

Magnitude of herbivory in
Posidonia oceanica (L.) Delile
and factors responsible
for spatial variation



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PUBLICACIÓ 1:

Extensive direct measurements of *Posidonia oceanica* defoliation confirm the importance of herbivory in temperate seagrass meadows

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RESUM:

Les taxes de defoliació exercides pel peix *Sarpa salpa* (L.) i per l'eriçó de mar *Paracentrotus lividus* (Lmk.) van ser avaluades mitjançant mètodes directes (pèrdues de àrees foliars) i indirectes (marques d'acció). El mostreig es va dur a terme estacionalment en deu praderies superficials de *Posidonia oceanica* (L.) de la costa mediterrània noroccidental, comprenent una superfície de més de 300 km. Els resultats indiquen que una gran proporció de la producció foliar primària (ca. 57%) es perd a conseqüència de la pressió exercida pels herbívors, si bé aquesta està subjecta a una considerable variació en l'espai. Tanmateix, els patrons de defoliació van mostrar una gran variabilitat anual, amb màximes durant l'estiu que poden excedir fins a ca. 2.5 vegades la producció foliar, i mínims durant l'hivern. De promig, *Sarpa salpa* és responsable d'un 70% de l'herbivorisme (ca. 40% de la producció foliar) i *Paracentrotus lividus* del restant 30% (ca. 17% de la producció foliar). La comparació entre mètodes d'avaluació directa i indirecta va evidenciar l'existència d'importants discrepàncies i suggereix que aquests últims són inadequats per arribar a estimes exactes de la pressió de l'herbivorisme.

Aquest estudi evidencia que, als ecosistemes de *Posidonia oceanica*, la pèrdua de biomassa foliar per l'efecte dels herbívors no és un procés marginal sinó generalitzat que ocorre en taxes molt més elevades del que havia estat estimat prèviament per mètodes indirectes (2%), replantejant així el paradigma de la importància de l'herbivorisme en els ecosistemes temperats.



INTRODUCTION

Herbivory is considered as one of the major forces shaping plant communities (Cyr & Pace 1993), playing a major role not only in trophic organization, but also in the control of plant abundance, distribution, and evolution. Yet, direct consumption of seagrass has been often considered to play a minor role. This is based on the generally low grazing rates reported, which represents about 10% of annual net aboveground primary production (Kikuchi & Peres 1977, Thayer et al. 1984, Zieman & Zieman 1989). Such low rates have been related to high C: N ratios in seagrass leaves, which have a lesser nutritional value than algae (Duarte 1990), as well as to the presence of cellulose, which cannot be easily digested by many marine organisms, and may act as a structural deterrent (Bjorndal 1980). Although sea turtles, sirenians (i.e. manatees and dugongs) and waterfowls are recognized as important seagrass consumers (Preen 1995, Nakaoka & Aioi 1999, Ganter 2000, Lefebvre et al. 2000), in their absence, herbivory has been usually considered as a marginal process in seagrass ecosystems. Nevertheless, there is increasing worldwide evidence that pressure exerted by marine herbivores other than these large vertebrates may also play an important role in the energetics and interaction network of seagrass ecosystems (see review by Valentine & Heck 1999, Heck & Valentine 2006). For instance, many species of sea urchins (Valentine & Heck 1991, Valentine et al. 1997, Valentine et al. 2000, Alcoverro & Mariani 2002) and herbivorous fish (Kirsch et al. 2002, Alcoverro & Mariani 2004, Tomas et al. 2005a) throughout the world feed regularly on seagrasses and can determine, at least in part, their distribution, abundance or the structure of their associated communities. However, up to date only few studies have used direct methods to estimate total rates of seagrass defoliation by herbivores and assessed the variability at the large-scale (but see Kirsch et al. 2002, Tomas et al. 2005a). These types of studies are necessary to clarify the role of grazing in seagrass ecosystems.

In particular, herbivory losses on the endemic Mediterranean species *Posidonia oceanica* (L.) Delile are amongst the lowest reported for seagrasses (Valentine & Heck 1999) with values around 2% of leaf production (Cebrián et al. 1996, 1997). These estimates,



although obtained from large-scale data (900 km), were based on indirect measures of herbivore bite marks. Such low values would seem in conflict with the relatively high abundance of the two main seagrass herbivores, the sea urchin *Paracentrotus lividus* (Lmk.) (Boudouresque & Verlaque 2001) and the fish *Sarpa salpa* (L.) whose schools are common in shallow Mediterranean waters (seagrass meadows and rocky bottoms; Verlaque 1990). Indeed, a recent study using direct measurements of seagrass losses has provided evidence that herbivory by *S. salpa* in undisturbed *P. oceanica* meadows can be substantial, with defoliation reducing up to 50% plant biomass (Tomas et al. 2005a). Moreover, overgrazing events by *P. lividus* and *S. salpa* have been repeatedly observed (e.g. Kirkman & Young 1981, Nedelec & Verlaque 1984, Ruiz et al. 2001, Tomas et al. 2005a). All these facts highlight the need for a broader re-assessment of the importance of herbivory in Mediterranean meadows.

Hence the objective of the present study was to re-examine the importance of herbivory in the temperate *Posidonia oceanica* ecosystem by quantification of the defoliation rates exerted by the two main *P. oceanica* consumers, the fish *Sarpa salpa* and the sea urchin *Paracentrotus lividus*. To do this, direct methods to estimate seagrass defoliation were undertaken across a spatial scale as large as possible (ca. 300 km), and taking into account the important temporal variability in fish activity (Tomas et al. 2005a).

MATERIALS AND METHODS

Study site and sampling design

Leaf production (Romero 1989) and herbivore pressure (Tomas et al. 2005a) are highest on shallow waters. The fish *Sarpa salpa* is commonly seen feeding at depths between 3-10 m (but up to 20 m), particularly during the warm period (i.e. late June to late September; Harmelin-Vivien 1983, Tomas et al. 2005a), and densities of the sea urchin *Paracentrotus lividus* are higher in the upper sublittoral (0.5 to 10 m, Boudouresque & Verlaque 2001). Therefore, the present study was undertaken within the depth range of maximum herbivore density (i.e. 5-8 m depth), where herbivores can potentially have a relevant effect on the



local communities of *Posidonia oceanica*. Seagrass defoliation by herbivores was examined in ten shallow *P. oceanica* beds in the Northeast Spanish coast and the south of France (NW Mediterranean), embracing a total extension of ca. 300 km. Selected sites were Montroig, Torredembarra, Fenals, Giverola, Medes Islands, Montgó, Montjoi, Port Lligat, Jugadora and Banyuls (see Fig. 1).

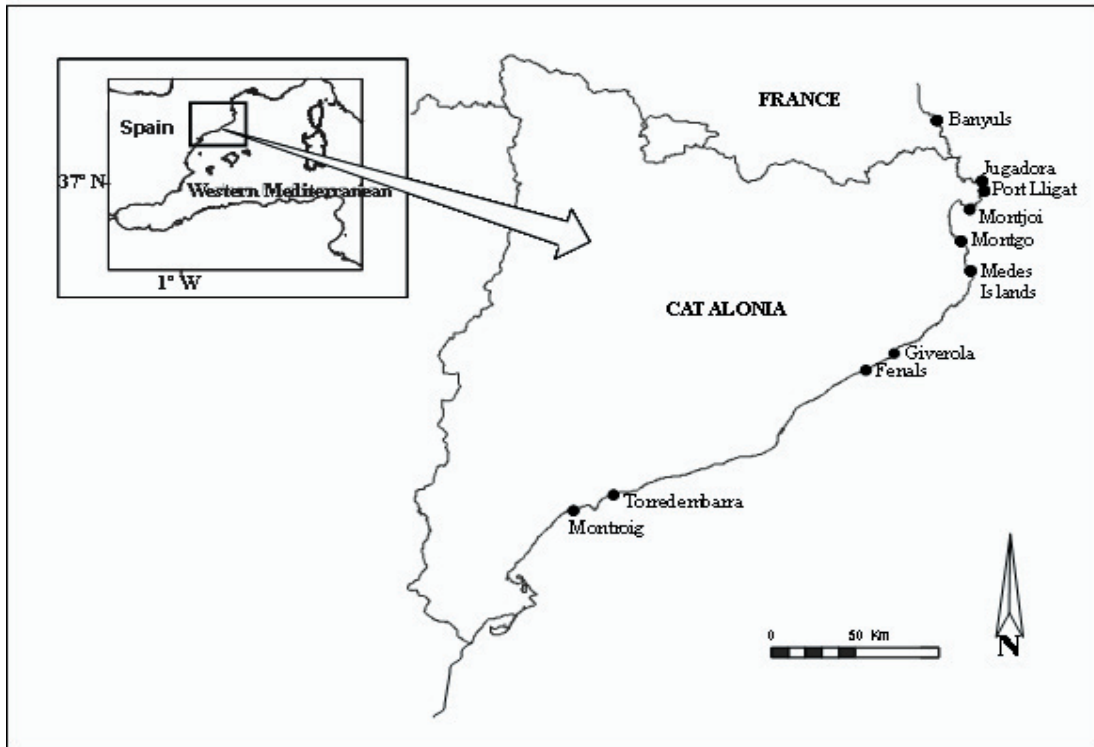


Fig. 1. Map of the NW Mediterranean showing the position of the study sites in the continental Spanish coast.

Sampling was performed at four different times of the year, to encompass the seasonal variation in densities and/or activity of herbivores, especially of *Sarpa salpa*. Large schools of this species start appearing in mid spring, as they leave wintering areas at greater depths (Verlaque 1990, Peirano et al. 2001). Fish densities in shallow seagrass beds are highest during the summer, decrease during the fall and reach annual minimums from late autumn to early spring (Verlaque 1990, Harmelin-Vivien & Francour 1992, Francour 1997, Peirano et al. 2001, Tomas et al. 2005a). Sampling was accordingly conducted in June 2004 (appearance period), August 2004 (period of maximum fish abundance), November 2004 (departure



period) and March 2005 (period of minimum abundance).

Measurements of seagrass defoliation and productivity

A tethering experiment (Mariani & Alcoverro 1999, Kirsch et al. 2002) was conducted to obtain direct quantification of *Posidonia oceanica* defoliation by macroherbivores. At each site, we collected 30 *P. oceanica* shoots haphazardly at 5-8 m depth, depending on the site. Care was taken to select shoots that had sufficient vertical rhizome to allow the safeguarding of leaves (typically 4-7) throughout the experiment. After collection, the tips of the leaves were cut to remove scars left by previous herbivore attacks, and the number of leaves and their length (to the nearest mm) were recorded. Shoots presenting leaves with lateral bites were discarded. The base of the leaves was also marked using a modified Zieman method (Romero 1989) in order to detect possible leaf elongation of uprooted shoots during the experiment. In order to optimize retrieval of samples, individual shoots were attached by their vertical rhizome to a labeled line of pickets, each line carrying a total of 5 labeled pickets. Shoots within a line were separated from each other by approximately 1.5 m. Four lines were set up inside the meadow at each site at the same depth of collection, lines being placed one approximately after the other and thus, each picket considered as an independent sample. When inserting pickets into the sediment, maximum care was taken to ensure that leaves were neither above nor below the average height of the leaf canopy. During the manipulation period, shoots were kept underwater to avoid potential stress and loss of epiphytes, thus minimizing potential tethering artefacts.

Tethered shoots were left at each study site during 2 weeks, as it has been shown that no significant changes in leaf quality occur during that period of time (Tomas et al. 2005a) and then retrieved for further sorting. Once in the laboratory, leaf length and width, and the number of leaves per shoot that were lost, broken (wave action), intact, or attacked by grazers and the numbers of bite marks per leaf were recorded. Both herbivores leave bite marks of identifiable shape (Boudouresque & Meisnez 1982). On the one hand, the sea urchin grinds seagrass leaves using the Aristotle's lantern which results on irregularly slashed scars. On the



other, the morphology of the fish jaw apparatus produces neat, semicircular bites (see Fig. 2a-b). Therefore, accurate estimates of leaf area removed by each of these bites can be obtained by scanning the leaves.

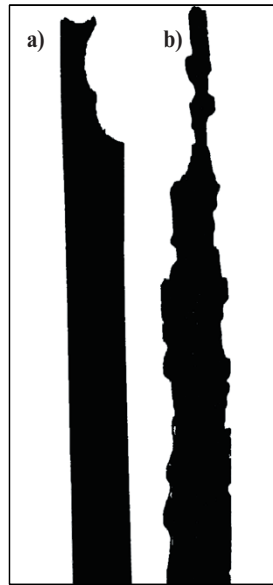


Fig. 2. Image of *Posidonia oceanica* leaves displaying morphologically distinctive bite marks of a) *Sarpa salpa* and b) *Paracentrotus lividus*.

Leaf elongation rate ($\text{cm}^2 \text{shoot}^{-1} \text{day}^{-1}$) of tethered shoots (the purpose of such assessment being only to correct defoliation estimates) was determined by dividing the area of new tissue produced by the number of days elapsed since marking (i.e. 15 d). These data were available for the sampling events in August, November and March, whereas those of June were estimated as the average between August and March values.

This extrapolation might represent a source of error but elongation rates of uprooted shoots were in any case low compared to attached shoots.

Seagrass defoliation was estimated by subtracting the leaf area remaining from each initial shoot measurement and by adding the growth area of the tethered shoots obtained after 2 weeks, and were expressed in $\text{cm}^2 \text{shoot}^{-1} \text{day}^{-1}$ (Kirsch et al. 2002). Leaves that were lost during this period were not included in the analyses and might underestimate the total

defoliation rates. The number of bite marks per shoot (the indirect method that has generally been used to estimate seagrass herbivory) and the leaf tissue consumed by each herbivore provided the means to test the accuracy of indirect versus direct methods to calculate herbivore pressure.

Monthly values of leaf productivity at the depth of study (i.e. 5 to 8 m) were compiled from available literature from different years and locations in the North-western Mediterranean. Rates of leaf production for each month of the year were expressed in terms of $\text{cm}^2 \text{ shoot}^{-1} \text{ d}^{-1}$ (i.e. leaf elongation) and then compared to seagrass defoliation obtained during the four different sampling times. To estimate annual defoliation rates, we assigned the obtained values to appropriate intervals as follows: January to May, March rates; June to July, June rates; August to September, August rates; October to November, November rates; December, March rates. These intervals were assigned based on available knowledge on the seasonal feeding behaviour of *Sarpa salpa* (e.g. Verlaque 1990, Harmelin-Vivien & Francour 1992, Francour 1997, Peirano et al. 2001, Jadot et al. 2002, Tomas et al. 2005a), and can be considered conservative, as we used a 6-months period (i.e. December-May) as the period of low feeding activity, which is an upper estimate. Moreover, our data have good temporal resolution during the period of maximum consumption.

Statistical analyses

Variability in the defoliation rates by *Sarpa salpa* and *Paracentrotus lividus*, and in the number of bite marks per shoot was assessed using a two-way ANOVA (Time fixed; Site random). ANOVA assumptions of normality (Chi-square test) and heteroscedasticity (Cochran's test) of data were not always achieved by transformation. Nonetheless, Underwood (1981) has indicated that despite violation of assumptions, the ANOVA F statistic is still able to provide robust results provided that the working sample size is large enough. Besides, for all analyses, the level of significance was set to $p < 0.01$ to minimize the risk of making a type I error (Underwood 1997). Significant differences among sampling Times and Sites were further investigated by Student-Newman-Keuls (SNK) post hoc comparisons.



The existence of an association between the number of bites by each herbivore (i.e. *Sarpa salpa* and *Paracentrotus lividus*), and their defoliation rate per shoot was assessed by regression analyses. To this end, shoots from each sampling site and period were pooled and average values (i.e. 10 Sites x 4 sampling Times) regressed to observed measures of defoliation.

RESULTS

Growth of tethered shoots

Elongation of uprooted tethered shoots was detected in all sampling times, with highest values in November (0.48 ± 0.055 S.E $\text{cm}^2 \text{shoot}^{-1} \text{d}^{-1}$), minimum in March (0.195 ± 0.036), and intermediate in August (0.26 ± 0.018 ; see Fig. 3). These values represented about one third of the growth of unmanipulated shoots, being the seasonal pattern different as well (Alcoverro et al. 1995).

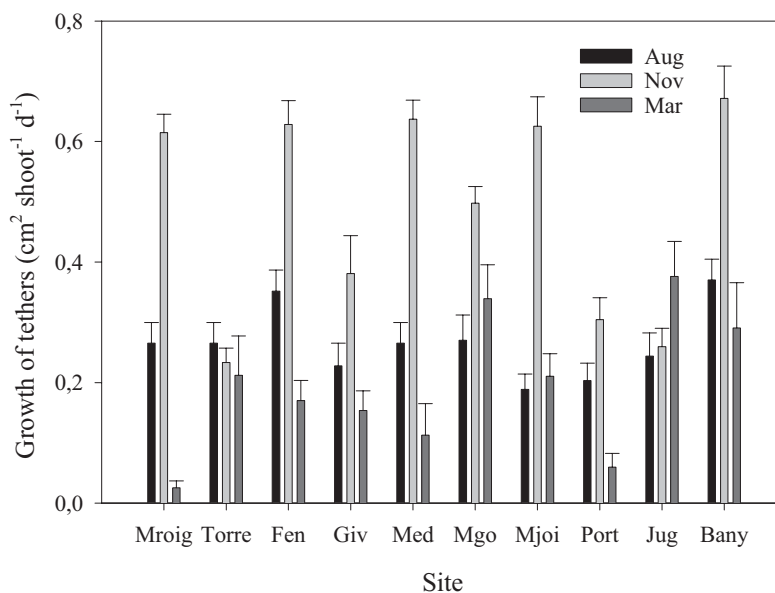


Fig. 3. Temporal differences in the growth of *Posidonia oceanica* tethers at each study site. Errors are S.E.

Seagrass defoliation

Mean annual defoliation of seagrass (i.e. all months and sites pooled) was estimated on ca. 0.523 ± 0.17 S.E $\text{cm}^2 \text{shoot}^{-1} \text{d}^{-1}$ while the mean leaf production obtained from monthly records available in the compiled literature (see Fig. 4) was ca. 0.91 ± 0.25 S.E $\text{cm}^2 \text{shoot}^{-1} \text{d}^{-1}$. Therefore, seagrass defoliation was grossly estimated as ca. 57% of leaf production and *Sarpa salpa* was confirmed as the main herbivore ($t_{39} = 3.68$; $p < 0.001$). In an annual basis (i.e. the mean resulting from pooling defoliation rates obtained from estimates of the 4 sampling times; see methods), fish accounted for mean values of seagrass defoliation of ca. 0.365 ± 0.08 $\text{cm}^2 \text{shoot}^{-1} \text{d}^{-1}$ (ca. 70% of total annual defoliation) whereas the sea urchin *Paracentrotus lividus* accounted for a lower rate (ca. 0.158 ± 0.04 $\text{cm}^2 \text{shoot}^{-1} \text{d}^{-1}$; ca. 30% of total annual defoliation).

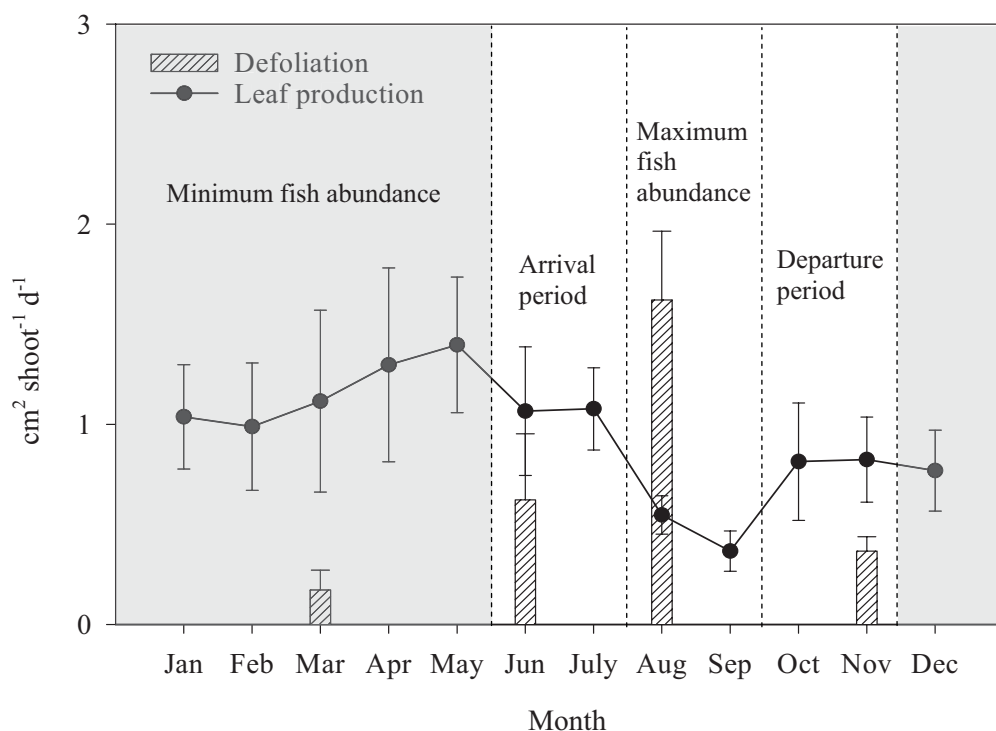


Fig. 4. Vertical bars indicate differences in the total rates of defoliation (i.e. *Sarpa salpa* and *Paracentrotus lividus*) at each sampling time (all Sites pooled). Simple straight lines show the monthly trends of leaf productivity compiled from the literature: Ott 1980, Wittmann 1984, Romero 1989, Esteban et al. 1990, Alcoverro et al. 1995, Cebrián et al. 1997. Dotted lines indicate the coherent periods for which measured rates of defoliation have been made extensive in the estimation of the total annual loss to herbivory (i.e. 57% of annual leaf production). Error bars are S.E.



Total seagrass defoliation during the study (i.e. *Sarpa salpa* and *Paracentrotus lividus*) showed both important spatial differences and a significant temporal variability (Table 1a; Fig. 5a-d).

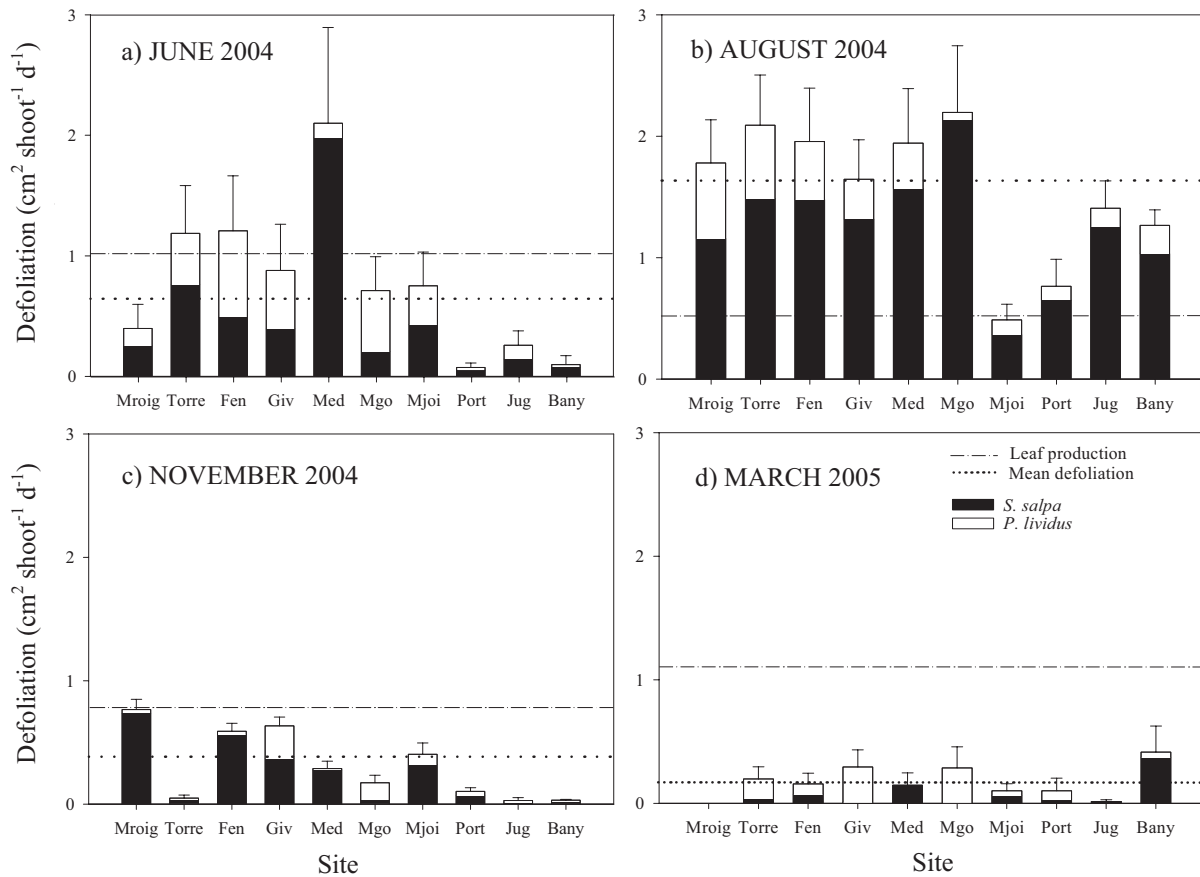


Fig. 5. Temporal differences in defoliation rates of *Posidonia oceanica* by *Sarpa salpa* and *Paracentrotus lividus* at each study site. Dotted lines stand for average values of leaf production from the literature expressed in cm² shoot⁻¹ d⁻¹ (see references in Fig. 4) and for mean seagrass losses to herbivores at each study site. Errors are S.E.

Differences among sites were generally high throughout the year; however, variability was higher during sampling events in late spring and during the fall and lowest in summer ($CV_{\text{jun}} = 96\%$, $CV_{\text{aug}} = 36\%$, $CV_{\text{nov}} = 80\%$, $CV_{\text{mar}} = 72\%$). In general terms, herbivore defoliation was clearly higher than leaf production in summer and lower in autumn and winter, while in early summer (i.e. June) it showed important variations subjected to the arrival of *Sarpa salpa* to each site.



Table 1. ANOVA results on seagrass losses to herbivores at the 4 different sampling times a) total defoliation b= defoliation by the fish *Sarpa salpa*; and c) defoliation by the sea urchin *Paracentrotus lividus* (Mar = March, Jun = June, Aug = August, Nov = November). C stands for Cochran's C statistic. Significant results are given in **bold**.

ANOVA	a) Total seagrass defoliation				b) Defoliation by <i>S. salpa</i>				c) Defoliation by <i>P. lividus</i>				
	Source of variation	df	MS Error	F	p	MS Error	F	p	MS Error	F	p	MS Error	F
Sampling Time = T	3	60.810	2.5058	24.267	0.0000	41.126	2.1646	18.999	0.0000	2.6678	0.4027	6.6243	0.0017
Site = S	9	5.115	0.8716	5.869	0.0000	2.641	0.7576	3.486	0.0003	0.8283	0.2443	3.3898	0.0004
T x S	27	2.506	0.8716	2.875	0.0000	2.165	0.7576	2.857	0.0000	0.4027	0.2443	1.6482	0.0212
		Transformation: -				Transformation: -				Transformation: -			
		C = 0.130; $p > 0.05$				C = 0.157; $p > 0.05$				C = 0.201; $p > 0.05$			
		SNK (T)				SNK (T)				SNK (T)			
		Mar < Nov < Jun < Aug				Mar < Jun = Nov < Aug				Mar < Jun = Aug < Nov			
		SNK (S)				SNK (S)				SNK (S)			
		P ≤ J = Mj = B ≤ Mr = Mg =				P = Mj = J = B = G = Mr =				P = J = B ≤ M = Mj = Mr =			
		G = T = F = M				T = Mg = F < M				Mg = T = F = G			



Hence, defoliation by fish showed remarkable spatial and temporal variation depending on the total period of time that fish remained in the shallow meadow (significant Site x Time interaction) though in general terms, defoliation increased from the sampling time in spring ($0.47 \pm 0.18 \text{ cm}^2 \text{ shoot}^{-1} \text{ d}^{-1}$), to mid summer ($1.24 \pm 0.15 \text{ cm}^2 \text{ shoot}^{-1} \text{ d}^{-1}$) and decreased in fall ($0.24 \pm 0.08 \text{ cm}^2 \text{ shoot}^{-1} \text{ d}^{-1}$) and winter (March; $0.075 \pm 0.03 \text{ cm}^2 \text{ shoot}^{-1} \text{ d}^{-1}$) (Table 1b; Fig. 5a-d). Similarly, spatial differences in rates of seagrass defoliation by *Paracentrotus lividus* were connected to the time of the sampling event (significant interaction Site x Time). Recorded values for this species were generally lower than those of *S. salpa* except for the winter sampling, when fish densities are at their lowest values. On the other hand, the influence of the sampling time was also made evident by generally higher defoliation rates in spring-summer ($0.29 \pm 0.07 \text{ cm}^2 \text{ shoot}^{-1} \text{ d}^{-1}$) and minimums in fall-winter ($0.08 \pm 0.03 \text{ cm}^2 \text{ shoot}^{-1} \text{ d}^{-1}$) (Table 1c; Fig. 5a-d).

Only a low percentage of the leaf losses recorded during the different sampling times ($2 \pm 1.2 \%$ in June, $2 \pm 0.9 \%$ in August, $4.7 \pm 4.4 \%$ in November and $3.9 \pm 1.8 \%$ in March) were attributed to mechanical breakage (wave action or other causes).

Direct vs. indirect methods

Frequency of *Sarpa salpa* bite marks also exhibited strong temporal and spatial variation, but post hoc comparisons indicated only two different groups with maximum values in August and minimum in March (see Table 2a). In contrast, spatial but no temporal differences were detected in sea urchin marks (Table 2b) despite observed differences in direct rates of seagrass defoliation (Table 1c). When mean values for each site and sampling time were regressed together ($n = 40$), only a weak association was found between defoliation rates and bite marks ($R^2 = 0.29$; $p < 0.01$ and $R^2 = 0.14$; $p < 0.05$, for both *S. salpa* and *Paracentrotus lividus*, respectively; Fig. 6).

ANOVA		b) <i>S. salpa</i> bite marks					c) <i>P. lividus</i> bite marks			
Source of variation	df	df Error	MS	MS Error	F	p	MS	MS Error	F	p
Time = T	3	670	890.28	212.61	4.187	0.0148	2.3578	2.6172	2.6172	0.4537
Site = S	9	670	135.71	13.686	9.916	0.0000	4.3594	0.9009	4.8390	0.0000
T x S	27	670	212.61	13.686	15.534	0.0000	2.6182	0.9009	2.9062	0.0000
Transformation: - C = 0.264; p > 0.05							Transformation: - C = 0.09; p > 0.05			
SNK (T)										
Mar = Jun < Nov = Aug										
SNK (S)					SNK (S)					
P ≤ J = B = Mj = T ≤ M =					J = P = M ≤ Mr = Mj = B =					
G ≤ F = Mg = Mr					F = T = G = Mg					

Table 2. ANOVA results on a) number of *Sarpa salpa* and b) *Paracentrotus lividus* bite marks after each time collection of tethered shoots (Mar = March, Jun = June, Aug = August, Nov = November). C stands for Cochran's C statistic. Significant results are given in **bold**.

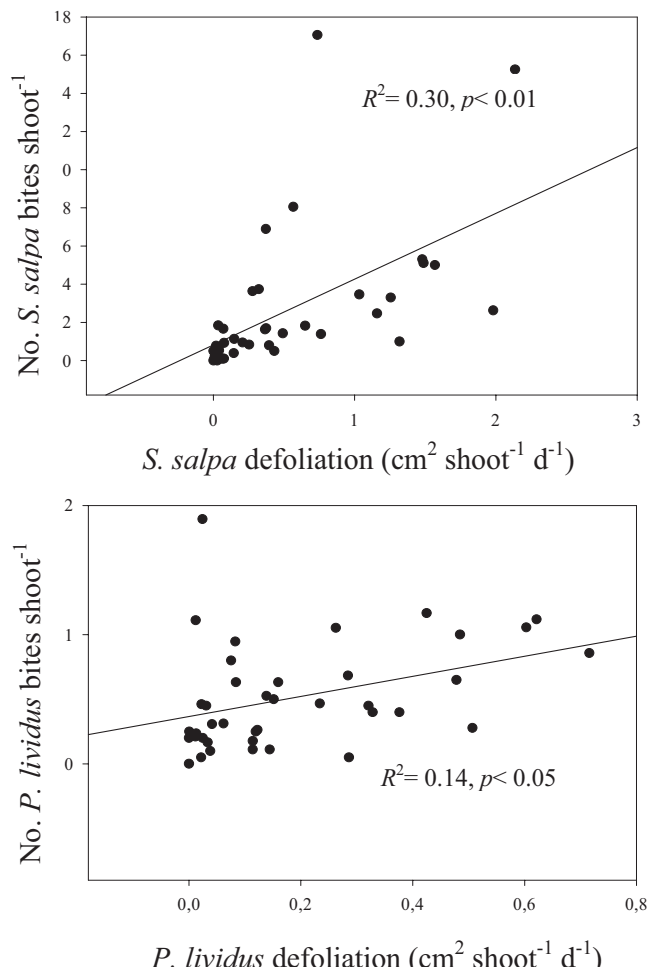


Fig.6. Relationship between the numbers of bite marks (i.e. indirect method) and the mean defoliation rates (i.e. direct method) by a) *Sarpa salpa* and b) *Paracentrotus lividus* at each study site (all sampling times included).

DISCUSSION

The results exposed here evidence the existence of a substantial defoliation of *Posidonia oceanica* in the examined meadows, reaching a gross annual estimate of ca. 57% of the annual leaf production. This is in contrast with previous reports obtained over a comparable depth range and geographic area (2%, Cebrián et al. 1996, 1997) using indirect estimates based on bite marks. In summer, since *Sarpa salpa* feeds in large schools (Harmelin-Vivivien 1983, Verlaque 1990) and aggregations ranging from 2-3 individuals of *Paracentrotus lividus* are not rare (Boudouresque & Verlaque 2001), repeated attacks to the same leaf may mask the marks of previous attacks, causing underestimation of defoliation rates (see Tomas et al. 2005a). Overall, herbivores are shown to play a much more important role in *P. oceanica* shallow meadows than previously thought, which is in accordance with recent views on seagrass ecosystems, whether tropical, subtropical or temperate (Valentine et al. 1997, Ganter 2000, Alcoverro & Mariani 2002, Kirsch et al. 2002, Alcoverro & Mariani 2004).

Sarpa salpa alone accounted for 70% of total annual losses to herbivores (ca. 40% of leaf production). Indeed, this species was consistently responsible for the majority of the removed leaf material in all the study sites and during most of the year, confirming the preeminence of fish in *Posidonia oceanica* herbivory (Cebrián et al. 1996, Alcoverro et al. 1997, Peirano et al. 2001). Defoliation by *S. salpa* clearly differed among sampling times (contribution to total seagrass leaves' losses from 80% in August to less than 50% in March). These differences are most probably caused by the seasonal migratory and feeding behaviour of this species (Verlaque 1990, Harmelin-Vivien & Francour 1992, Francour 1997, Peirano et al. 2001, Tomas et al. 2005a) which rules temporal variability in overall defoliation rates. However, spatial differences in the timing of obtained defoliation rates can be, at least in part, attributed to spatial differences in the periods of arrival and departure of fishes in spring and fall, respectively. From June to September, variability in the activity of *S. salpa* has been



associated to undergoing differences in the occupation of homing sites (either persistent or intermittent during the 24-hours cycle) depending on the local environment (Jadot et. al. 2002). For instance, spatial differences may arise from variability in local hydrodynamic conditions since shallow sheltered sites seem to sustain greater fish biomass than those unsheltered and/ or varying depth transitions (Francour 1997). Nevertheless, it does not seem to be the case of this study, since most of the study sites were located in sheltered areas and those few that were not, such as Torredembarra and Fenals, displayed important rates of defoliation (see Fig. 5). In contrast, other sources of variability such as fishing pressure and meadow size will need to be further investigated.

Sea urchins accounted for the remaining 30% of total annual losses to herbivores (i.e. 17% of leaf production). Defoliation rates by sea urchins also differed among sampling times, although less markedly than for fishes. These differences can be attributed to the influence of seasonal variables on the feeding activity such as temperature and the nature and abundance of trophic resources (Régis 1979, Frantzis & Grémare 1992). It is also possible that some underestimation of sea urchin defoliation occur in summer, in benefit of that of *Sarpa salpa*, due to the masking effect caused by the very high fish activity.

The effects of such important leaves' losses on the plant cannot be assessed from our data. It is clear that leaf growth and defoliation by herbivores are uncoupled. Growth exceeds defoliation most of the year, but defoliation largely exceeds growth in summer, causing reduction in leaf biomass and growth (Tomas et al. 2005a). In that period leaf production is at its annual lowest (Ott 1980, Romero 1989, Alcoverro et al. 1995, Cebrián et al. 1997), and the products of leaf photosynthesis accumulates as carbohydrates reserves in belowground organs (Alcoverro et al. 2001a). It is therefore possible that the decrease in leaf area caused by intense summer grazing would reduce plant reserves for over-wintering. However, it is also possible that biomass (including epiphytes) removal would alleviate the negative effect caused by self-shading (Dalla Via et al. 1998). In any case, strong grazing by *Sarpa salpa* in summer appears to be a relatively common phenomenon in shallow meadows which have persisted during decades (Harmelin-Vivien 1983, Velimirov 1984, Verlaque 1990, Tomas et



al. 2005ab). The period of higher herbivore activity coincides with the annual lowest nutrient content in seagrass leaves (Alcoverro et al. 1995, 1997) evidencing that N is not the force driving the feeding behaviour of *S. salpa*.

In the light of the new evidence obtained on the importance of herbivory processes in shallow *Posidonia oceanica* meadows, our views on carbon fluxes in such ecosystems should be modified, as the carbon transfer from the plant to higher levels becomes a major pathway (Fig. 7).

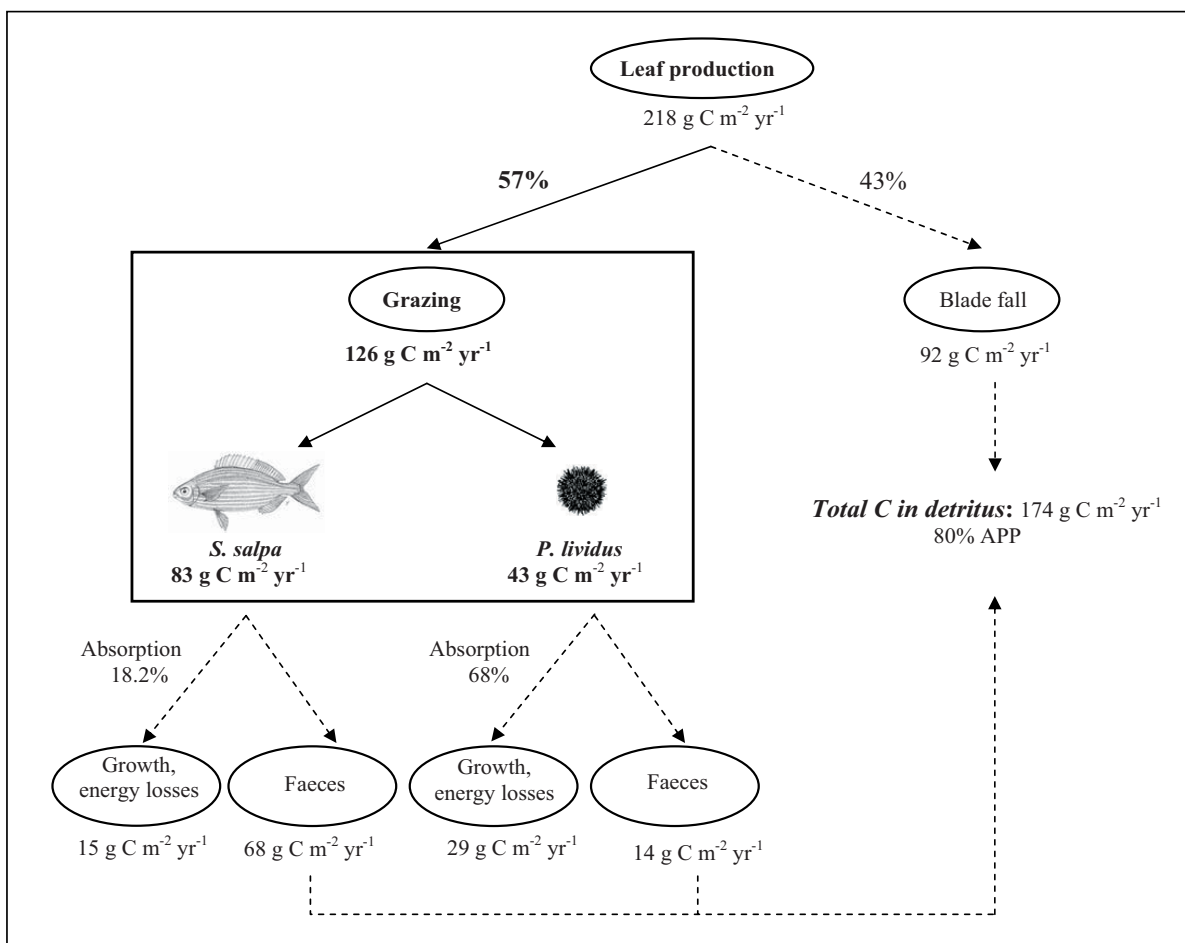


Fig. 7. Mean carbon fluxes in a Mediterranean *Posidonia oceanica* meadow from the continental coast. Values from this study are indicated in bold within the smaller square. Leaf productivity was calculated from the literature (see Fig. 4 for references) and then transformed in $\text{g C m}^{-2} \text{ yr}^{-1}$ with shoot density values for the same region in Alcoverro et al. 1995, Marbà et al. 1996a, Alcoverro et al. 2001b. Absorption efficiency for *S. salpa* from Velimirov 1984, and absorption efficiency for *P. lividus* from Frantzis & Grémare 1992.



However, in this budget model is necessary to remark that the amount of primary production entering the secondary food web through herbivory corresponds to the maximum possible estimate, assuming that the totality of defoliated tissues are consumed by herbivores. Consumption values for *S. salpa* may be slightly overestimated due to the fact that lateral bites exerted by large individuals may enhance leaf break by the effect of wave action; however, these cases were rare. Apparently, and due to the differential absorption efficiencies of *S. salpa* and *P. lividus* (ca. 18.2% and 68%, respectively; see Fig. 7 for references) the amount of seagrass C potentially reaching higher consumer levels through the sea urchin is higher ($29 \text{ g C m}^{-2} \text{ yr}^{-1}$) than that through the fish ($15 \text{ g C m}^{-2} \text{ yr}^{-1}$), if well this species allocates most of the ingested energy in respiration, excretion and secretion and only a small part to growth (Fernandez & Boudouresque 2000). However, the fraction of the primary production entering the litter stock, both by blade fall and by faecal rests is still the largest, with an estimate of ca. 80% of leaf production, confirming the importance of the detritic pathway (on average 70% of it; Pergent et al. 1994).

Given the bathymetric distribution of herbivores and the direct rates of seagrass leaves' losses to herbivory reported in this study there is enough evidence supporting that shallow *Posidonia oceanica* meadows (i.e. 5-8 m) are subjected to a differential functioning than those at greater depths in terms of both control of aboveground biomass and C flux. In fact, Pergent et al. (1997) evaluated the fate of primary production at depths ranging from 10 to 20 m and estimated that a lesser 3-10% of the C was lost to herbivores. Therefore, the productivity of deep seagrass meadows is closely controlled by the light gradient (Romero 1989, Marbà et al. 1996b) whereas herbivory pressure in shallow meadows may have a greater influence than previously thought.

In conclusion, this work strongly supports that the importance of herbivory in shallow *Posidonia oceanica* meadows in the Western Mediterranean is not simply anecdotal, and the reported cases of intense grazing (e.g. Ruiz et al. 2001, Tomas et al. 2005a) could be more the rule than the exception. Equally, the data we have presented suggest that the conventional



perception of temperate seagrass meadows as systems regulated by abiotic variables including nutrient dynamics needs to be reevaluated also in other regions and highlights the importance of using adequate (i.e. direct) methods to estimate seagrass leaves' losses to herbivores in the field.

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