

# Direct Evidence of Imbalanced Seagrass (*Posidonia oceanica*) Shoot Population Dynamics in the Spanish Mediterranean

NÚRIA MARBÀ<sup>1\*</sup>, CARLOS M. DUARTE<sup>1</sup>, ELENA DÍAZ-ALMELA<sup>1</sup>, JORGE TERRADOS<sup>1</sup>,  
ELVIRA ÁLVAREZ<sup>2</sup>, REGINO MARTÍNEZ<sup>1</sup>, ROCÍO SANTIAGO<sup>1</sup>, ESPERANÇA GACIA<sup>3</sup>, and  
ANTONI M. GRAU<sup>2</sup>

<sup>1</sup> Grup d'Oceanografia Interdisciplinària, Institut Mediterrani d'Estudis Avançats (Consejo Superior de Investigaciones Científicas-Universitat Illes Balears), Miquel Marqués 21, 07190 Esporles (Illes Balears), Spain

<sup>2</sup> Direcció General de Pesca, Conselleria d'Agricultura i Pesca, Govern de les Illes Balears, Foners 10, 07006 Palma de Mallorca, (Illes Balears), Spain

<sup>3</sup> Centre d'Estudis Avançats de Blanes, Accés a la Cala Sant Francesc, 14, 17300 Blanes (Girona), Spain

**ABSTRACT:** Direct census of shoots tagged in permanent plots was used to assess the present (2000–2002) *Posidonia oceanica* population dynamics in 25 meadows along the Spanish Mediterranean Coast. Shoot density ranged from  $154 \pm 8$  to  $1,551 \pm 454$  shoots  $m^{-2}$ , absolute shoot mortality from  $5 \pm 0$  to  $249 \pm 53$  shoots  $m^{-2} yr^{-1}$ , and absolute shoot recruitment from  $<5 \pm 1$  to  $62 \pm 42$  shoots  $m^{-2} yr^{-1}$ . Specific shoot mortality and recruitment rates, which are mathematically and statistically ( $p > 0.05$ ) independent of shoot density, varied from  $0.015 \pm 0.006$  to  $0.282 \pm 0.138$   $yr^{-1}$  and  $0.018 \pm 0.005$  to  $0.302 \pm 0.093$   $yr^{-1}$ , respectively. Absolute shoot mortality rate was scaled to shoot density (Pearson correlation,  $r = 0.78$ ,  $p < 0.0001$ ), and variability in specific shoot recruitment rate was partially due to differences in the percentage of growing apices, which produce most of the recruits within the population (Pearson correlation,  $r = 0.50$ ,  $p < 0.001$ ), demonstrating the existence of structural constraints on shoot demography. Shoot half-life was estimated to range from 2.5 to 60.4 yr and meadow turnover times between 6.7 yr and more than a century, provided current estimates of shoot mortality, recruitment rates, and density remain uniform. There were differences in shoot mortality and recruitment at the regional scale, with the meadows developing along the coast of the Spanish mainland experiencing the highest shoot mortality (Tukey test,  $p < 0.05$ ) and tending to exhibit the highest shoot recruitment. The low shoot recruitment did not balance shoot mortality in most (60%) of the meadows, showing a prevalence of declining populations among the 25 meadows studied (Wilcoxon ranked sign test,  $p < 0.0005$ ). This study demonstrates the power of direct census of seagrass shoots in permanent plots to evaluate the present status of seagrass meadows, to detect on-going population decline, and to provide some insight onto the possible factors involved. The incorporation of direct census of seagrass meadows to monitoring programs will help provide the early-warning signals necessary to support management decisions to conserve seagrass meadows.

## Introduction

Seagrasses, which provide valuable functions to coastal ecosystems (Duarte 2002), are experiencing worldwide declines derived from natural and man-made disturbances (Short and Wyllie-Echevarria 1996; Hemminga and Duarte 2000; Duarte 2002). There is evidence that seagrass decline is a nonlinear process that accelerates, through cascade effects, after reaching a certain level of disturbance (e.g., Duarte 1995, 2002; Hemminga 1998). Recovery of seagrass meadows is a slow process, requiring time scales up to centuries for slow-growing species (Duarte 1995, 2002; Hemminga and Duarte 2000). Detection of seagrass decline at the earliest stages of the process is crucial to pre-

vent large-scale and, at human time scales, often irreversible seagrass losses.

Efforts to detect seagrass decline prior to observing losses in vegetation cover are increasing through the proliferation of monitoring programs and methods world wide (e.g., Short and Coles 2001). Monitoring programs typically assess seagrass status through changes in the shoot density or cover. The error of these estimates is so large (Heidelbaugh and Nelson 1996) that seagrass decline can only be reliably detected when over half of the shoot population has already been lost. Decline of slow-growing species may proceed for years until it can be statistically resolved by monitoring programs based on density and cover estimates. As a result, there is considerable demand to generate new, reliable approaches to monitor the status of seagrass meadows. Shoot demography has been

\* Corresponding author; tele: 34 971/611720; fax: 34 971/611761; e-mail: nuria.marba@uib.es

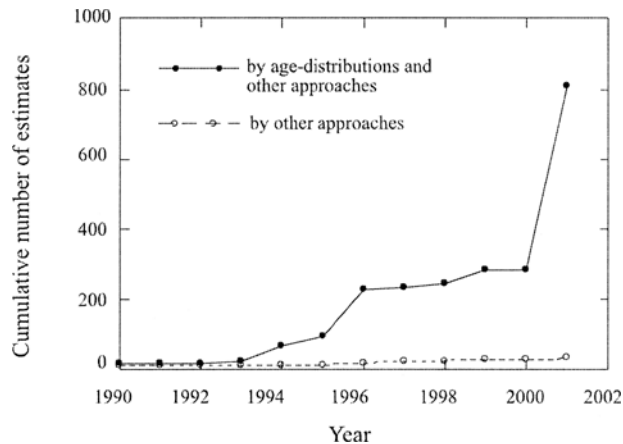


Fig. 1. The cumulative number of estimates for parameters relevant to seagrass population dynamics (mortality, recruitment, net rate of population growth, and median shoot age) since 1990. The cumulative number of total estimates (solid line) and that of values derived through methods other than the examination of age distributions (dotted line) are indicated. Data obtained from Patriquin (1973), Bigley and Harrison (1986), Duarte and Sand-Jensen (1990), Gallegos et al. (1993), Harrison (1993), Durako (1994), Gallegos et al. (1994), Olesen and Sand-Jensen (1994a,b), Perez et al. (1994), Vermaat et al. (1995), Duarte et al. (1996, 1997), Jensen et al. (1996), Marbà et al. (1996), Moore et al. (1996), Vidondo et al. (1997), Balestri et al. (1998), Kenworthy and Schwarzschild (1998), Manzanera et al. (1998), Laugier et al. (1999), Marbà and Walker (1999), Ramage and Schiel (1999), van Tussembroek (2000), Kamer-mans et al. (2001), Koch and Erskine (2001), Peterson and Fourqurean (2001), Rollon et al. (2001), and Ruiz and Romero (2001).

demonstrated to be a useful tool to assess seagrass population status, and it has been intensively used over the last decade to examine meadow status (e.g., Duarte and Sand-Jensen 1990; Durako 1994; Marbà et al. 1996; Kaldy et al. 1999; Peterson and Fourqurean 2001). Most available seagrass demographic estimates have been quantified retrospectively (Fig. 1), based on the age distribution of the living shoots of the population (Duarte et al. 1994). Demographic estimates based on the age distribution of the living shoots are subject to considerable uncertainty, as their use involves assumptions that often cannot be verified (Jensen et al. 1996, 1997; Kaldy et al. 1999; Ebert et al. 2002; Ebert and Williams 2003). Demographic estimates based on shoot age distributions provide retrospective assessments of the meadow dynamics over time scales up to years to decades over the past (Fourqurean et al. 2003) and do not necessarily accurately reflect the status of the meadow at the time of sampling and are less accurate in assessing the future (Jensen et al. 1996, 1997). Diagnostics on seagrass population status based on retrospective analyses involve, particularly for mortality estimates, assumptions that can rarely be verified

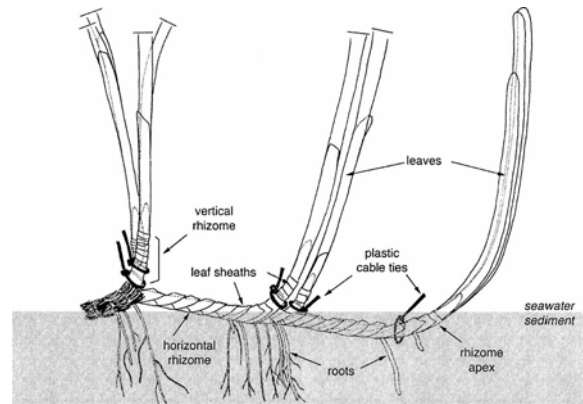


Fig. 2. Drawing of *Posidonia oceanica*. Morphological plant attributes and tagging procedure are shown.

(Ebert et al. 2002; Ebert and Williams 2003; Fourqurean et al. 2003).

The reliable early diagnosis of seagrass decline requires the use of alternative approaches to assess shoot population changes at short time scales. Direct censuses have been proposed as the most effective way to assess the current demographic status of seagrass populations (Short and Duarte 2001; Ebert et al. 2002). Direct shoot census has been successfully used to assess shoot demography in terrestrial clonal plants for decades (e.g., Harper 1977) but has seldom (Bigley and Harrison 1986; Laugier et al. 1999; Ruiz and Romero 2001) been applied to examine seagrass shoot demography, likely because the census of sufficient individually-tagged shoots is cumbersome and requires considerable dive time, manpower, and economic resources.

*Posidonia oceanica*, the dominant seagrass species in the Mediterranean Sea, forms highly productive meadows (Duarte and Chiscano 1999) extending about 50,000 km<sup>2</sup> (Bethoux and Copin-Montégut 1986). *P. oceanica* is a long-lived, slow-growing seagrass (a few centimeters per year; Duarte 1991) with sparse sexual reproduction (Meinesz and Lefèvre 1984; Buia and Mazzella 1991). Populations develop over millenary time scales (Mateo et al. 1997). Similar to all other seagrasses, the vast majority of shoots in *P. oceanica* meadows are vegetatively produced by horizontal rhizome apices and dividing vertical shoots (Fig. 2). *P. oceanica* is believed to be in decline across most of the Mediterranean basin, due to local anthropogenic forcing (e.g., Delgado et al. 1999; Duarte 2002) and possibly climate change (Duarte 2002). Retrospective examination of shoot demography along the Spanish Mediterranean Coast confirmed the reports of widespread decline in the recent past (1960–1990;

Marbà et al. 1996), but direct estimates of the present demographic status of the species are lacking.

We demonstrate the feasibility of the use of direct census of shoots tagged in permanent plots to assess the present (2000–2002) *P. oceanica* population dynamics in 25 meadows along the Spanish Mediterranean. We evaluated population status of the populations on the basis of examinations of the balance between the annual shoot mortality and shoot recruitment and the resulting net population growth rates.

## Materials and Methods

### STUDY SITE

The study was conducted in 25 *P. oceanica* meadows distributed along 2,500 km of the Spanish Mediterranean Coast coastline, the mainland, and the Balearic Islands. The populations examined developed at water depths ranging from 3 to 25 m and encompassed environments with contrasting anthropogenic pressure. All meadows, except those at Xilxes, Torre de la Sal, and Cabrera and Formentera Islands, were growing near tourist areas. The meadows at Xilxes and Torre de la Sal were located in an area with intense coastal erosion. Anthropogenic pressure at Cabrera Island has been low since it was expropriated for military activities in 1916 (Frontera et al. 1993) to become a national park in 1991 with conservation policies implemented to protect both the land and marine components (Marbà et al. 2002). Surface water temperature along the Spanish Mediterranean Coast varies about 3°C from north to south, and averages 13°C in winter and 25°C in summer (Flos 1985). The study sites were located in oligotrophic environments, as reflected in high water transparency (>15 m Secchi depth throughout) and low nutrient concentrations in seagrass leaves (Duarte and Fourqurean unpublished data). The meadows examined at the Balearic Islands grew over biogenic carbonate sediments while those on the Spanish mainland grew over a mixture of biogenic carbonate and terrigenous sediments.

Between June 2000 and August 2001, three permanent plots, of an area varying between 0.09 and 0.72 m<sup>2</sup> (as to include at least 100 shoots plot<sup>-1</sup>) were delimited at each of the selected sites by SCUBA divers by a string running around four metal poles inserted into the sediments at the corners of the plots. At Xilxes, where *P. oceanica* developed small isolated patches, regular plots could not be installed and 8 entire patches were selected for the study. All shoots present inside the plots, or the patches at Xilxes, were counted and tagged by SCUBA divers with a plastic cable tie placed around their vertical rhizomes, at least 2 cm below

the leaf meristem (Fig. 2). On average 101 ± 6 shoots were marked per plot, varying between 12 (the smallest patch at Xilxes) and 277 shoots plot<sup>-1</sup>, representing an average of 303 individually-tagged shoots per station and a total of 7,575 shoots tagged in this study. The plots were revisited once, at intervals between 292 and 436 d (Table 1), and the number of surviving shoots (i.e., tagged shoots) and newly recruited shoots (i.e., young, untagged shoots) were counted. All plots were revisited after summer 2001, and most of them (i.e., those located at Cabrera at >14 m depth, Mallorca, Girona, and Formentera) after fall 2001. The counting error was calibrated by counting replicated plots by independent observers, yielding an estimate of ±0.3 recruited shoots per plot and ±5 dead shoots per plot. The repeated shoot census allowed direct estimates of shoot density, absolute (shoots m<sup>-2</sup> yr<sup>-1</sup>) and specific (yr<sup>-1</sup>) rates of shoot mortality and recruitment, net population growth and shoot turnover rates, and shoot half-life at the meadows.

Absolute shoot mortality rate (AbsM; dead shoots m<sup>-2</sup> yr<sup>-1</sup>) was calculated as

$$\text{AbsM} = \frac{(\text{NT}_0 - \text{NS}_1) \times 365}{[A \times (t_1 - t_0)]}$$

NT<sub>0</sub> is the number of marked shoots at the start of the study (t<sub>0</sub>, d) at each plot, NS<sub>1</sub> is the number of marked shoots that survived at t<sub>1</sub> (d), and A is the plot area (m<sup>2</sup>). The specific shoot mortality rate (M; yr<sup>-1</sup>) was calculated as

$$M = \frac{[\ln(\text{NT}_0/\text{NS}_1)] \times 365}{t_1 - t_0}$$

Calculation of M allowed estimation of shoot half-life (Age; yr) as

$$\text{Age} = \frac{\ln 2}{M}$$

Absolute shoot recruitment rate (AbsR; recruited shoots m<sup>-2</sup> yr<sup>-1</sup>) was calculated as

$$\text{AbsR} = \frac{\text{NN}_1 \times 365}{[A \times (t_1 - t_0)]}$$

where NN<sub>1</sub> is the number of recruited (i.e., young not marked) shoots between t<sub>1</sub> and t<sub>0</sub>. Shoot turnover time (yr) is estimated by dividing shoot density at the beginning of the study by the absolute recruitment rate. The specific shoot recruitment rate (R; yr<sup>-1</sup>) was estimated as

$$R = \frac{[\ln(\text{NT}_1/\text{NS}_1)] \times 365}{t_1 - t_0}$$

where NT<sub>1</sub> is the number of living shoots at the end of the study at each plot, comprising both sur-

TABLE 1. Structure (i.e., shoot density at the beginning of the study, and percentage of rhizome apices) and absolute shoot mortality and recruitment rates of *Posidonia oceanica* meadows growing along the Spanish Mediterranean. All plots were revisited once. The date of plot set up and initial shoot census, and time elapsed in between initial and final shoot census are indicated. Number of mean values  $\pm$  standard error of mean values are provided. Number of plots = 3, except for those sites where one plot was lost during the study or shoot densities at  $t_0$  were lower than surviving shoot counts at  $t_1$  (\*), nd: no data available.

Region	Site	Latitude (degrees N)	Longitude (degrees E)	Depth (m)	Plot Set Up Date	Time Elapsed in Between Initial and Final Shoot Census (days)		Shoot Density $t_0$ (shoots m <sup>-2</sup> )	% Apices	Absolute Mortality Rate (dead shoots m <sup>-2</sup> yr <sup>-1</sup> )	Absolute Recruitment Rate (recruited shoots m <sup>-2</sup> yr <sup>-1</sup> )
						Initial Shoot Census	Final Shoot Census				
Formentera	Cala Torreta	38°47'45"	1°25'18"E	7	15-Jan-01	483	527.31*	3.08	46.18*	13.47 $\pm$ 5.07	
	Es Pujols	38°43'74"	1°27'27"E	4	25-April-01	389	745.83 $\pm$ 24.03	0.00	32.25 $\pm$ 8.80	17.59 $\pm$ 11.73	
	Illetes	38°45'37"	1°25'83"E	6	26-April-01	379	666.67 $\pm$ 14.58	0.60 $\pm$ 0.60	10.03 $\pm$ 4.01	18.06 $\pm$ 12.04	
Cabrera	El Castell	39°9'16"	2°35'83"E	5	16-Oct-00	367	704.00 $\pm$ 62.14	0.88 $\pm$ 0.88	62.33 $\pm$ 38.46	27.85 $\pm$ 12.15	
	El Castell	39°9'16"	2°55'82"E	10	26-Oct-00	357	535.42 $\pm$ 102.59	0.00	102.24 $\pm$ 46.23	10.65 $\pm$ 4.26	
	El Castell	39°9'16"	2°35'80"E	15	21-Nov-00	433	437.50 $\pm$ 26.02	0.65 $\pm$ 0.65	84.30 $\pm$ 13.26	14.05 $\pm$ 1.76	
	El Castell	39°9'18"	2°55'77"E	20	23-Nov-00	433	233.33*	0.00	7.89*	10.53 $\pm$ 5.27	
	El Castell	39°9'18"	2°35'76"E	25	23-Nov-00	434	159.38	0.00	5.26	5.26	
	Cala Sta Maria	39°9'07"	2°56'92"E	13.1	17-Oct-00	364	761.68 $\pm$ 31.19	0.00	135.82 $\pm$ 50.52	13.87 $\pm$ 4.29	
	Cala Sta Maria	39°9'00"	2°56'96"E	7	28-Oct-00	355	1000.00 $\pm$ 33.94	0.44 $\pm$ 0.44	163.75 $\pm$ 38.65	22.85 $\pm$ 11.42	
	Cala Sta Maria	39°9'16"	2°56'89"E	17	5-Feb-01	358	461.33*	2.37 $\pm$ 1.93	67.29*	23.11 $\pm$ 1.36	
	Sa Paret	39°8'81"	2°35'86"E	17	20-Nov-00	434	259.33*	1.08 $\pm$ 1.08	74.57*	8.49 $\pm$ 2.52	
	Mallorca	Porto Colom	39°25'05"	3°16'18"E	6.4	5-Jul-01	424	414.67 $\pm$ 80.74	5.36	55.09 $\pm$ 6.89	15.50 $\pm$ 5.17
Colonia St. Jordi		39°18'66"	2°59'96"E	4	26-Feb-01	434	980.00 $\pm$ 70.69	5.78 $\pm$ 2.81	115.50 $\pm$ 44.98	62.80 $\pm$ 42.30	
Mediterranean coast of Spanish mainland	Magahuf	39°30'25"	2°32'59"E	6	5-Oct-00	386	562.67 $\pm$ 54.76	0.00	64.30 $\pm$ 15.29	20.17 $\pm$ 10.77	
	Illetes-Calvià	39°32'10"	2°35'56"E	9	6-Aug-01	388	nd	2.24 $\pm$ 1.55	nd	nd	
	La Fossa	38°38'59"	0°4'56"E	3	28-Jun-00	436	1551.21 $\pm$ 454.06	0.00	249.01 $\pm$ 53.98	21.89 $\pm$ 12.13	
	L'Arenal	38°38'37"	0°3'06"E	6	27-Jun-00	436	430.67 $\pm$ 23.13	3.64 $\pm$ 3.05	87.06 $\pm$ 45.30	53.58 $\pm$ 3.87	
	L'Olla-										
	Campomanes	38°37'54"	0°0'57"W	5.3	29-Jun-00	292	426.67 $\pm$ 25.44	1.49 $\pm$ 0.32	108.33 $\pm$ 52.94	20.00 $\pm$ 15.00	
	Xilxes	39°45'13"	0°8'07"W	13.5	29-Jun-00	433	nd	20.61 $\pm$ 5.32	nd	nd	
	Torre de la Sal	40°8'13"	0°10'72"W	9	30-Jun-00	385	350.00 $\pm$ 42.70	0.84 $\pm$ 0.84	64.03 $\pm$ 11.41	14.05 $\pm$ 5.34	
	Fanals	41°41'58"	2°50'55"W	16	10-May-01	398	332.41 $\pm$ 23.48	nd	42.96 $\pm$ 7.85	5.15 $\pm$ 1.46	
	Civerola	41°44'15"	2°57'37"E	13	1-Jun-01	377	305.80 $\pm$ 60.20	nd	50.03 $\pm$ 16.80	24.24 $\pm$ 8.57	
Jonquet	42°18'19"	3°17'36"E	11.5	25-Jun-01	368	258.33 $\pm$ 19.90	nd	60.44	13.95		
Port Lligat	42°17'61"	3°17'58"E	12	26-Jun-01	366	154.63 $\pm$ 8.03	nd	30.93 $\pm$ 5.32	23.55 $\pm$ 2.77		

TABLE 2. Demographic parameters (i.e., specific mortality and recruitment rates, shoot half-life, shoot turnover time, and specific net population growth rate) of *Posidonia oceanica* meadows growing along the Spanish Mediterranean. All plots were revisited once. Number of mean values ( $\pm$  SE) are provided. Number of plots = 3, except for those sites where one plot was lost during the study or shoot densities at  $t_0$  were lower than surviving shoot counts at  $t_1$  (\*). nd = no data available.

Region	Site	Depth (m)	Mortality Rate ( $\text{yr}^{-1}$ )	Shoot Half Life (yr)	Recruitment Rate ( $\text{yr}^{-2}$ )	Shoot Turnover Time (yr)	Net Population Growth Rate ( $\text{yr}^{-1}$ )
Formentera	Cala Torreta	7	0.12*	31.08*	0.02 (0.01)	68.15 (17.86)	-0.10
	Es Pujols	4	0.04	17.04	0.02	80.04	-0.02
	Illetes	6	0.02 (0.01)	60.42 (18.06)	0.03 (0.02)	80.20 (32.50)	0.01 (0.01)
Cabrera	El Castell	5	0.11 (0.08)	15.69 (6.54)	0.04 (0.02)	37.67 (16.52)	-0.06 (0.08)
	El Castell	10	0.19 (0.07)	4.97 (1.98)	0.03 (0.02)	72.05 (27.55)	-0.16 (0.08)
	El Castell	15	0.22 (0.04)	3.33 (0.58)	0.04 (0.01)	32.43 (5.38)	-0.18 (0.04)
	El Castell	20	0.04*	25.09*	0.04 (0.02)	33.94 (12.58)	-0.01*
	El Castell	25	0.03	20.60	0.03	30.32	0.00
	Cala Sta Maria	13.1	0.21 (0.09)	5.00 (2.08)	0.02 (0.01)	63.82 (14.76)	-0.19 (0.09)
	Cala Sta Maria	7	0.18 (0.04)	4.27 (0.81)	0.03 (0.01)	64.68 (21.03)	-0.15 (0.03)
Mallorca	Cala Sta Maria	17	0.14*	5.77*	0.05 (0.01)	20.23 (3.26)	-0.09*
	Sa Paret	17	0.28	6.67	0.05 (0.02)	40.08 (16.50)	-0.25
	Porto Colom	6.4	0.17	4.33	0.06	31.36	-0.11
	Colonia St. Jordi	4	0.12 (0.04)	7.18 (2.34)	0.07 (0.05)	119.77 (104.92)	-0.05 (0.09)
	Magaluf	6	0.12 (0.02)	6.10 (0.95)	0.04 (0.02)	49.06 (22.15)	-0.08 (0.03)
	Illetes-Calvià	9	0.11	nd	0.03 (0.01)	nd	-0.07
	La Fossa	3	0.24 (0.08)	4.38 (2.20)	0.03 (0.02)	130.20 (56.14)	-0.19 (0.12)
Mediterranean coast of Spanish mainland	L'Arenal	6	0.24 (0.13)	4.75 (1.72)	0.15 (0.02)	8.11 (0.61)	-0.09 (0.11)
	L'Olla-						
	Campomanes	5.3	0.28 (0.14)	18.41 (16.72)	0.06 (0.04)	58.45 (25.17)	-0.23 (0.13)
	Xilxes	13.5	0.16 (0.04)	nd	0.30 (0.09)	nd	0.14 (0.11)
	Torre de la Sal	9	0.21 (0.03)	3.58 (0.68)	0.05 (0.02)	33.39 (11.22)	-0.16 (0.05)
	Fanals	16	0.14 (0.03)	5.27 (0.88)	0.02 (0.01)	75.45 (19.41)	-0.12 (0.02)
	Giverola	13	0.17 (0.05)	4.65 (1.18)	0.09 (0.02)	15.16 (5.24)	-0.08 (0.07)
	Jonquet	11.5	0.28	2.57	0.07	18.16	-0.21
	Port Lligat	12	0.23 (0.05)	3.41 (0.92)	0.18 (0.03)	6.80 (1.00)	-0.05 (0.04)

viving and recruited shoots. The specific net population growth rate ( $R_{\text{net}}$ ;  $\text{yr}^{-1}$ ) was estimated as  $R_{\text{net}} = R - M$ . Error terms refer to standard errors throughout unless indicated otherwise.

The existence of significant differences in demographic parameters among regions was examined using analysis of variance and Tukey multiple comparisons test. Pearson correlation coefficient was used to describe relationships between variables. Small-scale (i.e., 0.09–0.72  $\text{m}^2$ ) heterogeneity in shoot mortality and recruitment rates was quantified as the average of the coefficient of variation (CV; %) of these variables at each station. Wilcoxon ranked sign test, performed on the paired observations of average shoot mortality and recruitment rates of each population across all populations studied, was used to test for a significant large-scale trend of *P. oceanica* decline across the Spanish Mediterranean.

### Results

Shoot density in the meadows studied ranged between  $154 \pm 8$  and  $1,551 \pm 454$  shoots  $\text{m}^{-2}$  (Table 1), the variability observed partially being attributable to differences in water depth (Pearson correlation,  $r = 0.65$ ,  $p < 0.001$ ). Horizontal rhizome apexes were absent in 59% of the examined plots

(Table 1), and when present they represented on average 8.6% of total shoot density, and up to 55% of that in the isolated patches of Xilxes.

Absolute shoot mortality ranged from 5.26 to  $249.01 \pm 53.98$  shoots  $\text{m}^{-2} \text{yr}^{-1}$  with substantial (on average,  $\text{CV} = 53\%$ ) heterogeneity in absolute shoot mortality within meadows (Table 1). Absolute shoot mortality was scaled to shoot density (Pearson correlation,  $r = 0.78$ ,  $p < 0.0001$ ), with an average mortality of  $13.4\% \pm 2.2$  of the shoots present in the population. Specific mortality rates, which were independent of shoot density (Pearson correlation,  $p > 0.5$ ), provide a more robust basis to compare mortality rates. The specific shoot mortality rates ranged between  $0.02 \pm 0.01$  and  $0.28 \pm 0.14 \text{ yr}^{-1}$ , averaging  $0.16 \pm 0.08 \text{ yr}^{-1}$  (Table 2). The meadows growing along the coast of the Spanish mainland and Cabrera Island experienced the highest shoot mortality rates, whereas those at Formentera Island experienced the lowest mortality (Fig. 3). Significant (Tukey test,  $p < 0.05$ ) differences in shoot mortality rate were only observed when comparing meadows growing along the Spanish mainland with those at Formentera Island (Fig. 3). The rates of shoot mortality observed indicated that the half-life of the shoot population

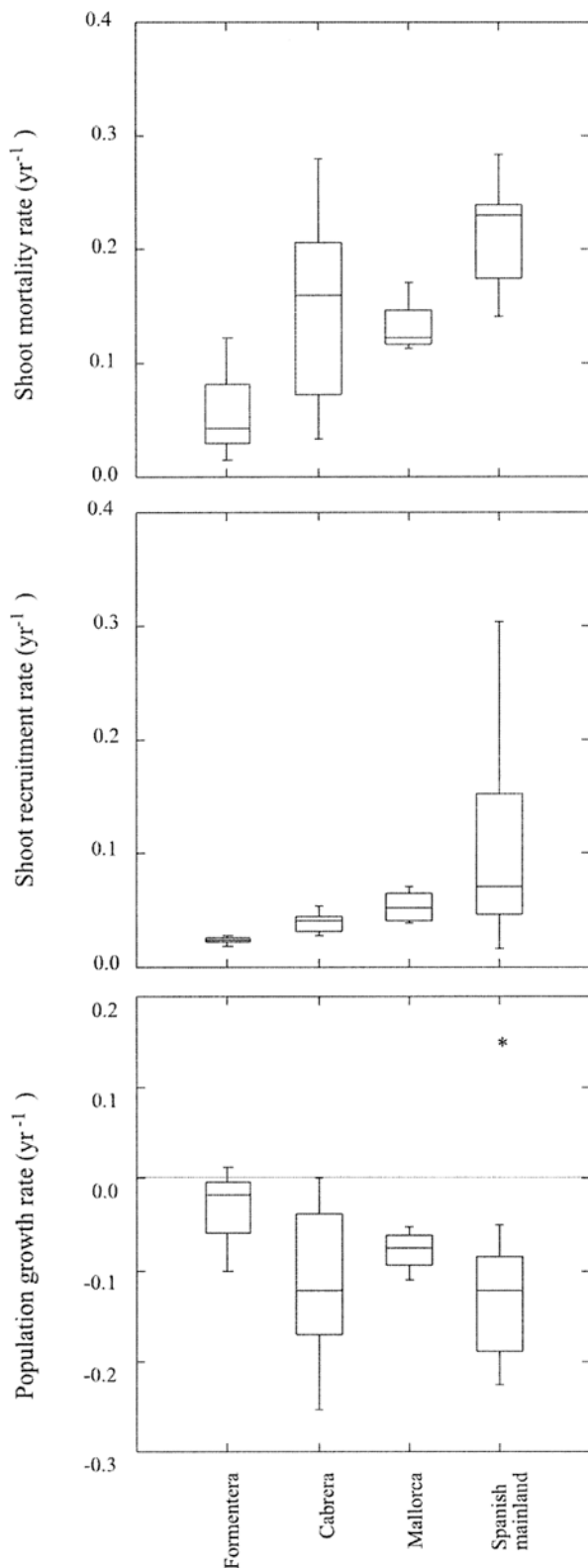


Fig. 3. *Posidonia oceanica* specific shoot mortality, specific shoot recruitment, and specific net population growth rates across the Spanish Mediterranean Coast regions studied.

varied from 2.5 to 60.4 yr, averaging 11.5 yr (Table 2).

*P. oceanica* recruited on average  $19 \pm 13$  shoots  $m^{-2} yr^{-1}$ , ranging from  $<5.26$  to  $62.8 \pm 42.3$  shoots  $m^{-2} yr^{-1}$  (Table 1). Shoot recruitment varied (on average  $CV = 59\%$ ) among contiguous plots (Table 1), partially due to differences in the percentage of growing apices, which produced most of the recruits within the population (Pearson correlation,  $r = 0.50$ ,  $p < 0.001$ ). The absolute rates of shoot recruitment indicate meadow turnover times for *P. oceanica* would range between  $6.8 \pm 1$  yr and more than a century (Table 2), provided current shoot recruitment and density remained uniform. The specific shoot recruitment rates ranged from  $0.02 \pm 0.01$  to  $0.30 \pm 0.09 yr^{-1}$  (Table 2). *P. oceanica* recruited shoots at the slowest rates at Cabrera and Formentera Islands, whereas the fastest specific shoot recruitment rates were observed along the Mediterranean coast of the Spanish mainland, although the differences were not statistically significant (Fig. 3 and Table 2).

The studied meadows experienced specific net population growth ranging from  $-0.25$  to  $0.14 \pm 0.11 yr^{-1}$ , encompassing strongly declining and expanding populations. The low shoot recruitment in most meadows examined was insufficient to compensate shoot mortality in most (60%) of the meadows (Tables 1 and 2), showing a prevalence of declining populations among the 25 meadows studied. Consideration of all meadows in concert showed a significant trend towards the decline of *P. oceanica* across this sample of populations in the Spanish Mediterranean Coast (Wilcoxon ranked sign test,  $p < 0.0005$ ).

### Discussion

The wide variability in the magnitude of shoot recruitment and mortality observed across *P. oceanica* meadows studied along the Spanish Mediterranean Coast (Tables 1 and 2) reflects the effect of regional and local environmental conditions, together with intrinsic factors (e.g., population structure, genetic variability), on *P. oceanica* population dynamics. *P. oceanica* shoot recruitment has been shown to be suppressed in carbonate sediments with increased sediment anoxia and sulphide due to even modest inputs of organic matter to the sediment (Holmer et al. 2003). Nutrient availability may limit *P. oceanica* growth (Alcoverro et al. 1997), and may constrain shoot recruitment at the most oligotrophic sites. The lowest *P. oceanica* shoot recruitment rates were observed in the meadows at Formentera and Cabrera Islands (Fig. 3 and Table 2), which grew on carbonate sediments and the most oligotrophic conditions present in the Spanish Mediterranean. The results reported also pro-

vide evidence of the role of intrinsic components of the meadow structure, such as shoot density and the density of meristem-bearing rhizome apices and the space available for colonization on *P. oceanica* population dynamics, with patchy, colonizing meadows exhibiting the highest shoot recruitment (Table 2).

The results presented clearly reveal an imbalanced *P. oceanica* population dynamics across the Spanish Mediterranean Coast during the years 2000–2002, involving an overall decline in shoot density during this period. The decline of *P. oceanica* meadows observed derived from the low shoot recruitment of the species, which ranks among the slowest of all the seagrasses (Hemminga and Duarte 2000), and the high shoot mortality experienced by the species (Table 2). Demographic estimates obtained in this study fall within the range of values reported for *P. oceanica* using retrospective approaches in the past (i.e., shoot recruitment rate: 0–0.44 yr<sup>-1</sup>, shoot mortality rate: 0.03–0.53 yr<sup>-1</sup>; Holmer et al. 2003; Marbà et al. 1996, 2002).

The current negative net population growth rate observed in Spanish Mediterranean Coast *P. oceanica* meadows predict, if sustained, a decline of 50% of shoot density within 2.7 and 69.3 yr (i.e., time =  $-\ln(2)/R_{net}$ ), generating concern about the conservation of these meadows. The net rates of population change recorded through the direct census approach used here is within the error of conventional quadrat count techniques used in most monitoring programs (Heidelbaugh and Nelson 1996). The widespread decline derived from our results would have remained hidden to monitoring programs, even for the fastest declining meadows (e.g., Sa Paret; Tables 1 and 2). Power analysis showed that the decline of shoot density by 50% after 2.7 yr for the meadow experiencing the fastest decline (Sa Paret at Cabrera Island) in this study, could only be detected from density counts with statistical confidence (i.e.,  $p < 0.05$ ) if 25 replicate quadrats were counted with a 1.5-yr interval. This is far larger than the effort any monitoring program may allocate, showing the superiority of direct censuses over standard procedures to detect seagrass decline.

The overall decline in *P. oceanica* shoot density observed across the Spanish Mediterranean Coast for the period 2000–2002 results from a combination of multiple causes. These include anthropogenic forcing and climatic disturbances operating at large spatial scales, which deteriorated the meadows. Anthropogenic forcing includes excess nutrient and organic inputs (Marbà et al. 2002; Holmer et al. 2003), along with physical disturbance caused by construction at the coastline (Duarte 2002). *P. oceanica* has been reported to be

highly sensitive to disturbance, such as the storms associated with the passage of low pressure systems or seawater warming (Marbà and Duarte 1997). In the summer of 2001 water temperature in the Balearic Islands reached anomalously high values of 28°C (Díaz-Almela unpublished data). The high water temperatures during the summer of 2001 probably stressed *P. oceanica*, both directly and through accelerated microbial metabolism in the sediments (Duarte 2002; Holmer et al. 2003), resulting in enhanced shoot mortality. The observation of a massive *P. oceanica* flowering event in fall 2001 across the meadows studied (Díaz-Almela unpublished data), provides additional evidence for abnormal stress to *P. oceanica* during the summer of 2001. In addition to high-temperature stress, passage of active low-pressure systems across the Spanish Mediterranean Coast in November 2001 resulted in severe storm and wave action, reaching record high proportions throughout most of the coast. This event resulted in important beach erosion and the detachment of large amounts of seagrass material. These climatic extremes may be responsible for much of the increased decline of *P. oceanica* over the period 2000–2002 relative to that in the preceding two decades. The finding of high specific shoot mortality rates at meadows from Cabrera Island, where visitors are forbidden since it was declared a National Park (i.e., meadows at Cala Santa Maria), points out extreme climatic events as important drivers of shoot mortality. Long time series of *P. oceanica* shoot demography are needed to identify the possible role of these disturbances on the observed seagrass decline. The balance of the role of anthropogenic versus climatic disturbances as causes of seagrass decline probably varies greatly across the meadows studied, such that actions to remediate the decline must be based on meadow-specific diagnostics, which could not be derived from the information presented here. This information is crucial to assess the capacity of the meadows to recover and to evaluate the magnitude of the decline observed.

Quantification of seagrass shoot demographic parameters and detection of on-going meadow decline can only be assessed using annual shoot census in permanent plots for seagrass stands experiencing specific (or per capita) shoot mortality rates  $< 1.0$  yr<sup>-1</sup>, and specific net shoot population growth rates  $> -2.99$  yr<sup>-1</sup> (i.e., shoot density decline not greater than 95% in one year). In order to use this method to detect long-term changes in seagrass shoot populations specific shoot mortality rate should be  $< 0.5$  yr<sup>-1</sup> and specific net shoot population growth rate should be  $> -0.30$  yr<sup>-1</sup> (i.e., shoot density decline not higher than 50% in one year). Populations experiencing changes be-

yond those limits would experience demographic oscillations too broad to be captured in annual census, so that closer observational intervals would be necessary, with an increase in the resources required to assess the annual rates. According to available data on seagrass demographics, annual shoot census would be an appropriated tool to detect decline in meadows of *P. oceanica* (Table 1), *Enhalus acoroides* (Vermaat et al. 1995), *Posidonia australis* and *Amphibolis antarctica* (Marbà and Walker 1999), and slowly declining and colonizing meadows of *Thalassia hemprichii* (Vermaat et al. 1995), *Thalassia testudinum* (e.g., Gallegos et al. 1993; Peterson and Fourqurean 2001) and *Posidonia sinuosa* (Marbà and Walker 1999). The use of shoot census is also restricted to seagrass species or populations with shoot meristems above the sediment surface and sufficiently robust as to accommodate the tags without disturbance.

This study demonstrates the power of direct censuses of seagrass shoots in permanent plots to evaluate the present status of seagrass meadows, and to detect on-going population decline. The study also demonstrates that large-scale monitoring based on direct census is feasible, although this requires significant resources. The average direct costs, excluding other costs such as training of personnel, acquisition of SCUBA gear, etc., required to set up and recensus a set of plots once was calculated at about 1,300 €, which translates into significant resources when scaled to the number of meadows and the geographic spread addressed in the present study. Subsequent visits to the plots revealed important losses of the permanent quadrats, due to storms and anchor disturbance. The resulting half-life of the plots was only about 618 d, which was much shorter than the half-life of *P. oceanica* shoot populations (Table 2). The number of replicate plots required for the long-term monitoring of seagrass meadows using permanent plots should be increased, to double that used here, in order to account for losses with time, also doubling the costs of this approach. Use of direct shoot census is particularly useful to assess recent population dynamics of slow-growing seagrass species, such as *P. oceanica*, where other approaches, such as shoot density monitoring using random quadrats, are ineffective. The results obtained portray a scenario of rapidly declining *P. oceanica* in the Spanish Mediterranean Coast and also provide some insight onto the possible factors involved. The incorporation of direct census of seagrass meadows to monitoring programs elsewhere will help them provide the early-warning signals necessary to assist in creating management decisions to conserve seagrass meadows. At a time that seagrass meadows are undergoing alarming worldwide decline, the results

presented here and the approach demonstrated provide an important basis to support managing policies informing of this problem before the meadows are lost.

#### ACKNOWLEDGMENTS

This study was funded by projects Posicost (IFD97-1654), Monitoring and Managing European Seagrasses. (EVK3-CT-2000-00044 and REN 2000-3091-CE/MAR), and LIFE-Posidonia (LIFE 2000/NAT/E/7303). We are grateful to C. Arrondo, C. Barrón, M. Alomar, and J. Klein for field assistance, and D. Jaume and G. Vizoso for artwork. We thank three anonymous reviewers for their comments.

#### LITERATURE CITED

- ALCOVERRO, T., J. ROMERO, C. M. DUARTE, AND N. I. LÓPEZ. 1997. Spatial and temporal variations in nutrient limitation of seagrass *Posidonia oceanica* growth in the NW Mediterranean. *Marine Ecology Progress Series* 146:155-161.
- BALESTRI, E., L. PIAZZI, AND F. CINELLI. 1998. Survival and growth of transplanted and natural seedlings of *Posidonia oceanica* (L.) Delile in a damaged coastal area. *Journal of Experimental Marine Biology and Ecology* 228:209-225.
- BETHOUX, J. P. AND G. COPIN-MONTEGUT. 1986. Biological fixation of atmospheric nitrogen in the Mediterranean Sea. *Limnology and Oceanography* 31:1353-1358.
- BIGLEY, R. E. AND P. C. HARRISON. 1986. Shoot demography and morphology of *Zostera japonica* and *Ruppia maritima* from British Columbia, Canada. *Aquatic Botany* 24:69-82.
- BUIA, M. C. AND L. MAZZELLA. 1991. Reproductive phenology of the Mediterranean seagrasses *Posidonia oceanica* (L.) Delile, *Cymodocea nodosa* (Ucria) Aschers., and *Zostera noltii* Hornem. *Aquatic Botany* 40:343-362.
- DELGADO, O., J. M. RUIZ, M. PÉREZ, J. ROMERO, AND E. BALLESTEROS. 1999. Effects of fish farming on seagrass (*Posidonia oceanica*) in a Mediterranean bay: Seagrass decline after organic loading cessation. *Oceanologica Acta* 22:109-117.
- DUARTE, C. M. 1991. Allometric scaling of seagrass form and productivity. *Marine Ecology Progress Series* 77:289-300.
- DUARTE, C. M. 1995. Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia* 41:87-112.
- DUARTE, C. M. 2002. The future of seagrass meadows. *Environmental Conservation* 29:192-206.
- DUARTE, C. M. AND C. L. CHISCANO. 1999. Seagrass biomass and production: A reassessment. *Aquatic Botany* 65:159-174.
- DUARTE, C. M., M. A. HEMMINGA, AND N. MARBÀ. 1996. Growth and population dynamics of *Thalassodendron ciliatum*. *Aquatic Botany* 55:1-11.
- DUARTE, C. M., N. MARBÀ, N. AGAWIN, J. CEBRIÁN, S. ENRÍQUEZ, M. D. FORTES, M. E. GALLEGOS, M. MERINO, B. OLESEN, K. SAND-JENSEN, J. URI, AND J. VERMAAT. 1994. Reconstruction of seagrass dynamics: Age determinations and associated tools for the seagrass ecologist. *Marine Ecology Progress Series* 107:195-209.
- DUARTE, C. M. AND K. SAND-JENSEN. 1990. Seagrass colonization: Biomass development and shoot demography in *Cymodocea nodosa* patches. *Marine Ecology Progress Series* 67:97-103.
- DUARTE, C. M., J. TERRADOS, N. S. R. AGAWIN, M. D. FORTES, S. BACH, AND W. J. KENWORTHY. 1997. Response of a mixed Philippine seagrass meadow to experimental burial. *Marine Ecology Progress Series* 147:285-294.
- DURAKO, M. J. 1994. Seagrass die-off in Florida Bay (USA): Changes in shoot demographics in *Thalassia testudinum*. *Marine Ecology Progress Series* 110:59-66.
- EBERT, T. A. AND S. L. WILLIAMS. 2003. Rejoinder to Fourqurean et al. (2003). *Limnology and Oceanography* 48:2074-2075.
- EBERT, T. A., S. L. WILLIAMS, AND P. J. EWANCHUK. 2002. Mortality



- estimates from age distributions: Critique of a method used to study age distributions. *Limnology and Oceanography* 47:600–603.
- FLOS, J. 1985. The driving machine, p. 60–99. In R. Margalef (ed.), *Western Mediterranean*. Pergamon Press, Oxford, U.K.
- FOURQUREAN, J. W., N. MARBÀ, AND C. M. DUARTE. 2003. Elucidating seagrass population dynamics: Theory, constraints, and practice. *Limnology and Oceanography* 48:2070–2074.
- FRONTERA, M., V. FORTEZA, AND P. TOMÁS. 1993. Home i natura: Els usos tradicionals del sòl i la pesca, p. 749–762. In J. A. Alcover, E. Ballesteros, and J. J. Fornós (eds.), *Història Natural de l'Arxipèlag de Cabrera*. Monografies de la societat d'Història Natural de les Illes Balears 2, Editorial Moll-CSIC. Palma de Mallorca, Spain.
- GALLEGOS, M., M. MERINO, N. MARBÀ, AND C. M. DUARTE. 1993. Biomass and dynamics of *Thalassia testudinum* in the Mexican Caribbean: Elucidating rhizome growth. *Marine Ecology Progress Series* 95:185–192.
- GALLEGOS, M., M. MERINO, A. RODRÍGUEZ, N. MARBÀ, AND C. M. DUARTE. 1994. Growth patterns and demography of pioneer Caribbean seagrasses (*Halodule wrightii* and *Syringodium filiforme*). *Marine Ecology Progress Series* 109:99–104.
- HARPER, J. L. 1977. *Population Biology of Plants*. Academic Press, London, U.K.
- HARRISON, P. G. 1993. Variations in demography of *Zostera marina* and *Z. noltii* on an intertidal gradient. *Aquatic Botany* 45: 63–77.
- HEIDELBAUGH, W. S. N. AND W. G. NELSON. 1996. A power analysis of methods for assessment of change in seagrass cover. *Aquatic Botany* 53:227–233.
- HEMMINGA, M. A. 1998. The root/rhizome system of seagrasses: An asset and a burden. *Journal of Sea Research* 39:183–196.
- HEMMINGA, M. A. AND C. M. DUARTE. 2000. *Seagrass Ecology*. Cambridge University Press, London, U.K.
- HOLMER, M., C. M. DUARTE, AND N. MARBÀ. 2003. Fast sulfur turnover in carbonate seagrass (*Posidonia oceanica*) sediments. *Marine Biogeochemistry* 66:223–239.
- JENSEN, S. L., B. D. ROBBINS, AND S. S. BELL. 1996. Predicting population decline: Seagrass demographics and the reconstructive technique. *Marine Ecology Progress Series* 136:267–276.
- JENSEN, S. L., B. D. ROBBINS, AND S. S. BELL. 1997. On the use of the reconstructive technique: Criticisms, comments, and questions. *Marine Ecology Progress Series* 146:305–309.
- KALDY, J. E., N. FOWLER, AND K. H. DUNTON. 1999. Critical assessment of *Thalassia testudinum* (turtlegrass) aging techniques: Implications for demographic inferences. *Marine Ecology Progress Series* 181:279–288.
- KAMERMANS, P., M. A. HEMMINGA, N. MARBÀ, M. A. MATTEO, M. MYOLERA, AND J. STAPEL. 2001. Leaf production, shoot demography, and flowering of the seagrass *Thalassodendron ciliatum* along the east African coast. *Aquatic Botany* 70:243–258.
- KENWORTHY, W. J. AND A. C. SCHWARZSCHILD. 1998. Vertical growth and short-shoot demography of *Syringodium filiforme* in outer Florida Bay, USA. *Marine Ecology Progress Series* 173:25–37.
- KOCH, M. S. AND J. M. ERSKINE. 2001. Sulfide as a phytotoxin to the tropical seagrass *Thalassia testudinum*: Interactions with light, salinity, and temperature. *Journal of Experimental Marine Biology and Ecology* 266:81–95.
- LAUGIER, T., V. RIGOLLET, AND M. L. DE CASABIANCA. 1999. Seasonal dynamics in mixed eelgrass beds, *Zostera marina* L. and *Z. noltii* Hornem. in a Mediterranean coastal lagoon (Thau lagoon, France). *Aquatic Botany* 63:51–69.
- MANZANERA, M., M. PÉREZ, AND J. ROMERO. 1998. Seagrass mortality due to oversedimentation: An experimental approach. *Journal of Coastal Conservation* 4:67–70.
- MARBÀ, N. AND C. M. DUARTE. 1997. Decadal changes in seagrass (*Posidonia oceanica*) growth and environmental change in the Spanish Mediterranean Coastlittoral. *Limnology and Oceanography* 42:800–810.
- MARBÀ, N., C. M. DUARTE, J. CEBRIÁN, S. ENRÍQUEZ, M. E. GALLEGOS, B. OLESEN, AND K. SAND-JENSEN. 1996. Growth and population dynamics of *Posidonia oceanica* in the Spanish Mediterranean Coast: Elucidating seagrass decline. *Marine Ecology Progress Series* 137:203–213.
- MARBÀ, N., C. M. DUARTE, M. HOLMER, R. MARTÍNEZ, G. BASTERRETxea, A. ORFILA, A. JORDI, AND J. TINTORÉ. 2002. Assessing the effectiveness of protection on *Posidonia oceanica* populations in the Cabrera National Park (Spain). *Environmental Conservation* 29:509–518.
- MARBÀ, N. AND D. I. WALKER. 1999. Population dynamics of temperate western Australian seagrasses: Importance of growth and flowering for meadow maintenance. *Marine Ecology Progress Series* 184:105–118.
- MATEO, M. A., J. ROMERO, M. PÉREZ, M. M. LITTLER, AND D. S. LITTLER. 1997. Dynamics of millenary organic deposits resulting from the growth of the Mediterranean seagrass *Posidonia oceanica*. *Estuarine Coastal and Shelf Sciences* 44:103–111.
- MEINESZ, A. AND J. R. LEFÈVRE. 1984. Régénération d'un herbier de *Posidonia oceanica* quarante années après sa destruction par une bombe dans la rade de Villefranche (Alpes-425 Maritimes, France), p. 39–44. In C. F. Boudouresque, J. de Grissac, and J. Olivier (eds.), *International Workshop on Posidonia oceanica Beds*. GIS Posidonie Publisher, Marseille, Spain.
- MOORE, K. A., H. A. NECKLES, AND R. J. ORTH. 1996. *Zostera marina* (eelgrass) growth and survival along a gradient of nutrients and turbidity in the lower Chesapeake Bay. *Marine Ecology Progress Series* 142:247–259.
- OLESEN, B. AND K. SAND-JENSEN. 1994a. Demography of shallow eelgrass (*Zostera marina*) populations—Shoot dynamics and biomass development. *Journal of Ecology* 82:379–390.
- OLESEN, B. AND K. SAND-JENSEN. 1994b. Patch dynamics of eelgrass (*Zostera marina*). *Marine Ecology Progress Series* 106:147–156.
- PATRIQUIN, D. 1973. Estimation of growth rate, production and age of the marine angiosperm *Thalassia testudinum* König. *Caribbean Journal of Science* 13:111–123.
- PÉREZ, M., J. ROMERO, C. M. DUARTE, K. SAND-JENSEN, AND T. ALCOVERRO. 1994. Growth plasticity in *Cymodocea nodosa* stands: The importance of nutrient supply. *Aquatic Botany* 47: 249–264.
- PETERSON, B. J. AND J. W. FOURQUREAN. 2001. Large-scale patterns in seagrass (*Thalassia testudinum*) demographics in south Florida. *Limnology and Oceanography* 46:1077–1090.
- RAMAGE, D. L. AND D. R. SCHIEL. 1999. Patch dynamics and response to disturbance of the seagrass *Zostera novaezelandica* on intertidal platforms in southern New Zealand. *Marine Ecology Progress Series* 189:275–288.
- ROLLON, R. N., N. M. CAYABAY, AND M. D. FORTES. 2001. Vegetative dynamics and sexual reproduction of monospecific *Thalassia hemprichii* meadows in the Kalayaan Island group. *Aquatic Botany* 71:239–246.
- RUIZ, J. M. AND J. ROMERO. 2001. Effects of in situ experimental shading on the Mediterranean seagrass *Posidonia oceanica*. *Marine Ecology Progress Series* 215:107–120.
- SHORT, F. T. AND S. WYLIE-ECHEVARRIA. 1996. Natural and human-induced disturbance of seagrasses. *Environmental Conservation* 23:17–27.
- SHORT, F. T. AND C. M. DUARTE. 2001. Methods for the measurement of seagrass growth and reproduction, p. 155–182. In F. T. Short and R. G. Coles (eds.), *Global Seagrass Research Methods*. Elsevier Science B. V., Amsterdam, The Netherlands.
- SHORT, F. T. AND R. G. COLES. 2001. *Global Seagrass Research Methods*. Elsevier Science B. V., Amsterdam, The Netherlands.

- VERMAAT, J., N. AGAWIN, C. M. DUARTE, M. D. FORTES, N. MARBÀ, AND J. URI. 1995. Meadow maintenance, growth and productivity of a mixed Philippine bed. *Marine Ecology Progress Series* 124:215-225.
- VIDONDO, B., C. M. DUARTE, A. L. MIDDELBOE, K. STEFANSEN, T. LUTZEN, AND S. L. NIELSEN. 1997. Dynamics of a landscape mosaic: Size and age distributions, growth, and demography of seagrass *Cymodocea nodosa* patches. *Marine Ecology Progress Series* 158:131-138.

#### SOURCE OF UNPUBLISHED MATERIALS

FOURQUREAN, J. Unpublished Data. Department of Biology and Southeast Environmental Research Center, Florida International University, Miami, Florida 33199.

*Received, January 16, 2004*

*Revised, July 30, 2004*

*Accepted, September 21, 2004*