ORIGINAL ARTICLE

Red Lionfish (*Pterois volitans*) Invade San Salvador, Bahamas: No Early Effects on Coral and Fish Communities

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ABSTRACT

The red lionfish, *Pterois volitans*, was first reported at San Salvador, Bahamas in January 2006; by 2009 they were common in waters 2 to 40 m deep around the island. Among the 5,078 fish observed on shallow patch reefs in 2007, only two were *P. volitans*; they were much more prevalent in deeper water along San Salvador's platform wall. Captured *P. volitans* ranged in size from 19-32 cm, all longer than maturity length. Pallid goby (*Coryphopterus eidolon*), blackcap basslet (*Gramma melacara*) and red night shrimp (*Rynchocienetes rigens*) were the most commonly identified stomach contents. Our study in 2007 also collected data on coral and fish communities at three, near-shore patch reef complexes (Rice Bay, Rocky Point, Lindsay Reef, and compared the results to a similar study done in 2001, before *P. volitans* was discovered at San Salvador. Scleractinian and, therefore, total coral species richness decreased significantly from 2001 to 2007; however, coral percentage cover increased significantly by approximately 50% during the same period, probably due to a more precise estimation procedure rather than a real increase. Even after adjustment for CPUE (2.25 more effort in 2007 than in 2001), significantly more fish were observed in 2007 than in 2001. Continued monitoring of lionfish numbers and potentially associated changes in patch reef ecology is recommended.

INTRODUCTION

Biological invaders are one of the leading contributors to the loss of biodiversity in natural ecosystems, a loss that is considered by some to be a great risk to natural ecology and human well-being (Wilcove, Rothstein, Dubow, Phillips, & Losos, 1998; Helfman, 2007). Biological invaders enter an ecosystem through natural range extensions or from human-induced introductions, and are only considered invasive if they survive, reproduce and disperse into an ecosystem where their species did not previously exist (Carlton, 1989).

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In the past, marine invasions have been rare or rarely reported as compared to freshwater and terrestrial invasions. Yet, in the last two decades human-mediated invasions have become more prevalent and anthropogenic dispersals among marine environments are increasing the rate at which invasions occur. These invasions have the potential to modify marine ecosystem processes, food-web dynamics or community compositions (Ruiz, Carlton, Grosholz, & Hines, 1997; Wilcove et al., 1998; Cuddington & Hastings, 2003; Semmens, Buhle, Salomon, & Pattengill-Semmens, 2004).

Although freshwater fish invasions have proven on many occasions to be devastating to native communities, limited research on the relatively small number of successful marine fish invasions has left the possible consequences arising from them uncertain (Ruiz et al., 1997; Whitfield et al., 2002; Albins & Hixon, 2008). Also, characteristics of a species in one community can be a poor indicator of the consequences that species may have in a new community. Therefore, the effects of an invasive in its new environment are not easily predicted based upon the species life history in its native range (Ruiz et al., 1997).

One such marine invader, for which potential effects on native communities are of concern, is the red lionfish, *Pterois volitans* and its difficult-to-distinguish relative, *P. miles* (U.S. Geological Survey, 2011). It is a scorpionfish (family Scorpaenidae, order Scorpaeniformes, subclass Teleostei), which has a native range throughout the tropical and subtropical Indo-Pacific from southern Japan southward to Australia and eastward to the islands of the South Pacific (Schultz, 1986; Meister et al., 2005). It is a popular aquarium fish and was one of the top ten most valuable marine fish imported to the United States (Ruiz-Carus, Matheson, Roberts, & Whitfield, 2006).

How *P. volitans* was first released into the southwest Atlantic and Caribbean is unknown, but it is believed that it was introduced into Florida waters by the aquarium trade (NOAA, 2007). Whitfield et al. (2002) believed that both intentional and unintentional releases from aquaria have been the most likely mechanisms for the introduction of *P. volitans*. Regardless of the method of introduction, *P. volitans* has rapidly expanded its range. Since its discovery in Florida waters in 1985 (U.S. Geological Survey, 2011), lionfish have spread up the coast of the eastern United States as far north as Rhode Island, eastward to Bermuda, southward into the Caribbean, Turks and Caicos, Cayman Islands, Puerto Rico, Greater Antilles (Cuba, Jamaica, Haiti, Dominican Republic), and to Central and South America (Mexico, Belize, Honduras, Nicaragua, Costa Rica, Panama, Columbia, Venezuela; Whitfield et al., 2002; Albins & Hixon, 2008; Guerrero & Franco, 2008; Schofield, Morris, Langston, & Fuller, 2011).

The first lionfish counts at 17 locations off North Carolina in 2004 averaged 21/ha. By 2008, mean counts rose to 150/ha, with some sites having nearly 350 lionfish/ha. In the Bahamas there were similar reports of high densities of lionfish, and results showing that lionfish were thriving in both warm temperate and subtropical reaches of the Atlantic. Data collected in the Bahamas show that lionfish densities are orders of magnitude higher than observed in their native range (Morris & Whitfield, 2009).

Although it is not reported by U.S. Geological Survey (2011), the first documented lionfish sighting at the island of San Salvador in the Bahamas was at Pigeon Creek, a tidal estuary and nursery habitat (Figure 1), in January 2006 (B. Baldwin, St. Lawrence University, Canton, NY, personal communication). By January 2007, a few lionfish were observed at various patch reefs near San Salvador (Gerace Research Centre students, personal communication). These data suggested that *P. volitans* was in the early stages of a successful invasion and, therefore, collection of the initial invasion data at patch reefs near San Salvador was necessary to understand potential changes that may occur due to the presumably larger populations of *P. volitans* to come.

Figure 1. Map of San Salvador showing the three study reef complexes: Lindsay Reef, Rocky Point and Rice Bay. Base map from Krumhansl, McLaughlin, Sataloff, Grove, & Baldwin (2007). Reproduced with permission.

Walter and Haynes (2006) characterized coral and fish communities at three patch reef complexes near San Salvador. Since the first lionfish was not reported until 2006, the data collected by Walter (2002) provide pre-lionfish invasion reef community characteristics. Our study examined population characteristics (preferred habitat, prey selection, quantity of consumption) of *P. volitans* during the initial phase of colonization and replicated Walter's (2002) study. We did not expect to find major differences in the coral and fish communities between 2001 and 2007 because lionfish had only been observed at San Salvador for 18 months before our study, their population size was small, and any detectable changes in the native coral and fish communities due to lionfish were unlikely.

Material and Methods

Study Area

Coral and fish communities were surveyed at three, shallow (< 5 m) patch reef complexes with contrasting physical characteristics: Rice Bay (RB), Rocky Point (RP) and Lindsay Reef (LR), at the small Bahamian island of San Salvador (Figure 1). Lionfish were also surveyed and collected along the wall of the western edge of the island's platform. San Salvador is located at 24° 3'N latitude and 74° 30'W longitude, 640 km east southeast of Miami, Florida.

Objectives

Our first objective was to determine population characteristics of *P. volitans* near San Salvador during the initial invasion phase. Our second and third objectives were to compare the pre- (2001) and initial post- (2007) invasion coral and fish communities at each of the three patch reef complexes.

Objective 1: Determine prey selection, quantity of consumption and preferred habitat of *P. volitans* near San Salvador during the initial invasion phase.

From May 24 to June 2, 2007 we did dives and snorkels at shallow artificial reefs and patch reefs (other than RB, RP and LR) and in the mangrove habitat at Pigeon Creek (Figure 1) to search for *P. volitans*. From May 29 to June 15, 2007, a local diving company at the Riding Rock Inn recorded *P. volitans* sightings and speared 21 specimens in waters 10 to 40 m deep, the safe depth range for recreational scuba diving. Location, depth, date, time and approximate length were recorded for each *P. volitans* sighted. Speared lionfish were brought to the surface, immediately put on ice and transported to the Gerace Research Centre. On the day of capture, data collected from the fish included total length (in cm) and identification and volume of stomach contents.

Objective 2: To describe differences, if any, in the coral communities between 2001 and 2007 on the three selected reefs.

Transect lines were placed on each of the three reef complexes to create study plots. At RP and LR, a 30-m baseline was run perpendicular to the shore. From the baseline, four 40-m transect lines were laid out haphazardly in various directions; all were entirely on the reef and did not overlap. After placement, each of the 40-m transect lines was divided evenly into four 10-m by 5-m (50 m^2) box plots (N = 16 per site). Due to the small reef surface area at RB, a baseline transect could not be used. Therefore, sixteen 10-m lines were placed entirely on top of the reef so they did not overlap. Each 10-m line at RB became one box plot. The corners of each box plot were marked with a nail and fluorescent flagging tape. Each nail was hammered into a dead part of the reef and removed at the end of the study to minimize disturbance.

For the coral survey, 1-m^2 quadrats were constructed from PVC pipe. Four evenly spaced holes were drilled 20 cm apart through each edge of the quadrat, and string was used to make a grid (N = 25, 400 cm^2 boxes) inside the quadrat frame. The frame was haphazardly placed within each 50-m^2 box plot ten times (N = 160 per reef) and coral species percentage cover was estimated by counting the number of 400 cm^2 boxes each coral species filled within the quadrat. Our quadrat design differed slightly from that of Walter (2002) in that he did not put a string grid inside his frame but instead used the visual estimation technique employed by Ormond, Roberts, and Jan (1996). China markers, transparencies and a clip board were used to record the data in the water; all observations were done by snorkeling. From the ten samples in each box plot, mean percentage coral cover (total, Scleractinia, Gorgonacea, Milleporidae) and species richness, diversity and equitability were calculated for each of the 16 box plots on each reef.

Objective 3: To describe differences, if any, in the fish communities between 2001 and 2007 on the three selected reefs.

Fish surveys were conducted in the same 50-m^2 box plots as the coral surveys. In each of the 16 plots we conducted two stationary point counts and one perimeter swim. Each stationary count was for 7.5 minutes or until no new fish was seen after 5 minutes, whichever came first. For stationary counts, each 50-m^2 box plot was visually divided into two, 5-m by 5-m plots. One stationary count was taken while hovering above the perimeter of the box plot on one 10-m side ~2.5 m from the corner. The second stationary count was done diagonally on the opposite 10-m side of the box plot. After the point counts, one swimming count was done along the inside perimeter (30 m) of the box plot to look for demersal, hiding and cryptic individuals. The three counts were summed to give a total fish count per box plot. At the same time, a second observer independently counted in the opposite half of the box plot and did her swimming count in the opposite direction.

Walter (2002) sampled in a slightly different way, so we adjusted his catch per unit effort (CPUE) to ours. In most box plots we did two, 7.5-minute stationary and 30 m of swimming counts. Walter observed each box plot twice and then took the average of the two counts: each count included two, 2.5-min stationary counts and two, 10 m swimming counts. Therefore, we had 1.5 times the stationary effort and 0.75 times the swimming effort of Walter (2002), so we multiplied his numbers by 2.25 (2 replicates x 1.5 x 0.75) to achieve equivalent CPUE.

Data Analysis

Following Walter (2002), the mean percentage cover of each coral species was aggregated in total and by group: hard corals (order Scleractinia) soft corals, (order Gorgonacea) and hydrocorals (family Milleporidae). Fish abundance data were aggregated in total and by major family (Acanthruidae, Labridae, Pomacentridae, Scaridae) and feeding guild (herbivores, planktivores, invertivores, piscivores, detritivores; Hiatt & Strasburg, 1960; Humann & Deloach, 2002). Biodiversity parameters for fish and coral communities were calculated using Microsoft Excel: species richness (S), Shannon's Diversity Index ($H' = -\sum p_i \ln(p_i)$, where p_i is the proportion of individuals of the i^{th} species) and equitability (species evenness) ($E = H'/\ln S$).

To promote equal variances, coral percentage cover values received arcsine(x) transformations and fish abundance values received *log*(x + 1) transformations (Excel) before analysis (Statistix, 2003). General Linear Models (GLMs), followed by Tukey's Honestly Significant Difference (HSD) tests to provide experiment-wise error rates, were used to distinguish values of the coral and fish variables among the three reefs (RB, RP, LR) and between the two years/observers (2001/Walter and 2007/Alexander). The 16 box plots of coral and fish data per reef were replicates in the GLMs.

Walter (2002) deliberately chose to sample reefs with contrasting physical conditions and coral communities (McGrath & Smith, 2003); as expected, the GLMs revealed many statistically significant differences among the three reefs. Since the objective of our study was to examine differences in coral and fish communities between 2001 and 2007, and not differences among reefs, differences in community characteristics among reefs will not be discussed (see Alexander, 2011 for these data).

Ecological changes or observer bias both could contribute to differences in the coral and fish communities observed in 2001 and 2007. To address the issue of inter-observer reliability, fish counts were made independently by two observers in 2007.

Results and Discussion

Pterois volitans

Shallow water hunts. From May 24 to June 2, 2007, no *P.* volitans were observed during 8.75 hours of snorkeling and diving at artificial reefs, shallow patch reefs (other than the three study sites) and in a mangrove habitat at Pigeon Creek (Figure 1). By 2009 *P. volitans* were seen frequently at all shallow patch reefs near San Salvador (J. M. Haynes, personal observation).

Deep water hunts. From May 29 to June 15, 2007, 46 *P. volitans* were observed during 21 of 22 deep water dives performed in collaboration with the local diving company. Depths ranged from 9 to 43 m and visually-estimated *P. volitans* lengths ranged from 12 to 25 cm. Lionfish were much more prevalent in the deeper waters surrounding San Salvador than at the shallow reef systems in 2007.

During nine of the deep water dives only single *P. volitans* were observed; during 12 dives they were observed in groups of two to five. These groups of lionfish were prominent during the first two weeks of June. *P. volitans* are found in large groups as juveniles but adults are normally solitary, only congregating in groups of three to eight during the initial stages of courtship (Whitfield et al., 2002; Schofield et al., 2011). Several local also reported seeing large groups of *P. volitans* in early June. During the 3rd week of June, Alexander surveyed a site where a fisherman reported seeing a large group of lionfish in early June, but none were seen. Before our study began, a Master Diver from the local diving company started his own, informal log of *P. volitans* sightings during deep water dives. During March 2007, he observed *P. volitans* on 16 dives but only recorded three occurrences of more than one together.

Maturity. Among the 46 *P. volitans* observed during deep water dives, 21 were speared; they ranged from 19-32 cm total length (24± 0.9 cm). Female *P. volitans* mature at 18 cm and males at 10 cm; therefore, all of the speared fish were adults (Morris & Whitfield, 2009). According to recent research, *P. volitans* spawn year round in the Bahamas, about every four days, with an average annual fecundity of over two million eggs per female (Morris & Whitfield, 2009). Yet our size and aggregation data suggest that *P. volitans* were engaged in courtship, and thus spawned, only in late May/early June. This inconsistency requires further research.

Diet. Small fish and shrimp were the foods of choice for the *P. volitans* we dissected; pallid goby (*Coryphopterus eidolon*), blackcap basslet (*Gramma melacara*) and red night shrimp (*Rynchocienetes rigens*) were the most common identifiable stomach contents. Other research showed that adult lionfish in the Bahamas feed on more than 40 species of fish, including many that are important in the diets of economically important species such as snappers and groupers (Morris & Whitfield, 2009). During dissections, we were often surprised by the large quantities of food found in stomachs relative to the size of the *P. volitans*. This is explained by the lionfish's ability to expand its stomach to over 30 times initial volume during consumption, an evolutionary adaptation thought to allow it to withstand long periods of fasting (Morris & Whitfield, 2009).

Ecology. Albins and Hixon (2008) reported reduced recruitment of coral reef fishes after lionfish invasion. They hypothesized that lionfish decrease the abundance of ecologically important species such as parrot- and other herbivorous fishes that keep macroalgae from overgrowing corals. If this potential impact materializes, the currently high rates of macroalgae overgrowth on corals at San Salvador (A. K. Alexander and J. M. Haynes, personal observations) could increase.

Shrimp populations could also suffer from increased predatory demands by *P. volitans*. Smaller shrimp populations may then lead to adverse effects on both coral and reef fish communities. One very important niche that certain shrimp species fill in reef ecosystems is providing "cleaning stations," a place where a shrimp removes parasites from fish and other crustaceans on a regular basis. Some shrimp species also live in facultative or obligate partnerships with corals, anemones, mollusks and echinoderms. Others are detrital feeders that play an essential part in keeping the reef ecosystem clean (Spalding, Ravilious, & Green, 2001).

Competition for prey and habitat between *P. volitans* and native fishes may also become an issue near San Salvador if the lionfish population continues to increase. Lionfish abundance, distribution and predation rates should be monitored within reef habitats and also within areas that native fish rely on for nursery habitat, such as the extensive mangroves along Pigeon Creek at San Salvador (Conboy & Haynes, 2011; Figure 1).

Corals

Corals were surveyed in January and May-June in 2001 and May-June in 2007. In 2007, 39 coral species were identified: 24 Scleractinia, 12 Gorgonacea and three Milleporidae. In 2001, 35 coral species were identified: 22 Scleractinia, 11 Gorgonacea and two Milleporidae (Table 1 see Appendix).

Scleractinia. Scleractinia observed in 2007 and not in 2001 were *Stephanocoenia intersepts*, *Meandrina meandrites* and *Mycetophyllia aliciae*. *S. intersepts* had low percentage cover at RB and LR (0.09% and

0.01% cover, respectively), *M. meandrites* also had low percentage cover at RB and LR (0.25% and 0.20%, respectively), and *M. aliciae* was found only at LR at 0.10% relative abundance (Table 1). According to a study done in the Florida Keys, *M. aliciae* was rarely observed and then only in low abundance (Rutten, Chiappone, Swanson, & Miller, 2008). Scleractinians observed in 2001 and not in 2007 were *Mussa angulosa* and *Scolymia* spp. *M. angulosa* was found only at LR (0.60%) and *Scolymia* spp. was found at RP and LR (0.11% and 2.15%, respectively; Table 1). These five rare scleractinians likely were present in both years but not consistently observed.

Gorgonacea. All gorgonians observed in 2001 were observed in 2007. The only Gorgonacean species observed in 2007 but not in 2001 was *Muricea muricata*. Its percent cover was 0.15% at RB, 0.01% at RP and 0.02% at LR (Table 1).

Identifying Gorgonacea is difficult; fewer than half of the 60 to 70 reef forms can be identified to species underwater; positive identification requires microscopic examination (Humann & Deloach, 2002). Often we took small samples of Gorgonaceans back to the lab, examining specimens microscopically and using keys to identify them (Humann & Deloach, 2002; Sanchez & Wirshing, 2005; Janes & Wah, 2005). *M. muricata* could easily be misidentified as other gorgonaceans in the field, such as *Eunicea succinea*. We recommend collecting small samples from confusing gorgonaceans in future studies.

Milleporidae. Among fire corals (Table 1), *Millepora alcicomis* and *M. complanata* were found both years and *M. squarrosa* only in 2007 (0.10% cover at LR). In both years the percentage cover of Milleporidae was very low. Glynn and Weerdt (1991) suggested that *Millepora* spp. are especially sensitive to higher than normal water temperatures, which have occurred twice at San Salvador since 2001. With rising concerns about global warming and its potential to increase the ocean temperatures enough to adversely affect reef ecosystems (e.g., coral bleaching; Toren, Landau, Kushmaro, Loya, & Rosenberg, 1998), future research at San Salvador should explore changes in *Millepora* spp. cover in relation to temperature fluctuations in the shallow patch reef systems.

Changes from 2001 to 2007.

Mean total species richness (p = .003, -15.4%) and scleractinian species richness (p < .0001, -22.7%) per box plot were significantly less in 2007 than in 2001. There were no significant differences for gorgonian species richness (p = .239), Shannon's H′ (p = .934) and Equitability (p = .230) between years (Table 2 see appendix). Except for lower scleractinian species richness and, therefore, lower total coral cover species richness, the coral communities at the three reef complexes studied near San Salvador had similar diversity in 2001 (Walter, 2002) and 2007.

Percentage cover of total corals (p < .0001, +50%), scleractinians (p < .0001, +56.3%) and gorgonians (p = .009, +43.8%) was significantly greater in 2007 than in 2001. Milleporid cover did not differ significantly between years (p = .674), as shown in Table 2. The coral community in 2007 may have had a higher percentage of coral cover in 2007 than in 2001 but the differences observed were more likely related to the differing estimation techniques used by Walter (2002). He estimated percentage cover for each coral species within an entire 1-m^2 frame, while we estimated cover more precisely in each of 25, 400-cm^2 panels within a 1-m^2 frame.

From the mid-1980s to 2000, scleractinian cover at reefs near San Salvador (including our study sites) suffered a massive decline from ~20% to 4-5% (McGrath & Smith, 2003). The percentage cover of live coral observed in 2001 (3.2%, Walter 2002) and 2007 (5%, Table 2) was consistent with McGrath and Smith (2003). Due to its greater precision, we recommend that the 2007 method for sampling corals be used in future studies at the three study reef complexes.

Fishes

Seventy-one fish species were recorded, 50 at RB, 45 at RP and 49 at LR; 37, 32 and 46 species were recorded at the three reefs, respectively, in 2001 (Table 3 see appendix). Fifteen species observed in 2007 were not seen in 2001. (*Sargocentron coruscum*, *Ocyurus chrysurus*, *Lutjanus mahogani*, *Haemulon flavolineatum*, *Haemulon chrysargyreum*, *Haemulon plumieri*, *Haemulon carbonarium*, *Holacanthus ciliaris*, *Stegastes partitus*, *Abudefduf saxatilis*, *Doratonotus megalepis*, *Sphyraena barracuda*, *Canthidermis sufflamen*, *Aluterus schoepfii*, *Urobatis jamaicensis*), and three species seen in 2001 were not seen in 2007 (*Chaetodon ocellatus*, *Acanthostracion polygonius*, *Rypticus saponaceus*). All 18 species were at densities < 0.5/50 m^2, usually < 0.2/50 m^2 (Table 3); therefore, they were easy to miss during sampling. Among the 5,078 fish recorded on the three shallow patch reef complexes in 2007, only two were *P. volitans*, both at RP.

Changes from 2001 to 2007.

Total fish counts (p = .031, +17%), Shannon's H′ (p < .0001, +35.5%) and Equitability (p = .002, +14%), but not species richness (p = .393), were significantly greater in 2007 than in 2001 (Table 4 see appendix). Among the major families and feeding guilds, Pomacentridae (damselfishes, p = .007, +28.6%), invertivores (p = .025, +26.6%) and piscivores (p = .037, +6.1%) were significantly more abundant in 2007 than in 2001. Only detritivores, the least abundant of the feeding guilds, were observed more often in 2001 than in 2007 (p = .030, -66.7%).

General fish discussion.

In the tropics, the May-July period is associated with high abundance of juveniles of many species. Fish were surveyed from mid-May to mid-June in 2001 and 2007, so we expected that the same species and age classes would be present. For example, the most abundant fish in both years was the bluehead, *Thalassoma bifasciatum*. However, bluehead counts were much higher in 2007 than in 2001 (reflected in both Labridae and invertivore counts; Table 4), and most of those observed in 2007 were juveniles. Observer counts of fish species in box plots in 2001 (N = 1) and 2007 (N = 2) and observer counts of total fish in box plots in 2007 (N = 2) were nearly identical (Table 4). Walter in 2001, and the two observers in 2007 had equivalent in-water training at San Salvador (prior undergraduate courses at SUNY College at Brockport) and demonstrated excellent observation and identification skills in the water (J. M. Haynes, personal communication). Therefore, the increases in fish counts from 2001 to 2007 are probably real and due mostly to higher numbers of juvenile blueheads in 2007. These results most likely reflect large natural variations in year class strength in most fish populations.

Differences in the results between the 2001 and 2007 fish studies illustrate the importance of using precisely the same methods for comparative studies. With 2.25 times more sampling effort than Walter (2002), we observed a net of 12 more species (although not more species per box plot) and 17% more fish (Table 4). Although our methods required more time in the water, we recommend them for future studies.

CONCLUSION

Among the 21 *P. volitans* captured in 2007, all were the size of mature adults, and small fishes and shrimps were their foods of choice. *P. volitans'* ability to eat large amounts of prey is a concern because of the potential for substantial reductions of fish and shrimp prey populations. Decreases in prey species could lead to increases in algal growth, competition for prey with native reef fishes, or disruptions of symbiotic relationships between some shrimps and fishes or other reef animals.

The coral communities at the three reef complexes studied at San Salvador had lower mean diversity in 2007 than in 2001 but percentage cover of total corals, scleractinians and gorgonians was significantly greater in 2007 than in 2001, changes most likely associated with somewhat different sampling methods between years. The percentage cover of live scleractinians observed in 2001 (Walter, 2002) and in 2007 was ≤ 5% and consistent with the ~75% decline from the mid-1980s to 2000 reported by McGrath and Smith (2003). Given rising concerns about global warming and other anthropogenic impacts on coral ecosystems and their global decline (Hughes et al., 2003), especially in the Caribbean (Gardner, Cote, Gill, Grant, & Watkinson, 2003), changes in coral community characteristics at San Salvador from the mid-1980s to 2007 likely reflect long-term impoverishment more than any other factor.

Although fish community parameters were generally more robust in 2007 than in 2001, these results likely reflect natural variations in year class strength (e.g., *T. bifasciatum*) and greater sampling effort in 2007 (2.25 times the 2001 effort). Our results are not due to the recent invasion of *P. volitans*, because only two were observed on the three study reef complexes in 2007.

In 2007 *P. volitans* was commonly observed in waters 10-40 m deep along San Salvador's western wall. By 2009 it was common on shallow patch reefs, including the three study reef complexes. It is evident that *P. volitans* has successfully invaded the waters near San Salvador, Bahamas. The effects of its increasing population on Sal Salvador's reef ecosystem are uncertain at this time but research conducted elsewhere in the Bahamas (Morris & Whitfield, 2009) does not suggest a positive outcome. Future monitoring will be needed to assess *P. volitans'* full impacts and potentially execute population control measures at San Salvador.

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TABLES 1-4

Table 1.
Percent cover of coral species observed in 2001 and 2007 at Rice Bay, Rocky Point and Lindsay Reef.

Taxonomic name	Common name	Rice	Bay	Rocky	Point	Lindsay	Reef
Year		01	07	01	07	01	07
Hydrozoa							
Milleporidae							
Millepora alcicornis	branching fire	2.44	0.38	0.24	1.13	0.38	0.38
Millepora complanata	blade fire	1.33	0.52	3.06	0.28	2.82	0.49
Millepora squarrosa	encrusting fire	0.00	0.00	0.00	0.00	0.00	0.10
Anthozoa							
Zooantharia							
Scleractinia							
Astrocoeniia							
Acroporidae							
Acropora palmata	elkhorn	0.00	0.00	0.02	0.10	0.00	0.00
Fungiida							
Agariciidae							
Agaricia agaricites	lettuce	0.78	0.28	3.70	0.12	4.38	0.14
Poritidae							
Porites astreoides	mustard hill	6.04	1.64	22.4	24.9	14.0	7.30
Porites branneri	finger	0.28	0.34	0.25	1.17	0.00	0.00
Porites porites	finger	2.61	1.41	2.08	1.16	4.01	2.93
Porites porites divaricata	finger	0.00	0.00	0.11	0.00	0.29	0.35
Porites porites frucata	finger	0.00	0.10	0.11	0.30	0.08	0.00
Siderastreidae							
Siderastrea siderea	greater starlet	0.83	0.00	0.25	0.00	0.17	0.05
Siderastrea radians	lesser starlet	3.66	0.13	0.74	0.21	0.17	0.23
Astrocoeniidae							
Stephanocoenia intersepts	blushing starlet	0.00	0.09	0.00	0.00	0.00	0.01
Caryophylliida							
Caryophyllidae							
Eusmilia fastigiata	smooth flower	0.61	0.01	0.00	0.20	0.00	0.05
Faviida							
Faviidae							
Diploria clivosa	knobby brain	4.44	0.00	1.81	0.48	0.08	0.00
Diploria labyrinthiformes	grooved brain	0.00	0.01	2.82	0.00	0.42	0.23
Diploria strigosa	symmetrical brain	3.38	0.74	2.33	0.83	2.77	0.16
Favia fragrum	golfball	3.33	0.12	1.14	0.17	1.26	0.18
Manicina areolata	rose	5.10	0.45	0.00	0.00	0.86	0.08
Montastrea annularis	lobed star	3.99	0.33	4.37	1.16	24.8	6.44
Montastrea cavernosa	cavernous star	0.33	0.17	0.00	0.15	0.02	0.00
Montastrea faveolata	mountainous star	3.33	0.00	0.00	0.00	0.00	0.70
Meandrinidae							
Meandrina meandrites	maze	0.00	0.25	0.00	0.00	0.00	0.20

Taxonomic name	Common name	Rice	Bay	Rocky	Point	Lindsay	Reef
Year		01	07	01	07	01	07
Dichocoenia stokesii	elliptical star	2.99	0.59	0.13	0.15	0.71	0.37
Mussidae							
Isophyllia sinuosa	sinuous cactus	0.00	0.00	0.00	0.00	0.54	0.02
Mussa angulosa	spiny flower	0.00	0.00	0.00	0.00	0.60	0.00
Scolymia spp.	disk	0.00	0.00	0.11	0.00	2.15	0.00
Mycetophyllia aliciae	knobby cactus	0.00	0.10	0.00	0.00	0.00	0.00
Octocorallia							
Gorgonacea							
Scleraxonia							
Briareidae							
Briareum asbestinum	corky sea finger	6.26	1.06	1.15	0.95	1.25	1.24
Anthothelidae							
E. caribaeorum	carpet gorgonian	0.67	1.28	0.47	0.37	2.57	0.11
Holaxonia							
Plexauridae							
Muricea muricata	spiny sea fan	0.00	0.15	0.00	0.01	0.00	0.20
Eunicea calyculata	warty sea rod	1.44	0.22	0.47	0.17	0.00	0.00
Eunicea mammosa	swollen-knob sea rod	2.16	2.18	4.61	3.02	2.27	0.34
Eunicea succinea	shelf-knob sea rod	2.16	1.23	4.61	0.77	2.27	0.72
Plexaura flexuosa	bent sea rod	0.00	0.14	0.38	3.39	0.00	0.00
Plexaura homomalla	black sea rod	8.20	2.82	12.61	5.00	13.02	6.40
Plexaurella spp.	slit-pore sea rod	1.72	0.14	0.11	0.20	4.01	0.00
Pseudoplexaura spp.	porous sea rod	16.0	1.75	7.84	2.16	2.19	0.05
Gorgoniidae							
Pseudopterogorgia spp.	sea plumes	4.55	0.73	6.14	0.79	0.67	0.00
Gorgonia flabellum	venus sea fan	0.78	0.96	7.94	2.95	8.52	6.25
Gorgonia ventalina	common sea fan	10.2	3.24	12.5	3.11	5.02	1.67

Table 2.
*Summary statistics for coral assemblages (Rice Bay, Rocky Point and Lindsay Reef combined) in 2001 and 2007 (N = 16 sample plots/reef/year; % Change = [(2007-2001)/2001]*100, where negative values indicate a decrease and positive values indicate an increase from 2001 to 2007; P-values from GLMs, including arcsin[X] transformations for percent cover).*

	2001			**2007**		**% Change**	***P***
	Mean	SE		Mean	SE		
Species Richness	13.6	0.50		11.5	0.52	-15.4	.003
Scleractinia	7.5	0.29		5.8	0.30	-22.7	<.0001
Gorgonacea	5.4	0.29		5.9	0.34	9.3	.239
Shannon's H'	1.824	0.067		1.832	0.068	0.4	.934
Equitability E	0.801	0.041		0.747	0.027	-6.7	.230
Percent Cover							
Total	6.6	0.006		9.9	0.007	50.0	<.0001
Scleractinia	3.2	0.003		5	0.005	56.3	<.0001
Gorgonacea	3.2	0.004		4.6	0.004	43.8	.009
Milleporidae	0.002	0.0006		0.003	0.0006	50.0	.674

Table 3.
List of fish species observed in 2001 and 2007 with their relative percent abundances (50 m^{-2}) for each reef: Rice Bay, Rocky Point and Lindsay Reef.

Taxonomic name	Common name	Rice	Bay	Rocky	Point	Lindsay	Reef
Year		01	07	01	07	01	07
Actinopterygii							
Atheriniformes							
Atherinidae							
Atherinomorus stipes	hard-head silverside	0.0	0.0	2.2	0.8	0.0	3.9
Beryciformes							
Holocentridae							
Holocentrus rufus	longspine squirrelfish	0.5	0.4	0.0	0.0	0.3	0.1
Holocentrus coruscum	reef squirrelfish	0.0	0.1	0.0	0.2	0.0	0.1
Gasterosteiformes							
Aulostomidae							
Aulostomus maculatus	trumpetfish	0.3	0.1	0.0	0.2	0.1	0.1
Perciformes							
Percoidei							
Serranidae							
Cephalopholis cruentata	graysby	0.3	0.1	0.0	0.0	0.1	0.0
Cephalopholis fulvus	coney	0.0	0.8	0.9	1.2	2.1	2.5
Epinephelus guttatus	red hind	0.3	0.1	0.0	0.0	0.4	0.3
Epinephelus striatus	Nassau grouper	0.0	0.2	0.0	0.1	0.0	0.1
Mycteroperca tigris	tiger grouper	0.3	0.0	0.0	0.1	0.1	0.3
Rypticus saponaceus	soapfish	0.3	0.0	0.0	0.0	0.0	0.0
Grammatidae							
Gramma loreto	fairy basslet	0.8	1.1	0.1	1.6	1.5	6.9
Priacanthidae							
Heteropriacanthus cruentatus	glasseye snapper	0.0	0.1	0.0	0.1	0.1	0.1
Malacanthidae							
Malacanthus plumieri	sand tilefish	0.3	0.0	0.0	0.0	0.0	0.1
Carangidae							
Caranx ruber	bar jack	1.1	1.4	0.0	0.4	1.5	5.3
Lutjanidae							
Lutjanus apodus	schoolmaster	0.3	1.0	0.1	0.2	0.1	0.0
Ocyurus chrysurus	yellowtail snapper	0.0	0.0	0.0	0.1	0.0	0.0
Lutjanus mahogani	mahogany snapper	0.0	0.1	0.0	0.0	0.0	0.1
Gerreidae							
Gerres cinereus	yellowfin mojarra	0.3	0.0	0.0	0.4	0.4	0.9
Haemulidae							
Hemulon sciurus	bluestriped grunt	0.8	0.2	0.0	0.1	0.3	0.2
Haemulon flavolineatum	french grunt	0.0	1.1	0.0	0.0	0.0	0.0
Haemulon chrysargyreum	small mouth grunt	0.0	0.1	0.0	0.0	0.0	0.0
Haemulon plumierii	white grunt	0.0	0.1	0.0	0.0	0.0	0.0
Haemulon carbonarium	caesar grunt	0.0	0.1	0.0	0.0	0.0	0.0
Mullidae							
Mulloidichthys martinicus	yellow goatfish	0.0	0.1	0.6	0.0	0.7	0.0
Pseudupeneus maculatus	spotted goatfish	2.7	3.6	0.1	0.2	1.5	0.6
Kyphosidae							
Kyphosus sectatrix	chub	1.1	0.0	1.8	10.4	2.1	0.1
Chaetodontidae							
Chaetodon capistratus	four-eye butterfly	0.3	0.2	0.0	0.0	0.4	0.7
Chaetodon ocellatus	spotfin butterfly	0.3	0.0	0.0	0.0	0.0	0.0
Chaetodon striatus	banded butterfly	1.1	1.0	0.6	0.2	0.5	0.4

Taxonomic name	Common name	Rice	Bay	Rocky	Point	Lindsay	Reef
Year		01	07	01	07	01	07
Pomacanthidae							
Holocanthus tricolor	rock beauty	0.0	0.0	0.0	0.1	0.1	0.0
Holacanthus ciliaris	queen angelfish	0.0	0.0	0.0	0.0	0.0	0.1
Pomacentridae							
Chromis cyaneus	blue chromis	0.0	0.8	0.3	0.0	0.4	0.0
Microspathodon chrysurus	yellowtail damse	0.0	0.0	1.3	1.5	0.0	0.0
Stegastes partitus	bicolor damsel	0.0	0.0	0.0	0.1	0.0	0.2
Stegastes dorsopunicans	dusky damsel	0.8	0.9	3.0	0.6	2.7	0.6
Stegastes leucostictus	beaugregory	4.1	1.4	0.3	0.6	0.4	1.1
Stegastes planifrons	threespot damsel	0.0	0.3	0.3	0.0	0.1	0.0
Stegastes diencaeus	longfin damsel	0.0	2.9	0.0	1.8	0.1	2.3
Stegastes variabilis	cocoa damsel	1.1	0.5	1.9	1.1	0.9	1.0
Abudefduf saxatilis	sergeant major	0.0	0.0	0.0	0.0	0.0	0.4
Labridae							
Bodianus rufus	spanish hogfish	0.3	0.1	0.3	0.2	0.1	0.1
Halichoeres bivattatus	slippery dick	1.0	1.6	2.4	2.1	0.3	0.0
Halichoeres garnoti	yellowhead wrasse	0.8	0.4	1.3	2.0	2.5	0.3
Halichoeres maculipinna	clown wrasse	0.8	1.4	1.2	7.2	0.0	0.0
Halichoeres radiatus	puddingwife	0.8	0.9	2.2	2.0	2.3	2.0
Thalassoma bifasciatum	bluehead	32	40	45	41	35	36
Doratonotus megalepis	dwarf wrasse	0.0	0.1	0.0	0.0	0.0	0.0
Scaridae							
Scaridae sp	UNID parrotfish	1.1	0.0	0.0	0.0	2.5	0.0
Scarus croicensis	striped parrotfish	4.6	4.4	3.7	0.1	10.4	3.0
Scarus taeniopterus	princess parrotfish	0.0	0.3	0.4	0.3	0.3	0.7
Scarus vetula	queen parrotfish	0.0	1.2	0.4	0.3	0.1	0.6
Sparisoma aurofrenatum	redband parrotfish	1.1	5.6	1.6	1.6	2.1	3.0
Sparisoma rubripinne	yellowtail parrotfish	0.0	1.2	0.3	0.5	0.1	0.2
Sparisoma viride	stoplight parrotfish	5.1	5.4	5.2	3.3	6.9	7.8
Clinidae							
Malacoctenus macropus	rosy blenny	0.3	1.0	0.0	0.0	0.0	0.2
Malacoctenus triangulatus	saddled blenny	2.4	1.6	0.3	1.5	3.3	2.1
Blenniidae							
Blenniidae sp.	UNID blenny	0.0	0.0	0.0	0.0	0.1	0.0
Ophioblennius atlanticus	red-lip blenny	0.0	0.0	1.5	0.3	0.0	0.0
Gobiidae							
Coryphopterus glaucofraenum	bridled goby	1.1	0.2	0.0	0.3	1.6	1.0
Gnatholepis thompsoni	goldspot goby	0.0	0.0	0.0	0.0	0.1	0.2
Gobiosoma genie	cleaning goby	0.0	0.1	0.0	0.0	2.8	0.3
A Acanthuridae							
Acanthurus bahianus	ocean surgeon	14	8.2	11	9.2	6.2	6.0
Acanthurus coeruleus	blue tang	6.0	5.5	9.2	5.9	5.0	7.9
Sphyraenidae							
Sphyraena barracuda	great barracuda	0.0	0.1	0.0	0.0	0.0	0.1
Pleuronectiformes							
Bothidae							
Bothus lunatus	peacock flounder	0.0	0.1	0.0	0.0	0.1	0.0
Scorpaeniformes							
Scorpaenidae							
Pterois volitans	red lionfish	0.0	0.0	0.0	0.1	0.0	0.0

Taxonomic name	**Common name**	**Rice**	**Bay**	**Rocky**	**Point**	**Lindsay**	**Reef**
Year		01	07	01	07	01	07
Tetraodontiformes							
Balistidae							
Canthidermis sufflamen	ocean triggerfish	0.0	0.0	0.0	0.1	0.0	0.0
Monacanthidae							
Aluterus schoepfii	orange filefish	0.0	0.0	0.0	0.1	0.0	0.0
Ostraciidae							
Lactophrys bicaudalis	spotted trunkfish	0.0	0.1	0.0	0.0	0.1	0.1
Lactophrys trigonus	honeycomb cowfish	0.3	0.0	0.0	0.0	0.0	0.0
Lactophrys triqueter	smooth trunkfish	0.0	0.0	0.1	0.1	0.0	0.1
Tetraodontidae							
Canthigaster rostrata	sharp-nosed puffer	2.4	2.1	0.1	0.1	0.9	0.3
Elasmobranchii							
Rajiformes							
Dasyatidae							
Dasyatis americana	southern stingray	0.0	0.1	0.0	0.2	0.0	0.0
Urotrygonidae							
Urobatis jamaicensis	yellow stingray	0.0	0.0	0.0	0.0	0.0	0.2

Table 4.
Summary statistics for fish assemblages (Rice Bay, Rocky Point and Lindsay Reef combined) in 2001 and 2007 (*N* = 16 sample plots/reef/year; % Change = [(2007a-2001)/2001] x 100, where negative values indicate a decrease and positive values indicate an increase from 2001 to 2007; *p* values from GLMs using untransformed species counts and ln[*N* + 1]-transformed fish counts).

	2001		**2007a**		**2007b**		**% Change**	***P***
	Mean	SE	Mean	SE	Mean	SE		
Species Richness	18.5	1.06	17.3	0.55	18.4	0.54	-6.5	.393
Shannon's H'	1.786	0.059	2.438	0.0376	-	-	35.5	<.0001
Equitability E	0.765	0.041	0.872	0.0009	-	-	14.0	.002
Counts (50 m^{-2})								
Total	86.8	5.47	101.7	5.28	105.67	5.25	17	.031
Major Families								
Acanthuridae	13.9	1.15	16.9	1.67	-	-	21.6	.993
Labridae	38.5	2.69	48.3	3.42	-	-	25.5	.660
Pomacentridae	4.9	0.66	6.3	0.53	-	-	28.6	.007
Scaridae	13.7	1.55	13.4	0.99	-	-	-2.2	.063
Feeding Guilds					-	-		
Herbivores	34.6	2.48	36.5	2.14	-	-	5.5	.316
Planktivores	0.8	0.21	2.33	1.07	-	-	191.3	.319
Detritivores	2.1	0.43	0.7	0.17	-	-	-66.7	.030
Invertivores	53.7	4.04	68.0	4.16	-	-	26.6	.025
Piscivores	5.3	0.77	7.0	1.03	-	-	6.1	.037