Trophic ecology of sea urchins in coral-rocky reef systems, Ecuador

Nancy Cabanillas-Terán, Peggy Loor-Andrade, Ruber Rodríguez-Barreras, Jorge Cortés

Sea urchins are important grazers and influence reef development in the Eastern Tropical Pacific (ETP). *Diadema mexicanum* and *Eucidaris thouarsii* are the most important sea urchins on the Ecuadorian coastal reefs. This study provided a trophic scenario for these two species of echinoids in the coral-rocky reef bottoms of the Ecuadorian coast, using stable isotopes. We evaluated the relative proportion of algal resources assimilated, and trophic niche of the two sea urchins in the most southern coral-rocky reefs of the ETP in two sites with different disturbance level. Bayesian models were used to estimate the contribution of algal sources, niche breadth, and trophic overlap between the two species. The sea urchins behaved as opportunistic feeders, although they showed differential resource assimilation. *Eucidaris thouarsii* is the dominant species in disturbed environments; likewise, their niche amplitude was broader than that of *D. mexicanum* when conditions were not optimal. However, there was no niche overlap between the species. The Stable Isotope Analysis in R (SIAR) indicated that both sea urchins shared limiting resources in the disturbed area, mainly *Dictyota* spp. (contributions of up to 85% for *D. mexicanum* and up to 75% for *E. thouarsii*). The Stable Isotope Bayesian Ellipses in R (SIBER) analysis results indicated less interspecific competition in the undisturbed site. Our results suggested a trophic niche partitioning between sympatric sea urchin species in coastal areas of the ETP, but the limitation of resources could lead to trophic overlap and stronger habitat degradation.

1   **Trophic ecology of sea urchins in coral-rocky reef systems, Ecuador**

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24 **Abstract**

25 Sea urchins are important grazers and influence reef development in the Eastern Tropical Pacific

26 (ETP). *Diadema mexicanum* and *Eucidaris thouarsii* are the most important sea urchins on the

27 Ecuadorian coastal reefs. This study provided a trophic scenario for these two species of

28 echinoids in the coral-rocky reef bottoms of the Ecuadorian coast, using stable isotopes. We

29 evaluated the relative proportion of algal resources assimilated, and trophic niche of the two sea

30 urchins in the most southern coral-rocky reefs of the ETP in two sites with different disturbance

31 level. Bayesian models were used to estimate the contribution of algal sources, niche breadth,

32 and trophic overlap between the two species. The sea urchins behaved as opportunistic feeders,

33 although they showed differential resource assimilation. *Eucidaris thouarsii* is the dominant

34 species in disturbed environments; likewise, their niche amplitude was broader than that of *D.*

35 *mexicanum* when conditions were not optimal. However, there was no niche overlap between the

36 species. The Stable Isotope Analysis in R (SIAR) indicated that both sea urchins shared limiting

37 resources in the disturbed area, mainly *Dictyota* spp. (contributions of up to 85% for *D.*

38 *mexicanum* and up to 75% for *E. thouarsii*). The Stable Isotope Bayesian Ellipses in R (SIBER)

39 analysis results indicated less interspecific competition in the undisturbed site. Our results

40 suggested a trophic niche partitioning between sympatric sea urchin species in coastal areas of

41 the ETP, but the limitation of resources could lead to trophic overlap and stronger habitat

42 degradation.

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53   **Introduction**

54   As a consequence of increasing human pressure, coastal ecosystems are facing a wide range of

55   threats, such as resource exploitation and habitat modification (Wilkinson, 1999; Dumas et al.,

56   2007; Costello et al., 2010; Rossi, 2013). Several studies have evaluated the development of

57   rocky bottom disturbances by analyzing the densities of echinoids and the development stage of

58   habitats (Phillips & Shima, 2006; Alvarado, Cortés & Reyes-Bonilla, 2012; Hereu et al., 2012).

59   Some of these studies have correlated different phases of benthic substrate degradation,

60   considering sea urchin density and their association with functional algae groups (Steneck, 1983;

61   Steneck & Dethier, 1994). Another approach to decipher benthic dynamics is through the trophic

62   relationships between consumers and resources using stable isotopes (Behmer & Joern, 2008).

63   Stable isotope analysis (SIA) has been a powerful tool to study trophic ecology, especially for

64   those species with foraging habits for which it is difficult to use traditional techniques, such as

65   stomach contents. Several studies have focused on sea urchins from a stable isotope approach

66   (e.g., Minagawa & Wada, 1984; Tomas et al., 2006; Vanderklift, Kendrick & Smith, 2006; Wing

67   et al., 2008; Cabanillas-Terán, 2009; Rodríguez-Barreras et al., 2015).

68   Stable carbon and nitrogen isotope ratios provide time-integrated information regarding feeding

69   relationships and energy flow through food webs (DeNiro & Epstein, 1981; Peterson & Fry,

70   1987; Vander-Zanden & Rasmussen, 2001; Carabel et al., 2006). Stable isotopes can be used to

71   study the trophic niche of a species due to the "δ-space". This is comparable to the n-dimensional

72   space that ecologists refer to as a niche because an animal's chemical composition is directly

73   influenced by what it consumes, as well as the habitat in which it lives (Newsome et al., 2007;

74   Parnell et al., 2010; Boecklen et al., 2011).

75   Carbon is a conservative tracer used to track energy sources in food webs, while nitrogen helps

76   determine the trophic position (Minagawa & Wada, 1984; Vander-Zanden & Rasmussen, 2001;

77   Post, 2002; Phillips, 2012; Phillips et al., 2014). Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable

78   isotopes have been used in marine ecosystems to determine the food habits of species (Peterson

79   & Fry, 1987), nutrient migrations within food webs, the trophic position of organisms and their

80   contribution at every level (Vander-Zanden & Rasmussen, 1996), the origin and transformation

81   of the ingested organic matter (Peterson, Howarth & Garrett, 1985), or how some ecosystems

82 have organisms that occupy similar trophic positions coexisting in high densities (Vanderklift,

83 Kendrick & Smith, 2006). Moreover, SIA are useful to assess the ecosystem health (e.g., Cole et

84 al., 2004; Hamaoka et al., 2010; Karube et al., 2010). For example human influence on lake

85 ecosystems were studied by Karube et al. (2010) and those authors found that signatures of $\delta^{13}C$

86 and $\delta^{15}N$ in macroinvertebrates of the littoral zone are indicators of anthropogenic impacts from

87 the watershed. Inorganic nitrogen loading from the watershed was recorded in $\delta^{15}N$ of snails.

88

89 Reef degradation currently has significant consequences for morpho-functionality of marine

90 environments (Hoegh-Guldberg, 1999; Mumby, Foster & Fahy, 2005), and the Ecuadorian reefs

91 are no exception (Glynn & Wellington, 1983; Glynn, 1993; Guzmán & Cortés, 1993; Glynn,

92 2003). Anthropogenic stressors can have synergistic effects on reefs, such as the harmful algae

93 blooms that are becoming increasingly important drivers of variation in the sea urchin

94 populations, as seen in other areas (Hunter & Price, 1992; Lapointe et al., 2005; Lapointe et al.,

95 2010).

96

97 Coral-rocky reefs have rarely been studied along the Ecuadorian mainland, despite the serious

98 threat by eutrophication, fisheries and other anthropogenic impacts (Guzmán & Cortés, 1993;

99 Cortés, 1997; Cortés, 2011). Ecuadorian coral communities are important because they represent

100 the southernmost distribution in the Eastern Tropical Pacific (ETP). Ecuador has no extensive

101 reef systems, as the majority of reefs are small rocky patches with some coral colonies.

102 Nevertheless, those areas are characterized by high biodiversity, including more than a quarter of

103 the Ecuadorian continental fishes and a great number of echinoderms, sea fans, and scleractinian

104 corals (Glynn et al., 2001; Glynn, 2003; Rivera & Martínez, 2011).

105

106 Sea urchins have the capability to modify the community structure through foraging, as several

107 authors have previously mentioned (e.g., Carpenter, 1981; Carpenter, 1986; Hay, 1984; Hay &

108 Fenical, 1988; Sala, Boudouresque & Harmelin-Vivien, 1998), and we need to elucidate what

109 occurs in areas where there are more than one sea urchin species which dominate the substratum
110 and their role in controlling fleshy macroalgae. The sea urchins *Diadema mexicanum* (Agassiz,
111 1863) and *Eucidaris thouarsii* (Agassiz & Desor, 1846) are two of the most dominant benthic
112 grazers in the ETP (Guzmán & Cortés, 1993). These two echinoids exert a strong influence on
113 the community structure (Lawrence, 1975; Glynn, Wellington & Birkeland, 1979; Andrew,
114 1989; Underwood, 1992). In the ETP, the sea urchin *E. thouarsii* could be described as a major
115 herbivore in rocky reef bottoms. Its preferential resource appeared to be benthic algal turf and
116 macroalgae, but if those were not available, it feeds on other organisms, such as the corals
117 *Pavona clavus*, *Pocillopora* spp. and *Porites lobata* (Glynn et al., 1979; Glynn & Wellington,
118 1983; Reaka-Kudla, Feingold & Glynn, 1996).

119

120 The ratios of δ^{15}N and δ^{13}C in consumers are strongly influenced by their food resources
121 (Phillips et al., 2014) and it is necessary to identify their ecological role, not only by their
122 capacity to structure the environment, but to understand the dynamics of coexistence of the sea
123 urchin populations along the Ecuadorian coast. The relative position of δ^{13}C vs. δ^{15}N echinoids
124 species can be displayed in a bi-plot and help to understand food web structure and organism
125 responses to niche shifts, diet variability and human impact (Layman et al., 2007). The aim of
126 this study was to improve the knowledge and understanding of the trophic biology of *D.*
127 *mexicanum* and *E. thouarsii* in Ecuadorian rocky reefs. We determined the stable isotopes of
128 carbon and nitrogen isotope for both sea urchin species. The complexity of the littoral zone was
129 analyzed using stable isotopes to understand the trophic interactions of these two echinoids in
130 areas with different degree of human impact. We assume that the more developed rocky-reef and
131 substrate associated to coral coverage will favor habitats with complex trophic interactions (see
132 Duffy et al., 2007; Álvarez-Filip, et al., 2009; Graham & Nash, 2013), resulting in wider isotopic
133 echinoids niche breadth.

134 **Material & Methods**

135 *Site descriptions:* This study was conducted between May and September of 2013, at two
136 localities, Los Ahorcados (LA: 01°40'42"S; 80°51'58"W) and Perpetuo Socorro (PS: 0°55'40"S;
137 80°44'25"W), in Manabí province, Ecuador (Fig. 1). The LA site was a small group of rocky
138 islets located near Machalilla National Park. Although this area was not considered a protected

139   area, it had a very high diversity of scleractinians and octocorals (Rivera & Martínez, 2011). LA

140   presented a rocky bottom with clear geomorphologic differences between the leeward and

141   windward areas. The leeward area were 25 m depth, and the windward side was mainly build by

142   octocorals (22 species), and hexacorals, such as *Pavona* spp., the branching corals *Pocillopora*

143   spp. and solitary corals. The PS site is located in front of the Port of Manta (1.5 km), one of the

144   most important ports in Ecuador for large pelagic fisheries (Villón & Beltrán, 1998a; Villón &

145   Beltrán, 1998b; Martínez-Ortíz *et al.*, 2007) and greatly impacted by anthropogenic activities

146   (See details in Table 1). PS rocky reef is a homogenous bottom of 7-9 m depth, and had a

147   substrate consisted mainly of a mixture of rock and sand with scarce scleractinian corals (*Pavona*

148   spp. and *Pocillopora* spp.) and gorgonians (mainly *Leptogorgia alba*).

149   In order to distinguish both sites, a coral-rocky reef category was used for this study, which was

150   developed taking into account habitat complexity and type of disturbance to establish two

151   categories, namely disturbed and undisturbed (Table 1). The distance of human impact to the

152   sites, size of the fleet and type of human disturbance were considered. The rugosity index (RI),

153   which is the ratio of a length of chain following the reef contour to the linear distance between its

154   start and end point (modified of Risk, 1972) was used. To calculate the RI, we used a three-meter

155   chain five times equitably-distributed along 15 transects (20m). The average RI obtained with

156   transects was used to determine the rugosity level per site, where larger numbers indicate higher

157   complexity following Alvarez-Filip et al. (2009) and Alvarez-Filip et al. (2011). Therefore

158   values of RI <1.5 were considered low complexity and RI >1.5 were defined as complex.

159

160   *Collecting and processing data*: We collected algal samples for identification, to calculate

161   biomass, and to carry out SIA. Algal biomass was measured using twelve 50 x 50 cm quadrats

162   per site. The quadrats were located randomly within the sea urchin habitat. The substrate inside

163   each quadrat was scrapped, carefully removed, collected in bags, and frozen for later analysis.

164   Macroalgae were identified to the lowest possible taxonomic level using the available keys

165   (Abbot & Hollenberg, 1976; Afonso-Carillo & Sansón, 1999; Littler & Littler, 2010). The

166   sampled invertebrate and algal species for this study are not threatened. The necessary permits

167   were obtained from the Ministry of Environment of Ecuador (014AT-DPAM-MAE).

168   In areas where the algal cover was dominated mainly by turf species (following the morpho-

169   functional category of Guidetti, 2006), we used a sniffer with a dense mesh bag coupled to a

170   compressed air tank. In the laboratory, individuals were separated into species and gently washed

171   with distilled water and dried in an oven at 50 °C for 24 h to measure the dry weight.

172   We collected four individuals of *D. mexicanum* and six of *E. thouarsii* in LA and twelve

173   individuals of *D. mexicanum* and eight of *E. thouarsii* in PS at the same depth range (8-10 m).

174   Only individuals greater than 5.0 cm in test diameter were collected to avoid any effect of the

175   development stage. The samples were frozen shortly after collection and processed at the

176   laboratory. The muscles of Aristotle´s lanterns were removed carefully and washed from the

177   stomach contents to estimate algal assimilation by *D. mexicanum* and *E. thouarsii*. This tissue

178   provides a time-integrated measure of assimilated sources (e.g., Michener & Schell, 1994; Ben-

179   David & Schell, 2001; Polunin et al., 2001; Phillips & Koch, 2002; Rodríguez, 2003; Tomas et

180   al., 2006).

181   The algal and echinoids muscle samples were rinsed with filtered water, dried at 50 °C during 24

182   hours, ground to a fine powder and placed in glass vial for isotope analyses. To remove

183   carbonates from some algal species (*Lobophora variegata* and *Polysiphonia* spp.), the samples

184   were washed with diluted HCl at 1 N prior to drying to avoid disturbance in the mass

185   spectrometer reading. A subsample was taken of each alga and muscle (~1 mg) to evaluate the

186     $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios using a Thermo Electron Delta V Advantage Mass Spectrometer.

187   Carbon and nitrogen samples were analyzed in a dual isotope mode at the Geology Department,

188   University of Florida, Gainesville, Florida.

189   The isotope samples were loaded into Eppendorf capsules and placed in a 50-position automated

190   Zero Blank sample carousel on a Carlo Erba NA1500 CNS elemental analyzer. After combustion

191   in a quartz column at 1020 °C in an oxygen-rich atmosphere, the sample gas was transported in a

192   He carrier stream and passed through a hot reduction column (650 °C) consisting of elemental

193   copper to remove oxygen. The effluent stream then passed through a chemical (magnesium

194   perchlorate) trap to remove water, followed by a 3 m Gas chromatography (GC) column at 45 °C

195   to separate N_2 from CO_2. The sample gas next passed into a ConFlo II preparation system and

196   into the inlet of a mass spectrometer running in continuous flow mode, where the sample gas was

197 measured relative to laboratory reference N_2 and CO_2 gases. The carbon isotopic results were

198 expressed in standard delta notation relative to Vienna Pee Dee Belemnite (VPDB). The nitrogen

199 isotopic results were expressed in standard delta notation relative to atmospheric air. The

200 standard deviations of $\delta^{13}C$ and $\delta^{15}N$ replicate analyses were estimated; the precision values were

201 0.074 and 0.148 for carbon and nitrogen isotope measurements, respectively. Carbon and

202 nitrogen samples were analyzed in a dual isotope mode. Ratios are expressed as:

203 δX (‰) = [($R_{sample}/ R_{standard}$) -1)] x 1000; where $R_{sample}= {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$.

204

205 *Data analysis*: The relative contribution of algae to the diet of the sea urchins *D. mexicanum* and

206 *E. thouarsii* was estimated with a Bayesian isotopic mixing model (SIAR, Parnell & Jackson,

207 2013), which included the isotopic signatures, fractionation and variability to estimate the

208 probability distribution of the contribution of the food source to a mixture. This procedure

209 supplied accurate information about the contribution of algal species to the sea urchin tissues

210 recognized the main components of the diet under different conditions (Peterson, 1999; Fry

211 2006; Wing et al., 2008). Lipid extractions in sea urchins was not necessary since Aristotle

212 lantern´s muscle is low in lipids, on the other hand when the C:N ratios are lower than 3.5 it is

213 not recommended (Post et al., 2007) see Table S1. The isotopic discrimination factor values used

214 to run the model were 2.4±1.6 ‰ (mean ± SD) for $\delta^{15}N$, and 0.4 ±1.3 ‰ for $\delta^{13}C$ (Fry & Sherr,

215 1984; Minagwa & Wada, 1984; Michener & Schell, 1994; Moore & Semmens, 2008). The

216 results of the mixing model showing the calculated sea urchin dietary proportions were

217 represented as box plots, indicating the 25%, 75%, and 95% of credibility intervals (Fig 2).

218 The niche width and overlap for the sea urchins were estimated with Stable Isotope Bayesian

219 Ellipses in R (SIBER) (Jackson et al., 2011) from the SIAR package (Parnell & Jackson, 2013).

220 This analysis uses metrics based on ellipses and provides the standard ellipse corrected area

221 (SEA_c) used as the trophic niche breadth and the overlap between ellipses, where values close to

222 1 represent a higher trophic overlap.

223 Prior to the statistical analysis, the homogeneity and normality of variance were tested by

224 performing a Kolmogorov-Smirnov and a Cochran's test (Zar, 2010). Statistical difference was

225 performed comparing $\delta^{15}N$ and $\delta^{13}C$ values between species. In addition, the algal biomass

226   between sites was evaluated with a one-way ANOVA, with site as a fixed factor. The statistical

227   analyses were performed using R with an alpha of 0.05 (R Core Team, 2014).

228

229   **Results**

230   The benthic communities in Ecuadorian rocky reefs ranged between habitats dominated by

231   macroalgae and live corals (LA), and habitats dominated by turf and coral skeletons (PS). Site

232   estimates for perturbation and complexity are outlined in Table 1. LA is a site with structural

233   complexity and dominance of branched erect algae, while PS has low structural complexity and

234   dominance of turf (Table 1).

235

236   The algae collected in LA were *Asparagopsis armata*, *Dictyota dichotoma*, *Lobophora*

237   *variegata*, *Polysiphonia* spp., and *Sargassum* spp, while in PS were *D. dichotoma*, *L. variegata*,

238   and *Polysiphonia* spp. The greatest algal biomass was recorded for *L. variegata* at both sites,

239   while *D. dichotoma* was the algae with the lowest biomass at both localities (Table 2). Overall,

240   the biomass average values ranged from 35.8 ± 9.73 g (dry weight) m^{-2} for PS to 143.00 ± 20.67

241   g m^{-2} in LA. We found significant differences between both sites (ANOVA, df= 1, F= 3.60, p<

242   0.01). The overall algal δ^{15}N fluctuated from 5.05 to 9.49‰ (Table 3). PS displayed the highest

243   mean values of nitrogen with *D. dichotoma* (7.60 ± 0.53‰). At LA, *Polysiphonia* spp. exhibited

244   the highest mean value for nitrogen (7.19 ± 1.13‰). We found significant differences in δ^{15}N

245   between sites (ANOVA, df= 1, F= 5.29, p= 0.02), taking into account all the algae isotopic

246   signatures. As for δ^{13}C, ratios fluctuated from -23.65 to -6.90‰, with LA displaying the most

247   negative values (*A. armata*). There was no significant difference in δ^{13}C among sites (ANOVA,

248   DF=1, F= 1.41, p>0.05).

249

250   Values of δ^{15}N were particularly different between the two species of sea urchins (ANOVA, df=

251   1, F= 20.10, p < 0.001). The isotopic value of δ^{15}N for *D. mexicanum* ranged from 11.38 to

252   12.99‰, whereas *E. thouarsii* displayed values from 12.31 to 14.15‰. The average values of

253   δ^{13}C and δ^{15}N estimated for *D. mexicanum* in LA were -16.67 ± 0.04 and 11.53 ± 0.14‰,

254   respectively, while *E. thouarsii* displayed -15.46 ± 0.16‰ and 12.84 ± 0.40‰, respectively. In

255   PS, the *D. mexicanum* isotopic signals were -16.25 ± 0.39‰ for δ¹³C and 12.62 ± 0.22‰ for

256   δ¹⁵N; while *E. thouarsii* displayed -15.41 ± 0.43‰ for δ¹³C and 13.54 ± 0.47‰ for δ¹⁵N. We

257   found significant differences in δ¹³C between species (ANOVA, df 1, F= 49.31, p < 0.0001), and

258   the most negative values were found at LA. The δ¹⁵N showed the same patterns as those algae

259   (higher values for PS). δ¹⁵N ratios of both sea urchins differed between the study sites, as LA

260   reported lower values than PS (ANOVA, df 1, F= 7.59, p < 0.01). The most notorious difference

261   was due to *D. mexicanum* (ANOVA, df 1, F= 82.41, p < 0.0001).

262

263   The mixing models provided evidence for the contribution of different algal resources for both

264   sites and species. The SIAR analysis showed that *Sargassum* spp. was the most important

265   resource for *D. mexicanum* in LA (up to 43%), followed by *D. dichotoma* and *A. armata* as

266   secondary resources (up to 37% for both). Likewise, *Sargassum* spp. was the main algal resource

267   for *E. thouarsii* in the same locality (up to 44%), followed by *Polysiphonia* spp. (up to 41%)

268   (Table 4). Contrasting, at PS the main macroalgal contributor was *D. dichotoma* for both sea

269   urchins (Fig. 2), with up to 85% of the proportional contribution for *D. mexicanum* and close to

270   75% for *E. thouarsii.* Table 5 shows data on isotopic niche breadth as measured by the corrected

271   standard ellipse area (SEAc). The main difference in the trophic niche breadth was caused by *E.*

272   *thouarsii* with a difference probability of 52%; overlap between species isotopic niches was not

273   found in any case (Fig. 3), but the SEAc was higher for *E. thouarsii* in both sites with 0.25 in LA

274   and 0.46 in PS (Table 5).

275

276   **Discussion**

277   There is very little information on the ecology of the Ecuadorian coast, and no data pertaining to

278   trophic relationships among sea urchins, apart from this study. The majority of the available

279   information on Ecuador came from studies conducted on Galapagos reefs (Glynn, Wellington &

280   Birkeland, 1979; Glynn & Wellington, 1983; Glynn, 2003; Glynn 2004; Glynn et al., 2009). The

281   rocky reefs examined in this study were selected to establish the baseline of the trophic ecology

282   of two rocky reef areas, with different disturbance levels in the Ecuadorian mainland coast. The

283   presence of *D. mexicanum* was related to the rocky bottoms of LA, where algal presence were

284   more frequent than in the disturbed site (PS). The population density of *E. thouarsii* was higher

285   at the disturbed site (N. Cabanillas-Terán, unpublished data). This study demonstrated that algal

286   abundance is not always equivalent to assimilation by the consumer. For instance, *L. variegata*

287   displayed the lowest dietary contribution at PS and LA for both sea urchins, although it exhibited

288   the highest average biomass at both sites. Grazing preference by *D. mexicanum* and *E. thouarsii*

289   was not related to algal biomass.

290   The isotopic results characterized different algal assemblages that were specific to each rocky

291   reef bottom (branched macroalgae for LA and turf for PS). The values of $\delta^{15}N$ in algae in this

292   study ranged from 5.05‰ to 9.49‰. This result agreed with the ranges of variation reported in

293   other studies (Owens, 1987). The values of $\delta^{13}C$ fluctuated from -23.65 to -6.90‰ and agreed

294   with data from Fry & Sherr (1984), who reviewed the $\delta^{13}C$ data of benthic algae, noting that

295   values ranged between -30 to -5‰. The different algae species constituting the community of LA

296   showed isotopic values that were closer together, but with a broader cloud distribution in the C

297   vs N biplot of points relative to what was observed in PS. This suggests a more complex trophic

298   net and shows how primary consumers interact with their resources (McClanahan, 1988; Phillips

299   & Gregg, 2003).

300   The isotopic ratios of $\delta^{15}N$ could be influenced by two main factors. One factor pertains to

301   changes in dissolved nitrogen, although these changes primarily affect the microscopic algal

302   communities or communities living near upwelling zones (Jennings et al., 1997; Polunin &

303   Pinnegar, 2002). The other factor is the anthropogenic impact (Bode, Alvarez-Ossorio & Varela,

304   2006), affecting the communities near the coastline. In this case, the community most affected by

305   urban impact was PS, located in front of Manta Port. In this port, human density is higher than

306   1000 ind/km^{-2}, and artisanal and industrial fishery contribute to nitrogen input, as well as the

307   hotel zone and discharges from tuna processing.

308

309   For algae found in both sites (*D. dichotoma*, *L. variegata* and *Polysiphonia* spp.), the average

310    $\delta^{15}N$ were higher in PS. This agrees with other areas with high anthropogenic influence where

311    $\delta^{15}N$ values tended to be higher (Wada, Kadonaga & Matsuo, 1975; Michener & Schell, 1994).

312   Although both localities shared species, the isotopic values for both localities were different

313   because each system had its own structure. The erected branched algae *A. armata* and *Sargassum*

314   spp. (not found in PS), contributed to the structural complexity founded in LA.

315

316   Variations in carbon and nitrogen ratios gave us information on trophic spectrum inherent to

317   each site and the contribution of algal species to the sea urchin tissues display information about

318   how consumers assimilate the resources when they inhabit disturbed and/or undisturbed sites.

319   Although both sea urchin species can share the same food resources, we found that their

320   ecological roles were different and there are differences between species in terms of assimilation.

321   This could explain the fact that $\delta^{15}N$ values in the tissues of *E. thouarsii* were higher for both

322   localities, even though both sea urchin species showed a preference for the same species *D.*

323   *dichotoma*. No overlap of isotope niche breadth of the echinoids was found between the two

324   species (Fig. 3), but the isotopic values between species at PS were closer, suggesting increased

325   competition due to the lack of resources. This result coincided with the mixing model because

326   the two species of sea urchins preferentially consumed similar proportions of the same species.

327   Moreover the SEAc was larger for *E. thouarsii* at both sites, and in LA the niche trophic distance

328   between *D. mexicanum* and *E. thouarsii* was very conspicuous, while in PS the two species of

329   sea urchins are closer (Fig. 3). A low degree of feeding specialization suggests that the sea

330   urchins adapt their foraging behavior to algae availability, being most evident for *E. thouarsii*,

331   that exhibits a broader trophic niche.

332   The grazing behavior of these sea urchins agreed with the findings by Glynn, Wellington &

333   Birkeland (1979) in the Galápagos Islands, as their grazing was stronger in those areas with 30%

334   or less coral cover. Previous studies highlighted that *E. thouarsii* limited coral growth, as this

335   echinoid interfered with the development of the reef frame and with the ability to modify the

336   habitat structure (Bak, 1994; Carpenter, 1981; Sonnenholzner, Ladah & Lafferty, 2009). We

337   considered *D. mexicanum* to be an important grazer for the rocky bottoms ecosystems,

338   considering that changes in its population caused significant changes in the algal cover of those

339   areas.

340   Our results supported the evidence that *D. mexicanum* and *E. thouarsii* were coexistent species

341   that play a significant role as herbivores. Nevertheless, they apparently eat whatever they find,

342   and the food items are incorporated differentially between the species. *Diadema mexicanum*

343 grazing effect on algal diversity and community structure is important in the process of
344 formation and maintenance of rocky reefs in Ecuador. This has also been observed in other areas
345 of the ETP where *D. mexicanum* has a relevant role in the recruitment of corals (Alvarado,
346 Cortés & Reyes-Bonilla, 2012). This was also observed in Caribbean reefs with *D. antillarum*
347 (Macintyre, Glynn & Hinds, 2005; Mumby et al., 2006; Idjadi, Haring & Precht, 2010; Sandin &
348 McNamara, 2012), and in sublittoral ecosystems of the Canary Islands with *D. africanum* (Alves
349 et al., 2003; Tuya et al., 2004; Hernández et al., 2005; Hernández et al., 2008; Sangil et al., 2014;
350 Cabanillas-Terán et al., 2015).

351 The standard ellipses areas values (Table 5) indicated that niche partitioning may vary depending
352 on different disturbance levels between sites; however, the diets of *D. mexicanum* and *E.*
353 *thouarsii* not only depend on the disturbance condition. For instance, *Dictyota dichotoma* was an
354 important component of the diet of *D. mexicanum* and *E. thouarsii* in the disturbed and
355 undisturbed sites, while *Polysiphonia* spp. was important in disturbed bottoms, where isotopic
356 algal signals are closer to each other. This could lead to a greater number of resource overlap at
357 PS than at LA.

358 Differential assimilation and niche partitioning are just snapshots, It is important to depict how
359 the shape of the food web varies in time and space (Layman et al., 2007 & Schmidt et al., 2007),
360 so it is necessary to carry out more extensive spatial and temporal research. Likewise it is
361 necessary to deepen research to analyze if the narrower niche amplitude (SEAc) of *D.*
362 *mexicanum* and its associated presence to scleractian corals (at LA) is consistent to what is
363 happening in the Caribbean, where its presence provides suitable habitat for coral recruitment.
364 The feeding success of herbivores is associated with the competition level for resources;
365 therefore, sympatric species are exposed to a potential trophic overlap. The most pristine zone
366 (LA) exhibited smaller SEAc (considering values per species) and nitrogen values, which
367 indicate a trophic niche partitioning between the main sea urchins on the Ecuadorian coast. But,
368 the limitation of resources could lead to trophic overlap and stronger habitat degradation.
369

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375

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644   **Figures**
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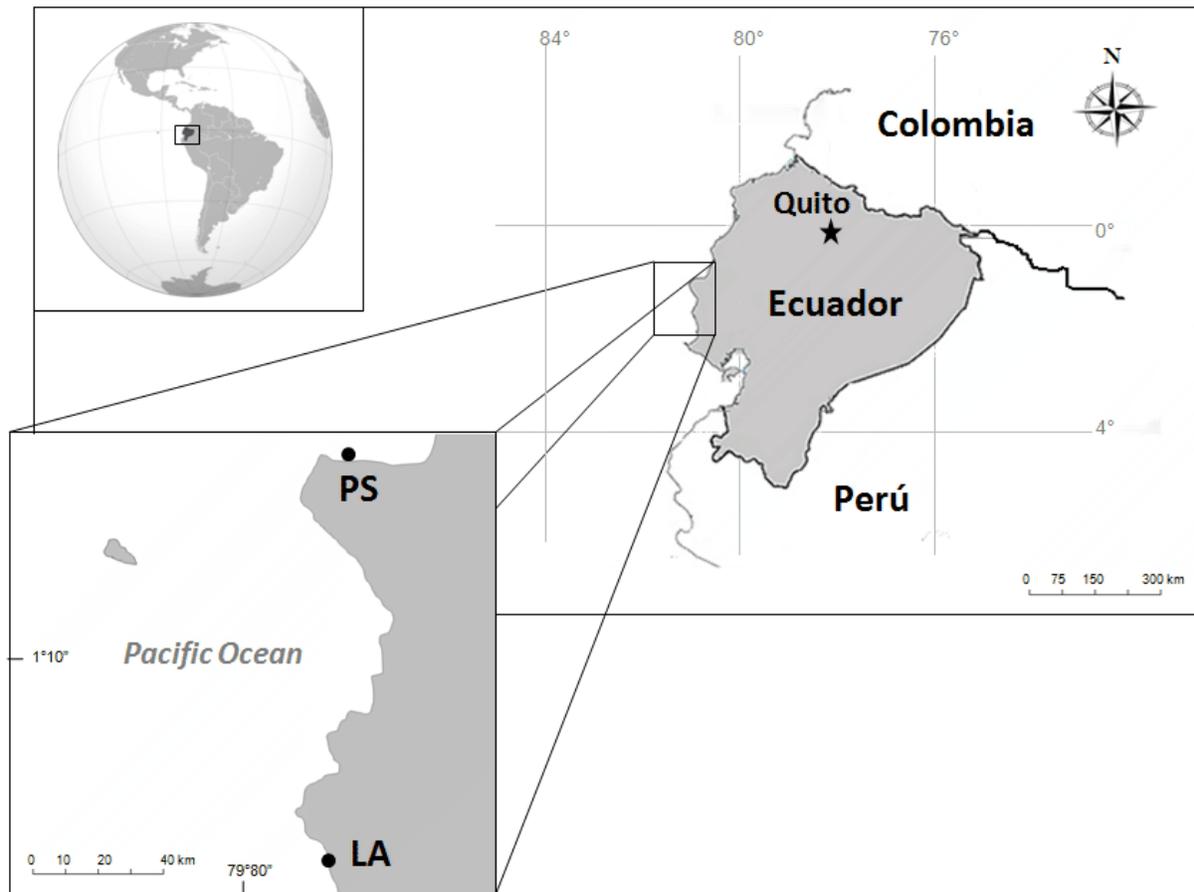
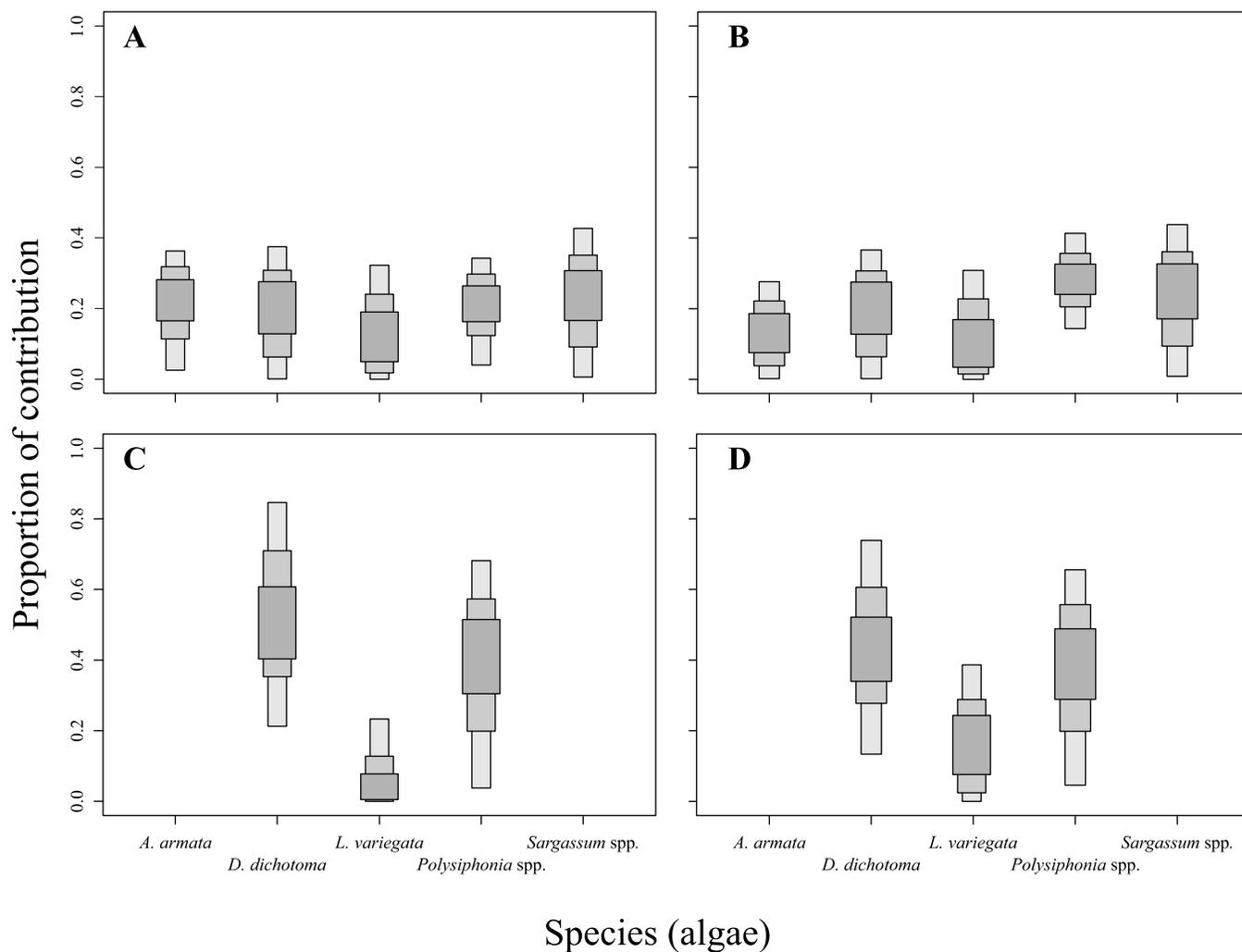

647
648   **Figure 1.** Study area and sampling sites in the coast of Ecuador: Los Ahorcados (LA) and
649   Perpetuo Socorro (PS).

651
652   **Figure 2.** Contribution rates of algae to the diet of the two sea urchin species. Results are shown
653   as 25, 75 and 95% of credibility intervals. A) Represents the contribution for *Diadema*
654   *mexicanum* in Los Ahorcados (LA), B) for *Eucidaris thouarsii* in LA, C) *D. mexicanum* in
655   Perpetuo Socorro (PS), and D) *E. thouarsii* in PS.

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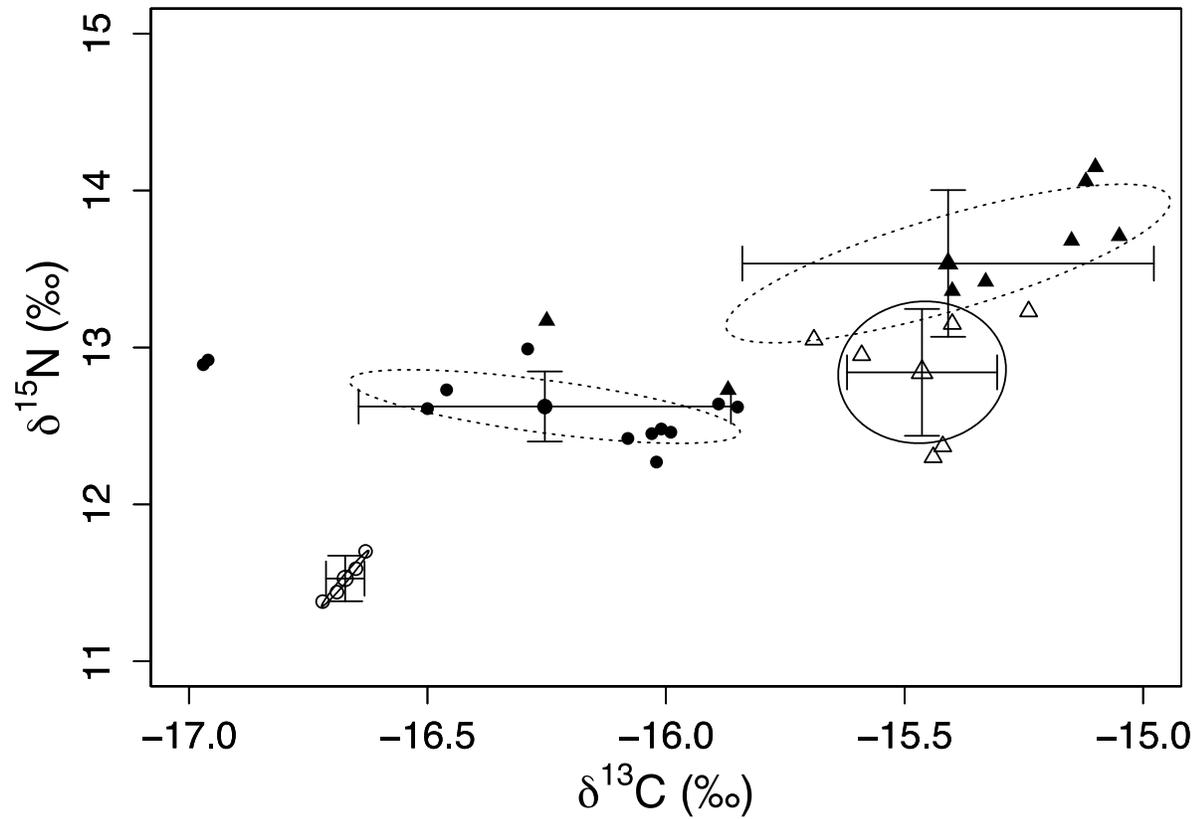
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659 **Figure 3.** Isotope niche breadth of the echinoids, *D. mexicanum* (circles) and *E. thouarsii*
660 (triangles) in Los Ahorcados (white symbols and solid line) and Perpetuo Socorro (black
661 symbols and dotted line).

663 **Tables**
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665
666 **Table 1.** Category of coral-rocky reef sites and source of human impact.
667

Site	Source of human impact	Human population density (ind·km⁻²)	Distance from sampling site to Source of human impact (km)	Rugosity Index (RI)	Category
Los Ahorcados (LA)	Artesanal Fishery + hotel zone	54.55	17.24	2.32	Undisturbed
Perpetuo Socorro (PS)	Artesanal and industrial Fishery+ hotel zone+ industry discharge	1046.34	3.43	1.10	Disturbed

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672 **Table 2.** Average algal biomass in grams (dry weight) m^{-2} ± standard deviation at Los Ahorcados
673 (LA) and Perpetuo Socorro (PS).
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Species	LA	PS
A. armata	34.32 ± 16.98	-
D. dichotoma	4.69 ± 1.90	0.60 ± 0.20
L. variegata	66.77 ± 24.52	23.26 ± 12.61
Polysiphonia spp.	30.73 ± 12.82	16.38 ± 6.26
Sargassum spp.	5.94 ± 3.09	-

686

Table 3. Mean ± standard deviation values of $\delta^{13}C$ and $\delta^{15}N$ of algal genus considered in the mixing model analysis taken from Los Ahorcados and Perpetuo Socorro.

	Los Ahorcados			Perpetuo Socorro		
Species	**$\delta^{13}C$**		**$\delta^{15}N$**	**Species**	**$\delta^{13}C$**	**$\delta^{15}N$**
A. armata (n=4)	-23.63 ±0.10	5.68	±0.02	-	-	-	-
D. dichotomaa (n=4)	-17.30 ±1.94	6.65	±0.791	*D. dichotoma* (n=3)	-15.27 ±3.05	7.60 ±0.53
L. variegata (n=4)	-15.73 ±3.331	5.89	±0.638	*L. variegata* (n=3)	-12.02 ±0.60	7.06 ±1.08
Polysiphonia spp. (n=6)	-9.33 ±1.759	7.19	±1.129	*Polysiphonia* spp. (n=4)	-14.72 ±3.04	7.38 ±0.36
Sargassum spp. (n=4)	-18.30 ±0.07	6.97	±0.06	-	-	-	-

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692 **Table 4.** Average percentage (%) contribution of algal **species** to the diet of the sea urchins *D.*
693 *mexicanum* and *E. thouarsii* at Los Ahorcados (LA) and Perpetuo Socorro (PS) produced by the
694 SIAR model using isotope values from algae. Minimum and maximum values for each algae are
695 shown in parentheses.

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Species	Diadema mexicanum		Eucidaris thouarsii	
	LA	PS	LA	PS
A. armata	21 (2-37)	-	14 (0-28)	-
D. dichotoma	20 (0-37)	52 (21-85)	19 (0-37)	44 (13-75)
L. variegata	16 (0-32)	9 (0-23)	15 (0-31)	19 (0-38)
Polysiphonia spp.	20 (04-35)	38 (3-67)	28 (15-41)	38 (4-66)
Sargassum spp.	23 (1-43)	-	24 (1-44)	-

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699 **Table 5.** Trophic niche breadth of sea urchins calculated by SIBER analysis of muscle values.
700 SEAc: corrected standard ellipse area. The right column shows statistical differences in SEA.
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Species	SEAc	Ellipses areas: Group differences probability (%)
D. mexicanum (LA)	0.005	
		1 vs 2 (10.4)*
D. mexicanum (PS)	0.218	
E. thouarsii (LA)	0.250	
		1 vs 2 (52.0)*
E. thouarsii (PS)	0.457	

*Group 1: Los Ahorcados (LA); Group 2: Perpetuo Socorro (PS)

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