Understanding the Lionfish Invasion in Bonaire to Develop the Best Strategy for Trinidad and Tobago

Comprensión de la Invasión del Pez León en Bonaire para Desarrollar la Mejor Estrategia para Trinidad y Tobago

Comprendre l'Invasion de Poissons-papillons a Bonaire pour Élaborer la Meilleure Stratégie de Trinidad et Tobago

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ABSTRACT

Lionfish are venomous, predatory reef fish native to the Indo-Pacific region, but have become widely distributed due to its popularity as an aquarium fish. Due to high fecundity, adaptability to non-native habitats and tolerance to large temperature and depth ranges, the lionfish invasion has the potential to become the most detrimental in history. Lionfish were first confirmed in Bonaire on 26th October, 2009. Since then, despite active eradication attempts, they have increased in abundance, occupying habitats at a range of depths. Trinidad and Tobago however have yet to be invaded by lionfish, but the presence of lionfish in aquariums in Trinidad and the availability of suitable prey and habitat, together with confirmed lionfish sightings in neighbouring territories make the lionfish invasion imminent. Questionnaires were conducted with target groups (lionfish-hunters, divers, dive-shops, fishermen and pet-shop owners) in Bonaire and Trinidad and Tobago. These revealed that there was a significant difference in the level of opinions and awareness between the invaded territory (Bonaire) and the un-invaded territory (Trinidad and Tobago). The current lionfish management strategies in Bonaire and the Caribbean were also appraised to suggest the best approach for Trinidad and Tobago in dealing with the future threat of lionfish.

KEY WORDS: Lionfish, invasive species, prevention, management, control

INTRODUCTION

The Red Lionfish (*Pterois volitans*) signifies the first marine fish invader from the Western Pacific to the Atlantic and is believed to have been a result of unintentional and/or intentional releases (Whitfield et al. 2002, Morris et al. 2010, Johnson and Purkis 2011, Morris et al. 2011b). The accidental release of six individuals from Biscayne Bay as a result of Hurricane Andrew in 1992 was accepted as the most likely method of lionfish introduction. However, this testimony has been questioned. A confirmed lionfish sighting made by a Lobster fisherman off Dania, Florida in 1985 actually pre-dates Hurricane Andrew (Morris and Akins 2009, Schofield et al. 2010). Betancur et al. (2011) suggested, based on genetic studies, that the minimum number of founding individuals required to account for the observed genetic diversity in the western Atlantic lionfish lies between eight and twelve individuals, rather than six.

The dispersal of lionfish seemingly occurs during the pelagic larval phase whereby dispersal can occur over great distances (Whitfield et al. 2007, Morris et al. 2009). Lionfish represent a species complex whose native range extends from Southern Japan, south to Lord Howe Island, throughout Indonesia, Micronesia and French Polynesia (Ruiz-Carus et al. 2006, Gonzales et al. 2009). In their native range, lionfish occupy the higher levels of the food chain (Hare and Whitfield 2003, Bervoets 2009) and are predominantly piscivores, but are renowned for also feeding on invertebrates (Morris 2009). Lionfish are benthic associated, and in its native range they occur over coral, sand, and hard-bottom substrates from the surface to 50 m (Whitfield et al. 2002, 2007, Vasquez-Yeomans et al. 2011). Lionfish are adaptable to many habitats and have colonized areas ranging from 1 to 140 m on reef walls, patch reefs, rocky areas, hard bottoms, ledges, crevices, mangrove creeks, isolated coral heads, blue holes, ship wrecks, and man-made structures (NOAA CoRIS 2009). Lionfish tend to live in small groups as juveniles and during reproduction, but disperse and hide in reef shadows when they are adults (Fishelson 1997).

Lionfish were first confirmed in Bonaire on October 26th, 2009; however their actual method of introduction to this region of the Caribbean remains unknown (Figure 1). Despite a constantly active eradication program, lionfish have continued to increase in abundance and size, occupying a range of habitats and depths. Trinidad and Tobago however have yet to be invaded by lionfish, but the presence of lionfish in aquariums in Trinidad and the ample availability of suitable prey and habitat, coupled with confirmed lionfish sightings in neighboring territories such as Venezuela and the Netherland Antilles make the lionfish invasion imminent. The aim of this study was to analyze the lionfish invasion and management strategies in Bonaire thus far in order to make suggestions and safeguard Trinidad and Tobago.

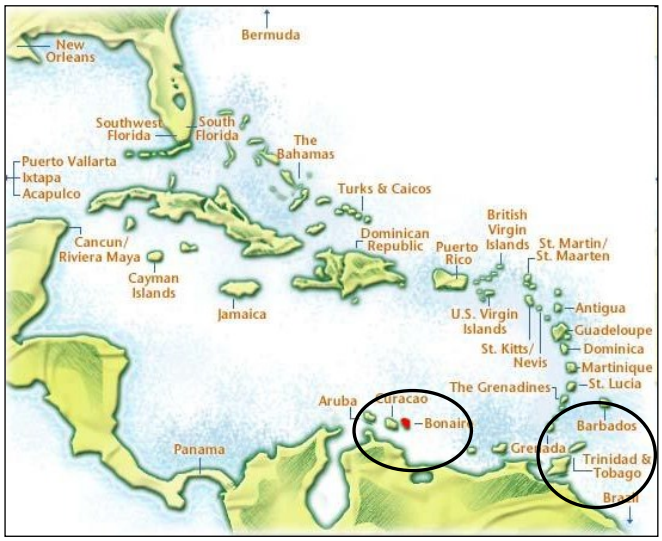


Figure 1. Location of Bonaire and Trinidad & Tobago.

METHODS

Collection of Lionfish

Lionfish were collected in Bonaire between October 26th, 2009 and July 14th, 2011. Specimens were collected either by Bonaire National Marine Park (BNMP) employees or trained volunteers (lionfish hunters) using SCUBA gear at over 90 dive-sites throughout Bonaire. Whilst diving, if a lionfish is observed, divers mark the area by tying a lionfish marker to a dead piece of coral or a piece of rubble. The date and time of sighting; approximate depth and distance from the mooring (and directions of how to find the lionfish) are uploaded onto the 'lionfish database'. Lionfish hunters then use this database to check which dive-sites require lionfish removal. Gloves, hand nets, vinyl dry bags and more recently the ELF tool (Eradicating Lionfish Tool) were used to capture lionfish. Captured lionfish were submitted to CIEE Research Station Laboratory for further analysis.

Lionfish Dissections and Stomach Content Analysis

Data including location, time and depth of capture was recorded along with the standard length (from snout to posterior end), total length (from snout to end of tail) and wet weight of the lionfish. Following dissection, the stomach was severed from the lionfish using a scalpel. The stomach lining was carefully cut and turned inside out with the stomach contents being emptied into a watch glass. Any contents that may have remained in the stomach were washed out with ethanol using a dropper. Individual prey items were examined under the microscope to be identified to the lowest possible taxon. For volumetric analysis, each individual prey item was measured in terms of length, weight and the volume of ethanol displaced (Hyslop 1980).

Questionnaires

Surveys were conducted in both territories with different target groups (divers, dive-shops, fishermen, lionfish hunters and pet shops). Questionnaires were distributed at dive-shops, dive resorts, dive-sites, fishing villages and other public places. Prior to conducting the questionnaire, individuals were asked to point out lionfish on a picture sheet to ensure the validity of their responses. The questionnaires consisted of a mix of likert scale and open answer questions. Amongst the different target groups' questionnaires, the first section consisted of questions focused to the group whilst the second section was identical with the other target groups. This allowed for comparison of people's opinions in different target groups and also territories. In Bonaire, face-to-face questionnaire surveys were conducted with dive-shops, divers, fishermen and lionfish hunters (and some 'divers' questionnaires were left at dive-shops for completion). In Trinidad and Tobago, face-to-face questionnaire surveys were conducted with dive-shops and fishermen, whilst both phone and face-to-face questionnaires were conducted with the pet shops.

Diver Spot Checks, Dive shop Examination and Orientation

Each dive shop was analyzed regarding the presence of lionfish posters and the availability of markers (Bonaire). Where feasible, orientation sessions were attended in Bonaire whereby dive-shops were appraised on the information they included about lionfish. The Bonaire National Marine Park (BNMP) requires that every diver coming to Bonaire attend an orientation session at their hotel and also a check-out dive with a local dive-master or instructor. Divers were randomly chosen and questioned about whether they had a lionfish marker, and if they knew how to use them. Lionfish markers were given to any divers not already possessing markers.

RESULTS

Lionfish Capture in Bonaire

For the duration of this research, the total number of lionfish captured was 2,214. The majority of lionfish captures in Bonaire occurred between 11:00 to 13:00 (n = 506), with a considerable quantity of lionfish being removed 15:00 to 17:00 (n = 461); 13:00 to 15:00 (n = 399) and 09:00 to 11:00 (n = 360) (Figure 2). Smaller quantities of lionfish were captured between 17:00 to 19:00 (n =143) and 07:00 to 09:00 (n = 25) with only ten lionfish being removed between 19:00 and 23:00.

The majority of lionfish captures (44%) occurred between February and April (Figure 3). However, between July and December there were considerably less lionfish captured as the total amount of lionfish captured over this 5 month time frame accounted for only 25% of all captures in Bonaire.

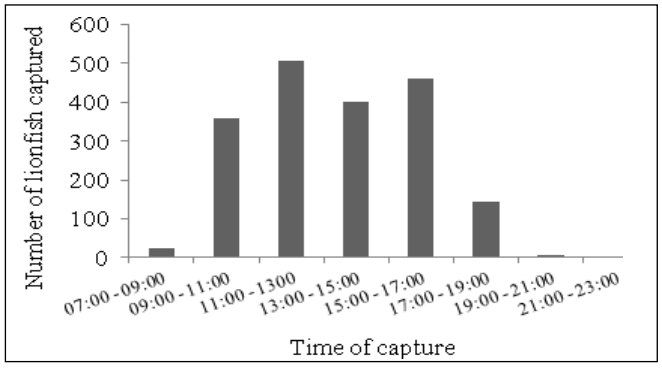


Figure 2. Range of times lionfish were captured in Bonaire.

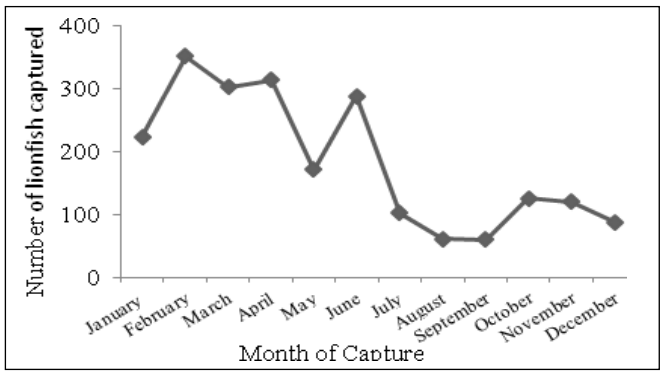


Figure 3. Distribution in the months in which lionfish were captured.

Lionfish Distribution in Bonaire

From their first introduction on October 26th 2009, there has been a continuous increase in the total length (TL) of the first generation of lionfish. However, on June 16th 2010, a lionfish of TL 5.5 cm was captured which indicated the beginning of the second generation, where there was a subsequent increase in the TL of both the first and second generations.

Depth of Capture

Lionfish were captured in Bonaire at depths ranging from 0.9 – 42.7 m. Figure 4a revealed that in Generation 1, there was a slight correlation between the TL of lionfish and the depth of their capture i.e. that as TL increased; there was also an increase in the depth of capture. A One-Way Analysis of Variance revealed that for Generation 1, the differences in the mean values among the different size classes are greater than what would be expected by chance, thus there is a statistically significant difference ($p < 0.001$). The second generation of lionfish also inhabited a range of depths, with there also being a slight correlation between lionfish TL and depth of capture (Figure 4b). This correlation was not as distinct as that observed for Generation 1 as lionfish in the 12.6 to 15.0cm category occurred at shallower depths than those in the 10.1 to 12.5cm category. Nonetheless, a One-Way Analysis of Variance revealed that for Generation 2, the differences in the mean values among the different size classes are greater than what would be expected by chance, thus there is a statistically significant difference ($p < 0.001$).

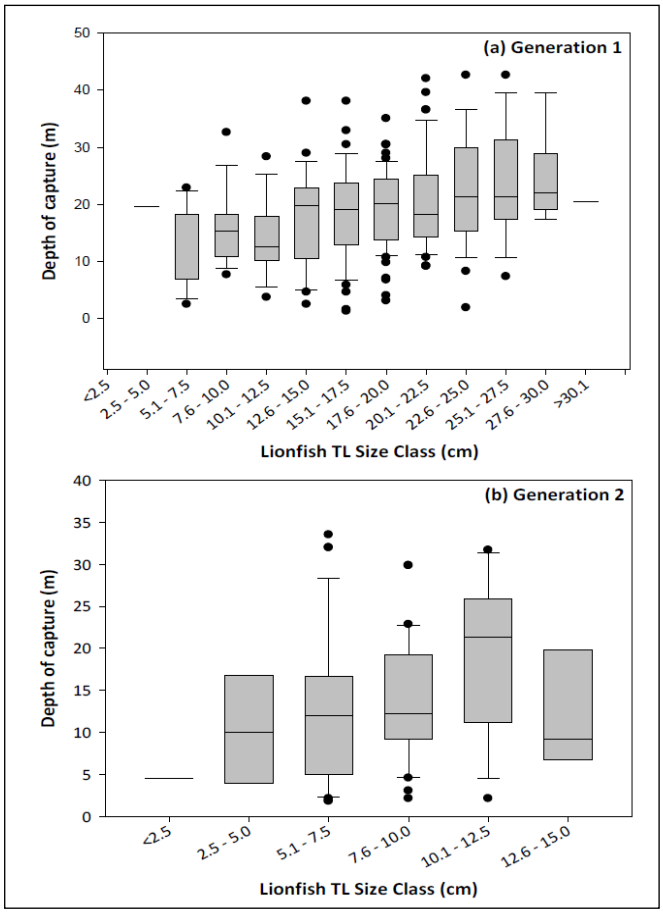


Figure 4. Comparison of the depth of capture of different size classes of Generation 1 and 2 of *Pterois volitans*.

Stomach Content Analysis

Analysis on captured lionfish revealed four main categories of stomach contents: fish only; invertebrates only; a mixed diet (i.e. fish and invertebrates) and empty stomachs. Stomachs that were too digested for analysis were ignored in this study.

Lionfish Prey Composition

Lionfish stomach analysis revealed that the ten most dominant prey families varied by frequency, number and volume (Table 1). Pomacentridae, Apogonidae, Grammatidae and Labridae almost constantly rank amongst the top four according to frequency, number and volume. Serranidae, Gobiidae, and Lutjanidae occupy the mid rank (five to seven) whilst Blennidae, Scaridae and Haemulidae complete the top ten in terms of lionfish feeding preferences.

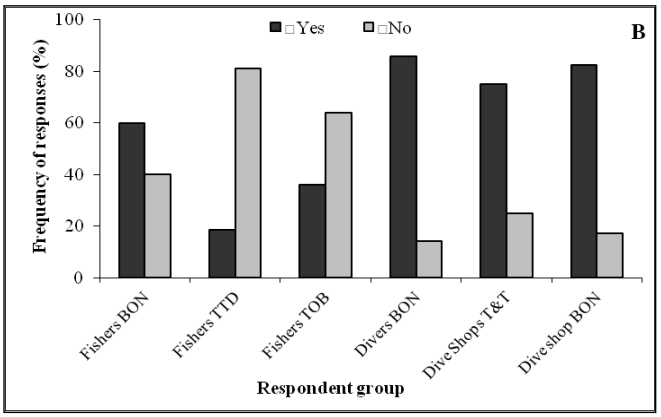
Table 1. Top ten prey families of *Pterois volitans* according to frequency, number and volume.

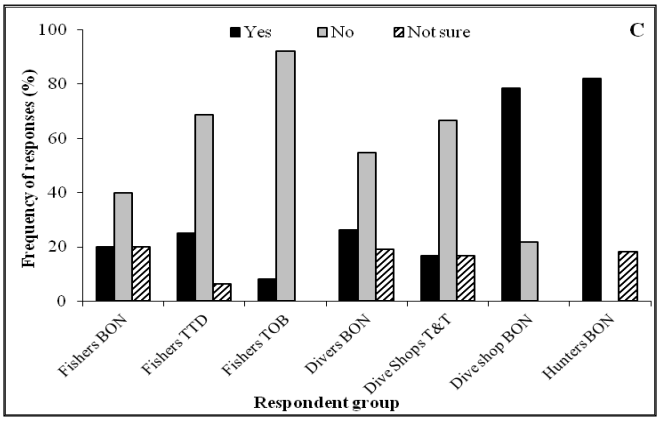
Rank	% Frequency	% Number	% Volume
1	Pomacentridae	Pomacentridae	Pomacentridae
2	Apogonidae	Apogonidae	Serranidae
3	Grammatidae	Grammatidae	Grammatidae
4	Labridae	Labridae	Apogonidae
5	Serranidae	Serranidae	Labridae
6	Gobiidae	Gobiidae	Lutjanidae
7	Lutjanidae	Blennidae	Gobiidae
8	Blennidae	Lutjanidae	Scaridae
9	Scaridae	Scaridae	Blennidae
10	Holocentridae	Haemulidae	Haemulidae

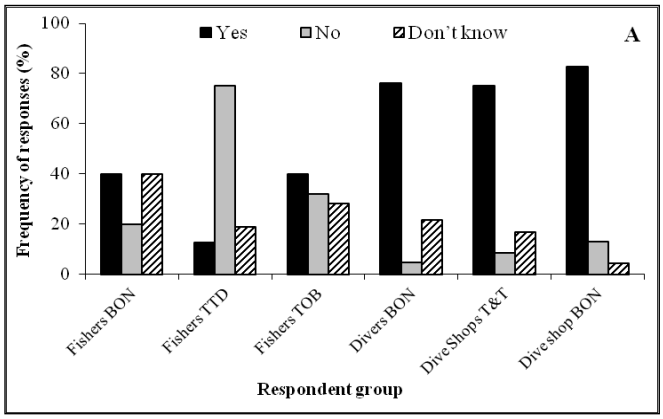
Questionnaire Data

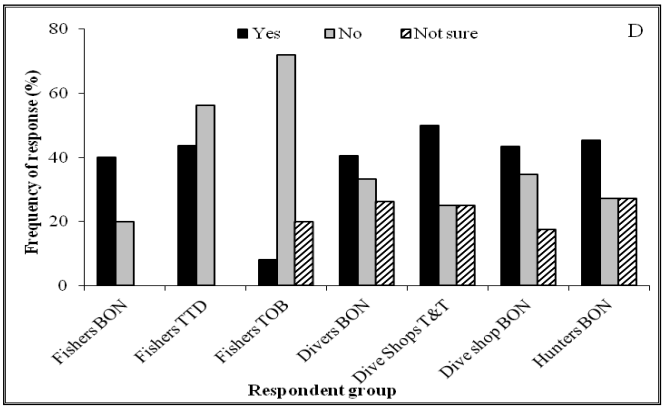
Regarding whether lionfish could be a problem, in Bonaire and Tobago, the majority of the divers and dive shops replied 'Yes', but in Trinidad, 75% of the fishermen replied 'No'. (Figure 5a). Chi-Squared Analysis revealed that there was a statistically significant association ($p = < 0.001$) between respondent group and their awareness of whether lionfish could be a problem. Regarding the awareness of the effects of lionfish, in Bonaire and Trinidad and Tobago, the majority of the divers and dive-shops stated that they were aware. However, the majority of fishermen in Trinidad and Tobago stated that they were unaware of the effects of lionfish on the Caribbean. (Figure 5b). Chi-Squared Analysis revealed that there was a statistically significant association ($p = < 0.001$) between respondent group and their awareness of the effects of lionfish on the Caribbean.

Concerning their willingness to eat lionfish, responses were generally mixed. The majority of fishermen in all territories replied 'No': (Bonaire: 40%; Trinidad: 69%; Tobago 92%). There was a similar unwillingness to eat lionfish with the divers in Bonaire and the dive-shops in Trinidad and Tobago replying. However in Bonaire, the hunters and dive shops were generally willing to eat lionfish (Figure 5c). Chi-Squared Analysis revealed that there was a statistically significant association ($p = <$









[BON: Bonaire; TTD: Trinidad; TOB: Tobago; T&T: Trinidad & Tobago]

Figure 5. Responses of groups in Bonaire and Trinidad and Tobago in relation to **(A)** Whether lionfish could be a problem; **(B)** Awareness of the effects of lionfish; **(C)** Willingness to eat lionfish and **(D)** Whether they are in favour of the creation of a fishing industry for lionfish.

0.001) between respondent group and their willingness to eat lionfish. Regarding the creation of a fishing industry for lionfish there were mixed responses amongst the different groups in all territories. Chi-Squared Analysis revealed that there was a statistically significant association ($p = < 0.05$) between respondent group and their willingness for the creation of a fishing industry for lionfish.

DISCUSSION

Depth

In their native range lionfish inhabit depths of over 50 m (Fishelson 1975), but Vasquez-Yeomans et al. (2011) suggests that they occur at depths over 300 m. Lionfish have been found to inhabit deeper (40 - 99 m) continental shelf depths off southeastern U.S. than the 38 - 43 m and 24 - 76 m reported by Whitfield et al. (2002) and Hare and Whitfield (2003), respectively. Meister et al. (2005) insinuated that this occurrence of lionfish at greater depths off south-eastern U.S. than in their native range actually follows a pattern observed for other subtropical reef fish. Meister et al. (2005) proposed that the occurrence of lionfish at greater depths is related to the larger size of the collected species (120 - 389 mm versus 100 - 184 mm TL) compared to those observed and collected by Whitfield et al. (2002). Other reef fish in the Caribbean have been reported to exhibit a similar positive trend between size and water depth (Wyanski et al. 2000). The restricted depth range owing to the use of SCUBA could account for the smaller size of lionfish suggested by Whitfield et al. (2002).

It is debatable whether lionfish in Bonaire are conforming to literature, i.e. inhabiting deeper waters as they increase in size. Although Figure 4 at first glance appears to indicate that depth of capture increased as lionfish size increased, there is also a wide range of depth occurrence in each size category. In Generation 1, the size classes within the 10 – 30 cm range occupied the full depth spectrum, i.e. ranging from less than 1 m to more than 40 m. A similar occurrence was observed in Generation 2, but this pattern began earlier; with fish in the 5.1 – 7.5 cm size class possessing depth ranges from less than 1 m to 35 m. The depths in which lionfish are occupying in Bonaire suggest further factors which need to be considered for management. The occurrence of lionfish at less than 1 m deep may have negative impacts on tourism as their venomous spines and their cryptic nature may make people disinclined to enter into the water. In the long term, hotel resorts may have to construct nets or other barriers to protect their guests from lionfish.

This extensive depth range which lionfish occupies confirms how resilient a species lionfish are. This makes lionfish management activities increasingly difficult, as resources cannot be directed to removing certain size classes at particular depths. Green and Cote (2009) revealed that targeted removal of certain size classes were successful, however, in the future, the main obstacle will be the efficient channeling of resources.

Feeding

The large numbers of teleost families in the stomach contents indicate that lionfish in Bonaire fed on a wide variety of available prey items, which is consistent with the literature (Morris 2009). However, it is important to note that stomach contents represent the last meal before capture and not necessarily the lionfish's dietary preference.

The families of prey consumed (Table 2) each have different habitat preferences and behavioural ecology. Additionally, Cerino (2010) suggested that the diet composition of lionfish is variable and often correlated with local species community. However in Bonaire, lionfish are feeding in an unpredictable manner and have fed on fish species ranging from the 1st to the 193rd most abundant (REEF 2011). Furthermore, Morris and Akins (2009) revealed the incidence of Atherinidae, Mullidae, and Monocanthidae in the top ten families in lionfish diets. However, these families were absent in lionfish diets in Bonaire. The reason for this is unknown as there is especially an abundance of these families throughout Bonaire.

Management in Bonaire

The success of lionfish control and management in Bonaire is due to the availability of a strong volunteer base. Morris et al. (2010) suggested that for small-scale populations with low connectivity to larger populations, control via fishing mortality and targeted removal may be a viable management strategy. Green and Cote (2009) found that targeting all individuals more than 15 cm removed 89% of the population; more than 20 cm removed 87% and more than 25 cm removed 79% of the population. These results signify that size selectivity in removal efforts can significantly affect the success of lionfish population management efforts (Green and Cote 2009).

Based on Figure 4 there is an evident difference in lionfish awareness between those involved in diving and fishing industries, in both territories. In Bonaire, there have been widespread lionfish awareness schemes whereby posters are visible at all dive-shops, fishing areas and other public venues such as shops, bars and notice boards. Furthermore, as mandated by the Bonaire National Marine Park, every diver visiting Bonaire is required to attend an orientation session at their hotel/resort. Through this orientation, divers are briefly educated about the lionfish invasion, and the procedure to follow if a lionfish is spotted whilst diving. Divers are also educated about the lionfish marking and reporting procedure.

Lionfish Awareness in Trinidad and Tobago

Within Trinidad and Tobago, a territory yet to be invaded by lionfish, the management procedures currently in place are still in their infancy. Trinidad and Tobago has instated a ban on the import of lionfish in July 2010 which is an important step in managing invasives. Claydon and Calosso (2008) suggested that a total ban should be placed on the import of lionfish and owning lionfish in aquaria. However, they also mandated that any lionfish already held in aquaria should be presented to the relevant authorities, live or dead. Therefore, this is one area which Trinidad needs to address in the future. Furthermore, there has been little or no lionfish awareness other than a newspaper article. Regarding the fishermen in Trinidad, the 10% that claimed to be aware of lionfish (Figure 4) had actually heard of lionfish independently, i.e. via documentaries on National Geographic, reading magazines, or seeing live lionfish at pet shops.

The Department of Marine Resources and Fisheries in Tobago is responsible for the lionfish awareness scheme, whereby posters have been erected in all dive-shops and most fishing villages. This accounts for the difference in awareness between fishermen in Trinidad and Tobago. Nonetheless, within Tobago, there are differences in the level of success of these posters. In the more developed areas of Tobago, most fishermen were able to correctly identify lionfish, and had some knowledge of the effects of lionfish, based on what they read on the posters. However in the more rural areas, there was considerably less awareness of lionfish, despite numerous, visible posters. Differences in the literacy levels could account for this since, although posters are available in this area, because the target audience may only be partially literate, the success rate of posters is affected.

Interestingly, the content matter of the posters also affected the knowledge level of individuals. In Bonaire, posters supply information on how to correctly mark and report lionfish to the BNMP and information on the actual impacts of lionfish and why they are a problem. Tobago alternatively provides information on what numbers to call when a lionfish is spotted, and also a description of lionfish. It is also highlighted that lionfish are poisonous, and importantly 'Do Not Touch'. This feature affects people's willingness to eat lionfish. Based on the posters, many fishermen believe lionfish (meat) is poisonous and are hesitant to eat lionfish. Lionfish are considered a food fish in their native range (Morris and Whitfield 2009) whilst the Scorpaenidae family is a delicacy in Mediterranean cuisine (Morris et al. 2011a). Fishermen in the Caribbean are familiar with native Scorpionfish which they know are poisonous. So the 'unknown' about lionfish coupled with past Scorpionfish experience account for the unwillingness to eat lionfish.

Lionfish Management in Trinidad and Tobago

Interviews with pet shops in Trinidad revealed the occurrence of lionfish within Trinidad. The main importer of lionfish in Trinidad claimed to import his fish directly from the Indo-Pacific Region. This is problematic, as the release of any of these individuals adds new genes to the already established population, thereby further strengthening their genetic diversity. The pet-shops/importers interviewed suggested that there was little demand for lionfish and many did not stock lionfish. Lionfish are saltwater, predatory species and require special, separate tanks, a resource which many shops do not posses. Furthermore, very few pet-shops actually specialize in salt water tanks. However, as suggested by one respondent, the fact that lionfish are predators, and now banned may actually increase the demand, similar to when piranhas were banned in Trinidad.

Lessons Learnt from Bonaire

The first step that Trinidad and Tobago needs to take is the development of a Lionfish Response Management Plan. As part of this, co-ordination and communication with relevant stakeholders and education and outreach are priorities (Table 2). The development of a response plan in April 2009 allowed Bonaire to respond quickly once lionfish arrived in Bonaire. In Bonaire, monitoring activities were concentrated in the Bonaire National Marine Park. A similar suggestion should be made for Trinidad and Tobago (Table 2).

The Buccoo Reef Marine Park (BRMP) covers an area of 150 ha with a terrestrial area of 300 ha (Brown et al. 2001). This protected area includes coral reef, sea grass lagoon and fringing mangrove (Brown 2002); habits suitable for lionfish (Albins and Hixon 2008, Barbour et al. 2010, Schofield et al. 2010). Buccoo Reef is deemed an IUCN Category IV Protected Area; however, no effective management has been executed since its designation as a protected area (Laydoo 1998, Da Costa 2010). The BRMP represents an area of suitable habitat with an abundance of prey and its location in relation to Venezuela and the Netherland Antilles makes this area of Tobago a likely point of introduction.

CONCLUSION

The best strategy for Trinidad and Tobago as lionfish have not yet arrived will be the strategy to focus on popular areas and marine parks. Instead of spreading resources to monitor the entire island, focusing more of the sampling effort on the Buccoo Reef Marine Park (BRMP) would be the best strategy for immediate implementation.

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Table 2. Recommended strategy for Trinidad and Tobago.

Aspects	Description	Recommendations for Trinidad and Tobago
Co-ordination and Communication	Essential for co-ordination with agencies and stakeholders such as the Government, health services, marine parks, fisheries personnel and dive and tourism industries. Can be achieved via lionfish workshops and educational sessions.	Bonaire's success was due to stakeholder involvement. Thus in Tobago the formation of a partnership with the dive shops is required so that dive tanks and lionfish removal equipment can be provided to lionfish hunters.
Education and outreach	Development of a plan to inform the general public and stakeholders about the effects of lionfish, and the proper way to report lionfish sightings and how to safely handle specimen. Communication should be established within the health sector in order to prepare for possible envenomations.	Tobago has already begun a lionfish awareness scheme, with focus on divers, dive shops and fishermen. However, scheme needs to be introduced to Trinidad. Initiate partnership with health-care facilities to be prepared for lionfish envenomations
Likely method of introduction to Trinidad and Tobago	Betancur et al. (2011) suggested that the minimum number of founding individuals required to account for the observed genetic diversity in the western Atlantic lionfish, lies between 8 to 12 individuals. Surveys of pet shops in Trinidad revealed that there are already at least 12 individuals, enough to foster a viable lionfish population if released. Confirmation of lionfish in Venezuela and the Netherland Antilles suggests that dispersal via oceanic currents is another vector of introduction.	Further to the already instated ban on lionfish, all lionfish need to be issued to the relevant authorities (e.g. Institute of Marine Affairs in Trinidad and the Department of Marine Resources and Fisheries in Tobago) either alive or dead (Claydon and Calosso 2008). Due to limited resources, monitoring efforts should be targeted to the Buccoo Reef Marine Park.
Lionfish ecology	*Feeding Ecology:* Based on lionfish stomach contents in Bonaire, lionfish possess a very broad diet and are not limited by certain species. Thus the abundance of suitable prey fish within Tobago means that lionfish will flourish if introduced. Impacts are likely to be exacerbated due to venomous defense and also the availability of vacant niches (Makjovic and Leeuwen 2008; Albins and Hixon 2011) as a result of overfishing top predators like snappers and groupers (Leung et al. 2011). *Habitat Preference*: Research on lionfish in Bonaire and the wider Caribbean revealed that lionfish inhabit a variety of habitats ranging from coral reefs to mangroves and sandy bottoms. Tobago's Buccoo Reef is an ideal ecosystem for lionfish due to the variety of habitats and its proximity to Venezuela makes this area of Tobago may be the first point of introduction.	Monitoring efforts should be targeted to Buccoo Reef Marine Park. By targeting popular areas and marine parks, this approach minimises contact with lionfish and selective eradication in the future can lead to an overall reduction in lionfish populations.

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.

Albins, M.A. and M.A. Hixon. [2011]. Worst case scenario: potential long-term effects of invasive predatory lionfish (*Pterois volitans*) on Atlantic and Caribbean coral reef communities. *Environmental Biology of Fishes.* In Press.

Barbour, A.B., M.L. Montgomery, A.A. Adamson, E. Diaz-Ferguson, and R.R. Siliman. 2010. Mangrove use by the invasive lionfish *Pterois volitans. Marine Ecology Progress Series* **401**:291-294.

Bervoets, T. 2009. Lionfish Response Plan, St Eustatius National Marine Park. [Online] Accessed February 16th, 2010 from: http://www.nacri.org/downloads/STENAPALionfishResponsePlan2009.pdf.

Betancur, R.R., A. Hines, A., Acero, G. Orti, A.E. Wilbur, and D.W. Freshwater. 2011. Reconstructing the lionfish invasion: insights into Greater Caribbean biogeography. *Journal of Biogeography* **38** (7):1281-1293.

Brown, K., W.N. Adger, E. Tompkins, P. Bacon, D. Shim, and K. Young. 2001. Trade-off analysis for marine protected area management, *Ecological Economics* **37**:417-434.

Brown, K. 2002. Innovations for Conservation and Development. *The Geographic Journal* **168**(1):6-17.

Cerino, D.S. 2010. Bioenergetics and trophic impacts of invasive Indo-Pacific lionfish. Masters of Science Thesis, East Carolina University, Greenville, North Carolina USA. [Online], Accessed February 8th, 2011 from: http://thescholarship.ecu.edu/bitstream/handle/10342/2724/Cerino_ecu_0600M_10151.pdf.

Claydon, J.A.B. and M.C. Calosso. 2008. A strategy to reduce the impact of the invasive red lionfish (*Pterois volitans/miles*) in the Turks and Caicos Islands. Technical Report, School for Field Studies, Center for Marine Resource Studies, South Caicos, Turks and Caicos Islands. [Online] Accessed March 23rd, 2011 from: http://www.marineresourcestci.com/Turks_and_Caicos_marine_resources/Lionfish_conclusions_Turks_and_caicos.html.

Da Costa, D.J. 2010. An Economic Valuation Analysis of Buccoo Reef Marine Park, Tobago, West Indies. FIL Electronic Theses and Dissertations, Paper 290. [Online], Accessed April 19th, 2011 from: http://digitalcommons.fiu.edu/etd/290/.

Fishelson, L. 1975. Ethology and reproduction of pteroid fishes found in the Gulf of Aqaba (Red Sea), especially *Dendrochirus brachypterus* (Cuvier) (Pteroidae, Teleostei), *Publication of Statistical Zoology, Napoli* **39**:635-656.

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.

Gonzales, J., M. Grijalba-Bendeck, A.P. Acero, and R.R. Betancur. 2009. The invasive red lionfish, *Pterois volitans* (Linnaeus 1758), in the Southwestern Caribbean Sea. *Aquatic Invasions* **4**(3):501-510.

Green, S. and I. Côté. 2009. Consumption Potential of Invasive Lionfish (Pterois volitans) on Caribbean Coral Reefs. *Proceedings of the 62nd Gulf and Caribbean Fisheries Institute*. **62**:366-367.

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 2.

Hyslop, E.J. 1980.Stomach contents analysis- a review of methods and their application. *Fish Biology* **17**:411-429.

Johnson, M.W. and S.J. Purkis. 2011. Spatial analysis of the invasion of lionfish in the western Atlantic and Caribbean. *Marine Pollution Bulletin* **62**:1218-1226.

Laydoo, R.S., K. Bonaire, and G. Alleng. 1998. Buccoo Reef and Bon Accord Lagoon, Tobago, Republic of Trinidad and Tobago, Caribbean Coastal Marine Productivity, (CARICOMP) Coral Reef, Seagrass and Mangrove Site Characteristics, UNESCO, Paris, France..

Leung, M-R., D. Padilla, N. Shemer, J. Vinagera, and B. Song. 2011. A Symmetric Intraguild Predation Model for the Invasive Lionfish and Native Grouper, Mathematical and Theoretical Biology Institute, Arizona State University, [Online] Accessed October 4th, 2011 from: http://mtbi.asu.edu/files/lionfish_paper.pdf.

Majkovic, A., and T.E. Leeuwen. 2008. Predation on the invasive red lionfish, *Pterois volitans* (Pisces: Scorpaenidae), by native groupers in the Bahamas. *Coral Reefs* **27**:501.

Meister, H.S., D.M. Wyanski, J.K. Loefer, S.W. Ross, A.M. Quattrini, and K.J. Sulak. 2005. Further Evidence for the Invasion and Establishment of *Pterois volitans* (Teleostei: Scorpaenidae) Along the Atlantic Coast of the United States. *Southeastern Naturalist* **4** (2):193-206.

Morris, Jr., J.A. 2009. *The Biology and Ecology of the Invasive Indo-Pacific Lionfish*. Ph.D. Dissertation, North Carolina State University, Raleigh, North Carolina USA.

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

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

Morris, Jr., J.A. and P.E. Whitfield. 2009. Biology, Ecology, Control and Management of the Invasive Indo Pacific Lionfish: An Updated Integrated Assessment. NOAA Technical Memorandum NOS NCCOS 99.

Morris, Jr., J.A., K.W. Shertzer, and J.A. Rice. 2010. A stage based matrix population model of invasive lionfish with implications for control. *Biological Invasions* **13**(1):7-12.

Morris, Jr., J.A., A. Thomas, A.L. Rhyne, N. Breen, L. Akins, and D. Nash. 2011a. Nutritional properties of the invasive lionfish: A delicious and nutritious approach for controlling the invasion, Aquaculture, Aquarium, Conservation & Legislation. *International Journal of the Bioflux Society* **4**(1):21-26.

Morris, Jr., J.A., C.V. Sullivan, and J.J. Govoni 2011b. Oogenesis and spawn formation in the invasive lionfish, *Pterois miles* and *Pterois volitans*. *Scientia Marina* **75**(1):147-154.

National Oceanic and Atmospheric Administration Coral Reef Information System [NOAAs CoRIS]. 2009.The Indo-Pacific Lionfish Invasion of the U.S. South Atlantic Sea Coast and Caribbean Sea. [Online], Accessed: December 21st, 2009 from http://coris.noaa.gov/exchanges/lionfish/.

Reef Environmental Education Foundation (REEF). 2011.Geographic Zone Report. [Online], Accessed February 11th, 2011 from: http://www.reef.org/db/reports/geo/TWA/8503.

Ruiz-Carus, R., R.E. Matheson, Jr., D.E. Roberts Jr., 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.

Schofield, P.J., J.A. Morris Jr., J.N. Langston, and P.L. Fuler. 2010. *Pterois volitans/miles*. US Geological Survey Nonindigenous Aquatic Species Data Base, Gainesville, Florida USA. [Online] Accessed April 15th 2011 from: http://nas.er.usgs.gov/queries/FactSheet.asp?speciesID=963.

Vasquez-Yeomans, L., L. Carillo, S. Morales, E. Malca, J.A. Morris, Jr. T. Schultz, and J.T. Lamkin. [2011]. First larval record of *Pterois volitans* (Pisces: Scorpaenidae) collected from the ichthyoplankton in the Atlantic. *Biological Invasions* In Press.

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. Munoz, and C.M. Addison. 2007. Abundance estimatesof the Indo-Pacific Lionfish *Pterois volitans/miles* complex in the Western North Atlantic. *Biological Invasions* **9**:53-64.

Wyanski, D.M., D.B. White, and C.A. Barans. 2000. Growth, population age structure, and aspects of the reproductive biology of snowy grouper, *Epinephelus niveatus*, off North Carolina and South Carolina. *Fishery Bulletin* **98**:199-218.