

Evidence of multiple vicariance in a marine suture-zone in the Gulf of Mexico

David S. Portnoy* and John R. Gold

Center for Biosystematics and Biodiversity,
Texas A&M University, College Station, TX
77843-2258, USA

ABSTRACT

Aim Our aim was to assess whether single or multiple vicariance event(s) have occurred in a marine suture-zone in the northern Gulf of Mexico. We estimated the divergence time of two genetically distinct groups of lane snapper (*Lutjanus synagris*), distributed on either side of this zone, and compared it to the timing of other vicariance events described previously in the area.

Location The northern Gulf of Mexico from the Texas coastline to the Atlantic coast of South Florida, USA. The marine suture-zone is proximal to Mobile Bay in Alabama.

Methods A Bayesian Markov chain Monte Carlo (MCMC) approach was used to estimate mutation-corrected divergence and genetic migration between eastern and western groups of lane snapper, based on genotypic differences at 13 nuclear-encoded microsatellites obtained previously from 77 and 171 individual samples, respectively. A second estimate of divergence time for eastern and western groups of lane snapper was generated, based on 590 base pairs of DNA sequence from the mitochondrially encoded NADH dehydrogenase subunit 4 (*ND4*) obtained previously from 45 and 93 individual samples, respectively.

Results Both classes of genetic markers (microsatellites and mtDNA) indicated a fairly recent divergence. Confidence intervals for microsatellite-based estimates suggested that divergence began less than 21 thousand years ago (ka), while confidence intervals for mitochondrial DNA-based estimates suggested divergence began less than 130 ka. These estimates were not consistent with vicariance events in the literature, which are hypothesized to have occurred well before 135 ka.

Main conclusions These results indicate that the marine suture-zone in the northern Gulf of Mexico features multiple vicariance events and may be characterized by a complex geological/environmental history. We suggest that processes during or after the Wisconsin glaciation (*c.* 110–18 ka) may have created a previously unrecognized barrier for lane snapper and possibly other species as well.

Keywords

Coalescent approach, Gulf of Mexico, Last Glacial Maximum, Lutjanidae, *Lutjanus synagris*, marine biogeography, snapper, suture-zone, vicariance.

*Correspondence: David S. Portnoy, Texas A&M University, Center for Biosystematics and Biodiversity, Old Herman Heep Building, College Station, TX 77843-2258, USA. E-mail: dsport@tamu.edu

INTRODUCTION

Remington (1968, p. 322) defined a suture-zone as 'a band ... of geographic overlap between major biotic assemblages, including pairs of species or semispecies which hybridize in

the zone'. Although the term has generated controversy (Swenson & Howard, 2004), it is clear that there are major transition zones where distinct lineages (sister species, subspecies and/or distinct phylogenetic assemblages) across a wide variety of taxa exist in sympatry (Wiley & Mayden, 1985; Avise,

2001). Many such zones are well studied in terrestrial systems and there are a variety of hypotheses for the mechanisms generating these patterns, including fusion of glacial refugia, opening of mountain passes, and anthropogenic influences (Anderson, 1948; Hewitt, 2000). Suture-zones have received less attention in the marine environment, in part due to difficulties in detecting hybrid zones and/or historical geographical/geological barriers (Hobbs *et al.*, 2009). An important component of suture-zone theory is that genealogical concordance for a wide variety of biota across taxa reflects a single vicariance event (Avice, 2000; Coyne & Orr, 2004; Whinnett *et al.*, 2005).

A vicariant zone has been described in the north-eastern Gulf of Mexico (hereafter Gulf), (Dahlberg, 1970; McClure & McEachran, 1992). At least 15 pairs of fishes and invertebrates described as sister taxa (species, subspecies, or genetically distinct populations) meet in this region, with evidence of hybridization occurring between several of the taxa (Table 1, Fig. 1). A comparison of distributional data obtained for each pair of sister taxa demarcates an area from *c.* 84° W, near Apalachee Bay, Florida, to *c.* 89° W, near Chandeleur Sound, Louisiana (Fig. 1, and see Appendix S1 in Supporting Information). The region meets the criteria laid out in Remington's definition of suture-zones and, additionally, is proximate to a recognized terrestrial suture-zone extending across northern

Florida into Alabama (Remington, 1968; McClure & McEachran, 1992).

Because the suture-zone is located to the east of the Mississippi River outflow, historical vicariance events have been invoked to explain the observed patterns of divergence. These include: (1) a physical barrier, similar to the Florida Peninsula, that arose *c.* 2.5 million years ago (Ma) during the Pliocene (Ginsburg, 1952), (2) an ecological barrier, perhaps a river that drained the Tennessee River basin directly into the Gulf, that existed approximately 2.4 Ma (Simpson, 1900; Ginsburg, 1952), (3) a strong current that flowed from the Gulf to the Atlantic through the Suwanee Straits approximately 1.75 Ma (Bert, 1986), and (4) extended cooling during early Pleistocene glaciations occurring *c.* 700–135 thousand years ago (ka) (Dahlberg, 1970).

In this study we analysed microsatellite and mitochondrial DNA (mtDNA) sequence data previously used by Karlsson *et al.* (2009) to demonstrate the existence of two genetically distinct groups of lane snapper, *Lutjanus synagris* (Linnaeus, 1758), on either side the Gulf suture-zone. The primary purpose of our analysis was to determine if estimated divergence times in lane snapper were consistent with the timing of hypothesized vicariance events in the suture-zone area, in order to distinguish whether the Gulf suture-zone is characterized by a single or multiple vicariance event(s).

Table 1 Sister taxa that are found in the Gulf of Mexico suture-zone, with an indication of whether there is evidence of introgrades (Int) between taxa. Distributional data, obtained from literature references and presented as a series of distributional maps, for all taxa may be found in Appendix S1 in Supporting Information.

Order	Family	East	West	Int	Source
Anguilliformes	Muraenidae	<i>Gymnothorax saxicola</i>	<i>Gymnothorax nigromarginatus</i>	Yes	McEachran & Fechhelm, 1998; Böhlke & Smith, 2002
	Ophichthidae	<i>Bascanichthys scuticaris</i>	<i>Bascanichthys bascanium</i>	No	McCosker <i>et al.</i> , 1989; McEachran & Fechhelm, 1998
		<i>Echiophis intertinctus</i>	<i>Echiophis punctifer</i>	No	McCosker <i>et al.</i> , 1989; McEachran & Fechhelm, 1998
	Congridae	<i>Rhynchoconger gracilior</i>	<i>Rhynchoconger flavus</i>	No	Smith, 1989; McEachran & Fechhelm, 1998
Clupeiformes	Clupeidae	<i>Brevoortia smithi</i>	<i>Brevoortia gunteri</i>	Yes	Dahlberg, 1970; Munroe & Nizinski, 2002
Lophiiformes	Ogcocephalidae	<i>Halieutichthys bispinosus</i>	<i>Halieutichthys intermedius</i>	No	Ho <i>et al.</i> , 2010
		<i>Ogcocephalus cubifrons</i>	<i>Ogcocephalus pantostictus</i>	No	Bradbury, 1980
		<i>Ogcocephalus parvus</i>	<i>Ogcocephalus declivirostris</i>	No	Bradbury, 1980
Scorpaeniformes	Triglidae	<i>Prionotus alatus</i>	<i>Prionotus paralatus</i>	Yes	McClure & McEachran, 1992
Perciformes	Blenniidae	<i>Chasmodes saburrae</i>	<i>Chasmodes bosquianus</i>	No	Williams, 1983; McEachran & Fechhelm, 2005
		<i>Archosargus p. probatocephalus</i>	<i>Archosargus p. oviceps</i>	Yes	Caldwell, 1965; Anderson <i>et al.</i> , 2008
Tetraodontiformes	Tetraodontidae	<i>Sphoeroides nephelus</i>	<i>Sphoeroides parvus</i>	No	Shipp, 1974, 2002
Pleuronectiformes	Achiridae	<i>Gymnachirus melas</i>	<i>Gymnachirus texae</i>	No	Dawson, 1964; McEachran & Fechhelm, 2005
Decapoda	Menippidae	<i>Menippe mercenaria</i>	<i>Menippe adina</i>	Yes	Williams & Felder, 1986; Bert & Harrison, 1988
Cephalopoda	Loliginidae	<i>Loligo plei</i> B	<i>Loligo plei</i> A	NA	Herke & Foltz, 2002

NA, not applicable.

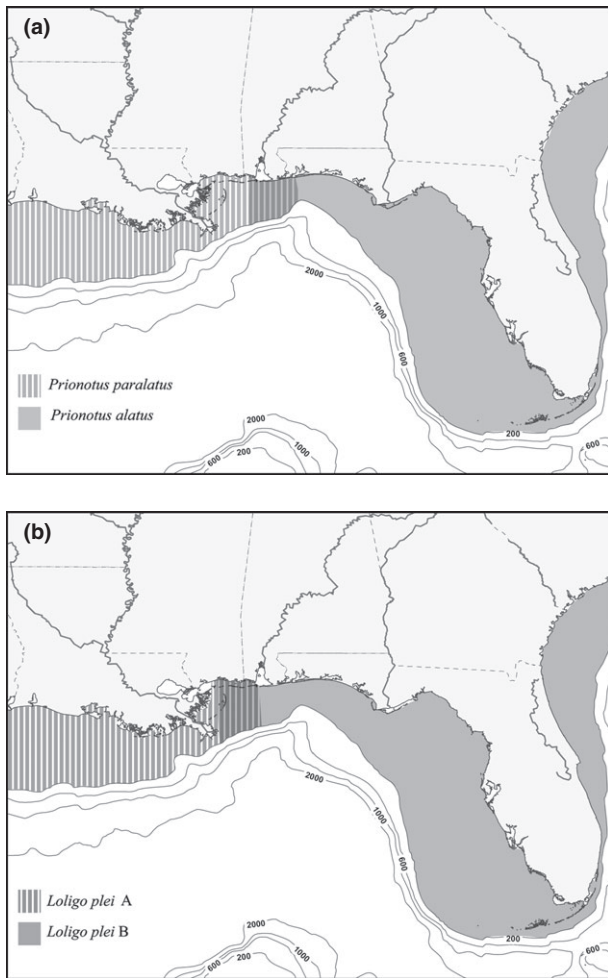


Figure 1 Approximate distributions, obtained from the literature, of two pairs of sister taxa that meet in the Gulf of Mexico suture-zone. Taxa in panel (a) are sister species; taxa in panel (b) are populations defined by genetic differences. References used to create the maps can be found in Table 1. Maps for 15 pairs of sister taxa may be found in Appendix S1 in Supporting Information. [Correction added after online publication, 27 March 2012: Key in Figure 1b amended.]

MATERIALS AND METHODS

The historical relationship and time of divergence between the two groups of lane snapper was assessed using genotypes at 13 nuclear-encoded microsatellites and the Bayesian Markov chain Monte Carlo (MCMC) approach employed in IMA (Hey & Nielsen, 2004). Parameters estimated were t (mutation-scaled time since divergence), m (mutation-scaled migration between groups), and q_a , q_e and q_w ; the latter three are estimates of θ ($4N_e\mu$) for the ancestral population and for the contemporary eastern and western populations. A null model of no migration between the two groups was also tested (Won & Hey, 2005; Hey & Nielsen, 2007). Genotypes of 248 individuals sampled from nine geographical localities were used in the analysis. Genotypes at each sample locality may be found at <http://agrilife.org/wfsc/doc/> under the file name 'lane snapper microsatellite geno-

types'; sample sizes per locality are given in Karlsson *et al.* (2009). The eastern group of lane snappers included 77 individuals from localities offshore of the west coast of Florida, the Florida Keys, and the east coast of Florida; the western group included 171 individuals sampled from localities offshore of Alabama, Louisiana, and four sites (near Galveston, Port Lavaca, Port Aransas and Brownsville) along the Texas coast.

Preliminary runs with IMA were used to determine appropriate priors for t and m and run times for subsequent runs. Final runs incorporating these priors were replicated, with different starting points to ensure that independent runs converged. Final runs consisted of a burn-in period of 1,000,000 generations and a post-burn-in of 8,000,000 generations. Each run included 50 chains with geometric heating and heating parameters of $h_1 = 0.8$ and $h_2 = 0.75$. The two final runs were combined by sampling half of the genealogies from each to generate final parameter estimates.

The model behind IMA assumes that each population is panmictic and that the genealogical relationship between a pair of populations is unaffected by input from other populations. While neither assumption is likely to be correct in most cases, the model is able to distinguish between different scenarios: no divergence, divergence with gene flow, and complete isolation (Niemiller *et al.*, 2008). Two scenarios were considered in this study: (1) high gene flow and deep divergence times, and (2) recent divergence with little to no gene flow. Posterior probability distributions of t were examined to evaluate the probability of zero time since divergence, indicating a lack of divergence (J. Hey, Rutgers University, pers. comm.). Given non-zero divergence, posterior probability distributions of m were examined to evaluate the probability of zero gene flow, indicating isolation (Won & Hey, 2005; Niemiller *et al.*, 2008). Log-likelihood ratio (LLR) tests were used to examine whether a null model with zero gene flow fit the data (Hey & Nielsen, 2007). Due to uncertainty caused by violations of the assumptions of the model (Wakeley, 2000; Strasburg & Rieseberg, 2010), and the absence of reliable point estimates of mutation rates for microsatellites in perciform fishes, t was converted to time in years in two ways. First, the posterior probability distribution of t was combined with the posterior probability distribution of μ across all loci, generated in *MSVAR* v. 1.3 (Beaumont, 1999) and corrected for a generation time of 7 years (Karlsson *et al.*, 2009). The resulting joint probabilities were plotted in *MATLAB* (The Mathworks, 2007, Natick, MA, USA) as a three-dimensional surface against t and μ . Because points on the resulting probability surface represent estimates of t and μ , they could be converted to time in years. Estimates of time were then overlain on the probability surface, providing a robust and intuitive way to explore all probable divergence times. Second, posterior probability distributions of t were centred on hypothesized times of vicariance events in the suture-zone as described in the literature (Ginsburg, 1952; Dahlberg, 1970; Bert, 1986). The most recent time estimate was used for each of the hypothesized vicariance events that persisted over long periods of time. This allowed for the calculation of a hypothetical μ consistent with the timing of

each vicariance event, which was then compared to estimates of microsatellite mean mutation rates (MMR) for vertebrates as reported in the literature.

In order to generate a second independent estimate of divergence time, MEGA 4.0 (Tamura *et al.*, 2007) was used to estimate sequence divergence between a subset of individuals from the two groups of lane snapper, using a 590 base pair (bp) fragment of the mitochondrially encoded NADH dehydrogenase subunit 4 (*ND4*). The subset included 45 individuals from the eastern group and 93 individuals from the western group; mtDNA haplotypes by locality may be found in Appendix S2. Net divergence between the two groups in the *ND4* fragment was estimated using a Kimura 2-parameter model (Kimura, 1980), with no rate variation among nucleotide positions. The standard error was estimated using 1000 bootstrap replicates. Net divergence was estimated in order to account for the within-group component of divergence. In order to convert the divergence estimate into time, a divergence rate for *ND4* was calibrated using a divergence rate of 1.2% per million years for cytochrome *c* oxidase subunit I (*COI*), previously estimated for marine fishes from eight geminate species pairs, including one pair in the genus *Lutjanus*, distributed across the Isthmus of Panama (Birmingham *et al.*, 1997). Following procedures used in Manthey *et al.* (2011), the overall mean divergence for both a 652 bp fragment of *COI* and a 590 bp fragment of *ND4* was calculated for a clade of lutjanids that included 48 individuals spread across 23 species. Sequence data were obtained from Gold *et al.* (2011). Overall mean divergence was calculated as the mean of all pairwise distances between individuals, using the Kimura 2-parameter model (Kimura, 1980) as implemented in MEGA. The ratio of overall mean divergences (*ND4/COI*) was then multiplied by the estimated molecular rate for *COI* of 1.2% per million years to arrive at a divergence rate for *ND4*. To validate the molecular rate calculated for *ND4*, sequence divergence between a geminate pair of lutjanids (*Lutjanus campechanus* versus *Lutjanus peru* – Clade C, Fig. 2) that are distributed on either side of the Isthmus of Panama was calculated. Sequence divergence was also calculated between

this geminate pair, as a group, and their sister species (*Lutjanus vivanus* – Clade B, Fig. 2). The estimates of sequence divergence were then converted into time, using the molecular rate estimated for *ND4*. If the rate calculated is reasonable, these divergence times should bracket the closure of the Isthmus of Panama, roughly 3 Ma (Keigwin, 1978, 1982).

RESULTS

Bayesian analysis generated a narrow, peaked posterior probability distribution of *t* with a point estimate of divergence time of 3578 years ($t = 0.1375$) for the eastern and western groups of lane snapper when a modal μ , obtained from *MSVAR*, of 2.69×10^{-4} mutations per generation was applied. When using the slowest mutation rate obtained from *MSVAR* (4.47×10^{-5} mutations per generation), the estimate of divergence time increased to 21,532 years. When this mutation rate (4.47×10^{-5}) and the largest estimates of *t* (0.2475) were combined, divergence times were still less than 40 ka. The combined posterior probabilities of μ and *t* strongly support a divergence occurring between *c.* 3.6 and 21 ka, with more than 98% of the probability surface having corresponding time estimates of less than 20 ka (Fig. 3). To generate an estimate of divergence time that corresponds to the most recent previously hypothesized vicariance event (*c.* 770–135 ka; Dahlberg, 1970) would require a mean mutation rate (MMR) $\ll 1.5 \times 10^{-5}$ if the largest estimate of *t* (0.2475) is used. This would be slower than the microsatellite MMR reported for other vertebrates (MMR: 5.5×10^{-4} – 1.07×10^{-2} ; Bulut *et al.*, 2009). The distributions of posterior probability for *m* (mutation-scaled migration) from east to west and from west to east overlapped and neither parameter could be differentiated from a rate of zero. However, a null model of zero migration was rejected [$2LLR_{(2)} = 7.3243$, $P = 0.026$] and both distributions peaked before zero, indicating that migration is likely to have occurred after separation but that the effective number of migrants in either direction is small. Estimates of theta suggest a relatively small ancestral size prior to divergence ($q_a = 5.12$), with larger post-divergence sizes for both eastern and western groups

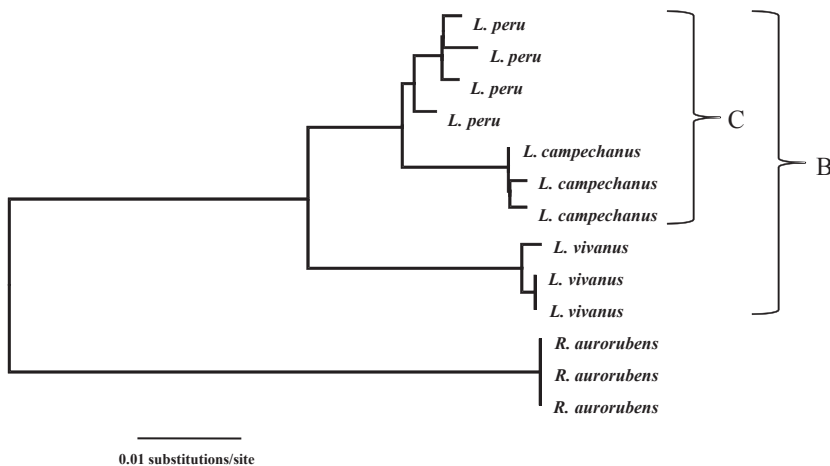


Figure 2 Neighbour-joining tree demonstrating relationships among species in the subfamily Lutjaninae, after Gold *et al.* (2011), which were used for calibration and validation of *ND4* divergence rate. Group C contains the geminate species pair *Lutjanus campechanus* and *L. peru* distributed across the Isthmus of Panama. Group B contains *L. campechanus*, *L. peru* and their sister species *L. vivanus*. The outgroup is *Rhomboplites aurorubens*. The letters correspond to group columns in Table 1.

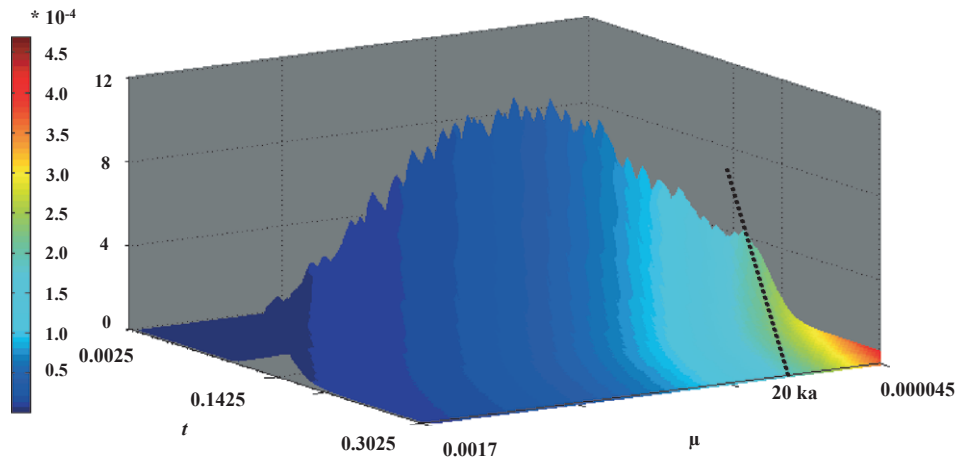


Figure 3 Three-dimensional surface of the combined posterior probability obtained from estimate of t (mutation-scaled divergence time of eastern and western Gulf of Mexico lane snapper, *Lutjanus synagris*) and μ (mutation rate per generation). Colour corresponds to time in years obtained for the combined estimated parameters, corrected for a generation time of 7 years. The proportion of posterior probabilities less than 20 ka is indicated.

($q_e = 35.83$, $q_w = 37.58$). Likelihood curves for estimated parameters can be found in Appendix S3.

The mean overall divergence of the 590 bp fragment of *ND4* among lutjanine snapper species was 1.26 times greater than mean overall divergence of the 652 bp fragment of *COI* among lutjanine snapper species in the phylogeny of Gold *et al.* (2011). When the estimated divergence rate for *COI* (Birmingham *et al.*, 1997) was multiplied by that ratio, the resulting divergence rate for *ND4* was 1.51% per million years. Using this divergence rate for *ND4*, the estimated time of divergence between taxa that split prior to the closure of the Isthmus of Panama (*L. vivanus* versus *L. campechanus* and *L. peru*; Clade C, Fig. 2) was between 3.86 and 1.7 Ma (Table 2), while the estimated time of divergence between taxa that split after the closure of the Isthmus of Panama (*L. campechanus* versus *L. peru*; Clade B, Fig. 2) was between 1.86 and 0.52 Ma

Table 2 Mean sequence divergence between clades of lutjanine fishes, based on 590 bp of *ND4*. Divergence in Clade B (Fig. 2) is that between *Lutjanus vivanus* and the geminate species pair (*L. campechanus* and *L. peru*) distributed on either side of the Isthmus of Panama. Divergence in Clade C (Fig. 2) is that between *L. campechanus* and *L. peru*. Divergence in E_W is that between the eastern and western groups of lane snappers, *L. synagris*, in the Gulf of Mexico. Divergence time is in millions of years ago (Ma), calculated using a divergence rate for *ND4* of 1.51% per million years. ‘Upper’ and ‘Lower’ are bounds of the 95% confidence interval, in Ma, calculated using a divergence rate for *ND4* of 1.51% per million years.

Clade	<i>ND4</i>	Divergence		
		time (Ma)	Upper (Ma)	Lower (Ma)
B	4.21	2.78	3.86	1.7
C	1.8	1.19	1.86	0.52
E_W	0.076	0.050	0.132	0.0

(Table 2). Because these estimates roughly bracket 3 Ma, the estimated rate of sequence divergence for *ND4* appears reasonable. When the calculated net sequence divergence between the two groups of lane snapper is multiplied by the estimated molecular rate for *ND4*, the estimated time of divergence between the eastern and western groups of *L. synagris* was 50 ka (95% confidence interval: 132 to 0 ka).

DISCUSSION

Vicariance events occurring at $c. \geq 2.5$ Ma, ≥ 1.7 Ma and 700–135 ka have been hypothesized by Ginsburg (1952), Bert (1986) and Dahlberg (1970), respectively, to explain faunal discontinuities in the northern Gulf. Results of our analysis strongly indicate that divergence between the two groups of lane snapper occurred much more recently. More than 95% of the microsatellite-based estimates of divergence were less than 21 ka, while the average time of divergence in the mtDNA fragment was 50 ka. The upper bound of the mtDNA based estimate (132 ka) is close to the end of the late Illinoian Glaciation and the beginning of the interglacial that followed ($c. 135$ ka; Hewitt, 1996); the majority of estimates contained within the 95% confidence interval, however, are much more recent. In addition, because molecular clocks may be faster over short time scales (< 1 – 2 Ma), relative to longer time scales (Ho *et al.*, 2005), the mtDNA-based estimate of divergence time may be upwardly biased.

Vicariance hypotheses involving the suture-zone

Ginsburg (1952) suggested a physical or ecological barrier that occurred during the Pliocene (> 2.5 Ma) and resulted in a vicariant zone in the north-eastern Gulf. He hypothesized that it could have been peninsular in nature, based on the observation that ichthyofaunal discontinuities in the

north-eastern Gulf mirrored those caused by the Florida Peninsula. During the Pliocene, the upper Tennessee drainage met the river systems of Mobile Bay, forming what has been called the Appalachian River (Hayes & Campbell, 1894) which drained through Mobile Bay into the north-eastern Gulf near the suture-zone (Simpson, 1900; Fig. 4). The existence of this river has support in terms of both faunal similarities between currently isolated river systems and the geology of the region (Mayden, 1988). This river could have been Ginsburg's (1952) ecological barrier, as large freshwater outflows may effectively halt dispersal of marine species (Rocha *et al.*, 2002).

Bert (1986), alternatively, suggested that the Suwannee Straits may have been important for the isolation of eastern and western biota in the northern Gulf. This hypothesis was based on estimates of molecular divergence between morphologically and genetically distinct western and eastern Gulf populations of the stone crab, *Menippe mercenaria*, and by the observation that the marine break is proximal to Remington's (1968) terrestrial Florida suture-zone. The powerful current in the Suwannee Straits ran from the Gulf to the Atlantic through the Okefenokee Trough, separated Florida from the mainland (Fig. 4), and may have been open as recently as 1.75 Ma (Bert, 1986). Such a current could have been a powerful barrier for marine dispersal. A final note is that there is also a terrestrial suture-zone that extends to the west into Alabama, perhaps supporting the notion that despite their proximity, different vicariance events are necessary to explain the marine and terrestrial suture-zones (Wiley & Mayden, 1985; McClure & McEachran, 1992).

Another possibility is that marine species were forced into different refugia during the repeated glacial events of the Pleistocene and came into secondary contact following glacial retreat (Hewitt, 1996). This scenario was invoked by Dahlberg

(1970) to explain the presence of sister species of menhaden, *Brevoortia gunteri* and *Brevoortia smithi*, distributed on either side of the Gulf suture-zone. Because earlier glacial cycles, between 700 and 135 ka, were more extended in time (Neil, 1957; Hewitt, 1996), these two sister species may have diverged well before the last glaciation (Dahlberg, 1970).

Estimates of divergence time for the two groups of lane snapper are not inconsistent with a glacial refugia hypothesis, as confidence intervals generated from both marker types include the Wisconsin Glaciation (c. 110–18 ka). However, characteristics of that glacial period and the biology of the lane snapper suggest that this hypothesis may be unlikely. First, estimated water temperatures during the winter across the northern Gulf during the last glaciation were approximately 18 °C (Brunner & Cooley, 1976), well within the range of thermal tolerance for lane snappers (Rivas, 1970). Second, although the sea level in the northern Gulf declined by as much as 150 m during the Last Glacial Maximum (Simms *et al.*, 2007), there remained a continuous shallow shelf occupying the area up to what currently is the 200-m isobath (Kennett & Shackleton, 1975). This would have been suitable habitat for lane snapper. Finally, more than 95% of divergence estimates from microsatellite data occur earlier than 21 ka.

An alternative possibility is that large pulses of cold freshwater from the Mississippi River caused by recession of the Laurentide Ice Sheet between 16 and 9 ka (Kennett & Shackleton, 1975; Aharon, 2003) generated simultaneous thermal and salinity barriers. Such pulses would have substantial impact on marine fauna in shallow-shelf environments, particularly around the suture-zone, which is in close proximity to the Mississippi outflow (Fig. 4). The two lane snapper groups could also have diverged sympatrically or parapatrically (Karlsson *et al.*, 2009), as the region is

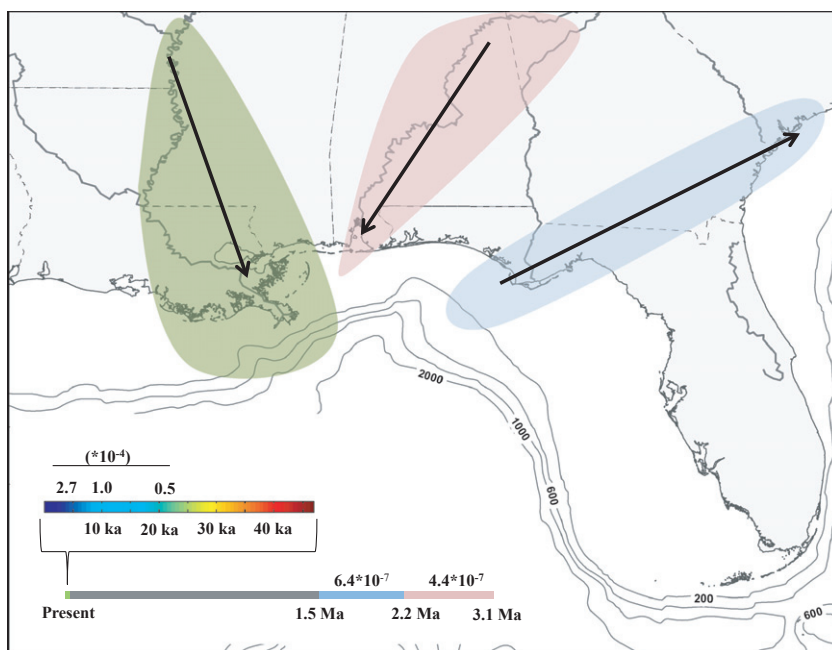


Figure 4 Map of the northern Gulf of Mexico with locations of three hypothesized vicariance events overlaid in colour: green – pulses of cold freshwater from the Mississippi River outflow occurring at the end of the last ice age (Aharon, 2003); red – ancient drainage of the Tennessee River system (Simpson, 1900); and blue – Suwannee Straits (Bert, 1986). Arrows represent the primary direction of current flow. Colours in the upper band correspond to colours (and times in thousand years ago, ka) in the time bar shown in Figure 3. The lower bar reflects time (in million years ago, Ma) for vicariance events hypothesized for the suture-zone. Required microsatellite mutation rates for given divergence time estimates are given above the bars.

characterized by an east to west shift from carbonate sediments to a mud and silt bottom (Bert, 1986). Because lane snappers readily occupy both habitat types (Luckhurst *et al.*, 2000), it may be that associated ecological differences accelerated divergence after a brief vicariance event and could be important in maintaining low levels of gene flow today.

While the exact event(s) that separated lane snapper in the north-eastern Gulf cannot be determined, divergence appears to have begun far more recently than timeframes hypothesized in the literature for other marine taxa. This suggests the complex geological and biological history of the north-eastern Gulf included multiple vicariance events that occurred in or near the suture-zone. Further study in this and other marine suture-zones will be necessary to confirm such a 'multiple-event' hypothesis and to determine if this is a common characteristic of marine suture-zones.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Distributional maps for 15 taxa found on either side of the Gulf suture-zone.

Appendix S2 Distribution of mtDNA haplotypes across geographical samples of lane snapper.

Appendix S3 Posterior probability distributions for parameters estimated using IMA.

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BIOSKETCHES

David S. Portnoy is a Research Associate in the Centre for Biosystematics and Biodiversity and a member of the Ecology and Evolutionary Biology group at Texas A&M University. His research is centred on the conservation genetics and historical zoogeography of long-lived, exploited marine fishes.

John R. Gold is Regents Professor at Texas A&M University. His research centres on genetics of fishes.

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