

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

Juan Carlos Villaseñor-Derbez¹, Sean Fitzgerald¹

¹Bren School of Environmental Sciences and Management, University of California Santa Barbara, Santa Barbara, California, USA

Corresponding author:

Juan Carlos Villaseñor-Derbez¹

Email address: jvillasenor@bren.ucsb.edu

ABSTRACT

Lionfish (*Pterois volitans/miles*) are an invasive species in the Western Atlantic and the Caribbean. Improving management of invasive lionfish populations requires accurate estimates of total biomass, which in turn depend on accurate definition of the length-weight relationship. Here, we reviewed published length-weight relationships of lionfish taken from throughout their invasive range and found that lionfish of equal lengths have lower body mass in the Caribbean than in the Atlantic or Gulf of Mexico. Additionally, we report a new pair of length-weight parameters ($a = 3.2056 \times 10^{-6}$; $b = 3.235$) for organisms sampled in the central Mexican Caribbean region. The substantial spatial variation in length-weight parameters highlights the importance of using site-specific information when estimating lionfish biomass using length observations. 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.

INTRODUCTION

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 invasive marine vertebrates established along the North Atlantic Caribbean 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). Invasive lionfish are primarily studied in coral reef ecosystems, where their impacts are far-reaching. 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, and increased lionfish biomass coincided with a 65% reduction in the biomass of native prey fishes along Bahamian coral reefs in just two years (Green et al., 2012). Lionfish have also established invasive populations in other habitats such as estuaries, mangroves, hard-bottomed areas, and mesophotic reefs (Jud et al., 2011; Barbour et al., 2010; Muñoz et al., 2011; Andradi-Brown et al., 2017; J.A.B. et al., 2012).

A substantial amount of research describes lionfish feeding ecology from North Carolina to Costa Rica (Muñoz et al., 2011; Morris and Akins, 2009; Cote et al., 2013; Dahl and Patterson, 2014; Valdez-Moreno et al., 2012; Villaseñor-Derbez and Herrera-Pérez, 2014; Hackerott et al., 2017; Sandel et al., 2015). 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 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 (Albins and Hixon, 2008; Green et al., 2012; 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 tracking the spread of established lionfish populations through time (Schofield, 2009, 2010) and by predicting invasion ranges under future climates (Grieve et al., 2016). Trophic impacts of lionfish

46 can be minimized if local lionfish biomass is controlled by by culling (Arias-Gonzalez et al., 2011).
47 However, the feasibility of controlling local populations remains a topic of debate (Côté et al., 2014).

48 Governments and non-profit organizations have sought to reduce lionfish densities through removal
49 programs and incentivizing its consumption (Chin et al., 2016). In some cases, these have shown to
50 significantly reduce –but not quite eliminate– lionfish abundances at local scales (Sandel et al., 2015;
51 Chin et al., 2016; de Leon et al., 2013). In addition, culling programs can help stabilize or grow native
52 prey fish populations (Côté et al., 2014). Complete eradication of lionfish through fishing is unlikely
53 because of their rapid recovery rates and ongoing recruitment to shallow-water areas from their persistent
54 populations in mesophotic coral ecosystems (Barbour et al., 2011; Andradi-Brown et al., 2017). However,
55 promoting lionfish consumption might create a level of demand capable of sustaining a stable fishery,
56 which can help control shallow-water populations while providing alternative livelihoods and avoiding
57 further impacts to local reef biota (Chin et al., 2016).

58 The feasibility of establishing fisheries through lionfish removal programs has been extensively
59 evaluated through field observations and empirical modeling (Barbour et al., 2011; Morris et al., 2011; de
60 Leon et al., 2013; Johnston and Purkis, 2015; Sandel et al., 2015; Chin et al., 2016; Usseglio et al., 2017).
61 One contributing factor to the success of many removal programs is the sedentary nature of adult lionfish
62 (Jud and Layman, 2012). Culling programs are effective in reducing adult populations largely because
63 lionfish exhibit high levels of site fidelity and rarely leave their home range in most cases (Fishelson,
64 1997; Côté et al., 2014; Kochzius and Blohm, 2005) – But see Andradi-Brown et al. (2017) for cases
65 when deep-water populations maintain shallow-water populations. Fish with this sedentary behavior are
66 likely to exhibit high levels of spatial variation in important life history characteristics such as growth or
67 natural mortality rate (Hutchinson, 2008; Wilson et al., 2012). The importance of considering spatial
68 heterogeneity is well-documented in terms of assessing and managing sedentary species (Gunderson et al.,
69 2008; Guan et al., 2013), and such variation should be accounted for when evaluating the feasibility of
70 establishing lionfish fisheries as well.

71 Empirical modeling efforts examining the feasibility of establishing fisheries for lionfish involve
72 modeling changes in biomass in response to changes in mortality (*i.e.* culling). A common way to
73 model this is via length-structured population models, where fish lengths are converted to weight in order
74 to calculate total biomass (Côté et al., 2014; Barbour et al., 2011; Andradi-Brown et al., 2017). The
75 length-weight relationship is therefore an essential component of these models, but this relationship can
76 vary across regions as a response to biotic (e.g. local food availability) and abiotic (e.g. water temperature)
77 conditions (Johnson and Swenarton, 2016). Literature suggests that site-specific parameters are necessary
78 in order to accurately estimate biomass when length-weight relationships are spatially variable, and this
79 variability becomes increasingly important when estimating the potential effectiveness of (and resources
80 needed for) lionfish culling programs or when identifying total biomass available for harvest by fishers
81 (Barbour et al., 2011; Morris et al., 2011; Johnston and Purkis, 2015; Chin et al., 2016; Côté et al.,
82 2014). In addition to environmentally-driven spatial variation, genetic analysis of invasive lionfish
83 suggest biological differences due to the existence of two genetically distinct subpopulations between
84 the northwest Atlantic and the Caribbean (Betancur-R et al., 2011). To date, no studies have examined
85 region-wide differences in length-weight parameters despite the large number of studies reporting this
86 relationship for lionfish.

87 The objective of this paper is to describe the spatial pattern of length-weight relationships of lionfish
88 in the Caribbean and Western Atlantic and evaluate the implications of these spatial differences. Length-
89 weight relationships for lionfish exist for North Carolina, Northern and Southern Gulf of Mexico, the
90 Southern Mexican Caribbean, Bahamas, Little Cayman, Jamaica, Bonaire, Puerto Rico, and Costa Rica
91 (Barbour et al., 2011; Fogg et al., 2013; Dahl and Patterson, 2014; Aguilar-Perera and Quijano-Puerto,
92 2016; Sabido-Itza et al., 2016; Sabido-Itzá et al., 2016; Darling et al., 2011; Edwards et al., 2014; Chin
93 et al., 2016; de Leon et al., 2013; Toledo-Hernández, 2014; Sandel et al., 2015). This study also provides
94 the first length-weight relationship for the central Mexican Caribbean.

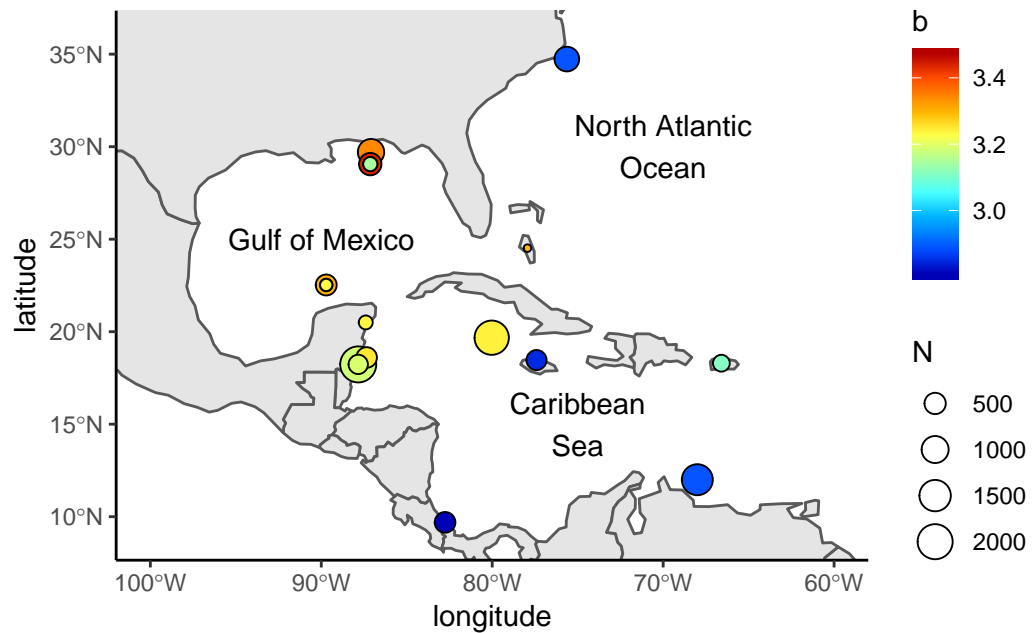


Figure 1. Locations where allometric growth parameters of lionfish (*Pterois spp*) have been reported. Circle sizes indicate sample size from each study, colors indicate the b coefficient from Eq. 1.

MATERIALS AND METHODS

We reviewed 12 published studies and obtained 17 length-weight relationships for the North Atlantic ($n = 1$), Gulf of Mexico ($n = 7$), and Caribbean ($n = 10$, Table 1, Fig 3). We collected information on sampling methods, sex differentiation, location, and depth ranges from each study when available, and assumed both genders were included in a study if gender was unspecified. Two studies reported parameters for genders combined and separated (Aguilar-Perera and Quijano-Puerto, 2016; Fogg et al., 2013), while the rest presented pooled results. Reviewed studies presented information for organisms obtained at depths between 0.5 and 57 m. Three studies explicitly stated that their organisms were sampled with pole spears (Aguilar-Perera and Quijano-Puerto, 2016; Chin et al., 2016; Dahl and Patterson, 2014; Sabido-Itzá et al., 2016), and five 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 (Sandel et al., 2015; Barbour et al., 2011; Fogg et al., 2013; Edwards et al., 2014; Sabido-Itza et al., 2016; Sabido-Itzá et al., 2016; Toledo-Hernández, 2014), and two studies did not specify how organisms were sampled (de Leon et al., 2013; Darling et al., 2011). Fogg et al. (2013) use spine-less weight in the length-weight relationship estimation, and thus their parameters likely underestimate whole weight. Since no spine-less to whole weight conversions were available, these parameters were taken as reported.

We also collected data from 10 sampling sites along the central 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 better representation of small sizes by eliminating gear selectivity. Organisms were euthanized via pithing and Total Length (TL; mm) and Total Weight (TW; g) were recorded.

The weight at length relationship for lionfish in the central Mexican Caribbean was calculated with

118 the allometric growth function:

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

119 Where a is the ponderal index and b is the scaling exponent or allometric parameter. When $b = 3$,
120 it is said that the organism exhibits a perfect isometric growth. Transforming this equation via base-10
121 logarithms:

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

122 This can be simplified and re-written as:

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

123 Where $Y = \log_{10}(TW)$, $X = \log_{10}(TL)$, and $c = \log_{10}(a)$. The coefficients (c and b) were estimated
124 with an Ordinary Least Squares Regression and heteroskedastic-robust standard error correction (Zeileis,
125 2004). The b coefficient was tested against the null hypothesis of isometric growth (*i.e.* $H_0 : b =$
126 3). Coefficients were tested with a two-tailed Student's t , and the significance of the regression was
127 corroborated with an F-test.

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

133 Combining the length-weight parameters extracted from the literature and the additional pair calculated
134 here, we obtain a total of 18 pairs. We use the central Mexican Caribbean as a case study of how the use
135 of *ex situ* parameters influences the accuracy of weight estimates for lionfish. We estimated TW from the
136 TL observations we collected in the central Mexican Caribbean ($n = 109$) using each of the 18 parameter
137 pairs and divided predicted weights by known observed weights to obtain a simple measure of over- or
138 underestimation. Difference in mean weight ratios across the different parameter pairs were tested with a
139 one-way analysis of variance (ANOVA). All analyses were performed in R version 3.5.0 (R Core Team,
140 2018). Raw data and code used in this work are available at dryad.org.

141 RESULTS

142 Inserting TL observations for the central Mexican Caribbean into 2 Eq. 2 and converting to 3 resulted
143 in the coefficient values $b = 3.2347391$ and $c = -5.4940866$ ($R^2 = 0.977$, $F(df = 1; 107) = 6928.67$,
144 $p < 0.001$). The length-weight coefficients estimated in this study were within the range identified by
145 studies in other regions (Table 1). The significant difference between this allometric factor (b) and the
146 isometric growth factor $b = 3$ ($t(107) = 6.04$; $p < 0.001$) indicated that lionfish present allometric growth,
147 which is consistent with other studies. Figure 2 shows the relationship between TL and TW for this region,
148 and more information on model fit is presented in Table S2.

149 Parameters from models fit to males or females exclusively tend to have a higher steepness (*i.e.* higher
150 allometric parameter), with mean \pm standard deviation values of $b = 3.27 \pm 0.06$ and $b = 3.31 \pm 0.23$
151 for males and females respectively, compared to parameters from models for pooled genders with a
152 mean \pm standard deviation value of $b = 3.14 \pm 0.20$. In the case of the ponderal index (a) and its
153 \log_{10} transformation (c), values were higher for parameters for pooled genders. Figure 3 shows the
154 length-weight relationships with parameters from all studies.

155 There were significant differences in our predicted weights for the central Mexican Caribbean when
156 using the different pairs of parameters ($F(df = 15; 1728) = 38.26$; $p < 0.001$). The lowest weight
157 estimates resulted from using the allometric parameters from Banco Chinchorro in the Caribbean Sabido-
158 Itzá et al. (2016), and the highest weight estimates came from the Northern Atlantic Barbour et al. (2011).
159 The calculated ratio of predicted-to-observed weight ranged from 0.80 ± 0.19 to 1.76 ± 0.50 (mean \pm
160 SD). Predicted-to-observed weight ratios are presented in Figure 4. Spine-less weight parameters from
161 Fogg et al. (2013) still produced predicted-to-observed weight ratios > 1 .

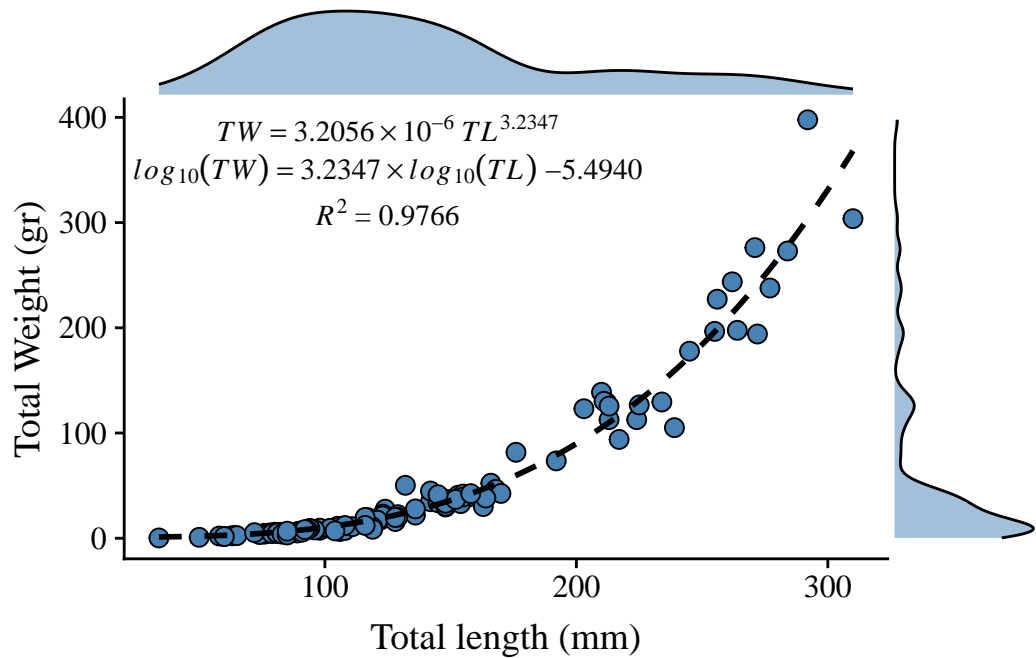


Figure 2. Length-weight relationship for 109 lionfish sampled in the central Mexican Caribbean. Points indicate samples, dashed black line indicates curve of best fit, marginal plots represent the density distribution of each variable.

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 $\times 10^{-5}$), 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	c	R^2	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
NorthAtlantic	B	774	2.9	2.89	-4.54	-	Barbour et al., 2011

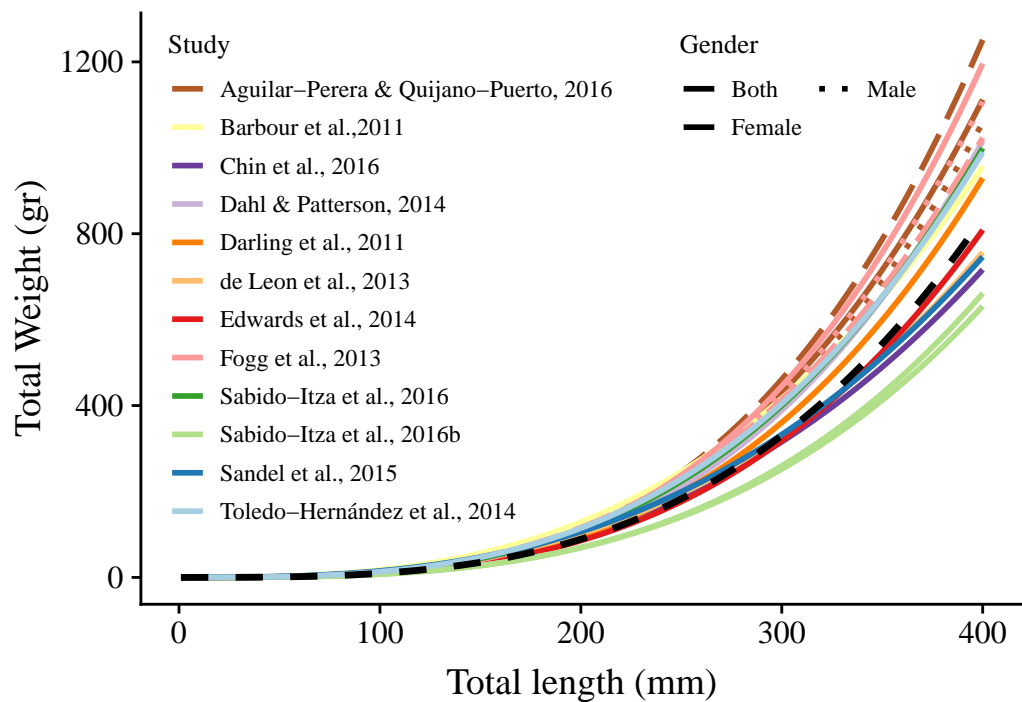


Figure 3. Length-weight relationships ($n = 18$) for 12 studies and this study. Colors indicate studies from which the parameters were extracted. Solid lines indicate that the fit was performed for males and females pooled together. Dotted lines indicate that the regression was performed on females, and dashed lines indicate it was performed for males. The dashed black line represents the relationship estimated in this study.

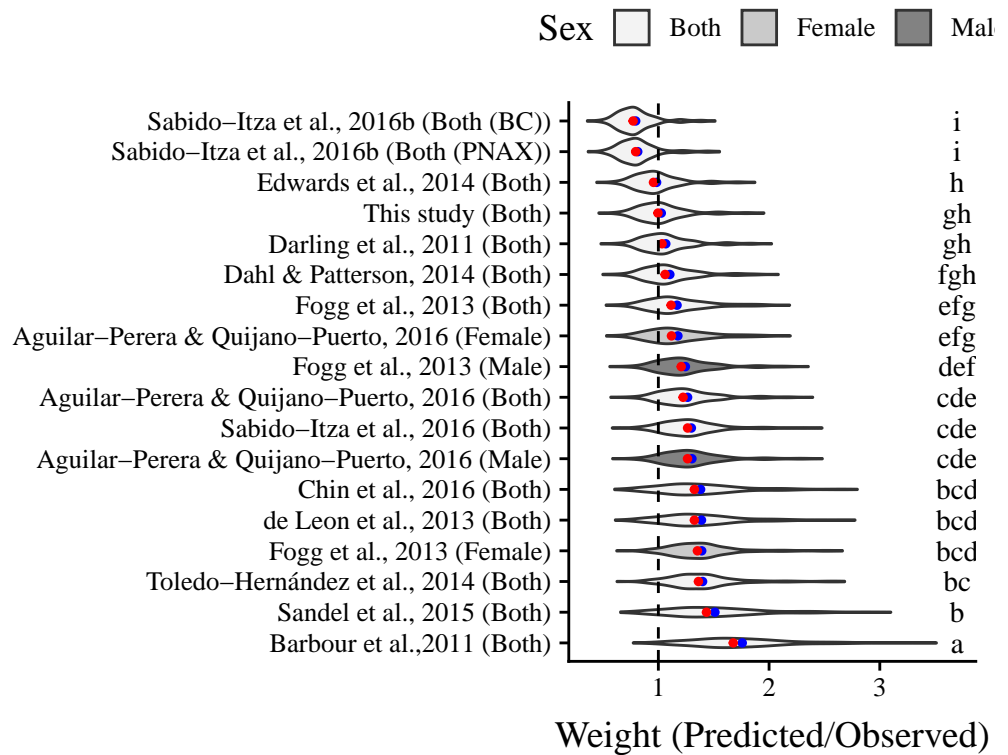


Figure 4. Violin plot of predicted to observed weight ratios for 18 pairs of allometric parameters. Red and blue circles indicate median and mean values, respectively. Like letters indicate values that do not differ significantly (Tukey's HSD; $p < 0.05$).

DISCUSSION

We detected substantial differences in weight-at-length between organisms from the Caribbean and Gulf of Mexico / North-Western Atlantic. Weight estimates using parameters from the Gulf of Mexico and North-Western Atlantic were higher on average than those from the Caribbean. The average predicted-to-observed weight ratios from these three regions were 1.24 ± 0.309 , 1.76 ± 0.496 , and Caribbean 1.17 ± 0.398 , respectively. These length-weight differences mirror similar findings of regional variability in age-at-length relationships of lionfish across both their invaded and native regions (Pusack et al., 2016). These differences may be driven by genetic variation or by organisms being exposed 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 differences may be driven by climate. Differences in weight-at-length could also reflect differences in energy input (*i.e.* in some regions, lionfish eat more) or differential usage of this energy (*e.g.* regional differences in predator abundances lead to different usage of energy), or a combination of both. Future research is needed to determine which processes are at work here.

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 (*Sebastes rastrelliger*) 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 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.

The results presented here have major 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. They showed that using the 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 up to a threefold TW overestimation. These differences become especially important when allocating resources for removal programs, incentivizing its fishery as 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. This work additionally highlights the need for more basic research that furthers our understanding of the invasive lionfish.

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