

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

Juan Carlos Villaseñor-Derbez<sup>1</sup>, Sean Fitzgerald<sup>1</sup>

<sup>1</sup>Bren School of Environmental Sciences and Management, University of California Santa Barbara, Santa Barbara, California, U.S.

Corresponding author:

Juan Carlos Villaseñor-Derbez<sup>1</sup>

Email address: jvillasenor@bren.ucsb.edu

## 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 17 length-weight relationships reported in 12 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

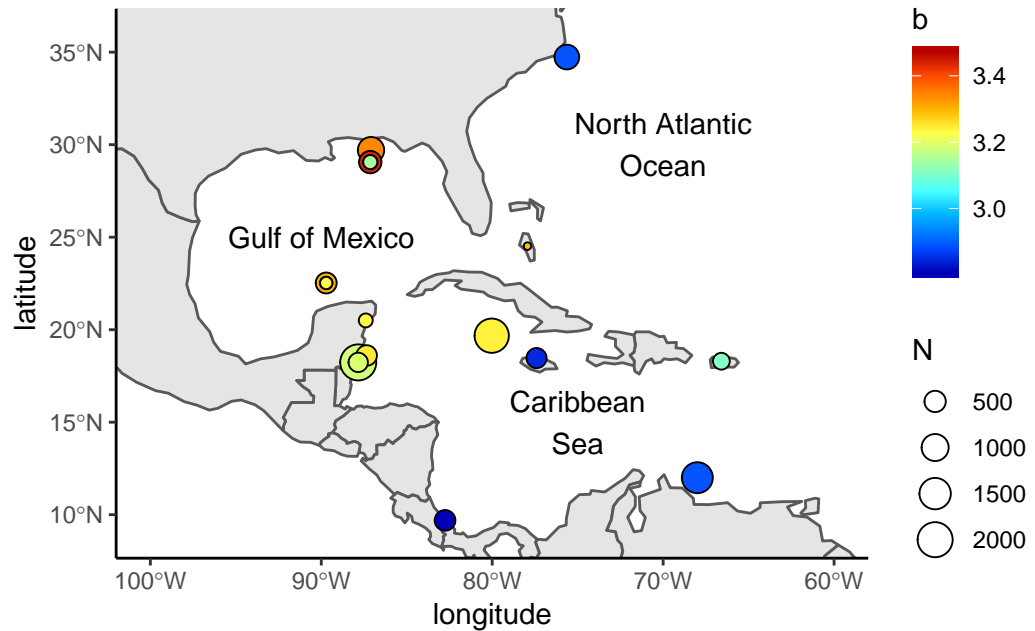
(Schofield, 2009, 2010) and predicting invasion ranges under future climates (Grieve et al., 2016). By combining information from these disciplines, researchers have been able to predict the trophic impacts of lionfish (Arias-Gonzalez et al., 2011), which can then be translated into ecosystem-level and 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 shallow-water populations while providing alternative livelihoods and avoiding further impacts to local reef biota (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). A common way to model this is via age- or length-structured population models (Côté et al., 2014; Barbour et al., 2011; Andradi-Brown et al., 2017), which convert fish length or age to weight to then calculate total biomass. Therefore, length-weight relationships are an essential component of these models. However, the length-weight relationship 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). Literature suggests that site-specific parameters are necessary to obtain accurate biomass estimates when length-weight relationships present spatial variation. This becomes increasingly important when estimating the potential effectiveness (and resources needed) of lionfish culling programs or identifying total biomass available for harvest by fishers (Barbour et al., 2011; Morris et al., 2011; Johnston and Purkis, 2015; Chin et al., 2016; Côté et al., 2014). Genetic analysis of invasive lionfish suggest that two distinct population groups exist (Betancur-R et al., 2011), and as such we would expect their biology to differ. Despite the large number of studies reporting site-specific length-weight relationships, no studies have described region-wide differences in these.

The objective of this paper is to describe the spatial pattern of length-weight relationships of lionfish in the Caribbean and Western Atlantic and identify whether these differences are trivial. Length-weight relationships 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; Sabido-Itzá 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). This study also provides the first length-weight relationship for this region.



**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

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 filed observations in the central Mexican Caribbean.

Length-weight relationships ( $n = 17$ ) identified in literature were obtained for the North Atlantic ( $n = 1$ ), Gulf of Mexico ( $n = 7$ ), and Caribbean ( $n = 10$ ). Information on sampling methods, sex differentiation, location, and depth ranges of each study was retrieved when available. Studies were assumed to include both genders if gender was unspecified. Locations where allometric studies have been performed are shown in Figure 1 and Table 1.

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.

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.

Combining the length-weight parameters extracted from the literature and the additional pair calculated here, we obtain a total of 18 pairs. We test whether using *ex situ* parameters produces differences in weight estimates by estimating TW from the 109 length observations of lionfish from the central Mexican Caribbean with each of the 18 relationships. Predicted weights were divided by known observed weights to obtain a simple measurement of over- or underestimation. Difference in mean weight ratios across studies were tested with a one-way analysis of variance (ANOVA). All analyses were performed in R version 3.5.0 (R Core Team, 2018). Raw data and code used in this work are available at [dryad.org](https://dryad.org).

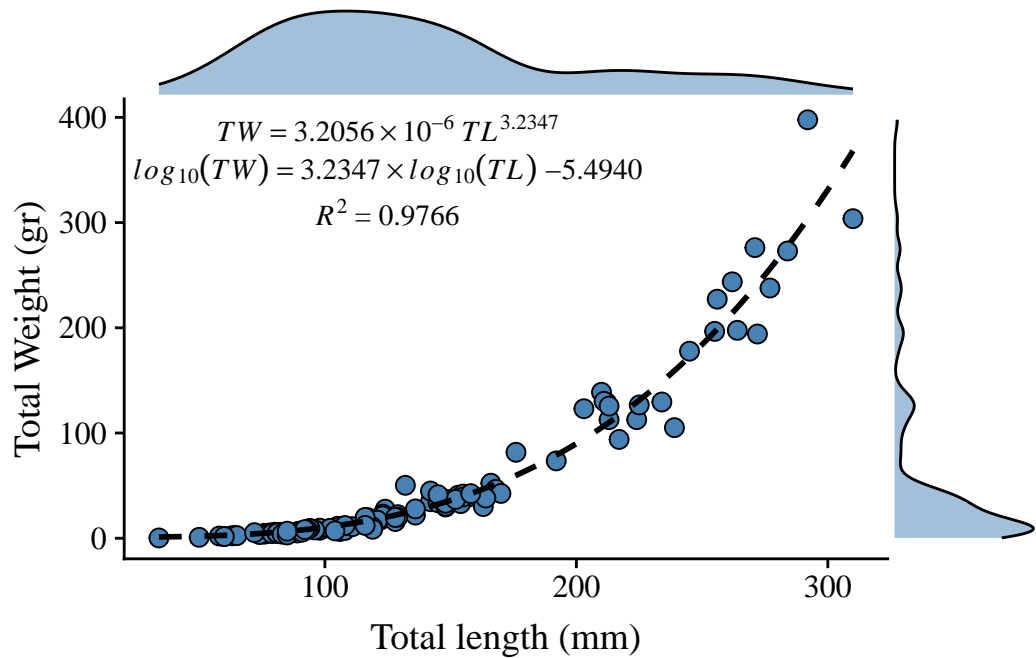
## RESULTS

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 12 peer-reviewed studies that reported length-weight parameters for *P. volitans* 17 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; 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.

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  $b = 3.14 \pm 0.20$ . 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.

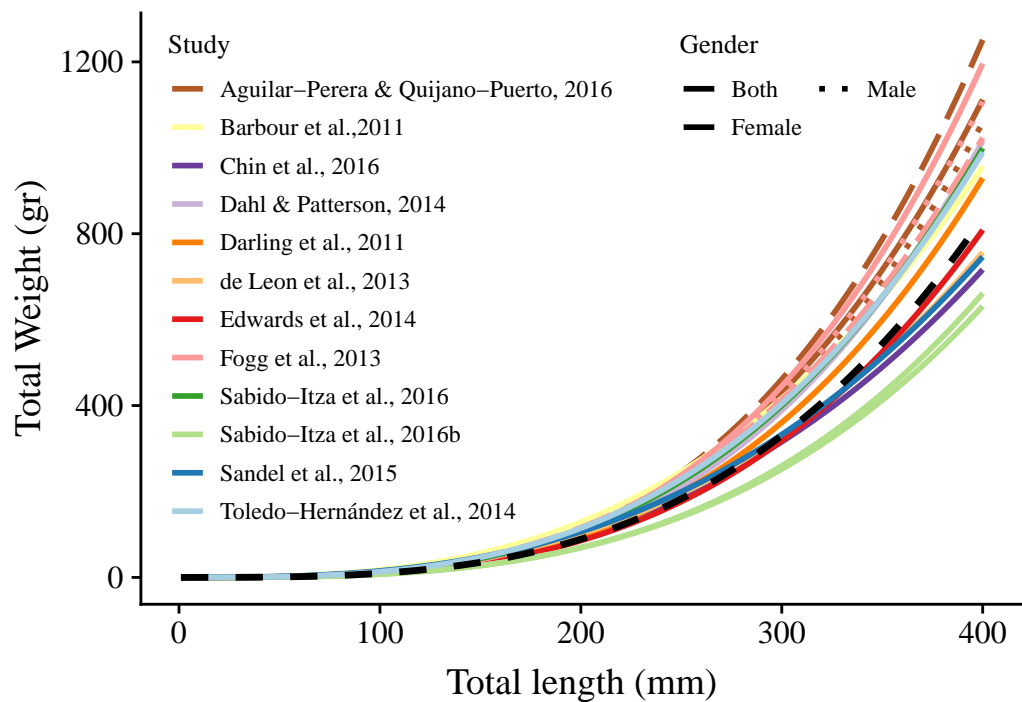
There were significant differences in predicted-to-observed weight ratios estimated for each pair of parameters ( $F(df = 15; 1728) = 38.26$ ;  $p < 0.001$ ). From all allometric parameters reviewed, those of Sabido-Itzá et al. (2016) in Banco Chinchorro, (Caribbean) provided the lowest weight estimates, with a predicted-to-observed weight ratio of  $0.80 \pm 0.19$  (mean  $\pm$  SD). On the other hand, Barbour et al. (2011) in the Northern Atlantic yielded the highest weight estimates, with a mean ( $\pm$  SD) predicted-to-observed weight ratio of  $1.76 \pm 0.50$ . Predicted-to-observed weight ratios are presented in Figure 4.



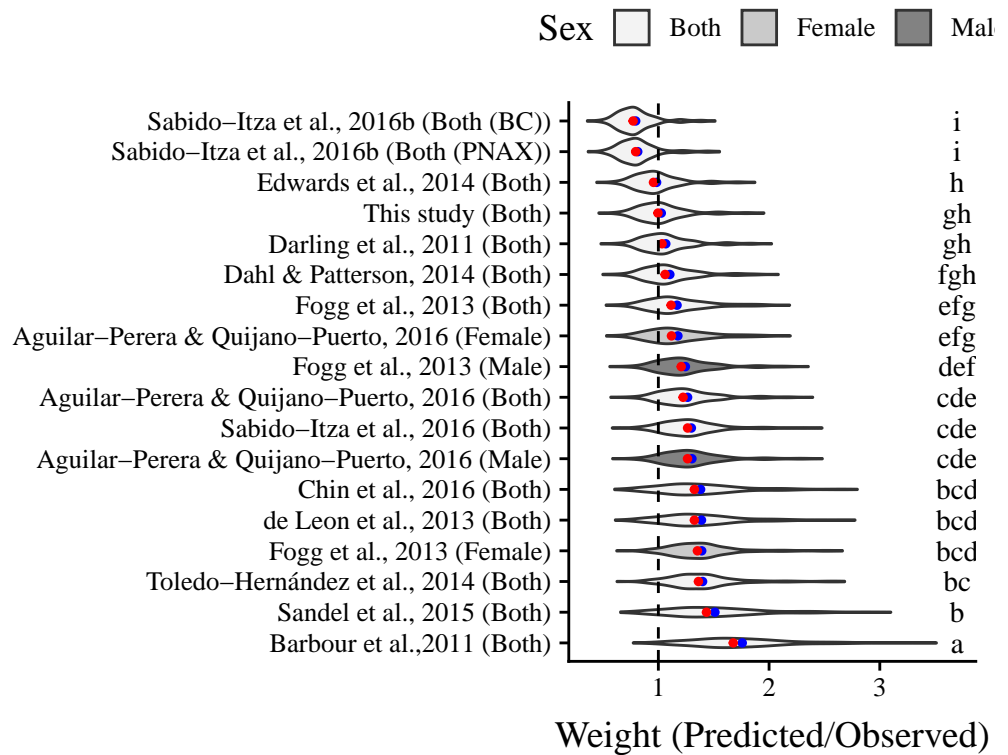
**Figure 2.** Length-weight relationship for 109 lionfish sampled in the central Mexican Caribbean. Points indicate samples, dashed black line indicates curve of best fit, marginal plots represent the density distribution of each variable.

**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 showing the distribution 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

A new pair of allometric growth parameters for lionfish in the central Mexican Caribbean are provided, complimenting existing literature for other sites in the Mexican Caribbean (Sabido-Itza et al., 2016; Sabido-Itzá 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 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; Edwards et al., 2014), 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” (Betancur-R et al., 2011). 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. For example, Edwards et al. (2014) simulate lionfish culling using parameters from North Carolina and Little Cayman, and identify that the difference in time required for the population to recover to 90% of its initial biomass after removals cease was of up to four years. 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 difference becomes especially relevant when estimating biomass available for harvest, predicting effects on local ecosystems, or evaluating the effectiveness of removal programs. 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).

## ACKNOWLEDGEMENTS

I would like to thank Nils Van Der Haar and Michael Doodey from Dive Aventuras as well as Guillermo Lotz-Cador who provided help to collect samples.

## REFERENCES

- Aguilar-Perera, A. and Quijano-Puerto, L. (2016). Relations between fish length to weight, and otolith length and weight, of the lionfish *Pterois volitans* in the parque nacional arrecife alacranes, southern gulf of Mexico. *Rev. biol. mar. oceanogr.*, 51(2):469–474.
- Aguilar-Perera, A. and Tuz-Sulub, A. (2010). Non-native, invasive red lionfish (*Pterois volitans* [Linnaeus, 1758]: Scorpaenidae), is first recorded in the southern gulf of Mexico, off the northern Yucatan peninsula, Mexico. *AI*, 5(Supplement 1):S9–S12.
- Albins, M. and Hixon, M. (2008). Invasive Indo-Pacific lionfish *Pterois volitans* reduce recruitment of Atlantic coral-reef fishes. *Mar. Ecol. Prog. Ser.*, 367:233–238.
- Andradi-Brown, D. A., Grey, R., Hendrix, A., Hitchner, D., Hunt, C. L., Gress, E., Madej, K., Parry, R. L., Régnier-McKellar, C., Jones, O. P., Arteaga, M., Izaguirre, A. P., Rogers, A. D., and Exton, D. A.



- (2017). Depth-dependent effects of culling-do mesophotic lionfish populations undermine current management? *R Soc Open Sci*, 4(5):170027.
- Arias-Gonzalez, J. E., Gonzalez-Gandara, C., Luis Cabrera, J., and Christensen, V. (2011). Predicted impact of the invasive lionfish *pterois volitans* on the food web of a caribbean coral reef. *Environ Res*, 111(7):917–925.
- Barbour, A., Montgomery, M., Adamson, A., D'az-Ferguson, E., and Silliman, B. (2010). Mangrove use by the invasive lionfish *pterois volitans*. *Mar. Ecol. Prog. Ser.*, 401:291–294.
- Barbour, A. B., Allen, M. S., Frazer, T. K., and Sherman, K. D. (2011). Evaluating the potential efficacy of invasive lionfish (*pterois volitans*) removals. *PLoS ONE*, 6(5):e19666.
- Bax, N., Williamson, A., Aguero, M., Gonzalez, E., and Geeves, W. (2003). Marine invasive alien species: a threat to global biodiversity. *Marine Policy*, 27(4):313–323.
- Betancur-R, R., Hines, A., Acero, A., Orti, G., Wilbur, A., and Freshwater, D. (2011). Reconstructing the lionfish invasion: insights into greater caribbean biogeography. *J Biogeography*, 38:1281–1293.
- Chin, D. A., Aiken, K. A., and Buddo, D. (2016). Lionfish population density in discovery bay, jamaica. *International Journal of Scientific & Engineering Research*, 7(12):1327 – 1331.
- Cote, I., Green, S., Morris, J., Akins, J., and Steinke, D. (2013). Diet richness of invasive indo-pacific lionfish revealed by dna barcoding. *Mar. Ecol. Prog. Ser.*, 472:249–256.
- Côté, I. M., Akins, L., Underwood, E., Curtis-Quick, J., and Green, S. J. (2014). Setting the record straight on invasive lionfish control: Culling works.
- Dahl, K. A. and Patterson, W. F. (2014). Habitat-specific density and diet of rapidly expanding invasive red lionfish, *pterois volitans*, populations in the northern gulf of mexico. *PLoS ONE*, 9(8):e105852.
- Darling, E. S., Green, S. J., O'Leary, J. K., and Côté, I. M. (2011). Indo-pacific lionfish are larger and more abundant on invaded reefs: a comparison of kenyan and bahamian lionfish populations. *Biol Invasions*, 13(9):2045–2051.
- Davis, M. A. (2003). Biotic globalization: Does competition from introduced species threaten biodiversity? *Bioscience*, 53(5):481.
- de Leon, R., Vane, K., Bertuol, P., Chamberland, V. C., Simal, F., Imms, E., and Vermeij, M. J. A. (2013). Effectiveness of lionfish removal efforts in the southern caribbean. *Endanger Species Res*, 22(2):175–182.
- Edwards, M. A., Frazer, T. K., and Jacoby, C. A. (2014). Age and growth of invasive lionfish (*pterois* spp.) in the caribbean sea, with implications for management. *BMS*, 90(4):953–966.
- Fishelson, L. (1997). Experiments and observations on food consumption, growth and starvation in *dendrochirus brachypterus* and *pterois volitans* (*pteroinae*, *scorpaenidae*). *Environmental Biology of Fishes*, 50(4):391–403.
- Fogg, A. Q., Evans, J. T., Ingram JR, G. W., Peterson, M. S., and Brown-Peterson, N. J. (2015). Comparing age and growth patterns of invasive lionfish among three ecoregions of the northern gulf of mexico. In GCFI, G. and Institute, C. F., editors, *Proceedings of the 68 th Gulf and Caribbean Fisheries Institute*, Panama City. Gulf and Caribbean Fisheries Institute.
- Fogg, A. Q., Hoffmayer, E. R., Driggers, W. B., Campbell, M. D., Pellegrin, G. J., and Stein, W. (2013). Distribution and length frequency of invasive lionfish (*pterois* sp.) in the northern gulf of mexico. *GCR*, 25.
- Green, S. J., Akins, J. L., Maljković, A., and Côté, I. M. (2012). Invasive lionfish drive atlantic coral reef fish declines. *PLoS ONE*, 7(3):e32596.
- Grieve, B., Curchitser, E., and Rykaczewski, R. (2016). Range expansion of the invasive lionfish in the northwest atlantic with climate change. *Mar. Ecol. Prog. Ser.*, 546:225–237.
- Guan, W., Cao, J., Chen, Y., and Cieri, M. (2013). Impacts of population and fishery spatial structures on fishery stock assessment. *Can. J. Fish. Aquat. Sci.*, 70(8):1178–1189.
- Gunderson, D. R., Parma, A. M., Hilborn, R., Cope, J. M., Fluharty, D. L., Miller, M. L., Vetter, R. D., Heppell, S. S., and Greene, H. G. (2008). The challenge of managing nearshore rocky reef resources. *Fisheries*, 33(4):172–179.
- Gurevitch, J. and Padilla, D. K. (2004). Are invasive species a major cause of extinctions? *Trends Ecol Evol (Amst)*, 19(9):470–474.
- Hackerott, S., Valdivia, A., Cox, C. E., Silbiger, N. J., and Bruno, J. F. (2017). Invasive lionfish had no measurable effect on prey fish community structure across the belizean barrier reef. *PeerJ*, 5:e3270.
- Hixon, M., Green, S., Albins, M., Akins, J., and Morris, J. (2016). Lionfish: a major marine invasion.

267 *Mar. Ecol. Prog. Ser.*, 558:161–165.

268 Hutchinson, W. F. (2008). The dangers of ignoring stock complexity in fishery management: the case of  
 269 the north sea cod. *Biol Lett*, 4(6):693–695.

270 Johnson, E. G. and Swenarton, M. K. (2016). Age, growth and population structure of invasive lionfish  
 271 (pterois volitans/miles) in northeast florida using a length-based, age-structured population model.  
 272 *PeerJ*, 4:e2730.

273 Johnston, M. and Purkis, S. (2015). A coordinated and sustained international strategy is required to turn  
 274 the tide on the atlantic lionfish invasion. *Mar. Ecol. Prog. Ser.*, 533:219–235.

275 Jud, Z., Layman, C., Lee, J., and Arrington, D. (2011). Recent invasion of a florida (usa) estuarine system  
 276 by lionfish pterois volitans / p. miles. *Aquat. Biol.*, 13(1):21–26.

277 Jud, Z. R. and Layman, C. A. (2012). Site fidelity and movement patterns of invasive lionfish, pterois  
 278 spp., in a florida estuary. *Journal of Experimental Marine Biology and Ecology*, 414-415:69–74.

279 Kochzius, M. and Blohm, D. (2005). Genetic population structure of the lionfish pterois miles (scor-  
 280 paenidae, pteroinae) in the gulf of aqaba and northern red sea. *Gene*, 347(2):295–301.

281 Molnar, J. L., Gamboa, R. L., Revenga, C., and Spalding, M. D. (2008). Assessing the global threat of  
 282 invasive species to marine biodiversity. *Frontiers in Ecology and the Environment*, 6(9):485–492.

283 Morris, J. A. and Akins, J. L. (2009). Feeding ecology of invasive lionfish (pterois volitans) in the  
 284 bahamian archipelago. *Environ. Biol. Fishes*, 86(3):389–398.

285 Morris, J. A., Shertzer, K. W., and Rice, J. A. (2011). A stage-based matrix population model of invasive  
 286 lionfish with implications for control. *Biol Invasions*, 13(1):7–12.

287 Muñoz, R., Currin, C., and Whitfield, P. (2011). Diet of invasive lionfish on hard bottom reefs of the  
 288 southeast usa: insights from stomach contents and stable isotopes. *Mar. Ecol. Prog. Ser.*, 432:181–193.

289 Peake, J., Bogdanoff, A. K., Layman, C. A., Castillo, B., Reale-Munroe, K., Chapman, J., Dahl, K.,  
 290 Patterson III, W. F., Eddy, C., Ellis, R. D., Faletti, M., Higgs, N., Johnston, M. A., Muñoz, R. C.,  
 291 Sandel, V., Villaseñor-Derbez, J. C., and Morris, J. A. (2018). Feeding ecology of invasive lionfish  
 292 (pterois volitans and pterois miles) in the temperate and tropical western atlantic. *Biol Invasions*.

293 Pimentel, D., Zuniga, R., and Morrison, D. (2005). Update on the environmental and economic costs  
 294 associated with alien-invasive species in the united states. *Ecological Economics*, 52(3):273–288.

295 Pusack, T. J., Benkwitt, C. E., Cure, K., and Kindinger, T. L. (2016). Invasive red lionfish (pterois  
 296 volitans) grow faster in the atlantic ocean than in their native pacific range. *Environ. Biol. Fishes*,  
 297 99(6-7):571–579.

298 R Core Team (2018). *R: A Language and Environment for Statistical Computing*. R Foundation for  
 299 Statistical Computing, Vienna, Austria.

300 Rocha, L. A., Rocha, C. R., Baldwin, C. C., Weigt, L. A., and McField, M. (2015). Invasive lionfish  
 301 preying on critically endangered reef fish. *Coral Reefs*, 34(3):803–806.

302 Sabido-Itzá, M., Aguilar-Perera, A., and Medina-Quej, A. (2016). Length–weight and length–length  
 303 relations, and relative condition factor of red lionfish, pterois volitans (actinopterygii: Scorpaeniformes:  
 304 Scorpaenidae), from two natural protected areas in the mexican caribbean. *Acta Ich et Piscat*,  
 305 46(4):279–285.

306 Sabido-Itza, M., Medina-Quej, A., De Jesus-Navarrete, A., Gomez-Poot, J., and Garcia-Rivas, M. (2016).  
 307 Uso de la estructura de tallas como evidencia del establecimiento poblacional del pez le?n pterois  
 308 volitans (scorpaeniformes: Scorpaenidae) en el sur del caribe mexicano. *RBT*, 64(1):353.

309 Sandel, V., Martínez-Fernández, D., Wangpraseurt, D., and Sierra, L. (2015). Ecology and management  
 310 of the invasive lionfish pterois volitans/miles complex (perciformes: Scorpaenidae) in southern costa  
 311 rica. *Rev Biol Trop*, 63(1):213–221.

312 Schofield, P. (2009). Geographic extent and chronology of the invasion of non-native lionfish (pterois  
 313 volitans [linnaeus 1758] and p. miles [bennett 1828]) in the western north atlantic and caribbean sea.  
 314 *AI*, 4(3):473–479.

315 Schofield, P. (2010). Update on geographic spread of invasive lionfishes (pterois volitans [linnaeus, 1758]  
 316 and p. miles [bennett, 1828]) in the western north atlantic ocean, caribbean sea and gulf of mexico. *AI*,  
 317 5(Supplement 1):S117–S122.

318 Toledo-Hernández, C. (2014). Population ecology and genetics of the invasive lionfish in puerto rico. *AI*,  
 319 9(2):227–237.

320 Usseglio, P., Selwyn, J. D., Downey-Wall, A. M., and Hogan, J. D. (2017). Effectiveness of removals of  
 321 the invasive lionfish: how many dives are needed to deplete a reef? *PeerJ*, 5:e3043.

- 322 Valdez-Moreno, M., Quintal-Lizama, C., Gómez-Lozano, R., and a Del Carmen García-Rivas, M. (2012).  
323 Monitoring an alien invasion: Dna barcoding and the identification of lionfish and their prey on coral  
324 reefs of the mexican caribbean. *PLoS ONE*, 7(6):e36636.
- 325 Villaseñor-Derbez, J. C. and Herrera-Pérez, R. (2014). Brief description of prey selectivity and ontogenetic  
326 changes in the diet of the invasive lionfish pterois volitans (actinopterygii, scorpaenidae) in the mexican  
327 caribbean. *PANAMJAS*, 9(2):131–135.
- 328 Wilson, J. R., Kay, M. C., Colgate, J., Qi, R., and Lenihan, H. S. (2012). Small-scale spatial variation in  
329 population dynamics and fishermen response in a coastal marine fishery. *PLoS ONE*, 7(12):e52837.
- 330 Zeileis, A. (2004). Econometric computing with hc and hac covariance matrix estimators. *J Stat Softw*,  
331 11(10).