

Temporal and Spatial Variability in Juvenile Red Snapper Otolith Elemental Signatures in the Northern Gulf of Mexico

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Abstract.—We examined otolith chemistry of age-0 red snapper *Lutjanus campechanus* in U.S. waters of the northern Gulf of Mexico (GOM) to determine if otolith elemental signatures could be employed as natural tags to estimate postsettlement population connectivity. Fish ($n = 755$) belonging to five successive year-classes (1996–2000) were sampled from three GOM regions. Solution-based analysis of otolith chemistry was accomplished with sector field-inductively coupled plasma-mass spectrometry (Ba, Mg, Mn, and Sr) and inductively coupled plasma-optical emissions spectrometry (Ca). Several regional trends observed for individual elements were consistent among year-classes, yet elemental signatures were significantly different among years as well as among regions (multivariate analysis of variance [MANOVA]; $p < 0.001$). Jackknifed classification accuracies from linear discriminant function analysis approached 80% (mean = 78.4%) in all years except 1998 (62.4%). Overall, these results indicate otolith elemental signatures may serve as effective region-specific natural tags of GOM red snapper. Significant differences in otolith chemistry among year-classes indicates year-class-specific analysis is required to derive natural tags. Furthermore, regional differences in elemental signatures may be insufficient in some years to be employed as accurate natural tags.

Red snapper *Lutjanus campechanus* is among the most economically and ecologically important reef fishes in the U.S. Gulf of Mexico (GOM). Significant bycatch mortality caused by shrimp trawling in juvenile snapper habitats on the continental shelf, as well as high exploitation rates by directed recreational and commercial fisheries, have resulted in an estimated 90% reduction in red snapper biomass since the 1970s (Goodyear and Phares 1990). Despite increasingly restrictive fishing regulations since the early 1990s, GOM red snapper have been estimated to be significantly overfished for well over a decade (SEDAR7 2004; Porch 2007). Significant research has been directed in recent years at examining red snapper population ecology to enhance fishery conservation efforts. In particular, studies examining popula-

tion structure and population dynamics have greatly increased knowledge of red snapper ecology.

Red snapper have been managed historically as a single unit stock in the GOM. That approach was supported by results of early genetics studies that employed a variety of markers to examine population structure. Several authors reported that differences in mitochondrial (mt)DNA allele distributions among GOM regions were insufficient to reject the null hypothesis of panmixia (Camper et al. 1993; Gold et al. 1994; Garber et al. 2004). Gold et al. (2001) reported similar findings based on nuclear DNA microsatellite distributions. Saillant and Gold (2006) examined spatial and temporal variability in microsatellites among three GOM regions and two red snapper cohorts and found little evidence of significant spatial heterogeneity among regions. However, they also reported that significant differences in genetic effective population size existed among regions, which they inferred to indicate the existence of different “demographic stocks” in the northern GOM. Pruett et al. (2005) stated that the current spatial distribution of mtDNA alleles in the northern GOM indicated a complex history of isolation and dispersal. They

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suggested results of nested clade analysis indicated GOM red snapper constituted a metapopulation, the sub-units of which may exist for long periods as somewhat isolated assemblages but are tied together by periodic dispersal instigated by environmental factors (e.g., glacial advance or retreat, habitat changes, and hydrologic variability).

Recent studies of GOM red snapper population dynamics are consistent with genetic studies that indicate regional differences in population demographics. Patterson et al. (2001a) reported no significant difference existed in growth rates between red snapper sampled off Alabama and fish sampled off Louisiana west of the Mississippi River terminus. Fischer et al. (2004) also reported that growth was not significantly different between Alabama and Louisiana samples, but fish sampled off Texas were significantly smaller at age than fish from the other two regions. Further evidence of significant regional differences in population demographics was reported in Woods et al. (2003). They reported fish off Alabama reached sexual maturity at smaller sizes and younger ages than in the western GOM, where size-specific fecundity was greater. Collectively, results reported by Fischer et al. (2004) and Woods et al. (2003) indicate significant variability in GOM red snapper population dynamics and demographics exists among regions, despite lack of genetic divergence in selectively neutral markers (Gold et al. 2001; Pruett et al. 2005; Saillant and Gold 2006).

Pruett et al. (2005) indicated that precise estimates of rates of exchange among GOM regions would permit greater examination of red snapper population structure. Goodyear (1995) hypothesized that the lack of genetic divergence among regions may result from hydrographic transport of eggs and larvae or diffusion of juveniles and adults away from centers of abundance. To our knowledge, no data exist with which to estimate larval dispersal or quantify presettlement connectivity among GOM regions, but postsettlement movement of juveniles and adults has been estimated in myriad conventional and ultrasonic tagging studies. Direct estimates of red snapper site fidelity to individual reefs or reef patches range from 25% to 50% per year (Patterson and Cowan 2003; Schroepfer and Szedlmayer 2006; Strelcheck et al. 2007). Movement estimated from tag returns in conventional tagging studies generally followed a negative binomial distribution in which a large percentage (e.g., 50%) of recoveries were made less than 1 km from their release sites and distance moved of the remaining recoveries followed a lognormal distribution (reviewed in Patterson et al. 2001b). While most recoveries have been reported near their site of release, several tagged fish

have moved over 100 km. Despite the obvious value of tagging data in examining red snapper postsettlement movement, the utility of conventional and ultrasonic approaches is compromised by tag loss or short battery life, respectively, relative to red snapper life history (Szedlmayer 1997; Schroepfer and Szedlmayer 2006; Westmeyer et al. 2007).

Recent advances in applying otolith elemental signatures as natural tags to estimate nursery source region and population connectivity in marine fishes suggest otolith chemistry may be useful to estimate population connectivity in GOM red snapper. Key to that approach is the fact that otoliths are metabolically inert once formed; thus, area-specific chemical signatures incorporated in their structure function as permanent natural tags (Campana 1999). Otolith chemical signatures have been applied successfully to examine population connectivity in several marine fishes, including weakfish *Cynoscion regalis* (Thorrold et al. 2001), pink snapper *Pagrus auratus* (Hamer et al. 2005), and Atlantic bluefin tuna *Thunnus thynnus* (Rooker et al. 2003).

The current study was part of a larger multidisciplinary effort to examine population structure in red snapper among GOM regions with population genetics (Pruett et al. 2005; Saillant and Gold 2006), population dynamics (Fischer et al. 2004; Jackson et al. 2007), and otolith chemistry approaches. Our first objective was to examine temporal and spatial variability in red snapper otolith elemental signatures to determine if otolith chemistry could be utilized as a natural tag to examine population connectivity in the northern GOM. We report region-specific otolith elemental signatures for five successive year-classes of age-0 red snapper. Univariate and multivariate statistical techniques were employed to test if regions could be distinguished accurately based on otolith chemistry. Temporal variability in region-specific signatures also was tested among the five year classes examined.

Methods

Age-0 red snapper were sampled from three regions in the northern GOM during October and November in 1996 through 2000 (Figure 1). The boundary between our northwest GOM (NWG) and north-central GOM (NCG) region was latitude 89.0°W, and the boundary between the NWG region and the southwest GOM (SWG) region was latitude 94.5°W. These regions were established a priori for several reasons. First, genetic and population dynamics components of the larger study were aimed at detecting differences in red snapper populations at this regional scale (Fischer et al. 2004; Pruett et al. 2005; Saillant and Gold 2006; Jackson et al. 2007). With respect to otolith chemistry,

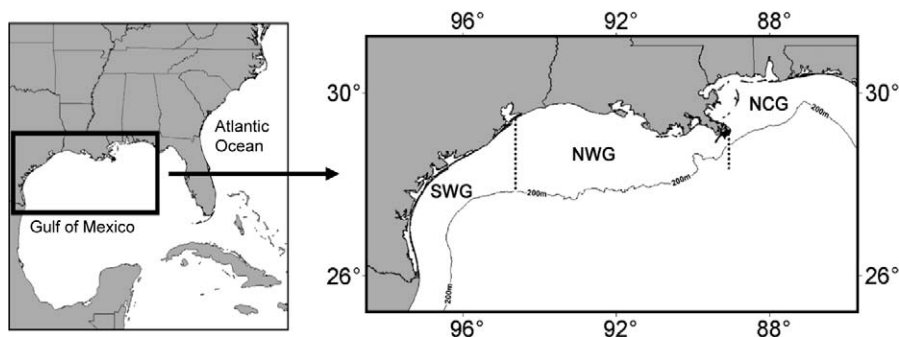


FIGURE 1.—Map of northern Gulf of Mexico regions from which age-0 red snapper were sampled in fall 1996–2000. The 200 m isobath indicates the edge of the continental shelf. Dotted lines indicate divisions between regions. SWG = southwest Gulf; NWG = northwest Gulf; and NCG = north-central Gulf.

predominant oceanographic features among regions suggested differences in hydrographic parameters and freshwater inputs that affect water chemistry would be persistent on this spatial scale (Cochrane and Kelly 1986; Justić et al. 2002; Rabalais et al. 2002; Dagg and Breed 2003). Patterson et al. (1998) reported juvenile red snapper otolith elemental signatures distinguished these northern GOM nursery regions with a mean jackknifed classification accuracy of 92% from linear discriminant function analysis (L DFA), although that study relied on small sample sizes ($n = 20$ per region) and some elements used may not be suitable for use as natural tags (e.g., SE, As, and Al).

Samples were collected in each region using otter trawls aboard the United States' National Oceanographic and Atmospheric Administration's (NOAA) RV *Oregon II* and the Dauphin Island Sea Laboratory's RV *A.E. Verrill* during the National Marine Fisheries Service's (NMFS) Fall Groundfish Survey in each year. Trawl stations were selected by NMFS biologists with stratified random sampling among depth strata and our sample sites were selected randomly from those stations. Fish were subsampled from a given station's trawl catch with systematic random sampling after first ordering individuals according to length. Immediately following selection, fish were placed in plastic bags and frozen.

In the laboratory, fish were thawed, weighed to the nearest milligram, and measured to standard length (SL). Sagittae were extracted using glass probes and polyethylene tweezers; all materials that came in contact with extracted otoliths were acid-washed and triple-rinsed with 18 M Ω double-deionized water (DDIH₂O). Extracted otoliths were scrubbed with a synthetic bristle brush, rinsed with DDIH₂O, and placed in acid-leached polyethylene vials to air-dry. Further otolith cleaning and sample preparation took place in a class-100 clean room in the Department of

Geology at Louisiana State University (LSU). Otoliths were cleaned with 2% ultrapure nitric acid for 10 s, flooded repeatedly with DDIH₂O, and allowed to air-dry in acid-leached cell wells placed under a class-10 laminar flow cabinet. Dry otoliths were weighed to the nearest 0.01 mg and placed in acid-leached polyethylene vials for dissolution. Otoliths were dissolved in 10% ultrapure nitric acid at 1 mL acid per 0.2 mg otolith; volumes of added acid and transferred solution aliquots (see below) were confirmed by mass with a precision balance (0.01 mg). Following dissolution, otolith solutions were diluted with 1% ultrapure nitric acid until final dilution factors were 750 \times . Analytical blanks were created by adding 1% ultrapure acid to empty acid-leached polyethylene vials. Otolith solutions and blanks were spiked with Indium (2.5 parts per billion) as an internal standard and their elemental composition (Ba, Mg, Mn, and Sr) was analyzed with a Finnigan MAT Element II magnetic sector field inductively coupled plasma-mass spectrometer (SF-ICP-MS) at the Department of Marine Science, University of Southern Mississippi. Otolith solutions were further diluted (dilution factor = 5×10^5) and analyzed for Ca on a Perkin-Elmer 3300 DV inductively coupled plasma-optical emissions spectrometer (ICP-OES) at the Department of Geology, LSU. Percent recovery for each element (except Ca) was estimated with the method of standard addition ($n = 3$), and the limit of detection (LOD) for each element was estimated as 3σ of blank concentrations.

Univariate and multivariate statistical techniques were employed to determine otolith elemental signatures unique to each nursery region; all statistical tests were performed in Statistical Analysis System (SAS; SAS Institute, Inc., 1996). First, we tested for potential ontogenetic effects on elemental concentrations. Analyses of covariance tested for differences among areas in the relationship between otolith mass and fish SL in

TABLE 1.—Number of trawl stations and sample sizes of age-0 red snapper sampled in three regions of the northern Gulf of Mexico from 1996–2000. SWG = southwest Gulf; NWG = northwest Gulf; and NCG = north-central Gulf.

Year	Region	Trawl stations	Sample size
1996	SWG	2	28
	NWG	2	24
	NCG	4	30
1997	SWG	4	50
	NWG	5	57
	NCG	4	57
1998	SWG	10	63
	NWG	8	62
	NCG	5	37
1999	SWG	10	64
	NWG	10	67
	NCG	7	38
2000	SWG	12	65
	NWG	12	64
	NCG	6	44

each year. Correlation analysis was performed to test if significant relationships existed between otolith mass and element concentrations within and among nursery regions and years.

Differences in otolith elemental signatures (Ba, Ca, Mg, Mn, and Sr) among nursery regions and sampling years were tested with multivariate analysis of variance (MANOVA) and analysis of variance (ANOVA). First, we tested normality with the Shapiro-Wilk test and the assumption of homogeneity of covariance matrices was tested with Barlett's test. The ability of elemental signatures (Ba, Mg, Mn, and Sr) to distinguish nurseries was evaluated by computing cohort-specific linear discriminant function (LDF) models. Classification accuracy of individual LDF models was estimated with the jackknife crossvalidation procedure in SAS's PROC DISCRIM.

Results

In all, 755 age-0 red snapper were sampled for analysis of otolith elemental signatures (Table 1). Sample sizes were lowest in 1996, but were consistently higher thereafter. The spatial distribution of trawl stations within each region also was broader after 1996 (Figure 2). Analyses of covariance revealed significant differences existed in the relationship between otolith mass and fish mass among regions for the 1996 and 1997 cohorts ($p < 0.05$ for tests of equal intercepts and equal slopes in both years). However, the relationships were similar among regions in the other years and differences in 1996 and 1997 were driven by a few outliers (Figure 3).

Concentrations of all elements were all at least three orders of magnitude higher in otolith solutions than LODs computed from analysis of analytical blanks

(LOD = 0.002, 8.30, 0.018, 0.003, and 1.00 ng/g¹ for Ba, Ca, Mg, Mn, and Sr, respectively). Mean percent recovery estimated by standard addition was 102.1% for Ba, 91.4% for Mg, 98.7% for Mn, and 105.1% for Sr. Otolith elemental concentrations were significantly correlated with otolith mass for Mn and Mg (Figure 4). We removed the effect of otolith mass from Mn and Mg concentration by subtracting the common slope of the least squares linear relationship between the two variables.

No difference in within-group covariance matrices was detected and the assumption of normality was met for most treatment levels of individual elements. Elemental signatures (Ba, Ca, Mg, Mn, and Sr) were significantly different among nursery regions (MANOVA, Pillai's Trace $F_{10;1,472} = 31.95$; $p < 0.001$) and years (MANOVA, Pillai's Trace $F_{20;2,956} = 85.92$; $p < 0.001$), and the interaction of region and year also was significant (MANOVA, Pillai's Trace $F_{40;3,700} = 11.85$; $p < 0.001$). Region and year effects and their interaction were highly significant (ANOVA, $p < 0.001$) for each element individually except Ca (ANOVA, $p = 0.664$ for region effect, $p = 0.580$ for year effect, and $p = 0.658$ for region \times year interaction; Figure 5). Cohort-specific LDF models (dependent variables = Ba, Mn, Mg, and Sr) yielded overall classification accuracies near 80% for all years except 1998 (Figure 6). Low mean classification success for the 1998 cohort resulted from poor jackknifed classification of samples from the NCG (60%) and SWG (45%) regions.

Discussion

Results from this study clearly demonstrate the potential for employing otolith elemental signatures as natural tags to estimate postsettlement movement and population connectivity in GOM red snapper. High classification accuracies for most year-classes examined are consistent with results reported by Patterson et al. (1998). However, some elements (e.g., Se, As, and Al) analyzed in that study may be less suitable for the purpose of deriving natural tags of nursery regions than the suite of elements analyzed in the current study. Campana (1999, 2005) and Campana and Thorrold (2001) suggested that the most appropriate elements to use for otolith elemental signatures are divalent cations that substitute directly for Ca in the otolith matrix, are incorporated into otoliths relative to their concentration in seawater, and are not significantly affected by various physiological processes. Incorporation of Ba and Sr in otoliths has been shown to be proportional to ambient elemental concentrations in water, with salinity and temperature interacting with ambient water concentration to affect otolith concentration (Bath et al.

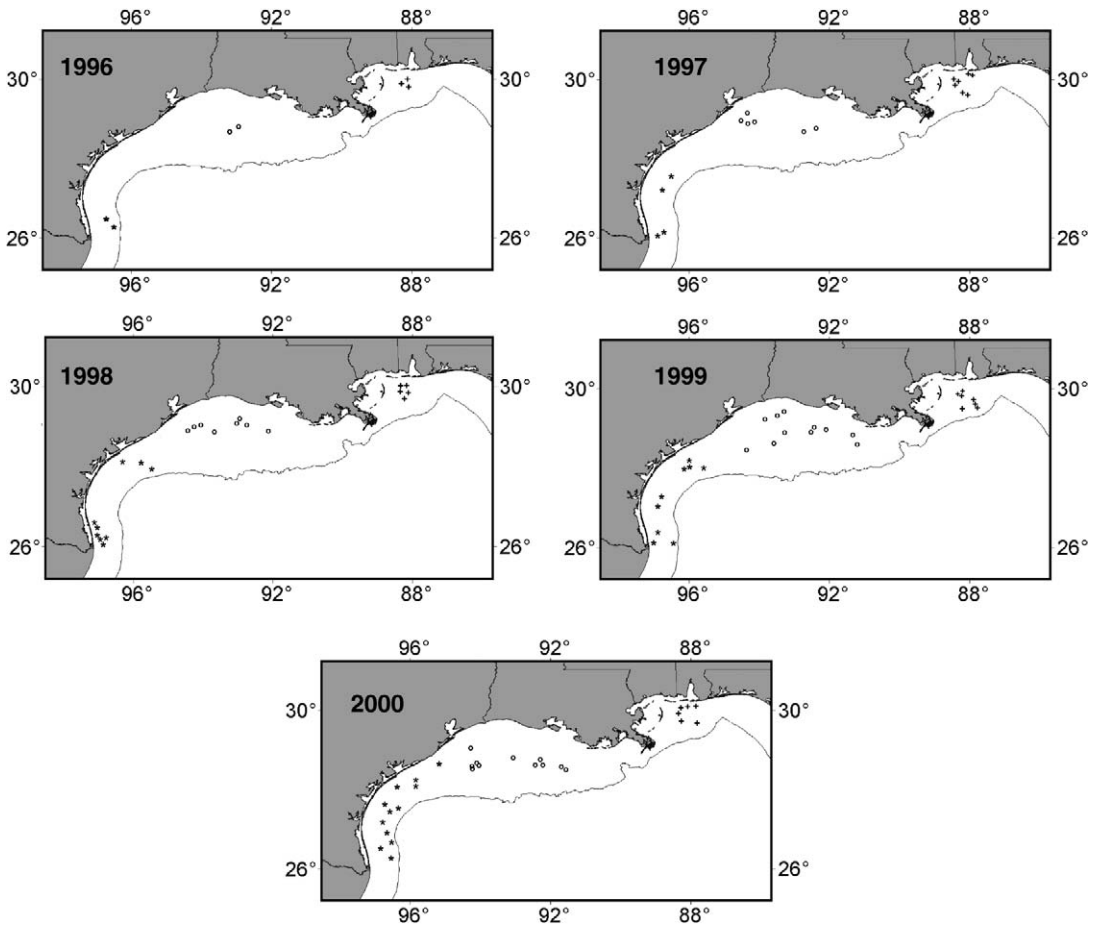


FIGURE 2.—Locations of trawling stations where age-0 red snapper were sampled in fall 1996–2000. Asterisks indicate stations within the southwest Gulf of Mexico (GOM) region. Circles indicate stations within the northwest GOM region. Crosses indicate stations within the north-central GOM region.

2000; Kraus and Secor 2004; Elsdon and Gillanders 2005; Martin and Wuenschel 2006). Martin and Thorrold (2005) reported temperature and salinity affected Mn incorporation in juvenile spot *Leiostomus xanthurus* otoliths. They also reported otolith Mg concentration was not affected by temperature or salinity, but was correlated with somatic growth. Similar results for Mg were reported by Elsdon and Gillanders (2002) in juvenile black bream *Acanthopagrus butcheri* thus highlighting the complex nature of elemental incorporation into otoliths and the potential for physiological effects to influence elemental deposition, particularly in the case of Mg.

The significant difference we report among year-classes in age-0 red snapper otolith elemental signatures is similar to interannual differences in otolith chemistry reported for other marine fishes (reviewed in

Campana 1999 and Gillanders 2005). Despite interannual differences, there were distinct trends in otolith elemental concentration among nursery regions that were similar for most elements among the cohorts. For example, Ba and Mg typically were lowest in the NCG and highest in the SWG. Strontium typically was lowest in the NCG, with the SWG and NWG having similar concentrations. Manganese typically was lowest in the NWG, with the NCG and SWG having similar concentrations. Therefore, it is evident that trends in environmental signals were somewhat consistent among years even if absolute otolith concentrations, and presumably ambient elemental concentrations, varied. No data exist, however, to correlate elemental concentration in seawater with red snapper otolith concentrations.

Hanson et al. (2004) suggested that latitudinal trends

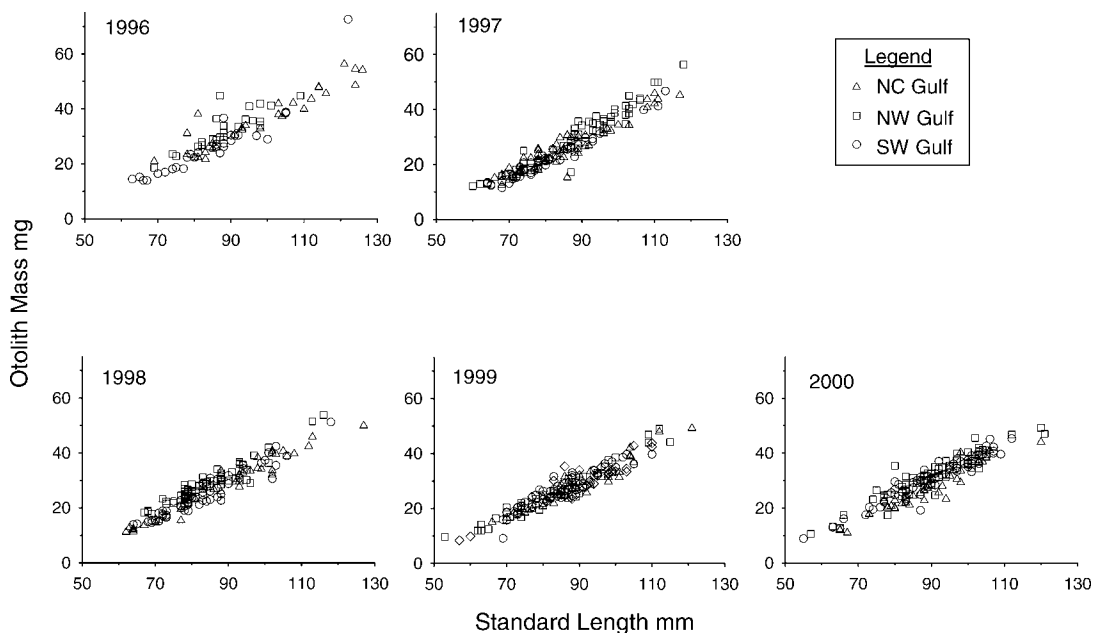


FIGURE 3.—Scatterplots of otolith mass versus standard length for age-0 red snapper sampled in fall 1996–2000 from the northern Gulf of Mexico.

along the west coast of Florida in gag *Mycteroperca microlepis* Sr and Mn otolith concentrations were generated by differential groundwater Sr and sediment Mn (mediated by redox chemistry) that showed similar latitudinal trends as otolith concentrations. Wells et al. (2003) reported significant regressions between Sr : Ca and Ba : Ca ratios in freshwater streams and the same ratios in otoliths of one-year-old westslope cutthroat trout *Oncorhynchus clarki lewisi*. Results of those studies, coupled with results of laboratory studies cited above, provide evidence that otolith chemistry reflects ambient water concentrations for Sr, Ba, and Mn, with the case of Mg incorporation still unresolved. Therefore, we infer ambient elemental concentrations in seawater likely displayed similar consistent differences among GOM red snapper nursery regions in the current study.

Persistent regional differences in hydrographic conditions (e.g., freshwater input, salinity, temperature, dissolved oxygen) among study regions also probably affected age-0 red snapper otolith elemental concentrations. The predominant source of both freshwater input and nutrient load in the northern GOM is the outflow of the Mississippi River (Justic et al. 2002; Rabalais et al. 2002; Dagg and Breed 2003). Low-frequency surface circulation over the Texas–Louisiana continental shelf entrains Mississippi River water during much of the year and establishes three main

oceanographic provinces on the northern GOM shelf that correspond to our three study regions (Cochrane and Kelly 1986; Patterson et al. 1998; Nowlin et al. 2005). High nutrient concentrations from the Mississippi River affect high levels of phytoplankton production and significant benthic-pelagic coupling over the Louisiana shelf (Rabalais et al. 2001, 2002; Justic et al. 2002; Dagg and Breed 2003). In most summers, hypoxic and anoxic conditions set up in large areas (10^3 km²) of the Louisiana shelf (Rabalais and Turner 2001; Rabalais et al. 2002). These oceanographic

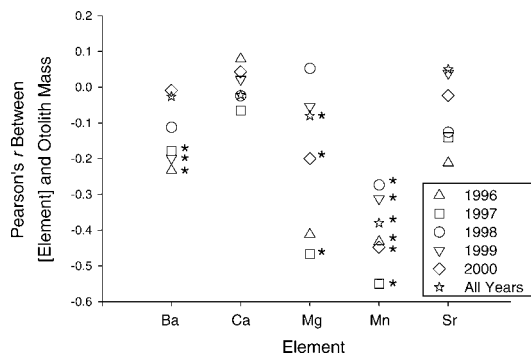


FIGURE 4.—Linear correlations between otolith elemental concentration and otolith mass for 1996–2000 age-0 red snapper cohorts. Asterisks denote significant correlations ($\alpha = 0.05$).

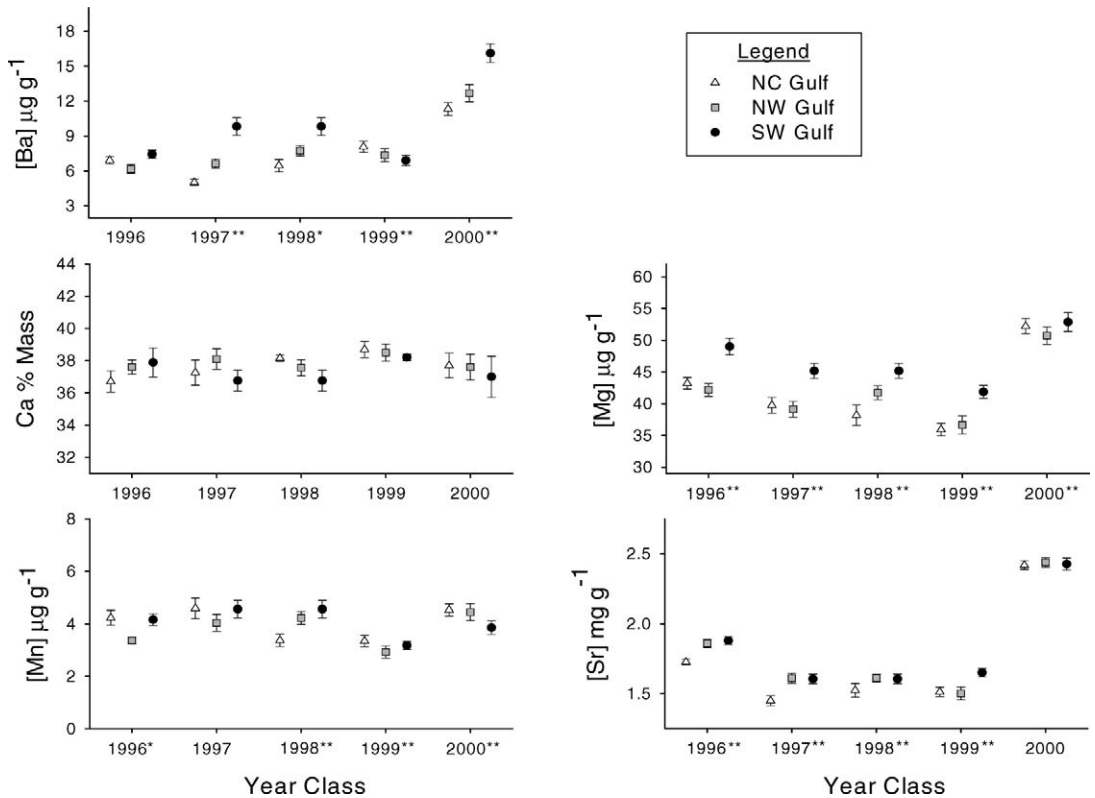


FIGURE 5.—Region- and cohort-specific mean otolith concentrations ($\pm 2\text{SE}$) of five elements analyzed with sector field-inductively coupled plasma-mass spectrometry (Ba, Mg, Mn, and Sr) or inductively coupled plasma-atomic emissions spectrometry (Ca) in age-0 red snapper otoliths. Asterisks denote regional differences were significance at $\alpha = 0.05$. Double asterisks indicate highly significant ($p < 0.01$) differences among regions.

graphic and biological phenomena provide a dynamic system in which trace elements are injected onto the shelf by the Mississippi River (Shiller 1993, 1997), but also may be rapidly absorbed by phytoplankton as micro nutrients (Lea et al. 1989; Beck et al. 2002), transported to the benthos with particulate organic material (POM; Sokolowski et al. 2001; Pohl et al. 2004), or affected by dynamic redox conditions at and just above the sediment–water interface (Warnken et al. 2001; Hanson et al. 2004). Similar oceanographic conditions may exist in the NCG, but the predominant freshwater source to that region, the plume of Mobile Bay, is a much less significant factor than the Mississippi River (Morey et al. 2003). Off Texas, upcoast winds in summer drive surface waters offshore resulting in high salinity bottom water being upwelled onto the shelf (Frolov et al. 2004; Nowlin et al. 2005).

Persistent oceanographic and hydrologic differences among regions likely exerted a strong affect on age-0 red snapper otolith chemistry among regions and year-classes examined. That a significant difference was

found in otolith elemental chemistry among year-classes probably resulted from dynamic, interannual differences in freshwater input and oceanographic conditions. Poor discrimination in 1998 occurred during a drought year in which low freshwater outflow of the Mississippi River resulted in hypoxia conditions existing in approximately 50% less area on the Louisiana shelf than in 1996, 1997, or 1999. However, Mississippi River outflow was even lower in 2000 than in 1998, resulting in one of the smallest spatial extents of hypoxia in the 20 years of near continuous observation (Rabalais and Turner 2001; Rabalais et al. 2002), yet discrimination accuracy among regions in 2000 was high. It may be more likely that an anomalous oceanographic event that occurred in the NCG in the summer of 1998 was the overriding factor that resulted in weak differences in red snapper otolith chemistry among regions. El Niño conditions in 1998 resulted in higher than average rainfall in the eastern GOM and predominant wind conditions that favored upwelling on the NCG shelf (Muller-Karger 2000;

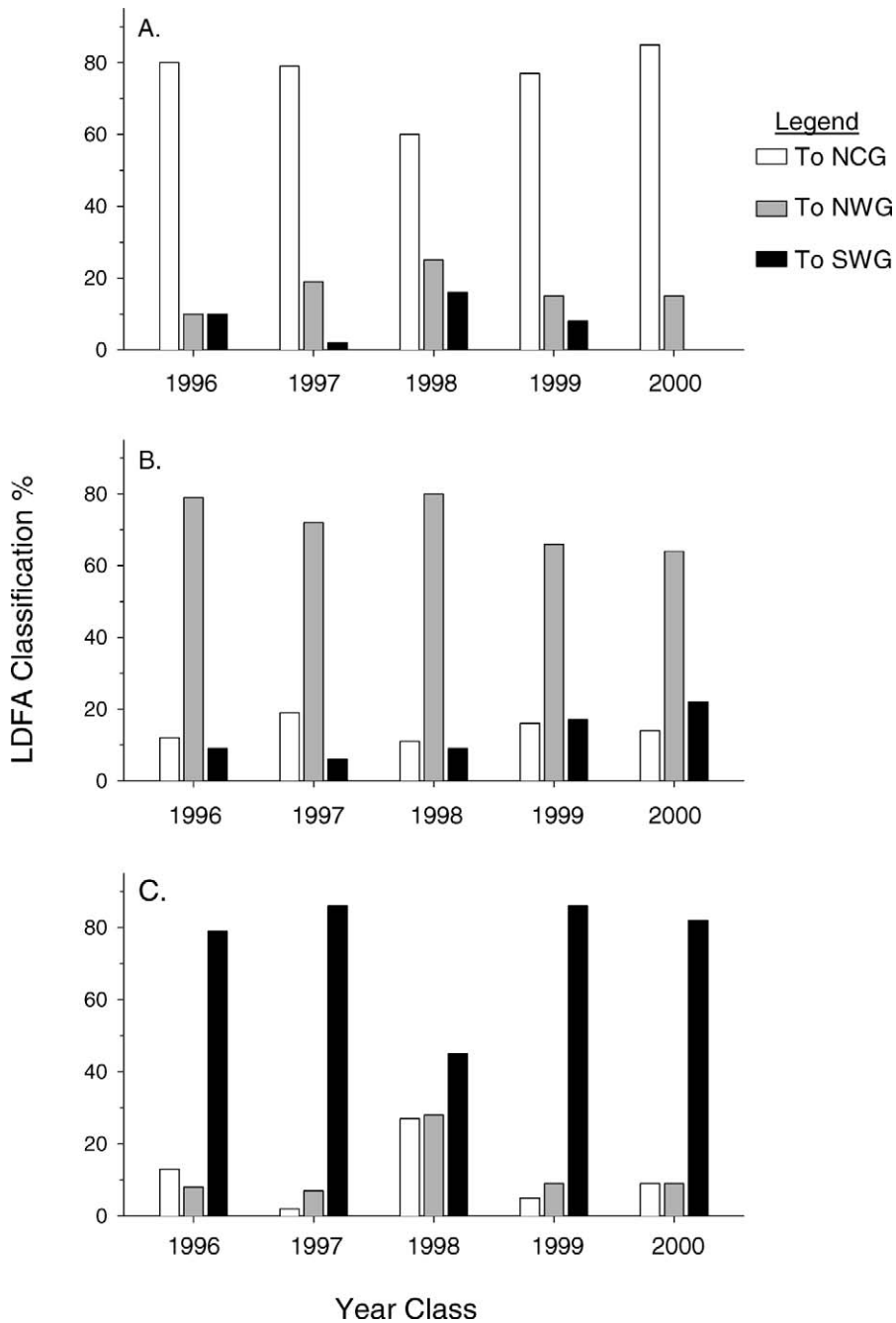


FIGURE 6.—Jackknifed classification percentages of individual age-0 red snapper to three northern Gulf of Mexico (GOM) regions estimated with linear discriminant function analysis (LDFA) of elemental signatures (Ba, Mg, Mn, and Sr) for fish collected in (A) the north-central GOM (NCG), (B) the northwestern GOM (NWG), and (C) the southwestern GOM (SWG).

Nowlin et al. 2000). The combination of those phenomena resulted in dense algal blooms and high biological oxygen demand in spring. As dead algae and POM sunk to the benthos, a stable water column in summer prevented vertical mixing and extensive hypoxia was observed on the NCG shelf (Collard and Lugo-Fernández 1999). Although we have no direct evidence to support our inference, it is likely the combination of this anomalous event and the low Mississippi River flow resulted in weaker than average differences in age-0 red snapper otolith chemistry in 1998.

Overall, interannual differences indicate age-0 red snapper elemental signatures must be analyzed on a year-class-specific basis. However, it should be stressed that high classification in most years is somewhat remarkable given the extended spawning season of red snapper (Jackson et al. 2006), thus resulting in differential environmental exposure histories of juveniles within each region. It is likely that for some year-classes, such as 1998, differences in elemental signatures will not be robust enough to derive meaningful region-specific natural tags. In four out of five years of the current study, however, elemental signatures clearly were sufficiently distinct among regions to be applied as natural tags to examine postsettlement movement and population connectivity. Having a suite of year-class-specific and region-specific otolith elemental signatures available should prove especially powerful as cohort-specific and time-specific approaches can be applied to estimate movement dynamics and connectivity.

Applying otolith elemental signatures to estimate postsettlement connectivity in fishes with life cycles that are exclusively marine has lagged behind research directed at fishes that display estuarine-dependency in early life (but see Rooper et al. 2003; Ashford et al. 2005; Bergenius et al. 2005; Warner et al. 2005). This study corroborates earlier work suggesting otolith microchemistry can be applied as a natural tag for a demersal continental shelf species if the scale of environmental variability driving differences in otolith chemistry matches the scale of the eventual application. In the case of red snapper, oceanographic and hydrographic differences among regions imparted region-specific natural tags in otoliths that can be applied to examine large-scale questions of postsettlement mixing and metapopulation structure. Studies of other reef fishes (e.g., Patterson et al. 1999; Hanson et al. 2004; Chittaro et al. 2006) have been successful in distinguishing nursery habitats for subsequent postsettlement movement analysis. However, most reef species examined to date have early life stages that are estuarine-dependent. In the current study, the

approach of employing otolith chemistry as a natural tag has been extended to a reef fish that spends its entire life cycle on the shelf.

The ultimate goal of our research on red snapper otolith elemental signatures is to apply these natural tags to examine metapopulation structure and source-sink population dynamics. Otolith elemental signatures reported herein provide natural tags for a series of year classes. These permanent tags should prove especially powerful in examining postsettlement movement in a fish that can live 60 years (Patterson et al. 2001b; Wilson and Nieland 2001). Future work also should concentrate on exploring other elements that may impart environmental signatures in otoliths, as well as examining the potential for stable isotopes of oxygen and carbon to increase our ability to distinguish nursery regions. Last, the geographic scope of the present study should be expanded to the entire GOM basin to examine population connectivity and, potentially, metapopulation structure throughout red snapper's GOM range.

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