

Seasonal grazing and food preference of herbivores in a *Posidonia oceanica* meadow*

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SUMMARY: Seasonal grazing of the fish *Sarpa salpa* (L.), the urchin *Paracentrotus lividus* Lamarck and the isopods *Idotea* spp. was compared with the C/N ratio of adult and intermediate leaves and epiphytes of *Posidonia oceanica* (L.) Delile, collected at three different depths. Despite seasonal differences in grazing, herbivores showed preferences throughout the year for adult leaves with more epiphyte and higher N contents. The maximum grazing on adult and intermediate leaves was observed in September and in June for fish and in March for urchins, whereas it was irregular for isopods. Grazing by the three herbivores was not related to their preference for leaves or epiphytes, notwithstanding the seasonal differences in their C and N contents. We concluded that herbivores show no preference for food type throughout the year and that seasonal consumption of *P. oceanica* is related mainly to herbivore behaviour.

Key words: grazing, C/N ratio, seagrass, epiphytes.

INTRODUCTION

Leaf production in the Mediterranean seagrass *Posidonia oceanica* (L.) Delile begins in August and attains its maximum in March, followed by a period of slow growth (Ott, 1980). The leaves and their epiphytes sustain a large number of organisms that either actively feed on them or eat their remains, which enter the food chain (Romero *et al.*, 1992; Mateo and Romero, 1997). Among grazers, a major role is played by the fish *Sarpa salpa* (Velimirov, 1984; Francour, 1997), the urchin *Paracentrotus lividus* (Ott and Maurer, 1977; Kirkman and Young, 1981), and the isopods *Idotea* spp. (Cebrian *et al.*, 1996).

Reviewing plant-animal trophic relationships in the *P. oceanica* ecosystem, Mazzella *et al.* (1992)

pointed out the difficulty of defining a general strategy for grazers, the latter depending both on the nutritional value of leaves and epiphytes and on the occurrence of herbivores.

The quality as a food (palatability) of the seagrass and its epiphytes, which can be expressed in terms of C/N ratios (Mazzella *et al.*, 1992), may vary according to season and within sites and depths, in relation to both environmental factors and the taxa that colonise the leaves (Pirc and Wollenweber, 1988; Alcoverro *et al.*, 1995; Alcoverro *et al.*, 1997a). Moreover, a large presence of herbivores may exert a controlling influence on epiphyte biomass and on shoot size and leaf length (Alcoverro *et al.*, 1997b). Data collected along the Spanish Mediterranean coast were used to evaluate the magnitude of herbivore consumption both on a local and a large scale (Alcoverro *et al.*, 1997b; Cebrian *et al.*,

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1996) and showed that the percentage of leaf production removed by herbivores in summer was correlated with both leaf specific growth rates and leaf production per shoot (Cebrian and Duarte, 1998).

Differences in grazing might also be explained by different behaviour of the grazers. Massive schools of the fish *S. salpa* actively feed on *P. oceanica* leaves in Summer to accumulate reserves for reproduction. In winter, adults migrate to greater depths, whereas young fish, in shallow waters, eat preferentially small crustaceans (Bini, 1968; Tortonese, 1975, Francour, 1997) and turf epilithic algae (Havelange *et al.*, 1997).

P. lividus forms true populations in *P. oceanica* meadows, where high densities may have a heavy impact on the meadow (Kirkman and Young; Nedelec and Verlaque, 1984). Even though the urchins reproduce throughout the year (Tortonese, 1965; Fenaux 1968), major spawning is concentrated in spring and summer (Fenaux 1968; Azzolina and Willsie, 1987) and is related to the lowest consumption of seagrass (Semroud and Kada, 1987). While the young urchins feed on both rhizomes and leaves, the adults (>2 cm diameter) have a low-specialised diet and graze preferentially, on the highly epiphytized distal part of the leaves at night (Nedelec and Verlaque, 1984; Zupo and Fresi, 1984).

Little is known about the behaviour of the isopods. The diet of the isopods *I. baltica balsteri* was investigated by Lorenti and Fresi (1982), who observed prolonged survival of the animal feeding on living leaves of *P. oceanica*.

Until now, it is not clear whether seasonal grazing is related to leaf or epiphyte quality of food or depends on other factors. The aim of the present work is to assess the relationships between grazing pressure and food availability and C and N contents, both in time and space. For this purpose three stations along a depth gradient were observed during one year. Two levels of food were considered: a) leaves (adult and intermediate) and b) epiphytes (divided into major taxa). Seasonal variations in food quality were analysed in terms of C and N contents and were compared with grazing pressure by *Sarpa salpa*, *Paracentrotus lividus* and *Idotea* spp.

MATERIALS AND METHODS

The study was carried out in the Bay of Monterosso, in the "Cinque Terre" Marine Protected Area (La Spezia, Ligurian Sea).

Twenty orthotropic shoots were collected seasonally on 28 September 1995, 11 December 1995, 21 March 1996 and 10 June 1996 at 5 m (the upper limit of the meadow), 10 m and 17 m (close to the lower limit). At each station, density was estimated by counting shoots in three random quadrats of 1 m². In the laboratory leaves were measured and divided into adult and intermediate (Giraud, 1977). Herbivore consumption was estimated by counting the number of leaves with grazed tips. Leaf marks were attributed to the fish *Sarpa salpa*, the urchin *Paracentrotus lividus* or the isopods *Idotea* spp. following Boudouresque and Meisnez (1982).

Epiphytism on leaves was calculated seasonally on five shoots per station using the Index of Epiphytism, IE (Morri, 1991), which is the portion of the leaf surface covered by each category of epiphyte with respect to the total leaf surface. The following epiphyte categories were taken into account: Algae (encrusting, erected, algal mat) Hydroids (*Sertularia perpusilla*, *Plumularia obliqua*, others), Bryozoa (*Electra posidoniae*, others), and other animals. Epiphytes were carefully scraped from leaves with a razor and leaves and epiphytes were desiccated for 48 h at 80°C and then weighed (Mazzella and Ott, 1984). Total C and N contents of leaves and epiphytes were estimated on three homogenised replicates with a CHN-analyser mod. Carlo Erba 1106. The C values were corrected following the procedures of Nieuwenhuize *et al.* (1994) to evaluate the calcium carbonate that might still be present on the blades after scraping.

Data were analysed using ANOVA and homogeneity of group variances controlled with the Bartlett test. To satisfy the assumption of homoscedasticity, the number of grazed leaves was log₁₀(X + 0.5) transformed. When data did not satisfy the assumption of homogeneity of variance, the Kruskal-Wallis non-parametric one-way analysis of variance was applied.

Correlations between grazing activity of the fish *S. salpa*, the urchin *P. lividus* and the isopods *Idotea* spp. and C, N contents of leaves and epiphytes and the IE indexes were investigated.

RESULTS

Shoot density showed differences between the three sampling depths (one-way ANOVA, P = 0.031). Recorded values (293.1 shoots·m⁻² at 5 m depth, 233.7 shoots·m⁻² at 10 m and 159 shoots·m⁻² at

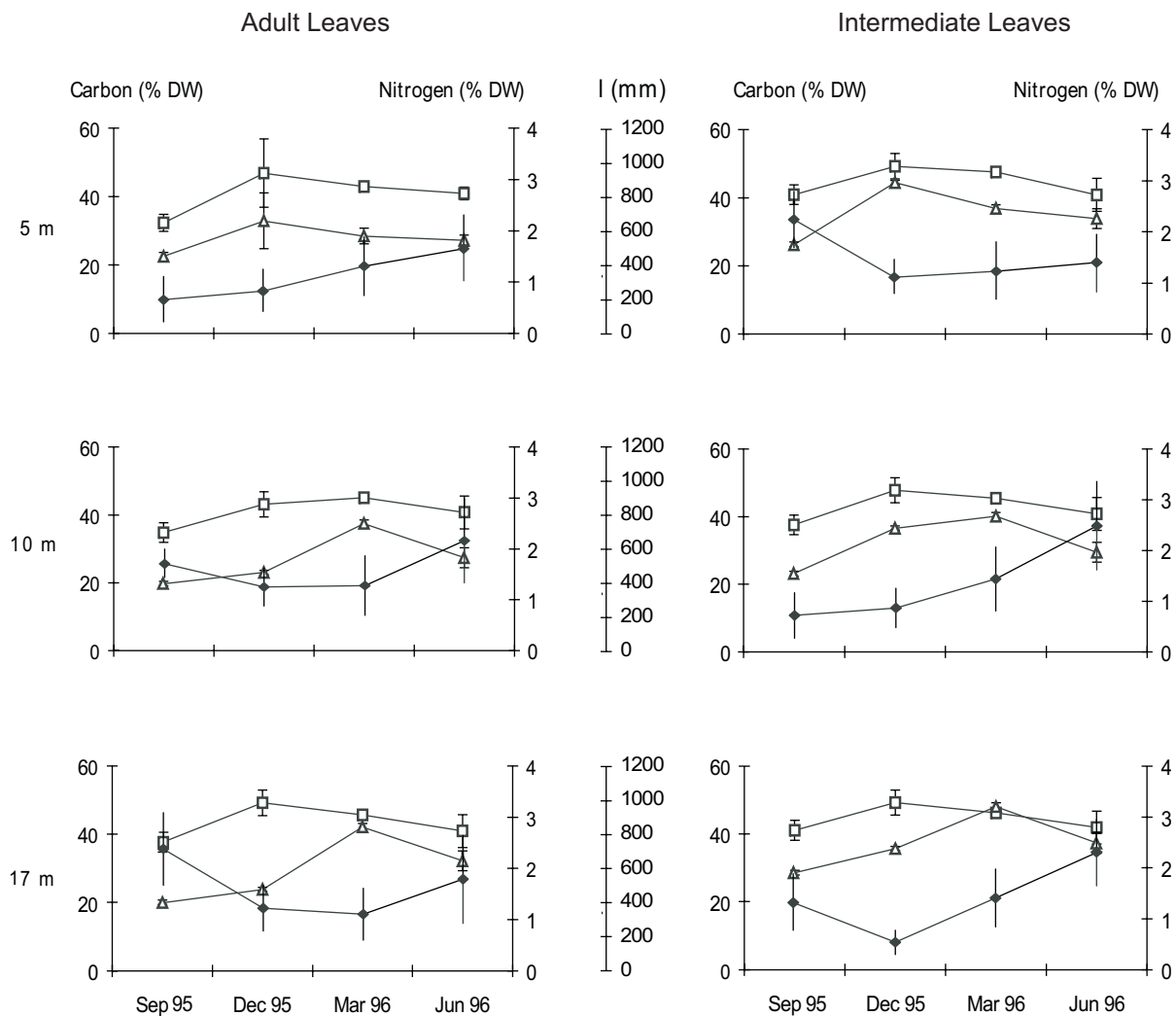


FIG. 1. – Seasonal variations of carbon (o) and nitrogen (Δ) contents in adult and intermediate leaves. Mean leaf length (l) in mm (u). Standard deviations are indicated with bars.

17 m) are characteristic of the present status of the Ligurian *Posidonia oceanica* meadows, which have regressed in response to large coastal impacts (Peirano and Bianchi, 1997).

Kruskall-Wallis analysis of variance performed on leaf length showed differences between months ($P < 0.0001$), with the longest leaves in June and September (Fig. 1). Differences were also found between depths and between adult and intermediate leaves ($P < 0.05$) in all months, with the single exception of March. Adult leaves, always longer than intermediate ones, attained their maximum length at 17 m depth in September (Fig. 1).

Total carbon contents of leaves varied seasonally and between adult and intermediate leaves (Table 1 and Fig. 1). The C contents of intermediate leaves was greater than in adult leaves in all stations, in

agreement with Romero *et al.* (1992). The recorded values (37.32-49.07%) were similar to those obtained by Augier *et al.* (1982) in France (31-45%) and Enriquez *et al.* (1995) in Spain (38.12%). The maximum C content was recorded in December and March in both adult and intermediate leaves.

Nitrogen showed seasonal differences between intermediate and adult leaves and between depths (Table 1 and Fig. 1). The N content showed higher levels in intermediate leaves. The analyses showed a seasonal trend at all depths, with minimum values in September and maximum ones in December and March.

Epiphyte cover, expressed as the index of epiphitism (IE), showed differences between adult and intermediate leaves and between seasons and depths (Fig. 2). Adult leaves were more epiphytised than intermediate ones and IE reached the highest

TABLE 1. – Three-way analysis of variance of leaves and their C and N contents (%) using leaf type (intermediate or adult), depth (station at 5, 10 and 17 m depth) and season (September, December, March and June) as factors. Significant differences are showed with asterisks (*).

	DF	MS	F	P
C (%)				
Season	3	340.70	18.144	<0.0001***
Depth	2	23.611	1.257	0.295
Leaf type	1	89.976	4.792	0.034*
Leaf Type x Depth	2	9.779	0.521	0.598
Leaf Type x Season	3	15.180	0.808	0.496
Season x Depth	6	4.555	0.243	0.960
Leaf Type x Depth x Season	6	6.354	0.338	0.913
Error	42	18.778		
N (%)				
Season	3	2.819	42.517	<0.0001***
Depth	2	0.345	5.208	0.010**
Leaf type	1	3.441	51.894	<0.0001***
Leaf Type x Depth	2	0.042	0.627	0.539
Leaf Type x Season	3	0.233	3.520	0.023*
Season x Depth	6	0.506	7.630	<0.0001***
Leaf Type x Depth x Season	6	0.030	0.459	0.835
Error	42	0.066		

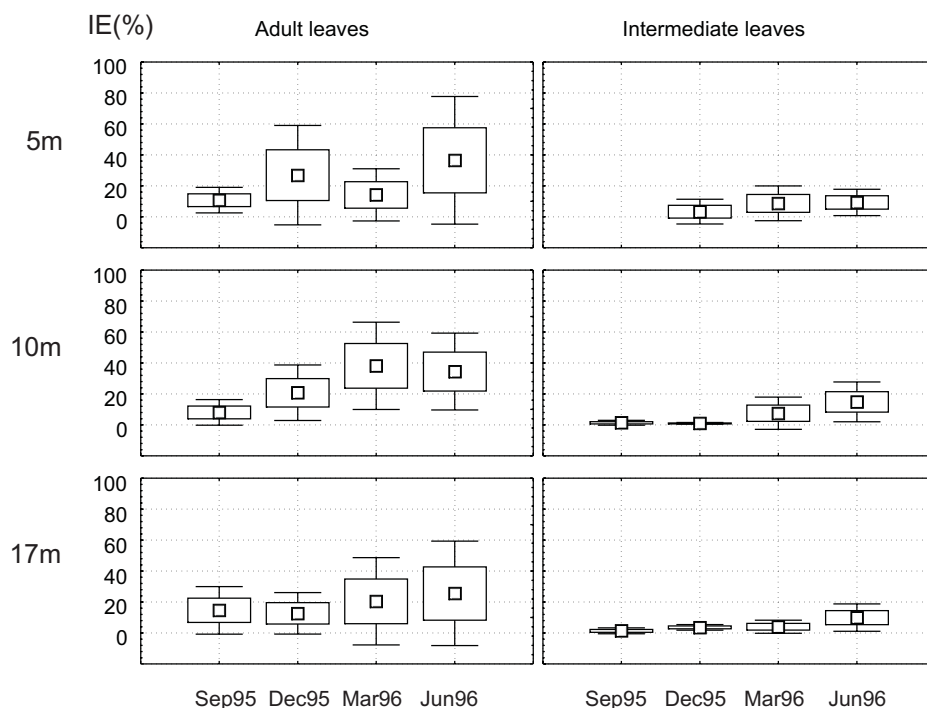


FIG. 2. – Mean Seasonal variation of the index of epiphytism (IE) in adult and intermediate leaves. Boxes indicate \pm standard deviations, bars the 95% confidence limits of the means.

values at all depths in June and decreased regularly until December. Encrusting algae dominated in September and December while *Electra posidoniae*, other Bryozoan and *Plumularia obliqua* colonised most of the leaves in March and June (Fig. 3). In intermediate leaves epiphyte colonisation varied considerably between depths. In September and December epiphyte colonisation differed within

depths and in adult leaves; in March and June, the predominance of *Electra posidoniae* in intermediate leaves sometimes reached and exceeded that of adult leaves. Carbon and nitrogen contents of epiphytes were seasonally related in most cases (Table 2 and Fig. 2) and showed increasing values from September to June in accordance with the period of maximum leaf colonisation.

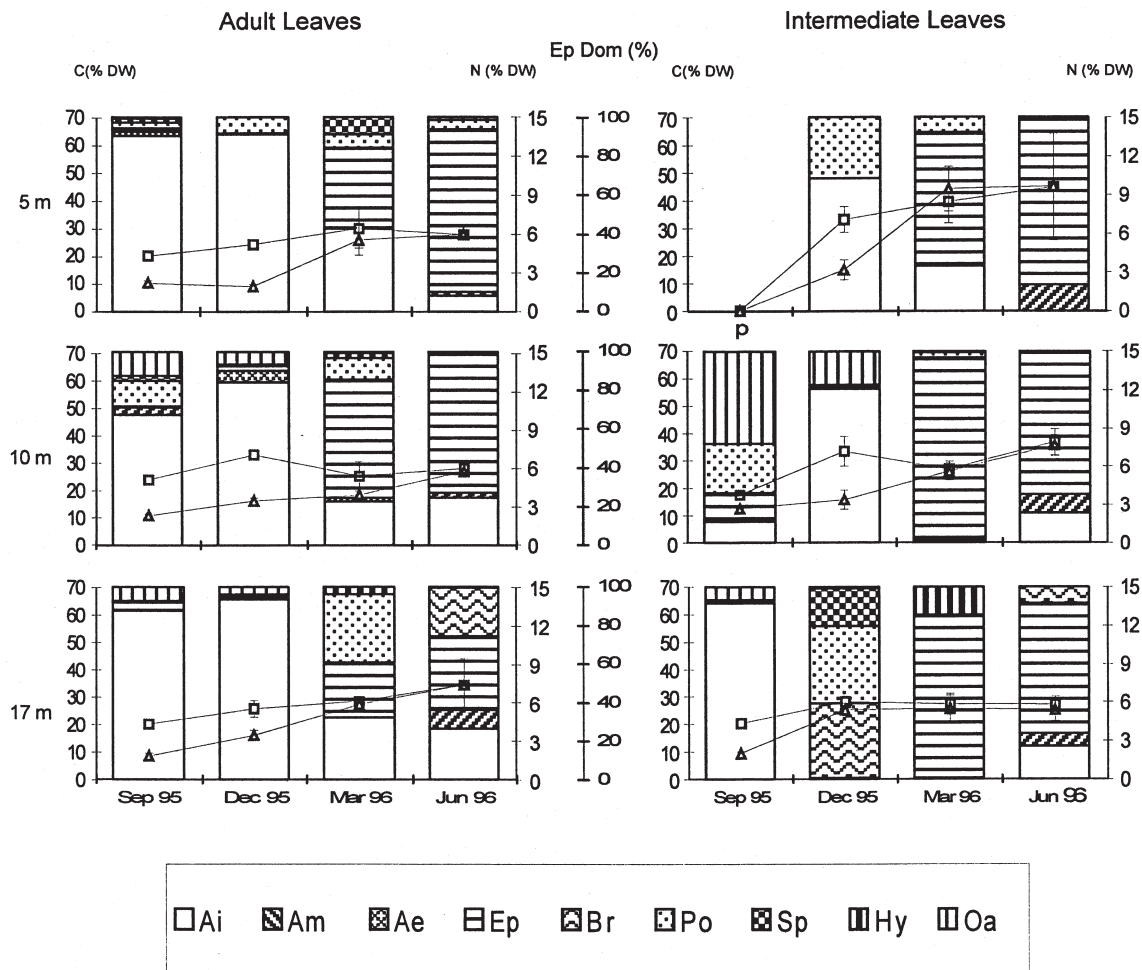


FIG. 3. – Seasonal percent dominance of epiphytes (Ep Dom) and variations in epiphyte carbon (○) and nitrogen (Δ) contents in adult and intermediate leaves. Standard deviations are indicated with vertical bars. A= algae (i= incrusting, m= mat, e= erected); Ep= *Electra posidoniae*; Br= other Bryozoa; Po= *Plumularia obliqua*; Sp= *Sertularia perpusilla*; Hy= other Hydroids; Oa= Other animals.

TABLE 2. – Annual mean values (\pm SD) of epiphyte C and N contents (Ce and Ne) and annual mean number of grazed leaves per shoot (Gl) and leaf type= Lt (A= adult and I= intermediate). Seasonal differences are indicated with the following symbols: N.S.= non significant difference; * = $0.05 \leq P < 0.01$; ** = $0.01 \leq P < 0.001$; *** = $P \leq 0.001$. The Kruskal-Wallis test is indicated with the notation (1).

Depth	Lt	Ce (%)	Ne (%)	Gl (n)
5 m	A	27.6 \pm 3.9 N.S. (1)	3.9 \pm 1.3 ***	0.9 \pm 0.7 *** (1)
	I	34.2 \pm 15.2 N.S. (1)	5.8 \pm 4.3 * (1)	0.9 \pm 1 *** (1)
10 m	A	24.7 \pm 6.2 N.S. (1)	4 \pm 1.9 * (1)	0.8 \pm 1 *** (1)
	I	29.4 \pm 7.9 *	4.6 \pm 2.4 ***	0.3 \pm 0.6 * (1)
17 m	A	27.3 \pm 7.2 * (1)	4.7 \pm 2.5 * (1)	0.3 \pm 0.5 * (1)
	I	20.6 \pm 12.7 ***	4.1 \pm 2.6 ***	0.1 \pm 0.03 N.S (1)

Herbivore pressure, in terms of number of leaves with grazed tips, showed differences between seasons at all depths in both adult and intermediate leaves with only one exception (Table 2). IE of grazed and non-grazed leaves did not show differences either in adult or intermediate leaves at each station and season considered (t-test, $P > 0.05$).

To test the indirect effects of each herbivore type on availability of food to other grazers, the IE of leaves grazed by fishes, urchins and isopods was compared at each station and season. No differences were found (Anova one-way, $P > 0.05$).

To test the preference of each herbivore for a specific item or prey, the grazing frequencies of each herbivore were compared to the IE of different epi-

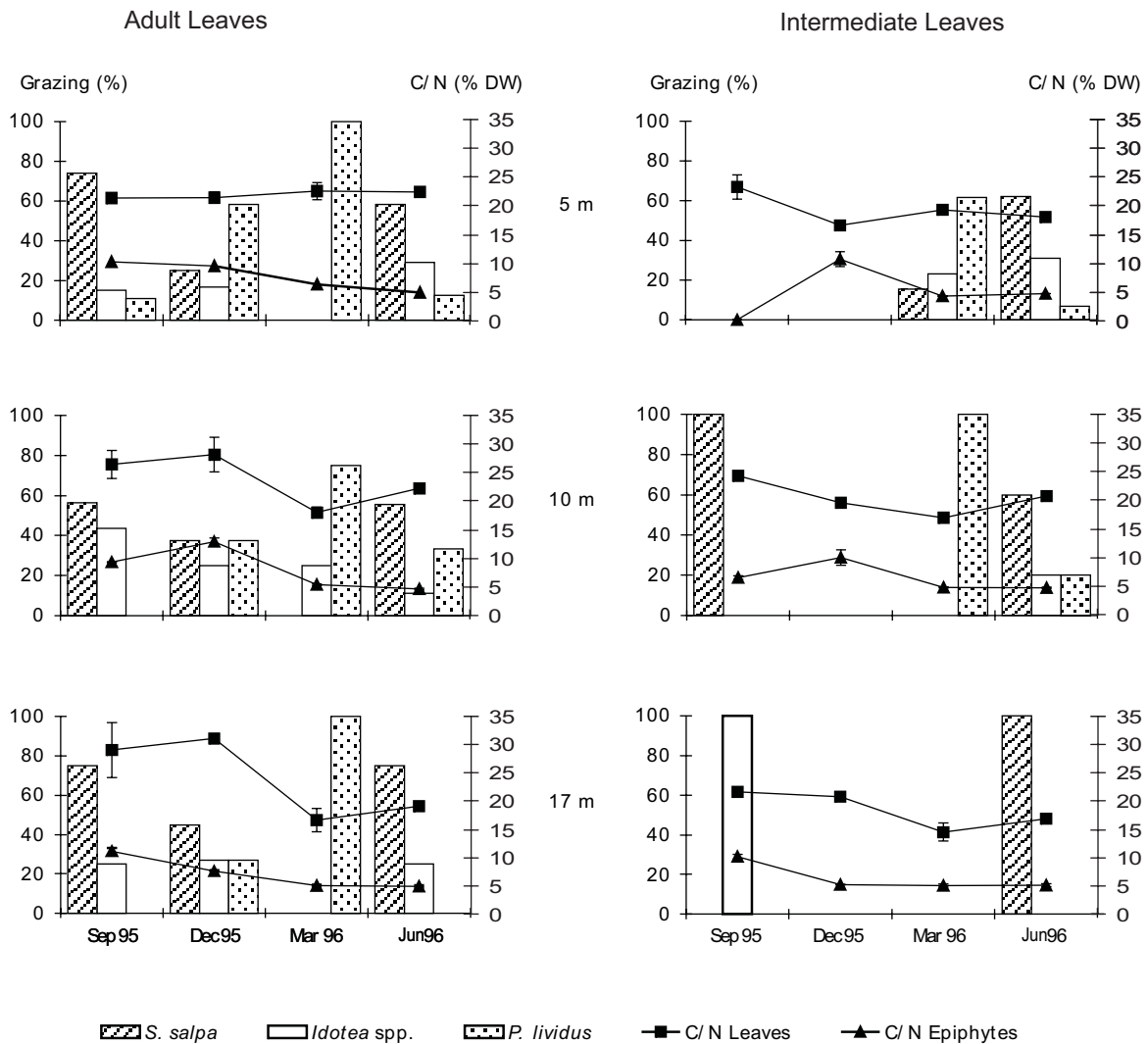


FIG. 4. – Grazing pressure of *S. sarpa*, *P. lividus* and *Idotea* spp. in term of percent seasonal grazing (%), and seasonal C/N ratio of leaves (n) and epiphytes (s).

phytic taxa. No relationships were found (Pearson correlation, $P > 0.05$).

Adult leaves were preferred by herbivores throughout the year at all depths (Fig. 4). The fish *Sarpa sarpa* had periods of grazing with maximum levels in June and September. A significant difference in the C/N ratio of epiphytes ($P < 0.001$) was found in these months in accordance with different taxa colonising *P. oceanica* leaves (incrusting algae in September and *E. posidoniae* in June). The urchin *Paracentrotus lividus* attained maximum grazing in March and minimum grazing in June (Fig. 4). Neither leaves nor epiphytes showed differences ($P > 0.05$) in C/N ratios in the two months. The isopods (*Idotea* spp.) may be considered to be a constant grazer of *P. oceanica* for virtually the whole year, grazing preferentially on adult to intermediate

leaves with only two exceptions (the shallowest station in March and the deepest station in September).

No correlations ($P > 0.05$) were found between the percentage of grazing by fish, urchins and isopods and the C and N contents of leaves and epiphytes.

DISCUSSION

C and N leaf contents are consistent with data from Pirc (1985), Pirc and Wollenweber (1988) and Alcoverro *et al.* (1997a), who indicated winter as the period of maximum nutrient absorption in the plant.

The timing and succession of epiphytes did not differ from previous studies made in Liguria (Relini Orsi *et al.*, 1977; Boero *et al.*, 1985), despite the dif-

ference in latitude and in the status of the meadow, both in terms of shoot density and depth of colonisation, from data collected at Ischia Island (Mazzella *et al.*, 1989; Chessa *et al.*, 1982). Hence, notwithstanding past regression, the meadow is in equilibrium with the environment and *Posidonia oceanica* shows a regular cycle in both plant growth and succession of epiphyte colonisation.

Adult leaves, which showed the greatest colonisation by epiphytes, were preferred by herbivores throughout the year at all depths.

Even though the three herbivores considered showed a different timing in grazing activity throughout the year, a preference for food type consisting of either leaves or epiphytes was not found. Hence, grazing might be related to the behaviour of the three species. At all depths grazing trends were accountable to *Sarpa salpa* behaviour. Fish grazing in June-September is due to the presence of massive schools that actively feed on *P. oceanica* to accumulate reserves for the winter period, when fish eat less, and to prepare adult fish for reproduction. In March, while *S. salpa* adults migrated deeply, juveniles lived and fed in shallow, rocky bottoms. Also minimum grazing of *Paracentrotus lividus* in June and September is consistent with its reproductive behaviour.

No food preference could be pointed out for the isopods (*Idotea* spp.) which may be considered as constant grazers of *P. oceanica* during virtually the whole year, grazing preferentially on adult to intermediate leaves with only two exceptions (the shallowest station in March and the deepest station in September).

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