

1 Biometry of the invasive lionfish (*Pterois volitans*) in the Central
2 Mexican Caribbean, and a review of allometric growth parameters
3 across the invasion range

4 **Running title:** Allometric growth of *Pterois volitans*

5 Juan Carlos VILLASEÑOR-DERBEZ¹

6 ¹ Bren School of Environmental Sciences and Management, University of California Santa
7 Barbara, Santa Barbara, California, U.S.

8 * Correspondence: Juan Carlos Villaseñor-Derbez, Bren Hall, University of California at
9 Santa Barbara, Santa Barbara, CA, 93106, US phone: +1 207 205 8435, e-mail: jvillasenor@
10 bren.ucsb.edu

Background. Lionfish (*Pterois volitans/miles*) are an invasive species in the North-Western Atlantic and the Caribbean. In order to better manage the invasion, inform lionfish removal programs, predict their possible impacts, and estimate biomass available for harvest, we must be able to accurately estimate their total biomass. Previous work has identified that lionfish age-at-length relationships are spatially variable across the invasion range. This work had two main objectives: i) compare length-weight relationships of the invasive lionfish through the invasion range; and ii) Report the length-weight frequency for lionfish in the Central Mexican Caribbean.

Materials and methods. A total of 13 length-weight relationships reported in eight peer-reviewed studies and FishBase were used to calculate expected biomass of organisms ($n = 109$) sampled from the Central Mexican Caribbean, whose Total Length (TL) and Total Weight (TW) were known. For each length-weight relationship, expected-to-observed weight ratio was calculated for each organism. Differences in mean expected-to-observed weight ratios were tested with a one-way ANOVA; Tukey's HSD was used as a post-hoc test to identify groups of non-statistically significant differences. Additionally, the length-weight relationship of the 109 organisms was calculated. Total Length (TL) and Total weight (TW) were log10-transformed to fit a linear model describing the linearized length-weight relationship. The model was fit using Ordinary Least Squares and Heteroskedastik-robust standard errors were computed.

Results. Expected-to-observed weight ratios ranged from 0.44 to 3.51, and differences in weight-at-length were spatially consistent. For a given length, parameters from the Caribbean yielded lower weights than those from the Gulf of Mexico and Atlantic, indicating that weight-at-length is spatially variable. 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.

Conclusion. The large differences between observed and expected biomass when using parameters from other locations highlights the importance of using site-specific parameters

37 to estimate biomass from length observations. Findings from this work can aid managers
38 and decision makers to better select length-weight parameters when these are not available
39 for their region of interest.

40 **Key words**

41 lionfish, *Pterois volitans*, length-weight relationship, allometric growth, Mexico

INTRODUCTION

At least 84% of the marine eco-regions have reported the presence of an invasive species (Molnar et al., 2008). These represent a major threat to local biodiversity and the economic activities that depend on it, like tourism or fisheries (Bax et al., 2003). Invasive species may also threaten native species through competition (DAVIS, 2003) or predation. By 2005, the economic cost of invasive species to the United States was estimated at \$120 billion per year and nearly 42% of species that have been included in the Endangered or Threatened species list have been labeled as such due to presence of invasive species (Pimentel, Zuniga & Morrison, 2005). This highlights the importance of understanding, managing, and preventing ecological invasions.

Lionfish (*Pterois volitans/miles* complex) are an invasive species in the North-Western Atlantic and the Caribbean, likely introduced through liberation of aquarium-kept organisms (Betancur-R et al., 2011). They are the first marine vertebrates to establish in North Atlantic (Schofield, 2009, 2010) and Caribbean coasts (Sabido-Itza et al., 2016). Lionfish have been widely reported in coral reefs (Aguilar-Perera & Tuz-Sulub, 2010), but also in other habitats such as estuaries (Jud et al., 2011), mangroves (Barbour et al., 2010), areas with hard-bottoms (Muñoz, Currin & Whitfield, 2011), and mesophotic reefs (Andradi-Brown et al., 2017). Due to its threat to local biodiversity, the speed of their spread, and its difficulty of management, their presence in these waters has been labeled as a major marine invasion (Hixon et al., 2016).

A significant amount of research has been done to describe lionfish feeding ecology in North Carolina (Muñoz, Currin & Whitfield, 2011), the Bahamas (Morris & Akins, 2009; Cote et al., 2013), Northern Gulf of Mexico (Dahl & Patterson, 2014), Mexican Caribbean (Valdez-Moreno et al., 2012; Villaseñor-Derbez & Herrera-Pérez, 2014), Belize (Hackerott et al., 2017), and Costa Rica (Sandel et al., 2015). Their feeding behavior and high consumption rates can reduce recruitment (Albins & Hixon, 2008) and population sizes (Green et al.,

2012) of native reef-fish species, and further the endangerment of critically endangered reef fish (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 composition of prey fishes). Major efforts have also 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 climate change scenarios (Grieve, Curchitser & Rykaczewski, 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.

Seeking to reduce lionfish densities, governments and non-profit organizations have promoted removal programs and incentivized its consumption (Chin, Aiken & Buddo, 2016). In some cases, these have shown to significantly reduce -but not quite eliminate- lionfish abundances at local scales (Sandel et al., 2015, Chin, Aiken & Buddo (2016), de Leon et al. (2013)). The rapid recovery rates exhibited by lionfish (Barbour et al., 2011) and the persistent populations in mesophotic coral ecosystems (Andradi-Brown et al., 2017) -which can contribute with recruitment to shallow-water populations- make of complete eradication through fishing effort an unlikely solution. However, further incentivizing its consumption might create a demand big enough to promote and sustain a stable fishery (Chin, Aiken & Buddo, 2016), which can reduce local abundances and control -not eradicate- the invasion while providing alternative livelihoods.

The feasibility of lionfish removal programs has been extensively evaluated through field observations (Sandel et al., 2015, Chin, Aiken & Buddo (2016), de Leon et al. (2013); Usseglio et al., 2017) and empirical modeling (Barbour et al., 2011; Morris, Shertzer & Rice, 2011; Johnston & Purkis, 2015). The latter measure changes in biomass or density (Barbour et al., 2011; Johnston & Purkis, 2015) in response to increased mortality (*i.e.* lionfish removal). In this case, biomass represents the sum of all fish's individual weight. Total Weight (TW)

can be estimated from Total Length (TL) observations using the allometric growth equation ($TW = aTL^b$). Parameters a and b for this equation exist for North Carolina (Barbour et al., 2011), Northern (Fogg et al., 2013) and Southern Gulf of Mexico (Aguilar-Perera & Quijano-Puerto, 2016), the Southern Mexican Caribbean (Sabido-Itza et al., 2016), Little Cayman (Edwards, Frazer & Jacoby, 2014), Jamaica (Chin, Aiken & Buddo, 2016), Bonaire (de Leon et al., 2013) and Costa Rica (Sandel et al., 2015), but remain unavailable for the central Mexican Caribbean. The weight-at-length of a species can vary across regions as a response to biotic (*e.g.* local food availability) and abiotic (*e.g.* water temperature) conditions (Johnson & Swenarton, 2016). Thus, when using biomass-informed models or estimating biomass from length observations, it is important to use site-specific parameters to obtain an accurate estimate. This is especially important when research involves identifying the total biomass available for harvest by fishers (Chin, Aiken & Buddo, 2016) or the efficacy of lionfish removals (Barbour et al., 2011; Morris, Shertzer & Rice, 2011; Johnston & Purkis, 2015).

Here, I provide the first allometric growth parameters for the invasive lionfish in the central Mexican Caribbean region. At the same time, I highlight the importance of using site-specific parameters by estimating biomass with parameters from other regions across the invasion range and comparing them to observed biomass. I also provide other 13 standardized parameters from eight studies through the invasion range, making them readily accessible for future research. Finally, I discuss the way in which allometric parameters are reported, and call for standardization to facilitate their use.

MATERIALS AND METHODS

Area of study. The study took place off the coasts of Playa del Carmen, in the Mexican Caribbean (**Fig. 1**). The region represents the northernmost section of the Mesoamerican Barrier Reef System (Ruiz-Zarate & Arias-Gonzalez, 2004). Coral reefs and mangroves are locally important habitats that represent important sources of income in terms of extractive (*e.g.* recreational fishing) and non-extractive (*e.g.* SCUBA diving) activities related to tourism, the main source of income to the local economy (Murray, 2007).

The reef profile has been described by Arias-Gonzalez (1998), indicating that the reef lagoon extends about 500 m from the coast, until the reef crest is reached. The reef becomes deeper, leading to the reef front often found at 700 m from the coastline and extends for an additional 300 m. At approximately 1000 m away from shore and 30 - 40 m depth, the reef leads to a drop-off. Along a perpendicular profile to the coast, bands of reef are interrupted by sand patches at 8 - 12 m deep and 16-18 m deep. Along the coast, these reefs have been reported to be under significant anthropogenic pressure, likely causing a shift in structure and function (Bozec et al., 2008).

Fish sampling. A total of 33 SCUBA immersions were performed in 10 sampling sites along the coast in 2010 (Fig. 1, Table 1). Sampling locations included wall and carpet reefs at depths between 5.7 m and 38.1 m. All observed organisms ($n = 109$) were collected using hand nets and numbered collection bottles. The use of hand nets prevented any weight loss due to bleeding and allowed a better representation of small sizes, often ignored due to gear selectivity when spearing. Organisms were euthanized and frozen within 30 minutes of completing the dive and stored for posterior analysis. Total Length (TL; mm) and Total Weight (TW; gr) were recorded for all organisms.

Data analysis. The weight at length relationship between the observed variables is described by the allometric growth function:

$$TW = aTL^b$$

Where TW is the Total Weight (gr), TL is the Total Length (mm), 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. The dependent and independent variables were transformed via base-10 logarithms, thus the equation becomes:

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

This can be simplified and re-written as:

$$Y = mX + c$$

Where $Y = \log_{10}(TW)$, $X = \log_{10}(TL)$, $m = b$, 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 Square Regression and heteroskedastic-robust standard error correction was performed. Both coefficients were tested against the null hypothesis of no change (*i.e.* $H_0 : c = 0$ and $H_0 : b = 0$). Additionally, the allometric parameter was tested against the null hypothesis of isometric growth ($H_0 : b = 3$). Coefficients were tested with a two-tailed Student's t-test. The significance of the regression was corroborated with an F-test.

Other length-weight relationships ($n = 13$) were extracted from peer-reviewed literature. Parameters were obtained for North Carolina ($n = 1$; Barbour et al., 2011), Northern ($n = 3$; Fogg et al., 2013) and Southern Gulf of Mexico ($n = 3$; Aguilar-Perera & Quijano-Puerto, 2016), the Southern Mexican Caribbean ($n = 1$; Sabido-Itza et al., 2016), Little Cayman ($n = 1$; Edwards, Frazer & Jacoby, 2014), Jamaica ($n = 1$; Chin, Aiken & Buddo, 2016), Bonaire ($n = 1$; de Leon et al., 2013) and Costa Rica ($n = 1$; Sandel et al., 2015) and Fishbase ($n = 1$;

158 Froese & Pauly, 2016) were also included. When available, information on sampling methods,
 159 gender differentiation, location, and depth ranges of each study was retrieved. Whenever
 160 gender was not specified, it was assumed that the results were presented for pooled genders.
 161 During the review process, some papers indistinctly used a to report either the ponderal index
 162 in eq. 1 or the y-intercept (c) in eq. 3, which might sometimes be overlooked. Furthermore,
 163 some studies reported their parameters as mm-to-gr conversions, but a rapid evaluation
 164 of such parameters indicated that they were estimated as cm-to-gr conversions. Here, all
 165 parameters are reported as TL(mm) to TW(gr) conversions. When required, values from
 166 other studies were transformed for consistency.

167 Since uncertainty around estimated relationships was not reported in some of the reviewed
 168 studies, it was not possible to test for statistical differences between relationships. Instead,
 169 the 13 length-weight relationships were used to calculate expected weight for the organisms
 170 sampled in the Central Mexican Caribbean ($n = 109$). Expected weights were divided by
 171 the observed weights to obtain a ratio. Difference in mean weight ratios across studies were
 172 tested with a one-way Analysis of Variance (ANOVA).

173 All hypothesis testing was performed with an *a priori* confidence level of $\alpha = 0.01$ in R
 174 version 3.4.0 (R Core Team, 2017). Data wrangling was done with the tidyverse package
 175 (Wickham, 2017). Maps were created with a mix of functions from the sp (Pebesma & Bivand,
 176 2005), rgdal (Bivand, Keitt & Rowlingson, 2017), tmap (Tennekes, 2017a), and tmaptools
 177 (Tennekes, 2017b) packages. Heteroskedastic-robust standard errors were calculated with
 178 the sandwich (Zeileis, 2004) and lmtest (Zeileis & Hothorn, 2002) packages. Models were
 179 manipulated with the broom package (Robinson, 2017). RefManageR (McLean, 2014)
 180 was used to keep track of citations. Raw data and code used in this work is available at
 181 github.com/jcvdav/lionfish_biometry.

RESULTS

Organism TL ranged between 34 and 310 mm and TW between 0.3 and 397.7 gr. The smallest organism (TL = 34.00 mm) was also the lightest organism (TW = 0.30 gr). However, the largest organism (TL = 310.00 mm) was not the heaviest (TW = 303.70 gr), and the heaviest organism (TW = 397.70 gr) was 292.00 mm in total length. Kernell density plots (Fig. 2) show the distribution for TL and TW for all sampled organisms. Both measures were positively skewed, with skewness of 0.87 for TL and 2.25 for TW.

Length-weight relationship. The model adjusted to eq. 3 estimated the coefficient values at $b = 3.2347391$ and $c = -5.4940866$. Thus, TW (gr) can be calculated from TL (mm) as a linear equation: $\log_{10}(TW) = 3.2347391 \times \log_{10}(TL) - 5.4940866$, or its exponential form: $TW = 3.2056297 \times 10^{-6} \times TL^{3.2347391}$. The intercept (c) and slope (b) were significantly different from zero ($t(107) = -66.17; p < 0.01$ and $t(107) = 83.24; p < 0.01$, respectively), rejecting the null hypothesis of no change. Additionally, the allometric factor (b) was significantly different from the value of isometric growth of $b = 3$ ($t(107) = 6.04; p < 0.01$), indicating that lionfish present allometric growth. More information on model fit and confidence intervals for the estimated coefficients is presented in Table 2. The relationship between Total Length and Total Weight is presented in Figure 3.

Comparison of allometric parameters. From the eight peer-reviewed studies including information on growth parameters for *P. volitans* and Fishbase (Froese & Pauly, 2016), 13 parameters were identified (Table 3). Two studies (Fogg et al., 2013; Aguilar-Perera & Quijano-Puerto, 2016) reported gender-level and pooled parameters, while the rest presented pooled results. The smallest coefficient of determination was presented by Chin, Aiken & Buddo (2016) with $R^2 = 0.8715$, while Sabido-Itza et al. (2016) reported the highest value at $R^2 = 0.9907$. Reviewed studies presented information for organisms obtained at depths between 0.5 and 57 m. Two studies (Aguilar-Perera & Quijano-Puerto, 2016; Chin, Aiken & Buddo, 2016) explicitly stated that their organisms were sampled with pole spears. Five

studies (Barbour et al., 2011; Fogg et al., 2013; Edwards, Frazer & Jacoby, 2014; Sandel et al., 2015; Sabido-Itza et al., 2016) mentioned that some of their organisms were obtained with pole spears (or other type of harpoon). A single study (de Leon et al., 2013) did not specify how organisms were sampled.

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 $b = 3.09 \pm 0.22$. In the case of the ponderal index (a) and its \log_{10} transformed parameter (c), values were higher for parameters for pooled genders. Figure 4 shows the predicted weights for organisms within the size range of these study using the 14 parameters previously described.

There were significant differences in expected-to-observed weight ratios estimated for each pair of parameters ($F(13, 1512) = 39.28$; $p < 0.05$). From all allometric parameters reviewed, those of Edwards, Frazer & Jacoby (2014) provided the lowest weight estimates, with an expected-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) expected-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 5.

DISCUSSION

This study provides the first pair of allometric growth parameters specific to the Central Mexican Caribbean, complementing other studies performed in Mexican waters in the Alacranes Reef (Aguilar-Perera & Quijano-Puerto, 2016) and Xcalak National Park (Sabido-Itza et al., 2016). By using hand nets instead of spears, we are able to sample a wider range of sizes often ignored by pole spear samples, allowing us to include smaller organisms.

232 Estimating parameters by including smaller organisms ensures better estimation of weight
233 for smaller sizes. This is especially important when biomass is calculated from visual census,
234 where small organisms can be registered. Thus, this study also increases certainty in weight
235 estimation of small organisms.

236 The length-weight coefficients estimated in this study were within the range identified by
237 studies in other regions (Barbour et al., 2011; de Leon et al., 2013; Fogg et al., 2013; Edwards,
238 Frazer & Jacoby, 2014; Sandel et al., 2015; Aguilar-Perera & Quijano-Puerto, 2016; Chin,
239 Aiken & Buddo, 2016; Sabido-Itza et al., 2016). However, the ones presented here provide
240 lower weight estimates for a same length. Until about $TL = 200$ mm, there are no appreciable
241 differences between the parameters for organisms from the Mexican Caribbean and those
242 for little Cayman (Edwards, Frazer & Jacoby, 2014) and Jamaica (Chin, Aiken & Buddo,
243 2016). Yet, for larger organisms ($TL > 270$ mm) parameters from Costa Rica (Sandel et
244 al., 2015) and Bonaire (de Leon et al., 2013) provide similar estimates to those from this
245 study. Conversely, these same studies tend to estimate higher weights—as compared to the
246 ones reported here—for smaller organisms, likely due to the lack of small organisms in the
247 samples used to estimate their parameters. When ever possible, future works should consider
248 the use of hand nets to obtain the samples not only for studies on weight-at-length, but also
249 diet, behavior and life history, where length can be an important factor.

250 There are evident differences in weight-at-length between organisms from the Caribbean
251 and Gulf of Mexico / North-Western Atlantic. Weight estimates with parameters from
252 the Gulf of Mexico and North-Western Atlantic (Barbour et al., 2011; Fogg et al., 2013;
253 Aguilar-Perera & Quijano-Puerto, 2016; Sabido-Itza et al., 2016) tend to be higher than those
254 from the Caribbean (de Leon et al., 2013; Edwards, Frazer & Jacoby, 2014; Sandel et al.,
255 2015; Chin, Aiken & Buddo, 2016), except for the ones from Xcalak National Park, Mexico
256 (Sabido-Itza et al., 2016). This indicates that there are differences between lionfish across
257 the invasion range. Similar regional variation exist for age-at-length relationships of lionfish

(Fogg et al., 2015). These differences can have major implications in management, especially when estimating biomass available for harvest or 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 & Swenarton, 2016).

While performing the literature review, it was often unclear if parameters were presented for eq.1 or eq. 3. Sometimes, they were even mislabeled and yielded senseless results when using the suggested conversion equation. On other cases, parameters were said to be reported for mm-to-gr conversions, when they were actually reported as cm-to-gr conversions. Perhaps these minor discrepancies can be easily solved by the trained eye, but why should they exist in the first place? It is important that we report our information in a standard way, making it readily available for other researchers and managers. In this particular case, I provide my humble opinion through 5 guidelines to report allometric parameters:

1. Be explicit in the methods section. What may seem obvious to you as an author —because you have been deeply immersed throughout the process— may not be clear to the reader. Specify any transformation performed on the data. When using log-transformations, mention the base used to transform. Do not assume that “data were log-transformed” means $\log_{10}(X)$. These assumptions vary across disciplines and software and can be a source of confusion. For example, in biology we often assume “log-transformed” indicates the use of base 10, however in R the proper command is `log10()` and not `log()`, which uses base e .

2. Use mm and gr to measure TL and TW, respectively. While conversion is always

possible, we should aim at using standard units to report these parameters. If you prefer to use cm to gr conversions, that is certainly valid, but make sure to explicitly mention units when presenting the parameters.

3. Specify the equation for which parameters are presented by including an explicit example with the parameters substituted into it, as done by some of the papers reviewed (de Leon et al., 2013; Sandel et al., 2015; Chin, Aiken & Buddo, 2016; Sabido-Itza et al., 2016). If possible, present the relationship in their exponential (eq. 1) and linear (eq. 3) forms.
4. Report standard errors and/or confidence intervals around the obtained estimates. Given that small changes in a , c , and b can result in important changes in estimated weight, it is important that we report uncertainty around each parameter and not just general model fit and coefficient significance. Reporting uncertainty around parameters allows researchers and managers to include upper and lower bounds in their predictions.
5. Make your data and code available. Even if this is not required by the journal or publisher, you can use free cloud data storage services or third-party repositories to make your research accessible to others. Resources will always be limited and budget will rarely be enough. It is important that we take advantage of open science tools that promote the advancement of knowledge and foster collaboration. Ultimately, this promotes transparency, allows replicability of research, and advances science.

This study provides a new pair of allometric growth parameters for lionfish from the central Mexican Caribbean, where they exhibit different weight-at-length. Furthermore, regional differences in length-weight relationships were identified, highlighting the importance of using site-specific parameters.

307 **ACKNOWLEDGEMENTS**

308 I would like to thank thank Nils Van Der Haar and Michael Doodey from Dive Aventuras
309 as well as Guillermo Lotz-Cador who provided help to collect samples. I would also like to
310 (anticipatedly) thank the editor and reviewers, who significantly improved the quality of this
311 work. This research was partially funded by the “Consejo Nacional de Ciencias y Tecnología”
312 (CONACyT) and the Latin American Fisheries Fellowship Program.

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TABLES

Table 1: Coordinates, minimum, maximum and mean depth (m), and number of samples for each location.

Location	Lat.	Long.	Min. Depth	Max. Depth	Mean Depth	n
Canones	20.477	-87.233	15.0	31.2	21.6	11
Castillo	20.496	-87.220	12.5	30.5	27.5	18
Cuevitas	20.478	-87.244	7.4	12.8	11.2	4
Islas	20.490	-87.228	14.0	19.4	16.7	10
Paamul	20.513	-87.192	9.9	22.7	15.5	31
Paraiso	20.484	-87.226	9.4	38.1	17.7	16
Pared	20.502	-87.212	12.1	21.0	16.3	12
Pedregal	20.507	-87.204	14.4	14.9	14.7	3
Santos	20.493	-87.222	5.7	26.6	16.2	2
Tzimin-Ha	20.393	-87.307	21.2	24.6	22.9	2
Total			5.7	38.1	18.6	109

462 Table 2: Regression table for the linear model fit between log10-transformed Total Weight
463 (dependent variable) and Total Length (independent variable). Numbers in parentheses next
464 to coefficient estimates indicate heteroskedastic-robust standard errors. The asterisks (*)
465 indicate the statistical significance. 95% Confidence intervals are provided for each parameter.

Table 2:	
	<i>Dependent variable:</i>
	log10(TW)
c	-5.494 (0.083)***
b	3.235 (0.039)***
95% CI for c	(-5.657-5.331)
85% CI for b	(3.159-3.311)
F Statistic	6928.67*** (df = 1; 107)
Observations	109
Adjusted R ²	0.976
Residual Std. Error	0.096 (df = 107)
<i>Note:</i>	*p<0.1; **p<0.05; ***p<0.01

Table 3: Summary of 13 allometric growth parameters available for lionfish in the invaded range from eight peer-reviewed papers, Fishbase (Froese & Pauly, 2016), and this study. All parameters have been adjusted to convert from millimeters to grams. n = Sample size, a = scaling parameter for eq. 1, 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. $mDepth$ and $MDepth$ indicate minimum and maximum depths (m), respectively, at which organisms were sampled. The $Spear$ column indicates if the study collected organisms with pole spears. An asterisk (*) indicates that some portion of organisms were sampled with pole spears. 1 = Aguilar-Perera & Quijano-Puerto (2016), 2 = Sandel et al. (2015), 3 = Chin, Aiken & Buddo (2016), 4 = Barbour et al. (2011), 5 = de Leon et al. (2013), 6 = Fogg et al. (2013), 7 = Edwards, Frazer & Jacoby (2014), 8 = Sabido-Itza et al. (2016), 9 = Froese & Pauly (2016), 10 = This study.

Reference	Region	Sex	a	c	b	R2	n	mDepth	MDepth	Spear
1	Arrecife Alacranes, Mexico	Both	472	0	-5.5400	3	0.95	5	20	Yes
1	Arrecife Alacranes, Mexico	Female	67	0	-5.9300	3	0.95	5	20	Yes
1	Arrecife Alacranes, Mexico	Male	59	0	-5.3800	3	0.95	5	20	Yes
2	Southern Caribbean Coast of Costa Rica	Both	458	0	-4.4400	3	-	-	-	Yes*
3	Discovery Bay, Jamaica	Both	419	0	-4.5600	3	0.8715	18.3	18.3	Yes
4	North Carolina	Both	774	0	-4.5391	3	-	27	45	Yes*
5	Bonaire	Both	1450	0	-4.6411	3	0.96	-	-	NA
6	Northern Gulf of Mexico	Both	582	0	-5.8600	3	0.99	-	-	Yes*
6	Northern Gulf of Mexico	Male	119	0	-5.5700	3	0.97	-	-	Yes*
6	Northern Gulf of Mexico	Female	115	0	-5.1700	3	0.94	-	-	Yes*
7	Little Cayman	Both	1887	0	-5.5229	3	0.97	15	30	Yes*
8	Parque Nacional Arrecifes de Xcalak, Mexico	Both	2143	0	-5.2828	3	0.9907	0.5	57	Yes*
9	NA	Both	NA	0	-5.0293	3	-	-	-	NA
10	Puerto Aventuras, Mexico	Both	109	0	-5.4941	3	0.9766	5.7	38.1	No

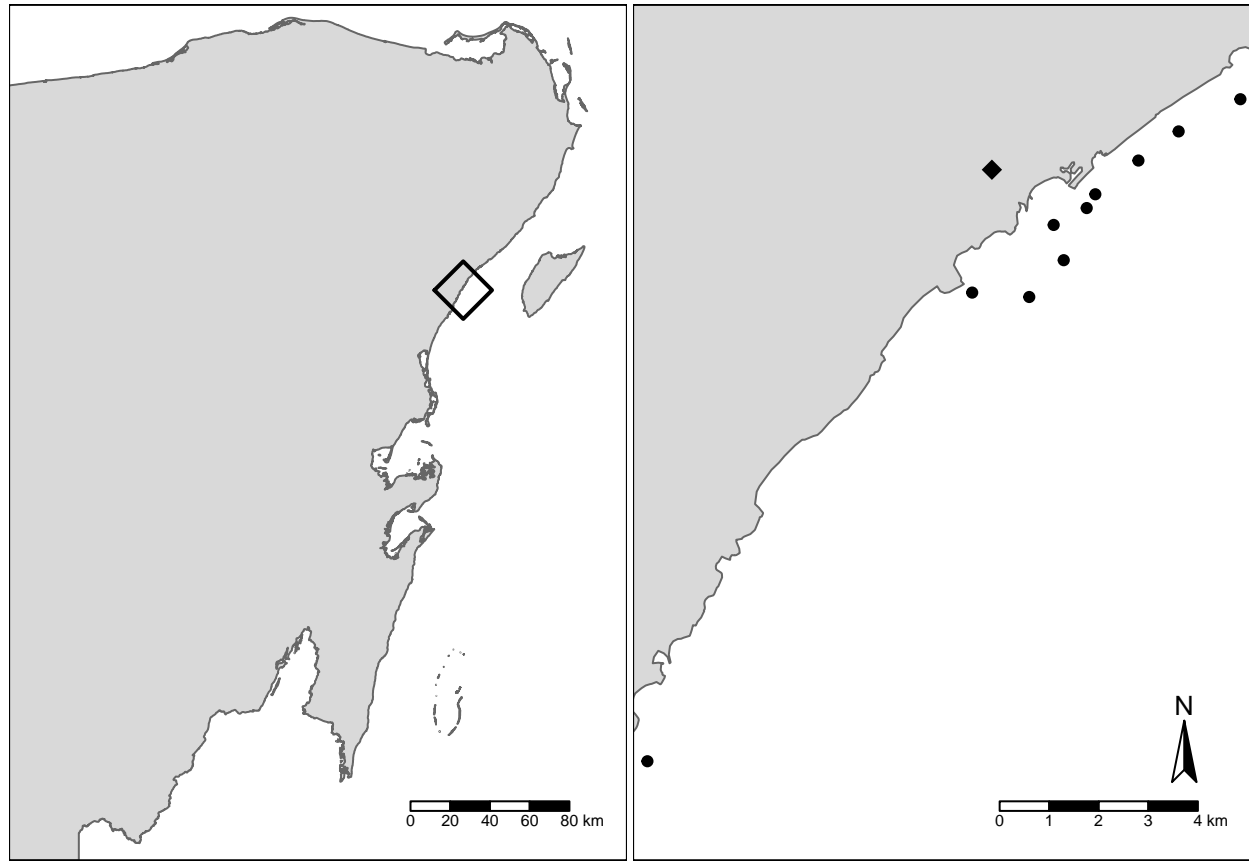


Figure 1: Map of the study area. The black inset on the left (Yucatan Peninsula) indicates the location where study sites are distributed. On the right, circular markers indicate sampling sites and the black romboid indicates location of Puerto Aventuras, Mexico.

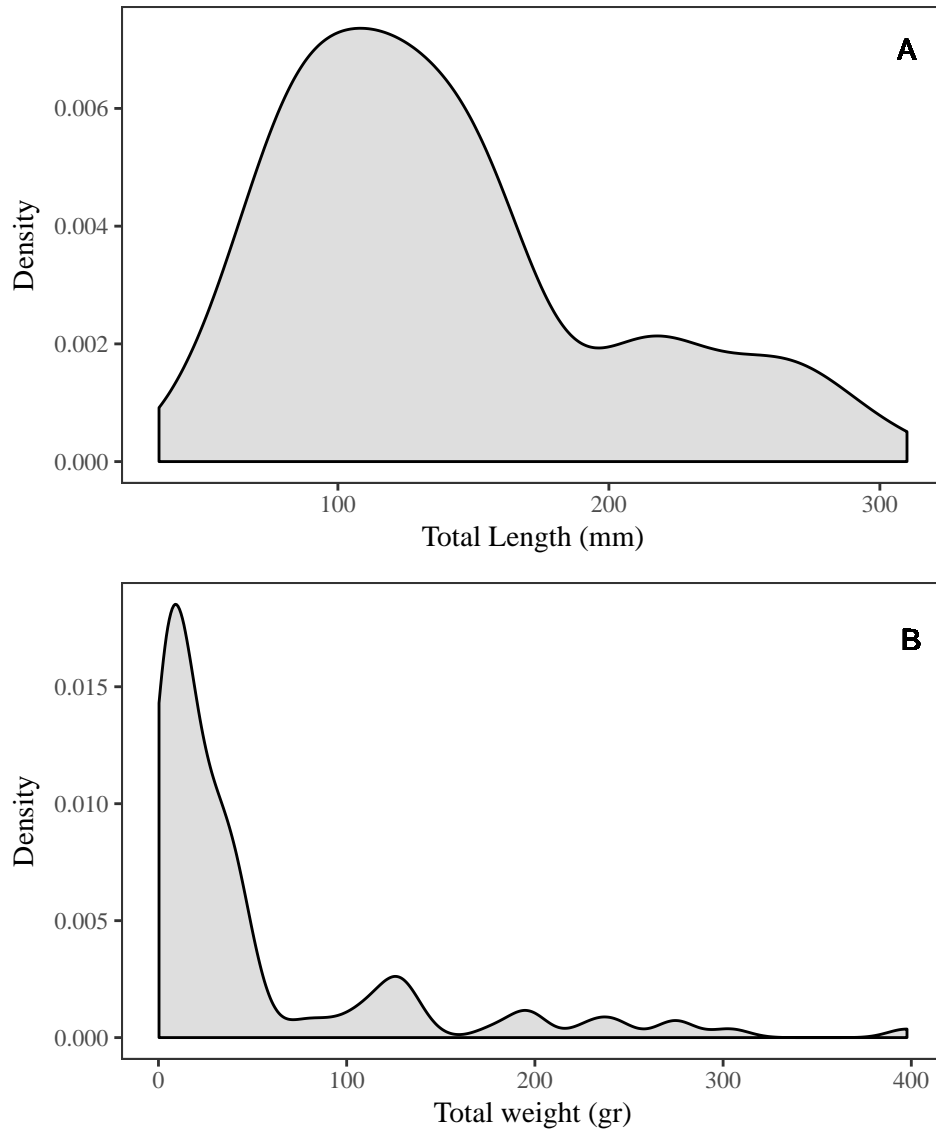


Figure 2: Kernell density plots for a) Total length (mm) and b) Total weight (gr) for 109 lionfish sampled in the central Mexican Caribbean.

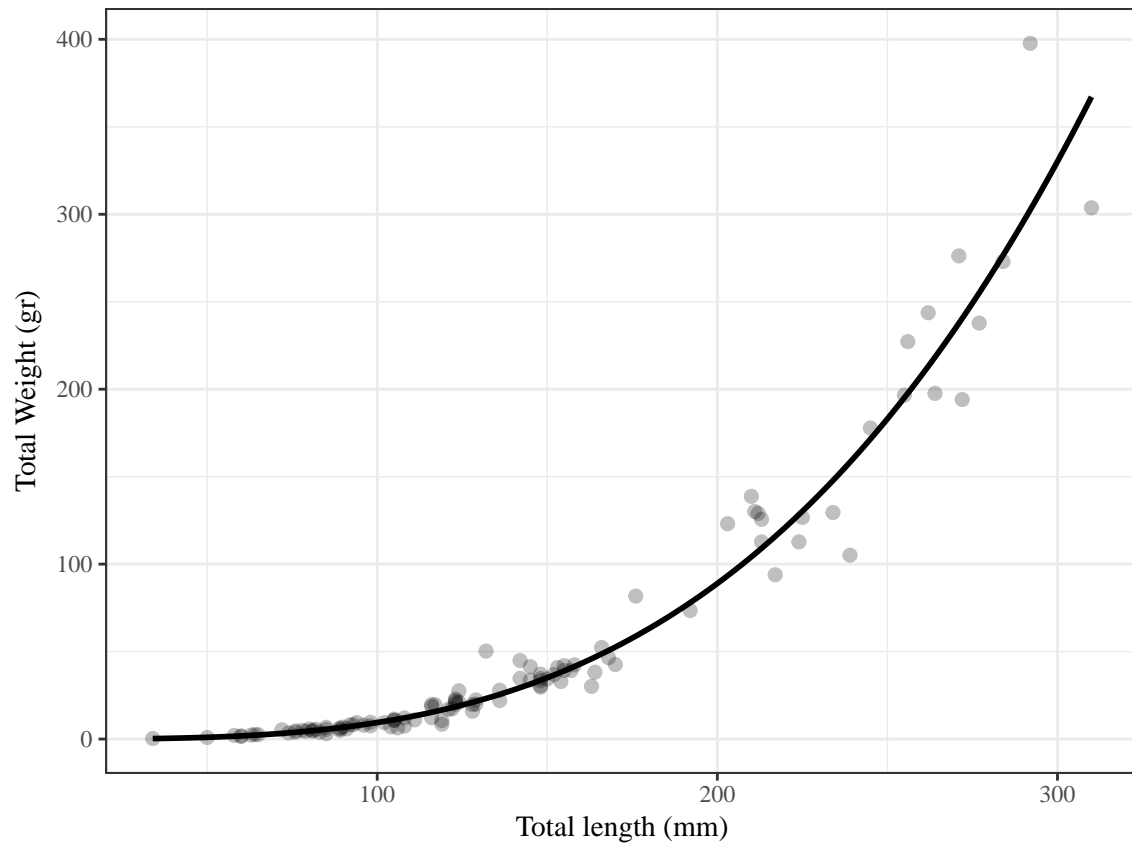


Figure 3: Length-weight relationship for 109 lionfish sampled in the central Mexican Caribbean. Points indicate samples, solid line indicates curve of best fit.

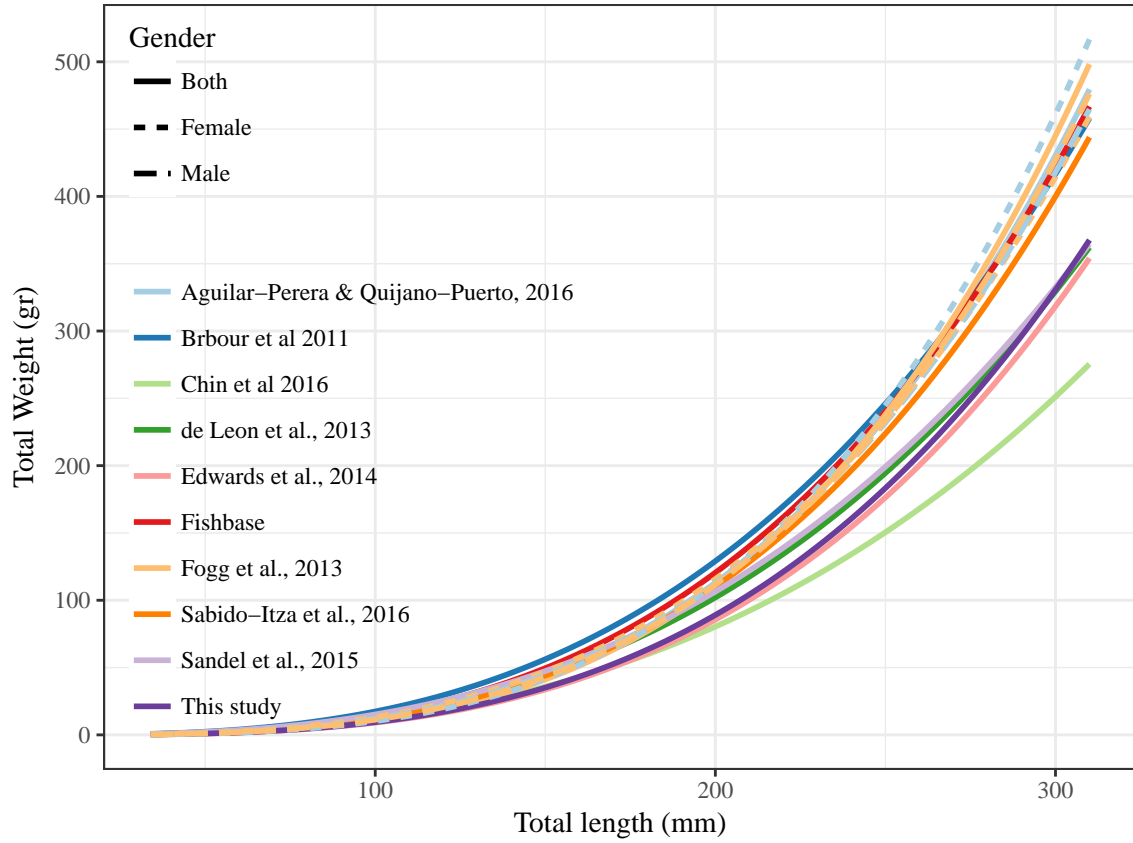


Figure 4: Length-weight relationships ($n = 14$) for eight studies, this study, and Fishbase. Colors indicate studies from which the parameters were extracted. Solid lines indicate that the fit was performed for males and females pooled together. Dotted lines indicate that the regression was performed on females, and dashed lines indicate it was performed for males.

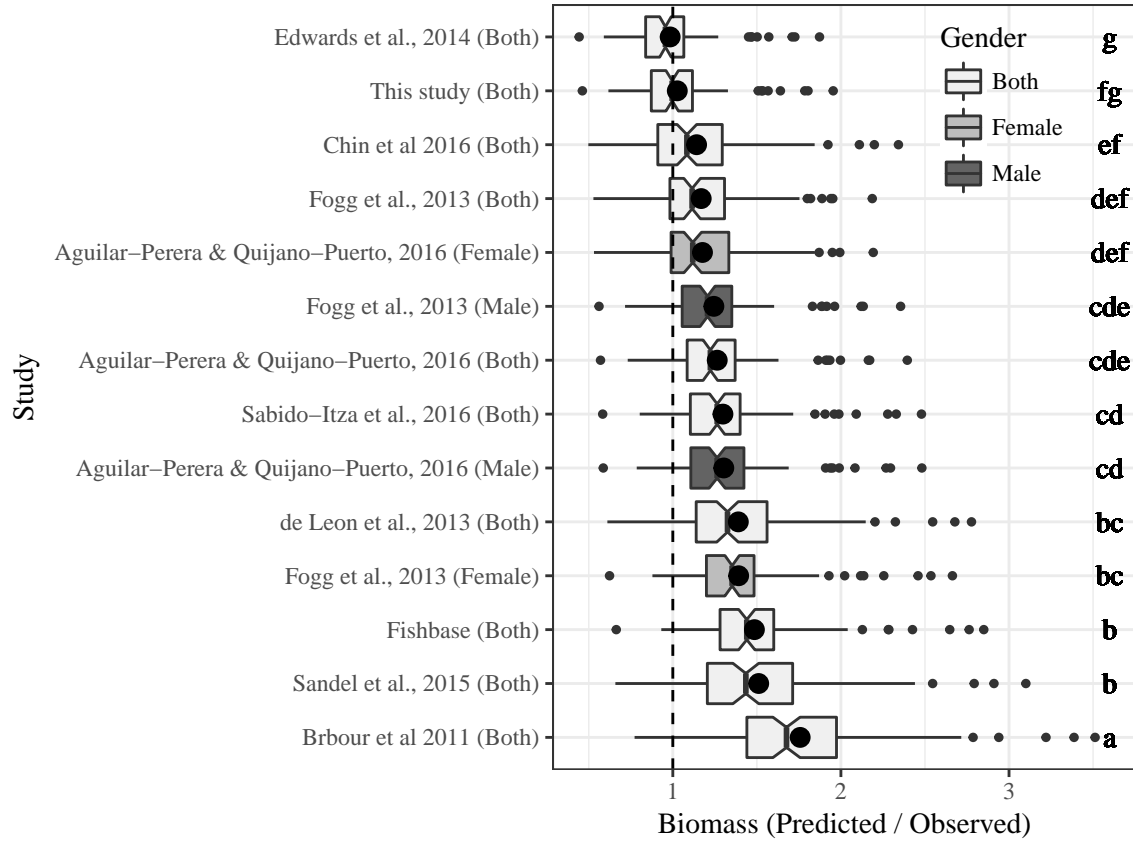


Figure 5: . Box and whiskers plot showing the distribution of predicted to observed biomass ratios for 14 pairs of allometric parameters. Lines indicate median values, circles indicate mean values, notches represent 95% confidence intervals around the median, lower and upper hinges correspond to the first and third quartiles, whiskers extend to the largest and lowest values within 1.5 inter-quartile range of the hinge, small points represent outliers further away than the whiskers. Like letters indicate values that do not differ significantly (Tukey's HSD; $p < 0.05$).