Ontogenetic foraging activity and feeding selectivity of the Brazilian endemic parrotfish *Scarus zelindae*

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Parrotfish are fundamental species in controlling algae phase-shifts and ensuring the resilience of coral reefs. Nevertheless, little is known on their ecological role in the South-western Atlantic Ocean. The present study analysed the ontogenetic foraging activity and feeding selectivity of the Brazilian endemic parrotfish *Scarus zelindae* using behavioural observation and benthic composition analyses. We found a significant negative relationship between fish size and feeding rates for *S. zelindae* individuals. Thus, terminal phase individuals forage with lower feeding rates compared to juveniles and initial phase individuals. The highest relative foraging frequency of *S. zelindae* was on epilithic algae matrix (EAM) with similar values for juveniles (86.6%), initial phase (88.1%) and terminal phase (88.6%) individuals. The second preferred benthos for juveniles was sponge (11.6%) compared with initial (4.5%) and terminal life phases (1.3%). Different life phases of *S. zelindae* foraged on different benthos according to their availability. Based on Ivlev's electivity index, juveniles selected EAM and sponge, while initial phase and terminal phase individuals only selected EAM. Our findings demonstrate that the foraging frequency of the endemic parrotfish *S. zelindae* is reduced according to body size and that there is a slight ontogenetic change in feeding selectivity. Therefore, ecological knowledge of ontogenetic variations on resource use is critical for the remaining parrotfish populations which have been dramatically reduced in the Southwestern Atlantic Ocean.

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Abstract

Parrotfish are fundamental species in controlling algae phase-shifts and ensuring the resilience of coral reefs. Nevertheless, little is known on their ecological role in the South-western Atlantic Ocean. The present study analysed the ontogenetic foraging activity and feeding selectivity of the Brazilian endemic parrotfish *Scarus zelindae* using behavioural observation and benthic composition analyses. We found a significant negative relationship between fish size and feeding rates for *S. zelindae* individuals. Thus, terminal phase individuals forage with lower feeding rates compared to juveniles and initial phase individuals. The highest relative foraging frequency of *S. zelindae* was on epilithic algae matrix (EAM) with similar values for juveniles (86.6%), initial phase (88.1%) and terminal phase (88.6%) individuals. The second preferred benthos for juveniles was sponge (11.6%) compared with initial (4.5%) and terminal life phases (1.3%). Different life phases of *S. zelindae* foraged on different benthos according to their availability. Based on Ivlev's electivity index, juveniles selected EAM and sponge, while initial phase and terminal phase individuals only selected EAM. Our findings demonstrate that the foraging frequency of the endemic parrotfish *S. zelindae* is reduced according to body size and that there is a slight ontogenetic change in feeding selectivity. Therefore, ecological knowledge of ontogenetic variations on resource use is critical for the remaining parrotfish populations, which have been dramatically reduced in the Southwestern Atlantic Ocean.

51 **Introduction**

52 Species may select vital resources (*e.g.* habitat, food and mates) according to

53 their availability in natural communities. Yet, these resources are subjected to temporal

54 and spatial fluctuation that influences species patterns of resource use (Holling, 1973,

55 Holt et al., 2008, Pekkonen et al., 2013). Many coral reef fishes change their

56 distribution and diet according to the availability of food resources; a trend that has

57 already been investigated for many families such as Haemulidae (Pereira and Ferreira,

58 2013), Pomacentridae (Frédérich et al., 2009, Waldner and Robertson, 1980) and

59 Scaridae (Plass-Johnson et al., 2013). For instance, parrotfish behavior seems to change

60 in response to food resource availability, meaning local variation in algae abundance

61 can influence fish feeding preferences and modify parrotfish patterns of abundance

62 (Russ, 2003, Hoey et al., 2011).

63 Parrotfishes are believed to be important contributors to healthy reefs because

64 they consume algae that compete with corals for space in tropical waters (Hughes et al.,

65 2003, Graham et al., 2013). Grazing activity also provides open space for coral

66 recruitment, securing better conditions for coral reef development during recent strong

67 impacts such as climate change and global warming (Bennett et al., 2015). As a

68 generalist group, parrotfish foraging activity varies strongly according to morphology,

69 life phase, and food availability (Bonaldo et al., 2014). They are usually classified in

70 three main functional groups: browsers, scrapers and excavators (Bellwood and Choat,

71 1990, Streelman et al., 2002, Francini-Filho et al., 2008, Bonaldo et al., 2014). *Browsers*

72 tend to cut off macroalgae, leaving no scars on the substrate (e.g. *Sparisoma* spp.),

73 *scrapers* feed at high rates leaving only a superficial scrape and normally do not damage

74 coral surface (e.g. *Scarus* spp.) and *excavators* feed at low rates removing large portions

75 of the substratum or coral using their robust jaws, leaving noticeable scars (e.g.

76 *Bolbometopon muricatum*) (Bellwood and Choat, 1990, Streelman et al., 2002).

77   Ontogenetic changes in foraging activity and feeding preference are relevant for

78 many coral reef fishes, including parrotfish (Bellwood, 1988, Pereira and Ferreira,

79 2013). Bellwood et al. (2006) suggested that newly settled *Scarus* individuals feed on

80 crustaceans, whilst larger juveniles almost exclusively ingest algae and detritus.

81 Additionally, morphological and anatomical body changes throughout ontogeny also

82 directly influence parrotfish feeding preferences. As parrotfish grow, the enlargement

83 and development of the oral jaws and associated musculature allow them to bite deeper

84 into the benthos, effectively scraping or even excavating the substratum (Bellwood and

85 Choat, 1990, Bonaldo et al., 2014, Francini-Filho et al., 2008). Although much research

86 has been conducted analysing ontogenetic changes on parrotfish ecology in the Indo-

87 Pacific and Caribbean, few studies have attempted to analyse variations on foraging

88 activity and feeding preference across different life stages in endemic parrotfish species

89 of the Southwestern Atlantic Ocean.

90   *Scarus zelindae* is an endemic parrotfish from Brazilian waters occurring on

91 coral and rocky reefs at depths up to 60 m. Previous studies have shown that *S.*

92 *zelindae* is predominantly herbivorous, ingesting algae and detritus (Ferreira and

93 Gonçalves, 2006). Francini-Filho et al. (2010) found *S. zelindae* had a preference for

94 turf algae and classified this species as a scraper. However, larger terminal phase

95 individuals can also act as excavators (Francini-Filho et al., 2008; Francini-Filho et al.,

96 2010,) whereas juveniles have been recorded feeding on *Millepora* spp. fire-corals with

97 feeding rates of up to 0.58 ± 0.35 bites/min (Pereira et al., 2012). Nevertheless, these

98 preliminary studies were more naturalist and did not systematically test for ontogenetic

99 changes on *S. zelindae* resource use. Therefore, the relationship of their ontogenetic

100 foraging activity and feeding selectivity is still unclear. The ecological role of parrotfish

101 on tropical coral reefs is evident; hence, it is critical to better understand ontogenetic

102 changes in their feeding patterns and the different effects parrotfish have on benthic

103 communities according to size. Adults are normally targeted by local fisheries and the

104 large bodied individuals could be the most effective individuals controlling algal

105 growth. However, this has never been analysed for *Scarus* individuals in the

106 Southwestern Atlantic Ocean. If *S. zelindae* display ontogenetic changes in feeding

107 activity and foraging preferences, then individuals of different life phases could have a

108 disproportional ecological role in shaping benthic communities.

109   The present study aims to understand the ontogenetic foraging activity and

110 feeding selectivity of the endemic parrotfish *Scarus zelindae* on tropical coral reefs. To

111 achieve this goal, the foraging intensity and feeding behaviour of juvenile, initial phase

112 (IP) and terminal life phase (TP) individuals were recorded using behavioural

113 observations. The benthic composition at foraging sites was also examined to determine

114 resource availability relative to foraging behavior. Specifically, we analysed if

115 individuals of different life phases selected food resources according to substratum

116 availability or whether they showed preferences for particular food types.

117

118 **Methods**

119

120 *Study area*

121   The studied coral reef complex is located within the limits of the "Costa dos

122 Corais" marine protected area (MPA) which encompasses 135 km of coastline in

123 Pernambuco State of North-eastern Brazil. The "Costa dos Corais" MPA was the first

124 Brazilian federal conservation area that included coastal reefs and is the largest

125   multiple-use MPA in the country (Maida & Ferreira, 1997). Deeper reefs (from 25 to 35

126   meters depth) (8°49' S and 35° 03' W) were used as sampling sites. These reefs are a

127   series of continuous long blocks with sand intervals and high structural complexity. The

128   benthic community is mainly composed of epilithic algae matrix, coralline algae,

129   sponges and hard corals (Supplementary material - Video S1). Deeper reefs were used

130   as sampling sites considering that the shallow reefs have been extremely impacted by

131   spearfishing and it is currently difficult to observe *S. zelindae* terminal phase individuals

132   in these areas (author's personal observation). Therefore, these deeper reefs represent a

133   unique opportunity to analyse parrotfish ontogenetic foraging activity and feeding

134   selectivity because all the different life phases have a representative abundance for

135   behavioural observations.

136

137   *Foraging activity*

138   Feeding rates (bites per minute) of *Scarus zelindae* individuals were obtained

139   from animal focal sampling always carried out by one observer (SiSBio − 16109)

140   (Altmann, 1974). Dives were conducted by SCUBA from December 2014 to March

141   2015. Individuals were observed over 5 minute intervals, except when the individuals

142   evaded the observer. On average, a minimum distance of 5 meters was maintained

143   between the observer and each fish in order to reduce observer impact on fish behaviour

144   (Pereira et al., 2016) whilst increasing identification accuracy of feeding selectivity.

145   During each observation session divers recorded feeding rates (total number of bites) of

146   each individual and the substratum type where feeding was observed. Fish size (total

147   length - TL) was visually estimated and individuals were categorized as juvenile, initial

148   and terminal phase according to size. Individuals were also classified into different life

149   phases based upon variation in their patterns of coloration (Figure 1). A total of 20

150   individuals from each life phase (juvenile, initial and terminal phase) where recorded

151   during 5 min observation sessions totalling 300 minutes of direct observation.

152

153   ***Benthic community***

154   The benthic composition was also analyzed in the reef complex where the

155   foraging behaviour of *S. zelindae* was recorded, using the point intercept transect

156   method (Meese and Tomich, 1992). A 20 meter transect belt was used in which the

157   diver registered the substrate at 0.5 m intervals. In order to avoid temporal variations in

158   resource availability all the benthic surveys were performed during the same dives and

159   same period as feeding behavioral observations (from December 2014 to March 2015).

160   A total of 20 randomly distributed belt transects were conducted along the top of the

161   reef at an average depth of 25 m. The benthic community was classified using the

162   categories: epilithic algal matrix (EAM), coralline algae, sand, sponge, hard coral,

163   macroalgae and bare rock.

164

165   ***Data analyses***

166   One-way analysis of variance (ANOVA) was used to compare mean feeding

167   rates of *S. zelindae* individuals on different life phases. Post hoc comparisons based on

168   Tukey HSD test were subsequently made for the significant factors using Statistica 10

169   (StatSoft Inc. 2011). Linear regressions were used to compare the bite rates (bites/min^{-1})

170   with parrotfish body size (cm).

171   To test differences between the relative foraging frequency of *S. zelindae*

172   individuals on different benthic categories we applied a permutational multivariate

173   analysis of variance (PERMANOVA). *S. zelindae* foraging frequency data on different

174   benthic categories were log transformed (X+1) and reassembled in a Bray-Curtis

175 similarity matrix. Unrestricted permutation of raw data was used as the best technique

176 for analyzing one factor. A permutational analysis of multivariate dispersions

177 (PERMIDISP) was also applied to analyze whether the multivariate variations were

178 homogeneous or not (Anderson 2001, Anderson and Walsh, 2013). PERMANOVA and

179 PERMIDISP were conducted using Primer-e 6 PERMANOVA+1.0 software (Ver.

180 6.1.14) 227 (Anderson and Gorley, 2007).

181 Principal component analysis (PCA) was used to investigate correlations

182 between *S. zelindae* feeding preferences and individual life phases, with the total

183 number of bites per substratum category used as the main data. All the data were

184 standardized and log-transformed prior to multivariate analyses. PCA was performed

185 using Primer-e 6 PERMANOVA+1.0 software (Ver. 6.1.14)

186 Ivlev's electivity index (Ivlev, 1961) was calculated to examine the ontogenetic

187 feeding selectivity of *S. zelindae* individuals. The index was calculated using the

188 following equation:

$$E_i = \frac{r_i - p_i}{r_i + p_i}$$

189

190 where electivity for the benthic category i (E_i) was considered the percentage of

191 availability of the benthic category i (p_i) in the field and the percentage of feeding rates

192 on this specific benthic category i (r_i). E values vary from -1.0 to $+1.0$ once negative

193 values indicate avoidance, zero indicates random selection, and positive values indicate

194 active selection. In order to estimate 95% confidence intervals of Ivlev's index values,

195 bootstrapping procedures (9999 simulations) were performed on individual feeding

196 rates (keeping resource availability constant). Variability analyses were performed

197 following procedures used by Smith (1982).

198

199

200   **Results**

201   *Feeding activity*

202   The feeding rate of *S. zelindae* was 34.6 ± 6.6 (bites/min^{-1}) mean ± s.d. for

203   juveniles, 17.9 ± 4.9 for initial phase and 14.9 ± 4.6 for terminal phase individuals.

204   Significant differences in foraging rates were observed among life phases (ANOVA; F

205   = 224.56; $p < 0.01$). Tukey HSD test showed significant differences between juveniles

206   and initial phase ($p < 0.01$) and also between juveniles and terminal phase ($p <$

207   0.01). However, no significant difference in foraging rate was observed between initial

208   phase and terminal phase ($p = 0.10$).

209   There was a significant negative relationship between fish size (cm) and feeding

210   rates (bites/min^{-1}) for *S. zelindae* individuals ($R^2 = 0.51$; $p = 0.008$) emphasising a

211   reduction on feeding rates according to fish growth (Figure 2).

212   The relative foraging frequency of *S. zelindae* was highest on the EMA and this

213   was similar for all life phases; juveniles (86.6%), initial phase (88.1%) and terminal

214   phase (88.6%) (Figure 3). On the other hand, sponge was the second highest preferred

215   feeding substratum for juveniles (11.6%) foraged at a higher percentage compared with

216   other life phases: initial phase (4.5%) and terminal phase (1.3%). Terminal phase

217   individuals displayed a considerable foraging frequency on coralline algae (4.3%) and

218   macroalgae (4.5%) (Figure 3). No significant difference was recorded for the relative

219   frequency of foraging comparing *S. zelindae* individuals at different life phases

220   (PERMANOVA; Pseudo F = 1.31; $p = 0.21$).

221   The PCA analysis of *S. zelindae* foraging preference explained 98.1% of the

222   total variability; 76.8% PC1 and 21.4% PC2, respectively. The eigenvalue for PC1 was

223   262 and 73 for PC2. The analysis confirmed that EAM was the most used food resource

224   for all life phases (Figure 4). However, in juvenile individuals sponge was the second

225 most foraged resource, whereas, in terminal phase individuals it was macroalgae (Figure

226 4).

227

Substratum availability

229 The benthic substratum on feeding sites of *S. zelindae* was mainly composed by

230 EAM (38.0 %), coralline algae (18.7 %) and sand (13.5 %), which together represented

231 more than 70% of the benthic composition. The less representative categories were rock

232 (5.2 %) and macroalgae (7.2) which represented less than 15% of the benthos (Figure3).

233

Foraging selectivity

235 *S. zelindae* individuals at different life phases foraged on different benthos

236 according to their availability. Based on the Ivlev's electivity index, juveniles selected

237 EAM and sponge; however initial phase and terminal phase individuals only selected

238 EAM (Figure 5). The benthic categories sand, rock, coralline algae and hard coral were

239 negatively selected for all life phases. However, sponge and macroalgae were selected

240 differently during *S. zelindae* foraging activity; juveniles used sponge as a food resource

241 and terminal phase individuals had a low rejection for macroalgae (Figure 5).

242

Discussion

244 Parrotfish populations are under intense decline in the Southwestern Atlantic

245 Ocean with many species already accounted for a 50% reduction in their total

246 abundance in the last decades (Floeter et al., 2008, Bender et al., 2014). Despite this

247 evident decline, baseline knowledge on parrotfish ecological role, such as foraging

248 activity and ontogenetic changes in resource use are still scarce in the Atlantic Ocean.

249 Our findings demonstrate that the foraging activity of *S. zelindae* diminishes according

250 to body size. Additionally, we have shown that EAM was the preferred foraging

251 benthos for all life phases, with a lower rejection of sponge in juveniles and macroalgae

252 in terminal phase individuals. Based on the Ivlev's electivity index, juveniles positively

253 selected EAM and sponge; however, initial phase and terminal phase individuals only

254 selected EAM. It is worth mentioning that Ivlev's electivity index (i.e. foraging

255 selectivity) is the only variable that accounts for resource/food availability; therefore

256 Ivlev's electivity index is more likely to represent true foraging preferences.

257 Understanding variation in foraging can inform how fishing, which targets adult

258 parrotfish, may be altering the overall ecological role of parrotfishes in enhancing the

259 resilience of coral reefs. Removal of large parrotfish due to fishing can cause a release

260 of grazing pressure on EAM, thus allowing macroalgae to grow and outcompete with

261 corals.

262 Ecomorphological patterns of many Southwestern Atlantic Ocean parrotfish

263 species were recently analysed by Lellys (2014) using premaxilla, dentary and mouth

264 configuration data. Lellys (2014) demonstrated that the weaker and more mobile oral

265 apparatus of smaller *S. zelindae* individuals classify them as *scrapers*. Additionally, the

266 teeth cutting edges exhibited by small size *S. zelindae* individuals increases the contact

267 area of the jaw, spreading the force over the substrate during feeding behaviour and

268 therefore reducing bite force (Bellwood and Choat, 1990, Lellys 2014). In contrast,

269 according to Francini-Filho et al. (2010), *S. zelindae* terminal phase individuals could be

270 classified as *excavators*, feeding at low rates and remove large portions of the

271 substratum using their robust jaws, leaving noticeable scars. Results from the present

272 study confirm Francini-Filho et al. (2010) findings once the lowest feeding rates were

273 observed for terminal phase individuals that foraged primarily on EAM and coralline

274   algae. Larger parrotfish may feed at low rates taking fewer bites, because they are able

275   to acquire large amounts of food per bite due to larger bites.

276   Additionally, during our field observations we have recorded large *S. zelindae*

277   individuals removing portions of the substratum and ascertained some scars on the

278   benthic community (*e.g. Siderastrea stellata* coral colonies). Although variations in *S.*

279   *zelindae* foray size were not specifically analysed in the present study, terminal phase

280   individuals could have a higher impact on benthic communities compared to juveniles

281   and initial phase individuals due to larger jaw size as previously shown for other

282   parrotfishes (Bonaldo et al., 2014). Hence, larger bodied individuals are not only likely

283   taking larger bites but those bites are likely having a larger impact on the benthos due to

284   force/bite intensity. Future research using foray measurements could elucidate this

285   impact on benthic communities (*e.g.* bioerosion) and test the hypothesis that adults,

286   normally targeted by local fisheries, could be the most effective individuals controlling

287   algal growth.

288   Terminal phase individuals recorded in the present study displayed smaller

289   feeding rates compared to juveniles and initial phase individuals. This could be

290   associated with patrolling behaviour observed for larger parrotfish size classes, on a few

291   occasions during this study, which is likely to reduce their feeding rates once energy is

292   allocated for mating and patrolling (Van Rooij et al. 1996; Bonaldo et al., 2006).

293   Haremic parrotfish also tend to increase their territory size and therefore more time

294   should be used to protect this area (Mumby and Wabnitz 2002). Additionally, it has

295   been suggested recently that observer presence could reduce feeding rates of fishes on

296   coral reefs (Pereira et al., 2016). Consequently, the impact of observer presence could

297   be intensified on terminal phase individuals who are normally patrolling much more

298   often than individuals of other size classes.

299   Spatial variation in the availability of benthic resource could potentially

300   influence *S. zelindae* feeding preference during the present study. Therefore, we have

301   assessed the benthic community in foraging areas, to understand the ontogenetic

302   selective patterns according to resource availability. According to Bonaldo et al. (2014)

303   the availability and productivity of surfaces covered by EAM, the main feeding

304   substratum for most parrotfish, may directly influence the distribution and feeding

305   habitats of parrotfish. It is likely that EAM could be the most important food resource

306   for the Brazilian endemic parrotfish throughout the specie`s life due to their natural

307   preference for EAM and also the availability. However, juveniles also selected sponges

308   in the benthic community. The use of sponges as a food resource for juvenile

309   parrotfishes is uncommon; therefore, juveniles could be foraging on the mucus

310   associated with the sponges as well as ingesting algae biofilm that grow on top of

311   sponges (Randall and Hartman 1968, Wulff 2006). Similarly, Pereira et al. (2012)

312   observed juveniles of *S. zelindae* feeding on *Millepora* spp. fire-corals on Brazilian

313   coral reefs.

314   Fishing pressure on coral reefs (mainly spearfishing) normally targets larger

315   individuals, known as terminal phase. According to (Nunes et al., 2012) recreational

316   spearfishing often captures endemic and larger herbivorous species in Brazilian waters,

317   such as the endangered species *Scarus trispinosus* (Labridae). During many years of

318   diving on the coral reefs analysed in the present study, only a few rare individuals of

319   *Scarus trispinosus* were recorded. Additionally, following interviews conducted with

320   the local community in 2015, a dramatic reduction in the abundance of this endangered

321   species was reported (Pereira, PHC unpublished data). Hence, *Scarus trispinosus* is

322   becoming functionally extinct in Pernambuco state, outside of non-take zones, which is

323   a worrying trajectory that *S. zelindae* population seems to also be following. The

324   herbivore community at the deeper reefs (> 25m) was previously analysed in a pilot

325   study and the three most current abundant species were *Sparisoma axillare* (7.01

326   ind./100m²), *Scarus zelindae* (6.28 ind./100m²) and *Sparisoma frondosum* (3.39

327   ind./100m²) (authors unpublished data). By removing larger bodied individuals of

328   parrotfish we could be losing a unique and critical functional group on Southwestern

329   Atlantic Ocean.

330   As previously discussed, the creation of new marine protected areas ranks within

331   priority actions for reef fish conservation in Brazilian waters, due to high levels of

332   endemism (up to 30% in reef fishes) (Floeter et al., 2008, Schiavetti et al., 2013).

333   However, the effective supervision of the few existing marine protected areas in Brazil

334   represent the most urgent conservation action to protect *S. zelindae* and other large

335   Brazilian endemic parrotfish (Francini-Filho et al., 2010). Despite the fact that the reefs

336   analysed in the present study are included in the largest Brazilian marine protected area

337   (MPA), the abundance of large herbivores has been dramatically reduced in the last

338   decades. This trend highlights the fact that the creation of more MPAs is probably not

339   the most effective way to increase protection of endangered coral reef fishes.

340   Accordingly, it is important to increase surveillance and monitoring on already created

341   MPAs. Environmental education programmes and alternative livelihoods for local

342   communities are also important strategies to reduce fishing pressure on endangered

343   parrotfish species as previously observed in other developing countries such as Kenya

344   (Cinner et al., 2012, Carter and Garaway, 2013,) and Thailand (Bennett and Dearden,

345   2014).

346   Much discussion has arisen, mainly in the last decades, regarding the abundance

347   of parrotfishes and the resilience of coral reef ecosystems. Nevertheless, Adam et al.

348   (2015) suggested in a recent review that the evidence is mixed in showing that increases

349 in herbivory can promote coral recovery on Caribbean reefs. The impacts of herbivores

350 on coral reef ecosystems will vary greatly in space and time and will depend on

351 herbivore diversity and species identity. Additionally, Suchley et al., (2016) findings

352 contrast the coral reef top-down herbivore control paradigm and suggest that the role of

353 external factors could be important in making environmental conditions more

354 favourable for algae growth. Brazilian coral reefs are dominated by higher abundances

355 of algae and macroalgae abundance seems to explain a large proportion of variance in

356 reef fish abundance and species richness (Pereira et al., 2014). Therefore, it is critical to

357 better understand the ecological role of herbivorous parrotfish and the real ontogenetic

358 influence of these species on algae dominated reefs throughout the Southwestern

359 Atlantic Ocean.

360

361 **Acknowledgments**

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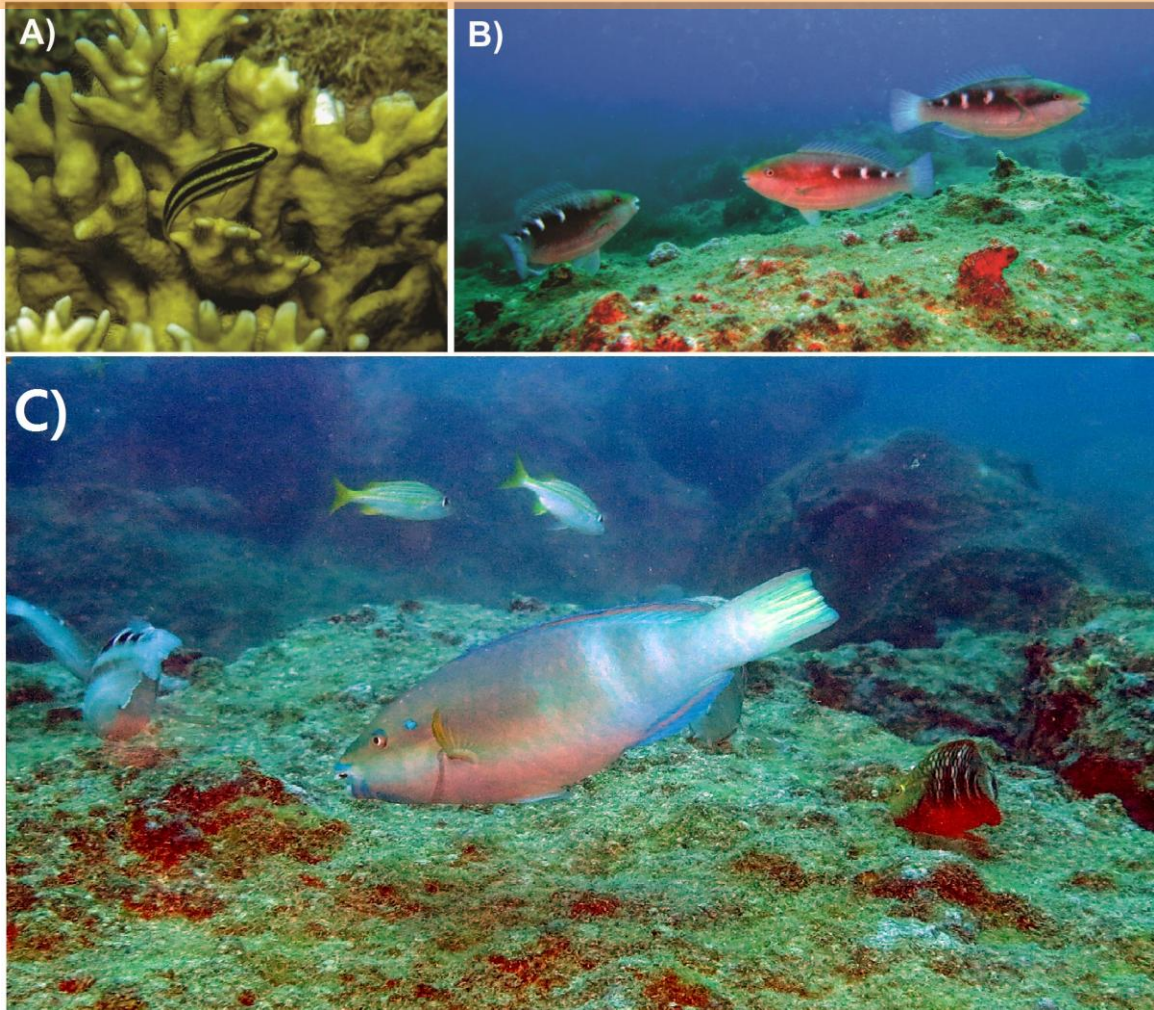
Figure 1 – *Scarus zelindae* life phase classification highlighting different color pattern.

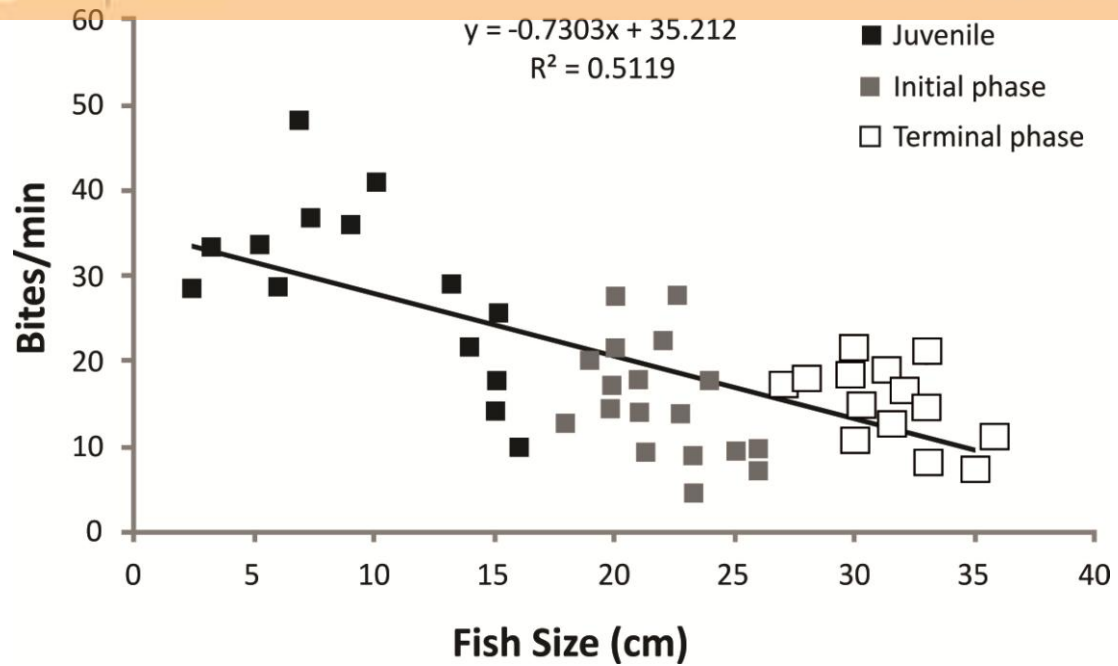A) Juvenile; B) Initial Phase (IP) and C) Terminal Phase (TP).

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Figure with axes: x-axis "Fish Size (cm)" ranging 0 to 40, y-axis "Bites/min" ranging 0 to 60. Regression equation $y = -0.7303x + 35.212$, $R^2 = 0.5119$. Legend: Juvenile (black squares), Initial phase (gray squares), Terminal phase (open squares).

Figure 2 – Linear regression of *S. zelindae* feeding rates (bites/min^{-1}) compared with fish size (cm). Each point represents an individual. Size of *S. zelindae* ranged from 2.5 cm to 36 cm.
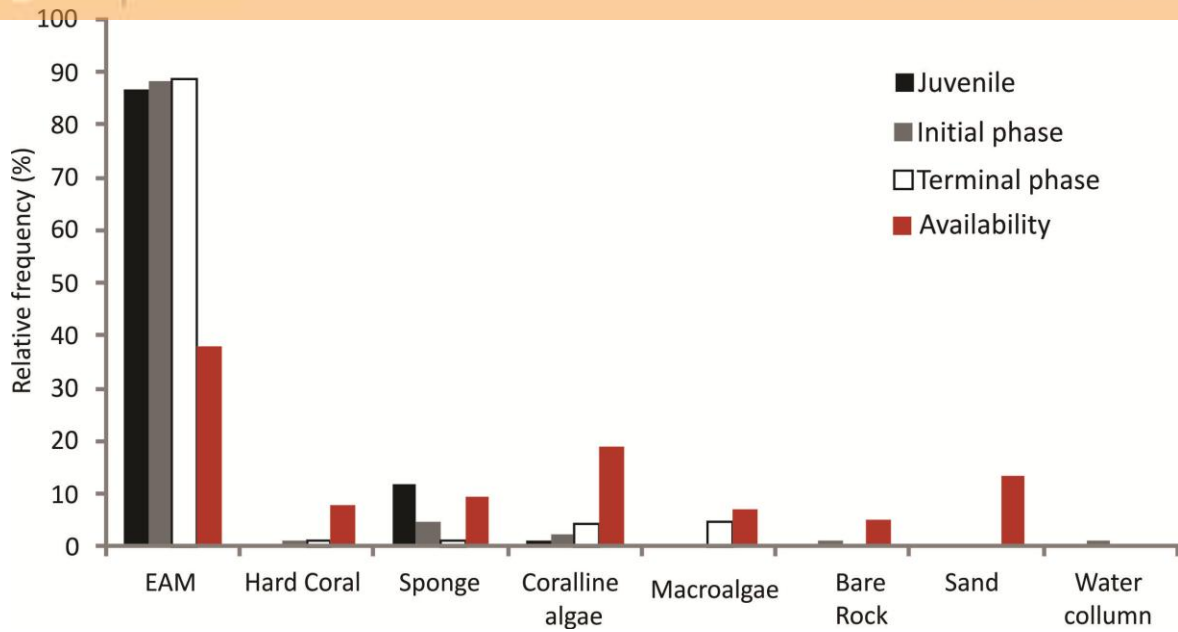
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Figure 3 – Relative frequency in foraging of *S. zelindae* individuals on different substratum per life phase and relative abundance of the benthic composition (resource availability).
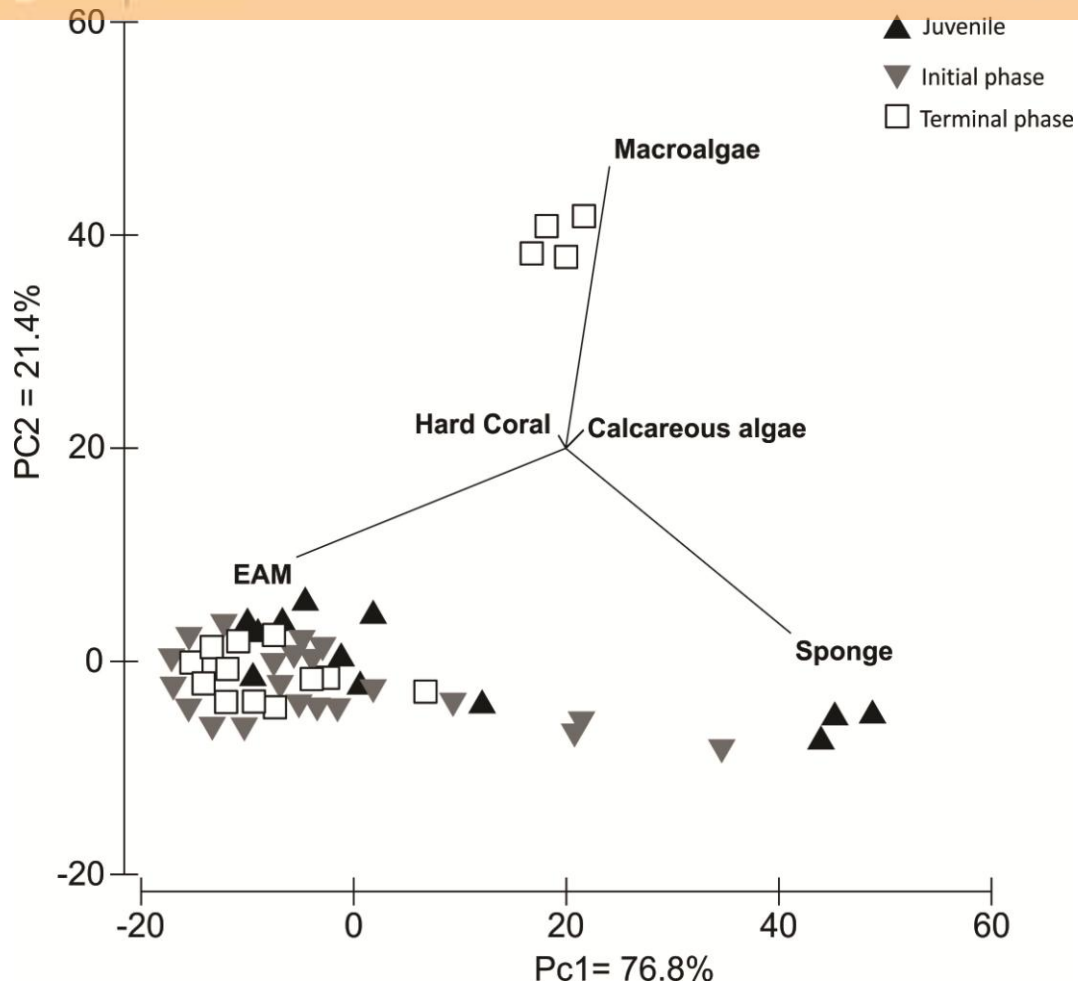
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Figure 4 – Principal components analysis with data clustered by types of substrata used as a food resource for *S. zelindae* at different life phases.
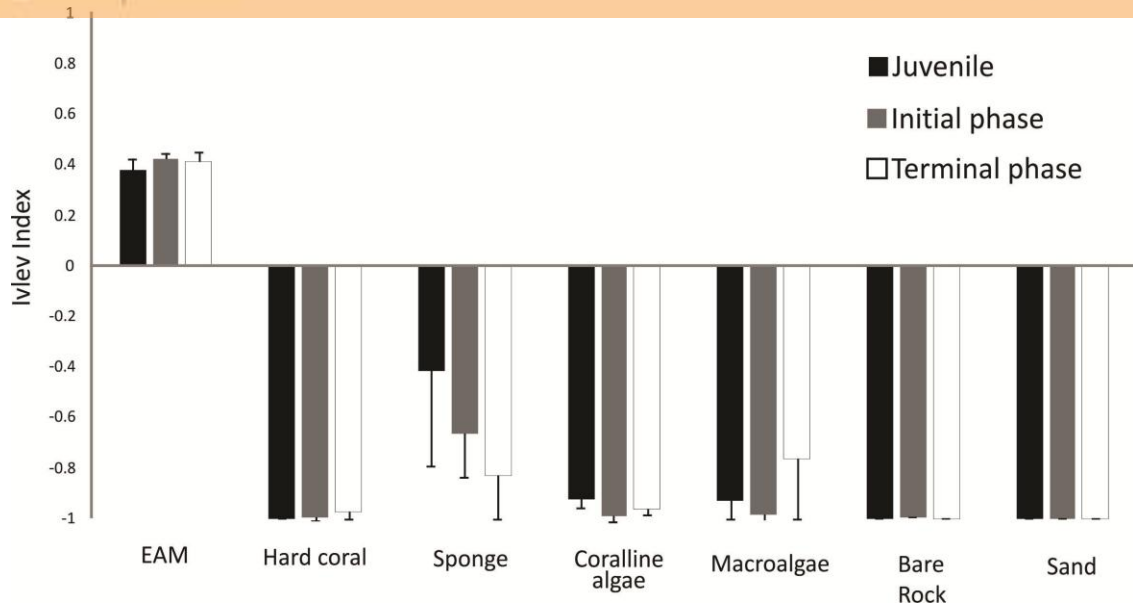
Figure 5 - Ivlev's electivity index of *S. zelindae* based off relative feeding rates and relative abundance of the benthos composition at foraging site. Bars in the figure represent 95% confidence intervals.