

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.

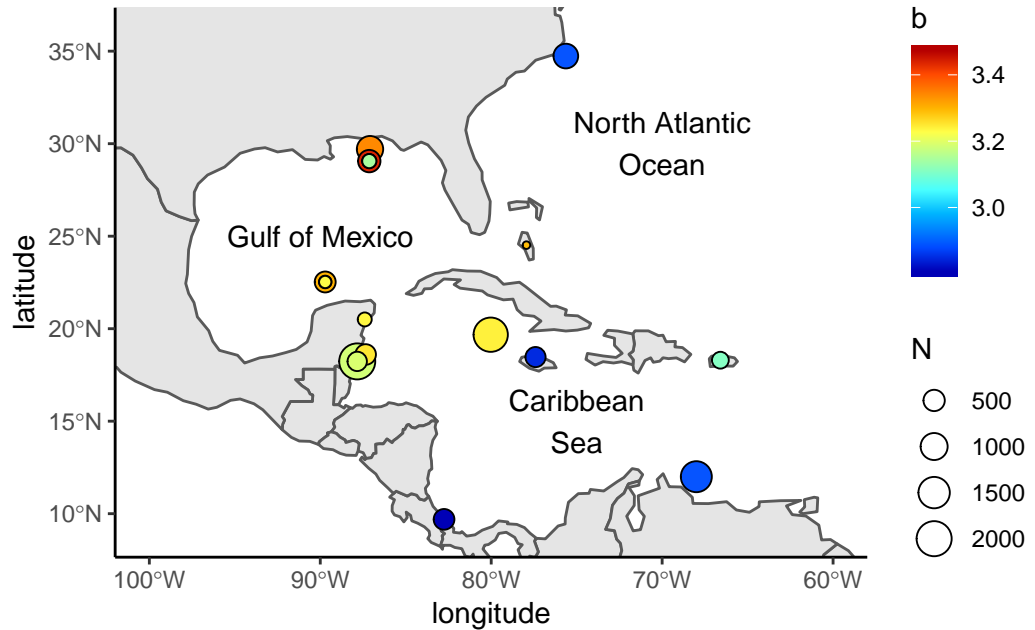


Figure 1. Locations where allometric growth parameters of lionfish (*Pterois spp*) have been reported. Circle sizes indicate sample size from each study, colors indicate the b coefficient from Eq. 1.

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 ²	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

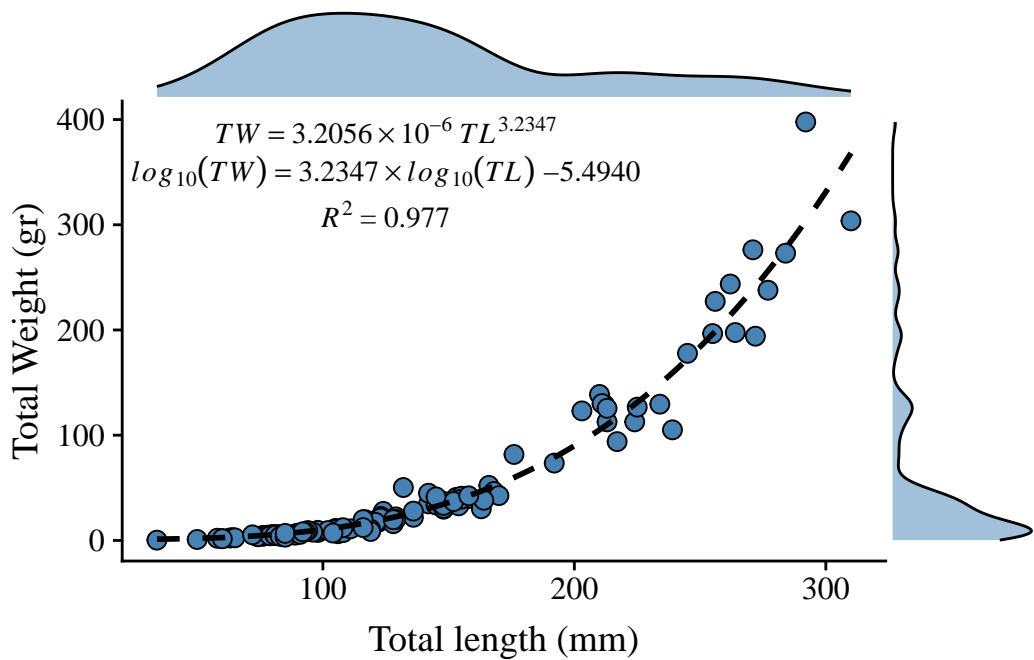


Figure 2. Length-weight relationship for 109 lionfish sampled in the central Mexican Caribbean. Points indicate samples, dashed black line indicates curve of best fit, marginal plots represent the density distribution of each variable.

137 mean \pm SD of 40.37 ± 58.74 gr (Sabido-Itzá et al., 2016), and the highest weight estimates came from
 138 the Northern Atlantic with 73.76 ± 96.11 gr (Barbour et al., 2011). To put this in context, true observed
 139 weights were 52.56 ± 76.58 gr. These correspond to predicted-to-observed weights ratios of 0.80 ± 0.19
 140 and 1.76 ± 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 ± 0.309 , 1.76 ± 0.496 , and 1.17 ± 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

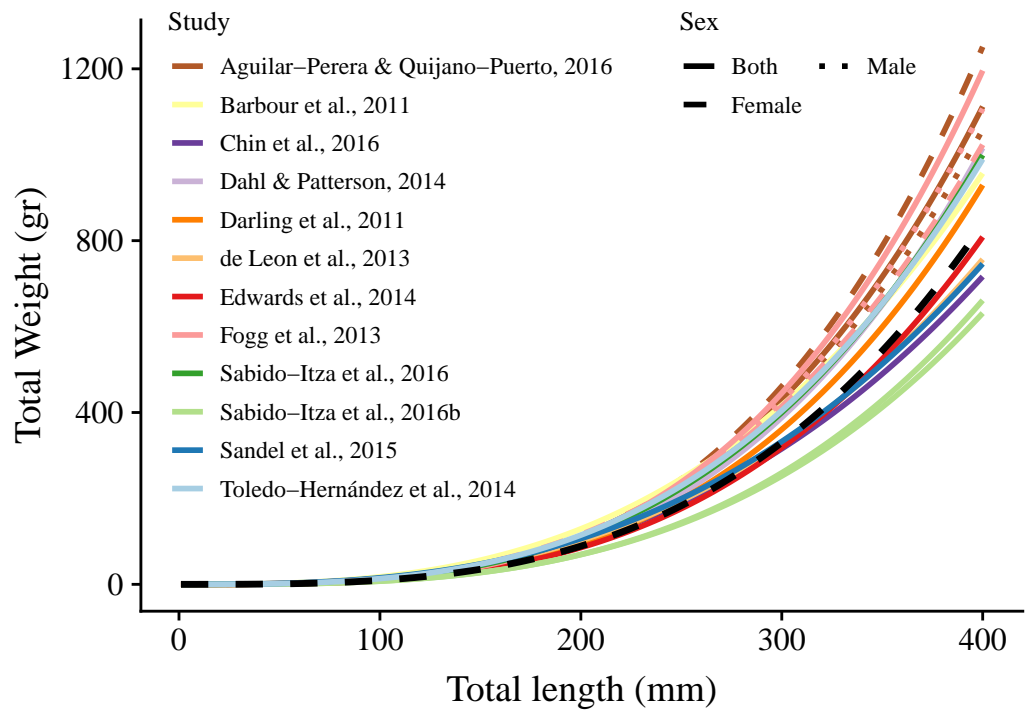


Figure 3. Length-weight relationships ($n = 18$) for 12 studies and this study. Colors indicate studies from which the parameters were extracted. Dotted, dashed and solid lines show models for males, females, and combined sexes, respectively. The dashed black line represents the relationship estimated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

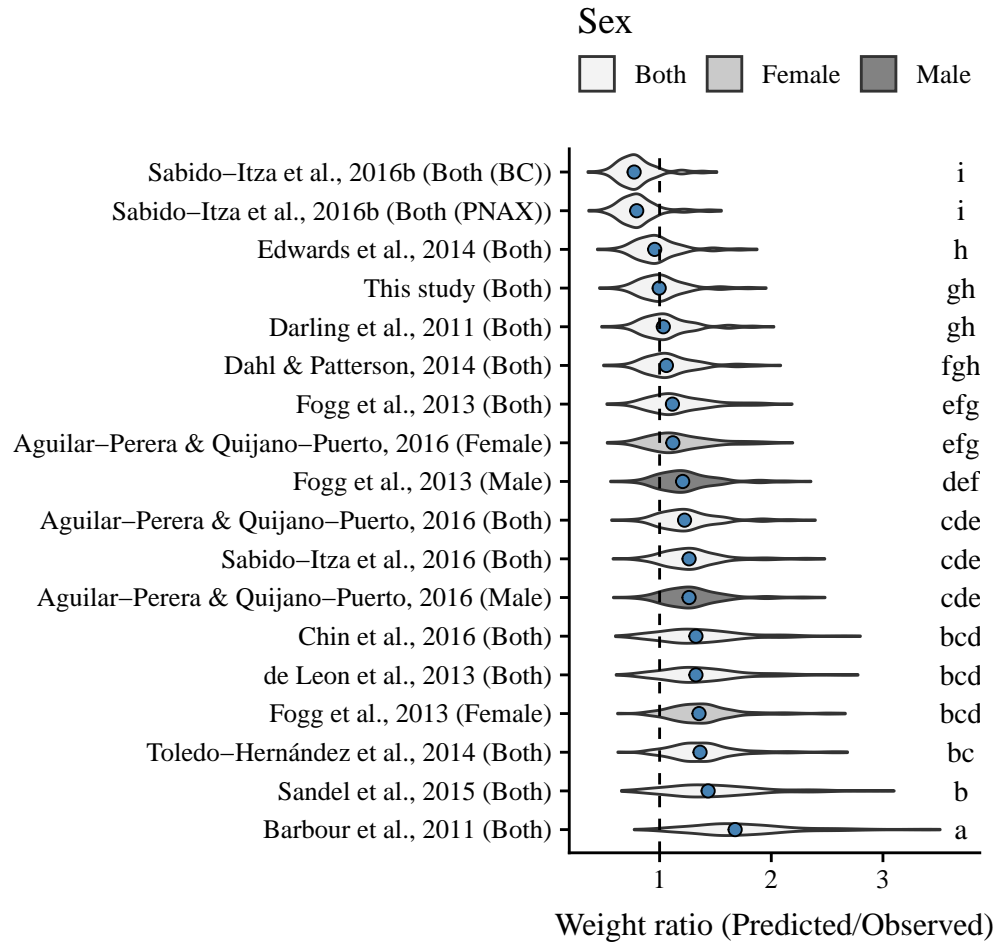


Figure 4. Violin plot of predicted-to-observed weight ratios for 18 pairs of allometric parameters. Blue circles indicate median values and Like letters indicate values that do not differ significantly.

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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