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Invertebrate borers in the Mediterranean sea grass *Posidonia oceanica*: biological impact and ecological implications

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The effects of polychaete (*Lysidice ninetta*, *L. collaris*, *Nematonereis unicornis* (Annelida: Polychaeta)) and limnoriid isopod (*Limnoria tuberculata* (Crustacea: Isopoda)) borers in the Mediterranean sea grass *Posidonia oceanica* (Potamogetonaceae) were assessed in the meadows of Olbia and Genoa (western Mediterranean Sea). Borer invertebrates were mainly found into the old leaf sheaths of the sea grass. At Olbia, a mean density of borers (202.6 ± 34.8 ind m^{-2}) significantly higher than at Genoa (23.2 ± 7.3 ind m^{-2}) was observed. In 3.3% of samples from Olbia, large polychaetes and isopods were also observed boring into living plant tissues. Only fractions from 0.8–3.9% of the sheath production was actually removed by borers at the two studied meadows. The fact that sheath weight loss with time was higher at Genoa than at Olbia regardless of the presence of borers suggests that other factors than the activity of such organisms are important in the sheath decay process.

INTRODUCTION

Marine phanerogams are significant primary producers in shallow coastal environments world wide (Ott, 1980; Phillips & McRoy, 1980). Although herbivory on sea grasses has been believed to be generally modest (<10–15% of sea grass production removed; Den Hartog, 1970; Ott, 1981; Thayer et al., 1984), recent papers provided evidence of a high variability in this phenomenon. Consumption by herbivores, for instance, may vary from 5 to 50% and 5–60% of the leaf production of *Thalassia testudinum* and *T. hemprichii* (Cebriàn & Duarte, 1998), respectively. Consumers of living sea grass tissues, however, are not numerous and specialist feeders on sea grass are not well documented in literature (Mazzella et al., 1992).

In the Mediterranean Sea, *Posidonia oceanica* (L.) Delile contributes most of the primary production in the littoral zone (Ott, 1980). Potential consumers classically include the sparid fish *Sarpa salpa* L., the sea urchin *Paracentrotus lividus* Lam. and the isopod *Idotea baltica* Pall. (Cebriàn et al., 1996b). The relatively low number of studies focused on the assessment of herbivory in *Posidonia oceanica* revealed a variability ranging from 2 to 37% of the leaf production (Velimirov, 1984; Cebriàn et al., 1996b; Pergent et al., 1997). In most cases, however, only a small fraction of the productivity is consumed directly by herbivores (Cebriàn et al., 1996b). The bulk of the *P. oceanica* leaf production is considered to: (1) be channelled in the detrital pathways and utilized *in situ* or exported to other systems (Wolff, 1976; Ott, 1980; Pergent et al., 1994; Mateo & Romero, 1997); and (2) be buried into the sediment (Romero et al., 1992).

Previous studies on herbivory have only considered the consumption of leaf blades of *P. oceanica*, and little attention has been focused on other compartments of this sea grass. For example, the basal portion of leaves, named as sheaths, account for a large fraction of the total biomass in *P. oceanica* systems (Mazzella et al., 1998) and may persist for many years on the rhizomes (Pergent et al., 1989). Their importance is also testified by the fact that sheath production represents about one fifth of the total leaf production (Pergent-Martini et al., 1994; Pergent et al., 1997; Guidetti et al., 2000).

In recent years the consumption of living and dead tissues of different sea grass species by small crustacean limnoriid isopods was described in southern Australia with considerable potential effects on tissue health and sea grass growth (Brearley & Walker, 1993, 1995, 1996). Guidetti et al. (1997), moreover, first reported the occurrence of borer organisms of *P. oceanica* in the Mediterranean Sea and, more precisely, along the Italian coasts. Eunicid polychaetes [*Lysidice ninetta* Audouin and M. Edwards, *Lysidice collaris* (Grube) and *Nematonereis unicornis* (Grube)] and limnoriid isopods [*Limnoria tuberculata* (Sowinski)], reaching in some cases a total number of up to 278 ind m^{-2}, were identified as responsible for burrowing in the mesophyll of old *P. oceanica* sheaths. Although in a few cases, large polychaetes were reported to pierce through entire leaf bases, sometimes affecting the living meristem and causing the detachment of the whole living shoot (Guidetti et al., 1997).

From the above issues, two interesting ecological implications could be represented by: (1) the direct consumption of living meristem, young leaves and sheaths still bearing leaves, which may negatively affect leaf growth and shoot production (partial damage) or shoot survival (total damage); (2) the burrowing in dead sheaths persisting along the rhizomes, which may result, directly, in a mechanical disrupting of the sheath tissues and, indirectly, in an enhancement of the microbial activity.

Therefore, this paper aims: to provide additional data on the occurrence of invertebrate borers in *P. oceanica*

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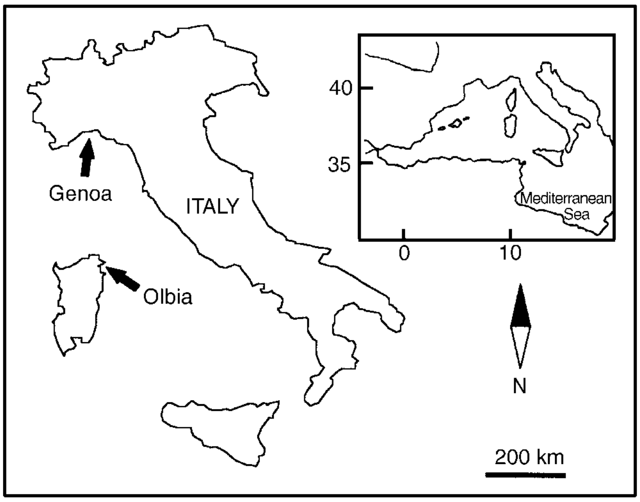

Figure 1. Location of the investigated meadows.

beds; to evaluate the impact of invertebrate borers on living plant tissue; to evaluate the fraction of sheath production removed by borers; and to contribute to the understanding of the ecological role of borer organisms in *P. oceanica* systems.

MATERIALS AND METHODS

Study areas

Samples of *Posidonia oceanica* were collected in December 1996 at Olbia (Sardinia Island, Italy: 40°55′N 09°34′E) at 6 m depth and at Genoa (Ligurian Sea, Italy: 44°23′N 09°0′E) at 8 m depth (Figure 1). The meadow of Olbia was located just outside the Olbia Gulf, in a locality named Capo Ceraso; the area was characterized by a gentle slope and low wave action. *Posidonia oceanica* was growing on coarse sand and distributed quite homogeneously with rare sand patches. The Genoa bed was located in front of the eastern part of Genoa city, in a locality named Genoa-Quinto; it was characterized by higher hydrodynamic conditions than the Olbia meadow. At Genoa, *P. oceanica* was growing on sand and, to a lesser extent, on a rocky substrate and was more patchy in distribution.

Field sampling

The shoot density (number of shoots m^{-2}) was measured by using a frame of 40×40 cm (ten replicates at each site) and the resulting values were converted to a square metre. It is well known that the shoot density of *P. oceanica* does not show significant variations with season, in contrast to the majority of other sea grasses (den Hartog, 1970). The bed covering was estimated according to Romero (1986) as percentage cover of *Posidonia* shoots over the total bottom surface.

A total number of 280 orthotropic (vertical growth) rhizomes with living shoots of *P. oceanica*, 160 (40 rhizomes × four replicates carried out in different portions of the meadow at least 50 m apart each other) from Olbia and 120 (30 rhizomes × four replicates) from Genoa, respectively, were randomly collected and examined for evidence of borers. A total of 50 orthotropic shoots from each site were randomly taken for estimating leaf production. In addition, ten plagiothropic rhizomes (horizontal growth) from each site were collected in order to preliminary observe the presence of borers in this category of rhizomes.

Laboratory analysis

Rhizomes with leaf shoots were examined for evidence of living borers, to note empty burrows made in the dead sheaths and the damage to living tissues (piercing of sheaths still bearing leaf blades and attack to young leaves and meristem localized in the centre of the leaf shoot). On the basis of the general structure of burrows (Guidetti et al., 1997) or the actual presence of borers, sheaths mined by polychaetes and isopods were distinguished. When present, borers were extracted from the sheaths, preserved in 4% formalin and classified at species level. In addition, the presence of fungal peritecia within the sheaths (with or without borers) was also noted.

To quantify the consumption of sheath tissue by borers, a similar approach utilized by Cebriàn & Duarte (1998) for the evaluation of patterns in leaf herbivory on sea grasses was followed. Thus, rhizomes with and without borers or their tracks were considered separately: rhizomes without damage were treated as controls, the sheath loss exhibited by these being supposed to be due to factors other than borers, such as abiotic agents (i.e. water movements). Sheath loss exhibited by mined rhizomes (with living borers or their tracks) was considered to be due to both the activity of borer organisms and other agents. The sheath loss by borers was therefore calculated as the difference between sheath weight loss with time exhibited by mined and not mined rhizomes. For this purpose, sheaths were assigned to different annual age-classes by using the lepidochronological technique (Pergent et al., 1989) and dried at 60°C until constant weight.

To quantify borer activity, the primary leaf production (blades and sheaths) of *P. oceanica* shoots from the two investigated meadows was estimated using the lepidochronological technique (Pergent-Martini et al., 1994). This method is based on the existence of annual cyclic variations (minima in spring and maxima in autumn) in the thickness of sheaths, which may persist along the *P. oceanica* rhizomes for many years after the leaf blade fall. The term 'lepidochronological year' is conventionally used for the time period between two minima and prevents any confusion with the calendar year. Each sheath was carefully detached from the rhizomes according to their distical rank insertion, from the oldest (towards the rhizome base) to the most recent (close to living leaves). Sheath thickness was measured with a manual micrometer, on a transverse section cut at 10–12 mm above the insertion point on the rhizome. The number of leaves produced per year was calculated on the basis of the number of old sheaths between each pair of minima in sheath thickness. Mean blade and sheath lengths were evaluated on the oldest leaves still bearing their apex in living shoots. The blade and sheath densities, that is the blade and sheath weight (DW) per length unit, were calculated only for the oldest leaves, just before shedding. Oldest leaves were thus scraped with a razor blade to eliminate epiphytes before drying. The positive

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Table 1. *Abundance of borers m^{-2}, number of shoots m^{-2} mined by borers or infested by fungal peritecia (mean ±SD). Differences between the two investigated sites evaluated by* t*-test or Mann–Whitney test (see Materials and Methods).*

	Olbia	Genoa	Difference
Number of borers	202.6 ±34.8	23.2 ±7.9	***
Number of *Lysidice ninetta*	42.5 ±10.1	0	***
Number of *L. collaris*	33.6 ±1.3	0	***
Number of *Nematonereis unicornis*	16.4 ±13.0	15.9 ±5.0	ns
Number of isopod borers	110.1 ±36.0	7.4 ±10.4	**
Shoots mined (living borers and/or tracks)	398.8 ±11.7	102.0 ±10.5	***
Shoots with borers' tracks	287.8 ±43.1	82.5 ±11.5	***
Shoots with polychaete tracks	146.3 ±31.3	80.1 ±10.4	*
Shoots with isopod tracks	188.1 ±66.6	2.3 ±3.2	**
Shoots with living borers	154.7 ±20.7	23.2 ±7.9	***
Shoots with living tissues attacked	15.2 ±10.7	0	***
Shoots with fungal peritecia	63.3 ±4.4	0	***

ns, not significant; *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$.

correlation between the sheath length of the oldest living leaves and their leaf blade length, was used to estimate the total length of fallen leaves on the basis of the length of their persisting sheaths.

On the basis of the above parameters, primary production (PI), for blades and sheaths separately, were calculated, according to Pergent-Martini et al. (1994), by:

$$PI = N \times L \times D \qquad (1)$$

where N=mean leaf number, L=mean blade/sheath length and D=blade/sheath density.

Data analysis

Statistical differences between the two investigated sites were performed by *t*-test or Mann–Whitney test on the basis of the assessment of normal distribution of data performed by Kolmogorov–Smirnov test (Sokal & Rohlf, 1981). Data on borers' abundance and on the number of rhizomes bearing sheaths infested by borers and fungal peritecia were converted to a metre square before comparisons. This was necessary because of the different number of shoots in the two series of replicates.

Since sheaths from different sites often show marked differences in length, thickness and, consequently, in the absolute weight, and as there is variability in the number of leaves produced per year (Pergent et al., 1989; Guidetti et al., 2000), sheath biomass was normalized for an ideal average sheath (Romero et al., 1992). Weight sheath loss with time was analysed by three-way ANOVA to test the null hypothesis that the sheath weight does not change with time (years), between sites and in relation to the borers' activity (presence vs absence). All three factors were considered to be fixed. Before analysis, data were tested by Kolmogorov–Smirnov test for normality and by Cochran's test ($P>0.05$) to meet the assumption of homogeneity of variances (Underwood, 1981).

RESULTS

Abundance, distribution and damage caused by borers

Borer organisms recorded at Olbia were represented by three species of polychaetes, namely *Lysidice ninetta* Audouin and M. Edwards, *L. collaris* (Grube) and *Nematonereis unicornis* (Grube), and the crustacean isopod *Limnoria tuberculata* (Sowinski). In some cases, the co-occurrence of more than one borer in the same rhizome or in the same sheath was observed. Thus, one individual of *Lysidice collaris* and another one of *N. unicornis*, in one case, and two specimens of *L. ninetta*, in other two cases, were found in the same rhizome, but not in the same sheath. On the other hand, more than one isopod was recorded in the same rhizome; in five cases two or three isopods were found in the same sheath, and in one case an isopod co-occurred in the same rhizome with two specimens of *L. collaris*. At the Genoa bed, borers were represented only by the polychaete *N. unicornis* and the isopod *Limnoria tuberculata*. In a single case, one specimen of *N. unicornis* was found in the same rhizome together with an individual of *L. tuberculata*.

At the Olbia meadow, *Lysidice ninetta* and *L. collaris* showed comparable abundances, while *N. unicornis* was less represented than the two former species. Isopods were more abundant than polychaetes (Table 1). At Genoa, polychaetes of the species *N. unicornis* were more abundant than isopods (Table 1).

Comparisons between the abundance of borers at the two investigated sites are shown in Table 1. *Lysidice ninetta* and *L. collaris* were present only at Olbia; the mean abundance of *N. unicornis* was not significantly different between Olbia and Genoa meadows, while at the former site the mean abundance of isopods was significantly higher.

At both meadows, isopods burrowed younger sheaths (close to living leaves) and polychaetes the older ones, although some large polychaetes of the genus *Lysidice* were also found in sheaths adjacent to living leaves. It is worth noting that the bulk of living borers were concentrated in sheaths at the most 4-y old. Moreover, not all sheaths along a rhizome were mined. The distribution of mined sheaths was patchy, approximately 4–10 adjacent sheaths, often located on the same side of the rhizome.

On the whole, most of rhizomes from Olbia were mined (85.9%) and 63.1% of these contained sheaths with empty burrows (with approximately similar frequencies for polychaetes and isopods). At Genoa, instead, only 28.9% of rhizomes were mined by borers; 23.4% showed

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Table 2. *Main structural features, annual leaf production per shoot, annual sheath production per shoot, sheath loss per rhizome and the percentage of leaf production lost by borers at the two meadows studied (mean ±SD).*

Site	Olbia	Genoa
Shoot density (shoots m^{-2})	456.4 ±53.7	353.3 ±48.9
Cover (%)	79.0 ±9.8	63.7 ±9.6
Total leaf production (mg DW $shoot^{-1}\,y^{-1}$)	924	1197
Sheath production (mg DW $shoot^{-1}\,y^{-1}$)	172.3	241.5
Total leaf production (g DW $m^{-2}\,y^{-1}$)	421.7	422.9
Sheath thickness (mm)	0.5 ±0.2	0.6 ±0.3
No. leaves produced y^{-1}	6.9 ±0.3	6.3 ±0.2
Total sheath loss (mg DW $shoot^{-1}\,y^{-1}$)	112.1	192.2
Sheath loss by borers (mg DW $shoot^{-1}\,y^{-1}$)	6.7	1.9
Sheath production lost by borers (%)	3.9	0.8

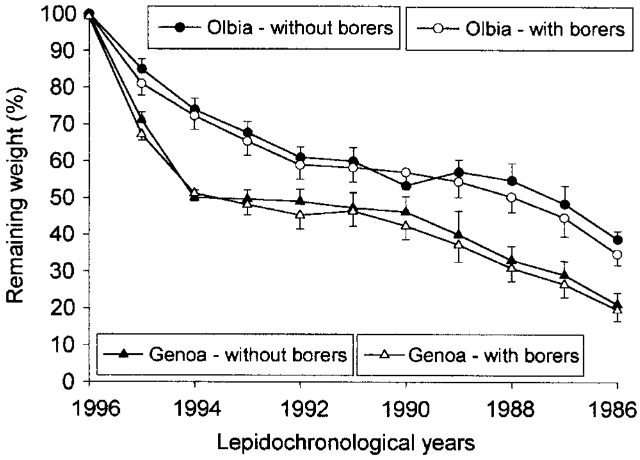

Figure 2. Weight change with time in sheath data derived from lepidochronological measurements (bars indicate standard errors).

sheaths with empty burrows (mainly due to polychaetes), while only 6.6% were actually infested by living borers.

A low proportion of shoots (3.3%) from Olbia only showed damage to living tissues. When the proportion of shoots with mined meristem or young leaves is reported to a square metre, a number of about 15 shoots m^{-2} can be calculated. In contrast, no damage to living plant tissues was detected in shoots from the Genoa meadow.

Different levels of damage to plant living tissues were observed. In three different shoots, two isopods and one individual of *L. ninetta* were found to attack sheaths bearing adult external living leaves. These tracks, however, were less marked than those observed in dead sheaths and seemed to be 'attempts' or 'tastings', since damage was limited. On the other hand, in two other cases (one shoot infested by a large *L. collaris* and another with clear tracks of a large polychaete) the author observed the total destruction of young leaves (<0.5 cm in length) and the meristematic tissue, both protected in the centre of the leaf shoot, and the partial removal of the basal portion of other growing leaves some centimetres long, appeared in the leaf bundles and with clear signs of suffering. In these cases, a clear track of a transverse piercing from the oldest external living leaves to the centre of the shoot was noted, meaning that penetration, which seems to be relatively easy for very large polychaetes, happens from outside.

Table 3. *Analysis of variance for the effects of sites (S), years (Y) and borers (B; presence vs absence) on the weight loss in* Posidonia oceanica *sheaths. Cochran's test:* C=*0.23,* P>*0.05. Data not transformed.*

Source of variation	df	MS	*F*	*P*
S	1	4.209	194.318	***
B	1	0.037	1.690	ns
Y	10	3.020	147.786	***
S×B	1	0.028	1.298	ns
S×Y	10	0.915	4.224	***
B×Y	10	0.037	0.172	ns
S×B×Y	10	0.032	0.146	ns
Residual	882	0.022	—	—
Total	925	0.063	—	—

ns, not significant; *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$.

No borers or their tracks were found in horizontal rhizomes from Olbia nor Genoa.

Leaf production and sheath tissue removal by borers

Both the mean shoot density and the mean percent bed covering were significantly higher ($P<0.01$) at Olbia than at Genoa (Table 2). At Olbia, the total leaf production (blades plus sheaths) was lower than at Genoa (Table 2); at both meadows a fraction of about 18–20% of the total leaf production was in the sheaths. When data of leaf production are reported to a metre square, very similar values were observed at the Olbia and Genoa beds (Table 2).

The mean sheath thickness was significantly lower at Olbia than at Genoa (*t*-test, $P=0.002$), while at the former site a significantly higher mean number of leaves was produced annually (*t*-test, $P<0.001$) (Table 2).

The lepidochronological technique allowed analysis of the weight loss in sheaths from the current year to sheaths 10-y old (Figure 2). Analysis of variance (Table 3), moreover, showed that differences were statistically significant between sites ($P<0.001$) and among years ($P<0.001$), while differences due to the effects of borers were not significant ($P=0.194$). In addition, ANOVA revealed a significant interaction only between site and year factors ($P<0.001$).

The difference between the mean sheath losses from mined and not mined rhizomes were not statistically

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significant mainly because of the comparatively high variability of this weight loss. This variability was also due to the low number of sheaths on damaged rhizomes actually mined by borers.

Total losses in the sheath production per year were 112.1 and 192.2 mg DW shoot^{-1}y^{-1} at Olbia and Genoa meadows, respectively (Table 2). However, fractions of 3.9% (6.7 mg DW shoot^{-1}y^{-1}) and 0.8% (1.9 mg DW shoot^{-1}y^{-1}) were actually attributable to the borers' removal (Table 2), corresponding to 2.6 g DW m^{-2}y^{-1} and 0.08 g DW m^{-2}y^{-1} at the Olbia and Genoa beds, respectively.

It is worth noting that the sheath weight loss is not constant in time, higher losses occurring during the first four years at Olbia (about 60% lost of the initial weight) and the first two years at the Genoa meadow (about 51% lost of the initial weight) (Figure 2).

Presence of fungal peritecia and relationships with boring invertebrates

In approximately 20% of rhizomes from Olbia (corresponding to up to 60 rhizome m^{-2}; Table 1), old sheaths at most 3-y old were infested by fungal peritecia localized in the sheath mesophyll just below the epidermis. These fungal peritecia resemble to those of the genus *Lulworthia*, previously reported in *Posidonia oceanica* (Cuomo et al., 1985). More detailed taxonomic analyses are still in progress.

All but one of the rhizomes with fungi were infested by isopods or showed their tracks in the same or in adjacent sheaths in which fungal peritecia occurred. Only one third of these rhizomes, instead, were concerned by the co-occurrence of polychaetes or their tracks.

DISCUSSIONS AND CONCLUSION

Boring invertebrates found at the Olbia and Genoa *Posidonia oceanica* beds belonged to the same species reported by Guidetti et al. (1997). The density of boring organisms found at Olbia was in the range of the data by Guidetti et al. (1997), who estimated a number varying from 75–278 borers m^{-2} at the Noli and Coda Cavallo beds located in the Ligurian and Tyrrhenian Seas (Italy), respectively. In contrast, very low densities of borers were observed at the Genoa meadow. No further data exist so far in literature on Mediterranean sea grass borers, neither on vagile invertebrates of the two *P. oceanica* beds object of the present study, which could contribute to the understanding of the observed distribution of borers.

Among the more important reasons involved in the regulation of borers' density, differences in the meadow density and patches could play a major role, borers' infestation being potentially favoured in a more dense and homogenous meadow. In this respect, Guidetti et al. (1997) reported higher densities of borers (mainly of isopods) in meadow stands where the shoot density was higher. Similarly, Brearley & Walker (1993) suggested that proximity of sea grass shoots could be favourable for the borers' infestation. Another potentially important factor regulating the borer abundance could be represented by the sheath toughness, which could mechanically hinder burrowing by borers. Sheaths from the Genoa meadow, for instance, were thicker, tougher and more lignified, and revealed lower densities of borers. Observations made on sheaths of plagiotropic shoots, whose thickness and toughness are higher than in orthotropic shoots, revealed the absolute absence of borers. Furthermore, since hydrodynamic conditions are commonly considered important factors influencing grazing rates in sea grass systems (Cebriàn et al., 1996a), they could also be invoked in affecting density of borers. Brearley & Walker (1996) suggested, for instance, that damages to Australian *Posidonia* sp. by *Limnoria agrostisa* were found most often where the sea grass grows in shallow sheltered areas.

The results of this study provided evidence that factors other than grazing by borers are responsible for sheath decay, since the weight losses were approximately 65% and 80% of the initial weight at Olbia and Genoa beds, respectively, after about 10 y. Romero et al. (1992) suggested that the local hydrodynamics could play a major role in this process. This could at the basis of the fact that at Genoa the sheath decay was significantly higher, in spite of the significantly lower borers' density.

The results of damage to living tissues and, in particular, to the meristem and young leaves were low at Olbia (the more impacted meadow) and null at Genoa and confirm the results reported by Guidetti et al. (1997). Thus, it is seems to be unlikely that borers really threaten the health of *P. oceanica* at the meadow scale, a greater number of borer organisms favouring old sheaths rather than living tissues. The results of this study and the few available data from the literature, however, are not yet sufficient to quantitatively assess the broad-scale biological impact of borer organisms on *P. oceanica* beds. As with the annual growth dynamics of *P. oceanica*, where variability due to local factors has been demonstrated (Alcoverro et al., 1995), density of borers and their impact may widely differ between meadows and, to a lesser extent, within meadows at different depths (Guidetti et al., 1997).

In Australian *Posidonia* systems, Brearley & Walker (1993, 1996) reported that truncation of vascular tissue may result in reduced transport of nutrients and photosynthates, in a loss of solutes and in a premature leaf fall, with a consequent reduced photosynthetic area, this leading ultimately to a severe reduction in the meadow productivity. Further, Brearley & Walker (1993, 1995) hypothesized that burrows may allow entry of water, bacteria and fungi, while Guidetti et al. (1997) suggested that borers, apart from the mechanical disruption of the dead sheath tissue, could enhance the microbial activity through deposition of faecal pellets into the tunnels. These hypotheses could be supported by the occurrence of fungal perithecia in dead sheaths of *P. oceanica*. Marine fungi possess a wide range of ligno–cellulosic enzymes able to degradate *P. oceanica* tissues (Cuomo et al., 1987). Fungi could facilitate the activity of borers by preconditioning of tissues and as an additional nutritional source during boring, as observed for marine wood borers (Eltringham, 1971). Hence, invertebrate borers and fungi could play a complementary role in the conversion of a fraction of sheath biomass in a form available for consumers at higher trophic levels.

In conclusion, the results presented here suggest that the effects of invertebrate borers on growth dynamics and

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production of *P. oceanica* appear to be minor. Nevertheless, as the effects of borers on *P. oceanica* could vary in relation to local environmental conditions and depth, additional studies are necessary for a quantitative assessment of their distribution patterns at different spatial scales and for an overall evaluation of their effects in the Mediterranean.

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