

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. In order to better manage the invasion, we must be able to accurately estimate their total biomass. This work compares length-weight relationships of the invasive lionfish through the invasion range. A review of 15 length-weight relationships reported in 11 peer-reviewed studies shows that lionfish exhibit spatial variation in weight-at-length. The reviewed parameters indicate that, for the same length, lionfish in the Caribbean have lower body mass than in the Atlantic or Gulf of Mexico. This highlights the importance of using site-specific parameters to estimate biomass from length observations. This study also reports 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. These findings can have major implications in management, especially when estimating biomass available for harvest, predicting effects on local ecosystems, or evaluating the effectiveness of removal programs.

INTRODUCTION

At least 84% of marine eco-regions have reported the presence of an invasive species (Molnar et al., 2008), which represent a major threat to local biodiversity and the economic activities that depend on it (Bax et al., 2003). Invasive species may threaten native species through predation, competition, or indirect habitat effects (Davis, 2003; Gurevitch and Padilla, 2004). By 2005, the economic cost of invasive species to the United States was estimated at USD \$120 billion per year (Pimentel et al., 2005).

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). Lionfish have been widely reported in coral reefs (Aguilar-Perera and Tuz-Sulub, 2010), but also in other habitats such as estuaries (Jud et al., 2011), mangroves (Barbour et al., 2010), hard-bottomed areas (Muñoz et al., 2011), and mesophotic reefs (Andradi-Brown et al., 2017). Their presence in these waters has been labeled as a major marine invasion because they threaten local biodiversity, spread rapidly, and are difficult to manage (Hixon et al., 2016).

A substantial amount of research has been done to describe lionfish feeding ecology in North Carolina (Muñoz et al., 2011), the Bahamas (Morris and Akins, 2009; Cote et al., 2013), Northern Gulf of Mexico (Dahl and Patterson, 2014), Mexican Caribbean (Valdez-Moreno et al., 2012; Villaseñor-Derbez and Herrera-Pérez, 2014), Belize (Hackerott et al., 2017), and Costa Rica (Sandel et al., 2015). Peake et al. (2018) show 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 keeping track of its range through time

(Schofield, 2009, 2010) and predicting invasion ranges under future climates (Grieve et al., 2016). By combining information from these disciplines, researchers have been able to predict the trophic impacts of lionfish (Arias-Gonzalez et al., 2011), which can then be translated into ecosystem-level and economic impacts.

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 (Sandel et al., 2015; Chin et al., 2016; de Leon et al., 2013). In addition, culling programs can help stabilize or grow native prey fish populations (Côté et al., 2014). Complete eradication of lionfish through fishing is unlikely because of their rapid recovery rates and ongoing recruitment to shallow-water areas from their persistent populations in mesophotic coral ecosystems (Barbour et al., 2011; Andradi-Brown et al., 2017). However, promoting its consumption might create a level of demand capable of sustaining a stable fishery, which can help control invasive populations while providing alternative livelihoods (Chin et al., 2016).

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

Empirical modeling efforts examining the feasibility of establishing fisheries for lionfish involve modeling changes in biomass in response to changes in mortality (*i.e.* culling (Côté et al., 2014; Barbour et al., 2011; Andradi-Brown et al., 2017)). In this case, biomass represents the sum of all individual fish weights. The individual weight (W) of an organism can be estimated from its length using the allometric growth equation, $W = aL^b$, where L is an organism's length and a and b are constants. This length-weight relationship for any given species is an essential component of biomass-based modeling, and can vary across regions as a response to biotic (*e.g.* local food availability) and abiotic (*e.g.* water temperature) conditions (Johnson and Swenarton, 2016). Site-specific parameters are therefore necessary in order to obtain accurate biomass estimates in a given region, especially when research involves identifying the total biomass available for harvest by fishers (Barbour et al., 2011; Morris et al., 2011; Johnston and Purkis, 2015; Chin et al., 2016). Equation parameters for lionfish exist for North Carolina, Northern and Southern Gulf of Mexico, the Southern Mexican Caribbean, Bahamas, Little Cayman, Jamaica, Bonaire, Puerto Rico, and Costa Rica, but remain unavailable for the central Mexican Caribbean (Barbour et al., 2011; Fogg et al., 2013; Dahl and Patterson, 2014; Aguilar-Perera and Quijano-Puerto, 2016; Sabido-Itza et al., 2016; Darling et al., 2011; Edwards et al., 2014; Chin et al., 2016; de Leon et al., 2013; Toledo-Hernández, 2014; Sandel et al., 2015).

Here, we review lionfish allometric growth parameters throughout its invasion range and examine spatial differences in the equation constants. We also provide a new pair of parameters specific to the central Mexican Caribbean. Results suggest there are important regional-scale variations in allometric growth patterns of lionfish, and these differences highlight the importance of using site-specific parameters when developing or informing invasion management strategies.

MATERIALS AND METHODS

The main objective of this work was to compare allometric growth of lionfish throughout their invasion range. Allometric parameters were retrieved from scientific literature, and an additional pair of parameters was calculated from field observations in the central Mexican Caribbean.

Length-weight relationships ($n = 15$) identified in literature were obtained for the North Atlantic ($n = 1$), Gulf of Mexico ($n = 7$), and Caribbean ($n = 8$). Information on sampling methods, sex differentiation, location, and depth ranges of each study was retrieved when available. Studies were assumed to include

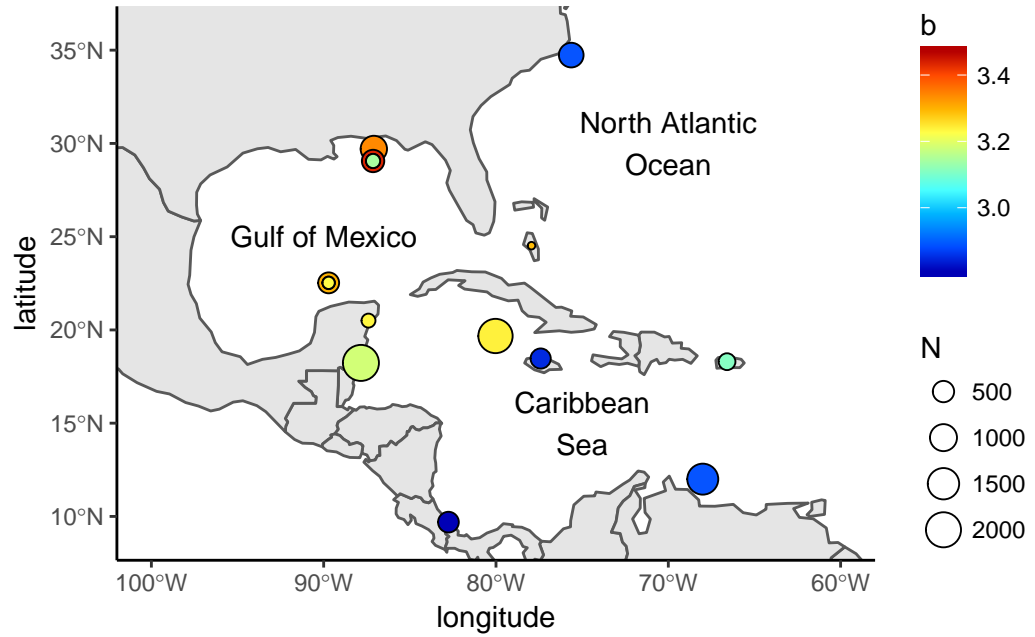


Figure 1. Locations where allometric growth parameters of lionfish (*Pterois spp*) have been reported. Circle sizes indicate sample size from each study, colors indicate the b coefficient from Eq. 1.

both genders if gender was unspecified. Locations where allometric studies were performed are shown in Figure 1 and Table 1.

Parameters from the central Mexican Caribbean were obtained from data collected in 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 before freezing organisms.

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:

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

This can be simplified and re-written as:

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

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

Studies inconsistently defined a as either the ponderal index from Eq. 1 or the y-intercept (c) from Eq. 3. Other studies incorrectly reported parameters as mm-to-g conversions when they were in fact cm-to-g conversions. Here, all parameters are reported as TL(mm) to TW(gr) conversions. When required, values from other studies were transformed for consistency.

Since uncertainty around estimated relationships was not reported in some of the reviewed studies, it was not possible to test for statistical differences between relationships. Instead, the 16 length-weight relationships were used to calculate predicted weight from length observations of the organisms sampled from the central Mexican Caribbean. Predicted weights were divided by the observed weights to obtain a ratio. Difference in mean weight ratios across studies were tested with a one-way Analysis of Variance (ANOVA). All analyses were performed in R version 3.4.4 (R Core Team, 2018). Raw data and code used in this work are available at dryad.org.

RESULTS

The model adjusted to Eq. 3 estimated the coefficient values at $b = 3.2347391$ and $c = -5.4940866$ ($R^2 = 0.977$, $F(df = 1; 107) = 6928.67$, $p < 0.001$). The allometric factor (b) was significantly different from the value of isometric growth of $b = 3$ ($t(107) = 6.04$; $p < 0.001$), indicating that lionfish present allometric growth. More information on model fit is presented in TableS2. The relationship between TL and TW is presented in Figure 2.

From this study in the central Mexican Caribbean and the 11 peer-reviewed studies that reported length-weight parameters for *P. volitans* 15 parameters were identified (Table 1, Fig 3). Two studies (Aguilar-Perera and Quijano-Puerto, 2016; Fogg et al., 2013) reported gender-level and pooled parameters, 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), 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; 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.

Parameters from models fit to males or females exclusively tend to have a higher steepness (*i.e.* higher allometric parameter), with mean \pm standard deviation values of $b = 3.27 \pm 0.06$ and $b = 3.31 \pm 0.23$ for males and females respectively, compared to parameters from models for pooled genders with a mean \pm standard deviation value of $b = 3.13 \pm 0.22$. In the case of the ponderal index (a) and its \log_{10} transformation (c), values were higher for parameters for pooled genders. Figure 3 shows the length-weight relationships with parameters from all studies.

There were significant differences in predicted-to-observed weight ratios estimated for each pair of parameters ($F(df = 15; 1728) = 38.26$; $p < 0.001$). From all allometric parameters reviewed, those of Edwards et al. (2014) provided the lowest weight estimates, with an predicted-to-observed weight ratio of 0.98 ± 0.23 (mean \pm SD). On the other hand, Barbour et al. (2011) yielded the highest weight estimates, with a mean (\pm SD) predicted-to-observed weight ratio of 1.76 ± 0.50 . Predicted-to-observed weight ratios and groups identified by Tukey's HSD ($\alpha = 0.05$) are presented in Figure 4.

DISCUSSION

A new pair of allometric growth parameters for lionfish in the central Mexican Caribbean are provided. This compliments existing literature for other sites in the Mexican Caribbean (Sabido-Itza et al., 2016). Additionally, the study identifies regional differences in length-weight relationships.

The length-weight coefficients estimated in this study were within the range identified by studies in other regions (Table 1). However, the ones presented here provide lower weight estimates for similar lengths. Until about $TL = 200$ mm, there are no appreciable differences between the parameters for

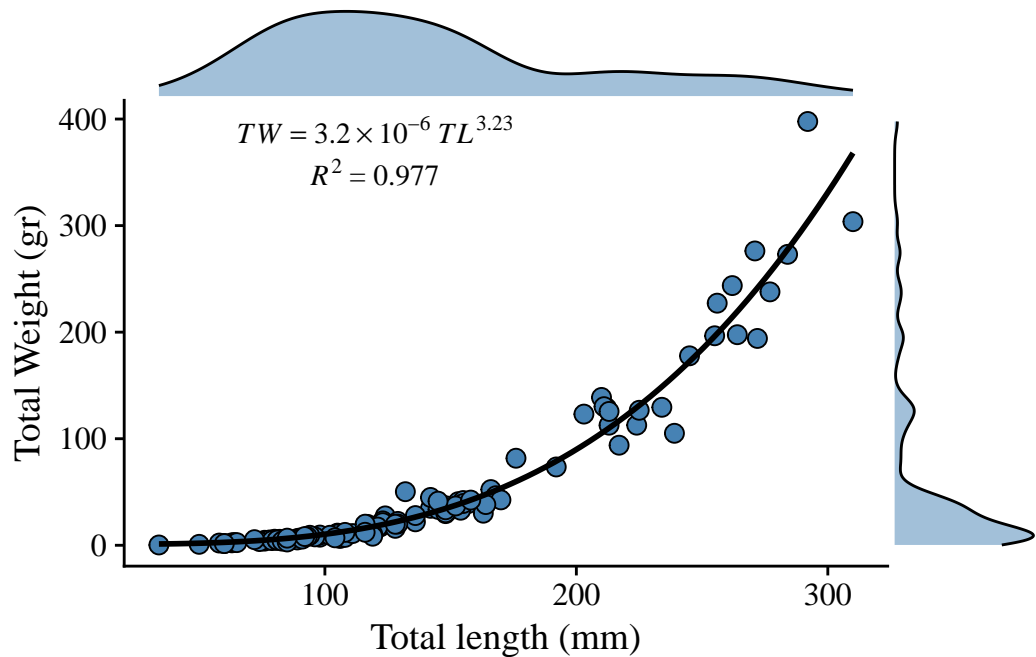


Figure 2. Length-weight relationship for 109 lionfish sampled in the central Mexican Caribbean. Points indicate samples, solid line indicates curve of best fit, marginal plots represent the density distribution of each variable.

Table 1. Summary of 16 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 | 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 |

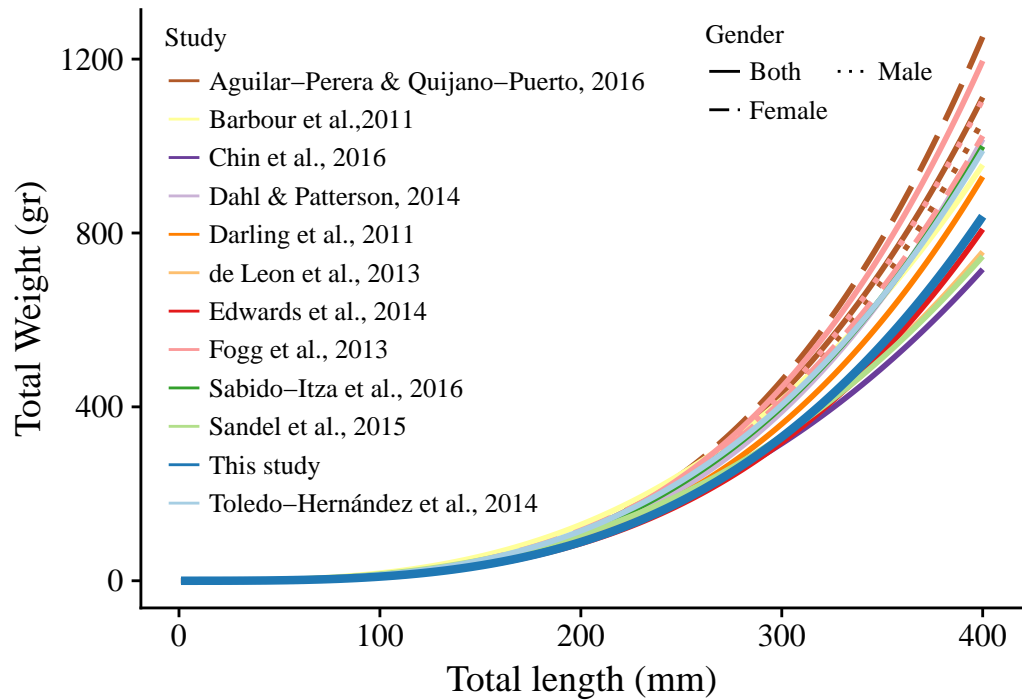


Figure 3. Length-weight relationships ($n = 16$) for 11 studies and this study. Colors indicate studies from which the parameters were extracted. Solid lines indicate that the fit was performed for males and females pooled together. Dotted lines indicate that the regression was performed on females, and dashed lines indicate it was performed for males.

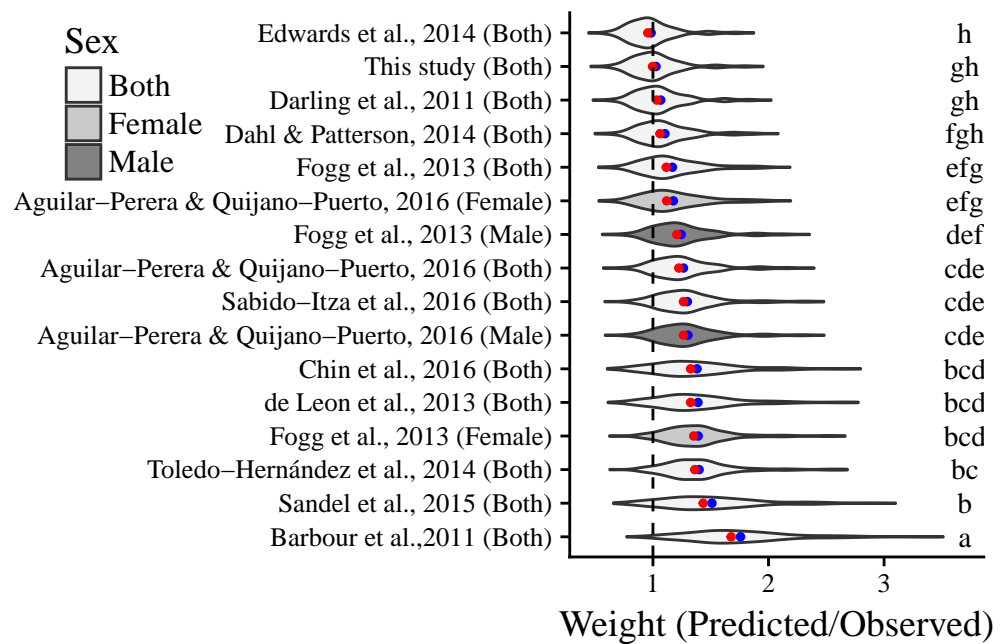


Figure 4. Violin plot showing the distribution of predicted to observed weight ratios for 16 pairs of allometric parameters. Red and blue circles indicate median and mean values, respectively. Like letters indicate values that do not differ significantly (Tukey's HSD; $p < 0.05$).

organisms from the Mexican Caribbean and those for little Cayman (Edwards et al., 2014) and Jamaica (Chin et al., 2016). Yet, for larger organisms (TL > 270 mm) parameters from Costa Rica (Sandel et al., 2015) and Bonaire (de Leon et al., 2013) provide similar estimates to those from this study. Conversely, these same studies tend to estimate higher weights –as compared to the ones reported here– for smaller organisms, likely due to the lack of small organisms in the samples used to estimate their parameters.

There are evident differences in weight-at-length between organisms from the Caribbean and Gulf of Mexico / North-Western Atlantic. Weight estimates with parameters from the Gulf of Mexico and North-Western Atlantic tend to be higher than those from the Caribbean. Similar regional variation has been reported for age-at-length relationships of this species across the invaded region (Fogg et al., 2015), or when comparing populations from the invasion and native ranges (Pusack et al., 2016). These may be driven by genetic differences or organisms being exposed to distinct environmental conditions. For example, work on mitochondrial DNA has shown two distinct population groups, identified as the “Caribbean group” and “Northern Group” (?). Alternatively, Fogg et al. (2015) suggest that differences observed in age-at-length “may be more related to climate rather than other biological and ecological factors”. 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 should focus on identifying which occurs here.

The results presented in this paper can have major implications for management. Our results show that, for a given length, using one set of parameters or the other can result in a threefold increase in estimated weight. This becomes especially relevant when estimating biomass available for harvest, predicting effects on local ecosystems, or evaluating the effectiveness of removal programs. Using site-specific values provides a more accurate estimate of fish biomass. Future research should try to use, to the extent possible, parameters calculated for their region, or use different parameters to provide upper and lower bounds in their results. At the same time, this highlights the need for more basic research that furthers our understanding of lionfish biology. To better manage the invasion, we must perform research that can describe biologically important information of lionfish throughout its invasion range (Johnson and Swenarton, 2016).

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