1 **Simulated green turtle grazing affects benthic infauna abundance and community**

2 **composition but not diversity in a *Thalassia testudinum* seagrass meadow**

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17 **Abstract**

18 Seagrass meadows host diverse invertebrate faunal communities. Infaunal organisms residing in

19 the sediments of meadows play important roles in the functioning of these ecosystems, such as

20 the breakdown of organic matter. Disturbance to the benthic environment through grazing by

21 megaherbivores, such as dugongs (*Dugong dugon*), can reduce infauna abundance within

22 localized areas in a meadow. However, it is not known how removal of the aboveground canopy

23 of a meadow without severe physical disturbance to the benthic habitat, such as through grazing

24 by green turtles (*Chelonia mydas*), affects seagrass meadow infaunal communities. Increasing

25 green turtle abundance will likely lead to greater areas of grazed seagrass with implications for

26 the invertebrate infaunal communities within meadows. We experimentally simulated green

27 turtle grazing for 16 months in a *Thalassia testudinum* seagrass meadow in The Bahamas to test

28 effects of grazing on meadow infaunal communities. Total abundance of the infaunal community

29 was reduced by 59% within six months of simulated grazing and thereafter remained lower

30 throughout the experiment. Six out of eleven individual infaunal groups present (e.g. nematodes)

31 also decreased in abundance following simulated grazing, but temporal abundance dynamics

32 varied among groups. Simulated grazing had no effect on Simpson's Diversity Index of the

33 infaunal community inhabiting the meadow at any point during the 16-month experiment.

34 Though diversity was not affected, relative abundance of individual groups varied over time, and

35 simulated grazing led to a significant change in infaunal community composition. These results

36 demonstrate how green turtle grazing may affect the infaunal communities of shallow seagrass

37 meadows with potential implications for the ecosystem services provided by these important

38 habitats.

39

40   **Key words:** seagrass, invertebrate, infauna, green turtle, *Chelonia mydas*, grazing, benthic

41

42 **1. Introduction**

43   Seagrass ecosystems host abundant and diverse invertebrate infaunal communities

44 (animals inhabiting the benthic environment) (Hemminga and Duarte, 2000; Orth et al., 1984;

45 York et al., 2018). Different infaunal species play many important roles in the functioning of

46 seagrass meadows. Polychaetes act as pollinators for *Thalassia testudinum* seagrass in the

47 Caribbean, suggesting that infauna play a role in the health and longevity of seagrass meadows

48 (van Tussenbroek et al., 2016). Detritivorous species of infauna consume organic matter at the

49 sediment surface and are important for recycling nutrients and organic matter within meadows

50 (Edgar and Shaw, 1995; Hemminga and Duarte, 2000; Klumpp et al., 1989). The infaunal

51 community can also serve as a large source of prey for consumers, including small fishes, within

52 meadows (Hemminga and Duarte, 2000; Virnstein, 1977), thereby transferring energy from the

53 bacterial and detrital pathways to higher order consumers within the meadow food web (Edgar

54 and Shaw, 1995).

55   The role that infauna play in the cycling of organic matter within seagrass meadows is

56 likely to make the infaunal community susceptible to changes in organic matter input to the

57 benthic environment. By removing seagrass and algal biomass, grazers decrease the amount of

58 primary production within a meadow available for incorporation into the benthic detritus. While

59 many small grazers, such as fishes, may not remove large amounts of biomass (Cebrián and

60 Duarte, 1998; Hemminga and Duarte, 2000), megagrazers, such as dugongs (*Dugong dugon*) and

61 green turtles (*Chelonia mydas*), consume large amounts of seagrass (Scott et al., 2018; Thayer et

62 al., 1984; Williams, 1988) and are likely to have a greater effect on the amount of seagrass and

63 algal material entering the detrital pathway. Dugongs create "feeding trails" within meadows in

64 which they consume both above- and belowground seagrass plant material (Preen, 1995). The

65   large physical disturbance to the benthic environment caused by this feeding strategy decreases

66   the abundance of infauna within these trails relative to the surrounding seagrass habitat (Skilleter

67   et al., 2007). Green turtles typically exhibit a different foraging strategy from that of dugongs,

68   however, with a notable exception in Indonesia where an unusually high density of turtles within

69   a protected area led to individuals digging for and consuming belowground seagrass rhizomes

70   (Christianen et al., 2014). Under normal grazing conditions in areas such as the Caribbean, green

71   turtles only consume the aboveground portions of seagrass, cropping blades to a short height

72   above the sediment surface (Bjorndal, 1980). Green turtles repeatedly re-graze the same areas,

73   creating distinct "grazing patches" which may remain in a grazed state for months or years

74   (Bjorndal, 1980; Fourqurean et al., 2010; Hernández and van Tussenbroek, 2014). When

75   cropping only aboveground seagrass blades, green turtles alter the amount of seagrass biomass in

76   a meadow without creating direct physical disturbance to the benthic environment such as

77   dugongs do within their feeding trails.

78   Successful long-term conservation efforts have led to increasing green turtle abundance

79   in many areas (Mazaris et al., 2017), including the Caribbean (Chaloupka et al., 2008; USFWS

80   and NOAA, 2016). Greater numbers of green turtles will lead to higher grazing pressure and

81   more seagrass area being returned to a natural grazed state. Effects of green turtle grazing on the

82   infaunal communities of seagrass meadows are not well understood, however. Changes to the

83   seagrass infaunal community are likely to have effects not only on the amount of infauna

84   available as a source of prey for consumers, but also on detrital matter consumption and the

85   recycling of nutrients and organic matter within meadows. It is therefore critical to understand

86   what effects grazing has on infaunal communities to better understand how seagrass meadow

87   functioning may be affected by increasing green turtle abundance and grazing.

88   Seagrass meadows host significantly higher densities of infauna compared to unvegetated

89   sediments (Orth et al., 1984), with higher infauna densities found in meadows with greater

90   seagrass biomass (Skilleter et al., 2007; Stoner, 1980; Stoner and Lewis, 1985). As green turtle

91   grazing directly reduces seagrass biomass, we predicted that grazing would lead to a decrease in

92   infauna abundance. We further predicted that grazing would decrease infaunal diversity and lead

93   to differences in the composition of the infaunal community within grazed areas, similar to

94   changes observed following dugong grazing (Skilleter et al., 2007). To test our predictions, we

95   analyzed infauna collections made during a long-term clipping experiment (16 months) in a

96   *Thalassia testudinum* seagrass meadow in The Bahamas to simulate green turtle grazing (Moran

97   and Bjorndal, 2007, 2005). We characterized the infaunal community and aspects of the seagrass

98   meadow in both experimentally clipped and unclipped reference plots prior to clipping initiation

99   and throughout the 16-month simulated grazing experiment to evaluate changes in abundance,

100   diversity, and community composition.

101

102   **2. Methods**

103   *2.1 Site description and experimental design*

104   This study took place at the Perry Institute for Marine Science's Caribbean Marine

105   Research Center on Lee Stocking Island, Exuma, The Bahamas (23.772963, -76.106910) from

106   July 1999 to November 2000. The experiment was conducted in a large, monospecific *Thalassia*

107   *testudinum* seagrass meadow 400 m to the southwest of the island. Water depth was ~3 m at low

108   tide with a tidal range of ~1.5 m. Mean shoot density was moderate within the meadow (589 ±

109   16.5 (SE) shoots m^{-2}), and mean canopy height of the meadow was 12.4 ± 0.5 (SE) cm at the

110   beginning of the study. The substrate was composed of sandy carbonate sediments within the

111   study area.

112   Thirty 3 x 3 m plots were established in the *T. testudinum* seagrass meadow to the

113   southwest of Lee Stocking Island in a blocked design. Three blocks of ten plots each were

114   established roughly 50 m apart, with each block consisting of five plot pairs. Each pair of plots

115   consisted of one experimentally clipped plot to simulate green turtle grazing, and one plot that

116   was left unclipped to serve as an ungrazed reference. All plots were spaced 4 m apart within

117   blocks. Simulated grazing was initiated in clipped plots by clipping all seagrass blades at the

118   blade-sheath junction (~2 cm above the sediment surface) with stainless steel scissors to mimic

119   natural green turtle grazing (Bjorndal, 1980; Moran and Bjorndal, 2005). All blades within

120   experimentally clipped plots were re-clipped every time mean blade length in the plot reached 5

121   cm, consistent with natural green turtle grazing behavior in the Caribbean region (Bjorndal,

122   1980; Ogden, 1980). Intervals between clipping events varied between 12 and 37 days, as blade

123   growth varies with temperature (Moran and Bjorndal, 2005), and clipped plots were maintained

124   for the entire 16-month duration of the study. Seagrass blades were removed from plots at the

125   time of clipping to simulate the removal of biomass and nutrients when green turtles graze an

126   area. Rhizomes were severed around the perimeters of clipped plots at the beginning of the

127   experiment and every 6 – 8 weeks thereafter with a flat-bladed shovel to prevent nutrient

128   translocation into the experimental plots. A 0.5 m wide buffer zone was established around the

129   edge within each plot, and all samples were collected from the remaining inner 2 x 2 m area, to

130   avoid possible edge-effects created by the surrounding unclipped meadow.

131   Results from this experiment on the effects of simulated grazing (clipping) on the growth

132   and morphometry of seagrass have been described previously (Moran and Bjorndal, 2005). Some

133   results are presented again here to aid in the interpretation of results of experimental grazing on

134   the invertebrate infauna community.

135

136   *2.2 Infaunal sample collection and analysis*

137   The invertebrate infaunal community was sampled from all plots, clipped and reference,

138   prior to initiation of the clipping experiment (July 1999; 0 months), and at 2, 6, 11, and 16

139   months following the initiation of experimental clipping. Infauna communities were sampled

140   from sediment cores collected within each plot with a 7.62 cm inner diameter PVC corer inserted

141   to a depth of 25 cm (1140 cm^3 total sample volume). One core was collected from a randomly

142   selected location within the inner 2 x 2 m sampling area of each plot at each sampling time,

143   taking care to not resample the same locations as previous coring events.

144   Cores were washed with seawater over a series of two metal mesh sieves (2.0 and 0.5

145   mm) in the laboratory, and seagrass root and rhizome material was removed. Only organisms

146   >0.5 mm were retained on the sieves, with smaller particles and organisms being washed

147   through. The organisms retained on each sieve were transferred to jars and preserved with a

148   mixture of 5% buffered formalin and seawater. Samples were left in this buffered formalin

149   mixture for at least two weeks, during which time a few drops of Rose Bengal mixed with

150   ethanol were added to each jar as a staining agent. After this period of preservation and staining,

151   samples were rinsed of the buffered formalin mixture and transferred to 70% ethanol in glass

152   scintillation vials for storage. The >2.0 mm and 0.5 – 2.0 mm size-fractions were kept separate

153   during this process. Infauna data were analyzed separately for each of these size-fractions in

154   addition to analyses conducted with pooled size-fraction data.

155   Infaunal organisms were counted and identified under a dissecting microscope. Most

156   organisms were identified to class or order. Aschelminth phyla were split into two groups during

157   identification: the nematodes (phylum: Nematoda) and all other aschelminthes (referred to here

158   as "non-nematode aschelminthes"). Infaunal communities were enumerated for eight clipped-

159   reference plot pairs selected from two of the experimental blocks (section 2.1). Samples were

160   enumerated for the same eight plot pairs at each time point during the experiment.

161

162   *2.3 Seagrass and sediment sample collection and analyses*

163   Seagrass meadow characteristics—*Thalassia testudinum* shoot density, blade length and

164   width, aboveground seagrass biomass, and belowground seagrass biomass—were measured at

165   regular intervals throughout the study in all experimentally clipped and reference plots. Seagrass

166   structural parameters were measured bi-weekly in all plots. Shoot density was measured from

167   three randomly placed 25 x 25 cm quadrats (0.0625 m^2), and blade length and width were

168   measured from 30 randomly selected blades from each plot. Aboveground seagrass biomass was

169   measured in all plots, clipped and reference, prior to the initiation of clipping (July 1999; 0

170   months). Thereafter, aboveground biomass was measured in clipped plots at each clipping event

171   (when blade length reached 5 cm), and in reference plots at 2, 6, 11, and 16 months following

172   initiation of the experiment. In clipped plots, all blades from the inner 4 m^2 of each plot were

173   collected for biomass, and in reference plots all blades from three randomly placed 25 x 25 cm

174   quadrats were collected. Collected blades were rinsed in seawater in the laboratory to remove

175   sediments and dried to a constant weight at 60° C for dry mass. Belowground seagrass biomass

176   (roots and rhizomes) was collected prior to the initiation of clipping (0 months) and at 2, 6, 11,

177   and 16 months following clipping from the same cores as infauna samples. Roots and rhizomes

178 were separated from the surrounding sediment in the laboratory (at the time infauna samples

179 were collected on sieves), rinsed in seawater, and dried to a constant weight at 60° C for dry

180 mass.

181 Characteristics of the surface sediments (where most infauna reside) in the meadow were

182 measured in all plots throughout the experiment. The depth of the detrital layer (layer of loose

183 particles and detritus at the sediment surface) was measured bi-weekly by inserting a rigid ruler

184 into the sediment until resistance was met within each of the three randomly placed quadrats

185 used for measuring seagrass shoot density. Organic matter content and particle size distribution

186 in the surface sediments of the meadow were measured from three shallow sediment cores (5.08

187 cm I.D.; 15 cm depth; 304 cm^3 volume) collected in each plot prior to clipping initiation (0

188 months), and at 2, 6, 11, and 16 months. Seagrass material and large invertebrates that were

189 visible were removed in the laboratory. Sediment samples were then dried to a constant weight at

190 60° C, ground with a mortar and pestle to pass through a 1 mm mesh sieve, and re-dried at 105°

191 C for at least 16 hours for dry mass measurement. Organic matter content was measured by

192 combusting dried sediment samples at 500° C for 3 hours in a muffle furnace. Sediment particle

193 size was measured using the hydrometer technique (Buoyoucus, 1936; Gee and Bauder, 1986).

194 Particle size-classes were assigned as follows: sand, >0.05 mm; silt, 0.002 – 0.05 mm; clay,

195 <0.002 mm.

196

197 *2.4 Data analyses*

198 For variables collected more frequently than infauna samples from plots (e.g. seagrass

199 density, collected bi-weekly), only data corresponding to the times of infauna collection were

200 used for analyses (i.e. sampling times at 0, 2, 6, 11, and 16 months). Mean values were

201 calculated for variables for which multiple measurements were collected at each time point (e.g.

202 seagrass density, three quadrats from each plot), and these mean values (i.e. single value per plot

203 per sampling time) were used for analyses.

204   Effects of clipping on infauna abundance over time were analyzed using linear mixed-

205 effects models, where treatment and time (sampling event) were treated as fixed effects, and

206 experimental plot blocks were treated as a random effect. Effects of clipping on meadow and

207 environmental factors over time (e.g. aboveground seagrass biomass, depth of detrital layer)

208 were analyzed using linear mixed-effects models in the same manner. Differences in variables

209 (infauna abundance, seagrass and sediment parameters) between clipped and reference plots at

210 the end of the 16-month clipping experiment were analyzed with a linear mixed-effects model

211 with treatment as a fixed effect and experimental plot block as a random effect. Relationships

212 between infauna abundance and meadow variables (e.g. aboveground seagrass biomass) were

213 analyzed using linear regression, and infauna abundance data were square-root transformed prior

214 to analysis to meet normality assumptions.

215   Simpson's Diversity Index was used to measure the diversity of the infaunal community.

216 This index accounts for both group richness and abundance and is a good measure of diversity in

217 situations when one or a few groups are considerably more abundant than others (e.g. nematodes

218 in this study). A linear mixed-effects model was used to analyze effects of clipping over time on

219 the diversity of the infauna community, where treatment and time were treated as fixed effects,

220 and block was treated as a random effect. Differences in measures of infaunal diversity between

221 treatments at the end of the experiment were analyzed with a linear mixed-effects model with

222 treatment as a fixed effect and block as a random effect. In addition to Simpson's Diversity

223   Index, infaunal group richness and evenness were also evaluated across treatments and sampling

224   events.

225   Changes to the composition of the infauna community over time as a result of

226   experimental clipping were analyzed using permutational multivariate analysis of variance

227   (PERMANOVA) (Anderson, 2001) with treatment and time as factors. Differences in the

228   community composition between treatments (clipped and reference plots) at the beginning (0

229   months) and end of the experiment (16 months) were analyzed using PERMANOVA with

230   treatment as the only factor. PERMANOVA calculations were based on a Bray-Curtis distance

231   matrix for community composition. Differences in community composition in multidimensional

232   space between treatments were visualized in two dimensions using non-metric multidimensional

233   scaling (NMDS).

234   All analyses were performed in R version 3.5.1 (R Core Team, 2018) using the 'nlme'

235   package for mixed-effects models (Pinheiro et al., 2018) and the 'vegan' package for

236   PERMANOVA tests and NMDS plots (Oksanen et al., 2018). Significance for all tests was

237   evaluated at an alpha value of 0.05.

238

239   **3. Results**

240   Most of the infaunal organisms identified in this study were from the 0.5 – 2.0 mm size-

241   fraction, and results for infauna abundance from this size-fraction were the same as results from

242   all data when both size-fractions were pooled. There were not enough data for multiple groups in

243   the >2.0 mm size-fraction to evaluate infauna abundance, and abundance was low for remaining

244   groups. Because including or omitting data from the >2.0 mm size-fraction from analyses did not

245   affect results, only results from the pooled data are presented.

246

247 *3.1 Effects of simulated grazing on the infaunal community*

248   Effects of experimental clipping on the seagrass meadow infaunal community occurred

249 relatively quickly—within six months—following the onset of simulated grazing. Changes were

250 not yet apparent two months post-clipping, however, total infauna abundance decreased by 59%

251 within clipped plots between two- and six-months post-clipping (Fig. 1), becoming significantly

252 different over time from unclipped reference plots (linear mixed-effects model (LME); $F_{1,41}$ =

253 36.7, $p < 0.01$).

254   The decrease in total infauna abundance was driven by a decrease in abundance observed

255 across all individual infaunal groups within clipped plots between two- and six-months post-

256 clipping (Fig. 2). The decline in abundance between two- and six-months within clipped plots

257 was greater in some groups (e.g. copepods) than others (e.g. oligochaetes). For six of the eleven

258 individual infaunal groups, abundances became significantly different over time between clipped

259 plots and reference plots after six months (Table S1). There was also a significant increase in the

260 number of crab claws within clipped plots between two- and six-months (Table S1, Fig. 2),

261 potentially a sign of increased predation. Nematodes were the most abundant individual infaunal

262 group and comprised on average ~30 – 40% of total infauna abundance within the meadow. As a

263 result, total infauna abundance was strongly, positively related to nematode abundance (linear

264 regression; $R^2 = 0.69$, $p < 0.01$), and the decrease in total infauna abundance was likely largely

265 driven by the decrease in nematode abundance.

266   Infaunal diversity (Simpson's Index) was slightly greater in clipped plots (0.79) than

267 reference plots (0.74) (LME; $F_{1,13}$ = 4.6, $p = 0.05$) prior to clipping initiation; however,

268 Simpson's Diversity Index did not differ between clipped and reference plots during the

269   experiment (LME; $F_{1,55} = 1.4$, p = 0.25) (Fig. 3). Infaunal group richness and evenness did not

270   differ between treatments prior to clipping (p = 0.39 and p = 0.47, respectively). Following the

271   onset of clipping, infaunal group richness decreased in clipped plots, while group evenness

272   increased, resulting in the lack of a difference in Simpson's Diversity Index over time between

273   clipped and reference plots.

274   Though the diversity of the infaunal community was not affected by clipping, the relative

275   abundance of individual groups comprising the community varied during the experiment (Fig.

276   S1). As a result, the composition of the infaunal community became significantly different

277   between clipped and reference plots during the experiment (PERMANOVA; full model, Table

278   1). Community composition did not differ between treatments prior to clipping (0 months, Table

279   1).

280

281   *3.2 Effects of long-term simulated grazing on the infaunal community*

282   Following 16 months of experimental clipping, total infauna abundance remained

283   significantly lower in clipped plots compared to reference plots (LME; $F_{1,13} = 9.6$, p = 0.01;

284   Table S2). Not all the individual groups that displayed differences after six months followed this

285   long-term pattern, however. By the end of the clipping experiment, only nematodes (p < 0.01)

286   and peracarids (p = 0.01) still had significantly lower abundances within clipped plots compared

287   to reference plots (in addition to total infauna abundance) (Table S2). Infauna abundances of the

288   remaining groups that had been lower in clipped plots became similar to those in reference plots,

289   whether due to an increase in abundance in clipped plots (e.g. polychaetes), or a decrease in

290   abundance within reference plots (e.g. gastropods) (Fig. 2).

291   Simpson's Diversity Index did not differ between clipped and reference plots at the end

292   of 16 months (LME; $F_{1,13} = 0.4$, p = 0.56). Though infaunal group richness and evenness

293   exhibited temporal variation within clipped plots, by the end of the 16-month experiment both

294   richness and evenness had become similar between clipped and reference plots again (richness;

295     $F_{1,13} = 0.3$, p = 0.59; evenness; $F_{1,13} = 0.3$, p = 0.60). All infaunal groups were present at all

296   sampling times, though abundances were temporally variable. This variation led to shifting

297   relative dominance among individual groups, which affected the community composition. The

298   significant differences in infaunal community composition observed between clipped and

299   reference plots during the experiment (section 3.1) were still present at the end of the clipping

300   experiment (PERMANOVA; 16 months, Table 1; Fig. 4).

301

302   *3.3 Effects of simulated grazing on meadow characteristics*

303   Experimental clipping significantly altered the aboveground seagrass canopy compared

304   to reference plots that remained unclipped (Table 2). Canopy height (measured from blade

305   length) was significantly lower in clipped plots than reference plots throughout the experiment

306   (LME; $F_{1,55} = 537.7$, p < 0.01). Seagrass blade width in clipped plots also became significantly

307   narrower than within reference plots by the end of the experiment (16 months; LME; $F_{1,13} = 35.9$,

308   p < 0.01). Aboveground seagrass biomass was of course also lower in clipped plots than

309   reference plots during the experiment (LME; $F_{1,55} = 322.8$, p < 0.01), as the clipping regime

310   mimicked the natural grazing strategy of green turtles—cropping all blades to short heights

311   above the sediment surface and removing the majority of biomass. Seagrass shoot density did not

312   differ between clipped and reference plots following 16 months of clipping (LME; $F_{1,13} = 0.9$, p

313   = 0.35).

314   Experimental clipping of the seagrass canopy also affected surface sediments in the

315   meadow (Table 3). The depth of the detrital layer—loose surface layer of unconsolidated

316   sediment and organic matter—was reduced in clipped plots compared to reference plots over the

317   course of the experiment (LME; $F_{1,55} = 5.0$, $p = 0.03$). Though the detrital layer became thinner

318   in clipped plots, the organic matter content of the surface sediments was not affected by clipping

319   (LME; $F_{1,55} = 2.7$, $p = 0.10$). The composition of the sediment (percent sand, silt, and clay)

320   varied significantly over the course of the experiment (significant time component) in both

321   treatments but did not differ between clipped and reference treatments.

322

323   *3.4 Relationships between infauna abundance and meadow characteristics*

324   We investigated potential relationships between abundance of infaunal groups and

325   characteristics of the seagrass meadow with linear regression. Total infauna abundance was

326   significantly, positively related to aboveground seagrass biomass ($p < 0.01$; Fig. S2a), meadow

327   canopy height ($p < 0.01$), and blade surface area ($p < 0.01$). Each of these meadow

328   characteristics explained similar amounts of variation in total abundance ($R^2 = 0.15$, $R^2 = 0.18$,

329     $R^2 = 0.17$, respectively), as all three are directly related to each other. Total infauna abundance

330   was not significantly related to belowground seagrass biomass ($R^2 = 0.01$, $p = 0.16$). However,

331   belowground biomass did not differ between clipped and reference plots during the experiment

332   (LME; $F_{1,55} = 0.17$, $p = 0.68$), as did measures of the aboveground canopy. With the exception of

333   organic matter content, infauna abundance was not related to any measured sediment

334   characteristics (i.e. detrital layer depth, percent sand, percent silt, percent clay) in the meadow.

335   Total infauna abundance was positively related to the organic matter content of the surface

336   sediments across all plots ($R^2 = 0.04$, p = 0.04); however, the relationship was weak and

337   differences in organic matter explained little of the variation in abundance (Fig. S2b).

338

339   **4. Discussion**

340   Infauna play important roles within seagrass meadows, and with successful conservation

341   efforts leading to increasing green turtle abundance (Chaloupka et al., 2008; Mazaris et al., 2017;

342   USFWS and NOAA, 2016)—which will result in more grazed seagrass—it is important to

343   understand how infaunal communities are affected by grazing. Our results demonstrate that

344   removal of the seagrass canopy through simulated green turtle grazing can affect both the

345   abundance and composition of the seagrass meadow infaunal community.

346   Infaunal groups comprising the community exhibited different responses to green turtle

347   grazing, and temporal dynamics varied within and among individual groups. Infauna abundance

348   exhibited high variation within both clipped and reference treatments in our study, which is

349   typical of seagrass meadow invertebrate communities (Brito et al., 2005; Jankowska et al., 2014).

350   Simulated grazing led to significantly reduced abundance (compared to ungrazed reference plots)

351   for six infaunal groups during the experiment (Table S1). However, four of these groups returned

352   to levels comparable to abundances in unclipped reference plots by the end of the experiment.

353   This recovery suggests that the initial decrease in abundance for some infaunal groups may have

354   been a response to the perturbation to the ecosystem from which the population was able to

355   recover as it adapted to the altered ecosystem state. Nematodes and peracarids, following a

356   decrease between two- and six-months post-clipping, remained at lower abundance levels for the

357   duration of simulated grazing, suggesting a different long-term response to canopy removal than

358   those groups exhibiting a recovery following the perturbation. Abundance may have been more

359   strongly affected by environmental factors (e.g. turbulence at the sediment surface) for some

360   groups, whereas predation pressure may have been the stronger driver for others. Infauna

361   abundance can be affected by changes to food source inputs (Bishop et al., 2010), and an

362   increase in a source, such as benthic microalgae, following canopy removal may also have

363   facilitated increases in abundance for some infauna in the long-term.

364   Though abundances were not reduced by clipping in the long-term for nine of the eleven

365   infaunal groups present in the meadow, the total abundance of the infaunal community was

366   reduced as a result of long-term simulated grazing. This was likely driven by the long-term

367   decline in nematode abundance within clipped plots, as nematodes were by far the most

368   numerous infaunal organisms at our study site (comprising ~30 – 40% of total abundance on

369   average). Given the lack of a long-term reduction for the majority of infaunal groups at our study

370   site, it is possible that total infauna abundance dynamics may exhibit a different response to

371   canopy removal through grazing in other seagrass systems differing in their infaunal

372   communities.

373   Though abundance dynamics were temporally variable within and among infaunal

374   groups, diversity of the infaunal community was not affected by simulated grazing. Dominance

375   (relative abundance) varied among infaunal groups over the course of the experiment; however,

376   all infaunal groups remained present throughout the experiment (Fig. S1). Many of these

377   infaunal groups exhibit high within-group diversity at lower taxonomic levels with

378   accompanying diversity in life-history traits (Ambrose, 1984; Lebreton et al., 2012). Differential

379   effects of grazing based on infaunal life-histories, such as feeding strategy (e.g. consumption of

380   detritus vs. microphytobenthos), could have important implications for ecosystem processes,

381   such as organic matter cycling, in seagrass meadows. It is possible that within-group species

382   dynamics may exhibit different responses to grazing based upon life-history traits of the infauna,

383   and these effects (if present) would be masked in the current study. Examining species-level

384   differences and life-histories were beyond the scope of this study; however, these would be

385   useful future research directions for understanding effects of grazing on diversity in seagrass

386   meadows.

387   While infaunal group diversity was not affected by experimental clipping, shifting

388   relative dominance among groups during the experiment (Fig. S1) led to significantly different

389   infaunal community composition between treatments after 16 months (Fig. 4; Table 1). Infaunal

390   communities differ among seagrass meadows (Ansari et al., 1991), and some infauna have even

391   been found to be associated with specific species of seagrass (Liao et al., 2016). It is possible that

392   other meadows, differing in their seagrass species and infaunal communities, may respond

393   differently to green turtle grazing from that in the present study. However, grazing is likely to

394   affect the composition of the infaunal community regardless of the community composition prior

395   to grazing. Unless abundance decreases proportionally across all groups inhabiting a meadow (so

396   infaunal group evenness is unaffected), changes to the composition of the community will occur.

397   Green turtle grazing may lead to additional indirect effects within seagrass meadows

398   through changes to the infaunal community. As abundance and composition of the community

399   change, other ecosystem functions and services may also be affected, such as prey availability

400   for juvenile fishes using the meadow as foraging habitat. These effects of grazing may not affect

401   entire seagrass meadows, however, as green turtles do not often graze entire meadows (though

402   there are exceptions; e.g. Christianen et al., 2014). Green turtles in the Caribbean create discrete

403   foraging patches within a meadow (Bjorndal, 1980), resulting in a mosaic of grazed and

404   ungrazed areas of seagrass. The effects of green turtle grazing—on the infaunal community and

405   indirect effects stemming therefrom—may scale to the amount of grazing within a meadow.

406   However, the distance to which edge effects may propagate beyond a grazed area may differ

407   among infaunal groups (Bell et al., 2001; Tanner, 2005; York et al., 2018), and it is possible

408   certain groups may be affected across an area greater than that which is grazed by turtles. Indeed,

409   decapod and mollusc abundance can be negatively affected up to 5 m from the edges of propeller

410   scars within meadows (Uhrin and Holmquist, 2003). Green turtle grazing patches differ from

411   other forms of disturbance (e.g. propeller scars, dugong grazing trails) in important ways,

412   however. For example, they have a lower edge-to-area ratio and both their size and shape may

413   change over time with turtle behavior (Hernández and van Tussenbroek, 2014). Understanding

414   edge-effects and grazing patch dynamics on infaunal communities will be an important avenue

415   for future research. With increasing green turtle abundance and grazing in areas such as the

416   Caribbean (Chaloupka et al., 2008), more seagrass area will return to a natural grazed state, and

417   the effects on ecosystem functions mediated by the infaunal communities within seagrass

418   meadows will become more wide-spread.

419   Many infaunal species are detritivores and play an essential role in the recycling of

420   organic matter in meadows (Hemminga and Duarte, 2000). Seagrass meadow canopies baffle

421   waves and reduce current speed, creating a calmer microhabitat near the sediment surface

422   (Fonseca et al., 1982; Gacia et al., 1999; Reidenbach and Thomas, 2018) thereby trapping

423   organic matter which may be incorporated into the detrital layer (Gacia et al., 2002; Kennedy et

424   al., 2010). A change in the detritivorous infauna community within a meadow may affect organic

425   matter and nutrient recycling; however, green turtle grazing is known to increase organic matter

426   cycling rates in *Thalassia testudinum* meadows (Thayer et al., 1982). To further our

427   understanding of how grazing affects seagrass ecosystem functioning through changes to

428   infaunal communities, future studies should target meadows dominated by species other than *T.*

429   *testudinum* in which canopy structure differs from that in the present study.

430   Foraging habitat for juveniles of many fish species is an important ecosystem service

431   provided by seagrass meadows, and changes to the infaunal community through grazing may

432   affect these consumer populations. The sediment surface becomes more exposed following

433   grazing, potentially creating a habitat in which foraging for infauna becomes easier. The

434   decrease in abundance observed across many infaunal groups may have been a result of

435   increased predation following removal of the seagrass canopy. Fauna inhabiting the benthic

436   surface, such as small crabs, may be especially vulnerable within grazed areas, and we measured

437   the abundance of crab claws within plots as a potential sign of predation to investigate this. The

438   significant increase in crab claws within clipped plots during the study, preceded by a sharp

439   decline in decapod abundance (Fig. 2), suggests that predation increased following removal of

440   the protective seagrass canopy. An increase in predation of infauna by fishes within

441   experimentally clipped plots was not directly observed during this study. However, normal fish

442   behavior may have been altered by the presence of divers within the meadow. Additionally, all

443   activities were conducted during daytime, so any potential nighttime or crepuscular predation by

444   fishes or other consumers would not have been observed. Hydrodynamics could also have led to

445   horizontal transport of crab claws into or out of experimental plots, leading to the observed

446   changes; however, the coupled decapod-crab claw dynamics were only observed within clipped

447   plots, not reference plots. Further research is needed to better understand the cause of declines in

448   infauna abundance following grazing.

449   Green turtles affect the infaunal communities inhabiting seagrass ecosystems through

450   grazing of the aboveground canopy, likely with further effects on ecosystem functions mediated

451   by aspects of the infaunal community. Infaunal communities are comprised of many species

452   (Edgar et al., 1994; Liao et al., 2016; Skilleter et al., 2007) which play important roles in

453   seagrass ecosystems, from affecting the rate at which organic matter and nutrients are passed

454   through the detrital cycle, to acting as a source of prey for numerous consumers such as juvenile

455   fishes. Infauna therefore affect rates of energy and nutrient flow through seagrass food webs. As

456   green turtle populations increase, more seagrass will be consumed, and greater areas of seagrass

457   meadows will be returned to a naturally grazed state. Given the roles infauna play in seagrass

458   ecosystems, effects on these communities should be taken into account when evaluating the

459   effects of green turtles in seagrass habitats.

471

472   **Author Contributions**

473   KMH (née Kathleen L. Moran), ABB, and KAB designed the study. KMH collected the data.

474   RAJ analyzed the data and led the writing of the manuscript with contributions from all authors.

475

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611

612   **Table 1**. Results of the permutational multivariate analysis of variance (PERMANOVA)

613   evaluating infaunal community composition using Bray-Curtis distances. Differences in

614   community composition between clipped and reference plots were evaluated over the course of

615   the clipping experiment (full model), as well as between treatments (i.e. no time component) at

616   zero months (pre-clipping) and 16 months (end of the clipping experiment). Infaunal

617   communities differed in their composition both throughout and at the end of the experiment but

618   did not differ prior to experimental clipping. Significant results are in bold and denoted with an

619   (*).

620

	df	MS	F	p	
Full Model					
treatment	1	0.95	7.67	**<0.01**	*
time	2	0.20	1.58	0.10	
treatment:time	2	0.16	1.32	0.20	
Residuals	42	0.12			
Total	47				
Zero Months					
treatment	1	0.13	0.94	0.47	
Residuals	14	0.14			
Total	15				
Sixteen months					
treatment	1	0.43	4.97	**0.01**	*
Residuals	14	0.09			
Total	15				

621

622

623 **Table 2**. Seagrass meadow characteristics in experimentally clipped and unclipped reference

624 plots during the experiment. Data are mean ± SE of the eight plots sampled for each treatment.

625

Treatment	Blade length	Blade width	Shoot density	AG biomass	BG biomass
	cm	cm	shoots m^{-2}	g DM m^{-2}	g DM m^{-2}
Pre-clipping					
0 months					
Clipped	12.6 ± 0.4	0.7 ± 0.0	599.3 ± 16.5	80.7 ± 5.8	682.5 ± 79.5
Reference	12.2 ± 1.0	0.7 ± 0.0	579.3 ± 29.6	79.6 ± 2.8	590.7 ± 94.1
Post-clipping					
2 months					
Clipped	8.0 ± 0.3	0.6 ± 0.0	697.3 ± 42.3	30.8 ± 2.2	748.8 ± 108.6
Reference	12.5 ± 0.7	0.7 ± 0.0	772.0 ± 38.7	63.2 ± 5.2	715.1 ± 59.0
6 months					
Clipped	2.9 ± 0.3	0.6 ± 0.0	668.0 ± 41.1	15.1 ± 0.7	797.1 ± 156.5
Reference	11.9 ± 0.6	0.7 ± 0.0	716.0 ± 45.3	59.3 ± 4.6	837.4 ± 110.4
11 months					
Clipped	4.0 ± 0.5	0.6 ± 0.0	732.7 ± 46.1	25.9 ± 2.1	572.0 ± 97.4
Reference	11.7 ± 0.4	0.7 ± 0.0	779.3 ± 50.7	60.4 ± 4.1	756.8 ± 164.7
16 months					
Clipped	4.5 ± 0.2	0.6 ± 0.0	698.0 ± 43.8	14.0 ± 0.6	718.4 ± 178.5
Reference	13.9 ± 0.6	0.7 ± 0.0	761.3 ± 48.2	67.6 ± 4.2	657.8 ± 111.6

626 AG: aboveground; BG: belowground; DM: dry mass

627

628   **Table 3**. Sediment characteristics in experimentally clipped and unclipped reference plots in the

629   seagrass meadow during the experiment. Data are mean ± SE of the eight plots sampled for each

630   treatment.

631

Treatment	Detrital depth cm	OM %	Sand %	Silt %	Clay %
Pre-clipping					
0 months					
Clipped	1.9 ± 0.2	4.6 ± 0.2	85.7 ± 1.3	11.4 ± 1.2	2.9 ± 0.2
Reference	1.9 ± 0.1	4.5 ± 0.1	84.1 ± 1.5	13.0 ± 1.2	2.8 ± 0.3
Post-clipping					
2 months					
Clipped	3.5 ± 0.5	4.7 ± 0.1	84.5 ± 2.4	12.0 ± 2.1	3.4 ± 0.4
Reference	4.0 ± 0.6	4.7 ± 0.1	87.0 ± 1.4	10.1 ± 1.3	3.0 ± 0.3
6 months					
Clipped	2.7 ± 0.2	4.7 ± 0.1	74.1 ± 0.8	22.9 ± 0.9	3.0 ± 0.2
Reference	3.0 ± 0.3	4.8 ± 0.1	73.6 ± 0.9	23.5 ± 0.9	2.9 ± 0.3
11 months					
Clipped	2.4 ± 0.2	4.3 ± 0.1	73.3 ± 1.3	23.5 ± 1.4	3.2 ± 0.3
Reference	2.9 ± 0.2	4.7 ± 0.1	71.7 ± 2.1	24.3 ± 1.9	4.0 ± 0.4
16 months					
Clipped	2.7 ± 0.2	4.7 ± 0.1	76.0 ± 2.7	19.6 ± 2.1	4.4 ± 0.7
Reference	3.5 ± 0.3	4.7 ± 0.1	76.7 ± 3.3	18.5 ± 2.7	4.7 ± 0.6

632   OM: organic matter
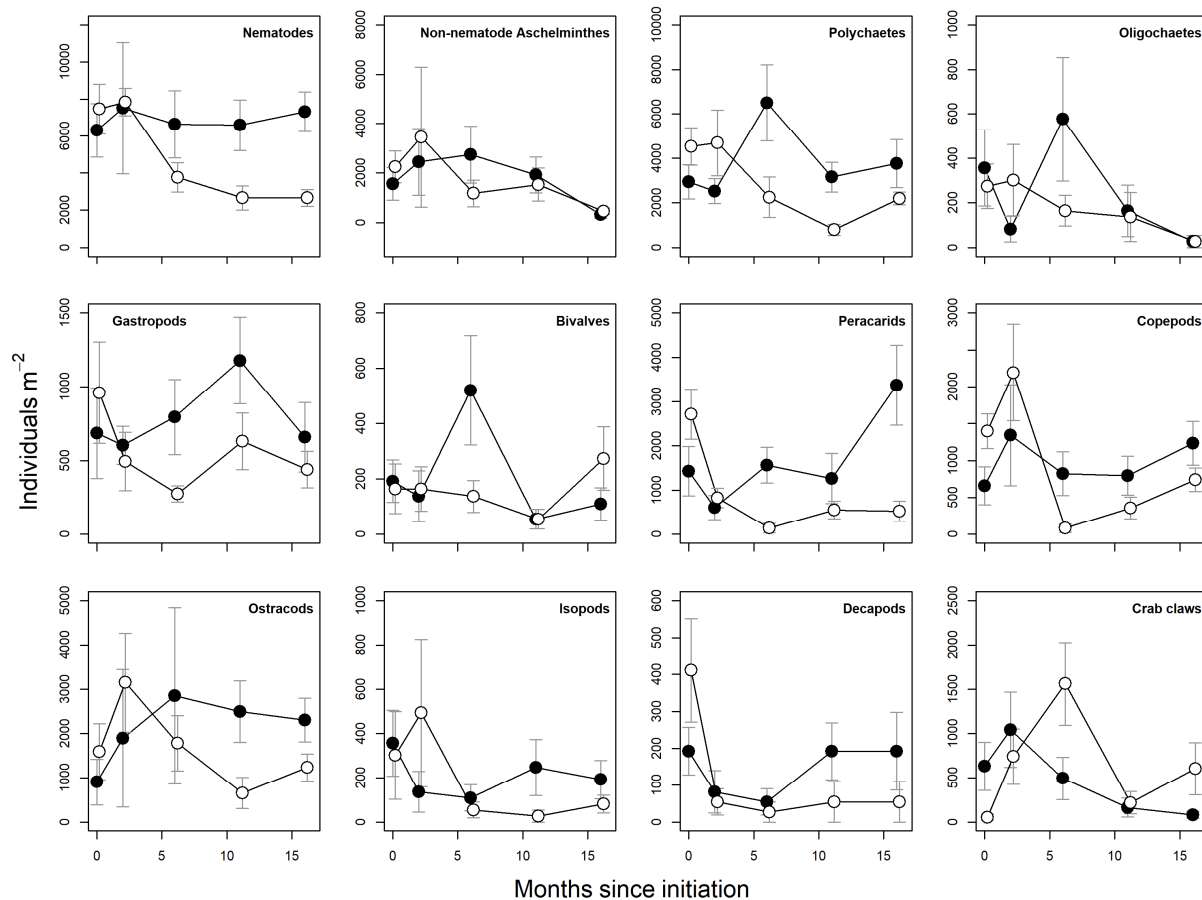
633
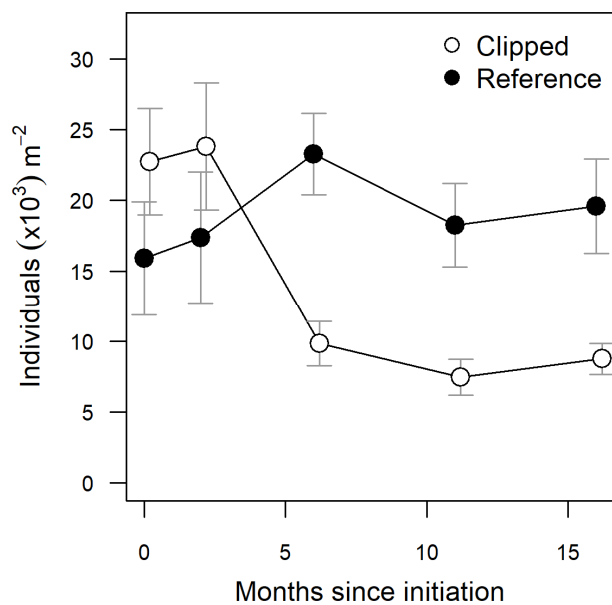
Figure 1. Total infauna abundance over the course of the 16-month clipping experiment in clipped (open points) and reference (closed points) plots. Data are mean ± SE. Abundance was significantly different between clipped and reference plots at 16 months (LME; $F_{1,13} = 9.6$, p = 0.01). Sampling at zero months was prior to clipping initiation.

**Figure 2**. Abundance of individual infaunal groups (and crab claws) over the course of the 16-month clipping experiment in clipped (open points) and reference (closed points) plots. Abundance was significantly different between clipped and reference plots at 16 months for only nematodes and peracarids (see Table S2). Sampling at zero months was prior to clipping initiation. Data are mean ± SE. Note differences in y-axis scales.

647
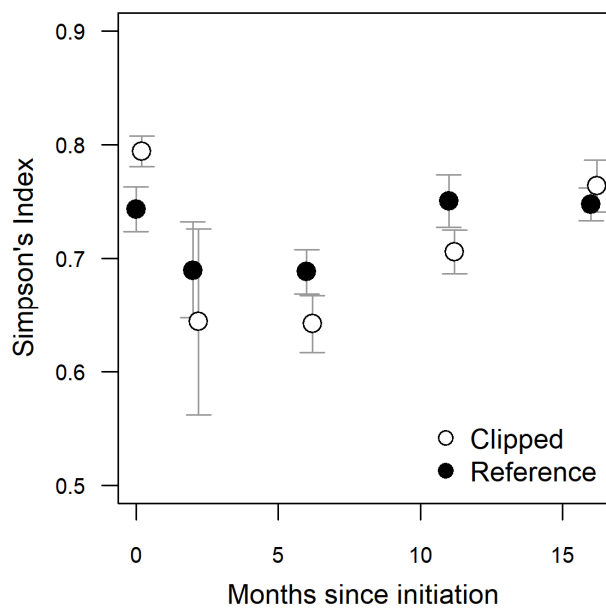
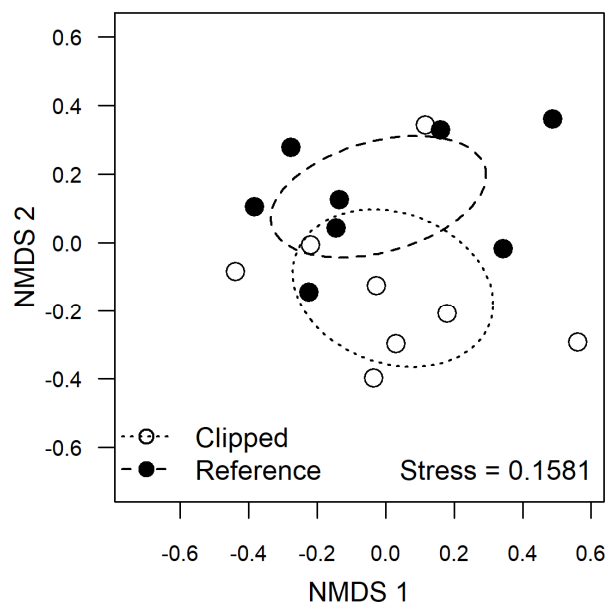**Figure 3**. Simpson's Diversity Index of the infaunal communities in clipped (open points) and

reference (closed points) plots over the course of the 16-month clipping experiment. Data are

mean ± SE. Diversity was not significantly affected by clipping over the course of the

experiment. Sampling at zero months was prior to clipping initiation.

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Figure 4. Non-metric multidimensional scaling (NMDS) plot showing separation in infaunal

community composition between clipped (open points, dotted ellipse) and reference plots (closed

points, dashed ellipse) at the end of the experiment (16 months). Difference in community

composition was significant (PERMANOVA; see Table 1). Each point is a single plot (n=8 for

each treatment) for which the infaunal community was enumerated. Two-dimensional stress was

calculated following square-root transformation and a Wisconsin double standardization of the

data.

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