Hydrobiologia
DOI 10.1007/s10750-017-3421-y

PRIMARY RESEARCH PAPER

Submerged benthic macrophytes in Mediterranean lagoons: distribution patterns in relation to water chemistry and depth

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Received: 2 May 2017 / Revised: 11 October 2017 / Accepted: 23 October 2017

Abstract A large spectrum of coastal lagoon types with a wide range of environmental conditions is observed along the French Mediterranean coast. These comprise wide trophic and salinity gradients, ranging from oligotrophic to hypertrophic status, and from nearly freshwater to slightly above marine Mediterranean Sea water salinities, respectively. The statistical analysis of a long-term dataset, including water column variables and observations of macrophyte genera, showed that salinity, depth, and then trophic status, were important factors explaining the distribution of benthic macrophytes for the soft-bottom sediments in the 34 studied French Mediterranean lagoons. Based on this, we assumed that the vegetation succession along the eutrophication gradient was different according to the lagoon salinity ranges. Euhaline and polyhaline lagoons follow the well-known Schramm schematic model, where aquatic angiosperm such as seagrasses dominate under oligotrophic conditions, and opportunistic macroalgae and phytoplankton dominate under eutrophic and hypertrophic conditions. In oligohaline and mesohaline lagoons, the succession is probably an intermediate scheme between the successions observed in small temperate lakes and in marine coastal ecosystems due to the presence of both brackish and freshwater

Handling editor: Pierluigi Viaroli

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10750-017-3421-y) contains supplementary material, which is available to authorized users.

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Published online: 31 October 2017

species. We thus propose a conceptual scheme for the oligohaline and mesohaline lagoons.

Keywords French coastal lagoons · Submerged aquatic vegetation (SAV) · Eutrophication · Salinity · Depth · Canonical correspondence analysis (CCA)

Introduction

Coastal lagoons are generally defined as shallow water bodies, separated from the sea by a barrier and connected to the sea by one or more restricted inlets (Barnes, 1980; Kjerfve, 1994). They occupy around 13% of the coastline worldwide and about 5.3% of the European coast, where they are particularly abundant around the Mediterranean Sea (Cromwell, 1971). Coastal lagoons rank among the most productive ecosystems in the world and provide a wide range of ecosystem services and resources (Kennish & Paerl, 2010). They support important fisheries and are also used for aquaculture exploitation, recreation, and tourism (Pérez-Ruzafa et al., 2011). Located at the interface between the continental coastal zone and the sea, they support strong physical and ecological gradients. They are influenced by both marine and freshwater inputs from the catchment area; indeed, the salinity can vary from nearly freshwater to hypersaline water, depending on the hydrological balance (Kjerfve, 1994). Variation in salinity and other environmental factors can also be observed within a lagoon, both spatially and temporally. Since coastal lagoons are often subdivided into different rather homogenous hydrological basins (Tagliapietra & Ghirardini, 2006; Fiandrino et al., 2017), different ecological conditions can be met even in neighboring basins.

Hence, despite their common features, coastal lagoons present a wide variability of their environmental conditions. These depend particularly on freshwater inputs from their watershed and the magnitude of water exchanges with the sea, which are the main driver of the hydrological processes within the different basins, as well as on their geomorphology and human activities. Although depth in coastal lagoons generally averages less than 2 m, deeper waters may be encountered according to their geomorphological origin. Hence, coastal lagoons with a tectonic origin, like Diana, Urbino (Corsica), or Thau (South of France), are deeper than brackish lagoons with a deltaic (e.g., Camargue in Rhône delta in France, Po and Ebro delta in Italy and Spain, respectively) or sedimentary origin (e.g., Palavasian lagoons, south of France (Guerlorget & Perthuisot, 1992; Schramm & Nienhuis, 1996; De Wit, 2011). A great number of Mediterranean coastal lagoons are more strongly influenced by waves than by tides and wind direction and speed are key elements for the genesis of waves. Microtidal (< 2 m) conditions predominate in many coastal lagoons (Eisma, 1998). The Mediterranean coast of continental South of France and Corsica are subjected to tidal ranges below 0.5 m and lagoons can be defined as nanotidal, as suggested by Tagliapietra & Ghirardini (2006). Tidal range determines the morphology and grain size distribution of sediment; in nanotidal lagoons, the deepest zones tend to be in the center of the basin (Tagliapietra & Ghirardini, 2006). The majority of the bottoms in coastal lagoons are composed of soft-bottom sediments.

Because of their shallowness, local meteorological conditions strongly influence water temperature and other physical and chemical parameters in coastal lagoons. Under Mediterranean climates (characterized by warm to hot dry summers and mild to cool winters), coastal lagoons support a high variability of seasonal events (such as precipitations, high temperature). All these features would make lagoons vulnerable to global climatic change. Sea level, temperature, precipitations, and storms are expected to impact coastal lagoons (Anthony et al., 2009; De Wit, 2011). Furthermore, coastal lagoons have been subjected to development of human activities on their watershed and thus, an increase in nutrient and chemical contaminant inputs (e.g., urban sewage, waste water treatment plants, agricultural effluents) have often occurred (Barnes, 1980; Castel et al., 1996; Kennish & Paerl, 2010; Munaron et al., 2012). Their restricted water exchanges with the sea, confinement, long water residence times, and their potential to accumulate elevated levels of nutrients supplied from their watersheds and internal loading make coastal lagoons particularly sensitive to eutrophication processes (Barnes, 1980; Kjerfve, 1994; Glibert et al., 2014).

Both the natural and anthropogenic perturbations mentioned above may affect the diversity as well as the physiological and ecological adaptation of the species inhabiting coastal lagoons. They can highly

influence not only the composition and size structure of phytoplankton communities (Bec et al., 2011; Leruste et al., 2016) but also the sessile organisms such as benthic fauna and macrophytes (Sfriso et al., 1992; Charpentier et al., 2005). Submerged macrophytes, composed of macroalgae and aquatic angiosperms, are of particular interest in coastal lagoons, because these are important primary producers. Many species can be considered as ecosystem engineers by creating habitats for aquatic organisms and birds (Duarte & Cebrián, 1996; Levin et al., 2001; Vizzini & Mazzola, 2008) and by structuring the physical environments in coastal ecosystems (Hartvig et al., 2009; Thomaz & da Cunha, 2010). Benthic macrophytes form highly productive (Agostini et al., 2003) and extensive meadows in many coastal lagoons. Hence, in coastal lagoons, macrophytes play an important role not only in benthic oxygen and nutrient fluxes (Viaroli et al., 1996), in biogeochemical cycles (Plus et al., 2003) but also in driving sediment microbial processes (Hansen et al., 2000).

Knowledge on the ecology of macrophytes is paramount both for the fundamental knowledge of the ecosystem functioning in coastal lagoons as well as for more applied aspects, including their use as ecological indicators of environmental health and ecological status (Sfriso et al., 2009; Sargian et al., 2013; Orfanidis et al., 2014). Accordingly, in the European Water Framework Directive (WFD) (European Commission (EC), 2000), macrophytes are recognized as important biological quality elements for determining the ecological status of transitional waters, including coastal lagoons.

Growth and distribution of macrophytes in coastal ecosystems are influenced by both biotic (e.g., grazing, competition) and abiotic factors such as nutrients and light availability (Dennison, 1987; Duarte, 1991, 1995), pattern of currents (Fonseca & Kenworthy, 1987), temperature (Larkum et al., 2006; Hurd et al., 2014), and salinity (Lirman et al., 2008; Steinhardt & Selig, 2011). In Mediterranean lagoons, many species start growing in spring and often form the densest biomass late spring or during the summer (Menéndez & Comín, 2000; Agostini et al., 2003; Sfriso & Facca, 2007; Obrador & Pretus, 2010). Angiosperms and macroalgae are sensitive to anthropogenic stress (Orth et al., 2006), particularly to excessive nutrient inputs (Cloern, 2001; de Jonge et al., 2002; McGlathery et al., 2007). Both macroalgae and submerged aquatic angiosperms such as seagrasses and Potamogetonaceae take up nutrients directly from the water column, whereas, in addition, aquatic angiosperms can also take up nutrients from the sediment through their roots. Submerged macrophytes have morphological, physiological, and ecological adaptations to face environmental fluctuations (e.g., variations of salinity, water level, temperature, and light) (Littler & Littler, 1984; Brock, 1986). Under low nutrient and clear water conditions, seagrasses or other angiosperms are dominant on soft bottoms and perennial macroalgae on hard substrata. In contrast, under high nutrient and high turbidity conditions, macrophyte community compositions shift from aquatic angiosperms and perennial macroalgae to fast-growing opportunistic macroalgae and phytoplankton. Finally, under hypertrophic conditions, phytoplankton becomes the main primary producer (Schramm, 1999; Viaroli et al., 2008). This scheme, representing the changes of macrophyte communities along a eutrophication gradient, is known as the "Schramm schematic model" (Schramm, 1999). It has been used as a framework for the use of macrophytes as indicators of water quality in coastal ecosystems (Sfriso et al., 2009; Sargian et al., 2013; Orfanidis et al., 2014). Expert judgment has been used to create the French macrophyte index (examination tool for coastal lagoon macrophyte ecological status, EXCLAME) developed for the Water Framework Directive (WFD) (Ifremer et al., 2011; Sargian et al., 2013) and a slightly different macrophytes index was used in the Lagoon Monitoring Network (RSL, Réseau de Suivi Lagunaire, Ifremer, 2007). After almost two decades of intensive monitoring of macrophyte communities and hydrological parameters in coastal lagoons, it is now possible to study, in a statistically rigorous way, the link between environmental conditions and the occurrence of macrophyte taxa in coastal lagoons and check the general validity of the Schramm scheme (Schramm, 1999).

In this paper, we test the hypothesis that water chemistry and depth of the coastal lagoons determine the communities of aquatic macrophytes that dominate during late spring and early summer on the soft bottoms of the coastal lagoons. Particularly, we aim to disentangle the impacts of the eutrophication status, depth, and the salinity on these communities. Therefore, we study 34 French Mediterranean coastal lagoons, comprising different salinities, depths, and

trophic status and use the data from different monitoring programs such as the RSL, the WFD, and smaller lagoon monitoring projects pursued by lagoon managers. These were compiled in a coherent large and single database. Hence, the aims of this study were i) to determine and rank the main environmental factors driving the distribution of these macrophytes in Mediterranean coastal lagoons characterized by large trophic and salinity gradients, ranging from oligotrophic to hypertrophic status, and from nearly freshwater to slightly above Mediterranean sea water salinities, ii) to investigate the distribution patterns of macrophyte communities in these Mediterranean lagoons.

Methods

Study sites

In the French Mediterranean area, most coastal lagoons are located in the Gulf of Lions (NW Mediterranean Sea), where these systems constitute more than 50% of the coastline. In addition, coastal lagoons occur along the coasts of the Côte d'Azur and the Tyrrhenian Sea (E. Corsica). This study covered 34 lagoons from these different areas (Fig. 1) belonging to the administrative regions of Occitanie, Provence-Alpes-Côte d'Azur and Corse. Some lagoons were divided into sectors corresponding to hydrodynamic sub-basins empirically defined on the basis of their bathymetry in order to individualize sectors belonging to the same lagoon but displaying significant differences (Souchu et al., 2010). Hence, a total of 43 sectors were defined for 34 lagoons. General morphometric data on the studied coastal lagoons are provided in Table 1, together with the identified sectors and occurrence of shellfish farming within the lagoons and additional information on freshwater tributaries from their watersheds. In general, the studied lagoons are shallow water bodies (mean depth smaller than 2 m); only six lagoons have a mean depth higher than 2 m: Berre (BER, VAI), Diana (DIA), Leucate (the south part LES), Thau (TW, TE), and Urbino (URB) (Table 1).

Many lagoons in the South of France still have the typical geomorphological features including narrow sandy barriers and one or several restricted inlets (Table 1), although many inlets have been highly modified by humans. In addition, a significant proportion of the coastal lagoons have been very strongly modified by humans and have either lost their inlets or lost a natural connection to their watersheds (e.g., freshwater inflows through channels). In addition, some of the lagoons in the deltaic settings nowadays occur inland, several kms separated from the sea, because of accretion of the delta, while still communicating with the sea through an artificial canal (Table 1). Other lagoons have been compartmentalized by humans into a complex of several adjacent lagoons. This is the case for the Palavasian lagoons (close to Montpellier city) where a navigation canal—the Rhône to Sète canal—was built through the former Melgueil lagoon running parallel to the coastline. Together with other types of human interventions and natural infilling, this has resulted in creating five "seafront" lagoons and four "inland" lagoons (Fig. 1). The "seafront" lagoons have an inlet, but are separated from their watershed by the Rhône to Sète canal; the "inland" lagoons are separated from the sea by this canal from which they receive seawater indirectly (Leruste et al., 2016).

Data collection

Environmental variables

We used water column data collected through the Lagoon Monitoring Network (RSL) and the Water Framework Directive (WFD) (Ifremer, Quadrige data bank). We considered nine variables from these databases: depth, turbidity, salinity, concentrations of chlorophyll *a*, total nitrogen, total phosphorus, and concentrations of ammonium, nitrate plus nitrite, and phosphate. Samplings were carried out during late spring and summer periods between 1998 and 2015 (Table S1 in Supplementary Material). Water was sampled at a single station per lagoon sector three times per year, i.e., once a month from June to August. No water samplings were available for Les Mouettes (MOU). This lagoon communicated directly with the adjacent Ingril Sud (INS) lagoon; therefore, Ingril Sud (INS) water column data were taken as a proxy for Les Mouettes (MOU). Water samples were collected (1) through a Niskin bottle or (2) with 2 l polypropylene bottles according to the accessibility of lagoons. Samples for total nitrogen and phosphorus, as well as Chl *a* were transported at 4°C and filtered in the

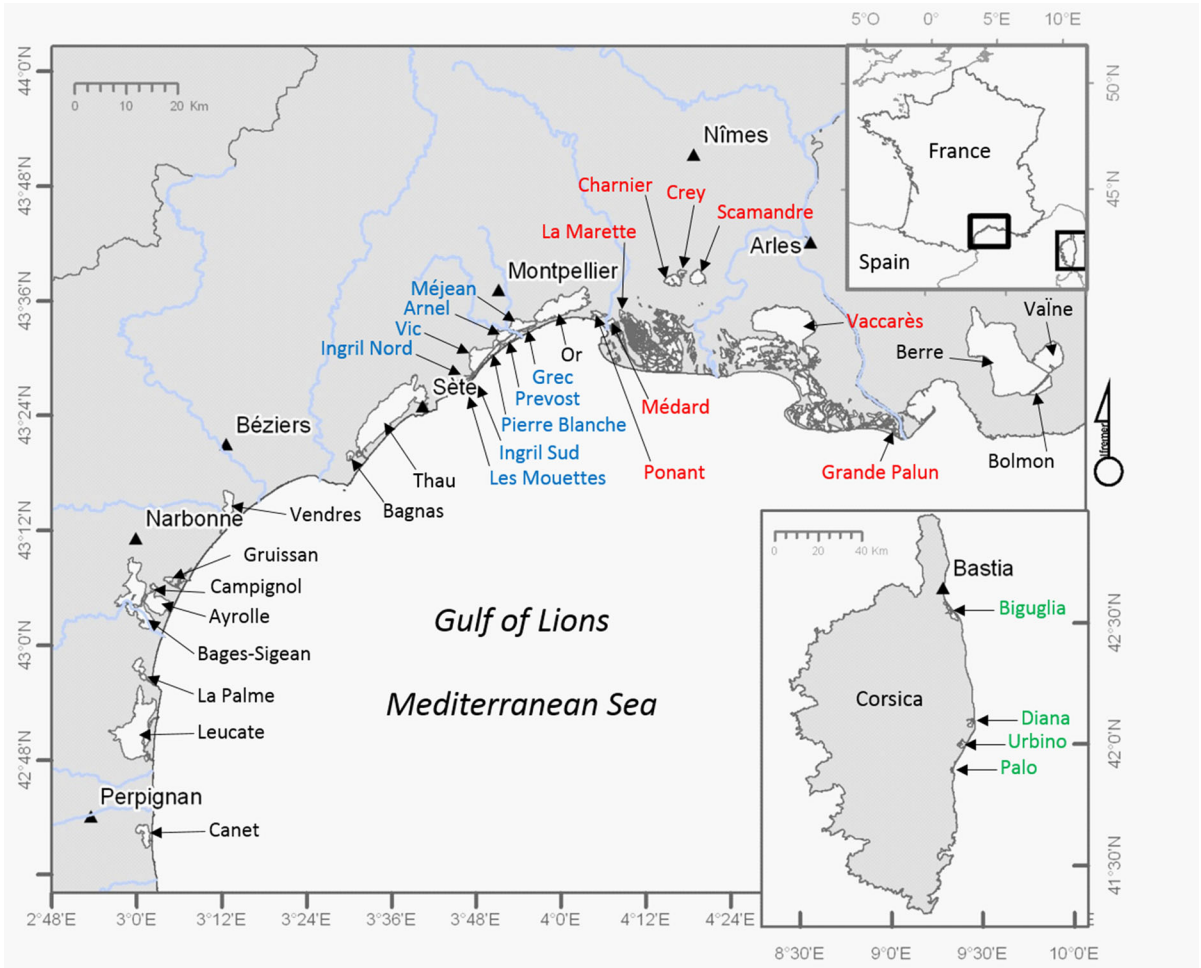

Fig. 1 Overview of the study area showing the 34 lagoons studied. In blue: lagoons from the Palavasian complex, in red: Camargue lagoons, in green: Corsican lagoons. In this study, some lagoons were divided into sectors corresponding to hydrodynamic sub-basins. The number and the names of sectors corresponding to each lagoon are presented in Table 1

laboratory within 3 h after sampling. Inorganic nutrients samples were pre-filtered (1) directly in the field or (2) in the laboratory through 20-µm nylon filters. Salinity was recorded with a WTW LF 197 field sensor. Turbidity was measured at the laboratory with an optic turbidimeter (2100N IS turbidimeter ISO 7027). Chlorophyll *a* concentration, used as a proxy for phytoplankton biomass, was measured by spectrofluorimetry (Neveux & Lantoine, 1993). The analytical protocols of nutrients have been described in detail by Souchu et al. (2010) and details of filtration, conservation, and analysis of phytoplankton have been described by Bec et al. (2011).

Benthic sampling

The data were obtained from different monitoring networks: the RSL and WFD database (Ifremer/Quadrige) and data collected by lagoon managers for the Berre (BER) and Vaccarès (VAC) lagoons. The monitoring surveys were conducted between 1998 and 2015. Macrophyte samplings were performed at benthic stations. To cope with the spatial heterogeneity of the benthos, 1–54 benthic sampling stations were chosen in the studied lagoon sectors depending on the surface of the sector (see Supplementary Material). However, macrophyte samplings were only performed every 2–4 years. The number of benthic stations and the years of macrophyte sampling in the different lagoon

Table 1 Characteristics of the 34 studied lagoons along the French Mediterranean coast comment

Lagoon	Label of the sector	Lagoon Area (km^2)	Mean depth by sector (m)	Connection to the sea through an inlet	Main freshwater tributary	Shellfish farming
Canet	CNN, CNS	6.5	0.6–0.6	np^2	River	
Leucate	LEN, LES	52.7	1.6–2.2	p	Karst	×
La Palme	LAP	6.1	0.7	np^1	Karst	
Bages-Sigean	BGN, BGM, BGS	37.7	1.5–1.5–1.2	p	River	
Ayrolle	AYR	13.4	0.7	p	Wetland	
Campignol	CAM	1.0	0.7	–	Canal	
Gruissan	GRU	1.4	0.7	p	Canal	
Vendres	VDR	6.6	0.6	–	Indirectly to the river	
Bagnas	BAN	1.7	0.6	–	Canal	
Thau	TE, TW	68.0	5.2–3.3	p	River, Canal (RSC)	×
Palavasian complex: (in blue in Fig. 1)						
Les Mouettes	MOU	0.4	0.8	–	Connected to Ingril Sud	
Ingril Nord	INN	3.2	0.7	–	Canal (RSC)	
Ingril Sud	INS	3.6	0.8	p	Canal (RSC)	
Pierre Blanche	PBL	3.3	0.6	–	Canal (RSC)	
Vic	VIC	12.0	1	–	Canal (RSC)	
Prevost	PRE, PRW	2.4	0.9–0.7	p	Canal (RSC)	×
Arnel	ARN	5.9	0.6	–	Canal (RSC)	
Mejean	MEE, MEW	7.2	0.7–0.7	–	Canal (RSC)	
Grec	GRC	1.2	0.5	–	Canal (RSC)	
Or	ORE, ORW	31.8	1.1–1.2	np^2	Canal (RSC)	
Camargue: (in red in Fig. 1)						
Ponant	PON	1.9	2.6	p	River	
Medard	MED	1.4	0.7	–	Canal (RSC)	
La Marette	MARN, MARS	1.3	0.7–0.6	–	Canal	
Vaccares	VAC	101.3	1.4	np^2	Canal	
Grande Palun	GP	3.0	0.6	–	River	
Scamandre	SC	5.5	1.2	–	Canal	
Charnier	CH	5.2	0.9	–	Canal	
Crey	CR	1.7	0.9	–	Canal	
Berre	BER, VAI	132.5	4.9	p	River, Canal	
Bolmon	BOL	6.0	1.3	–	River, Canal	
Corsica: (in green in Fig. 1)						
Biguglia	BIG	13.8	1.5	np^1	River, Canal	
Diana	DIA	5.4	3.5	p	River	×
Urbino	URB	7.6	4.2	np^1	River	×
Palo	PAL	1.1	0.8	np^1	Wetland, Stream	

Legend (p) permanent connection to the sea through an inlet; (np) non-permanent connection to the sea, natural (1) or artificial (2); (−) lagoons without inlets, indirectly connected to the sea through an artificial canal or another lagoon. × indicates the presence of shellfish farming. RSC is the Rhône to Sète canal

sectors are shown in Table S1 (see the Supplementary Material). The macrophyte sampling campaigns were generally carried out in late spring or early summer, during the maximal growth and production rates. Unlike water column data, the protocol and the macrophyte sampling methods can be different according to the monitoring program and the sampling date. These methods are identified in Table S1 and described in the Supplementary Material. Only stations with soft bottoms were considered in this study.

In each lagoon, the depth was measured at each benthic station. In the deepest stations, the depth was measured with a depth gauge by SCUBA divers, whereas in the shallowest lagoons, the depth was measured with a graduated ruler. The mean depth was calculated for each lagoon sector.

Macrophyte taxonomy

The taxonomic resolution of macrophyte determinations was heterogeneous among and within the monitoring programs, ranging from the species to the genus level. To homogenize and standardize the data, all the statistical analyses were carried out at the genus level. Taxonomic nomenclature followed AlgaeBase (Guiry & Guiry, 2016) and World Register of Marine Species (WoRMS Editorial Board, 2016).

Data analyses

The water column data were not normally distributed; therefore median values and interquartile ranges (IQR) were calculated.

A canonical correspondence analysis (CCA) (Ter Braak, 1986, 1987) was used to explore the relationship among macrophyte genera and environmental variables in the lagoons. CCA aims to visualize a pattern of community variation and the main features of species distribution along environmental variables (Ter Braak, 1987), based on unimodal taxon–environment relationships. CCA can be considered as the constrained form of a correspondence analysis (CA) in which the axes are linear combinations of the environmental variables. CCA results are displayed by an ordination diagram in which the taxa scores (represented by points) and the environmental variables (represented by arrows), together reflect the taxa distributions along the different environmental variables (Ter Braak, 1986), with further details about its interpretation provided by Ter Braak (1987).

CCA produces two kind of site scores (Ter Braak, 1986; Palmer, 1993; McCune, 1997): linear combination (LC) scores which are linear combinations of constraining variables and weighted averages (WA) scores which are weighted averages of species scores. Some controversy exists regarding the choice of the site scores (Palmer, 1993; Ter Braak, 1994; McCune, 1997; Oksanen, 2016). According to Graffelman & Tuft, (2004) WA and LC, scores have different properties that are pertinent for the interpretation of results. We chose the LC scores because these have been reported to give better results in simulation (Palmer, 1993; Ter Braak, 1994) and they are interpretable with respect to both taxa and variable markers (Graffelman & Tuft, 2004).

The CCA involved 34 lagoons representing 43 different sectors, 50 genera (after removing rare genera, i.e., genera that have a frequency of occurrence $< 1\%$), and nine environmental variables: Chlorophyll a (CHLa), salinity (SALINITY), turbidity (TURB), depth (DEPTH), total nitrogen (TN), total phosphorus (TP), nitrate plus nitrite (NO3_NO2), ammonium (NH4), and phosphate (PO4). Table 2 list all observed macrophyte taxa and indicates which genera have been used for the CCA analyses. Samplings with non-determined taxa or without macrophytes were removed before the analysis because CCA cannot cope with missing or zero values. Due to the heterogeneity of the macrophyte sampling methods, only the presence–absence data were used. All 43 studied sectors comprised different numbers of benthic stations (see above and Table S1). This allowed us to calculate at each sampling date the relative frequency of occurrence for each taxon in the different sectors by dividing the number of occurrences by the total number of benthic stations in the lagoon sector. This relative frequency of each taxon per sector was used in the CCA.

All abiotic variables were inspected for outliers and the asymmetry and the normality of their distributions were tested (Shapiro–Wilk normality test). All variables, except salinity, have a right-skewed distribution. To improve the distribution of these abiotic variables (make them closer to the normal distribution), with the exception of salinity, all other environmental variables were transformed either as log (x) or as log (x + 1) (i.e., TP, PO4 and NO3_NO2, because

Table 2 List of macrophytes recorded in the 34 studied lagoons

Phylum	Genus	Code used in CCA	Species	Author citation
Charophyta	*Chara*	Cha	*Chara aspera*	C.L. Willdenow, 1809
			Chara galioides	A.P. De Candolle, 1813
			Chara hispida	Linnaeus, 1753
			Chara tomentosa	Linnaeus, 1753
	Lamprothamnium	Lam	*Lamprothamnium papulosum*	(K. Wallroth) J.Groves, 1916
Chlorophyta	*Acetabularia*	Ace	*Acetabularia acetabulum*	(Linnaeus) P.C.Silva, 1952
	Bryopsis	Bry	*Bryopsis hypnoides*	J.V. Lamouroux, 1809
			Bryopsis muscosa	J.V. Lamouroux, 1809
			Bryopsis plumosa	(Hudson) C. Agardh, 1823
	Chaetomorpha	Che	*Chaetomorpha aerea*	(Dillwyn) Kützing, 1849
			Chaetomorpha linum	(O.F.Müller) Kützing, 1845
	Cladophora	Cla	*Cladophora albida*	(Nees) Kützing, 1843
			Cladophora battersii	van den Hoek, 1963
			Cladophora coelothrix	Kützing, 1844
			Cladophora glomerata	(Linnaeus) Kützing, 1843
			Cladophora lehmanniana	(Lindenberg) Kützing, 1843
			Cladophora liniformis	Kützing, 1849
			Cladophora pellucida	(Hudson) Kützing, 1843
			Cladophora socialis	Kützing, 1849
			Cladophora vadorum	(Areschoug) Kützing, 1849
			Cladophora vagabunda	(Linnaeus) van den Hoek, 1963
	Codium	Cod	*Codium fragile*[1]	(Suringar) Hariot, 1889
			Codium tomentosum	Stackhouse, 1797
	Monostroma	Mon	*Monostroma grevillei*	(Thuret) Wittrock, 1866
	Spirogyra	Spi *		Link, 1820
	Ulva	Ulv	*Ulva clathrata*	(Roth) C. Agardh, 1811
			Ulva compressa	Linnaeus, 1753
			Ulva intestinalis	Linnaeus, 1753
			Ulva lactuca	Linnaeus, 1753
			Ulva linza	Linnaeus, 1753
			Ulva rigida	C. Agardh, 1823
			Ulva rotundata	Bliding, 1968
	Ulvaria	Ulr	*Ulvaria obscura*[1]	(Kützing) P. Gayral ex C. Bliding, 1969
	Valonia	Val	*Valonia aegagropila*	C. Agardh, 1823
			Valonia utricularis	(Roth) C. Agardh, 1823
Ochrophyta	*Aglaozonia*	Agl *	*Aglaozonia melanoidea*	Sauvageau, 1899
			Aglaozonia parvula	(Greville) Zanardini, 1843
	Chorda	Cho	*Chorda filum*[1]	(Linnaeus) Stackhouse, 1797
	Cladosiphon	Cld *	*Cladosiphon mediterraneus*	Kützing, 1843
	Cladostephus	Cls	*Cladostephus spongiosus*	(Hudson) C. Agardh, 1817
	Colpomenia	Col	*Colpomenia peregrina*[1]	Sauvageau, 1927
			Colpomenia sinuosa	(Mertens ex Roth) Derbès & Solier, 1851
	Cutleria	Cut	*Cutleria adspersa*	(Mertens ex Roth) De Notaris, 1842
			Cutleria multifida	(Turner) Greville, 1830

Table 2 continued

Phylum	Genus	Code used in CCA	Species	Author citation
	Cystoseira	Cys	*Cystoseira barbata*	(Stackhouse) C. Agardh, 1842
			Cystoseira compressa	(Esper) Gerloff & Nizamuddin, 1975
	Desmarestia	Des	*Desmarestia viridis*[1]	(O.F.Müller) J.V. Lamouroux, 1813
	Dictyota	Dic	*Dictyota dichotoma*	(Hudson) J.V. Lamouroux, 1809
			Dictyota spiralis	Montagne, 1846
	Feldmannia	Fel *	*Feldmannia irregularis*	(Kützing) G.Hamel, 1939
	Halopteris	Hao *	*Halopteris filicina*	(Grateloup) Kützing, 1843
	Padina	Pad *	*Padina pavonica*	(Linnaeus) Thivy, 1960
	Sargassum	Sar	*Sargassum muticum*[1]	(Yendo) Fensholt, 1955
	Scytosiphon	Scy *	*Scytosiphon lomentaria*	(Lyngbye) Link, 1833
	Sphacelaria	Sph		Lyngbye, 1818
	Sphaerotrichia	Spe *	*Sphaerotrichia divaricata*[1]	(C. Agardh) Kylin, 1940
	Stictyosiphon	Sti	*Stictyosiphon adriaticus*	Kützing, 1843
	Taonia	Tao *	*Taonia atomaria*	(Woodward) J. Agardh, 1848
	Vaucheria	Vau		A.P de Candolle, 1801
Rhodophyta	*Acrochaetium*	Acc *		Nägeli, 1858
	Agardhiella	Aga	*Agardhiella subulata*[1]	(C. Agardh) Kraft & M.J. Wynne, 1979
	Aglaothamnion	Ago *	*Aglaothamnion pseudobyssoides*	(P.L. Crouan & H.M. Crouan) Halos, 1965
	Ahnfeltiopsis	Ahn	*Ahnfeltiopsis flabelliformis*[1]	(Harvey) Masuda, 1993
	Alsidium	Als	*Alsidium corallinum*	C. Agardh, 1827
	Antithamnion	Ant *	*Antithamnion cruciatum*	(C. Agardh) Nägeli, 1847
	Callithamnion	Cal	*Callithamnion corymbosum*	(J.E. Smith) Lyngbye, 1819
			Callithamnion tetragonum	(Withering) S.F.Gray, 1821
	Centroceras	Cen	*Centroceras clavulatum*	(C. Agardh) Montagne, 1846
	Ceramium	Cer	*Ceramium codii*	(H. Richards) Feldmann-Mazoyer, 1938
			Ceramium comptum	Børgesen, 1924
			Ceramium diaphanum	(Lightfoot) Roth, 1806
			Ceramium strictum	(Kützing) Rabenhorst, 1847
			Ceramium tenerrimum	(G. Martens) Okamura, 1921
			Ceramium tenuissimum	(Roth) J. Agardh, 1851
			Ceramium virgatum	Roth, 1797
	Chondracanthus	Chc	*Chondracanthus acicularis*	(Roth) Fredericq, 1993
	Chondria	Chn	*Chondria capillaris*	(Hudson) M.J. Wynne, 1991
			Chondria simplisiuscula	Weber-van Bosse, 1913
	Chondrus	Chd	*Chondrus giganteus*[1]	Yendo, 1920
	Chrysymenia	Chr	*Chrysymenia wrightii*[1]	(Harvey) Yamada, 1932
	Chylocladia	Chy	*Chylocladia verticillata*	(Lightfoot) Bliding, 1928
	Corallina	Cor *	*Corallina elongata*	J.Ellis & Solander, 1786
	Dasya	Das	*Dasya hutchinsiae*	Harvey, 1833
			Dasya pedicellata	(C. Agardh) C. Agardh, 1824

Table 2 continued

Phylum	Genus	Code used in CCA	Species	Author citation
			Dasya sessilis[1]	Yamada, 1928
	Falkenbergia	Fal	*Falkenbergia rufolanosa*	(Harvey) F. Schmitz, 1897
	Gelidium	Gel *	*Gelidium crinale*	(Hare ex Turner) Gaillon, 1828
	Gracilaria	Gra	*Gracilaria bursa-pastoris*	(S.G. Gmelin) P.C. Silva, 1952
			Gracilaria dura	(C. Agardh) J. Agardh, 1842
			Gracilaria gracilis	(Stackhouse) M. Steentoft, L.M. Irvine & F. Farnham, 1995
	Gracilariopsis	Grc	*Gracilariopsis longissima*	(S.G.Gmelin) M. Steentoft, L.M. Irvine & F. Farnham, 1995
	Grateloupia	Grt	*Grateloupia doryphora*	(Montagne) M. Howe, 1914
			Grateloupia filicina[1]	(J.V. Lamouroux) C. Agardh, 1822
	Griffithsia	Gri	*Griffithsia corallinoides*[1]	(Linnaeus) Trevisan, 1845
	Gymnogongrus	Gym	*Gymnogongrus griffithsiae*	(Turner) Martius, 1833
	Halopithys	Hal	*Halopithys incurva*	(Hudson) Batters, 1902
	Halymenia	Hay	*Halymenia floresii*	(Clemente) C. Agardh, 1817
	Hypnea	Hyp *	*Hypnea valentiae*[1]	(Turner) Montagne, 1841
	Laurencia	Lau	*Laurencia coronopus*	J. Agardh, 1852
			Laurencia microcladia	Kützing, 1865
			Laurencia obtusa	(Hudson) J.V. Lamouroux, 1813
	Lomentaria	Lom	*Lomentaria clavellosa*	(Lightfoot ex Turner) Gaillon, 1828
	Lophosiphonia	Lop	*Lophosiphonia obscura*	(C. Agardh) Falkenberg, 1897
			Lophosiphonia subadunca	(Kützing) Falkenberg, 1901
	Nitophyllum	Nit *	*Nitophyllum punctatum*	(Stackhouse) Greville, 1830
	Osmundea	Osm	*Osmundea hybrida*	(A.P. de Candolle) K.W. Nam, 1994
			Osmundea pinnatifida	(Hudson) Stackhouse, 1809
	Polysiphonia	Pol	*Polysiphonia denudata*	(Dillwyn) Greville ex Harvey, 1833
			Polysiphonia elongata	(Hudson) Sprengel, 1827
			Polysiphonia mottei	Lauret, 1967
			Polysiphonia opaca	(C. Agardh) Moris & De Notaris, 1839
			Polysiphonia scopulorum	Harvey, 1855
			Polysiphonia sertularioides	(Grateloup) J. Agardh, 1863
			Polysiphonia setigera	Kützing, 1849
	Pterosiphonia	Pte	*Pterosiphonia parasitica*	(Hudson) Falkenberg, 1901
			Pterosiphonia pennata	(C. Agardh) Sauvageau, 1897
	Radicilingua	Rad	*Radicilingua thysanorhizans*	(Holmes) Papenfuss, 1956
	Rytiphlaea	Ryt	*Rytiphlaea tinctoria*	(Clemente) C. Agardh, 1824
	Solieria	Sol	*Solieria chordalis*	(C.Agardh) J. Agardh, 1842
			Solieria filiformis[1]	(Kützing) P.W. Gabrielson, 1985
	Sphaerococcus	Sph	*Sphaerococcus coronopifolius*	Stackhouse, 1797
	Spyridia	Spy	*Spyridia filamentosa*	(Wulfen) Harvey, 1833

Table 2 continued

Phylum	Genus	Code used in CCA	Species	Author citation
Tracheophyta	*Ceratophyllum*	Cea *	*Ceratophyllum demersum*	Linnaeus, 1753
	Cymodocea	Cym	*Cymodocea nodosa*	(Ucria) Ascherson, 1870
	Myriophyllum	Myr	*Myriophyllum spicatum*	Linnaeus, 1753
	Potamogeton	Pot*	*Potamogeton crispus*	Linnaeus, 1753
	Stuckenia	Stu	*Stuckenia pectinata*	(Linnaeus) Börner, 1912
	Ruppia	Rup	*Ruppia cirrhosa*	(Petagna) Grande, 1918
			Ruppia maritima	Linnaeus, 1753
	Zostera	Zos	*Zostera marina*	Linnaeus, 1753
			Zostera noltei	Horneman, 1832

Species with (1) are introduced species (Verlaque 2000, 2001, 2002). Genus codes marked with an asterisk represent the rare genera with a frequency of occurrence < 1%; these rare genera have been removed before the CCA analysis

of the presence of zero values). The water column samples were usually collected during the late spring and mid-summer period, whereas macrophyte samples were collected during late spring or early summer, generally in May–June. Thus, it would not be correct to directly associate the macrophyte data with the environmental variables. Moreover, we assumed that the presence–absence of macrophytes in a site is not exclusively explained by the environmental condition of the year of sampling "*y*," but also by the conditions prevailing during the previous years (particularly for perennial species). Therefore, the macrophyte samplings of the year "*y*" were associated with the mean of each environmental variable integrated over a period of 3 years (y, $y - 1$, and $y - 2$). The statistical significance of the relationship between the species and the whole set of environmental variables was evaluated with a permutation test (Monte Carlo).

An agglomerative hierarchical clustering (AHC) was done after the CCA analysis using the Ward's aggregation method in order to identify groups of lagoons according to the environmental variables and macrophytes composition. The *K*-means method using the Calinski–Harabasz criterion (Calinski & Harabasz, 1974) was used to determine the number of clusters in the AHC.

The CCA analysis and all statistical tests were implemented using the R software version 3.1.1 (R development team, 2016), ade4 package (Dray & Dufour, 2007), and vegan package (Oksanen et al., 2016).

Results

Environments

Salinity

The salinity in the different sectors of the coastal lagoons shown in Fig. 2 ranged from oligohaline (salinity between 0.5 and 5) to hyperhaline (salinity > 40). The majority (65%) of the lagoon sectors had a median in the polyhaline and euhaline ranges, 33% in oligohaline to mesohaline range, and 2% in the hyperaline range. Only five lagoons had oligohaline waters, i.e., Campignol (CAM) and the Camargue lagoons Grande Palun (GP), Scamandre (SC), Charnier (CH), and Crey (CR). The Lowest and highest median salinities (0.9 and 41.6) were recorded in the Grande Palun lagoon (GP) and in the western sector of the Pierre-Blanche lagoon (PBW), respectively (Fig. 2). Salinity showed important between-year fluctuations in the Canet lagoon sectors (CNN, CNS), whereas deeper lagoon sectors with a greater marine influence such as Thau (TW, TE), Diana (DIA), and Urbino (URB) showed minor salinity fluctuations. For Scamandre (SC), Charnier (CH), and Crey (CR), the salinity was only recorded in 2013. A north–south salinity gradient was observed in Bages lagoon with a lowest median salinity recorded in the north part of the lagoon (BGN, 15.5), whereas the highest median salinity was recorded in the south part (BGS, 29.6), which is connected to sea by an inlet. In

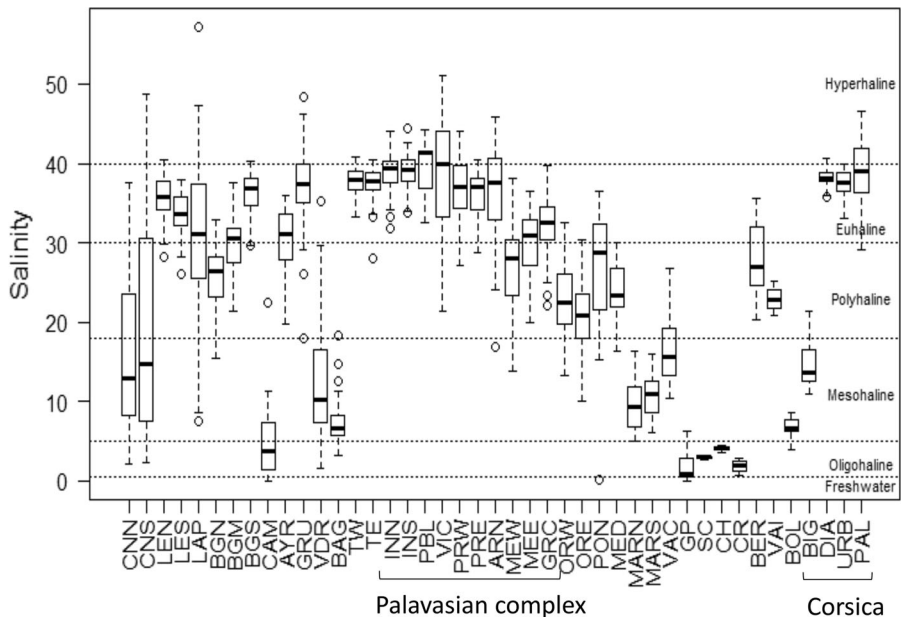

Fig. 2 Distribution of the salinity in the 43 Mediterranean lagoon sectors ordered geographically from west to east along the French Mediterranean coast. Box and whiskers plots from data (June, July, and August) between years: the whiskers represent the 5th and the 95th percentiles, the outer edges of the boxes represent the 25th and 75th percentiles, and the horizontal line within the boxes represents the median. Salinity range from oligohaline and hyperhaline was defined according to the Venice System (1958)

Table 3 Overall median values and ranges (minimum, maximum) of the environmental variables. The codes and transformations used in the CCA are also indicated

Quantitative variables	Median	Min	Max	Code used in CCA	Transformation used in CCA
Salinity	33.9	0.1	47.8	Salinity	
Turbidity (NTU)	3.4	0.5	211	Turb	Log
Depth (m)	1.5	0.5	5.2	Depth	Log
Chlorophylle a ($\mu g.l^{-1}$)	3.9	0.2	397	Chl *a*	Log
Total nitrogen (µM)	39.4	6.03	463	TN	Log
Total phosphorus (µM)	1.33	0.13	57.3	TP	Log $(x + 1)$
Nitrate + nitrite (µM)	0.23	0.00	71.9	NO3_NO2	Log $(x + 1)$
Ammonium (µM)	0.58	0.00	107	NH4	Log
Phosphate (µM)	0.18	0.00	27.3	PO4	Log $(x + 1)$

the Palavasian lagoons, higher salinities were recorded in the west part (INN, INS, VIC, and PBL) than in the east part (PRW, PRE, MEW, MEE, and GRC). Among the Corsican lagoons studied, only Biguglia (BIG) had mesohaline water, the other Corsican lagoons (DIA, URB, PAL) had euhaline waters.

Nutrient, Chlorophyll a, and turbidity

Table 3 shows the overall median, minimum and maximum values recorded for the nutrients, the turbidity, and the Chl *a* concentrations in the lagoon sectors. The mesohaline Canet lagoon (CNN), close to the Pyrenees (Fig. 1) showed the highest concentrations in PO4 (16.4 µM, IQR = 11.3 µM) and TP (30.5 µM, IQR = 14.0 µM), combined with high median values for Chl *a* concentrations and turbidity. PO4 and TP concentrations were 91- and 23-fold higher, respectively, than their corresponding grand median values for all lagoons together (cf., 0.18 µM for PO4 and 1.33 µM for the TP see Table 3). High concentrations of TP (> 5 µM) were also recorded in Vendres (VDR), Bolmon (BOL), Or (ORW, ORE), and in the east part of the Palavasian complex (MEW, MEE, and GRC). The Camargue lagoons (SC, CH, CR), Vendres (VDR), and Or (OR, ORE) lagoons had the highest concentrations in TN, Chl *a*, and turbidity with median values higher than

130 µM for TN, 50 µg l^{-1} for the Chl *a* and 20 NTU for the turbidity. The turbidity was also high (29.9 NTU, IQR = 22.4 NTU) in the Grande Palun lagoon (GP), whereas the TN concentration (37.2 µM, IQR = 14.8 µM) and Chl *a* (14.5 µg l^{-1}, IQR = 6.55 µg l^{-1}) were lower than those observed in other oligohaline lagoons from the Camargue area. An east–west gradient was observed along the Palavasian complex with higher turbidity, Chl *a*, and TN concentrations recorded in the east part (PRW, PRE, ARN, MEW, MEE, and GRC) than the west part (INN, INS, VIC, PBL). Furthermore, all the values recorded for these three parameters were higher in the Palavasian complex than the grand median values calculated for all lagoons studied (Table 3). The lowest median values for all the parameters were recorded in lagoons such as Ayrolle (AYR, i.e., PO4 < 0.07 µM, NO3_NO2 = 0.10 µM, TURB < 1.5 NTU), Leucate (LEN, LES), and the Corsican lagoons Urbino (URB) and Diana (DIA). The latter showed the lowest median values for TP (TP < 0.5 µM), while the lowest TN was observed in Diana (12.7 µM).

Macrophytes

A total of 127 species belonging to 76 genera were observed in the 43 lagoon sectors during the study period (Table 2). Fifty-one percent of the genera belonged to the phylum Rhodophyta, 25% to Ochrophyta, 13% to Chlorophyta, 8% to Tracheophyta (vascular plants), and 3% to the phylum Charophyta (*Chara* and *Lamprothamnium* genera). The six Tracheophyta belonged to the genera *Ceratophyllum*, *Myriophyllum*, *Cymodocea*, *Stuckenia*, *Zostera*, and *Ruppia.* Three different species of seagrasses "sensu stricto" according to (Larkum et al., 2006), were found, i.e., *Zostera marina* Linnaeus, *Zostera noltei* Horneman, and *Cymodocea nodosa* (Ucria) Ascherson, and two species belonging to the Potamogetonaceae, i.e., *Ruppia cirrhosa* (Petagna) Grande, and *Stuckenia pectinata* (Linnaeus) Börner. Figure 3

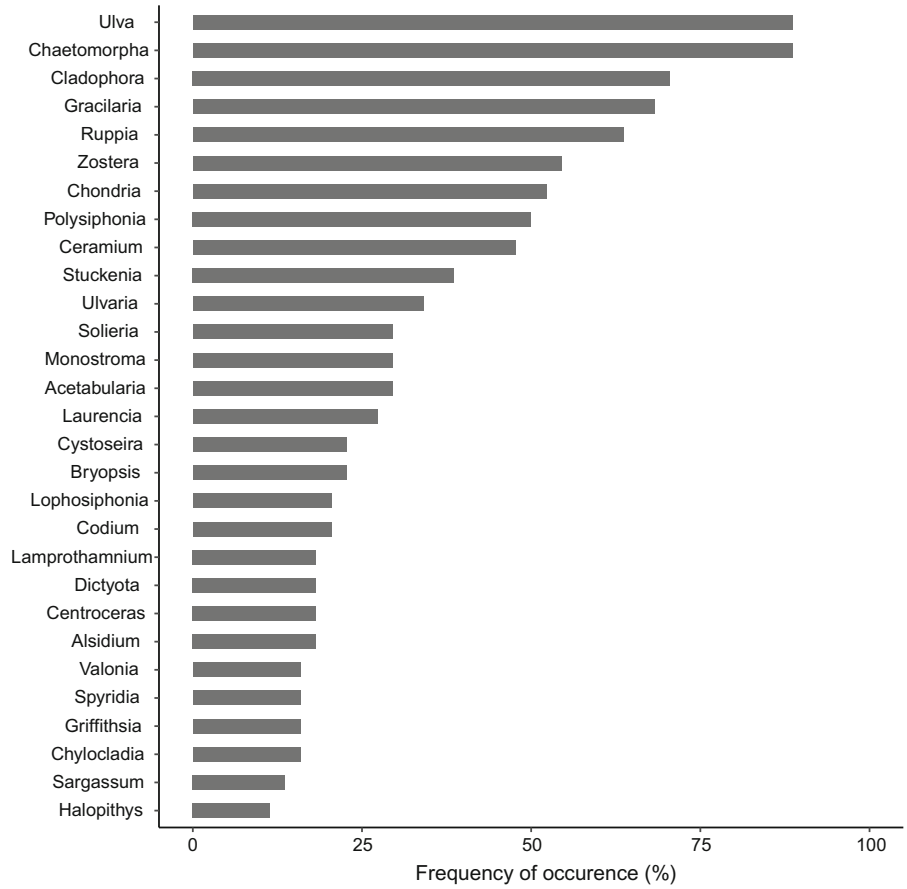

Fig. 3 Frequency of occurrence of the genera in the 43 lagoon sectors. Only genera with a frequency of occurrence > 10% are presented

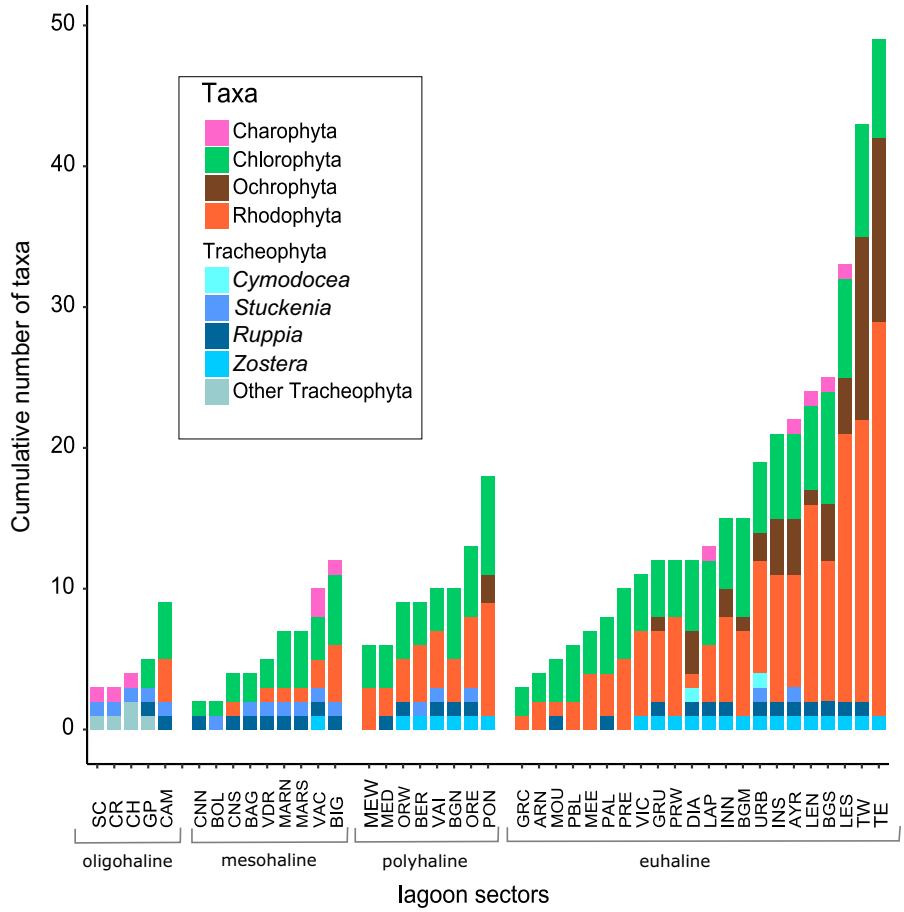

Fig. 4 Cumulative number of genera over the study periods in lagoon sectors. Sectors are grouped according to the salinity classification (see Fig. 2). The number of genera per phylum is represented as well as the main angiosperms (*Cymodocea*, *Stuckenia*, *Ruppia*, *Zostera*) belonging to the phylum Tracheophyta

shows the frequency of occurrence of the different macroalgal genera in the 43 Mediterranean lagoon sectors studied. The three most commonly occurring genera were the green algae *Ulva*, *Chaetomorpha*, and *Cladophora*. These taxa were found in more than 70% of the lagoon sectors. The Tracheophyta *Ruppia* and *Zostera*, as well as the red algae *Gracilaria, Chondria*, and *Polysiphonia* were present in more than 50% of the sectors (Fig. 3).

The cumulative numbers of taxa (at the genus level) observed throughout the study period in the different sectors are shown in Fig. 4. This maximum varied between 2, both in Bolmon (BOL) and in the North part of Canet (CNN), and 49 in the east part of the Thau lagoon (TE, Fig. 4). Lagoons with less than five genera observed were Bagnas (BAG), Arnel (ARN), Canet (CNN, CNS), Grec (GRC), Scamandre (SC), Charnier (CH), and Crey (CR). In contrast, Thau (TW, TE), Leucate (LEN, LES), Bages sud (BGS), Ayrolle (AYR), and Ingril sud (INS) had more than 20 genera observed. On average, oligohaline and mesohaline sectors had lower maximum genera numbers than polyhaline and euhaline sectors. However, large variation was observed in the euhaline group, where the maximum number of genera ranged from 3 in Grec (GRC) to 49 in the east part of the Thau lagoon (TE).

Only nine lagoons presented genera belonging to the phylum Charophyta: the species *Lamprothamnium papulosum* (K. Wallroth) J. Groves was present in Leucate (LES, LEN), Bages sud (BGS), Ayrolle (AYR), La Palme (LAP), Biguglia (BIG), Vaccarès (VAC); different species from the genus *Chara* were present in the Camargue lagoons Scamandre (SC), Charnier (CH), Crey (CR), and Vaccarès (VAC). The

brown algae were present in nine lagoons: Thau (TW, TE), Leucate (LEN, LES), Bages (BGS, BGM), Ayrolle (AYR), Gruissan (GRU), Ingril nord (INN), Ingril sud (INS), Ponant (PON), Urbino (URB), and Diana (DIA). Genera from the phylum Tracheophyta were present in all the lagoons except in the eastern part of the Palavasian complex in Arnel (ARN), Prevost (PRE), Pierre Blanche (PBL), Méjean (MEW, MEE), and Grec (GRC). The seagrass *C. nodosa* was only observed in the Corsican lagoons Urbino (URB) and Diana (DIA). In the oligohaline Camargue lagoons, Scamandre (SC), Charnier (CH), and Crey (CR) no genera belonging to the Chlorophyta nor to the Rhodophyta phylum were observed (Fig. 4).

Relationship between macrophytes and environment

The CCA included the 43 lagoons sectors, the 50 genera, and the nine environmental variables listed above. The first three axes were highly significant ($P < 0.001$, 999 permutation) and accounted for 43.9, 17.7, and 14.7% of the total inertia, respectively (Table 4).

The ordination diagram of CCA shows, in an approximate way, the centers of the genera distributions along each environmental variable (Fig. 5) and the position of the sites (Fig. 6). The first axis was highly positively correlated with salinity and negatively with turbidity and TN (Table 4). Genera on the left side of axis 1 were found at lower salinities, higher turbidities, and higher TN concentrations (Fig. 5a). The genera *Chara* and *Myriophyllum* were mainly found in oligohaline lagoons such as Scamandre (SC), Charnier (CH), and Crey (CR) (Figs. 5a, 6a). *Stuckenia* was mainly found in oligohaline and mesohaline lagoons such as Grande Palun (GP), Bagnas (BAG), Bolmon (BOL), or Biguglia (BIG). Genera on the right side of axis 1 were mainly found in polyhaline and euhaline lagoon sectors. The second axis reflected a depth gradient (Fig. 5b), with taxa located on the lower side such as *Halopithys*, *Griffithsia*, or *Rytiphlaea* related to deeper euhaline lagoons sectors such as Thau (TW, TE), Leucate (LES), Urbino (URB), and Diana (DIA). Some taxa were only present in one single lagoon: *Grateloupia*, *Colpomenia*, *Cutleria*, and *Chorda* were only found in the Thau lagoon (TW, TE), whereas the seagrass *Cymodocea nodosa* was only found in the Corsican lagoons Urbino (URB) and Diana (DIA) (Figs. 5b, 6). Genera located in the upper part of the second axis, such as *Lamprothamnium* and *Acetabularia* were found mainly in shallow lagoons such as Ayrolle (AYR) and La Palme (LAP). Finally, the third axis reflects TP, Chl *a*, and PO4 gradients (Table 4; Fig. 5c). This axis can be defined as a gradient of trophic status. According to the level of eutrophication, two groups of lagoon sectors can be distinguished on this third axis (Fig. 6b). Lagoon sectors with lower Chl *a*, TP, and PO4 concentrations as in Ayrolle (AYR), La Palme (LAP), or Bages (BGN, BGM, and BGS) were projected on the positive part of the third axis (Fig. 6b). In these lagoons, taxa such as *Acetabularia*, *Zostera*, *Valonia*, *Centroceras*, *Lamprothamnium*, or *Spyridia* were observed (Fig. 5d). On the negative part of axis 3, lagoon sectors from the Palavasian complex (e.g., GRC, MEW, MEE, PBL, ARN) were characterized by higher Chl *a*, TP, and PO4 concentrations and by the genera *Ulva*, *Gracilaria*, or *Solieria* (Figs. 5d, 6b). *Ulva*, *Gracilaria*, and *Solieria*, located on the lower central part of the diagram are ubiquist genera present in many lagoons. However, they were mainly present in the most eutrophicated sectors with high concentrations of Chl *a* and TP and PO4.

Following the CCA analysis, the clustering allowed to classify the lagoon sectors according to the presence of genera and environmental parameters (Fig. 6a, b). Thus, five groups were identified according to the Calinski–Harabasz criterion: one group comprising oligohaline and mesohaline sectors, one intermediate

Table 4 Percentage of variation, relative eigenvalues, and correlation coefficients between environmental variables and the first three CCA axes

	Axis 1	Axis 2	Axis 3
Variation (%)	43.90	17.73	14.69
Eigenvalues	0.43	0.17	0.14
Salinity	0.84	0.24	−0.08
Turb	−0.73	−0.02	−0.54
Depth	0.55	−0.78	0.12
Chl *a*	−0.58	−0.33	−0.70
TN	−0.72	0.09	−0.51
TP	−0.54	−0.02	−0.77
NO3_NO2	−0.31	0.02	−0.28
NH4	−0.34	0.07	−0.39
PO4	−0.24	0.05	−0.70

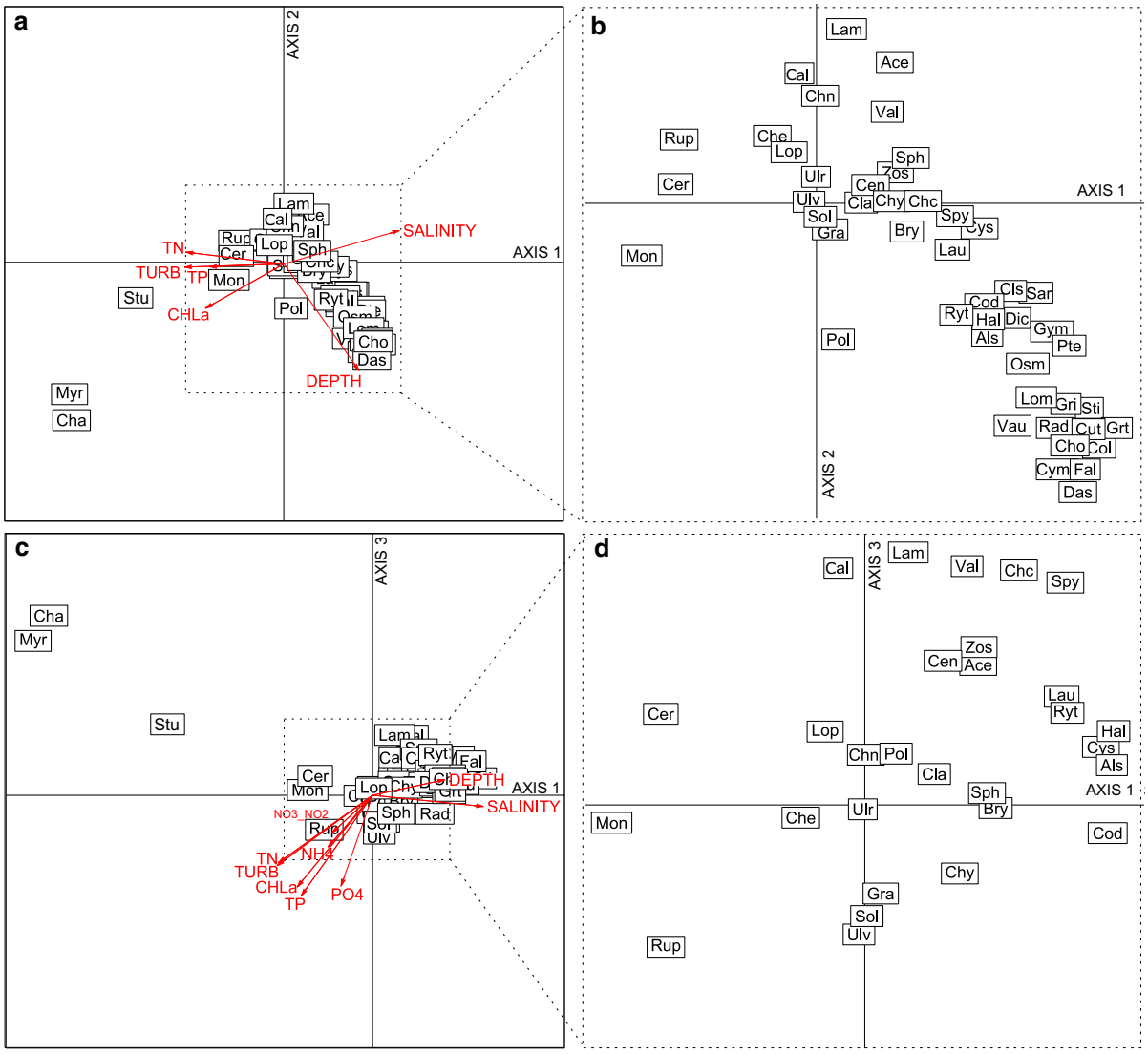

Fig. 5 CCA biplots with the genera (in boxes) and environmental variables (red arrows) in the factorial planes 1–2 (**a**, **b**) and 1–3 (**c**, **d**). Arrows are drawn for the most important variables only. See Table 2 for the environmental variable abbreviations. The dotted line squares (**b**, **d**) represent a zoom of the biplots offering a more detailed view of the genera. The names of the genus codes are defined in Table 3. Rare genera (< 1%) were not included in the analysis

group mainly comprising mesohaline sectors but also some oligohaline and polyhaline sectors during certain periods, and three groups among the polyhaline and euhaline sectors i.e., (i) deep lagoon sectors, (ii) oligotrophic and mesotrophic sectors, and (iii) eutrophic to hypertrophic lagoon sectors (Fig. 6a, b). Hence, water column depth and trophic status clearly impact the macrophyte community composition in the polyhaline and euhaline lagoons. Large variations of nutrient concentrations occurred both among oligohaline and mesohaline lagoons. Nevertheless for the oligohaline and mesohaline sectors, the CCA did not show the very strong differences in macrophyte genera in relation to the variable nutrient concentrations, as observed in polyhaline and euhaline sectors. In addition, the oligohaline and mesohaline lagoons studied were all shallow (< 1.5 m), which did not allow us to study depth as a structuring factor for these lagoons. Hence, in our analysis, neither depth, nor nutrient concentrations were clearly discernable as

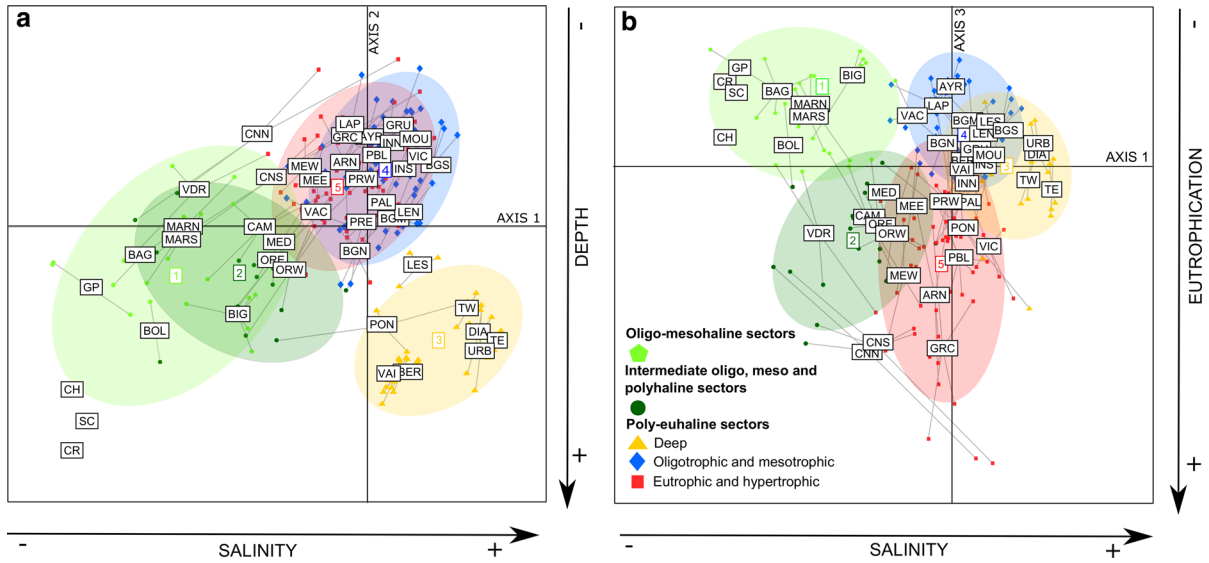

Fig. 6 Visualization of the CCA diagram showing the spatial ordination of lagoon sectors in the factorial planes 1–2 (**a**) and 1–3 (**b**). Points associated to each sector by a line represent a sampling date. In the factorial plane 1–2 (**a**), the hierarchical clustering reveals 2 main groups according to the salinity along the first axis: oligohaline and mesohaline groups (in light green polygons and dark green circles), polyhaline and euhaline groups (blue diamonds, red squares, and yellow triangles). The second axis is related to depth and deeper sectors are represented by yellow squares. On the third axis (**b**), lagoon sectors are distributed along an eutrophication gradient, separating oligotrophic and mesotrophic sectors (blue diamonds) from eutrophic and hypertrophic sectors (red squares). Ellipse contains 95% of points

structuring factors for the macrophyte communities in oligohaline and mesohaline lagoons.

Discussion

The French Mediterranean lagoons located in the adjacent Gulf of Lion, Côte d'Azur and Tyrrhenian Sea (E. Corsica), for which we studied 43 lagoon sectors in 34 lagoons, represent a large spectrum of lagoon types and a wide range of environmental conditions. Our hypothesis that water chemistry and depth determine the communities of aquatic macrophytes in these coastal lagoons is clearly supported by our analysis of the long-term dataset, as we were able to explain 76.3% of the variability of aquatic macrophyte communities in the CCA by the selected factors. Our study, however, focused on the macrophyte communities during late spring or early summer, and, therefore, we have overlooked some cold-loving species that may develop in autumn or winter as e.g., Ochrophyta. Another drawback in our study is that the water chemistry was only sampled from June to August, which does not give a full description of the annual fluctuations of nutrient concentrations and salinities, although this period of sampling provides a very good indicator for the eutrophication status (Souchu et al., 2010). Salinities are maximal during summer. Nevertheless, we checked our classification of salinity classes with the classification based on annual salinity measurements (Bec et al., 2011; Sanchez & Grillas, 2012) and generally found good agreement. Thus, we found that the observed salinity was the main variable driving the distribution of submerged macrophytes in late spring and summer, explaining more than 40% of the variance. Collectively, the environmental and macrophyte data allowed to identify four different groups of lagoon sectors. Two major groups of lagoon sectors were separated according to the salinity gradient. Nested within the group of euhaline and polyhaline sectors, we identified a group of deep lagoon sectors and two groups of shallow lagoon sectors distributed along a eutrophication gradient. In the following discussion, we aim to disentangle the impacts of salinities and the eutrophication status on these communities.

Salinity

CCA analysis showed that salinity was the main variable explaining the distribution of submerged macrophytes (43.9% of the variance). This is in agreement with many studies that have shown that the distribution and abundances of macrophytes are related to the tolerated salinity range (Vaquer & Heurteaux, 1989; Adams et al., 1992; Menéndez et al., 2002; Greve & Binzer, 2004; Vincent et al., 2006; Casagranda & Boudouresque, 2007; Christia & Papastergiadou, 2007; Lirman et al., 2008; Obrador & Pretus, 2008; Schubert et al., 2011; Antunes et al., 2012). Along this gradient, two main groups emerged from the CCA, i.e., a group comprising oligohaline and mesohaline sectors and another group comprising polyhaline and euhaline sectors. In addition, an intermediate group emerged, mainly comprising mesohaline sectors with high salinity variability. Oligohaline and mesohaline sectors harbor freshwater macrophytes tolerant to brackish conditions. One characteristic example is *Stuckenia pectinata*, which tolerates brackish waters with salinity up to 10 (Van Wijk, 1988). This species is highly productive at salinities of 0 and 5 (Teeter, 1965; Borgnis & Boyer, 2016). Although it is less productive at a salinity of 10, it is able to double in biomass and increase the shoot number. In addition, a previous study found that a salinity of 15 reduced production or proved fatal for many plants (Teeter, 1965). Inversely, polyhaline and euhaline lagoon sectors harbor both brackish and marine taxa.

Furthermore, the CCA analysis also showed that the presence of the genera in oligohaline lagoon sectors was also related to higher turbidity and total nitrogen content. In coastal lagoons, nutrient inputs and eutrophication can lead to an increase of the turbidity in the water column. Although increasing turbidity is often caused by phytoplankton growth due to nutrient inputs, turbidity could also be due to sediment resuspension. In fact, in shallow coastal lagoons, type of substrate, sediment resuspension due to the wind (Lawson et al., 2007; Millet et al., 2010), and bioturbation (Scheffer et al., 1993) can increase the amount of suspended solids in the water column. Moreover, turbidity is more persistent in oligohaline lagoons due to very low settling velocity of suspended solids (at salinity < 5), thus reducing light availability for plants (Charpentier et al., 2005). Hence, frequent natural windy conditions, which are common in the South of France favor sediment resuspension that persists in oligohaline lagoons for longer periods (Sanchez & Grillas, 2013).

Turbidity impacts the abundance and the distribution of submerged macrophytes in aquatic environments (Scheffer et al., 1992; Obrador & Pretus, 2008; Zaldívar et al., 2008). However, taxa such as *Stuckenia pectinata* have a specific strategy of extended stem growth thus locating its leaves just below the water surface in a floating canopy. This strategy allows this species to use light resources more efficiently (Van Wijk, 1988). As observed in other regions of the Mediterranean sea (Verhoeven, 1980; Christia & Papastergiadou, 2007; Prado et al., 2013), *S. pectinata* can coexist in oligohaline lagoons with taxa such as *Myriophyllum spicatum* Linnaeus and charophytes, i.e., *Chara aspera* C.L Willdenow, *Chara tomentosa* Linnaeus, and *Chara hispida* Linnaeus. *S. pectinata* is therefore a better competitor for light compared with submerged macrophytes such as the bottom-covering *Chara* species (den Berg et al., 1999; Bakker et al., 2010). In oligohaline lagoons, most of charophytes are sensitive to eutrophication and have a low tolerance to turbidity (Blindow, 1992; Coops, 2002; Mouronval & Baudouin, 2010). *M. spicatum* is a very competitive freshwater species which can develop in turbid and eutrophicated waters (Mouronval & Baudouin, 2010), this fast-growing species often forms a thick canopy shading out other aquatic plants. Because *S. pectinata* is more salt tolerant than *M. spicatum,* it is a better competitor at the salinities occurring in oligohaline lagoons. Moreover, *S. pectinata* is also dominant in mesohaline lagoons. These species co-exists with brackish and marine taxa such as *R. cirrhosa* and *Z. noltei*. However, a suite of life history traits makes *S. pectinata* more competitive than *R. cirrhosa* at lower salinity (< 10) and at lower water transparency (Verhoeven, 1980; Van Wijk, 1988; Menéndez & Comín, 1989; Prado et al., 2013). In the same way, seagrasses, such as *Zostera*, are well adapted to sudden changes and could grow at salinities ranging between 5 and 45 (Greve & Binzer, 2004), but they are less competitive than *S. pectinata* in oligo-mesohaline waters.

Remane (1934) showed a minimum of diversity for invertebrates along the salinity gradient and a critical salinity zone (5–8) was defined by Kinne (1971) where species number was lower. Recently, Telesh et al.

(2013) showed that such a critical salinity zone also exist for macrophytes. The same trend was observed in oligo-mesohaline lagoons where the number of taxa was generally lower than in poly-euhaline lagoons (Fig. 4).

The macrophyte distribution in polyhaline and euhaline lagoons was explained by two other factors, i.e., depth (17.7% of the variance in the CCA) and eutrophication level (14.7% of the variance). Hereafter, the macrophyte distribution patterns are sequentially discussed for these two factors.

Depth

Depth is also an important structuring factor in the distribution of aquatic macrophytes (Vincent et al., 2006; Christia & Papastergiadou, 2007). In most of the deepest lagoon sectors e.g., Thau (TW, TE), south part of Leucate (LES), Diana (DIA), Urbino (URB), a higher salinity (euhaline) was observed, with less fluctuation than in shallowest sectors. Due to their higher volume, and their connection to the sea, these lagoons are less affected by salinity variations. Deep lagoons, in particular Thau lagoon, have a higher number of taxa than other lagoons: the seagrasses *Z. marina* and *Z. noltei*, marine macroalgae such as the red algae *Halopithys incurva* (Hudson) Batters, *Alsidium corralinum* C. Agardh, and also marine exotic species such as *Griffithsia corralinoides* (Linnaeus), Trevisan, *Sargassum muticum* (Yendo) Fensholt, or *Codium fragile* (Suringar), Hariot. *H. incurva* often associated with *Zostera*, *Rytiphlaeae tinctoria* (Clemente),C. Agardh, and *A. corallinum* constituted a permanent group in the west part of this lagoon (Dubois & Lauret, 1991; Gerbal & Verlaque, 1995).

Both quality and quantity of light change with depth. Irradiance decreases with depth and water strongly absorbs the red radiations of the light spectrum. For most submerged aquatic vegetation, light defines the lower limit of their depth distribution (Greve & Binzer, 2004). Hence, some macrophytes and most red algae are more adapted to lower irradiance and usually thrive best in deeper water (Häder & Figueroa, 1997). Seagrasses are able to colonize down to the depth receiving, on the average 11% of the surface light (Duarte, 1991). *Zostera noltei* generally found in shallow waters was observed at 7.5-m deep in TE, whereas *Zostera marina* was found in deeper sites until 9-m deep (Gerbal & Verlaque, 1995). In the Thau lagoon (TE, TW), the red algae *Solieria chordalis* (C. Agardh), J. Agardh, characteristic of deep areas (Gerbal & Verlaque, 1995), was mainly present in depth higher than 4 m. Nevertheless, this species was also found in eutrophicated lagoon sectors with high turbidity levels such as Arnel (ARN), Méjean (MEW, MEE), and Prévost (PRW, PRE).

In addition, deep lagoons showed high proportion of exotic species. This is probably not only related to depth as an ecological driver, but rather the result of the fact that most of the deeper lagoons are used for shellfish farming. Verlaque (2001) described the Thau lagoon as a hot spot of marine species introduction in Europe. More than 20% of the macrophytes species of the Thau lagoon were introduced through shellfish farming. The majority (43 genera) may originate from the Pacific region; the transfer of oysters is a highly probable vector of macrophytes introduction, particularly for those genera that develop on hard substrates. Although many introduced species in Thau and Leucate lagoons have been mainly reported for hard substrates (Verlaque, 2000), we observed some exotic species on soft-bottom substrate (Table 3).

Eutrophication

A third major gradient corresponding to the eutrophication level (14.7% of the variance in the CCA) divided the polyhaline and euhaline lagoon sectors into two groups: on one hand, hypertrophic and eutrophic sectors, and on the other hand, mesotrophic and oligotrophic sectors. Our study showed that lagoons with a low nutrient and Chl *a* concentrations e.g., Ayrolle (AYR), La Palme (LAP), were characterized by the presence of perennial macrophytes such as *Zostera* (*Z. marina* and *Z. noltei*), the Charophyte *Lamprothamnium papulosum* (the only representative of this phylum in these lagoons), and macroalgae such as *Acetabularia acetabulum* (Linnaeus) P.C. Silva or *Centroceras clavulatum* (C. Agardh) Montagne. Inversely, sectors with higher turbidity, Chl *a* and nutrient concentrations in the water column e.g., east part of the Palavasian complex: Méjean (MEW, MEE), Prévost (PRW, PRE), Grec (GRC), Arnel (ARN) were characterized by the presence of opportunistic algae from the genus *Ulva*, *Gracilaria*, or *Solieria*. The high level of eutrophication in these lagoon sectors is due to excess nutrient inputs over the last decades (Leruste et al., 2016). Hence, our results

confirm and illustrate the schematic model of Schramm (Schramm & Nienhuis, 1996; Schramm, 1999) and observations made by several authors in lagoons and coastal ecosystems (Sand-Jensen & Borum, 1991; Duarte, 1995; Schramm & Nienhuis, 1996; Burkholder et al., 2007; Viaroli et al., 2008; Zaldívar et al., 2008) where under low nutrient and clear water conditions, extensive meadows of perennial seagrass species dominate, whereas increasing nutrient inputs enhance the growth of phytoplankton, fast-growing epiphytic macroalgae, and finally floating ephemeral macroalgae which alternate with phytoplankton communities. Under hypertrophic conditions, phytoplankton becomes the dominant primary producer and macroalgae disappear.

This community shift results not only in a loss of ecosystem components, but also in an impoverishment of the ecosystem complexity and organization (Viaroli et al., 2008). Our results showed a lower diversity in the most eutrophicated lagoon sectors with only few genera observed (e.g., *Gracilaria*, *Ulva*, *Solieria*) and the absence of brown algae and angiosperms (Fig. 4). However, macroalgal blooms involve relatively few taxa. Among these taxa, we can cite the opportunistic, free floating macroalgae: *Gracilaria* and *Ulva* which indicate a degraded-eutrophic status which is characterized by high nutrient conditions. These taxa outcompete with benthic perennial macrophytes because they are more adapted to high turbidity, lower irradiance, and nutrient supply. *Ulva* and *Gracilaria* are nitrophilic species (Gerbal & Verlaque, 1995) and the rate of growth of these fast-growing macroalgae increases with increasing dissolved inorganic nitrogen supply (Teichberg et al., 2010). Hence, *Ulva* and red algae such as *Gracilaria* or *Solieria* outcompete other primary producers due to their ability to store nitrogen and phosphorus, but also in the case of the *Gracilaria* to lower light intensity requirement. In our results, the excess of DIP and the high TP concentrations in the most eutrophicated lagoons (e.g., MEW, GRC), suggest that P was not limiting the primary production as described by Souchu et al. (2010). These authors conclude in a studied of 20 coastal French Mediterranean lagoons, that increase of DIP along the eutrophication gradient is explained by the P content of lagoon sediments and that recycling processes strongly affect inorganic nutrient concentrations in the water column. The nitrogen limitation in eutrophicated lagoons is thus related to high TP and PO4 concentrations in the water column. The primary growth limiting nutrient may shift from P alone in oligotrophic lagoons to N alone as eutrophication proceeds (Souchu et al., 2010).

We showed that the vegetal succession along a eutrophication gradient described by Schramm (Schramm & Nienhuis, 1996; Schramm, 1999) is clearly applicable for the shallow polyhaline and euhaline coastal lagoons (Fig. 7), at least for the NW Mediterranean region. The submerged aquatic vegetation under oligotrophic conditions comprises seagrasses and slow-growing algae (Orfanidis et al. 2008), while opportunistic macroalgae and phytoplankton dominate under eutrophic and hypertrophic conditions, respectively (see Fig. 7d). Viaroli et al. (2008) argue that the two successional stages, i.e., the rooted angiosperms and the opportunistic macroalgae, represent two alternative stable states. Nevertheless, our analysis did not allow us to show that these two stages represented coexisting attraction basins representing clearly alternative states for a given window of environmental conditions. In contrast, for the oligohaline and mesohaline lagoons, the Schramm scheme does not fully comply. This is related to the predominance of members from the Potamogetonaceae in these lagoons that have a particular growth form capable of extended stem growth with many floating leaves (Van Wijk, 1988). This strategy allows these species to expose their leaves to the high light intensities in the surface layer of the lagoon and thus, to escape from the shading caused by dense phytoplankton and floating macroalgae. This way, these Potamogetonaceae species are able to coexist with the latter and can, therefore, persist at higher levels of eutrophication than the typical seagrass species in the polyhaline and euhaline lagoons. Therefore, we hypothesize that the succession of primary producer's along a eutrophication gradient in oligohaline and mesohaline lagoons (Fig. 7b, c) resembles the scheme described by (Sand-Jensen & Borum, 1991) for small temperate lakes, which is depicted in Fig. 7a. In agreement with our results and observations, we assume that in oligohaline and mesohaline lagoons, smaller submerged bottom dwelling macrophytes (e.g., particularly Charophytes in oligohaline lagoons) dominate in the oligotrophic status, although often coexisting with small populations of *S. pectinata*. With increasing eutrophication level, this Potamogetonaceae increase in biomass in concert with

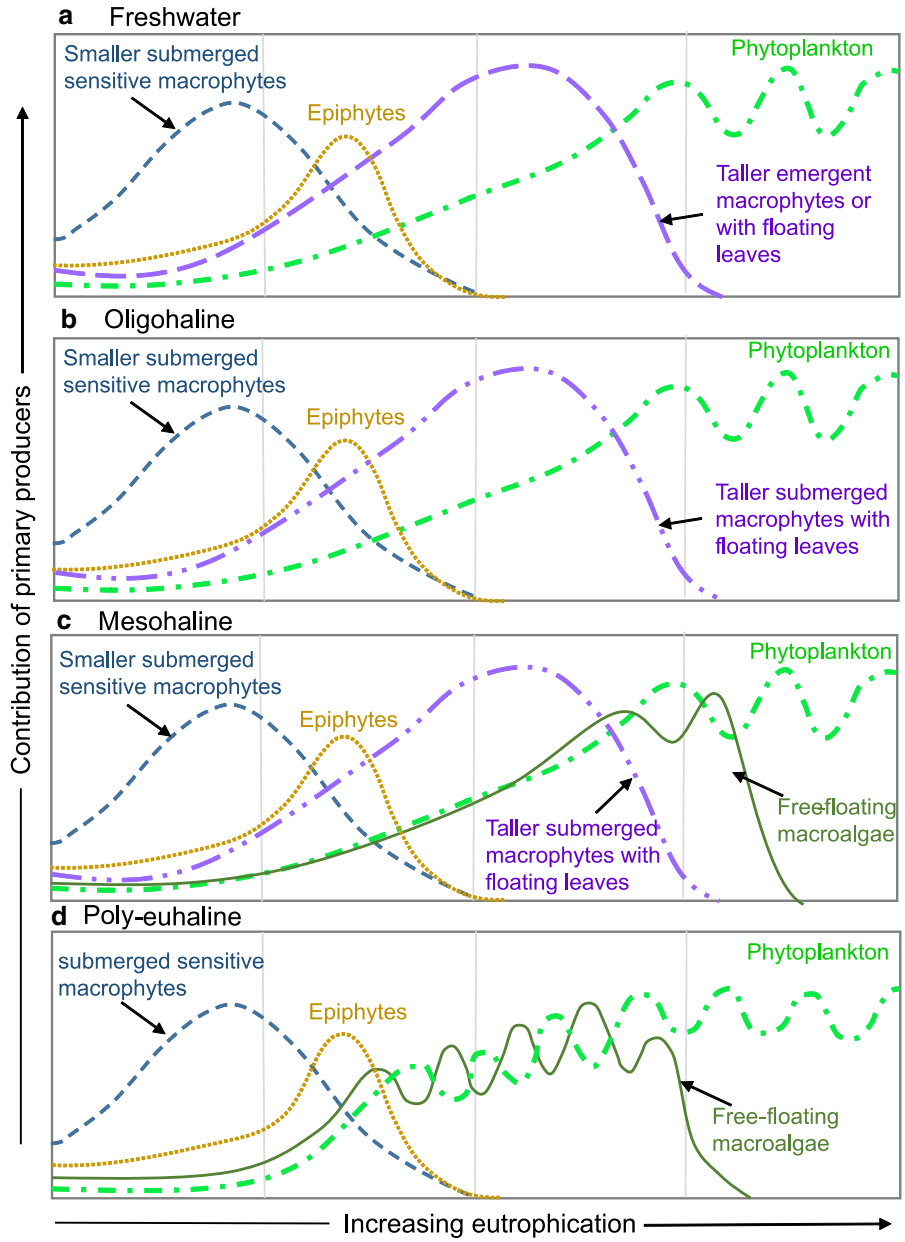

Fig. 7 Conceptual representation of the relative succession of primary producers along an increasing eutrophication gradient in (**a**) shallow temperate lakes [modified from Sand-Jensen (1980), Sand-Jensen and Borum (1991)], (**b**) oligohaline and (**c**) mesohaline lagoons [this study],(**d**) polyhaline and euhaline lagoons [modified from Schramm (Schramm & Nienhuis, 1996)]

phytoplankton and with opportunistic macroalgae, the latter particularly in mesohaline lagoons (Fig. 7c). The fact that *S. pectinata* are present over a very wide range of eutrophication levels explains why in our CCA analysis we could not discern the impact of eutrophication levels as a structuring driver for the macrophyte community composition in the oligohaline and mesohaline lagoons. The conceptual scheme we propose in Fig. 7 needs to be validated by more data on biomass and coverage of macrophyte taxa in oligohaline and mesohaline lagoons with contrasting trophic levels.

The general trend of macrophyte taxa suggested in Fig. 7 is probably more adapted in the French lagoons or Mediterranean lagoons with nanotidal conditions and less pertinent for the microtidal Italian lagoons in the Norther Adriatic Sea. However, nanotidal conditions are widespread in the Mediterranean and tides exceeding 50 cm only occur in the Northern Adriatic and the Gulf of Gabès (Tunisia). Nevertheless, the

coexistence of Charophytes and *S. pectinata* has also been observed in a Western Greek lagoon by Christia & Papastergiadou (2007) under low salinity and small fluctuation of this parameter. However, more biogeographic data are needed to extrapolate our findings to the ensemble of nanotidal lagoons in the whole Mediterranean Sea.

Other factors

Even though a significant portion of the macrophyte distribution could be attributed to salinity, depth, and trophic status, yet a portion (24% of the CCA) remains unexplained. The two main reasons for undetermined variation are the lack of other relevant explanatory variables and stochastic variations in taxa distribution. Stochastic fluctuations are impossible to quantify and remain unexplained in a statistic analysis (Borcard et al., 1992). Other abiotic and biotic factors may drive the macrophyte community structure. These may include, other factors related to water chemistry as e.g., oxygen, pH, and chemical contaminants. In this respect, pH and oxygen are subject to strong diurnal fluctuations related to the community metabolism in the lagoon and we were, therefore, unable to take these into account due to the large variability of sampling in our database. Non-chemical factors include hydrodynamics, physical exposure, substratum, grazing, interspecific, and intraspecific competition. Among these factors, hydrodynamics play an important role in spatial and temporal distribution of macroalgae, transporting plants and influencing chemical characteristics in the water column and in the sediment (Flindt et al., 1999), impacting the connectivity between the adjacent Mediterranean sea and the lagoons (Fiandrino et al., 2017). Furthermore, coastal lagoons can be highly impacted by chemical contaminants (Munaron et al., 2012) and some of these compounds can impact the photosynthesis and the growth of macrophytes (Haynes et al., 2000; Chesworth et al., 2004). Future studies need to focus on the impact of these factors on the macrophyte communities.

Acknowledgements This study was supported by a Ph.D. Grant for Ines Le Fur, financed by Ifremer and the French Water Agency (Agence de l'Eau Rhône Méditerranée Corse). The authors thank the staff of the Ifremer laboratory in Languedoc-Roussillon and PACA, the Tour du Valat institute, lagoons managers of the GIPREB and of the Réserve Nationale de Camargue and all surveyors involved in the collection of the data on which this article is based.

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