

1 Running head: Positive effects of mesograzers on epiphytes

2 **Positive effects of mesograzers on epiphytes in an eelgrass system**

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26 ABSTRACT

27 Traditionally, consumer-prey interactions have been considered as purely negative, but
28 herbivores may have positive effects on plants and their productivity. Grazing may enhance
29 prey biomass-specific productivity via directly or indirectly reducing the competition for
30 light, nutrients, and space. We studied the effect of four common mesograzers, the isopod
31 *Idotea baltica*, the amphipod *Gammarus oceanicus*, and the gastropods *Littorina littorea* and
32 *Rissoa membranacea* on epiphytes in an eelgrass (*Zostera marina* L.) system. Eelgrass was
33 grown in laboratory mesocosms for a set of experiments manipulating mesograzer species
34 identity, mesograzer density and nutrient concentration. We measured epiphyte biomass-
35 specific productivity via incorporation of radioactive carbon. Herbivore effects on epiphyte
36 photosynthetic capacity were strongly positive for *Rissoa*, moderately positive for *Littorina*
37 and *Idotea* and zero for *Gammarus* under low nutrient supply. Both gastropods increased the
38 nitrogen content of epiphytes, especially the small gastropod *Rissoa*, and enhanced epiphyte
39 growth. The crustacean species did not increase epiphyte nutrient content, but *Idotea* probably
40 enhanced epiphyte productivity by removing the overstory of algal cells, and thus reducing
41 competition for light, nutrients, and space. The positive effect of the two gastropod species
42 disappeared under higher nutrient supply implying the importance of nutrient limitation for
43 this interaction. The positive effect of *Idotea* remained at moderate grazer densities despite
44 the higher nutrient concentrations.

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50 KEYWORDS: mutualism, grazing, periphyton, herbivores, *Littorina*, *Idotea*, *Gammarus*,
51 *Rissoa*, nutrients

INTRODUCTION

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53 Predation, competition, physical disturbances and physiological stress have been
54 demonstrated to strongly influence the structure of marine ecosystems through negative
55 interactions with community components (Bertness et al. 2001). However, recent research
56 suggests that positive interactions play a more important role in organizing communities than
57 previously assumed, and should be explicitly included in ecological theory (Bruno et al. 2003,
58 Hay et al. 2004, Bulleri et al. 2008, Gross 2008). Facilitation in aquatic systems includes
59 symbiotic relationships as between corals and zooxanthellae, which provide the structure for
60 one of the most diverse ecosystems worldwide, foundation species like seagrasses or kelp,
61 which create three-dimensional structure in an otherwise monotonous environment, and the
62 so-called “dangerous liaisons”, i.e. consumer-prey interactions and parasite-host mutualism
63 (Hay et al. 2004).

64 Negative interactions which become positive in a community context are found in many
65 consumer-prey interactions. Herbivorous chitons feed on encrusting coralline algae, which are
66 resistant to most grazers. When the chitons are experimentally removed, the coralline algae
67 are overgrown by epiphytic algae that attract parrotfish. These feed on epiphytes and the
68 coralline host algae causing far more damage to the coralline algae than the chitons (Littler et
69 al. 1995). Territorial herbivorous damsel fish, which aggressively defend their algal mats,
70 create patches of intermediate grazing intensity in coral reefs where algal species richness and
71 evenness are increased compared to adjacent areas. The presence of this fish species also
72 enhances algal productivity, although the mechanisms that cause this effect remain unclear
73 (Hixon & Brostoff 1996, Ceccarelli et al. 2001).

74 The stimulation of seagrass productivity by herbivory is another positive effect of consumer-
75 prey interactions. Valentine et al. (1997) found that sea urchin grazing caused a 40% increase
76 in the productivity of subtropical turtle grass. The sea urchins removed large parts of the

77 seagrass biomass, but the simultaneous enhancement of productivity compensated this loss.
78 Despite the strong grazing pressure there was no significant reduction of seagrass biomass.
79 Nacken and Reise (2000) even proposed that autumnal herbivory by brent geese and wigeon
80 is essential to the survival of dwarf eelgrass. A field enclosure experiment showed that
81 grazing caused a 45% reduction of biomass including rhizomes, which are important storage
82 organs. In the next vegetation period, however, the grazed sites had a significantly higher
83 growth rate compared to former enclosure sites.

84 Small consumers (mesograzers) such as amphipods, isopods, and gastropods increase seagrass
85 growth by removing the epiphytes from its surface (Hughes et al. 2004). The resulting
86 reduction in competition for light and nutrients can increase seagrass productivity, but the
87 effect of mesograzers is species-specific (Duffy et al. 2001, Jaschinski & Sommer 2008).
88 Overgrazing of eelgrass meadows by mesograzers is known, but is believed to be a rare
89 incident occurring only under high mesograzer densities (Fredriksen et al. 2004). Seagrasses
90 provide mesograzers with food (epiphytes), a structure to live on, and a refuge from
91 predation. The strong positive interactions between mesograzers and seagrasses are supposed
92 to be fundamental for the health and continued existence of these ecologically and
93 economically important ecosystems.

94 In addition to this mutualism, mesograzers may increase the photosynthetic capacity
95 (production per biomass) of their prey the algal assemblage growing on seagrasses or other
96 substrates. The increase in the photosynthetic capacity of periphyton by small invertebrate
97 grazers is thought to be caused by two mechanisms. First, the removal of the overstory of
98 cells and the destruction of the boundary layer that impedes nutrient diffusion reduce the
99 competition for space, light and nutrients and are likely to boost the biomass-specific
100 productivity of the algae (McCormick & Stevenson 1991). Second, sloppy feeding and
101 excretory products of grazers may directly increase the availability of nutrients (Grimm 1988,
102 Mulholland et al. 1991, Kahlert & Baunsgaard 1999). Some experiments have shown a

103 positive effect of grazers on periphyton nutrient content (Hunter & Russel-Hunter 1983,
104 Rosemond 1993, Hillebrand & Kahlert 2001, Hillebrand et al. 2004) but only one study has
105 directly measured the photosynthetic capacity of a marine epilithic community (Kaehler &
106 Froneman 2002). The enhanced epilithion productivity observed by Kaehler & Froneman
107 (2002) was not caused by the mechanisms described above, however, but via a change in
108 community composition. The remaining algae assemblage was composed of very productive
109 species.

110 We manipulated the abundance of four mesograzers in experimental eelgrass systems to test
111 their effect on epiphyte nutrient content and photosynthetic capacity. The isopod *Idotea*
112 *baltica* (hereafter *Idotea*), the amphipod *Gammarus oceanicus* (hereafter *Gammarus*), and the
113 two gastropod species *Littorina littorea* (hereafter *Littorina*) and *Rissoa membranacea*
114 (hereafter *Rissoa*) are potentially dominant grazers in eelgrass systems. All four mesograzer
115 species are known to graze on epiphytes, but they have different feeding modes (crustaceans
116 = ‘lawn-mower’, gastropods = ‘bulldozer’ Sommer 1999a) and vary in their selectivity.
117 Seasonal abundance patterns differ strongly for the studied species (unpublished data),
118 implying that their impact on epiphytes also varies in the course of the year. Additionally, we
119 varied nutrient supply to determine, if the hypothesized positive impacts of mesograzers on
120 epiphytes would persist under eutrophic conditions.

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MATERIAL AND METHODS

123 **Experimental design.** We conducted seven mesocosm experiments to test the impact of four
124 common mesograzer species on the nutrient content and photosynthetic capacity of epiphytes
125 in an eelgrass system under ambient and high nutrient supply. The experiments took place in
126 summer 2002 one after the other from June to September. A preliminary field study had
127 shown that the qualitative and quantitative composition of epiphytes is relatively constant
128 during this period. Each experiment included four treatments: a grazer-free control and low,

129 moderate and high abundances of one grazer species (Table 1). Experimental aquaria were
130 divided into four compartments each, and treatments were assigned to compartments
131 according to a randomized block design. There were six aquaria, such that there were six
132 independent replicates of each experimental treatment. Mesograzer abundances were chosen
133 based on species-specific numerical densities per square meter in summer according to
134 monitoring data for eelgrass associated macrofauna in the Kiel Bight (4 stations, 1997-2001).
135 The average of all stations and years was used as moderate density for the four consumer
136 species. Half of this abundance represented the low density treatment and we doubled the
137 average in the high density treatment.

138 The experiments took place in a constant temperature chamber. The six replicate aquaria were
139 125 l (50 cm x 50 cm x 50 cm) each, and were divided into four compartments with 1 mm
140 metal mesh, resulting in 24 “mesocosms” of 25 cm x 25 cm x 50 cm. This corresponds to the
141 minimum mesocosm size recommended for experiments with seagrass (Short et al. 2001).
142 Summer conditions found in eelgrass systems in the western Baltic Sea were established
143 concerning light, temperature and nutrients. The aquaria were illuminated by HQI-lamps with
144 a 16 h day and 8 h night cycle. The light intensity was $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ at the water surface.
145 The temperature in the constant temperature chamber was set to 17 °C. However, due to a
146 warming-effect of the lamps the water temperature in the aquaria was slightly higher (18.6 °C
147 ± 0.3). Sand-filtered brackish deep water from the Kiel Fjord (salinity: $14.1 \text{ PSU} \pm 2.2$) was
148 used and additionally filtered with a $0.8 \mu\text{m}$ membrane filter to avoid contamination with
149 plankton species. Nutrient concentrations in the four experiments under ambient nutrient
150 conditions were $5 \mu\text{mol l}^{-1}$ nitrate and $0.25 \mu\text{mol l}^{-1}$ phosphate. In the three experiments under
151 higher nutrient supply the values were three-fold enriched. Silicate levels were high (14.5
152 $\mu\text{mol l}^{-1}$).

153 Continuous water circulation was created using pumps and the water was exchanged (up to
154 90% of the total volume) every day. Periphyton growing on the walls of the aquaria was
155 removed every day before the water exchange.

156 The mesocosms were filled with 1 mm-sieved homogenized sediment (5 cm depth), which
157 consisted mainly of fine sand with low organic content. After 24 h, 20 freshly harvested
158 eelgrass shoots were planted in each mesocosm (320 shoots m⁻², average abundance in the
159 Kiel Fjord in summer). Only shoots with at least four leaves were selected and the average
160 length of shoots was 40 cm. We measured the initial biomass of epiphytes (chl *a*) on 10
161 eelgrass shoots in each experiment. There was no significant difference in initial epiphyte
162 biomass between experiments. On the following day, the mesocosms were stocked with
163 grazers. All experimental material was collected at Falkenstein Beach in the inner Kiel Fjord,
164 Germany (54°21'10"9'). The experiment was terminated after ten days. At this time, the
165 eelgrass was harvested, placed in plastic bags and stored frozen until further processing.

166 A preliminary experiment had shown that the optimal experimental duration was ten days,
167 because overgrazing, cannibalism and reproduction occurred soon after 10 days in the
168 crustacean treatments.

169 **Epiphyte productivity.** Primary productivity estimates, based on ¹⁴C-measurements were
170 carried out on the last day of the experiment. Four eelgrass shoots were randomly selected
171 from each mesocosm and the mid section of each shoot (10 cm) was transferred into a
172 transparent Nalgene plastic bottle containing 250 ml seawater (0,2 µm filtered). Only shoots
173 with four leaves were used. After inoculation with 26.4 µCi ¹⁴C-Na₂CO₃, three hour
174 incubations (between 10.00 and 14.00 h) were carried out under experimental conditions. One
175 bottle out of each mesocosm was wrapped up in aluminium foil and used as dark incubation.
176 After incubation all eelgrass shoots were placed in plastic bags and stored frozen until further
177 processing.

178 We measured water temperature, salinity and pH of the used seawater to calculate available
179 carbon via alkalinity according to Buch (1945). A standard carbon concentration can be used
180 in marine water with an average salinity of 35, but the available carbon must be calculated via
181 alkalinity in brackish and fresh water.

182 Epiphytes were separated from the eelgrass blades by carefully scraping the blades using a
183 plastic scraper and a scalpel and then transferred into small amounts of filtered sea water. This
184 suspension was filtered on pre-weighed 0.2 µm membrane filters (cellulose nitrate, Sartorius).
185 The filters were dried for 48 h at 60 °C and weighted to calculate dry weight. Then the filters
186 were transferred into scintillation vials containing 10 ml Lumagel (Perkins Elmer).
187 Radioactivity was measured in a Liquid Scintillation Counter. All counts were corrected for
188 background and counting efficiency.

189 Productivity was calculated as follows:

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$$191 \quad \text{dpm}_1 * ^{12}\text{CO}_2 * 1.06$$
$$192 \quad \text{mg C (g dry wt)}^{-1} \text{ h}^{-1} = \frac{\text{dpm}_1 * ^{12}\text{CO}_2 * 1.06}{\text{dpm}^2 * \text{wt} * t},$$
$$193 \quad \text{dpm}^2 * \text{wt} * t$$

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195 where dpm_1 is the activity (decay per minute) of the samples minus the activity in the dark
196 incubation as correction for non-photosynthetic uptake of ^{14}C , dpm_2 the activity of the isotope
197 added to the bottles and $^{12}\text{CO}_2$ the mg available inorganic carbon. The factor 1.06 is a
198 correction for isotope discrimination. Wt is the dry weight of the epiphyte sample and t the
199 length of the incubation period in hours (Penhale 1977).

200 **Elemental composition.** Two eelgrass shoots from each mesocosm were washed in filtered
201 seawater to remove detritus and faecal pellets. Observations with a dissecting microscope
202 after the cleaning procedure showed the successful removal of unwanted material. Epiphytes
203 were carefully scraped from the eelgrass blades using a plastic scraper and a scalpel and

204 transferred to small amounts of filtered sea water. This suspension was filtered on
205 precombusted (450 °C, 24 h) Whatmann GF/F filters. After drying (24 h, 60°C) the samples
206 were stored in a desiccator until combustion in a CHN-analyser (Fisons, 1500N) to measure C
207 and N content. The C:N ratios were calculated in molar units.

208 **Chlorophyll *a* and phaeophytin.** We measured the photosynthetic pigment chlorophyll *a* and
209 its degradation product phaeophytin and used the proportion of phaeophytin as a proxy for the
210 proportion of dead and senescent cells in the epiphyte assemblages. Six eelgrass shoots were
211 randomly selected from each mesocosm. Epiphytes were carefully scraped from the eelgrass
212 blades and collected on GF/F filters as described in the previous section. Pigment analyses
213 with HPLC, carried out on scraped eelgrass blades and epiphytes, indicated that removal
214 efficiency by scraping was up to 99%. Chlorophyll *a* and phaeophytin concentrations were
215 calculated according to Lorenzen (1967). The cleaned eelgrass blades were dried to a constant
216 weight for 48 h at 60 °C and subsequently combusted for 8 h at 540 °C to determine the ash-
217 free dry mass (AFDM). The eelgrass surface area was calculated using the formula surface
218 (mm^2) = AFDM (g) x 588.88 ($R^2=0.97$), determined by measuring and weighing 100 eelgrass
219 shoots. All epiphytic chlorophyll *a* and phaeophytin concentrations were normalized to unit
220 eelgrass surface area.

221 **Comparative effects.** To compare the per biomass effect of the four studied grazer species on
222 epiphyte photosynthetic capacity and nitrogen content, grazer effects on epiphytes and
223 eelgrass were calculated as the raw difference between control and grazer treatments with the
224 same biomass level (0.96 mg AFDM m^{-2} , Tab. 1).

225 **Statistics.** We performed one-way ANOVAs to analyse the influence of mesograzer
226 abundance on epiphytes biomass-specific productivity and C:N for each independent
227 experiment. Initially we analysed the data using randomized block ANOVAs, in which the
228 different abundances were considered fixed factors. The block effect was non-significant in

229 all analyses, therefore the block factor was ignored and the data were reanalysed with a one-
230 way ANOVA. Differences between treatments were tested with Tukey`s test.
231 We calculated the effect size (Hedges`d) of the mesograzers` impact on epiphyte biomass-
232 specific productivity and C:N ratio for the treatments with the same biomass of mesograzers.
233 This effect measure represents the standardized difference between treatment and control
234 means divided by the combined SD of both treatments (Gurevitch & Hedges 1993).

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236

RESULTS

237 **Epiphyte photosynthetic capacity.** With the exception of *Gammarus*, epiphyte biomass-
238 specific productivity ($\mu\text{g C}\cdot\text{mg DW epiphytes}^{-1}\cdot\text{h}^{-1}$) increased significantly with the presence
239 of grazers (Fig. 1, Table 2). *Rissoa* had the strongest effect on epiphyte biomass-specific
240 productivity; even medium abundances of this species significantly enhanced this parameter
241 and high abundances of this species nearly doubled epiphyte productivity compared to
242 controls. *Idotea* and *Littorina* showed significant effects only in the high abundance
243 treatments. Epiphyte biomass-specific productivity increased by 47% and 80% in the high
244 abundance treatments of *Idotea* and *Littorina*. *Gammarus* had no significant impact on
245 epiphyte photosynthetic capacity.

246 The effect on epiphyte biomass-specific productivity differed substantially among the four
247 grazers when the treatments with the same grazer biomass are compared (Fig. 3A). The
248 magnitude of the effect was approximately equally positive for *Idotea* (Hedges`d = 1.2) and
249 *Littorina* (d = 1.0). *Rissoa* had the highest positive effect on epiphyte biomass-specific
250 productivity (d = 5.5) and *Gammarus* had no effect at all (d = -0.1, not significantly different
251 from zero).

252 **Epiphyte C:N.** Initial values of epiphyte C:N ratio ranged from 12.1 to 12.5 indicating a
253 deficiency of nitrogen in summer. Epiphyte C:N values from 7.5 to 8.9 were observed under
254 higher nutrient conditions in spring and autumn (unpubl. data). In the experiments with *Idotea*

255 and *Gammarus*, the initial values remained basically unchanged. In contrast, *Littorina* and
256 *Rissoa* had a significant positive effect on the nitrogen content of epiphytes (Fig. 2, Table 2).
257 *Rissoa* reduced the C:N ratio most strongly ($d = -11.8$) in the treatments with the same grazer
258 biomass, whereas the impact of *Littorina* ($d = -1.4$) was one order of magnitude smaller (Fig.
259 3B). *Gammarus* and *Idotea* exerted no significant effect on the C:N ratio ($d = 0.1$, not
260 significantly different from zero).

261 **Dead and senescent algal cells.** The proportion of phaeophytin was not significantly
262 different in grazer treatments and controls in the four experiments. Phaeophytin accounted for
263 17-23% of the algal chlorophyll *a*.

264 **Comparison of positive and negative effects of grazers on epiphyte biomass.**

265 To compare the positive and negative effects of mesograzers on epiphyte biomass we
266 calculated the removal by grazing and the increase caused by indirect grazing effects ($\mu\text{g Chl}$
267 $a \cdot \text{cm}^{-2} \text{eelgrass} \cdot \text{d}^{-1}$), assuming that these processes are constant during the experiment.

268 Positive and negative effects varied between mesograzer species and density (Table 3). The
269 importance of positive effects in comparison to negative effects changed accordingly (Fig. 4).
270 *Rissoa* increased the biomass of epiphytes about 26% compared to the negative impact of this
271 mesograzer at low grazer densities. This percentage decreased to 7% at high densities.

272 *Littorina* caused a smaller percentaged increase ranging from 7% at low density of this grazer
273 to 1% at high density. *Idotea* had an intermediate positive impact (about 13%).

274 **Grazer impact on epiphyte photosynthetic capacity and C:N ratio under high nutrient** 275 **supply.**

276 Epiphyte biomass-specific productivity only increased significantly in the presence of
277 moderate densities of *Idotea* ($P = 0.040$) under high nutrient supply (Fig. 5). Furthermore, we
278 found a significant decrease of epiphyte biomass-specific productivity between the moderate
279 and high density treatment of *Idotea* ($P < 0.001$). The presence of *Littorina* and *Rissoa* had no

280 effect on epiphyte photosynthetic capacity. No grazer species had a significant impact on
281 epiphyte C:N ratio.

282 **DISCUSSION**

283 In contrast to the traditional view according to which the interaction of consumers and their
284 plant prey has been regarded as a unidirectional negative relationship, a growing number of
285 studies emphasize the importance of positive effects of grazing (Sterner 1986, Kahlert &
286 Baunsgaard 1999, Hay et al 2004, Hillebrand et al. 2004). Our study supports the hypotheses
287 that consumers can enhance the biomass-specific productivity of primary producers.

288 Consumer effects on epiphyte biomass-specific productivity were strongly positive for
289 *Rissoa*, moderately positive for *Littorina* and *Idotea* and essentially zero for *Gammarus*.

290 It has previously been assumed that grazers can influence the photosynthetic capacity of
291 biofilms in a positive way by directly or indirectly reducing competition for nutrients
292 (McCormick & Stevenson 1991, Mulholland et al. 1991, Kahlert & Baunsgaard 1999,
293 Hillebrand & Kahlert 2001). Marine herbivores can provide their plant prey with nitrogen by
294 direct excretion of mainly ammonium and by production of faecal pellets. The strong negative
295 impact of *Rissoa* and *Littorina* on epiphyte C:N ratio supports the assumption that, in contrast
296 to the tested crustaceans, gastropods enhanced the photosynthetic capacity of epiphytes via
297 excretory products in our study. Especially in the *Rissoa* treatments, many faecal pellets were
298 observed, which adhered to the epiphyte assemblages. Apparently, this had immediate
299 consequences for the nutrient availability in adjacent algal patches. Epiphytes under *Rissoa*
300 grazing had the strongest increase in nitrogen content compared to ungrazed algal
301 assemblages. Nitrogen is the limiting nutrient in epiphytic assemblages on eelgrass from late
302 spring to autumn (Jaschinski, unpublished data). The use of nutrient ratios to indicate nutritive
303 status of microalgae is commonly used for phytoplankton, but the interpretation of such data
304 for periphyton has to be treated with caution, because detritus and heterotrophic elements

305 could influence the nutrient ratios. However, microscopic observations showed that neither
306 changes in detritus and heterotrophs nor changes in algal composition compromised our data.
307 A positive effect of grazers on nutrient content of microalgae has been previously reported in
308 freshwater systems (Rosemond et al. 1993, Hillebrand et al. 2004, Liess et al. 2006) and one
309 intertidal periphyton community (Hunter & Russell-Hunter 1983). All studies used gastropods
310 including *Littorina* as grazers, which live in close association with their food sources. The
311 more mobile crustacean grazers have the potential to supply a significant amount of nitrogen
312 via ammonium excretion to the plant community (Taylor & Rees 1998), but experimental
313 evidence on the importance of nutrient recycling via grazing so far exists only for slow
314 moving or sessile organisms like gastropods, bryozoans and barnacles (Hurd et al. 1994,
315 Williamson & Rees 1994). In our experiments, sinking faecal pellets of *Idotea* and *Gammarus*
316 may have enriched the microphytobenthos; the nitrogen content of eelgrass was not
317 influenced by the different treatments (unpubl. data). Our experimental design did not allow
318 testing for potential ammonium enrichment in the water. However, the dispersal and dilution
319 of waste products is thought to restrict the importance of this mechanism in free-swimming
320 mesograzers (Probyn & Chapman 1983).

321 Gastropod and crustacean mesograzers differ in their feeding mode. *Idotea* and *Gammarus*
322 are generally considered to reduce the microalgal community homogenously (“lawn-mower”
323 type of grazer), whereas *Littorina* and *Rissoa* produce a feeding trail by scraping the surface
324 with their radula (“bulldozer” type of grazer, Sommer 1999). The taenioglossan radula of the
325 studied gastropods enables these species to completely remove the epiphytic layer on
326 eelgrass leaves (van Montfrans et al. 1982). These differences influence the mesograzer
327 impact on epiphyte photosynthetic capacity.

328 The difference in the impact on epiphyte biomass-specific productivity between *Idotea*
329 (positive effect) and *Gammarus* (no effect) strengthens the conjecture that the removal of the
330 biofilm’s canopy layer, and thus a reduction of competition for light and space, also played

331 an important role in the enhancement of the photosynthetic capacity of epiphytes by
332 mesograzers. The different selectivity of these mesograzers influences their effect on epiphyte
333 community composition and structure. Epiphyte composition was clearly dominated by
334 diatoms, which constituted 74 to 99% of epiphyte biovolume, but small filamentous algae –
335 mostly the red alga *Acrochaetium secundatum* and the brown alga *Myrionema sp.* - were also
336 present. The diatoms showed a high level of differentiation in growth form and cell size. The
337 most important prostrate diatom species was the strongly adhering *Cocconeis scutellum*,
338 stalked forms mainly consisted of *Licmophora* species, the only tube-living diatom was
339 *Berkeleya rutilans* and diatom chains were represented by *Melosira nummuloides* and
340 *Grammatophora marina*. *Idotea* fed on diatom chains, filamentous algae, and stalked
341 diatoms; whereas *Gammarus* is only capable of removing some of the filamentous growth
342 forms (Jaschinski et al. sub.). The stronger impact of *Idotea* on the structure of the algal
343 assemblage might have mediated the availability of light and space to the epiphyte
344 community. Self-shading can reduce primary production in lower layers in ungrazed
345 periphyton communities, and thus decrease the photosynthetic capacity of the assemblage
346 (Brush 2002).

347 The removal of senescent or dead algal cells does not seem to be important for the positive
348 effect of grazing on epiphyte photosynthetic capacity. The proportion of phaeophytin, the
349 degradation product of chlorophyll *a*, was not significantly different in consumer and control
350 treatments. Phaeophytin accounted for 17-23% of epiphyte chlorophyll *a*. Lamberti and Resh
351 (1983) found similar values for stream periphyton under caddisfly grazing. This consumer
352 likewise fed indiscriminately with respect to living versus dead algae.

353 Several freshwater studies reported an increase of periphyton photosynthetic capacity
354 mediated by consumers (Lamberti & Resh 1983, Lamberti et al 1987, Steward 1987, Hill &
355 Harvey 1990), but two experiments found a reduction of chlorophyll-specific productivity.
356 The consumers had created a community dominated mainly by grazing- resistant species,

357 which as a trade-off had relatively low growth rates (Rosemond et al. 1983, Hill et al. 1992).
358 We found a similar trend for *Idotea* grazing in the experiment with higher nutrient supply.
359 High abundances of *Idotea* reduced epiphyte photosynthetic capacity, probably via
360 preferentially feeding on the fast-growing chain-forming diatom *Melosira nummuloides*,
361 which profited most from nutrient enrichment. This change in epiphyte composition via
362 grazing had a negative effect on the photosynthetic capacity of the algal community.
363 We clearly showed an enhancement of epiphyte productivity via grazing, but the positive
364 effects did not compensate for the consumptive losses, i.e., the presence of mesograzers did
365 not increase epiphyte biomass (Jaschinski & Sommer 2008). Nevertheless, estimations of
366 positive and negative grazing effects on epiphyte biomass showed that the promotion of
367 epiphyte productivity can counterbalance up to 26% of biomass losses (*Rissoa*). *Idotea*
368 increased epiphyte biomass about 13% compared to negative effects and *Littorina* produced
369 the smallest positive effect (mean 4%). Although these data should be treated with caution,
370 our results imply that beneficial effects of mesograzers may play a relevant role in optimizing
371 plant productivity as models predict. Thus, the effect of mesograzers on epiphytes can be
372 considered at least partly mutualistic (De Mazancourt et al. 1998). The importance of this
373 interaction, however, depends on the nutrient supply of the community. The positive effect of
374 the gastropods on epiphyte nitrogen content and accordingly epiphyte productivity found
375 under relatively low nutrient conditions disappeared with higher nutrient supply. This is in
376 good accordance with a model showing that the positive effect of herbivores depends on the
377 strength of plant nutrient limitation (De Mazancourt et al. 1998). *Idotea* enhanced epiphyte
378 photosynthetic capacity at moderate densities despite the nutrient enrichment implying that
379 the supposed removal of the overstory of cells, and thus the increased light intensities
380 reaching deeper layers, may be of importance even in more eutrophic systems.
381 In conclusion, the positive interactions between mesograzers and their periphyton prey
382 depend on consumer identity, grazing pressure and environmental conditions. Recent studies

383 found that species-level characteristics of mesograzers had important effects in seagrass
384 systems (Duffy et al. 2001, Jaschinski & Sommer 2008). Our study showed that functional
385 diversity of mesograzers is also an issue concerning the potential positive effects on epiphyte
386 productivity with possible consequences for the functioning of ecosystems as the dominance
387 of grazer changes with season and location. Higher nutrient supply via direct or indirect
388 consumer effects seems to be more important in nutrient poor conditions, the reduction of
389 competition for space and/or light may additionally enhance the productivity under higher
390 nutrient supply, when nutrients are not limiting.

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398 /20). We declare that our experiments comply with the current laws of Germany.

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508 Table 1. Grazer abundances in all experiments. *Gammarus*, *Idotea* and *Littorina* were about
509 10 mm long, *Rissoa* 6 mm. Treatments with the same biomass are shown in bold.

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Grazer abundances	Density (m ⁻²)			Biomass (g AFDM*m ⁻²)		
	low	moderate	high	low	moderate	high
<i>Gammarus</i>	80	160	320	0.24	0.48	0.96
<i>Idotea</i>	128	256	512	0.48	0.96	1.92
<i>Littorina</i>	64	128	256	0.96	1.92	3.84
<i>Rissoa</i>	320	640	1280	0.24	0.48	0.96

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528 Table 2. Results of the ANOVAs of mesograzer impact on epiphyte photosynthetic capacity
 529 and C:N. Significant effects on epiphyte photosynthetic capacity were always positive, the
 530 significant effects on C:N always decreased this ratio because of increasing nitrogen
 531 concentrations.

Grazer	Density	Epiphyte productivity (P-level)			Epiphyte C:N (P-level)		
		control	low	moderate	control	low	moderate
<i>Gammarus</i>	low	0.773			0.990		
	moderate	0.941	0.978		0.981	0.999	
	high	0.993	0.898	0.991	0.982	0.999	0.999
<i>Idotea</i>	low	0.646			0.978		
	moderate	0.150	0.724		0.995	0.999	
	high	0.002	0.020	0.159	0.938	0.999	0.986
<i>Littorina</i>	low	0.154			0.032		
	moderate	0.131	0.999		0.048	0.997	
	high	< 0.001	0.025	0.030	< 0.001	< 0.001	< 0.001
<i>Rissoa</i>	low	0.088			< 0.001		
	moderate	< 0.001	0.042		< 0.001	0.335	
	high	< 0.001	< 0.001	0.044	< 0.001	< 0.001	< 0.001

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545 Table 3 Effects of mesograzers on epiphyte biomass ($\mu\text{g Chl a}\cdot\text{cm}^{-2}$ eelgrass $\cdot\text{d}^{-1}$). Shown are
 546 the removal of biomass via grazing (negative effect) and the increase of biomass caused by
 547 indirect grazing effects (positive effect).

Grazer	Density	Positive effect	Negative effect
<i>Idotea</i>	low	0.0008	0.0057
	moderate	0.0009	0.0096
	high	0.0016	0.0104
<i>Littorina</i>	low	0.0007	0.0107
	moderate	0.0005	0.0163
	high	0.0003	0.0216
<i>Rissoa</i>	low	0.0011	0.0042
	moderate	0.0012	0.0119
	high	0.0011	0.0151

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565 Figure legends

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567 Fig. 1. Impact of grazer abundance on epiphyte biomass-specific productivity (mean and
568 standard deviation) under low nutrient conditions. Capital letters indicate significant
569 differences between treatments.

570

571 Fig. 2. Impact of grazer abundance on epiphyte C:N (mean and standard deviation) under low
572 nutrient conditions. Capital letters indicate significant difference between treatments.

573

574 Fig. 3. Per biomass effects of grazer species on epiphyte biomass-specific productivity (A)
575 and epiphyte C:N (B). Shown are the raw, arithmetic differences between grazer treatments
576 and grazer-free controls corrected for biomass (g AFDM).

577

578 Fig. 4. Increase in epiphyte biomass caused by positive grazing effects shown as percentage
579 of the decrease of epiphyte biomass by grazing (both effects were calculated as $\mu\text{g Chl } a \cdot \text{cm}^{-2}$
580 $\text{eelgrass} \cdot \text{d}^{-1}$).

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582 Fig. 5. Impact of grazer abundance on epiphyte biomass-specific productivity (mean and
583 standard deviation) under high nutrient conditions. Capital letters indicate significant
584 differences between treatments.

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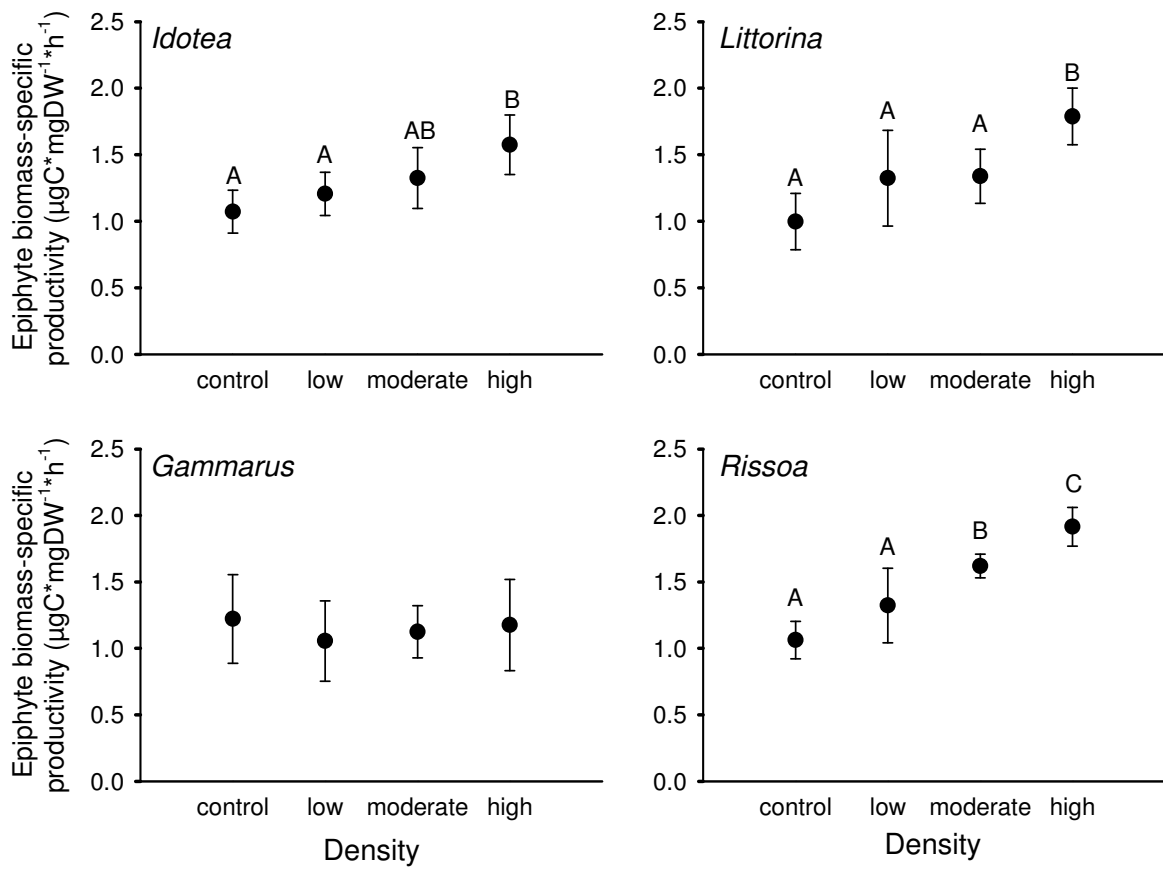
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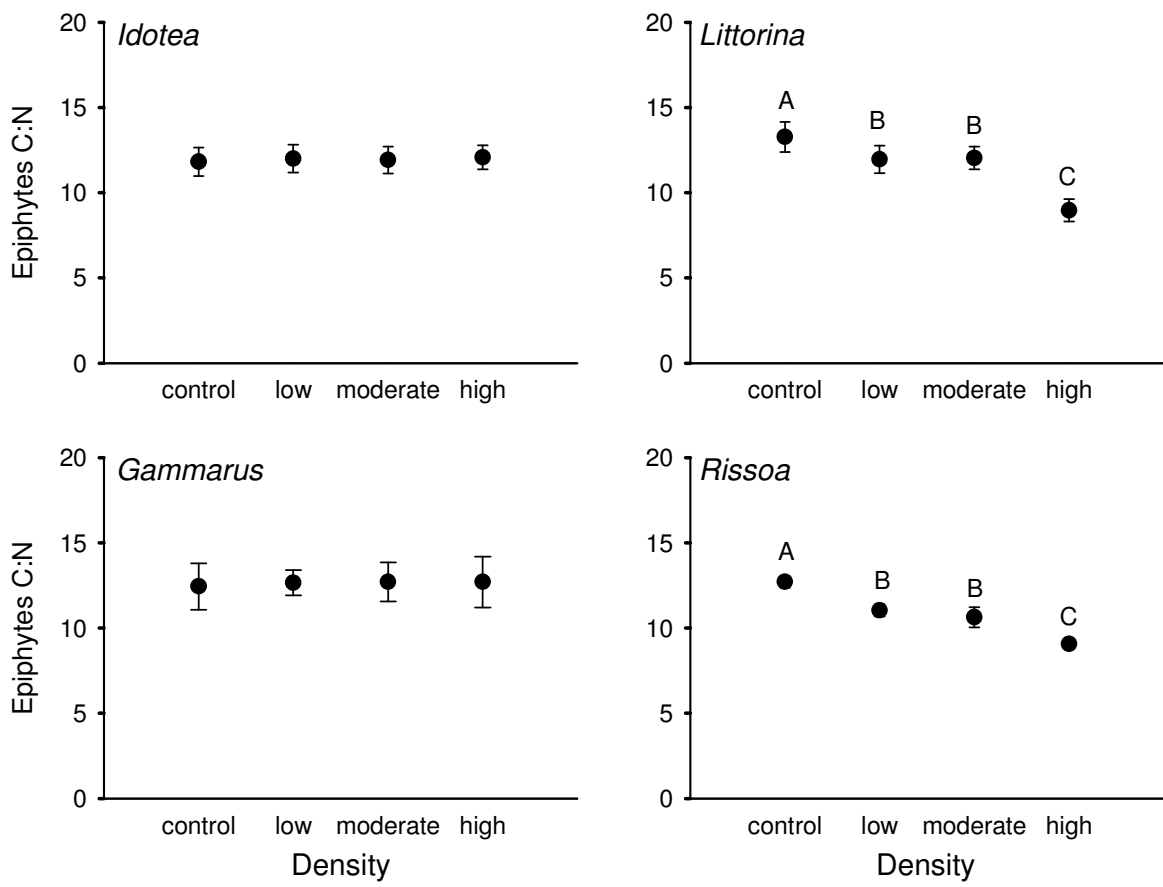
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605 Figure 2



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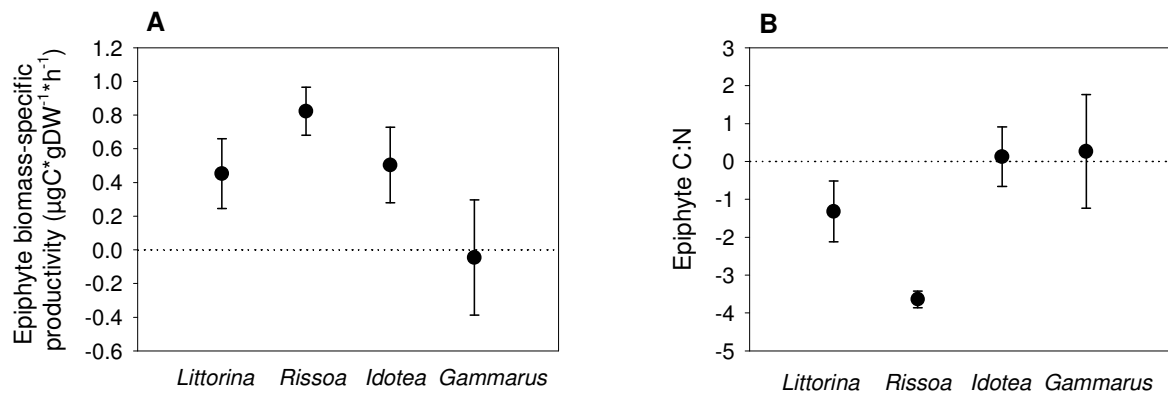
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618 Figure 3



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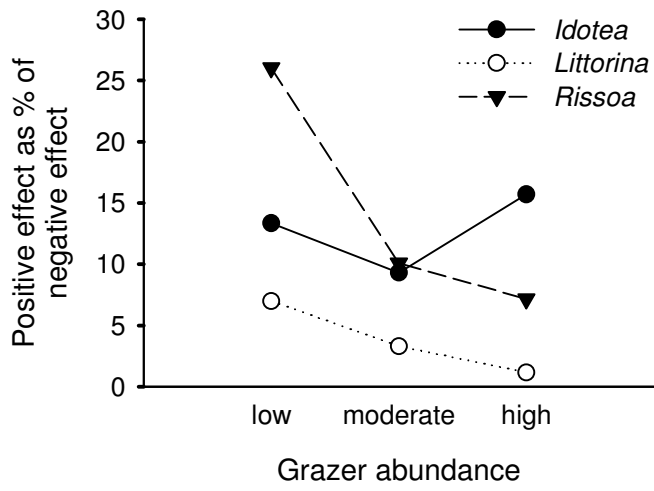
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639 Figure 4



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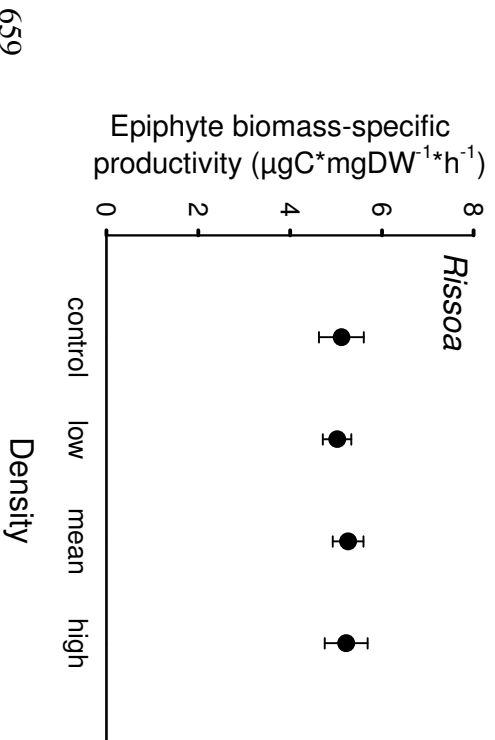
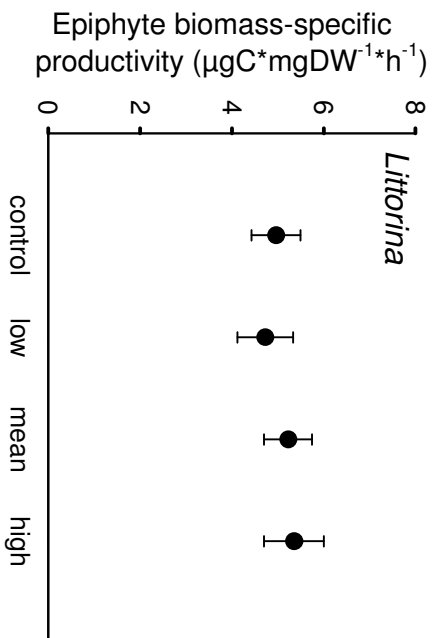
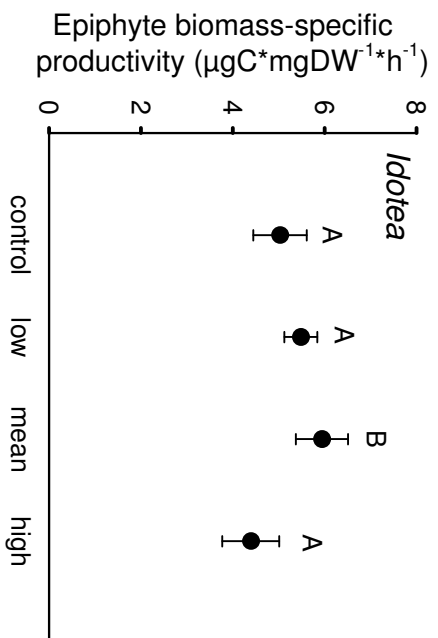
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658 Figure 5



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Density