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Co-occurrence of dinoflagellate blooms and high pH in marine enclosures

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ABSTRACT: High abundances of dinoflagellates in mixed phytoplankton populations in marine enclosures were strongly correlated with high pH during 23 enclosure-years of weekly samples. Diatom blooms were not similarly correlated with high pH. The correlation with high pH was not the result of dinoflagellate blooms themselves drawing down the CO_2 and driving up the seawater pH. Examination of individual blooms of >500 cells ml^{-1} indicates that dinoflagellate cell counts increased only after the pH was driven high (i.e. >8.5). High pH occurred either by natural processes (diatom blooms) or, in one case, by an artificial manipulation of the pH in the enclosure. There were 9 periods in which the seawater pH exceeded 8.5. Dinoflagellate blooms occurred during 7 of those events. A high pH affinity for dinoflagellates could help explain reported successional sequences of diatom blooms followed by dinoflagellate blooms and the association of dinoflagellate blooms with eutrophication. Seawater pH should probably be included with other environmental factors in studies of the mechanisms that control the occurrence of field dinoflagellate blooms.

INTRODUCTION

Regular temporal patterns of marine phytoplankton species abundance, or succession, have often been reported (Margalef 1963, Harris 1980, Smayda 1980 and references therein, Karentz & Smayda 1984, Evans 1988). In one such sequence, dinoflagellates have been reported to follow large diatom blooms, especially the winter-spring bloom found in many coastal environments (Gran & Braarud 1935, Riley 1957, Patten et al. 1963, Loeblich 1984, Taylor & Pollinger 1987). The dinoflagellates include red tide and toxigenic species, so it would be particularly interesting to determine specific factors responsible for their appearance.

Reviews of general dinoflagellate ecology (Guillard & Keller 1984, Loeblich 1984, Taylor & Pollinger 1987), of nuisance blooms in particular (Steidinger & Baden 1984, Paerl 1988, Cosper et al. 1989, Okaichi et al. 1989, Graneli et al. 1990, Riegman 1991), and studies of phytoplankton succession (e.g. Margalef 1958, Watling et al. 1979, Smayda 1980 and references therein, Levasseur et al. 1984, Pagou & Ignatiades 1988) do not list pH as a factor influencing marine dinoflagellate growth or distribution. This is in sharp contrast to the case in freshwater where the pH of lakes is determined from examination of the phytoplankton assemblages (e.g. ter Braak & van Dam 1989, Dixit et al. 1992).

Recently, Yoo (1991) found pH to be the leading factor correlating with the abundance of dinoflagellates (a positive correlation between abundance and pH) in Masan Bay, Korea. Data from marine enclosures are reported here. They also suggest pH is an important factor contributing to the regulation of dinoflagellate blooms in a coastal marine environment. Specifically, the data suggest the hypothesis that high seawater pH permits dinoflagellate blooms to develop.

It is frequently assumed that pH in relatively well-buffered seawater is essentially constant. It is not the purpose here to review pH data for coastal environments. However, a cursory examination of surface water data from other coastal marine ecosystems indicates that high pH values in surface seawater are not uncommon. For example, the German Bight in the North Sea may have pH values of 8.7 (Pegler & Kempe 1988). The Chesapeake Bay main stem and the Potomac River (USA) may have pH values of 9.0 and 9.25 respectively (Hires et al. 1963). A small coastal pond on Cape Cod (USA) has values up to 9.0 (Emery 1969).

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A more detailed example is shown in Fig. 1. The pH in lower Narragansett Bay (Rhode Island, USA) fluctuated by ca 1 pH unit in 1989–1990. This part of Narragansett Bay (typical salinities of 29 to 30 ‰) is probably only slightly altered by cultural eutrophication (Hinga et al. 1989). The seasonal pH variability in Narragansett Bay is caused by an exchange of carbon between the CO_2 in seawater and organic matter (Rudnick & Oviatt 1986). During the winter-spring bloom, CO_2 has a net fixation into phytoplankton and storage in benthic sediments with a resultant rise in seawater pH. As temperatures warm in summer, there is a net regeneration of CO_2 driving the seawater pH down. Variability around the annual pattern probably reflects individual phytoplankton blooms. In this system, CO_2 equilibration with the atmosphere and flushing do not occur fast enough to prevent the pH excursions. Similar bloom-CO_2 dynamics have been observed in lake systems, albeit with a greater pH range (Talling 1976).

There is a considerable inter-annual variation in the phytoplankton dynamics in Narragansett Bay. Without further data, it is not correct to assume that the magnitude and timing of extremes of pH shown in Fig. 1 will be the same every year. Although it is tempting to do so, it is not valid to compare the pH pattern found in one year in one part of the bay (e.g. Fig. 1) with phytoplankton data from other years or in other parts of the bay.

As presented in the review by Smayda (1980), successional patterns may be caused by allogenic (external) or autogenic (community-caused) factors. Allogenic factors include changes in salinity, temperature, light, turbulence, or anthropogenic influences. These provide conditions in the environment suitable for different species or groups of phytoplankton over time. Autogenic factors include life cycle, nutrients, water quality, ectocrines, predation and light (especially at high cell densities). Seawater pH is affected by both the phytoplankton community and by external factors such as discharge of organic matter. Hence, pH may be both an autogenic and allogenic factor in phytoplankton succession.

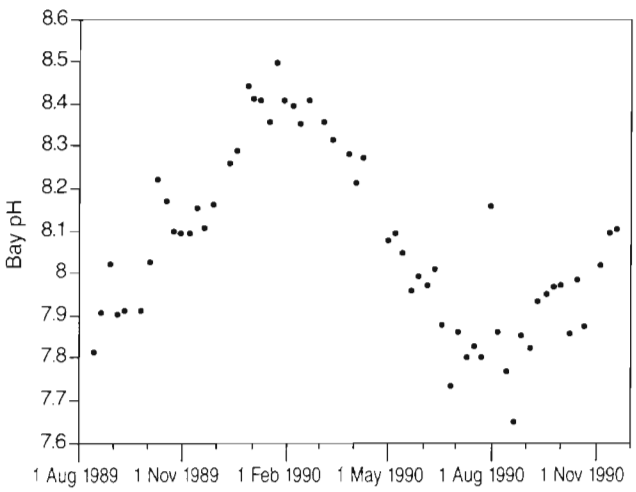

Fig. 1. pH of seawater at the Graduate School of Oceanography pier in lower Narragansett Bay (Rhode Island, USA)

MATERIALS AND METHODS

Data collected during 2 marine enclosure experiments at the Marine Ecosystems Research Laboratory (MERL) of the University of Rhode Island were re-examined for this analysis. One experiment was a 9 enclosure 28 mo eutrophication experiment (Nixon et al. 1984, Kelly et al. 1985, Oviatt et al. 1986a, b, 1989, Keller 1988a, b, 1989, Keller & Rice 1989, Hinga 1990). The other experiment was a 4 enclosure 15 mo carbon isotope fractionation experiment (M. A. Arthur, K. Hinga & M. E. Q. Pilson unpubl.). The enclosures were part of an outdoor tank farm of 14 enclosures (often called mesocosms). Each enclosure had a 37 cm layer of sediment in the bottom, 13 m^3 of overlying water, a water column depth of 5 m, turbulence induced by means of a vertical plunger (running 2 h of each 6 h), and temperature held to within 1 to 2 °C of the adjacent bay. For the initiation of each experiment, a benthic community was collected from a silt-clay area in Narragansett Bay with a box corer, which maintains the sediments in a structurally undisturbed condition, and transferred to the tanks in a tray the internal diameter of the enclosure tanks. Unfiltered seawater, with its water column community intact, was transferred from the adjacent bay with non-disruptive displacement pumps. When left unmanipulated, the biology and biogeochemistry of the enclosures have been found to be very similar to that found in lower Narragansett Bay even for long periods of time (Pilson et al. 1980, Pilson 1985).

In the nutrient addition experiment, 3 tanks were held as unmanipulated controls and 6 tanks were given daily additions of nutrients (Oviatt et al. 1986a). The nutrient addition tanks were given different amounts of nutrients to create a gradient of treatment using the 6 enclosures. In the CO_2 experiment, the concentrations of CO_2 and the alkalinity were initially adjusted to give elevated CO_2 concentrations without altering the seawater pH. This manipulation required that gaseous CO_2 be regularly introduced by bubbling into the seawater in the treated tanks to balance CO_2 loss to the atmosphere and maintain the pH.

A useful feature of these experiments for this study is that the phytoplankton populations present in the enclosures after the first few weeks were primarily those that grew in the enclosures. The water, and

hence phytoplankton, exchange with bay water was either slow (3.7 % d^{-1} in the nutrient addition experiment) or nonexistent (in the carbon isotope fractionation experiment). Samples were always taken during a mixing period in the enclosures to assure a representative sample. The water in the enclosures has been found to be homogenized after mixing with vertical plungers for 30 min.

The phytoplankton counts and pH data from the nutrient addition experiment have been previously published (Frithsen et al. 1985). Species names are used here as they were listed in the original data reports (Frithsen et al. 1985, and examination of archived computer files for less common species). The data from the CO_2 experiment is unpublished. The counts were made by several different persons. There is no way to check the species identifications or consistency of identifications in the data reports. Some dinoflagellate identifications are only to genera, but this does not interfere with the analysis conducted here. It seems unlikely that the trained technicians making the counts would misidentify major dinoflagellate populations for diatoms or other groups. Neither experiment was run with controls to investigate the effect of pH. Hence, the data should be viewed as a collection of unreplicated time-series field observations from coastal ecosystems.

Dinoflagellate abundances of >100 dinoflagellate cells ml^{-1} and blooms of >500 dinoflagellate cells ml^{-1} were chosen for this analysis. The analyses are not sensitive to the exact abundance levels chosen. The same results emerge if somewhat higher or lower values are used.

RESULTS

Dinoflagellate abundances of >100 cells ml^{-1} occurred almost exclusively when the pH in the systems was high (Fig. 2). Phytoplankton blooms themselves draw down ΣCO_2 and raise the pH. Hence, one would expect some shift in the frequency of occurrence of all phytoplankton blooms toward high pH. This can be seen in the small shift in the distribution of diatom abundances of >100 cells ml^{-1} to higher pH than the distribution of all samples (Fig. 2). The median pH of the distribution of all samples, samples with diatom abundances >100 cells ml^{-1}, and samples with dinoflagellate abundances >100 cells ml^{-1} are 7.96, 8.16 and 8.52 respectively. The probability that the pH distribution of samples with high dinoflagellate abundances is not different from the pH distribution of all samples is very low ($p \leq 0.0005$; 1-sample *t*-test).

Dinoflagellate abundances >100 cells ml^{-1} were found in all the months January through September.

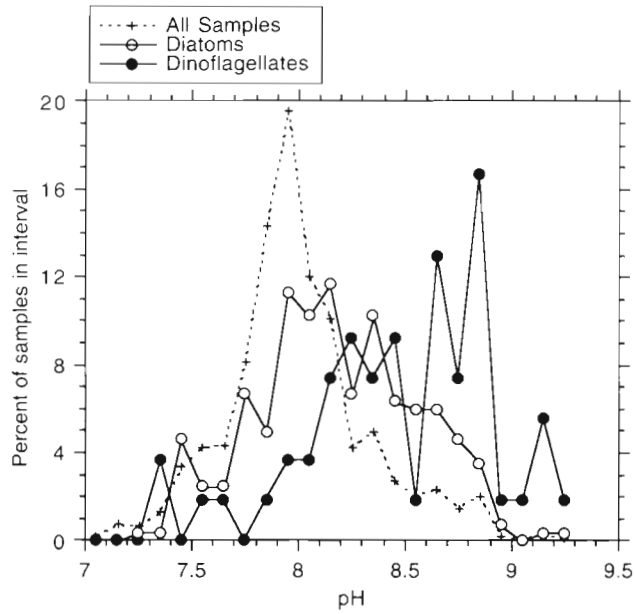

Fig. 2. Frequency of occurrence, in 0.1 pH unit intervals, of dinoflagellate and diatom abundances of over 100 cells ml^{-1} and the frequency of all pH measurements where phytoplankton cells were counted

No high dinoflagellate abundances occurred in October through December when the pH was rarely above 8.1 (with only a single occurrence as high as pH 8.3). Individual observations of high dinoflagellate abundances were usually composed of single species but occasionally were 2 or more species.

Dinoflagellates found in high abundance were reported as: *Peridinium* spp. (by far the most common), *Heterocapsa triquetra*, *Exuviaella* sp., *Amphidinium* sp., *Gymnodinium* sp., *Scrippsiella* sp., *Dissodium lenticulum*, *Prorocentrum redfieldi*, *Prorocentrum gracile* and *Dinophysis acuminata*.

Not all dinoflagellate species occurred in high abundances at high pH. The 2 *Prorocentrum* spp. (abundant in 3 samples) were found at pH of ca 8.0 to 8.1. *Dinophysis acuminata* was found in high abundance in a single month-long bloom that occurred at very low pH, <7.5. The remaining dinoflagellate species all had occurrences associated with high pH.

There were 6 dinoflagellate blooms >500 cells ml^{-1} during the nutrient addition experiment. The blooms occurred between late March and mid May and consisted of 1 bloom each of *Heterocapsa triquetra* and an *Exuviaella* sp. and 4 *Peridinium* spp. blooms. In each case, the pH changed in response to a winter-spring diatom bloom before the dinoflagellate bloom began (e.g. Fig. 3). High abundances in each of these large blooms was developed at pH 8.4 or greater.

In the elevated CO_2 experiment, the sole dinoflagellate bloom (a mixed *Amphidinium* sp. and *Gymno-*

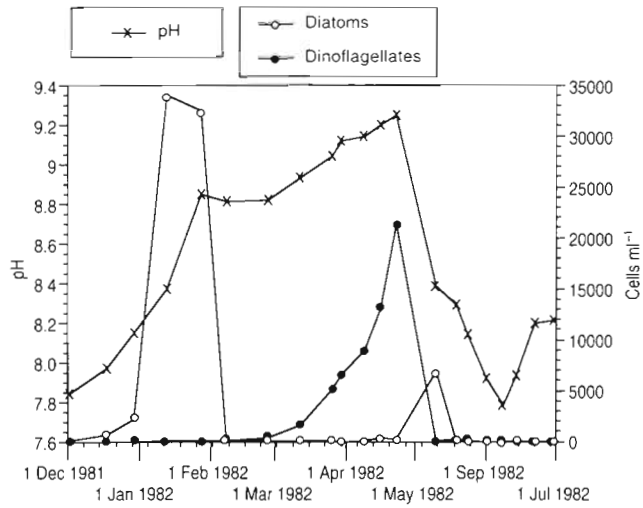

Fig. 3. Time course of a *Peridinium* sp. bloom in Mesocosm No. 4 during the MERL nutrient addition experiment.

dinium sp. bloom) occurred in late June. This occurred when a failure in the CO_2 injection system for one of the tanks resulted in a net loss of CO_2 to the atmosphere and permitted a rise in pH to 8.4 (Fig. 4).

When there were periods of high pH, how likely was a dinoflagellate bloom to develop? There were 8 periods in the nutrient addition experiment (where phytoplankton counts were available) where the pH was above 8.5. (Unfortunately, a 3 mo hiatus in phytoplankton counts occurred during the second spring period of the experiment when high pH were found. This significantly reduced the number of observed periods.) The CO_2 experiment provided 1 period of high pH. Hence, there were a total of 9 periods of observation where the pH in the enclosures exceeded 8.5. Dinoflagellate blooms of >500 cells ml^{-1} developed during 7 of those 9 periods.

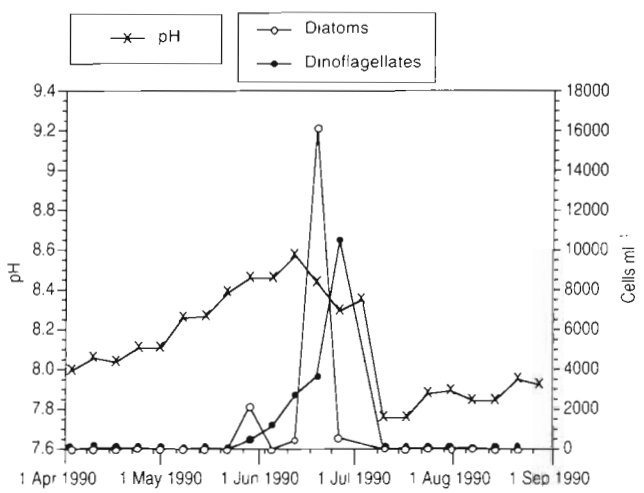

Fig. 4. Time course of a mixed *Amphidinium* sp. and *Gymnodinium* sp. during the elevated CO_2 experiment

DISCUSSION

The correlation between high pH and high dinoflagellate abundance in these enclosures strongly suggest that pH is a factor that contributes to the control of dinoflagellate blooms. Similarly, in a stepwise multiple regression, Yoo (1991) found pH to be the leading environmental variable correlating with the abundance of dinoflagellates in a Korean bay. As both Yoo's results and these are based upon correlative evidence, it is possible that the similar timing of high dinoflagellate abundance and high pH are chance. However, as noted above for the enclosure studies, there is a very low probability that the pH distribution of samples with high dinoflagellate abundances is not different from the distribution of pH distribution of all samples.

Several factors that might be expected to control the occurrence of dinoflagellates were not important in these experiments, at least at the abundance levels considered. Low concentrations of silicate have been suggested to promote dinoflagellates over diatoms. In the nutrient addition experiment, nutrients were added in constant ratios. There was always an adequate supply of silicate, except in the control (no nutrient addition) tanks for short periods. High dinoflagellate abundances occurred almost exclusively in the nutrient addition tanks. The silicate concentrations during the CO_2 experiment were also high relative to the inorganic nitrogen and phosphate. Temperature does not appear to be a direct factor During the October through December period there were no occurrences of high dinoflagellate abundances. The temperatures in the enclosures during this period were similar to temperatures when high abundances of dinoflagellates were usually found (March through May). Calm, stratified conditions are often associated with dinoflagellate blooms (Taylor & Pollinger 1987). Physical mixing conditions in the enclosures, however, were constant (completely mixed 4 times a day) for the entire length of these experiments.

Assemblages of freshwater phytoplankton are sensitive to pH (e.g. ter Braak & van Dam 1989, Dixit et al. 1992). The pH of lake water can often be determined to within a fraction of a pH unit by observing the diatom assemblage. It seems reasonable to also expect pH changes of 1 to 2 pH units to have some effect on the composition of marine phytoplankton. Unfortunately, there is a rather sparse literature addressing pH effects on marine phytoplankton. One study with marine phytoplankton (Goldman et al. 1982a) showed how pH can affect species dominance in competition experiments. Growth rate experiments with a few individual species of prymnesiophytes (Kain & Fogg 1958, Paasche 1964, Swift & Taylor 1966) and diatoms

(Bachrach & Lucciardi 1932, Goldman et al. 1982b, Chen 1986) generally show optimum growth near pH 8.1 and a decrease in growth rate at higher pH, especially above pH 8.5. Chen (1986) found that the carbon fixation rate of natural phytoplankton assemblages (composed primarily of a *Phaeocystis* sp. and diatoms) decreased sharply with pH greater than pH 7.8 to 8.1 even though the assemblages were collected in waters with pH 8.8 to 9.1. In contrast, Barker (1935) found highest growth rates for 3 dinoflagellate species in cultures initiated at pH 8.5 to 9.5. The pH decreased during the culture periods so the growth optima were not well constrained. Nevertheless, the growth optima in these experiments were clearly well on the alkaline side of normal seawater pH. Blackburn & Oshima (1989) found a growth optimum for the dinoflagellate *Pyrodinium bahamense* near pH 8.0, so not all dinoflagellates have elevated pH optima. It should be noted that it is not necessary that dinoflagellates have optimum growth at high pH to account for the observed high pH effect (e.g. Goldman 1982a). It is only necessary that at high pH, the dinoflagellates can better tolerate the conditions and outcompete other phytoplankton groups in the initial population.

If high pH is found to be an important factor in the occurrence of field populations of dinoflagellates, the pH factor could be a causal link between the suggested association of eutrophication and red tides (e.g. Anderson 1989, Smayda 1991). The pH of seawater in a coastal ecosystem can be driven to greater extremes by nutrient additions than would occur without nutrient additions. When more nutrients are available, blooms may reach greater magnitudes hence drawing down the CO_2 and raising the pH to greater extents. As an example, during the marine enclosure eutrophication experiments discussed above, the pH in the 3 enclosures without nutrient additions rarely exceeded 8.5 and was quite similar to the bay data shown in Fig. 1. The enclosures given nutrient additions had greater extremes of pH and sometimes exceeded a pH of 9.0 (Frithsen et al. 1985).

A pH effect might help explain why dinoflagellate blooms do not always occur with eutrophication. Organic carbon is often introduced along with nutrients in pollution sources such as sewage and fish waste. The CO_2 generated from the remineralization of the organic carbon will tend to keep pH low. However, once the organic carbon is exhausted, and after the excess CO_2 vents to the atmosphere, the nutrients may stimulate phytoplankton blooms that raise the pH. The nutrients may have been fixed into biota and remineralized one or more times before they are able to stimulate a bloom that raises the pH. If this process is important in the field, it is likely that pH-induced blooms may occur somewhat offshore rather than at the point of introduction of the nutrients and organic carbon.

Stratified conditions and low oxygen in bottom waters are also associated with field blooms of dinoflagellates (Taylor & Pollinger 1987). A carbon-driven pH mechanism could contribute to this effect if the bloom species are promoted by high pH. When phytoplankton grow in a stratified water column they convert CO_2 in the water to particulate materials. Some of the particulate carbon is transported to deeper waters through settling and zooplankton grazing and fecal pellet production. Where there is sufficient downward transport of particulate material, the organic carbon will not remineralize in the upper waters to replace the CO_2 taken up by primary production. This will result in a rise in pH in the surface waters and provide an opportunity for high-pH species. The high pH may persist until the water overturns or the surface water CO_2 reequilibrates with the atmosphere.

The data presented here do not identify the mechanism, or mechanisms, by which pH could create an environment suitable to different species. There are many possibilities. The speciation (chemical form) of many compounds in seawater is affected by pH (e.g. Kester 1986). Consequently, a wide variety of compounds might be involved in creating favorable conditions for dinoflagellates at high pH. One example is copper. At least some dinoflagellates are particularly sensitive to cupric ions (e.g. Anderson & Morel 1978). The availability of the cupric ion is partially controlled by pH. Cupric ion concentrations decrease with increasing pH (Kester 1986). However, Chen (1986) found that the direct effect of pH on growth rate of 2 *Thalassiosira* spp. was much greater than the effect of cupric ions. Some more direct physiological mechanism might be limiting growth rates of these diatoms at high pH. Chen (1986) suggested carbon limitation may be responsible for the effect.

It is interesting to consider the implications phytoplankton cell growth in a high pH environment. In order for a cell to grow, it must take up CO_2 across the cell membrane (either by passive diffusion or active transport). The CO_2 can be the negatively charged HCO_3^- or the uncharged CO_2aq (defined here as dissolved free CO_2 plus H_2CO_3). If a cell takes up CO_2aq, there is no impact upon the internal charge balance and pH for the cell. However, CO_2aq is not very abundant in seawater with only ca 20 µmol l^{-1} for seawater in equilibrium with the atmosphere. The concentration of CO_2aq decreases even further at high pH. If phytoplankton start growing in seawater at pH 8.1 and an initial concentration of 1910 µmol l^{-1} of ΣCO_2, by the time the 180 µmol l^{-1} CO_2 has been removed (a bloom requiring 1.7 µmol l^{-1} of phosphate), the pH will have risen to 8.6. During this small change in ΣCO_2, the concentration of CO_2aq decreases from ca 20 to 5 µmol l^{-1} (Fig. 5).

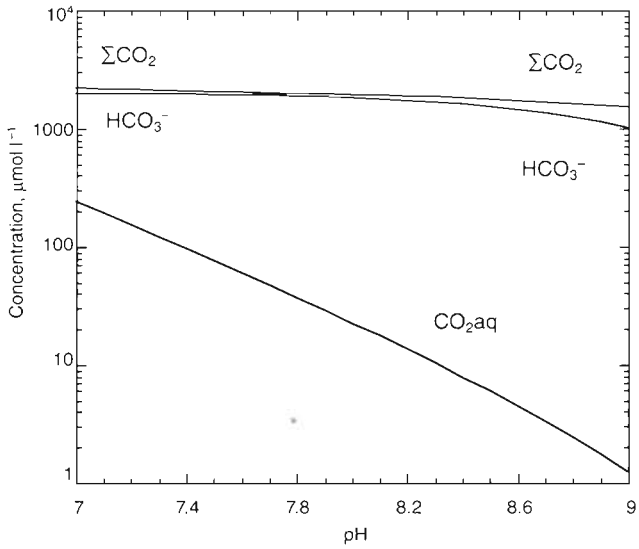

Fig. 5. Concentrations of ΣCO_2, HCO_3^-, and CO_2aq plotted against pH. These are calculated for seawater conditions of 15 °C, 29.5 ‰ and an alkalinity of 2.00 meq l^{-1} Small changes in ΣCO_2 resulting from the uptake of CO_2 by phytoplankton or the remineralization of organic matter causes significant changes in the pH and large changes in the concentration of CO_2aq

If the cell takes up the more abundant HCO_3^-, it must convert it to CO_2aq before carboxylation by the photosynthetic enzymes through the reaction:

$$HCO_3^- + H^+ \rightarrow CO_2aq + H_2O.$$

High pH seawater is a relatively proton-poor environment for marine phytoplankton. In order for a cell to maintain its internal pH in a high pH environment it must minimize its loss of protons (Raven 1980). The extra demand for protons necessary for use of HCO_3^- may make it difficult for a cells utilizing HCO_3^- to grow at high pH.

Some dinoflagellates are capable of heterotrophic uptake of dissolved or particulate carbon. Many forms of organic carbon would have little impact on the charge balance of the cell when taken up across the cell membrane. The respiration of the organic carbon would provide both energy and a source of CO_2 that does not require protons before photosynthetic fixation. Perhaps heterotrophy allows some dinoflagellates to out compete obligate autotrophs in a high pH environment where uptake of inorganic carbon is difficult. Whatever the mechanism involved, if some groups of phytoplankton have an ability to tolerate high pH environments, they may be expected to outcompete other less tolerant groups and develop their highest abundances during periods of high seawater pH.

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