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Spatiotemporal dynamics of submerged macrophyte status and watershed exploitation in a Mediterranean coastal lagoon: Understanding critical factors in ecosystem degradation and restoration

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Abstract :

Increases in the intensity of disturbances in coastal lagoons can lead to shifts in vegetation from aquatic angiosperms to macroalgal or phytoplankton communities. Such abrupt and discontinuous responses are facilitated by instability in the equilibrium controlling the trajectory of the community response. We hypothesized that the shift in macrophyte populations is reversible, and that this reversibility is dependent on changes in the pressures exerted on the watershed and lagoon functioning. Biguglia lagoon (Mediterranean Sea, Corsica) is an interesting case study for the evaluation of long-term coastal lagoon ecosystem functioning and the trajectory of submerged macrophyte responses to disturbances, to facilitate the appropriate restoration of ecosystems. We used historical data for a two hundred-year period to assess changes in human activities on the watershed of the Biguglia lagoon. Macrophyte mapping (from 1970) and monitoring data for dynamics (from 1999) were used to investigate the trajectory of the community response. The changes observed in this watershed included a large number of hydrological developments affecting salinity and resulting in changes in macrophyte distribution. Nutrient inputs over the last 40 years have led to a shift in the aquatic vegetation from predominantly aquatic angiosperm community to macroalgae and phytoplankton in 2007 (dystrophic crisis). Changes in hydrological management and improvements in sewage treatment after 2007 led to a significant increase of aquatic angiosperms over a relatively short period of time (4–5 years), particularly for Ruppia cirrhosa and Stuckenia pectinata. There has been a significant resurgence of Najas marina, due to changes in salinity. The observed community shift suggests that Biguglia lagoon is resilient and that the transition may be reversible. The restored communities closely resemble those present before disturbance. These findings demonstrate the need to understand watershed exploitation and ecosystem variability in lagoon restoration.

Keywords : Coastal lagoons, Human pressures, Long-term changes, Submerged macrophytes, Community shifts

1. Introduction

Coastal lagoons provide essential ecosystem services and have a high economic potential (Kjerfve, 1994). They are intrinsically unstable due to their transitional location between continental and marine biota, morphodynamics and environmental factors, potentially resulting in profound spatiotemporal changes in physical, chemical and biological conditions (Barnes, 1980; Bird, 1994; Day et al., 2000). Coastal lagoons have been among the most disturbed coastal ecosystems worldwide since the mid-20th century (De Jonge et al., 2002). Jennerjahn and Mitchell (2013) identified three categories of major hazards to ecosystems: human activities, climate change and extreme events. For example, increases in population density along coastlines, changes in watershed activities, hydrological regulation and eutrophication can strongly affect the physicochemical conditions in coastal lagoons (Nixon, 1995; Cloern, 2001; Lloret et al., 2008; Downing, 2014). Nevertheless, estuaries subject to anthropogenic and natural stresses often have similar characteristics, making it difficult to distinguish between them and, thus, to determine the nature of the anthropogenic stress (Jennerjahn and Mitchell, 2013). Increases in disturbance intensity and abrupt changes in disturbances can lead to persistent radical changes, resulting in the dominance of one or a few species (Folke et al., 2004; Cloern and Jassby, 2012). Folke et al. (2010) characterized the dynamics of complex social-ecological systems by studying three aspects: resilience, adaptability and transformability. Changes in system dynamics are referred to as regime shifts, and such shifts may be reversible or irreversible (Scheffer et al., 2001). Abrupt and discontinuous responses are facilitated by instability of the equilibrium controlling the trajectory of the community response (Collie et al., 2004; Suding et al., 2004; Schröder et al., 2005). Elliot et al. (2007) showed that disturbances affected both the structure and functioning of the ecosystem.

Submerged macrophytes are essential coastal lagoon species, with important structural and ecological functions (Sfriso et al., 2001, 2003; Duarte et al., 2002; Marzano et al., 2003; Garrido et al., 2013). They can be used as bioindicators of ecosystem health, because they display community-level responses to nutrients in the water, in terms of species diversity, structure and cover density (Pasqualini et al., 2006). Eutrophication can lead to vegetation shifts, described as a transition between alternative states, from pristine slow-growing benthic plants (aquatic angiosperms) to rapidly growing ephemeral plants (macroalgal or phytoplankton communities; Duarte, 1995; Viaroli et al., 1996; Valiela et al., 1997; Schramm, 1999; Dahlgren and Kautsky, 2004; Orfanidis et al., 2008a, 2008b; Viaroli et al., 2008). Under the low-nutrient and clear-water conditions of the pristine oligotrophic state, the late-successional angiosperms *Ruppia* and *Zostera* spp. become dominant (Pergent-Martini et al., 2005; Pergent et al., 2006). By contrast, opportunistic seaweeds, such as *Gracilaria, Ulva* and *Cladophora* spp., together with cyanobacteria and picophytoplankton, are indicators of the degraded eutrophic state, in which nutrient levels are high (Bec et al., 2011). The first conceptual model was proposed by Nienhuis (1992), and was based on a phase succession (aquatic angiosperms > aquatic angiosperms+epiphytes > macroalgae+phytoplankton). Schramm (1999) developed a model based on a similar successional representation (perennial benthic macrophytes > macrophytes+fast growing epiphytes > free floating macroalgae+phytoplankton > phytoplankton) adding a more detailed explanation of possible causes and trends. Viaroli et al. (2008) and Fong and Kennison (2010) also included cyanobacteria in their model. The primary causes of shifts and succession in the macrophyte community are nutrient loading (mostly nitrogen and phosphorus from watershed activities; Valiela et al., 1997; Dahlgren and Kautsky, 2004), changes in coastal hydrology and interactions between these factors. Primary producer succession may be strongly favored or prevented by water residence time (Flindt et al., 1997), as described by Valiela et al. (1997), Hauxwell and Valiela (2004), Dahlgreen and Kautsky (2004), where the effects of nutrients are related to hydrodynamics.

An understanding of the mechanisms controlling the capacity of an ecosystem to recover after disturbances and of the ways in which human activities can alter this capacity is crucial to the success of ecosystem restoration (Folke et al., 2004). A pronounced degradation of trophic state and decrease in macroalgal biomass has been recorded in Venice lagoon, together with a progressive expansion of seagrass meadows (Facca et al., 2014). Excess nutrients are thought to induce the shift between the two alternative states (Viaroli et al., 2008), both of which are thought to be resilient, due to the existence of feedback mechanisms (Carpenter et al., 2001). According to Clewell and Aronson (2007), it is not possible to separate humans and ecosystems entirely, and the satisfactory restoration of ecosystems is therefore dependent on attention being paid to the interactions between humans and the natural environment. A retrospective view of human activities is essential, to improve understanding, for the restoration of processes (Fukami and Wardle, 2005), particularly in unstable lagoon environments. One useful approach to understanding the long-term ecological dynamics of coastal lagoons is based on analyses of historical data concerning watershed activities, including changes to land use/cover and hydrological regulations in particular (Kemp et al., 2005; Steyaert et al., 2007). An understanding of the resilience of coastal lagoons and their capacity to recover efficiently after exposure to human stressors requires spatial and temporal data for submerged macrophytes (aquatic angiosperms and macroalgae), phytoplankton and environmental parameters reflecting water quality.

In this study, we analyzed the overall functioning of a coastal lagoon ecosystem, to determine the trajectory of the vegetation community response to the major human pressures, with a view to optimizing the restoration of the ecosystem. We focused on two particular objectives: (i) characterizing the functioning of the coastal lagoon in the medium and long term, as a function of pressures relating to watershed activities and local meteorological and hydrological conditions and (ii) following the spatiotemporal dynamics of macrophyte populations in response to recent anthropogenic pressures. In this context, Biguglia lagoon (Mediterranean Sea, Corsica, France; Fig.1) is an interesting case study, because data concerning anthropogenic pressures and macrophyte populations are available for a recent 15-year period. We hypothesized that the succession or shift in macrophyte populations is reversible, and that this reversibility depends on changes in the pressures exerted on the watershed and lagoon functioning. The key questions to be addressed are: (i) Are coastal lagoons resilient to changes in these pressures? (ii) If they are, then how similar are the pristine and restored communities? (iii) If they are not, what is the disturbance threshold beyond which they cannot recover?

2. Material and methods

2.1. Study site

Biguglia lagoon (42°36’N; 9°28’E) is a confined, shallow, brackish coastal lagoon (maximum depth: 1.8 m) covering 14.5 km² that is separated from the Mediterranean Sea by a long sandy beach (11 km; Fig. 1). The lagoon is linked to the Mediterranean Sea through a long (1.5 km), narrow, shallow natural channel to the north (Fig. 1). Marine water inputs are limited (Mouillot et al., 2000) because the sea channel tends to close (due to the accumulation of sand), and human intervention is sometimes required to open it again. Biguglia lagoon receives freshwater from the rivers draining its watershed (180 km²), mostly in the north-western part, from the River Golo (through an artificial channel: the Fossone canal) and from pumping stations draining the agricultural plain in the southern part of the watershed, sewage plants and rainfall (Fig. 1; Frisoni and Dutrieux, 1992). Freshwater inputs dominate the water budget (≈ 90 Mm^3 per year, for a total lagoon volume of 10.2 Mm^3) and lagoon renewal is rapid (< two months; Mouillot et al., 2000). This confined ecosystem has increasingly been disturbed by eutrophication associated with an intensification of agriculture and an increase in the density of urban settlements in the watershed, together with additional pressure due to the presence of tourists in the area in the summer (Frisoni and Dutrieux, 1992; Orsoni et al., 2001; Andral et al., 2007; Département de la Haute-Corse, 2012). Nutrient concentrations in this lagoon are higher than in most other Mediterranean lagoons (e.g. total nitrogen, ammonium in 1998; Orsoni et al., 2001; Souchu et al., 2010), due to the existence of fewer opportunities for dilution with seawater. High levels of silt and organic matter accumulation have been recorded across the entire lagoon (Orsoni et al., 2001). This lagoon has a Mediterranean climate, with large, unpredictable fluctuations in rainfall between years (Chauvelon et al., 2003). Biguglia lagoon was included in the RAMSAR list of wetlands of international importance in 1991, and has been classified as a nature reserve since 1994. It is managed by a local government agency (Département de la Haute-Corse, 2013). The lagoon is mostly used for professional fishing.

2.2. Environmental data

We used historical documents and maps to analyze the functioning of Biguglia lagoon and to identify the major anthropogenic pressures acting on the watershed in the long term (from the 18th century). Human population history between the early 19th century and the present day was assessed for all human settlements, based on the number of inhabitants per town (four towns in the watershed). The following population data were available: (i) from 1800 to 1999, population data collected at intervals of about five years (http://cassini.ehess.fr/cassini/fr/html/6_index.htm) and (ii) French National Statistics and

Economic Studies Agency (INSEE) data for 1999 to 2011, collected at intervals of seven to nine years. We used two maps to analyze historical land cover in the watershed. The first map of Corsica, *Plan Terrier*, was ordered in 1774 by Louis XV of France, to provide an inventory of the natural resources of the island after its acquisition (Caratini, 1995). This map is precise, at a scale of 1:10,000 (Source: *Archives départementales de Corse du Sud*; Albitreccia, 1942), and it was georeferenced with ArcGis version 10.0 (ESRI®). Land-cover patches were represented as polygons on a schematic topographic background. The polygons were redrawn in vector format, by tracing the lines of the scanned and georeferenced map. The CORINE land-cover program established a precise land-cover map of the study site for 2006 (http://www.statistiques.developpement-durable.gouv.fr/donnees-ligne/li/1825/1097/occupation-sols-corine-land-cover.html). For all these numerical vector maps, data were georeferenced with Lambert 93 coordinates, and we considered three generic land-cover types, as defined by the CORINE land cover program: forests and shrublands, farmland, and urban areas. The surface areas corresponding to these three generic land-cover types were calculated for the two maps (1774 and 2006). An additional survey was conducted in this area by the French fiscal services (Source: *Archives départementales de Haute-Corse*; Corvol, 1999). This survey provided information about the composition of the landscape for the year 1879, but in a non-spatial format. We used these data to obtain an intermediate update of landscape composition.

More detailed information about local meteorological and hydrological functioning began to become available from the 19th century onwards. Météo-France® has recorded annual spring and summer cumulative rainfall levels since 1948 at Bastia Airport, which is located close to the lagoon. Mean summer lagoon salinity data for the northern and southern basins were obtained from records published since 1930 (1930; 1978; 1982; 1983; 1990;

Burelli et al., 1979; Frisoni and Dutrieux, 1992; Orsoni et al., 2001; IFREMER data) and from recordings made during this study (from 1999 to 2014).

We used 10 parameters for the short-term analysis of water quality: salinity (PSU: practical salinity units), water temperature (°C), turbidity (NTU: nephelometric turbidity units), dissolved oxygen (O_2, %), nitrate (NO_3, µM), ammonium (NH_4, µM), nitrite (NO_2, µM), dissolved inorganic nitrogen ($DIN=NO_3+NH_4+NO_2$, µM), phosphate (DIP, µM), total nitrogen (TN, µM), total phosphorus (TP, µM) and chlorophyll *a* (chl *a*; $µg.L^{-1}$) concentrations. The database developed by the Lagoon Monitoring Network (*Réseau de Suivi Lagunaire*) can be used to assess the eutrophication status of lagoons (Souchu et al., 2010). Sampling was carried once monthly during the summer period (June, July and August) from 1999 to 2014 (but not in 2000, 2001 and 2005, due to technical problems), at two stations in the lagoon (the northern and southern basins; Fig. 1). Water was sampled principally during the summer period, corresponding to the peak of primary production in Mediterranean lagoons (Souchu et al., 2010; Bec et al., 2011). We avoided the collection of samples during periods of sediment resuspension, by not sampling for three days after any period in which wind speed exceeded 25 $m.s^{-1}$. For each sampling station, subsurface salinity, temperature, turbidity and dissolved oxygen measurements were performed *in situ* with a multiparameter water quality probe (YSI Environmental Monitoring Systems, 6600 V2-2). At each station, we collected subsamples of water (80 mL), which were stored in polyethylene bottles at -20°C until nutrient analysis. DIN and DIP concentrations were determined by manual colorimetric methods, as described by Aminot and Kérouel (2004). Total nitrogen and total phosphorus concentrations were determined by wet oxidation and automated colorimetry (Raimbault et al., 1999). For chlorophyll *a* determinations, we filtered 50 mL of a water sample through Whatman GF/F membranes (0.7 µm pores) under vacuum (<10 cm Hg). The filters were then placed in glass tubes and stored at -20°C. Filters were ground in acetone

(90%) and incubated for 24 h in the dark at 4°C. Pigment levels were measured by spectrofluorimetry (Neveux and Lantoine, 1993). Concentrations are expressed in µg.L^{-1} (precision ±5%).

2.3. Macrophyte mapping and monitoring of dynamics

Earlier maps of the main macrophytes and bottom types in Biguglia lagoon were available for studies of the change in macrophyte distribution. The first two maps were produced by De Casabianca et al. (1973) and Frisoni and Dutrieux (1992), at a scale of 1:20,000, and were based mostly on *in situ* observations. Each map was scanned and georeferenced with ArcGis version 10.0 (ESRI®). The areas of aquatic angiosperms and macroalgae were redrawn in vector format, by tracing polygons on the scanned and georeferenced maps. Pasqualini et al. (2006) made accurate maps of the main macrophytes and bottom types in Biguglia lagoon in 1999. Aerial photographs were used for image processing, as described by Pasqualini et al. (1997). The resulting map was then georeferenced with Lambert 93 coordinates and converted to vector format in a GIS database. The current distribution of macrophytes and other bottom types within Biguglia lagoon was determined by mapping with the same method (Pasqualini et al., 1997; Garrido et al., 2013), from color aerial photographs (May 2010, 1:10,000 scale; International Air Photo®) and field observations (Spring-Summer 2010, 35 transects distributed throughout the lagoon and recorded by differential GPS). This technique combines a high level of precision and rapid processing (Pasqualini et al., 1997; 2001). Image processing (ENVI software) led to the identification of six main bottom types: *Najas marina* L., *Ruppia cirrhosa* (Petagna) Grande and/or *Stuckenia pectinata* (L.) Börner (formerly known as *Potamogeton pectinatus*), mixed aquatic angiosperms (*Najas marina*, *Ruppia cirrhosa*, and/or *Stuckenia pectinata*), silt, macroalgae, *Posidonia oceanica* (Linnaeus) Delile litter and sand. Three images, corresponding to the three different layers (i.e., red, green and blue), were obtained from aerial photographs. The dynamics of each layer was adjusted by enhancing image contrast (linear contrast enhancement) to improve precision and clarity. Principal component analysis (PCA) was carried out on the green and blue layers. A supervised classification (by the generalized hypercube method) was applied to color composition. The polygons were then positioned on the basis of field observations *in situ*. The final images were occasionally corrected on the basis of the field data. All the maps (1972/1973, 1991, 1999 and 2010) were georeferenced with Lambert 93 coordinates and converted to a vector format in a GIS database.

Macrophyte dynamics were monitored from 1999 onwards, to assess the eutrophication status of Biguglia lagoon according to the Lagoon Monitoring Network method (*Réseau de Suivi Lagunaire*; Souchu et al., 2010; Ferreira et al., 2011), which meets the requirements of the Water Framework Directive (2000/60/CE). Macrophyte community coverage was estimated in 1999, 2003, 2009, 2012 and 2014, at 15 stations in Biguglia lagoon (Fig. 1), in June, during the period of maximal macrophyte growth before the summer senescence period. At each station, macrophyte coverage was estimated *in situ* on areas of about 120 m² corresponding to a circle with a radius of about 6 m. This surface area was considered suitable for the detection of all the taxa present in the selected areas (Ferreira et al., 2011). The total vegetation cover and the percentage cover for each aquatic angiosperm and macroalgal species were determined by eye, and a representative sample was systematically collected for the validation of species-level identifications in the laboratory.

2.4. Statistical analysis

We used XLStat® V2011 5.01 statistical software for comparisons. We used nonparametric Kruskal-Wallis one-way analysis of variance on ranks to evaluate the significance of differences in environmental data between stations and between sampling years. The Conover-Iman test was then used to highlight differences between years. This test calculates stochastic dominance and reports results for multiple pairwise comparisons. We used nonparametric Spearman's rank correlation (ρ) analysis to identify potential relationships between environmental variables. Values of $p<0.05$ were considered significant. Principal component analysis (PCA) was carried out with the FactoMineR package of R software to highlight potential links between abiotic and biotic parameters, and similarities between sampling stations and years of sampling. This multivariate analysis method is particularly suitable for ecological data, as it makes no assumptions about the structure between samples or about the normality of the data distribution. Biotic and abiotic data collected over the same sampling period were included in the PCA analysis: June 1999, June 2003, June 2009, June 2012 and June 2014. Only variables without missing values and with low Spearman correlation coefficients were included as active variables in the PCA, to prevent bias. Meteorological variables (rainfall levels and water temperature) were added as illustrative variables. For comparison with the abiotic data collected at the two water sampling stations (N and S; Fig. 1), percentage coverage data for macroalgae, and for the macrophytes *Ruppia cirrhosa* and of *Stuckenia pectinata* were averaged for the stations of the lagoon.

3. Results

3.1. Environmental data

The number of inhabitants of the Biguglia watershed remained relatively small and constant from the early 19th century to the mid-20th century (about 2,000 inhabitants; Table 1). However, whereas farmland accounted for less than 40% of the watershed in the late of 18th century, it accounted for more than 80% at the end of the 19th century (Table 1). The number of inhabitants has increased considerably since 1970 (reaching about 25,000 in 2011), and this increase was associated with an increase in the size of urban areas and a decrease in the areas covered by farmland or forests and shrublands (Table 1).

Rainfall in the Biguglia watershed has varied considerably between years since 1948. Annual rainfall ranged from 330 mm in 1952 to 1371 mm in 2008, with a mean value of 765 mm (CV=26.8%). Rainfall levels were significantly higher in the spring and fall than in the winter and summer (Spearman, $p<0.05$). Mean summer salinity data were available from 1930 onwards and ranged from 11.0 PSU in 2014 to 27.2 PSU in 2012 for the northern basin, and from 7.3 PSU in 2014 to 14.5 PSU in 2012 in the southern basin. Mean summer salinity differed between the northern and southern basins (Spearman, $p<0.05$). Salinity was significantly correlated with summer rainfall levels (Spearman, $p<0.05$).

Between 1999 and 2014, summer parameters displayed interannual variability at Biguglia lagoon (Fig. 2; Table 2). In the northern basin, salinity, turbidity and ammonium concentration varied from year to year (Fig. 2; Table 2). In the southern basin, interannual variation was observed for a larger number of parameters, including salinity, turbidity, nitrates, ammonium, total nitrogen, total phosphorus and chlorophyll *a* concentrations (Fig. 2; Table 2). Significant differences were observed for many parameters in 2007 (Fig. 2; Table 2). In the summer of 2007, Biguglia lagoon suffered a dystrophic crisis associated with the massive development of a potentially toxic cyanobacterium, *Anabaenopsis circularis* (G.S. West) Woloszynnska & V. Miller (IFREMER data). In the other years, significant differences were observed for only one or two parameters, which were influenced by very large peaks (e.g. peak in 2014 for nitrates in the southern basin; Fig. 2; Table 2).

3.2. Macrophyte mapping and monitoring of dynamics

The map produced by De Casabianca et al. (1973) for 1972-1973 revealed a predominance of aquatic angiosperms (84% of the total lagoon area; Table 3). Four aquatic angiosperms were present in Biguglia lagoon: *Zostera noltei* Hornemann close to the sea channel in the north, *Ruppia cirrhosa* and *Stuckenia pectinata* throughout the lagoon and *Najas marina* in the southern basin. *Ulva* sp. was also present, but with a low prevalence. Conversely, in 1991 (Frisoni and Dutrieux, 1992), *Ulva* sp. occupied 65% of the total area of the lagoon, with aquatic angiosperms covering only 51% (Table 3). In 1991, two aquatic angiosperm species were encountered (*Ruppia maritima* Linnaeus and *Stuckenia pectinata*). Aquatic angiosperm levels were lowest in 1999 (Pasqualini et al., 2006), when these plants covered only 13% of the total area, whereas *Ulva* sp. and *Gracilaria* sp. covered 7% of the lagoon (Table 3). Four aquatic angiosperms were present in Biguglia lagoon: *Zostera noltei* close to the sea channel, *Ruppia cirrhosa* (95% of the aquatic angiosperms present) and *Ruppia maritima* throughout the lagoon, and *Stuckenia pectinata*, mostly in the south-western part of the lagoon. *Najas marina* was not observed in 1999. In 2010, analysis of the Biguglia lagoon map revealed a predominance of aquatic angiosperms (62% of the total area; Table 3), mostly in the southern basin for *Najas marina* (17%), throughout the lagoon for *Ruppia cirrhosa* and/or *Stuckenia pectinata* (40%), and in the southern basin for mixed aquatic angiosperms (5%; *Stuckenia pectinata* and *Najas marina*; Fig. 3). Macroalgal formations were observed mostly in the northern basin (14%), in the form of tufts within the *Ruppia cirrhosa* meadows (Fig. 3; Table 3). *Posidonia oceanica*, an exclusively marine species, was found only as litter, close to the points of communication with the sea and partly blocking the connecting channel (Fig. 3).

The monitoring of macrophyte dynamics between 1999 and 2014 showed interannual variability in aquatic angiosperm coverage (Fig. 4). Essentially, two species were encountered (*Ruppia cirrhosa* and *Stuckenia pectinata*), with *Ruppia cirrhosa* predominating in the northern basin (notably in 2014) and *Stuckenia pectinata* predominating in the southern basin (notably in 2012). Aquatic angiosperms were less prevalent in Biguglia lagoon in 1999, 2003 and 2009. Macroalgal community diversity and coverage also varied between years (Fig. 4). Coverage was highest in 1999 and 2003, for both basins, whereas only one macroalga (*Ulva instestinalis* Linnaeus) was observed in 2009, with low coverage. *Gracilaria dura* (C.Agardh) J.Agardh was well represented, particularly in the southern basin, in 1999 and 2003. In these years, *Ulvaria obscura* (Kützing) P.Gayral ex C.Bliding (formerly known as *Monostroma obscurum*), *Ulva rigida* C.Agardh, *Gracilaria gracilis* (Stackhouse) M.Steentoft, L.M.Irvine & W.F.Farnham and *Neosiphonia sertularioides* (Grateloup) K.W.Nam & P.J.Kang (formerly known as *Polysiphonia sertularioides*) were also detected, particularly in the northern basin (Fig. 4). Intermediate results were obtained for 2012 and 2014, with a predominance of macroalgae in the northern basin in 2014 (Fig. 4). *Gracilaria gracilis* was present in 2012, notably in the northern basin, whereas *Gracilaria bursa-pastoris* (S.G.Gmelin) P.C.Silva was found throughout the lagoon in 2014. In these years, *Neosiphonia sertularioides*, *Chaetomorpha aerea* (Dillwyn) Kützing and *Cladophora vagabunda* (Linnaeus) Hoek were also sampled (Fig. 4)

3.3. Relationships between environmental and macrophyte data

The PCA analysis was performed on 9 active variables (chlorophyll *a*, DIP, DIN, turbidity, dissolved oxygen, salinity, cover percentages for macroalgae, *Ruppia cirrhosa* and *Stuckenia pectinata*). NH_4, NO_2 and NO_3 were considered to be illustrative variables because they were highly correlated with DIN (Spearman, $p<0.5$; $r=0.81$, 0.77, 0.77, respectively). TN and TP were not retained in the analysis because of missing values in 1999 and 2009, and because these variables were significantly correlated with chlorophyll *a* levels (Spearman, $p<0.5$; $r=0.61$, 0.50, respectively). The first two principal components (PC) accounted for

57.58% of the total variance (PC1: 23.76%, PC2: 33.82%; Fig. 5a). Turbidity and chlorophyll *a* concentration contributed to the construction of PC1 with strong negative correlations (loadings: -0.91, -0.87, respectively; Fig. 5a), probably largely due to the production of phytoplankton. By contrast, a positive correlation was observed for salinity (loading: 0.70), but this variable made a smaller contribution to PC2 (Fig. 5a). PC2 was positively correlated with DIP and negatively correlated with *Stuckenia pectinata* coverage (loadings: 0.70 and -0.67, respectively).

The graphical locations of stations centroid in the plane formed by the PC1-PC2 axes highlights the opposition between the two basins along the first axis, with higher eutrophication and lower salinity levels for the southern basin (Fig. 5b). PC2 was driven by changes in DIP and *Stuckenia pectinata* coverage levels over time in the southern basin. Evolution trajectory of the southern basin in PC1-PC2 axes plane highlighted macroalgae coverage increasing from June 1999 to June 2003. In June 2009, macroalgal coverage and DIP had decreased and chlorophyll *a* levels had increased, these changes being associated with high levels of summer rainfall and low salinity. *Stuckenia pectinata* coverage increased between 2009 and 2012, but subsequently decreased in June 2014, when phytoplankton biomass increased. Data for the northern basin made a smaller contribution to PC1 and PC2 than data for the southern basin.

4. Discussion

An understanding of the patterns of change in anthropogenic pressures that have occurred in the past can help us to determine the most appropriate management measures for the restoration of Mediterranean lagoons. In this context, the historical data available for the watershed of the Biguglia lagoon provide useful information to improve our understanding of the patterns of change in the hydrological and ecological functioning of lagoons. Two key factors have had a major effect on the benthic vegetation succession/shift of the Biguglia lagoon: salinity and nutrient enrichment.

There is currently a steep salinity gradient between the northern and southern basins of the lagoon. This gradient may change considerably with the configuration of the lagoon, the hydrological watershed, and meteorological conditions (rainfall). The configuration of the lagoon at the end of the 18th century was identical to that today, with a channel communicating with the sea at the north of the lagoon (Fig. 1; Letteron, 1923; Plan Terrier map of 1774). However, drainage measures have been implemented since the end of the 18th century, with the establishment of canals to favor cultivation of the watershed, and periodic interventions to open the lagoon to the sea, to ensure efficient emptying of the lagoon (Jaujou, 1954). Agricultural areas occupied less than 40% of the watershed in 1774, and the population was small. The Fossone Canal connecting the River Golo and the south of the lagoon (Fig. 1; 4 km long) was created at about this time. A new remediation program was initiated at the end of the 19th century, with the establishment of a drainage canal around the lagoon to drain the adjacent marshes, and the installation of five pumping stations (Fig. 1; Département de la Haute-Corse, 2012). Agricultural land occupied more than 80% of the watershed, but the population remained small. The watershed gradually became more suitable for human settlement, and a significant increase in the number of inhabitants was observed from the 1970s onwards (suburban extension of Bastia and changes in land use in the Mediterranean mountains; San Roman Sanz et al., 2013). The current network of drainage canals and pumping stations does not satisfy agricultural needs and clearly affects lagoon salinity. Freshwater inputs currently dominate the water budget (≈ 90 Mm^3 for a total lagoon volume of 10.2 Mm^3; Mouillot et al., 2000). Biguglia lagoon has salinity levels corresponding to polyhaline and mesohaline ecosystems (Battaglia, 1959). Salinity levels vary from year to year and are dependent on meteorological conditions (spring and fall rainfall), which exert tight control over the *in situ* environmental conditions, particularly in Mediterranean climates (Tagliapietra and Ghirardini, 2006). Nevertheless, the salinity of the Biguglia lagoon decreased steadily from 1999 to 2011, in both the northern and southern basins. The rapid increase in salinity observed in 2012 reflected the mechanical opening of the current channel of communication with the sea (significant salt water input) by the managers of the natural reserve.

The quality of freshwater inputs has declined, and this process has undoubtedly been exacerbated by a sewerage system that has not yet been adapted to deal with the increase in the number of inhabitants in the watershed (Département de la Haute-Corse, 2012). Biguglia lagoon remains a major site of agricultural and urban activities, favoring large nitrogen inputs. The total and dissolved inorganic nitrogen concentrations obtained during the summer months in this study are higher than those reported for other Mediterranean lagoons, such as Sacca di Goro in Italy (Viaroli et al., 2006; Giorgani et al., 2009), or other French lagoons (Souchu et al., 2010). Conversely, summer nitrate concentrations in Biguglia lagoon are much lower than those measured annually in some estuaries, such as the Ebro delta (nitrates > 0.2 mM; Vidal et al., 1997). The available data for nutrient levels in other seasons indicate that ammonium and nitrate concentrations can be high in Biguglia lagoon (> 80 µM for ammonium and > 20 µM for nitrate; Orsoni et al., 2001; Garrido et al., 2016). Some of the phosphorus concentrations obtained for this lagoon during the summer months were higher than those reported for other French lagoons (Souchu et al., 2010), and exceeded the annual concentrations measured in some coastal embayments (Lie et al., 2011; Saeck et al., 2013). The northern basin of Biguglia lagoon may be considered mesotrophic, and the southern basin eutrophic (Souchu et al., 2010). The inorganic nutrients in the waters of lagoons subject to anthropogenic pressure reflect the cumulative effects of inputs from rivers and sewage, uptake, grazing, sediment-water fluxes, recycling processes, and stock (Fisher et al., 1992). Total nutrient-based approaches for predicting algal (phytoplankton and macroalgae) biomass are very efficient in lagoons (Souchu et al., 2010). Typically, in mesotrophic to hypertrophic lagoons with a high stock of P-rich sediment, shallow water and resuspension, high summer temperatures and anoxic events, the concentration of P in the water column results partly from sediment fluxes (De Wit et al., 2001; Thouzeau et al., 2007). However, extreme events, such as dystrophic crises, or instantaneous events (peak of ammonium concentration and recent increases in nitrate concentration) may occur.

Variations of salinity and nutrient input are known to affect the growth of macroalgae and aquatic angiosperms (Cloern, 2001; De Jonge et al., 2002; Charpentier et al., 2005; Orfanidis et al., 2008b). Our sampling strategy focused on the summer period and did not, therefore, highlight seasonal changes in macrophyte levels, but the data obtained made it possible to compare years, in conditions of maximal primary production. The variability of the dataset resulted mostly from variations of chlorophyll *a* and turbidity. The relationship between turbidity/chlorophyll *a* and salinity/summer rainfall indicated that the observed turbidity resulted principally from phytoplankton production that seemed to be linked to freshwater inputs. It also highlights the independence of these 4 variables and DIP and NH_4, due to instantaneous peaks of dissolved nutrient concentrations in the southern basin in 1999 and 2003. Finally, our analysis revealed no clear relationship between the water column and macrophyte data, except for the negative correlation between chlorophyll *a* and macroalgae levels, due to the dystrophic crisis in 2007, resulting in a shift in the vegetation from macroalgae to phytoplankton between 2003 and 2009. Additional correlation analyses performed separately for the two basins of the lagoon revealed significant relationships between *Ruppia cirrhosa* and salinity and between *Stuckenia pectinata* and NO_2 (Spearman, r=-0.80 and 0.67, respectively) in the northern basin, and between *Stuckenia pectinata* and spring rainfall and temperature in the southern basin (Spearman, r=0.97). All these results suggest that turbidity and chlorophyll *a* levels have a larger effect on macroalgae than on *Ruppia cirrhosa* and *Stuckenia pectinata*, which seem to be more strongly influenced by abiotic parameters.

Three periods of benthic vegetation succession have been observed in Biguglia lagoon: from 1970 to 2007, the year 2007 and from 2007 to the present (Fig. 6). Between 1970 and 2007, changes were observed in the abundance of aquatic angiosperm species (Fig. 6). *Zostera noltei* was present throughout the study period, but only in the northern basin of the lagoon, close to the sea channel. This euryhaline species thrives in almost all salinity conditions, from near freshwater to a salinity of more than 30, including situations in which salinity changes rapidly (Hemminga and Duarte, 2000; Charpentier et al., 2005). Conversely, *Ruppia cirrhosa* was found throughout the lagoon, but the area covered by this species decreased considerably over the 1970-2007 period. *Ruppia* is a cosmopolitan genus, tolerant to salinity fluctuations, and is typically found in coastal lagoons (Verhoeven, 1979; Menéndez, 2002). In Europe, *Ruppia cirrhosa* grows in water with salinities of 3 to 100 PSU (Verhoeven, 1979). This remarkable tolerance to salinity variations makes *Ruppia cirrhosa* a good bioindicator for coastal lagoons, because salinity fluctuations are unlikely to be responsible for major changes and discontinuities in the community. *Stuckenia pectinata* was found only in the center and south of the lagoon, and the area occupied by this species decreased from 1970 to 2007. This species is a perennial annual submerged pondweed with large numbers of long narrow leaves. It grows on sediments in still or flowing eutrophic fresh water, lakes, rivers and in brackish lagoons (Menéndez and Comin, 1989). *Najas marina* was present in the 1970s but disappeared from the lagoon in the 2000s, undoubtedly due to changes in salinity. *Najas marina* is widespread at the freshwater to slightly oligohaline end of the salinity gradient, in ponds, lakes, coastal and inland marshes, although it is generally found at lower abundances in these environments (Handley and Davy, 2002). In addition to the significant impact of nitrogen inputs in Biguglia lagoon, the north-south salinity gradient has also clearly affected the distribution of aquatic angiosperms. The northern basin is consistently saltier than the southern basin, due to the input of salt water via the communication channel with the sea (short residence time; mostly *Zostera noltei* and *Ruppia cirrhosa*). The southern basin is less salty and more confined, with a longer water residence time (mostly *Ruppia cirrhosa*, *Stuckenia pectinata and Najas marina).*

By contrast to aquatic angiosperms, the populations of macroalgae increased considerably during the 1970-2007 period (Fig. 6). Under conditions of nutrient excess and high turbidity, there is a shift in species composition from aquatic angiosperms to the dominance of opportunistic macroalgae (Schramm, 1999; Viaroli et al., 2008). This situation reflects the efficiency of nutrient assimilation by these opportunistic macroalgae (Duarte, 1995). Opportunistic macroalgae have lower light requirements for growth than rooted aquatic angiosperms (Hemminga and Duarte, 2000), and the displacement of aquatic angiosperms seems to be induced principally by nitrogen, rather than by phosphorus (Touchette and Burkholder, 2000). *Ulva* sp. was present at low frequency in 1970, and *Gracilaria dura*, *Ulvaria obscura* and *Ulva* sp. populations developed in the early 2000s (Fig. 6). The increase in the populations of these macroalgae and their subsequent decomposition may have resulted in anoxic conditions unfavorable for aquatic angiosperms (Coffaro and Bocci, 1997). A qualitative shift from the pristine aquatic angiosperm community to macroalgal blooms in Mediterranean lagoons until the mid-1970s has been demonstrated, with aquatic angiosperm populations decreasing in nutrient-rich waters (Viaroli et al., 2008). Several shallow lagoons were covered with extensive meadows of *Ruppia* and/or *Zostera* in the past, but increases in nutrient inputs in recent decades have led to the rapid development of *Ulva* sp. and *Gracilaria* sp. blooms and the displacement of aquatic angiosperms (Sfriso and Marcomini, 1996; Bombelli and Lenzi, 1996; Viaroli et al., 2006; Sfriso and Facca, 2007).

During the summer of 2007, a dystrophic crisis occurred in Biguglia lagoon, with the recording of high chlorophyll *a* concentrations (up to 200 $\mu g.L^{-1}$). It was difficult to identify the trigger elements, but this dystrophic crisis was associated with massive development of the potentially toxic cyanobacteria *Anabaenopsis circularis* (IFREMER data; Fig. 6). The *Anabaenopsis circularis* (freshwater species) bloom was a direct consequence of the decrease in salinity (Pulina et al. 2011), which was associated with high nutrient concentrations. By cascading effect, cyanobacteria bloom and salinity decrease concomitant with temperature increase in summer engendered the accumulation of organic matter by phytoplankton and the death of macroalgae in the Biguglia lagoon, causing strong anoxia. The capacity of aquatic angiosperms to retain nitrogen is dependent on an internal control system that keeps the nitrogen cycle balanced and counteracts shifts in the community towards macroalgae or phytoplankton (Valiela et al., 1997). When nutrient loads increase, massive macroalgal development can induce physical and chemical changes in the water. Floating mats of algae decrease light penetration into the water, leading to the formation of layers of water with different properties, with oxygen-rich water towards the surface and anoxic conditions towards the bottom (Souchu et al., 1998; Brush and Nixon, 2003). Sulfide and nutrients released into the water act as a stressor for aquatic angiosperm and macroalgae (Azzoni et al., 2001). The last phase of the transition from healthy to stressed ecosystems is dominated by phytoplankton, as observed during the dystrophic crisis of the summer of 2007. Phytoplankton levels are often high in heavily degraded lagoons (Sfriso and Facca, 2007) and play a crucial role in controlling the flows of matter and energy in coastal environments (Bec et al., 2011). However, the paradigm that increasing nutrient load causes an irreversible transition from aquatic angiosperms to macroalgae or phytoplankton communities can now be called into question, because this paradigm is not well-supported by quantitative theories or models (Nixon et al., 2001). However, after 2007, the chlorophyll *a* concentrations measured in Biguglia lagoon in the summer were similar to those in other Mediterranean lagoons (Souchu et al., 2010; Giordani et al., 2009), or coastal embayments (Saeck et al., 2013; Lie et al., 2011).

Recent deteriorations in water quality led the managers of the Biguglia lagoon nature reserve to take various remedial measures, such as periodically opening up the current channel of communication with the sea by mechanical means (significant salt water input; particularly during 2012, with an exceptional increase in the salinity of the lagoon) and cleaning the Fossone Canal from 2009 to 2012 (significant freshwater inputs), to decrease the confinement of the southern basin (Département de la Haute-Corse, 2013). Substantial efforts have also been made to improve sewage treatment in the watershed under the *Schéma d'Aménagement et de Gestion des Eaux* (SAGE; Département de la Haute-Corse, 2012). After 2007, the abundance of aquatic angiosperms increased in this lagoon (Fig. 6), particularly for *Ruppia cirrhosa* across the lagoon, and *Stuckenia pectinata* in the south, with a resurgence of *Najas marina* in the southern basin of the lagoon (low salinity). The macroalgae *Gracilaria bursa-pastoris* and *Gracilaria dura* appeared during this period, but only in a small area (Fig. 6). The point at which a system shifts from one state to another depends on the external nutrient load and the water exchange time (Dahlgren and Kautsky, 2004). Primary producer succession is often favored by hydrological and hydrodynamic conditions, such as currents and flushing, which disperse the phytoplankton community (Flindt et al., 1997). In the system studied here, such hydrological management measures improved the quality of the water column, favoring the development of aquatic angiosperms over a relatively short period of time (4-5 years). Biguglia lagoon seems to be very resilient, and the shifts observed may be reversible. Improvements in wastewater treatment in the watershed, to decrease nutrient inputs, will also be essential, to prolong the effects of these management efforts and to allow the system to recover.

In conclusion, Biguglia lagoon remains vulnerable to sporadic shifts, due to several factors: (i) hydrological management of the watershed and the communication channel with the sea, with effects on salinity, (ii) nutrient inputs from the watershed, (iii) natural climatic phenomena (rainfall, wind) or climate change (Lloret et al., 2008). As evidence of ecosystem degradation accumulates, it is often difficult to distinguish between natural variations of the state of the ecosystem and human-induced changes. We used long-term (two hundred years) historical data to determine the pattern of change in human activities on the watershed of Biguglia lagoon, including the many hydrological developments affecting salinity and, thus, the distribution of aquatic angiosperms. Many changes in salinity have occurred in Biguglia lagoon, and there is still a steep spatial gradient of salinity, but aquatic angiosperms have adapted to cope with such abrupt changes. Over the last 40 years, human activities have profoundly altered the Biguglia lagoon, with changes in the aquatic vegetation, from a predominance of aquatic angiosperms to macroalgae and phytoplankton during a dystrophic crisis in 2007. The observed shift in the community suggests that Biguglia lagoon is resilient and that the transition may be reversible. The restored communities closely resemble the pristine communities. The disturbances at this lagoon do not, therefore, seem to have exceeded the threshold beyond which lagoons cannot recover. Actions aiming to restore the ecosystem of this lagoon should take this resilience into account, but should also consider the desired ecosystem services.

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Figure captions

Fig. 1. Location of Biguglia lagoon (Corsica, France, Mediterranean Sea) and the stations sampled.

Fig. 2. Spatiotemporal variations of subsurface salinity, temperature, nitrate, ammonium, phosphate, total nitrogen, total phosphorus, and chlorophyll *a* (chl a) concentrations, registered during each of the summer months from 1999 to 2014 in Biguglia lagoon.

Fig. 3. Spatial distribution of macrophytes and bottom types in Biguglia lagoon in 2010.

Fig. 4. Monitoring of macrophyte dynamics at 15 sampling stations (S1 to S15) in Biguglia lagoon between 1999 and 2014 (Ca: *Chaetomorpha aerea*; Cv: *Cladophora vagabunda*; Gd: *Gracilaria dura*; Gg: *Gracilaria gracilis*; Gb: *Gracilaria bursa-pastoris*; Ns: *Neosiphonia sertularioides*; Ui: *Ulva instestinalis*; Uo: *Ulvaria obscura*; Ur: *Ulva rigida;* nd: not determined; The values shown correspond to the percentage cover of the species concerned).

Fig. 5. Principal component analysis of water column, meteorological and macrophyte data for the southern (station BIS) and northern (station BIN) basins of Biguglia lagoon in June 1999, 2003, 2009, 2012 and 2014. Loadings of the 9 active variables (illustrative variables in gray) on the plane defined by PC1 and PC2 (a). Location of stations centroids by year on the plane PC1-PC2 (b). The numbers following station names correspond to the sampling year (ex: BIS:09 = Biguglia south, year 2009).

Fig. 6. Conceptual representation of the succession of aquatic vegetation with eutrophication and salinity variations in Biguglia lagoon.

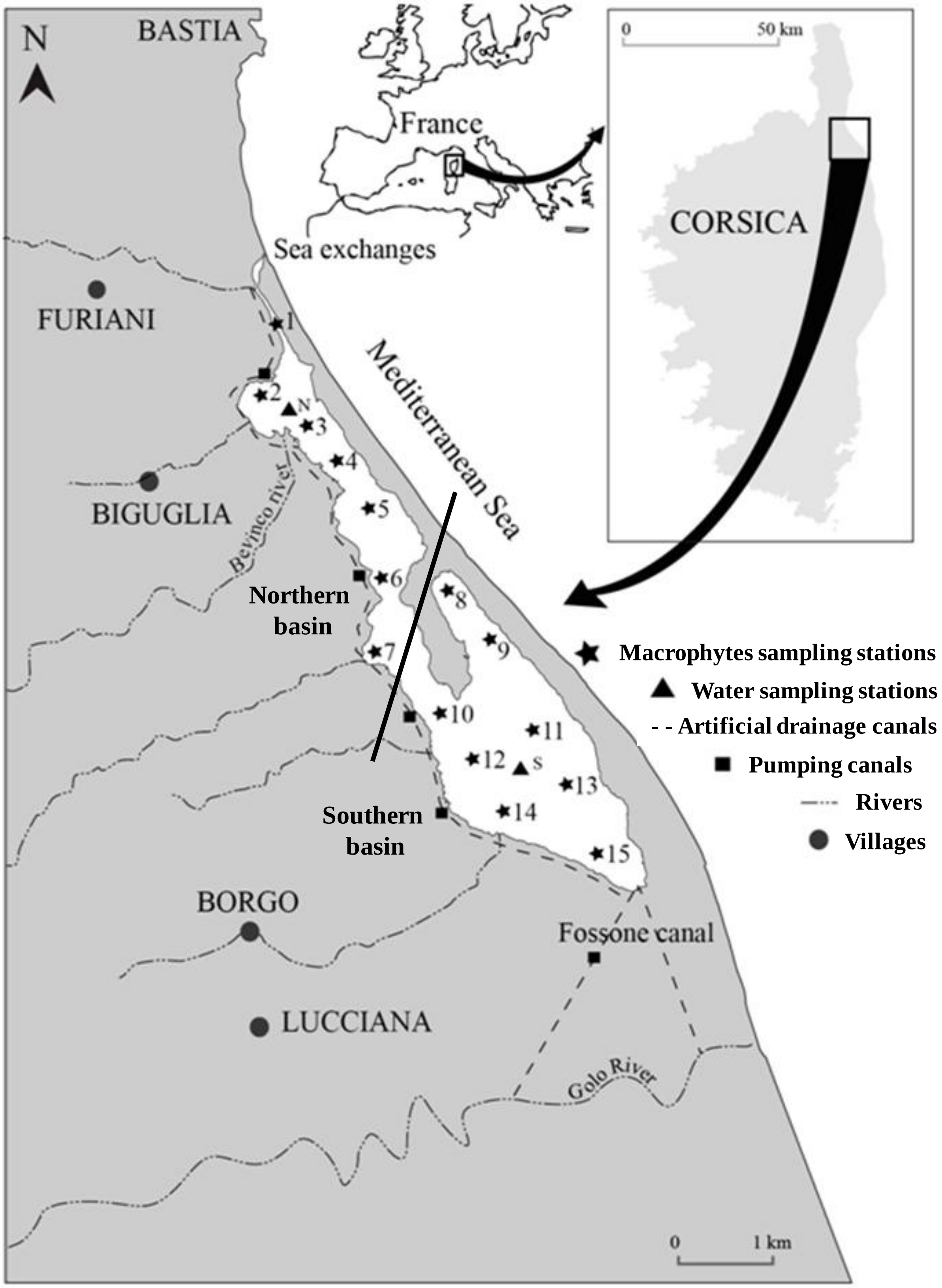

N
BASTIA
France
0
50 km
CORSICA
Sea exchanges
FURIANI
1
2
N
3
4
5
BIGUGLIA
Bevinco river
Mediterranean Sea
6
Northern basin
7
8
9
10
11
12
S
13
14
15
Southern basin
Macrophytes sampling stations
Water sampling stations
- - Artificial drainage canals
Pumping canals
Rivers
Villages
BORGO
Fossone canal
LUCCIANA
Golo River
0
1 km

Fig. 1.

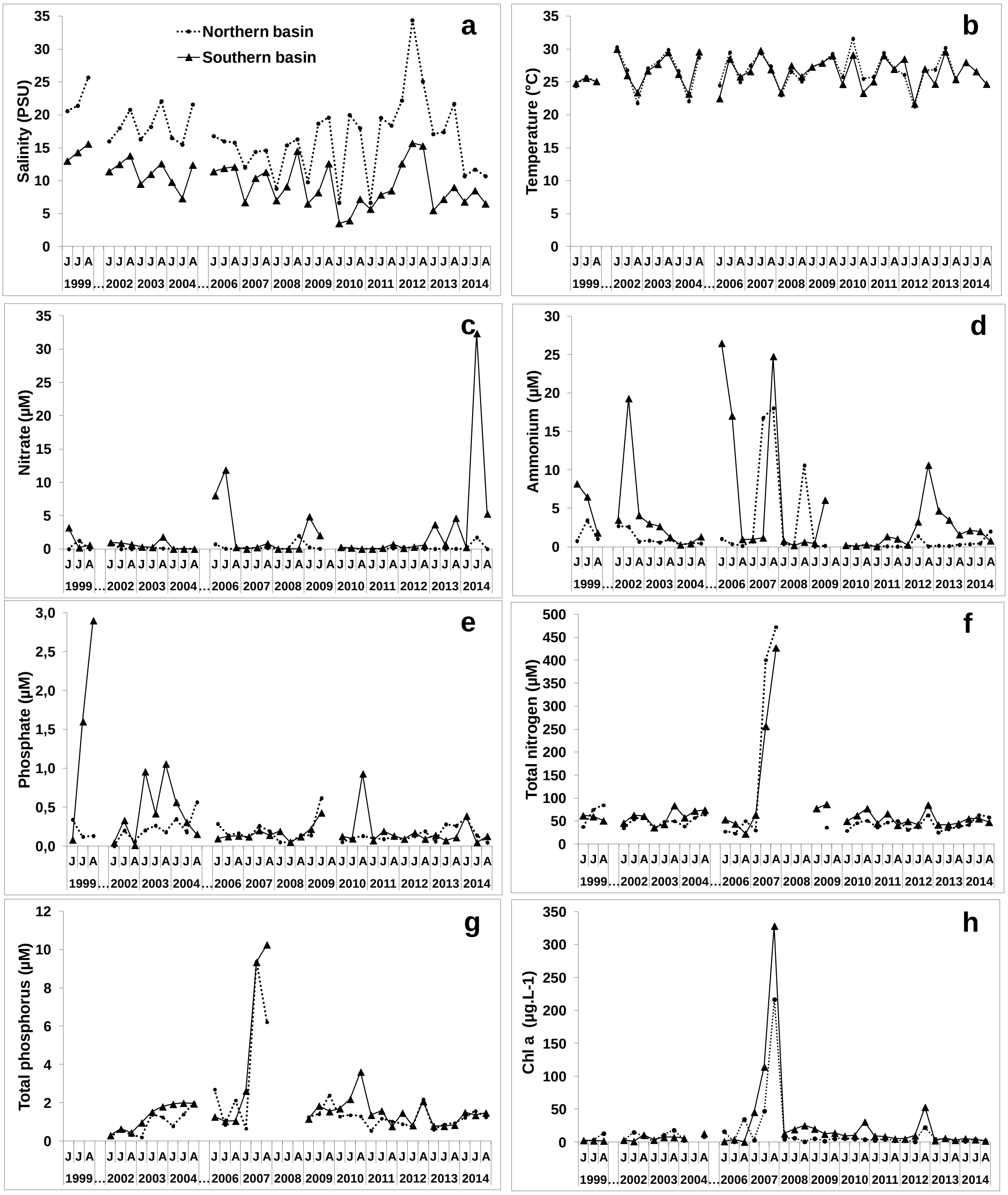
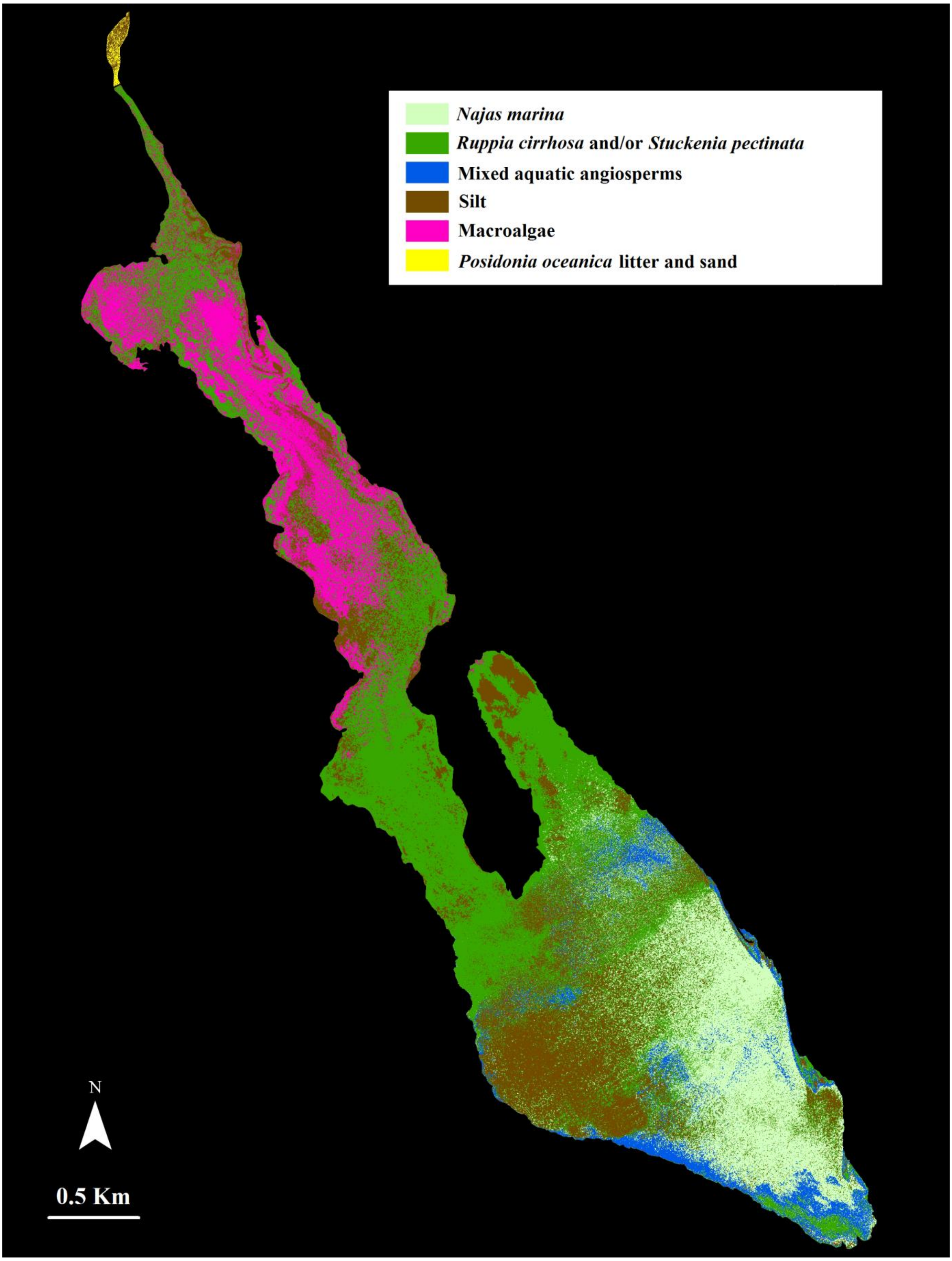

a
Northern basin
Southern basin
Salinity (PSU)
b
Temperature (°C)
c
Nitrate (µM)
d
Ammonium (µM)
e
Phosphate (µM)
f
Total nitrogen (µM)
g
Total phosphorus (µM)
h
Chl a (µg.L-1)
J J A
1999…
2002
2003
2004…
2006
2007
2008
2009
2010
2011
2012
2013
2014

Fig. 2.



Najas marina
Ruppia cirrhosa and/or Stuckenia pectinata
Mixed aquatic angiosperms
Silt
Macroalgae
Posidonia oceanica litter and sand
N
0.5 Km

Fig. 3.

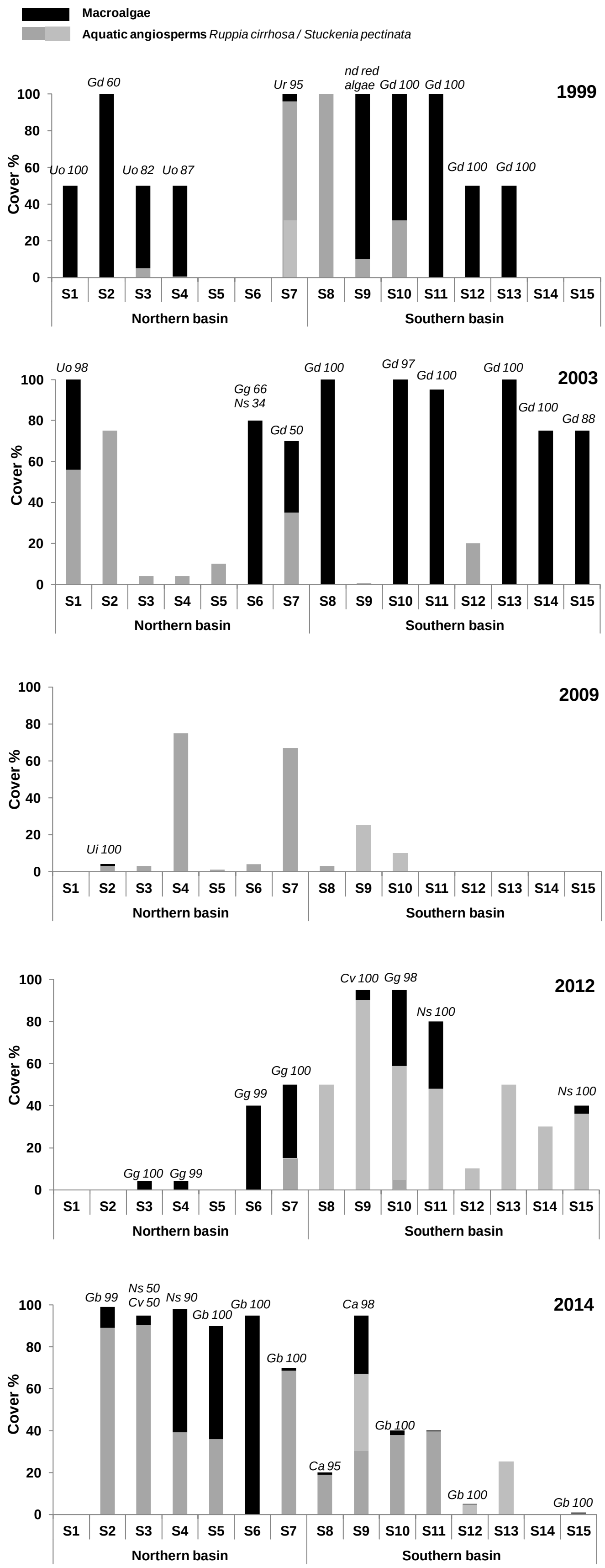

Macroalgae
Aquatic angiosperms Ruppia cirrhosa / Stuckenia pectinata
1999
2003
2009
2012
2014
Cover %
0
20
40
60
80
100
S1
S2
S3
S4
S5
S6
S7
S8
S9
S10
S11
S12
S13
S14
S15
Northern basin
Southern basin
Uo 100
Gd 60
Uo 82
Uo 87
Ur 95
nd red algae
Gd 100
Gd 100
Gd 100
Gd 100
Uo 98
Gg 66
Ns 34
Gd 50
Gd 100
Gd 97
Gd 100
Gd 100
Gd 100
Gd 88
Ui 100
Cv 100
Gg 98
Ns 100
Gg 100
Gg 99
Ns 100
Gg 100
Gg 99
Gb 99
Ns 50
Cv 50
Ns 90
Gb 100
Gb 100
Ca 98
Gb 100
Gb 100
Ca 95
Gb 100
Gb 100

Fig. 4.

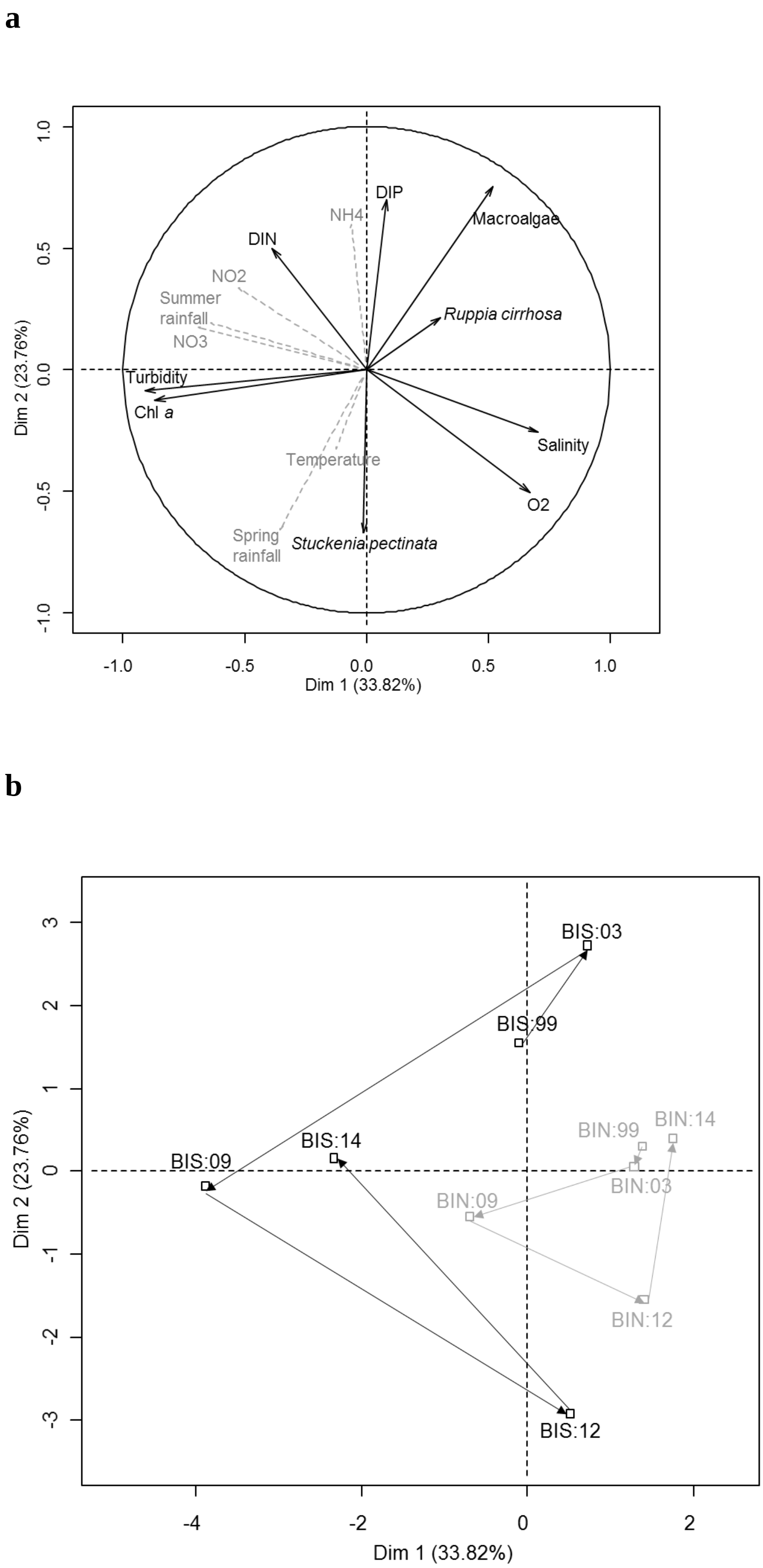

a
Dim 2 (23.76%)
Dim 1 (33.82%)
1.0
0.5
0.0
-0.5
-1.0
-1.0
-0.5
0.0
0.5
1.0
DIP
NH4
Macroalgae
DIN
NO2
Summer
rainfall
Ruppia cirrhosa
NO3
Turbidity
Chl a
Salinity
Temperature
O2
Spring
rainfall
Stuckenia pectinata
b
Dim 2 (23.76%)
Dim 1 (33.82%)
3
2
1
0
-1
-2
-3
-4
-2
0
2
BIS:03
BIS:99
BIN:99
BIN:14
BIS:14
BIS:09
BIN:03
BIN:09
BIN:12
BIS:12

Fig. 5.

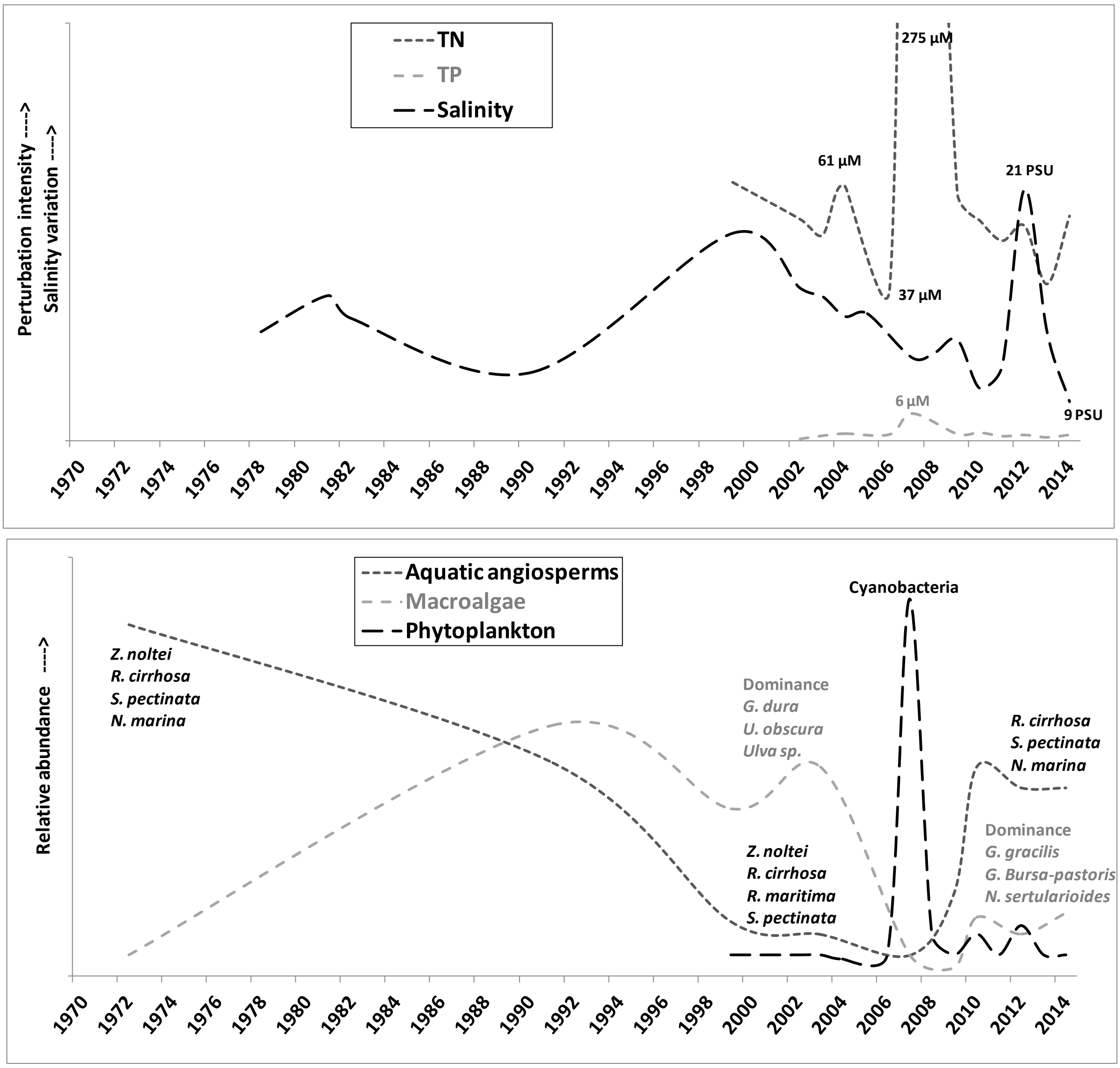

TN
TP
Salinity
Perturbation intensity ---->
Salinity variation ---->
61 µM
275 µM
37 µM
21 PSU
6 µM
9 PSU
1970
1972
1974
1976
1978
1980
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
2012
2014
Aquatic angiosperms
Macroalgae
Phytoplankton
Relative abundance ---->
Cyanobacteria
Z. noltei
R. cirrhosa
S. pectinata
N. marina
Dominance
G. dura
U. obscura
Ulva sp.
R. cirrhosa
S. pectinata
N. marina
Z. noltei
R. cirrhosa
R. maritima
S. pectinata
Dominance
G. gracilis
G. Bursa-pastoris
N. sertularioides

Fig. 6.

Table 1

Historical changes in Biguglia lagoon in terms of the human population and major land uses in the watershed from the 18th century to the present day.

Human population			
Year	**1800**	**1881**	**2011**
Number of inhabitants	1290	1863	25663

Major land uses (% of total land)			
Year	**1774**	**1879**	**2006**
Forests and Shrublands	56	12	42
Farmland	40	84	40
Urban areas	4	4	17

Table 2

Kruskal-Wallis one-way analysis of variance on ranks for the environmental data for Biguglia lagoon.

Difference between years										
Parameters	**Salinity**	**Temperature**	**Turbidity**	**Dissolved oxygen**	**Nitrates**	**Ammonium**	**Phosphates**	**Total nitrogen**	**Total phosphorus**	**Chlorophyll *a***
Northern basin										
Kruskal-Wallis: p-values (significant in bold)	**0.031**	0.431	**0.009**	0.094	0.576	**0.016**	0.194	0.334	0.052	0.829
Conover-Iman test: years different to other years (lower values)	2007 2014		2003			2011				
Conover-Iman test: years different to other years (higher values)	2012		2007			1999 2002 2007				
Southern basin										
Kruskal-Wallis: p-values (significant in bold)	**0.008**	0.855	**0.006**	0.692	**0.016**	0.055	0.212	0.070	**0.002**	**0.004**
Conover-Iman test: years different to other years (lower values)	2010		2003		2004				2002 2013	1999 2006
Conover-Iman test: years different to other years (higher values)	1999 2012		2007		2006 2009 2013 2014				2007	2007

Table 3

Temporal changes in the aquatic angiosperm and macroalgae communities of Biguglia lagoon.

Year	**1972/1973**	**1991**	**1999**	**2010**
References	De Casabianca et al., 1973	Frisoni and Dutrieux, 1992	Pasqualini et al., 2006	This study
Aquatic angiosperms	*Zostera noltei* *Ruppia cirrhosa* *Stuckenia pectinata* *Najas marina*	*Ruppia maritima* *Stuckenia pectinata*	*Zostera noltei* *Ruppia cirrhosa* *Ruppia maritima* *Stuckenia pectinata*	*Ruppia cirrhosa* *Stuckenia pectinata* *Najas marina*
Percentages of aquatic angiosperms	84	51	13	62
Main macroalgae	*Ulva* sp.	*Ulva* sp.	*Gracilaria* sp. *Ulva* sp.	*Gracilaria* sp *Ulva* sp.
Percentage or presence of main macroalgae	Weak presence (not calculated)	65	7	14