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Genetic structure of Atlantic and Gulf of Mexico populations of sea bass, menhaden, and sturgeon: influence of zoogeographic factors and life-history patterns*

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Abstract. To assess the influence of zoogeographic factors and life-history parameters (effective population size, generation length, and dispersal) on the evolutionary genetic structure of marine fishes in the southeastern USA, phylogeographic patterns of mitochondrial DNA (mtDNA) were compared between disjunct Atlantic and Gulf of Mexico populations in three coastal marine fishes whose juveniles require an estuarine or freshwater habitat for development. Black sea bass (*Centropristis striata*), menhaden (*Brevoortia tyrannus* and *B. patronus*) and sturgeon (*Acipenser oxyrhynchus*) samples were collected between 1986 and 1988. All species showed significant haplotype frequency differences between the Atlantic and Gulf, but the magnitude and distribution of mtDNA variation differed greatly among these taxa: sea bass showed little within-region mtDNA polymorphism and a clear phylogenetic distinction between the Atlantic and Gulf; menhaden showed extensive within-region polymorphism and a paraphyletic relationship between Atlantic and Gulf populations; and sturgeon exhibited very low mtDNA diversity both within regions and overall. Evolutionary effective sizes of the female populations ($N_{f(e)}$) estimated from the mtDNA data ranged from $N_{f(e)} = 50$ (Gulf of Mexico sturgeon) to $N_{f(e)} = 800\,000$ (Atlantic menhaden), and showed a strong rank-order agreement with the current-day census sizes of these species. The relationship between $N_{f(e)}$ and the estimated times of divergence (t) among mtDNA lineages (from conventional clock calibrations) predicts the observed phylogenetic distinction between Atlantic and Gulf sea bass, as well as the paraphyletic pattern in menhaden, provided the populations have been separated by the same long-standing zoogeographic barriers thought to have influenced other coastal taxa in the southeastern USA. However, vicariant scenarios alone cannot explain other phylogenetic aspects of the menhaden (and sturgeon) mtDNA data and, for these species, recent gene flow between the Atlantic and Gulf coasts is strongly implicated. These data are relevant to management and conservation issues for these species.

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Introduction

The geographic structure of any species is a product of both historical and contemporary gene flow (Slatkin 1987), and is likely to have been affected by such factors as geographic or ecologic impediments to movement and inherent dispersal capability. An important issue in evolutionary biology concerns whether general and predictable relationships exist between the phylogeographic structures of species and their environmental requirements and life-histories. For example, freshwater fishes tend to be physically confined to particular bodies of water, and their populations commonly exhibit extensive geographic population structure reflecting historical patterns of drainage isolation and coalescence (Bermingham and Avise 1986, Avise et al. 1987a). In contrast, many oceanic and reef-based marine organisms exhibit extensive movement as larvae and/or adults (Rosenblatt 1963, Scheltema 1971), and at least some surveyed species show relatively little population genetic structure over huge areas (Winans 1980, Graves et al. 1984, Shaklee 1984, Avise et al. 1986, Gyllensten 1986, Avise 1987).

However, marine species themselves exhibit a great diversity of life-history patterns with respect to dispersal. For example, in species that lay demersal eggs (e.g. toadfish), or in anadromous species that reproduce in freshwater (e.g. salmon), long-distance gene flow must occur primarily through movements of sub-adults or adults. Conversely, gene flow in species that are benthic as adults (e.g. oysters) may occur exclusively via movement of pelagic gametes or larvae. Many species exhibit extensive movements both as pelagic larvae and adults (e.g. tuna), while in comparison others show limited movement at all life-history stages (e.g. horseshoe crabs).

Phylogeographic patterns in coastal marine species may be intermediate between freshwater and pelagic marine types, because the potential for dispersal is tempered by habitat availability along a linear zoogeographic regime. The distributional limits of coastal species are typically defined by major geographic or hydrologic boundaries, such as at Cape Cod, Cape Hatteras, and the Florida peninsula along the east coast of the USA (Hilde-

brand and Schroeder 1928, Bigelow and Schroeder 1953, Briggs 1974). The Florida peninsula is of special interest because it divides the temperate coastal fauna of the southeastern USA into Atlantic and Gulf of Mexico provinces (Hoese and Moore 1977). Warm, subtropical conditions extend northward to central Florida on both sides of the peninsula, and at the present time divide some elements of the temperate fauna into allopatric units.

In general, coastal marine fishes (and many invertebrates) utilize near-shore or estuarine habitat as nursery grounds for larvae and juveniles. In contrast to pelagic or reef-based species, where reproduction often involves long-distance transport of larvae, such coastal species have developed strategies to minimize offshore transplant (and loss) of larvae (Checkley et al. 1988).

Here we examine mitochondrial DNA (mtDNA) population structure in three temperate coastal marine fishes that require an estuarine or freshwater habitat for juvenile development. Mitochondrial DNA is especially useful for elucidating population structure because this non-recombining molecule evolves rapidly and provides character states whose phylogenetic relationships readily can be deduced (Brown et al. 1979, Wilson et al. 1985, Avise 1986, 1989, Moritz et al. 1987). The geographic distribution of branches in an intraspecific mtDNA phylogeny constitutes the maternal "phylogeographic" pattern of a species (Avise et al. 1987a). Our major goals are to: (1) further assess the influence of historical geographic factors and life-history pattern on the genetic structure of the marine fauna of the southeastern US; (2) provide genetic data that may be of relevance to management and conservation decisions for these species; and (3) assess two additional, seldom-considered factors in phylogeographic outcomes – the significance of differing effective population sizes and generation lengths on the distributions of gene lineages within and among populations.

Taxonomy and life-history background

Black sea bass

The Atlantic subspecies of black sea bass, *Centropristis striata striata*, is distributed on the Atlantic continental shelf from Massachusetts to central Florida (Grosslein and Azarovitz 1982), with occasional strays in south Florida (Miller 1959). The Gulf subspecies, *C. striata melana*, occurs in the Gulf of Mexico from northern Florida to Texas. Miller suggested that the paucity of records in southwestern Florida may be due to inadequate sampling, but Houde (1982) noted that sea bass eggs and larvae are rarely found in this region. The Atlantic and Gulf forms of black sea bass were originally described as separate species (Ginsburg 1952), but broad overlap in meristic characters prompted demotion to the current subspecies status (Miller 1959, Bortone 1977).

In spring, adult sea bass inhabit coastal spawning areas while subadults return to estuarine nursery areas (Musick and Mercer 1977). Pelagic eggs hatch in 3 or 4 d and post-larvae enter the estuarine habitat (Hildebrand and Schroeder 1928, Dahlberg 1972, Kendall 1972). Juveniles and adults migrate to offshore areas in the fall (Musick and Mercer 1977).

Menhaden

Brevoortia tyrannus, the Atlantic menhaden, and *B. patronus*, the Gulf menhaden, have been accorded specific status based on differences in meristic characters, external morphology, fecundity, and maximum size and age (Hildebrand 1948, Dahlberg 1970). The Atlantic menhaden is distributed from Nova Scotia to east central Florida, and the Gulf menhaden ranges from Mexico to west central Florida, with occasional reports from south Florida (Hildebrand 1948, Briggs 1958, Christmas and Gunter 1960, Reintjes 1964, Dahlberg 1970). Atlantic and Gulf menhaden populations are thus apparently disjunct, with a gap on the Atlantic side of south Florida (Dahlberg 1970). However, at the southern ends of their ranges, both forms hybridize with the yellowfin menhaden *B. smithi* (Reintjes 1960, Hettler 1968, Dahlberg 1970), providing a possible avenue of gene flow between the Atlantic and Gulf.

On the Atlantic coast, menhaden undergo extensive seasonal migration, moving northward and inshore during spring, and southward and offshore in autumn (Massman et al. 1954, Nicholson 1978). Seasonal migration appears to be less extensive in south Atlantic (and Gulf) menhaden populations (Hildebrand 1963, Roithmayr and Waller 1963). A large aggregate of juveniles and adults off North Carolina is believed to constitute the primary overwintering population for the Atlantic species (Nicholson 1972). Based on meristic characters, spawning time, and migratory behavior, several researchers have suggested that discrete populations of Atlantic menhaden may exist (June 1958, 1965, Sutherland 1963, June and Nicholson 1964, Dahlberg 1970). However, tagging data indicate that considerable mixing occurs between areas (Dryfoos et al. 1973), and Nicholson (1978) concluded that extensive migration and intermingling on overwintering grounds precluded the likelihood of significant population structure in *Brevoortia tyrannus*.

Based on egg and larval surveys, spawning occurs through most of the year, with the highest concentration of eggs observed off North Carolina in December through February (Kendall and Reintjes 1975, Judy and Lewis 1983). Eggs hatch in 36 to 48 h and larvae subsequently enter the upper estuarine habitat (June and Chamberlin 1959, Reintjes 1961). Like many coastal species, reproductive success in menhaden is strongly linked to Eckman transport of larvae into estuaries (Lewis et al. 1972, Weinstein et al. 1980, Checkley et al. 1988).

Menhaden support major fisheries on both sides of the Florida peninsula, in peak years yielding over one billion kilograms, or one-fourth of the fish biomass harvested annually in the USA (Chapoton 1972). Despite recent evidence of overfishing, menhaden must currently number in the tens or hundreds of billions.

Atlantic sturgeon

The Atlantic subspecies of sturgeon, *Acipenser oxyrhynchus oxyrhynchus*, is distributed from Labrador to north Florida, with strays reported from central Florida during exceptionally cold weather (Backus 1951, Bigelow and Schroeder 1953, Wooley and Crateau 1985). The Gulf subspecies, *A. oxyrhynchus desotoi*, is historically recorded from the Mississippi River to central Florida, but has also been observed at the southern tip of the peninsula in cold weather (Vladykov and Greeley 1963, Wooley and Crateau 1985). An appropriate freshwater habitat for sturgeon is effectively absent through most of south Florida, so Atlantic and Gulf subspecies are considered geographically disjunct (Rivas 1954). However, the distribution and migratory behavior of mature specimens on the continental shelf are largely unknown (Van Den Avyle 1984). Based on two specimens, Vladykov (1955) described the Gulf sturgeon as a distinct subspecies, but subsequent analysis of a larger sample demonstrated that only one internal character (relative spleen length) is nearly diagnostic, and apparently no external character unequivocally separates Atlantic from Gulf specimens (Wooley 1985).

Acipenser oxyrhynchus is a slow growing anadromous species, which reaches an age of at least 60 yr (Magnin 1964). Mature sturgeon inhabit rivers through the summer, and tagging data indicate that adults return to the same drainage in subsequent seasons (Wooley and Crateau 1985). Juveniles remain in freshwater for 1 to 8 yr, moving into neritic waters more frequently with increasing age (Vladykov and Greeley 1963, Huff 1975). While some immature individuals may remain in the vicinity of their natal drainage, others move extensively along the coast (Vladykov and Greeley 1963). Based on long-distance tag returns (up to 645 km), Holland and Yelverton (1973) concluded that juveniles have no strong affinity for their natal drainage system.

Sturgeon were common through the late nineteenth century, after which several factors including development of a significant fishery (Vladykov and Greeley 1963), dam construction which inhibited access to upstream spawning areas (Murawski and Pacheco 1977), and incidental harvest of juveniles by other fisheries (Leland 1968), have had devastating effects on the populations. Atlantic and Gulf sturgeon are now absent from many areas of former abundance, and are scarce through most of the range (Huff 1975, Murawski and Pacheco 1977).

Materials and methods

Black sea bass (*Centropristis striata*) were obtained from upper and lower Chesapeake Bay, Maryland and Virginia ($n=10$), Brunswick, Georgia ($n=9$), and Panacea, Florida ($n=9$). Atlantic menhaden (*Brevoortia tyrannus*) were collected in upper Chesapeake Bay, Maryland ($n=8$) and Brunswick, Georgia ($n=9$), and Gulf menhaden (*Brevoortia patronus*) were collected in Ocean Springer, Mississippi ($n=16$). Sturgeon (*Acipenser oxyrhynchus*) were collected from four Georgia drainages – the Altamaha ($n=9$), Ogeechee ($n=5$), Satilla ($n=4$) and Savannah Rivers ($n=3$), and also from the Apalachicola ($n=3$) and Suwannee Rivers ($n=12$) on the Gulf coast of Florida. Tissue sources for the mtDNA isolations included heart, liver, and eggs, which usually were removed in the field and shipped within 7 d to the laboratory on MSB buffer: 0.21 *M* mannitol, 0.07 *M* sucrose, 0.05 *M* tris-HCl (pH 7.5), 0.01 *M* EDTA (Lansman et al. 1981). From some specimens, freshly dissected tissues, as well as frozen ovaries and eggs, were also employed with success.

Purified mtDNA was obtained by CsCl-ethidium bromide density-gradient centrifugation (Lansman et al. 1981). MtDNA was then dialized against 1 *M* sodium acetate for 48 h, and against TE buffer (0.01 *M* tris-HCl, 0.5 m*M* EDTA, pH 8.0) twice for periods of 24 h. MtDNAs were then digested with 12 to 18 informative restriction enzymes (Table 1) under conditions recommended by the manufacturer. Enzymes were deemed informative if they generated two or more mtDNA restriction fragments in at least some samples of a given species. MtDNA fragments were end-labeled with ^{35}S-radionucleotides and separated on 1.0 to 1.6% agarose gels (Maniatis et al. 1982). Digestion products were detected by autoradiography and compared in size to fragments in a one kilobase (kbase) ladder (Bethesda Research Laboratories). Usually, we did not attempt to score fragments smaller than 0.5 kbase.

Nucleotide sequence divergence (p) was estimated by the site approach of Nei and Li (1979), based on mtDNA fragment profile changes which were clearly attributable to restriction-site gains or losses (details in Avise et al. 1989). MtDNA variation was also summarized by the nucleotide and genotypic diversity indices of Nei and Tajima (1981) and Nei (1987), which are defined in the footnotes to Table 2. Genetic-distance matrices were clustered using the unweighted pair-group method with arithmetic means (UPGMA). Parsimony networks based on the qualitative restriction-fragment data were generated by the approach described in Avise et al. (1979).

Results

Black sea bass

Individual sea bass, *Centropristis striata*, were scored on average for 61 mtDNA restriction sites, revealed by the 13 informative restriction enzymes listed in Table 1. Among the 29 assayed sea bass, 5 different mtDNA haplotypes were observed (Table 1), and overall genotypic diversity was 0.566 (Table 2). In the UPGMA phenogram, the genotypes grouped into two distinct clusters whose members differed on average by about 0.9% sequence divergence (Fig. 1). Genotypes "a" and "b" differed consistently from "c"–"e" in digestion profiles for *Eco*RI, *Hin*cII, *Hin*dIII, *Stu*I, and *Xba*I (Table 1: Columns 8, 10, 11, 21, 22; and Fig. 2). These two clusters align perfectly with the geographic source of the samples (Atlantic vs Gulf coast; Fig. 2). Since nucleotide diversity within either *C. striata striata* or *C. striata melana* was

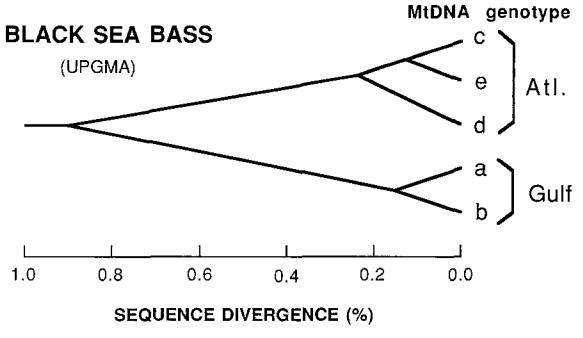

Fig. 1. *Centropristis striata.* UPGMA (unweighted pair-group method of analysis) phenogram summarizing relationships among the five mitochondrial DNA (mtDNA) clones observed in Atlantic and Gulf of Mexico populations

Table 1. *Centropristis striata*, *Brevoortia tyrannus* and *B. patronus*, and *Acipenser oxyrhynchus*. Descriptions of mtDNA clones observed in Atlantic (At) and Gulf Coast (Gu) populations. Genotypic descriptions present 22 columns representing 22 endonucleases: 1: *Ava*I; 2. *Ava*II; 3: *Bcl*I; 4: *Bgl*I; 5: *Bgl*II; 6: *Bst*EII; 7: *Cla*I; 8: *Eco*RI; 9: *Eco*RV; 10: *Hin*cII; 11: *Hin*dIII; 12: *Kpn*I; 13: *Msp*I; 14: *Nde*I; 15: *Pst*I; 16: *Pvu*II; 17: *Sac*I; 18: *Sal*I; 19: *Spe*I; 20: *Sst*II; 21: *Stu*I; 22: *Xba*I. Capital letters in these columns represent digestion profiles, whereby C indicates most common pattern within each species, and remaining letters indicate variant digestion profiles (letters shared by different groups do not imply identity of fragment profiles). −: not assayed; +: assayed but uninformative (zero or only one cut in the mtDNA). In menhaden, patterns "o" and "cc" differ only in gel patterns produced by *Ava*II and *Hin*cII, two enzymes not included in sequence-divergence calculations due to complexity of fragment patterns produced. Diagrams of digestion profiles are available from authors on request, *N*: no. of individuals

Clone type	mtDNA description (by enzyme no.)																					*N* and (coast)
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	
Black sea bass																							
a	C	−	+	C	C	C	+	C	C	C	C	+	−	C	+	C	+	−	−	C	C	C	8 (Gu)
b	C	−	+	C	C	C	+	C	C	B	C	+	−	C	+	C	+	−	−	C	C	C	1 (Gu)
c	C	−	+	C	C	C	+	D	C	D	D	+	−	C	+	C	+	−	−	C	D	D	17 (At)
d	C	−	+	C	C	C	+	D	C	E	D	+	−	C	+	C	+	−	−	C	D	D	1 (At)
e	C	−	+	C	C	C	+	D	C	D	D	+	−	C	+	C	+	−	−	C	B	D	1 (At)
Menhaden																							
a	G	A	C	D	B	C	C	C	F	I	C	G	−	D	A	F	C	−	F	−	H	−	1 (At)
b	C	B	C	C	B	B	C	C	C	E	C	B	−	C	B	I	C	−	C	−	C	−	1 (At)
c, v	C	C	C	C	C	B	C	C	C	E	C	B	−	C	B	J	C	−	B	−	D	−	2 (At, Gu)
d	C	D	C	C	C	B	C	C	C	H	C	C	−	C	B	E	C	−	C	−	C	−	1 (At)
e	E	E	C	C	C	B	B	C	B	K	C	C	−	C	B	B	C	−	B	−	C	−	1 (At)
f	F	A	C	D	B	C	C	C	A	I	C	G	−	D	A	F	C	−	F	−	H	−	1 (At)
g	C	F	C	C	B	B	C	C	A	B	C	B	−	C	E	K	C	−	C	−	B	−	1 (At)
h	G	G	C	D	B	G	C	C	A	I	C	F	−	D	D	F	C	−	F	−	I	−	1 (At)
i	F	A	C	D	B	F	C	C	A	I	C	G	−	D	A	F	D	−	F	−	H	−	1 (At)
j	C	H	C	C	E	B	D	C	C	L	C	B	−	C	F	E	C	−	C	−	C	−	1 (At)
k	G	I	C	D	B	C	C	C	A	J	C	G	−	D	A	F	C	−	F	−	G	−	1 (At)
l	C	J	C	C	D	B	B	D	C	E	C	E	−	C	C	I	C	−	C	−	C	−	1 (At)
m	C	H	C	C	C	B	B	C	A	E	C	B	−	D	B	E	C	−	C	−	C	−	1 (At)
n	C	D	C	C	C	B	C	C	C	E	C	D	−	C	B	L	C	−	C	−	D	−	1 (At)
o	C	K	C	C	B	D	C	C	B	A	C	B	−	C	B	H	C	−	A	−	B	−	1 (At)
p	G	G	C	D	B	C	C	C	A	I	C	F	−	D	A	G	C	−	F	−	H	−	1 (At)
q	C	D	C	C	C	B	C	C	A	E	C	B	−	C	C	E	C	−	C	−	C	−	1 (At)
r	C	D	C	C	C	B	C	C	C	F	C	B	−	C	B	J	C	−	C	−	C	−	1 (Gu)
s	C	L	C	C	C	B	B	C	C	E	C	A	−	C	B	B	C	−	C	−	C	−	1 (Gu)
t	C	M	C	C	B	B	B	C	C	E	C	B	−	C	B	I	C	−	C	−	F	−	1 (Gu)
u	C	J	C	C	C	B	C	C	C	H	C	D	−	C	B	H	C	−	D	−	C	−	1 (Gu)
w	C	N	C	C	C	B	C	C	C	F	C	C	−	C	B	A	C	−	C	−	C	−	1 (Gu)
x	C	J	C	C	C	B	B	C	D	G	C	B	−	C	B	D	C	−	C	−	C	−	1 (Gu)
y	C	O	C	C	C	B	C	C	C	D	C	D	−	C	B	J	C	−	C	−	D	−	1 (Gu)
z	C	L	C	C	C	B	C	C	C	E	C	C	−	C	B	C	C	−	C	−	C	−	1 (Gu)
aa	C	O	C	C	C	B	C	C	C	D	C	B	−	C	B	J	C	−	C	−	D	−	1 (Gu)
bb	C	P	C	C	C	B	E	C	E	C	C	B	−	C	B	J	C	−	B	−	D	−	1 (Gu)
cc	C	F	C	C	B	D	C	C	B	B	C	B	−	C	B	H	C	−	A	−	B	−	1 (Gu)
dd	C	J	C	A	C	B	C	C	C	E	C	B	−	C	H	H	C	−	B	−	E	−	1 (Gu)
ee	D	J	C	C	C	B	C	C	B	H	C	C	−	C	B	H	C	−	C	−	F	−	1 (Gu)
ff	E	Q	C	C	C	E	B	C	C	H	C	B	−	C	B	H	C	−	E	−	C	−	1 (Gu)
gg	C	R	C	C	C	B	B	C	C	E	C	C	−	C	B	E	C	−	D	−	C	−	1 (Gu)
Sturgeon																							
a	−	C	C	C	+	C	+	C	C	C	C	−	C	+	C	+	+	C	C	C	C	C	17 (At, Gu)
b	−	C	C	B	+	C	+	C	C	C	C	−	C	+	C	+	+	C	C	C	C	C	1 (Gu)
c	−	C	C	C	+	C	+	C	C	C	C	−	D	+	C	+	+	C	C	C	C	C	12 (At)
d	−	C	C	C	+	C	+	C	B	C	C	−	C	+	C	+	+	C	C	C	C	C	4 (At)
e	−	C	C	C	+	C	+	C	D	C	C	−	C	+	C	+	+	C	C	C	C	C	1 (At)
f	−	C	C	C	+	C	+	C	C	D	C	−	C	+	C	+	+	C	C	C	C	C	1 (At)

very low, the net nucleotide divergence between the two nominal subspecies remained $p_{corr} = 0.007$ (Table 2).

Menhaden

Menhaden (*Brevoortia tyrannus* and *B. patronus*) exhibited extensive mtDNA diversity, the molecular basis of which includes both restriction-site and mtDNA size differences, as detailed by Avise et al. (1989). The following statements are based solely on the mtDNA restriction-site differences, since these are most relevant to calculations of sequence divergence and phylogeny estimation. Among the 33 assayed specimens of *B. tyrannus* and *B. patronus*, 31 different mtDNA genotypes were observed (Table 1), yielding a genotypic diversity estimate of 0.996, close to the maximum assumable value of 1.0

Population	No. of: individuals	genotypes	Nucleotide diversity (mean sequence divergence)[a]	Genotypic diversity[b]
Black sea bass				
Atlantic	19	3	0.0003	0.205
Gulf	9	2	0.0003	0.222
Composite	28	5	0.0037	0.566
Atlantic vs Gulf			0.0075 (uncorrected)	
			0.0072 (corrected[c])	
Menhaden				
Atlantic	17	17	0.0316	1.000
Gulf	16	16	0.0099	1.000
Composite	33	31	0.0239	0.996
Atlantic vs Gulf			0.0261 (uncorrected)	
			0.0054 (corrected[c])	
Sturgeon				
Atlantic	21	5	0.0017	0.643
Gulf	15	2	<0.0001	0.133
Composite	36	6	0.0014	0.670
Atlantic vs Gulf			0.0016 (uncorrected)	
			0.0008 (corrected[c])	

Table 2. *Centropristis striata, Brevoortia tyrannus* and *B. patronus*, and *Acipenser oxyrhynchus*. Estimates of mtDNA variation and differentiation in Atlantic and Gulf coast populations

[a] $p=[n/(n-1)]\,\Sigma f_i f_j p_{ij}$, where f_i and f_j are frequencies of ith and jth sequences in a sample of size n, and p_{ij} is estimated divergence between ith and jth sequences (Nei 1987; p. 256)

[b] $[n/(n-1)]\,(1-\Sigma f_i^2)$

[c] $p_{\text{corrected}}=p_{xy}-0.5\,(p_x+p_y)$, where p_{xy} is the mean divergence between mtDNA sequences in Atlantic and Gulf populations ($p_{\text{uncorrected}}$), and p_x and p_y are mean divergences between mtDNA sequences within Atlantic and Gulf populations, respectively

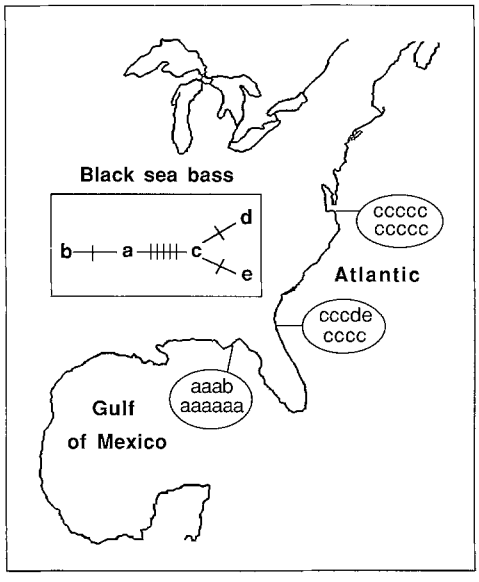

Fig. 2. *Centropristis striata.* Geographic distributions of the five observed mtDNA clones (labeled "a" through "e", as in Table 1). Inset: parsimony network interconnecting these genotypes; short bars crossing branches indicate numbers of restriction-site changes along a path. Network could be generated without homoplasy

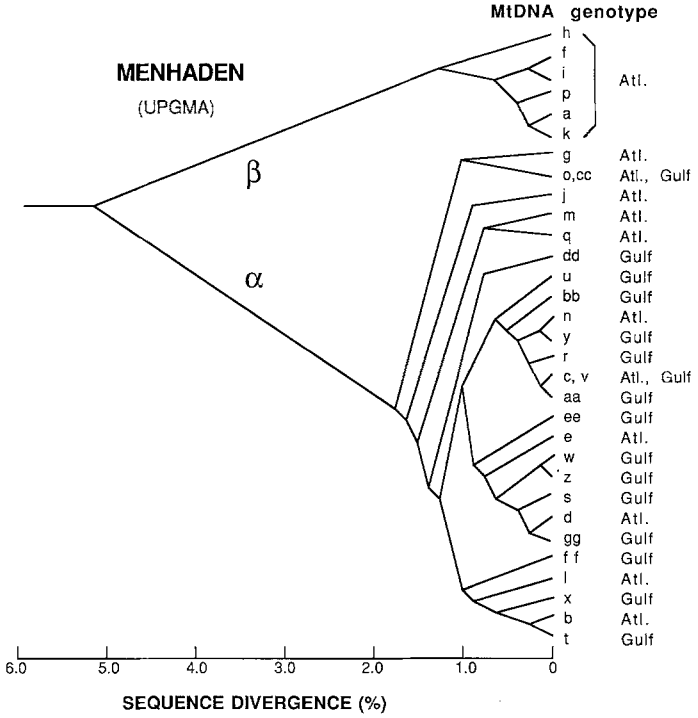

Fig. 3. *Brevoortia tyrannus* and *B. patronus.* UPGMA phenogram summarizing relationships among mtDNA clones observed in Atlantic and Gulf of Mexico populations

(Table 2). This represents the highest value yet reported for any species (Avise et al. 1989). No assayed individuals within either the Atlantic or Gulf populations shared an mtDNA genotype, although two pairs of *B. tyrannus*/*B. patronus* individuals were identical at all 49 to 51 restriction sites scored.

On average, a random pair of sampled menhaden differed by an estimated 2.4% sequence divergence, with somewhat higher nucleotide diversity observed in *Brevoortia tyrannus* (Atlantic) than in *B. patronus* (Gulf) (Table 2). The 31 mtDNA genotypes clustered into two distinct groups (α and β, Fig. 3), one of which was observed only in Atlantic menhaden, while the other was observed in both Atlantic and Gulf populations (Fig. 4). The frequencies of α and β were significantly different in our Atlantic and Gulf collections. In a G-test for heterogeneity (Sokal and Rohlf 1981), $G_H = 8.4$, $P<0.01$. Representatives of these two genotypic clusters differed on average by about 5% sequence divergence. However, since representatives of both genotypic arrays were

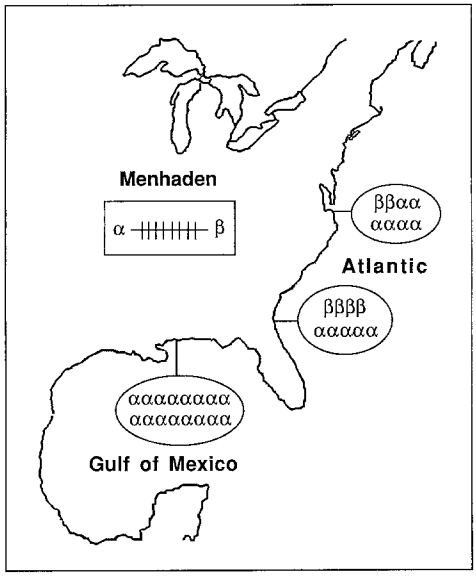

Fig. 4. *Brevoortia tyrannus* and *B. patronus*. Geographic distributions of the two major mtDNA lineages (α and β in Fig. 3) observed. Representatives of these two lineages typically differed by at least eight assayed restriction-site changes, as indicated by the short bars crossing network branch connecting them (inset)

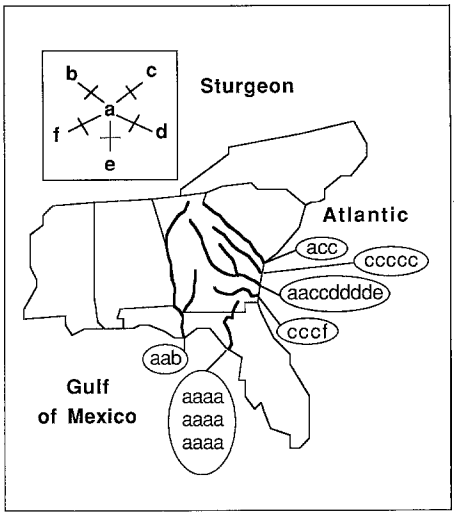

Fig. 6. *Acipenser oxyrhynchus*. Geographic distributions of the six observed mtDNA clones (labeled "a" through "f", as in Table 1). River drainages indicated by heavier lines (clockwise from the northeast) are as follows: Savannah, Ogeechee, Altamaha, Satilla, Suwannee, and and Apalachicola. Inset:parsimony network interconnecting mtDNA genotypes; short bars crossing branches indicate numbers of digestion profile changes along a path; network could be generated without homoplasy

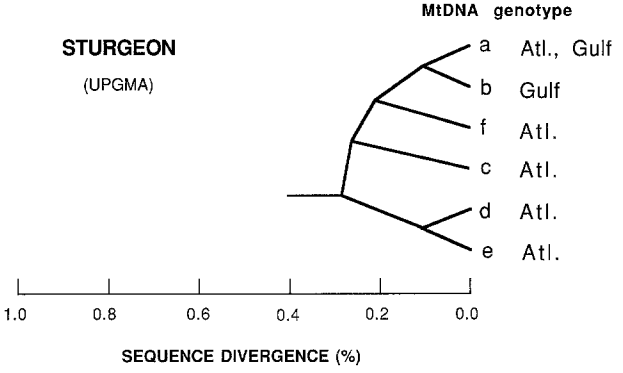

Fig. 5. *Acipenser oxyrhynchus*. UPGMA phenogram summarizing relationships among mtDNA clones observed in Atlantic and Gulf of Mexico populations

observed in *B. tyrannus*, the net sequence divergence between *B. tyrannus* and *B. patronus* was only $p_{corr} = 0.005$ (Table 2).

Atlantic sturgeon

Individual sturgeon, *Acipenser oxyrhynchus*, were scored, on average, for 68 mtDNA restriction sites, revealed by 15 informative restriction enzymes (Table 1). Among the 36 assayed sturgeon, 6 different mtDNA haplotypes were observed (Table 1), and mean genotypic diversity was 0.670 overall (Table 2). All genotypes were very closely related, and showed no clear separations in the UPGMA phenogram (Fig. 5). The most common genotype, "a", was observed on both coasts (Fig. 6), although in significantly different frequencies in the Atlantic and Gulf of Mexico ($G_H = 25.2$, $P \ll 0.01$). Each other haplotype differed from "a" by an independent, single restriction-site change (Fig. 6), such that all estimates of nucleotide sequence divergence were very low (maximum $p = 0.004$). Net nucleotide divergence between the Atlantic and Gulf collections was $p_{corr} = 0.0008$ (Table 2).

Discussion

Zoogeographic background

Previous studies have used molecular markers to appraise genetic differentiation between Atlantic and Gulf populations of several coastal-restricted species in the southeastern USA, including horseshoe crabs (Saunders et al. 1986), American oysters (Reeb and Avise 1990), stone crabs (Bert 1986), marine toadfish and catfish (Avise et al. 1987b), diamondback terrapins (Lamb and Avise in preparation), and seaside sparrows (Avise and Nelson 1989). With the exception of the marine catfish, all these taxa exhibit a striking pattern of phylogeographic concordance involving a clear genetic distinction of most populations in the Gulf of Mexico (and sometimes southeastern Florida) from those along the remainder of the Atlantic coast (reviews in Reeb and Avise 1990 and Avise and Ball 1990).

These phylogenetic separations exhibited by a significant fraction of the southeastern coastal fauna were probably initiated by population disjunctions dating to the late Pliocene or Pleistocene, and presumably are maintained today by contemporary ecologic or hydrologic limits to gene flow in peninsular Florida (review in Reeb and Avise 1990). One scenario of historical popula-

tion separation in the region involves changes in sea level associated with the several glacial advances of the past 2 m.yr. During glacial periods, the massive Florida and Yucutan peninsulas were apparently arid and bordered by coastlines that provided poor habitat for freshwater- or estuarine-adapted species. Thus, during glacial maxima (low sea level), the western Gulf of Mexico may have been an isolated refugium for estuarine populations formerly connected to those along the Atlantic coast. An alternative hypothesis associates vicariant separations with the interglacial periods. During interglacial times (such as at present), temperate-adapted marine species may have been isolated into Atlantic and Gulf populations by the subtropical and tropical ecological conditions of south Florida. During glacial advances, climatic cooling caused southward shifts in geographic range, such that temperate-adapted marine faunas extended well south of the Florida peninsula (Hedgpeth 1954). Thus, range shifts at times of glacial maxima may have provided periodic opportunities for contact among Atlantic and Gulf populations that were otherwise separated by the Florida peninsula.

While the estimates of genetic distance (and calibrations of molecular evolutionary rate) for any of these species are not yet precise enough to provide firm associations with *particular* glacial or interglacial episodes during the Pleistocene, it remains of interest to consider the relative roles of historical vicariant events and contemporary gene flow, as well as other demographic and life-history factors, in shaping the genetic architectures of the southeastern marine fauna.

Magnitudes and patterns of mtDNA divergence

All three groups of fishes examined in this study (*Centropristis striata*, *Brevoortia tyrannus* and *B. patronus*, and *Acipenser oxyrhynchus*) exhibit significant shifts in mtDNA genotype frequency between Atlantic and Gulf coast sample locations (Figs. 2, 4, 6). Nonetheless, the magnitudes and patterns of mtDNA variation differ dramatically among these taxa (Figs. 1, 3, 5): black sea bass showed very low mtDNA diversity within regions, moderate levels of mtDNA sequence divergence, and a sharp genetic distinction between the Atlantic and Gulf coast; menhaden showed extremely high genotypic diversity within populations, large sequence differences among mtDNA genotypes, and considerable sharing of particular clones and clonal assemblages between Atlantic and Gulf coast locales; sturgeon exhibited low genotypic diversity, small sequence differences between mtDNA genotypes, and limited sharing of genotypes between the two coasts. Can these diverse patterns be understood in terms of the historical demographies and life histories of these species?

One important consideration may be the effective sizes of female populations over evolutionary time, since under neutrality theory, $N_{f(e)}$ (the effective population size of females) should be related directly to: (a) the standing crop of mtDNA diversity and sequence divergence within populations (Nei 1987, Avise et al. 1988); and (b) the evolutionary time required for two completely isolated populations to evolve to a status of reciprocal monophyly (that is, for the gene tree to become concordant with the population tree). In particular, the mean time to common ancestry for random pairs of mtDNA genotypes within a random-mating population is about $N_{f(e)}$ generations (Avise et al. 1988), and gene trees are likely to be concordant with population subdivisions only after $2N_{f(e)}$ generations of isolation (Neigel and Avise 1986, Pamilo and Nei 1988). One consequence of these considerations is that, all else being equal, larger population size and longer generation length can both be expected to increase the chronological times required for gene lineages within an ancestral population to be converted to gene lineage differences between isolated daughter populations.

For sake of argument, assume that the Atlantic and Gulf populations of each of the assayed fish groups have indeed been separated by historical impediments to gene flow [as discussed, for example, by Bert (1986) and Reeb and Avise (1990) for other taxa]. For black sea bass, the observed mtDNA pattern is certainly compatible with this possibility, since our samples in the Atlantic and Gulf are fixed for distinct mtDNA genotypes that exhibit far greater sequence differences between- than within-regions ($p_{corr} = 0.007$, Table 2). Under a conventional mtDNA "clock" calibration for vertebrates (2% sequence divergence per million years: Brown et al. 1979, Wilson et al. 1985, Shields and Wilson 1987), the level of genetic divergence in sea bass corresponds to about 350 000 yr of separation (Avise 1989), or roughly 100 000 generations (assuming 3.5 yr per generation). Thus if $N_{f(e)}$ within sea bass populations has been considerably less than about 200 000 individuals, isolated Atlantic and Gulf coast stocks are indeed expected to have evolved to the observed status of reciprocal monophyly. The mean mtDNA sequence divergence within Atlantic or Gulf populations, $p = 0.0003$ (Table 2), corresponds to a mean time of lineage separation of about 15 000 yr, or 5 000 sea bass generations. This yields a within-region estimate of $N_{f(e)} \cong 5\,000$. Thus, for the black sea bass, the low mtDNA sequence diversity observed within regions (Table 2), as well as the fixed and significant sequence differences between regions (Fig. 2), are both consistent with relatively low values of $N_{f(e)}$ (in contrast to menhaden – see below).

Assume for argument that a similar historical scenario has influenced the population genetic structure of menhaden. At face value, two major aspects of the *Brevoortia* spp. mtDNA data then appear compatible with vastly larger $N_{f(e)}$'s for this group: (1) the high nucleotide and genotypic diversities within regions (Table 2); and (2) the lack of concordance between the mtDNA gene tree and the Atlantic vs Gulf coast sampling locales (Fig. 3). For example, nucleotide diversity within the Atlantic *B. tyrannus*, $p = 0.032$ (Table 2), corresponds under a conventional evolutionary clock to 1.6 myr of mtDNA lineage separation, or about 800 000 menhaden generations (assuming 2 yr per generation). This yields a within-Atlantic estimate of $N_{f(e)} \cong 800\,000$ (similar calculations for the Gulf *B. patronus* yield $N_{f(e)} \cong 250\,000$). While these

estimates of evolutionary effective population size are vastly lower than present-day census sizes (N) of these taxa (see "Taxonomy and life-history background", e.g. "Menhaden"), many demographic factors, such as high variances in progeny survival among females, or fluctuations in population size, can greatly reduce $N_{f(e)}$ relative to contemporary N. For example, in the case of Atlantic menhaden, a collapse of the east-coast fishery in the late 1960's and 1970's implied a significant but apparently temporary recent reduction in population size. Other cases in which $N_{f(e)} \ll N$ have been reported previously for vertebrate species from mtDNA data (Avise et al. 1988).

In any event, the estimated $N_{f(e)}$'s for menhaden are vastly larger than those for the black sea bass, a finding consistent with the relative abundances of these taxa today. If menhaden $N_{f(e)}$'s are indeed on the order of several hundred thousand, and if (as in the sea bass) population separation between the Atlantic and Gulf occurred perhaps 350 000 yr ago (175 000 menhaden generations), then insufficient time (number of generations less than $2N_{f(e)}$) may have elapsed for the menhaden mtDNA lineages to evolve to a status of reciprocal monophyly between the two regions. Indeed, a phylogenetic interpretation of the mtDNA dendrogram in Fig. 3 suggests a paraphyletic situation (Neigel and Avise 1986) – some menhaden mtDNA lineages in the Atlantic are more closely related to some lineages in the Gulf than they are to others in the Atlantic.

However, the mtDNA data in menhaden cannot be interpreted solely from consideration of $N_{f(e)}$'s and a vicariant population history, for the following reason. If menhaden populations in the Atlantic and Gulf had indeed been separated for several hundred thousand years, the genetic differences between mtDNA genotypes shared by these regions (Fig. 3) should in all cases date to genic divergences *older* than the population separation. But several clusters of mtDNA genotypes shared by Atlantic and Gulf locales are very closely related, and in two cases, shared clones were identical at all 49 to 51 assayed restriction sites (o, cc and c, v in Fig. 3). Thus, while the extensive mtDNA polymorphism in menhaden may be attributable to large effective population sizes, the "paraphyletic" appearance of the menhaden mtDNA history is more plausibly attributable to recent gene flow between regions, rather than a retention of mtDNA variants from a polymorphic ancestral stock divided by a historical vicariant event.

In sturgeon, the mtDNA data appear most consistent with relatively small $N_{f(e)}$'s within Atlantic and Gulf populations, as well as recent contact between the two regions. Assuming the conventional mtDNA clock, the observed nucleotide diversities (Table 2) suggest mean times to common mtDNA ancestry within the Atlantic and Gulf of 85 000 and 500 yr, respectively. Since sturgeon exhibit a generation length of roughly 10 yr (Huff 1975), the times elapsed since random pairs of individuals within the Atlantic or Gulf last shared a common maternal ancestor may be only about 8 500 and 50 generations, respectively. These latter values also correspond to the respective estimates of $N_{f(e)}$ for the two regions. And these estimates of $N_{f(e)}$ may be generous, since they assume random mating among sturgeon in different drainages [any historical population subdivision among rivers would inhibit lineage extinction on a regional basis, and further increase the expected depths of the mtDNA lineage separations; particularly in our Atlantic collections, there is some preliminary evidence for mtDNA frequency shifts among rivers (Fig. 6), although samples sizes are too small for firm conclusions]. In any event, the small estimates of $N_{f(e)}$ for the sturgeon, particularly compared to those of the menhaden, appear qualitatively consistent with the probable relative abundances of these species today. Relationships between the $N_{f(e)}$'s estimated from the mtDNA data, and the present-day population sizes of the three taxa considered in this report, are summarized in Table 3.

Table 3. *Centropristis striata, Brevoortia tyrannus, B. patronus* and *Acipenser oxyrhynchus*. Comparisons of evolutionary effective size of female populations, $N_{f(e)}$ (estimated from mtDNA nucleotide diversities) with present-day female population size, N. (See "Discussion–Magnitudes and patterns of mtDNA divergence" for procedures). Present-day population size estimates are admittedly crude and impressionistic: rare, $N < 10^4$; common, $N \cong 10^6$ to 10^8; abundant, $N > 10^8$

Species and location	$N_{f(e)}$	N
Menhaden		
Gulf	250 000	abundant
Atlantic	800 000	abundant
Black sea bass		
Gulf	5 000	common
Atlantic	5 000	common
Sturgeon		
Gulf	50	rare
Atlantic	8 500	rare

In contrast to the menhaden, the shallow evolutionary depth of the mtDNA history in sturgeon precludes clear distinctions between alternative hypotheses for the sharing of genotypes between Atlantic and Gulf locales. Thus, the presence of the "a" mtDNA genotype in both the Atlantic and Gulf of Mexico drainages (Fig. 6) could be due to retention of the plesiomorphic condition from a near ancestor, and/or recent gene flow between the two coasts (either around south Florida, or conceivably via the Okefenokee Swamp along the Florida-Georgia boundary).

Management and conservation

Among the marine fishes considered in this report, only black sea bass exhibited a clear distinction in mtDNA phylogeny between Atlantic and Gulf coast populations. Thus, the available genetic evidence suggests a fairly long time of population separation, and supports the current recognition of the two distinct subspecies of black sea bass.

In menhaden and sturgeon, several mtDNA clones or clonal arrays shared by Atlantic and Gulf populations strongly suggests relatively recent genetic contact be-

tween these regions. Tagging data demonstrate that menhaden and juvenile sturgeon are capable of long-distance movement along coasts (Holland and Yelverton 1973, Nicholson 1978), while sea bass migrations appear largely confined to seasonal inshore-offshore movement (Musick and Mercer 1977). Thus, the contrast in phylogenetic pattern among these species may be attributable in part to differences in their dispersal characteristics. Among the 11 species of southeastern coastal vertebrates and invertebrates thus far genetically surveyed (see "Discussion – Zoogeographic background"), only menhaden, sturgeon, hardhead catfish (*Arius felis*), and gafftopsail catfish (*Bagre marinus*) have failed to exhibit clear disjunctions in phylogenetic history between the south Atlantic and the Gulf of Mexico. These four species are all strong and active swimmers as adults and, in each case, recent gene flow between Atlantic and Gulf populations may have blurred the evidence for any historical population disjunctions. On the other hand, in both the menhaden and sturgeon, significant differences in mtDNA genotype frequency between the Atlantic and Gulf coasts suggest that recent gene flow between these regions has been quite limited.

Black sea bass, menhaden, and sturgeon continue to support commercial fisheries, and management biologists must assess the impact of harvest on population maintenance. For example, if fish at any particular locale are overharvested, will the population be significantly replenished by recruitment and migration from other areas? This raises the issue of a distinction that should be drawn between populations in an evolutionary sense, and populations or stocks in a management sense.

Over the ecological timescales of a few years or decades relevant to harvesting strategies, it is probable that not only are Atlantic and Gulf populations largely distinct demographically, but that subpopulations within either region may also be demographically independent. For example, our limited samples of sturgeon showed preliminary evidence for genetic structuring among Atlantic drainages and, more to the point, sturgeon breeding colonies that were extirpated by overfishing a century ago have not yet been recolonized by fish from other drainages (Wooley and Crateau 1985). Since sturgeon are severely depleted by habitat destruction and overfishing throughout their range, it would seem prudent to afford strong protection measures for all remaining spawning locales.

Other kinds of management decisions may benefit from the proper recognition of population stocks in an evolutionary sense. For example, should overfished populations in one region be supplemented by man-directed transplantations of fishes from other areas? In the case of sturgeon, extirpated Gulf populations might wisely be reseeded from Atlantic populations without fear of mixing highly diverged stocks, since the Atlantic and Gulf populations have quite clearly been in contact in recent evolutionary time. In contrast, transplantations between Atlantic and Gulf coast populations of black sea bass would compromise the integrity of genetic differences that appear to have accumulated over many tens or hundreds of thousands of years.

Geographic populations of a species can be phylogenetically structured at many levels, ranging from short-term separations to long-term evolutionary disjunctions. Integration of information from molecular genetics and contemporary dispersal and life-history studies should reveal the kinds of timescales involved, and thereby provide constructive input for conservation and management decisions.

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