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# Spatial variation in allometric growth of invasive lionfish has management implications

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Lionfish (*Pterois volitans / miles*) are an invasive species in the Western Atlantic and the Caribbean. Improving management of invasive lionfish populations requires accurate total biomass estimates, which depend on accurate estimates of allometric growth. Sedentary species like lionfish often exhibit high levels of spatial variation in life history characteristics. We review 17 published length-weight relationships for lionfish taken throughout their invasive range and found substantial regional differences in allometric growth parameters. The spatial pattern we observed is consistent with findings from other studies focusing on genetics or age-at-length. We show that the use of *ex situ* parameters can result in up to a threefold under- or overestimation of total weight, but using parameters from nearby regions reduces this error. These findings can have major implications for management in terms of predicting effects on local ecosystems, evaluating the effectiveness of removal programs, or estimating biomass available for harvest.

# 1 Spatial variation in allometric growth of 2 invasive lionfish has management 3 implications

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## 10 ABSTRACT

11 Lionfish (*Pterois volitans / miles*) are an invasive species in the Western Atlantic and the Caribbean.  
12 Improving management of invasive lionfish populations requires accurate total biomass estimates, which  
13 depend on accurate estimates of allometric growth. Sedentary species like lionfish often exhibit high  
14 levels of spatial variation in life history characteristics. We review 17 published length-weight relationships  
15 for lionfish taken throughout their invasive range and found substantial regional differences in allometric  
16 growth parameters. The spatial pattern we observed is consistent with findings from other studies  
17 focusing on genetics or age-at-length. We show that the use of *ex situ* parameters can result in up to a  
18 threefold under- or overestimation of total weight, but using parameters from nearby regions reduces  
19 this error. These findings can have major implications for management in terms of predicting effects on  
20 local ecosystems, evaluating the effectiveness of removal programs, or estimating biomass available for  
21 harvest.

## 22 INTRODUCTION

23 Lionfish (*Pterois volitans/miles* complex) are an invasive species in the western Atlantic and Caribbean  
24 Sea, likely introduced through liberation of aquarium-kept organisms (Betancur-R et al., 2011). They  
25 are the first invasive marine vertebrates established along the North Atlantic Caribbean coasts (Schofield,  
26 2009, 2010; Sabido-Itza et al., 2016) and their presence has been labeled as a major marine invasion  
27 because they threaten local biodiversity, spread rapidly, and are difficult to manage (Hixon et al., 2016).  
28 Lionfish have established invasive populations in coral reefs, estuaries, mangroves, hard-bottomed areas,  
29 and mesophotic reefs (Barbour et al., 2010; Jud et al., 2011; Muñoz et al., 2011; Claydon et al., 2012;  
30 Andradi-Brown et al., 2017; Gress et al., 2017).

31 A substantial amount of research describes lionfish impacts throughout its invaded range. A meta-  
32 analysis by Peake et al. (2018) showed that invasive lionfish prey on at least 167 different species across  
33 the tropical and temperate North Atlantic. Their feeding behavior and high consumption rates can reduce  
34 recruitment and population sizes of native reef-fish species, and can further endanger reef fish (Green et al.  
35 (2012); Rocha et al. (2015); but see Hackerott et al. (2017)). For example, field experiments by Albins  
36 and Hixon (2008) showed that lionfish establishment led to reduced recruitment of native fishes by nearly  
37 80% over a five-week period in Florida. Green et al. (2012) reported that prey fish biomass declined by  
38 65% over two years as lionfish biomass increased along Bahamian coral reefs. Their trophic impacts can  
39 be minimized if local lionfish biomass is controlled by culling (Arias-Gonzalez et al., 2011).

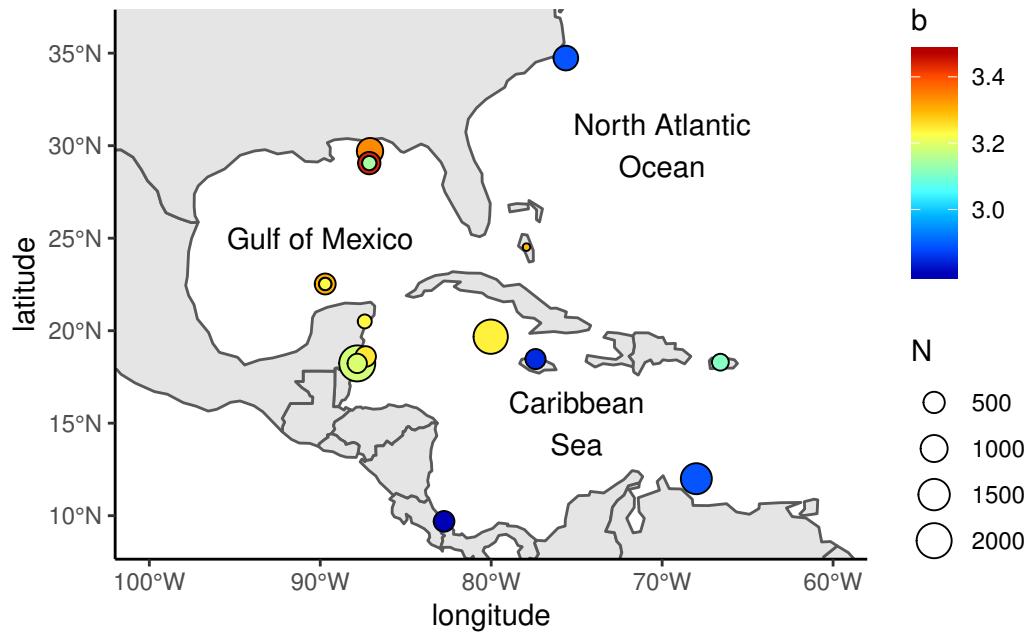
40 Governments and non-profit organizations have sought to reduce lionfish densities through removal  
41 programs and incentivizing its consumption (Chin et al., 2016). In some cases, these have shown to  
42 significantly reduce –but not quite eliminate– lionfish abundances at local scales (de Leon et al., 2013;  
43 Sandel et al., 2015). Complete eradication of lionfish through fishing is unlikely because of their rapid  
44 recovery rates and ongoing recruitment to shallow-water areas from persistent populations in mesophotic  
45 ecosystems (Barbour et al., 2011; Andradi-Brown et al., 2017). However, promoting lionfish consumption

46 might create a level of demand capable of incentivizing a stable fishery while controlling shallow-water  
47 populations, thus creating alternative livelihoods and avoiding further impacts to local biota.

48 The feasibility of establishing fisheries through lionfish removal programs has been extensively  
49 evaluated through field observations and empirical modeling (Barbour et al., 2011; Morris et al., 2011; de  
50 Leon et al., 2013; Johnston and Purkis, 2015; Sandel et al., 2015; Usseglio et al., 2017). Determining the  
51 feasibility of such initiatives requires modeling the change in biomass in response to changes in fishing  
52 mortality (*i.e.* culling). A common way to model this is via length-structured population models, where  
53 fish lengths are converted to weight to calculate total biomass (Barbour et al., 2011; Côté et al., 2014;  
54 Andradi-Brown et al., 2017). The allometric length-weight relationship is thus an essential component of  
55 these models, but this relationship can vary across regions as a response to biotic and abiotic conditions  
56 (Johnson and Swenarton, 2016).

57 Outcomes of previous studies suggest lionfish are likely to exhibit spatial heterogeneity in the length-  
58 weight relationship, which we summarize in two main causes. First, culling programs are effective in  
59 reducing local adult populations largely because lionfish exhibit high levels of site fidelity and small home  
60 ranges (Fishelson, 1997; Kochzius and Blohm, 2005; Jud and Layman, 2012; Côté et al., 2014). It is  
61 known that fish with sedentary behavior are likely to exhibit high levels of spatial variation in important life  
62 history characteristics such as growth or natural mortality rates (Gunderson et al., 2008; Hutchinson, 2008;  
63 Wilson et al., 2012; Guan et al., 2013). Second, genetic analysis of lionfish suggests biological differences  
64 due to the existence of two genetically distinct invasive subpopulations between the northwest Atlantic  
65 and the Caribbean (Betancur-R et al., 2011). Site-specific parameters are necessary to accurately estimate  
66 biomass when allometric relationships are spatially variable, and this variability is increasingly important  
67 when estimating the potential effectiveness of lionfish culling programs (Barbour et al., 2011; Morris et al.,  
68 2011; Côté et al., 2014; Johnston and Purkis, 2015). However, the region-wide differences in allometric  
69 growth parameters has remained unexplored for lionfish, despite the large number of site-specific studies  
70 reporting the length-weight relationship.

71 Here, we compare previously published length-weight relationships for lionfish populations in North  
72 Carolina, Northern and Southern Gulf of Mexico, the Southern Mexican Caribbean, Bahamas, Little  
73 Cayman, Jamaica, Bonaire, Puerto Rico, and Costa Rica (Barbour et al., 2011; Darling et al., 2011; de  
74 Leon et al., 2013; Fogg et al., 2013; Dahl and Patterson, 2014; Edwards et al., 2014; Toledo-Hernández,  
75 2014; Sandel et al., 2015; Aguilar-Perera and Quijano-Puerto, 2016; Sabido-Itza et al., 2016; Sabido-Itzá  
76 et al., 2016; Chin et al., 2016). We also collected lionfish length and weight data in the central Mexican  
77 Caribbean and report the first allometric growth equation for this region. The objective of this paper is to  
78 describe the spatial pattern of length-weight relationships of lionfish across the Caribbean and Western  
79 Atlantic and to discuss implications of these spatial differences.



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

## 80 METHODS

81 We reviewed 12 published studies and obtained 17 length-weight relationships for the North Atlantic  
 82 ( $n = 1$ ), Gulf of Mexico ( $n = 7$ ), and Caribbean ( $n = 9$ , Table 2, Fig 3). We collected information on  
 83 sampling methods, sex differentiation, location, and depth ranges from each study when available. Only  
 84 two studies reported parameters for each gender (Aguilar-Perera and Quijano-Puerto, 2016; Fogg et al.,  
 85 2013), so we assumed both genders were included in a study if gender was unspecified. Reviewed studies  
 86 presented information for organisms obtained at depths between 0.5 m and 57 m. Three studies explicitly  
 87 stated that their organisms were sampled with pole spears (Dahl and Patterson, 2014; Aguilar-Perera and  
 88 Quijano-Puerto, 2016; Chin et al., 2016; Sabido-Itzá et al., 2016), and five studies mentioned that some of  
 89 their organisms were obtained with pole spears (or other type of harpoon) but also hand-held nets or fish  
 90 traps (Barbour et al., 2011; Fogg et al., 2013; Edwards et al., 2014; Toledo-Hernández, 2014; Sandel et al.,  
 91 2015; Sabido-Itza et al., 2016; Sabido-Itzá et al., 2016), and two studies did not specify how organisms  
 92 were sampled (Darling et al., 2011; de Leon et al., 2013). Fogg et al. (2013) use spineless weight in their  
 93 calculations, so their parameters likely underestimated total weight. Since no spineless to total weight  
 94 conversions were available, these parameters were taken as reported.

95 We also used data from Villaseñor-Derbez and Herrera-Pérez (2014), who collected organisms from  
 96 10 sampling sites along the central Mexican Caribbean coast in 2010 (Supplementary Table 1). Sampling  
 97 locations included wall and carpet reefs at depths between 5.7 m and 38.1 m. All observed lionfish ( $n$   
 98  $= 109$ ) were collected using hand nets and numbered collection bottles. The use of hand nets prevented  
 99 any weight loss due to bleeding and allowed better representation of small sizes by eliminating gear  
 100 selectivity. Organisms were euthanized via pithing and Total Length (TL; mm) and Total Weight (TW; g)  
 101 were recorded.

102 The weight-at-length relationship for lionfish in the central Mexican Caribbean was calculated with  
 103 the allometric growth function:

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

104 Where  $a$  is the ponderal index and  $b$  is the scaling exponent or allometric parameter.

105 Transforming this equation via base-10 logarithms we obtain:

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

106 This can be simplified and re-written as:

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

107 Where  $Y = \log_{10}(TW)$ ,  $X = \log_{10}(TL)$ , and  $c = \log_{10}(a)$ . The coefficients ( $c$  and  $b$ ) were estimated  
108 with an Ordinary Least Squares Regression and heteroskedastic-robust standard error correction (Zeileis,  
109 2004). When the  $b = 3$ , it is said that the organism exhibits a perfect isometric growth, so the  $b$  coefficient  
110 was tested against the null hypothesis of isometric growth (*i.e.*  $H_0 : b = 3$ ). Coefficients were tested with  
111 a two-tailed Student's  $t$ , and the significance of the regression was corroborated with an F-test.

112 Some of the reviewed studies inconsistently defined  $a$  as either the ponderal index from Eq. 1 or  
113 the y-intercept ( $c$ ) from Eq. 3. Other studies incorrectly reported parameters as mm-to-g conversions  
114 when they were in fact cm-to-g conversions. We standardized each study by converting coefficients and  
115 report all parameters as TL(mm) to TW (gr) conversions. Locations where allometric studies have been  
116 performed are shown in Figure 1 and summarized in Table 2.

117 We obtained a total of 18 parameter pairs by combining length-weight parameters extracted from  
118 the literature and the additional pair calculated here. We used the central Mexican Caribbean as a case  
119 study of how the use of *ex situ* parameters influences the accuracy of weight estimates for lionfish. We  
120 estimated TW from the TL observations we collected in the central Mexican Caribbean ( $n = 109$ , with  
121  $TL \in (34, 310)$ ) using each of the 18 parameter pairs and divided predicted weights by known observed  
122 weights to obtain a simple measure of over- or underestimation. Difference in mean weight ratios across  
123 the different parameter pairs were tested with a one-way analysis of variance (ANOVA) and Tukey's test  
124 was used for *post-hoc* tests. All analyses were performed in R version 3.5.1 (R Core Team, 2018). Raw  
125 data and code used in this work are available on github.

## 126 RESULTS

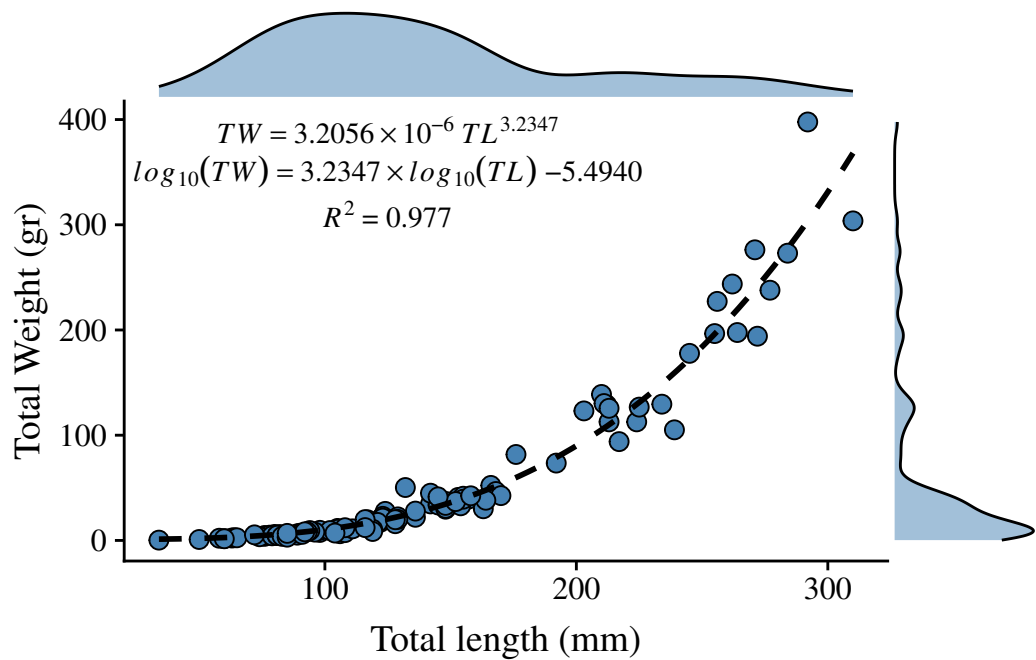
127 The length-weight relationship for organisms from the central Mexican Caribbean resulted in the  
128 coefficient values  $a = 3.2056297 \times 10^{-6}$ ,  $b = 3.2347391$  and  $c = -5.4940866$  ( $R^2 = 0.977$ ,  $F(df =$   
129  $1; 107) = 6928.67$ ,  $p < 0.001$ ). The allometric factor ( $b$ ) was significantly different from  $b = 3$   
130 ( $t(107) = 6.04$ ;  $p < 0.001$ ) indicating that lionfish present allometric growth. The length-weight co-  
131 efficients estimated in this study were within the range identified by studies in other regions (Table 2).  
132 Figure 2 shows the relationship between TL and TW for this region, and model fit statistics are presented  
133 in Table 1.

**Table 1.** Coefficients of the linear model fit to Eq 3. Numbers in parentheses represent heteroskedastic-robust standard errors.

	$\log_{10}(TW)$
c	-5.494 (0.083)***
b	3.235 (0.039)***
F Statistic	6928.67*** (df = 1; 107)
Observations	109
Adjusted R <sup>2</sup>	0.976
Residual Std. Error	0.096 (df = 107)

Note: \* $p < 0.1$ ; \*\* $p < 0.05$ ; \*\*\* $p < 0.01$

134 There were significant differences in our predicted weights for the central Mexican Caribbean when  
135 using the different pairs of parameters ( $F(df = 17; 1944) = 61.55$ ;  $p < 0.001$ ). The lowest weight  
136 estimates resulted from using the allometric parameters from Banco Chinchorro in the Caribbean, with



**Figure 2.** Length-weight relationship for 109 lionfish sampled in the central Mexican Caribbean. Points indicate samples, dashed black line indicates curve of best fit, marginal plots represent the density distribution of each variable.

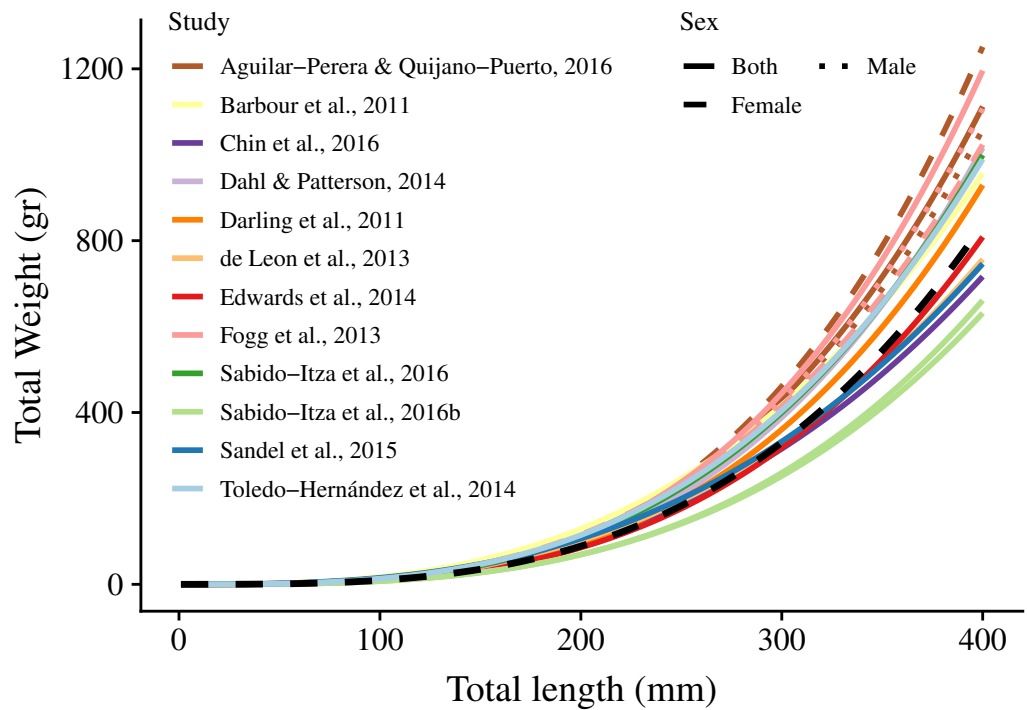
137 mean  $\pm$  SD of  $40.37 \pm 58.74$  gr (Sabido-Itzá et al., 2016), and the highest weight estimates came from  
 138 the Northern Atlantic with  $73.76 \pm 96.11$  gr (Barbour et al., 2011). To put this in context, true observed  
 139 weights were  $52.56 \pm 76.58$  gr. These correspond to predicted-to-observed weights ratios of  $0.80 \pm 0.19$   
 140 and  $1.76 \pm 0.50$  (mean  $\pm$  SD), respectively.

141 The calculated ratio of predicted-to-observed weight ranged from 0.36 to 3.51, indicating that *ex situ*  
 142 parameters can result in major under- and overestimation. Tukey's *post-hoc* test suggests that weight ratios  
 143 for the central Mexican Caribbean were not different from those obtained with parameters from Little  
 144 Cayman, the Bahamas, and some sites in the Gulf of Mexico (Tukey's HSD  $p > 0.05$ ). Weight estimates  
 145 using parameters from the Gulf of Mexico and North-Western Atlantic were higher on average than those  
 146 from the Caribbean (Fig 3). The average ( $\pm$  SD) predicted-to-observed weight ratios from these three  
 147 regions were  $1.24 \pm 0.309$ ,  $1.76 \pm 0.496$ , and  $1.17 \pm 0.398$ , respectively. Predicted-to-observed weight  
 148 ratios are presented in Figure 4. Spineless weight parameters from Fogg et al. (2013) still produced  
 149 predicted-to-observed weight ratios  $> 1$ .

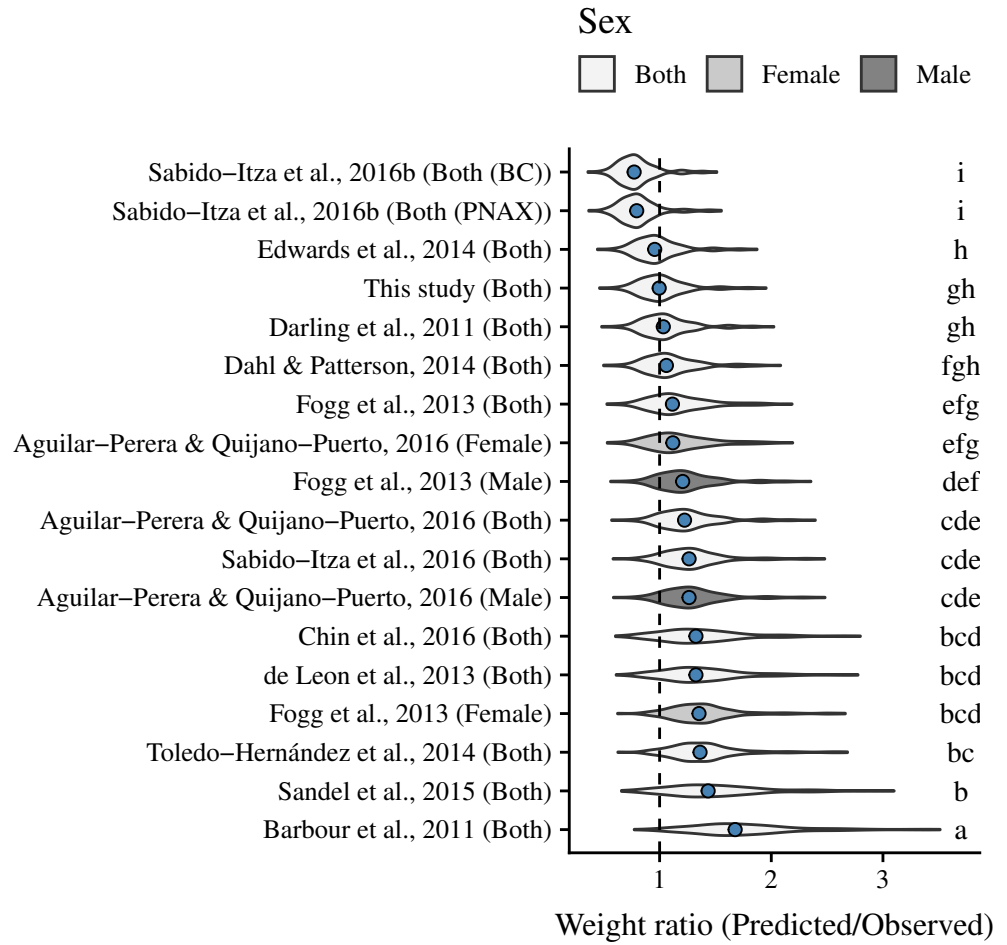
**Table 2.** Summary of 18 allometric growth parameters available for lionfish in the invaded range from peer-reviewed literature and this study. All parameters have been adjusted to convert from millimeters to grams. n = Sample size, Sex specifies whether data was presented for Females (F), Males (M), or both genders combined (B), a = scaling parameter for Eq. 1 (presented in  $\times 10^{-5}$ ), c = y-intercept for Eq. 3, b = exponent or slope for Eq. 1 or Eq. 3, respectively. The Fit column contains the reported  $R^2$  of the model fit.

Region	Sex	n	a	b	c	Fit	Reference
Caribbean	B	458	3.6	2.81	-4.44	-	Sandel et al., 2015
Caribbean	B	419	2.8	2.85	-4.56	0.8715	Chin et al., 2016
Caribbean	B	1450	2.3	2.89	-4.64	0.96	de Leon et al., 2013
Caribbean	B	1887	0.3	3.24	-5.52	0.97	Edwards et al., 2014
Caribbean	B	-	0.25	3.29	-5.60	-	Darling et al., 2011
Caribbean	B	2143	0.52	3.18	-5.28	0.9907	Sabido-Itza et al., 2016
Caribbean	B	227	0.8	3.11	-5.10	0.958	Toledo-Hernández et al., 2014
Caribbean	B	449	0.23	3.25	-5.64	0.97	Sabido-Itza et al., 2016b
Caribbean	B	368	0.32	3.19	-5.50	0.98	Sabido-Itza et al., 2016b
Caribbean	B	109	0.32	3.23	-5.49	0.9766	This study
GoM	B	934	0.21	3.34	-5.68	0.98	Dahl & Patterson, 2014
GoM	B	472	0.29	3.30	-5.54	0.95	Aguilar-Perera & Quijano-Puerto, 2016
GoM	F	67	0.12	3.47	-5.93	0.95	Aguilar-Perera & Quijano-Puerto, 2016
GoM	M	59	0.42	3.23	-5.38	0.95	Aguilar-Perera & Quijano-Puerto, 2016
GoM	B	582	0.14	3.43	-5.86	0.99	Fogg et al., 2013
GoM	M	119	0.27	3.31	-5.57	0.97	Fogg et al., 2013
GoM	F	115	0.68	3.14	-5.17	0.94	Fogg et al., 2013
North Atlantic	B	774	2.9	2.89	-4.54	-	Barbour et al., 2011





**Figure 3.** Length-weight relationships ( $n = 18$ ) for 12 studies and this study. Colors indicate studies from which the parameters were extracted. Dotted, dashed and solid lines show models for males, females, and combined sexes, respectively. The dashed black line represents the relationship estimated in this study.



**Figure 4.** Violin plot of predicted-to-observed weight ratios for 18 pairs of allometric parameters. Blue circles indicate median values and Like letters indicate values that do not differ significantly.

## 150 DISCUSSION

151 Our results suggest that lionfish exhibit highly variable allometric relationships across the invaded range,  
152 and that this variation is related to space. Moreover, we show that the use of *ex situ* parameters may  
153 lead to highly biased weight estimates. Our comparison of observed weights to those predicted with  
154 locally-informed parameters and *ex situ* parameters showed that weight can be overestimated by more  
155 than a three-fold, and highlights the need to use local information. Here we discuss the implications of  
156 our findings and highlight potential future research directions.

157 We detected substantial differences in weight-at-length between organisms from the Caribbean, Gulf  
158 of Mexico, and North-Western Atlantic. Groupings of predicted-to-observed weight ratios aligned with  
159 the spatial distribution of the examined studies, suggesting that these differences are mediated by space.  
160 These regional allometric differences mirror similar patterns in age-at-length of lionfish across both their  
161 invaded and native regions (Pusack et al., 2016). Variation may be driven by genetics or by organisms'  
162 exposure to distinct environmental conditions. For example, Betancur-R et al. (2011) used mitochondrial  
163 DNA to demonstrate the existence of two distinct population groups, identified as the “Caribbean group”  
164 and “Northern Group”, and Fogg et al. (2015) alternatively suggested that age-at-length differences may  
165 be climate-driven. Differences in weight-at-length could also reflect differential energy input or usage, or  
166 a combination of both. Future research is needed to determine which processes are at work here.

167 Differences in length-weight relationships have traditionally been highlighted as potential pitfalls to  
168 fishery management. For example, Wilson et al. (2012) show that small-scale variations in length-at-age  
169 and fishing mortality in other Scorpaeniformes translate to differential landings, effort, and catch per  
170 unit effort in the live fish fishery of California, and that these differences must be taken into account in  
171 management plans. The lionfish case poses the opposite scenario, where the manager desires to eradicate  
172 the species. To accurately gauge both the effectiveness of lionfish removal efforts and the resources  
173 needed to successfully manage an invasion, we must acknowledge and understand regional biological  
174 differences in important variables such as allometric growth parameters.

175 The results presented here have major implications for management. For example, Edwards et al.  
176 (2014) simulated a lionfish culling program under two scenarios, one using length-at-age and length-to-  
177 weight parameters from North Carolina and one using parameters from Little Cayman. Their results show  
178 that using different parameters caused up to a four-year difference in the time required for the simulated  
179 lionfish population to recover to 90% of its initial biomass after removals ceased. Here, we show that  
180 using one set of length-weight parameters versus another for a given length can result in more than a  
181 threefold under- or overestimation of total weight. These spatially-driven differences become especially  
182 important when allocating resources for lionfish removal programs, incentivizing lionfish fisheries as a  
183 source of alternative livelihoods, or estimating ecosystem impacts. Research efforts focused on invasive  
184 lionfish populations need to use parameters calculated for their region to the extent possible, or at least  
185 use reasonable sets of different parameters that provide upper and lower bounds in their results.

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189 Conflict of Interest: The authors declare that they have no conflict of interest.

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