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## Water flux management and phytoplankton communities in a Mediterranean coastal lagoon. Part II: Mixotrophy of dinoflagellates as an adaptive strategy?

P. Cecchi <sup>a,\*</sup>, M. Garrido <sup>b,2</sup>, Y. Collos <sup>a,1</sup>, V. Pasqualini <sup>b</sup>

<sup>a</sup> UMR MARBEC, IRD – CNRS – Ifremer – University of Montpellier, CC093, 34095 Montpellier Cedex 5, France

<sup>b</sup> UMR 6134 CNRS Sciences for the Environment, UMS 3514 CNRS, Stella Mare, University of Corsica, BP 52, 20250 Corte, France

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## ABSTRACT

Dinoflagellate proliferation is common in coastal waters, and trophic strategies are often advanced to explain the success of these organisms. The Biguglia lagoon is a Mediterranean brackish ecosystem where eutrophication has long been an issue, and where dominance of dinoflagellates has persisted for several years. Monthly monitoring of fluorescence-based properties of phytoplankton communities carried out in 2010 suggested that photosynthesis alone could not support the observed situation all year round. Contrasting food webs developed depending on the hydrological season, with a gradual shift from autotrophy to heterotrophy. Progressively, microphytoplankton assemblages became unequivocally dominated by a *Prorocentrum minimum* bloom, which exhibited very weak effective photosynthetic performance, whereas paradoxically its theoretical capacities remained fully operational. Different environmental hypotheses explaining this discrepancy were examined, but rejected. We conclude that *P. minimum* bloom persistence is sustained by mixotrophic strategies, with complex compromises between phototrophy and phagotrophy, as evidenced by fluorescence-based observations.

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## 1. Introduction

Coastal lagoons are among the richest reservoirs of ecological diversity and biological productivity, and support many different important ecosystem services (Nixon, 1982; Costanza et al., 1997; Barbier et al., 2011). Owing to their transitional location between continental and marine biota, these ecosystems are naturally subject to various environmental stresses that induce deep spatiotemporal changes in their physical, chemical and biological properties (Barnes, 1980; Day et al., 2000; Telesh and Khlebovich, 2010). However, coastal lagoons are also severely impacted by increasing anthropogenic pressures: more than 40% of the world's population already lives within 100 km of a coastline, and an even larger proportion is forecasted for the forthcoming decades (Martinez et al., 2007; Duxbury and Dickinson, 2007). Land use dynamics on watersheds strongly controls fluxes towards aquatic ecosystems, which are becoming more and more polluted, over-enriched in nutrients and light-depleted. This combination of disturbances greatly influences their metabolism, as regularly documented for Mediterranean coastal wetlands (Alvarez-Cobelas et al., 2005; La Jeunesse et al., 2002;

Plus et al., 2006; Serrano et al., 2006; Flo et al., 2011). Chemical contamination and 'cultural eutrophication' are widespread threats that can dramatically compromise the ecological integrity of these valuable ecosystems. In addition, the erosion of local biodiversity and the modification of natural habitat (mainly for commercial and recreational purposes) may help to promote the successful installation of opportunistic and potentially invasive organisms (Garcès and Camp, 2012). On Mediterranean coasts, the conjunction of these factors has been postulated as the main explanation for the increasing frequency of phytoplankton blooms, sometimes facilitated by anthropogenic introduction of exotic species through the transfer of ballast water or shellfish stocks (Estrada and Vaqué, 2014).

Phytoplankton blooms correspond primarily to a natural component of plankton community dynamics in marine ecosystems (Margalef, 1978; Wyatt, 2014), with in particular diatoms flourishing seasonally in coastal waters. However, for several decades, the expansion of dinoflagellate blooms (red tides and/or harmful algal blooms – HABs) has become a worldwide societal and research concern (Hallegraeff, 1993, 2003). In the Mediterranean Sea, blooms (>100,000 cells L<sup>-1</sup>) and more specifically HABs, have been rarely documented before the 1980s (Jacques and Sournia, 1978–1979; Fig. 1A), and no significant toxic episodes had ever been recorded in this area (Smayda, 1990; Hallegraeff, 1993; Masó and Garcès, 2006). Since then, the focused interest of researchers concerned by this international issue, together with the current expansion of plankton blooms, has prompted the publication of numerous reports (Silva, 1985; Paulmier, 1986;

\* Corresponding author.

E-mail addresses: [Philippe.Cecchi@ird.fr](mailto:Philippe.Cecchi@ird.fr) (P. Cecchi), [Marie.Garrido@oec.fr](mailto:Marie.Garrido@oec.fr) (M. Garrido), [pasquali@univ-corse.fr](mailto:pasquali@univ-corse.fr) (V. Pasqualini).<sup>1</sup> Deceased.<sup>2</sup> Present address: OEC - Office de l'Environnement de la Corse, Avenue Paul Giacobbi, 20600 Bastia, France.

Denardou-Queneherve et al., 1999; Garcès et al., 1999; Caroppo et al., 2001; Vila et al., 2001; Luglie et al., 2003; Koukaras and Nikolaidis, 2004; Chomérat, 2005; Vila et al., 2005; Frehi et al., 2007; Nincevic-Gladan et al., 2008; Souchu et al., 2010; Zingone, 2010; Laabir et al., 2011; Garrido et al., 2016; Fig. 1B).

The underlying causes of this global increase remained poorly understood for a long time, but the relationship between increased abundance of harmful algae and increasing nutrient loads is now universally recognized as a world-wide expression of eutrophication in coastal ecosystems (Anderson et al., 2002, 2008; Glibert et al., 2005; Glibert and Burkholder, 2006; Heisler et al., 2008). The species-specific response of phytoplankton assemblages remains however hardly predictable, as it depends on the physiology of the potentially involved organisms, environmental conditions, and the chemical form of the supplied nutrients (Glibert and Burkholder, 2006; Burkholder et al., 2008). As outlined by Smayda (2008), this is particularly true when considering the potential relationships linking the trophic status of aquatic ecosystems (along a gradient from oligotrophic waters to hypertrophic waters) and the occurrence of dinoflagellate proliferation. For example, and in line with historical evidence, toxic events associated with *Alexandrium minimum* proliferation along Mediterranean coasts have been linked to excessive nutrient loads carried by local inputs (Vila et al., 2005). Conversely, recurrent blooms of *Alexandrium catenella* [recently renamed *A. pacificum*, John et al., 2014a, 2014b] documented in the Thau lagoon (French Mediterranean coastal ecosystem) have been primarily associated with the 'oligotrophication' of the water masses (Collos et al., 2009). In fact, dinoflagellate blooms can occur over a broad range of trophic situations, even if they have lower nutrient uptake affinities than diatoms, their next largest competitors. Planktonic dinoflagellates have accordingly developed different but complementary adaptive strategies for the acquisition of nutrients under imbalance conditions (Stoecker, 1998; Dagenais-Bellefeuille and Morse, 2013; Johnson, 2015).

Many attempts have been made to formalize the conditions required for blooms to develop and to maintain. The model of phytoplankton life-forms defined by Margalef in 1978 has long been the best guide to describe marine phytoplankton assemblages and their successions (Margalef, 1978). It summarizes the coupled effects of water motion (turbulence and light) and trophic status (nutrient availability) on phytoplankton selection, and provides a matrix in which phytoplankton growth strategies can be organized. Within this framework, HABs were said to correspond to 'spectacular local accumulation rather than *in situ* growth' [p. 450 in Smayda and Reynolds (2001)]. However, the low nutrient uptake affinities (elevated  $K_s$  values) regularly observed for bloom-forming dinoflagellates (Smayda, 1997; Fig. 1 in Kudela et al., 2010; Table 2 in Glibert et al., 2012) conflicted with the Margalef model. This apparent paradox was later clarified by Smayda and Reynolds (2001), who again used the life-form concept for describing HAB events, but in decoupling nutrient availability and turbulence, whose interdependency had previously been denied (Reynolds, 1986). This enabled the authors to propose a gradient of life-form properties along a continuum of progressively decreasing nutrient resources and reduced vertical mixing. Ultimately, a model with nine life-form types having distinctive morphotype traits and habitat preferences was proposed, encompassing all known characters of dinoflagellate HAB events [see Fig. 5 in Smayda and Reynolds (2001)]. One of the major outcomes of the ordination of dinoflagellates along this continuum is the explicit recognition of the different adaptive strategies they develop to satisfy their nutrient requirements despite their weak intrinsic physiological capacities (elevated  $K_s$  values are ecologically disadvantageous). For Smayda (1997), four main adaptations are involved: (i) motility and vertical migrations toward nutrient-rich horizons, (ii) allelochemical interactions to alleviate interspecific competition, (iii) allelopathy potential to enhance defense, and (iv) mixotrophic nutritional strategies to meet carbon and/or inorganic nutrient requirements for photosynthesis, growth and reproduction.

Mixotrophy is defined by the simultaneous presence and some combination of both autotrophic and heterotrophic modes of nutrition, i.e., use of different sources of carbon and energy, for the same phytoplankton cell (Hansen, 2011). Three main physiological modes of mixotrophic behavior have been historically hypothesized (Stoecker, 1998; Matantseva and Skarlato, 2013), spaced along a gradient ranging between a pure photoautotrophy and a pure heterotrophy. Ideal mixotrophs for which phototrophy and phagotrophy are balanced (Model I) lie at one end, phagotrophic algae which are primarily phototrophic (Model II, with three sub-types) lie in the middle, and photosynthetic protozoa which are firstly phagotrophic (Model III, with two sub-types) lie at the other end. Model II seems to be largely shared by many photosynthetic organisms (except for diatoms, Stoecker et al., 2009) that depend firstly on light and inorganic nutrients, but are also able to assimilate organic materials, either for their growth in nutrient-depleted environments, or to meet their energy requirements under insufficient irradiance, or even in the dark. This strategy has long been considered to offer an important mode of nutrition in oligotrophic environments, but also increasingly to help explain the sustainable success of bloom-forming dinoflagellates in eutrophic coastal waters (Burkholder et al., 2008). It seems now recognized that mixotrophy should be considered as a unifying rule among aquatic photosynthetic protists (except for cyanobacteria and diatoms), and not as a strange characteristic of some of them (Flynn et al., 2013; Glibert et al., 2016); or at least that mixotrophs do constitute an important and distinct plankton group in terms of their functional traits, ecology and biogeochemical functions (Barton et al., 2013).

The bloom-forming dinoflagellate *Prorocentrum minimum* is representative of the Model IIA strategy (i.e. mixotrophy enhanced by nutrient imbalance), and has been extensively studied because of its impact on local microbial food webs, where it proliferates (Heil et al., 2005). It has recently been confirmed that the mixotrophic pathway adopted by this organism not only responds to inorganic nitrogen limitation (as previously documented by Stoecker et al. (1997)), but is also very strongly stimulated under P-limiting conditions (Johnson, 2015). This last author convincingly shows in particular that both N and P starvation promote mixotrophy, but by simultaneously inducing marked changes in photosynthetic parameters of *P. minimum* with a very significant diminution of its photochemical efficiency, corresponding to a reduced photoautotrophy performance. This could be associated with the necessary trade-offs between the two nutritional strategies when shared simultaneously within the same cell by a single organism (Flynn and Mitra, 2009).

Here we report on intriguing functional responses recently observed during a long-lasting bloom of *P. minimum* in a Mediterranean coastal lagoon in Corsica. Our initial aim was to document the impacts of a remediation operation (the management of water fluxes to alleviate the confinement of the lagoon) on phytoplankton communities, using data collected monthly over one year (2010) in the Biguglia lagoon. The evolution of their taxonomy and their pigment composition was studied, highlighting how this operation has perniciously promoted dinoflagellate dominance and facilitated the durable installation of a large *P. minimum* bloom in an ecosystem historically described as diatoms-dominated (see companion paper, Garrido et al., 2016). During this monitoring, fluorescence-based analyses (Phyto-PAM) were also performed. They gave meaningful insights into the seasonal fluctuations of the fitness of phytoplankton assemblages, but they also highlighted the peculiar physiological properties of *P. Prorocentrum* when its bloom expanded univocally over the whole lagoon. In the following sections, we will first summarize the main features of the environmental, spatial and temporal variability observed in 2010, and briefly present the evolution of phytoplankton communities during the survey. We will then introduce the two studied fluorescence proxies, in underlining their progressive but unexpected disconnection along the course of the monitoring. First, a series of alternative (external) environmental

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