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Role of DOP on the alkaline phosphatase activity of size fractionated plankton in coastal waters in the NW Mediterranean Sea (Toulon Bay, France)

Gérard Bogé *, Magali Lespilette, Dominique Jamet, Jean-Louis Jamet

Laboratoire PROTEE-EBMA (EA 3819), Université de Toulon, CS 60584, 83041 Toulon Cedex 9, France

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ABSTRACT

The particulate material was fractionated into 5 size classes (>90 μ, 50–90 μ, 6–50 μ, 1–6 μ, and <1 μ). DOP was analysed as easily (DOPh, DOPpa) and less easily hydrolysable compounds (DOPox). Based on Vmax, 94% of the high affinity AP activity was due to <50 μ cells and 77% to <1 μ cells. 83% of the low affinity activity was due to >90 μ cells. The high affinity activities were negatively correlated with DOP for the <50 μ classes. These correlations came mostly from DOPox. They were more significant when $NO_3 + NO_2$ concentrations were high, when DIP concentrations were low and when N/P ratio was >10. At lower N/P ratios, AP was more significantly correlated with DIP. The low affinity activities showed significant negative correlation with DIP and with DOP and DOPox for the >90 μ class. The inhibition of AP activities by DOPox may originate from stable compounds interfering with DIP for the control of AP synthesis.

1. Introduction

In water, phosphorus is present as inorganic or organic compounds (Benitez-Nelson, 2000; Paytan and McLaughlin, 2007). The inorganic phosphorus is directly used by plankton. In the Mediterranean, one of the most oligotrophic seas in the world, DIP concentrations are particularly low, especially in the eastern basin and they are rapidly insufficient to cover phosphorus requirements of the living matter (Thingstad et al., 1998, 2005; Céa et al., 2015; Van Wambeke et al., 2002; Pujo-Pay et al., 2011; Lazzari et al., 2016). In such conditions, various strategies are implemented by plankton to reach their nutrients needs, to sustain their production rate and growth and to limit the decrease of biomass.

Plankton cells have the capacity to use phosphorus stored as polyphosphate (Orchard et al., 2010), to replace membrane phospholipids by non-phosphorus molecules (Martin et al., 2011), and to synthesize high affinity DIP transporters in order to extract phosphate at lower concentrations and energy coast (Chung et al., 2003; Yao et al., 2011). A selection of small species with higher Surface/Volume ratio ensures also a more efficient nutrient uptake (Ignatiades et al., 2002; Tambi et al., 2009; Litchman, 2007).

But the most efficient strategies concern DOP utilization. DOP comprises bioavailable compounds among which phosphoric esters are the most commonly used by plankton (Nausch and Nausch, 2004, 2006; McLaughlin et al., 2013; Ivančić et al., 2009, 2010, 2016). Ectoenzymes such as alkaline phosphatase hydrolyse monoesters, and nucleotidases hydrolyse diesters (Suzumura et al., 1998; Ammerman and Azam, 1985; Sato et al., 2013). DOP is thus converted to biodisponible phosphate, phosphorus being recycled several times per day (Nausch and Nausch, 2006; McLaughlin et al., 2013). When the nutrient deficiency is particularly severe, compounds more resistant to hydrolysis such as phosphonates are dephosphorylated by intracellular enzymes, notably CP lyase (Villarreal-Chiu et al., 2012; Dyhrman et al., 2007).

The synthesis of these ecto- and intracellular enzymes is regulated via the Pi signal transduction pathway (PHO) (Hsieh and Wanner, 2010; Dick et al., 2011). This synthesis is repressed at high DIP concentrations and is derepressed at low concentrations. (Jansson et al., 1988). Phosphate sensors inside and outside the cells adjust the phosphate response to cellular needs (Mouillon and Persson, 2006) so that enzyme activities are negatively correlated to external or intracellular phosphate concentrations (Jansson et al., 1988; Litchman and Nguyen, 2008).

These strategies depend on DIP concentrations but also on NO_3/PO_4 ratios. In the marine environment, this ratio is close to 16 (Redfield et al., 1963). When this ratio exhibits higher values, the production is limited

Abbreviations: AP, alkaline phosphatase; SRP, soluble reactive phosphorus; DIP, dissolved inorganic phosphorus; DOPpa, AP hydrolysable dissolved organic phosphorus; DOPh, acid hydrolysable dissolved organic phosphorus; DOPox, Non hydrolysable dissolved organic phosphorus; DOP, total dissolved organic phosphorus; Pi, Inorganic Phosphorus.

* Corresponding author.
E-mail addresses: boge@univ-tln.fr (G. Bogé), m_lespilette@yahoo.fr (M. Lespilette), d.jamet@univ-tln.fr (D. Jamet), jamet@univ-tln.fr (J.-L. Jamet).

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by phosphorus and the species capable of using organic phosphorus are selected. In the Mediterranean, this ratio is often close to 22, which denotes a limitation by phosphorus (Pujo-Pay et al., 2011; Tanhua et al., 2013; Lazzari et al., 2016). In coastal waters, increased terrestrial inputs of N and P are greatly modifying nutrient cycling and thereby plankton production can be limited by nitrogen, phosphorus or colimited by the two elements (Sardans et al., 2012).

For several years, we study the alkaline phosphatase activity from plankton in Toulon bay and its relation with dissolved phosphorus compounds (Bogé et al., 2006, 2012, 2013, 2014). The analysis of the data collected monthly in Toulon Bay in 2005/2006 has already shown that: a) the bulk AP activity resulted from dissolved and particulate activities (Bogé et al., 2012) ; b) the dissolved and the particulate activities were described by multiphasic kinetics with low and high affinities (Bogé et al., 2013), c) the particulate activity was negatively correlated with DIP when DOP concentrations were low, and with DOP especially when DIP concentrations were low (Bogé et al., 2012, 2013, 2014); d) non AP-hydrolyable compounds were mostly responsible for the negative correlations with the particulate activity (Bogé et al., 2014).

This work was intended to deeper investigate the impact of DOP on AP activity from the particular material of different size classes. The contribution of each size class to the total activity was first examined. Thereafter, the correlations between the activity of each size class and DOP concentrations were analyzed in relation with the concentrations of DIP, $NO_3 + NO_2$ and with the N/P ratios. DOP included easily hydrolysable compounds (acid hydrolysable phosphorus: DOPh, and Alkaline Phosphatase-hydrolysable phosphorus: DOPpa), and compounds which were more difficult to hydrolyse (non acid hydrolysable but oxydable phosphorus: DOPox).

2. Methodology

2.1. Study sites

Toulon Bay is located on the southern coast of France on the Mediterranean Sea (Lat. 43°5′ N and Long. 6°0′ E) (Fig. 1). Toulon Bay is subdivided into two zones: “Little Bay” (LiB) and “Large Bay” (LaB), separated by an artificial breakwater. Little Bay is semi-enclosed and shelters the naval port and the commercial port of Toulon. It received the Las River. Large Bay is open to the sea and receives the Eygoutier River.

2.2. Sampling procedure

Seawater was collected monthly in Little Bay (Fig. 1: S1) and in Large Bay (Fig. 1: S2) in 2005 (19.04, 30.05, 15.06, 05.07, 24.08, 12.09, 04.10, 14.11, 15.12) and in 2006 (10.01, 28.02, 14.03), between 0.8:00 AM and 10:00 AM using a Niskin bottle.

2.3. Analysis

2.3.1. Phosphorus

This analysis was carried out on samples passed through filters with 0.45 µ pores. Phosphorus was analysed as Dissolved Inorganic Phosphorus (DIP), Dissolved Organic Phosphorus (DOP), acid hydrolysable phosphorus (DOPh), Alkaline Phosphatase-hydrolysable phosphorus (DOPpa) and oxydable non hydrolysable phosphorus (DOPox).

DIP was quantified as soluble reactive phosphorus (SRP) measured according to the standard phosphomolybdate blue method (Murphy and Riley, 1962).

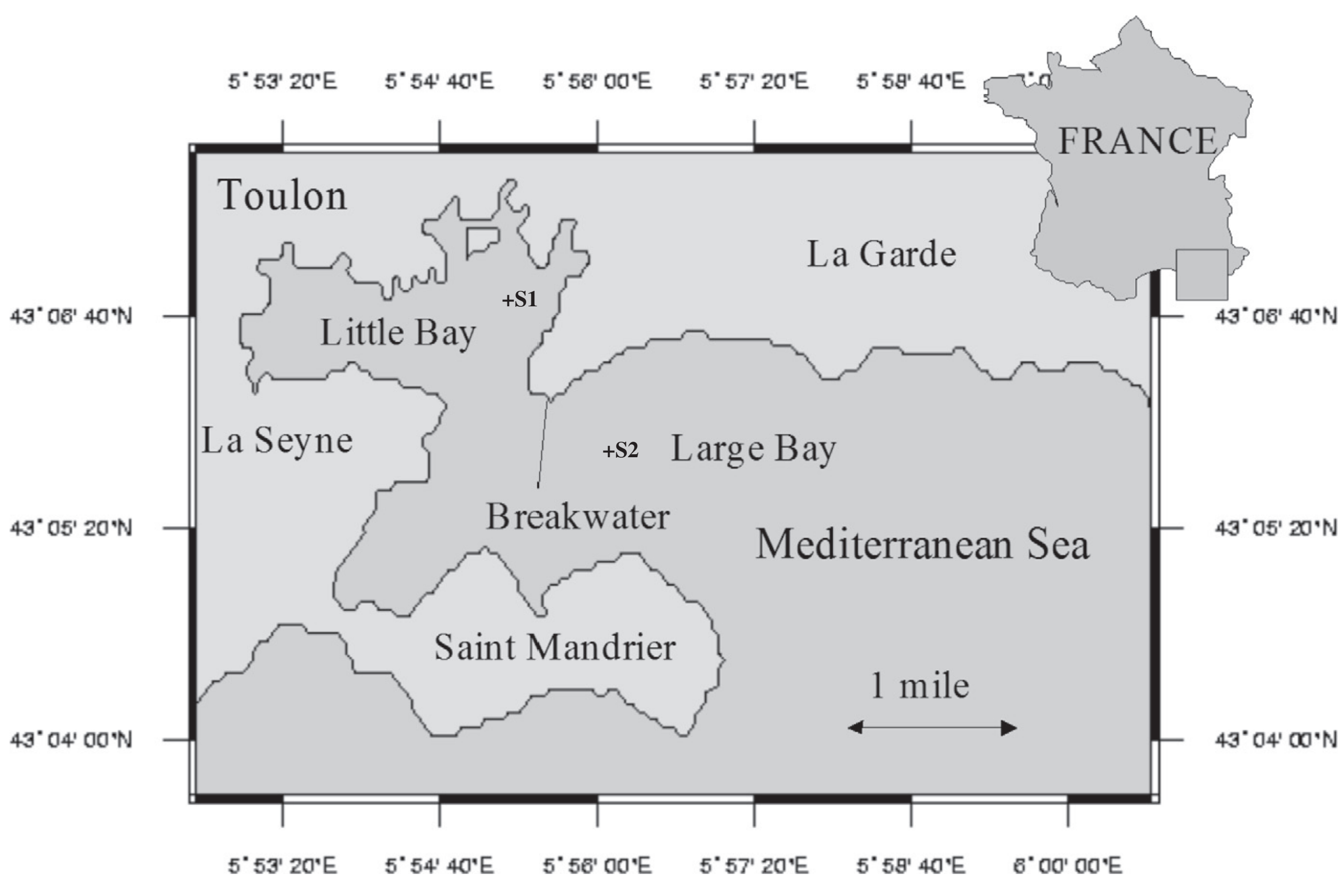

Fig. 1. Map of Toulon Bay.