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# Seasonal Recruitment and Survival Strategies of Palisada Cervicornis Comb. Nov. (Ceramiales, Rhodophyta) in Coral Reefs

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1 SEASONAL RECRUITMENT AND SURVIVAL STRATEGIES OF *PALISADA*  
2 *CERVICORNIS* COMB. NOV. (CERAMIALES, RHODOPHYTA) IN CORAL REEFS <sup>1</sup>

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28 Running title: Survival strategies of *Palisada cervicornis* comb. nov.

29

30 Abstract

31 As marine tropical ecosystems deteriorate and lose biodiversity, their communities are shifting to  
32 dominance of a few species, altering ecosystem's functioning and services. Macroalgae are  
33 becoming dominant on coral reefs, and frequently observed outcompeting corals. Turf algal  
34 assemblages are the base of energy flow in these systems and one of the most abundant types of  
35 macroalgae on coral reefs, but little is known about their biology and diversity. Through  
36 molecular and morphological analyses, we established the proper identity of the turf-forming  
37 species *Laurencia cervicornis*, and by studying seasonal recruitment and the impact of  
38 herbivorous fishes on its abundance, we describe its survival strategy. The molecular analyses  
39 using a total of 45 *rbcL* gene sequences including eight current genera within the *Laurencia*  
40 complex and two new sequences of *L. cervicornis*, strongly support the new combination of  
41 *Palisada cervicornis* comb. nov. In addition, a detailed morphological characterization including  
42 the description of reproductive structures, is provided. *P. cervicornis* was seen recruiting in all  
43 seasons but was typically in low abundance. Specimens grown on tiles in fish enclosure cages  
44 were devoured in less than 4 hours when offered to fishes. Even though many species of the  
45 *Laurencia* complex have chemicals that deter herbivory, species within the genus *Palisada* lack

46 feeding deterrents and are highly palatable. We suggest that *P. cervicornis* is a palatable species  
47 that seems to survive in the community by obtaining a size-refuge from herbivory within turf  
48 communities..

49

50

51 Key words: Algal recruitment, Florida, herbivory, *Laurencia cervicornis*, *Palisada cervicornis*,  
52 phylogeny, *rbcL* gene, Rhodomelaceae, taxonomy, turf algae.

53

54 Abbreviations: BI, Bayesian inference; bp, base pairs; ML, maximum likelihood; NJ, neighbor  
55 joining; *rbcL* gene, large subunit of the Ribulose 1,5-bisphosphate carboxylase/oxygenase gene.

56

57 Introduction

58 Tropical coastal ecosystems are exposed to major anthropogenic stressors that are causing a shift  
59 in dominance and/or composition of species, altering the ecosystem's diversity and functioning  
60 (Duarte 2000, McGlathery 2001). Particularly on coral reefs, reduced grazing pressure and  
61 increases in nutrients have facilitated a shift from coral-to macroalgae-dominated systems  
62 (Hughes 1994, Gardner et al. 2003, Doropoulos et al. 2013). Field monitoring and experimental  
63 studies (e.g. Artmitage et al. 2005, Collado-Vides et al. 2007, Mumby 2009, Duran et al. 2016)  
64 have reported that different groups of macroalgae have the ability to dominate coral reefs  
65 depending upon nutrient availability and levels of herbivory.

66 Marine macroalgae encompass over 10,000 species globally (Guiry, 2012). For the  
67 Caribbean Sea, Littler and Littler (2000) described around 553 species of macroalgae, and more  
68 recently Dawes and Mathieson (2008) described 693 algal species in Florida alone. This vast

69 taxonomic and morphological diversity has resulted in a relatively low taxonomic resolution of  
70 most ecological studies. The vast majority of studies reporting shifts of species dominance are  
71 carried out using the word ‘macroalgae’ as their unit of measurement, while other studies use  
72 form-functional groups as their measurement unit (Bruno et al. 2009, Suchley et al. 2016), and  
73 still fewer studies have reported results at the genus and species level (Burkepile 2009,  
74 Ceccarelli et al. 2011, Duran et al. 2016). However, particular macroalgal species can have  
75 profound effects on coral-algae interactions; for example, crustose coralline algae (CCA) are  
76 known to be an important group of algae related with coral settlement; however, only a few CCA  
77 species actually facilitate coral recruitment (Harrington et al. 2004). Moreover, it is expected that  
78 future changes in temperature and CO<sub>2</sub> will affect the composition of macroalgae and their  
79 interactions with corals due to species-specific physiological tolerances and increasing algal  
80 allelopathic strength (Ober et al. 2016, Del Monaco et al. (2017).).

81         Macroalgal turf, a loosely defined assemblage of aggregated compact small algae  
82 (Connell et al. 2014 for a review of the term), likely play important roles in coral reef  
83 communities, such as primary producers, structure providers, nitrogen fixers, and facilitate the  
84 accumulation of sediments (McCook 1999 for a review). Moreover, algal turfs can have both  
85 positive and negative effects on coral recruits (Arnold et al. 2010, Venera-Ponton et al. 2011),  
86 and through direct contact, turfs can negatively affect coral growth (Wild et al. 2014). Turfs in  
87 the Caribbean Sea are composed of species from such genera as: *Laurencia* J.V. Lamouroux,  
88 *Sphacelaria* Lyngbye, and *Gelidium* J. V. Lamouroux, and small filamentous species of all four  
89 algal phyla and cyanobacteria (Hay 1981, Carpenter 1986, Littler and Littler 2013). In the  
90 Florida Keys coral reefs, species of the *Laurencia* complex are frequently observed , but their  
91 abundance falls into the lower end of the dominant groups of algae, while brown algae such as

92 *Dictyota* spp., *Lobophora* spp. and the green calcareous *Halimeda* spp. occupy more of the reef  
93 (Yñiguez et al. 2015). However, recruitment and successional studies in the area show that  
94 *Laurencia* species are more abundant than previously recognized (Duran et al. 2016) but difficult  
95 field identification and consistent removal via high grazing pressure limit their recognition.  
96 Furthermore, because *Laurencia* spp. are turf-forming, their abundance might be frequently  
97 underestimated. Thus, studies may frequently overlook species with potentially important roles  
98 on coral reefs.

99         Regulation of algal abundance has been related to the abundance of herbivorous fishes.  
100 Several experimental studies demonstrate that fish grazing can substantially influence the  
101 abundance of different macroalgal species (e.g. Bellwood et al. 2006, Blanco et al. 2011).  
102 However, algae can avoid grazing by producing biologically active compounds that deter  
103 herbivory (Gressler et al. 2010, 2011). *Laurencia* spp. are some of the most chemically defended  
104 seaweeds and produce a large number of secondary metabolites (Pereira et al. 2003, Manilal  
105 2011), 400 of which might have some deterrent effect on fishes (Hay et al. 1988). This might  
106 explain why herbivory is relatively low for some *Laurencia* species (Loffler et al. 2014).  
107 However, some species within the genus contain similar secondary compounds that do not affect  
108 grazing (Hay et al. 1988). Furthermore, some species, such as *Laurencia intricata* J.V.  
109 Lamouroux, are nutritionally rich in lipids, protein, amino acids and fatty acids (Gressler et al.  
110 2010) making them highly palatable. Although species-level identification of algae is difficult  
111 and often requires specialized methods that go beyond morphological characterization, proper  
112 identification of species provides important information about many characteristics of organisms  
113 that clarify their role in the ecosystem (Knowlton and Jackson 1994, De Clerck et al. 2013, Fong  
114 and Fong 2014).

115           The taxonomy of the red algal genus *Laurencia* is extremely complicated due to the large  
116 degree of morphological plasticity, the worldwide distribution from temperate to tropical oceans,  
117 and the diversity of environments in which it is observed (Fujii et al. 2011). Consequently, the  
118 taxonomic position of species within the *Laurencia* complex has rapidly changed as new  
119 morphological and molecular data are recognized. Over the past two hundred years, since the  
120 establishment of the genus *Laurencia* (Lamouroux 1813), many taxonomic changes have been  
121 proposed resulting in the current *Laurencia* complex. Currently, it is composed of eight  
122 formally proposed genera: *Laurencia* J.V. Lamouroux *sensu stricto*, *Osmundea* Stackhouse  
123 (1809), *Chondrophycus* (Tokida & Y. Saito) Garbary & J.T. Harper (Garbary and Harper 1998),  
124 *Palisada* (Yamada) K. W. Nam (Nam 2007), *Yuzurua* (K.W. Nam) Martin-Lescanne (Martin-  
125 Lescanne et al. 2010), *Laurenciella* Cassano, Gil-Rodríguez, Sentías, Díaz-Larrea, M. C.  
126 Oliveira & M. T. Fujii (Cassano et al. 2012a), *Coronaphycus* Metti (Metti et al. 2015), and the  
127 most recently established *Ohelopapa* F. Rousseau, Martin-Lescanne, Payri & L. Le Gall  
128 (Rousseau et al. 2017). Within this complicated taxonomic reality, it is difficult to come up with  
129 proper identification of this important complex of species on coral reefs, causing potential  
130 underestimation of their diversity and abundance.

131           In this study, taxonomists and ecologists joined forces to properly identify a turf-forming  
132 species in coral reefs, and understand the causes of its low abundance. During a recruitment and  
133 successional study of macroalgae in the Florida Keys (Duran et al. 2016), we noticed the  
134 presence of a unique tiny turf-forming species that we identified as *Laurencia cervicornis*  
135 Harvey. This tiny (< 1 cm tall) species was previously merged by Howe with *Laurencia*  
136 *corallopsis* (Howe 1918), now known as *Palisada corallopsis* (Montagne) Sentías, M.T. Fujii &  
137 Díaz-Larrea (Sentías and Díaz-Larrea 2008); however, Littler and Littler (2000), and Wynne *et*



138 *al.* (2005) did not recognize this merger, keeping both species: *L. cervicornis* and *P. corallopsis*  
139 as taxonomically distinct entities. Furthermore, the previously known *Laurencia coelenterata* D.  
140 L. Ballantine & Aponte, now established as *Osmundea coelenterata* (D. L. Ballantine & Aponte)  
141 M. T. Fujii, Senties & Areces (Fujii et al. 2016), is also a small species that in the field can easily  
142 be confused with *L. cervicornis* or *P. corallopsis* unless clear iridescence is observed. We were  
143 able to identify and study this species only by growing it on tiles kept in the laboratory under  
144 controlled conditions in the total absence of grazers. Therefore, the first goal of this study was to  
145 determine the taxonomic identity of our specimens and provide a detailed morphological and  
146 molecular analysis of this species. Secondly, to understand the forces controlling the extremely  
147 low abundance of *Laurencia cervicornis* in the Florida Keys, we asked the following questions:  
148 1) Is *L. cervicornis* regularly recruiting? And if so, how frequent is this species recruiting in the  
149 study site? 2) If recruitment is frequent, why is the species not abundantly present? We expected  
150 to find recruits of *L. cervicornis* throughout the year, but its abundance would be rapidly  
151 controlled by herbivores, which could explain the extremely low abundance of this species in the  
152 field.

153

## 154 Materials and Methods

### 155 *Study site*

156 This study was conducted in the Florida Reef Track, near Pickles Reef (Key Largo,  
157 Florida 25°00'05" N, 80°24'55" W) in a spur and groove reef at a mid-depth area (5-6 m).  
158 Parrotfish and surgeonfish are the dominant herbivorous fishes on Pickles Reef with an average  
159 abundance of 5087.17 g per 100 m<sup>2</sup> while the long-spined urchin, *Diadema antillarum* Philippi  
160 (1845), is present, only at very low densities (<1 individual per 50 m<sup>2</sup>) (Duran et al. 2016). Water

161 temperature varies seasonally ranging from 24 °C in winter (December and January) to 30 °C  
162 during summer. Collection of material and experiments were conducted with the approval of the  
163 Florida Keys National Marine Sanctuary (permits: FKNMS-2009-047 and FKNMS-2011-090).

#### 164 *Taxonomic approach*

165 Samples of *Laurencia cervicornis* were collected from Pickles Reef, Key Largo, Florida,  
166 USA (Table S1).

#### 167 *Molecular analyses*

168 The samples used for molecular analysis were dried in silica gel. The total DNA was  
169 extracted, using the DNeasy Plant Mini Kit (Qiagen, Valencia, CA, USA) according to the  
170 manufacturer's instructions. DNA was amplified by polymerase chain reaction (PCR) using the  
171 reaction mix of the Promega® (Madison, WI, USA) in a final volume of 25 µL. The samples  
172 were amplified in three overlapping parts with the primer pairs: FrbcLstart - R753, F492 - R1150  
173 and F993 - RrbcS (Freshwater and Rueness 1994). Successfully amplified products were purified  
174 with the column MicroSpin™ S-300 HR (GE Healthcare, Buckinghamshire, UK) following the  
175 manufacturer's protocol. Sequencing reactions were performed with BigDye™ Terminator v3.1  
176 Cycle Sequencing Kit (Applied Biosystems, Foster City, USA) on an ABI PRISM 3100 Genetic  
177 Analyzer (Applied Biosystems). The primers used for sequencing were the same used for the  
178 PCR amplification.

#### 179 *Sequence alignments and phylogenetic analysis*

180 DNA sequences were analyzed and manually edited in BioEdit v7.0.9.0 (Hall 1999).  
181 Identity of generated sequences was checked through BLAST available at the NCBI website  
182 (<http://www.ncbi.nlm.nih.gov>).

183 The model used in the Bayesian inference (BI) and maximum likelihood (ML) analyses  
184 was the general-time-reversible model of nucleotide substitution with invariant sites and gamma  
185 distributed rates for the variable sites (GTR + I + G). This model was selected using jModeltest  
186 2.1.10 (Darriba et al. 2012) under the Akaike information criterion (AIC) as implemented on the  
187 CIPRES Science Gateway v3.3. For Bayesian inference analysis, two runs of four chains of the  
188 Markov chain Monte Carlo (one hot and three cold) of 10,000,000 generations, with sampling  
189 every 1,000 generations, and the initial 10,000 generations in both runs were discarded as ‘burn  
190 in’ to build the consensus tree using MrBayes (v3.2) (Ronquist et al. 2012) implemented on the  
191 CIPRES portal. Maximum Likelihood (ML) was performed with PhyML (Guindon and Gascuel  
192 2003) using TOPALi v2.5 graphical interface (Milne et al. 2004) under heuristic search with 100  
193 bootstrap replicates. Neighbor-Joining (NJ) analysis was performed under heuristic search with  
194 2,000 bootstrap replicates using PAUP 4.0b8 (Swofford 2002). Pairwise distances were  
195 calculated using the uncorrected ‘p’ distances in PAUP.

#### 196 *Morphology*

197 Voucher specimens and material for morphological studies were fixed in 4%  
198 formalin/seawater solution or pressed as herbarium sheets. Transverse and longitudinal hand-  
199 sections were obtained with a razor blade and stained with 0.5% aqueous aniline blue solution  
200 acidified with dilute 1N HCl. The microscopic measurements were obtained from the middle  
201 portions of the thallus using a calibrated ocular micrometer. Photomicrographs were obtained  
202 using a Zeiss Axiocam ERC-5S digital camera (Göttingen, Germany) coupled to an Axio skop 2  
203 Zeiss microscope (Göttingen, Germany) and Stemi SV6 Zeiss stereomicroscope (Göttingen,  
204 Germany). The vouchers were deposited in the herbaria of the Botanical Institute, São Paulo  
205 (SP), Brazil, of the University of São Paulo (SPF), and Fairchild Tropical Botanical Garden

206 Herbarium (FTG 167768). Abbreviations follow on-line Index Herbariorum:  
207 <http://sciweb.nybg.org/science2/IndexHerbariorum.asp> (Thiers 2017, continuously updated).

208

209 *Ecological approach*

210 *Recruitment experiment*

211         Eight experimental plots (9 m<sup>2</sup>: 3 x 3 m) were established in June 2009 to examine the  
212 effects of herbivory on benthic community dynamics. Briefly, within each plot we established 2  
213 1 x 1m herbivore exclusion cages and 2 exclusion cage controls made of three walls to mimic the  
214 effects on flow but an open top to allow herbivores access (for a detailed explanation of methods  
215 see Zaneveld et al. 2016). Recruitment of *Laurencia cervicornis* was assessed using 10 x 10 cm  
216 limestone tiles (obtained from quarried South Florida Pleistocene limestone) attached to plastic  
217 mesh with plastic cable ties and secured to the ground with galvanized staples. Two tiles were  
218 placed in each enclosure cage (n = 8 plots x 2 exclusion cages x 2 exclusion control cages = 32  
219 tiles) and left in the field for three months. To assess seasonal variability, tiles were collected and  
220 replaced with new tiles every three months. A total of three deployments covering three seasons:  
221 fall (September - December 2011), winter (December 2011 - March 2012) and spring (March -  
222 June, 2012) were accomplished. Collected tiles were brought to the laboratory and placed in  
223 individual aquaria to allow algae to grow to a size that allowed species identification. Aquaria  
224 were previously prepared to replicate optimal conditions (12:12 light-dark period, salinity: 35-36  
225 PSU, temperature: 25-28 °C, constant water circulation and air pump). Within a week of  
226 collection, the percent cover of *L. cervicornis* was visually quantified and sorted out into the  
227 following categories: 0.1 % for a single individual occupying <0.5% of the tile; 0.5% for less  
228 than three sparse individuals that occupied <1% cover; 1% for >1 individuals that occupied <5%

229 cover; and then multiples of 5 were used from 5 to 100% coverage. After inspection, tiles were  
230 returned to their corresponding aquaria and maintained for three more months to promote growth  
231 and to discover reproductive structures in the recruited specimens.

232 The average percent cover of the two tiles placed within each cage for the eight plots was  
233 used to calculate seasonal abundance and compared across seasons using ANOVA. All analyses  
234 were conducted using R program from R Development Core Team (2012), version 3.2.2.

#### 235 *Impact of herbivorous fishes on Laurencia cervicornis experiment*

236 Feeding assays were used to assess herbivory impact on the abundance of *L. cervicornis*.  
237 In May 2015, 50 limestone tiles (similar to those described above) were deployed for 6 months  
238 within a single 2 x 1 x 0.5 m (length x width x height, mesh size 2.5 cm diameter) cage at a 12 m  
239 depth to study recruitment and growth of macroalgae, including *L. cervicornis*. The cage was  
240 located off Key Largo (24.9500° N, 80.4540° W), approximately 50 m from the Aquarius Reef  
241 Base. From November 9-13 of 2015, nine tiles per day were removed from the enclosure and  
242 exposed to herbivorous fishes each day. Divers surveyed and photographed each tile at 4-hour  
243 intervals. The first photographs were taken as soon as the tiles were removed from the cage and  
244 were employed as a baseline in the morning at ~08:00 (initial t = 0). Additional photographs  
245 were taken midday (~12:00; t = +4 hours) and late afternoon (~16:00; t = +8 hours). We  
246 calculated the percent cover of *L. cervicornis* from photos at each time point using Vidana spatial  
247 ecology software (<http://www.marinespatialecologylab.org/resources/vidana/>). Percent cover was  
248 averaged within time points (initial, noon and evening) and repeated measurement ANOVA was  
249 used to compare removal rate of *Laurencia cervicornis* within the treatment day. All analyses  
250 were conducted using the R program (R Development Core Team 2012, version 3.2.2).

251

252 Results

253 *Laurencia cervicornis* is a tiny iridescent species living intermingled with other small  
254 turf-forming species. In the study area, turfs were frequently covered by sediments making it  
255 difficult to distinguish species. We discovered *L. cervicornis* in recruitment tiles kept in aquaria  
256 in the laboratory. In the field, it was necessary to flush the sediments covering turfs in order to  
257 detect some small iridescent tips intermingled with the rest of turf-forming species. Accordingly,  
258 it was impossible to estimate *L. cervicornis* abundance in the field and the results presented here  
259 are restricted to observations from our recruitment tiles.

260 *Molecular analysis*

261 A total of 45 *rbcL* gene sequences were used in this study, including three newly  
262 generated sequences, two of *L. cervicornis* and one of *P. corallopsis* from Florida, US. The  
263 remaining sequences were obtained from GenBank. Two species of Rhodomelaceae were used  
264 as outgroups, *Chondria collinsiana* M. Howe and *C. dasyphylla* (Woodward) C. Agardh (Table  
265 S1). The final *rbcL* gene alignment consisted of 1,446 bp. The topology of the consensus tree is  
266 shown in Fig. 1. The *Laurencia* complex was resolved as monophyletic with full support based  
267 on the models applied to the sequences analyzed. Species of the *Laurencia* complex were  
268 separated into eight clades corresponding to the current genera of the complex: *Chondrophyucus*,  
269 *Coronaphycus*, *Laurencia*, *Laurenciella*, *Palisada*, *Osmundea*, *Ohelopapa* and *Yuzurua*, with  
270 high to moderate support values, except *Ohelopapa* that joined the *Palisada* but without support.  
271 Within the *Palisada* assemblage, two main subclades were recognized, both with high support.  
272 The two samples of *L. cervicornis* grouped with full support and the intraspecific divergence was  
273 0.2%. *L. cervicornis* is closest phylogenetically to *P. furcata* and *P. corallopsis* from which it  
274 diverged by 3.1-3.5% and 2.7-3.3%, respectively. *Palisada corallopsis* from Florida diverged

275 from the sample from Mexico by 0.4%, indicating that both are the same taxonomic entity. The  
276 interspecific divergence within the *Palisada* clade ranged from 1.4% (*P. cf. perforata* and *P. cf.*  
277 *cruciata* from New Caledonia) to 6.8 % (*P. corallopsis* from Mexico and *P. perforata* from the  
278 Canary Islands).

279 Our phylogenetic analyses strongly support the transfer of *Laurencia cervicornis* to the genus  
280 *Palisada*, and the nomenclatural change is proposed here:

281 ***Palisada cervicornis*** (Harvey) Collado-Vides, Cassano et M. T. Fujii **comb. nov.**

282 Basionym: *Laurencia cervicornis* Harvey, Smithsonian Contributions to Knowledge 5(5): 73, pl.  
283 18C, 1853.

#### 284 *Morphology*

285 Plants grown in aquaria were erect, forming reddish brown tufts or hemispherical clumps  
286 up to 5-6 cm high but were never observed over 1 cm high in the field. The plant exhibits blue  
287 iridescent rings throughout the thalli (Fig. 2A). The thalli are terete, cartilaginous in texture, and  
288 are 0.7-1.2 mm in diameter. Erect axes arise from a single discoid holdfast. Upright branches are  
289 scarcely ramified; branching is irregular to dichotomous usually with 1-2 orders of branches  
290 (Fig. 2A). Cells in surface view are polygonal, isodiametric, 22-48  $\mu\text{m}$  long and 16-34  $\mu\text{m}$  wide.  
291 Secondary pit connections between cortical cells are present (Fig. 2B). In the transverse section,  
292 the thalli have one or two layers of pigmented cortical cells 17-23  $\mu\text{m}$  long and 19-32  $\mu\text{m}$  in  
293 diameter, and four or five layers of colorless medullary cells, rounded or slightly radially  
294 elongated, 51-101  $\mu\text{m}$  long and 30-83  $\mu\text{m}$  wide. Medullary cell walls are uniformly thickened,  
295 but lenticular thickenings are absent. Each vegetative axial segment produces two pericentral  
296 cells (Fig. 2C). Tetrasporangial branchlets are cylindrical, simple or compound, 1.0–2.7 mm long  
297 and 0.5–1.2 mm wide. The arrangement of the tetrasporangia is in a right-angle pattern in

298 relation to fertile branchlets. Mature tetrasporangia are tetrahedrally divided, 38-91  $\mu\text{m}$  in  
299 diameter. In female thalli, cystocarps are conical with a protuberant ostiole, developed at the  
300 subapical portions, partly immersed in the branches, 578-852  $\mu\text{m}$  in diameter. Carposporangia  
301 are clavate, 78-113  $\mu\text{m}$  long and 24-95  $\mu\text{m}$  in diameter (Fig. 2D). Male branches are  
302 characteristically swollen, 0.5-1.2 mm in diameter. In longitudinal section through a fertile  
303 branchlet, the spermatangial pits are cup shaped, and an axial cell row is discernible at the base  
304 (Fig. 2E). Spermatangial trichoblasts arise from axial cells, consisting of fertile and sterile  
305 branches (Fig. 2F); the fertile branches produce many ovoid spermatangia, 7-10  $\mu\text{m}$  long and  
306 3.5-5.8  $\mu\text{m}$  in diameter, and terminate in vesicular sterile cells, 19-30  $\mu\text{m}$  long and 13-21  $\mu\text{m}$  in  
307 diameter; each spermatium possesses an apical nucleus (Fig. 2F).

308

### 309 *Ecological approach*

#### 310 *Recruitment and seasonality*

311 *Palisada cervicornis* recruited to each of the 32 tiles throughout the study period; no significant  
312 differences were found between enclosure and control treatments (ANOVA,  $F_{1,69} = 0.011$ ,  $p =$   
313 0.917). Seasonal differences in recruitment were significant with highest abundance in spring  
314 compared with fall and winter (Fig. 3; ANOVA,  $F_{2,69} = 4.499$ ,  $p = 0.014$ ; Tukey posthoc., spring  
315  $\neq$  (fall = winter),  $p = 0.013$ ).

#### 316 *Herbivory impact on Palisada cervicornis abundance:*

317 After six months growing inside an enclosure cage, all 50 recruitment tiles were colonized by *P.*  
318 *cervicornis*, with an average of 5% percent cover. As soon as the tiles were exposed to fish  
319 grazing, the abundance of *P. cervicornis* rapidly decreased, with the maximum reduction  
320 occurring in the first 4 hours of exposure (ANOVA,  $F_{2,111} = 43.361$ ,  $p < 0.0001$ , Tukey posthoc,  $p$



321 < 0.0001, am  $\neq$  (noon = afternoon)); when total consumption of *P. cervicornis* was observed  
322 (Fig. 4).

323

## 324 Discussion

325         Discovering a tiny, inconspicuous species during an ecological study provided us with  
326 the opportunity to address taxonomic and ecological questions in a combined effort. Using  
327 molecular tools, we properly identified the species and readjusted its nomenclature status, and  
328 through field and laboratory experiments we identified survival strategies of *Palisada*  
329 *cervicornis* in a Florida coral reef.

### 330 *Taxonomic approach*

331         The samples from the Florida Reef Track, clearly grouped in the *Palisada* clade distant  
332 from the *Laurencia* and *Chondrophyucus* clades. Therefore, the sequences from Florida strongly  
333 support the new combination here proposed. Intraspecific divergence was minimal (0.2%) and  
334 within the range of other *Laurencia* complex species that had divergences of 0.01% to 0.02% for  
335 *Palisada poiteaui* (Díaz-Larrea et al. 2007), 0%-0.4% for *Palisada perforata* (Cassano et al.  
336 2009), and 0%-0.9% for *Laurencia dendroidea* (Cassano et al. 2012b). Furthermore, the  
337 divergence between *P. cervicornis* and *P. corallopsis* (2.7-3.3%) establish these two species as  
338 separate taxonomic entities, solving the previously proposed merger of those species (Howe  
339 1918). Even though the type locality for *Palisada cervicornis* is Key West and the samples for  
340 this study come from the upper Keys, this sequence can be representative for the type locality as  
341 it belongs to the Florida Reef Track. As for *P. corallopsis*, this is the first reported sequence for  
342 the species in Florida, differing by only 0.4% from the sequence reported for the Mexican  
343 Caribbean (Díaz-Larrea et al. 2007). The sequenced sample of *P. corallopsis* is from a region

344 near its type locality, which is Cuba (Howe 1918). Therefore, we consider this sequence as  
345 representative of the species.

346         Although *Palisada cervicornis* (as *Laurencia cervicornis*) has been reported in several  
347 sites around the world, many of those reports do not include a morphological description (Suárez  
348 2005, Wynne et al. 2005, Wynne 2011, Tsuda and Walsh 2013); or the descriptions are for  
349 juvenile organisms (Littler and Littler 2000, Dawes and Mathieson 2010). Thanks to the  
350 cultivation of the specimens of *P. cervicornis* in aquaria, we were able to describe the  
351 morphology, including for the first time a detailed description of its reproductive structures and  
352 other observations allowing us to differentiate this species from other similar species in the  
353 region.

354         Morphologically, *Palisada cervicornis* is easily confused with *Osmundea coelenterata*  
355 (originally described as *Laurencia coelenterata*), *Yuzurua iridescens* (M.J. Wynne & D.L.  
356 Ballantine) Senties & M.J. Wynne and *P. corallopsis* due to the compact and small thalli and  
357 their turf-forming habit. All four species share morphological features such as, two pericentral  
358 cells per vegetative axial segment, and arrangement of the tetrasporangia at a right-angle.  
359 Furthermore, three of the four species show secondary pit connections between adjacent cortical  
360 cells, with the exception being *P. corallopsis*. However, each one possesses its own distinctive  
361 characteristics; for example, *Osmundea coelenterata* has the filament-type of spermatangial  
362 branches originating from cortical cells, and tetrasporangia are cut off randomly from the cortical  
363 cells, both typical of *Osmundea* (Fujii et al. 2016). *Yuzurua iridescens* possesses all generic  
364 features established by Nam (1999, as subgenus *Yuzurua*) (Senties et al. 2015), and differs from  
365 *P. cervicornis* by the presence of cortical cell walls near apices markedly projecting with  
366 apiculate tips. *P. cervicornis* and *P. corallopsis* both form small turfs, but *P. corallopsis* presents

367 a height of up to 8 cm and no iridescence. *O. coelenterata* shows a partial iridescence in the  
368 apical section of the branchlets (*in situ* observations), and very small size (to 4 mm), while *P.*  
369 *cervicornis* is larger (2.5 cm in the field, but grows larger in the tanks) and exhibits iridescence  
370 along all branches. An examination of a paratype specimen of *O. coelenterata* (as *L.*  
371 *coelenterata*) from Puerto Rico (#4551) revealed iridescent rings throughout the thalli, the same  
372 as *P. cervicornis*; however, the differences in both species are at the genus level. The results of  
373 the molecular analyses, and the in-depth morphological observations obtained in the present  
374 study corroborate the current taxonomic position of these closely related species of the  
375 *Laurencia* complex.

376 *Ecological aspects of the turf-forming alga Palisada cervicornis.*

377 Coral reef systems have been characterized as grazing controlled ecosystems (Burkepile  
378 et al. 2013), where highly productive algal turfs support large grazer communities (Poulin and  
379 Klumpp 1992). In turn, these herbivores often affect the abundance and diversity of the algal  
380 species present (Hay 1981, Duran et al. 2016) and their productivity (Carpenter 1986, Russ  
381 2013). We show that although *Palisada cervicornis* is inconspicuous, it is a common member of  
382 the turf community in the Florida Keys that recruits year-round. However, when allowed to grow  
383 in herbivore exclusion cages, large *P. cervicornis* are promptly consumed upon exposure to  
384 herbivorous fishes (100% consumption after 4 hours of exposure to grazing). In general, the  
385 survival of species within the *Laurencia* complex is attributed to the chemical deterrents the  
386 algae produce (Hay et al. 1988, Pereira et al. 2003, Malinal 2011). For example, *Laurencia*  
387 *dendroidea* (as *L. obtusa*) produces elatol, which significantly deters herbivory and has been  
388 found in *Laurencia* species worldwide (Pereira et al. 2003). Importantly, not all species in the  
389 *Laurencia* complex show similar chemical characteristics, particularly species of the genus

390 *Palisada*, which lack elatol, as well as terpenes and acetogenins that are present in all *Laurencia*  
391 species tested so far (Fujii et al. 2011). Thus, *P. cervicornis* seems to persist in the community by  
392 obtaining a size-refuge from herbivory within turf communities rather than through chemical  
393 defenses commonly found in *Laurencia* species (e.g. Carpenter 1986; Verges 2011).

#### 394 *Integration*

395         Understanding species interactions and their consequences for ecosystem dynamics  
396 remains a challenge. On coral reefs, herbivore control of macroalgae has been one of the most  
397 important and well-studied interactions, with direct consequences on management and the  
398 development of strategies to protect and facilitate the recovery of these important ecosystems  
399 (Hughes et al. 2010, Mumby 2009).

400         Through the combined efforts of taxonomists and ecologists, we are able to explain the  
401 rapid consumption of what was previously believed to be, a heavily-defended *Laurencia* species.  
402 Further, our recruitment experiments showed that *P. cervicornis* recruits year round; thus helping  
403 explain how such a palatable species is able to persist in a heavily grazed system. In an era in  
404 which biodiversity loss is a major environmental crisis (Rockstrom et al. 2009), our report of a  
405 new taxonomic combination and first molecular sequence near the type locality of the species,  
406 sheds light on the ecology of *P. cervicornis* and furthers our knowledge of the algal biodiversity  
407 on the Florida Reef track.

408

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713 Legend of Tables and Figures

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716 Table S1. Taxa used in this study for phylogenetic analysis.

717

718 FIG. 1. Consensus tree derived from Neighbor-Joining analysis of *rbcL* gene sequences.

719 Bootstrap supports for NJ (2000 replicates) and ML (100 replicates) (>60%) and Bayesian

720 posterior probabilities (>0.6) are shown at the nodes; - indicates lack of support; \* indicates full

721 support (99-100% bootstrap value for NJ/ML, and 1.00 for PP). Taxa marked in bold indicate newly

722 generated sequences.

723

724

725 FIG. 2. Morphological features of *Palisada cervicornis* comb. nov. (A) Habit of a specimen,

726 scale bar = 3 mm. (B) Cortical cells in surface view, showing secondary pit-connections

727 (arrows), scale bar = 20  $\mu\text{m}$ . (C) Transverse section of the upper portion of a branch showing an

728 axial cell (a) and two pericentral cells (p), scale bar = 25  $\mu\text{m}$ . (D) Longitudinal section through a

729 female branchlet showing immersed cystocarp, scale bar = 100  $\mu\text{m}$ . (E) Longitudinal section

730 through a male branchlet showing spermatangial branches in cup-shaped tips, scale bar =

731 100  $\mu\text{m}$ . (F) Detail of spermatangial branches on trichoblast with two laterals, sterile (arrow) and  
732 spermatangial (arrowhead) branches on its suprabasal cell (sbt). Note spermatangia with an  
733 apical nucleus, scale bar = 25  $\mu\text{m}$ .

734

735 FIG. 3- Seasonal abundance of *Palisada cervicornis* in recruitment tiles.

736

737 FIG. 4- Experimental herbivory impact on *Palisada cervicornis*.