Age, growth and population structure of invasive lionfish (*Pterois volitans/miles*) in northeast Florida using a length-based, age-structured population model

Eric G. Johnson[*] and Mary Katherine Swenarton[*]

Department of Biology, University of North Florida, Jacksonville, FL, United States
[*] These authors contributed equally to this work.

ABSTRACT

The effective management of invasive species requires detailed understanding of the invader's life history. This information is essential for modeling population growth and predicting rates of expansion, quantifying ecological impacts and assessing the efficacy of removal and control strategies. Indo-Pacific lionfish (*Pterois volitans/miles*) have rapidly invaded the western Atlantic, Gulf of Mexico and Caribbean Sea with documented negative impacts on native ecosystems. To better understand the life history of this species, we developed and validated a length-based, age-structured model to investigate age, growth and population structure in northeast Florida. The main findings of this study were: (1) lionfish exhibited rapid growth with seasonal variation in growth rates; (2) distinct cohorts were clearly identifiable in the length-frequency data, suggesting that lionfish are recruiting during a relatively short period in summer; and (3) the majority of lionfish were less than two years old with no lionfish older than three years of age, which may be the result of culling efforts as well as ontogenetic habitat shifts to deeper water.

INTRODUCTION

Invasive species are organisms that have been introduced to areas where they do not naturally occur, and whose establishment adversely affect native biotas and ecosystems. The establishment of an invasive species can have far reaching effects on invaded ecosystems through predation (*Race, 1982*), competition for prey or habitat (*Mills et al., 1993*; *Byers, 2009*), or by introducing novel pathogens or parasites (*Crowl et al., 2008*). Ultimately, invasives can lead to declines in the abundance and diversity or even extinction of native organisms (*Grosholz et al., 2000*) with cascading effects on ecosystem structure and function (*Vitousek, 1990*). Historically, research on biological invasions has focused heavily on terrestrial plant species (*Lowry et al., 2013*), yet invasions in marine ecosystems have received increasing attention (*Verling et al., 2005*; *Rilov & Crooks, 2009*). Recent interest in marine systems has been driven in part by high profile marine invasions (e.g., *Carcinus maenus* (*Carlton & Cohen, 2003*), *Caleurpa taxifola*

(*Meinesz, 1999*), *Didemnum vexillum* (*Lambert, 2009*)) and because the principal vectors of marine introductions (e.g., commercial shipping, aquaculture, aquarium trade) have increased dramatically in magnitude (*Minchin et al., 2009*).

A marine invasive species of particular concern is the lionfish (*Pterois volitans/miles*), now established throughout the western Atlantic, Gulf of Mexico, and Caribbean Sea (*Schofield, 2009*; *Morris Jr, 2012*; *Dahl & Patterson, 2014*). Lionfish have long venomous spines that deter predation, exhibit rapid growth (*Barbour et al., 2011*; *Edwards, Frazer & Jacoby, 2014*; *Pusack et al., 2016*), mature early and reproduce year-round (*Morris Jr, 2009*), and are capable of long distance dispersal during egg and larval stages (*Ahrenholz & Morris, 2010*; *Johnston & Purkis, 2011*). This combination of life history characteristics has allowed this species to establish and spread rapidly (see *Côté, Green & Hixon, 2013* and references therein for review); lionfish are now among the most abundant predatory fishes in many areas of the invaded range (*Whitfield et al., 2007*; *Dahl & Patterson, 2014*). Lionfish prey on an array of reef fishes (*Morris Jr & Akins, 2009*) and are capable of reducing native fish recruitment by nearly 80% (*Albins & Hixon, 2008*) and overall fish biomass by 65% (*Green et al., 2012*) with potential cascading impacts on ecosystem structure and function, including extirpations (*Albins, 2015*; *Ingeman, 2016*). Current evidence suggests that biotic resistance is not likely to present a significant barrier to the lionfish invasion (*Albins, 2013*; *Hackerott et al., 2013*; *Valdivia et al., 2014*) prompting human intervention to help control this species. Harvest is now actively promoted by management agencies throughout the western Atlantic Ocean and Caribbean Sea and has shown promise in reducing densities of this invasive species at local scales (*Frazer et al., 2012*; *Albins & Hixon, 2013*; *de León et al., 2013*; *Green et al., 2014*).

Previous empirical and modeling studies suggest high levels of sustained removal effort will be required to reduce lionfish biomass and minimize impacts (*Barbour et al., 2011*; *Morris Jr, Shertzer & Rice, 2011*; *Johnston & Purkis, 2015*). Many of these studies employ population modeling approaches that rely on key estimates of life history (e.g., growth, mortality, fecundity) with considerable uncertainty that may also vary in space or over time (*Fogg et al., 2015*). Moreover, these models, which typically evaluate the effects of varying control and harvest strategies on lionfish population density or biomass (*Barbour et al., 2011*; *Johnston & Purkis, 2015*) and the response of native fish communities (*Green et al., 2014*), can be highly sensitive to changes in life history inputs (*Morris Jr, Shertzer & Rice, 2011*). Consequently, considerable effort has been directed at estimating vital rates for lionfish in the invaded range. In particular, growth has been the focus of numerous studies (*Potts, Berrane & Morris Jr, 2010*; *Barbour et al., 2011*; *Jud & Layman, 2012*; *Benkwitt, 2013*; *Akins, Morris Jr & Green, 2014*; *Edwards, Frazer & Jacoby, 2014*; *Fogg et al., 2015*; *Rodríguez-Cortés, Aguilar-Perera & Bonilla-Gómez, 2015*; *Pusack et al., 2016*). Growth is critically important since body size strongly influences predator–prey interactions (*Rice et al., 1993*; *Sogard, 1997*; *Lorenzen, 2006*), winter mortality in temperate species (*Henderson, Holmes & Bamber, 1988*; *Hurst, 2007*) and is a key determinant of reproductive output in fishes (*Hixon, Johnson & Sogard, 2013*).

Current estimates of lionfish growth are available from the temperate Atlantic (*Potts, Berrane & Morris Jr, 2010*; *Barbour et al., 2011*), Gulf of Mexico (*Fogg et al., 2015*;

Rodríguez-Cortés, Aguilar-Perera & Bonilla-Gómez, 2015) and Caribbean Sea (*Edwards, Frazer & Jacoby, 2014*; *Pusack et al., 2016*), but are unavailable in many regions including the southern South Atlantic Bight which was one of the first areas to be colonized after introduction (*Schofield, 2009*). Because growth can vary with ecological factors (e.g., population density, food availability) and the abiotic environment (e.g., temperature), spatially-explicit estimates are often required to describe growth accurately. Previous age and growth estimates for lionfish have typically been generated from analyses of otoliths (*Potts, Berrane & Morris Jr, 2010*; *Barbour et al., 2011*; *Edwards, Frazer & Jacoby, 2014*; *Fogg et al., 2015*) or tagging (*Jud & Layman, 2012*; *Akins, Morris Jr & Green, 2014*; *Pusack et al., 2016*); both being effective but time consuming and effort intensive methodologies. Estimating growth from length-frequency data has a long history in fisheries management and can be an effective alternative approach, particularly when age data are sparse or not available (*Pauly & David, 1981*; *Pauly & Morgan, 1987*; *Fournier et al., 1990*); and has recently been applied to lionfish (*Rodríguez-Cortés, Aguilar-Perera & Bonilla-Gómez, 2015*). Herein, we describe a flexible length-based, age-structured model to provide insight into the life history of lionfish in northeast Florida. The purpose of this study was to (1) construct a statistical length-based model for estimating age, growth and population structure of lionfish, (2) evaluate the performance of our model using validation from otolith analysis and external length-frequency data, and (3) provide estimates of vital rates and population structure of lionfish in northeast Florida where such information is not currently available.

METHODS

Ethics statement

All lionfish used in this study were handled in strict accordance with a UNF IACUC protocol (IACUC#13-004) and tissues of opportunity waivers approved by the University of North Florida. UNF IACUC defines tissues of opportunity as samples collected: (1) during the course of another project with an approved IACUC protocol from another institution; (2) during normal veterinary care by appropriately permitted facilities; or (3) from free-ranging animals by appropriately permitted facilities. Lionfish removals are encouraged by the State of Florida and sample collection locations did not require any specific permissions. No endangered or protected species were harmed during the course of this study.

Sample collections

Lionfish were collected from locations offshore of northeast Florida by trained spearfishermen (Fig. 1). Sampling occurred primarily during several large-scale public removal events in 2013, 2014 and 2015 (April and August) and during opportunistic sampling by recreational spearfishermen in 2014 (July, September, October, November) and early 2015 (January). All lionfish were captured offshore (>15 km) on hardbottom and artificial reef habitats in approximately 20–35 m of depth. Lionfish were measured in the field for standard (SL) and total length (TL) to the nearest 1 mm. A subset of lionfish from each tournament, and all lionfish from the opportunistic samples, were transported to
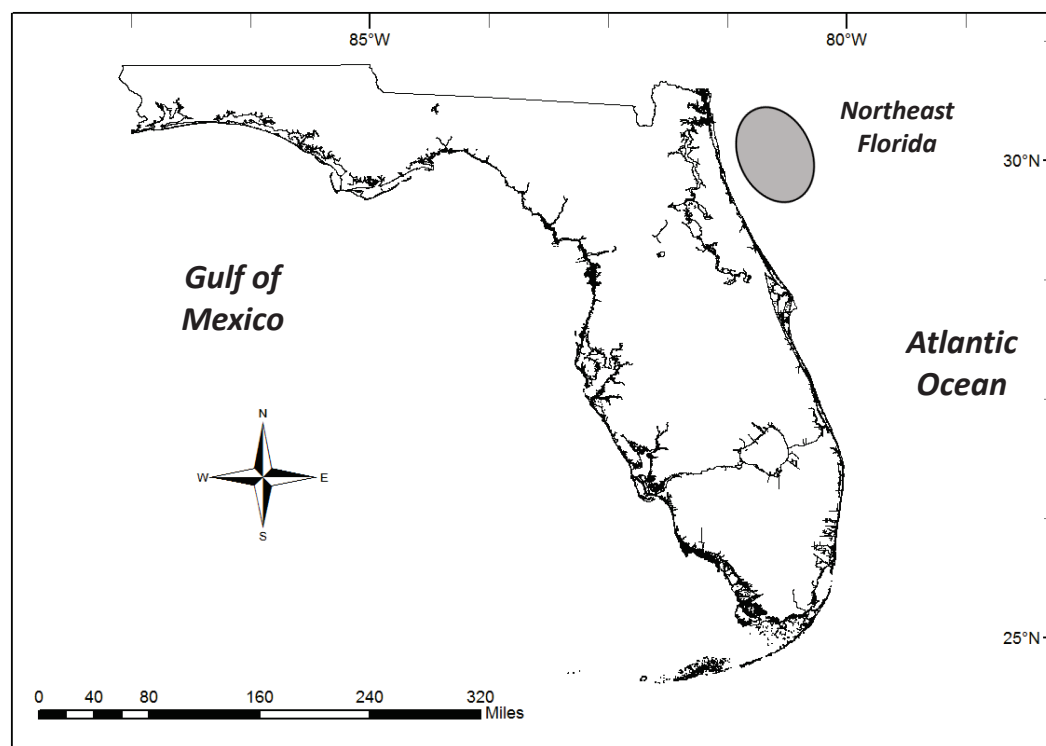
Figure 1 Lionfish collection region (shaded oval) off the coast of northeast Florida.

the University of North Florida for further processing. In the laboratory, lionfish were measured (SL and TL), weighed to the nearest 0.1 g and sexed. Some small lionfish were difficult to accurately sex and were considered immature (*Morris Jr, 2009*). A subset of lionfish ($n = 100$) had their sagittal otoliths removed, which were used to determine lionfish age directly and in model validation.

Length-based, age-structured model

Lionfish TL data from 2014 were used to construct length-frequency histograms for the observed data from 0 to 450 mm (TL) using 10 mm increments (46 length bins) for each collection month separately (Fig. 2). Length-frequency data from 2013 and 2015 were not used in model fitting because of low temporal resolution; however these data were used to assess model performance (see *Model validation*). Because sex was not determined for many lionfish, length-frequency data were pooled. Growth and population age structure were estimated by fitting a length-based, age-structured model to the observed length-frequency data.

The model uses length as a proxy for age and estimates the proportion of fish of a given size in each age class using a maximum likelihood approach by fitting a predicted length frequency distribution to the observed data (*Pauly & David, 1981*; *Johnson, 2004*). To generate the predicted length-frequency distribution, the mean size-at-age was first estimated using either the traditional (*von Bertalanffy, 1938*; *Beverton & Holt, 1957*) or seasonalized (*Somers, 1988*; *García-Berthou et al., 2012*) formulation of the von Bertalanffy
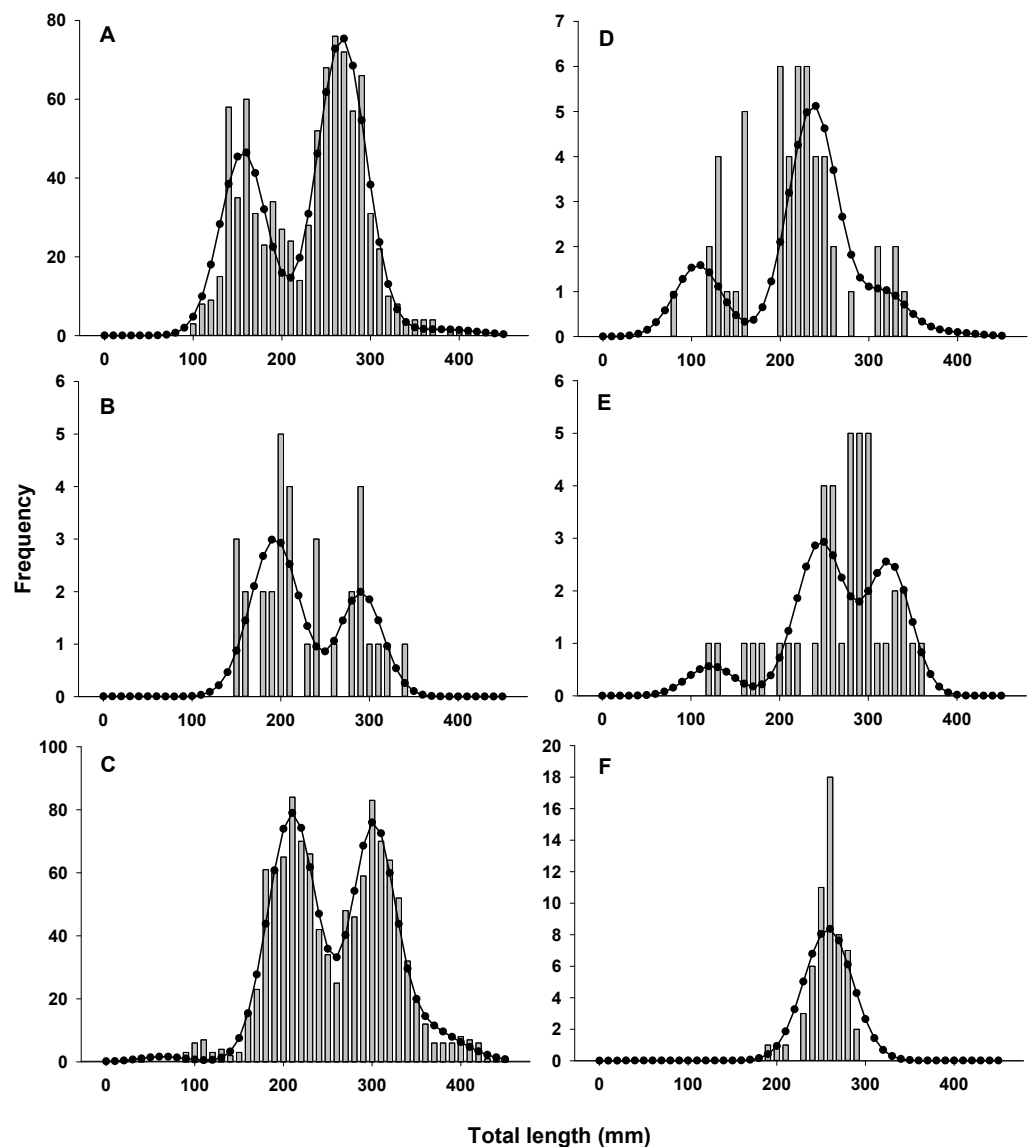
Figure 2 Observed length frequency histograms of lionfish collected from northeast Florida used in model parameterization. Length-frequency of lionfish collected in (A) April 2014, (B) July 2014, (C) August 2014, (D) October 2014, (E) November 2014, and (F) January 2015 (grey bars). The black curve in each panel symbolizes the predicted length frequency distribution of lionfish from the best fit candidate model (Model 1, see Table 1).

growth function (VBGF) which expresses fish length as a function of age. The traditional formulation of the VBGF is given below (Eq. 1):

$$L_t = L_\infty \left[1 - e^{-(K(t - t_0))} \right] \qquad (1)$$

where L_t is the length of a fish at age t, L_∞ is the asymptotic maximum length, K is the Brody growth coefficient, and t_0 is the theoretical time at which a fish was length 0. The seasonalized VBGF (Eq. 2) extends the traditional VBGF to allow the growth rate to vary seasonally, and may better reflect the growth of fishes in temperate regions which

Table 1 Summary of model diagnostics and fit for four candidate population models. Model diagnostics ($-\ln$ (L)), number of parameters (K), Akaike Information Criteria (AIC), corrected AIC (AIC_c), and model weights) for the four candidate models. Seasonal indicates whether a seasonalized (Yes) or traditional (No) von Bertalanffy growth function was fit to the data. Variance at age indicates whether variance in size-at-age was held constant across ages (Fixed) or allowed to vary among ages (Variable).

Model	Seasonal	σ^2 at age	$-\ln(L)$	K	AIC	AIC_c	ΔAIC_c	ω_i
1	Yes	Variable	648.92	32	1361.84	1370.53	0.00	1.00
2	Yes	Fixed	659.09	29	1376.18	1383.26	12.72	0.00
3	No	Variable	667.38	30	1394.76	1402.35	31.82	0.00
4	No	Fixed	672.25	27	1398.51	1404.60	34.07	0.00

experience pronounced seasonal temperature fluctuations. The seasonalized VBGF (*Somers, 1988*) is given in the series of equations below (Eqs. 2–4):

$$L_t = L_\infty\left[1 - e^{-(K(t-t_0)-S(t)+S(t_0))}\right] \tag{2}$$

$$S(t) = \left(\frac{CK}{2\pi}\right)\sin\pi(t-t_s) \tag{3}$$

$$S(t_0) = \left(\frac{CK}{2\pi}\right)\sin\pi(t_0-t_s) \tag{4}$$

where L_t, L_∞, K, t_0 are the same as previously defined (Eq. 1), t_s sets the timing of seasonal growth oscillations relative to t_0 ($t_s + 0.5 =$ winter point (t_w); the time of slowest growth), and C is the intensity of seasonal growth oscillation ($0 \le C \le 1$). A value of $C = 0$ indicates no seasonality in growth, while $C = 1$ indicates extreme seasonality and complete cessation of growth at t_w. Because the VBGF only estimates the mean size-at-age over time; variation in the size of individual fish within each age class was estimated by including variance in size-at-age (σ_a^2) as a model parameter. The proportion of lionfish in each age class during each sampling month and year was also estimated within the model ($P_{a,t}$). The expected number of individuals of age a in size class i in month t ($n_{a,i,t}$) was then calculated:

$$n_{a,i,t} = N_t \cdot P_{a,t} \cdot P\left(L_{\text{lower}} \le L_i \le L_{\text{upper}} \mid N(\overline{L}_{a,t}, \sigma_a^2)\right) \tag{5}$$

where N_t is the total number of individuals captured in month t, $P_{a,t}$ is the probability of a fish captured in month t being age a, L_{lower} and L_{upper} are the lower and upper bounds of a predicted 10 mm size bin (e.g., 230 and 240 mm), and $N(\overline{L}_{a,t}, \sigma_a)$ defines a normal probability density function with the mean length $\overline{L}_{a,t}$ of fish of age a in month t estimated from the VBGF (Eqs. 1 or 2–4), and model estimated standard deviation at age, σ_a. Because size distributions overlap across ages, the total number of expected fish of size i in month t was then calculated by summing the expected contributions to size class i from each age:

$$N_{i,t} = \sum_{a=0}^{3} n_{i,a,t}. \tag{6}$$

Table 2 Parameter estimates from a length-based, age structured population model. (Top) Model parameter estimates (von Bertalanffy growth parameters, estimated date of birth and variation in size-at-age) for lionfish from northeast Florida estimated from four candidate models (see Table 1). (Bottom) Results of sensitivity runs using the best fit model (Model 1); parameter values were fixed at $-10\%/+10\%$ of best fit estimates to examine the effect on remaining model parameters. As in the best fit model base run, L_∞ was also fixed in most sensitivity runs to ensure biologically realistic parameter values.

Candidate models		VBGF parameters				DOB	σ (size at age)			
Seasonal	σ^2 at age	L_∞	K	C	t_s	t_b	Age 0	Age 1	Age 2	Age 3
Yes	Variable	448*	0.47	0.61	0.21	0.42	26.29	27.48	24.13	40.30
Yes	Fixed	448*	0.46	0.63	0.24	0.40	26.47	26.47	26.47	26.47
No	Variable	448*	0.47	n/a	n/a	0.36	28.41	27.24	25.21	37.21
No	Fixed	448*	0.46	n/a	n/a	0.34	26.87	26.87	26.87	26.87

Sensitivity runs	L_∞	K	C	t_s	t_b	Age 0	Age 1	Age 2	Age 3
L_∞ (-10%)	403.2*	0.59	0.54	0.14	0.49	26.45	27.27	24.21	29.29
L_∞ ($+10\%$)	492.8*	0.39	0.66	0.27	0.35	26.19	27.57	24.12	48.03
K (-10%)	472.6	0.42*	0.58	0.23	0.38	26.37	27.51	24.07	45.08
K ($+10\%$)	429.5	0.52*	0.58	0.17	0.45	26.38	27.46	24.17	37.50
C (-10%)	448*	0.47	0.55*	0.20	0.42	26.30	27.48	24.13	40.33
C ($+10\%$)	448*	0.47	0.67*	0.21	0.42	26.28	27.48	24.13	40.28
t_s (-10%)	448*	0.47	0.34	0.13*	0.40	26.30	27.52	24.12	40.75
t_s ($+10\%$)	448*	0.46	0.68	0.28*	0.38	26.97	27.13	24.29	35.48
t_b (-10%)	448*	0.46	0.31	0.14	0.38*	26.42	27.41	24.08	38.33
t_b ($+10\%$)	448*	0.47	1.00	0.20	0.46*	26.26	27.57	24.22	42.39

Notes.

*Parameter value was fixed to ensure biologically realistic values (see text for details).

Four different candidate models were compared based on all combinations of two possible model structures (1) seasonal versus non-seasonal growth and (2) fixed versus variable variance in size-at-age (Table 2). Model fit was assessed by varying model parameters to minimize the log-likelihood between observed and predicted (Eq. 6) monthly length-frequency data using the SOLVER optimization routine in Microsoft Excel (MS Excel 2013, Microsoft, Inc. Seattle, WA, USA). Akaike's Information Criterion corrected for sample size (AICc) was used to select the best model from the candidate set and quantify the relative support of each model given the data (ω_i).

The key assumptions of all candidate models were as follows: (1) predicted length-at-age follows a normal distribution with mean $\overline{L}_a$ and standard deviation σ_a, (2) there are only four age classes present in the observed length-frequency samples (age 0, 1, 2, and 3; this assumption was verified by aging of sagittal otoliths from a subset of lionfish ($n = 100$) which found that only 8% of individuals were age three (despite non-random sampling that was biased to select larger individuals), and no individuals were age four or older (see *Model Validation*), and (3) lionfish recruitment is assumed to occur at a single point during the year and was estimated in the model by the parameter, t_b, the estimated birth date of an annual cohort. This simplifying assumption is surely violated to some degree (every fish is not born on the same day), yet model outputs are not significantly

affected because t_b in essence represents the average birth date with the variance in size-at -age (σ_a^2) reflecting a combination of variation in birth dates confounded with the variability in growth rates among individual fish. We further assumed that (4) because diver effort varied across time and the pattern of selectivity for lionfish of varying ages is unknown, the proportion of lionfish in each age class may not accurately reflect overall population structure. While this assumption does not directly impact our estimates of model parameters, it does limit the some of the conclusions that can be drawn from the data. As a result, no attempt is made to make quantitative inferences regarding relative changes in abundance of cohorts between years or over time (e.g., recruitment strength, natural mortality).

Model performance and sensitivity

Two types of analyses were conducted to examine the robustness of our model and associated parameter estimates: (1) a randomized grid search designed to evaluate the ability of the model to converge on a consistent solution from randomly generated sets of initial parameter values (±25% best fit values) and (2) the sensitivity of model outputs was assessed by fixing individual model parameters at ±10% of their best fit values, allowing the model to converge on a new constrained solution, and examining the resulting effect on model fit and parameter estimates.

Model validation

Direct aging of a 100 fish subsample using sagittal otolith analysis was performed to verify ages and provide external validation for model outputs. Otoliths were extracted by first making a transverse cut into the skull, and removing the otoliths from under the brain cavity. Otoliths were rinsed and stored dry in envelopes until processing. Aging analysis was conducted by the Florida Fish and Wildlife Research Institute (FWRI) following the procedures outlined in *VanderKooy & Guindon-Tisdel (2003)*. Briefly, a singular otolith from each fish was embedded in casting resin and 500 μm sections were cut using a Buehler low-speed Isomet saw. Sections were then mounted on glass slides with histomount and viewed under reflected light with a dissecting microscope at 32× magnification. Marginal increment analysis was conducted and the distance from the most recent annulus to the otolith margin was scored 1–4. Two readers aged the otoliths independently. If the ages did not agree, the otolith was removed from further analysis ($n = 7$). Otolith ages were then reconciled with the model chronology using Eq. (7) which generates the actual age (A_a) at the time of the first annulus formation in years (time elapsed from the estimated date of birth (t_b) to deposition of the first annulus):

$$A_a = t_w + 1 - t_b \qquad (7)$$

where A_a is the actual fractional age in years, t_w is the winter point from the seasonal VBGF, and t_b is the model estimated birth date. This adjustment is valid assuming that annuli deposition is coincident with the winter point (t_w) when growth is slowest. To generate ages for older fish (1+) we simply added a year for each additional annulus present. To evaluate model performance, the VBGF from the best fit model was plotted

against observed size-at-age from otolith analysis to examine the level of agreement in the two independent measures of growth.

As a further evaluation of model performance, we fit the best model to three sets of observed lionfish length-frequency data from northeast Florida that were not used in parameter estimation and thus external to the model (Fig. 3). These were not used in model fitting because available samples in those years (2013, 2015) lacked sufficient temporal resolution to evaluate seasonal growth models.

RESULTS

General

The total lengths of lionfish sampled ($n = 2,137$) ranged from 41 to 448 mm in northeast Florida over the study period. Maximum length (448 mm) and minimum length (41 mm) were both recorded in August of 2014. Some fish were not sexed and some fish were immature, but of the fish that were sexed there were 466 females present and 727 males.

Model selection

There was almost complete support for model 1 as the best fit model ($\omega_i \approx 1$), which assumed seasonal variability in growth and age dependent variance in size-at-age (Table 1). Models that did not assume seasonal variability in growth or had fixed variance in size-at-age fit the data poorly and had essentially no support ($\omega_i \approx 0$). The best model fit observed length-frequency distributions well (Fig. 2), particularly in months with large sample sizes. The best model converged on biologically realistic values for life history parameters (Table 2) with the exception of L_∞ (see below). A grid search using randomly generated initial parameter values consistently converged on the same set of parameter values indicating a global minimum and robust solution were reached. Sensitivity analyses revealed that parameter estimates were generally robust with the exception of L_∞ and k which were inversely correlated (Table 2).

Growth

The best fit model allowed for seasonal growth (Tables 1 and 2; Figs. 2 and 4); traditional VBGF formulations generated poor fits to the data (Table 1). The estimated seasonalized VBGF from the model was:

$$L_t = 448 \, \text{mm} \left[1 - e^{-0.47(t-0) + \left[\frac{(0.61*0.47)}{2\pi} \sin \pi (t-0.71) \right] - \left[\frac{0.61*0.47}{2\pi} \sin \pi (0.71) \right]} \right]. \tag{8}$$

All growth parameters were freely estimated with the exception of L_∞ which was fixed at the maximum observed size of 448 mm TL, a common convention (*Sammons & Maceina, 2009*). Constraining L_∞ was required because relatively few old fish were captured and the length data contained little information about maximum size. Consequently, the model produced biologically unrealistic estimates of L_∞ in excess of 800 mm TL when this parameter was not constrained. This is a commonly reported problem since K and L_∞ are negatively correlated and adequate fits can

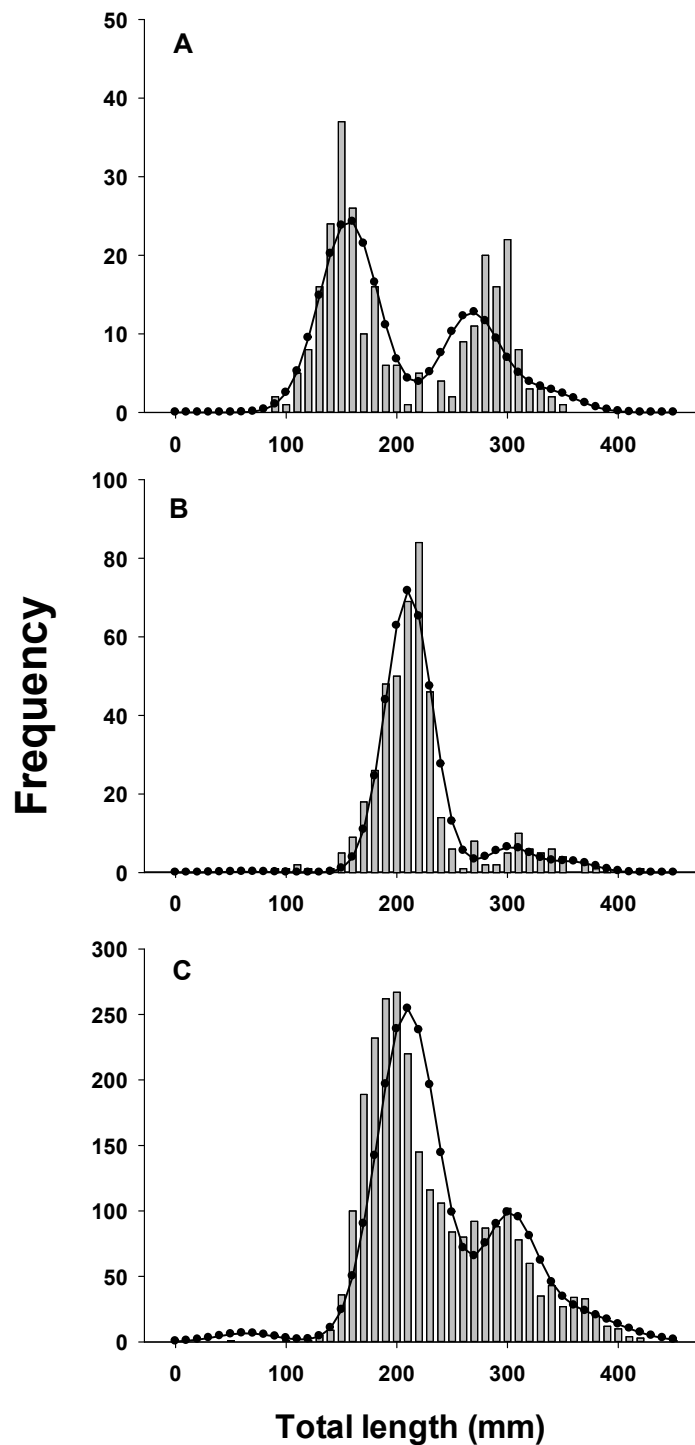**Figure 3** **Observed length frequency histograms of lionfish collected from northeast Florida used in model validation.** Length-frequency of lionfish collected in (A) April 2013, (B) April 2015, (C) August 2015 (grey bars). The black curve in each panel symbolizes the predicted length frequency distribution of lionfish from the best fit candidate model (Model 1, see Table 1). Observed data were not used in model fit.
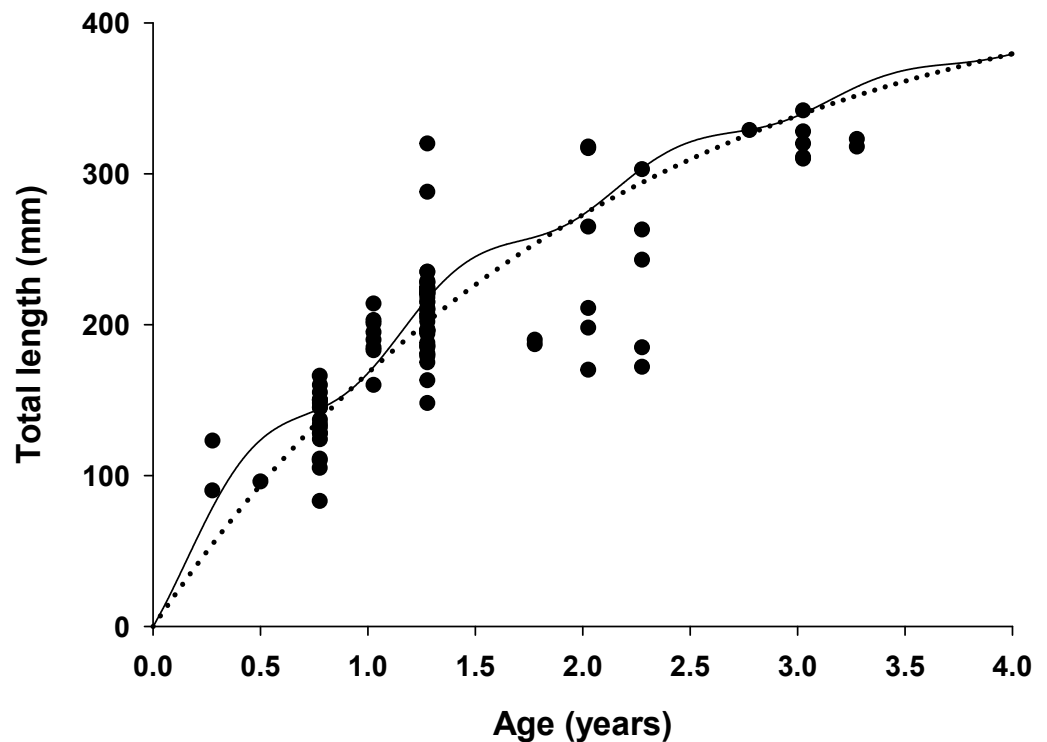
Figure 4 **Estimated growth of lionfish using two growth models.** Traditional (dotted line) and seasonalized (solid line) von Bertalanffy growth functions predicting size-at-age generated from the best fit traditional (Model 3) and seasonal (Model 1) models (see Table 1). The estimated ages of lionfish from sagittal otolith analysis are plotted as solid circles.

be achieved over a broad range of parameter values (*Shepherd, 1987*). We also effectively fixed t_0 at 0 by removing it from the model; this nuisance parameter was not required since the time of birth (t_b) was independently estimated within the model (*Gulland & Rosenberg, 1992*; *Taylor, Walters & Martell, 2005*). The estimated value for C was 0.61 indicating relatively strong seasonality in growth with slowest growth occurring on February 13th ($t_w + t_b = 0.12$). The seasonal VBGF for lionfish predicted patterns in external (not used in model fitting) observed length-frequency data collected in 2013 and 2015 well, although some evidence for interannual variation in growth is apparent (Fig. 3) and were in close agreement with size-at-age determined from otolith analysis (Fig. 4).

Recruitment

Annual lionfish recruitment was estimated to occur as a single event in early summer ($t_b = 0.41$ = June 2nd). The distinct bimodal distribution of total lengths among early ages in all years is consistent with a brief period of annual recruitment (Figs. 2 and 3) and also with results from otolith aging where 94% and 75% of otoliths from lionfish collected in April and August, respectively, had the same marginal increment. Moreover, the observed marginal increment relative to annuli deposition was consistent with a birth date in summer.

Table 3 Age structure of the lionfish population from northeast Florida. The estimated proportion of the population in each age class (P_{age}) in each sampling month from April 2014 to January 2015 estimated from the best fit model (Table 1). Mean proportions ($\bar{x}$) from monthly model estimates were calculated as a weighted average ($\sum(P_{a,m} * n)/N$, where N is the total number of fish captured in all months ($N = 2{,}137$).

Model	P_a 0	1	2	3	n
April	0.37	0.62	0.00	0.02	850
July	0.00	0.63	0.37	0.00	33
August	0.01	0.50	0.40	0.10	1,102
October	0.20	0.67	0.10	0.02	53
November	0.09	0.49	0.37	0.04	41
January	0.00	1.00	0.00	0.00	58
$\bar{x}$	0.16	0.56	0.22	0.06	
Otoliths	0.09	0.69	0.14	0.09	

Population age structure

The lionfish population in northeast Florida was relatively young. Aged otoliths ranged from age 0 to age 3 (Fig. 4) with age 0, 1, 2, 3 fish comprising 9%, 69%, 14% and 9% of the population, respectively (Table 3). Otolith analysis identified no fish greater than 3 years of age supporting the model assumption of only four age classes in the population (Figs. 2 and 4). Older lionfish are probably more common than suggested by our data since the primary goal of otolith analysis was model validation and the largest fish aged in this study was smaller (342 mm TL) than the maximum size captured (448 mm TL). However, this bias is likely small since very few lionfish were larger than 342 mm TL (6.1%) and only 0.8% were greater than 400 mm TL. Model estimated population age structure generally agreed with the results from otolith aging (Table 3, Fig. 4), but direct quantitative comparisons between otolith samples and model outputs are not possible because we selectively aged larger fish, for which age is more uncertain, for model validation. For all months, the highest proportions of fish were age 1 and age 2 (Table 3). The highest proportion of age 0 fish occurred in April just prior to the cohorts estimated first birthday ($A_a = 0.91$) on June 2nd ($t_b = 0.41$; see above) when these fish, although not fully recruited to the fishery, were large enough (TL = 151 mm) to be effectively targeted by divers (*Barbour et al., 2011*; *Edwards, Frazer & Jacoby, 2014*). Newly recruited age 0 fish were largely absent during July and August, likely because fish at this age are translucent and cryptic and too small (TL = 32–59 mm) to be captured by spearfishers. Model predicted proportions at age indicate that older fish were rare in all months with Age 3 fish comprising only 6% of the population on average (Table 3).

DISCUSSION

This study developed and validated a length-based, age-structured model to estimate age, growth and population structure of lionfish from length-frequency data in northeast Florida. The results of the model provide some key insights: (1) lionfish in this region grow rapidly, (2) lionfish exhibit seasonal growth, (3) peak recruitment of lionfish to

northeast Florida occurs during a short window in early summer, (4) the population of lionfish in northeast Florida is young with older fish virtually absent, likely reflecting the removal of older lionfish by spearfishers in combination with the movement of lionfish to deeper water with age. These findings add to our growing understanding of lionfish biology and provide the first estimates of lionfish vital rates in the region.

Lionfish grew exceptionally fast, much faster than in their native range (*Pusack et al., 2016*), mirroring the findings of many other studies (*Potts, Berrane & Morris Jr, 2010*; *Barbour et al., 2011*; *Jud & Layman, 2012*; *Albins, 2013*; *Benkwitt, 2013*; *Akins, Morris Jr & Green, 2014*; *Edwards, Frazer & Jacoby, 2014*; *Fogg et al., 2015*; *Rodríguez-Cortés, Aguilar-Perera & Bonilla-Gómez, 2015*; *Pusack et al., 2016*). Rapid growth is a trait positively correlated with invasibility and coupled with other life history information (*Morris Jr, 2009*; *Ahrenholz & Morris, 2010*; *Côté et al., 2013*) may help to explain the successful establishment and rapid invasion and of the species and is concerning for potential lionfish impacts in this region through both competition and predation. Other fish in the region that are competing on the same trophic level as lionfish (*Layman & Allgeier, 2012*) such as black sea bass (*Centropristis striatus*) and vermillion snapper (*Rhomboplites aurorubens*), take a longer time to grow to reproductive size (*Hood, Godcharles & Barco, 1994*; *Zhao, McGovern & Harris, 1997*). With both a low size at maturity and fast growth rates, lionfish have the potential to reach a large size and reproduce well before their native competitors.

Our reported values for L_∞ and K are broadly consistent with previous studies (Table 4), although some variability exists across locations which may reflect differences in collection methods and sampling intensity, elapsed time since colonization, or regional differences in environmental or ecological factors. However, comparisons of individual growth parameters in isolation across regions can be problematic because L_∞, K, and t_0 are typically strongly correlated (*Shepherd, 1987*) and actual realized growth rates (size-at-age) are a combination of all three values (*Gwinn, Allen & Rogers, 2010*; *Pardo, Cooper & Dulvy, 2013*). To compare growth across regions directly, we used reported VBGF parameters from previous studies to calculate mean size-at-age for lionfish at age 1, 2 and 3 ($\bar{L}_1$, $\bar{L}_2$, $\bar{L}_3$; Table 4). In particular, while K was variable across studies ($\bar{x} = 0.64$; Coefficient of Variation (CV) = sd/$\bar{x}$ = 52%); these differences were reduced when comparing mean size-at-age from the VBGF (CV = 14, 9, and 8% for $\bar{L}_1$, $\bar{L}_2$, $\bar{L}_3$, respectively across all studies; Table 4). Two exceptions were studies in the southern Gulf of Mexico (*Rodríguez-Cortés, Aguilar-Perera & Bonilla-Gómez, 2015*) where lionfish grew faster than other locations and in the Cayman Islands (*Edwards, Frazer & Jacoby, 2014*) where growth was much slower. Rapid growth in the first study (*Rodríguez-Cortés, Aguilar-Perera & Bonilla-Gómez, 2015*) may be driven by the warmer temperatures in the southern Gulf of Mexico compared to where our study was conducted in northeast Florida (Table 4). Growth rates from northeast Florida were most similar to those in North Carolina (*Potts, Berrane & Morris Jr, 2010*; *Barbour et al., 2011*) and the northern Gulf of Mexico (*Fogg et al., 2015*) providing additional support for temperature as an important factor underlying variation in growth in this species (Table 4). Such a relationship would not be unusual; temperature is well known to strongly influence growth rates in fishes (*Pauly, 1980*; *Gislason et al., 2010*) and the seasonal growth observed in this study clearly demonstrates

Table 4 Summary of available growth estimates for lionfish in the invaded range. Von Bertalanffy growth parameters (L_∞, k, t_0), estimated size at age at 1, 2 and 3 years ($\overline{L}_1, \overline{L}_2, \overline{L}_3$), observed maximum size (L_{max}) and age (L_a), and method of estimation for available studies of lionfish growth in the invaded and native range.

Location	Sex	L_∞	K	t_0	$\overline{L}_1$	$\overline{L}_2$	$\overline{L}_3$	L_{max}	A_{max}	Method	Temp (°C)[a]	Reference
Atlantic Ocean												
North Carolina	Combined	455	0.32	−1.22	231	293	337	464	8.0	Otoliths	22.1	*Potts, Berrane & Morris Jr (2010)*
North Carolina	Combined	425	0.47	−0.50[b]	169	265	325	464	8.0	Otoliths	22.1	*Barbour et al. (2011)*[b]
Northeast Florida	Combined	448	0.47	0.00[b]	168	273	339	448	3.3[c]	Length-based	21.4	Present study
Gulf of Mexico												
Northeast	Combined[d]	393	0.54	−0.08	174	265	319	434[e]	4.5	Otoliths	21.8	*Fogg et al. (2015)*
West	Combined[d]	389	0.54	−0.34	200	279	325	434[e]	4.0	Otoliths	21.7	*Fogg et al. (2015)*
Southeast	Combined[d]	429	0.57	−0.16	208	304	358	434[e]	4.5	Otoliths	25.1	*Fogg et al. (2015)*
Yucatan	Combined	420	0.88	0.11	228	340	387	389	n/a	Length-based	29.3	*Rodríguez-Cortés, Aguilar-Perera & Bonilla-Gómez (2015)*
Florida Keys												
Key Largo	Combined	411	0.70	0.00[b]	207	310	361	452	n/a	Length-based	26.3	*Swenarton, Johnson & Akins (2014)*
Caribbean Sea												
Little Cayman	Female	286	0.57	−1.01[b]	195	235	257	333	3.0	Otoliths	30.0	*Edwards, Frazer & Jacoby (2014)*
Little Cayman	Male	382	0.38	−1.01[b]	204	260	299	391	5.0	Otoliths	30.0	*Edwards, Frazer & Jacoby (2014)*
Little Cayman	Combined[f]	349	0.42	−1.01[b]	199	250	284	391	5.0	Otoliths	30.0	*Edwards, Frazer & Jacoby (2014)*
Caymans/ Bahamas	Combined	322	1.48	−0.07[b]	256	307	319	n/a	n/a	Tagging	29.7/28.7	*Pusack et al. (2016)*

Table 4 (*continued*)

Location	Sex	L_∞	K	t_0	$\bar{L}_1$	$\bar{L}_2$	$\bar{L}_3$	L_{max}	A_{max}	Method	Temp (°C)[a]	Reference
Indo-Pacific												
Philippines/ Marianas	Combined	225	1.62	−0.07[b]	175	215	223	n/a	n/a	Tagging	30.2/28.1	*Pusack et al. (2016)*
	$\bar{x}$ [g]	404.1	0.64	−0.33	204.0	288.6	335.4	429.7	4.9			
	σ	42.2	0.33	0.45	28.9	27.2	28.4	32.2	1.6			
	CV	10.4	52.2	138.7	14.1	9.4	8.5	7.5	33.4			

Notes.

[a] Average temperatures represent regional long-term annual averages and do not reflect conditions at study locations at the time they were conducted.

[b] Parameter value was fixed during growth curve fitting.

[c] Re-analysis of data obtained from *Potts, Berrane & Morris Jr (2010)*.

[d] Maximum age adjusted for interval between estimated birth date and first annulus.

[e] L_{max} was not reported on a site-specific basis in *Fogg et al. (2015)* and represents combined data for all regions.

[f] The estimates reflect combined data from both sexes from *Edwards, Frazer & Jacoby (2014)*.

[g] Values include combined data from the invaded range and only independent estimates (e.g., A_{max} from *Potts, Berrane & Morris Jr, 2010* and *Barbour et al., 2011* is only included once because they use the same data set).

the effect of temperature on growth for lionfish. Conversely, the slower growth of lionfish in one study in the Cayman Islands (*Edwards, Frazer & Jacoby, 2014*) cannot be explained by temperature. Slow growth in this study may be explained by other environmental or ecological factors (although *Pusack et al. (2016)* demonstrate faster growth in this region), be an artifact of curve fitting procedures or result from the recency of colonization as discussed by the authors (*Edwards, Frazer & Jacoby, 2014*). Further studies of lionfish growth in the wider Caribbean will help to more clearly identify the various mechanisms underlying regional differences in growth rates.

We constrained L_∞ to 448 mm TL, the largest fish observed in our data set ($n = 2,137$) because unconstrained fits produced biologically unrealistic values ($L_\infty > 800$ mm TL). In practice, this approach is often required when data contain few old fish and consequently little information about L_∞ (*Shepherd, 1987*). In such cases, fixing L_∞ to the maximum observed size (L_{max}) is a common convention (*Sammons & Maceina, 2009*). Our value of L_8 is similar to those predicted from empirically derived relationships between L_∞ and size at maturity (190 mm TL; *Gardner et al., 2015*) and L_{max} (448 mm TL; this study) which are 421 and 450 mm TL, respectively (*Froese & Biholan, 2000*) and is also consistent with previously reported estimates of L_∞ (Table 4) and with maximum reported lengths in the catch from the invaded range (476 mm TL; *Morris Jr, 2012*).

One key finding from our model was the strong support for seasonal growth rates ($C = 0.61$) which were correlated with seasonal fluctuations in bottom water temperatures (Table 1, Fig. 4). Temperature has a large effect on growth in fishes, resulting in seasonal cycles in growth rates in temperate areas and more uniform growth in tropical regions (*Pauly, 1980*). Our model estimated the winter point to be 0.12 which corresponds to a calendar date of February 13th. This is in strong agreement with known climatology for waters of the southeastern continental shelf of the US where bottom temperatures are typically coldest in late winter (*Atkinson et al., 1983*). Seasonal growth resulted in substantial changes in intra-annual size-at-age for young fish relative to the traditional VBGF; but not in overall annual estimates of growth ($K = 0.47$ for both seasonal and traditional VBGFs; Table 2, Fig. 4). The greatest difference was observed for age 0 fish which were estimated to be 38% larger than predicted by the traditional VBGF by late summer in their first year (111 mm vs 80 mm TL; Fig. 4). Seasonal growth could have important implications for predator–prey dynamics between lionfish and native fishes. Predation risk in marine fishes is typically inversely related to body size (*Rice et al., 1993*; *Lorenzen, 1996*) and this relationship can be particularly strong for the prey of gape-limited predators. However, seasonal growth is probably not likely to substantially impact predation on lionfish. While many of the native predators documented to consume lionfish are gape-limited, suction feeders (Nassau grouper, *Epinephelus striatus* (*Maljković, Van Leeuwen & Cove, 2008*; *Diller, Frazer & Jacoby, 2014*); tiger grouper, *Mycteroperca tigris* (*Maljković, Van Leeuwen & Cove, 2008*), and nurse sharks (*Ginglyostoma cirratum*, *Diller, Frazer & Jacoby, 2014*); direct observations of predation on lionfish are scarce and most evidence indicates that native predators are not effective at controlling lionfish populations (*Hackerott et al., 2013*; *Valdivia et al., 2014*). Conversely, seasonal growth in temperate regions, may allow gape-limited

lionfish (*Muñoz, Currin & Whitfield, 2011*; *Green et al., 2012*) access to larger prey earlier in their life history than previously thought. While this finding does not significantly alter our understanding of lionfish trophic dynamics because this effect is inherent in field observations of prey consumption, abundance and size-structure (*Albins & Hixon, 2008*; *Green et al., 2012*); seasonal growth should be considered in predictive models which use the VBGF to ensure accurate estimates of lionfish growth in temperate regions. For example, the predictions from bioenergetic (*Cerino et al., 2013*), removal efficacy (*Barbour et al., 2011*) and prey consumption models (*Green et al., 2014*) all rely on biological and ecological relationships that scale with lionfish body size (e.g., maximum prey size) or mass (e.g., consumption rates, metabolism) which are underestimated when assuming non-seasonal growth.

Although not important for tropical areas of the invaded range, seasonal growth may lower the risk of winter mortality for juvenile lionfish in temperate regions where winter water temperatures approach thermal minima for lionfish. Overwinter mortality in fishes can be substantial in coastal systems and is often size-selective with larger individuals more resistant to mortality from both thermal stress (*Lankford & Targett, 2001*) and starvation (*Henderson, Holmes & Bamber, 1988*; *Hurst, 2007*). Lionfish are a tropical species and generally intolerant of cold temperatures (*Kimball et al., 2004*). Thus, larger size at the onset of winter may at least partially mitigate the negative effects of low water temperatures in temperate regions.

Lastly, as fisheries for lionfish develop and intensify in the invaded range, resource managers may begin to apply various population and stock assessment models (i.e., catch curves, yield-per-recruit) to this species. Seasonal growth must be considered in many of these models, which generate biased outputs (e.g., natural mortality) and associated management reference points when assuming a traditional VBGF (*Sparre, 1990*; *Pauly, 1990*; *Hufnagl, Huebert & Temming, 2013*).

Distinct annual cohorts are clearly identifiable in our length-frequency data, particularly in months with large sample sizes (Figs. 2A, 2C and 3). Several non-mutually exclusive hypotheses could explain this observed pattern. One explanation is that peak spawning of lionfish in regions that contribute to recruitment in northeast Florida varies seasonally. Further, to coincide with the predicted timing of lionfish recruitment in our region, peak spawning in source populations would be need to occur in summer. Although lionfish are capable of spawning throughout the year (*Morris Jr, 2009*), most studies do provide support for increased reproductive activity in summer. *Gardner et al. (2015)* reported two peak spawning periods for lionfish in the Cayman Islands occurring in spring and late summer, and spawning activity also peaks in summer in the eastern Gulf of Mexico (*Fogg, Brown-Peterson & Peterson, 2013*), North Carolina and The Bahamas (*Morris Jr, 2009*). Source populations for larvae settling in northeast Florida are not definitively known, but evidence from population genetics (*Freshwater et al., 2009*; *Butterfield et al., 2015*), biophysical modeling (*Cowen, Paris & Srinivasan, 2006*; *Johnston & Purkis, 2011*; *Johnston & Purkis, 2015*) and chronology of invasion history (*Schofield, 2009*) suggest a combination of self-recruitment and subsidies from upstream locations such as southern Florida and northern Cuba. Unfortunately, little is

known about reproductive biology of lionfish in these regions. Alternatively, recruitment of lionfish in summer may be enhanced by seasonal physical oceanographic conditions promoting the delivery and/or retention of larvae to the region or by seasonal differences in post-settlement survival, or a combination of these processes. Although the causative factors driving this recruitment cannot be determined from this study, identifying factors that may limit lionfish larval supply or survival is inherently important to lionfish management and control efforts (*Johnston & Purkis, 2011*; *Johnston & Purkis, 2015*; *Morris Jr, Shertzer & Rice, 2011*).

Both the observed otolith ages and model predicted age structure indicate that a majority of the sampled population in northeast Florida is three years of age or younger, a recurring pattern in numerous studies with lionfish (*Barbour et al., 2011*; *Edwards, Frazer & Jacoby, 2014*; *Fogg et al., 2015*). Lionfish live for decades in aquaria (*Potts, Berrane & Morris Jr, 2010*) and older fish are reported from North Carolina (*Barbour et al., 2011*) and the more recently invaded Caribbean (*Edwards, Frazer & Jacoby, 2014*), so this finding is unexpected given that lionfish have been established in northeast Florida for almost two decades (*Schofield, 2009*). The absence of older cohorts is unlikely to be explained by high natural mortality given their large size and a lack of evidence for substantial predation on lionfish by native fishes (*Valdivia et al., 2014*). The observed age-structure in our study is likely explained by a combination of non-mutually exclusive factors: (1) local culling activities that target larger lionfish; (2) ontogenetic movement of lionfish to deeper water over time; and (3) limitations our otolith analysis which was primarily designed to validate the growth model (although this effect is likely small relative to the others). Repeated culling may reduce the number of older, larger fish over time as is commonly observed in fishery species (*Worm et al., 2009*); shifts towards smaller size of lionfish at fished relative to unfished locations have been reported in several studies (*De León et al., 2011*; *Frazer et al., 2012*). Although lionfish removal efforts in northeast Florida have intensified in recent years, lionfish are not easily accessible (>15 km offshore) and overall directed effort for this species in this region is still low. Thus, regional fishing pressure certainly contributes to the truncated population age-structure but is not likely to be the sole driver. The absence of older lionfish in our study may also be partially explained by ecological factors. For example, the observed population age structure is consistent with an ontogenetic shift of older lionfish to deeper waters likely occurring in winter (older fish (2+) are common during summer and fall but almost completely absent in collections from January and April; Table 3). Ontogenetic shifts are well documented for many marine fishes (*Eggleston, Dahlgren & Johnson, 2004*; *Eggleston, Grover & Lipcius, 1998*; *Johnson, 2004*), and have been hypothesized to explain the presence of larger lionfish at depth (*Barbour et al., 2011*; *Claydon, Calosso & Traiger, 2012*; *Swenarton, 2016*). Surveys employing other gear types (e.g., ROVs, otter trawls) report that lionfish are abundant at depth in both the Gulf of Mexico (*Nuttall et al., 2014*; *Switzer, Tremain & Keenan, 2015*, *Aguilar-Perera, Quijano-Puerto & Hernández-Landa, 2016*) and western Atlantic Ocean (*Meister et al., 2005*), although none of the studies report lionfish size distributions. The presence of deep water refuges is a major concern for lionfish management and control, since lionfish residing at depth are inaccessible to spearfishers (currently the primary

method of removal), and culling efforts in shallow depths may be replenished by larval export from lionfish at depth (*Morris Jr, 2009*; *Green et al., 2014*). If lionfish are moving to deeper waters as they grow, a major unresolved question is determining the proportion of deep water lionfish that are immigrants from shallow water relative to the proportion that initially settled at depth. Thus, further studies using traditional tagging, acoustic telemetry or biogeochemical approaches will be needed to address this question and should be prioritized.

Overall, our model generated biologically realistic parameters, provided good fits to observed length-frequency data, and was in close agreement with the results from otolith aging analysis (Fig. 4) and when fit to length-frequency data external to model (Fig. 3). The length-based approach described here may offer a more practical alternative to aging by otoliths alone which is time and labor intensive and can be particularly difficult for fishes in tropical regions which often lack defined annuli (*Edwards, Frazer & Jacoby, 2014*). Moreover, this approach requires only length data which are easily collected and widely available. Thus this approach could be applied to existing data from lionfish populations throughout the invaded range. Such spatially-explicit information on lionfish biology would aid management agencies seeking to develop effective localized removal and harvest strategies.

ACKNOWLEDGEMENTS

ADDITIONAL INFORMATION AND DECLARATIONS

Funding

Program, UNF Coastal Biology Program, UNF Department of Biology and the Guy Harvey Ocean Foundation. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests

The authors declare there are no competing interests.

Author Contributions

- Eric G. Johnson conceived and designed the experiments, performed the experiments, analyzed the data, wrote the paper, prepared figures and/or tables.
- Mary Katherine Swenarton conceived and designed the experiments, performed the experiments, analyzed the data, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.

Animal Ethics

The following information was supplied relating to ethical approvals (i.e., approving body and any reference numbers):

All lionfish used in this study were handled in strict accordance with a UNF IACUC protocol (IACUC#13-004) and tissues of opportunity waivers approved by the University of North Florida. UNF IACUC defines tissues of opportunity as samples collected: (1) during the course of another project with an approved IACUC protocol from another institution; (2) during normal veterinary care by appropriately permitted facilities; or (3) from free-ranging animals by appropriately permitted facilities. Lionfish removals are encouraged by the State of Florida and sample collection locations did not require any specific permissions. No endangered or protected species were harmed during the course of this study.

Data Deposition

The following information was supplied regarding data availability:

The raw data has been supplied as a Supplemental Information 1.

Supplemental Information

Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.2730#supplemental-information.

REFERENCES

Aguilar-Perera A, Quijano-Puerto L, Hernández-Landa RC. 2016. Lionfish invaded the mesophotic coral ecosystem of the Parque Nacional; Arrecife Alancranes, Southern Gulf of Mexico. *Marine Biodiversity* Epub ahead of print June 25 2016 DOI 10.1007/s12526-016-0536-8.

Ahrenholz DW, Morris Jr JA. 2010. Larval duration of the lionfish, *Pterois volitans* along the Bahamian Archipelago. *Environmental Biology of Fishes* **88**(**4**):305–309 DOI 10.1007/s10641-010-9647-4.

Akins JL, Morris Jr JA, Green SJ. 2014. *In situ* tagging technique for fishes provides insight into growth and movement of invasive lionfish. *Ecology and Evolution* **4**(**19**):2768–2777 DOI 10.1002/ece3.1171.

Albins MA. 2013. Effects of invasive Pacific red lionfish (*Pterois volitans*) versus a native predator on Bahamian coral-reef fish communities. *Biological Invasions* **15**:29–43 DOI 10.1007/s10530-012-0266-1.

Albins MA. 2015. Invasive Pacific lionfish *Pterois volitans* reduce abundance and species richness of native Bahamian coral-reef fishes. *Marine Ecology Progress Series* **522**:231–243 DOI 10.3354/meps11159.

Albins MA, Hixon MA. 2008. Invasive Indo-Pacific lionfish *Pterois volitans* reduce recruitment of Atlantic coral-reef fishes. *Marine Ecology Progress Series* **367**:233–238 DOI 10.3354/meps07620.

Albins MA, Hixon MA. 2013. Worst case scenario: potential long-term effects of invasive predatory lionfish (*Pterois volitans*) on Atlantic and Caribbean coral reef communities. *Environmental Biology of Fishes* **196**:1151–1157 DOI 10.1007/s10641-011-9795-1.

Atkinson LP, Lee TN, Blanton JO, Chandler WS. 1983. Climatology of the southeastern United States continental shelf waters. *Journal of Geophysical Research* **88**:4705–4718 DOI 10.1029/JC088iC08p04705.

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.

Benkwitt CE. 2013. Density-dependent growth in invasive lionfish (*Pterois volitans*). *PLoS ONE* **8**(**6**):e66995 DOI 10.1371/journal.pone.0066995.

Beverton RJH, Holt SJ. 1957. *On the dynamics of exploited fish populations. Fisheries Investment Series 2*, vol. 19. London: Ministry of Agriculture and Fisheries.

Butterfield JSS, Díaz-Ferguson E, Silliman BR, Saunders JW, Buddo D, Mignucci-Giannoni AA, Searle L, Allen AC, Hunter ME. 2015. Wide-ranging phylogenetic structure of invasive red lionfish in the western Atlantic and Greater Caribbean. *Marine Biology* **162**:733–781 DOI 10.1007/s00227-015-2618-8.

Byers JE. 2009. Competition in marine invasions. In: Rilov G, Crooks JA, eds. *Biological invasions in marine ecosystems. Ecological Studies*, vol. 204. Berlin: Springer-Verlag, 245–260.

Carlton JT, Cohen AN. 2003. Episodic global dispersal in shallow water marine organisms: the case history of the European shore crabs *Carcinus maenas* and *C. aestuarii*. *Journal of Biogeography* **30**:1809–1820 DOI 10.1111/j.1365-2699.2003.00962.x.

Cerino D, Overton AS, Rice JA, Morris Jr JA. 2013. Bioenergetics and trophic impacts of the invasive Indo-Pacific lionfish. *Transactions of the American Fisheries Society* **142**(**6**):1522–1534 DOI 10.1080/00028487.2013.811098.

Claydon JAB, Calosso MC, Traiger SB. 2012. Progression of invasive lionfish in seagrass, mangrove and reef habitats. *Marine Ecology Progress Series* **448**:119–129 DOI 10.3354/meps09534.

Côté IM, Green SJ, Hixon MA. 2013. Predatory fish invaders: insights from Indo-Pacific lionfish in the western Atlantic and Caribbean. *Biological Conservation* **164**:50–61 DOI 10.1016/j.biocon.2013.04.014.

Côté IM, Green SJ, Morris Jr JA, Akins JL, Steinke D. 2013. Diet richness of invasive Indo-Pacific lionfish revealed by DNA barcoding. *Marine Ecology Progress Series* **472**:249–256 DOI 10.3354/meps09992.

Cowen RK, Paris CB, Srinivasan A. 2006. Scaling of connectivity in marine populations. *Science* **311**:522–527 DOI 10.1126/science.1122039.

Crowl TA, Crist TO, Parmente RR, Belovsky G, Lugo AE. 2008. The spread of invasive species and infectious disease as drivers of ecosystem change. *Frontiers in Ecology and Evolution* **6(5)**:238–246 DOI 10.1890/070151.

Dahl KA, Patterson III 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.

de León R, Vane K, Bertuol P, Chamberland VC, Simal F, Imms E, Vermeij MJA. 2013. Effectiveness of lionfish removal efforts in the southern Caribbean. *Endangered Species Research* **22**:175–182 DOI 10.3354/esr00542.

De León R, Vane K, Vermeij M, Bertoul P, Simal F. 2011. Overfishing works: a comparison of the effectiveness of lionfish control efforts in Bonaire and Curacao. *Proceedings of the Gulf and Caribbean Fisheries Institute* **64**:65–66.

Diller JL, Frazer TK, Jacoby CA. 2014. Coping with the lionfish invasion: evidence that naïve, native predators can learn to help. *Journal of Experimental Marine Biology and Ecology* **455**:45–49 DOI 10.1016/j.jembe.2014.02.014.

Edwards MA, Frazer TK, Jacoby CA. 2014. Age and growth of invasive lionfish (*Pterois spp.*) in the Caribbean Sea, with implications for management. *Bulletin of Marine Science* **90(4)**:953–966 DOI 10.5343/bms.2014.1022.

Eggleston DB, Dahlgren CP, Johnson EG. 2004. Fish Density, diversity, and size-structure within multiple back reef habitats of Key West National Wildlife Refuge. *Bulletin of Marine Science* **75(2)**:175–204.

Eggleston DB, Grover JJ, Lipcius RN. 1998. Ontogenetic diet shifts in Nassau grouper: trophic linkages and predatory impact. *Bulletin of Marine Science* **63(1)**:111–126.

Fogg AQ, Brown-Peterson NJ, Peterson MS. 2013. Northern Gulf of Mexico lionfish: insights into their reproductive life history. *Proceedings of the Gulf and Caribbean Fisheries Institute* **66**:206–207 DOI 10.18785/gcr.2501.08.

Fogg AQ, Evans JT, Ingram Jr WG, Peterson MS, Brown-Peterson NJ. 2015. Comparing age and growth patterns of invasive lionfish among three ecoregions of the northern Gulf of Mexico [Abstract 88]. *Proceedings of the Gulf and Caribbean Fisheries Institute* **68**.

Fournier DA, Sibert JR, Majkowski J, Hampton J. 1990. MULTIFAN: a likelihood-based model for estimating growth parameters and age composition from multiple

length frequency data sets illustrated by using data for southern bluefin tuna (*Thunnus maccoyii*). *Canadian Journal of Fisheries and Aquatic Sciences* **47**:301–317 DOI 10.1139/f90-032.

Frazer TK, Jacoby CJ, Edwards MA, Barry SC, Manfrino CM. 2012. Coping with the lionfish invasion: can targeted removals yield beneficial effects? *Reviews in Fisheries Science* **20**:185–191 DOI 10.1080/10641262.2012.700655.

Freshwater DW, Hines A, Parham S, Wilbur A, Sabaoun M, Woodhead J, Akins L, Purdy B, Whitfield PE, Paris CB. 2009. Mitochondrial control region sequence analyses indicate dispersal from the US East Coast as the source of the invasive Indo-Pacific lionfish *Pterois volitans* in the Bahamas. *Marine Biology* **156**:1213–1221 DOI 10.1007/s00227-009-1163-8.

Froese R, Biholan C. 2000. Empirical relationships to estimate asymptotic length, length at first maturity and length at maximum yield per recruit in fishes, with a simple method to evaluate length frequency data. *Journal of Fish Biology* **56**:758–773 DOI 10.1111/j.1095-8649.2000.tb00870.x.

García-Berthou E, Carmona-Catot G, Merciai R, Ogle DH. 2012. A technical note of seasonal growth models. *Reviews in Fish Biology and Fisheries* **22**:635–640 DOI 10.1007/s11160-012-9262-x.

Gardner PG, Frazer TK, Jacoby CA, Yanong RP. 2015. Reproductive biology of invasive lionfish (*Pterois* spp.). *Frontiers in Marine Science* **2(7)**:1–10.

Gislason H, Dean N, Rice JC, Pope JC. 2010. Size, growth, temperature and the natural mortality of marine fish. *Fish and Fisheries* **11**:149–155 DOI 10.1111/j.1467-2979.2009.00350.x.

Green SJ, Akins JL, Malijkovic A, Côté IM. 2012. Invasive lionfish drive coral reef declines. *PLoS ONE* **7(3)**:e32596 DOI 10.1371/journal.pone.0032596.

Green SJ, Dulvy NK, Brooks ALM, Akins JL, Cooper AB, Miller S, Côté IM. 2014. Linking removal targets to the ecological effects of invaders: a predictive model and field test. *Ecological Applications* **24(6)**:1311–1322 DOI 10.1890/13-0979.1.

Grosholz ED, Ruiz GM, Dean CA, Shirley KA, Maron JL, Connors PG. 2000. The impacts of a nonindigenous predator in a California bay. *Ecology* **81**:1206–1224 DOI 10.1890/0012-9658(2000)081[1206:TIOANM]2.0.CO;2.

Gulland JA, Rosenberg AA. 1992. A review of length-based approaches to assessing fish stocks. In: *FAO Fisheries Technical Paper. No. 323.* Rome: FAO.

Gwinn DC, Allen MS, Rogers MW. 2010. Evaluation of procedures to reduce bias in fish growth parameter estimates resulting from size-selective sampling. *Fisheries Research* **105**:75–79.

Hackerott S, Valdivia A, Green SJ, Coté IM, Cox CE, Akins JL, Layman CA, Precht WF, Bruno JM. 2013. Native predators do not influence invasion success of Pacific lionfish on Caribbean reefs. *PLoS ONE* **8(7)**:e68259 DOI 10.1371/journal.pone.0068259.

Henderson PA, Holmes RHA, Bamber RN. 1988. Size-selective overwintering mortality in the sand smelt, *Atherina boyeri* Risso, and its role in population regulation. *Journal of Fish Biology* **33**:221–233.

Hixon MA, Johnson DW, Sogard SM. 2013. BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. *ICES Journal of Marine Science* **71(8)**:2171–2185 DOI 10.1093/icesjms/fst200.

Hood PB, Godcharles MF, Barco RS. 1994. Age, growth, reproduction, and the feeding ecology of black sea bass, *Centropristis striata*, in the Eastern Gulf of Mexico. *Bulletin of Marine Science* **54(1)**:24–37.

Hufnagl M, Huebert KB, Temming A. 2013. How does seasonal variability in growth, recruitment, and mortality affect the performance of length-based mortality and asymptotic length estimates in aquatic resources? *ICES Journal of Marine Science* **70**:329–341 DOI 10.1093/icesjms/fss163.

Hurst TP. 2007. Causes and consequences of winter mortality in fishes. *Journal of Fish Biology* **71**:315–345 DOI 10.1111/j.1095-8649.2007.01596.x.

Ingeman KE. 2016. Lionfish cause increased mortality rates and drive local extirpation of native prey. *Marine Ecology Progress Series* **558**:235–245.

Johnson EG. 2004. Population dynamics and stock assessment of the blue crab in North Carolina. D. Phil. Thesis, North Carolina State University.

Johnston MW, Purkis SJ. 2011. Spatial analysis of the invasion of lionfish in the western Atlantic and Caribbean. *Marine Pollution Bulletin* **62**:1218–1226 DOI 10.1016/j.marpolbul.2011.03.028.

Johnston MW, Purkis SJ. 2015. A coordinated and sustained international strategy is required to turn the tide on the Atlantic lionfish invasion. *Marine Ecology Progress Series* **533**:219–235 DOI 10.3354/meps11399.

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**:69–74 DOI 10.1016/j.jembe.2012.01.015.

Kimball M, Miller JM, Whitfield PE, Hare JA. 2004. Thermal tolerance and potential distribution of invasive lionfish (*Pterois volitans/miles* complex) on the east coast of the United States. *Marine Ecology Progress Series* **283**:269–278 DOI 10.3354/meps283269.

Lambert G. 2009. Adventures of a sea squirt sleuth: unraveling the identity of *Didemnum vexillum*, a global ascidian invader. *Aquatic Invasions* **4(1)**:5–28 DOI 10.3391/ai.2009.4.1.2.

Lankford TE, Targett TE. 2001. Low-temperature tolerance of age-0 Atlantic croakers; recruitment implications for US mid-Atlantic estuaries. *Transactions of the American Fisheries Society* **130**:236–249 DOI 10.1577/1548-8659(2001)130<0236:LTTOAA>2.0.CO;2.

Layman CA, Allgeier JE. 2012. Characterizing trophic ecology of generalist consumers: a case study of the invasive lionfish in The Bahamas. *Marine Ecology Progress Series* **448**:131–141 DOI 10.3354/meps09511.

Lorenzen K. 1996. The relationship between body weight and natural mortality in fish: a comparison of natural ecosystems and aquaculture. *Journal of Fish Biology* **49**:627–647 DOI 10.1111/j.1095-8649.1996.tb00060.x.

Lorenzen K. 2006. Population management in fisheries enhancement: gaining key information from release experiments through use of a size-dependent mortality model. *Fisheries Research* **80**:19–27.

Lowry E, Rollinson EJ, Laybourn AJ, Scott TE, Aiello-Lammens ME, Gray SM, Mickley J, Gurevitch J. 2013. Biological invasions: a field synopsis, systematic review, and database of the literature. *Ecology and Evolution* **3(1)**:182–196 DOI 10.1002/ece3.431.

Maljković A, Van Leeuwen TE, Cove SN. 2008. Predation on the invasive red lionfish, *Pterois volitans* (Pisces: Scorpaenidae), by the native groupers in the Bahamas. *Corals Reefs* **27**:501 DOI 10.1007/s00338-008-0372-9.

Meinesz A. 1999. *Killer algae.* Chicago: University of Chicago Press.

Meister HS, Wyanski DM, Loefer JK, Ross SW, Quattrini AM, Sulak KJ. 2005. Further evidence for the invasion and establishment of *Pterois volitans* (Teleostei: Scorpaenidae) along the Atlantic coast of the United States. *Southeastern Naturalist* **4**:193–206 DOI 10.1656/1528-7092(2005)004[0193:FEFTIA]2.0.CO;2.

Mills EL, Dermott RM, Roseman EF, Dustin D, Mellina E, Conn DB, Spidle AB. 1993. Colonization, ecology, and population structure of the "Quagga" mussel (Bivalvia: Dreissenidae) in the lower great lakes. *Canadian Journal of Fisheries and Aquatic Sciences* **50(11)**:2305–2314 DOI 10.1139/f93-255.

Minchin D, Gollasch S, Cohen AN, Hewitt CL, Olenin S. 2009. Characterizing vectors of marine invasion. In: Rilov G, Crooks JA, eds. *Biological Invasions in Marine Ecosystems.* Berlin: Springer-Verlag, 109–116.

Morris Jr JA. 2009. The biology and ecology of the invasive Indo-Pacific lionfish. D. Phil. Thesis, North Carolina State University.

Morris Jr JA. 2012. *Invasive Lionfish: a guide to Control and Management. Gulf and caribbean fisheries institute special publication series number 1.* Marathon: Gulf and Caribbean Fisheries Institute.

Morris Jr JA, Akins JL. 2009. Feeding ecology of invasive lionfish (*Pterois volitans*) in the Bahamian archipelago. *Environmental Biology of Fishes* **86**:389–398 DOI 10.1007/s10641-009-9538-8.

Morris Jr JA, Shertzer KW, Rice JA. 2011. A stage-based population matrix model of invasive lionfish with implications for control. *Biological Invasions* **13**:7–12 DOI 10.1007/s10530-010-9786-8.

Muñoz RC, Currin CA, Whitfield PE. 2011. Diet of invasive lionfish on hard bottom reefs of the Southeast USA: insights from stomach contents and stable isotopes. *Marine Ecology Progress Series* **432**:181–193 DOI 10.3354/meps09154.

Nuttall MF, Johnston MA, Eckert RJ, Embesi JA, Hickerson L, Schmahl GP. 2014. Lionfish (*Pterois volitans* [Linnaeus, 1758] and *P. miles* [Bennett, 1828]) records within mesophotic depth ranges on natural banks in the Northwestern Gulf of Mexico. *BioInvasions Records* **3(2)**:111–115.

Pardo SA, Cooper AB, Dulvy NK. 2013. Avoiding fishy growth curves. *Methods in Ecology and Evolution* **4(4)**:353–360.

Pauly D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *ICES Journal of Marine Science: Journal du Conseil* **39(20)**:175–192 DOI 10.1093/icesjms/39.2.175.

Pauly D. 1990. Length-converted catch curves and the seasonal growth of fishes. *Fishbyte* **8(3)**:24–29.

Pauly D, David N. 1981. ELEFAN I, a BASIC program for the objective extraction of growth parameters from length-frequencies data. *Meeresforsch* **28(4)**:205–211.

Pauly D, Morgan GR. 1987. Length-based methods in fisheries research. In: *ICLARM conference proceedings no. 13*. Manila: International Center for Living Aquatic Resources Management.

Potts JC, Berrane D, Morris Jr JA. 2010. Age and growth of lionfish from the Western North Atlantic. In: *Proceedings of the 63rd Gulf Caribbean Fisheries Institute*.

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. *Environmental Biology of Fishes* **99**:571–579 DOI 10.1007/s10641-016-0499-4.

Race MS. 1982. Competitive displacement and predation between introduced and native mud snails. *Oecologia* **54**:169–179.

Rice JA, Miller TJ, Rose KA, Crowder LB, Marschall EA, Trebitz AS, DeAngelis DL. 1993. Growth rate variation and larval survival: inferences from an individual-based size-dependent predation model. *Canadian Journal of Fisheries and Aquatic Sciences* **50(1)**:133–142 DOI 10.1139/f93-015.

Rilov G, Crooks JA. 2009. *Biological invasions in marine ecosystems: ecological, management, and geographic perspectives.* Berlin: Springer-Verlag.

Rodríguez-Cortés KD, Aguilar-Perera A, Bonilla-Gómez JL. 2015. Growth and mortality of Red Lionfish, *Pterois volitans* (Actinopterygii: Scorpaeniformes: Scopaenidae), in the Parque Nacional Arrecife Alacranes, southern Gulf of Mexico, as determined by size-frequency analysis. *Acta Ichthyologica et Piscatoria* **45(2)**:175–179 DOI 10.3750/AIP2014.45.2.07.

Sammons SM, Maceina MJ. 2009. Variation in growth and survival of Bluegills and Redbreast Sunfish in Georgia rivers. *North American Journal of Fisheries Management* **29**:101–108 DOI 10.1577/M07-140.1.

Schofield PJ. 2009. Geographic extent and chronology of the invasion of non-native lionfish (*Petrois volitans* [Linnaeus 1758] and *P. miles* [Bennett 1828]) in the Western North Atlantic and Caribbean Sea. *Aquatic Invasions* **4(3)**:473–479 DOI 10.3391/ai.2009.4.3.5.

Shepherd JG. 1987. A weekly parametric method for estimating growth parameters from length composition data. In: Pauly D, Morgan GR, eds. *Length-based methods in fisheries research*, vol. 13, 113–119.

Sogard SM. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bulletin of Marine Science* **60(3)**:1129–1157.

Somers IF. 1988. On a seasonally oscillating growth function. *Fishbyte* **6(1)**:8–11.

Sparre P. 1990. Can we use traditional length-based fish stock assessment when growth in seasonal? *Fishbyte* **8(3)**:29–32.

Swenarton MK. 2016. Population ecology of the invasive lionfish (*Pterois volitans/miles*) in the South Atlantic Bight. M.S. Thesis, University of North Florida.

Swenarton MK, Johnson RG, Akins JL. 2014. Regional comparisons of lionfish (*Pterois* spp.) population demographics from the East Coast of Florida. *Proceedings of the Gulf and Caribbean Fisheries Institute* **67**:215–216.

Switzer TS, Tremain DM, Keenan SF. 2015. Temporal and spatial Dynamics of the lionfish invasion in the Eastern Gulf of Mexico: perspectives from a broadscale trawl survey. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* **7**:1–8 DOI 10.1080/19425120.2014.987888.

Taylor NG, Walters CJ, Martell SJD. 2005. A new likelihood for simultaneously estimating von Bertalanffy growth parameters, gear selectivity, and natural and fishing mortality. *Canadian. Journal of Fisheries and Aquatic Sciences* **62**:215–223.

Valdivia A, Bruno JF, Cox CE, Hackerott S, Green SJ. 2014. Re-examining the relationship between invasive lionfish and native grouper in the Caribbean. *PeerJ* **2**:e348 DOI 10.7717/peerJ.348.

VanderKooy S, Guindon-Tisdel K. 2003. *A practical handbook for determining the age of Gulf of Mexico fishes.* Ocean Springs: Gulf States Marine Fisheries Commission.

Verling E, Ruiz GM, Smith LD, Galil B, Miller AW, Murphy KR. 2005. Supply-side invasion ecology: characterizing propagule pressure in coastal ecosystems. *Proceedings of the Royal Society B* **272**:1249–1257 DOI 10.1098/rspb.2005.3090.

Vitousek PM. 1990. Biological invasions and ecosystem processes—towards an integration of population biology and ecosystem studies. *Oikos* **57(1)**:7–13 DOI 10.2307/3565731.

von Bertalanffy L. 1938. A quantitative theory of organic growth. *Human Biology* **10**:181–213.

Whitfield PE, Hare JA, David AW, Harter SL, Muñoz RC, Addison CM. 2007. Abundance estimates of the Indo-Pacific lionfish *Pterois volitans/miles* complex in the western North Atlantic. *Biological Invasions* **9**:53–64 DOI 10.1007/s10530-006-9005-9.

Worm B, Hilborn R, Baum JK, Branch TA, Collie JS, Costello C, Fogarty MJ, Fulton EA, Hutchings JA, Jennings S, Jensen OP, Lotze HK, Mace PM, McClanahan TR, Minto C, Palumbi SR, Parma AM, Ricard D, Rosenberg AA, Watson R, Zeller D. 2009. Rebuilding global fisheries. *Science* **325**:578–585 DOI 10.1126/science.1173146.

Zhao B, McGovern JC, Harris PJ. 1997. Age, growth, and temporal change in size of the vermillion snapper from the South Atlantic Bight. *Transactions of the American Fisheries Society* **126(2)**:181–193 DOI 10.1577/1548-8659(1997)126<0181:AGATCI>2.3.CO;2.