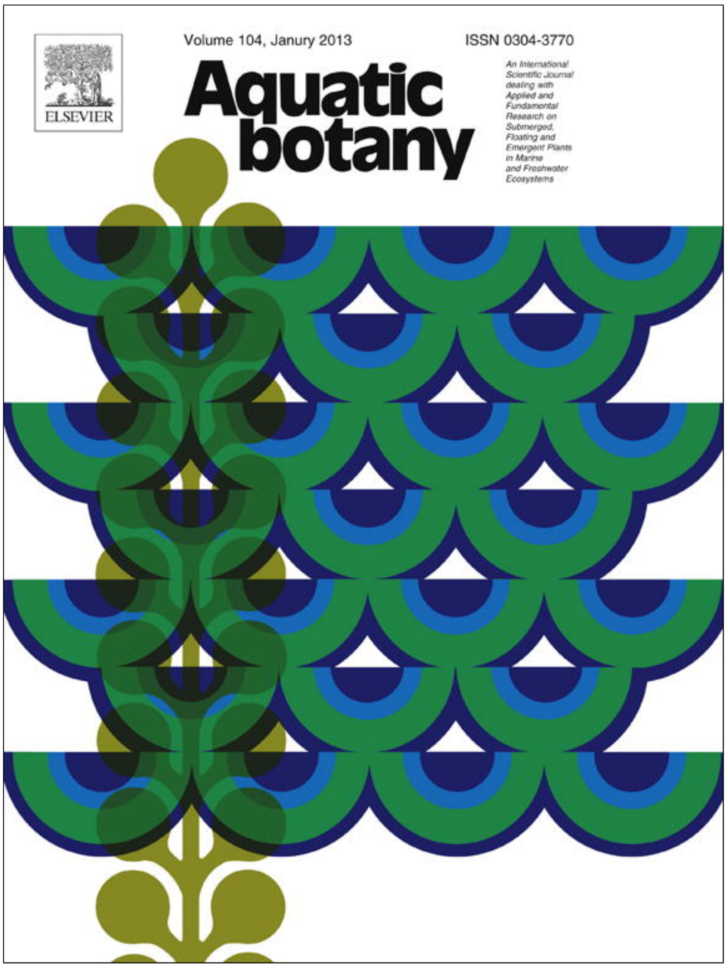
Volume 104, Janury 2013
ISSN 0304-3770
Aquatic botany
An International Scientific Journal dealing with Applied and Fundamental Research on Submerged, Floating and Emergent Plants in Marine and Freshwater Ecosystems
ELSEVIER

Aquatic Botany 104 (2013) 193–203

Contents lists available at SciVerse ScienceDirect

Aquatic Botany

journal homepage: www.elsevier.com/locate/aquabot

Seagrasses in Portugal: A most endangered marine habitat

Alexandra H. Cunha*, Jorge F. Assis, Ester A. Serrão

CCMAR – Centro de Ciências do Mar, Edifício 7, Universidade do Algarve, Campus de Gambelas, 8005-139 Faro, Portugal

ARTICLE INFO

Article history:
Received 23 July 2010
Received in revised form 22 August 2011
Accepted 26 August 2011
Available online 6 September 2011

Keywords:
Geographic distribution
Habitat extinction
Long-term change
Marine conservation
Population decline
Portugal
Seagrass cover
Seagrass decline

ABSTRACT

Numerous reports of seagrass decline around the world indicate that seagrass habitats are undergoing a global crisis with important consequences for coastal biodiversity, environmental status and economy, reflecting their vulnerable and overlooked status within many conservation agendas.

This paper describes the results of the first extensive survey of this habitat in Portugal. It shows the present cover distribution and declining trends of seagrasses on the Portuguese coast (1980–2010), identifies environmental and conservation issues, and discusses challenges for long-term survival.

Seagrass populations of the Portuguese coast are also facing an unprecedented decline in distribution, matching the general trends described for most world seagrasses. The results of this investigation show a dramatic decrease of seagrass cover in Portugal in the last 20 years. This decrease followed different trends for the three species present on this coast. *Zostera noltii*, having disappeared from some systems by almost 75%, is still the most abundant species, present in 10 of the 18 sites assessed. *Zostera marina* is presently the most endangered seagrass species in Portugal, as it disappeared from six of eight historical locations and faces extinction from the Portuguese territory if measures are not taken to assure the protection of the last regions left with populations. *Cymodocea nodosa* has a geographic distribution range limited to the southern/southwestern coasts, and its current conservation status is uncertain, although there is evidence for the recent occurrence of several population bottlenecks.

Management questions are discussed and actions to improve habitat conservation are suggested.

1. Introduction

Seagrass meadows are declining around the world at an unprecedented rate, suggesting a global crisis, yet most of the references are from a few highly developed countries (Orth et al., 2006; Duarte et al., 2009). Indeed, along extensive coastlines, there is no published information on seagrass distribution patterns and historical trends are unknown (Duarte et al., 2008). Reported losses (29% of the maximum area measured; Waycott et al., 2009), probably represent a small fraction of those that have occurred, many losses remain unreported, and real losses may never be known because most will disappear without ever having been reported to have occurred (Duarte et al., 2008). Striking seagrass losses have been documented in North America, Europe and Australia (Orth et al., 2006; Waycott et al., 2009). Major gaps in knowledge of seagrass cover and distribution exist for West Africa (Duarte et al., 2008; Cunha and Araújo, 2009), northeast South America, the northwest Pacific and the tropical Indo-Pacific (from East Africa to Hawaii) where seagrasses are widespread and abundant (Waycott et al., 2009).

In southern Europe and the Mediterranean, with some localized exceptions for *Posidonia oceanica*, information on seagrass distribution and abundance trends are scarce. Portugal, although entirely on the Atlantic coast, forms a biogeographic admixture zone where Atlantic species at their southernmost distributional limits encounter Mediterranean and African species that extend northwards. Furthermore, signatures of past climatic events, possibly interacting with local adaptation traits for these seagrass species with contrasting environmental affinities, have resulted in a unique population genetic constellation of the seagrasses along the Portuguese coast (Olsen et al., 2004; Coyer et al., 2004; Diekmann et al., 2005; Alberto et al., 2008).

The Portuguese coast is the northern limit in the Atlantic for *Cymodocea nodosa* (Ucria) Ascherson, and it is presently the southern distributional limit for *Zostera marina* Linnaeus 1753 (Cabaço and Santos, 2010; Bull et al., 2010). It is also the center of the distributional range for *Zostera noltii* Hornemann 1832, a mostly intertidal species ranging from Mauritania (Cunha and Araújo, 2009), to the southern fjords of Norway (den Hartog, 1970). Among all four native seagrass species of Europe (*sensu stricto*) only the Mediterranean endemic *P. oceanica* (Linnaeus) Delile is not present in Portugal, making this coastline particularly unique in terms of European seagrass biodiversity. Two other more typically brackish aquatic plant species are present on the Portuguese coastal ecosystems, *Ruppia maritima* and *Ruppia cirrhosa*. They are present in

* Corresponding author. Tel.: +351 289 800 051; fax: +351 289 800 051.
E-mail address: acunha@ualg.pt (A.H. Cunha).

0304-3770/$ – see front matter © 2011 Elsevier B.V. All rights reserved.
doi:10.1016/j.aquabot.2011.08.007

coastal lagoons with higher influence of freshwater and, although they were not target species in this study, their distribution is briefly reported for some sites, particularly where they mix in with the 3 seagrass species.

This paper depicts the first full assessment of the distribution, cover and conservation status of the Portuguese seagrasses. We report decreases in seagrass cover or even total disappearance along the Portuguese coast and highlight the need to evaluate past versus current distribution and ascertain the conservation status of Portuguese seagrasses.

2. Materials and methods

2.1. Study site

The Portuguese west coast extends for ca. 800 km along a straight North-South orientation, whereas the south coast, extends for ca. 200 km West–East (Fig. 1). Estuaries along this coastline vary significantly in geomorphologic and hydrologic features. While the Tagus and the Sado rivers estuaries have the broadest areas (ranges 320–180 km^2), the Mondego, Mira, Arade and Guadiana rivers are channel-like (ranges 20–5 km^2). Ria de Aveiro, Ria de Alvor and Ria Formosa are shallow coastal barrier islands lagoon systems (ranges 6–91 km^2). Annual river flow is markedly different, with the Tagus estuary presenting mean values above 250 $m^3 s^{-1}$, and the Mira and the Ria Formosa discharging on average below 5 $m^3 s^{-1}$ (Vinagre et al., 2010). Salinity varies seasonally from a mean of 21.2 (9.3–31.8) in Mondego river, to 36.9 (35.0–39.0) in Sado river (Vinagre et al., 2010). The two coasts are subject to different climate and storm regimes, with the northern coast subjected to more intense westerly and northern winds. Both are very exposed to southern storms, which can be frequent and very intense in certain times of the year. Because of different current exposure and latitude water temperature ranges are very wide between the study sites with lowest means of 14 °C in the Arrábida coast in winter, to highest means of 27 °C in Ria Formosa and Guadiana river in summer (Vinagre et al., 2010).

2.2. Distribution and cover assessment techniques

The current distributional patterns of seagrasses in Portugal were assessed from 2007 to 2010 during the LIFE Biomares project (LIFE 06 NAT/P/192) that aimed at restoration of a seagrass meadow in the Marine Park Luiz Saldanha, on the Arrábida coast (Cunha et al., 2009, in press). Sites surveyed were selected because they had either previous written or oral records of present or past seagrass presence, or because seagrass-like cover areas were identified in aerial photos or Google Earth® images.

The methods used for seagrass cover assessment are described in detail in Cunha et al. (2009). Different approaches were used because the sites varied in their availability of prior information and in access to the field sites. For intertidal and shallow subtidal field sites with clear water conditions and inaccessible by boat, map-

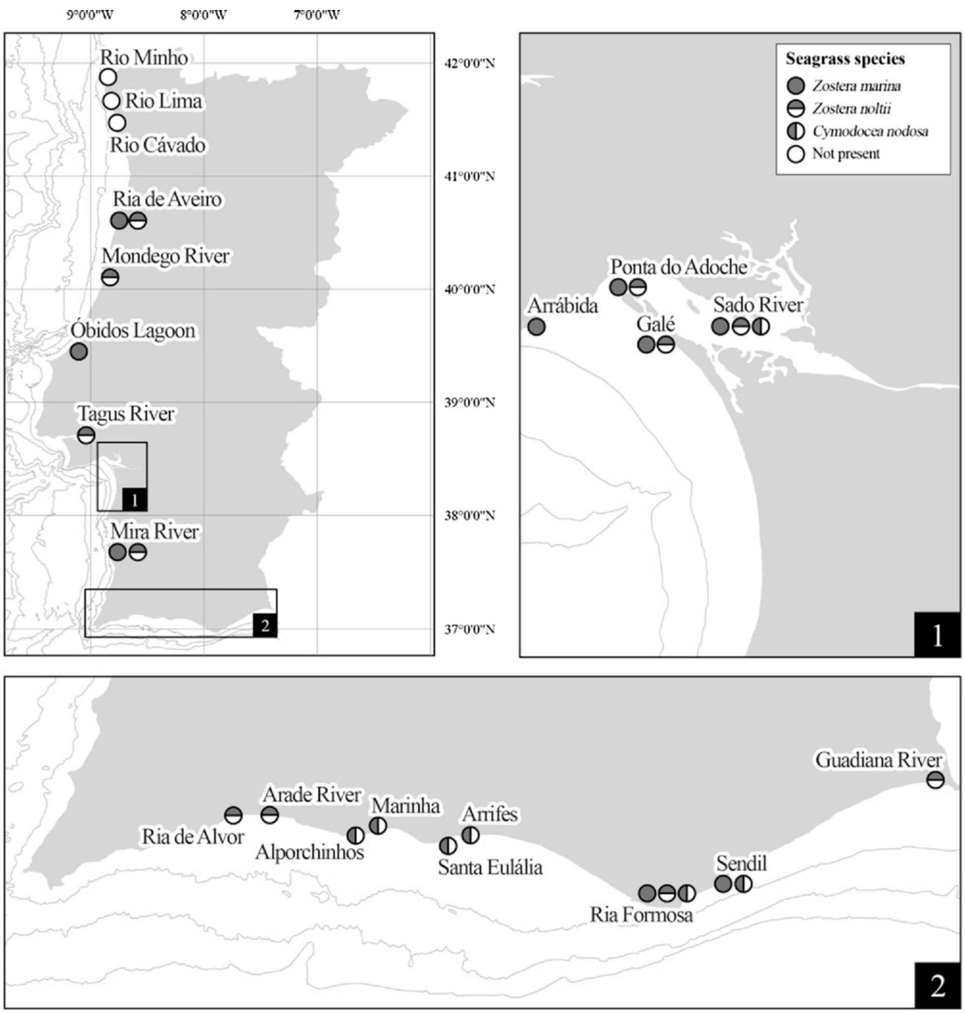

Fig. 1. Seagrass distribution in the Portuguese coast, depicting the 21 sites visited and information on seagrass presence/absence, and species present.

ping and distribution assessment was made by walking along the shore line, and by free diving (snorkeling), accurately registering GPS points and creating tracks around the seagrass patches, that were transferred to the project GIS. Deep water or low visibility subtidal sites were visually evaluated by means of scuba diving, placing the GPS unit to float on the water's surface, in a housing attached to a buoy, vertically positioned over the scuba diver. For large open sites with clear water, long distance boat/canoe transects were made, using a crystal glass tube to visually groundtruth underwater field features. Patches were delineated by GPS and transferred to the GIS. Intense field prospection and "bare foot mapping" were used to explore new areas. Intertidal and subtidal areas were surveyed for all regions except for Ria Formosa, where data from intertidal zone was available from a previous study (Guimarães, 2007; Guimarães et al., in press). Estimated seagrass area per region was calculated for each species with the help of a GIS. Moreover, seagrass habitat maps were generated for each studied region to visually evaluate the most diverse localities in terms of seagrass species, number and area of seagrass meadows. This information is digitally available in the project GIS.

2.3. Historical distribution assessment

During the field work several fishermen or clam and bait collectors were informally interviewed about the past existence of seagrass meadows. This method known as "bare foot mapping", was very useful because it was possible to obtain interesting information that do not have a formal record. Most people interviewed were familiar about the existence of seagrass, its present and historical distribution as well as their importance as support of fisheries. Furthermore, a lot of information about past seagrass distribution was obtained from fellow biologists, that had in some period of their lives, worked or studied these systems. Historical distribution records were also retrieved from scientific seagrass literature when existent, but mostly from "grey" literature. "Grey" literature used in this study comprised documents about seagrasses for the general public, field campaign reports from students or governmental institutes, and master's and doctoral theses that were never published in peer reviewed journals, but that could be obtained directly from the authors or from institution's libraries. Most scientific references were identified via searches of electronic library databases (Aquatic Sciences and Web of Science), and personal communications with national and international seagrass researchers were obtained directly by asking/emailing fellow researchers from the research centers in Portugal and Spain.

3. Results and discussion

3.1. Summary of seagrass distribution and abundance in Portugal

Presently, there are seagrasses in 18 of the 21 sites visited during this study (Fig. 1). The most widely distributed seagrass on the Portuguese coast is *Z. noltii* (15.74 km^2) which occurs in 10 of the 18 sites with seagrasses in the estuaries of Mondego, Tagus, Sado, Mira, Arade and Guadiana rivers, and in Ria de Aveiro, Ria de Alvor and Ria Formosa coastal lagoons. In some locations such as in Ria de Aveiro (Canal de Ovar), Sado estuary, Mira estuary and Ria Formosa it is still possible to observe extensive meadows. It is interesting to note that *Z. noltii* is not present in the Óbidos Lagoon neither in the Costa da Galé sites, where *Z. marina* forms extensive meadows, whereas in other similar and adjacent areas the two species occur together.

Z. marina appears to be the most endangered seagrass species on the Portuguese coast, taking into account its historical patterns. From the eight sites where this plant was once abundant, only two had *Z. marina* populations in 2010, with a total coverage of 0.075 km^2. The populations at these two sites (Lagoa de Óbidos and Ria Formosa) are subject to continued use of bivalve hand trawling and intense boat mooring, in addition to recent channel dredging and the opening of inlets (in Ria Formosa). The future of this species in Portugal is therefore, at the moment, uncertain. Furthermore, restoration attempts with this species on the Arrábida coast were not successful, particularly due to winter storms and fish grazing (Cunha et al., in press). As for *C. nodosa*, there are 3 main populations identified, with an acreage of approximately 1.09 km^2. Nevertheless, it is hard to acknowledge the cover distribution trends as this species was often confused with *Z. marina*, and was never referred to in documents prior to 1992. Still, due to its limited distribution and low clonal diversity with a unique genetic background, it is a species of special concern and action should be taken to avoid its local disappearance.

From the 21 sites visited, the three that did not have seagrasses (Fig. 1) were the Northern estuaries of the Minho, Lima and Cávado rivers, for which there are no previous records of seagrass presence. Further north, on the coast of Spain, only 200 km away from Ria de Aveiro, there are populations of *Z. marina* and *Z. noltii*, and so a distributional gap occurs here.

From the 18 sites where seagrasses were presently recorded, 14 had previous records. Five other sites identified in this work had never been cited before for the presence of seagrasses. Scientific information about seagrass distribution, ecology and biology in Portugal is recent, and historical information is mostly available in grey literature. Presently, 100 publications about seagrasses of the Portuguese coast were identified, but these include grey literature, public outreach articles and scientific papers. Worldwide, publications on seagrasses started in 1960 but only in the 1990s, scientists responded to the need for more information on seagrass ecology that resulted in a 100-fold increase in the annual number of papers published, which represented a sustained publication growth rate of 12.8% per year (Orth et al., 2006). In Portugal, it was also during the 1990s that scientific publications picked up, and during the last 10 years the publications increased 11-fold, with 55 published papers, representing a 9.9% increase during that period. Despite all this effort on seagrass research in Portugal, the causes for seagrass disappearance are still not totally understood. Some causes are particularly well understood, as the case of *Z. noltii* in Mondego (Ferreira et al., 2007; Lillebø et al., 2007; Baeta et al., 2009) and the evident impact of mechanical removal of seagrasses for human activities such as bivalve culturing, bivalve harvesting, boat mooring, or channel dredging.

3.2. Patterns of seagrass distribution and abundance of *Z. noltii*

3.2.1. Current distribution in Ria de Aveiro

In Ria de Aveiro coastal lagoon, the most northern site where *Z. noltii* is found, an area estimated as 0.43 km^2 was mapped in 2010, in the Canal de Ovar (north channel) and an area of 0.13 km^2 was mapped in the Costa Nova channel (Table 1). All meadows mapped were seagrass beds with very dense stands. It is possible that the acreage in the northern part of the lagoon is underestimated in this study, because it was not possible to visit some remote and secondary channel areas difficult to access.

3.2.2. Historical cover in Ria de Aveiro

Z. noltii used to cover up to 8 km^2 in 1984 (Silva et al., 2004), but by 2004 it had fallen to 3 km^2 (Silva et al., 2009). Erosion over the last decades caused deepening of major channels (Silva and Duck, 2001; Silva et al., 2004, 2009), and the combined action of increasing water current, loss of fine sediments and nutrients, and decline in intertidal area contributed to seagrass decrease (Silva et al., 2009). Until 1960, a large part of the area had a dense coverage

Table 1
Location and cover distribution (area in km² and m²) of seagrass species in the Portuguese coast from 2007 to 2010 (n.p.: not present; very rare: <10 shoots were found in the area).

Sites	Date survey	*Zostera marina*	*Zostera noltii*	*Cymodocea nodosa*	Latitude	Longitude
Ria de Aveiro (Mira channel)	2008	10 patches (<2 m)	0.130 km²	n.p.	40°36′31.47″N	8°44′40.34″W
Ria de Aveiro (Ovar channel)	2010	n.p.	0.431 km²	n.p.	40°43′33.69″N	8°41′09.64″W
Mondego river	2009	n.p.	0.044 km²	n.p.	40°07′47.63″N	8°50′52.69″W
Óbidos Lagoon	2010	0.0105 km²	n.p.	n.p.	40°07′47.63″N	8°50′52.69″W
Tagus river	2009	n.p.	0.21 km²	n.p.	38°43′57.94″N	9°0′46.87″W
Arrábida	2007	n.p.	n.p.	n.p.	38°28′36.21″N	8°58′48.62″W
Sado river	2007	n.p.	0.29 km²	0.022 km²	38°27′46.47″N	8°51′32.85″W
Ponta do Adoche	2009	0.0121 km²	Not-measured	n.p.	38°29′32.27″N	8°54′31.03″W
	2010	Very rare	Very rare	n.p.		
Costa da Galé	2009	0.0013 km²	n.p.	n.p.	38°29′2.37″N	8°54′22.00″W
	2010	Very rare	Very rare	n.p.		
Mira river	2009	400 m²	Not-measured	n.p.	37°43′21.15″N	8°46′29.50″W
	2010	Very rare	0.075 km²	n.p.		
Ria de Alvor	2009	n.p.	0.01 km²	n.p.	37°07′42.20″N	8°36′22.19″W
Arade river	2009	n.p.	0.004 km²	n.p.	37°10′0.99″N	8°29′33.17″W
Alporchinhos Beach	2009	n.p.	n.p.	<100 m²	37°05′21.53″N	8°24′46.66″W
Marinha Beach	2009	n.p.	n.p.	800 m²	37°05′21.47″N	8°24′46.68″W
Santa Eulália Beach	2009	n.p.	n.p.	0.15 km²	37°05′06.19″N	8°13′1.62″W
Arrifes Beach	2009	n.p.	n.p.	1000 m²	37°04′33.87″N	8°16′33.96″W
Ria Formosa	2007	0.05 km²	14.49 km² [a]	0.913 km²	37°00′0.67″N	7°49′56.48″W
Sendil	2007	50.3 m²	n.p.	508.4 m²	37°00′58.67″N	7°47′35.50″W
Guadiana river	2009	n.p.	0.054 km²	n.p.	37°12′20.10″N	7°24′53.84″W

[a] Both intertidal and subtidal populations from Guimarães (2007) and Cunha et al. (2009).

of SAV, including *Potamogeton pectinatus*, *R. cirrhosa*, *Z. noltii* and *Z. marina*. The historical descriptions about the amount of seagrasses and other aquatic vegetation that used to cover Ria de Aveiro are quite impressive. Viana de Lemos (1933), Taborda de Morais (1937), and Silva et al. (1974a,b) described the aquatic vegetation cover of Ria de Aveiro as luxuriant, but also acknowledged the alarming decrease of seagrasses observed in some areas. Ria de Aveiro was known by the traditional activity of collecting "moliço" a mixture of aquatic plants that included mostly *Z. marina* and *Z. noltii*, which was used as fertilizer and supported important agricultural activity in the fields in the vicinity of the lagoon. In 1955 there were 800 boats ("moliceiros") operating, which in turn collected more than 100,000 tons of aquatic vegetation per year (Silva et al., 2004). The decrease in seagrass and other SAV area within Ria de Aveiro over the past five decades is well described in Silva and Duck (2001) and Silva et al. (2004, 2009), which explain the effects of the construction of the inlet piers (Barra Nova), the dredging associated with the engineering works that channelized and deepened the water channel, increased water currents, promoting the transport and redistribution of sandy sediments. Furthermore, increased siltation, turbidity, and nutrients washing, which are associated with faster tidal flows, changed the physical forcing in the system leading to the disappearance of subtidal meadows of aquatic vegetation. *Z. noltii*, is now restricted to some intertidal flats that are usually less exposed to tidal currents relative to adjacent areas (Silva et al., 2009).

3.2.3. *Current distribution in Mondego river*

Another site in the north of Portugal where *Z. noltii* had a dramatic decrease in cover area was the Mondego estuary. The estuary, 7 km in length, consists of two different arms separated by an alluvium-formed island (Murraceira Island; Martins et al., 2005). In the southern arm there is a *Z. noltii* meadow, that presently extends up to 4.4 m² (Table 1).

3.2.4. *Historical distribution*

Z. noltii used to be present in an upper and a lower reach, having disappeared from the upper reaches without trace more than 20 years ago. The meadow in the lower reach, identified as the richest area in the system with regard to macrofaunal abundance and biodiversity (Lillebø et al., 1999; Pardal et al., 2000, 2004; Cardoso et al., 2004a,b; Dolbeth et al., 2003), had almost disappeared by 1997 (Pardal et al., 2004; Ferreira et al., 2007). The main cause for this decrease was the interruption of the upstream communication between the two arms of the estuary in the early 1990s, which increased water residence time and nutrient concentrations. These became major driving forces for seasonal *Ulva* spp. blooms and a concomitant severe reduction of the area occupied by *Z. noltii* beds from approximately 150,000 m² in 1986 to 200 m² (Cardoso et al., 2005; Pardal et al., 2004; Martins et al., 2005). A recovery plan promoted by Coimbra University and implemented by the Water Management Authority, which manage the freshwater inputs to the system, resulted in a decrease in nutrient loading and *Ulva* spp. blooms and increased water transparency (Ferreira et al., 2007; Lillebø et al., 2007; Baeta et al., 2009). Further physical protection of the remaining few shoots and rhizomes, and seagrass transplantation resulted in increased *Z. noltii* abundance since 1998 (Neto, 2004; Pardal et al., 2004; Martins et al., 2005; Baeta et al., 2009). Despite this recent management success, the main threat to this population, the increased eutrophication of the system, is still on, caused by important inputs of nutrients from agricultural and urban origin (Pardal et al., 2000; Lillebø et al., 2004, 2005; Baeta et al., 2009). The combination of nutrient surplus with the natural variation in other factors (e.g. low hydrodynamics, high salinity) causes, in some periods, significant growth of green algae, mainly *Ulva* spp. (Martins et al., 2001) and the non-indigenous *Asparagopsis armata* (Cunha, pers. obs.). Another anthropogenic source of disturbance is the intensive macro invertebrate harvesting for fishing bait still observed nowadays (Cunha, pers. obs.).

3.2.5. *Current distribution in the Tagus river*

A meadow of *Z. noltii*, of at least 0.21 km² was identified in the lower reach of the Tagus river estuary (Salinas de Alcochete) in 2008 (Fig. 1 and Table 1). The meadow expands throughout an intertidal platform that has been growing since the construction of the

Vasco da Gama bridge, that appears to have created a sediment accumulation zone there (João Carlos Farinha, pers. commun.).

3.2.6. Historical distribution

Images from Google Earth, show that in 2002 this *Z. noltii* meadow was already present. Despite being one of the most studied estuaries in Portugal, there are no previous seagrass references for this estuary. Nevertheless, there is an historical reference from 1868 to "the threat that the collection of marine plants that protected the natural oyster banks posed to the sustainability of the oyster culture" (Baldaque da Silva, 1893), which we suspect that might be a reference to *Z. noltii*, because oysters are still found within *Z. noltii* banks, in other natural areas. An intertidal patch of *Z. noltii* was observed in this estuary, in Ponta dos Corvos (Alfeite, sapal de Corroios) in 1989 (E. Serrão, pers. obs.). The main threat to seagrasses observed in the recently mapped meadow, was clam ("lamejinha") harvesting with a "fork" that is widely used in the area.

3.2.7. Current distribution in Sado river

The Sado estuary has extensive *Z. noltii* meadows in the intertidal flats and lower subtidal areas, estimated to cover 0.29 km^2 (Table 1; Cunha et al., 2009). Near the river mouth at Ponta do Adoche, a belt of *Z. noltii* at a depth of 3 m, surrounded the *Z. marina* bed that existed until November 2009. All the above ground canopy and great part of the rhizomes disappeared during the winter storms of 2009/2010 and by September 2010 only very slight recovering had occurred.

3.2.8. Historical distribution

Historical records for this site, including aerial photographs, are very limited. The region used to support one of the richest oyster productions of the Portuguese coast, which disappeared in the 1980s (Leal, 1984). It is very likely that seagrass meadows also covered larger areas before the development of the commercial port, paper mill industry and ship construction plants, because channel dredging, salt marsh occupation and organic and inorganic pollution affected intensively the estuary (Caeiro et al., 2005). Furthermore, the Sado river supports the most active rice fields in Portugal, which release a vast amount of fertilizers and pesticides in the estuary (Vale et al., 1993).

3.2.9. Current distribution in Mira river

Z. noltii population from the Mira estuary had disappeared almost completely in January 2007, after a major flood event in November 2006 which left behind a muddy area, full of dead rhizomes and very sparse *Z. noltii* shoots (Adão, Cunha, pers. obs.; Cunha et al., 2009). The population rebound in the summer of 2008, and in 2009. *Z. noltii* was present up to 4.5 km from the river mouth and had a total cover of 0.075 km^2, most of it at the southern margin (Table 1). It was noteworthy that the patches were very high on the river margin, next to the *Spartina* marshes, a possible response to increased water turbidity associated with heavy river sediment load.

3.2.10. Historical distribution

The *Z. noltii* habitat of the Mira river estuary has been studied since 1984 (Andrade, 1986). The roughly estimated cover area for the 2 species (*Z. noltii* and *Z. marina*) at that time was, approximately, 0.8 km^2. Subsequent studies focused on the associated fauna (Almeida, 1988; Costa et al., 1994; Ferreira, 1994; Adão, 2003) and not specifically on the seagrass population ecology or distribution. The *Z. noltii* population biomass varies seasonally with maxima in spring and summer, under higher temperature and light conditions (Ferreira, 1994; Adão, 2003). Before the 2007 population bottleneck, a continuous meadow of *Z. noltii* in the lower reach had one of the highest genotypic (i.e., clonal) diversities in southwest Iberia (Diekmann et al., 2005), meaning that each sampled plant had its origin in a distinct seed, instead of predominant clonal propagation so common in seagrasses. This might be related with the frequency of disturbance by flooding events that carry vast amounts of sediment from a poor managed watershed (fires, forestry operations, intensive agriculture) periodically killing most vegetative shoots. It is possible that population resilience here is dependent on the germination of seeds that are buried in the sediment and germinate in the summer, after major flooding events. Clam and fish bait collection (Adão, 2003; Cunha, pers. obs., 2007–2009) and blooms of the non-indigenous red alga *A. armata* (Cunha, pers. obs., 2007–2009) are also potential threats to these populations.

3.2.11. Current distribution in Ria de Alvor

Ria de Alvor is a small estuarine system with an area of 14.5 km^2, formed by two rivers on the southern coast of Portugal. It is delimited by two barrier peninsulas and connected to the sea by a single inlet. In 2009 the *Z. noltii* cover was approximately 5000 m^2, and consisted of several fragmented patches at the upper intertidal level, near the salt marsh zone, and a central mudflat with very few shoots. In September 2010, these patches had almost disappeared, covered by a layer of sediment, apparently originated by the dredging of a new channel.

3.2.12. Historical distribution

Duarte and Mendonça (1988) and Antunes and Cunha (1988) were the first to report that the seagrasses and seaweeds of the area were important for the eggs and juveniles of commercial fish. In the eighties Santos and Salgado (1988) mapped and estimated the biomass of seagrasses and seaweeds of this system. They used aerial photos from April 1986, and refer, that the seagrass distribution looked stable compared with aerial photos from 1973. They identified seven *Z. noltii* meadows with a total cover of 19,600 m^2 and estimated the biomass in 27.2 tons (wet weight). This same area was reassessed using aerial photography in December 1991, just before intensive dredging and construction operations (fish harbor, nautical recreation area and two piers), and the same 7 meadows were identified and measured with a total cover of 15,880 m^2 and total biomass of 14.6 tons (wet weight) (Cunha, 1991). In 2009, all seven patches had disappeared, the *Z. noltii* cover was reduced by almost 75% and its biomass was negligible. The main threats identified in this area are habitat loss (channel dredging and aquaculture practices), eutrophication (nutrients washed off from agriculture fields and golf courses), and intensive collection of bivalves and bait.

3.2.13. Current distribution in Arade river

In 2009, the *Z. noltii* beds of Arade river estuary had 3 patches in a total of 4000 m^2 (Table 1).

3.2.14. Historical distribution

In 2004, a submerged aquatic vegetation (SAV) assessment estimated that 18,000 m^2 of *Z. noltii* meadows extended along the river margins, with other aquatic vegetation such as *R. maritima* and *Fucus vesiculosus* (Santos et al., 2004). Within 5 years, the *Z. noltii* cover was reduced by almost 78% and *F. vesiculosus* and *R. maritima* have completely disappeared. The Arade estuary has become increasingly impacted since a river dam was built in the sixties decreasing freshwater flow and increasing sediment. Large areas of saltmarsh and mudflats of the estuary are now occupied by fish aquaculture, and a fish harbor and a commercial port, that destroyed large seagrass beds that can be assumed as having been *Z. noltii*. Some minor clam and bait collection is still conducted in the river margins and over the remnant seagrass patches.

3.2.15. Current distribution in Ria Formosa

Guimarães (2007) mapped the intertidal *Z. noltii* meadows in Ria Formosa, which is the largest population in Portugal (13.04 km^2) and occupies 45% of the intertidal area of the lagoon. From those, at least 3.95 km^2 that were *Z. noltii* beds are now occupied by clam farms, although this acreage is underestimated (Guimarães et al., in press). There is also subtidal *Z. noltii* in Ria Formosa, estimated to be 5.51 km^2 (Cunha et al., 2009), but because it also mixes with *Z. marina* patches it is possible that the acreage is higher.

3.2.16. Historical distribution

The first references to the presence of seagrasses (*Z. noltii*) in Ria Formosa (Olhão, Fuseta, Tavira) are from Baldaque da Silva (1893), and later by Rocha Peixoto (1903), that described the use of seagrasses for fertilizer. Later studies of seagrasses from Ria Formosa focused on light absorption (Enríquez et al., 1992), macrobenthic secondary production (Sprung, 1994), and vegetation descriptions (Costa et al., 1996). Since then, research on *Z. noltii* in Ria Formosa has grown exponentially, focusing on the biology and ecology (Cabaço, 2007; Cabaço et al., 2007, 2009; Alexandre et al., 2006; Santos et al., 2004), physiology (Alexandre, 2004; Peralta et al., 2005; Machás et al., 2003, 2006; Massa et al., 2009; Silva and Santos, 2003; Silva et al., 2005), genetics (Diekmann et al., 2005) and anthropogenic effects (Cabaço et al., 2007, 2008; Alexandre et al., 2005). Tidal delta migration and inlet opening can cause sharp reductions in mixed seagrass beds in this system, as described for a large seagrass patch (0.51 km^2) including *Z. noltii* (Cunha et al., 2005; Cunha and Santos, 2009). Because there were no previous seagrass cover assessments it is not possible to estimate the historical losses or gains in Ria Formosa. Many areas that used to have *Z. noltii* beds are now occupied by clam farms (Guimarães et al., in press), harbors, industries and coastal constructions, or dredged to open and maintain navigation channels, such as the opening of a new inlet in Fuseta island and channel dredging (May 2011, Cunha pers. obs.) that are destroying vast areas of this species. Other major impacts on *Z. noltii* beds in Ria Formosa are bait and clam seed collection that are done by digging in *Z. noltii* beds and the frequent propeller scarring and anchoring that are widespread on the mudflats of the lagoon.

3.2.17. Current distribution in Guadiana river

The Guadiana river estuary, which sets the border with Spain, has a narrow (2–3 m) *Z. noltii* meadow that extends along the Portuguese margin of the river for 2 km (Fig. 1 and Table 1). *Z. noltii* beds are also present on the Spanish border of the Guadiana river, but were not included in this study. Information on the presence of *Z. noltii* in the Guadiana is limited to incidental reports by Lousã (1986) and Bettencourt and Ramos (2003) with no cover data. We expect that this seagrass had a wider distribution and cover prior to the extensive waterfront development that started in the 1960s.

3.3. Patterns of seagrass distribution and abundance of Z. marina

3.3.1. Current distribution in Óbidos and Ria Formosa

Z. marina was found only in the Óbidos Lagoon and in Ria Formosa (Fig. 1 and Table 1), having recently disappeared from several other sites during this study. Two areas in the Óbidos Lagoon have *Z. marina*, a shallow area behind a sand bar (Ponta do Arinho) with 36 single patches (1–2 m diameter), and a second large meadow, in the center of the lagoon (depth 4–6 m). In Ria Formosa, the seagrass population of the Fuseta channel was represented by 11 small patches (0.5–2.5 m diameter), growing on the channel margin at a low depth (2 m) in May 2010. This population is highly menaced by the recent opening (January 2011) of a new inlet in the Fuseta island. The Culatra channel population is the largest, with 5 meadows identified along the channel margins and 2 others in mudflats and shallow channels.

During this study we observed the disappearance of six *Z. marina* populations. Considered extinct from Ria de Aveiro (Silva et al., 2004), *Z. marina* was identified and geo-referenced during the Biomares field campaign in 2009, that found one patch of *Z. marina* in the Ovar channel and 10 very small patches (about 1–2 m in diameter) in a mud flat in front of the Costa Nova do Prado. Later, in May 2010 (after the stormy winter of 2009/2010), those patches had disappeared. In Portinho da Arrábida, the remnant seagrass meadow that was last seen in October 2006 had disappeared by January 2007 and has not been found in subsequent surveys (2008–2011). In the Tróia peninsula, the Ponta do Adoche and Costa da Galé meadows, mapped and monitored in 2009, were not observed in April 2010 after strong southern storms affected the area in the winter 2009/2010, and the populations of Rio Mira were not observed in 2007 (a small patch with 7 shoots, appeared again in 2009). In Ria Formosa, from the 10 patches studied by Billingham et al. (2003), only four were found in May 2010.

3.3.2. Historical distribution

It is hard to have a precise idea of the historical distribution of *Z. marina* on the Portuguese coast, given the lack of information. Nevertheless, some historical records exist for the Ria de Aveiro, such as Viana de Lemos (1933) who described the distribution of submerged aquatic vegetation in Ria de Aveiro, referring to the once extensive meadows of *Z. marina*, and reporting their decrease. In a later publication, Taborda de Morais (1937) states that *Z. marina* disappeared from Ria de Aveiro because of the wasting disease (the only reference to the presence of this disease in Portugal). Póvoa do Reis in 1974, identified the presence of *Z. marina* in more than 30 locations in the Mira channel and Nova Costa do Prado, both in the south area of Ria de Aveiro (Silva et al., 1974a,b). In his hand-drawn map, another species identified as *Zostera intermedia P. Póvoa*, was also referenced for 9 locations mixed with *Z. marina*.

The Arrábida coast, which used to have luxuriant *Z. marina* beds (Palminha, 1958; L. Cancela da Fonseca; M. Guerra; E. Gonçalves, pers. commun., 2010) showed a decreasing trend since the eighties (Palmeirim et al., 1977; Ameida, 1997). Silva (2004), based on aerial photo analyses, described in detail the decrease in cover of *Z. marina* in the bay Portinho da Arrábida. The oldest photos available (1946), show the existence of a 10 ha continuous meadow. Subsequent photos show an increase in fragmentation due to intensive clam collection by scuba diving, industrial clam trawling and free anchoring that led to the almost disappearance of seagrasses. The last major patch had about 60 m^2 in 2004 when, only 4 clones were found in a sample of 33 shoots, and was last recorded in 2006 (Diekmann et al., unpublished). By January 2007, the condition of this seagrass habitat had deteriorated significantly, consisting of only dead rhizomes colonized by the invasive red alga *A. armata*. This patch therefore disappeared in the 2006/2007 winter and was not observed in August 2011.

Ponta do Adoche and Costa da Galé are two areas on the outer coast of Tróia peninsula that had *Z. marina* meadows mapped and monitored during this study. Genetic data revealed that both meadows were genetically diverse and resulted almost entirely from massive seed-based recruitment, a pattern that contrasts with the highly clonal neighboring Sado and Arrábida populations (Diekmann et al., unpublished). Ponta do Adoche has been monitored by Andrade (2006, 2007) and Andrade and Ferreira (2011) for the Environmental Impact Assessment Studies of the Tróia Resort Marina. These studies showed that *Z. marina* had a seasonal growth pattern correlated with solar irradiance, and maximum summer cover of 10,839 m^2, coincident with our 2009 quantification (Table 1). This represents an increase, since Google Earth images from the

2003 summer show that this meadow covered 6500 m^2 then. Illegal fisheries with nets still occur at this location (Andrade, 2006, 2007), which is very rich in commercially valuable crustaceans; hundreds of mating snow crabs are commonly seen in the spring camouflaged under *Z. noltii* leaves. Bait and clam collection on the seagrass was also practiced during low tides by many beach users. Despite the strong currents in the area, blooms of the filamentous brown alga *Acitenospora crinita* (Ectocarpacea), possibly of estuarine origin, completely covered these meadows for several weeks in 2007 and 2008 (Cunha, pers. obs.).

The Costa da Galé population was first referenced in July 2008, when the Biomares team was exploring for new seagrass areas. The area, very close to the shore (beach), had 41 patches that were mapped in 2009 covering 1300 m^2. Patches were spread along a 0.1 km^2 area, had circular shape with sizes varying from 1 to 12 m^2, and their distributional pattern as isolated circular patches suggested a single seed origin for each patch. These patches did not exist in Google Earth images of 2003, and in 2006 only 11 patches (about 7.3 m^2) were identified in the photos. This coast was reported by L. Cancela da Fonseca (pers. commun.) as having had extended seagrass meadows along the beaches during the eighties, and this was confirmed by fishermen that described the historical existence of large seagrass beds in the area. Both refer having seen the destruction of these meadows by the industrial bivalve trawling fleet that still operates in the area, the effects of which (i.e., scar marks on the bottom) can be seen in Google Earth images from 2006. Last seen in October 2009, both seagrass meadows (Ponta do Adoche and Costa da Galé) were not found by April 2010, the start of the annual monitoring campaigns (Andrade and Cunha, pers. obs.). The winter 2009/2010 was extremely strong, with an unusually high frequency of southern storms to which these patches are fully exposed, as well as intensive rain and flooding which caused the coastal waters to be brown full of sediments in suspension and leaving little light for about four winter months. The few shoots found at the site had also evident signs of herbivory. This was the first time in the last 20 years that the Ponta do Adoche meadows were not observed (Andrade, pers. commun.).

The *Z. marina* population from the Mira estuary was mapped in 1985 by Andrade (1986). The map depicted the cover distribution of *Z. marina* on both river margins, at lower and upper of the estuary, with approximately 0.004 km^2. In the summer of 2006, the *Z. marina* patches from the lower reach and southern margins were surveyed for genetics and looked profuse (Diekmann, pers. commun.). Flood events during November 2006 possibly contributed to the disappearance of these patches because in January 2007 no vestige of the former populations could be found (Adão, Cunha, pers. obs.). In the summer of 2009 we mapped a meadow of 200 m × 2 m (400 m^2), in the previously identified areas, in the lower reach and southern margin, but by February 2010, only a very small patch (40 cm × 40 cm) with ca. 30 shoots very impacted by herbivory, was found (Fig. 1 and Table 1). At present it is uncertain whether this species still occurs in this river.

The Óbidos Lagoon, on the west coast of Portugal, is shallow with a mean depth of 2 m and a wet area of 7 km^2, connected to the ocean by a single narrow inlet (Carvalho et al., 2006). Seagrasses appear to have occurred there for at least a century. It was estimated that 150 ton/year of seagrasses were collected in the Óbidos Lagoon (Baldaque da Silva, 1893). The presence of *Z. marina* in this lagoon was briefly referred to in the benthic fauna studies of Quintino (1988). Old fishermen referred that *Z. marina* used to cover the entire area up to the upper half of the lagoon 50 years ago, which according to old maps would have been approximately 1.5 km^2. In 2008, ten patches of *Z. marina* occurred near Ponta do Arinho and one in the center of the lagoon. In July 2010, the central patch was mapped, as well as more 36 patches in Ponta do Arinho, showing a large increase in the number of *Z. marina* patches between 2008 and 2010. These were surrounded by many patches of *R. maritima*, which were not seen during the 2008 field campaign, and also formed some isolated and larger patches. The total estimated cover of *Z. marina* in the lagoon was 0.0105 km^2 (Fig. 1 and Table 1).

In the Ria Formosa lagoon, the first reference to the presence of *Z. marina* was in Cacela-a-Velha in 1991 (Duarte, Serrão, pers. obs., 1991; see also Enríquez et al., 1992). Costa et al. (1996) refers to this species in the list of species of Ria Formosa Natural Park and Cunha and Duarte (2005, 2007) reported small patches scattered between *C. nodosa* meadows. In a post-dredging seagrass recovery assessment project in 2001, the Ria Formosa was extensively searched for *Z. marina* over a distance of 25 km from Praia de Faro to Fuseta, and also in the area of Cacela-a-Velha where several patches of *Z. marina* had been reported and sampled in 1991 (Enríquez et al., 1992). During this survey, *Z. marina* was identified at 12 sites, with patches ranging from 1 m^2 to 4000 m^2, totalling 9450 m^2, which were mapped and sampled for genetics (Billingham et al., 2003). Most of these were located around Culatra channel, and one site at Ludo (Esteiro do Baião) separated by about 15 km from the remaining ones. No *Z. marina* was observed in the two above-mentioned sites where it had been previously documented: Faro Island and Cacela-a-Velha. At Faro Island channel the disappearance was due to dredging of this channel (by dredging activities that started in 1996 to deepen the channels), whereas at Cacela the causes for disappearance are unknown but might possibly also be related to the intense interventions in this area during 1996/1997, that included channel dredging, closing a recent inlet and refilling barrier island dunes (Ceia, 2009). The Ludo (Baião) meadow had been reduced from ca. 300 m^2 in the spring of 2001 to about 10 m^2 in December 2004, and in April 2005 only a single living shoot was observed among a dead rhizome mat covered by a decaying *Ulva* spp. bloom (Serrão and Diekmann, pers. obs.). In our 2007 survey, 42 meadows were mapped inside the lagoon, totalling 0.0501 km^2 including 3 patches in the Fuseta channel (Cunha et al., 2009). By 2010, at Culatra channel and Coco Island, only 6 of the 12 sites identified in 2001 by Billingham et al. (2003) were present, including a large patch identified and mapped in Esteiro da Regueira (Culatra). In the Fuseta channel, 9 more patches were found showing an increase of 500 m^2 in area in 3 years (Table 1). Besides these 2 populations inside the lagoon (Fuseta and Culatra), 2 patches were also found outside, in a sheltered bay called "Lugar do Sendil", in the Armona beach. The local fishermen indicated that the area occupied by seagrass meadows was much wider, and the fishermen used to come and fish for eels with "redinha", a fishing gear similar to hand trawl. These patches are set on the sandy beach of Armona Island, 100 m from the shore and about 800 m northeast of the inlet (Table 1). They are composed of 2 circular and adjacent patches of *Z. marina* covering 50.30 m^2. These patches are threatened by the huge amount of algae, mostly *Ulva* spp. that floats on the bottom and accumulates in this sheltered area. There are references to the existence of much more extensive seagrass meadows in the area outside the Ria Formosa (Cancela da Fonseca, pers. commun. observed in 1960–1970), namely: (1) at Ilha de Tavira, from Praia do Barril (Santa Luzia) westwards until the Fuseta inlet (observed in the early 1990s), (2) at Quarteira (observed in the 1970s), and (3) near Vila Real de Santo António, in the Montegordo-Manta Rota region (observed in the 1970s). These were subtidal meadows but it is not known whether the species was *Z. marina* or *C. nodosa*. The disappearance of these meadows coincided with observation of industrial bivalve harvesting in the area using a clam trawler named "ganchorra" particularly commonly observed during the mid 1980s (Cancela da Fonseca, pers. commun.).

3.4. Patterns of seagrass distribution and abundance of C. nodosa

3.4.1. Current distribution

The Sado estuary is the northern limit of *C. nodosa* in the Atlantic, where it is isolated by more than 250 km from its nearest meadow on the open Algarve coast (Alberto et al., 2001, 2008). It consists of several meadows along the inner part of the Tróia peninsula, which occupy a band between 2 and 4 m depth with an estimated cover of 0.032 km^2 (Cunha et al., 2009).

On the southern coast of Portugal (Alporchinhos, Marinha, Santa Eulália, and Arrifes Beaches), *C. nodosa* occurs on the open coast on mixed soft and hard bottom. These meadows grow in intertidal rocky pools, on rocky surfaces and sand substrate to 4 m depth and can be partially exposed during spring low tides. The Santa Eulália meadow is the largest one with approximately 0.0491 km^2, and only 3 clones were found by Alberto et al. (2008) among 30 shoots. Like in all other *C. nodosa* meadows in Portugal, which are also currently composed by very few clones (Alberto et al., 2008, and unpublished data), this indicates that seed recruitment is rare and meadows are mainly maintained by clonal propagation.

In Ria Formosa, *C. nodosa* extends through the edges of the main and secondary channels over an area of 0.913 km^2, to a maximum depth of 2 m (Table 1; Cunha et al., 2009). In the summer months, these plants can attain very high shoot densities and long leaves, and can be confounded with *Z. marina*. Just outside Ria Formosa, in Lugar do Sendil (Armona Island beach) a patch of 508.4 m^2 was mapped in 2007 (Table 1). The inner patch was dense, with many runners on the edges. Leaves were small, compared to the ones inside the Ria Formosa lagoon (about 20 cm long). As reported for *Z. marina* at this site, the patches were covered by large amounts of algae, mostly *Ulva* spp. Larger seagrass meadows were reported in the area (Cancela da Fonseca, pers. commun.) and fishermen refer to the richness of eels in this seagrass area before industrial bivalve trawlers started operating in the region.

C. nodosa is the only seagrass present in insular Portuguese territory, in Madeira island (Wirtz, 1995) and was sampled for a genetic biogeographic study in 2002 (Alberto et al., 2008). There are still small, sparse patches of *C. nodosa* in several places along the south coast of Madeira (e.g. near the Clube Naval, Lido, Funchal and east of Ribeira Brava; P. Neves, 2010; Wirtz, 2011, pers. commun.). One of those was formed by only a few plants per square meter, immediately to the southeast of the Clube Naval, Funchal. A larger (at least 200 m × 400 m) dense bed covered the eastern half of the bay of Machico, starting at a depth of approximately 7–9 m and ending rather abruptly at a depth of 16 m. Then, the wall of Machico harbor was extended and the water from Machico river was re-directed and covered that area with mud (Wirtz, pers. commun., 2011). The *C. nodosa* sampled in Lido had no genotypic (i.e., clonal) diversity, a single clone was detected in the site, a pattern similar to the other *C. nodosa* populations found along the Portuguese mainland coast, which may be the result of either severe demographic bottlenecks from previously larger populations or founder effects (Alberto et al., 2008). The Madeira population is however genetically closer to the populations in the Canary islands and Mauritania than to the Portuguese mainland (Alberto et al., 2008).

3.4.2. Historical records

The first references for *C. nodosa* in Ria Formosa were by Enríquez et al. (1992) and Costa et al. (1996). Biomass, leaf production, horizontal and vertical growth were estimated by Cunha and Duarte (2005, 2007) and found to be among the largest found for the species. These meadows, like all mainland Portugal, consist of an admixture contact zone of genetically differentiated types, with a mixture of alleles that are otherwise exclusively Mediterranean or exclusively Atlantic (Alberto et al., 2005, 2008). However, they lack genotypic (i.e., clonal) variability (Alberto et al., 2005, 2008). Most of the Ria Formosa is presently occupied by a huge single male plant of *C. nodosa* (Alberto et al., 2008) a pattern that can well explain the lack of seed-based recovery following channel dredging; recovery was seen only where a few patches of seagrass were left on the sides of the channels (Alberto and Billingham, pers. obs.).

3.5. Distribution and abundance of Ruppia spp.

3.5.1. Current distribution

Widgeon grass (*R. maritima* and *R. cirrhosa*) cover distribution is poorly known in Portugal but is known to occur in coastal lagoons and salt marshes. During this study we observed and mapped *R. maritima* in the Óbidos Lagoon (7 patches were mapped in 2008, most in a inner zone of the lagoon, with an estimated an area of 0.083 km^2). In 2010, the area covered was much larger (area not estimated) and extended to several areas of the inner and outer lagoon, mixed in the *Z. marina* meadows mapped in 2010. This is the first and unique report of *R. maritima* growing together with *Z. marina* in Portugal.

3.5.2. Historical records

R. maritima occurred in the Arade river (Santos et al., 2004) but was not observed in 2009 (this study), and it also occurred in Ria Formosa at Ludo (Gonçalves, pers. obs., 2010). *R. cirrhosa* occurred at Lagoa de Santo André (Calado and Duarte, 2000) and Ria de Aveiro (Silva et al., 2004). In Lagoa de Albufeira it covered 0.425 km^2 (Salgado and Santos, 1985) and occurred in all margins of both the inner and outer lagoon. During our surveys in this area widgeon grass was not observed in the inner lagoon, and the cover estimated for the outer lagoon (0.037 km^2), was much smaller than the area depicted in the hand-map done by Salgado and Santos (1985). Many other locations need urgently to be assessed for these species, believed to have been suffering from the same trends towards extinction as their less eurihaline counterparts. Further difficulties in assessing their distribution and cover are that *Ruppia* spp. can be annual or perennial and this varies in space and time, and they can persist as a seed bank, making their cover assessment more challenging.

4. Genetic uniqueness of Portuguese seagrass meadows

The Portuguese seagrass meadows are unique, genetically differentiated from all other worldwide populations surveyed in Europe and throughout the rest of the world (Olsen et al., 2004; Coyer et al., 2004; Alberto et al., 2008). In addition to their differentiation from other world regions, there is isolation and distinct genetic patterns within Portugal, even at considerably short distances. This was the case for the now vanished *Z. marina* meadows distant by only 15 km at Esteiro do Baião and Ponta da Culatra, which were genetically distinct (Billingham et al., 2003) and possibly locally adapted, as indicated by outbreeding depression when crossed (Billingham et al., 2007). The *Z. noltii* populations along the Portuguese coast are all genetically distinct from each other, reflecting low dispersal between sites. However, the most striking boundary is in the central region, where populations located North of the Tagus river are genetically differentiated from the southern ones, a pattern which may be related to the coastal morphology and nearshore current patterns (Diekmann et al., 2005). Portuguese *C. nodosa* populations are all composed of few clones (i.e., are not maintained predominantly by seed propagation), and those clones have a mixture of Mediterranean and Atlantic (African) genetic characteristics, and therefore are a unique genetic make-up only found in this contact zone (Alberto et al., 2008). The high clonality of *C. nodosa* in Portugal may result from either (1) founder effects caused by initial colonization by very few clones which have

Table 2
Major habitat loss factors, threats identified in the seagrass ecosystem of the Portuguese coast and management needs for improving conservation status.

Factors	Threats	Management needs
Meadow destruction	Construction of marinas, ports, other coastal construction; channel dredging; beach filling, bivalve (clam and oyster) culturing	Environment policy enforcement; public and coastal management institutions awareness
Meadow fragmentation	Free mooring; boat propeller scarring; clam and bait hand collection; industrial clam trawling and with hand trawlers	Permanent buoys; better channel signalization; public information with boat license; policy law enforcement; banning of clam trawling from seagrass habitats; creation of management plan for clam/bait collection areas, public awareness programs; implementation of clam hatcheries and bait farms with progressive abandonment of collection of this species from the wild
Habitat sedimentation	Dredging operations, inlet opening Bad watershed soil practices Winter storms	Improvement of water drainage practices (agriculture and natural barriers) Better practices in dredging activities – observer on board Environment policy enforcement Implementation of Water Framework Directive
Water eutrophication	Urban and industrial sewage Bad watershed soil practices Algae blooms	Implementation of watershed good practices Implementation of Water Framework Directive Public and coastal management institutions awareness Implementation of management plans for exotic species

persisted and expanded, or by (2) bottlenecks caused by heavy disturbance on pre-existing meadows followed by recolonization from a few local surviving clones. The previous reports of extensive seagrass meadows on the Algarve coast in the 1960s (see above, pers. obs., by Cancela da Fonseca) and the fact that the remaining meadows on the open Algarve coast are located on rock or around rocky areas suggest that these might be the survivors of heavy disturbance, spared from the intensive bivalve dredging (not done on rocky shores) that could be seen on the Algarve coast during the 1980s. The species *C. nodosa* is dioecious (plants are only male or female), which confers higher level of susceptibility to population bottlenecks. Most of the Ria Formosa is presently occupied by a huge single male plant of *C. nodosa* (Alberto et al., 2008); in Marinha Beach another single male was found. Single males cannot produce seeds, a likely reason for the lack of seed-based recovery following channel dredging monitored in 2001; *C. nodosa* recovered only where a few patches were left by the dredges on the sides of the channels, allowing for clonal propagation (Alberto and Billingham, pers. obs.).

5. Implications

Seagrass meadows provide critical habitat for a wide range of species and supports different and more abundant and diverse fish assemblages than non-vegetated habitats (e.g. Heck et al., 1989; Heck and Valentine, 2006; Connolly, 1994; Guidetti, 2000; Guidetti and Bessotti, 2000; Duarte, 2002). Despite efforts to quantify the economic value of the seagrass ecosystem (e.g. 19,004$ ha^{-1} y^{-1}; Costanza et al., 1997), it is evident that the economic losses so far published related to seagrass disappearance, are underestimated.

The declining of seagrasses along the Portuguese coast has been causing great marine biodiversity loss, contributed to coastal fisheries impoverishment, decrease in coastal water quality, and increased coastal erosion, with loss of a very valuable resource for the Portuguese economy: beach sand. The Portuguese estuaries currently have poor conditions for annular seabream (*Diplodus annularis* L.) juveniles due to low abundance of seagrass habitats (Vinagre et al., 2010). Fish assemblages associated with seagrass and sandy sites (as those left after seagrass loss) are substantially different, as the seagrass supported a much more abundant and diverse fish community, and was an important juvenile fish habitat for more species than sand, as quantified in Ria Formosa (Ribeiro et al., 2006). In the Mondego river, the *Z. noltii* meadow was quantified as the richest in macrofaunal abundance and biodiversity (Lillebø et al., 1999; Pardal et al., 2000, 2004; Cardoso et al., 2004a,b, 2005; Dolbeth et al., 2003, 2007). In the Mira river, seagrass habitat was the most important feature in determining abundance and distribution of estuarine fishes (Almeida, 1988, 1999; Costa et al., 1994).

Management actions can be put in place to invert the decreasing trend observed (Table 2) notably because seagrasses have received recognition as important indicators of a good ecological status under the Water Framework Directive. Means to invert the seagrass decline along Portuguese coast would have to involve:

- a general raise in awareness among coastal users, managers, politicians, environmental groups, and the general public;
- real integration of coastal plans in political decisions;
- measures to minimize the impact of clam and bait harvesting (e.g. regulate permits for clam farms in seagrass meadows, regulating bivalve and bait collection, establishing protection zones around meadows);
- establishment of protected areas under the Habitat Directive where coastal impacts could be halted;
- increasing awareness of fishermen and nautical recreation groups to minimize seagrass meadow scarring by boat propellers and anchoring;
- implement best dredging practices and review dredging projects that have the potential to impact seagrass habitat, and coastal constructions (harbors, marinas, inlets) should consider alternative locations that minimize the impact on seagrass beds;
- work towards a full implementation of a good status for water quality as stated in the WFD.

A major involvement of society, scientists, politicians and resource managers is needed to invert the losses depicted in this paper. More effort is required into research and study of these ecosystems, in actions to promote seagrass self-recovery and restoration.

Acknowledgments

Results presented in this paper were possible due to the help of many colleagues who provided personal information and access to reports, and paddling friends and volunteers that helped in the seagrass mapping field trips. Special thanks to J. Banha and J. Pereira and to the technicians of the Biomares project, L. Gonçalves, V. Ferreira, T. Repolho, D. Paulo, J. Boavida, S. Rodrigues, F. Pires, that collaborate actively in the seagrass mapping operations. E. Berecibar identified the alga *C. acitenospora*. This research was funded by the European commission through the LIFE Biomares project (LIFE 06 NAT/P/192). Comments from three anonymous reviewers substantially improved this manuscript.

References

Adão, M.H.S.M., 2003. Dinâmica das comunidades de meiofauna em sedimentos associados aos povoamentos de *Zostera noltii* no estuário do rio Mira. Dissertação apresentada para obtenção do grau de Doutor. Universidade de Évora, Évora, Portugal.

Alberto, F., Gouveia, L., Arnaud-haond, S., Péres-lloréns, J., Duarte, C.M., Serrão, E., 2005. Within-population spatial genetic structure, neighbourhood size and clonal subrange in the seagrass *Cymodocea nodosa*. Mol. Ecol. 14, 2669–2681.

Alberto, F., Massa, S., Manent, P., Diaz-Almela, E., Arnaud-Haond, S., Duarte, C.M., Serrão, E.A., 2008. Genetic differentiation and secondary contact zone in the seagrass *Cymodocea nodosa* across the Mediterranean–Atlantic transition region. J. Biogeogr. 35, 1279–1294.

Alberto, F., Mata, L., Santos, R., 2001. Genetic homogeneity in the seagras *Cymodocea nodosa* at its northern Atlantic limit revealed through RAPD. Mar. Ecol. Prog. Ser. 221, 299–301.

Alexandre, A., 2004. Impacto da actividade de marisqueio na floração e no esforço de reprodução sexual em *Zostera noltii* Hornemann na Ria Formosa. Master Thesis. University of the Algarve, Faro, Portugal.

Alexandre, A., Cabaço, S., Santos, R., Serrão, E.A., 2006. Timing and success of reproductive stages in the seagrass *Zostera noltii*. Aquat. Bot. 85, 219–223.

Alexandre, A., Santos, R., Serrão, E.A., 2005. Effects of clam harvesting on sexual reproduction of the seagrass *Zostera noltii*. Mar. Ecol. Prog. Ser. 298, 115–122.

Almeida, A., 1988. Estrutura, dinâmica e produção da macrofauna acompanhante dos povoamentos de *Zostera noltii* e *Zostera marina* no estuário do Rio Mira. PhD Thesis. Faculty of Sciences of the University of Lisbon, Lisbon, Portugal.

Almeida, A.J., 1999. The role of seagrass beds on the conservation of littoral fish. In: Almada, V.C., Oliveira, R.F., Gonçalves, E.J. (Eds.), Behaviour and Conservation of Littoral Fishes. I.S.P.A., Lisboa, Portugal (CB), pp. 521–529.

Ameida, A.J., 1997. "As pradarias submarinas" de angióspermicas marinhas. Liberne, Revista da Liga para a Protecção da Natureza 61, 18–20.

Andrade, F., 1986. O estuário do Mira: caracterização geral e análise quantitativa da estrutura dos macropovoamentos bentónicos. PhD Thesis. Faculty of Sciences of the University of Lisbon, Portugal.

Andrade, F., 2006, 2007. Relatório do Programa de Monitorização Ambiental do projecto da Marina e novo Cais dos "ferries" do Troiaresort. Instituto do Mar, Lisboa, Portugal.

Andrade, F., Ferreira, A., 2011. A method for monitoring shallow seagrass meadows (*Zostera* spp.) using terrestrial oblique large-scale photography. Aquat. Bot. 95, 103–109.

Antunes, M.P., Cunha, P.,1988. Ecologia da ictiofauna na Ria de Alvor. In: Actas do 5º Congresso do Algarve. Racal Club, Silves, Portugal.

Baeta, A., Valiela, I., Rossi, F., Pinto, R., Richard, P., Niquil, N., Marques, J.C., 2009. Eutrophication and trophic structure in response to the presence of the eelgrasss *Zostera noltii*. Mar. Biol. 156, 2107–2120.

Baldaque da Silva, A.,1893. Estado actual das pescas. Imprensa Nacional, Lisboa, Portugal.

Bettencourt, A., Ramos, L., 2003. Estuários Portugueses, Ministério das Cidades, Ordenamento do Território e Ambiente. Instituto da Água, Lisboa.

Billingham, M., Reusch, T.B., Alberto, F., Serrão, E.A., 2003. Is asexual reproduction more important at geographical limits? A genetic test of the seagrass *Zostera marina* in the Ria Formosa, Portugal. Mar. Ecol. Prog. Ser. 265, 77–83.

Billingham, M., Simões, T., Reusch, T.B.H., Serrão, E.A., 2007. Genetic sub-structure and intermediate optimal outcrossing distance in the marine angiosperm *Zostera marina*. Mar. Biol. 157, 793–801.

Bull, J.C., Kenyon, E.J., Edmunds, D., Cook, K.J., 2010. Recent loss of Gibraltar seagrasses. Bot. Mar. 53, 89–91.

Cabaço, C., Machás, R., Santos, R., 2007. Biomass-density relationships of the seagrass *Zostera noltii*: a tool for monitoring anthropogenic nutrient disturbance. Estuar. Coast. Shelf. Sci. 74, 557–564.

Cabaço, S., 2007. Impact of anthropogenic activities on the seagrass *Zostera noltii*. PhD Thesis. University of the Algarve, Faro, Portugal.

Cabaço, S., Machás, R., Santos, R., 2009. Individual and population plasticity of the seagrass *Zostera noltii* along a vertical intertidal gradient. Estuar. Coast. Shelf. Sci. 82, 301–308.

Cabaço, S., Machas, R., Vieira, V., Santos, R., 2008. Impacts of urban wastewater discharge on seagrass meadows (*Zostera noltii*). Estuar. Coast. Shelf. Sci. 78, 1–13.

Cabaço, S., Santos, R., 2010. Reproduction of *Zostera marina* at the species southern distributional limit in the eastern Atlantic. Mar. Ecol. 31, 300–308.

Caeiro, S., Costa, M.H., Ramos, T.B., Fernandes, F., Silveira, N., Coimbra, A., Medeiros, G., Painho, M., 2005. Assessing heavy metal contamination in Sado estuary sediment: an index analysis approach. Ecol. Indic. 5, 151–169.

Calado, G., Duarte, P., 2000. Modelling growth of *R. cirrhosa*. Aquat. Bot. 68, 29–44.

Cardoso, P.G., Brandão, A., Pardal, M.A., Raffaelli, D., Marques, J.C., 2005. Resilience of *Hydrobia ulvae* populations to anthropogenic and natural disturbances. Mar. Ecol. Prog. Ser. 289, 191–199.

Cardoso, P.G., Pardal, M.A., Lillebø, A.I., Ferreira, S.M., Raffaelli, D., Marques, J.C., 2004a. Dynamic changes in seagrass assemblages under eutrophication and implications for recovery. J. Exp. Mar. Biol. Ecol. 302, 233–248.

Cardoso, P.G., Pardal, M.A., Raffaelli, D., Baeta, A., Marques, J.C., 2004b. Macroinvertebrate response to different species of macroalgal mats and the role of disturbance history. J. Exp. Mar. Biol. Ecol. 308, 207–220.

Carvalho, S., Gaspar, M.B., Moura, A., Vale, C., Antunes, P., Gil, O., Fonseca, L.C., Falcão, M., 2006. The use of marine biotic index AMBI in the assessment of the ecological status of the Óbidos Lagoon. Mar. Pollut. Bull. 52, 1414–1424 (Portugal).

Ceia, F.R., 2009. Barrier-islands vulnerability and Ria Formosa dynamics under a management viewpoint. J. Integr. Coast. Zone Manage. 9, 57–77.

Connolly, R.M., 1994. A comparison of fish assemblages from seagrass and sand habitats of a southern Australian estuary. Aust. J. Mar. Fresh. Res. 45, 759–770.

Costa, J.C., Lousã, M., Santos, M.D.E., 1996. A vegetação do Parque Natural da Ria Formosa. Stud. Bot. Ediciones Univ. de Salamanca 15, 69–157 (Algarve, Portugal).

Costa, M., Costa, J., Raposo, P., Assis, C., 1994. Do eelgrass beds and salt marsh borders act as preferential nurseries and spawning grounds for fish? An example of the Mira estuary in Portugal. Ecol. Eng. 3, 187–195.

Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P., van den Belt, M., 1997. The value of the world's ecosystem services and natural capital. Nature 387, 253–260.

Coyer, J.A., Diekmann, O.E., Serrão, E.A., Procaccini, G., Milchakova, N.G.A., Pearson, G.A., Stam, W.T., Olsen, J.L., 2004. Population genetics of dwarf eelgrass *Zostera noltii* throughout its biogeographic range. Mar. Ecol. Prog. Ser. 281, 51–62.

Cunha, A.H., 1991. Monitorização dos bancos de *Zostera noltii* da Ria de Alvor. Relatório de projecto. Portisub, Clube Subaquático de Portimão, Portimão, p. 15.

Cunha, A.H., Erzini, K., Serrão, E., Gonçalves E., Gonçalves V., Henriques, M., Guerra, M., Duarte, C.M., Marbá, N. Biomares a LIFE project to restore and manage the biodiversity of the marine park site Arrábida-Espichel (PTCON0010) LIFE06 NAT/P/192. J. Coast. Conserv., in press.

Cunha, A.H., Araújo, A., 2009. New distribution limits of seagrass beds in West Africa. J. Biogeogr. 36, 1621–1622.

Cunha, A.H., Assis, J., Serrão, E., 2009. Estimation of available seagrass meadow area in Portugal for transplanting purposes. J. Coast. Res. 56, 1100–1104.

Cunha, A.H., Duarte, C.M., 2005. Population age structure and rhizome growth of *Cymodocea nodosa* (Ucria) Ascherson in Ria Formosa (Southern Portugal). Mar. Biol. 146, 841–847.

Cunha, A.H., Duarte, C.M., 2007. Biomass and leaf production of *Cymodocea nodosa* (Ucria) Ascherson in an Atlantic lagoon: the Ria Formosa (South of Portugal). Bot. Mar. 50, 1–7.

Cunha, A.H., Santos, R., 2009. The use of fractals to assess seagrass landscape stability: a case study from the barrier island system of Ria Formosa (South of Portugal). Estuar. Coast. Shelf Sci. 84, 584–590.

Cunha, A.H., Santos, R., Gaspar, A.P., Bairros, M., 2005. Seagrass landscape-scale changes in response to disturbance by barrier-islands dynamics: a case study from Ria Formosa (South of Portugal). Estuar. Coast. Shelf Sci. 64, 636–644.

den Hartog, C., 1970. The sea-grasses of the World. Verhandl. der Koninklijke Nederlandse Akademie van Wetenschappen, Afd. Natuurk. 59 (1).

Diekmann, O.E., Coyer, J.A., Ferreira, J., Olsen, J.L., Stam, W.T., Pearson, G.A., Serrão, E.A., 2005. Population genetics of *Zostera noltii* along the west Iberian coast: consequences of small population size, habitat discontinuity and nearshore currents. Mar. Ecol. Prog. Ser. 290, 89–96.

Dolbeth, M., Cardoso, P.G., Ferreira, S.M., Verdelhos, T., Raffaelli, D., Pardal, M.A., 2007. Anthropogenic and natural disturbance effects on a macrobenthic estuarine community over a 10-year period. Mar. Ecol. Prog. Ser. 54, 576–585.

Dolbeth, M., Pardal, M.A., Lillebø, A.I., Azeiteiro, U.M., Marques, J.C., 2003. Short and long-term effects of eutrophication on the secondary production of an intertidal macrobenthic community. Mar. Biol. 143, 1229–1238.

Duarte, C.M., 2002. The future of seagrass meadows. Environ. Conserv. 29, 192–206.

Duarte, A.P., Mendonça, E.,1988. Caracterização ecológica da Ria de Alvor – Estudo componente ictioplancton. In: Actas do 5° Congresso do Algarve. Racal Club, Silves, Portugal.

Duarte, C.M., Borum, J., Short, F., Walker, D., 2008. Seagrass ecosystems: their global status and prospects. In: Poluin, N. (Ed.), Aquatic Ecosystems. Cambridge University Press, Foundation for Environmental Conservation, pp. 281–294 (Chapter 18).

Duarte, C.M., Culbertson, J., Dennison, W.C., Fulweiler, R.W., Hughes, T., Kinney, E.L., Marbá, N., Nixon, S., Peacock, E.E., Smith, S., Valiela, I., 2009. Global Loss of Coastal Habitats: Rates, Causes and Consequences. Carlos Duarte Fundacion BBVA, Bilbao, Spain, p. 175.

Enríquez, S., Agustí, Duarte, C.M., 1992. Light absorption by seagrass *Posidonia oceanica* leaves. Mar. Ecol. Prog. Ser. 86, 201–204.

Ferreira, C., 1994. Estrutura trófica da comunidade macrobentónica dos povoamentos de *Zostera noltii* (Hornem.) e de *Zostera marina* L. no estuário do Rio Mira (Portugal). Master Thesis. University of Coimbra, Portugal.

Ferreira, S.M., Brandão, A., Baeta, A., Neto, J.M., Lillebø, A.I., Jensen, K.T., Pardal, M.A., 2007. Effects of restoration management on the estuarine isopod *Cyathura carinata*: mediation by trematodes and habitat change. Mar. Biol. 151, 109–118.

Guidetti, P., 2000. Differences among fish assemblages associated with nearshore *Posidonia oceanica* seagrass beds, rocky-algal reefs and unvegetated sand habitats in the Adriatic Sea. Estuar. Coast. Shelf. Sci. 50, 515–529.

Guidetti, P., Bessotti, S., 2000. Fish fauna of a mixed meadow composed by the seagrasses *Cymodocea nodosa* and *Zostera noltii* in the western Mediterranean. Oceanol. Acta 23, 759–770.

Guimarães, H., Cunha, A.H., Nzinga, R., Marques, J. The distribution of seagrass (*Zostera noltii* Hornem.) in the Ria Formosa lagoon system and the implications of clam farming on its conservation. J. Nat. Conserv., in press.

Guimarães, M.H.M.E., 2007. Contribuição para a elaboração de um plano integrado de gestão dos campos de *Z. noltii* na Ria Formosa. Master Thesis. University of Algarve, Faro, Portugal.
Heck Jr., K.L., Valentine, J.F., 2006. Plant–herbivore interactions in seagrass meadows. J. Exp. Mar. Biol. Ecol. 330, 420–436.
Heck Jr., K.L., Able, K.W., Fahay, M.P., Roman, C.T., 1989. Fishes and decapod crustaceans of Cape Cod eelgrass meadows: species composition seasonal abundance and comparison with unvegetated substrates. Estuaries 12, 59–65.
Leal, A.M., 1984. Estado actual das ostreiras dos estuários do Tagus, Sado, Mira e do 404 Algarve. In: INIP/APRH (Ed.), Seminário sobre aquacultura Lisboa. , pp. 71–86.
Lillebø, A.I., Teixeira, H., Pardal, M.A., Marques, J.C., 2007. Applying quality status criteria to a temperate estuary before and after the mitigation measures to reduce eutrophication symptoms. Estuar. Coast. Shelf Sci. 72, 177–187.
Lillebø, A.I., Flindt, M.R., Pardal, M.A., Marques, J.C., 1999. The effect of macrofauna, meiofauna and microfauna on the degradation of *Spartina maritima* detritus from a salt marsh area. In: Marques, Gamito, Ré (Eds.), Processes and Flows in Marine Benthic Ecosystems. Acta Oecol. 20, 249–258.
Lillebø, A.I., Neto, J.M., Flindt, M.R., Marques, J.C., Pardal, M.A., 2004. Phosphorous dynamics in a temperate intertidal estuary. Estuar. Coast. Shelf Sci. 61, 101–109.
Lillebø, A.I., Neto, J.M., Martins, I., Verdelhos, T., Leston, S., Cardoso, P.G., Ferreira, S.M., Marques, J.C., Pardal, M.A., 2005. Management of a shallow temperate estuary to control eutrophication: the effect of hydrodynamics on the system nutrient loading. Estuar. Coast. Shelf Sci. 65, 697–707.
Lousã, M.F., 1986. Comunidades Halofílicas da Reserva Natural de Castro Marim-Vila Real de Santo António. Universidade Técnica de Lisboa-Instituto Superior de Agonomia, Lisboa, p. 157.
Machás, R., Santos, R., Peterson, B., 2003. Tracing the flow of organic matter fromprimary producers to filter feeders in Ria Formosa lagoon, Southern Portugal. Estuaries 26, 846–856.
Machás, R., Santos, R., Peterson, B., 2006. Elemental and stable isotope composition of *Zostera noltii* (Horneman) leaves during the early phases of decay in a temperate mesotidal lagoon. Estuar. Coast. Shelf Sci. 66, 21–29.
Martins, I., Neto, J.M., Fontes, M.G., Marques, J.C., Pardal, M.A., 2005. Seasonal variation in short-term survival of *Zostera noltii* transplants in a declining meadow in Portugal. Aquat. Bot. 82, 132–142.
Martins, I., Pardal, M.A., Lillebø, A.I., Flindt, M.R., Marques, J.C., 2001. Hydrodynamics as a major factor controlling the occurrence of green macroalgal blooms in a eutrophic estuary: a case study on the influence of precipitation and river management. Estuar. Coast. Shelf Sci. 52, 165–177.
Massa, S.I., Arnaud-Haond, S., Pearson, G.A., Serrão, E.A., 2009. Temperature tolerance and survival of intertidal populations of the seagrass *Zostera noltii* (Hornemann.) in Southern Europe (Ria Formosa, Portugal). Hydrobiologia 619, 195–201.
Neto, J.M., 2004. Nutrient enrichment in a temperate macro-tidal system. Scenario analysis and contribution to coastal management. PhD Thesis in Biology. University of Coimbra, Portugal.
Olsen, J.L., Stam, W.T., Coyer, J.A., Reusch, T.B.H., Billingham, M., Bostrom, C., Calvert, E., Christie, H., Granger, S., La Lumiere, R., Milchakova, N., Oudot-Le Secq, M.P., Procaccini, G., Sanjabi, B., Serrão, E., Veldsink, J., Widdecombe, S., Wyllie-Echeverria, S., 2004. North Atlantic phylogeography and large-scale populations differentiation of the seagrass *Zostera marina* L. Mol. Ecol. 13, 1923–1941.
Orth, R.J., Carruthers, T.J.B., Dennison, W.C., Duarte, C.M., Fourqurean, J.W., Heck, K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Olyarnik, S., Short, F.T., Waycott, M., Williams, S.L., 2006. A global crisis for seagrass ecosystems. Bioscience 56, 987–996.
Palmeirim, J.M., Luis, O.J., Ribeiro, V.M.A., 1977. Dados sobre as populaçõesde *Zostera marina* do Portinho da Arrábida. Trabalho de avaliação e conhecimentos da cadeira de Oceanografia Biológica II. Faculty of Sciences of the University of Lisbon, Portugal, p. 31.
Palminha, F., 1958. As algas marinhas de zona costeira da Arrábida e sua protecção (contribuição para o estudo ecológico), A Serra da Arrábida e a Protecção à Natureza. Publicações da Liga para a Protecção XIV, Lisboa, Portugal, pp. 5–23.
Pardal, M.A., Cardoso, P.G., Sousa, J.P., Marques, J.C., Raffaelli, D., 2004. Assessing environmental quality: a novel approach. Mar. Ecol. Prog. Ser. 267, 1–8.
Pardal, M.A., Marques, J.C., Metelo, I., Lillebø, A., Flindt, M.R., 2000. Impact of eutrophication on the life cycle, population dynamics and production of *Amphitoe valida* (Amphipoda) along an estuarine spatial gradient (Mondego estuary, Portugal). Mar. Ecol. Prog. Ser. 196, 207–219.
Peralta, G., Brun, F.G., Hernández, I., Vergara, J.J., Pérez-Lloréns, J.L., 2005. Morphometric variations as acclimation mechanisms in *Zostera noltii* beds. Estuar. Coast. Shelf Sci. 64, 347–356.
Quintino, V.M.S., 1988. Structure et cinétique comparées des communautés de macrofaune benthique de deux systémes lagunaires de la cote ouest de Portugal: Óbidos et Albufeira. PhD Dissertation. University of Paris, France.
Ribeiro, J., Bentes, L., Coelho, R., Gonçalves, J.M.S., Lino, P.G., Monteiro, P., Erzini, K., 2006. Seasonal, tidal and diurnal changes in fish assemblages in the Ria Formosa lagoon (Portugal). Estuar. Coast. Shelf Sci. 67, 461–474.
Rocha Peixoto, R., 1903. Os Palheiros Do Litoral. Portugália I. Porto, Portugal, pp. 79–96.
Salgado, P., Santos, R., 1985. Estudo da distribuição da componente macrofitobentónica da Lagoa de Albufeira (Relatório de Síntese). Laboratório Nacional de Engenharia e Tecnologia Industrial, Ministério da Indústria e Tecnologia Industrial, Sacavém, Portugal, pp. 131–149.
Santos, R., Salgado, P., 1988. Cartografia e abundância por fotointerpretação dos macrófitos aquáticos da Ria de Alvor. In: Actas do 5° Congresso do Algarve, Silves, Portugal, pp. 419–426.
Santos, R., Silva, J., Cunha, A., 2004. Relatório final do estudo de caracterização dos bancos de fanerogâmicas e macroalgas no estuário do Rio Arade. Centre of Marine Sciences, Faro, Portugal, p. 15.
Silva, J.M., Santos, R., Calleja, M.L., Duarte, C.M., 2005. Submerged versus air-exposed intertidal macrophyte productivity: from physiological to community-level assessments. J. Exp. Mar. Biol. Ecol. 317, 87–95.
Silva, J., Santos, R., 2003. Daily variation patterns in seagrass photosynthesis along a vertical gradient. Mar. Ecol. Prog. Ser. 257, 37–44.
Silva, J.A.M., 2004. Estudos iniciais para a recuperação da população de fanerogâmicas marinhas do Parque Marinho da Arrábida, Setúbal, Portugal. Master Thesis. University of the Algarve, Faro, Portugal.
Silva, J.F., Duck, R.W., 2001. Historical changes of bottom topography and tidal amplitude in the Ria de Aveiro, Portugal – trends for future evolution. Clim. Res. 18, 17–24.
Silva, J.F., Duck, R.W., Catarino, J.B., 2004. Seagrass and sediment response to changing physical forcing in a coastal lagoon. Hydrol. Earth Syst. Sci. 8, 151–159.
Silva, J.F., Duck, R.W., Catarino, J.B., 2009. Nutrient retention in the sediments and the submerged aquatic vegetation of the coastal lagoon of the Ria de Aveiro, Portugal. J. Sea Res. 62, 276–285.
Silva, J.F., Vieira, M., Carvalho, M., Póvoa dos Reis, M., 1974a. Sobre a existência de um híbrido entre *Zostera marina* L. e *Z. nana* Roth na Ria de Aveiro, vol. III. I.D.E.S.O., Ria de Aveiro, pp. 23–27, 3 tab.
Silva, J.F., Vieira, M., Carvalho, M., Póvoa dos Reis, M., 1974b. Três comunidades de *Zostera* L. na Ria de Aveiro, vol. III. I.D.E.S.O., Ria de Aveiro, pp. 34–40.
Sprung, M., 1994. Macrobenthic secondary production in the intertidal zone of Ria Formosa – a lagoon in Southern Portugal. Estuar. Coast. Shelf Sci. 38, 539–558.
Taborda de Morais, 1937. Boletim da Sociedade Broteriana, 2ª série, pp. 12–221.
Vale, C., Cortesão, C., Castro, O., Ferreira, A.M., 1993. Suspended sediment response to pulses in river flow and semi-diurnal and fortnightly tidal variations in a mesotidal estuary. Mar. Chem. 43, 21–31.
Viana de Lemos, A., 1933. Moliço da Ria de Aveiro. Revista da Faculdade de Ciências da Universidade de Coimbra 3, 416–433.
Vinagre, C., Cabral, H.N., Costa, M.J., 2010. Relative importance of estuarine nurseries for species of the genus *Diplodus* (Sparidae) along the Portuguese coast. Estuar. Coast. Shelf Sci. 86, 197–202.
Waycott, M., Duarte, C.M., Carruthers, T.J.B., Orth, R.J., Dennison, W.C., Olyarnik, S., Calladine, A., Fourqurean, J.W., Heck, K.L., Hughes, A.R., Kendrick, G.G.A., Kenworthy, W.J., Short, F.T., Williams, S.W., 2009. Accelerating loss of seagrass across the globe threatens coastal ecosystems. Ecol. PNA, 1–5.
Wirtz, P., 1995. One vascular plant and ten invertebrates new for the marine fauna and flora of Madeira. Arquipelago 13A, 11–124.