MANAGEMENT AND RESTORATION OF MEDITERRANEAN COASTAL LAGOONS IN EUROPE

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(Coordinators)

CÀTEDRA
D'ECOSISTEMES
LITORALS
MEDITERRANIS

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This publication is included in the project “Life Pletera” (LIFE13 NAT/ES/001001)

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CÀTEDRA D'ECOSISTEMES LITORALS MEDITERRANIS

Ajuntament de Torroella de Montgrí

GrupoTragsa

Generalitat de Catalunya
Departament de Territori i Sostenibilitat

Parc Natural
del Montgrí, les Illes Medes i el Baix Ter

can Quintana Museu de la Mediterrània

With the support of:

Diputació de Girona

Universitat de Girona

Edition

Càtedra d'Ecosistemes Litorals Mediterranis

Parc Natural del Montgrí, les Illes Medes i el Baix Ter

Museu de la Mediterrània

Coordinators of the volume

Xavier Quintana, Dani Boix, Stéphanie Gascón, Jordi Sala

Collection Coordinator "Recerca i Territori"

Xavier Quintana

Graphic Design

Glòria Martí Romaní

Printing

Gràfiques Agustí

Printed on recycled paper Cyclus print

ISSN: 2013-5939

Dipòsit legal: GI 661-2018

With the support of:

FUNDACIÓ MASCORT TORROELLA DE MONTGRÍ

associació del llibre de la festa major

Universitat de Girona Consell Social

Ajuntament de Girona

Sumary

Introduction: an integrative approach for the restoration of Mediterranean coastal lagoons

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Introduction

The restoration of degraded ecosystems has developed during the past three decades, progressing from simple trial-and-error experiences to an approach based on a reference system to guide and test restoration projects (Van Andel & Aronson, 2006). A common approach has been using an ecosystem in good ecological state and a degraded ecosystem as references to study and evaluate the results of the restoration actions (Rey-Benayas et al., 2009). This method allows comparing the characteristics of the restored ecosystem with those of the same degraded ecosystem before implementing restoration actions. Recent studies have also acknowledged the importance of incorporating social and economic aspects, together with scientific-technical aspects, in restoration projects. Comín et al. (2018) have recently proposed a restoration approach based on the evaluation of the ecosystem services to restore territories made of a mosaic of ecosystems as watersheds. Restoration ecology has also been progressing rapidly in the past decades, providing the fundamentals to stimulate ecological restoration initiatives and projects including those related to coastal ecosystems and socioecological drivers (De Wit et al., 2017).

Many Mediterranean coastal lagoons (MCL) are degraded because of land use transformations around the lagoons and ongoing pollutant discharges from continental human activities. Global coastal changes have been mostly caused by direct and indirect impacts of human populations (Valiela, 2006). Therefore, most of the causes of the degradation of coastal lagoons are extraneous to the lagoons, so their restoration should mainly target actions outside the coastal lagoons. Intense degradation of MCL took place after some major socioecological changes. The regulation of river flows decreased the amount of sediment transported and deposited along coastlines, reducing their geomorphological transformations and the formation of new coastal lagoons. Urbanisation of Mediterranean coasts reduced their capacity to form new lagoon areas. Climate change is both a challenge and an opportunity for the recovery of MCL, as an intense geomorphological activity is taking place along Mediterranean coasts due to frequent sea storms and other impacts of climate change.

The general ecology of MCL was described by Guelorguet & Perthuissot (1983), who proposed a simple model of ecological characteristics of different coastal lagoons in relation with the freshwater-seawater gradient on one side and the evaporation gradient on the other side (Fig. 1). Basically, the degree of mixing of freshwater and seawater and water turnover are the major factors that determine the structural and functional characteristics of coastal lagoons, as both biological communities and biogeochemical processes, as well as socioeconomic ones, (Anthony et al., 2009) are tightly related to the freshwater-seawater gradient (Kjerfve, 1994) and its associated characteristics. In fact, the biological communities of coastal lagoons are the result of the evolutionary process of adaptation to water salinity, which is a major ecophysiological factor regulating species' capacity to live in water with different salt concentrations. The mix of seawater and freshwater and the evaporation of water are the major physical processes regulating the rest of the ecological characteristics of coastal lagoons that are closely related to the hydrodynamic processes taking place in the coastal zone (Ayala-Castañares & Phleger, 1969).

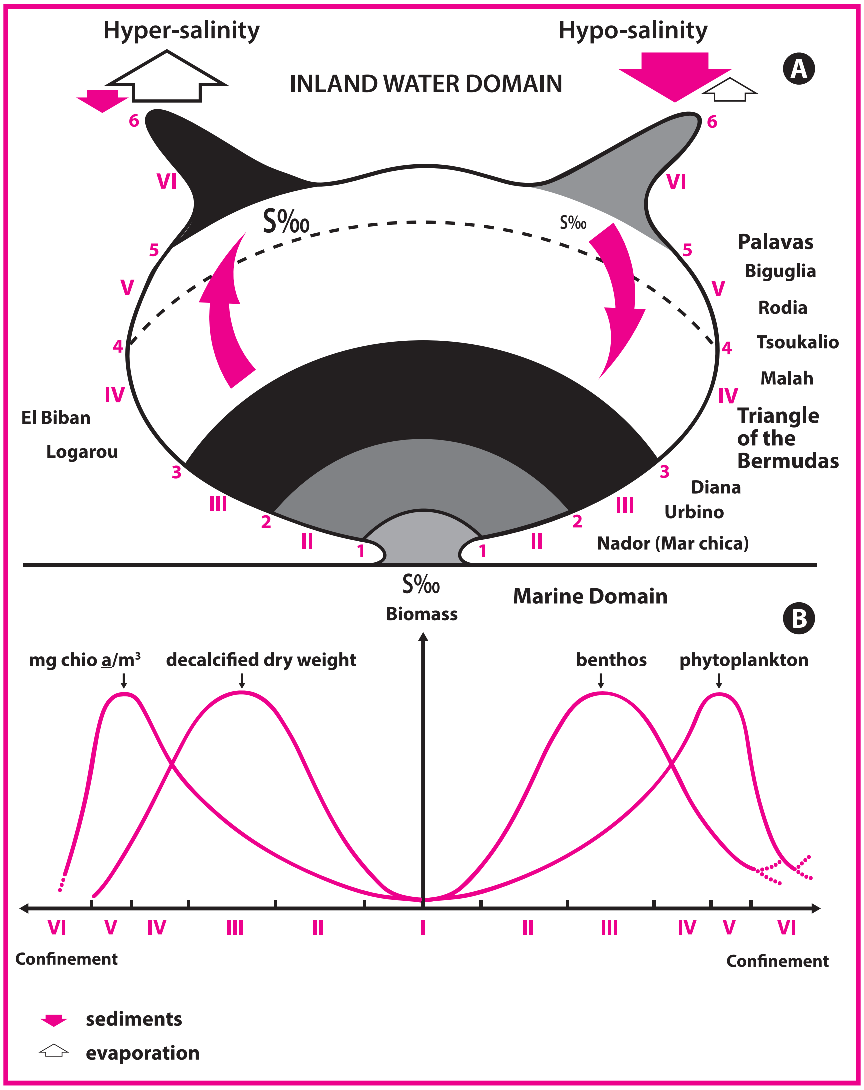

Fig. 1. "*Le domain paralique*" model of ecological characteristics across gradients of confinement (Guelorguet & Perthisot 1983) illustrated with examples of different MCL.

Cloern (2001) showed the direct relationship between increased nutrient inputs and other stressors (intensive fishing and aquaculture, invasive species, toxic pollutants) and their impacts on coastal aquatic systems in terms of eutrophication, human health, and socioeconomic costs, and suggested some potential actions to reverse the effect of these stressors. However, the reverse process after the stressors are removed is not straightforward, since it may take alternative ways. However, a general trend towards the improvement of the ecosystem's characteristics is observed on the long term, especially if the removal of stressors is combined with hydrogeomorphic improvements to facilitate sea-coastal lagoon exchanges (Viaroli et al., 2007; Viaroli et al., 2008).

The foundation of the Society for Ecological Restoration in 1987 and the UN Conference on Environment and Development in 1992, increased the environmental concern on restoring degraded ecosystems. Several meetings between governmental and non-governmental agencies during the 20th century established commitments to put into practice ecological restoration at large scale. These and many other initiatives indicate the interest in providing both the scientific fundamentals and the technical experience to plan, perform, and monitor ecological restoration programs, actions, and projects. This paper reviews some of the major aspects to be considered for the restoration of MCL.

The framework for the restoration of Mediterranean coastal lagoons

Coastal lagoons are typical ecosystems of sedimentary coasts where a sandbar deposited by sea currents limits and progressively closes an area of the sea attached to the continent or to the terrestrial part of an island. The present coastal lagoons were formed after the last glaciation, when the sea level rise stabilised. Their geomorphological features are regulated by the interaction between the sea and continental water and sediment flows, which may be strongly regulated by human action, as well as other factors such as wind and biotic interactions (Carter, 1988). Coastal lagoons are distributed along the low coasts of the Mediterranean shore (Fig. 2).

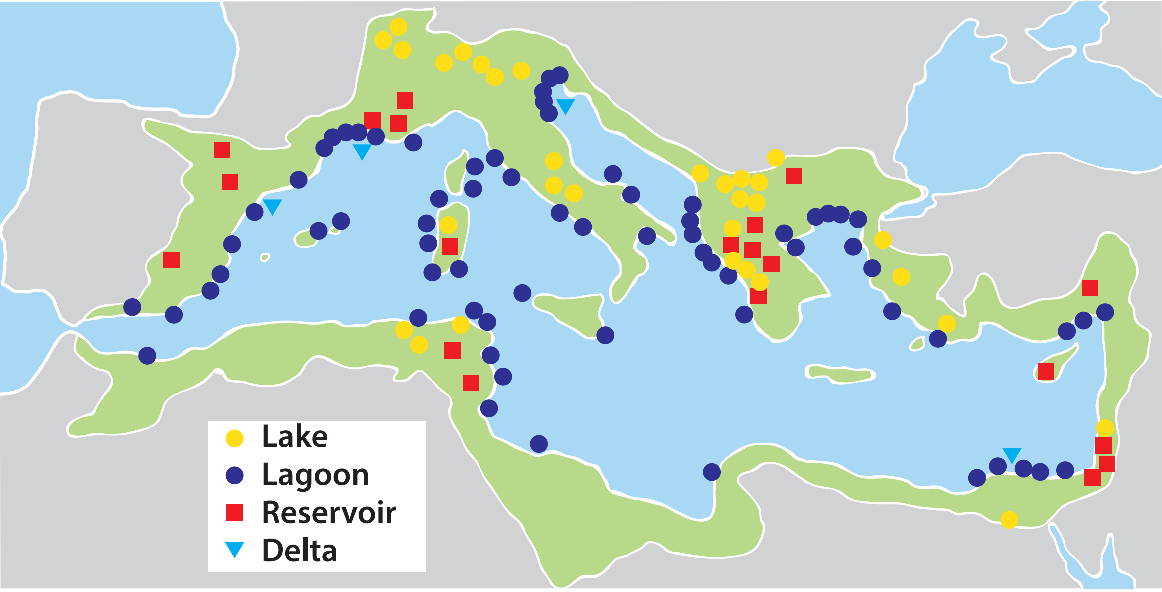

Fig. 2. Distribution of major coastal lagoon systems in the Mediterranean coasts (adapted from Pearce & Crivelli 1994).

The driver-pressure-state-impact-response (DPSIR) framework (Fig. 3) is a useful approach to understand the restoration options for degraded coastal lagoons (Pirrone et al., 2005; Pastres & Solidoro, 2012). Regulated continental inflows caused siltation and loss of water quality of many MCL (Comín & Valiela, 1993; Menéndez & Comín, 2000). Coastal dynamics, including sea currents and waves, should be a major driver of MCL evolution. However, because of the small amplitude of Mediterranean tides (with the exception of a few coastal zones such as the north Adriatic coast), the tidal energy is very low to drive the major characteristics of MCL. In contrast, more frequent sea storms and the sea level rise caused by climate change are important geomorphological drivers of the MCL-sea exchanges.

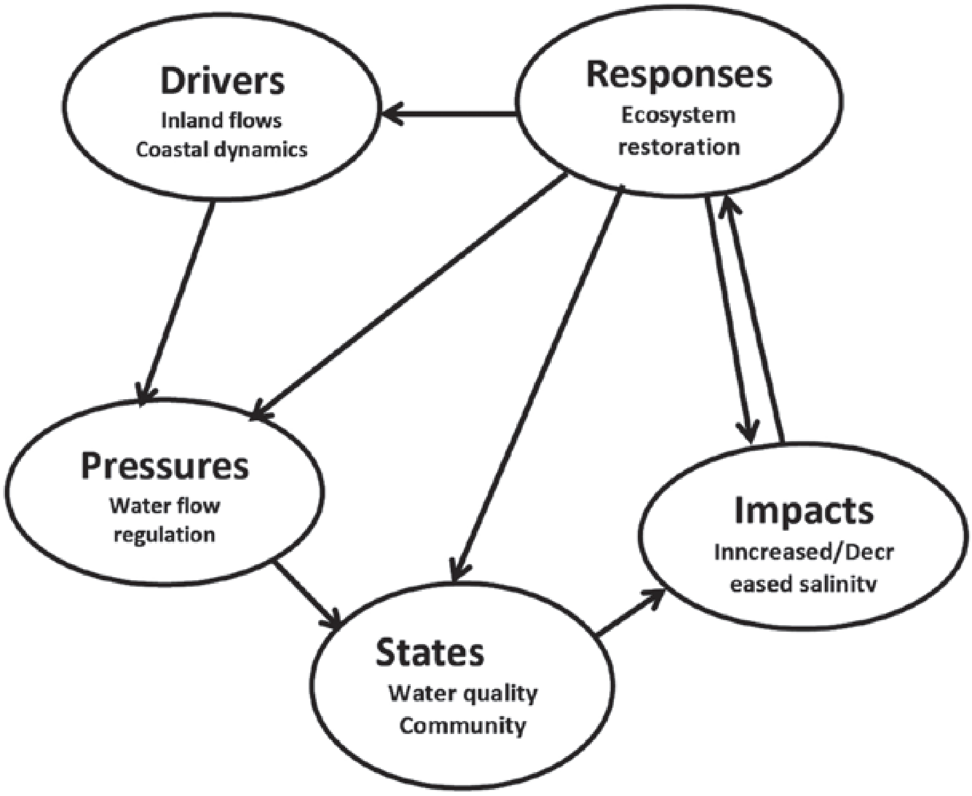

Fig. 3. Scheme showing some of the major drivers, pressures, state characteristics, impacts and responses of coastal lagoons.

Changes in the amounts and characteristics of the continental water flowing into MCL put pressure on their ecological functioning. For example, alterations of the trophic web of some MCL took place following intensive discharges of pesticides associated with agricultural sewage. Increasing continental water flows (or decreasing lagoon-sea exchanges), decrease MCL salinity and put significant pressure on the ecology of MCL, as they alter the freshwater-seawater water budget of the lagoons. MCL are quite closed systems and are not submitted to intensive hydrodynamics. So, in general, increasing lagoon-sea water exchanges will have a positive effect for the ecological status of a coastal lagoon, a rejuvenating effect in its geomorphological history. However, inflows of polluted seawaters to pristine lagoons will cause a degradation of their ecological characteristics.

The state of many MCL is poor because of artificialisation of their shorelines and especially the inflow channels both from the continent and those connecting the lagoon with the sea. Also, many of them have low water quality because of the altered water balance, which affects all the ecological aspects of the ecosystem, from the physical and chemical characteristics of the water to fisheries. Invasive species cause significant changes in the biological structure of some MCL.

Loss of biodiversity, decreased or increased salinity, and eutrophication significantly affect coastal lagoons (Perez-Ruzafa et al., 2011). Most frequently, the actions to mitigate these impacts on coastal lagoons are based on partial aspects of their ecological functioning. Reducing the discharge of pollutants, removing invasive species, regulating fishing, and removing excess accumulated sediment are usual responses to improve the state of degraded MCL. However, restoration requires an ecosystem approach and actions targeted at eliminating the causes of degradation and not just their effects. For example, removing the sediment accumulated by an excess of continental inflows requires changing the inflows and not only removing the sediment, as the latter action will only work temporarily but will not remove the cause of sediment accumulation.

In addition, a restoration plan requires taking into account the socioecological framework of the system to be restored, which is particularly relevant in the coastal zone where so many socioeconomic aspects depend on the state and management of natural resources. For example, the important clam industry developed in some lagoons could be negatively affected if freshwater inflows are restricted because nutrients associated to freshwater flows favour phytoplankton growth which feeds bivalves. However, bivalves cultivated in pans may cause an excess of organic matter accumulation in the sediment with respect to the oxidative capacity of the lagoon and, consequently, eutrophication (Marinow et al., 2008).

The restoration of Mediterranean coastal lagoons

Because of the small amplitude of Mediterranean tides (20 cm on average, with some exceptions, such as the North Adriatic coast), the wave energy is relatively low. In contrast, the continental inflows have been polluting and discharging materials since the mid-twentieth century, after intensification of agricultural practices. These factors, together with the loss of habitats because of land cover changes, have been the major drivers of the degradation of Mediterranean coastal lagoons. Agricultural sprawl during the past century and urbanisation during the past half century have negatively affected the state of MCL.

The restoration of coastal lagoons should first focus on the dynamics of the coastline and its geomorphological capacity to create new lagoons. Coastal lagoons, particularly MCL, are ephemeral. They tend to close their connections with the sea and to accumulate sediments, decreasing the open water areas, and finally become marshlands. This natural process can take hundreds to thousands of years. Along a coastline modelled by natural geomorphological processes, new coastal lagoons are formed, as the aggradation of old lagoons takes place on this time scale. However, because of anthropomorphic pressures, these natural processes are restricted nowadays, and the formation of new coastal lagoons is very limited along the Mediterranean coastline, with a few exceptions at the mouths of some deltas. However, even in these zones the formation of new lagoons is altered because of intense river flow regulations.

Sea level rise as a consequence of climate change may be an opportunity to recreate coastal lagoons. More intense and frequent sea storms will increase the communication of coastal lagoons with the sea and will favour the deposition of sediments in coastal bars. This passive restoration, together with an adaptive strategy to use the coastal zone for anthropic activities, may contribute to improving the state of degraded MCL on the short-medium term and to recreating new ones on the long term. It can be argued that it will also cause the salinisation of continental coastal zones. However, in many cases, these zones were marine zones and marshlands filled artificially with sediment for agricultural purposes or urbanised. Also, the increasing continental-sea interaction will favour coastal fisheries due to nutrient release from flooded soils and will increase natural marshlands in the Mediterranean coastal zone, which decreased their land cover as a consequence of intense agriculture, industrial, and urbanisation processes. Adapting to sea level rise and more frequent sea storms is a challenge to ensure the life of people living in people living along Mediterranean coasts and for recovering artificialized and degraded coastal environments. This will be a more efficient socioeconomic approach than refilling the sand of beaches with sand from close seas and constructing barriers. The ICZM-Integrated Coastal Zone Management approach tries to incorporate these points of view with support of the UNEP (http://www.unep.org). However, adaptation to changes of the marine dynamics will not be efficient if major pressures on MCL, such as urban sprawl and land cover and use changes, take place faster than—and against—the adaptive strategy (El Asmar et al., 2012).

The first step to planning the ecological restoration of MCL is to remove the causes of degradation of the lagoon. It is critical to know the coastal dynamics and its geomorphological capacity to recreate lagoons (Carter, 1988), because this knowledge can guide or at least set up the framework to prioritise restoration actions on large spatial and temporal scales (Fig. 4).

A physical intervention may be required to restore the adequate seawater and continental water inflows, and the habitats surrounding a coastal lagoon are an important part of it. Both freshwater wetlands and marshlands play key roles not just in water and sediment dynamics, but also in removing pollutants entering the MCL and providing habitats for many species. The interplay between open water and the surrounding wetlands is also a key part of the biogeochemical processes in the whole ecosystem. Sediment removal is an efficient action to rejuvenate the state of small eutrophic coastal lagoons or to facilitate water flows in tidal creeks and inflow channels. From this point of view, it is important to know the cryptodepression depth (the depth of the water column below sea level) because it is the portion of the water column facilitating the inflow of seawater. Moreover, in lagoons perpendicular to the coastline originated from abandoned river mouths, this part of the water column can become anoxic because of the establishment of an halocline (Armengol et al., 1983; Rojo & Miracle 1989; Paches et al., 2014), particularly if these lagoons have been subjected to organic pollution (Koutsodendris et al., 2015).

Water turnover is a key characteristic of the MCL. In general, seawater turnover is very low (lower than 6 months) because most MCL are quite closed and seawater exchange is restricted due to the microtidal regime in most Mediterranean coasts. Therefore, the water may remain in the lagoon for 1-6 months, accumulating sediment and organic matter, which stresses the ecosystem metabolism. In any case, water turnover is a key characteristic to take as a reference for most biogeochemical and biological processes. Chemical treatments are not efficient to improve the water quality of coastal lagoons because of their common high water volumes, dynamics, and mixture of freshwater and marine water.

Modifying the trophic web of MCL may be a good strategy to recover the biological structure and water quality. For example, planting and facilitating the growth of submerged macrophytes will cause the sedimentation of suspended solids and decrease water turbidity. A similar effect can be obtained favouring zooplankton filtration on phytoplankton, facilitating the development of some zooplankton species. However, these approaches will have no significant effect in large lagoons or with different lagoon sea mouths which hamper the control of water flows and biological populations.

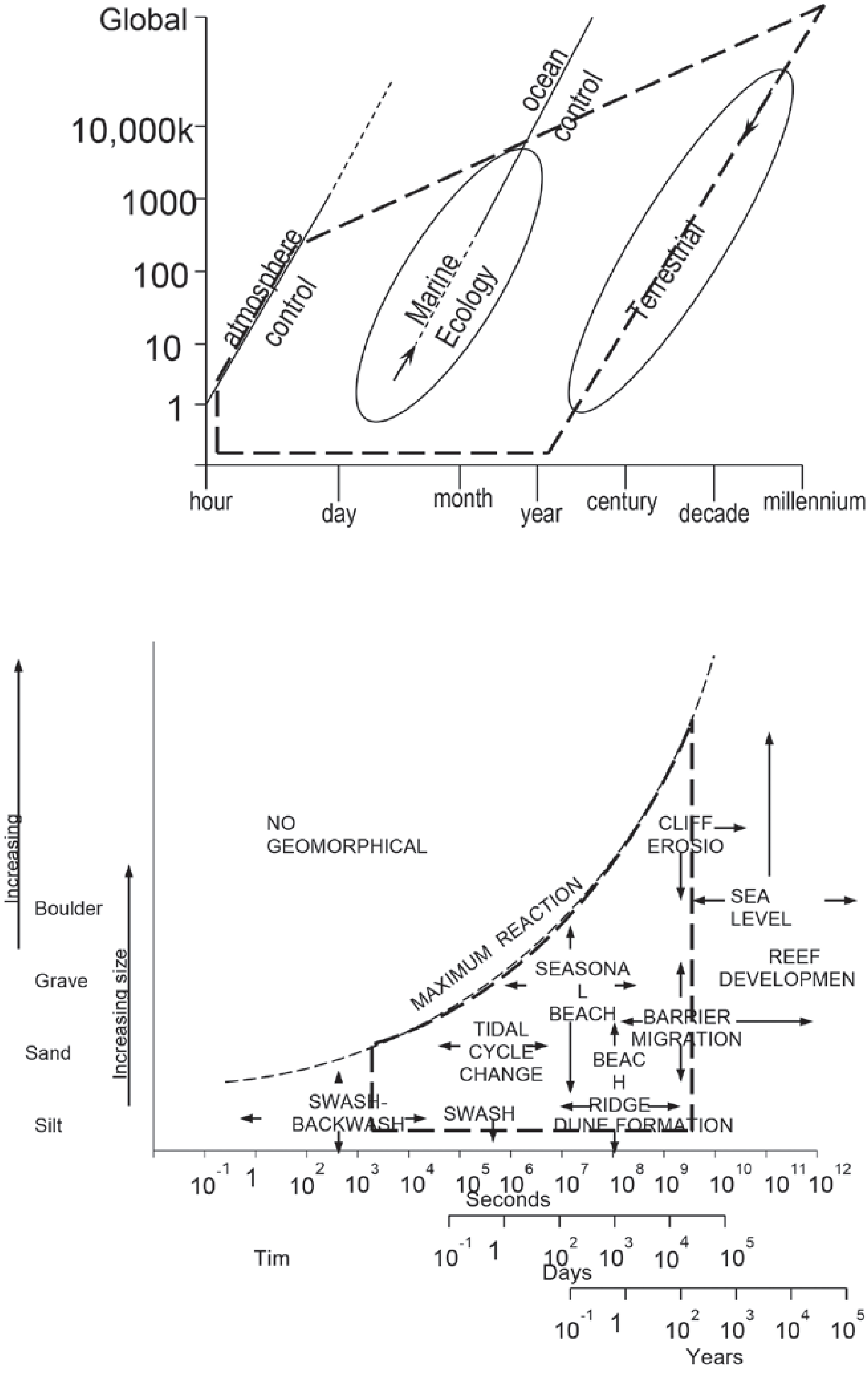

Fig. 4. Major processes regulating the ecological characteristics of coastal lagoons at different spatial and temporal scales (Comín *et al.* 2004).

All these suggestions are efficient tools in aquatic ecosystems with small water volume and much lower water turnover than those of coastal lagoons. So, these suggestions must be evaluated taking into account the extension of the lagoon, the water volume, and the exchanges with the continent and the sea, which will make it difficult to apply these measures. For example, removal of fish, which eat or uproot macrophytes, facilitating sediment resuspension and turbid waters, is not easy in large-volume coastal lagoons, but it may be a good strategy for small coastal lagoons with a very restricted connection and very low water exchange with the sea, such as coastal ponds with intense urban or agricultural pressures found along some Mediterranean coasts. In fact, intensive commercial fishing and aquaculture practiced in some MCL are ways of regulating the trophic web of the system, favouring an extractive activity which produces some socioeconomic benefits (Cataudella et al., 2015).

Integrating the scientific-technical, social, and economic aspects of restoration

The scientific-technical aspects for the restoration of MCL are clear. Some of the major ones have been presented above. Improving the hydrological connectivity with the sea and restricting pollutants discharged in inland water flows are required for the restoration of MCL, as confirmed by all the papers presented in this volume. Another major aspect required and frequently quoted is recovering natural habitats surrounding the lagoons. Both marshes and open-water systems around the lagoon are part of the the open sea-beach-sandbar-marsh-lagoon-marsh complex, which should be considered as one ecosystem tightly connected with respect to water and inorganic and organic solid flows, and to the biological communities living in and moving across the system.

However, the ecological restoration of an ecosystem requires the integration of social and economic aspects together with the scientific-technical ones (Rezende & Oliveira, 2008). The approval and participation of the local people is required for the success of any restoration project. Otherwise, it may not be possible to change private land and water rights. Even in the case of private property of a lagoon or some of its surrounding zones, the participation of local people is important, as they can contribute to the wise management of the natural resources and to the accomplishment of their expected economic benefits.

In fact, this is the objective of integrating the scientific-technical, social, and economic aspects when restoring a degraded ecosystem (Comín et al., 2005). As the provision of ecosystem services is not yet valued in our socioeconomic system, facilitating the sustainable use of natural resources and providing direct or indirect economic benefits for local people can be achieved while performing the ecological restoration of MCL and later through their management. This is particularly important in front of the challenges ahead for the management of the Mediterranean coastline and particularly of MCL: excess of urbanisation, generalised eutrophication after increased contaminated freshwater inflows, restricted water exchange with the sea, and impacts of climate change. Direct economic benefits can be achieved through the rational exploitation of the lagoon’s natural resources (e.g., fisheries). Indirect economic benefits can be obtained if the restoration actions avoid negative impacts on the exploited natural resources (Alam, 2008; Costa et al., 2013). Further development of the Water Framework Directive may be required for this type of transitional waters (Orfanidis et al., 2005; Basset et al., 2012).

Trabucchi et al. (2013) have proposed an approach based on the evaluation of ecosystem services to plan the ecological restoration of a territory made of a mosaic of ecosystems, which is usually the prevailing land cover of the inland watersheds of coastal lagoons. The evaluation of ecosystem services used to rank the sites to be evaluated and the actions to restore the different sites can combine both social and economic aspects. However, this strategy requires the active participation of local or expert people in the assessment of ecosystem services (Comín et al., 2018). In any case, planning and performing the ecological restoration of MCL requires the integrative participation of stakeholders to agree upon the objectives and priorities at site and coastal zone scales. This is required to achieve the major objective for the restoration of MCL on the long term, recovering natural habitats around degraded lagoons (for the restoration of the coastal systems and for the formation of new ones while others get closed and filled), allowing the recovery of coastal hydrodynamics. Therefore, this is the best strategy to adapt to and mitigate the impacts of global changes.

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The role of Mediterranean salt marsh vegetation and soil in the global carbon balance

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1. Introduction

In recent decades, climate changes have impacted natural and human systems in all continents and oceans. The main cause of this climate alteration is the increase of anthropogenic greenhouse gas emissions since the pre-industrial era. Some of the risks associated with the consequences of climate change are increased global average temperature, more frequent extreme weather events such as floods and storms, and sea level rise (IPCC, 2014). Ecosystems have direct and indirect influence on local and global climate. At local scale, land use changes can affect temperature and humidity conditions, while at global scale, ecosystems play a key role in climate, either sequestering or emitting greenhouse gases. In fact, global climate regulation was already recognized as an ecosystem service in the Millennium Ecosystem Assessment Report (United Nations, 2005).

Coastal lagoons are very often surrounded by salt marshes dominated by dense halophytic vegetation, generating what the Water Framework Directive (2000/60/EEC) defines as transitional waters. Both coastal lagoons and salt marshes are part of estuarine ecosystems (Britton & Crivelli, 1993; Farinha et al., 1996). Regarding climate regulation, salt marshes, and wetlands in general, play an important role in the global carbon balance through carbon capture and emission. In fact, even if salt marshes cover a relatively small portion of the earth surface (4–6%) (Mitsch & Gosselink, 2000), an estimated 25–30% of the global soil carbon reservoir is stored in these ecosystems (Lal, 2008). This large amount of stored carbon is due to high primary productivity and slow rates of soil organic matter decomposition caused by anaerobic soil conditions during flooding periods (Chmura et al., 2003; Kairanly et al., 2010).

In addition to climate change regulation, salt marshes provide several ecosystem services, such as water regulation and purification, control of soil erosion, control of flooding and storm protection, and food supply for wildlife support, among others (Costanza et al., 1997). However, historically, but still nowadays, these ecosystems have suffered large area losses due to anthropic activities, such as drainage and conversion to agriculture, grazing, water storage, fisheries, mineral exploitation, hunting, harvest of wetland vegetation, urban development, tourism, and water sports (Airoldi & Beck, 2007). Some estimates suggest losses of coastal habitats around 67% over time (Lotze et al., 2006).

Salt marshes are present along oceanic and marine coasts ranging from the subarctic to the tropics, but they are most extensive at mid-latitudes (Murray et al., 2010; Mitsch & Gosselink, 2000). Hence, our main goal is to review the available information from Northern Hemisphere mid-latitude salt marshes (from 23.5o to 66.5o N), especially from those located in the Mediterranean basin, and highlight the role of these salt marshes in the global carbon balance in comparison with other mid-latitude salt marshes (Pacific and Atlantic coast). Indeed, despite the ecological interest and high sensitivity to anthropogenic activities of Mediterranean salt marshes, only scarce data are available regarding their role in the global carbon balance.

In this review, we differentiate north mid-latitude *tidal* and *non-tidal* salt marshes. The first correspond to salt marshes located along oceanic coasts, such as the Atlantic and the Pacific, subjected to intense daily movement of the water table, with daily astronomical tides ranging from 1 to 10 m. In contrast, non-tidal salt marshes correspond to those of the Mediterranean basin, where tides are almost imperceptible (generally 0.2–0.3 m). In fact, in the salt marshes of the Mediterranean coasts, meteorological events (strong rainfall and winds) and river overflows affect flooding more than astronomical tides, being these salt marshes flooded only during some periods of the year (usually during autumn and spring) (Ibañez et al., 2000). While the presence of lagoons and deltas is common along the Mediterranean coasts, extensive plain estuaries are typical of ocean coasts.

In terms of climate, the salt marshes reviewed in this study can be classified as temperate or Mediterranean. Temperate salt marshes are located along the Atlantic coasts, where climate is mainly characterized by mild temperatures and rainfall distributed throughout the year. Conversely, Mediterranean-climate salt marshes are those located in the Mediterranean basin and along the Pacific coast of the United States (California) and are subjected to dry summer periods with high temperatures. Consequently, a main characteristic of Mediterranean salt marshes, especially of those located in the Mediterranean basin and in the upper zone of the Pacific salt marshes, is the hypersalinity of the soils in summer (Cameron, 1972; Berger et al., 1978). Dominant vegetation communities also differ depending on climate, with perennial succulent plants of the genera *Sarcocornia* and *Arthrocnemum* being dominant in Mediterranean marshes, and species of the genera *Spartina* and *Juncus* in temperate marshes (Ibañez et al., 2000).

2. Carbon reservoirs

Salt marshes are widely recognized as one of the most productive ecosystems in the world (Gattuso et al., 1998; Mitsch & Gosselink, 2000). Active photosynthetic organisms remove carbon dioxide (CO_2) from the atmosphere and transform it into organic carbon. Some of this carbon returns to the atmosphere via respiration from living organisms, while another fraction is stored in living biomass (aboveground and belowground), non-living biomass (dead stems and roots, and litter), and soil organic carbon (Murray, 2010; McLeod et al., 2011). Because well-preserved salt marshes typically have mature vegetation that maintains a steady stock, most of the carbon sequestered is buried as soil carbon stock (Murray, 2010). In these ecosystems, flooding can promote anoxic conditions in the soil, which slow down the decomposition of organic matter, favouring its accumulation and incomplete degradation (Chmura et al., 2003). As a consequence, salt marshes keep large amounts of carbon, both over the short term (decennial) in biomass, and over the long term (millennial) in soil (Duarte et al., 2005; Lo Iacono et al., 2008). Therefore, conservation of salt marshes has key importance in the maintaining of carbon reservoirs over time.

2.1 Carbon reservoir in vegetation

Autotrophic organisms remove carbon dioxide from the atmosphere through photosynthesis and fix it in carbohydrate molecules. This process, per unit area and time, is called gross primary production (GPP). Nevertheless, some of the CO_2 removed from the atmosphere through photosynthesis (GPP) can be released by autotrophic and soil (heterotrophic) respiration (R). The difference between GPP and R, the net ecosystem production (NEP), represents the carbon that will be finally incorporated into the ecosystem. If we compare the NEP of different coastal ecosystems (Table 1), salt marshes are among the most productive per unit area, and, thus, they are considered important ecosystems in the mitigation of climate change.

Ecosystem	Surface area (10^{12} m^2)	GPP (g C m^{-2} y^{-1})	R (g C m^{-2} y^{-1})	NEP (g C m^{-2} y^{-1})
Mangroves	0.2	2087	1866	221
Salt Marshes	0.4	3595	2010	1585
Seagrass	0.3	1903	692	1211
Macroalgae	1.4	3702	2116	1587
Coral Reefs	0.6	1720	1572	148

Table 1. Surface area, gross primary production (GPP), respiration rate (R) and net ecosystem production (NEP=GPP-R) for coastal vegetated ecosystems. Source: Duarte et al., (2005).

2.1.1. Net primary production of vascular vegetation

Many studies of primary production of vascular plants in salt marshes have been performed around the world, but particularly on Atlantic coast salt marshes. Nonetheless, studies on net primary production of Mediterranean salt marshes are still scarce, although more research has been done since the ‘90s (Scarton et al., 1998; Ibañez et al., 1999; Curco et al., 2002; Palomo & Niell, 2009). The temporal and spatial variability and the use of different methods make comparisons among studies difficult (Ibañez et al., 2000), but, in general, net aboveground production (NAP) is higher in the tidal salt marshes of the Atlantic and Pacific coasts than in the salt marshes of the Mediterranean basin (Table 2). This is mostly due to the lack of flooding during summer in Mediterranean basin salt marshes, along with low rainfall and high temperatures, which cause high salt and water stress to plants (Ibañez et al., 2000).

Ocean/Sea	Climate	Study area	Species	NAP (g m^{-2} y^{-1})	References
Atlantic	Temperate	Delacroix, Louisiana, (USA)	*Distichlis spicata* *Juncus roemerianus* *Spartina alterniflora* *Spartina cynosuroides* *Spartina patens*	1162-1967 1806-3295 1381-2895 1134 1342-4159	White et al. (1978); Hopkinson et al (1980)
Atlantic	Temperate	Gulf coast of Mississippi, Louisiana (USA)	*Distichlis spicata* *Juncus roemerianus* *Spartina alterniflora* *Spartina patens*	1300 1072 1089 1242	De la Cruz (1974)
Atlantic	Temperate	Bar Harbor, Maine (USA)	*Juncus gerardii* *Spartina alterniflora* *Spartina patens*	618-4449 1629-1756 6048	Linthurst and Reimold (1978)
Atlantic	Temperate	Delaware Bay (USA)	*Distichlis spicata* *Juncus gerardii* *Phragmites communis* *Spartina alterniflora* *Spartina patens*	1995 1556 1592 1487 785	Linthurst and Reimold (1978)
Atlantic	Temperate	Sapelo Island, Georgia (USA)	*Distichlis spicata* *Spartina cynosuroides* *Spartina patens* *Sporobulus virginicus*	4214 5996 3824 1372	Linthurst and Reimold (1978)
Atlantic	Temperate	Bay of Fundy, New Brunswick (Canada)	*Plantago maritima* *Spartina patens* *Spartina alterniflora*	296 500 718	Connor (1995)

Atlantic	Temperate	Netherlands	*Spartina anglica* *Triglochin maritima* *Elytrigia pungens* *Atriplex portulacoides*	1162-1649 568-783 478-878 790-1434	Groenendijk (1984)
Pacific	Mediterranean	San Francisco Bay and san Diego Bay, California (USA)	*Spartina foliosa*	280-1700	Mahall and Park (1976); Cameron (1972)
Atlantic	Mediterranean	Guadiana River (Portugal)	*Limonium monopetalum* *Atriplex portulacoides*	2516 598	Neves et al (2007)
Atlantic	Temperate	Indian River, Florida (USA)	*Sarcocornia pacifica*	835-2316	Rey et al (1990)
Pacific	Mediterranean	San Francisco Bay and san Diego Bay, California (USA)	*Sarcocornia pacifica*	215-2858	Mahall and Park (1976); Cameron (1972) (Zedler et al (1980)
Mediterranean	Mediterranean	Palmones estuary (Spain)	*Sarcocornia perennis* ssp. *alpini*	2973	Palomo and Niell (2009)
Mediterranean	Mediterranean	Ebre delta (Spain)	*Arthrocnemum macrostachyum* *Sarcocornia fruticosa*	189 581	Curco et al. (2002)
Mediterranean	Mediterranean	Po delta (Italy)	*Sarcocornia fruticosa* *Phragmites australis*	683 876	(Scarton et al. (2002)
Mediterranean	Mediterranean	Rhone delta (France)	*Arthrocnemum macrostachyum* *Sarcocornia fruticosa*	187-294 948-1262	(Berger (1978); Ibañez (1999)

Table 2. Range of maximum net aboveground production (NAP, g m^{-2} y^{-1}) in dominant salt marsh species of Atlantic, Pacific and Mediterranean coasts.

According to previous studies, the maximum NAP values of dominant species of salt marshes of the Atlantic coast of North America (i.e., species of the genera *Juncus* and *Spartina*) range from 500 to 6048 g m^{-2} y^{-1} (Table 2). Conversely, in the salt marshes of the Pacific coast, which are affected by tidal movement but are under Mediterranean climatic conditions, the maximum NAP values for *Spartina foliosa* were only 1700 g m^{-2} y^{-1} (Table 2). Moreover, typical halophytic perennial species of Mediterranean basin salt marshes, such as *Arthrocnemum macrostachyum* and *Sarcocornia fruticosa,* present the lowest NAP values reported. In particular, *A. macrostachyum* showed the lowest NAP values, ranging from 187 to 294 g m^{-2} y^{-1}, and *S. fruticosa*, the highest, ranging from 581 to 1262 g m^{-2} y^{-1} (Table 2). These values are also very low in comparison to maximum NAP from other similar perennial succulent plants, such as *Sarcocornia pacifica*, from the upper zone of the salt marshes in the coasts of Florida and California (2316–2858 g m^{-2} y^{-1}) (Table 2). Hence, overall data indicate that salt marshes subjected to Mediterranean climate, especially those in the Mediterranean basin, have the lowest NAP values. Nevertheless, NAP values found for *Sarcocornia perennis* subsp. *alpini* in the marsh of the Palmones River (southern Spain) were remarkably high (2973 g m^{-2} y^{-1}), even exceeding previous data reported for the Mediterranean basin and close to NAP values of similar species from the coast of Florida and California (Palomo & Niell, 2009). One of the reasons given by the authors to explain this elevated production is the high level of eutrophication in the Palmones River estuary, which causes a high nutrient supply.

Most of the production studies performed in salt marshes have focused on net primary aerial production. However, it has been demonstrated that belowground biomass is also important, since in some cases, it can be higher than aboveground biomass (Table 3). For instance, in tidal salt marshes of the Atlantic coast of the United States, with species of the genera *Spartina* and *Plantago*, and also in a tidal Atlantic salt marsh of the coast of the Iberian Peninsula, with *Limonium monopetalum* and *Atriplex portulacoides*, the net belowground production (NBP) was between two and four fold higher than the value of NAP (Table 3). In a similar way, in the Mediterranean basin, the values of NBP for *S. fruticosa* and for *Phragmites australis* were about two fold higher than the value of NAP (Table 3). Nevertheless, it is known that, also in the Mediterranean basin, NBP values were only one third of NAP values in salt marshes with dominance of *A. macrostachyum* and *S. perennis* subsp. *alpini*. Hence, the importance of the belowground production seems to depend on the dominant plant species. Subterranean biomass can also play a key role in the increase of soil organic carbon and marsh accretion (see section 2.2).

Ocean/Sea	**Climate**	**Study area**	**Species**	**NAP (g m^{-2} y^{-1})**	**NBP (g m^{-2} y^{-1})**	**References**
Atlantic	Temperate	Bay of Fundy, New Brunswick (Canada)	*Plantago maritima* *Spartina patens* *Spartina alterniflora*	296 500 718	648 1113 1575	Connor (1995)
Atlantic	Temperate	Delaware Bay (USA)	*Spartina patens* *Spartina alterniflora*	785 1487	3300 6500	Roman and Daiber (1984)
Atlantic	Mediterranean	Guadiana River (Portugal)	*Limonium monopetalum* *Atriplex portulacoides*	2516 598	2752 1601	Neves et al (2007)
Mediterranean	Mediterranean	Palmones estuary (Spain)	*Sarcocornia perennis* ssp. *alpini*	2973	1022	Palomo and Niell (2009)
Mediterranean	Mediterranean	Ebre delta (Spain)	*Arthrocnemum macrostachyum* *Sarcocornia fruticosa*	189 581	50 950	Curco et al. (2002)
Mediterranean	Mediterranean	Po delta (Italy)	*Sarcocornia fruticosa* *Phragmites australis*	683 876	1260 2263	(Scarton et al. (2002)

Table 3. Maximum net aboveground and belowground production (NAP and NBP, respectively; g m^{-2} y^{-1}) in dominant salt marsh species of Atlantic and Mediterranean coasts.

2.1.2. Net primary production of microbial mat

Vascular plants are the most conspicuous fraction of salt marsh vegetation, but even though this naked eye assessment seems true, it is incomplete in floristic and primary production terms. In soils apparently unvegetated, where vascular plants are absent, as well as in vegetated soils under marsh canopy, there are diverse assemblages of cyanobacteria and eukaryotic algae, forming the microbial mat, which plays an important role in the primary production of salt marshes (Sullivan & Currin, 2000). The values of annual microalgal production (MP) in some salt marshes of the Atlantic and Pacific coasts of the United States range from 28 to 341 g C m^{-2} y^{-1} (Table 4). In particular, in salt marshes of the Atlantic coast where species of the genus *Spartina* are dominant, the percentage of microalgal production can reach 60% of the global net aerial production of salt marshes (Table 4). Even higher percentages (76–140%)

of microalgal production were found in a salt marsh in southern California subjected to Mediterranean climate (Table 4) (Zedler, 1980). Hence, it has been hypothesized that arid conditions and hypersaline soils of Mediterranean salt marshes disfavour vascular plant growth, but promote microalgal production (Zedler, 1980). Nevertheless, more studies are needed to assess the role of microbial mat in the global net aerial production of salt marshes in general, and specifically in salt marshes of the Mediterranean basin in comparison to tidal salt marshes.

State	**BMP (g C m^{-2} y^{-1})**	**BMP/NAP**	**Reference**
Massachusetts	105	25	Van Raalte et al. (1976)
Delaware	61-99	33	Gallagher and Daiber (1974)
South Carolina	98-234	12-58	Pinckney and Zingmark (1993)
Georgia	200	25	Pomeroy (1959)
Georgia	150	25	Pomeroy et al. (1981)
Mississippi	28-151	10-61	Sullivan and Moncreiff (1988)
Texas	71	8-13	Hall and Fisher (1985)
California	185-341	76-140	Zedler (1980)

Table 4. Microalgal production (MP; g C m^{-2} y^{-1}) and ratio of microalgal to vascular plant net aerial production (MP/NAP x 100%) in different salt marshes of Atlantic and Pacific coasts of USA. Source: Sullivan and Currin (2000).

2.2 Carbon reservoir in soils

Soil organic carbon comes principally from vegetation (Chmura, 2011). When both aerial and subterranean vegetal tissues die, the decomposition process begins, carried out by heterotrophic microorganisms. Depending on its duration, flooding can create anoxic conditions in the soil, reducing the efficiency of organic matter decomposition and favouring soil carbon sequestration (Chmura et al., 2003; Megonigal et al., 2004). As a consequence, the main carbon reservoir in salt marshes is soil organic carbon. If we compare carbon stocks in wetlands and in other terrestrial ecosystems (Figure 1), wetlands have remarkably high values, due mainly to low organic matter decomposition rates. In fact, maximum values of soil carbon accumulation rates are 1 or 2 orders of magnitude higher in coastal vegetated ecosystems than in terrestrial forests (Figure 2). The great capacity of coastal soils and sediment to sequester carbon was highlighted by Duarte et al. (2005), who found maximum values for salt marshes (151 g C m^{-2} y^{-1}), followed by mangroves (139 g C m^{-2} y^{-1}), seagrasses (83 g C m^{-2} y^{-1}), estuaries (45 g C m^{-2} y^{-1}), and continental shelf (17 g C m^{-2} y^{-1}).

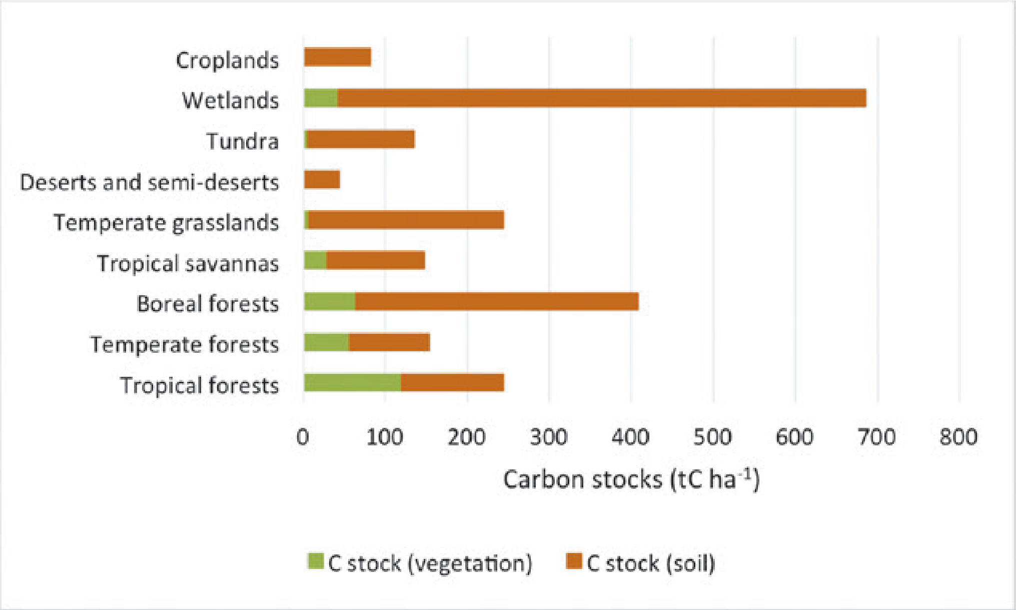

Figure 1. Carbon stocks in vegetation and soils (0-1 m depth) in different ecosystems. Source: Dalal and Allen (2008).

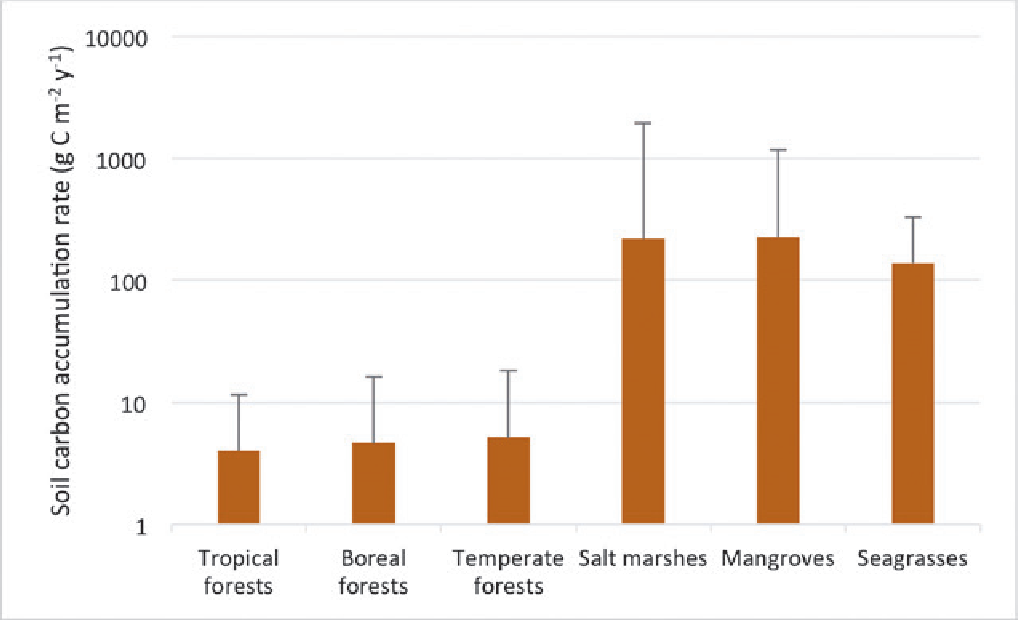

Figure 2. Mean long-term carbon accumulation (g C m^{-2} y^{-1}) in soils of forest and coastal vegetated ecosystems using a log scale. Maximum rates of accumulation are indicated using error bars. Source: Mcleod et al. (2011).

Currently, there is still a lack of information on soil carbon accumulation in salt marshes of the Mediterranean basin. From 96 studies collected by Chmura et al. (2003), only one included data from this area (Hensel et al., 1999; Figure 3). Since then, a few more studies on soil carbon content and sequestration in Mediterranean salt marshes have been done, which give support to previous results obtained for tidal salt marshes. For instance, the soil carbon accumulation rate in the Rhône delta was 161 g C m^{-2} y^{-1} (Hensel et al., 1999), and in the Palmones estuary, 560 g C m^{-2} y^{-1} (Palomo & Niell, 2009), while the average given mainly for tidal salt marshes was 218 ± 24 g C m^{-2} y^{-1} (Chmura et al., 2003). On the other hand, the values of soil carbon density in the Mediterranean basin salt marshes of the Rhône delta (Hensel et al., 1999), Ebro delta (Curco et al., 2002), and Po delta (Scarton et al., 2002) were 0.073, 0.055, and 0.081 g C cm^{-3}, respectively. These values are similar to the results of all sites included in the study by Chmura et al. (2003), in which the average soil carbon density was 0.043 ± 0.002 g C cm^{-3} (ranging from 0.009 to 0.121 g C cm^{-3}), being estimations made from 0 to 5 cm depth.

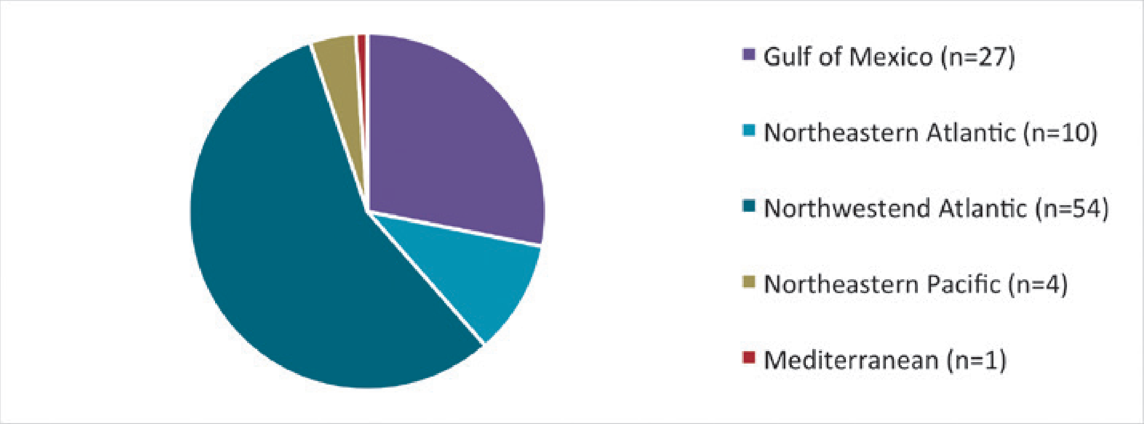

Figure 3. Number of studies reporting soil data on carbon accumulation rates in salt marshes of different locations, compiled by Chmura et al. (2003).

Therefore, with some exceptions, similar values of soil carbon sequestration rates and soil organic carbon content have been reported for Mediterranean salt marshes compared to Atlantic and Pacific tidal salt marshes. However, if organic soil carbon comes mainly from salt marsh vegetation, we would expect lower soil carbon values in Mediterranean basin salt marshes than in Atlantic and Pacific temperate salt marshes, since, as seen before, the peaks of primary production are lower in the former. One possible explanation is that in tidal marshes, according to the outwelling hypothesis (Odum, 1980), daily water movements caused by tidal inundation transport large amounts of organic carbon (belonging to aboveground biomass) from the marsh into the boundary areas. Conversely, this fact does not occur in Mediterranean salt marshes, where there is a low tidal range, and, thus, export of particulate organic matter is low and irregular (Ibañez et al., 2000; Palomo & Niell, 2009). Hence, in Mediterranean coastal marshes, especially in those where dense vegetal coverture avoids litter removal by strong winds and marine storms, such as the typical marshes dominated by *S. fruticosa* and *P. australis* (Ibañez et al., 1999), litter accumulation is an important process that allows enhanced carbon storage in the soil.

In relation to carbon exportation, the contribution of belowground biomass to soil organic carbon is remarkable. While aboveground biomass is susceptible to be exported outside the marsh, belowground biomass remains stored in the soil, ready to be decomposed in situ. For example, Palomo & Niell (2009) found a higher contribution of belowground than aboveground biomass to soil organic carbon. In addition, belowground biomass plays a key role in soil vertical accretion, which is important to preserve salt marshes, since it maintains soil elevation with respect to the sea level. Also related to marsh accretion and soil carbon accumulation, dense banks of vegetation in Mediterranean salt marshes can act as traps of particulate carbon suspended and transported by strong winds and marine storms (Hensel, 1998).

3. Carbon losses

As discussed before, carbon inputs by photosynthetic activity into salt marshes contribute to the decrease of atmospheric CO_2 concentrations. However, at the same time, ecosystem respiration promotes CO_2 release into the atmosphere. Nevertheless, atmospheric CO_2 removal by plant photosynthesis (GPP) is usually higher than emissions through respiration (R) (Table 1), making the net balance positive (i.e., atmospheric carbon is incorporated into the ecosystem).

Annual CH_4 emissions (g CH_4 m^{-2} y^{-1})

	Average ± SD	CV	Maximum	Minimum	n
Estuary	539 ± 603	112	1620	1.70	6
Lake	64 ± 345	537	2576	0.11	55
River	465 ± 669	144	2266	62.05	12
Wetland	470 ± 2300	489	19044	0.06	126

Table 5. Annual CH_4 emissions in different coastal and aquatic ecosystems. SD: standard deviation; CV: coefficient of variation; n: number of data. Source: Ortiz-Llorente and Alvarez-Cobelas (2012).

Soil organic matter decomposition, despite being the main process related to the incorporation of carbon into the soil, also favours the emission of carbon compounds, such as CO_2 and methane (CH_4), as products of the decomposition process. If the soil presents aerobic conditions, organic matter can be oxidized completely by heterotrophic microorganisms to CO_2. However, during flooding periods that cause anoxic conditions in the soil, aerobic respiration is replaced by fermentation and methanogenesis (Mitsch & Gosselink, 2000). In fact, ecosystems that usually, or at least during some periods of the year, have submerged soils are among the major sources of CH_4 (Dalal & Allen, 2008). Natural wetlands emit about 25% of the total emissions of CH_4 from all anthropogenic and natural sources (Whalen, 2005). Moreover, by comparing annual CH_4 emission rates of different coastal and aquatic ecosystems, researchers found the highest CH_4 values in wetlands, followed by lakes, rivers, and estuaries (Ortiz-Llorente & Alvarez-Cobelas, 2012). Hence, the role of wetlands, including salt marshes, as carbon sinks might depend on CH4 emissions.

Several environmental variables can affect CH_4 emissions in wetlands. The water table predominantly controls the flux of CH_4 through its influence on the extent of oxic and anoxic soil horizons and, consequently, on the ratio between CH_4 production and CH_4 oxidation (Kelley et al., 1995; Christensen et al., 2001). High temperatures can favour CH_4 emission by increasing primary production and consequently substrate supply (Withing & Chanton, 2001) and decomposition of organic carbon (Ding & Cai, 2007). Methane emissions have been studied more broadly in freshwater wetlands (Whiting & Chanton, 2001; Kayranli 2010) than in salt marshes. However, some comparisons of CH_4 emissions between the 2 ecosystems have been done. In particular, Bartlett & Harris (1993) compared averages of annual CH_4 emissions between salt marshes and freshwater wetlands of the United States, finding lower emission rates in the former than in the latter. The average of CH_4 emissions in salt marshes ranged from -0.8 to 15.8 mg m^{-2} d^{-1}, while in freshwater forested swamps and freshwater marshes, they ranged from 39.8 to 155 mg m^{-2} d^{-1} and from 29.4 to 587 mg m^{-2} d^{-1}, respectively. One reason explaining this difference is related to soil salinity, since several studies have found that CH_4 flux is negatively affected by salinity (Barlett & Harris, 1993; Poffenbarger et al., 2011; Livesley & Andrusiak, 2012). Hence, lower values of CH_4 emissions would be expected in salt marshes compared to freshwater wetlands, due to the competition for oxidizable substrate between sulfate-reducing bacteria and methanogens that usually occurs in salt marshes (Mitsch & Gosselink, 2000).

4. Concluding remarks and importance for conservation

- The results obtained so far show that Mediterranean basin salt marshes have lower values of net aboveground primary production than tidal salt marshes of the Pacific and Atlantic coasts, mainly due to the high salt and water stress suffered by plants during summer.

- The net primary production of microbial mat is expected to be higher in Mediterranean basin salt marshes than in salt marshes of the tidal Pacific and Atlantic coasts.

- In general, soil carbon sequestration rates and soil organic carbon content are similar between Mediterranean basin salt marshes and Atlantic and Pacific tidal salt marshes.

- In Mediterranean coastal marshes, especially in those where dense vegetal coverture hinders litter removal by strong winds and marine storms, litter accumulation is an important process that allows the enhancement of carbon storage in the soil.

- Although CH_4 emissions might be high in wetlands, making the carbon balance negative, lower values of CH_4 emissions would be expected in salt marshes than in freshwater wetlands, due to the competition for oxidizable substrate between sulfate-reducing bacteria and methanogens that usually occurs in salt marshes.

Salt marshes need to be preserved, among other reasons, because:

- Vascular plants of the salt marsh favour the removal of atmospheric CO_2 and its incorporation into the ecosystem.

- Salt marshes maintain large amounts of carbon stored in biomass and, especially, in the soil, avoiding its release to the atmosphere.

- Salt marshes are important ecosystems for climate change mitigation, due to their high capacity of atmospheric CO_2 sequestration and their low emission of CH_4.

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Protecting and restoring the salt marshes and seagrasses in the lagoon of Venice

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1. The lagoon of Venice

The Lagoon of Venice is one of the largest and most important coastal transitional ecosystems of the Mediterranean (Tagliapietra et al., 2009). Human presence has constantly modified the original estuarine structure, so nowadays the lagoon can be considered a human-oriented ecosystem that still maintains strong natural traits. It is located in the north-western part of the Adriatic Sea between the current mouths of the Sile and Brenta rivers, between 45.18° and 45.57° N latitude and 12.12° and 12.63° E longitude (Fig. 1).

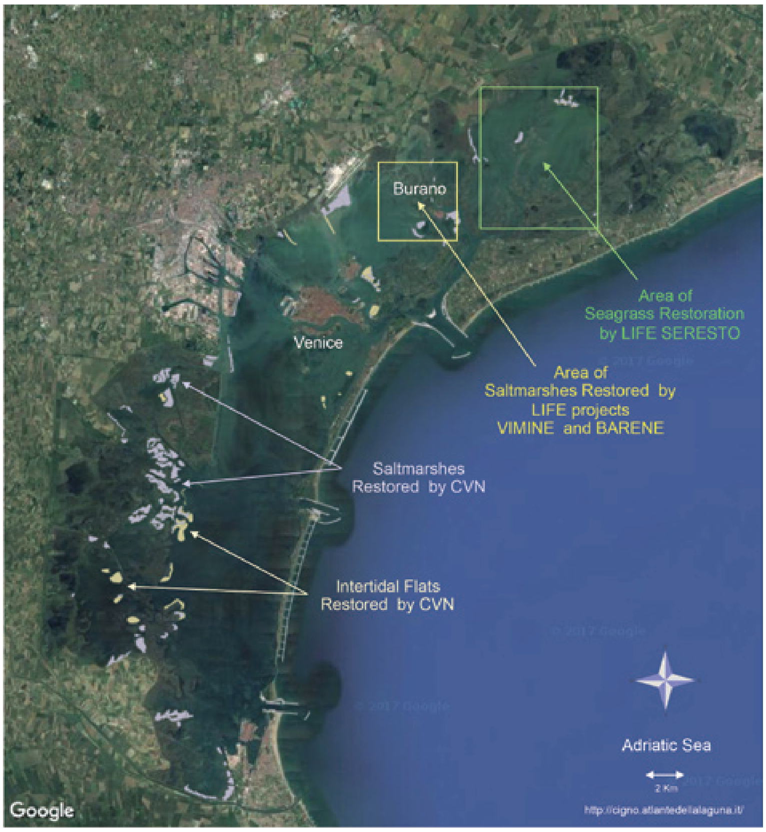


Figure 1: Map of the lagoon of Venice showing the places in which the different restoration projects were made (from the “Atlas of the Lagoon”, http://cigno.atlantedellalaguna.it/).

The lagoon is connected to the sea by 3 inlets, and the physical separation between the lagoon and the Adriatic Sea comprises 2 barrier islands and 2 spits. The lagoon is about 50 km long and 10 km wide, and covers an area of about 540 km^2. Of this area, 36 km^2 are salt marshes, 30 km^2 are islands (excluding the barrier islands), and the rest is covered by water. The mean depth of the water column is about 1.2 m, with only 5% of the lagoon deeper than 5 m (Molinaroli et al., 2009). The maximum depth is 47 m, at a scour located at the lagoon side of the Malamocco Inlet. The lagoon contains about 628 million m^3 of water. According to Kjerfve (1994), the Lagoon of Venice can be defined as a “restricted” coastal lagoon. The 3 inlets (Lido, Malamocco, and Chioggia) allow tidal flushing twice a day: every day the Lagoon of Venice exchanges with the Adriatic Sea about 400 million m^3 of water, while the inflow from the inland through the rivers and subsoil is about 3.7 million m^3 (Bernstein & Montobbio, 2011). Tides are a main factor in shaping the morphology of the lagoon and driving water exchange, dissolved oxygen, salinity, nutrients, and sediment distribution. The North Adriatic tides are the largest in the Mediterranean. In the Lagoon of Venice tides are mixed, predominantly semidiurnal, and microtidal (Tagliapietra & Ghirardini, 2006) with a mean tidal range of 61 cm and an intertidal range of 121 cm from the highest to the lowest astronomical tidal level (calculated for 1986–2004).

The drainage basin is about 1850 km^2, 40% of which is reclaimed land lying under the sea level. According to the Köppen–Geiger–Pohl Climatic Classification (Geiger & Pohl, 1953), the lagoon experiences a humid subtropical climate with hot summers (Cfa). Due to the shallowness of the lagoon, water temperature follows strictly the seasonal trends of air temperature, ranging from 0°C (seldom freezing) to above 30°C. Precipitations distributed throughout the year contribute to an average freshwater input of about 35.5 m^3 s^{-1} as recorded in 1999 (Zuliani et al., 2005), with the most important tributaries located in the northern basin. Freshwater input and tides produce a salinity gradient, ranging from marine (ca. 37 psu) to almost freshwater near the bayhead estuaries and freshwater inlets. The gradient is compressed towards the mainland, due to the preponderant tidal contribution resulting in an average value of ca. 30 psu. Therefore, most of the lagoon can be classified as mixoeuhaline/(mixo-)polyhaline according to the Venice System (D'Ancona 1959).

Due to the uniqueness and peculiarity of its cultural values, which are made up of an exceptional cultural heritage and, above all, integrated into an extraordinary environmental context, "Venice and its Lagoon" has been listed in the UNESCO World Heritage List since 1987. The Lagoon of Venice can be considered a "cultural landscape" where over time the work of human and nature has been intertwined under the influence of environmental, social, and economic constraints and opportunities (Fig. 2). The Lagoon of Venice is one of the most studied coastal sites in the world, both ecologically and culturally, belonging to the international Long-Term Ecological Research network (LTER). Detailed information can be found in the "Atlas of the Lagoon" (www.atlantedellalaguna.it).

Figure 2: The unique landscape of the lagoon. Salt marshes around Burano (author P. Nascimbeni).

2. Changes during the past century

The lagoon has undergone major changes especially during the twentieth century. The most important were the construction of large jetties at the sea inlets but, above all, the progressive construction of an industrial zone on the mainland behind Venice, reclaiming a large salt marsh zone. This culminated in the 1960s with the excavation of a large canal linking the Malamocco Inlet with the industrial zone to bring tankers to the developing petrochemical pole. This canal strongly affected the central part of the lagoon by changing its hydrology and consequently its ecology, bringing large masses of seawater near the mainland. The hydrologic imbalance has also been heightened by the progressive reduction of freshwater inputs from the catchment area, mainly due to the use of water for irrigation purposes. The construction of jetties at the lagoon inlets at the beginning of the twentieth century also had the effect of reducing the intake of sediments, both of marine and estuarine origin, from the sea (D'Alpaos 2010).

In the 1970–1990, it was estimated that the catchment provided the lagoon with 30 000 m^3 y^{-1} of sediments, and about 1 100 000 m^3 y^{-1} were released into the sea. Later, 2005 estimates gave unchanged contributions from the catchment and almost half the outflows to the sea (580 000 m^3 y^{-1}). During the 2 periods, sediment movements in the lagoon were almost equal (i.e., about 2 000 000 m^3 y^{-1})(Bernstein & Montobbio, 2011).

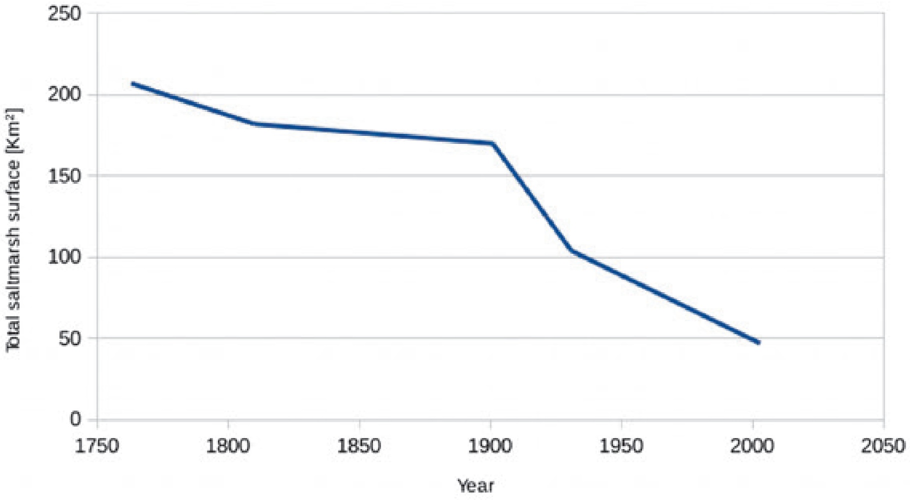


Figure 3: Total salt marsh surface (km^2) (data from D'Alpaos, 2010).

Since the first maps of the lagoon were created in 1763 (D'Alpaos, 2010, Fig. 3), the total surface of salt marshes has continuously decreased, and the lagoon has progressively deepened, with a strong increase in the area of subtidal flats at the expense of the intertidal flats, usually covered by seagrasses (Sarretta et al., 2010). These impacts are much more evident in the central part of the lagoon than in the southern one, while the northern lagoon has kept a more natural fit. If, on the one hand, the increase of sediment resuspension (Sfriso et al., 2005a,b) favoured the loss of the fine fraction into the sea, on the other hand, a strong erosion of landforms with a general flattening and the infilling of many natural channels and waterways was recorded. At the same time, nutrient loading to the lagoon increased mainly due to the production of fertilizers in the industrial zone, the development of chemical fertilisation in agriculture, and the use of phosphorus in detergents. Both phosphorus and nitrogen inputs almost triplicated from the 1950s to the 1980s (Solidoro et al., 2010), leading to a progressive eutrophication of the lagoon, which culminated with the dystrophic crises recorded between the 1980s and the 1990s. Seagrass beds were almost completely replaced by opportunistic macroalgae such as the Ulvaceae, Cladophoraceae, Gracilariaceae, and Solieriaceae, and phytoplankton also declined (Sfriso & Facca, 2007). Later, the banning of phosphorus from detergent formulations, the improvement of sewage systems and agricultural practices on the mainland, and other factors such as climatic changes (Sfriso & Marcomini, 1996) strongly reduced the macroalgal production and the dystrophic events. The reduction of macroalgal cover favoured the demographic explosion of the non-native Manila clam (*Tapes philippinarum*), introduced in the lagoon in 1983 for economic purposes (Cesari & Pellizzato, 1985), which took advantage of the sediments and water still rich in organic matter and phytoplankton and from the almost complete absence of competitors and predators. The wild hydraulic and mechanical harvesting of this new fishing resource reworked continuously the lagoon bottom, causing sediment resuspension, water turbidity, and loss of fine sediments (Sfriso et al., 2005a,b) with consequent increased sediment loss to the sea. Benthic communities were strongly impacted both directly and indirectly by water turbidity and sedimentation rates up to the beginning of this century, when clam harvesting was strongly regulated and public aquaculture concessions were set, for a total area of 1870 ha in 2014. Manila clam harvesting declined from ca. 35 000–40 000 tonnes/year in the period 1995–2000 to ca. 20 000–25 000 in 2001–2008; there was a big drop to 5600 tonnes in 2009 and then a constant decline up to ca. 1700 tonnes in 2012 (Pessa et al., 2013, 2014).

3. Loss of priority habitats

Human activity during the twentieth century has endangered two of the key habitats of the Lagoon of Venice, the salt marshes and the seagrass beds (Fig. 4), for which environmental conservation and restoration programmes have been put in place.

Figure 4: Seagrass meadows penetrating the salt marshes (author P. Nascimbeni).

3.1. Salt marshes (the “Barene”) (Eunis habitat A2.54)

In the Lagoon of Venice salt marshes resemble low silty tabular islands rising 30–40 cm above the mean sea level. They are covered with halophytes and exist in a dynamic equilibrium between sedimentation and erosion. They form a band that extends predominantly from the middle reach of the lagoon to its mainland edge. The periodicity and amplitude of the tides, at different moments of their daily and monthly cycles, determine the periods of submersion and emersion and the sediment deposition patterns, and hence the structure of the salt marshes and the development of a rich network of creeks and ponds (Fig. 5). In almost the whole Mediterranean, the tidal range is very low, so the landforms the tides generate are often destroyed by the action of waves and other physical agents. Mediterranean tidal salt marshes are therefore very rare, and this alone would be enough reason to protect this habitat. In addition, the vegetation succession, which in oceanic salt marshes develops on a metre scale, in the Lagoon of Venice develops on a centimetre scale. A few centimetres of altitude difference are sufficient to change the plant composition and animal biocoenosis associated with it, making the salt marshes of the Lagoon of Venice very vulnerable to variations in hydrology induced by both humans and climate change.

Figure 5: The hydrological network of a salt marsh (author P. Nascimbeni).

Salt marshes show spatial heterogeneity at the landscape scale, their morphogenesis being generated by the actions of both river and sea. Their features blend along the land-sea gradient. Riverine salt marshes are more silty-clayey, while marine salt marshes are sandy-silty. The carbonate content is higher in the marine ones, even exceeding 70%. Salt marsh soils have been formed through a long paedogenetic process that, due to the growth of vegetation and allochthonous inputs, leads to organic matter accumulation, salt and carbonate dissolution, oxidation of sulphides, and progressive acidification. There are also continental salt marshes created by the submersion of previously emerged soil. The variation of tidal levels according to astronomical phases differentiates depositional areas and elevations, which in turn affect permeability, oxygenation, and biogeochemistry. It follows that within the same salt marsh we can recognise different subunits of soil containing characteristic vegetal associations. An indicator of the various marshsoil composition are the different iron oxides and their colours, changing from the reddish of the more permeable and oxygenated soils to the grey of longer submerged areas; for instance, the higher reddish soils can contain *Halimione potulacoides* and *Salicornia fruticosa*, whereas the grey soils of the low marshes commonly contain *Spartina stricta* (Bonometto, 2003; Lang et al., 2006). In principle, therefore, salt marsh restoration should be aimed at restoring the conditions that have allowed the formation of this habitat allowing sufficient time for the genesis of soils and the establishment of their complex hydrobiology. This would require large-scale operations ranging from a replanning of agriculture on the mainland to the restoration of estuarine conditions and the recalibration of the lagoon hydrology. This would be the way to rebalance the salt marshes, reverse the degradation process, and gain an eco-physiologically sound habitat. This scientific and technical process requires long-term strategies and political foresight. In any case, we must take into account the sea-level-rise scenarios induced by climate change, which may modify completely our vision of the lagoon.

3.2. Seagrass Meadows (Eunis habitat A2.61)

Seagrasses are marine vascular plants (phanerogams) which carry out their entire life cycle submerged in marine or brackish waters. The success of these plants in lagoon environments is due to the evolution of various physiological and morphological adaptations ranging from the resistance to saline conditions and a constant submersion, to the development of a root system based on horizontal rhizomes that confer them resistance to swell, and to hydrophilic pollination and dissemination. In pristine or healthy lagoons, seagrasses can form extensive populations or even real underwater meadows (Orfanidis et al., 2003; Viaroli et al., 2008). Seagrasses are included among the marine and brackish species protected at international and national level, as reported in several conventions (Bern Convention 23/06/1979 and SPAMI-Barcelona Convention 1995). Seagrasses are also included among the species of greater attention in the Action Plan for the Conservation of Marine Vegetation in the Mediterranean Sea (RACs / SPAs - Regional Activity Centre for Specially Protected Areas), and the Water Framework Directive (EU 2000/60) gives them utmost importance as indicators of good ecological status.

The meadows have a strong bottom-stabilising action, trapping sediments, and a key role in water oxygenation, nutrient removal, and CO_2 sequestration because, as opposed to most of the macroalgae, seagrasses are perennial species. It was estimated that the CO_2 trapped by seagrass meadows in the Lagoon of Venice, based on the 2003 meadow extension, is ca. 40 000 tons (Sfriso & Facca, 2007). In addition, a quantity of CO_2 at least double is estimated to be trapped in the calcareous organisms (small calcareous macroalgae and worms, gastropods, and bivalves) living in the meadows. Seagrasses form a three-dimensional canopy that hosts a rich and diversified community, which contributes significantly to the lagoon trophic web and is an optimal nursery for many species of marine fish and invertebrates. Therefore, seagrass meadows are also extremely important for fishery and represent a grazing area for wild fowl. Seagrasses are very susceptible to a series of disturbance factors (Table 1), such as water turbidity caused by suspended solids or excessive phytoplankton, which reduces the supply of light they need for photosynthesis to the leaves. Suspended solids may also deposit on the leaves, suffocating the marine herbs. Nutrients trigger the production of thionitrophilic macroalgae, such as Ulvaceae and Cladophoraceae, resulting in a strong competition for light and space and causing dystrophic crises. Seagrasses favour sedimentation, hold sediments, and trap organic matter, so their loss leads to increased bottom erosion (Sfriso et al., 2005a) (Fig. 6).

Figure 6: The edge between a seagrass meadow and muddy sediment with *Ulva* sp. (author SELC).

Code	Description
F02.02	Professional active fishing
F02.02.05	Professional active fishing with benthic dredging
F01.03	Marine and Freshwater Aquaculture with bottom culture
G05.02	Shallow surface abrasion/mechanical damage to seabed surface
H03	Marine and brackish water pollution
I01	Invasive non-native species (Both animal and vegetal)
J02.02.02	Removal of sediments (by estuarine and coastal dredging)
J02.05.01	Modification of water flow (tidal & marine currents)
J02.05.06	Wave exposure changes
J02.12.01	Sea defence or coast protection works, tidal barrages
J02.11	Siltation rate changes, dumping, depositing of dredged deposits

Table 1: Factors of pressure and disturbance acting on seagrasses, identified and coded during the activities of the DG Environment and the European Environment Agency concerning the implementation of European Directives Habitat (92/43/EEC) and Birds Habitat (2009/147/EC) (Curiel et al., 2014).

In the Lagoon of Venice, 3 seagrasses, *Cymodocea nodosa, Zostera marina,* and *Z. noltei*, are present. In addition, 2 aquatic plants, *Ruppia maritima* and *R. cirrhosa*, colonise the most confined areas. In general, all these species are found along the estuarine gradient from the seaward areas to the most confined zones, but inside the lagoons many microhabitats are present, with patches of different species. *Cymodocea nodosa* is a subtropical species that colonises areas with high salinity and coarse sediments. This species is affected by a strong seasonality linked to water temperature variations, so its foliage is largely reduced in winter. It lives mostly in the areas closest to the sea inlets on silty-sandy substrates. In the lagoon, however, this plant is more developed than in other parts of the Mediterranean Sea, reaching a height of 1.5 m, probably due to the nutrient-rich waters. *Zostera marina* lives on silty sediments with little clay and has leaves that can reach 1.3 m in length and 5–6 mm in width. It forms dense populations living in shallow waters; at low tide the leaves often float on the water surface. *Zostera noltei* is a species characteristic of the most inner areas with predominantly silty sediments, low water, and muddy plains emerging at low tide. The shoots have a shape similar to that of *Zostera marina* but are smaller, up to 0.6 m high and only 0.7–1.5 mm wide. *Zostera marina* and *Z. noltei* grow all year round, but faster during spring. In confined areas where water can freeze, they can lose their leaves and stop growing in winter. In warm years, they can significantly reduce their growth also in summer. *Ruppia cirrhosa* and mostly *R. maritima* have limited distribution in the brackish areas of the inner lagoon. The latter lives only in the small ponds inside the salt marshes (Sfriso, 2010).

There are indications of a very large or almost total cover of the lagoon bottom until the beginning of 1900, based on anecdotal evidence and qualitative scientific reports. Some information for limited areas is from aerial photographs from World War II. The first indications of a very rapid reduction of seagrasses are reported in Sfriso (1987). Seagrass reduction, especially in the areas characterised by low water renewal, was highest during the period of great algal proliferation between the ’70s and the ’80s (Sfriso et al., 1987), but the first seagrass mapping dates back to 1990 (Caniglia et al., 1992). Other maps followed in 2002, 2004, and 2010. The map comparison (Curiel et al., 2014, Table 2) shows a small regression between 1990 and 2002, while between 2002 and 2004 a wider loss was recorded, particularly for *Zostera marina* and mostly for *Z. noltei*, which were replaced by macroalgae especially in the central and northern basin of the lagoon.

	1990 (ha)	**2002 (ha)**	**2004 (ha)**	**2010 (ha)**
Monospecific *Cymodocea nodosa*	391	1.777	1.714	2.276
Monospecific *Zostera marina*	266	2.195	1.130	1.404
Monospecific *Zostera noltei*	1.436	70	21	57
Mixed *Z. noltei* + *C. nodosa*	2.157	220	75	21
Mixed *Z. noltei* + *Z. marina*	692	825	527	27
Mixed *Z. marina* + *C. nodosa*	23	141	69	12
Mixed *Z. noltei* + *Z. marina* + *C. nodosa*	528	203	136	11
Total	**5.493**	**5.431**	**3.672**	**3.808**

Table 2: Seagrass coverage reported in 1990, 2002, 2004, and 2010 (Curiel et al., 2014).

The main causes that led to the disappearance of *Z. marina* in the northern basin were the increase of thionitrophilic macroalgae, the loss of habitats, and the increase in water turbidity (Sfriso and Facca, 2007). In addition, the weather conditions of 2002, a year with very high rainfall, and 2003, a very hot year, were anomalous and triggered extensive blooms of phytoplankton, which affected the residual seagrass populations. In the following years, between 2004 and 2010, a modest seagrass recruitment was observed (3808 ha, ca. 12% of the lagoon bottoms investigated) (Provincia di Venezia, 2014; Rismondo et al., 2005; Sfriso et al., 2009).

4. Different scales of intervention

The idea of a basin-scale policy (not extended to the mainland yet) was contained in the "Special law for Venice"(Italian government Law 171, 1973,). Environmental restoration in Venice also falls within Italian law, since "the preservation of Venice and its lagoon is declared a problem of paramount national interest". After the huge flooding of 1966, in 1973 a special law was issued for the safeguarding of Venice and its lagoon from floods. In 1984 the general criteria were defined, and they include "studies, projects, experiments and works for the hydrogeological balance of the lagoon, to stop and reverse the degradation of the basin".

The Italian state entrusted a consortium of Italian companies (Consorzio Venezia Nuova, CVN) with the works for the safeguarding of Venice and the lagoon under the jurisdiction of the Italian state and as the sole concessionaire of the Water Authority of Venice (Magistrato alle Acque di Venezia, now Provveditorato Interregionale per le Opere Pubbliche del Triveneto). Their main work was the design and construction of mobile gates at the sea-inlets of the lagoon known as MOSE (acronym for MOdulo Sperimentale Elettromeccanico), nevertheless, in 1992 it was specified that works on the gates would be subordinate to the hydrogeological re-equilibrium of the lagoon. In 2005, the European Commission issued the Italian government an infringement procedure for the MOSE impacts relative to the Birds Directive 79/409 and the Habitat Directive 92/43 (infringement procedure 2003/4762). As a consequence, in 2007–2011, the Venice Water Authority set up a plan for the compensation, conservation, and requalification of the Venetian Sites of Community Importance IT3250003, IT3250023, IT3250030, and IT3250031, and Special Protection Area IT3250046. Compensatory measures include, among others, the reconstruction of salt marshes and tidal flats, and transplantation of seagrasses.

The Italian state funding for environmental restoration in the lagoon will be much more limited in the future than it has been in the past. So, the local regional government and the Water Authority of Venice will have to pursue more targeted projects that focus on the concept of constant care and maintenance, rather than emergency interventions, to foster ecological processes that naturally preserve and restore habitats. Funding could be sought at regional and European level, but the economic self-sustainability of actions over time must be emphasised.

This situation motivates the search for novel solutions, allowing scientists from universities and research institutes, cooperatives, and local companies to interact with Venetian authorities in drafting and implementing targeted projects. In this sense, over the past decade, the Lagoon of Venice has been successful in obtaining funding from the LIFE programme (Fig. 1). Through this programme, the European Union finances environmental and nature protection projects aimed at improving the conservation of endangered species and habitats. The purpose of the LIFE programme is to contribute to the implementation of the Birds and Habitats Directives and the establishment of the Natura 2000 network of protected areas. However, in order to be successful, these pilot projects that pursue the EU's goal of halting biodiversity loss need to seek forms of medium- or long-term sustainability with the involvement of local authorities and stakeholders.

5. Large-scale salt marsh restoration

During the past century, erosion, redistribution, and export to the sea of lagoon sediments have produced a loss of geomorphological diversity. The objectives of large-scale restoration, inspired by the Venice Special law, were to encourage a rebalancing of the hydrological and ecological environmental functions of the lagoon through a geomorphological recovery. These works were entrusted by the Italian government and the Venice Water Authority to the CVN as part of the safeguard programme. The restoration works have been included in a general framework ranging from the excavation of canals to the reconstruction of intertidal flats and salt marshes, to the re-naturalisation of lagoon areas that had been reclaimed for the construction of the industrial zone, to interventions on subtidal bottoms to reduce wave shear stress and increase consolidation through seagrass transplantation. It is therefore a vast plan of works of which salt marsh restoration is only a part, albeit substantial.

The results are significant: over the past 25 years, 106 salt marshes have been restored or constructed for a total area of 11 km^2, equal to 27% of the natural existing salt marshes and 30% of those eroded from 1930 to the present. In addition, 18 tidal flats were built (surface area of 2 km^2) (Volpe, 2012).

The environmental restoration of salt marshes involves technical, environmental, economic, and aesthetic aspects, which are addressed through modular solutions for engineering works of protection, containment, and consolidation and through soft techniques and careful application of vegetational, paedological, and faunistic knowledge for biotope restoration. The works were based on historical analyses of the morphological changes occurred in the past century and on hydraulic optimisation studies. Salt marsh restoration works included the rebuilding of the parts that had been eroded, the protection of the eroding edges, the re-elevation of low salt marshes, and the construction of new salt marshes (Nascimbeni, 2007).

One of the tenets of the geomorphological environmental restoration in the lagoon is the reuse of sediments within the lagoon itself. The second is to not build new supratidal morphological structures (i.e., islands and islets) subtracting “water spaces” to the lagoon. Therefore, muds from the dredging of the lagoon canals were used as a valuable resource. The works started in 1988 were mainly aimed at the reuse of sediment from dredging the canals inside the lagoon while simultaneously producing artificial morphological structures mimicking salt marshes and intertidal flats. At a later stage, the work was focused on the lagoon ecology through the improvement of morphodynamic functions and increasing biodiversity and resilience of the system, contributing to an overall re-naturalisation of the environment (Nascimbeni, 2007).

The management of sediments in the Lagoon of Venice is not simple, and their use is governed by the law L.360/1991 and the following “Memorandum of Understanding” of 1993 “Environmental safety criteria for the excavation and re-use of muds extracted from the Canals of Venice”. The memorandum classifies sediments in 4 classes (A, B, C, and over C; Tab. 3), according to an increasing level of pollution and subdivides lagoonal sediments as a function of reuse for morphological recovery and reconstruction, in order to avoid or limit environmental impacts.

Class	Allowed use
A	Restoration of landforms involving the direct or indirect contact of the sediments with the waters of the lagoon
B	Sediments must be confined so as not to come into contact with circulating water
C	Sediments can be used on Islands never submersed and secluded by deep foundations
Over C	if not considered toxic waste, sediment can be used outside the lagoon surrounded by waterproof barriers

Table 3: Sediment classes and the allowed reuse for morphological recovery and reconstruction (Ministero dell’Ambiente, 1993).

The “mimic salt marshes” can therefore be constructed using class A sediment (Ufficio di Piano, 2010). Based on this classification, most surficial sediments of the lagoon fall into in class B (Castellani & Barbanti, 2010). It follows that, if no new classification scheme is adopted, the use of sediments from the lagoon will be greatly reduced, leading to additional costs for restoration activities. The scientific community has deepened its research on the chemical geospeciation and the bioavailable fraction of chemical species that can exert toxic effects on organisms. It resulted that the Memorandum of Understanding classes, based solely on chemical concentration, although precautionary, are not adequate to represent the actual sediment ecotoxicity. The “one out all out” concept underlying the sediment classification under the Memorandum of Understanding must necessarily be overcomed, and the addresses of the European Directives (e.g., REACH) and of Italian decrees for classification of surface water bodies status (Dlgs 152/2006, DM. 260/2010) pointing out the importance on considering a wide range of pollutants, including new-generation ones, should be included in new classification schemes. The review of the Memorandum of Understanding is currently actively discussed, but it seems clear that it will lead to the overcoming of the classic chemical approach in favour of an integrated chemical-ecotoxicological approach. The ecotoxicological assessment has to be founded on the choice of adequate endpoints suitable for the protection of the peculiar estuarine environment and its biota (Losso & Volpi Ghirardini, 2010; Losso et al., 2010). As a consequence, on the one hand, a considerable part of class B sediments can be reconsidered for environmental restoration (Castellani & Barbanti, 2010), whereas on the other hand, other hotspots of toxicity not revealed before could be evidenced (Losso et al., 2010; Picone et al., 2016). This new, more articulate approach that is in synergy and complementarity with ecotoxicological aspects is the basis of the proposals for new criteria for classification and management of lagoon sediments (Corami et al., 2014; Losso et al., 2010; Picone et al., 2016).

Hence, 19.5 million m^3 of sediments suitable for salt marsh restoration were obtained from the excavation of about 200 km of lagoon canals needed to restore water circulation and allow navigation (Bernstein & Zonta, 2010; Volpe 2012). Considering the volumes and surfaces of the works, very pragmatic engineering techniques were adopted. The construction technique of this type of salt marshes consists essentially in creating a containment barrier along the designed perimeter and then pumping inside fluidised mud up to the desired height. However, pragmatism in construction does not imply a simplistic design. On the contrary, the need to adapt to heterogeneous lagoon morphologies and contexts has led to the development of a modular approach and the experimentation of several module structures, often used in combination. These modules mainly refer to barriers, whether they are part of a containing barrier or aimed to protect the salt marsh edges, or with a breakwater function on the shoals. Depending on the specific features of the environments to be protected (morphology, vegetation, exposure to physical agents), the modules used differ in design, material compositions, and set-up schemes. The main kind of modules are timber piles, brushwood fascines, bags, rolls, and mattresses made of and filled with different materials (*“burghe“* and *“buzzoni”*), such as polymeric fibres, natural fibres, stones, brushwood, and shells.

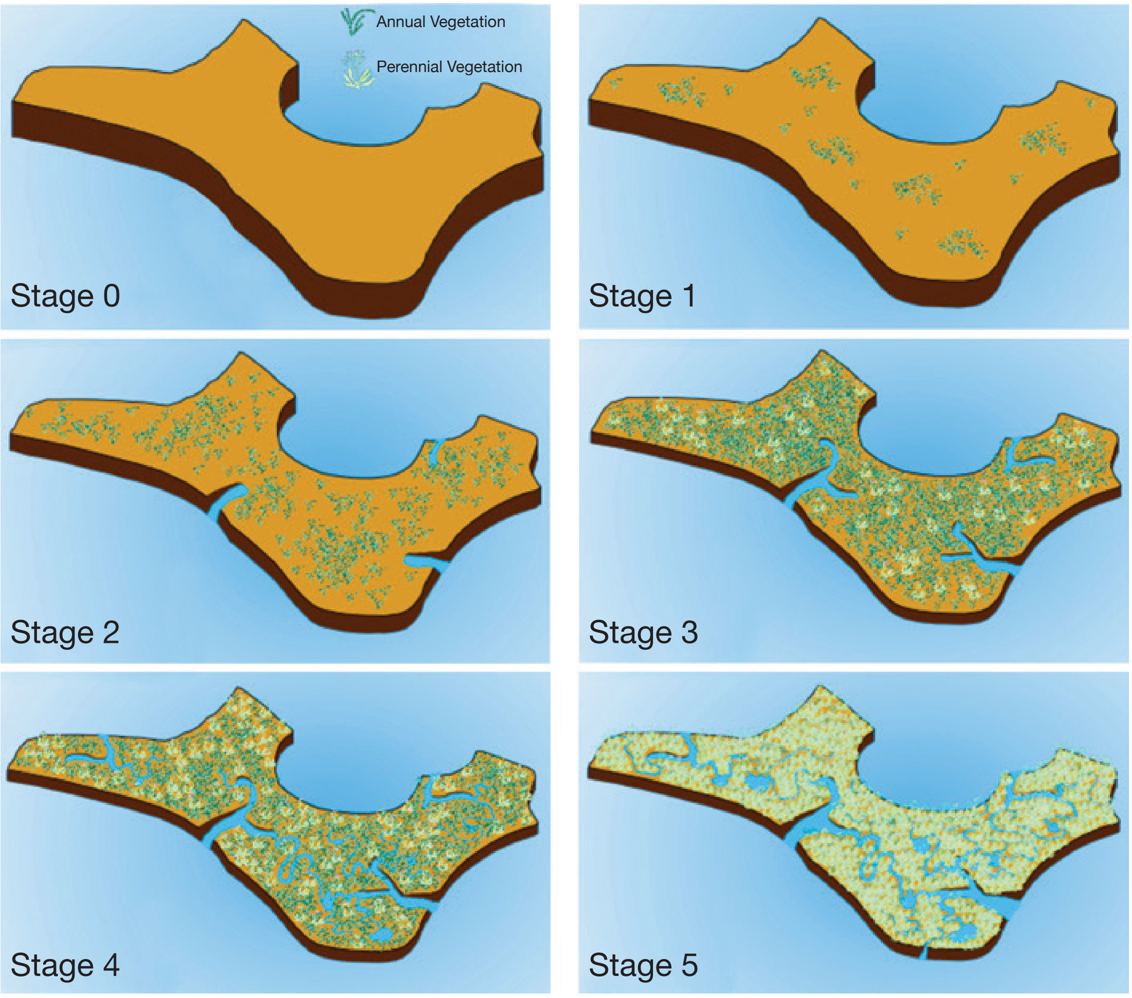
Until 1998, the barriers were constructed of timber pilings differently arranged. The use of wooden poles was required by the Superintendence of the Architectural Heritage and Landscape of Venice and its Lagoon (Soprintendenza ai Beni architettonici e Paesaggistici per Venezia e Laguna). The constraint of the use of wood limited the design of the barriers, which often resulted not adequate for the protection of the salt marsh edges and sometimes difficult to integrate in the landscape. In fact, the use of timber poles has caused some problems of durability, as these poles are rapidly attacked by marine woodborers, which are extremely active in the lagoon. The ecological footprint and impact on possible underlying archaeological structures is another aspect that should be carefully considered when using wooden poles. There may also be safety issues for navigation, since once broken, the log stubs drift in the lagoon. Based on these considerations, the use of rolls and mattresses was initially authorised in 1998. The rolls and mattresses were initially made of double twisted wire mesh, which were very effective for dampening boat-induced waves. Since 2000, polyester wires and modules with different degrees of degradability have also been tested. These wires and modules are made of natural-fibre woven grids and are filled with various materials, such as wood, coconut fibres, soil mixtures, halophyte turfs, and reed fascines. Considering their effectiveness in dampening the energy of the waves, mattresses made of polyester grids have been used along the lagoon channels under intense boat traffic and in areas subject to wind waves. The modular structures made of biodegradable natural materials are effective in protected areas with little wave energy (Nascimbeni, 2007). Lines of wood piles and brushwood fascines were deployed along some salt marsh edges for sediment trapping, but with questionable results. The new substrate of the reconstructed salt marshes cannot have that stratified structure given by the tidal deposition and vegetation typical of the natural salt marshes even when the slurry mud is sprayed on the surface at different times. Nevertheless, similarly to what happens in a sea-flooded plain, mimic salt marshes undergo a process of maturation that, over many years, makes them look natural.

Figure 7 shows the 6 evolutionary stages that have been identified, each with its own characteristics in relation to the age of artificial salt marshes (Patassini & Magro, 2016, based on CVN studies).

6. Life Natura 1999 salt marshes at Palude dei Laghi

From 1999 to 2002 a LIFE Project (LIFE NATURA 1999 “Barene: protezione e recupero con tecniche di ingegneria naturalistica”) was conducted, and it was aimed at the protection and redevelopment of a limited pilot area of the northern basin of the Lagoon of Venice with traditional techniques and new concepts experimented in Venice and in the Wadden Sea (Lower Saxony, Germany). The main partners of the project were the Venice Water Authority, City of Venice, Coastal Research Centre, Lower Saxony Ministry for Environment, Technical University of Berlin (DE), and Consorzio Venezia Nuova.

The techniques consisted in placing stone rolls (*“burghe”*) and biodegradable rolls (*“buzzoni”*) close to the salt marsh edges, in areas less exposed to erosion. Stone rolls are modular cylindrical elements made of



Stage	Time (years)	Elevation asl (cm)	Vegetation	Coverage surface	Creeks	Creek % of surface	Birds (nesting species)
0 (end of the work)	> 0.17	+70 / +100	none	-	none	-	none
1 (Compaction)	0.17 - 1	+60 / +70	*Salicornia* spp.	scattered cover	none	-	*Charadrius alexandrinus,* *Sterna albifrons,* *Haematopus ostralegus,* *Larus michahellis*
2 (Compaction / colonization)	1 - 3	+45 cm	*Salicornia,* *Sarcocornia*	about 50%	beginning of formation	up to 5%	As the previouse stage
3 (Colonization)	3 - 6	+30 cm	*Sarcocornia fruticosa,* *Limonium narbonense,* *Halimione portulacoides*	about 90%	in development	5 - 10%	Among the birds species the *Tringa totanus* can be found
4 (Colonization)	6 - 10		40-90% perennial (associations with *Sarcocornia* and *Halimione portulacoides*)	Total coverage	well-defined creeks and ponds system	10 - 15 %	*Tringa totanus,* *Haematopus ostralegus,* *Charadrius alexandrinus,* *Himantopus himantopus,* *Recurvirostra avosetta*
5 (Stability)	> 10		Perennial halophytes		network of creeks, canals, ponds is morphologically well-developed	15 - 25%	Bird species are those of the previous stage

Figure 7: The 6 stages summarising the evolution of an artificial salt marsh and the related main features, elevation above mean sea level, type of vegetation and coverage, creek formation, and main nesting bird species (author Irene Guarneri).

a high-strength grid filled with pebbles or sand and placed a short distance away from the salt marsh edge to counteract erosion. Biodegradable rolls are modular cylindrical elements made of differently degradable fabrics and filled with natural material such as wooden chips, vegetal soil, coconut fibres, and even *Spartina stricta* sods. There has been extensive use of brushwood fascines to retain sediments in the more internal areas of the Palude dei Laghi (for techniques, see Nascimbeni, 2007). In addition to the fascines, to promote sedimentation, artificial “algae” (i.e., floating polypropylene bundles) were also tested. The purpose was to slow down the water currents and intercept suspended sediments that are deposited on the bottom. However, this technique was discarded, since it introduces artificial elements into the environment without important results.

An interesting aspect of the project was the transplantation of halophytes in the salt marshes of the Lagoon of Venice: a halophyte nursery and a greenhouse were set up in a lagoon islet, Isola dei Laghi, located north of Burano, in order to stock and obtain the required plants.

The nursery was equipped for halophytes production and for the recovery of turfs detached from natural salt marshes due to boat-induced waves that, along with currents, cause erosion at the base of the salt marsh edges. The most successful species, both in cultivation and replanting, were the Graminae *Puccinellia palustris* and *Spartina maritima*.

Transplantations were optimised depending on the substrate by choosing different types of plant packaging. The plants were housed using a number of methods (sods, mattresses, small coconut baskets), the soil was prepared by harrowing, and sometimes sand was added near the transplants in order to favour the colonisation of adjacent areas.

This project also involved local fishermen working on the salt marshes’ maintenance when they were not engaged in fishing. The project showed that the techniques and small-scale approach used are valid; however, it was discontinued because of lack of funding.

7. Life Vimine salt marsh soil-bioengineering

LIFE VIMINE (2013–2017) was a demonstrative project in the northern Lagoon of Venice aimed to define and test an “integrated approach” to protecting the innermost salt marshes from erosion (Barausse et al., 2015). These salt marshes, located far from large channels, are surrounded by very shallow waters (a few tens of centimetres) but still undergo erosion; thus, specific conservation techniques are needed. Innermost salt marshes are among the most natural salt marsh habitats of the lagoon, and reconstructed salt marshes cannot substitute them, because they differ in soil structure (and, sometimes, elevation), fauna, morphology, and edge plasticity (Bonometto, 2003). VIMINE recognised that salt marshes should be protected as a system: protecting a salt marsh stretch also means protecting other habitats benefitting from its wave-breaking function such as other salt marshes, mudflats, or lagoon bottoms. For this reason, no single large protection works were made but, rather, many, small and spatially diffuse defences on strategic stretches selected to achieve the *prevention* of erosion.

Figure 8: Fascine barrier during low tide (author C. Ferrari).

Figure 9: A groyne (author C. Ferrari).

Figure 10: Sediment nourishment (author SELC).

Figure 11: Nourished mud covered by transplanted and natural salt marsh vegetation (author SELC).

Salt marsh conservation was achieved through nature-based solutions or soil-bioengineering techniques, which use biodegradable and natural materials (living plants, wood, sediments) and take advantage of natural processes such as the ability of plants to consolidate soil, enrich it with carbon, and make it accrete, and trap suspended sediments. The basic protection module was a brushwood fascine (Fig. 8 and 9) with a length of about 2 m and a diameter of 35–40 cm, sometimes wrapped in a coconut net, and tied with vegetal cords (e.g., sisal) or iron wire—all biodegradable or quickly degradable materials. Fascines were used to construct specific protections, designed depending on the local morphology and its evolutionary trend. The most common protection was the fascine barrier (from 2 m to tens of metres): fascines, placed in 2 or 3 superimposed lines sticking to the salt marsh edge, are anchored to wooden poles planted in the lagoon bottom. The barrier protects the salt marsh edge and favours sedimentation without blocking water exchange. To increase fascine durability, the small spaces between fascines and the salt marsh edge are filled with sediments, taken from nearby mudflats manually or, if large quantities are needed, using a small pump. These sediments are similar to those of the nearby salt marshes and reduce the costs and impacts of the works. Nourishment by pumping sediments behind fascines was also used to reconstruct completely eroded salt marsh edges or to refill internal salt marshes losing elevation (Fig. 10 and 11). The small scale of nourishment (from a few square meters to about one hundred) was essential to carefully recreate the proper soil elevation to favour the growth of halophytes, which quickly colonise the new sediment, strengthening it and making it accrete at a speed comparable to local sea level rise (Sarretta et al., 2010). The overall goal was thus to recreate natural salt marsh defences against lateral and vertical erosion and to concurrently restore small habitat surfaces. Fascines were also used for constructing wind barriers (2.5–25 m) placed up to 10–15 m off the salt marsh edge and crossing the dominant wind direction, and groynes, extending from the salt marsh edge for about 1.5–9 m, with the twofold aim of slowing currents down and dampening waves.

The choice of biodegradable materials and soft technologies is in line with the salt marsh plastic nature and the reversibility required by the Special Law for Venice, although these solutions cannot be applied along heavy-traffic channels, which demand more resistant protections (Bonometto, 2003; Barausse et al., 2015). Small, diffuse, and biodegradable protections, mostly created through semi-manual labour and using small boats and mechanical means, minimise environmental and landscape impacts on innermost salt marshes as well as costs, and are fit to contrast a spatially diffuse erosion by focusing on critical spots.

Regular monitoring and maintenance of biodegradable materials is needed to quickly identify and repair damaged protections, and monitoring is also key to promptly detecting and protecting new eroding spots and preventing erosion. Such ordinary surveillance was carried out by workers who regularly patrolled the lagoon, but it was made more efficient and sustainable by the participation of local communities, a cornerstone of the “integrated approach”. In VIMINE, a deliberate choice was made: the fascines were assembled and the protection works were constructed, monitored, and maintained also by local workers, such as fishermen of the Burano island. Choosing local workers has advantages: they efficiently navigate the shallow, mazy northern lagoon, which they know well; they can constantly monitor salt marshes during their daily fishing activities, promptly reporting maintenance needs; and hiring local workers allows to indirectly raise awareness of the erosion issue and of the value of salt marshes among local communities, as well as to create local jobs. Working to protect their own territory can be a reason for local communities to stay in the lagoon, which is depopulating, and rediscover the value of its natural habitats: VIMINE thus tackles the issue of salt marsh erosion together with the “erosion” of the lagoon communities, to demonstrate that conservation and sustainable local development can reinforce each other. This is why VIMINE implemented wider stakeholder participation activities, promoted local businesses depending on salt marsh conservation such as ecotourism, and created a short supply chain of wood to construct fascines, which was also a source of local sustainable jobs (Barausse et al., 2015). An assessment of the costs and benefits of conserving salt marshes through an integrated approach was carried out as a decision support tool for public bodies to plan investments in salt marsh maintenance; the results indicated that the cost of preventing erosion through soil-bioengineering is outweighed by the value of the created jobs and of the safeguarded ecosystem services (Barausse et al., 2015).

8. Seagrass transplantations

Over the past 25 years, various lagoon authorities have carried out seagrass transplantations both for technical experiments and for proper environmental restoration.

In 1992–1997 the City of Venice conducted a series of small-scale (4–5 m^2 plot) experiments of seagrass transplants in the central and southern basin of the lagoon that allowed the identification of edaphic and hydrological requirements of the seagrass species living in the lagoon (*Zostera marina, Z. noltei*, and *Cymodocea nodosa*). These experiments provided the background necessary to apply and adapt to the lagoon the various transplant techniques reported in the literature, such as rhizome transplantation and turf transplantation.

The Water Authority of Venice performed several restoration works through seagrass transplantation. Considering the extension of some works, in addition to the manual transplant technique (Fig. 12–14), mechanised transplant techniques were also experimented and applied (Fig. 15). These techniques allowed the transplants to be more resilient because of the larger size of the transfused turf compared to the size of the manually transplanted ones.

Figure 12: Manual seagrass transplantation (author SELC).

Figure 13: Transplanted sods (author SELC).

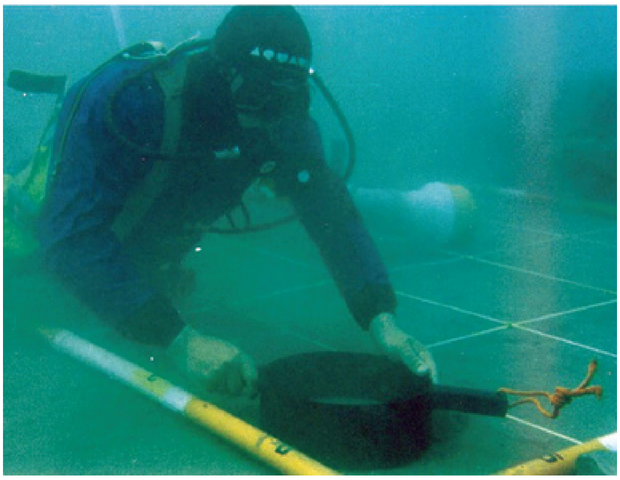


Figure 14: Transplanting seagrasses in a subtidal flat (author SELC).

Figure 15: Large seagrass turfs prepared for mechanical transplantation (author SELC).

In 1994 the Venice Architecture School (IUAV) and the Consorzio Thetis, Venice, conducted a pilot study for the transplantation of some tens of square metres of *Zostera noltei* in a shallow marshpond in the brackish zone of the northern Lagoon of Venice, once rich in seagrasses. At the beginning, the experiment gave positive results both in the survival and recolonization capability of the implanted sods (Zitelli & Rossetto, 1996) but after some years, the transplantation failed due to the harsh condition of the secluded area.

In 1996–1997, the possibility of explanting seagrass sods from a donor site without damaging the meadow vitality was tested. Two different techniques, sod transplantation and the rhizome method (bundles of rhizomes with shoots held in the superficial sediments with plastic clips, Fig. 16), were tested in 5 stations with *Cymodocea nodosa* and 5 stations with *Zostera marina*. The survival rate, coverage, shoot density, and biomass were measured at the 10 sites for both methods (in total 20 plots, 5 m by 5 m each, hosting 25 sods or bundles). After 2 growing seasons, both transplanting methods showed successful results (Tab 4). Statistically significant differences between the 2 transplantation methods were observed only for *C. nodosa* biomass, which was higher for the sod technique (Curiel et al., 2003) (Fig. 17).

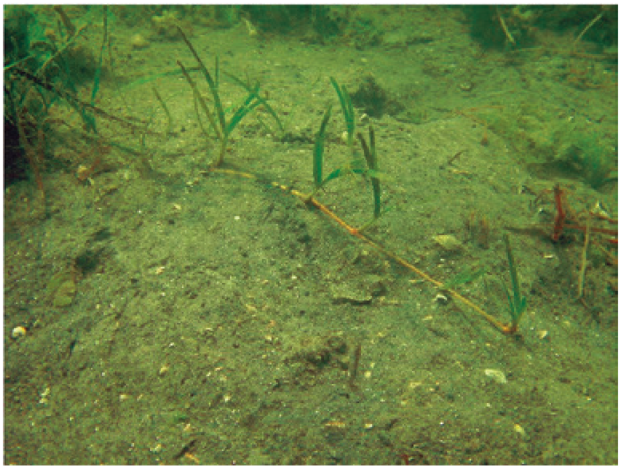


Figure 16: Rhizome colonising the bare sediment adjacent to the transplant (author SELC).

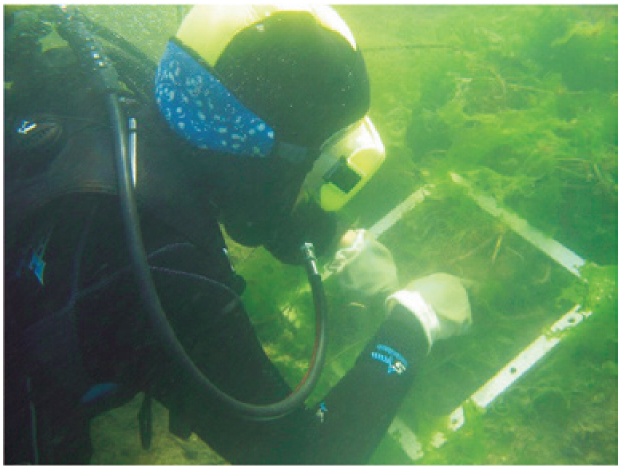


Figure 17: Seagrass growth monitoring (author SELC).

C. nodosa	**Beginning**		**After two growing seasons**	
	Sod	**Rhizome**	**Sod**	**Rhizome**
Survival (%)	100	100	74	73
Coverage (% total cell area)	4.1	1,2	86	76
Density (shoots·m^{2})	45	13.4	681	563
Biomass transplant (g.d.w.·m^{2})	-	-	402.9	177
Biomass control (g.d.w.·m^{2})	-	-	1116.9	

Z. marina	Beginning		After two growing seasons	
	Sod	**Rhizome**	**Sod**	**Rhizome**
Survival (%)	100	100	48	60
Coverage (%)	4.1	1.2	70	74,4
Density (shoots·m^2)	16.2	7.8	107.5	130.6
Biomass transplant (g.d.w.·m^2)	-	-	167.2	107.8
Biomass control (g.d.w.·m^2)	-	-	308.3	

Table 4: Average values of parameters monitored for *C. nodosa* and *Z. marina* (Curiel et al., 2003).

A large seagrass transplantation was carried out for the conservation and upgrading of the Sites of Community Importance and Special Protection Areas of the Lagoon of Venice (spring to summer 2010). The activity envisaged the use of a mechanised method that allowed to obtain 2250 m^2 of *Cymodocea nodosa* sods from donor sites with high seagrass coverage. The seagrasses were re-implanted in the southern lagoon basin in plots of approximately 350 m^2 each; the sods were deployed in a staggered array at about 1.30 m from each other. Site monitoring at the end of the third vegetative season showed coverage of 80–100%, and an increase in the vegetated area of 3.2–3.8 times as well as low mortality rates of transplanted sods (6–13%). After 3 years, the donor sites returned to a coverage of about 100%, recolonising the explantations (Scarton et al., 2017).

9. Life Seresto seagrass restoration

In order to favour a faster bottom seagrass colonisation in the northern part of the north lagoon basin, where seagrasses had almost completely disappeared, in 2012, the European Community funded the project SeResto “Habitat 1150* (Coastal lagoon) recovery by SEagrass RESTOration. A new strategic approach to meet HD & WFD objectives” (http://www.lifeseresto.eu/). The aim was the recovery of the ecological status of this area through the restoration and preservation of habitat 1150* (coastal lagoon) in the site of Community Interest (SCI) Laguna Superiore di Venezia (IT3250031), where this habitat covers approx. 3660 ha, by means of widespread transplantations of seagrasses. The implementation of the project was possible thanks to recent regulations that had strongly limited disturbance elements, by reducing the nutrient inflow (especially phosphorus) from the watershed (“Ronchi Costa” Decrees, 28 April 1998) and regulating the harvesting of the Manila clam (*Tapes philippinarum*) (Orel et al., 2000). In addition, clam fishing in this area stopped also because of the strong reduction of this resource by overfishing. The area is almost completely enclosed amongst islands, salt marshes, and the mainland, and without the widespread transplantation of small sods (15–30 cm) and rhizomes the recolonization would have required much more time.

During the first 3 years, small transplantations of submerged marine angiosperms (approx. 42 670 rhizomes) were carried out on a large scale in 35 sites. The aim was not to make large transplantations but to act through various small transplantations of small sods or single rhizomes with fishermen’s direct interventions. Then, the natural growth of the transplanted plants, recorded to be 0.16–0.22 cm day^{-1} (i.e., 58–80 cm y^{-1}) and the reproduction capacity (approx. 50 seeds per shoot) supported by marine tides and winds favoured the plant dispersion and a progressive recolonisation of the area.

The technical proposal is characterised by low effort and costs. It is expected that angiosperm populations will colonise salt marsh edges and natural channels within 3–4 years and 25–30% of the entire intervention area will be completely colonised by seagrass meadows with different levels of development within 5–10 years, depending on the different ecological conditions.

Plant transplantation and dispersion are mainly made by local fishermen and hunters (associated with project partner Laguna Venexiana ONLUS), who were specifically trained in the framework of the project. They are constantly assisted by the project's scientific partners (DAIS-Ca' Foscari University Venice and ISPRA) on license of PROVV OOPP, who contributed directly also to the seagrass transplantations. In this way, the project is raising both local population's and stakeholders' awareness of the need for preserving the lagoon environment. Transplantation activities are flanked by close environmental monitoring surveys, in order to test the effectiveness of the proposed actions. The monitoring is considering the ecologic quality of waters, sediments, and biologic communities (macrophytes, benthic fauna, and fish fauna). One more action will quantify and assess the ecosystem services provided by the restored habitat.

The results of the first 3 years show that rhizome transplantations were successful in 33 sites out of 35 where the colonisation has exceeded 60% with a high dispersion along salt marsh and canal edges. In the successful sites, the overall ecological status recorded by the Macrophyte Quality Index (MaQI, Sfriso et al., 2014) and the Habitat Fish Bioindicator Index (HFBI, Zucchetta et al., in preparation) changed from "Poor" to "Good".

10. Conclusions

The Lagoon of Venice is an important training ground for the development of environmental restoration techniques in a highly sensitive context from both an environmental and a cultural point of view, and even more considering the unique degree of intertwining of natural and cultural values.

The addresses given by the special law for the safeguarding of the Lagoon of Venice have greatly motivated the search for large-scale solutions. As it has been pointed out, however, long-term sustainability also relies on the management of the environmental dynamics, starting with the abatement, or mitigation, of the pressures causing lagoon degradation.

Small-scale and soft bioengineering solutions are nonetheless needed for maintenance, and a point of emergent importance is the constant care of the environment through the involvement of local stakeholders and workers.

Also of crucial importance is the predictive analysis of future trends, as an environmental restoration cannot be successful if it is opposed to strong and unidirectional evolutionary trends. Maybe restoration strategies should consider following the trend and adapting to it, instead of aiming at reconstructing landforms and habitats exactly as they were a century ago in the same way as if the situation were immutable. Constant care and routine actions are the key for preventing the loss of these delicate habitats. Therefore, the focus should be on promoting the natural processes leading to the formation of salt marshes and seagrass beds by tuning environmental restoration according to the new environmental dynamics. Among the new dynamics, we should not forget those induced by climate change, which could, in the course of this century, render useless any attempt to bring the lagoon back to a configuration now distant in time.

Acknowledgments

The authors thank Dr. Piero Nascimbeni and Dr. Claudia Ferrari for the beautiful pictures.

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When maintaining ecological integrity and complexity is the best restoring tool: The case of the Mar Menor lagoon

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1. Introduction

Coastal lagoons and estuarine environments are naturally stressed systems due to their high physicochemical variability (Elliott & Quintino, 2007). The species living in these environments are tolerant to such stress, adapting their physiology and behaviour to a broad spectrum of fluctuations. Thus, like communities in the initial stages of ecological succession or contaminated by human activity (Odum, 1969; 1985), estuarine benthic communities are expected to show low diversity, with few species of small size, very abundant, and typical opportunistic *r*-strategists (Margalef, 1969; Michel, 1979; Barnes, 1980; Kjerfve, 1994; Carrada & Fresi, 1988; Reizopoulou & Nicolaidou, 2004). The communities would then be controlled by the physical environment, and the interspecific relationships would not be very developed (Sanders, 1968). Therefore, estuarine ecosystems are expected to be conformed by a simple and uniform benthic community represented by the euryhaline and eurythermal biocoenosis described by Pérès & Picard (1964). Such acceptation of uniformity has been maintained through time by different authors (Augier, 1982; Carrada & Fresi, 1988; European Environment Agency, 2015; Gubbay et al., 2016), habitat lists, and conservation agreements (OSPAR, Barcelona or Eunis).

As commented, these ecosystems tolerate adverse environmental conditions well. So, as it is assumed that estuarine communities have the same characteristics as contaminated areas suffering from human-induced stress, the consequence is that biological indicators are incapable of differentiating between natural and stressed states. This is the “estuarine quality paradox” (Dauvin, 2007; Elliot & Quintino, 2007; Dauvin & Ruellet, 2009).

Under these conditions, the system would be bottom-up controlled and exposed to eutrophication processes and dystrophic crises (Elliott & Quintino, 2007). This would imply that recovering from impacts does not mean to have large individuals and a high representation of *k*-strategists, and should assume a status with naturally lower biomass-abundance ratio, higher production-biomass and higher abundance-species richness ratios, and a trophic system dominated by detritus feeder invertebrates and nutrient-reflecting algae (Margalef, 1969; Elliott & Quintino, 2007), including ephemeral species of filamentous algae such as *Chaetomorpha linum, Cladophora dalmatica, C. vagabunda, Ceramium diaphanum,* or thin tubular or blade forms such as *Ulva compressa, U. intestinalis, U. prolifera,* or *U. rigida* (Wilkinson et al., 1995; Pérez-Ruzafa et al., 2011a).

However, most of these assumptions are under reconsideration (Pérez-Ruzafa et al., 2011a), and coastal lagoons can be more heterogeneous and complex than expected (Pérez-Ruzafa et al., 2004; 2005a; 2007a; 2008), showing complex autoregulation mechanisms based on their spatial and temporal heterogeneity (Pérez-Ruzafa et al., 2005a).

1.1. Estuarine vs. lagoon paradox: Can a coastal lagoon be complex at the same time as productive?

Due to the physiographic characteristics of coastal lagoons, such as shallowness, number and intensity of physicochemical gradients, and terrestrial influence, including nutrient inputs, these ecosystems are among the most productive of the planet (Nixon, 1982; Carrada & Fresi, 1988; Alongi, 1998). This biological productivity is exploited by humans mainly in the form of fisheries (Nixon, 1982; Pérez-Ruzafa et al., 2011b) and aquaculture developments.

However, according to the theory of ecological succession (Odum, 1969), highly productive ecosystems must correspond to early stages in succession, were ecosystems' constituents coincide with quick growth species, with short life cycles and high fecundity (i.e., *r*-strategists). This would be in agreement with the existing general assumptions on coastal lagoon characteristics and the estuarine paradox. How is then possible that at the same time that they are so productive, some coastal lagoons can be complex and with sophisticated homeostatic mechanisms typical of mature systems (Pérez-Ruzafa et al., 2002; 2005b)? This apparent paradox can be explained taking into account that while productivity in these environments is enhanced by the strong physicochemical gradients, at the same time, introducing restrictions to the energy flow would permit to produce a work that can be used to generate physical, hydrological, and biological structures, leading to a very complex spatiotemporal heterogeneity and homeostatic behaviour. In coastal lagoons, this restriction role is performed mainly by the inlets or communication channels with the open sea, but also by benthic vegetation and meadows, stones, and rocky boulders, either natural or introduced by humans to build breakwaters and docks (Pérez-Ruzafa, 2015).

This emerging complexity differentiates coastal lagoons from estuaries (Pérez-Ruzafa et al., 2011c) and results in the development of the aforementioned homeostatic mechanism of self-regulation, which makes it difficult to detect the stress to which the ecosystem may be subjected and the effects of eutrophication or the inputs of contaminants on it (Pérez-Ruzafa & Marcos, 2015). At the same time, any ecological restoration attempt should take it into account.

The restoration process or the prevention of remoteness from ecological integrity of an ecosystem must be put in the context of ecological succession and its responses to increasing stress (Figure 1). Ecosystems, like individuals, can face moderate environmental stress and maintain their integrity, regulating their main ecological or physiological functions and parameters within certain margins of variation. These are known as homeostatic or homeorhetic mechanisms, the last term used by Odum (2000) to refer to the capability to maintain the energy flow through the system using feedback regulations. It is a laxer control mechanism than homeostasis at the individual level, and shows a more chaotic behaviour and pulses, and not so much equilibrium states (Odum & Barret, 2006). In this phase, the organisms or ecosystems can show alterations in some parameters that simply indicate that they are adjusting to the new environmental conditions, but not necessarily that these changes are harmful to them. Under higher or persistent stress conditions, organisms and ecosystems start to show increasingly deeper changes and reach a breaking point, when significant deterioration occurs. Finally, they can reach a point of no-return, when irreparable damage takes place, leading to death in the case of individuals or to a different community or ecosystem. At both points, sudden and dramatic changes can occur in the framework of catastrophe theory sensu Thom (1989).

Usually, restoration approaches consider conceptual models of changes of the state of a system with increasing pressure that include these phases. The homeostatic region would correspond to the concept of resistance, that is the degree of change of structural indicators under stress conditions but without the system losing its ecological integrity and functions (Pimm, 1984; Tett et al., 2007) (grey area in Fig. 1). It is assumed that an ecosystem that has surpassed its homeostatic capacity but has not yet reached the point of no-return maintains the ability to return to its original state and to regain its integrity (path II in Fig. 1). This capability is known as resilience and is measured in time units (Pimm, 1984; Tett et al., 2007). After the no-return point, the system can no longer reach its original status and evolves to a new type of ecosystem (path III in figure 1). The new ecosystem will have lower structure and autoregulation capabilities but, as it is made up of a higher component of *r*-strategist species, it can tolerate higher stress before reaching the new breaking point (path IV).

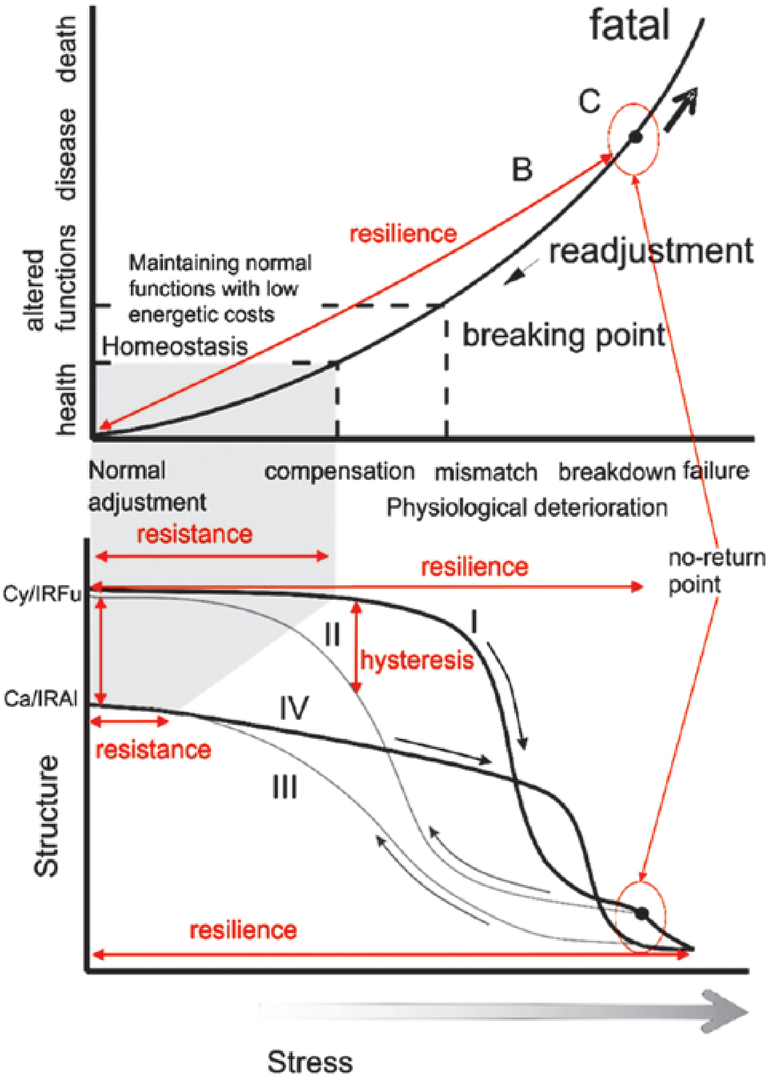

Figure 1. Changes in functional status, from health to different degrees of disability, of an organism or ecosystem, and physiological or structural impairment when exposed to increasing stress (modified from Lloyd, 1972 and Elliott et al., 2007). Black lines represent the paths under increasing stress. The grey area corresponds to the homeostatic or homeorhetic regions where the system maintains its structural and functional parameters within the limits for normal functioning (resistance). When the stress exceeds the self-regulation capacity of the system, the system loses part of its properties and malfunctions, showing symptoms of alteration. If the stress persists, a break point is reached where suddenly the structure and functions of the system are significantly altered. In these conditions, if the stress stops, the system can still recover (grey lines represent the recovering paths). The extent of the change that still allows a recovery is called resilience. However, if stress persists or increases, the system can reach a point of no-return, which leads to death or a state of new equilibrium, usually with the structure and functions diminished. Most of the indicators currently used, both at physiological and community and ecosystem level, are useful for detecting changes in the region B. However, we need to find good indicators and understand the processes in the homeostatic region and breakdown and no-return points to anticipate significant deterioration or irreparable damage, respectively. In both regions, the transition phase can be difficult to anticipate because sudden and dramatic changes can occur in the framework of catastrophe theory. Cy/IRFu—*Cymodocea nodosa* meadows / Infralittoral rock with Fucales; Ca/IRAl—*Caulerpa prolifera* meadow / Infralittoral rock with *Alsidium corallinum*.

Unfortunately, most of these considerations and models are conceptual, and there is very little information about when the breaking or the no-return point will be reached. On the other hand, it is quite probable that in the vicinity of the no-return point, the system does not recover completely its original structure and homeostatic capabilities when the stress ceases. This difference is named hysteresis (Tett et al., 2007) or hysteresis type II (Elliot et al., 2007).

Ecological restoration is an intentional activity aimed at recovering the health of an ecosystem and returning it to its historic evolution (SER, 2002). In practice, the experience of restoring marine and coastal systems is limited, and there are few examples of successful recovery (Elliot et al., 2007; Duarte et al., 2015). Lagoon ecosystems in particular suffer from numerous and varied pressures that make it difficult to find generalisable restoration methods. It is therefore necessary to understand the functioning of these complex ecosystems and the processes that are altered both by human pressures and by the possible measures to be taken, in order to devise restoration methods that make compatible the human uses with the ecosystem integrity and its sustainability.

Because of this, in many cases, the best available option, while the non-return point is still not reached, may be only to remove the stressor and permit the ecosystem to recover its integrity in a natural way. However, it should be kept in mind that following the evolution of ecosystems under stress conditions, and after their elimination, may be the best way to develop a scientific knowledge that allows anticipating changes and recommending active management actions (including, for example, habitat enhancement or creation, maintenance works in the channels, or introduction or eradication of species) that help the system recover in future situations.

2. The Mar Menor: a complex ecosystem under human pressure

Located on the southeastern coast of Spain, with an area of 135 km^2 and an average depth of 4.5 m, Mar Menor is among the biggest coastal lagoons in the Mediterranean (Fig. 2). Until less than 20 years ago, it differed from most of the other coastal lagoons by the oligotrophy and traditional cleanliness of its water while maintaining high fishing yields. Additionally, it is characterised by the presence of rocky outcrops and islands, which contribute to increasing its environmental heterogeneity and biodiversity. As in most coastal lagoons, due to the intrinsic characteristics of its environment, the Mar Menor lagoon is a provider of goods and services for humans thanks to its high biological productivity and its suitability for health care activities, nautical sports, and leisure activities.

The history of human pressure on the lagoon dates back to Phoenician and Roman times, when mining activities in the surrounding mountains allowed waste with heavy metals, mainly lead and zinc, to enter the lagoon and accumulate in its sediments.

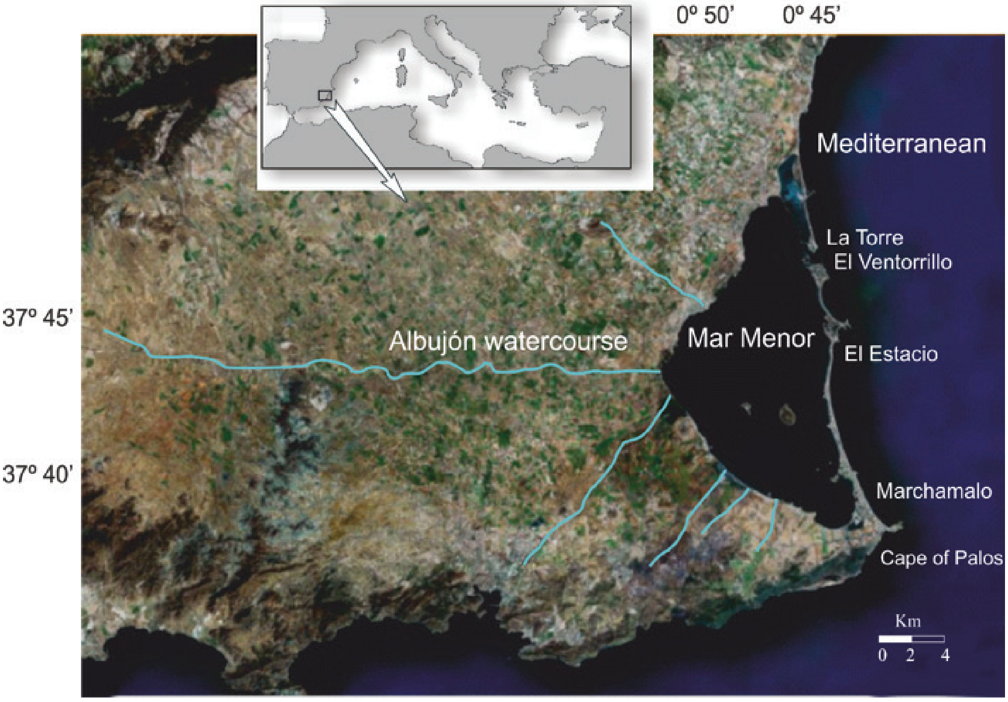

Figure 2. Location of the Mar Menor lagoon.

Of all human activities in the lagoon’s recent history, 3 have induced and continue to induce drastic changes in the lagoon’s hydrographic, sedimentological, and ecological processes, and therefore in its biological assemblages. On the one hand, the hydrodynamic changes due to the enlargement of the El Estacio inlet in 1972 produced an increase in water renewal rates, reducing salinity and extreme temperatures, thus allowing colonisation by new species, in a process of “Mediterranization” of the lagoon (Pérez-Ruzafa et al., 1987; 1991). At the same time, tourist and urban development initiated a series of transformations in the geomorphology of the lagoon and waste inputs, including land reclamation, building of sport harbours, artificial beach creation, etc., with important consequences for the lagoon’s hydrological conditions and fisheries. Since then, changes in salinity and temperature have been observed with the expansion of colonisers, such as the algae *Caulerpa prolifera*, that covered the entire basin in a few years (Pérez-Ruzafa et al., 1989). On the other hand, the stress induced by coastal works and the removal and resuspension of sediments is increasing the expansion of *C. prolifera* and the associated muddy bottoms, and leads to the disappearance of the original communities (Pérez-Ruzafa et al., 2006). Finally, more recently, and correlated with changes in agricultural practices in the drainage basin and the introduction of intensively irrigated crops, the alteration of the nutrient entry regime has produced a chain of changes that affect the trophic status and the ecological integrity of the lagoon (Pérez-Ruzafa et al., 2002) and pose risks in the entry and bioaccumulation of pesticides and other pollutants (Pérez-Ruzafa et al., 2000; Conesa-Alcaraz et al., 2010; Campillo et al., 2013; León et al., 2013; Moreno-González et al., 2013a,b; 2014; Traverso-Soto et al., 2015).

The lagoon is, therefore, subject of concern due to its high rate of change over the recent decades, with a detrimental impact on water quality and the structure of the lagoon’s biological assemblages and dynamics. The correct management of the lagoon, not only as a natural area but also as a heritage and economic resource of the Murcia Region, requires a comprehensive knowledge of the functioning of its environmental system, as well as taking measures coherent with its goals of conservation and enjoyment.

2.1. Opening channels

The hydrographic conditions of coastal lagoons, as in the case of Mar Menor, change throughout their geological history depending on fluctuations in sea level, the development of the sandbar that separates the lagoon from the open sea, the communication channels between the two systems, and the occurrence of storms that can temporary break the sandbar. The biological populations of the lagoons will vary according to their degree of isolation and the associated environmental conditions. In the Mar Menor lagoon, salinity increased after the last sea level regression in the Quaternary and the progressive isolation that took place during the eighteenth century, reaching a maximum at the end of that century with values of 70 g of salt per litre. After this period, there were several sporadic episodes in which storms broke the sandbar, producing changes in salinity and allowing the colonisation of several species, mainly fish such as the gilthead seabream (*Sparus aurata*), seabass (*Dicentrarchus labrax*), and grey mullet (Mugilidae spp.) (Butigieg, 1927; Navarro, 1927; Dezileau et al., 2016). The last of these events, which occurred in 1869, caused a significant decrease in salinity, from 60–70 to 50–53 PSU, probably reinforced by the opening of artificial inlets that increased the communication of the lagoon with the Mediterranean (the construction of the Marchamalo started in 1769 and that of El Charco, in 1878) for the installation of fishing devices (locally called "encañizadas") to catch fish during their reproductive migrations. This implied a strong change in the lagoon biology with the introduction of different species of phanerogams (*Cymodocea nodosa* and *Zostera noltii*) that expanded throughout the basin. In addition, about 30 new species of molluscs and fish settled in the lagoon (Pérez-Ruzafa et al., 1987).

One of the most drastic transformations in the recent history of the Mar Menor lagoon took place after the enlargement, at the beginning of the 1970s, of the El Estacio inlet (previously an artificial "encañizada") to construct a navigable channel up to 30 m wide and 5 m deep. The increase in water renewal rates led to a significant drop in salinity from 44.8–52.9 to 43–45 and reduced extreme temperatures (Pérez-Ruzafa et al., 1987; 1991), allowing the colonisation and the establishment of new marine species (Pérez-Ruzafa & Marcos, 1992; 1993). The number of mollusc and fish species doubled in just 15 years (Pérez-Ruzafa et al., 1987; Pérez-Ruzafa, A., 1989) to the detriment of typical lagoon species, many of them of fishing interest (such as the grey mullet).

As a part of the same process, other alien species, such as the jellyfish *Cotylorhiza tuberculata* and *Rhizostoma pulmo*, entered the lagoon from the Mediterranean in the mid-1980s (Pérez-Ruzafa, A., 1989) and, after a period of population growth, proliferated massively as a consequence of the changes in the trophic state of the lagoon, causing serious problems to the tourist activity (Pérez-Ruzafa et al., 2002).

But some of the most important changes affecting the physiography and functioning of the Mar Menor ecosystem occurred at the level of the benthic meadows and communities. The populations of *Ceramium ciliatum* var. *robustum* and *Cladophora* sp. (García-Carrascosa, 1982) in the photophilic community were mostly replaced by *Acetabularia acetabulum, Jania rubens, Padina pavonica* facies and, depending on the area, by *Palisada tenerrima* (Pérez-Ruzafa, I.M., 1989). *C. nodosa, Zostera marina*, and *Z. noltii* dominated the Mar Menor soft bottoms before 1970 (Lozano, 1954; Simonneau, 1973). Some records (Simonneau, 1973) indicate the presence of *Posidonia oceanica* in sandy shallow areas of the southern basin. Although, given the salinity limit of tolerance of this plant, it is unlikely that this species would be able to constitute stable or extensive meadows, some scattered specimens were maintained rooted until 1980 near the Marchamalo and El Estacio inlets (Pérez-Ruzafa et al., 1987; Pérez-Ruzafa, A., 1989). Currently, the benthic vegetation of the Mar Menor lagoon mainly consists of a monospecific meadow of *Caulerpa prolifera* or a mixed *Caulerpa-Cymodocea* meadow, dominated by *C. prolifera*, on muddy and some rocky substrates, covering more than 80% of the lagoon's bottom, favouring high contents of organic matter in the sediment and low oxygen concentrations. *C. nodosa* grasses are now scattered and restricted to shallow sandy bottoms, and some more or less dense patches of *Ruppia cirrhosa* are also observed in the shallowest areas protected from hydrodynamism (Pérez-Ruzafa et al., 1989).

The expansion of *C. prolifera*, beginning in the northern area of the lagoon, has been progressive since the enlargement of the El Estacio channel. From 1982 to 1987, the mean biomass in the areas deeper than 2 m increased from 63.62 to 103.06 gDW · m^{-2} and maintained this value until recent years. On the contrary, the mean biomass of *C. nodosa* showed a strong decrease from 49.61 to 2.69 gDW · m^{-2} in the same period (Pérez-Ruzafa et al., 1989; 2012).

The initial colonisation of *C. prolifera* was probably due to increasing minimum temperatures, since this alga poorly tolerates temperatures below 10°C (Meinesz, 1979), which were frequently reached before El Estacio was enlarged. On the other hand, it grows almost continuously throughout the year and has a high capacity of vegetative generation of new stalks from any fragment ripened by hydrodynamism, which gives it a high rate of colonisation. From that point onward, the progressive variation of the lagoon's environmental conditions, and the increase in sediment stress and nutrients in the water in a subsequent phase, favoured the algae and disfavoured the phanerogam *C. nodosa*. Sediments colonised by *C. prolifera* increase quickly in silt-clay fractions and in organic matter content that lead to sediment anoxia. Although anoxia per se does not explain the regression of *C. nodosa*, as this species is adapted to live in anoxic environments (Terrados et al., 1999), anoxia may have contributed to accelerating the plant's regression in zones with limited light. In fact, sediment instability is more advantageous for macroalgae than for phanerogams, and the combination of limited light and sediment anoxia has been shown to have negative effects on various species of marine phanerogams (Hemminga & Duarte, 2000). *C. nodosa* declined sharply when the silt and clay content of the sediment exceeded 15% (Terrados et al., 1998) and, in the Mar Menor lagoon, *C. nodosa* is very scarce and shows very low biomass when organic matter content is higher than 9% and the silt-clay fraction is higher than 44% (Pérez-Ruzafa et al., 2012). Therefore, although it is not clear if *C. prolifera* and *C. nodosa* are species in competition, there is strong evidence that the sediment transformations produced by *C. prolifera* strongly affect the phanerogam.

2.1.1. Impact of enlarging channels on fishing activity

The degree of communication between lagoons and the sea not only determines species diversity and the colonisation of marine species, but also the fishing activity and biological productivity (Pérez-Ruzafa et al., 1991; 2007b; Lae, 1994; Pombo et al., 2002). But the effect of dredging coastal lagoon inlets on fishing production is not clear and may vary considerably depending on the lagoon (Pérez-Ruzafa et al., 2012).

The increase in biodiversity in the Mar Menor lagoon, as a result of the colonisation processes occurring at the end of the nineteenth century after the opening of the El Charco artificial inlet and later after the enlargement of the El Estacio channel in the 1970s, has been linked to a decrease in the catches of the main commercial species, mainly grey mullet and gilthead seabream.

The decrease in the lagoon's total catch was more pronounced in the case of El Charco modifications due to the extremely high and almost monospecific or mono-taxonomic yield based on grey mullet species at that time. The fall in fishing yields produced by El Charco works formed the object of study of 2 scientific reports (Butigieg, 1927; Navarro, 1927) which sought an explanation for it. These studies attributed the decline in catches to the drop in salinity, colonisation of new species (such as *S. aurata*), and expansion of *C. nodosa* meadows. However, other factors could be responsible, such as the fall in productivity itself, both benthic and planktonic, associated with a lower intensity of the salinity gradient.

In the case of El Estacio works, the drop in the catch affected both *S. aurata* and Mugilidae, being also related to the increase in fish diversity and to a new drop in salinity, but mainly to the colonisation and rapid expansion of the algae *Caulerpa prolifera*, which produced a high degree of organic matter accumulation and anoxia in the sediments (Pérez-Ruzafa & Marcos, 1987; Pérez-Ruzafa et al., 2005b).

In both cases, there was a significant increase in the number of species fished and in the contribution of Mediterranean species to the total catch of the fleet, especially after El Estacio was enlarged. In this framework, human activities (e.g., modification of the inlets) affect, as we have seen, the fishery in terms of abundance and species composition. However, the fisheries in the Mar Menor lagoon seem to be offset by a homeostatic adaptability of the system. As a result, a dynamic equilibrium is maintained in which total catch remains around the maximum sustainable yield (MSY) as a combination of fishing efforts both inside and outside the lagoon, the alternation in species abundance, and the incorporation of new species in the fishery. The whole system is maintained by the productivity associated with the intense physicochemical gradients existing in coastal lagoons, and it is regulated by the restrictions imposed by the inlets on both water and species fluxes (Marcos et al., 2015). Other factors that are operating include temperature oscillations and trends linked to climate change acting on both short- and long-term scales (Marcos et al., 2015).

2.1.2. Management of the inlets as a restoration or management tool

Maintenance of the exchange between coastal lagoons and the sea through inlets is usually considered essential for the biological functioning of a lagoon (Quignard, 1984) and avoiding dystrophic crises (Rossi, 1984). Furthermore, as fishing in coastal lagoons is based mainly on marine migrants, opening or closing one or more inlets and completing maintenance dredging operations in the channels are usual management practices in coastal lagoons over the world (Pérez-Ruzafa & Marcos, 2012). However, the effects of dredging or building new communication channels may vary considerably from one lagoon to other, and the ways in which inlets are managed must be carefully analysed (Pérez-Ruzafa & Marcos, 2012). While in some lagoons increasing the interchange with the sea can improve fisheries (Castro, 1984), in others it can lead to a drop in fishing yields (Peja et al., 1996; Marcos et al., 2016). As commented before, fishing yields in coastal lagoons are mainly related to the intensity of physicochemical gradients, increasing with the hydrographic differences with the sea and the complexity of the perimeter, and also increasing when the mean depth of the lagoon is low (Jojeux & Ward, 1998; Pérez-Ruzafa et al., 2007b; Pérez-Ruzafa & Marcos, 2012). Therefore, depending on the initial geomorphological and hydrodynamic conditions, dredging the channels can in some cases avoid excessive isolation of the lagoon facilitating an active gradient, and, in other cases, increase excessively the communication with the sea, homogenizing the system and reducing the intensity of the gradients, leading to an increase or fall of the fishing yields, respectively.

These practices, whether or not linked to fishing activity, can also lead to significant changes in environmental conditions, the introduction of new species, and the distribution of benthic macrophytes, having strong consequences on lagoon communities (Pérez-Ruzafa et al., 1991; Dye, 2005; Gamito et al., 2005). The degree of marine influence and the geomorphology of the inlets, which regulate colonisation rates of marine organisms and introduce restrictions to the flux of organisms (including genes), are key elements to determine species richness and the spatial heterogeneity and internal structure of lagoon communities (Pérez-Ruzafa & Marcos, 1992; Pérez-Ruzafa et al., 2007b). The resulting spatio-temporal variability and ecosystem complexity is one of the bases of the homeostatic capability of these environments (Pérez-Ruzafa et al., 2005a; Pérez-Ruzafa, 2015). Therefore, these complex effects of modifying the geomorphology of the inlets on the general biodiversity and structure of lagoon communities should be taken into account in any restoration or integrated management plan for these ecosystems.

2.2. Impact of coastal works and beach creation

Some of the most important changes in coastal lagoons have occurred because of coastal works, generally for the development of tourist and urban infrastructures (land filling, urban development and associated services, construction of marinas, sport harbours, dikes, etc.). In the case of the Mar Menor lagoon, there have been different actions aimed at gaining land at sea, such as those in the 1970s that produced the disappearance of “El Vivero”, a shallow area in the south of La Manga (the sandy barrier separating the lagoon from the Mediterranean), known by fishermen as the place of recruitment and nursery of numerous fish species. Later, in 1986, the Spanish Ministry of Public Works initiated a plan to create artificial beaches in the lagoon. The actions consisted in the dredging of sandy sediments in the shallow areas north of La Manga and their pumping in the shallow areas on the west coast of the lagoon. The stability of the beaches was reinforced by the installation of rocky dikes perpendicular to the coast.

As a consequence of these actions, both dredging and spill areas showed changes in habitat characteristics. Both zones were originally shallow, with depths less than 1.5 m, and sandy, with no vegetation cover or isolated spots of *C. nodosa*. A dense *Caulerpa prolifera* meadow started to form at the deep boundary of the 2 areas, at depths greater than 1.5 m. After dredging and pumping works, an increase in the primary production of microphytobenthos (Figure 3a) took place, leading to an increase in organic matter and fine particles in the sediment (Figure 3b). At the same time, the reduction in light penetration in the shallow areas due to turbidity favoured the quick expansion of *C. prolifera*, which behaves as a shade-adapted species with a low photoprotective capacity (García-Sánchez et al., 2012) (Figure 3c). This process was faster in dredged areas, where 50% of the holes were densely colonised by *C. prolifera* or *Chaetomorpha linum* (Pérez-Ruzafa et al., 1991; 2006). As a result, in both dredging and pumping areas, the alteration of the substrate produced a change in the composition of the lagoon bottom. The sandy bottom dominated by coarse and fine sand and low in silt, clay, and organic matter (always less than 0.5%) was replaced by a muddy bottom with dense *C. prolifera* meadows, dominated by fine sand and with high percentages of silt, clay, and organic matter that exceeded 8% in a few months and increase yearly.

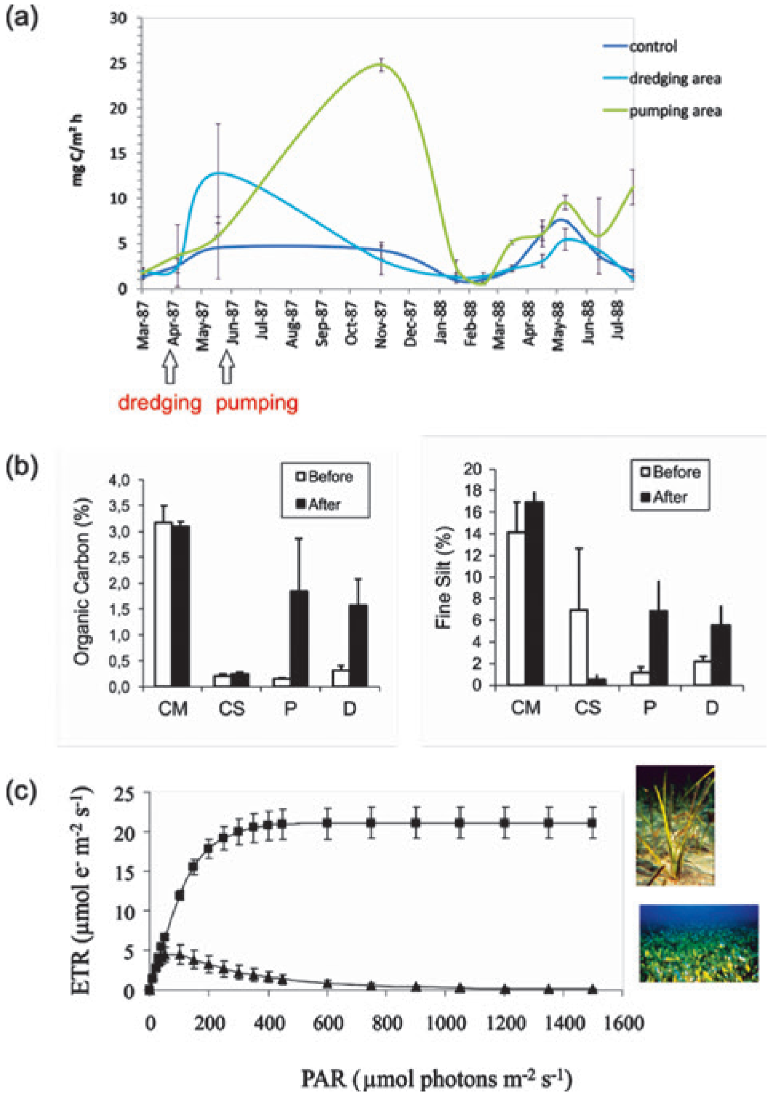

Figure 3. Sequence of events after dredging and pumping of sediments for beach creation in the Mar Menor lagoon: (a) after dredging and pumping operations in sandy bottoms, the primary production of microphytobenthos increases compared to control areas; (b) as a consequence, organic carbon content and fine particles in the sediment increase in both pumping and dredging zones, which change from being typical sandy bottoms to be similar to *Caulerpa prolifera* meadow bottoms (CM—control on *Caulerpa* meadows; CS—control on sandy bottoms; P—pumping area; D—dredging area); (c) as photosynthetic efficiency measured as electron transport rate (ETR) show inhibition in *C. prolifera* (triangle) at lower light intensity than *C. nodosa* (square), due to turbidity during operations, *C. prolifera* spread in the working areas where its growth was previously limited by high irradiance. Modified from Pérez-Ruzafa et al., 1991 (a); Pérez-Ruzafa et al., 2006 (b) and García-Sánchez et al., 2012 (c).

As a consequence of changes in vegetation and sediment characteristics, fish assemblages also changed radically. The observed changes can be interpreted against a framework of a general response to perturbations. Stress increased fish abundance, in a first step, after increasing productivity and substituting *k*-strategist species by opportunistic ones. Species richness and diversity increased under moderate perturbations (in pumping areas and areas surrounding the dredging zone) after the first impact, according to the intermediate disturbance hypothesis (Connell, 1978), but decreased strongly in greatly affected areas (inside the holes). Finally, the colonisation by *C. prolifera* meadows led to a significant change in the fish assemblage by substituting the characteristic community of sandy bottoms, dominated by *Pomatoschistus marmoratus, Gobius niger,* and *Callionymus* spp., by a community dominated by *G. niger*, significantly impoverishing both abundance and species richness (Pérez-Ruzafa et al., 2006). All attempts to extract the produced mud and refill with sand made during the past 20 years have produced the same effects, making the situation even worse year after year.

2.2.1. Introduction of artificial habitats

One aspect of coastal works is the introduction of new substrates, usually rocky or wooden, for the construction of poles, jetties, breakwaters, and dikes. Some of these elements, such as signalling and mooring poles in Venice, or piers in Mar Menor, form an important part of the typical landscape of these lagoons.

These constructions offer a hard substrate, which is usually scarce in most coastal lagoons, and is colonised—in a process similar to that observed in artificial reefs—by species of algae, invertebrates, and fish that otherwise could not inhabit these environments. The community of brekwaters and dikes is similar to those living on natural rocky bottoms in the lagoon, both in terms of species composition and assemblage structure. However, the structural complexity of artificial constructions may be greater than that of the natural rocky substrates, favouring the abundance and specific richness of the assemblages. Studies in the Mar Menor lagoon show that colonisation takes place in a few months after the installation of artificial substrata. Abundance tends to remain constant through time, although the arrival of new species and the process of assemblage structuring can continue throughout the years. In addition, the blocks, and especially the piers on pillars, generate low-illumination environments appropriate for the development of complex communities of benthic organisms, mainly filter-feeders (Photo 1).

The moderate introduction of hard substrates could be considered, by itself, a way to increase the environmental diversity in coastal lagoons. Artificial hard substrates could have a positive impact under certain conditions, because they add species richness, biological diversity, and spatial heterogeneity to the original assemblages. However, it should be considered that depending on their design and size, these structures, as breakwaters built for harbours and beach creation, can modify the hydrodynamic regime in the surrounding areas, and sandy bottoms will be substituted by muddy ones as a consequence of the processes of sedimentation and retention of dead biomass. Hence, the suitability of installing breakwaters or other artificial rocky substrata, their effect on hydrodynamics, and, as a result, on sedimentation rates and bottom characteristics in their area of influence should be considered during the planning stage (Pérez-Ruzafa et al., 2006).

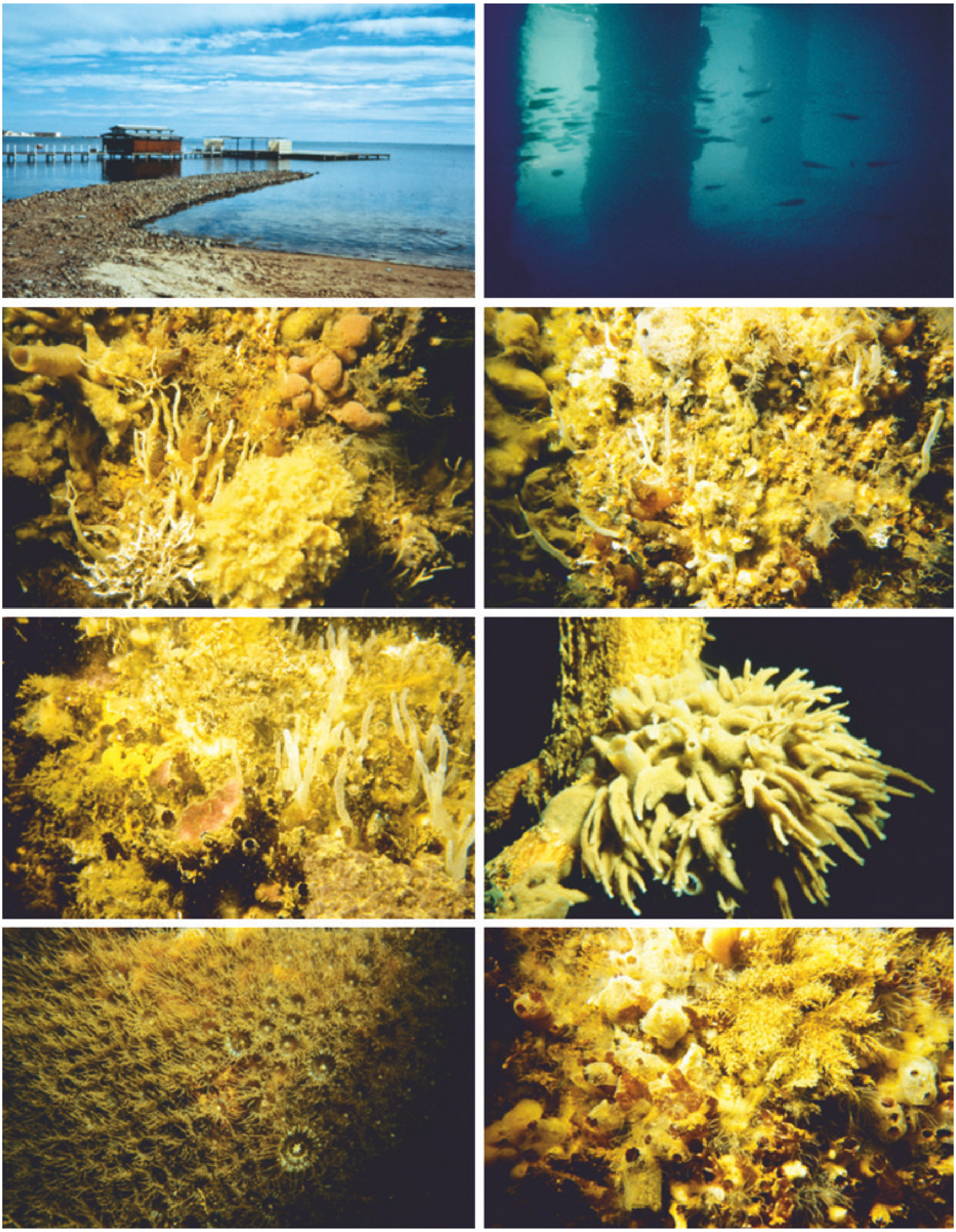

Photo 1. Traditional piers are a better choice for bathing in coastal lagoons than artificial beaches maintained with breakwaters or dikes. The pillars under the pier maintain a well-structured community of sciaphilic filtering organisms typical of caves. Close-up photos show different aspects of the community dominated by sponges, cnidarians, polychaetes, bryozoans, and ascidians, which contribute to maintaining water quality and increasing lagoon biodiversity.

2.3. Eutrophication process

Until the 1970s, Mar Menor was markedly oligotrophic, its main distinctive feature being the transparency of its waters compared to the great majority of coastal lagoons. The primary production was mainly benthic, with the phanerogam *C. nodosa* being the main macrophyte, which was replaced after the enlargement of the El Estacio inlet by a *Cymodocea-Caulerpa* mixed bed, with a biomass of approximately 280 gDW · m^{-2} (Pérez-Ruzafa, A., 1989; Pérez- Ruzafa et al., 1989; Terrados & Ros, 1991). At that time, the high benthic biomass of macrophytes contrasted with the low phytoplankton density (Ros & Miracle, 1984) and water oligotrophy (Gilabert, 2001). Based on data from the mid-1980s, it was estimated that 63.18% of the total primary production of the lagoon was due to *C. prolifera*, 0.42% to *C. nodosa*, 0.24% to photophilic algae, 11.62% to microphytobenthos, and 24.53% to phytoplankton (Terrados & Ros, 1991). However, this trophic status has been lost in the past decade, with the recent history of nutrient inputs to the lagoon being closely related to urban and agricultural development, either at the coastline or in the drainage basin.

Eutrophication is not a trophic state, but a process derived from the increase in the supply of organic matter to the ecosystem (Likens, 1972; Nixon, 1995; Gamito et al., 2005). It is generally associated with the increase in the input of inorganic nutrients favouring primary production in the ecosystem (European Environment Agency, 2001), which leads to a progressive replacement of marine phanerogams and slow-growing algae by fast-growing algae and, finally, by phytoplankton, which eventually dominates the system (Gamito et al., 2005). This process has been described in many coastal lagoons (Reyes & Merino, 1991; Boynton et al., 1996; Taylor et al., 1999) and has been modelled (Giusti et al., 2010). When eutrophication is chronic, its effects include anoxia states, toxic phytoplankton blooms, massive death of benthic organisms, and drastic changes in species distribution. Once the process is triggered, it is difficult to slow down. Due to the progressive release of nutrients accumulated in the sediment during its development, the impoverishment in species, and the simplification of the food web, the eutrophic state can be prolonged for a long time, even if the nutrient intake ceases (Nienhuis, 1992).

In general, coastal lagoons and estuaries are considered particularly sensitive to the effects of nutrient inputs (European Environment Agency, 1999; Taylor et al., 1999; NRC, 2000). Urban discharges are commonly regarded as the main source of phosphorus in aquatic systems and many coastal lagoons (Vaulot & Frisoni, 1986), while agriculture is often regarded as the main source of nitrogen.

The alteration of the nutrient cycle is considered one of the main causes of algal blooms, which are often stimulated by the availability of nitrogen (Valiela et al., 1997; Taylor et al., 1999), and usually lead to dystrophic crises in some lagoons (Amanieu et al., 1975; Boutiere et al., 1982; Reyes and Merino, 1991; Ferrari et al., 1993; Sfriso et al., 1995; Viaroli et al., 1996; Guyoneaud et al., 1998; Bachelet et al., 2000; Sakka Hlaili et al., 2007; Specchiulli et al., 2009; Giusti et al., 2010). Drastic fluctuations in primary production, whether seasonal or daily, produce a strong mismatch in the oxygen balance. The system moves from being oversaturated during the ephemeral phases of high autotrophic production and accumulation of organic matter, to anoxia periods, when it moves to the heterotrophic phases with a high consumption of oxygen (D'Avanzo et al., 1996; Viaroli et al., 2001; Viaroli & Christian, 2003).

The data collected in the Mar Menor lagoon over the past 20 years provide evidence for the existence of the classical process of eutrophication, but with some deviations. Intense tourism and urban development began in the early 1970s. During this period, primary production, both benthic (Terrados & Ros, 1991) and in the water column, was limited by the low nitrogen inputs, which entered mainly through runoff, principally during the rainy season in winter, while phosphorus penetrated directly from urban water leaks, principally in the summer and in most cases without any treatment (Gilabert, 2001). In the mid-1980s, nitrate concentrations were low and always below 1 µmol $NO_3^-·L^{-1}$, contrasting with the higher phosphate values. Subsequently, in the late-1980s, sewage networks and treatment plants for the main urban areas were implemented, reducing phosphorous inputs except in some overflow events from the water collection system. When the water treatment plants were operative, the agricultural activity began to transform from rain fed with low use of fertilisers to irrigations with an overfertilisation with nitrogen compounds. At the end of the 1990s, nitrate in lagoon waters reached concentrations up to 8 µmol $N·L^{-1}$, $NO_3^-·L^{-1}$, especially during spring and summer, stimulating the growth of large phytoplanktonic algae (Pérez-Ruzafa et al., 2002). Therefore, phosphorus became the limiting factor for biological productivity in the lagoon, with nitrogen concentration being high most of the time.

As a result of changes in the nutrient entry regime, the water column in the lagoon changed from oligotrophic to eutrophic, providing the conditions for the growth of larger phytoplanktonic cells, so that communities dominated by small flagellates (*Rhodomonas* and *Cryptomonas*) in winter, and diatoms and dinoflagellates from spring to autumn, were replaced by large diatoms such as *Coscinodiscus* spp. and *Asterionella* spp. present throughout the year.

However, contrary to expectations in a system with high nutrient loads, during 20 years, from the early 1990s, when started irrigation practices, to early 2010s, Mar Menor lagoon still maintained a low phytoplankton biomass and there was no significant increase in chlorophyll concentration (Pérez-Ruzafa et al., 2002) (Fig. 4).

Since 1995, there has also been a strong proliferation of the jellyfish *Rhyzostoma pulmo* and *Cotylorhiza tuberculata*, which colonised the Mar Menor lagoon after the El Estacio enlargement. *Aurelia aurita*, the only native jellyfish of Mar Menor, became the least abundant, having the highest density in spring (April and May). *R. pulmo* begins to proliferate in May, while *C. tuberculata* has its peak abundance in July and August, reaching more than 12 individuals per 100 m^3 (Fig. 5). In the mid-summer of 1997, the jellyfish population across the lagoon was estimated to be about 40 million individuals (Pérez-Ruzafa et al., 2002).

Notwithstanding the process of eutrophication, a comparison of the seasonal dynamics between 1988, when nitrate concentration was low, and 1997, after nutrient inputs increased considerably, indicates no significant changes in the slope of the biomass spectra of the pelagic trophic web. This was due to the combined direct and indirect top-down control exerted by these allochthonous jellyfish (*R. pulmo* and *C. tuberculata*) feeding on large diatoms, tintinnids, veliger larvae, and copepods (Pérez-Ruzafa et al., 2002) (Fig. 6a). The concentration of chlorophyll *a* showed a negative relationship with nutrient concentration and a positive relationship with the abundance of ichthyoplankton, suggesting that phytoplankton controls nutrient concentration, while herbivores are controlled by fish larvae (Fig. 5a, c), reinforcing the evidence of a top-down control of the trophic web (Pérez-Ruzafa et al., 2005a). In addition, the variation in the relationships between the abundance of fish larvae and chlorophyll *a* concentration showed a highly defined seasonal dynamic with a limiting cycle (Fig. 6b). The combination of direct and indirect effects on different stretches of the size spectrum (e.g., the effect of jellyfish on tintinnids and copepods, permitting the growth of small phytoplankton) and control mechanisms such as bottom-up and top-down (Lehman, 1991; Cottingham, 1999) translates into a different size structure than would be expected under eutrophic conditions.

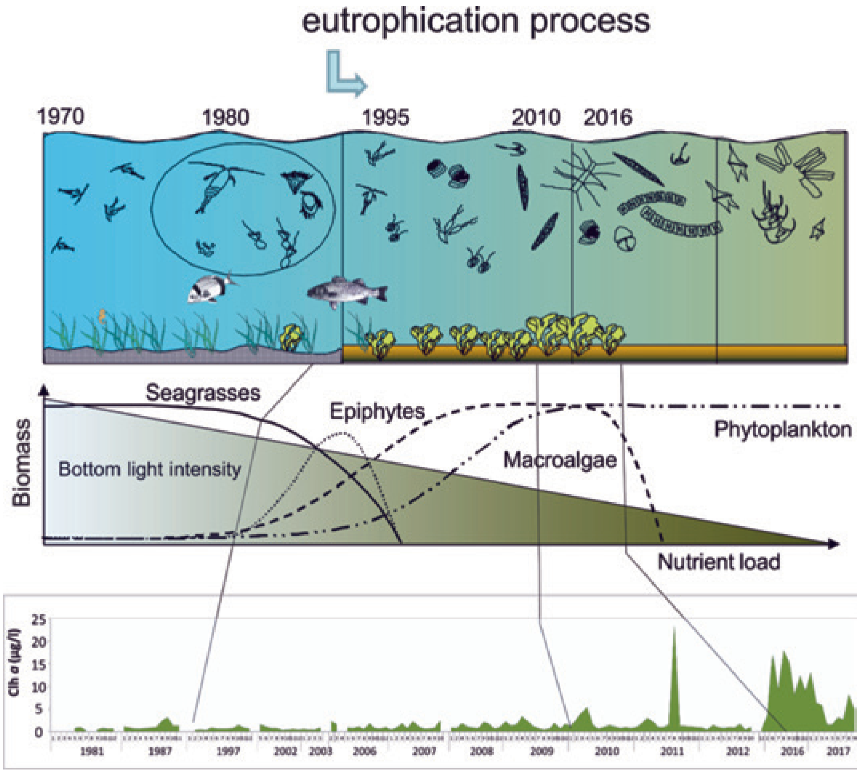

Figure 4. Conceptual model of the eutrophication process and timing of the principal changes observed in the case of the Mar Menor coastal lagoon. The lower graph shows the temporal dynamics of the chlorophyll *a* concentration in the water column throughout the process. Adapted from Gamito et al. (2005).

The oscillations and spatial variations in the amplitude of the limit cycle (Fig. 6c) can be explained biologically as resulting from overflows produced by the delayed response in herbivore density to food availability, or as being due to differences in community structure and species life cycles (Scheffer, 1998), which result in homeorrhetic control mechanisms (sensu Odum, 2000) and delays in the response along the different levels of the trophic web. The temporal stability of the regulation mechanisms in the Mar Menor lagoon, and probably in other systems, may be due to the seasonal mismatches in the reproduction and life cycle of the different estuarine species (Pérez-Ruzafa et al., 2004; 2005a), the immigration of marine species, and, in general, to the spatial and temporal heterogeneity of the biological assemblages determined by the restrictions to the colonisation of species from the open sea through the inlets. The plankton-benthos connections may also play an important role. In fact, the importance of top-down control over phytoplankton exerted by filtering bivalves and other benthic organisms has been described in different coastal bays (Heck & Valentine, 2007; Newell et al., 2007; Lonsdale et al., 2009).

This situation changed dramatically since the year 2015. The sustained intake of nitrates, rising temperatures, and anomalies in the winter thermal cycle, which reduced jellyfish populations to a minimum for 2 years, led to a deterioration of water quality in the lagoon. The depth of visibility of the Secchi disk was reduced from around 6 m to less than 0.5 m, whereby the compensation depth was above the average depth of the lagoon, with the consequent mortality of the meadows located at more than 2 m depth. Since then, the water column has been dominated by dense populations of *Synechococcus* sp. In the infralittoral benthic assemblages on hard substrates the photophilic community on rocks with Fucales (IRFu) was replaced by a photophilic community dominated by *Alsidium corallinum* (IRAl) and Ulvales (Fig. 1).

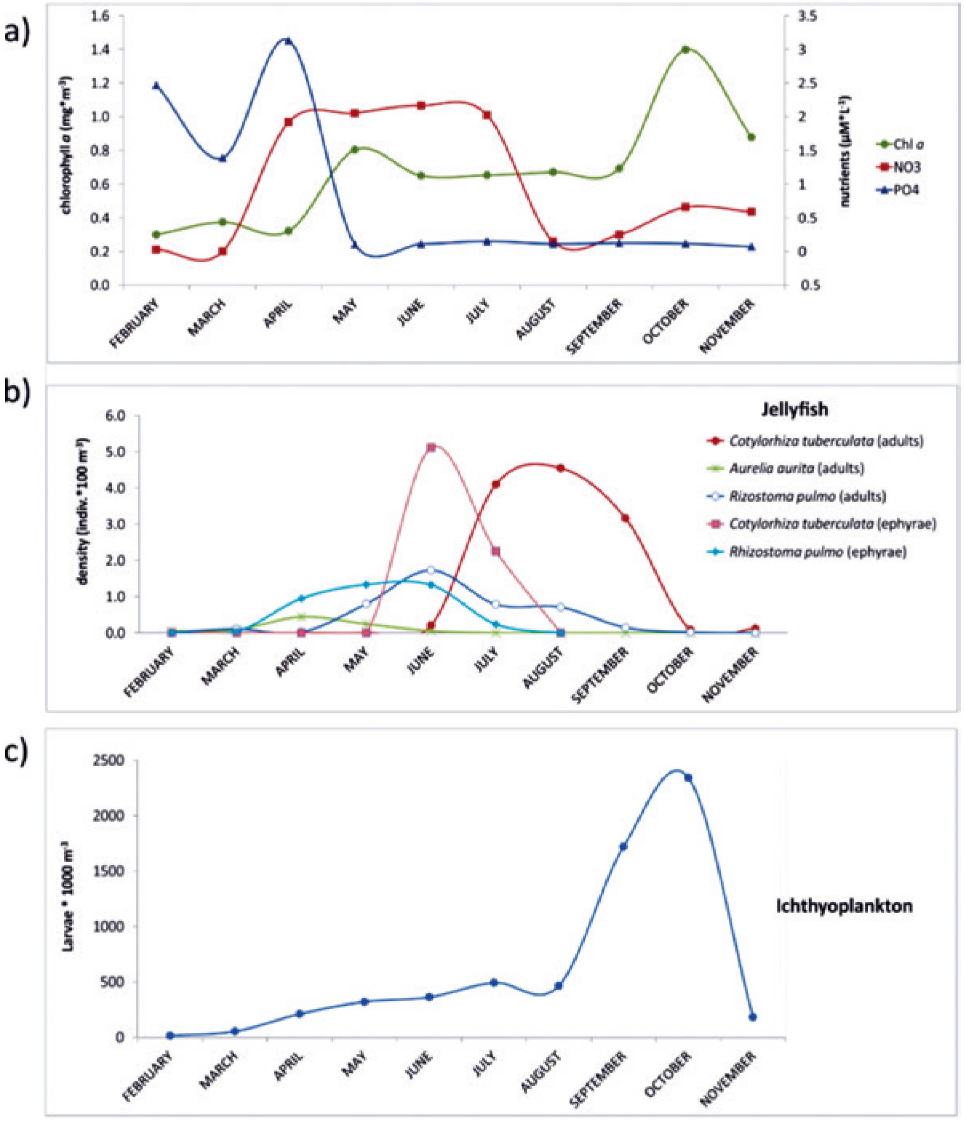

Figure 5. Seasonal dynamic in (a) nutrients (NO_3^- and PO_4^{-3}) and chlorophyll *a* concentration; (b) jellyfish abundance (including ephyra and adult phases of *Rhizostoma pulmo* and *Cotylorhiza tuberculata*, and adults of *Aurelia aurita*); and (c) ichthyoplankton density. Adapted from Pérez-Ruzafa et al. (2011a).

The lagoon is currently in a critical situation, with forced fluctuations by increasingly unpredictable climatology, and with heavy autumn and winter rains that have drastically affected its salinity for months. Because of this, it is difficult to anticipate its evolution. However, the lagoon still responded to management measures aimed at reducing nutrient wastes, recovering water transparency (reaching a Secchi disc visibility of up to 5 m) during the spring and the beginning of the summer of 2017, but losing it again after the rise in temperatures in mid-summer.

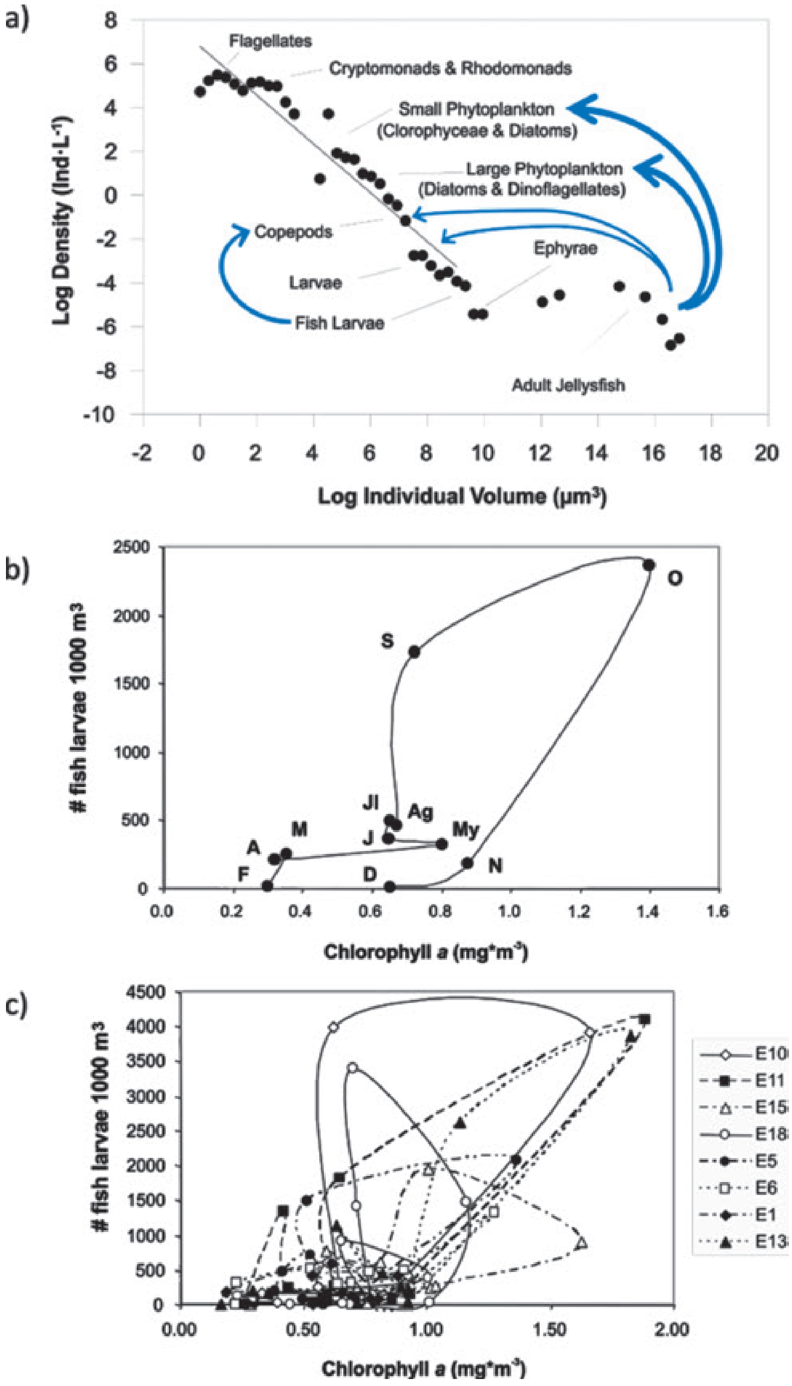

Figure 6. (a) Top-down control exerted by jellyfish and ichthyoplankton on the different compartments of the Mar Menor food web, showed on a representation of the pelagic biomass size-spectrum ranking from small flagellates (2 µm diameter) to adult jellyfish (up to 40 cm diameter), according to Pérez-Ruzafa et al. (2002); (b) averaged and (c) spatio-temporal variability (symbols represent different sampling stations: E1 to E18) of the regular seasonal cycle of the relationship between fish larvae density and chlorophyll a concentration in the Mar Menor lagoon, adapted from Pérez-Ruzafa et al. (2005).

Final remarks

The Mar Menor lagoon is a good example of how not taking into account the functioning of ecological processes has led to critical situations, with the decline of fishing production and the loss of traditional arts, deterioration of bathing areas, loss of water quality, and a serious eutrophication process. The failure of previous management measures, based on counteracting the consequences of certain actions with more actions of the same type, shows that in order to find the right solutions, we need a deep knowledge of the unique processes that take place in coastal lagoons. Many of the consequences of these actions involve potential risks to human uses of the lagoon and local economy, and this must be taken into account in addition to the environmental and biological characteristics that are at risk (Pérez-Ruzafa & Marcos, 2005). In fact, the economical activities of coastal lagoons depend closely on ecological processes. Any management measure must take into account the balances that maintain the biological productivity inherent in coastal lagoons, as well as the constraints on hydrodynamic and biological flows that allow the emergence of spatiotemporal heterogeneity and ecological complexity, which are the key to these ecosystems' self-regulation capacity. Restoration measures may consider introducing hard substrates and structures, restoring sediments, or maintaining communication channels. However, these solutions will only work if they keep the natural gradients and spatio-temporal heterogeneity; emulate the natural processes produced by currents, waves, and natural dynamics in intensity and duration; and take into account the adaptations and complex interactions between species in the different affected communities. On the one hand, productivity can be increased by intensifying the gradients and energy inputs into the system. This role is played by organic or nutrient inputs, which promote biological productivity; freshwater discharges, which increase the difference in salinity with the sea; coastal works and land reclamation, which usually increase the lagoon perimeter; dredging and pumping sediments which increase nutrient transfer into the water column; or the loss of depth or lagoon surface which intensify the physico-chemical gradients. An excess of production can lead to processes of eutrophication and loss of water quality and simplification of the ecosystem. On the other hand, the complexity and heterogeneity of the system, which contribute to the maintenance of beta diversity and to the preservation of homeostatic and self-regulation functions, can be kept by restricting hydrodynamic and energy flows, mainly by regulating exchanges in the channels of communication with the sea, but also by maintaining seagrass meadows or artificial structures. The balance between one effect and the others is essential if we want to preserve a productive system able to sustain fisheries or water bird assemblages without evolving into overly fast and simple states in which self-regulation mechanisms are lost. This requires a good understanding of the complex cause-effect relationships that take place as a result of different human actions (Fig. 7). The construction of conceptual and numerical models based on scientific knowledge and the results of the scientific monitoring of previous actions are essential to anticipate problems and help in decision making.

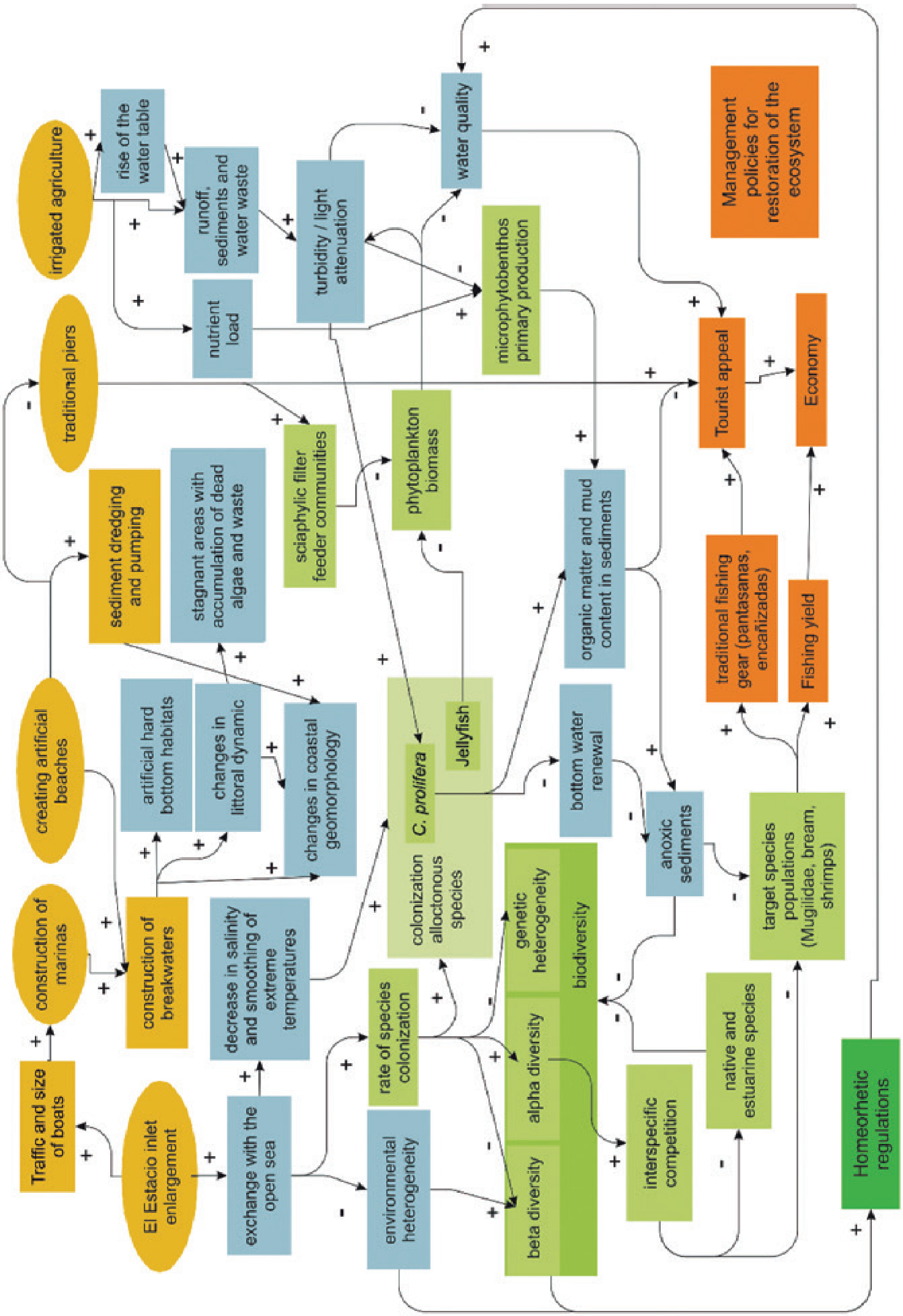

Figure 7. Diagram of the cause-effect relationships between main human activities (yellow boxes), environmental conditions (blue boxes), biological process and descriptors (green), and socio-economic aspects (orange). The plus sign indicates increasing effects, and the minus sign indicates decreasing effects.

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Tancat de la Pipa: a case study of ecological reallocation-restoration within the Albufera de València Natural Park

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1. Introduction

The Albufera de València Natural Park (AVNP hereafter) is an ecologically valuable Spanish wetland located on the Mediterranean coast. It is nationally and internationally recognised: it was declared Natural Park in 1986 by the Valencian Autonomous Government, has been included in the Ramsar List of Wetlands of International Importance since 1990, and has been considered a relevant habitat under the EU Bird Directive (79/409/EEC) since 1991, in addition to possessing species and habitats treated in the EU Habitats Directive (92/43/EEC). The park contains one of the largest littoral lagoons (2300 ha) in the Iberian Peninsula, the Albufera de València lagoon (AV lagoon hereafter). The park also consists of 14000 ha of fields for rice cultivation and an associated drainage system surrounding the AV lagoon. In the past, the AV lagoon harboured rich communities of submerged vegetation, both vascular plants and charophytes (Pardo, 1942; Rodrigo et al., 2009; Rodrigo et al., 2010). Unfortunately, this lagoon is currently a hypertrophic turbid phytoplankton-dominated system (Rodrigo et al., 2013a) as the result of eutrophication. This process began in the 1960s with the discharge of completely untreated sewage waters from industrial, agricultural, and urban sources, and continued for many years afterwards (Dafauce, 1975). As a consequence, the submerged vegetation in the lagoon was lost many years ago. In recent years, several actions have been carried out in the AVNP to reduce the external nutrient load (e.g., by improving the sanitation infrastructures and the wastewater treatment). However, these measures have not been sufficient for achieving a good ecological potential.

In order to meet the requirements of the European Union Water Framework Directive for the AVNP, in 2007, the Spanish Water Authority initiated an effort to (i) restore the previous aquatic habitats, to increase species and habitat biodiversity, and (ii) improve the water quality of inflows entering the AV lagoon, to assist in its restoration. One of the actions taken was the transformation of a 40-ha area of AV surrounding rice fields, called Tancat de la Pipa, into a naturalised zone designed as an eutrophication remediation system, with 3 types of aquatic ecosystems: (i) several units of water surface-flow constructed wetlands, (ii) 2 small lagoons at the end of the system, and (iii) a basin fed by groundwater inputs that tried to mimic the typical springs formerly common in the AVNP. In 2009, the new Tancat de la Pipa system started to be monitored, and the area protected, after being designated as a Reserve Area by the Valencian Autonomous Government due to the ecosystem services it provides. Tancat de la Pipa, located on the north shore of the AV lagoon, was part of this lagoon in the 18th century, but was later turned into rice fields (Sanchis-Ibor, 2001). Thus, the Tancat de la Pipa area represents a case study of ecological reallocation-restoration that contributes to the conservation of priority natural habitats in the context of the European global biodiversity conservation strategy. Tancat de la Pipa also provides a unique opportunity to investigate the ecological key factors and the interactive processes, synchronised and synergistic most of the time, that are relevant for the success of restoration and the conservation of species and habitats (Rodrigo et al., 2013a, b; Calero et al., 2015; Rodrigo et al., 2015).

Over the last few years, constructed wetlands have been used in natural environments to treat eutrophicated waters (Tang et al., 2009), as they increase biodiversity, cost relatively little, and treat water efficiently (Vymazal, 2011). Shallow lagoons are also widely used in ecological engineering and are often considered to be constructed wetlands because they improve water quality and enhance ecological functioning (Vymazal, 2011). These lagoons are extensively used to control diffuse pollution from agricultural runoff (Mitsch et al., 2012) and to serve as ecological buffers; lagoons are also used in stormwater treatment (Jenkins et al., 2012) or as polishing units in constructed wetlands (Vera et al., 2011). Treatment efficiency in constructed wetlands and shallow lagoons is always measured in terms of nutrient removal and, in urban wastewater treatments, also in terms of bacterial and pathogenic parasite removal. However, few studies have focused on the plankton community inhabiting these wetlands as indicators of the improvement in water quality, and still fewer studies have dealt with the role of plankton in the eutrophication reversion. Furthermore, zooplankton in particular has been largely ignored, although it may play a key role in reducing eutrophication (Calero et al., 2015). This chapter (sections 3 and 4) presents the analyses of the role of plankton from the water surface-flow constructed wetlands and the 2 small lagoons in the eutrophication reversion in the first 3.5 years of operation of the new Tancat de la Pipa.

The maintenance or recovery of submerged macrophyte stands is an important goal (Crisman et al., 2005) in the restoration and management of lagoons, due to their beneficial effect on water quality. Submerged macrophytes enhance the structural complexity of the water column (Jeppesen et al., 1997) and tend to promote species diversity (Declerck et al., 2007). Macrophytes buffer the harmful consequences of anthropogenic eutrophication by reducing phytoplankton biomass through either direct or indirect mechanisms (Scheffer, 1998). However, avoiding the loss of submerged vegetation in eutrophic lagoons and reintroducing vegetation after it is lost are difficult issues in the restoration of aquatic systems, because many factors, both biotic and abiotic, affect these processes. Nutrient concentrations above a certain threshold are known to cause the disappearance of vegetation (González-Sagrario et al., 2005). Eutrophication promotes abundant microalgal production (phytoplankton and periphyton), resulting in reduced light availability for submerged vegetation (Roberts et al., 2003). In regard to animals, exotic fish species, such as carp, negatively affect macrophytes by direct or indirect actions (Angeler et al., 2002; van de Bund & van Donk, 2004). Invasive red swamp crayfish have been shown to damage macrophytes by direct feeding (Anastacio et al., 2005) or other actions (Angeler et al., 2001). Consumption pressure by waterfowl has been reported to cause reductions in submerged vegetation biomass and cover (Noordhuis et al., 2002; Matuszak et al., 2012). Charophytes, a component of submerged vegetation, are one of the groups that are most sensitive to nutrient enrichment (Blindow, 1992), and are responsible for the establishment and maintenance of clear-water states in many cases (Coops, 2002). Moreover, some authors have described the preferential feeding of waterfowl on charophytes rather than on higher plants (Cirujano et al., 2004). The synergistic negative combination of all of the above-mentioned factors may be a determinant of the continuity of submerged vegetation in lagoons under restoration. Therefore, our major purpose was to discover the control factors influencing the macrophyte (angiosperms and charophytes) dynamics in the recently created Tancat de la Pipa lagoons (section 4), mainly those factors causing the total disappearance of submerged vegetation and preventing revegetation. Since the seed sediment bank is crucial to assess its potential as a source of future vegetation (Rodrigo et al., 2010; Hong et al., 2012) and to re-establish local and regional macrophyte species (Kentula, 2000), we also characterized the seed sediment bank in the lagoons. Finally, in the last section, we present the main contributions of our work for the management and restoration of Mediterranean lagoons.

2. The new ecosystems of Tancat de la Pipa: design and functioning of a wetland for eutrophication remediation and biodiversity increase

The 40 ha of the former rice fields of Tancat de la Pipa (Fig. 1; 39° 21’ 51” N, 0° 20’ 47” W) were transformed in (i) about 9 ha free water surface-flow constructed wetlands (FWSCWs hereafter): FG, fp (made up of 3 cells placed in series), and F4; (ii) 2 small lagoons: the Educative lagoon (0.35 m mean depth, 6 ha) and the Reserve lagoon (same mean depth, 8 ha); and (iii) a basin (1 m mean depth, 4.5 ha) fed by subterranean waters provided by a deep artesian well to mimic typical springs of the area, locally called “ullals”, and to promote the diversity of submerged macrophytes and other groups. The whole system was flooded and started to operate in April 2009. There was a monitoring program from this date to the end of 2012.

Inflow eutrophicated waters from the AV lagoon—with mean values of 0.35 mg $P{\cdot}L^{-1}$, 4.5 mg $N{\cdot}L^{-1}$, and 50 µg chl-*a*$\cdot L^{-1}$ for 2009–2012—entered continuously by gravity from a gully and a channel in the north of the system to a distribution channel. Water flowed slowly above the substrate (exposed to air and sunlight) and within it across the 3 FWSCWs units. Vertical sluice gates at the entrance and exit controlled the water depth (0.20 ± 0.05 m, annual average) and residence time in each unit. FG and fp units had been planted with emergent vegetation (such as cattails in the first 2 cells, and cattails and rushes in the third one) in January and February 2009. Water left the FWSCWs and flowed through a central distribution channel that discharged to the marsh composed of the Educative and Reserve lagoons. In the created spring, the outlet fed the Educative lagoon as well. The complete water circulation ended when the water was pumped out back to the AV lagoon after crossing the Educative and Reserve lagoons. The water authorities stipulated target total suspended solids, total phosphorus, and total nitrogen concentrations below 10 $mg{\cdot}L^{-1}$, 0.1 mg $P{\cdot}L^{-1}$, and 3 mg $N{\cdot}L^{-1}$, respectively, in the Tancat de la Pipa outflows before discharge to the AV lagoon.

A brief description of the time course of emergent vegetation in the FWSCWs is necessary to further understand some changes observed in plankton communities and water quality dynamics: at the end of the first growing season, the aboveground biomass of the cattails reached 800–1500 g dry mass m^{-2}, with a 100% cover in the 2 first cells, whereas in the third one was only 20% (Martín et al., 2013). At the end of the second growing season there was a 100% cover in the third cell. The macrophytes of the first cells were harvested at the end of 2009 (and the intermediate cell of fp in September 2010). After harvesting, emergent plants did not fully recover, because of the pressure from herbivorous waterfowl (mainly *Porphyrio porphyrio*). Some cells were never harvested, but the predation pressure also affected them (Martín et al., 2013).

Since restoration efforts are sometimes based on the establishment of founder colonies of macrophytes to give rise to submerged vegetation meadows that contribute to the maintenance of water in good condition (Smart & Dick, 1999), in 2008, the managers planted in both lagoons several species of submerged macrophytes that were typical of the area (*Myriophyllum spicatum, Ceratophyllum demersum, Potamogeton pectinatus, P. nodosus, P. crispus, Zannichellia peltata*, and *Ranunculus peltatus*) in order to prevent the phytoplankton blooms that would most likely result from high nutrient concentrations, and to simultaneously accelerate vegetation recovery. But the vegetation cover disappeared after the second year. Moreover, 2 singular events in the hydraulic management of the Educative and Reserve lagoons have to be highlighted: first, in the summer of 2011, the input gates to the lagoons were closed because the FWSCWs were dried for maintenance, causing the water level to drop significantly in the lagoons; second, in the summer of 2012, the lagoons were desiccated to reduce the fish populations and in an attempt to mimic the temporary flooding regime, because drying after wetting promotes the loss of dormancy in sediment seeds and increases germination of certain species of submerged vegetation.

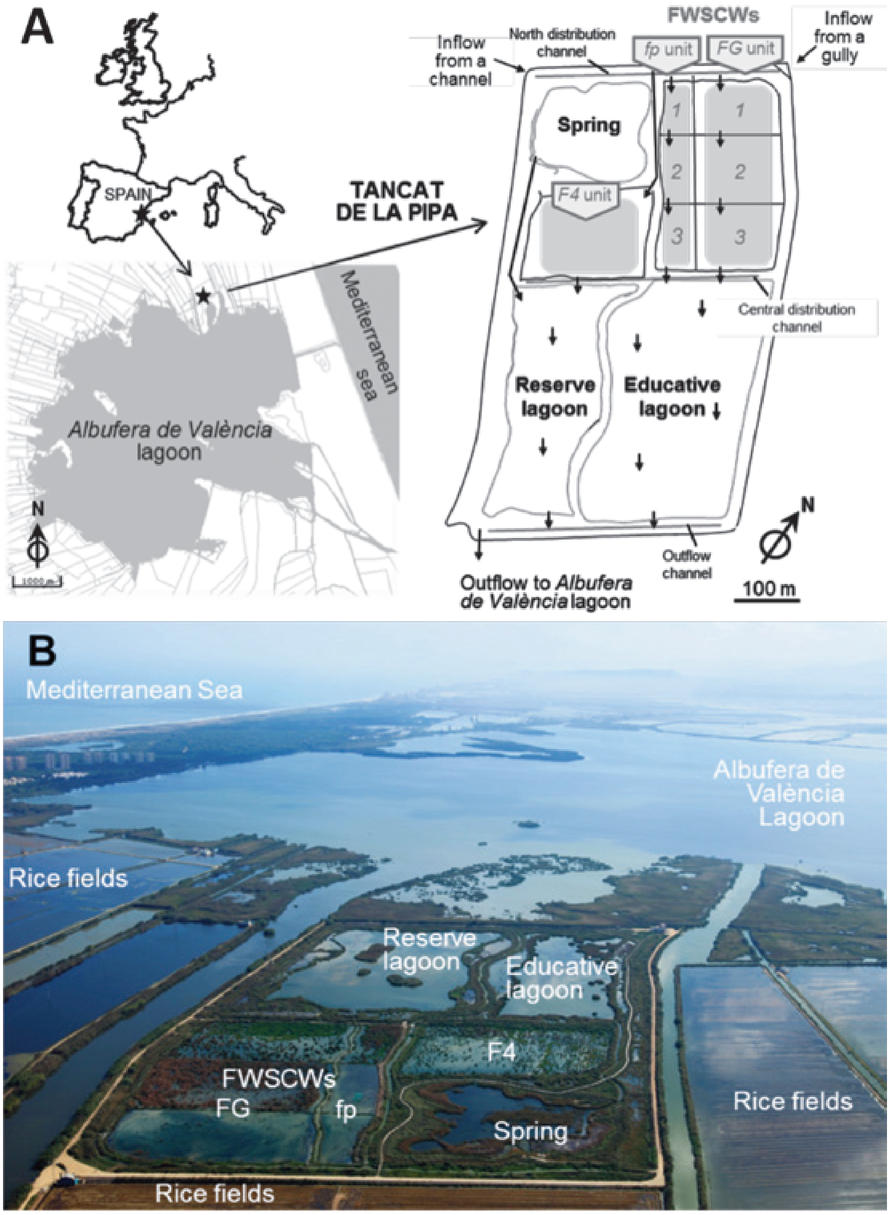

Figure 1: A: Location of Tancat de la Pipa within Albufera de València Natural Park, and design of the remediation system. B: Aerial view of Tancat de la Pipa with all the new aquatic systems (Photo: Confederació Hidrogràfica del Xúquer).

The springs, locally called “ullals”, were formerly abundant in the AVNP (Roselló i Verger, 1995), and most of them fed the AV lagoon with freshwater; however, several decades ago they deteriorated, due to desiccation and pollution. The creation of the Tancat de la Pipa spring provided an opportunity to investigate the influence of underground inputs on the system, to have a place that provides local submerged vegetation for restoration, and to evaluate the ecological role of submerged macrophytes in the trophic status of this new ecosystem. The inflow was approximately 4 L·s^{-1}, but 1 year later it gradually started to decrease and stopped in January 2012. The artesian well was rebuilt in February, and the groundwater inflow was re-established. The managers initially planted some founder colonies of *M. spicatum*, but they did not develop successfully. Only charophytes were able to colonise and grow as a result of the germination of sediment bank propagules, and these were used as founder colonies when the Educative and Reserve lagoons were under revegetation. Unfortunately, the flow definitively stopped, and this fact, together with other facts, negatively affected the whole community of the spring (for more details, see Rodrigo et al., 2015).

Because the Tancat de la Pipa system is connected to the channels and gullies that discharge into the AV lagoon, the fish fauna is shared. It includes autochthonous species and many exotic species that were intentionally released for fishery activities prior to the area being declared a Natural Park (the exotic fish species carp, *Cyprinus carpio*; goldfish, *Carassius auratus*; pumpkinseed sunfish, *Lepomis gibbosus*; mosquitofish, *Gambusia holbrooki*). The introduced red swamp crayfish, *Procambarus clarkii*, is also very abundant in the area (Dies et al., 2003). In regard to herbivorous waterfowl, up to 8 species of Anatidae are found, the mallard, *Anas platyrhynchos* being the dominant. Among coots, the Eurasian coot, *Fulica atra*, is the most abundant (Vera & Giménez, 2011).

3. The free water-surface constructed wetlands: the role of plankton in eutrophication reduction

Input water quality to the whole Tancat de la Pipa system was clearly improved by the action of the FWSCWs: a 70% reduction in total phosphorus and total suspended solids and a reduction of nearly 80% in total nitrogen (see Martín et al., 2013) were observed. But what happened with the plankton?

3.1. Phytoplankton and zooplankton dynamics. Removal and production rates

The phytoplankton biomass distribution changed after crossing the FWSCWs (Fig. 2A; Calero et al., 2015). On average, Cryptophyceae and Bacillariophyceae dominated the microalgal assemblage at the inflow, whereas Euglenophyceae (*Euglena* spp., *Phacus* cf. *parvulus*, and *Trachelomonas volvocina*) became the greatest contributor at all outflows. Acting as consumers, they would represent an energy input to the plankton community from the microbial food web and a link between both nutrient flows (Jones, 2000). Euglenophyceae richness also increased through the FWSCWs: 5–9 more species appeared at the outflows. Overall, the number of phytoplankton species grew slightly after crossing the FWSCWs. Chlorophyceae was the most diverse group, with 75 species from a total of 191. All these changes in the taxonomical composition of phytoplankton assemblages caused variations in the autotrophy/mixotrophy ratio. The potential mixotrophical microalgae dominated (ratio below 1) during 78–83% of sampling dates at the outflows, 20% more than at the inflow to the system. Only 3 and 6 species of potentially toxic cyanobacteria were detected in FG and fp, respectively. These populations appeared at low concentrations, below the toxicity limit of 2 mm^3 L^{-1} established for the AV lagoon (Romo et al., 2013). The phytoplankton assemblages changed after passing through the FWSCWs during the majority of sampling dates, according to the analysis of similarity based on Pearson correlation coefficients (Calero et al., 2015).

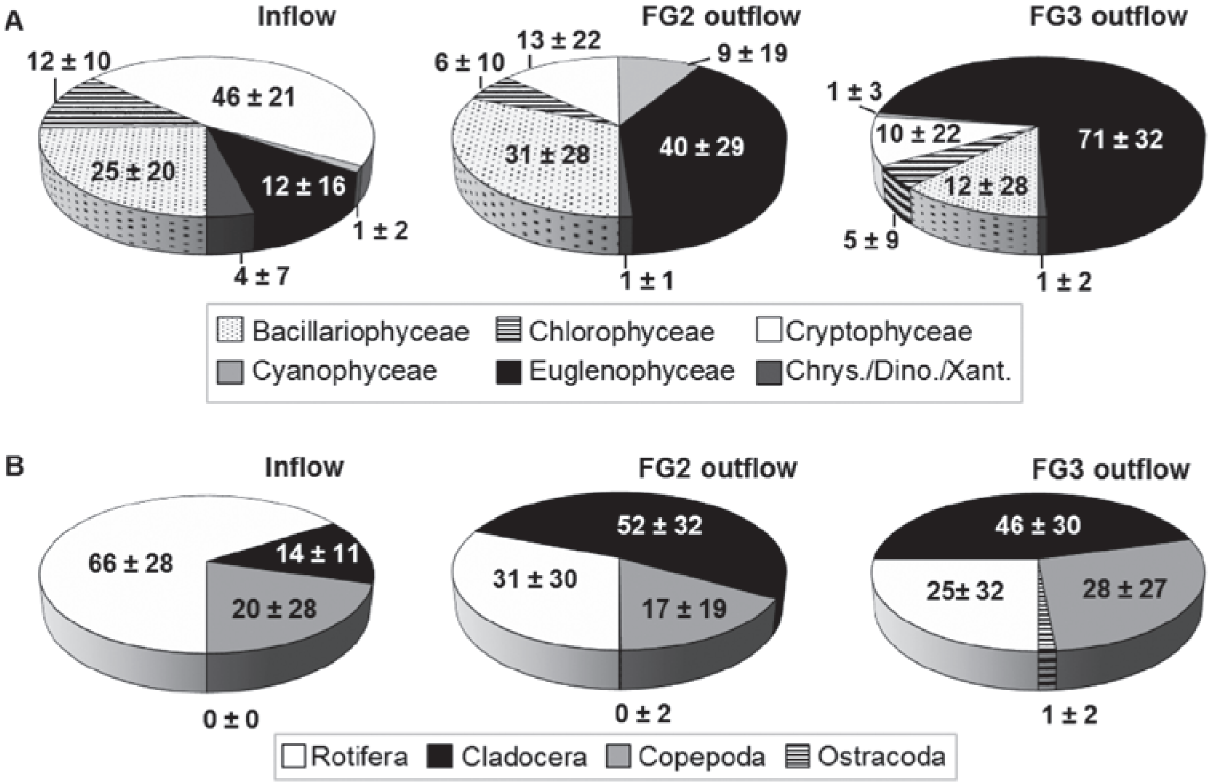

Figure 2: Distribution of biomass percentage between the different phytoplankton (A) and zooplankton groups (B) at the inflow of the FWSCWs and the outflows of 2 of the cells from FG (FG2 and FG3) over a year, from September 2011 to September 2012 (means and S.D. shown; n = 11); Chrys.: Chrysophyceae; Dino.: Dinophyceae; Xant.: Xantophyceae. Adapted from Calero et al., 2015.

The FWSCWs removed between 48% and 88% of biovolume when the different microalgal groups were considered separately, except for Euglenophyceae. As this group was produced within FWSCWs at 77–87% efficiency for most of the time, the total phytoplankton removal was lower than by groups (50%). From April 2009 to September 2011, the first 2 cells of both units removed a total cumulative mass of 1466 kg dry weight (DW) of phytoplankton (Fig. 3A) at a rate up to 151 mm·m^{-2}·d^{-1} during the first year of operation (Table 1). During the last year, however, the FG unit produced 613 kg DW of phytoplankton. In terms of chlorophyll *a* (hereafter, chl-*a*), the reduction was similar to that achieved by total microalgae biomass. All cells accounted for a reduction of 137 kg of chl-*a* during the 3.5 years of operation, although periods of reduction and production alternated (Fig. 3B), and the reduction took place at different rates (Table 1).

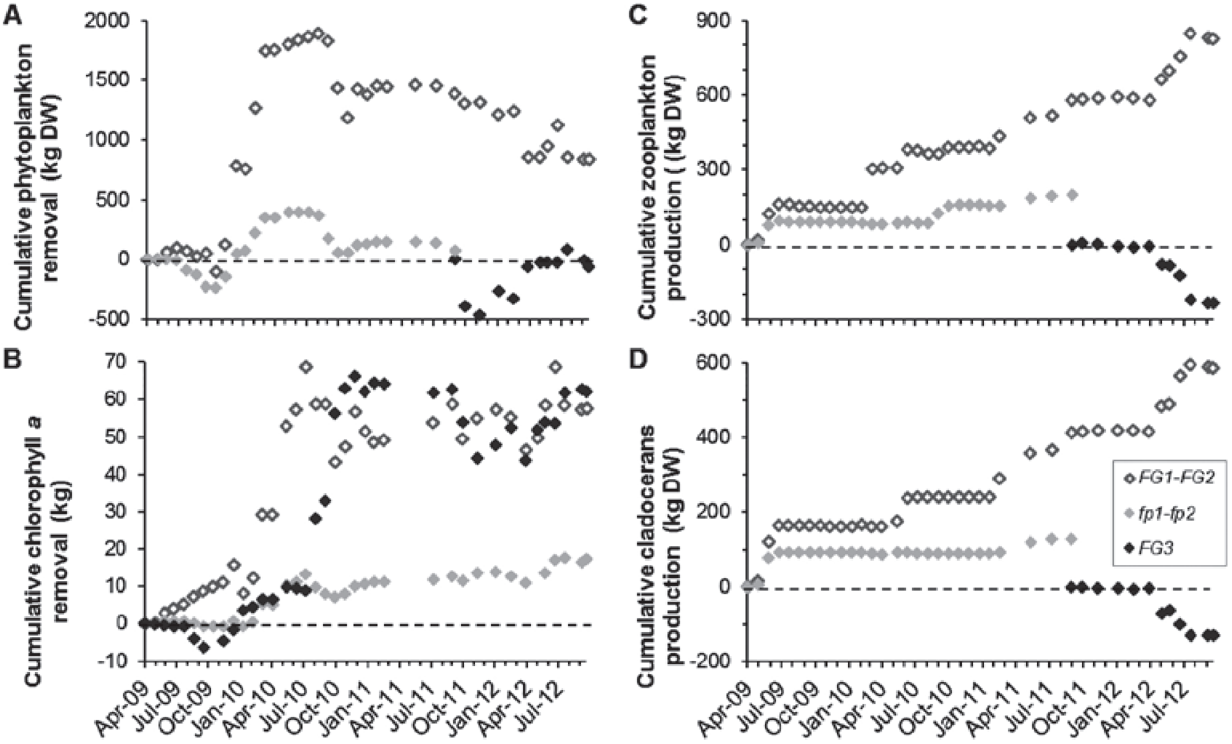

Figure 3: Cumulative mass removal of phytoplankton biomass (A) and chlorophyll *a* (B), and cumulative mass production of zooplankton (C) and, in particular, cladocerans (D) for the first 2 cells of both FWSCWs (FG1–FG2 and fp1–fp2) and for the last cell of the FG unit (FG3). When removal series decrease, this implies that the last added value is of opposite sign, then net production occurs. When production series decrease, this implies than the last added value was of opposite sign, then net loss occurs. Adapted from Calero et al., 2015.

	Removal rate						Production rate					
	Chlorophyll *a*			**Total phytoplankton**			**Total zooplankton**			**Cladocerans**		
Cell	1st y	2nd y	3rd y	1st y	2nd y	3rd y	1st y	2nd y	3rd y	1st y	2nd y	3rd y
FG1-FG2	2.5	1.8	-0.1	151.4	-25.7	-46.7	26.5	14.4	21.1	13.8	14.4	14.7
FG3	1.0	9.1	0.0	n.d.	n.d.	-10.0	n.d.	n.d.	-36.6	n.d.	n.d.	-20.2
fp1-fp2	0.7	0.8	0.5	44.6	19.1	n.d.	26.4	27.5	n.d.	27.6	5.9	n.d.

Table 1: Removal rates (mg m^{-2} d^{-1}) for chlorophyll *a* and total phytoplankton biomass, and production rates (mg m^{-2} d^{-1}) for total zooplankton and cladocerans, in each cell of the FWSCWs. The first year rates (1st y) refer to data from April 2009 to April 2010; the second year rates (2nd y), to data from April 2010 to April 2011; and the third year rates (3rd y), to data from September 2011 to September 2012.

The biomass distribution of zooplankton changed seasonally: rotifers dominated in summer, copepods in winter, and cladocerans appeared during spring, vanishing in the coldest and warmest periods. This seasonal replacement between rotifers and copepods is typical for Mediterranean wetlands (Rojo & Rodrigo, 2010), interrupted by the spring bloom of cladocerans (Gyllström & Hansson, 2004). As the nearby rice fields have the appropriate conditions to favour the hatching of cladocerans' diapausing eggs (Rodrigues et al., 2011), some cladocerans were carried to the FWSCWs inflow when, from January to March, the rice farmers released the excess irrigation water into the gully. The biomass distribution also changed after water had passed through FWSCWs: rotifers dominated at the inflow to the system, whereas cladocerans dominated at all outflows (Fig. 2B). During the last year, rotifer percentage dropped from 66% of total zooplankton biomass at the inflow to 25% at the FG outflow, while the percentage of cladocerans increased from 14% to 46%. Cladocerans reached 98% of total zooplankton biomass within the FWSCWs in spring. They were produced internally, because the calm and shallow waters, with emergent plants where diapausing eggs can be attached to, stimulated the production of cladocerans (Gyllström & Hansson, 2004) tenfold faster than in the subsequent lagoons, which had emergent vegetation only on the shores (Rodrigo et al., 2013a). The FWSCWs also promoted a higher cladoceran richness (up to 6 more species were identified at the outflows). The most abundant species were *Alona rectangula, Moina micrura*, and *Daphnia magna*. The most diverse group was the rotifers, with *Brachionus angularis* and *Synchaeta oblonga* dominating in density; the most abundant copepods were cyclopoids. Comparing biomass distribution with Pearson correlation coefficients revealed that the zooplankton assemblages differed between inflows and outflows on most of the sampling dates (Calero et al., 2015). After crossing the FWSCWs, water contained 50–65% more zooplankton biomass during 25–64% of the time. The highest production efficiencies (85–100%) were observed in ostracods in 33–42% of the sampling dates; cladocerans were produced seasonally (in 42–61% of the sampling dates) with an efficiency of 55–89%. From April 2009 to September 2011, the first 2 cells of both units produced a total cumulative mass of 780 kg DW of zooplankton (Fig. 3C) at rates around 20 $mg \cdot m^{-2} \cdot d^{-1}$ (Table 1). During the last year, the production rate for the first 2 cells of the FG unit remained nearly stable, at 246 kg DW (Fig. 3C). The third cell, however, produced 234 kg DW. Around 70% of the produced zooplankton mass corresponded to cladocerans (Fig. 3D). The most abundant cladocerans species were herbivores of different sizes (from 0.2 to 5 mm of length), with a wide filtering capacity. Different sizes of zooplankton imply a high variety of predators and so a wider grazing spectrum over phytoplankton (Sommer & Sommer, 2006). The result was that the water released in the Educative and Reserve lagoons was dominated by cladocerans, small autotrophic algae, and large mixotrophic algae such as Euglenophyceae, which can also consume bacteria and organic matter.

3.2. Concluding remarks

The plankton composition of the inflow lotic waters to FWSCWs, with weak top–down control, shifted towards a community with high efficiency in resource use and complex trophic relationships, typical of lentic shallow systems. The observed negative correlation between cladocerans and phytoplankton within the FWSCWs might indicate a top–down control over microalgae, besides the bottom–up control shown by the positive correlation detected between water nutrients and phytoplankton. Thus, both nutrients and cladocerans seem to have affected phytoplankton in the outflows, controlling its biomass and improving the quality of the water discharged to the small lagoons. Moreover, the production of ostracods within the FWSCWs has to be highlighted, particularly because this group has experienced an important loss of biodiversity in western Mediterranean wetlands (Poquet et al., 2008) and also in the AV lagoon, due to eutrophication and pollution. Habitats such as constructed wetlands contribute to the recuperation of this group of zooplankton and benthic organisms.

Total phytoplankton biomass and chl-*a* decreased with good efficiency during the study period, especially in the first year. The yearly difference may have been mainly caused by variations in the presence of vegetation, especially in the first 2 cells of fp and in the first cell of FG (Martín et al., 2013; Vymazal, 2013). The lack of emergent plants, which promoted higher solar radiation to the water and higher wind exposure, would have benefited phytoplankton also due to a lack of competition, with the result of producing microalgae internally and lowering the removal efficiency of the first cells of the FWSCWs. According to the areal removal rate constants, the last cell of FG unit, which was never harvested, removed phytoplankton chl-*a* at the highest average rate. The release of water poor in filamentous cyanobacteria, rich in small algae, and with high zooplankton biomass, mainly cladocerans, produced within the FWSCWs and released to the small lagoons is positively relevant for the AV lagoon, particularly in the critical spring periods.

4. The 2 small lagoons: the role of plankton and submerged vegetation in eutrophication reduction

The average mass removal efficiencies of the FWSCWs were as high as 65–75% for water quality parameters such as total phosphorus and total suspended solids (Martín et al., 2013). In spite of this, the final nutrient concentrations in the FWSCWs outflows were still not as low as desired, because of the large amounts of nutrients in the inflows to the Tancat de la Pipa system. Thus, the Educative and Reserve lagoons provided a suitable scenario for measuring the cooperative role of these small lagoons in nutrient retention, and simultaneous reduction of phytoplankton biomass, within the whole system. Additionally, they offered an opportunity to create small surfaces of permanent water within the AVNP to recover and harbour submerged macrophytes communities.

4.1. Phytoplankton and zooplankton dynamics. Removal and production rates

The phytoplankton dynamics alternated between periods of high microalgal production (corresponding to more than 100 µg chl-*a*·L^{-1} and 100 $mm^3 \cdot L^{-1}$ of biovolume; Fig. 4A, B, D, and E) and clear-water phases in both lagoons (1–3 µg chl-*a*·L^{-1} and 0.04–less than 1 $mm^3 \cdot L^{-1}$). In the summer, the high nutrient concentrations and warm temperatures stimulated phytoplankton growth within the lagoons. In the spring, the microalgal biomass was strongly reduced by the grazing effect of the zooplankton, particularly the large-bodied cladocerans. After the first desiccation of the lagoons, the algal biomass increased sharply. The release of nutrients (particularly TP) from the sediment after flooding, as was observed in other wetlands during intermittent dry periods (Sánchez-Carrillo & Angeler, 2010), enhanced the algal biomass. Cyanobacteria were dominant over the summer of 2009, representing more than 50% of the total biovolume, but decreased with time. Genera and species of potentially toxic Cyanobacteria (*Anabaena* sp., *Aphanizomenon* sp., *Cylindrospermopsis raciborskii, Microcystis aeruginosa, M. wesenbergii, Oscillatoria* sp., *Planktothrix agardhii,* and *Planktothrix* sp.) were detected at low concentrations (0.1–0.8 $mm^3 \cdot L^{-1}$) in both lagoons. Later, Cryptophyceae such as *Cryptomonas erosa* and Euglenophyceae (*Euglena* spp.) were primarily dominant. The autotrophic/mixotrophic phytoplankton index was below 1 for most of the study. The values were mainly due to the dominance of Euglenophyceae. As described above, inflow waters were already rich in mixotrophic organisms whose growth was propitiated in the FWSCWs.

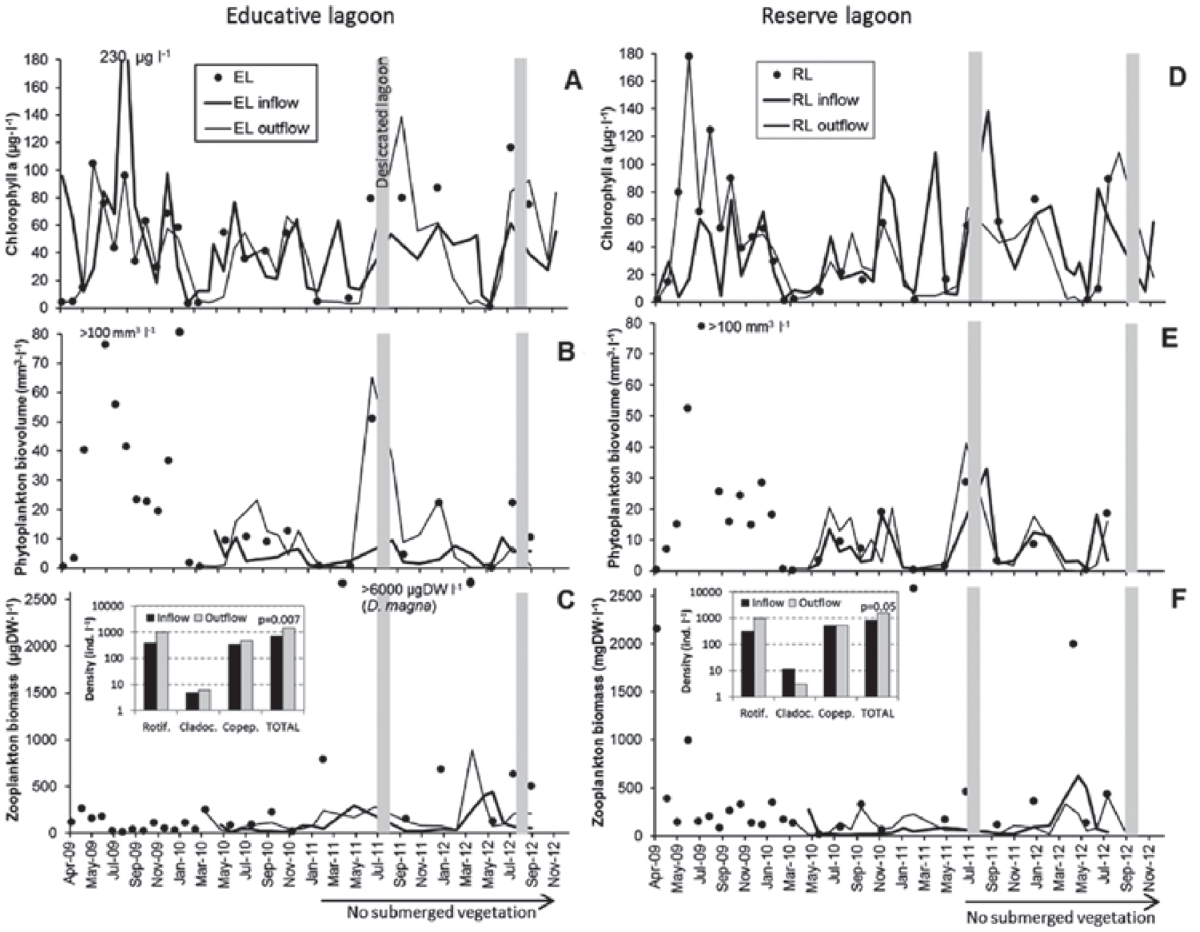

Figure 4: Dynamics of chlorophyll *a*, phytoplankton biovolume, and zooplankton biomass in the Educative (left) and Reserve lagoon (right) (within the lagoon and in the inflow and outflow); the top-left-hand graph in C and F shows the mean density of each zooplanktonic group and the total zooplankton for the inflow and outflow; the ANOVA test result (probability) is shown for the total zooplankton. Grey vertical bars indicate periods when both lagoons were desiccated. Adapted from Rodrigo et al., 2013b.

There was an overall increase in the phytoplankton richness in the outflows, particularly in the Educative lagoon (Bacillariophyceae represented the greatest increase, 45%). The taxonomic composition of the phytoplankton assemblages shifted after passing through the lagoons only during some periods (Rodrigo et al., 2013b). During the first few years, these similar and different periods alternated; however, from the end of 2011 onwards, the phytoplankton assemblage structures were completely transformed within the lagoons for 75% of the dates.

The total phytoplankton biovolume was only reduced in the outflows relative to the inflows in approximately 40% of the samples, in which the decrease in the phytoplankton biomass was as high as 77% and 66% in the Educative and Reserve lagoons, respectively. The biovolume of all of the taxonomic groups was reduced by a similar magnitude. There was a high phytoplankton removal efficiency (in terms of chl-*a*) of 50% in the first year of operation in the Educative lagoon; however, there was a negative phytoplankton removal efficiency in the Reserve lagoon. These efficiencies inverted over time, such that the efficiency was higher for the Reserve lagoon (22–42%) than for the Educative lagoon (1–8%). The final mean removal rate was 0.25–0.42 mg chl-$a \cdot m^{-2} \cdot d^{-1}$. At the end of the study period, the cumulative removal was 45 and 21 kg of chl-*a* for the Reserve and Educative lagoons, respectively (Fig. 5A).

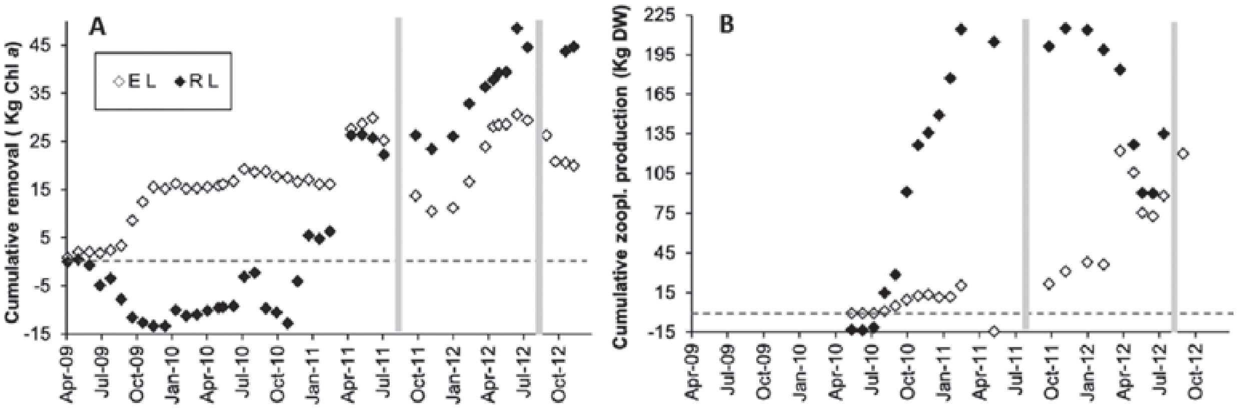

Figure 5: Cumulative mass removal of chlorophyll *a* (A) and cumulative mass production of zooplankton (B) in the Educative (ER) and Reserve lagoon (RL); the vertical grey bars indicate dry periods. Adapted from Rodrigo et al., 2013b.

As in the FWSCWs, the zooplankton biomass dynamics reflected the typical seasonal substitution of taxonomic groups in this type of Mediterranean waterbodies. The dominant cladocerans were *Simocephalus vetulus* and *Daphnia magna*; the dominant rotifers were *Brachionus angularis* and *Synchaeta oblonga*; and the dominant copepods were *Acanthocyclops americanus* and *Microcyclops rubellus*. A considerably higher zooplankton biomass was measured within the lagoons than in the inflows (Fig. 4C, F). High zooplankton biomass peaks (over 6000 µg DW·L^{-1}) were observed at some times, coinciding with low phytoplankton biovolume (0.04–0.6 mm^{3}·L^{-1}). The zooplankton richness also increased in the outflows, particularly in the Educative lagoon. Cladocerans were the taxonomic group that was primarily exported (90–96% of biomass increased in the outflow) for 50% of the samples, particularly in the spring. The mean rate of zooplankton mass production, in terms of the balance between the inflows and the outflows, over the study period was approximately 2 mg DW·m^{-2}·d^{-1} for both lagoons. The maximum production in the Reserve lagoon occurred in the autumn and winter of 2010, at 13 mg DW·m^{-2}·d^{-1}. From the end of 2011 to the beginning of 2012, small changes were observed in the dynamics of the cumulative zooplankton production in the Educative lagoon (Fig. 5B), where 36 kg DW of zooplankton were released to the AV lagoon. From this period to the end of 2012, the zooplankton cumulative production tripled and 120 kg were finally released to the AV lagoon. In contrast, the cumulative zooplankton production exhibited different dynamics in the Reserve lagoon (Fig. 5B). The production fitted a unimodal pattern: the zooplankton production increased until more than 200 kg of zooplankton were released cumulatively in February 2011; a stable balance was maintained in the zooplankton biomass among the inflows and the outflows until 1 year later, when the cumulative zooplankton production decreased to approximately 100 kg, the same value as the final production values in the Educative lagoon. In both lagoons, the cumulative zooplankton production was inversely correlated with the cumulative phytoplankton removal dynamics. During the period in which the lagoons were partially covered by submerged vegetation (see below), there was a much higher zooplankton biomass in the vegetated areas for both lagoons. This is typical for shallow lakes, where large-bodied zooplankton can seek refuge from predators among the macrophytes (Lauridsen & Lodge, 1996). However, following the disappearance of the vegetation, the lagoons continued to produce and export zooplankton. *Daphnia magna* specimens from Mediterranean shallow lakes prefer to hide near the sediment when exposed to predation risk (Tavsanoglu et al., 2012). This strategy may have been adopted by the large cladocerans in the Educative and Reserve lagoons in the absence of vegetation, resulting in the large populations observed in 2011 and 2012. The absence of vegetation left all of the sediment surfaces exposed; large carps then disturbed the sediment (Rodrigo et al., 2013a), resulting in large hatching rates and the subsequently large populations of cladocerans observed.

4.2. Submerged macrophytes dynamics. Determinants factors for a successful revegetation

We tried to elucidate the factors that caused the total disappearance and prevented the regeneration of submerged vegetation cover in both lagoons. For this purpose, we used different approaches: characterization of the seed sediment bank, monitoring of the submerged macrophytes dynamics, and a field experiment with exclosures (Rodrigo et al., 2013a).

4.2.1. Seed bank. Sediment potential previous to plantation

Most plant seeds in the sediment cores taken from each lagoon in 2008, prior to the planting of macrophytes by the managers, corresponded to charophyte fructifications; no angiosperm seeds were found in considerable numbers. Eleven taxa of charophyte remains were identified: *Chara aspera, C. baltica, C. braunii, C. globularis, C. hispida, C. vulgaris, C.* sp., *Nitella hyalina, Lamprothamnium papulosum, Tolypella glomerata,* and *T. prolifera*. The fructifications of *C. hispida* and *T. glomerata* were the most abundant in the Educative lagoon, and those of *L. papulosum* and *N. hyalina*, in the Reserve lagoon. The work to transform the former rice field in the current Reserve Area (construction of lagoon basins using machinery) moved upward the deep sediments corresponding to the saline period of the AV lagoon (Rodrigo et al., 2010). This process accounts for the finding in the surficial sediments of fructifications formed by species that are characteristic of fluctuating and high saline conditions, such as *L. papulosum* (Soulié-Märsche, 1998; Alonso-Guillén, 2011; Rodrigo & Alonso-Guillén, 2013). The highest proportion of apparently viable fructifications was that of *T. glomerata*. The apparent oospore viability was verified based on the germination of several species in both lagoons (4 of the 6 species—not including species from saline environment—whose fructifications could potentially germinate in the environmental conditions of the present lagoons), even though the charophytes did not form wide meadows.

4.2.2. Submerged macrophyte dynamics after plantation

Of the 7 planted species by the managers, *Myriophyllum spicatum* was the dominant macrophyte (Figs. 6–7), and it covered almost the entire free water surface in both lagoons. When nutrient levels are high in an aquatic ecosystem, a submerged diverse plant community is usually replaced by a submerged monoculture of a fast-growing species (van Zuidam et al., 2012). The dominance of *M. spicatum* over the other planted species was not surprising, because this species grows well in shallow eutrophic waters such as those found in the lagoons (Madsen, 1998). *M. spicatum* showed an annual cycle pattern; it reached its highest biomass and flowered during the warm season, became less abundant during the winter, and reappeared in the spring. The mean biomass during the warm seasons was higher for 2009 (Fig. 7). In the Educative lagoon, the estimated total biomass decreased in the summer of 2010 as a result of the lower biomass per unit surface area and the smaller cover, which was due primarily to the increased helophyte expansion. In the Reserve lagoon, the total biomass increased more than 1 order of magnitude from the summer of 2009 to the summer of 2010, primarily because of the increased coverage. *M. spicatum* never recovered after the winter of 2010–2011 in the Educative lagoon, and remained only until August 2011 in the Reserve lagoon, with low biomass and coverage. Even the desiccation period imposed by the managers during August 2011 did not promote the natural recruitment of vegetation during the spring of 2012 in either lagoon.

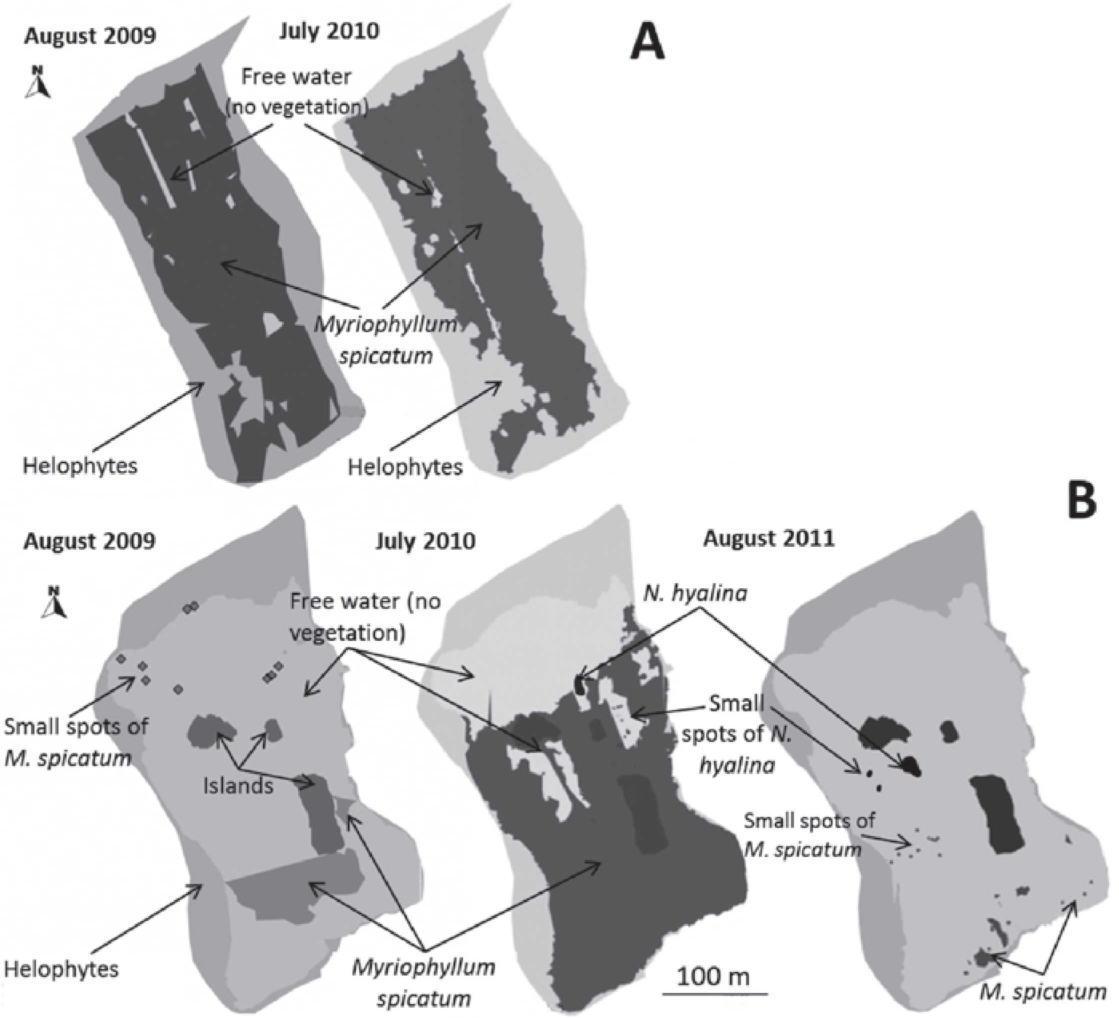

Figure 6: Maps of vegetation cover in the Educative (A) and Reserve (B) lagoons in the summers of 2009–2011. No submerged vegetation was found in the Educative lagoon in August 2011. Adapted from Rodrigo et al., 2013a.

Zannichellia peltata, Potamogeton pectinatus, P. crispus, Ruppia maritima, C. hispida, and *T. glomerata* in the Educative lagoon and *Z. peltata, P. pectinatus, N. hyalina*, and *C. vulgaris* in the Reserve lagoon were detected sporadically. *Cladophora* sp. and *Enteromorpha* sp. were present during the warm periods in both lagoons.

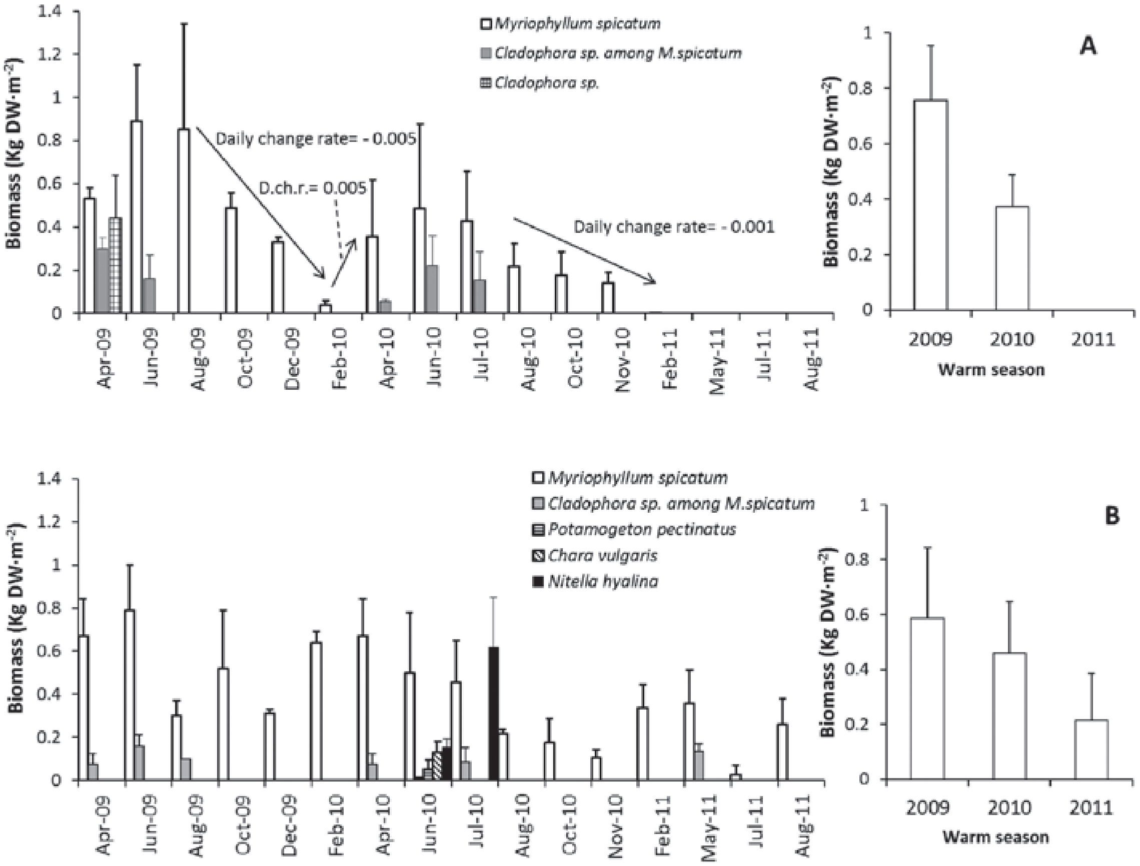

Figure 7: Left: Time course of macrophyte biomass in the Educative (A) and Reserve (B) lagoons. The vertical bars indicate standard deviation of the data from 3 sampling stations. Right: Means of *M. spicatum* biomass during the warm periods (from April–May 2009 to August 2011). The vertical bars indicate standard deviation from the monthly data. Adapted from Rodrigo et al., 2013a.

4.2.3. Seed bank. Sediment potential after more than 2 years of vegetation growth

Seeds of most of the angiosperm species originally planted by the managers were found in the sediments of both lagoons taken after almost 3 years of vegetation development. However, the average seed density was low. Some seeds were found in a very small number of samples, confirming that seed banks typically exhibit clustered spatial distributions. The percentage of sediment samples containing *M. spicatum* seeds was 37% higher in the Educative lagoon than in the Reserve lagoon, and the mean density was also statistically higher in the Educative lagoon; this finding can be explained by the wider spatial distribution of this macrophyte in the smaller lagoon. *Potamogeton* seed density was slightly higher than that of *M. spicatum.* Seeds of *R. maritima* were scarce in both lagoons. *Vallisneria spiralis* (not observed previously in the lagoons) seeds were also detected. During germination trials in the laboratory, the first germlings were observed 10 days after flooding the sediments. Germlings of charophytes (primarily *C. vulgaris*), *M. spicatum* (very low numbers), and *V. spiralis* were detected. The low germination rates obtained during the trials were consistent with the low numbers of seeds found in the sediments of both lagoons. Thus, the potential of the sediments that had previously supported vegetation to serve as a source of vegetation recruitment appeared to be very low.

4.2.4. Field experiment. Unravelling factors that affect revegetation

The factors that negatively affect submerged vegetation may include negative biotic relationships such as those related to the presence of fish and crayfish, waterfowl grazing, phytoplankton, and epiphytic development that causes shading, and abiotic factors, such as water nutrient concentration. The synergistic negative combination of all of these factors may be a determinant of the continuity of submerged vegetation in aquatic ecosystems under restoration. Thus, we performed a field experiment in March 2012 to unravel the major negative factors affecting macrophyte replanting. Three different types (treatments) of 1 m^2 exclosures were set up and planted with macrophyte cultures that formed 3 different assemblages: *Chara hispida* alone; a mixture of *C. vulgaris, C. baltica*, and *Nitella hyalina*; and a mixture of higher plants (*M. spicatum, C. demersum*, and *Potamogeton pectinatus*). The "Open" type of exclosure permitted the entrance of fish, crayfish, and birds. The "Lateral" exclosure prevented the entry of fish. The "Closed" exclosure also prevented bird grazing (Rodrigo et al., 2013a).

Most plants and charophytes cultures disappeared in the "Open" and "Lateral" exclosures 9 weeks after plantation. However, in the "Closed" exclosures almost 100% of the plant cultures were present and had grown and developed a dense meadow for all 3 of the communities 3 weeks after plantation. The percentage of individual plant culture survival decreased in "Mixed charophytes" assemblages, primarily because of the disappearance of *N. hyalina* specimens; only *C. vulgaris* individuals remained in the "Closed" exclosures after 6 and 9 weeks. The percentage of macrophyte coverage for both the "Mixed charophytes" and "Higher plants" assemblages was significantly higher in the "Closed" than in the "Lateral" exclosures (Fig. 8). In the "Closed" exclosures, the top net was removed after 9 weeks of plant growth in 2 out of 3 replicates for each assemblage to allow birds (and presumably crayfish) to enter. Later, almost 100% of the vegetation had disappeared in the uncovered exclosures, with only a few plant remains found very close to the lateral nets. The macrophyte communities remained intact in the exclosures in which the top net was not removed.

The abundant growth of epiphytes on plants and charophytes and the development of filamentous algae were visually evident in both lagoons, particularly in the "Lateral" and "Closed" exclosures, because the nets facilitated the retention of such organisms. Reductions in light availability resulting from periphyton growth were as high as 45%. The mean percentage of light reduction was 36 ± 6% for the lagoons combined, and the differences between them were not statistically significant. The reduction measured here (through the incubation of acetate squares, see Rodrigo et al., 2013a) is not exactly the same as that of the plants, because they have mechanisms that harm epiphytes through allelopathic interactions (Berger & Schagerl, 2004; Rojo et al., 2013). However, there is also evidence for lower sensitivity of epiphytic algae towards allelochemicals (Hilt, 2006).

The results from the "Closed" exclosures demonstrated that all of the assayed species of higher plants can grow under the chemical conditions of the water in the Educative lagoon, even when competing with the other species (in mixed assemblage treatments) and when covered by large amounts of periphyton. Nutrient contents in both lagoons were high and displayed sharp fluctuations; however, on most occasions, they were below the thresholds that produce the disappearance of submerged vegetation in shallow temperate lakes (1.2–2.0 mg $TN \cdot L^{-1}$ and 0.13–0.20 mg $TP \cdot L^{-1}$; González-Sagrario et al., 2005). As expected, charophytes were found to be more sensitive than plants to high nutrient concentrations in the lagoons, because charophytes have been described to disappear first in cases of an increasing trophic level (Blindow, 1992; van den Berg et al., 1998). This property presumably explains why they (specifically *C. hispida*) were lost even from the “Closed” exclosures in the Reserve lagoon and did not proliferate to form wide meadows in the lagoons. Birds used primarily the “Closed” exclosures as resting areas by alighting on the top net; while the birds rested, their defecations dropped into the exclosures and presumably resulted in locally increased nutrient concentrations. The other limnological variables examined during the spring, which is a crucial period for vegetation development, did not show major differences, particularly during the last 3 years of the study. Water level fluctuations were not sufficiently different among years to negatively affect submerged vegetation. A clear-water phase took place when the exclosures were set up, but, in spite of the high water transparency during this period, macrophytes did not proliferate spontaneously except for those planted by us. There was no detectable germination from the seed bank in the lagoons and no progress of the macrophyte cultures that were planted without protection from fish or crayfish, waterfowl, or both.

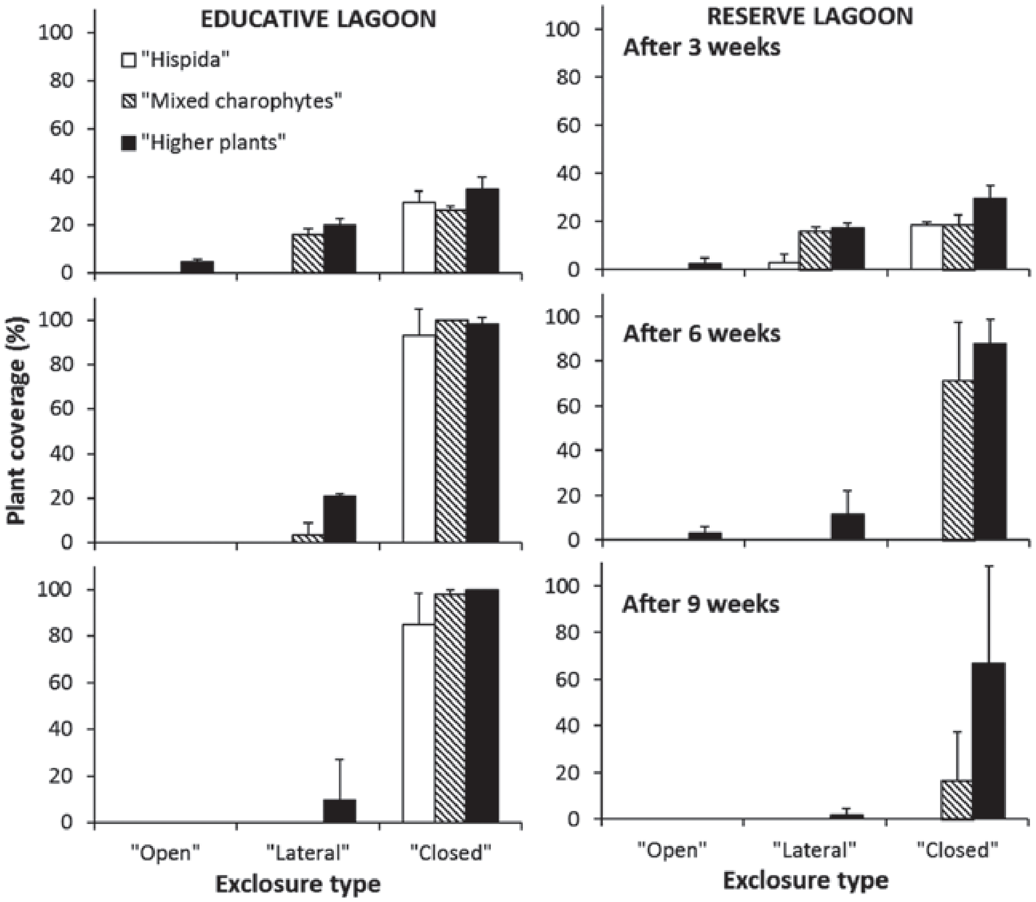

Figure 8: Success of revegetation indicated as a percentage of coverage by plants in the exclosures in the Educative (left) and Reserve (right) lagoons. The vertical bars indicate standard deviation of 3 exclosure results per treatment. Adapted from Rodrigo et al., 2013a.

Submerged vegetation in both lagoons was able to support the bird grazing pressure for 2 complete annual cycles but not for a third cycle. Waterfowl density was higher in both lagoons in the early spring of 2010 than in 2011 (Rodrigo et al., 2013b). Macrophytes have been reported to produce new growth rapidly after partial reduction of biomass, thereby compensating for the loss caused by bird grazing (Matuszak et al., 2012). However, intensive grazing pressure from relatively high bird densities can lead to a complete removal of macrophytes that cannot be easily compensated (Torn et al., 2010). On the other hand, low numbers of waterfowl may also reduce submerged vegetation when there is relatively low vegetation density (Marklund et al., 2002). Because of the shallowness of the Educative and Reserve lagoons, both ducks and coots can easily forage on submerged vegetation, diving (with low energy expenditure) to find food or eating at the surface when the vegetation easily reaches the water surface. The vegetation damage caused by waterfowl is greater than that of the foraging activity per se because birds uproot more vegetation than they actually consume (Matuszak et al., 2012). We observed that birds could take heavy parts of plants in that we found several peat pots outside of the “Lateral” exclosures to which only birds had access. In spite of the absence of submerged vegetation in both lagoons since 2011, coots and particularly ducks continued to visit the lagoons. Therefore, coots’ search for food in the sediments contributed to sediment disturbance, and also had a negative effect on the recruitment of vegetation.

Factors other than changes in waterfowl grazing pressure that affect submerged vegetation, such as fish densities, may have undergone interannual variation. The relationship between the intensity of fish disturbance and plant density is most likely not smooth. Critical breakpoints or thresholds for plant density presumably occur at certain intensities of fish disturbance (Dugdale et al., 2006). A higher plant density may be sustainable in the presence of fish disturbance, but for a lower plant density, the equivalent fish disturbance may cause a substantial reduction in biomass. In both lagoons, because of the design of water circulation in Tancat de la Pipa, small fish can easily enter the lagoons, but it is almost impossible for larger fish to escape through the water pump that extracts water to the AV lagoon. Fish populations were therefore composed of very large individuals (particularly carp, which may weigh more than 2 kg; Lasalle M., pers. comm.) that cannot be consumed by natural predators such as herons, grebes, and cormorants. It is difficult to conclude from our field experiment whether the fish contributed to the elimination of macrophyte communities in the lagoons directly (e.g., grazing) or indirectly (e.g., by releasing nutrient-rich excrement or disturbing the sediments). Unfortunately, we do not have yearly quantitative data on fish biomass for comparison. However, we observed during our visits to the exclosures that the large carp swim so fast that they are able to cross the lagoons in a few seconds, disturbing large quantities of sediment. Such activity may cause the uprooting of germlings that would eventually germinate from the sediments and the deterioration of the plants in the culture pots. Invasive red swamp crayfish are another biotic agent that may damage macrophytes. It was not possible to evaluate crayfish populations during the study. However, we had evidence that they were able to enter the “Lateral” exclosures (possibly by climbing or drilling the sediment below the lateral net) because we found several live individuals and sheddings inside the exclosures during our visits.

4.3. Concluding remarks

The water quality was also improved significantly by the 2 small lagoons even though the input pollutant concentrations were not as high as those received by the FWSCWs, which made further reduction difficult. Overall, the 2 lagoons facilitated more than 30% mass removal of chl-*a* for the entire Tancat de la Pipa system, with both lagoons acting as a zooplankton production system, clearly involved in water clearance. The charophyte fructification sediment bank in both lagoons before plantation was quite dense; however, the conditions in the lagoons did not allow an extensive growth of charophytes. Natural submerged vegetation, particularly that in restored aquatic ecosystems, frequently undergoes large fluctuations in biomass and diversity (Hilt et al., 2010), and the causes of such variation are difficult to determine. In the Educative and Reserve lagoons, even when the initial founder plant colonies had no protection from biotic agents, they became established and self-sustaining and spread over most parts of the lagoons from 2008 to 2011. However, it seems that the increased grazing pressure and sediment disturbance performed by biotic factors mainly caused the disappearance of vegetation and prevented further revegetation.

5. What did we learn from this case study about management, restoration, and conservation of mediterranean lagoons?

- A system such as the Tancat de la Pipa is able to reduce eutrophication with a reasonably satisfactory efficiency in terms of nutrients. Physical, chemical, and biological processes, particularly regarding food web and plankton participation, were important to improve water quality across the system.

- The FWSCWs and the Educative and Reserve lagoons reduced microalgal biomass and exported potential heterotrophic phytoplankton and herbivorous zooplankton, particularly cladocerans (a key contributor to the clear-water phases of the AV lagoon). The FWSCWs exported 200 kg DW of zooplankton per year to the small lagoons, and these lagoons exported 60 kg DW of zooplankton per year to the AV lagoon. During the second year of operation, the Tancat de la Pipa outflow positively affected the AV area directly influenced by it: a 75% reduction of chlorophyll *a* concentration was determined in the AV lagoon waters in comparison to the first year; this fact increased water transparency and permitted submerged vegetation to appear and grow in the surroundings.

- Each lagoon developed unique characteristics, such as hydraulic features and submerged vegetation cover, and exhibited different stages of removal efficiencies of nutrients and phytoplankton and different stages of zooplankton production. However, the result of improving the water quality of the outflows and enhancing planktonic biodiversity was similar for both lagoons.

- The ecosystem services provided by the lagoons motivate us to highly recommend the configuration of this type of ecosystems as a supplementary action to FWSCWs in the management of eutrophicated waters on protected sites such as the AVNP. Some of the measures that could enhance the lagoon treatment effectiveness include improvement in the hydrodynamical conditions (prolonging mean water residence time, thereby improving nutrient retention efficiency), managing the emergent vegetation, and constructing specific structures in the lagoons (e.g., smaller islands than those in the Reserve lagoon).

- We unravelled the synergistic factors that triggered the disappearance of submerged macrophytes and their failure to become re-established in the small lagoons. High nutrient concentrations were not the key factor preventing macrophyte expansion and re-establishment in the lagoons, but the synergistic negative effects of both fish or crayfish and waterfowl on plants. More areas with permanent submerged vegetation in the AVNP during the critical periods of dried rice fields (spring) are required to decrease bird herbivory pressure on Tancat de la Pipa ecosystems. The eradication of exotic fish populations in the lagoons was impossible because of the high degree of connections with the main lagoon and the surrounding channels. However, fish populations should be reduced to a level that is compatible with macrophyte survival in the short term and should not be allowed to recover sufficiently to affect the survival and expansion of macrophyte transplants (set-up of nets at the inlet sites of the lagoons, continued net-based fishing, etc.). A reduction in nutrient concentrations in the inflows to the lagoons is desirable to prevent periphytic shading of submerged vegetation and phytoplankton growth. Macrophyte plantation to restore the lagoons is also necessary, because of the low potential to recover a diversity of vegetation in these systems from the sediment angiosperm propagule bank. The future development of submerged vegetation will contribute to the maintenance of longer clear-water phases and consequently to the increase in overall diversity.

- We highlight that experimental approaches, both in the laboratory and in the field, are also required for understanding the interactive processes, synchronised and synergistic most of the time, that affect the capability of these complex and vulnerable small aquatic ecosystems as natural sources of biological diversity.

- Finally, we encourage the construction of more systems like the Tancat de la Pipa in the AVNP to reduce the nutrient load on the main lagoon. More similar eutrophication remediation systems will enhance planktonic and macrophyte biodiversity, in particular, and promote biological development, in general.

Acknowledgements

This study was funded by the contracts of University of Valencia with TRAGSA under the directive of the Xúquer River Water Authorities and project CGL 2009 10292 of the Spanish Ministry of Economy and Competitiveness to MAR. We acknowledge the dedication of Javier Ferrer-Polo, Teodoro Estrela, Mamen Regidor, and Sara Jiménez (CHJ). We are also grateful for the collaboration of (in alphabetical order) Aruca Sebastian, Carlos Peña, Carmen Hernández, Fidel Rubio, Francesco Mazzei, Francisco Cortés, Jara García, Joan Miquel Benavent, José Luis Alonso-Guillén, Lourdes Ribera, Lucía Moreno, María Belenguer, Mario Giménez, Matthieu Lassalle, Miguel Martín, Núria Oliver, Pablo Vera, Sara Gargallo, and William Colom.

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Restoration and management of coastal lagoons in the Ebro Delta

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1. Human impacts, reference conditions, and ecological status

With a length of 910 km and a drainage area of 85 362 km^2, the Ebro River is one of the most important tributaries to the Mediterranean Sea (Figure 1). The Ebro River creates one of the largest deltas (320 km^2) in the north-western Mediterranean Basin. The largest area (65%) of the delta is dedicated to rice farming, and natural areas cover only about 80 km^2. These protected areas, which were declared Natural Park in 1983, include different aquatic ecosystems, such as coastal lagoons, salt marshes, and bays. Coastal lagoons are amongst the most important habitat types due to the ecosystem services they provide (shoreline protection, water quality improvement, fisheries resources, habitat and food for migratory and resident animals, and recreational areas), and the biodiversity they hold (Levin et al., 2001).

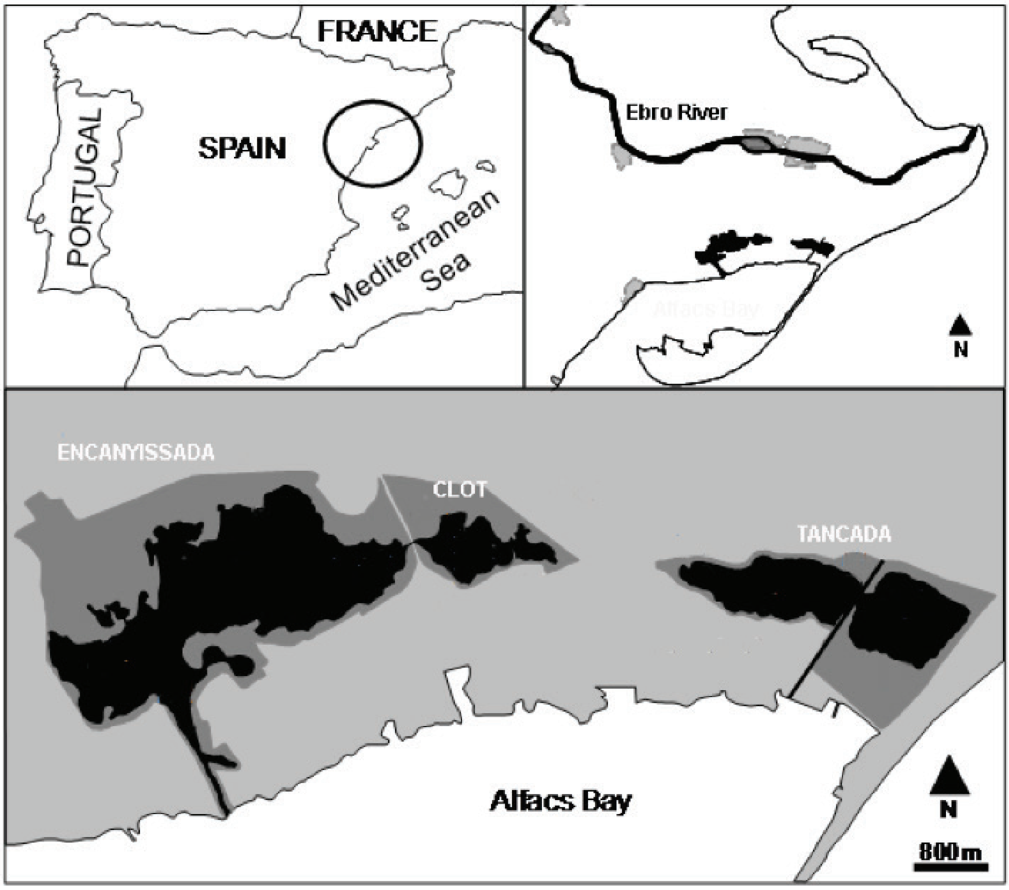

Figure 1. Location of Ebro Delta coastal lagoons (in black). Names are indicated for those that have been subjected to restoration projects.

Surrounded by vast extensions of rice fields, the Ebro Delta coastal lagoons have undergone intense human interference since the nineteenth century (Ibáñez & Caiola, 2016). Until late 1980s, most of the agricultural wastewater, rich in particulate organic matter, nutrients, and some chemical herbicides and pesticides (e.g., organochlorinated contaminants such as PCBs, DDTs, and HCB, now banned by law), was released into the lagoons from May to October (Comín, 1984; Comín et al., 1991). As a result, the emerged vegetation (mostly reed beds) expanded and the submerged vegetation declined by more than 80% in most of the lagoons. In addition, the lagoons' ecological functioning shifted to a phytoplankton-dominated primary production with high turbidity due to high chlorophyll concentration and resuspension of fine sediments during wind forcing events (Ferrer & Comín, 1982; Comín et al., 1990; 1991; Ibáñez et al., 2000). Fish populations and waterfowl abundance also declined, and target local fisheries and recreational activities were severely impacted (Forés, 1992; Ibáñez et al., 2000; Rodríguez-Climent et al., 2012).

In late 1980s, the regional government and Natural Park authorities implemented new hydrological infrastructures (pumping stations and drainage canals surrounding the lagoons) to establish a new water management scheme aimed at reducing, not eradicating, drainage water inputs from rice fields to the lagoons. However, reduced but significant freshwater inflows with better water quality have persisted through all these years from May to November. This present management scheme involves bringing in freshwater from the Ebro River with lower organic matter, nutrients, and agricultural chemicals to favour the development of macrophytes over phytoplankton (Comín et al., 1991) and with the final aim of restoring the habitat for protected species and gaming birds.

The ecological status, as defined by the Water Framework Directive, or WFD (European Commission, 2000), is an expression of the quality, structure, and functioning of aquatic ecosystems. This means that good water quality is not enough to ensure good ecological status. To measure the ecological status, the WFD established a set of indicators that are to be assessed in a homogenous way by all European Union member states. The common trait of the ecological quality elements (water quality, hydromorfology, and biological assemblages) is that their quantitative measure should represent the difference between the present status and reference conditions (i.e., conditions without human impacts). Before intensive human settlement in the past 2 centuries, the coastal lagoons from the Ebro Delta used to be saltwater systems (Benito et al., 2014). Unfortunately, scientific information on the biological communities under reference conditions is lacking and this fact makes difficult a sound assessment of their ecological status.

In the past 2 decades, the water quality of the lower Ebro River, estuary, and lagoons has improved due to the decreased nutrient loading and chemical pollutants (Ibáñez et al., 2012; Prado et al., 2014a). Regardless, however, the improvement of water quality, a good ecological status will not be achieved with the present water management scheme, as this is based on artificial freshwater inputs that favour certain species, causing an important deviation from the reference conditions. Current ecological quality assessment of Ebro Delta coastal lagoons carried out by the Catalan Water Agency following the WFD procedure show that their status is in most cases moderate or poor (Boix et al., 2010). Moreover, several studies showed that low salinities have favoured the presence of non-native species (Caiola & Sostoa, 2002; Franch et al., 2008; Rodríguez-Climent et al., 2013) and that marine species supporting local fisheries have not recovered (Rodríguez-Climent et al., 2012). Therefore, restoration criteria should take into account not only improving water quality, but also recovering the ecological processes in order to re-establish reference conditions and, thus, meet the EU WFD criteria of good ecological status.

2. Current management and ecological features

As a result of the current water management scheme, the Ebro Delta coastal lagoons are subjected to contrasting salinity regimes from May to November (3.6 to 11.6‰ in the Clot lagoon, 12.5 to 27.1‰ in the Encanyissada lagoon, and 18.6 to 28.1‰ in the Tancada lagoon; Prado et al., 2013a), but have more similar ranges (from 13‰ in the Clot to 28–31‰ in the Encanyissada and Tancada) during the rest of the year, with minimal freshwater inflows.

2.1. Submerged vegetation

According to vegetation surveys conducted between 1976 and 1977 (Curcó, 1994) *Potamogeton pectinatus* (optimal growth at salinities of ca. 5; Van Wijk et al., 1988) and to a lesser extent *Najas marina* (freshwater species; Agami & Waisel, 1985) were the dominant macrophyte species in the Encanyissada and Clot lagoons, and the largest part of the Tancada lagoon, indicative of significant agricultural freshwater inflows and eutrophic conditions (Grillas, 1990; Adams et al. 1992; Ibáñez et al. 2000). During the late ’80s, both *Ruppia cirrhosa* and *P. pectinatus* could be found in mixed and monospecific stands in the Tancada lagoon, particularly in the west basin (e.g., Menéndez & Comín, 1989), but no information is available from the other lagoons. Today, after the reduction of freshwater inputs and the improvement of water quality, *R. cirrhosa* (optimal growth in meso- to polyhaline waters from 12 to 30‰; Adams et al., 1992) is the dominant species in the Encanyissada lagoon (only mixed in low abundance with *P. pectinatus* in northern sites) and the only macrophyte found in the Tancada lagoon (see Figure 2a). In the Clot lagoon, lower salinities (ca. 3.6‰) have allowed the persistence of dominant populations of *P. pectinatus* interspersed with *R. cirrhosa* (capable of growing from 0 to 75‰; Adams & Bate, 1994) and mixed stands of *P. pectinatus* and *N. marina* in some reduced areas (Figure 2b).

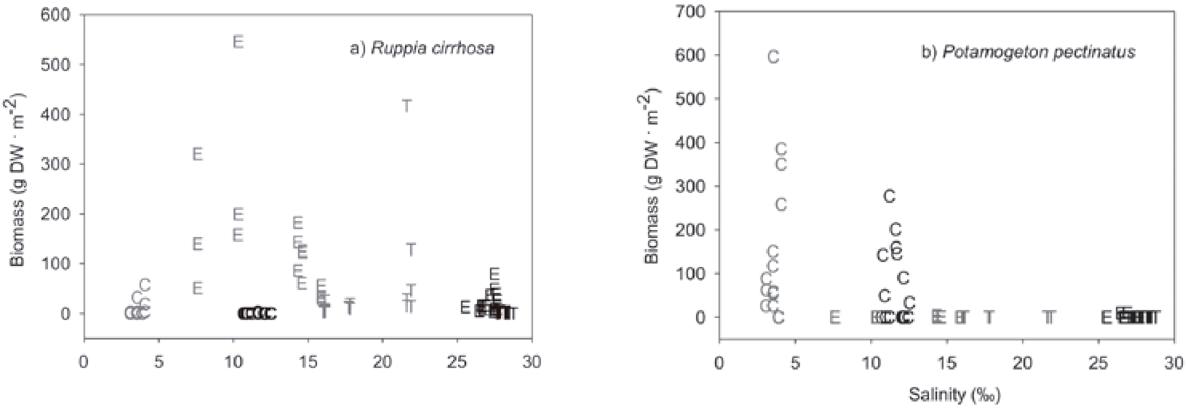

Figure 2. Seasonal variation of: a) the biomass of *R. cirrhosa* and, b) the biomass of *P. pectinatus* in relation to mean annual salinity (i.e., averaged summer and winter values) in the three study lagoons. C: Clot, E: Encanyissada, and T: Tancada. Summer values (August) are indicated in grey and winter values (February) in black. Figure from Prado et al., (2013a) with permission.

Current biomass stands of *R. cirrhosa* are subjected to considerable seasonal variability with maximum standing stock values in summer (0–308 g DW·m^{-2} in the Encanyissada lagoon and 4–153 g DW·m^{-2} in the Tancada lagoon) and minimum in winter (0–45 g DW·m^{-2} and 0 to 2.3 g DW·m^{-2}, respectively), closely mirrored by patterns of estimates of annual net production (Prado et al., 2013a). In the Encanyissada lagoon, a large variability in plant abundance is reported (ca. 10 fold), possibly resulting from differences in winter salinity (from 24 to 34‰), from shading effects by drift marine macroalgae entering from eutrophicated areas of the Alfacs Bay (Prado et al. 2013a), or both. In the Tancada lagoon, contrasting summer biomasses are also observed between the west and eastern basins (9 and 107 g DW·m^{-2}, respectively; Prado et al., 2013a), and previous studies reported notably higher biomass estimates in 1986–1989 (Menéndez & Comín, 1989: ca. 25–687 g DW·m^{-2}; Menéndez, 2002: 9–840 g DW·m^{-2}). These differences between basins are possibly associated with the higher salinity compared to the one recorded in the '90s (Comín et al., 1991). The higher salinity eliminated large areas covered with *P. pectinatus*, destabilising sediments and enhancing turbidity, thus hindering the recolonisation and survival of *R. cirrhosa* (see also Charpentier et al., 2005). For *P. pectinatus* (mostly developing in the Clot lagoon), seasonality is less marked than for *R. cirrhosa*, with higher biomass values in summer (0–331 g DW·m^{-2}) than in winter (0–168 g DW·m^{-2}). Although no historical records are available for the Clot lagoon, these biomass values are much lower than those reported for several brackish habitats in the Camargue at similar salinities (376 to 668 g DW·m^{-2}; Van Wijk, 1988) and suggest suboptimal growth conditions for this species adapted to fresher water conditions. In summer, *N. marina* (57 g DW·m^{-2}) mixed with *P. pectinatus* (58.5 g DW·m^{-2}) also develops in the area closest to the connection with the Encanyissada lagoon. Overall, peak biomasses reported by Prado et al. (2013a) were 88–95% lower than maximum values reported in the literature at similar salinities, and there is little or no recovery in some areas compared to the latest reports from more than 20 years ago. Aside the distribution patterns along the salinity gradient, other factors such as nutrient loading, turbidity, and low oxygen concentrations (e.g., 3-4 mg·L^{-1} in the Clot lagoon and ca. 6 mg·L^{-1} in the Tancada) may account for suboptimal conditions for plant growth in these coastal lagoons. Based on the existing information, we conclude that past restoration efforts and current water management have shifted the habitat towards saltier conditions, replacing *P. pectinatus* with *R. cirrhosa* in many cases, but still away from saltwater reference conditions. However, the current salinity regime throughout the year may not be optimal for any of the existing macrophyte species.

2.2. Planktonic communities

Phytoplankton and zooplankton communities in Ebro Delta coastal lagoons also display contrasting patterns of abundance during the summer period, with higher numbers of total zooplankton and lower numbers of total phytoplankton at higher salinities (Prado et al., 2017a). Structural differences are also observed at the assemblages' level, particularly between the Clot and Tancada lagoon during the summer period (Figure 3, Table 2). Among phytoplankton, benthic Bacillariophyceae are one of the commonest groups, with highest summer abundances in the Clot and Encanyissada lagoons being presumably the result of enhanced light conditions and sediment resuspension (Prado et al., 2017a). Chlorophyceae, and to a lesser extent Cyanophyceae, and Euglenophyceae (all generally less than 1%) are also more abundant in the Clot lagoon in summer (as may occur in freshwater environments; Nicholls, 1976), and decrease in the Encanyissada and Tancada lagoons. Conversely, Dinophyceae, a typical marine group commonly found in Ebro Delta Bays (M. Fernández, pers. comm.), show the highest abundances in the Tancada lagoon and the lowest in the Clot lagoon (53% and 1%, respectively), indicating that Dinophyceae entered the lagoons through connecting channels with Alfacs Bay (absent in the Clot). The zooplankton community is dominated by copepod life stages with lesser abundance of other taxa, especially during the winter period. The osmoconformer calanoid *Calanipeda aquadulcis* (Svetlichny et al., 2012) is the most widespread taxa across lagoons (see also Menéndez & Comín, 1986), with more adults in summer and copepodits in winter. The harpacticoid copepod *Canuella perplexa*, widely distributed in coastal lagoons at salinities from 16 to

32 (Ceccherelli & Mistri, 1991), is largely responsible for the higher total numbers of total zooplankton at greater salinities. Other copepod species are present in marginal numbers and generally show higher summer abundances in the Encanyissada and Tancada lagoons. Cladocerans, which are common in oligohaline environments (Brucet et al., 2009), are present in low abundance, particularly in the Tancada lagoon during the winter period (higher salinity). Ostracoda are also present in low numbers, consistently with patterns found in other coastal Mediterranean lagoons (e.g., Brucet et al., 2009; 2010). Among other zooplankton groups, rotifers have been indicated to attain high summer biomasses in Catalan lagoons (Badosa et al., 2007; Brucet et al., 2009), but are more abundant in winter, particularly at lower salinities (Prado et al., 2017a). Overall, temperature and salinity were the most important factors determining the structure of assemblages (ca. 60% and 72% of phytoplankton and zooplankton variance, respectively). Salinity alone accounts for ca. 44% of the variation in the taxa abundance and composition of phytoplankton and for ca. 20% of the variation of zooplankton (see Prado et al., 2017a). Yet, compared to the period of high agricultural runoff ca. 30 years ago, present conditions show an important decrease in the overall abundance of phytoplankton (more than 50%), whereas zooplankton abundances are ca. 6 times higher (see Comín 1984; Menéndez & Comín 1986). Current low phytoplanktonic abundances may be explained by a sharp reduction in the nutrient loading from rice fields into the lagoons following the construction of circumvallation channels, and to the reappearance of macrophyte communities (Prado et al., 2013a).

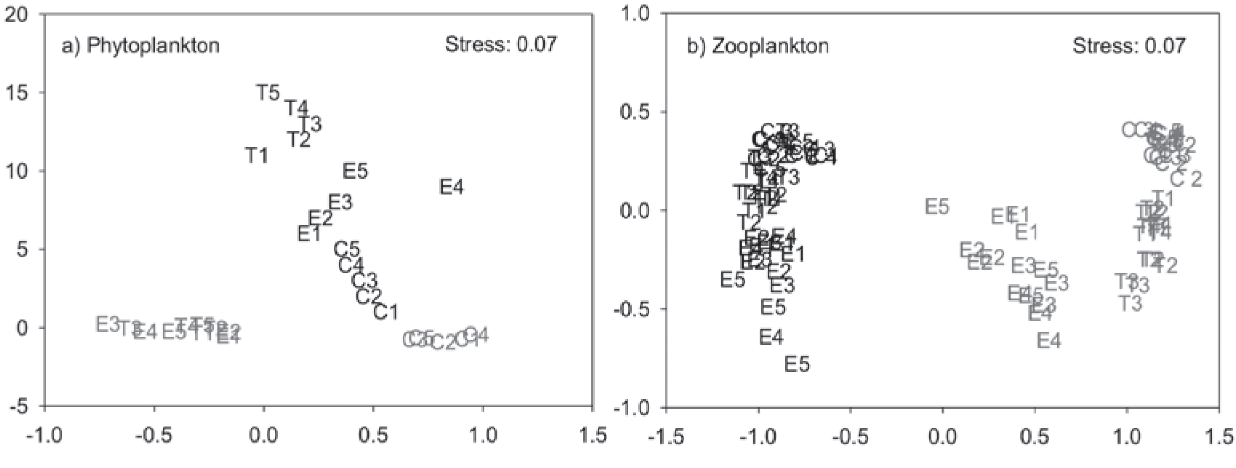

Figure 3. n-MDS ordination showing differences in phytoplankton and zooplankton assemblages across lagoons and seasons. Symbol labels as in Fig. 1. Figure from Prado et al., (2017a) with permission.

	Phytoplankton				**Zooplankton**		
	R	*p (%)*	Sim./Diss (%)		R	*p (%)*	Sim./Diss (%)
Lagoon	0.784	**0.1**		Lagoon	0.848	**0.1**	
C-T	1	**0.2**	54.57	C-T	0.914	**0.1**	50.81
C-E	0.828	**0.1**	29.71	C-E	0.868	**0.1**	32.62
T-E	0.578	**0.2**	37.47	T-E	0.847	**0.1**	41.72
C			89.82	C			84.80
E			85.36	E			81.22
T			85.64	T			74.58
Season	0.960	**0.1**	34.69	Season	1	**0.1**	86.90
W			87.67	W			80.64
S			86.20	S			79.77

Table 1. Results of two-way ANOSIM (global effects and pairwise comparisons) and SIMPER analyses (similarities/dissimilarities) for phytoplankton and zooplankton assemblages based on dissimilarity matrices derived from taxa abundances (log (x + 1) transformation). *R*—ANOSIM statistics; *p*—significance level of sample statistics (%). In ANOSIM analyses, significant results are indicated in bold. In SIMPER results, pairwise comparisons indicate dissimilarities and single group similarities.

	Macroinvertebrates		
	R	*p (%)*	Sim./Diss (%)
Lagoon	0.756	**0.1**	
C-T	0.899	**0.1**	57.57
C-E	0.676	**0.1**	44.16
T-E	0.752	**0.1**	49.90
C			69.79
E			71.46
T			65.8
Season	0.559	**0.1**	46
W			76.72
S			61.32

Table 2. Results of two-way ANOSIM (global effects and pairwise comparisons) and SIMPER analyses (similarities/dissimilarities) based on dissimilarity matrices derived from abundance of macroinvertebrate taxa (log (x + 1) transformation). *R*—ANOSIM statistics; *p*—significance level of sample statistics (%). In ANOSIM analyses, significant results are indicated in bold. In SIMPER results, pairwise comparisons indicate dissimilarities and single group similarities.

2.3. Macroinvertebrate communities

Prado et al. (2014a) showed that patterns of macrofaunal assemblages in Ebro Delta lagoons are strongly influenced by the interactive effects of freshwater inflows and the seasonal forcing. According to their findings, species richness and diversity were positively associated with salinity (i.e., higher in the Tancada and Encanyissada lagoons and lower in the Clot lagoon), particularly in summer, when salinity conditions are more contrasting. Assemblages displayed 22 taxa, which included crustaceans, insects, gastropods, and bivalves, and featured contrasting patterns across the salinity gradient and the study seasons (Figure 4, Table 2).

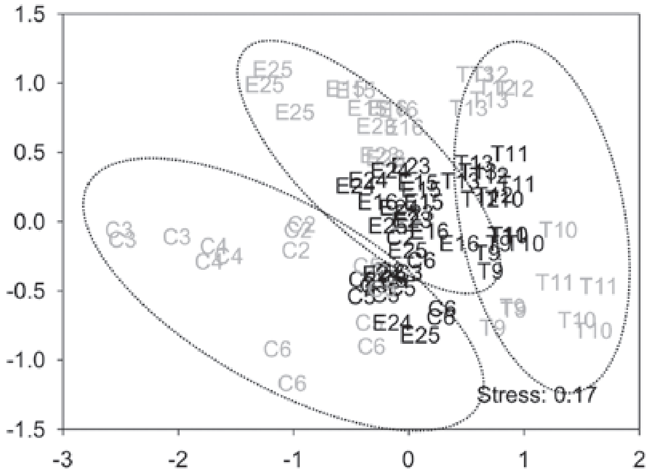

Figure 4.n-MDS ordination showing differences in macrofaunal assemblages found among the three study lagoons. Circles point out grouping patterns across zones and lagoons. Symbol labels as in Fig. 1. Data were Log (x + 1) transformed. Figure from Prado et al., (2014a) with permission.

Among crustaceans, the euryhaline amphipods *Gammarus aequicauda* and *Corophium volutator* (McLusky, 1970; Prato & Biandolino, 2003) are abundant in all the lagoons, particularly in the Tancada. The isopods *Idotea baltica* and *Cyathura carinata* are not found in the Clot lagoon and are most abundant in the Tancada, due to a more efficient osmoregulatory ability at salinities above 10 (Hørlyck, 1973). In contrast, the isopod *Lekanesphaera hookeri* is very abundant in the Clot lagoon but is absent from the Tancada, also in agreement with ranges of salinity tolerance (Jansen, 1970). Among insects, *Chironomus salinarius* and Orthocladiinae are more abundant at the lower Clot salinities (see also Cartier, 2011), and in summer, larvae of the Lepidoptera *Acentria ephemerella* appear associated with *P. pectinatus* in the Clot lagoon and the northern zone of the Encanyissada lagoon. Among molluscs, the gastropod *Hydrobia* sp. is extremely abundant in the Encanyissada and lower in the other lagoons, particularly in the Clot, due to its marked preference for meso- to polyhaline waters (Khlebovich & Kondratenkov, 1973). The remaining gastropod (*Haminoea navicula, Gibbula* sp., and *Theodoxus fluviatilis*) and bivalve (*Cerastoderma* sp. and *Scrobicularia plana*) species observed are characteristic of marine waters (López-Cotelo et al., 1982; Baden & Boström, 2001; Malaquias & Cervera, 2006) and are found in higher numbers in the Tancada lagoon. Up to 56–60% of these variations in macroinvertebrate assemblages was explained by environmental factors, with salinity and temperature accounting for the largest contributions (approx. 14% and 10%, respectively), whereas biomass was mostly controlled by temperature and nutrients (Prado et al., 2014a). To a minor extent, other explanatory factors also included distinctive levels of oxygen and organic matter across the lagoons, apparently associated with the freshwater influx (Prado et al., 2014a).

2.4. Vertebrate communities

Brackish water macrophytes such as *P. pectinatus, N. marina,* and *R. cirrhosa* among others are known to be a preferred food and habitat for waterfowl species such as ducks and coots (Perrow et al., 1997; Rodríguez-Pérez & Green, 2006) and appear to have favoured the development of large populations of certain aquatic birds (Mateo et al., 2000; Farré & Duro, 2010) after the restoration efforts (Ibáñez et al., 2000). Actually, during breeding season large populations of waterbirds use the habitats of these macrophytes to breed. These waterbirds include ducks (*Anas platyrhynchos* mostly), little grebes (*Tachybaptus ruficollis*), Eurasian coots (*Fulica atra*), colonies of several species of herons (*Ixobrychus minutus, Nycticorax nycticorax, Ardeola ralloides, Bubulcus ibis, Egretta garzetta* and *Ardea purpurea*), and also large numbers of glossy ibis (*Plegadis falcinellus*) and the purple swamphen (*Porphyrio porphyrio*). The coastal lagoons are also important breeding territories for terns (*Sterna albifrons, Gelochelidon nilotica, Chlidonias hybrida, Sterna sandvicensis,* and *S. hirundo*) and gulls (*Chroicocephalus genei, C. ridibundus,* and *Larus audouinii*). During migration seasons and winter, ducks (*Anas penelope, A. strepera, A. crecca, A. acuta, A. clypeata, Netta rufina,* and *Aythya ferina*) are very common, and so are grebes (*Podiceps cristatus* and *P. nigricollis*), waders (*Limosa limosa, L. lapponica, Calidris ferruginea, C. alba, C. minuta, Tringa totanus,* and *T. nebularia*) and herons (*A. alba* and *A. cinerea*). Finally, during winter thousands of greater flamingos (*Phoenicopterus roseus*) use the lagoons as preferred habitat.

In contrast, fish populations adapted to live in saltwater and brackish water declined during the 1970s and 1980s, with the low freshwater quality inputs, and total catch yields have never recovered in most of the lagoons from the ca. 70% biomass decline during the late 1980s (Ibáñez et al., 2000). Moreover, lower salinities also favoured invasion by non-native fish species with low commercial value such as the bleak (*Alburnus alburnus*), the goldfish (*Carassius auratus*), the common carp (*Cyprinus carpio*), the topmouth Stone Moroko (*Pseudorasbora parva*), the pike perch (*Sander lucioperca*), the wels catfish (*Silurus glanis*), and the pond loach (*Misgurnus anguillicaudatus*) (Caiola & Sostoa, 2002; Franch et al., 2008; Rodríguez-Climent et al., 2012). The mosquitofish, *Gambusia holbrooki*, deserves special attention due to its negative effects on the conservation of endangered Iberian toothcarp, *Aphanius iberus* (Caiola & Sostoa, 2005). Hence, poor conservation status of these species might be partly due to an altered food-web structure or to changes in the availability of trophic resources such as macroinvertebrates, zooplankton, and phytoplankton; and intensified by constricted patterns of food search, particularly in permanent lagoon residents such as the mugilids (*Liza aurata, L. saliens, L. ramada, Mugil cephalus,* and *Chelon labrosus*), the eel (*Anguilla anguilla*), the sand smelt (*Atherina boyeri*), the common goby (*Pomatoschistus microps*), and the black-striped pipefish (*Syngnathus abaster*). These ecological alterations also negatively affected non-resident species that used to be more abundant, such as the sea bass (*Dicentrarchus labrax*), the gilthead seabream (*Sparus aurata*), and the sole (*Solea senegalensis*).

Alterations in the quality and abundance of submerged habitats and food resources caused by differences in salinity have been shown to impact the dietary composition of major fish species in Ebro Delta lagoons (Prado et al., 2014b). Variability in $\delta^{13}C$ signatures across lagoons is particularly strong throughout the food web, with consistently lower values in the Clot lagoon and higher in the Tancada lagoon (Figure 5). These differences are in agreement with patterns observed in other systems with variable contributions from marine and continental material (e.g., Deegan & Garritt, 1997; Vizzini et al., 2005; Garcia et al., 2007; Obrador & Pretus, 2012). For $\delta^{15}N$, a negative relationship with the salinity gradient is detected in sediments, zooplankton, and invertebrate communities (Prado et al., 2014b), possibly due to past inputs of $\delta^{15}N$-enriched water from anthropogenic sources (e.g., Vizzini & Mazzola, 2004; Vizzini et al., 2005). Yet, enduring processes of eutrophication appear to cause little effects in the $\delta^{15}N$ signatures of fish species (as a proxy of trophic position; Figure 5). The mixing models used for the evaluation of fish dietary contributions show that trophic pathways of the most abundant fish species (Liza spp.), sand smelt (*Atherina boyeri*), the common goby (*P. microps*), the Iberian toothcarp (*A. iberus*), and the Eastern mosquitofish (*G. holbrooki*) are dominated by zooplankton in the Encanyissada, and by macroinvertebrates in the Clot and Tancada lagoons (Prado et al., 2014b). A plausible hypothesis for these results is that consumer choices along the salinity gradient may have been influenced by differences on prey availability (Prado et al., 2014a). In contrast, although fish populations in Ebro Delta lagoons have experienced an important overall decline since the ’80s (Ibáñez et al. 2000), the biomass of fish species does not seem to have a clear association with salinity, except for the invasive mosquitofish, *G. holbrookii*, which was more abundant in the Clot lagoon (Prado et al., 2014b).

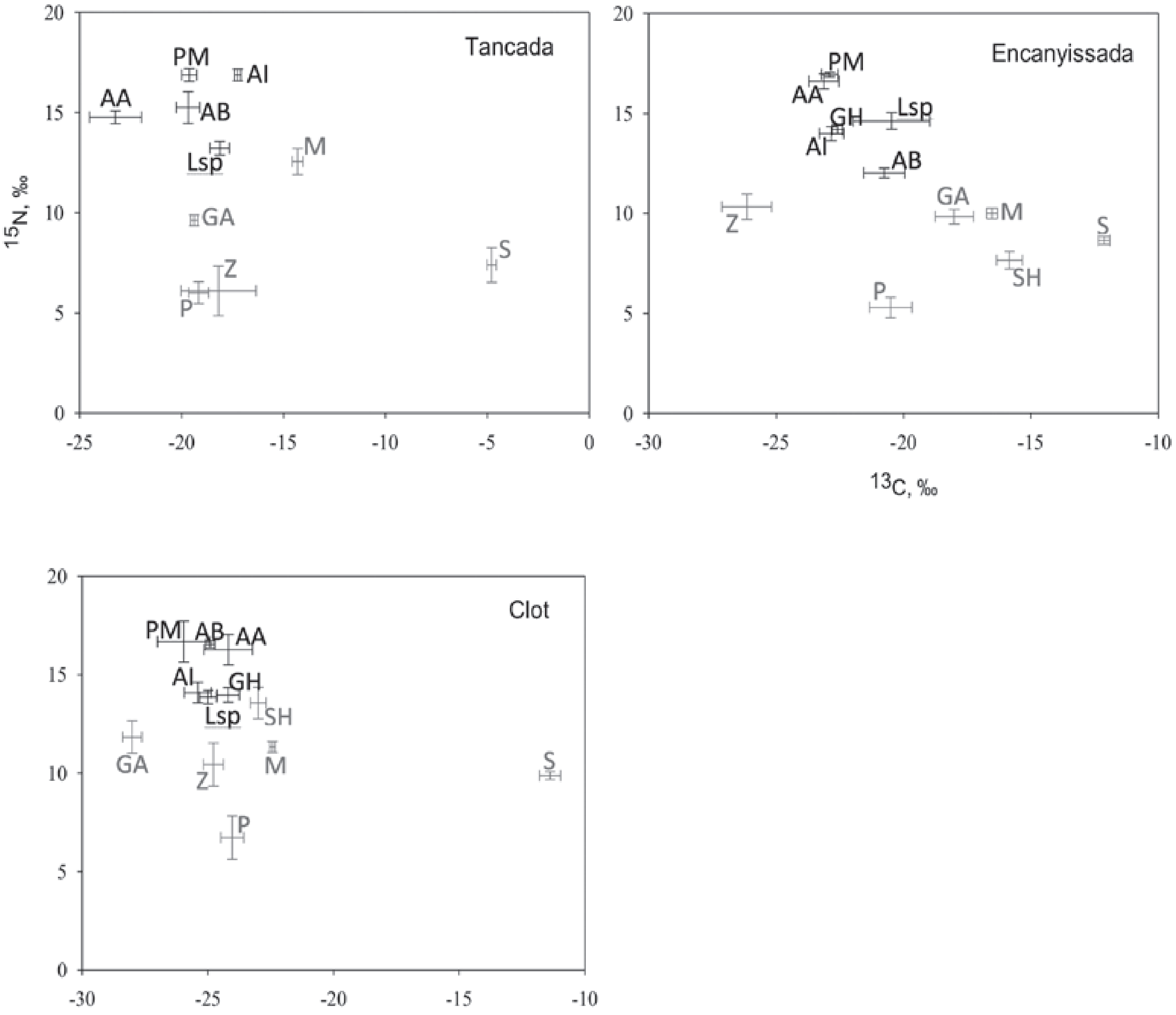

Figure 5. δ^{13}C and δ^{15}N fish species (black) and food sources (grey) in the three investigated lagoons in the Ebro Delta across the salinity gradient. Lsp= *Liza* spp.; AA= *Anguilaanguila*; PM= *Potamochistusmicrops*; AB= *Atherinaboyeri*; AI= *Aphaniusiberus*; GH= *Gambusiaholbrook*i; GM= *Gammarusaequicauda*; SH= *Sphaeromahookeri*; M= Macrophytes; S= Sediment; F= Phytoplankton; Z= Zooplankton. Error bars are SE. Figure from Prado et al., (2014b) with permission.

2.5. Food web structure

The throughout investigation of the entire food web—from phytoplankton to birds—using network analyses (Ecopath with Ecosim software) showed contrasting trophic functioning in the 3 lagoons, but they were mostly due to bottom-up processes related to salinity effects on habitat type (see Prado et al., 2013b). Since the 2 higher-salinity lagoons, Encanyissada and Tancada, are dominated by the annual macrophyte *R. cirrhosa*, plant and epiphyte biomasses are sufficient to sustain fish and macroinvertebrate communities in summer, but not in winter, when almost all biomass is lost. Hence, a swift to detrital consumption is necessary for balancing the trophic models of these lagoons. Conversely in the Clot lagoon, since macrophyte communities are dominated by the pseudo-annual species *Potamogeton pectinatus*, which persists all year but registers a certain decline in winter, consumers do not experience any seasonal limitation. In addition, seasonal differences in some commonly used ecosystem metrics such as NPP: biomass ratios, total system troughoutput (TST), and ascendancy are also the lowest in the Clot lagoon, suggesting a more stable trophic functioning, which does not depend so much on variability in the abundance of phytoplankton (Prado et al., 2013b). This influence of salinity, coupled with nutrient availability, in the trophic functioning of these systems is further confirmed by a strong positive association with the ratio of planktonic to benthic pathways, thus suggesting enhanced planktonic processes when plants are limited. In addition, seasonal variation in habitat availability (refugees provided by vegetation) may indirectly impact the abundance of higher trophic levels (Green & Short, 2003). Yet, although considering the target environments as a closed system is an accepted modelling approach (Christian & Luczcovich, 1999; Prado et al., 2013b), it might also provide an oversimplistic perspective of the real fluxes of energy and organic matter entering the lagoons from marine and continental sources. For instance, Prado et al. (2014b) showed that $\delta^{13}C$ signatures of macrophytes strongly mirrored the salinity gradient (-14.31 ± 0.26‰, -16.26 ± 0.37‰, and -22.59 ± 0.41‰, respectively, in the Tancada, Encanyissada, and Clot lagoon). Hence, POM from more depleted C3 plants (less than 25 to 19‰) such as rice, spreading over ca. 70% of the delta surface, might be an important source of carbon in the Clot lagoon, which features the highest freshwater inputs through irrigation channels. Similarly, the seagrass *Cymodocea nodosa,* which thrives in Alfacs Bay and is amongst the most enriched sources of vegetal carbon (approx. 7.5‰; Vizzini & Mazzola, 2003) could be subsidising POM into the Encanyissada and Tancada lagoons through connecting marine channels.

3. Analysis of restoration efforts in Ebro Delta coastal lagoons

The ecological restoration efforts in the Ebro Delta started early in the ’90s in the Encanyissada lagoon, the biggest coastal lagoon of the Ebro Delta, and were focused on the improvement of water quality by changing the existent hydrological connections to restore the macrophyte cover of the lagoon. Also in the ’90s an experimental restoration of wetlands from abandoned rice fields near the Tancada lagoon was performed to test the efficiency of these restored areas in reducing the nutrient content of wastewater and to study vegetation and waterbird dynamics in such areas during the restoration process. Both restoration efforts were promoted by the Ebro Delta Natural Park and the University of Barcelona.

A third restoration action, promoted by the Natural Park, was performed in Buda island after the regional government purchased half of the island in 1992 to undertake actions to enhance biodiversity and preserve and improve protected habitats. This intervention was included in a LIFE Natura project aiming at boosting biodiversity and counteracting existing threats such as poor water quality of the coastal lagoons, loss of riverine woodland, and favourable habitats for the nesting of some protected species such as the pratincole (*Glareola pratincola*) and the bittern (*Botaurus stellaris*), as well as the decline in the populations of the endangered Iberian toothcarp (*A. iberus*).

After these first efforts to improve the ecological status of some of the lagoons of the Ebro Delta, in the following decade habitat rehabilitation was not a priority. The most remarkable was the restoration of a small lagoon and wetlands (Riet Vell) as a result of another LIFE Natura project carried out by the NGO SEO/BirdLife. Then, after 2010 some important restoration projects were performed, including the creation of green filters and coastal lagoons in former rice fields and abandoned fish farm facilities, as well as the hydrological restoration of other existing lagoons.

Next, we analyse in more detail the main restoration projects carried out in the Ebro Delta coastal lagoons during the past 25 years to improve the ecological quality of these priority wetland habitats, which were impacted by land management policies that favour agriculture, hunting, and fishing and also significantly reduced their surface.

3.1. The Encanyissada lagoon functional restoration (1991–1992)

The aim of this first restoration action in this lagoon, with an average depth of 80 cm, was to improve its water quality (eutrophication and pesticide pollution) and recover the submerged vegetation, of great importance for waterbird and fish populations that had decreased by then (Forès, 1992).

Therefore, to revert the pollution problems, the construction of a bypass canal around the lagoon was undertaken to avoid the entrance of drainage water from the rice fields, detouring it to the Alfacs Bay. In addition, a new lower input of freshwater of better quality from the Ebro River was set up using an existing irrigation canal (Forès et al., 2002). The lagoon-seawater exchanges increased as the freshwater inputs decreased, and this further helped to reduce nutrient loading because of the relatively low nutrient content of seawater (Comín et al., 1990).

At the same time, during the spring of 1991, the Clot lagoon was dried out on purpose. This small lagoon (0.56 km^2) is part of the Encanyissada lagoon system, but is separated by a floodgate. This floodgate made it possible to isolate the small lagoon from the main lagoon, to enable the aeration of the sediment and decrease the flux of nutrients (especially phosphorus) from sediment to water during subsequent flooding.

The Clot lagoon was completely dry for almost a year, and it was then filled with irrigation water with lower inputs of phosphorus and nitrogen in the form of ammonia usually present in the rice field drainage water. Some laboratory experiments were made before to find the appropriate characteristics of the future flooding water and choose the best procedure. Taking into account water availability and topography, the best option was a first flooding with seawater followed by successive flooding episodes with freshwater

(Forès, 1992). Two years after the restoration, the macrophyte cover exceeded 70%, leading to the quick recovery of fish and wildfowl populations; these results showed that the input of drainage water is one of the main causes of the disappearance of macrophytes and the proliferation of phytoplankton in the Ebro Delta coastal lagoons (Forès at al., 2002). Therefore, the restoration was successful in terms of recovery of ecosystem health (recovery of macrophyte community, waterfowl, etc.) rather than in terms of ecosystem integrity (reference conditions), since the lagoon system still keeps significant freshwater inputs, especially in the case of El Clot.

3.2. Restoration of wetlands in the Tancada lagoon (1993–1998)

This experimental restoration (Comín et al., 2001) consisted in the conversion of abandoned rice fields to wetlands along the shore of the Tancada lagoon (2.6 km^2) to test its efficiency for nitrogen and phosphorus removal from agricultural wastewater that was used to flood the restored wetlands. The dynamics of the restored vegetation was investigated, as well as which stage of succession was most suitable for wetland birds. Finally, the study determined the degree of potential recovery of landscape diversity that would occur if the restoration activity carried out was applied to a larger area covering the whole vegetation belt surrounding a coastal lagoon.

The inflowing and outflowing water from the experimental area were controlled and compared, and showed that wetlands converted from rice paddies after spontaneous revegetation appear to be very efficient at retaining nitrogen from surface water (50–95% of the total incoming nitrogen) but much less so at retaining phosphorus (less than 50% of the incoming phosphorus). Therefore, if wetlands restored from rice fields are used as filters to remove nutrients, it is possible to achieve an improvement of the water quality drained from agricultural systems that is discharged to coastal ecosystems (lagoons, bays, and open sea).

The colonisation process of the vegetation after restoration of freshwater wetlands showed typical characteristics of secondary succession: flooding the area with freshwater during the growing season and maintaining a low (up to 30 cm) water level favoured the development of the common reed (*Phragmites australis*). By the fourth year, the restored wetlands were densely covered by this plant community. The dominant plant species varied during the first 4 years after rice fields were abandoned, changing from *Echinochloa* sp. and *Scirpus maritimus* dominance in the first year to *Typha latifolia* in the second and to *Scirpus lacustris* in the third, before the common reed was established in the following years. The aboveground dry biomass of the emergent vegetation increased progressively with the ageing of the wetlands, which means that a net accumulation of plant detritus occurred during all years.

As in the case of emergent vegetation, the seasonal growth of macrophytes in these wetlands followed a similar pattern to those of other populations of the same species located in areas close to the experimental site but subjected to natural water fluxes and not to regulated flooding (Comín et al., 1997).

Waterbirds preferred wetlands at an intermediate stage of succession, selecting the *Thypha* and *Scirpus* dominated habitats over rice fields and open wetlands, which provide little protection, and over older wetlands with dense vegetation, which hinder bird movements while feeding or breeding. Therefore, to improve bird habitat, the vegetation in dense old wetlands should be managed in order to maximise diversity. Nevertheless, after the restoration, farmers who cultivated neighbouring rice fields complained about aquatic birds that lived in the restored sites and fed on the farmers' rice fields. This led to the transformation of the restored sites into dry grasslands to decrease the number of aquatic birds (Comín et al., 2005).

Overall, the study showed that wetland restoration can simultaneously achieve different objectives such as nutrient removal and biodiversity conservation, among others. Another conclusion is that habitat restoration can be rapidly achieved after intensive human use has ended, because wetland recuperation from rice fields takes place in a relatively short period of time.

3.3. Wetland restoration in Buda island lagoons (1996–2000)

The Buda island (1280 ha) is a natural reserve of the Ebro Delta Natural Park that includes 2 coastal lagoons, the Calaix Gran and the Calaix de Mar, as well as rice fields, reed beds, and salt marshes. The restoration carried out in the island was part of the conservation actions established by the project "Restoration and integrated management of the island of Buda" supported by the LIFE Natura Program of the European Union (LIFE 96/E/003180).

In 1996 the activities carried out on the island included hunting, fishing, and rice cultivation, this last one having some negative effects on coastal lagoons due to the fertilisers and agrichemicals used that were discharged directly into the lagoons. The most important restoration actions targeted the improvement of the natural hydrological connectivity with the surrounding wetlands and avoiding the entrance of nutrients and contaminants from the rice fields into the lagoons, to reduce the high level of eutrophication and hypoxia before the restoration. The project also allowed the conversion of rice fields into brackish and salt marshes through the abandonment of more than 0.3 km^2 of rice fields to restore them to a green filter and pasture area. The formerly cultivated rice fields were flooded with brackish water and were then left untouched to allow vegetation recovery. This habitat restoration and the management carried afterwards had an almost immediate positive response in terms of bird species that was already visible before the end of the project. Remarkably, 20–30 pairs of collared pratincole (*G. pratincola*) bred in former rice fields in 1997, and the great egret (*Ardea alba*) was recorded breeding for the first time in the Iberian Peninsula. The reintroduction of 2500 individuals of Iberian toothcarp (*A. iberus*) and Valencia toothcarp (*Valencia hispanica*), 2 priority species of the Habitats Directive, in 2 small brackish lagoons (100 m^2) created in purpose, was successful. The breeding success of these species was confirmed by capturing young fishes during monitoring census.

By the end of the project, macrophytes had recolonised the coastal lagoons thanks to the improvement of water quality by avoiding inflows of polluted water and by creating green filters for the water coming from the island's rice fields prior to reaching the lagoons.

3.4. The creation of 2 constructed wetlands (2010)

Under the Integral Plan for the Protection of the Ebro Delta and promoted by the Spanish and Catalan Governments, 2 artificial wetland areas were created after the abandonment of rice fields, with the objective of improving the quality of the water draining from surrounding cultivated paddy fields. These

2 newly constructed wetlands, one in the north Ebro Delta (“Illa de Mar”—45.37 ha) and the other in the south Ebro Delta (“The Embut”—77.63 ha) were designed to act as biological filters to improve water quality by reducing the amount of nutrients and pollutants being delivered to the coastal lagoons and bays, where aquaculture and fishing are important economic activities. The wetlands also act as sediment traps and carbon sinks, increasing land elevation, thus compensating for sea level rise and subsidence. Despite being constructed in 2010, only recently (2014) did these wetlands start to operate, because of previous lack of funds and a suitable management plan.

The 2014–2018 LIFE Natura project “Adaptation and mitigation measures to climate change in the Ebro Delta” (LIFE13 ENV/ES/001182) includes a management action focused on the optimisation of the constructed wetlands. The objective of this action is to optimise the operation of the wetlands in order to maximise the rate of carbon sequestration and soil elevation, and the reduction of nutrients and pollutants. To establish the best management plan for both areas, it is necessary to carry out several pilot tests that consist in the manipulation of the water column and turnover rate. The result of the pilot tests are currently being analysed, and the main variables monitored are organic and inorganic nutrient concentration in water and soil, water physicochemistry, heavy metals and pesticides of water and soil, total carbon and nitrogen of soil, chlorophyll, suspended matter, biological and chemical oxygen demand, etc. For the estimation of soil elevation, the Surface Elevation Table (SET; Cahoon et al., 2002) is used, as well as marker horizons. Above- and belowground biomass and vegetation composition are also monitored. The optimisation plan is expected to result in the retention of 70% of total dissolved nitrogen, the reduction of 30% of pesticides and heavy metals, a mean soil elevation rate of 0.5 $\text{cm}\cdot\text{year}^{-1}$, and a carbon sequestration rate of 80 $\text{g}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$.

3.5. Habitat restoration and management of the Alfacada and Tancada lagoons (2011–2017)

The last major habitat restoration performed in the Ebro Delta was supported by the LIFE Natura Program of the European Union (LIFE09 NAT/ES/000520) and took place in the Alfacada and Tancada coastal lagoons, located in the Ebro Delta Natural Park. Although the Alfacada lagoon is a protected area, it was until recently a private estate used for hunting; this has led to isolation from the sea and the river and the introduction of freshwater from the surrounding rice field irrigation system. The Alfacada lagoon is also vulnerable to the effects of climate change and sediment deficit, since the area is close to the river mouth and is quickly retreating. Therefore, specific management and restoration measures were necessary to mitigate these negative effects. The other restored area was the salt marshes of the Tancada lagoon, in particular the former Sant Antoni saltpans (abandoned in the ’50s), which were partially transformed during the ’90s to intensive fish farming activities. Much work was then required to restore this recently protected area to its natural state, recovering its connectivity with the sea (Alfacs Bay) through the removal of the dikes of 60 shallow ponds of the former fish farm.

The main objective of the project was to improve the ecological status of both coastal lagoons through habitat restoration and management measures, such as the improvement of natural hydrological connectivity, the removal of infrastructures that interfere with this connectivity, the creation of new coastal lagoon habitats in existing rice fields, and the restoration of salt marsh habitats. Specifically, the restoration objectives were (a) to improve the ecological status of the Alfacada lagoon through a better connection of the lagoon to the sea and river; (b) to implement restoration measures designed to mitigate the effects of coastal erosion and climate change; (c) to improve the conservation status of priority habitats and species, including 10 coastal and migratory wading birds listed in the annexes of the Birds Directive; (d) to increase the Alfacada lagoon habitat, restoring part of the original lagoon areas that had been converted to rice fields; and (e) to improve the ecological status and the hydrological connectivity with the sea of the old saltpans of Sant Antoni, through the restoration of areas affected by abandoned aquaculture facilities.

Several measures have been implemented to deal with the consequences of sea level rise and coastal erosion. In the context of climate change, the main adaptation measure to increase coastal resilience was reconnecting the lagoons and the sea (opening connections through the existing coastal dike), in order to increase the sediment inputs to the lagoons during marine storms.

3.5.1. The Alfacada lagoon

The habitat restoration of the lagoon started with an improvement of its hydrological network, by widening the canals that bypass the lagoon and building a new canal that connects the lagoon with the Ebro River. In addition, the hydrological connection of some salt marshes was restored; previously, these marshes had been divided by dikes, forming isolated plots. Also, the connection of the salt marshes with the lagoon itself was improved, since formerly it had been impeded by a dike to avoid the entrance of seawater during marine storms. Once the hydrological functioning of the lagoon was improved, the reintroduction of the European pond turtle (*Emys orbicularis*) was initiated. A new population of some 100 individuals of this species was progressively created. Current monitoring indicates that these turtles are acclimatising to their new habitat and will be able to establish a reproductive population in 8–10 years.

Recently (2016–2017), the project converted some 50 ha of rice fields back to coastal lagoon habitat, including 2 brackish coastal lagoons surrounded by reed beds and areas of riparian forest.

3.5.2. The Tancada lagoon and Sant Antoni saltpans

The main restoration action in this area was the naturalisation of an old aquaculture facility back to salt marsh habitat. Intensive fish farming has had a negative impact on the southern part of the Tancada lagoon, and the closure of an aquaculture facility in the area of the Sant Antoni old saltpans was an opportunity to restore 16 ha of coastal ponds and salt marshes to their original habitat. The restoration works were constrained by the fact that the area hosted one of the main populations of the endangered Iberian toothcarp (*A. iberus*). Therefore, a special monitoring of this fish species was carried out before, during, and after the restoration. Ultimately, the restoration efforts created hydrological conditions and a landscape configuration more similar to those occurring in the area prior to human alteration. Although enhanced fish diversity and abundance were not met on the short term, subtler changes in the distribution of assemblages indicated a gradual improvement of the ecological quality status following the restoration. The Iberian toothcarp population of the area showed a significant decrease in the abundance of individuals after the restoration works, but similar patterns were also detected in the non-restored reservoir ponds, thus suggesting the influence of natural processes (i.e., temperature) rather than restoration works themselves (Prado et al., 2017b).

The creation of artificial islets in the former saltpans has allowed a number of endangered bird species to breed. In the first 2 years following the restoration, the establishment of colonies of the slender-billed gull (*Chroicocephalus genei*), Audouin's gull (*Larus audouinii*), little tern (*Sterna albifrons*), and gull-billed tern (*Gelochelidon nilotica*) was recorded. In the case of the slender-billed gull, these were the first breeding pairs observed in a decade.

The success of the restoration in terms of bird conservation was also due to the elimination of land accesses to the restored areas and other sensitive areas nearby, as well as to the physical protection of another coastal salt marsh area using a fence of poles and ropes, which was necessary to mitigate the impacts of predators and human frequentation.

Finally, to improve the landscape quality and avoid bird collisions, all the electric power lines that previously crossed the area were buried.

4. Recommendations for future restoration and management goals

Mediterranean coastal lagoons such as the ones reported herby for Ebro Delta were in most cases saltwater lagoons under reference conditions (brackish in a few cases), and they should be permanently or temporarily hypersaline during the summer period due to enhanced evaporation rates. Since the annual cycle of vegetation depends on species type, salinity ranges are a central factor controlling the seasonal dynamics of ecosystems and their stability throughout the year. Likely, perennial seagrass species such as *Cymodocea nodosa* (the dominant macrophyte in the Alfacs Bay) or *Zostera noltii* (present along the Northern Bay shore, associated with agricultural freshwater discharge areas) were formerly present within the Ebro Delta lagoons, as they are in other similar Mediterranean lagoons (Laugier at al., 1999; Agostini et al., 2003). Therefore, management practices should aim to recover local Mediterranean seagrasses by significantly reducing freshwater inflows (especially in summer) that prevent colonisation from the bays. Although *Z. noltii* has been indicated to have a wide tolerance to low salinities (e.g., in the Sea of Azov it grows across a salinity gradient of 2–26‰), it most commonly develops in the same euryhaline waters (35–37‰) as *C. nodosa* (Green & Short, 2003). However, germination and development of seedlings are favoured by lower salinities: 2–6 days at 15–20‰ followed by rising to ca. 27‰ for *C. nodosa* (Caye & Meinesz, 1986) and 10‰ for *Z. noltii* (Loques et al., 1990), which naturally occur during river floods and rainy seasons.

The implemented restoration projects imply there were 2 main types of restoration approaches in the coastal lagoons and wetlands of the Ebro Delta: the functional restoration and the structural restoration. The functional restoration is directed at recovering the fluxes of water and sediment, and the connectivity of the lagoons and surrounding marshes (i.e., the Alfacada lagoon project). The structural restoration is directed at recovering the habitats or some components of the biological communities (i.e., birds, fish, etc., as in the Buda island project). In most of cases, the restoration works have taken into account both functional and structural goals, but so far the restoration projects have had an individual nature, without any global scheme to adapt the restoration goals to the whole deltaic system. Therefore, the main recommendation for future restoration and management efforts is to frame individual projects within a global strategy for the whole Ebro Delta, following some general principles:

- Increase the surface of coastal lagoons to recover part of the habitat lost in the nineteenth and twentieth centuries. Benito et al. (2014) estimated a loss of 77% in the coastal lagoon area.

- Ensure a coherent functional and structural restoration in order to get as close as possible to achieving the reference conditions and good ecological status. This means more connectivity with the sea (increasing the number and width of outlets), higher and less fluctuant salinity, and higher cover of macrophytes such as *Z. noltii* and *Cymodocea nodosa*.

- Reduce artificial freshwater inputs as much as possible, trying to mimic the natural hydrological cycle of the lagoons. Reduced freshwater flows should be mostly allocated in spring and autumn, the rainy periods in which river floods occurred in the past. In addition, avoid salinities below 15 to prevent the spread of freshwater invasive species, such as the mosquitofish (*G. holbrooki*) and favour endangered species such as the Iberian toothcarp (*A. iberus*).

- Increase the surface of marshes surrounding the lagoons (especially salt marshes), since they are a key part of the ecological functioning of coastal lagoons, especially for nutrient cycling, carbon sequestration, accretion, and habitat for breeding and feeding of many species.

- Promote the reintroduction and recovery of endangered species once the habitat is restored to conditions that are suitable for their survival, such as adequate salinity and water quality or proper habitat structure.

- Prioritise management schemes that follow the principles of adaptive management and allow the recovery of the good ecological status and species of conservation concern, avoiding the schemes directed to goals such as increasing the population of gaming birds.

- Promote applied research on coastal lagoon restoration in order to improve the technical groundworks of future restoration works, as well as monitoring directed to quantify the results and evolution of restoration projects.

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The importance of hydrological connectivity for coastal lagoon management: Cal Tet and La Ricarda (Llobregat Delta, Spain) case studies

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Introduction

Coastal lagoons are transition zones, halfway between the mainland and the sea, that receive both freshwater (river and stream) and seawater inputs. As a result, their hydrological functioning is complex, with marked fluctuations in salinity and nutrient concentrations both in space and in time (Barnes, 1980; Kjerfve, 1986). Thus, the environmental filters which the organisms pass are very strong, and change significantly from one lagoon to another depending on the existing hydrological dynamics. That is why local biodiversity (α) is often low (only few organisms can adapt to the particular environmental conditions of a given lagoon), while regional diversity (diversity γ) is usually high (Cognetti & Maltagliati, 2000; Basset et al., 2006). The high regional diversity results from the high spatial and temporal environmental heterogeneity (each lagoon has particular environmental conditions ideal for a type of organisms) and the high productivity of these ecosystems (Levin et al., 2001). Lagoon waters receive nutrients both from the rivers and streams, which transport nutrients along their beds, and the ocean, which transports nutrients through currents and waves. This large accumulation of nutrients in lagoons stimulates the proliferation of invertebrates (e.g., crustaceans and aquatic insects), which in turn serve as food for fish and waterfowl. It is therefore not surprising that coastal lagoons are one of the preferred stops of migratory birds during their long seasonal migrations (McLusky & Elliott, 2004).

Thus, due to this great accumulation of nutrients, coastal lagoons are one of the most precious ecosystems for humans in terms of provided goods and services (Costanza et al., 1997). However, at the same time, this great accumulation of nutrients implies coastal lagoons are under a constant threat of eutrophication, especially systems affected by human activities. The rivers and streams that flow into coastal lagoons receive discharges of agricultural, industrial, and urban wastewater, which carry high concentrations of nutrients (Newton et al., 2012). The excessive accumulation of nutrients leads to eutrophy. Phytoplanktonic algae proliferate massively and do not allow light to penetrate to the bottom of the lagoon, which implies a decrease (or disappearance) of the primary producers and a drastic reduction in dissolved oxygen. Coastal lagoons are particularly vulnerable to this phenomenon, which leads to significant losses of biodiversity (Zaldívar et al., 2008), including resident and migratory birds (Fernández et al., 2005).

The ability of coastal lagoons to avoid their ecological degradation due to eutrophication (i.e., their self-purification capacity) depends to a large extent on their water renewal rate (Tett et al., 2003). The frequent (or continuous) entry of seawater in the lagoon helps enormously to renew its waters and to decrease the concentration of nutrients (Roselli et al., 2013). Thus, hydrological balance and water renewal are key factors in the management of coastal lagoons if we want to preserve their biodiversity and the goods and services they provide us. Unfortunately, the vast majority of coastal lagoons now undergo drastic hydrology modifications. The multiple inputs of freshwater from rivers and streams have been reduced to a few inputs, usually in the form of wastewater or return water from irrigation, and seawater inputs have been reduced due to the inability of the lagoons to break the sandbars that separate them from the sea. In this chapter we exemplify this situation with 2 case studies in the Llobregat Delta (Barcelona, Spain): the lagoons of Cal Tet and La Ricarda. In both cases, hydrology has been the key factor in determining their current status of eutrophy. We present these cases as a future learning opportunity to improve the current situation of ecological degradation that affects most of the coastal lagoons around the world (Lotze et al., 2006).

Case study 1: the Cal Tet lagoon

Introduction

The year 1994 saw the beginning of an ambitious project of 6 750 million euros called Delta Plan. Its main objective was to turn the Llobregat River delta into one of Europe's largest logistic platforms. The plan included the following projects: (1) extension of the airport; (2) extension of the port of Barcelona and creation of a large area for logistics activities; (3) diversion of the final section of the river; (4) construction of hydraulic infrastructures (sewage treatment plant and desalination plant); and (5) construction of transport infrastructures (roads and railways). The establishment of the Pla Delta caused the disappearance of wetlands and lagoons of important natural value, both for migratory bird populations and for numerous species of fish, reptiles, amphibians, aquatic invertebrates, macrophytes, and algae (Llorente, 2005). One of the measures used to mitigate the impact of this project, namely the diversion of the river, was the creation of the Cal Tet lagoon, thought to be a refuge of biodiversity in the threatened environment of the delta.

Figure 1: Photo of the study area in 1996 (before the construction of the Cal Tet lagoon, top left), 2003 (when the construction of the lagoon was finished and before the new Llobregat River mouth was excavated, top right), and now (below). In the most recent photograph, the wastewater station of the Llobregat basin, the new mouth of the Llobregat River, and the purification reeds receiving the effluent from the tertiary treatment plant have been marked. Pictures sourced from Google Earth.

The lagoon extends over 95 ha in the flood plain of the river estuary that was formerly occupied by crops and grazing pastures, and it belongs to the network of protected areas of the Llobregat Delta. Cal Tet was created before the new Llobregat River estuary was dug (Figure 1). Land clearing began in 2002, and the works were completed in January 2003 (Seguí & Flor-Arnau, 2015). The lagoon is 1 km long, has a maximum width of 150 m, and occupies an area of 13 ha. Its maximum depth varies between 1.80 and 2.40 m, depending on the time of year (Seguí & Flor-Arnau, 2015).

The proximity of Cal Tet to the sea would qualify it as a coastal lagoon; however, the absence of a direct connection with the sea is completely inconsistent with this type of ecosystem (Kjerfve, 1986). Therefore, it is a system of artificial and atypical origin, fed exclusively from the surface aquifer and rainwater. As shown later in this chapter, during some periods the lagoon was connected to a sewage treatment pond (Figure 1), receiving freshwater with relatively high concentrations of nutrients. This resulted in peculiar hydrological conditions, very different from those expected in a natural system. In this chapter, we will examine in depth the evolution of the abiotic and biotic features of the lagoon from its creation in 2003 to 2016, in order to exemplify the importance of hydrology for the ecological functioning of coastal lagoons and their associated biodiversity.

Materials and methods

The data presented in this article were compiled from several sources. On the one hand, the University of Barcelona generated data in the project called “Monitoring of biological parameters and detection of bioindicators of the system status during the creation of new infrastructures in the Delta del Llobregat” (2003–2005), financed by the Department of Environment and Housing of the Generalitat de Catalunya. On the other hand, Josep Maria Seguí and Núria Flor Arnau collected more data from monitoring macrophytes as indicators of the ecological status of the water bodies, thanks to funding by the Consortium for Protection and Management of the Natural Areas of the Delta del Llobregat (Delta Consortium onwards) and the City Council of Prat de Llobregat. In addition, we have had access to a historical series of water and water quality data generated as a result of the management and monitoring of the lagoon by the Delta Consortium with the collaboration of the municipal laboratory of Aigües del Prat. Finally, we consulted the census of nesting birds in the lagoon, compiled in an unpublished report (Santaeufemia, 2009).

Macrophytes

During the years 2003–2005 and 2009–2016, samplings took place during the months of May and July (Seguí & Pérez, 2006; Seguí & Flor-Arnau, 2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016). Eight sampling points were marked in the lagoon, and a visual inspection was carried out within a 10-m radius. In those areas with presence of macrophytes a hook was thrown in 3 directions, noting the species collected and evaluating the percentage of coating of the area.

Aquatic macroinvertebrates

From June 2004 to July 2005, samples of epiphytic and benthic aquatic macroinvertebrates, and multi-habitat samples (Cañedo-Argüelles & Rieradevall, 2011) were collected monthly. Epiphytic macroinvertebrates were collected using the Kornijów & Kairesalo method (1994), which consists in isolating several stems of *Phragmites australis* (dominant helophyte in the Cal Tet) using a PVC tube

6 cm wide and 50 cm high, and cutting them so that they remain floating inside the tube. The water with the stems was then poured into a tray and the surface was gently scraped to remove the aquatic invertebrates. The surface of the cut stems was measured in order to calculate the density of invertebrates (i.e., individuals per square metre). The benthic macroinvertebrates were sampled using a Van Veen dredge (with a total area of 299 cm^2) in the deepest part of the lagoon. The sediment collected with the dredge was washed and filtered by a 250-µm mesh designed to retain aquatic macroinvertebrates. Finally, the multi-habitat samples were collected by kicking the bottom of the lagoon in the coastal zone, and removing sediment and roots from the helophytes for 1 minute. All the suspended material was captured using a 250-µm mesh. All invertebrate samples were preserved in 70% ethanol and were taken to the laboratory, where all specimens were identified at the lowest possible taxonomic resolution (genus or species for most groups, including Chironomids) following different identification guides and publications (Cranston et al., 1983; Barnes, 1995; Puig, 1999; Tachet et al., 2000; Epler, 2001). Invertebrate biomass was estimated by determining the ash-free weight (550°C for 4 hours) of at least 10 representative individuals of each taxon.

Results

The water level in the lagoon, according to the records of the limnimeter located in one of its arms (Figure 2), has gone through 3 distinct phases. In the first phase, from the lagoon's creation in 2003 to 1500 days later (year 2007), seasonal water level variations were very marked. Water levels dropped dramatically in summer, especially in 2003 and 2005, because the lagoon received water exclusively from the rain and the water table. Both sources of water are notably reduced in summer (precipitation decreases and groundwater level decreases due to reduced aquifer recharge) and, at the same time, higher temperatures lead to greater evapotranspiration.

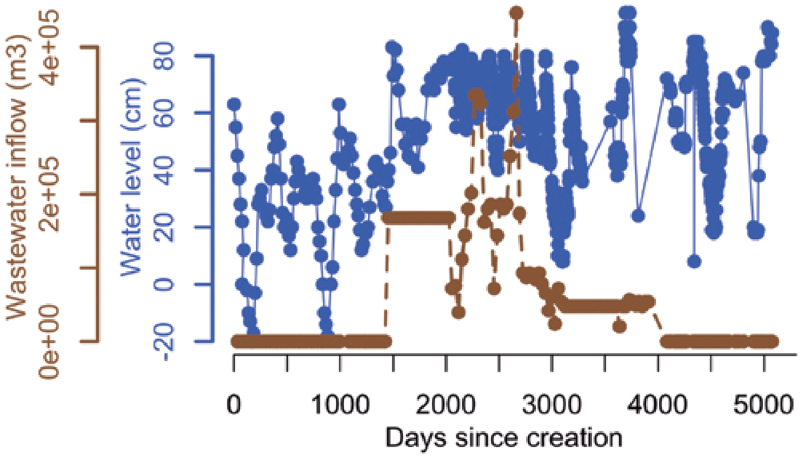

Figure 2: In blue, variations in the water level of Cal Tet lagoon (cm) according to the reading of a limnimeter set in one of the arms of the lagoon. In brown, residual water inputs (m^3 per month) to the lagoon from the purification reeds. The x-axis marks the days since the creation of the lagoon in January 2003.

Aware of the situation, the managers of the lagoon (Delta Consortium) decided to connect the lagoon to the water treatment reeds from the tertiary treatment of the sewage treatment plant. In the second phase, from 1500 to 3000 days (October 2010) after the lagoon was created (Figure 2), tertiary water input led to a significant increase in the lagoon level (from 28 to 64 cm on average) and its stabilization throughout the year (seasonal variability was softened as the residual water inputs were relatively constant). Thereafter the residual water inputs were reduced (third phase), until they stopped about 4000 days after the creation of the lagoon (March 2014). This caused a return to seasonality at the lagoon level, although it remained high (mean of 50 cm) with respect to the first phase (mean of 28 cm).

These hydrological changes in the lagoon were accompanied by significant variations in water quality (Figure 3). Nutrient concentrations increased significantly during the period when the lagoon was connected to the constructed wetlands built for the tertiary treatment of the WWTP. The conductivity increased rapidly during the first phase (mean of 6140 µS·cm^{-1}, maximum of 9800 µS·cm^{-1}), with values especially high in summer. This was due to the decrease in the water level of the lagoon, which brought about an increase in the concentration of dissolved salts (mainly from the intrusion of seawater into the surface aquifer). In the second phase, freshwater inflow from the purification tanks caused a significant decrease in conductivity (mean of 3565 µS·cm^{-1}, maximum of 4733 µS·cm^{-1}). Finally, when the wastewater inputs were removed (March 2014), the conductivity did not increase significantly (Figure 3), probably due to the recharge of the surface aquifer with residual water during the second phase and early third phase. In addition, in the spring of 2014, the meadows surrounding the lagoon began to flood with rainwater and agricultural surplus, which in turn recharged the aquifer with freshwater.

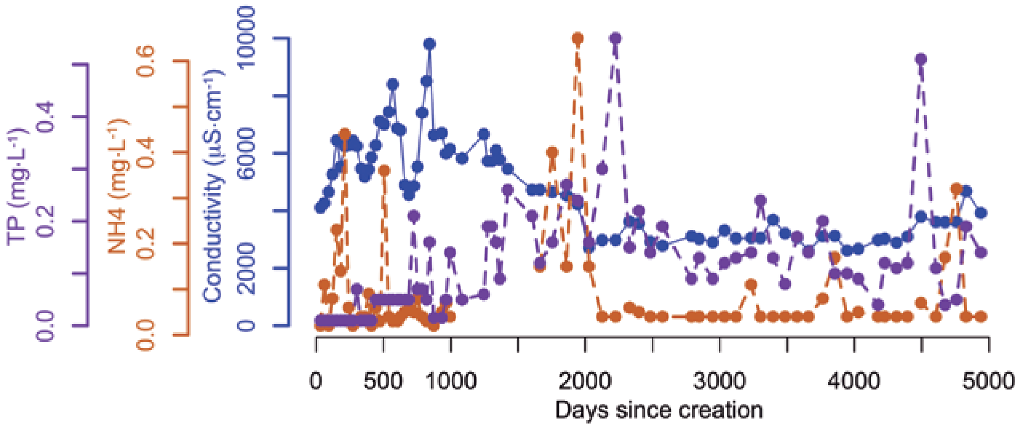

Figure 3: In blue, conductivity (µS·cm^{-1}) and the concentrations (mg·L^{-1}) of ammonia (in orange) and total phosphorus (in lilac) over time (the x-axis marks the days since the creation of the lagoon in January 2003).

Hydrological changes also produced changes in primary production (Figure 4), probably as a consequence of changes in water quality and a complex network of biological interactions (see discussion). During the first phase, the concentration of phytoplankton chlorophyll *a* remained low and relatively constant (mean of 3.56 ± 2.73 µg·L^{-1}, maximum of 28 µg·L^{-1}). In the second and third phases, however, much higher values (mean of 21 ± 25 µg·L^{-1}, maximum of 156 µg·L^{-1}) were recorded. Dissolved oxygen, which is closely linked to primary production, remained around the saturation point (mean of 103 ± 7%, minimum of 73%) in the first phase, whereas in the second and third phases it oscillated more markedly (mean of 87 ± 12%, minimum of 18.3%), and the lagoon even registered anoxic conditions at certain times.

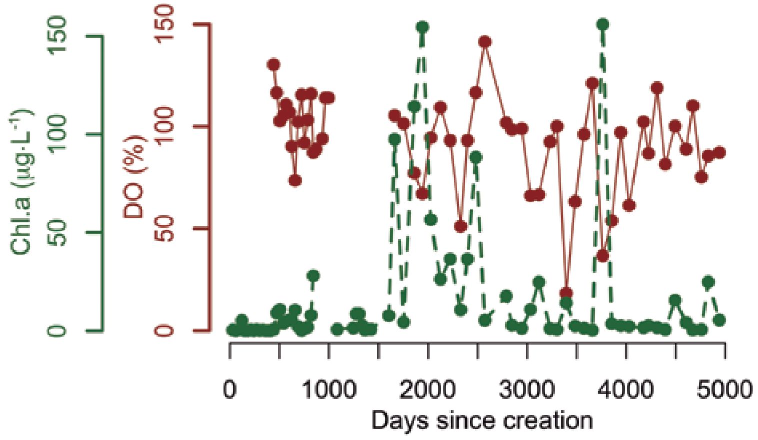

Figure 4: Variation of dissolved oxygen (in red, measured in percentages) and concentration (µg·L^{-1}) of chlorophyll *a* phytoplankton (green) over time (the x-axis marks the days since the creation of the lagoon in January 2003).

Macrophyte populations also showed significant changes over time (Table 1). During the years 2003 and 2004, the community of macrophytes was diverse (11 species in total), and was dominated by abundant populations of charophytes, accompanied by bryophyte *Riella cossoniana* and the angiosperm *Potamogeton pectinatus*. Thereafter, biodiversity declined drastically (4 species in total) and became dominated exclusively by *P. pectinatus*. In response to these changes in the macrophyte community, the community of benthic macroinvertebrates decreased in abundance, biomass, and richness, and became exclusively dominated by the chironomid *Chironomus riparius* (Figure 5). In contrast, the epiphytic community and the lagoon littoral (multi-habitat samples) recorded seasonal variations outside the changes in the macrophyte community (Figure 5). Finally, according to data for the period 2003–2009, bird populations increased significantly during the first year of life of the lagoon (Table 2) and recorded their maximum in 2007 (67 nesting pairs). The most abundant species were the Eurasian coot (*Fulica atra*) and the European little grebe (*Tachybaptus ruficollis*).

	2003	2004	2005	2009	2010	2011	2012	2013	2014	2015	2016
BRYOPHYTES											
Riella cossoniana	++	++	-	-	-	-	-	-	-	-	-
CAROPHYTES											
Chara aspera	+	+	+	-	+	+	+	+	-	-	-
Chara braunii	+	-	-	-	-	-		-	-	-	-
Chara globularis	+++	+++	+	-	+	-		-	-	-	-
Chara vulgaris var vulgaris	++	++	-	-	-	-		-	-	-	-
Chara vulgaris var longibracteata	+++	+++	+	-	+	-	+	-	-	-	-
Chara vulgaris var contraria	-	+	-	-	-	-		-	-	-	-
Nitella hyalina	-	-	-	-	-	-	-	-	-	-	+
Tolypella glomerata	+	+	-	-	-	-		-	-	-	-
ANGIOSPERMS											
Potamogeton pectinatus	++	+++	+++	-	++	+++	+++	+++	+++	+++	+++
Ruppia maritima	+	-	-	-	-	-		-	-	-	-
Zannichellia palustris	+	+	-	-	-	-		-	-	-	-

	Abundance (%)
+++	> 40
++	15 - 40
+	1 - 15
-	0

Table 1: Abundance (by lagoon bottom ranges) of the different macrophyte species in the Cal Tet lagoon over time (Seguí & Pérez, 2006; Seguí & Flor-Arnau, 2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016).

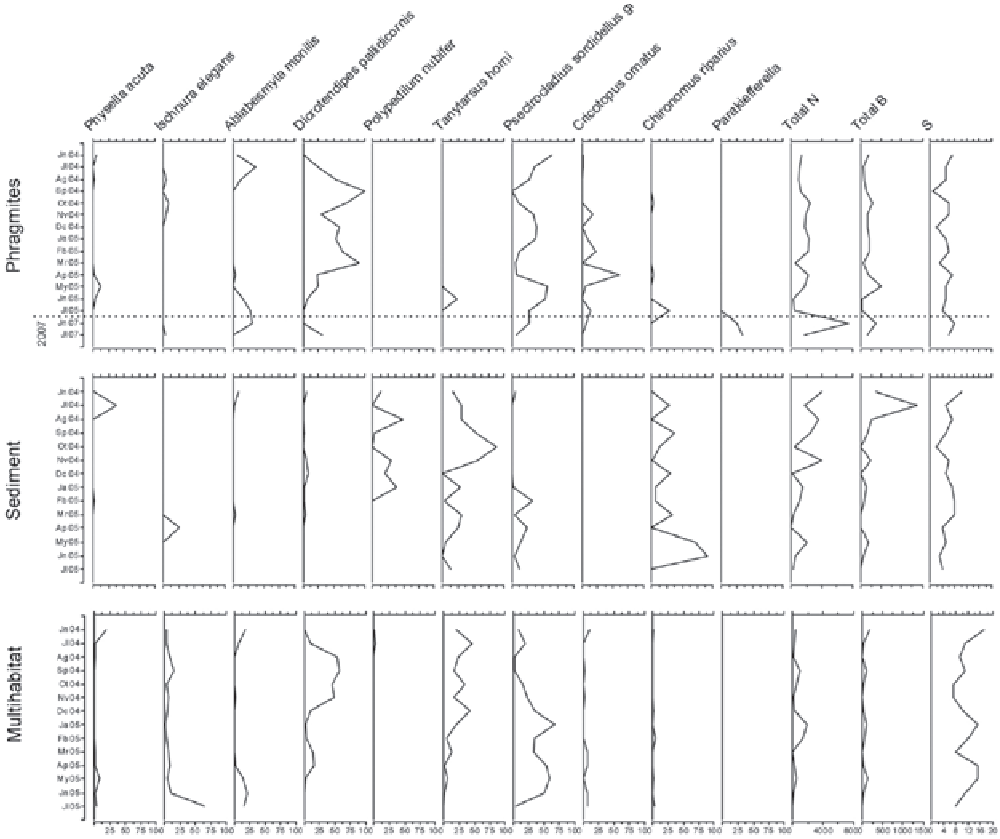

Figure 5: Abundance of the different species of macroinvertebrates in the *Phragmites australis* (top), sediment (centre), and multi-habitat samples (bottom) over time. Abundance (Total N), biomass (Total B), and total richness (S) of invertebrates are also shown.

	2003	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**
Anas strepera	-	-	-	-	-	1	-
Fulica atra	2	22	12	11	40	11	10
Ixobrychus minutus	-	-	1	-	3	4	3
Netta rufina	-	1	2	3	2	-	2
Porphyrio porphyrio	-	-	-	1	2	1	4
Tachybaptus ruficollis	1	12	3	7	20	7	6
Tadorna tadorna	1	2	-	2	-	-	1
Total	4	37	18	24	67	24	26

Table 2: Number of nesting pairs of dominant bird species in the Cal Tet lagoon during the years 2003–2009 (Santaeufemia, 2009).

Discussion

The changes registered in the Cal Tet lagoon from its creation until 2016 show the great importance of hydrological functioning for the biodiversity of the coastal lagoons. During this period, Cal Tet changed from a mesotrophic and oligohaline system characterised by clear waters and dominance of macrophytes to a eutrophic and mesohaline system characterised by turbid water dominated by blooms of phytoplanktonic algae and episodes of oxygen deprivation.

These sudden state changes have been previously described in shallow lakes around the world and are related to the competition between macrophytes and phytoplankton algae for light and nutrients (Scheffer et al., 1993; Scheffer & Jeppesen, 2007). In the case of Cal Tet, the salinity increase is the main factor that motivated the change of state, but many other elements of the ecosystem played a relevant role (Figure 6). Since there was no other water input than the surface aquifer and rainfall, the lagoon dried during the first years of production, causing a drastic increase in salt concentration (initial conductivity of 4110 µS·cm^{-1}; maximum conductivity before receiving water from the retention reeds of 9800 µS·cm^{-1}). This increase in conductivity was probably very damaging to charophyte populations, which usually have maximum salinity tolerances below 3000 µS·cm^{-1} (García, 1999), and benefited the angiosperm *Potamogeton pectinatus*, which is a superior competitor in conditions of high salinity (Lovvorn et al., 1999).

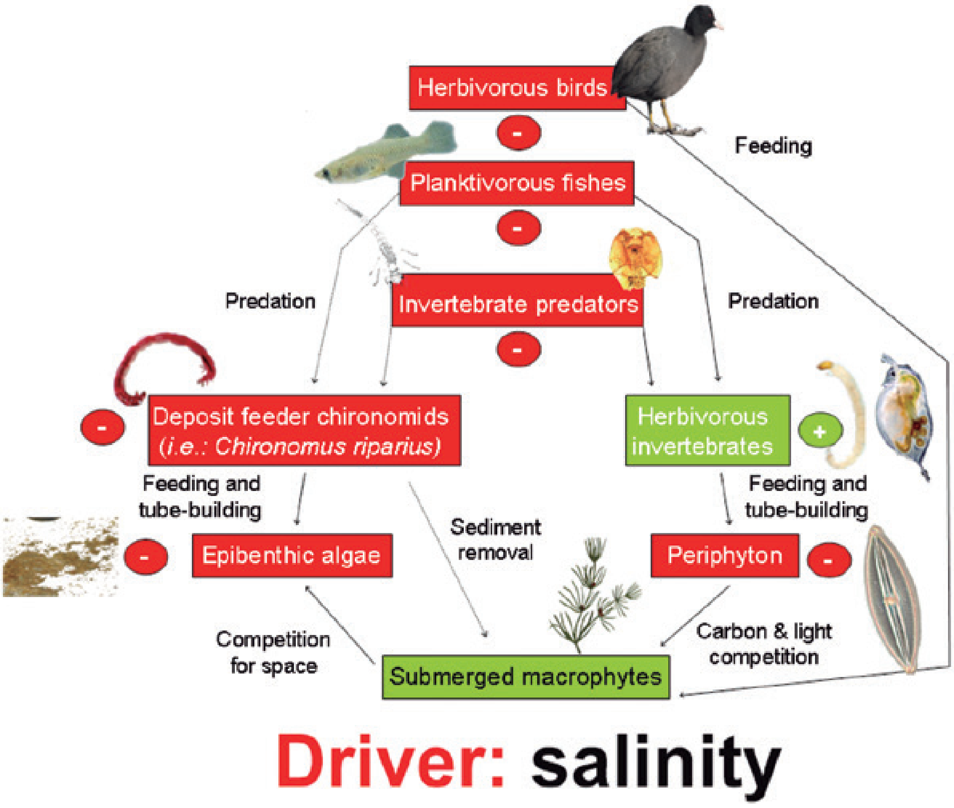

Figure 6: Diagram of the different elements of the ecosystem related to the change of state of the Cal Tet lagoon from a clear phase, dominated by macrophytes, to a turbid phase, dominated by phytoplankton algae. In red, the factors detrimental to the survival of the macrophytes, and in green those that benefit them. Adapted from Cañedo-Argüelles (2009).

At the same time, the populations of cladocera (mainly *Daphnia*) present in the lagoon (Cañedo-Argüelles, 2009) could be reduced due to the increased conductivity, since they do not tolerate salts (Cowgill & Milazzo, 1990; Mount et al., 1997; Bailey et al., 2004; Kefford et al., 2004, 2007). As previous studies have shown, this may have been key to the disappearance of charophytes, since cladocera feed on phytoplanktonic algae, keeping the water clear and allowing light to penetrate to the sediment, where the macrophytes bloom (Bales et al., 1993; Jeppesen et al., 2007). The populations of cladocera were also reduced following the increase in the density of mosquitofish (*Gambusia holbrooki*) (Caiola et al., 2005), which voraciously feeds on zooplankton (Cardona, 2006). Finally, the populations of

Eurasian coot (*Fulica atra*) probably promoted the disappearance of the charophytes, since these constitute one of Eurasian coot's favourite sources of food (van den Berg et al., 1998; Noordhuis et al., 2002).

Beginning in March 2014, the input of regenerated water from the treatment plant to this wetland was stopped in an attempt to restore the lagoon's initial state of clear water and stable macrophyte populations. However, once the change of state occurred (with the replacement of the charophytes by *Potamogeton pectinatus* and blooms of phytoplanktonic algae), different mechanisms prevented the return of the lagoon to the phase of clear water. For example, the disappearance of charophytes, together with the predatory pressure of *Gambusia holbrooki*, led to an impoverishment of the community of benthic macroinvertebrates, which became dominated exclusively by *Chironomus riparius*. This is because charophytes are a key habitat for benthic aquatic macroinvertebrates, as charophytes provide macroinvertebrates with shelter from predators and food in the form of epiphytic algae (Hargeby, 1990; Hargeby et al., 1994; van den Berg et al., 1997, 1998, 1999; Brodersen et al., 2001). Once *Chironomus riparius* became the dominant benthic species, it probably contributed to increasing turbidity by removing the sediment in search of shelter and food (Armitage et al., 1995). At the same time, as the macrophytes disappeared, the shelter for zooplankton was reduced, and zooplankton was then exposed to predation by the fish (Jeppesen et al., 1997, 1998). Finally, the blooms of phytoplanktonic algae prevented the reestablishment of the macrophytes by stopping light from reaching the bottom of the lagoon. At the same time, the absence of primary producers in the lagoon bed, together with the great demand for oxygen that results from the microbial decomposition of dead algae, causes periods of oxygen deprivation (Cañedo-Argüelles et al., 2012a). This prevents the reestablishment of macrophytes and limits the survival of benthic macroinvertebrates to species that tolerate the lack of oxygen, such as *Chironomus riparius* (Penttinen & Holopainen, 1995; Stief et al., 2005), which in turn promotes turbidity. This is called a hysterical response; once the phase is changed, it is not enough to restore the initial conditions of water quality (nutrients and salinity) and return to the phase of clear water (Scheffer et al., 1993; Scheffer & Jeppesen, 2007).

We can conclude that the Cal Tet lagoon is stagnant in a state of turbid waters characterised by the dominance of the angiosperm *Potamogeton pectinatus* and blooms of phytoplanktonic algae. While this does not appear to have significantly affected some organisms (e.g., macroinvertebrate populations on the coast or certain bird populations), it is obvious that the lagoon is not reaching its full potential in biodiversity development. This is due to the artificial hydrology of the lagoon, which makes managing water inputs difficult. On the one hand, depriving the lagoon of water inputs from the water purification reeds of the tertiary process of the treatment plant progressively lowers the water level of the lagoon, increasing the conductivity (something that is detrimental to the charophytes and zooplankton and thus promotes the turbid water phase). On the other hand, the input of freshwater loaded with nutrients from the purification reeds also promotes turbidity, since the nutrients stimulate the growth of phytoplankton algae. Therefore, the return of the lagoon to the clear-water phase is problematic and would require a "naturalisation" of the system hydrology (either by connecting it to the sea or by allowing the entry of oligohaline and oligotrophic waters). In this regard, the recharge of the surface aquifer that has been carried out since 2014 by flooding with runoff water from the wet meadows and marsh rush surrounding the lagoon is a positive step forward, since it stabilises the water level and keeps the conductivity in a fairly stable range.

Case study 2: la laguna de La Ricarda

Introduction

The lagoon of La Ricarda is located 2 km from the present mouth of the Llobregat River (Figure 7), in the municipality of El Prat de Llobregat. It covers an area of approximately 29 ha and is 1.3 km long and maximum 150 m wide. It is a natural lagoon that formerly had been a mouth of the Llobregat River and that fed on freshwater coming from it. In humid seasons, the lagoon received an important quantity of freshwater, which caused a decrease in salinity, mainly in the high part of the lagoon; in addition, the water level increased sharply during the floods of the river or during storms, breaking the sandbar that separates the lagoon from the sea and causing saltwater input. As a consequence, during these stages, the lagoon had much higher salinities near its mouth. In addition, in summer, due to the lack of rainwater and high temperatures, freshwater input was usually scarce and evapotranspiration increased significantly, which caused an increase in the salinity of the lagoon (Hernández & Vázquez-Suñé, 1995). In this way, the lagoon maintained a water dynamics that allowed the renewal of its water and variations of salinity that caused a very wide saline gradient.

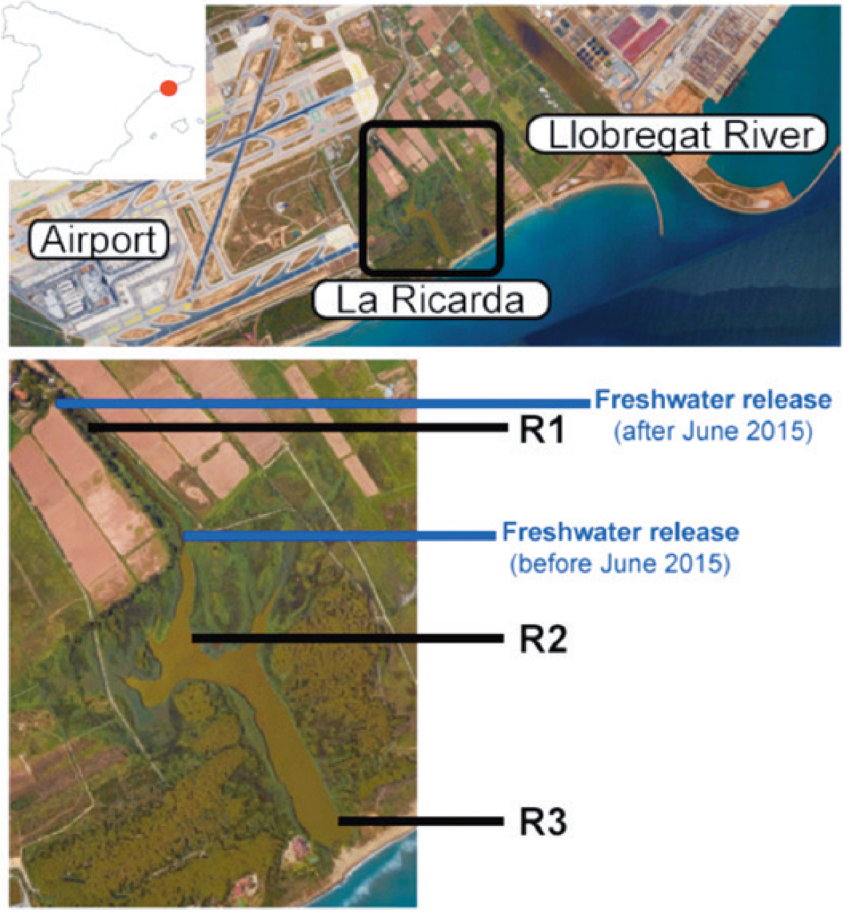

Figure 7: Location (top) and extension (bottom) of the study area in 2017. The 3 sampling points (R1, R2, and R3) and the freshwater inputs from the Barcelona Airport have been marked on the extension of the study area. Pictures sourced from Google Earth.

The expansion of the Barcelona Airport caused the disappearance of the agricultural area draining to the lagoon, and so the lagoon lost its main freshwater input (Figure 8). Later, when the Barcelona Airport expansion project was completed, in 2009, water contributions became almost non-existent and the lagoon level decreased drastically. Thus, during this last period the sandbar could not be broken due to the minimum level that the lagoon had all year round, aggravated by the coastal regression of this stretch of coast. In short, the water dynamics of this lagoon has been clearly affected in recent years.

Figure 8: Photographs of the Barcelona Airport in 2001 (above) and 2016 (below). The agricultural area draining to the lagoon before the expansion of the airport is left blank. Pictures sourced from Google Earth.

In an attempt to restore the balance of the lagoon, the Barcelona Airport, per the Environmental Impact Statement of the airport expansion project, began to provide an artificial freshwater flow to La Ricarda lagoon in 2003 (with well water and water from a deep aquifer). Between 2008 and 2014 these contributions became reused water, and in July 2014 more water from rainfalls and pumped from the aquifer started to flow into the lagoon. In December 2014, the sandbar was artificially opened, but it closed again 3 days later. In June 2015, the location of the tube that contributed the artificial flows of freshwater changed, and is now at the head of the lagoon (Figure 7).

Materials and methods

The data presented here were compiled from data generated by the University of Barcelona and the Delta Consortium. In addition, data from the macroinvertebrate communities of the lagoon for the 2004–2005 period (Cañedo-Argüelles & Rieradevall, 2010) were consulted.

This study is based on a 1-year sampling campaign (June 2014–June 2015). The first sampling took place just before the start of the artificial freshwater supply by the Barcelona Airport. Therefore, data are available prior to the input. Afterwards, subsequent monthly data were collected. Sampling took place at 3 points in the lagoon: a first point very close to the pier (R1); a second point in the central part of the lagoon, at the confluence of the different arms of the lagoon (R2); and a third point very close to the mouth (R3) (Figure 7).

Physicochemical analysis of water

Temperature (°C), conductivity ($\mu S \cdot cm^{-1}$), specific conductance (SPC, $\mu S \cdot cm^{-1}$), pH, oxygen saturation percentage (%), and oxygen concentration ($mg \cdot L^{-1}$) were collected using a multi-parameter probe (WTW, multi-parameter model 197i). In addition, water samples were collected for the analysis of ammonium, nitrates, phosphates, total phosphorus, and chlorophyll *a* in the laboratory following standardised methodologies (Greenberg et al., 2005).

Identification and quantification of plankton

Two types of samples were collected: samples collected with a surface dip net, to identify qualitatively the organisms present, and a volume of 100 ml of water, to analyse quantitatively the individuals present. The samples were preserved in ethanol. In order to proceed to the qualitative and quantitative identification of the organisms present in the samples, the sedimentation protocol in buckets was used, as proposed in the methodology for establishing the ecological status of water bodies, according to the Water Framework Directive (European Commission Directive 2000/60/EC). Once the results were obtained, a SIMPER statistical analysis was performed to establish which species contributed to a higher degree in the differentiation of the groups.

Identification of macroinvertebrates

The sediment samples were collected from the bottom of the lagoon using a dredge; the surface samples were collected with a dip net. The samples were preserved in formol. Due to the minimal presence of macroinvertebrates in the collected samples, the entire volume of all collected samples was observed; so, a total of 19 samples were examined. The organisms were identified at the family level, using the taxonomic key of Tachet et al. (2000). Due to their large indicator role and species richness (Cañedo-Argüelles et al. 2012), Chironomids were identified at the species level under the microscope, following the key of Andersen et al. (2013).

Results

The conductivity profile (Figure 8) shows differences between several sampling points over time can be observed. Point R1, located near the pier, had a lower conductivity than R2 and R3, but the range of variation was relatively low. Point R1 had values between 6000 and 7000 $\mu S \cdot cm^{-1}$, while the closest point to the mouth, R3, had a conductivity range between 7000 and 9000 µS·cm^{-1}. In February, after the sandbar separating the lagoon from the sea opened, the conductivity increased considerably at the 3 sampling points (R1, R2, and R3). However, in the next sampling, conducted in April, the conductivity dropped to values similar to those recorded before the sandbar opening. Finally, the effect of the change of location of the tube that contributes the artificial water input to the lagoon was evident in the values of conductivity of point R1, exactly where the current water supply occurs. The conductivity at this point decreased dramatically in the June 2015 sampling, when the tube location was changed, but no effects were observed on R2 or R3.

In general, the values of dissolved oxygen were low for all the samples (4–10 mg·L^{-1}, Figure 8), except for samples taken in February, after the opening of the sandbar (13–17 mg·L^{-1}, Figure 9). However, it is necessary to emphasise the anoxia phenomena in the deepest layers during the month of October. In the last sampling, in June 2015, once the change of location of the tube supplying the artificial water input to the lagoon had taken place, R1 presented more dissolved oxygen than R2 and R3, unlike in the previous sampling, in April, when R1 was the point where a lower concentration of dissolved oxygen could be observed.

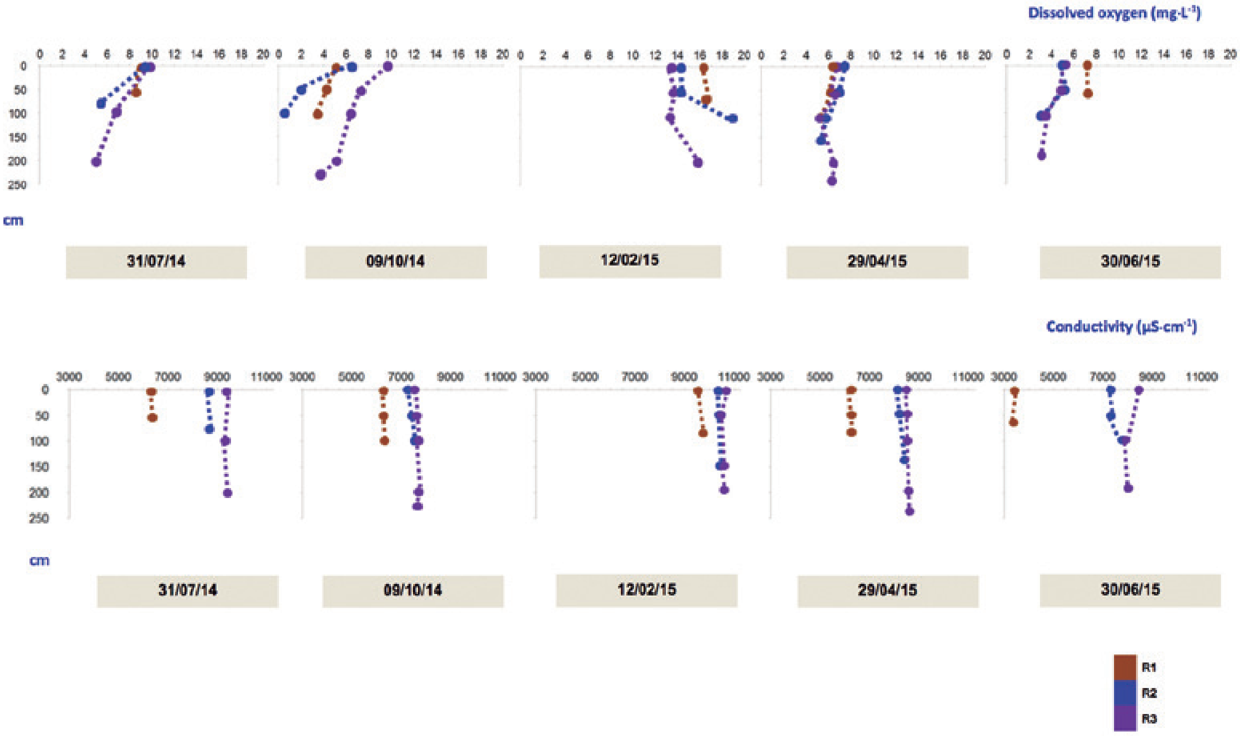

Figure 9: Depth profiles of dissolved oxygen (top) and conductivity (bottom) for each sampling point in the La Ricarda lagoon over the study period.

Phosphorus concentrations were very high, with values between 0.09 and 0.67 mgP·L^{-1} (Table 4). In contrast, phosphate concentrations were very low. The depth of the Secchi disk varied between 19 and 50 cm, and the concentrations of chlorophyll *a*, between 1.19 and 33.5 mg/m^{3}.

Date	**Pier level (cm)**	**Sample point**	**Secchi disk (cm)**	**Total Phosphorus (mg·L^{-1})**	**Phosphate (mg·L^{-1})**	**Nitrate (mg·L^{-1})**	**Ammonia (mg·L^{-1})**	**Chlorophyll *a* (mg·m^{-3})**	**N/P ratio**
ju-14	**60**	**R1**	19	0,67	0,0016	<2	0,06	5,37	3,1
		R2	25	0,29	0,0000	<2	<0,04	12,5	7,0
		R3	28	0,28	0,0006	<2	0,11	26,9	7,5
jul-14	**60**	**R1**	28	0,39	0,0003	<2	0,14	10,6	5,5
		R2	34	0,31	0,0005	<2	<0,04	15,8	6,6
		R3	48	0,3	0,0003	<2	<0,04	17,3	6,8
oct-14	**92**	**R1**	38	0,34	0,0008	1,5	<0,04	24,5	4,5
		R2	33	0,61	0,0013	0	<0,04	15,0	0,1
		R3	35	0,18	0,0005	0	<0,04	33,5	0,2
dec-14	**108**	**R1**	30	0,35	0,0003	0	<0,04	28,6	0,1
		R2	38	0,34	0,0014	0	0,16	2,77	0,5
		R3	40	0,27	0,0003	0	<0,04	23,2	0,1
feb-15	**82**	**R1**	32	0,21	0,0004	1,1	<0,04	10,9	5,4
		R2	29	0,31	0,0009	1,2	<0,04	18,7	4,0
		R3	35	0,09	0,0003	1,1	<0,04	15,4	12,7
apr-15	**80**	**R1**	32	0,22	0,0003	0	0,05	6,81	0,2
		R2	33	0,27	0,0005	0,2	<0,04	1,19	0,9
		R3	42	0,22	0,0008	0,0	<0,04	2,68	0,2
ju-15	**65**	**R1**	50	0,30	0,0004	1,0	0,15	7,64	3,8
		R2	30	0,23	0,0002	0,2	<0,04	17,1	1,0
		R3	29	0,13	0,0002	0,2	<0,04	28,0	1,8

Table 4: Data of the lagoon level, Secchi disk, and concentrations of nutrients and phytoplankton chlorophyll *a* recorded in the lagoon of La Ricarda.

Phytoplankton

A total of 17 phytoplankton species were identified, and the most abundant were *Chlamydomonas* sp. pl. (54.6% relative abundance), *Cryptomonas* sp. pl (36.6% relative abundance), and Peridinium sp. pl. (2.5% relative abundance) (Table 5). It is worth noting the presence of 2 species of potentially toxic cyanobacteria: *Aphanizomenon* sp. pl. and *Anabaenopsis* sp. pl.

Sample	*Aphanizomenon* sp. pl	*Euglena* sp. pl	*Euglena acus*	*Scenedesmus* sp. pl	*Cyclotella* sp. pl	*Synechocystis* sp. pl	*Monoraphidium* sp. pl	*Katodinium* sp
R1_Ju14	43,69	8,74	48,06	4,37	26,21	-	-	-
R2_Jul14	-	17,48	-	-	26,21	-	-	-
R3_Ju14	26,21	-	17,48	-	39,32	-	-	8,74
R1_Oct14	30,58	4,37	-	-	52,43	-	-	-
R2_Oct14	17,48	17,48	-	-	13,11	-	-	-
R3_Oct14	8,74	4,37	74,28	-	4,37	-	-	43,69
R1_Dec14	21,85	-	-	-	-	-	-	-
R2_Dec14	-	-	136,94	-	109,55	-	-	-
R3_Dec14	-	-	82,17	-	82,17	-	-	-
R1_Feb15	4,37	-	-	-	-	-	-	-
R2_Feb15	-	8,74	78,64	-	13,11	-	-	-
R3_Feb15	-	-	-	-	-	-	-	-
R1_Apr15	34,95	21,85	4,37	-	8,74	-	-	-
R2_Apr15	21,85	4,37	48,06	8,74	21,85	-	196,61	-
R3_Apr15	17,48	-	43,69	13,11	8,74	-	524,3	-
R1_Jun15	4,37	-	-	4,37	21,85	-	-	-
R2_Jun15	21,85	26,21	30,58	4,37	65,54	34,95	-	-
R3_Jun15	56,8	8,74	100,49	-	30,58	52,43	-	8,74

Sample	*Anabaenobsis* sp. pl	*Crucigenia tetrapedia*	*Oscillatoria* sp. pl	*Phacus* sp. pl	*Spirulina*	*Goniocloris fallax*	*Peridinium* sp. pl	*Chlamydomonas* sp. pl	*Cryptomonas* sp. pl
R1_Ju14	-	-	-	-	-	-	-	415,07	109,23
R2_Jul14	13,11	-	-	-	-	-	-	655,37	218,46
R3_Ju14	26,21	-	-	4,37	-	4,37	-	218,46	873,83
R1_Oct14	4,37	-	-	-	-	-	594,2	87,38	65,54
R2_Oct14	-	-	-	-	-	-	166,03	174,77	43,69
R3_Oct14	-	-	-	-	-	-	-	436,91	3058,39
R1_Dec14	-	-	4,37	-	-	-	-	2621,48	131,07
R2_Dec14	-	-	-	-	-	-	-	7668,8	1095,54
R3_Dec14	-	-	-	-	-		-	1369,43	5477,71
R1_Feb15	-	-	4,37	-	-	-	-	3495,3	218,46
R2_Feb15	-	-	-	-	-	-	-	3932,22	655,37
R3_Feb15	-	-	-	-	-	-	-	436,91	2403,02
R1_Apr15	4,37	-	-	-	-	-	157,29	131,07	52,43
R2_Apr15	-	-	-	-	-	-	34,95	1223,36	174,77
R3_Apr15	-	-	-	-	-	4,37	-	87,38	611,68
R1_Jun15	4,37	-	-	-	4,37	-	-	87,38	34,95
R2_Jun15	56,8	8,74	-	-	-	8,74	157,29	1135,97	43,69
R3_Jun15	113,6	13,11	-	-	-	4,37	-	218,46	1092,28

Table 5: Abundance of each species of phytoplankton observed in a millilitre of water from the La Ricarda lagoon.

According to the SIMPER analysis, the community of the sampling point located near the sea (R3) was significantly different from that of the middle part (R2) and the head (R1) of the lagoon. Nevertheless, the majority of the species present in summer and winter were different from the rest of the year and similar to each other.

Taking into account the spatial factor, the species significantly associated with each group were the following:

R1: *Chlamydomonas* sp. pl. (47% contribution to group differentiation, being the species that contributed the most), *Cryptomonas* sp. pl., *Aphanizomenon* sp. pl., *Cyclotella* sp. pl.

R2: *Chlamydomonas* sp. pl. (53% contribution to group differentiation, being the species that contributed the most), *Cryptomonas* sp. pl., *Cyclotella* sp. pl., *Euglena* sp. pl., *E. acus.*

R3: *Cryptomonas* sp. pl. (58% contribution to group differentiation, being the species that contributed the most), *Chlamydomonas* sp. pl., *E. acus.*

Taking into account the spatial factor, the species significantly associated with each group were the following:

Winter: *Chlamydomonas* sp. pl. (63% contribution to group differentiation, being the species that contributed the most), *Cryptomonas* sp. pl.

Summer: *Chlamydomonas* sp. pl. (38% contribution to group differentiation, being the species that contributed the most). The contribution in this group is much more distributed among the different species, *Cryptomonas* sp. pl., *Cyclotella* sp. pl., *Aphanizomenon* sp. pl., *Anabaenopsis* sp. pl., *E. acus*.

Macroinvertebrates

In the sediment samples of the lagoon (including the 3 sampling points and all the sampling sites), only 5 individuals of macroinvertebrates were found: an individual belonging to the family (R3 30/06/2015) *Gammaridae* and 4 individuals of the family (R3 10/12/2014) *Planorbidae*. A total of 6 families were found in the littoral samples (collected the 29/04/2015): *Chironomidae, Gammaridae, Mysidacea, Limonidae, Baetidae*, and *Hydrophilidae*. Even so, only 1 individual of each species was found, except in the case of chironomids and gammarids, of which there were 10 and 30 individuals, respectively.

Chironomidae exuviae were identified at species level, and 2 species were identified: *Chironomus nuditarsis*, a species with a wide distribution area and which can be found in water bodies with low concentrations of dissolved oxygen; and another species of the genus *Cricotopus* sp., which could not be classified, due to the lack of its respiratory organ.

Discussion

Firstly, it is important to consider that the contribution of freshwater to the lagoon of La Ricarda was not enough to increase its level considerably and, consequently, the sandbar that separates it from the sea could only be broken once throughout the study period. Therefore, the lagoon's hydrological balance was not restored, since 2 of the factors that influence this balance, the input of freshwater and seawater (Bird, 1994; Smith, 1994; Rosselli et al. 2013) were affected. The reduction of freshwater inputs and the minimum contact of the lagoon with the sea favour the confinement of the lagoon (Tett et al. 2003). The imbalance of the hydrological dynamics of the lagoon also affects the nutrient cycle and favours eutrophic processes (Zaldívar et al. 2008). The eutrophic state of La Ricarda is clearly reflected in several factors. On the one hand, the depth of the Secchi disk was very low, indicating high water turbidity. On the other hand, there were high concentrations of nutrients, especially the concentration of total phosphorus, which was between 10 and 20 times higher than 0.02 mg·m^{-3}, the concentration above which it is considered that a mass of water can suffer eutrophic problems (Vollenweider & Kerekes, 1982). In many cases, the phosphorus concentration exceeded the limit separating eutrophy from hypertrophy, 0.08 mg·m^{-3} (Vollenweider & Kerekes, 1982). In contrast, the phosphate-to-total-phosphorus ratio was very low; this seems to indicate that phosphorus was not dissolved as phosphate in the lagoon water, but it could be in other forms, or organic matter could be present. This may be related to the abundance of cyanobacteria in the lagoon (Aldasoro et al., 2004).

The high oxygen values measured in July 2014, when the lagoon was in a eutrophic situation, are striking (100–130%). At that time, the temperature was high and so was the nutrient concentration, and the algae biomass had grown exponentially, resulting in a period of primary overproduction. This caused excessive algal growth, probably leading to an increase in organic matter (Cloern, 2001; Smith, 2003). The next sampling, in October, indicated that the temperature had dropped and a lot of organic matter had begun to decompose, with the consequent need for oxygen. These processes generate a demand for oxygen that the system cannot supply and, therefore, anoxia phenomena occur (Cloern, 2001; Smith, 2003), as observed in this study. The shallow depth of the lagoon and the fact that the wind can mix it could be favouring the resuspension of the sediments from the bottom of the lagoon and the phosphorus that contains, producing the feedback of the dark phase that is undergoing. All this would mean an internal recycling of nutrients and a high degree of eutrophication of the water body. In short, the hydrological balance of the lagoon has been altered, causing a critical situation of confinement and a typical scenario of a hypertrophic environment.

Our results show important spatial differences in phytoplankton communities. On the one hand, the high conductivity of the R3 point resulted in the dominance of euryhaline species (e.g., *Cryptomonas* sp. pl.), whereas points R1 and R2 were dominated by species more characteristic of freshwaters (e.g., *Chlamydomonas* sp. pl.). Temporality also affected the composition of species and their abundance. Despite these differences, the vast majority of species present in the lagoon are typical of eutrophic environments (Aldasoro et al., 2004). It is important to highlight the presence of *Aphanizomenon* sp. pl. and *Anabaenopsis* sp. pl., 2 species with toxic potential. Their presence was more significant in the summer samples and is entirely related to eutrophic processes. It would be necessary to conduct a specific study to determine if there are toxins in the water of the lagoon or in the trophic network.

The invertebrate communities reflect the state of eutrophy in which the lagoon is now. The sediment of the lagoon was practically devoid of invertebrates throughout the study, indicating that the anoxic conditions of the bottom of the lagoon prevented the survival of aquatic fauna. Coastal samples also reflected an impoverished community, dominated by species tolerant to pollution. This is the case of the chironomid *Chironomus nuditarsis*, capable of living in eutrophic environments with low oxygen availability (Real et al., 2000).

In general terms, it can be concluded that the lagoon of La Ricarda is in a poor state of conservation, immersed in eutrophy. This degradation has been relatively recent, since studies carried out in 2004 and 2005 showed good oxygenation of the water column during most of the year and much lower concentrations of chlorophyll and nutrients (Cañedo-Argüelles et al., 2012a), in addition to an assemblage of macroinvertebrates significantly more abundant and rich in species (Cañedo-Argüelles & Rieradevall, 2010). Therefore, there is an urgent need to improve management to reverse the eutrophication process. This must happen, since it is a protected natural area, classified in the Habitats Directive as a Site of Community Importance (SCI) and declared a Priority Interest Site with the main goal of preserving it.

General conclusions

In this chapter we showed the importance of hydrology in the self-purification capacity of coastal lagoons. In the case of Cal Tet, the confinement of its waters led progressively to a situation of salinization that caused an undesired change of state (from a phase of clear waters to a phase of turbid waters). In the absence of natural freshwater inputs from rivers and streams, it was decided to reverse the situation using wastewater passed through a green filter. This led to a drastic increase in nutrient concentration that strengthened the turbid water phase due to the exponential growth of phytoplanktonic algae. This phase still continues to this day, even though the wastewater supply stopped years ago. In the case of La Ricarda, the reduction of freshwater inputs has led to the confinement of the lagoon (unable to break the sandbar that separates it from the sea due to the lagoon's low water level). In addition, the fact that freshwater inputs occur from a single point has led to the formation of a marked saline gradient (freshwater at the head, seawater at the mouth), unlike the previous state, characterised by brackish water, resulting from the continuous mix of freshwater and seawater inputs. All this has led to an unprecedented eutrophic situation and a worrying reduction of biodiversity.

Taking into account the data presented in this chapter, it seems obvious that both ecosystems would significantly improve if they received sufficient good quality freshwater inputs. This would not only help dilute current nutrient concentrations and improve water transparency, but it would also (in the case of La Ricarda) give the lagoon sufficient hydraulic boost to break the sandbar that separates it from the sea. The connection of the lagoons with the sea supposes an input of water well oxygenated and poor in nutrients, helping enormously in the purification of the water of the lagoon. Although the solution seems relatively simple, it is actually very complicated. In a world where river water is a precious commodity, the freshwater inputs that should be received by coastal lagoons have been used by farmers, industries, and cities, or diverted to the sea to avoid flooding airports and urban areas. Claiming these contributions to safeguard the health and integrity of these ecosystems is therefore difficult, because it conflicts directly with the maintenance of human well-being as we understand it today. Perhaps in the future, hopefully not too long, we will reflect on the great benefits that these ecosystems provide us, as they are vital for the biodiversity of invertebrates, amphibians, reptiles, fish, and birds. Finding a balance between maintaining this extraordinary biodiversity and meeting our needs is complicated but not impossible. Therefore, a joint effort of all the parties involved in the management of the territory becomes indispensable to improve water management so that the water belonging to these ecosystems returns to them if possible, once human needs are met.

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Management and Restoration Actions of Confined Mediterranean Coastal Lagoons in the Empordà and Baix Ter Wetlands

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1. Introduction

In the coast of Girona (NE of the Iberian Peninsula), there are several wetlands associated with the deltaic progradation of the Ter river (Baix Ter wetlands) and of the Muga and Fluvià rivers (Alt Empordà wetlands). Among other coastal water bodies with more or less freshwater influence, there are some brackish or even hyperhaline coastal lagoons, where continuous surface freshwater inputs are inexistent or very scarce. The hydrology of these brackish ecosystems is strongly determined by the sea, although they are separated from the sea for most of the year since the low tidal oscillation in this area poorly affects the lagoons' water level. Because of their isolation from surface freshwater and marine inputs, they have been defined as confined coastal lagoons. Their hydrology is dominated by sudden inputs during sea storms or freshwater flooding events, followed by long periods of confinement without surface water inputs, when lagoons tend to dry out and to increase their salinity (Quintana et al., 1998; Quintana, 2002; Badosa et al., 2006).

Nowadays, confined coastal lagoons in Girona are scarce, restricted to the 2 main nuclei cited (the Alt Empordà and Baix Ter wetlands), both included in the Natura 2000 network. However, it is highly probable that this type of ecosystems was much more abundant in the past, not only in Girona but also in other floodplain areas around the Mediterranean coast (Britton & Crivelli, 1993; Quintana & Marí, 2004; Quintana et al., 2009). Most of these water bodies were desiccated and substituted by residential areas for touristic purposes during the second half of the 20th century (Figures 1 and 2). The factors that probably facilitated it were their location, immediately behind the coastal sand bar, and the relatively easy way to desiccate them (as they are shallow waters, which are not fed by continuous water inputs). Thus, confined coastal lagoons are probably one of the coastal aquatic ecosystems that have suffered more reduction and degradation due to the human development in the Mediterranean shoreline.

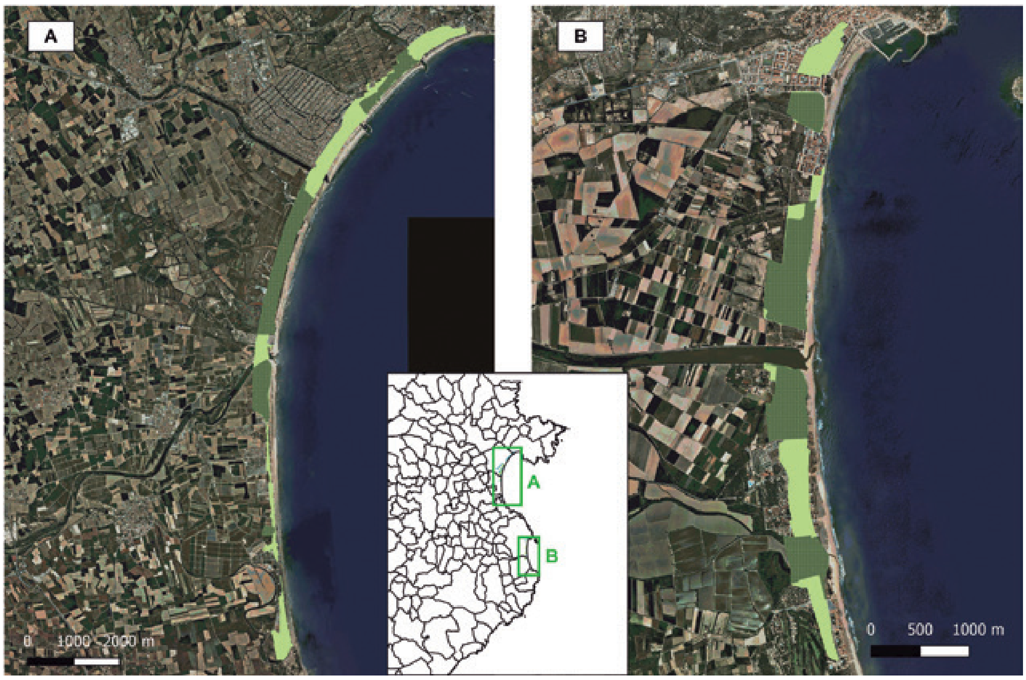

Figure 1: Map showing the current confined coastal lagoons (dark green) very close to the coast (first 100m) in Girona and the probable coastal ecosystems existing in 1950 (light green) and disappeared during the second half of the 20th century.

Figure 2: Comparison of a general view of the town of l'Estartit (Baix Ter) around 1925 (above) and in 2015 (below). A indicates the position of a representative building (Casa Salieti) for reference; B is the position of a confined coastal lagoon, which nowadays has been substituted by a roundabout; C is the old salt marsh surrounding this lagoon, also disappeared and substituted by buildings. *Photos: Museu de la Mediterrània and Josep Pascual.*

The remaining confined coastal lagoons still keep the natural hydrological characteristics based on a flooding-confinement pattern which, in turn, determines nutrient dynamics and species composition in these habitats. Because of the irregular flooding, water level fluctuations are strong (Figure 3), as it is characteristic of Mediterranean aquatic ecosystems (Alvarez-Cobelas et al., 2005; Beklioglu et al,. 2007). Fluctuations in salinity are also strong, depending on the relative amount of marine and freshwater inputs (Table 1). In most of the coastal ecosystems in the Mediterranean Sea, hydrology is strongly modified by humans for irrigation supply or waste water evacuation (Britton & Crivelli, 1993; Morillo & Gonzalez, 1996; Gönenç & Wolflin, 2005). This is not the case of the remaining confined coastal ecosystems, as their hydrology is less affected by human activities. Consequently, confined coastal lagoons still keep several species particularly adapted to these characteristic hydrological conditions. These species are in strong regression due to the fast disappearance of these environments during the last decades (Gosálbez et al., 1994; Quintana & Marí, 2004; Gesti, 2006; Quintana et al., 2009). The importance of the habitats appearing in these environments has been widely recognized by the European Commission, with the inclusion of most of them in the Habitats Directive (92/43/EEC). Some examples of habitats listed in this Directive with a relevant presence in confined coastal ecosystems are habitats of *Salicornia* and other annuals colonizing mud and sand (habitat 1310); Mediterranean salt meadows of *Juncetalia maritimi* (habitat 1410); Mediterranean and thermo-Atlantic halophilous shrubs of *Arthrocnemetalia fructicosae* (habitat 1420); and, finally, coastal lagoons (habitat 1150), which are defined as a priority natural habitat type. Thus, conservation of these environments is essential in a context of global biodiversity conservation in Europe.

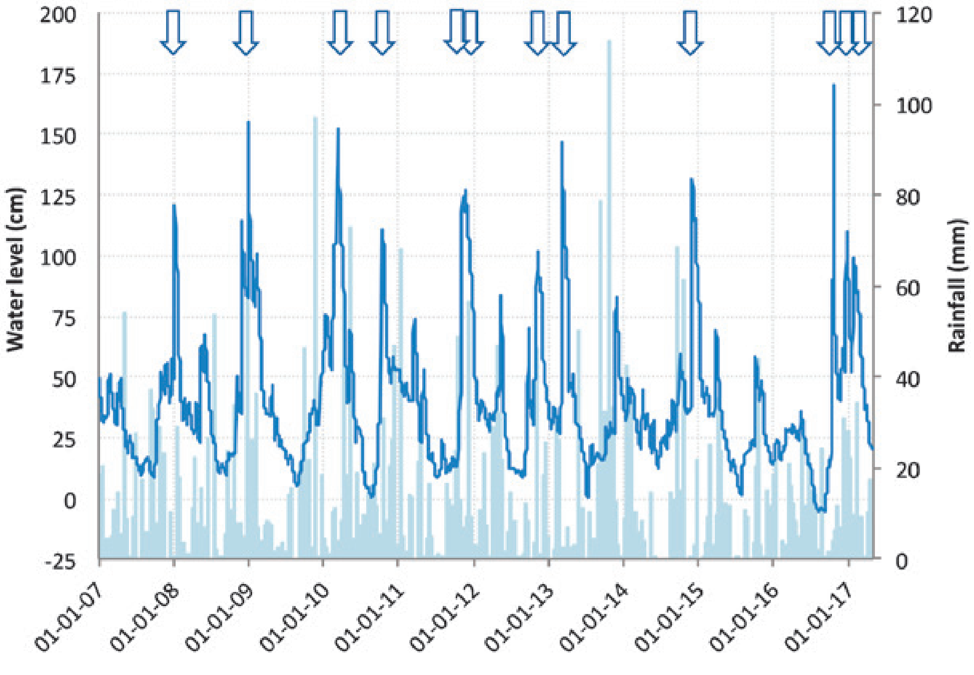

Figure 3: Variations in water level in the Fra Ramon lagoon (Baix Ter Wetlands) during 10 hydrological cycles. The water level is the elevation above sea level of the water surface. Zero water level corresponds to the average sea level in the area between 1990 and 1995. The bars represent rainfall (in mm). Strong water level increases coincide with sea storm events (arrows).

Area	Water body	Period	Conductivity (EC_{25})	NO_3^- (µM)	SRP (µM)	Total N (µM)	Total P (µM)	Chlorophyll (µg·L^{-1})	References
Alt Empordà Wetlands	Connectada	1989/91	34.7 (16.0-51.2)	1.19 (0-9.8)	1.64 (0-5.74)	NA	NA	8.24 (0.25-52)	Quintana et al. (1998)
	Bassa Tamariu	1989/91	25.4 (6.3-41.0)	1.25 (0-8.4)	0.82 (0-2.94)	NA	NA	13.3 (0.25-96)	
	Connectada	1996/98	31.5 (4.4-79.0)	7.19 (0-203)	1.76 (0-46.2)	123.8 (16-616)	4.66 (0.85-46)	12.6 (0.58-120)	Brucet et al. (2005)
	Bassa Tamariu	1996/98	34.9 (4.4-64.0)	3.23 (0-149)	0.90 (0-34.6)	153.1 (46-380)	4.44 (0.63-36)	16.6 (0.46-131)	
	Litoral	1996/98	32.7 (1.2-89.7)	12.1 (0-428)	7.73 (0-73.5)	213.5 (44-1005)	20.3 (0.9-182)	19.6 (0.83-164)	
	Rogera	1996/98	24.3 (6.0-66.1)	8.35 (0-194)	1.92 (0-24.3)	135.3 (45-380)	4.02 (0.59-18)	25.7 (3.34-109)	
	Estany d'en Túries	1996/98	31.4 (6.3-81.4)	6.37 (0-37.3)	3.98 (0-49.6)	186.5 (45-555)	9.43 (0.65-48)	18.0 (0.28-131)	
Baix Ter Wetlands	Fra Ramon	2002/03	41.9 (15-68.3)	1.52 (0.22-6)	0.57 (0-1.54)	223 (78-357)	10.23 (3.74-26)	19.75 (0-137)	Badosa et al. (2006)
	Bassa Pi	2002/03	60.3 (2.5-129)	12.9 (0-126)	2.78 (0.6-6.3)	432 (170-677)	27.7 (3.15-99)	44.8 (0-204)	
	Pletera G02[(1)]	2002/03	31.3 (8.3-56.4)	4.21 (0-34.7)	0.92 (0-3.86)	145 (73-220)	4.48 (1.35-9.9)	5.62 (0-30.8)	
	Fra Ramon	2016/17	63.9 (32.6-91.5)	1.48 (0.28-2.69)	1.60 (0.2-5.65)	418 (3.57-786)	9.21 (1.95-21.7)	NA	This study
	Bassa Pi	2016/17	87.1 (12.8-193)	2.87 (1.6-28.4)	2.97 (0.3-12)	943 (188-2257)	12.34 (0.99-25.5)	NA	
	Pletera G02[(1)]	2016/17	47.5 (19.2-84.4)	1.44 (0.2-1.79)	1.30 (0.2-4.93)	297 (3.57-739)	6.54 (0.92-16.6)	NA	
	Pletera M03[(2)]	2016/17	57.1 (23.5-114)	1.44 (0.21-1.64)	0.39 (0.1-1.18)	323 (3.57-866)	5.86 (2.4-19.22)	NA	

Table 1: Mean and range (in brackets) of conductivity and nutrients of some confined coastal lagoons (surface waters) in the Alt Empordà and Baix Ter wetlands. SRP, soluble reactive phosphate. (1) Artificial lagoon created in 2002 in the framework of the life project LIFE99NAT/E/006386. (2) Artificial lagoon created in 2016 in the framework of the life project LIFE13NAT/ES/001001. NA, non-available data.

2. Ecological characteristics of confined coastal lagoons and associated salt marshes

2.1. Hydrology

The hydrology based on a flooding-confinement pattern is one of the main characteristics of these ecosystems. In these lagoons, the main inputs occur during strong storm events, when not only surface but also subsurface and groundwater inputs take place. These episodes restrict to very few days, and coincide with sea storms and strong flooding events. After them, lagoons remain disconnected from the sea and from any surface freshwater source. As it is typical of Mediterranean climate events, flooding events occur randomly along the year with no clear seasonal pattern, except that they are more frequent in winter and are especially rare in summer. The frequency of the sea storms per year is also variable and has increased during the last decades, from 2-3 per year during the 70s to 5-6 per year in the first decade of the 21st century (Pascual et al., 2012). No more surface water inputs are significant apart from the flooding events, but groundwater inputs feed the lagoons for a longer time period (1-2 months after the flooding event, depending on its intensity). Groundwater inputs are very important in this system since they allow the persistence of these lagoons during dry periods. These inputs consist of a mixture of sea and fresh groundwater, which may suppose, for instance, between 20 and 60% of freshwater in Fra Ramon lagoon (Menció et al., 2017).

Most of the year these lagoons remain confined, with much reduced surface and groundwater inputs, especially in summer (Figure 4). During confinement, water level decreases and salinity increases due to evaporation. The degree of confinement, together with the mixture of sea water, freshwater and groundwater, determines the salinity of the lagoons. Salinity usually ranges from brackish (conductivity close to 20 $mS{\cdot}cm^{-1}$) to hyperhaline (more than 60 $mS{\cdot}cm^{-1}$) but outlayer values of <1 and >120 $mS{\cdot}cm^{-1}$ are also recorded (Table 1). A high degree of salinity stratification may appear at a short depth during groundwater inputs and it tends to disappear with confinement (Figure 5). Thus, not only a high salinity but also its high temporal and spatial variability are features of this type of lagoons (Quintana et al., 1998; Brucet et al., 2005; Badosa et al., 2006).

2.2. Nutrient dynamics

The flooding-confinement pattern strongly determines nutrient dynamics, which is more related to internal loading processes than to external nutrient supplies, as it is characteristic of chocked coastal ecosystems (Gilbert et al., 2010). During confinement, lagoons concentrate organic matter and total nutrients, which are especially high in summer (Table 1). However, different patterns were observed in inorganic nutrients (Quintana et al., 1998; Badosa et al., 2006; López-Flores et al., 2006a; 2014): while phosphate tends to accumulate with confinement as organic matter does, inorganic nitrogen concentrations peak with flooding events, but disappear fast with confinement (Figure 6).

Figure 4: Aerial view of *els estanys d'en Túries* coastal lagoons (Alt Empordà wetlands) in the period previous to desiccation, when confinement is the highest. *Photo: Parc Natural dels Aiguamolls de l'Empordà.*

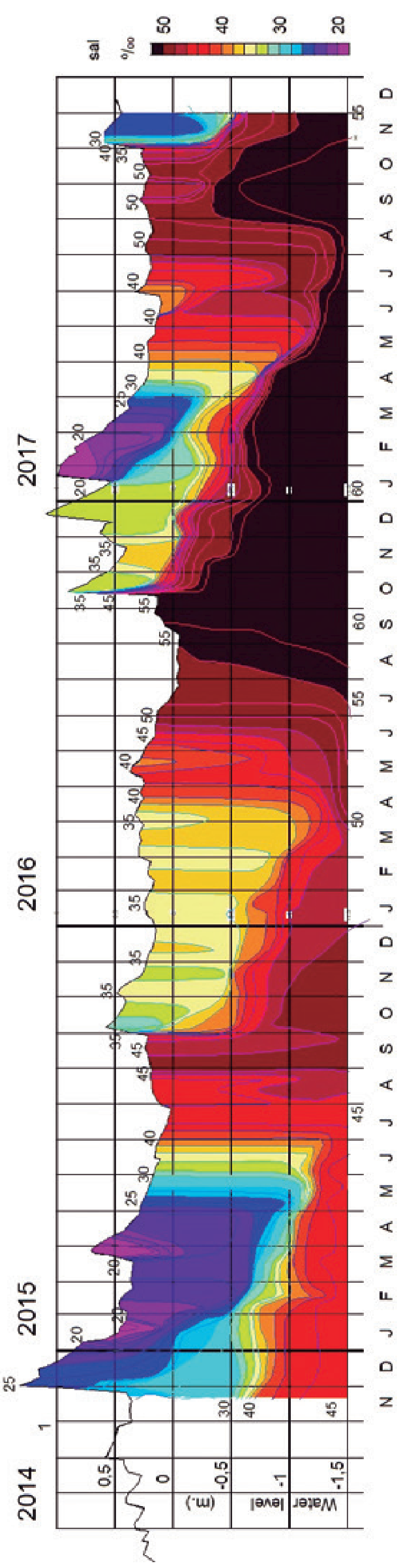

Figure 5: Salinity isolines (‰) in Fra Ramon lagoon (Baix Ter Wetlands) during several annual cycles (2014-2017). The vertical axis represents the elevation (in m) of the lagoon surface above the sea level in this zone between 1990 and 1995. The figure also shows the stratification in winter due to groundwater inputs and the uniform increase of salinity during summer due to confinement.

López-Flores et al. (2014) found that denitrification rates are always higher than nitrification ones, resulting in a net loss of inorganic nitrogen if nitrogen inputs do not compensate it. Thus, the balance between nitrification and denitrification processes may explain these intense nitrogen losses. This pattern affects all the inorganic forms of nitrogen since reduced nitrogen forms (such as the ammonia generated with organic matter mineralization) are firstly oxidized to nitrate via nitrification, but later lost to the atmosphere via denitrification. On the other hand, phosphate dilutes during flooding events and tends to concentrate during confinement. The simultaneous accumulation of phosphate and loss of inorganic nitrogen lead to especially low N/P ratios, what has been defined as a differential confinement of nutrients (Quintana et al., 1998). The consequence is the nitrogen limitation for phytoplankton growth (López-Flores et al., 2006a; 2009; 2014). Such differences in accumulation in other conservative and non-conservative compounds were also found: some persistent pesticides and heavy metals tend to concentrate during confinement, while some more degradable pesticides appear only when the water turnover rate is high due to runoff (López-Flores et al., 2003; Salvadó et al., 2006).

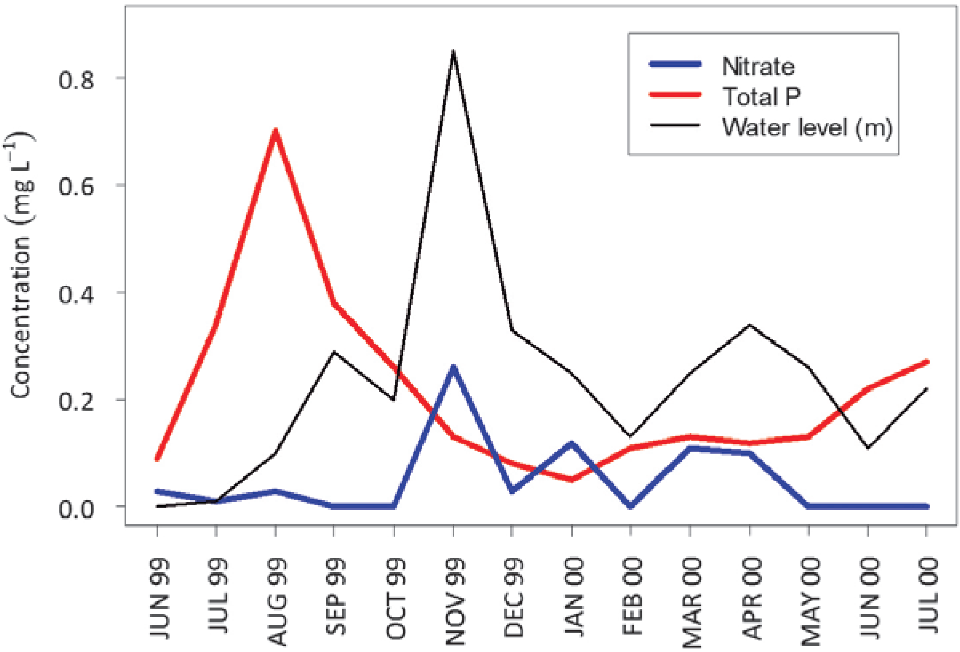

Figure 6: Variations in nitrate and total phosphorus concentrations in Fra Ramon lagoon (Baix Ter Wetlands) during an annual cycle. Adapted from Badosa et al. (2006).

2.3. Community structure

Water level fluctuations, salinity variability and nutrient dynamics resulting from the flooding-confinement pattern strongly determine species composition and community structure in confined coastal lagoons (Brucet et al., 2005; Gascón et al., 2005; López-Flores et al., 2006b; Quintana et al., 2006). Although a lot of marine or freshwater species may arrive during flooding events, only a few euryhaline species that tolerate the adverse conditions found in these habitats achieve stable populations. Thus, some compartments of the trophic structure are frequently covered by close-to-monospecific assemblages. This is the case of macrophyte meadows, dominated by a single species of *Ruppia* genus (Gesti, 2006), which adapts its reproductive behaviour as it grows in temporary or permanent areas (Gesti et al., 2005). The surrounding vegetation is also composed of few species tolerating inundation with saline water, such as *Salicornia patula, Sarcocornia fruticosa, Juncus acutus, J. maritimus*, and *Halimione portulacoides*, organized in a topographic gradient, depending on their tolerance to flooding duration (Gesti, 2006). The lack of inorganic nitrogen in water strongly determines phytoplankton species. Thus, species composition of planktonic primary producers is dominated by unicellular *Synechococcus*-like cyanobacteria, which can fix atmospheric nitrogen, or by mixotrophic species, such as dinoflagellates, haptophytes or cryptophytes, which can uptake nitrogen by consuming bacteria. Organisms more dependent on dissolved inorganic nitrogen, such as diatoms or chlorophytes, are scarce (Quintana & Moreno-Amich, 2002; López-Flores et al., 2009; 2014). Microbial community structure has been traditionally overlooked in Mediterranean coastal lagoons. As a recent study found out (Frederic Gich, unpublished data), the bacterial functional gene *nosZ* involved in the last denitrification enzymatic step and the functional gene *nrfA* involved in dissimilatory nitrate reduction to ammonia (DNRA) are present in several Baix Ter lagoons at similar gene copy numbers (from 10^4 to 10^7 gene copy numbers per milliliter). Thus it demonstrates the genetic potential of the community to reduce nitrate to nitrogen gas or ammonia. Since DNRA is favoured when there is a high availability of organic matter relative to nitrate (Fazzolari et al., 1998; Nizzoli et al., 2010), we can envisage that ammonification could be important during confinement periods. Then, surrounding plant detritus containing nitrogenous macromolecules, such as nucleic acids, proteins and amino sugars, would be decomposed to ammonia in anoxic conditions while denitrification could be predominant after freshwater inputs containing nitrate.

In the absence of fish, such as in temporary or semi-permanent lagoons, dominances of different species of invertebrates follow one another over time according to the flooding-confinement gradient. Rotifers (*Synchaeta* spp.) dominate in flooding periods, but they are then substituted by calanoid copepods (mainly *Eurytemora velox* or *Calanipeda aquaedulcis*). During stable conditions when water level is close to desiccation dominant species depends on trophic state: rotifers (*Brachionus* spp.), amphipods (*Gammarus aequicauda*) or jellyfish (*Odessia maeotica*) (Figure 7). Cladocera are absent or very scarce. Calanoid dominances exceeding 90% of total individuals remain during weeks or even months if stable conditions are not interrupted by any hydrological disturbance (Brucet et al., 2005). During calanoid dominances body size arises as an important factor in the structuring of aquatic invertebrate community (Brucet et al., 2006): adults and juveniles of the same species play a different trophic role, thus reducing intraspecific competition when nutrient availability is scarce (Brucet et al., 2008; Quintana et al., 2015). Benthic community structure is not so dependent on the temporal flooding-confinement pattern (Gascón et al., 2005). While water column assemblages are similar in different water bodies, but with a high temporal variability, benthic macroinvertebrates depend more on space related variables, such as water permanence or substrate granulometry (Gascón et al., 2007).

One of the most characteristic fish species of confined coastal lagoons is the Iberian toothcarp (*Aphanius iberus*), an endangered cyprinodontid fish, endemic of the Iberian Peninsula, included in annex I of the Habitats Directive (Doadrio et al., 2011). Dense monospecific populations of the Iberian toothcarp are common in fish assemblages, especially during confinement, when the water level is the lowest and fish concentrate in permanent water refuges (Moreno-Amich et al., 1999). Iberian toothcarp strongly adapts to the fluctuating conditions of these waters tolerating a wide range of salinity. It also acts as a top predator, originating a conspicuous size-based trophic cascade

(Compte et al., 2012), which causes an increase in water clarity and macrophyte density. Besides habitat reduction, one of the main problems of Iberian toothcarp conservation is the presence of the mosquitofish (*Gambusia holbrooki*), an invasive North American species, introduced in the Mediterranean area at the beginning of the 20th Century for mosquito and malaria control purposes (Doadrio et al., 2011). Nowadays, due to the presence of mosquitofish, Iberian toothcarp is relegated to habitats with high salinity fluctuations that limit mosquitofish invasive success (Alcaraz & Garcia-Berthou, 2007; Ruiz-Navarro et al., 2011).

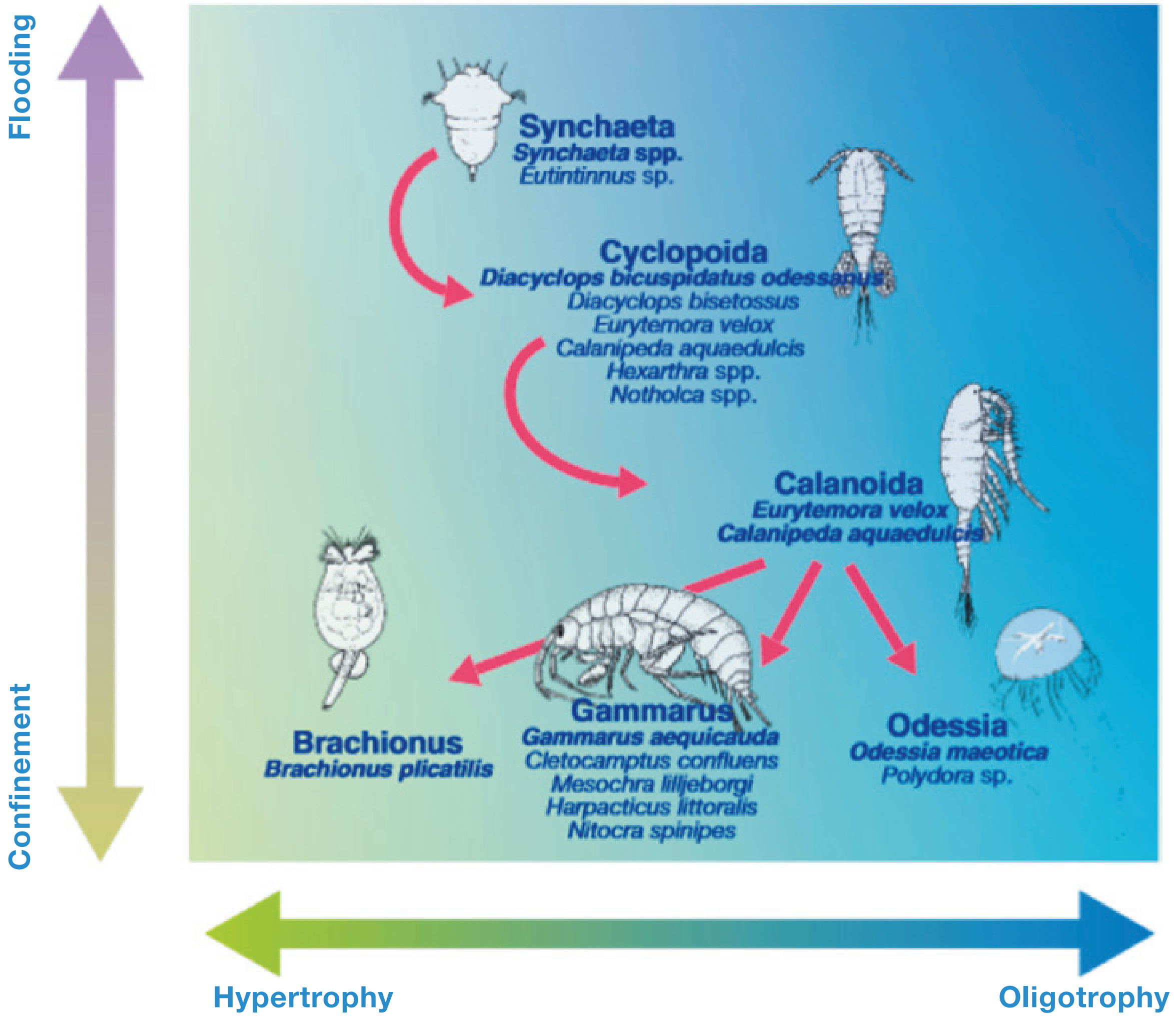

Figure 7: Conceptual model of plankton succession in fishless confined coastal lagoons. Drawing by J. Corbera reproduced from Boix et al. (2015) with permission.

3. Management and restoration of confined coastal lagoons

3.1. Flux regulation in Alt Empordà salt marshes and their ecological consequences

In 1989, few years after the creation of the Empordà Wetlands Natural Park in Alt Empordà wetlands, managers of the new park decided to increase the flooding duration in the salt marshes. The arguments were clear: in the 1950s a drainage channel was built to drain the salt marsh and to reduce flooding duration. Later, in the '70s, a residential project was proposed in the area, but it was cancelled, because people protested against the descruction of the salt marsh. Therefore, with the creation of the Natural Park, it was high time to recover the flooded surface. With this purpose, park managers installed a sluice gate in the drainage channel built in the 50s, thus deviating surface freshwater inputs to the confined coastal lagoons. Due to this flux regulation, surface freshwater flooding mainly circulated through the coastal lagoons instead of evacuating directly to the Fluvià river estuary and the sea (Figure 8). This change in the flooding pattern caused several effects in nutrient dynamics and species composition of these lagoons (Quintana et al., 1998; 1999; Brucet et al., 2005):

- As expected and desired, water level remained higher than before, enlarging the hydroperiod of the salt marshes.

- Average salinity tended to decrease with the increase of freshwater inputs, as salinity variability did.

- Together with freshwater inputs, there was an increase of nitrate inputs, which caused a change in the N/P ratio. An N limitation before flux regulation (NO_3^-/SRP<1) changed to a high availability of inorganic N during freshwater flooding (NO_3^-/SRP>100).

- The high amount of nitrate entering in a strong N limited system caused eutrophication of the lagoons and the increase of the frequency of hypertrophic events during confinement periods.

- Species composition changed dramatically, with a strong reduction of species adapted to confinement conditions and their substitution by species typical from eutrophic oligohaline waters.

After seeing this negative effect, park managers decided to change how the sluice gate works. Currently, the sluice gate is used to control water level so that it avoids the excessive drainage of the salt marsh but ensures that the excess of freshwater floods directly to the sea and is not diverted to the confined lagoons.

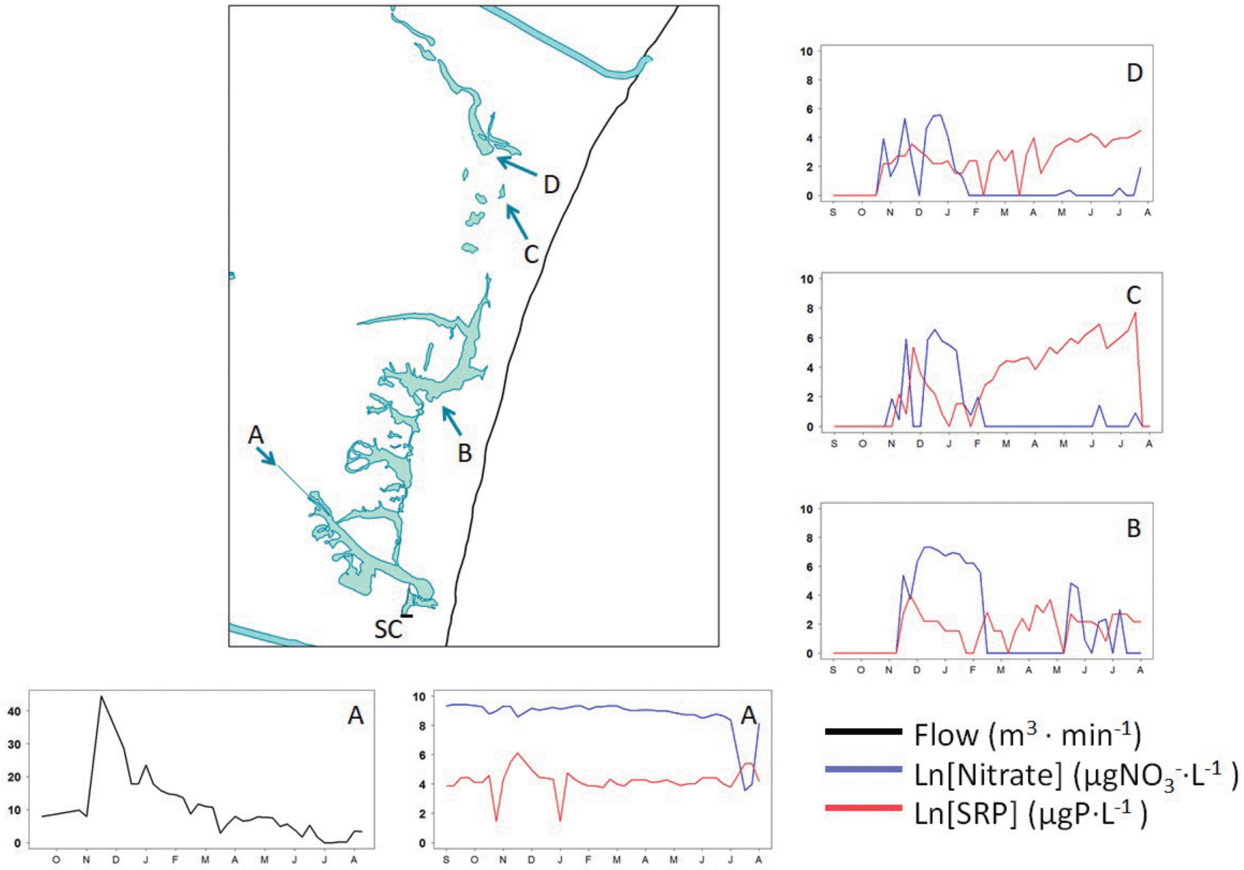

Figure 8: Flux regulation effects in Alt Empordà salt marshes as a consequence of the installation of a sluice gate (SC) in the output channel. The figure shows seasonal variations of freshwater inflow entering through *Rec Corredor* (A) and of nitrate and SRP concentrations in different water bodies. High N/P ratio waters from the *Rec Corredor* flooded low N/P ratio waters from the coastal lagoons (B, C, and D) causing eutrophication. Nitrate picked during the flooding period (December-March) while phosphate increased during confinement, coinciding with hypertrophic events. SRP, soluble reactive phosphate. Adapted from Quintana et al. (1999).

3.2. Iberian toothcarp conservation efforts

The Iberian toothcarp is an example of species negatively affected by the flux regulation during the 90s in the Alt Empordà salt marshes (Moreno-Amich et al. 1999). The increase in eutrophication, as well as the reduction of average salinity and variability, allowed the spread of the invasive mosquitofish, which is more adapted to those new freshwater flooding conditions (Rincón, 2002; Alcaraz & Garcia-Berthou, 2007; Ruiz-Navarro et al., 2011). The current management of the sluice gate and the consequent reduction of freshwater flooding in the confined lagoons have promoted the recovery of the Iberian toothcarp populations in the Alt Empordà salt marshes.

In La Pletera salt marshes, in Baix Ter wetlands, three new permanent lagoons were created in 2002, in the framework of a Life Nature project (Life Ter Vell-Pletera, LIFE99NAT/E/006386). The aim of the project was to increase the number of refuges for the Iberian toothcarp populations in this area (Quintana & Marí, 2004; Quintana et al., 2009). The recent lagoons were repopulated with close to 400 Iberian toothcarp individuals immediately after their creation. Short term repopulation was successful, and Iberian toothcarp density increased one order of magnitude per year (Badosa, 2007). However, on the long term, Iberian toothcarp density declined due to the arrival of mosquitofish, affecting not only the created lagoons but also the natural ones (Pou-Rovira, 2009). A very strong freshwater flooding event caused by strong rainfall in October 2005 (Pascual et al., 2006) might be the cause of mosquitofish arrival to La Pletera confined coastal lagoons. Since then, the Iberian toothcarp and the mosquitofish coexist in the area, with strong population oscillations in both species, being mosquitofish more abundant in oligohaline waters and Iberian toothcarp in conditions of high salinity fluctuations. Thus, a high salinity concentration or variability is basic for the conservation of the Iberian toothcarp populations in lagoons where mosquitofish is present.

One relevant aspect that was not considered during the construction of the lagoons in 2002 is the importance of the sedimentary pattern and the groundwater supplies. In La Pletera salt marshes, groundwater may account up to 80% of the total water circulation (Menció et al., 2017). A thin sediment layer with very low permeability situated at shallow depth (between 30 and 90 cm from the surface) makes the input of groundwater in the lagoons difficult (Geoservei, 2016). The creation of lagoons in 2002 was simply based on the building of a hole below sea level, which ensured water permanency all year round. However, substrate composition was not considered, so the impermeable layer was most probably removed during the works. The high permeability of the new lagoons may facilitate the input of groundwater, with a salinity close to 20 $mS \cdot cm^{-1}$, which enables mosquitofish persistence.

3.3. Criteria for restoration of confined coastal lagoons in Baix Ter wetlands

In Baix Ter wetlands a restoration project was developed in La Pletera salt marshes (Life Pletera; LIFE13NAT/ES/001001). This zone was affected by building works for a residential estate in the late 80s, and then discontinued in the 90s. The aim of the project was to recover the ecological values of these salt marshes, altered by the building works. With this purpose, the remaining urban features (promenade, accesses, filling material, breakwaters, and debris) were dismantled and substituted by a coastal ecosystem. Several confined coastal lagoons were surrounded by the corresponding salt marsh vegetation, separated from the sea by a well-constituted dune (Figure 9). Five criteria prevailed in the excavations for lagoon creation and removal of the human-made elements. Their order was hierarchical so that none of them applied unless the former criteria were met. These criteria were:

1) The conservation of the ecological functioning of the coastal ecosystem. The new structure of the restored salt marsh must guarantee that the typical ecological processes of the lagoons (described in section 2) will work properly in the future. With this purpose, the restored ecosystem was organized following the usual spatial structure of confined coastal wetlands in natural conditions, which consist of the following bands running parallel to the coastline:

- a band of coastal dunes made up of mobile dunes and the foredune;
- a gradient band consisting of a mixture zone of dunes and salt marshes;
- a band of lagoons formed by several permanent confined lagoons distributed parallel to the sea;
- a band of salt marshes formed by halophilic vegetation allowing lagoons to overflow during flooding events.

Figure 9: Aerial view of the restored area in La Pletera (Baix Ter wetlands) before (up) and after (down) the restoration.

Hydrology must follow the flooding-confinement pattern with no continuous inputs of surface freshwater sources. It will maintain the characteristic nutrient dynamics and community structure of these habitats, as described in sections 2.2 and 2.3.

2) The improvement of the existing colony of the Iberian toothcarp with the creation of more population nuclei. Two issues were considered here. Firstly, several permanent water bodies remain isolated during confinement periods but connected during flooding events. This structure promotes habitat diversification and ensures the permanent availability of refuges suitable for Iberian toothcarp, either during dry or wet years. Secondly, permanent water bodies were built by excavating the sediment below sea level, but taking into account the sedimentary pattern, and ensuring that the impermeable layer was not removed (Geoservei, 2016). It facilitates higher salinity conditions during confinement, which are suitable for Iberian toothcarp permanence (as discussed in section 3.2.).

3) The non-intervention in areas still keeping salt marsh vegetation, since the filling done during the urbanization process did not fill up the whole salt marsh area. Thus, the remaining areas still covered by coastal habitats included in the Habitats Directive (such as those listed in section 1) should be kept.

4) The recovery of the topographical levels existing before the urbanization process. It is important to stand out that this is not the main restoration rule, as it is in most restoration projects. It means that we did not use the morphology of the original salt marsh as a reference for the building of the new morphology. On the other hand, we only apply it when the three former criteria were met. Trying to reproduce the old morphology does not make sense when the salt marsh has been strongly altered by the building works.

5) The design of a new topographic distribution that in the future recalls the existence of an unfinished development process in the area. It is not the aim to reproduce a pristine salt marsh as if it was never altered and destroyed, but to remember that there was a failed urbanization process and that the salt marsh ecosystem is not an original system, but rather a restored and recovered one. With this idea, the old accesses and promenades turned into lagoons and depressions; the old roundabouts became separations between permanent water bodies and one of the old electric transformers now shelters a hide for bird watching.

3.4. Restoration in a global change scenario

In the current context of global change, the area of La Pletera has recorded an average increase of sea level of 5 mm·year^{-1}, an increase in the average frequency of sea storms, and a backward of the coastline of about 1 m·year^{-1} during the last decades (Pascual et al., 2012). Occasional river flooding events, which can regenerate the confined lagoons, are not possible in the area as long as the last reach of the Ter River is dammed and channelled, and rock armour embankments on both shores protect it from overflowing. Nowadays, the relatively short dimensions of the area and the unpredictability of the effects of a river flooding advise against the occasional river flooding through the salt marsh.

In the short term, a modelling approach (Figure 10) of the current possible effects of a strong sea storm compared with those of the presence of the withdrawn human-made elements shows that the removal of the human-made structures in La Pletera increases the capacity of the salt marsh to laminate water during sea storms and reduces sea water intrusion into adjacent crop fields (Solà et al., 2016). In the very long term, one of the main problems on the coast of Catalonia is the presence of infrastructures close to the sea (train rails, motorways, promenades, breakwaters), which do not allow a gradual shift of the sea coast and of the coastal ecosystems into land (Sabater et al., 2017). The designed soft structure, based on bands and with the absence of any hard barrier, appears to be the best way to mitigate climate change effects in this coast.

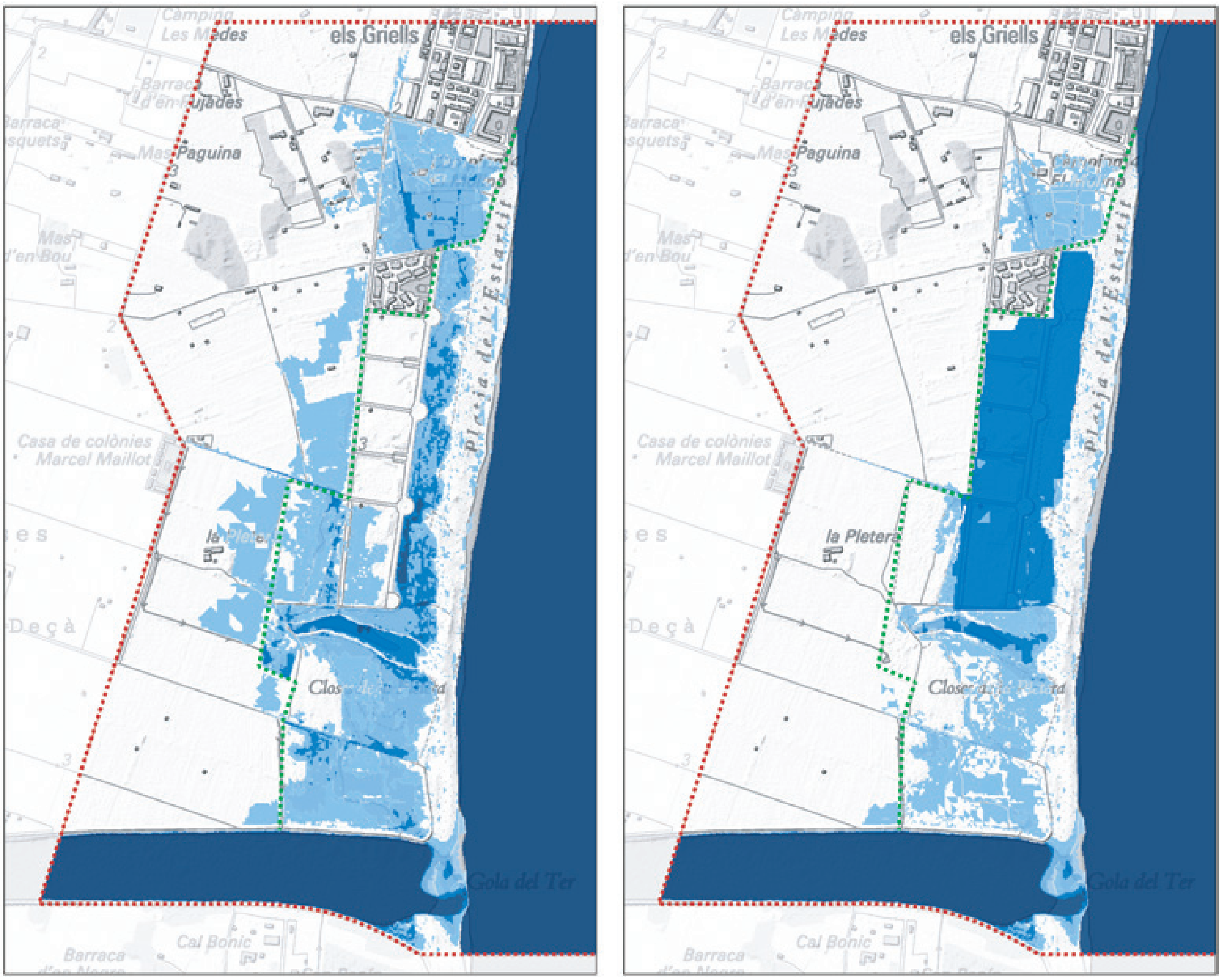

Figure 10: Results of the hydraulic model, developed in the framework of the projects Life Pletera (LIFE13 NAT/ES/001001) and Life Medacc (LIFE12ENV/ES/000536), showing the expected effects of an intense sea storm in the area of La Pletera salt marshes before and after the restoration actions. The presence of the man-made elements before the restoration (left) avoided the flooding of the salt marsh and caused marine intrusion in the adjacent farmlands. With the removal of these elements (right) the sea water inputs during a sea storm do not overcome the salt marsh area. Red dotted line, limit of the Nature 2000 area; green dotted line, limit of the public coastal domain.

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The “malladas” of La Devesa de El Saler: The recovery of a set of coastal interdunal lagoons in the Albufera Natural Park

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1. Introduction

The Albufera Natural Park (Valencia, Spain) is a protected area, partially surrounded by the city of Valencia and its metropolitan area, which shelters around a million and a half inhabitants (Figure 1). Broadly speaking, the park comprises three types of ecosystems: 1) a shallow freshwater lake (approx. 2800 ha), homonymous to the park, connected to the sea by artificial channels, called *golas*; 2) the marsh surrounding the lake on the north, south, and west, and now almost entirely occupied by rice paddies, which at the same time act as wetlands during flooding of the crop (in late spring for rice cultivation, and in late autumn to early winter, for hunting); and 3) a sandy bar, or *restinga*, located on the east, between the lake and the Mediterranean Sea. This sandy bar, known as *La Devesa de El Saler*, is about 1 km wide and 14 km long and it is formed by several dune strands parallel to the coast and their respective interdunal depressions. Water usually accumulates in these basins during certain periods of the year, forming a system of ponds locally known as *malladas*. It should be noted that *La Devesa de El Saler* is currently a recreation area widely frequented by both the local population and tourists.

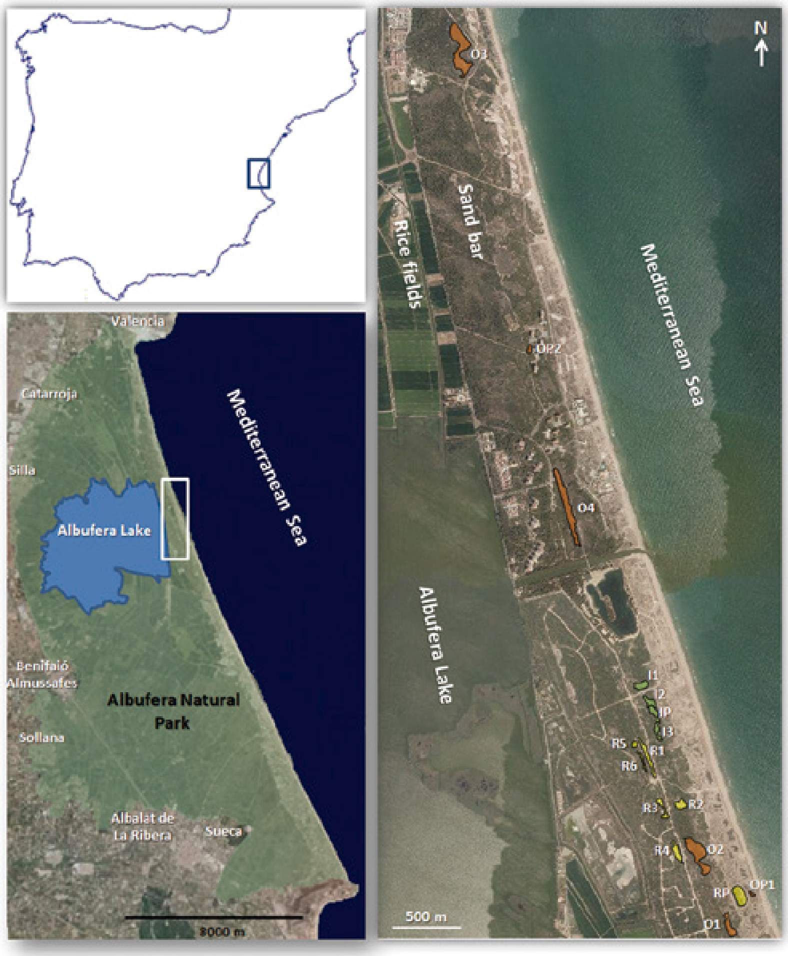

Figure 1. Left: Location of the study area in the Iberian Peninsula (top) and the Albufera Natural Park (bottom). Right: Detail of the area with the location and code of some of the studied *malladas*. The colours indicate their age of restoration: yellow, green, and orange correspond to the projects of restoration in 2007, 2003, and 1998, respectively. (Modified from Olmo 2016).

The area was declared Natural Park in 1986 (Decree 89/1986, 8 July), -the first in the Valencian region-, and included in the Ramsar List of Wetlands of International Importance in 1989. The whole area also belongs to the Natura 2000 Network, because it is considered a Site of Community Interest (Council Directive 92/43/EEC) and Special Protected Area for Birds (Council Directive 2009/147/EC). The protection of the Natural Park is regulated by two autonomous regulations, the Natural Resources Management Plan (Decree 96/1995) and the Master Plan for Use and Management (Decree 259/2004). Like many other Mediterranean coastal areas and despite the high level of protection, the area was historically under strong anthropogenic pressures due to the high population density located in its vicinity.

In particular, the sandy bar ecosystem, *La Devesa de El Saler*, has undergone several transformations, the most intense in the 20th century (Figure 2).

Figure 2. Pictures of *La Devesa de El Saler* and restoration of some *malladas*: (a) in the 60's during the development plan; (b) aerial view in 2002; (c) restoration work in the *mallada* R1; (d) installation of a footbridge in the *mallada* O4; (e) *mallada* R1 right after its restoration in the summer of 2007; and (f) *mallada* R1 after its first filling in October 2007. (From Olmo 2016).

At the time, as an endemic area of malaria, the *malladas* were considered unhealthy places where mosquito populations, vectors of the disease, had to be eradicated. Therefore, these ponds were drilled, breaking their impermeability, to promote drainage towards the groundwater (Cambó Law of 1918). Later, in the 60's, an urbanization project called "Management and Development Project of *Monte de La Devesa*" was approved. Its goal was the urbanization of the beach barrier, including a set of residential complexes with several towers of apartments, single-family houses, hotels and recreation areas, in addition to a sewerage system, car parks, secondary roads, and a sea promenade.

All these actions involved the levelling of the land, which resulted in the complete disappearance of the dune strands near the sea, along with many of the associated ponds. The *malladas* were artificially filled with the sand of the dunes and with debris (mud, rubble, etc.) from the River Turia flooding of the city of Valencia in 1957.

In the mid-1970s, the political change in Spain (from dictatorship to democracy) prompted the rise of a series of social and environmental movements against the urbanization project; many of them promoted by prominent naturalists of the time, such as the well-known Felix Rodríguez de la Fuente. As a consequence, the urbanization project of *La Devesa de El Saler* was only partially implemented. Valencian citizens, under the slogan *"El Saler per al poble"* (*El Saler* for the people), managed to stop the construction of most of the facilities planned, mainly the bulk of residential units. However, not until the end of the 1980s did the environmental policies at European, national, and regional level adopted action frameworks in an attempt to recover the ecological value of the area (Sanjaume 1998; Rey Benayas et al. 2003). Since then, the coastal dunes and the buried ponds were tried to be brought to their previous state through successive restoration projects.

The first of these projects was carried out between 1988 and 1998 by the local government, who restored one part of the affected area. Later, two Life Natura projects were done in the region, *Life Duna* (LIFE00 NAT/E/007339), between 2003 and 2005, and *Life Enebro* (LIFE04 NAT/E/000044), between 2007 and 2009, co-financed by the European Commission. In these projects, infrastructures such as roads were eliminated, and part of the coastal dune strand and some dune slacks were restored. The old basins were silted, although during periods of heavy rains, they could maintain a thin layer of water. Consequently, the vegetation was dominated by reeds along with other terrestrial plants that tolerate some degree of flooding, such as species of the *Inula* or *Dittrichia* genera. The first step for the restoration of the *malladas* was to define the boundaries of the old basins using aerial photographs and other historical records. Subsequently, heavy machinery was used to extract the sediments (Figure 2c) above the layer of silts limiting the waterproof zone (between 50 and 100 cm below ground level). Most of the *malladas* were restored to be temporary (Antón-Pardo & Armengol 2010; Olmo et al. 2016). Nevertheless, some were excavated deeper to maintain a water column throughout the year and thus create reservoirs for endemic and threatened cyprinodont fish species (Benavent Olmos et al. 2004): *fartet* or Iberian toothcarp (*Aphanius iberus*) and *samaruc* or Valencian toothcarp (*Valencia hispanica*). In some of these permanent *malladas*, submerged macrophytes (mainly of the *Chara* and *Potamogeton* genera) and specimens of the above-mentioned fish were introduced. For the rest of the *malladas*, a natural recolonization of those local plant species adapted to these environments was chosen (Benavent Olmos et al. 2004). The shores of the ponds were given a gentle slope to facilitate the access of fauna.

The *malladas* are listed in the Habitats Directive (92/43/EEC) as "Humid dune slacks (Code 2190)". As general features, these interdunal ponds are endorheic, shallow, slightly brackish, and small, hardly extending beyond one hectare. The water of the temporary ponds comes from rainfall, whereas the water of the permanent ponds also derives from groundwater. Temporality has an annual dynamic defined by the Mediterranean climate of the region, where the heaviest rains fall in autumn and spring, while summers are dry and hot. Accordingly, the hydrological year starts in September and ends in August the following year. Given the unpredictability of the Mediterranean climate, temporary *malladas* can have different alternating periods (hydroperiods) of filling and drought within the same hydrological year and with different durations.

In the area of *La Devesa* there are over 40 water bodies (Rueda-Sevilla et al. 2006; Rueda 2015). The main *malladas*, following the traditional toponymy and from north to south, are: *mallada del Quarter, del Saler, de La Rambla, Redona, del Garrofer, Llarga, de la Mata del Fang, de l'Hospitalet, de la Torre, Malladeta,* and *del Canyar*. There is also an area with restored lagoons in the *Racó de l'Olla*, a reserve area closer to Albufera Lake. Most *malladas* are separated by old firewalls (*tallafocs*); however, some that are sequential can be found connected during extreme flooding events (for example in the winter of 2017 we observed the connection of the *malladas de La Rambla* and *Redona*, and the latter also with *del Garrofer*). Some of these old *malladas* are very fragmented, and some include isolated water bodies. For instance, following the restoration carried out in 2003 (*Life Duna* project) where the old *mallada Mata del Fang* was located, four *malladas* were created, three of them (two temporary and one permanent) connect to each other when the water level is very high, and a fourth temporary one is separated from the other three by a path. The last of the completed projects restored two temporary *malladas* in the summer of 2016 (*Rambla* and *Redona*), and new actions are planned.

The aquatic systems of the Albufera Natural Park have been the subject of research in the field of limnology. Since the beginning of the 20th century many of these studies have focused on the Albufera Lake (Arévalo 1916, 1918; Blanco 1976). Since the 1980s, under the direction of Dr. Rosa Miracle, limnological studies intensified (e.g. Miracle et al., 1984; Oltra & Miracle 1984, 1992; Oltra 1993; Romo & Miracle 1994) and extended to other aquatic systems of the natural park, such as rice fields, ditches, springs (locally known as *ullals*), and some of the old *malladas* (Soria & Alfonso 1993; Alfonso, 1996; Soria, 1997). More recently, after the restorations carried out by the projects *Life Duna* and *Life Enebro*, several limnologic aspects of the *malladas* were studied (Rueda-Sevilla et al. 2006; Antón-Pardo & Armengol 2010; Olmo et al. 2015, 2016; Rueda 2015; Antón-Pardo et al. 2016; Olmo 2016; Romo et al. 2016).

This chapter documents the effects that different restoration projects have had on the environmental features and the zooplankton assemblages of the *malladas*. We emphasize the colonization, establishment, and configuration of various groups of zooplankton in these aquatic habitats, comparing those recently restored *malladas* with the firstly restored ones, which will be used as reference systems. We have used a nomenclature related to the different ages of restoration (Figure 1): R (recently restored, in 2007), I (intermediate restoration, in 2004), and O (old *malladas* restored in 1998); and P will refer to the permanent *malladas*. Zooplankton is an excellent model for understanding community ecology and ecological restoration (Louette et al. 2009; Badosa et al. 2010), and the studies presented below provide detailed information on how the development of restoration works can affect these communities.

2. The effect of the restoration on the environmental characteristics of the “malladas”

The successive restorations carried out in the *malladas* have affected diverse environmental characteristics including the limnological ones. To examine the effects of restoration on these characteristics an exhaustive study during four hydrological years was launched: since October 2007, after the first filling of the recently restored *malladas*, until May 2011, after the summer drying of all the temporary ones. In the set of the 17 studied *malladas*, (13 temporary and four permanent) the different ages of restoration are well represented (7 recently restored, 4 intermediate and 6 old *malladas*).

During the study period, the air temperature was similar, with mean values close to 18°C (Figure 3). However, rains were more variable between the different hydrological years. In the first three years, the accumulated annual precipitation was higher than 650 mm per year, while in the last hydrological year, it was less than 400 mm. In this last year, the hydroperiods of the temporary ponds were more intermittent and ephemeral (Figure 4). In the permanent *malladas*, the water level fluctuated with a variation of 90 cm, indicative of seasonal and interannual rainfall variability. Since the spring of 2011, the temporary *malladas* remained virtually dry due to a long lasting drought. Following that episode of xericity, the complete filling of all the basins took place at the end of the autumn of 2016, after strong rainfall.

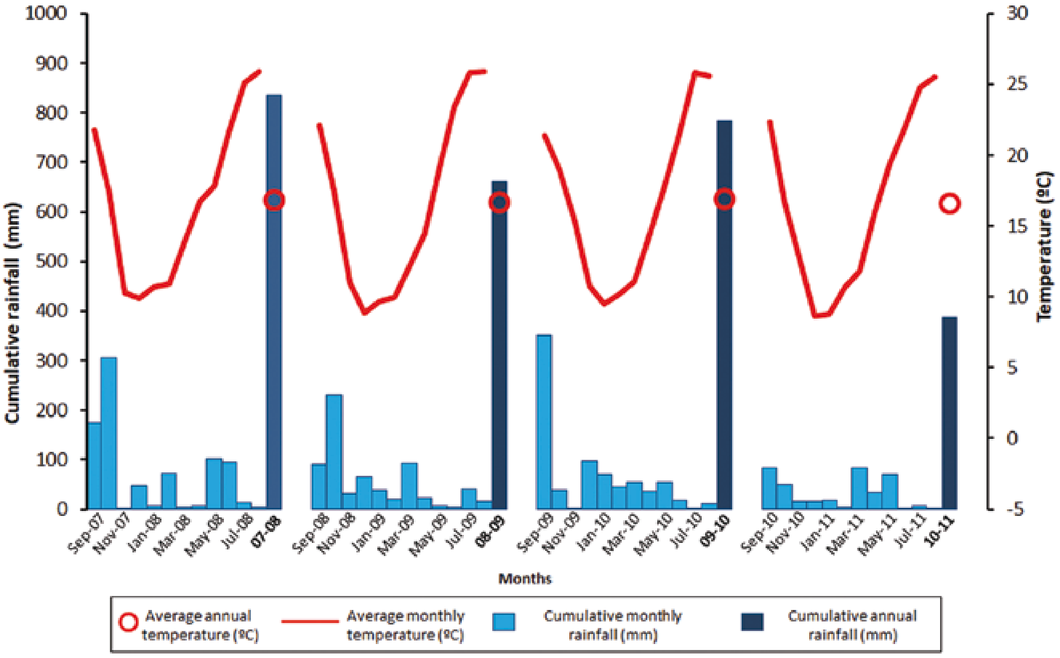

Figure 3. Cumulative precipitation (monthly and annual) and average temperature (monthly and annual) recorded during the four hydrological study years (September 2007-July 2011) at the Benifaió meteorological station, located 12 km from the study area. (Modified from Olmo 2016).

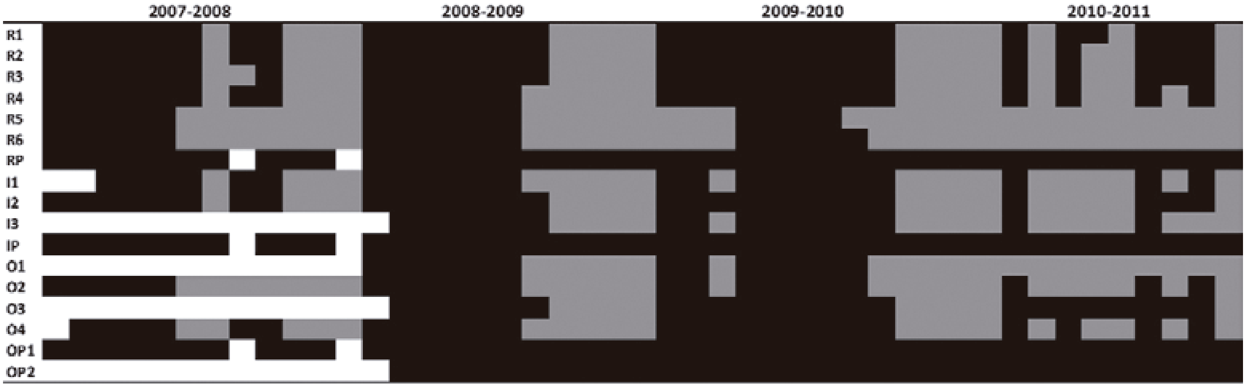

Figure 4. Representation of the hydroperiod of the 17 *malladas* from 2007 to 2009. Black: flood periods; grey: dry periods; white: no data available.

During this four-year hydrological period, the *malladas* were visited monthly, and during the inundation periods a series of limnological variables were measured: conductivity, water temperature, pH, dissolved oxygen, depth, and chlorophyll *a*, nitrate, and soluble reactive phosphate concentrations. Other variables such as the percentage of vegetation cover or the presence of macroinvertebrates and waterfowl were also registered.

In the case of the temporary ponds, the vegetation cover comprised almost exclusively helophytes, whereas the permanent ponds also developed macrophytes in the beds of their basins. The temporary *malladas* restored in 2007 evolved from lacking vegetation in the first year of study to having a vegetation cover of 10–20% at the end of the four years. The cover of the temporary *malladas* restored in 1998 and 2003 remained around 75–90% and 50–70%, respectively. On the other hand, the cover of the recent permanent *mallada* (RP) reached up to 70%, while the permanent older ones (IP, OP1, and OP2) had around 40% of total coverage.

In general terms, and despite the intrinsic characteristics of each pond, younger *malladas* had higher levels of pH, oxygen, conductivity and depth (Figure 5). This could be related to the increase in plant cover that occurs with time since restoration. The increase in plant cover imply a higher supply of organic matter to the older basins sediments, which should have two main consequences: 1) increase of silting speed, with the consequent reduction of depth and shortening of the hydroperiod; and 2) increase of decomposition rate, which could imply a reduction of pH and dissolved oxygen.

In calcareous regions, like ours, pH is regulated by the carbonate buffer system (Wetzel 2001). However, other natural processes such as respiration, photosynthesis, decomposition, and the presence of humic compounds also influence this variable. In general, the pH value changes as the balance between primary production and decomposition changes (by the uptake or release of CO_2 dissolved in water), and this causes daily, seasonal, or interannual pH fluctuations. If the production exceeds the decomposition, pH will be higher; on the contrary, if the decomposition dominates, pH will be lower (Brönmark & Hansson 2010). In our pond system, pH is generally around 8 to 9 (Alfonso 1996; Antón-Pardo & Armengol 2010). The lower pH values in the older *malladas* imply the dominance of decomposition over production (Scheffer 2004) due to the increase of organic matter from vegetation. On the contrary, in the recent *malladas*, production apparently dominates, as they have small inputs of organic matter due to the scarce vegetal cover. The same processes may also be the cause of the decrease in oxygen as the time since the restoration increases.

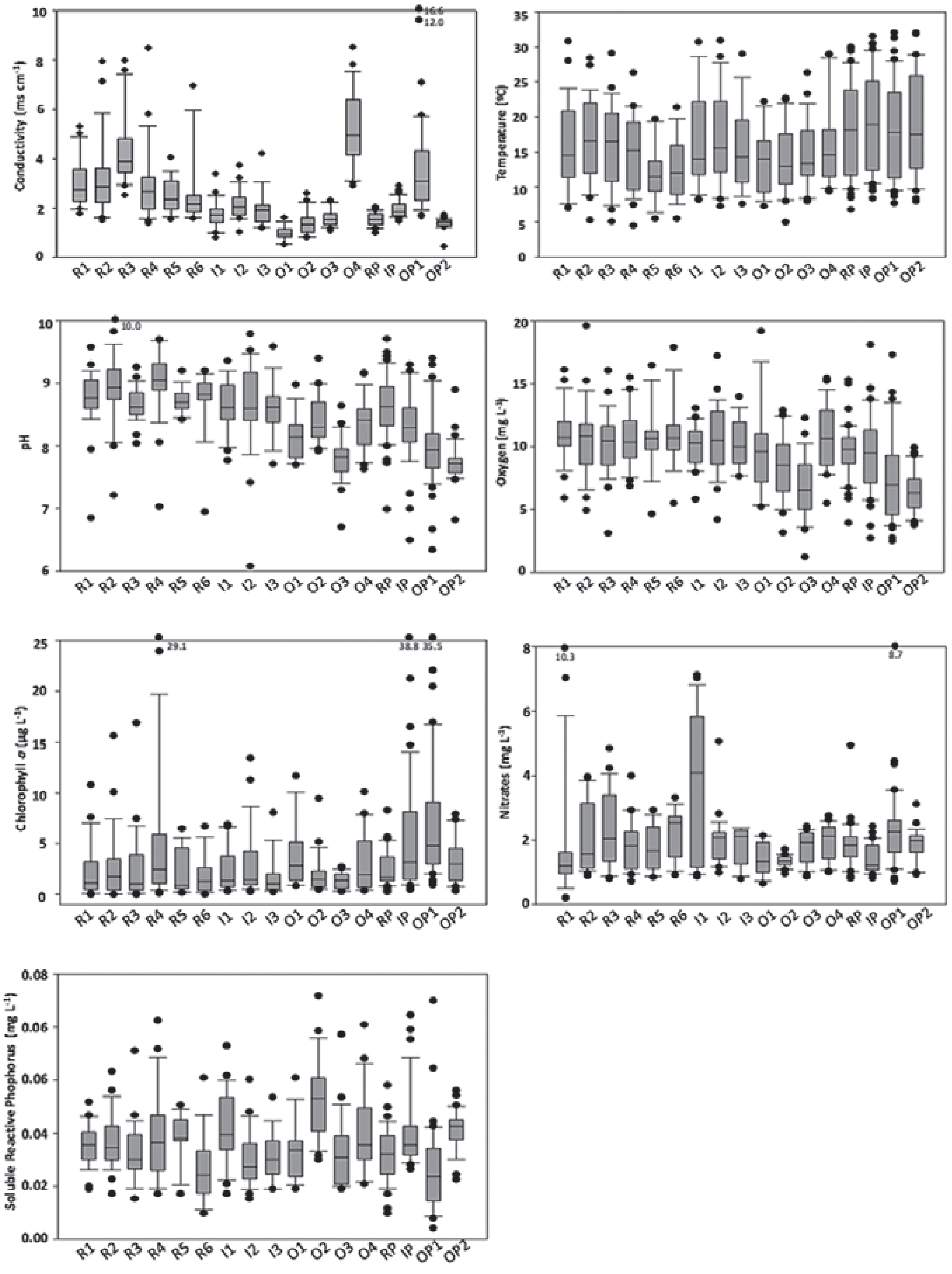

Figure 5. Box and whisker diagrams of conductivity, temperature, pH, oxygen, chlorophyll *a*, nitrates, and soluble reactive phosphorus for each *mallada* during the study period. The boundaries of the boxes indicate the 25th and 75th percentiles; the line inside each box is the median. Error bars indicate the 90th and 10th percentiles, with black dots being the extreme values.

In respect to conductivity, coastal ponds tend to concentrate salts due to the influence of groundwater, which is usually brackish, and of marine spray (Reyes et al. 2006). However, a reduction in salinity from the first year of restoration until the end of the study was observed in recent *malladas*. The restoration works exposed layers of sediment containing an accumulation of salts, which possibly favoured a higher conductivity during the first hydroperiod, when compared to the older ponds. In our system, the progressive reduction of conductivity could be due to the leaching of the salts to deeper layers of the sediment. Two of the oldest lagoons (O4 and OP1) had higher conductivities than the rest, because of the presence of an old zone with high salinity in the bed of the temporary *mallada* O4 and the punctual input of marine water in the permanent *mallada* OP1 (near the beach) during sea storms.

Water level variations in both permanent and temporary wetlands are theoretically the result of the interaction of a complex set of processes such as precipitation, infiltration, evaporation, and plant transpiration (Mitsch & Gosselink 2007). The morphology of the basins, including their depth, has a significant influence on these variations. In our system, depth generally decreases with age, and this could also be related to the increase in vegetation cover over time, which favours a quicker silting of the basin. Increased coverage could also contribute to the drying of ponds by evapotranspiration and filtration since root systems alter and break impermeable silt strata, facilitating the loss of water to deeper layers (Mitsch & Gosselink 1993).

For other environmental variables, however, no clear patterns apparently derived from the age of restoration. In all *malladas*, the mean values of chlorophyll *a* in the water were around 5 µg L^{-1}, which is the boundary between oligotrophy and mesotrophy (OECD 1982), although the permanent ponds had slightly higher mean concentrations (Figure 5). Regarding the dissolved nutrients, nitrates and phosphates were detected in all samples, but with very low concentrations and without a defined pattern related to the hydroregime or the age of the restoration of the ponds.

In order to explore the general patterns of the environmental characteristics in the set of ponds, we performed a principal component analysis (PCA). The first axis (CP1) explained 57% of the variance and appeared positively related to pH (Figure 6). It ordered the ponds according to the age of restoration, with the most recent lagoons located in the positive side of the axis, and the oldest ones in the negative side. The second axis (CP2) explained 17.8% of the variance. This axis ordered the lagoons according to their hydroperiod, and it clearly separates the permanent lagoons (on the positive side of the axis) from the temporary ones (on the negative side). This axis correlated positively with depth, pH, and chlorophyll *a*, and negatively with conductivity.

Other ordination analyses performed with samples from the temporary and permanent lagoons independently revealed similar patterns. On one hand, in the absence of the hydroperiod (permanence vs. temporality), these analyses also highlighted the importance of pH in relation to the age of restoration, with a lower value in older lagoons that were clearly isolated from recent and intermediate ones. On the other hand, our sites were also related to chlorophyll *a* and depth, with deeper ponds presenting lower values of chlorophyll *a*, which is probably related to the seasonal and interannual variations.

Based on these results, we can conclude that the heterogeneity in our pond system is highly determined by the age of restoration, or the number of years that have passed since the restoration.

Our goal was to unravel and quantify the main factors that explain the environmental differences between the age groups, since information on the abiotic context will help us to better understand the biotic framework in which we will focus in the rest of the chapter: the assemblage of zooplankton communities.

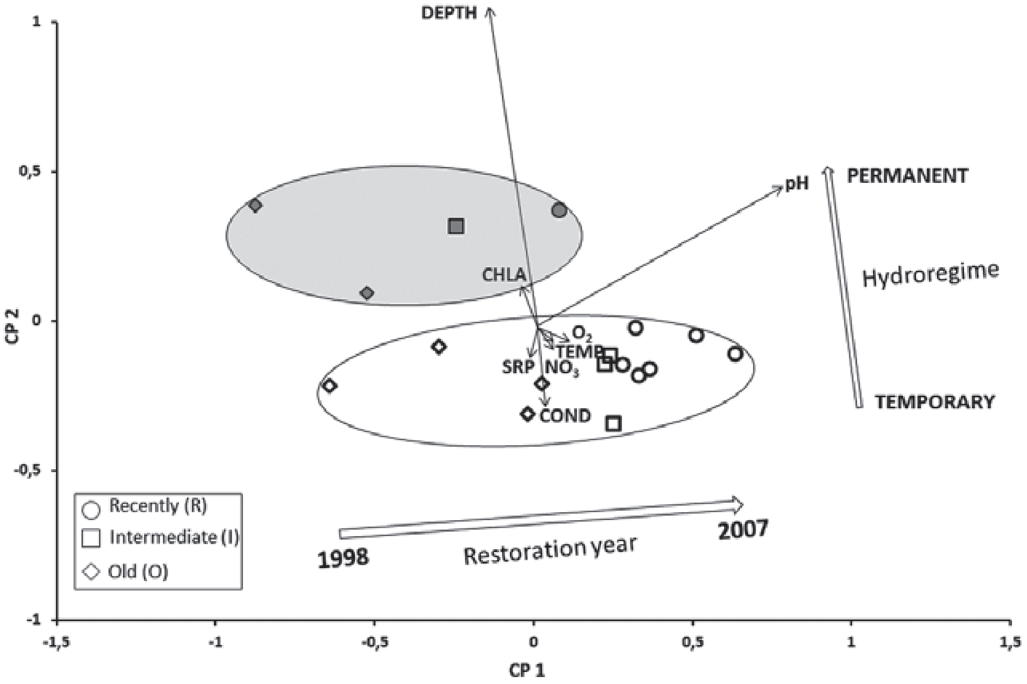

Figure 6. Ordination diagram of the Principal component analysis made with the limnological variables in 17 *malladas*. Each symbol corresponds to the average position of all the samples of a pond in the studied period. The grey and empty symbols correspond to the permanent and temporary *malladas*, respectively. COND: conductivity; TEMP: temperature; CHLA: chlorophyll *a* and SRP: soluble reactive phosphorus.

3. The effect of restoration on the zooplankton of the "malladas"

The results on zooplankton come mainly from two studies: a preliminary one including eight *malladas* restored in 2003 and 1998, with samples taken in the hydrological cycle 2006–2007, and another one with 17 *malladas* (including the previous ones and others restored in 2007) that were studied during the 2007–2011 period.

3.1. The zooplankton of the "malladas": composition and dominant groups

During the hydrological cycle 2006–2007, some *malladas* including temporary and permanent ones were studied three years after the project *Life Duna*. In that study, we took samples fortnightly and identified 100 species of zooplankton, among which rotifers dominated with 71 species, followed by cladocerans (15 species), copepods (13), and a species of anostracan (Antón-Pardo & Armengol

2010; Antón-Pardo et al. 2016). The accumulated species richness during that year had its highest values in the permanent freshwater pond IP (Table 1). Values of average density were around 200–300 ind L^{-1} in most of the ponds, but they fluctuated greatly, with highest abundances due to juveniles of cyclopid copepods and to rotifers. This result coincides with the pattern of dominance that has been found in other shallow Mediterranean systems (Ortega-Mayagoitia et al. 2000, Rodrigo et al. 2003; Brucet et al. 2010). The species found during this period were generally cosmopolitan, frequent in the region and in this type of Mediterranean coastal systems with saltwater influence (e.g., Antón-Pardo & Armengol 2012, 2014) and therefore subject to salinity fluctuations characteristic of these ecosystems (Badosa et al. 2005; Serrano & Fahd 2005).

REFERENCE	**Abundance (Ind L^{-1})**	**Mean richness**	**Cumulative richness**
IP	211.8 ± 121.4	16.8 ± 4.7	62
OP1	334.8 ± 174.6	12.4 ± 5.4	40
O3	117.6 ± 94.7	14.8 ± 3.8	39
I2	249.0 ± 377.7	6.6 ± 2.4	26
O2	212.6 ± 465.9	7.9 ± 3.3	21
I1	231.9 ± 300.5	7.1 ± 2.2	19
O4	938.6 ± 865.1	7.3 ± 2.2	18
O1	280.5 ± 249.7	12.3 ± 1.2	28

Table 1. Average values of density, mean richness and accumulated richness in the set of *malladas* studied in 2006–2007 and which were used as reference systems in other studies.

In terms of species composition, the genera of rotifers *Lecane* and *Brachionus* were the richest, while *Hexarthra, Polyarthra*, and *Keratella* had the highest densities. Cyclopids dominated among the copepods: the most abundant species was *Acanthocyclops americanus*, which was previously cited as present in the area by another name (*A. robustus*); and it is very abundant in the whole area (Soria & Alfonso 1993; Alfonso 1996; Oltra & Miracle 1992) and tolerates brackish and eutrophic waters (Dussart 1969; Miracle et al. 2013). There were also remarkable abundances of *Diacyclops bisetosus, D. bicuspidatus,* and *Tropocyclops prasinus*, which are also euryhaline (Dussart 1969; Alonso 1998). Only one *mallada* (O3) registered the presence of a species of calanoid copepod, the diaptomid *Mixodiaptomus kupelweseri*, which was previously cited as present in the area (Alfonso 1996). As for Cladocera, *D. magna* was found at higher densities, which is understandable given its tolerance to high ranges of salinity (Boronat et al. 2001; Ortells et al. 2005). Conductivity tends to be negatively related to the diversity of cladocerans since most species of this group have little tolerance for this factor (Jeppesen et al. 1994; Moss 1994). Other species of cladocerans less tolerant to mineralization such as *Ceriodaphnia quadrangula, Simocephalus vetulus*, or *Daphnia pulicaria* (Alonso 1998; Boronat et al. 2001) were also found. The results of this work show that the permanent ponds and those with longer hydroperiod accumulated greater species richness during the study period, but it also emphasizes the importance of the restoration age on zooplankton, as well as the conductivity and the system's productivity-related aspects (Antón-Pardo & Armengol 2010; Antón-Pardo 2011; Antón-Pardo et al. 2016).

Many studies have found that the duration of the hydroperiod (here correlated with depth) is the primary factor determining the structure and composition of the community in aquatic systems (e.g. Wellborn et al. 1996; Boix et al. 2001; Eitam et al. 2004). Generally, species richness is greater in permanent ponds (e.g., Collison et al. 1995; Alonso 1998; Spencer et al. 1999) or in temporary pools with longer hydroperiods (e.g. Fahd et al. 2000; Boix et al. 2001). However, comparing systems with different hydroperiods is complicated because of two reasons: first, the greater number of samples (the sampling effort) can influence the number of species found in the permanent systems or with longer hydroperiods; and second, the hydroperiod is often associated with variables that increase environmental heterogeneity (depth or aquatic vegetation) or with the abundance of Anatidae, which may act as dispersal vectors of zooplankton (Figuerola & Green 2002).

The influence of salinity on the structure of the pond community has also been widely studied (Williams 1999; Brock et al. 2005; Toumi et al. 2005; Waterkeyn et al. 2008) and, as in the *malladas*, its influence on the zooplankton assemblage is significant (e.g. Boronat et al. 2001; Frisch et al. 2006; Martinoy et al. 2006; Waterkeyn et al. 2008). Apart from the effects on species richness, which will be discussed in the next section, this variable had a positive effect on the abundance of zooplankton; the three most brackish ponds were those with the highest average abundance of zooplankton. The relationship between salinity and productivity has long been known, since brackish ponds are systems where nutrients are not usually limiting and where a few well-adapted species can develop significantly (Hammer 1986).

Finally, we note the presence of the Anostraca *Tanymastix stagnalis*, a rare species in the Iberian Peninsula (Boix 2002), which was only found in one *mallada* (O2) with one of the most irregular hydroperiods. Rueda-Sevilla et al. (2006) found three populations of this species in the same area: one population in O2 and the other populations in two *malladas* which are not included in this study. Although this species has been classified as a cold-water species, in this area it appears at higher temperature ranges. Large branchiopods like this may be more efficient competitors than smaller filterers such as cladocerans or rotifers (Waterkeyn et al. 2011), but being larger are also more susceptible to predation by fish and invertebrates (Bohonak & Whiteman 1999). Therefore, species of large branchiopods usually appear in temporary systems, where large predators (mainly fish) are absent (Schneider & Frost 1996). Experiments carried out with this species showed the importance of conductivity in the maintenance and development of its populations. This fact, together with their obligate sexuality and with the fact that their dispersal capacity may not be as high as that of other branchiopods, would explain the isolation of their populations (Olmo et al. 2015).

3.2. The effect of restoration on zooplankton in permanent ponds

As already mentioned, the permanent *malladas* presented higher zooplankton species richness, which in our case can be associated with several factors: (i) high habitat heterogeneity and environmental conditions related to a diversification of niches; (ii) the annual permanence of water, which facilitates assemblage succession; (iii) the temporal variety in the environmental conditions favouring different hatching stimuli; (iv) a constant water column that helps the establishment of waterfowl, which are significant dispersal vectors (e.g., Figuerola & Green, 2002); and (v) the presence of fish populations and other predatory macroinvertebrates that imposes an intense predation pressure, preventing the dominance of a few species (e.g. Spencer et al. 1999) and making competitive exclusion difficult. In addition, the expansion of the old basins (in area and depth) and the introduction of aquatic flora and fauna species carried out during the restoration may have helped to increase the effect of these factors. This is because, together with the introduced fish and plants, diverse species of zooplankton or its forms of resistance associated with the water and the sediment of the plants may have entered. This fact could contribute to the quick increase of the species richness in these permanent ponds.

To illustrate the effect of the restoration on the zooplankton of permanent systems, we will present two examples that were studied in detail: the case of the permanent pond *Mata del Fang* (PI), restored in 2003, and the case of the new pond created in the old *mallada del Canyar* (RP).

1. *Mallada de la Mata del Fang* (IP): This pond was not completely silted during the development of the area in the 60's, leaving a small channel-shaped lagoon with an area of about 300 m^2 and a depth of 1 m that was used to provide water to the urbanization works. A study of this pond carried out in 1987 along a year (Soria & Alfonso 1993) found a high density of emergent vegetation and low water quality. The dissolved oxygen was low (4.7 ± 2.4 mg L^{-1}) and the concentration of chlorophyll *a* was 27.7 ± 10.7 µg L^{-1}, so the pond was described as mesotrophic (OECD 1982). As part of the project *Life Duna* (in 2003), the area of the basin was increased (up to 4000 m^2), and the basin was excavated to an approximate depth of 2 m. Different species of macrophytes (*Chara hispida, Potamogeton pectinatus*, and *Zannichellia peltata*), as well as specimens of the endemic fish above-mentioned, were introduced. In the post-restoration years (2006 to 2009), there were significant changes in both environmental variables and aquatic communities (Antón-Pardo et al. 2013). In addition to the development of submerged vegetation, there was a significant colonization of helophytes, mainly of *Phragmites, Typha, Juncus*, and *Scirpus* genera. As a consequence of the new submerged vegetation and the increase in depth, there was an increase in dissolved oxygen levels. Moreover, between three and six years after restoration, the mean concentration of chlorophyll *a* decreased to values below 5 µg L^{-1}, so the pond entered a state of oligotrophy (OECD 1982). As for zooplankton, the richness of all groups increased substantially, which implied important changes in the structure of the communities (Antón-Pardo 2011; Antón-Pardo et al. 2011). Between February 1987 and January 1988 (Alfonso 1996), a total of 14 species of rotifers were found, with a clear dominance of *Keratella tropica*. Only two species of crustaceans were observed, the cladoceran *Daphnia magna* at very low densities and the copepod *Tropocyclops prasinus*, whose juveniles (mainly nauplii) reached the maximum densities. In the years after the restoration, the *mallada* held 78 species of zooplankton, with 60 species of rotifers in total, 5 copepods, and 13 species of cladocerans (Antón-Pardo et al. 2013). The increase in species of this latter group is particularly relevant for the system functioning, since its greater efficiency in phytoplankton filtration (as compared to rotifers and nauplii microfilters) helps in the processes of water clarification and facilitates the existence of clear phases in shallow habitats (Scheffer et al. 1993).

2. *Mallada del Canyar* (RP): In this case, the pond was excavated in an area where there was no previous basin. The excavation took place in the summer of 2007 as part of the project *Life Enebro.* The final dimensions of the pond were approximately 5900 m^2 in area and maximum 1.5 m in depth. Unlike the restored temporary systems, in this case, the excavation reached the groundwater table, so the pond had water before the autumn rains (Figure 7). Endemic fish and submerged vegetation were also introduced, similar in composition to that detailed in the description of *mallada* IP. Gradually from its first filling (October 2007), the pond had a significant colonization of helophytes (similar species to IP) in the basin and its rim (Antón-Garrido et al. 2013; Calero et al. 2015). There was a quick development of submerged vegetation with the colonization and establishment of new species of macrophytes belonging to genera *Nitella* and *Utricularia*, which eventually developed large submerged beds (Calero et al. 2015). This *mallada* was sampled after filling for four hydrologic years: nutrient and conductivity values increased over time, while oxygen values decreased after the second year and chlorophyll *a* was generally low in the same period.

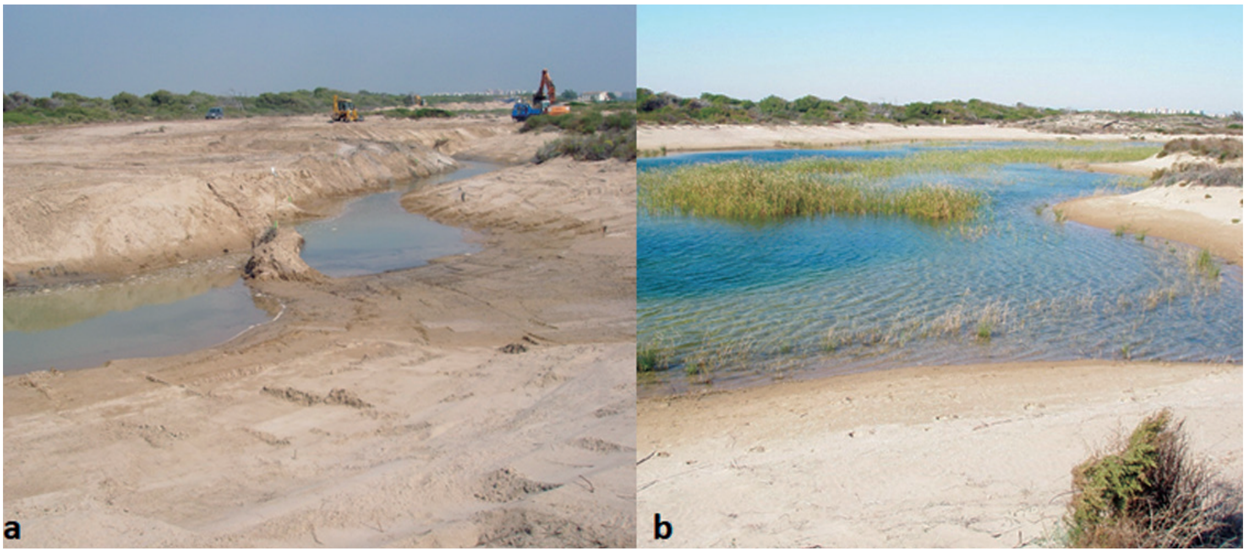

Figure 7. (a) Detail of the excavation work in the permanent mallada PR in summer 2007 (before the autumn rains). Note that the water table is exceeded in depth; (b) the same *mallada* in the autumn of 2008.

Many species of zooplankton quickly colonized this newly created *mallada*. Figure 8 shows the species richness accumulated in this pond during the four years of the study, indicating a high richness already from the first sampling (12 species of rotifers and one of cladoceran), and a progressive increase in the number of species until the slope softened two years after its creation. After four years, the accumulated species richness reached 80 species, mostly rotifers (61 species), followed by cladocerans (13 species) and, finally, copepods (six species). The most abundant group was the rotifers, especially in the first months, with abundances above 1000 ind L^{-1}. The most abundant species of this assemblage were *Anuraeopsis fissa, Polyarthra dolichoptera, K. tropica, Hexarthra oxyuris*, and *Trichocerca pusilla*. The cladocerans showed lower and more constant abundances during the whole period (maximum of 29 ind L^{-1}). In the later years of the study, copepods were more relevant, due to the juvenile stages, whose average densities increased from 103 ind L^{-1} to 406 ind L^{-1} from the first to the last year of the study, respectively.

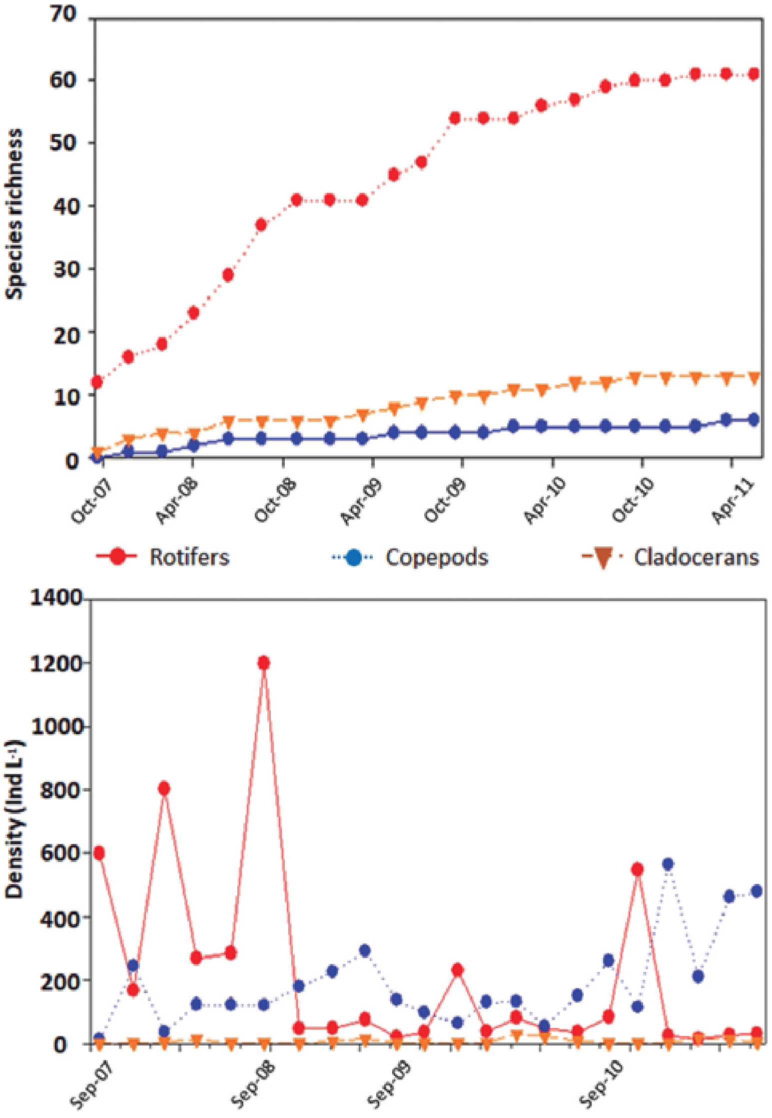

Figure 8. Top: Cumulative richness of rotifers, copepods, and cladocerans of the *mallada* RP from September 2007 to March 2011 in bimonthly intervals. Bottom: Zooplankton density of the three main groups of zooplankton during the same period.

3.3. The effect of restoration on zooplankton in temporary ponds

Most of the lagoons we have studied are temporary, so in this section, we will discuss some noticeable aspects of the zooplankton of this type of systems undergoing restoration, such as early colonization, egg bank, and ecological succession.

1. Early colonization: The six temporary *malladas* recently restored by the project *Life Enebro* (R1 to R6, Figure 1) were sampled 15 days after the first rainfall at the end of September 2007, which was quite abundant, so the lagoons filled quickly. We could thus document the colonization of the main zooplankton groups from the beginning. Furthermore, we had the opportunity to compare these pioneer communities with those from a set of eight *malladas* restored in 1998 and 2003, which we have considered as reference and which have been described in more detail in section 3.1.

In the first sampling performed after the restoration, 30 species in total were identified in the six recently restored *malladas*: 24 rotifers, four copepods, and two cladocerans (Figure 9). In the recent *malladas*, the richness value had a wide range: from five species in R6 to 19 in R1. But for two species of rotifers of the genus *Cephalodella*, the rest had already appeared in the reference *malladas* during the previous hydroperiod (2006-2007). Out of 100 species previously reported, 28% were detected in the first filling of the recent *malladas* (31% of the 71 species of rotifers, 14% of the 15 species of cladocerans, 27% of the 13 species of copepods, and the only species of anostracan was not found). In some of them, high densities were reached, with rotifers dominating in richness and abundance: some species, such as *H. fennica, P. dolichoptera*, and *B. angularis*, had densities of more than 150 ind L^{-1}. In contrast, *malladas* with low richness also showed low densities (R5 and R6).

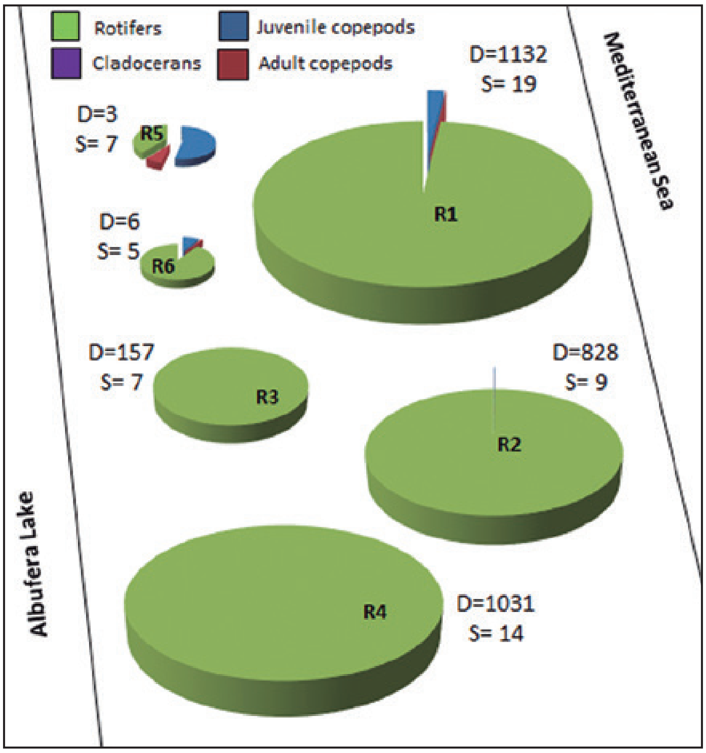

Figure 9. Proportion of the different zooplankton groups in the first sampling of newly created ponds (R1–R6) carried out in October 2007. The location of the graphs shows the relative position of each *mallada*, and its size is proportional to the zooplankton density.

These six *malladas* are not connected and thus, main dispersal vectors for zooplankton arrival relies on wind and animals (humans included). A large number of waterfowl (mainly Anatidae) was detected in some of the ponds right after the first filling. As dispersion is apparently not a limiting factor for the arrival of zooplankton (Antón-Pardo et al. 2016), these new *malladas* act as sinks of immigrants arriving from older neighbouring *malladas*, which in turn serve as a source of the regional species pool, as suggested by several studies (Caley & Schluter 1997; Leibold et al. 2004; Vanschoenwinkel et al. 2007). Data show that the colonization of zooplankton occurred very quickly in the restored ponds, indicating their good dispersive abilities, according to other studies (Louette & De Meester 2004; Frisch & Green 2007; Badosa et al. 2010). The results evidenced the colonizing capacity of organisms with shorter development times and quick response to hatching such as rotifers (Brendonck & De Meester 2003; Frisch et al. 2012; Lopes et al. 2014). Likewise, they benefitted from the absence of their direct competitors, the cladocerans, which were only detected in two ponds and at very low density. Despite their high regional diversity (15 species in 2006–2007), cladocerans have longer generation times, so it would take them longer to colonize new waterbodies (Jenkins & Buikema 1998).

Bearing in mind that the natural recolonization of restored aquatic systems is strongly influenced by a propagule bank in the previous basin (Olmo et al. 2012), we cannot discard the recruitment from a remnant eggs bank before restoration, although the maintenance of this egg bank was not taken into consideration during excavation works. Moreover, the early appearance of adult copepods (including ovigerous females) in active communities could also be indicating that the egg bank before restoration was not completely withdrawn. According to Frisch & Green (2007), the cyclopids can colonize and become dominant in a few hours after the rehydration of their anhydrobiotic resistance forms. Other indicator of this remnant egg bank would be the results obtained from genetic analysis of *D. magna*, which revealed that some recent *malladas* had a high clonal richness, comparable to the reference *malladas* and far superior to that expected after reproduction among the colonizing clones after a growing season (Ortells et al. 2012).

2. Egg bank: A short period after the restoration should be sufficient for a pond to accumulate a large number of species, aided by the high dispersal rate and recruitment from the egg bank (Louette et al. 2006; Badosa et al. 2010). The start of the hydroperiod represents the moment of greater recruitment of species (Olmo et al. 2012) that configures the communities thereafter (Boix et al. 2004). In these early stages, residents are mainly recruited from the bank of resting eggs accumulated in the sediment of the basins.

The accumulation of these resistance forms increases with time (in quantity and diversity), and it represents an archive of the local biodiversity of each pond (Hairston 1996; Caceres 1998). For this reason, the abundance and diversity of the egg bank should have a considerable impact on the structure and dynamics of the communities in this type of pond (Marcus et al. 1994; Hairston 1996; Caceres 1998). It is thus expected that the age of restoration—especially in this case, where the sediment was removed from the lagoon—acts as a limiting factor of richness in the recently restored *malladas* in comparison to older ones with a more developed resting egg bank.

In addition to the study of active communities in the water column, the analysis of egg banks is a useful tool for studying the diversity of zooplankton communities (Vandekerkhove et al. 2004) as it integrates spatial and temporal scales (Brendonck & De Meester 2003). In this sense, hatching experiments with the viable egg bank are useful for comparing pond communities with different characteristics (Frisch et al. 2009). In September 2010 we took sediment samples from three temporary *malladas* of different restoration ages (R1, I1, and O2). Using samples of homogenized sediment from each pond, we carried out an *ex situ* experiment of hatching in aquaria for a month (October-November 2010, at the same time as the ponds flooded). The number of hatching species was 13, 15, and 18 in R1, I1, and O2, respectively. All the aquaria reached some stabilization in the accumulated richness between days 14 and 18 of the experiment. No hatching of copepods was observed, but the ostracods were common to all of them. The rotifers, with quick response to hatching, were the dominant group in richness: seven species were common to the three ponds, against a single species of cladoceran, *D. magna*. Finally, in all cases, benthic species dominated over the four planktonic species (*A. fissa, H. fennica, D. magna*, and *T. stagnalis*). In contrast, the number of exclusive species increased with the age of restoration: three, five, and eight in R1, I1, and O2, respectively. Among these particular species, the anostracan T. stagnalis only hatched in the aquaria with sediment from O2, the only pond that had an active population of this branchiopod. Also, a delay in hatching time (sensu Vandekerkhove et al. 2004) was detected associated with the age of the *mallada*. This observation is in line with several studies that suggest that egg bank age influences hatching rate, since older eggs do not hatch as easily as new ones (Hairston et al. 1995; Weider et al. 1997) due to a progressive degradation of photosensitive components that induce hatching (De Meester et al. 1998, Nielsen et al. 2015). An additional reason for the hatching delay in the oldest *mallada* could be a temporary adjustment due to the competitive pressure exerted by the branchiopod *T. stagnalis*. This group may even competitively exclude cladocerans, rotifers, and copepods, which would hatch in later stages of filling when the branchiopods disappear from the water column (De Meester et al. 2016).

3. Ecological succession: Ecological succession is related to the temporal changes that occur in the communities. In this case, to evaluate the effects of the restoration on succession in the zooplankton community, we selected a recently restored *mallada* (R1) and compared it with two older ones (I1 and O2), restored respectively in 2004 and 1998. We have considered them as reference systems with which to compare the data of the new one. The three *malladas* were sampled monthly during four hydrological cycles: from the first filling of R1 in the autumn of 2007 to drying in the spring of 2011. Furthermore, they are all temporary, and during the study period, they presented a similar hydroperiod (Figure 4), with longer water permanence phases in the first years and more ephemeral water in the last year. Thus, differences in the zooplankton community due to the hydroperiod are minimized. As previously described, the new *malladas* presented slightly different environmental conditions than the older ones. R1 had higher values of conductivity, oxygen concentration, and depth. Regarding species richness per sample, the largest differences were observed in the oldest *mallada* O2 (17.6 ± 3.7) compared to the most recent ones (I1: 10.9 ± 3.4, R1: 10.5 ± 4.2). The species accumulation curves (Figure 10) showed in R1 and I1 a significant increase in the first year, while the slope softened in recent years. On the other hand, in O2 the substantial increase in the number of species occurred in both the first and second years. In this way, O2 is the *mallada* with the highest number of accumulated species (60 species), as compared to 43 of I1 and 52 of R1 (Figure 10). Regarding the composition of the zooplankton community in the new *mallada*, the first year it was dominated by rotifers and juveniles of copepods, typical pioneer organisms (Firsch & Green 2007; Badosa et al. 2010). However, from the second year onwards, although juveniles of copepods continued to dominate, cladoceran abundance increased considerably, achieving a similar proportion as in the older ponds (Figure 11). These results showed an increase in the complexity of the zooplankton community in R1, which would gradually resemble that of the older *malladas*. This increase in diversity in R1 could also be favoured by vegetation development (which enhances the availability of microhabitats) and by a change in environmental variables (Olmo et al. 2016). Other studies indicate that species richness is higher in older aquatic habitats, due to greater accumulation of resting eggs in the sediment (Badosa et al. 2010; Miguel-Chinchilla et al. 2014), as in O2. However, the most recent *mallada* is set in an intermediate position. This *mallada* was quickly colonized by different species immediately after filling, and probably the greater range of variation in environmental conditions (mainly variations in conductivity and chlorophyll) would have allowed the presence of a larger number of species than in I1, with a more stable environment. To sum up, the restoration in R1 produced an immediate and quick transition to similar conditions to the ones in older *malladas*. While greater differences were observed in the zooplankton communities in the first year, from the second year on, the R1 *mallada* showed more similarities with the reference *malladas* and a more complex community.

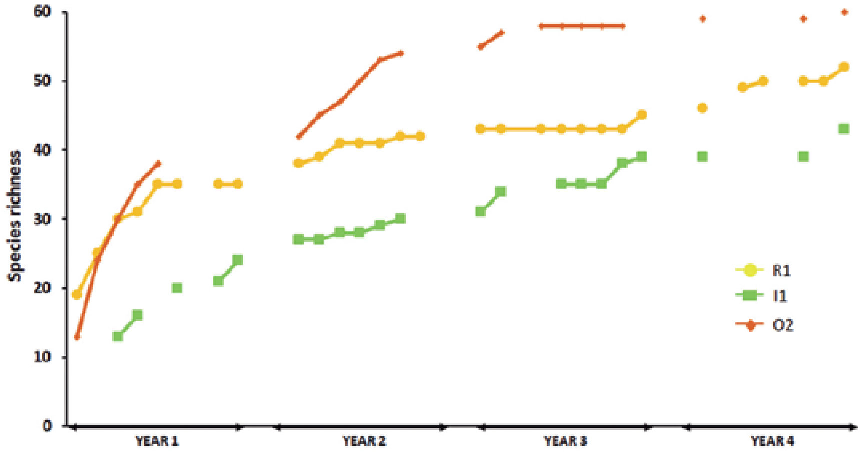

Figure 10. Accumulated richness of zooplankton in three *malladas* with different restoration ages: R1 (recent), I1 (intermediate), and O2 (old) during four hydrological cycles between 2007 and 2011. The line indicates the continuity in the inundation period.

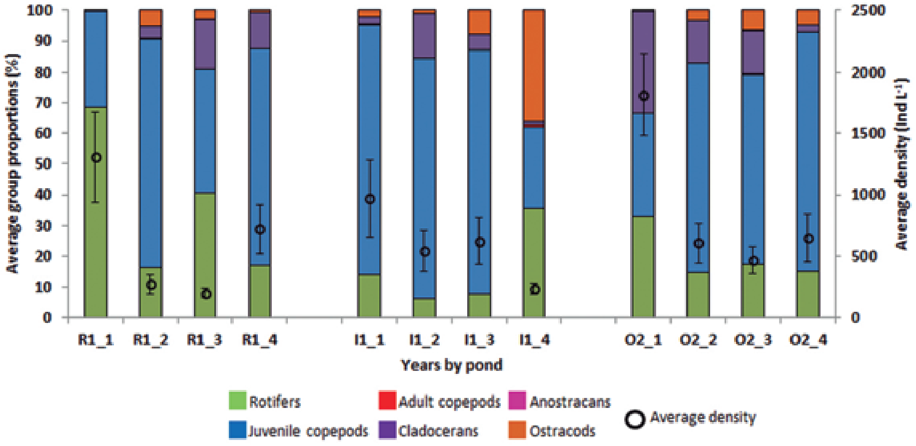

Figure 11. Relative abundance (bars) and average density (dots) of the main zooplankton groups in three *malladas* with different restoration ages: R1 (recent), I1 (intermediate), and O2 (old), during four hydrologic cycles (1–4) between 2007 and 2011.

4. General conclusions

Restored aquatic habitats provide a unique opportunity to understand the resilience of their communities and the ecological succession (De Meester et al. 2005). The different restoration projects that were carried out in *La Devesa de El Saler* produced a mosaic of aquatic ecosystems that had been restored at various times and therefore, with different ages. This opportunity helped to monitor the environmental and zooplankton conditions in these ponds, especially those that were restored in 2007, since colonization and succession were studied from the moment of the restoration of the habitats. On the other hand, zooplanktonic organisms, with short life cycles and quick responses to environmental variations, can be appropriate indicators to evaluate the success of the restoration (e. g. Jenkins 2003; Williams et al. 2008; Antón-Pardo et al. 2013).

Regarding the **environmental factors**, the successive restorations have shown, on the one hand, the high velocity of change, and on the other, a clear pattern that was related to a rapid colonization by helophytes, a reduction of conductivity, a decrease of depth by clogging, and an increase of the quantity of organic matter in the sediment, which was accompanied by a decrease in dissolved oxygen and pH. The levels of nutrients and chlorophyll fluctuated, but remained low.

Concerning **zooplankton communities**, initially, the new habitats were colonized by species with high rates of dispersal and growth (mainly rotifers) which mostly were already present in the regional reservoir of species. This may indicate that colonization and establishment of species occurred from older habitats; but, given the rapidity of colonization in some cases, we cannot rule out the presence of a residual egg bank that remained viable in the sediment in spite of the silting and the restoration, and that in these new environmental conditions, eggs hatched again and recolonized the waterbodies. The results also highlight the importance of the **hydroperiod** on species richness. The richness was greater in the permanent systems than in the temporary ones. In the temporary systems, richness was higher in longer hydroperiods, although, in the case of permanent systems, this great richness may have been affected by the introduction of species associated with repopulation with fish and macrophytes. Other factors such as conductivity and those related to system productivity were also important in structuring zooplankton communities. Finally, the **age of restoration** strongly reflects in the zooplankton communities, since it had a great importance in the ordination of the communities. Moreover, total richness, especially richness of microcrustaceans and in particular of cladocerans, was strongly influenced by the age of restoration. These parameters could therefore be good indicators to evaluate the success in restoration. In spite of the small difference in the age of restoration among the ponds, the study of the hatching of the zooplankton egg bank helped us to distinguish the age of the ponds based on the richness, the number of exclusive species, and the moment of hatching.

A remarkable aspect of our study is the rapidity with which the new waterbodies, both permanent and temporary, have been transformed and colonised. This shows that in these systems, where there is a good dispersal of zooplankton, in a few years (though few years are equivalent to several generations of zooplankton), the communities of the new ponds become similar to the old ones, which can be considered reference sites in the absence of unaltered systems.

These studies show that the removal of sediment (as a form of restoration) from the silted ponds, either naturally or artificially, has improved the characteristics of the systems and their functionality, enabling a rapid colonization by zooplankton (and by the whole aquatic community). Changes in environmental variables and vegetation occurred rapidly, but in these shallow systems, given the abundance of emergent vegetation, the processes of clogging accelerate and in a few years (approximately 10–15) ponds lose depth and hydroperiod length. At present, new partial interventions that remove part of the sediment (leaving some as a source of propagules) and of the helophytes in some areas of the lagoon would allow them to maintain a high heterogeneity, greater biodiversity, and better limnological functioning.

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