Posidonia oceanica meadows are not declining globally. Analysis of population dynamics in marine protected areas of the Mediterranean Sea

José M. González-Correa, Just T. Bayle Sempere*, Pablo Sánchez-Jerez, Carlos Valle

Department of Marine Sciences and Applied Biology, University of Alicante, PO Box 99, Alicante 03080, Spain

ABSTRACT: Many studies have reported a worldwide decline in seagrasses, including *Posidonia oceanica,* with evidence of regression on a global scale for different reasons. With the aim of assessing the population dynamics of *P. oceanica* in the Mediterranean Sea, we chose 6 protected and pristine areas, separated by 200 to 3000 km, to determine whether an overall decline is occurring. Within each locality, we randomly selected 2 sites separated by 2 to 4 km. At each site, we sampled seagrass at 2 fixed depths (10 and 20 m). At each sampled depth, 10 principal plagiotropic rhizomes, separated by 1 to 5 m, were collected. We used lepidochronology to study seagrass dynamics, and analysis of variance (ANOVA) and permutational multivariate ANOVA (PERMANOVA) to analyze the data, testing the 3 main factors of locality, site, and depth. Our results showed positive population dynamics of *P. oceanica* in all localities and for all studied parameters. We observed exceptional vegetative growth around Zembra Island, Tunisia. We did not find statistically different vegetative growth between the northernmost and the warmer localities, showing a high level of plasticity in this species. This study demonstrates that global processes are not causing an overall decline in *P. oceanica* meadows around the Mediterranean Sea and attributes the decline reported in the literature to cumulative effects derived from different natural and anthropogenic local processes.

KEY WORDS: *Posidonia oceanica* · Population dynamics · Marine protected areas · Vegetative growth · Decline · Impacts · Global processes

INTRODUCTION

Many authors have reported the decline of seagrasses throughout the world (see review by Duarte 2002). The permanency of seagrasses over a geological scale has been questioned by Larkum & West (1983), who proposed that seagrasses may not be as well adapted to their environment as previously supposed. Moreover, they remarked that a permanent seagrass community should be defined over spatial scales of 10 to 1000 km², and that stability may be maintained at one scale but not at another. These changes have been noticed not only in the broad decline of seagrasses worldwide during the past century, but also in their paleobiogeographical history (Larkum & den Hartog 1989). The origin of decline in seagrass beds had been attributed to natural and anthropogenic causes that can act on a local or global scale, including meteorological events (Poiner et al. 1989), geological processes (e.g. earthquakes, volcanic eruptions; Short & Wyllie-Echevarria 1996), breakdowns of natural cycles (e.g. changes in some *Zostera marina* populations; Glémarec 1979), wasting disease by *Labyrinthula* sp. infections (e.g. in North Atlantic *Z. marina* beds in the 1930s; Rasmussen 1977), herbivore pressure (Ruíz et al. 2001), evolutionary constraints (Molinier & Picard 1952), multiple anthropogenic impacts (e.g. otter-bottom trawling, Sánchez Lizaso et al. 1990; coastal construction, Meinesz 1982, Guidetti & Fabiano 2000; beach nourishment, outfall sewage, Cambridge et al. 1986), and climate change (Short & Neckles 1999).

In the Mediterranean Sea, *Posidonia oceanica* is a slow-growing species that constitutes a large steady

community at its climax in soft sea-beds (Duarte 1991); some beds have been estimated to be older than 6000 yr (Picard 1965). This species plays an important role in the function of Mediterranean ecosystems (Hemminga & Duarte 2000). Losses of this species have been widely reported for different reasons, including those indicated above, suggesting that *P. oceanica* shows evidence of regression on a global scale (Pérès 1984, Marbà et al. 1996). This conclusion, however, was based on observational approaches, without distinguishing the real causes that have produced the observed declines.

If a global regression is currently in effect, it would mean that some global process (e.g. climate change, wasting diseases, herbivore pressure, and evolutionary constraints) should also be working on *Posidonia oceanica* meadows in the Mediterranean Sea. Studying pristine natural areas, such as marine protected areas, that are free of local anthropogenic impacts (e.g. otter trawl fishing, coastal construction, outfall sewage) could help us to understand the effects derived from global or local causes of decline. Thus, the general aim of this study was to assess the population dynamics of *P. oceanica* meadows in 6 selected pristine areas, with different levels of protection, around the Mediterranean Sea to assess the global decline of this species. In this sense, we hypothesized that a negative branch population growth in *P. oceanica* meadows should be found in these pristine areas if a global process of regression were occurring.

MATERIALS AND METHODS

Study area and sampling design. The study was carried out between 2002 and 2004 in 6 well conserved *Posidonia oceanica* meadows that were never subject to any local impact. The sites were selected randomly around the Mediterranean coast, separated by 200 to 3000 km, and included the following: Marine Protected Area of Carry-le-Rouet (Carry-le-Rouet, France; mean shoot density: 302 ± 15 at 10 m and 221 ± 17 at 20 m depth), Special Area of Conservation of Cape Blanco (Cape Blanco, Balearic Islands, Spain; mean shoot density: 477 ± 13 at 10 m and 376 ± 12 at 20 m), Special Area of Conservation of Alicante (Alicante, Spain; mean shoot density: 380 ± 11 at 10 m and 190 ± 12 at 20 m), Marine Protected Area of Cape Gata-Nijar (Cape Gata, Almeria, Spain; mean shoot density: 460 ± 30 at 10 m and 380 ± 25 at 20 m), Marine Protected Area of Zembra Island (Zembra Island, Tunisia; mean shoot density: 601 ± 14 at 10 m and 400 ± 13 at 20 m), and Marine Protected Area of Cape Greco (Agia Napa, Cyprus; mean shoot density: 379 ± 10 at 10 m, and 299 ± 7 at 20 m; Fig. 1). At each locality, we randomly choose 2 sites separated by 2 to 4 km that represented a medium spatial scale. At each site, we sampled at 2 fixed depths (10 and 20 m).

Seagrass dynamics. Branch dynamics of *Posidonia oceanica* populations were studied directly by counting live and dead branches along a principal plagiotropic rhizome. A principal plagiotropic rhizome was defined as an expanding branch that bore secondary, tertiary, etc., new branches, and was considered the main ex-
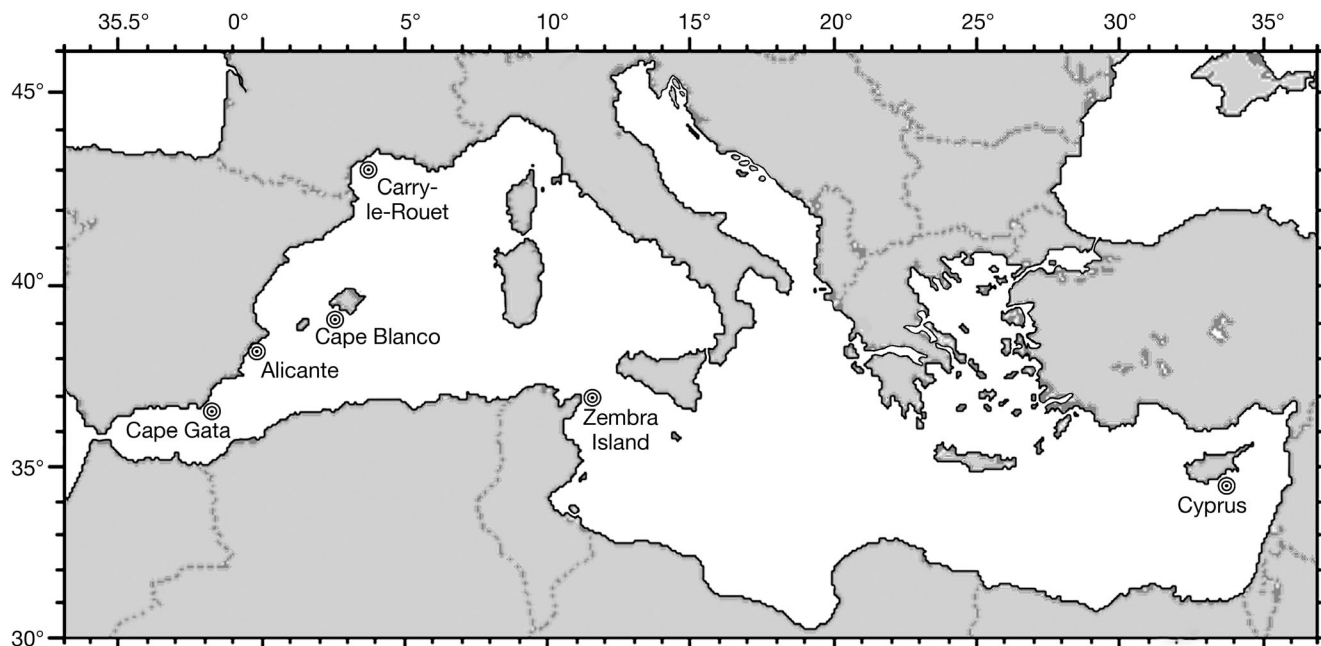

Fig. 1. Study sites of pristine *Posidonia oceanica* meadows around the Mediterranean Sea

panding unit of the plant where all vegetative events are registered consecutively over time. Plagiotropic runner rhizomes of *P. oceanica*, which exhibit a high degree of meristem dependency, are the parts of the plant that accomplish this condition and are therefore responsible for expanding meadows (Tomlinson 1974). This method allowed us to calculate the branch balance directly with no other extrapolation. Following this protocol, 10 principal plagiotropic rhizomes separated by 1 to 5 m were collected by SCUBA diving at each sampling depth in the center of each meadow. Each rhizome bore a variable number of lateral orthotropic branches.

We used the reconstruction technique of lepidochronology (Pergent 1990), which has been widely used to study seagrass dynamics (e.g. Guidetti & Fabiano 2000). This method is based on the thickness of *Posidonia oceanica* sheaths, which develop over an annual cycle. Each annual cycle comprises 2 minima of sheath thickness (Pergent 1987). These annual cycles are only clearly identifiable in vertical branches and not in the basal, plagiotropic rhizomes (Pergent 1987). To date plagiotropic rhizomes, we dated the oldest orthotropic rhizome that branched from the plagiotropic rhizome. We considered that its age was the same as the remaining plagiotropic rhizomes (from the insertion of the oldest vertical rhizome to the end of the plagiotropic rhizome, Fig. 2). However, this method is not sensitive enough to date horizontal rhizomes younger than 1 yr; therefore, we selected only rhizomes older than 3 yr to minimize such imprecision. Further, only principal plagiotropic rhizomes were used to minimize variability in estimations; the lateral plagiotropic branches borne by a principal plagiotropic rhizome have differentiated growth with respect to the principal rhizome (Molenaar et al. 2000).

The dating of plagiotropic and orthotropic rhizomes allowed us to estimate annual values of seagrass variables. These included colonization rate measured as the length of the sea bed covered by plagiotropic rhizomes (image projected in cm yr^{-1}); and elongation rate (mm yr^{-1}) of orthotropic (accuracy of ±0.1 mm) and plagiotropic (cm yr^{-1}, accuracy of ±1 mm) rhizomes, which was obtained by measuring their contours using a tape measure. Leaf production (leaves yr^{-1}) was estimated by counting sheaths; rhizome production (g DW yr^{-1}) was estimated after drying rhizomes for 24 h at 80°C, and branch balance (branches yr^{-1}) was calculated as the difference between the total branches produced and the dead branches along each plagiotropic rhizome divided by the age of the plagiotropic rhizome (i.e. age of the oldest living orthotropic rhi-
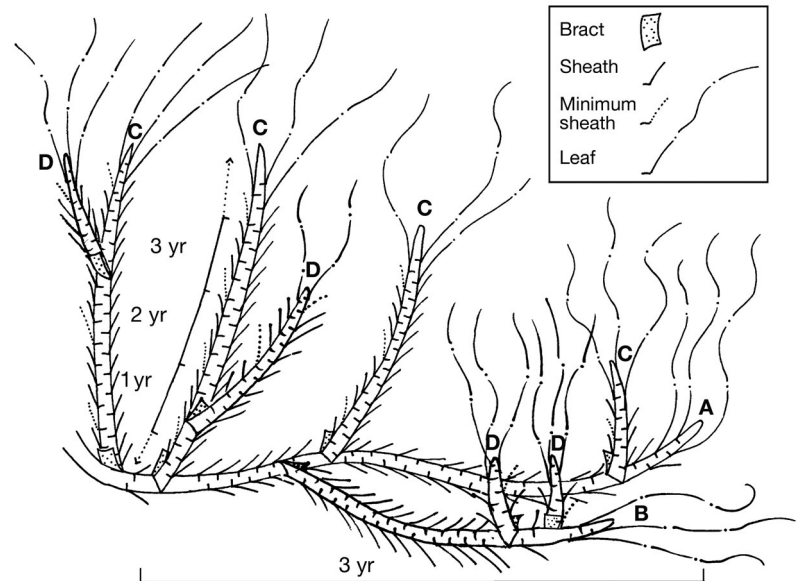

Fig. 2. Representation of the indirect method used to date plagiotropic rhizomes. A: primary plagiotropic; B: secondary plagiotropic; C: secondary orthotropic; D: tertiary branches

zome) bearing them. We distinguished among secondary orthotropic and plagiotropic rhizomes that branched from both primary plagiotropic rhizomes, and tertiary rhizomes that branched from those secondary rhizomes (Molenaar et al. 2000). The global balance of branches was estimated and added to the different branch balances mentioned above. Finally, aborted branches (aborted branches yr^{-1}) that emerged from primary plagiotropic rhizomes were also estimated. We considered dead rhizomes to be those with symptoms of necrosis in the meristem of their leaves (multiple fine, dark sheaths and rhizomes that were not sectioned), and aborted branches were those that were not developed and showed only 1 fine sheath and its corresponding bract.

Data analysis. A mixed analysis of variance (ANOVA) design was employed in testing parameters from seagrass dynamics for the 3 main factors considered: locality, site, and depth. The linear model for this analysis was

$$X_{ijkn} = \mu + L_i + S(L)_{j(i)} + D_k + L \times D_{ixk} + S(L) \times D_{j(i)xk} + \text{Residual}_{n[j(i)xk]}$$

where L_i is the effect of the ith localities, which estimates variability at the larger spatial scale; $S(L)_{j(i)}$ is the effect of the jth sites at each level of the locality factor, which estimates spatial variability at the medium spatial scale; and D_k is the effect due to depth. Residual$_{n[j(i)xk]}$ is the error term that estimates variability at a smaller spatial scale. L_i and $S(L)_{j(i)}$ were randomized factors, and D_k was a fixed factor.

Before the analysis, Cochran's test was used to test for homogeneity of variance for all variables. Where significant differences were found, the data were $\ln(x+1)$ transformed. When transformations did not remove heterogeneity, analyses were performed on the untransformed data by setting the F-test alpha to 0.01, since ANOVA is quite robust to departures from its assumptions, especially when the design is balanced and contains a large number of samples or treatments (Underwood 1997). When the factors showed significant differences, *a posteriori* pair-wise comparisons of means were performed using the Student-Newman-Keuls test.

A permutational multivariate ANOVA (PERMANOVA software; Anderson 2001) was used to test simultaneous responses of the *Posidonia oceanica* variables to the factors locality, site, and depth. The linear model used for this analysis is the one previously mentioned. When the factors showed significant differences, pairwise *a posteriori* comparisons of levels of each factor

were performed. We tested the homogeneity of data using pair-wise comparisons and the associated nonmetric multidimensional scaling (MDS) plot.

RESULTS

Seagrass structure

In total, 240 principal plagiotropic rhizomes containing their apex were processed, of which only about 2% were dead. Principal plagiotropic rhizomes were on average 5.1 ± 0.7 yr old (ranging from 3 to 15 yr old). During this period, colonization and elongation showed similar differences among locations, with the highest values at Zembra Island (7.2 ± 0.6 and 8.6 ± 0.7 cm yr^{-1} respectively, $p = 0.05$, Table 1; Fig. 3A,B). Carry-le-Rouet showed the lowest values but without statistical differences from the other locations (3.8 ± 0.5

Table 1. *Posidonia oceanica*. Summary of analysis of variance (ANOVA) results comparing variations in colonization, elongation, leaf production, rhizome production, aborted branches, balance of secondary orthotropic and plagiotropic branches, balance of tertiary branches, and global balance of primary plagiotropic rhizomes sampled at 2 depths (10 and 20 m) and at 2 sites in each locality. A: Alicante; Z: Zembra island; G: Cape Gata; C: Cyprus; B: Cape Blanco; CR: Carry-le-Rouet. SNK: Student-Newman-Keuls test. **p < 0.01; *p < 0.05

Source of variation	df	Colonization		Elongation		Leaf production	
		MS	F	MS	F	MS	F
Locality	5	5811.40	6.28*	7326.05	8.29*	123.11	12.09**
Site (Locality)	6	924.70	2.84*	883.21	2.14*	10.18	1.01
Depth	1	261.46	0.22	628.04	0.38	11.16	0.24
Locality × Depth	5	1205.47	1.18	1660.09	0.96	46.16	0.91
Site (Locality) × Depth	6	1022.29	3.14	1724.35	4.17**	50.63	5.04**
Residual	216	325.08		413.61		10.05	
SNK		Z > A = G = B = C = CR		Z > A = G = B = C = CR		CR < Z = A = G = C = B	

Source of variation	df	Rhizome production		Aborted branches		Balance of secondary branches	
		MS	F	MS	F	MS	F
Locality	5	9.921	16.53**	0.0296	1.52	11.014	17.21**
Site (Locality)	6	0.6	1.76	0.0195	3.41**	0.64	1.16
Depth	1	0.0001	0.0001	0.0358	5.53	0.103	0.03
Locality × Depth	5	0.806	0.6	0.0065	0.88	3.083	3.14
Site (Locality) × Depth	6	1.336	3.91**	0.0073	1.28	0.981	1.78
Residual	216	0.341		0.0057		0.551	
SNK		Z > A = G = C = B = CR				Ambiguous result	

| Source of variation	df	Balance of secondary plagiotropic branches		Balance of tertiary branches		Global balance	
		MS	F	MS	F	MS	F
Locality	5	0.191	3.31	0.914	2.96	1.336	6.39*
Site (Locality)	6	0.058	1.75	0.309	1.71	0.209	1.67
Depth	1	0.017	0.18	2.448	8.21*	0.392	0.99
Locality × Depth	5	0.097	2.85	0.298	1.72	0.396	3.02
Site (Locality) × Depth	6	0.034	1.03	0.174	0.96	0.131	1.04
Residual	216	0.033		0.181		0.125	
SNK				10 m depth > 20 m depth		Ambiguous result	
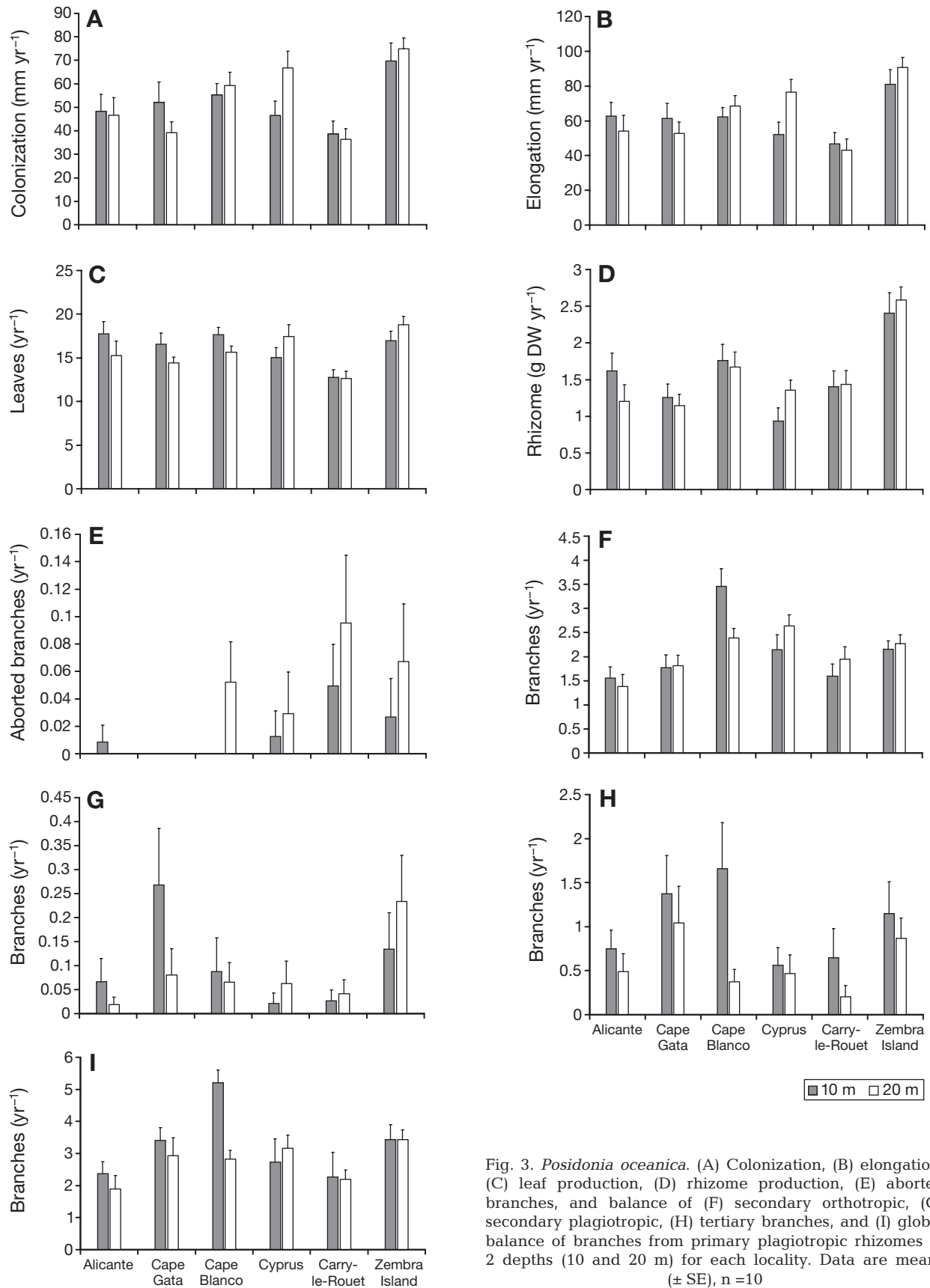
Fig. 3. *Posidonia oceanica*. (A) Colonization, (B) elongation, (C) leaf production, (D) rhizome production, (E) aborted branches, and balance of (F) secondary orthotropic, (G) secondary plagiotropic, (H) tertiary branches, and (I) global balance of branches from primary plagiotropic rhizomes at 2 depths (10 and 20 m) for each locality. Data are means (± SE), n =10

and 4.5 ± 0.6 cm yr^{-1}, respectively). Leaf production was significantly lower at Carry-le-Rouet (12.7 ± 0.9 leaves yr^{-1}), while the remaining localities ranged between 16.5 ± 1.6 (Alicante) and 17.8 ± 1.1 leaves yr^{-1} (Zembra Island; Fig 3C). Rhizome production reached the highest values at Zembra Island: 2.5 ± 0.2 g DW yr^{-1} vs. 1.3 ± 0.1 g DW yr^{-1} on average for the other localities (p = 0.01, Table 1, Fig 3D). Aborted branches showed a high rate of variability among localities and depths (Fig 3E), with a maximum value at 20 m depth at Carry-le-Rouet (0.11 ± 0.05 aborted branches yr^{-1}) and with no aborted branches at Cape Gata. The global balance of branches from a primary plagiotropic rhizome ranged from 2.1 ± 0.4 at Alicante to 3.2 ± 0.6 branches yr^{-1} at Cape Gata. Cape Blanco was an exception, reaching 4.0 ± 0.7 branches yr^{-1} on average (p = 0.05, Table 1, Fig 3I). We found the highest value of balance of secondary and tertiary orthotropic rhizomes at Cape Blanco at 10 m depth (3.5 ± 0.3 and 1.7 ± 0.5, respectively; Fig. 3F,H), but statistical differences were only observed in the balance of secondary orthotropic rhizomes among localities (p = 0.01, Table 1). Balance of secondary plagiotropic branches showed the highest rates at 10 m depth at Cape Gata and at 20 m depth at Zembra Island, with a value around 0.25 branches yr^{-1}, whereas the other localities and depths ranged between 0.02 ± 0.01 and 0.13 ± 0.07 branches yr^{-1} (Fig. 3G).

For secondary orthotropic rhizomes, we found significant differences for leaf production among localities (p = 0.01, 9.1 ± 1.0 leaves yr^{-1} at Zembra Island and Cape Gata, >8.4 ± 0.9 leaves yr^{-1} at Alicante and Cape Blanco, >7.6 ± 0.9 leaves yr^{-1} at Cyprus and Carry-le-Rouet, Table 2, Fig. 4A); homogeneity in elongation, ranging between and 5.9 ± 0.9 mm yr^{-1} at Carry-le-Rouet and 8.9 ± 1.1 mm yr^{-1} at Zembra Island, with significant differences only at a medium scale (p = 0.01, Table 2, Fig 4B); and finally significantly lower rhizome production at Cyprus (p = 0.01, 0.06 ± 0.01 vs. a
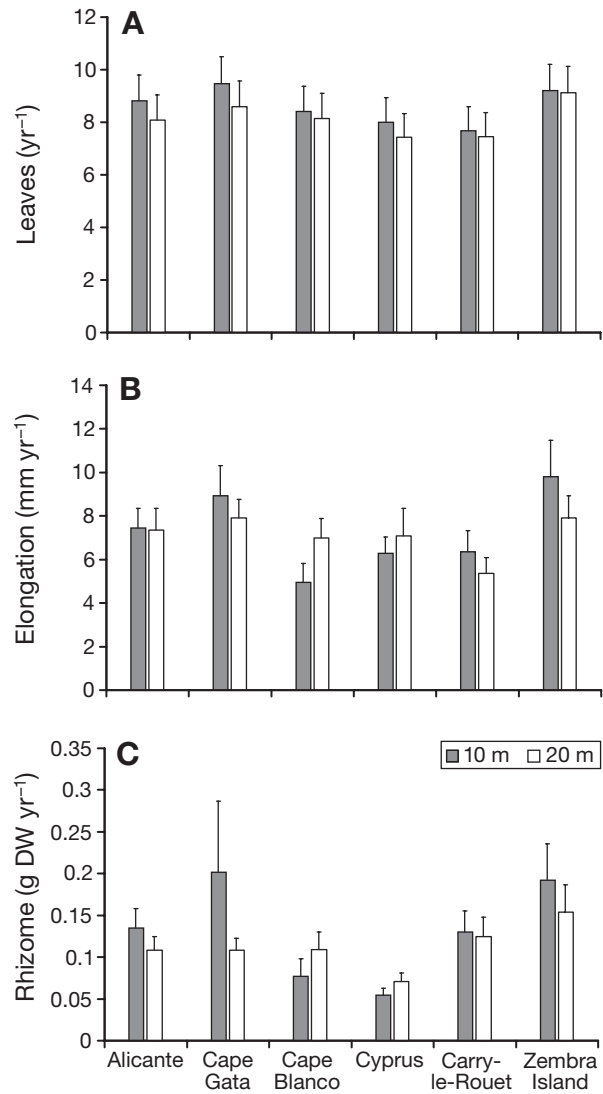

Fig 4. *Posidonia oceanica*. (A) Leaf production, (B) elongation, (C) rhizome production in orthotropic rhizomes at 2 depths (10 and 20 m) for each locality. Data are means (± SE), n = 10

Table 2. *Posidonia oceanica*. Summary of analysis of variance (ANOVA) results comparing variation in elongation, leaf production, and rhizome production of secondary orthotropic branches at 2 depths (10 and 20 m) and 2 sites in each locality. Definitions of abbreviations as in Table 1. **p < 0.01; *p < 0.05

Source of variation	df	Elongation		Leaf production		Rhizome production	
		MS	F	MS	F	MS	F
Locality	5	0.929	2.38	17.25	28.12**	0.065	9.01**
Site (Locality)	6	0.389	3.26**	0.614	0.89	0.007	0.7
Depth	1	0.002	0.01	12.51	12.38*	0.022	1.10
Locality × Depth	5	0.293	1.9	1.01	1.29	0.019	2.82
Site (Locality) × Depth	6	0.154	1.29	0.78	1.13	0.007	0.69
Residual	216	0.120		0.69		0.01	
SNK				C = CR < A = B < Z =G			
				10 m depth > 20 m depth			

range between 0.093 ± 0.009 and 0.172 ± 0.038 g DW yr^{-1}, Table 2, Fig 4C).

Focusing on depth, only the averages of leaf production in secondary branches (8.6 ± 0.1 at 10 m vs. 8.1 ± 0.1 leaves yr^{-1} at 20 m, p = 0.05, Table 2) and tertiary branch balance (p = 0.05, 0.571 ± 0.045 at 10 m vs. 0.369 ± 0.035 branches yr^{-1} at 20 m) were significant between the depths sampled in this study. The multivariate response of plant descriptors showed significant differences among localities, differentiating Zembra Island from the other localities (p = 0.01, Table 3, Fig. 5, MDS).

Fig. 5. *Posidonia oceanica*. Non-metric multidimensional scaling (MDS) plot of vegetative variables for the locality factor

DISCUSSION

The studied seagrass meadows included types IV to II as proposed by Giraud (1977) in terms of shoot density, and matched the range of densities reported by Pergent-Martini et al. (1994) over a depth gradient. The population dynamics of *Posidonia oceanica* meadows during the last 5 yr on average were positive in every locality studied. This occurred independently of global features such as latitude, longitude, temperature, and depth, indicating a healthy situation in these marine protected areas with no signs of decline. Among the meadows analyzed, Zembra Island showed exceptional vegetative growth compared to the other localities. Our results contrast with those obtained by Marbà et al. (1996), who recorded a general decline of *P. oceanica* meadows along the Spanish Mediterranean coast.

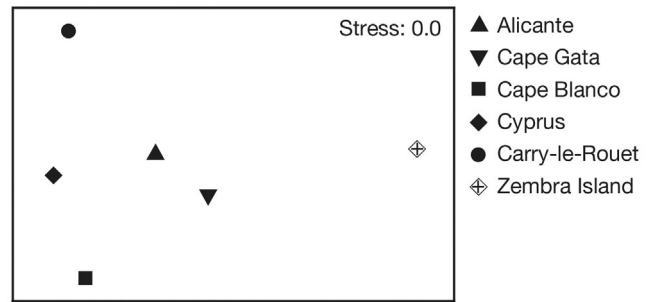*Posidonia oceanica* has been considered to be maladapted to the current oceanographic conditions and

to be an evolutionary constrained species, at least along the northernmost shores (Molinier & Picard 1952, Pérès 1984). This may be a consequence of displacement by continental drift to zones with minimum temperatures below the tolerance of this genus (12–13 to 25°C). Based on our results, the effect of temperature does not seem to determine negative vegetative growth due to a maladaptation. In this sense, results from the northernmost locality did not show statistically different vegetative growth with respect to other warmer localities (e.g. Cyprus, Alicante, and Cape Gata), although the locality had lower values for some parameters. Our results verify a high level of plasticity of *P. oceanica*, which has been discussed by other authors (Marbà et al. 1996) and was evident in different patterns of vegetative growth independent of the considered spatial scale (site, locality) and depth. Plasticity is expressed as variability in values of different parameters studied over different spatial scales (even among rhizomes), which has also been found in other

Table 3. *Posidonia oceanica*. Non-parametric permutational analysis of variance (PERMANOVA) on Euclidean distances for vegetatives variables of seagrass from 2 sites at each depth and 2 depths (10 m, 20 m) for each locality and 6 localities around the Mediterranean Sea. Comparisons: pair-wise *a posteriori* tests were performed between localities to determine significant differences. Definitions of abbreviations as in Table 1. **p < 0.01; *p < 0.05

Variables	Source of variation	df	MS	*F*
For plagiotropic rhizomes:	Locality	5	7559.88	8.203**
elongation, leaf and rhizome production,	Site (Locality)	6	921.65	2.111
and global balance	Depth	1	668.55	0.385
	Locality × Depth	5	1738.05	0.973
For orthotropic rhizomes:	Site (Locality) × Depth	6	1786.04	4.09**
elongation, leaf and rhizome production	Residual	216	436.69	

Comparisons	*t*	Comparisons	*t*	Comparisons	*t*
A vs. G	0.3936	G vs. B	1.2579	B vs. CR	2.2185
A vs. B	1.4878	G vs. C	1.2005	B vs. Z	4.2232*
A vs. C	1.5481	G vs. CR	1.2991	C vs. CR	2.2096
A vs. CR	1.6421	G vs. Z	4.9706*	C vs. Z	5.6408*
A vs. Z	8.9505*	B vs. C	0.3482	CR vs. Z	4.8190*

studies for very small spatial scales and between different environmental conditions (González-Correa et al. 2005). This high variability suggests the existence of processes that work on very local scales and can be derived from morphological responses to local variability in source availability (Pergent-Martini et al. 1995) or due to internal growth dynamics of shoots and rhizomes (Gobert et al. 2003).

Related to the changes due to depth, our results showed that *Posidonia oceanica* accommodates some structural features, diminishing tertiary branches and leaf number, in orthotropic branches in deeper meadows. We interpreted this to be a plastic response of the plants to avoid an 'umbrella effect' among shoots, providing better use of the lower intensity of light. This pattern of variation in some vegetative growth parameters along depth gradients has been reported previously (e.g. Pergent-Martini et al. 1994) and is considered one of the main factors conditioning the distribution and growth of *P. oceanica* meadows. The direction and extent of plastic response are prime components of the adaptability of individuals carrying the specific genotype, and as such are subject to strong selection. Unavoidable responses to extreme environmental conditions (e.g. lower elongation, number of leaves, and global balance of branches, and high numbers of aborted branches in northernmost localities) may seem non-adaptive, but over evolutionary time even these seemingly non-functional responses may have been selected as preferred alternatives to more a drastic outcomes such as death (Schlichting & Smith 2002). This plasticity is a clear adaptation to heterogeneous environmental conditions of *P. oceanica*, and it cannot be considered characteristic of a maladapted and evolutionary constrained species.

Our results suggest that the decline of *Posidonia oceanica* meadows reported by other authors is probably due to cumulative effects derived from different anthropogenic local processes. These events can have widespread effects throughout larger areas: e.g. damage caused by otter-trawling over 30 yr along 7 km of meadows from 13 to 24 m depths near a fishing harbor (Sánchez Lizaso et al. 1990). The massive regression (44%) of *P. oceanica* meadows close to the city of Marseille has been linked to outfall sewage for 12 yr (Pergent-Martini 1994); the waste material dumped for 17 yr from an asbestos quarry on the island of Corsica caused the decline of 230 ha of *P. oceanica* meadow (Pasqualini et al. 1999); 11.2 ha were lost and 9.8 ha were significantly degraded due to aquaculture activities during 10 yr (Ruíz et al. 2001); and the construction of 2 ports harboring 1404 small to medium boats have caused the destruction of at least 11 ha of *P. oceanica* meadows and the degradation of another 14 ha (Fernández Torquemada et al. 2005). Natural phenomena

can also play an important role at local scales. For example, major storms could affect these meadows at scales of tens of km^2, although this has still not been reported for *P. oceanica*. The importance of human activities in the decline of species is not a new issue and has been confirmed over the last 50 millennia (Burney & Flannery 2005). The interaction of all of these local events along the Mediterranean coastline may produce a misunderstanding about the regression of *P. oceanica* at a global scale.

The data obtained in this study from these marine protected areas demonstrate that no global decline of *Posidonia oceanica* meadows is occurring in the Mediterranean Sea. The implications derived from the fact that the causes of decline were global or local have great importance for policies of restoration and conservation of this species and the associated assemblages. A global degradation caused by global processes could not be stopped by management of coastal areas, and, even if it were possible, the time needed to solve the problem would exceed human time scales. We argue that the widespread reported decline of *P. oceanica* meadows in the Mediterranean is really due to an accumulation of local events, and we suggest that it is possible to act upon these local causes that produce local regressions. This fact is supported by 2 reported recoveries of *P. oceanica* meadows after stopping the causes of damage: the elimination of otter-bottom trawling by means of anti-trawling reefs (González-Correa et al. 2005) and the establishment of a waste-water-treatment plant (Pergent-Martini et al. 2002). The anti-trawling reefs have enabled a positive branch balance (0.96 ± 0.06 branches yr^{-1} from primary plagio-tropic rhizomes) in the disturbed *P. oceanica* meadows 8 yr after protection, and 0.18 ha over a 12 yr period were recovered after opening the wastewater-treatment plant. These studies estimated that although the effects of recovery can be detected within several years after the cessation of the impact, complete natural restoration will be achieved over 100 yr.

On the other hand, recent findings about the export of seeds and the success of seedling settlement (Balestri & Cinelli 2003, Y. Fernández Torquemada & J. M. González-Correa unpubl. data) suggest an important value of pristine areas in the restoration of disturbed *Posidonia oceanica* meadows that export seeds and fragmented rhizomes. Consequently, if there is no natural global regression of *P. oceanica* meadows in the Mediterranean Sea, the management of coastal areas should reduce the environmental impacts and preserve the *P. oceanica* meadows areas around the Mediterranean Sea. However, it will be necessary to monitor changes in vegetative growth parameters in the Mediterranean Sea to assess the possible consequences of global processes such as global warming.

LITERATURE CITED

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26:32–46

Balestri E, Cinelli F (2003) Sexual reproductive success in *Posidonia oceanica.* Aquat Bot 75(1):21–32

Burney DA, Flannery TF (2005) Fifty millennia of catastrophic extinctions after human contact. Trends Ecol Evol 20(7):395–401

Cambridge ML, Chiffings AW, Brittan C, Moore L, McComb AJ (1986) The loss of seagrass in Cockburn Sound, Western Australia: II. Causes of decline. Aquat Bot 24:269–285

Duarte CM (1991) Allometric scaling of seagrass form and productivity. Mar Ecol Prog Ser 77:289–300

Duarte CM (2002) The future of seagrass meadows. Environ Conserv 29(2):192–206

Fernández Torquemada Y, González-Correa JM, Mártinez JE, Sánchez Lizaso JL (2005) Evaluation of the effects produced by the construction and expansion of marinas on *Posidonia oceanica* (L.) Delile meadows. J Coast Res 49:94–99.

Giraud G (1977) Essai de classement des herbiers de *Posidonia oceanica* (Linne) Delile. Bot Mar 20(8):487–491

Gobert S, Kyramarios M, Lepoint G, Pergent-Martini C, Bouquegneau JM (2003) Variations at different spatial scales of *Posidonia oceanica* (L.) Delile beds; effects on the physico-chemical parameters of the sediment. Oceanol Acta 26:199–207

González-Correa JM, Bayle JT, Sánchez-Lizaso JL, Valle C, Sánchez-Jerez P, Ruiz JM (2005) Recovery of deep *Posidonia oceanica* meadows degraded by trawling. J Exp Mar Biol Ecol 320(1):65–76

Glémarec M (1979) Les fluctuations temporelles des peuplements benthiques liées aux fluctuations climatiques. Oceanol Acta 2:365–371

Guidetti P, Fabiano M (2000) The use of lepidochronology to assess the impact of terrigenous discharges on the primary leaf production of the Mediterranean seagrass *Posidonia oceanica*. Mar Pollut Bull 40(5):449–453

Hemminga M, Duarte CM (2000) Seagrass ecology. Cambridge University Press, Cambridge

Larkum AWD, West RJ (1983) Stability, depletion and restoration of seagrass beds. Proc Linn Soc N S W 106:201–212

Larkum AWD, den Hartog C (1989) Evolution and biogeography of seagrasses. In: Larkum AWD, McComb AJ, Shepherd SA (eds) Biology of seagrasses. Elsevier, Amsterdam, p 112–156

Marbà N, Duarte CM, Cebrián J, Gallegos ME, Olesen B, Sand-Jensen K (1996) Growth and population dynamics of *Posidonia oceanica* on the Spanish Mediterranean coast: elucidating seagrass decline. Mar Ecol Prog Ser 137:203–213

Meinesz A (1982) Aménagements touristiques et protection de la zone marine littorale. Vie Nature Environnement 30:8–12

Molenaar H, Barthélémy D, Reffye P, Meinesz A, Mialet I (2000) Modelling and growth patterns of *Posidonia oceanica*. Aquat Bot 66:85–99

Molinier R, Picard J (1952) Recherches sur les herbiers de Phanérogames marines du littoral méditerranéen français. Ann Inst Océanogr 27:157–234

Pasqualini V, Pergent-Martini C, Pergent G (1999) Environmental impact identification along the Corsican coast (Mediterranean Sea) using image processing. Aquat Bot 65:311–320

Pérès J (1984) La regresion des herbiers à *Posidonia oceanica*. In: Boudouresque CF, Jeudy de Grissac A, Olivier J (eds) International workshop on *Posidonia oceanica* beds, Vol 1. GIS Posidonie, Marseille, p 445–454

Pergent G (1987) Recherches lépidocronologiques chez *Posidonia oceanica* (Potamogetonaceae). Fluctuations des paramètres anatomiques et morphologiques des écailles des rhizomes. PhD dissertation, University Aix-Marseille II

Pergent G (1990) Lepidochronological analysis in the seagrass *Posidonia oceanica*: a standardized approach. Aquat Bot 37:39–54

Pergent-Martini C (1994) Impact d'un rejet d'eaux useés urbaines sur l'herbier à *Posidonia oceanica*, avant et après la mise en service d'une station depuration. PhD dissertation, University of Corsica

Pergent-Martini C, Rico-Raimondino V, Pergent G (1994) Primary production of *Posidonia oceanica* in the Mediterranean Basin. Mar Biol 120:9–15

Pergent-Martini C, Rico-Raimondino V, Pergent G (1995) Nutrient impact on *Posidonia oceanica* seagrass meadows: preliminary data. Mar Life 5:3–9

Pergent-Martini C, Pasqualini V, Pergent G, Ferrat L (2002) Effect of a newly set up wastewater-treatment plant on a marine phanerogam seagrass bed—a medium-term monitoring program. Bull Mar Sci 71(3):1227–1236

Picard J (1965) Recherches qualitatives sur les biocénoses marines des substrats meubles dragables de la région marseillaise. Rec Trav Stat Mar Endoume–Marseille 52:3–160

Poiner IR, Walker DI, Coles RG (1989) Regional studies—seagrasses of tropical Australia. In: Larkum AWD, McComb AJ, Shepherd SA (eds) Biology of seagrasses. Elsevier, Amsterdam, p 279–303

Rasmussen E (1977) The wasting disease of eelgrass (*Zostera marina*) and its effects on environmental factors and fauna. In: McRoy CP, Helfferich CA (eds) Seagrass ecosystems: a scientific perspective. Marcel Dekker, New York, p 1–51

Ruíz JM, Pérez M, Romero J (2001) Effects of fish farm loadings on seagrass (*Posidonia oceanica*) distribution, growth and photosynthesis. Mar Pollut Bull 42(9):749–760

Sánchez Lizaso JL, Guillén-Nieto JE, Ramos-Esplà AA (1990) The regression of *Posidonia oceanica* meadows in El Campello (Spain). Rapp Comm Int Mer Medit 32:7

Schlichting CD, Smith H (2002) Phenotypic plasticity: linking molecular mechanisms with evolutionary outcomes. Evol Ecol 16:189–211

Short FT, Wyllie-Echevarria S (1996) Natural and human induced disturbance of seagrasses. Environ Conserv 23:17–27

Short FT, Neckles HA (1999) The effect of global climate change on seagrasses. Aquat Bot 63:169–196

Tomlinson PB (1974) Vegetative morphology and meristem dependence—the foundation of productivity in seagrasses. Aquaculture 4:107–130

Underwood AJ (1997) Experiments in ecology. Their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge