The Impacts of the Indo-Pacific Lionfish (*P. volitans* and *P. miles*) on Fish Assemblages in Near Shore Benthic Reef Habitats of the Central and Southern Bahamas

KEY WORDS: Lionfish, invasive species, habitat alteration, marine ecology, The Bahamas

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ABSTRACT

Since the first recorded Tropical Western Atlantic sightings of the Indo-Pacific Lionfish (*P. volitans* and *P. miles*) in the 1990s, this mid-level predator has become a common component of shallow-water fish assemblages from mangrove creeks to coral reefs. Although the origins of this cryptic invasion are unknown, the success of lionfish, specifically in the near shore waters of The Bahamas, has been document through increased abundance and increase in the number of benthic habitats utilized since 2005. The long term impact of lionfish on near shore fish assemblages in the wider Caribbean is not known, but invasive species management planning requires some information on changes in the abundance and diversity of reef fishes, especially species commercially exploited. This large synoptic survey of fish assemblages from four types of reef habitats on two islands in The Bahamas examines how the presence of lionfish can alter shallow-water tropical fish assemblages. Patch reefs, hard bottom, fringing reefs and channels reefs adjacent to the islands of Great Exuma (Central Bahamas) and Great Inagua (Southern Bahamas) were evaluated via a rapid assessment methodology. Roving diver fish surveys were carried out with a coastal assessment of anthropogenic impacts (ranking) from development and/or fishing pressure. Univariate and Multivariate statistics were used to determine if the presence of lionfish is significantly altering the recorded fish assemblages when compared to sites with no lionfish present. This community-level assessment can be applied in the understanding of how the lionfish invasion may affect near shore reef habitats, and ultimately the production of commercially important fisheries species.

Los Impactos del Pez León *P. volitans* y *P. miles*

PALABRAS CLAVE: Pez león, impactos, Bahamas

Les Impacts du Poisson-Lion Originaire de L'Océan Indien et Pacifique (*P. Volitans* and *P. miles*) sur les Assemblages de Poissons des Habitats des Récifs Près de la Côte Benthique dans le Centre et le Sud des Bahamas

MOTS CLÉS: Poisson-lion, impacts, habitats des récifs, Bahamas

INTRODUCTION

The range expansion of the Indo-Pacific Lionfishes *P. volitans* and *P. miles* has been well documented along the east coast of the United States and throughout the islands and continental coasts of the Tropical Western Atlantic since the early 1990s (Whitfield et al. 2002, Morris and Whitfield 2009). This invasive alien species (IAS) was originally brought from Asia through the aquarium trade and has been known to occupy a variety of benthic habitats throughout its introduced range (Ruiz-Carus et al. 2006).

Following the modern approach in the study of invasion ecology by Elton (1958), a series of classification schemes to categorize and describe IAS have been presented in the literature. The method used by Davis and Thompson (2000) recognizes that not all invasion events are similar, therefore leading to the development of three organizing criteria: dispersal distance, uniqueness, and ecosystem impacts. These organizing criteria can be applied to any invasion to better determine its long-term ecological ramifications. By applying these same criteria to the recent lionfish invasion, it may be possible to predict future impacts based on established studies of other marine invaders. Lionfish have invaded across the largest shallow-water tropical province – the Tropical Western Atlantic, thus the success of their dynamic dispersal distance, both uniqueness and impact appear to be very habitat specific (Green and Côté 2009).

The diversity of marine habitats – reefal and non-reefal across the coastal shelf to platform margins and slopes – are only now being characterized with some rigor in benthic system classifications, thus it is critical to identify habitat-specific data to infer potential impacts based on Davis and Thompson's methods. The question remains: what impact does established invasion ecology theory predict an IAS, such as lionfish, may have on native ecosystems? This is an especially critical question for islands of the wider Caribbean as islands are particularly vulnerable to invasion impacts, and reef resources of the region are already degraded from a range of threats (Reigl et al. 2009). Carlton (1996) predicts changes at community level with the introduction of new species due in part to fundamental changes in the flow of matter and energy within an ecosystem. Along the same lines, Shae and Chesson (2002) cite the establishment and growth of an

IAS as critical factors that help determine impacts at the species assemblages that make up the community.

Although Morris and Akins (2009) have been be initiated on the feeding and reproductive biology of the lionfish, we wish to examine the broad assemblage of shallow-water tropical fishes associated with near shore reef resources to determine if lionfish are indeed changing the flow of energy/matter in specific habitat. Additionally, learning more about how lionfish interact with the assemblages of fishes on specific reef habitats, via predation and competition, can further substantiate long term ecological implications of this IAS.

Lionfish tend to act as opportunistic mid-level ambush predators with feeding preference dominated by juvenile crustaceans, wrasses, and grunts (Albins and Hixon 2008). With voracious appetites consuming 8.5 g of prey items per day (Fishelson 1997), lionfish also have the potential to reduce survivorship of newly recruited reef fishes, possibly resulting in the displacement and out-competition of other native species in similar trophic levels (Snyder and Burgess 2007). Analyzing a shift in abundance for both prey and competitor species may help to substantiate impacts on a species specific level; however, the impact of lionfish invasion may be difficult to examine when competitors, like groupers, are also heavily exploited (Sadovy and Eklund 1999).

As the lionfish are already well established, and populations appear to have progressed to the growth phase (Shae and Chesson 2002), invasion theory suggests we look for the presence of an observable shift in the abundance of other species (not competitors) through predation and mortality impacts on juveniles (Elton 1958). Novel predation on small individuals/juveniles of other fish species could drastically alter the population dynamics of those species, especially if only limited predation existed on juvenile fish prior to the introduction of an invasive species (Albins and Hixon 2008). Consequences of these new events should result in an overall decrease in community diversity of fishes.

Evidence from natural lionfish range expansion from Southeast Asia into East Africa shows a historical preference for expansion into highly impacted systems (Schultz 1986). This may help to explain why lionfish have been so successful invading island reef habitats in the Tropical Western Atlantic, which also have a history of exposure to overfishing, land-based sources of pollution, and other direct threats to reef health (Reigl et al. 2009, Sullivan Sealey et al. 2008). Although the success of lionfish is clearly related to the ability of this invader to act as a habitat generalist within its introduced range, this is not to say that lionfish occur everywhere. Also, within the areas where lionfish are found the level of impact may vary between individual habitats (Shae and Chesson 2002). It may even be possible that in some habitats lionfish display little or no impact, but rather remain as a persistent, marginal component of the fish community. Building upon this hypothesis, our study aims at quantifying specific, measurable changes in reef fish diversity throughout different near shore habitats to better understand the role of lionfish as an IAS.

Two islands in The Bahamas were selected for characterization of reef fish assemblages as these islands has small populations, moderate fishing pressure, and historical roving diver data recording occurrence and abundance of fishes dating back to 1996. We wish to look at how near shore fish assemblages have changed over space and time in the southern Bahamas; with attention to changes that may have occurred since the first reported sightings of lionfish in 2006.

If lionfish are changing the flow of energy and matter through a community, then there are several questions to be addressed:

i) What and how much piscine prey are they eating and what will be the long term implications of this increased mortality on prey populations?; and
ii) What mid-level predators are they competing against? Assessment of the larger shallow-water reef fish assemblages can help identify species or guilds of species impacted by this invasion.

METHODS

For this survey of near shore benthic habitats we have chosen to focus on two unique island systems within the Bahamas: Great Exuma in the central Bahamas and Great Inagua in the southern Bahamas (Figure 1). Situated in the heart of the archipelago, Great Exuma offers some of the best natural harbors in the country. With historic importance since the late 18th century and a population of 4,000 permanent residents (Sealey 1990), this island system has had a history of anthropogenic impacts on the near shore benthos. Great Inagua, which is the 3rd largest island in the Bahamas, has also played a major role in the historical development of the nation. Natural salt pans have been exploited in Great Inagua since the 18th century, and today a majority of the 800 residents continue to work in the world's largest solar salt operation run by Morton (Sealey 1990). However, the establishment of a national park occupying the eastern two thirds of the island has maintained many of the prisitine ecosystems unique to Great Inagua.

Nero and Sealey (2005) describe a great variety in near shore fish communities, even within the same habitat type, between islands in the Bahamas. Therefore, to determine the species present and relative fish abundances at the sites surveyed in Great Exuma and Great Inagua, roving diver fish surveys (Schmitt and Sullivan 1996) were utilized. These surveys employed the effort of one or more trained individuals who snorkeled randomly, traversing a defined survey area within each of the sites. The duration of these surveyed varied; however, the average survey time was 45 minutes per diver. During the surveys every fish species sighted was noted and given a relative abundance on a four tier scale ((1) - 1, (2)2 - 10, (3)11 - 99, (4)100+) (Schmitt and Sullivan 1996). Lionfish abundance was also noted at each site and tallied on an individual basis. Following the completion of each survey where lionfish were present, every effort was made to remove them from the survey site in accordance with best management practices established in the Bahamas (Sullivan Sealey et al. 2009). Data and bottom time for each individual survey was aggregated inter-annually by site into a spreadsheet for record keeping and analysis.

To determine the relationships between lionfish presence/absence and the community diversity for each of the sites surveyed, univariate and multivariate statistical analyses were used in this study. PRIMER (Plymouth Routines in Multivariate Ecological Research) software was used to calculate the Berger-Parker (d) and Shannon (H') diversity indices (Clarke and Warwick 1994) to give an estimate of diversity. Similarity Percentage analysis (SIMPER) was used to assess species specific contributions (Clarke 1993), whereby the Bray-Curtis dissimilarity between the three habitat types (Patch reefs, Fringing reefs, and Hardbar) was calculated, thus yielding the average percentage contribution that each species contributes towards any difference in community diversity. Finally, principle component analysis (Shaw 2003) allowed for the isolation of specific fish species contributing to the difference in community diversity over time. For the purpose of this analysis, sites were grouped according to habitat type regardless of the island with which they are associated.

RESULTS

Figure 1. A map of the Bahamian archipelago showing the location of the two islands surveyed: Great Exuma and Great Inagua.

To best assess if temporal changes in fish biodiversity at the study stations is an artifact of the lionfish introduction since 2006, surveys of five stations in Great Exuma were separated into three discrete groups based on three to four year survey intervals. Table 1 is a summary of the stations and survey effort used in this study. All stations included in this analysis had aggregate bottom time surveys in excess of 180 minutes, which provides ample data to conduct rapid assessments of fish assemblages (Schmitt et al. 2002). While bottom time for these sites does not reach the 20 hours necessary to observe ~95% of the species diversity at a given site (Schmitt and Sullivan 1996), other variables were considered to maximize statistical accuracy. To create the best description of the near shore habitats on these islands (Mumby et al. 1996), stations surveyed ranged in habitat diversity (channel reefs, patch reefs, fringing reefs, hardbar). Also, surveys were staggered between 7:00 (dawn) and 18:00 (dusk) to insure that a maximum number of species at each site could be accounted for, regardless of temporal variation in behavioral/ feeding patterns (Nero and Sealey 2005). Furthermore, surveys conducted in Great Exuma were staggered seasonally as well, with a majority of surveys conducted in January (winter) and June (summer).

Initial analysis of the Shannon (H') and Berger-Parker (d) diversity indices for Great Exuma from 1996 until 2010 (Table 2) reveals a relatively high measure of biodiversity across all sites as represented by species evenness and abundance respectively (Clarke and Warwick 1994). Nevertheless, there is a decrease in diversity for all sites in Great Exuma of over 2% in the average H' index (4.149 in 1996 - 1999 to 3.956 in 2007 - 2010) and over 7% in the average d index (14.28 in 1996 - 1999 to 12.24 in 2007-2010). While this decrease in biodiversity corresponds with the introduction of lionfish into the region, other factors (climate change, pollution, etc.) may also play a role in this notable shift. With no historical data for Great Inagua there it is not possible to determine changes in diversity as thoroughly as in Great Exuma. However, based on the diversity indices derived for surveys between 2009 - 2010 it is evident that all sites surveyed, regardless of location or habitat type, across the island display unusually high levels of diversity. This is to be expected in a relatively pristine, un-impacted marine ecosystem with little anthropogenic pressure.

Examining differences in the average diversity indices between habitat types on both islands, the channel reef site (EX-FC) displays significantly higher Shannon (4.237) and Berger-Parker (15.132) diversity than all other habitat types. These findings are likely due to a high species evenness present on this habitat as many species swim through during migration to other habitat types (Schmitt et al. 2002). Average diversity index values for the six patch reef sites surveyed are also high (H' = 3.96, d = 12.249), followed by three hardbar sites (H' = 3.94, d = 11.917) and one fringe reef (H' = 3.978, d = 11.865).

The geometrically scaled abundance was transformed (square root) and Bray Curtis Similarity indices calculated comparing each survey station. Cluster diagrams show the relatedness between surveys highlighting the large differences between islands and reef habitat types, and the smaller differences in fish assemblages over the 14-year time period of surveys. Figure 2 shows the similarity comparisions between all stations of different habitat types across the 14 year survey history. This cluster diagram clearly illustrates that, with the exception of IN-027 AR, patch reef stations share the largest degree of similarities (61.91%). The hardbar habitats analyzed displayed little similarities between sites in different island groups, and the one fringing reef station (IN-013) and channel reef station (EX-FC) show great dissimilarities from all other sties. Five sites that have been surveyed for over 14 years show temporal shifts in fish assemblages over the three time periods: 1996 to 1999, 2002 to 2006 and 2007 to 2010 (when lionfish were documented on the sites) (Figure 3). Changes within habitats are detectable when habitats are segregated.

Priniciple component analysis was carried out to understand which fish species (variables) were contributing to both the "between habitat" differences and the "between time periods" differences. The patch reefs in Great Exuma show changes over time primariy in grunt (cottonwick, sailors choice, bluestripe grunt) and mojarra (yellowfin and flagfin) abundance. For all hardbar habitats there was significant variation in lionfish abundance, along with changes in hogfish and brown chromis occurrence. EX-FC (channel reef) in Great Exuma showed the greatest temporal changes over 14 years attributed to changes in silversides, sergeant majors, french grunts, and Nassau groupers (Figure 4).

DISCUSSION

Since the onset of a rapid proliferation of lionfish across the Bahamian archipelago, the consensus amongst the scientific and stakeholder communities has been that the lionfish, as an IAS, poses an immediate threat to delicate reef ecosystems (Morris and Whitefield 2009). While these *a priori* conclusions may have some validity, the diversity in benthic habitats throughout the Caribbean presents a challenge in generalizing any potential impacts of this cryptic invasion. With most prior studies focusing on reef habitats deeper than 10 m (Green and Côté 2009), our results offers a novel view of community-level impacts that lionfish may be having in these dynamic near shore environments.

Based on studies of other marine invasive species, one would expect lionfish to exhibit similar behavior by significantly altering the overall community diversity, as well as some specific species abundances, throughout its range (Elton 1958). Our analysis reveals that, despite apparent high values for diversity, there are observable shifts in fish assemblages seen at the community level over time and between specific near shore habitats. With an overall decline in abundances of grunts, silversides, chromis, and damselfish, all of which are known to be predated on by lionfish (Albins and Hixon 2008, Morris and Akins 2009), this shift could be the result of lionfish invasion. Additionally, the significant decline of juvenile Nassau groupers characertistic of these near shore environments at the channel reef station (EX-FC), which by far had the highest diversity of any habitat surveyed, may be related to broader regional factors relating to fishing and recruitment as well as the increase in lionfish abundance.

Although the relative good health of Bahamian near shore reefal habitats has allowed for the maintenance of a high species diversity despite the introduction of lionfish, our survey has also indicated a noticeable decline in overall biodiversity for all habitats in Great Exuma over the past 14 years. Over time, these near shore habitats have lost some components of their fish assemblages, notably butterfly fish, eels and other specialized feeders, which further indicates a shift in fish assemblages at the community level. Since measures of biodiversity take into

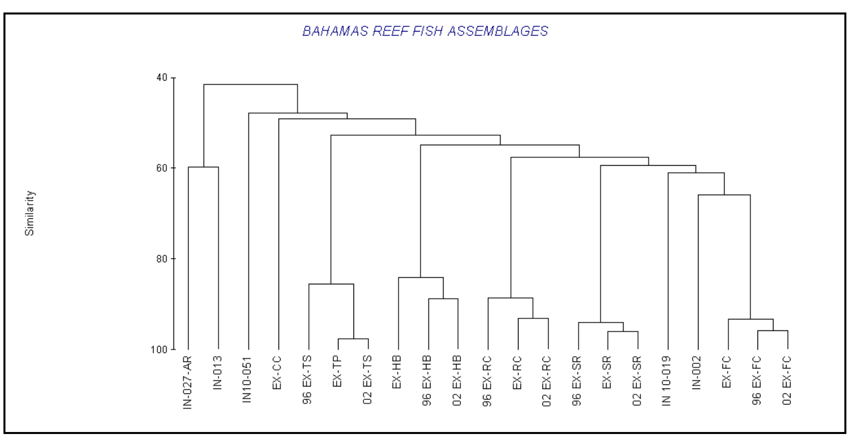

Figure 2. Bray Curtis Similarity Dendogram comparing all habitats surveyed across both islands. The y-axis represents the percent similarity that sites share with each other.

TABLE 1: Summary of stations

STATION	CODE	ISLAND	HABITAT	DATE OF FIRST SURVEYS	DATES OF LAST SURVEYS	Bottom time (minutes)	Bottom Time (hours)	LIONFISH ABUNDANCE
ROLLE CAY	96 EX-RC	EXUMA	Patch reef	1996	1999	180	3.0	0
HOOPERS BAY	96 EX-HB	EXUMA	Patch reefs	1996	1999	310	5.2	0
STUDENTS PATCH REEF	96 EX-SR	EXUMA	Patch Reef	1996	1999	220	3.7	0
FOWL CAY REEF	96 EX-FC	EXUMA	Channel reef	1996	1999	240	4.0	0
TRIPLETS/ SAND DOLLAR	96 EX-TS	EXUMA	Patch Reef	1996	1999	180	3.0	0
ROLLE CAY	02 EX-RC	EXUMA	Patch reef	2002	2006	270	4.5	0
HOOPERS BAY	02 EX-HB	EXUMA	Patch reefs	2002	2006	185	3.1	0
STUDENTS PATCH REEF	02 EX-SR	EXUMA	Patch Reef	2002	2006	210	3.5	0
FOWL CAY REEF	02 EX-FC	EXUMA	Channel reef	2006	2010	260	4.3	0
TRIPLETS/ SAND DOLLAR	02 EX-TS	EXUMA	Patch Reef	2007	2010	200	3.3	0
ROLLE CAY	EX-RC	EXUMA	Patch reef	2006	2010	240	4.0	1
HOOPERS BAY	EX-HB	EXUMA	Patch reefs	2007	2010	210	3.5	2
STUDENTS PATCH REEF	EX-SR	EXUMA	Patch Reef	2006	2010	425	7.1	2
CRAB CAY NEARSHORE	EX-CC	EXUMA	Hard bar	2007	2010	320	5.3	2
FOWL CAY REEF	EX-FC	EXUMA	Channel reef	2006	2010	310	5.2	2
TRIPLETS/ SAND DOLLAR	EX-TS	EXUMA	Patch Reef	2007	2010	290	4.8	0
MORTON BAY NORTHERN PATCHES	IN-09	INAGUA	Patch Reef	2009	2010	370	6.2	2
MORTON BAY SOUTHERN HARDBAR	1n-051	INAGUA	Hard bar	2009	2010	210	3.5	2
TROPIC BIRD COVE	IN-019	INAGUA	Hard bar	2009	2010	240	4.0	1
MATHEW TOWN AR PATCH	IN-027AR	INAGUA	Patch Reef - Artificial	2009	2010	240	4.0	2
CULVERT FRINGING REEF	IN-013	INAGUA	Fringing Reef	2009	2010	180	3.0	2

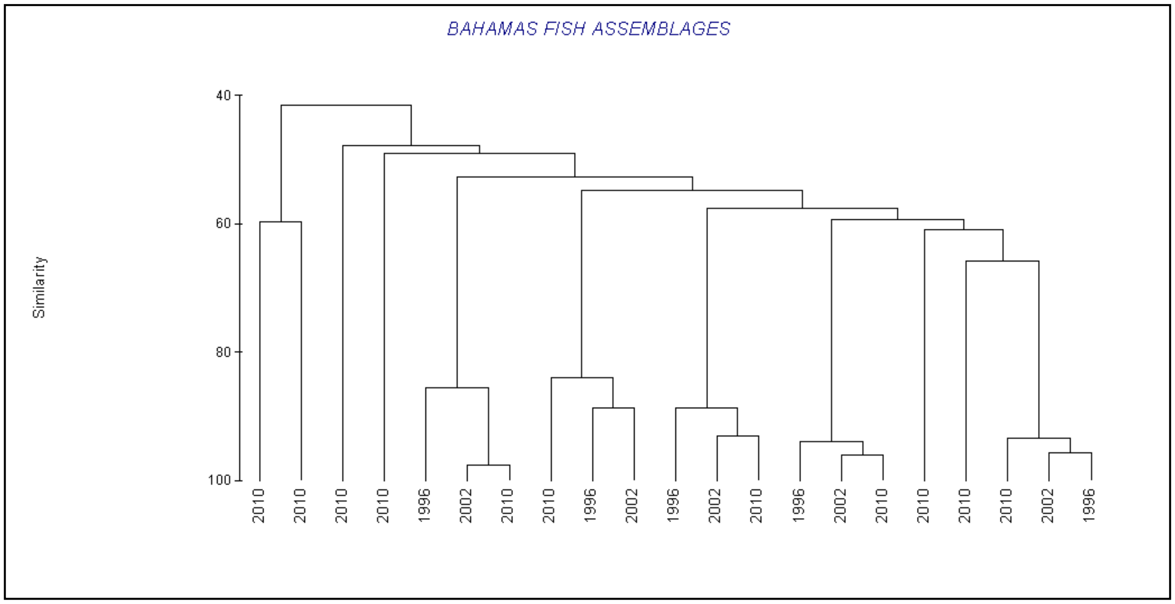

Figure 3. Bray Curtis Similarity Dendogram showing inter annual comparisons for the surveys conducted over a 14 year period. Each year correlates to a station in the same location as referenced in Figure 2.

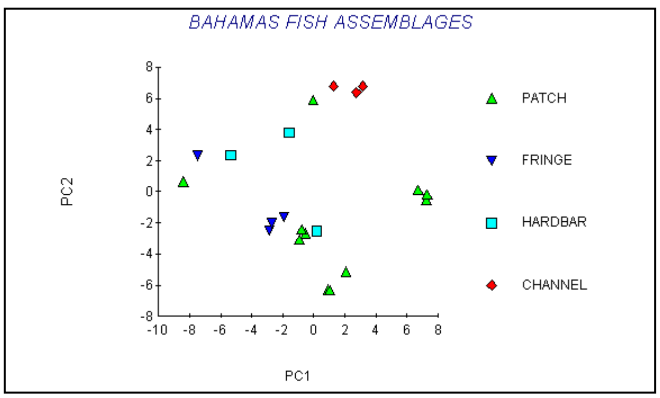

Figure 4. PCA cluster diagram comparing different habitat types. Closely grouped clusters of points show temporal variation in community level species diversity for the same sites in Great Exuma. The unrelated string of points in the upper left corner of the plot represents sites from Great

account species evenness, it is possible that lionfish may be having the greatest impact on the more diverse communities, like those seen in the Bahamas, compared to more degraded reefs in the southern Caribbean. The long-term study of a variety of near shore reef habitats can help identify the complex of threats to these systems, from local to regional in scale, including climate change, coastal development and land-based sources of pollution (Reigl et al. 2009).

Prior to the lionfish invasion, the future of the unique inshore reefal habitats of the Bahamas was already at risk from a variety of anthropogenic and natural threats. The introduction of lionfish poses many unanswered questions as to the ability of these ecosystems to cope long-term. If these community level changes evidenced by our results are even partially caused by lionfish, then they should also be habitat-specific in accordance with established theories on invasion ecology (Davis and Thompson 2000). Through future research we may be able to identify if lionfish display habitat preference in their introduced range, which may in turn lead to better management of this IAS. Removal of breeding stock from these preferential habitats may ultimately impact abundances in marginal habitats, thereby reducing potential impacts of lionfish in specific habitats.

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