

Biology and Ecology of the Invasive Lionfishes, *Pterois miles* and *Pterois volitans*

JAMES A. MORRIS, JR.¹, J.L. AKINS², A. BARSE³, D. CERINO¹, D.W. FRESHWATER⁴,
S.J. GREEN⁵, R.C. MUÑOZ¹, C. PARIS⁶, and P.E. WHITFIELD¹

¹National Oceanic and Atmospheric Administration, 101 Pivers Island Road, Beaufort, North Carolina 28516 USA, ²Reef Environmental Education Foundation, 98300 Overseas Hwy, Key Largo, Florida 33037 USA, ³Department of Biology, Salisbury University, 1101 Camden Avenue, Salisbury, Maryland 21801 USA, ⁴University of North Carolina Wilmington, Center for Marine Science, 5600 Marvin Moss Lane, Wilmington, North Carolina 28409 USA, ⁵Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia, V5A 1S6, Canada, ⁶Applied Marine Physics, Rosenstiel School of Marine and Atmospheric Science, 4600 Rickenbacker Causeway, Miami, Florida 33149 USA

ABSTRACT

The Indo-Pacific lionfishes, *Pterois miles* and *P. volitans*, are now established along the U.S. southeast coast, Bermuda, Bahamas, and are becoming established in the Caribbean. While these lionfish are popular in the aquarium trade, their biology and ecology are poorly understood in their native range. Given the rapid establishment and potential adverse impacts of these invaders, comprehensive studies of their biology and ecology are warranted. Here we provide a synopsis of lionfish biology and ecology including invasion chronology, taxonomy, local abundance, reproduction, early life history and dispersal, venomology, feeding ecology, parasitology, potential impacts, and control and management. This information was collected through review of the primary literature and published reports and by summarizing current observations. Suggestions for future research on invasive lionfish in their invaded regions are provided.

KEY WORDS: Lionfish, invasive species, *Pterois*

Biología y Ecología del Pez León Invasor, *Pterois miles* y *Pterois volitans*

Los peces león del Indo-Pacífico, *Pterois volitans* and *Pterois miles*, se están estableciendo a lo largo de la costa sur oriental de los Estados Unidos, Bermuda, Bahamas y han comenzado a invadir el Caribe. Aunque los peces leones son populares en el comercio de acuarios, poco es conocido de su biología y ecología. Dado el rápido establecimiento de los peces león y su impacto potencial de estos invasores, los estudios comprensivos acerca de su biología y ecología son necesarios. Aquí proporcionamos una sinopsis de la biología y ecología del pez león incluyendo la cronología de la invasión, taxonomía, abundancia local, reproducción, historia temprana de la vida y dispersión, venomology, ecología de alimentación, parasitología, los impactos potenciales, y control y gerencia. Esta información fue recogida por medio de la revisión de la literatura primaria y informes públicos y resumiendo observaciones actuales. Las sugerencias para la investigación futura sobre el invasor pez león en las regiones invadidas son proporcionadas.

PALABRAS CLAVES: peces león, especie invasora, *Pterois*

Biologie et Ecologie de Rascasses volantes Invasives, *Pterois miles* et *Pterois volitans*

Les rascasses volantes, *Pterois volitans* et *Pterois miles*, originaires de la zone tropicale indo-Pacifique sont aussi retrouvées le long des côtes sud-est américaines, aux Bermudes, aux Bahamas, et sont actuellement entrain d'envahir les Caraïbes. Alors que ces poissons sont très demandés dans le commerce des poissons d'aquarium, peu de données relatives à leur biologie et à leur écologie sont connues. Dans ce contexte, d'invasion rapide de ce poisson et des impacts potentiels sur les communautés de poissons récifaux endogènes, nous essayons de mettre en évidence la biologie de reproduction, les habitudes alimentaires et les caractères venimeux en utilisant les observations menées en laboratoire et sur le terrain. Concernant la reproduction de ce poisson, les observations menées montrent que c'est un animal itéropare, asynchrone avec de multiples pontes par saison (le nombre de ponte étant indéterminé). Les mesures visant à déterminer la périodicité de ponte montrent que ces poissons pondent mensuellement, avec des périodes de ponte au cours de la plupart des mois du calendrier d'où le caractère invasif de cette espèce. Les expérimentations conduites au laboratoire sur la prédation des rascasses juvéniles ont montré que ces derniers ne constituent pas de véritables proies pour les poissons récifaux endémiques à cause de leurs défenses venimeuses. L'analyse du contenu stomacal révèle essentiellement des crustacés et des poissons des espèces fourragères incluant les poissons dévolus à la pêche commerciale ou de loisirs, comme le vivaneau et le mérour. Ces travaux fournissent un nouvel éclairage en ce qui concerne la biologie intégrée et l'écologie des rascasses volantes non endémiques, et démontrent le besoin d'une détection précoce et systématique de cette espèce et la mise en œuvre de solution rapide pour faire face à cette invasion dans l'écosystème marin.

MOTS CLÉS: Rascasses volantes ,espèce invasion, *Pterois*

INTRODUCTION

The lionfish invasion in the Northwestern Atlantic and the Caribbean represents one of the most rapid marine finfish invasions in history. Despite being a popular member of the marine ornamental aquarium trade, little was known regarding the biology and ecology of these

lionfishes prior to this invasion. Information on lionfish abundance, dietary habits, predators, and seasonality of reproduction are scarce. Most of what has been published on lionfish relates largely to lionfish envenomations, which commonly occur during aquarium husbandry or as a result of poor handling by home aquarists.

Invasive lionfish are a concern to coastal managers due to their potential threat to fisheries resources, native fish communities, and human health. Since 2000, National Oceanic and Atmospheric Administration (NOAA) researchers have partnered with non-governmental organizations, academics, and other federal and state agencies to develop a programmatic response to the lionfish invasion. The following provides a synopsis of information on the biology and ecology of the invasive lionfishes that have invaded the Northwestern Atlantic and Caribbean, and a discussion of future research needs and management options.

Invasion Chronology

Many non-native marine ornamental fishes have been reported along the U.S. East Coast, with a “hotspot” of introductions occurring in South Florida (Semmens *et al.* 2004). Lionfish have been documented off Palm Beach, Boca Raton, and Miami, Florida beginning in 1992; and Bermuda, North Carolina, South Carolina and Georgia beginning in 2000 (Hare and Whitfield 2003, REEF 2008, USGS 2008, Whitfield *et al.* 2002). Since 2004, lionfish have become widespread in the Bahamas (REEF 2008, USGS 2008, Whitfield *et al.* 2007). More recently, lionfish were reported in the Turks and Caicos and Cuba (Chevalier *et al.* 2008) in 2007, and in the Cayman Islands, Jamaica, Dominican Republic (Guerrero and Franco 2008), U.S. Virgin Islands, Belize, and Barbados in 2008 (REEF 2008, USGS 2008). Juvenile lionfishes have also been reported along the U.S. northeast coast including Virginia, New York, Rhode Island, and Massachusetts since 2001. These northeastern specimens are incapable, however, of overwintering due to thermal intolerance (Kimball *et al.* 2004), and they are not considered established.

It is nearly impossible to determine which introduction event(s) allowed lionfish to become established. Research on the genetic variation of the lionfish populations is providing insight into the minimum number of lionfish and the geographic origin of founder population(s) (Hamner *et al.* 2007). Interestingly, this is not the first documented invasion of *Pterois* sp. as Golani and Sonin (1992) reported a Mediterranean invasion of *P. miles* from the Red Sea via the Suez Canal.

Taxonomy

Pterois miles and *P. volitans* are morphologically similar and distinguishable in their native range by meristics, with *P. volitans* exhibiting one higher count of dorsal and anal fin rays when compared to *P. miles*. This difference was documented by Schultz (1986) who reported that *P. miles* is found in the Red Sea, Persian Gulf, and Indian Ocean (excluding Western Australia) and *P. volitans* is found in the Western and Central Pacific and Western Australia. Kochzius *et al.* (2003) used mitochondrial DNA analyses to show that specimens identified as *P. miles* and *P. volitans* were genetically distinct. Their

geographic sampling did not allow the determination of whether this distinction was at the species or population level. Hamner *et al.* (2007) analyzed specimens identified as *P. miles* and *P. volitans* from additional areas of their native range, including Indonesia, where they are sympatric. They found that the two taxa are clearly distinct supporting the designation of two species. Analyses with different molecular markers and additional geographic samples of species in *Pterois* and the out-group comparison with the closely related genus *Dendrochirus*, support the classification of *P. miles* and *P. volitans* as separate species. Recent efforts by Hamner *et al.* (2007) have confirmed that:

- i) Both *P. miles* and *P. volitans* were introduced along the U.S. East Coast,
- ii) *P. volitans* comprises approximately 93% of the population, and
- iii) A strong founder effect (*i.e.* low genetic diversity) is evident among Atlantic specimens.

The genetic structure of invasive lionfish in the Caribbean is presently unknown. Only one species (*P. volitans*) has been confirmed along the Bahamian archipelago. Documentation of genetic change and adaptation of lionfish populations in their invaded range is warranted (*e.g.*, Morris and Freshwater 2008). Greater understanding of lionfish genetics could assist with validation of reef fish dispersal and connectivity models in the Northwestern Atlantic, Caribbean, and Gulf of Mexico.

Local Abundance

Whitfield *et al.* (2007) provided the first assessment of lionfish densities off North Carolina and reported an average of 21 lionfish per hectare across 17 locations in 2004. Lionfish densities off North Carolina have continued to increase. Recent assessments off New Providence, Bahamas indicate lionfish densities are more than 18 times higher than the 2004 North Carolina estimates (Green and Côté 2008). The cryptic nature of lionfish make them difficult to census. It is likely that estimates of lionfish on complex coral reef habitats under-represent local abundance of juveniles. Thus, these density estimates should be considered conservative. Further, lionfish densities in the Bahamas are more than eight times higher than estimates from their native range (Green and Côté 2008). Few published data are available, however, from the Indo-Pacific region providing high uncertainty for this comparison. In their invaded Atlantic and Caribbean ranges, it is unclear when lionfish densities will reach carrying capacity. Given that many reef fishes along the east coast of the U.S. and Caribbean are overfished (Hare and Whitfield 2003), lionfish might be utilizing vacated niche attributes such as increased availability of forage fishes and reef space.

Monitoring of lionfish densities across habitat types using standardized indices of abundance is needed to

determine when lionfish abundances reach carrying capacity. Lionfish densities are expected to vary depending on such factors as seasonality, local recruitment, local niche availability, and fishing pressure. Studies assessing the drivers controlling lionfish densities in specific habitats are needed to support lionfish control measures and to identify potential pathways for new invaders.

Reproduction

The Pteroinae, including *P. miles* and *P. volitans*, are gonochoristic; males and females exhibit minor sexual dimorphism only during reproduction (see Fishelson 1975). Lionfish courtship has been well described by Fishelson (1975) who provided a detailed description for the pigmy lionfish, *Dendrochirus brachypterus*, and reported similar courtship behaviors for *Pterois* sp. According to Fishelson, lionfish courtship, which includes circling, side winding, following, and leading, begins shortly before dark and extends well into nighttime hours. Following the courtship phase, the female releases two buoyant egg masses that are fertilized by the male and ascend to the surface. The eggs and later embryos are bound in adhesive mucus that disintegrates within a few days, after which the embryos and/or larvae become free floating.

P. miles and *P. volitans* ovarian morphology is similar to that reported for *D. brachypterus* (Fishelson 1978) in that these fishes exhibit cystovarian type ovaries (Hoar 1957) with oocytes developing on stalks or peduncles. The oocytes are terminally positioned near the ovary wall, which secretes the encompassing mucus shortly before spawning. The seasonality of lionfish reproduction throughout their native range is unknown. Invasive lionfish collected off North Carolina and in the Bahamas suggests that lionfish are reproducing during all seasons of the year.

Early Life History and Dispersal

Larval stage descriptions for *P. miles* and *P. volitans* are incomplete with only one report by Imamura and Yabe (1996) describing five *P. volitans* larvae collected off northwestern Australia. Scorpaenid larvae exhibit two morphologically distinct groups characterized as “morph A” and “morph B” by Leis and Rennis (2000). Pteroinae larvae are grouped among the “morph B” morphotypes, whose traits include: large head, relatively long and triangular snout, long and serrated head spines, robust pelvic spine, and pigment confined to the pectoral fins (Leis and Rennis 2000) and postanal ventral and dorsal midlines (Washington et al. 1984). *Pterois* sp. meristic characters are reported as 12 - 13 dorsal spines, 9 - 12 dorsal rays, three anal spines, 5 - 8 anal rays, 12 - 18 pectoral rays, one pelvic spine, five pelvic rays, and 24 vertebrae (Imamura and Yabe 1996; Leis and Rennis 2000).

The size of *P. miles* or *P. volitans* larvae at hatching is unmeasured, but is likely to be approximately 1.5 mm

based on reports for *P. lunulata* (Mito and Uchida 1958; Mito 1963). The specific planktonic larval duration of lionfish is also unknown, although Hare and Whitfield (2003) estimated it to be between 25 to 40 days based estimates for *Scorpaena* (Laidig and Sakuma 1998).

Dispersal of lionfish presumably occurs during the pelagic larval phase during which larvae can be dispersed across great distances. For example, lionfish eggs released in the Bahamas are capable of dispersing to New England via the Gulf Stream. Larval connectivity models for reef fishes (e.g., Cowen et al. 2006) provide insight into lionfish larval dispersal and are valuable for predicting the spread of lionfish as evidenced by the recent establishment of lionfish in the Caribbean. Further lionfish dispersal into the lower Caribbean and the Gulf of Mexico seems imminent. Assuming a planktonic larval duration of 25 to 40 days (Hare and Whitfield 2003), the Caribbean and Yucatan currents are capable of dispersing lionfish larvae into the Gulf of Mexico from locations in the Caribbean where lionfish are already resident (i.e., Cuba, Jamaica, Cayman Islands) (Cowen et al. 2006). Based on the rapidity of lionfish establishment along the U.S. East Coast and the Bahamas, lionfish establishment along the southern edges of Central America (Nicaragua, Costa Rica, and Panama), the Yucatan peninsula, and the western Gulf of Mexico is likely within a few years or less. Establishment would also be facilitated by gyres such as the Columbia-Panama Gyre and the Gulf of Mexico loop current, which could provide a mechanism for lionfish to become established in the Florida Keys.

Venomology

Lionfish are venomous with their spines containing apocrine-type venom glands. Each spine of the lionfish (except caudal spines) is venomous including 13 dorsal spines, three anal spines, and two pelvic spines. The spines are encased in an integumentary sheath or skin and contain two grooves of glandular epithelium that comprises the venom producing tissue. Spine glandular tissue extends approximately three quarters the distance from the base of the spine towards the tip (Halstead et al. 1955).

Lionfish envenomation occurs when the spine's integumentary sheath is depressed as it enters the victim. This process tears the glandular tissue allowing the venom to diffuse into the puncture wound (Saunders and Taylor 1959). The toxin in lionfish venom contains acetylcholine and a neurotoxin that affects neuromuscular transmission (Cohen and Olek 1989). Lionfish venom has been found to cause cardiovascular, neuromuscular, and cytolytic effects ranging from mild reactions such as swelling to extreme pain and paralysis in upper and lower extremities (Kizer et al. 1985). Antivenom of the related stonefish (*Synanceia* spp.) is highly effective in neutralizing lionfish venom activity (Shiomi et al. 1989, Church and Hodgson 2002).

The severity of sting reactions in humans is dependent upon such factors as the amount of venom delivered, the

immune system of the victim, and the location of the sting. Records of home aquarists stung by lionfish provide a comprehensive assessment of how lionfish stings affect humans (Kizer *et al.* 1985, Vetrano *et al.* 2002). The probability of lionfish envenomation is higher when handling smaller-sized lionfish because the venom glandular tissue is closer to the tip of the spine and the spine tip is smaller and sharper (Halstead *et al.* 1955).

The effectiveness of lionfish venom defense in their invaded range is in question. Maljković *et al.* (2008) reported that lionfish were found in the stomachs of groupers; however, this observation provides no assessment of the frequency of lionfish consumption by grouper. Furthermore, laboratory behavioral experiments suggest that groupers actively avoid lionfish, even during periods of extreme starvation. Additional research is needed towards understanding predatory interactions between lionfish and native predators.

Work by Sri Balasubashini *et al.* (2006a, 2006b) indicated that lionfish (*P. volitans*) venom contains antitumor, hepatoprotective, and antimetastatic effects in mice suggesting a promising application for cancer research. Depending on the outcome of this research and the subsequent demand for lionfish venom, bioprospecting of venom from invasive lionfish could assist with fishery development.

Feeding Ecology

In the Red Sea, lionfish (*P. miles*) have been reported to feed on assorted taxa of benthic fishes including damselfish, cardinal fish, and anthias (Fishelson 1975, Fishelson 1997). However, in the Pacific Ocean, *P. lunulata* were observed to feed primarily on invertebrates including penaeid and mysid shrimps (Matsumiya *et al.* 1980, Williams and Williams 1986). Assessments of invasive lionfish feeding suggests that lionfish are largely piscivorous, but also feed on a number of crustaceans. The particular taxa of highest importance in invasive lionfish diet will likely vary by habitat type and prey availability.

Feeding, growth, and starvation of *P. volitans* from the Red Sea was investigated by Fishelson (1997) who reported that lionfish stomachs can expand over 30 times in volume when consuming a large meal. This capability supported Fishelson's hypothesis that lionfish were capable of longterm fasting, and demonstrated their ability to withstand starvation for periods of over 12 weeks without mortality. Fishelson (1997) also measured daily consumption rates in the laboratory for six size classes of lionfish ranging from 30 - 300g and found that lionfish consumed approximately 2.5 - 6.0% of their body weight per day at 25 - 26 °C. Preliminary observations suggest that lionfish in their invaded range can consume piscine prey at rates greater than reported earlier by Fishelson (1997). Quantification of the feeding ecology of lionfish including consumption rates and prey selectivity will permit better assessment of the impacts of their predation on local reef

fish communities.

Parasitology

Knowledge of the parasites infecting native and non-native lionfish is scant. No comprehensive survey of protozoan or metazoan parasites of either host (*P. miles* or *P. volitans*) has been published. There are, however, a few isolated records of single parasite species such as monogeneans from the Red Sea (Paperna 1972, Colorni and Diamant 2005) and Japan (Ogawa *et al.* 1995), copepods also from Japan (Dojiri and Ho 1988), and leeches from Japan (Paperna 1976) and the Florida coast (Ruiz-Carus *et al.* 2006). Most published records of lionfish parasites are of ectoparasites; the only record of an endoparasite is of a new myxosporean species, *Sphaeromyxa zaharoni* which was found in a lionfish gall bladder from the Red Sea (Diamant *et al.* 2004). Recent observations of invasive lionfish collected off North Carolina and in the Bahamas have found low prevalence of endo- and ectoparasites when compared to parasites of native reef fishes. Future research describing parasites of invasive lionfish will provide a unique study of opportunistic parasitism by common parasites of marine reef fishes.

Potential Impacts

Potential ecological impacts of lionfish on local reef fish communities will vary depending on the abundance of top level predators, the forage fish community, the density of lionfish, and the geographic location. Local studies providing observations of lionfish impacts on community structure and the abundance of forage fishes are needed. The first evidence of lionfish impacts in their new range was provided by Albins and Hixon (2008) who reported a 79% reduction in forage fish recruitment on experimental patch reefs in the Bahamas during a five week observation period. Analysis of the potential impact of lionfish consumption on whole coral reef fish communities is also being documented in the Bahamas, where data on stomach contents are being combined with abundance estimates of the prey community across various habitat types and seasons. Given the high levels of lionfish biomass found at some locations (Whitfield *et al.* 2007, Green and Côté 2008), the predatory removal of forage fishes is a growing concern, because many other top level predators (i.e., potential food competitors with lionfish) are overfished or in low abundance (Hare and Whitfield 2003).

It is unclear if lionfish predation on economically important species such as juvenile serranids will harm stock rebuilding efforts. Economically important species were observed in the diet of lionfish in the Bahamas. Research that monitors lionfish predation on economically important species is needed.

Lionfish impacts on tourist recreational activities have been observed. Some locations have posted warning signs advising of the potential for lionfish envenomation. As lionfish densities increase, so too does the risk of enveno-

mations. It is unknown whether increasing lionfish densities will reduce recreational activities and cause economic hardship. This will be dependent on factors such as the prevalence of warning signs, the density of lionfish, the rate of human encounters, and the effectiveness of education and outreach.

Control and Management

Management of marine finfish invasions are confounded by highly diverse and wide-ranging habitats, swift ocean currents, and jurisdictional constraints. Prevention is the least expensive and most effective management option. There are currently two lionfish management and control efforts in Bermuda and the Bahamas. Bermuda initiated a lionfish culling program in 2008 that included a training program, collecting license, and a special dive flag allowing commercial and recreational fishers to spear lionfish along nearshore reefs. A video description of this program can be seen at <http://www.youtube.com/watch?v=LnbKjiUCGRU>. Bahamian fisheries officials instituted a lionfish kill order to fishermen in 2007. They have also actively engaged the public with educational seminars devoted to promoting lionfish as a food fish with the hopes that human consumption will support fishery development. Grassroots, "adopt a reef programs", are also being utilized to encourage local citizens to take ownership of small reefs and to protect them from lionfish impacts. Some tourist locations, such as resorts, are physically removing lionfish by spearfishing and handnets to reduce the risk of swimmer interaction. The effectiveness of these approaches is unclear, because too little is known about the rate of lionfish recruitment and movement among the various habitat types. Recently, NOAA researchers have developed techniques to trap lionfish, thus providing a means of removal from deeper waters and larger areas that are impractical for diver removal.

An early detection and rapid response program has been developed (NOAA/REEF/USGS) in south Florida (a hotspot for marine introductions), which utilizes and coordinates resources from over thirty state, federal, and non-governmental organizations in the region. Workshops utilizing this model are being conducted in regions of the Caribbean to improve local response to marine invasions. Programs such as this represent the first line of defense for marine introductions and should be endorsed and supported by local managers.

CONCLUSIONS

The lionfish introduction provides a reminder of how rapid a non-native species can become established and potentially compete with native fishes for resources. Early detection and rapid response efforts are of utmost importance in the marine environment due to the complexity and ineffectiveness of eradication measures. Future research on invasive lionfish should focus on understanding and reducing their ecological impacts, the scale of which is yet

to be determined.

ACKNOWLEDGEMENTS

We thank the NOAA Aquatic Invasive Species Program, NOAA National Centers for Coastal Ocean Science, the NOAA Undersea Research Program (Grant No. NA030AR4300088), the National Science Foundation (Grants OCE0825625, OCE0550732, PEET No.0328491, DBI-MRI No.0618453), the GEF Coral Reef Targeted Research Program, Connectivity Working Group, and the Natural Sciences and Engineering Research Council of Canada for funding support. We also thank J. Langston and P. Schofield (USGS) for providing lionfish sightings records and D. Ahrenholz, D. Evans, and J. Govoni for their helpful review of this manuscript.

LITERATURE CITED

- 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.
- Chevalier, P.O., E. Gutierrez, D. Ibarzabal, S. Romero, V. Isla, and J. Calderin, and E. Hernandez. 2008. First record of *Pterois volitans* (Pisces: Scorpaenidae) for Cuban waters. *Solenodon* **7**:37-40.
- Church, J.E. and W.C. Hodgson. 2002. The pharmacological activity of fish venoms. *Toxicon* **40**:1083-1093.
- Cohen, A.S. and A.J. Olek. 1989. An extract of lionfish (*Pterois volitans*) spine tissue contains acetylcholine and a toxin that affects neuromuscular-transmission. *Toxicon* **27**:1367-1376.
- Colorni, A. and A. Diamant. 2005. Hyperparasitism of trichodinid ciliates on monogenean gill flukes of two marine fish. *Diseases of Aquatic Organisms* **65**:177-180.
- Cowen R.K., C.B. Paris, and A. Srinivasan. 2006. Scaling of connectivity in marine populations. *Science* **311**:522-526.
- Diamant, A., C.M. Whipps, and M.L. Kent. 2004. A new species of *Sphaeromyxa* (Myxosporae: Sphaeromyxina: Sphaeromyxidae) in devil firefish, *Pterois miles* (Scorpaenidae), from the Northern Red Sea: morphology, ultrastructure, and phylogeny. *Journal of Parasitology* **90**:1434.
- Dojiri, M. and J.S. Ho. 1988. Two Species of Acanthochondria Copepoda Poecilostomatoida parasitic on fishes of Japan." Report of the Sado Marine Biological Station, Niigata University **18**:47-56.
- Fishelson, L. 1975. Ethology and reproduction of pteroid fishes found in the Gulf of Agaba (Red Sea), especially *Dendrochirus brachypterus* (Cuvier), (Pteroidae, Teleostei). *Pubblicazioni della Stazione zoologica di Napoli* **39**:635-656.
- Fishelson, L. 1978. Oogenesis and spawn formation in the pigmy lionfish *Dendrochirus brachypterus* Pteroidae. *Marine Biology* **46**:341-348.
- Fishelson, L. 1997. Experiments and observations on food consumption, growth and starvation in *Dendrochirus brachypterus* and *Pterois volitans* (Pteroinae, Scorpaenidae). *Environmental Biology of Fishes* **50**:391-403.
- Golani, D. and O. Sonin. 1992. New records of the Red Sea fishes, *Pterois miles* (Scorpaenidae) and *Pteragogus pelycus* (Labridae) from the eastern Mediterranean Sea. *Japanese Journal of Ichthyology* **39**:167-169.
- Green, S.J. and I.M. Côté. 2008. Record densities of Indo-Pacific lionfish on Bahamian coral reefs. *Coral Reefs* DOI 10.1007/s00338-008-0446-8.
- Guerrero, K.A. and A.L. Franco. 2008. First record of the Indo-Pacific red lionfish *Pterois volitans* (Linnaeus, 1758) for the Dominican Republic. *Aquatic Invasions* **3**:255-256.
- Halstead, B., M.J. Chitwood, and F.R. Modglin. 1955. The anatomy of the venom apparatus of the zebrafish, *Pterois volitans* (Linnaeus). *Anatomical Record*: **122**:317-333.
- Hamner R.M., D.W. Freshwater, and P.E. Whitfield. 2007. Mitochondrial cytochrome b analysis reveals two invasive lionfish species with strong founder effects in the western Atlantic. *Journal of Fish Biology* **71**:214-222.
- Hare, J. A. and P.E. Whitfield. 2003. An integrated assessment of the introduction of lionfish (*Pterois volitans/miles* complex) to the

- Western Atlantic Ocean. *NOAA Technical Memorandum NOS NCCOS* p 21.
- Hoar, W.S. 1957. The gonads and reproduction. Pages 287-321 in: M.E. Brown (ed.). *Physiology of Fishes*. Academic Press. New York, New York, USA.
- Imamara, H. and M. Yabe. 1996. Larval record of a red firefish, *Pterois volitans*, from northwestern Australia (Pisces: Scorpaeniformes). *Bulletin of the Faculty of Fisheries, Hokkaido University* **47**:41-46.
- Kimball M.E., J.M. Miller, P.E. Whitfield, and J.A. Hare. 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.
- Kizer, K.W., H.E. McKinney, and P.S. Auerbach. 1985. Scorpaenidae envenomations: A five-year poison center experience. *Journal of the American Medical Association* **253**:807-810.
- Kochzius, M., R. Soller, M.A. Khalaf, and D. Blohm. 2003. Molecular phylogeny of the lionfish genera *Dendrochirus* and *Pterois* (Scorpaenidae, Pteroinae) based on mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* **28**:396-403.
- Laidig, T.E. and K.M. Sakuma. 1998. Description of pelagic larval and juvenile grass rockfish, *Sebastes rastrelliger* (family Scorpaenidae), with an examination of age and growth. *Fisheries Bulletin* **96**:788-796.
- Leis, J.M. and D.S. Rennis. 2000. Scorpaenidae (Scorpionfishes, Stonefishes). Pages 217-255 in: J.M. Leis and B.M. Carson-Ewart, (eds.) *Fauna Malesiana Handbooks. The larvae of Indo-Pacific coastal fishes. An identification guide to marine fish larvae*. Brill, Leiden, The Netherlands.
- Maljković, A., T.E. Van Leeuwen, and S.N. Cove. 2008. Predation on the invasive red lionfish, *Pterois volitans* (Pisces: Scorpaenidae), by native groupers in the Bahamas. *Coral Reefs* **27**:501-501.
- Matsumiya, Y., I. Kinoshita, and M. Oka. 1980. Stomach contents examination of the piscivorous demersal fishes in Shijiki Bay Japan. *Bulletin of the Seikai National Fisheries Research Institute* **55**:333-342.
- Mito, S. 1963. Pelagic fish eggs from Japanese waters – III. Percina, VIII. Cottina. IX. Echeneida and Pleuronectida. *Japanese Journal of Ichthyology* **11**:39-102.
- Mito, S. and K. Uchida. 1958. On the egg development and hatched larvae of a scorpaenid fish, *Pterois lunulata* Temminck et Schlegel. *Scientific Bulletin of the Faculty of Agriculture, Kyushu University* **16**:381-385.
- Morris, J.A., Jr. and D.W. Freshwater. 2008. Phenotypic variation of lionfish supraocular tentacles. *Environmental Biology of Fishes* **83**:237-241.
- Ogawa, K., M.G. Bondad-Reantaso, and H. Wakabayashi. 1995. Redescription of *Benedenia epinepheli* (Yamaguti, 1937) Meserve, 1938 (Monogenea: Capsalidae) from cultured and aquarium marine fishes of Japan. *Canadian Journal of Fisheries and Aquatic Sciences* **52** (Suppl 1):62-70.
- Paperna, I. 1972. Monogenea of Red Sea fishes. III. Dactylogyridae from littoral and reef fishes. *Journal of Helminthology* **46**:47.
- Paperna, I. 1976. Parasitological survey of fishes of the Red Sea and Indian Ocean. Pages 82. in: Z. Reiss and I. Paperna: *Fifth report of the H. Steinitz Marine Biology Laboratory*, Elat 1975-1976.
- Reef Environmental Education Foundation (REEF) 2008. REEF database. <http://www.reef.org/db/reports>. Cited 1 November 2008.
- Ruiz-Carus, R., R.E. Matheson, D.E. Roberts and P.E. Whitfield. 2006. The western Pacific red lionfish, *Pterois volitans* (Scorpaenidae), in Florida: Evidence for reproduction and parasitism in the first exotic marine fish established in state waters. *Biological Conservation* **128**:384-390.
- Saunders, P.R. and P.B. Taylor. 1959. Venom of the lionfish *Pterois volitans*. *American Journal of Physiology* **197**:437-440.
- Schultz, E. T. 1986. *Pterois volitans* and *Pterois miles*: two valid species. *Copeia* **1986**:686-690.
- Semmens, B.X., E. Buhle, A. Salomon, and C. Pattengill-Semmens. 2004. A hotspot of non-native marine fishes: evidence for the aquarium trade as an invasion pathway. *Marine Ecology Progress Series* **266**:239-244.
- Shiomi, K. M. Hosaka, S. Fujita, H. Yamanaka, and T. Kikuchi. 1989. Venoms from six species of marine fish: lethal and hymolytic activities and their neutralization by commercial stonefish antivenom. *Marine Biology* **103**:285-289.
- Sri Balasubashini, M., S. Karthigayan, S.T. Somasundaram, T. Balasubramanian, P. Viswanathan, and V.P. Menon. 2006a. *In vivo* and *in vitro* characterization of the biochemical and pathological changes induced by lionfish (*Pterois volitans*) venom in mice. *Toxicology Mechanisms and Methods* **16**:525-531.
- Sri Balasubashini, M., S. Karthigayan, S.T. Somasundaram, T. Balasubramanian, P. Viswanathan, P. Raveendran, and V.P. Menon. 2006b. Fish venom (*Pterois volitans*) peptide reduces tumor burden and ameliorates oxidative stress in Ehrlich's ascites carcinoma xenografted mice. *Bioorganic and Medicinal Chemistry Letters* **16**:6219-6225.
- United States Geological Survey (USGS) (2008). Non-indigenous aquatic species database query: Lionfish Sightings Distribution. <http://nas.er.usgs.gov/taxgroup/fish/lionfishdistribution.htm> Cited 1 November 2008.
- Vetrano, S.J., J.B. Lebowitz, and S. Marcus. 2002. Lionfish envenomation. *Journal of Emergency Medicine* **23**:379-382.
- Washington, B.B., H.G. Moser, W.A. Laroche, and W.J. Richards. 1984. Scorpaeniformes: development. Pages 405-428 in: H.G. Moser, J. Richards, D.M. Cohen, M.P. Fahay, A.W. Kendall, S.L. Richards (eds.) *Ontogeny and Systematics of Fishes*. Special Publication 1 of the American Society of Ichthyologists and Herpetologists.
- Whitfield P.E., T. Gardner, S.P. Vives, M.R. Gilligan, W.R. Courtenay, G.C. Ray, and J.A. Hare. 2002. Biological invasion of the Indo-Pacific lionfish *Pterois volitans* along the Atlantic coast of North America. *Marine Ecology Progress Series* **235**:289-297.
- Whitfield P.E., J.A. Hare, A.W. David, S.L. Harter, R.C. Muñoz, and C.M. Addison. 2007. Abundance estimates of the Indo-Pacific lionfish *Pterois volitans/miles* complex in the Western North Atlantic. *Biological Invasions* **9**:53-64.
- Williams, L.B. and E.H. Williams, Jr. 1986. Ichthyological notes about fishes collected for parasite examination around Sesoko Island, Okinawa. *Galaxea* **5**:217-221.