1 **Grazer diversity effects in an eelgrass-epiphyte-microphytobenthos system**

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22 **Abstract**

23 The dramatic loss of biodiversity and its consequences for ecosystem processes have been of

24 considerable interest in recent ecological studies. However, the complex and interacting

25 processes influencing diversity effects in multitrophic systems are still poorly understood. We

26 used an experimental eelgrass system to study the effects of changing richness of three consumer

27 species on the biomass, diversity and taxonomic composition of both epiphytic and benthic

28 microalgal assemblages. After 1 week, consumer richness enhanced the grazing impact on

29 epiphyte biomass relative to single consumer treatments and a positive effect of consumer

30 richness on prey diversity was found. Moreover, strong effects of consumer species identity on

31 taxonomic composition were found in both microalgal assemblages. However, the effects of

32 consumer richness were not consistent over time. The consequences of high nutrient availability

33 seemed to have masked consumer richness effects.

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Introduction

Numerous studies in terrestrial food webs have shown that the diversity of primary producers can strongly influence ecosystem functioning (see Hooper et al. 2005 for overview). However, the consequences of the loss of consumer diversity have been studied only recently (Jonsson and Malmquist 2000; Duffy et al. 2001, 2005; O'Connor and Crowe 2005; Gamfeldt et al. 2005). Since all natural ecosystems include more than one trophic level and consumer species can exert strong impacts on ecosystem processes and community structure (Duffy 2002), it is important to consider the effects of diversity in multitrophic systems. Furthermore, the fact that species at higher trophic levels seem to be more often subject to extinction than species at lower trophic levels (Jackson et al. 2001; Petchey et al. 2004) underpins the necessity of exploring the consequences of losses in consumer diversity.

Conceptual models predict that changes in consumer diversity and composition can generate a wider range of effects on ecosystem processes than changes in primary producer diversity alone (Thébault and Loreau 2003; Petchey et al. 2004; Fox 2004). Resource availability, food web structure, functional traits of lost species and bidirectional effects can create complex responses of ecosystem processes to changes in diversity in a multitrophic system (Duffy 2002; Worm and Duffy 2003; Hillebrand and Cardinale 2004).

In this study we focus on these questions:

1. How does consumer richness affect total prey biomass?

2. Does consumer richness have a positive influence on prey diversity?

3. Does high nutrient supply affect the impact of grazer richness?

There are two classes of biodiversity effects: the selection and the complementarity effect (Loreau and Hector 2001, Hooper et al. 2005). The selection effect hypothesis postulates that

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67 species with a large impact on prey biomass are more likely to be present with increasing

68 diversity and thus dominate the mixtures. The complementarity effect enhances resource use via

69 niche partitioning and facilitation. Experimental studies addressing the impact of consumer

70 diversity on primary producer biomass are rare in marine systems and the results are ambiguous.

71 Gamfeldt et al. (2005) reported a reduction of microalgae biomass with growing ciliate diversity.

72 No evidence for mesograzer diversity effects were found on algae biomass in rock-pools

73 (Matthiessen et al. 2006), whereas Duffy et al. (2005) documented that mesograzer diversity

74 enhanced epiphyte grazing only in the presence of predators.

75 　　Consumer pressure shows a unimodal relationship with prey diversity (Worm et al. 2002),

76 but the relationship of diversity effects on different trophic levels remains unclear (Hunter and

77 Price 1992; Terborgh 1992). Dyer and Letourneau (2003) reported a positive effect of consumer

78 diversity on prey diversity in an endophytic system as postulated by conceptual models (Dunne et

79 al. 2002; Thébault and Loreau 2003; Petchey et al. 2004), but increasing mesograzer species

80 richness decreased total benthic community diversity in a seagrass system (Duffy et al. 2003).

81 　　The diversity/productivity relationship at the primary producer level has been the topic of

82 much debate in terrestrial ecology for more than 50 years (see Tilman 1999 for review). More

83 recent studies focus on the influence of nutrient availability and productivity on the relationship

84 between consumers and prey diversity (Proulx and Mazumder 1998; Hillebrand 2003).

85 Multivariate models and empirical studies show that these factors have interactive effects on prey

86 diversity (Kondoh 2001; Worm et al. 2002). High nutrient supply, and thus high productivity at

87 the primary producer level, may change the effect of consumer richness in two ways. First,

88 diversity effects may have a small impact in comparison with the availability of resources, as

89 found for plant diversity and production (Huston 1994) and the effect of consumer richness on

90 the decomposition of leaves (Bärlocher and Corkum 2003). Second, niche complementarity and

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91 facilitation may decrease in importance when the food supply is high. We found that high

92 nutrient supply, and thus high epiphyte biomass, reduced the selectivity of grazers (S. Jaschinski

93 unpublished data).

94   Here, we present the results of a mesocosm experiment testing the effect of grazer diversity

95 on epiphyte and microphytobenthos assemblages within a multi-trophic eelgrass system.

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97 **Materials and methods**

98 **The study system**

99 The eelgrass *Zostera marina* is one of the most abundant marine macrophytes in northern

100 temperate regions and it is a structuring species of ecologically and economically important

101 ecosystems. Some of the organisms associated with eelgrass, the so-called mesograzers (mainly

102 small crustaceans and gastropods), play an important role in this system as they remove the

103 epiphytes, and thus enhance eelgrass growth and survival (see Hughes et al. 2004 for overview).

104 Furthermore, they are a crucial link between primary producers and higher trophic levels (Edgar

105 and Shaw 1995).

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107 **Experimental design**

108 We manipulated grazer species richness in 54 indoor mesocosm units (diameter 30 cm; height 60

109 cm), equally distributed in nine tanks (117 x 93 x 60 cm). Each mesocosm was filled with sieved

110 (2 mm) sediment from the field (height 10 cm). Each experimental unit was planted with 20

111 freshly harvested eelgrass shoots (average abundance in the Kiel Fjord in summer, ~350 shoots

112 m^{-2}) and left undisturbed for 4 days. Three common mesograzers, the isopod *Idotea baltica*

113 (*Idotea*, hereafter), the amphipod *Gammarus salinus* (*Gammarus*, hereafter) and the periwinkle

114   *Littorina littorea* (*Littorina*, hereafter), were used as consumers. In addition to the start and the

115   control (no grazer) treatments, three richness levels were used (1, 2, 3, all combinations). Each

116   treatment was replicated in six independent mesocosms in a randomised design. Grazer

117   abundances introduced into the grazer treatments were related to average natural abundances in

118   summer (Gohse-Reimann 2007). The initial grazer biomass was 60 mg ash-free dry mass

119   (AFDM) corresponding to 18 *Idotea*, 24 *Gammarus* or 6 *Littorina* in the single grazer treatments.

120   Mixed-grazer treatments were stocked using a substitutive design whereby the biomass of all

121   grazers was kept constant.

122   The mesocosms were supplied independently with a constant flow of sand-filtered brackish

123   deep water from the Kiel Fjord (salinity 14.7 PSU $\pm$ 0.7). Water flowed out of each tank

124   continuously through a hole, 2 cm in diameter, that was covered with a 1-mm plastic mesh.

125   Nutrients from the inflow to the experimental units were determined on a daily basis by using an

126   auto-sampler (Skalar SAN$^+$ System). Nutrient concentrations of the inflowing water were as

127   follows: nitrate 9.1 μmol l^{-1} $\pm$ 2.7, ammonium 3.7 μmol l^{-1} $\pm$ 1.2, phosphate 0.8 μmol l^{-1} $\pm$ 0.3 and

128   silicate 18.4 μmol l^{-1} $\pm$ 1.2. The nutrient concentrations in the Kiel Fjord were as follows: nitrate

129   1.6 μmol l^{-1}, ammonium 1.3 μmol l^{-1}, phosphate 0.2 μmol l^{-1} and silicate 5.1 μmol l^{-1}. Thus, the

130   experimental nutrient concentrations were about 4 times enriched compared to the field data. The

131   light and temperature regime was adapted to summer conditions with a 16-h day and 8-h night

132   cycle (100 μmol s^{-1} m^{-2}, 18.5ºC).

133   In our experiment, we focused on the microalgae assemblages in the experimental eelgrass-

134   system. Microalgae can be successfully used as model systems to explore the consequences of

135   diversity loss at the consumer level (Gamfeldt et al. 2005; Matthiessen et al. 2006). Results can

136   be obtained over a short period because of the short generation time of the microalgae.

137   Mesocosms have the additional advantage of providing a more natural environment than small-

138   scale experiments.

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140   **Sampling and sample processing**

141   Samples were taken at the beginning (time 0, three control mesocosms), after 7 days (three

142   mesocosms of each treatment) and after 21 days (three mesocosms of each treatment).

143   Microphytobenthos on the sediment surface was sampled according to Aberle and Wiltshire

144   (2006). Subsequently, the sediment samples were preserved with liquid nitrogen by using the

145   cryolander-technique (Wiltshire et al. 1997). The micro-slicing of the sediment surface was

146   carried out according to Wiltshire (2000) and the sediment layers were fixed with Lugol's

147   solution. For the determination of the number of algal cells, their biovolume, and taxonomic

148   composition, the samples were transferred to a Sedgewick Rafter chamber. After settlement the

149   sampled cells were counted under an inverted microscope and converted to biovolume following

150   the methods of Hillebrand et al. (1999).

151   After the sediment samples were taken, all eelgrass shoots were uprooted and transferred to a

152   container with filtered seawater to collect attached grazers. Subsequently, the eelgrass was placed

153   in plastic bags and stored frozen until further processing. Two eelgrass shoots out of each

154   mesocosm were carefully scraped to transfer attached epiphytes to a defined volume of filtered

155   seawater. The samples were fixed with 1% Lugol's iodine and counted under an inverted

156   microscope in 3 ml Utermöhl-chambers. A minimum of 400 cells was counted for dominant

157   species and the whole chamber was counted to account for rare species. Biovolume was used as

158   proxy for biomass.

159   The eelgrass shoots were dried to constant weight for 48 h at 60°C and subsequently

160   combusted for 8 h at 540°C to determine AFDM. The eelgrass surface area was calculated using

161   the formula: surface (mm^2) = AFDM (g) x 588.88 (R^2 = 0.97, $P \leq 0.001$), determined by

162   measuring and weighing 100 eelgrass shoots (Jaschinski and Sommer 2008). Eelgrass leaf

163   production was measured by a variation of the leaf-marking technique: at the beginning of the

164   experiment all the eelgrass shoots were marked with a needle hole 1 cm above the first node with

165   roots. Six shoots from each mesocosm were cut at the marking place and the length and the width

166   of new leaves (without hole) and the growth of old leaves were measured. The production of

167   biomass was calculated as AFDM per day using the formula above.

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169   **Statistics**

170   To test for significant differences between grazer treatments one-way ANOVAs were

171   implemented using the factor grazer composition and the response variables microalgal

172   biovolume and diversity, and eelgrass and secondary production, followed by Newman-Keuls

173   post hoc tests (composition effect). To detect significant grazer species richness effects, planned

174   contrasts comparing the three-grazer treatment against all single-grazer treatments were applied

175   (richness effect).

176   Net biodiversity effects (ΔY) were calculated according to Loreau and Hector (2001) as an

177   additional estimate of diversity effects. ΔY was tested against zero with a two-sided *t*-test. A

178   significant net biodiversity effect shows that the effect in the combinations is higher than

179   expected from the single-grazer treatments. To calculate the expected share of each species in the

180   combinations (*Idotea-Gammarus*, *Idotea-Littorina*, *Gammarus-Littorina*, *Idotea-Gammarus-*

181   *Littorina*), we used the means of the single-grazer treatments (n = 3). The increase in net

182   biodiversity effects from two to three grazer species was tested with a linear regression.

183   Multivariate ANOVAs were used to test the significant impact of grazer treatments on the

184 proportional contribution of algal growth forms to epiphyte and microphytobenthos composition.

185 Data were arcsine square root transformed. The analysis was performed with the Pillai`s trace

186 statistic (PT), recommended for interdependent response variables (Scheiner 1993).

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188 **Results**

189 **Consumer effects on ecosystem processes**

190 After the first 7 days of the experiment, epiphyte biomass detected as biovolume was highest in

191 the control treatment and decreased with consumer species richness (Fig. 1a). Grazer species

192 richness (Table 1) and species identity showed significant effects; *Idotea* and *Gammarus* reduced

193 epiphyte biomass significantly more effectively than *Littorina* ($P \leq 0.001$). Neither grazer species

194 richness nor species identity had significant effects on microphytobenthos biomass (Fig. 1b). The

195 total algal biomass at the sediment surface was generally 1 order of magnitude lower than the

196 epiphyte biomass.

197   Epiphyte species richness and diversity (*H'*, based on the Shannon-Wiener function) were

198 lowest in the control treatment and increased with grazer species richness (Fig. 1c, e). We found

199 significant effects of grazer species richness on epiphyte species richness and diversity (Table 1).

200 The impact of *Littorina* differed significantly from *Idotea* and *Gammarus* as the periwinkle had a

201 less positive effect on epiphyte diversity than the two crustacean species ($P \leq 0.001$), but there

202 was no significant effect of grazer species identity on epiphyte species richness. Epiphyte

203 evenness showed the same trend and was significantly affected by grazer species richness (Table

204 1) and grazer species identity ($P \leq 0.001$). Microphytobenthos taxon richness and diversity

205 provided similar values for the control and the grazer treatments after 7 days (Fig. 1d, f). The

206 diversity increased slightly with increasing grazer richness and *Littorina* had a more negative

207 impact on microphytobenthos diversity than *Gammarus* and *Idotea*, but these differences were

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208   not significant ($P > 0.05$). We found no significant effects on microphytobenthos evenness.

209   After 21 days, the control treatment had the highest epiphyte biomass, but no significant effect of

210   grazer species richness on epiphyte biomass was found (Fig. 2a; Table 1). Species identity

211   significantly affected epiphyte biomass and *Littorina* showed the weakest impact on epiphyte

212   biomass ($P \leq 0.001$). Neither grazer species richness nor species combination was significantly

213   correlated with microphytobenthos biomass (Fig. 2b; Table 1). Epiphyte and microphytobenthos

214   biomass increased in all treatments by as much as 2-20 times compared to the sampling after 7

215   days (Figs. 1, 2).

216   After 21 days, control treatments showed the lowest epiphyte species richness, and grazer

217   richness had no significant impact on epiphyte species richness (Fig 2c, Table 1). The diversity

218   (H') of epiphytes was highest in the single grazer treatments (Fig. 2e), whereas two- and three-

219   grazer treatments were similar to the control treatment. Both crustacean species had a

220   significantly more positive effect on epiphyte diversity than *Littorina* ($P \leq 0.001$). Grazer species

221   richness and combination did not significantly affect microphytobenthos taxon richness (Fig. 2d).

222   However, we found a similar trend for diversity (Fig. 2f) as in the epiphyte assemblages. Overall,

223   epiphyte and microphytobenthos diversity declined in all treatments after 21 days compared to

224   the sampling after 7 days (Figs. 1, 2).

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226   **Net biodiversity effects**

227   Significant net diversity effects of grazer richness were found for epiphyte biovolume and

228   epiphyte diversity after 7 days (Fig. 3). Epiphyte biomass was significantly lower and epiphyte

229   diversity was significantly higher in the combinations (two species and three species,

230   respectively) than the expected values from the single-grazer treatments. We found no significant

231 difference between the effect of the two species and the three species mixtures on net diversity

232 effects.

233

234 **Algal growth forms and taxonomic composition**

235 Both microalgal assemblages were dominated by diatoms at the beginning of the experiment

236 (microphytobenthos, 99%; epiphytes, 80% with 20% small brown algae mostly *Acrochaetium*

237 *secundatum*). The diatoms in the epiphyte community mostly consisted of stalked forms (37%).

238 Prostrate diatoms and diatom chains contributed roughly equal shares (20 and 22%, respectively).

239 Tube-dwelling forms represented 1% of the total algal biovolume. In contrast, the

240 microphytobenthos community was dominated by prostrate forms (over 90%) with only 7%

241 comprising chain forming, and 0.4% stalked diatom genera.

242   After 7 days, a significant impact of the different grazer treatments on epiphyte composition

243 was seen (Fig. 4a; PT = 2.27, F = 1.94, P = 0.012). The effect on microphytobenthos composition

244 was not significant (Fig. 4b; PT = 1.82, F = 1.33, P = 0.16). Significantly different impacts on

245 algal growth forms between all single-grazer treatments were found in the epiphyte assemblage

246 for stalked forms ($P \leq 0.04$) and diatom chains ($P \leq 0.05$). In the microphytobenthos

247 assemblages, *Idotea* had a significant different impact on prostrate ($P \leq 0.02$) and *Littorina* on

248 stalked diatoms ($P \leq 0.04$). The effect on green algae differed significantly between all three

249 grazer species (P = 0.0003).

250   After 21 days, clear composition changes were detected in all treatments and an overall

251 dominance of chain-forming diatoms appeared in both microalgal assemblages (Fig. 4c, d).

252 *Melosira*, present initially in small amounts in the epiphyte assemblages, dominated both

253 communities and made up between 60% and 92% and between 45% and 77% of epiphytes and

254 microphytobenthos, respectively. Macroalgae were almost eliminated in most treatments.

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255 We found a significant impact of the different grazer treatments on epiphyte composition (PT =

256 2.23, $F = 1.9$, $P = 0.016$). The effect on microphytobenthos composition was not significant (PT

257 = 1.45, $F = 0.95$, $P = 0.55$). *Littorina* had a different impact on epiphytes than *Idotea* and

258 *Gammarus*. Significant effects on prostrate ($P \leq 0.015$) and stalked ($P = 0.025$) and chain-

259 forming diatoms ($P \leq 0.005$) were observed. *Gammarus* had a significantly different impact on

260 tube-living diatoms ($P \leq 0.0004$). For the microphytobenthos assemblages, we found no

261 significant differences between the three grazers.

262

263 **Discussion**

264 We found diverse impacts of grazer richness on microalgal biomass, diversity, and taxonomic

265 composition within the experimental seagrass communities. The studied consumers, the isopod

266 *Idotea*, the amphipod *Gammarus*, and the periwinkle *Littorina*, showed a significant impact on

267 biomass and diversity of the epiphytic assemblages only. Strong effects on algal growth forms

268 and taxonomic composition occurred in both microalgal assemblages. The consumer richness

269 effects on epiphyte biomass and species richness were not consistent with time under a high

270 nutrient regime.

271   After 7 days, our results showed that even low consumer richness can affect primary

272 production in an eelgrass community. Epiphyte biomass was significantly reduced with

273 increasing consumer species richness after 7 days. Thus, our results corroborate the findings of

274 recent studies in aquatic foodwebs. Higher diversity of protists had strong negative effects on

275 microalgae biomass (Naeem and Li 1998; Gamfeldt et al. 2005) and higher diversity of snails

276 increased the grazing impact on epiphyton and periphyton in a freshwater macrophyte system

277 (Wojdak 2005).

278   Theoretical framework in the literature has proposed that biodiversity effects on ecosystem

279   processes can be grouped into two classes: the selection and the complementarity effect (Loreau

280   and Hector 2001). The selection effect operates on the higher probability of dominance of species

281   with strong effects, while the complementary effect includes resource partitioning via niche

282   differentiation and facilitation. The diverse impact of the studied consumers on the taxonomic

283   composition of the microalgal assemblages supported the possibility that niche differentiation

284   played a role in our experiment. Facilitation may have been another mechanism that increased the

285   grazing impact. The growth of *Littorina* was significantly higher in the presence of other grazers

286   (Gohse-Reimann 2007).

287   The different qualitative grazing behaviour of co-occurring consumer species (specialists)

288   seems to be fundamentally important to the relationship between consumer diversity and

289   ecosystem function (Chapin et al. 1997; Duffy 2002; Gamfeldt et al. 2005). Consumers with

290   identical feeding behaviour were not found to have a positive diversity–production relationship

291   (Fox 2004). Our findings here of strong species effects on the composition of microalgal

292   assemblages are in good correspondence with recent models (Thébault and Loreau 2003; Fox

293   2004). In these, it is predicted that a high degree of specialisation of consumers is necessary to

294   cause significant effects of consumer diversity on prey biomass.

295   The biomass of the microphytobenthos community was not affected by grazer richness,

296   species identity or combination in this study. Such an insusceptibility of microphytobenthos

297   biomass to grazing impacts by macrofauna organisms is in good agreement with studies

298   conducted by Hillebrand and Kahlert (2002). These authors found that in contrast to epilithic

299   algae, the effect of grazing on the microphytobenthos was negligible. Although grazers like

300   *Idotea*, *Gammarus* and *Littorina* are known to graze on microphytobenthos, their effect is

301   considered less strong than   the impact of very effective microphytobenthos grazers such as

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302 hydrobiid snails and *Corophium* sp. (Gerdol and Hughes 1994). Additionally, the epiphyte

303 biomass was 10-20 times higher than the microphytobenthos biomass, and thus greater

304 availability of epiphytes could have partially neutralized the negative impact of macrofauna

305 grazing on microphytobenthos biomass in our study.

306   In our experiment, high consumer diversity caused increasing epiphyte species richness at

307   first. This positive effect of consumer diversity on prey diversity is in good agreement with

308 theoretical predictions (Dunne et al. 2002; Thébault and Loreau 2003; Petchey et al. 2004) and

309 with results from a field study in an eelgrass bed, where macroalgae diversity was positively

310 related to animal diversity (Parker et al. 2001). A plausible explanation for such top-down

311 diversity effects is the capability of consumers to mediate coexistence of their prey by feeding on

312 the competitive dominant prey species, and thus confining competitive exclusion at the prey level

313 (Paine 1966; Hillebrand 2003; Petchey et al. 2004). Consumer effects show a unimodal

314 relationship with prey diversity, with the highest prey diversity related to "intermediate"

315 mortality (Huston 1979). In our study, the grazing efficiency increased with growing mesograzer

316 richness and this effect had the adequate strength and was directed towards the dominant algae

317 species, such that it positively affected epiphyte diversity. In contrast, Duffy et al. (2003)

318 reported a negative effect of growing mesograzer richness on benthic diversity. The mesograzer

319 abundance in this study was about double compared to our experiment. The strong grazing

320 pressure may have prevented a positive effect. Positive top-down effects of diversity have also

321 been reported in a terrestrial endophytic community, but not in a detrital food web (Dyer and

322 Letourneau 2003). Some authors have argued that the likelihood of top-down effects declines

323 from aquatic to terrestrial and decomposer food webs (Polis and Strong 1996; Shurin et al. 2002).

324 More tests of cascading effects of consumer diversity in different ecosystems and under different

325 consumer pressures and nutrient supplies are necessary to obtain a conclusion which is applicable

326 over.

327   After 3 weeks of incubation, we found a drastic change in our experimental units: the

328 consumer richness effects on epiphyte biomass and species richness disappeared, although the

329 effect of consumer species identity remained constant. An explanation for this change in impact

330 of consumer richness with time is the high nutrient availability. The counteracting processes of

331 herbivore grazing and nutrient enrichment on autotrophic biomass and diversity have received a

332 lot of attention recently (Hillebrand and Kahlert 2002; Hillebrand 2003; Hughes et al. 2004).

333 These studies reported that grazing pressure and nutrient availability can have strong antagonistic

334 effects on prey biomass and diversity. Some studies focus on the influence of nutrient availability

335 and accordingly productivity on the relationship between consumers and prey diversity (Proulx

336 and Mazumder 1998; Hillebrand 2003). Multivariate models and empirical studies show that

337 these factors have interactive effects on prey diversity (Kondoh 2001; Worm et al. 2002).

338 The influence of resource availability on consumer diversity effects has so far only been tested in

339 a freshwater gastropod-macrophyte system (Wojdak 2005). In contrast to our results, the

340 consumer diversity effects were stronger than the nutrient effects and remained constant under

341 high nutrient supply. However, Bärlocher and Corkum (2003) found that nutrient enrichment

342 overwhelms diversity effects in leaf decomposition. This result agrees with Huston (1994) who

343 concluded that the effects of plant diversity are small compared to strong effects nutrient

344 availability.

345   The nutrient concentrations in our experiment were in the range of moderate enrichment

346 reported for estuaries in the case of anthropogenic eutrophication (Valiela 1992). However, the

347 nitrogen and phosphorus concentrations were 4 times higher than the usual summer

348 concentrations in the Kiel Fjord. During the experiment, we found an overall increase in epiphyte

349 and microphytobenthos biomass and a decrease in diversity in both microalgal assemblages. Such

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350 phenomena are usually found in communities under nutrient enrichment (Sundbäck and Snoeijs

351 1991; Hillebrand 2003; Hughes et al. 2004). Furthermore, effects on taxonomic composition were

352 substantial in all treatments: both microalgal assemblages changed into monoculture-like

353 communities consisting mainly of the highly productive filamentous diatom *Melosira*

354 *nummuloides*. This species and its congener, *Melosira moniliformis*, are known for their ability to

355 respond rapidly to nutrient enrichment, especially at high silicate concentrations as in our

356 experiment (Hillebrand et al. 2000). Our results support the hypothesis that nutrient effects –

357 resulting in a high productivity – can neutralize consumer diversity effects.

358 In general, our data supported the hypothesis that in a prey-consumer system higher

359 consumer diversity can lead to a more efficient resource utilisation and consequently, to a

360 stronger control of prey biomass. The importance of species identity and functional traits was

361 emphasized. We showed that diversity at the prey level can be affected by diversity changes at

362 the consumer level. The inconsistency of consumer diversity effects with time revealed the

363 overall importance of collateral factors, e.g. nutrient conditions in a multitrophic system.

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490 Table 1

491 Results of planned contrasts with the fixed factor grazer species richness.

492 Significant results are shown in bold ($P < 0.05$)

Grazer richness effects	7 Days		21 Days	
	F	P	F	P
MPB biovolume	0.62	0.4446	0.2	0.6572
Epiphyte biovolume	**26.04**	**0.0002**	1.32	0.2695
MPB taxon richness	2.21	0.1592	0.33	0.5729
Epiphyte species richness	**11.22**	**0.0048**	0.39	0.542
MPB diversity	0.01	0.9435	**13.89**	**0.0023**
Epiphyte diversity	**27.29**	**0.0001**	**10.59**	**0.0058**
MPB evenness	0.85	0.3728	**14.65**	**0.0018**
Epiphyte evenness	**18.17**	**0.0008**	**11.26**	**0.0047**
Eelgrass growth	0.94	0.3478	0.76	0.398
Secondary production	0.37	0.552	0.003	0.9576

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504   Figure 1: Effects of grazer diversity on ecosystem properties after 7 days of incubation. Filled

505   circles represent means with SE. Single-species treatments and two-species combinations are

506   represented by unfilled symbols (means with SE, n = 3), consumers are identified by first letter of

507   the genus name (I = *Idotea*, G = *Gammarus*, and L = *Littorina*). Lines show significant responses

508   to grazer species richness. Epiphyte biovolume (a), microphytobenthos (MPB) biovolume (b),

509   epiphyte species richness (c), MPB taxon richness (d), epiphyte diversity(e), and MPB diversity

510   (f).

511

512   Figure 2: Effects of grazer diversity on ecosystem properties after 21 days of incubation. Filled

513   circles represent means with SE. Single-species treatments and two-species combinations are

514   represented by unfilled symbols (means with SE, n = 3), consumers are identified by first letter of

515   the genus name (I = *Idotea*, G = *Gammarus*, and L = *Littorina*). Lines show significant responses

516   to grazer species richness. Epiphyte biovolume (a), microphytobenthos (MPB) biovolume (b),

517   epiphyte species richness (c), MPB taxon richness (d), epiphyte diversity (e), and MPB diversity

518   (f).

519

520   Figure 3: Net biodiversity effects for the different grazer combinations after 7 days of incubation.

521   Shown are the significant values with a higher grazer effect in the combinations than expected

522   from the single-grazer treatments (I = *Idotea*, G = *Gammarus*, and L = *Littorina*).

523

524   Figure 4: Effects of grazer richness and combination on algal composition. Shown are the

525   proportional contributions of algal growth forms (n = 3). Epiphyte growth forms after 7 days of

526   incubation (a), microphytobenthos (MPB) growth forms after 7 days of incubation (b), epiphyte

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527   growth forms after 21 days of incubation (c), and MPB growth forms after 21 days of incubation

528   (d). Treatments are identified by first letter of genus name (I = *Idotea*, G = *Gammarus*, L =

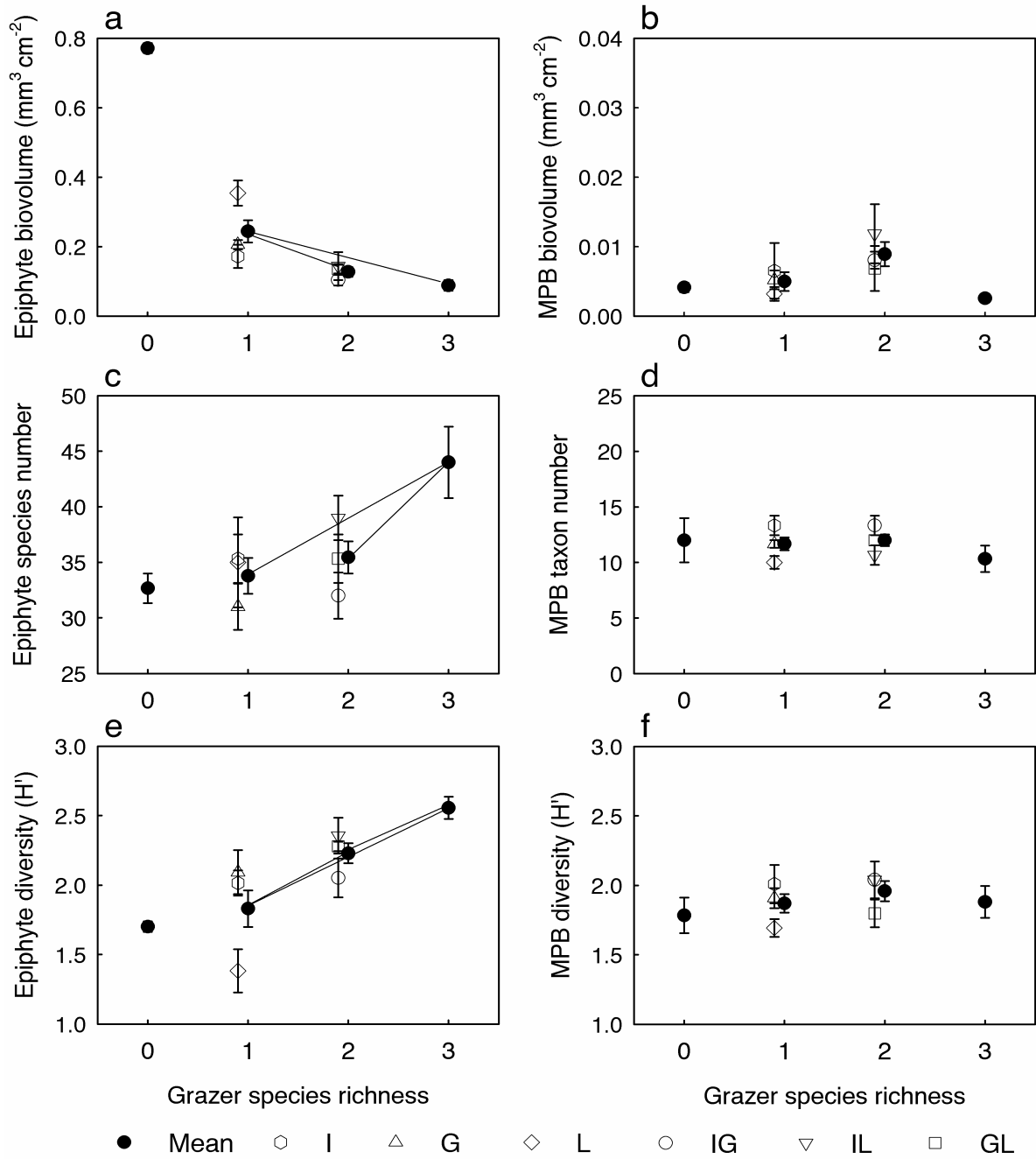529   *Littorina*, and Ctrl = consumer-free controls).
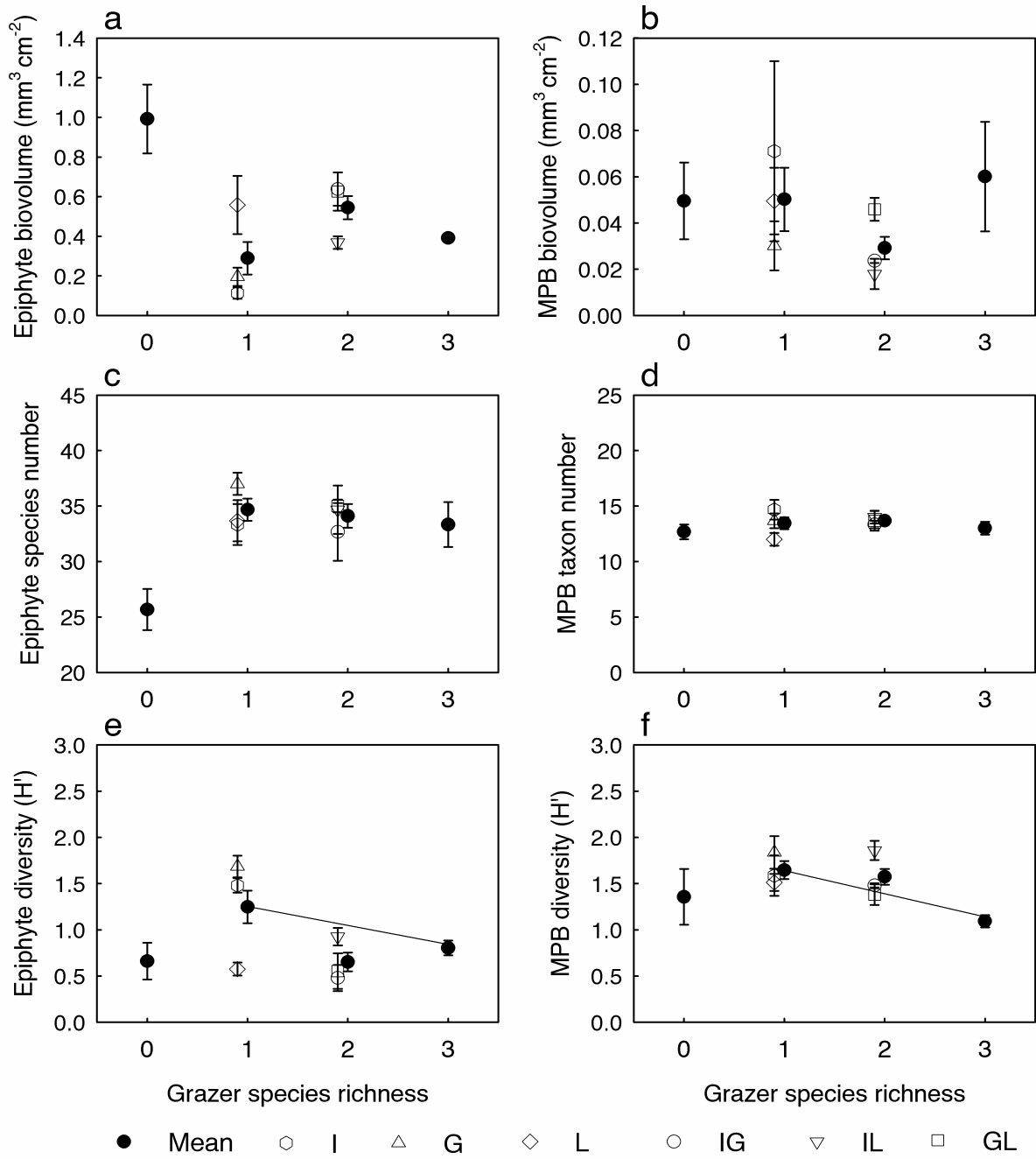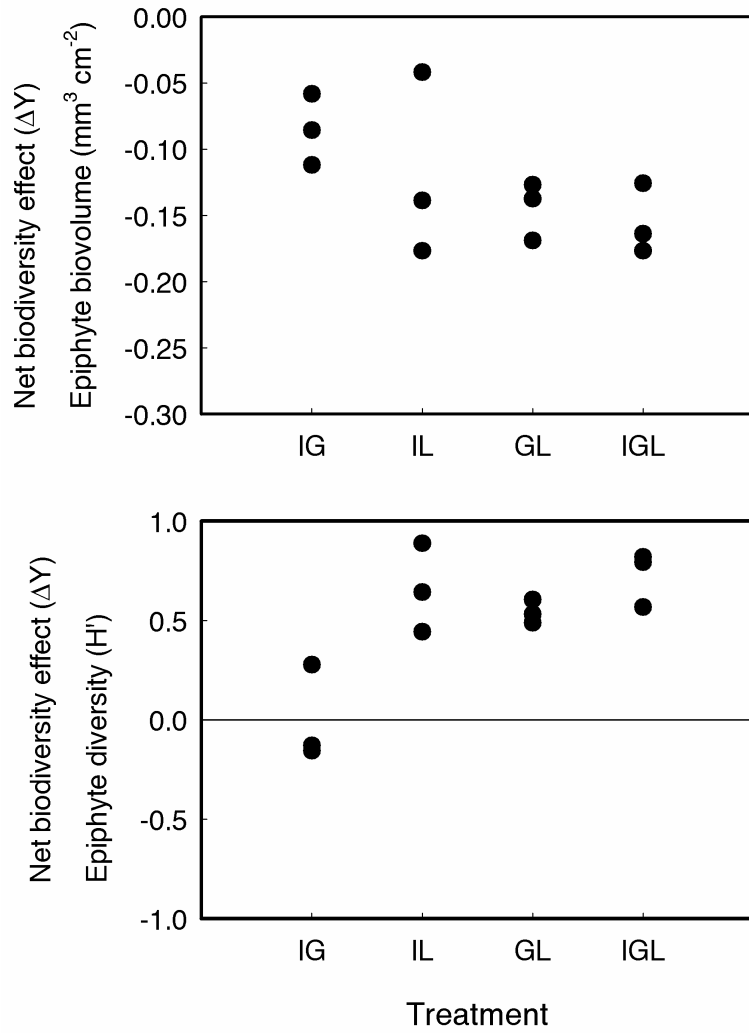
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Fig. 1

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