

Spatial and temporal distribution of the invasive lionfish *Pterois volitans* in coral reefs of Tayrona National Natural Park, Colombian Caribbean

The lionfish *Pterois volitans* is an invasive species throughout the Western Atlantic that disturbs functioning of local ecosystems such as coral reefs via fast and intense consumption of small fish and invertebrates. In 2009, lionfish populated the bays of Tayrona National Natural Park (TNNP), a biodiversity hotspot in the Colombian Caribbean that is strongly influenced by changing environmental conditions due to a rainy and dry season. So far, the spatial and temporal distribution of *P. volitans* in the bays of TNNP is unknown. Therefore, this study assessed the abundance and body lengths of *P. volitans* during monthly surveys throughout the year 2012 in four bays (thereof two bays where lionfish removals were undertaken) of TNNP at 10 m water depth in coral reefs using transect tools. Findings revealed lionfish abundances of 2.9 ± 0.9 individuals ha^{-1} with lengths of 20 - 25 cm for TNNP, hinting to an established, mostly adult local population. Actual TNNP lionfish abundances are thereby very similar to those at Indo-Pacific reef locations where the invasive lionfish formerly originated from. Significant spatial differences for lionfish abundances and body lengths between different bays in TNNP suggest habitat preferences of *P. volitans* depending on age. Lionfish abundances were highly variable over time, but without significant differences between seasons. Removals could not reduce lionfish abundances significantly during the period of study. This study therefore recommends improved management actions in order to control the already established invasive lionfish population in TNNP.

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9 Introduction

10 The Indo-Pacific lionfish *Pterois volitans* belongs to the family Scorpaenidae and is an invasive
11 marine fish that was introduced in the Western Atlantic during the 1980's (Whitfield et al. 2002;
12 Morris and Whitfield 2009; Schofield 2010; Albins and Hixon 2011; Arias-González et al. 2011).
13 Lionfish in invaded areas have many advantages over native fauna e.g. their generalist diet on a
14 variety of smaller fishes, shrimps and small mobile invertebrates (Morris and Akins 2009),
15 defensive venomous spines (Morris and Whitfield 2009; Albins and Hixon 2011), rapid growth
16 (Albins and Hixon 2011), low parasite load (Morris 2009), and habitat generality (Barbour et al.
17 2010; Albins and Hixon 2011). These characteristics make lionfish dramatically decrease local
18 populations in invaded areas (Albins and Hixon 2008; Arias-González et al. 2011) with strong
19 implications for the trophic web structures of the marine ecosystem (Mack et al. 2000).
20 Additional features of lionfish such as high fecundity (Morris 2009; Morris and Whitfield 2009),
21 effective larval dispersal mechanisms (Morris and Whitfield 2009), and efficient predation
22 (Albins and Hixon 2008; 2011; Côté and Maljković 2010) increase their probability of invasion
23 success.

24 In Colombia, lionfish arrived to the oceanic islands of San Andrés and Providencia in 2008
25 and invaded the entire continental coast of the country in the course of the following year. For the
26 Tayrona National Natural Park (TNNP; Fig. 1) in the northeast Colombian coast, the presence of

27 *P. volitans* was first recorded in May - July 2009 at water depths between 12 – 20 m over coral
28 patches (González et al. 2009). In 2010, juvenile *P. volitans* (3 – 10 cm lengths) were observed in
29 the mangrove ecosystem of Chengue Bay (Arbeláez and Acero P. 2011). The ecological
30 consequences of lionfish are of particular interest for the TNNP area due to its major coastal
31 biodiversity (Garzón-Ferreira and Cano 1991). The TNNP is a fishing restricted area
32 administrated by the National Natural Parks of Colombia dealing with all territories of marine
33 parks and reserves. Generally, the TNNP includes different coastal bays with complex structural
34 bottoms offering heterogeneity of habitats suitable for a high marine biodiversity. A record
35 diversity was reported especially for macroalgae (Bula-Meyer and Norris 2001; Diaz-Pulido and
36 Garzón-Ferreira 2002; Diaz-Pulido and Díaz Ruiz 2003) but also for other marine organisms (e.g.
37 mollusks; Díaz 1995; Diaz-Pulido 1998).

38 So far, little is known about the spatial and temporal distribution of lionfish in TNNP.
39 Therefore, the aim of the present study was to assess monthly *P. volitans* abundances and
40 estimated body lengths throughout one year (2012) for four bays within TNNP. The first
41 objective was to compare lionfish data from TNNP with other invaded areas and also with its
42 native locations in the Indo-Pacific. The second objective was to determine whether lionfish
43 abundances change over time and if differences between a rainy and dry season, coinciding with
44 a seasonal upwelling, exist. This objective focused on possible effects of strong seasonal
45 variation in physicochemical parameters (temperature, salinity, wind, water currents, surplus of
46 inorganic nutrients; Bayraktarov et al. 2013, 2014) during seasonal upwelling on lionfish
47 distribution, as concluded for the factor temperature by the experimental study of Kimball et al.
48 2004 indicating ceased feeding of lionfish at 16°C with lethal consequences at 10°C. The third
49 objective addressed the efficiency of management actions (removals) that started in May 2012 in
50 two TNNP bays by comparing lionfish abundances before removals with data collected after
51 removals for two of the four bays. The present study provides recent and comprehensive lionfish
52 distribution data and establishes an actual baseline with high temporal and spatial resolution for
53 TNNP reefs in the Colombian Caribbean. Further needs of management actions to control the
54 already established invasive lionfish population in TNNP are discussed.

55 **Materials and Methods**

56 *Study site*

57 All necessary permits were obtained for the described study by Instituto de Investigaciones
58 Marinas y Costeras ‘José Benito Vives de Andrés’ (Invemar) in Santa Marta, Colombia which
59 complied with all relevant regulations (decree # 302 and # 309).

60 The Tayrona National Natural Park (TNNP) is located at the northeastern coast of Colombia,
61 between 11°17' – 11°22' N and 73°53' – 74°12' W (Fig. 1). The region contains a rocky coastline
62 with capes, inlets and bays with sandy beaches covering over 40 km (Garzón-Ferreira and Cano
63 1991; Díaz et al. 2000; Martínez and Acosta 2005). The area of survey included the main TNNP
64 bays Chengue, Gayraca, Neguanje, and Cinto (Fig. 1) which experience strong seasonal changes
65 due to a rainy season (> 80 % of the annual rainfall, May to November) and a dry season
66 (December to April) characterized by a seasonal upwelling with strong changes in temperature
67 (decrease from 28 to 21°C), salinity (increase from 33 to 38), increased wind and water currents
68 (Salzwedel and Müller 1983; Mesa et al. 1997; Bayraktarov et al. 2013; 2014). Increased
69 concentration of inorganic nutrients and chlorophyll *a* during periods of upwelling (dry season)
70 result in mesotrophic conditions, compared with oligotrophic settings during the non-upwelling
71 periods (rainy season; Franco-Herrera et al. 2007; Arévalo-Martínez and Franco-Herrera 2008;
72 Bayraktarov et al. 2014).

73 Coral reef formations can be found growing on both sides of each bay between water depths of
74 5 to 20 m (Werding and Erhardt 1976; Werding and Sánchez 1989; Garzón-Ferreira and Cano
75 1991) and represent a habitat for over 180 reef fish species (Olaya-Restrepo et al. 2008).
76 Additionally, the bays harbor mangrove ecosystems and seagrass beds (Fig. 1; Garzón-Ferreira
77 and Cano 1991).

78 *Lionfish assessment in space and time*

79 In order to address the goals of the study, *P. volitans* abundances were monitored monthly in four
80 bays of TNNP. Surveys comprised monitoring along line transects of 50 m length and 5 m width
81 in triplicates that were located at the western and at the eastern flank of each bay (Fig. 1) in order
82 to encompass a representative area for lionfish distribution. Transects were located at water
83 depths between 9 and 11 m, parallel to the coastline, and were separated by > 5 m to ensure
84 independence between samples. The investigated area covered 1500 m² per bay and a total of
85 6000 m² within the TNNP. The method of visual census was applied by SCUBA (English et al.

86 1997; Lang et al. 2010). The total number of *P. volitans* observed during a time of 25 min per
87 replicate was counted (Morris 2009). Places where lionfish may hide such as holes and cavities
88 between rocks and coral framework were carefully examined. Estimated total body lengths (TL)
89 of lionfish were recorded *in situ* in 5 cm intervals for each localized individual from the tip of the
90 snout to the tip of the caudal fin. The surveys were performed between the second and the third
91 week of each month, between 8:00 am. and 3:00 pm.

92 We were informed that lionfish removals were planned to start in May 2012 as a joint project
93 between Universidad Nacional de Colombia, Universidad Jorge Tadeo Lozano, Universidad del
94 Magdalena, Instituto de Investigaciones Marinas y Costeras ‘José Benito Vives de Andrés’
95 (Invemar) and the National Natural Parks of Colombia. Removals were performed monthly by
96 spearing and netting at variable depths (5 – 25 m) by SCUBA diving, and to our knowledge,
97 exclusively in the TNNP bays Chengue and Cinto. Additional unregistered removals of lionfish
98 by dive centers or fishermen could not be considered in the present survey.

99 *Data analysis*

100 Mean monthly abundances of *P. volitans* in the TNNP bays Chengue, Gayraca, Neguanje and
101 Cinto (Fig. 2a) were calculated from data collected over 12 months with a replication of 6
102 transects per bay and month and were converted into individuals per hectare (ind ha^{-1} ; Fig. 2a).
103 Monthly abundance before onset of removals in May were estimated by calculating the
104 abundance for the time period January to April, whereas lionfish data collected between May and
105 December were used to determine the monthly mean abundance after removals (Fig. 2b). For
106 calculation of the temporal lionfish distribution, all lionfish transect data were aggregated per
107 month resulting in a replication of $n = 24$ transects (Fig. 3a). Annual mean abundance was
108 determined for each bay and the whole TNNP area by pooling the data collected over 12 months
109 resulting in a transect replication of $n = 69$ transects for Chengue and Neguanje, and $n = 72$ for
110 Gayraca and Cinto (total of 282 transects). Mean estimated sizes of lionfish (Fig. 3b) were
111 calculated from total estimated body lengths of fishes observed along the transects in the
112 respective bay.

113 Differences in *P. volitans* abundances between bays and months were tested by a Generalized
114 Linear Model (GLM) for Poisson-distributed data and the software R (R Development Core

115 Team 2008). Multiple comparisons between bays (Chengue, Gayraca, Neguanje and Cinto) and
116 months were performed by a Tukey's Honestly Significant Difference (HSD) *post hoc* test on
117 data before (January – April; 93 transects) and after onset of removal (May – December; 189
118 transects). For a quantification of possible removal effects, GLMs for Poisson-distributed data
119 and Tukey's HSD *post hoc* tests were performed before and after removal in the bays Chengue
120 and Cinto, individually.

121 **Results**

122 *Spatial distribution of lionfish in TNNP*

123 Throughout the year 2012, 123 individuals of *Pterois volitans* were counted during 12 months in
124 four bays over a total monitored area of 6000 m². Before removals, lowest mean lionfish
125 abundance was found in Chengue Bay with 1.7 ± 1.0 ind ha⁻¹ (monthly mean \pm SE for the months
126 January - April), followed by Cinto with 2.5 ± 0.3 , and Neguanje with 3.9 ± 1.0 ind ha⁻¹. Highest
127 numbers of monthly lionfish were present in Gayraca with 5.8 ± 3.6 ind ha⁻¹. Significant
128 differences in lionfish abundances during the months before removal were present between the
129 bays Chengue and Gayraca (GLM, Tukey's HSD *post hoc*, $p = 0.033$) with higher lionfish
130 abundance in Gayraca. After onset of monthly removal in May, lowest monthly lionfish
131 abundance was observed in Neguanje with 0.8 ± 0.5 ind ha⁻¹, followed by Chengue with 1.3 ± 0.6
132 and Cinto with 3.9 ± 2.0 ind ha⁻¹. Highest monthly lionfish abundance was still observed in
133 Gayraca Bay with 4.4 ± 1.7 ind ha⁻¹. After removal, significant differences were found between
134 Chengue and Cinto ($p = 0.017$), Chengue and Gayraca ($p = 0.004$), Gayraca and Neguanje ($p <$
135 0.001) and Neguanje and Cinto ($p = 0.003$).

136 Our monthly lionfish censuses demonstrated temporal and spatial variability in lionfish
137 abundances among TNNP bays, which varied between 0 and 16.7 ind ha⁻¹ (Fig. 2a). In Chengue
138 (a removal bay), lionfish abundances were below 5 ind ha⁻¹ (monthly mean \pm SE) until July and
139 disappeared thereafter completely until December, where 1.1 ± 1.1 ind ha⁻¹ were registered.
140 Highest abundances were observed in Gayraca during January with 16.7 ± 10.3 ind ha⁻¹ and
141 August with 12.2 ± 4.6 ind ha⁻¹, while intermediate abundances were present during September
142 with 10.0 ± 5.6 ind ha⁻¹ and December with 7.8 ± 6.5 ind ha⁻¹ in this bay. In Neguanje, highest

143 lionfish abundances were recorded in January with 5.6 ± 5.6 ind ha⁻¹ and February with 5.6 ± 3.6
144 ind ha⁻¹. Here, no lionfish were observed between July and December, except for September
145 where 2.2 ± 2.2 ind ha⁻¹ were registered. In Cinto, lionfish abundances peaked during September
146 with 16.7 ± 5.6 ind ha⁻¹ and June with 6.7 ± 2.4 ind ha⁻¹, but were otherwise below 5 ind ha⁻¹.
147 Mean lionfish abundance before removal was 10.0 ± 5.8 ind ha⁻¹ for Chengue, 35.0 ± 21.8 ind ha⁻¹
148 for Gayraca, 21.7 ± 6.9 ind ha⁻¹ for Neguanje, and 15.0 ± 1.7 ind ha⁻¹ for Cinto (Fig. 2b).
149 Lionfish abundance for the months during which removal actions were performed changed the
150 values to 5.0 ± 3.3 , 28.3 ± 9.8 , 5.0 ± 2.7 , and 23.3 ± 12.1 ind ha⁻¹, respectively (Fig. 2b).

151 *Temporal distribution of lionfish in TNNP*

152 On the temporal scale, highest abundance of lionfish was observed in September with 7.2 ± 2.4
153 ind ha⁻¹ (monthly TNNP mean \pm SE; Fig. 3a) and January with 6.4 ± 3.0 ind ha⁻¹; lowest during
154 November with 0.3 ± 0.3 ind ha⁻¹ and July with 0.8 ± 0.6 individuals ha⁻¹ ind ha⁻¹. Significant
155 differences between months were present between September and April (GLM, Tukey's HSD
156 *post hoc*, $p = 0.05$), July and January ($p = 0.04$), September and July ($p = 0.02$), September and
157 May ($p = 0.03$), and between September and October ($p = 0.03$). However, lionfish abundances
158 were not significantly different between rainy (May – November) and dry season (December –
159 April).

160 Largest estimated lionfish body lengths of 40 cm were registered for Cinto in January and
161 August, and Neguanje in September (Fig. 3b). Largest body lengths were present in Gayraca and
162 Cinto with mean sizes of 20 – 25 cm, followed by Neguanje with 15 – 20 cm, and smallest in
163 Chengue with 10 – 15 cm. A total of 75 % of all lionfish observed had a body length larger than
164 17.5 cm TL (20 – 25 cm) representing the size of 50 % maturity for females (Morris 2009).
165 Before removal, mature lionfish accounted for 80 % and 72 % after initiation of removal efforts.
166 Adults were distributed as 13 % in Chengue, 51 % in Gayraca, 21 % in Neguanje, and 15 % in
167 Cinto before removal which changed to 4 %, 49 %, 8 %, and 40 % after removal, respectively.

168 *The effect of fish removal*

169 Individual GLM analyses showed no significant differences in lionfish abundance before
170 (January – April) and after removal (May – December) for both removal bays, Chengue (GLM,
171 Tukey's HSD *post hoc*, $p = 0.53$) and Cinto ($p = 0.25$). Since no significant differences were
172 observed before and after removal, transect data were pooled to calculate an annual mean of $2.9 \pm$
173 0.9 ind ha^{-1} (annual mean \pm SE) for the TNNP region. The annual mean for Chengue was $1.4 \pm$
174 1.3 ind ha^{-1} , $4.9 \pm 1.3 \text{ ind ha}^{-1}$ for Gayraca, $1.8 \pm 0.6 \text{ ind ha}^{-1}$ for Neguanje, and $3.4 \pm 0.8 \text{ ind ha}^{-1}$
175 for Cinto, respectively (Table 1).

176 **Discussion**177 *Spatial and temporal distribution of *P. volitans**

178 Our data on *P. volitans* distribution in Tayrona National Natural Park (TNNP; Colombian
179 Caribbean) show that a local population with mean body length of 20 – 25 cm has developed in
180 the bays Chengue, Gayraca, Neguanje and Cinto. These lionfish total body lengths (TL) hint to a
181 population mostly dominated by adult fishes that are able to sexually reproduce, based on Morris
182 (2009) who reported 17.5 cm TL as the size of 50 % maturity for females.

183 With an annual mean of 2.9 ind ha^{-1} , lionfish abundance in TNNP was similar to some
184 locations in the Indo-Pacific where it originated from, e.g. Palau Archipelago with 2.2 ind ha^{-1}
185 (Grubich et al. 2009), but below $\sim 80 \text{ ind ha}^{-1}$ reported for the Gulf of Aqaba/ Red Sea (Fishelson
186 1997). Table 1 shows a comparison of lionfish abundance in TNNP to other invaded and native
187 habitats worldwide, however data should be considered as estimates as methods of monitoring
188 were not always comparable (e.g. rotenone-sampling over small areas; Fishelson 1997). Lionfish
189 abundances in TNNP were below the values reported for other invaded areas of the Western
190 Atlantic such as the Bahamas with 393 (Green and Côté 2009) or the coast of North Carolina/
191 USA with 150 ind ha^{-1} (Morris and Whitfield 2009) which may be due to the relatively recent
192 invasion of TNNP in 2009 (González et al. 2009) vs. an invasion of the Bahamas in 2004
193 (Schofield 2009). High abundances of lionfish in invaded areas are likely the result of
194 unrestricted growth and reproduction due to the availability of food sources and lack of natural

195 predators. Some predators obviously learned to target lionfish as potential prey (Bernadsky and
196 Goulet 1991; Maljković et al. 2008). So far, two Caribbean large-bodied grouper species,
197 *Epinephelus striatus* and *Mycteroperca tigris*, were captured with lionfish in their stomach
198 contents (Maljković et al. 2008). However, *E. striatus* is one of the species categorized as
199 endangered in the Colombian Caribbean red list of marine fishes (Mejía and Acero P. 2002).
200 Mumby et al. (2011) presented data on the reduction of lionfish biomass by groupers which may
201 thus serve as natural biocontrol of growing lionfish populations. However, the lack of these
202 natural lionfish predators in TNNP (Olaya-Restrepo et al. 2008) and the wider Caribbean (Sadovy
203 2005) is alarming. In contrast to Mumby et al. (2011), the study of Hackerott et al. (2013)
204 concluded that the abundance of lionfish was not influenced by interaction with native predators
205 in 71 reefs and different biogeographic regions in the Caribbean. The hypothesis of groupers as
206 natural biocontrol against invasive lionfish is currently a subject of active debate (Bruno et al.
207 2013, Green et al. (in press), Mumby et al. 2013). These conflicting results once more stress the
208 necessity of immediate and improved management actions to control further lionfish reproduction
209 and invasion.

210 Our monthly *P. volitans* distribution data over four bays in TNNP showed no seasonal pattern
211 between a rainy and a dry season, characterized by seasonal upwelling and the consequently
212 altered environmental conditions (temperature, salinity, water currents, and surplus of inorganic
213 nutrients; Salzwedel and Müller 1983; Bayraktarov et al. 2013; 2014) did not appear to affect the
214 abundance of lionfish in TNNP. An effect of seawater temperature decrease from 28 to 21 °C
215 (Bayraktarov et al. 2014) on lionfish distribution within the area could not be detected. This
216 finding is supported by the laboratory study by Kimball et al. 2004 showing that the critical
217 temperature at which lionfish ceases feeding was 16 °C with lethal consequences at 10 °C, which
218 is more than 10 °C lower than the coldest temperature so far reported for the TNNP upwelling
219 region (20 °C, Bayraktarov et al. 2014).

220 *Effect of lionfish removal*

221 Abundances and body lengths of *P. volitans* for Chengue Bay, in which removals were
222 performed, were smaller than for the uncontrolled Gayraca and Neguanje. However, removals
223 could not effectively reduce lionfish abundances in Cinto which were lower than abundances in
224 Gayraca but higher than in Neguanje. Body lengths found in Cinto corresponded to those in

225 Gayraca. The smallest body lengths observed in Chengue indicate that a mostly juvenile
226 population may have developed in this bay and thereby may indicate a habitat preference
227 dependent on age. However, it cannot be excluded that the smaller body lengths of lionfish in
228 Chengue are a consequence of removal during management actions targeting predominantly
229 larger adult individuals which are easier to observe and catch. Smaller juveniles may hide
230 between the roots of mangroves (Arbeláez and Acero P. 2011) or in crevices and holes of the reef
231 framework which are especially extensive for Chengue Bay (personal observation). Additionally,
232 Chengue Bay comprises a highly developed mangrove ecosystem (Garzón-Ferreira and Cano
233 1991) which may serve as nursery for lionfish larvae and juveniles. This is further supported by
234 the study of Arbeláez and Acero P. (2011), who found lionfish juveniles of 3 – 10 cm lengths at
235 the submerged roots of the mangroves bordering the entrance to the southern lagoon in Chengue
236 Bay.

237 Factors affecting fish populations that cannot be excluded are the differences in coral reef
238 complexity between the bays and the potential food sources for lionfish. These important points
239 need to be addressed in further studies.

240 Our study suggests that management actions for the TNNP require further improvement in
241 terms of removal frequencies and a larger removal area in order to significantly reduce the
242 established lionfish population. Targeted removals were shown to represent a viable strategy in
243 reducing the direct impacts of invasive lionfish on marine ecosystems (Frazer et al. 2012). Frazer
244 et al. (2012) further suggest that management actions should involve long-term monitoring of
245 lionfish distribution, data on recruitment, growth, and reproduction as well as studies on the
246 direct and indirect effects by invasive lionfish on other fish assemblages. The implementation and
247 improvement of management actions in order to preserve the condition of TNNP coral reef
248 ecosystems during *P. volitans* invasion are crucially essential. The national plan to control and
249 manage lionfish invasion in Colombia is focused on three focal strategy points: 1.) realization of
250 fundamental research, 2.) implementation of management actions and 3.) focus on education and
251 control (MADS et al. 2013). Whereas the first two points are addressed by research groups of
252 universities and institutes, the third point is coordinated by the National Natural Parks of
253 Colombia dealing with all territories of marine parks and reserves. The removal of lionfish
254 outside the marine parks territories lies in the hands of regional environmental officers confronted
255 by an environmental and societal challenge.

256 *Recommendations*

257 Considering the national plan to control and manage lionfish invasion, potential management
258 actions required for the Colombian Caribbean region may further focus on raising the
259 community's awareness by introducing the lionfish problem and the consequences of its invasion.
260 Removals on a wider scale can be promoted by consumption of lionfish on a local and
261 commercial scale. Public outreach should focus especially on lionfish as a good candidate for
262 human nutrition. Morris et al. 2011 reported a relatively high content of lionfish fillet yield (30.5
263 %) comparable to groupers, graysbys, and coney. Lionfish meat had also higher content of
264 essential n-3 fatty acids and a relatively low amount of saturated fatty acids as compared to other
265 marine reef fish species (e.g. red snapper, dolphinfish, blue fin tuna, triggerfish, grouper and
266 tilapia; Morris et al. 2011). The authors suggested that public outreach should especially focus on
267 education about lionfish invasion, handling and cleaning of *P. volitans* in order to minimize risks
268 for envenomation (Morris et al. 2011).

269 The establishment of marine reserves can effectively protect larger fishes (Halpern 2003) such
270 as groupers that could prey on lionfish as reported for the fishing-restricted Exuma Cays Land
271 and Sea Park / Bahamas by Mumby et al. 2011. As long as it is not clear whether native predators
272 are able to effectively prey on lionfish, further controlled fishing restrictions especially on native
273 apex predator populations will become imperative for lionfish invasion control.

274 The invasion of *P. volitans* in the Western Atlantic and the Caribbean is considered as one of
275 the top global threats to conservation of biodiversity (Sutherland et al. 2010). Local lionfish
276 populations may disturb functioning of coral reefs through high consumption of small
277 herbivorous fishes, including parrotfishes (Albins and Hixon, 2008; Morris and Akins 2009), thus
278 indirectly promote the outcompeting of corals by naturally uncontrolled growth of seaweeds
279 (Mumby et al. 2006; Mumby and Steneck 2008; Lesser and Slattery 2011). Under the combined
280 effects of overfishing, lionfish invasion (Albins and Hixon 2011), global climate change (Hoegh-
281 Guldborg et al. 2011), and local environmental degradations, the future of coral ecosystems is
282 severely endangered (Jackson 2010) in the Western Atlantic and Caribbean.

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Figure 1

Area of survey in the Tayrona National Natural Park (TNNP).

The points indicate the sampling locations at the western and eastern flank of each bay.

Source: Invemar 2014.

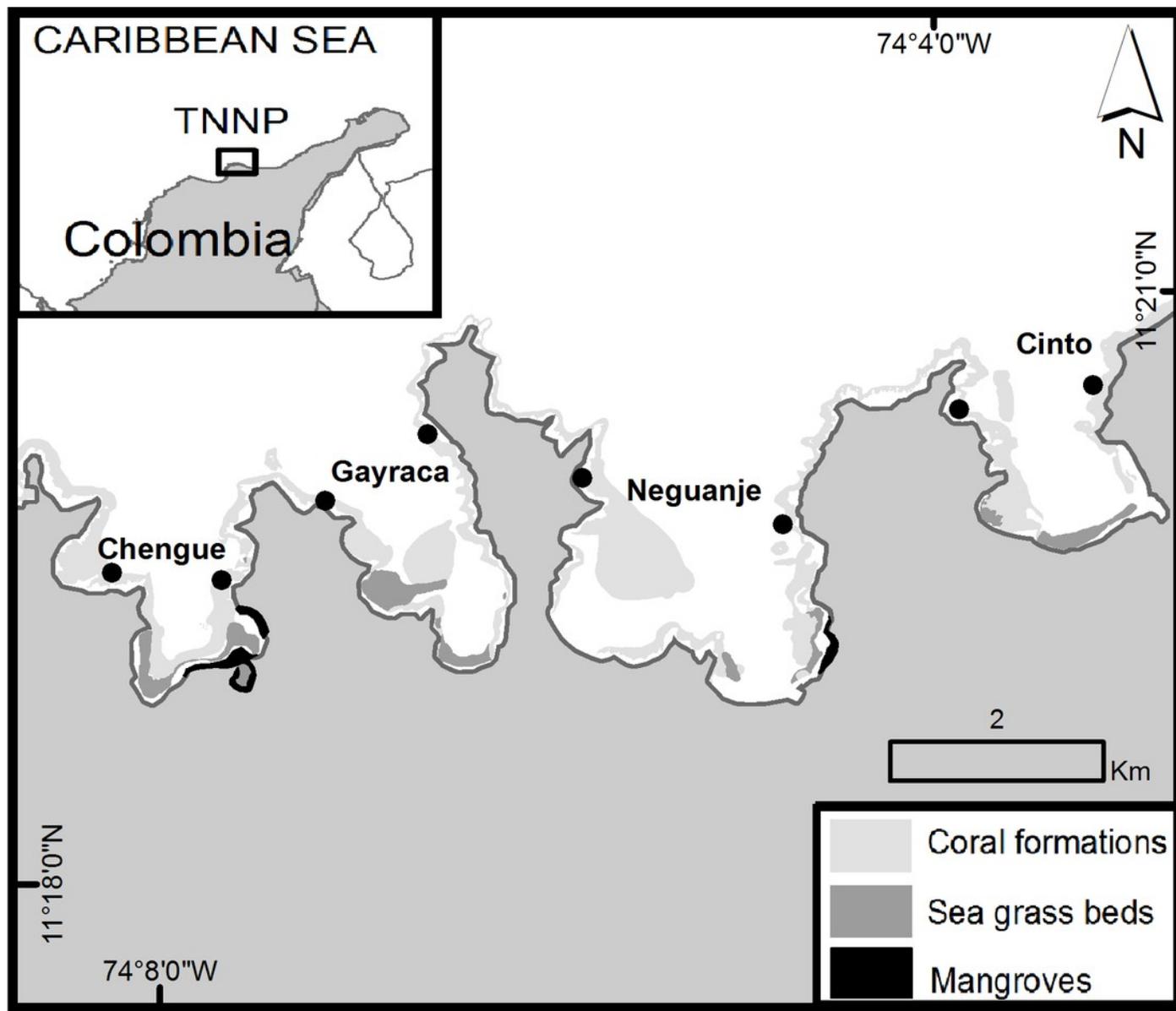


Figure 2

Lionfish abundances in Tayrona National Natural Park before and after removal.

A) Abundances (monthly mean \pm SE) of *Pterois volitans* in the bays Chengue, Gayraca, Neguanje and Cinto throughout the months of 2012. The red line indicates the starting period of monthly removals (May 2012) from the bays Chengue and Cinto. Removal bays (Chengue and Cinto) are indicated by solid symbols, while non-removal bays have open symbols. B) Mean lionfish abundances (+ SE) before (January – April) and after removal (May – December). Abbreviations: Chengue (Ch), Gayraca (Ga), Neguanje (Ne), and Cinto (Ci).

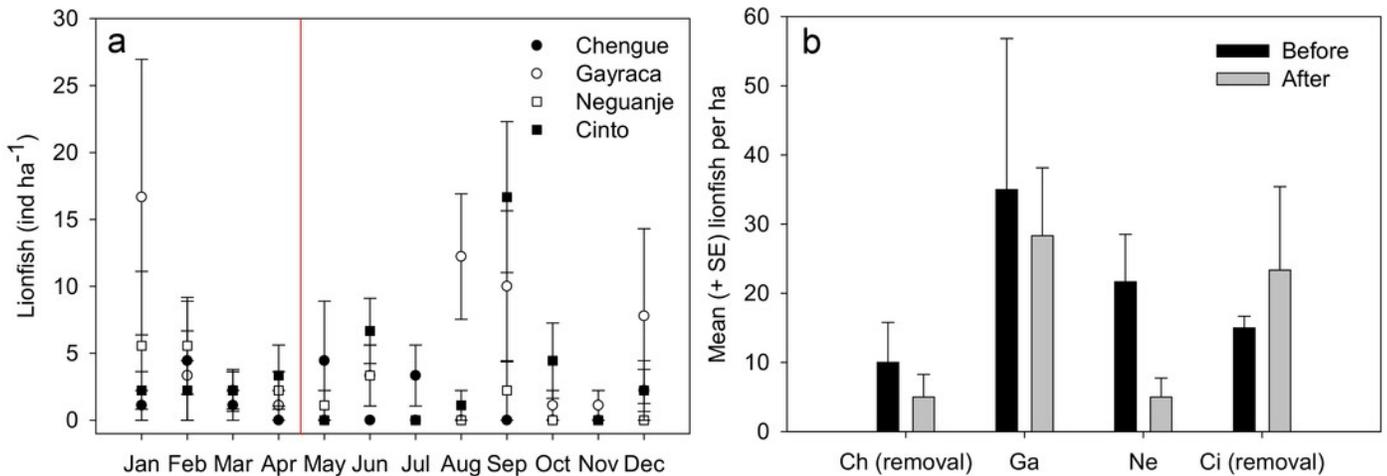


Figure 3

Monthly abundances of *Pterois volitans*.

A) Monthly mean \pm SE; aggregate of four bays for Tayrona National Natural Park and B) estimated body lengths for the bays Chengue, Gayraca, Neguanje, and Cinto. Missing error bars represent sample sizes which did not allow the calculation of a mean and SE at some locations and months.

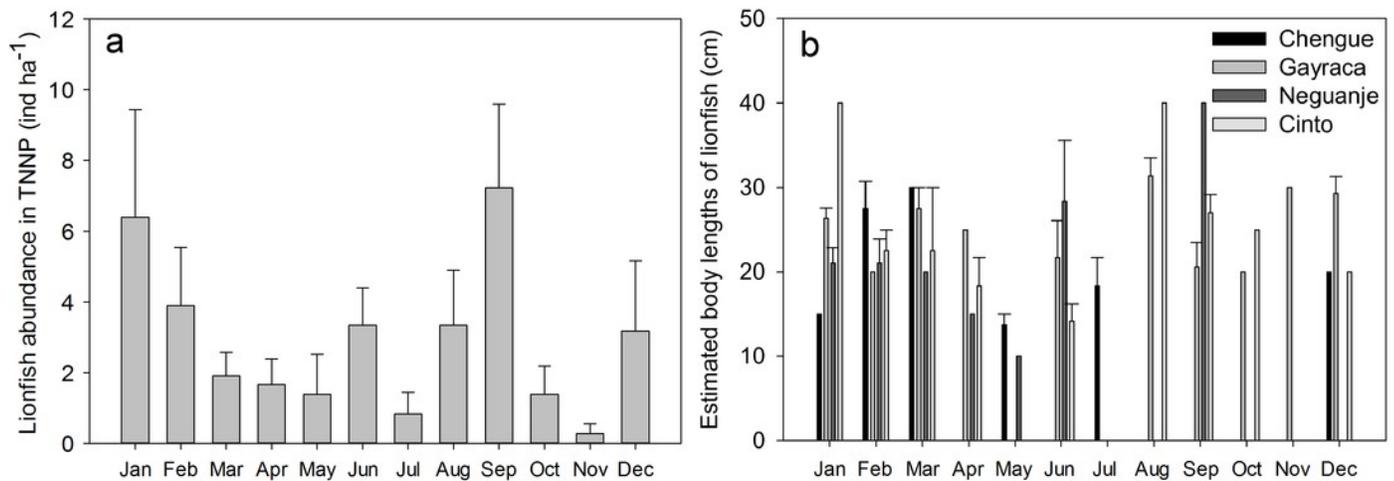


Table 1 (on next page)

Comparison of *Pterois volitans* abundance in Tayrona National Natural Park (TNNP) with worldwide reports on invaded and native habitats.

Region and Year	Habitat for lionfish	Reported abundance (ind ha ⁻¹)	Source
Chengue Bay (TNNP, Colombian Caribbean), 2012	invasive	1.4 ± 0.6	this study
Gayraca Bay (TNNP, Colombian Caribbean), 2012	invasive	4.9 ± 1.3	this study
Neguanje Bay (TNNP, Colombian Caribbean), 2012	invasive	1.8 ± 0.6	this study
Cinto Bay (TNNP, Colombian Caribbean), 2012	invasive	3.4 ± 0.8	this study
TNNP, Colombian Caribbean, 2012	invasive	2.9 ± 0.9	this study
New Providence, Bahamas, Western Atlantic, 2008	invasive	393.3 ± 144.4	Green and Côté (2009)
Coast off North Carolina, USA, Western Atlantic, 2004	invasive	21.2 ± 5.1	Whitfield et al. (2007)
Coast off North Carolina, USA, Western Atlantic, 2008	invasive	150	Morris and Whitfield (2009)
Palau Archipelago, Western Pacific, 2008	native	2.2	Grubich et al. (2009)
Gulf of Aqaba, Red Sea, 1997	native	~ 80	Fishelson (1997)