Abundance modulates the ecosystem functional contributions of two sympatric Caribbean sea cucumbers

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Abstract

In highly diverse systems such as coral reefs, many species appear to fulfil similar ecological roles, suggesting that they might be ecologically equivalent. However, even if species provide similar functions, the magnitude of those roles could modulate their impact within ecosystems. Here, we compare the functional contributions of two common, co-occurring Caribbean sea cucumber species, *Holothuria mexicana* and *Actynopyga agassizii*, in terms of ammonium provisioning and sediment processing on Bahamian patch reefs. We quantified these functions through empirical measures of ammonium excretion, and in situ observations of sediment processing coupled with fecal pellet collections. On a per-individual level, *H. mexicana* excreted approximately 23% more ammonium and processed approximately 53% more sediment per hour than *A. agassizii*. However, when we combined these species-specific functional rates to species abundances to produce reef-wide estimates, we found that *A. agassizii* contributed more than *H. mexicana* to sediment processing at 57% of reefs (1.9 times more per unit area across all surveyed reefs), and more to ammonium excretion at 83% of reefs (5.6 times more ammonium per unit area across all surveyed reefs), owing to its higher abundance. We conclude that sea cucumber species can differ in the rates at which they deliver per capita ecosystem functions but their ecological impacts at the population level depend on their abundance at a given location.

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Introduction

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43   Ecosystem functioning is described by the movement of energy and material within an

44   ecosystem, the fluxes of which are controlled by the identity and abundance of species within it

45   (Loreau, 2000; Cardinale et al., 2006; Tilman, Isbel & Cowles, 2014). Trait-based approaches

46   have been used to predict how species influence core ecosystem processes (Zwart et al., 2015;

47   Cadotte, 2017; Carturan et al., 2018), which on coral reefs include herbivore–algae interactions,

48   ⁻ ⁻ predator–prey interactions, nutrient cycling, and carbonate dynamics (Brandl et al. 2019).

49   These approaches have been useful when applied to highly biodiverse ecosystems where an

50   ecological function is fulfilled by multiple species that share one or more characteristics relevant

51   to that function (Strong et al., 2015; Brandl et al., 2019; Wolfe et al., 2020). Traits such as body

52   mass, trophic group, and nutrient stoichiometrics are widely used as proxies for functional

53   richness to predict the role of groups of species on ecosystem functioning (McGill et al., 2006;

54   Bellwood et al., 2019). However, the use of trait-dependent groups or guilds can mask significant

55   interspecific variation, often oversimplifying species contributions to ecological processes

56   (Semmler et al., 2021). For instance, parrotfishes contribute to the process of carbonate dynamics

57   through coral grazing and bioerosion, but species differences in body size can lead to

58   disproportionate contributions to bioerosion by large species at the reef-wide scale (Lange et al.,

59   2020). For example, one species of bioeroding parrotfish was found to remove 27 times more

60   material per year than another co-occurring and closely related species (Bellwood, 1995). There

61   is therefore value in empirically measuring individual-level functional rates to infer the

62   importance of species to specific ecosystem processes, even within functional guilds (Lange et

63   al., 2020).

64   The role of vertebrates, especially fishes, has dominated studies of ecosystem functioning on

65   coral reefs (Allgeier, Burkepile & Layman, 2017), even though invertebrates are dominant

66   contributors to coral reef ecosystem diversity (Glynn & Enochs, 2011). Specifically, mobile

67   invertebrates only make up a small proportion (7.3%) of the literature on species' functional

68   niches (Bellwood et al., 2019) yet can make up a substantial proportion of biomass and play a

69   range of ecological roles. For example, sea cucumbers (Echinodermata: Holothuroidea) are

70   found at high densities (up to 3 individuals per m^2) in seagrass beds and near reef flats (e.g., Lee

71   et al., 2018). They serve functional roles in nutrient recycling, sediment processing, and benthic

72   primary productivity in tropical systems (Uthicke & Klumpp, 1998; Uthicke, 1999, 2001a;

73   Wolkenhauer et al., 2010; MacTavish et al., 2012; Purcell et al., 2016). As detritivores that feed

74   on epibenthic organic material and meiofauna, holothuroids can turnover 64-250 kg of sediment

75   individual^{-1} yr^{-1} (Wolfe & Byrne, 2017; Hammond, Meyers & Purcell, 2020; Williamson et al.,

76   2021), with some of this activity occurring nocturnally (Hammond, 1982; Navarro et al., 1983).

77   Sediments egested by sea cucumbers are often lower in organic matter than the sediment

78   consumed (Mercier, 1999), demonstrating the role deposit-feeding sea cucumbers can play in re-

79   mineralization of surface sediments (MacTavish et al., 2012). Some sea cucumber species can

80   cause changes in sediment grain size, potentially through calcium carbonate dissolution and

81   sediment abrasion during digestive processes (Hammond, 1981; Schneider et al., 2011).

82   Additionally, sea cucumbers excrete inorganic nitrogen as ammonium (NH_4^+), providing a

83   nitrogenous source for benthic microalgae (Mukai et al., 1989; Uthicke & Klumpp, 1988;

84   Uthicke, 2001a), macroalgae (Felaco, Olvera-Novoa, and Robledo, 2020) and seagrass

85   (Wolkenhauer et al., 2010; Arnull et al., 2021). For example, in the Indo-Pacfic, field enclosures

86   with high densities of the sea cucumber *Holothuria scabra* resulted in a 30% increase in seagrass

87   leaf extension rate compared to low-density enclosures (Arnull et al., 2021). Owing to their high

88   densities in some habitats, sea cucumber populations have the potential to contribute a consistent

89   'press' of ammonium within marine systems (Allgeier et al., 2017). This is especially important

90   on oligotrophic coral reefs, which primarily rely on nutrient recycling to bolster benthic primary

91   productivity (Hatcher, 1988; Allgeier, Burkepile & Layman, 2017). Taken together, the

92   functional roles provided by sea cucumbers can form a link in transferring energy to other

93   marine trophic levels through the functions of nutrient recycling and sediment processing

94   (Purcell et al., 2016; Wolfe et al., 2020).

95   In this study, we investigated the nutrient provisioning and sediment processing functions

96   of two common sea cucumber species in a shallow coral reef–seagrass ecosystem in The

97   Bahamas. Our research objectives were to use empirical measures of ammonium excretion rates

98   and field observations of sediment processing rates to estimate and compare per capita and reef-

99   wide contributions by *Holothuria mexicana* and *Actinopyga agassizii* to both ecosystem

100 processes. Since *H. mexicana* is exploited disproportionately more in the Caribbean than *A.*

101 *agassizii* (Rogers et al., 2018), determining the magnitude of nutrient contribution and sediment

102 processing by these species to coral reefs will provide insight into the potential functional loss

103 associated with current and future sea cucumber fisheries.

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106 **Materials & Methods**
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108 **Study location and study species**
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110 Research was conducted under a Marine Scientific Research Permit issued by the Department of

111 Marine Resources, Government of The Bahamas, to the Cape Eleuthera Institute, and in

112 accordance with the Canadian Council of Animal Care (Protocol No. 1301B-19).

113   The study was conducted on 35 separate coral reef patches along the southwestern coast

114   of Eleuthera Island, The Bahamas, from May to August 2019 (Fig. 1a). Reef patches were

115   located in Rock Sound, a large, shallow (< 5 m depth) sandy basin. They ranged in hard-bottom

116   area from 2 to 209 m^2 (mean ± sd: 35 ± 43 m^2) and depth from 2.6 to 4.5 m (mean ± sd: 3 ± 0.5

117   m) and were separated from the nearest patch by a minimum of 100 m. All patch reefs were

118   immediately surrounded by a halo of seagrass, *Thalassia testudinum*, that extended up to 9.6 m

119   away from the patch edge (Fig. 1b). Beyond this distance, seagrass was either sparse or absent.

120   The two focal sea cucumber species, *H. mexicana* and *A. agassizii* (family Holothuriidae; Fig.

121   1c), are distributed widely across the Caribbean region (Hendler et al. 1995). In Rock Sound, we

122   found both species co-occurring in seagrass beds and on or near coral patches. *Holothuria*

123   *mexicana* feeds approximately 12 h per day, whereas *A. agassizii* feeds approximately 10 h each

124   day (Hammond, 1982). There was no sea cucumber fishery in The Bahamas at the time of this

125   study. A small experimental sea cucumber fishery in the Bahamas took place in 2010 on Andros

126   Island but closed after 11 months due to stock depletion (Sherman et al., 2018).

127

128   **Seagrass area, sea cucumber body sizes and density**

129   We estimated seagrass area at each patch by measuring the circumference at the outer edge of the

130   high-density seagrass halo (Fig. 1b), as well as that of the hard-bottom area of the coral patch

131   reef itself. We converted perimeters to areas and subtracted the hard-bottom area from the total

132   area to obtain seagrass area. Divers counted, identified to species, and measured the length and

133   midbody girth of every sea cucumber encountered on reefs and within the dense seagrass halo.

134   Beginning at a recognizable landmark and moving in a clockwise fashion, two divers swam side-

135   by-side, and systematically searched in the seagrass for sea cucumbers, and then searched the

136 reef, carefully looking in crevices and overhangs for sea cucumbers. Sea cucumber species

137 density is expressed as individuals per m² of seagrass area.

138

139 **Sediment processing and movement**

140 We quantified hourly sediment processing by *A. agassizii* and *H. mexicana* following Lee et al.

141 (2018, adapted from Uthicke, 1999), where we assumed that the quantity of sediment egested is

142 equal to the quantity ingested. We selected *A. agassizii* (mean length ± sd = 20 ± 2 cm, range: 14

143 – 23 cm, *n* = 20) and *H. mexicana* (mean length ± sd = 24 ± 3 cm, range: 18 – 30 cm, *n* = 20)

144 individuals that represented the commonest size classes across Rock Sound. We measured

145 sediment processing and movement for 20 individuals of each species from 11:00 to 16:00 hrs in

146 July 2019 on two patch reefs that were separate from our 35 survey patches. To do so, divers

147 tracked sea cucumbers by planting a metal stake labelled with flagging tape in the sediment at a

148 standardized distance (ca. 1 cm) from the posterior end of the focal sea cucumber. At the end of

149 each hour (for three consecutive hours), the number of fecal pellets egested by each individual

150 was counted, and the linear distance moved by each individual was recorded. The stake was re-

151 placed near the posterior end of the focal individual to serve as starting point for the next hour-

152 long observation. After the last observation period, up to 10 (average = 9 ± 0.4 pellets; median =

153 10 pellets; range = 0-10 pellets) of the most recently defecated fecal pellets for each individual

154 (i.e., the pellets closest to the individual) were collected in Falcon® tubes. More recently

155 released pellets were chosen because they are easier to collect as they have not yet disintegrated.

156 The length and girth of each sea cucumber were also measured. Fecal pellets were frozen and

157 transported to Simon Fraser University.

158   After thawing and combining pellets for each individual, we placed them in a drying

159   oven for 24 h at 60°C. Pellets were then weighed to determine dry weight (DW) on an analytical

160   balance to the nearest 0.001 g. Dried pellet samples were transferred into porcelain crucibles,

161   placed in a muffle furnace for 2 h at 550°C, then reweighed to obtain ash weight (AW). We

162   calculated ash-free dry weight (AFDW = DW − AW) to determine the organic matter (OM)

163   content in the fecal pellets.

164

165   **Empirical estimates of ammonium excretion**

166   To measure excretion rates of *A. agassizii* and *H. mexicana*, divers collected individuals of both

167   species haphazardly from various reef patches that were separate from our sediment processing

168   and movement observations. We made excretion estimates by following well-established

169   methods by Layman et al. (2011) and Francis & Côté (2018) who modified slightly the methods

170   of Schaus et al. (1997),Whiles et al. (2009), and Taylor et al. (2007). Individual *H. mexicana* and

171   *A. agassizii* ($n = 20$ for each species) were brought to the Cape Eleuthera Institute (CEI, 24°

172   49'54.46" N, 76° 19'56.28" W) and allowed to recover in sea tables connected to a flow-through

173   seawater system pumped directly from the ocean for 1-2 h before being placed gently but rapidly

174   in individual 20-L acid-washed bags filled with a known volume of pre-filtered (0.7 μm

175   Whatman GF-F filters) sea water. Bags containing sea cucumbers ($n = 20$ per species) and

176   control bags of filtered sea water containing no sea cucumbers ($n = 3$ empty bags) were sealed

177   and placed in sea tables to maintain ambient temperature (29 – 31°C) for 60 min. Although

178   handling might have increased excretion rate initially, the relatively long incubation period

179   makes it likely that sea cucumbers were near resting rates for most of this period. At the end of

180   the incubation period, we collected one 100 ml water sample from each bag using a sterile plastic

181   syringe. Samples were filtered (0.45 μm Whatman GF-F filters), placed in dark bottles and

182   refrigerated for immediate analysis of ammonium (NH_4^+) content, a proxy for inorganic nitrogen,

183   using fluorometric methods (Taylor et al., 2007). After incubation, we measured the wet weight

184   (g), total length (cm), and midbody girth (cm) of each sea cucumber and allowed them to recover

185   in sea tables for several hours before release onto their reef of capture. We randomized with

186   respect to species the order in which we measured ammonium excretion of individuals.

187

188   **Data analyses**

189   We transformed sea cucumber counts at each patch into densities (i.e., numbers per m^2 of

190   seagrass). We ran a Welch's t-test to assess differences in mean density and mean proportion of

191   total density between sea cucumber species across Rock Sound. To test for differences in size

192   distributions between *A. agassizii* and *H. mexicana*, we ran a two-sample Kolmogorov-Smirnov

193   test on sea cucumber length.

194

195   *Individual-level estimates*

196   To test for species differences in sediment processing, we ran t-tests to examine the effect of

197   species on four metrics related to sediment processing: (1) fecal pellet egestion rate (pellets h^{-1}),

198   (2) weight per pellet (g), (3) sediment processing rate (g of sediment h^{-1}), and (4) organic matter

199   (% OM). In calculating sediment processing rate, we assumed that the quantity of sediment

200   egested is equal to the quantity of sediment ingested (Uthicke, 1999). Additionally, we ran a *t*-

201   test to test for differences in speed (m h^{-1}) between *A. agassizii* and *H. mexicana*.

202   To provide a longer-term perspective on the contributions of individual sea cucumbers

203   and increase comparability with other studies, we extrapolated individual hourly sediment

204 processing rates to individual annual rates. To do so, we converted individual hourly rates of

205 sediment processing from g h^{-1} to kg yr^{-1}, assuming sediment processing rates remain constant

206 throughout the year. Following Lee et al. (2018), we multiplied the egestion rate (pellets h^{-1}) of

207 each species by 12 h and 10 h of activity for *H. mexicana* and *A. agassizii*, respectively

208 (Hammond, 1982) to obtain a daily rate of fecal pellet egestion (pellets d^{-1}). We then multiplied

209 this rate by the average pellet weight for each species (g pellet^{-1}), which gave sediment weight

210 processed per day (g d^{-1}). Finally, we extrapolated this rate to an annual rate in kg of sediment

211 processed y^{-1} per individual.

212   To test for species differences in hourly ammonium excretion rate (μmol NH$_4^+$ h^{-1}), we

213 ran a linear model with sea cucumber wet weight (data-centred), species and their interaction as

214 model predictors. We used wet weight as a predictor in our model so it could be compared to

215 other studies (see Discussion).

216

217 *Reef-level estimates*

218 We used the individual-level estimates of sediment processing (g h^{-1}) and ammonium excretion

219 (μmol NH$_4^+$ h^{-1}) described above to generate reef-level estimates of sediment processing (kg m^{-2}

220 yr^{-1}) and ammonium excretion (μmol NH$_4^+$ m^{-2} h^{-1}) for each species on each of the 35 reefs by

221 bootstrapping confidence intervals (following Fieberg, Vitense & Johnson, 2020).

222   To generate annual reef-level estimates of sediment processing (kg m^{-2} yr^{-1}) for each

223 species, we first used a t-test to test the effect of species on sediment processing rate (g h^{-1}). To

224 incorporate uncertainty around this relationship, we bootstrapped reef-specific 'populations' of

225 sediment processing rates for 5,000 iterations to obtain reef-level estimates at each reef for each

226 species, accounting for the number of individuals of each species at each site. We then converted

227   our bootstrapped estimates from g h^{-1} to kg yr^{-1}. Finally, we divided the bootstrapped estimates

228   of sediment processing by seagrass area to obtain annual sediment processing rate per unit area

229   of seagrass (kg m^{-2} yr^{-1}).

230   We used the same method to estimate reef-level estimates of ammonium contribution

231   (μmol NH$_4^+$ m^{-2} h^{-1}) by each species on each of the 35 reefs. However, because we could record

232   length but not wet weight of sea cucumbers during underwater surveys, we first converted all

233   observed sea cucumber total lengths of both species to wet weight, using the significant

234   relationship generated between these two variables from the sea cucumbers used to estimate

235   ammonium excretion rates (linear model; $F_{1,36} = 15.56$, $p < 0.001$ for both species). This allowed

236   us to predict ammonium excretion (μmol h^{-1}) as a function of wet weight for each species. To

237   incorporate uncertainty around this relationship, we bootstrapped each reef-specific 'population'

238   of wet weights (5,000 iterations) to predict total ammonium excretion rates for each species at

239   each patch reef, using the model from our empirical excretion measurements. Lastly, we divided

240   our bootstrapped estimates of total ammonium excretion by the seagrass area at each reef to

241   obtain excretion estimates per unit area of seagrass (μmol NH$_4^+$ m^{-2} h^{-1}). All statistical analyses

242   were conducted in R (R Core Team 2020, version 1.3.959) using the tidyverse (Wickham et al.,

243   2019), ggspatial (Dunnington, 2020), dunn.test (Dinno, 2017), cowplot (Wilke, 2019), and

244   viridis (Garnier, 2018) packages.

245

246   **Results**

247

248   **Body size and density**

249   Across all patches surveyed, *H. mexicana* was significantly larger than *A. agassizii* (mean ± CI

250   (range); *Hm*: 27 cm [25.9, 27.2] (17 – 47 cm), *Aa*: 22 cm [21.5, 22.3](13 – 45 cm), $p < 0.001$).

251 The length distributions of the two species were also significantly different ($p < 0.001$; Fig. 2).

252 There were, on average, 15 ($\pm$ 2 SE) sea cucumbers per patch (range: 1 – 62; Fig. 1). There were

253 significantly more *A. agassizii* (11 $\pm$ 2) present, on average, than *H. mexicana* (4 $\pm$ 1) per patch

254 ($p = 0.003$). Mean patch size was 35 ($\pm$ 7 SE; range 1.3 – 209) m^2 and mean seagrass area was

255 54 ($\pm$ 10 SE; range 5.3 – 296) m^2, yielding a mean overall density of 0.3 ($\pm$ 0 SE; range 0.02 –

256 1.3) sea cucumbers per m^2 of seagrass area.

257

258 **Sediment processing and movement**

259 *Actinopyga agassizii* egested fecal pellets at approximately four times the rate of *H. mexicana* (p

260 $= 0.008$; Fig. 3a). However, the fecal pellets egested by *H. mexicana* were seven times heavier

261 than those egested by *A. agassizii* ($p < 0.001$; Fig. 3b). Combining these measures together,

262 individual *H. mexicana* processed three times more reef sediment per hour, on average, than

263 individual *A. agassizii* ($p < 0.001$; Fig. 3c). Fecal pellets egested by *A. agassizii* had a

264 significantly higher OM by approximately 1.5% than those of *H. mexicana* ($p < 0.001$; Fig. 3d).

265 *Holothuria mexicana* moved a maximum of 170 cm in a three-hour observation, while *A.*

266 *agassizii* moved at most 125 cm. Speed did not differ significantly between *A. agassizii* (0.1 $\pm$

267 0.03 m h^{-1}) and *H. mexican*a (0.2 $\pm$ 0.04 m h^{-1}) ($p = 0.17$; Fig. 3e).

268 Through extrapolation of egestion rates and quantities, we found that individual *A.*

269 *agassizii* and *H. mexicana* have the potential to process 5.9 (range: 4.3 – 7.5) and 12.5 (range:

270 9.4 – 16) kg of sediment y^{-1}, respectively. When we scaled up these individual egestion rates to

271 population-level rates, *A. agassizii* populations turned over, on average, significantly more

272 sediment (1.9 $\pm$ 0.2 SE kg m^{-2} yr^{-1}) than *H. mexicana* (1.0 $\pm$ 0.4 SE kg m^{-2} yr^{-1}; $p = 0.019$; Fig.

273 4). However, this difference appears due mainly to the absence of *H. mexicana* from several

274   reefs. When we considered only reefs where both species were present (24 of 35 reef patches), *A.*

275   *agassizii* populations turned over sediment at a similar rate (1.6 ± 0.2 SE kg m^{-2} yr^{-1}) compared

276   to *H. mexicana* populations (1.4 ± 0.5 SE kg m^{-2} yr^{-1}; p = 0.77; Fig. 4). At reefs with both

277   species, *Actinopyga agassizii* contributed more to sediment processing at 57% of reefs, *H.*

278   *mexicana* contributed more at 40% of these reefs, and both contributed equally at a single reef

279   (Fig. S1).

280

281   **Ammonium excretion**

282   The sea cucumbers used to assess ammonium excretion rates were slightly larger, on average,

283   than those found on the study reefs, but they spanned the ranges of lengths observed on reefs

284   (Fig. 2). We used slightly (~11%) larger *H. mexicana* individuals (mean ± SE [range]; 787 ± 69

285   [361 – 1397] g) on average, than *A. agassizii* individuals (mean ± SE [range]; 706 ± 55 [110 –

286   1080] g) to obtain ammonium excretion rates. Species identity had a significant effect on sea

287   cucumber ammonium excretion rate (p = 0.04), but there was no effect of wet weight (p = 0.07,

288   r^2 = 0.17) (Fig. S2). On average, individual *Holothuria mexicana* excreted NH_4^+ at a rate that

289   was approximately 23% higher than individual *A. agassizii* (mean ± SE; *Hm*: 15.6 ± 1.1 μmol

290   NH_4^+ h^{-1}, *Aa*: 12.0 ± 1.0 μmol NH_4^+ h^{-1}) (p = 0.023).

291

292   Reef-level estimates of excretion contributions showed that *A. agassizii* populations

293   contributed 5.7 times more ammonium per unit area (3.1 ± 0.5 μmol NH_4^+ m^{-2} h^{-1}) than *H.*

294   *mexicana* populations (0.54 ± 0.1 μmol NH_4^+ m^{-2} h^{-1}; p < 0.001; Fig. 4). When considering only

295   reefs where both species occurred, *A. agassizii* populations contributed 3.3 times more

296   ammonium per unit area (2.5 ± 0.6 μmol NH_4^+ m^{-2} h^{-1}) than *H. mexicana* populations (0.75 ± 0.1

297   μmol NH_4^+ m^{-2} h^{-1}; $p < 0.001$; Fig. 4). When both species were present, *A. agassizii* contributed

298   more ammonium at 83% of reefs, *H. mexicana* contributed more at 13% of reefs, and both

299   species contributed equally at one reef (Fig. S3).

300
301
302
303   **Discussion**

304   This is the first study to evaluate the functional roles of *H. mexicana* and *A. agassizii* in relation

305   to two important ecological processes. Rates of sediment processing and ammonium excretion

306   for *H. mexicana* and *A. agassizii* were species-specific, providing evidence that the two species

307   provide these functions at different magnitudes. Although individual *H. mexicana* processed

308   approximately 53% more sediment and excreted approximately 23% more ammonium per hour

309   than individual *A. agassizii*, differences in abundance between the two species resulted in larger

310   reef-wide contributions to both functions by *A. agassizii* across sites. This suggests that, in the

311   coral reef–seagrass ecosystem we studied, differences in population density can reverse the

312   individual-level differences in the magnitude of the functions provided by these two species of

313   sea cucumbers. Elsewhere, sea cucumber density could simply attenuate or even exacerbate

314   differences in individual rates, depending on both species-specific contributions and abundance.

315

316   **Sediment processing and movement**

317   We highlight the ecological roles of *H. mexicana* and *A. agassizii* as motile sediment processors

318   of patch reef sediments. At the individual level, *A. agassizii* egested pellets faster than *H.*

319   *mexicana*, but their pellets were smaller. Assuming the total amount of sediment egested reflects

320   the amount ingested (Uthicke, 1999; Lee et al., 2018), individual *H. mexicana* processed three

321 times more sediment per hour than individual *A. agassizii*. The sediment processing rates of both

322 species were within the range of Mediterranean species (Coulon & Jangoux, 1993) but

323 considerably lower than those of Indo-Pacific species (Uthicke, 1999; Wolfe & Byrne, 2017; Lee

324 et al., 2018).

325   At the reef scale, however, *A. agassizii* had a higher estimated sediment processing

326 potential because of its higher abundance. *Actinopyga agassizii* populations processed 1.9 times

327 more sediment per unit area than *H. mexicana* populations. Note that our estimates of sediment

328 processing rates across patch reefs are likely conservative because we could only measure

329 sediment processing rates of sea cucumbers between 09:00 and 16:00 hrs but both species feed

330 and are active at night (Hammond, 1982). There is no information, to our knowledge, on the

331 ecological consequences of sediment processing by our two target species. However, the

332 ingestion and release of fecal casts and disturbance caused by locomotion by other deposit-

333 feeding sea cucumbers play a role in redistributing surface sediments and influencing biotic

334 interactions occurring at the sediment–water interface (Purcell et al., 2016). Moreover, halting

335 bioturbation and feeding functions by experimental removal of sea cucumbers led to the

336 development of cyanobacterial mats and a reduction in oxygen penetration depth into sediments

337 (Moriarty et al., 1985; Uthicke, 1999; Michio et al., 2003; Lee et al., 2018).

338   *Actinopyga agassizii* egested fecal pellets with higher OM content than *H. mexicana*.

339 This might make pellets of *A. agassizii* more prone to bacterial and fungal growth, and result in a

340 more rapid loosening of the mucous membrane that holds the fecal material and hence faster

341 resuspension of organic matter (Conde, Diaz & Sambrano, 1991). The interspecific difference

342 may stem from differences in the time each species spends on various substratum types. For

343 example, in Jamaica, *A. agassizii* was observed mainly on algal turf and on macroalgae, whereas

344   *H. mexicana* spent 90% of its time on sand (Hammond, 1982). Alternatively, interspecific

345   differences may be attributed to the resident time of sediment in the digestive tract, where one

346   species could be less 'thorough' in sediment processing than another, resulting in fecal pellets

347   with higher organic matter. The fecal pellets of *A. agassizii* could also be higher in OM because

348   they are smaller, meaning that there is more organic material surrounding the pellet relative to

349   the amount of sediment inside the pellet, assuming that organic matter is concentrated on the

350   surface of the pellet where most digestive reactions take place. Future studies should (1) use a

351   stable isotope approach to identify the specific origins and diet sources of *H. mexicana* and *A.*

352   *agassizii* (e.g., Slater & Carton, 2010), (2) determine pellet grain size distribution between

353   species, which may have an effect on organic matter content and could reveal niche

354   differentiation, and (3) quantify nocturnal sediment processing (and ammonium excretion) rates

355   of sea cucumbers.

356

357   **Ammonium excretion**

358   Individual ammonium excretion rates by *H. mexicana* and *A. agassizii* were species specific but

359   did not significantly vary with body size. The average rates estimated here for *A. agassizii* (12.0

360   μmol NH_4^+ h^{-1}) and *H. mexicana* (15.6 μmol NH_4^+ h^{-1}) are at the high end of the range reported

361   for Western Pacific tropical species (1 − 18 μM; Mukai et al., 1989; Uthicke, 2001a; Wheeling,

362   Verde & Nestler, 2007). Though *H. mexicana* had a higher average excretion rate, both species

363   showed the same weak relationship with body size, indicating that individual *H. mexicana*

364   excrete more nutrients than individual *A. agassizii* of the same size. Note that the relationship

365   between ammonium excretion rate and sea cucumber body size was weaker than expected from

366   physiology and mass–balance theory. Obtaining accurate but non-destructive mass and

367 morphology measurements of holothuroids is notoriously difficult because they readily change

368 shape and retain water in their body cavity (Wheeling, Verde & Nestler, 2007).

369  Despite having a lower per capita excretion rate, *A. agassizii* contributed more

370 ammonium than *H. mexicana* at the reef scale owing to its higher abundance. *Actinopyga*

371 *agassizii* contributed more to ammonium excretion at 83% of our study reefs and, on average,

372 excreted 5.6 times more ammonium per unit area than *H. mexicana.* Ammonium excretion by

373 tropical sea cucumbers has been shown to be an important source of limiting nutrients that

374 promotes growth of microalgae (e.g., Uthicke, 2001b; MacTavish et al., 2012) and seagrass (e.g.,

375 Wolkenhauer et al., 2010).

376  Both sea cucumber species together contributed approximately 15% of the ammonium

377 released by coral reef fishes on patch reefs in Rock Sound. We estimated that *A. agassizii* and *H.*

378 *mexicana* excreted 3.1 ± 0.5 μmol NH_4^+ m^{-2} h^{-1} and 0.5 ± 0.1 μmol NH_4^+ m^{-2} h^{-1}, respectively. In

379 Rock Sound, all resident fishes together contribute, on average, ~25 μmol m^{-2} h^{-1} during the

380 daytime (Francis & Côté, 2018). These fishes included more than 45 species across 17 families.

381 On a per-species basis, the role of sea cucumbers as nutrient providers is therefore substantial,

382 and given their nocturnal behaviour, they may contribute more to the overall diel nutrient budget

383 at night compared to daytime. In addition, migratory grunts (Haemulidae), which contribute

384 more than twice as other reef-associated fishes, migrate seasonally and annually, resulting in an

385 unpredictable nutrient supply (Francis & Côté, 2018). In contrast, some species of sea cucumbers

386 are known to exhibit high site fidelity for years over time (Wolfe & Byrne, 2017), meaning that

387 sea cucumbers may contribute more consistently to seagrass beds adjacent to reefs than reef fish

388 do. In this way, sea cucumbers act as a 'press' of nutrient inputs, operating on time scales of days

389 to months, or even years (Allgeier et al., 2017).

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Conclusions

393   The two sea cucumber species we studied differed in the per-capita rates at which they deliver

394   two ecosystem functions, but their ecological impacts at the population level depended on their

395   abundance. We draw two main insights from these findings. First, our results are likely place-

396   specific. We examined only two of the many functional roles of sea cucumbers; however, it

397   should be expected that other functions, such as modulation of alkalinity and provision of habitat

398   for symbionts (Purcell et al., 2016), will also depend on abundance. This means that the relative

399   importance of co-occurring sea cucumber species in fulfilling these various functions will vary

400   spatially and reflect local patterns of relative species abundance. Second, our results suggest that

401   activities (e.g., fishing) or events (e.g., disease epidemics) that could reduce overall densities will

402   have substantial impacts on the ecological functions provided by sea cucumbers. Moreover, the

403   impacts will be exacerbated if these disturbances affect primarily the species that provide

404   ecological functions at higher per-capita rates. This is the case for sea cucumbers in the

405   Caribbean region, where *H. mexicana* has already been heavily exploited (Rogers et al. 2018). In

406   Belize, *H. mexicana* makes up between 65-90% of total sea cucumber catch, while *A. agassizii*

407   makes up approximately 1% (Rogers et al. 2018). Identifying the species and populations that

408   contribute disproportionately to ecosystem processes is increasingly important in a time when

409   ecosystems are being transformed and diversity is being lost across ecosystems (Loreau et al.,

410   2001).

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417

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420

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626   Figure captions

627

628   **Figure 1. (a)** Map of Eleuthera Island (inset), The Bahamas, and the study area, Rock Sound (main

629   panel). Each dot is a patch reef, whose colour represents the total density of sea cucumbers at each patch,

630   within the surrounding halo of dense seagrass (size of dots not drawn to scale). **(b)** One of 35 patch reefs

631   surveyed in this study, and **(c)** co-occurring *Actinopyga agassizii* (left) and *Holothuria mexicana* (right).

632

633   **Figure 2.** Size distribution of length for *H. mexicana* (26.5 ± 0.33 cm long, range: $17 – 47$ cm, $n = 223$)

634   and *A. agassizii* (21.9 ± 0.20 cm long, range: $13 – 45$ cm, $n = 462$) from 35 reef patches in Eleuthera, The

635   Bahamas. Density is the proportion of data points in each length bin, which sums to 1.

636

637   **Figure 3.** Dot and whisker plots of **(a)** fecal pellet egestion rate (number h^{-1}), and **(b)** weight per fecal

638   pellet, **(c)** sediment processing rate (g h^{-1}), **(d)** % organic matter content of egested fecal pellets, and **(e)**

639   movement speed of *H. mexicana* and *A. agassizii* ($n = 20$ for each species). Dots display the mean, and

640   whiskers display the 95% confidence intervals. Asterisks denote significant differences between species.

641

642   **Figure 4.** Estimates of **(a)** annual sediment processing rate (kg $m^{-2}yr^{-1}$) and **(b)** hourly ammonium

643   excretion rate (mol NH_4^+ m^{-2} h^{-1}) of *H. mexicana* and *A. agassizii* populations across 35 patch reefs in

644   Rock Sound, The Bahamas. Each point represents a patch reef. Horizontal and vertical error bars

645   represent the standard error (standard deviation of 5,000 bootstrap resamples) of contributions by *H.*

646   *mexicana* and *A. agassizii* populations at each site, respectively. The dashed line represents equal

647   contributions by both species.

648

Figure 1

(a) Map of Eleuthera Island (inset), The Bahamas, and the study area, Rock Sound (main panel), (b) One of 35 patch reefs surveyed in this study, and (c) co-occurring *Actinopyga agassizii* (left) and *Holothuria mexicana* (right).

In (a), each dot is a patch reef, whose colour represents the total density of sea cucumbers at each patch, within the surrounding halo of dense seagrass (size of dots not drawn to scale).
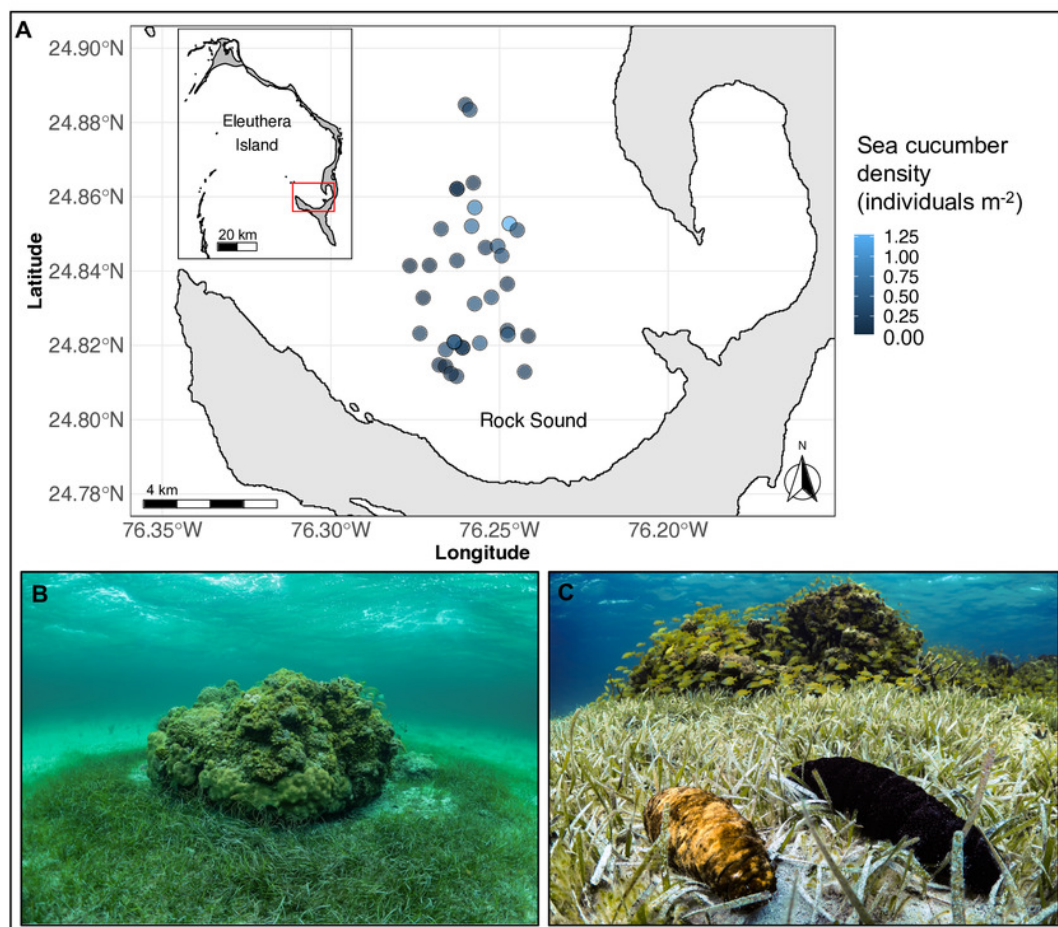
Figure 2

Size distribution of length for *H. mexicana* (26.5 ± 0.33 cm long, range: 17 – 47 cm, *n* = 223) and *A. agassizii* (21.9 ± 0.20 cm long, range: 13 – 45 cm, *n* = 462) from 35 reef patches in Eleuthera, The Bahamas.

Density is the proportion of data points in each length bin, which sums to 1.
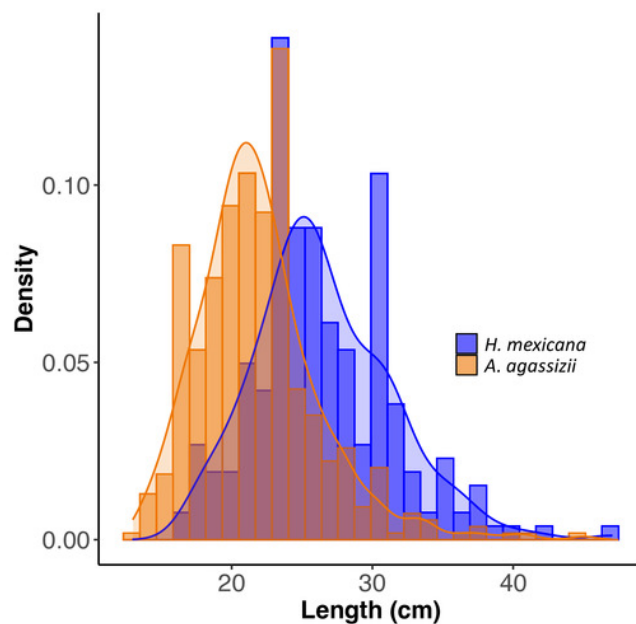
Figure 3

Dot and whisker plots of (a) fecal pellet egestion rate (number h^{-1}), and (b) weight per fecal pellet, (c) sediment processing rate (g h^{-1}), (d) % organic matter content of egested fecal pellets, and (e) movement speed of [i]H. mexican

Dots display the mean, and whiskers display the 95% confidence intervals. Asterisks denote significant differences between species.
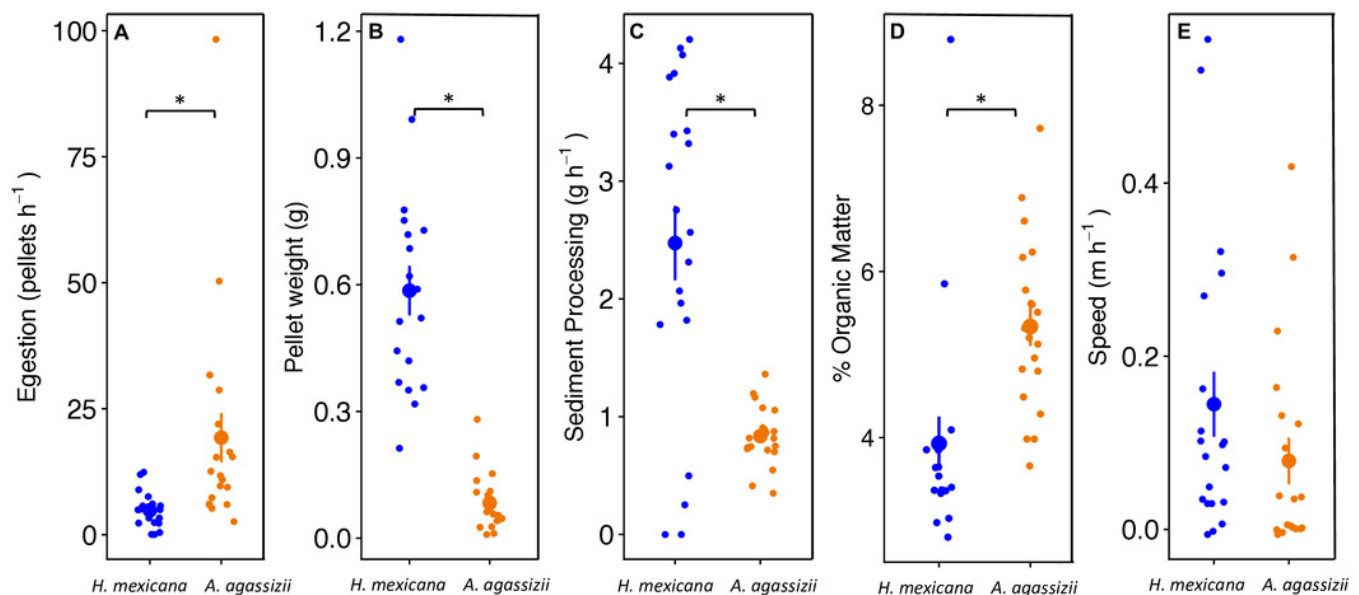
Figure 4

Estimates of (a) annual sediment processing rate (kg m^{-2}yr^{-1}) and (b) hourly ammonium excretion rate (mol NH$_4^+$ m^{-2} h^{-1}) of *H. mexicana* and *A. agassizii* populations across 35 pat

Each point represents a patch reef. Horizontal and vertical error bars represent the standard error (standard deviation of 5,000 bootstrap resamples) of contributions by *H. mexicana* and *A. agassizii* populations at each site, respectively. The dashed line represents equal contributions by both species.