LONG-TERM POPULATION DYNAMICS IN A HEALTHY
Posidonia oceanica MEADOW

GONZÁLEZ-CORREA, JOSÉ MIGUEL[1,2]*, SÁNCHEZ LIZASO, JOSÉ LUIS[1],
FERNÁNDEZ TORQUEMADA, YOLANDA[1] & FORCADA, AITOR[1]

(1) Department of Science of Sea and Applied Biology. Universidad de Alicante, carretera S. Vicente s/n. Alicante (03690).

(2) Corresponding autor. Centro de Investigaciones Marinas de Santa Pola (CIMAR). Torre d´Enmig s/n, Cabo de Sta Pola. Sta Pola, Alicante (03130). E-mail address: jogonzalezco@aemet.es

ABSTRACT

Wide losses of *Posidonia oceanica* led some authors to suggest this species showed evidence of decline in a global scale. Our aim was to survey the long-term evolution of a healthy and mature meadow of *Posidonia oceanica* at Tabarca Island (SE, Spanish coast). We surveyed cover and density at three depths (-4, -12 and -20m) and the dynamics at border meadows (erosion fronts vs adjacent edges) by one transect laid from -0,5m to -12m depth. Sexual reproduction as a repair mechanism was tested by monitoring the survival of seedling in five random sites. At each sampling site, sea-bottom roughness was estimated. Density and cover at sampling depths of -12 and -20 m were steady for 22 years (1988-2010), but both descriptors significantly decreased at upper limit (-4m) in 2010. Erosion fronts measured on transect went back -0.87 ± 0.75 m y^{-1}, though this fact was compensated by the progress of its adjacent edges in 0.6 ± 0.69 m y^{-1}. Density of survival seedlings has maintained a steady state for two years after settlement and it was strongly correlated with sea-bottom roughness. Our results suggest *P. oceanica* meadows of Tabarca Island could have remained stable long-term. But we detected "hot areas", such as those placed in upper limit or in erosion fronts, where likely a quick decline by natural causes (e.g. waves) was offset by natural repair mechanisms (e.g. settlement of seedlings and vegetative growth).

Key words: *Posidonia oceanica*, seagrasses, repair mechanisms, long-term dynamics, steady state.

RESUMEN

Amplias perdidas de praderas de *Posidonia oceanica* condujeron a algunos autores a sugerir que esta especie mostraba evidencias de un declive a escala global. Nuestro objetivo fue estudiar la evolución a largo plazo de una pradera madura y sana de *Posidonia oceanica* de la Isla de Tabarca (costa SE de España). Medimos la cobertura y densidad en tres profundidades (-4, -12 y -20 m) y la dinámica en el borde de la pradera (frentes de erosión frente a los bordes adyacentes) mediante un transepto establecido desde -0,5 a -12 m de profundidad. Se comprobó además, si la reproducción sexual funcionaba como un mecanismo de reparación de las praderas, mediante la monitorización de la supervivencia de plántulas en cinco sitios aleatorios. La rugosidad del fondo marino se estimó en cada sitio de muestreo. Las densidades y coberturas en las profundidades de -12 y -20 m fueron estables durante 22 años (1988-2010); aunque ambos descriptores disminuyeron significativamente en el limite superior (- 4 m), en 2010. Los frentes de erosión retrocedieron en el transepto fijo -0.87 ± 0.75 m a^{-1}, aunque este hecho fue compensado por el progreso de su borde adyacente con 0.6 ± 0.69 m a^{-1} de nueva pradera. La densidad de las plántulas supervivientes se mantuvo estable durante dos años después de su enraizamiento y se encontró fuertemente correlacionada con la rugosidad del fondo marino. Nuestros resultados sugieren que las praderas de *P. oceanica* de la isla de Tabarca permanecieron estable durante un largo periodo. Aunque, hemos detectado "áreas calientes", como aquellas situadas en el límite superior o en los frentes de erosión, donde probablemente un rápido declive causado por causas naturales (por ejemplo olas) fue seguido por mecanismos de reparación natural (por ejemplo asentamiento de plántulas y crecimiento vegetativo).

Palabras clave: *Posidonia oceanica*, fanerógamas marinas, mecanismos de reparación, dinámica a largo plazo, estado estable.
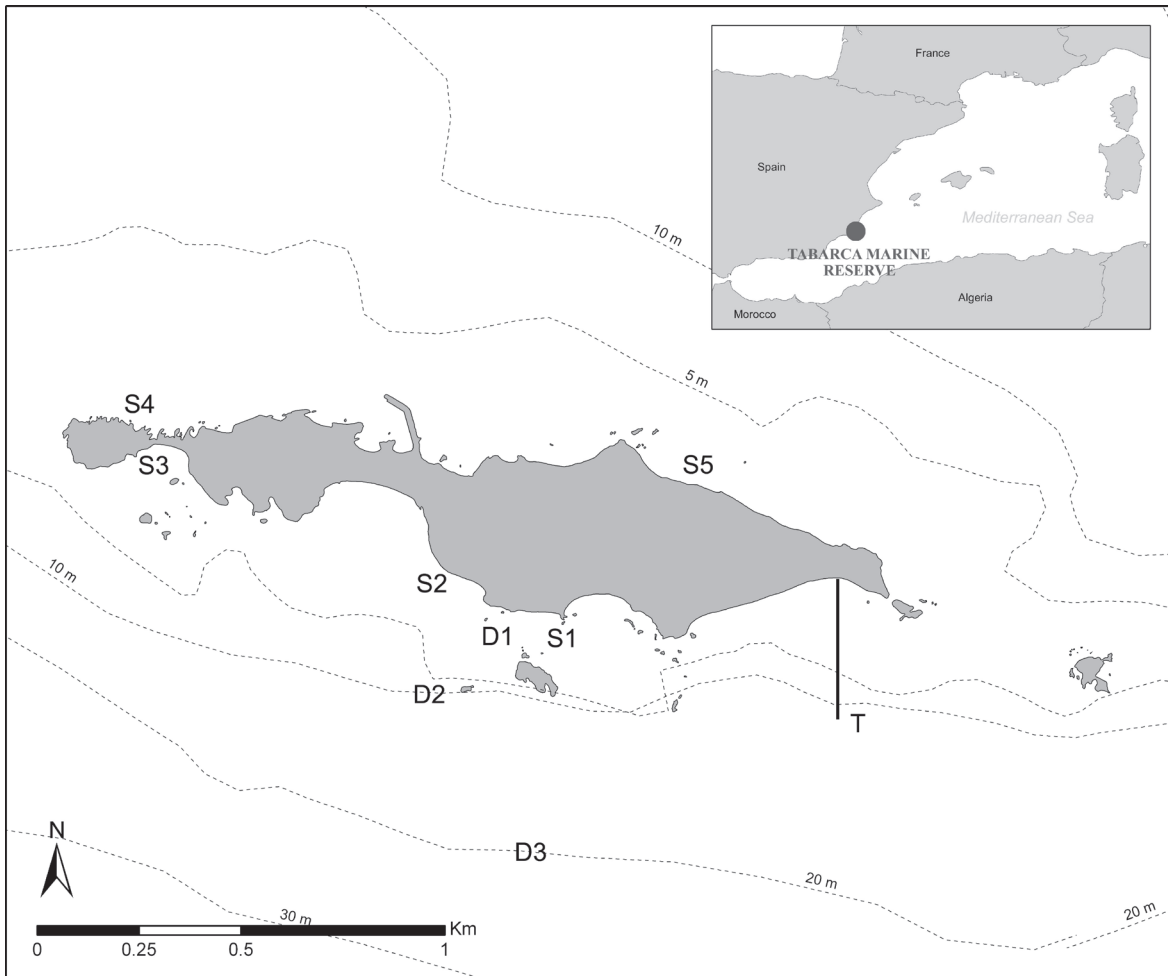
Figure 1:

Situation of Tabarca Island in Western Mediterranean. T depicts transect laid from surface to -12 m depth in order to assess dynamics of borders. D1, D2, D3 depict sampling sites at -4, -12 and -20 m respectively, where shoot dynamics of meadow was evaluated. S1, S2, S3, S4 and S5 are samplings sites in upper limit where the viability of seedling settlement was tested in order to check its role as repair mechanisms.

INTRODUCTION

One in five seagrass species is now listed as endangered, vulnerable, or near threatened, having a heightened risk of extinction under the IUCN Red List Criteria (Short *et al.* 2011). *Posidonia oceanica* is an endemic seagrass which spreads for 25000-50000 km² on sea bottom of Mediterranean Sea. It is responsible for very important ecological functions such as to support one of richest ecosystems on the earth, oxygenating surrounding water, trapping sediments or protecting littoral from energy of waves (Gacia *et al.* 1999, Gacia & Duarte 2001, Serrano *et al.* 2012). Their meadows do not reach the threshold to be considered at risk of extinction according to above-mentioned criteria; although it was estimated that they are decreasing by 5% per year (Short *et al.* 2011). Decreasing has been attributed to mechanical

damage from trawling (Martín *et al.* 1997, González-Correa *et al.* 2005) and anchoring (Francour *et al.* 1999, Milazzo *et al.* 2004), coastal development (Fernández-Torquemada *et al.* 2005, Leriche *et al.* 2006, González-Correa *et al.* 2008) and eutrophication (Pérès and Picard 1975, Díaz Almela *et al.* 2008(a), Holmer *et al.* 2008). Wide losses of this species led some authors to suggest that *P. oceanica* showed evidence of decline on a global scale (Pérès 1984, Marbà *et al.* 1996 a, Jordá *et al.* 2012). Conversely, González Correa *et al.* (2007 a) proposed that decline was restricted only to damaged areas by local or medium-scale impacts. It was based on shoot dynamics assessment in six pristine areas around the Mediterranean Sea, free of impacts, which showed good health.

An important handicap for the study of temporal trends in *P. oceanica* meadows is the slow vegetative
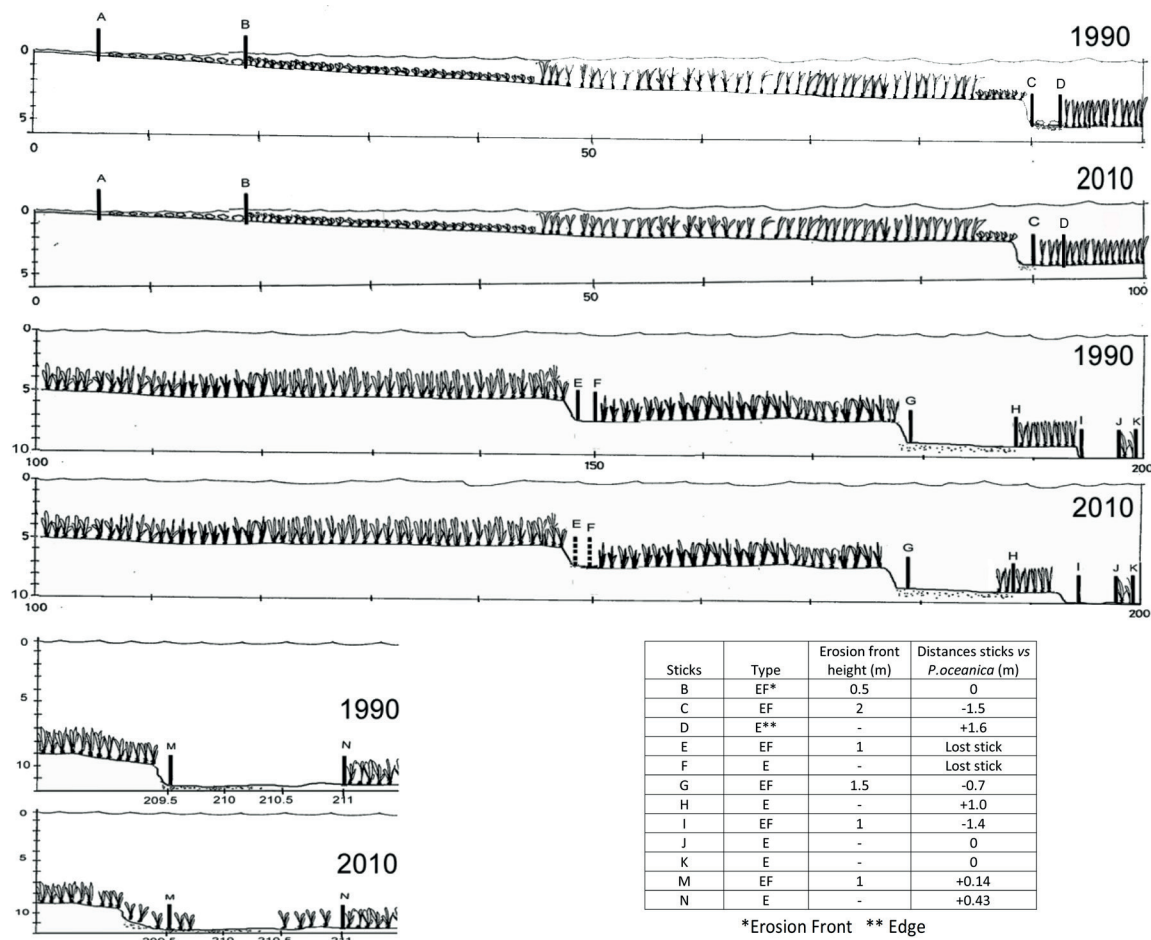
Sticks	Type	Erosion front height (m)	Distances sticks *vs* *P.oceanica* (m)
B	EF*	0.5	0
C	EF	2	-1.5
D	E**	-	+1.6
E	EF	1	Lost stick
F	E	-	Lost stick
G	EF	1.5	-0.7
H	E	-	+1.0
I	EF	1	-1.4
J	E	-	0
K	E	-	0
M	EF	1	+0.14
N	E	-	+0.43

*Erosion Front ** Edge

Figure 2:

Comparison of erosion fronts and edges locations between 1990 and 2010. Sticks are depicted by vertical bars labelled with capital letters.

Dotted vertical bars depict lost sticks.

growth. In fact, it is the slowest among seagrasses around the world, with averages of horizontal growth of 4.5±0.6 to 8.6±0.7 cm year^{-1} and averages of global recruitment rates for a primary plagiotropic rhizome between 2.1±0.4 to 4±0.7 shoots year^{-1} (González Correa *et al.* 2007a). Consequently, if *P. oceanica* meadows are free of strong impacts responsible for quick changes, sensitive changes due to light trends are detected only by long-term monitoring (c.a. > 20 years).

To solve this problem, indirect techniques based on age structure of vertical shoots (Duarte *et al.* 1994) have often been used (Marbà *et al.* 1996 a, Olesen *et al.* 2002, Brun *et al.* 2006), but its accuracy has been questioned versus direct techniques (Ebert *et al.* 2002, Ebert & Williams 2003, Fourqurean *et al.* 2003, González-Correa et al. 2007b). Unfortunately, direct

techniques have been scarcely used in population dynamics literature because a continuous sampling effort over many years is necessary. Hence, reliable studies about long-term trends in healthy *P. oceanica* meadows are very scarce (Peirano *et al.* 2011), as well as, for others template, (Bull *et al.* 2012, Lobelle et al. 2013) and tropical (Rasheed and Unsworth 2011) species.

On the other hand, studies about analysis of trends of *P. oceanica* meadows did not pay attention to the role of sexual reproduction, as it was considered that vegetative growth is the main mechanism responsible for maintaining *P. oceanica* meadows (Marbà & Duarte 1998). In fact, survival of seedling into mature *P. oceanica* meadows, with high shoot densities, is very unlikely (Domínguez *et al.* 2012). But, if seed settling
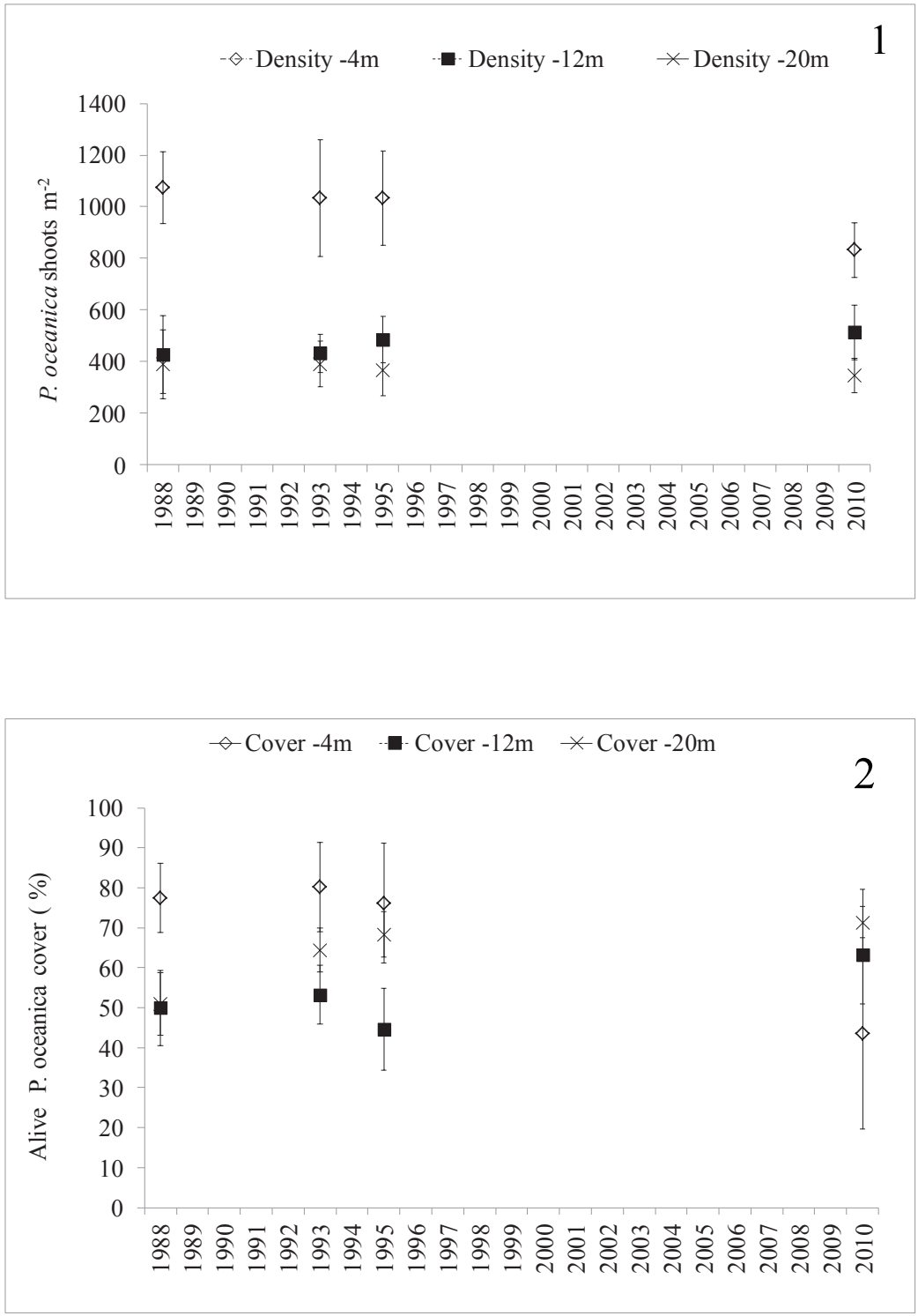
Figure 3:

Evolution of 1) shoots density and 2) live P. oceanica cover at -4m, -12m and -20 m during the study time (1988, 1993, 1995, 2010). Bars depict standard deviation (shoot densities n=15; cover n=4).
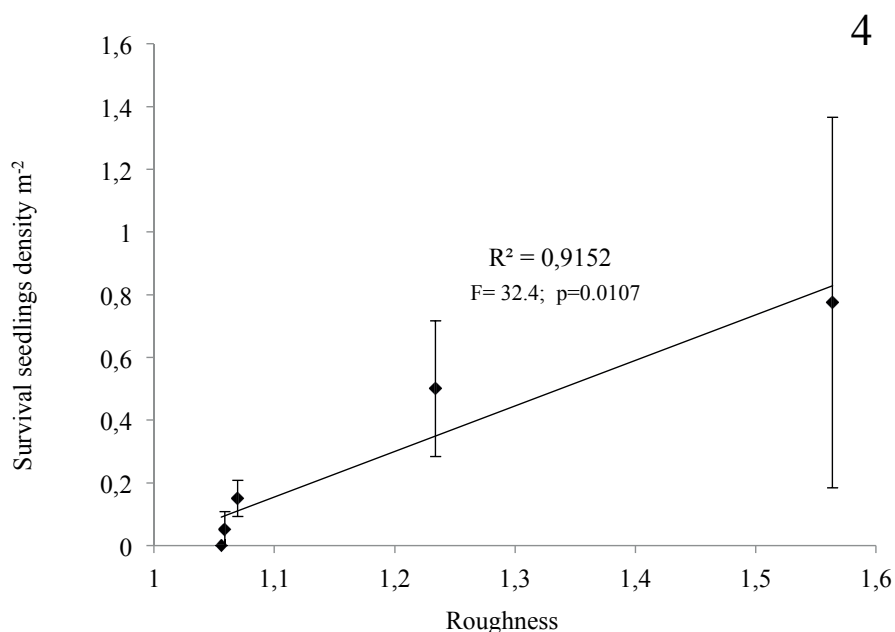
Figure 4:

Mean settled seedlings density at each site as a function of roughness. A linear regression is shown. Bars depict standard deviation (n=4).

is into small patches of *P. oceanica* (1 to 150 shoots; Díaz Almela *et al.* 2008b, Domínguez *et al.* 2012) or into depositional micro-environments (substrate depressions, algal turfs; Balestri & Lardicci 2008), then recruitment is successful.

Here, our aim was to survey the long-term evolution of a mature meadow free of anthropogenic impacts. We hypothesized that a protected and mature *P. oceanica* meadow would stay steady in a long-term scale, as opposed to general decreasing trend (5 % per year, Short *et al.* 2011). In addition, we proposed that stable state is based on repair mechanisms. Dynamics population of meadow was checked by direct techniques: i) dynamics in erosion front was tested following its evolution in relation with demarcation sticks for 20 years; ii) shoot population dynamics, in inner *P. oceanica* meadows, was surveyed by shoot densities and cover measurements for 22 years; iii) viability of settled seedlings at upper limit was assessed for two years in order to check its role as repair mechanisms. In addition, sea-bottom roughness was linked to final survival seedlings density.

MATERIAL AND METHODS

Study area and origin of historical data

The study was carried out on Nueva Tabarca Island (SW, Mediterranean Sea, Figure 1), where the *P. oceanica* meadow constitutes the predominant benthic assemblage.

It has not suffered sensitive impacts during study time because Tabarca Island became the first Marine Protected Area in the Spanish coast in 1986. Our research group was responsible for earlier protection actions and carried out initial surveys (Ramos 1985, Sánchez Lizaso 1993) thus, we had a series of unpublished historic data, which allowed us a long-term comparison of state of *P. oceanica* meadow.

Assessment of P. oceanica meadow evolution

Dynamics of borders was checked by a 210 meters length transect that spread from -0.5 m to -12 m depth (Figure 1). It descended on successive terraces, separated by jumps, or erosion fronts, which ranged from 2 m to 0.5 m (Figure 2). These erosion fronts were considered "hot areas" for meadow dynamics, so we marked them in 1990 by two 1.5 m length sticks, at each jump (-1.5, -3, -5, -12 m): one stick was hammered into the base of the erosion front and the other one into the edge of contiguous *P. oceanica* terrace (Figure 2). In 2010, distances between sticks and *P. oceanica* meadows were measured and they were considered positive (progressive) if the meadow exceeded the sticks and negative (regressive) if plants receded.

Shoot population dynamics at inner meadow was surveyed at micro-scale by shoot densities and at medium-scale by cover measurements in three depths: -4, -12 and -20 m (Figure 1). At each depth, shoot density and live *P.*

Table 1: *Results from the two-way ANOVA applied to assess the evolution of shoot density and cover of live P. oceanica meadow during sampling times (1988, 1995, 1993 and 2010) and three depths (-4, -12 and -12 m). Post hoc analysis SNK was used to identify homogeneous values in significant interaction Time x Depth.*

	Source	d.f.	M.S.	F	F-*versus*
Shoot density	Time	3	9.65	1.44[n.s]	Residual
	Depth	2	2537.67	379.04[***]	Residual
	Time × Depth	6	27.69	4.14[***]	Residual
	Residual	168	6.70		
	Total	179			
	SNK (Time × Depth)	Shoot densities at -4m depth in relation with time: (1993=1995=1988)>2010			
Cover of live P. oceanica	Time	3	121.38	0.92[n.s.]	Residual
	Depth	2	1143.07	8.63[n.s.]	Residual
	Time × Depth	6	818.12	6.17[***]	Residual
	Residual	36	132.52		
	Total	47			
	SNK (Time × Depth)	Cover of live P. oceanica at -4m depth in relation with time: (1993=1995=1988)>2010			

d.f.: degrees of freedom; M.S.: mean square; F: F ratio. Significance level: *** = p<0.001, n.s. = not significant.

oceanica cover was estimated by 15 random plots (40x40 cm) and four transects of 25 meters length respectively. It was conducted in 1988, 1993, 1995 and 2010.

Assessment of sexual reproduction as repairing mechanism

In spring 2004, there was a seed production peak at the Western Mediterranean Sea (Díaz Almela *et al.* 2006). This strong peak of seedlings was used to evaluate whether sexual reproduction had a repair role of gaps into upper limit of *P. oceanica* meadow. Surveys were performed in eight randomised sampling times for two years; at each time, five random sites around Tabarca Island (-4 m depth) were sampled (Figure 1) and at each site, survival seedling density was estimated by four random rectangles of 10x1 m. In addition, at each site, roughness of sea bottom was estimated by randomly laying, three times, a 10-meter chain on outline of sea bottom. Linear distance between the beginning and the end of chain (DBE) was measured. The ratio 10/DBE represented an estimation of sea-bottom roughness.

Statistical analysis

A two tailed paired t-test was used to check the evolution of both erosion fronts and its adjacent meadows. Each paired comparison was composed of the measurement taken in 2010 and zero, representing the initial position of *P. oceanica* meadow with respect to the sticks (in 1990).

To assess inner dynamics of meadows, two-way ANOVA was applied to test for significant differences in shoot density and cover of *P. oceanica* meadow. Two factors were comprised into the model: *Time* (four levels, fixed and orthogonal) and *Depth* (three levels, fixed and orthogonal).Two-way ANOVA was also applied to test for significant differences in settled seedlings density considering as factors: *Time* (eight levels, random and orthogonal) and *Site* (five levels, random and orthogonal). When the factors showed significant differences, the Student-Newman-Keuls test was used for posteriori pairwise comparisons. Before analysis, Cochran´s test was used to test homogeneity of variance for all variables.

Finally, linear regression was used to assess whether settled seedlings density was related with sea-bottom roughness. The significance of the linear regression model was tested by mean of ANOVA. The analyses of residuals confirmed the goodness-of-fit of the model. Finally, linear regression was used to assess whether settled seedlings density was related with sea-bottom roughness. The significance of the linear regression model was tested by mean of ANOVA. The analyses of residuals confirmed the goodness-of-fit of the model.

RESULTS

Border of *P. oceanica* meadows showed a equilibrium dynamics: erosion fronts move back an average of -0.87±0.75 m y^{-1}; but its adjacent edges move forward an average of 0.6±0.69 m y^{-1} (Figure 2). As a result, no significant differences were found in whole dynamics of *P.oceanica* meadow borders (t_9=0.140, p=0.892).

Density (Figure 3.1) and cover (Figure 3.2) of live

Table 2: *Results from the two-way ANOVA applied to test for significant differences among sampling times and sites in settled seedlings density in upper limit of P. oceanica meadow around Tabarca Island.*

	Source	d.f.	M.S.	F	F *versus*
Survival seedlings	Time	7	0.2594	$0.7^{n.s.}$	Time x Site
	Site	4	4.1057	11.12^{***}	Time x Site
	Time x Site	28	0.3692	2.61^{***}	Residual
	Residual	120	0.1414		
	Total	159			
			SNK´s test		
Sites			Times		
S1			J4 A4 N4 D4 F5 A5 J5 N6		
S2			J4 A4 N4 D4 F5 A5 J5 N6		
S3			J4 A4 N4 D4 F5 A5 J5 N6		
S4			A4 N4 J4 F5 J5 D4 N6 A5		
S5			D4 J4 N6 J5 A5 A4 N4 F5		

d.f.: degrees of freedom; M.S.: mean square; F: F ratio. Significance level: *** = p<0.001, n.s. = not significant.

Times codification: J4= June 2004, A4= August 2004, N4= November 2004, D4= December 2004, F5= February 2005, A5= April 2005, J5= June 2005, N6= November 2006.

P. oceanica did not change significantly for 22 years at medium and deep meadows (-12 and -20m), however, both descriptors showed a significant decrease at shallow meadows (-4m) in 2010 (Table 1).

Survival seedlings density did not show significant differences among sampling times, remaining steady for two years post the seedling peak event. Interaction of survival seedlings in time with sites was significant (Table 2). Additionally, the final survival seedlings density was strongly correlated with sea-bottom roughness (Figure 4).

DISCUSSION

The *P. oceanica* meadow, in middle and deep sampling areas, remained stable for 22 years; but it regressed at shallow sampling areas, where shoot density and live *P. oceanica* cover decreased in 2010. We think stability could be linked to the marine protection status and to intrinsic components of *P. oceanica*. This is a long-lived species, which has demonstrated how intrinsic factors, such as resource storage and its re-allocation among modules, can buffer external environmental forcing. Conversely, responses of small seagrasses amplify external environmental forcing (Marbà *et al.* 1996 b). This strong resilience, let settling healthy meadows when they are protected against direct anthropogenic impacts such as it was demonstrated in eight *P. oceanica*

meadows around Mediterranean Sea (Gonzalez-Correa *et al.* 2005).

We attribute regression to damages by strong storms events, because no known anthropogenic impacts had taken place in this Marine Protected Area during the study time (wastes, anchoring out of anchor areas, etc.) and, in addition, high quantities of *P. oceanica* debris was normally accumulated on coastline for whole study time (Mateo *et al.* 2003). Physical disturbances are one of the major mechanisms to generate favourable conditions for recruitment, growth and reproduction. Disturbances not only reduce or eliminate the cover of resident organisms, thereby lessening competition for resources that are present on the site (Sousa 1984). In this sense, the success of seeds settling has been linked to sea bottom with null or reduced *P. oceanica* density (Díaz Almela *et al.* 2008b, Domínguez *et al.* 2012) and to sheltered microstructure of sea bottom such as substrate depression or algal turfs (Balestri *et al.* 2008). We attribute to coastal hydrodynamics two kinds of effects on *P. oceanica* meadows: gaps into shallow meadows and regression at erosion fronts. New gaps constituted an ideal settlement area, such as was demonstrated by the perdurable seedling settlement reported for two years in this study after flowering peak of 2003, especially on high roughness sea bottom. Records of flowering events at short-term scales are irregular in space and time, but it becomes a

relevant event when we consider long-term scales. As an example, five massive flowerings linked to summer temperature peaks were reported by Díaz Almela *et al.* (2006) around Western Mediterranean Sea in 30 years (1973-75, 1982-83, 1992-94, 2001 and 2003). Focusing on Tabarca Island, light events of flowerings occurred in 1976, 1979, 1983, 1987, 1989 and 1992, with flowering intensity (f.i.) of 0.6% at 4 m, 0.7% at 12 m and 3.4% at 19 m respectively (Sánchez Lizaso 1993). In addition to these light events, two strong flowerings were recorded at Tabarca Island: in 1986 (22.5% f.i.; Sánchez Lizaso 1993); and in 2003 (direct observation by authors). As a consequence, at large-temporal scale, sexual reproduction could be considered an important repairing mechanism. Repairing role of sexual recruitment has been allocated as a common strategy for accelerating recovery in some terrestrial shrubs and herbs after canopy removal (Hughes & Fahey 1991). We think that shallow meadow showed a long-term equilibrium dynamics: rough weather would cause the regression of erosion fronts and would generate gaps; whereas seeds settling speeded up its reparation. Settling of vegetative fragments of *P. oceanica* has been attributed by literature as repairing mechanism too, especially in strong roughness bottom (Di Carlo *et al.* 2005). The height of erosion fronts was up to 2 m (Figure 2); which would constitute a significant obstacle for vegetative fragments and it would promote their settling.

Findings of erosion front transect suggest coastal hydrodynamics forces could modify erosion fronts position. They had an average regression of -0.87±0.75 m y^{-1}, but this was compensated by an average progression of 0.6±0.69 m y^{-1} in its adjacent edges. We think regression and progression could follow a discontinuous sequence: the front would be eroded for a long term by hydrodynamics forces, until they collapsed as consequence of a strong event (i.e. a storm). Thereafter, fallen plants would form an unstable slope such as we observed in "M" stick (Figure 2). Some of these plants would disappear by hydrodynamics erosion because they were not solidly anchored and, as consequence, a new erosion front would be formed in a rearmost position. However, other ones would take root and become part of the new edge promoting a significant leap forward, helping the natural vegetative recovery of edge plants.

Our results suggest *P. oceanica* meadows of Tabarca Island could have remained stable on the long-term. But we detected "hot areas", such as those placed in upper limit or in erosion fronts, where likely a quick decline by natural causes (e.g. waves) was offset by natural repair mechanisms (e.g. settlement of seedlings and vegetative growth).

REFERENCES

Balestri E, Lardicci C (2008). First evidence of a massive recruitment event in *Posidonia oceanica*: Spatial variation in first-year seedling abundance on a heterogeneous substrate, Estuarine Coastal Shelf Science, 76: 634-41.

Brun FG, Vergara JJ, Peralta G, García-Sánchez MP, Hernández I, Perez-Llorens JL (2006). Clonal building, simple growth rules and phylloclimate as key steps to develop functional-structural seagrass models, Marine Ecology Progress Series, 323: 133-48.

Bull JC, Kenyon EJ, Cook KJ (2012). Wasting disease regulates long-term population dynamics in a threatened seagrass, Oecologia, 169: 135-142.Cochran WG (1951). Testing a linear relation among variances, Biometrics, 7: 17-32.

Diaz-Almela E, Marbà N, Álvarez E, Balestri E, Ruiz-Fernández JM, Duarte CM (2006). Patterns of seagrass (*Posidonia oceanica*) flowering in the western Mediterranean, Marine Biology, 148: 723-742.

Díaz-Almela E, Marbà N, Duarte CM (2007). Consequences of Mediterranean warming events in seagrass (*Posidonia oceanica*) flowering records, Global Change Biology, 13: 224-35.

Díaz Almela E, Marbà N, Álvarez E, Santiago R, Holmer M, Grau A, Mirto S, Danovaro R, Petrou A, Argyrou M, Karakassis I, Duarte CM, (2008ª). Benthic input rates predict seagrass (*Posidonia oceanica*) fish farm-induced decline, Marine Pollution Bulletin, 56: 1332-42.

Díaz Almela E, Marbà N, Álvarez E, Santiago R, Martínez R, Duarte CM (2008b). Patch dynamics of the Mediterranean seagrass *Posidonia oceanica*: Implications for recolonisation process, Aquatic Botany, 89: 397-493.

Di Carlo G, Badalamenti F, Jensen AC, Koch EW, Riggio S (2005). Colonisation process of vegetative fragments of *Posidonia oceanica* (L.) Delile on rubble mounds. Marine Biology, 147: 1261-70.

Domínguez M, Celdrán D, Muñoz-Vera A, Infantes E. Martinez-Baños P, Marín A, Terrados J (2012). Experimental evaluation of the restoration capacity of a fish-farm impacted area with *Posidonia oceanica* (L.) Delile seedlings, Restoration Ecology, 20: 180-7.

Duarte CM, Marbá N, Agawin N, Cebrian J, Enriquez S, Fortes MD, Gallegos ME, Merino M, Olesen B, Sand-Jensen K (1994). Reconstruction of seagrass dynamics: age determinations and associated tools for the seagrass ecologist, Marine Ecology Progress Series, 107: 195-209.

Ebert TA, Williams SL, Ewanchuk PJ, (2002). Mortality estimates from age distributions: Critique of a method used to study seagrass dynamics. Limnology Oceanography, 47: 600-603.

Ebert TA, Williams SL (2003). Rejoinder to Fourqurean *et al.* (2003). Limnology Oceanography, 48: 2074-75.

Fernández-Torquemada Y, Sánchez-Lizaso JL, González-Correa JM, (2005). Preliminary results of the monitoring of the

brine discharge produced by the SWRO desalination plant of Alicante (SE Spain). Desalination, 182: 395-402.

Fourqurean JW, Marbà N, Duarte CM, (2003). Elucidating seagrass population dynamics: Theory, constraints, and practice. Limnology Oceanography, 48: 2070-2074.

Francour P, Ganteaume A, Poulain M (1999). Effects of boat anchoring in *Posidonia oceanica* seagrass beds in the Port-Cros national park (north-western Mediterranean sea) Aquatic Conservation: Marine Freshwater Ecosystem, 9: 391-400.

Gacia E, Granata TC, Duarte CM (1999). An approach to measurement of particle flux and sediment retention within seagrass (*Posidonia oceanica*) meadows, Aquatic Botany, 65: 255-268.

Gacia E, Duarte CM (2001). Sediment retention by a Mediterranean *Posidonia oceanica* meadow: The balance between deposition and resuspension, Estuarine Coastal Shelf Science, 52: 505-14.

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, Journal of Experimental Marine Biology and Ecology, 320: 65-76.

González-Correa JM, Bayle Sempere JT, Sánchez-Jerez P, Valle C (2007ª). *Posidonia oceanica* meadows are not declining globally. Analysis of population dynamics in marine protected areas of the Mediterranean Sea, Marine Ecology Progress Series, 336: 111-119.

González-Correa JM, Fernández-Torquemada Y, Sánchez-Lizaso JL (2007b). Comparing shoot population dynamics methods on *Posidonia oceanica* meadows, Journal Experimental Marine Biology and Ecology, 353: 115-125.

González-Correa JM, Fernández Torquemada Y, Sánchez Lizaso JL (2008). Long-term effect of beach replenishment on natural recovery of shallow *Posidonia oceanica* meadows. Estuarine Coastal Shelf Science, 6: 834-844.

Holmer M, Argyrou M, Dalsgaard T, Danovaro R, Diaz-Almela E, Duarte CM, Frederiksen M, Grau A, Karakassis I, Marbà N, Mirto S, Pérez M, Pusceddu A, Tsapakis M (2008). Effects of fish farm waste on *Posidonia oceanica* meadows: Synthesis and provision of monitoring and management tools, Marine Pollution Bulletin, 56: 1618-1629.

Hughes JW, Fahey TJ (1991) Colonization dynamics of herbs and shrubs in a disturbed northern hardwood forest. Journal of Ecology, 79: 605-16.

Jordá G, Marbà N, Duarte C (2012). Mediterranean seagrass vulnerable to regional climate warming, Nature Climate Change, D.O.I: 10.1038/NCLIMATE1533

Leriche A, Pasqualini V, Boudouresque CF, Bernard G, Bonhomme P, Clabaut P, Denis J (2006). Spatial, temporal and structural variations of a *Posidonia oceanica* seagrass meadow facing human activities, Aquatic Botany, 84: 287-293.

Lobelle D, Kenyon EJ, Cook KJ, Bull JC (2013). Local competition and metapopulation processes drive long-term

seagrass epiphyte population dynamics, Plos one, 8, e57072.

Marbà N, Duarte CM, Cebrian J, Gallegos ME, Olesen B, Sand-Jensen K (1996 a). Growth and population dynamics of *Posidonia oceanica* on the Spanish Mediterranean coast: Elucidating seagrass decline, Marine Ecology Progress Series, 137: 203-213.

Marbà N, Cebrian J, Enriquez S, Duarte CM (1996 b). Growth patterns of Western Mediterranean seagrasses: species-specific responses to seasonal forcing, Marine Ecology Progress Series, 133: 203-215.

Marbà N, Duarte CM, (1998). Rhizome elongation and seagrass clonal growth, Marine Ecology Progress Series, 174: 269-280.

Martín MA, Sánchez Lizaso JL, Ramos Esplá AA (1997). Cuantificación del impacto de las artes de arrastre sobre la pradera de *Posidonia oceanica* (L.) Delile, 1813, Publicaciones Especiales Instituto Español de Oceanografía, 23: 243-53.

Mateo MA, Sánchez-Lizaso JL, Romero J (2003). *Posidonia oceanica* 'banquettes': A preliminary assessment of the relevance for meadow carbon and nutrients budget, Estuarine Coastal Shelf Science, 56: 85-90.

Milazzo M, Badalamenti F, Ceccherelli G, Chemello R (2004). Boat anchoring on *Posidonia oceanica* beds in a marine protected area (Italy, western Mediterranean): Effect of anchor types in different anchoring stages, Journal of Experimental Marine Biology and Ecology, 299: 51-62.

Olesen B, Enríquez S, Duarte CM, Sand-Jensen K (2002). Depth-acclimation of photosynthesis, morphology and demography of *Posidonia oceanica* and Cymodocea nodosa in the Spanish Mediterranean Sea. Marine Ecology Progress Series, 236: 89-97.

Peirano A, Cocito S, Banfi V, Roberta C, Damasso V, Farina G, Lombardi C, Mauro R, Morri C, Roncarolo I, Saldaña S, Savini D, Sgorbini S, Silvestri C, Stoppelli N, Torricelli L, Bianchi CN (2011). Phenology of the Mediterranean seagrass *Posidonia oceanica* (L.) Delile: Medium and long-term cycles and climate inferences, Aquatic Botany, 94: 77-92.

Pérès JM, Picard J (1975). Causes of decrease and disappearance of the seagrass *Posidonia oceanica* on the French Mediterranean coast, Aquatic Botany, 1: 133-139.

Pérès JM (1984). La régression des hèrbiers à *Posidonia oceanica*. In: Boudouresque CF, Jeudy de Grissac A, Olivier J, eds, International workshop on *Posidonia oceanica* beds, GIS Posidonie Publications,1, Marseille, 445-454.

Ramos AA (1985). La reserva marina de la isla plana o nueva tabarca. 2nd ed, Secretariado de Publicaciones de la Universidad de Alicante. Alicante.

Rasheed MA, Unsworth RKF (2011). Long-term climate-associated dynamics of a tropical seagrass meadow: implication for the future. Marine Ecology Progress Series, 422: 93-103.

Sánchez Lizaso JL (1993). Estudio de la pradera de *Posidonia*

oceanica (L.) Delile de la reserva marina de Tabarca (Alicante): Fenología y producción primaria. Universidad de Alicante, Alicante.

Serrano O, Mateo MA, Renom P, Julià R (2012). Characterization of soils beneath a *Posidonia oceanica* meadow, Geoderma, 185-186: 26-36.

Short FT, Polidoro B, Livingstone SR, Carpenter KE, Bandeira S, Bujang JS, Calumpong HP, Carruthers TJ, Coles RG, Dennison WC, Erftemeijer PL, Fortes M, Freeman AS, Jagtap TG, Kamal AH, Kendrick GA, Judson W, La Nafie YA, Nasution IM, Orth RJ, Prathep A, Sanciangco JC, Tussenbroek BV, Vergara SG, Waycott M, Zieman JC (2011). Extinction risk assessment of the world's seagrass species, Biology Conservation, 144: 1961-1971.

Sousa WP (1984). The role of disturbance in natural communities, Annual Reviews of Ecology, Evolution and Systematics, 15: 353-391.

Underwood AJ (1981). Techniques of analysis of variance in experimental marine biology and ecology, Oceanography Marine Biology Annual Reviews, 19: 513-605.