



Native fish community structure and Indo-Pacific lionfish *Pterois volitans* densities along a depth-temperature gradient in Onslow Bay, North Carolina, USA

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ABSTRACT: We quantified native fish densities along a depth-temperature gradient within a temperate-tropical marine transition zone (North Carolina continental shelf) to examine the role of depth and temperature in structuring these communities. We also examined the distribution of invasive lionfish (*Pterois volitans*, *P. miles*) to evaluate a laboratory-derived thermal minimum for lionfish. We collected year-round continuous bottom water temperature data from 2000 to 2010 and surveyed lionfish (2004 to 2010), conspicuous fishes (2006 to 2010) and cryptic smaller-bodied fishes (2007 to 2010) at depths from 5 to 46 m using SCUBA. Bottom water temperatures were constant across the depth gradient during summer and increased from inshore to offshore during winter. The conspicuous fish community was structured by 3 depth zones, 5–14, 15–37 and 38–46 m, that corresponded with winter mean temperatures of 13.9, 17.9 and 20.9°C, respectively. The cryptic fish community was structured by 4 depth zones, 5–15, 18–24, 27–38.5 and 39.5–46 m, with corresponding winter mean bottom temperatures of 13.8, 15.6, 18.7 and 20.9°C. In contrast, summer temperatures were not important in structuring either the conspicuous or the cryptic fish community. Thus, fish communities in the spring/summer appear to be structured by the pattern of bottom water temperature experienced the previous winter, supporting previous studies that indicate winter minimum temperature is important for determining fish distribution and abundance in temperate marine ecosystems. In addition, the deeper fish communities were dominated by tropical species. Lionfish, a tropical species, was found in the highest densities from 38 to 46 m and present in locations with a winter mean of 15.3°C and higher. Increasing temperatures could favor a potential expansion of invasive lionfish and native tropical species into the nearshore waters on the North Carolina shelf, resulting in unforeseen community structure and trophic disruptions.

KEY WORDS: Lionfish · *Pterois volitans* · Conspicuous fish · Cryptic fish · Winter mean temperature · Depth · North Carolina · Hard bottom habitat · Climate change

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INTRODUCTION

Warming global temperature is linked to spatial shifts in species distributions (Parmesan & Yohe 2003, IPCC 2007). In recent years, shifts in fish distributions have been documented as generally poleward and

changing depths as fishes follow their optimal temperature range (Perry et al. 2005, Nye et al. 2009, Sorte et al. 2010a). The extent of these distribution shifts varies depending on the regional biogeography and species physiology. For example, in the North Sea and northeastern United States, species at the south-

ern extent of their range exhibited the greatest distribution shifts poleward, while those at the northern boundary shifted poleward and in some cases deeper (Perry et al. 2005, Nye et al. 2009). Fish communities in transition zones off the western coast of Australia and in the northern Gulf of Mexico and the Mediterranean Sea are becoming more tropical (Ben Rais Lasram & Mouillot 2009, Fodrie et al. 2010, Wernberg et al. 2013). Projections off the eastern coast of Australia and the United States are for warmer winter temperatures to increase overwintering survival of tropical fishes, resulting in range expansions (Figueira & Booth 2010, Hare et al. 2012b). Thus, marine boundaries that represent zoogeographic transitions (e.g. temperate-tropical) may be important areas to detect evidence consistent with climate change impacts. In warm-temperate locations such as the Carolinian biogeographic province, shifts in distribution may result in changes in fish communities from temperate species to subtropical and tropical species (Parker & Dixon 1998, Ben Rais Lasram & Mouillot 2009, Nye et al. 2009, Fodrie et al. 2010), possibly leading to local extirpation of some species and colonization by others (Fodrie et al. 2010, Cheung et al. 2012, 2013).

In the Southeast US Continental Shelf Large Marine Ecosystem (hereafter Southeast US Shelf), Cape Hatteras, North Carolina, represents the northern boundary, where cooler temperate waters originating from the Labrador Current converge with warmer tropical Gulf Stream waters from the south, resulting in a year-round north-south gradient in water temperature. Thus, Cape Hatteras represents both a southern and northern boundary for many temperate and tropical species, respectively. In addition, just south of Cape Hatteras, there is a winter-induced inshore-offshore thermal gradient characterized by colder near-coastal waters and warmer offshore waters that are thermally moderated year-round by the Gulf Stream (Atkinson et al. 1983). This thermal gradient is caused by winter cooling of inshore shallow waters, while offshore the Gulf Stream continues to provide warm water from more southern areas (Atkinson et al. 1983).

The winter inshore-offshore temperature gradient on the Southeast US Shelf is coincident with the shelf depth gradient and likely influences fish community structure year-round. Previous studies in this region found that fish communities shift from temperate to tropical based on depth, with colder winter temperatures usually attributed as the main factor in this shift (i.e. distance from the Gulf Stream) (Miller & Richards 1980, Grimes et al. 1982, Chester et al. 1984, Sedberry & Van Dolah 1984). Temperature-linked overwinter

survival is an important factor in determining abundance and distribution of marine species along the eastern coast of the United States (Hurst 2007). If ocean warming trends continue as projected (IPCC 2007), the Southeast US Shelf should warm, resulting in an inshore shift in species distributions, analogous to poleward shifts seen elsewhere (Perry et al. 2005, Ben Rais Lasram & Mouillot 2009, Fodrie et al. 2010). Species-specific differential shifts in distributions could potentially alter interspecific interactions and food webs and have important impacts on fisheries (Nye et al. 2009, Cheung et al. 2012, 2013). However, to date there has not been a quantitative examination of depth and bottom water temperature influence on fish community structure within this region.

Climate change is one of multiple stressors acting on marine ecosystems (Breitburg & Riedel 2005). The Southeast US Shelf is also under stress from the invasion of the Indo-Pacific lionfish (*Pterois volitans*, *P. miles*), and the present overwintering distribution of lionfish extends from Cape Hatteras south to the northern coast of South America (Betancur-R et al. 2011). Lionfish are considered a major threat to Atlantic reefs by reducing reef fish recruitment and biomass and have been implicated in cascading impacts such as decreased coral cover on coral reefs (Albins & Hixon 2008, Lesser & Slattery 2011, Green et al. 2012). Water temperature is thought to be one of the few abiotic factors to control lionfish distribution on a large scale. The thermal tolerance of lionfish was established experimentally by Kimball et al. (2004); lionfish perish at 10°C. Thus, in addition to potential changes in fish community structure, warming temperatures in the Southeast US Shelf should make the area more favorable to lionfish.

Our goal was to document the role of depth and bottom temperature in influencing fish community structure within the Southeast US Shelf near its northern boundary. We examined both summer and winter bottom temperature to evaluate the importance of maximum and minimum temperatures. Baseline community data combined with concomitant collection of key environmental variables are necessary to establish causality between the environment and community change (Parmesan & Yohe 2003) and for the development of predictive tools to examine the consequences of change (Cheung et al. 2012, 2013, Hare et al. 2012a, Wuenschel et al. 2012). To establish the biological baseline, we surveyed the fish community of larger mobile species along with smaller-bodied cryptic fishes that appear to show increased sensitivity to changes in temperature (Perry et al. 2005). To establish the environmental baseline,

we deployed temperature sensors at the survey sites and quantified summer and winter bottom temperature, a key variable structuring fish communities in this region and elsewhere (Parker & Dixon 1998, Kimball et al. 2004, Figueira & Booth 2010, Wuen-schel et al. 2012). We used the temperature data to calculate temperature preference for several of the abundant species in the survey and to evaluate the laboratory-defined thermal tolerance of lionfish.

MATERIALS AND METHODS

Site characteristics

Fish surveys were conducted annually from 2004 to 2010 on natural hard bottom reefs (calcium carbonate rock outcroppings), rock jetties and shipwreck sites across the shelf in Onslow Bay, North Carolina, from depths of 5 to 46 m (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m509p241_supp.pdf). Sites were chosen to represent a gradient of depth and, by proxy, winter bottom water temperature. However, the closeness of the shallower locations to the authors' home port resulted in an uneven distribution of samples across Onslow Bay, North Carolina (Fig. 1). Surveys were conducted annually between April and September based on ship time availability.

Data loggers (HOBO® Water Temp Pro V1 and V2, HOBO® TidBit v.1) were used to collect bottom water temperatures and were deployed opportunistically at up to 20 locations across the shelf for differing time periods (maximum of 10 yr) (see Table S2 in the Supplement). In some cases, temperature loggers were deployed prior to commencement of fish surveys. On reef sites, loggers were attached near the substrate to small moorings with attached subsurface floats, whereas on shipwrecks, loggers were attached directly to the structure. Data loggers recorded 1 observation every 30 min and were retrieved annually (Fig. 1). Depth at each site was confirmed *in situ*, but for analyses (below), depths were derived from NOAA chart number 11520.

Bottom water temperature analysis

To characterize the climatology of Onslow Bay during the 2001 to 2010 time period, we calculated the mean winter and mean summer bottom water temperature for each year and site based on the daily average from the 3 coldest winter months (January, February and March) and the 3 warmest months

(August, September and October), respectively. The relationship between mean winter temperature and depth was examined using linear regression analysis, with temperature as the dependent variable and depth as the independent variable. The relationship between mean summer temperature and depth was examined using non-parametric Spearman correlation, as the data could not be transformed to meet the assumptions of parametric statistics. We also calculated winter bottom temperature at selected depths across the shelf to illustrate the overall trend in bottom temperature throughout the time period of the study.

Fish surveys

Fish abundance has been estimated within the Southeast US Shelf using hook and line (Grimes et al. 1982, Chester et al. 1984), trawling (Sedberry & Van Dolah 1984), stationary point counts (Parker & Dixon 1998) and video surveys (Burge et al. 2012). However, with the exception of stationary point counts and video surveys, these methods do not effectively census smaller benthic-oriented (cryptic) fishes (Willis 2001). To address these deficiencies, we utilized 2 different diver-based underwater visual census (UVC) band transects (Samoilys & Carlos 2000), hereafter referred to as conspicuous and cryptic fish surveys. Conspicuous fish surveys examined highly mobile conspicuous fish of all sizes (area sampled: $50 \times 10 \text{ m} = 500 \text{ m}^2$) from 2006 to 2010. Cryptic fish surveys (area sampled: $50 \times 2 \text{ m} = 100 \text{ m}^2$) characterized only the smaller-bodied (<10 cm total length) cryptic (or juvenile) fishes (Willis 2001) from 2007 to 2010. For those species observed on both transect types, the adults were generally observed on the conspicuous transects, and the juveniles were generally observed on the cryptic transects. Lionfish were surveyed from 2004 to 2010 using the same method as conspicuous fish, with lionfish-specific surveys occurring 2 yr prior to commencement of community surveys. Our surveys for lionfish and other native fishes were the same and predated recommendations of lionfish-specific survey methods from coral reef habitats (Green 2012). We routinely looked underneath ledge overhangs and within crevices and found that in the hard bottom habitats of Onslow Bay, lionfish were easily visible either on top of the habitat structure, at the base/sand interface of ledges or underneath ledge overhangs. All fish were identified to the lowest taxonomic level (generally species) and assigned a biogeographic designation of temperate, subtropical or tropical based on published sources from FishBase (Froese & Pauly 2014).

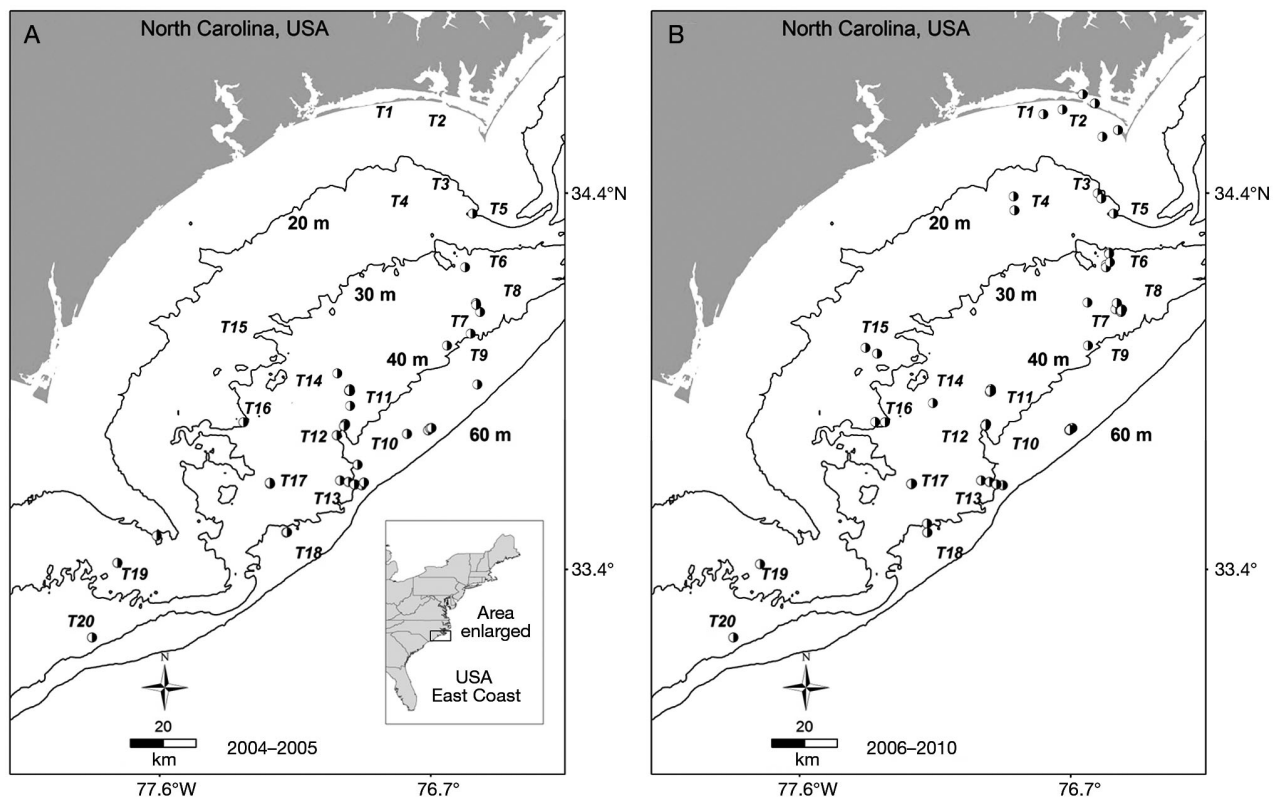


Fig. 1. (A) Lionfish surveys (●) from 2004 to 2005. (B) Lionfish and native conspicuous and cryptic fish surveys from 2006 to 2010 (not all sites surveyed every year). 'T' followed by a number indicates general location of each temperature sensor. Details on number of years for each location are shown in Table S2 in the Supplement at www.int-res.com/articles/suppl/m509p241_supp.pdf

Fish data analysis: relationships to temperature and depth

Multivariate analyses

Conspicuous and cryptic fish densities were first square root transformed to reduce the influence of common species, converted into resemblance matrices using Bray-Curtis similarity and visually examined as multi-dimensional scaling plots in PRIMER (Clarke & Warwick 2001, Clarke & Gorley 2006). We used the similarity profile (SIMPROF) procedure to determine if there was significant structure within the data to warrant further analysis. The categorical variable year was examined using ANOSIM. The influence of continuous environmental variables (mean summer and winter bottom temperature and depth) on fish community structure was examined using the global BEST and LINKTREE procedures (Clarke et al. 2008). In addition, we added lionfish and predator densities (i.e. groupers) to the global BEST and LINKTREE analyses for the cryptic fish community to examine the potential influence of these factors on cryptic fish

community structure. The global BEST procedure determines the combination of environmental variables that 'best' explains fish community structure. Environmental covariates that were found to be collinear (Spearman rank correlation $\rho > 0.9$) were identified and removed prior to BEST analysis (Clarke et al. 2008). Thus, in the case of conspicuous fish, the environmental data consisted of depth and each temperature variable (analyzed separately), and for cryptic fish, the variables depth, winter and summer temperature, lionfish and predator densities (derived from the conspicuous fish transects) were examined, with depth and the temperature variables alternately removed. Following the methods outlined in Clarke & Warwick (2001), the environmental data were observed in draftsman plots, transformed (if needed to correct skewness), normalized and converted to resemblance matrices using the Euclidean distance coefficient. Variable(s) in global BEST with the highest Spearman rank correlations with the fish resemblance matrices were explored further in LINKTREE, with the SIMPROF test set at the 0.05 significance level. We further constrained the results so that groups with

less than 4 sites would not be split further. The LINKTREE procedure is a form of constrained cluster analysis that uses a sequence of SIMPROF tests to identify the specific breaks or 'cutoffs' of the values within the environmental data that best explain the structure within the biotic community (Clarke et al. 2008). SIMPER analysis was conducted to determine the individual species (or taxa) that comprise the different LINKTREE-derived depth zones.

Univariate analyses

The relationship between Shannon diversity for both conspicuous and cryptic communities and depth and winter temperature was examined using regression analysis, with diversity as the dependent variable and either depth or winter temperature as independent variables. Only winter temperatures were analyzed because multivariate analyses found no effect of summer bottom temperatures on fish community structure. To examine the influence of depth and winter temperature on the tropical composition within the fish assemblage, we calculated a Tropicalization Index (TI) based on the percentage contribution of tropical species to the entire fish community at each site (Wernberg et al. 2013). We conducted regression analyses using the index as the dependent variable and depth as the independent variable. The conspicuous fish data were ranked to meet the assumptions for parametric linear regression analyses.

We also calculated a median temperature of occurrence for many of the conspicuous and cryptic species and examined the temperature distribution of lionfish in more detail. Relatively abundant species were included in this analysis: average density over the whole study period $>100 \text{ ind. ha}^{-1}$ and >20 occurrences (conspicuous) and >15 occurrences (cryptic). Mean winter temperature and \log_{10} -transformed fish abundance were used; data were transformed to reduce the influence of highly abundant observations. Median temperature of occurrence was calculated using a quotient analysis (van der Lingen et al. 2005) as modified by Röckmann et al. (2011). Bootstrapping was used to calculate 95% confidence intervals for the median temperature of occurrence estimate; specifically, winter temperature and abundance observations were re-sampled with replacement to generate replicate datasets of the same size as the original data set for each species.

Three analyses were conducted to examine lionfish distribution by depth and temperature in more detail. First, lionfish densities were examined by depth zone

(from LINKTREE results) and year, using a Kruskal-Wallis 1-way ANOVA on ranks to examine lionfish density differences across year and depth zone. Second, the temperature limit of lionfish (based on mean winter temperature) was estimated using the probability density function of temperature of occurrence. The confidence intervals derived from bootstrapping were used to determine the temperature at which the probability of lionfish abundance exceeds 0. Third, the relationship between lionfish densities and summer temperatures were examined using linear regression analysis. Lionfish densities were ranked to meet assumptions for parametric statistics.

RESULTS

Depth and bottom water temperature relationship

We found a strong linear relationship between depth and winter temperature within Onslow Bay (Fig. 2A, linear regression, temperature $^{\circ}\text{C} = 8.892 + [0.241 \times \text{depth}]$, $R^2 = 0.72$, $p < 0.001$). There was no relationship between summer bottom temperature and depth (Spearman rank correlation $\rho = -0.032$, $p = 0.755$), with summer temperature nearly homogeneous across Onslow Bay (Fig. 2B). Winter temperature by year and depth show a consistent pattern by year across the shelf, with shallow areas being the coldest and deeper areas being the warmest, with no interannual trend for increasing temperatures during the time period of this study (Fig. 2C). In fact, there was a consistent decrease across the shelf in winter temperature during the winter of 2008 to 2009. Depth and winter temperature are collinear variables ($\rho > 0.9$); as such, multivariate analyses were conducted separately with winter temperature, summer temperature and depth to avoid statistical problems related to covariance (Clarke et al. 2008).

Fish community analyses

Multivariate analyses

In 2006 to 2010, 142 taxa from 42 families were observed on the conspicuous fish transects, and in 2007 to 2010, 101 taxa from 28 families were observed on the cryptic fish transects (see Table S3 in the Supplement). We found inherent multivariate structure within the conspicuous and cryptic communities, warranting further multivariate investigation (SIMPROF, conspicuous $\Pi = 4.182$, $p = 0.001$; cryptic

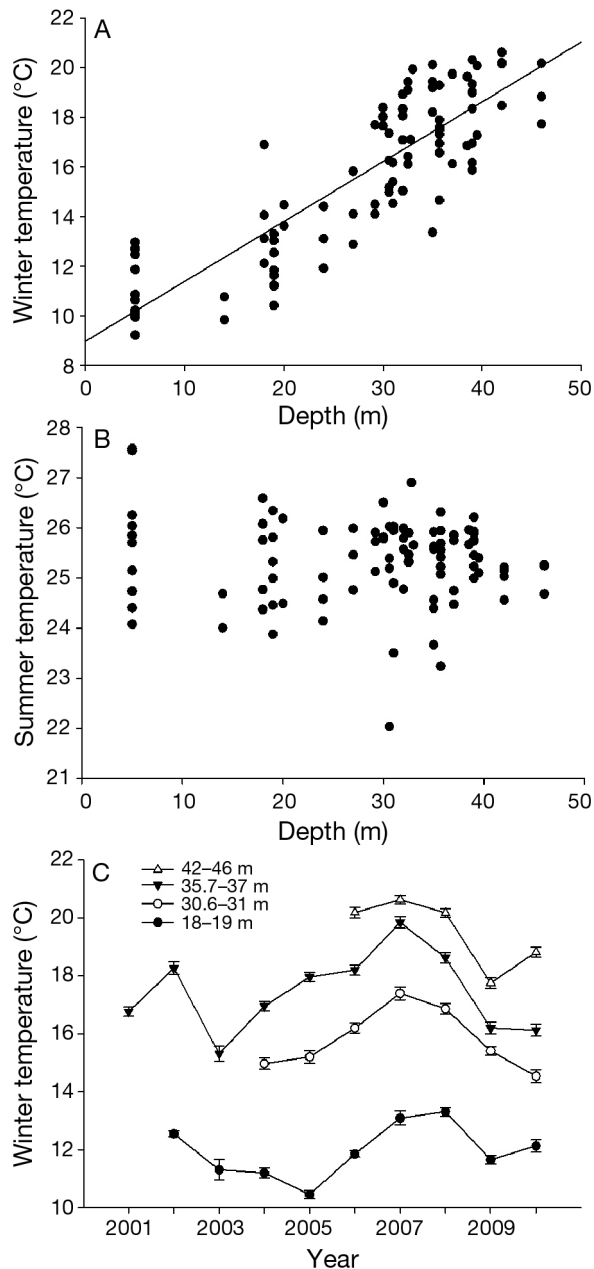


Fig. 2. (A) Mean winter bottom temperature (°C) and depth (m) and the associated regression line (see 'Results: Depth and bottom water temperature relationship'). (B) Scatter plot of summer mean bottom temperature (°C) by depth, illustrating no trend in summer temperatures by depth. (C) Winter bottom temperature (°C) across selected sites within different depths. Each point represents 1 location or an average of up to 2 sites within the depth

$\Pi = 3.933$, $p = 0.001$). There was no difference among years for the conspicuous (ANOSIM $R = 0.03$, $p = 0.29$) or cryptic (ANOSIM $R = 0.047$, $p = 0.09$) fish communities; thus, all data were pooled across years for subsequent analyses. Depth provided a slightly better fit for describing fish community structure

(global BEST depth: conspicuous $\rho = 0.687$, $p = 0.001$; cryptic $\rho = 0.644$, $p = 0.001$) than mean winter temperature (global BEST winter temperature: conspicuous $\rho = 0.560$, $p = 0.001$; cryptic $\rho = 0.577$, $p = 0.001$). Summer temperature was found to be the least important in describing fish community structure (global BEST summer temperature: conspicuous $\rho = 0.261$, $p = 0.001$; cryptic $\rho = 0.231$, $p = 0.001$). Depth structured the conspicuous fish community into 3 main clusters (LINKTREE $B > 66\%$ separation), 5–14, 15–37 and 38–46 m (Fig. 3A), with the greatest separation or difference among groups occurring at depths <14 m and >15 m ($B = 85\%$). These depth zones corresponded with winter mean temperatures of 13.9, 17.9 and 20.9°C, respectively. The cryptic community was separated by 4 depth categories ($B > 61\%$), 5–15, 18–24, 27–38.5 and 39.5–46 m (Fig. 3B), with the greatest community separation ($B = 84\%$) between depths <24 m and >27 m. These depth zones corresponded to winter mean temperatures of 13.8, 15.6, 18.7 and 20.9 °C, respectively.

Results of the conspicuous fish SIMPER analysis indicated 8 species responsible for 90.7 % of the similarity within 5 to 14 m (Table 1). The top 5 species responsible for characterizing this depth zone were *Diplodus holbrookii*, *Centropristis striata*, *Archosargus probatocephalus*, *Halichoeres bivittatus* and *Equetus punctatus*. Seventeen species comprised 90.9 % of the similarity within 15 to 37 m, and the top 5 species were *Haemulon aurolineatum*, *Haemulon plumieri*, *C. striata*, *Mycteroperca microlepis* and *Mycteroperca phenax*. Lionfish were ranked ninth in percent contribution within this depth zone. Twenty-five species comprised 90.2 % of the similarity within 38 to 46 m, with lionfish ranking the highest in percent contribution (19.4 %) within this depth zone, along with *Holocentrus adscensionis*, *Holacanthus bermudensis*, *Balistes capriscus* and *M. phenax* in order of decreasing contribution (Table 1).

Winter temperature preference of individual species was consistent with the depth and temperature groupings found in the multivariate analysis (Fig. 4A). Some warm-water species were found in the deep depth zone, and some warm-water and intermediate-temperature species were found in the mid-depth zone. Only cooler-water species were found in the inshore zone. The mean temperature preference of lionfish was 17.7°C; the lionfish was one of the warm-water species but was found in both the deep and mid-depth zones.

Similar to conspicuous fish, the number of cryptic fish species representative of the individual depth zones tended to increase with depth across the shelf.

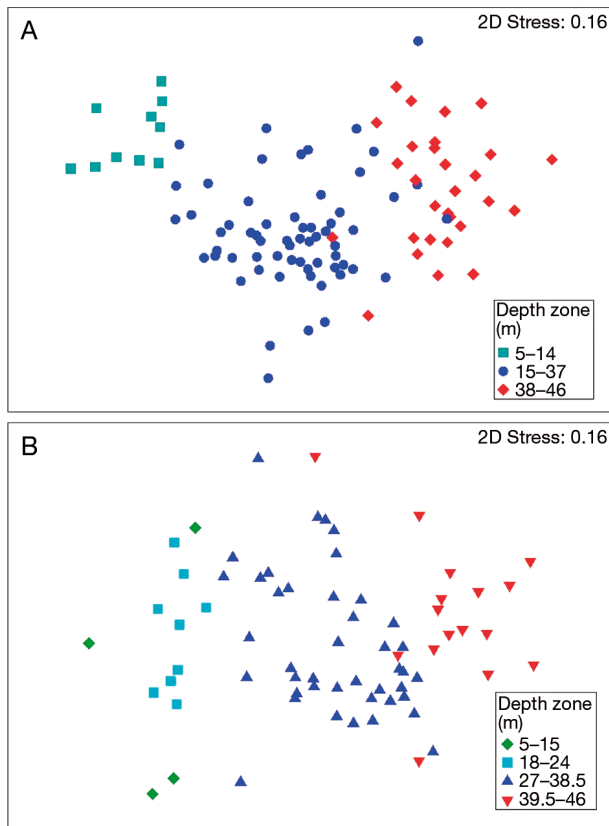


Fig. 3. Multi-dimensional scaling plots color coded by statistically significant depth zone groups based on results from the LINKTREE analysis ($p < 0.001$). (A) Conspicuous fish densities, 2006 to 2010. (B) Cryptic fish community structure, 2007 to 2010

Five species accounted for 94.9% of the similarity within the 5 to 15 m depth zone (Table 2). In order of decreasing contribution, these species were *Serranus subligarius*, *H. bivittatus*, *D. holbrookii*, *Chaetodon ocellatus* and *H. plumieri*. Seven species comprised 90.2% of the similarity within 18 to 24 m; the top 5 species were *H. bivittatus*, *S. subligarius*, *H. aurolineatum*, *Parablennius marmoreus* and *Pareques umbrosus*. Eleven species comprised 91.4% of the similarity within 27 to 38.5 m; the top 5 species were *Chromis scotti*, *H. bivittatus*, *Chromis enchrysurus*, *H. aurolineatum* and *Thalassoma bifasciatum*. Nine species comprised 90.6% of the similarity within the 39.5 to 46 m depth zone; the top 5 species were *Hali-choeres garnoti*, *C. enchrysurus*, *Stegastes partitus*, *T. bifasciatum* and *C. scotti* (Table 2).

Winter temperature preference of individual cryptic species was similar to the results of the conspicuous community and consistent with the depth and temperature groupings found in the multivariate analysis (Fig. 4B). The results of this analysis indicate

Table 1. Dominant species (top 90% based on SIMPER analysis) from 3 depth zones across the North Carolina continental shelf. Species are listed in descending order of contribution to similarity within each depth zone from 2006 to 2010. Density = mean (+SE). 5–14 m, N = 10; 15–37 m, N = 61; 38–46 m, N = 30. (t) = tropical, (st) = subtropical, (tm) = temperate species according to FishBase published sources (Froese & Pauly 2014). Sim. = average percent similarity, T = average winter temperature ($^{\circ}\text{C}$)

Species	Density (ind. ha ⁻¹)	Contribution (%)
5–14 m (Sim. = 35.9, T = 13.9 ± 0.02)		
<i>Diplodus holbrookii</i> (st)	1773.9 (970)	31.5
<i>Centropomus striata</i> (tm)	509.4 (286)	20.2
<i>Archosargus probatocephalus</i> (st)	365.7 (172)	13.4
<i>Halichoeres bivittatus</i> (t)	137.6 (52)	7.1
<i>Equetus punctatus</i> (t)	258.6 (216)	5.9
<i>Eucinostomus species</i> (t)	184.7 (113)	5.5
<i>Chaetodipterus faber</i> (st)	28.3 (13)	3.8
<i>Lagodon rhomboides</i> (st)	85.5 (43)	3.2
Cumulative contribution (%)		90.7
15–37 m (Sim. = 33.9, T = 17.9 ± 0.02)		
<i>Haemulon aurolineatum</i> (st)	7749.1 (1808)	33.4
<i>Haemulon plumieri</i> (st)	234.2 (33)	8.2
<i>Centropomus striata</i> (tm)	209.7 (57)	5.8
<i>Mycteroperca microlepis</i> (st)	92.2 (14)	5.4
<i>Mycteroperca phenax</i> (st)	83.4 (12)	5.2
<i>Pareques umbrosus</i> (st)	177.7 (27)	4.9
<i>Diplodus holbrookii</i> (st)	718.5 (269)	4.3
<i>Holacanthus bermudensis</i> (st)	48.1 (7)	3.3
<i>Pterois volitans</i> (t)	84.6 (15)	3.1
<i>Centropomus ocyurus</i> (st)	97.3 (21)	3.1
<i>Halichoeres bivittatus</i> (t)	82.5 (16)	2.9
<i>Calamus species</i> (st)	219.3 (164)	2.5
<i>Seriola dumerili</i> (st)	208.8 (83)	2.2
<i>Rhomboplites aurorubens</i> (st)	1931.5 (937)	1.9
<i>Chromis scotti</i> (t)	166.0 (48)	1.8
<i>Balistes caprisus</i> (st)	30.1 (6)	1.6
<i>Decapterus species</i> (st)	2046.9 (899)	1.6
Cumulative contribution (%)		90.9
38–46 m (Sim. = 29.9, T = 20.9 ± 0.01)		
<i>Pterois volitans</i> (t)	176.4 (24)	19.4
<i>Holocentrus adscensionis</i> (st)	210.4 (131)	8.7
<i>Holacanthus bermudensis</i> (st)	49.7 (8)	7.4
<i>Balistes caprisus</i> (st)	52.4 (11)	5.6
<i>Mycteroperca phenax</i> (st)	60.4 (16)	4.3
<i>Chaetodon sedentarius</i> (st)	28.3 (5)	4.2
<i>Lachnolaimus maximus</i> (st)	37.7 (10)	4.1
<i>Calamus species</i> (st)	44.0 (10)	3.9
<i>Haemulon plumieri</i> (st)	220.9 (94)	3.8
<i>Cephalopholis cruentatus</i> (st)	36.1 (8)	3.2
<i>Priacanthus arenatus</i> (st)	72.2 (23)	3.1
<i>Halichoeres garnoti</i> (t)	39.0 (12)	3.1
<i>Bodianus pulchellus</i> (t)	35.5 (10)	2.4
<i>Seriola dumerili</i> (st)	48.3 (17)	2.3
<i>Malacanthus plumieri</i> (st)	15.8 (4)	2.2
<i>Holacanthus tricolor</i> (t)	25.1 (6)	2.2
<i>Acanthurus coeruleus</i> (t)	31.5 (10)	1.7
<i>Acanthurus bahianus</i> (t)	51.3 (26)	1.5
<i>Pagrus pagrus</i> (st)	42.0 (16)	1.3
<i>Epinephelus morio</i> (st)	8.8 (2)	1.2
<i>Pomacanthus paru</i> (st)	11.2 (3)	1.1
<i>Chaetodon ocellatus</i> (t)	16.4 (5)	1.0
<i>Panulirus argus</i> (t)	19.1 (6)	0.9
<i>Stegastes partitus</i> (t)	12.1 (4)	0.9
<i>Seriola rivoliana</i> (st)	26.1 (11)	0.9
Cumulative contribution (%)		90.2

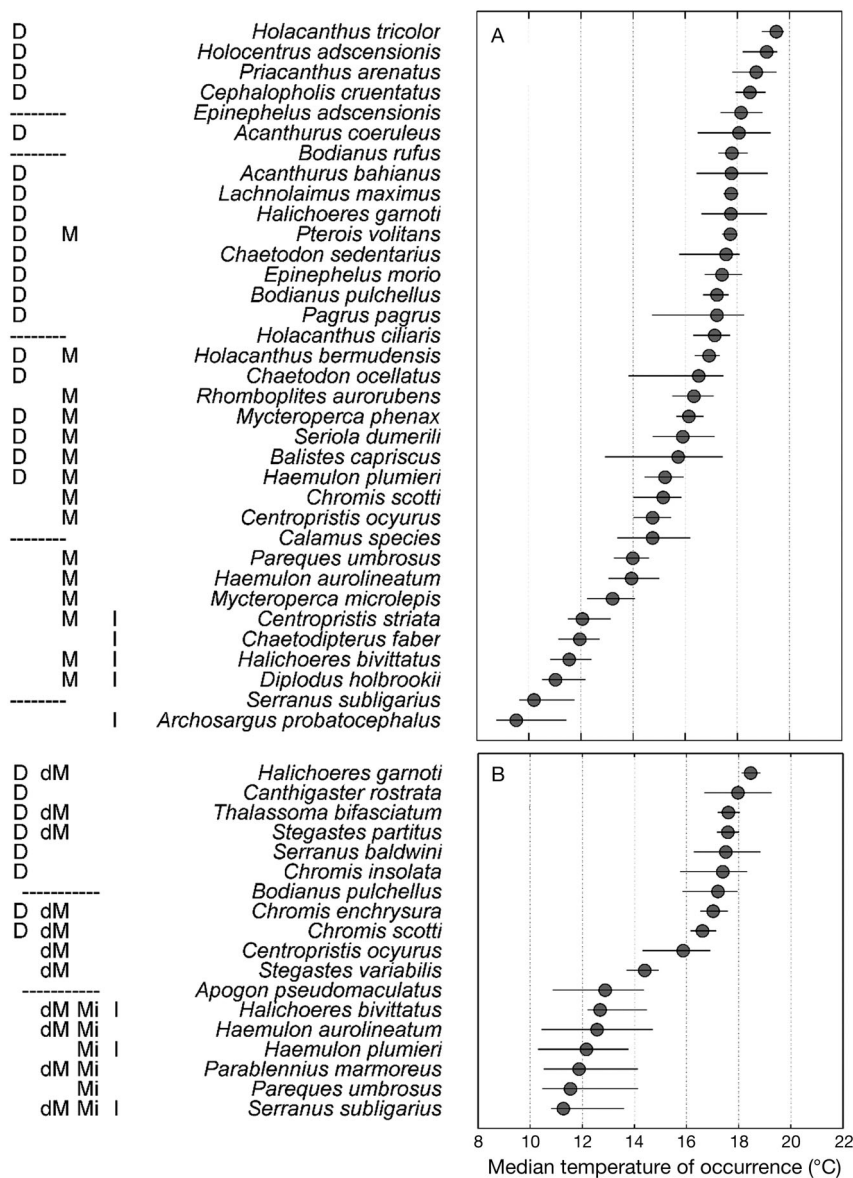


Fig. 4. (A) Median winter temperature preference of conspicuous species. Depth zone designation from the multivariate analyses are provided on the left: I = 5–14 m, M = 15–37 m, D = 38–46 m. Species for which designations were not possible are denoted by -----; these species were not observed frequently enough to use the quotient analysis. (B) Median winter temperature preference of cryptic species. Depth zone designation from the multivariate analyses are provided on the left: I = 5–15 m, Mi = 18–24 m, dM = 27–38.5 m, D = 39.5–46 m. Error bars: 95% confidence intervals

2 main groupings, the cooler water species, occurring in shallower water and with a median temperature preference between 11.2 and 13.0°C, and the warmer-water species, occurring in deeper water with temperatures between 16.0 and 18.3°C. The temperature preference of *Stegastes variabilis* occurs between the 2 groups, at a median temperature of occurrence of 14.2°C.

Univariate analyses

A positive relationship was found between conspicuous fish diversity and depth (linear regression Shannon diversity = $2.025 + [0.0166 \times \text{depth}]$ [$R^2 = 0.25$, $p < 0.001$]), but no relationship was found between cryptic fish diversity and depth ($R^2 = 0.0022$, $p = 0.7$). For both the conspicuous and cryptic fish communities, a positive relationship was found between the Tropicalization Index (TI) and depth ($R^2 = 0.32$, $p < 0.001$, regression: rank (TI) = $4.633 + (1.500 \times \text{depth})$; $R^2 = 0.54$, $p < 0.001$, regression: TI = $7.808 + (1.790 \times \text{depth})$, respectively, Fig. 5). Overall, the cryptic fish community had a higher TI than conspicuous fishes. The TI for cryptic fishes ranged from 12.5 to 100 with an average of 65, and the index for conspicuous fishes ranged from 4.8 to 60 with an average of 26.8.

Lionfish were found within the 15 to 37 and 38 to 46 m depth zones throughout the study, with densities ranging from 0 to 440 ind. ha^{-1} . Overall, lionfish densities increased from 2004 to 2007 then in 2009 decreased back to pre-2006 levels (Fig. 6). This decrease may in part be attributed to colder winter bottom temperatures that occurred during the winter of 2008 to 2009 (Fig. 6). The highest lionfish densities were found in the 38 to 46 m depth zone. However, there was no significant difference in lionfish densities between depth zones (15–37 and 38–46 m, $p = 0.259$) or among years ($p = 0.113$).

The probability density function indicated that lionfish are absent from areas where mean winter temperature falls below 14°C and start to occur at temperatures between 14 and 16°C (Fig. 7); site-specific data show that lionfish were only observed in locations with a winter mean temperature of above 15.3°C and higher. There was no relationship between lionfish density and summer temperature ($F = 0.00204$, $p > 0.964$).

Table 2. Dominant cryptic fish species (top ~90 % based on SIMPER analysis) from 4 depth zones across the North Carolina continental shelf. Species are listed in descending order of contribution to similarity within each depth zone from 2007 to 2010. Density = mean (+SE). 5–15 m, N = 4; 18–24 m, N = 10; 27–38.5 m, N = 41; 39.5–46 m, N = 16. (t) = tropical, (st) = subtropical, (tm) = temperate species according to FishBase published sources (Froese & Pauly 2014). Sim. = average percent similarity, T = average winter temperature (°C)

Species	Density (ind. ha ⁻¹)	Contribution (%)
5–15 m (Sim. = 20.2, T = 13.8 ± 0.04)		
<i>Serranus subligarius</i> (st)	987.5 (649)	25.9
<i>Halichoeres bivittatus</i> (t)	513.4 (209)	25.2
<i>Diplodus holbrookii</i> (st)	17034 (13902)	16.8
<i>Chaetodon ocellatus</i> (t)	145.2 (83)	15.0
<i>Haemulon plumieri</i> (st)	101.5 (45)	11.9
Cumulative contribution (%)		94.9
18–24 m (Sim. = 42.1, T = 15.6 ± 0.01)		
<i>Halichoeres bivittatus</i> (t)	2786.2 (324)	31.9
<i>Serranus subligarius</i> (st)	1227.5 (134)	22.2
<i>Haemulon</i>		
<i>aurolineatum</i> (st)	7073.8 (2873)	10.7
<i>Parablennius marmoreus</i> (st)	492.5 (161)	8.1
<i>Pareques umbrosus</i> (st)	721.2 (310)	8.1
<i>Haemulon plumieri</i> (st)	1825.0 (707)	5.2
<i>Centropristis striata</i> (st)	245.0 (92)	4.1
Cumulative contribution (%)		90.2
27–38.5 m (Sim. = 34.4, T = 18.7 ± 0.02)		
<i>Chromis scotti</i> (t)	4863.8 (726)	32.5
<i>Halichoeres bivittatus</i> (t)	964.0 (164)	12.0
<i>Chromis enchrysurus</i> (t)	1216.0 (206)	11.8
<i>Haemulon aurolineatum</i> (t)	18285.8(6272)	10.5
<i>Thalassoma bifasciatum</i> (t)	1021.8 (208)	8.2
<i>Stegastes partitus</i> (t)	391.6 (102)	5.4
<i>Halichoeres garnoti</i> (t)	285.6 (84)	3.2
<i>Serranus subligarius</i> (st)	288.3 (87)	2.4
<i>Stegastes variabilis</i> (t)	229.1 (65)	2.2
<i>Parablennius marmoreus</i> (st)	341.6 (179)	1.6
<i>Centropristis ocyurus</i> (st)	208.1 (111)	1.5
Cumulative contribution (%)		91.4
39.5–46 m (Sim. = 32.1, T = 20.9 ± 0.02)		
<i>Halichoeres garnoti</i> (t)	880.7 (227)	27.0
<i>Chromis enchrysurus</i> (t)	1961.8 (796)	22.5
<i>Stegastes partitus</i> (t)	305.1 (64)	11.7
<i>Thalassoma bifasciatum</i> (t)	350.6 (152)	7.9
<i>Chromis scotti</i> (t)	2263.8 (1590)	6.7
<i>Serranus baldwini</i> (t)	153.0 (44)	5.0
<i>Canthigaster rostrata</i> (t)	130.3 (64)	3.8
<i>Serranus phoebe</i> (st)	125.4 (44)	3.5
<i>Chromis insulatus</i> (t)	221.4 (120)	2.6
Cumulative contribution (%)		90.6

DISCUSSION

The North Carolina shelf is characterized by a winter temperature gradient of increasing bottom water temperatures that coincides with increasing depth, where the offshore waters are moderated year-round by the presence of the warm Gulf Stream current (Atkinson et al. 1983). This temperature gradient is strongest during the coldest months of the year: Jan-

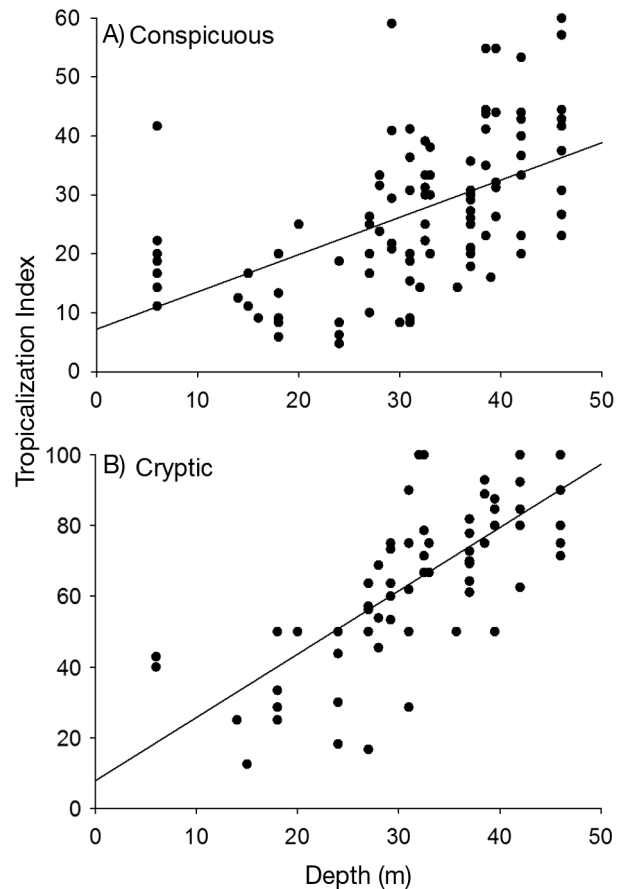


Fig. 5. Tropicalization Index (TI) by depth (m) with resulting linear regression line (see 'Results: Univariate analyses'). (A) Conspicuous species, (B) cryptic species. Note change in y-axis scale

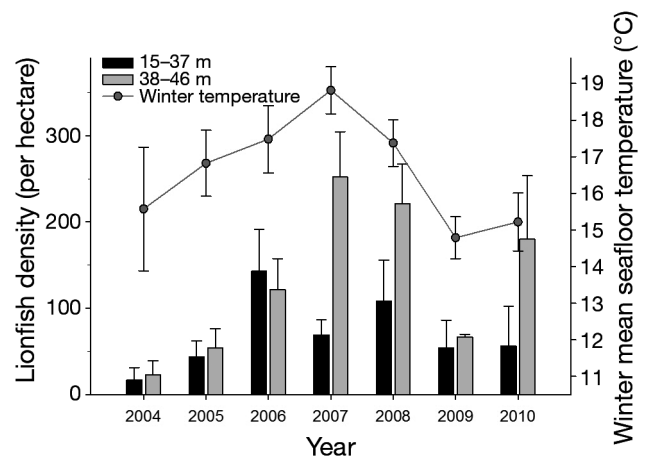


Fig. 6. Lionfish densities in Onslow Bay by year and depth zone with winter mean bottom water temperature overlaid. This mean temperature is an average of the 15–37 and 38–46 m depth zones; lionfish were never observed within the 5–14 m depth zone during the study. Error bars: SE

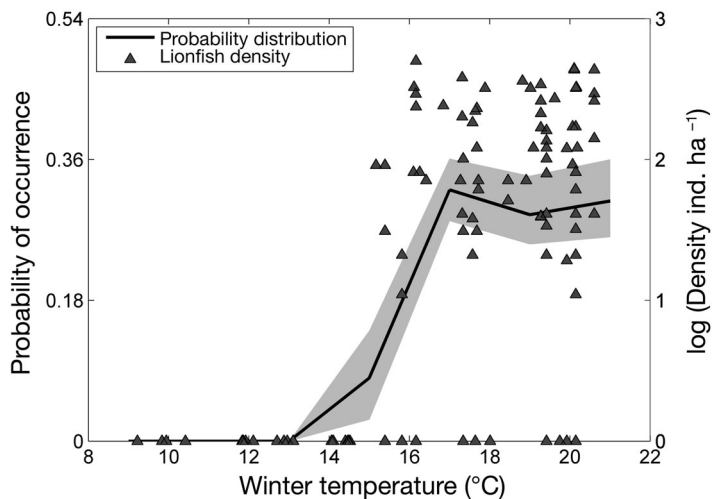


Fig. 7. Probability density of lionfish occurrence as a function of mean winter temperature. The probability density was calculated as a single parameter quotient (see 'Materials and methods: Univariate analyses'). Also shown are lionfish densities as a function of mean winter temperature estimated during the conspicuous fish surveys.

Gray area indicates 95% confidence intervals

uary, February and March. In contrast, during the summer months, the temperature across the shelf is homogeneous. The correlation of winter temperature with depth makes it difficult to distinguish the role of either in structuring fish communities in Onslow Bay. However, evidence of winter temperature as an important factor in structuring these fish communities exists. First, many of the warm-water species observed only in the deepest depth zone are found in shallow waters in more tropical areas (Froese & Pauly 2014). Second, an increasingly tropical fish community composition with depth and increasing bottom temperatures was found for both the conspicuous and cryptic fish communities. The shift to a more tropical composition with increasing depth has been observed and attributed to warmer winter bottom temperatures in previous studies within the Southeast US Shelf (Miller & Richards 1980, Grimes et al. 1982, Chester et al. 1984, Sedberry & Van Dolah 1984). Third, lionfish are found in shallow waters throughout much of the western Atlantic, but off North Carolina, they are restricted to deeper and warmer waters. Since there was no bias toward greater habitat structure (presumably preferred habitat) in the deeper waters (Table S1 in the Supplement), these data suggest that temperature is responsible for the cross-shelf pattern in fish community off North Carolina. However, other biotic and abiotic factors cannot be ruled out. Some of these factors include pH, dissolved oxygen, habitat complexity, predator and prey distributions, and differential

recruitment. These factors were not measured in the present study, but our work provides a baseline pattern of community structure that is at least partially explained by winter bottom temperature and depth. These baseline data can now be used to detect future changes to the fish communities such as continued tropicalization (Parker & Dixon 1998) and species range shifts (Figueira & Booth 2010), as suggested by Booth et al. (2011).

One of the objectives of this work was to evaluate the laboratory-derived thermal minimum for lionfish in the field. Lionfish perished in the laboratory at 10°C (the chronic lethal minimum), regardless of the rate of temperature decline or the acclimation temperature of lionfish (Kimball et al. 2004). This differs from the field-derived minimum thermal threshold of 15.3°C (mean winter temperature) found in this study. However, 15.3°C is a mean value that represents a threshold for detecting lionfish presence/absence in the field, while 10°C

is the temperature where lionfish death occurred in the laboratory. Thus, perfect correspondence between the laboratory-derived chronic lethal minimum and the field-derived presence/absence minimum threshold is not expected, and differences between laboratory-derived and observed minimum thresholds have been found in previous studies (Figueira et al. 2009, Figueira & Booth 2010). Further, Kimball et al. (2004) found that lionfish ceased feeding at 15.3°C and became 'stationary and lethargic' at 13°C, which may increase their susceptibility to predation (Maljkovic et al. 2008). These physiological and behavioral limits appear to have an effect on lionfish distribution within the bounds determined by direct lethal effects of temperature. It is not known whether lionfish move in response to cold winter temperatures or stay and perish (McBride & Able 1998); juveniles and young adults in an estuary displayed high site fidelity (Jud & Layman 2012), but Green et al. (2011) examined adult lionfish on patch reefs and showed that movements of at least 130 m were possible. Whether lionfish move or not, their distribution continues to be limited to the deeper, warmer waters offshore of North Carolina, suggesting that winter bottom temperature is an important mechanism controlling their distribution in the field (Kimball et al. 2004).

The issue of fish movement is relevant to the community analyses conducted here. Depth and winter temperature are important environmental variables. Depth is fixed over the annual cycle, whereas tem-

perature varies (warm in the summer, cold in the winter). We found a strong relationship between depth, winter temperature and community structure, which was measured during the spring and summer. Either depth is a dominant factor shaping distributions, or winter temperature is dominant, and movement between winter and spring/summer is minimal. Under this latter hypothesis, the distributions observed in the spring/summer reflect the pattern of bottom temperature experienced the winter before. The question of depth or bottom temperature regulation of fish distribution is important (Hare et al. 2012a), and continued research in Onslow Bay could evaluate which factor is most important. As Onslow Bay continues to warm, if temperature is more important, warmer-water species should move into shallower water. If depth is more important, warmer-water species should remain within preferred depth ranges. In addition to these longer-term studies, shorter-term studies could be conducted to examine the scale of annual and seasonal movements of lionfish and other abundant fishes using acoustic telemetry or traditional tagging.

In the future, the greatest rate of community change in the Southeast US Shelf is likely to be in the nearshore waters (Simpson et al. 2011). Range expansions of tropical and subtropical species north of Cape Hatteras are also expected (Hare et al. 2012b), similar to poleward expansions predicted off the eastern coast of Australia (Figueira et al. 2009, Figueira & Booth 2010). However, it is difficult to predict specific winners and losers with continued warming, but given the high abundance of lionfish and their invasion success within the Atlantic, lionfish are likely to be one of the species to expand their range if winter temperatures become more physiologically hospitable (Sorte et al. 2010a,b). Lionfish have additional value as a potential indicator species for detecting community change in this region for 3 main reasons: (1) they have an established *in situ* thermal minimum threshold based on mean winter bottom temperature (they are present in temperatures of 15.3°C and higher), (2) there are few factors known to limit their distribution on a large scale other than temperature and (3) they are easily recognized. If lionfish become established year-round in areas previously known to be uninhabitable (e.g. habitats <27 m depth off North Carolina), then this could indicate that the thermal regime is shifting to favor more tropical species in general. Predicting future range

expansions or contractions of other species is more problematic, since thermal tolerance data are not available for most species (but see Figueira & Booth 2010, Hare et al. 2012b). However, our analyses revealed several tropical species (in addition to lionfish) that are abundant yet restricted to warmer offshore depths in Onslow Bay but have wide depth distributions within the tropics (Tables 1, 2 & 3). We propose that these fishes (*Halichoeres garnoti*, *Thalassoma bifasciatum*, *Holacanthus tricolor*, *Chromis enchrysurus*, *C. scotti* and *C. insolatus*) (Tables 1 & 2) may be good candidates as species most likely to expand their distributions shoreward and/or northward (Hare et al. 2012b) under current global warming scenarios (IPCC 2007). Collectively, this group of species could be considered an ecological indicator if (like lionfish) they become established year-round in areas previously uninhabitable (Table 3). In addition, the temperature thresholds calculated in this study can now be used to project future fish community distributions based on various carbon emissions projections (Figs. 6 & 7) (Cheung et al. 2012, 2013, Hare et al. 2012b, Wuenschel et al. 2012).

There is limited evidence that tropicalization of the fish community is already occurring within Onslow Bay, North Carolina (Parker & Dixon 1998), as it is in the northern Gulf of Mexico (Fodrie et al. 2010), Mediterranean Sea (Ben Rais Lasram & Mouillot 2009) and western Australian coast (Wernberg et al. 2013). At one location in Onslow Bay (~29 m depth), Parker & Dixon (1998) documented 29 new tropical species and increased abundance in 28 other species between the 1970s and early 1990s. In addition, 3

Table 3. List of common tropical fish species, with reportedly wide depth distributions (FishBase, Froese & Pauly 2014) compared to the truncated depth distributions found in this study off North Carolina (NC). Mean winter temperature ranges are from this study. All species were ranked within the top ~90% within their respective depth zones based on similarity analyses (Tables 1 & 2)

Species	— Depth range (m) —		Mean winter temperature range (°C)
	FishBase	NC, this study	
<i>Halichoeres garnoti</i>	2–80	29.2–46	14.1–20.6
<i>Thalassoma bifasciatum</i>	0–40	28–46	16.8–20.6
<i>Stegastes partitus</i>	0–100	28–46	15.3–20.6
<i>Chromis enchrysurus</i>	5–146	27–46	14.1–20.6
<i>Chromis insolatus</i>	20–100	29.2–42	17.6–19.6
<i>Holacanthus tricolor</i>	3–92	29.2–42	17.2–20.6
<i>Chromis scotti</i>	15–116	27–42	12.9–20.2
<i>Pterois volitans</i>	2–55 ^a	27–46	15.3–20.6

^a Lionfish in its native range; lionfish occur up to 304.8 m in invaded range (R. Gilmore unpubl. data)

species (1 subtropical, 2 tropical) observed in this study (cherub fish *Centropyge argi*, orange back bass *Serranus anularis* and the greater soapfish *Ryp-ticus saponaceous*) (see Table S3 in the Supplement) were recently documented as new species to North Carolina by Quattrini et al. (2004). Although it is unclear whether these reports are because of more effective sampling of the cryptic fish communities (i.e. UVC, video) or a northern range expansion, the overall trend toward more tropical composition is expected to continue based on current global carbon emissions projections (IPCC 2007, Cheung et al. 2012). In fact, in our study we found the cryptic fish community to be dominated by tropical species, consistent with the idea that smaller-bodied fishes with short generation times have a demonstrated sensitivity to changing climate conditions (Perry et al. 2005, Bellwood et al. 2006). However, we found that detecting community change using comparisons with previous studies of conspicuous and cryptic fishes within the depths that we examined is problematic because of either the biases associated with the various methods themselves (Connell et al. 1998, Bennett et al. 2009, Burge et al. 2012) or, in the case of cryptic species (Table 2), the lack of previous data. Investigations examining fish community structure in response to changing climatic conditions that do not consider cryptic fishes may fail to detect community shifts if they occur (Bellwood et al. 2006).

Most previous studies in the region used extractive sampling techniques such as angling, which targets larger, economically valuable species (Grimes et al. 1982, Chester et al. 1984), or trawling, which can underestimate larger mobile species and is restricted to low-relief habitat (Sedberry & Van Dolah 1984). Others used direct observation methods such as stationary point counts using video and divers (Parker & Dixon 1998, Burge et al. 2012). Fish community differences between extractive sampling and direct observation methods are common (Connell et al. 1998) and have been most recently noted in the North Carolina region by Burge et al. (2012). Burge et al. (2012) used video and diver stationary point counts to survey fishes and summarized differences between the 18 most frequently encountered species in their study and 7 previous studies (Appendix 3, Burge et al. 2012). Because of the variety of sampling methods and the location and scale of the studies, robust conclusions regarding community change are difficult. However, the taxa and general order of importance of species within our study (Table 1) were in broad agreement with the species most important in Burge et al. (2012), and the top-ranking species identified in several previous

studies (Grimes et al. 1982, Chester et al. 1984, Sedberry & Van Dolah 1984) were also represented within the top 90% of identified fish taxa here (Table 1).

CONCLUSIONS

Temperate-tropical marine transition zones such as the coastal waters along the North Carolina coast may be areas that will undergo the most ecosystem change as a result of warming ocean temperatures, and previous studies highlighted the importance of these regions as climate change hotspots (Booth et al. 2011). The baseline data collected in this study will assist in detecting climate change impacts, such as the expansion of tropical fish communities into areas previously uninhabited, and will allow the projection of species distribution shifts based on future carbon emissions (IPCC 2007) and the temperature thresholds we report. A diverse assemblage of ecologically and economically valuable fishes can be found on North Carolina temperate reefs, many of which are considered overfished and have suffered population declines in recent years (Rudershausen et al. 2008). If winter temperatures are indeed the overriding factor in structuring these hard bottom reef communities, the continued warming of global temperatures may cause further changes to fish community structure. Increasing temperatures also favor a potential expansion of the invasive lionfish population across the shelf (and northward). These 3 factors combined could further stress native fish communities, potentially leading to unforeseen fish community structure and trophic disruptions as the marine community responds to warmer temperatures (Sorte et al. 2010a), complicating recovery efforts for some species (Nye et al. 2009).

Disclaimer. The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the authors and do not necessarily reflect the views of NOAA or the Department of Commerce.

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