

Monitoring of the lower limit of *Posidonia oceanica* meadows at Port-Cros Island, Provence, Mediterranean Sea

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Abstract. The lower limit (31-34 m) of the *Posidonia oceanica* seagrass meadow was monitored, between 2002 and 2008, at Port-Cros Island (Provence, France, northwestern Mediterranean Sea), a National Park where the biota and benthic communities are considered to be in pristine condition. Two sets of concrete markers were laid down on the northern and southeastern coast, respectively, at the boundary between the meadow and the bottom which extends downwards. Shoot density and cover were measured in the vicinity of each marker in 2002, 2005 and 2008 (northern site) and in 2006 and 2008 (southeastern site). In addition, shoots were numbered within selected patches. Shoot density (northern site only), number of shoots within patches and cover dramatically declined over the period studied. Taking into account data from other monitoring sites in the northwestern Mediterranean, results point to four possible main causes: **(i)** direct or indirect effects of the North Atlantic Oscillation (NAO), via e.g. rainfall, cloudiness, river discharge and plankton abundance; **(ii)** a rise in relative sea-level, resulting in a decrease of light availability at depth; **(iii)** a negative impact, at least at a depth, of seawater warming; and **(iv)** the presence of the introduced Chlorobionta *Caulerpa cylindracea*.

Résumé. Surveillance de la limite inférieure de l'herbier à *Posidonia oceanica* à Port-Cros, Provence, Méditerranée. La limite inférieure (31-34 m) de l'herbier à *Posidonia oceanica* a été surveillée, entre 2002 et 2008, à Port-Cros (France, Méditerranée nord-occidentale). L'île de Port-Cros est un Parc national dont les espèces patrimoniales et les communautés sont considérées comme étant dans un bon état de conservation. Deux groupes de balises en ciment ont été placés à la limite inférieure de l'herbier, l'un sur la côte Nord et l'autre sur la côte Sud-Est de l'île. La densité des faisceaux et le recouvrement

de l'herbier ont été mesurés au voisinage des balises, en 2002, 2005 et 2008 (Nord) et en 2006 et 2008 (Sud-Est). Par ailleurs, le nombre de faisceaux a été compté dans des taches exactement localisées. La densité des faisceaux (Nord uniquement), le nombre de faisceaux dans les taches exactement localisées et le recouvrement ont diminué de façon spectaculaire au cours de la période étudiée. En prenant en compte les données d'autres sites de Méditerranée nord-occidentale, cette régression peut être expliquée par quatre causes principales : **(i)** les effets directs ou indirects de la NAO (Oscillation Nord-Atlantique), au travers des précipitations, de la nébulosité, du débit des fleuves et de la prolifération du plancton ; **(ii)** la remontée relative du niveau marin, qui détermine la diminution de la quantité de lumière qui atteint le fond ; **(iii)** un impact négatif, au moins en profondeur, du réchauffement de l'eau ; et **(iv)** la présence du Chlorobionte introduit *Caulerpa cylindracea*.

INTRODUCTION

The seagrass *Posidonia oceanica* (Linnaeus) Delile (Magnoliophyta) is the engineer species of a key Mediterranean ecosystem. Like many other seagrasses worldwide, it provides many valuable ecological and economic services (Costanza *et al.*, 1997), e.g. **(i)** a very high primary production rate, **(ii)** the export of a large part of this production towards other ecosystems where it enters the local food web, **(iii)** a spawning site and nursery for many species of crustaceans and fish of commercial importance and **(iv)** control of sediment fluxes and protection of beaches against erosion (Pergent *et al.*, 1994; Francour, 1997; Boudouresque *et al.*, 2006a, 2006b; Ruíz *et al.*, 2009). The *P. oceanica* ecosystem exhibits some unique characteristics which may explain why such a rich and luxuriant ecosystem can thrive in such oligotrophic waters, namely the Mediterranean Sea, a feature shared with coral reefs, in the tropical realm (Boudouresque *et al.*, 2006b).

Posidonia oceanica meadows are very sensitive to disturbance caused by human activity. As a result, the loss of *P. oceanica* beds has been observed in a number of regions. Human-induced losses of *P. oceanica* have been mainly related to coastal development, pollution, trawling, fish farming, mooring, dredging, dumping and introduced species (Meinesz *et al.*, 1981; Boudouresque and Jeudy de Grissac, 1983; Ardizzone and Pelusi, 1984; Meinesz *et al.*, 1991; Pasqualini *et al.*, 2000; Ruiz and Romero, 2001; Boudouresque *et al.*, 2006a; Pergent-Martini *et al.*, 2006; Boudouresque *et al.*, 2009).

The purpose of the monitoring of *P. oceanica* meadows is twofold. **(i)** To monitor a high value natural heritage in order to quickly detect any new loss. **(ii)** To utilize this ecosystem as a biological indicator in order to allow overall assessment of the quality of the marine environment and to evaluate the efficiency of management policies (Harmelin, 1976; Meinesz, 1977; Boudouresque *et al.*, 1990; Pergent *et al.*, 1995; Boudouresque *et al.*, 2000; Pergent-Martini *et al.*, 2005; Boudouresque *et al.*, 2006a, 2007). These goals particularly matter within a marine protected area (MPA), the National Park of Port-Cros (Provence, France, northwestern Mediterranean Sea).

In order to evidence possible changes in the Port-Cros *P. oceanica* meadow, concrete markers were set up at its deep limit in 1970 and 1972, at six sites, from 30 m (Grande Vayre Cove) to 38 m depth (La Gabinière Islet) (Harmelin, 1976). Four years later, no change was observed (Harmelin, 1977). The meadow has been therefore considered a pristine ecosystem, despite some localized losses in the Port-Cros and Port-Man Bays (Augier and Boudouresque, 1970a, 1970b; Robert, 1983). Overall, in the early 1970s, the depth limit ranged between (30) 34-36 (38) m (Harmelin, 1976; Harmelin and Laborel, 1976). Unfortunately, the position of the 1970 and 1972 markers was subsequently lost. The Port-Cros *P. oceanica* meadow was accurately mapped in 1999 by Belsher *et al.* (2005). The deep meadow limit was then mainly located between 30 and 33 m. A withdrawal, with regard to the 1970s, cannot be ruled out, since the reliability of the 1970s depth gauges was not as poor as is often thought nowadays (Jean-Georges Harmelin, pers. comm.).

Here, we describe the laying down of two new sets of concrete markers at the lower limit of the Port-Cros *P. oceanica* meadow and the subsequent monitoring of the meadow adjacent to these markers.

MATERIAL AND METHODS

Two monitoring sites were chosen at the lower limit of the *Posidonia oceanica* meadow (Fig. 1). The first one (hereafter “La Palud”) is located on the northern coast of Port-Cros island, between La Palud Cove and Pointe Miladou, at a depth ranging between 32.5 and 34.0 m. It was established in September 2002. The second monitoring site (hereafter “Vaisseau-Tuf”) is located on the southeastern coast, between Pointe du Vaisseau and Pointe du Tuf, at a depth ranging between 31.2 and 34.2 m. It was established in September-October 2006.

Each monitoring site consists of 10 concrete markers laid down at the exact lower limit of the *P. oceanica* meadow, i.e. at the boundary between the meadow and the dead matte or the coastal detritic community (sand) which extends downwards and offshore (Fig. 2). Markers are landmarks used in topographical and cadastral work to mark boundaries (Faynot polyroc®; Fig. 3, 4). A marker consists of a nearly cubic concrete head, 11-cm side and 12-cm high, a 60-cm anchorage peg which is driven into the matte and firmly fixes the head to the bottom, and an upward racket-like device used to label the marker. A 1.5-m high “photo-stand” is placed 1 m ahead of each marker, facing the meadow limit; it is driven vertically into the sediment, with 50 cm laid outside (Tables 1 and 2). During the field survey, three photographs of the marker, a graduated scale and the surrounding meadow are taken from the top of the photo-stand (Boudouresque *et al.*, 2007).

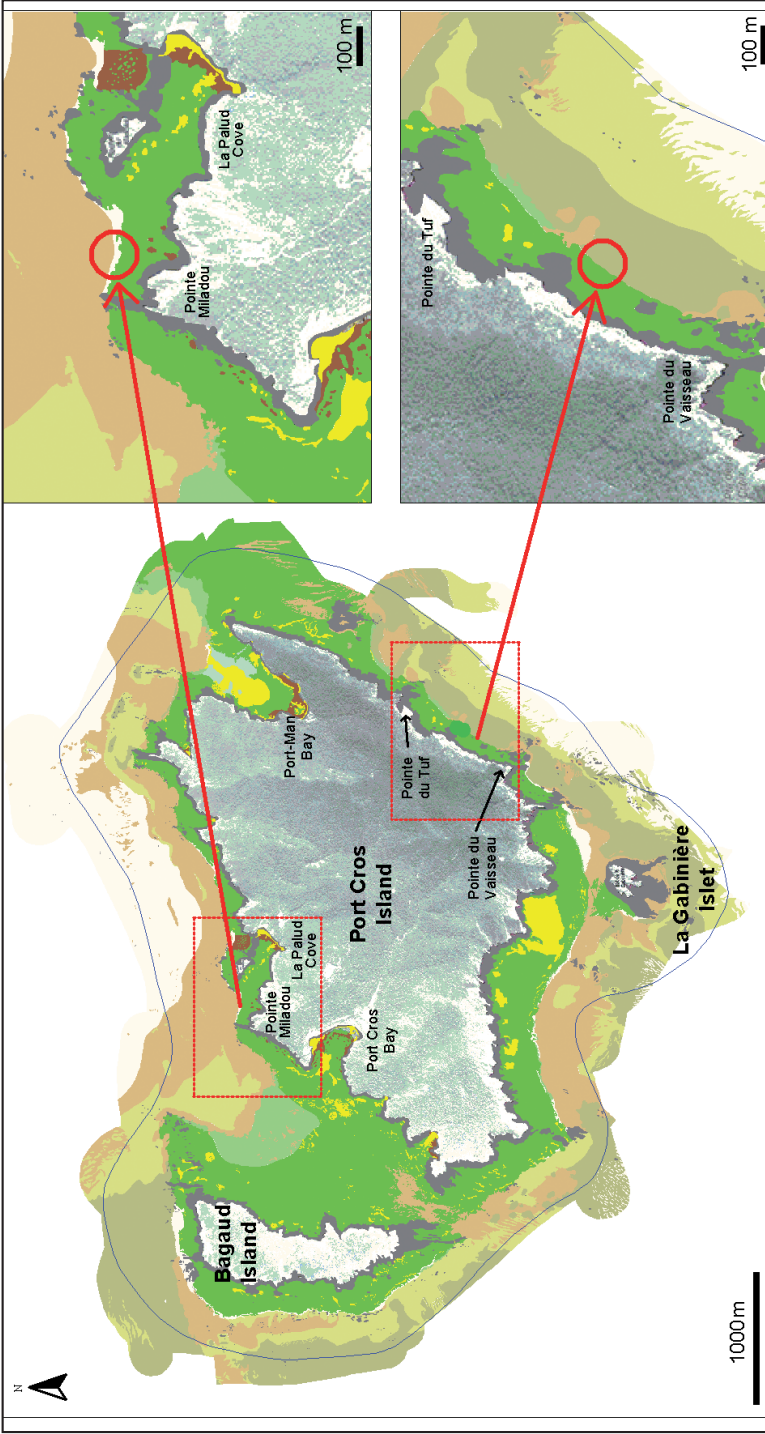


Figure 1. Map of marine benthic communities of the Port-Cros National Park (from Belsher et al., 2005). The *Posidonia oceanica* meadow is represented in green. In the inserts, localization of the two monitoring sites: La Palud (above, on the northern coast) and Vaisseau-Tuf (below, on the southeastern coast). Blue line = limit of the National Park (600 m offshore).

Table 1. Position of concrete markers (LP) and photo-stands (LPS) at the monitoring site La Palud. 43°00.877 N, 6°23.087 E (WGS 84).

Markers	Distance between markers (m)	Orientation (from a marker to the next)	Photo-stand to marker	Orientation (from photo-stand to marker)
LP1 to LP2	5.0	357°	LPS1 to LP1	205°
LP2 to LP3	8.0	320°	LPS2 to LP2	245°
LP3 to LP4	6.7	277°	LPS3 to LP3	175°
LP4 to LP5	5.1	270°	LPS4 to LP4	200°
LP5 to LP6	8.2	335°	LPS5 to LP5	190°
LP6 to LP7	7.6	305°	LPS6 to LP6	205°
LP7 to LP8	11.0	300°	LPS7 to LP7	185°
LP8 to LP9	7.3	300°	LPS8 to LP8	165°
LP9 to LP10	6.0	260°	LPS9 to LP9	170°
			LPS10 to LP10	185°

Table 2. Position of concrete markers (VT) and photo-stands (VTS) at the monitoring site Vaisseau-Tuf. From VT1 to VT5: 20.8 m; from VT1 to VT10: 44.9 m. md = missing data. VT1: 42°59.921N, 6°24.595 E; VT10: 42°59.949 N, 6°24.612 E (WGS 84).

Markers	Distance between markers (m)	Orientation (from a marker to the next)	Photo-stand to marker	Orientation (from photo-stand to marker)
VT1 to VT2	12.9	355°	VTS1 to VT1	100°
VT2 to VT3	4.4	90°	VTS2 to VT2	120°
VT3 to VT4	7.0	40°	VTS3 to VT3	120°
VT4 to VT5	5.0	5°	VTS4 to VT4	125°
VT5 to VT6	2.7	75°	VTS5 to VT5	160°
VT6 to VT7	3.8	15°	VTS6 to VT6	135°
VT7 to VT8	6.3	40°	VTS7 to VT7	150°
VT8 to VT9	3.9	70°	VTS8 to VT8	md
VT9 to VT10	5.4	30°	VTS9 to VT9	30°
			VTS10 to VT10	140°

Field surveys were performed on September 2002 (baseline), October 2005 and October 2008 (La Palud site) and on October 2006 (baseline) and October 2008 (Vaisseau-Tuf site).

The *P. oceanica* shoot density was measured in the vicinity of each marker by means of a 20 cm x 20 cm frame randomly placed (three replicates). Shoots were counted within the frame. In addition, shoots were numbered within some (2-5) patches exactly localized (distance, direction) with regard to the marker (Table 3); these patches (number and location), when available, were arbitrarily selected by the diver. Due to severe shoot loss within the patches initially selected (see results), new shoot patches were subsequently selected in the vicinity of the markers in 2005 and 2008 (La Palud site) and in 2008 (Vaisseau-Tuf site).

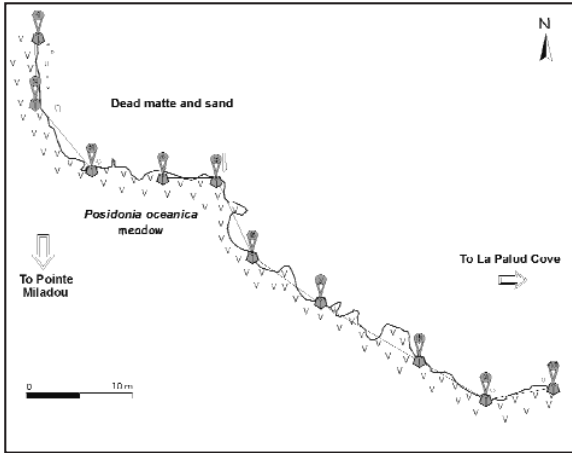


Figure 2. Position of the concrete markers (LP1 through LP10) at the monitoring site La Palud. Photo-stands are not shown.

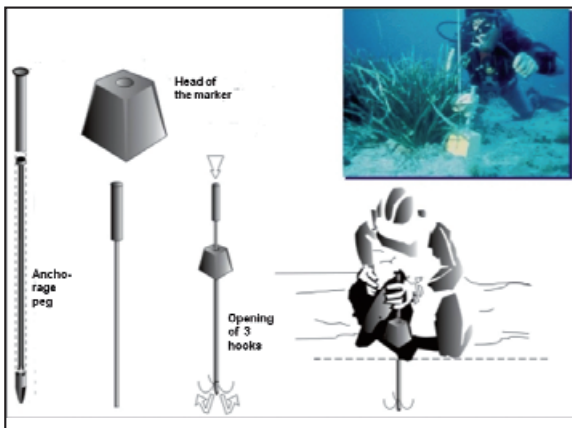


Figure 3. The marker used. Above right: the setting up of a marker by a diver (photo Alexis Rosenfeld©).

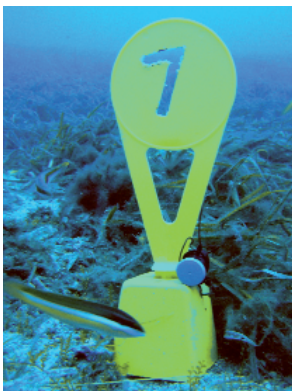


Figure 4. A concrete marker with the upward racket-like device used to label it. The blue cylinder, at the top right of the marker, contains a temperature recorder.

Table 3. Example of shoot numbering within selected shoot patches, in the vicinity of the marker LP1 (monitoring site La Palud), at the lower limit of the *Posidonia oceanica* meadow.

	2002	2005	2008
Patch LP1a	2	2	2
Patch LP1b	4	1	0
Patch LP1c	3	2	0
Patch LP1d	3	0	0
Patch LP1e	15	4	1
Total	27	9	3

The cover is the mean percentage of substrate covered by the *P. oceanica* meadow (whatever the shoot density within the meadow or within patches of *P. oceanica*); the cover was measured by means of a 30 cm x 30 cm see-through plastic sheet divided into nine 100 cm² squares (three replicates), according to the method described by Boudouresque *et al.* (2006a, 2007).

Caulerpa cylindracea Sonder (= *C. racemosa* (Forsskål) C. Agardh var. *cylindracea* (Sonder) Verlaque, Huisman *et Boudouresque*) is a Chlorobionta (Viridiplantae, Plantae) introduced into the Mediterranean Sea (Durand *et al.*, 2002; Verlaque *et al.*, 2003, 2004) and a possible competitor of *Posidonia oceanica*. Its presence and abundance was noted in the vicinity of each marker.

RESULTS

The mean shoot density of the *Posidonia oceanica* meadow near its deep limit significantly declined from 123 to 48 shoots/m² between 2002 and 2008 at La Palud (Tables 4, 10). The annual rate of decline was 14-15%. In contrast, at Vaisseau-Tuf, no change in mean shoot density was recorded (Tables 7, 10).

Table 4. *Posidonia oceanica* shoot density (mean number of shoots per m²) at the monitoring site La Palud (34 m deep). Density was measured in 2002, 2005 and 2008.

Year	Concrete markers (LP1 through LP10)										Mean
	LP1	LP2	LP3	LP4	LP5	LP6	LP7	LP8	LP9	LP10	
2002	75	100	150	150	108	83	175	150	117	108	123
2005	42	92	104	67	42	40	115	110	67	83	76
2008	58	58	117	8	33	17	58	33	58	42	48

The number of shoots within selected patches severely declined at both monitoring sites (Tables 5, 8, 10), at an annual rate of 19% and 30% (La Palud, 2002-2005 and 2005-2008 respectively) and 15% (Vaisseau-Tuf, 2006-2008). At the Vaisseau-Tuf site, there was no significant correlation between the depth and the rate of change in the number of shoots (Table 8).

Table 5. Cumulative number of shoots within the selected patches of shoots in the vicinity of the markers, at the monitoring site La Palud (34 m deep). Shoots were numbered in 2002, 2005 and 2008.

Year	Concrete markers (LP1 through LP10). Patches selected in 2002										Total
	LP1	LP2	LP3	LP4	LP5	LP6	LP7	LP8	LP9	LP10	
2002	27	30	13	13	43	14	16	16	22	19	213
2005	9	13	13	6	21	5	15	7	12	12	113
2008	3	2	12	0	2	2	9	0	7	2	39
	New patches selected in 2005										
2005	3	2	1	-	2	-	4	7	-	15	34
2008	2	0	0	-	0	-	4	0	-	4	10
	New patches selected in 2008										
2008	6	3	6	14	4	5	3	6	-	5	52

Table 6. Bottom cover (%) of the *Posidonia oceanica* meadow at the monitoring site La Palud (34 m deep). Cover was measured in 2002, 2005 and 2008.

Year	Concrete markers (LP1 through LP10)										Mean
	LP1	LP2	LP3	LP4	LP5	LP6	LP7	LP8	LP9	LP10	
2002	41	35	28	22	17	15	26	19	19	24	24%
2005	24	30	17	24	22	17	17	19	31	11	21%
2008	15	19	11	19	11	15	19	22	26	11	17%

Table 7. *Posidonia oceanica* shoot density (mean number of shoots per m²) at the monitoring site Vaisseau-Tuf (31-34 m deep). Density was measured in 2006 and 2008.

Year	Concrete markers (VT1 through VT10)										Mean
	VT1	VT2	VT3	VT4	VT5	VT6	VT7	VT8	VT9	VT10	
2006	67	108	83	83	200	133	67	117	92	108	106
2008	67	100	92	67	125	142	67	125	108	133	103

Table 8. Cumulative number of shoots within the selected patches of shoots in the vicinity of the markers, at the monitoring site Vaisseau-Tuf. Shoots were numbered in 2006 and 2008.

Year	Concrete markers (VT1 through VT10) and depth. Patches selected in 2006										Total
	VT1	VT2	VT3	VT4	VT5	VT6	VT7	VT8	VT9	VT10	
	34 m	31 m	33 m	32 m	32 m	32 m	32 m	32 m	33 m	33 m	
2006	27	13	8	13	48	44	15	24	27	30	249
2008	6	11	8	7	45	35	8	14	15	31	180
	New patches selected in 2008										
2008	5	-	-	-	-	-	8	17	11	10	51

Table 9. Bottom cover (%) of the *Posidonia oceanica* meadow at the monitoring site Vaisseau-Tuf. Cover was measured in 2006 and 2008.

Year	Concrete markers (VT1 through VT10) and depth										Mean
	VT1	VT2	VT3	VT4	VT5	VT6	VT7	VT8	VT9	VT10	
	34 m	31 m	33 m	32 m	32 m	32 m	32 m	32 m	33 m	33 m	
2006	22	83	39	48	31	57	54	80	63	57	53%
2008	19	39	26	33	43	44	41	37	30	28	34%

Table 10. Wilcoxon signed-rank test for shoot density, bottom cover and cumulative number of shoots within selected shoot patches. ns = not significant.

Monitoring site	Parameter and compared years	Z	p	Significance
La Palud	Shoot density			
	2002 vs 2005	2.803 060	0.005	**
	2005 vs 2008	2.089 553	0.037	*
	2002 vs 2008	2.803 060	0.005	**
	Bottom cover			
	2002 vs 2005	1.066 228	0.286	ns
	2005 vs 2008	2.132 456	0.033	*
	2002 vs 2008	1.954 751	0.038	*
	Cumulative number of shoots			
	2002 vs 2005	2.665570	0.008	**
2005 vs 2008	2.803060	0.005	**	
2002 vs 2008	2.803060	0.005	**	
Vaisseau-Tuf	Shoot density			
	2006 vs 2008	0.420084	0.674	ns
	Bottom cover			
	2006 vs 2008	2.599201	0.009	**
Cumulative number of shoots				
2006 vs 2008	2.547100	0.011	*	

The cover of the *P. oceanica* meadow significantly declined at both sites (Tables 6, 9, 10), at an annual mean rate of 4-7% (La Palud site) and 20% (Vaisseau-Tuf site). With regard to the number of shoots within selected patches, there was no significant correlation between the depth and the rate of change in the cover (Table 9).

The introduced Chlorobionta *Caulerpa cylindracea* was absent at La Palud when the markers were laid down; a small patch was observed in 2005; subsequently, in 2008, it became widespread, both within the meadow at its boundary and further seawards; however, its overall abundance was low. At the Vaisseau-Tuf site, *C. cylindracea* was densely present since 2006.

DISCUSSION

According to Mayot *et al.* (2006), the decline in shoot density constitutes a harbinger of the *P. oceanica* deep limit withdrawal. The Port-

Cros Island deep *P. oceanica* meadow can therefore be considered as in regression, although shoot density still falls within the range of “normal densities” (according to Pergent *et al.*, 1995) for a pristine meadow at the depths considered (61-285 shoots/m² at 31 m depth, 38-262 at 34 m). This is a completely unexpected result, since the Port-Cros National Park, localized off the Provence coast, and therefore beyond impact of coastal pollution and urbanization, is usually regarded as a non-polluted and non-disturbed site, harbouring pristine biota and ecosystems (Harmelin and Marinopoulos, 1993; Harmelin and Robert, 2001; Boudouresque *et al.*, 2004; Belsher *et al.*, 2005; GEM, 2007; Harmelin and Ruitton, 2007; Cadiou *et al.*, 2009).

The question which arises is: why has such a decline occurred at Port-Cros Island? Since the withdrawal of the deep limit of *P. oceanica* meadow constitutes a general feature everywhere in the northwestern Mediterranean Sea, whatever the proximity of disturbance and pollution sources (Boudouresque *et al.*, 2000; Mayot, 2007), it can be expected that the causes are not local factors but forcings acting over a large geographical area.

Trawling is regarded as a major cause of regression of deep *P. oceanica* meadows throughout the Mediterranean Sea (Ardizzone and Pelusi, 1984; Ramos-Esplá *et al.*, 1994; Pasqualini *et al.*, 2000; Ganteaume *et al.*, 2005; González-Correa *et al.*, 2005; Boudouresque *et al.*, 2006a; Jackson *et al.*, 2006; Boudouresque *et al.*, 2009; González-Correa, 2009). However, trawling has been banned around Port-Cros Island since the founding of the National Park, in 1963, and fishers strictly abide by this rule. Therefore, trawling cannot be a plausible cause of *P. oceanica* regression.

The competition between *P. oceanica* and introduced species means a physiological cost for both competitors, whichever may be the winner and even if there is no winner (Villèle and Verlaque, 1994, 1995; Ceccherelli *et al.*, 2000; Pergent *et al.*, 2008). In addition, the introduced Chlorobionta *Caulerpa cylindracea* affects the sediment biogeochemical conditions by increasing organic matter pools, microbial activity, and sulfide pools of the sediments (Holmer *et al.*, 2009); the meristematic activity of *P. oceanica* shoots declines strongly when the plant is growing on sediments with a sulfide pool > 0.001 mol AVS (acid volatile sulfides)/m² (Garcias-Bonet *et al.*, 2008). Therefore, it cannot be ruled out that the occurrence of *C. cylindracea* at La Palud from 2005, and its abundance at Vaisseau-Tuf, may weaken *P. oceanica* and play a role in its regression.

An increase in turbidity (e.g. enrichment in inorganic and organic particles and dissolved compounds, plankton blooms due to eutrophic conditions) reduces transparency of the water and penetration of light, and can consequently induce a withdrawal of the *P. oceanica* lower limit (Boudouresque *et al.*, 2009).

The North Atlantic Oscillation (NAO) can also be influential with regard to light penetration into the water column. NAO is a non-cyclical climatic phenomenon. A high NAO index (denoted NAO+) corresponds to a northward shift of the storm track and to a significant increase of storminess in Northern Europe, while dry conditions and mild winters are dominant in Southern Europe, the Mediterranean Sea and North Africa. In contrast, when the NAO index is low (NAO-), the impact is more or less reversed and Southern Europe and the Mediterranean receive increased rainfall, with increased river discharge and cloudiness (Kerr, 2000; Visbeck *et al.*, 2001; Turre, 2002). The NAO index fluctuates over decadal periods; it was generally negative in the 1950s and 1960s, and generally positive in the 1980s and 1990s (Visbeck *et al.*, 2001; Stenseth *et al.*, 2002; Cassou and Terray, 2003). The NAO index decreased from 2002 to 2006, then slightly increased in 2006-2008. Locally, the NAO often results in disruption of the wind regime, water mass stratification and thermocline depth and unicellular plankton abundance (Leterme *et al.*, 2005; Molinero *et al.*, 2005). The NAO can therefore account, directly or indirectly, for a subtle deficit in light availability at depth.

The rise in relative sea-level is also to be considered as a possible cause for the deep *P. oceanica* regression. About 20 000 years ago, at the time of the Last Glacial Maximum (LGM), the sea-level was 130 m below that of today (Henderson, 2005). From 19 000 years BP to the present, the sea-level has never stopped rising (Laborel *et al.*, 1983, 1994; Miller *et al.*, 2005). The “Greek” level, 2 600 years ago, was about 60-80 cm below the present level (Morhange, 2003). Between 1870 and 2004, at a world scale, the relative sea-level rise was 20 cm (Church and White, 2006). Between 1945 and 2000, in the western Mediterranean, the sea-level rose at a mean rate of 0.5-1.0 mm. a⁻¹ (Calafat and Gomis, 2009). Any rise in the sea-level results in a withdrawal of the lower limit of the *P. oceanica* meadow, which matches the compensation depth of the species (i.e. the depth where production *via* photosynthesis is equal to loss from respiration); for instance, in sites with a gently sloping bottom, a 1-m rise in sea-level can lead, at depth, to a 100-m wide belt becoming unsuitable for the seagrass (Bruun, 1962; Boudouresque *et al.*, 2009).

Finally, may the warming of Mediterranean sea-water play a role in the deep *P. oceanica* regression? During the Little Ice Age (LIA, from the 13th to the early 19th century), temperature dropped conspicuously (Le Roy Ladurie, 2004; Luterbacher *et al.*, 2004; Hopkin, 2007). The subsequent rapid warming, from the mid-19th century, constitutes in part a natural phenomenon; however, the present day release of greenhouse gas, due to human activity, obviously enhances this natural trend (Stott *et al.*, 2000). During the severe warm-water episode which occurred in

summer 1999 from Liguria (Italy) to the Gulf of Lions (Cerrano *et al.*, 2000; Perez *et al.*, 2000), a negative impact on *P. oceanica* was observed at its depth limit, near Marseille (Provence) (Mayot *et al.*, 2003, 2005; Mayot, 2007). This result was surprising, since the site is located near the cold distribution limit of the species, and therefore a positive rather than a negative effect of this warming event would have been expected. The possible link, either direct or indirect, between seawater warming and regression of the depth limit is only a working hypothesis that does not rest on any identified physiological process (Mayot *et al.*, 2005; Boudouresque *et al.*, 2009).

A body of co-operating causes may therefore account for the regression of the depth limit of *P. oceanica* meadows in the northwestern Mediterranean, a regression which not only continues today, but has accelerated during the 1990s and 2000s. The general improvement of coastal water quality and the recovery trend of shallow *P. oceanica* meadows (Boudouresque *et al.*, 2000; Mayot, 2007) do not support the idea that pollution plays a major role. The fact that trawling was banned decades ago around Port-Cros Island rules out (at least locally) its involvement in the present day deep meadow regression. Our results suggest that direct or indirect consequences of the current episode of the North Atlantic Oscillation, the sea-level rise, the warming of the sea water and colonization by *Caulerpa cylindracea* could be plausible candidates to account for the observed regression of the depth limit of the *P. oceanica* meadow, at least at the scale of the Port-Cros National Park.

With regard to current sea water warming, Hobo-tidbit® temperature recorders were fixed to a concrete marker of La Palud and Vaisseau-Tuf sites (Figure 4), in order to shed light on the possible role of the temperature.

CONCLUSION

The monitoring of the depth limit (31-34 m) of the *Posidonia oceanica* seagrass meadow, 2002 through 2008 within the Port-Cros National Park, a locality where the biota and communities are considered to be in pristine condition, led to a rather unexpected result: a conspicuous loss.

Taking into account data from other monitoring sites in the northwestern Mediterranean Sea, our results point to four possible main causes: **(i)** direct or indirect effects of the North Atlantic Oscillation (NAO), *via* e.g. rainfall, cloudiness, river discharge (nutrient, silt) and plankton abundance, resulting in a decrease of light availability at depth, **(ii)** a rise in relative sea-level, also resulting in a decrease of light availability at depth, **(iii)** a negative impact, at least at depth, of the seawater warming, whose physiological basis remains unclear, and **(iv)** the presence of the introduced Chlorobionta *Caulerpa cylindracea*.

A long-term monitoring survey, straddling at least two NAO climatic episodes, and accurate records of deep water temperature, are essential to disentangle the role played by pollution, NAO, relative sea-level rise and warming, in the regression of deep *P. oceanica* meadows.

The present study highlights the importance of Marine Protected Areas (MPAs) as reference areas. They are crucial for solving global environmental questions. The present study also emphasizes that MPAs are not “islands” of nature, equilibrium and tranquility, independent of the surrounding areas and the natural processes and human-induced impacts, but just a small part of the region to which they belong and the global environment; legal protection is not enough; *P. oceanica* meadows in a marine protected area may be no healthier than those in unprotected areas (Boudouresque and Verlaque, 2005; Montefalcone *et al.*, 2009).

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