



ELSEVIER

Aquatic Botany 76 (2003) 65–77

**Aquatic
botany**

www.elsevier.com/locate/aquabot

Mesofaunal borers in seagrasses: world-wide occurrence and a new record of boring polychaetes in the Mexican Caribbean

Maria Cristina Gambi^a, Brigitta I. van Tussenbroek^{b,*},
Anne Brearley^c

^a Laboratorio di Ecologia del Benthos—Stazione Zoologica “Anton Dohrn” Napoli,
Punta S. Pietro, 80077 Ischia Napoli, Italy

^b Unidad Académica Puerto Morelos, Instituto de Ciencias del Mar y Limnología, Universidad Nacional
Autónoma de México, Apdo. Postal 1152, Cancún 77500 Q. Roo, Mexico

^c School of Plant Biology, The University of Western Australia, 35 Stirling Highway, Crawley 6009, Australia

Received 10 April 2002; received in revised form 27 November 2002; accepted 13 January 2003

Abstract

In the last decade, an increasing number of mesofaunal crustaceans and polychaetes have been reported to bore into seagrass tissues. Crustacean borers have been found in seagrasses from different oceans (Indo-West Pacific, Mediterranean, and Caribbean), but until present, boring polychaetes had only been registered in the Mediterranean. Here, a new record of polychaete borers within sheaths of the seagrass *Thalassia testudinum* (Banks ex König) off the Mexican Caribbean coast (Puerto Morelos) is reported. The polychaetes were found in sheaths of plants collected at two stations in a shallow meadow (3–4 m depth), and except for slight morphological differences, were similar to *Lysidice ninetta* Audouin and Milne Edwards, *Lysidice collaris* Grube, and *Nematonereis unicornis* Grube; taxa previously recorded in sheaths of the Mediterranean seagrass *Posidonia oceanica* (L.) Delile. A synthesis of present knowledge of fauna burrowing into seagrass tissues, suggests the existence of specific associations between particular seagrasses and specialized members of crustaceans (orders Isopoda and Tanaidacea) or polychaetes (family: Eunicidae). The boring crustaceans can be classified as mesoherbivores because they consume the living tissues they burrow into. Each species bores into specific tissues which are either leaf blades, leaf sheaths, rhizomes or seeds. The polychaetes, in contrast, bore into the dead sheath tissues which remain attached to the vertical rhizomes after abscission of the green blades, and can thus considered to be detritivores. © 2003 Elsevier Science B.V. All rights reserved.

Keywords: Seagrasses; Borers; Mesofauna; Polychaeta; Eunicidae; Crustacea; Isopoda

* Corresponding author. Tel.: +52-987-10219; fax: +52-987-10138.

E-mail address: vantuss@mar.icmyl.unam.mx (B.I. van Tussenbroek).

1. Introduction

Although there are many reports on the wide array of fauna associated with seagrass beds (e.g. Howard et al., 1989; Hutchings, 1982; Jernakoff et al., 1996; Scipione et al., 1996; Solis-Weiss and Carreno, 1986), organisms boring (excavating or burrowing) into the seagrasses have been largely overlooked. Small animals burrowing into plant tissues can be considered to be a specialised guild of mesofauna, because they produce their own shelter and microhabitat, represented by their canals or chambers inside the plants (Brawley, 1992). The first report on borers in seagrasses is that of Kussakin in 1979 (in Cookson, 1990), who reported a limnoriid isopod in the rhizome tissue of *Phyllospadix iwatensis* Makino. Cookson (1990) subsequently designated three other limnoriid isopods as seagrass borers, based on the presence of a rasp and file on the mandibles and their association with seagrass rhizomes, although damage to the seagrass tissue was not recorded. More extensive and conclusive investigations of isopods burrowing in leaves of various Australian seagrasses were initiated a decade ago (Brearley and Walker, 1993, 1995, 1996). Since these first works, various publications have appeared on this topic, and isopod borers were found in seagrasses at several other sites apart from Australia (Cookson and Lorenti, 2001; Guidetti et al., 1997; van Tussenbroek and Brearley, 1998). Recently, Nakaoka (2002) described the boring habit of a tanaid crustacean in fertile spathes of *Zostera* spp. in Japan. Annelid polychaetes have also been reported to inhabit seagrasses, but they had only been reported associated with sheaths of *Posidonia oceanica* in the Mediterranean (Gambi et al., 1997). The aim of this note is to report the first evidence of occurrence of polychaete borers in a shallow meadow of the seagrass *Thalassia testudinum* (Banks ex König) along the Caribbean coast of Mexico, and to summarise the present knowledge on mesofaunal borers in seagrasses.

2. Material and methods

Several sheaths containing polychaete borers, collected in December 2000, were fixed in 4% formaldehyde and then preserved in 70% ethanol for species identification. Species were classified according to the available literature for the Gulf of Mexico (Gathof, 1984; Salazar-Vallejo, 1996; Salazar-Vallejo and Carrera-Parra, 1997) and compared to those from the Mediterranean (Martin, 1987).

Sections of vertical rhizomes with attached live and dead leaf tissue of *T. testudinum* were collected during December 2000 and November 2001, by severing them from the horizontal rhizome with a sharp knife below the substratum. Collections were made at two sampling sites (Research Station, 20°52'02"N; 86°51'54"W, and Punta Caracol, 20°53'20"N; 86°51'20"W), located in a shallow meadow (3–4 m depth) off Puerto Morelos in the Mexican Caribbean. Live and dead sheaths on the vertical rhizomes of *T. testudinum* were examined for evidence of polychaete borers ($N = 40$ shoots per sampling station). Each sheath was examined under a stereomicroscope and location of the polychaetes was recorded, together with details concerning borer patterns. Index of borer occurrence (IB) was calculated as the percentage of shoots hosting borers over the total shoots examined (Gambi, 2000; Zupo et al., 2001). Thickness of the sheaths containing polychaete borers was measured using

dial calipers with 0.01 mm precision. For each examined shoot, the total number of live and dead sheaths was recorded. This number, together with the average number of leaves produced per shoot per year at the same sampling stations (van Tussenbroek, 1996), allowed estimation of the time that sheaths remained attached to the vertical rhizomes. For example, the number of leaf sheaths on a shoot is 30; if 15 leaves are formed on average on a shoot, the oldest attached (dead) sheath has an estimated age of 2 years, which is the time sheaths remained attached to the vertical rhizome of this shoot.

Nomenclature for the morphology of *T. testudinum* follows van Tussenbroek (1998). A leaf consists of a colourless sheath and green blade. After abscission of the green blades, sheaths remain attached to the vertical rhizome forming a bundle of dead sheath tissue. A shoot is the conjunction of a vertical rhizome and its corresponding dead or living leaf tissue. Borer is a general term for an organism which excavates in any type of plant tissue, making characteristic burrows, canals or chambers within this tissue.

3. Results

3.1. First record of polychaete borers into the sheaths of *Thalassia testudinum*

The analysis of the polychaete borers in *T. testudinum* sheaths off Puerto Morelos revealed three species belonging to Eunicidae, which resembled *Lysidice ninetta* Audouin and Milne Edwards (sensu Gathof, 1984; Salazar-Vallejo and Carrera-Parra, 1997), *Lysidice collaris* Grube (sensu Martin, 1987), and *Nematonereis unicornis* Grube (sensu Gathof, 1984; Salazar-Vallejo and Carrera-Parra, 1997) from the Mediterranean, but slight differences between the specimens from Caribbean and Mediterranean were detected. *L. ninetta* from the Mediterranean had three short antennae of similar length, while the middle antenna of the Caribbean specimens were almost twice as long as the others, although not extending over the slightly bilobed prostomium. Colour pattern also differed; Mediterranean specimens were reddish with minute white spots, with a white or cream collar on third to fifth segment, while Caribbean specimens were white or pale in colour. *L. collaris* from this study resembled Mediterranean specimens described by Martin (1987): the three antennae having similar length and being slightly longer than the prostomium, shape of the eyes reniform, and prostomium more clearly bilobed than in *L. ninetta*. In some specimen, a pale red collar with white small spots was observed on the sixth segment, a characteristic not present in the Mediterranean specimens. The Caribbean specimens of *N. unicornis*, in synonymy with *Nematonereis hebes* Verrill, 1900 (Salazar-Vallejo and Carrera-Parra, 1997, and references therein), also differed slightly from the Mediterranean ones (K. Fauchald, personal communication). Because of the slight differences in morphology in comparison with the specimen from the Mediterranean, the polychaete species from the present study will be indicated as *L. cf ninetta*, *L. cf collaris* and *N. cf unicornis*.

The polychaetes associated with *T. testudinum* could be divided into two size groups; small (between 0.20 and 0.50 mm wide, and 0.70 and 2.0 cm long) and larger borers (0.50–0.96 mm wide, and 2.08–3.61 cm long). The small borers were either *N. cf unicornis* and small specimens of *L. cf ninetta* and *L. cf collaris*, while the larger borers only



Fig. 1. Small boring polychaetes (*Nematoneis* cf. *unicornis*) in the sheaths of *Thalassia testudinum* (arrows).

belonged to both species of *Lysidice*. Small polychaetes were found within sheaths from which the green blade had most recently abscised (first dead sheath) until the fourth dead sheath. They were located inside burrows made in the mesophyll of a sheath (Fig. 1). These burrows were quite regular, narrow (\approx similar to the width of the polychaete) and linear or sinuous, following the nerves of the sheath, located in the upper part of the sheath (upper 1–3 cm, Fig. 1). Larger polychaetes entered the bundle of dead sheath tissue through small holes bored in the outer sheath about 1.3–2.0 cm from the leaf base (Figs. 2 and 3). Subsequently, traces of burrowing by large polychaetes extended through a large part of the bundle of dead sheath tissue, from the outermost until the fifth to third dead sheath (Fig. 3). Empty burrows, formed by both small and larger worms, were filled with sediment, and often hosted other species of non-burrowing polychaetes (spionids, capitellids, sabellids, dorvilleids, syllids, cirratulids, nereidids), or sipunculids. None of the boring polychaetes settled in sheaths of living leaves which still had attached green blades.

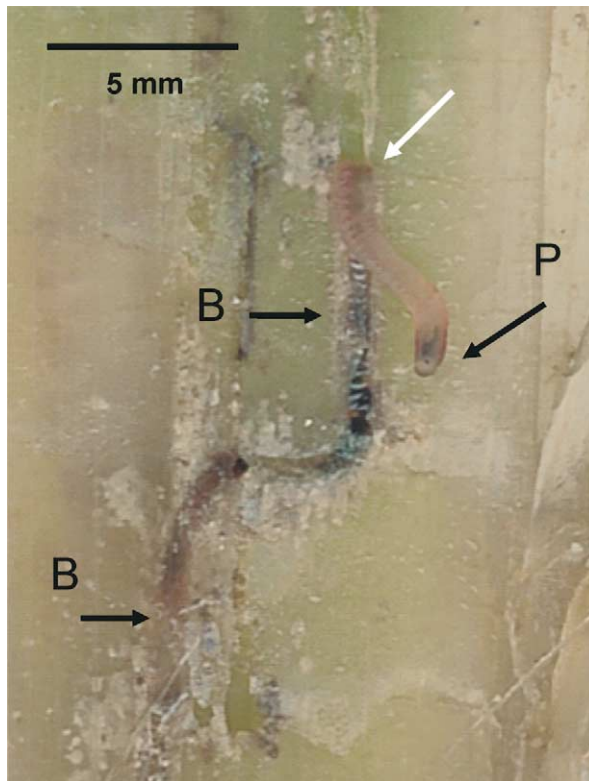


Fig. 2. Large boring polychaete (*Lysidice cf. ninetta*) in a burrow made in the sheath tissue of *Thalassia testudinum*. On the picture part of the polychaete which is outside the burrows is folded backwards (white arrow), showing the underside of the worm. (P) Prostomium, (B) parts of the polychaete inside the burrow.

At Punta Caracol, all shoots examined had burrowing marks of small or large polychaetes, whereas at the Research Station site, 36 out of 40 examined shoots had marks of polychaete borers, resulting in an index of borer occurrence of 100 and 90%, respectively. Generally, 1–2 specimens were observed per single shoot, but up to six small specimens were recorded in one shoot. The thickness of sheaths with small polychaetes borers varied between 0.51 and 0.57 mm at the Research Station site, and between 0.50 and 0.59 at Punta Caracol. Large polychaetes bored through several sheaths within a bundle, with thickness varying between 0.10 and 0.50 mm. At both stations, vertical rhizomes had 15 to 49 attached sheaths which were still relatively complete. With advanced age, the sheaths gradually transformed into threadlike filaments attached to the vertical rhizome. Calculations based on the number of attached (live and dead) sheaths to the vertical rhizome, and the mean annual production of leaves per shoot (15 leaves per year), indicated that the sheaths remained relatively intact for a period of ~1–3 years. Sheaths damaged by small polychaete borers were probably between 2 and 5 months old (since appearance of the leaf), whereas the age of sheaths bored by the larger polychaetes ranged from 3 months to 3 years.

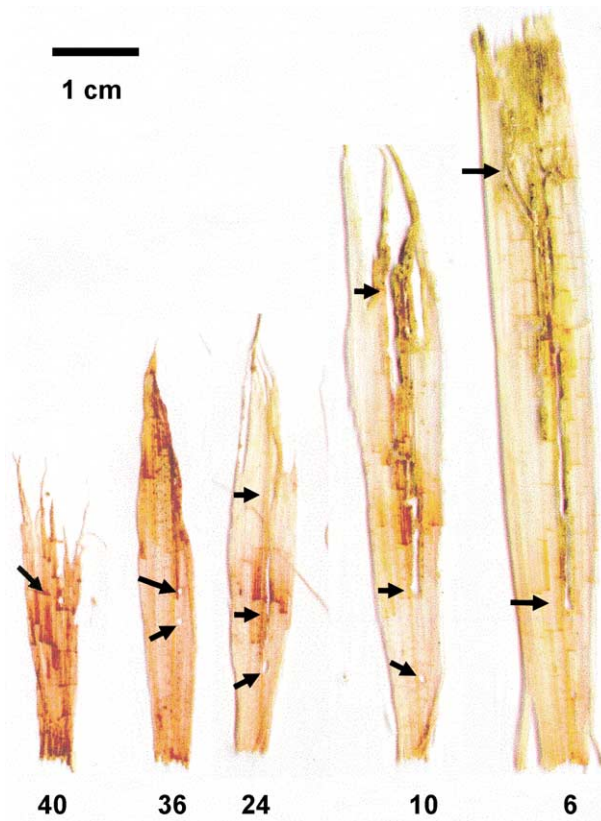


Fig. 3. Sheaths of a *Thalassia testudinum* shoot damaged by a large polychaete borer (*Lysidice* cf. *ninetta* or *L.* cf. *collaris*). The numbers represent the sheath number; numbering starting with the youngest (live) sheath. Because the leaves alternate on the vertical rhizome, every other sheath number has burrowing marks of the same large polychaete. Inclined arrows in the oldest sheaths indicate small holes made when the polychaete bored into the sheath bundle, and horizontal arrows indicate the longitudinal burrows in the younger sheath tissue.

4. Discussion and summary of present knowledge

4.1. Polychaete borers in *Thalassia testudinum* from the Caribbean

The polychaete species in *T. testudinum* were similar to the taxa boring sheaths (scales) of *P. oceanica* from the Mediterranean (Gambi et al., 1997), but slight differences in morphology from Mediterranean specimen were detected. *L. ninetta* is pantropical including the Caribbean (George and Hartmann-Schröder, 1985; Cantone, 1993), but it has very few clearly distinguishable characteristics and Salazar-Vallejo and Carrera-Parra (1997), suggested that specimens from different areas most likely belong to different species. *L. collaris* has an Indo-Pacific distribution, and was introduced into the Mediterranean through the Suez canal (Ben-Eliahu, 1972). *L. collaris* has not been reported in the Caribbean until

date; the morphological description of *L. ninetta* by Gathof (1984) included some features of *L. collaris*, but Fauchald (1970) considered that the two species belonged to the same taxon (*L. ninetta*). In the Mediterranean and South Africa, these two species of *Lysidice* are morphologically well defined (Martin, 1987; Day, 1967), and the distinction is supported for the Mediterranean specimen through genetic analysis by Talia (2001). It is likely that the specimens from the present study (*L. cf ninetta*, and *L. cf collaris*) are new local species, and further morphological analyses, as well as genetic comparisons (DNA-marker analyses), are in progress to clarify the taxonomic status.

Dimensions of the small polychaetes within the sheaths of *T. testudinum* were lower (max. width and length were 0.50 mm, and ~2 cm, respectively) than those recorded for the polychaetes within the sheaths (or scales) of *P. oceanica* (max. width 1.2 mm, max. length ~6 cm; Cafiero, 1998; Guidetti et al., 1997). The size of animals that colonise the sheaths of *P. oceanica* is constrained by their thickness (Gambi et al., 2000a,b; Guidetti et al., 1997), thus size of the polychaetes in *T. testudinum* may also be limited by sheath thickness (0.50–0.59 mm for sheaths containing small polychaetes).

Both the small polychaetes and the isopod *Limnoria simulata* Menzies (van Tussenbroek and Brearley, 1998) start burrowing in the upper end of the sheath tissue (at the abscission line of the green blades) of *T. testudinum*, working downwards. The burrows made by polychaetes, however, were clearly distinguishable from those by isopods. Isopods generally colonised the younger leaves (those with an intact green blade), their burrows formed a network of canals in the mesophyll and the epidermis of the inner face of the sheath, and they bored into adjacent leaves. Traces of the small polychaetes were always found in sheaths of old leaves with abscised blades, and the burrows were made in the mesophyll tissue (leaving the epidermis on both sides of the sheath intact), and they followed leaf nerves. Occasionally, burrows of both small polychaetes and the isopod *L. simulata* were found in the same sheath, a feature also noted in *P. oceanica* in the Mediterranean by Cafiero (1998) and Gambi (2000). In *P. oceanica*, isopods were also common in the younger, more recent sheaths ('scales'), and had irregular or "alveolar" burrows, whereas the polychaetes made sinuous burrows in older sheaths (Gambi et al., 2000a,b).

Polychaete borers were very abundant in *T. testudinum* at both sampling stations (IB was 90 and 100% at Research Station and Punta Caracol, respectively), but a more extensive quantitative analysis is required to verify whether this is a general pattern throughout the area. In the Mediterranean, the number of polychaete borers ranged from several tens to several hundreds per m² of *P. oceanica* bed; they occurred throughout the year without a specific seasonal pattern (Gambi, 2000, in press; Gambi and Cafiero, 2001); and annual mean IB values ranged from 3 to 68% in four examined beds, never exceeding 82% (Gambi, 2000, in press).

4.2. Current knowledge on seagrass borers

The association of a few mesofaunal species with particular seagrasses, suggests that the borers represent a guild with morphological and functional adaptations for utilising seagrass tissues (Brearley and Walker, 1996; Gambi et al., 2000a,b; Guidetti et al., 1997). Borers have been reported in the leaves, rhizomes and seeds of the seagrasses (Table 1). Little is known concerning the boring habits of mesofauna in other than leaf tissue (except for the recent

Table 1
Summary of registered associations between seagrasses and mesofaunal borers

Borer taxon	Host seagrass	Tissue	Other substrata	Location of seagrass-borer association	Remarks	Reference
Crustacea, order: Isopoda, family: Limnoriidae						
<i>Limnoria zinovae</i> Kussakin	<i>Phyllospadix iwatensis</i> Makino	Rhizomes?	None	Seas of Japan and Okhots ^b	Boring habit assumed on basis of mandible structure	Kussakin (1979, in: Cookson, 1990)
<i>Limnoria agrostisa</i> Cookson	<i>Amphibolis griffithii</i> (J.M. Black) Den Hartog	Living sheaths	None	Southern Australia ^a	Rasp in mandible not reduced as it is in other limnoriid seagrass borers	Brearely and Walker (1993); Cookson (1990); Cookson and Poore (1994)
<i>Limnoria agrostisa</i> Cookson	<i>Posidonia</i> spp. ^c	Rhizomes, vertical shoots	None	Southern Australia ^a		Brearely and Walker (1996); Brearely (unpublished data)
<i>Limnoria rarustissima</i> Cookson	<i>Heterozostera</i> , <i>Zostera</i> , <i>Amphibolis</i> , <i>Posidonia</i> ^d	Rhizomes?	Red algae?	South Australia and Vict. ^a	Boring habit assumed on basis of mandible structure	Cookson (1990)
<i>Limnoria simulata</i> Menzies	<i>Thalassia testudinum</i> Banks ex König	Living sheaths	None	Mexican Caribbean ^b	Müller (1988) supposed this species was a rhizome borer, but boring habit was not described	van Tussenbroek and Brearely (1998)
<i>Limnoria mazzellae</i> Cookson and Lorenti	<i>Posidonia oceanica</i> (L.) Delile	Dead sheaths	None	Mediterranean ^a	Bores younger sheaths than the polychaetes	Guidetti et al. (1997); Cookson and Lorenti (2001)
<i>Limnoria foveolata</i> Menzies	Unknown	?	None	Kai Islands, Indonesia ^b	Boring habit assumed on basis of mandible structure	Cookson (1990)
<i>Lyniseia himantopoda</i> Poore	<i>Heterozostera tasmanica</i> Martens ex Ascherson	Green blades	None	South Western and Southern Australia ^a	Boring resembles mining of insects in terrestrial plants	Brearely and Walker (1993, 1996) and Cookson (1990)
<i>Lyniseia amae</i> Cookson and Poore	<i>Posidonia</i> spp. ^c	Green blades	None	South-Western and Southern Australia ^a	Boring resembles mining of insects in terrestrial plants	Brearely and Walker (1993, 1995, 1996)
<i>Lyniseia diana</i> Cookson and Poore	<i>Posidonia ostenfeldii</i> Den Hartog	Green blades	None	Southern Australia ^a	Boring resembles mining of insects in terrestrial plants	Brearely and Walker (1993); Cookson (1990)
Crustacea, order: Tanaidacea, family: Tanaidae						
<i>Zeuxo</i> sp.	<i>Zostera marina</i> L., <i>Zostera caulescens</i> Miki	Seeds in fertile spades	Unknown	NE Japan ^b		Nakaoka (2002)

Polychaeta, order: Eunicida, family: Eunicidae

<i>Nematonereis unicornis</i> Grube	<i>Posidonia oceanica</i> (L.) Delile	Dead sheaths	Coarse sediments	Mediterranean ^a	Smallest recorded borer polychaete	Guidetti et al. (1997); Gambi (2000)
<i>Nematonereis cf. unicornis</i> (local form)	<i>Thalassia testudinum</i> Banks ex König	Dead sheaths	Sediments	Mexican Caribbean ^b	Synonymous with <i>N. hebes</i> Verrill	Present study
<i>Lysidice ninetta</i> Adouin & Milne Edwards	<i>Posidonia oceanica</i> (L.) Delile	Dead sheaths	Calcareous red algae, algal covered hard bottoms	Mediterranean ^a	Most common borer, large specimen occasionally consumes living sheaths	Guidetti et al. (1997); Gambi and Cafiero (2001)
<i>Lysidice cf. ninetta</i> (local form)	<i>Thalassia testudinum</i> Banks ex König	Dead sheaths	Corals, and coralline sediments	Mexican Caribbean ^b		Present study
<i>Lysidice collaris</i> Grube	<i>Posidonia oceanica</i> (L.) Delile	Dead sheaths	As <i>L. ninetta</i>	Mediterranean ^a	Large specimens occasionally consume living sheaths	Guidetti et al. (1997); Gambi and Cafiero (2001)
<i>Lysidice cf. collaris</i> (local form)	<i>Thalassia testudinum</i> Banks ex König	Dead sheaths	Corals, and coralline sediments	Mexican Caribbean ^b		Present study
<i>Marphysa fallax</i> Marion & Bobretzky	<i>Posidonia oceanica</i> (L.) Delile	Dead sheaths	Coralligenous formations	Mediterranean ^a	Less common than other boring polychaetes	Gambi (2000); Gambi and Cafiero (2001)

^a Seagrass-borer association registered throughout major sections of seagrass distribution range.

^b Seagrass-borer association registered at one or few specific locations.

^c *P. australis* Hooker, *P. sinuosa* Cambridge and Kuo and *P. angustifolia* Cambridge and Kuo (Cambridge and Kuo, 1982; Kuo and Cambridge, 1984).

^d Cookson (1990) did not mention the species of the seagrasses.

study by Nakaoka, 2002), and this review will cover leaf-boring isopods and polychaetes, but the boring habits and roles of the crustaceans in rhizomes and seeds certainly merit further investigation.

Isopod borers belong to the genera *Limnoria* and *Lynseia* of the family Limnoriidae (Cookson, 1990, 1997; Cookson and Poore, 1994; Cookson and Lorenti, 2001; Müller, 1988; Poore, 1987). Limnoriid isopods in general, are borers in plant material (wood, holdfasts of seaweeds, seagrasses), although the specific habits of some seagrass borers are still unknown, the loss of the rasp and file on the mandible appears to be a diagnostic characteristic associated with use of softer substrates such as seagrass rather than wood (Cookson, 1990). Leaf boring *Limnoria* spp. bore into living sheath tissue, removing mesophyll and epidermal tissue. The body form of members of the more specialised genus *Lynseia* is more elongated than that of *Limnoria* spp., and the particular morphology of their limbs provide special adaptations for a burrowing habit within the mesophyll of living green blades (Cookson and Poore, 1994). The ecological role of the isopod borers on the seagrasses is not yet clear, but there are indications that they may be important top-down regulators in some seagrass beds. Most of the isopod borers infest living tissue, the exception being *Limnoria mazzellae* (Cookson and Lorenti, 2001) which bored into dead *P. oceanica* sheaths (Cafiero, 1998; Cookson and Lorenti, 2001; Guidetti et al., 1997). Thus, in general, the isopod borers can be considered to be a special class of mesoherbivores. Although the quantity of sheath tissue removed by the borers is small or negligible (e.g. 11% tissue removal of *P. oceanica* by *L. mazzellae*, Gambi et al., 2000a,b), isopod borers belonging to the genus *Limnoria* have a potential to severely damage seagrasses, as they burrow near or in the meristemic regions of the leaves. To date, no records of bed destruction by these isopods has been reported, but Brearley and Walker (1993) showed considerable damage in meristemic tissue of *Amphibolis griffithii* by *L. agrostisa* resulting in leaf malformation and sometimes in mortality of the leaf cluster (max. 8% of all leaf clusters). Leaf growth may also be affected as was shown by van Tussenbroek and Brearley (1998) for *T. testudinum* infested with *L. simulata*. The effects of leaf mining of *Lynseia* in *Posidonia* spp. are less clear; tissue around burrows in the green blades of the leaves generally appears healthy although lines of weakness along burrows contribute to leaf fragmentation during storms and may facilitate entry of water and of pathogens.

The polychaete borers in seagrasses belong to the family Eunicidae (George and Hartmann-Schröder, 1985; Martin, 1987). The jaw apparatus of the members of this family are multifunctional and amongst the most complex of polychaetes, permitting an herbivorous, carnivorous or detritivorous feeding habit (Fauchald and Jumars, 1979). Gut content analysis of the two most abundant species of polychaetes associated with *P. oceanica* (*Lysidice* spp.) showed that a relatively high percentage of the food consisted of *P. oceanica* tissues (Gambi et al., 2000a,b), which demonstrated that the scale tissues removed during burrowing activity were ingested. In addition, for both seagrass boring species of *Lysidice*, cellulolytic activity was detected in the posterior, intestinal body portion (Cigliano et al., in press), indicating that they are capable to utilise the plant material as a food source. In contrast to the isopods, the known polychaete borers are not restricted to seagrasses, and the same species have also been found in other habitats (Table 1). All polychaete borers from the Mediterranean and the Caribbean infested dead sheath tissues, and can thus be considered to be detritivores: albeit specialised ones as they consume tissue which is still attached to

the plants. Their burrowing activities enhance scale fragmentation, and their faecal pellets, deposited within the burrows, enhance microbial activity, thus they may play a role in accelerating sheath decay and their recycling (Gambi et al., 2000a; Guidetti, 2000). The mass of dead tissue removed by polychaetes is modest, comprising on average 1.3% of the total weight of the sheath bundles of *P. oceanica* (Gambi et al., 2000a,b; Gambi, in press). However, dead sheaths of *T. testudinum* infested by polychaetes decayed considerably faster than uninfested ones (van Tussenbroek, unpublished data), thus direct tissue removal might not be a correct indicator of the degree of tissue refraction.

Leaf borers have only been recorded in a limited numbers of seagrasses, suggesting that certain morphological characteristics of the seagrasses are required to render these a suitable burrowing habitat. Both isopod and polychaete borers require linear (strap shaped) leaves, thick enough to allow the formation of burrows. Polychaete borers, additionally, require dead sheath tissue of relatively long persistence (at least several months) before it is removed through decay. The present study showed that the dead sheath tissue can either be fibrous or membraceous, but it probably has to form bundles at the base of the plant to serve as a cryptic habitat for these organisms. Various seagrasses belonging to the genera *Cymodocea*, *Zostera*, *Enhalus* and *Phyllospadix* could fulfil these requirements, but until date, leaf borers have not been found in any of their corresponding species. However, research into seagrass borers is relatively recent, and the list of borers in seagrasses might increase as more collections are made.

Acknowledgements

The authors are grateful to Daniel Gasca Flores for collecting the samples. Thanks are due to S. Salazar-Vallejo, Vivianne Solis-Weiss, and Kristian Fauchald for bibliographic and taxonomic advice, and to Maurizio Lorenti for critical reading of the manuscript.

References

- Ben-Eliahu, M.N., 1972. Littoral Polychaeta from Cyprus. *Tethys* 4, 85–94.
- Brawley, S.H., 1992. Mesoherbivory. In: D.M., John, Hawkins, S.J., J.H., Price (Eds.), *Plant–Animal Interactions in the Marine Benthos*. The Systematic Association, vol. 46. Clarendon Press, Oxford, pp. 235–263.
- Brearley, A., Walker, D.I., 1993. Isopod borers in seagrass species from south-western Australia. In: Wells, F.E., Walker, D.I., Kirkman, H., Lethbridge, R. (Eds.), *Proceedings of the Fifth International Marine Biological Workshop: The Marine Flora and Fauna of Rottnest Island*, vol. 2. Western Australian Museum, Perth, Western Australia, pp. 415–428.
- Brearley, A., Walker, D.I., 1995. Isopod miners in the leaves of two Western Australian *Posidonia* species. *Aquat. Bot.* 52, 163–181.
- Brearley, A., Walker, D.I., 1996. Burrow structure and effects of burrowing isopods (Limnoriidae) in south-western Australian *Posidonia* meadows. In: Kuo, J., Phillips, R.C., Walker, D.I., Kirkman, H. (Eds.), *Proceedings of an International Workshop on Seagrass Biology*. Faculty of Sciences, The University of Western Australia, pp. 261–268.
- Cafiero, G., 1998. Distribuzione spazio-temporale ed autoecologia di invertebrati perforatori di scaglie di *Posidonia oceanica* (L.) Delile. M.Sc. Thesis, University of Siena, Italy, 73 pp.
- Cambridge, M., Kuo, J., 1982. Morphology, anatomy and histochemistry of the Australian seagrasses of the genus *Posidonia* Konig (Posidoniaceae). III. *Posidonia sinuosa* Cambridge and Kuo. *Aquat. Bot.* 14, 1–14.

- Cantone, G., 1993. Censimento dei Policheti dei mari italiani: Eunicidae, Berthold, 1927. Atti. Soc. Tosc. Sci. Nat. Mem. Serie B 100, 229–243.
- Cigliano, M., Manini, E., Gambi, M.C., in press. First data on the cellulolytic enzyme activity of polychaetes borers of the sheaths of *Posidonia oceanica*. Biol. Mar. Medit. 10.
- Cookson, L.S., 1990. Australasian species of Limnoriidae (Crustacea: Isopoda). Memoirs Mus. Vict. 52, 137–262.
- Cookson, L.S., 1997. Additions to the taxonomy of the Limnoriidae (Crustacea: Isopoda). Memoirs Mus. Vict. 56, 129–143.
- Cookson, L.S., Poore, G.C.B., 1994. New species of *Lynseia* and transfer to the genus to Limnoriidae (Crustacea: Isopoda). Memoirs Mus. Vict. 54, 179–189.
- Cookson, L.S., Lorenti, M., 2001. A new species of Limnoriid isopod borer from the Mediterranean. Crustaceana 74, 339–346.
- Day, J.H., 1967. A monograph on the Polychaeta of Southern Africa. Part I. Errantia. Trustees of the British Museum, Natural History. London, pp. 377–404.
- Fauchald, K., 1970. Polychaetous annelids of the family Eunicidae, Lumbrineridae, Iphitimidae and Dorvilleidae from western Mexico. Allan Hancock Monogr. Mar. Biol. 5, 1–335.
- Fauchald, K., Jumars, P.A., 1979. The diet of the worms: a study of polychaete feeding guilds. Oceanogr. Mar. Biol. Ann. Rev. 17, 193–284.
- Gambi, M.C., in press. Spatio-temporal distribution and ecological role of polychaetes borers of *Posidonia oceanica* (L.) Delile scales. Bull. Mar. Sci.
- Gambi, M.C., 2000. Polychaete borers of *Posidonia oceanica* (L.) Delile scales: distribution patterns and ecological role. In: Pergent, G., Pergent-Martini, C., Buia, M.C., Gambi, M.C. (Eds.), Proceedings of the 4th International Seagrass Biology Workshop, Corsica, 26 September–2 October 2000. Biol. Mar. Medit. 7, 215–219.
- Gambi, M.C., Cafiero, G., 2001. Functional diversity in the *Posidonia oceanica* ecosystem: an example with polychaete borers of the scales. In: Faranda, F., Guglielmo, L., Spezie, G.C. (Eds.), Mediterranean Ecosystems: Structure and Processes. Springer, Milano, Italy, pp. 387–393 (Chapter 51).
- Gambi, M.C., Lorenti, M., Bussotti, S., Guidetti, P., 1997. Borers in *Posidonia oceanica* scales: taxonomical composition and occurrence. Biol. Mar. Medit. 4, 384–387.
- Gambi, M.C., Zupo, V., Lorenti, M., 2000a. Organism borers of *Posidonia oceanica* scales: trophic role and ecological implications for the ecosystem. Biol. Mar. Medit. 7, 253–261.
- Gambi, M.C., Zupo, V., Mazzella, L., Buia, M.C., 2000b. Feeding ecology of the polychaete *Platynereis dumerilii* (Audouin and Milne-Edwards) (Nereididae) in the *Posidonia oceanica* system: the role of the epiphytic flora. Ophelia 53, 189–202.
- Gathof, J.M., 1984. Family Eunicidae Savigny, 1818. In: Uebelacker, J.M., Johnson, P.G. (Eds.), Atlas of the Polychaetes of the Northern Gulf of Mexico, vol. 6. Barry Victor and Associates, pp. 1–31 (Chapter 40).
- George, J.D., Hartmann-Schröder, G., 1985. Polychaetes: British Amphinomida, Spinttherida and Eunicida. In: Kermack, D.M., Barnes, R.S.K. (Eds.), Synopses of the British Fauna (New Series), vol. 32. Published for The Linnean Society of London and The Estuarine and Brackish Water Sciences Association by Brill, E.J., Backhuys, W., 221 pp.
- Guidetti, P., 2000. Invertebrate borers in the Mediterranean seagrass *Posidonia oceanica*: biological impact and ecological implications. J. Mar. Biol. Ass. U.K. 80, 725–730.
- Guidetti, P., Bussotti, S., Gambi, M.C., Lorenti, M., 1997. Invertebrate borers in *Posidonia oceanica* scales: relationships between their distribution and lepidochronological parameters. Aquat. Bot. 58, 151–164.
- Howard, R.K., Edgar, G.J., Hutchings, P.A., 1989. Faunal assemblages of seagrass beds. In: Larkum, A.W.D., McComb, A.J., Shepherd, S. (Eds.), Biology of Seagrasses: A Treatise on the Biology of Seagrasses with Special Reference to the Australian Region. Elsevier, Amsterdam, pp. 536–564.
- Hutchings, P.A., 1982. The fauna of Australian seagrass beds. Proc. Linn. Soc. N.S.W. 106, 181–200.
- Jernakoff, P., Brearley, A., Nielsen, J., 1996. Factors affecting grazer–epiphyte interactions in temperate seagrass meadows. Oceanogr. Mar. Biol. Ann. Rev. 34, 109–162.
- Kuo, J., Cambridge, M., 1984. A taxonomic study of the *Posidonia ostenfeldii* complex (Posidoniaceae) with descriptions of four new Australian seagrasses. Aquat. Bot. 20, 267–295.
- Martin, D., 1987. Anélidos Poliquetos asociados a las concreciones de algas calcáreas del litoral catalan. Misc. Zool. 11, 61–75.
- Müller, H.G., 1988. Redescription, synonymy, and ecology of *Limnoria simulata* Menzies 1957 from the Caribbean Sea of N-Colombia. Senckenbergiana Biol. 69, 397–403.

- Nakaoka, M., 2002. Predation on seeds of seagrass *Zostera marina* and *Zostera caulescens* by a tanaid crustacean *Zeuxo* sp. *Aquat. Bot.* 72, 99–106.
- Poore, G.C.B., 1987. Lynseiidae (Isopoda: Flabellifera): a new monotypic family from Australia. *J. Crust. Biol.* 7, 258–264.
- Salazar-Vallejo, S.I., 1996. Lista de especies y bibliografía de poliquetos (Polychaeta) del Gran Caribe. *Anales. Inst. Biol. Univ. Nac. Auton. Mexico, Ser. Zool.* 67 (1), 11–50.
- Salazar-Vallejo, S.I., Carrera-Parra, L.F., 1997. Eunicidos (Polychaeta) del Caribe mexicano con claves para las especies del Gran Caribe: *Fauchaldius*, *Lysidice*, *Marphysa*, *Nematoneireis* y *Palola*. *Rev. Biol. Trop.* 45 (4), 1481–1498.
- Scipione, M.B., Gambi, M.C., Lorenti, M., Russo, G.F., Zupo, V., 1996. Vagile fauna of the leaf stratum of *Posidonia oceanica* and *Cymodocea nodosa* in the Mediterranean Sea. In: Kuo, J., Phillips, R.C., Walker, D.I., Kirkman, H. (Eds.), *Proceedings of an International Workshop on the Seagrass Biology*. Rottneest Island, WA, 25–29 January 1996, pp. 249–260.
- Solis-Weiss, V., Carreno, S., 1986. Estudio prospectivo de la macrofauna bentica asociada a las praderas de *Thalassia testudinum* en la Laguna de Terminos, Campeche. *An. Inst. Cienc. Mar. Limnol. Univ. Nal. Autón. México* 13, 201–216.
- Talia, M., 2001. Filogeografía comparata nell'ecosistema a *Posidonia oceanica* (L.) Delile: la pianta e gli organismi scavatori. M. Sc. Thesis, University Federico II, Napoli, 119 pp., unpublished (in Italian, available from M.C. Gambi).
- van Tussenbroek, B.I., 1996. Techniques of rapid assessment of seagrass production yield, applied to *Thalassia testudinum* in a Mexican tropical reef lagoon. In: Kuo, J., Phillips, R.C., Walker, D.I., Kirkman, H. (Eds.), *Proceedings of an International Workshop on the Seagrass Biology*. Rottneest Island, WA, 25–29 January 1996, pp. 131–138.
- van Tussenbroek, B.I., 1998. Above- and below-ground biomass and production of *Thalassia testudinum* in a tropical reef lagoon. *Aquat. Bot.* 61, 69–82.
- van Tussenbroek, B.I., Brearley, A., 1998. Isopod burrowing in leaves of turtle grass, *Thalassia testudinum*, in a Mexican Caribbean reef lagoon. *Mar. Freshwater Res.* 49, 525–531.
- Zupo, V., Nelson, W., Gambi, M.C., 2001. Measuring invertebrate grazing on seagrass and epiphytes. In: Short, F.T., Coles, R.C. (Eds.), *Global Seagrass Research Methods*. Elsevier, Amsterdam, pp. 371–382 (Chapter 14).