Biol Invasions (2019) 21:3013–3018
https://doi.org/10.1007/s10530-019-02070-1

INVASION NOTE

There’s a new kid in town: lionfish invasion of the plankton

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Received: 26 February 2019 / Accepted: 31 July 2019 / Published online: 5 August 2019

Abstract Invasion of the western Atlantic Ocean, Caribbean Sea, and Gulf of Mexico by the Indo-Pacific lionfish, *Pterois volitans/miles* (Scopaenidae), has caused well-documented critical changes to coral reef ecosystems throughout the region. Most efforts to quantify these changes have focused on the charismatic adult stage; much less is known about the pelagic larval stage. While dispersal by the larval stage has likely been the main contributor to the rapid population expansion throughout the region, there are very few documented cases of larvae being collected anywhere in the invaded region where adult lionfish are abundant. We compared ichthyoplankton collected using identical sampling gear from the Straits of Florida in 2007–2008 (pre-lionfish population expansion to the Florida Keys) to those collected in 2014–2015 (during the ongoing expansion), providing the opportunity to test for a temporal change in the ichthyoplankton. Despite a substantially greater sampling effort in 2007–2008 [total of 938,126 m^3 of water sampled compared to approximately 144,013 m^3 ($\sim$ 15%) sampled in 2014–2015], we collected no lionfish larvae in 2007–2008, whereas in 2014–2015, 76 larvae were collected. The overall mean density in 2014–2015 of 0.4–0.7 lionfish larvae 1000 m^{-3} is comparable to a number of common reef fish families and is likely beginning to have an ecological impact on plankton constituents. As the invasion continues, additional studies of the ecological role of lionfish larvae in the plankton are warranted.

Keywords Lionfish invasion · Subtropical ichthyoplankton · Plankton ecology

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Within the last several decades, the Indo-Pacific lionfish, *Pterois volitans/miles* (Scopaenidae; hereafter referred to as *P. volitans* for brevity), has invaded and become established in the western Atlantic Ocean, the Caribbean Sea, and Gulf of Mexico (reviewed in Côté and Smith 2018). Lionfish are voracious predators on small fishes and crustaceans (Morris and Atkins 2009) and are causing well-documented critical changes to coral reef ecosystems throughout the region (Albins and Hixon 2013; Green et al. 2012). While numerous efforts are underway to understand the effects of and control this invasion, most of these efforts are focused on the adult life stage. We know relatively little about the pelagic larval stage.

The larval stage of lionfish (Fig. 1) is widely understood to have played a key role in the invasion. Sedentary, site-attached adults spawn year-round, producing buoyant, mucous-encapsulated eggs that hatch into pelagic larvae that spend 20–35 days in the plankton before settling to the benthos (reviewed in Kulbicki et al. 2012). Dispersal by this pelagic stage has likely been the main contributor to the rapid population expansion throughout the Caribbean Sea, western Atlantic Ocean, and Gulf of Mexico (Betancur-R et al. 2011), yet there are very few documented cases of larvae being collected anywhere in the invaded region where adult lionfish are abundant [but see Vasquez-Yeomans et al. (2011), Kitchens et al. (2017) for reports of 1–3 individuals]. Consequently, their potential effect on plankton ecology is entirely unknown.

To examine the potential effects of increasing populations of *P. volitans* on the plankton, we compared ichthyoplankton collected from the Straits of Florida (SOF) in 2007–2008 (pre-lionfish population expansion to the Florida Keys; Ruttenberg et al. 2012) to those collected in 2014–2015 (during the ongoing expansion). Although conducted for different research purposes, these two sets of 2-year sampling programs utilized identical sampling gear in roughly the same geographic area, providing the opportunity to test for a temporal change in the ichthyoplankton. Based on regional population expansion and increasing reproductive success, we anticipated that the abundance of lionfish larvae in the SOF would be significantly higher in recent years relative to the past.

Fig. 1 Larval *Pterois volitans* collected from the Straits of Florida in 2015. This specimen was collected at station 6EM-B (26.00246, − 79.35606) in Net 0 which sampled from the surface to 30 m depth. At 14.2 mm, standard length, this specimen is larger than the maximum reported here as the comparison across years included only net samples from discrete depths. Photo credit: Cedric Guigand, University of Miami

In both 2-year studies we sampled multiple transects across the SOF with a Multiple Opening and Closing Net and Environmental Sampling System (MOCNESS) equipped with 1-mm mesh nets and a 4-m^2 opening (Fig. 2). This system enabled the collection of depth-discrete samples throughout the top 80 m of the water column. In 2007–2008, larvae were sampled at four depth bins: 0–20, 20–40, 40–60, and 60–80 m, encompassing the depths at which scorpaenid larvae are typically collected (Huebert et al. 2010; Shulzitski et al. 2018). In 2014–2015, three discrete depths were sampled: 15, 30, and 60 m. Samples were fixed in 95% ethanol for transport to the laboratory, where they were sorted to remove larval fishes. All fish larvae were identified based on standard morphology, meristics, a regional ichthyoplankton guide (Richards 2005), and genetically-confirmed morphological descriptions of *P. volitans* (Vasquez-Yeomans et al. 2011; Kitchens et al. 2017). Key morphological characteristics that were used to distinguish *P. volitans* from other scorpaenids found in the western Atlantic include a more cigar-shaped body, less robust head spines, long and lightly pigmented pectoral fins, and pigment on the dorsal margin at the base of the dorsal fin with opposing pigment along the ventral margin (E. Malca, A. Jugovich, NOAA SEFSC, pers. comm.). Putative *P. volitans* larvae were individually confirmed by multiple ichthyoplankton experts, especially Peter Konstantinidis, Ichthyoplankton Taxonomist and Curator of Vertebrates at Oregon State University. Together these two sets of ichthyoplankton surveys, conducted during the peak reproductive period for most reef fishes, provide the most extensive time-series data available to evaluate subtropical plankton communities in this region at a time of increasing adult lionfish populations.

Our overall sampling effort was substantially greater in 2007–2008 with a total of 938,126 m^3 of water sampled compared to approximately 144,013 m^3 sampled in 2014–2015 ($\sim$ 15% of 2007–2008 volume). We collected 2742 scorpaenid larvae in 2007–2008 and 482 in 2014–2015. No fish

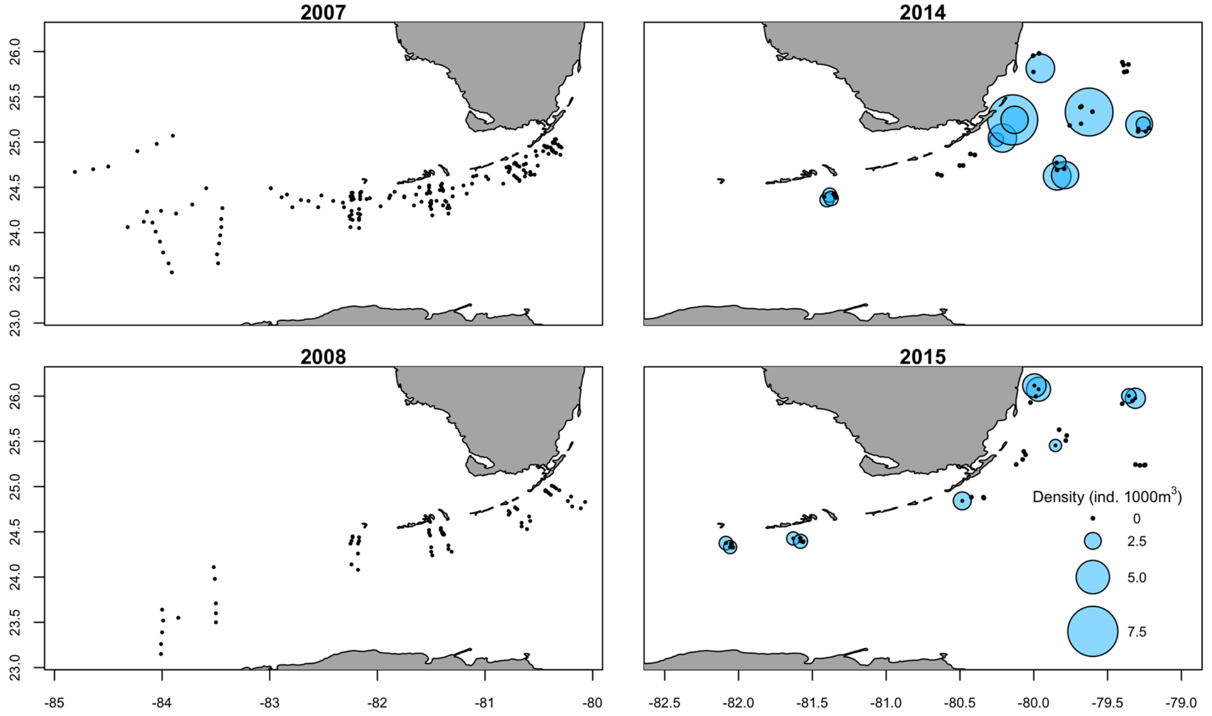

Fig. 2 Stations sampled for larval fishes in the Straits of Florida in summers of 2007 (n = 186), 2008 (n = 68), 2014 (n = 43), and 2015 (n = 32). Blue circles indicate the mean density (individuals·1000 m^{-3}) of *Pterois volitans* larvae sampled at each station; black dots indicate stations where *P. volitans* larvae were absent. Station densities are a mean of the 4 m^2 MOCNESS nets (n = 4) that sampled at each station

larvae were identified as *P. volitans* in the 2007–2008 samples; however, in 2014–2015, despite the greatly reduced sampling effort, we collected 76 *P. volitans* larvae (Fig. 2, Table 1). These numbers amount to an overall mean density in 2014–2015 of 0.4–0.7 *P. volitans*·1000 m^{-3}, although densities were variable among stations and ranged up to a maximum of 12.7 *P. volitans*·1000 m^{-3} in a single net sample (Fig. 2). Overall, scorpaenids comprised ~ 2–3% of all larval fishes across all years and in 2014–2015, *P. volitans* comprised 0.4–0.5% of all larval fishes, and ~ 13–26% of all scorpaenids. Examples of other scorpaenid larvae in the samples include *Scorpaena agassizii* (longfin scorpionfish), *Pontinus rathbuni* (highfin scorpionfish), *Neomerinthe hemingwayi* (spinycheek scorpionfish), *Scorpeana brasiliensis* (barbfish), *Scorpaena plumeri* (spotted scorpionfish), and *Setarches guentheri* (channeled rockfish) (*unpubl. data*). Larval *P. volitans* were collected from all three depths sampled, but most (63%) were found in the 30 m depth bin (35% were collected from 15 m depth; 1% from 60 m). Individuals were sampled from nearshore stations up to 100 km offshore of Florida (Fig. 2). The size distribution of larvae ranged from 2.72 to 11.63 mm standard length (mean = 4.79 mm); the larger larvae exhibiting elaborate morphological coloration (Fig. 1).

This comparison of extensive ichthyoplankton collections over a 10-year period demonstrates that ecological changes are now underway in the plankton. Lionfish larvae have increased from 0 to an average density of 0.4–0.7 individuals·1000 m^{-3}, comparable to mean 2014–2015 densities of common reef fish families such as squirrelfishes (Holocentridae: 0.75·1000 m^{-3}), barracudas (Sphyraenidae: 0.70·1000 m^{-3}), mahi mahi (Coryphaenidae: 0.54·1000 m^{-3}), pufferfishes (Tetraodontidae: 0.48·1000 m^{-3}), and triggerfishes (Balistidae: 0.39·1000 m^{-3}); and higher than many others such as butterflyfishes (Chaetodontidae: 0.31·1000 m^{-3}), angelfishes (Pomacanthidae: 0.30·1000 m^{-3}), lizardfishes (Synodontidae: 0.26·1000 m^{-3}), pipefishes (Syngnathidae: 0.09·1000 m^{-3}), and blennies (Blenniodei: 0.03·1000 m^{-3}). Peak larval lionfish densities in individual net hauls of 12.7

larvae·1000 m^{-3} is a density roughly comparable to peak densities of common fish families such as triggerfishes (Balistidae: 14.4·1000 m^{-3}), big-eyes (Priacanthidae: 14.3·1000 m^{-3}), mahi mahi (Coryphaenidae: 13.6·1000 m^{-3}), and barracudas (Sphyraenidae: 11.5·1000 m^{-3}) (M.R. Gleiber, S. Sponaugle, R.K. Cowen, 2019, unpublished).

Despite sampling only 15% of the water volume sampled in 2007–2008, our 2014–2015 ichthyoplankton collections revealed a major change in larval fish assemblages in that larvae of the invasive Indo-Pacific lionfish are now abundant. Efforts to control the invasion through diver removal of adult lionfish (Green et al. 2014, Usseglio et al. 2017), while moderately successful on shallow coral reefs frequented by divers are not likely to succeed due to the extensive successful spread of the species and the diverse habitats it occupies. Abundant lionfish populations at depths far beyond those regularly accessed by divers (Kulbicki et al. 2012) translate to a virtually unlimited supply of eggs and larvae that can continue to disperse to a wide range of nearshore habitats (reviewed in Sponaugle and Cowen 2019). Continued uncontrolled population expansion of the Indo-Pacific lionfish is having severely negative direct and indirect impacts on coastal marine food webs, marine biodiversity, and the communities of both shallow coral and deep mesophotic reefs (reviewed in Côté and Smith 2018) and their larvae are now common in the plankton.

As populations continue to expand, there are likely to be increasing numbers of lionfish larvae in the plankton who may deplete prey and displace the larvae of other reef fishes. These tropical and subtropical pelagic habitats are oligotrophic and thus may be more readily susceptible to periods of food limitation. Will lionfish larvae outcompete other species for food, or even function as predators on other fish larvae? Although data exist on ichthyoplankton assemblages (Richardson et al. 2010; Huebert et al. 2010; Shulzitski et al. 2018) and species-specific larval fish diets (Llopiz and Cowen 2009; Llopiz et al. 2010) for this region, other interactions among plankton constituents remain undocumented. Thus, the ecological consequences of lionfish larvae on other plankton constituents and the planktonic food web are entirely unknown. While it will be challenging to quantify these consequences due to the vast three-dimensional habitat that is home to a high diversity of often diffuse

Table 1 Sampling effort and density of ichthyoplankton collections in the Straits of Florida in 2007–2008 and 2014–2015

Year	Volume sampled (m^3)	No. of larval fishes	No. of scorpaenids	No. of *P. volitans*	Mean larval fish density (ind·1000 m^{-3})	Mean scorpaenid density (ind·1000 m^{-3})	Mean *P. volitans* density (ind·1000 m^{-3})	Percent scorpaenids/all larval fishes	Percent *P. volitans*/all larval fishes	Percent *P. volitans*/scorpaenids
2007	714,776	109,954	1897	0	153.8	2.7	0.0	1.7	0.0	0.0
2008	223,350	32,457	845	0	145.3	3.8	0.0	2.6	0.0	0.0
2014	74,246	12,330	379	49	166.1	5.1	0.7	3.1	0.4	12.9
2015	69,767	5235	103	27	75.0	1.5	0.4	2.0	0.5	26.2

planktonic organisms (Cowen et al. 2007), this planktonic invasion is worthy of study.

Members of the plankton contribute substantially to the earth's carbon cycle (Field et al. 1998; Behrenfeld 2014) and underlie most marine food webs, including those supporting valuable fisheries species (e.g., Cury et al. 2008). Quantification of the ecological interactions of plankton constituents will allow us to better understand and predict changes to globally relevant processes. As most marine fishes possess a larval stage that must survive and grow for a period of time in the plankton before entering the juvenile or adult population, the invasion of this ecosystem by a new predator could have important ramifications. The impacts of larval lionfish on planktonic communities will influence adult populations in ways that are currently difficult to predict. Likewise, population growth of lionfish, as in most marine fishes, should be very sensitive to larval mortality (Morris et al. 2011), yet we have no knowledge of rates of larval lionfish growth or survivorship. The role of lionfish larvae in the plankton is a gaping hole in our knowledge of this invasive species that is having a disproportionate effect on a diversity of marine ecosystems. As this population expansion continues, additional intensive ichthyoplankton studies will be needed to begin to quantify the ecological effects of lionfish in the plankton of subtropical oceans. The exponential increase in juvenile and adult lionfish in nearshore habitats is now apparent in elevated numbers of lionfish larvae in the plankton which will likely cascade through the pelagic food web with the potential to substantially impact plankton prey and other larval fish species.

Acknowledgements We thank the scientific party and R/V Walton Smith crew for their contributions to the field sampling. We are particularly grateful to Cedric Guigand who participated in the cruises and took the photo of the live lionfish larva collected in 2015. We thank the many lab assistants and volunteers who helped with sample collection and processing over the years as well as expert advice on larval fish identification from Joel Llopiz. We are indebted to Peter Konstantinidis at Oregon State University and Emma Jugovich and Estrella Malca at NOAA's Southeast Fisheries Science Center for assistance in confirming the identification of lionfish larvae. National Science Foundation (NSF) OCE Grant 0550732 supported the collection and processing of the 2007–2008 samples, and NSF OCE Grant 1419987 supported the 2014–2015 study. Raw collection data are available at www.bco-dmo.org/dataset/661268.

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