

Invasive lionfish present region-wide variation of allometric growth in the Western Atlantic

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ABSTRACT

Lionfish (*Pterois volitans/miles*) are an invasive species in the North-Western Atlantic and the Caribbean. In order to better manage the invasion, inform lionfish removal programs, and estimate biomass available for harvest, we must be able to accurately estimate their total biomass, frequently from length observations. This work compares length-weight relationships of the invasive lionfish through the invasion with the addition of parameters for the Central Mexican Caribbean. A review of 15 length-weight relationships reported in 10 peer-reviewed studies shows that lionfish exhibit spatial variation in weight-at-length. The reviewed parameters indicate that, for the same length, lionfish in the Caribbean have lower body mass than in the Atlantic or Gulf of Mexico. This highlights the importance of using site-specific parameters to estimate biomass from length observations. This study also reports a new pair of length-weight parameters ($a = 3.2056 \times 10^{-6}$; $b = 3.235$) for organisms sampled in the Central Mexican Caribbean. Findings from this work can aid managers and decision makers to better select length-weight parameters when these are not available for their region of interest.

1 INTRODUCTION

At least 84% of the marine eco-regions have reported the presence of an invasive species (Molnar et al., 2008), which represent a major threat to local biodiversity and the economic activities that depend on it (Bax et al., 2003). Invasive species may threaten native species through predation, competition, or indirect habitat effects (Davis, 2003; Gurevitch and Padilla, 2004). By 2005, the economic cost of invasive species to the United States was estimated at USD\$120 billion per year (Pimentel et al., 2005).

Lionfish (*Pterois volitans/miles* complex) are an invasive species in the Western Atlantic and the Caribbean, likely introduced through liberation of aquarium-kept organisms (Betancur-R et al., 2011). They are the first marine vertebrates to establish in North Atlantic (Schofield, 2009, 2010) and Caribbean coasts (Sabido-Itza et al., 2016). Lionfish have been widely reported in coral reefs (Aguilar-Perera and Tuz-Sulub, 2010), but also in other habitats such as estuaries (Jud et al., 2011), mangroves (Barbour et al., 2010), areas with hard-bottoms (Muñoz et al., 2011), and mesophotic reefs (Andradi-Brown et al., 2017). Due to their threat to local biodiversity, the speed of their spread, and difficulty of management, their presence in these waters has been labeled as a major marine invasion (Hixon et al., 2016).

A significant amount of research has been done to describe lionfish feeding ecology in North Carolina (Muñoz et al., 2011), the Bahamas (Morris and Akins, 2009; Cote et al., 2013), Northern Gulf of Mexico (Dahl and Patterson, 2014), Mexican Caribbean (Valdez-Moreno et al., 2012; Villaseñor-Derbez and Herrera-Pérez, 2014), Belize (Hackerott et al., 2017), and Costa Rica (Sandel et al., 2015). Their feeding behavior and high consumption rates can reduce recruitment (Albins and Hixon, 2008) and population sizes (Green et al., 2012) of native reef-fish species, and further the endangerment of critically endangered reef fish (Rocha et al., 2015). (However, see Hackerott et al. (2017) for a case where there was no evidence that lionfish affected the density, richness, or community composition of prey fishes). Major efforts have been made to understand the possible impacts of the invasion by keeping track of its range through time

(Schofield, 2009, 2010) and predicting invasion ranges under future climates (Grieve et al., 2016). By combining information from these disciplines, researchers have been able to predict the trophic impacts of lionfish (Arias-Gonzalez et al., 2011), which can then be translated into ecosystem-level and economic impacts.

Seeking to reduce lionfish densities, governments and non-profit organizations have promoted removal programs and incentivized its consumption (Chin et al., 2016). In some cases, these have shown to significantly reduce –but not quite eliminate– lionfish abundances at local scales (Sandel et al., 2015; Chin et al., 2016; de Leon et al., 2013). The rapid recovery rates exhibited by lionfish (Barbour et al., 2011) and the persistent populations in mesophotic coral ecosystems (Andradi-Brown et al., 2017) –which can contribute with recruitment to shallow-water populations– make of complete eradication through fishing effort an unlikely solution. However, further incentivizing its consumption might create a demand big enough to promote and sustain a stable fishery (Chin et al., 2016), which can reduce local abundances and control the invasion while providing alternative livelihoods.

The feasibility of lionfish removal programs has been extensively evaluated through field observations (Usseglio et al., 2017; Sandel et al., 2015; Chin et al., 2016; de Leon et al., 2013) and empirical modeling (Barbour et al., 2011; Morris et al., 2011; Johnston and Purkis, 2015). The latter approach models changes in biomass in response to changes in mortality (*i.e.* culling). In this case, biomass represents the sum of all fish's individual weight. The individual weight of an organism (Total Weight; TW) can be estimated from its Total Length (TL) using the allometric growth equation ($TW = aTL^b$). Parameters a and b for this equation exist for North Carolina (Barbour et al., 2011), Northern (Fogg et al., 2013; Dahl and Patterson, 2014) and Southern Gulf of Mexico (Aguilar-Perera and Quijano-Puerto, 2016), the Southern Mexican Caribbean (Sabido-Itza et al., 2016), Bahamas (Darling et al., 2011), Little Cayman (Edwards et al., 2014), Jamaica (Chin et al., 2016), Bonaire (de Leon et al., 2013) Puerto Rico (Toledo-Hernández, 2014), and Costa Rica (Sandel et al., 2015), but remain unavailable for the central Mexican Caribbean. The weight-at-length of a species can vary across regions as a response to biotic (*e.g.* local food availability) and abiotic (*e.g.* water temperature) conditions (Johnson and Swenarton, 2016). Thus, when using biomass-informed models or estimating weights from length observations, it is important to use site-specific parameters. This is especially important when research involves identifying the total biomass available for harvest by fishers (Chin et al., 2016) or the efficacy of lionfish removals (Barbour et al., 2011; Morris et al., 2011; Johnston and Purkis, 2015).

This study reviews lionfish allometric growth throughout the invasion range, and provides a new pair of parameters specific to the central Mexican Caribbean. The results suggest there are important regional-scale variations in allometric growth patterns of lionfish. The observed differences highlight the importance of using site-specific parameters, especially when informing invasion management strategies.

2 MATERIALS AND METHODS

The main objective of this work was to compare allometric growth of lionfish throughout the invasion range. Allometric parameters were retrieved from scientific literature, and an additional pair of parameters was calculated from field observations in the central Mexican Caribbean.

Length-weight relationships ($n = 15$) identified in literature were obtained for North Carolina ($n = 1$, Barbour et al. (2011)), Northern ($n = 3$, Fogg et al. (2013)) and Southern Gulf of Mexico ($n = 3$, Aguilar-Perera and Quijano-Puerto (2016)), the Southern Mexican Caribbean ($n = 1$, Sabido-Itza et al. (2016)), Little Cayman ($n = 1$, Edwards et al. (2014)), Jamaica ($n = 1$, Chin et al. (2016)), Bonaire ($n = 1$, de Leon et al. (2013)) and Costa Rica ($n = 1$, Sandel et al. (2015)). Locations with allometric parameters are shown in Figure 1. When available, information on sampling methods, gender differentiation, location, and depth ranges of each study was retrieved. Whenever gender was not specified, it was assumed that the results were presented for pooled genders.

Parameters from the central Mexican Caribbean were obtained from data collected in 10 sampling sites along the Mexican Caribbean coast in 2010 (Table S1). Sampling locations included wall and carpet reefs at depths between 5.7 m and 38.1 m. All observed lionfish ($n = 109$) were collected using hand nets and numbered collection bottles. The use of hand nets prevented any weight loss due to bleeding and allowed a better representation of small sizes by eliminating gear selectivity. Organisms were euthanized (via pithing) and Total Length (TL; mm) and Total Weight (TW; gr) were recorded before freezing organisms.

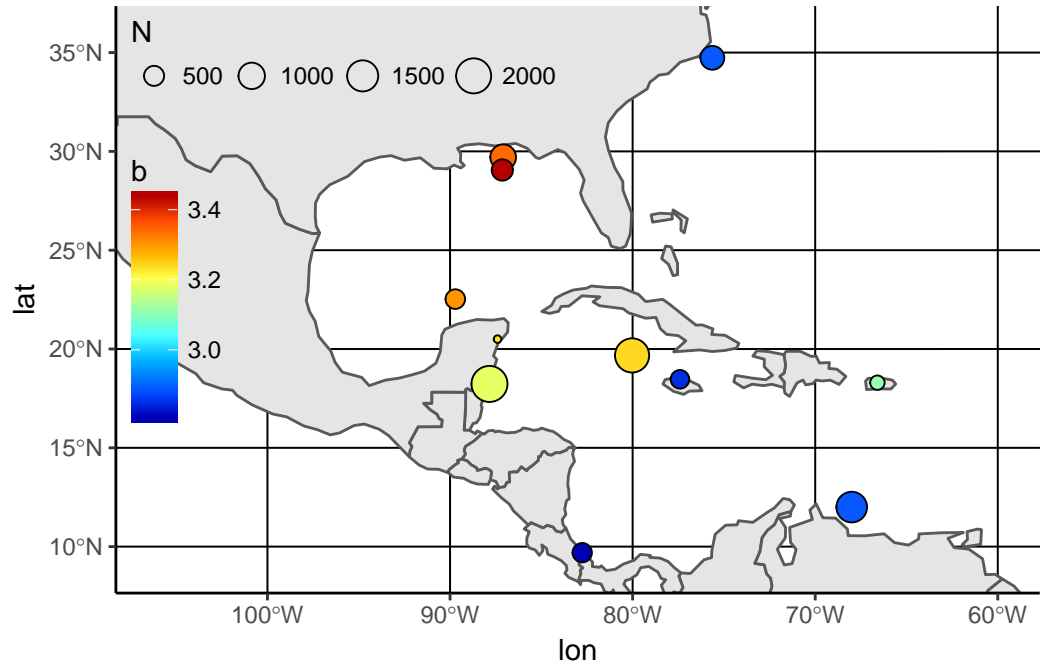


Figure 1. Locations where allometric growth of lionfish (*Pterois spp*) have been reported. Sizes indicate sample size of each study, colors indicate the b coefficient in Eq 1

98 The weight at length relationship for lionfish in the central Mexican Caribbean was calculated with
99 the allometric growth function:

$$TW = aTL^b \quad (1)$$

100 Where TW is the Total Weight (gr), TL is the Total Length (mm), a is the ponderal index and b is
101 the scaling exponent or allometric parameter. When $b = 3$, it is said that the organism exhibits a perfect
102 isometric growth. The dependent and independent variables were transformed via base-10 logarithms,
103 thus the equation becomes:

$$\log_{10}(TW) = b \times \log_{10}(TL) + \log_{10}(a) \quad (2)$$

104 This can be simplified and re-written as:

$$Y = mX + c \quad (3)$$

105 Where $Y = \log_{10}(TW)$, $X = \log_{10}(TL)$, $m = b$, and $c = \log_{10}(a)$. Since $b = m$, we will only use b
106 throughout the paper for simplicity. The coefficients (c and b) were estimated with an Ordinary Least
107 Square Regression and heteroskedastic-robust standard error correction (Zeileis, 2004). Both coefficients
108 were tested against the null hypothesis of no change (i.e. $H_0 : c = 0$ and $H_0 : b = 0$). Additionally, the
109 allometric parameter was tested against the null hypothesis of isometric growth ($H_0 : b = 3$). Coefficients
110 were tested with a two-tailed Student's t -test. The significance of the regression was corroborated with an
111 F-test.

During the review process, some studies indistinctly used a to report either the ponderal index in 1 or the y-intercept (c) in 3. Others reported their parameters as mm-to-gr conversions, but a rapid evaluation of such parameters indicated that they were estimated as cm-to-gr conversions. Here, all parameters are reported as TL(mm) to TW(gr) conversions. When required, values from other studies were transformed for consistency.

Since uncertainty around estimated relationships was not reported in some of the reviewed studies, it was not possible to test for statistical differences between relationships. Instead, the 16 length-weight relationships were used to calculate expected weight length observations of the organisms sampled from the Central Mexican Caribbean ($n = 109$). Expected weights were divided by the observed weights to obtain a ratio. Difference in mean weight ratios across studies were tested with a one-way Analysis of Variance (ANOVA).

All hypothesis testing was performed with an *a priori* confidence level of $\alpha = 0.01$ in R version 3.4.0 (R Core Team, 2017). Raw data and code used in this work is available at dryad.org.

3 RESULTS

The model adjusted to 3 estimated the coefficient values at $b = 3.2347391$ and $c = -5.4940866$. Thus, TW (gr) can be calculated from TL (mm) as a linear equation: $\log_{10}(TW) = 3.2347391 \times \log_{10}(TL) - 5.4940866$, or its exponential form: $TW = 3.2056297 \times 10^{-6} \times TL^{3.2347391}$. The intercept (c) and slope (b) were significantly different from zero ($t(107) = -66.17; p < 0.001$ and $t(107) = 83.24; p < 0.001$, respectively), rejecting the null hypothesis of no change. Additionally, the allometric factor (b) was significantly different from the value of isometric growth of $b = 3$ ($t(107) = 6.04; p < 0.001$), indicating that lionfish present allometric growth. More information on model fit and confidence intervals for the estimated coefficients is presented in TableS2. The relationship between Total Length and Total Weight is presented in Figure 2.

From the 11 peer-reviewed studies including information on growth parameters for *P. volitans* and the additional calculated for the central Mexican Caribbean, 16 parameters were identified (Table 1, Fig 3). Two studies (Aguilar-Perera and Quijano-Puerto, 2016; Fogg et al., 2013) reported gender-level and pooled parameters, while the rest presented pooled results. The smallest coefficient of determination was presented by Chin et al. (2016) with $R^2 = 0.8715$, while Sabido-Itza et al. (2016) reported the highest value at $R^2 = 0.9907$. Reviewed studies presented information for organisms obtained at depths between 0.5 and 57 m. Three studies (Aguilar-Perera and Quijano-Puerto, 2016; Chin et al., 2016; Dahl and Patterson, 2014) explicitly stated that their organisms were sampled with pole spears. Five studies (Sandel et al., 2015; Barbour et al., 2011; Fogg et al., 2013; Edwards et al., 2014; Sabido-Itza et al., 2016; Toledo-Hernández, 2014) mentioned that some of their organisms were obtained with pole spears (or other type of harpoon), but also hand-held nets or fish traps. Two studies (de Leon et al., 2013; Darling et al., 2011) did not specify how organisms were sampled.

Parameters from models fit to males or females exclusively tend to have a higher steepness (*i.e.* higher allometric parameter), with mean \pm standard deviation values of $b = 3.27 \pm 0.06$ and $b = 3.31 \pm 0.23$ for males and females respectively, compared to parameters from models for pooled genders with a mean \pm standard deviation value of $b = 3.13 \pm 0.22$. In the case of the ponderal index (a) and its \log_{10} transformation (c), values were higher for parameters for pooled genders. Figure 3 shows the weight-at-length relationships with parameters from all studies.

There were significant differences in expected-to-observed weight ratios estimated for each pair of parameters ($F(15, 1728) = 38.26; p < 0.001$). From all allometric parameters reviewed, those of Edwards et al. (2014) provided the lowest weight estimates, with an expected-to-observed weight ratio of 0.98 ± 0.23 (mean \pm SD). On the other hand, Barbour et al. (2011) yielded the highest weight estimates, with a mean (\pm SD) expected-to-observed weight ratio of 1.76 ± 0.50 . Predicted-to-observed weight ratios and groups identified by Tukey's HSD ($\alpha = 0.05$) are presented in Figure 4.

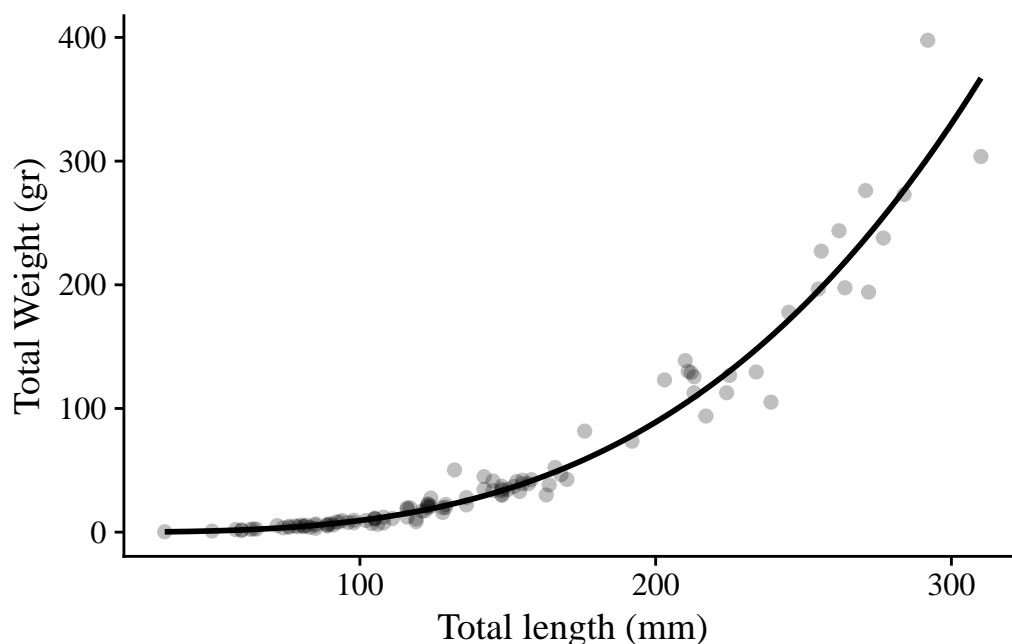


Figure 2. Length-weight relationship for 109 lionfish sampled in the Central Mexican Caribbean. Points indicate samples, solid line indicates curve of best fit (See Table S1).

Table 1. Summary of 13 allometric growth parameters available for lionfish in the invaded range from peer-reviewed literature and this study. All parameters have been adjusted to convert from millimeters to grams. n = Sample size, a = scaling parameter for eq. 1, c = y-intercept for eq. 3, b = exponent or slope for eq. 1 or eq. 3, respectively. The R^2 column indicates reported model fit.

Region	Sex	n	a	b	R2	Reference
Alacranes Reef, Mexico	B	472	2.90e-06	3.30	0.95	Aguilar-Perera & Quijano-Puerto, 2016
Alacranes Reef, Mexico	F	67	1.20e-06	3.47	0.95	Aguilar-Perera & Quijano-Puerto, 2016
Alacranes Reef, Mexico	M	59	4.20e-06	3.23	0.95	Aguilar-Perera & Quijano-Puerto, 2016
Bahamas	B	-	2.50e-06	3.29	-	Darling et al., 2011
Bonaire	B	1450	2.28e-05	2.89	0.96	de Leon et al., 2013
Costa Rica	B	458	3.64e-05	2.81	-	Sandel et al., 2015
Discovery Bay, Jamaica	B	419	2.75e-05	2.85	0.8715	Chin et al 2016
Little Cayman	B	1887	3.00e-06	3.24	0.97	Edwards et al., 2014
North Carolina	B	774	2.89e-05	2.89	-	Brbour et al 2011
Northern Gulf of Mexico	B	934	2.10e-06	3.34	0.98	Dahl & Patterson, 2014
Northern Gulf of Mexico	B	582	1.40e-06	3.43	0.99	Fogg et al., 2013
Northern Gulf of Mexico	M	119	2.70e-06	3.31	0.97	Fogg et al., 2013
Northern Gulf of Mexico	F	115	6.80e-06	3.14	0.94	Fogg et al., 2013
Puerto Aventuras, Mexico	B	109	3.20e-06	3.23	0.9766	This study
Puerto Rico	B	227	8.00e-06	3.11	0.958	Toledo-Hernández et al., 2014
Xcalak, Mexico	B	2143	5.20e-06	3.18	0.9907	Sabido-Itza et al., 2016

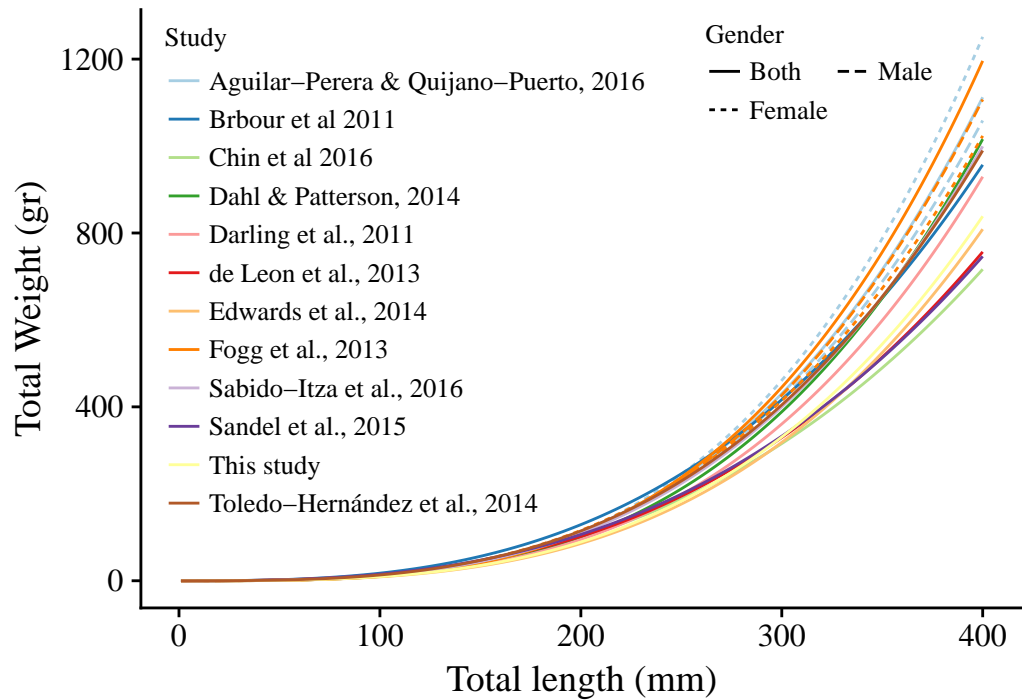


Figure 3. Length-weight relationships ($n = 16$) for eight studies, this study, and Fishbase. Colors indicate studies from which the parameters were extracted. Solid lines indicate that the fit was performed for males and females pooled together. Dotted lines indicate that the regression was performed on females, and dashed lines indicate it was performed for males.

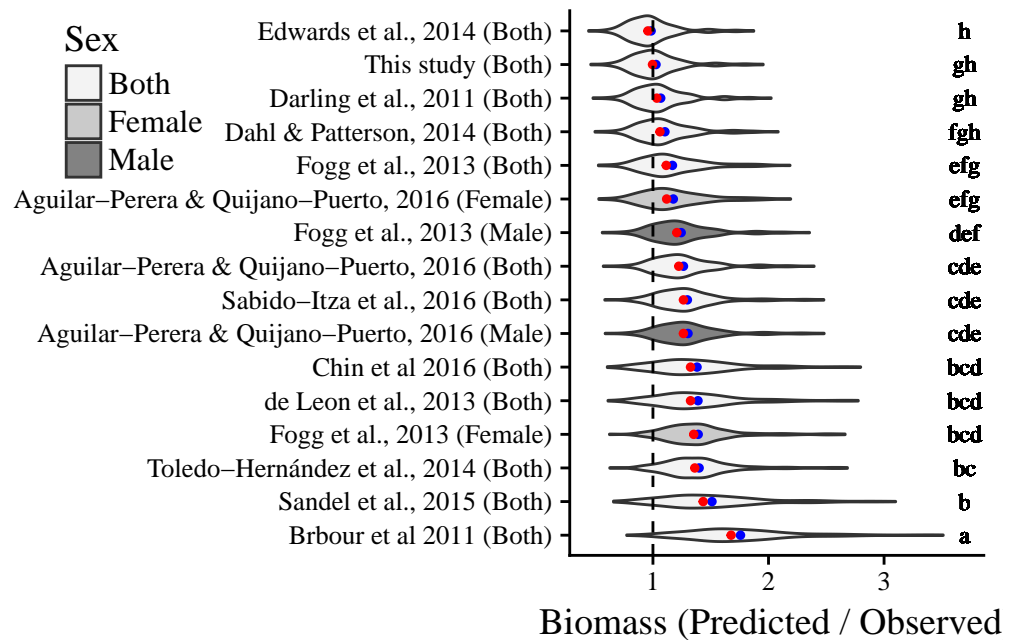


Figure 4. Violin plot showing the distribution of predicted to observed biomass ratios for 16 pairs of allometric parameters. Red and blue circles indicate median and mean values, respectively. Like letters indicate values that do not differ significantly (Tukey's HSD; $p < 0.05$).

4 DISCUSSION

Fogg et al. (2013) uses Spine-less weight

Toledo-Hernández (2014) compares young and wold growth

A new pair of allometric growth parameters for lionfish in the central Mexican Caribbean are provided. This compliments existing literature for other sites in the north (*i.e.* Alacranes Reef (Aguilar-Perera and Quijano-Puerto, 2016)) and South (Xcalak (Sabido-Itza et al., 2016)) of the Mexican Caribbean. Additionally, the study identifies regional differences in length-weight relationships. Here, we focus the discussion on plausible causes of these differences.

The length-weight coefficients estimated in this study were within the range identified by studies in other regions (Barbour et al., 2011; Fogg et al., 2013; Aguilar-Perera and Quijano-Puerto, 2016; Sabido-Itza et al., 2016; Edwards et al., 2014; Chin et al., 2016; de Leon et al., 2013; Sandel et al., 2015). However, the ones presented here provide lower weight estimates for a same length. Until about TL = 200 mm, there are no appreciable differences between the parameters for organisms from the Mexican Caribbean and those for little Cayman (Edwards et al., 2014) and Jamaica (Chin et al., 2016). Yet, for larger organisms (TL > 270 mm) parameters from Costa Rica (Sandel et al., 2015) and Bonaire (de Leon et al., 2013) provide similar estimates to those from this study. Conversely, these same studies tend to estimate higher weights –as compared to the ones reported here– for smaller organisms, likely due to the lack of small organisms in the samples used to estimate their parameters.

There are evident differences in weight-at-length between organisms from the Caribbean and Gulf of Mexico / North-Western Atlantic. Weight estimates with parameters from the Gulf of Mexico and North-Western Atlantic tend to be higher than those from the Caribbean. This indicates that there are differences between lionfish across the invasion range. Similar regional variation has been reported for age-at-length relationships of this species (Fogg et al., 2015; Pusack et al., 2016).

Causas de las diferencias...

These differences can have major implications in management, especially when estimating biomass available for harvest or predicting effects on local ecosystems, or evaluating the effectiveness of removal programs. Using site-specific values provides a more accurate estimate of fish biomass. Future research should try to use, to the extent possible, parameters calculated for their region, or use different parameters to provide upper and lower bounds in their results. At the same time, this highlights the need for more basic research that furthers our understanding of lionfish biology. To better manage the invasion, we must perform research that can describe biologically important information of lionfish throughout its invasion range (Johnson and Swenarton, 2016).

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