

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



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## PUBLICACIÓ 2:

### Habitat loss and fishing pressure alter herbivory in *Posidonia oceanica* seagrass beds

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RESUM:

La influència de la pèrdua d'hàbitat i la pressió pesquera a les poblacions de *Sarpa salpa* (L.) i *Paracentrotus lividus* (Lmk.) i a les seves taxes d'herbivorisme va ser investigades a nou praderies superficials de la Mediterrània Noroccidental amb diferent disponibilitat de *Posidonia oceanica* (L.) Delile (densitat, cobertura i àrea de la praderia), dins i fora d'àrees protegides.

L'efecte de la pressió pesquera va ser avaluat mitjançant un mostreig asimètric on una reserva marina (MPA, protegida durant més de vint anys) es va comparar amb tres àrees no protegides (controls), respectivament per praderies de mitjana i petita mida. L'efecte de la disponibilitat de *Posidonia oceanica* va ser investigat mitjançant l'anàlisi de regressió amb la mida de la praderia com a variable explicativa. Les localitats incloses dins l'anàlisi van ser aquelles on no existeix pressió pesquera. L'abundància i la distribució de talles del peix herbívor *Sarpa salpa* i de l'eriç de mar *Paracentrotus lividus*, així com les seves taxes d'herbivorisme sobre les fulles de *P. oceanica* van ser quantificades a cada localitat i en funció dels dos dissenys de mostreig.

Independentment del tamany de l'hàbitat, les poblacions de *Sarpa salpa* (sobretot els individus de ca. 30 cm) van assolir una major biomassa a les reserves marines, mentre que l'abundància de *Paracentrotus lividus* va mostrar un cert efecte de la depredació en praderies petites. L'herbivorisme exercit per *S. salpa* va reflectir aquestes tendències: assolir majors valors dins d'àrees protegides, mentre que els valors van ser inferiors per a *P. lividus* dins l'àrea protegida de menor tamany. Tanmateix, la disponibilitat d'hàbitat de *Posidonia oceanica* va exercir una clara influència en l'abundància de *S. salpa* ( $R^2= 0.82, p< 0.01$ ) i, en conseqüència, en les seves taxes d'herbivorisme ( $R^2= 0.73, p< 0.05$ ). Pel contrari, *P. lividus* no va mostrar cap efecte ni a les seves densitats ( $R^2= 0.15, p> 0.05$ ) ni en les taxes d'herbivorisme ( $R^2= 0.15, p> 0.05$ ). Per tant, la major pressió dels herbívors va ser detectada a les àrees amb menor disponibilitat de *P. oceanica* ja que aquestes suporten les majors densitats i biomasses de *S. salpa*.



Aquest estudi evidencia que la pesca i la pressió de l'herbivorisme són factors clau en el control de les interaccions tròfiques als ecosistemes de fanerògames marines. No obstant, aquest estudi també evidencia que, en absència de pesca, les característiques del paisatge, a banda de la disponibilitat de *Posidonia oceanica* "per se", tenen també un paper crucial en les taxes locals d'herbivorisme. Els mecanismes que poden explicar aquestes interaccions se exposen.



## INTRODUCTION

Herbivory plays a vital role in terrestrial and aquatic systems, and is of particular importance in some marine habitats, such as algal communities, where grazing rates can be more than three times higher than in terrestrial systems (Cyr & Pace 1993). Recent studies have shown that herbivory also plays a central role in seagrass meadows ecology, by directly removing plant biomass, inducing nutrient export, and modifying plant production (see review by Heck & Valentine 2006, and references therein). Increased rates of herbivory (overgrazing events) can result in significant alterations in the structure and functioning of marine ecosystems (Lawrence 1975, Harrold & Spence 1987). Similarly, reduced rates of herbivory through top-down effects can also lead to major changes in ecosystem functioning, such as the dramatic “phase shifts” witnessed in many coral reefs (Done 1992, Hughes 1995, McCook 2001, Szmant 2002). Several causes altering plant-herbivore interactions have been identified. Among them, probably the most relevant are overexploitation (hunting and overfishing) and habitat loss (Turner et al. 1999, Jackson 2001a, Jackson et al. 2001).

Terrestrial and marine ecosystems are highly vulnerable to anthropogenic impacts inducing indirect deterioration (e.g. climate change, global biogeochemistry, biotic additions and losses) or direct fragmentation and destruction (e.g. land clearing, bottom trawling and urban development) of key habitats (see Vitousek et al. 1997 for a review). Some of these impacts affect ecosystems by reducing the effective habitat size, but also by fragmenting formerly continuous areas, which causes disruption of key ecological processes, such as herbivory (e.g. Barnett et al. 1977, Roland 1993, Kruess & Tschamkete 1994, McArthur 2000). Herbivore densities and the associated grazing pressure can be stable, increase or decreased following habitat size. The main mechanisms driving those spatial patterns being differential recruitment, predation, and migration occurring as a function of the habitat size (Bender et al. 1998). The role of recruitment and predation in controlling the abundance of individuals over time has been well-established (Matter 1999) and may account for herbivore crowds in small patches that have been released from predation pressure (Cappuccino et

al. 1998, Kondoh 2003). Conversely, the influence of migration appears to be the object of discrepancies across studies (Debinski & Holt 2000). In particular, the resource concentration hypothesis (Tahvanainen & Root 1972, Root 1973) predicts that higher numbers of individuals will arrive to larger or denser patches of the targeted plant because the probability of finding the resource is enhanced. However, many other landscape and biological aspects of species may influence the dispersal capacity of organisms and often a resource dilution rather than concentration is observed in some biological systems (Yamamura 2002, Otway et al. 2005, Hambäck & Englund 2005). Those patterns are closely linked to the herbivore movement capacity, sensorial ability or the foraging behaviour – whether they do not search, have some form of orientation, or are attracted to resource areas in a manner that is proportionate to the resource availability and patch size (Kunin 1999, Bowman et al. 2002, Bukovinszky et al. 2005).

The role of fishing in modifying ecosystem functions has been the subject of considerable research, as marine ecosystems collapse under the increasing pressure of the global demand for fish (Pauly et al. 1998, 2002, Steneck et al. 2004). Seagrass systems are affected by overfishing in much the same way as many other nearshore communities (Jackson & Sala 2001). By preferentially targeting top predators, long-term sustained fisheries lead to simplification of the food-webs and induce the outburst of otherwise controlled species through trophic cascades (Pauly et al. 2002). For instance, sea urchins populations which have been released from predation pressure have caused widespread overgrazing of marine macrophytes (Estes & Duggins 1995, Estes et al. 1998). Alternatively, herbivores themselves (dugongs, waterfowl, turtles, herbivorous fish, and others) can also be subjected to direct hunting pressure or bycatch as non-target species (Bertram & Bertram 1973, Madsen 1998a,b, Jackson 2001b) thus reducing the impact that these may cause on plant biomass and the flux of nutrients to higher trophic levels.

Our study was conducted in the western Mediterranean on meadows of the endemic seagrass *Posidonia oceanica* (L.) Delile. Declared a priority marine habitat in 1992 (Habitat Directive 92/43/EEC), human activities still cause, however, habitat loss in certain areas





(Sánchez-Jerez & Ramos-Espla 1996, Gonzalez–Correa et al. 2005) and were likely an important cause of overall decline prior that date (EEA 1999). The dominant herbivores, the sparid fish *Sarpa salpa* (L.) and the sea urchin *Paracentrotus lividus* (Lmk.), are also potentially affected by harvesting: *S. salpa* populations are a common non-target species caught in fishing nets (García-Rubies 1997, Cuccu et al. 1999), whereas *P. lividus* is an edible sea urchin that is commonly consumed (Guidetti et al. 2004). In this paper we seek to understand how seagrass herbivores and herbivory pressure can be affected by concurrent effects of habitat loss and overfishing. The influence of the habitat loss in herbivore processes was investigated along a gradient of seagrass habitat sizes whereas often hazardous assessment of fishing-related mortality in ‘trash’ species (Chopin et al. 1996) was circumvented by comparing trends in the population structure of fish in seagrass meadows located inside and outside no-take marine protected areas (Sanchez Lizaso et al. 2000, Willis & Millar 2005).

## MATERIALS AND METHODS

**Sampling design and study sites.** Sampling was undertaken in nine shallow *Posidonia oceanica* meadows in the NW Mediterranean, outside and inside long-term marine protected areas and with seagrass meadows of different sizes.

The influence of fishing pressure was investigated following an asymmetrical sampling design in meadows with small and medium seagrass habitat size. The two selected marine protected areas (MPA) were Banyuls, representing the small habitat size and, Medes Island, representing the medium habitat size, both of them effectively protected for more than 20 years (Bell 1983, Ros et al. 1984). This period ensures an effective recover of the fish populations (effectives and sizes), including herbivore groups (McClanahan & Arthur 2000, Russ & Alcalá 2004, McClanahan & Graham 2005) and the recovery of top-down control on sea urchins (McClanahan 2000). These two MPAs were each compared to three control meadows of equivalent habitat size class (see Fig. 1). One of the control sites, Jugadora, is



inside a relatively recently declared marine protected area (4-5 years prior to this study), although traditional fishing is permitted, and no sign of fish recovery has been detected yet (see results).

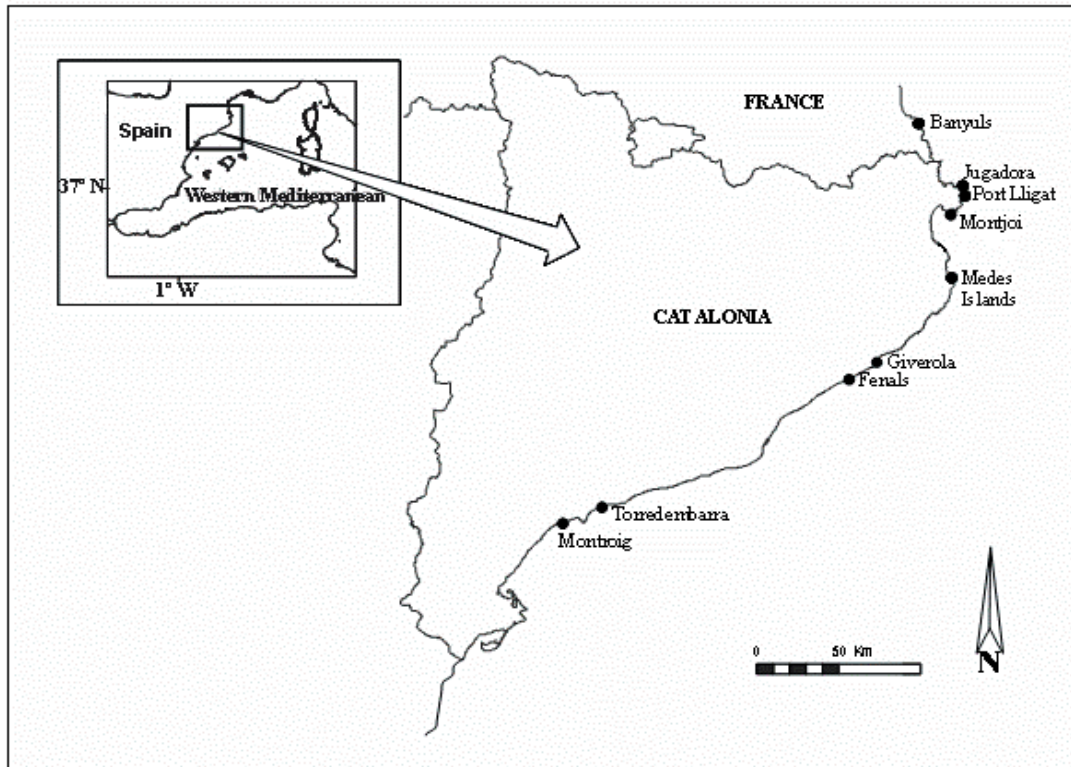


Fig.1. Map of the NW Mediterranean showing the nine study sites along the Catalan coast and the south of France. Small sites were: Banyuls (Marine Protected Area for more than 20 years), Jugadora, Giverola and Fenals; medium sites were: Medes Islands (MPA for more than 20 years), Montjoi, Port Lligat and Torredembarra; large site: Montroig (FHS hypothesis only; see text for further details).

The effect of the habitat size was tested in the six control meadows mentioned above, and including an additional large meadow (Montroig, Fig. 1) to increase the habitat size range.

The study was purposely conducted in (i) summer, from mid June to mid August, since this period concentrates the largest herbivory activity, especially that of the fish *Sarpa salpa* (Peirano et al. 2001, Tomas et al. 2005, Prado et al. in press) and (ii) in shallow meadows, within the 0.5 and 10 m depth isolines, which are known to assemble the majority



of fish and sea urchin individuals (Harmelin-Vivien 1983, Francour 1997, Boudouresque & Verlaque 2001, Tomas et al. 2005).

**Estimation of habitat size.** In all localities, the study area was set accordingly to the summer home range described for *Sarpa salpa* (4.3 ha; Jadot et al. 2002), considering the central point of such study area the centre of the mentioned depth ranges (i.e. between 0.5m and 10 m depth). The area occupied by *Posidonia oceanica* (i.e. the habitat size) within the fish home range was obtained from available local cartography. This area was then multiplied by the seagrass cover and shoot density (see below) as these two factors can influence considerably the real seagrass available for dwelling fish, to obtain Food Habitat Size (FHS, see Table 1). Seagrass shoot density and percent cover were assessed with twelve 40 x 40 cm and with eighteen 50 x 50 cm haphazardly located quadrates respectively (see Alcoverro et al. 1995). Shoot density, percent cover, shallow (i.e. 0-10 m) area with *Posidonia oceanica* and the resulting food habitat size (FSH) at each study site. Banyuls= B; Fenals= F; Jugadora= J; Giverola= G; Medes Islands= M; Torredembarra= T; Port Lligat= P; Montjoi= Mj; Montroig= Mr.

Site	Protection	Density (No. shoots m <sup>-2</sup> )	Cover (%)	Seagrass area (ha)	FHS
B	MPA (small)	418 ± 47	37 ± 4	2.34	36.3
F		559 ± 44	30 ± 7	0.17	2.9
J		360 ± 32	70 ± 6	0.89	22.6
G		1001 ± 50	46 ± 8	1.20	55.2
M	MPA (Medium)	467 ± 46	66 ± 6	2.39	73.6
T		667 ± 49	62 ± 7	1.47	60.8
P		361 ± 32	65 ± 4	3.06	72.0
Mj		478 ± 22	55 ± 3	3.76	99.6
Mr	Control (Large)	479 ± 62	84 ± 3	4.20	169.7

**Abundance of grazers.** *Sarpa salpa* and *Paracentrotus lividus* abundance and size structure were investigated in two consecutive summers (July-August 2003 and 2004) at each locality. In the study area (4.3 ha approximately) the methodology used to assess populations of *S. salpa* consisted on visual transect censuses. Size distribution was obtained by counting individuals and assigning them to one of three size classes: small (5-15 cm), medium (20-



30 cm) and large (> 30 cm), within 50 x 10 m strip transects (Francour 1999). In order to incorporate the large temporal variability resulting from fish mobility patterns in this species (Jadot et al. 2002) we conducted transects at different times and in different days within the two sampling periods. Each transect 30 per site, was considered an independent replicate. Fish biomass ( $\text{g WW} * 10 \text{ m}^{-2}$ ) was estimated using the size-weight conversion factors given in Francour (1997) (small: 5-15 cm = 15 g WW; medium: 20-30 cm = 155 g WW; large: > 30 cm = 552 g WW). The population of *P. lividus* in each meadow was assessed within the same area as the fish population, with fifteen 50 x 50 haphazard quadrates. In each quadrate, sea urchin test diameter was measured using a calliper. Individuals were separated into juvenile (0.5 to 3 cm) and adult size classes (3 to 8 cm), coherently with age-dependent patterns of predation reported for this species (Sala 1997).

**Seagrass herbivory.** *Posidonia oceanica* herbivory rates were measured in summer 2005 at the same study sites and area than herbivore densities through direct estimates of leaf area loss in individual shoots. At the beginning of the study interval, 20 seagrass shoots were haphazardly selected at each shallow meadow, tagged for identification and connected by a series of ropes (4 per study site, connecting 5 shoots each) for easy recovery. For each shoot the number of leaves, leaf length and width, and the number and type of bite marks (i.e. fish or sea urchin; see Prado et al. in press) were measured underwater without detaching the shoot. In addition, shoots were punched at the base to evaluate shoot elongation (Romero 1989). Shoots were collected 45 days later, and measured in the laboratory for the same variables reported above. Leaf elongation was measured as well. For each shoot, biomass loss was estimated as the difference between the initial length and that at the time of collection (45 days later), corrected for leaf elongation (i.e. subtraction of leaf length increases during the study interval), and attributed to each herbivore accordingly to the bite mark left at the end of the leaf. Since the objective of the study was to account for large spatial differences, leaf losses resulting from lateral bite marks or leaf fall were not included in calculations; due to this, final herbivory values may be slightly underestimated. Herbivory rates were transformed from length values ( $\text{cm shoot}^{-1} \text{ d}^{-1}$ ) to biomass values ( $\text{g DW shoot}^{-1} \text{ d}^{-1}$ ) using appropriate

conversion factors (Kirsch et al. 2002, Tomas et al. 2005).

**Statistical analyses.** Asymmetrical analyses of variance (Underwood 1993, 1994) were performed to investigate the effect of long-term protection for both herbivore abundance (*Sarpa salpa* and *Paracentrotus lividus*) as well as on fish and sea urchin herbivory rates. In such analyses, 'Protection' effects are obtained, for each FHS, by weighting differences in one-way ANOVA results (Site random factor) in all study sites (4 levels) against differences in control sites (3 levels). Separate asymmetric ANOVAs were conducted for small and medium FHS. In the particular case of *S. salpa*, the effect of the fishing restriction is probably age-dependent (Bell 1983) and consequently, was tested separately for each size-class (i.e. small, medium and large; see above) and for the total number of individuals. In addition, since differences in fish body weight among size classes may influence herbivory rates due to distinctive energetic requirements, individuals of *S. salpa* were consistently investigated in terms of fish biomass (i.e. g WW 10 m<sup>-2</sup>). For *P. lividus*, the influence of protection was examined in terms of densities of juvenile, adult and total number of individuals. Abundances were first analysed for interannual differences with a one-way ANOVA and then data were pooled ( $F_{\text{year}} = 0.482; p > 0.05$ ) and included in the asymmetrical one-way design described above.

ANOVA assumptions of normality (Chi-square test) and heterocedasticity (Cochran's test) were not always achieved by transformation. Nonetheless, Underwood (1981) has indicated the ANOVA F statistic is robust despite violation of assumptions, provided that the working sample size is large enough. When such assumptions were not met, we set the significance level to  $p < 0.01$  to minimize the risk of making a type I error.

The significance of the habitat size effect on herbivore abundance and consumption rates was investigated by regression analysis. Specific aims were to test the effect of the FHS on: (a) *Sarpa salpa* total biomass and herbivory rates, and (b) *Paracentrotus lividus* densities and herbivory rates. In addition, the existence of an association between herbivory rates and herbivore abundance was assessed by correlation analyses.



## RESULTS

**Abundance of herbivores.** The distribution of *Sarpa salpa* exhibited important large-scale variation, in terms of both density of individuals (from  $0.3 \pm 0.1$  [S.E] ind.  $10 \text{ m}^{-2}$  in Montroig (data not shown) to  $1.4 \pm 0.3$  [S.E] g WW  $10 \text{ m}^{-2}$  in the Medas MPA) and biomass (from  $21 \pm 8$  [S.E] g WW  $10 \text{ m}^{-2}$  in Montroig to  $666 \pm 243$  [S.E] g WW  $10 \text{ m}^{-2}$  in the Banyuls MPA) (see Fig. 2a,b). Total biomass but not density of *S. salpa* was higher in the long-term MPAs than in control areas (Table 2). Patterns of biomass and density of large fish mirrored those of total biomass and density in the two MPAs since large individuals formed the bulk of sampled populations in these sites. The effect in medium fish sizes depended on the FHS: both biomass and density of individuals were significantly lower in the small MPA but remained unaffected in the medium MPA. Small fish sizes showed no significant effect of long-term protection in either small or medium FHS sites (Table 2).

Densities of *Paracentrotus lividus* also exhibited differences among study sites, with values ranging from  $2.4 \pm 1.3$  [S.E] ind.  $\text{m}^{-2}$  in Banyuls MPA to  $18.8 \pm 7.2$  [S.E] ind.  $\text{m}^{-2}$  in Giverola (Fig. 3). Mean values in Montroig (i.e. the large FSH site, not shown in Fig. 3) were  $6.13 \pm 3.3$  [S.E] ind.  $\text{m}^{-2}$ . The influence of the long-term protection showed no effects in total and juvenile densities of sea urchins. However, adult effects were inconsistent at the two levels of FHS; significantly lower numbers were observed in the small MPA but not in the medium MPA (Table 3, Fig. 3). There was a significant negative relationship between fish biomass and the FHS ( $R^2 = 0.82$ , slope =  $-1.5 \text{ E}^{-3}$ ,  $p < 0.01$ ) whereas no correlation was detected between sea urchin densities and those same FHS sites ( $R^2 = 0.15$ , slope =  $-4.3 \text{ E}^{-5}$ ,  $p > 0.05$ ; Fig. 4a,b).



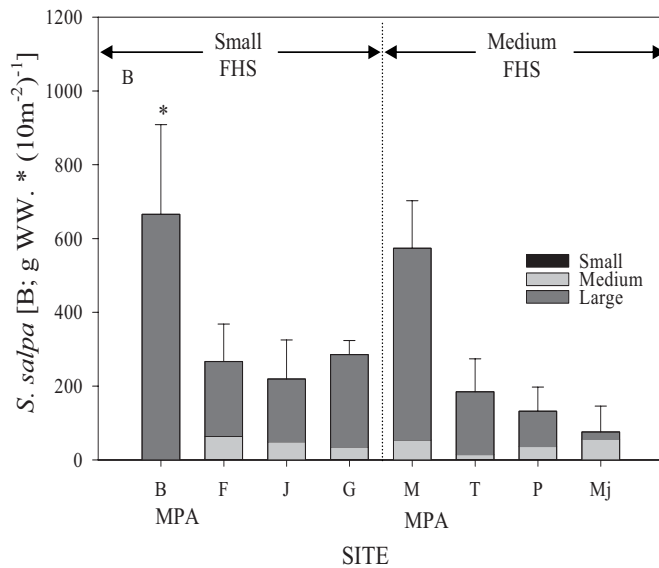
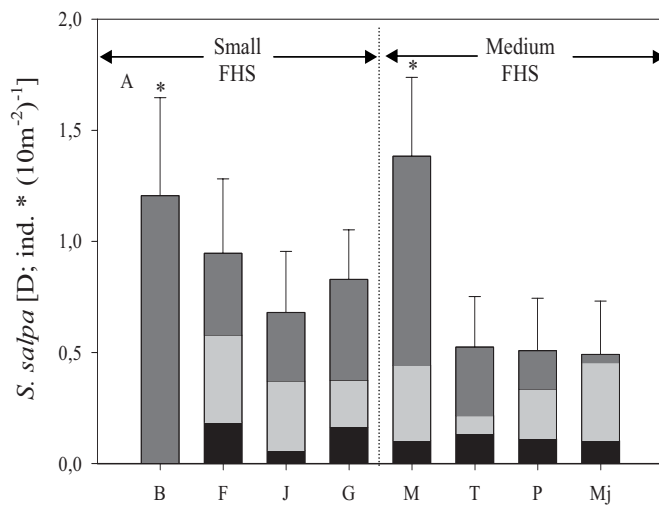


Fig. 2. Abundance of the fish *Sarpa salpa* by size classes at each study site expressed as a) No. of ind. \* 10m<sup>-2</sup> and, b) biomass (g WW \* 10m<sup>-2</sup>). The existence of significant differences in either total, adult or medium individuals of *S. salpa* (see Table 2) between long term MPAs and non MPAs is indicated for each FHS. Errors bars are S.E.

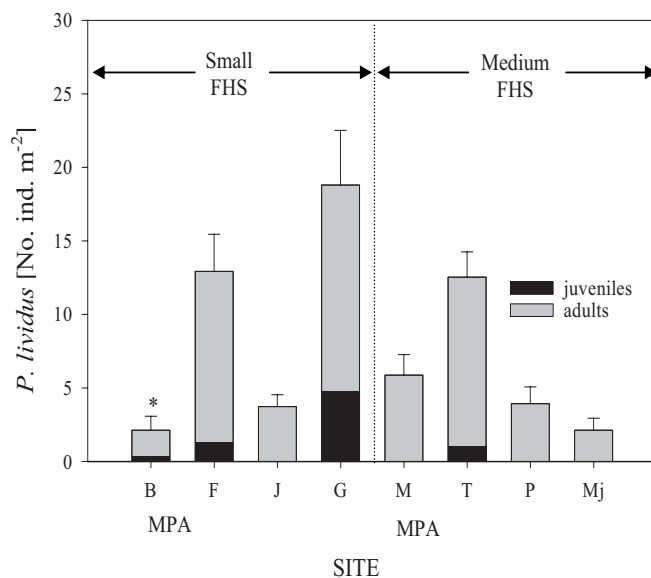


Fig. 3. Densities of juvenile and adult *Paracentrotus lividus* at each study site. The existence of significant differences in the abundance of *P. lividus* (adults) between long term MPAs and control sites are indicated with asterisks for each FHS (see Table 3). Site names as in Table 1. Error bars are S.E.



Table 2. Summaries of asymmetric ANOVAs (All sites vs. non-reserves) testing for differences in a) fish density: total, large, medium and small number of individuals of *Sarpa salpa* per 10 m<sup>-2</sup> and b) fish biomass: total and large, medium and small (g WW (10 m<sup>-2</sup>)<sup>-1</sup>) between long-term MPAs and unprotected areas. Significant differences are indicated in **bold**.

		Total <i>S. salpa</i>			Large <i>S. salpa</i>			Medium <i>S. salpa</i>			Small <i>S. salpa</i>			
FISH DENSITY	Protection effect	df	MS	F	p	MS	F	p	MS	F	p	MS	F	p
	Low FHS	1	3.372	6.178	0.1383	21.637	130.974	<b>0.0076</b>	17.317	111.939	<b>0.00882</b>	0.4396	3.039	0.2209
			Transformation: - C = 0.771			Transformation: - C = 0.889			Transformation: - C = 0.810			Transformation: - C = 0.790		
	Medium FHS	1	MS	F	p	MS	F	p	MS	F	p	MS	F	p
			22.252	105.710	<b>0.00933</b>	60.321	109.099	<b>0.00904</b>	0.250	0.3505	0.61383	0.0918	1.0774	0.4083
			Transformation: - C = 0.844			Transformation: - C = 0.829			Transformation: - C = 0.766			Transformation: - C = 0.834		
		Total <i>S. salpa</i>			Large <i>S. salpa</i>			Medium <i>S. salpa</i>			Small <i>S. salpa</i>			
FISH BIOMASS	Protection effect	df	MS	F	p	MS	F	p	MS	F	p	MS	F	p
	Low FHS	1	414.64E4	312.777	<b>0.0032</b>	521.10E4	3483.76	<b>0.0003</b>	93.74E2	102.615	<b>0.0096</b>	211.231	1.0339	0.4162
			Transformation: - C = 0.850			Transformation: - C = 0.880			Transformation: - C = 0.840			Transformation: - C = 0.810		
	Medium FHS	1	MS	F	p	MS	F	p	MS	F	p	MS	F	p
			425.84E4	153.224	<b>0.0065</b>	392.61E4	76.32	<b>0.0129</b>	8628.8	0.859	0.4518	102.692	2.514	0.2537
			Transformation: Arc sen x C = 0.579 (n.s)			Transformation: Arc sen x C = 0.553 (n.s)			Transformation: Arc sen x C = 0.568 (n.s)			Transformation: Arc sen x C = 0.542 (n.s)		





## Habitat size and fishing pressure alter herbivory in seagrass ecosystems

Table 3. Summaries of asymmetric ANOVAs (All sites vs. non-reserves) testing for differences in densities of juvenile (0.5 to 3 cm) and adult *Paracentrotus lividus* (3 to 8 cm) between long-term MPAs and unprotected areas. Significant differences are indicated in **bold**.

SEA URCHIN DENSITY		Total <i>P. lividus</i>			Adult <i>P. lividus</i>			Juvenile <i>P. lividus</i>		
Protection effect	df	MS	F	p	MS	F	p	MS	F	p
Low FSH	1	622.44	2.529	0.2527	1049.38	22.405	<b>0.04185</b>	12.167	0.330	0.6251
		Transformation: $\sqrt{\sqrt{x}}$ C = 0.691 (n.s)			Transformation: $\sqrt{\sqrt{x}}$ C = 0.749 (n.s)			Transformation: $\sqrt{\sqrt{x}}$ C = 0.661 (n.s)		
Medium FSH	1	6.52	0.036	0.8666	2.772	0.019	0.9012			
		Transformation: $\sqrt{x}$ C = 0.785 (n.s)			Transformation: $\sqrt{x}$ C = 0.754 (n.s)					

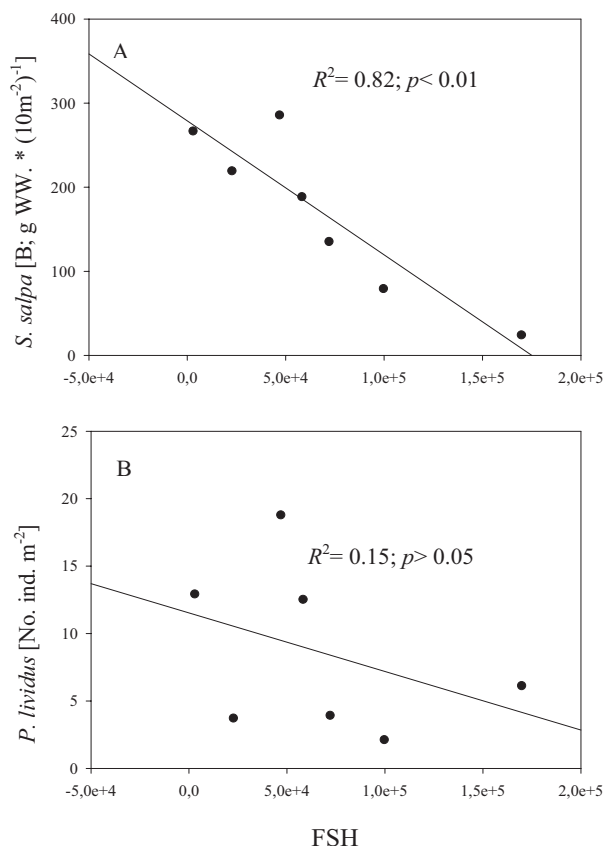


Fig. 4. Regression analyses (unprotected areas only) between the Food Habitat Size (FHS) and a) the total biomass of *Sarpa salpa* and, b) densities of the sea urchin *Paracentrotus lividus*.



**Seagrass herbivory.** Seagrass herbivory rates (including both herbivores) in the Catalan Coast during the summer period reached mean values of  $2.9 \pm 0.5$  [S.E] g DW shoot<sup>-1</sup> d<sup>-1</sup> (149% of leaf production in that period), but varied from  $0.6 \pm 0.2$  to  $5.1 \pm 1.7$  [S.E] g DW shoot<sup>-1</sup> d<sup>-1</sup> in Montroig (data not shown) and Giverola, respectively (Fig. 5a). *Sarpa salpa*, accounted for 67 % of total herbivory ( $1.95 \pm 0.4$  g DW shoot<sup>-1</sup> d<sup>-1</sup>) and the sea urchin *Paracentrotus lividus* for the remaining 33% ( $0.95 \pm 0.4$  g DW shoot<sup>-1</sup> d<sup>-1</sup>), with both species exhibiting substantial differences among study sites (Fig. 5b,c). Fish and sea urchin herbivory rates were strongly associated to fish biomass and sea urchin density, respectively (*S. salpa*:  $r = 0.87$ , slope =  $5.2 \text{ E}^{-3}$ ,  $p < 0.01$ ; *P. lividus*:  $r = 0.79$ , slope =  $0.16$ ,  $p < 0.01$ ).

Herbivory rates in MPAs were ca. 32% higher than in control study sites. *Sarpa salpa* herbivory was notably affected by protection status independently of habitat size (see Table 4). In contrast, for small meadows, the effect of protection displayed a trend towards decreased herbivory rates of *Paracentrotus lividus* but it was not significant (Table 4; Fig. 5c). For medium FHS sites and consistently with abundance patterns, no significant sea urchin herbivory effect or trend was detected.

Fish herbivory was strongly associated to the FHS ( $R^2 = 0.73$ ; slope =  $-2.5 \text{ E}^{-5}$ ;  $p < 0.05$ ) whereas sea urchin herbivory was not ( $R^2 = 0.15$ ; slope =  $-8.9 \text{ E}^{-6}$ ;  $p > 0.05$ ) (Fig. 6a,b).

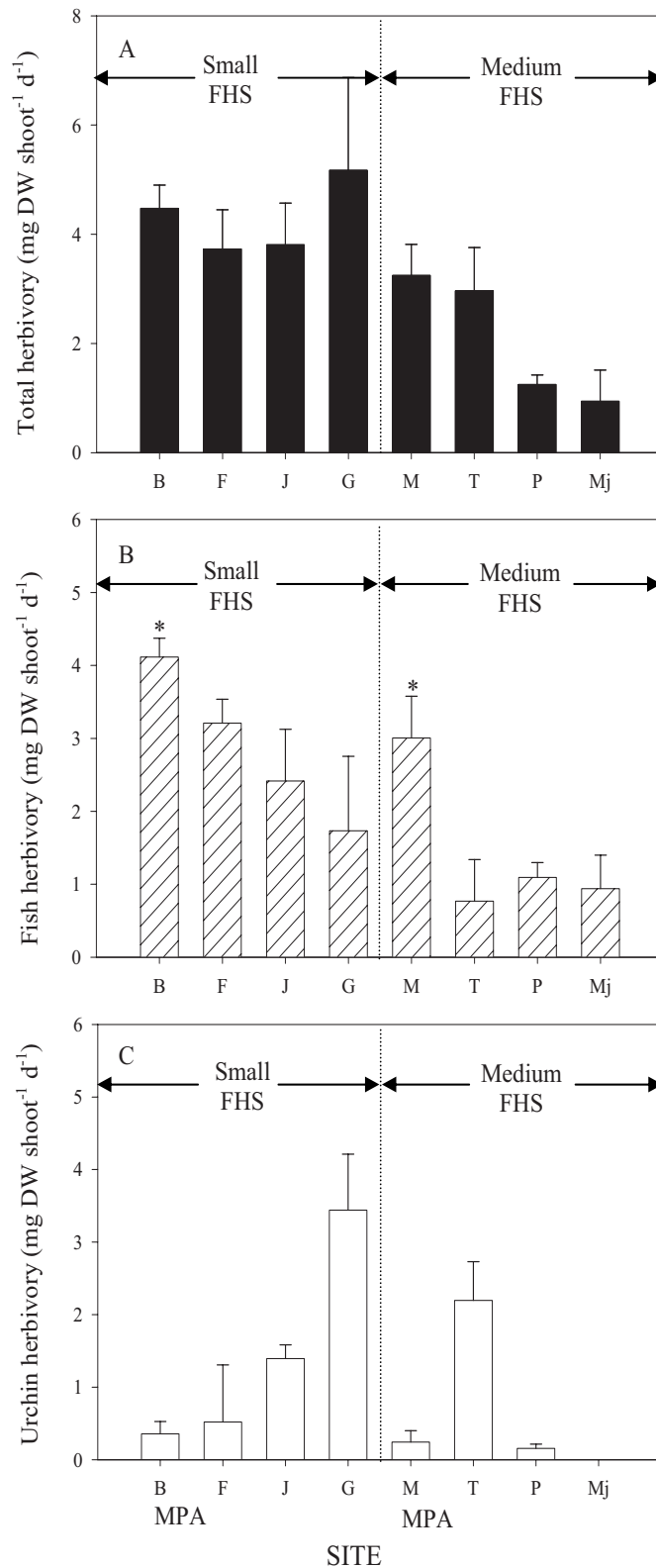


Fig. 5. Herbivory rates measured at each site (mg DW shoot<sup>-1</sup> d<sup>-1</sup>): a) total (fish and sea urchin), b) *Sarpa salpa*, and b) *Paracentrotus lividus*. Significant differences in each herbivory rate between long term MPAs and non MPAs are indicated for each FHS (see Table 4). Errors bars are S.E.



Table 4. Summaries of asymmetric ANOVAs (All sites vs. non-reserves) testing for differences in seagrass herbivory (mg DW shoot<sup>-1</sup> d<sup>-1</sup>) by a) the fish *Sarpa salpa* and b) the sea urchin *Paracentrotus lividus* between MPAs and unprotected areas. Significant differences are indicated in **bold**.

HERBIVORY		<i>S. salpa</i>			<i>P. lividus</i>		
Protection effect	df	MS	<i>F</i>	<i>p</i>	MS	<i>F</i>	<i>p</i>
<b>Low FHS</b>	1	247.061	24.096	<b>0.03908</b>	24.906	0.598	0.51994
		Transformation: - C = 0.614 (n.s)			Transformation: - C = 0.890		
<b>Medium FHS</b>	1	MS	<i>F</i>	<i>p</i>	MS	<i>F</i>	<i>p</i>
		47.5836	99.194	<b>0.00993</b>	4.105	0.1515	0.73456
		Transformation: $\sqrt{x}$ C = 0.612 (n.s)			Transformation: - C = 0.830		

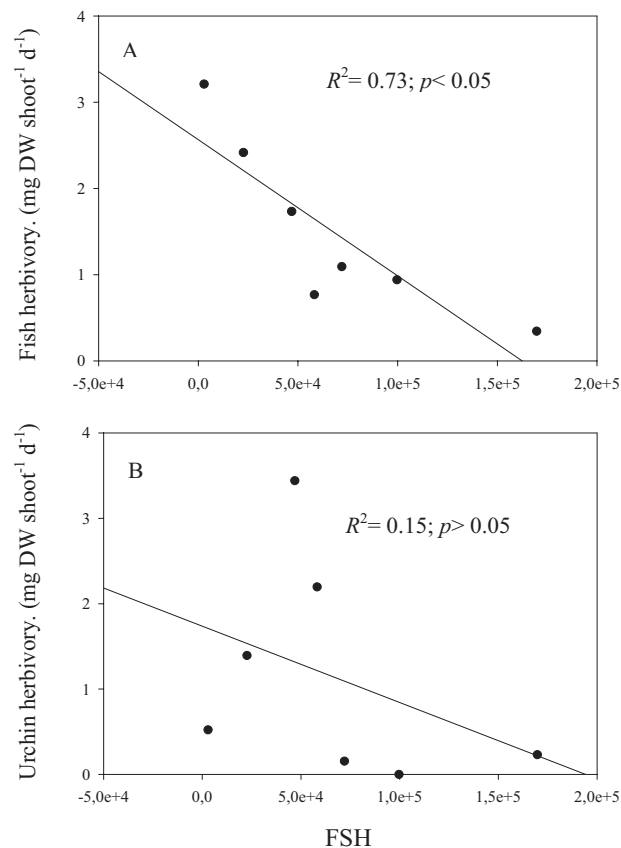


Fig. 6. Regression analyses between the Food Habitat Size (FHS) and herbivory rates by a) *Sarpa salpa*, and b) *Paracentrotus lividus* in unprotected areas.



## DISCUSSION

Our study provides evidence that in the Western Mediterranean the size of seagrass habitat has a substantial influence in fish herbivory in seagrass ecosystems. Moreover, fishing pressure also alters grazing rates, decreasing fish grazing and increasing, albeit to a lesser extent, sea urchin grazing. In many instances, the influence of seagrass habitat loss (Sánchez-Lizaso et al. 1990, Short & Wyllie-Echeverria 1996, Orth et al. 2006) and declining herbivore populations due to overexploitation (review by Jackson et al. 2001) in ecosystem functioning have mostly been studied independently, yet our results suggest that fishing pressure and landscape characteristics may have counteracting effects on key ecological processes such as herbivory. In fact, the negative correlation between fish grazing and food habitat size suggests that any loss of *Posidonia oceanica* habitat could cause the aggregation of herbivore fishes within the remnant habitat patches, offsetting the release in grazing pressure caused by fishing in most marine systems.

Populations of the herbivorous fish *Sarpa salpa*, but not those of the sea urchin *Paracentrotus lividus*, attain higher abundances in meadows with relatively low abundance of *Posidonia oceanica* (low shoot density, cover and/or reduced surface). Accordingly, areas with small FHS revealed herbivore impacts that were several orders of magnitude greater than those in large FHS. The fish *S. salpa* is not a permanent inhabitant of seagrass beds, but moves across different habitats (Verlaque 1990). Besides fishing pressure, the abundance of *S. salpa* seems to be driven by recruitment and mortality processes (see Macpherson et al. 1997) not directly connected to the *P. oceanica* ecosystem and thus, most probably independent from features of meadow vitality or extension. *S. salpa* recruitment occurs in very shallow rocky bottoms (Leboulleux 1992, Harmelin-Vivien et al. 1995) and individuals do not feed on macrophytes until they reach ca. 13 cm (Christensen 1978). Juveniles and adults are mid-



water visual foragers moving widely within their summer home range (4.3 ha Jadot et al. 2002) which may include seagrass meadows, rocky substrates and sandy areas. In mobile species with such wide ranges, negative density-area relationships have been associated to either random searching patterns (Bowman et al. 2002) or the use of visual or olfactory cues to find the resources (Bukovinszky et al. 2005). Large schools of *S. salpa* are common browsers in *P. oceanica* but also feed on a variety of benthic macroalgae (Verlaque 1990) suggesting that seagrass availability is not a limiting factor for the growth of fish populations. However, large individuals of *S. salpa* seem to have a higher contribution of seagrass to their diet (Havelange et al. 1997) and are typically found aggregating in meadows. Consequently, the lower the seagrass availability within the home range, the higher the local fish abundance within the seagrass bed.

Conversely, *Paracentrotus lividus* displayed no correlation with FHS. In fact, perimeter-area ratios, rather than the size of habitat itself, appear to influence the abundance of organisms with small movement ranges, or with a foraging behaviour relying on contact search, such as sea urchins (Hambäck & Englund 2005). Particularly, for *P. lividus*, the spatial distribution of individuals appears to be dependent on both the presence of bare rhizomes (mat structure) of *Posidonia oceanica* for local recruitment, and on the degree of connection between the seagrass and the adjacent hard substrate that facilitates the migration from the later to the former (Tomas et al. 2004, Prado et al. 2006). It has to be taken into account that *P. lividus* does not migrate across large tracts of sandy habitat (Dance 1987), possibly because it would be exposed to higher predation levels. Presumably, the final within-bed population abundance and structure results from density-dependent migration from the rocky habitat, the local bed recruitment (Prado et al. 2006) and processes like predation (see below).

Medes and Banyuls marine protected areas presented a clear increase in the biomass of the fish *Sarpa salpa* as already observed by other authors (Macpherson et al. 2002) and this resulted in enhanced grazing pressure (ca. 32% higher than in the respective control sites). Although *Sarpa salpa* is not a clear fishing target in the study region (García-Rubies 1997), fish populations can be affected by conspicuous non-selective fishing practices operating





in seagrass meadows (Sánchez-Jerez & Ramos-Esplá 1996, 2000) or by the fishing of commercial species (van der Walt & Govender 2003). More specifically, our study indicates that fishing pressure can effectively influence the fish size distribution, by reducing the abundance of large size-classes and increasing intermediate size-classes, resulting in an overall biomass decrease. These results are coherent with many studies documenting the impacts of fishing on population and community structure (review by Rochet & Trenkel 2003) as well as with studies examining the benefits of no take areas to fish populations (Bell 1983, Macpherson et al. 2002, Willis & Millar 2005). It is possible that this observed effect inside MPAs (increase in the abundance of large sizes and decrease in medium ones) is also due to the increase of carnivores' abundance (Russ & Alcala 1996, Babcock et al. 1999, McClanahan 2000), although the predators of *S. salpa* are few (Triay 2005) and, consequently, this effect would seem of minor importance. In contrast, numerous studies have evidenced the existence of top-down control of sea urchin populations resulting from enhanced predation in MPAs, in terms of both density (Babcock et al. 1999, McClanahan et al. 1999, Shears & Babcock 2003) and size distribution (Sala 1997, Shears & Babcock 2002, Guidetti 2004). We found such effects but only in the MPA with small FHS, where probably a higher predation pressure exists (see also Westera 2003 for inconsistent top-down effects).

As already described for Indo-Pacific seagrass beds (Alcoverro & Mariani 2004), fishing restrictions appear to affect both herbivores in an opposite manner, increasing *Sarpa salpa* and decreasing *Paracentrotus lividus* herbivory, although sea urchins are largely affected by other processes. As a result, the two sites with major herbivory pressure have a completely different functioning one is a fishing-protected meadow dominated by *S. salpa* (Banyuls MPA) and the other, an unprotected meadow dominated by *P. lividus* (Giverola). However, the effect of protection did not disrupt the trends caused by FHS (i.e. concentration effect) since *S. salpa* was the only species affected (see Moericke et al. 1975, Fahrig & Paloheimo 1987, Gillespie 1987, for similar effects in other species).

The results presented here indicate that overfishing and the loss or deterioration of seagrass habitat can modify the demographic structure of keystone herbivores in *Posidonia*



*oceanica* ecosystems, and cause profound functional alterations in shallow Mediterranean seagrass meadows. A reduction in seagrass area (or cover, or density) due to increasing anthropogenic pressure, would imply that the remnant seagrass would be further exposed to increased herbivory rates, eventually leading to its additional decline (Ruiz et al. 2001). Therefore, the inclusion of critical seagrass areas within the design of future marine reserves should deserve more attention to prevent possible overgrazing events. In this study we detected 9-fold differences in herbivory rates related to the gradient of meadow sizes. This raises some key questions that require further research, such as the threshold of herbivory that can be tolerated by a seagrass meadow without deterioration. In any case, we have provided evidence that herbivory in marine systems is not only controlled by features of the populations or communities concerned, but also by landscape features, highlighting the importance of including this reciprocal perspective in conservation concerns.

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