

## Spatial variation in allometric growth of invasive lionfish has management implications

Juan Carlos Villaseñor-Derbez · Sean Fitzgerald ·

Received: date / Accepted: date

**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 substantial regional differences in allometric growth parameters. The spatial pattern we observed is consistent with findings from other studies focusing on genetics or age-at-length. 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 major implications for management in terms of predicting effects on local ecosystems, evaluating the effectiveness of removal programs, or estimating biomass available for harvest.

**Keywords** Lionfish · invasive species · length-weight · allometric growth · regional variations ·

---

Juan Carlos Villaseñor-Derbez  
Bren School of Environmental Science and Management, University of California Santa Barbara, Santa Barbara, California, United States, 93117 | ORCID: 0000-0003-1245-589X  
E-mail: [jvillasenor@bren.ucsb.edu](mailto:jvillasenor@bren.ucsb.edu)

Sean Fitzgerald  
Bren School of Environmental Science and Management, University of California Santa Barbara, Santa Barbara, California, United States, 93117

## 1 Introduction

Lionfish (*Pterois volitans/miles* complex) are an invasive species in the western Atlantic and Caribbean Sea, likely introduced through liberation of aquarium-kept organisms (Betancur-R et al, 2011). They are the first invasive marine vertebrates established along the North Atlantic Caribbean coasts (Schofield, 2009, 2010; Sabido-Itza et al, 2016) and their presence has been labeled as a major marine invasion because they threaten local biodiversity, spread rapidly, and are difficult to manage (Hixon et al, 2016). 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 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 (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 Florida. Green et al (2012) reported that prey fish biomass declined by 65% over two years as lionfish biomass increased along Bahamian coral reefs. 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 ecosystems (Barbour et al, 2011; Andradi-Brown et al, 2017). However, promoting lionfish consumption might create a level of demand capable of incentivizing a stable fishery while controlling shallow-water populations, thus creating alternative livelihoods and avoiding further impacts to local biota.

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; Usseglio et al, 2017). Determining the feasibility of such initiatives requires modeling the change in biomass in response to changes in fishing mortality (*i.e.* culling). A common way to model this is via length-structured population models, where fish lengths are converted to weight to calculate total biomass (Barbour et al, 2011; Côté et al, 2014; Andradi-Brown et al, 2017). The allometric length-weight relationship is thus an essential component of these models, but this relationship can vary across

regions as a response to biotic and abiotic conditions (Johnson and Swenarton, 2016).

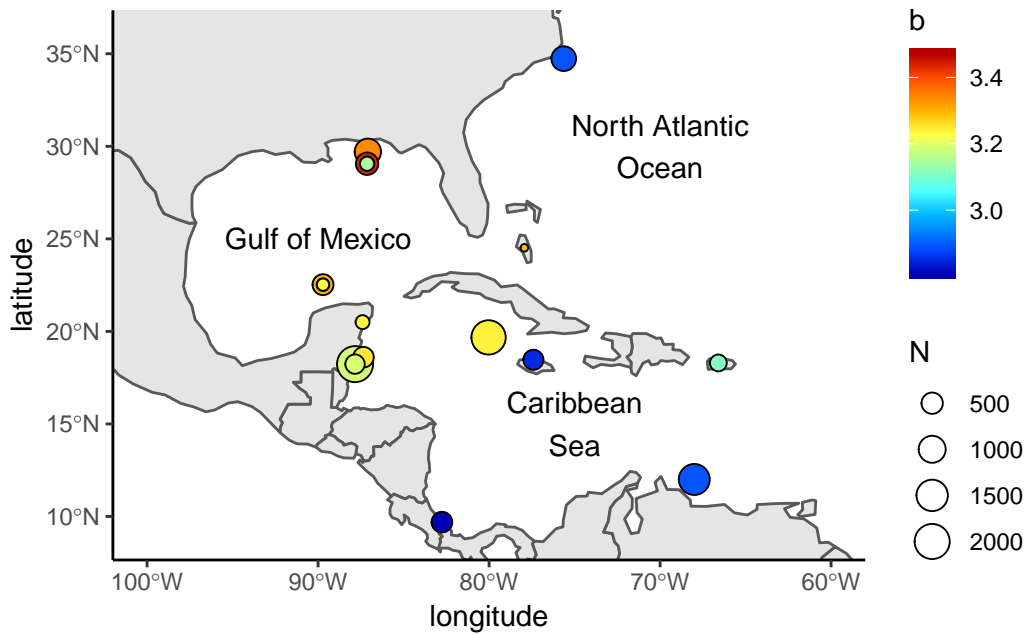
Outcomes of previous studies suggest lionfish are likely to exhibit spatial heterogeneity in the length-weight relationship, which we summarize in two main causes. First, culling programs are effective in reducing local adult populations largely because lionfish exhibit high levels of site fidelity and small home ranges (Fishelson, 1997; Kochzius and Blohm, 2005; Jud and Layman, 2012; Côté et al, 2014). It is known that fish with sedentary behavior are likely to exhibit high levels of spatial variation in important life history characteristics such as growth or natural mortality rates (Gunderson et al, 2008; Hutchinson, 2008; Wilson et al, 2012; Guan et al, 2013). Second, genetic analysis of lionfish suggests biological differences due to the existence of two genetically distinct invasive subpopulations between the northwest Atlantic and the Caribbean (Betancur-R et al, 2011). Site-specific parameters are necessary to accurately estimate biomass when allometric relationships are spatially variable, and this variability is increasingly important when estimating the potential effectiveness of lionfish culling programs (Barbour et al, 2011; Morris et al, 2011; Côté et al, 2014; Johnston and Purkis, 2015). However, the region-wide differences in allometric growth parameters has remained unexplored for lionfish, despite the large number of site-specific studies reporting the length-weight relationship.

Here, we compare previously published length-weight relationships for lionfish populations in North Carolina, Northern and Southern Gulf of Mexico, the Southern Mexican Caribbean, Bahamas, Little Cayman, Jamaica, Bonaire, Puerto Rico, and Costa Rica (Barbour et al, 2011; Darling et al, 2011; de Leon et al, 2013; Fogg et al, 2013; Dahl and Patterson, 2014; Edwards et al, 2014; Toledo-Hernández, 2014; Sandel et al, 2015; Aguilar-Perera and Quijano-Puerto, 2016; Sabido-Itza et al, 2016; Sabido-Itzá et al, 2016; Chin et al, 2016). We also collected lionfish length and weight data in the central Mexican Caribbean and report the first allometric growth equation for this region. The objective of this paper is to describe the spatial pattern of length-weight relationships of lionfish across the Caribbean and Western Atlantic and to discuss implications of these spatial differences.

## 2 Materials and Methods

We reviewed 12 published studies and obtained 17 length-weight relationships for the North Atlantic ( $n = 1$ ), Gulf of Mexico ( $n = 7$ ), and Caribbean ( $n = 9$ , Table 2, Fig 3). We collected information on sampling methods, sex differentiation, location, and depth ranges 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 obtained at depths between 0.5 m and 57 m. Three 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 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 (Barbour et al, 2011; Fogg et al, 2013; Edwards et al, 2014; Toledo-Hernández, 2014; Sandel et al, 2015; Sabido-Itza et al, 2016; Sabido-Itzá et al, 2016), and two studies did not specify how organisms were sampled (Darling et al, 2011; de Leon et al, 2013). Fogg et al (2013) use spineless weight in their calculations, so their parameters likely underestimated total weight. Since no spineless to total weight conversions were available, these parameters were taken as reported.



**Fig. 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.

We also collected data from 10 sampling sites along the central Mexican Caribbean coast in 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 eliminating gear selectivity. Organisms were euthanized via pithing and Total Length (TL; mm) and Total Weight (TW; g) were recorded.

The weight-at-length relationship for lionfish in the central Mexican Caribbean was calculated with the allometric growth function:

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

Where  $a$  is the ponderal index and  $b$  is the scaling exponent or allometric parameter. Transforming this equation via base-10 logarithms we obtain:

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

This can be simplified and re-written as:

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

Where  $Y = \log_{10}(TW)$ ,  $X = \log_{10}(TL)$ , and  $c = \log_{10}(a)$ . The coefficients ( $c$  and  $b$ ) were estimated with an Ordinary Least Squares Regression and heteroskedastic-robust standard error correction (Zeileis, 2004). When the  $b = 3$ , 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.

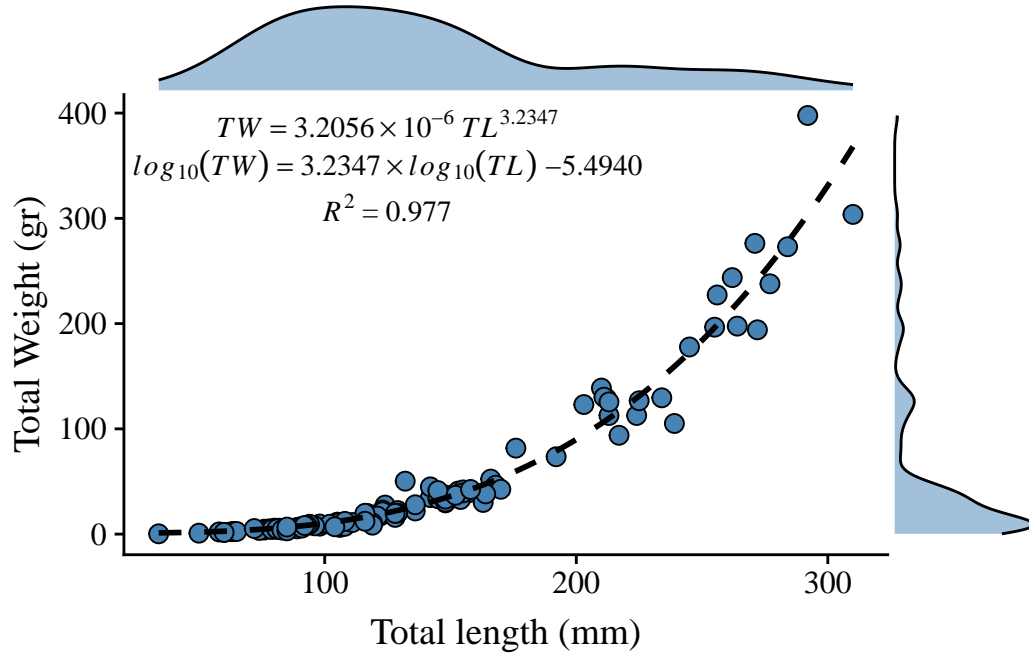
Some of the reviewed studies inconsistently defined  $a$  as either the ponderal index from Eq. 1 or the y-intercept ( $c$ ) from Eq. 3. Other studies incorrectly reported parameters as mm-to-g conversions when they were in fact cm-to-g conversions. We standardized each study by converting coefficients and report all parameters as TL(mm) to TW (gr) conversions. Locations where allometric studies have been performed are shown in Figure 1 and summarized in Table 2.

We obtained a total of 18 parameter pairs by combining length-weight parameters extracted from the literature and the additional pair calculated here. 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 ( $n = 109$ ) 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 across the different parameter pairs were tested with a one-way analysis of variance (ANOVA) and Tukey's test was used for *post-hoc* tests. All analyses were performed in R version 3.5.0 (R Core Team, 2018). Raw data and code used in this work are available on github.

### 3 Results

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



**Fig. 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** Coefficients of the linear model fit to Eq 3. Numbers in parentheses represent heteroskedastic-robust standard errors.

	$\log_{10}(TW)$
c	-5.494 (0.083)***
b	3.235 (0.039)***
F Statistic	6928.67*** (df = 1; 107)
Observations	109
Adjusted R <sup>2</sup>	0.976
Residual Std. Error	0.096 (df = 107)

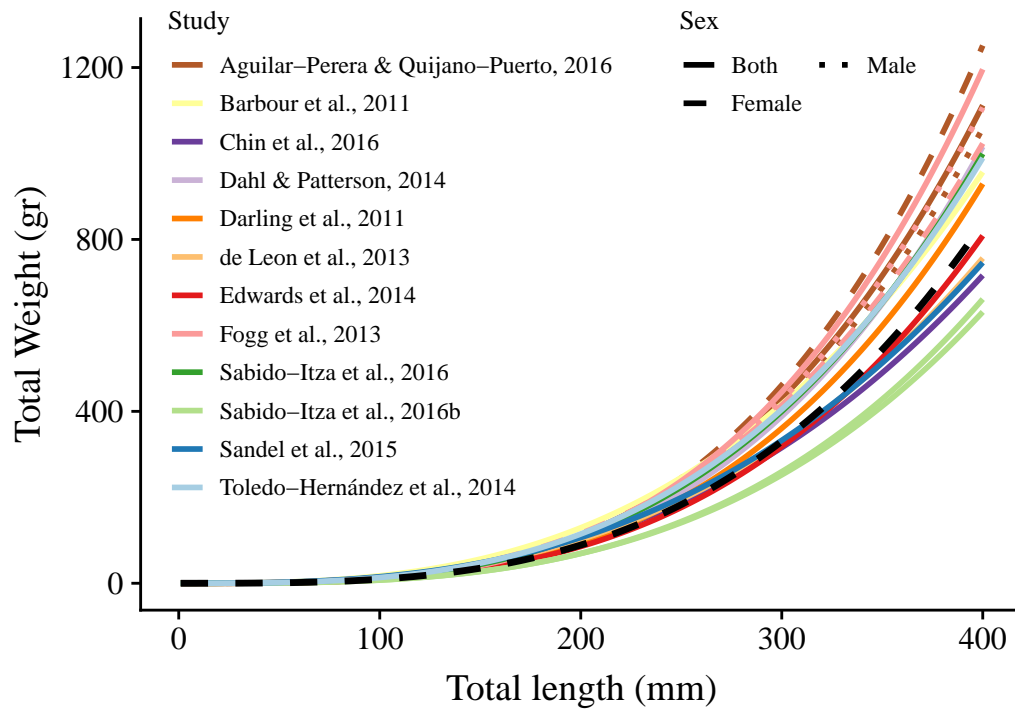
Note: \*p<0.1; \*\*p<0.05; \*\*\*p<0.01

**Table 2** 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 Fit column contains the reported  $R^2$  of the model fit.

Region	Sex	n	a	b	c	Fit	Reference
Caribbean	B	458	3.6	2.81	-4.44	-	Sandel et al., 2015
Caribbean	B	419	2.8	2.85	-4.56	0.8715	Chin et al., 2016
Caribbean	B	1450	2.3	2.89	-4.64	0.96	de Leon et al., 2013
Caribbean	B	1887	0.3	3.24	-5.52	0.97	Edwards et al., 2014
Caribbean	B	-	0.25	3.29	-5.60	-	Darling et al., 2011
Caribbean	B	2143	0.52	3.18	-5.28	0.9907	Sabido-Itza et al., 2016
Caribbean	B	227	0.8	3.11	-5.10	0.958	Toledo-Hernández et al., 2014
Caribbean	B	449	0.23	3.25	-5.64	0.97	Sabido-Itza et al., 2016b
Caribbean	B	368	0.32	3.19	-5.50	0.98	Sabido-Itza et al., 2016b
Caribbean	B	109	0.32	3.23	-5.49	0.9766	This study
GoM	B	934	0.21	3.34	-5.68	0.98	Dahl & Patterson, 2014
GoM	B	472	0.29	3.30	-5.54	0.95	Aguilar-Perera & Quijano-Puerto, 2016
GoM	F	67	0.12	3.47	-5.93	0.95	Aguilar-Perera & Quijano-Puerto, 2016
GoM	M	59	0.42	3.23	-5.38	0.95	Aguilar-Perera & Quijano-Puerto, 2016
GoM	B	582	0.14	3.43	-5.86	0.99	Fogg et al., 2013
GoM	M	119	0.27	3.31	-5.57	0.97	Fogg et al., 2013
GoM	F	115	0.68	3.14	-5.17	0.94	Fogg et al., 2013
North Atlantic	B	774	2.9	2.89	-4.54	-	Barbour et al., 2011

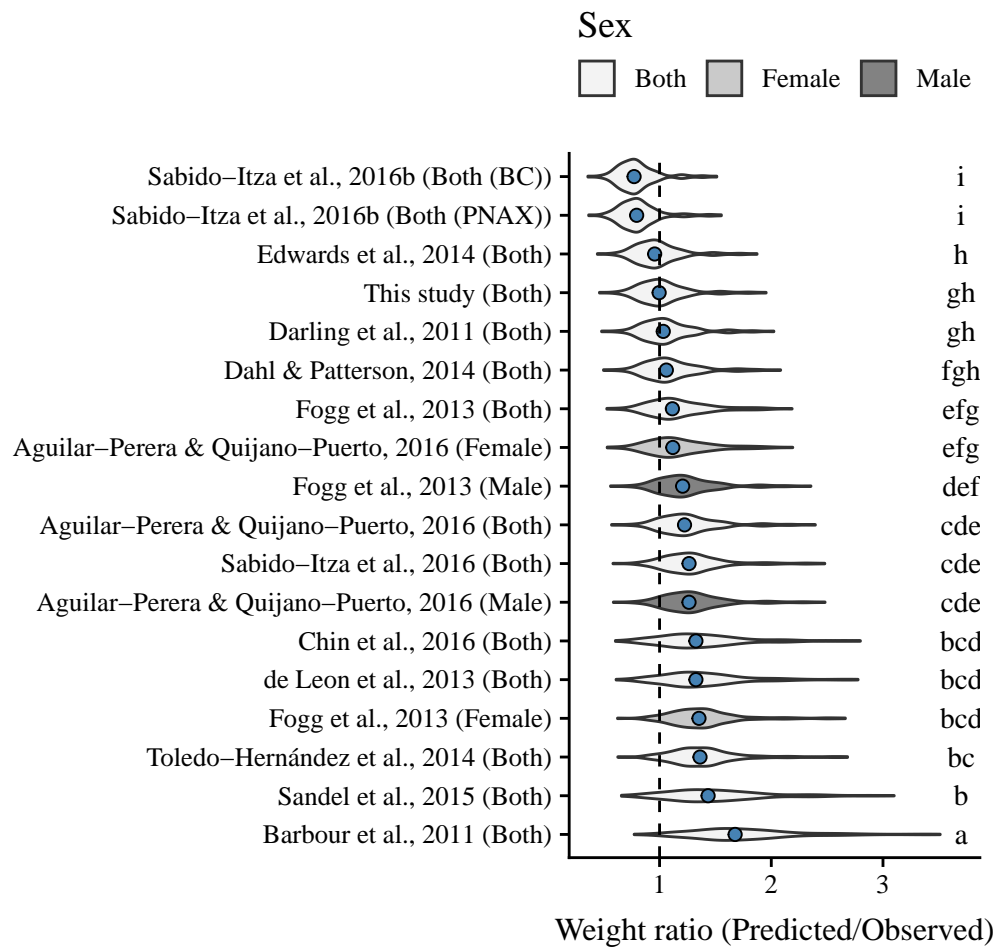
There were significant differences in our predicted weights for the central Mexican Caribbean when using the different pairs of parameters ( $F(df = 17; 1944) = 61.55; p < 0.001$ ). The lowest weight estimates resulted from using the allometric parameters from Banco Chinchorro in the Caribbean, with mean  $\pm$  SD of  $40.37 \pm 58.74$  gr (Sabido-Itzá et al, 2016), and the highest weight estimates came from the Northern Atlantic with  $73.76 \pm 96.11$  gr (Barbour et al, 2011). To put this in context, true observed weights were  $52.56 \pm 76.58$  gr. These correspond to predicted-to-observed weights ratios of  $0.80 \pm 0.19$  and  $1.76 \pm 0.50$  (mean  $\pm$  SD), respectively.

The calculated ratio of predicted-to-observed weight ranged from 0.36 to 3.51, indicating that *ex situ* parameters can result in major under- and over-estimations. 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 (Tukeys HSD  $p > 0.05$ ). Weight estimates using parameters from the Gulf of Mexico and North-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  $1.24 \pm 0.309$ ,  $1.76 \pm 0.496$ , and  $1.17 \pm 0.398$ , respectively. Predicted-to-observed weight ratios are presented in Figure 4. Spineless weight parameters from Fogg et al (2013) still produced predicted-to-observed weight ratios  $> 1$ .



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





**Fig. 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.

## 4 Discussion

We detected substantial differences in weight-at-length between organisms from the Caribbean, Gulf of Mexico, and North-Western Atlantic. Groupings of predicted-to-observed weight ratios aligned with the spatial distribution of the examined studies, suggesting that these differences are mediated by space. These regional allometric differences mirror similar patterns in age-at-length 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 age-at-length differences may be climate-driven. Differences in weight-at-length could also reflect differential energy input or usage, or a combination of both. Future research is needed to determine which processes are at work here.

Differences in length-weight relationships have traditionally been highlighted as potential pitfalls to fishery management. For example, Wilson et al (2012) show that small-scale variations in length-at-age and fishing mortality in other Scorpaeniformes translate to differential landings, effort, and catch per unit effort in the live fish fishery of California, and that these differences must be taken into account in management plans. The lionfish case poses the opposite scenario, where the manager desires to eradicate species. To accurately gauge both the effectiveness of lionfish removal efforts and the resources needed to successfully manage an invasion, we must acknowledge and understand regional biological differences in important variables such as allometric growth parameters.

The results presented here have major implications for management. For example, Edwards et al (2014) simulated a lionfish culling program under two scenarios, one using length-at-age and length-to-weight parameters from North Carolina and one using parameters from Little Cayman. Their results show that using different parameters caused up to a four-year difference in the time required for the simulated lionfish population to recover to 90% of its initial biomass after removals ceased. Here, we show that using one set of length-weight parameters versus another for a given length can result in more than a threefold under- or overestimation of total weight. These spatially-driven 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 use reasonable sets of different parameters that provide upper and lower bounds in their results.

## 5 Acknowledgements

The authors 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.

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

## References

- Aguilar-Perera A, 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, DOI 10.4067/S0718-19572016000200025, URL [http://www.scielo.cl/scielo.php?script=sci\\_arttext&pid=S0718-19572016000200025&lng=en&nrm=iso&tlng=en](http://www.scielo.cl/scielo.php?script=sci_arttext&pid=S0718-19572016000200025&lng=en&nrm=iso&tlng=en)
- Albins M, Hixon M (2008) Invasive indo-pacific lionfish *Pterois volitans* reduce recruitment of atlantic coral-reef fishes. *Mar Ecol Prog Ser* 367:233–238, DOI 10.3354/meps07620, URL <http://www.int-res.com/abstracts/meps/v367/p233-238/>
- Andradi-Brown DA, Grey R, Hendrix A, Hitchner D, Hunt CL, Gress E, Madej K, Parry RL, Régnier-McKellar C, Jones OP, Arteaga M, Izaguirre AP, Rogers AD, Exton DA (2017) Depth-dependent effects of culling-do mesophotic lionfish populations undermine current management? *R Soc Open Sci* 4(5):170027, DOI 10.1098/rsos.170027, URL <http://dx.doi.org/10.1098/rsos.170027>
- Arias-Gonzalez JE, Gonzalez-Gandara C, Luis Cabrera J, 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, DOI 10.1016/j.envres.2011.07.008, URL <http://dx.doi.org/10.1016/j.envres.2011.07.008>
- Barbour A, Montgomery M, Adamson A, Diaz-Ferguson E, Silliman B (2010) Mangrove use by the invasive lionfish *Pterois volitans*. *Mar Ecol Prog Ser* 401:291–294, DOI 10.3354/meps08373, URL <http://www.int-res.com/abstracts/meps/v401/p291-294/>
- Barbour AB, Allen MS, Frazer TK, Sherman KD (2011) Evaluating the potential efficacy of invasive lionfish (*Pterois volitans*) removals. *PLoS ONE* 6(5):e19666, DOI 10.1371/journal.pone.0019666, URL <http://dx.doi.org/10.1371/journal.pone.0019666>
- Betancur-R R, Hines A, Acero A, Orti G, Wilbur A, Freshwater D (2011) Reconstructing the lionfish invasion: insights into greater caribbean biogeography. *J Biogeography* 38:1281–1293, DOI 10.1111/j.1365-2699.2011.02496.x, URL <http://dx.doi.org/10.1111/j.1365-2699.2011.02496.x>

- Chin DA, Aiken KA, Buddo D (2016) Lionfish population density in discovery bay, jamaica. *International Journal of Scientific & Engineering Research* 7(12):1327 – 1331
- Claydon J, Calosso M, Traiger S (2012) Progression of invasive lionfish in sea-grass, mangrove and reef habitats. *Mar Ecol Prog Ser* 448:119–129, DOI 10.3354/meps09534, URL <http://www.int-res.com/abstracts/meps/v448/p119-129/>
- Côté IM, Akins L, Underwood E, Curtis-Quick J, Green SJ (2014) Setting the record straight on invasive lionfish control: Culling works. *PeerJ* DOI 10.7287/peerj.preprints.398v1, URL <https://peerj.com/preprints/398v1>
- Dahl KA, Patterson WF (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, DOI 10.1371/journal.pone.0105852, URL <http://dx.doi.org/10.1371/journal.pone.0105852>
- Darling ES, Green SJ, O'Leary JK, Côté IM (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, DOI 10.1007/s10530-011-0020-0, URL <http://link.springer.com/10.1007/s10530-011-0020-0>
- de Leon R, Vane K, Bertuol P, Chamberland VC, Simal F, Imms E, Vermeij MJA (2013) Effectiveness of lionfish removal efforts in the southern caribbean. *Endanger Species Res* 22(2):175–182, DOI 10.3354/esr00542, URL <http://www.int-res.com/abstracts/esr/v22/n2/p175-182/>
- Edwards MA, Frazer TK, Jacoby CA (2014) Age and growth of invasive lionfish (*pterois* spp.) in the caribbean sea, with implications for management. *BMS* 90(4):953–966, DOI 10.5343/bms.2014.1022, URL <http://openurl.ingenta.com/content/xref?genre=article&issn=0007-4977&volume=90&issue=4&spage=953>
- 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, DOI 10.1023/A:1007331304122, URL <https://doi.org/10.1023/A:1007331304122>
- Fogg AQ, Hoffmayer ER, Driggers WB, Campbell MD, Pellegrin GJ, Stein W (2013) Distribution and length frequency of invasive lionfish (*pterois* sp.) in the northern gulf of mexico. *GCR* 25, DOI 10.18785/gcr.2501.08, URL <http://aquila.usm.edu/gcr/vol25/iss1/9>
- Fogg AQ, Evans JT, Ingram JR GW, Peterson MS, Brown-Peterson NJ (2015) Comparing age and growth patterns of invasive lionfish among three ecoregions of the northern gulf of mexico. In: GCFI G, Institute CF (eds) *Proceedings of the 68 th Gulf and Caribbean Fisheries Institute, Gulf and Caribbean Fisheries Institute, Panama City*
- Green SJ, Akins JL, Maljković A, Côté IM (2012) Invasive lionfish drive atlantic coral reef fish declines. *PLoS ONE* 7(3):e32596, DOI 10.1371/journal.pone.0032596, URL <http://dx.doi.org/10.1371/journal.pone.0032596>

- Gress E, Andradi-Brown DA, Woodall L, Schofield PJ, Stanley K, Rogers AD (2017) Lionfish (pterois spp.) invade the upper-bathyal zone in the western atlantic. *PeerJ* 5:e3683, DOI 10.7717/peerj.3683, URL <http://dx.doi.org/10.7717/peerj.3683>
- Guan W, Cao J, Chen Y, Cieri M (2013) Impacts of population and fishery spatial structures on fishery stock assessment. *Can J Fish Aquat Sci* 70(8):1178–1189, DOI 10.1139/cjfas-2012-0364, URL <http://www.nrcresearchpress.com/doi/10.1139/cjfas-2012-0364>
- Gunderson DR, Parma AM, Hilborn R, Cope JM, Fluharty DL, Miller ML, Vetter RD, Heppell SS, Greene HG (2008) The challenge of managing nearshore rocky reef resources. *Fisheries* 33(4):172–179, DOI 10.1577/1548-8446-33.4.172, URL <http://doi.wiley.com/10.1577/1548-8446-33.4.172>
- Hackerott S, Valdivia A, Cox CE, Silbiger NJ, Bruno JF (2017) Invasive lionfish had no measurable effect on prey fish community structure across the belizean barrier reef. *PeerJ* 5:e3270, DOI 10.7717/peerj.3270, URL <http://dx.doi.org/10.7717/peerj.3270>
- Hixon M, Green S, Albins M, Akins J, Morris J (2016) Lionfish: a major marine invasion. *Mar Ecol Prog Ser* 558:161–165, DOI 10.3354/meps11909, URL <http://www.int-res.com/abstracts/meps/v558/p161-165/>
- Hutchinson WF (2008) The dangers of ignoring stock complexity in fishery management: the case of the north sea cod. *Biol Lett* 4(6):693–695, DOI 10.1098/rsbl.2008.0443, URL <http://rsbl.royalsocietypublishing.org/cgi/doi/10.1098/rsbl.2008.0443>
- Johnson EG, Swenarton MK (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, DOI 10.7717/peerj.2730, URL <http://dx.doi.org/10.7717/peerj.2730>
- Johnston R, 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, DOI 10.3354/meps11399, URL <http://www.int-res.com/abstracts/meps/v533/p219-235/>
- Jud Z, Layman C, Lee J, Arrington D (2011) Recent invasion of a florida (usa) estuarine system by lionfish pterois volitans / p. miles. *Aquat Biol* 13(1):21–26, DOI 10.3354/ab00351, URL <http://www.int-res.com/abstracts/ab/v13/n1/p21-26/>
- Jud ZR, Layman CA (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, DOI 10.1016/j.jembe.2012.01.015, URL <http://linkinghub.elsevier.com/retrieve/pii/S0022098112000305>
- Kochzius M, 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, DOI 10.1016/j.gene.2004.12.032, URL <http://dx.doi.org/10.1016/j.gene.2004.12.032>
- Morris JA, Shertzer KW, Rice JA (2011) A stage-based matrix population model of invasive lionfish with implications for control. *Biol In-*

- vasions 13(1):7–12, DOI 10.1007/s10530-010-9786-8, URL <http://link.springer.com/10.1007/s10530-010-9786-8>
- Muñoz R, Currin C, 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, DOI 10.3354/meps09154, URL <http://www.int-res.com/abstracts/meps/v432/p181-193/>
- Peake J, Bogdanoff AK, Layman CA, Castillo B, Reale-Munroe K, Chapman J, Dahl K, Patterson III WF, Eddy C, Ellis RD, Faletti M, Higgs N, Johnston MA, Muñoz RC, Sandel V, Villaseñor-Derbez JC, Morris JA (2018) Feeding ecology of invasive lionfish (pterois volitans and pterois miles) in the temperate and tropical western atlantic. *Biol Invasions* DOI 10.1007/s10530-018-1720-5, URL <http://link.springer.com/10.1007/s10530-018-1720-5>
- Pusack TJ, Benkwitt CE, Cure K, Kindinger TL (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, DOI 10.1007/s10641-016-0499-4, URL <http://link.springer.com/10.1007/s10641-016-0499-4>
- R Core Team (2018) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, URL <https://www.R-project.org/>
- Rocha LA, Rocha CR, Baldwin CC, Weigt LA, McField M (2015) Invasive lionfish preying on critically endangered reef fish. *Coral Reefs* 34(3):803–806, DOI 10.1007/s00338-015-1293-z, URL <http://link.springer.com/10.1007/s00338-015-1293-z>
- Sabido-Itzá M, Aguilar-Perera A, 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, DOI 10.3750/{AIP2016}.46.4.01, URL [http://www.aiep.pl/volumes/2010/7\\_4/txt/txt\\_01.php](http://www.aiep.pl/volumes/2010/7_4/txt/txt_01.php)
- Sabido-Itza M, Medina-Quej A, De Jesus-Navarrete A, Gomez-Poot J, 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, DOI 10.15517/rbt.v64i1.18943, URL <http://revistas.ucr.ac.cr/index.php/rbt/article/view/18943>
- Sandel V, Martínez-Fernández D, Wangpraseurt D, 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, URL <http://www.ncbi.nlm.nih.gov/pubmed/26299126>
- 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, DOI 10.3391/ai.2009.4.3.5, URL <http://www.aquaticinvasions.net/2009/index3.html>
- Schofield P (2010) Update on geographic spread of invasive lionfishes (pterois volitans [linnaeus, 1758] and p. miles [bennett, 1828]) in the west-

- ern north atlantic ocean, caribbean sea and gulf of mexico. AI 5(Supplement 1):S117–S122, DOI 10.3391/ai.2010.5.S1.024, URL <http://www.aquaticinvasions.net/2010/supplement1.html>
- Toledo-Hernández C (2014) Population ecology and genetics of the invasive lionfish in puerto rico. AI 9(2):227–237, DOI 10.3391/ai.2014.9.2.12, URL <http://www.aquaticinvasions.net/2014/issue2.html>
- Usseglio P, Selwyn JD, Downey-Wall AM, Hogan JD (2017) Effectiveness of removals of the invasive lionfish: how many dives are needed to deplete a reef? PeerJ 5:e3043, DOI 10.7717/peerj.3043, URL <http://dx.doi.org/10.7717/peerj.3043>
- Wilson JR, Kay MC, Colgate J, Qi R, Lenihan HS (2012) Small-scale spatial variation in population dynamics and fishermen response in a coastal marine fishery. PLoS ONE 7(12):e52837, DOI 10.1371/journal.pone.0052837, URL <http://dx.doi.org/10.1371/journal.pone.0052837>
- Zeileis A (2004) Econometric computing with hc and hac covariance matrix estimators. J Stat Softw 11(10), DOI 10.18637/jss.v011.i10, URL <http://www.jstatsoft.org/v11/i10/>