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Edited by **Darryl L. Felder**
and **David K. Camp**



Population Genetics and Biogeography of the Gulf of Mexico

Joseph E. Neigel

Marine biogeography and population genetics have undergone fundamental changes since the publication of “Bulletin 89.” In marine biogeography the most important change was the eventual acceptance of plate tectonics as a mechanism that shapes global biogeographic patterns. From this perspective, vicariance biogeography brought a rigorous phylogenetic approach to biogeographic analysis (Nelson and Platnick 1981), and *Marine Zoogeography* (Briggs 1974) synthesized what was then known about the distributions of marine faunas. In population genetics there were 2 major transformations. The first was brought about by the introduction of allozyme methods in the mid-1960s, which made it possible to survey Mendelian variation in virtually any species (Hubby and Lewontin 1966). This sudden influx of data revitalized the field and led to a greater emphasis on the genetics of natural populations (Lewontin 1974). The second and still ongoing transformation was a shift away from the classical perspective of allele frequencies toward the molecular perspective of variation in DNA sequences (Lewontin 1985). The DNA sequences were recognized as a richer source of information than allele frequencies and required new analytical approaches. The parallel rise of molecular perspectives in population genetics, systematics, physiology, and other fields engendered new areas of synthesis. A prime example is intraspecific phylogeography, which began with the application of cladistic principles from biogeography to the geographic distributions of mitochondrial DNA lineages within species (Avice, Reeb, and Saunders 1987). Phylogeography not only led to new insights in

biogeography and population genetics but also prepared a generation of evolutionary biologists to work on both systematic and population genetic questions.

Planktonic larval dispersal in marine species is certain to have important demographic and evolutionary consequences. However, as several authors have noted, there is much that we still do not know about dispersal distances, connectivity between populations, and the nature of barriers to gene flow in the marine realm (Neigel 1997, Grosberg and Cunningham 2000, Warner and Cowen 2002). Population genetic methods can be used to address these questions but the results are often frustratingly ambiguous. Most measures of dispersal based on population genetics are indirect, requiring a theoretical model to link observable distributions of genetic markers to parameters that represent gene flow (Slatkin 1985, 1987, Neigel 1997). The reliability of these measures is open to question because the distributions of genetic markers are also affected by forces other than gene flow, notably genetic drift, selection, and mutation. For marine species we typically know even less about these other forces than we do about dispersal. Fortunately, this conundrum appears to be at least partly solvable with new approaches that are just beginning to yield results (see for example Bilodeau, Felder, and Neigel 2005). If these approaches are successful, it is possible that much of the literature reviewed here could become outdated. Nevertheless, this is an opportune time to review what has been learned from surveys of genetic variation within species of the Gulf of Mexico (GMx). This body of work shows that the GMx is richer in

evolutionary diversity and endemism than has been generally appreciated. Also, some notable genetic phenomena have been found in the GMx, such as genetic breaks associated with the Floridian disjuncture of the Carolinian marine province. These important findings from the GMx figure prominently in the field of marine population genetics as a whole.

Surveys of Genetic Markers in the GMx

In the peer-reviewed literature there are about 100 published surveys of genetic markers in marine and estuarine species that occur in the GMx (see list of population genetic surveys), with some publications reporting surveys of multiple species. This total does not include surveys of morphological variation (the genetic basis of which is usually not determined) or studies of a primarily systematic focus that are based on small numbers of individuals from each species. (If any population genetic surveys were omitted from this review at the time of this writing, 2006, it was unintentional, and it would be appreciated if they were brought to the author's attention.) In the selection of taxa to survey there has been a strong bias in favor of those of commercial or recreational value. Indeed, some fishery species (e.g., *Sciaenops ocellatus*) have been surveyed repeatedly for a variety of genetic markers. Most surveys were intended primarily to detect regional patterns of differentiation such as would correspond to stocks that could be managed as units. However, despite this emphasis on large regional scales, many surveys were restricted to U.S. coastlines and often omitted substantial portions of a species range. A large proportion of the surveys included an explicit comparison between populations from the GMx and those from the NW Atlantic. I have included some discussion of genetic "breaks" found in these comparisons, even if their locations fall slightly outside the GMx (typically the Atlantic coast of Florida). This is because all of these findings have contributed to our growing understanding of the forces that have shaped the population genetics and biogeography of the GMx (Avisé 1992).

The selection of genetic markers for surveys of genetic variation in the GMx has paralleled the general trend in population genetics: the earliest studies used allozymes; later ones introduced restriction fragment length polymorphisms (RFLPs) of mitochondrial DNA (mtDNA), followed by mtDNA sequences, and most recently, microsatellites and nuclear DNA sequences. However, all of these types of genetic markers continue to be used, and it

has often been illuminating to compare results from different markers.

There have been enough surveys of genetic variation in GMx species to suggest the possibility of a detailed comparative analysis that might reveal hitherto unnoticed patterns and suggest novel hypotheses. However, meaningful comparisons among genetic surveys are limited by differences in methodology, including differences in type of genetic marker, sampled localities, and methods of data analysis. There are no common yardsticks of genetic variation or differentiation, even though the same statistics can be calculated from different data sets. For example, Wright's F_{ST} is often viewed as a common measure of genetic differentiation among populations. However, estimates of F_{ST} are strongly dependent on the type of genetic marker used and the scale at which populations are defined. Estimates of F_{ST} based on moderately polymorphic markers, such as allozymes, are generally much higher than estimates based on highly polymorphic markers such as microsatellites (Neigel 1997, Hedrick 1999, Neigel 2002). Populations are usually defined by arbitrary geographic boundaries, which might range in scale from a few hundred meters of shoreline to entire ocean basins. Measures of genetic differentiation at such different scales cannot be meaningfully compared. In theory it would be possible to compare genetic surveys on the basis of common demographic parameters, such as migration rates, that were estimated for comparable geographic units. However, this would require reanalysis of the raw genetic data from every survey, and raw data are often not provided in publications (Leberg and Neigel 1999).

Within the limitations set by differences in methodology, general inferences about gene flow among marine populations are usually based on how much of the observed variation in genetic markers is distributed among geographic samples (Grosberg and Cunningham 2000, Hellberg et al. 2002). Four levels of genetic differentiation are conventionally recognized: (1) fixed differences in allelic composition or reciprocal monophyly in gene genealogies; (2) moderate differences in allele frequencies or haplotypes; (3) slight but statistically significant differences in genetic markers; and (4) no significant differences. Fixed differences in allozyme alleles between populations or reciprocal monophyly of DNA sequences are considered evidence of a complete barrier to gene flow that has persisted for at least thousands of years. Whether or not such genetically isolated populations are viewed as separate species can be influenced by previous taxonomic work. For example, mitochondrial DNA and allozyme

frequency differences between the nominally conspecific northeastern GMx and northwestern GMx populations of the thalassinidean *Callichirus islagrande* are greater than those between the brachyuran species *Menippe adina* and *M. mercenaria*, although only the latter pair exhibits obvious phenotypic differences and formal taxonomic recognition (Bert 1986, Williams and Felder 1986, Staton and Felder 1995, Schneider-Broussard et al. 1998, Bilodeau, Felder, and Neigel 2005).

Moderate differences in the frequencies of genetic markers between populations are interpreted as evidence of either a partial barrier to gene flow or an inconstant barrier that may have recently formed or broken down; although recent could mean many thousands of years. Classical methods of data analysis cannot distinguish these alternatives, although newer methods potentially can (Knowles and Maddison 2002). Differences in the frequencies of genetic markers that are slight but statistically significant are the most difficult to interpret. Much depends on assumptions about the strength of genetic drift, which has been a subject of broad speculation for marine populations. If it is assumed that genetic drift is weak because populations are very large (often the case for marine species), then even a slight amount of genetic differentiation implies that gene flow must also be very weak not to have completely overcome genetic drift. This leads to the interpretation that there is very little migration among the populations, because even low rates of gene flow should be able to abolish any detectable levels of differentiation. However, it is also conceivable that genetic drift is in fact very strong in marine populations because entire cohorts of recruits could be spawned by only a few individuals, a scenario known as “sweepstakes reproduction” (Hedgecock 1994). In this view, low levels of genetic differentiation imply that gene flow must be very strong to overcome the strong genetic drift associated with sweepstakes reproduction, and this leads to the interpretation that gene flow (and hence migration) is very high among populations. An additional factor that is probably not considered often enough is the role of natural selection. Selection can either increase or decrease differentiation among populations to any extent and at any scale. This lack of a specific prediction has made it difficult to test hypotheses based on selection and has caused some marine geneticists to avoid giving it much consideration (Hellberg et al. 2002). From this discussion it should be evident that there is a broad range of plausible interpretations for slight genetic differentiation among marine populations.

Complete absence of genetic differentiation implies

extensive gene flow, or panmixia, among populations. However, the difference between finding slight differentiation rather than no differentiation is often simply a matter of statistical power. For example, statistically significant differences in genetic markers among populations of *Sciaenops ocellatus* were found only when large sample sizes and sufficiently polymorphic genetic markers were surveyed (see list). Because many surveys have been limited in these respects it would be difficult to counter the proposition that with large enough samples and suitable genetic markers statistically significant geographic variation could be detected in any marine species. Thus, the problem of interpreting slight genetic differentiation is probably also relevant to cases in which no differentiation has been detected. In the list, 3 levels of genetic differentiation are distinguished: no statistically significant differentiation, differences in frequencies of genetic markers, and fixed differences at some loci or reciprocal monophyly for gene genealogies. No distinction is made between slight and moderate differences in the frequencies of genetic markers. This represents a compromise between the provision of what would be generally accepted as valid and useful characterization of levels of genetic differentiation and the ambiguities, discussed above, inherent in such characterizations.

Biogeographic Context

The regional patterns of genetic variation that are detected in studies of GMx species are usually interpreted in terms of historical biogeography. There is an underlying assumption that larger-scale patterns develop over longer periods of time and thus reflect deeper historical processes. This assumption is supported by both population genetics theory, which predicts that genetic drift takes place more slowly in larger units of population structure (Wright 1951), and by empirical evidence such as hierarchically nested phylogeographic patterns (Neigel, Ball, and Avise 1991).

Biogeographically, the GMx is part of a larger system that includes the western Atlantic and Caribbean. The northern GMx has been considered part of the warm-temperate Carolinian Marine Province, which also includes the northwestern Atlantic coast from Cape Hatteras, North Carolina, to Cape Canaveral, Florida. In contrast, the southern GMx is tropical, and along with the Caribbean is considered part of the Tropical Northwestern Atlantic Province. The approximate boundaries between warm-temperate and tropical conditions in

the GMx are Cape Rojo, Mexico, to the west and Cape Romano, Florida, to the east (Briggs 1974). The Carolinian Province is interrupted by the portion of the Florida peninsula that extends into tropical waters, and the ranges of some Carolinian species are broken at this disjunction while other, more eurythermic species continue through it. Another recognized biogeographic division separates the northeastern GMx from the northwestern GMx, with the boundary placed at either the mouth of the Mississippi River or at Mobile Bay, Alabama (Briggs 1974, McClure and McEachran 1992). Geologically, sediments in the northwestern GMx are predominately terrigenous, whereas those in the northeastern GMx are carbonate, with corresponding differences in the distribution and types of benthic habitats and communities. This longitudinal division is reinforced by the outflows of the Mississippi and Atchafalaya rivers. Low salinity water loaded with sediments and nutrients are carried by surface currents to the west during winter and to the east during summer (Ohlmann and Niiler 2005). These river outflows have dramatic effects on coastal habitats and disrupt the ranges of some coastal species.

The GMx has had a relatively long and tectonically stable history since its formation in the late Jurassic, approximately 150 mybp. Geological, climatological, and oceanographical changes that occurred during the Neogene Period (23 my to present) are potential influences on the generation of species diversity and the shaping of genetic variation within species of the GMx. A singular tectonic change that occurred during this period was the emergence of the Central American Isthmus in the Pliocene, which closed the Tropical American Seaway that connected the Pacific Ocean and the Caribbean Sea. The closure severed biotic connections between the 2 basins and profoundly altered patterns of oceanic circulation in the Caribbean and GMx. Throughout the Neogene there have been repeated cycles of glaciation, which altered sea levels and climates and induced shifts in ranges that are likely to have both fragmented species and brought previously isolated fragments back into contact. It can be assumed that practically all GMx species have experienced these effects because the most recent glacial period ended just 12,000 years ago. Indeed, because there have been as many as 15 glacial cycles during the Pleistocene, it is likely that their effects on the biogeography of contemporary species are compounded in ways that may be difficult to unravel. Three vicariant mechanisms have received the most attention: (1) the emergence of the Central American Isthmus; (2) the opening and closing of the Suwannee

straits across Florida; and (3) changes associated with glacial cycles. These are each considered in detail below.

The Emergence of the Central American Isthmus

Paleontological records indicate that the emergence of the Central American Isthmus began to alter patterns of surface circulation, carbonate deposition, and evolution in the Caribbean Sea by the late Miocene (Collins, Budd, and Coates 1996). Complete closure of the Tropical American Seaway between the Pacific Ocean and the Caribbean Sea occurred in the mid-Pliocene, about 3.5 million years before the present (Keigwin 1982, Coates et al. 1992). An important consequence was the redirection of the North Equatorial Current northward into the Gulf Stream, through the Yucatán Straits and into the GMx. The closure of the Tropical American Seaway was a vicariant event that isolated populations of marine species on either side of the Isthmus of Panama. Sister species created by this event, referred to as geminate species, are often used as standards for the estimation of the rate of mitochondrial DNA sequence evolution. These estimates, or “molecular clock calibrations,” can be used to date other cladogenic events from mtDNA sequence data.

Suwannee Straits. In the mid-Miocene (Haq, Hardenbol, and Vail 1987) and possibly the late Pliocene (Ward and Strickland 1986), high sea levels created a deepwater channel, the Okeefenokee Trough, which separated Florida from the mainland of North America. The Suwannee straits flowed through this channel from the GMx to the Atlantic (Olsen 1968, Brooks 1973, Riggs 1984). It has been hypothesized that the Suwannee straits allowed stone crabs (*Menippe adina*) from the GMx to migrate through the Okeefenokee Trough and hybridize with crabs of their sister species, *M. mercenaria*, on the Atlantic coast (Bert and Harrison 1988). The existence of a relict hybrid zone would explain why crabs from the coast of Georgia have some of the phenotypic characteristics and allozyme allele frequencies that are otherwise characteristic of *M. adina* from the GMx (Bert 1986). As a biogeographic scenario, introgression through the Okeefenokee Trough requires that the 2 species of *Menippe* diverged prior to the opening of the Suwannee straits and that the hybrid population on the coast of Georgia has been isolated from GMx *M. adina* since the closure of the straits. These events would have occurred at least several million years ago, a time scale that is amenable to testing by molecular clock estimates of DNA sequence divergence between the 2 nominal species and between *M. adina* in

the GMx and “*adina*-like” crabs from the putative relict hybrid zone of the coast of Georgia. Based on an analysis of mitochondrial 16S ribosomal DNA sequences, the estimated divergence times for both comparisons were much less than predicted by the Suwannee straits hypothesis. Indeed, *M. adina* and *M. mercenaria* appear to have separated very recently, so much so that they share some identical 16S haplotypes (as well as multiple nuclear DNA markers; Schneider-Broussard et al. 1998).

The example of the stone crabs illustrates how a correspondence between a genetic pattern and the location of a known vicariant event can be misleading. For highly vagile marine species, we should not expect to see the geographic imprints of remote events to be preserved in their genetic structures unless they are maintained by present day conditions. For example, if a genetic break is found at the mouth of the Mississippi River, we should not assume that the river created the break. An alternative possibility is that 2 races of the species were formed elsewhere in the past and subsequently shifted to their present day ranges. The river mouth could now be acting as a barrier to dispersal or simply mark the point at which a critical change in environmental conditions occurs. The dating of cladogenic events by molecular clock estimates provides one means to test hypotheses about cause and effect relationships between past geological events and present day genetic structure.

The Florida Vicariant Zone

The pattern of genetic breaks associated with the interruption of the Carolinian Province in southern Florida is one of the best-studied cases in the field of phylogeography (Avice 1992, 2000). Pleistocene cycles of glaciation could have caused repeated episodes of contact and separation between GMx and Atlantic populations by at least 2 mechanisms (Avice 1992). First, glacial cooling would eliminate the tropical zone in southern Florida and bring previously allopatric populations from the 2 sides of the disjunction into contact (Hedgepeth 1954). The second mechanism would have the opposite effect of increasing isolation of GMx and Atlantic populations of estuarine species during glaciations. Drops in sea level would expose large areas of the Florida and Yucatán peninsulas, and along with decreased rainfall, could have eliminated estuarine habitats that previously bridged the northern GMx and Atlantic. These climate-induced events could have occurred as recently as the most recent glaciation only 12,000 years ago, or during any of the many other glaciations that occurred during the Pleistocene, Pliocene, or Miocene.

Genetic differentiation associated with the Florida disjuncture of the Carolinian Province has been found for many species (see list). The amount of differentiation varies from none to fixed allelic differences and/or reciprocal monophyly. Surprisingly, differentiation is found not only in species with ranges that are broken by the disjuncture but also in species with apparently continuous ranges (Avice 1992, Cunningham and Collins 1998). Although in some comparisons the extent of genetic differentiation appears to be inversely related to dispersal ability, this relationship fails to hold when more than a few species are considered (Cunningham and Collins 1998, Gold and Richardson 1998a). Molecular clock estimates indicate that genetic breaks associated with the Carolinian disjuncture do not date to any single event, which is to be expected given the cyclical nature of glacial effects. This has led to the characterization of these congruent breaks as a case of “pseudoconvergence” (P. Cunningham and Collins 1994, C. Cunningham and Collins 1998).

A full explanation of any case of genetic divergence between GMx and Atlantic populations must not only account for its origins, but also its maintenance under present conditions. High rates of gene flow for even a few generations can eliminate genetic differentiation between populations. It thus seems necessary that either oceanographic barriers to dispersal or selection against migrants (or hybrids) must be acting to maintain geographic variation. However, to determine which of these mechanisms predominates has been very difficult. For example, within the U.S. GMx the American oyster, *Crassostrea virginica*, is divided into 2 distinct genetic units that are reciprocally monophyletic for mtDNA (Reeb and Avice 1990) and have fixed allelic differences for some nuclear DNA markers (Karl and Avice 1992, Hare and Avice 1998). These genetic units meet at Cape Canaveral, Florida, where they form a narrow hybrid zone. Detailed analysis of genetic markers within this cline could not determine whether it was maintained primarily by selection or by restricted gene flow (Hare and Avice 1996).

A recent study demonstrates the importance of considering the Carolinian disjuncture in a regional context that includes the tropical GMx and Caribbean. A survey of genetic markers in the *Brachidontes exustus* (scorched mussel) species complex throughout the GMx and Caribbean revealed that the genetic break associated with the Carolinian disjuncture is just one of many regional disjunctions, and that northwestern Atlantic populations are more closely related to some Caribbean populations than to Carolinian populations in the GMx (Lee and Ó Foighil

2005). Their findings led the authors of this study to suggest that while the genetic units were created by past cladogenic events, their present locations and maintenance are controlled by postrecruitment selection rather than oceanographic barriers to larval dispersal.

For some species, genetic differentiation has been found within the GMx. Shifts in the frequencies of genetic markers have been found to coincide with the mouth of the Mississippi River; the Chenier Plains off the coast Louisiana; Laguna Madre, Texas; and with single, anomalous populations (see list). Temporal variation in allele frequencies has also been observed (e.g., McMillen-Jackson, Bert, and Steele 1994) and in one widely cited case greatly exceeded the magnitude of geographic variation in allele frequencies (Kordos and Burton 1993). These intriguing phenomena suggest that gene flow within the GMx is not always strong enough to overcome both genetic drift and natural selection. Limited gene flow is also suggested by a study that found significant differentiation among microsatellite allele frequencies in the ghost shrimp *Callichirus islagrande* among locations on a geographic scale of just tens of kilometers (Bilodeau, Felder, and Neigel 2005).

In conclusion, genetic surveys of the species of the GMx have revealed patterns of geographic differentiation that are not fully understood but seem to suggest the action of several factors that include past isolation, barriers to dispersal, and natural selection. The very existence of these patterns could be considered remarkable because of the potential for planktonic larval dispersal to affect high levels of gene flow. The challenge now is to determine the relative importance and role of each of the forces that shape patterns of geographic differentiation in the GMx and to apply this new understanding to basic questions about the evolution of marine species as well as to fisheries management and the conservation of biodiversity.

Abbreviations

Abbreviations used in column headers of the list of population genetic surveys are as follows: Allo = number of polymorphic allozyme loci; Caribb = Caribbean; GMx/Atl = between Gulf of Mexico and Atlantic; w/GMx = among populations within Gulf of Mexico; Msat = microsatellite; mtDNA = mitochondrial DNA; nucDNA = nuclear DNA; NW Atl = northwest Atlantic; Other = other genetic markers; Ref = reference. Abbreviations used in columns are as follows: AI = actin gene intron; ANON = anonymous locus; BIN = bindin gene; CI = calmodulin intron; COI = cytochrome oxidase subunit I gene; CR =

control region; HC = hemocyanin protein polymorphism; ITS = ribosomal internal transcribed spacer; LDH = lactate dehydrogenase; ND4 = mitochondrial NADH dehydrogenase subunit 4; PCR-RFLP = restriction fragment polymorphism within DNA amplified by the polymerase chain reaction; rbcl = ribulose-biphosphate carboxylase; RFLP = restriction fragment polymorphism; SEQ = DNA sequence; Y = yes; N = no; NA = not available; 0 = no statistically significant difference; 1 = difference in frequencies of markers; 2 = fixed allelic differences or reciprocal monophyly of sequences; 16S = large subunit ribosomal RNA gene; 28S = 28S ribosomal RNA gene. Numbers in "Markers" columns denote number of marker loci. Italic numbers refer to numbered references; superscripts refer to endnotes at end of table.

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References

1. Adams, L. D., and P. E. Rosel. 2006. Population differentiation of the Atlantic spotted dolphin (*Stenella frontalis*) in the western North Atlantic, including the Gulf of Mexico. *Marine Biology* 148: 671–681.
2. Avise, J. C. 1992. Molecular population structure and the biogeographic history of a regional fauna: a case-history with lessons for conservation biology. *Oikos* 63: 62–76.
3. Avise, J. C. 2000. *Phylogeography: The History and Formation of Species*. Harvard University Press, Cambridge, Massachusetts. 464 pp.
4. Avise, J. C., C. A. Reeb, and N. C. Saunders. 1987. Geographic population structure and species differences in mitochondrial DNA of mouthbrooding marine catfishes (Ariidae) and demersal spawning toadfishes (Batrachoididae). *Evolution* 41: 991–1002.
5. Bagley, M. J., D. G. Lindquist, and J. B. Geller. 1999. Microsatellite variation, effective population size, and population genetic structure of vermilion snapper, *Rhomboplites aurorubens*, off the southeastern USA. *Marine Biology* 134: 609–620.
6. Ball, A. O., and R. W. Chapman. 2003. Population genetic analysis of white shrimp, *Litopenaeus setiferus*, using microsatellite genetic markers. *Molecular Ecology* 12: 2319–2330.
7. Bert, T. M. 1986. Speciation in western Atlantic stone crabs (Genus *Menippe*): the role of geological processes

- and climatic events in the formation and distribution of species. *Marine Biology* 93: 157–170.
8. Bert, T. M., and R. G. Harrison. 1988. Hybridization in western Atlantic stone crabs (genus *Menippe*): evolutionary history and ecological context influence species interactions. *Evolution* 42: 528–544.
 9. Bilodeau, A. L., D. L. Felder, and J. E. Neigel. 2005. Population structure at two geographic scales in the burrowing crustacean *Callichirus islagrande* (Decapoda, Thalassinidea): historical and contemporary barriers to planktonic dispersal. *Evolution* 59: 2125–2138.
 10. Blandon, L. R., R. Ward, T. L. King, W. J. Karel, and J. P. Monaghan. 2001. Preliminary genetic population structure of southern flounder, *Paralichthys lethostigma*, along the Atlantic Coast and Gulf of Mexico. *Fishery Bulletin (U.S.)* 99: 671–678.
 11. Bohlmeier, D. A., and J. R. Gold. 1991. Genetic studies in marine fishes. 2. A protein electrophoretic analysis of population structure in the Red Drum *Sciaenops ocellatus*. *Marine Biology* 108: 197–206.
 12. Bowen, B. W., and J. C. Avise. 1990. Genetic structure of Atlantic and Gulf of Mexico populations of Sea Bass, Menhaden, and Sturgeon: influence of zoogeographic factors and life-history patterns. *Marine Biology* 107: 371–381.
 13. Brazeau, D. A., P. W. Sammarco, and D. F. Gleason. 2005. A multi-locus genetic assignment technique to assess sources of *Agaricia agaricites* larvae on coral reefs. *Marine Biology* 147: 1141–1148.
 14. Briggs, J. C. 1974. *Marine Zoogeography*. McGraw Hill, New York. 475 pp.
 15. Brooks, H. K. 1973. *Geological oceanography*. Pp. IIE1–IIE49 in J. I. Jones, R. E. Ring, M. O. Rinkel, and R. E. Smith, eds. *A Summary of Knowledge of Eastern Gulf of Mexico*. State University System of Florida Institute of Oceanography, St. Petersburg, Florida.
 16. Broughton, R. E., L. B. Stewart, and J. R. Gold. 2002. Microsatellite variation suggests substantial gene flow between king mackerel (*Scomberomorus cavalla*) in the western Atlantic Ocean and Gulf of Mexico. *Fisheries Research* 54: 305–316.
 17. Buonaccorsi, V. P., E. Starkey, and J. E. Graves. 2001. Mitochondrial and nuclear DNA analysis of population subdivision among young-of-the-year Spanish mackerel (*Scomberomorus maculatus*) from the western Atlantic and Gulf of Mexico. *Marine Biology* 138: 37–45.
 18. Buroker, N. E. 1983. Population genetics of the American Oyster *Crassostrea virginica* along the Atlantic coast and the Gulf of Mexico. *Marine Biology* 75: 99–112.
 19. Chapman, R. W., A. O. Ball, and L. R. Mash. 2002. Spatial homogeneity and temporal heterogeneity of red drum (*Sciaenops ocellatus*) microsatellites: effective population sizes and management implications. *Marine Biotechnology* 4: 589–603.
 20. Coates, A. G., J. B. C. Jackson, L. S. Collins, T. M. Cronin, H. J. Dowsett, L. M. Bybell, P. Jung, and J. A. Obando. 1992. Closure of the Isthmus of Panama: the near-shore marine record of Costa Rica and western Panama. *Geological Society of America Bulletin* 104: 814–828.
 21. Collins, L. S., A. F. Budd, and A. G. Coates. 1996. Earliest evolution associated with closure of the Tropical American Seaway. *Proceedings of the National Academy of Sciences of the United States of America* 93: 6069–6072.
 22. Cunningham, C. W., and T. M. Collins. 1998. Beyond area relationships: extinction and recolonization in molecular marine biogeography. Pp. 297–321 in R. DeSalle and B. Schierwater, eds. *Molecular Approaches to Ecology and Evolution*. Birkhauser Verlag, Basel.
 23. Cunningham, P., and T. M. Collins. 1994. Developing model systems for molecular biogeography: vicariance and interchange in marine invertebrates. Pp. 405–433 in B. Schierwater, B. Streit, G. P. Wagner, and R. DeSalle, eds. *Molecular Ecology and Evolution: Approaches and Applications*. Birkhauser Verlag, Basel.
 24. Diaz, M., G. M. Leclerc, and B. Ely. 1997. Nuclear DNA markers reveal low levels of genetic divergence among Atlantic and Gulf of Mexico populations of striped bass. *Transactions of the American Fisheries Society* 126: 163–165.
 25. Dowling, T. E., and W. M. Brown. 1993. Population structure of the bottlenose dolphin (*Tursiops truncatus*) as determined by restriction endonuclease analysis of mitochondrial DNA. *Marine Mammal Science* 9: 138–155.
 26. Felder, D. L., and J. L. Staton. 1994. Genetic differentiation in trans-Floridian species complexes of *Sesarma* and *Uca* (Decapoda, Brachyura). *Journal of Crustacean Biology* 14: 191–209.
 27. Foighil, D. Ó, T. J. Hilbish, and R. M. Showman. 1996. Mitochondrial gene variation in *Mercenaria* clam sibling species reveals a relict secondary contact zone in the western Gulf of Mexico. *Marine Biology* 126: 675–683.
 28. Garber, A. F., M. D. Tringali, and J. S. Franks. 2005. Population genetic and phylogeographic structure of wahoo, *Acanthocybium solandri*, from the western central Atlantic and central Pacific Oceans. *Marine Biology* 147: 205–214.

29. Garber, A. F., M. D. Tringali, and K. C. Stuck. 2004. Population structure and variation in red snapper (*Lutjanus campechanus*) from the Gulf of Mexico and Atlantic coast of Florida as determined from mitochondrial DNA control region sequence. *Marine Biotechnology* 6: 175–185.
30. Gold, J. R., and C. P. Burrige. 2004. Historical population dynamics of red snapper (*Lutjanus campechanus*) in the northern Gulf of Mexico. *Texas Journal of Science* 56: 157–170.
31. Gold, J. R., T. L. King, L. R. Richardson, D. A. Bohlmeier, and G. C. Matlock. 1994a. Allozyme differentiation within and between Red Drum (*Sciaenops ocellatus*) from the Gulf of Mexico and Atlantic Ocean. *Journal of Fish Biology* 44: 567–590.
32. Gold, J. R., A. Y. Kristmundsdottir, and L. R. Richardson. 1997a. Mitochondrial DNA variation in king mackerel (*Scomberomorus cavalla*) from the western Atlantic Ocean and Gulf of Mexico. *Marine Biology* 129: 221–232.
33. Gold, J. R., E. Pak, and D. A. DeVries. 2002. Population structure of king mackerel (*Scomberomorus cavalla*) around peninsular Florida, as revealed by microsatellite DNA. *Fishery Bulletin (U.S.)* 100: 491–509.
34. Gold, J. R., E. Pak, and L. R. Richardson. 2001. Microsatellite variation among red snapper (*Lutjanus campechanus*) from the Gulf of Mexico. *Marine Biotechnology* 3: 293–304.
35. Gold, J. R., and L. R. Richardson. 1991. Genetic studies in marine fishes. IV. An analysis of population structure in the Red Drum (*Sciaenops ocellatus*) using mitochondrial DNA. *Fisheries Research* 12: 213–241.
36. Gold, J. R., and L. R. Richardson. 1994. Mitochondrial DNA variation among red fishes from the Gulf of Mexico. *Fisheries Research* 20: 137–150.
37. Gold, J. R., and L. R. Richardson. 1998a. Mitochondrial DNA diversification and population structure in fishes from the Gulf of Mexico and western Atlantic. *Journal of Heredity* 89: 404–414.
38. Gold, J. R., and L. R. Richardson. 1998b. Population genetic structure in greater amberjack, *Seriola dumerili*, from the Gulf of Mexico and western Atlantic Ocean. *Fishery Bulletin (U.S.)* 96: 767–778.
39. Gold, J. R., L. R. Richardson, C. Furman, and T. L. King. 1993. Mitochondrial DNA differentiation and population structure in Red Drum (*Sciaenops ocellatus*) from the Gulf of Mexico and Atlantic Ocean. *Marine Biology* 116: 175–185.
40. Gold, J. R., L. R. Richardson, C. Furman, and F. Sun. 1994b. Mitochondrial DNA diversity and population structure in marine fish species from the Gulf of Mexico. *Canadian Journal of Fisheries and Aquatic Sciences* 51: 205–214.
41. Gold, J. R., L. R. Richardson, and T. F. Turner. 1999. Temporal stability and spatial divergence of mitochondrial DNA haplotype frequencies in red drum (*Sciaenops ocellatus*) from coastal regions of the western Atlantic Ocean and Gulf of Mexico. *Marine Biology* 133: 593–602.
42. Gold, J. R., F. Sun, and L. R. Richardson. 1997b. Population structure of red snapper from the Gulf of Mexico as inferred from analysis of mitochondrial DNA. *Transactions of the American Fisheries Society* 126: 386–396.
43. Gold, J. R., and T. F. Turner. 2002. Population structure of red drum (*Sciaenops ocellatus*) in the northern Gulf of Mexico, as inferred from variation in nuclear-encoded microsatellites. *Marine Biology* 140: 249–265.
44. Grosberg, R., and C. W. Cunningham. 2000. Genetic structure in the sea: from populations to communities. Pp. 61–84 in M. D. Bertness, S. D. Gaines, and M. E. Hay, eds. *Marine Community Ecology*. Sinauer Associates, Sunderland, Mass.
45. Groue, K. J., and L. J. Lester. 1982. A morphological and genetic analysis of geographic variation among oysters in the Gulf of Mexico. *Veliger* 24: 331–335.
46. Gurgel, C. F. D., S. Fredericq, and J. N. Norris. 2004. Phylogeography of *Gracilaria tikvahiae* (Gracilariaceae, Rhodophyta): a study of genetic discontinuity in a continuously distributed species based on molecular evidence. *Journal of Phycology* 40: 748–758.
47. Haq, B. U., J. Hardenbol, and P. R. Vail. 1987. Chronology of fluctuating sea levels since the Triassic. *Science* 235: 1156–1167.
48. Hare, M. P., and J. C. Avise. 1996. Molecular genetic analysis of a stepped multilocus cline in the American oyster (*Crassostrea virginica*). *Evolution* 50: 2305–2315.
49. Hare, M. P., and J. C. Avise. 1998. Population structure in the American oyster as inferred by nuclear gene genealogies. *Molecular Biology and Evolution* 15: 119–128.
50. Hare, M. P., and J. R. Weinberg. 2005. Phylogeography of surfclams, *Spisula solidissima*, in the western North Atlantic based on mitochondrial and nuclear DNA sequences. *Marine Biology* 146: 707–716.
51. Hedgecock, D. 1994. Does variance in reproductive success limit effective population sizes of marine organisms? Pp. 199–207 in T. Kawasaki, S. Tanaka, Y. Toba, and A. Taniguchi, eds. *Long-Term Variability of Pelagic Fish Populations and Their Environment*. Pergamon Press, Oxford, United Kingdom.
52. Hedgpeth, J. W. 1954. *An introduction to the zoogeogra-*

- phy of the northern Gulf of Mexico with reference to the invertebrate fauna. *Publications of the Institute for Marine Science, University of Texas* 3: 111–211.
53. Hedrick, P. W. 1999. Perspective: highly variable loci and their interpretation in evolution and conservation. *Evolution* 53: 313–318.
 54. Heist, E. J., and J. R. Gold. 1999. Genetic identification of sharks in the US Atlantic large coastal shark fishery. *Fishery Bulletin (U.S.)* 97: 53–61.
 55. Heist, E. J., and J. R. Gold. 2000. DNA microsatellite loci and genetic structure of red snapper in the Gulf of Mexico. *Transactions of the American Fisheries Society* 129: 469–475.
 56. Heist, E. J., J. E. Graves, and J. A. Musick. 1995. Population genetics of the sandbar shark (*Carcharhinus plumbeus*) in the Gulf of Mexico and Mid-Atlantic Bight. *Copeia*: 555–562.
 57. Heist, E. J., J. A. Musick, and J. E. Graves. 1996. Mitochondrial DNA diversity and divergence among sharpnose sharks, *Rhizoprionodon terraenovae*, from the Gulf of Mexico and Mid-Atlantic Bight. *Fishery Bulletin (U.S.)* 94: 664–668.
 58. Hellberg, M. E., R. S. Burton, J. E. Neigel, and S. R. Palumbi. 2002. Genetic assessment of connectivity among marine populations. *Bulletin of Marine Science* 70(1, Supplement): 273–290.
 59. Herke, S. W., and D. W. Foltz. 2002. Phylogeography of two squid (*Loligo pealei* and *L. plei*) in the Gulf of Mexico and northwestern Atlantic Ocean. *Marine Biology* 140: 103–115.
 60. Hoover, C. A., and P. M. Gaffney. 2005. Geographic variation in nuclear genes of the eastern oyster, *Crassostrea virginica* Gmelin. *Journal of Shellfish Research* 24: 103–112.
 61. Hubby, J. L., and R. C. Lewontin. 1966. A molecular approach to the study of genic heterozygosity in natural populations. I. The number of alleles at different loci in *Drosophila pseudoobscura*. *Genetics* 54: 577–594.
 62. Karl, S. A., and J. C. Avise. 1992. Balancing selection at allozyme loci in oysters: implications from nuclear RFLPs. *Science* 256: 100–102.
 63. Keeney, D. B., M. Heupel, R. E. Hueter, and E. J. Heist. 2003. Genetic heterogeneity among blacktip shark, *Carcharhinus limbatus*, continental nurseries along the US Atlantic and Gulf of Mexico. *Marine Biology* 143: 1039–1046.
 64. Keeney, D. B., M. R. Heupel, R. E. Hueter, and E. J. Heist. 2005. Microsatellite and mitochondrial DNA analyses of the genetic structure of blacktip shark (*Carcharhinus limbatus*) nurseries in the northwestern Atlantic, Gulf of Mexico, and Caribbean Sea. *Molecular Ecology* 14: 1911–1923.
 65. Keigwin, L. 1982. Isotopic paleoceanography of the Caribbean and East Pacific: role of Panama uplift in late Neogene time. *Science* 217: 350–352.
 66. King, T. L., R. Ward, and E. G. Zimmerman. 1994. Population structure of eastern oysters (*Crassostrea virginica*) inhabiting the Laguna Madre, Texas, and adjacent bay systems. *Canadian Journal of Fisheries and Aquatic Sciences* 51: 215–222.
 67. Knowles, L. L., and W. P. Maddison. 2002. Statistical phylogeography. *Molecular Ecology* 11: 2623–2635.
 68. Kordos, L. M., and R. S. Burton. 1993. Genetic differentiation of Texas Gulf Coast populations of the blue crab *Callinectes sapidus*. *Marine Biology* 117: 227–233.
 69. Lankford, T. E., T. E. Targett, and P. M. Gaffney. 1999. Mitochondrial DNA analysis of population structure in the Atlantic croaker, *Micropogonias undulatus* (Perciformes: Sciaenidae). *Fishery Bulletin (U.S.)* 97: 884–890.
 70. Leberg, P. L., and J. E. Neigel. 1999. Enhancing the retrievability of population genetic survey data? An assessment of animal mitochondrial DNA studies. *Evolution* 53: 1961–1965.
 71. Lee, T., and D. Ó Foighil. 2004. Hidden Floridian biodiversity: mitochondrial and nuclear gene trees reveal four cryptic species within the scorched mussel, *Brachidontes exustus*, species complex. *Molecular Ecology* 13: 3527–3542.
 72. Lee, T., and D. Ó Foighil. 2005. Placing the Floridian marine genetic disjunction into a regional evolutionary context using the scorched mussel, *Brachidontes exustus*, species complex. *Evolution* 59: 2139–2158.
 73. Lewontin, R. C. 1974. *The Genetic Basis of Evolutionary Change*. Columbia University Press, New York. 346 pp.
 74. Lewontin, R. C. 1985. Population genetics. Pp. 3–18 in P. J. Greenwood, P. H. Harvey, and M. Slatkin, eds. *Evolution: Essays in Honour of John Maynard Smith*. Cambridge University Press, Cambridge, United Kingdom.
 75. Mangum, C. P., and A. L. McKenney. 1996. Subunit composition of the crustacean hemocyanins: divergence in incipient speciation. *Biological Bulletin* 191: 33–41.
 76. McClure, M. R., and J. D. McEachran. 1992. Hybridization between *Prionotus alatus* and *P. paralatus* in the northern Gulf of Mexico (Pisces, Triglidae). *Copeia*: 1039–1046.
 77. McCommas, S. A. 1982. Biochemical genetics of the sea

- anemone *Bunodosoma cavernata* and the zoogeography of the Gulf of Mexico. *Marine Biology* 68: 169–173.
78. McMillen-Jackson, A. L., and T. M. Bert. 2003. Disparate patterns of population genetic structure and population history in two sympatric penaeid shrimp species (*Farfantepenaeus aztecus* and *Litopenaeus setiferus*) in the eastern United States. *Molecular Ecology* 12: 2895–2905.
 79. McMillen-Jackson, A. L., and T. M. Bert. 2004. Genetic diversity in the mtDNA control region and population structure in the pink shrimp *Farfantepenaeus duorarum*. *Journal of Crustacean Biology* 24: 101–109.
 80. McMillen-Jackson, A. L., T. M. Bert, and P. Steele. 1994. Population genetics of the blue crab *Callinectes sapidus*: modest population structuring in a background of high gene flow. *Marine Biology* 118: 53–65.
 81. Neigel, J. E. 1997. A comparison of alternative strategies for estimating gene flow from genetic markers. *Annual Review of Ecology and Systematics* 28: 105–128.
 82. Neigel, J. E. 2002. Is F_{ST} Obsolete? *Conservation Genetics* 3: 167–173.
 83. Neigel, J. E., R. M. Ball, and J. C. Avise. 1991. Estimation of single generation migration distances from geographic variation in animal mitochondrial DNA. *Evolution* 45: 423–432.
 84. Nelson, G., and N. I. Platnick. 1981. *Systematics and Biogeography: Cladistics and Vicariance*. Columbia University Press, New York. 567 pp.
 85. Ohlmann, J. C., and P. P. Niiler. 2005. Circulation over the continental shelf in the northern Gulf of Mexico. *Progress in Oceanography* 64: 45–81.
 86. Olsen, S. J. 1968. Miocene vertebrates and north Florida shorelines. *Palaeogeography, Palaeoclimatology and Palaeoecology* 5: 127–143.
 87. Pruett, C., E. Saillant, and J. Gold. 2005. Historical population demography of red snapper (*Lutjanus campechanus*) from the northern Gulf of Mexico based on analysis of sequences of mitochondrial DNA. *Marine Biology* 147: 593–602.
 88. Quattro, J. M., D. S. Stoner, W. B. Driggers, C. A. Anderson, K. A. Priede, E. C. Hoppmann, N. H. Campbell, K. M. Duncan, and J. M. Grady. 2006. Genetic evidence of cryptic speciation within hammerhead sharks (Genus *Sphyrna*). *Marine Biology* 148: 1143–1155.
 89. Reeb, C. A., and J. C. Avise. 1990. A genetic discontinuity in a continuously distributed species: mitochondrial DNA in the American oyster, *Crassostrea virginica*. *Genetics* 124: 397–406.
 90. Riggs, S. R. 1984. Paleooceanographic model of Neogene phosphorite deposition, U.S. Atlantic continental margin. *Science* 223: 123–131.
 91. Saunders, N. C., L. G. Kessler, and J. C. Avise. 1986. Genetic variation and geographic differentiation in mitochondrial DNA of the horseshoe crab, *Limulus polyphemus*. *Genetics* 112: 613–627.
 92. Schneider-Broussard, R., D. L. Felder, C. A. Chlan, and J. E. Neigel. 1998. Tests of phylogeographic models with nuclear and mitochondrial DNA sequence variation in the stone crabs, *Menippe adina* and *Menippe mercenaria*. *Evolution* 52: 1671–1678.
 93. Schulze, S. R., S. A. Rice, J. L. Simon, and S. A. Karl. 2000. Evolution of poecilogony and the biogeography of North American populations of the polychaete *Streblospio*. *Evolution* 54: 1247–1259.
 94. Selander, R. K., S. Y. Yang, R. C. Lewontin, and W. E. Johnson. 1970. Genetic variation in the horseshoe crab (*Limulus polyphemus*), a phylogenetic “relic.” *Evolution* 24: 402–414.
 95. Sellas, A. B., R. S. Wells, and P. E. Rosel. 2005. Mitochondrial and nuclear DNA analyses reveal fine scale geographic structure in bottlenose dolphins (*Tursiops truncatus*) in the Gulf of Mexico. *Conservation Genetics* 6: 715–728.
 96. Slatkin, M. 1985. Gene flow in natural populations. *Annual Review of Ecology and Systematics* 16: 393–430.
 97. Slatkin, M. 1987. Gene flow and the geographic structure of natural populations. *Science* 236: 787–792.
 98. Staton, J. L., and D. L. Felder. 1995. Genetic variation in populations of the ghost shrimp genus *Callichirus* (Crustacea, Decapoda, Thalassinidea) in the western Atlantic and Gulf of Mexico. *Bulletin of Marine Science* 56: 523–536.
 99. Staton, J. L., D. W. Foltz, and D. L. Felder. 2000. Genetic variation and systematic diversity in the ghost shrimp genus *Lepidophthalmus* (Decapoda: Thalassinidea: Callianassidae). *Journal of Crustacean Biology* 20: 157–169.
 100. Street, G. T., and P. A. Montagna. 1996. Loss of genetic diversity in Harpacticoida near offshore platforms. *Marine Biology* 126: 271–282.
 101. Tam, Y. K., I. Kornfield, and F. P. Ojeda. 1996. Divergence and zoogeography of mole crabs, *Emerita* spp. (Decapoda: Hippidae), in the Americas. *Marine Biology* 125: 489–497.
 102. Tringali, M. D., and T. M. Bert. 1996. The genetic stock structure of common snook (*Centropomus undecimalis*).

- Canadian Journal of Fisheries and Aquatic Sciences 53: 974–984.
103. Tringali, M. D., and R. R. Wilson. 1993. Differences in haplotype frequencies of mtDNA of the Spanish Sardine *Sardinella aurita* between specimens from the Eastern Gulf of Mexico and Southern Brazil. *Fishery Bulletin (U.S.)* 91: 362–370.
 104. Turner, T. F., L. R. Richardson, and J. R. Gold. 1999. Temporal genetic variation of mitochondrial DNA and the female effective population size of red drum (*Sciaenops ocellatus*) in the northern Gulf of Mexico. *Molecular Ecology* 8: 1223–1229.
 105. Turner, T. F., J. P. Wares, and J. R. Gold. 2002. Genetic effective size is three orders of magnitude smaller than adult census size in an abundant, estuarine-dependent marine fish (*Sciaenops ocellatus*). *Genetics* 162: 1329–1339.
 106. Ward, L. W., and G. L. Strickland. 1986. Outline of tertiary stratigraphy and depositional history of the U.S. Atlantic coastal plain. Pp. 87–123 in C. W. Poag, ed. *Geologic Evolution of the United States Atlantic Margin*. Van Nostrand Reinhold Company, New York.
 107. Warner, R. R., and R. K. Cowen. 2002. Local retention of production in marine populations: evidence, mechanisms, and consequences. *Bulletin of Marine Science* 70: 245–249.
 108. Williams, A. B., and D. L. Felder. 1986. Analysis of stone crabs: *Menippe mercenaria* (Say), restricted, and a previously unrecognized species described (Decapoda: Xanthidae). *Proceeding of the Biological Society of Washington* 99: 517–543.
 109. Wilson, R. R., and P. D. Alberdi. 1991. An electrophoretic study of Spanish sardine suggests a single predominant species in the eastern Gulf of Mexico, *Sardinella aurita*. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 792–798.
 110. Wirgin, I., L. Maceda, J. Stabile, and C. Mesing. 1997. An evaluation of introgression of Atlantic coast striped bass mitochondrial DNA in a Gulf of Mexico population using formalin-preserved museum collections. *Molecular Ecology* 6: 907–916.
 111. Wirgin, I., J. Waldman, J. Stabile, B. Lubinski, and T. King. 2002. Comparison of mitochondrial DNA control region sequence and microsatellite DNA analyses in estimating population structure and gene flow rates in Atlantic sturgeon *Acipenser oxyrinchus*. *Journal of Applied Ichthyology* 18: 313–319.
 112. Wright, S. 1951. The genetical structure of populations. *Annals of Eugenics* 15: 323–353.
 113. Young, A. M., C. Torres, J. E. Mack, and C. W. Cunningham. 2002. Morphological and genetic evidence for vicariance and refugium in Atlantic and Gulf of Mexico populations of the hermit crab *Pagurus longicarpus*. *Marine Biology* 140: 1059–1066.
 114. Zatcoff, M. S., A. O. Ball, and G. R. Sedberry. 2004. Population genetic analysis of red grouper, *Epinephelus morio*, and Scamp, *Mycteroperca phenax*, from the southeastern US Atlantic and Gulf of Mexico. *Marine Biology* 144: 769–777.
 115. Zigler, K. S., and H. A. Lessios. 2004. Speciation on the coasts of the New World: phylogeography and the evolution of bindin in the sea urchin genus *Lytechinus*. *Evolution* 58: 1225–1241.

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List of population genetic surveys of species that occur in the Gulf of Mexico.

Species	Common Name	Markers			Non-GMx Locations			Explicit Comparisons		Ref	
		Allo	mtDNA	nucDNA	Msat	Other	NW Atl	Caribb	GMx/Atl		w/GMx
Kingdom: Animalia											
Phylum: Annelida											
Class: Polychaeta											
Order: Spionida											
Family: Spionidae											
<i>Streblospio benedicti</i>	Spionid polychaete		SEQ COI				Y	N	2	NA	93
<i>Streblospio gynobranchiata</i>	Spionid polychaete		SEQ COI				N	N	NA	2	93
Phylum: Arthropoda											
Class: Malacostraca											
Order: Decapoda											
Infraorder: Anomura											
Superfamily: Hippoidea											
Family: Hippidae											
<i>Emerita talpoida</i>	Atlantic sand crab		SEQ 16S, SEQ CR				Y	N	2	NA	101
Superfamily: Paguroidea											
Family: Paguridae											
<i>Pagurus longicarpus</i>	Longwrist hermit crab	2	SEQ COI				Y	N	2	NA	113
Infraorder: Brachyura											
Superfamily: Grapsoidea											
Family: Sesamidae											
<i>Sesarma reticulatum</i>	Purple marsh crab	13					Y	N	2	1	26
<i>Sesarma reticulatum</i>	Purple marsh crab						Y	N	2	0	75
Superfamily: Ocypodoidea											
Family: Ocypoididae											
<i>Uca minax</i>	Red-joint fiddler crab	13					Y	N	1	1	26
<i>Uca minax</i>	Red-joint fiddler crab						Y	N	1	0	75
Superfamily: Portunoidea											
Family: Portunidae											
<i>Callinectes sapidus</i>	Blue crab	3					N	N	NA	1	68 ¹
<i>Callinectes sapidus</i>	Blue crab	9					Y	N	0	1	80
Superfamily: Xanthoidea											
Family: Menippidae											
<i>Menippe mercenaria</i> & <i>M. adina</i>	Stone crab	26	SEQ 16S				Y	N	2	1	7 ²
<i>Menippe mercenaria</i> & <i>M. adina</i>	Stone crab						Y	N	1	NA	92

SEQ 16S pseudo-genes; RFLP ANON

Infraorder: Thalassinidae										
Superfamily: Callianassoidea										
Family: Callianassidae										
<i>Callichirus isagrande</i>										9 ³
<i>Callichirus isagrande</i>										98
<i>Callichirus major</i>										98
<i>Lepidophthalmus louisianensis</i>										99
Superfamily: Penaeoidea										
Family: Penaeidae										
<i>Farfantepenaeus aztecus</i>										78
<i>Farfantepenaeus duorarum</i>										79
<i>Litopenaeus setiferus</i>										6
<i>Litopenaeus setiferus</i>										78 ⁴
Class: Maxillopoda										
Order: Harpacticoida										
Family: Cletoidea										
<i>Cletodes</i> sp.										
<i>Enhydrosoma peritoense</i>										
Family: Diosaccidae										
<i>Robertsonia</i> sp.										100
Family: Normanellidae										
<i>Normanella</i> sp.										100
Family: Tisbidae										
<i>Tachidiella</i> sp.										100
Class: Merostomata										
Order: Xiphosura										
Family: Limulidae										
<i>Limulus polyphemus</i>										91
<i>Limulus polyphemus</i>										94
Phylum: Chordata										
Class: Actinopterygii										
Order: Acipenseriformes										
Family: Acipenseridae										
<i>Acipenser oxyrinchus</i>										12
<i>Acipenser oxyrinchus</i>										111
Order: Batrachoidiformes										
Family: Batrachoididae										
<i>Opsanus beta</i>										4

(continued)

List of population genetic surveys of species that occur in the Gulf of Mexico. (continued)

Species	Common Name	Markers			Non-GMx Locations			Explicit Comparisons		Ref
		Allo	mtDNA	nucDNA	Msat	Other	NW Atl	Caribb	GMx/Atl	
Order: Clupeiformes										
Family: Clupeidae										
<i>Brevoortia tyrannus</i> & <i>B. patronus</i>	Menhaden		RFLP			Y	N	1	NA	12 ⁵
<i>Sardinella aurita</i>	Spanish sardine		RFLP			N	N	NA	0	103
<i>Sardinella aurita</i>	Spanish sardine	14				Y	N	NA	1	109
Order: Perciformes										
Family: Carangidae										
<i>Seriola dumerili</i>	Greater amberjack		RFLP			Y	N	1	0	38
Family: Centropomidae										
<i>Centropomus undecimalis</i>	Common snook	8	RFLP			Y	Y	1	1	102
Family: Lutjanidae										
<i>Lutjanus campechanus</i>	Red snapper		SEQ CR			Y	N	0	1	29 ⁶
<i>Lutjanus campechanus</i>	Red snapper		RFLP			N	N	NA	0	40
<i>Lutjanus campechanus</i>	Red snapper		RFLP			N	N	NA	0	36
<i>Lutjanus campechanus</i>	Red snapper		RFLP			N	N	NA	1	42
<i>Lutjanus campechanus</i>	Red snapper		RFLP		20	N	N	NA	0	34
<i>Lutjanus campechanus</i>	Red snapper		RFLP			N	N	NA	0	30
<i>Lutjanus campechanus</i>	Red snapper				5	N	N	NA	0	55
<i>Lutjanus campechanus</i>	Red snapper		SEQ ND4			N	N	NA	0	87
<i>Rhomboplites aurorubens</i>	Vermilion snapper				7	Y	N	0	NA	5
Family: Moronidae										
<i>Morone saxatilis</i>	Striped bass					Y	N	1	NA	24
<i>Morone saxatilis</i>	Striped bass			RFLP 3 ANON		Y	N	1	1	110 ⁷
Family: Sciaenidae										
<i>Microponogonias undulatus</i>	Atlantic croaker		PCR-RFLP			Y	N	1	NA	69
<i>Pogonias cromis</i>	Black drum		RFLP			N	N	NA	0	40 ⁸
<i>Sciaenops ocellatus</i>	Red drum	9				Y	N	1	1	11
<i>Sciaenops ocellatus</i>	Red drum				5	Y	N	1	NA	19
<i>Sciaenops ocellatus</i>	Red drum		RFLP			Y	N	1	0	35
<i>Sciaenops ocellatus</i>	Red drum		RFLP			Y	N	1	0	39
<i>Sciaenops ocellatus</i>	Red drum		RFLP			N	N	NA	0	40
<i>Sciaenops ocellatus</i>	Red drum	9				Y	N	1	0	31
<i>Sciaenops ocellatus</i>	Red drum		RFLP			N	N	NA	0	36 ⁹
<i>Sciaenops ocellatus</i>	Red drum		RFLP			Y	N	1	1	41
<i>Sciaenops ocellatus</i>	Red drum				8	N	N	NA	1	43
<i>Sciaenops ocellatus</i>	Red drum		RFLP			N	N	NA	NA	104

	Red drum	8 loci	N	N	NA	NA	105
<i>Sciaenops ocellatus</i>	Red drum		N	N	NA	NA	105
Family: Scombridae							
<i>Acanthocybium solandri</i>	Wahoo	SEQ CR	Y	Y	0	NA	28
<i>Scomberomorus cavalla</i>	King mackerel		Y	N	0	1	16 ¹⁰
<i>Scomberomorus cavalla</i>	King mackerel	1 RFLP	Y	N	1	0	32
<i>Scomberomorus cavalla</i>	King mackerel		Y	N	1	NA	33
<i>Scomberomorus maculatus</i>	Spanish mackerel	RFLP ND4	Y	N	0	1	17
Family: Serranidae							
<i>Centropristis striata</i>	Black sea bass	RFLP	Y	N	2	NA	12
<i>Epinephelus morio</i>	Red grouper	RFLP	N	N	NA	0	36
<i>Epinephelus morio</i>	Red grouper		Y	N	0	0	114
<i>Mycteroperca phenax</i>	Scamp		Y	N	0	0	114
Order: Pleuronectiformes							
Family: Paralichthyidae							
<i>Paralichthys lethostigma</i>	Southern flounder		Y	N	0	1	10 ¹¹
Order: Siluriformes							
Family: Ariidae							
<i>Arius felis</i>	Hardhead catfish	RFLP	Y	N	0	0	4
<i>Bagre marinus</i>	Gafftopsail	RFLP	Y	N	0	0	4
Class: Chondrichthyes							
Order: Carcharhiniformes							
Family: Carcharhinidae							
<i>Carcharhinus limbatus</i>	Blacktip shark	SEQ CR	Y	N	1	0	63
<i>Carcharhinus limbatus</i>	Blacktip shark	SEQ CR	Y	Y	1	1	64 ¹²
<i>Carcharhinus plumbeus</i>	Sandbar shark	RFLP	Y	N	0	0	56 ¹³
<i>Carcharhinus plumbeus</i>	Sandbar shark		Y	N	0	NA	54
<i>Rhizoprionodon terraenovae</i>	Sharpnose shark	RFLP	Y	N	0	NA	57
<i>Sphyrna lewini</i>	Scalloped hammerhead	SEQ CR, SEQ COI	Y	N	2	NA	88
Class: Mammalia							
Order: Cetacea							
Family: Delphinidae							
<i>Stenella frontalis</i>	Atlantic spotted dolphin	SEQ CR	Y	N	1	NA	1
<i>Tursiops truncatus</i>	Bottlenose dolphin	SEQ CR	N	N	NA	1	95
<i>Tursiops truncatus</i>	Bottlenose dolphin	RFLP	Y	N	1	0	25
Phylum: Cnidaria							
Class: Anthozoa							
Order: Actiniaria							
Family: Actiniidae	Wharty sea anemone		Y	Y	2	0	77 ¹⁴
<i>Bunodosoma cavernata</i>							

(continued)

List of population genetic surveys of species that occur in the Gulf of Mexico. (continued)

Species	Common Name	Markers			Non-GMx Locations			Explicit Comparisons		Ref	
		Allo	mtDNA	nucDNA	Msat	Other	NW Atl	Caribb	GMx/Atl		w/GMx
Order: Scleractinia											
Family: Agariciidae											
<i>Agaricia agaricites</i>	Lettuce coral					45 AFLP	Y	Y	NA	NA	13 ¹⁵
Phylum: Echinodermata											
Class: Echinoidea											
Order: Temnopleuroidea											
Family: Toxopneustidae											
<i>Lytechinus variegatus carolinus</i>	Green sea urchin		SEQ COI	SEQ BIN			Y	N	0	0	115
Phylum: Mollusca											
Class: Bivalvia											
Order: Mtiloidea											
Family: Mytilidae											
<i>Brachidontes exustus</i> complex	Scorched mussel		SEQ COI	SEQ 28S, SEQ ITS1			Y	Y	2	NA	71
<i>Brachidontes exustus</i> complex	Scorched mussel		SEQ COI	SEQ 28S, SEQ ITS1			Y	Y	2	1	72
Order: Ostreoida											
Family: Ostreidae											
<i>Crassostrea virginica</i>	American oyster	21					Y	N	NA	1	18 ¹⁶
<i>Crassostrea virginica</i>	American oyster	5					N	N	NA	1	45 ¹⁷
<i>Crassostrea virginica</i>	American oyster			SEQ 3 ANON			Y	N	1	NA	49
<i>Crassostrea virginica</i>	American oyster			PCR-RFLP 4			Y	N	1	1	60
<i>Crassostrea virginica</i>	American oyster			PCR-RFLP 4 ANON			Y	N	2	NA	62
<i>Crassostrea virginica</i>	American oyster	15					N	N	NA	1	66
<i>Crassostrea virginica</i>	American oyster		RFLP				Y	N	2	0	89
Order: Veneroidea											
Family: Mactridae											
<i>Spisula solidissima</i>	Atlantic surfclam		SEQ COI	SEQ 2 CI			Y	N	2	NA	50
Family: Veneridae											
<i>Mercenaria campechiensis</i>	Southern quahog		SEQ 16S				N	N	NA	1	27 ¹⁸
Class: Cephalopoda											
Order: Teuthida											
Family: Loliginidae											
<i>Loligo pealei</i>	Long-finned squid		RFLP				Y	N	1	0	59
<i>Loligo plei</i>	Slender inshore squid		RFLP				Y	N	0	1	59 ¹⁹

Kingdom: Plantae
Phylum: Rhodophyta
Class: Rhodophyceae
Order: Gracilariales
Family: Gracilariaceae
Gracilaria tikvahiae

Red alga

rbcl

Y

N

I

I

46²⁰

ITS

- ¹ Temporal variation in allele frequencies exceeded geographic variation.
- ² Geographic variation includes a hybrid zone between the nominal species *M. adina* and *M. mercenaria*.
- ³ A phylogenetic break occurs at the Chenier plain off the coast of Louisiana.
- ⁴ A phylogenetic break occurred between Atlantic and E GMx populations and W GMx populations.
- ⁵ Two nominal species, *Brevoortia tyrannus* and *B. patonus*, with a paraphyletic distribution of haplotypes.
- ⁶ Geographic variation was restricted to one distinct population off the coast of Mississippi.
- ⁷ Historically, GMx populations have been stocked with fish from Atlantic populations.
- ⁸ Geographic variation was clinal.
- ⁹ Pattern of variation was interpreted as the result of isolation by distance.
- ¹⁰ Populations in the northern GMx were distinct from others.
- ¹¹ A shift in allele frequencies was observed at Galveston Bay, Texas.
- ¹² Reciprocal monophyly with Caribbean populations.
- ¹³ Extremely low polymorphism.
- ¹⁴ Caribbean and Atlantic populations were similar and GMx populations were distinct.
- ¹⁵ GMx and Caribbean populations were distinct.
- ¹⁶ A large shift in allele frequencies was observed for a population near Brownsville, Texas.
- ¹⁷ Population near Laguna Madre, Texas, was distinct from others.
- ¹⁸ Paraphyletic distribution of haplotypes interpreted as evidence of past hybridization with Atlantic congener.
- ¹⁹ Genetic break occurred at Mississippi River mouth.
- ²⁰ Sample sizes for some localities were very small.