

Spatial variation in allometric growth of invasive lionfish has management implications

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ABSTRACT

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 regional differences that led to significant under- and overestimation of weight estimates. The spatial pattern we observed is consistent with findings from other studies focusing on genetics or length-at-age. 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 substantial implications for management in terms of predicting effects on local ecosystems, evaluating the effectiveness of removal programs, or estimating biomass available for harvest.

INTRODUCTION

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

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

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

46 ecosystems (Barbour et al., 2011; Andradi-Brown et al., 2017). However, promoting lionfish consumption
47 might create a level of demand capable of incentivizing a stable fishery while controlling shallow-water
48 populations, thus creating alternative livelihoods and avoiding further ~~impacts~~ negative effects to local
49 biota.

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

59 Outcomes of previous studies suggest lionfish are likely to exhibit spatial heterogeneity in the length-
60 weight relationship, which we summarize in two main causes. First, culling programs are effective in
61 reducing local adult populations largely because lionfish exhibit high levels of site fidelity and small home
62 ranges (Fishelson, 1997; Kochzius and Blohm, 2005; Jud and Layman, 2012; Côté et al., 2014). It is ~~know~~
63 known that fish with sedentary behavior are likely to exhibit high levels of spatial variation in important
64 life history ~~charactersties~~ characteristics such as growth or natural mortality rates (Gunderson et al., 2008;
65 Hutchinson, 2008; Wilson et al., 2012; Guan et al., 2013). Second, genetic analysis of lionfish suggests
66 biological differences due to the existence of two genetically distinct invasive subpopulations between
67 the ~~northwest~~ Western Atlantic and the Caribbean (Betancur-R et al., 2011). ~~Site-specific parameters~~
68 ~~are necessary to accurately estimate biomass when allometric relationships are spatially variable, and~~
69 ~~this variability is~~ The large number of site-specific studies reporting the length-weight relationship of
70 lionfish provide variable estimates. These differences may be increasingly important when estimating the
71 potential effectiveness of lionfish culling programs (Barbour et al., 2011; Morris et al., 2011; Côté et al.,
72 2014; Johnston and Purkis, 2015). However, the ~~region-wide differences in allometric growth parameters~~
73 ~~has remained unexplored for lionfish, despite the large number of site-specific studies reporting the~~
74 ~~length-weight relationship~~ magnitude of the error caused by using *ex situ* parameters to estimate total
75 weight from length observations remains unexplored.

76 Here, we ~~compare~~ use previously published length-weight relationships for lionfish populations in
77 North Carolina, Northern and Southern Gulf of Mexico, the Southern Mexican Caribbean, Bahamas, Little
78 Cayman, Jamaica, Bonaire, Puerto Rico, and Costa Rica (~~Barbour et al., 2011; Darling et al., 2011; de Leon et al., 2013;~~
79 to quantify the magnitude of the error caused by using *ex situ* parameters to estimate lionfish weight from
80 length observations. We also collected lionfish length and weight data in the central Mexican Caribbean
81 and report the first ~~allometric growth equation~~ length-weight relationship for this region. ~~The objective of~~
82 ~~this paper is to describe the spatial pattern of length-weight relationships of lionfish across the Caribbean~~
83 ~~and Western Atlantic and to discuss implications of these spatial differences.~~

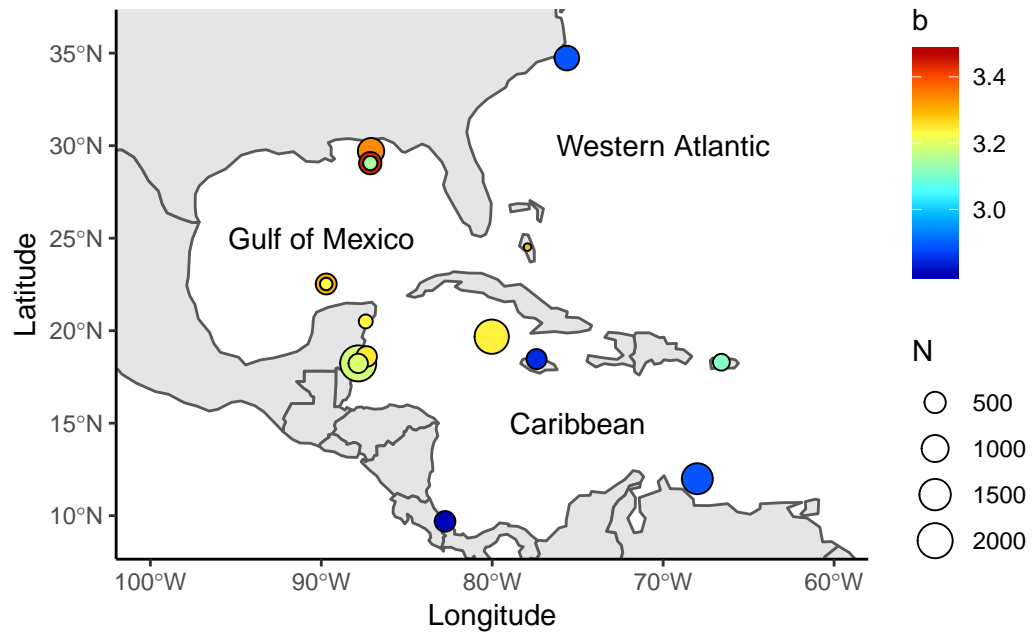


Figure 1. Locations where allometric growth parameters of lionfish (*Pterois spp*) have been reported. Circle sizes indicate sample size from each study, colors indicate the b coefficient from Eq. 1.

METHODS

We reviewed 12 published studies and obtained 17 length-weight relationships for the ~~North-Western~~ Atlantic ($n = 12$), Gulf of Mexico ($n = 7$), and Caribbean ($n = 98$, Table 1, Fig 31). We collected information on ~~sampling methods~~, sex differentiation, location, ~~length~~ and depth ranges ~~and sampling methods~~ from each study when available. Only two studies reported parameters for each gender (Aguilar-Perera and Quijano-Puerto, 2016; Fogg et al., 2013), so we assumed both genders were included in a study if gender was unspecified. Reviewed studies presented information for organisms ~~ranging between 25 mm and 475 mm in Total Length (TL), and that were~~ obtained at depths between 0.5 m and 57 m. ~~Three-Four~~ studies explicitly stated that their organisms were sampled with pole spears (Dahl and Patterson, 2014; Aguilar-Perera and Quijano-Puerto, 2016; Chin et al., 2016; Sabido-Itzá et al., 2016), and ~~five-six~~ studies mentioned that some of their organisms were obtained with pole spears (or other type of harpoon) but also hand-held nets or fish traps (~~Barbour et al., 2011; Fogg et al., 2013; Edwards et al., 2014; Toledo-Hernández, 2014; Sandel et al., 2015; Sabido-Itzá et al., 2016~~), and two studies did not specify how organisms were sampled (Darling et al., 2011; de Leon et al., 2013). ~~Fogg et al. (2013) use spineless weight in their calculations, so their parameters likely underestimated total weight. Since no spineless to total weight conversions were available, these parameters were taken as reported.~~

We also ~~collected data from~~ ~~used data from~~ Villaseñor-Derbez and Herrera-Pérez (2014), who collected ~~organisms from~~ 10 sampling sites along the central Mexican Caribbean coast in ~~the Summer of~~ 2010 (Supplementary Table 1). 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 better representation of small sizes by ~~eliminating-avoiding~~ gear selectivity. Organisms were euthanized via pithing and Total Length (TL; mm) and Total Weight (TW; g) were recorded.

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

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

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

111 ~~Transforming this equation via base-10 logarithms we obtain:-~~

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

112 ~~This can be simplified and re-written as:-~~

$$Y = bX + c$$

113 ~~Where $Y = \log_{10}(TW)$, $X = \log_{10}(TL)$, and $c = \log_{10}(a)$~~ The above equation was linearized using
114 ~~\log_{10} -transformation.~~ The coefficients ~~(c and b)~~ were estimated with an Ordinary Least Squares Regres-
115 sion, and heteroskedastic-robust standard error correction was applied (Zeileis, 2004). When ~~the~~ $b = 3$, it
116 is said that the organism exhibits a perfect isometric growth, so the b coefficient was tested against the
117 null hypothesis of isometric growth (*i.e.* $H_0 : b = 3$). Coefficients were tested with a two-tailed Student's
118 t , and the significance of the regression was corroborated with an F-test.

119 Some of the reviewed studies inconsistently defined a as either the ponderal index from Eq. 1 or
120 the y-intercept ~~(c) from Eq. ??~~ from the linearized log-transformed equation. Other studies incorrectly
121 reported parameters as mm-to-g conversions when they were in fact cm-to-g conversions. We standardized
122 each study by converting coefficients and report all parameters as TL (mm) to TW (g) conversions.
123 Locations where allometric studies have been performed are shown in Figure 1 and summarized in Table
124 1.

125 We obtained a total of 18 parameter pairs by combining length-weight parameters extracted from the
126 literature and the additional pair calculated here. Recall that the objective of this study is not to describe
127 variations between populations, but rather to estimate how the use of *ex situ* parameters influences weight
128 estimates. We used the central Mexican Caribbean as a case study of how the use of *ex situ* parameters
129 influences the accuracy of weight estimates for lionfish. We estimated ~~TW from the TL~~ TW from
130 the TL observations we collected in the central Mexican Caribbean ($n = 109$, with $TL \in (34, 310)$ TL
131 ranging from 34 mm to 310 mm) using each of the 18 parameter pairs and divided predicted weights
132 by known observed weights to obtain a simple measure of over- or underestimation. Difference in
133 mean weight ratios across the different parameter pairs were tested with a one-way analysis of variance
134 (ANOVA) and an analysis of covariance (ANCOVA), where the sources of variation were the study and
135 TL. Ratios were logit-transformed prior to analysis, and a *post-hoc* Tukey's test was used for *post-hoc*
136 tests to identify groups where mean ratios did not differ. All analyses were performed in R version
137 3.5.1-2 (R Core Team, 2018). Raw data and code used in this work are available on github —at
138 github.com/jcvdav/lionfish_biometry.

139 RESULTS

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

147 Coefficients of the linear model fit to Eq ???. Numbers in parentheses represent heteroskedastic-robust
148 standard errors: $c = -5.494 (0.083)***$ $b = 3.235 (0.039)***$ F Statistic 6928.67*** (df = 1; 107) Observations
149 109 Adjusted R^2 0.976 Residual Std. Error 0.096 (df = 107) Note:

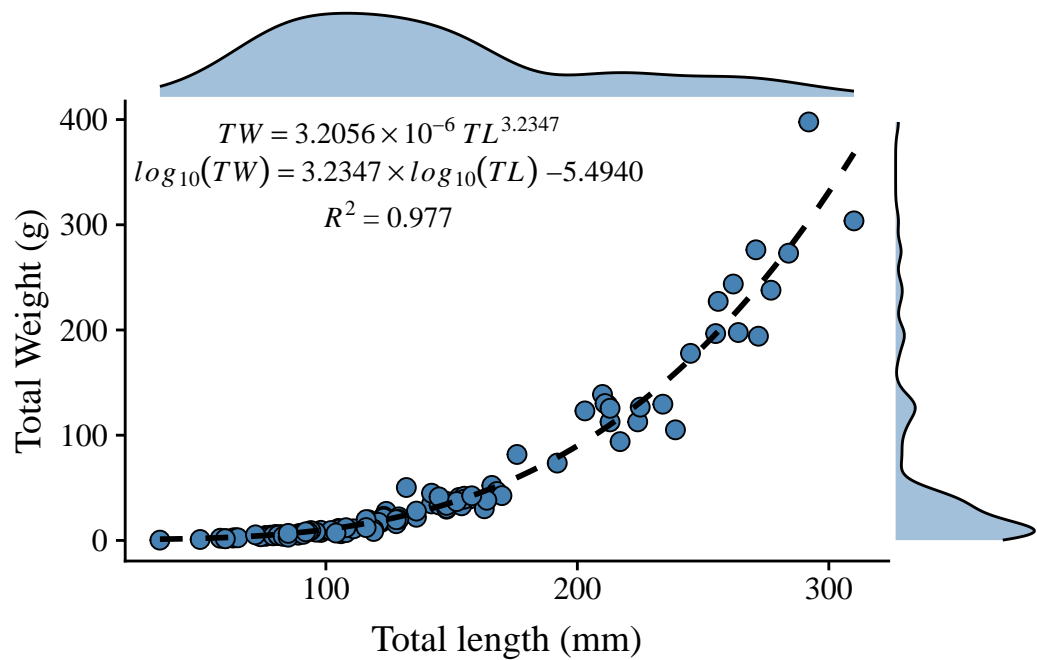


Figure 2. Length-weight relationship for 109 lionfish sampled in the central Mexican Caribbean. Points indicate samples, dashed black line indicates curve of best fit, marginal plots represent the density distribution of each variable.

There were significant differences in our predicted weights for the central Mexican Caribbean when using each of the different pairs of parameters ($F(df = 17; 1944) = 61.55; p < 0.001$, $F(df = 17; 1943) = 24.96; p < 0.001$). The lowest weight estimates for the observed lengths resulted from using the allometric parameters from Banco Chinchorro in the Caribbean, with mean \pm SD of 40.37 ± 58.74 gr (Sabido-Itzá et al., 2016), and g (Sabido-Itzá et al., 2016). In contrast, the highest weight estimates came from the Northern-Western Atlantic with 73.76 ± 96.11 gr-g (Barbour et al., 2011). To put this in context, true observed weights were have a mean of 52.56 ± 76.58 gr. These correspond to g. Weights predicted from these extreme parameters correspond to mean \pm SD predicted-to-observed weights ratios of 0.80 ± 0.19 and 1.76 ± 0.50 (mean \pm SD), respectively.

The calculated ratio of predicted-to-observed weight ranged from The largest under- and overestimations resulted in ratios of 0.36 to and 3.51 of the actual observed weight, indicating that *ex situ* parameters can result in major substantial weight under- and overestimations. overestimation.

Tukey's *post-hoc* test suggests that weight ratios for the central Mexican Caribbean were not different from those obtained with parameters from Little Cayman, the Bahamas, and some sites in the Gulf of Mexico (Tukeys-Tukey's HSD $p > 0.05$). Weight estimates using parameters from the Gulf of Mexico and North-Western-Western Atlantic were higher on average than those from the Caribbean (Fig 3). The average (\pm SD) predicted-to-observed weight ratios from these three regions were 1.24 ± 0.309 , 1.76 ± 0.496 , and 1.17 ± 0.398 , respectively. This suggest that the smallest errors are observed when using parameters other locations in the Caribbean. Predicted-to-observed weight ratios are presented in Figure 4. Spineless weight parameters from Fogg et al. (2013) still produced predicted-to-observed weight ratios > 1 .

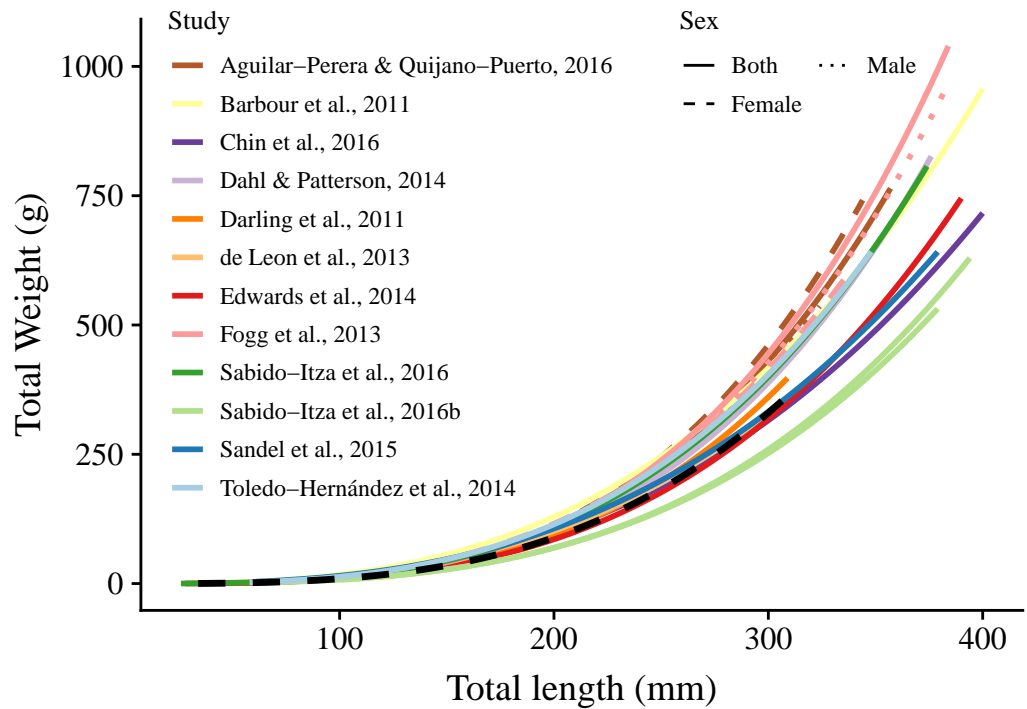


Figure 3. Length-weight relationships ($n = 18$) for 12 studies and this study. [The curves are shown for the range of lengths reported in each study \(See Supplementary Table 2\); when ranges were not present, we use the ones found in this study \(34 mm - 310 mm\).](#) Colors indicate studies from which 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. [There are two solid green lines for Sabido-Itza et al, 2016b, one for each of the two sites for which they report parameters. A log-log version of this figure is presented in Figure S4.](#)

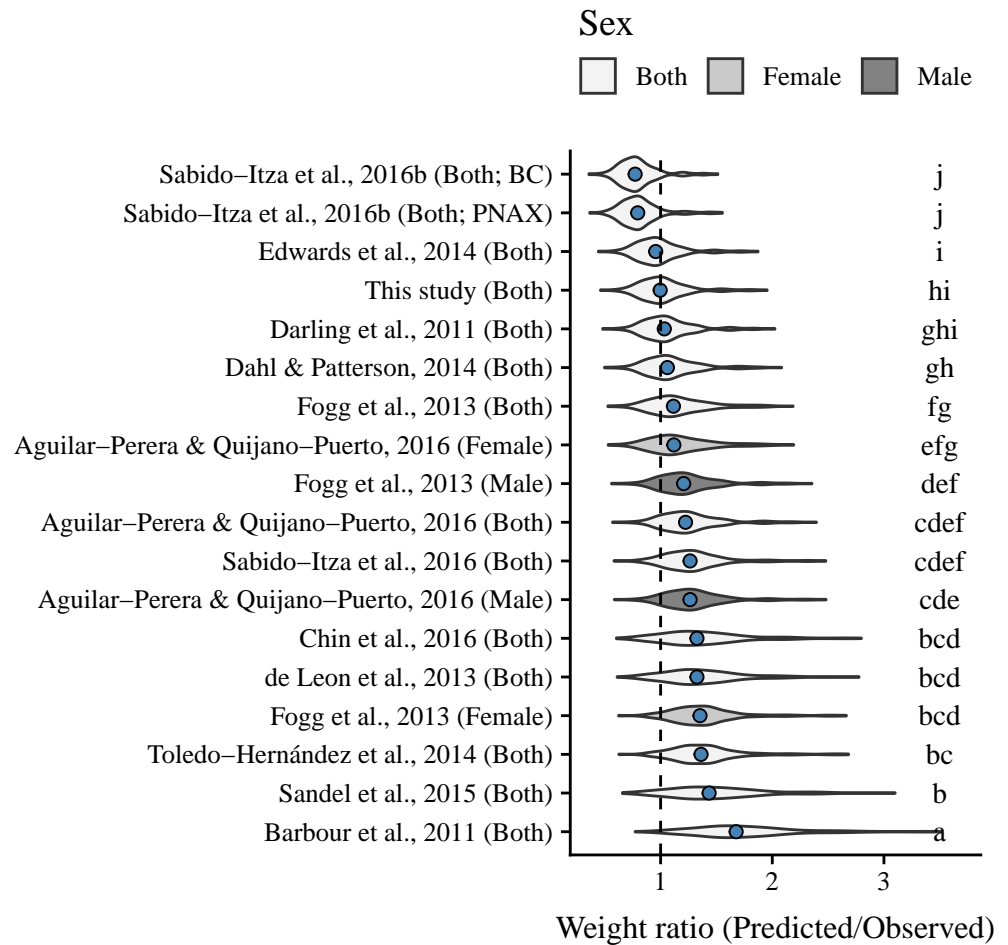


Figure 4. Violin plot of predicted-to-observed weight ratios for 18 pairs of allometric parameters. Blue circles indicate median values and **Like-like** letters indicate values that do not differ significantly. [For Sabido-Itza et al., 2016b, BC and PNAX make reference to Banco Chichorro and Parque Nacional Arrecifes de Xcalak, two sites for which they report parameters.](#)

Table 1. 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 $\times 10^{-5}$), e = 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	e- R^2	Fit-Reference
Caribbean-Western Atlantic	B	458-774	3.6-2.9	2.81-2.89	-4.44-	Sandel-Barbour et al., 2011
Caribbean-Western Atlantic	B	419-	2.8-0.25	2.85-3.29	-4.56-	0.8715-Chin-Darling et al., 2013
Caribbean-GoM	B	1450-934	2.3-0.21	2.89-3.34	-4.64-0.98	0.96-de Leon et al., 2013
Caribbean-GoM	B	1887-472	0.3-0.29	3.24-3.30	-5.52-0.95	0.97-Edwards et al., 2014
Caribbean-GoM	B-F	-67	0.25-0.12	3.29-3.47	-5.60-0.95	-Darling et al., 2014-Aguilar-Perera et al., 2014
Caribbean-GoM	B-M	2143-59	0.52-0.42	3.18-3.23	-5.28-0.95	0.9907-Sabido-Itza et al., 2014
Caribbean-GoM	B	227-582	0.8-0.14	3.11-3.43	-5.10-0.99	0.958-Toledo-Hernández et al., 2014
Caribbean-GoM	B-M	449-119	0.23-0.27	3.25-3.31	-5.64-0.97	Sabido-Itza-Fogg et al., 2014
Caribbean-GoM	B-F	368-115	0.32-0.68	3.19-3.14	-5.50-0.94	0.98-Sabido-Itza-Fogg et al., 2014
Caribbean	B	109-458	0.32-3.6	3.23-2.81	-5.49-	0.9766-This study-Sandel et al., 2011
GoM-Caribbean	B	934-419	0.21-2.8	3.34-2.85	-5.68-0.87	0.98-Dahl & Patterson, 2001
GoM-Caribbean	B	472-1450	0.29-2.3	3.30-2.89	-5.54-0.92	0.95-Aguilar-Perera & Chin, 2013
GoM-Caribbean	F-B	67-1887	0.12-0.3	3.47-3.24	-5.93-0.97	0.95-Aguilar-Perera & Chin, 2013
GoM-Caribbean	M-B	59-2143	0.42-0.52	3.23-3.18	-5.38-0.99	0.95-Aguilar-Perera & Chin, 2013
GoM-Caribbean	B	582-227	0.14-0.8	3.43-3.11	-5.86-0.96	0.99-Fogg-Toledo-Hernández et al., 2014
GoM-Caribbean	M-B	119-449	0.27-0.23	3.31-3.25	-5.57-0.97	Fogg-Sabido-Itza et al., 2014
GoM-Caribbean	F-B	115-368	0.68-0.32	3.14-3.19	-5.17-0.98	0.94-Fogg-Sabido-Itza et al., 2014
North-Atlantic-Caribbean	B	774-109	2.9-0.32	2.89-3.23	-4.54-0.98	-Barbour et al., 2011-Thompson et al., 2011

DISCUSSION

Our results suggest that lionfish exhibit highly variable allometric relationships across the invaded range, and that this variation is ~~related to space~~ spatially heterogeneous and relevant for management of the invasion. Moreover, we ~~shot show~~ that the use of *ex situ* parameters may lead to highly biased weight estimates. Our comparison of observed weights to those predicted with locally-informed parameters and *ex situ* parameters showed that weight can be overestimated by more than a three-fold, and highlights the need to use local information. Here we discuss the implications of our findings, ~~possible shortcomings in our analyses~~, and highlight potential future research directions.

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

We detected substantial differences in weight-at-length between organisms from the Caribbean, Gulf of Mexico, and ~~North-Western Western~~ Atlantic. Groupings of predicted-to-observed weight ratios identified in our *post hoc* testing aligned with the spatial distribution of the examined studies, suggesting that these differences ~~are may be~~ mediated by space. These regional allometric differences mirror similar patterns in ~~age-at-length length-at-age~~ of lionfish across both their invaded and native regions (Pusack et al., 2016). Variation may be driven by genetics or by organisms' exposure to distinct environmental conditions. For example, Betancur-R et al. (2011) used mitochondrial DNA to demonstrate the existence of two distinct population groups, identified as the "Caribbean group" and "Northern Group", and Fogg et al. (2015) alternatively suggested that ~~age-at-length length-at-age~~ differences may be ~~climate-driven driven by the environment~~.

We might be inclined to attribute all variation to the spatial origin of these parameters. However, these were not only collected for different locations, but also using a range of different sampling methods and at different points in time (See Supplementary Table 2 for an extended version of Table 1). While we are not able to evaluate how these factors influence previous estimates (raw data from all studies would be needed), it is certain that the lack of locally-calculated parameters may induce significant bias when calculating weight from length observations. Differences in weight-at-length could also reflect differential energy input or usage, or a combination of both. ~~Future research is needed to determine which processes are at work here.~~

~~Differences in~~ The magnitude of the bias and our lack of understanding of the source of variation highlights the need to simultaneously collect length-weight relationships have traditionally been highlighted as potential pitfalls to fishery management. For example, Wilson et al. (2012) show that small-scale variations in length-at-age and fishing mortality in other Scorpaeniformes translate to differential landings, effort, and catch per unit effort in the live fish fishery of California, and that these differences must be taken into account in management plans. The lionfish case poses the opposite scenario, where the manager desires to eradicate the species. To accurately gauge both the effectiveness of lionfish removal efforts and the resources needed to successfully manage an invasion, we must acknowledge and understand regional biological differences in important variables such as allometric growth parameters ~~information~~ across the invaded range to test for spatially-induced patterns and link these to previously suggested environmental and genetic structures. Such an endeavor would provide insights into lionfish biology and better inform management.

Applying parameters estimates to lengths outside the range of lengths originally used to estimate the parameters may also induce error. Our smallest observed organism was 34 mm in *TL*, and only two studies estimated parameters with smaller organisms (Sabido-Itza et al., 2016; Edwards et al., 2014). On the other hand, our largest organism had a *TL* of 310 mm, which is well within the range of all other studies (maximum observed lengths varied from 325 mm to 475 mm; See Supplementary Table 2). Due to the power-function describing the allometric relationship, the error is higher when extrapolation is done for lengths that are larger than the maximum length used to estimate the parameters. This means that not only must managers use locally-informed data, but that these local data must also include the full range of lengths present in the region to reduce error caused by extrapolation.

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

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

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