Alkaline phosphatase activities among planktonic communities in the northern Red Sea

Hong Li[1], Marcel J. W. Veldhuis[2], Anton F. Post[1,*]

[1]H. Steinitz Marine Biology Laboratory, The Interuniversity Institute for Marine Science, PO Box 469, 88193 Eilat, Israel
[2]Nederlands Instituut voor Onderzoek der Zee (NIOZ), PO Box 59, 1790 AB Den Burg, Texel, The Netherlands

ABSTRACT: During a June 1996 cruise in the northern Red Sea, we studied spatial distributions of alkaline phosphatase (AP) activities in different plankton size fractions and in the aqueous fraction which passes through 0.2 µm filters. AP proved to be a highly stable compound in the Red Sea and has potential use as an indicator for inorganic P-availability to planktonic communities. Depth profiles showed that aqueous and particulate alkaline phosphatase activities were highest in surface waters. The contribution of the aqueous fraction to total alkaline phosphatase activity varied between 42 and 74%. The bulk of particulate alkaline phosphatase activity was associated with picoplankton (50 to 71%) at all sampling sites. A good correlation was found between depth distributions of alkaline phosphatase activities and *Synechococcus*, suggesting that this abundant picoplanktonic cyanobacterium is a significant contributor to the enzyme activity in the northern half of the Gulf of Aqaba. Chlorophyll *a*-specific alkaline phosphatase activities were highest for plankton communities in the surface layers of the northern half of the Gulf. Alkaline phosphatase activities increased in the Gulf of Aqaba in water bodies traveling north, further away from the Straits of Tiran. At this narrow and shallow entrance to the Gulf, local turbulent conditions and coral reef flats inject phosphate into the productive layer. Plankton communities immediately north of the Straits showed basal levels of alkaline phosphatase activity, and phosphate supply presumably satisfied their P-demands. Based on the regulation of alkaline phosphatase synthesis, its secretion and stability, we proposed the use of alkaline phosphatase activities for a (partial) assessment of the P-status of marine planktonic communities. Such an assessment indicated that inorganic phosphate availability in the waters of the northern Gulf of Aqaba was persistently low during the period prior to sampling.

KEY WORDS: Marine picoplankton · Phosphate · P$_i$-limitation · Alkaline phosphatase activity · *Synechococcus*

INTRODUCTION

Assessment of which nutrient limits the primary production of marine phytoplankton is the subject of continuing research effort and debate. Although nitrogen is commonly considered as the growth limiting nutrient, no rigorous demonstration of nitrogen limitation has been presented (Hecky & Kilham 1988). Evidence is largely based on the high demand of phytoplankton productivity for combined nitrogen; ambient concentrations of nitrate, nitrite and ammonium that are, more often than not, below detection limits; low Redfield ratios for N:P and geo-evolutionary considerations (Harrison 1990, Garside & Garside 1993, Falkowski 1997). Other evidence, however, challenges this notion as it has been shown that iron and phosphorus rather than nitrogen may become the limiting nutrient for marine productivity in certain bodies of water. Iron has been reported as the factor limiting phytoplankton productivity in large sections of the equatorial Pacific and the Southern Ocean (Martin et al. 1994, Coale et al. 1996). P-limitation of phytoplankton production was reported for the eastern basin of the Mediterranean Sea (Krom et al. 1991, Krom et al. 1993). Cell cycle studies of the abundant phytoplanktonic cyanobacterium *Synechococcus* in Mediterranean waters following phosphate additions suggest that P-limitation might be encountered more frequently than previously

thought (Vaulot et al. 1996). Moreover, the N:P ratio in the Sargasso Sea is often in excess of the Redfield ratio (16:1), and bacterial communities from this sea were demonstrated to be P-limited (Cotner et al. 1997).

Orthophosphate is the main, and possibly sole, P-source taken up directly by algal and bacterial planktonic communities. However, orthophosphate concentrations in many bodies of water are too low to support their growth and biomass production. A variable fraction of dissolved phosphate in the marine environment is bound to organic compounds, and phosphate supply depends to a large extent on its regeneration from dissolved organic matter (Harrison 1980, 1992). Alkaline phosphatase (AP) and 5'-nucleotidase activities contribute significantly to phosphate regeneration in aquatic ecosystems (see e.g. Ammerman & Azam 1985, 1991a, b, Chróst 1991, James et al. 1991). Both enzymes are localized to the cell surface, but they differ in substrate specificity. 5'-Nucleotidase is capable of hydrolyzing nucleotides only and its activities appear to be a function of bacterial density rather than P-availability (Ammerman & Azam 1991a, b). AP is capable of hydrolyzing a wide range of organic P-compounds. AP therefore has potential importance in inorganic phosphate-deplete, oligotrophic waters where growth of plankton depends on P-regeneration (Cotner et al. 1997). Extracellular AP activity is inducible, that is, the biosynthesis of the enzyme is switched on when inorganic phosphate supply is low and the enzyme is subsequently localized to the cell exterior. This activity has been used as an indicator of the P-status of phytoplankton communities in freshwater ecosystems (Healey 1978, Cotner & Wetzel 1991). In the common cyanobacterium *Synechococcus* both P-limitation and supply of organic P-sources induce AP activities in parallel with an enhanced phosphate uptake capacity (Ray et al. 1991, Aiba et al. 1993, Scanlan et al. 1993, Donald et al. 1997). Marine phytoplankton species like *Synechococcus* and *Prochlorococcus* are abundantly present in environments where the inorganic P-supply is low (Parpais et al. 1996, Vaulot et al. 1996) and they would thus benefit from this adaptive potential in the competition for available phosphorus.

The Gulf of Aqaba is a warm, stratified body of water and its photic layer is depleted of inorganic nutrients during most of the year, comparable to other oligotrophic seas. Primary production in the Gulf of Aqaba and the northern Red Sea ranges from 20 to 110 mg C m^{-2} d^{-1} and chlorophyll a concentrations vary between 0.02 and 0.8 mg m^{-3} (Levanon-Spanier et al. 1979). Both combined inorganic nitrogen and phosphate drop below detection limits during the summer stratification period (Klinker et al. 1978, Lindell & Post 1995). Although little is known about nutrient control of primary productivity in the Gulf of Aqaba, phosphate

should be considered a potentially limiting nutrient (Reiss & Hottinger 1984). In order to assess the inorganic P-status for planktonic communities in the northern Red Sea, where both dissolved inorganic nitrogen and phosphorus compounds are below detection levels, we used AP activity as an assay. Although AP activities have been studied in marine algae (Yentsch et al. 1972, Vargo & Shanley 1985, Tomas & Baden 1993) and in mesocosms (Carlsson & Graneli 1993, Sobecky et al. 1996), its potential as an indicator for P-limitation in nutrient poor, subtropical seas has not been reported.

MATERIALS AND METHODS

Study area. The Gulf of Aqaba, a side-arm of the northern Red Sea, is a narrow, deep basin which is 180 km long, on average 14 km wide and has a maximum depth of 1800 m. It is connected to the Red Sea by the Straits of Tiran, a shallow sill with a maximum depth of 242 m. Being surrounded by desert, the Gulf has high evaporation rates averaging 1 cm d^{-1}. Nutrient levels, chlorophyll a concentrations and primary productivity all testify to its oligotrophic nature during the stratification period (Reiss & Hottinger 1984). The input of freshwater and inorganic nutrients from land based sources is negligible. The Straits of Tiran and the prevailing climatic conditions cause a thermohaline circulation in the Gulf of Aqaba with an influx of warm, nutrient-depleted surface waters from the Red Sea counterbalanced by an efflux of deep more dense waters (Klinker et al. 1976, Reiss & Hottinger 1984, Wolf-Vecht et al. 1992).

Sampling. During a research cruise on board the RV 'University I' between 2 and 10 June 1996, water samples were taken from the Gulf of Aqaba and the northern Red Sea. Hydrocast samples were taken at 3 sampling stations (A, B and M) located in the northern half of the Gulf of Aqaba (Fig. 1). Water was sampled with 5 l Niskin bottles equipped with reversing pressure gauges (SiS GmbH model RPM 2000) at depths of 1, 20, 40, 60, 80, 100, 125, 150 and 200 m. In addition we collected surface samples from a further 9 sites spaced at roughly equal distances on a transect, from its entrance at the Straits of Tiran to the northern tip of the Gulf (Fig. 1).

Size fractionation. Water samples were passed immediately through a 100 µm mesh to exclude large zooplankton and phytoplankton. The samples were subsequently fractionated into different size groups. Total plankton (0.2 to 100 µm) was obtained by filtering 100 ml water samples onto 0.2 µm polycarbonate filters (Poretics) by filtration at <125 mm Hg. Nanoplankton (2 to 20 µm) was collected on 2 µm polycar-

bonate filters (Poretics) after passing the sample through a 20 µm mesh. Picoplankton (0.2 to 2 µm) was collected on 0.2 µm polycarbonate filters after passing the sample through a 2.0 µm polycarbonate filter (Poretics) by vacuum filtration at <125 mm Hg. Microplankton (20 to 100 µm) was estimated by subtraction of the combined nanoplankton and picoplankton fraction (0.2 to 20 µm) from total plankton. The aqueous phase was sampled by collecting the filtrate of samples passed through a 0.2 µm polycarbonate filter. All samples were stored in the dark at 4°C in 20 ml vials prior to analysis.

Determinations. For the determination of soluble reactive phosphorus, 250 ml seawater were precipitated with 6.25 ml 1 M NaOH (Karl & Tien 1992) and stored at 4°C. Samples were then centrifuged for 15 min at 3000 rpm (1470 × g) and the pellet was redissolved in 0.2 M HCl . Phosphate was then determined spectrophotometrically at 800 nm in 10 cm cuvettes according to Murphy & Riley (1962). The detection limit of this method is about 10 nM.

Chlorophyll a was determined from 250 ml water samples filtered on 25 mm GF/F filters and subsequently extracted in 10 ml 90% acetone for 24 h at 4°C. Chlorophyll a concentrations were calculated from values of fluorescence emission of extracts before and after acidification with HCl as measured on a Turner Designs 10-000R fluorometer (Venrick et al. 1987). Two 2 ml water samples were preserved with paraformaldehyde at pH 7.0 at a final concentration of 0.4% v/v and directly frozen and stored in liquid nitrogen. Phytoplankton counts were performed with an Epics XL (Coulter Inc.) flow cytometer. Phytoplankton groups were distinguished on the basis of forward scatter relative to 0.474 µm beads (cell size) and pigment fluorescence. Yellow (phycoerythrin) and red (chlorophyll a) fluorescence were determined from excitation at 488 nm.

In comparison to high biomass bodies of water and laboratory cultures, AP activities per unit volume in oligotrophic seawater are low. For this reason 100 to 200 ml of (size fractionated) seawater samples were concentrated on 0.2 µm polycarbonate filters (Poretics) and immersed in 2 ml of filtered seawater. AP activity was determined after addition of 100 µl of 10 mM p-nitrophenylphosphate (PNP) as a substrate, 270 µl tris-glycine buffer (50 mM, pH 8.5) and 27 µl of 1 mM MgCl$_2$. Following incubation for 24 h at 37°C on an
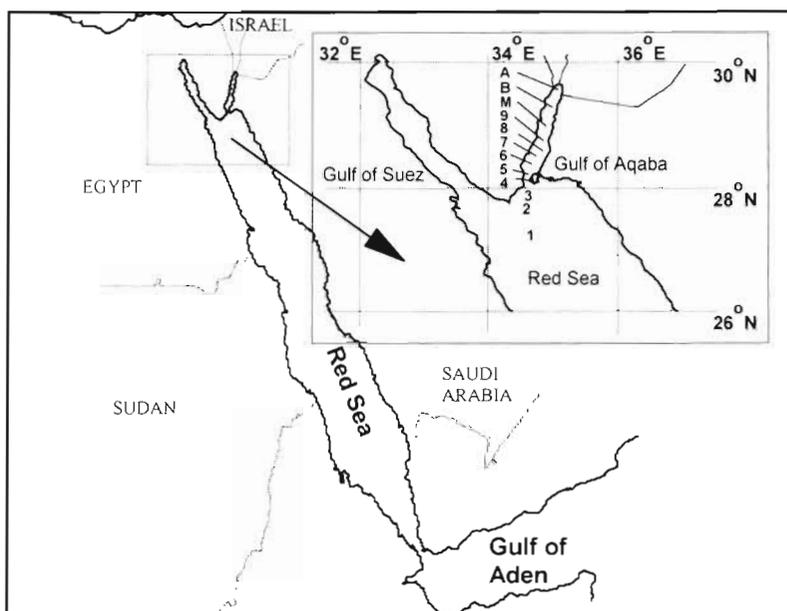

Fig. 1. Gulf of Aqaba and the northern Red Sea with locations of the sampling stations visited during the 2 to 10 June 1996 research cruise

orbital shaker at 100 rpm, the concentration of p-nitrophenol formed in the reaction was determined spectrophotometrically from the absorbance at 400 nm, using a molar extinction coefficient of 18000 cm^{-1} (Wynne 1981). Appropriate incubation times were determined by testing triplicate filtered seawater samples over a 48 h incubation period. AP activities were detectable after 10 h and increased in a linear fashion over 24 h incubation periods and longer (data not shown). In order to assess the stability of AP activity in seawater, 0.2 µm filtered seawater samples were incubated in both darkness at 4°C and light at 40 µmol photons m^{-2} s^{-1} and 24°C, simulating sample storage and natural conditions respectively. Triplicate samples over a 50 d time series were transferred to −75°C until assayed as described above. Statistical analyses were performed using the 'Statistica for Windows' software package (Statsoft, Inc.).

RESULTS

Stability of alkaline phosphatase in seawater

AP is an enzyme which is released to the environment through either cell lysis or excretion. Depending on its own lifetime and the prevailing environmental conditions, the enzyme may remain active outside the cell, and should then be detectable in the aqueous phase as freely dissolved activity. Boiled seawater and distilled water incubations, run as control experiments,
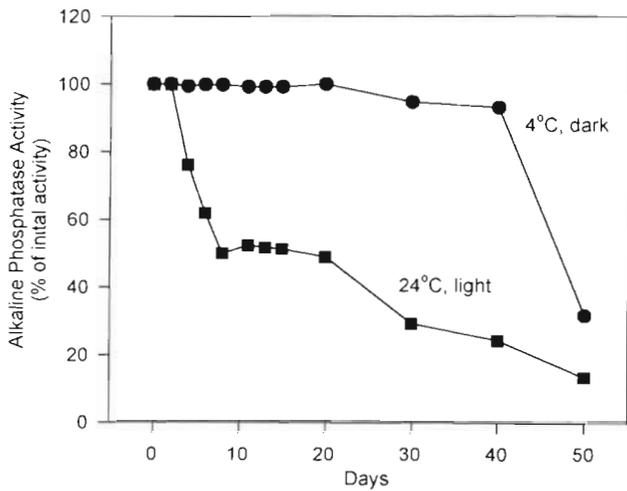
Fig. 2. Time-dependent change in alkaline phosphatase activity (expressed as percentage of initial activity) in particle-free seawater incubated in darkness at 4°C (●) and in the light (40 μmol photons m^{-2} s^{-1}) at 24°C (■). Data are average values of triplicate samples

inorganic phosphate (P$_i$) history of the plankton community over a period of up to 1.5 mo. This consideration formed the basis for our subsequent study of the spatial patterns in AP activities in the Gulf of Aqaba.

Depth profiles of alkaline phosphatase activity

The waters in the northern half of the Gulf of Aqaba exhibited a complex thermal structure with multilayer stratification in June 1996 (Fig. 3). P$_i$ concentrations were near the detection limit in the upper 200 m of the water column. Average concentrations along the depth profiles were 9.6 ± 2.2, 14.1 ± 10.7 and 9.8 ± 5.1 nmol l^{-1} at Stns A, B and M respectively. Chlorophyll a showed typical depth distributions, with concentrations ranging between 0.05 and 0.25 μg l^{-1} and the presence of a deep chlorophyll maximum apparent at all sites

did not show any PNP degradation. Filtered (0.2 μm), particle-free seawater samples from the head of the Gulf, kept in the dark at 4°C, retained AP activities at the level of initial activity (10 nmol PNP ml^{-1} h^{-1}) over a 40 d period (Fig. 2). AP activities declined drastically after Day 40 and on Day 50 AP activity was reduced to 25%. When identical water samples were kept at an irradiance of 40 μmol photons m^{-2} s^{-1} at 24°C, AP activities remained stable for 2 d, after which they steadily decreased to about 50% of the initial activity in 8 d and to 25 to 30% activity only after 30 to 40 d (Fig. 2). Light and temperature conditions used can be considered representative of those encountered in the northern Red Sea. In the presence of suitable organic P-sources, aqueous AP may thus contribute significantly to P-regeneration in these waters. AP activities thus potentially reflect the
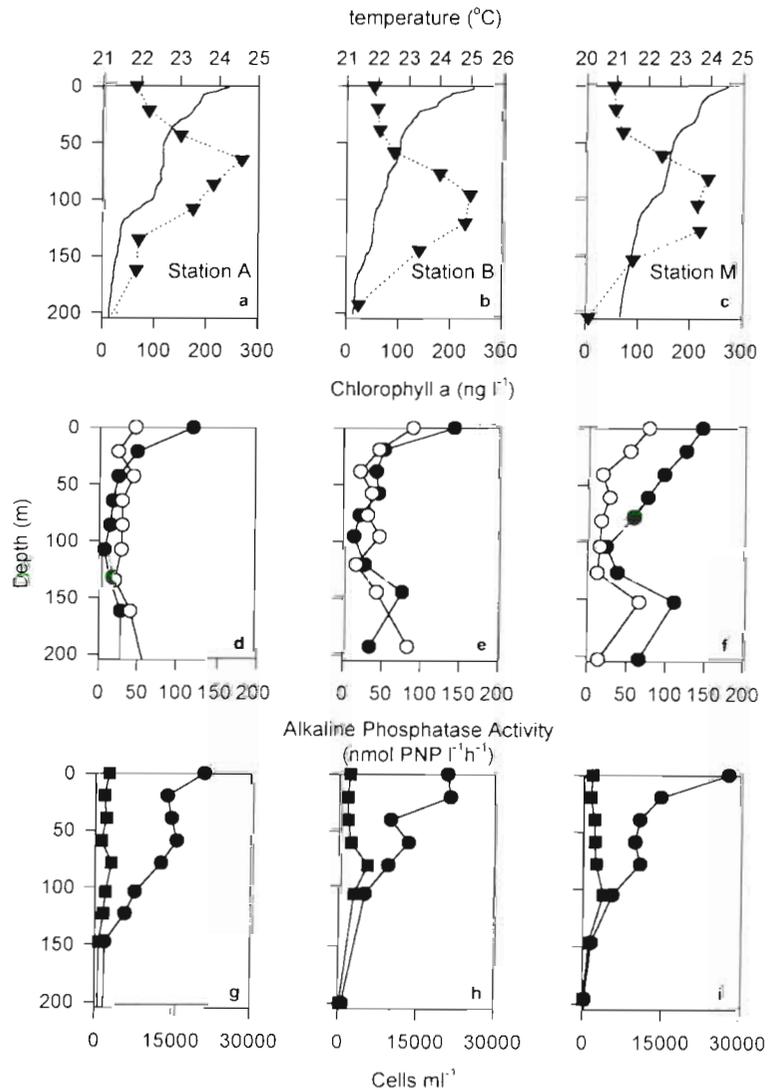

Fig. 3. (a, b, c) Depth distributions of seawater temperature (solid line) and chlorophyll a concentration (▼) at sampling Stns A, B and M respectively. (d, e, f) Aqueous alkaline phosphatase activity (●) and alkaline phosphatase activities associated with particulate matter (0.2 to 100 μm) (○) at Stns A, B and M. (g, h, i) Depth distributions of Synechococcus (●) and picoeukaryotic algae (■) at Stns A, B and M

(Fig. 3). Depth profiles of AP activities associated with the total particulate (0.2 to 100 µm) and aqueous (<0.2 µm) fractions showed very similar patterns at all sampling stations (Fig. 3). AP activities of both the aqueous and particulate fractions were highest in the surface layers with typical values of 150 and 40 to 80 nmol PNP l^{-1} h^{-1} respectively. AP activities quickly decreased with depth for both fractions and they reached a minimum at depths of 100 to 125 m, the bottom of the photic zone. Depth distributions showed that the layers with highest AP activities were located near the surface, well above the deep chlorophyll maximum (Fig. 3). Depth distributions of picophytoplankton showed that *Synechococcus* was abundantly present in near the surface layers with concentrations reaching 2.5×10^4 cells ml^{-1} (Fig. 3). Eukaryotic algae were present at 2 to 3×10^3 cells ml^{-1} with a slight maximum at the depths of the chlorophyll maximum. The smallest picophytoplankton representative, *Prochlorococcus*, was present in insignificant numbers ($<10^3$ cells ml^{-1}) and thus its contribution to phytoplankton biomass was negligible. Depth profiles determined during a second visit to the sampling sites in the same week confirmed the previous observed patterns for all parameters with the distinction of slightly lower AP activities in surface layer samples: mean AP activities for all stations were 113 ± 46 nmol PNP l^{-1} h^{-1} (aqueous fraction) and 55 ± 24 nmol PNP l^{-1} h^{-1} (particulate fraction). A closer inspection of the depth profile data showed a trend whereby the percentage contribution of aqueous AP activity at all depths increased with distance from the head of the Gulf. Aqueous AP activity contributed 42 ± 17% and 51 ± 13% of the combined aqueous and particulate activities at Stns A and B in the northern section of the Gulf to 74 ± 13% at Stn M in the central section.

Alkaline phosphatase activity along a surface water transect

During stratification, P$_i$-input into the photic layer of the Gulf of Aqaba occurs only with the entry of Red Sea waters through the Straits of Tiran. P$_i$ is injected into the surface waters of the Gulf with the passage of water over extensive coral reef flats (Korpal 1991) and from deeper layers by local turbulence at the Straits (Murray et al. 1984). One thus expects a gradient of decreasing P$_i$-availability when travelling from the Straits to the more northern parts of the Gulf, with this being reflected in increasing AP activities. Since AP activity
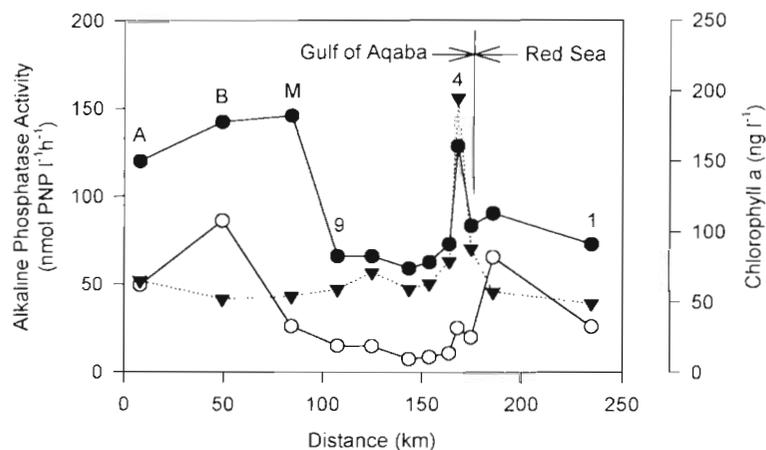

Fig. 4. Aqueous (●) and particulate (○) alkaline phosphatase activity and chlorophyll a concentrations (▼) in surface waters of the northern Red Sea and the Gulf of Aqaba along a south-north transect

was most pronounced in the surface layers of the water column, we decided to determine surface AP activities along a transect from the northern Red Sea to Stn A in the northern tip of the Gulf of Aqaba. The AP activities in the aqueous fraction were significantly higher than those of the particulate fraction at all sampling sites (Fig. 4) and accounted for 79 ± 10% of the combined activities. In the northern half of the Gulf of Aqaba both particulate and aqueous AP activities were obviously higher than those in the southern half. Whereas aqueous and particulate AP activities along the transect showed parallel spatial patterns, these differed from the pattern of surface chlorophyll a concentrations, which were higher in the southern half of the Gulf (Fig. 4). At Stn 4, just north of the Straits, we observed a 4-fold increase in chlorophyll a. AP activities of the particulate and aqueous fractions were strongly correlated (Pearson correlation coefficient, r$_p$ = 0.52; p < 0.001; n = 54) for both samples taken along depth profiles in the northern section of the Gulf and along the surface transect (Fig. 5). This finding suggest a relationship between the 2 activities and both may be indicators of the P-status of the plankton community.

Alkaline phosphatase activities in different plankton size fractions

The typical spatial distribution of AP activities described above raises questions about the source of the aqueous AP activity. In order to assess the contribution of different plankton size fractions to overall activity we size-fractionated plankton samples into pico-, nano-, and microplankton fractions and determined AP activities of each separately. Picoplankton
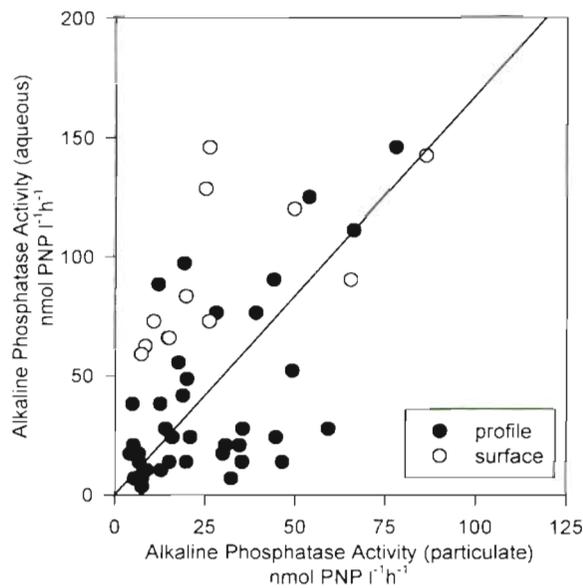
Fig. 5. Aqueous akaline phosphatase activity as a function of particulate alkaline phosphatase activity for depth profiles (●) at Stns A, B and M in the Gulf of Aqaba and surface samples (O) of the northern Red Sea and the Gulf of Aqaba along a south-north transect
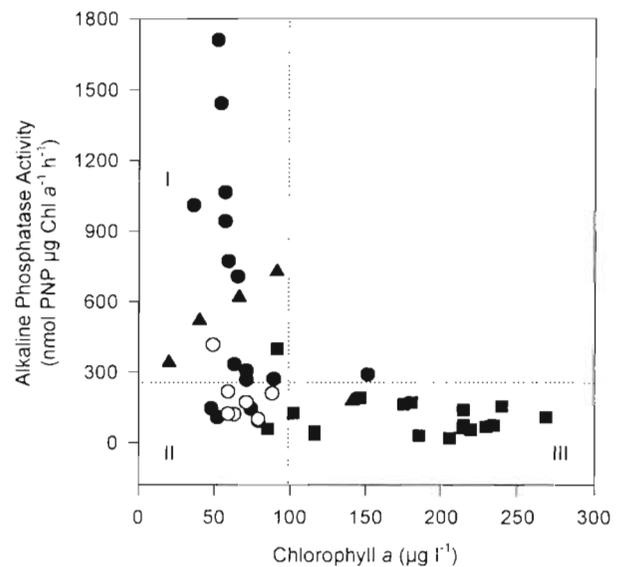

Fig. 6. Chlorophyll a-specific alkaline phosphatase activities as a function of chlorophyll a concentrations for samples taken from 0 to 60 m in the northern half (●) and southern half (O) of the Gulf, from 60 to 120 m (■), and from >120 m (▲). I, II and III denote arbitrary areas consistent with P-depleted, low P and P-replete conditions respectively

contributed 63% of total particulate activity for all samples taken at Stns A, B and M. Nanoplankton contributed 20% and microplankton 17%. While the picoplankton contribution was always most pronounced, the relative contribution of pico-, nano-, and microplankton fractions to total particulate AP activities varied with location in the Gulf of Aqaba (Table 1). Interestingly, the picoplankton contribution rose from 50 to 71% moving south, with a decline in contribution from 37 to 3% by microplankton. Size-fractionated activities for surface samples taken along the south-north transect were similar to the mean of those observed along depth profiles (Table 1). Stepwise mul-

Table 1. Relative contribution (mean ± SE) of different plankton size fractions to alkaline phosphatase activities associated with total particulate matter along depth gradients at Stns A, B and M and in surface waters along a transect from the northern Red Sea (Stn 1) to the northern tip of the Gulf of Aqaba (Stn A)

Sampling site	Alkaline phosphatase activity (% of total)		
	Pico-plankton (0.2–2.0 µm)	Nano-plankton (2.0–20 µm)	Micro-plankton (>20 µm)
Stn A (depth profile)	50 ± 13	12 ± 4	37 ± 15
Stn B (depth profile)	66 ± 18	20 ± 8	14 ± 15
Stn M (depth profile)	71 ± 5	27 ± 8	3 ± 4
Surface transect	62 ± 18	20 ± 9	18 ± 18

tiple regression of aqueous AP activity versus distance from head of the Gulf, depth and the different size fractions revealed that approximately 44% of the variance in the aqueous AP activity was derived from the picoplankton fraction, 16% from differences in distance and only 3% from differences in depth (multiple $R = 0.72$; adjusted $R^2 = 0.45$; $n = 35$; $p < 0.002$). These findings suggest that most AP activity in the water column (particulate and aqueous) was derived from the picoplankton fraction. The depth distributions of the abundant picoplankter Synechococcus were similar to those of AP activities (Fig. 3) and its abundance showed a strong correlation with both aqueous ($r_p = 0.73$; $p < 0.001$; $n = 20$) and particulate ($r_p = 0.63$; $p < 0.005$; $n = 20$) AP activities. This indicates that 53% of variation in aqueous activity and 39% of that in particulate activity can be explained from variation in Synechococcus cell numbers.

Patterns of chlorophyll a concentrations along depth profiles and the surface transect were distinctly different from those for AP activities. A plot of all combined data of chlorophyll a specific AP activity versus chlorophyll a concentration shows an exponential decrease in activity with increasing chlorophyll a levels (Fig. 6). Inspection of 3 arbitrarily defined regions (I, II and III in Fig. 6) reveals that group III consists nearly exclusively of observations from the bottom half of the photic zone (60 to 150 m deep). Groups I and II were both made up of observations from the upper half of the photic layer (0 to 60 m), with the distinction that

most data points from the southern half of the Gulf of Aqaba (open circles) were located in group II and data in group I were mostly from the northern half (solid circles).

DISCUSSION

The major findings of our study are (1) planktonic communities showed AP activities in P_i-depleted waters, (2) AP activities in particle-free seawater showed a surprising longevity and (3) depth distributions of AP activity correlated with those of the abundant picoplankter *Synechococcus* AP activitities were detected in both aqueous and particulate fractions throughout the stratified photic layer of the Gulf of Aqaba, but were maximal in the surface layer. Aqueous activities were stable over extended periods (2 to 40 d), after which enzyme activities reached a minimal level at both low and ambient temperatures. The relevance of long AP life-times has not been discussed for the marine environment so far. The strong correlation between particulate and aqueous AP activities implies that the AP produced by the planktonic community is subsequently released to the surrounding waters. During a period of stable stratification in June 1996, inorganic phosphate (P_i) concentrations were <15 nM in the upper 150 to 200 m, low enough to become limiting for phytoplankton productivity (Krom et al. 1991, Krom et al. 1993, Vaulot et al. 1996, Scanlan et al. 1997). In contrast to other plankton groups phytoplankton satisfy their P-demand from P_i-supply (Harrison 1980). They may therefore be responsible for significant extracellular AP activity (Ammerman & Azam 1991b, Cotner & Wetzel 1991). Samples from the upper 60 m of the water column in the northern half of the Gulf were characterized by low chlorophyll *a* concentrations and high AP activities (see Figs. 3 & 6). These findings are consistent with the occurrence of P_i-limiting conditions in the northern part of the Gulf which are reflected in an adaptive response of the planktonic community to low ambient P_i-levels. Samples from the southern half of the Gulf had experienced phosphate-replete conditions in their recent past at the Straits of Tiran. Here, phosphate is injected into Gulf of Aqaba surface waters from deeper layers by local turbulence at this location (Murray et al. 1984) and through P-losses from coral reef communities (Korpal 1991). Indeed we observed elevated chlorophyll *a* concentrations and low chlorophyll *a*-specific alkaline phosphatase activities in surface samples from the southerly half of the Gulf.

Although picoplankton have a high surface:volume ratio, advantageous for meeting their nutrient de-

mands (Chisholm 1992), AP activities were mostly associated with this size fraction, suggesting that they respond most strongly to P_i-depletion. Depth distributions of AP activities in the Gulf of Aqaba bore a high similarity to those of the picoplanktonic cyanobacterium *Synechococcus*, whose maximal concentrations are found in the upper 50 m. *Prochlorococcus* (when present), eukaryotic algae and heterotrophic bacteria have distinctly different depth distributions (Lindell & Post 1995, Post & Angel unpubl. results). P_i-depletion causes a prompt induction of AP activity by the freshwater *Synechococcus* strain PCC 7942, and a large part of this activity is found as free dissolved enzyme activity (Block & Grossman 1988). Marine *Synechococcus* strain WH7803 responds to P_i-limitation with induced synthesis of a high affinity phosphate uptake system (Scanlan et al. 1993) and of organic P-uptake capacity (Donald et al. 1997). Recently, *Synechococcus* was shown to contribute significantly to ATP (a substrate for AP) and P_i-uptake in the P_i-deplete waters of the Sargasso Sea (Cotner et al. 1998). *Synechococcus* was shown to be more susceptible to P_i-limitation than *Prochlorococcus* (Parpais et al. 1996, Vaulot et al. 1996) and can thus be expected to induce AP synthesis at a less advanced stage of P-depletion.

Induction of extracellular AP activities is a common response of planktonic communities to low inorganic P-supply and it may convey information about their P-history (see e.g. Chróst 1991, Wynne & Bergstein-Ben Dan 1995, Cotner et al. 1997). P_i-starvation immediately induces the synthesis of AP, following which maximal activity can be detected at the cell's exterior within 2 to 12 h (Vargo & Shanley 1985, Block & Grossman 1988). In the freshwater *Synechococcus* strain PCC 7942, AP may be released to the aqueous environment and these activities are detected between 4 to 12 h (Block & Grossman 1988). Its long lifetime (2 to 40 d, this study) exceeds the average generation time of most phytoplankton species (Lande et al. 1989, Vaulot & Partensky 1992, DiTullio et al. 1993, Liu et al. 1995). On the basis of these considerations we can compare the relative levels of aqueous and particulate AP activities and consider the hypothetical model for P_i-availability and AP levels of planktonic communities found in Table 2.

Table 2. Hypothetical model for P_i-availability and AP levels of planktonic communities

Aqueous	Particulate	P-history
Absent	Low or absent	No P_i-limitation
Low	High	Recent P_i-limitation (h to d)
High	High	Persisting P_i-limitation (d to wk)
High	Low or absent	Recent relief from P_i-limitation

On the basis of this division we consider the situation encountered in the northern half of the Gulf of Aqaba, where aqueous AP contributed 42 to 74% of combined particulate and aqueous activity, as one of persistent P_i-limitation. The fact that aqueous AP activities were proportional to those of the particulate matter at all depths suggests that both aqueous and particulate AP activities reflect the low P_i- history of this body of water up to the day of sampling.

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