

Recovery of deep *Posidonia oceanica* meadows degraded by trawling

José M. González-Correa^a, Just T. Bayle^{a,*}, José L. Sánchez-Lizaso^a, Carlos Valle^a,
Pablo Sánchez-Jerez^a, Juan M. Ruiz^b

^aDepartment of Marine Sciences and Applied Biology, University of Alicante, P.O. Box 99,0 E-03080-Alicante, Spain

^bInstituto Español de Oceanografía, Centro Oceanográfico de Murcia, Lo Pagán, 30740 San Pedro del Pinatar, Murcia, Spain

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Abstract

The recovery capacity of meadows of the Mediterranean seagrass *Posidonia oceanica* (L.) Delile in an area affected by illegal trawling were assessed after protection by anti-trawling reefs. The differences in vegetative growth between two impacted and two undisturbed localities were tested using growth, shoot balance, aborted branches, and leaf and rhizome production of both plagiotropic and orthotropic rhizomes. The organic matter in sediments, silt clay fraction and light intensity incident on the bottom were also measured in order to evaluate the physical conditions. Environmental and plant variables were measured in three sites placed inside each locality. The vegetative growth was positive in both impacted and control meadows but growth rates were lower in impacted than in control meadows. Average growth, production and shoot balance were greater in plagiotropic rhizomes from undisturbed localities (40.7 ± 1.75 vs. 28.4 ± 1.34 mm/year, 1133 ± 0.06 vs. 708 ± 0.04 mg DW/shoot/year, 1.36 ± 0.08 vs. 0.96 ± 0.06 shoots/year, respectively). Significantly greater values were also found in undisturbed localities for orthotropic rhizomes in terms of shoot balance and rhizome production (0.07 ± 0.01 vs. 0.01 ± 0.003 shoots/shoot/year and 155 vs. 124 mg DW/shoot/year, respectively). Of the physical parameters measured, only light intensity differed significantly between impacted and undisturbed localities. This parameter was 15.5% to 67.6% lower in impacted localities than in undisturbed localities, and this is the factor that causes the retardation of vegetative growth. The results show that recovery of *P. oceanica* meadows is possible after eliminating the cause of the impact. However, the very low rates of vegetative growth may prolong the time to total recuperation to almost 100 years. Therefore, effective management of *P. oceanica* meadows should aim to prevent meadow loss.

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1. Introduction

Declines in the cover of *Posidonia oceanica* (L.) Delile meadows have been recorded in many parts of

* Corresponding author. Tel.: +34 965903400x2977; fax: +34 965903464.

E-mail address: bayle@ua.es (J.T. Bayle).

the Mediterranean Sea, and have been attributed to several natural and anthropogenic impacts (Pérès, 1984; Bourcier, 1989; Guidetti and Fabiano, 2000; Ruiz et al., 2001). Illegal otter trawling has been identified as one of the most important direct causes of large scale degradation of *P. oceanica* meadows, particularly deep meadows (between 15 and 30 m depth, Ardizzone and Migliulo, 1982; Ardizzone and Pelusi, 1983; Ardizzone et al., 2000). Repeated passes of trawl gear over the seabed causes the mechanical degradation of *P. oceanica* meadows by pulling up leaves and rhizomes. It reduces plant density and cover predominantly in deep seagrass meadows (i.e. between 15 and 30 m depth; Sánchez Lizaso et al., 1990). This degradation changes the structure and dynamics of the associated biological assemblages, and can modify sediment composition and structure and enhance nutrient fluxes (Sanchez Jerez and Ramos Esplá, 1996; Jimenez et al., 1997; Ramos-Esplá et al., 1997; Moser et al., 1998; Auster and Langton, 1999; Hall et al., 2000; Kaiser and Jennings, 2002; U.S. National Research Council, 2002). The sediment structure is also modified by the otter trawl boards, which resuspend and mix the layers of sediment into the column water (i.e. siltation; Jones, 1992).

Anti-trawling artificial reefs have been widely used to avoid illegal trawling along the Spanish Mediterranean coast (Guillén et al., 1994; Ramos et al., 2000) with the main objective of restoring *P. oceanica* meadows (Revenge et al., 2000). It is expected that *P. oceanica* plants that survived trawling could recover in these unvegetated areas by vegetative growth. Recolonization would occur mainly by horizontal rhizome growth that, even though considered a very slow process ($1\text{--}7\text{ cm year}^{-1}$; Caye, 1982; Marbà and Duarte, 1998), is the most effective method by which *P. oceanica* spreads because plant establishment by means of broken rhizomes and successful sexual reproduction are both considered infrequent (Meinesz and Lefèvre, 1984; Balestri and Cinelli, 2003).

The natural capacity of seagrass to recover may also be constrained by the effects of habitat alterations caused by trawling. Both the reduction of plant abundance and siltation can favour sediment resuspension by hydrodynamics, increasing turbidity and nutrient concentrations in the water column (Bulthuis et al., 1984; Gacia et al., 1999; Gacia and Duarte,

2001; Ruiz and Romero, 2003). This, in turn, reduces light availability for plant photosynthesis either directly (Ruiz and Romero, 2001) or indirectly, such as through the enhancement of epiphyte growth on leaves (Sand Jensen, 1977; Silverstein et al., 1986; Neverauskas, 1987; Cebrian et al., 1999), reducing plant growth or causing even further seagrass mortality. These effects persist for long periods, affecting the natural recovery rates of degraded meadows and the performance of applied management actions.

Despite their importance, the long term indirect effects of trawling impacts on the initial recovery of *P. oceanica* meadows have not been evaluated yet. The general aim of the present study was to evaluate the recovery capacity of degraded *P. oceanica* meadows protected by anti-trawling reefs for 8 years (Guillén et al., 1994), through comparisons between heavily impacted and relatively undisturbed localities. We hypothesized that the reduced cover and siltation on degraded meadows produces a press impact that reduces available light, which in turn influences the capacity of damaged *P. oceanica* meadows to recover.

2. Materials and methods

2.1. Study area and sampling design

The study was carried out between August 1999 and December 2000 on the *P. oceanica* meadows located offshore from El Campello and Villajoyosa (Alicante, SE Spain, SW Mediterranean Sea). The seabed in this area was partially modified by illegal otter trawling, with 40% of the *P. oceanica* seagrass beds between depths of 14 and 28 m (290 ha, over 7 km of shoreline) estimated to be damaged (Sánchez Lizaso et al., 1990). In 1992, it was protected from trawling through the installation of an anti-trawling artificial reef (Guillén et al., 1994).

The selection of sampling localities was based on previous studies (Sánchez Lizaso et al., 1990; Sanchez Jerez and Ramos Esplá, 1996; Sánchez Jerez et al., 1999; 2000) and preliminary surveys specifically conducted for this study. These studies demonstrated that areas impacted by trawling can be identified based on measurements of meadow spatial structure such as shoot density and meadow cover. Shoot density was measured by counting all living shoots in

three random 40×40 cm quadrats, and seagrass cover was estimated as the proportion of substrata occupied by living seagrass patches along a 25 m transect (Sánchez Lizaso, 1993). On average, the impacted areas within the protected area contained 52.08 shoots/m², about 15% meadow cover and a global density (sensu Romero, 1985) of 7.812 shoots/m² of bottom, which contrasts with neighbouring, undisturbed areas with considerably higher shoot density (146.5 shoots/m²), meadow cover (~85%) and global density (124.5 shoots/m² of bottom). In the impacted meadow, two localities (Baeza and El Carritxal) were chosen for comparison with two other localities (Piteras and El Charco), located in the neighbouring undisturbed meadows (Fig. 1). Localities within each meadow were separated by 2000 m and positioned at the same depth (20 m) to avoid the influence of this factor. Inside each location, we randomly chose three sampling sites separated by 100 s of m to prevent spatial pseudoreplication (Hurlbert, 1984).

2.2. Environmental parameters

For sediment characterization, a 10×20 cm core was taken at each sampling site and kept frozen in the

laboratory for further analysis. Each core was divided horizontally into three portions of about 5 cm in height. We used the upper 5 cm portions of each core to estimate the percentage of organic matter and percentage of silt and clay (<0.062 mm) following Buchanan (1984).

To assess light conditions at each location, light intensity (lm m⁻²) was measured in situ by means of ONSET StowAway LI logger photometers with an accuracy of ±0.01 lm m⁻². Photometers were attached to vertical steel bars pushed into the sediment and were located 1.5 m above the bottom, just above the seagrass canopy. Light measurements were continuously recorded at 15 min intervals for 10-day periods, which we considered short enough to prevent shading effects by fouling. Sampling was performed in autumn, winter, spring and summer. A daily average light intensity was estimated from data recorded between 11:00 AM and 1:00 PM and used to estimate an overall mean for each period.

2.3. Seagrass dynamics

In each sampling site, 10 principal plagiotropic rhizomes bearing a variable number of lateral

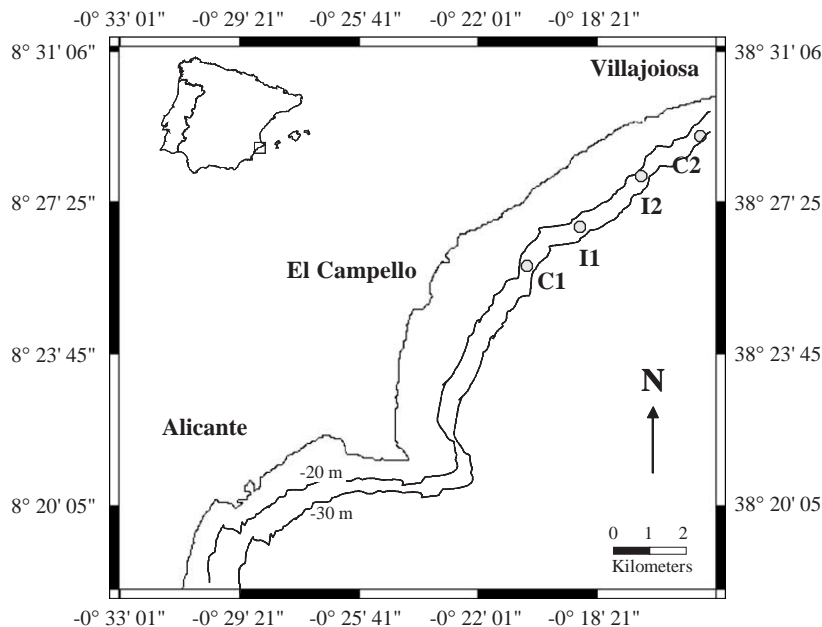


Fig. 1. Study area; localities of the *P. oceanica* meadows investigated in the Western Mediterranean Sea: Piteras (C1), Charco (C2) undisturbed localities and Baeza (I1), Carritxal (I2) impacted localities.

orthotropic shoots were taken by SCUBA diving. We chose only these plagiotropic runner rhizomes because *P. oceanica* exhibits a high degree of meristem dependency which is the reason why they are responsible for expanding meadows (Tomlinson, 1974).

We used the reconstruction technique of lepidochronology (Pergent, 1990), which has been widely used to study seagrass dynamics (Guidetti and Fabiano, 2000; Guidetti, 2001). It is based on the thickness of *P. oceanica* sheaths, which develop over an annual cycle and each cycle (i.e. the segment of rhizome contained between two minima of sheath thickness) corresponds to 1 year and the length of the rhizome segment comprised by each cycle (Pergent, 1987). These annual cycles are only clearly identifiable in vertical shoots and not in the basal, horizontal stem (Pergent, 1987). In order to date plagiotropic rhizomes we employed a novel indirect method: the difference in age of two consecutive vertical branches along the same horizontal rhizome corresponds to time (Fig. 2). However, the method is not sensitive for dating horizontal rhizomes younger

than 1 year; therefore, we selected only shoots older than 3 years in order to minimize such imprecision. Further, only principal plagiotropic rhizomes were used in order 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 made annual estimations of numerous seagrass variables possible. These included: growth (mm/year); rhizome production (g DW/year), estimated after drying rhizomes for 24 h at 80 °C (Romero et al., 1998); leaf production (leaves/year) estimated by counts of sheets; shoot balance (shoots/year), calculated as the difference between living and dead shoots per year; and aborted branches (aborted branches/year). We considered those rhizomes with symptoms of necrosis in the meristem of their leaves as dead (multiple fine, dark sheets and the rhizome is not sectioned) and we considered those branches that were not developed, with only a few fine sheets, as aborted.

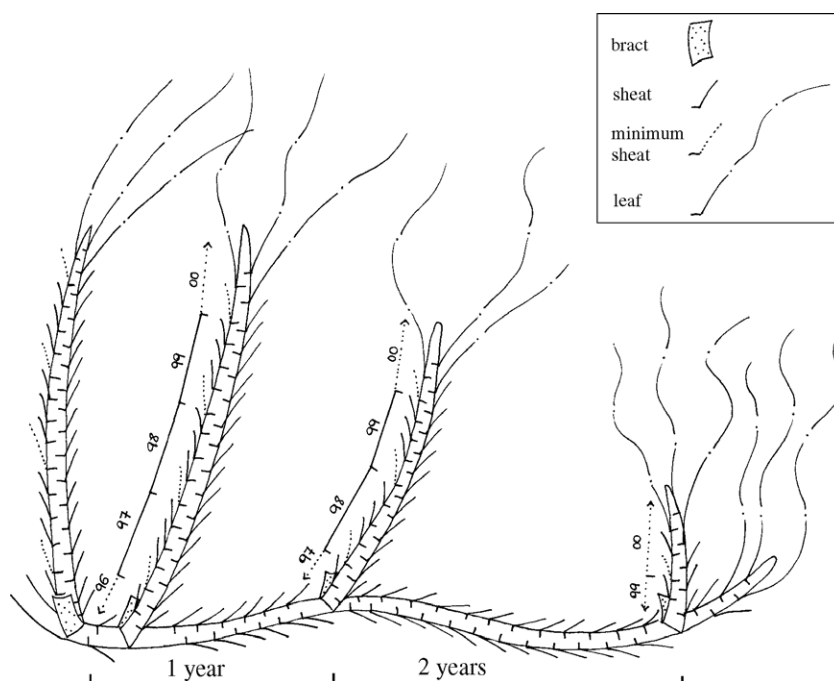


Fig. 2. Representation of the indirect method used to date plagiotropic rhizomes.

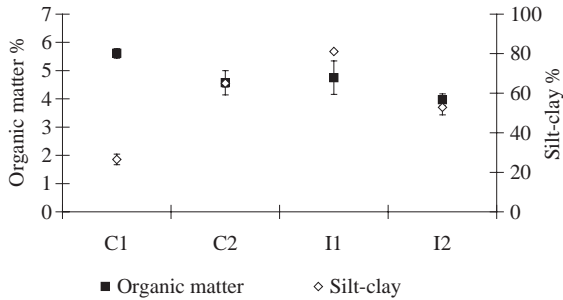


Fig. 3. Proportion of organic matter and silt-clay in undisturbed and impacted meadows. Data are means (\pm S.E.), $n=3$.

2.4. Data analysis

A mixed analysis of variance design (ANOVA; Underwood, 1981) was employed in testing parameters from seagrass structure and rhizome growth for the three main factors considered: trawling impact (hereafter referred to as impact), location and site. The linear model for this analysis was:

$$X_{ijkn} = \mu + I_i + L(I)_{j(i)} + S(L(I))_{k(j(i))} + \text{Residual}_{n(k(j(i)))},$$

where X_{ijkn} is each dependent variable, μ is the overall mean, I_i is the impact factor, $L(I)_{j(i)}$ is the effect of the j th locality in each level of the impact factor that estimates variability at the medium spatial scale, and $S(L(I))_{k(j(i))}$ is the effect of k th sites in each level of the locality factor, estimating spatial variability at the small spatial scale. $\text{Residual}_{n(k(j(i)))}$ is the error term that estimates variability among samples. I_i was a fixed factor, and $L(I)_{j(i)}$ and $S(L(I))_{k(j(i))}$ were random factors. Parameters from sediment analysis were tested with a similar design but with the smallest spatial factor removed. Data on light intensity level was analysed with a mixed model including an orthogonal factor related to seasonal variability and without the smallest spatial factor. For this, the linear model was:

$$X_{ijkn} = \mu + I_i + L(I)_{j(i)} + T_k + I_i \times T_k + L(I)_{j(i)} \times T_k + \text{Residual}_{n(kji)},$$

where T_k was the effect of k th seasons.

Before analysis, Cochran's test (Cochran, 1947) was used to test for homogeneity of variance for all

variables. Where significant differences were found, the data were $\ln(x)$ or $\ln(x+1)$ transformed. When transformations did not remove heterogeneity, analyses were performed on the untransformed data by setting the F -test alpha at 0.01, since analysis of variance is quite robust to departures from their assumptions, especially when the design is balanced and contains a large number of samples or treatments (Underwood, 1997). Moreover, when possible, pooling was done with those non-significant nested factors, testing them previously at $p \geq 0.25$. This procedure increases test power and improves the results of analysis (Underwood, 1991). The proportion of variation explained by each factor was calculated following Burdick and Graybill (1992) in order to determine their relative importance.

3. Results

3.1. Environmental parameters

The average silt-clay fraction value was lower in undisturbed meadows ($45.79 \pm 8.73\%$ vs. $66.99 \pm 6.54\%$; Fig. 3), although significant differences were not found for the Impact factor (Table 1). Organic matter fractions did not show significant differences among undisturbed and impacted meadows ($5 \pm 0.20\%$ vs. $4.36 \pm 0.17\%$, Fig. 3). We only found significant differences for these parameters between localities (Table 1).

Light intensity was significantly lower in the impacted meadows and this pattern was consistent across all seasons (Fig. 4, Table 2). Light values were 15.5% to 67.6% lower in impacted localities, showing the greatest difference during winter. Light intensity showed different patterns between localities among

Table 1

Summary of the results of analysis of variance (ANOVA) comparing variations in silt-clay (%) and organic matter (%) at localities between impacted and undisturbed meadows

Source of variation	df	F-versus	Silt-clay (%)		Organic matter (%)	
			MS	F	MS	F
I	1	L(I)	1432.27	0.80 ^{n.s.}	3.83	0.83 ^{n.s.}
L(I)	2	Residual	1785.65	99.32**	4.59	12.35**
Residual	8		17.98		0.37	

** $p < 0.01$; n.s.: not significant.

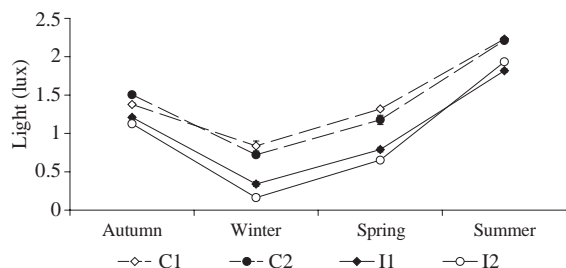


Fig. 4. Light level (lx) estimated in undisturbed and impacted meadows in each season for a year. Data are means (\pm S.E.), $n=80$.

the different seasons, resulting in a significant interaction term for these factors.

3.2. Seagrass structure

Average growth for plagiotropic rhizomes was 40.7 ± 1.75 mm/year in undisturbed localities, and 28.4 ± 1.34 mm/year in impacted meadows (Fig. 5(1)). Rhizome production was 1133 ± 0.06 mg DW/sh/year in undisturbed, and only 708 ± 0.04 mg DW/sh/year in impacted meadows (Fig. 5(2)). In both, leaf production was around 11 leaves/year (Fig. 5(3)). Shoot balance was higher at undisturbed than at impacted meadows (1.36 ± 0.08 vs. 0.96 ± 0.06 shoots/year; Fig. 5(4)). Moreover, aborted shoots were more abundant at undisturbed meadows (0.12 ± 0.04 vs. 0.07 ± 0.01 ; Fig. 5(5)). Extrapolated to global density, new branches resulting from these balance rate values would be 19–27 shoots/year m^2 in undisturbed and 1–1.2 shoots/year m^2 in impacted localities (including both plagiotropic and orthotropic rhizomes). Differences were significant for growth rate, rhizome production, shoot balance and aborted shoots (most

Table 2

Summary of the results of analysis of variance (ANOVA) comparing variations in level light (lx) between impacted and undisturbed meadows for a year

Source of variation	df	F-versus	MS	F
I	1	$L(I)$	55.96	108.64**
$L(I)$	2	–	0.515	–
T	3	$T \times L(I)$	132.72	208.32**
$T \times I$	3	$T \times L(I)$	1.34	2.10 ^{n.s.}
$T \times L(I)$	6	Residual	0.64	7.56**
Residual	1264		0.08	

** $p < 0.01$; n.s.: not significant.

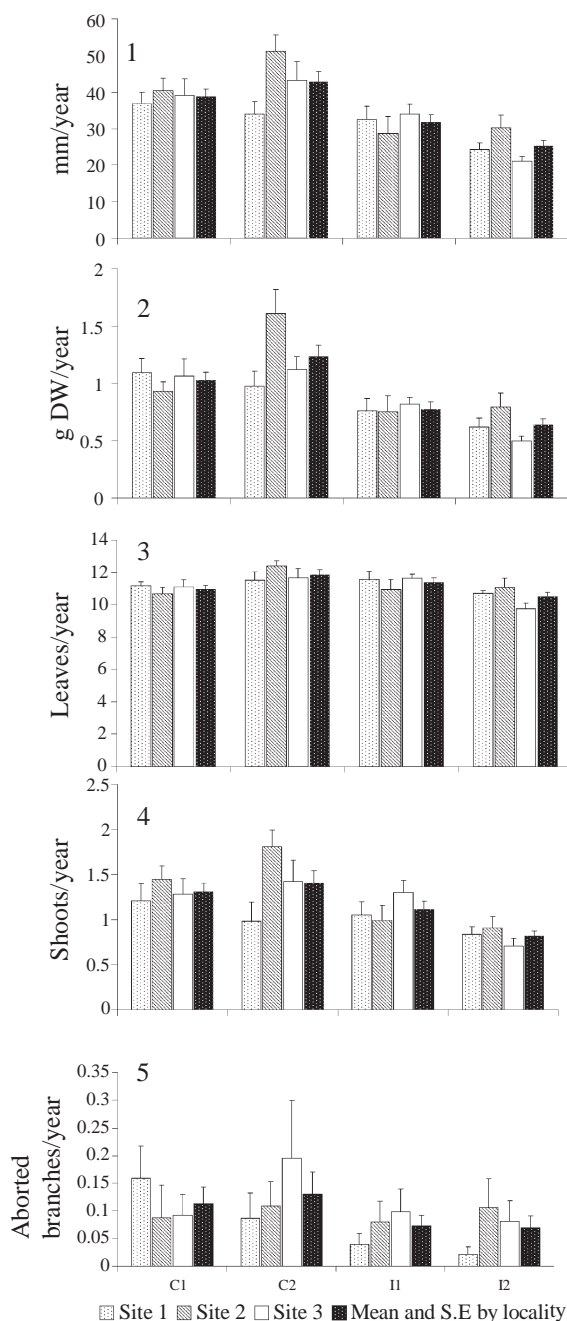


Fig. 5. (1) Growth, (2) rhizome production, (3) leaf production, (4) shoot balance and (5) aborted branches in plagiotropic rhizomes at sites and localities in impacted and undisturbed meadows. Data are means (\pm S.E.), $n=10$.

of them after pooling data) (Table 3). In contrast, the number of leaves produced per year did not differ between impacted and undisturbed meadows. At smaller spatial scales, significant differences were found for the number of leaves among localities, and for shoot balance and growth among sites.

For orthotropic rhizomes, average growth was 6.97 ± 0.27 mm/year at undisturbed localities, and 5.69 ± 0.16 mm/year at impacted meadows (Fig. 6(1)). Rhizome production was 155 ± 0.01 mg DW/shoot/year at undisturbed and 94 ± 0.004 mg DW/shoot/year at impacted meadows (Fig. 6(2)). Leaf production was around 8 leaves/year (Fig. 6(3)). The shoot balance rate was seven-fold greater at undisturbed than at impacted meadows (0.07 and 0.01 shoots/shoot/year, respectively; Fig. 6(4)). Aborted shoots were also more common at undisturbed meadows (average: 0.016 ± 0.006 vs. 0.009 ± 0.004 ; Fig. 6(5)). Significant differences between undisturbed and impacted meadows were found for both production and shoot balance (Table 4). At smaller spatial scales, significant differences were found for growth and numbers of aborted shoots at the locality level and for growth, rhizome

production, shoot balance and number of leaves at the site level.

4. Discussion

Impacted *P. oceanica* meadows protected by anti-trawling reefs showed a positive shoot balance after a period of 8 years of protection, which demonstrates that meadows have the capacity to recover. However, heavily impacted meadows have a very slow recovery rate when compared to undisturbed meadows in terms of rhizome growth, rhizome production and shoot balance. Differences increased drastically when these results were extrapolated to the global density of *P. oceanica* on the seafloor.

Differences in light intensity between undisturbed and impacted meadows were considerable and consistent among all seasons, despite otter trawling being halted 8 years ago. The main cause of these differences was the resuspension of silt–clay observed in the impacted meadows, rather than differences in the characteristics of the sediments. *P. oceanica* signifi-

Table 3

Summary of the results of analysis of variance (ANOVA) comparing variations in growth, rhizome production, shoots balance, aborted branches and leaf production of plagiotropic rhizomes at sites and localities between impacted and undisturbed meadows

	Source of variation	df	F-versus	MS	F	% of total variation
Growth (mm year ⁻¹)	I	1	L(I)	4531.5	15.0**	31.05
	L(I)	2	S(L(I))	446.90	1.68 ^{n.s.}	2.75
	S(L(i))	8	Residual	266.01	2.02*	6.12
	Residual	108		131.74		60.08
Rhizome production (g DW year ⁻¹)	I	1	L(I)	5.40	14.62**	32.20
	L(I)	2	S(L(I))	0.47	1.33 ^{n.s.}	1.53
	S(L(i))	8	Residual	0.35	2.37 ^{n.s.}	7.98
	Residual	108		0.15		58.29
Shoot balance (shoots year ⁻¹)	I	1	L(I)	4.65	7.88**	17.84
	L(I)	2	S(L(I))	0.72	1.3 ^{n.s.}	1.52
	S(L(i))	8	Residual	0.56	2.09*	7.90
	Residual	108		0.27		72.74
Aborted branches (aborted branches year ⁻¹)	I	1	L(I)	0.08	32.85*	4.59
	L(I)	2	S(L(I))	0.00	0.12 ^{n.s.}	0.00
	S(L(i))	8	Residual	0.02	0.74 ^{n.s.}	0.00
	Residual	108		0.03		95.41
Leaf production (leaves year ⁻¹)	I	1	L(I)	6.68	0.58 ^{n.s.}	0.00
	L(I)	2	S(L(I))	11.54	5.02*	13.63
	S(L(i))	8	Residual	2.30	1.20 ^{n.s.}	1.70
	Residual	108		1.91		84.67

Variance was partitioned (as % of total variation) into the different factors. F-values in bold were calculated with pooling of L(I)+S(L(I)).

* $p < 0.05$; ** $p < 0.01$; n.s.: not significant.

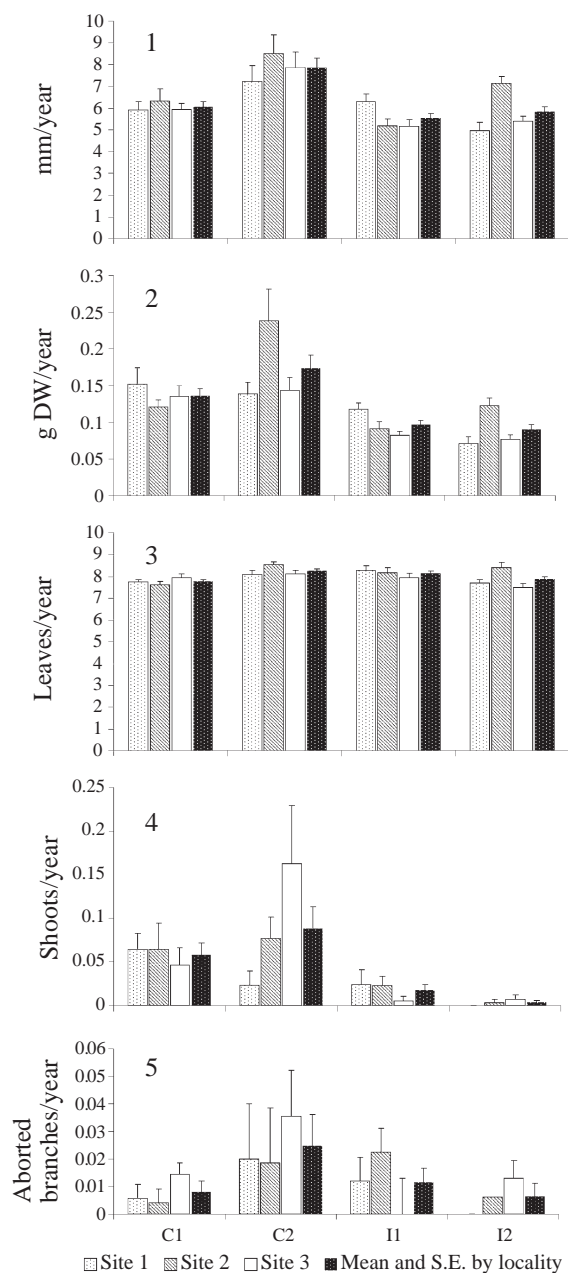


Fig 6. (1) Growth, (2) rhizome production, (3) leaf production, (4) shoot balance and (5) aborted branches in orthotropic rhizomes at sites and localities in impacted and undisturbed meadows. Data are means (\pm S.E.), $n=10$.

cantly buffers sediment resuspension and increases sediment retention (Gacia et al., 1999; Heiss et al., 2000; Terrados and Duarte, 2000), and this capacity is

directly related to the density and cover of meadows. Otter trawling has greatly altered the structure of *P. oceanica* meadows along the Campello-Villajoyosa shore. In the impacted localities, the abrasive trawling gear has eliminated approximately 60% of the cover of seagrass from the seafloor and reduced the shoot density in the mattes that survived by more than 40%. These effects are the consequence of the highly destructive trawling gear that can remove between 100 000 and 360 000 shoots/h (Martín et al., 1997). Thus, the low cover favours the resuspension of fine sediments in the impacted meadow and decreases the available levels of light for the plants. Light intensity is one of the most important physical factors that restricts the distribution of *P. oceanica* meadows and affects their vigour (Romero et al., 1998). Reduction in light intensity negatively affects photosynthetic activity and the total carbon budget, thereby reducing growth, production, the number of leaves and the survival of shoots (Ruiz and Romero, 2001).

The impact of otter trawling gives rise to a “press” impact (i.e., sustained alterations in the time after an impact; Underwood, 1991) upon the environment that results in a press response of *P. oceanica* meadows in terms of vegetative growth (Guidetti, 2001; Ruiz and Romero, 2003). Nevertheless, the positive shoot balance suggests that the press response will diminish slowly with time.

The lower levels of light available to the impacted meadows explains most of the difference in vegetative growth between impacted and undisturbed meadows. However, significant differences in growth also occurred at smaller spatial scales for some parameters, reflecting the influence of other biological environmental factors (Livingston, 1987). The highest percentage of variance was explained by differences among rhizomes followed by the factor for trawling impact. Sites and localities showed very low values of percentage of variance. These results agree with those obtained by Alcoverro et al. (1995), in the sense that the vegetative growth of deep *P. oceanica* meadows is controlled at large spatial scales by light availability and local conditions (the scale of localities and sites in this study) play a lesser role in deep environments.

High variability in vegetative growth among rhizomes has been documented previously (Alcoverro et al., 1995; Molenaar et al., 2000) and suggests the existence of processes that work at very local scales

Table 4

Summary of the results of analysis of variance (ANOVA) comparing variations in growth, rhizome production, leaves production, shoots balance, aborted branches and of orthotropic rhizomes at sites and localities between impacted and undisturbed meadows

	Sources of variation	df	F-versus	MS	F	% of total variation
Growth (mm year ⁻¹)	<i>I</i>	1	<i>L(I)</i>	47.11	1.79 ^{n.s.}	9.18
	<i>L(I)</i>	2	<i>S(L(I))</i>	26.39	4.7*	18.38
	<i>S(L(i))</i>	8	Residual	5.63	2.34*	8.57
	Residual	108		2.40		63.87
Rhizome production (g DW year ⁻¹)	<i>I</i>	1	<i>L(I)</i>	0.12	10.65**	32.20
	<i>L(I)</i>	2	<i>S(L(I))</i>	0.01	0.89 ^{n.s.}	1.52
	<i>S(L(i))</i>	8	Residual	0.01	3.70 ^{n.s.}	7.98
	Residual	108		0.01		58.29
Shoot balance (shoots year ⁻¹)	<i>I</i>	1	<i>L(I)</i>	0.12	9.75*	21.33
	<i>L(I)</i>	2	<i>S(L(I))</i>	0.01	0.62 ^{n.s.}	0
	<i>S(L(i))</i>	8	Residual	0.01	2.08*	8.22
	Residual	108		0.01		70.45
Aborted branches (aborted branches year ⁻¹)	<i>I</i>	1	<i>L(I)</i>	0.01	0.34 ^{n.s.}	0
	<i>L(I)</i>	2	<i>S(L(I))</i>	0.01	4.76*	6.25
	<i>S(L(i))</i>	8	Residual	0.01	0.45 ^{n.s.}	0
	Residual	108		0.01		93.75
Leaf production (leaves year ⁻¹)	<i>I</i>	1	<i>L(I)</i>	0.01	0.01 ^{n.s.}	0
	<i>L(I)</i>	2	<i>S(L(I))</i>	2.17	2.41 ^{n.s.}	9.94
	<i>S(L(i))</i>	8	Residual	0.90	2.76*	13.53
	Residual	108		0.33		76.54

Variance was partitioned (as % of total variation) into the different factors. *F*-values in bold were calculated with pooling of *L(I)*+*S(L(I))*.

p*<0.05; *p*<0.01; n.s.: not significant.

(distance of metres among rhizomes). These differences among rhizomes may be derived from morphological responses to local variability in resource availability. Fourqurean et al. (1992) and Pergent-Martini et al. (1995) found a relationship between the nutrients contained in sediments and foliage parameters; however Gobert et al. (2003) explained this local variability as due only to the internal growth dynamics of shoots and rhizomes.

This study has demonstrated that protection of a disturbed *P. oceanica* meadow is effective in order to achieve recovery. The vegetative growth in this species is characterized by two important features. It is the main mechanism for colonization (Tomlinson, 1974; Marbà and Duarte, 1998), since the frequency of establishment of broken rhizomes is very low (3/ha/year; Meinesz and Lefèvre, 1984) and successful sexual reproduction is infrequent, although not impossible (at Tabarca Island (SW-Spain), 0.295 ± 0.08 new plants took root per m² in spring 2004; unpublished data). Compared to all other seagrass species, *P. oceanica* has the lowest growth rate (Marbà and Duarte, 1998). Due to these two

features, the capacity of *P. oceanica* to colonize areas is highly sensitive to decreases in vegetative growth produced by illegal trawling. The estimated production of new shoots based on the plagiotropic and orthotropic rhizomes shoot balance and global density was 1.265 and 24.96 shoots/m² of bottom at impacted and undisturbed meadows, respectively. This translates to an approximately 20-fold greater colonization capacity at control meadows than disturbed meadows. Such low production rates of new shoots at impacted localities imply that a long period of time is necessary for recovery. If recovery time=(global density at undisturbed localities–global density at impacted localities)/ production of new shoots at impacted localities year⁻¹ m⁻² of seafloor, we estimate a recovery time of 91.9 years (124.1–7.812)/1.265). It will take around 100 years for impacted meadows to reach the same average global density recorded in the control meadows in this study.

While this estimation is linear, we expect that recovery could become exponential as shoot density and cover increase, as demonstrated for *Cymodocea*

nodosa (Vidondo et al., 1997). A feedback process may be involved in *P. oceanica* recovery, with the resuspension of sediments decreasing as plant cover increases. Such a process would increase recovery speed, and a threshold level of plant cover may exist whereby turbidity decreases markedly and triggers higher vegetative growth rates. Whether such a threshold level exists would be an interesting goal for future studies.

The process and rate of recovery could also differ depending on the level of meadow alteration before protection and the nature of the impact. In this sense, the greater the shoot density and cover in the perturbed meadows, the greater will be the potential meadow spreading rates. The effects of the impact will differ depending on the duration of the direct (i.e. damage by trawling) and indirect causes (i.e. resuspension of silt–clay). In this study, the disturbed *P. oceanica* meadows were still suffering the effects of the indirect impact 8 years after the cessation of illegal trawling. This implies a slow vegetative growth resulting in an increased time for recovery.

In summary, we have demonstrated the capacity of a damaged *P. oceanica* meadow to recover. The spreading rate of plants is controlled mainly by light intensity occurring at larger spatial scales, but some processes operating at the scale of metres regulate the vegetative growth of rhizomes significantly. Due to this differential pattern, information about spatial scales of variation is, therefore, fundamentally important when postulating hypotheses from field observations (Ebherhart and Thomas, 1991) and for obtaining unconfounded results. We conclude that anti-trawling artificial reefs can be used effectively to stop the regression of meadows and enhance their recovery although at extremely slow rates.

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