

## Herbivory on the seagrass *Cymodocea nodosa* (Ucria) Ascherson in contrasting Spanish Mediterranean habitats

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### Abstract

We assess the magnitude and variability of herbivory (i.e. leaf consumption and sloughing caused by herbivore bites) on the seagrass *Cymodocea nodosa* along the Spanish Mediterranean coast and test the hypothesis that this is higher in meadows growing in sheltered bays than in exposed, open zones. Total leaf loss by herbivores varied by about three orders of magnitude along the Spanish Mediterranean coast, from < 1 to 130 mg DW shoot<sup>-1</sup> yr<sup>-1</sup>. These differences were paralleled by a great variation in the fraction of leaf production lost by herbivores, which ranged from < 1 to about 50%. Most (75%) of the populations, however, supported modest losses of leaf production (< 10%). A significant fraction (30%) of the variance in herbivory was explained by meadow exposure, the meadows growing in sheltered bays suffering about five times the losses encountered in open sites. These results suggest that the trophic importance of *C. nodosa* as a food resource for herbivores, and the role of herbivores on the control of the seagrass production, increases notably from exposed to sheltered meadows in the Spanish Mediterranean and point to the importance of considering the degree of exposure when addressing herbivory on other seagrass species.

**Keywords:** Seagrass; *Cymodocea nodosa*; Herbivory; Sheltered bays; Spanish Mediterranean

### 1. Introduction

*Cymodocea nodosa* (Ucria) Ascherson is a common (den Hartog, 1970) and highly productive seagrass (Pedeutzi and Vukovic, 1990; Terrados and Ros, 1992; Pérez and

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Romero, 1994) in the Mediterranean Sea. The presence of many herbivore marks on its leaves suggests that *C. nodosa* is an important food source for herbivores (Cebrián, pers. obs.), and points to herbivory as an important control of seagrass production (Thayer et al., 1984). However, the loss of *C. nodosa* leaf production to herbivores has not been evaluated as yet.

Seagrass meadows growing in sheltered bays and coastal lagoons provide habitat for spawning and juvenile growth (Costa and Bruxelas, 1989; Costa et al., 1994) and offer foraging areas for many adult fishes and birds (Valentine and Heck, 1991). As a consequence, seagrass meadows in protected sites tend to maintain more abundant faunal communities, including higher numbers of herbivorous species, than those in exposed zones (Heck and Thoman, 1984; Orth et al., 1984; Costa et al., 1994). This suggests that seagrass meadows in enclosed, protected bays may support higher herbivory than those in exposed coastal zones and that habitat exposure may be a significant source of variability in herbivory on seagrasses.

Here we examine the extent of herbivory on *C. nodosa* leaf production, both as consumption and sloughing following herbivore bites, along 20 coastal populations in the Spanish Mediterranean and test the hypothesis that *C. nodosa* populations growing in sheltered bays support greater herbivory than those in open coastal systems.

## 2. Methods

We sampled 20 *C. nodosa* populations along the Spanish Mediterranean coast (Fig. 1) in June and July when *C. nodosa* reaches its maximum biomass (Terrados and Ros, 1992; Pérez and Romero, 1994; Marbà et al., 1996). The sites were classified as enclosed, sheltered bays or open, exposed areas (Fig. 1 Table 1). The sheltered bays sampled had a narrow connection with the open sea relative to their extent, had smaller fetches than the open sites due to their restricted extension (Falqués, 1989), and exhibited much lower wave heights (25 cm on average; Terrados, 1986 Falqués, 1989) than the open sites (75 cm on average; Conde, 1991; Cebrián et al., 1996a). The number of protected and exposed populations sampled, reflects the natural abundance of sheltered bays and open beaches along the area surveyed (Fig. 1).

In every population we collected 50 shoots randomly distributed within the seagrass bed. The depth of sampling ranged from 50 cm, in the shallowest populations, to about 5 m in the deepest ones. The shoots were dug out by hand and care was taken to extract intact, long pieces of vertical rhizome for estimation of the leaf formation rate (see below). We recorded the length, width, age rank and the number of marks left by herbivore bites (Cebrián et al., 1996b) of every leaf on the sampled shoots. Leaf nutrient (N, P) concentrations (% DW), as an estimator of the seagrass nutritional quality for herbivores (Thayer et al., 1984), were measured in duplicate subsamples of dried leaves using a Carlo-Erba autoanalyzer for nitrogen (N) concentrations, and a colorimetric method, following wet acid digestion, for phosphorus (P) concentrations (Koroleff, 1983).

*C. nodosa* bears narrow leaves and only few marks remain apparent under intense

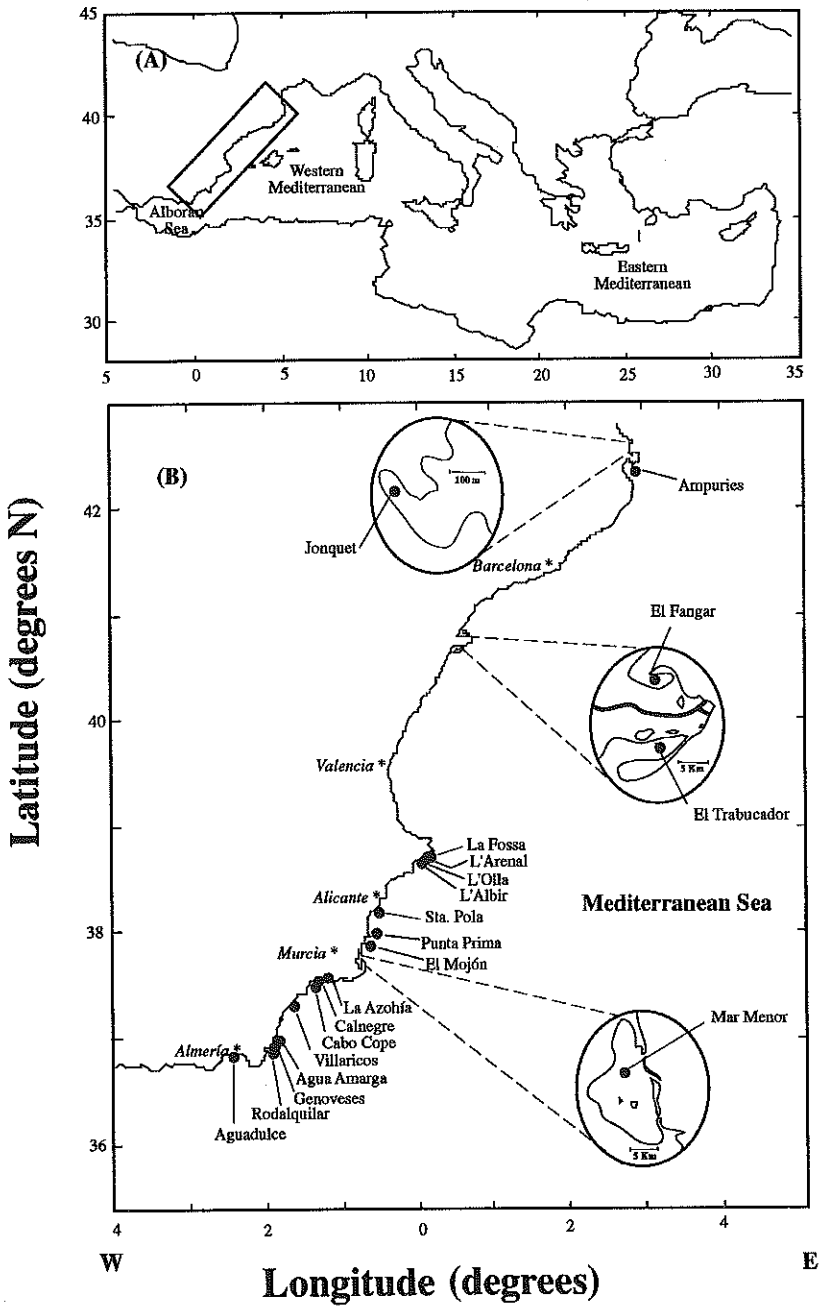


Fig. 1. (A) Location of the area studied in the Mediterranean Sea and (B) location of the sampled populations of *C. nodosa* along the Spanish coast. The sheltered bays have been amplified.

Table 1  
The type of location (sheltered bay or open site), the annual leaf production per shoot, the leaf nitrogen (N) and phosphorus (P) concentrations, the leaf loss per shoot and the percentage of leaf production lost by herbivory for all the populations examined

Population	Type	Leaf production (mg DW shoot <sup>-1</sup> y <sup>-1</sup> )	N (% DW)	P (% DW)	Leaf loss by herbivory (mg DW shoot <sup>-1</sup> y <sup>-1</sup> )	Percentage of leaf production lost by herbivory
Jonquet	sheltered bay	95.1	2.65	0.27	35.6	37.5
Ampuries	open site	181.1	3.16	0.21	54.3	30
El Fangar	sheltered bay	312.9	3.13	0.25	133	42.5
El Trabucador	sheltered bay	199.2	3.01	0.24	14.3	7.2
La Fossa	open site	87.8			8.8	10
L'Arenal	open site	123.9	1.97	0.22	7	5.7
L' Olla	open site	228.4	1.45	0.18	0.3	0.1
L'Albir	open site	136.3	2.37	0.09	0.8	0.6
St. Pola	open site	153.3	1.75	0.11	0.5	0.3
Punta Prima	open site	146.6	2.05	0.24	0.5	0.3
El Mojón	open site	226	3	0.14	0.9	0.4
Mar Menor	sheltered bay	156.6	1.94	0.15	19.1	12.2
La Azohía	open site	99.7	1.82	0.13	13.9	14
Calnegre	open site	323.5	2.18	0.20	50	15.5
Cabo Cope	open site	92.3	1.88	0.17	0.6	0.6
Villaricos	open site	218.6	1.73		1.9	0.9
Agua amarga	open site	113.6	2.08	0.23	2.1	1.9
Genoveses	open site	135.6	2.53	0.18	2	1.5
Rodalquilar	open site	219.3	1.74	0.16	4.8	2.2
Aguadulce	open site	97.1	2.54	0.13	2.3	2.4
Mean ± SE		167.3 ± 16.1	2.26 ± 0.12	0.18 ± 0.12	17.6 ± 7.3	9.3 ± 3

herbivory (Laborel and Laborel-Dequen, 1977; Zieman et al., 1984). Moreover, sloughing of leaf apical portions after bites by herbivores may be an important loss factor (Zieman et al., 1979). Hence, herbivory was derived by comparing the leaf length increment with leaf age between intact and bitten leaves. To do so, we derived continuous values of leaf age using the procedure presented by Cebrián et al. (1994) and defined, for intact and bitten leaves respectively, the pattern of leaf growth with leaf age by plotting leaf length vs leaf age and depicting the LOWESS (robust locally weighted regression) smoothed trend (Cleveland, 1979). We then estimated the mean maximum leaf biomass reached by intact and bitten leaves as the plateau attained over the leaf life-span by their respective patterns of leaf growth with leaf age and after transforming leaf length to biomass from the specific weight and width of the leaves ( $\text{g DW cm}^{-2}$ ). Bitten and intact leaves were supposed to have similar growth rates, as supported by experimental clipping of *C. nodosa* leaves (Cebrián et al., unpubl. obs.).

If the mean maximum leaf biomass reached by intact leaves differed from that reached by bitten leaves (Student-*t*,  $P < 0.05$ ; the variance of the mean maximum leaf biomass was estimated from the leaves having reached the plateau), we then derived the average maximum leaf loss ( $\text{mg DW leaf}^{-1}$ ) as the product of this difference and the fraction of fully-grown (i.e. having reached the plateau) leaves that had been bitten. Conversely, provided there was no significant difference in the mean maximum leaf biomass between intact and bitten leaves ( $P > 0.05$ ), herbivory was estimated by regressing leaf consumption, derived from the area covered by the leaf marks, on leaf age using least-square regression analyses (Jacobsen and Sand-Jensen, 1995; Cebrián et al., 1996b). In this case, we then estimated the average maximum leaf loss ( $\text{mg DW leaf}^{-1}$ ) as the maximum consumption value over the leaf life-span (Cebrián et al., 1994; Cebrián et al., 1996b).

The mean number of leaves produced annually per shoot ( $\text{leaves shoot}^{-1} \text{y}^{-1}$ ) was derived, for each population, from determination of the mean number of nodes (i.e. one node corresponds to one leaf) produced per annual cycle of the internodal length sequence imprinted on the five oldest vertical shoots sampled in the population (Duarte et al., 1994). In turn, this estimate allowed us to derive (1) the mean chronological equivalence of the plastochrone interval (in days  $\text{PI}^{-1}$ , estimated as the inverse value of the mean number of leaves produced annually per shoot), required to derive the leaf age estimates (Cebrián et al., 1994) and (2) the mean leaf production per shoot and the mean leaf loss per shoot by herbivory (both in  $\text{mg DW shoot}^{-1} \text{y}^{-1}$ ) when multiplied, respectively, by the mean maximum leaf biomass reached by the intact leaves and by the average maximum leaf loss (both in  $\text{mg DW leaf}^{-1}$ ). Because *C. nodosa* growth is strongly seasonal (Pérez and Romero, 1994; Marbà et al., 1996), which must consequently be the case for herbivory on *C. nodosa*, the error made when extrapolating production and herbivory values recorded during the sampling period to the entire year must be low.

Relationships between variables were described by the Pearson correlation coefficients (*r*) and least-squares linear regression analyses, after log-transforming the variables when necessary. ANOVA techniques were used to analyse the variability between the enclosed, protected and open, exposed populations.

## Herbivory

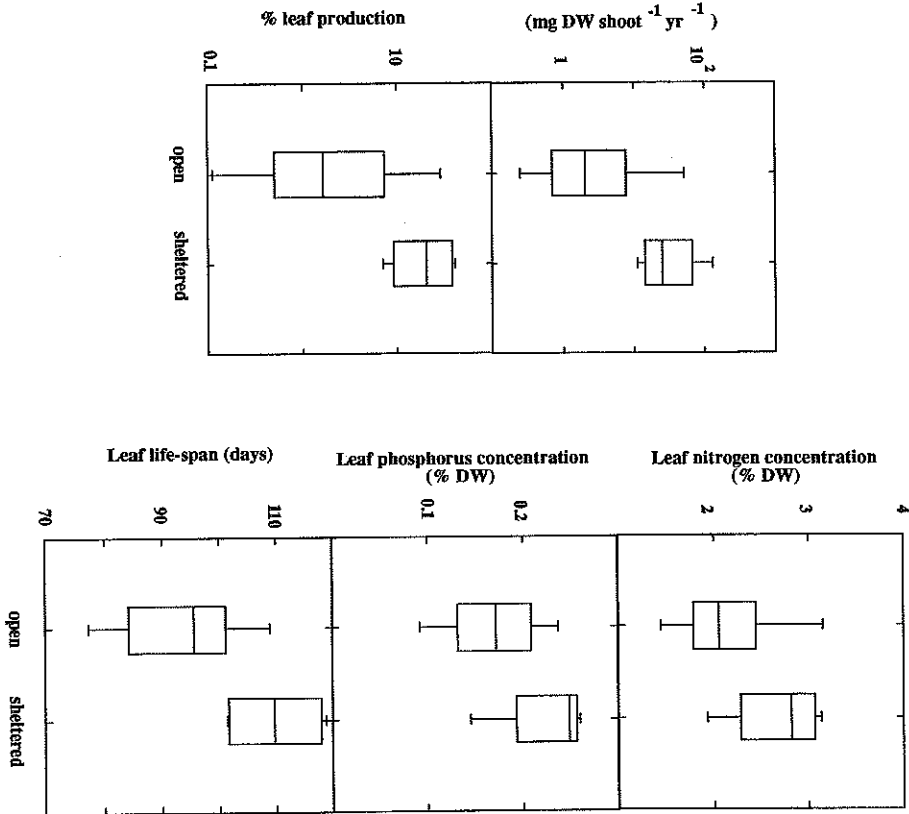


Fig. 2. Box plots comparing the leaf loss by herbivory, both in absolute amount and percentage of leaf production, the leaf nutrient (nitrogen and phosphorus) concentration and the leaf life-span, between the sheltered bays and the open sites. Boxes encompass 25% and 75% quartiles and the central line represents the median, and bars encompass 95% of the values.

### 3. Results

Shoot leaf losses by herbivory varied by more than two orders of magnitude among populations, although most of the populations (80%) supported losses  $< 20$  mg DW shoot<sup>-1</sup> y<sup>-1</sup> (Table 1). The fractional leaf production removed by herbivores also varied greatly among populations but was modest ( $< 5\%$ ) for most (55%) of the populations examined (Table 1). The mean leaf nutrient concentration of the *C. nodosa* populations sampled ranged from 1.5 to 3.2% of DW and from 0.09 to 0.27% of DW for nitrogen and phosphorus, respectively (Table 1). Herbivory, both as the absolute and proportional loss of leaf production, was correlated with both nitrogen ( $r = 0.52$  and  $0.48$ ,  $P < 0.05$ , respectively) and phosphorus ( $r = 0.44$  and  $0.40$ ,  $P < 0.05$ , respectively) concentrations

in *C. nodosa* leaves. Conversely, neither herbivory nor the nutrient leaf content were correlated with leaf production per shoot ( $P > 0.05$ ).

The great variability of herbivory on *C. nodosa* was partially attributable to the exposure (sheltered vs exposed) of the sites where the plants were growing (ANOVA,  $P < 0.05$ , 30% of the variance in herbivory explained), with the populations growing in sheltered bays supporting higher leaf losses by herbivory than those in open sites (Fig. 2). Plants growing in sheltered sites also tended to have higher leaf nitrogen (ANOVA,  $P = 0.07$ ) and phosphorus (ANOVA,  $P < 0.05$ ) concentrations (Fig. 2). In fact, the association between herbivory and leaf nutrient contents was linked to meadow exposure (ANCOVA,  $P < 0.05$  for the four relationships shown above). In addition, the populations growing in sheltered bays had longer leaf life-spans (ANOVA,  $P < 0.05$ , Fig. 2), so that their leaves were exposed longer to herbivore attack.

#### 4. Discussion

Our results are indicative of a significant role of *C. nodosa* leaves as a food source for herbivores in the Mediterranean littoral zone. The fraction of *C. nodosa* leaf production lost by herbivory (Table 1) is within the range of values for other seagrass species (1–50%, cf. Klumpp et al., 1993; Cebrián and Duarte, 1994). Given our estimate of mean leaf loss per shoot by herbivory (Table 1) and the mean shoot density of *C. nodosa* for some of the sampled populations (i.e.  $1630 \pm 402$  shoots  $m^{-2}$ ; Marbà et al., unpubl. obs.), we estimated the average areal leaf loss by herbivory to be about  $30 \text{ g DW } m^{-2} y^{-1}$ . Considering that the sloughed portion of leaf biomass due to herbivore bites could account for an important fraction of this average total leaf loss, this value is comparable to the reported range of leaf consumption for other seagrass species (cf. Klumpp et al., 1993; Cebrián and Duarte, 1994).

Nevertheless, we show that loss of *C. nodosa* leaf production by herbivory varies by more than two orders of magnitude in the Spanish Mediterranean, this variance being partially explained (30%) by the degree of meadow exposure (Fig. 2). These data strongly suggest that herbivore impact on *C. nodosa* leaf production depends on whether the meadow grows in a sheltered or an exposed site. In open coastal zones, the fractional loss of *C. nodosa* leaf production by herbivory (Table 1) is similar to the range of fractional consumption recorded for other temperate species (2–20%, Cebrián and Duarte, 1994). On the other hand, the fractional removal of *C. nodosa* leaf production by herbivores in sheltered bays (Table 1) is one of the highest reported to date, only comparable with the highest values registered in tropical seagrass meadows (> 50% leaf production removed, Greenway, 1976; Keller, 1983; Valentine and Heck, 1991).

The high variance in herbivory on *C. nodosa* along the Spanish Mediterranean seems to be a common trait in seagrass ecology (cf. Thayer et al., 1984; Klumpp et al., 1993; Cebrián et al., 1996b). This high variance has been partially attributed to changes in herbivore abundance as a consequence of the interaction among recruitment rates (Camp et al., 1973), predation effects (McClanahan et al., 1994) or overfishing (Klumpp et al., 1993). The variation in herbivore biomass may also partially account for the much

greater (5-fold, on average) herbivory on the *C. nodosa* populations growing in sheltered bays because seagrass meadows growing within these locations tend to support higher herbivore abundances than those inhabiting open, exposed sites (Costa and Bruxelas, 1989; Costa et al., 1994). The higher leaf nutrient concentration and leaf life-span of the *C. nodosa* populations growing in sheltered bays (Fig. 2), which may respectively render the leaves more palatable for herbivores (Thayer et al., 1984) and longer exposed to them (Sand-Jensen et al., 1994), could also account for the higher herbivory on *C. nodosa* in sheltered bays than in open sites.

In summary, we conclude that loss of *C. nodosa* leaf production by herbivory, albeit similar on average to many other seagrasses, varies greatly in the Spanish Mediterranean. A significant (30%) fraction of this variance is explained by meadow exposure (sheltered vs exposed sites). In sheltered meadows herbivores may remove up to 50% of the seagrass leaf production, which is among the highest values reported so far for seagrasses, compared with five times lower values, on average, in exposed meadows. Hence, our results indicate that both the trophic importance of *C. nodosa* as a food resource for herbivores and their role on the control of the seagrass production must be much greater in sheltered than in exposed meadows in the Spanish Mediterranean. The degree of exposure of seagrass populations, through changes in the associated herbivore biomass, may be also a significant factor accounting for the variability of herbivory on other seagrass species.

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