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The fate of phosphate in an in situ Lagrangian addition experiment in the Eastern Mediterranean

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Abstract

The Eastern Mediterranean is the largest oceanic ecosystem that is phosphate-limited. To determine the impact of a transient input we executed a phosphate addition experiment in the surface waters of the Cyprus Eddy (33.3°N 32.3°E), and compared the ecosystem response with surrounding unperturbed water. A tracer, sulphur hexafluoride (SF_6), added with the phosphate, enabled tracking of the patch when phosphate concentration declined to detection limits, and provided quantitative estimates of mixing, dilution and patch volume. The patch expanded to $>400\,km^2$ over 9 days with a lateral diffusion rate of $23\pm2\,m^2/s$ that was consistent with previous tracer releases in eddies. Mixed layer phosphate concentration was ~110 nmol/l immediately post-release, and declined to <5 nmol/l after 6 days. A phosphate budget was developed using SF_6 as a proxy to discriminate between dilution and biological pathways, with dilution resulting in loss of ~75% of added phosphate from the patch centre by day 3. Non-conservative phosphate loss was largely due to biological incorporation into particulate-P, of which 50% accumulated at the patch centre whilst the remainder was removed by lateral dilution by day 3. Non-conservative phosphate loss at the patch centre was 15–15.5 nmol/l by day 4, which was equal to the cumulative biological P uptake of 15.6 (±5.6) nmol/l P and concurred with two other independent estimates of P uptake. This closure of the phosphate budget infers that the transfer of added P to mesozooplankton and higher consumers was not significant within the timescale of the experiment, despite the observed biomass increase that followed phosphate addition. Although patch dilution significantly reduced phosphate concentration and particulate accumulation, and so the apparent biological response to the added phosphate, analysis suggests that lateral mixing would not prevent bacterial biomass accumulation at the growth rates observed, suggesting that another factor such as grazing was responsible.

Keywords: Dilution; Phosphate; Phytoplankton; Bacteria; Eastern Mediterranean; Phosphate enrichment; Diffusion

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1. Introduction

The Eastern Mediterranean is an ultra-oligotrophic body of water that is recognised as the largest open ocean region in which primary production is limited by phosphate availability (Krom et al., 1991). Phosphate and nitrate in surface waters are extremely low during spring-summer, and this is reflected in low phytoplankton biomass, with chlorophyll *a* at less than 0.5 mg m^{-3} (Krom et al., 2005; Psarra et al., 2005). Over winter surface water nutrients are replenished by deep mixing with Levantine Intermediate Water that has an inorganic N:P ratio of 29. As this represents the primary source of nutrients for autotrophic production it is perhaps not surprising that, following biological uptake, excess dissolved inorganic nitrogen remains (0.5–1 μmol/l), whereas phosphate is undetectable using conventional micromolar analytical techniques (Krom et al., 1992, 2003). Phosphate limitation during late winter-spring has also been inferred from microcosm experiments which have shown increases in phosphate uptake and phytoplankton biomass upon phosphate addition or combined phosphate and nitrate additions, but not with nitrate addition alone (Bonin et al., 1989). Phytoplankton and heterotrophic bacterial production were also shown to be P-limited during winter in both the Levantine Basin and Cretan Sea (Zohary and Robarts, 1998; Christaki et al., 2001). The presence of Alkaline Phosphatase, an enzyme produced in response to low phosphate, is further evidence of physiological P limitation in spring (Thingstad and Mantoura, 2005). However, the situation appears more equivocal in summer, when the absence of both nitrate and phosphate in surface waters, and the observed biological response to addition of either nutrient in microcosm experiments, suggests seasonal co-limitation (Krom et al., 2003; Zohary et al., 2005).

The uncertainty regarding P limitation, or N and P co-limitation, makes it difficult to predict how the Eastern Mediterranean will respond to chronic or acute change in nutrient supply. Allochthonous nutrient sources in the Eastern Mediterranean to the coastal margins include aeolian deposition, terrestrial run-off, mariculture and sewage outfalls, although the impact of the latter examples is localised. The region receives significant dust deposition originating from the Sahara, which has been identified as both a potential sink (Krom et al., 1991), and source of N and P (Carbo et al., 2005; Herut et al., 1999, 2005). Climate change may potentially result in variability in wind mass trajectory and aridification that may alter both the composition, and the frequency and duration of aeolian input to the E. Mediterranean (Carbo et al., 2005), with potential implications for microbial community structure and productivity. Aeolian dust input currently maintains availability of the micronutrient iron in the Eastern Mediterranean at levels that exceed the global average for the open ocean (Krom et al., 2003), which may influence nitrogen fixation in this region (Gruber and Sarmiento, 1997). Climate forcing may also influence nutrient supply to the Eastern Mediterranean via water mass circulation. Recent reported changes in deep water formation (Roether et al., 1996) indicate increased upward mixing in the Levantine basin and shoaling of the nutricline (Klein et al., 1999), which may alter long term productivity and community composition.

Although the Eastern Mediterranean is highly vulnerable to change, the ecosystem response to variation in nutrient supply has received little attention. This is in contrast to other regions such as high nitrate low chlorophyll (HNLC) waters, in which ecosystem response to the limiting micronutrient, iron, is well documented. Increases in iron availability in HNLC waters generally stimulates a strong response in the larger autotrophs, with significant biomass accumulation by diatoms (Boyd et al., 2000), whereas the response of the heterotrophic and autotrophic picoplankton is limited by microzooplankton grazing (Hall and Safi, 2001). However, in contrast to HNLC waters, heterotrophic bacteria and phytoplankton biomasses are of similar magnitude in low nutrient low chlorophyll (LNLC) regions such as the Eastern Mediterranean (Pitta et al., 2005; Li et al., 1992). In addition, the potential for N and P co-limitation, or switching of limiting nutrient when the other is available, confirms that HNLC regions are not appropriate models for LNLC regions. Although our current understanding of nutrient limitation in the E. Mediterranean is primarily based upon microcosm experiments (Bonin et al., 1989; Zohary and Robarts, 1998), the observations from such experiments may not reflect the in situ response due to artefacts such as exclusion of larger consumers, altered cycles of light, mixing and turbulence, surface effects and potential nutrient contamination (Banse, 1991). Mesoscale in situ addition experiments have successfully overcome the limitations of