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Harmful algal blooms: Their ecophysiology and general relevance to phytoplankton blooms in the sea

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Abstract

From 60 to 80 species of phytoplankton have been reported to be harmful; of these, 90% are flagellates, notably dinoflagellates. The effects of turbulence on harmful algal bloom (HAB) taxa, their photoadaptive strategies, growth rate, and nutrient uptake affinity (K_s) are considered. Flagellates, including HAB taxa, collectively have a lower nutrient uptake affinity than diatoms. Four major adaptations are suggested to have been evolved to offset the ecological disadvantages of their low nutrient affinity: nutrient retrieval migrations; mixotrophic tendencies; allelochemically enhanced interspecific competition; and allelopathic, antipredation defense mechanisms. Motility-based behavioral features of flagellates contributing to their blooms include: phototaxis, vertical migration, pattern swimming, and aggregation, which facilitate nutrient retrieval, trace metal detoxification, antipredation, depth-keeping, and turbulence avoidance. Neither a general physiological syndrome nor distinctive physiological profile distinguishes harmful flagellate species from nonharmful taxa. However, HAB flagellates exhibit significant ecophysiological differences when compared to diatoms, including greater biophysical vulnerability to turbulence, greater bloom dependence on water-mass stratification, greater nutritional diversity involving mixotrophic tendencies, greater potential use of allelochemical mechanisms in interspecific competition and antipredation defenses, and unique behaviorial consequences of their motility. Flagellates use a "swim" strategy; diatoms a "sink" strategy.

About 300 (7%) of the estimated 3,400–4,100 phytoplankton species have been reported to produce "red tides," including diatoms, dinoflagellates, silicoflagellates, prymnesiophytes, and raphidophytes (Sournia 1995). Excluding diatoms decreases this number to ~200; moreover, most red tide species do not produce harmful blooms. Only 60–80 species (2%) of the 300 taxa are actually harmful or toxic as a result of their biotoxins, physical damage, anoxia, irradiance reduction, nutritional unsuitability, etc. Of these, flagellate species account for 90% and, among flagellates, dinoflagellates stand out as a particularly noxious group. They account for 75% (45–60 taxa) of all harmful algal bloom (HAB) species. The exceptional importance of dinoflagellates is further evident from their pre-eminence among the species, perhaps 10–12, primarily responsible for the current expansion and regional spreading of HAB outbreaks in the sea (Anderson 1989; Hallegraeff 1993; Smayda 1989*a*, 1990).

Harmful algal taxa may be nonmotile or motile; pico-, nano-, or larger sized; photoautotrophic, mixotrophic, or obligate heterotrophs; siliceous or nonsiliceous species, etc., and have diverse modes of inimical action. The considerable physiological and phylogenetic diversity represented in the phytoplankton in general, and among HAB species in particular, prompt a basic question: what cellular processes and environmental mechanisms select for which HAB species, or strains, will bloom, particularly from among those species which co-occur and share overlapping niches? Resolution of this should be a major priority of future research. The equally relevant, better understood question focused upon here is: what common properties of a HAB event must be accommodated ecophysiologically for HAB taxa to bloom? In this analysis, selected ecophysiological attributes of HAB taxa are contrasted with those of diatoms. Diatoms are selected for comparison as the "norm," because their ecophysiology is better understood than it is for other phylogenetic groups, and with few notable exceptions their blooms do not disrupt food-web processes. Also, the spring bloom-diatom bias and whole-community approach (Smayda 1997) have deflected research away from red tide and HAB events which, until recently, have been generally viewed as periodic, rogue blooms of peripheral scientific interest. Harmful algal blooms, however, provide unique opportunities to evaluate entrenched views based on the spring bloom-diatom template. I consider HAB events to be a scientific Rosetta Stone allowing deeper insights into the underlying principles and processes regulating phytoplankton growth in the sea generally and that of the different phylogenetic groups which have diversified the phytoplanktonic life mode. The selection and treatment of topics in this analysis reflect this view.

The need to distinguish between cellular, population, and community growth in bloom dynamics

Phytoplankton growth is classically measured as a whole-community response, with chlorophyll used as an index of abundance against which rate processes are normalized. Community growth measurements have two presumptions: the community's taxonomic elements are physiologically equivalent, and chlorophyll-based estimates of community growth rate adequately measure behavior of the dominant taxa. Although these unlikely assumptions have yet to be evaluated, estimates of community growth rate are of considerable biogeochemical value and essential in analyses of mass balance and nutrient flow. However, they provide limited insight into bloom dynamics. In reality, community growth is only one of three different, concurrent growth modes which characterize phytoplankton population dynamics: cellular growth, population growth, and community growth. In analyses of HAB events, community growth is the least significant of the three growth modes, masking many ecophysiological processes whose resolution is essential for proper understanding of HAB dynamics.

Cellular growth is the active, basic growth unit. It is the outcome of coupled physiological processes under genetic and multifactorial control, particularly irradiance and nutrient levels. It is also influenced by the physiological fitness and adaptability of the individual cells. Cellular genetics sets the maximal potential growth rates ($\mu_{\max}$) of the individual taxa, occurrence of clonal variability, niche requirements, parameter tolerance ranges, etc. The instantaneous cellular growth rates (μ) reflect the multiplicative interactions of the changing habitat conditions, often following a Monod type of kinetic.

Population growth is the environmentally modified outcome of cellular growth, the recruitment term; it is also the bloom unit. Population growth is dependent upon the cellular growth rates, but the factors regulating cellular and population growth rates are not identical. Grazing and advection, for example, influence population growth rate, but are irrelevant to cellular growth rates. Nutrients directly (=physiologically) influence the latter, but their effect on population growth is indirect via increased recruitment and(or) yield-dose relationships which influence population carrying capacity. Population growth rates of a given taxon are always lower than its cellular growth rates.

The *community* is an assemblage of multiple, concurrent species' blooms equal to the total number of taxa present, each in different bloom cycle stages, and each regulated by different combinations of growth factors. Thus, the primary instantaneous regulator of Species A may be grazing; allelochemical inhibition to Species B, etc. With regard to HAB events, and specifically selection and dynamics of the bloom species, it is essential to distinguish among and analyze the three different growth modes which are operative simultaneously. For HAB events, just as all blooms, are the outcome of a continuous, differential regulation of cellular and population growth rates of the multiple species making up the community. Measurements of cellular growth rate and their regulation alone will not explain regulation of population growth rate dynamics, nor vice versa. Measurements of both cellular and population growth rates and their regulation must be undertaken. Restricting analyses to whole-community growth rate approaches, as traditionally done, obliterates resolution of these processes. Community dynamics are a consequence of cellular and population growth—not the determinant of the latter.

Cellular growth

Effects and roles of turbulence—It is often contended that reduced vertical mixing is a major precondition for red tide outbreaks. Supportive field evidence includes the intermittent dinoflagellate blooms during upwelling relaxation periods (Blasco 1977) and shifts from diatom to flagellate-dominated communities in experimental mesocosms during reduced vertical mixing (Parsons et al. 1978). A mean coefficient of eddy diffusivity of 0.4 $cm^2 s^{-1}$ is the suggested transition state between diatom and dinoflagellate predominance (Margalef 1978), with diatoms occurring in regions of high turbulence (2–100 $cm^2 s^{-1}$) and dinoflagellates at lower turbulence (0.02–1 $cm^2 s^{-1}$). Turbulence induced by winds >350 cm s^{-1} disrupts dinoflagellate blooms in the Dead Sea (Pollingher and Zemel 1981), and inhibition of near-surface blooms of *Lingulodinium* (*Gonyaulax*) *polyedra* is predicted to occur at wind speeds >210 cm s^{-1} (Thomas and Gibson 1990*a*). Margalef's classical mandala predicts the selection of HAB species and their blooms based on the interactions between turbulence and nutrient concentrations (Margalef 1978; Margalef et al. 1979).

The magnitude and ratio (=balance) of the two primary parameters of turbulence—shear stress and rates of strain—determine whether cellular growth will be impaired or favored (Thomas and Gibson 1990*a,b*). White (1976) and Pollingher and Zemel (1981) were among the first to demonstrate experimentally that turbulence inhibits dinoflagellate growth rate and can lead to mortality, if sustained or intensified. Turbulence disrupts the cellular clock, mitotic cycle, and alters nucleic acid concentrations (Pollingher and Zemel 1981; Berdalet and Estrada 1993). Motile cells of *L. polyedra* exposed to high shear lose their longitudinal flagellum and ability to swim forward; such cells spin in place (Thomas and Gibson 1990*a*). High shear rates can also induce cellular disintegration (Berdalet and Estrada 1993). Naked flagellates may then shed their scales, a loss possibly detrimental to their cellular protection against allelochemical inhibition (Estep and MacIntyre 1989). Turbulence can therefore negatively influence dinoflagellate blooming by three mechanisms: physical damage, physiological impairment, and behavioral modification. In the latter case, the loss of flagella and increased turbulence can disrupt cellular swarming (=aggregation), phototaxis, and diel vertical migration (i.e. behaviorisms presumably beneficial in bloom formation). Interspecific variability among dinoflagellates in their vulnerability to turbulent shear and strain (Berdalet and Estrada 1993) thus may be a factor in selection of bloom species.

Turbulence, stability, and stratification are usually used interchangeably in relating phytoplankton dynamics to water-mass mixing characteristics. This presumed synonymy may misrepresent actual dynamics, given the diverse cellular, physiological, and behavioral impacts of turbulence. Consider the well-documented observation that red tides often follow a sequence of intense rainfall, runoff, and period of intense irradiance. Triggering of these blooms usually is attributed to increased stratification induced by runoff. However, the water mass invariably is already well stratified (because of seasonal warming). Hence, the proposed reduction in turbulence stimulating the bloom would appear to be needless. *The required precondition of reduced turbulence for a HAB event to occur is already present!* I suggest that the "turbulence parameter" has two ecologically distinct components. First, there is turbulence (=mixing) per se, which through shear stress primarily impacts cellular integrity, physiology, and behavior. It is a biophysical parameter operative primarily at the cellular level. It influences the ability of cells to grow, the survival of seed populations, and impacts those cellular processes and structural features which are vulnerable to biophysical disruption.

Stratification, the second component of the turbulence parameter, is a habitat parameter operative at the population level. Modifiable by winds, heating, or runoff, the associated variations in microhabitat structure and growth conditions influence population growth. Kierstead and Slobodkin (1951) have discussed the importance of "critical patch size," below which the rate of horizontal diffusion will exceed the growth rate and thwart bloom development. Viewed in the context of the rainfall-runoff-increased irradiance paradigm, the lenses of freshened waters formed during this sequence represent zones of improved population growth conditions and reduced dispersal. Growth initially improves, not because of reduced turbulence or increased stratification per se (i.e. as physical growth promoters), but because the boluses of stratified waters are microhabitats of increased nutrient and(or) improved water quality conditions! These microhabitats, with their improved growth conditions and entrained populations, will persist until nutrients are utilized, or the lenses are broken up by diffusion or increased turbulence. The latter may have a dual effect: dispersal of the bloom population and biophysical impairment of the individual cells. In this perspective, turbulence primarily influences cellular processes, whereas stratification, particularly microstratification, primarily influences population dynamics.

Diatoms, in contrast to dinoflagellates and probably flagellates generally, are considerably less sensitive to turbulence and may even be biophysically stimulated by motion. Schöne's (1970) study reveals that although turbulence can break up diatom chains, it may also stimulate cellular growth and induce division synchrony, as in *Skeletonema costatum.* The chlorophyte *Dunaliella tertiolecta, Isochrysis galbana* (chrysophyte), *Heterosigma akashiwo* (raphidophyte), and the diatom *Thalassiosira weissflogii* were unimpaired (chlorophyll based) at agitation rates inhibitory to dinoflagellates (Berdalet and Estrada 1993). Thomas and Gibson (1990*b*) suggested the following phylogenetic tolerance to turbulence: green algae > blue-green algae > diatoms > dinoflagellates. Alignment of blue-green algae as less sensitive than diatoms to turbulence seems incorrect, given bloom dynamics of oceanic *Trichodesmium* spp. and noxious cyanobacterial blooms in the Baltic Sea (Kononen 1992).

Photosynthesis, irradiance, and photoadaptive strategies—Photoadaptive strategies to accommodate fluctuations (natural and auto-induced) in irradiance levels are a major aspect of flagellate ecology, since they have several behavioral traits based on photoreception. Their auto-regulated, aggregational behaviorisms and physically induced patchiness attenuate irradiance, leading to self-shading stresses. This is aggravated during periods of increased population growth, furthering the need for rapid photoadaptive compensation. There are several lines of evidence for such capability. Frequent bloom events following the previously mentioned rainfall-runoff-increased irradiance sequence reveal the capacity for rapid response to high irradiance levels after exposure to reduced irradiance. Chlorophyll *a* levels in dinoflagellates ranging in cell size from 600 to 40,000 μm^3 exceeded diatom levels by 3.3-fold (Hitchcock 1982). Peridinin, the major accessory pigment of most dinoflagellates and highly efficient in energy transfer, responds more rapidly than chlorophyll to increased irradiance levels (Prezelin 1987). Flagellates in situ will swim either through or to pycnoclines in response to photo-induced motility (Edler and Olsson 1985), with frequent attraction to pycnocline microhabitats often characterized by elevated nutrient levels and low irradiance (Holligan 1987). Collectively, these responses reveal the persistent need and ability of HAB dinoflagellates to respond and adapt to low levels of irradiance. This requirement seems paradoxical, given the tendency of dinoflagellates and flagellates generally to predominate seasonally and regionally under conditions of high irradiance, long daylength, and reduced water-column turbidity.

Phytoplankton exposed to low irradiance levels usually increase their chlorophyll levels (Paasche 1968). In most dinoflagellates, this follows one of two photoadaptive strategies: either the size or the number of photosynthetic units (PSU) increases (Prézelin 1987). *Prorocentrum minimum* combines both strategies (Harding et al. 1983). In the strategy of increased PSU size, the increased light-harvesting pigments elevate light-limited photosynthesis to light-saturation rates. In the strategy of increasing the number of photosynthetic units, but keeping their size constant, photosynthetic rates at both light-limiting and saturating intensities increase in proportion to chlorophyll content. The assimilation number in this strategy is similar at both high and low irradiances; in the strategy of increased PSU size, they differ with irradiance. Both strategies enhance photosynthesis at lower irradiances, with maximal cell division rates sometimes maintained, even though the parameters of the photosynthesis vs. irradiance curves vary between strategies (Prézelin 1987). Cells adapted to low irradiance and then exposed to higher intensities, as during the rainfall-runoff-increased irradiance-HAB bloom sequence, will achieve more sustained growth using the strategy that increases PSU number.

The photoadaptive strategies characterizing other phytoplanktonic groups are unresolved (Prézelin 1987). Although similar *P* vs. *I* responses at low irradiance levels characterize the diatom *S. costatum,* the raphidophyte *H. akashiwo,* and the toxic dinoflagellate *Alexandrium tamarense,* their light curves for growth differ significantly (Langdon 1987, 1988). The compensation intensity (1.1 μEinst $m^{-2}s^{-1}$) for *S. costatum* was 35 times lower than that for *A. tamarense*; that for *H. akashiwo* was intermediate (9 μEinst $m^{-2}s^{-1}$). Among the phylogenetic groups, consistent with their responses to turbulence, dinoflagellates seem to have the lowest growth efficiencies and highest compensation intensities, while diatoms are best adapted for growth at low irradiance.

Growth rate—Population expansions result from divisions of individual, free-living cells; palmelloid growth, as in the nuisance species *Phaeocystis pouchetii,* is uncommon. Release of swarmers from palmelloid and epibenthic vegetative stages, dormant morphs, or immigration may also provide "seed" stock initiating population growth, but do not sustain it. Red tide species are commonly assumed to be relatively slow growing, with blooms resulting from low grazing pressure and (or) physical accumulation. Margalef et al. (1979) reasoned that mass balance calculations would show in situ nutrient fluxes are often lower than the supply rates needed

Table 1. Maximum daily growth rates (μ_{max} d^{-1}) in situ and in culture, and frequency of occurrence (%) for various phytoplankton groups exclusive of coccolithophorids. (Source: tables 3–5 of Furnas 1990.)

	≥1.0 (%)	≥1.5 (%)	≥2.0 (%)	≥3.0 (%)	≥3.5 (%)	≥4.0 (%)
Diatoms (n = 58; range 0.2–5.9 d^{-1}):						
	53(91)	50(88)	41(70)	23(40)	15(26)	14(24)
Dinoflagellates (n = 24; range 0.1–2.7 d^{-1}):						
	10(42)	7(29)	3(12)	0	0	0
Other flagellates (n = 22; range 1.3–5.2 d^{-1}):						
	22(100)	17(77)	10(45)	1(5)	1(5)	0

to produce observed HAB populations, and thus their blooms reflect physical accumulations (however, *see* LeCorre et al. 1993). The common occurrence of red tide patches shows this mechanism can indeed lead to spectacular, localized blooms. However, the extensive literature describing blooms clearly shows there are enough exceptions to invalidate this as a general mechanism of HAB bloom formation. The following evaluates the slow growth view.

The early experimental literature generally suggests that daily growth rates of dinoflagellates are $\sim k = 0.3$ d^{-1}, or a generation time of 3 d. Reviews of some of the phytoplankton growth literature (Banse 1982; Furnas 1990; Tang 1995) confirm that diatom growth rates are generally much higher than those for dinoflagellates based on equivalent body mass. Banse concluded that size-based diatom growth rates would exceed dinoflagellate rates by ~3-fold. Table 1 summarizes growth rates for diatoms and flagellates. Maximal rates span a 60-fold range, from $k = 0.1$ to 5.9 d^{-1}. Although these rates were measured in different ways, and undoubtedly include observations at suboptimal growth conditions, the generally superior growth rate of diatoms relative to flagellates is evident. About 40% of the diatom taxa exceeded $k = 3.0$ d^{-1}; only one phytoflagellate (*Micromonas pusilla*) and no dinoflagellates achieved this rate. About 50% of the phytoflagellate taxa achieved rates of $k = \sim 2.0$ d^{-1}, whereas half of the dinoflagellate taxa grew at rates <1.0 d^{-1} (Table 1). These comparisons generally support the dogma that dinoflagellate cellular growth rates are usually lower than those of other phylogenetic groups, including the diverse phytoflagellates against which dinoflagellates often compete. Tang (1995) has attributed this to a lower photosynthetic capacity per unit biomass.

Confronted with the problem of high growth rates (≥1.0 d^{-1}) for some dinoflagellates (excluded from his allometry), Banse (1982) suggested some dinoflagellates may have "unusually high growth rates." Although Tang reported a mean growth rate of 0.65 d^{-1} for 31 dinoflagellate taxa (with a range from 0.16 to 1.46 d^{-1}), eight taxa (25%) exhibited rates ≥1.0 d^{-1} (*see* figure 3 of Tang 1995), and two rates >1.46 d^{-1} excluded by Banse and (apparently) Tang. Contrary to the entrenched view that dinoflagellates are intrinsically slow growers (i.e. with 2–3-d generation times), Smayda (1996) found high growth rates were common among the 898 daily rates determined during the population growth curves for 14 taxa incubated in situ at ambient temperature and irradiance conditions (Table 2). Species-specific maximal growth rates ranged from $k = 0.86$ to 3.54 d^{-1}, i.e. generation times (G) of 7–28 h. All species, excluding *L. polyedra,* were capable of at least 1.0 d^{-1}. Rates for seven species exceeded 2.0 d^{-1}, with *P. minimum* (clone EX)

Table 2. Maximum daily growth rates, μ_{max} (d^{-1}), generation times, G, and frequencies of growth rates (k) ≥ 2.0 d^{-1} and ≥ 1.0 d^{-1} of dinoflagellates during monospecific population experiments (Smayda 1996; Smayda and Karentz in prep.).

Species + clone	μ_{max} (±)	G (h)	≥2.0	≥1.0
Prorocentrum minimum EX	3.54(0.21)	7	3	15
Amphidinium carterae AMPHI 1	2.89(0.08)	8	5	27
Prorocentrum minimum EXUV	2.37(0.12)	10	4	24
Glenodinium halli OBB	2.19(0.11)	11	2	6
Prorocentrum redfieldii N95B	2.17(0.22)	14	1	4
Heterocapsa pygmaea CP	2.12(0.30)	11	2	23
Prorocentrum micans PRED 1	2.04(0.10)	12	1	9
Glenodinium foliaceum GF	1.73(0.14)	14	0	3
Gymnodinium splendens GS	1.53	16	0	3
Gymnodinium nelsoni GSBL	1.43(0.17)	17	0	5
Heterocapsa triquetra Ptri	1.34(0.22)	18	0	9
Scrippsiella trochoidea Ptro	1.25(0.22)	19	0	6
Alexandrium tamarense GGT19	1.03(0.13)	23	0	1
Lingulodinium polyedra Gpd	0.86	28	0	0
Totals			18	138

achieving the maximal rate observed (3.54 d^{-1}); its next highest rate (2.84 d^{-1}) was similar to the maximum for *Amphidinium carterae.* (High growth rates of this species were among those excluded by Banse and Tang.) Of 138 growth rates, about 15% of the total exceeded 1.0 d^{-1}; 18 rates (2%) exceeded 2.0 d^{-1}. Rapid growth rates were usually multiple occurrences. For example, $k = > 2.0\ d^{-1}$ was achieved five times by *A. carterae* and seven times by the two *P. minimum* clones. These taxa and *Heterocapsa pygmaea* exceeded $k = 1.0\ d^{-1}$ more than 20 times—a rate even achieved by *A. tamarense.* These high experimental growth rates contradict the slow, intrinsic growth behavior (i.e. 48–72 h generation times) generally attributed to dinoflagellates. They also challenge the derivative view that physical accumulation of the slow growing dinoflagellates and(or) reduced grazing are the mechanisms most likely triggering their blooms. The results suggest that some dinoflagellates are indeed capable of rapid, though not necessarily sustained, growth and that their HAB outbreaks may follow a period of rapid cellular growth independent of physical and grazing control.

Affinity coefficient, K_s, *and nutrient acquisition*—Red tide blooms occur at both extremes of the nutrient gradient: in oligotrophic and nutrient-enhanced habitats. Best known for their occurrences in nutrient-depleted waters having a steep, shallow thermocline overlying a deeper reservoir of high nutrient levels, harmful blooms in nutrient-enriched waters are increasingly reported (Smayda 1989*a*, 1990). Nutrient availability influences nutrient uptake rates and sets the biomass carrying capacity and, therefore, cellular, population, and community growth rates. At the cellular level, nutrient uptake follows Droop's (1973) cell quota model, which approximates a hyperbolic function when related to external nutrient concentrations, and is empirically described by the Monod equation (Eppley et al. 1969):

$$V = (V_{max}S)/(K_s + S).$$

V is the rate of nutrient uptake, V_{max} the maximal rate of uptake, S the substrate concentration, and K_s the half-saturation, or affinity constant. Uptake in steady state systems depends on the external nutrient concentration; growth (at low external concentrations) depends on the internal (=cellular) nutrient concentration. The specific rate of uptake is the product of the specific growth rate and internal nutrient concentration. These complex kinetics, the in situ occurrences of transient nutrient pulses and patches, and luxury consumption and cellular storage of nutrients in internal pools preclude assessment of whether a given water mass will support a HAB event (if such taxa are present) based on nutrient measurements alone. Neither do whole-community approaches apply; the needed level of resolution requires analyses of cellular processes initially, and subsequently population dynamics. A major stumbling block has been the derivation of predictive, cellular level, nutrient uptake kinetics to quantify the relationship between a given species' cellular growth response and the nutrient field. Two parameters of the nutrient uptake equation have been focused upon in such efforts: the maximum uptake rate, V_{max}, known also as the *velocity coefficient* and, particularly, the half-saturation coefficient, K_s, termed the *affinity coefficient.* These cellular constants have been broadened into specific organismal strategies, with three modes of nutrient uptake strategies proposed: affinity strategy, growth strategy, and storage strategy (Sommer 1989).

Growth-strategy species presumably have elevated maximal uptake rates (V_{max})—an adaptation to ensure high velocity uptake of ambient nutrients and pulsed accretions from grazer excretions, transient physical advections, or other opportunistic encounters. This strategy would seem to be a variant of the surge uptake capacity of phytoplankton (Conway et al. 1976; McCarthy and Goldman 1979), which is probably a commonplace adaptation to the phytoplanktonic life mode. Therefore, for growth-strategy species to qualify as such, they presumably have basal V_{max} rates even greater than surge uptake rates of other species. Given the limited availability of V_{max} data, it is not possible to identify any HAB taxa as using a velocity-adapted growth strategy, if it occurs.

Storage-strategy species build up intracellular storage pools for future growth. In growth-strategy species, such a capability would be advantageous in nutrient-depleted habitats. The data are too limited to assess their representation among HAB taxa, but nutrient storage capability seems to be commonplace (*see below*). This suggests that exceptional storage enhancement mechanisms are the basis of this presumed strategy.

Of the three strategies, affinity adaptation has received the most attention. In this, K_s is considered an index of a species' potential competitive ability at low nutrient concentrations. Because affinity-adapted species have low K_s constants, their selection is hypothesized to be favored in seasons and regions of chronically low nutrient supply rates, where they are expected to outcompete higher K_s species. The corollary is that species with high K_s coefficients will dominate in high nutrient regimes. Margalef (1978) concluded that diatoms collectively have high K_s coefficients and dinoflagellates lower ones. He reasoned that turbulence, elevated nutrients, and high K_s species should co-occur, because turbulence augments nutrient levels leading to prominent spring and upwelling blooms of diatoms. In contrast, stratification, depleted nutrients, and low K_s species are predicted to co-occur.

K_s values for NH_4, NO_3, and PO_4 uptake by dinoflagellates, selected phytoflagellates, and representative diatoms are compared in Table 3. This limited data set ($n = 37$) does not confirm the expectation that diatoms generally have high K_s coefficients and dinoflagellates lower ones. The opposite pattern is evident: dinoflagellate K_s values are not only generally higher than diatom coefficients, but substantially so. In fact, they even exceed macroalgal coefficients (Hanisak 1983). The highest diatom K_s value (5.5 μM NH_4) (*Coscinodiscus wailesii*) contrasts with maximal dinoflagellate coefficients of 27 μM for NH_4 uptake, 29 μM for NO_3, and 6.3 μM for PO_4. When all dinoflagellate data are combined ($n = 22$), K_s exceeds 1.0 μM in 18 cases (82%), is >2.0 μM in 15 cases (68%), and >5.0 μM in seven cases (32%); only 18% of the values are <1.0 μM. Corresponding values for all diatom data ($n = 28$) are 16 (57%), six (18%), and two (7%), with ~43% of the coefficients <1.0 μM. Some of the low (<1.0) K_s values (Table 3) are for growth, these coefficients being considerably lower than those for nutrient

Table 3. Half-saturation constants (K_S, μM) for nitrogen and phosphorus uptake by dinoflagellates, other flagellates, and diatoms.

	NH_4	NO_3	PO_4	Source*
Dinoflagellates				
Alexandrium tamarense	2.0	1.5–2.8	—	13
A. tamarense	—	—	0.40	2
A. tamarense	—	—	1.85	28
Amphidinium carterae	—	—	0.01	3
A. carterae	—	~2.0	—	10
Crypthecodinium microadriaticum	—	—	0.01	3
Gonyaulax polyedra	5.3–5.7	8.6–10.3	—	7
G. polyedra (red tide populations)	7.5–15.0	—	—	9
Gymnodinium bogoriense	20.0	—	3.2	12
Gymnodinium breve	—	—	0.18†	25
Gymnodinium nagasakiense	0.6†	—	0.14†	27
Gymnodinium sanguineum (=*splendens*)				
18°C	1.1	3.8	—	7
18°C	—	1.02†	—	22
25°C	—	6.55†	—	22
Heterocapsa triquetra	—	—	3.1	4
Peridinium cinctum	27.0	29.0	0.18–0.31	21
Peridinium sp.	3.6	—	—	24
Peridinium sp.	—	—	6.3	11
Prorocentrum minimum	—	—	1.96	2
Pyrocystis noctiluca	—	—	1.7–2.8	18
P. noctiluca	—	—	0.15†	19
Raphidophytes, others				
Chattonella antiqua	2.2	2.8	—	14
C. antiqua	—	3.0	1.9	16
C. antiqua	0.23†	0.65†	0.25†	15
C. antiqua	—	0.87†	0.29†	16
Dunaliella tertiolecta	0.1	1.4	0.73	4, 7
Dunaliella sp. 18°C	—	0.23†	—	22
Dunaliella sp. 25°C	—	0.95†	—	22
Heterosigma akashiwo	2.0–2.3	2.0–2.5	1.0–1.98	23
Isochrysis galbana	—	0.1	—	7
Monochrysis lutheri	0.5	0.6	—	7
Phaeocystis pouchetii				
colonies	—	—	3.08	26
single cells	—	—	0.31	26
Diatoms				
Asterionellopsis glacialis	0.6–1.5	0.7–1.3	—	7
A. glacialis	—	0.9–1.1	—	20
Chaetoceros gracilis	0.3–0.5	0.1–0.3	—	7
C. gracilis	—	—	0.12	22
Coscinodiscus lineatus	1.2–2.8	2.4–2.8	—	7
Coscinodiscus wailesii	4.3–5.5	2.1–5.1	—	7
Ditylum brightwelli	—	2.0	—	5
D. brightwelli	1.1	0.6	—	7
Fragilaria pinnata	—	0.6–1.5	—	1
Leptocylindrus danicus	0.5–3.4	1.2–1.3	—	7
Rhizosolenia stolterfothii	0.5	1.7	—	7
Skeletonema costatum	0.8–3.6	0.4–0.5	—	7
S. costatum	—	2.1	—	20
Thalassiosira oceanica	0.4	0.3–0.7	—	7
T. oceanica	0.22–0.66	0.5–1.0	—	6
T. oceanica	—	—	0.6–0.7	17
Thalassiosira pseudonana	—	1.87	—	1
Thalassiosira weissflogii	—	—	1.72	8

* 1—Carpenter and Guillard 1971; 2—Cembella et al. 1984; 3—Deane and O'Brien 1981; 4—Doremus 1982; 5—Eppley and Coatsworth 1968; 6—Eppley and Renger 1974; 7—Eppley et al. 1969; 8—Fuhs et al. 1972; 9—Harrison 1976; 10—Hersey and Swift 1976; 11—Lehman 1976; 12—Lieberman et al. 1994; 13—MacIsaac et al. 1979; 14—Nakamura 1985*a*; 15—Nakamura 1985*b*; 16—Nakamura and Watanabe 1983; 17—Perry 1976; 18—Rivkin and Swift 1982; 19—Rivkin and Swift 1985; 20—Romeo and Fisher 1982; 21—Sherr et al. 1982; 22—Thomas and Dodson 1974; 23—Tomas 1979; 24—van Rijn et al. 1987; 25—Vargo and Howard-Shamblott 1990; 26—Veldhuis et al. 1991; 27—Yamaguchi 1994; 28—Yamamoto and Tarutani 1996.
† For growth.

uptake. The K_s ratios of uptake-to-growth for these species are: *D. tertiolecta* (~5 : 1, NO_3); *Gymnodinium sanguineum* (~4 : 1, NO_3); *Pyrocystis noctiluca* (~13 : 1, PO_4); *Chattonella antiqua* (~9 : 1, NH_4; ~4 : 1, NO_3; ~7 : 1, PO_4). These normalized values strengthen the observed trend which shows that higher uptake coefficients characterize flagellates relative to diatoms, as do Doucette and Harrison's (1990) K_s data for iron uptake. K_s for iron uptake by *G. sanguineum* exceeded by >2-fold the coefficients for six diatoms and a coccolithophorid. High K_s coefficients (≥ 2.0 μM) also characterize the harmful raphidophytes, *C. antiqua* and *H. akashiwo,* and the nuisance species, *P. pouchetii,* which exceed coefficients for benign phytoflagellates (Table 3). This general occurrence of high K_s values among HAB taxa is notable.

The K_s data and their phylogenetic patterns suggest a paradox: collectively, HAB species lack the expected high affinity for nutrient uptake thought to be essential for their frequent bloom occurrences in nutrient-depleted waters. The collective high affinity of diatoms adds to this paradox. This high affinity is seemingly a needless adaptation, since diatoms thrive in enriched seas. Based on limnetic dinoflagellate blooms, Lieberman et al. (1994) suggested that K_s-based conclusions regarding competition strategies may be valid in mixed habitats, but in stratified environments—the preferred habitat of HAB taxa—both K_s and V_{max} have poor predictive power. In stratified waters, they argued, low K_s coefficients and high V_{max} may not be significantly advantageous, because other factors determine competitive outcome. Use of K_s differences only, whether in arriving at the above paradox or to predict competitive success leading to selection and growth of bloom dominants is also problematic for other reasons. The covariance between K_s and V_{max} (Healey 1980; Aksnes and Egge 1991) and the occurrence of surge (=high velocity) uptake (Conway et al. 1976; McCarthy and Goldman 1979) are some physiological features compromising such use. There are also ecological constraints. Healey (1980) has suggested that the ratio of $V_{max} : K_s$ (i.e. the slope of the Michaelis-Menton equation at lower nutrient concentrations) is a more appropriate affinity constant. This ratio, thought to represent the sum of the total affinity at all nutrient uptake sites (=cellular affinity), has been likened to an "ion clearance" or "filtration affinity" measurement (Aksnes and Egge 1991), in contrast to the site-specific affinity indicated by K_s. In terms of competitive advantage, higher ratios indicate higher rates of nutrient uptake at lower concentrations (Healey 1980). Competitive advantage can result from either an increase in V_{max} or decrease in K_s, with four velocity-affinity combinations potentially represented among the phytoplankton: species whose V_{max}, K_s = high velocity, high affinity (++); those with low velocity, high affinity (−+); those with high velocity, low affinity (+−); those with low velocity, low affinity (−−). The extent to which these variants of affinity adaptation are represented among HAB taxa and phytoplankton generally remains to be established.

Correlates of a high K_s

Although interactive K_s and V_{max} kinetics determine cellular responses to available nutrients and influence interspecific competition and subsequent population growth, the high K_s coefficients characteristic of HAB taxa suggest strong selection pressure has occurred for compensatory mechanisms to minimize this competitive disadvantage. Admittedly, it is not clear from known evolutionary patterns of the phytoplankton whether the observed K_s trends are primitive traits or derived characteristics. However, I suggest flagellates generally have evolved four major adaptations to offset the ecological disadvantages of a high K_s:

1. Nutrient-retrieval migrations.
2. Mixotrophic nutritional tendency.
3. Allelochemically enhanced interspecific competition.
4. Allelopathic antipredation defense mechanisms.

Nutrient retrieval—Eppley and Harrison (1975) sketched the basic mechanism of a vertical nutrient-retrieval strategy: diel migration of nutrient-depleted dinoflagellates into NO_3-rich subsurface layers would access nutrients needed to outcompete diatoms and favor red tide blooms. The advantages of a nutrient-retrieval strategy are obvious. Consider the extreme condition of the dual stress of nitrogen limitation and the progressively reduced N-uptake affinity which accompany seasonal warming (Thomas and Dodson 1974). That temperature influences K_s is shown by the 6- and 3-fold increases in affinity for NO_3 by *G. sanguineum* and *Dunaliella* sp., respectively, between 18° and 25°C (Table 3; *see also* Eppley et al. 1969). Nutrient-retrieval migrations into cooler, deeper layers would both increase affinity, i.e. lower K_s and increase $V_{max} : K_s$ (magnitude depends on the degree of vertical thermal change), and facilitate uptake by the cells now exposed to elevated NO_3 concentrations. At the organismal (=cellular) level, the benefits of this strategy may include improved survival capacity and retention within the community, with delay of resting stage formation. These benefits are not dependent on bloom occurrences. The population would benefit from enhanced cellular competitive ability and growth rate. Migratory, nutrient-retrieval strategies are suggested to provide much greater competitive advantage than low cellular K_s and high V_{max} coefficients (Lieberman et al. 1994). The extent to which nutrient-retrieval strategies are a factor in pycnocline blooms of flagellates (*see* Holligan 1987; Lindahl 1986) is unresolved.

Nutrient retrieval involves numerous behavioral, physiological, cellular, population dynamics, and habitat features, including the need for dark uptake capability, synchronous diel variations in nitrate reductase activity, ecologically suitable time-courses of adaptation, etc. Experimental evidence that dinoflagellates have a nutrient-retrieval strategy is growing; the observations of Cullen and Horrigan (1981), Cullen (1985), and Cullen et al. (1985) are summarized here. The photic regulation of diel migrations by nutrient-sufficient cells is well documented; but for nitrogen-deficient cells the vertical nitrogen field overrides such regulation. Daylight populations of nutrient-deficient *G. sanguineum,* for example, accumulate near the depth at which irradiance saturates photosynthesis, which is often close to the nitracline. At night, migration below the nitracline results in dark uptake of NO_3, and although there is considerable interspecific variability in this capability (*see* Paasche et al. 1984), reductions in nutrient levels within the enriched layer have been measured (*see also* Olsson and Granéli 1991). Thus, dinoflagellates exhibit two of the basic prerequisites for an operative nutrient-retrieval strategy: directed migration toward increased concentrations of the deficient nutrient, and induced dark uptake. This strategy is not restricted to dinoflagellates. Nutrient-retrieval migrations of phosphate-deficient cells, with dark uptake capability, are undertaken by the harmful raphidophytes *C. antiqua* and *H. akashiwo* (Nakamura and Watanabe 1983; Watanabe et al. 1988, 1990). Even though N-sufficient, synchronous uptake of nitrogen accompanied dark PO_4 uptake! Hence, nutrient-retrieval migrations to remedy nutrient deficiency may also increase access to, and uptake of nonlimiting nutrients; that is, nutrient-retrieval migrations may also function as a "nutrient pump."

The cellular and population benefits of nutrient retrieval require metabolic coupling between daylight photosynthesis and nocturnal nutrient uptake. The following diel integration of migration, energy storage in the light, with nutrient assimilation and accumulation in the dark, has been proposed for N-deficient dinoflagellates (Cullen 1985; Cullen et al. 1985). Migration into the N-deficient euphotic zone shunts photosynthate into carbohydrate pathways and cellular accumulation. Dinoflagellates intrinsically have higher carbohydrate content (~2.5-fold greater) and metabolism than diatoms, irrespective of whether they have cellulosic thecal plates (Hitchcock 1982). These carbohydrate reserves stimulate subsequent dark assimilation of nitrogen at depth which, upon migration back into the euphotic zone, results in protein synthesis and cellular and population growth. P-deficient *C. antiqua,* unlike many microalgae, does not store polyphosphate (Nakamura and Watanabe 1983). During nutrient retrieval, dark-assimilated PO_4 is stored in internal, inorganic phosphorus pools, with photophosphorylated incorporation into growth pathways occurring upon migration into the euphotic zone. The nuisance species, *P. pouchetii,* exhibits a remarkable strategy and mechanism of nutrient storage and retrieval (Lancelot and Mathot 1985; Veldhuis and Admiraal 1985). Photosynthetic products are secreted as carbohydrates and stored within the mucilaginous colony envelope, particularly during nutrient limitation. Their reassimilation during the dark period together with that of intracellular reserve products provides the cellular carbon and energetic needs for maintenance and, given an adequate nitrogen supply, protein synthesis.

Although the potential for a nutrient-retrieval strategy is clearly present, the extent to which natural populations utilize this strategy is uncertain. It has yet to be shown whether the time constants of the various behavioral and physiological adaptations required in nutrient-retrieval strategies are attainable by in situ populations. Multifactorial regulation of HAB taxa and dynamics also impact the success of this strategy. Most likely, flagellate nutrient-retrieval strategies probably occur in variable formats. In fact, a nutrient-retrieval strategy may be an intrinsic aspect of the phytoplanktonic life mode! Consider diatoms which, when nutrient deficient, increase their sinking rates until exposed to elevated nutrient levels; their sinking rate then decreases and enhanced nutrient uptake occurs (*see* Smayda 1970). The break up of diatom chains during nutrient deficiency prolongs retention within the euphotic zone, facilitating the search for nutrient-enriched microzones. These analogous migrational-gravitational responses would appear to maximize encounters with increased nutrient deficiency. Another diatom nutrient-retrieval strategy more closely analogous to flagellate behavior occurs via passive, upward migrations of large *Rhizosolenia* mats which transport NO_3 from subnitracline layers in oceanic habitats (Villareal et al. 1993). Uptake of NO_3 at depth leads to positive buoyancy and ascension into surface waters, followed by sinking of nutrient-depleted mats to depth, NO_3 retrieval, and ascension once again. Smaller diatoms are incapable of this particular nutrient-retrieval mechanism; their morphometric constraints restrict their nutrient-retrieval strategy to the more passive, aforementioned gravitational mechanisms.

The ecologically significant aspect of nutrient retrieval is not the specific cellular and behavioral mechanisms used to access increased nutrients during deprivation (=deficiency), but that nutrients are taken up when encountered. Flagellates achieve this through a "swim" strategy; diatoms through a "sink" strategy. Flagellates, through their motility and nutrient-retrieval migrations, can potentially access nutrients thoughout the water column, whereas diatoms are less efficient in this regard. The greater tolerance of diatoms to turbulence and associated vertical dispersal increases access both to physically induced nutrient pulsing and residual water-column nutrients. Flagellates and diatoms therefore seem to have analogous strategies of nutrient retrieval during deficiency. This re-enforces the notion that nutrient-retrieval mechanisms are a generally adaptive phytoplanktonic strategy.

Mixotrophic nutrition—Utilization of dissolved organic and particulate nutrients would help offset the ecological disadvantages of a high K_s in an oligotrophic niche. The high nutritional diversity among flagellates generally, in contrast to the limited heterotrophy of diatoms, suggests such adaptations occur (Gaines and Elbrächter 1987; Schnepf and Elbrächter 1992). About half of all dinoflagellate taxa are obligate heterotrophs; some have evolved elaborate phagotrophic-feeding mechanisms activated by chemodetection of prey. *Dinophysis rotundata,* for example, pierces its prey with a tubular peduncle, through which it aspirates their cellular contents (Hansen 1991). Some species use swimming motions to envelope an extruded feeding veil (=*pallium*) around captured diatom and other prey for extracellular digestion (Gaines and Taylor 1984). *Noctiluca,* a voracious, indiscriminate predator, is the most prominent HAB taxon exhibiting such obligate phagotrophy (Kimor 1979). The remarkable, ichthyotoxic coastal dinoflagellate, *Pfiesteria piscicida,* characterized by a triphasic life cycle of at least 19 different flagellate, amoeboid, and cyst stages, and capable of at least three different nutritional modes, is an "ambush predator" activated by secretions from live fish (Burkholder et al. 1995; Mallin et al. 1995).

Almost all HAB taxa are obligate phototrophs, however; their use of supplemental nutritional modes is thus of great interest. Phototrophic flagellates collectively exhibit two primary nutrient supplement strategies: uptake of dissolved organic substances (=osmotrophy) and ingestion of particulate matter (=mixo-phagotrophy). Osmotrophic uptake data are rare, although there is general experience from laboratory cultivation that various dissolved organic compounds enhance growth and(or) survival of dinoflagellates (Iwasaki 1979; Gaines and Elbrächter 1987). More quantitative evidence links uptake of exogenous organic molecules with increased toxicity of *Gymnodinium breve* (Shimizu et al. 1995). Among phytoflagellates, low irradiance (not darkness) stimulated uptake of dissolved organic carbon in three species of the harmful prymnesiophyte genus *Chrysochromulina* (Pintner and Provasoli 1968). Nonetheless, nutritional use of dissolved organic substances seems to be a relatively ineffective adaptation to a high K_s, partly because of limited in situ availability and flux of dissolved organic substrate.

Mixo-phagotrophy utilizes particulate nitrogen and phosphorus sources when inorganic concentrations are limiting or in short supply. Growing evidence suggests that this mode of nutritional supplementation is common among dinoflagellates (Gaines and Elbrächter 1987) and other flagellates. Species of *Chrysochromulina*, responsible for an epidemic of toxic blooms in Scandinavian waters (Eikrem and Throndsen 1993; Granéli et al. 1993), ingest bacteria and small flagellates during P limitation (Jones et al. 1993; Nygaard and Tobiesen 1993). Bactivorous feeding by 10 flagellate species, including the harmful taxa *A. tamarense* and *H. akashiwo*, was an important source of phosphorus in vitro during blooms of *Prymnesium parvum* and *Chrysochromulina polylepis* (Nygaard and Tobiesen 1993). The rates of bacterial ingestion and accumulation of phosphorus are impressive: maximal ingestion rates for the toxic flagellates ranged from 57 bacteria cell^{-1} h^{-1} (*C. polylepis*) to 113 h^{-1} (*H. akashiwo*) to 706 h^{-1} (*A. tamarense*). Ingestion of the P-rich bacteria, which increased with phosphate limitation, provided 3.5- to ~10-fold more phosphorus than required to maintain the equilibrium population growth rates of $k = 0.3$ d^{-1} in continuous culture.

Mixo-phagotrophy is clearly a strategy utilized by high K_s taxa. It is apparently heightened during P deficiency and is found among all phylogenetic groups having HAB taxa (excluding diatoms). Murray (1995) hypothesized that phytoplankton secrete dissolved organic matter purposely to achieve antiviral protection. In this, the organic exudates stimulate growth of bacteria and heterotrophic flagellates. Ingestion of viruses by the latter reduces the probability of viral infection of phytoplankton cells, thought to be a major cause of their mortality. I suggest a related, auto-regulated "bacterial farming" strategy may be among the nutritional augmentation strategies used by mixo-phagotrophic flagellates. Their secretion of carbon is expected to stimulate bacterial growth within the phycosphere (i.e. not the cellularly attached bacteria) leading to their phagotrophic ingestion of the proliferating bacteria. This bacterial farming strategy would have multiple advantages. Ingestion of farmed bacteria would provide nutrients, as reported by Nygaard and Tobiesen (1993); allow direct predation on, and population control of, bacterial predators and, through this, indirectly control viral particles. It may not be coincidental that increased toxicity accompanies P deficiency in at least two harmful taxa, *C. polylepis* (Edvardsen et al. 1990) and *A. tamarense* (Boyer et al. 1985), capable of bactivory during P deficiency. Estep and MacIntyre (1989) also propose another novel mechanism of supplemental nutrient acquisition: *dasmotrophy*, a mechanism of "remote parasitism." Based on *Chrysochromulina* physiology, they propose that it secretes exudates which increase the cellular permeability of prey (=other phytoplankton) resulting in partial leakage of cellular material which is then utilized by *Chrysochromulina*. In this strategy, the role of the "toxin" is to induce cellular leakage, not mortality.

These limited observations suggest mixo-phagotrophic supplementation by photosynthetic HAB taxa and among flagellate taxa generally has evolved as an adaptation to high K_s coefficients. The co-occurrence of obligate phototrophy, osmotrophy, and mixo-phagotrophy in harmful *C. polylepis*, for example, and variations along this nutritional gradient among congeneric species, show the range of nutritional adaptations that can occur. I suggest that these are an important ecophysiological feature of HAB taxa.

Allelochemically enhanced interspecific competition—Allelochemical will refer to chemically regulated interspecific competition, and allelopathic to antipredation regulation. Phycotoxins (i.e. saxitoxin, brevetoxin, domoic acid, okadaic acid) are distinguished from allelopathic and allelochemical secondary metabolites because of probable differences in their biosynthesis, chemical nature, and specific effects. Their ecophysiological consequences may overlap, however; phycotoxins may mask co-occurring allelochemical and allelopathic metabolites, and the latter may mimic phycotoxins. Phycotoxins and secondary metabolites produced by the same species of certain dinoflagellates and raphidophytes have similar antimicrobial activity (e.g. Nagai et al. 1990). A major difference between phycotoxins and allelo-metabolites is that phycotoxins can be vectored through the food web, accompanied by broad-based trophodynamic effects, whereas allelochemicals are usually directly targeted (Smayda 1992).

Experimental evidence suggests five types of allelochemical relationships potentially influence in situ interspecific competition: mutually advantageous interactions; mutually exclusive interactions; selective inhibition; selective stimulation; and indifference (i.e. without effect). Allelochemic mechanisms seem to function primarily via secretions of bioactive metabolites, although a novel, recently described mechanism is "contact immobilization" which leads to cell lysis of *Gyrodinium instriatum* when grown together with a *Heterocapsa* sp. (Uchida et al. 1995). Estep and MacIntyre (1989) suggested that the allelochemic mechanism of dasmotrophy has the dual advantage of providing *C. polylepis* with nutrients and inhibiting growth of competing species. Some allelochemic mode examples:

- Mutually advantageous interactions characterized bi-algal pairings of the HAB taxa *C. antiqua-Chattonella* cf. *akashiwo*, *C. antiqua-Rhodomonas ovalis* (Iwasaki 1979), and among various ciguatoxic *Prorocentrum* spp. (Bomber 1990). Mutually exclusive interactions occurred between various *Chattonella* spp. and *Alexandrium catenella* (Iwasaki

1979) and between ciguatoxic *Prorocentrum concavum* and *Gambierdiscus toxicus* (Bomber 1990).

- Selective, interspecific inhibition among dinoflagellates and dinoflagellate inhibition of flagellates and(or) diatoms are particularly well documented. Among dinoflagellates, *P. minimum* inhibited *Prorocentrum micans* and *A. catenella* inhibited *P. micans* (Iwasaki 1979). Dinoflagellate taxa which inhibit nondinoflagellate taxa include *A. catenella* (Iwasaki 1979), *P. micans* (Uchida 1977), *Gyrodinium aureolum* (Arzul et al. 1995; Gentien and Arzul 1990), *G. breve* (Freeberg et al. 1979), and *Alexandrium lusitanicum* (Blanco and Campos 1988). The raphidophyte, *H. akashiwo*, is antagonistic against the diatom *S. costatum* (Pratt 1966; Honjo 1993) but stimulates *P. minimum* (Honjo 1992). In contrast, media conditioned by *H. akashiwo* in low abundance stimulated *S. costatum* (Pratt 1966), whereas stationary phase *Skeletonema* inhibits *C. antiqua* and *Chattonella marina* (Imada et al. 1991).
- Selective allelochemic stimulation (excluding auxotrophic use of secreted vitamins) has also been documented. "Luxuriant growth" of *S. costatum* stimulated "most red tide flagellates," including *P. minimum, P. micans, Chattonella* spp., and *A. catenella* (Iwasaki 1979). Related information on allelochemic effects can be found in the review of Maestrini and Bonin (1981).
- Species can also be influenced by their own allelochemic secretions, with three general responses having been recorded: auto-stimulation; auto-inhibition; and indifference. Exudates of *Chattonella* spp. are auto-stimulatory; those secreted by *P. minimum* are not (Iwasaki 1979). Auto-stimulation would seem to be competitively awkward, if re-assimilation of the exudate in some form is required, followed by subsequent biochemical transformation, utilization, and end-product secretion back into the environment. Alternatively, auto-stimulation might result from trace metal detoxication by secreted complexation compounds (*see section on behavior*), from other types of habitat improvement resulting from physical-chemistry effects, or from the mixo-phagotrophic strategy of bacterial farming proposed earlier.
- Auto-inhibition has been well-documented for *Chattonella* spp., *A. catenella, P. micans,* and *S. costatum* (Iwasaki 1979; Imada et al. 1991; Blanchemain et al. 1994). Auto-inhibition of *G. sanguineum* begins during the late exponential growth phase; competing dinoflagellates were not inhibited until exposed to more potent filtrates produced during stationary phase (Kayser 1979). Auto-inhibition may be attributable to a physical-chemical influence on buffering capacity (Blanchemain et al. 1994). Auto-inhibition and increased phycotoxin production during stationary growth are puzzling aspects of allelochemical strategies.

Collectively, this evidence reveals allelochemic substances have multiple effects: they influence growth rate and induce death-lysis; affect yield (=carrying capacity), which influences cellular abundance; influence population growth curves, notably duration of lag phases; and probably also influence survival and life cycle stages. In contrast, the allelochemic potential of diatoms seems to be less well developed than among flagellates (Smayda 1963; Maestrini and Bonin 1981), notwithstanding a recent report (Subba Rao et al. 1995) otherwise. Despite this evidence for a potentially high allelochemic capacity among flagellates, its relevance to in situ dynamics is uncertain. The frequent co-occurrences of HAB blooms and dead fish, and shellfish-borne and fish-borne (ciguatera) toxicities have fostered the anecdotal notion that such blooms develop because the bloom species are phycotoxic or allelochemically active. However, there is no clear field evidence that HAB outbreaks (i.e. *not the consequences*) indeed depend upon phycotoxins or secondary metabolites. Since most red tide species are benign (Sournia 1995) and harmful blooms of species lacking phycotoxins are common, their blooms and any associated inimical effects must have other explanations. Pratt's (1966) classical study on in vitro inhibition of *S. costatum* by *H. akashiwo,* and derivative studies (Stuart 1972; Maestrini and Bonin 1981; Tomas 1980; Honjo 1993) illustrate the problem of extrapolation to natural populations. The interannual and annual variations in summer blooms of *Skeletonema* in Narragansett Bay that Pratt attributed to allelochemical inhibition by *Heterosigma,* and as observed in bi-algal cultures, were subsequently shown to be either a short-lived effect in situ (Stuart 1972), or not expressed (Tomas 1980). The *Heterosigma-Skeletonema* exclusionary blooms have since been linked to differences in nitrogen metabolism and top-down trophic effects, within which a combination of allelochemic and allelopathic effects is embedded (French and Smayda 1995). Until studies are carried out with pure phycotoxins and allelochemic metabolites, or there is definitive chemical characterization of the active metabolites, and these are unequivocably linked to a particular regulatory process, allelochemical involvement in HAB events remains speculative.

Allelopathic defense against predation—First-feeding and late-larval stages of many fish species nutritionally depend upon dinoflagellates. Larvae of 15 of 20 fish species in natural populations begin to feed on dinoflagellates while still in yolk sac stage (Last 1980). First-feeding northern anchovy, *Engraulis mordax,* ingested four dinoflagellate species offered as prey, but rejected diatoms and naked flagellates (Scura and Jerde 1977). Thus, there is selective pressure for allelopathic defense against fish predation. Experimental results indicate that some dinoflagellates and other flagellates have this capability (*see* Smayda 1992). Examples include ingestion of only 6–11 cells of phycotoxic *A. tamarense* was lethal to first-feeding sea bream (*Pagrus major*) (White et al. 1989), and ingestion of only one cell of a more toxic strain was lethal to larval capelin (*Mallotus villolus*) and herring (*Clupea harengus harengus*) (Gosselin et al. 1989). The ichthyotoxins produced by flagellates are a diverse complex of chemical structures having different physical and toxicological properties and modes of action. They may be water- or lipid-soluble; potent as secreted exotoxins, or upon contact, and have cytolytic, hemolytic, or neurotoxic activity (Shimizu 1989; Yasumoto 1989). Gill filaments rather than prey ingestion often function as the primary toxin uptake sites, with asphyxiation resulting from interference with osmoregulation and gas exchange (Endo et al. 1985; Onoue and Nozawa 1989; Toyoshima et al. 1989). Physiological and behavioral dysfunction of herring, pollock, winter flounder, Atlantic salmon, and cod began within 5 min after toxin injection, leading to death (White 1984). Juvenile sea bream died within 4–10 min of exposure to the neurotoxic fraction from three red tide species (Onoue and Nozawa 1989).

Although direct demonstration of allelopathy in situ during HAB events is lacking, there is strong, indirect evidence. The most vivid manifestations of allelopathy are ichthyotoxic blooms, including those of *G. breve* renowned for its massive fish kills in the Gulf of Mexico. The 1988 bloom of *C. polylepis* in southern Scandinavian waters killed off much of 0-yr cod, whiting, pollock, and saithe (Dundas et al. 1989). Blooms of *C. antiqua, C. marina, Chattonella subsala,* and *H. akashiwo* have chronically devastated fish farms in the Seto Inland Sea (Okaichi 1989). Allelopathic induction of fish avoidance responses is also known. During noxious *G. aureolum* blooms, adult fish seek refuge in bottom waters; larval stages undertake exit migrations and return following bloom demise (Potts and Edwards 1987). Similar emigrations of adult stocks occur during dense blooms of the cyanobacterium *Nodularia spumigena* (Lenanton et al. 1985). The enigma of such apparent in situ allelopathy against fish, and a remarkable feature of ichthyotoxins produced by dinoflagellates, is that the toxic principle and its potent derivatives are frequently vectored through the food web. This often results in indiscriminant die-offs of predators several trophic levels removed from the toxic flagellate (*see* Smayda 1992; White 1977) in addition to any directly targeted, antipredator effects.

As in fish predation, many flagellate taxa are extensively grazed upon, often preferentially, by zooplankton and microbial loop components. Space restrictions allow only representative examples from the literature considered in greater detail elsewhere (Smayda 1992; Turner and Tester 1997). Egg production of *Acartia tonsa* and *Pseudocalanus parvus* was 10-fold greater when fed *L. polyedra* than a diatom diet of *Leptocylindrus danicus* or *Chaetoceros curvisetus* (Morey-Gaines 1979). *Calanus helgolandicus* attained maturity more quickly when fed *G. sanguineum* than *S. costatum* and *Lauderia borealis* (Paffenhöfer 1970). Zooplankton grazing of dinoflagellates in situ can be extensive, as observed during a toxic *A. tamarense* bloom (Watras et al. 1985). Because dinoflagellate caloric values are 3–5.5-fold greater than those of diatoms over a size range of 600–40,000 μm^3 (Hitchcock 1982), prey selected based on size would yield about three to five times more calories when the ingested cell is a dinoflagellate than a diatom of equivalent size.

Some dinoflagellates and other flagellates exhibit allelopathic defense against copepod predation. Their allelopathic metabolites may cause death or physiologically impair, stun, or repel the immediate grazer. Some examples: natural populations of migratory cladoceran, copepod, and larvacean species avoided dense, subsurface layer patches of *G. sanguineum* and exhibited feeding inhibition (Fiedler 1982). Filtration rates of the five dominant copepod species were 2–6-fold lower in "patch" water. A *Gymnodinium flavum* bloom suppressed grazing of *Calanus pacificus*; its filtration rates were then 30-fold lower than when fed a small diatom (Huntley 1982). In vitro experiments confirm that despite active copepod grazing on dinoflagellates allowing growth and reproduction, allelopathy against zooplankton predation occurs. Of 21 flagellate species and clones tested as prey for four copepod species, nine were rejected; seven produced phycotoxins (Huntley et al. 1986; Uye and Takamatsu 1990). The nontoxic *Scrippsiella trochoidea* was also rejected, so allelopathy is obviously not the only determinant of prey suitability.

Significant behavioral and physiological modifications can accompany ingestion of cells which are allelopathic, but not lethal (Huntley et al. 1986; Sykes and Huntley 1987). Ingestion of *G. breve* by *C. pacificus* resulted in regurgitation, increased heartbeat (>400 bpm), erratic mouthpart movements, twitching, and loss of motor control, followed by 100% mortality after 3 d. These abnormal physiological and behavioral responses were reversible; normal feeding resumed on nontoxic *Gyrodinium resplendens.* [Some copepods which co-occur with *G. breve* can graze on it without apparent ill-effects (*see* Turner and Tester 1997).] Ichthyotoxic *P. piscicida* and diatoms are equally nutritious to *A. tonsa,* but ingestion of *Pfiesteria* leads to erratic and impaired swimming behavior (Mallin et al. 1995). Cellular ingestion is not the only allelopathic routing. Some dinoflagellates secrete exudates inhibitory to copepods and a tintinnid (*Favella ehrenbergii*) (Hansen 1989; Huntley et al. 1986; Uye and Takamatsu 1990). Five ichthyotoxic raphidophycean species were either rejected by copepods or supported very low egg production rates (Uye and Takamatsu 1990). *H. akashiwo* is a remarkably broad-spectrum antagonist against microzooplankton, copepods, benthic larvae, fish, and a poor food source for many benthic invertebrates (Tomas and Deason 1981). Ichthyotoxic flagellates (*G. breve, Chattonella* spp., *H. akashiwo*) can also be allelopathic against copepods.

There is considerable evidence, therefore, that HAB flagellates have a diverse allelopathy against a broad spectrum of microbial, zooplanktonic, nektonic, and benthic taxa and of potential significance in natural population dynamics. Poulet et al. (1994) have generalized from experimental evidence that diatoms have evolved an allelopathic, antipredation strategy to reduce copepod population levels by inhibiting their reproductive success. The preponderance of available evidence suggests, however, that allelopathy is more widely a flagellate trait than a diatom trait. The high allelopathic potential of HAB taxa is consistent with their predominance in stratified waters where metabolites are expected to be more effective than in the well-mixed waters preferred by diatoms. This facilitates both detection of prey and allelochemical countermeasures. Margalef (1978) suggested grazing pressure tends to be indiscriminate on nonmotile cells and in turbulent water, whereas flagellates in low turbulence systems are more easily tracked and captured by grazers. Allelopathic strategies, however, may be a mixed blessing. Because excretion by grazers is an important source of recycled nutrients, allelopathic success disrupts this supply of nutrients. The nutrient-retrieval and mixo-phagotrophic strategies of HAB flagellates would appear to partially resolve this, with allelopathy providing antipredation protection and allelochemic metabolites helping in interspecific competition. This combination of adaptations to elevated K_s coefficients would be beneficial at all growth modes, balancing off cellular survival needs with those of population dynamics and community status.

Behavior

Dinoflagellates when nonmotile (=dead; narcotized) sink at size-dependent rates similar to those of diatoms (Kamykowski et al. 1992). Species >25 μm in cell size have a swim : sink ratio of 7.6 : 1 which significantly over-compensates gravitational sinking. Swimming, which has low energetic costs (Raven and Richardson 1984), allows several distinctive flagellate behaviorisms. Collectively, flagellates use a "swim" strategy; diatoms a "sink" strategy. Differences in the degree of internal vs. external control of bloom dynamics may be one consequence of these two basic phytoplanktonic strategies. Phytoplankton, generally, are considered to have little internal control over community organization and bloom events, unlike terrestrial floral communities, because of frequent physical disturbances (Margalef 1978). However, the association of flagellate blooms with water-mass stratification and of diatom blooms with more mixed waters suggests the bloom dynamics of flagellate-dominated communities are under greater, relative internal control (through their behavioral adaptations) than those dominated by diatoms. If true, a paradox emerges: diatom blooms and successional events, seemingly under greater external regulation, are more predictable than those of the highly unpredictable, and presumably more auto-regulated flagellate communities. The motility-dependent behaviorisms of flagellates that may facilitate this greater internal control are phototaxis, vertical migration, pattern swimming, and aggregation.

Phototaxis as a general mechanism provides directed behavior, such as depth-keeping, environmental surveillence (=habitat information gathering) leading to microhabitat relocation and environmental coupling between irradiance and nutrients (i.e. the two fundamental energy sources of phytoplankton growth). Swimming behavior also makes possible the other behaviorisms dependent upon motility.

Vertical migration allows flagellates to access nutrients throughout the water column and to implement the nutrient-retrieval strategy discussed previously, although motility per se is not an effective nutrient uptake mechanism (Aksnes and Egge 1991). Chemosensory ability, such as that which allows the flagellate *C. antiqua* to detect elevated inorganic phosphate concentrations, is an associated behavioral adaptation of flagellate swim strategies (Ikegami et al. 1995). The closest, analogous diatom behavior is probably their exploitation of micronutrient patches that increased sinking confers. However, the passive nutrient-collection strategy of all but the largest planktonic diatoms associated with sinking is rudimentary in contrast.

Pattern swimming and auto-regulated aggregation have multiple benefits which vary with life cycle stage and growth phase. Physically induced aggregation (=patchiness) is of lesser interest than swarming behavior but may confer some of the benefits of auto-regulated aggregation. The most obvious benefit of aggregation is that it favors increased anti-predation protection classically associated with schooling behavior and possibly also provides antiviral defense (Murray 1995). Dinoflagellates exhibit well-known sensitivity to trace metals, with toxicity—particularly from copper—a problem. This suggests organic complexation of trace metals is needed for survival and growth. Aggregation may play a role in such habitat detoxication. Smayda (1989*b*) has proposed that the secretion of weak complexation substances reported for flagellates (Ishida 1968) may become concentrated within the microhabitats of the aggregated cells and detoxify these sites, leading to improved growth.

Aggregation also increases self-shading. This may facilitate rapid transition into the photosynthesis-irradiance photoadaptive strategies discussed previously and confer competitive advantage over shaded nonmotile taxa and competing taxa within the aggregated swarms. Aggregation facilitates genetic exchange, including inheritance of toxicity (Ishida et al. 1993), and mating reactions which induce transitions in life cycle stages (Sawayama et al. 1993). The increased intraspecific competition expected to accompany aggregation does not seem to deter auto-regulated behavior. This suggests that the limitations of reduced nutrient availability per cell and increased competition for nutrients induced by aggregation are of lesser significance than the limitations which flagellate swarming behavior protects against, or overcomes. The major disadvantage of cellular aggregation and patch accumulations may be in facilitating pathogen attack leading to demise of the population.

Clearly, HAB flagellates exhibit flexible, controlled behavior as a result of motility. The exact behavioral expression at a given time or spatial domain is a complex balance between physiological optimization and environmental stress (Kamykowski et al. 1992). The behavior of the chain-forming dinoflagellate *Gymnodinium catenatum* in Spanish upwelling rias (Fraga et al. 1989) provides an elegant example of the ecophysiological benefits to population dynamics of auto-regulated cellular behavior. The formation of longer chains by this toxic species, which can reach 64 cells per chain and 2 mm in length (Blackburn et al. 1989), increases swimming speed. Fraga et al. (1989) believed such strong motility allows *G. catenatum* to be retained during downwelling periods, when it then blooms. Diel migrations into the underlying nutrient reservoir accompany this behavior (Fraga and Bakun 1993). During nutrient deficiency, the serpentine swimming motion with synchronized propulsion and torsion of the chains is abandoned and a reduction in chain size occurs (Blackburn et al. 1989). The stationary phase cells then hang vertically within the water column.

Conclusions

The foregoing analyses suggest there is a dual answer to the issue of whether HAB taxa differ ecophysiologically from other taxa. Taken collectively, the physiologies of HAB species range over the gamut that generally characterizes phytoplankton, rather than being physiologically unique or sharing a characteristic physiological syndrome. There are no apparent major differences among these taxa in their cellular processes, physiological mechanisms, life cycle strategies, and population growth-curve dynamics. They exhibit common features and requirements in terms of inorganic nutrition, photosynthesis, and reliance on vegetative growth as the primary reproductive mode. Differences in physiological rates and growth processes are differences of degree, rather than fundamental. Nevertheless, significant ecophysiological differences in several attributes of HAB flagellates emerge when contrasted to diatoms. HAB flagellate taxa diverge from diatoms in their vulnerability to turbulence, in their low nutrient affinity, in their considerable nutritional diversity involving mixotrophic tendencies, in their generally lower growth rates, in their potential reliance on allelochemical regulation of interspecific competition and allelopathic predation defense, and in several behavioral consequences of their motility. Because such differences probably also characterize nonharmful flagellates, these characteristics may reflect more fundamental differences between nonmotile and motile cells in their adaptations to the phytoplanktonic life mode. With regard to nonmotile, harmful or nuisance taxa, ecophysiological differences between these and benign taxa are not evident. Their negative bloom consequences appear to result from population-density, or size-mismatch effects on upper trophic levels, rather than related to those traits (listed above) common to HAB flagellates.

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