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Phosphorus limitation of primary productivity in the eastern Mediterranean Sea

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Abstract

Although NO_3^- is generally considered to limit primary productivity in most of the world's oceans, previous studies have suggested the Mediterranean Sea may be an exception. In this study of the southeastern Mediterranean, we found that all the PO_4^{3-} was removed from the upper water column during the winter phytoplankton bloom in the core and boundary of a warm-core eddy, while measurable (0.3–0.6 μM) NO_3^- remained. The N:P ($NO_3^-:PO_4^{3-}$) ratio in the core and boundary of the Cyprus eddy was 27.4 and the slope of the linear portion of the N vs. P scattergram was 25.5 with a positive intercept of 0.5 μM on the NO_3^- axis. A similar N:P ratio (28–29), slope (21–23), and intercept (0.9–1.1) was found for the water column across much of the southern Levantine basin. These data, taken together with the results of incubation experiments, lead us to conclude that the southeastern Mediterranean is strongly P limited. The degree of P limitation increases from west to east across the entire basin. We suggest that removal of PO_4^{3-} by adsorbtion on Fe^- rich dust particles may be an important process controlling the concentration of P in the water column.

NO_3^- is generally considered to be the master chemical variable limiting primary productivity throughout much of the ocean (Codispoti 1989). It is based principally on considerations of the N:P ratios of upwelling waters which are generally <16:1 molar ratio, on nutrient enrichment experiments, and from observations of residual PO_4^{3-} when NO_3^- (plus NO_2^- and NH_3) has diminished to undetectable concentrations. There are, however, particular environments where the N supply keeps up with demand, such as the tropical lagoons studied by Smith and coworkers (Smith 1984).

Both NO_3^- and PO_4^{3-} are depleted in the Mediterranean Sea compared to the adjacent Atlantic Ocean principally because the waters flowing into the Mediterranean at Gibraltar are nutrient-depleted surface waters. The counterbalancing outflow is of relatively nutrient-enriched intermediate and deep waters. Berland et al. (1980) noted that the Mediterranean is different from most other major ocean basins in that P seems to play a more important role in phytoplankton limitation. Several studies carried out in the western basin have shown that P is either the principal limiting nutrient or is the limiting nutrient for part of the year (e.g. Fiala et al. 1976). However, more recently, Owens et al. (1989) suggested that on the balance of evidence, the western basin appears to be N limited. Pojed and Kveder (1977) working in the northern Adriatic Sea believed P was the limiting nutrient in the

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growth of phytoplankton. Vukudin and Stojanski (1976) were of the same opinion from their work in the middle and southern Adriatic.

In one of the few studies carried out in the eastern basin, Becacos-Kontos (1977) suggested that the factors limiting primary productivity in the waters of the Gulf of Saronique (Aegean Sea) were sometimes solely P and sometimes both P and N. MacIsaac and Dugdale (1972), in studies conducted near Greece, reported enhancement of NO_3^- uptake after addition of PO_4^{3-} but did not draw any definite conclusions on the limiting nutrient. Bonin et al. (1989) showed that C and P uptake by natural microplankton populations collected from two stations adjacent to the coast of Israel was enhanced by adding PO_4^{3-} and PO_4^{3-} + NO_3^- but not by adding NO_3^- alone. Similar results have been reported recently from stations farther offshore in the Levantine basin (Berland et al. 1987). Azov (1986) found a correlation between chlorophyll and PO_4^{3-} content at two locations off Haifa, Israel, which he suggested implied that the waters were P limited.

The tendency of deeper Mediterranean waters to be depleted in PO_4^{3-} relative to NO_3^- has been observed previously (Miller et al. 1970; Coste et al. 1984). Miller et al. (1970) found N : P ratios >16 in the deep waters from the Adriatic, Ionian, and Ligurian Seas, while he measured an N : P ratio of 16 : 1 in the Levantine basin. In the one station (No. 404) of the GEOSECS program in which nutrients were determined just east of the Strait of Sicily in the Mediterranean, N : P ratios of 24.1 were measured in the deep water (Spencer 1983).

In 1988 and 1989, we made a series of cruises to examine the physical structure and nutrient dynamics of a quasi-stationary, warm-core eddy situated south of Cyprus (Krom et al. in press.). To determine which element (N or P) limits phytoplankton productivity in the southeast basin of the Mediterranean, we present recent data on PO_4^{3-} and NO_3^- from the eddy and data from part of a survey cruise to the southern Levantine basin. With the available data, we offer a plausible explanation of the processes that might be important in controlling the observed nutrient limitation.

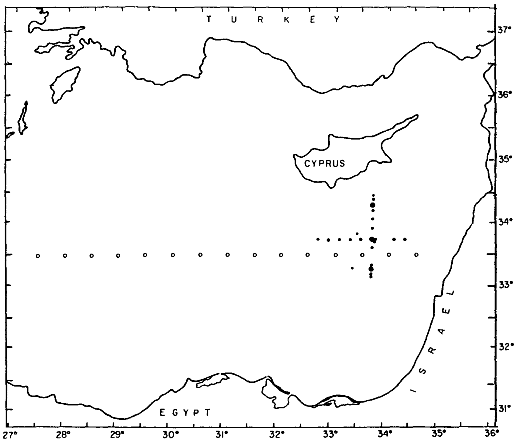

Fig. 1. Map of the southeastern Levantine basin showing the station locations used to sample the warm-core eddy in May 1989 as typical of all the eddy cruises (●) and those stations sampled across the eastern Mediterranean which have been used in this study (○).

Methods

Area of study—Field observations were taken aboard the RV *Shikmona* as part of a series of cruises to the Levantine basin in 1989. Four cruises were made to the Cyprus eddy. The cruises were made in February, May, September, and November 1989. Figure 1 indicates the May 1989 stations. A similar orthogonal series of stations was carried out for all the eddy cruises with the intersection of the sampling locations being the center of the eddy. The boundary station was located at the northern edge of the eddy. At the core and boundary locations, multiple sampling casts were made. In addition to the eddy cruises, a series of samples was taken during the LDSB-01 cruise to the Levantine basin in March 1989. Those stations from which data are presented are shown in Fig. 1.

Sampling and analysis—Water samples were collected with a General Oceanics rosette equipped with 10 1.5-liter Niskin bottles. The water was sampled for dissolved oxygen and then for nutrients as soon as the rosette was taken on-board. Duplicate samples were collected in 15-ml plastic scintillation vials which were either new or had

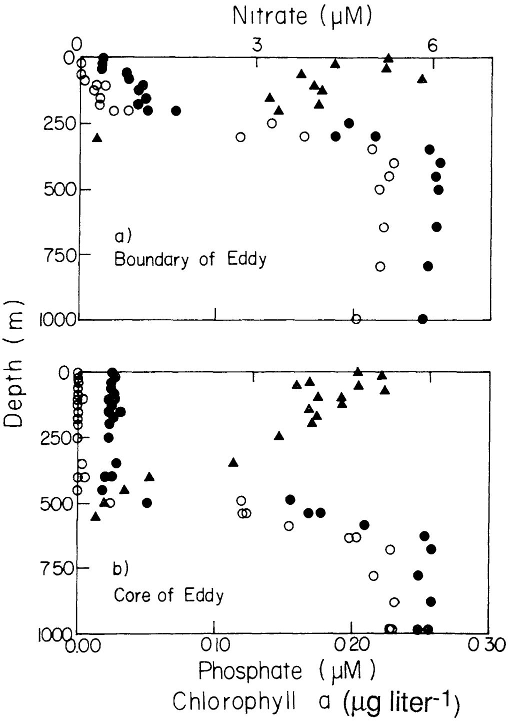

Fig. 2. NO_3^- (●), PO_4^{3-} (○), and Chl *a* (▲) vs. depth in the boundary and core stations of the Cyprus eddy sampled in February 1989.

been used previously only for eastern Mediterranean water samples. The vials were prewashed with 10% HCl and drained but not rinsed. At the time of sampling, the sample bottles were rinsed twice with the sample, filled with sample, and then immediately frozen in a custom-made rack. Special care was needed in preparing the sampling bottles because of the low levels of nutrients extant in the eastern Mediterranean. In the laboratory, the samples were thawed in warm water and analyzed within 1–2 h. Sample determination was generally carried out within 1 week of the completion of the cruise and always within 3 weeks.

The nutrient determinations were carried out on a hybrid autoanalyzer system with NO_3^- (and silicic acid) being measured on a rapid flow analysis Alpkem system attached to a Technicon AA-II sampler. PO_4^{3-} was measured on a Technicon AA-II AutoAnalyzer. NO_3^- was determined with a copperized Cd open-tube reactor method. NO_2^- was measured on several profiles. The results were all <0.07 μM, which was close to the limits of detection of the procedure used. Thus all data measured as $NO_3^- + NO_2^-$ are effectively NO_3^-. PO_4^{3-} was determined with the molybdate/hydrazine procedure of Atlas et al. (1971) and the modification that no wetting agent was used. Eastern Mediterranean surface water was used for the baseline. A sample of deionized, distilled water was run with each batch of samples to determine the nutrient content of the baseline sample after suitable correction was made for the refractive index effect (Atlas et al. 1971). The short-term precision (1 SD) determined with replicate samples collected in the field was 0.02 μM for NO_3^- and 0.003 μM for PO_4^{3-}. The limit of detection (2 × the SD of the blank) for the procedures was 0.05 μM for NO_3^- and 0.012 μM for PO_4^{3-}.

Samples (100 ml) for Chl *a* determination were filtered immediately after the water samples were taken. The samples were filtered onto GF/F glass-fiber filters after prefiltration through a 60-μm sieve. The samples were folded into Al foil and immediately frozen until they could be analyzed in the lab (within 2 weeks). Chl *a* was determined with the acetone extraction procedure of Strickland and Parsons (1972) and their equations.

Results

During the winter cruise (February) to the eddy, a mixed layer was observed with constant temperature and salinity to a depth of 200 m at the boundary station and 450 m at the core station (Krom et al. in press). At this time, in the boundary station, Chl *a* was scattered in the range of 0.15–0.25 μg $liter^{-1}$ in the upper 100 m and decreased to undetectable values at 300 m (Fig. 2a). In the core station, Chl *a* was also somewhat scattered (0.15–0.23 μg $liter^{-1}$) in the upper 100 m and decreased to zero at a depth of 550–600 m (Fig. 2b). PO_4^{3-} was undetectable (<0.01 μM) in the mixed zone of both stations, while the NO_3^- content was 0.3–0.6 μM at the boundary station and 0.5–0.7 μM in the core station. Below the mixed layer there was a similar-shaped nutricline at both stations, with a small nutrient maximum at 500 m at the boundary and at 750–

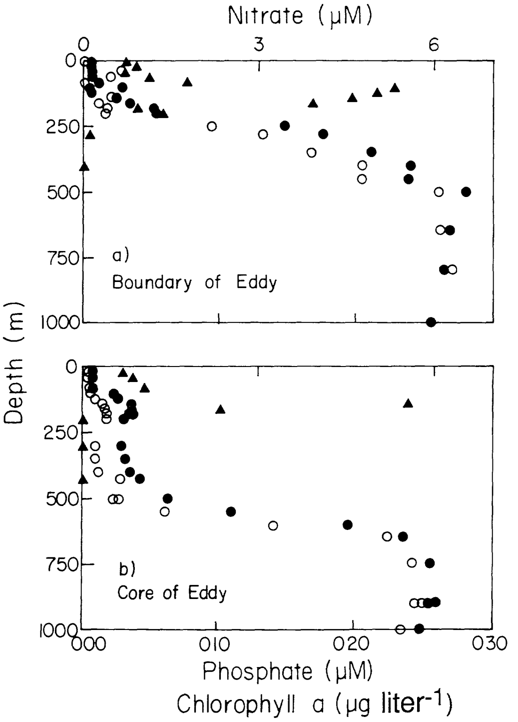

Fig. 3. As Fig. 2, but in May 1989 as typical of summer conditions.

800 m in the core and about constant values of 5.5 μM NO_3^- and 0.24 μM PO_4^{3-} below.

In May, a surface pycnocline developed at a depth of 30–50 m which remained until the end of the year (Krom et al. in press). During this period, a Chl *a* maximum was observed at a depth of 90–120 m which decreased to zero at ~200-m depth (Fig. 3). This pattern was similar to that observed elsewhere in the Levantine basin (Berman et al. 1986). The dissolved nutrient levels were at or close to the limits of analytical detection in the upper 100 m at both the boundary and core stations (Fig. 3). Below this depth at the boundary station, the main nutricline was observed in which nutrients increased to about constant levels at 500 m. In the core of the eddy, there was a zone from 100 to 450 m in which there was a small buildup of nutrients with the main nutricline being observed from 450 to 650 m. The N : P (NO_3^- : PO_4^{3-}) ratio was relatively low (2–25) in the upper 100 m at both boundary and core stations (Fig. 4). However both NO_3^- and PO_4^{3-} were close to the limits of the analytical precision in this depth range and therefore such ratios may not be reliable. At a depth of 100–300 m in the boundary station, the N : P ratio increased to values up to 120. From 300 m to the lowest depth sampled, the N : P ratio was constant at 27.3±2.5 (Table 1). In the core station the pattern was more complicated. In the depth range from 100 to 450 m there was a scatter of N : P ratios between 20 and 100. The highest values were observed at the top of the minor nutricline immediately below the Chl *a* maximum (100–200 m) and at the top of the major nutricline (450–550 m) in May. Below 550 m the N : P ratio was constant at 27.5±4.0. Similar ratios (~25) have been measured in samples taken in the eastern Mediterranean from the RV *Knorr* and measured on-board ship during 1988 (Boyle and Christiansen unpubl. data).

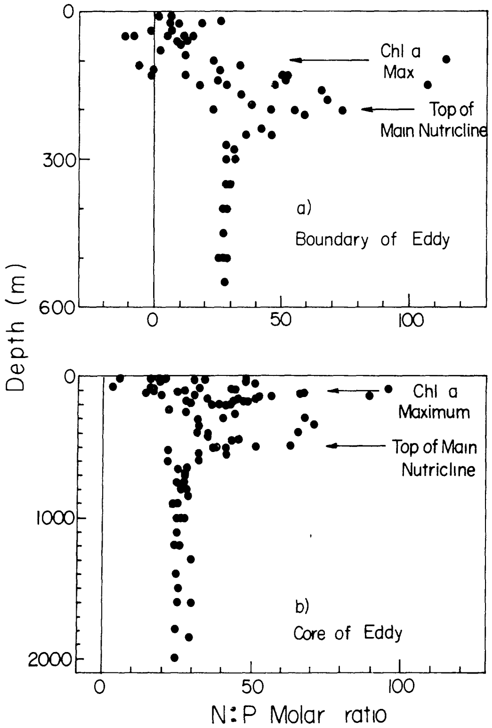

Fig. 4. N : P (NO_3^- : PO_4^{3-}) ratio vs. depth in the boundary and core stations of the Cyprus eddy. These figures combine data from May, September, and November 1989. The depth of the Chl *a* maximum and the top of the main nutricline are shown. Note the change in depth scale between panels.

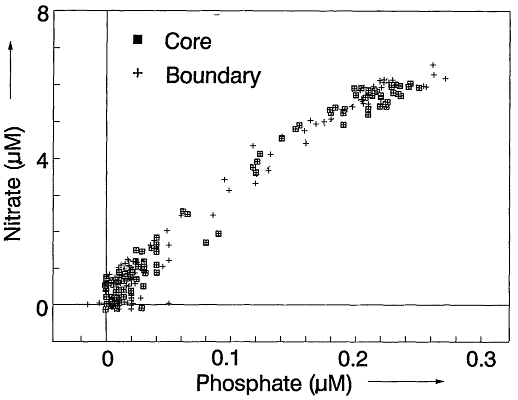

Fig. 5. NO_3^- vs. PO_4^{3-} in combined data from both the core and boundary stations of the Cyprus eddy. Data from February, May, September, and November 1989. Of the 272 data points included, 15 are from depths >1,000 m.

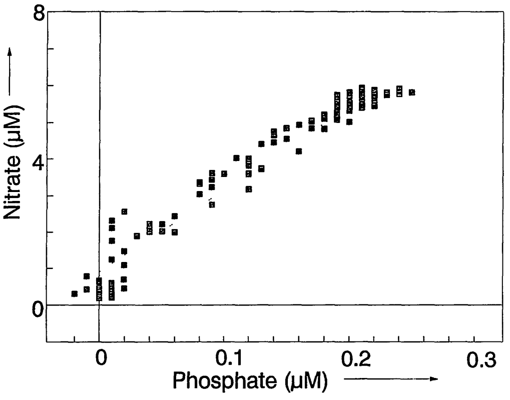

Fig. 6. NO_3^- vs. PO_4^{3-} from stations sampled across the southeastern Levantine basin at 33°30'N collected at 0.5° spacing from 34°30'E to 27°30'E. Of the 150 data points included, 10 are from depths >1,000 m.

Figure 5 shows all of the NO_3^- vs. PO_4^{3-} for the core and boundary stations of the eddy plotted together. Although the depth of the nutricline was shallower in the boundary than in the core due to the physical structure of the eddy (Krom et al. in press), the N vs. P relationship was similar at both locations. The increase in nutrient content can be represented by a straight line from 0.5 to >6 µM NO_3^- and 0 to >0.21 µM PO_4^{3-} with a variable low level of nutrients in the lowest range of concentration and some nonlinearity in the deepest samples where PO_4^{3-} increased by 0.02–0.03 µM but NO_3^- did not. A best-fit straight line for the linear portion of the data set calculated for the core station resulted in an equation with a slope of 25.6; for the boundary station, it was 25.3 (Table 1). Both data sets had a positive intercept of 0.5 µM NO_3^- when PO_4^{3-} was zero. The scattergram for a set of nutrient samples collected across the southeastern Levantine basin showed a similar pattern (Fig. 6) with a calculated slope for the linear portion of the data set

Table 1. Elemental ratio of dissolved nutrients (NO_3^- : PO_4^{3-}) in the water column across the Mediterranean basin.

Location	Regression equation*	r^2	N : P ratio	No. of data	Source
Cyprus eddy core station (500–2,000 m)	N = 21.1P + 1.1	0.89	27.5±4.0†	46	This study
Cyprus eddy boundary station (300–1,000 m)	N = 20.7P + 1.3	0.91	27.3±2.5	35	This study
SE Levantine basin (200–2,000 m)	N = 22.9P + 0.89	0.95	28.1±3.0	152	This study
Cretan Strait (0–2,000 m)	N = 20.8P + 1.13	0.95	28.9±4.6	203	This study
GEOSECS 404 (Sea of Crete, 100–4,000 m)	N = 18.7P + 1.08	0.98	24.3±0.7	20	Spencer 1983
Alboran Sea (Sta. 73; 100–2,800 m)	N = 19.1P + 1.12	0.96	22.5±1.6	18	Coste et al. 1984
GEOSECS 115 (N. Atlantic)	N = 14.5P + 0.75	0.99	15.2±0.7	53	Bainbridge 1981

* Regression line calculated for the linear portion of the data only. The surface-depleted zone and, when appropriate, the deepest samples were not included in this calculation.

† The N : P ratio was calculated excluding the data from 500–550-m depth because these appeared to have significantly higher N : P ratios than the remaining samples. A discussion of the possible reasons for this observation is given in the text.

of N = 22.9 P and an intercept of 0.9 μM NO_3^-. The N : P ratio across the southeastern Levantine basin was 28.1 ± 3.0.

Discussion

At the onset of deep winter mixing, the water column of the eddy was mixed to a depth of 450 m in the core of the eddy and 200 m in the boundary (Krom et al. in press). A phytoplankton bloom developed soon after the nutrients were supplied to the euphotic zone. During this bloom all the PO_4^{3-} was removed to a depth of 450 m in the core and 250 m in the boundary, while measurable amounts of NO_3^- (0.3–0.7 μM) remained (Fig. 2). Although the values of NO_3^- are low by "normal" oceanic standards, they are above the limit of detection for the analytical procedure used for these nutrient-poor eastern Mediterranean waters. By May, when the water column had thermally stratified, and for the rest of summer, the level of NO_3^- and PO_4^{3-} were both close to the limit of detection and cannot be used directly to determine which nutrient was limiting the observed productivity.

The elemental ratio of dissolved nutrients ($NO_3^- : PO_4^{3-}$) in the water column has been used in previous studies to suggest which element is limiting (Codispoti 1989). For most areas of the world's oceans, the phytoplankton uptake ratio of N : P should be close to the Redfield ratio of 16 : 1 (by atoms) in a healthy marine ecosystem (Codispoti 1989). It is based on phytoplankton growth experiments (Goldman et al. 1979) as well as a large-scale study of the ratio in particulate matter (Copin-Montegut and Copin-Montegut 1983). Although Takahashi et al. (1985) argued that the ratios for O : C : N : P obtained by Redfield et al. (1963) are too low, the ratio of N : P in their study was still 16 : 1.

The N : P ratio for the water column in the Cyprus eddy was 27.5 ± 4.0 (Table 1; Fig. 4). Similarly the N : P ratio for the southwestern Levantine basin below 200 m was 28.1 ± 3.0 (Table 1). Both ratios represent a major deviation from the normal elemental ratio of 15–16 : 1 as represented, for example, by station 115 of the GEOSECS program in the North Atlantic (Table 1).

In sampling across the eddy, unusually high N : P ratios (25–120) were found at the upper boundaries of the nutriclines. Similar high values for the N : P ratio have been observed in subsurface layers of the western Mediterranean (Raimbault and Coste 1990). Although these boundaries are below the 1% light level (90–120 m), measurable chlorophyll was observed. It is suggested here and by Raimbault and Coste (1990) that these values may be due to preferential uptake of PO_4^{3-} by nutrient-starved phytoplankton. They concluded that this observation represents additional evidence to that provided by nutrient ratios to confirm severe P limitation in the western Mediterranean. Below the upper level of the nutricline, the chlorophyll level dropped to zero and thus further nutrient uptake by phytoplankton cannot be occurring. At these depths the N : P ratios were relatively constant.

Limited but direct evidence for P limitation also exists from thymidine incorporation experiments. The addition of PO_4^{3-} to samples of water taken from the core of the warm core eddy in September resulted in a significant increase in the bacterial uptake of [^{3}H]thymidine in comparison to samples in which 15 μM glucose was added or controls with no additions were made (Wood et al. in prep.). Unfortunately, the comparable experiment made with NO_3^- addition was lost on-board ship. Such an increase in microbial activity is most simply explained as being due to P limitation in the sample. MacIsaac and Dugdale (1972) reported that they observed no simple pattern of increase in NO_3^- uptake while testing the response of a population of microplankton collected near Greece to the addition of five concentrations of NO_3^-. By contrast, the addition of PO_4^{3-} resulted in a significant increase in the rate of NO_3^- uptake. They noted that the enhancement of NO_3^- uptake with other nutrients had not been observed before and suggested that this might be because previous experiments had not been attempted in such infertile waters. A simpler explanation is that this observation supports the other evidence presented here that waters of the eastern Mediterranean are strongly PO_4^{3-} limited. Both

Bonin et al. (1989) and Berland et al. (1987) found that biological activity in natural microbial populations was enhanced by adding PO_4^{3-} and $PO_4^{3-} + NO_3^-$ but not by adding NO_3^- alone.

In this study, it has been shown that the N : P ratio increases in the Mediterranean from west to east with a value of 22.5 : 1 being found in the Alboran Sea, 24.3 : 1 being found at station 404 of GEOSECS in the Sea of Crete, and 27–29 : 1 measured in the eastern basin of the Mediterranean (Table 1). Similarly the calculated slope of the linear portion of the N vs. P scattergram increases systematically to the east (though the magnitude of the intercept does not). Although Berland et al. (1980) suggested that at least part of the western basin of the Mediterranean is P limited at least occasionally, Owens et al. (1989) suggested on the basis of "various nutritional status indices" that production over much of the western basin is slightly N limited. Our study clearly suggests that the eastern basin is PO_4^{3-} limited. Furthermore, the degree of P limitation seems to increase to the east although the pattern as shown, for example, by the N : P ratios in the water column is not simple (unpubl. data) and is complicated both by the complex structure of jets and eddies that are known to exist in the area (Hecht et al. 1988) and by the unknown time scales of the processes that are modifying the N : P ratio.

The regression line calculated from the linear portion of the scattergram plot for NO_3^- vs. PO_4^{3-} for the southern Levantine basin has a slope of 22.9 (Fig. 6, Table 1). The equation for the nutrient increase with depth in the eddy had a slope of 25.6 in the core and 25.3 in the boundary. These ratios are all significantly greater than the usual value of 14–16 found in most of the world's oceans and also somewhat greater than the ratio of 19 found in the western Mediterranean (Table 1). A linear regression relationship of the type observed in this study can be due to simple stochiometric regeneration of NO_3^- and PO_4^{3-} in the water column or to mixing of two water bodies with different initial nutrient contents or to a combination of both processes. Thus, Takahashi et al. (1985) argued that the normal Redfield ratio for organic matter composition in the Atlantic calculated with the simple slope of the NO_3^- vs. PO_4^{3-} regression line may be incorrect because the end-member water masses have different preformed nutrient contents. In the Levantine basin, the two relevant water mass end-members are Levantine Intermediate Water which is formed in the basin and has essentially no nutrients in it initially and Levantine Deep Water (LDW; Hecht et al. 1988). LDW forms principally in the Adriatic and then flows eastward across the basin.

Bethoux and Copin-Montegut (1986) noted that the outflowing waters at Gibraltar had an N : P ratio of 22 : 1. They suggested, in part, on the basis of a nutrient budget for the entire basin that this high ratio was due to unusually high rates of N fixation and that much of the fixation was probably due to extensive beds of seagrasses, principally *Posidonia.* If this hypothesis were correct, more N fixation should be occurring in the eastern basin of the Mediterranean than in the western basin. There are however no substantial beds of *Posidonia* (or any other N-fixing seagrass) found along the coast of Israel (recent observations made with a remote operated vehicle: B. Galil pers. comm.). Bonin et al. (1989) observed that when natural populations of microplankton from southeast Mediterranean coastal waters were enriched with PO_4^{3-} and incubated in the light for 5 d, a large increase in total N was observed. They proposed that N fixation, mediated by picocyanobacteria, may explain these findings. However, in order for substantial N fixation to occur, they noted that excess P must be present.

An alternative explanation, not considered in the previous studies that have examined these unusually high nutrient ratios, is removal of P from the water column by inorganic processes. The proposed mechanism may also be important in the Red Sea, which is the only other large body of marine water where the N : P ratio is significantly >16 : 1 (Naqvi et al. 1986). It is known that Fe oxyhydroxides have a strong affinity for PO_4^{3-} and adsorption coefficients in excess of 500–5,000 have been measured in oxic marine sediments (Berner 1973 *cited by* Krom and Berner 1980). Several studies have shown that substantial quantities of dust are blown across the Mediterranean, particularly the central and eastern basins (Guerzoni et al. 1989). Chester et al. (1977) found the overall average dust loading in the eastern Mediterranean (14 μg m^{-3} air) to be among the highest recorded for maritime soil-sized dusts. This dust comes from the Sahara Desert and also from local sources, particularly in summer when the area is dry. It contains a high proportion of Fe oxides and poorly crystalline clay minerals, both of which have a high affinity for dissolved PO_4^{3-}. We suggest that this dust removes PO_4^{3-} as it falls through the water column, particularly from the deeper layers where there is no competition by phytoplankton uptake and the PO_4^{3-} content is relatively higher. The total amount of PO_4^{3-} that would need to be removed from the deeper layers to produce the entire observed deficiency is ~0.1 μM.

In order to explain the observed slope of the regression line entirely as a result of simple regeneration, it is necessary that the N : P ratio of the decomposing organic matter be unusually high. Direct measurements of this quantity were not made during this study. The core of the eddy is effectively isolated from the surrounding waters and, as a result, Krom et al. (in press) were able to calculate the new production in the core of the eddy from the total annual nutrient budget for the euphotic zone of the eddy core. The N : P ratio for this new production was 18.7. Although this ratio is >16 : 1, it is substantially lower than that needed to explain the entire N : P anomaly as regeneration. In addition the C : N : P ratio measured for particulate organic matter sampled in the chlorophyll maximum at a series of stations 30–100 km from the coast of Egypt was 110 : 16.5 : 1 (Abdel-Moati 1990—close to normal Redfield ratios.

If this mechanism were important, the organic C : total P in the sediment of the eastern Mediterranean should be lower than that found elsewhere. Calvert (1983) measured the organic C : total P ratio in sediments (15 cm) from the Levantine basin to be 106 : 4.8, which is lower than the ratio of 106 : 0.8–1.4 found in sediments (10–30 cm) collected from a similar water depth in the eastern Atlantic (Hartmann et al. 1976). Furthermore because there is such a low input of organic matter into the sediment, the surface layers in the Levantine basin are expected to remain oxic to a substantial depth, and remobilization of PO_4^{3-} as it passes through the oxic–anoxic boundary (Krom and Berner 1981) is unlikely to result in a significant release of this inorganically bound PO_4^{3-} into the water column as occurs in nearshore sediments.

Graham and Duce (1979) showed that 36% of the total P present in atmospheric dust samples collected at Narragansett, Rhode Island, was released within 12 h when placed in low nutrient (<0.1 μM) Sargasso Sea water. This dust contained a mixture of natural and anthropogenic material. In comparison they quote Lepple (1975) as showing that only 8% of the total P present in Saharan dust is released. Both these experiments were conducted at levels of PO_4^{3-} in seawater where desorption would be expected to predominate; we are suggesting the adsorption of PO_4^{3-} is likely to occur in deeper waters. Our preliminary findings suggest that removal of P by adsorption onto mineral particles may be an important process in the eastern Mediterranean and demonstrate the need for a rigorous test of this hypothesis.

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