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Behavior, physiology and the niche of depth-regulating phytoplankton

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1. Introduction

To understand the population dynamics of phytoplankton species contributing to harmful algal blooms (HABs), we focus on physiological, biochemical, and behavioral features of phytoplankton that might influence ecological selection in different hydrographic regimes. Each species of phytoplankton has a different combination of adaptive characteristics that in many ways defines its niche, *i.e.*, the suite of ecological factors that determines its distribution and activities. By understanding the adaptations of different phytoplankton species, it should be possible to describe patterns of species abundance as functions of hydrographic processes, nutrient distributions and the potential impact of herbivores. This understanding could be applied to determine the principal causes of HABs (*e.g.*, eutrophication, upwelling, stratification, advection), to achieve better skill at forecasting their occurrence, and to predict the consequences for phytoplankton of environmental changes in coastal waters, such as might be associated with aquaculture, coastal engineering, or climate change. Because the ecological and commercial effects of algal blooms depend on the particular species involved, it is essential to focus on characteristics of phytoplankton that are likely to distinguish one species from another with respect to ecological selection during development and maintenance of a bloom.

Recognizing that many harmful algae can move vertically, we discuss depth regulation in phytoplankton as an ecological strategy, emphasizing physiological and biochemical adaptations that can strongly influence the growth and survival of phytoplankton species in different hydrographic regimes. We identify adaptive features that can be quantified experimentally, so that species can be compared and predictive models can be developed. This discussion is focused on marine systems; a comprehensive presentation, including a thorough review of the extensive literature on freshwater cyanobacteria (Zevenboom 1986; Oliver 1994) is beyond the scope of this chapter.

2. Hydrographic regimes and corresponding strategies for survival

Without denying the relevance of physiological adaptations to light, temperature, or nutrients, Margalef (1978) suggested that, with respect to ecological selection of phytoplankton species, the most important factor is the mechanical energy of the water column: “Water movement controls plankton communities.” Because nutrients are incorporated into particles, and particles tend to sink, the fate of a permanently stratified water column with no input of mechanical energy is complete segregation of the factors necessary for the growth of phytoplankton: light, but no nutrients near the surface; nutrients, but no light at depth. The productivity of such systems is minimal. Mechanical energy from winds, tides, and some types of currents displaces water and delivers nutrients to the photic zone through mixing and upwelling, leading to enhanced productivity (Yentsch 1980; Kiørboe 1993). There are limits, however: deep vertical mixing reduces mean irradiance for surface-layer phytoplankton, thereby diminishing primary productivity (Sverdrup 1953); in other places, upwelling can be too intense for the assimilatory responses of phytoplankton to keep pace (Dugdale and Wilkerson 1989). The phytoplankton that survive under specific regimes of turbulence have developed "adaptation syndromes…to recurrent patterns of selective factors" (Fig. 1; Margalef 1978). The dominant selective factor is turbulence. A principal mode of action is the delivery of nutrients to phytoplankton cells (Kiørboe 1993).

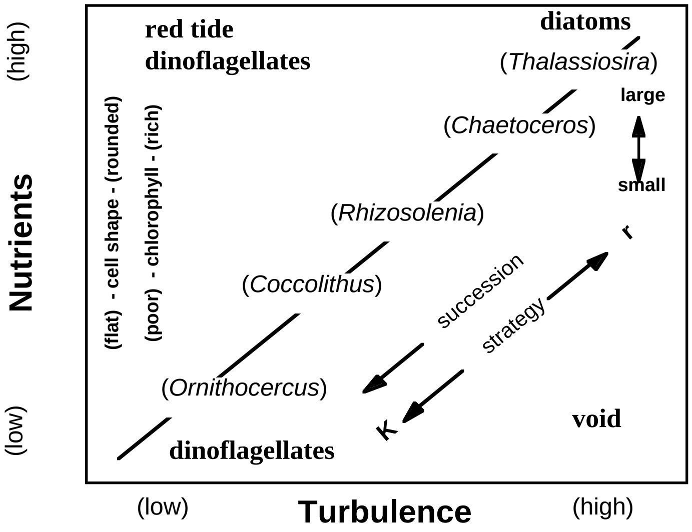

Fig. 1. Margalef's (1978) view of how life-forms of phytoplankton, represented by exemplary species, correspond to different regimes of turbulence and availability of nutrients. The trends in cell size, shape, pigment content, and ecological strategy are consistent with a strong influence of nutrient availability on selection. Depth regulation and vertical migration were not explicitly considered, although the dominance of red-tide dinoflagellates in low-turbulence, high-nutrient waters can be associated with swimming behavior (redrawn from Margalef, 1978).

Accepting that life forms of phytoplankton species reflect in large part alternative strategies for survival in different regimes of turbulence (Kiørboe 1993; Estrada and Berdalet, this volume), we describe in this chapter how our understanding of niche space defined by turbulence regimes is expanded when strategies of depth regulation by phytoplankton are considered. Some adaptations of depth-regulating phytoplankton are identified, and an attempt is made to describe adaptation syndromes that could enhance the success of particular phytoplankton species in particular regimes of turbulence or nutrients. One reason for doing this is to see if potentially harmful phytoplankton species have developed adaptations that would be selected for in response to changes in coastal waters, such as eutrophication (Smayda 1990; Hallegraeff 1993) or hydrographic shifts associated with climate change (Fraga and Bakun 1993; Tester *et al.* 1993).

2.1 Classification of adaptive strategies

Selective patterns of phytoplankton can be associated with water columns classified as high-energy, high-nutrients (deep vertical mixing or active upwelling), moderate-energy, moderate nutrients (transiently stratified water, nutricline well within the photic zone), and low-energy, low-nutrients (highly stratified, nutricline very deep in the photic zone or below it). The persistence of high nutrients in stratified marine waters can be viewed as an anomaly associated with external inputs of nutrients, conducive to dinoflagellate blooms (Fig. 1); because of coastal eutrophication, such conditions have become more common in recent decades (Smayda 1990).

With respect to depth regulation in different regimes of turbulence, there are three general strategies that require different combinations of physiological and behavioral adaptations (behavior is very loosely defined to include the regulation of buoyancy): mixing, migrating and layer-formation.

2.1.1 Mixers

In regimes of high turbulence, displacement of phytoplankton cells (m s^{-1}) is much greater than maximum sinking or swimming speeds (see Kamykowski *et al.*, this volume), thus, the phytoplankton ("mixers") go with the flow. Because elevated nutrients are generally associated with enhanced turbulence, mixers should have adaptations to exploit variable irradiance (Legendre and Demers 1984; Demers *et al.* 1991; Ibelings *et al.* 1994), rather than to acquire nutrients efficiently.

How important is depth regulation to mixers? In well-mixed surface layers (ignoring upwelling), losses due to sinking (l_s, d^{-1}) can be quantified: $l_s = w_s / z_m$, where w_s is sinking rate (m d^{-1}) and z_m (m) is mixed layer depth. Regulation of sinking rate is important to the extent that l_s makes a significant contribution to net growth rate (*i.e.*, the specific growth rate, μ (d^{-1}) minus specific loss rates to grazing, mixing and sinking). For example, a diatom with a sinking rate of 1 m d^{-1}, blooming in a mixed layer of 50 m, will not be affected much by sinking losses. See the review by Walsby and Reynolds (1980) for a comprehensive treatment.

When turbulence decays, for example when a mixed layer shoals and near-surface nutrients are depleted as phytoplankton grow and accumulate, sinking losses become more important (z_m decreases and μ decreases). One strategy for a mixer is capitulation by sinking from the system and entering a life-cycle that culminates in re-introduction to the surface layer when conditions are once again favorable (Smetacek 1985). This strategy could be facilitated by an increase in cell density in response to nutrient depletion (Richardson and Cullen 1995 and references therein) and also the production of mucilage, setae or microfibrils, which would promote aggregation, thereby accelerating the sinking rate by increasing the Stokes radius (Jackson 1990; Kiørboe 1993). For mixers, an alternative adaptation to decaying turbulence is to minimize sedimentation by reducing sinking rate when entering the nutrient-rich thermocline, thereby increasing the probability of resuspension into the mixed layer (Lande and Wood 1987). This strategic trend of nutrition-influenced vertical movement culminates in vertical migration, which is the next category.

2.1.2 Migrators

In lower-energy water columns, nutrients in the well-lighted surface layer can be depleted. By migrating vertically in such systems, phytoplankton can acquire nutrients at depths where light would limit growth rate, but also exploit saturating irradiance near the surface, where depletion of nutrients would otherwise restrict the accumulation of biomass (Holmes *et al.* 1967; Cullen 1985). Diel vertical migration (DVM) is the best studied and probably most common form of vertical migration (Blasco 1978; Heaney and Eppley 1981; Watanabe *et al.* 1991). However, cyclical vertical movements of phytoplankton likely occur over other temporal scales (Rivkin *et al.* 1984; Villareal *et al.* 1996). The environment of migrators is characterized by extreme, but in large part predictable variability in light and nutrients. Important adaptations for vertical migration include: the capacity to take up nutrients in low light or in the dark; photosynthetic physiology tuned to exploiting predictably varying irradiance; and behavioral responses (*i.e.*, changes in swimming behavior or cellular buoyancy) regulated effectively by environmental feedback (Richardson *et al.* 1996).

2.1.3 Layer-formers

Migration is but one adaptation for survival in low-energy water columns. Many species of phytoplankton segregate vertically in stratified waters, remaining in distinct strata (Venrick 1988). This layering can be described partly on the basis of population dynamics, *i.e.*, different local optima for net growth rates (Lande *et al.* 1989), but for some species, buoyancy regulation and active swimming certainly play a role. Some motile species aggregate and migrate vertically within a restricted range (Sommer 1985) but others aggregate and show little or no evidence of vertical migration during phases of their life cycles: examples include *Gyrodinium aureolum* (*Gymnodinium mikimotoi*) (Holligan 1978) and *Ceratium tripos* (Falkowski *et al.* 1980; Eppley *et al.* 1984). Such aggregating phytoplankton can be considered as layer-formers. They are found in environments characterized by maximum predictability of irradiance and nutrient supply. Efficiency of light-utilization would be an important selective factor for phytoplankton that form deep layers, whereas efficient nutrient utilization is very important for layer-formers that aggregate near the surface. Other adaptations to layer formation would include effective physiological controls on depth regulation, and the development of mechanisms to repel grazers (Turner *et al.*, this volume).

The three strategies — mixing, migrating, and layer formation are neither totally distinct nor relevant to all phytoplankton. These categories should be useful, however, for discussing adaptations of depth-regulating phytoplankton. In this chapter, we will focus on photosynthesis, nutrient utilization, behavior, and their interactions. Several other adaptive processes can be explored fruitfully without considering in detail the movements of phytoplankton in the water column. For example, special nutrient requirements (iron, vitamins, ammonium), allelopathy, mixotrophy, cyst formation and germination, as well as parasitism have all been studied in the context of HABs; they are discussed elsewhere in this volume.

3. Adaptations to environmental variability

Turbulence, solar radiation and depth-regulation behavior interact to determine the irradiance experienced by phytoplankton. Phytoplankton respond to changes in irradiance through a suite of adjustments called photoacclimation (Harding *et al.* 1987; Falkowski and LaRoche 1991). Adaptations of different taxa to irradiance have been compared in an analysis of strategies which revealed broad differences between dinoflagellates, diatoms, and green algae that were generally consistent with their patterns of dominance in aquatic environments (Richardson *et al.* 1983). In the hopes of finding key properties that might explain the dominance of phytoplankton species in particular hydrographic regimes, we build upon that analysis, looking at aspects of photoacclimation that might relate closely to strategies of depth regulation.

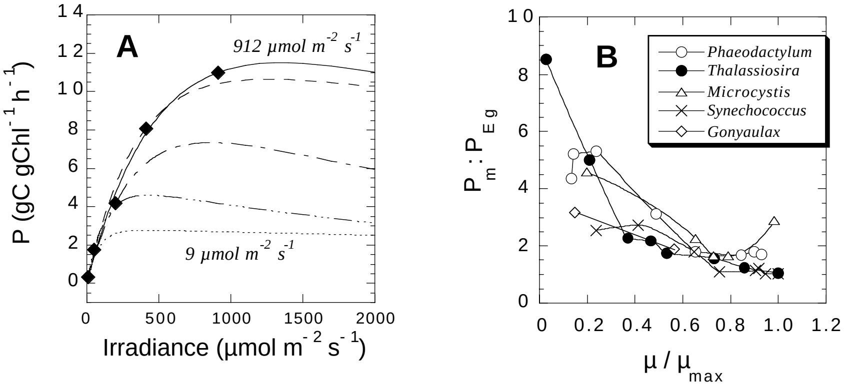

Fig. 2. Adaptations to exploit variable irradiance. A. Photosynthesis (gC $\mathrm{gChl}^{-1}\,\mathrm{h}^{-1}$) vs *E* for *Thalassiosira pseudonana* (3H) in semi-continuous cultures adapted to different irradiance (9, 50, 200, 410, and 912 μmol $\mathrm{m}^{-2}\,\mathrm{s}^{-1}$; lowest to highest curves, respectively) during the photoperiod of a 12h:12h light:dark cycle at 20°C. Photosynthesis was measured as ^{14}C-bicarbonate uptake for 24 subsamples over 20 min (Cullen *et al.* 1989), fit to the model of Platt *et al.* (1980). Closed diamonds mark photosynthesis at growth irradiance for each culture, $P_{E\mathrm{g}}$. B. Excess photosynthetic capacity, P_m:$P_{E\mathrm{g}}$, as a function of light-limited growth rate, relative to the maximum at that temperature (μ / μ_max). Cultures of *T. pseudonana* from A (•), along with data presented by Kana and Glibert (1987b) for *Phaeodactylum tricornutum* (o), *Microcystis aeruginosa* (Δ), *Synechococcus* WH7803 (x), and *Alexandrium* (*Gonyaulax*) *tamarense* (◊).

3.1. Excess photochemical capacity

The relationship between photosynthesis and irradiance (*P*-*E*; here we refer to photosynthesis normalized to chlorophyll, *P*, gC $\mathrm{gChl}^{-1}\,\mathrm{h}^{-1}$, but we omit the superscript B) is an adaptive feature of phytoplankton; it varies with growth irradiance (Fig. 2A, see also Falkowski 1980); nutrition (Cullen *et al.* 1992), and temperature (Li and Morris 1982; Maxwell *et al.* 1995). The *P*-*E* relationship can be characterized by an initial slope, α (gC $\mathrm{gChl}^{-1}\,\mathrm{h}^{-1}$ (μmol $\mathrm{m}^{-2}\,\mathrm{s}^{-1})^{-1}$), a maximum rate, P_m (gC $\mathrm{gChl}^{-1}\,\mathrm{h}^{-1}$), and a term characterizing the susceptibility to photoinhibition (*e.g.*, β, gC $\mathrm{gChl}^{-1}\,\mathrm{h}^{-1}$ (μmol $\mathrm{m}^{-2}\,\mathrm{s}^{-1})^{-1}$; Platt *et al.* 1980). For cultures grown under constant irradiance (E_g)

during the photoperiod, the ratio of maximal to adapted rate of photosynthesis, $P_m{:}P_{Eg}$ (where P_{Eg} is P at growth irradiance) is an index of excess photosynthetic capacity (Kana and Glibert 1987b), *i.e.*, the capacity to exploit irradiance greater than the mean. Excess photosynthetic capacity (EPC) represents genetically determined capability to exploit variable irradiance, especially exposures to bright light during vertical mixing.

The enzymes (principally ribulose bisphosphate carboxylase) and the reaction center proteins (Sukenik *et al.* 1987) required to maintain EPC represent a capital cost that carries with it a reduction in growth rate when irradiance does not vary much (Richardson *et al.* 1983). Hence, we would expect mixers to have maximal EPC, and layer-forming phytoplankton to have minimal excess capacity.

It is premature to generalize, but one can speculate that excess photochemical capacity indeed reflects depth-regulation strategy. A preliminary survey of available data (Fig. 2B; Kana and Glibert 1987b) suggests that the genetically determined photosynthetic responses of diatoms are consistent with what we would expect for mixers: high EPC for cultures grown in low irradiance. Two species have lower values of P_m/P_{Eg}: *Synechococcus* and *Alexandrium* (Fig. 2B). *Synechococcus*, too small to move very far in a day, seems adapted to stable water columns. *Alexandrium* can migrate vertically, but at least one strain forms a persistent layer near the surface when nutrients are replete (MacIntyre *et al.* 1997). A comprehensive survey of photosynthetic responses might reveal if EPC indicates the hydrographic regime to which different phytoplankton species are best adapted. The diagnostic is potentially useful for characterizing environmental preferences of harmful phytoplankton, and their potential responses to altered hydrography.

Differences in EPC, reflecting ecological selection linked to turbulence, could influence the interpretation of P_m in nature as a measure of photoacclimation (Falkowski 1981): for example, a relatively high P_m for phytoplankton in optically deep mixed layers with low mean irradiance has been interpreted as an adaptation to the highest irradiance encountered during vertical mixing (Vincent *et al.* 1994). In a sense, the mixing phytoplankton would indeed be adapted to exploit the highest irradiance encountered, but it may be the consequence of genotypic selection for mixers with high EPC rather than phenotypic photoacclimation to highest irradiance experienced during mixing.

3.2. Capacity for photoacclimation

Many species of phytoplankton cannot survive exposures to full sunlight. Hence, species of phytoplankton that form blooms at the surface should have adaptations for tolerating potentially harmful solar radiation. In this chapter, only photosynthetically available radiation (PAR) will be considered. Ultraviolet radiation (UV) can also be a factor; effects of UV and adaptive responses are reviewed elsewhere (Vincent and Roy 1993; Cullen and Neale 1994).

A first step in characterizing the growth responses of a phytoplankter (say, a species that forms harmful blooms) is to examine its growth rate as a function of irradiance. One can determine growth-irradiance relationships of phytoplankton (Langdon 1988) and generalize about tolerance of bright light or adaptation to low light, but caution is warranted: for example, the marine *Synechococcus* was originally thought to require low light regimes for growth (Glover 1986) but an oceanic clone was later shown to grow very well at irradiance levels approaching full sunlight (Kana and Glibert 1987a). To obtain high growth rates in bright light, it was crucial for Kana and Glibert (1987a) to introduce high irradiance gradually, because even though low-light-adapted *Synechococcus* had some excess photosynthetic capacity (Fig. 2B), it did not survive abrupt increases to supersaturating (*i.e.*, inhibiting) irradiance (Barlow and Alberte 1985). Oceanic *Synechococcus* are now known to be abundant over a broad range of depths in the photic zone (Campbell and Vaulot 1993). We can infer that adaptation of phytoplankton to variable environmental irradiance includes not only the capacity to exploit irradiance higher than the mean, but also mechanisms to tolerate excess irradiance long enough for effective adaptation to take place.

3.2.1. Short-term responses to excess irradiance

Phytoplankton respond to excess irradiance through a variety of mechanisms that operate over a range of time-scales (Harris 1986). An operating principle is that when irradiance is high enough to saturate photosynthetic systems, additional photons absorbed by photosynthetic pigments, especially those directed to photosystem II (PSII) reaction centers, are potentially damaging (Ibelings *et al.* 1994 and references therein). In this section, we discuss short-term diversion of excess absorbed irradiance away from sensitive sites, with concomitant changes in characteristics of *in vivo* fluorescence. Longer-term adjustments are examined below.

Rapid (seconds to minutes) responses to excessive irradiance involve processes that reduce the efficiency with which absorbed photons (excitons) are transferred to PSII reaction centers. The absorbed but diverted energy is dissipated as heat; the concomitant reduction in fluorescence yield is called nonphotochemical quenching. Nonphotochemical quenching can be effected by several processes (Krause and Weis 1991; Arsalane *et al.* 1994). In studies of phytoplankton, quenching through xanthophyll cycling (Demers *et al.* 1991; Olaizola *et al.* 1994) is recognized as being important in photoprotection; it is responsive to growth conditions (Arsalane *et al.* 1994), and variable among species (Demers *et al.* 1991). The xanthophyll cycle involves the physiologically harmless conversion of pigments with enzymatic reversion to complete the cycle. Activity of xanthophyll cycling is manifest in rapid (minutes), reversible reductions in chlorophyll fluorescence during exposure to bright light (Demers *et al.* 1991). Although quenching associated with xanthophyll cycling may provide only partial protection from excess irradiance (Olaizola *et al.* 1994), it seems likely that physiological regulation of xanthophyll pools is an adaptive feature of phytoplankton that would reflect the different strategies of mixers, migrators, and layer-formers (Demers *et al.* 1991; Ibelings *et al.* 1994).

If excess irradiance is not quenched or otherwise diverted, PSII reaction centers can be inactivated, leading to photoinhibition. Photoinhibition is defined here as a decrease in the rate of photosynthesis *during* exposure to supersaturating irradiance — *i.e.*, a reduction in the capacity for photosynthesis, concomitant with decreases in efficiency; (see Fig. 3 and Neale 1987). Strong, slowly reverting nonphotochemical quenching processes can also reduce the efficiency of photosynthesis (Ting and Owens 1994), but not necessarily the rate of photosynthesis in bright light (see Fig. 6C in Cullen *et al.*

1988). While such strong quenching is active, rates of photosynthesis would be maintained if cells remained at the surface, but the exposure to bright light would reduce subsequent photosynthesis if cells were mixed vertically (Ibelings *et al.* 1994). Mechanisms such as strong quenching and inactivation of PSII reaction centers are reversible and thus can protect the long-term integrity of PSII (Öquist *et al.* 1992; Ibelings *et al.* 1994), even though they reduce short-term photosynthesis in nature. If such "protective" mechanisms are not effective, more severe and possibly irreversible damage could occur. Hence, when trying to describe the photophysiology of a phytoplankter, it is important to explore long-term adaptability to bright light, as well as short-term responses. Note that a low-light adapted diatom (*Thalassiosira pseudonana*, presumably a mixer) showed strong inhibition of short-term photosynthesis during exposure to bright light, but it survived and adapted (Fig. 3A), whereas a layer-former, *Oscillatoria agardhii*, showed no inhibition of photosynthesis during short-term exposures to irradiance much higher than saturating irradiance, but would not survive (Fig. 3B).

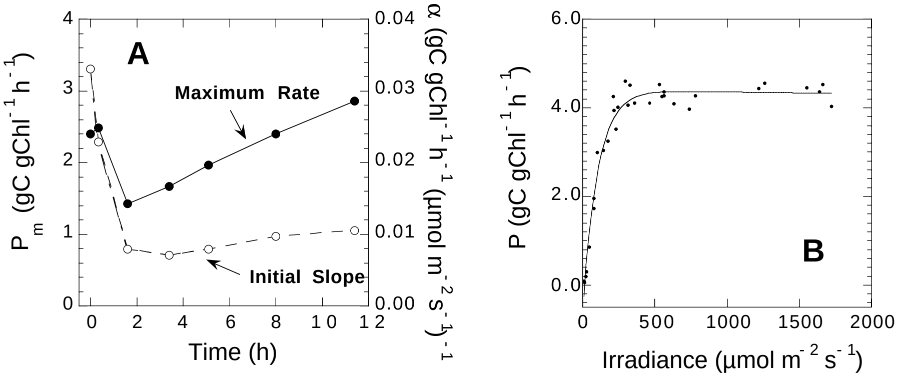

Fig. 3. Photosynthetic responses to increased irradiance of phytoplankton suited to different regimes of turbulence. A. *Thalassiosira pseudonana*, a coastal diatom, presumably adapted to turbulent environments: a culture adapted to low light, 20 µmol m^{-2} s^{-1} was shifted to 2000 µmol m^{-2} s^{-1} (Cullen and Lewis 1988); both the initial slope of the *P-E* curve (α) and the maximum rate P_m declined rapidly, consistent with nonphotochemical quenching and inactivation of PSII reaction centers, causing photoinhibition. After 2 hours, photosynthesis continued, chemical composition changed consistent with photoacclimation, photosynthetic capacity recovered, and the culture eventually acclimated to high light. B. *Oscillatoria agardhii*, a depth-regulating cyanobacterium, sampled from a low-light metalimnetic peak in an experimental mesocosm: *P* as a function of *E* (15 min incubations with ^{14}C bicarbonate) showed no short-term photoinhibition, even at $E > 10$ times the irradiance at which cells had aggregated. Cells did not survive after transfer to bright light, however (J.J. Cullen and A.R. Klemer, unpublished).

It thus seems possible that dynamic physiological responses to bright light, including those that might reduce short-term photosynthesis, are adaptations that promote survival of phytoplankton that move through the water column. Depth-regulating phytoplankton need not have these adaptations, if they can descend rapidly enough to avoid damaging conditions (Heaney and Talling 1980; Häder and Worrest 1991; Neale *et al.* 1991). Perhaps the existence of strong circadian rhythms in photosynthetic performance (Prézelin 1992) with maximal resistance to photoinhibition near midday (J.J. Cullen, unpublished data on *Heterocapsa niei*), is an adaptation to predictable exposures to bright light.

Experiments on the dynamic responses of phytoplankton to bright light should thus be helpful for inferring how species might compete in different turbulence environments. For example, research on freshwater bloom formers, especially cyanobacteria, has been very successful (Ibelings *et al.* 1994 and references therein). These studies have been noteworthy not only for the development and testing of hypotheses, but also for the application of powerful fluorescence techniques (Schreiber *et al.* 1986) to describe dynamic changes in photosynthetic physiology in an environmental context. Research on short-term photosynthetic responses of marine and estuarine phytoplankton has focused more on the oceanographic problem of describing photosynthetic responses to fluctuating light (Neale and Marra 1985; Kirkpatrick *et al.* 1990; Franks and Marra 1994) than on comparing species. However, Sakshaug *et al.* (1987) were able to identify differences in bright-light responses between two congeneric diatoms that could be related to the oceanic vs coastal environments from which they were isolated.

3.2.2. Longer-term photoacclimation through unbalanced growth

Aspects of the longer-term (hours-days) acclimation of phytoplankton to changes in irradiance have been studied very well (reviewed by Falkowski and LaRoche 1991). For example, the ratio of cellular C to chlorophyll (C:Chl) increases with growth irradiance (Geider 1987), along with the capacity for photosynthesis, P_m (Falkowski 1981). These changes are consistent with adaptive shifts in the allocation of photosynthate between three major cellular pools: light harvesting, maintenance, and storage (Shuter 1979; Lancelot *et al.* 1991; Geider *et al.* 1996). Rates of acclimation depend on growth conditions, magnitude and direction of the change, species, which property is measured, and what constituent is used in the denominator of a ratio (*e.g.,* C:Chl; Geider and Platt 1986; Cullen and Lewis 1988). In general, the time scales of change for C:Chl and P_m range from hours to a generation time or so (Prézelin and Matlick 1980; Post *et al.* 1984; Cullen and Lewis 1988). These changes are accomplished through unbalanced growth, the synthesis (or more precisely, the net accumulation) of some cellular components at different rates than others (Shuter 1979). An understanding of the regulation of unbalanced growth leads directly to an understanding of long-term photoacclimation (Geider *et al.* 1996).

Cellular chemical composition is sensitive to irradiance, but other factors also have a strong influence. In general, light harvesting capability is reduced (in essence, diluted; C increases relative to Chl) and storage products are accumulated in relatively bright light, under relatively low temperature, and in response to nutrient limitation. These are the conditions under which the absorption of light by photosystems (the *source* of photosynthetic electron flow: a function of pigmentation and irradiance) exceeds the cell's ability to utilize the light (the *sink* for photosynthetic electron flow: a function of assimilatory enzymes, temperature, and nutrients available for protein synthesis). In other words, the capacity to harvest light is reduced and photosynthate is stored when the source-sink ratio is high (Cullen 1985). When light is limiting (sink exceeds source), storage is reduced and photosynthate flows to light harvesting components. Using fluorescence induction methods, the balance between light absorption and utilization (source:sink) can be quantified as "excitation pressure", the reduction state of the electron acceptor pool in PSII (Maxwell *et al.* 1995). This measurement, as well as a related analytical representation (Geider *et al.* 1996), can be extremely useful in studies of photoacclimation through unbalanced growth.

Photoacclimation involves trade-offs, and thus ecological strategies probably exist. For example, adaptation to low light involves processes that maximize light harvesting (*e.g.*, accumulation of pigment) and minimize losses to respiration (Geider *et al.* 1986). Adaptation of mixers to low mean irradiance is thus an interesting problem. Excess photosynthetic capacity facilitates use of variable irradiance in deep mixed layers, but the adaptations to support exploitation and tolerance of bright light (high levels of photosynthetic enzymes, active photoprotective and repair mechanisms) come with a cost (elevated respiration, inefficient photosynthesis after exposure to bright light). The consequences of these kinds of physiological trade-offs have been considered by Ibelings et al. (1994); the topic merits careful examination in future studies of adaptation to different mixing regimes.

Deep layer-formers are expected to be small (internal self-shading of pigments is minimized, hence light absorption efficiency is maximized, Morel and Bricaud 1986) and to have inherently low respiration rates (Richardson *et al.* 1983). The existence of big cells in deep layers suggests that efficient photosynthesis is not always necessary: processes such as phagotrophy, osmotrophy or resistance to grazing are likely important to their ecology (discussed elsewhere in this volume). Vertical migrators that can reach the surface need not adapt to low light, unless the nutricline is so deep that saturating irradiance cannot be reached during a diurnal ascent. Size and swimming speed (or rates of sinking or floating) would then be factors (see Kamykowski *et al.*, this volume). Note that the energetic costs of swimming are small (Richardson *et al.* 1983), and not considered to be a major ecological factor for phytoplankton.

For ecological modeling, as well as for understanding adaptations to environmental variability and the physiological trade-offs that are involved, it is critical to understand the dynamic regulation of biosynthesis during photoacclimation. Some progress has been made (Shuter 1979; Lancelot *et al.* 1991; Geider *et al.* 1996). Source-sink regulation is central to the process of photoacclimation, and as we show in the following sections, it may be important to the nutrition and buoyancy regulation of vertically migrating phytoplankton.

4. Unbalanced growth, behavior, and nutrient assimilation

It has long been recognized that motility of marine phytoplankton allows them to exploit nutrients over a relatively large part of the water column (Gran 1929), thereby achieving concentrations greater than could be attained through growth at any one depth in stratified waters (Holmes *et al.* 1967). In coastal waters, this exploitation of nutrients is achieved principally through diel vertical migration. For a time, the ability of dinoflagellates to support growth by taking up nitrate during nocturnal descent of DVM was controversial (reviewed by Cullen 1985). Now, it is well established that vertically migrating flagellates can and do take up deep nutrients (N and/or P) to support growth in stratified water columns (Watanabe *et al.* 1995; MacIntyre *et al.* 1997 and references therein). Interest has been focused primarily on nitrate and phosphate uptake by flagellates during DVM, but there have been demonstrations (either direct or indirect) of deep nutrient acquisition by vertically cycling marine diatoms (cycle time of several days, Villareal *et al.* 1996) and marine cyanobacteria (Karl *et al.* 1992). Also, it has been suggested that through buoyancy regulation, mixed-layer diatoms can exploit deep nutrients obtained during periodic encounters with the thermocline (Lande and Wood 1987; Richardson and Cullen 1995). Buoyancy reversals in freshwater cyanobacteria, and regulation through light-nutrient interactions have been long recognized and well studied over the years (reviewed by Oliver 1994 and discussed by Klemer *et al*. 1996). For all examples, the strategy of deep-nutrient acquisition through vertical cycling involves close coupling between physiological condition and changes in buoyancy or swimming direction (see Kamykowski *et al.*, this volume).

4.1 Physiological adaptations for assimilation of deep nutrients

What are the physiological adaptations for the exploitation of deep nutrients? One is the ability to take up nutrient (*e.g.*, nitrate) in the dark, or in very low light. There is much to be learned by comparing the abilities of different species to take up nitrate in the dark (Paasche *et al.* 1984); one important observation is that for some dinoflagellates, the capability is induced only after a short period of N-starvation (Paasche *et al.* 1984; Cullen 1985).

Assimilation of nitrate into protein requires products of photosynthesis for energy, reductant, and carbon skeletons (Syrett 1981); when N-starved dinoflagellates were fed nitrate in the dark (thereby greatly increasing the sink for photosynthate), these requirements were satisfied by the mobilization of carbohydrate that had been stored during the light period. The stoichiometry (about 6 mol carbohydrate-C mobilized for each mol nitrate-N taken up and assimilated) is consistent with calculated demands (Cullen 1985). This mechanism of N-acquisition is apparently sustainable: a dinoflagellate could be maintained on nitrate supplied only in the dark (Harrison 1976).

Assimilation of nitrate and synthesis of protein at the expense of accumulated carbohydrate is one aspect of a general dependence of nocturnal protein synthesis on carbohydrate dynamics (Cuhel *et al.* 1985; Zenvenboom 1986). It can thus be concluded that uptake and assimilation of nitrate during nocturnal descent of DVM requires few, if any, special physiological adaptations. Accumulation of storage products is the consequence of being in nutrient-depleted surface layers during the day, consistent with photoacclimation to high excitation pressure (see 3.2.2). Mobilization of storage products for assimilation of nitrate in the dark is likewise consistent with source-sink regulation: exposure to inorganic nitrogen creates a large demand for photosynthate to provide carbon skeletons for protein synthesis. Under similar conditions, diatoms are capable of nocturnal nitrate uptake (Fig. 4), suggesting that the ability to take up nutrients in the dark is not a special adaptation of migrators.

Not all vertical migrators do so every day. For example, large diatoms (Villareal *et al.* 1996), the dinoflagellate *Pyrocystis* (Rivkin *et al.* 1984) and cyanobacteria of the genus *Trichodesmium* (Karl *et al.* 1992) in the open ocean are thought to migrate between the nutricline and surface waters with a period longer than a day. The large diatoms may cycle on the order of a generation time (Richardson *et al.* 1996). Mixed-layer diatoms might also cycle vertically through nutrient-dependent sinking and resuspension from the thermocline (Lande and Wood 1987); this would happen on an irregular basis. Buoyancy regulation in freshwater cyanobacteria is likewise tied more to physiological state than to the diel cycle (Oliver 1994). Adaptations for all these non-motile migrators include the ability to take up large amounts of nutrient during periodic exposures, along with the capacity to accumulate large amount of storage products to support nutrient assimilation at depth (Fig. 4B; Richardson *et al.* 1996). As shown in Fig. 4B, the accumulation of storage products acts as a buffer for environmental variability (Gibson and Jewson 1984). Species might vary in the amount they can store and in the time they can remain nutrient starved before survival is threatened (Fig. 5). Can some species of depth-regulating phytoplankton buffer

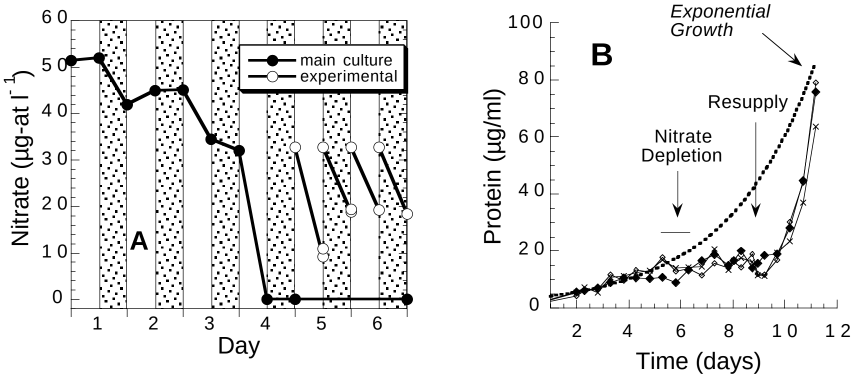

Fig. 4. Uptake and assimilation of nitrate after N-starvation. A. The diatom *Skeletonema costatum*, grown at 20°C on a 12h:12h light-dark cycle with nutrients in excess except for nitrate. Filled circles, nitrate in the culture; open circles, connected by lines, show responses of subsamples to the addition of 32 µg-at l^{-1} nitrate at the beginning or end of the light period. Conditions and manipulations are essentially the same as reported by Cullen (1985) for the dinoflagellate *Heterocapsa niei*, and results are very similar, showing capacity for the uptake of nitrate in the dark after brief N-starvation. Like in *Heterocapsa*, carbohydrate was mobilized during dark nitrate uptake in the stoichiometry appropriate for nitrate reduction and protein synthesis. However, *Skeletonema* took up only about half as much nitrate during the dark period. (M. Zhu and J.J. Cullen, unpublished). B. Changes of protein in triplicate cultures of the diatom *Thalassiosira weissflogii* during N-starvation and resupply of nitrate. From day 6 through 9, protein did not increase because N was unavailable. Photosynthate was accumulated as carbohydrate; changes in chemical composition were sufficient to explain increased sinking rate of the diatom. After nitrate was supplied on day 9, the uptake of nitrate proceeded in the light and in the dark; carbohydrate was mobilized to support protein synthesis, decreasing cell density in the process. By day 11, protein in the cultures was almost fully restored to what would have accumulated during unperturbed exponential growth. Carbohydrate acted as an environmental buffer (results from Richardson and Cullen 1995).

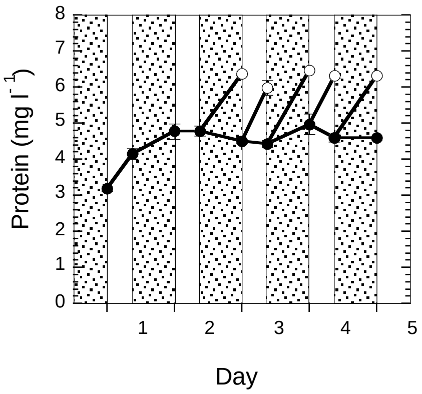

Fig. 5. Maintenance of the ability to assimilate nitrate during N-starvation. Protein concentration (closed circles ± s.e. of triplicates; method of Dorsey *et al.* 1978) for *Heterocapsa niei* grown to nitrate depletion on day 1 (conditions as in Fig. 4A, initial nitrate = 50 µM, but on a 9h:15h light-dark cycle). Open circles, increase of protein (±s.e.) after addition of 30 µM nitrate to subsamples. The ability to take up nitrate in the dark was undiminished after three days: essentially all added nitrate was consumed during the last dark period, and 79% of the nitrate appeared as protein (assuming protein is 16% N by weight; Dorsey *et al.* 1978). It is not known how long the capability for nitrate assimilation would persist or how other species might differ in this respect. Unpublished data of M. Zhu and J.J. Cullen.

more than one cell division? Can some buffer much less? Does it matter for ecological selection? These questions deserve further study.

4.2. Behavioral adaptations for deep nutrient assimilation

The preceding discussion has shown that physiological adaptations for deep nutrient acquisition are widespread. Thus, it may be the ability to cycle between deep nutrient pools and the surface layer, rather than the capacity to take up nutrients in the dark, that is key to exploitation of deep nutrient pools. Consequently, a variety of behavioral adaptations for deep nutrient acquisition are likely to exist.

4.2.1 Motile phytoplankton

For motile phytoplankton, vertical migration, though phased to solar irradiance, is governed by factors other than phototactic swimming, including temperature, cell size, cell density, and environmental feedback on swimming behavior (Kamykowski 1995). Not surprisingly, species differ in the depth or light level of aggregation during the day, extent of nocturnal descent, and timing of both descent and ascent. Further, migration patterns can be strongly influenced by nutrition (Heaney and Eppley 1981; MacIntyre *et al.* 1997) so that each species probably has a unique suite of nutrient- and light-dependent vertical migration patterns, each suited to a particular hydrographic regime (Cullen 1985). Indeed, each dinoflagellate studied to date has displayed a distinct suite of responses to altered regimes of nutrients or stratification. The challenge is to infer from field observation and experimental results where and why a particular species will bloom, or when its strategy might fail. For some species, bloom dynamics have been described as a function of the interactions between behavior, physiology, and regional hydrography (*e.g.*, Tyler and Seliger 1981; Watanabe *et al.* 1995; Figueiras *et al.* 1996). More studies using different species in experimental water columns may be effective in revealing physiologically-influenced behavioral and physiological adaptations that are suited for growth and survival in other hydrographic regimes.

4.2.2 Non-motile phytoplankton

Depth regulation in vacuolate freshwater cyanobacteria has been well described (Oliver and Walsby 1984). The synthesis and collapse of gas vesicles strongly influences buoyancy, but the accumulation of ballast (*e.g.*, polymeric carbohydrate) also affects sinking and floating. Vesicle synthesis, turgor collapse, and carbohydrate accumulation are influenced by interactions of light and nutrients, and the general tendency is for nutrient-rich, low-light cells to float and nutrient-starved, high-light cells to sink (Oliver 1994). The concept of nutritional effects on the accumulation and mobilization of carbohydrate ballast has been applied to marine cyanobacteria (Romans *et al.* 1994) and diatoms (Richardson and Cullen 1995) as well. Clearly, physiological responses to nutrients and light have a direct influence on vertical movements of non-motile phytoplankton. Research on marine forms will benefit from careful consideration of the extensive literature on freshwater cyanobacteria.

4.3. The mechanistic links between nutrition and vertical migration

Because nutrition influences vertical migration of motile phytoplankton, swimming behavior must be under physiological control. But how does light absorption and nutrition influence swimming? A direct link has been suggested (see Lieberman *et al.* 1994; Kamykowski 1995): accumulation of dense carbohydrate in the posterior region of a dinoflagellate, perhaps with lipid accumulation anteriorly, would direct swimming upward. The importance in nature of this mechanism of orientation is unknown and deserving of further study (Häder *et al.* 1991 and references therein).

Even if the exact mechanism of physiologically-induced behavior modification is unknown, there is a need to describe the environmental influences on swimming trajectories of motile phytoplankton so that the vertical movements of phytoplankton can be incorporated into hydrodynamic or ecological models. Phototaxis alone cannot explain migratory behavior of phytoplankton; modeling exercises show that even simple physiological control on migration behavior greatly improves predicted growth (Kamykowski *et al.*, this volume). However, the interaction of light and nutrients in influencing cellular orientation and consequently vertical distribution is poorly described. This is an important topic for future research. One approach would be to relate orientation patterns to internal stores of storage compounds. Another would be to calculate something akin to excitation pressure (Maxwell *et al.* 1995; Geider *et al.* 1996; see 3.2.2) and relate it to swimming orientation. Considering the rapid migratory response of a nitrogen-starved dinoflagellate to N addition (MacIntyre *et al.* 1997), we might focus on the source-sink balance as reflected in the enzymes of carbohydrate synthesis and mobilization (Cullen 1985) rather than on PSII, site for excitation pressure. A principal objective would be to provide appropriate algorithms for models of vertical migration. Another product, of course, would be a deeper appreciation of how migrating phytoplankton respond to their environment, and what response patterns are best suited to particular hydrographic regimes.

5. Summary and conclusions

We began this chapter by relating behavioral strategies of depth-regulating phytoplankton to different regimes of turbulence (see also Estrada and Berdalet, this volume). Recognizing that interactions of behavior and hydrography determine the temporal variability of irradiance and nutrient supply, we extended Margalef's (1978) search for "adaptation syndromes…to recurrent patterns of selective factors," looking for adaptations to dominant modes of environmental variability that are specific to different behavioral strategies. Distinct syndromes were identified: mixers should be adapted to highly variable irradiance, with some influence of nutrition on buoyancy; migrators should have a well-developed capacity for unbalanced growth and effective physiological control of vertical movements; and layer-formers should develop efficient systems for utilizing light or nutrients at the expense of tolerating environmental variability. Ecological trade-offs are associated with each adaptation, so there is wide latitude for differentiation between species. We suggest that differences in adaptation patterns can be related to ecological success in particular hydrographic regimes.

Quantifiable properties are associated with several key adaptations. Excess photochemical capacity, an index of the ability to exploit variable irradiance, should be high in mixers and low in layer-formers. Short-term photoprotective responses, detectable with fluorescence techniques, can have a strong influence on the survival of phytoplankton exposed to bright light during mixing or vertical migration. Photoacclimation and nutrient acquisition through unbalanced growth can be related to the ratio of light absorbed to light (*i.e.*, photosynthate) utilized: regulation of the allocation of photosynthate is subject to selection, so we expect adaptive differences between species. The process of unbalanced growth can be examined through a number of simple experiments (Figs. 4, 5; also Cullen and Lewis 1988) and described quantitatively in the context of recent models (Lancelot *et al*. 1991; Geider *et al*. 1996). Such models should also serve to describe nutrient uptake during vertical migration and the physiological control of buoyancy (Kromkamp and Walsby 1990) as well as vertical migration behavior (Kamykowski *et al*., this volume).

Because adaptation syndromes to different hydrographic regimes include physiological controls on depth regulation, many niches are available, associated with a range of behavioral responses to light and nutrients. By characterizing environmental influences on depth regulation for individual species, and the consequences for population dynamics, we may be able to define the niches of different phytoplankton species and identify the selective factors that promote their growth in particular environments. Progress has been made for freshwater cyanobacteria (Oliver 1994) and a few marine species (*e.g.*, Tyler and Seliger 1981; Richardson *et al.* 1996; Villareal *et al.* 1996), but appropriate experimental data for marine HAB phytoplankton is scarce (*e.g.*, Watanabe *et al.* 1995; MacIntyre *et al.*, 1997). We conclude that to describe the growth of depth-regulating phytoplankton in nature, the interaction of physiology and behavior must be considered. Because many HAB species can move vertically, new approaches, some of which have been outlined here, should be useful in trying to understand the physiological ecology of harmful algal blooms.

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