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Herbivory on *Zostera marina* by the gastropod *Smaragdia viridis*

José L. Rueda *, Carmen Salas, Javier Urra, Pablo Marina

Departamento de Biología Animal, Universidad de Málaga, Campus de Teatinos s/n, 29071-Málaga, Spain

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ABSTRACT

The feeding activity of the gastropod *Smaragdia viridis* on *Zostera marina* (eelgrass) was studied under laboratory conditions and from shoots collected in a deep eelgrass bed (12–14 m depth) in southern Spain (Alboran Sea). This gastropod preferentially ingested young leaf tissues, such as those located in the central leaf and first pair of adjacent leaves and at close distances from the junction of the leaves with the sheath. The ingestion rate of this gastropod was size dependent, ingesting up to 40.6 mm^2 of epidermal tissues in 24 h (for large individuals), however this value generally represented a very low percentage of the area of a single shoot (0.3–2.1%). The absorption of eelgrass tissues, in relation to digested/non-digested eelgrass cells in faecal pellets, was not size dependent and reached high values (75–90% cells digested). The grazing impact in an eelgrass bed, based on the affected area (length of radular marks by leaf width), also represented a very low value (0.3–1.1%) in relation to the total LAI (Leaf Area Index) available. A seasonal trend of herbivory was registered with maximum values in summer together with maximum densities of *S. viridis*.

1. Introduction

Seagrass beds represent an important habitat for a large number of species in different parts of their geographical distribution (Green and Short, 2003). Most of the associated species feed on a wide variety of food sources (e.g. detritus, periphyton, other organisms) and, rarely on the seagrass itself (Thayer et al., 1984; Hemminga and Duarte, 2000; Valentine and Duffy, 2006). This may be due to the fact that, unlike terrestrial species, only few marine species are able to feed directly on vascular plants and digest them. This group includes some species of vertebrates, such as sirenids, birds, sea turtles and fishes (Thayer et al., 1984; Baldwin and Lovvorn, 1994; Valentine and Duffy, 2006), and also invertebrates, generally sea urchins (Alcoverro and Mariani, 2004), crustaceans (Groenendijk, 1984; Nakaoka, 2002) and some molluscs (Carlton et al., 1991; Zimmerman et al., 1996; Hickman, 2005; Rueda and Salas, 2007). Nevertheless, there is increasing evidence that herbivory in seagrasses is more important than previously thought, and information on the role of small seagrass feeding invertebrates is still scarce (Heck and Valentine, 2006).

Molluscs are important components of seagrass beds and they generally play an important role in the trophic webs of these habitats (Hemminga and Duarte, 2000). Past studies indicated the importance of periphyton for some grazing mollusc species (Mazzella and Russo, 1989; Jernakoff et al., 1996; Hily et al., 2004) and the positive effects of their grazing activity on the plants (Jernakoff et al., 1996). On the other hand, few studies have focused on those small species (<1–2 cm), whether molluscs or not, that feed directly on the seagrass tissues (Carlton et al., 1991; Zimmerman et al., 1996; Hickman, 2005; Nakaoka, 2002; Valentine and Duffy, 2006). Moreover, these small herbivores probably provide important pathways for the mobilisation of seagrass carbon to higher trophic levels. Unlike large herbivores, these small species ingest a smaller quantity of seagrass tissues, but they can also have severe impacts on the plant, especially when occurring at high densities, by reducing its photosynthetic activity (e.g. *Tectura depicta*) (Zimmerman et al., 1996) or its reproductive output (e.g. *Zeuxo* sp.) (Nakaoka, 2002). The grazing activity of these small herbivores has rarely been studied and evaluated when compared to other seagrass feeders (Heck and Valentine, 2006) and, like some large herbivores, selective mechanisms of ingestion may play an important role in their feeding activity (Thayer et al., 1984; Yamamuro and Chirapart, 2005).

The emerald neritid *Smaragdia viridis* (Linnaeus, 1758) is the only native marine mollusc from the family Neritidae in the European coasts (Mediterranean Sea and Canary Islands) and it also occurs in the Caribbean Sea. In Europe, this small gastropod (shell height < 1 cm) is generally associated with *Zostera marina* (Rueda et al., 2008b; Rueda and Salas, 2008) and *Cymodocea nodosa* (Somaschini et al., 1998; Ballesteros et al., 2004) beds, and forms

* Corresponding author. Present address: Marine and Estuarine Ecology Unit, School of Integrative Biology, The University of Queensland, Brisbane, Qld 4072, Australia. Tel.: +61 7 3365 4821; fax: +61 7 3365 1655.
E-mail address: biologiamarina@uma.es (J.L. Rueda).

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therein stable populations. Recently, Rueda and Salas (2007) demonstrated that the strong association between this gastropod and the above mentioned seagrasses could be explained by its trophic dependence, representing the only known mollusc that feeds directly on seagrass tissues for the European malacofauna (both Atlantic and Mediterranean coasts). This is particularly interesting because most mollusc species inhabiting seagrass beds feed on other food sources such as periphyton (e.g. *Jujubinus striatus*, *Rissoa* spp.), detritus (e.g. *Tellina* spp., *Abra* spp.) or other invertebrates (e.g. Naticids, cephalopods) so their strict dependence on seagrasses is questionable (Rueda and Salas, 2008). Information on the feeding biology and grazing activity of *S. viridis* is completely absent, as is the case with most small seagrass grazers, especially molluscs (Heck and Valentine, 2006). The present research aims to study some aspects of the feeding biology of this small neritid (e.g. pre-ingestive selection, food ingestion and absorption) and to estimate its grazing incidence on eelgrass.

2. Materials and methods

2.1. Study sites and collection of gastropods and eelgrass for laboratory experiments

Eelgrass shoots and gastropods were collected by diving in (1) Cañuelo Bay (MPA "Paraje Natural de Acantilados de Maro-Cerro Gordo", southern Spain) in a deep *Z. marina* bed (12–14 m) in March, June, September and December 2004 and (2) Caleta de Vélez in a shallower eelgrass bed mixed with *C. nodosa* (5–7 m depth) in October 2006. The latter eelgrass bed had to be chosen because those in Cañuelo Bay and adjacent areas unfortunately experienced a strong decline due to illegal trawling by fishermen during 2005 and 2006 (Rueda et al., 2008a). The eelgrass bed at Cañuelo Bay covered ca. 38.8 ha (Bañares-España et al., 2002) and information on its phenology has been given in Rueda et al. (2008a). The eelgrass bed at Caleta de Vélez was smaller (less than one ha) and more fragmented than that of Cañuelo Bay and it is adjacent to a fishing harbour. In southern Spain (Alboran Sea), eelgrass beds generally occur in open bays at higher depths than those found in other Mediterranean or Atlantic locations of Europe (Green and Short, 2003; Rueda et al., 2008a).

A total of 16 live individuals of *S. viridis* of different size classes (shell height ranging from 1.7 to 7.2 mm) were collected (six in Cañuelo Bay and ten in Caleta de Vélez) and placed in containers with seawater. Eelgrass shoots for the experiments were also collected (>50 shoots) and transported separately to the laboratory. Prior to experiments, all individuals of *S. viridis* were acclimatized to laboratory conditions for at least 24 hours inside a glass container filled with filtered seawater, at room light and temperature (19.9 ± 0.9 °C; Mean of all experiments ± standard deviation). Shoots of *Z. marina* were cleared of mobile invertebrate species and placed in plastic containers separately with natural seawater. Shoots used in different experiments were similar regarding morphological features such as shoot height (32.1 ± 5.7 cm) or number of leaves (5.5 ± 0.5 leaves shoot^{-1}). This was also the case for those shoots collected in Cañuelo Bay and Caleta de Vélez.

2.2. Feeding biology of S. viridis under laboratory conditions

In each experimental set-up, one shoot of *Z. marina* was placed inside a plastic tray (35 cm × 24 cm) with natural seawater together with one individual of *S. viridis* that was always placed in the same corner of the tray (opposite to the base of the *Z. marina* shoot). All experiments were carried out at similar temperatures (19.9 ± 0.9 °C). Each experiment ran for 24 h and it was performed twice (except for one of the *S. viridis* individuals), resulting in a total of 31 experiments. After 24 h, the type of leaf grazed and location of the radular marks within the shoot (laboratory shoots) was annotated. According to the leaf type, the radular marks could be located in the central leaf (the youngest leaf), in the first pair of lateral leaves (adjacent to the central leaf), the second pair of lateral leaves (older than the first pair) or, in the third pair of lateral leaves (the oldest ones) (Fig. 1). The location within the leaf was measured as the distance from the junction of the leaves with the sheath to the middle point of the radular mark. Later on, the area of all radular marks produced by each individual in each experiment (24 h) was measured using image analysis with the software Visilog 6. This area was used for estimations of the ingestion rate (IR) of one individual during one day (mm^2 of *Z. marina* ingested d^{-1}) under laboratory conditions. In each case, the affected area in the shoot was computed as the length of the radular marks along the leaf by the leaf width. Length of the shoot (shoot height) as well as length (from junction of leaf with sheath to leaf apex) and width (middle part of the leaf) of each leaf contained in the shoots used in each experiment were also measured for estimations of the leaf area of the *Z. marina* shoot, assuming rectangle shapes.

Absorption of eelgrass tissues was studied from the faeces egested by each individual of *S. viridis* during each experiment. At the end of each experiment (24 h), most faecal pellets were collected using a Pasteur pipette and fixed in Lugol for further microscopic analyses. Gut passage time of *S. viridis* (or similar species) has not been quantified in this study and it is currently unknown as for most gastropod species. Nevertheless, individuals collected in a *C. nodosa* bed in summer 2007 were placed in separate containers with seawater and without food (seagrass leaves) and most faecal pellets were egested in the first 6–12 h

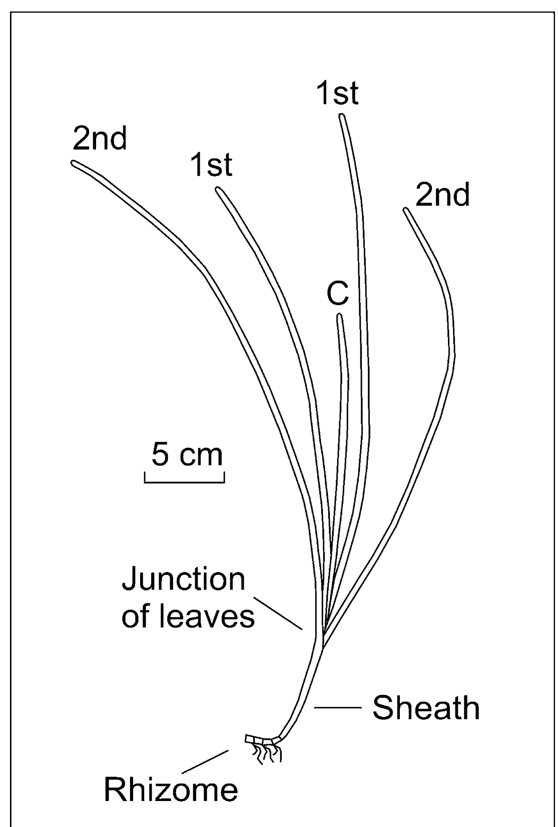

Fig. 1. Eelgrass shoot displaying the different parts and types of leaves. C: Central leaf; 1st: First pair of lateral leaves; 2nd: Second pair of lateral leaves.