

Posidonia oceanica in the Marmara Sea

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ABSTRACT

The seagrass *Posidonia oceanica* is a stenohaline species endemic to the Mediterranean Sea, where it normally lives at a salinity of between 36.5 and 39.5 ppt. Surveys carried out at the North-eastern distribution limits revealed large beds in the Dardanelles Strait and isolated beds in the Marmara Sea, where the salinity ranges between 21.5 and 28 ppt. Microsatellite analysis of these low-salinity tolerant *P. oceanica* beds, show different signs of genetic isolation: excess of heterozygosity and a presence of fixed alleles. These particularities are rarely found in the whole distributional range of the species. Moreover, all the populations considered in the analysis have a very low genetic diversity in comparison with most of the meadows sampled throughout the Mediterranean Sea. Taking into consideration the genetic data, rhizome expansion rate and the actual extent of the isolated beds in the Marmara Sea and knowing the reproductive rate and dissemination characteristics of *P. oceanica*, we hypothesize that the isolated population of the Marmara Sea has been established since the Middle Holocene, before the catastrophic intrusion of brackish water into the Marmara Sea and the strong and persistent flow coming from the Black Sea.

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1. Introduction

Posidonia oceanica (L.) Delile (Magnoliophyta) is the most abundant seagrass in the Mediterranean Sea and its distribution is fairly well recorded (Green and Short, 2003). However, its distribution limit is still unclear particularly at the narrow Dardanelle Strait where the Aegean Sea meets the Marmara Sea and previous records appear to be incorrect. The record of *P. oceanica* reported in the Marmara Sea in The World Atlas of Seagrasses (Green and Short, 2003), was in fact observed at Urla-Iskele, close to Izmir in the Aegean Sea (Short, pers. com.).

This endemic Mediterranean species is known to be stenohaline, living in a salinity range between 36.5 ppt (in the Alboran Sea: Ramirez et al., 2005) and 39.5 ppt (in the Aegean Sea: Beşiktepe, 2003). The species can occasionally tolerate very high salinity up to 48 ppt in semi-enclosed environments, such as the Stagnone coastal lagoon at Marsala (Di Maida et al., in press.), but up to now it has not been recorded in low salinity environments. The presence of the species in the Marmara Sea is exceptional because of its brackish water. Moreover, the regular and vigorous intrusion

of the Black Sea brackish waters, which flow at the subsurface (0–25 m depth) since the Holocene (Özsoy et al., 1995; Tuğrul et al., 1995; Polat and Tuğrul, 1996; Türkoğlu et al., 2004) limits the arrival of floating seeds and/or rhizomes from the Mediterranean Sea, thus probably isolating Marmara Sea meadows.

We quantified the distribution of *P. oceanica* in the Dardanelles Strait and in the Marmara Sea through SCUBA diving observations, beach surveys, discovering large beds in the straits of Dardanelles and isolated populations in the Sea of Marmara. In order to understand the level of genetic isolation of the newly discovered *Posidonia* meadows we assessed the clonal diversity and the genetic affinity with other Mediterranean populations.

2. Methods

The Marmara Sea is about 210 km long and 75 km wide (11,500 km²), with 800 km of coastline and connections to the Black Sea at its eastern side and the Mediterranean Sea (Aegean Sea) at its western side (Fig. 1). High density water coming from the Aegean Sea (salinity ranging 39–39.5 ppt) sink below the surface at the entrance and move along the bottom of the Dardanelles Strait (60–70 m depth) throughout the Marmara Sea, reaching the Black Sea after the Bosphorus Strait (310 km³ year⁻¹). Low density waters (salinity from 20 to 29 ppt) flow at the surface (between 0

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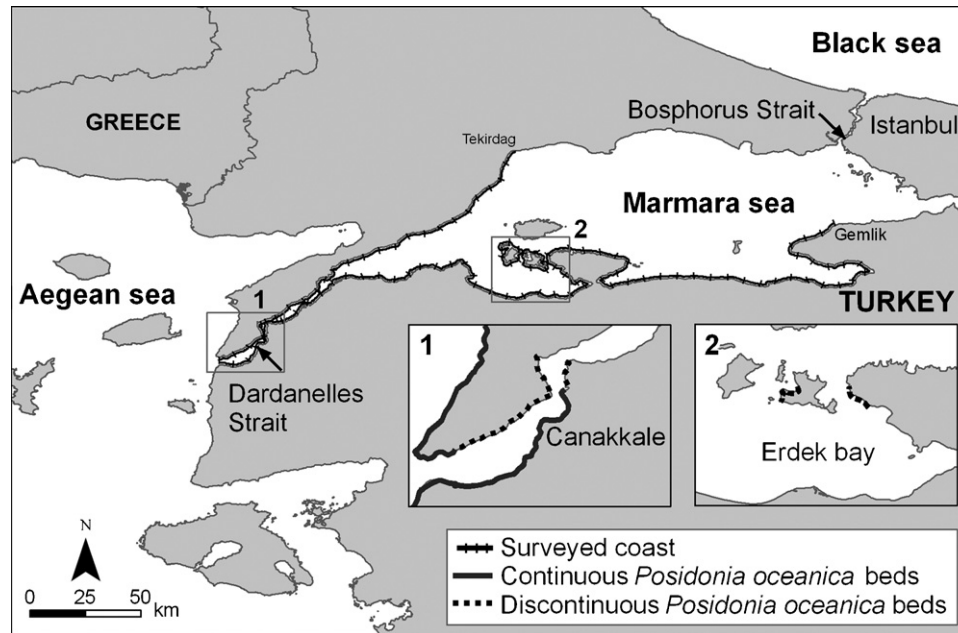


Fig. 1. Distribution of *Posidonia oceanica* in the Dardanelles Strait and in the Marmara Sea.

and 25 m depth) from the Black Sea to the Aegean Sea ($612 \text{ km}^3 \text{ year}^{-1}$). Mixing between the layers appears limited (Latif et al., 1991; Beşiktepe, 2003).

In order to study the distribution of *P. oceanica* all along the Marmara Sea coasts, we collected information about the presence of *P. oceanica* meadows from fishermen and divers in 2004–2005 (awareness by brochures and posters). A total of 30 days of direct surveys were undertaken from the Dardanelles Strait to the west coasts of the Marmara Sea (Gemlik peninsula in the South and Tekirdag in the North; Fig. 1) to record the occurrence of beached dead seagrass material. A total of fourteen surveys by SCUBA diving were performed in zones of potential presence of *P. oceanica* (dead leaves on the coast) and in places where *P. oceanica* was recorded (the first isolated bed of *P. oceanica* has been found in the central-southern part of the Marmara Sea by Yüksek and Okuş, 2004). For any *P. oceanica* bed discovered, the shallow and deep limits as well

as the extension along the shore were localised by GPS. Hydrological data available in the vicinity of each recorded meadow were gathered.

The *P. oceanica* meadows from the Marmara Sea and from the Dardanelles Strait recorded during the survey were sampled for genetic analysis. In addition, three other meadows were sampled in the Mediterranean region adjacent to the Dardanelles Strait (Table 1). Samples were collected for each meadow above 5 m depth, with intervals over 5 m, to reduce the possibility to collect different shoots from the same rhizome.

Leaf material was cleaned from epiphytes, blotted on tissue and dried in silica gel for further DNA extraction. Approximately $50 \mu\text{g}$ of dried tissue from each individual sample were ground in a Mixer Mill MM300 (QIAGEN). DNA extraction was carried out using the KIT Nucleospin Multi-96 Plant (Macherey-Nagel). Thirteen polymorphic microsatellite regions, 12 nuclear and 1 chloroplast

Table 1
Summary of genetic data for the five populations analyzed

	N	G	G/N	L	A	Fis	H_e	H_0	Wt	M	Ass
Erdek Latitude 40 28 Longitude 27 40	30	9	0.30	6	21	-0.704	0.246	0.426	***	-	-
Dardanos Latitude 40 02 Longitude 26 04	30	24	0.80	7	24	-0.073	0.263	0.288	NS	-	-
Küçukkuyu Latitude 39 31 Longitude 26 32	30	11	0.37	6	24	-0.189	0.213	0.261	NS	1 Dar	3 Dar
Lesbos (Eftalou) Latitude 39 22 Longitude 26 12	18	13	0.72	6	22	-0.306	0.234	0.314	**	-	1 Erd
Dikili Latitude 39 09 Longitude 26 47	30	14	0.47	7	25	0.017	0.231	0.234	NS	2 Ntu	2 Ntu

N: number of samples; G: number of genotypes; L: number of polymorphic loci; A: number of alleles; H_e : expected heterozygosity; H_0 : observed heterozygosity; Wt: Wilcoxon test for heterozygosity excess significant at 99% (***) or not significant (NS); M: number of first generation migrants and population of origin; Ass: number of genotypes assigned to any other population.

(Procaccini and Waycott, 1998; Alberto et al., 2003), were used to obtain individual multilocus genotypes. For PCR protocols and microsatellite scoring, see Migliaccio et al. (2005).

Multilocus genotypes were utilized for statistical analysis. The following parameters were calculated for each population using the software GENETIX 4.1 (Belkir et al., 1996–2002): total number of alleles (A), allele frequencies for each locus, observed (H_o) and expected (H_e) heterozygosity, and fixation index F_{is} (Weir and Cockerham, 1984). Heterozygosity and F_{is} values were calculated after exclusion of replicated genotypes and only for the nuclear loci.

Bottleneck analysis was performed with the software Bottleneck (Cornuet and Luikart, 1996), using a Wilcoxon sign-rank test applied on a two-phased model of mutation. Assignment and migration tests were performed with the software GeneClass2 (Piry et al., 2004) using a frequency-based method (Paetkau et al., 1995) and Monte-Carlo resampling (Paetkau et al., 2004). Factorial correspondence analysis on allele frequency was performed with GENETIX 4.1 (Belkir et al., 1996–2002).

3. Results

Large beds were found inside the Dardanelles Strait (between 0 and 25 m deep) and isolated beds in the Sea of Marmara (between 0 and 5 m deep) located 160 km from the north-eastern boundary of the species range in the Aegean Sea (Fig. 1).

In the Dardanelles Strait, salinity near the seagrass beds (surveys at -5 and -10 m in front of Canakale) ranges between 24 and 28 ppt throughout the year (and between 24 and 38 ppt at the lowest limit of the beds at 25 m depth). In the Marmara Sea (Erdek bay: Psalamini Islands and Narth), in the vicinity of the *P. oceanica* beds, the salinity ranges between 21.5 and 26.5 ppt throughout the year (surveys at the surface and at -5 m).

For the 5 populations examined, only 8 of the 13 loci utilized were polymorphic (Table 1). The number of polymorphic loci per population ranged from 6 to 7 (Table 1). Average number of alleles per population was 23.2, with the lowest number in Erdek ($A = 21$) and the highest in Dikili ($A = 25$). Genotypic diversity (G/N) ranged from 0.30 in Erdek, to 0.80 in the Dardanelles population. The Marmara Sea population was also characterized by the lowest F_{is} value (-0.704) and the highest heterozygosity excess. This is reflected in the high significance for the Wilcoxon test for the existence of a bottleneck ($p < 0.01$). The significance was lower for the population from Lesbos ($p < 0.05$) and the test was not significant for the other populations (Table 1).

Gene flow was very low among all the localities, with the two meadows, from Dardanelles and Marmara Sea, not being acceptors of any first-generation migrant from the other localities (Table 1). Assignment test almost completely agreed with the previous analysis, showing that only one individual from any other population (i.e. Lesbos) was assigned preferentially to the Marmara Sea population. Factorial correspondence analysis stressed that each single meadow was isolated from the others with a limited overlap of genotype clusters. The Marmara Sea meadow was the only one completely isolated from the others.

4. Discussion

We recorded here the presence of large *P. oceanica* meadows in the Marmara Sea and in the Dardanelles Strait. Our records better clarify the geographical distribution of this seagrass species in the north-eastern side of the Mediterranean basin and in the Marmara Sea, where *P. oceanica* was never reported in the past (Cirik and Güner, 1979; Zeybek et al., 1993; Taşkın et al., 2001).

In the Marmara Sea and in the Dardanelles Strait, *P. oceanica* beds grow in brackish waters with a salinity always lower than 28 ppt. These ecological conditions are exceptional for the species, considering that in the Mediterranean Sea salinity ranges from 36.5 to 39.5 ppt. *Posidonia oceanica*, in fact, is always absent from areas near river deltas, where salinity is lower than 37 ppt. Furthermore *P. oceanica* does not expand into the Atlantic Ocean where salinity is 35–36 ppt: its western boundaries in the Mediterranean Sea are located in the Alboran Sea, at Punta Chullera-Cala Sardina (Andalucia, Spain) in the north and at Sebka-bou-Areg, near the Chaffarines islands (between Morocco and Spain) in the south.

Up to now, the only evidence for long-term acclimation to a wider salinity range was in the Stagnone di Marsala coastal lagoon (western coasts of Sicily), where the species experiences seasonally salinity values ranging between 32 and 47 ppt (Di Maida et al., in press). Salinity could not have been so severe in the past but could have been affected by recent changes in the lagoon hydrodynamic regime, contributing to the impoverishment of the meadows growing inside the lagoon (Di Maida et al., in press). The only existing short-term mesocosm experiments show that in controlled conditions the species does not easily tolerate low salinity values, having a considerable mortality rate after 15 days of incubation at a salinity below 29 ppt (Fernández-Torquemada and Sánchez-Lizaso, 2005).

All the populations considered in the analysis have a very low genetic diversity in comparison with most of the meadows sampled all around the Mediterranean Sea (Arnaud-Haond et al., 2007). This reflects in the low number of polymorphic loci and especially in the low allelic diversity. The average number of alleles per population calculated in the present analysis ($A = 23.2$), in fact, is notably lower than the average number for Western ($A = 34$), Central ($A = 44$) and Eastern ($A = 36$) Mediterranean populations (Arnaud-Haond et al., 2007). The number for the Eastern group increases to 41 when the two North-Adriatic clonal populations are excluded. Differences in average number of alleles between the populations analyzed here and any other of the three population groups identified above are significant ($p < 0.01$) applying a Student t -test. The difference is not significant when North-Adriatic populations are included in the Eastern group. All these characteristics are indicative of populations present at the limits of a species distribution or at the extreme of the environmental tolerance. A decrease in allelic richness was also observed along a latitudinal gradient in the temperate seagrass species *Zostera noltii* and *Cymodocea nodosa* (Coyer et al., 2004; Alberto et al., 2006). Clonal diversity also varies at a limit of a species distribution (Billingham et al., 2003). Very low clonal diversity (G/N) was found in the North-Adriatic *P. oceanica* meadows (Ruggiero et al., 2002). In the present analysis we only found a distinct decline of the G/N value in the Marmara Sea population, where only 30% of the shoots collected represented different genotypes. In *P. oceanica*, low clonal diversity has been recorded for different localities and is not necessarily related with the spatial isolation of the meadow. Nevertheless, in our case many different parameters allow us to hypothesize a complete isolation of the Marmara Sea population. Together with the lower clonal diversity, we found here the higher excess of heterozygosity, the lowest number of alleles and a significant Wilcoxon test, suggesting the existence of bottleneck. Moreover, although all the populations analyzed appeared to be isolated, this is particularly evident in the Marmara Sea and the Dardanelles Strait, where no migrants from other populations were detected. The factorial correspondence analysis reinforces our idea, showing a complete isolation of the Marmara Sea meadows (Fig. 2). A possible scenario to explain the isolation observed includes an initial settlement by very few genotypes and/or a secondary

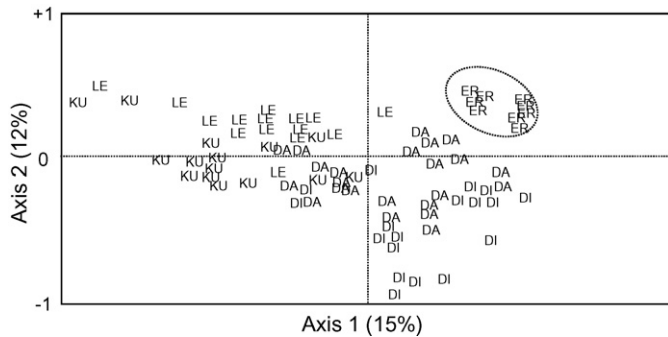


Fig. 2. Factorial correspondence analysis obtained on the allele frequency for five populations considered. DI: Dikili, DA: Dardanelles; KU: Küçukkuyu; LE: Lesbos; ER: Erdek -Marmara.

positive selection of few adapted genotypes. The excess of heterozygosity supports the adaptation of few individuals (heterozygote advantage) to the extreme environmental conditions encountered in the Marmara Sea. This hypothesis is also supported by the existence of fixed alleles that are rare throughout the entire distributional range of the species (Arnaud-Haond et al., 2005, 2007).

Genetic data clearly show that the population of the Marmara Sea is isolated since a long time. To understand the presence of these isolated populations the history of the hydrodynamic regime in the particularly complex communication among the Mediterranean Sea, the Marmara Sea and the Black Sea has to be taken into account.

Approximately 12,000 years ago, the salt waters of the Mediterranean Sea began to enter the Marmara Sea, which must have been a fresh water basin before that (Smith et al., 1995; Aksu et al., 1999; Major et al., 2002; Çağatay et al., 2000; Myers et al., 2003). Introduction of Mediterranean species into the Marmara Sea could have began after this time.

In light of contrasting hypotheses on the opening of the Bosphorus Strait, the event which favoured the fast changes of sea level and hydrodynamic conditions in the Marmara Sea and in the Black Sea was dated before 5300 years BP, and it was sometimes associated with the biblical story of Noah (Ryan et al., 1997; Ryan and Pitman, 1999; Aksu et al., 2002; Sperling et al., 2003). Geological data, based on the identification of biological remains in the sediment, clearly show that the outflow of surface low salinity water coming from the Black Sea is regular and persistent in the Marmara Sea for more than 5300 years (Aksu et al., 2002; Kerey et al., 2004).

According to that, how can we explain the presence of large, geographically and genetically isolated *P. oceanica* beds in the Marmara Sea?

Posidonia oceanica is a species with a theoretical long-distance dispersal potential, but the income of genotypes from the Mediterranean to the Marmara Sea is unlikely to have occurred recently. *P. oceanica*, in fact, can either disperse by rhizome fragmentation, or sexually by seed transport. In the first case, the negative buoyancy of rhizomes does not allow long-distance transport. Moreover, experimental transplanting have shown that re-implant of mature plants is not highly successful and that cuttings of rhizomes tend to die when settled deeper than where they originate (Molenaar and Meinesz, 1991). Buoyant fruits have higher dispersal potential, being able to float more than 15 days before releasing seeds which sink to the bottom and develop. Nevertheless, floating fruits would need a surface current from the Aegean Sea to the Marmara Sea, which is in the opposite direction of the current flowing since the Holocene.

Furthermore *P. oceanica* is an exceptional perennial species, the same individual can live for thousands of years by vegetative (clonal) expansion of the rhizomes (Marbà and Duarte, 1998). The dead rhizomes are imputrescible and, when the conditions are favourable for vertical growing, they pile into mattes. Matte remains were directly dated up to 4590 ± 140 years BP (Boudouresque et al., 1980; Mateo et al., 1997) while indirect estimates dated matte formations back to 6000–7000 years BP (Mateo et al., 1997). These exceptional characteristics show that a perennial bed of *P. oceanica* could have survived in isolated conditions of the Marmara Sea since the mid Holocene.

The *P. oceanica* beds found in the Marmara Sea are sparse, without established mattes and they grow in two main localities along 5–6 km of coastline. Lateral growth of *P. oceanica* beds is very slow, i.e. $1\text{--}6\text{ cm year}^{-1}$ (Meinesz and Lefèvre, 1984; Marbà and Duarte, 1998). According to this growth rate, the expansion from a single seed to a circular bed of 27 m radius would take about 600 years (Kendrick et al., 2005). The two large main beds (5–6 km wide) found in the Marmara Sea, although possibly originating from more recruitment events, should have taken much longer times to grow to their present size.

All these data strongly suggest that the presently isolated *Posidonia oceanica* beds in the Marmara Sea are a relic population composed of genotypes adapted to brackish waters and growing clonally since a long time. They could well have originated from an initial settlement of a few seeds entering the Marmara Sea after 12,000 years BP and not later than the incoming of brackish waters (between 10,000 and 5300 years BP) from the Black Sea.

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