

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

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ABSTRACT

Lionfish (*Pterois volitans* / *miles*) are an invasive species in the Western Atlantic and the Caribbean. Improving management of invasive lionfish populations requires accurate estimates of total biomass, which depend on accurate estimates of the length-weight relationship. Lionfish exhibit a sedentary behavior that is likely to result in high levels of spatial variation in some life history characteristics, such as the length-weight relationship. We review 12 published length-weight relationships of lionfish taken throughout their invasive range and describe the spatial variation and implications of these differences. The spatial pattern observed here is consistent with those reported in genetic studies or age-at-length studies. We show that the use of *ex situ* parameters can result in up to a three-fold overestimation of Total Weight, but that using parameters obtained nearby 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.

INTRODUCTION

Lionfish (*Pterois volitans/miles* complex) are an invasive species in the western Atlantic and Caribbean Sea, 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. Green et al. (2012) report that prey fish biomass declined 65% over two years as lionfish biomass increased along Bahamian coral reefs. 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 throughout the invaded range (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). It has been proposed that trophic

46 impacts of lionfish can be minimized if local lionfish biomass is controlled by culling (Arias-Gonzalez
47 et al., 2011).

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;
60 de Leon et al., 2013; Johnston and Purkis, 2015; Sandel et al., 2015; Chin et al., 2016; Usseglio et al.,
61 2017). One contributing factor to the success of many removal programs is the sedentary nature of adult
62 lionfish (Jud and Layman, 2012). Culling programs are effective in reducing local adult populations
63 largely because lionfish exhibit high levels of site fidelity and rarely leave their home range (Fishelson,
64 1997; Côté et al., 2014; Kochzius and Blohm, 2005). Fish with this sedentary behavior are likely to exhibit
65 high levels of spatial variation in important life history characteristics such as growth or natural mortality
66 rates (Hutchinson, 2008; Wilson et al., 2012). The importance of considering spatial heterogeneity is
67 well-documented in terms of assessing and managing sedentary species (Gunderson et al., 2008; Guan
68 et al., 2013), and such variation should be accounted for when evaluating the feasibility of establishing
69 lionfish fisheries as well.

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

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

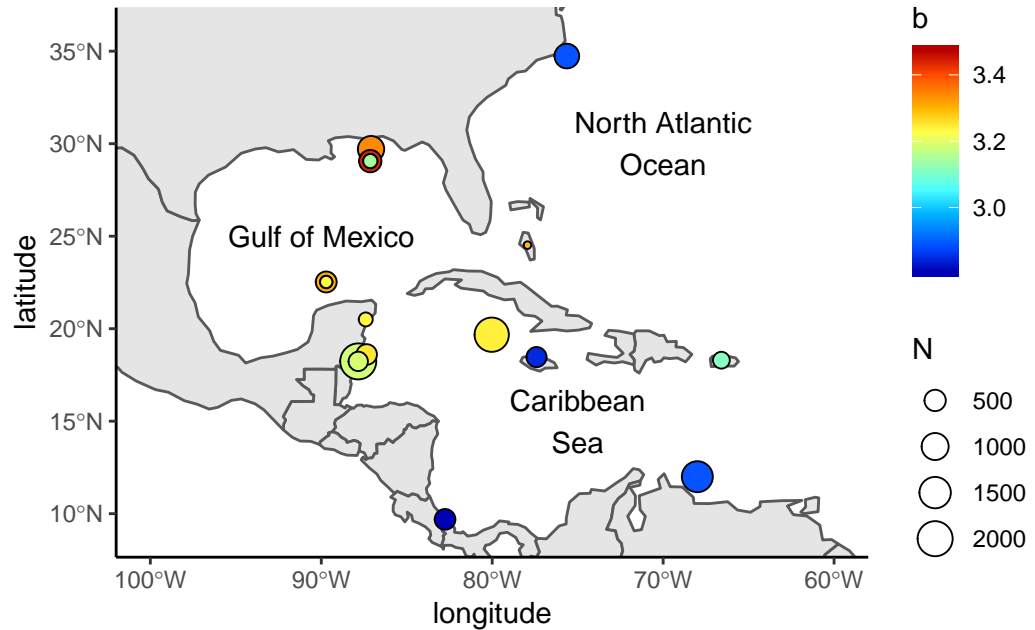


Figure 1. Locations where allometric growth parameters of lionfish (*Pterois spp*) have been reported. Circle sizes indicate sample size from each study, colors indicate the b coefficient from Eq. 1.

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. Only two studies reported parameters for each gender (Aguilar-Perera and Quijano-Puerto, 2016; Fogg et al., 2013). Reviewed studies presented information for organisms obtained at depths between 0.5 m 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 total weight. Since no spine-less to total 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 the allometric growth function:

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

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

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

119 This can be simplified and re-written as:

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

120 Where $Y = \log_{10}(TW)$, $X = \log_{10}(TL)$, and $c = \log_{10}(a)$. The coefficients (c and b) were estimated
121 with an Ordinary Least Squares Regression and heteroskedastic-robust standard error correction (Zeileis,
122 2004). The b coefficient was tested against the null hypothesis of isometric growth (*i.e.* $H_0 : b =$
123 3). Coefficients were tested with a two-tailed Student's t , and the significance of the regression was
124 corroborated with an F-test.

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

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

139 RESULTS

140 The length-weight relationship for organisms from the central Mexican Caribbean resulted in the
141 coefficient values $a = 3.2056297 \times 10^{-6}$, $b = 3.2347391$ and $c = -5.4940866$ ($R^2 = 0.977$, $F(df =$
142 $1; 107) = 6928.67$, $p < 0.001$). The allometric factor (b) was significantly different from $b = 3$
143 ($t(107) = 6.04$; $p < 0.001$) indicating that lionfish present allometric growth. The length-weight co-
144 efficients estimated in this study were within the range identified by studies in other regions (Table 1).
145 Figure 2 shows the relationship between TL and TW for this region, and more information on model fit is
146 presented in Table S2.

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

153 There were significant differences in our predicted weights for the central Mexican Caribbean when
154 using the different pairs of parameters ($F(df = 15; 1728) = 38.26$; $p < 0.001$). Weight estimates using
155 parameters from the Gulf of Mexico and North-Western Atlantic were higher on average than those from
156 the Caribbean. The average (\pm SD) predicted-to-observed weight ratios from these three regions were
157 1.24 ± 0.309 , 1.76 ± 0.496 , and 1.17 ± 0.398 , respectively. The lowest weight estimates resulted from
158 using the allometric parameters from Banco Chinchorro in the Caribbean Sabido-Itzá et al. (2016), and
159 the highest weight estimates came from the Northern Atlantic (Barbour et al., 2011). The calculated ratio
160 of predicted-to-observed weight ranged from 0.80 ± 0.19 to 1.76 ± 0.50 (mean \pm SD). Tukey's post-hoc
161 test suggests that weight ratios for the central Mexican Caribbean were not different from those obtained
162 with parameters from Little Cayman, the Bahamas, and some sites in the Gulf of Mexico (Tukey's HSD
163 $p > 0.05$). Predicted-to-observed weight ratios are presented in Figure 4. Spine-less weight parameters
164 from Fogg et al. (2013) still produced predicted-to-observed weight ratios > 1 .

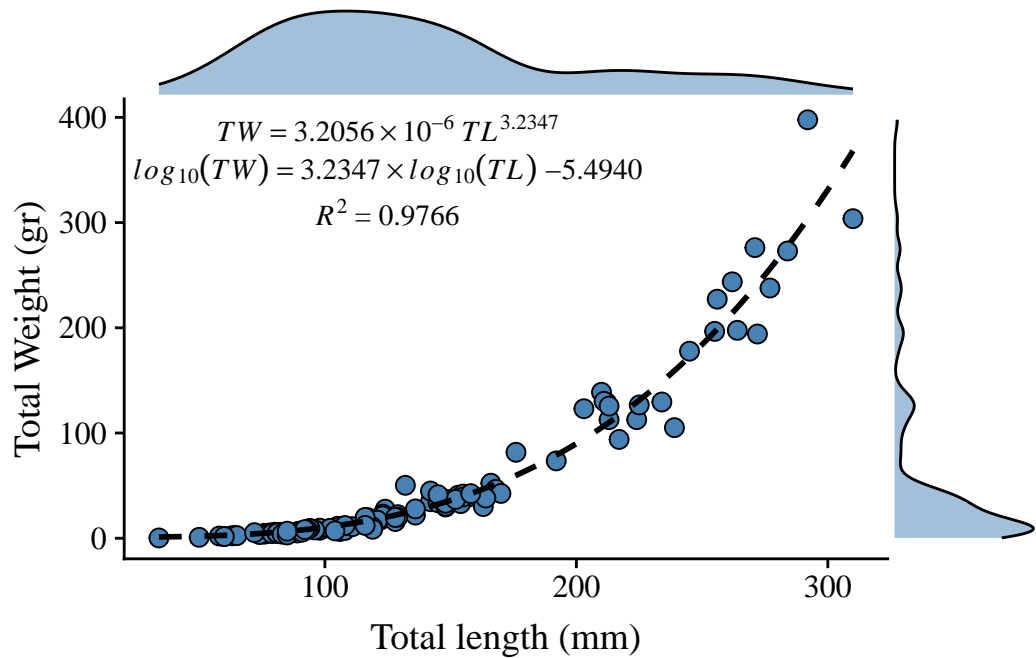


Figure 2. Length-weight relationship for 109 lionfish sampled in the central Mexican Caribbean. Points indicate samples, dashed black line indicates curve of best fit, marginal plots represent the density distribution of each variable.

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
North Atlantic	B	774	2.9	2.89	-4.54	-	Barbour et al., 2011

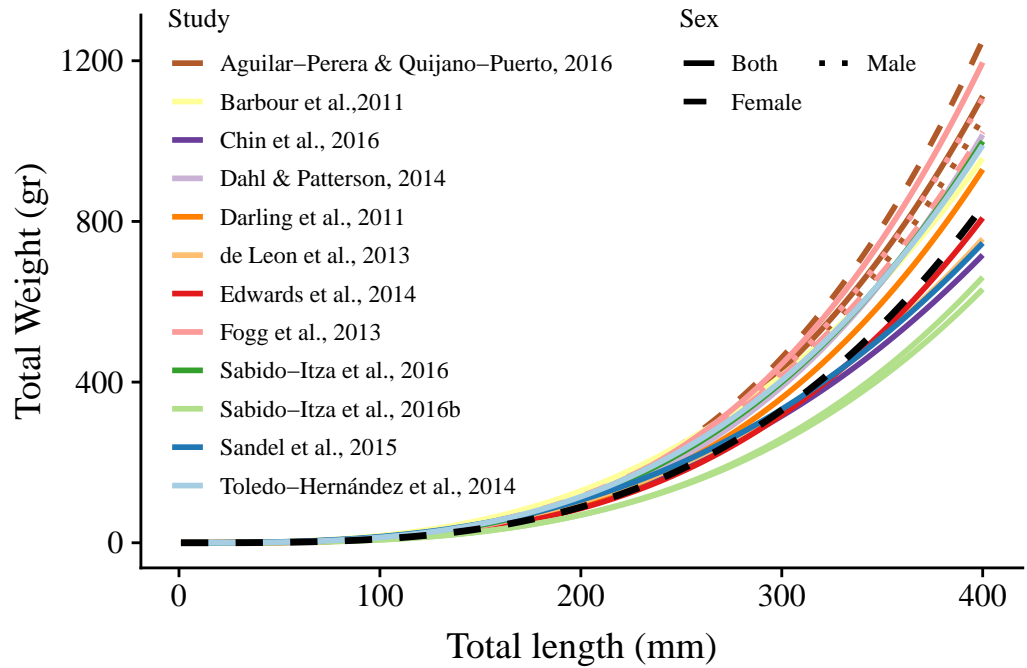


Figure 3. Length-weight relationships ($n = 18$) for 12 studies and this study. Colors indicate studies from which the parameters were extracted. Dotted, dashed and solid lines show models for males, females, and combined sexes, respectively. The dashed black line represents the relationship estimated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

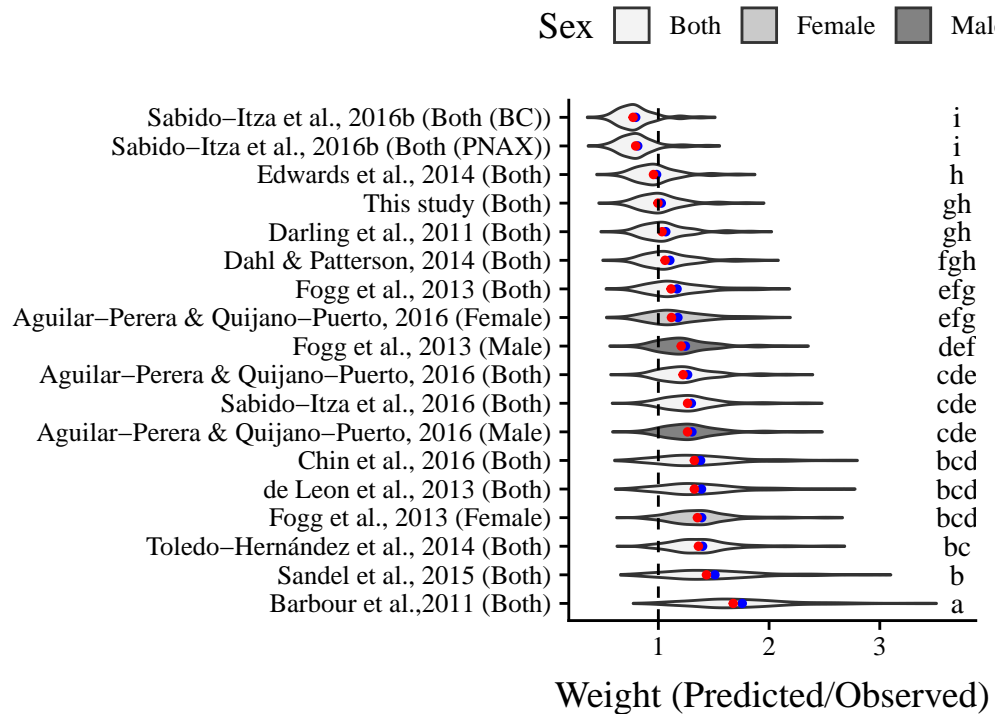


Figure 4. Violin plot of predicted-to-observed weight ratios for 18 pairs of allometric parameters. Red and blue circles indicate median and mean values, respectively. Like letters indicate values that do not differ significantly.

DISCUSSION

We detected substantial differences in weight-at-length between organisms from the Caribbean and Gulf of Mexico / North-Western Atlantic. The groupings of predicted-to-observed weight ratios were consistent with the spatial distribution of the studies, suggesting that these differences are mediated by space. 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 patterns 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 or differential usage of this 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 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. 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 up to a threefold TW overestimation. These spatially-driven differences become especially important when allocating resources for lionfish removal programs, incentivizing its fishery 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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