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Is *Posidonia oceanica* regression a general feature in the Mediterranean Sea?

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Abstract

Over the last few years, a widespread regression of *Posidonia oceanica* meadows has been noticed in the Mediterranean Sea. However, the magnitude of this decline is still debated. The objectives of this study are (i) to assess the spatio-temporal evolution of *Posidonia oceanica* around Cap Corse (Corsica) over time comparing available ancient maps (from 1960) with a new (2011) detailed map realized combining different techniques (aerial photographs, SSS, ROV, scuba diving); (ii) evaluate the reliability of ancient maps; (iii) discuss observed regression of the meadows in relation to human pressure along the 110 km of coast. Thus, comparison with previous data shows that, apart from sites clearly identified with the actual evolution, surfaces occupied by the seagrass *Posidonia oceanica* are relatively stable. The recorded differences seem more related to changes in mapping techniques. These results confirm that in areas characterized by moderate anthropogenic impact, *Posidonia oceanica* meadows are not subject to significant regression and that the changes due to the evolution of mapping techniques are not negligible. However, others facts should be taken into account before extrapolating to the Mediterranean Sea (e.g. currently mapped surfaces) and assessing the amplitude of actual regression.

Keywords: Anthropogenic pressure, Corsica, mapping techniques, Mediterranean Sea, Posidonia oceanica, regression.

Introduction

Several studies indicate a widespread regression of seagrass meadows over the last decades (Molinier & Picard, 1952; Larkum & West, 1983; Shepherd et al., 1989; Short & Wyllie-Echeverria, 1996; Duarte, 2002; Spalding et al., 2003; Jorda et al., 2012). Such regression varies according to species and geographical zones under consideration (Short & Wyllie-Echeverria, 2000; Orth et al., 2006; Boudouresque et al., 2009; Waycott et al., 2009). Although regressions can be related to natural processes (e.g. colonization and erosion dynamics, climate change, sea level change, weather events, exceptional tectonic events or diseases), it is clear that they are most often associated with human activities (Peres & Picard, 1975; Short & Wyllie-Echeverria, 1996; Duarte, 2002; Björk et al., 2008). If the reality of such regressions is well established, their magnitude must be critically analyzed. Indeed, the available estimates indicate a loss of 12,000 to 33,000 km² (Short & Wyllie-Echeverria, 2000; Short, 2003), but these values should be considered with prudence in the light of current knowledge, which is still very fragmentary on the topic of worldwide seagrass distribution (especially past and present; Green & Short, 2003).

The five marine species of Magnoliophyta found in the Mediterranean Sea undergo natural and anthropogenic pressures of a kind likely to lead to significant regressions (Marbà et al., 1996; Boudouresque et al., 2012, 2009), even if the available data primarily concerns the emblematic species Posidonia oceanica L. Delile (Boudouresque et al., 2009). The main regressions of marine seagrass meadows recorded in the Mediterranean are related to the restructuring of the shores (Meinesz et al., 1991; Ruiz & Romero 2003; Boudouresque et al., 2012), management of living resources (fisheries and aquaculture; Delgado et al., 1999; Pasqualini et al., 2000; Gonzalez-Correa et al., 2005; Pergent, 2006; Kiparissis et al., 2011), solid and liquid waste (Pergent-Martini et al., 1995; Boudouresque et al., 2012), the development of pleasure boats and tourism cruises (Boudouresque et al., 2012; Montefalcone et al., 2006) and the introduction of exotic species (Boudouresque et al., 2012). However, the amplitude of these regressions remains controversial. Thus, Boudouresque et al. (2009) estimated regression at between 0 and 10% during the 20th century and Gonzalez-Correa et al. (2007) considered that there is no overall decline of the species in the Mediterranean and attributes the decline reported in the literature to cumulative effects derived from different natural and anthropogenic local processes. On the other hand, for Marbà *et al.* (1996), this decline may be more important (5 to 8% per year); similarly, Jorda *et al.* (2012) predicted the functional extinction of *P. oceanica* meadows by the middle of this century (year 2049 ± 10). In addition, the lack of reliable baselines is a major obstacle to assessing the reality and importance of the regressions reported (Pergent-Martini & Pergent, 1996; Montefalcone *et al.*, 2013).

The aim of this work is to estimate the reliability of existing maps and to evaluate the spatio-temporal distribution of *Posidonia oceanica* meadows in an area affected by moderate anthropogenic impact (Lopez Y Royo *et al.*, 2009), that is to say lower than observed on the northern coast of the western basin (population pressure, industrial activities, coastal management) and higher than in the south of the eastern basin (e.g. Libya) (UNEP/MAP-PLAN BLEU, 2009). In this framework, a comparison with previous maps, as well as new maps based on previous raw data, will be taken into account.

Materials and Methods

Cap Corse, located in the north of Corsica (France, Mediterranean), although relatively preserved (low population density and limited industry) is home to the second largest city (Bastia, 45,000 ha) and the first port (2.5 million passengers and 2.4 million tons of cargo per year) of the island (OEC, AAMP, 2011). It is also subject to strong pressure from tourism during summer and increased pleasure boats traffic, significant exploitation of living resources (four fishing ports and five marine shelters, trawling activity; *in* OEC, AAMP, 2011) and the consequences of massive solid waste from the asbestos mine of Canari (burial funds and major source of contamination, particularly in terms of trace metals; Bernier *et al.*, 1997; Lafabrie *et al.*, 2007).

The map of main benthic assemblages and bottomtypes between 0 and 40 m depth was prepared between July 2010 and September 2011. The shallow zone (0 to 15 m) was mapped using a complete photographic coverage (146 colour aerial photographs at 1/5 000th, from the BD ORTHO® 2007 of National Geographic Institute) with a 0.5 m resolution.

Remote sensing was applied to each photograph using Envi 4.4® software following the method of Pasqualini *et al.* (1998) modified by Bonacorsi *et al.* (2011). The deep zone (15 to 50m) was mapped using exhaustive acoustic coverage (coupling a multibeam echosounder EM 1000TM and a side-scan sonar Klein 3000TM). This data, which was processed using the Caraibes 3.6® software programme, enables us to develop a Digital Terrain Model (DTM) and a mosaic (0.5m resolution). More than 500 observations *in situ* [bathyscaph, scuba-diving, and pictures taken by a "Remote Operated Vehicle" (ROV)] allowed us to validate the interpretation of the aerial photographs and sonar mosaics. All the data have been entered in a Geographic Information System (GIS; ArcGis 10®; projection Mercator-WGS84).

In order to gain a better understanding of the evolution of P. oceanica meadows, two complementary approaches were used: a general assessment of the distribution of seagrass along Cap Corse since 1960 (Molinier, 1960; Pasqualini, 1997) and a large-scale mapping of test-sites (Fig. 1). These sites are of interest to conservation (e.g. natural monuments in the Gulf of St Florent barrier-reef, platform reef and micro-atolls as described; in PNUE-UICN-GIS Posidonie, 1990; Boudouresque et al., 2012) or they show prior (e.g. Pietra Corbara) or recent (e.g. Macinaggio) damage. Historical data (the "Plan Terrier" of Corsica - Testevuide & Begidis, 1770, 1795), aerial photographs (from 1948 to 1994) and sonograms (survey in 1995) make it possible to reconstitute the temporal evolution of the main benthic assemblages and bottom-types at these sites. Moreover, remote sensing has been applied to raw data (aerial photographs from 1960 to 1997) in order to identify the origin of observed changes (improved mapping techniques or evolution of the distribution of assemblages).

The reliability of the maps obtained was evaluated using different reliability scales according to the methods (Pasqualini, 1997; Pasqualini *et al.*, 1998; Projet Mesh, 2008).

Results

The map produced enables us to identify six benthic assemblages and bottom-types in the 0 to 40m zone, which corresponds to the maximum bathymetric extension of the seagrass *Posidonia oceanica* in the studied area (Fig. 1).

Photophilous algae on rocks are present all along the studied coastline, although their surface is relatively limited (881.0 ha, 6.8% of mapped surfaces). Sandy bottoms occupy a larger area, estimated at 1914 ha (14.8%). They are sometimes colonized by the other seagrass *Cymodocea nodosa* (Ucria) Asch; small areas (66.5 ha, 0.5 %), which are probably under-estimated because of the difficulties in identifying them (low cover and biomass). Locally infralittoral pebbles (37.0 ha, 0.3%) can hide these soft substrates, in particular close to the outlets of coastal rivers, at the edge of Cap Corse (erosion of cliffs) and at the Canari site (spoils from the asbestos mine).

Posidonia oceanica meadows occupy the major part of the studied bathymetric area (up to 40 m deep on the eastern coast, and 30 to 35m deep on the western coast; Fig. 1) with an area of 9970 ha (77.2%). *P. oceanica* grows preferably on sandy bottoms on the east coast and in the Gulf of St Florent and on rocky bottoms on the north and west coast. The dead matte of *P. oceanica* (53.0 ha, 0.4%) is identified punctually only where it was not hidden by sediments: platform reef and barrier reef of



Fig. 1: Map of main benthic assemblages and bottom-types of the Cap Corse (test-sites are indicated by a frame).

the Gulf of St Florent, Pietra Corbara marina and Macinaggio shoreline.

The reliability of the map is high whatever the scale used (between 88% and 90%), compared to previous maps (Table 1).

At the St Florent site, the map obtained from aerial photographs, dated July 1960, (Fig. 2) provides a baseline for the main benthic assemblages and bottom-types prior to coastal development (e.g. port of St Florent, dikes and ripraps), whereas the map obtained from aerial photographs, dated May 2006, show the current situation (Fig. 3). *P. oceanica* meadows are essentially present at the *P. oceanica* platform reef (South) and the *P. oceanica* barrier reef (West) while the *Cymodocea nodosa* meadow is observed in the North-East (Fig. 2).

The reef has a traditional structure, parallel to the coast, marking a small lagoon occupied by a dead *P. oce-anica* matte (Figs 2 and 3). The platform reef has a specific structure in the shape of a triangle. Its central part consists of dead matte, occasionally covered by sand, and the outline of a micro-atoll can be noticed in the South-Western part of the structure (Fig. 2); this atoll is well developed in 2006 (Fig. 3).

The reliability of the map is at its maximum for the 2006 map (between 90% and 93%; Table 1). It is only 51% and 74% for the 1960 map, because of grayscale photo-

Medit. Mar. Sci., 14/1, 2013, 193-203

graphs and the lack of field data at that time (Table 1).

The study of the eastern coast of Cap Corse shows signs of degradation of the *P. oceanica* meadow. Thus, there are several circular structures at Pietra Corbara marina (aerial photographs of 2006; Fig. 4A) and rectilinear traces (2010 sonograms) up to 5m wide facing the port of Macinaggio (Fig. 4B).

The circular structure, which is the largest one (230m in diameter), corresponds to a depression occupied by soft substrate and dead matte. The observations made by scuba diving show that the rectilinear traces close to the port of Macinaggio correspond to deep furrows that cut a degraded *P. oceanica* meadow (mosaic of dead matte and meadow with very low percentage cover). These marks appear to result from the abrasion of the sea bottom by otter trawl panels.

The reliability of the map is between 90% and 93% for the Pietra Corbara test site and between 87% and 90% for the Macinaggio test site (Table 1).

Discussion

The first available mapping of Cap Corse reported a surface of 12,963 ha (Molinier, 1960), for the *P. ocean-ica* meadow, which results in a decrease of 23% (nearly 3000 ha) in the last fifty years.

The origin of these regressions can be sought at two levels:

(i) Anthropogenic pressures, especially the waste released from an old asbestos mine (over 11 million tons of debris between 1948 and 1965, *in* Bernier *et al.*, 1997). These releases have resulted in an early degradation of the *P. oceanica* meadow at the foot of the mine and a rise in the lower limit to 35m depth, already reported by Molinier (1960). These mechanisms have continued since with a rise in the lower limit to 25m and a disappearance of the meadow along more

Table 1: Reliability of different maps.

	Pasqualini <i>et al</i> ., 1998	Mesh, 2008
Whole map		
Molinier, 1960	_*	33 %
Pasqualini, 1997	69 %	79 %
This work	88 %	90 %
Test-sites		
St Florent, 1960	74 %	51 %
St Florent, 2006	90 %	93 %
Pietra Corbara, 1995	75 %	75 %
Pietra Corbara, 2006	90 %	93 %
Macinaggio, 1997	63 %	72 %
Macinaggio, 2012	87 %	90 %

*this scale is not applicable to this card because of the techniques used.



Fig. 2: Map of the main benthic assemblages and bottom-types at the site of St Florent in 1960.

than two kilometres of coastline (Pasqualini *et al.,* 1999). However, the magnitude of the phenomenon is relatively small (250 ha) and cannot be compared with the surfaces that have been "lost".

(ii) The accuracy of the reference map that was used (Molinier, 1960; Table 1). Indeed, this study is based on transect diving and samples gathered thanks to a dredge, two techniques that give a great part to interpolation. Thus, Pergent-Martini *et al.* (1995) and Leriche *et al.* (2004) showed, in the Marseille region, that the large differences in the distribution of *P. oceanica* meadows, are explained more by errors and inaccuracies in the old maps used as reference than by a real change in their distribution (Montefalcone *et al.*, 2013).

This last hypothesis seems to be confirmed by the fact that on maps made with more recent and comparable methods (Pasqualini, 1997), the total area of seagrass would have only decreased by 2% during the last sixteen



Fig. 3: Map of the main benthic assemblages and bottom-types at the site of St Florent in 2006.



Fig. 4: Anthropogenic impacts within the meadows of Posidonia oceanica as circular structures (a) at Pietra Corbara and rectilinean traces (b) at Macinaggio.

years (from 10,201 ha in 1995 to 9,970 ha in 2011). In addition, the method used by Pasqualini (1997) slightly overestimates the surfaces of the meadow, insofar as the author accurately maps upper and lower limits but considers that between them the meadow is continuous (interpolation on the intermediate bathymetric slice).

Thus, at the St Florent test site, the map obtained from the aerial photographs of March 2006 (Fig. 3) shows that the total area covered by *P. oceanica* has undergone a slight decrease (-9.5 %) since 1960, while the area covered by *C. nodosa* has been reduced significantly (- 59.8 %, Table 2).

However, at the barrier reef and platform reef, the surface of the *P. oceanica* meadow increased by 10% and 2%, respectively; the surface of the micro-atoll in turn has increased 72% since 1960 (Fig. 5).

At the reef barrier, the recorded growth occurs mainly at the internal front (decrease of dead matte surface) while the external front is stable.

At the reef platform, the slight increase is due to the

addition of the growth of the meadow at the base of the platform (south-east), and regression at the internal front (extended central dead matte). The "appearance" of dead matte at the base of the platform reef, particularly in the South-East, seems to result from the disappearance of the sediment that initially hid this structure.

The coastline's evolution over the last 200 years, based on remote sensing (Table 2), shows:

- A significant coastline progression, between the end of XVIIIth century and 1960. This littoral accretion is larger for the south-eastern part (+ 60 to 70 m) than for the western part (+ 45m on average) i.e. 0.27 to 0.39 m.y⁻¹, respectively.
- A significant coastline retreat between 1960 and 1974
 (- 2.7 m · y⁻¹), date of the construction of the port. This phenomenon is particularly visible in the southeastern area of the Gulf and on the coast behind the southern platform.
- A more regular and smaller scale coastline retreat since $1974 (-0.78 \text{ m} \cdot \text{y}^{-1})$, despite the construction of

Table 2: Evolution of coastline, s	size of P. oceanica micro-	atoll and percentage cove	r of main benthic	assemblages, betw	een 1960 and 2	2007 in
the Gulf of St Florent.						

	1960	1974	1985	1994	2006
Layouts presents	-	Harbour seawall	Riprap	-	-
Mean changes of the coastline / XVIII th century (m)	+ 40	+20	+12	+7	+3
<i>P. oceanica</i> micro-atoll: Diameter E/O (m) Diameter N/S (m)	6.7 6.1	7.4 7.2	9.3 10.2	9.7 10.8	10.3 11.7
<i>P. oceanica</i> plateform reef (ha) <i>P. oceanica</i> barrier reef (ha)	2.22	-	-	2.20	2.26
	5.90	4.90*		6.90	6.50
<i>P. oceanica</i> meadow Total area (ha)	11.29	-	-	10.72	10.21
Dead P. oceanica matte (ha)	4.06	-	-	6.63	8.31
<i>Cymodocea nodosa meadow</i> total area (ha)	11.70	-	-		4.70

* The quality of aerial photographs was uneven and did not allow an accurate evaluation of the P. oceanica barrier reef.



Fig. 5: Map of the principal *P. oceanica* micro-atoll of the Gulf of St Florent in 1960 and 2006. In 1960 and 2006, the dead matte of *P. oceanica* was partially covered by soft substrates.

riprap to protect the coastline from erosion.

The confrontation of the position of the rocky bottom (which is not highly influenced by erosion) according to the "plan Terrier" and to the current map shows an average difference of less than $6m (\pm 4m)$, which confirms the accuracy of this survey and allows it to be considered as a reference state, reliable for this sector.

This hypothesis is confirmed by the study at the Macinaggio site, where the interpolation performed by Pasqualini (1997) at the intermediate bathymetric slice (15-30m depth) reveals a continuous meadow with an estimated area of 169 ha, while the area is currently estimated at 159 ha. In the absence of reliable references, it is difficult to draw conclusions about an effective regression of the meadow (of about 6%) or to date it (before or after 1995).

Similarly, if the hypothesis of a deterioration of the meadow at its superficial layer (0-15m depth) cannot be ruled out, it seems likely that some of the changes observed since 1995 are due to the pixel size (5m; in Pasqualini, 1997), which does not allow to distinguish the small discontinuities in the meadow (e.g. patches of sand).

At the lower limit, there is an increase in dead matte surfaces in relation to the trawling pressure. This degradation caused by trawling, widely reported in the literature (Ardizzone & Pelusi 1984; Ramos-Esplá *et al.*, 1994; Martin *et al.*, 1997; Ardizzone *et al.*, 2000; Kiparissis *et al.*, 2011), was confirmed by scuba diving observations. Similarly, the comparison of characteristic spots on sonograms, acquired in 1995 and 2011, confirms a replacement of the *P. oceanica* meadow by dead matte, with increasing evidence of trawling, which often become confluent (Pergent *et al.*, 2011).

In total, this site (0-40m depth) records a maximum decrease of 12% of the surface of the *P. oceanica* meadow over 16 years (358 ha in 1995 and 315 ha in 2011; Fig. 6). However, this decline needs to be kept into perspective: this site (519 ha) represents only 4.0% of the total area mapped (12,921 ha).

The Pietra Corbara test site also shows extensive destruction of the *P. oceanica* meadow, which is replaced by soft sediments and dead matte. Covering an area of 6.0 ha, the circular structure has not been observed on aerial photographs prior to 1990 and does not seem to have evolved over the last two decades (6.0 ha in 1994). Similar circular structures have been identified on several occasions, both on the coast of Corsica (Pasqualini et al., 1998) and along the north-western Mediterranean coast (Lefevre & Meinesz, 1984; Tunesi & Boudouresque, 2006). They appear to be most frequently due to the impact of explosives (e.g. fishing with dynamite, bomb exploding during the last world war; Lefevre & Meinesz, 1984; Pergent-Martini & Pergent, 1996; Pasqualini et al., 1998). However, the absence of this structure on aerial photographs prior to 1990 (e.g. aerial photograph from 1975) does not allow us to accept the hypothesis of a bomb from the last war. Similarly, the large size of this structure does not seem compatible with the impact of small explosives. If we compare the current impacted surface (6.1 ha) with the data of Pasqualini (1997, 5.1 ha), the degradation of the *P. oceanica* meadow is estimated at 16%. However, the analysis of the images of 1994 used by Pasqualini (1997) with the method used in this study provides a larger surface (6.0 ha). It appears that the observed difference (1.6%) cannot be considered significant over a period of 17 years. Similarly, if natural recolonization phenomena are generally observed in similar situations (Lefevre & Meinesz, 1984; Pergent-Martini, 1994), these mechanisms have a very low rate (between 0.009 and 0.010 ha \cdot y⁻¹; Pergent-Martini *et al.*, 1995) and they require the presence of isolated shoots that are torn in the depression caused by the explosion, which does not seem to be the case here (field data).

The use of the same method (image processing, pixel size, positioning accuracy) on old photographs (since 1960) in the Gulf of St Florent make it possible to overcome imprecision (interpolation) and to gain a better understanding of the actual evolution of the areas covered by shallow *P. oceanica* meadows. Thus, it appears that, except for the north-east, where port construction works have resulted in a 9.5% reduction of the *P. oceanica* meadow, there is stability or even a progression:

(i) The areas occupied by *P. oceanica* on the platform



Fig. 6: Main benthic assemblages and bottom-types in 1997 and 2011, on the right of the port of Macinaggio. The isobaths -15, -30 and -40 m are shown in black.

reef have remained stable over the past fifty years, even at a site subjected to significant human pressure (port construction, beach activities, etc.). This data confirms the preliminary results of Pasqualini et al. (2001) who saw no major modifications in the area occupied by P. oceanica between 1960 and 1996. Indeed, the regressions of the central part, which correspond to the natural dynamics of this type of structure (Boudouresque et al., 2012) are offset along the coastline. The shrinking of the coastline, concomitant with the construction of the port, seems to favour a recolonization of P. oceanica on the dead matte located between the reef and the beach. This growth of about 3m since 1960 corresponds to a mean horizontal growth rate of 6cm per year, which is entirely consistent with the mean growth rate of plagiotropic rhizomes estimated by Caye (1982) (7.4 cm per year).

- (ii) The *P. oceanica* reef barrier follows similar dynamics, with an extension of the meadow at the internal front and stability at the external front (climb of matte). This increase is estimated at 1.2% with a horizontal grow rate of 5.3 cm per year since 1960.
- (iii) The *P. oceanica* micro-atoll located in the southwestern part of the reef (Atoll A – Figs 3 and 5), also shows significant growth, since its surface went from $21m^2$ in 1960 to $85m^2$ in 2006, which gives us a horizontal growth rate of 4.2 cm \cdot y⁻¹. Two similar structures (in-construction micro-atolls) also appear to have gone through a significant growth in this sector with a growth rate of 4.3 (± 0.3) cm \cdot y⁻¹ (Fig. 7).

Thus, it is clear that the *P. oceanica* meadow of the Gulf of St Florent is characterised by progressive dynamics. While this process is relatively limited, due to the growth rate of the plant, it is a unique example in the Mediterranean Sea since coastal development generally results in a decrease of the meadow (Meinesz *et al.* 1991; Tunesi & Boudouresque, 2006; Montefalcone *et al.* 2007; Boudouresque *et al.*, 2009).

Taken together, these results therefore show the relative stability of surfaces occupied by *P. oceanica* meadows between 1995 and 2011; with the exception of a few sites, well identified, where it has actually regressed (Macinaggio) or increased (St Florent). Recorded differences seem more related to the evolution of mapping techniques. These results confirm that in areas characterized by moderate anthropogenic pressure, *P. oceanica* meadows are not subject to significant regression (Boudouresque *et al.*, 2009). Similarly, LERICHE *et al.* (2006) did not find any significant regression of the *P. oceanica* meadow in the Bay of Saint-Cyr (France), despite the construction of two small pleasure harbours.

In addition, the bibliographic data, highlighting a significant regression of *Posidonia oceanica*, cannot be applied generally across the Mediterranean Sea. For example, the regression of 5 to 8% per year proposed for Spain by Marbà *et al.* (1996), would result today in a 75% decrease of all *P. oceanica* meadows, which is not in agreement with available data. Similarly, the regression values recorded in Liguria (Italy) by Lasagna *et al.* (2011) or in the Gulf of Gabes (Pergent & Kempf 1993), correspond to local situations characterized, usually, by



Fig. 7: Evolution of the size of P. oceanica micro-atolls of the Gulf of St Florent. Structure A: principal "micro-atoll" of the P. oceanica reef platform; structures B and C: P. oceanica "micro-atolls" in formation.

high anthropogenic pressure (Marbà *et al.*, 1996, 2002; Ardizzone *et al.*, 2006; Boudouresque *et al.*, 2012; Montefalcone *et al.*, 2007).

To gain a better understanding of the actual magnitude of the regression of *P. oceanica* meadows at Mediterranean scale, the following should be taken into account:

- (i) Currently mapped surfaces represent only about 35% (PNUE-PAM-CAR/ASP, 2009) of the total surface (35,000 km²; Pasqualini *et al.*, 1998). Although this value is constantly increasing, essential data from relatively undisturbed areas (e.g. Libya, Turkey) are still lacking.
- (ii) Available maps used to estimate changes do not constitute a reliable baseline because of their low accuracy (too ancient). This is highlighted by Pergent-Martini (1994) who showed that, depending on the chosen reference (maps surveyed at the end of the nineteenth century), the loss of *P. oceanica* meadows in the Marseille-Cortiou area during the 20th century varied from 5 to 43%.
- (iii) Part of the recorded regressions could be linked to the natural continuous rise in the sea level since 19,000 BP (Laborel *et al.*, 1994; Morhange *et al.*, 1996; Collina-Girard, 2003; Morhange, 2003; Clark *et al.*, 2009). Also, the presence of dead mattes, beyond the lower limit of *P. oceanica* meadows could, in some cases, be very old and unrelated to anthropogenic pressures (Boudouresque *et al.*, 2009; Vacchi *et al.*, 2010).

Thus, although it seems possible to specify the size of the last regression of *P. oceanica* meadows, considerable uncertainties weigh as to their future, particularly in the light of the changes brought about by climate change (Pergent *et al.*, 2012). According to Marbà & Duarte (2010) and Jorda *et al.* (2012), the vulnerability of this species in response to warming waters could lead to its functional extinction by 2049 (\pm 10 years), due to a rise in the early mortality of young shoots. The increased rate of extreme events including thermal anomalies resulting in an increase in water temperatures, above 28°C for several weeks, seems to exert stress on plants (e.g. decrease in the number of leaves; Mayot *et al.*, 2005; Marbà & Duarte, 2010).

However, Gonzales-Correa *et al.* (2007) believe that *P. oceanica* meadows will only be affected marginally, due to high plasticity.

Moreover, several authors have related increased frequency of flowering of *P. oceanica* with increasing water temperature and/or solar activity, which could constitute a functional response to the stress experienced by the plant (Marbà & Duarte, 2010; Montefalcone *et al.*, in press).

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