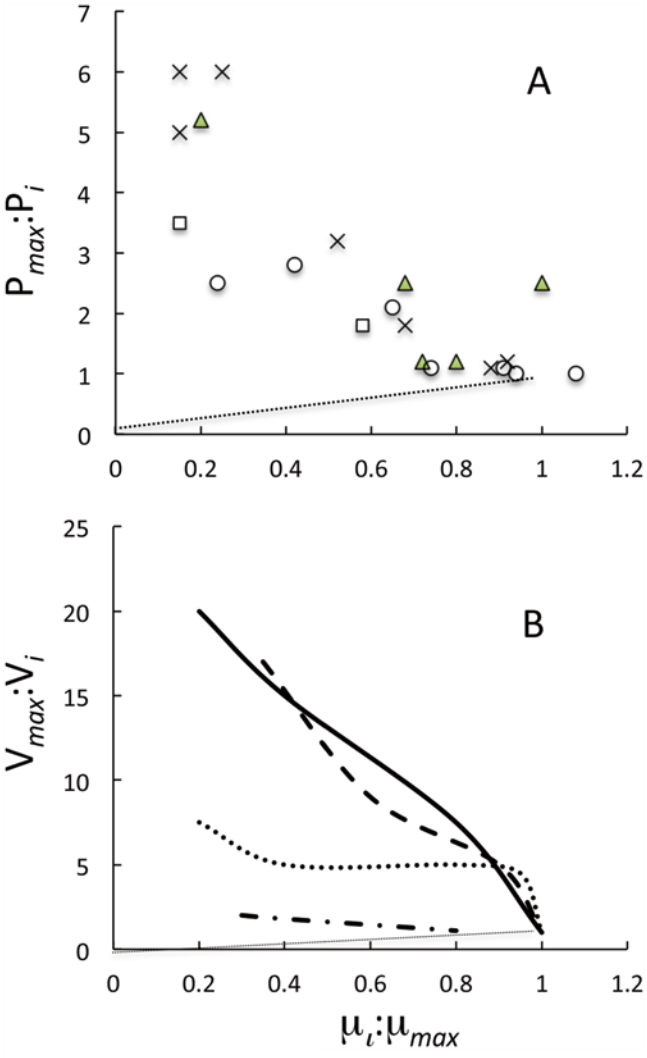

Fig. 2 Comparison of the relationships between P_{max}:P_i (**a**) and μ_i:μ_{max} and V_{max}:V_i and μ_i:μ_{max} (**b**). In panel (**a**) four species are compared: *circle*, *Synechococcus* WH7803; *triangle*, *Microcystis aeruginosa*; *crosses*, *Phaeodactylum tricornutum*; and *squares*, *Alexandrium tamarensis.* Figure redrawn from, and original data sources given in, Kana and Glibert 1987b. In panel (**b**) four species are compared: *solid line*, *Phaeodactylum tricornutum*; *dashed line*, *Thalassiosira weissflogii*; *dotted line*, *Chaetoceros simplex*; and *dot-dash line*, *Dunaliella teriolecta*. Figure redrawn from, and original data derived from Goldman and Glibert (1982). The fine *dashed lines* in both panels represent the equivalency of the rates

caused a shift in pigment-protein synthesis rate. The reduction state is directly related to the relative rates of reductant formation via light harvesting and reductant utilization via (principally) carbon assimilation. Thus, an increase in irradiance at constant utilization (e.g. at μ_{max}) increases the redox state and reduces the pigmentation that ultimately reduces the redox state to a new poise. The dynamic balance of pigment concentrations is one of several mechanisms that balance energy absorption with energy utilization, but it is an important mechanism for modelers of phytoplankton productivity because it relates pigment cellular concentrations to the environment (e.g. Li et al. 2010).

This irradiance-dependent energy balance concept led to a more general analysis relating "energy in" vs. "energy out", or light harvesting *vs* assimilation. This "balance" was formulated as a simple ratio (light absorption/assimilation) that served as a gradient signal that mediated pigment synthesis (Kana et al. 1997). A key assumption was that photosynthetic assimilation is constrained to μ_{max}, which is constrained independently by nutrient availability, temperature, and other growth-limiting factors (i.e. growth rate is the grand integrator). It was possible to model a cell that manifested pigment concentrations and PE curves that behaved according to experiments conducted across irradiance, temperature and nutrient gradients *and diverse species* (Geider et al. 1996, 1997, 1998; Kana et al. 1997). The "slow step" related to light-dependent μ_{max}, that in turn constrains P_{max}, and could be located among a number of bottlenecks ranging from PSII turnover time to rates of cellular metabolism outside of the photosynthetic apparatus. This provided a "rule" allowing the integration of diverse environmental factors into a single regulatory mechanism. Photoacclimative pigment concentrations could not be predicted from irradiance alone. It required knowledge of the ratio of absorption to assimilation.

In terms of nitrogen acquisition and assimilation, there are many parallels. The balance between carrier proteins and the enzymes for N assimilation is analogous to the balance between pigments and the enzymes of C assimilation. In nutrient acquisition, the carrier proteins at the cell surface are analogous to the light harvesting apparatus, and specifically in terms of NH_4^+ and NO_3^- acquisition, the transporters AMTs and NRTs, respectively, perform that role (e.g. Galván and Fernandez 2001; Rogato et al. 2015).

However, in terms of nutrient acquisition, the parallels with light acquisition are more complicated because not all nutrient substrates follow the same kinetics. In fact, even within the inorganic nitrogen forms, there are key differences in the nutrient uptake response as a function of variable substrate supply (e.g. Glibert et al. 2016). In general, NO_3^- transporters are induced by the presence of their substrate (NO_3^-), whereas NH_4^+ transporters are induced by the absence or deficiency of their substrates, or repressed by increased availability of their substrate, NH_4^+ (Glibert et al. 2016 and references therein). Thus, increasing concentrations of NO_3^- yield more NRTs, whereas increasing concentrations of NH_4^+ yield fewer AMTs. In this regard, the regulation of NH_4^+ acquisition is more similar to light acquisition in that absence leads to up-regulation of the acquisition pathways. Such

a phenomenon has been well documented in both culture and field experiments, where N limitation results in uptake rates that far exceed the nutrient that would be required to balance growth (e.g. Conway et al. 1976; McCarthy and Goldman 1979; Glibert and Goldman 1981; Fig. 2). This rapid or "surge uptake" is, in concept, the same as the excess PS capacity relative to balanced growth shown in low light grown cultures (Kana and Glibert 1987b; Fig. 2). Due to the differing nature of the regulation of NO_3^- vs NH_4^+ transporters, vis-à-vis what signals their up-regulation when substrate is limiting, rapid or surge uptake of NH_4^+ is more likely than that of NO_3^-. It, like light harvesting antennae, is "primed and ready" to respond to any increase in substrate availability, whereas the up-regulation of NO_3^- transporters in most cases require time to respond, the so-called "shift-up" response (e.g. Berges et al. 2004).

If the "light meter" for photosynthetic regulation is the energy pressure and state of the PQ pool, what is the "nutrient meter" and how does it sense a state of sufficiency or saturation? All nitrogen forms are ultimately reduced to NH_4^+ before assimilation into amino acids and proteins. Assimilation of NH_4^+, either derived from direct uptake or from reduction of NO_3^- or NO_2^-, occurs via a series of reactions involving (for most algal species) the enzymes glutamine (Gln) synthetase (GS) and glutamate (Glu) synthase (GOGAT; also known as glutamine-2-oxoglutarate amidotransferase). This pathway yields Glu, the product of Gln and oxoglutarate (2-OG) (Scanlan and Post 2008). The availability of Gln and the Gln/Glu ratio govern the NO_3^- reducing capacity in the cell; when Gln levels are low, and when NO_3^- is available, nitrate reductase (NR) is up-regulated. Alternatively, when Gln levels are high, NR activity levels are dialed back (Flynn et al. 1994; Campbell 1999). As the supply of NH_4^+ becomes insufficient to maintain a high internal N-status, indicated by a decline in internal Gln:Glu ratios (Flynn et al 1989, 1994), then the ability to transport and use NO_3^- is up-regulated. AMTs in some species are up-regulated by the depletion of NO_3^-, but the inverse relationship does not appear to be the case; that is they are not down-regulated by the prevalence of NO_3^- (e.g. Hockin et al. 2012; Glibert et al. 2016). Thus, the "nutrient meter" for all forms of N acquisition is the GS-GOGAT state and therefore the ability to assimilate NH_4^+ (directly or from reduction of NO_3^- or NO_2^-) relative to the ability to use that nitrogen downstream. In all, the cells have tuning knobs, the PQ redox state and the relative levels of Gln:Glu, that serve as the signals to up-regulate or down-regulate acquisition to meet the needs of the cells when resources are low, and to switch off acquisition when resources are sufficient.

Overall Perspective on Dynamic Kinetics

The ratio of light absorption to assimilation capacity turned out to be a robust modeling parameter that "self-regulated" cellular pigments under diverse environmental factors (Geider et al. 1996, 1997, 1998; Kana et al. 1997). Energy input was related

to irradiance and light harvesting (pigment content), whereas assimilation capacity was regulated by cellular limits determined by factors such as temperature and nutrient limitation. Effectively, these models scaled pigment responses to growth rate as the "grand rate setter" and by doing so, it was possible to coalesce diverse phytoplankton species variation for pigment regulation into a single regulatory structure for multiple environmental effects. This result also supports the notion described above that the cell does not "ride up and down" a PE curve but rather the PE curve is merely a consequence of the nature of light harvesting efficiency and maximum rate constraints at any given time—both of which lead to a saturating response curve. By the same token, a cell does not "ride up and down" a nutrient kinetic curve; the shape of the curve at any given time is a consequence of the nature of the nutrient acquisition machinery and the rate constants of the suite of nitrogen assimilating enzymes at any given point in time.

As is the case with photoacclimation, which is recognized to depend on the dynamic balance of energy flow through the entire photosynthetic apparatus and cell, nutrient assimilation should be recognized to depend on the balance of nutrient acquisition at the cell surface and the maximal rate at which these nutrients can be assimilated within the cell, a balance between surface uptake sites and internal enzymes (Smith et al. 2009). This dynamic balance approach recognizes that even at the level of saturation the cell continues to regulate its nutrient metabolism through processes of internal feedbacks and controls. Such a suite of feedbacks may result in considerable adjustment of nutrient uptake in the region where nutrients are normally considered "saturating". Such adjustments may lead to short-term uptake curves showing continued increase in uptake, leading to biphasic kinetics or even inhibition (Glibert et al. 2016). In fact, kinetic relationships should be viewed as continually varying within the bounds of a response surface and deviations from a single, classically defined kinetic relationship, should be viewed as the norm rather than the exception (Goldman and Glibert 1983; Smith et al. 2009; Glibert et al. 2013, 2016).

One approach that is showing promise in capturing dynamic regulation of nutrient kinetics is that of optimal kinetics (Aksnes and Egge 1991; Smith et al. 2009). This approach recognizes that the ability of the cell to up- or down-regulate nutrient uptake is a function of the potential maximum uptake sites, internal enzymes and rates of assimilation. Instead of a half-saturation constant, this approach calculates an affinity uptake rate:

$$V_{\text{aff}} = [(V_{\max} S) / ((V_{\max} / A) + S] \tag{3}$$

wherein the relationship substitutes the more classic half-saturation constant (K_s) with an affinity constant, $V_{\max}$ ratioed to A, the affinity. In such a formulation, both the affinity and $V_{\max}$ may vary with cellular physiology. Thus, as with the photosynthetic "regulatory term", light harvesting/assimilation, a ratio provides a more robust measure of the relative abilities of all species to compete for nutrients (Smith

et al. 2009). In essence, optimal kinetics assumes that the cells dynamically balance the efficiency of nutrient acquisition at the cell surface and the maximal rate at which these nutrients can be assimilated within the cell, a balance between surface uptake sites and internal enzymes (Smith et al. 2009; Pahlow and Oschlies 2013). Bonachela et al (2012) have also proposed a dynamic formulation of nutrient uptake in which a model cell allows for dynamic regulation of cell transport proteins, leading to flexibility in the maximal uptake rate as well as the limiting portion of the curve. Others (e.g. Klausmeier et al. 2007) have addressed model formulations that allow for flexibility in the uptake of more than one nutrient resource. Such an approach allows for dynamic changes in uptake and in allocation strategies of the different nutrients.

The implications of a dynamically varying, rather than fixed kinetic model are important. On the one hand, nutrient stress can develop before nutrient availability declines below the conventionally defined half saturation value (and bearing in mind how poorly this value is typically known), while on the other hand, regulation of nutrient uptake does not cease when availability of nutrient reaches values defined as "saturating" (Glibert et al. 2013). Thus, application of fixed kinetics to the concept of nutrient limitation fails to recognize the complexity of regulation that occurs across the entire range of substrate availability. Furthermore, regulation of nutrient uptake along this continuum may differ for different nutrients or for different forms of the same nutrient. Importantly not only are there differences in cellular nutrient content between taxa, but within taxa at any given time there are differences in the plasticity or flexibility in nutrient content. Such regulation is fine-tuned and balanced at steady state. However, natural communities are rarely growing at steady state under single nutrient sources and fixed concentrations and are composed typically of numerous taxa. Conceptualizing the relationships between physiological processes and growth as dynamic rather than as fixed kinetic relationships, and understanding how this regulation may differ for different nutrients, has further implications for understanding cell properties and ultimately for ecosystem metabolism.

The brief review above has emphasized that with both light acquisition and CO_2 assimilation as well as with nutrient acquisition and assimilation, there is strong biological regulation between the demand side (getting what is needed when the supply is low) and the assimilation of the resource (the maximal rate always set by biochemical reactions and their constants) for each set of environmental conditions. It is time to incorporate these tuning knobs in models rather than fixed half saturation or photosynthetic constants. Progress is being made. More needs to be done-both experimentally and computationally to move forward from our fixed and invariant notions of kinetics to better representation of the dynamics of biology.

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Todd M. Kana and Patricia M. Glibert

Ask each of us when we met and you will get a different answer (clearly one of us made a better impression on the other when we first met!). We do agree that we met in college, but we were attending different colleges. After several years of a long-distance relationship while we pursued our master's degrees and first job opportunities, we both applied to Harvard for our Ph.D.—and remarkably it was the only place that accepted us! We were married later that year, much to the surprise of many faculty and students who thought we had just met. Pat studied N cycling, but Todd was not aquatically oriented and studied plant autecology. Pat finished first and took a postdoc at Woods Hole Oceanographic Institution (WHOI). The writing was on the wall: we were going to be located at a marine lab, but WHOI at that time forbade spouses from both being hired. Nor were there opportunities for Todd's expertise. Todd learned that hanging out with oceanographers could be fun and he gravitated back to his interests in basic photosynthetic processes, but now in the context of the newly discovered marine *Synechococcus*. Pat stayed focused on how and why phytoplankton could cope with vanishingly low nitrogen in the oceans as well as becoming a first time mom (WHOI's first female scientist to give birth). A move to the Horn Point Laboratory in Maryland was welcome when positions for both of them were offered and when HPL was developing a core group of plankton ecologists and recognized the advantages of spousal hiring. Two more children, many challenges, wonderful colleagues, good students, and fun travels have filled our lives over the past 30+ years. Todd now spends more time on instrumentation and applications development and less time on photophysiology. Pat focuses on how and why phytoplankton can cope with all the excess nitrogen that has eutrophified our estuaries and coasts. The questions have changed; our work has evolved, but the excitement of the science has not.

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