Age and Growth of Invasive Lionfish: North Carolina, USA vs Bonaire, Dutch Caribbean

Edad y Crecimiento de Lionfish Invasivo: Carolina del Norte, EE.UU. Contra Bonaire, Caribeño Holandés

Âge et Croissance de Poisson-papillon Invasif: La Caroline du Nord, les USA Contre Bonaire, les Caraïbes Hollandaises

SAMANTHA D. FARQUHAR
University of North Carolina, Wilmington, North Carolina 28110 USA.
*farquharsamantha6@gmail.com

ABSTRACT

Lionfish are an invasive species that are now well established throughout the Atlantic. Originally from the Indo-Pacific, they have decimated local fish populations due to their rapid reproduction, broad environmental tolerance, voracious appetite, and lack of predators. Through the examination of otoliths paired with morphometric data, this study investigates the age and growth of lionfish (sp. *P. volitans)* from two locations: North Carolina, USA and Bonaire, Dutch Caribbean. Otoliths were extracted from lionfish samples, embedded in resin, and then sectioned so that age could be determined with microscopic analysis. These age estimates along with the corresponding total lengths were used to calculate growth rates via the von Bertalanffy growth equation. Results returned a K and L-infinity value of 0.32 cm and 42.5 cm for lionfish from NC and 0.39 cm and 38.7 cm for Bonaire, respectively. The average total length of lionfish collected in Bonaire was 12.8 cm while North Carolina lionfish was 27.6 cm. Furthermore, the age range of lionfish collected in North Carolina was 0.6–6.0 years old with an average age of 2 years old. Bonaire lionfish showed a range of 0.1 - 5.0 years old with an average age of 1 year. Statistical analyses showed a significant relationship between age and total length as well as location and total length. Overall, these findings suggest that lionfish from North Carolina survive longer, growing older and larger, than that of lionfish from Bonaire. This likely attributes to: the differing start dates of the invasion; Bergmann's Rule; and other environmental influences such as climate, resource accessibility, and removal efforts between the two localities

KEYWORDS: Lionfish; growth, North Carolina, Bonaire

INTRODUCTION

Lionfish are an invasive species native to the Indo-Pacific that have now come to thrive in the Atlantic and Caribbean. Invasive lionfish can be classified into two species, the fire devilfish (*P. miles)* and red lionfish, (*P. volitans)*. Both species look and behave very similarly; they both appear to have red and white zebra-like stripes, long pectoral fins, venomous spines, and a sedentary, fearless demeanor (Schultz 1986). However, meristic counts differ between the species. *P. miles* generally has 10 dorsal-fin rays and 6 anal-fin rays while *P. volitans* usually has 11 dorsal-fin rays and 7 anal-fin rays (Schultz 1986). For both species, the sexes are morphologically similar and can be only identified by dissection (Morris 2012). Species *P. volitans* has a wider geographic invasive range than *P. miles* (Schofield 2009). This study focuses on species *P. volitans*

The earliest sighting of lionfish in the Atlantic dates to 1985 off the southeastern coast of Florida and thought to be caused by negligent aquarists. Through mitochondria DNA analysis, this was shown to be likely source of the invasive (Freshwater et al. 2009). In 2000, multiple individuals were sighted off North Carolina. By 2004, the first assessment of lionfish densities in North Carolina revealed an average of 21 invasive lionfish ha-1 across 17 locations (Whitfield et al. 2007). By 2008, the maximum lionfish densities observed off North Carolina were approximately 450 lionfish/ha, with average densities around 150 lionfish/ha (Morris and Whitfield 2009, Morris 2012). Soon after, in 2009, lionfish were seen in Bonaire (de León et al. 2013). Presently, lionfish have been found as far south as Brazil and as far north as New York (Morris and Whitfield 2009, Freshwater et al. 2009, Green et al. 2012, Ferreira et al. 2015). This invasion is expected to continue spreading the throughout the remainder of the Caribbean and to continue southward along the coast of South America until the water temperatures fall below their thermal tolerance limit (Morris and Whitfield 2009). Additionally, invasive lionfish have been documented establishing themselves in the Red Sea and most recently undertaking a lessepsian migration into Mediterranean Sea (Barriche et al. 2016).

The population growth of lionfish, as with many invasive species, follows a predictable trajectory. This includes: a lag phase, a period of exponential growth, an invasion peak, and then equilibrium (Morris 2012). The peak is a particular concern as this is the point when the carrying capacity of an ecosystem can be exceeded causing a dramatic shift. It is not fully understood if this peak has been reached in all of the invaded area, but it is accepted that lionfish densities in the Atlantic are drastically higher than observed in their native range which are reported as a maximum of 26 individuals/ha (Kulbicki et al. 2012).

Lionfish are classified as generalist carnivores that feed on a wide variety of fishes and crustaceans (Morris and Akins 2009). Lionfish consume prey at high rates, largely during crepuscular periods (Green et al. 2012). Their hunting strategy is unique among predatory fishes within the Caribbean. Lionfish hover motionless over prey with their large pectoral fins extended and are able to approach their prey closely before making a rapid strike. They also can extrude water jets to orient the prey towards the mouth before striking (Albins and Lyons 2012). Their relentless predation wreaks havoc on communities. For example, a 79% reduction in fish recruitment on experimental patch reefs in the Bahamas was observed during a five-week observation period in the presence of a single small lionfish (Albins and Hixon 2008). Another study reported lionfish prey biomass reduced by an average of 65% over a two-year-period (Green et al. 2012). This type of predation results in the over-consumption of herbivore fishes which can lead to coral reef ecosystems shifting to algae dominated as shown by Lesser and Slattery (2011). These shifts that can effect both habitat and economy as seen during the mass extinction of the sea urchin, *Diadema antillarum* in the 1980s (Mumby et al. 2006).

Lionfish are extremely tolerant and adaptive. They have been reported from all major marine seafloor and substrate types within the invaded Atlantic, and they occupy a range of depths (Morris et al 2009). They have no known predators and a proven voracious appetite; this paired with their ability to reproduce every four days drives their success (Morris et al. 2009). Their reproduction consists of broadcast spawning. Their eggs and larvae are capable of dispersing great distances via geostrophic and wind-driven currents (Ahrenholz and Morris 2010). The socioeconomic impacts of the lionfish invasion remain an area of active research, but have the potential to be severe. Vulnerable sectors identified are fishing and tourism economies, which are critically important to many Caribbean and Atlantic nations (Morris 2012).

Through the analysis of otoliths and recorded total lengths, this study aims to:

i) Produce von Bertalanffy growth curves and
ii) Investigate the age structure and growth of *Pterois volitans* with regards to environmental influences for two very different locations: North Carolina, USA and Bonaire, Dutch Caribbean.

METHODS

Lionfish samples were obtained from both locations during the summer of 2015 (June – August) (Figure 1). In North Carolina, 21 lionfish were purchased from local fisherman after their returns from the Onslow Bay area. In Bonaire, 17 lionfish were speared and donated by locals. Bonaire samples all were from the west coast of the island. However, due to human or experimental error, only 13 otoliths from each location were able to be completely evaluated.

For all samples collected, the species was verified, total length (TL) recorded, and the sagittal otoliths were extracted. Otoliths are small bones that are found within fishes' craniums that help facilitate balance, orientation, and sound (Secor et al. 1991). As these bones grow, they form annual rings similar to like rings of a tree. These annuli can be counted to give age estimates and used in further calculations to produce growth curves (Secor et al. 1991). The otoliths were embedded in resin, mounted, and sectioned with an Isomet™ Low Speed Saw as described in Secor et al. (1991). Sections were then analyzed for annuli under a compound microscope to determine age. Further analysis for growth was conducted following protocol set forth by the FAO's (Food and Agriculture Organization of the United Nations) manual, *Introduction to Tropical Fish Stock Assessment* (Sparre and Venema 1998).

The age estimates from the otolith analyses along with the corresponding total lengths were used to calculate a growth rates via the von Bertalanffy growth equation (Table 1.):

$$L_t = L_\infty (1 - e^{(-K(t-t_0))}$$

Where L(t) is length at time, t(0) is the theoretical length at age 0, K is the growth rate and L_∞, termed 'L infinity' in fisheries science, is the asymptotic length at which growth is zero (von Bertalanffy 1934). This equation assumes that body length is a function of age. Parameters for this equation were calculated by the Ford-Walford plot. This plot graphs a fish's length at year (t+1) against the fish's length the previous year (t) producing the equation:

From this, the following parameters can be calculated from the linear regression via:

$$L_{t+1} = a + b\ L_t$$

$$K = -\ln(b)$$

$$L_\infty = a/(1 - b$$

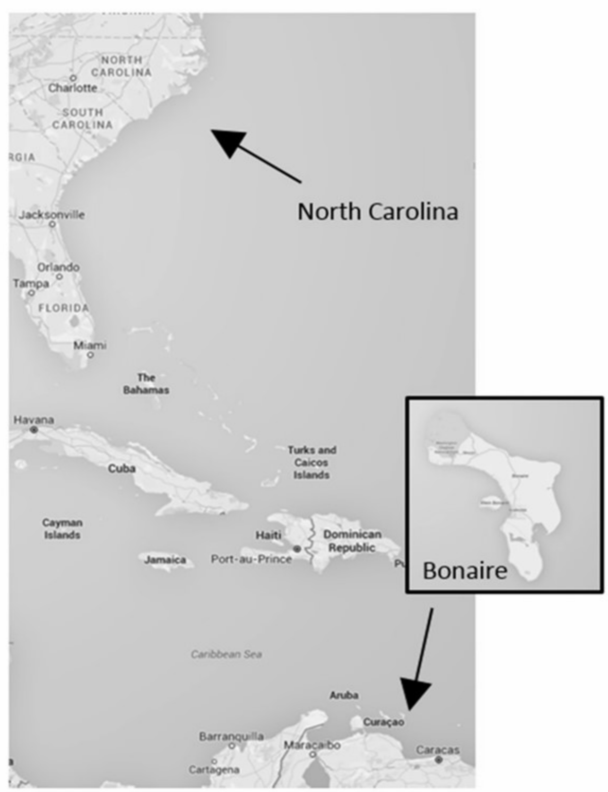

Figure 1. Map of study area.

The parameter, t(0) was calculated by creating a Von Bertalanffy plot. This plots age (t) against:

$$-\ln(1 - L(t) \quad / \quad L_\infty$$

From the linear regression of this plot, t(0) can be simply calculated by:

$$t_0 = -a/b$$

Furthermore, a one-way ANCOVA statistical analysis was ran on the data (Bonaire n = 13, North Carolina n = 13) using the program, XLSTAT, to test the significance between age, total length, and location. This analysis compares a response variable by both an independent factor and a continuous variable—the covariate. Total length was the dependent or response variable, while location acted as the independent factor and age as the independent variable of covariance. In this context, the ANCOVA adjusted the total length data for age and tested for significance in total length between both locations.

Lastly, a one-way ANOVA testing location and total length was run on compiled data from United States Geological Survey's (USGS) and North Carolina Division of Marine Fisheries' (NCDMF) records (Bonaire n = 89, North Carolina n = 56). ANOVAs test for mean differences between a continuous dependent variable and an independent factor. This data was generously made accessible by Dr. Pamela Schofield and spanned 2001 - 2007. The NCDMF data spanned a number of sporadic instances throughout 2005 - 2012 when lionfish were accidently caught during sampling programs that were being conducted (NCDMF, unpublished data). Overall, the Bonaire data ranged from 4.6 to 43 cm and the North Carolina data ranged from 5 to 43.5 cm.

RESULTS

Results return a K and L-infinity value of 0.32 and 42.5 cm for lionfish from NC and 0.39 and 38.7 cm for Bonaire, respectively (Table 2, Figure 2). The age range of lionfish collected in North Carolina was 0.6 - 6.0 years old with an average age of 2 years old (Figure 3). Bonaire collected lionfish had a range of 0.1 - 5.0 years old with an average age of 1 year (Figure 3). The mean total length of lionfish in Bonaire was 12.8 cm while North Carolina lionfish reported a mean of 27.6 cm.

The ANCOVA showed a significant relationship between age and length reporting a p-value of 0.0001. This ANCOVA reported no statistical significance between location and total length ($p < 0.26$) implying that age was not a predicting factor between length and location. This is summarized in Table 3. The second test, the ANOVA, reported a high level of significance between location and total length. ($p < .0001$) as seen in Table 4.

Table 1. Raw otolith and corresponding age data for samples from North Carolina and Bonaire

North Carolina		Bonaire	
Age (years)	Total Length (cm)	Age (years)	Total Length (cm)
0.6	15	0.1	10.2
0.6	14	0.2	10
0.8	17	0.3	13.4
1	28	0.5	16
1	30	0.7	16
2	34.5	0.8	20
2	35	1	26.7
2	36	1	20
3	31	1	32
3	32	2	34
4	35	3	25
4	36	3	27
6	40	5	43

Table 2. Comparison between parameters of von Bertalanffy growth equation for North Carolina and Bonaire.

Parameters	North Carolina	Bonaire
L_∞	42.5 cm	38.7 cm
K	0.32	0.39
T(0)	0.85	0.048

DISCUSSION

Overall, results indicated that North Carolina lionfish survive longer, growing older and statistically larger than Bonaire lionfish. However, Bonaire lionfish showed a slightly faster growth rate. These results are similar to those found in past studies from the Western Atlantic and Caribbean. One study from the Cayman Islands reported lionfish with a K growth coefficient of 0.42 and a L_∞ value of 34.9 cm (Edwards et al. 2014) while another from Onslow Bay, NC reported lionfish with a K growth coefficient of 0.32 and a L_∞ value of 45.5 cm (Potts et al. 2010). While the von Bertalanffy growth function (VBGF) is widely accepted, the assumptions and limitations should be recognized (Pardo et al. 2013). The VBGF is was not adjusted for seasonality which could produce variations in the growth coefficient. Additionally, bias in K has been shown based on the variation associated with using the calculated value of the length at age zero parameter, t (0), versus observed values (Pardo et al. 2013).

The one-way ANCOVA indicated that length and age have a significant relationship as expected. However, there was no statistical significance between location and age-adjusted total lengths (Table 3.). The ANOVA, however, did show a highly significant relationship between location and total length (Table 4.). It should be noted that these statistical analyses test for significance in different ways and the results of the ANCOVA do not necessarily contradict that of the ANOVA. While, it would have been expected to see age acting as covariate between location and total length since age and length are strongly correlated, discrepancies are likely due to sample size. The ANCOVA tested only 13 samples from each location while the ANOVA had much more (n = 89, n = 56). It is known that sample size strongly affect accuracy and consequently p-values of statistical analyses. It also should be noted that the sampling methods for the data could contain bias. The Bonaire lionfish were speared, while the majority of North Carolina

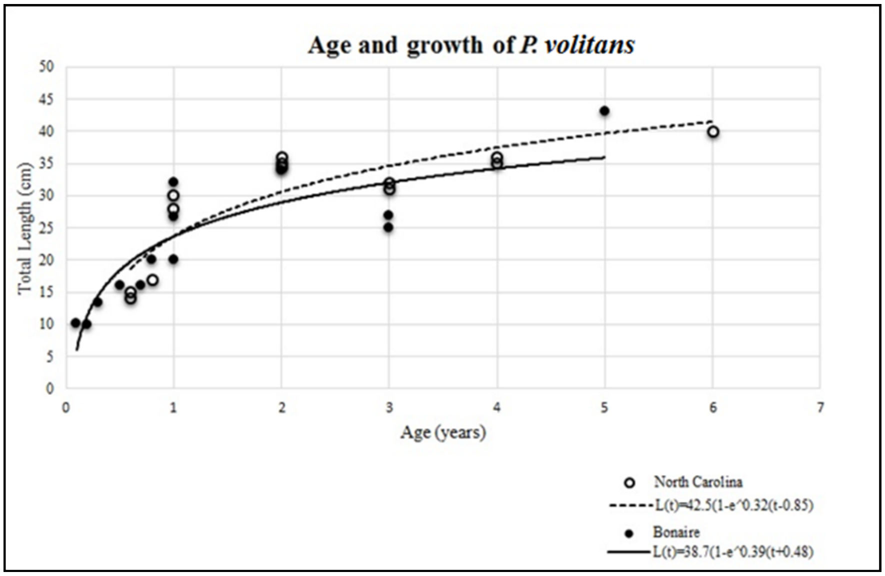

Figure 2. Von Bertalanffy growth curves calculated from lionfish samples from both North Carolina and Bonaire.

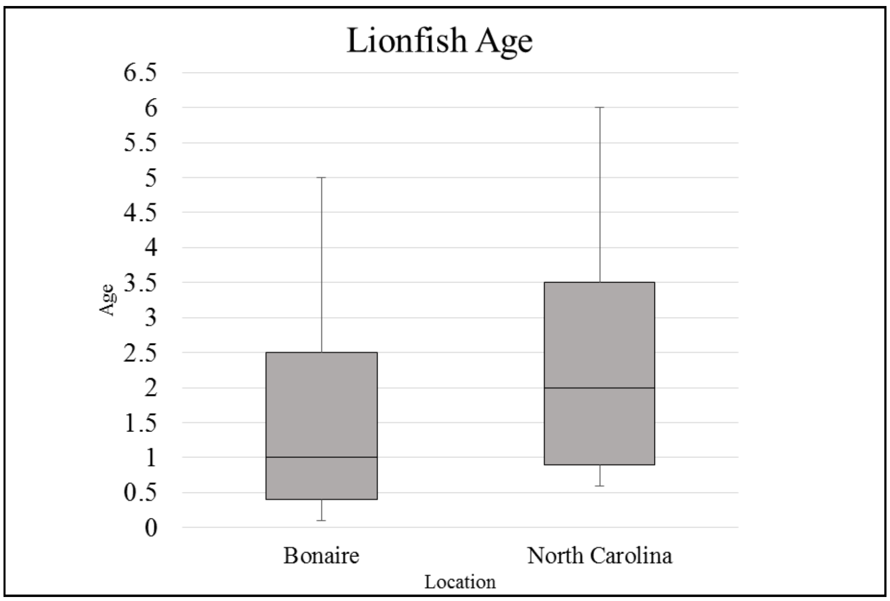

Figure 3. Age structure of lionfish samples from Bonaire and North Caroli-

Table 3. Summary of ANCOVA testing for significance between location and age-adjusted lengths (Bonaire n=13, North Carolina n=13), p-level of significance defined as $p < 0.05$

Source	Value	Standard error	t	Pr > |t|	Lower bound (95%)	Upper bound (95%)
Age	4.704	0.786	5.986	< 0.0001	3.078	6.330
Location	-2.814	2.428	-1.159	0.258	-7.836	2.209

Table 4. Summary of ANOVA with total length tested against age on compiled USGS and NCDMF lionfish data (Bonaire n = 89, North Carolina n=56), p-level of significance defined as $p < 0.05$.

Source	Value	Standard error	t	Pr > |t|	Lower bound (95%)	Upper bound (95%)
Location	-0.633	0.065	-9.785	< 0.0001	-0.761	-0.505

lionfish were from a variety of sources and using multiple types of fishing gears. These include citizen reports, state and federal monitoring programs, and other scientific surveys using spears, hook and lines, and trawls. Furthermore, out of the current study's samples, Bonaire contained many more young fish than that of North Carolina which can cause bias in statistical analyses. These discrepancies discussed could be remedied by mounting an expedition to collect larger sample sizes with a more even distribution of ages from both locations with a consistent sampling method.

The differences observed in age structure could be due to the differing start dates of the introduction (Figure 3). North Carolina has a seven year lead allowing for a higher abundance of older fish. Furthermore, the differences seen in total length between the two locations could be a prime example of Bergmann's rule. This ecogeographical rule states that populations and species of larger size are found in higher latitudes while species of smaller size are found in lower latitudes and consequently warmer regions. This rule has been shown to apply to marine fishes (Fisher et al. 2010).

Other differences and significance seen between growth, total length, and age are likely influenced by climate, resource accessibility, and removal efforts. Bonaire's year-round monthly average temperature is approximately 29°C (84°F). Bonaire is also a small island renowned for its convenience for pristine diving. Local efforts to eliminate lionfish and help protect and conserve Bonaire's reefs are strong. Government organizations (STINAPA), educational institutes (CIEE Research Station Bonaire), local dive shops, and visitors work closely together reporting and monitoring lionfish sightings to each other. These sightings are uploaded online to a 'lionfish database' that is open to the public. One can even go on to take a lionfish spearing course and after completion of the course receive a 'lionfish license', allowing them join the removal force. While these efforts target all lionfish, typically older, larger fish are the first to be removed. These types of collaborations and removal efforts have proven effective in reducing lionfish abundance (Ali 2015, Ali et al. 2013, Barbour et al. 2011, de León et al. 2013). The role of volunteers and group effort is described as essential as increased removal effort has both decreased lionfish and allowed researchers to collect a large sample size in a short time to collect further data (Ali 2015, Ali et al. 2013). Moreover, a study that compared fished and unfished areas of Bonaire over a two year period (2009 - 2011) found that lionfish biomass in fished locations on Bonaire was 2.76-fold lower than in unfished areas on the same island (de León et al. 2013).

Additionally, the culling of lionfish is not just beneficial for the environment; it has been shown to be tasty and nutritious as well. The fish is described to have a "delicate flakey white meat" and shown to have a high omega-3 content (Morris et al. 2011). Thus, it is not uncommon to see lionfish on the menu in restaurants or markets throughout the Caribbean.

As discussed, in Bonaire, lionfish are hunted often and are easily accessible to the public. However, in North Carolina this is not the case. Lionfish are found miles off the coast and in much deeper water (~40 m). Most importantly, their removal is not as popular, and there is less community involvement. There are some lionfish derbies that have proven successful in the area as well as educational outreach, but these removal efforts are not as consistent as that of Bonaire. Recent surveys from 2010 have shown that lionfish densities in Onslow Bay were as high as 200 lionfish per hectare (Whitfield et al. 2014). Thus, this number will likely increase unless a balance is found within the ecosystem or their removal and harvesting gains popularity.

This study has implications for the management, monitoring, and planning for the mitigation of the lionfish invasion. The produced von Bertalanffy growth curves (Figure 2) allow for an estimate of age based only on the total length measurement of a fish. This can save future researchers the cumbersome task of otolith extraction and analysis. Despite the fact that North Carolina has had more time to cope with the invasion than Bonaire, Bonaire's management is exceptionally better. While the accessibility of lionfish cannot be changed in North Carolina, other aspects from Bonaire's success could be adapted for North Carolina. Outreach education programs, community initiatives, and removal efforts all have the potential to be increased. Further, restaurants and grocers alike could be encouraged to offer lionfish. Overall, the same level of commitment applied to researching and remedying the lionfish invasion in the Caribbean needs to be employed in North Carolina.

LITERATURE CITED

Ahrenholz, D.W. and J.A. Morris, Jr. 2010. Larval duration of the lionfish, *Pterois volitans*, collected from the Bahamian Archipelago. *Environmental Biology of Fishes* **88**(4):305-309.

Albins, M.A. and M.A. Hixon. 2008. Invasive Indo-Pacific lionfish (*Pterois volitans*) reduce recruitment of Atlantic coral-reef fishes. *Marine Ecology Progress* Series **367**:233-238.

Albins, M.A. and P.J. Lyons. 2012. Invasive red lionfish-*Pterois volitans* blow directed jets of water at prey fish. *Marine Ecology Progress Series* **448**:1-5.

Ali, F., K. Collins, and R. Peachey. 2013. The role of volunteer divers in lionfish research and control in the Caribbean. In: MA Lang and MDJ Sayer (eds). *Proceedings of the Joint International Scientific Diving Symposium*. Curaçao, Netherland Antilles.

Ali, F. 2015. Does removal work? A one year comparison of lionfish removal efforts at Klein Bonaire. *Proceedings of the Gulf and Caribbean Fisheries Institute* **66**:210-211.

Barbour, A.B., M.S. Allen, T.K. Frazer, and K.D. Sherman. 2011. Evaluating the potential efficacy of invasive lionfish *(Pterois volitans*) removals. *PLoS ONE* **6**:e19666.

Bariche, M., M. Torres, and E. Azzurro. 2013. The presence of the invasive lionfish *Pterois miles* in the Mediterranean Sea. *Mediterranean Marine Science* **14**(2):292-294.

Edwards, M.A., T.K. Frazer, and C.A. Jacoby. 2014. Age and growth of invasive lionfish (*Pterois spp.)* in the Caribbean Sea, with implications for management. *Bulletin of Marine Science* **90**:953-966.

De León, R., K. Vane, P. Bertoul, V.C. Chamberland, F. Simal, E. Imms, and M.J.Vermejj. 2013. Effectiveness of lionfish removal efforts in the southern Caribbean. *Endangered Species Research* **22**(2):175-182.

Ferreira, C.E.L., O.J. Luiz, and S.R. Floeter. 2015. First record of invasive lionfish (*Pterois volitans*) for the Brazilian Coast. *PLoS ONE* **10** (4):e0123002.

Fisher, J.A.D., K.T. Frank, and W.C. Legett. 2010 Global variation in marine fish body size and its role in biodiversity-ecosystem functioning. *Marine Ecology Progress Series* **405**:1-13.

Freshwater, D.W., A. Hines, S. Parham, A. Wilbur, M. Sabaoun, J. Woodhead, L. Akins, B. Pury, P.E. Whitfield, and C.B. Paris. 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.

Green, S.J. and I.M. Côté. 2009. Record densities of Indo-Pacific lionfish on Bahamian coral reefs. *Coral Reefs* **28**:107.

Green, S.J., J.L. Akins, A. Maljković, and I.M. Côté. 2012. Invasive lionfish drive Atlantic coral reef fish declines. *PLoS One* **7**(3):e32596

Lesser, M.P. and M. Slattery. 2011. Phase shift to algal dominated communities at mesophotic depths associated with lionfish (*Pterois volitans*) invasion on a Bahamian coral reef. *Biological Invasions* **13**:1855–1868.

Kulbicki, M., J. Beets, P. Chapanet, K. Cure, et al. 2012. Distribution of Indo-Pacific lionfishes Pterois spp. in their native ranges: implications for the Atlantic invasion. *Marine Ecology Progress Series* **446**:189-205.

Morris, J.A., Jr. (ed.). 2012. *Invasive Lionfish: A Guide to Control and Management.* Gulf and Caribbean Fisheries Institute Special Publication Series Number 1. Marathon, Florida, USA. 113 pp.

Morris, J.A., Jr. and J.L. Akins. 2009. Feeding ecology of invasive lionfish (*Pterois volitans*) in the Bahamian archipelago. *Environmental Biology of Fishes* **86**:389-398.

Morris, J.A., Jr. and Whitfield, P.E. 2009. Biology, ecology, control and management of the invasive Indo-Pacific lionfish: An updated integrated assessment. Beaufort, NC, NOAA/National Ocean Service/ Center for Coastal Fisheries and Habitat Research, NOAA Technical Memorandum NOS NCCOS, 99 pp.

Morris, J.A., Jr., J.L. Akins, A. Barse, D. Cerino, D.W. Freshwater, S.J. Green, R.C. Muñoz, C.B. Paris, and P.E. Whitfield. 2009. Biology and ecology of the invasive lionfishes, *Pterois miles* and *Pterois volitans*. *Proceedings of the Gulf and Caribbean Fisheries Institute* **61**:409-414.

Morris, J.A., Jr., A. Thomas, A.L., Rhyne, N. Breen, L. Akins, and B. Nash. 2011. Nutritional properties of the invasive lionfish: a delicious and nutritious approach for controlling the invasion. *AACL Bioflux* **4**:21–26.

Mumby, P.J., J.D. Hedley, K. Zychaluk, A.R. Harborne, and P.G. Blackwell. 2006. Revisiting the catastrophic die-off of the urchin *Diadema antillarum* on Caribbean coral reefs: Fresh insights on resilience from a simulation model. *Ecological Modeling* **196**:131–148.

Pardo, S.A., A.B. Cooper, and N.K. Dulvy. 2013. Avoiding fishy growth curves. *Methods in Ecology and Evolution* **4**: 353–360.

Potts, J.C., D. Berrane, and J.A. Morris, Jr. 2010. Age and growth of lionfish from the western north Atlantic. *Proceedings of the Gulf and Caribbean Fisheries Institute* **63**:314.

Schofield, P.J. 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. *Aquatic Invasions* **4**:473-479.

Schultz, E.T. 1986. *Pterois volitans* and *Pterois miles*: two valid species. *Copeia* **1986**:686-690.

Secor, D.H., J.M. Dean, and E.H. Laban. 1991. *Manual for Otolith Removal and Preparation for Microstructural Examination.* University of South Carolina, Baruch Institute for Marine Biology and Coastal Research S.C. Technical Report 91-1.

Sparre, P. and S.C. Venema. 1998. Introduction to tropical fish stock assessment, Part 1: manual. FAO Fisheries Technical Papers 306/1, Rev. 2.

Thresher, R.E., J.A. Koslow, A.K. Morison, and D.C. Smith. 2007. Depth-mediated reversal of the effects of climate change on long-term growth rates of exploited marine fish. *Proceedings of the National Academy of Sciences of the United States of America* **104**(18):7461–7465.

U.S. Geological Survey. 2016. Nonindigenous Aquatic Species Database. Gainesville, Florida. https://nas.er.usgs.gov/.

Whitfield, P.E., R.C. Muñoz, C.A., Buckel, B.P. Degan, D.W. Freshwater, and J.A. Hare. 2014. Native fish community structure and Indo-Pacific lionfish *Pterois volitans* densities along a depth-temperature gradient in Onslow Bay, North Carolina, USA. *Marine Ecology Progress Series* **509**:241-254.