

Diet of invasive lionfish on hard bottom reefs of the Southeast USA: insights from stomach contents and stable isotopes

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ABSTRACT: The Indo-Pacific lionfish (*Pterois volitans* and *P. miles* complex) has become widely established along the United States Southeast coast and continues to colonize the Caribbean, yet its biology and ecology is only beginning to be understood. We used stomach contents and stable isotope analyses to determine the diet of lionfish in the warm-temperate hard bottom reef community in the Southeast US Atlantic Ocean. During June to August 2004 and 2006, we collected lionfish with SCUBA from 18 different locations in Onslow Bay, North Carolina, at depths of 30 to 45 m. In 2006, we also conducted visual surveys of small benthic fishes to estimate the abundances of potential prey. Analyses of stomach contents (n = 183) and stable isotopes (n = 115) suggest a generalist carnivorous diet, and prey categories were predominately fish (~99% of total volume) from 16 families. Major differences in the importance of prey occurred between years. Serranidae and Scaridae dominated the diet in 2004, while Haemulidae and Carangidae were important in 2006. Analyses of visual prey surveys did not reveal specialization on particular prey taxa but instead suggest that prey are consumed in relation to their local abundance. Given current theory pertaining to invasive species impacts, the expanding lionfish distribution, and observations that lionfish appear capable of settling to many different habitat types, the overall pattern of generalist piscivory emerging from these data indicates the potential for significant impacts to the invaded community.

KEY WORDS: Marine invasion · Rocky reef · Scorpaenidae · Warm temperate · Continental shelf · Piscivory · Diet · Prey

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INTRODUCTION

Invasive species are a major threat to biological diversity. They have the potential to transform marine habitats worldwide, and to cause hundreds of billions of dollars in economic damages (reviews in Strayer et al. 2006, Molnar et al. 2008). Predators are known to have profound effects on the structure of marine communities, and have been shown capable of enhancing species diversity (keystone species) and altering community structure (trophic cascades) (Paine 1966, Estes et al. 1998, Rilov 2009). Invasive predators have been implicated as one of the most important causes of declines and extinctions of species worldwide

(Vitousek et al. 1997). Generalist invasive predators that become established might potentially affect a wide range of species, but the risk of local extirpation for native species is thought to be lower than for specialized invasive predators. These, in contrast, would be expected to exert stronger direct impacts on a few species and possibly cause more extensive indirect effects, depending on the ecological status of the targeted prey (Rilov 2009). To determine the ecological impacts of invasive predators, we must understand how they interact with other members of the community and how their arrival and establishment affects community structure (Kalogirou et al. 2007, Rilov 2009).

Along the United States Southeast Atlantic coast, and in Bermuda and the Bahamas, red lionfish *Pterois volitans* and devil firefish *P. miles* are now established and are continuing to expand their range in the Caribbean (Morris et al. 2009, Schofield 2009). These 2 species are nearly morphologically identical and 93% of specimens sampled from the Atlantic as well as North Carolina were *P. volitans* (Hamner et al. 2007), so hereafter we refer to invasive specimens collectively as lionfish or *P. volitans*. Native to the subtropical and tropical regions of the South Pacific, Indian Ocean, and the Red Sea, lionfish are venomous predators whose popularity in the aquarium trade may have contributed to their introduction to Atlantic waters (Whitfield et al. 2002, Semmens et al. 2004, Ruiz-Carus et al. 2006). Classified as demersal mesocarnivores together with groupers (Serranidae) and snappers (Lutjanidae) (Cailliet et al. 1986), lionfish are believed to be opportunistic predators that consume fish, shrimp, and crabs in their native range (Hiatt & Strasburg 1960, Harmelin-Vivien & Bouchon 1976, Sano et al. 1984). However, until their recent invasion of the Atlantic and Caribbean, their biology and ecology were poorly understood beyond general descriptions because conclusions from these earlier studies were hampered by small sample sizes ($n = 1$ to 12; Hiatt & Strasburg 1960, Harmelin-Vivien & Bouchon 1976, Sano et al. 1984). For example, in the native range, lionfish are reported to have few natural predators (Bernadsky & Goulet 1991), to attain a size of 38 cm total length (TL), and to reach depths of 50 m (Randall et al. 1990). In contrast, lionfish in the invaded range have been found in the stomach contents of piscivorous groupers (Maljković et al. 2008) and have been observed to occur at greater depths (down to 304.8 m, R. Gilmore unpubl.) and attain sizes larger (47.6 cm TL; J. Morris unpubl.) than in the native range. These depth and size extensions, as well as novel observations of predation on lionfish in the invaded range, probably reflect the paucity of investigations in the native range.

Recent studies of lionfish in the Bahamas are beginning to shed light on their ecology and biology in their invaded range (Morris et al. 2009). Bahamian studies documented lionfish at 5 to 177 times higher densities than in their native range (Grubich et al. 2009), capable of reducing reef fish recruitment by 79% from experimental patch reefs, and preying mostly on fishes (78% by volume), including 41 species from 21 families (Albins & Hixon 2008, Green & Cote 2009, Morris & Akins 2009). Based on laboratory studies, 80 adult lionfish along a 1 km stretch of reef in Eilat (Red Sea) were estimated to cumulatively consume approximately 230 kg of mostly small-bodied prey fishes per year (Fishelson 1997). The size (and economic importance) of prey consumed in the invaded range may increase,

however, as increases in body size (relative to the native range) are known for a variety of invasive species, potentially including lionfish (Grosholz & Ruiz 2003).

The invaded range, and densities, size attained and depth distribution of lionfish in invaded habitats, together with laboratory studies of food consumption, all indicate the possibility for substantial impacts to both native prey communities and trophic competitors. A comprehensive understanding of the impacts of invasive species requires investigation of interactions at broad geographic scales (Crooks & Rilov 2009), because impacts may vary as invaders confront and respond to different ecological and physical factors in their invaded range. For example, the narrower depth distribution of lionfish in northern parts of the invaded range may be related to winter water temperatures (Whitfield et al. 2002, Kimball et al. 2004, Ruiz-Carus et al. 2006). Ultimately, the impact of lionfish on populations of potential prey and competitors cannot be assessed without detailed data on food habits (Meister et al. 2005, Ruiz-Carus et al. 2006).

Despite recent studies of potential impacts of lionfish to tropical reef communities in the Bahamas (Albins & Hixon 2008, Morris & Akins 2009, Cote & Maljković 2010), impacts to warm-temperate hard bottom reefs of the Southeast US Atlantic Ocean remain unknown. These hard bottom reefs are well recognized as essential fish habitats that support economically valuable commercial and sport fisheries and an increasingly popular sport diving industry (Struhsaker 1969, Parker & Ross 1986), and lionfish have become widespread residents in the region (Whitfield et al. 2007, Morris et al. 2009). Additional stressors in the Southeast US Atlantic include multiple non-native marine fish species (Semmens et al. 2004, Schofield et al. 2009), potential increases in winter bottom water temperatures (Parker & Dixon 1998), and the overfishing of many important predatory reef species (Coleman et al. 1999, Huntsman et al. 1999, Shertzer & Williams 2008).

We set out to contribute to the understanding of lionfish impacts in their invaded range by determining their diet on hard bottom communities of the Southeast US Atlantic Ocean. Our goal was to assess both immediate (stomach contents) and long-term (isotopes) lionfish diets in combination with data from prey community surveys to make inferences about the specialist or generalist predatory role of lionfish. Stomach contents provided information on ingested prey, representing the animal's diet over the last few hours to days, while stable isotopes offered additional information on the trophic status of lionfish by providing a long-term integration of the diet over previous weeks to months (Cocheret de la Morinière et al. 2003). We then considered these results within the context of native reef fish

diets, hard bottom community structure, and ecological stressors in the Southeast USA to infer potential impacts (trophic overlap and direct predation) of this invasive fish in these warm-temperate reef systems.

MATERIALS AND METHODS

During June to August 2004 and 2006, we collected lionfish with spears through daylight hours from 18 continental shelf locations in Onslow Bay, North Carolina, at depths from 30 to 45 m (Fig. 1, Table S1 in Supplement 1 at www.int-res.com/articles/suppl/m432p181_supp.pdf) using decompression diving techniques. In 2006, at each site ($n = 11$), we also conducted visual surveys of small benthic fishes to estimate the abundance of potential prey. Visual surveys always took place before collections. The prey fish surveys consisted of one 15 min underwater visual census per site, along a 25 m long transect (Brock 1954, Samoilys & Carlos 2000). The width of the transects was restricted to 2 m and targeted active cryptic (or juve-

nile) prey fishes 10 cm and less in TL, on or above the benthos. This group is often underestimated in surveys of larger conspicuous fishes. However, crevices were not searched, so sedentary or truly cryptic species such as scorpionfish (Scorpaenidae) are unlikely to have been sampled effectively. Because collection of fishes at depth may cause regurgitation (Bowen 1992), we immediately placed speared lionfish in plastic bags to prevent loss of regurgitated stomach contents.

Stomach contents. At the surface, fish were weighed and measured, mouth and gills examined for regurgitated prey (Parrish 1987), and stomachs removed and preserved in 95% ethanol. We identified prey items in the stomachs to the lowest practical level using a dissecting microscope and published taxonomic keys and reference texts (Dahlberg 1975, Robins et al. 1986, Bohlke & Chaplin 1993, Hoese & Moore 1998, McEachran & Fechhelm 1998, Carpenter 2002a,b, McEachran & Fechhelm 2006). We blotted the prey items dry, counted, measured and weighed them, and determined their volume by displacement (Hyslop 1980). In 2004, we also removed and froze muscle tissue for isotope analysis. In the laboratory, we rinsed muscle tissue in distilled water, dried it at 60°C for 48 h, and then ground the tissue prior to analysis. Results are expressed as δ values (‰), which represent deviations from the standard reference materials (Fry 1988). Samples were analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values with a mass spectrometer at University of California-Davis Stable Isotope Facility.

Isotope analysis. We used a simple 2-source mixing model (Vander Zanden & Rasmussen 2001) and lionfish $\delta^{13}\text{C}$ values to estimate the contribution of phytoplankton and benthic algae to the lionfish food web. We used a mean $\delta^{13}\text{C}$ value of -23.5 ‰ for phytoplankton (Fogel et al. 1999), which is consistent with other reports of coastal phytoplankton. There are few reported $\delta^{13}\text{C}$ values for the benthic macroalgae and microalgae, which occur on the shallow portions of the continental shelf and contribute significantly to primary production in the coastal ocean (Cahoon & Cooke 1992, Jahnke et al. 2000). We used a value of -17.0 ‰ for benthic algae, which is consistent with values reported from the West Florida Shelf (Fonseca et al. 2006), the Seto Inland Sea (Takai et al. 2002), and the known enrichment in $\delta^{13}\text{C}$ by benthic primary producers (France 1995). We estimated the trophic level at which lionfish are feeding by comparing the $\delta^{15}\text{N}$ values of the primary producers at the base of the food web with lionfish $\delta^{15}\text{N}$ values (Fry 1988, Vander Zanden & Rasmussen 2001). Fogel et al. (1999) report phytoplankton $\delta^{15}\text{N}$ values averaging $+4$ ‰ from the study area, and we assumed that benthic algae would have a similar N isotope value. We assumed that carnivorous fish muscle tissue is enriched by 3.4 ‰ from its

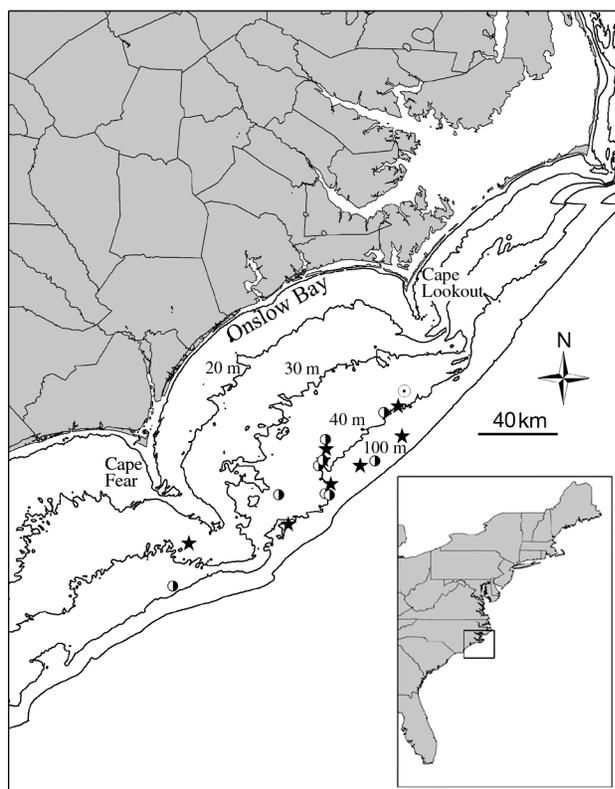


Fig. 1. Coastal North Carolina, showing bathymetric depth zones, (inset) the location of Onslow Bay on the US East Coast, and sampling locations in Onslow Bay in (★) 2004, (○) 2006, and (●) both years. Geographic extent of locations ranged from $34^{\circ}10.523' \text{N}$ and $76^{\circ}31.308' \text{W}$ in the north to $33^{\circ}11.653' \text{N}$ and $77^{\circ}48.434' \text{W}$ in the south

prey (Fry 1988, Vander Zanden & Rasmussen 2001) and that herbivorous fish and invertebrates are enriched by 2.4‰ from their food source (Vander Zanden & Rasmussen 2001, McCutchan et al. 2003).

Statistical analysis. We constructed cumulative prey curves to determine the adequacy of sample sizes (see Supplement 2 at www.int-res.com/articles/suppl/m432p181_supp.pdf). For each prey category, we calculated mean percent number (%n), volume (%V) and weight (%W) from the percentage representation of each prey category in the total number, volume and weight, respectively, of food items for individual lionfish. Rather than pooling prey items across stomachs (sacrificial pseudoreplication) and to quantify the variation around each dietary index, we calculated indices at the level of individual stomachs and then calculated mean values (Ferry & Caillet 1996, Graham et al. 2007). Frequency of occurrence (%O) was calculated as the number of stomachs that contained one or more of a given prey type expressed as a percentage of all lionfish examined. These data were used to calculate the percent index of relative importance (%IRI = $[IRI_i / \text{Total IRI}] \times 100$, where i = a given prey category, $IRI_i = (\%n_i + \%V_i) \times \%O_i$, and Total IRI = sum of individual IRIs for each prey category (Caillet 1977, Macdonald & Green 1983, Bowen 1992, Cortes 1997). Percent IRI limits the biases of the individual components of diet analysis and facilitates comparison with other diet studies (Cortes 1997).

We used 1-way analysis of similarities (ANOSIM) tests to examine differences in prey categories, lengths, volume, and number consumed between sampling years, and between prey categories consumed versus prey categories censused during field surveys (see Supplement 3 at www.int-res.com/articles/suppl/m432p181_supp.pdf). A 2-way ANOSIM with year and lionfish size class as factors was used to examine changes in lionfish diet with size while accounting for any differences between years (see Supplement 4 at www.int-res.com/articles/suppl/m432p181_supp.pdf). Where significant differences were found, similarity percentages (SIMPER) analyses were used to determine the contribution of particular categories responsible for the observed dissimilarities. We used the Mann-Whitney Rank Sum test to examine differences between sizes of lionfish collected between years and to compare the sizes of lionfish consuming crustaceans with those that did not, since these data were not normally distributed. As with nearly all studies of stomach contents from predatory fishes, we sampled specimens that contained prey items that could only be categorized as unidentifiable fish species. However, since different fish species are not expected to show differential digestion rates, we assumed that unidentifiable fish prey came from the same species and in similar pro-

portions as identifiable species (Pine et al. 2005). We incorporated unidentifiable fish prey for those analyses that did not depend on the identity of the particular prey item (cumulative prey curve, broad prey categories consumed, distributions of volume and number of prey consumed), and only used recognizable prey items for the remaining analyses. We examined the relationship between fish TL and both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with linear regression using all data.

RESULTS

We found lionfish on nearly all habitats we sampled, including high, medium, and low relief natural hard bottoms, algal sand plains, and artificial relief wreck sites. A total of 226 lionfish were collected, 115 in 2004 and 111 in 2006. Of these, 81 % contained food and of these 183 specimens, 96 % contained fish prey (see Table S1 in Supplement 1). Unidentifiable prey fishes accounted for 45 % by both volume and weight, and 57 % by number. The cumulative number of prey categories (18) recorded from these specimens had neared an asymptote and additional estimates of prey items indicated that only 1.5 to 3 prey categories may have been missed by sampling (see Fig. S1 in Supplement 2). In addition, the mean coefficient of variation (CV) of the mean cumulative number of prey taxa generated for the final 4 stomach samples was 0.59 %, suggesting that characterizing the diet of lionfish from these samples was sufficiently precise.

Analyses of stomach contents suggest a generalist carnivorous diet. Prey categories included decapod crustaceans (mean \pm SE volume per stomach = 0.45 ± 0.13 ml, $n = 17$ stomachs), cephalopod and bivalve mollusks (0.05 ± 0.05 ml, $n = 2$), and ophiuroid echinoderms (0.10 ml, $n = 1$), but these made up only a fraction of prey contents by volume and number (3.8 % invertebrates combined). In contrast, a diverse array of prey fishes from 16 different families was observed in the stomachs (3.77 ± 0.37 ml, $n = 176$; Table 1, Fig. 2). Goatfishes (Mullidae) and wrasses (Labridae) were the largest prey consumed and grunts (Haemulidae), parrotfishes (Scaridae), and sea basses (Serranidae) were consumed in the greatest abundance (Fig. 2).

Major differences in the importance of prey were seen between years. Serranidae and Scaridae dominated the diet in 2004 while Haemulidae, Carangidae (scad and jacks), and Crustacea were important in 2006 (Fig. 3, 1-way ANOSIM, $R = 0.306$, $p = 0.001$; SIMPER, % contribution to dissimilarity: Serranidae = 22.50, Scaridae = 10.19, Haemulidae = 20.38, Carangidae = 6.99, Crustacea = 10.54). These differences may have been due to the availability of prey or a reflection of the sizes of lionfish collected between years. Lion-

Table 1. *Pterois volitans*. Prey consumed by lionfish off North Carolina. IRI: Index of relative importance (see 'Materials and methods: statistical analysis' for details); n/a: stomach contents regurgitated from multiple fish while in a common holding tank. Unidentifiable fishes represented 45% of total volume (664 ml) and weight (616 g), and 57% of total number (826) of prey fishes recorded from lionfish stomachs

Prey category	Total no. consumed	%IRI 2004	%IRI 2006
Synodontidae	2	0.40	0
<i>Saurida normani</i>			
Scorpaenidae	1	0.07	0
Triglidae	1	0	0.08
Serranidae	52	70.15	0.08
Tattler bass <i>Serranus phoebe</i>			
Belted sandfish <i>S. subligarius</i>			
Harlequin bass <i>S. tigrinus</i>			
Lantern bass <i>S. baldwini</i>			
School bass <i>Schultzea beta</i>			
Sandperch <i>Diplectrum</i> spp.			
Apogonidae	11	0.40	0
Twospot cardinalfish			
<i>Apogon pseudomaculatus</i>			
Carangidae	31	0.40	6.94
<i>Selar crumenophthalmus</i>			
Haemulidae	150	0	72.83
<i>Haemulon aurolineatum</i>			
Mullidae	1	n/a	n/a
Pomacentridae	8	0.24	1.58
<i>Chromis enchrysur</i>			
Labridae	9	1.71	0.38
<i>Bodianus</i> spp., <i>Halichoeres</i> spp.			
<i>Thalassoma</i> spp.			
Scaridae	48	18.67	0.16
Bucktooth parrotfish			
<i>Sparisoma radians</i> , <i>Scarus</i> spp.			
Blenniidae	22	2.94	0.41
<i>Hypleurochilus geminates</i>			
Gobiidae	3	0	1.01
Acanthuridae	1	0	0.16
Bothidae	7	0.25	1.02
Monacanthidae	12	0.62	0.65
<i>Monacanthus ciliatus</i>			
Mollusca	3	0.10	0.16
Bivalvia, Cephalopoda			
Crustacea	29	4.06	14.55
Stomatopoda, Decapoda, Cirripedia			
Echinodermata	1	n/a	n/a
Ophiuroidea			

fish collected in 2004 were significantly larger than those collected in 2006 (mean ± SE TL in 2004 vs. 2006: 30.9 ± 0.53 vs. 28.4 ± 0.74 cm; Mann-Whitney Rank Sum test, $T = 13738$, $n_{2004} = 115$, $n_{2006} = 111$, $p = 0.02$); and lionfish consuming Crustacea were significantly smaller than lionfish that did not consume Crustacea (TL of samples containing Crustacea vs. those with no Crustacea: 25.9 ± 1.62 vs. 29.5 ± 0.49 cm; Mann-

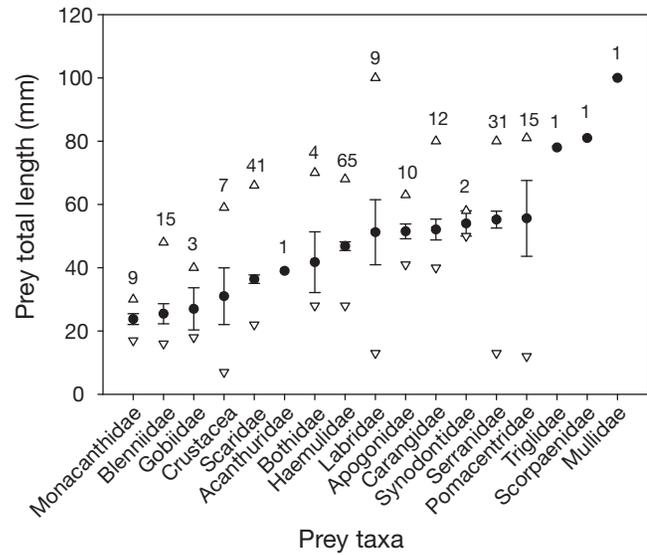


Fig. 2. *Pterois volitans*. Size characteristics (TL) of prey categories consumed by lionfish: (●) mean ± 1 SE, (Δ, ∇) maximum and minimum values. Numbers above symbols are number of prey consumed per category

Whitney Rank Sum test, $T = 1343$, $n_{Crustacea} = 20$, $n_{no\ Crustacea} = 163$, $p = 0.026$). The mean prey/predator TL ratio for 2004 was 0.18 ± 0.01 (max. 0.41, $n = 41$), compared with 0.16 ± 0.01 (max. 0.25, $n = 35$) for 2006 and the difference was not significant (t -test, $t_{74} = 1.84$, $p = 0.07$).

Subtle ontogenetic differences in predatory habit were apparent when examining changes in recognizable prey with lionfish size (2-way ANOSIM, $R_{year} = 0.344$, $p = 0.001$; $R_{size\ class} = 0.064$, $p = 0.029$). We found that the smallest lionfish contained the greatest proportion by volume of crustacean prey, and higher proportions of small bodied benthic fishes such as gobies (Gobiidae) and blennies (Blenniidae) (Fig. 4, Table S3 in Supplement 4). Their diet was distinct from all other size classes except fish of 25 to 29.9 cm TL (Table S2 in Supplement 4). With increasing size, the percent volume of larger-bodied prey such as sea basses, parrotfishes, and grunts increased, along with the variety of different prey categories consumed, but the diets of larger size classes of lionfish were not significantly different from each other (Fig. 4, Supplement 4).

Despite the differences in prey consumed between years, general characteristics of prey found in stomachs indicated consistency in lionfish predatory habits. Prey lengths, volumes of stomach contents, and numbers of prey consumed per stomach were similar between years. Mean ± SE TL of prey in 2004 vs. 2006 was 44.2 ± 1.7 mm, $n = 122$ vs. 43.9 ± 1.5 mm, $n = 94$ (Fig. 5A; 1-way ANOSIM, $R = 0.01$, $p > 0.05$); mean volume of prey in 2004 vs. 2006 was 3.4 ± 0.33 ml, $n = 104$ vs. 4.0 ± 0.72 ml, $n = 79$ (Fig. 5B; 1-way ANOSIM, $R =$

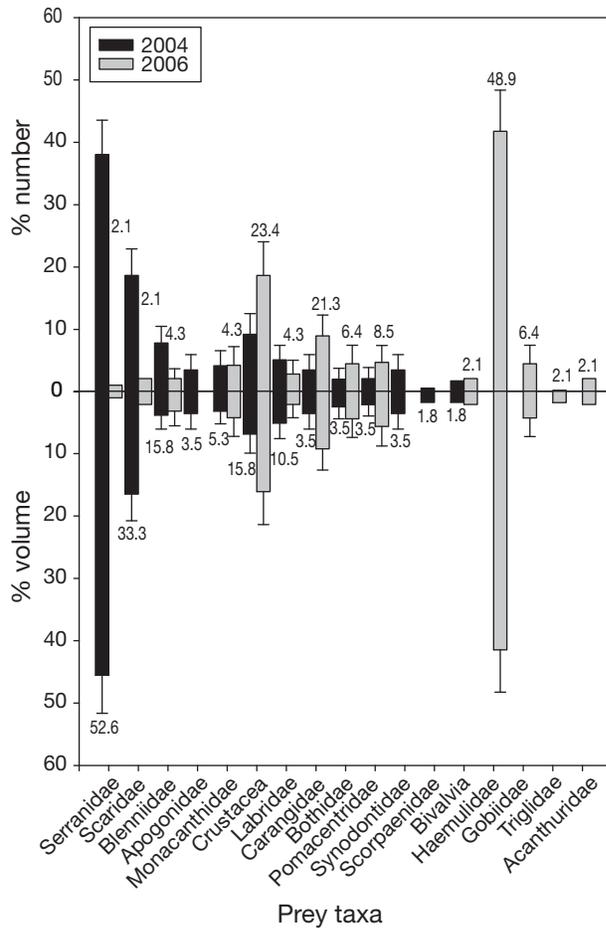


Fig. 3. *Pterois volitans*. Relative importance of prey categories consumed by lionfish from 2004 and 2006, shown as mean (+SE) percent of total number (upper panel) and total volume (lower panel) of prey consumed. Numbers above and below bars show percent frequency of occurrence for prey categories in 2006 and 2004, respectively

0.004, $p > 0.05$); mean number of prey per stomach in 2004 vs. 2006 was 4.0 ± 0.36 , $n = 104$ vs. 5.5 ± 1.0 , $n = 79$ (Fig. 5C; 1-way ANOSIM, $R = 0.015$, $p = 0.035$). In the case of number of prey, the low global R statistic indicates that the overall distribution of prey numbers consumed between years, although statistically significant (because of large sample sizes; Warwick 1993, Warwick & Clarke 2001), was not biologically significant. Visual surveys of prey availability compared with prey from stomach contents revealed that grunts were observed most frequently in the environment and also in the stomachs of lionfish (Fig. 6). Differences between damselfish (Pomacentridae) and scad that were censused versus eaten were not large enough to result in significant differences (1-way ANOSIM, $R = 0.367$, $p = 0.09$).

A total of 115 samples collected in 2004 from 17 sites were analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (see Table S1

in Supplement 1). The $\delta^{13}\text{C}$ values of lionfish muscle tissue exhibited little variability between samples, with an overall mean of $-16.60 \pm 0.02\text{‰}$ (range -16.0 to -17.2‰). The range in $\delta^{15}\text{N}$ values was greater (9.61 to 12.07‰), with an overall mean of $11.00 \pm 0.04\text{‰}$ (Fig. 7). There was no significant relationship between total length of specimens, which ranged between 14.5 and 45.0 cm, and either $\delta^{13}\text{C}$ ($F = 0.006$, $p = 0.9552$, adjusted $r^2 = 0.0088$, $df = 114$) or $\delta^{15}\text{N}$ ($F = 2.16$, $p = 0.1447$, adjusted $r^2 = 0.0100$, $df = 114$) values of lionfish tissue. Given our previous assumptions regarding $\delta^{15}\text{N}$ values for benthic algae and tissue enrichment for carnivorous fish, herbivorous fish, and invertebrates (see 'Materials and methods'), there are 2.3 trophic level steps between the mean lionfish $\delta^{15}\text{N}$ value and primary producers. Assuming a trophic level of 2.3 and a 0.8‰ increase in $\delta^{13}\text{C}$ per trophic step, the 2-source mixing model results indicated that benthic primary producers provide about 77% of the carbon in the lionfish food web.

DISCUSSION

Our study of stomach contents, prey surveys, and isotope analyses for *Pterois volitans* off North Carolina indicates a generalist feeding strategy for this invasive fish. Since stomach contents provide only a snapshot of prey consumed, we hoped that samples from multiple years would provide insight regarding the consistency or variability of targeted prey. We found that prey categories that were important (sea basses, parrotfishes) in 2004 were less important in 2006 (when grunts, crustaceans, and scad were the dominant prey items). Although lionfish that had consumed crustaceans were smaller than those that had not and lionfish collected in 2006 were smaller (by approx. 2 cm) than those collected in 2004, it is improbable that such dramatic differences in prey consumption were due to the slight size difference in specimens alone. Rather, differences between years are most likely driven by differences in prey availability.

Unfortunately, we did not conduct prey censuses in 2004 so we do not know if these differences in prey importance between years were a response to the local availability of prey. However, our prey community surveys from 2006 do suggest that lionfish consume prey in relation to their availability in the environment rather than preferentially consuming particular prey types, as grunts were the most abundant prey item seen and also the most abundant prey in stomachs. Additionally, although we found a mismatch between scad in stomachs (second most abundant prey species) versus censused (absent from visual surveys), subsequent surveys from multiple years and sites indicate

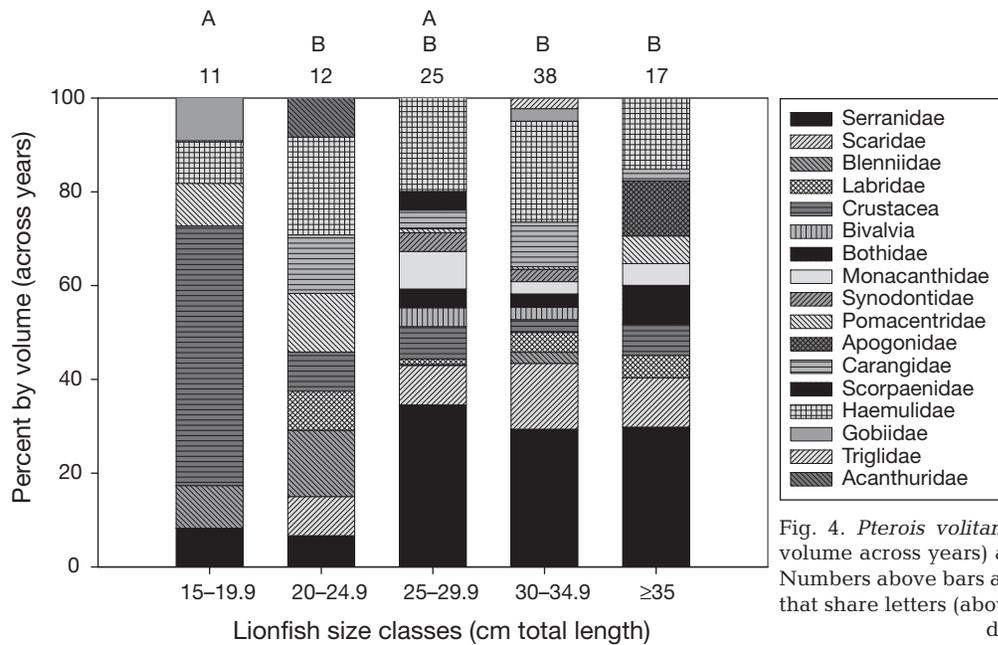


Fig. 4. *Pterois volitans*. Prey composition (% by volume across years) as a function of lionfish size. Numbers above bars are sample sizes. Size classes that share letters (above bars) are not significantly different

that scad is a patchily distributed species that occasionally visits benthic habitats in large (1100 to 40000 ind. ha⁻¹) schools while feeding (Parker et al. 1994, Kendall et al. 2009, P. Whitfield et al. unpubl.). Thus, due to their patchy distribution, our visual surveys were unlikely to have effectively censused scad. Tomato grunts *Haemulon aurolineatum* and scad *Decapterus* spp. can be the 2 most abundant species on hard bottom reefs (Parker et al. 1994, Kendall et al. 2009, P. Whitfield et al. unpubl.) and it is likely that scad was one of the most abundant potential prey species in our study area, resulting in a match between availability and consumption. Although the magnitude of damselfishes observed during censuses is greater than that recorded in stomach contents, this same pattern was also found for 2 other studies of piscivorous groupers in such disparate locations as the Great Barrier Reef (GBR) and Hawaii (Beukers-Stewart & Jones 2004, Dierking et al. 2009). These authors suggested that the close association by damselfishes with the shelter of reefs may make them less vulnerable to predation than mid-water schooling fishes. The groupers *Cephalopholis* spp. studied at the GBR ate a variety of prey but focused on the 2 most abundant families on the reefs: cardinalfishes (Apogonidae) and damselfishes (Beukers-Stewart & Jones 2004). When present, however, mid-water schooling herrings (Clupeidae) and fusiliers (Caesionidae) were selected over reef-associated species, similar to our observations of consumption of mid-water schooling grunts and scad. Predators may preferentially attack large schools if school size increases the conspicuousness and detectability of prey (Botham & Krause 2005), and not all

predators succumb equally to the confusion effect attributed to schools (Turesson & Brönmark 2004). Our density estimates for grunts, scad, and damselfishes suggest that the 3 most abundant prey items observed in lionfish stomachs were also the 3 most abundant prey in the environment. This suggests that prey are generally taken in relation to their local abundance but additional prey surveys coupled with stomach contents are needed to strengthen this conclusion.

The flexibility (across years) in prey consumption and apparent generalist feeding strategy observed for lionfish in this study is consistent with predatory strategies documented for other invasive fishes, including racer goby *Neogobius gymnotrachelus* and flathead catfish *Pylodictis olivaris* (Grabowska & Grabowski 2005, Pine et al. 2005). Available evidence suggests that the most successful fish invaders appear to be piscivorous or omnivorous and ecological generalists (Kolar & Lodge 2001, Unmack & Fagan 2004). Such predation strategies likely aid invasive species during establishment in novel environments where the food base may differ from the species' natural range (Grabowska & Grabowski 2005, Pine et al. 2005), providing an abundance of diverse potential prey resources that would only rarely be limiting (Grabowska & Grabowski 2005, Rehage et al. 2005). The generalist feeding strategy that we have documented for *Pterois volitans* indicates one potential mechanism for the success of this invasive piscivore.

Although we found crustaceans, mollusks, and echinoderms in lionfish stomachs, all measures of prey importance indicate that adult lionfish are essentially piscivorous. This designation does not discount the

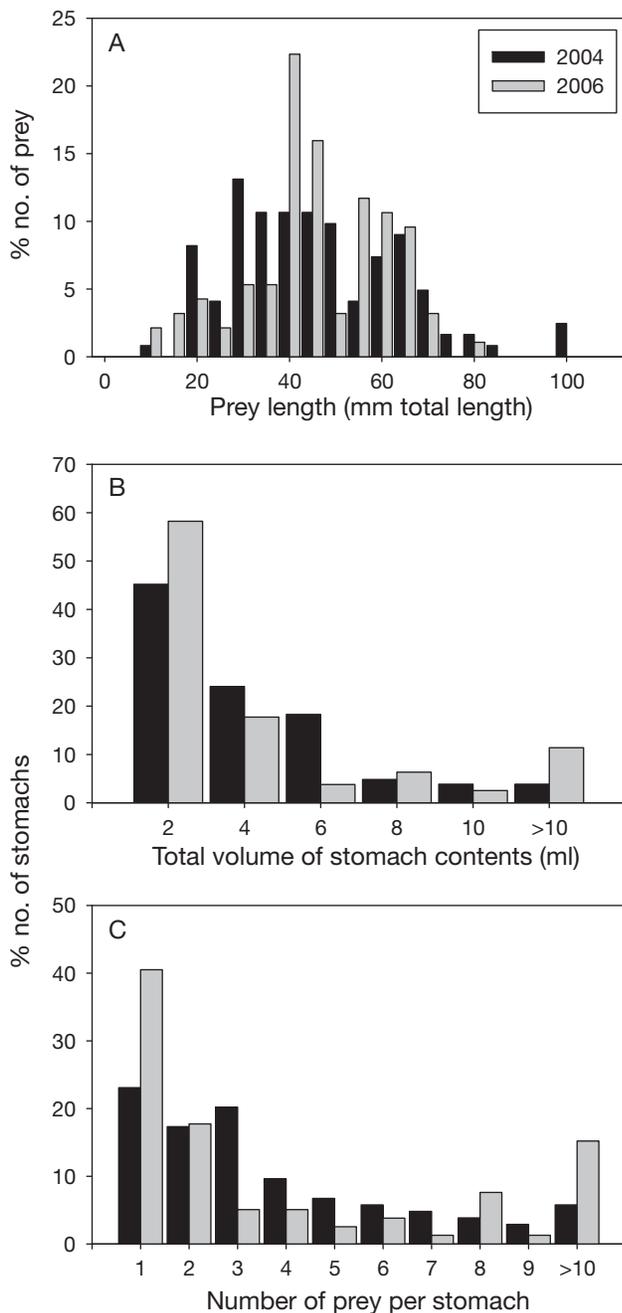


Fig. 5. *Pterois volitans*. Comparisons between collection years of (A) prey size, (B) volume of stomach contents and (C) number of prey consumed. Sample sizes in 2004 and 2006 respectively were: (A) 122 and 94 prey items, (B, C) 104 and 79 stomachs

finding that smaller lionfish may target invertebrate prey and smaller-bodied fishes, and gradually decrease the quantity of invertebrate prey with ontogeny. Such an ontogenetic shift is a general pattern for numerous piscivores and can result in increased growth rates following the shift (Reñones et al. 2002, Scharf et al. 2009). Morris and Akins (2009) examined

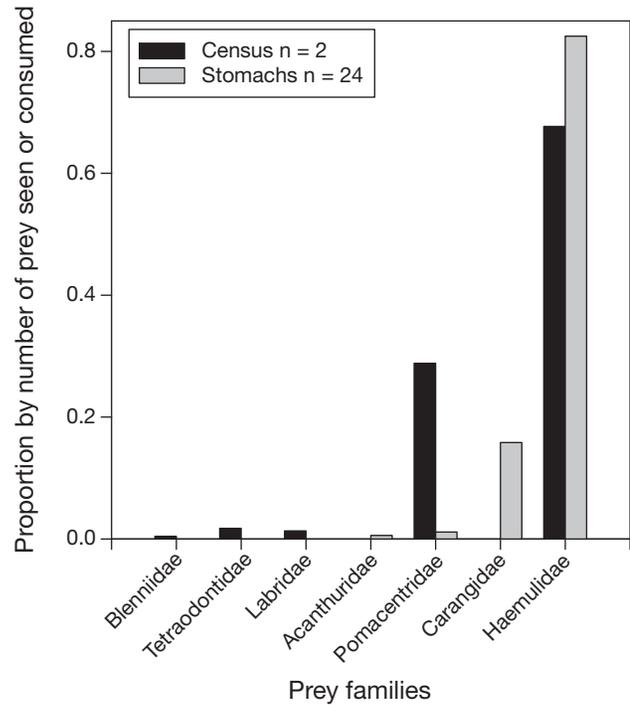


Fig. 6. *Pterois volitans*. Consumption of lionfish prey (determined from stomach samples) compared with prey availability (determined from prey censuses) in 2006. Data are from the Lobsterrock sites (see Table S1 in Supplement 1) that contained the largest number of stomachs with recognizable prey items

lionfish stomachs from the Bahamas and also found that the proportion of fishes in the diet increased with lionfish size. The specimens they examined were smaller on average (TL = 21.7 cm) than our North Carolina sample (TL = 28.4 to 30.9 cm, from 2006 and 2004) and this appears to have influenced the importance of prey as determined through dietary indices, because larger-bodied predators are typically capable of consuming larger-bodied prey (Unmack & Fagan 2004). Smaller-bodied fishes such as gobies, basslets (Grammatidae), and wrasses were ranked as the most important prey items in the Bahamas; whereas, typically larger-bodied prey (sea basses, grunts, parrotfishes) were most important off North Carolina. In addition, the average prey/predator TL ratio was slightly higher off North Carolina (0.16–0.18 vs. 0.15 in the Bahamas), though the maximum prey/predator TL ratio was higher in the Bahamas (0.48 vs. 0.25–0.41 in North Carolina) (Albins & Hixon 2008, Morris & Akins 2009). Morris & Akins (2009) found a greater number of families of fish prey (21 vs. 16 off North Carolina) in their samples but also had a larger sample size (n = 1069 vs. 183 in the present study). However, a number of prey families found in lionfish from the Bahamas were also found in lionfish from North Carolina. These include grunts, cardinalfish, damselfish, wrasses, par-

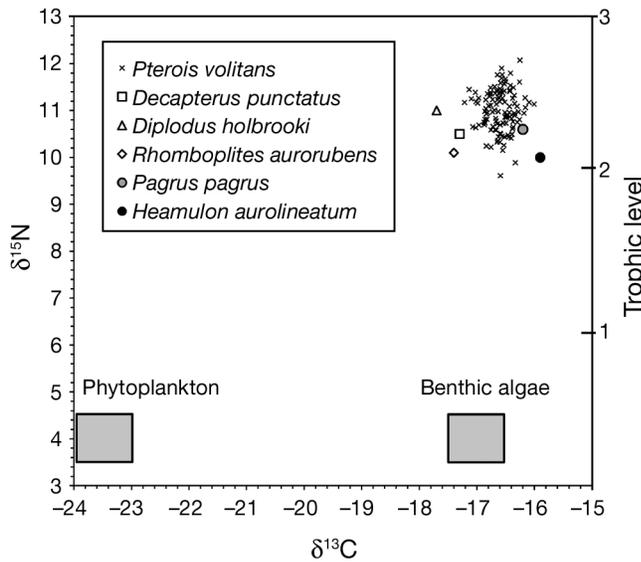


Fig. 7. Plot of stable C and N isotope values for *Pterois volitans* collected in this study (+) and mean values for Onslow Bay reef fishes (*Decapterus punctatus*, *Diplodus holbrooki*, *Rhomboplites aurorubens*, *Pagrus pagrus*, and *Haemulon aurolineatum*) from Thomas & Cahoon (1993). Onslow Bay reef fishes include those utilizing a benthic pathway (filled symbols) and pelagic pathway (open symbols). Estimated trophic level positions of fish are indicated on right side of graph. Boxes for phytoplankton and benthic algae represent the mean ± 0.5 ‰ of published isotope values which were used in the mixing model and trophic level calculations

rotfish, blennies, gobies, sea basses, lizardfish (Synodontidae), surgeonfish (Acanthuridae), filefish (Mona-canthidae), and goatfish. Prey families unique to North Carolina relative to the Bahamian studies include scorpionfish, sea robins (Triglidae), scad, and flounders (Bothidae).

Stable N isotopes provide another means of assessing ontogenetic changes in lionfish diets and the trophic level at which lionfish are feeding. The isotope values of muscle tissue integrate diet over a longer period of time than do stomach contents, and reflect the isotope values of all assimilated prey, rather than the identifiable remains of ingested prey. Despite the decrease in percentage of invertebrates found in stomach contents of larger lionfish, we did not see a significant relationship between total length and $\delta^{15}\text{N}$ values, suggesting that the observed increase in fish consumption with size did not result in a net increase in trophic level. Small fishes that replaced invertebrates in diets of larger lionfish are likely feeding at a similar trophic level as invertebrates, and the utilization of herbivorous fishes such as parrotfish may also contribute to the observed static trophic level with increasing lionfish size. Consumption of rapidly digested (e.g. soft-bodied invertebrates), lower trophic level prey which are not

evident in stomach contents (Bowen 1992) may also contribute to the observed $\delta^{15}\text{N}$ values. The lack of relationship between fish size and $\delta^{15}\text{N}$ values is in contrast to results from other studies examining marine benthic carnivorous fishes (Reñones et al. 2002, Cocheret de la Morinière et al. 2003), and supports the conclusion that lionfish are generalist feeders. Based on $\delta^{15}\text{N}$ values, we conclude that lionfish are feeding at a similar trophic level to multiple species of reef fish in Onslow Bay (spottail pinfish *Diplodus holbrooki*, vermilion snapper *Rhomboplites aurorubens*, round scad *Decapterus punctatus*, red porgy *Pagrus pagrus*, and tomtate *Haemulon aurolineatum*) reported by Thomas & Cahoon (1993) (Fig. 7).

The importance of benthic primary producers to the food web supporting lionfish, as determined by the 2-source mixing model, is consistent with analyses of the trophic importance of benthic algae to fishes occupying other shallow nearshore waters (Thomas & Cahoon 1993, Reñones et al. 2002, Takai et al. 2002, Fonseca et al. 2006). Lionfish C isotope values are also intermediate to those reported for the 5 species of reef fishes (-15.9 to -17.7 ‰) collected from Onslow Bay, which were described as representative of separate planktonic and benthic trophic pathways (Thomas & Cahoon 1993; our Fig. 7). The range and average $\delta^{13}\text{C}$ values (-16.0 to -17.2 , and -16.6 ‰, respectively) of lionfish collected off North Carolina overlap with values for piscivore (-16.3 to -17.6 ‰) and opportunistic generalist (-15.8 to -18.0 ‰) fishes from the literature (Fry 1988), providing additional support that lionfish feed as generalists.

Potential impacts—trophic overlap and direct predation

Since lionfish appear to be generalist predators that feed primarily on benthic fishes, there is potential in the invaded range for trophic overlap with native fishes that share prey resources (See Table S4 in Supplement 5 at www.int-res.com/articles/suppl/m432p181_supp.pdf) as well as direct impacts to prey community structure via predation (Randall 1967, Sano et al. 1984, Naughton & Saloman 1985, Matheson et al. 1986, Fishelson 1997). For example, economically important groupers in the genus *Mycteroperca* feed almost exclusively on fishes (Randall 1967, Dodrill et al. 1993), and scamp grouper (*M. phenax*) overlap in habitat utilization and size classes with lionfish (R. Muñoz & P. Whitfield unpubl.). Like lionfish, serranids, haemulids, and carangids are some of the most important food items in the scamp diet (Matheson et al. 1986), so comparably sized scamp and lionfish may be targeting similar prey, potentially resulting in negative

trophic impacts from the growing lionfish population if their shared prey resource became limited.

Our ongoing research examining juvenile and cryptic fish (lionfish prey) community structure on hard bottoms is shedding light on potential predatory impacts. Given that we found 100 mm prey items in lionfish stomachs, that maximum prey/predator TL ratios were 0.41 (or 0.48 if we use Bahamas estimates), and that a 47 cm (1435 g) lionfish was landed off North Carolina (J. Morris unpubl.), prey up to 22.5 cm TL could potentially be consumed by lionfish in the Southeast US Atlantic. This estimate is larger than the 8 to 9 cm TL reported by Fishelson (1997) in the laboratory, but the largest lionfish he studied also weighed less (1006 g) than the specimen from North Carolina. During our ongoing research, we regularly observe lionfish together with the juveniles of a variety of economically important species such as black seabass *Centropristis striata*, vermilion snapper, white grunt *Haemulon plumieri*, and scamp grouper at sizes (<10 to 20 cm) such that they could be directly consumed by lionfish (R. Muñoz & P. Whitfield unpubl.). Indeed, Morris & Akins (2009) found economically important yellowtail snapper *Ocyurus chrysurus* and Nassau grouper *Epinephelus striatus* in the stomachs collected from Bahamian lionfish.

On the other hand, numerous Atlantic fishes are capable of consuming venomous scorpaenids, including goosefish *Lophius americanus* and mutton snapper *Lutjanus analis*, which are known to consume the venomous scorpaenid blackbelly rosefish *Helicolenus dactylopterus* and spotted scorpionfish *Scorpaena plumieri*, respectively (Randall 1967, Bowman et al. 2000). In addition, lionfish were recently documented in the stomachs of tiger groupers *Mycteroperca tigris* and Nassau groupers in the Bahamas (Maljković et al. 2008). At this stage, however, the potential role of predation in decreasing the number of lionfish is unknown, as is the effect of lionfish on native predators. Predation by large carnivores such as groupers and sharks may represent one of the best controls for invasive lionfish (Albins & Hixon 2008), as low densities (~2.2 ind. ha⁻¹) of lionfish were observed in their native range on Palauan reefs with robust grouper populations (Grubich et al. 2009).

Lionfish: a permanent component of the Western Atlantic fish community

Piscivores are believed most capable of altering the communities which they invade (Marchetti et al. 2004) and the overall pattern of generalist piscivory emerging from this study and others (Albins & Hixon 2008, Morris & Akins 2009, Cote & Maljković 2010) indicates

the potential for significant impacts to the invaded community. In addition to the diversity of habitats occupied off the North Carolina coast (P. Whitfield et al. unpubl.), lionfish have also been found in Bahamian mangroves (Morris & Akins 2009, Barbour et al. 2010). Therefore, in southern locations where winter water temperatures more closely resemble those found in the native range, lionfish can be expected to eventually occupy a variety of inshore and offshore habitats. Because of their planktonic larval dispersal and their opportunistic colonization of habitats and use of food resources, we caution that eradication of lionfish will not be feasible. Sustained control measures may mitigate the eventual extent of lionfish populations, but only on a local scale, and the costs of these efforts will need to be carefully evaluated. Fortunately, lionfish are a popular food fish in their native range and aside from the care required in avoiding spines once collected, they are one of the easiest fishes to capture by spear. Therefore, developing and encouraging a fishery for lionfish should be an important part of local control efforts.

In addition to trophic and predatory impacts outlined here, further indirect effects are possible and remain to be investigated in the Southeast US Atlantic. These effects may be related to the overfishing of many groupers and other native predators (Coleman et al. 1999, Huntsman et al. 1999, NMFS 2010) or invasional meltdown (Simberloff & Von Holle 1999, Grosholz 2005) or interactions with other non-native marine fishes (Semmens et al. 2004, Schofield et al. 2009). The combined effects of overfishing, climate change, and multiple invasive species on ecosystems are not well understood but have been implicated in ecosystem state shifts and decline in several marine ecosystems (Harris & Tyrrell 2001, Stachowicz et al. 2002, Frank et al. 2005, Grosholz 2005).

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