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Biological invasion of the Indo-Pacific lionfish *Pterois volitans* along the Atlantic coast of North America

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ABSTRACT: The occurrence of lionfish *Pterois volitans* is reported from the western Atlantic Ocean. Adults were collected off the coasts of North Carolina, Georgia and Florida, and juveniles were collected along the shore of Long Island, New York. They have also been found around Bermuda. Lionfish are indigenous to tropical waters of the western Pacific and their occurrence along the east coast of the United States represents a human-induced introduction. Distribution of adults suggests lionfish are surviving in the western Atlantic and capture of juveniles provides putative evidence of reproduction. The most likely pathway of introduction is aquarium releases, but introduction via ballast water cannot be ruled out. The ecosystem of the southeastern United States continental shelf is already undergoing change: reef fish communities are becoming more tropical and many fish species are overfished. These ongoing changes, along with limited information regarding the biology of *P. volitans*, make predictions of long-term effects of the introduction difficult. This discovery represents the first, apparently successful introduction, of a marine fish from the western Pacific to Atlantic coastal waters of the United States.

KEY WORDS: Biological invasions · Nonindigenous species · Marine fish · Scorpaenidae · Marine introductions · Lionfish · *Pterois volitans* · Invasive species · Pteroinae

INTRODUCTION

Biological invasions consist of the arrival, survival, successful reproduction and dispersal of a species in an ecosystem where the species did not exist previously (Carlton 1989). Invasions can result from natural range extensions or from human-induced introductions (Carlton 1989). Over the past 2 decades, introductions of nonindigenous marine species have occurred more frequently, raising concerns over their impacts on marine ecosystems (Cohen & Carlton 1998, Ruiz et al. 2000). A number of studies have documented pathways of marine introductions (i.e. arrival) and outlined factors and mechanisms that lead to successful invasions (i.e. dispersal; Carlton 1985, Carlton & Geller 1993, Ruiz et al. 1997, Wonham et al. 2000, 2001).

There are striking differences in marine fish introductions compared to introductions of other marine species (Baltz 1991). First, marine fish introductions are relatively rare. Of the more than 200 established exotic species in the San Francisco Bay watershed (both freshwater and marine components), only 6 are marine and estuarine fish species (Cohen & Carlton 1998). Simi-

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larly, of the more than 550 fish introductions reported in the United States, less than 30 were marine fishes introduced to marine environments (Fuller et al. 1999[1]). Second, although some fish introductions have been linked to ballast water (Wonham et al. 2000), which is an important pathway for aquatic introductions generally (Carlton 1985, Carlton & Geller 1993, Ruiz et al. 1997, Wonham et al. 2001), most marine fish introductions have resulted from purposeful releases for fishery development or aquarium releases (Randall 1987). Third, success (i.e. reproduction and dispersal) of many marine fish introductions is often known (Randall 1987, Baltz 1991), whereas success of most other aquatic introductions can be difficult to determine (Ruiz et al. 1997).

Marine fish introductions are thought to have limited effects on ecosystems. It may be that as a result of limited marine fish introductions, and the equivocal effect of introduced fish species on native marine fishes, fisheries and communities, introduced marine fishes have not traditionally been thought of as an important threat (Ruiz et al. 1997). In a review of Hawaiian marine fish introductions, Randall (1987) noted few adverse effects of introduced marine fish species, yet little direct research has investigated potential effects. In addition, there is the specter of ecosystem consequences similar to those experienced in the Great Lakes, where introductions of the round goby *Neogobius melanostomus*, the European ruffe *Gymnocephalus cernuus* and the sea lamprey *Petromyzon marinus* have been implicated, along with overfishing and pollution, in the decline and extinction of several native fish species (Miller et al. 1989, Jude et al. 1995).

This paper documents the introduction and probable establishment of the Indo-Pacific lionfish *Pterois volitans* along the East Coast of North America. This represents the first, apparently successful introduction, of a marine fish from the western Pacific to Atlantic coastal waters of the United States. The establishment of lionfish is of particular importance due to its venomous spines, style of predation and lack of known predators. Further, the introduction of lionfish along the southeastern United States coast is of concern because a number of species at a similar trophic level are overfished and the overall fish fauna is already changing.

METHODS, RESULTS AND DISCUSSION

Pterois volitans along the Atlantic coast of North America

Nineteen substantiated observations and 1 specimen collection have been made of the western Pacific lion-

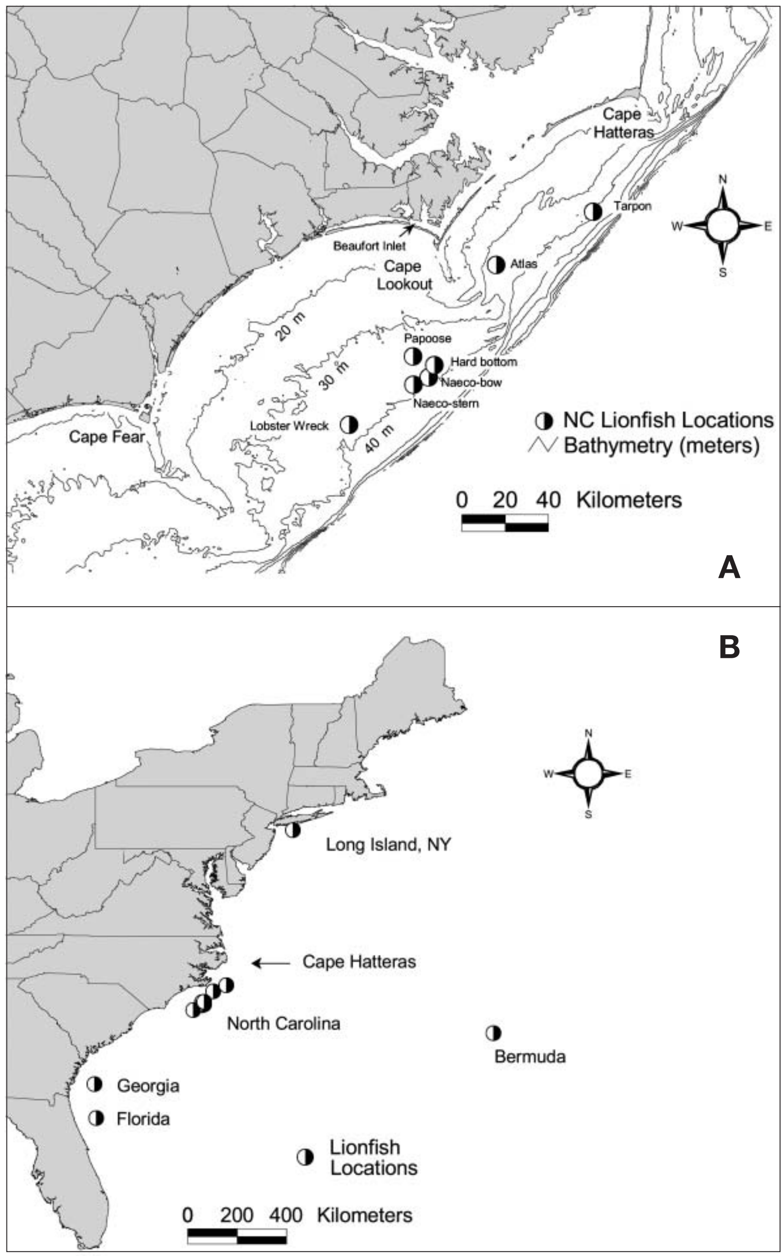

Fig. 1. *Pterois volitans.* (A) Lionfish sightings along North Carolina coast and (B) in the western Atlantic

[1]Available at http://nas.er.usgs.gov/fishes/

fish *Pterois volitans* at 8 different locations (Fig. 1A) on the North Carolina continental shelf over the period of 1 yr (Table 1). There have been other reports of lionfish in this area but only observations substantiated with photographs, video or specimen collection are included here. Multiple lionfish were observed on 2 occasions (Table 1). All fish observed off North Carolina were adults (Fig. 2A), and the specimen collected was female.

An adult male lionfish was collected (Fig. 2B) and 2 others observed off the Georgia coast during the summer of 2001 (Table 1). The Georgia site was approximately 500 km southwest of the North Carolina sites (Fig. 1B). There have been other sightings by SCUBA divers off the coast of Georgia but again, only observations supported by photographs, video or specimen collection are presented.

An adult lionfish (FSBC 19395, FWC-Florida Marine Research Institute) was also collected off the coast of St. Augustine, Florida (Fig. 1B). Multiple lionfish were also observed when the specimen was collected (Table 1).

Two juvenile lionfish (Fig. 2C) were collected on wood pilings along the south coast of Long Island, New York (Table 1) during summer 2001. There are other reports of lionfish sightings along the south coast of Long Island, but only substantiated observations are presented. The Long Island location is approximately 800 km north-northeast of the North Carolina locations.

In April 2001, a lionfish was entered at the Agricultural Exhibition in Bermuda as part of an aquarium exhibit. The lionfish (BAMZ 2001.198.001, Bermuda Natural History Museum) was collected as a juvenile from a tide pool at Devonshire Bay, south shore of Bermuda, in the late summer of 2000 and maintained in a private aquarium until April 2001 (W. Sterrer pers. comm.). In October 2001, several divers reported another lionfish sighting along the South Shore of Bermuda and photographs were taken (Table 1).

All lionfish specimens collected were positively identified as *Pterois volitans*. Identification is relatively straightforward. The subfamily Pteroinae (Pisces: Scorpaenidae) contains 5 genera, distinguishable based on presence/absence of unbranched pectoral rays, relative length of dorsal spines to dorsal rays and presence/absence of a tentacle from the lachrymal bone (Eschmeyer 1986). The genus *Pterois* contains 8 valid species (Eschmeyer 1998) that can be differentiated using meristics, coloration and scale type (Eschmeyer 1986, Schultz 1986). Within *Pterois* there are 2 allopatric sibling species, *P. volitans* and *P. miles*, that can be separated by dorsal and anal fin ray counts, relative length of the pectoral fin and relative size of the dorsal

Table 1. *Pterois volitans.* Observations in the western Atlantic Ocean. Meristics and total length (TL) are included if they could be determined. The number in parentheses in the number observed column is the number of lionfish collected

Location	Site name	Depth (m)	Date	Number observed	Estimated size (TL cm)	Dorsal rays	Anal rays	Observer	Evidence
North Carolina	Naeco-Stern	42	10 Aug 2000	1				Renate Eichinger	Photos
North Carolina	Tarpon	43	Fall 2000	1				John Pieno	Photos
North Carolina	Papoose	39	17 Jun 2001	1				Jeff Kuehn	Photos
								Paul Swenson	Photos
North Carolina	Hard-bottom Site 1	40	19 Jun 2001	4				Jim Smith	Video
North Carolina	Naeco-Bow	42	25 Jun 2001	1				Bobby Edwards	Video
North Carolina	Naeco-Stern	42	9 Aug 2001	2				Jennifer Roy	Video
North Carolina	Atlas	39	16 Aug 2001	1	12	11	7	Paula Whitfield	Video
								Cindy Burnham	Video
North Carolina	Naeco-Bow	42	18 Aug 2001	1	10	11	7	Paula Whitfield	Video
North Carolina	Atlas	39	31 Aug 2001	1	12			Paula Whitfield	Video
North Carolina	Hard-bottom Site 2	40	4 Sep 2001	5 (1)		11	7	John Wisniewski	Collection
								Ryan Tenant	Observer
								Mike Gerken	Observer
								George Purifoy	Photos
								Robert Purifoy	Observer
North Carolina	Lobster Wreck	39	28 Sep 2001	1				Bob Decker	Photos
Georgia	40 mile bottom	38	17 Aug 2001	3 (1)	17.6	11	7	Bob Phillips	Collection
Long Island	Fire Island Inlet	1	11 Sep 2001	1 (1)	2.5	11	7	Todd Gardner	Collection
Long Island	Fire Island Inlet	1	23 Sep 2001	1 (1)		11	7	Todd Gardner	Collection
Bermuda	Devonshire Bay	<1	Fall 2000	1 (1)	6.2			Horace Landy	Collection
Bermuda	Devonshire Bay		Fall 2001	1				Ian Murdoch	Photos
Florida	Offshore St. Augustine	38	Jan 2002	6 (1)	18.4			David Hagan	Collection/obs

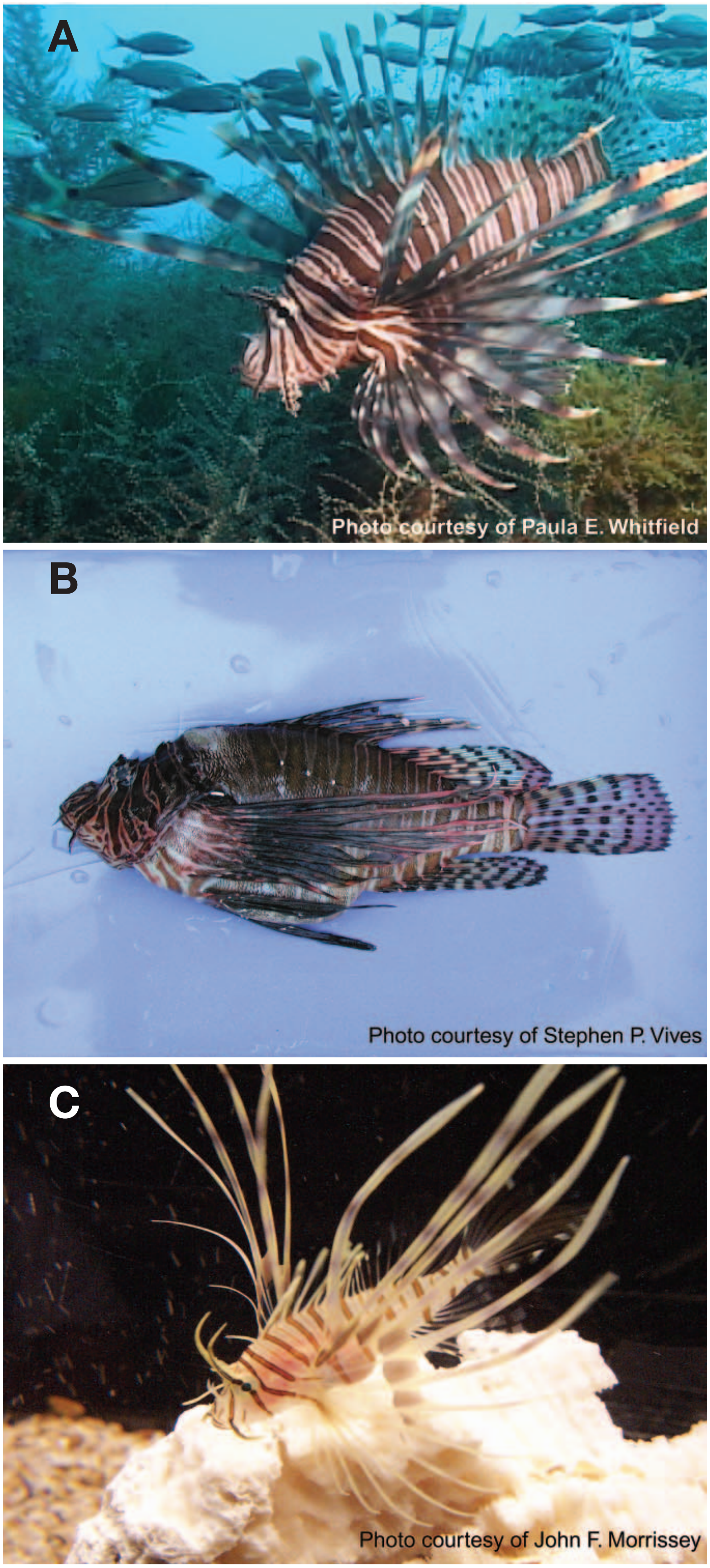

Fig. 2. *Pterois volitans.* (A) Image of a lionfish from a video taken at the Naeco-bow off of North Carolina. Tomtate *Haemulon aurolineatum* are in the background. (B) Image of lionfish specimen collected off the Georgia Coast. (C) Image of a juvenile lionfish collected alive off Long Island, New York

fin spots (Schultz 1986). The 5 specimens collected (1 adult female, NC; 1 adult male, GA, 2 juveniles, NY; 1 adult FL) were positively identified as *P. volitans* based on spot size (adults) and meristics (both adults and juveniles): dorsal XIII, 11; anal III,7; pectoral 14. In addition, 2 fish videotaped were positively identified as *P. volitans* by fin spine/ray counts. All other lionfish photographed and videotaped were assumed to be *P. volitans*, but some could have been *P. miles* (Table 1).

The native range of *Pterois volitans* extends from southern Japan, south to Lord Howe Island off the east coast of Australia, throughout Indonesia, Micronesia and French Polynesia (Schultz 1986). *P. miles* replaces *P. volitans* west of Sumatra, throughout the Indian Ocean and north to the Red Sea (Schultz 1986). Both species associate with rock and coral substrate from the surface to 50 m, and many records are from harbor areas (Schultz 1986). Both species have venomous dorsal, anal and pelvic spines and are popular in the aquarium trade (Thresher 1984). The presence of *P. volitans* along the Atlantic coast of North America represents introductions from the western 291 Pacific to the western North Atlantic.

Potential survival of *Pterois volitans* along the southeastern United States

The number and spatial distribution of observations suggest that adult *Pterois volitans* are surviving along the southeastern United States coast. Adult *P. volitans* were observed at 8 sites off of North Carolina, twice during 2000 and multiple times during 2001. Adults were also observed off the coast of Georgia in 2001 and Florida during 2002. The spatial extent and multiple observations of adults suggest that *P. volitans* is distributed over a large latitudinal portion of the southeastern United States continental shelf.

Temperature is likely an important factor affecting survival, reproduction and dispersal of *Pterois volitans* along the Atlantic coast of North America (Longhurst 1998). Two oceanographic and zoogeographic regimes are defined along the east coast of the United States. The southeastern United States continental shelf (Cape Hatteras to southern Florida) contains relatively saline (34 to 36 salinity) and warm (12 to 16°C winter minimum) water and a warm-temperate fish fauna (Briggs 1974, Stegmann & Yoder 1996). The northeastern United States continental shelf (Cape Hatteras to Gulf of Maine) is characterized by slightly fresher (30 to 33 salinity) and colder (5 to 10°C winter minimum) water and a cold-temperate fish fauna (Briggs 1974, Mountain & Holzwarth 1989). Temperature at sites where lionfish were observed on the North Carolina shelf ranged between 14 and 28°C, but cold periods (<15°C) lasted only for a few days (Fig. 3A). These winter temperatures are somewhat lower than winter temperatures off Lord Howe Island, the reported southern limit of *P. volitans* in the southern hemisphere (Fig. 3B). Observation of lionfish at many sites over 2 yr suggests that individuals have survived winter temperatures along the southeastern United States coast.

Winter water temperatures on the northeastern continental shelf are likely too cold to permit overwintering by lionfish. Juvenile stages of a number of tropical and warm-temperate species occur along the northeastern coast during summer (Smith 1899, Able & Fahay 1998) and these fish either perish (McBride & Able 1998) or successfully return to more southern winter habitats (Kendall & Walford 1979). Given the sedentary nature of lionfish (Fishelson 1975), it is likely that juvenile lionfish perish when water temperatures cool below the critical thermal minimum.

Water temperature in Bermuda will likely allow survival of lionfish. Bermuda's fish fauna is subtropical/tropical (Smith-Vaniz et al. 1999) and the subtropical shorefish fauna is more diverse than off North Carolina and Georgia. Thus, if lionfish can survive off the southeastern United States, they certainly can survive off Bermuda.

The occurrence of juveniles strongly suggests that introduced lionfish are reproducing in the western Atlantic Ocean. Also, observation of multiple individuals off North Carolina, Georgia and Florida (Table 1) suggests reproducing populations; Fishelson (1975) reported that *Pterois volitans* (= *P. miles* [Schultz 1986]) is solitary and observed in groups of 3 to 8 only during the initial stages of courtship. Although both sexes and juveniles have been collected, mating has not been observed.

Spawning along the southeastern United States continental shelf likely supplied juvenile lionfish to Long Island and Bermuda. Larval transport pathways from the southeastern shelf to the northeastern shelf and Bermuda have been described (Hare & Cowen 1991, 1996, Cowen et al. 1993, Schultz & Cowen 1994). *Pterois* sp. lays eggs in an egg mass, which is pelagic (Breder & Rosen 1966, Fishelson 1975). Larval duration of lionfish probably ranges between 25 and 40 d; settlement occurs at 10 to 12 mm (for *P. miles*, Fishelson 1975) and the typical growth rate for larval scorpaenids is 0.3 mm d^{-1} (Laidig & Sakuma 1998). This estimated larval duration is well within the range of transport times of other southeastern shelf species expatriated to coastal regions of the northeastern shelf (Hare & Cowen 1991, 1996) and Bermuda (Schultz & Cowen 1994).

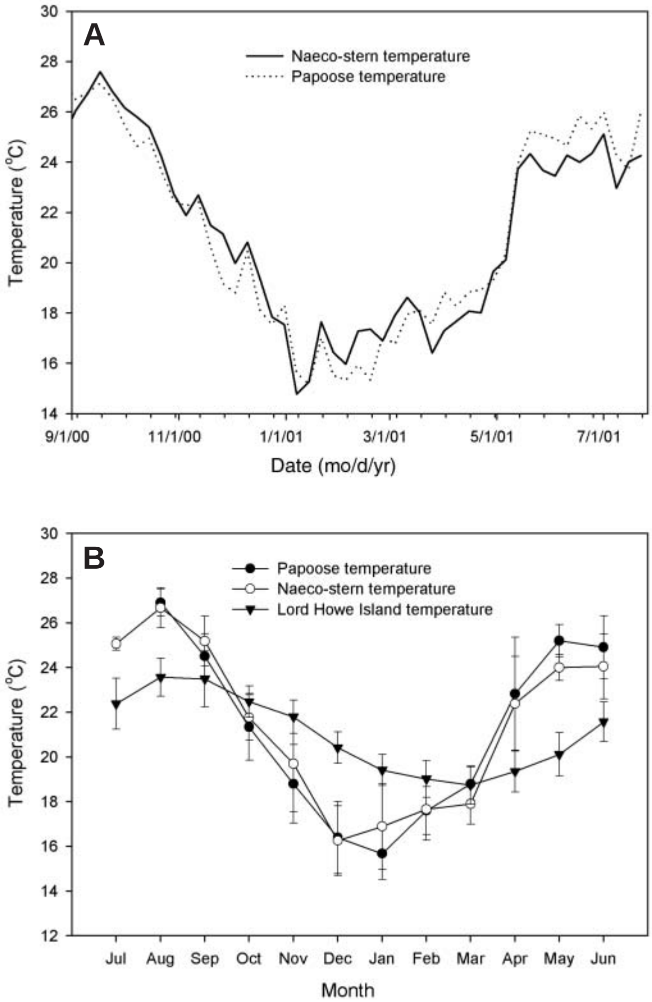

Fig. 3. (A) Mean weekly bottom water temperatures during the winter 2000/2001 at the Naeco-stern and Papoose off of North Carolina. (B) Mean monthly bottom water temperatures and standard deviation for the Naeco-stern, Papoose and Lord Howe Island near the poleward extent of lionfish *Pterois volitans* in its native range (Lord Howe Island coastal station data 1976–1987; CSIRO Division of Marine Research, Hobart)

In summary, lionfish are likely established along the southeastern United States continental shelf. Reproduction is supplying juveniles to the southeastern and northeastern continental shelves and Bermuda. Population survival is possible off Bermuda but not likely on the shelf north of Cape Hatteras due to cold winter temperatures.

Method of introduction

A variety of pathways has been described for biological invasions of marine fish species: natural range extensions, deliberate introductions to improve fisheries, movement of fishes through canals, transport in ballast water and unintentional or intentional aquarium or aquaculture releases (see also Baltz 1991, Courtenay 1993). Because there are vast distances and several biogeographic provinces between the native range of *Pterois volitans* and observations reported here (Briggs 1974), natural dispersal or movement through canals is unlikely. Further, lionfish would not be released for fishery purposes. Thus, ballast water or aquarium release are the 2 most likely introduction possibilities.

Ballast water has lead to introductions of approximately 35 fish species worldwide (Wonham et al. 2000). Most successful introductions are of species in 2 families: Gobiidae and Blennidae (Wonham et al. 2000). There are no reports of successful introductions of scorpaenids resulting from ballast water transport; however, 2 individual scorpaenids have been found in ballast water (Wonham et al. 2000). Additionally, lionfish are reported from several harbor areas (Schultz 1986) making an introduction via ballast water possible.

Nevertheless, accidental or intentional release from aquaria is the most likely mechanism of introduction. *Pterois volitans* is a popular aquarium fish (Thresher 1984) and an accidental release of lionfish was made from an aquarium into Biscayne Bay, Florida in 1992 (Courtenay 1995). Additionally, lionfish specimens collected off the coast of North Carolina, Georgia and Florida appear to be typical of individuals from the central portion of the native range that includes the Philippines and Indonesia (W. Eschmeyer pers. comm.); 85% of marine aquarium fishes exported to the United States come from the Philippines and Indonesia (Baquero 1999).

Ecosystem effects

Introduced species can have deleterious (Taylor et al. 1984, Carlton et al. 1990, Nichols et al. 1990, Carlton & Geller 1993) or minimal effects (Randall 1987) on invaded ecosystems. *Pterois volitans* feeds on a wide variety of smaller fishes, shrimps and crabs (Fishelson 1975, Sano et al. 1984). All of these prey items are abundant on southeastern United States reefs and wrecks (Wenner et al. 1983). The style of lionfish predation is a slight modification of the typical ambush predators that are common on southeastern reefs and wrecks (red grouper, frogfish, scorpion fish). Lionfish use their outstretched pectoral fins to slowly pursue and corner their prey (Allen & Eschmeyer 1973, authors' obs.). The lack of experience of prey species with this behavior may increase predation efficiency of lionfish on the southeastern United States. However, without knowledge of diet, dietary preferences and foraging requirements, the impact of lionfish on prey populations and potential competitors for food cannot be evaluated.

Similarly, interactions with potential lionfish predators are also unknown. Few predators of lionfish have been reported within the native range (Bernadsky & Goulet 1991). Moreover, predators along the southeastern United States have no experience with venomous spines of the lionfish (Ray & Coates 1958, Halstead 1967).

The southeastern United States reef ecosystem is already undergoing change. Many important reef fish predators are overfished (Huntsman et al. 1999). Simultaneously, the reef fish fauna of the North Carolina shelf is becoming more tropical (Parker & Dixon 1998) suggesting ecosystem changes that may be favorable to dispersal of lionfish from more tropical populations. These larger scale ecosystem changes make predicting effects of lionfish on southeastern reef ecosystems even more difficult.

At this time, negative effects on the ecosystem are unlikely as the number of lionfish observed is relatively few, but future effects on tropical and subtropical reef communities in the western central Atlantic may occur if reproduction and dispersal of this species results in population growth.

Future work

Documenting the spatial extent of the introduction and estimating the number of extant individuals are important goals for future research. Efforts should concentrate on reefs and wrecks on the southeastern United States shelf that are <50 and >30 m, based on maximum depth observed in the native range and the depth of individuals observed off the coast of North Carolina (Fig. 4). Efforts to find lionfish juveniles along the east coast of the United States and Bermuda should also continue. Additionally, bottom water temperature should be measured over a large spatial extent during the winter of 2001/2002 and beyond. Temperature data coupled with information on reef and wreck locations

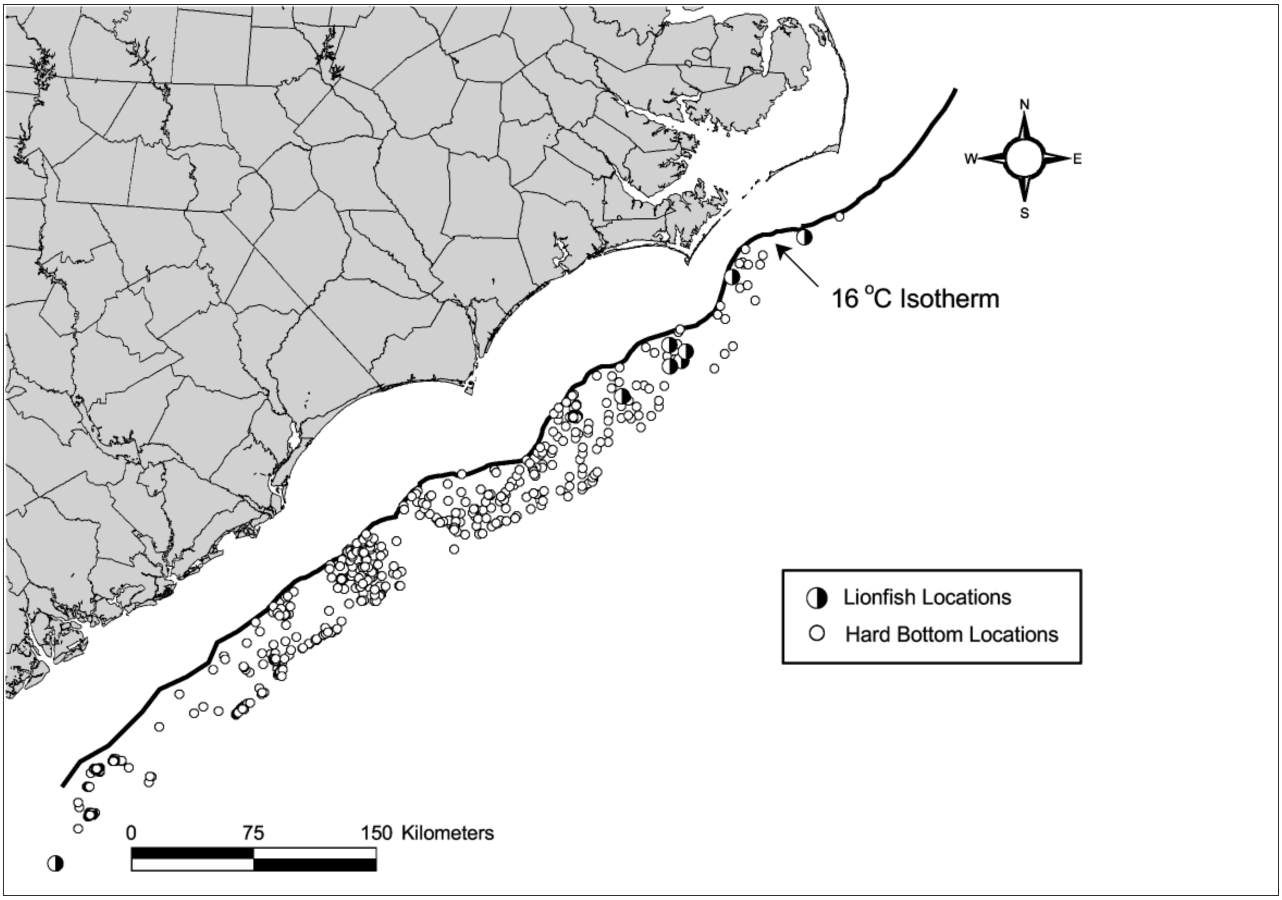

Fig. 4. Best estimate of potential habitat distribution of lionfish *Pterois volitans* along the southeastern continental shelf. Offshore limit is the 50 m isobath (Schultz 1986). The 16°C isotherm represents a likely inshore limit. The 16°C isotherm was taken from a 5 yr average of February sea surface temperature images (see Stegmann & Yoder 1996); temperature is generally vertically homogenous on the North Carolina shelf during winter and thus surface temperature estimates provide a reasonable measure of bottom temperatures

will refine our understanding of potential habitat distribution of *Pterois volitans*. Experiments to determine temperature tolerance of lionfish will further define potential range distribution along the southeastern shelf. Genetic studies similar to those of Planes & Lecaillon (1998) can provide information regarding effective population size and genetic variability of the introduced population. Additionally, genetic studies may be able to identify the source region of the native range which may elucidate the mechanism of introduction (Hauser et al. 1998). Collection of larger lionfish specimens for histological evaluation of their reproductive state will further our knowledge concerning reproduction and potential dispersal. Finally, modeling and/or drifter studies could be undertaken to estimate dispersal of lionfish from observed locations to better predict areas that may receive recruits (Hare et al. 1999).

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