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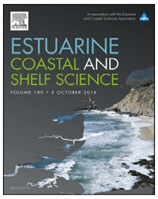

First steps of ecological restoration in Mediterranean lagoons: Shifts in phytoplankton communities

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ABSTRACT

Along the French Mediterranean coast, a complex of eight lagoons underwent intensive eutrophication over four decades, mainly related to nutrient over-enrichment from continuous sewage discharges. The lagoon complex displayed a wide trophic gradient from mesotrophy to hypertrophy and primary production was dominated by phytoplankton communities. In 2005, the implementation of an 11 km offshore outfall system diverted the treated sewage effluents leading to a drastic reduction of anthropogenic inputs of nitrogen and phosphorus into the lagoons. Time series data have been examined from 2000 to 2013 for physical, chemical and biological (phytoplankton) variables of the water column during the summer period. Since 2006, total nitrogen and phosphorus concentrations as well as chlorophyll biomass strongly decreased revealing an improvement in lagoon water quality. In summertime, the decline in phytoplankton biomass was accompanied by shifts in community structure and composition that could be explained by adopting a functional approach by considering the common functional traits of the main algal groups. These phytoplankton communities were dominated by functional groups of small-sized and fast-growing algae (diatoms, cryptophytes and green algae). The trajectories of summer phytoplankton communities displayed a complex response to changing nutrient loads over time. While diatoms were the major group in 2006 in all the lagoons, the summer phytoplankton composition in hypertrophic lagoons has shifted towards green algae, which are particularly well adapted to summertime conditions. All lagoons showed increasing proportion and occurrence of peridinin-rich dinophytes over time, probably related to their capacity for mixotrophy. The diversity patterns were marked by a strong variability in eutrophic and hypertrophic lagoons whereas phytoplankton community structure reached the highest diversity and stability in mesotrophic lagoons. We observe that during the re-oligotrophication process in coastal lagoons, phytoplankton shows complex trajectories with similarities with those observed in freshwater lake systems.

1. Introduction

Eutrophication has been defined as a suite of adverse symptoms resulting from the nutrient and organic inputs (De Jonge and Elliott, 2001). High biomass decreases light availability, favoring among the primary producers the community that is most competitive for light, *i.e.*, phytoplankton at the expense of macrophytes (Cebrian et al., 2014). This over-production causes a loss of diversity (Schramm, 1999; De Jonge and de Jong, 2002), habitat destruction and mortalities due to anoxia (Smith, 2006; Carlier et al., 2008). These phenomena negatively impact ecosystem health, result in increased vulnerability to disturbances (Heemsbergen et al., 2004; Worm and Lotze, 2006) and loss of ecosystem services (Bullock et al., 2011). In coastal areas, which are characterized by strong demographic growth, eutrophication has become a serious threat since the 1950s (Nixon, 1995). Coastal lagoons are particularly sensitive to eutrophication, since these systems tend to concentrate anthropogenic nutrient inputs (Knopper, 1994; Cloern, 2001; Kennish and Paerl, 2010) due to restricted exchanges with the sea and long water residence time (Boesch, 2002; Kennish and Paerl,

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2010; Glibert et al., 2011).

In 2000, The Water Framework Directive (WFD) was established in Europe requiring member states to monitor the ecological and chemical quality state of water bodies and implement ways to achieve good status by 2021 (Sherrard et al., 2006; Cartaxana et al., 2009). Efforts have been made in many parts of the world to combat eutrophication by reducing nutrient inputs from watersheds and initiate ecological restoration. Ecological restoration is well documented in lakes which have been subjected to water quality improvement programs since the 70s (Jeppesen et al., 2005, 2007). Studies on lake restoration have shown that the response trajectories during re-oligotrophication are not simply the inverse of the previous eutrophication processes and are characterized by hysteresis. Accordingly, the recovery of ecosystem functions often lagged behind the reduction of external nutrient loadings, due to nutrient regeneration from sediments or the persistence of turbid alternative states because of dense blooms of phytoplankton or the presence of a pool of easily resuspendable organic matter (Scheffer et al., 1993; Scheffer and Carpenter, 2003; Sondergaard et al., 2003; Ibelings et al., 2007). Because of these phenomena, re-oligotrophication processes are difficult to understand and predict for degraded systems (Van Donk et al., 2008). Hence, ecological restoration generally takes much longer than water degradation due to eutrophication. At first, it results in modifications of the composition and structure of primary producers communities. Phytoplankton is generally the first autotrophic compartment responding to the change of nutrient availability and other anthropogenic pressures (Livingston, 2000; Paerl et al., 2003). In restored lakes, this response has resulted in considerable changes of phytoplankton biomass, community structure and functional diversity (Ruggiu et al., 1998; Anneville and Pelletier, 2000; Katsiapi et al., 2013).

A functional approach to phytoplankton ecology appears particularly useful to study the adaptive responses of phytoplankton communities to re-oligotrophication. This approach is based on defining the functional traits of species that impact on their performance and survival (Violle et al., 2007) and, thus provides a better understanding of how phytoplankton communities respond to environmental changes. The functional approach has been used to understand how environmental changes or gradients drive phytoplankton community structure (Litchman et al., 2010). Some morphological and physiological traits particularly reflect the phytoplankton adaptations to nutrient availability, such as cell size, maximum growth rate and trophic regime (Litchman and Klausmeier, 2008; Litchman et al., 2010). During re-oligotrophication, the reduction of nutrient inputs could thus favor small cells, which compete more effectively for nutrient uptake and show high growth rates (Chisholm, 1992; Kamenir and Morabito, 2009; Litchman et al., 2010), and mixotrophic species that present some advantages over strictly autotrophic cells (Anneville and Pelletier, 2000). These functional traits highlight phytoplankton adaptations to the reduction of nutrient availability and represent an interesting tool to evaluate the impact of changing eutrophication status.

Since the implementation of the WFD, coastal waters represent a major issue for management and ecological restoration which has been used to reestablish ecosystems services. So far, little is known about the responses of coastal ecosystems to ecological restoration (Vidal et al., 1999; Duarte et al., 2009; Nixon, 2009). The recent literature describes a diversity of responses to restoration (Boesch, 2002; Elliott et al., 2007; Ho et al., 2008; Duarte et al., 2009), including a decrease of primary production while phytoplankton biomass remained stable (Philippart et al., 2007), reappearance of macrophyte communities (De Jonge and de Jong, 2002), and decrease of biomass and frequency of bloom occurrence (Lie et al., 2011). As shallow lakes, coastal lagoons have been particularly subjected to cultural eutrophication process due to nutrient over-enrichment from watersheds and long residence time (Kennish and Paerl, 2010; Glibert et al., 2011). Ecological restoration of coastal lagoons has started recently and studies of this process are still scarce. Given the high variability and dynamics of these systems, we can expect variable and complex restoration trajectories. During the re-oligotrophication process in a Mediterranean coastal lagoon (Collos et al., 2009), phytoplankton community changes were similar to those observed in some freshwater lakes, *i.e.* characterized by the appearance of dinophytes species and small-sized cyanobacteria (Ruggiu et al., 1998; Kamenir and Morabito, 2009). The results suggest some similar responses of lakes and coastal lagoons to re-oligotrophication process.

In the South of France, to improve the ecological quality of eight eutrophied coastal lagoons close to Montpellier, a drastic and persistent reduction of anthropogenic nutrient inputs has been achieved since December 2005, leading to a dynamic of ecological restoration. In the framework of a monitoring network, these lagoons and sixteen other lagoons have been monitored from 2000 to 2013 to assess their eutrophication status. These 24 lagoons presented a large eutrophication gradient ranging from oligotrophy to hypertrophy (Souchu et al., 2010), the most eutrophied lagoons showed phytoplankton dominance with high biomasses (>100 μgChla L^{-1}). The phytoplankton size structure was dominated by small eukaryotic algae (3–6 μm) with relatively high growth rates (Bec et al., 2008, 2011).

Prior to the reduction in nutrient loadings, the complex of eight lagoons represented a eutrophication gradient ranging from mesotrophic to hypertrophic, including the most hypertrophic lagoons of the region. This context offered us a unique opportunity to study how the initial eutrophication status of lagoons influences the re-oligotrophication trajectories and to assess the success of ecological restoration in these highly degraded systems. We focused on phytoplankton community shifts to investigate the impact of ecological restoration in coastal lagoons for this range of eutrophication levels. Using data from a 13-year monitoring program, we describe changes of phytoplankton biomass and structure (i.e., size class structure and community composition), by comparing two periods: before and after the nutrient reduction. In addition, after implementation of the nutrient reduction, HPLC pigment analyses were added to the monitoring program. This allowed us to study the dynamics of functional and taxonomic groups as well as phytoplankton diversity, based on pigment biomarkers, during re-oligotrophication trajectories.

2. Materials and methods

2.1. Studied sites

The Palavasian lagoon complex is located on the French Mediterranean coast, near Montpellier city (urban population 250,000 inhabitants). Since the 17th century, infilling and human constructions have compartmentalized a large natural lagoon to give rise to the current complex of eight interlinked shallow lagoons covering 38.8 km^2 (Fig. 1). A major human intervention was the building of a navigation canal through the natural lagoon oriented NE-SW, named the Rhône-to-Sète canal which divided the complex into two parts (inland and seafront lagoons). As a result, four of the eight lagoons (i.e., the inland lagoons North Ingril, Vic, Arnel, and Méjean lagoons) are bordered by wetland or salt marshes, which can act as a buffer zone and regulate freshwater inputs from the watershed. Four seafront lagoons (South Ingril, Pierre Blanche, Prévost, and Grec lagoons) are located between the Rhône-to-Sète canal and the lido. Among them, South Ingril and Prévost lagoons