



# The community diversity of two Caribbean MPAs invaded by lionfish does not support the biotic resistance hypothesis

Dorka Cobián-Rojas<sup>a</sup>, Juan J. Schmitter-Soto<sup>b,\*</sup>, Consuelo M. Aguilar Betancourt<sup>c</sup>, Alfonso Aguilar-Perera<sup>d</sup>, Miguel Á. Ruiz-Zárate<sup>b</sup>, Gaspar González-Sansón<sup>c</sup>, Pedro P. Chevalier Monteagudo<sup>e</sup>, Roberto Herrera Pavón<sup>b</sup>, Alain García Rodríguez<sup>f</sup>, Raúl I. Corrada Wong<sup>e</sup>, Delmis Cabrera Guerra<sup>e</sup>, Héctor Salvat Torres<sup>g</sup>, Susana Perera Valderrama<sup>h</sup>

<sup>a</sup> Parque Nacional Guanahacabibes, Centro de Investigaciones y Servicios Ambientales, Sandino 22100, Pinar del Río, Cuba

<sup>b</sup> El Colegio de la Frontera Sur, Departamento de Sistemática y Ecología Acuática, Av. Centenario km 5.5, 77014 Chetumal, Mexico

<sup>c</sup> Universidad de Guadalajara, Departamento de Estudios para el Desarrollo Sustentable de Zonas Costeras, Gómez Farias 82, 48980 San Patricio Melaque, Cihuatlán, Mexico

<sup>d</sup> Universidad Autónoma de Yucatán, Departamento de Biología Marina, Carr. Mérida-Xmatkuil km 15.5, 97100 Mérida, Mexico,

<sup>e</sup> Acuario Nacional de Cuba, Calle 1<sup>a</sup> #6002, 11300 Playa, Havana, Cuba

<sup>f</sup> Instituto de Oceanología, Ave. 1<sup>a</sup> #18406, 11600 Havana, Cuba

<sup>g</sup> Centro de Investigaciones de Ecosistemas Costeros, Cayo Coco, 69400 Ciego de Ávila, Cuba

<sup>h</sup> Centro Nacional de Áreas Protegidas, Calle 18A #4114, 11300 Miramar, Playa, Havana, Cuba

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## ABSTRACT

Marine protected areas (MPAs) conserve diversity and abundance of fish communities. According to the biotic resistance hypothesis, communities with higher diversity and abundance should resist invasions better. To test this idea, the presence of lionfish in two Caribbean MPAs was studied: Parque Nacional Guanahacabibes (PNG) in Cuba and Parque Nacional Arrecifes de Xcalak (PNAX) in Mexico. Selection of these MPAs was based on both their different levels of success with enforcement and different abundances of native fish, with a more abundant native fish fauna at PNG. Underwater visual censuses were used to evaluate both the native fish structure and composition and at the same time distribution and abundance of lionfish. The abundance of potential predators on lionfish was also measured to determine possible effects of lionfish on both the abundance and the size of its prey and competitors. Lionfish showed higher abundance and larger size in PNG compared to PNAX, even though its probable competitors and predators were also more abundant and larger in PNG. Prey abundance and size decreased after the invasion. No correlation was detected between potential predators and lionfish, which might indicate natural predation is not substantial. In PNAX, lower abundance of prey, potential competitors and predators can also be attributed to historical overfishing, but this did not provide an advantage to lionfish. Lionfish were less abundant and reached smaller sizes in PNAX compared to PNG. This work confirms the effectiveness of lionfish culling at PNAX, but does not support the biotic resistance hypothesis that native fish might have controlled this invasive species.

## 1. Introduction

Anthropogenic activity and natural events have degraded fish communities in Caribbean reefs (Doney et al., 2012). Overfishing, pollution, hurricanes, climatic change, disease outbreaks, and invasive species are among the most important drivers that have affected fish

communities, promoting declines of large carnivorous fish as well as herbivores (Myers and Worm, 2003; Edwards et al., 2014). Predators new to an ecosystem are especially detrimental (Salo et al., 2007).

According to the biotic resistance hypothesis, communities with higher diversity and abundance should resist invasions better, because the establishment of aliens requires “empty niches” in this region, with

\* Corresponding author.

E-mail addresses: [jschmitt@ecosur.mx](mailto:jschmitt@ecosur.mx) (J.J. Schmitter-Soto), [aaguilar@uady.mx](mailto:aaguilar@uady.mx) (A. Aguilar-Perera), [maruizzar@ecosur.mx](mailto:maruizzar@ecosur.mx) (M.Á. Ruiz-Zárate), [pedroc@acuaronacional.cu](mailto:pedroc@acuaronacional.cu) (P.P. Chevalier Monteagudo), [rherrera@ecosur.mx](mailto:rherrera@ecosur.mx) (R. Herrera Pavón), [raulc@acuaronacional.cu](mailto:raulc@acuaronacional.cu) (R.I. Corrada Wong), [delmisc@acuaronacional.cu](mailto:delmisc@acuaronacional.cu) (D. Cabrera Guerra).

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habitats in which there is little competition, atypical of mature and diverse ecosystems (Elton, 1958; Jeschke and Genovesi, 2011). The rapid invasion of lionfish *Pterois volitans* in the western Atlantic (Schofield, 2009) has been explained in part by a lack of native predators (Ward-Paige et al., 2010). Nevertheless, the evidence is equivocal, since Hackerott et al. (2013) found a high abundance of lionfish in protected reefs with abundant native predators.

Lionfish are mainly generalist piscivores (Layman and Allgeier, 2012; Valdéz-Moreno et al., 2012) and can be more abundant and voracious than native mesopredators (Albins, 2013). Albins and Hixon (2008) found lionfish affected native fish recruitment by nearly 80% over five weeks in experimental artificial reefs, and Green et al. (2012) detected an increase of lionfish abundance in the Bahamas with a decrease of 65% in prey biomass in just two years. Lionfish may compete with native species that share a similar niche (Côté et al., 2013; Hackerott et al., 2013; Albins, 2013; Arredondo-Chávez, 2016; Murillo Pérez, 2016).

The lionfish have become established in Cuba (Chevalier Monteagudo et al., 2008) and in Mexico, in the Caribbean (Sabido-Itzá et al., 2012) and southern Gulf of Mexico (Aguilar-Perera & Tuz-Sulub, 2010). These sites share a similar fish composition, and the lionfish has invaded them at about the same time; however, management policies and enforcement are different in strength and success, which is reflected in greater species diversity, abundance, and biomass at PNG. Thus, based on the biotic resistance hypothesis, which states that greater species richness implies better niche occupancy, less available resources, more potential competitors and predators, and hence fewer opportunities for invaders to succeed (Jeschke and Genovesi, 2011), it was expected that PNG would be more resistant to lionfish invasion.

The present study used an observational approach to contrast two marine protected areas (MPAs) under different management regimes. It examined the biotic resistance hypothesis by analyzing the correlation between abundance and size of lionfish and of its prey, and possible effects of competitors and predators, in two MPAs: Parque Nacional Guanahacabibes (PNG), Cuba, and Parque Nacional Arrecifes de Xcalak (PNAX), Mexico, which were invaded at the same time but have contrasting fish richness and biomass. The objectives and hypotheses are: (1) to analyze spatial and temporal variations of lionfish abundance, biomass, and size in both MPAs, with the expectation that more lionfish would be present in the MPA with the least diversity, (2) to analyze lionfish prey, in the anticipation that the better-protected MPA would witness less of an impact on the abundance and size structure of its prey by lionfish predation, (3) to determine if lionfish affect abundance and size of probable competitors, and (4) to determine if potential predators have any effect on lionfish abundance and size, expecting that there would be an inverse correlation or a significant negative change of competitors or predators due to the presence and increasing dominance of the invader.

## 2. Materials and methods

### 2.1. Study areas

The Parque Nacional Guanahacabibes (PNG), in western Cuba, has a marine extension of 15,950 ha (Fig. 1). The eastern zone of PNG has well-developed spurs and grooves, up to 10 m tall, with numerous caves, crevices, and tunnels. The western zone is less complex, and there is no clear reef crest (Perera Valderrama et al., 2013).

The Parque Nacional Arrecifes de Xcalak (PNAX), on the Mexican-Belizean border, has an extension of 13,495 ha (Fig. 1). A well-defined reef crest separates a 1–10 m deep reef lagoon, with *Thalassia testudinum* prairies and small coral patches, from a reef front, with spurs and grooves and isolated massive pillars up to 6 m tall; the lagoon width ranges from < 100 m at Mahahual in the north to > 1000 m at Xcalak, where coral cover is poorer (Ruiz-Zárte et al., 1998). From Xcalak southwards runs a submarine canyon known as La Poza.

Both MPAs were established in 2001. Other than the lionfish invasion in 2009, local impacts, virtually absent in PNG, have not changed in recent years; however, PNAX, although shifting gradually from extractive artisanal to catch-and-release fisheries, still faces illegal fishing pressure (Perera Valderrama et al., 2013).

### 2.2. Visual censuses and predator transects

Stationary visual censuses (Bohnsack and Bannerot, 1986) were performed at nine sites in each MPA (Fig. 1). Every site was surveyed four times and every visit consisted of 20 censuses per site. Number of individuals per species was recorded and fish size was estimated at 5-cm intervals. Surveys were done during the dry season (PNG: Feb 2014 and 2015; PNAX: Apr 2014 and 2015) and rainy season (PNG: Jun 2013 and 2014; PNAX: Sep 2014 and 2015). At PNG, the forereef was surveyed (four censuses at the drop-off, three at the first terrace, two over spur-and-groove habitat), whereas in PNAX one census was in the reef lagoon, over coral patches, and the rest in the forereef (five over spur-and-groove, two at the drop-off, one in crevices). In both MPAs, depth was 12–15 m in the forereef and 3–5 m in the reef lagoon.

Potential predators of lionfish (Table 1) were recorded at five sites in the forereef (PNG: Cuevas de Pedro, Encanto, Yemayá, Uvero Quemado, and Verraco; PNAX: Xahuayxol, Río Huach, Xcalak, La Poza, and Bacalar Chico), during two 800-m long × 10-m wide transects (Pina-Amargós et al., 2014). Potential fish competitors are listed after Chevalier Monteagudo et al. (2013) and Murillo Pérez (2016), and potential predators after Hackerott et al. (2013). Prey species were selected taking into account previous studies of the lionfish diet in both MPAs (Valdéz-Moreno et al., 2012; Cobián-Rojas et al., 2016). *Coryphopterus personatus* is not distinguishable from *C. hyalinus* underwater (Humann and DeLoach, 2011), so both gobiids were analyzed together.

### 2.3. Variations of abundance, biomass, and size

Abundance (as mean density, i.e. mean number of specimens sighted per census), biomass density (in g/m<sup>2</sup>), and body size (in cm) were averaged for each locality. Abundance was transformed by log ( $x + 1$ ) to achieve normality and homoscedasticity (Zar, 1996). Two-way ANOVAs were performed to explore effects of year and season on abundance, biomass, and size of native fish species. This was done separately for each MPA, because these were sampled in different years and their natural physiography is quite contrasting. Nevertheless, a comparison between MPAs was attempted by mixed nested ANOVA for abundance and size, with factor A: MPA (fixed effects, two levels), factor B: sites (nested in A, random effects, nine levels), and years (four levels). The same was done to compare total fish abundance and biomass. To detect differences in mean size of prey and probable competitors between MPAs, a one-way ANOVA was used. Simple-classification ANOVAs were performed to compare predator and lionfish abundance among sites in each country in the 800-m-long transects. A posteriori comparison of means was done with the Student-Newman-Keuls test.

Pearson correlations were performed between the abundance of lionfish and the abundance of every prey, probable competitor, and potential predator, pooling all data and also separately by MPA. To explore similarities in composition among MPAs, sites and season, a multidimensional scaling analysis was used, and the contribution of each species to every group was evaluated by a SIMPER analysis. Tests of dispersion homogeneity (PERMDISP) were applied on prey and probable competitors (Anderson et al., 2008). To test for significant differences, a nested two-way PERMANOVA was performed by MPA and site, both as fixed factors. For cluster analyses, data were transformed by fourth root and the distance used was the Bray-Curtis index. In all cases, significance was assessed at least at  $p < 0.05$ . Statistical packages used were Primer v6 with PERMANOVA+ (Anderson et al., 2008), Statistica 8.0 (Statsoft, 2007), and Statgraphics (StatPoint, 2010).

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