



ELSEVIER

Aquatic Botany 78 (2004) 183–195

**Aquatic  
botany**

[www.elsevier.com/locate/aquabot](http://www.elsevier.com/locate/aquabot)

# In vitro experimental assessment of the grazing pressure of two gastropods on *Zostera marina* L. epiphytic algae

Christian Hily<sup>a,\*</sup>, Solène Connan<sup>b</sup>, Coralie Raffin<sup>a</sup>,  
Sandy Wyllie-Echeverria<sup>c</sup>

<sup>a</sup> LEMAR, Institut Universitaire Européen de la Mer, Technopole Brest-Iroise,  
Place Nicolas Copernic, Plouzané 29280, France

<sup>b</sup> LEBHAM, Institut Universitaire Européen de la Mer, Plouzané, France

<sup>c</sup> School of Marine Affairs, University of Washington, Seattle, WA, USA

Received 3 October 2002; received in revised form 23 September 2003; accepted 14 October 2003

## Abstract

This study experimentally assessed the impact of gastropod grazing on epiphyton biomass and taxonomic composition on leaves of the seagrass *Zostera marina* L. along the coasts of Brittany, France. Image analysis was used to measure the same section of a leaf before and after grazing and assess grazing pressure. It was found that: (1) both grazers, *Gibbula umbilicalis* and *Jujubinus striatus*, were highly efficient in reducing epiphytic cover; (2) *J. striatus* showed a higher specific grazing rate than *G. umbilicalis* at an equivalent animal biomass; (3) *J. striatus* increased its activity when epiphytic biomass increased. Analysis of the variability of epiphytic cover along the leaves showed considerable heterogeneity from the basal part of the external leaves of a shoot to the apex. The development of long filamentous algae (mainly ectocarpales) in spring and summer and their concentration at the apex intensified shading impact on the seagrass bed. The grazing of both gastropod species was also concentrated at the apex, thereby enhancing their role in moderating the shading effect. © 2003 Elsevier B.V. All rights reserved.

**Keywords:** Seagrass; Snails; Microherbivores; Epiphytic algae; Seasonality

## 1. Introduction

The presence of periphyton enhances the habitat value of seagrass leaves and favors the development of a more complex habitat within the temperate seagrass canopy (Schneider and Mann, 1991). Generally speaking, the term “periphyton” covers microalgae, macroalgae,

\* Corresponding author. Tel.: +33-2-98-49-8640; fax: +33-2-98-49-8645.

E-mail address: [christian.hily@univ-brest.fr](mailto:christian.hily@univ-brest.fr) (C. Hily).

bacteria and small animals (hydrozoa, bryozoa) that live on plants. Periphyton constitutes a source of food and sometimes shelter (Mazzella et al., 1992; Bologna and Heck, 1999). The present study considered only micro- and macroalgae growing on seagrass leaves, which correspond to epiphyton. These algae, especially those of a filamentous nature, can also slow the rate at which suspended water-column particles move through the seagrass canopy, thereby enhancing the capacity of seagrass leaves to precipitate sedimentation (Van Montfrans et al., 1984).

Over the last few decades, a decrease in water clarity, often associated with an increase in nutrient loading, has had a negative impact on the seagrass habitat as a result of eutrophication (Short and Wyllie-Echeverria, 1996). Many *Zostera marina* beds in western Brittany (France) are threatened by anthropogenic impacts such as eutrophication, anchoring and dredging (Hily and Den Hartog, 1997). A eutrophic environment enhances epiphyte growth and plankton biomass, which in turn reduces the light available to seagrass (Mazzella and Alberte, 1986; Dennison, 1987), ultimately causing localized episodes of seagrass loss (Shepherd et al., 1989; Wetzel and Neckles, 1986). Sand-Jensen (1977) showed that heavy epiphyte cover reduces the photosynthetic capacity of the seagrass *Z. marina* by 31% and acts as a barrier to carbon uptake. Borum and Wium-Andersen (1980) reported that less than 10% of the light was transmitted through the dense epiphyte cover growing on the distal end of the oldest leaf blade of *Z. marina*. As light levels decrease, progressive invasion of the temperate seagrass zone by opportunistic macroalgae such as *Ulva* and *Enteromorpha* or filamentous epiphytic macroalgae and phytoplankton can ultimately cause a shift to algal dominance and the disappearance of seagrasses (Orth and Van Montfrans, 1984; Borum and Wium-Andersen, 1980).

The food source provided by epiphytes is exploited by microherbivore communities inhabiting the seagrass beds (Bologna and Heck, 1999; Van Montfrans et al., 1984). The grazing community associated with the seagrass habitat is very diverse (Borum, 1985, 1987; Mazzella et al., 1992; Hily and Bouteille, 1999). Some animals graze on epiphytes at the surface of the seagrass leaf, while others consume the entire leaf blade. This grazing activity plays a major role in structuring between-site variability in epiphyte biomass (Alcoverro et al., 1997). The effect of grazing on epiphyte depends on three factors: the diversity and abundance of grazer species (Hootsmans and Vermaat, 1985; Mazzella and Russo, 1989), the consumption rate and dietary preferences of species, and the growth rate of grazers and epiphytes (Borum, 1987; Mazzella and Russo, 1989).

Microherbivores may have the capacity to accommodate the increased epiphytic productivity and hence prevent seagrass decline through light deprivation. In controlled experiments, when grazers were excluded and nutrients and light were maintained at constant levels, Borum (1987) found that the epiphyte biomass on older seagrass leaves was 10 times higher than in natural conditions. Several studies have also considered the effect of a preferential grazing season for species, as a function of algal recruitment and succession (Howard and Short, 1986; Kitting et al., 1984; Neckles et al., 1993).

To quantify the potential and efficiency of seagrass grazers in removing epiphyte biomass, our study focused on two gastropod species, *Gibbula umbilicalis* and *Jujubinus striatus*, the most abundant microherbivores in *Z. marina* meadows of Brittany (Hily et al., 1999). *G. umbilicalis* (up to 10 mm in size) lives in various habitats of the intertidal zone, while *J. striatus* (up to 5 mm) is more specialized and largely restricted to *Z. marina* beds. Seasonal variation

in the grazing pressure of these two species was quantified using a precise, small-scale laboratory assessment method (Hily et al., 2000).

## 2. Materials and methods

### 2.1. Experimental design

The seagrass leaves used for the experiments were sampled in the intertidal *Z. marina* meadows of Brest Bay. For each experiment, both gastropod species were supplied with seagrass collected within 48 h of the feeding test. All *Z. marina* shoots (full-grown, on average 37.1 cm in length and 0.6 cm in width) were kept moist during transport from the field to the laboratory where they were placed in 200 l tanks equipped with a flow-through seawater system. Salinity was  $34.0 \pm 0.9\text{‰}$  and temperature varied from 9.7 °C in February to 18.5 °C in July. At the start of the experiment, two outer leaves were placed vertically in a Plexiglas tube (50 cm long and 10 cm in diameter) in another tank. The tube was closed with a sieve to prevent the snails from escaping. Leaves were maintained vertically in the tube by means of a weight attached to their base, which provided near natural conditions for snail grazing activity, apart from water movement, of course. All tubes were kept under running seawater and provided with light on a diurnal basis. Preliminary experiments to determine the optimal number of grazers (three, six or nine) per tube indicated that the food supply was adequate for nine individuals of a given species and that their grazing impact was sufficiently high in terms of cover rate to be easily measured by image analysis. A similar number can be observed under natural conditions in *Z. marina* meadows. Each experiment was conducted for 24 h, a period during which epiphytic growth was negligible and leaves did not deteriorate. As the effect of a species can change over time because of seasonal and annual variation in the recruitment of algae (Neckles et al., 1993; Kendrick and Burt, 1997), grazing was assessed during different seasons. Overall, nine experiments (six replicate tubes per species per experiment) were performed during 6 different months (five experiments with *J. striatus* in February, March, April, May and June; and four experiments with *G. umbilicalis* in April, May, June and July). Thus, comparisons between the two species were possible for three periods (April, May and June).

### 2.2. Sample processing

A camera with a macrophoto lens (100 mm) linked to a PC microcomputer run with Visilog 5.1 software was used to measure epiphytic cover (Hily et al., 2000). Measurement was based on differences in gray color between a leaf surface with or without epiphytes. The method was automated by a specific program, which compared the surfaces of two binary images of each leaf section (2.8 cm in length) before measurement. Grazing was regarded as the difference between epiphytic cover rates measured before and after the introduction of grazers into the tanks. The total length and width of each leaf were measured ( $\pm 0.5$  mm). From the apex to the basal part of the leaf, the sections were designated from 1 (apex) to *n* (base).

To determine the relationship between the cover and epiphyte biomass for each period, several seagrass leaves were scraped with a razor blade after cover measurement to remove all of the attached flora. The scraped material was collected onto pre-dried, pre-weighed GFC filter paper, which was then dried at 60 °C for 48 h for biomass [dry weight (DW)] determination. These epiphyton biomass data were standardized to a unit of seagrass leaf covered with epiphytes (cm<sup>2</sup>).

To compare the efficiency of the two grazers, the amount of epiphyton removed was expressed per mg of ash-free DW (AFDW) of animal. At the end of the experiment, grazers were dried (60 °C) for 48 h, total DW measured, and AFDW calculated from ash weight after combustion in an oven (450 °C for 4 h). The results obtained for the two species relative to experimental periods are expressed as the mean rate (%) of epiphytic biomass removed per day from each leaf section. Basal sections without epiphytes before experimentation were not taken into account.

Grazing rates are expressed per individual snail or biomass (i.e. the amount of epiphyton grazed by 1 mg of grazer organic matter).

### 2.3. Data analysis

Statistical tests were applied to compare epiphyte cover before and after grazing, as well as the grazing efficiency of the two species. The data were  $\log_{10}(x + 1)$  – transformed (biomass of epiphytes before/after an experiment) or  $\arcsin[\text{square root}(x/100)]$  – transformed (grazing rates) for variance homogenization (Scherrer, 1984). As recommended by Scherrer (1984) and Underwood (1999) for non-independent samples, before/after epiphytic biomass was compared by a paired *t*-test for every  $n_i$  leaf section. Epiphytic distribution along the leaves (from the apex to the basal part) was tested by multifactorial ANOVA. The efficiency of the two grazers was compared by multifactorial ANOVA for three periods (April, May and June) in terms of grazed biomass/leaf section, month and grazer species. Analyses were performed with Statgraphics statistical software.

## 3. Results

The proportion of epiphyton removed appeared to vary substantially between the two snails, but also among leaf sections and months (Fig. 1). The rate of epiphytes grazed by *J. striatus* was highest in June, median in February, April and May, and lowest in March. For *G. umbilicalis*, the rate was highest in April and then gradually decreased in May, June and July.

The highest epiphyte biomass before grazing was localized on apical sections and decreased gradually toward the basal part of the leaf (Fig. 2). Even though the grazing rate (%) was higher in the basal part of the leaf (Fig. 1), it is particularly noteworthy that the biomass (mg per section) grazed was greater in upper than lower sections (Fig. 2).

Considerable variation in epiphyte biomass was observed from month to month (Table 1). When the removal rate is expressed per individual, values are higher for *G. umbilicalis*, but when it is expressed at an equivalent animal biomass (mg mg<sup>-1</sup> grazer organic matter per day), these rates are higher for *J. striatus*. In April and June, weight-specific removal is

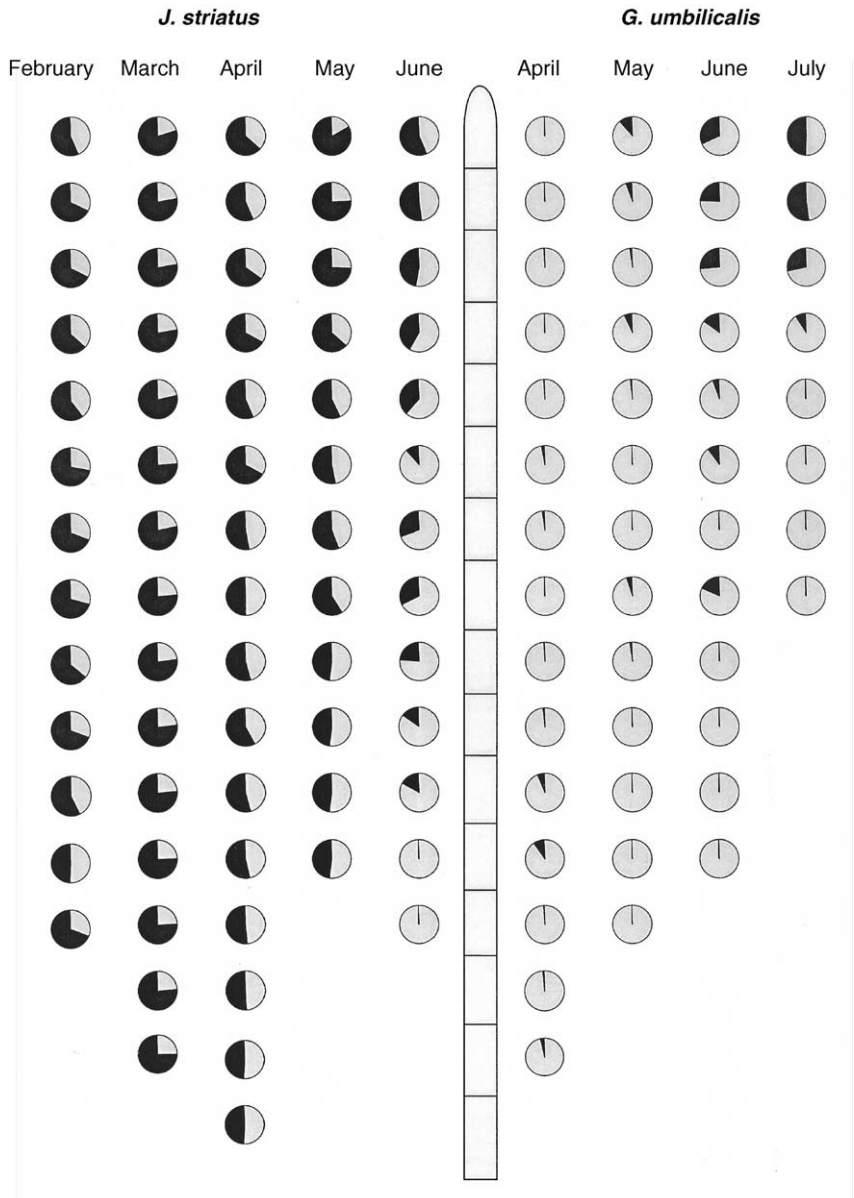


Fig. 1. Proportion of epiphyte biomass grazed (light areas) compared to initial biomass (light + shaded areas) according to grazing species, month of experiment and leaf section. Mean per experiment.

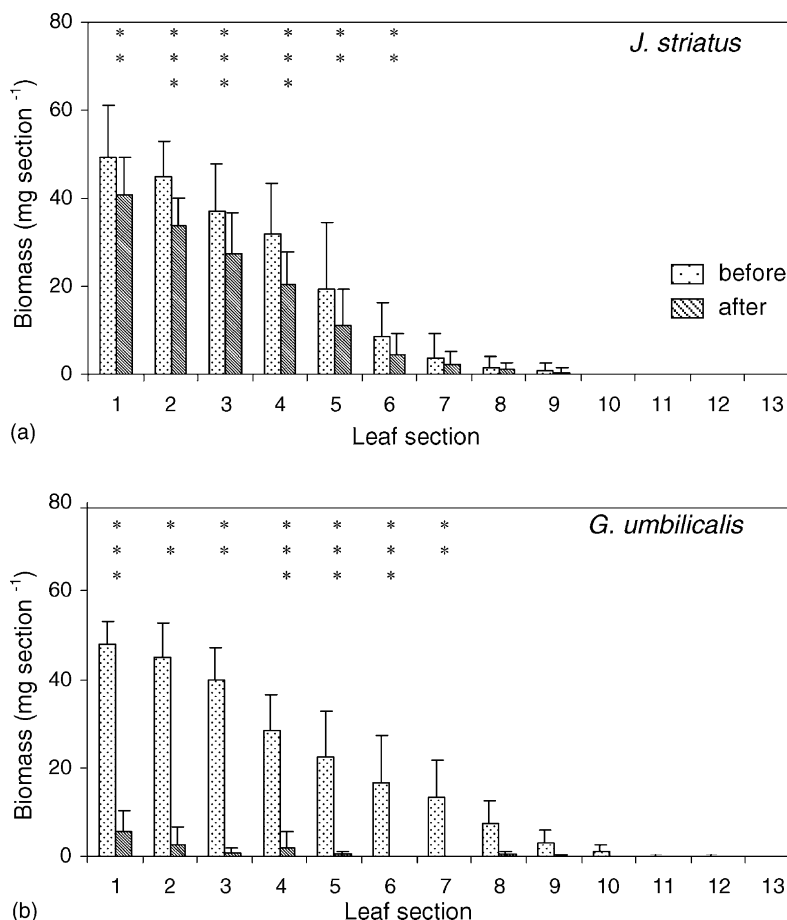


Fig. 2. Example of grazing activity (May experiment—mean  $\pm$  1 S.E.) over 24 h: epiphytic biomass before (□) and after grazing (▨) by *J. striatus* (a) and *G. umbilicalis* (b), as measured from the apex (section 1) to the basal part of the leaves. Each section was 2.8 cm long and 0.6–1.1 cm width. Results of paired *t*-test are indicated with asterics: \* ( $P < 0.05$ ), \*\* ( $P < 0.01$ ) or \*\*\* ( $P < 0.001$ ).

approximately three times as high for *J. striatus* as for *G. umbilicalis* (respectively 1.31 and 1.58 mg for *J. striatus* and 0.45 and 0.35 mg for *G. umbilicalis*). In May, the differences are lower (0.48 mg for *J. striatus* and 0.31 mg for *G. umbilicalis*).

The results for grazing activity show large differences between the periods of low (February) and high (April) epiphytic cover. Grazing was highest when epiphytic algae were most abundant (20.14 and 149.71 mg per day, respectively). This trend was also found for *J. striatus* when the grazed biomass was expressed in terms of grazer biomass units (i.e. mg of algae grazed in 24 h by 1 mg of grazer; Table 1). *G. umbilicalis*, on the contrary, exhibited a constant grazing rate when food was abundant, and a lower rate when epiphytic algal biomass was low.

Table 1

Removal of epiphyton by two microherbivorous snails, *J. striatus* and *G. umbilicalis*, from *Z. marina* leaves in different months

Month	Epiphyton density (mg DW cm <sup>-2</sup> )	Individual-based removal (mg DW per individual per day)	Weight-specific removal (g DW g per AFDW per day)
<i>J. striatus</i>			
February	3.2	2.2 ± 0.9	0.3 ± 0.1
March	6.6	8.3 ± 3.3	0.6 ± 0.2
April	6.6	16.6 ± 7.5	1.3 ± 0.5
May	9.5	6.2 ± 2.5	0.5 ± 0.2
June	18.5	21.9 ± 6.9	1.6 ± 0.5
<i>G. umbilicalis</i>			
April	6.6	32.0 ± 4.2	0.5 ± 0.1
May	9.5	26.7 ± 5.5	0.3 ± 0.2
June	18.5	29.5 ± 8.1	0.4 ± 0.2
July	4.3	7.9 ± 3.8	0.1 ± 0.0

Presented are mean epiphyton density (mg DW cm<sup>-2</sup> of seagrass leaf covered with epiphytes) at the start of each experiment, removal rates expressed per individual and per unit animal weight. Means of removal rates are ± 1 S.E. Removal rates (final vs. initial epiphyton density, paired *t*-tests) were all significant (*P* < 0.001). Replication was six.

Pooled over all experiments, significant differences existed in periphyton density along the length of the leaves (one-way ANOVA, *P* = 0.000). The paired *t*-test showed significant differences for both species between the biomass before and after grazing (Fig. 2 and Table 1). Multifactorial ANOVA ('species' × 'sections' and 'species' × 'months', Table 2)

Table 2

Effect of snail micrograzer species, leaf sections (apical = sections 1–4; median = sections 5–9; basal = sections 10–13) and months on two types of removal rate

Factors	df	SS	<i>P</i>	A posteriori results
Individual-based removal rate (mg DW per individual per day)				
Snail species	1	6.095	0.000	<i>G. umbilicalis</i> > <i>J. striatus</i>
Leaf sections	14	32.608	0.000	apical > median > basal part
Error	279	66.697		
Snail species	1	6.287	0.000	<i>G. umbilicalis</i> > <i>J. striatus</i>
Months	2	5.509	0.000	April = June > May
Error	297	93.796		
Grazer mass-specific removal rate (g DW g per AFDW per day)				
Snail species	1	0.005	0.000	<i>J. striatus</i> > <i>G. umbilicalis</i>
Leaf sections	14	0.026	0.000	apical > median > basal part
Error	285	0.031		
Snail species	1	0.004	0.000	<i>J. striatus</i> > <i>G. umbilicalis</i>
Months	2	0.006	0.000	April = June > May
Error	291	0.050		

Results of multifactorial ANOVA and a posteriori Fisher's LSD tests are presented (multifactorial ANOVA showed no significant interaction between the factors). The used conservative error rate for each comparison was 0.01.

indicated that (1) the individual-based removal rate was higher for *G. umbilicalis* than for *J. striatus*; (2) the weight-specific removal rate was higher for *J. striatus* than for *G. umbilicalis*; (3) removal rate was greater in the apical parts than in the median and basal parts; (4) removal rate was greater in April and June than in May. Interactions were not found to be significant. Comparison of individual weights showed that *G. umbilicalis* individuals were larger and had higher mean individual weights ( $83.36 \text{ mg AFDW} \pm 23.96$ ) than *J. striatus* ( $13.76 \text{ mg AFDW} \pm 1.53$ ).

Although this study was not intended to describe the qualitative succession of epiphytic macroalgal species on *Zostera* leaves during the year, some complementary observations may elucidate the results obtained for grazing activity: when long filamentous algae (ectocarpales) were present on leaves, the animals removed some without eating them. Moreover, variation in the seasonal biomass of epiphytic cover corresponded to a qualitative succession in species composition. During the winter period, algal cover consisted exclusively of calcareous crustose algae (*Pneophyllum* sp.), and our experiments showed that these plants were consumed by *J. striatus* (*G. umbilicalis* was not tested during this period, i.e. February; Table 1). Consumption rates remained low, however, until the development of filamentous algae began in March. Grazing rates at this time were two to four times higher ( $0.30 \text{ mg}$  per day in February,  $0.64 \text{ mg}$  per day in March and  $1.31 \text{ mg}$  per day in April). In March, filamentous algae developed rapidly in a succession of species, with ectocarpales followed by ceramiales.

Significant correlation between epiphytic biomass and weight-specific removal rate was found every month for *J. striatus* and *G. umbilicalis* (Fig. 3). Relations between weight-specific removal rate and water temperature were different for the two grazers (Fig. 4): except for  $13.8^\circ\text{C}$ , the removal rate increased with water temperature for *J. striatus* while it remained constant or decreased for *G. umbilicalis*.

## 4. Discussion

### 4.1. Variability in epiphytic cover

Epiphytic cover increased from the basal part to the apex of leaves, corresponding to a progressive colonization of surface area with increasing leaf age. This distribution probably increased the overall shading effect of epiphyton, which is mainly concentrated in the upper part the *Z. marina* canopy. Den Hartog (1983), Jacobs et al. (1983), and Novaczek (1987) showed that epiphytes are not evenly distributed over *Z. marina* leaves, but concentrated near the tips, whereas some species, such as *Rhodophysema georgii* or *Audouinella* sp., are generally observed on the edges.

The diversity of macroalgae changed with seasons, being lower during winter when crustose calcareous algae were dominant, and then higher when filamentous algae became dominant in spring, reaching a maximum in June. This strong development of filamentous epiphytes, mainly Ectocarpales, was also observed in Brittany by Jacobs et al. (1983) in the *Z. marina* meadows of Roscoff. These differences in taxonomic composition also led to large differences in biomass (maximal in June). Our observations are in agreement with those of other authors (Borum, 1985; Borum et al., 1984; Novaczek, 1987), who found a



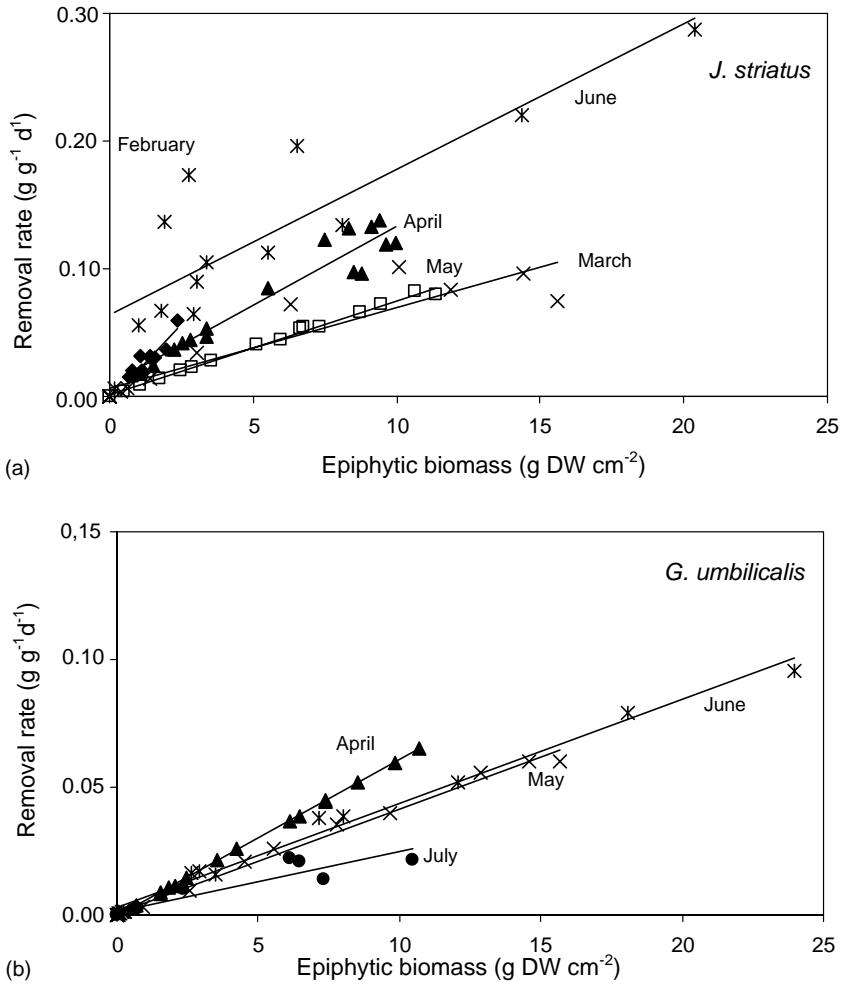


Fig. 3. Relations between standing epiphytic biomass and removal rate according to month of experiment for the two grazers: (a) *J. striatus*; (b) *G. umbilicalis*.  $R^2$  = correlation coefficient. Each point corresponds to a leaf section.

bimodal seasonal pattern, with a maximum at the end of spring and in autumn and low biomass in summer. This pattern corresponds to a “spring bloom”, with amplitude and duration depending on the overall environmental quality at a site (Borum, 1985).

#### 4.2. Grazing

*J. striatus* and *G. umbilicalis* were able to graze the filamentous and calcareous epiphytes present on the leaves during the study period. When individuals were placed in experimental tanks, epiphytic cover decreased all along the leaf, but especially at the apex. This suggests that the two species studied behave similarly, concentrating their activity on the

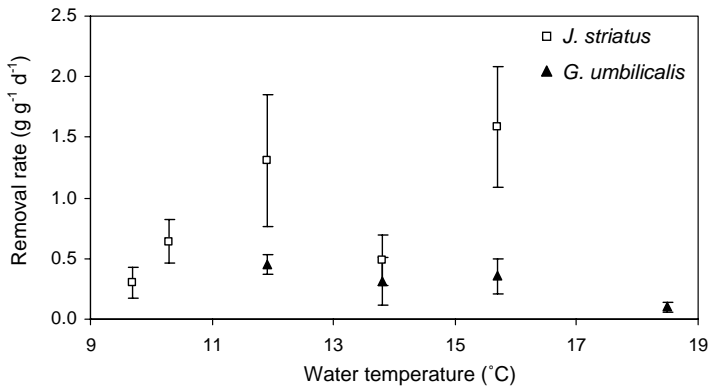


Fig. 4. Relations between weight-specific removal rate ( $\text{g g}^{-1}$  per day) and water temperature ( $^{\circ}\text{C}$ ) for the two grazers (white square for *J. striatus*; black triangle for *G. umbilicalis*—mean  $\pm 1$  S.E.).

highest epiphytic biomass. *J. striatus* showed weight-specific grazing rates that were positively correlated with epiphytic algae biomass, which implies that the animals increase their activity when food is more abundant. It is likely that *J. striatus* was able to adapt its feeding to the food available. In contrast, *G. umbilicalis* showed stable grazing pressure in all experimental periods.

The two species differed in grazing efficiency. As the mean individual weight of *G. umbilicalis* was higher than that of *J. striatus*, it removed more per individual. However, when grazing was expressed in grazer biomass units, *J. striatus* was more efficient than *G. umbilicalis*. A similar result was found by Hootsmans and Vermaat (1985) who found that the smaller *Hydrobia ulvae* had a higher weight-specific removal rate than the larger *Littorina littorea*. While *G. umbilicalis* is common in various coastal habitats with soft and hard substrates, *J. striatus* is found almost exclusively in eelgrass beds (Hily et al., 1999). Our personal observations also indicate that the smaller *J. striatus* is better adapted to the leaf substratum, both morphologically and functionally. This species moves rapidly along the leaves and is active even under quite strong water movement because of its small size (per. observ.). Water movement was not considered in our experiments which were performed under still conditions. However, it is likely that grazing pressure would be modulated by different hydrodynamic conditions.

The indirect role of epiphyte grazing on seagrass plants has already been demonstrated. Hootsmans and Vermaat (1985) showed that even low grazing pressure, causing no visible difference in periphyton cover, was sufficient to create better growing conditions for *Z. marina*. Several species of mesograzers are reported to increase *Z. marina* growth by reducing epiphytic biomass (reviewed in Jernakoff et al., 1996; Neckles et al., 1993). If algal epiphytes have a net negative effect on the growth of seagrass, as suggested in the literature (Orth and Van Montfrans, 1984; Van Montfrans et al., 1984; Jernakoff et al., 1996), then grazers may have a substantial and indirect impact on proliferation, biomass, reproductive potential and possibly even the persistence of seagrasses. This would have an indirect effect in increasing the fitness of *Z. marina* (Van Montfrans et al., 1982; Orth and Van Montfrans, 1984; Nelson, 1997).

Some authors have not observed grazing effects on coralline algae (Van Montfrans et al., 1982; Morgan and Kitting, 1984; Klumpp et al., 1992), but the present study shows that gastropods such as *J. striatus* are able to graze on encrusting coralline algae in the absence of other food resources and in winter conditions. Jacobs et al. (1983) suggested that the dominance of crustose red algae on *Z. marina* leaves in France is due to the presence of trochid gastropods that do not graze on them. Our results are compatible with the observations of Mazzella and Russo (1989), who used scanning electron microscopy to observe traces of rasping on calcareous red algae by *G. umbilicalis* and *G. ardent* on *Posidonia oceanica* leaves. Padilla (1985) also found that calcareous algae were often grazed, presumably because they are brittle and can thus be easily removed.

Finally, we observed that some of the material removed from *Z. marina* leaves by grazers was not eaten, but dropped to the sediment floor and was thus available as a food source for other groups of macrodetritivores and decomposers (e.g. amphipods and polychaetes). This suggests that energy calculations based on the AFDW of epiphytes scraped from the leaf may overestimate actual consumption by grazers.

## Acknowledgements

The authors are grateful to Alain Le Mercier for developing the computer program and automating the method and to Camille Buart, Florence Foucher, Maud Millet and Loïc Lancou for assistance with measurements, and to J. Gray for linguistic assistance. The study was supported by the CNRS and by a grant from the French program, “Dynamique de la Biodiversité et Environnement”.

## References

- Alcoverro, T., Romero, J., Duarte, C.M., Lopez, N.I., 1997. Spatial and temporal variation in nutrient limitation of seagrass *Posidonia oceanica* growth in the NW Mediterranean. Mar. Ecol. Prog. Ser. 146, 155–161.
- Bologna, P.A.X., Heck Jr., K.L., 1999. Macrofaunal associations with seagrass epiphytes: relative importance of trophic and structural characteristics. J. Exp. Mar. Biol. Ecol. 242, 21–39.
- Borum, J., 1985. Development of epiphytic communities on eelgrass (*Zostera marina*) along a nutrient gradient in a Danish estuary. Mar. Biol. 87, 211–218.
- Borum, J., 1987. Dynamics of epiphyton on eelgrass (*Zostera marina* L.) leaves: relative role of algal growth, herbivory and substratum turnover. Limnol. Oceanogr. 32, 986–992.
- Borum, J., Wium-Andersen, S., 1980. Biomass and production of epiphytes on eelgrass (*Zostera marina* L.) in the Øresund, Denmark. Ophelia Suppl. 1, 57–64.
- Borum, J., Kaas, H., Wium-Andersen, S., 1984. Biomass variation and autotrophic production of an epiphyte–macrophyte community in a coastal Danish area. II. Epiphyte species composition, biomass and production. Ophelia 23, 165–179.
- Den Hartog, C., 1983. Structural uniformity and diversity in *Zostera*-dominated communities in Western Europe. Mar. Technol. Soc. J. 17, 6–14.
- Dennison, W.C., 1987. Effects of light on seagrass photosynthesis, growth and depth distribution. Aquat. Bot. 27, 15–26.
- Hily, C., Bouteille, M., 1999. Modifications of the specific diversity and feeding guilds in an intertidal sediment colonized by an eelgrass meadow (*Zostera marina*) Brittany, France. C.R.A.S. (Paris, Life Sciences) 322, 1121–1131.

- Hily, C., Den Hartog, C., 1997. Les herbiers de zostères. In: Dauvin, (Ed.), *Les Biocénoses Marines et Littorales Françaises des Côtes Atlantiques, Manche et mer du nord: Synthèse, Menaces et Perspectives*. MNHN, Paris, pp. 140–143.
- Hily, C., Raffin, C., Connan, S., 1999. Les Herbiers de Zostères en Bretagne. Report Univ. Bretagne Occidentale/Direction Régionale de l'Environnement Bretagne.
- Hily, C., Raffin, C., Connan, S., Le Mercier, A., 2000. Quantification of the grazing activity on seagrass epiphyton with a new methodological approach: first application in *Zostera marina* meadows. *Biol. Mar. Medit.* 7, 223–226.
- Hootsmans, M.J.M., Vermaat, J.E., 1985. The effect of periphyton-grazing by three epifaunal species on the growth of *Zostera marina* L. under experimental conditions. *Aquat. Bot.* 22, 83–88.
- Howard, R.K., Short, F., 1986. Seagrass growth and survivorship under the influence of epiphyte grazers. *Aquat. Bot.* 24, 287–302.
- Jacobs, R.P.W.M., Hermelink, P.M., Van Geel, J., 1983. Epiphytic algae on eelgrass at Roscoff, France. *Aquat. Bot.* 15, 157–173.
- Jernakoff, P., Brearley, A., Nielsen, J., 1996. Factors affecting grazer–epiphyte interactions in temperate seagrass meadows. *Oceanogr. Mar. Biol. Rev.* 34, 109–162.
- Kendrick, G.A., Burt, J.S., 1997. Seasonal changes in epiphytic macro-algae assemblages between offshore exposed and inshore protected *Posidonia sinuosa* Cambridge et Kuo seagrass meadows, Western Australia. *Bot. Mar.* 40, 77–85.
- Kitting, C.L., Fry, B., Morgan, M.D., 1984. Detection of inconspicuous epiphytic algae supporting food webs in seagrass meadows. *Oecologia* 62, 145–149.
- Klumpp, D.W., Salita-Espinosa, J.S., Fortes, M.D., 1992. The role of epiphytic periphyton and macroinvertebrate grazers in the trophic flux of a tropical seagrass community. *Aquat. Bot.* 43, 327–349.
- Mazzella, L., Alberte, R.S., 1986. Light adaptation and the role of autotrophic epiphytes in primary production of the temperate seagrass, *Zostera marina* L. *J. Exp. Mar. Biol. Ecol.* 100, 165–180.
- Mazzella, L., Russo, G., 1989. Grazing effect of two *Gibbula* species (Mollusca, Archaeogastropoda) on the epiphytic community of *Posidonia oceanica* leaves. *Aquat. Bot.* 35, 357–373.
- Mazzella, L., Buia, M.C., Gambi, M.C., Lorenti, M., Russo, G.F., Scipione, M.B., Zupo, V., 1992. Plant–animal trophic relationships in the *Posidonia oceanica* ecosystems of the Mediterranean Sea: a review. In: John, S.J., Hawkins, S.J., Price, J.H. (Eds.), *Plant–Animal Interactions in the Marine Benthos*. Clarendon Press, Oxford, pp. 165–187.
- Morgan, M.D., Kitting, C.L., 1984. Productivity and utilization of the seagrass *Halodule wrightii* and its attached epiphytes. *Limnol. Oceanogr.* 29, 1066–1076.
- Neckles, H.A., Wetzel, R.L., Orth, R.J., 1993. Relative effects of nutrient enrichment and grazing on epiphyte–macrophyte (*Zostera marina* L.) dynamics. *Oecologia* 93, 285–295.
- Nelson, T.A., 1997. Epiphyte–grazer interactions on *Zostera marina* (Anthophyta: Monocotyledones): effects of density on community function. *J. Phycol.* 33, 743–752.
- Novaczek, I., 1987. Periodicity of epiphytes on *Zostera marina* in two embayments of the southern Gulf of St Lawrence. *Can. J. Bot.* 65, 1676–1681.
- Orth, R.J., Van Montfrans, J.V., 1984. Epiphyte–seagrass relationships with an emphasis on the role of micrograzing: a review. *Aquat. Bot.* 18, 43–69.
- Padilla, D.K., 1985. Structural resistance to herbivores: a biomechanical approach. *Mar. Biol.* 90, 103–109.
- Sand-Jensen, K., 1977. Effects of epiphytes on eelgrass photosynthesis. *Aquat. Bot.* 3, 55–63.
- Schneider, F.I., Mann, K.H., 1991. Species-specific relationships of invertebrates to vegetation in a seagrass bed. II. Experiments on the importance of macrophyte shape, epiphyte cover and predation. *J. Exp. Mar. Biol. Ecol.* 145, 119–139.
- Scherrer, B., 1984. In: G. Morin (Ed.), *Biostatistique*. Qué, Canada.
- Shepherd, S.A., McComb, A.J., Bulthuis, D.A., Neverauskas, V., Steffensen, D.A., West, R., 1989. Declines of seagrasses. In: *Biology of Seagrasses: A Treatise on the Biology of Seagrasses with Special References to the Australian Region*. Elsevier, Amsterdam, pp. 346–393.
- Short, F., Wyllie-Echeverria, S., 1996. Natural and human-induced disturbance of seagrasses. *Environ. Conserv.* 23, 17–27.
- Underwood, A.J., 1999. *Experiments in Ecology: their Logical Design and Interpretation using Analysis of Variance*. Cambridge University Press, United Kingdom.

- Van Montfrans, J.V., Orth, R.J., Vay, S.A., 1982. Preliminary studies of grazing by *Bittium varium* on eelgrass periphyton. Aquat. Bot. 14, 75–89.
- Van Montfrans, J., Wetzel, R.L., Orth, R.J., 1984. Epiphyte–grazer relationships in seagrass meadows: consequences for seagrass growth and production. Estuaries 7, 289–309.
- Wetzel, R.L., Neckles, H.A., 1986. A model of *Zostera marina* photosynthesis and growth, simulated effects of selected physical–chemical variables and biological interactions. Aquat. Bot. 26, 307–323.