

Spatial variation in allometric growth of invasive lionfish has management implications

Juan Carlos Villaseñor-Derbez¹ and Sean Fitzgerald¹

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

Corresponding author:

Juan Carlos Villaseñor-Derbez¹

Email address: juancarlos@ucsb.edu

ABSTRACT

Lionfish (*Pterois volitans* / *miles*) are an invasive species in the Western Atlantic and the Caribbean. Improving management of invasive lionfish populations requires accurate total biomass estimates, which depend on accurate estimates of allometric growth. Sedentary species like lionfish often exhibit high levels of spatial variation in life history characteristics. We review 17 published length-weight relationships for lionfish taken throughout their invasive range and found regional differences that led to significant under- and overestimation of weight estimates. The spatial pattern we observed is consistent with findings from other studies focusing on genetics or length-at-age. We show that the use of *ex situ* parameters can result in up to a threefold under- or overestimation of total weight, but using parameters from nearby regions reduces this error. These findings can have substantial 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 Ocean and Caribbean Sea, likely introduced through release of aquarium-kept organisms (Betancur-R et al., 2011). They are the first invasive marine vertebrates established along these 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). Lionfish have established invasive populations in coral reefs, estuaries, mangroves, hard-bottomed areas, and mesophotic reefs (Barbour et al., 2010; Jud et al., 2011; Muñoz et al., 2011; Claydon et al., 2012; Andradi-Brown et al., 2017; Gress et al., 2017).

A substantial amount of research describes lionfish impacts throughout its invaded range. A meta-analysis by Peake et al. (2018) showed that invasive lionfish prey on at least 167 different species across the tropical and temperate Western 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 (Green et al., 2012; Rocha et al., 2015); but see Hackerott et al. (2017). 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 the Bahamas. Green et al. (2012) reported that prey fish biomass declined by 65% over two years as lionfish biomass increased along Bahamian coral reefs. However, their trophic impacts can be minimized if local lionfish biomass is controlled by culling (Arias-Gonzalez et al., 2011).

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 (de Leon et al., 2013; Sandel et al., 2015). Complete eradication of lionfish through fishing is unlikely because of their rapid recovery rates and ongoing recruitment to shallow-water areas from persistent populations in mesophotic

46 ecosystems (Barbour et al., 2011; Andradi-Brown et al., 2017). However, promoting lionfish consumption
47 might create a level of demand capable of incentivizing a stable fishery while controlling shallow-water
48 populations, thus creating alternative livelihoods and avoiding further negative effects to local biota.

49 The feasibility of establishing fisheries through lionfish removal programs has been extensively
50 evaluated through field observations and empirical modeling (Barbour et al., 2011; Morris et al., 2011; de
51 Leon et al., 2013; Johnston and Purkis, 2015; Sandel et al., 2015; Usseglio et al., 2017). Determining the
52 feasibility of such initiatives requires modeling the change in biomass in response to changes in fishing
53 mortality (*i.e.* culling). A common way to model this is via length-structured population models, where
54 fish lengths are converted to weight to calculate total biomass (Barbour et al., 2011; Côté et al., 2014;
55 Andradi-Brown et al., 2017). The allometric length-weight relationship is thus an essential component of
56 these models, but this relationship can vary across regions as a response to biotic and abiotic conditions
57 (Johnson and Swenarton, 2016).

58 Outcomes of previous studies suggest lionfish are likely to exhibit spatial heterogeneity in the length-
59 weight relationship, which we summarize in two main causes. First, culling programs are effective in
60 reducing local adult populations largely because lionfish exhibit high levels of site fidelity and small
61 home ranges (Fishelson, 1997; Kochzius and Blohm, 2005; Jud and Layman, 2012; Côté et al., 2014).
62 It is known that fish with sedentary behavior are likely to exhibit high levels of spatial variation in
63 important life history characteristics such as growth or natural mortality rates (Gunderson et al., 2008;
64 Hutchinson, 2008; Wilson et al., 2012; Guan et al., 2013). Second, genetic analysis of lionfish suggests
65 biological differences due to the existence of two genetically distinct invasive subpopulations between the
66 Western Atlantic and the Caribbean (Betancur-R et al., 2011). The large number of site-specific studies
67 reporting the length-weight relationship of lionfish provide variable estimates. These differences may be
68 increasingly important when estimating the potential effectiveness of lionfish culling programs (Barbour
69 et al., 2011; Morris et al., 2011; Côté et al., 2014; Johnston and Purkis, 2015). However, the magnitude of
70 the error caused by using *ex situ* parameters to estimate total weight from length observations remains
71 unexplored.

72 Here, we use previously published length-weight relationships for lionfish populations in North
73 Carolina, Northern and Southern Gulf of Mexico, the Southern Mexican Caribbean, Bahamas, Little
74 Cayman, Jamaica, Bonaire, Puerto Rico, and Costa Rica to quantify the magnitude of the error caused by
75 using *ex situ* parameters to estimate lionfish weight from length observations. We also collected lionfish
76 length and weight data in the central Mexican Caribbean and report the first length-weight relationship for
77 this region.

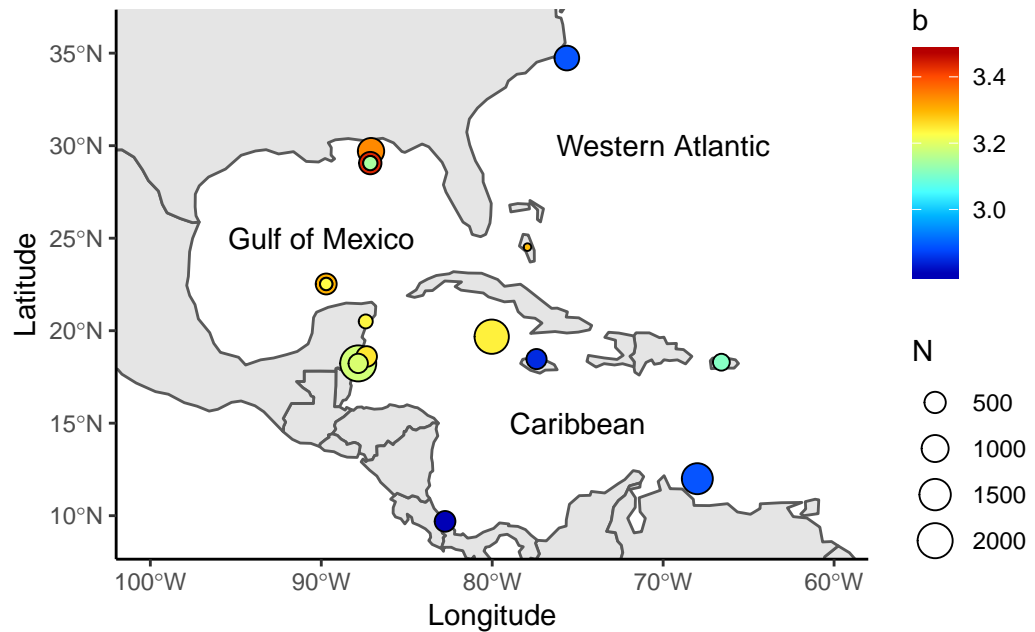


Figure 1. Locations where allometric growth parameters of lionfish (*Pterois spp*) have been reported. Circle sizes indicate sample size from each study, colors indicate the *b* coefficient from Eq. 1.

METHODS

We reviewed 12 published studies and obtained 17 length-weight relationships for the Western Atlantic ($n = 2$), Gulf of Mexico ($n = 7$), and Caribbean ($n = 8$, Table 1, Fig 1). We collected information on sex differentiation, location, length and depth ranges and sampling methods from each study when available. Only two studies reported parameters for each gender (Aguilar-Perera and Quijano-Puerto, 2016; Fogg et al., 2013), so we assumed both genders were included in a study if gender was unspecified. Reviewed studies presented information for organisms ranging between 25 mm and 475 mm in Total Length (TL), and that were obtained at depths between 0.5 m and 57 m. Four studies explicitly stated that their organisms were sampled with pole spears (Dahl and Patterson, 2014; Aguilar-Perera and Quijano-Puerto, 2016; Chin et al., 2016; Sabido-Itzá et al., 2016), and six 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 (Barbour et al., 2011; Fogg et al., 2013; Edwards et al., 2014; Toledo-Hernández, 2014; Sandel et al., 2015; Sabido-Itza et al., 2016), and two studies did not specify how organisms were sampled (Darling et al., 2011; de Leon et al., 2013).

We also used data from Villaseñor-Derbez and Herrera-Pérez (2014), who collected organisms from 10 sampling sites along the central Mexican Caribbean coast in the Summer of 2010 (Supplementary Table 1). 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 avoiding 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.

The above equation was linearized using \log_{10} -transformation. The coefficients were estimated with an Ordinary Least Squares Regression, and heteroskedastic-robust standard error correction was applied (Zeileis, 2004). When $b = 3$, it is said that the organism exhibits a perfect isometric growth, so 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.

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

We obtained a total of 18 parameter pairs by combining length-weight parameters extracted from the literature and the additional pair calculated here. Recall that the objective of this study is not to describe variations between populations, but rather to estimate how the use of *ex situ* parameters influences weight estimates. We used the central Mexican Caribbean as a case study of how the use of *ex situ* parameters influences the accuracy of weight estimates for lionfish. We estimated TW from the TL observations we collected in the central Mexican Caribbean ($n = 109$, with TL ranging from 34 mm to 310 mm) using each of the 18 parameter pairs and divided predicted weights by known observed weights to obtain a simple measure of over- or underestimation. Difference in mean weight ratios were tested with an analysis of covariance (ANCOVA), where the sources of variation were the study and TL . Ratios were logit-transformed prior to analysis, and a *post-hoc* Tukey's test was used to identify groups where mean ratios did not differ. All analyses were performed in R version 3.5.2 (R Core Team, 2018). Raw data and code used in this work are available on github at github.com/jcvdavid/lionfish_biometry.

RESULTS

The length-weight relationship for organisms from the central Mexican Caribbean resulted in coefficient values of $a = 3.2056297 \times 10^{-6}$ and $b = 3.2347391$ ($R^2 = 0.977$, $F(df = 1; 107) = 6928.67$, $p < 0.001$). The allometric factor (b) was significantly different from $b = 3$ ($t(107) = 6.04$; $p < 0.001$) corroborating that lionfish present allometric growth. The length-weight coefficients estimated in this study were within the range identified by studies in other regions (Table 1). Figure 2 shows the relationship between TL and TW for this region.

There were significant differences in our predicted weights for the central Mexican Caribbean when using each of the different pairs of parameters ($F(df = 17; 1943) = 24.96$; $p < 0.001$). The lowest weight estimates for the observed lengths resulted from using the allometric parameters from Banco Chinchorro in the Caribbean, with mean \pm SD of 40.37 ± 58.74 g (Sabido-Itzá et al., 2016). In contrast, the highest weight estimates came from the Western Atlantic with 73.76 ± 96.11 g (Barbour et al., 2011). To put this in context, true observed weights have a mean of 52.56 ± 76.58 g. Weights predicted from these extreme parameters correspond to mean \pm SD predicted-to-observed weights ratios of 0.80 ± 0.19 and 1.76 ± 0.50 (mean \pm SD), respectively. The largest under- and overestimations resulted in ratios of 0.36 and 3.51 of the actual observed weight, indicating that *ex situ* parameters can result in substantial weight under- and overestimation.

Tukey's *post-hoc* test suggests that weight ratios for the central Mexican Caribbean were not different from those obtained with parameters from Little Cayman, the Bahamas, and some sites in the Gulf of Mexico (Tukey's HSD $p > 0.05$). Weight estimates using parameters from the Gulf of Mexico and Western Atlantic were higher on average than those from the Caribbean (Fig 3). The average (\pm SD) predicted-to-observed weight ratios from these three regions were 1.24 ± 0.309 , 1.76 ± 0.496 , and 1.17 ± 0.398 , respectively. This suggest that the smallest errors are observed when using parameters other locations in the Caribbean. Predicted-to-observed weight ratios are presented in Figure 4.

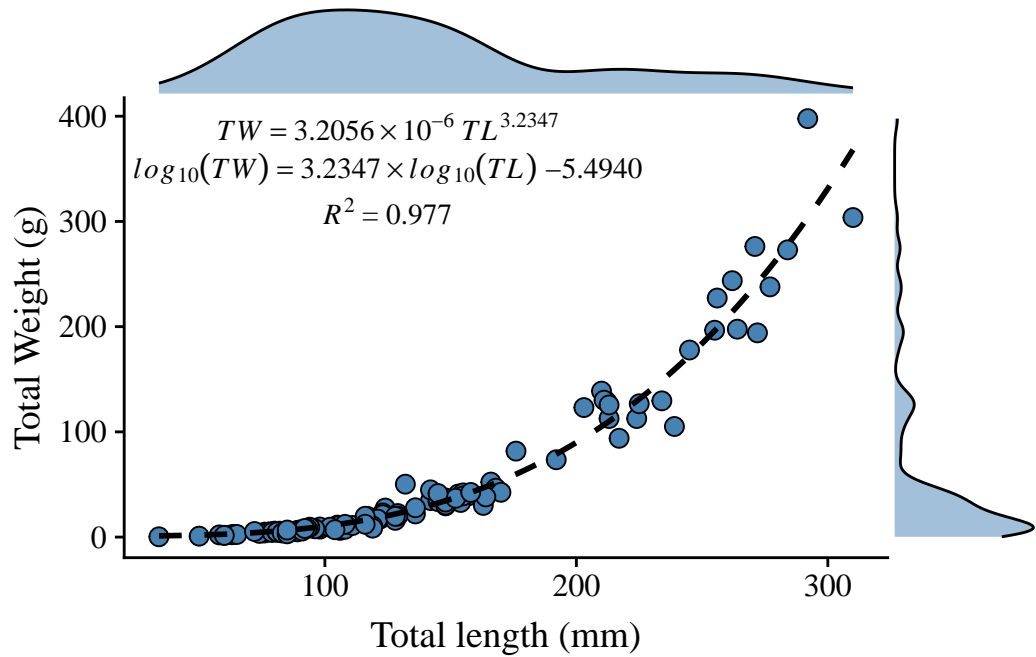


Figure 2. Length-weight relationship for 109 lionfish sampled in the central Mexican Caribbean. Points indicate samples, dashed black line indicates curve of best fit, marginal plots represent the density distribution of each variable.

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 (presented in $\times 10^{-5}$), b = exponent.

Region	Sex	n	a	b	R^2	Reference
Western Atlantic	B	774	2.9	2.89	-	Barbour et al., 2011
Western Atlantic	B	-	0.25	3.29	-	Darling et al., 2011
GoM	B	934	0.21	3.34	0.98	Dahl & Patterson, 2014
GoM	B	472	0.29	3.30	0.95	Aguilar-Perera & Quijano-Puerto, 2016
GoM	F	67	0.12	3.47	0.95	Aguilar-Perera & Quijano-Puerto, 2016
GoM	M	59	0.42	3.23	0.95	Aguilar-Perera & Quijano-Puerto, 2016
GoM	B	582	0.14	3.43	0.99	Fogg et al., 2013
GoM	M	119	0.27	3.31	0.97	Fogg et al., 2013
GoM	F	115	0.68	3.14	0.94	Fogg et al., 2013
Caribbean	B	458	3.6	2.81	-	Sandel et al., 2015
Caribbean	B	419	2.8	2.85	0.87	Chin et al., 2016
Caribbean	B	1450	2.3	2.89	0.92	de Leon et al., 2013
Caribbean	B	1887	0.3	3.24	0.97	Edwards et al., 2014
Caribbean	B	2143	0.52	3.18	0.99	Sabido-Itza et al., 2016
Caribbean	B	227	0.8	3.11	0.96	Toledo-Hernández et al., 2014
Caribbean	B	449	0.23	3.25	0.97	Sabido-Itza et al., 2016b
Caribbean	B	368	0.32	3.19	0.98	Sabido-Itza et al., 2016b
Caribbean	B	109	0.32	3.23	0.98	This study

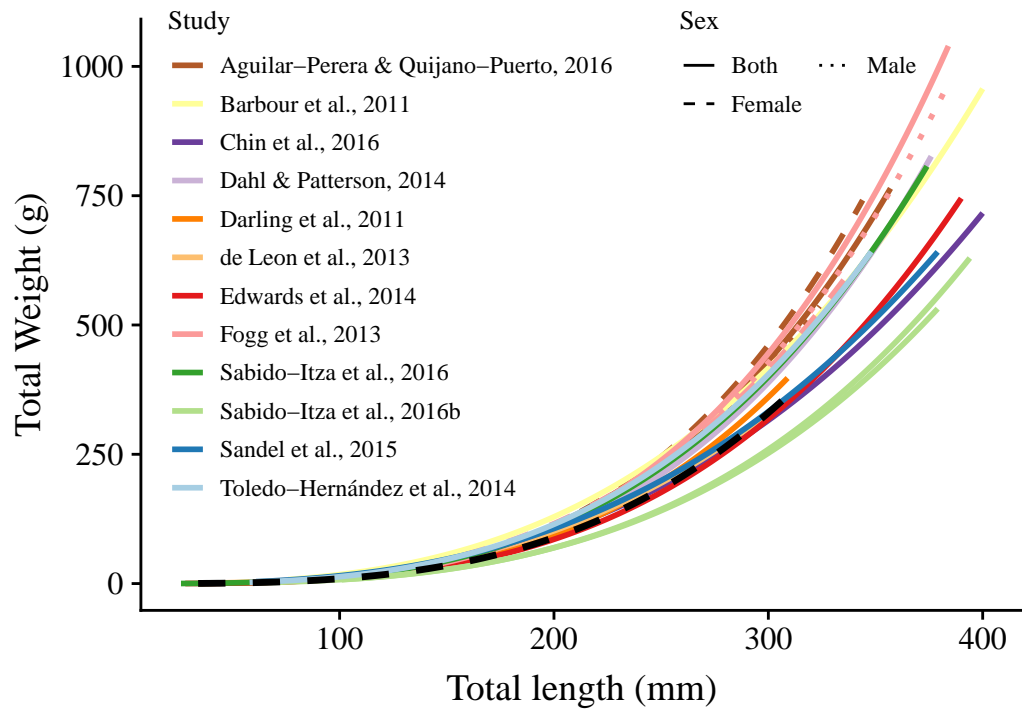


Figure 3. Length-weight relationships ($n = 18$) for 12 studies and this study. The curves are shown for the range of lengths reported in each study (See Supplementary Table 2); when ranges were not present, we use the ones found in this study (34 mm - 310 mm). Colors indicate studies from which the 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. There are two solid green lines for Sabido-Itza et al., 2016b, one for each of the two sites for which they report parameters. A log-log version of this figure is presented in Figure S4.

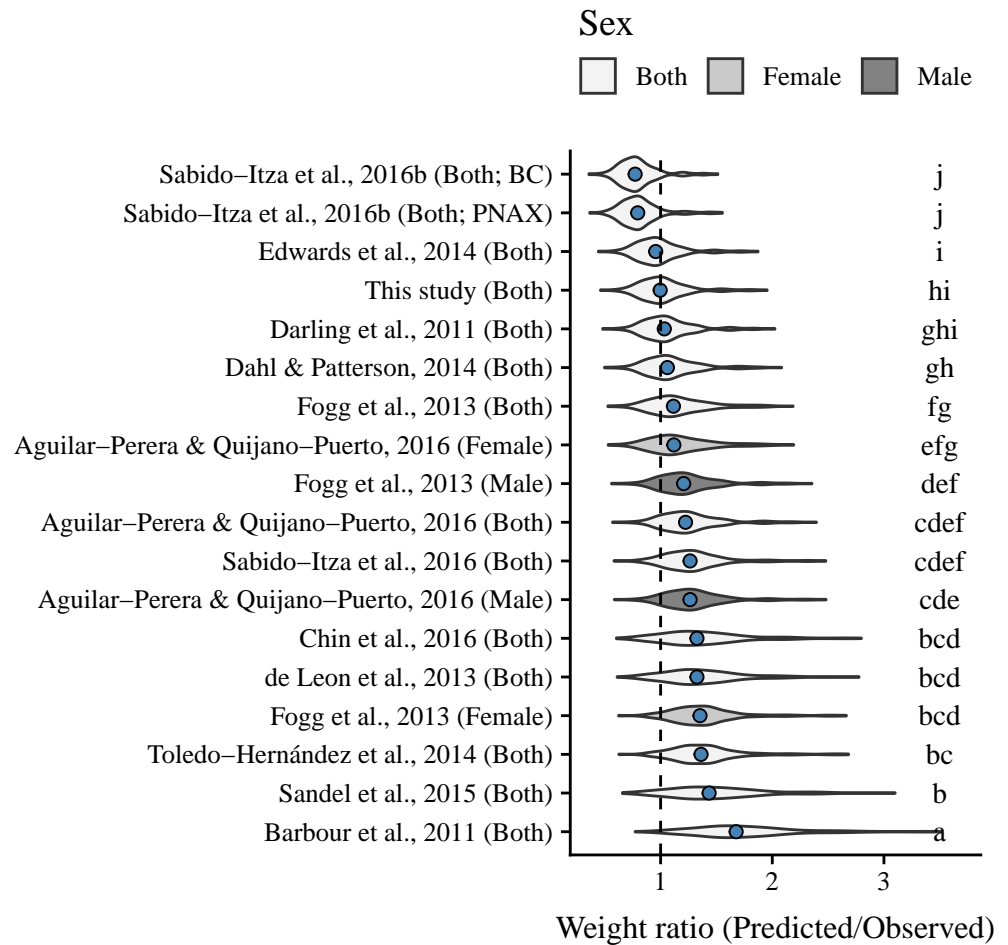


Figure 4. Violin plot of predicted-to-observed weight ratios for 18 pairs of allometric parameters. Blue circles indicate median values and like letters indicate values that do not differ significantly. For Sabido-Itza et al, 2016b, BC and PNAX make reference to Banco Chinchorro and Parque Nacional Arrecifes de Xcalak, two sites for which they report parameters.

DISCUSSION

Our results suggest that lionfish exhibit highly variable allometric relationships across the invaded range, and that this variation is spatially heterogeneous and relevant for management of the invasion. Moreover, we show that the use of *ex situ* parameters may lead to highly biased weight estimates. Our comparison of observed weights to those predicted with locally-informed parameters and *ex situ* parameters showed that weight can be overestimated by more than a three-fold, and highlights the need to use local information. Here we discuss the implications of our findings, possible shortcomings in our analyses, and highlight potential future research directions.

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 the 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.

We detected substantial differences in weight-at-length between organisms from the Caribbean, Gulf of Mexico, and Western Atlantic. Groupings of predicted-to-observed weight ratios identified in our *post hoc* testing aligned with the spatial distribution of the examined studies, suggesting that these differences may be mediated by space. These regional allometric differences mirror similar patterns in length-at-age of lionfish across both their invaded and native regions (Pusack et al., 2016). Variation may be driven by genetics or by organisms' exposure 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 length-at-age differences may be driven by the environment.

We might be inclined to attribute all variation to the spatial origin of these parameters. However, these were not only collected for different locations, but also using a range of different sampling methods and at different points in time (See Supplementary Table 2 for an extended version of Table 1). While we are not able to evaluate how these factors influence previous estimates (raw data from all studies would be needed), it is certain that the lack of locally-calculated parameters may induce significant bias when calculating weight from length observations. Differences in weight-at-length could also reflect differential energy input or usage, or a combination of both. The magnitude of the bias and our lack of understanding of the source of variation highlights the need to simultaneously collect length-weight information across the invaded range to test for spatially-induced patterns and link these to previously suggested environmental and genetic structures. Such an endeavor would provide insights into lionfish biology and better inform management.

Applying parameters estimates to lengths outside the range of lengths originally used to estimate the parameters may also induce error. Our smallest observed organism was 34 mm in *TL*, and only two studies estimated parameters with smaller organisms (Sabido-Itza et al., 2016; Edwards et al., 2014). On the other hand, our largest organism had a *TL* of 310 mm, which is well within the range of all other studies (maximum observed lengths varied from 325 mm to 475 mm; See Supplementary Table 2). Due to the power-function describing the allometric relationship, the error is higher when extrapolation is done for lengths that are larger than the maximum length used to estimate the parameters. This means that not only must managers use locally-informed data, but that these local data must also include the full range of lengths present in the region to reduce error caused by extrapolation.

The results presented here have fundamental 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 more than a threefold under- or overestimation of total weight. These differences become especially important when allocating resources for lionfish removal programs, incentivizing lionfish fisheries 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

203 use reasonable sets of different parameters that provide upper and lower bounds in their results.

204 ACKNOWLEDGEMENTS

205 The thank Nils Van Der Haar and Michael Doodey from Dive Aventuras as well as Guillermo Lotz-Cador
206 who provided help to collect samples. We are grateful for comments raised by the editor and two
207 anonymous reviewers, which significantly increased the quality of this work.

208 Conflict of Interest: The authors declare that they have no conflict of interest.

209 REFERENCES

- 210 Aguilar-Perera, A. and Quijano-Puerto, L. (2016). Relations between fish length to weight, and otolith
211 length and weight, of the lionfish pterois volitans in the parque nacional arrecife alacranes, southern
212 gulf of mexico. *Rev. biol. mar. oceanogr.*, 51(2):469–474.
- 213 Albins, M. and Hixon, M. (2008). Invasive indo-pacific lionfish pterois volitans reduce recruitment of
214 atlantic coral-reef fishes. *Mar. Ecol. Prog. Ser.*, 367:233–238.
- 215 Andradi-Brown, D. A., Grey, R., Hendrix, A., Hitchner, D., Hunt, C. L., Gress, E., Madej, K., Parry, R. L.,
216 Régnier-McKellar, C., Jones, O. P., a Arteaga, M., Izaguirre, A. P., Rogers, A. D., and Exton, D. A.
217 (2017). Depth-dependent effects of culling-do mesophotic lionfish populations undermine current
218 management? *R Soc Open Sci*, 4(5):170027.
- 219 Arias-Gonzalez, J. E., Gonzalez-Gandara, C., Luis Cabrera, J., and Christensen, V. (2011). Predicted
220 impact of the invasive lionfish pterois volitans on the food web of a caribbean coral reef. *Environ Res*,
221 111(7):917–925.
- 222 Barbour, A., Montgomery, M., Adamson, A., Diaz-Ferguson, E., and Silliman, B. (2010). Mangrove use
223 by the invasive lionfish pterois volitans. *Mar. Ecol. Prog. Ser.*, 401:291–294.
- 224 Barbour, A. B., Allen, M. S., Frazer, T. K., and Sherman, K. D. (2011). Evaluating the potential efficacy
225 of invasive lionfish (pterois volitans) removals. *PLoS ONE*, 6(5):e19666.
- 226 Betancur-R, R., Hines, A., Acero, A., Orti, G., Wilbur, A., and Freshwater, D. (2011). Reconstructing the
227 lionfish invasion: insights into greater caribbean biogeography. *J Biogeography*, 38:1281–1293.
- 228 Chin, D. A., Aiken, K. A., and Buddo, D. (2016). Lionfish population density in discovery bay, jamaica.
229 *International Journal of Scientific & Engineering Research*, 7(12):1327 – 1331.
- 230 Claydon, J., Calosso, M., and Traiger, S. (2012). Progression of invasive lionfish in seagrass, mangrove
231 and reef habitats. *Mar. Ecol. Prog. Ser.*, 448:119–129.
- 232 Côté, I. M., Akins, L., Underwood, E., Curtis-Quick, J., and Green, S. J. (2014). Setting the record
233 straight on invasive lionfish control: Culling works. *PeerJ*.
- 234 Dahl, K. A. and Patterson, W. F. (2014). Habitat-specific density and diet of rapidly expanding invasive
235 red lionfish, pterois volitans, populations in the northern gulf of mexico. *PLoS ONE*, 9(8):e105852.
- 236 Darling, E. S., Green, S. J., O’Leary, J. K., and Côté, I. M. (2011). Indo-pacific lionfish are larger and
237 more abundant on invaded reefs: a comparison of kenyan and bahamian lionfish populations. *Biol*
238 *Invasions*, 13(9):2045–2051.
- 239 de Leon, R., Vane, K., Bertuol, P., Chamberland, V. C., Simal, F., Imms, E., and Vermeij, M. J. A.
240 (2013). Effectiveness of lionfish removal efforts in the southern caribbean. *Endanger Species Res*,
241 22(2):175–182.
- 242 Edwards, M. A., Frazer, T. K., and Jacoby, C. A. (2014). Age and growth of invasive lionfish (pterois
243 spp.) in the caribbean sea, with implications for management. *BMS*, 90(4):953–966.
- 244 Fishelson, L. (1997). Experiments and observations on food consumption, growth and starvation in
245 dendrochirus brachypterus and pterois volitans (pteroinae, scorpaenidae). *Environmental Biology of*
246 *Fishes*, 50(4):391–403.
- 247 Fogg, A. Q., Evans, J. T., Ingram JR, G. W., Peterson, M. S., and Brown-Peterson, N. J. (2015). Comparing
248 age and growth patterns of invasive lionfish among three ecoregions of the northern gulf of mexico. In
249 GCFI, G. and Institute, C. F., editors, *Proceedings of the 68 th Gulf and Caribbean Fisheries Institute*,
250 Panama City. Gulf and Caribbean Fisheries Institute.
- 251 Fogg, A. Q., Hoffmayer, E. R., Driggers, W. B., Campbell, M. D., Pellegrin, G. J., and Stein, W. (2013).
252 Distribution and length frequency of invasive lionfish (pterois sp.) in the northern gulf of mexico. *GCR*,
253 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.
- Gress, E., Andradi-Brown, D. A., Woodall, L., Schofield, P. J., Stanley, K., and Rogers, A. D. (2017). Lionfish (pterois spp.) invade the upper-bathyal zone in the western atlantic. *PeerJ*, 5:e3683.
- 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.
- 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. *Mar. Ecol. Prog. Ser.*, 558:161–165.
- Hutchinson, W. F. (2008). The dangers of ignoring stock complexity in fishery management: the case of the north sea cod. *Biol Lett*, 4(6):693–695.
- Johnson, E. G. and Swenarton, M. K. (2016). Age, growth and population structure of invasive lionfish (pterois volitans/miles) in northeast florida using a length-based, age-structured population model. *PeerJ*, 4:e2730.
- Johnston, M. and Purkis, S. (2015). A coordinated and sustained international strategy is required to turn the tide on the atlantic lionfish invasion. *Mar. Ecol. Prog. Ser.*, 533:219–235.
- Jud, Z., Layman, C., Lee, J., and Arrington, D. (2011). Recent invasion of a florida (usa) estuarine system by lionfish pterois volitans / p. miles. *Aquat. Biol.*, 13(1):21–26.
- Jud, Z. R. and Layman, C. A. (2012). Site fidelity and movement patterns of invasive lionfish, pterois spp., in a florida estuary. *Journal of Experimental Marine Biology and Ecology*, 414–415:69–74.
- Kochzius, M. and Blohm, D. (2005). Genetic population structure of the lionfish pterois miles (scorpaenidae, pteroinae) in the gulf of aqaba and northern red sea. *Gene*, 347(2):295–301.
- Morris, J. A., Shertzer, K. W., and Rice, J. A. (2011). A stage-based matrix population model of invasive lionfish with implications for control. *Biol Invasions*, 13(1):7–12.
- Muñoz, R., Currin, C., and Whitfield, P. (2011). Diet of invasive lionfish on hard bottom reefs of the southeast usa: insights from stomach contents and stable isotopes. *Mar. Ecol. Prog. Ser.*, 432:181–193.
- Peake, J., Bogdanoff, A. K., Layman, C. A., Castillo, B., Reale-Munroe, K., Chapman, J., Dahl, K., Patterson III, W. F., Eddy, C., Ellis, R. D., Faletti, M., Higgs, N., Johnston, M. A., Muñoz, R. C., Sandel, V., Villaseñor-Derbez, J. C., and Morris, J. A. (2018). Feeding ecology of invasive lionfish (pterois volitans and pterois miles) in the temperate and tropical western atlantic. *Biol Invasions*.
- Pusack, T. J., Benkwitt, C. E., Cure, K., and Kindinger, T. L. (2016). Invasive red lionfish (pterois volitans) grow faster in the atlantic ocean than in their native pacific range. *Environ. Biol. Fishes*, 99(6-7):571–579.
- R Core Team (2018). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rocha, L. A., Rocha, C. R., Baldwin, C. C., Weigt, L. A., and McField, M. (2015). Invasive lionfish preying on critically endangered reef fish. *Coral Reefs*, 34(3):803–806.
- Sabido-Itzá, M., Aguilar-Perera, A., and Medina-Quej, A. (2016). Length–weight and length–length relations, and relative condition factor of red lionfish, pterois volitans (actinopterygii: Scorpaeniformes: Scorpaenidae), from two natural protected areas in the mexican caribbean. *Acta Ich et Piscat*, 46(4):279–285.
- Sabido-Itza, M., Medina-Quej, A., De Jesus-Navarrete, A., Gomez-Poot, J., and Garcia-Rivas, M. (2016). Uso de la estructura de tallas como evidencia del establecimiento poblacional del pez le?n pterois volitans (scorpaeniformes: Scorpaenidae) en el sur del caribe mexicano. *RBT*, 64(1):353.
- Sandel, V., Martínez-Fernández, D., Wangpraseurt, D., and Sierra, L. (2015). Ecology and management of the invasive lionfish pterois volitans/miles complex (perciformes: Scorpaenidae) in southern costa rica. *Rev Biol Trop*, 63(1):213–221.
- Schofield, P. (2009). Geographic extent and chronology of the invasion of non-native lionfish (pterois volitans [linnaeus 1758] and p. miles [bennett 1828]) in the western north atlantic and caribbean sea. *AI*, 4(3):473–479.
- Schofield, P. (2010). Update on geographic spread of invasive lionfishes (pterois volitans [linnaeus, 1758]

309 and p. miles [bennett, 1828]) in the western north atlantic ocean, caribbean sea and gulf of mexico. *AI*,
 310 5:S117–S122.
 311 Toledo-Hernández, C. (2014). Population ecology and genetics of the invasive lionfish in puerto rico. *AI*,
 312 9(2):227–237.
 313 Usseglio, P., Selwyn, J. D., Downey-Wall, A. M., and Hogan, J. D. (2017). Effectiveness of removals of
 314 the invasive lionfish: how many dives are needed to deplete a reef? *PeerJ*, 5:e3043.
 315 Villaseñor-Derbez, J. C. and Herrera-Pérez, R. (2014). Brief description of prey selectivity and ontogenetic
 316 changes in the diet of the invasive lionfish pterois volitans (actinopterygii, scorpaenidae) in the mexican
 317 caribbean. *PANAMJAS*, 9(2):131–135.
 318 Wilson, J. R., Kay, M. C., Colgate, J., Qi, R., and Lenihan, H. S. (2012). Small-scale spatial variation in
 319 population dynamics and fishermen response in a coastal marine fishery. *PLoS ONE*, 7(12):e52837.
 320 Zeileis, A. (2004). Econometric computing with hc and hac covariance matrix estimators. *J Stat Softw*,
 321 11(10).