

PATTERNS OF ENDEMISM AND SPECIES RICHNESS OF FISHES
OF THE WESTERN GULF SLOPE

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PATTERNS OF ENDEMISM AND SPECIES RICHNESS OF FISHES
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ABSTRACT

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Contemporary freshwater fish communities are influenced by selection mechanisms (i.e., species-area relationships; species-energy relationships) with the role of historical mechanisms (i.e., speciation and dispersal) poorly understood and largely understated. I assessed the influence of selection and historical mechanisms on species richness and endemism among fish communities of the Western Gulf Slope (WGS). Distributions within the WGS generally conformed to predictions generated from global freshwater fish distributions. Species richness was greatest ($P < 0.01$) in wetter regions, and endemism was greatest ($P < 0.01$) in drier regions of the WGS. To assess historical mechanisms, fish phylogenies were used to determine direction, origin, and timing of dispersion into the WGS. Based on these findings, multiple events of colonization into the WGS likely occurred from the late Miocene until the start of the Holocene. Contemporary lineages represent ancestral origins and routes from the north (28% of the

155 native fishes of the WGS; beginning during the Late Miocene), southwest (15%; Late Miocene/Early Pliocene), north-east (14%; Pleistocene), and east (44%; Pleistocene through Holocene). Recent colonizers (north-east and east) attributed to the greatest numbers (67 to 93%) of widespread taxa within the WGS, whereas older lineages (north and southwest) attributed to the greatest number (92%) of endemics. Furthermore, greatest species richness was in the eastern WGS, nearest the source (e.g., Mississippi River) of most recent colonizers during the last glacial maximum. Consequently, historical influences obscured contemporary influences of selection mechanisms. Nevertheless, a consistent pattern of colonization and extirpation has emerged since the Late Miocene, which likely will continue to influence species richness and endemism in the WGS and can be used to inform fish conservation policy.

CHAPTER I

PATTERNS OF ENDEMISM AND SPECIES RICHNESS OF FISHES OF THE WESTERN GULF SLOPE

INTRODUCTION

Ecological and evolutionary processes regulate contemporary community structure, although roles and influences of specific mechanisms (e.g. selection, drift, speciation, and dispersal) vary across time and space (Velland 2010). Contemporary fish communities are predominately influenced by environmental conditions (i.e., species-area relationships; species-energy relationships); however, the role of historical mechanisms (i.e., speciation and dispersal) is largely understated (Oberdorff et al. 2011). Historical mechanisms influence species pools from which contemporary communities are formed and therefore have an influence on contemporary communities. However, the influence of historical mechanisms is rarely implicated because of difficulties in testing historical influences at continental and intercontinental scales (Oberdorff et al. 2011). Assessments at smaller (regional) scales are necessary to inform global patterns in contemporary fish communities.

River systems within the Western Gulf Slope (WGS) drainages of North America are ideal riverscapes to assess the influence of selection and historical mechanisms on riverine fish communities because WGS drainages share a similar geological history, are

often isolated from one another by saltwater at river termini, but differ along contemporary precipitation gradient from west (24 mm per year) to east (150 mm per year). During the Pliocene (2.6 – 5.3 MA), the WGS experienced major geological and climatological changes. Southern drainages east of the continental divide flowed easterly into the Ancestral Southern Plains stream, likely near the present location of the Trinity River, and eventually into the Gulf of Mexico (Metcalf 1966, Conner 1977, Conner and Suttkus 1986, Cross et al. 1986, Mayden 1988). The north to south corridor of the Ancestral Southern Plains Stream, intersected by easterly flowing rivers, facilitated fish dispersion of north to south and east to west. Headward erosion of the Lower Pecos and Edwards Plateau rivers eventually captured and isolated the WGS streams (Woodruff 1977, Woodruff and Abbott 1979, Cross et al. 1986). During the Pleistocene (2.6 MA 10 12,000 YA), unglaciated areas of southern North America, including the WGS, were refugia for flora and fauna during glacial maxima (Soltis et al. 2006). During glacial periods and in the early stages of interglacials (i. e. the Early Holocene at 12,000 YA), lower sea levels and stream piracy enabled interconnectivity of many WGS river systems that facilitated fish dispersion along east and west gradients (Conner and Suttkus 1986). During interglacial periods, river systems gradually became more isolated as sea levels rose and river and terrestrial systems generally became drier and warmer (detailed in Al-Rabab'ah and Williams 2004).

Biotic responses since the last glacial maximum (LGM) are similar among flora and fauna. Species expansions were greatest before and at the start of interglacial periods, and population contractions and extirpations were greatest during interglacial periods. Climates of the WGS during interglacial periods tend towards increasing aridity as

glaciers migrate north but are punctuated by extreme dry periods, such as the Holocene Climate Optimum (2,500 to 5,000 year BP; Al-Rabab'ah and Williams 2004). Increasing aridity and lower water availability are directly related to population contractions and extirpation. Isolated drainages are less able to have dynamic equilibrium between dispersion and recolonization (Hugueny et al. 2010). Fishes found farther north and to the east of the WGS initially inhabited various drainages of the WGS but are now extirpated (Jurgens 2005, Johnson and Hill 2008). Some flora and fauna resisted extirpations and persist as relict populations, including odonates (Abbott 2001), salamanders of the genus *Plethodon* (Baird et al. 2006), short-tailed shrews *Blarina carolinensis* (Reilly et al. 2005), Texas Wild Rice *Zizania texana* (Horne and Kahn 1997), and loblolly pines *Pinus taeda* (Al-Rabab'ah and Williams 2004), eventually leading to higher numbers of endemic forms, especially among WGS fishes (Lee et al. 1980, Wiley and Mayden 1985, Eisenhour 2004, Near and Bernard 2004, Echelle et al. 2005, Schönhuth et al. 2008).

Purposes of this study were to assess the influences of contemporary factors (i.e., species-area relationships, climate, and species-energy relationships) and historical zoogeography on species richness, endemism, and distributions of WGS fishes. Fish distributions and factors influencing fish distributions have been reported for the WGS or parts of the WGS (i.e., Texas) (Evermann and Kendall 1892, Knapp 1953, Hubbs 1957, Conner 1977, Conner and Suttkus 1986, Smith and Miller 1986, Thomas et al. 2007, Hubbs et al. 2008) and provide invaluable observations of occurrence and native status of fishes before anthropogenic influences altered existing communities. My approach builds on the existing knowledge but also includes a finer resolution of fish distributions

at the sub-basin level based on updates in taxonomy, better understanding of species ranges, and updates in species phylogenies (Rauchenberger 1989, Richardson and Gold 1995 a & b, Broughton and Gold 2000, Johnson et al. 2001, Near et al. 2003, Eisenhour 2004, Near and Bernard 2004, Echelle et al. 2005, Blum et al. 2008, Schönhuth et al. 2008, Ayache and Near 2009) to inform ancestral histories and likely direction of dispersion among WGS fishes. Objectives of this study were to elucidate patterns in species richness and endemism across subdrainages of the WGS, to assess the relationships between species richness and endemism among HUC of areas, temperature, and productivity (using precipitation as a surrogate), and among ancestral origins of taxa and therefore infer directionality into and resident time within the WGS. I hypothesize that the numbers of species of fish per HUC will increase with water availability similar to Muneeppeerakul et al. (2008), that endemism rates to increase westward due to isolation in refugia of spring-fed systems (Oberdorff et al. 1999, Tribsch and Schönswetter 2003, Soltis et al. 2006, Reyjol et al. 2007), and that ancestral origins will have a quantifiable relationship with current distributions. Understanding of the role history and geological forces on contemporary fish communities within the WGS will inform how global fish communities are assembled in unglaciated regions but will also provide resource managers with predications on how past, current, and future communities will respond as the interglacial conditions continue to intensify and WGS climates move toward increasing aridity.

METHODS

Study area

The WGS encompasses the rivers that flow independently into the Gulf of Mexico from the Calcasieu in the east to the Rio Grande in the west (Figure 1). In total, WGS drains an area of 786,000 km². Study area includes the Calcasieu of Louisiana, all drainages of Texas except for the Red and Canadian rivers, and the Rio Grande and Pecos River of New Mexico and Colorado. Watersheds in the Rio Grande drainage of Mexico were eliminated in this study because of incomplete or incompatible data. Streams of the WGS flow through 14 US-EPA Level III Ecoregions including the Western Gulf Coastal Plains, South Central Plains, Texas Blackland Prairies, East Central Texas Plains, Southern Texas Plains, Cross Timbers, Edwards Plateau, Central Great Plains, Southwestern Tablelands, High Plains, Chihuahuan Deserts, Arizona/New Mexico Mountains, Arizona/New Mexico Plateau, and Southern Rockies (EPA 2011). Detailed physical descriptions of the rivers of the WGS can be found in Conner and Suttkus (1986) and Smith and Miller (1986). The WGS was divided into 196 sub-basins using USGS eight-digit Hydrologic Unit Codes (HUCs, Seaber et al 1987). Precipitation and temperature data were downloaded from <http://www.worldclim.org>, and the rasters were translated into annual averages by HUC using ArcGIS v. 9.2. The WGS has a largely east-to-west precipitation gradient from a maximum average annual precipitation of 150 cm in the Whiskey Chitto to a minimum of 24 cm in the Rio Grande-Fort Quitman HUC (Figure 2). The temperature gradient of the WGS is largely north to south, and ranges from a maximum annual average of 23°C in the Lower Rio Grande to a minimum annual

average of 0°C in the Rio Grande Headwaters HUC (Figure 3). Detailed summaries of the study area can be found in Conner and Suttkus (1986) and Smith and Miller (1986).

Fish

One hundred and fifty-five species of fish are considered native to the WGS based on available literature (Texas Freshwater Fishes, <http://www.bio.txstate.edu/~tbonner/txfishes/index.htm>, Conner and Suttkus 1986, Smith and Miller 1986, Hubbs et al. 2008, Hendrickson and Cohen 2010) and expert opinion. Fish were analyzed at the species level according to the latest accepted nomenclature (Nelson et al. 2004). Fifty-one species were determined to be endemic because all, or a vast majority, of their ranges were in the WGS. For some analyses, endemic fishes were further split into single-basin and regional endemics (Figure 4). *Catostomus plebeius*, *Notropis potteri*, *Cyprinodon rubrofluviatilis*, and *Percina macrolepida*, were categorized as endemic, although they are found in drainages adjacent to the WGS, their ranges are primarily in the WGS or show notable divergence from other populations outside of the WGS. One hundred and four species that occur in the WGS were considered to be widespread because their ranges extended over two or more geographical regions (i.e. the Western Gulf Slope as well as the Lower Mississippi Basin or the Eastern Gulf Slope) (similar to Morrone and Crisci 1995, Durand et al. 2003, and Reyjol et al. 2007). Some species were widespread and ubiquitous, and occur in drainages beyond the WGS as well as the Calcasieu and Rio Grande and most, if not all, basins in between (Figure 5). This term includes species with a southwestern range termination in the Rio Grande. Other

widespread species occurred in drainages beyond the WGS and had either their northeastern or southwestern range limit within the WGS (Figure 6). This group included species with disjunct (ranges interrupted by absence in one or more drainage basins between occupied drainages) populations within the WGS. Included within the fishes considered to be widespread with range terminations in the WGS were those with a northeastern range termination in the Rio Grande, but not widespread species with southwestern range terminations in the Rio Grande. Native ranges were delineated as the greatest extent reached before substantial anthropogenic habitat alteration, which began in the mid-1800s. Ranges of individual species (Appendix I, as maps) were determined by georeferencing data from written sources and 33 museum collections (Appendix II), using paper and electronic maps. Data on fish distributions were then entered into a matrix of occurrence by HUC. Literature and expert opinion were utilized to determine most probable recent native ranges. Temporal and spatial ancestral origins were determined using phylogenetic data (Rauchenberger 1989, Warren et al. 1994, Lydeard et al. 1995, Kristmundsdóttir and Gold 1996, Echelle and Echelle 1998, Simons and Mayden 1999, Broughton and Gold 2000, Bielawski and Gold 2001, Johnson et al. 2001, Raley and Wood 2001, Near et al. 2003, Underwood et al. 2003, Eisenhour 2004, Near and Benard 2004, Echelle et al. 2005, Blum et al. 2008, Schönhuth et al. 2008, Ayache and Near 2009, Bufalino and Mayden 2010) as well as ranges of present species and relatives within and beyond the WGS (Lee et al. 1980, Page and Burr 1991).

Statistical analyses

Linear regression models were used to test relationships among independent variables (e.g., HUC average annual precipitation, temperature, and area) and dependent variables (e.g., total species, number of endemic species, percentage of endemic species, percentage of northern origin fishes, percentage of eastern origin fishes, percentage of southwestern origin fishes, and percentage of northern/eastern origin fishes). Regression models were generated with SigmaPlot 10.0 (Systat Software, Inc. www.sigmaplot.com). HUCs containing fewer than four species were eliminated from the analyses due to lack of data, as well as HUCs in predominantly saline water due to their proximity to the coast and fluctuating salinities. Consequently, 149 of the available 196 HUCs of the WGS were retained for analysis (Figure 7). Average faunal similarity (AFS) analyses were conducted using PRIMER 6 (Primer-E, <http://www.primer-e.com/>). Drainages and HUCs were compared using the Kulczynski P/A method. Resemblances were analyzed by drainage using cluster analysis of grouped averages.

RESULTS

Fish community consisted of 23 families, 57 genera, and 155 native freshwater fishes among WGS drainages (Table 1). Ancestral origins of the 155 fishes were from the East (44%), North (28%), Southwest-West (15%), and North-East (14%) (Figure 8). Among drainages, richness ranged from 46 species in Nueces drainage to 87 species in the Calcasieu and Sabine drainages (Figure 9) with average faunal similarities among drainages ranging from 34% between the Rio Grande and Calcasieu to 97% between the

Neches and Sabine (Figure 10). Among 8-digit HUCs ($N = 149$), species richness ranged from four species in the Rio Grande headwaters, Conejos, and Rio Puerco, to 86 species in Lower Sabine (Figure 11). Thirty-five species (23%) were widespread and ubiquitous across the WGS, 69 species (45%) were widespread with range terminations in drainages of the WGS, and 51 species (33%) were endemic to the WGS (Table 1).

Among the 35 widespread ubiquitous fishes, five fishes occurred in drainages to the northeast and to the southwest of the WGS, and 30 fishes have southwestern range terminations in the Rio Grande drainage. Ancestral origins of fishes occurring in drainages to the northeast and to the southwest of the WGS were from the East ($N = 2$; *Atractosteus spatula*, *Fundulus grandis*), North-East ($N = 2$; *Cyprinella lutrensis*, *Aplodinotus grunniens*), and Southwest-West ($N = 1$; *Cyprinidon variegatus*). Ancestral origins of fishes with southwestern range terminations in the Rio Grande drainage were from the North-East (37%), East (30%), North (27%), and Southwest-West (7%).

Among the 69 widespread species with range terminations in the WGS, 66 fishes had southwestern range limits, of which 15 fishes had disjunct distributions, and three fishes had northeastern range limits (Table 1). Ancestral origins of fishes with southwestern range limits were from the East (82%), North-East (11%), and North (8%). Southwestern range terminations occurred predominantly in the Colorado ($N = 13$), San Jacinto ($N = 11$), Nueces ($N = 11$), and Brazos ($N = 9$).

Among fishes with disjunct distributions, eight species were disjunct among parallel drainages and had ancestral origins from the East (75%, *Notropis chalybaeus*, *Erimyzon sucetta*, *Minytrema melanops*, *Lepomis symmetricus*, *Etheostoma gracile*,

Percina shumardi), North (13%, *Phenacobius mirabilis*), and North-East (13%, *Macrhybopsis hyostoma*), three fishes were found in the Rio Grande and eastern drainages of the WGS but absent from multiple drainages within the WGS with ancestral origins from the north (*Pimephales promelas*, *Fundulus zebrinus*) and north-east (*Semotilus atromaculatus*), and four were only in central drainages of the WGS with ancestral origins from the North (75%, *Hybognathus placitus*, *Macrhybopsis storeriana*, *Etheostoma spectabile*) and the North-East (25%, *Notropis shumardi*).

Among the three widespread species with northeastern range terminations in the WGS, two occurred in the Rio Grande and one occurred in the Nueces River basin. Ancestral origins of species with range terminations in the Rio Grande were the North (*Campostoma ornatum*) and the Southwest (*Poecilia formosa*). Ancestral origin of the taxon with northeastern range termination in the Nueces River drainage was from the Southwest (*Asytanax mexicana*).

Among the 51 species endemic to the WGS, 37 fishes were restricted to one basin (basin endemics), and 14 fishes resided in two or more basins in the WGS (regional endemics) (Figures 12 and 13). Ancestral origins of endemic fishes were from the North (57%), Southwest-West (35%), East (6%), and North-East (2%).

Basin and regional endemics were predominantly found in the Rio Grande ($N = 35$), Guadalupe ($N = 14$), Colorado ($N = 11$), San Antonio ($N = 10$), Brazos ($N = 9$), and Nueces ($N = 6$). Among the HUCs, total number of WGS endemic fishes ranged from zero in Lower Clear Fork Brazos, Hubbard, Mission, Aransas, Lower Nueces, San Fernando, and Palo Blanco HUCs, to 17 in the Elm-Sycamore HUC in the Rio Grande

basin (Figure 16). HUCs within the Rio Grande Basin with large number of endemics were Elm-Sycamore ($N = 17$), Amistad Reservoir ($N = 16$), and Lower Devils River ($N = 16$). HUCs within the Pecos River Basin with large number of endemics were Lower Pecos ($N = 16$), Lower Pecos-Red Bluff Reservoir ($N = 14$), Upper Pecos-Black ($N = 13$), Upper Pecos-Long Arroyo ($N = 12$), Rio Hondo ($N = 12$), and Independence Creek ($N = 12$). HUCs within the Guadalupe River Basin with large number of endemics were Middle Guadalupe River ($N = 12$) and San Marcos ($N = 12$). In contrast, areas generally low in number of endemic fishes ($N \leq 1$) were the eastern third of the WGS, coastal drainages of Texas, and endorheic or highly xeric drainages in the western WGS.

Distribution associations

Fishes grouped by ancestral origins were not homogeneously distributed throughout the WGS. Species of eastern origin comprised a large percentage of fish communities in the eastern WGS, northern and southwestern origin fishes were prevalent in the western WGS, and north-east origin fishes were found throughout the WGS. Percentage of eastern origin fishes per HUC was positively associated with annual precipitation ($r^2 = 0.87, P < 0.01$) and weakly associated with annual temperature ($r^2 = 0.19, P < 0.01$) and area ($r^2 = 0.05, P < 0.01$) (Figure 15). Percentage of northern origin fishes per HUC was negatively associated ($r^2 = 0.54, P < 0.01$) with annual precipitation, negatively associated ($r^2 = 0.52, P < 0.01$) with annual temperature, and weakly associated with area ($r^2 = 0.08, P < 0.01$). Percentage of southwestern fishes per HUC was negatively associated ($r^2 = 0.50, P < 0.01$) with annual precipitation and weakly associated with

annual temperature ($r^2 = 0.06$, $P < 0.01$) (Figure 17). Percentage of North-East origin fishes per HUC was weakly associated with annual precipitation ($r^2 = 0.12$, $P < 0.01$) and with annual temperature ($r^2 = 0.05$, $P < 0.01$) (Figure 18).

Species richness and the number of endemic species were not homogeneously distributed among HUCs. Mean species richness was 67 (± 14 , $N = 30$) among HUCs with ≥ 100 cm annual precipitation (i.e., roughly east Texas and western Louisiana), 35 (± 14 , $N = 77$) among HUCs with $100 > X > 50$ cm annual precipitation, and 21 (± 10 , $N = 42$) among HUCs with ≤ 50 cm annual precipitation (i.e., Trans-Pecos region and northern extent of the Chihuahuah Desert). Species richness was positively associated ($r^2 = 0.72$, $P < 0.01$) with annual precipitation. Species richness was positively associated ($r^2 = 0.69$) with mean annual surface temperature by HUC, and no relationship was detected ($r^2 < 0.01$, $P = 0.68$) between species richness and surface area of HUC. Number of endemic fishes was negatively associated ($r^2 = 0.19$, $P < 0.01$) with annual precipitation totals (Figure 14), and was not associated ($r^2 < 0.01$, $P = 0.54$) with annual temperature or area of HUC ($r^2 = 0.05$, $P < 0.01$). Endemics as a percentage of total number of species was negatively associated ($r^2 = 0.56$, $P < 0.01$) with annual precipitation totals (Figure 19). Endemics as a percentage of total number of species was weakly associated ($r^2 = 0.25$, $P < 0.01$) with annual temperature, but not area of HUC ($r^2 = 0.07$, $P < 0.01$).

DISCUSSION

Zoogeographical analyses of the WGS fish community supports my initial predications that occurrence and persistence of the extant WGS fish community are attributed to timing and source of ancestral colonization and to productivity and water quantity of a basin. The occurrence and distribution of species or descendants from three directional sources of ancestral origin demonstrate that the contemporary WGS fish community is a result of colonization events occurring from several million years ago to as recent as the last glacial maximum. Fishes from Northern and Southwestern origins most likely represent lineages with the longest tenure in the WGS. Northern and Southwestern lineages comprise the largest proportion of endemic fishes (collectively 92% of all endemics), likely associated with their long tenure in the WGS and multiple dispersion opportunities starting with geologic upheavals of the Miocene and Pliocene, multiple isolation and extirpation events due to changing climates, and further dispersal events throughout the Pleistocene (Conner and Suttkus 1986).

Also during the Pleistocene, more recent invasions from Eastern ancestral lineages colonized the WGS, giving rise to the largest number of widespread forms (63% of all widespread forms). A fourth category of ancestral origins comprises fishes from both Northern and Eastern origins (North-East). Given that sister lineages reside north and east of the WGS (Richardson and Gold 1995b, Eisenhour 2004), these fishes most likely invaded from the north until the Miocene/Pliocene following the same routes as northern-origin species (Cross et al. 1986), and then invaded the WGS again from the east during the Pleistocene. North-East origin fishes generally have widespread

distributions within the WGS and comprise 19% of the total number of widespread species and 2% of endemic species. However, timing and ancestral source of colonization alone does not explain contemporary patterns in freshwater fish distributions within the WGS.

Persistence and radiation of ancestral forms within the WGS are associated with the contemporary precipitation gradient, which was used as a surrogate for productivity and water quantity. Species richness in the WGS was positively associated with areas of higher precipitation, supporting the theory that consistent water availability and associated productivity of a region are likely mechanisms for fish persistence (Schlosser 1995, Oberdorff et al. 1995, Oberdorff et al. 1997). Conversely, numbers of endemic fishes in the WGS were inversely associated with precipitation gradients, consistent with evolutionary theory that isolated and novel environments drive fish species radiation (Near and Benard 2004, Reyjol et al. 2007). Collectively, ancestral origin and contemporary water quantities were primary determinants of composition of fish communities within the WGS.

Contemporary biological communities are consequence of available species pools attributed to numerous invasions and colonization events through time (Taylor et al. 1990, Vermeij 1991, Ricklefs and Schluter 1994, Huston 1999). Among freshwater fish communities, ancestral stocks dispersed and colonized during Miocene and Pliocene era refuges from advancing glaciers and subsequent dispersal of fishes influenced fish communities throughout Europe and North America during the Pleistocene (Oberdorff et al. 1995, Oberdorff et al. 1997, Solitis et al. 2006, Reyjol et al. 2007). Conner and Suttkus (1986) recognized multiple routes and different times of colonization and

dispersal for fishes within WGS, but we further refined their classification scheme by including recently described species (i.e., *Macrhybopsis* spp. in Eisenhour 2004, *Dionda* spp. in Schonhuth et al. 2008), an updated distribution of fishes by HUC, and a more recent understanding of species phylogeny. Sources and timing of fish invasions into the WGS not only give clues about the ancestral biotic constraints of species, but also time of residence, which can influence probability of persistence and speciation.

The cohort of fishes with northern origins (28% of fishes) contains the species with longest times of residence in the WGS. Ancestors of northern origin species colonized from the Great Plains to the WGS and arrived in multiple waves from at the least the Late Miocene through the Pleistocene. Evidence of early waves of invasion from the north come from a Miocene/Pliocene divergence of *Dionda* species (Schonhuth et al. 2008), Pliocene divergence of the *Macrhybopsis aestivalis* complex (Eisenhour 2004), and a 6-4.5 mya divergence time of *Cyprinella luternsis* and *C. lepida* complex (Richardson and Gold 1995b). The earliest waves of extant fishes consisted of fishes travelling the hypothesized Ancestral Plains Stream basin that flowed southward from Kansas (Figure 20) until the glaciations of the Pleistocene (Metcalf 1966). Major ancestral drainages in the WGS flowed in an easterly direction, much like the upper reaches of present day drainages, and bounded by the Rocky Mountains to the west (Metcalf 1966, Conner 1977, Conner and Suttkus 1986, Cross et al. 1986, Mayden 1988). The north to south corridor of the Ancestral Plains Stream allowed active movement of fishes to the south, as well as passive transport of populations across WGS basins via stream captures and avulsions. Fishes originally of northern origin that dispersed initially into southern WGS and later northeastward include endemic forms such as *Dionda*,

Macrhybopsis, and some *Notropis* and *Cyprinella* species, which are similar routes of dispersal as the southwestern origin fishes.

The cohort of fishes with southwestern origin (15% of fishes) has inhabited the area since at least the Late Miocene or Early Pliocene. Echelle et al. (2005) suggests that the genus *Cyprinodon* diverged during Late Miocene, and clades containing the *Cyprinodon* of the WGS diverged in the Early Pliocene (~4.6-4.9 mya), which places their time of arrival and radiation in the WGS similar to those of northern origin fishes. Fishes of southwestern origin likely dispersed along inland and coastal routes. The inland route of dispersal was made possible by the active geology and variable climate of the Rio Grande/Pecos regions and drainages directly to the south (Smith and Miller 1986). *Gambusia* species penetrate further into the WGS than *Cyprinodon*, most likely attributable to the persistence of *Gambusia* in freshwater springs, whereas *Cyprinodon* species are extremophiles and are more able to persist in less reliable surface waters (i.e., non-spring environments) (Echelle and Echelle 1978). Coastal dispersal is suggested by the ranges of *Cyprinodon variegatus*, *Gambusia affinis*, and *Poecilia latipinna*, which exhibit widespread distributions along the coast beyond the WGS. Salt tolerances of these three species (Brown and Feldmeth 1971, Page and Burr 1991, Hubbs 2000) suggest probable coastal dispersal since the Pliocene, punctuated in the Pleistocene during drastic sea-level fluctuations, and continuing through present time.

The cohort of fishes with eastern origin (44% of current species) arrived in the WGS more recently than those of northern or southwestern descent. Westward range extensions of eastern fishes are attributed to incremental movements toward the west when sea levels fell during numerous glacial advancements during the Pleistocene and

rivers sharing bay systems (Sabine-Neches, Trinity-San Jacinto, and Guadalupe-San Antonio) merged together via downstream connections (Figure 21), such as the Sabine-Neches-Trinity (Phillips 2009), Sabine-Calcasieu, Colorado-Brazos, and at times a single stream that contained the Colorado, Brazos, San Jacinto, and Trinity (Conner 1977, Conner and Suttkus 1986). Concurrent or subsequent connections also occurred in basins via stream avulsions (Phillips 2009), such as numerous stream captures that occurred throughout the Edwards Plateau region (Woodruff, 1977), Navasota River from the Trinity basin to the Brazos River basin (Rozenburg et al. 1972, Phillips 2009), and the capture of west-east flowing streams by the Pecos (Smith and Miller 1986).

In this study, 14% of the fishes were classified as north-east origin. The majority of these fishes were previously designated by Conner and Suttkus (1986) as residual species; however, part of their definition of residual was that these fishes were widespread in preglacial drainages. The ubiquitous nature of fishes across the WGS does not necessarily translate to being residual. Fishes classified as of north-east origin colonized the WGS via northern routes, such as upper and middle reaches of the Pecos River, Rio Grande, and Trinity River. Fishes of N/E origin show little or no evidence of recent speciation, suggesting that populations which faced similar environmental conditions as northern-derived fishes have had either existing gene pools bolstered by later waves of invasion or the populations were derived from recent colonization events. Occurrences of north-east fishes in eastern and coastal drainages that would have been, at various times during the Pleistocene, inundated by the sea (i.e. the Mission, Lavaca/Navidad, San Bernard, and San Jacinto) (Belcher 1975, Richardson and Gold 1995a) suggest subsequent eastern re-invasion of these species. Eisenhour (2004) found

that Brazos River and Colorado River populations of *Macrhybopsis hyostoma* were more similar to Southern Plains populations to the north of the WGS, whereas *M. hyostoma* of the Sabine River were more similar to populations in the Central Coastal Plain.

Morphology of *M. hyostoma* coupled with its absence from the Trinity and San Jacinto suggests waves of invasion from the North as well as the East. Populations of *Micropterus salmoides* in WGS show signs of divergence, and suggest multiple invasions over time (Edwards 1980, Lutz-Carrillo et al. 2006). *Micropterus treculii* is included in the N/E group because of a complex history with mtDNA suggesting close relationships to *M. salmoides*, *M. dolomieu*, and *M. punctulatus* (Johnson 2001, Near 2003), and nuclear DNA suggesting *M. henshalli* is the sister species with a divergence time of 2.5 mya (Tom Near, personal communication). The complex mitochondrial history suggests a long history of introgression, which still occurs today (Garrett 1991, Littrell 2007)

In addition to various past colonization events, contemporary biological communities are a consequence of environmental filters (Oberdorff et al. 1995, Oberdorff et al. 1997). Three commonly-used environmental filters (precipitation, temperature, and HUC area) differed in their association with species richness and number of endemics within the WGS. Precipitation, used as a surrogate for productivity but also might be a surrogate for area, was an adequate predictor of species richness and number of endemics, whereas temperature and HUC area were poor predictors of richness and endemics. Species richness was positively associated with precipitation, with larger numbers of species occurring in eastern part of the WGS. In contrast, the numbers of endemics were negatively associated with precipitation, specifically larger numbers of endemics in the western part of the WGS. Positive relationships between species

richness and precipitation (i.e., productivity, area, and water availability) in the WGS are similar to trends reported for numerous flora and fauna within drainages (Angermeier and Schlosser 1989), across drainages (Muneepeerakul et al. 2008) including the WGS (Lee 1980, Owen and Dixon 1989), and within continents (McAllister et al. 1986, Pearson and Carroll 1998, Hubbell 2001). Globally, the effects of productivity on species richness are disputed, but often show a unimodal or positive linear relationship (Huston 1979, Huston 1999, Waide et al. 1999, Mittelbach et al. 2001), and a positive linear relationship with productivity would be expected at the scale of this study. Endemism is linked to not only productivity (or water availability), but also to a predominant historical element of isolation in refugia (Oberdorff et al. 1999, Tribsch and Schönswetter 2003, Soltis et al. 2006, Reyjol et al. 2007). The differences between the patterns of endemism between this study and those of Oberdorff et al. (1999) and Reyjol et al. (2007) are possibly scaling issues, as those studies assessed regional and continental patterns and not patterns within a region as this study did.

Collectively, patterns in species richness, endemism, ancestral origins, and environmental associations provide the basic elements of a generalized conceptual model that describes the origin of the WGS fish community. Since the Miocene era, multiple waves of colonizing fish entered the WGS via numerous interconnections of the watersheds, either by inland connections or by lower sea levels. Once in the WGS, changing environmental conditions allowed some fishes to persist while others are extirpated. Isolation frequently occurs with sea level rise when a river terminus enters the saltwater environments of the Gulf of Mexico. It is likely that isolation and restriction of gene flow, along with environmental novelties across the large geographic

span of the WGS facilitated speciation. Since the Pleistocene, numerous glacial advances and declining sea levels facilitated westward movement of eastern fishes into the WGS, whereas numerous glacial retreats and rising sea levels isolated drainages and fishes.

During the last glacial event (Wisconsin Glacial Episode: 110,000 to 12,000 years ago), lower sea levels and cooler and wetter climates, generating mean annual discharges up to 400% greater than today within the WGS (Sylvia and Galloway 2006) allowed fishes to colonize or recolonize the inland waters of the WGS. Since the Holocene interglacial climate shifts and glacial retreats have increased aridity (drier and warmer) within the WGS. The persistent North American gradient of increased aridity from west to east since the end of the Pleistocene has not been constant (Al-Rabab'ah and Williams 2004), but is marked with periods of extreme dryness followed by cooler and wetter climates.

The fish communities of the WGS have experienced an eastward shift as rainfall has decreased westward since the LGM, where with increasing aridity, increasing extinction rates and more frequent isolation events in novel arid environments leading to speciation. (this study, Hewitt 2000, Davis and Shaw 2001, Al-Rabab'ah and Williams 2004). This process, repeated during each of the previous interglacial events, is the likely isolating mechanism leading to restriction of gene flow and higher rates of speciation and endemism in the western WGS but also higher extinction (lower richness; Cracraft 1985). Consequently, species richness is highest in the eastern WGS primarily because the eastern drainages are nearest to the most recent direction of colonization and also because higher precipitation and water quantity dampens environmental extremes that could lead

to extinction. Endemism is highest in the western WGS because of past and current isolation and environmental novelties of a more arid region.

Two areas within the WGS had slightly higher rates of endemism than expected: upper reaches of the Brazos River basin and the Edwards Plateau region of Texas. The Brazos is the second-largest river in the region (the Rio Grande/Pecos is the largest), and spans seven ecoregions. Unlike WGS rivers to the east, a large portion of the Brazos experiences harsh plains and highland conditions (including the refugia provided by karst aquifers) in the upper reaches, and more stable, low gradient conditions in the lower reaches. The Edwards Plateau is another unique feature within the WGS with a large and vast karst groundwater source (Edwards and Trinity aquifers) producing stable spring flows and highly reliable surface flows in streams and rivers. Karst aquifers differ from other types of aquifers in a number of features (White 1988), but the most relevant is the permanency of surface water. With perennial contribution to base flows, some of the rivers originating in the Edwards Plateau likely had more permanent water than in other regions of WGS, creating refugia for aquatic biota especially in extreme dry periods during interglacial times, such as the most recent altithermal period. As such, extinction rates were limited by the more permanent groundwater sources, and isolation persisted increasing the probability of speciation.

Assuming that our generalized conceptual model of fish origins in the WGS is accurate, we note some interesting trends in fish conservation and can make some predictions about the future of fishes within the WGS. The number of threatened and endangered species is highest out west. This is expected because these species face the greatest threat of extinctions and have isolated populations with restricted ranges, but

these are natural phenomena. As natural resource managers, we have limited options when it comes to protecting species with small distributions in environments with high extinction rates (Olden et al. 2010). Maintaining species only in hatcheries, by using translocation, and assisted migration (Mueller and Hellmann 2008) to maintain reproductive viability poses economic and conservation challenges. In the future, unless something diverts the current trajectory of climate, we predict that the extirpation front will continue moving eastward as it leaves even higher probabilities of extinction in its wake westward.

Eventually, climate may shift back to being cooler and wetter in the WGS with lower sea levels, and we should expect that fish will recolonize the region from refugia in the East, as they have throughout the glacial cycles. For this reason, there should be increased efforts to protect the species rich, but endemic poor, areas in the eastern drainages of the WGS. Maintaining source populations for future colonization is a better conservation strategy than focusing efforts only on saving rare and endemic species, which may be doomed to extinction due to natural processes, and are, in effect, sinks.

Table 1. Natural fish occurrences by basin with ancestral origin, distributional designation, and range termination. (Origin: N = North, SW = Southwest, N/E = North and East, E = East. Designation: W = Widespread, E = Regional Endemic, E* = Basin Endemic. Termination: S = Southern or Southeastern, N = Northern or Northeastern. Numbers in (parentheses) are total number of species.)

Family	Species	Drainage											Origin	Designation	Termination
		Rio Grande (73)	Nueces (46)	San Antonio (50)	Guadalupe (60)	Colorado (71)	Brazos (76)	San Jacinto (73)	Trinity (82)	Neches (83)	Sabine (87)	Calcasieu (87)			
Petromyzontidae	<i>Ichthyomyzon castaneus</i>									X	X	X	E	W	S
	<i>Ichthyomyzon gagei</i>							X	X	X	X	X	E	W	S
Acipenseridae	<i>Scaphirhynchus platyrhynchus</i>	X											N	W	S
Polyodontidae	<i>Polyodon spathula</i>							X	X	X	X	X	E	W	S
Lepisostidae	<i>Atractosteus spatula</i>	X	X	X	X	X	X	X	X	X	X	X	E	W	
	<i>Lepisosteus oculatus</i>	X	X	X	X	X	X	X	X	X	X	X	E	W	S
	<i>Lepisosteus osseus</i>	X	X	X	X	X	X	X	X	X	X	X	E	W	S
	<i>Lepisosteus platostomus</i>											X	E	W	S
Amiidae	<i>Amia calva</i>					X	X	X	X	X	X	X	E	W	S
Clupeidae	<i>Dorosoma cepedianum</i>	X	X	X	X	X	X	X	X	X	X	X	N/E	W	S
	<i>Dorosoma petenense</i>	X	X	X	X	X	X	X	X	X	X	X	E	W	S

Table 1-Continued

Family	Species	RG	Nu	SA	G	C	B	SJ	T	Ne	S	C	Or	Des	Term	
Cyprinidae	<i>Campostoma anomalum</i>	X	X	X	X	X	X		X				N	W	S	
	<i>Campostoma ornatum</i>	X											N	W	N	
	<i>Cyprinella lepida complex</i>		X	X	X								N	E		
	<i>Cyprinella lutrensis</i>	X	X	X	X	X	X	X	X	X	X	X	N/E	W		
	<i>Cyprinella proserpina</i>	X											N	E*		
	<i>Cyprinella venusta</i>	X	X	X	X	X	X	X	X	X	X	X	E	W	S	
	<i>Dionda argentosa</i>	X											N	E*		
	<i>Dionda diaboli</i>	X											N	E*		
	<i>Dionda episcopa</i>	X											N	E*		
	<i>Dionda nigrotaeniata</i>			X	X	X							N	E		
	<i>Dionda serena</i>		X										N	E*		
	<i>Gila pandora</i>	X											SW	E*		
	<i>Hybognathus amarus</i>	X											N	E*		
	<i>Hybognathus hayi</i>											X	X	E	W	S
	<i>Hybognathus nuchalis</i>							X	X	X	X	X	X	E	W	S
	<i>Hybognathus placitus</i>						X	X						N	W	S
	<i>Hybopsis ammis</i>				X	X	X	X	X	X	X	X	X	E	W	S
	<i>Lythrurus fumeus</i>					X	X	X	X	X	X	X	X	E	W	S
	<i>Lythrurus umbratilis</i>								X	X	X	X	X	E	W	S
	<i>Macrhybopsis aestivalis</i>	X												N	E*	
	<i>Macrhybopsis hyostoma</i>						X	X			X	X	X	N/E	W	S
	<i>Macrhybopsis marconis</i>			X	X	X								N	E	
	<i>Macrhybopsis storeriana</i>							X						N	W	S
	<i>Notemigonus crysoleucas</i>		X	X	X	X	X	X	X	X	X	X	X	N/E	W	S
	<i>Notropis amabilis</i>	X	X	X	X	X								N	E	

Table 1-Continued

Family	Species	RG	Nu	SA	G	C	B	SJ	T	Ne	S	C	Or	Des	Term
	<i>Notropis atherinoides</i>								X	X	X	X	N	W	S
	<i>Notropis atrocaudalis</i>						X	X	X	X	X	X	E	E	
	<i>Notropis braytoni</i>	X											N	E*	
	<i>Notropis buccula</i>						X						N	E*	
	<i>Notropis buchanani</i>	X	X	X	X	X	X		X	X	X	X	N/E	W	S
	<i>Notropis chalybaeus</i>				X						X		E	W	S
	<i>Notropis chihuahua</i>	X											N	E*	
	<i>Notropis jemezanus</i>	X											N	E*	
	<i>Notropis orca</i>	X											N	E*	
	<i>Notropis oxyrhynchus</i>						X						N	E*	
	<i>Notropis potteri</i>					X	X	X	X				N	E	
	<i>Notropis sabiniae</i>							X	X	X	X	X	E	W	S
	<i>Notropis shumardi</i>					X	X		X				N/E	W	S
	<i>Notropis simus</i>	X											N	E*	
	<i>Notropis stramineus</i>	X	X	X	X	X							N	W	S
	<i>Notropis texanus</i>		X	X	X	X	X	X	X	X	X	X	E	W	S
	<i>Notropis volucellus</i>		X	X	X	X	X	X	X	X	X	X	E	W	S
	<i>Opsopoeodus emiliae</i>		X	X	X	X	X	X	X	X	X	X	E	W	S
	<i>Phenacobius mirabilis</i>					X			X	X	X		N	W	S
	<i>Pimephales promelas</i>	X				X	X		X				N	W	S
	<i>Pimephales vigilax</i>	X	X	X	X	X	X	X	X	X	X	X	E	W	S
	<i>Platygobio gracilis</i>	X											N	W	S
	<i>Rhinichthys cataractae</i>	X											N	W	S
	<i>Semotilus atromaculatus</i>	X							X	X	X	X	N/E	W	S
Catostomidae	<i>Carpiodes carpio</i>	X	X	X	X	X	X	X	X	X	X		N/E	W	S

Table 1-Continued

Family	Species	RG	Nu	SA	G	C	B	SJ	T	Ne	S	C	Or	Des	Term
	<i>Catastomus commersoni</i>	X											N	W	S
	<i>Catostomus plebeius</i>	X											N	E	
	<i>Cycleptus elongatus</i>		X	X	X	X	X	X	X	X	X	X	N/E	W	S
	<i>Cycleptus sp. Rio Grande</i>	X											N	E*	
	<i>Erimyzon oblongus</i>							X	X	X	X	X	E	W	S
	<i>Erimyzon sucetta</i>				X		X	X	X	X	X	X	E	W	S
	<i>Ictiobus bubalus</i>	X	X	X	X	X	X	X	X	X	X	X	E	W	S
	<i>Minytrema melanops</i>					X	X	X	X	X	X	X	E	W	S
	<i>Moxostoma austrinum</i>	X											N	E*	
	<i>Moxostoma congestum</i>	X	X	X	X	X	X						N	E	
	<i>Moxostoma poecilurum</i>							X	X	X	X	X	E	W	S
Characidae															
	<i>Astyanax mexicanus</i>	X	X										SW	W	N
Ictaluridae															
	<i>Ameiurus melas</i>		X	X	X	X	X	X	X	X	X	X	E	W	S
	<i>Ameiurus natalis</i>		X	X	X	X	X	X	X	X	X	X	E	W	S
	<i>Ictalurus furcatus</i>	X	X	X	X	X	X	X	X	X	X	X	N/E	W	S
	<i>Ictalurus lupus</i>	X	X	X	X	X							N	E	
	<i>Ictalurus punctatus</i>	X	X	X	X	X	X	X	X	X	X	X	N/E	W	S
	<i>Noturus gyrinus</i>		X	X	X	X	X	X	X	X	X	X	E	W	S
	<i>Noturus nocturnus</i>						X	X	X	X	X	X	E	W	S
	<i>Pylodictis olivaris</i>	X	X	X	X	X	X	X	X	X	X	X	N/E	W	S
Esocidae															
	<i>Esox americanus</i>						X	X	X	X	X	X	E	W	S
	<i>Esox niger</i>										X	X	E	W	S

Table 1-Continued

Family	Species	RG	Nu	SA	G	C	B	SJ	T	Ne	S	C	Or	Des	Term
Salmonidae	<i>Oncorhynchus clarkii virginalis</i>	X											N	E*	
Aphredoderidae	<i>Aphredoderus sayanus</i>					X	X	X	X	X	X	X	E	W	S
Atherinopsidae	<i>Labidesthes sicculus</i>							X	X	X	X	X	E	W	S
	<i>Menidia beryllina</i>	X	X	X	X	X	X	X	X	X	X	X	E	W	S
Fundulidae	<i>Fundulus blairae</i>						X	X	X	X	X	X	E	W	S
	<i>Fundulus chrysotus</i>					X	X	X	X	X	X	X	E	W	S
	<i>Fundulus grandis</i>	X	X			X	X	X	X	X	X	X	E	W	
	<i>Fundulus notatus</i>			X	X	X	X	X	X	X	X	X	E	W	S
	<i>Fundulus olivaceus</i>						X	X	X	X	X	X	E	W	S
	<i>Fundulus zebrinus</i>	X				X	X		X				N	W	S
	<i>Lucania parva</i>	X	X			X		X	X	X	X	X	E	W	S
Poeciliidae	<i>Heterandria formosa</i>										X	X	E	W	S
	<i>Gambusia affinis</i>	X	X	X	X	X	X	X	X	X	X	X	SW	W	S
	<i>Gambusia amistadensis</i>	X											SW	E*	
	<i>Gambusia clarkhubbsi</i>	X											SW	E*	
	<i>Gambusia gaigei</i>	X											SW	E*	
	<i>Gambusia geiseri</i>				X								SW	E*	
	<i>Gambusia georgei</i>				X								SW	E*	
	<i>Gambusia heterochir</i>					X							SW	E*	
	<i>Gambusia nobilis</i>	X											SW	E*	

Table 1-Continued

Family	Species	RG	Nu	SA	G	C	B	SJ	T	Ne	S	C	Or	Des	Term
	<i>Gambusia senilis</i>	X											SW	E*	
	<i>Gambusia speciosa</i>	X											SW	E*	
	<i>Poecilia formosa</i>	X											SW	W	N
	<i>Poecilia latipinna</i>	X	X	X	X	X	X	X	X	X	X	X	SW	W	S
Cyprinodontidae															
	<i>Cyprinodon bovinus</i>	X											SW	E*	
	<i>Cyprinodon elegans</i>	X											SW	E*	
	<i>Cyprinodon eximius</i>	X											SW	E*	
	<i>Cyprinodon eximiussp.</i>	X											SW	E*	
	<i>Cyprinodon pecosensis</i>	X											SW	E*	
	<i>Cyprinodon rubrofluviatilis</i>						X						SW	E	
	<i>Cyprinodon talarosa</i>	X											SW	E*	
	<i>Cyprinodon variegatus</i>	X	X		X	X	X	X	X	X	X	X	SW	W	
Moronidae															
	<i>Morone mississippiensis</i>							X	X	X	X	X	E	W	S
Centrarchidae															
	<i>Centrarchus macropterus</i>							X	X	X	X	X	E	W	S
	<i>Lepomis cyanellus</i>	X	X	X	X	X	X	X	X	X	X	X	N/E	W	S
	<i>Lepomis gulosus</i>		X	X	X	X	X	X	X	X	X	X	N/E	W	S
	<i>Lepomis humilis</i>					X	X	X	X	X	X	X	N/E	W	S
	<i>Lepomis macrochirus</i>	X	X	X	X	X	X	X	X	X	X	X	N/E	W	S
	<i>Lepomis marginatus</i>						X	X	X	X	X	X	E	W	S
	<i>Lepomis megalotis</i>	X	X	X	X	X	X	X	X	X	X	X	N/E	W	S
	<i>Lepomis microlophus</i>				X	X	X	X	X	X	X	X	E	W	S
	<i>Lepomis miniatus</i>	X	X	X	X	X	X	X	X	X	X	X	E	W	S
	<i>Lepomis symmetricus</i>					X	X	X	X	X	X	X	E	W	S

Table 1-Continued

Family	Species	RG	Nu	SA	G	C	B	SJ	T	Ne	S	C	Or	Des	Term
	<i>Micropterus punctulatus</i>			X	X	X	X	X	X	X	X	X	N/E	W	S
	<i>Micropterus salmoides</i>	X	X	X	X	X	X	X	X	X	X	X	N/E	W	S
	<i>Micropterus treculii</i>			X	X	X	X						N/E	E	
	<i>Pomoxis annularis</i>		X	X	X	X	X	X	X	X	X	X	E	W	S
	<i>Pomoxis nigromaculatus</i>						X	X	X	X	X	X	E	W	S
Percidae	<i>Ammocrypta vivax</i>							X	X	X	X	X	E	W	S
	<i>Ammocrypta clara</i>									X	X	X	E	W	S
	<i>Etheostoma artesia</i>									X	X	X	E	W	S
	<i>Etheostoma asprigene</i>									X	X	X	E	W	S
	<i>Etheostoma chlorosomum</i>			X	X	X	X	X	X	X	X	X	E	W	S
	<i>Etheostoma collettei</i>											X	E	W	S
	<i>Etheostoma fonticola</i>				X								E	E*	
	<i>Etheostoma fusiforme</i>											X	E	W	S
	<i>Etheostoma gracile</i>		X		X	X	X	X	X	X	X	X	E	W	S
	<i>Etheostoma grahami</i>	X											N	E*	
	<i>Etheostoma histrio</i>									X	X	X	E	W	S
	<i>Etheostoma lepidum</i>	X	X	X	X	X							N	E	
	<i>Etheostoma parvipinne</i>					X	X	X	X	X	X	X	E	W	S
	<i>Etheostoma proelieri</i>							X	X	X	X	X	E	W	S
	<i>Etheostoma spectabile</i>			X	X	X	X		X				N	W	S
	<i>Percina apristis</i>				X								E	E*	
	<i>Percina carbonaria</i>			X	X	X	X						N	E	
	<i>Percina macrolepida</i>	X		X	X	X	X	X	X	X	X	X	N	E	
	<i>Percina maculata</i>											X	E	W	S
	<i>Percina sciera</i>					X	X	X	X	X	X	X	E	W	S

Table 1-Continued

Family	Species	RG	Nu	SA	G	C	B	SJ	T	Ne	S	C	Or	Des	Term
	<i>Percina shumardi</i>			X	X					X	X		E	W	S
Sciaenidae	<i>Aplodinotus grunniens</i>	X	X	X	X	X	X	X	X	X	X	X	N/E	W	
Elassomatidae	<i>Elassoma zonatum</i>						X	X	X	X	X	X	E	W	S
Cichlidae	<i>Herichthys cyanoguttatus</i>	X											SW	E*	



Figure 1. Western Gulf Slope divided into eight-digit HUCs.

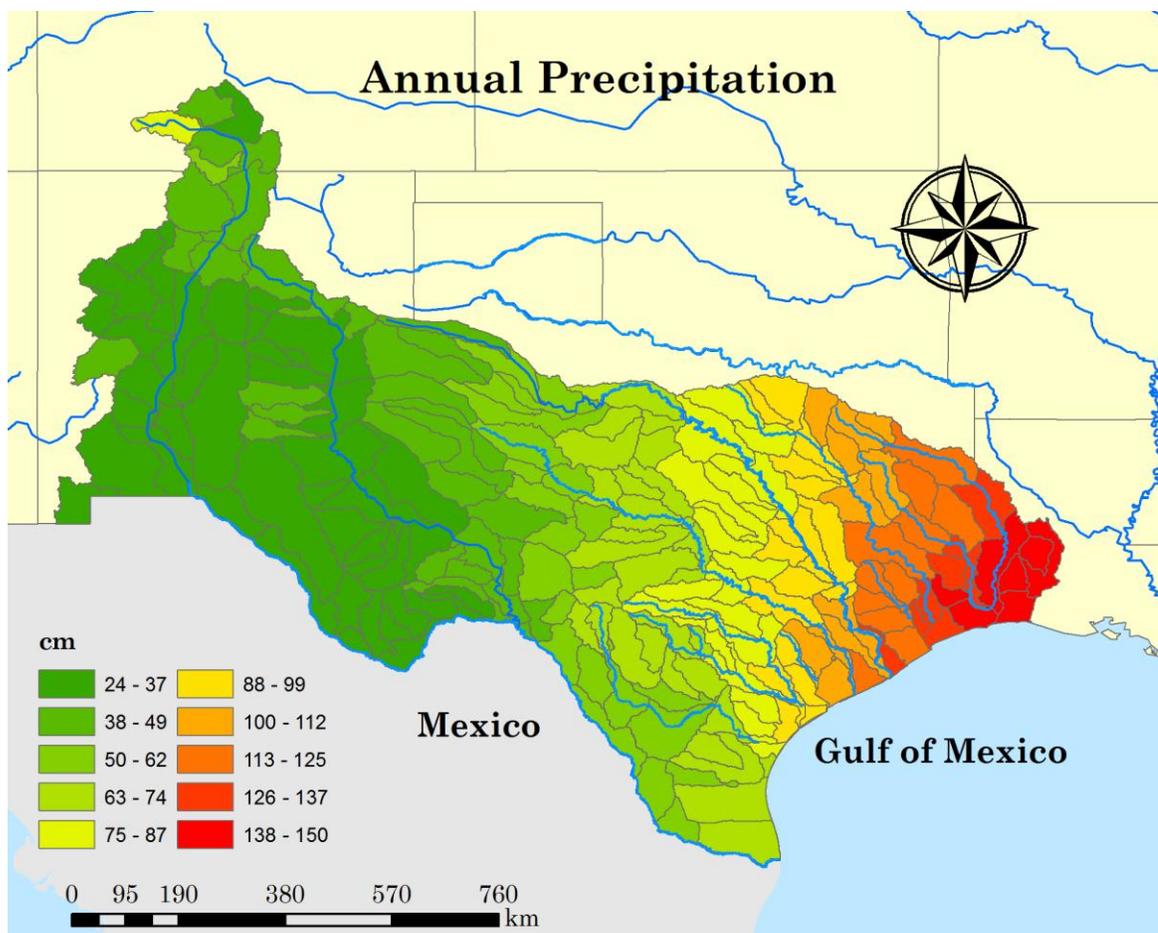


Figure 2. Average annual precipitation in the WGS.

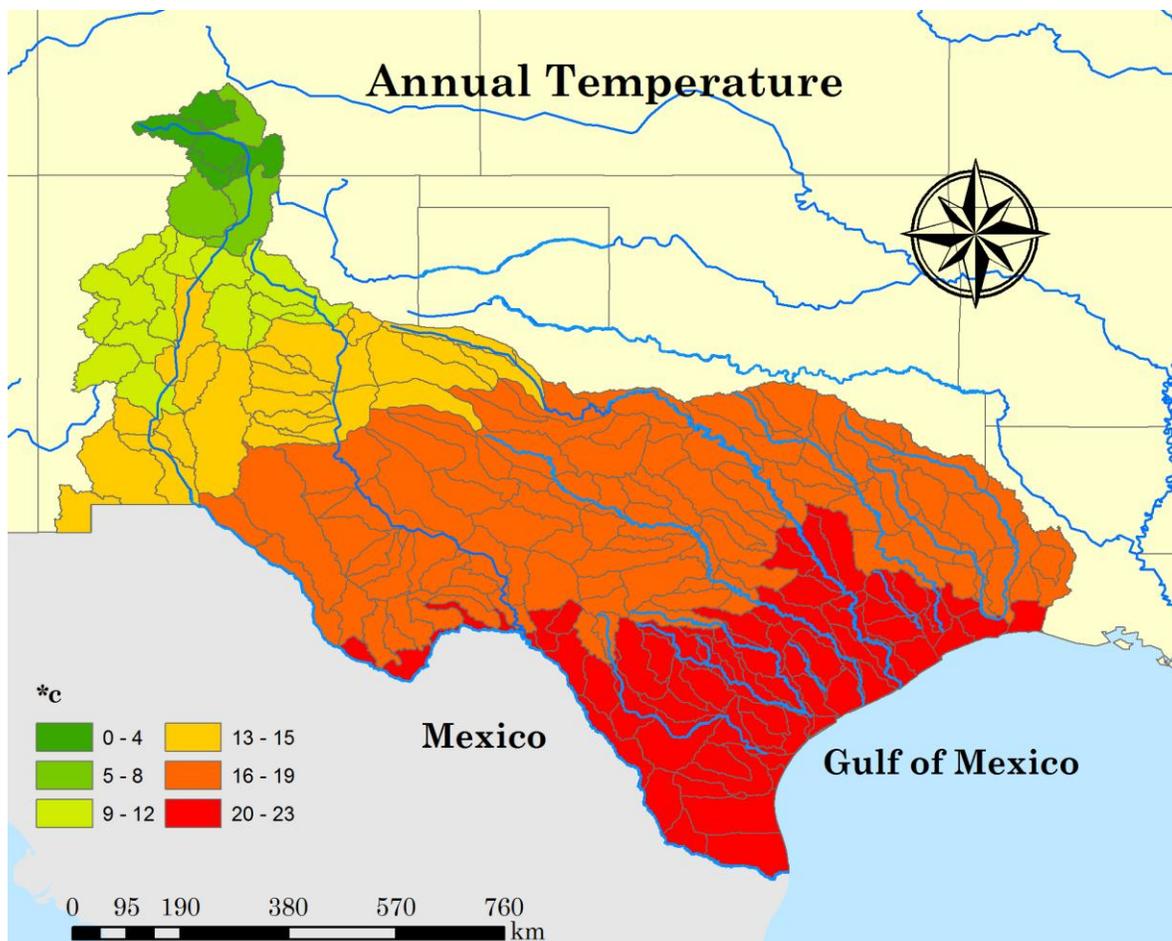


Figure 3. Average annual temperature in the WGS.

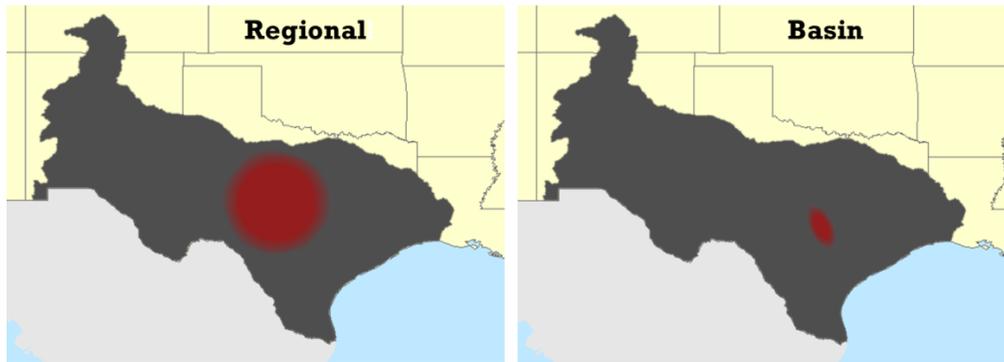


Figure 4. Conceptual graphic of distributions of regional and basin endemic species.

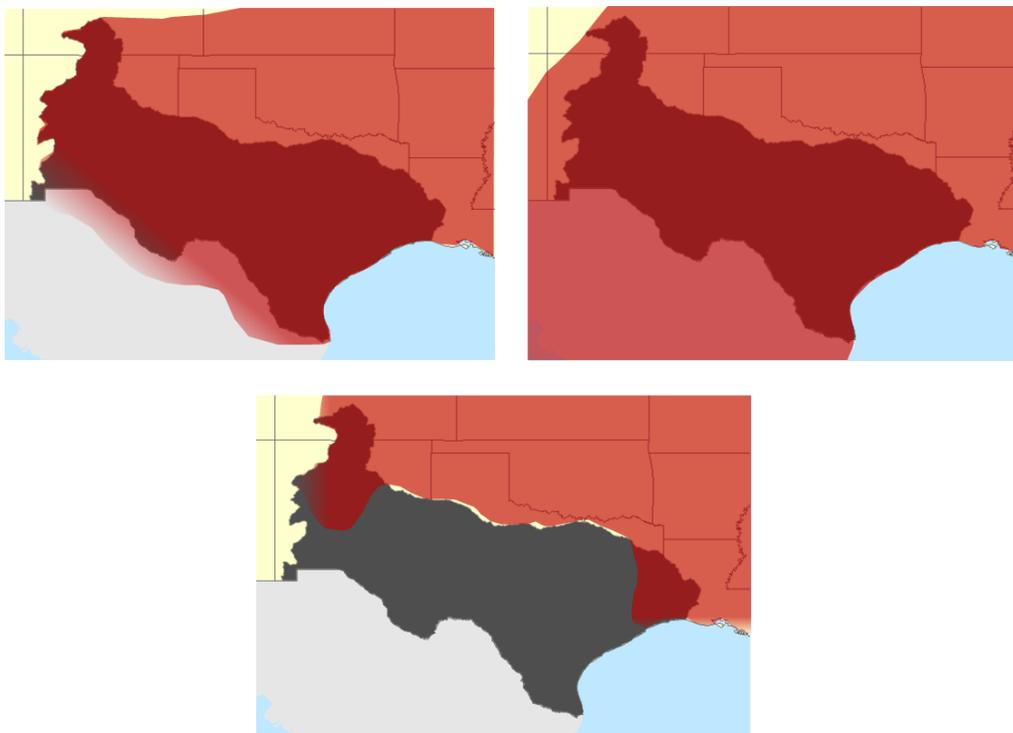


Figure 5. Conceptual graphic of distributions of widespread ubiquitous species.

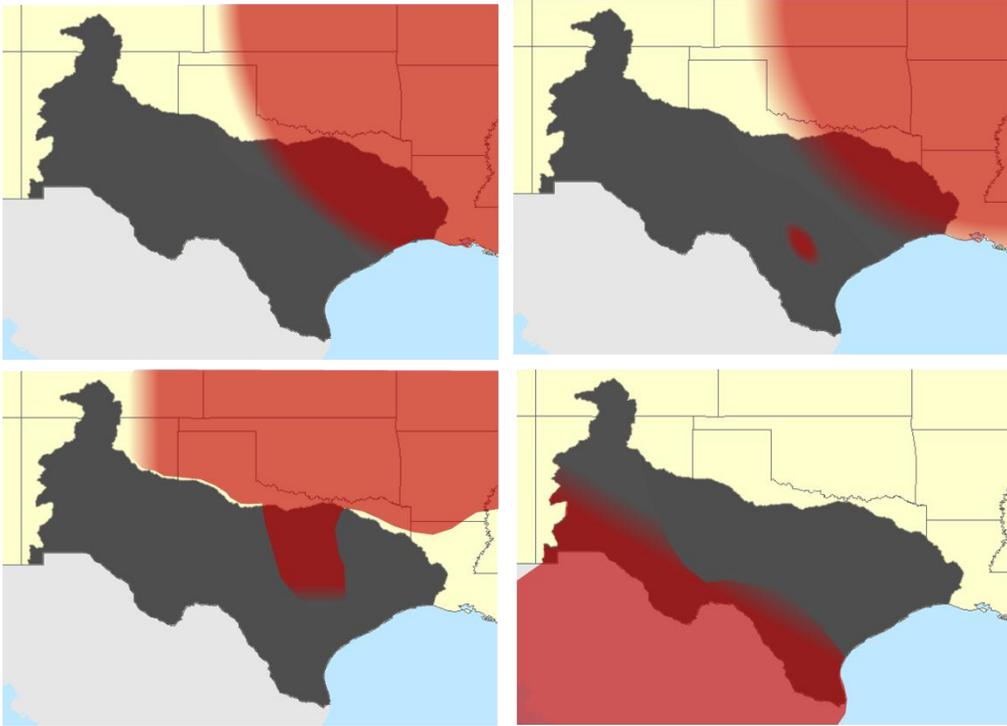


Figure 6. Conceptual graphic of distributions of widespread range terminating species.

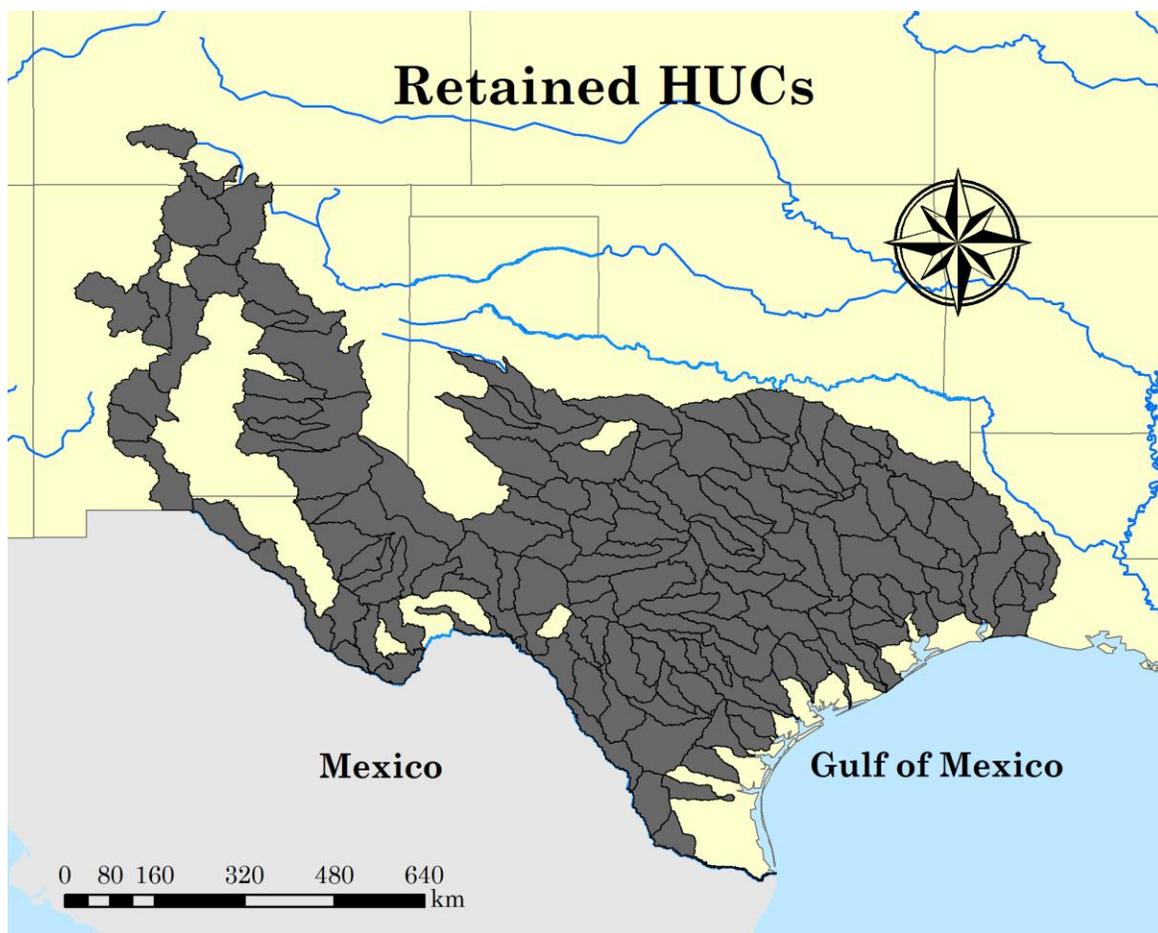


Figure 7. HUCs retained for analysis.

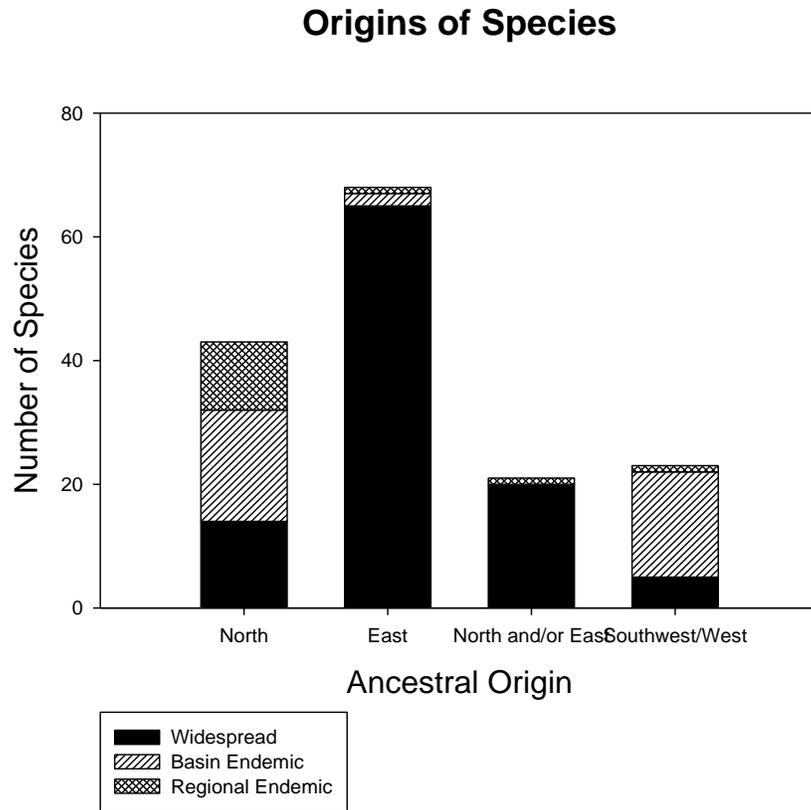


Figure 8. Ancestral origins of fish species in the Western Gulf Slope.

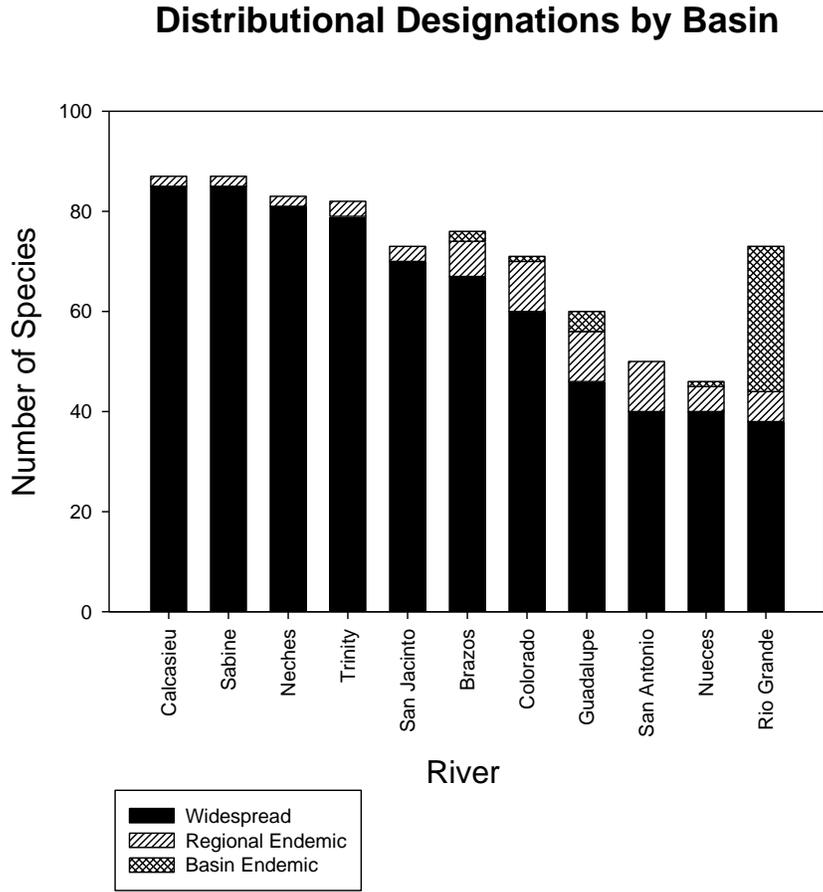


Figure 9. Distributional designation by basin.

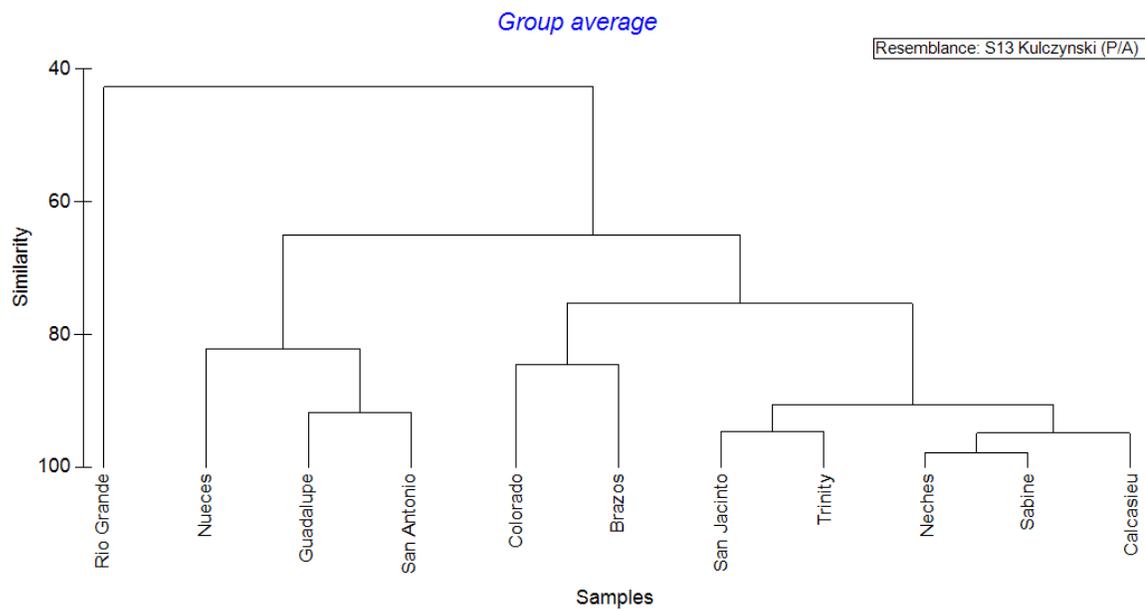


Figure 10. Average faunal similarity between basins.

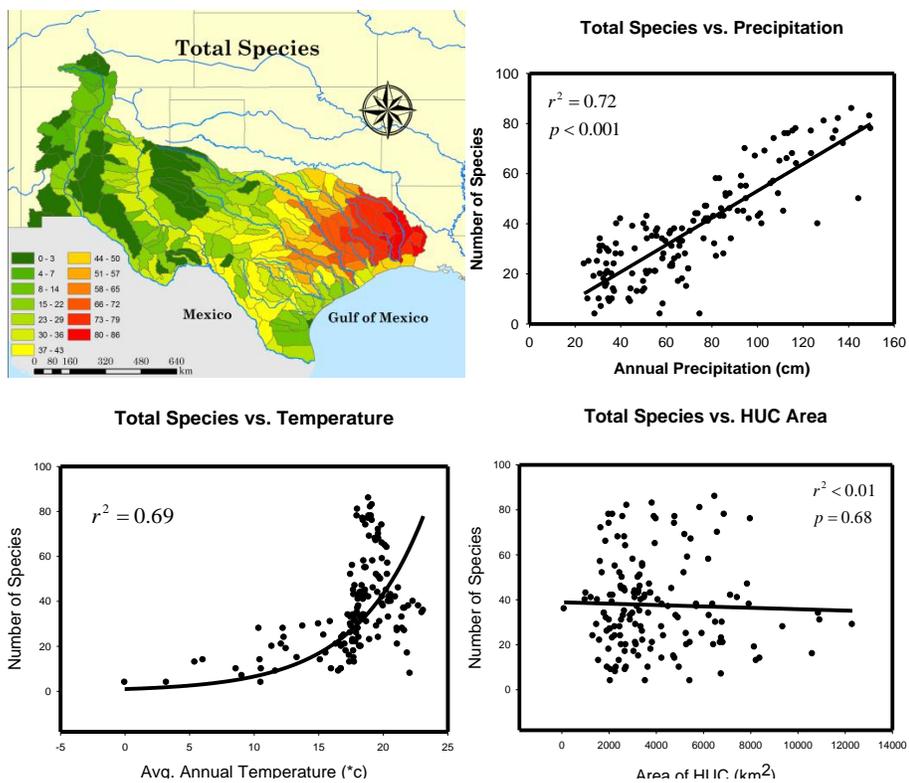


Figure 11. Total number of fish species per HUC.

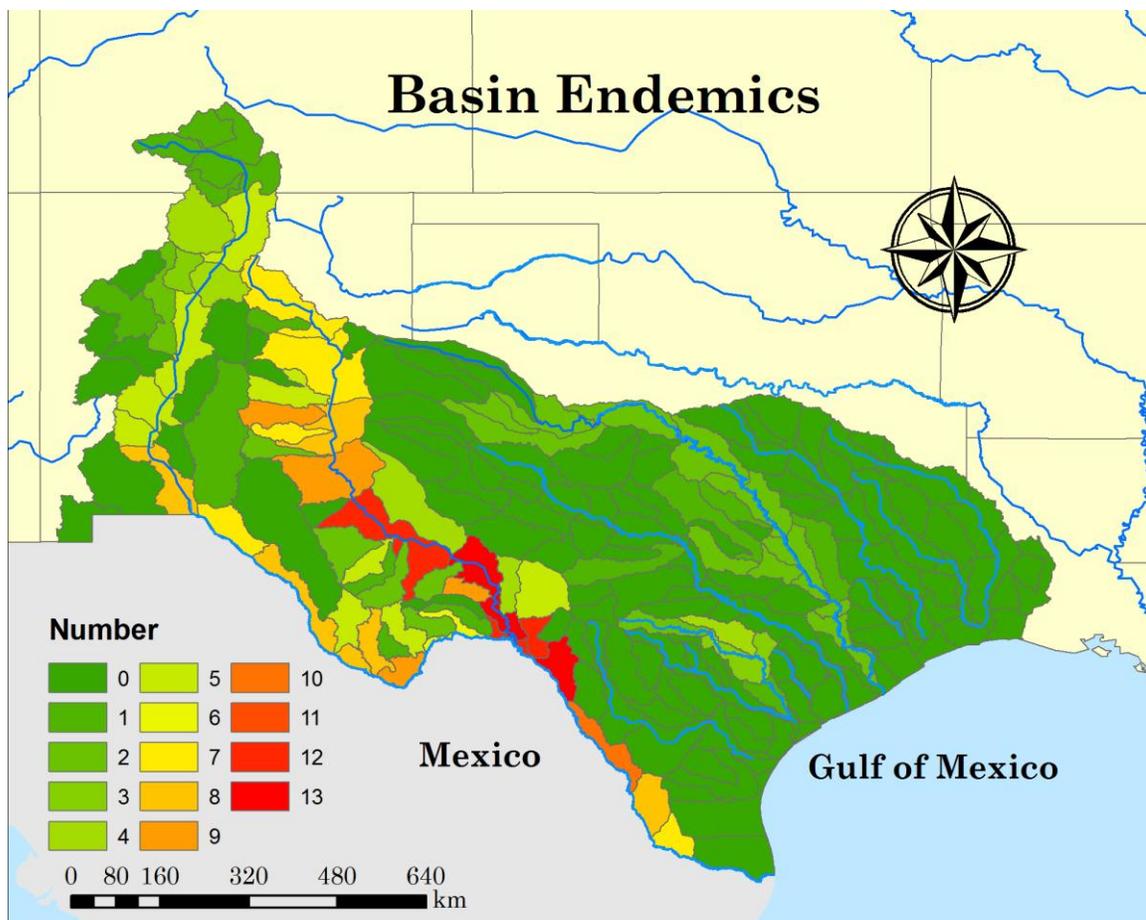


Figure 12. Number of basin endemics per HUC.

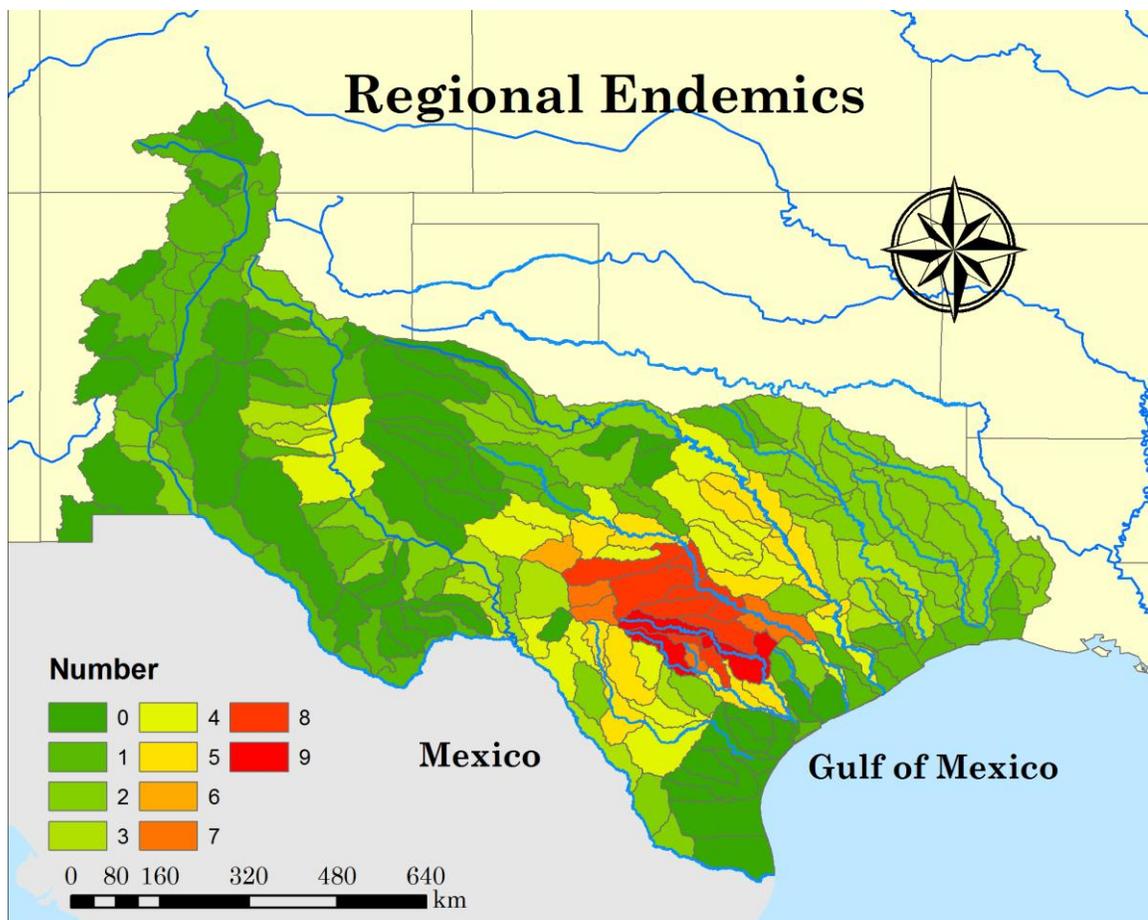


Figure 13. Number of regional endemics per HUC.

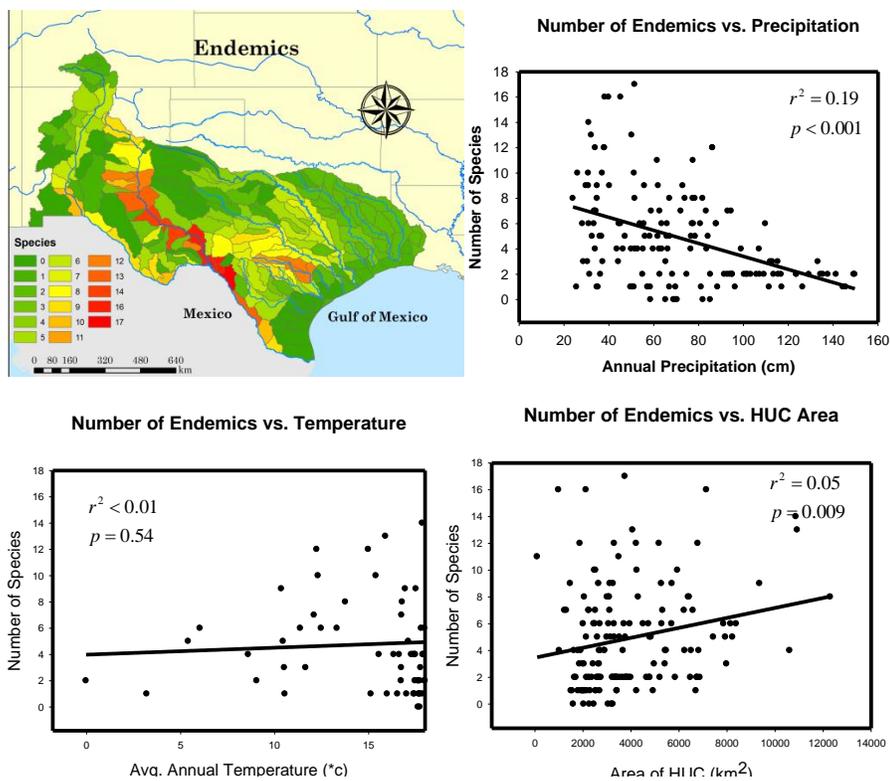


Figure 14. Total number of endemic fish species per HUC.

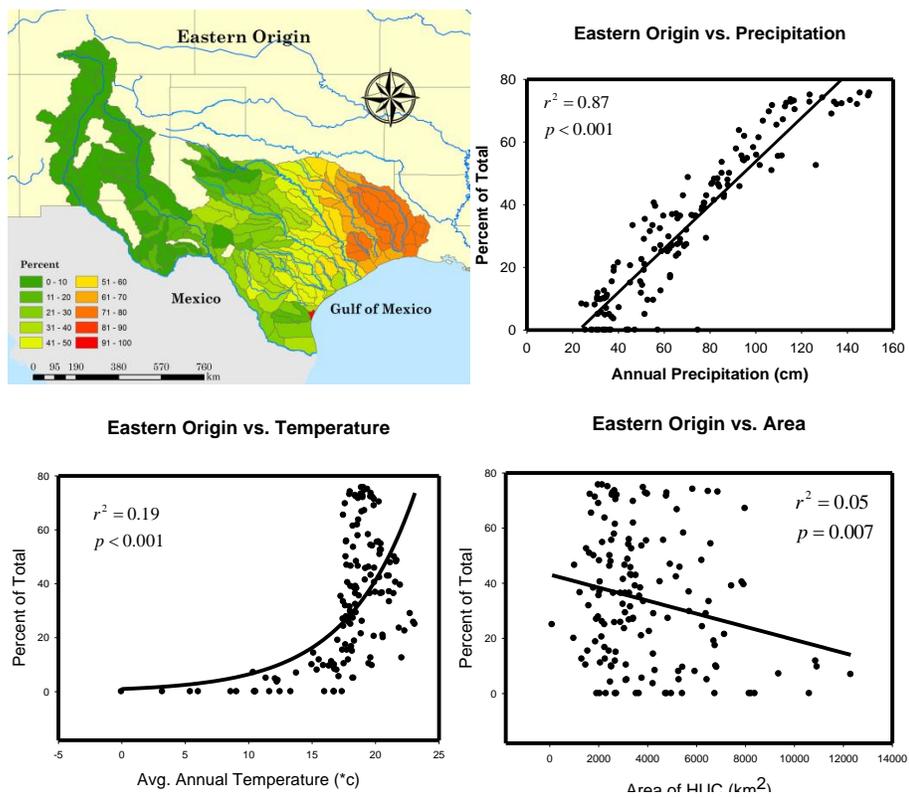


Figure 15. Percentage of eastern origin species per HUC.

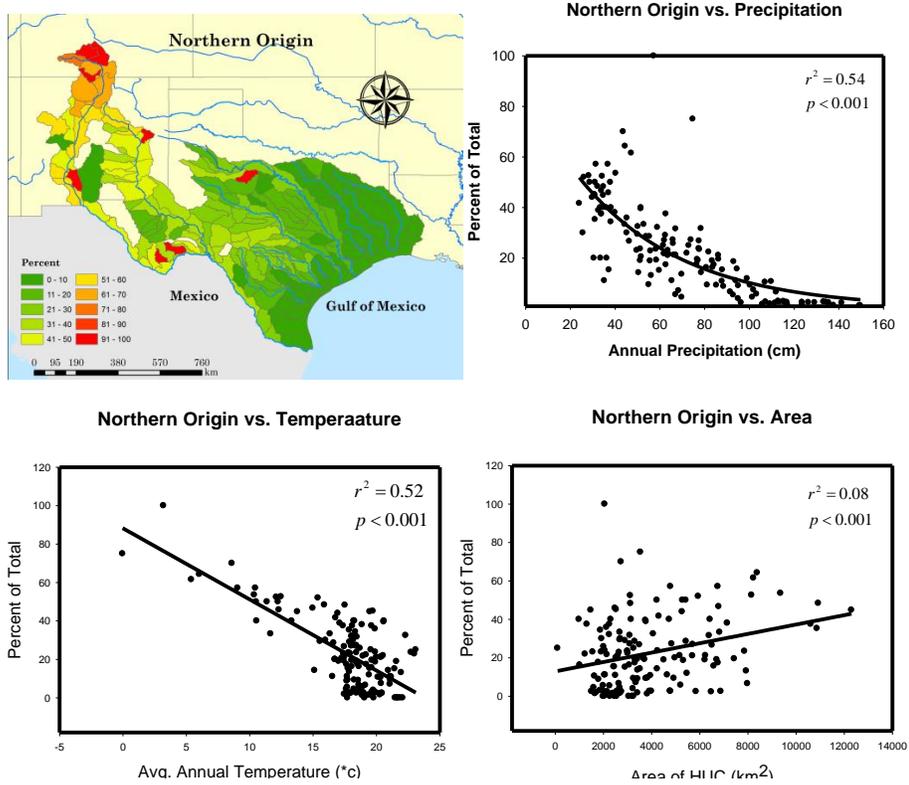


Figure 16. Percentage of northern origin fish species per HUC.

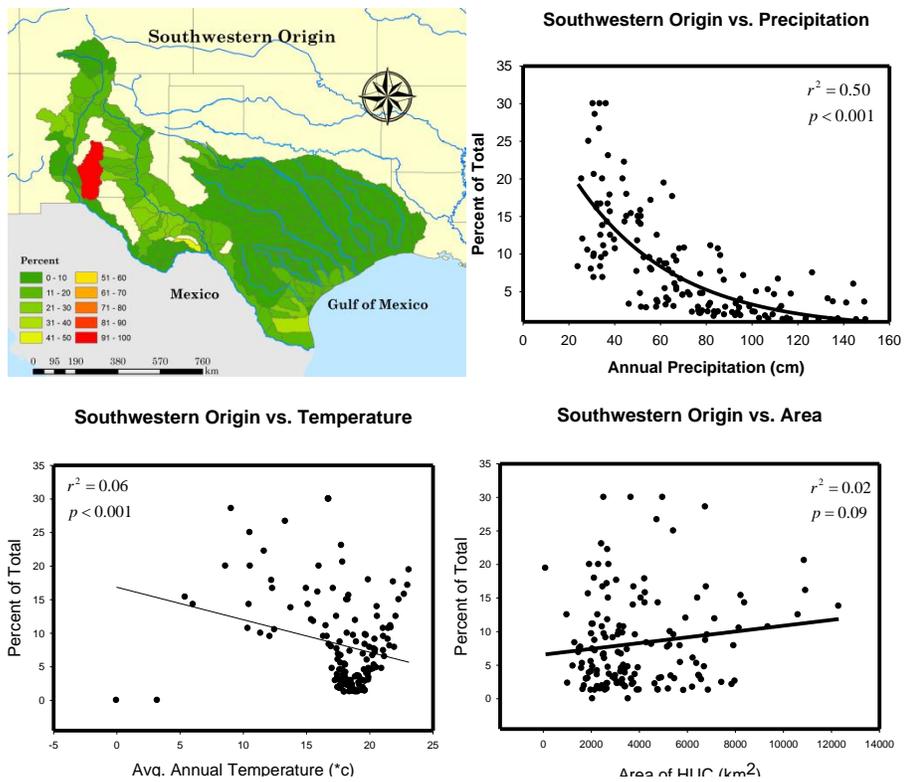


Figure 17. Percentage of southwestern origin fish species per HUC.

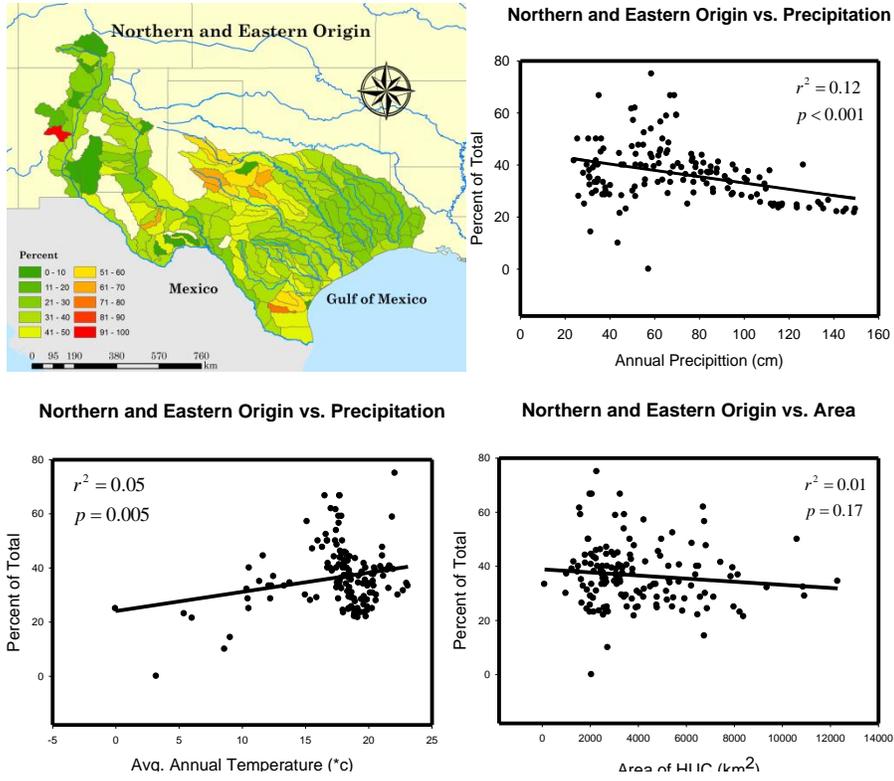


Figure 18. Percentage of northern and eastern origin fish species per HUC.

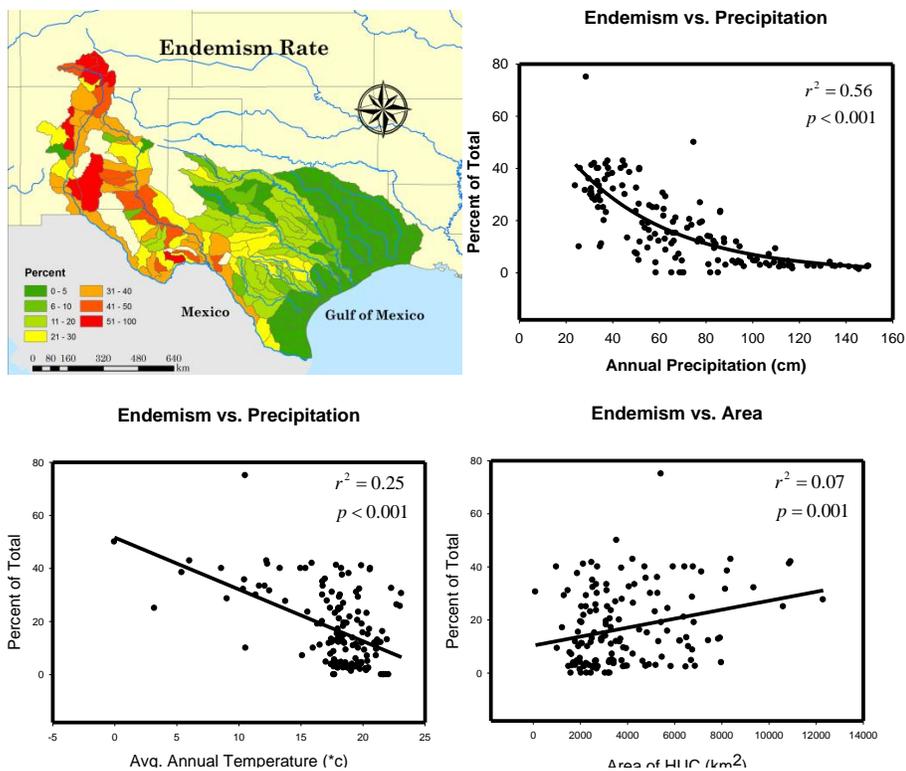


Figure 19. Endemic fishes as a percentage of the total species per HUC.

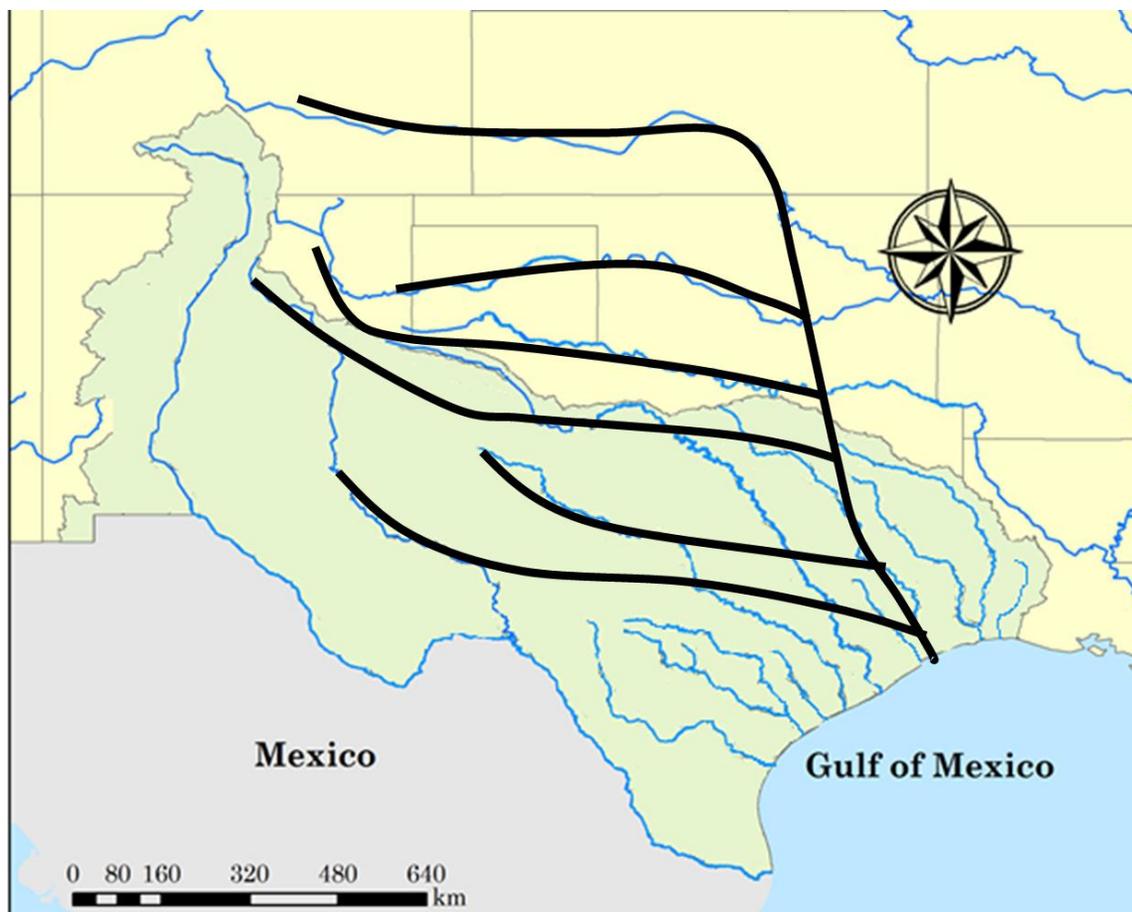


Figure 20. Conceptual graphic of the Ancestral Southern Plains Stream (Metcalf 1966, Conner 1977, Conner and Suttkus 1986, Cross et al. 1986, Mayden 1988).

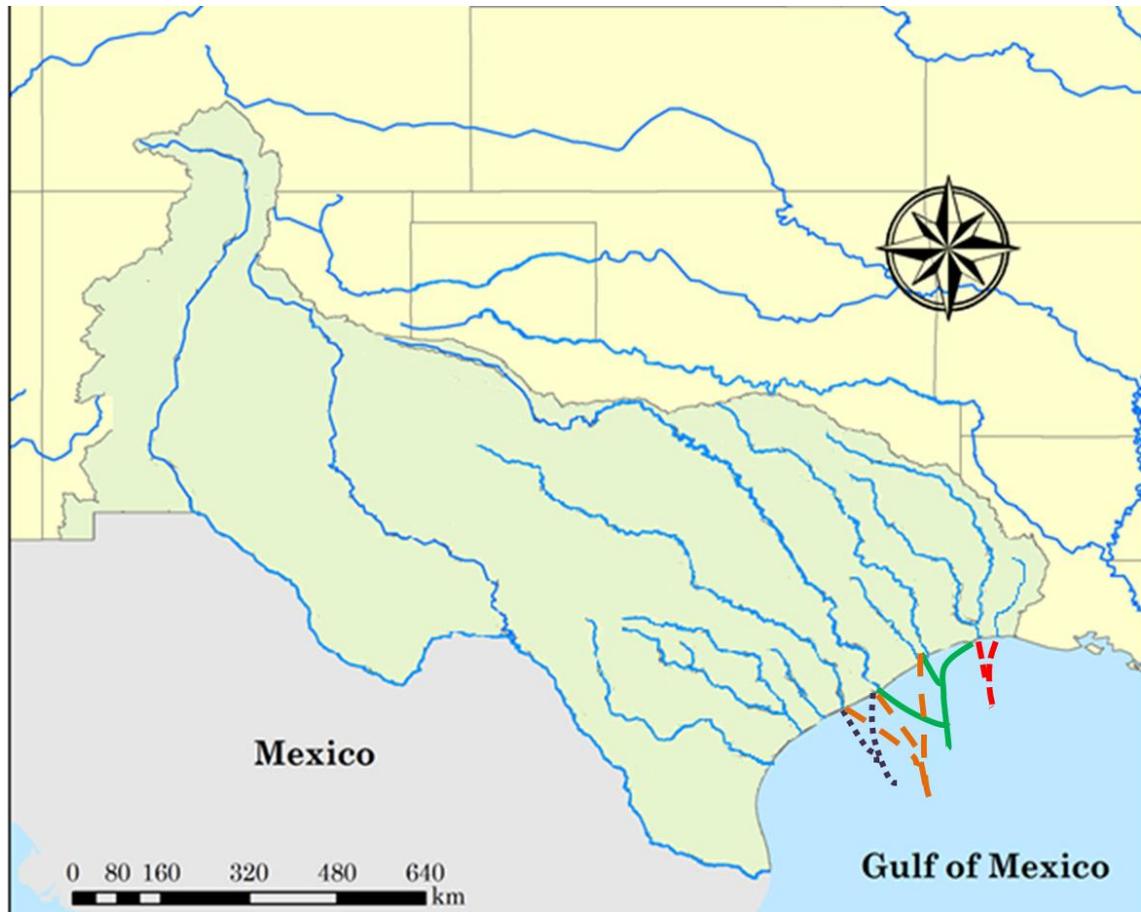


Figure 21. Conceptual Graphic of downstream Pleistocene stream connections adapted (Conner 1977, Conner and Suttkus 1986, Phillips 2009, Prather et al. 2012).

APPENDIX I

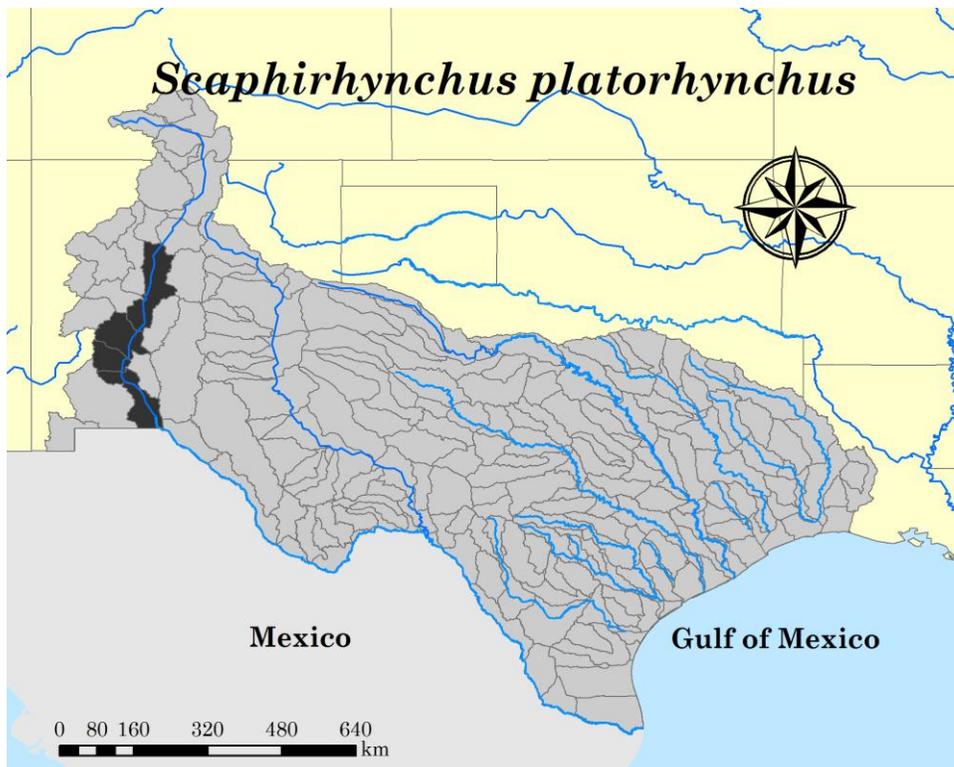
RANGE MAPS OF WESTERN GULF SLOPE FISHES

Petromyzontidae





Acipenseridae

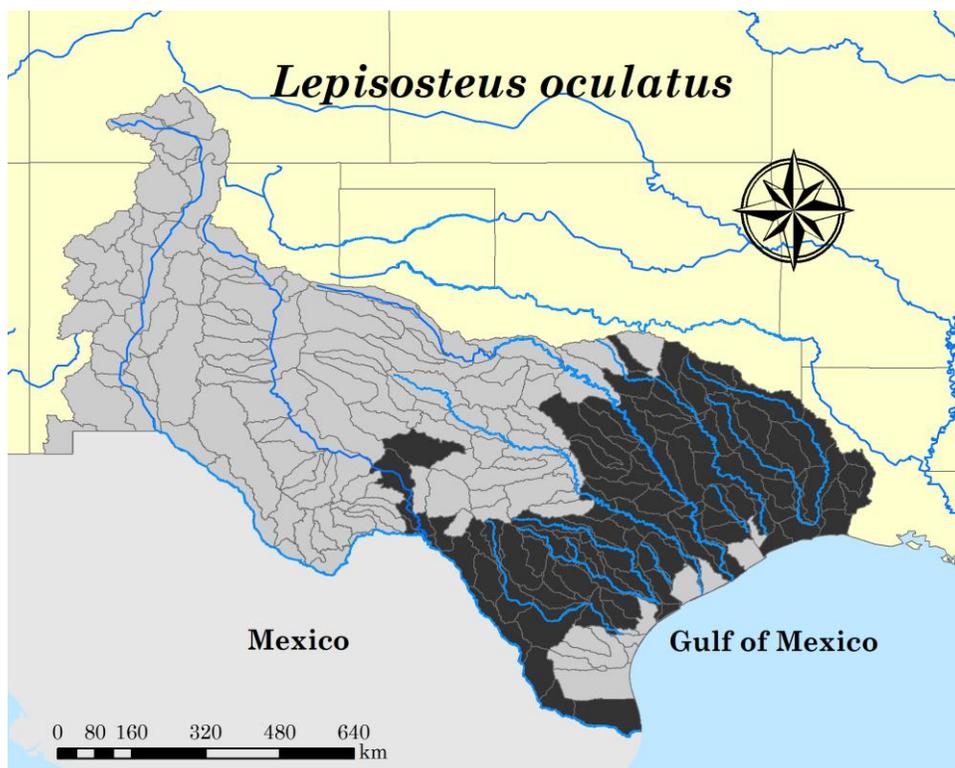


Polyodontidae



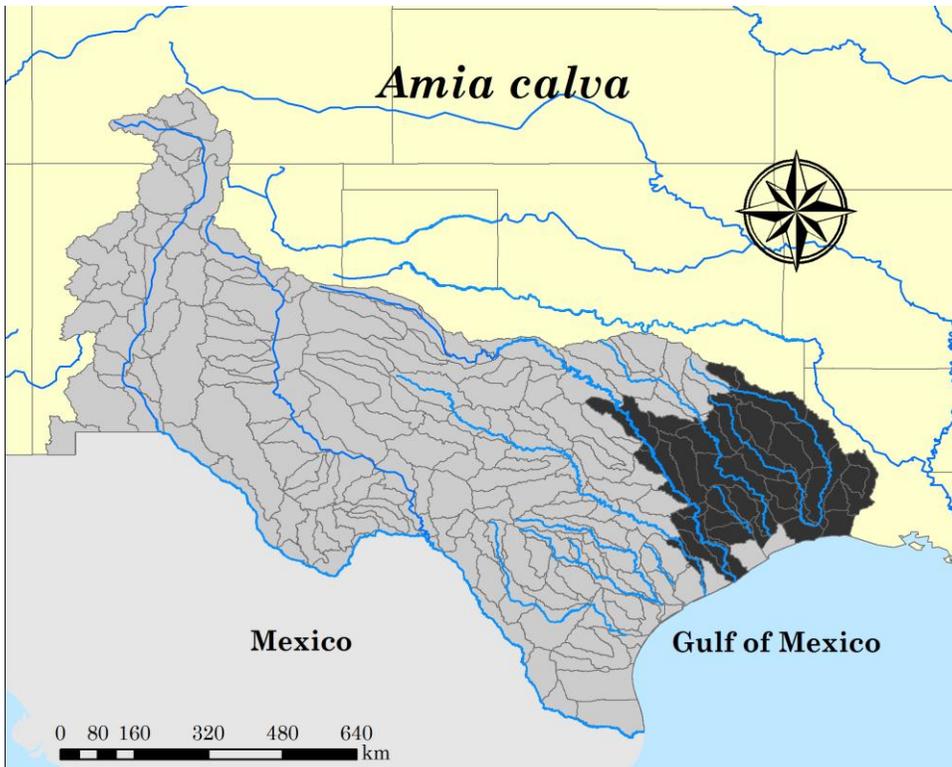
Lepisosteidae



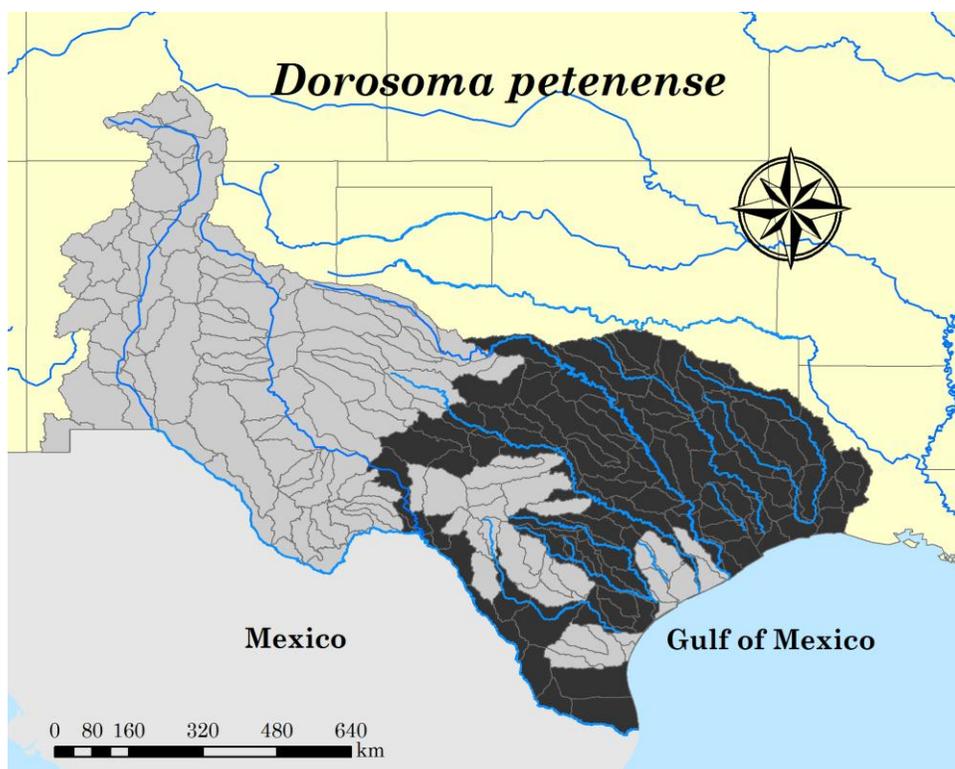




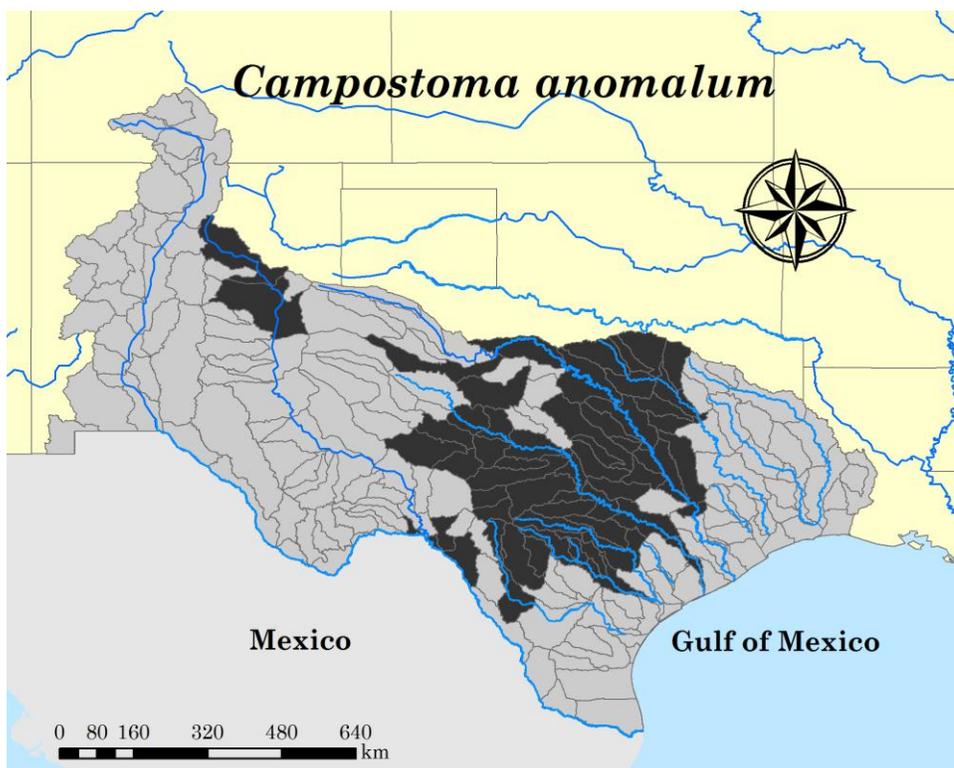
Amiidae

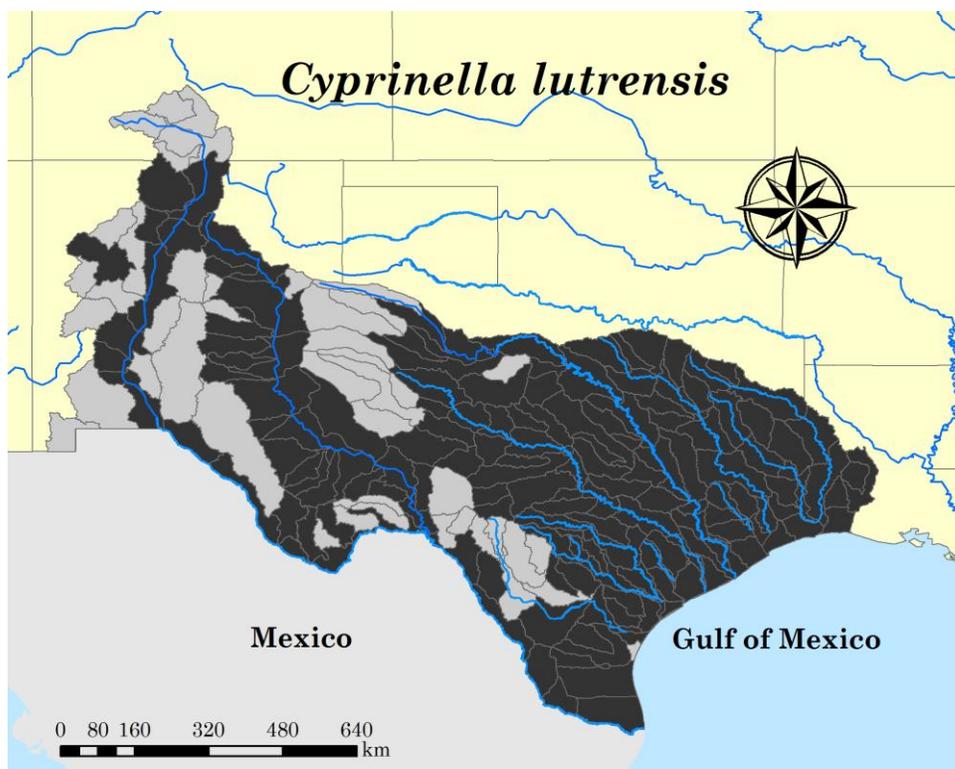
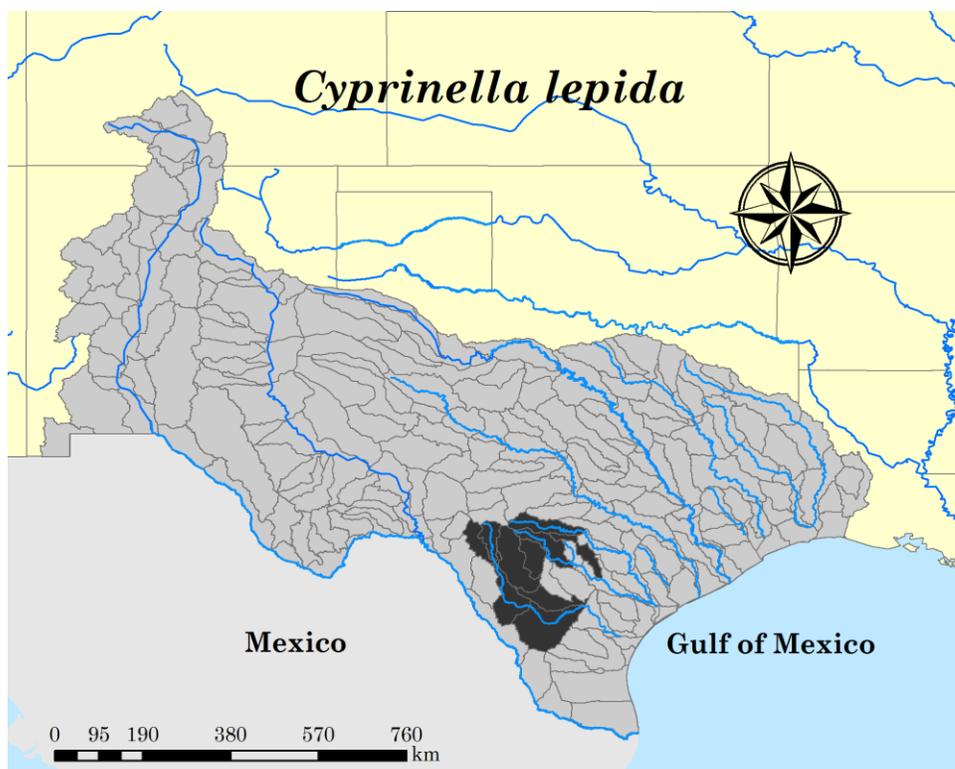


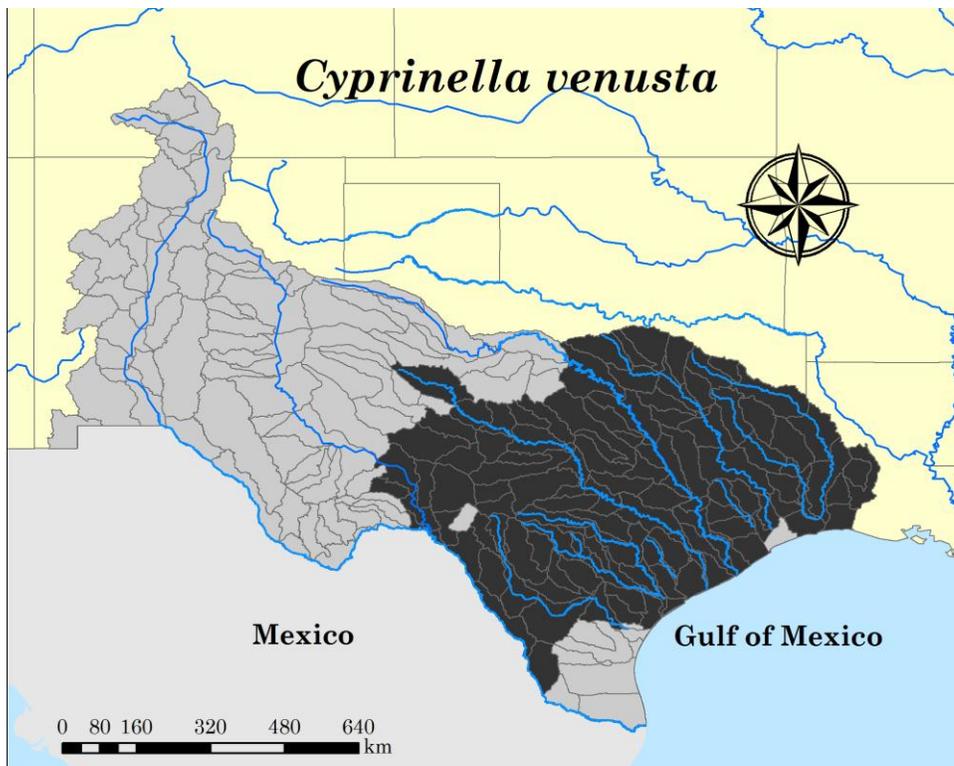
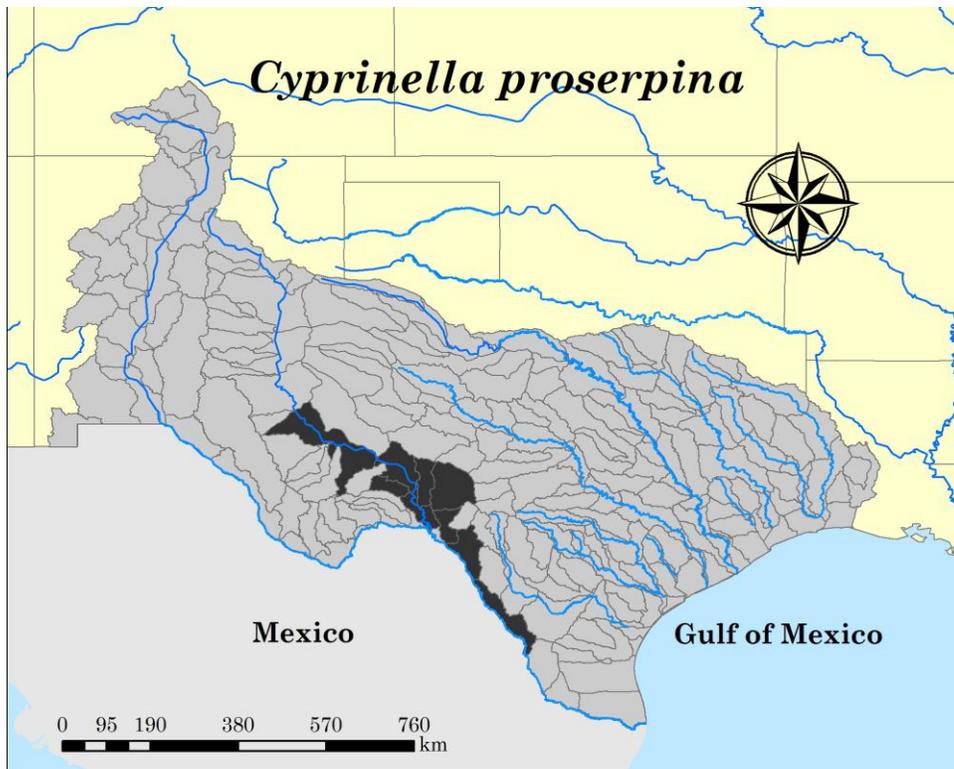
Clupeidae



Cyprinidae

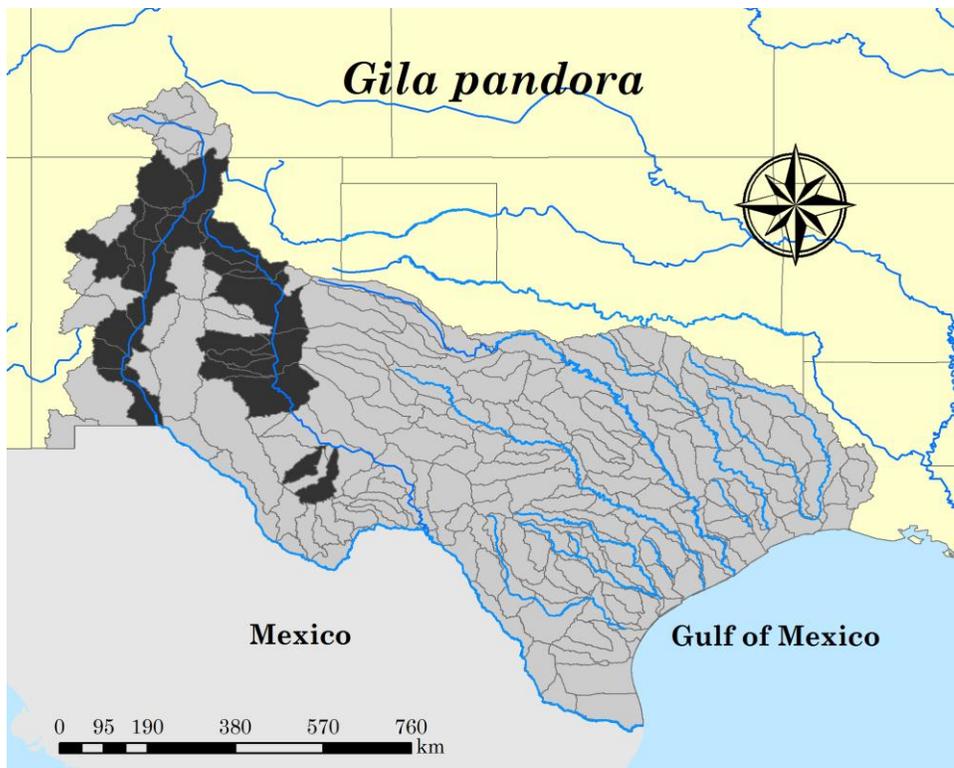
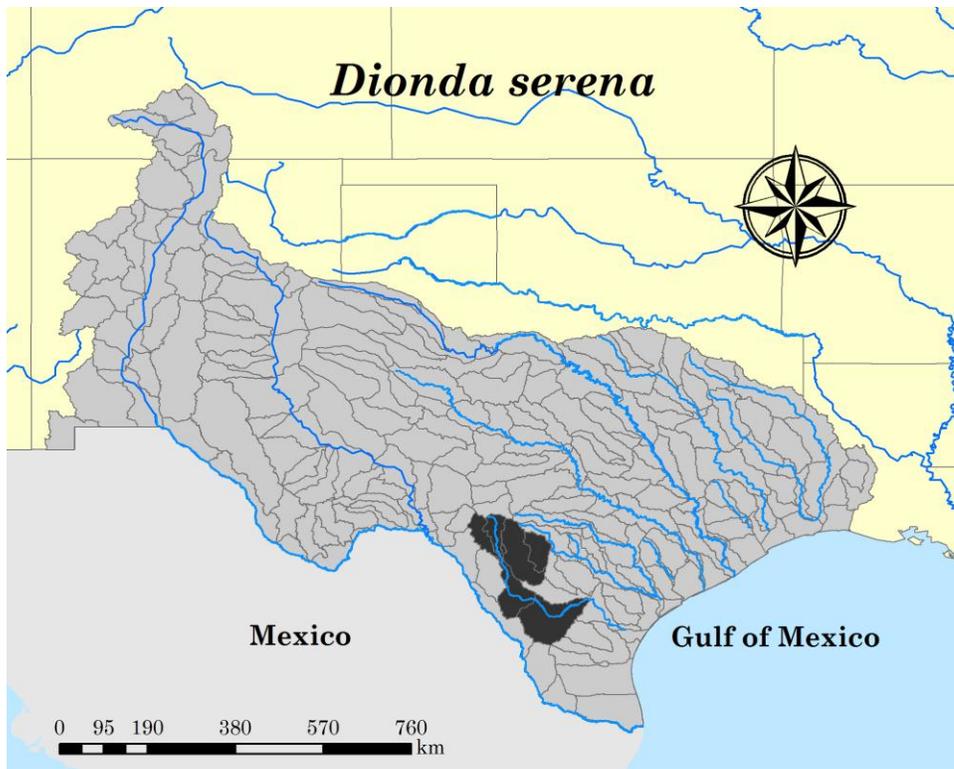




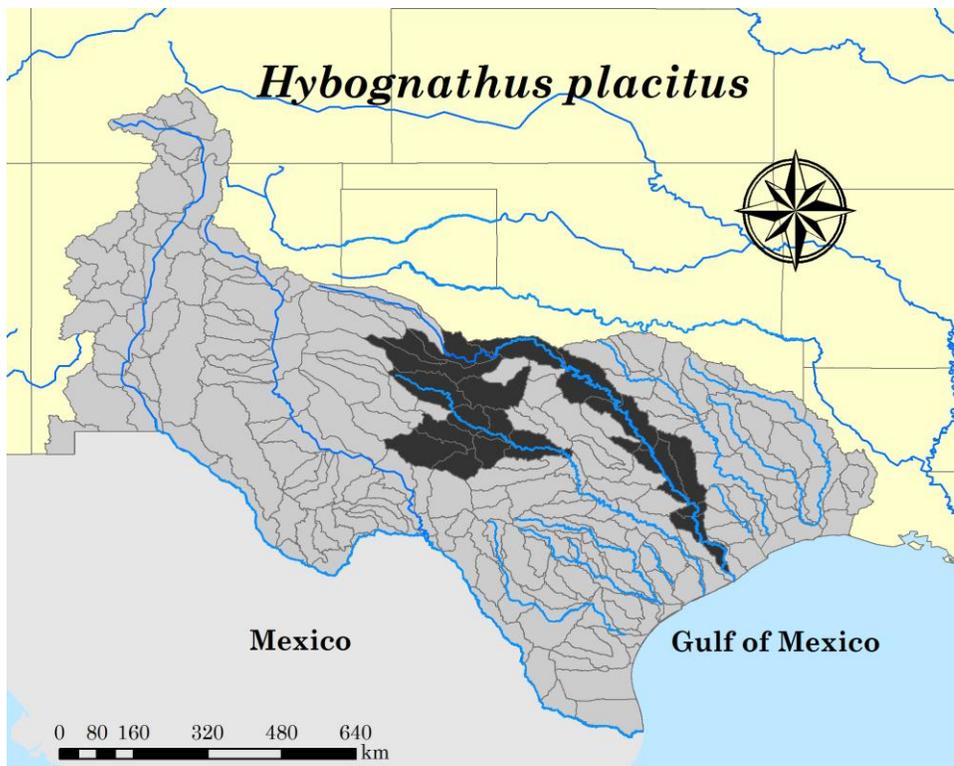
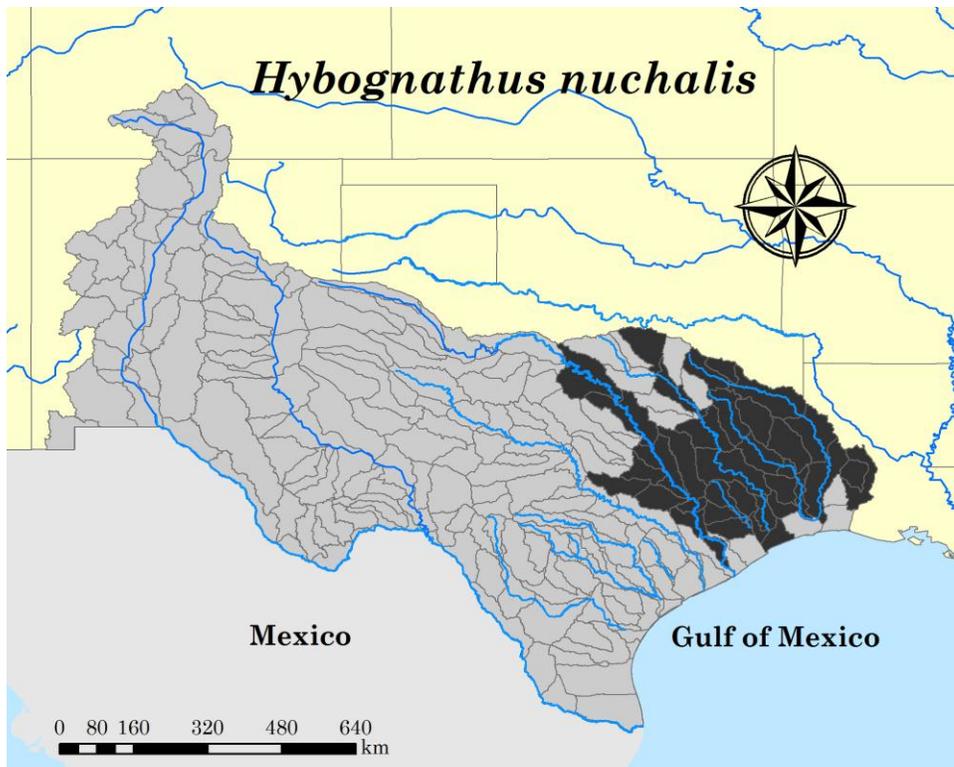


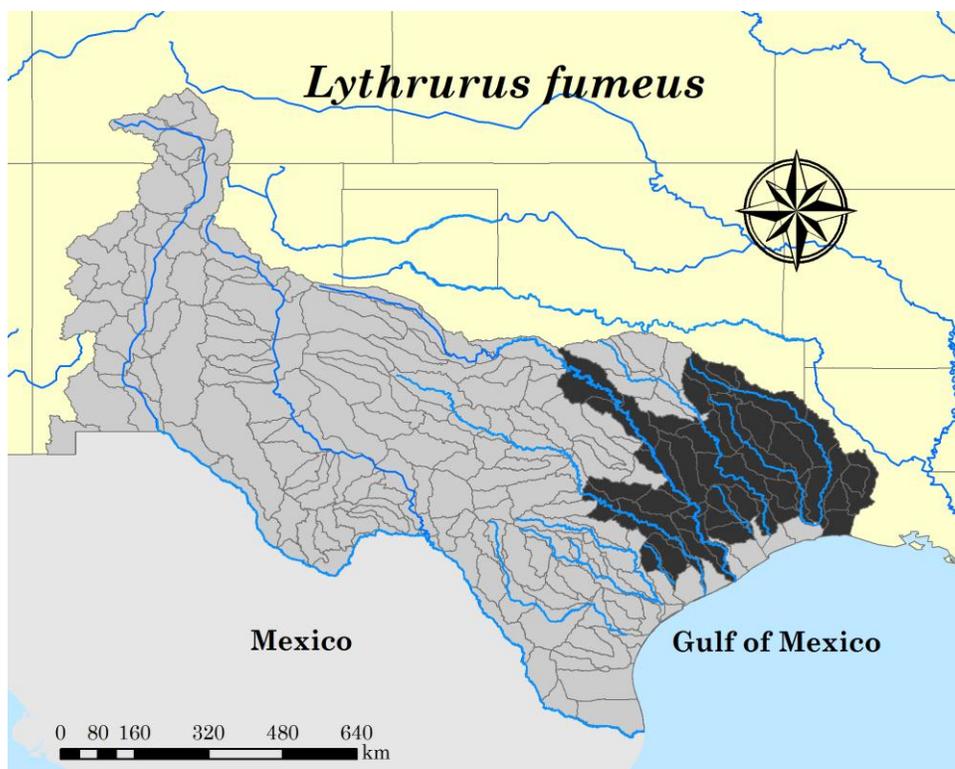
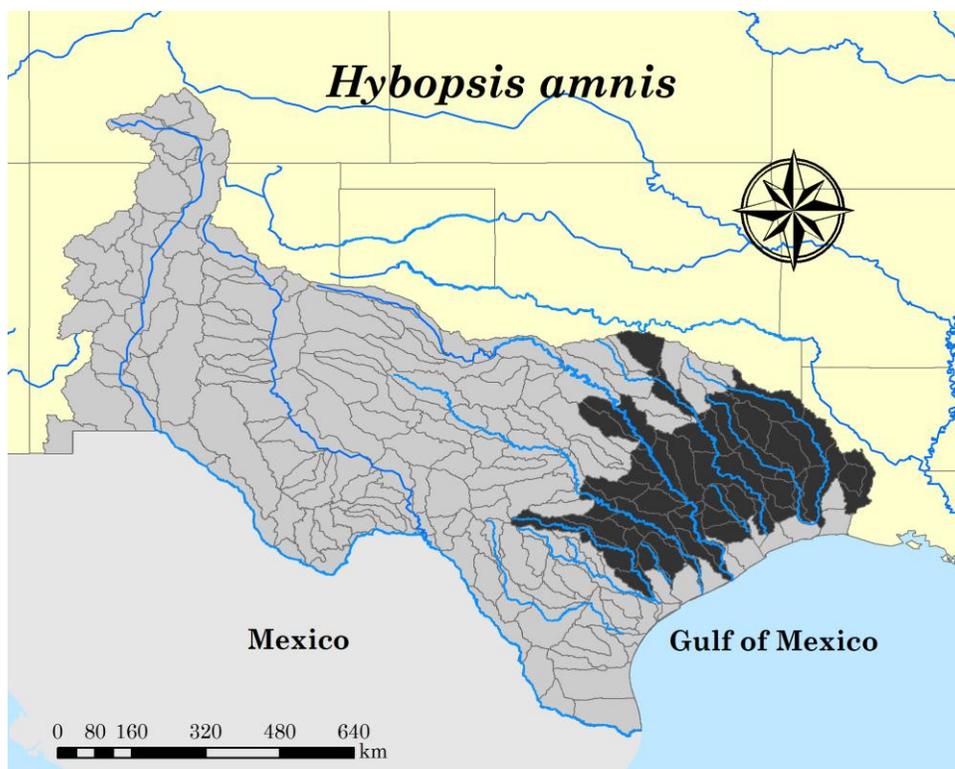




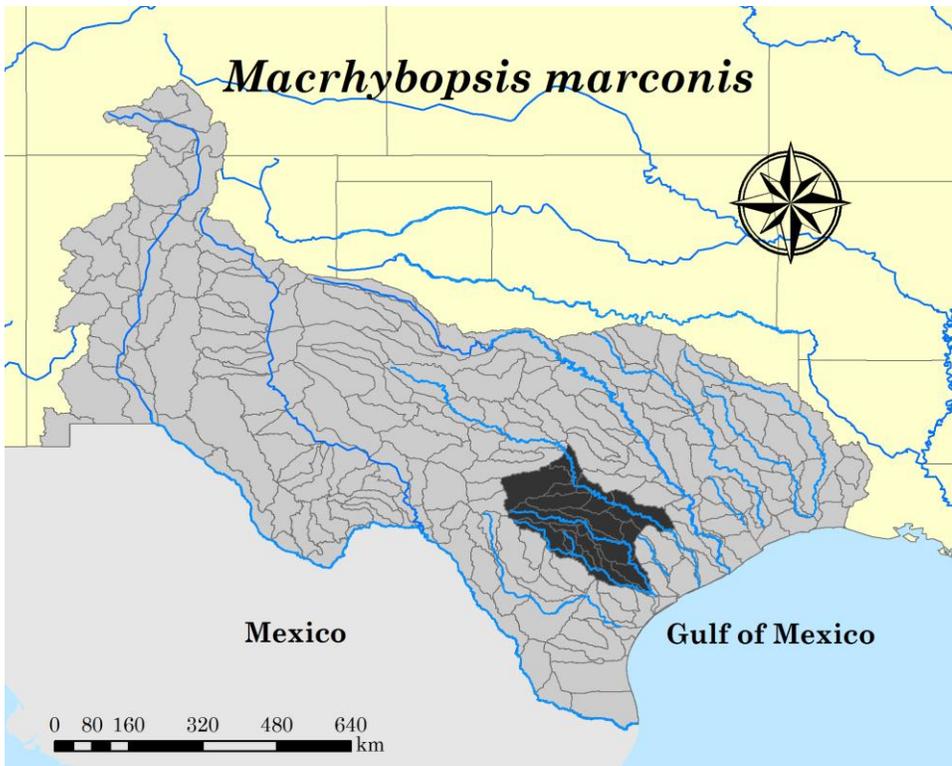
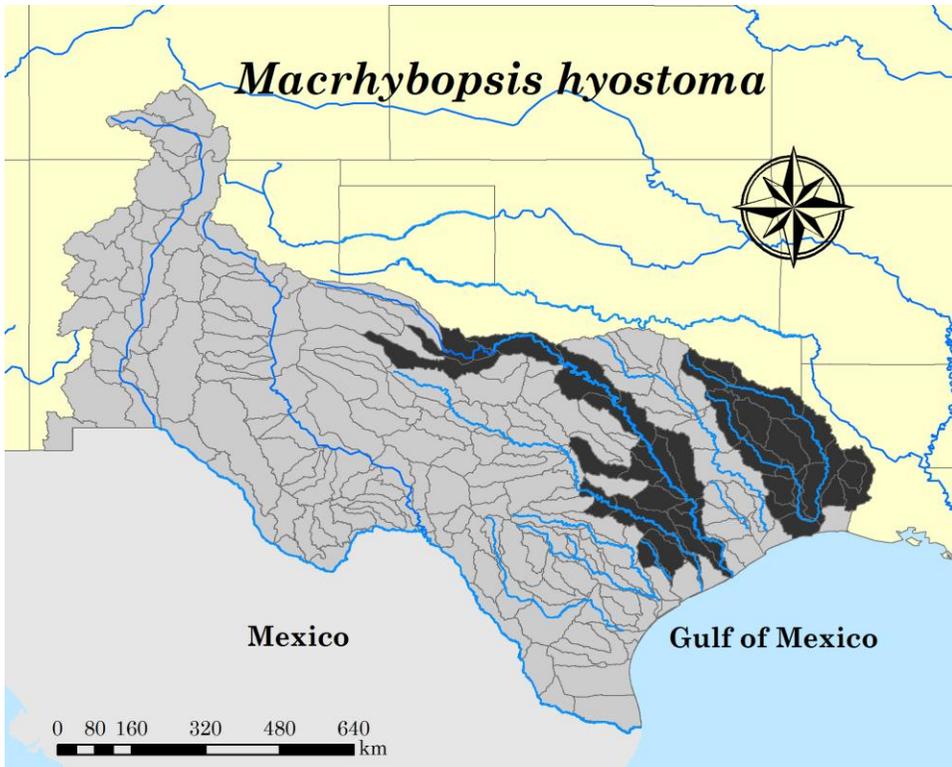


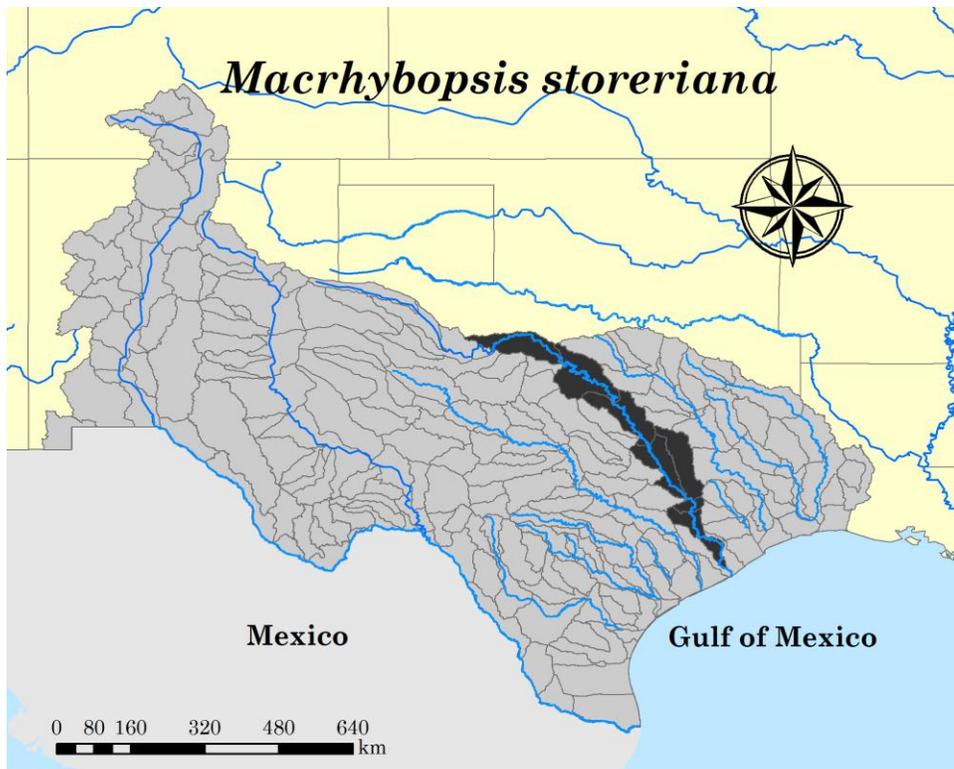


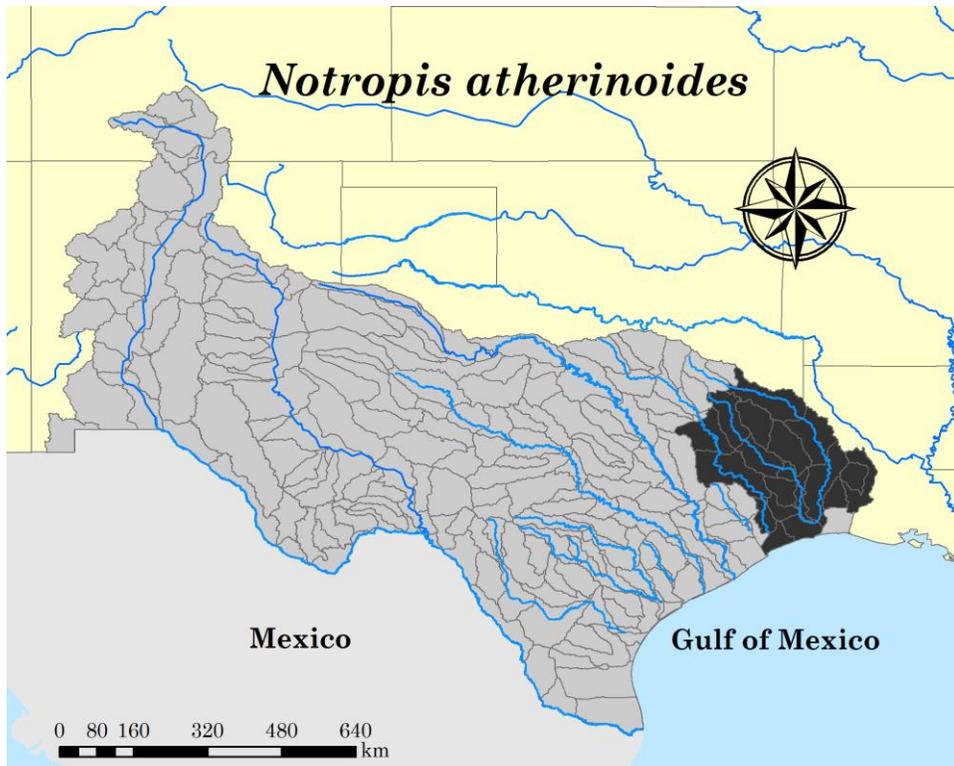
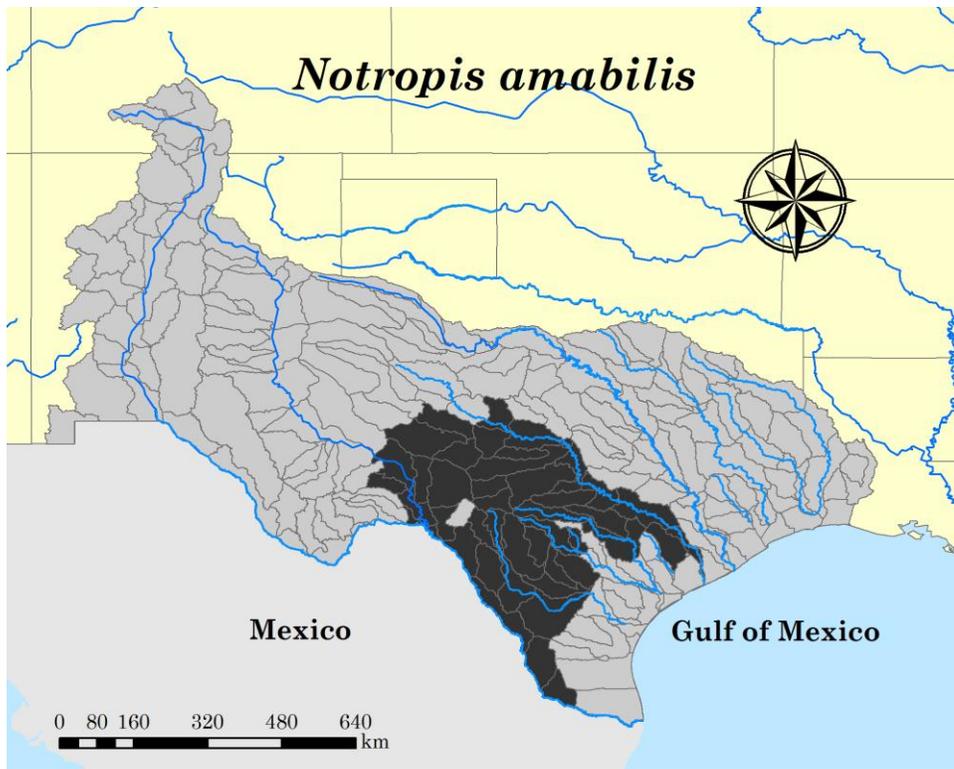




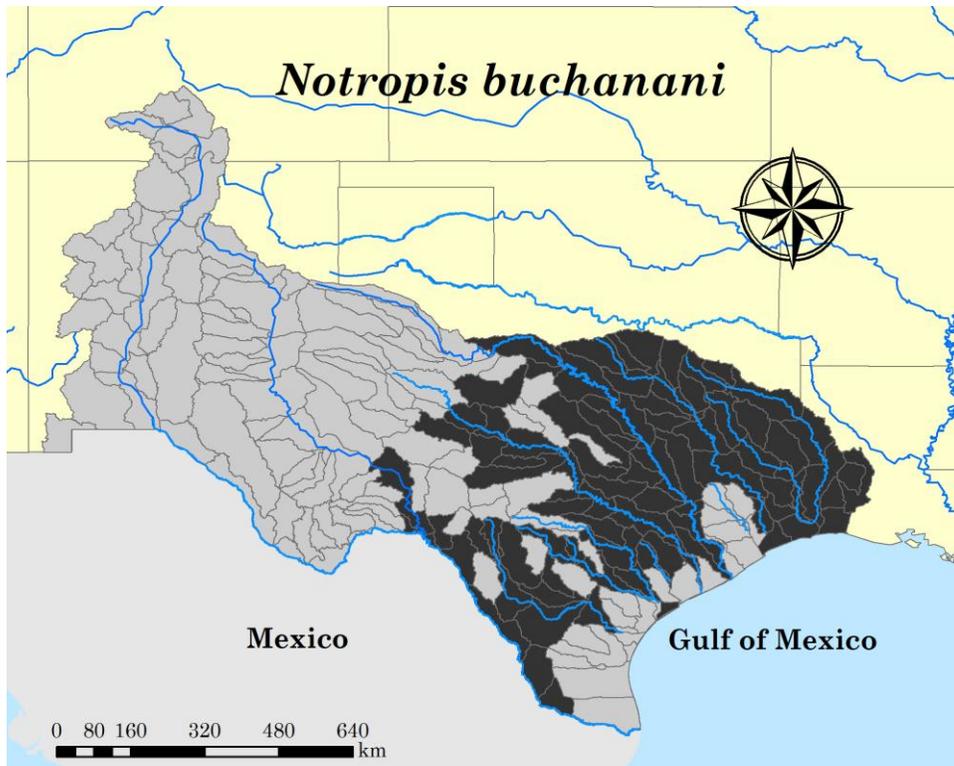
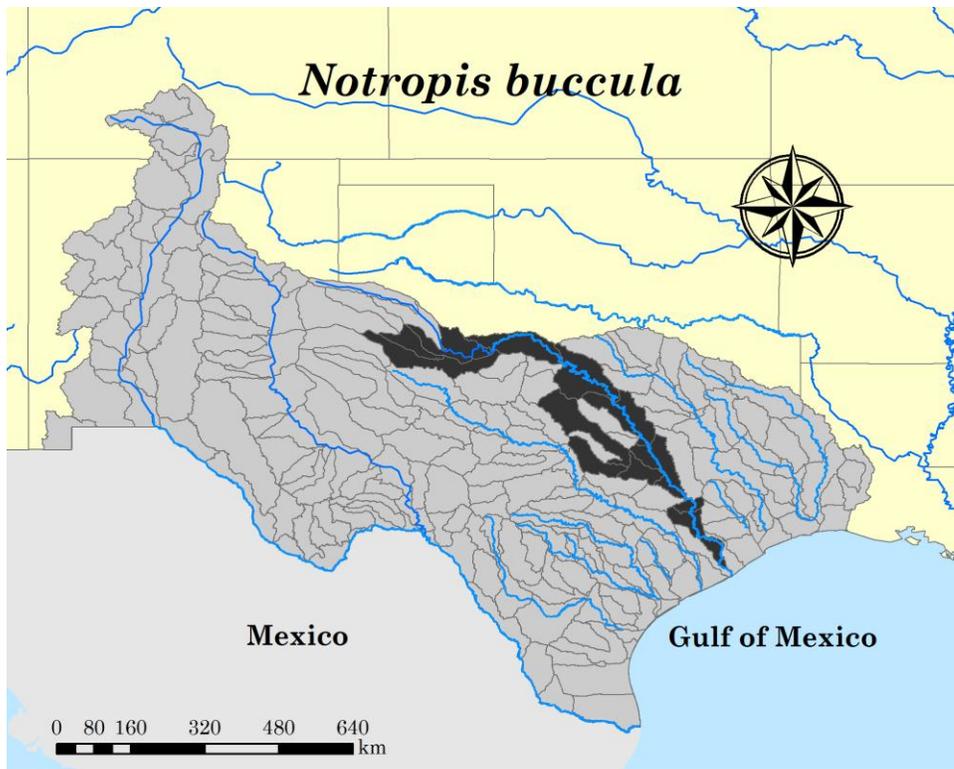


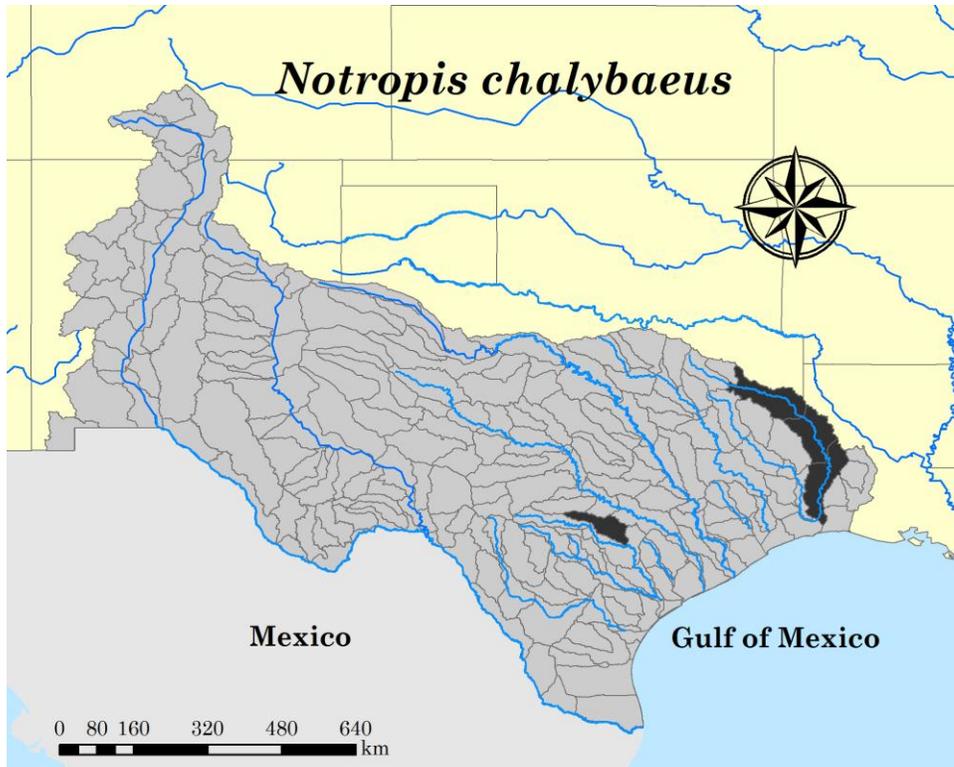


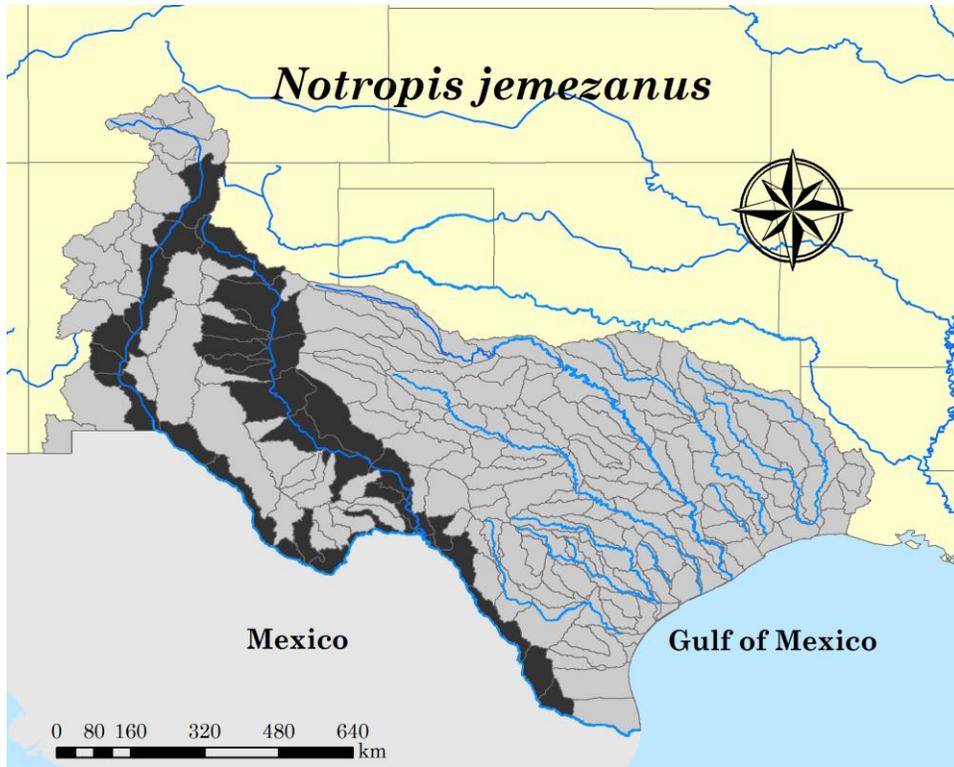


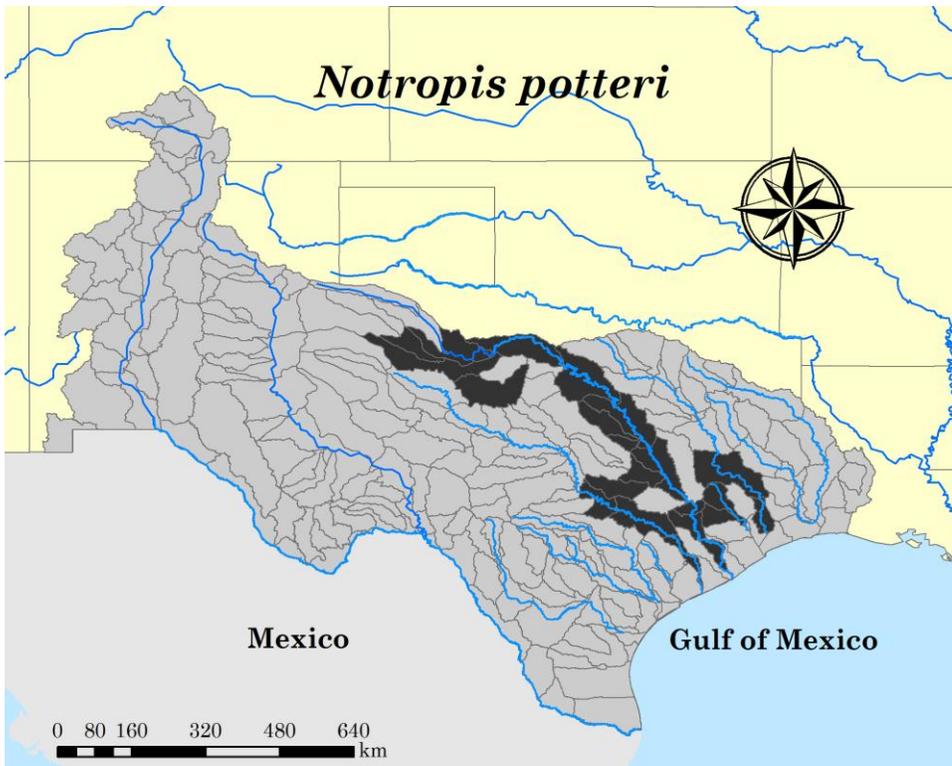
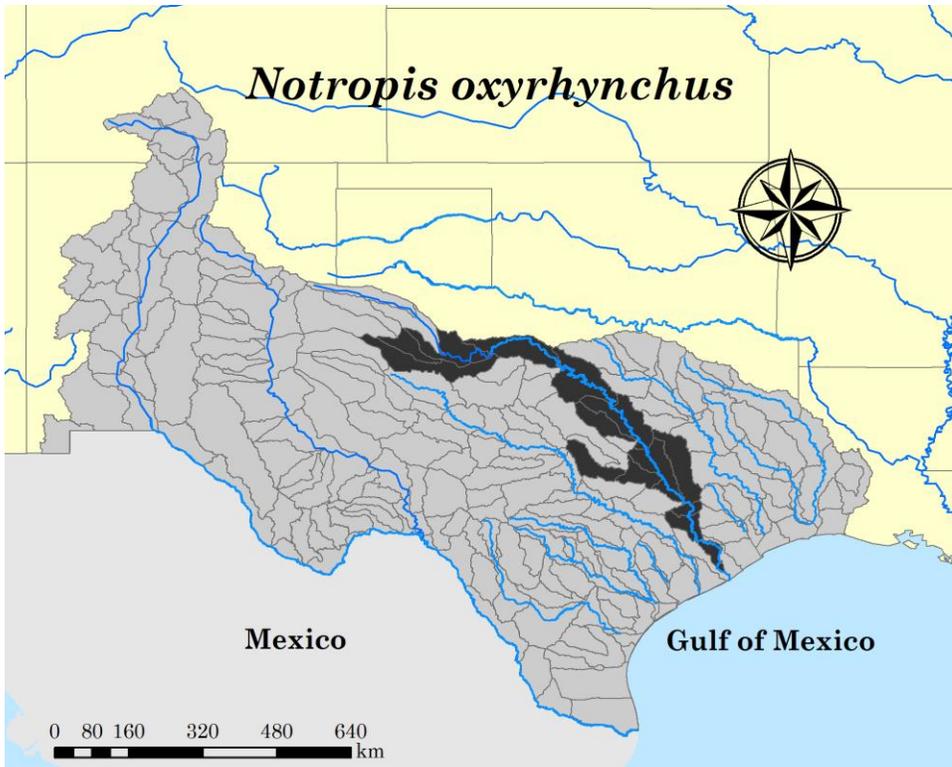


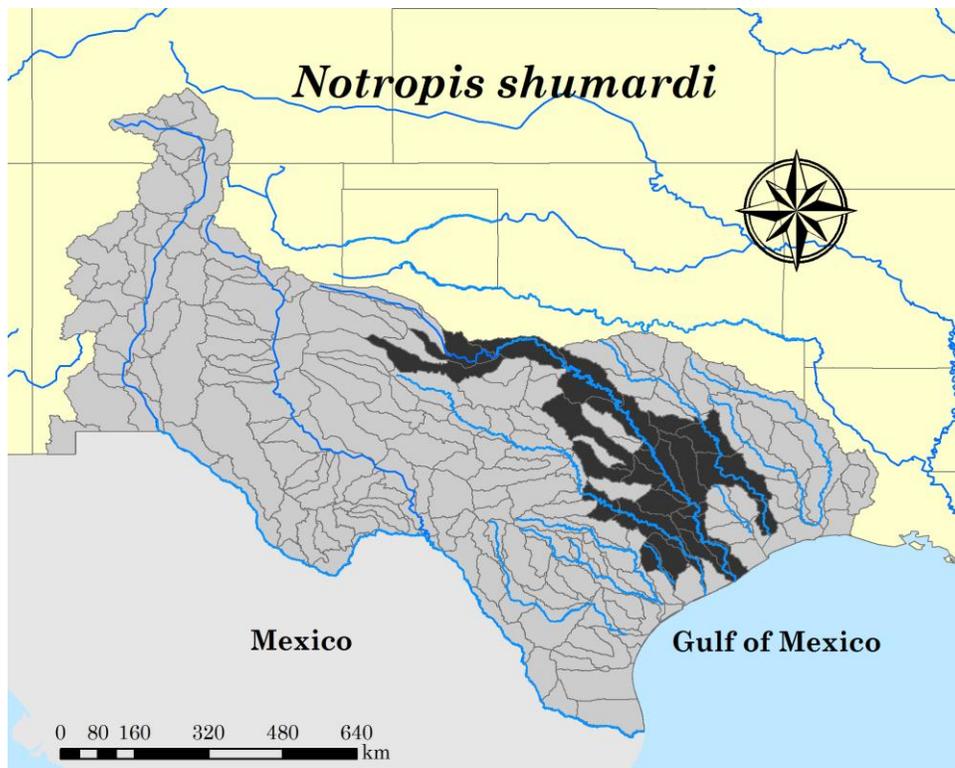
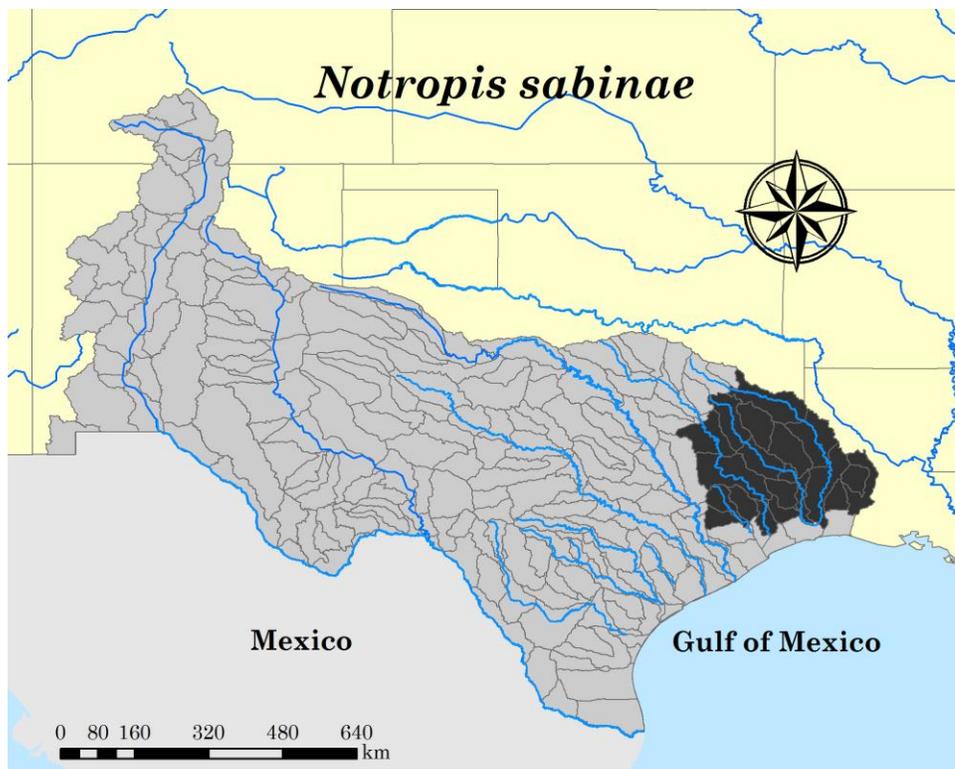


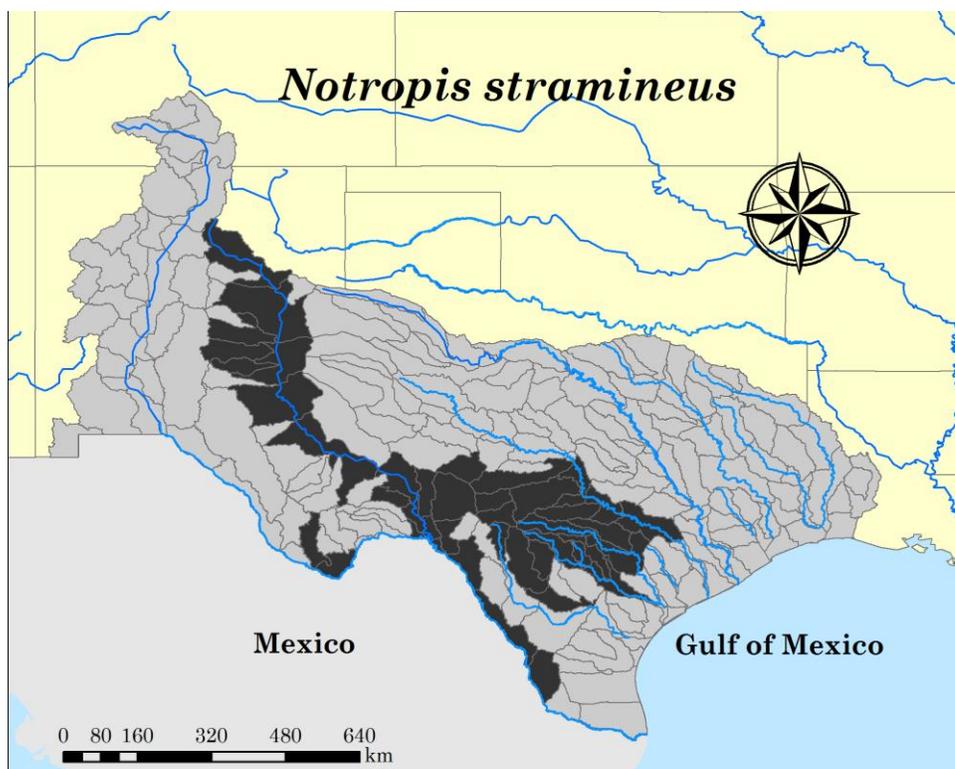
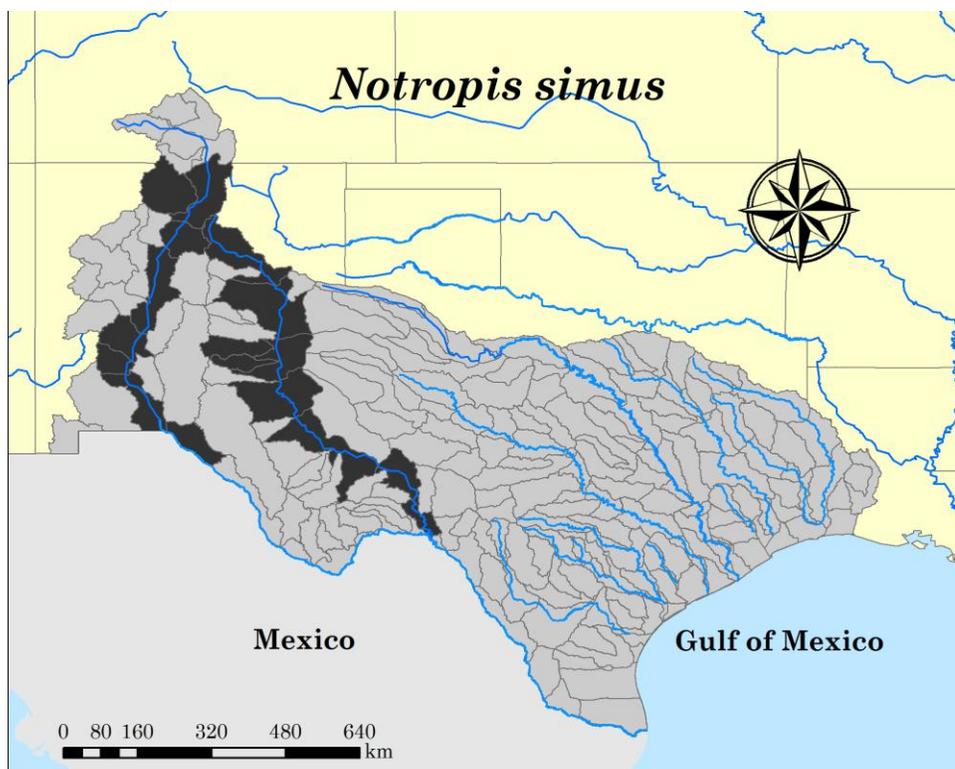


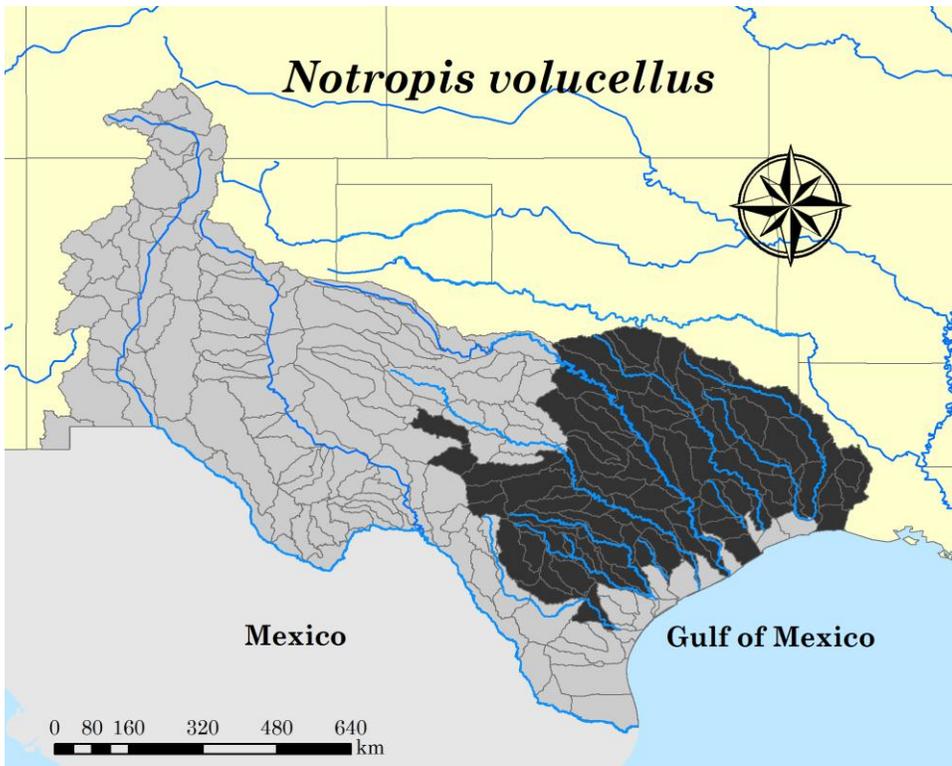
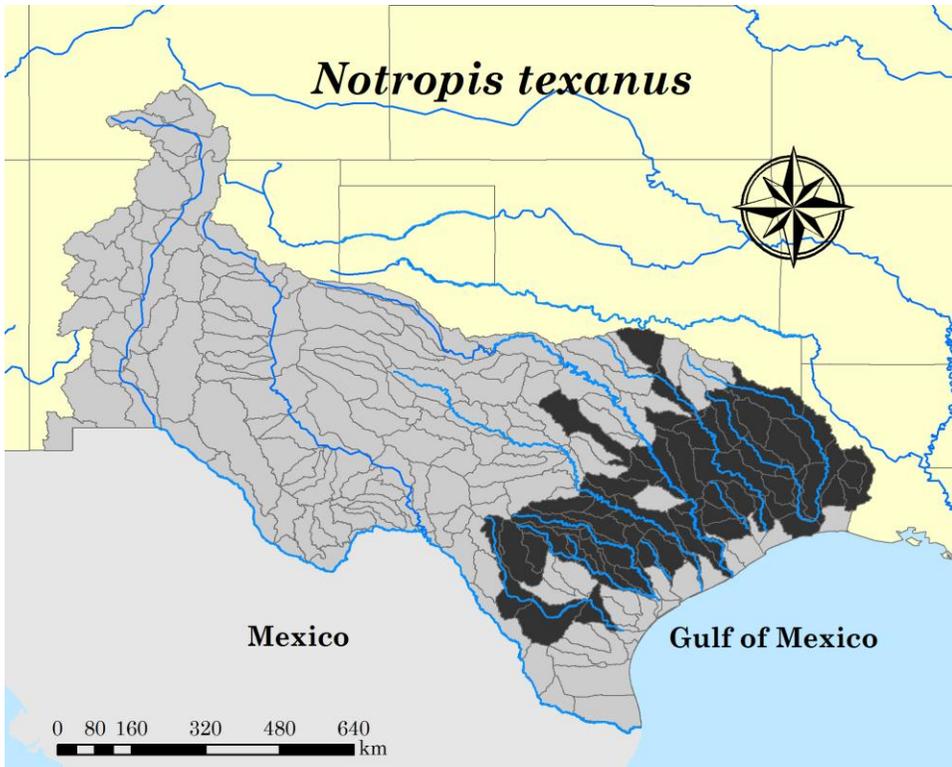


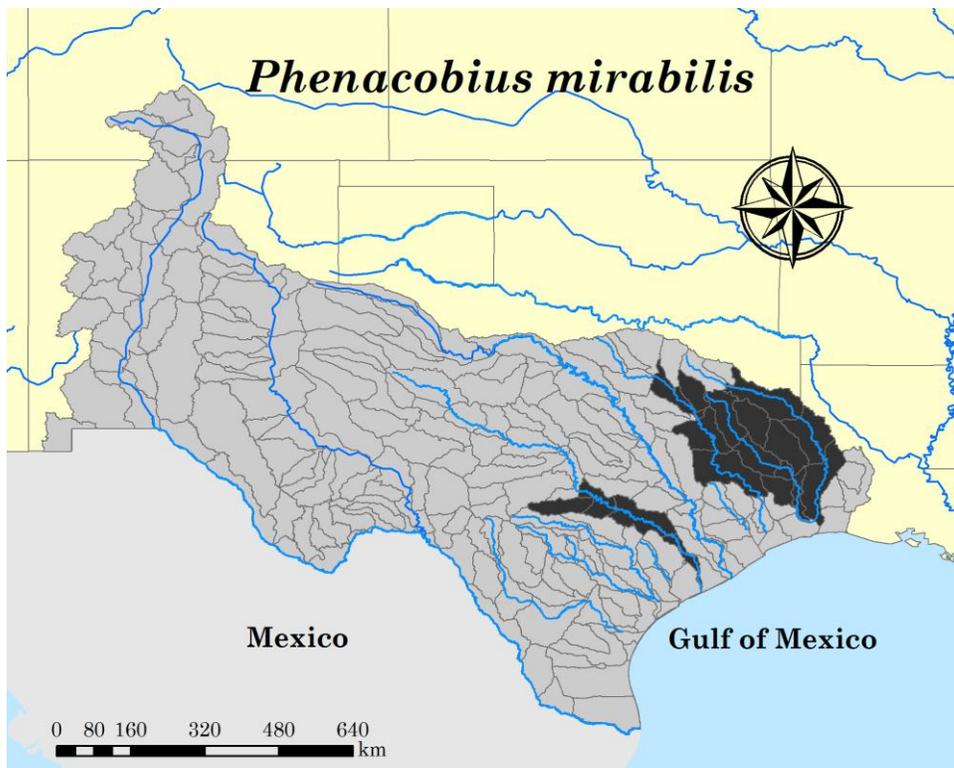
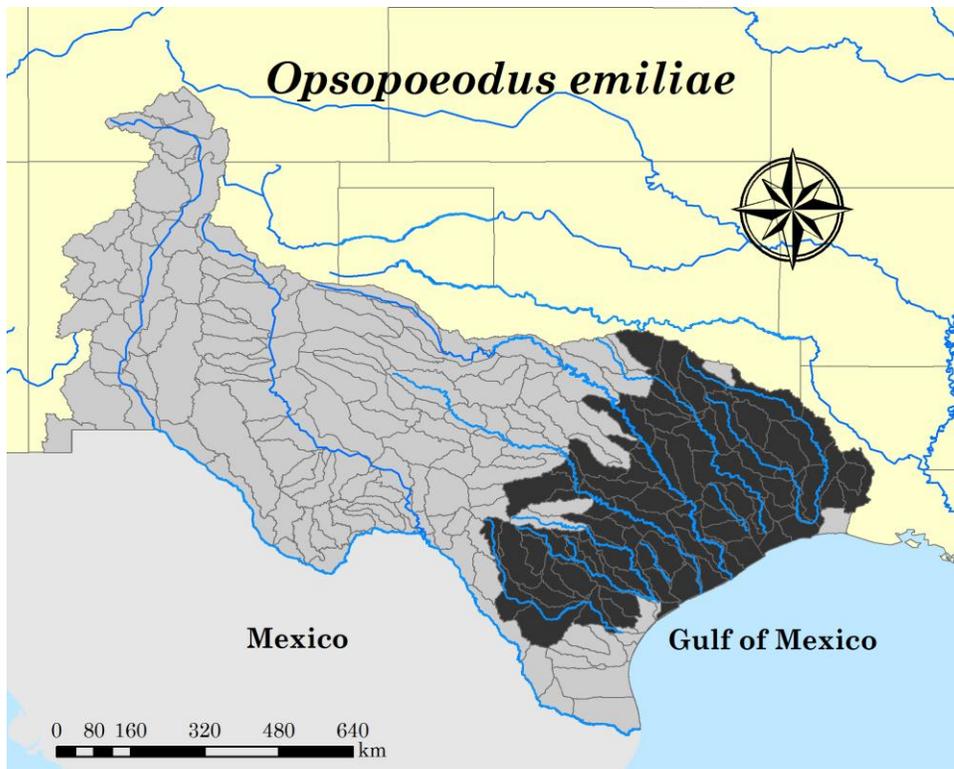


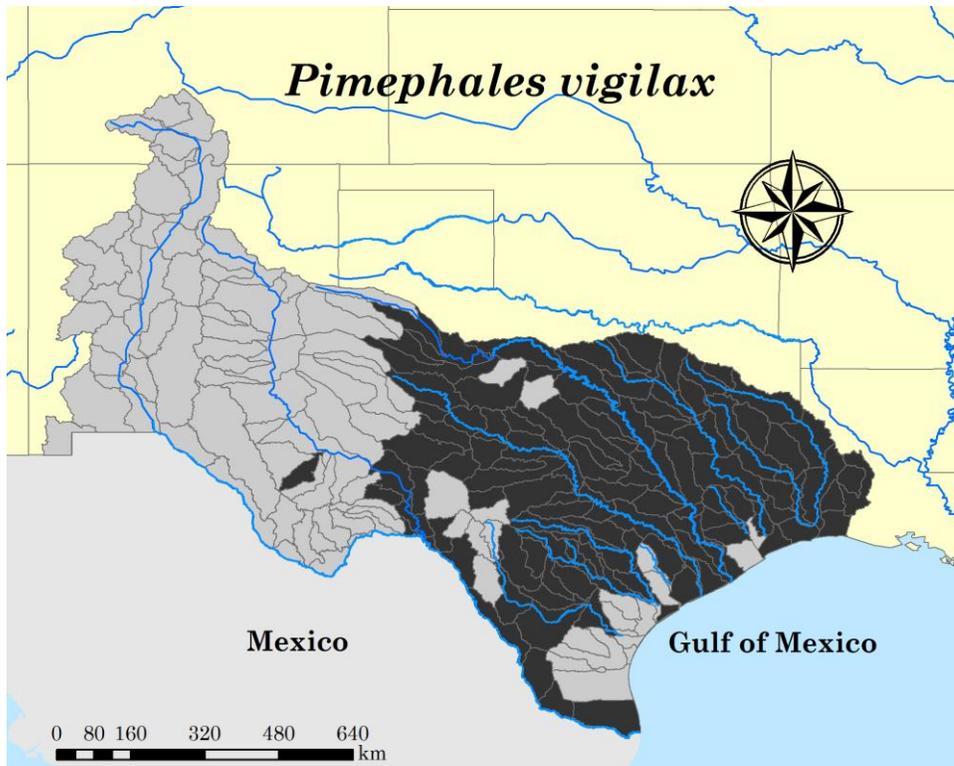
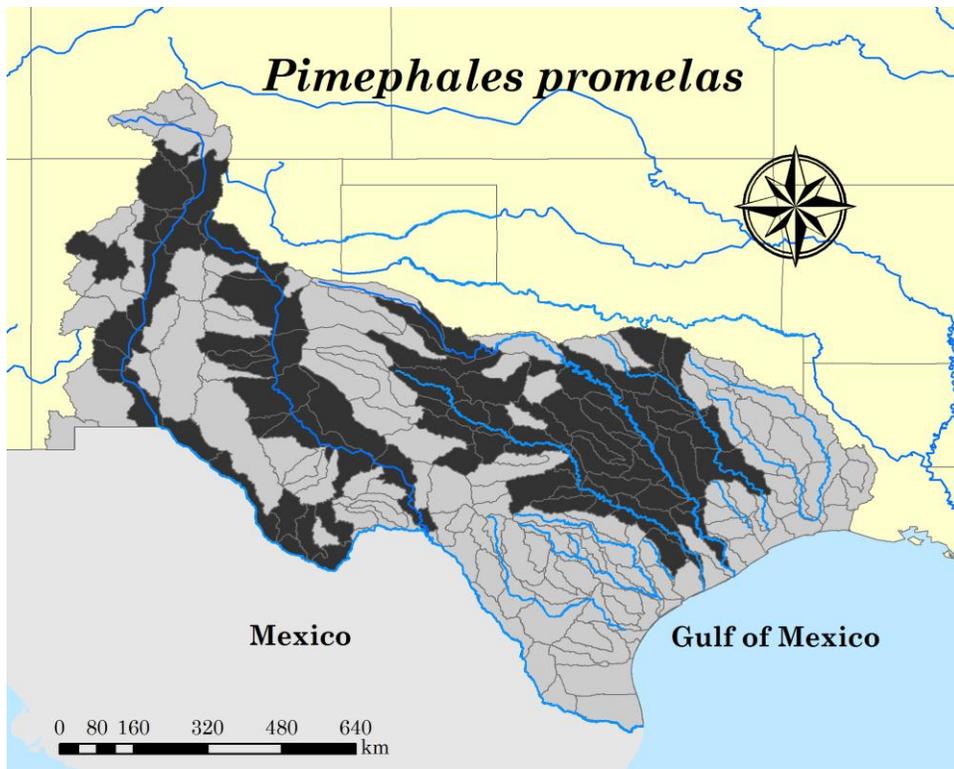


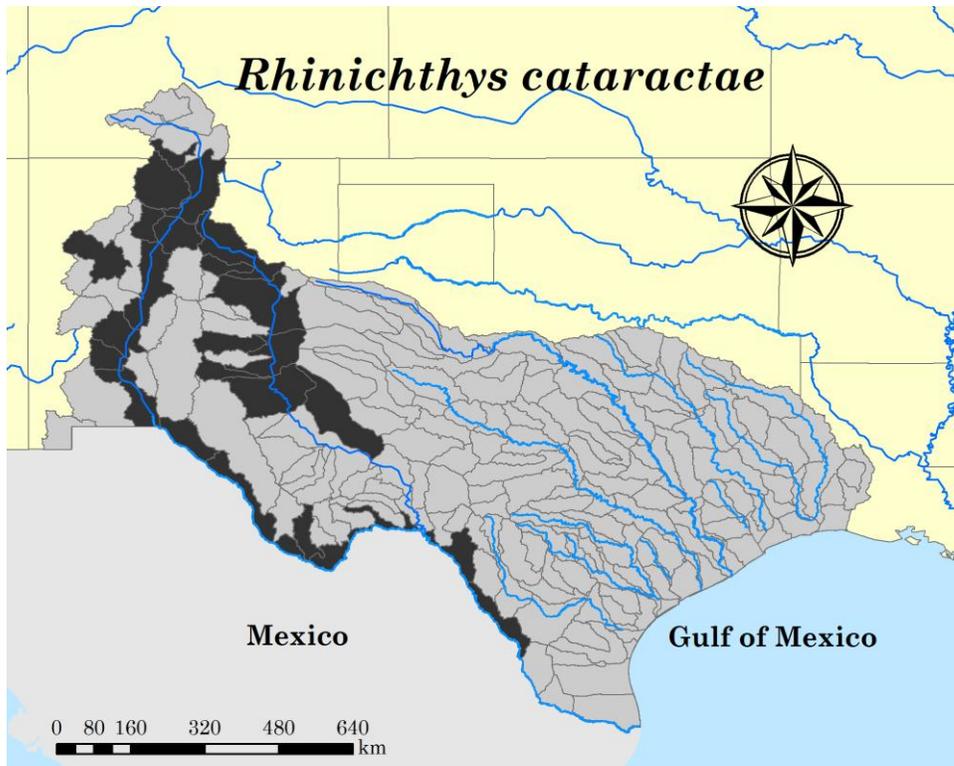
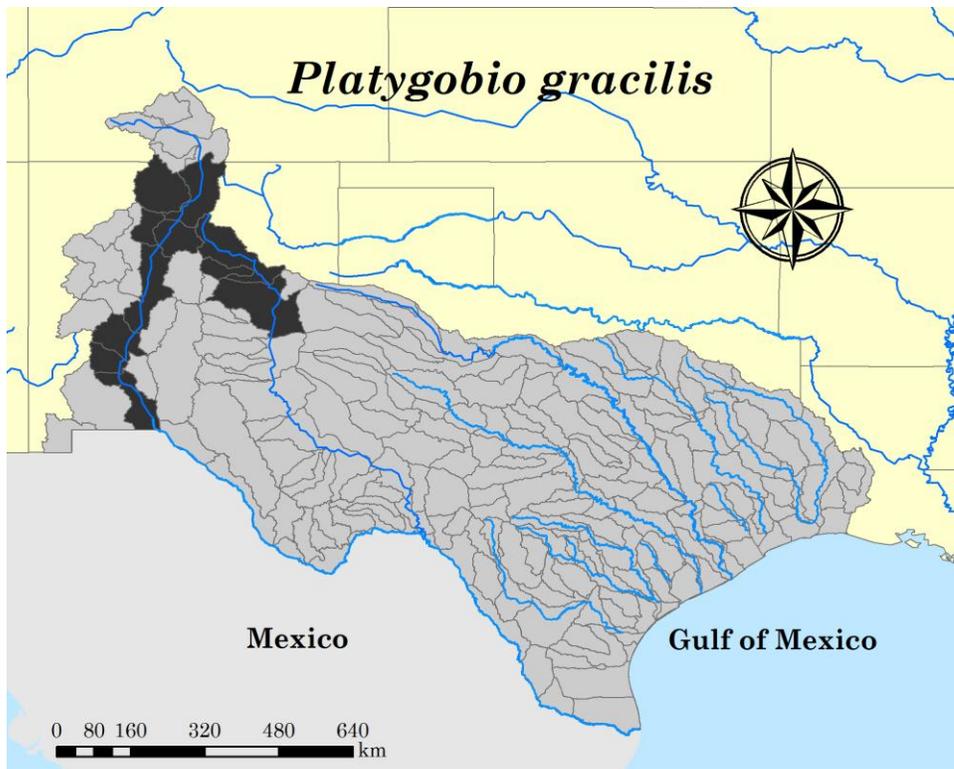


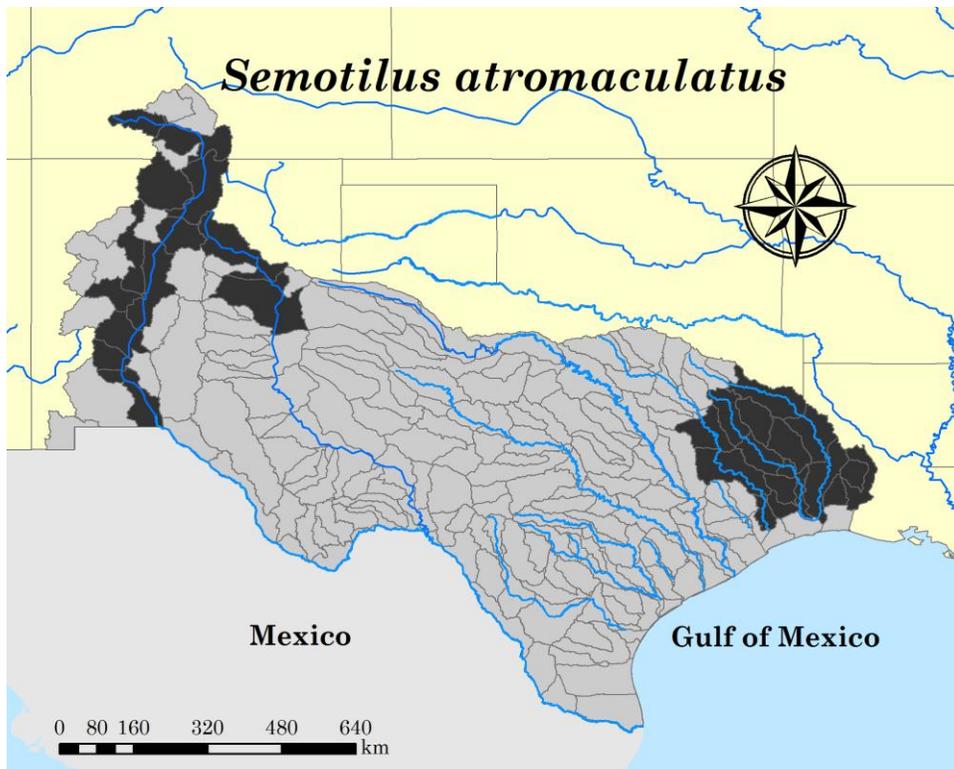




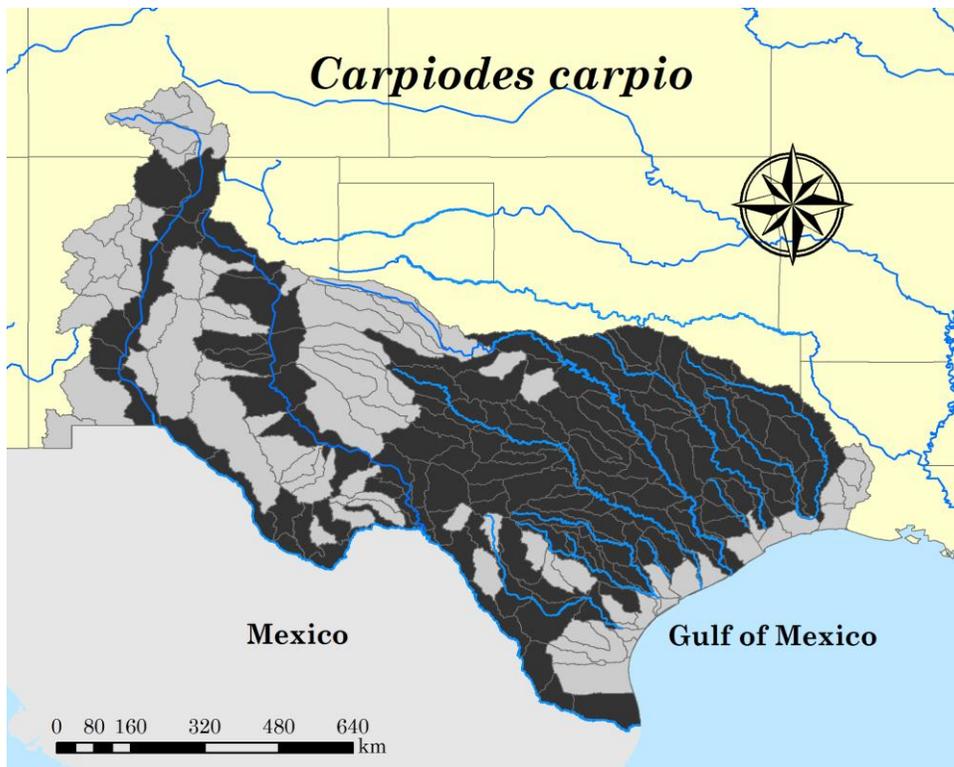


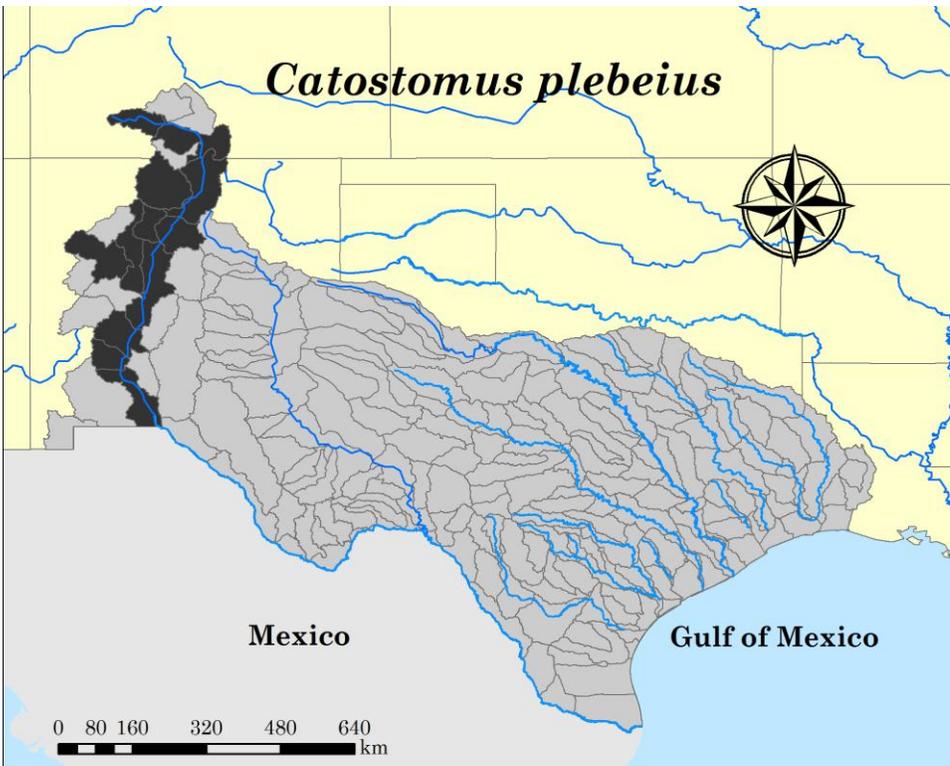
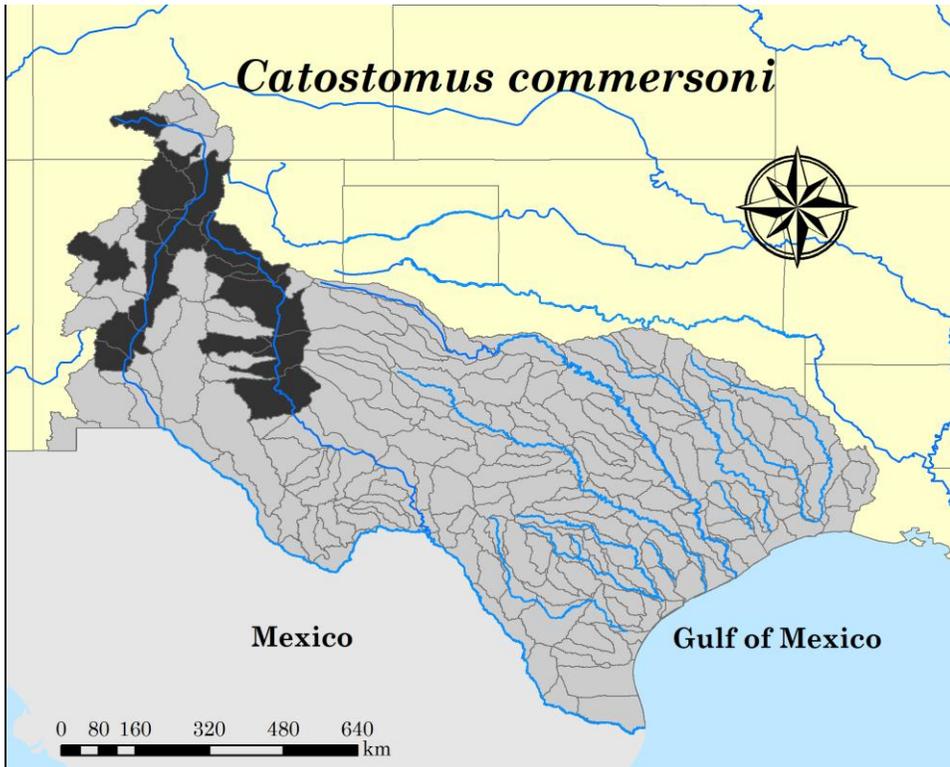


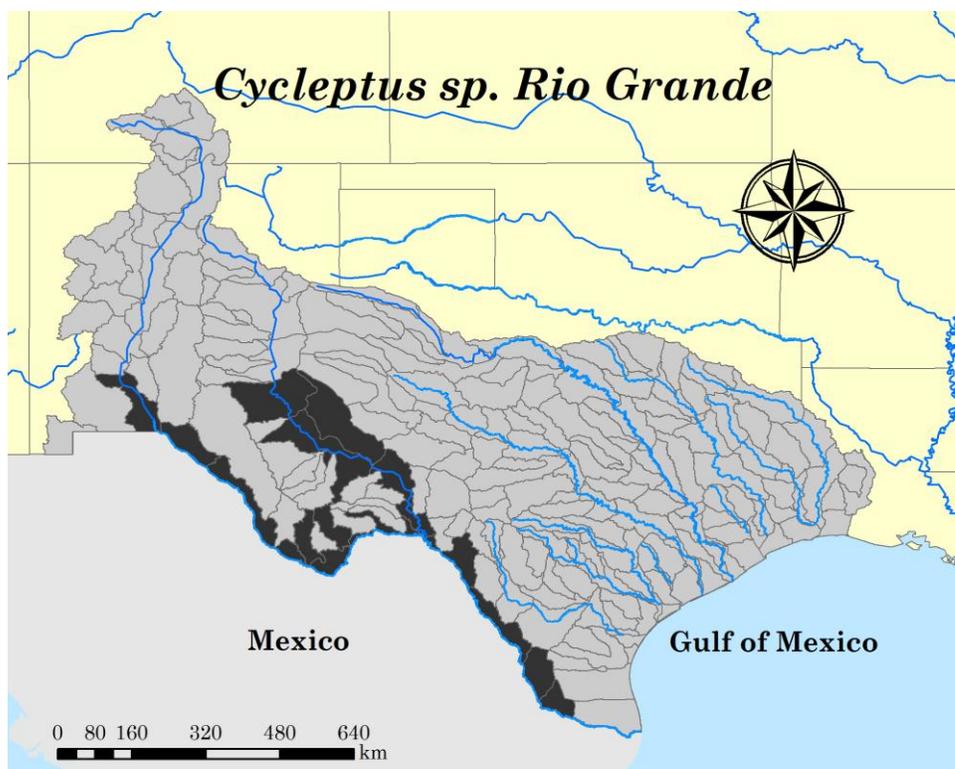
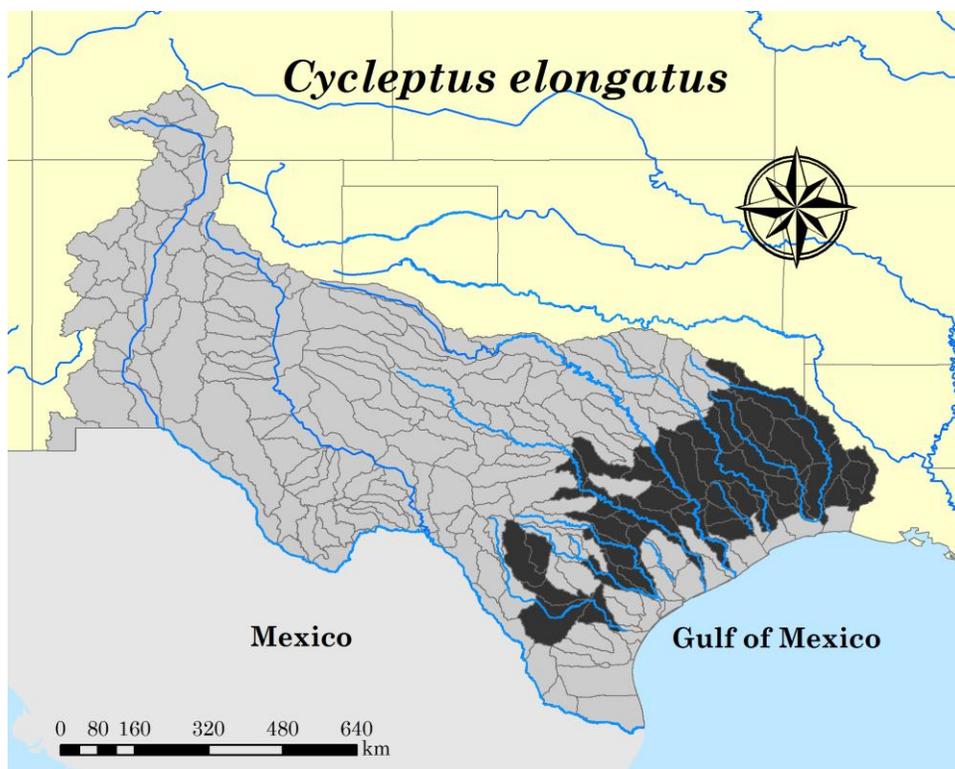


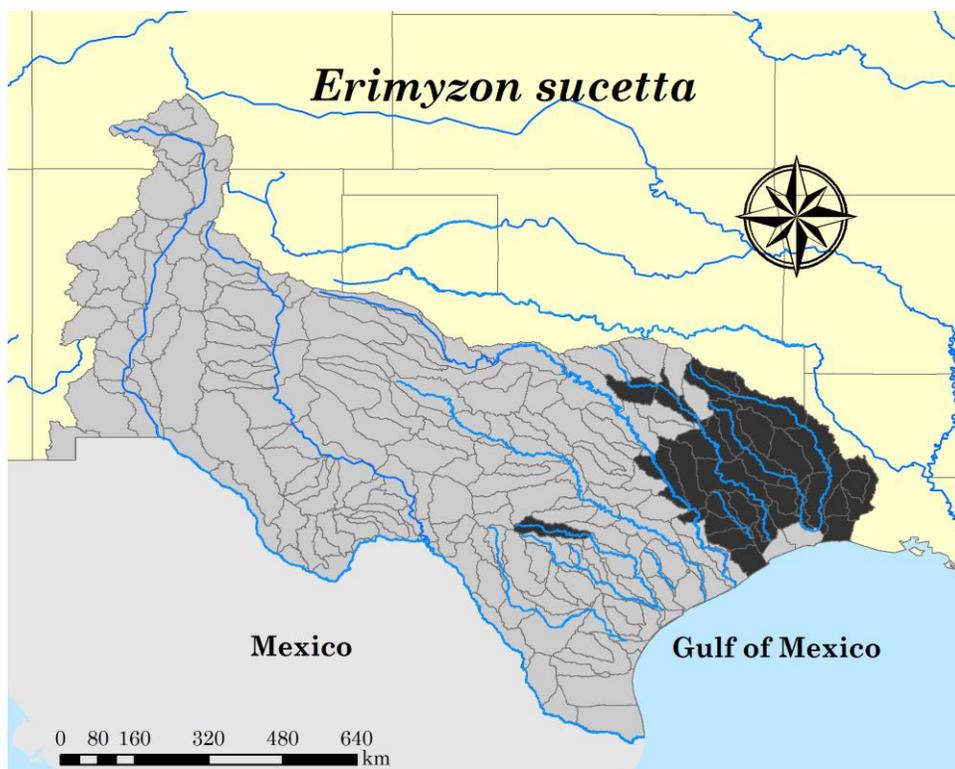


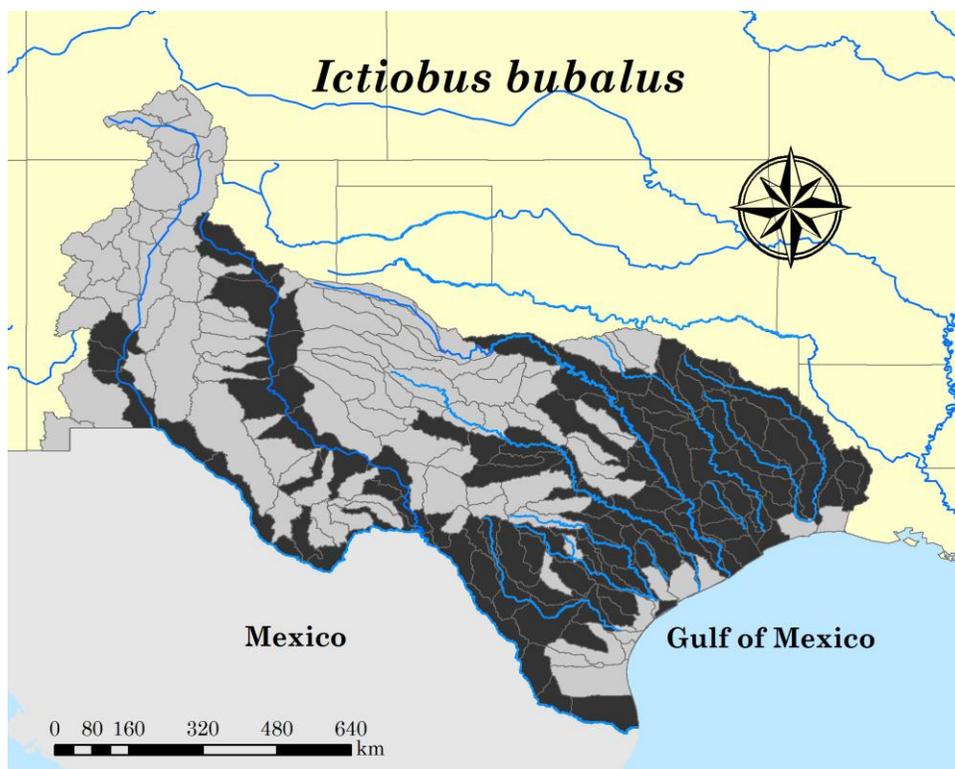
Catostomidae









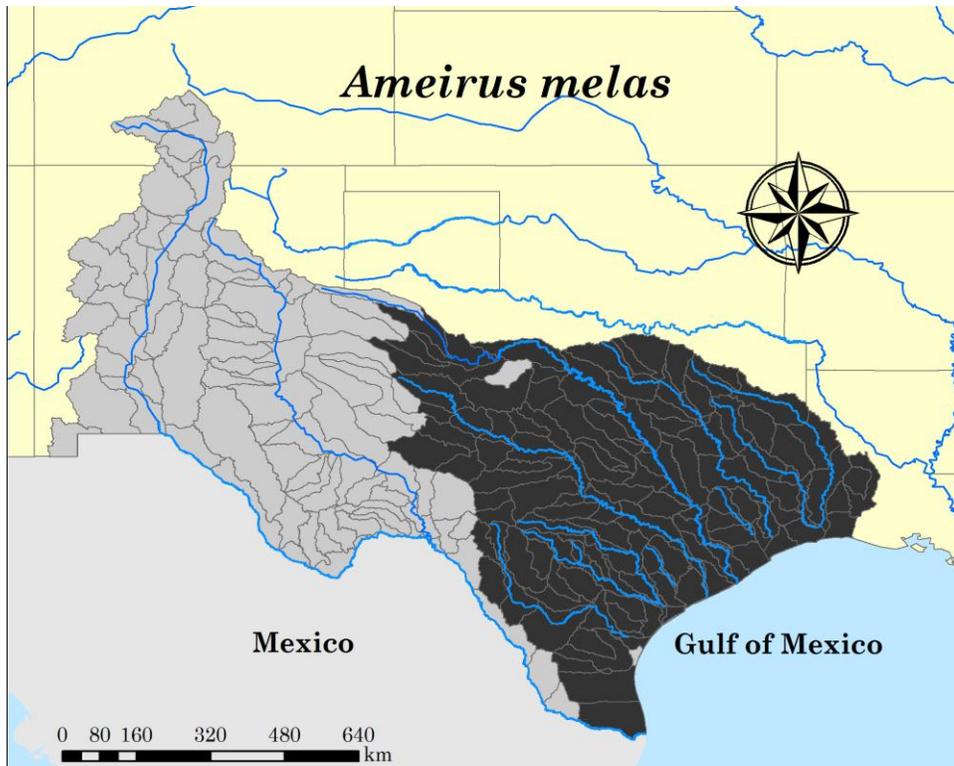


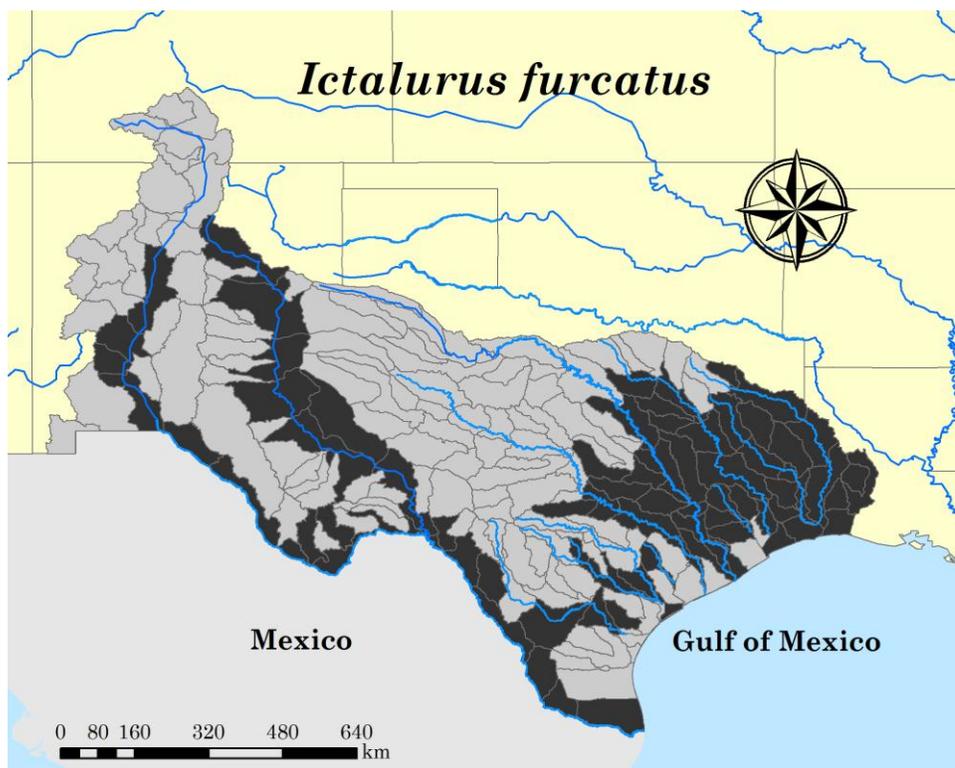
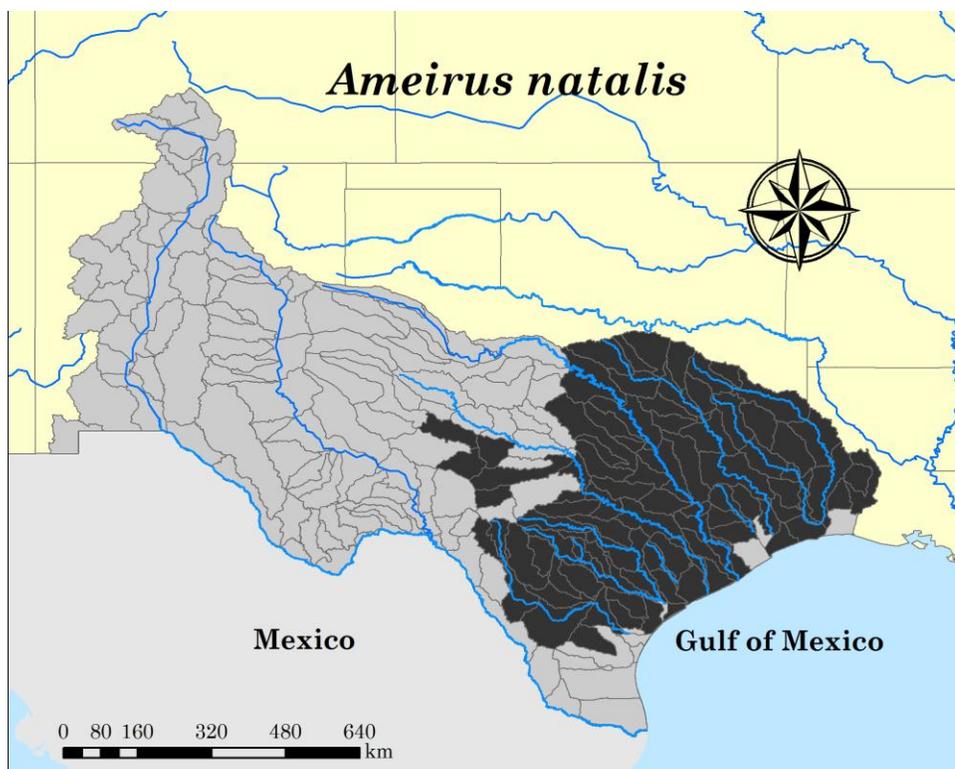


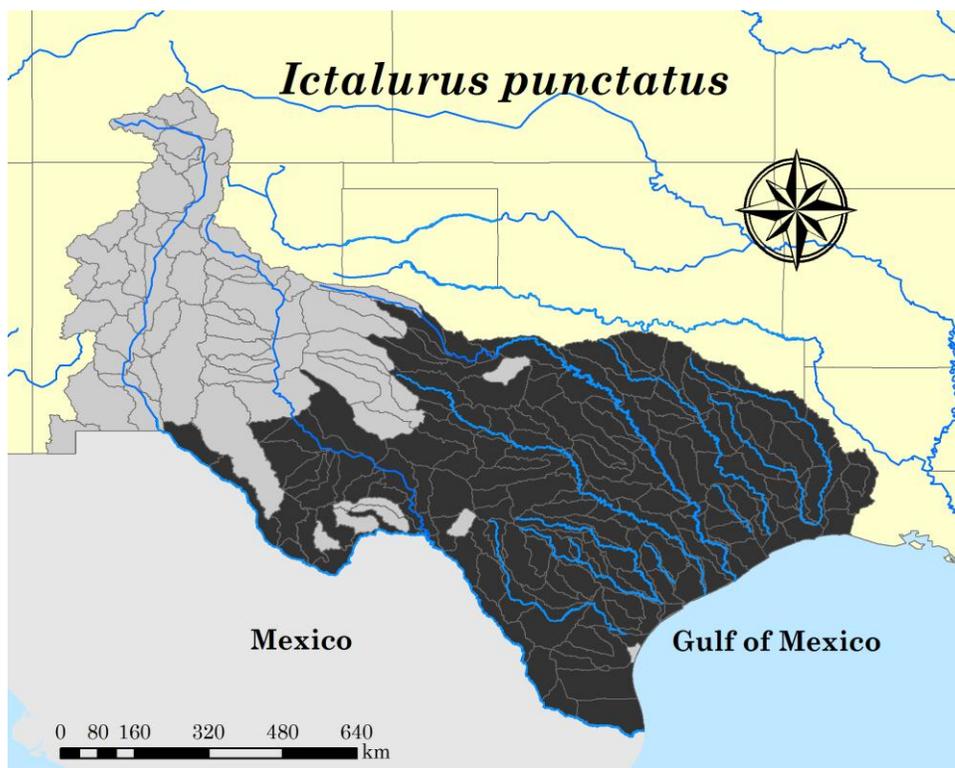
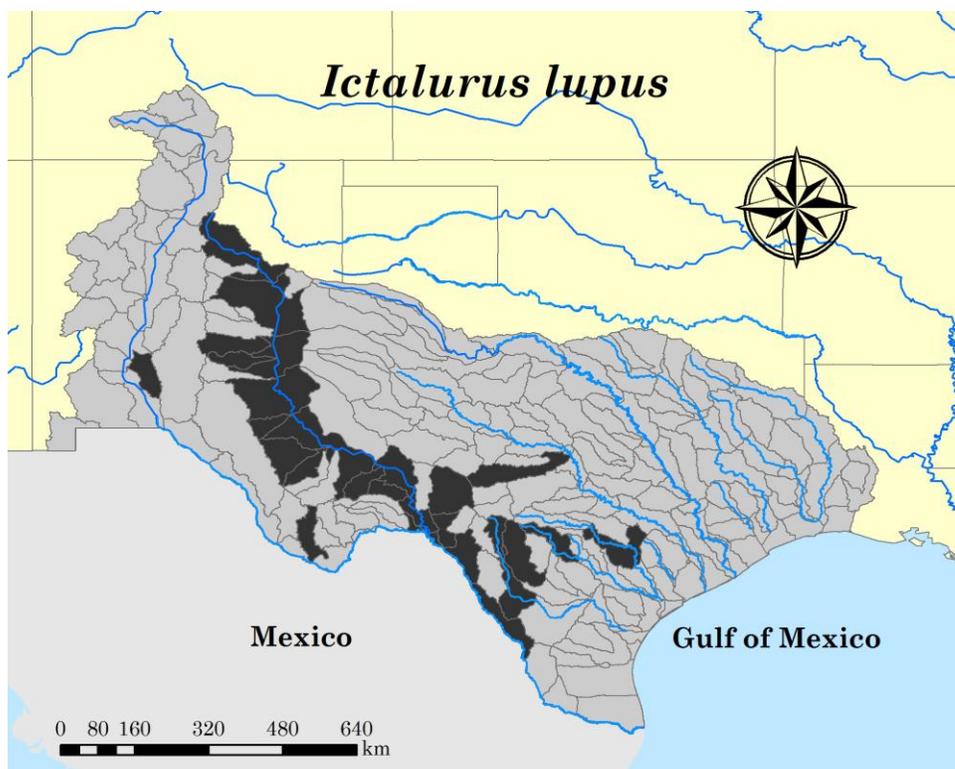
Characidae

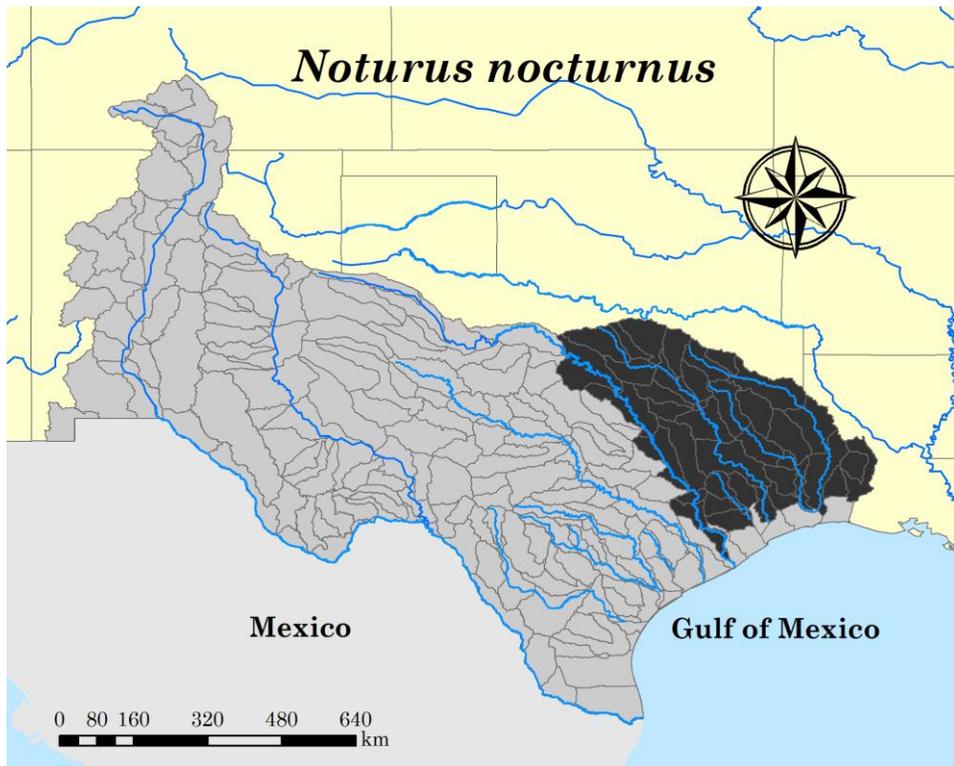


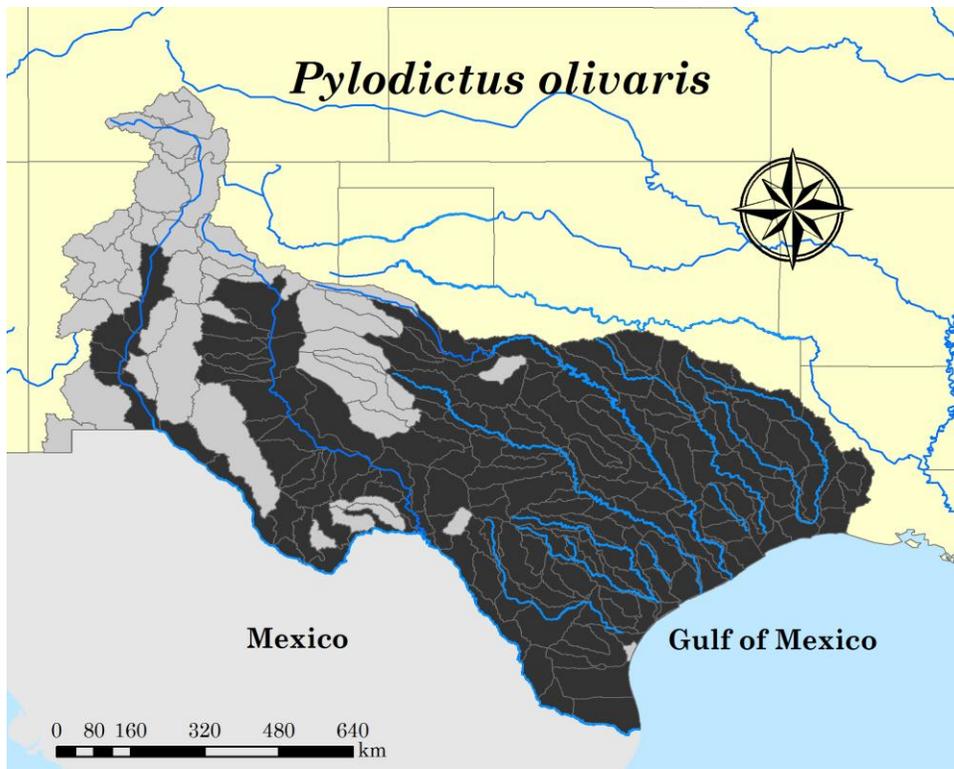
Ictaluridae



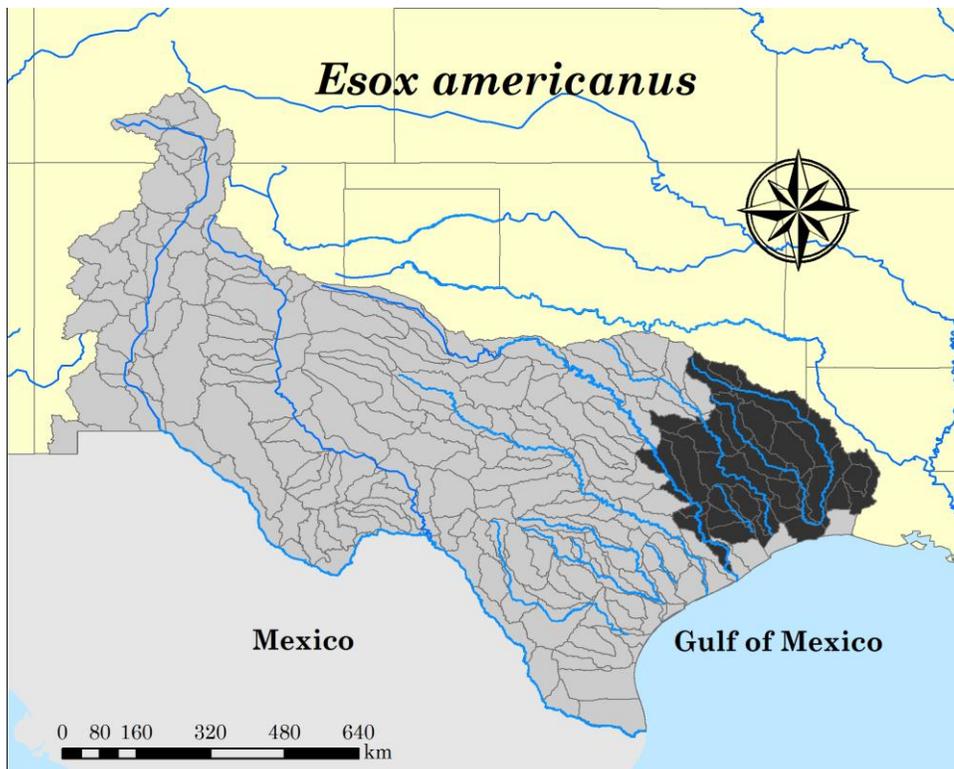






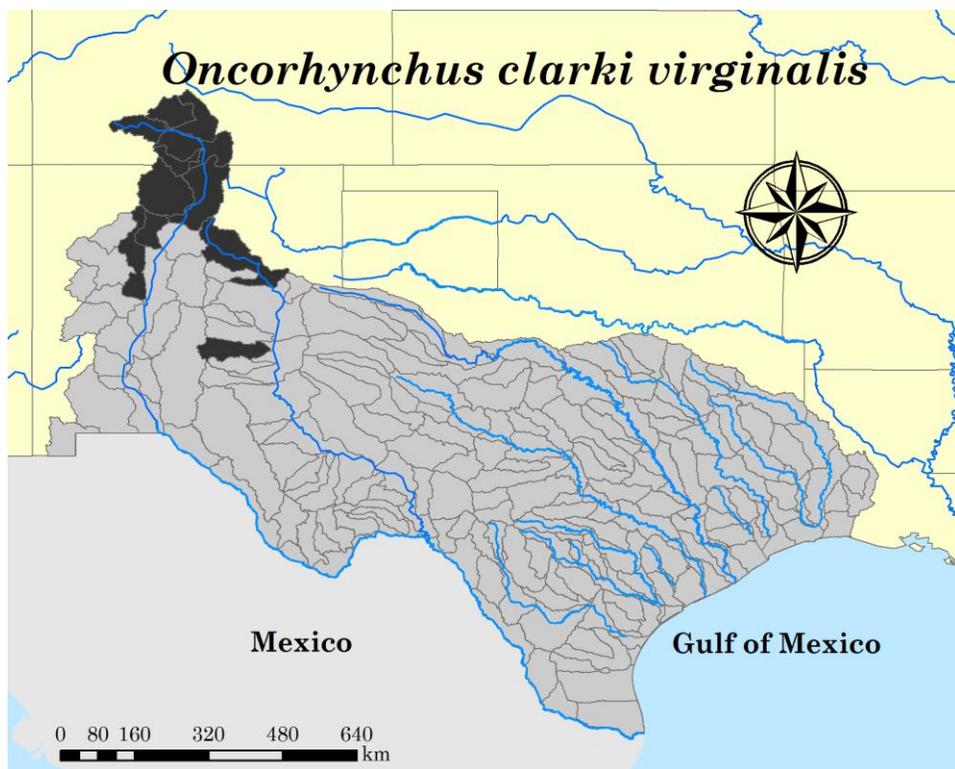


Esocidae





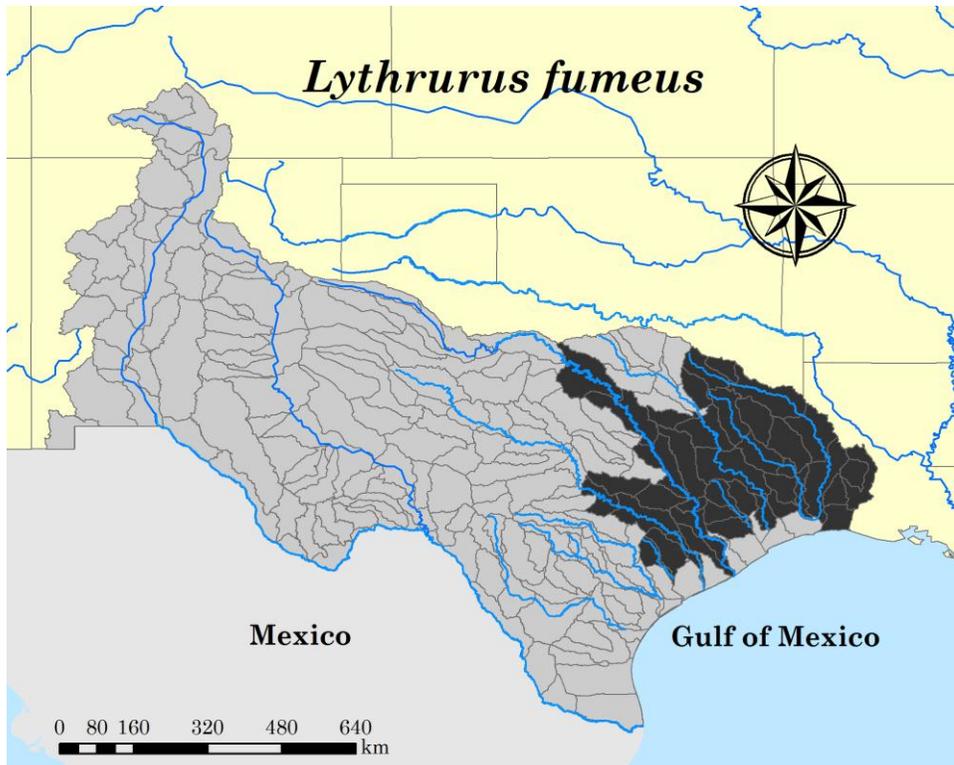
Salmonidae

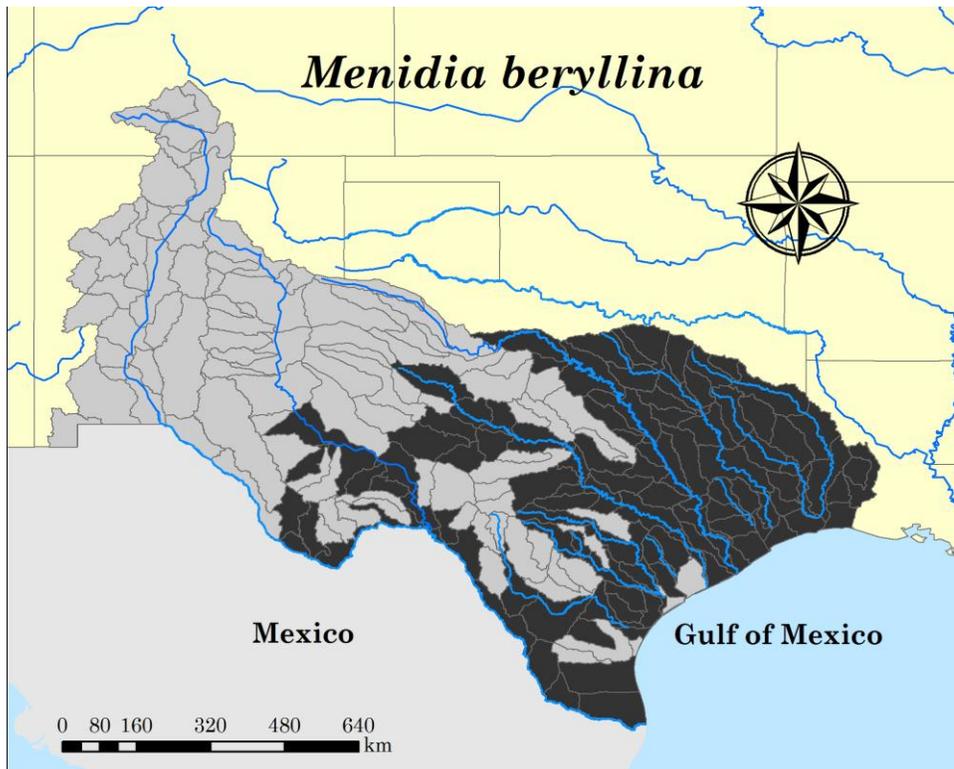


Aphredoderidae

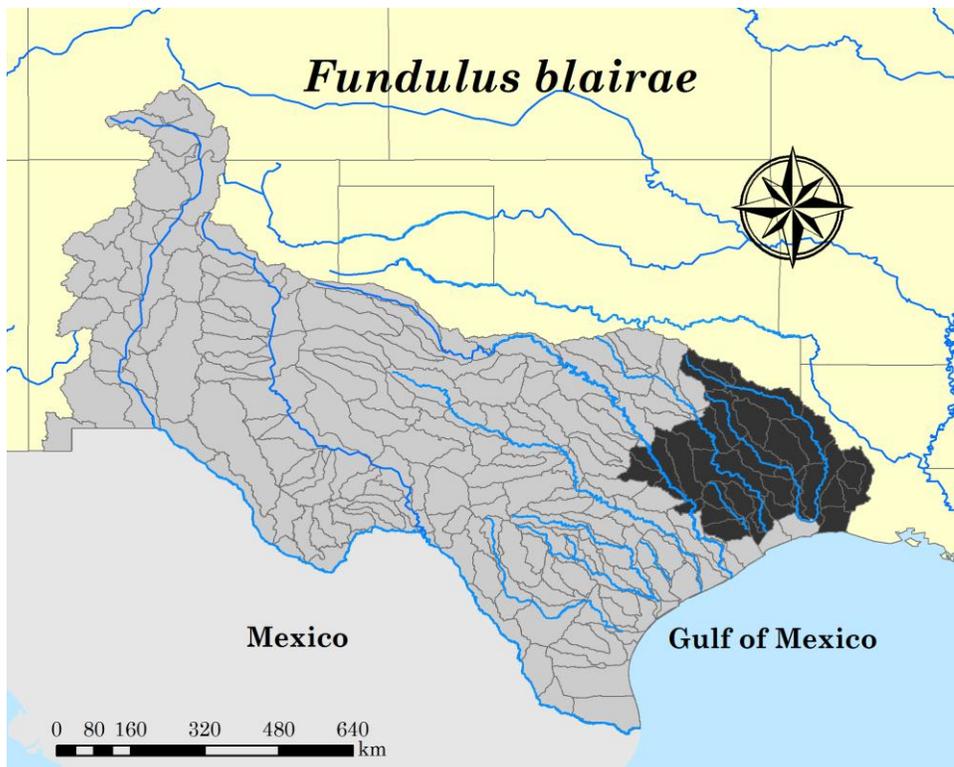


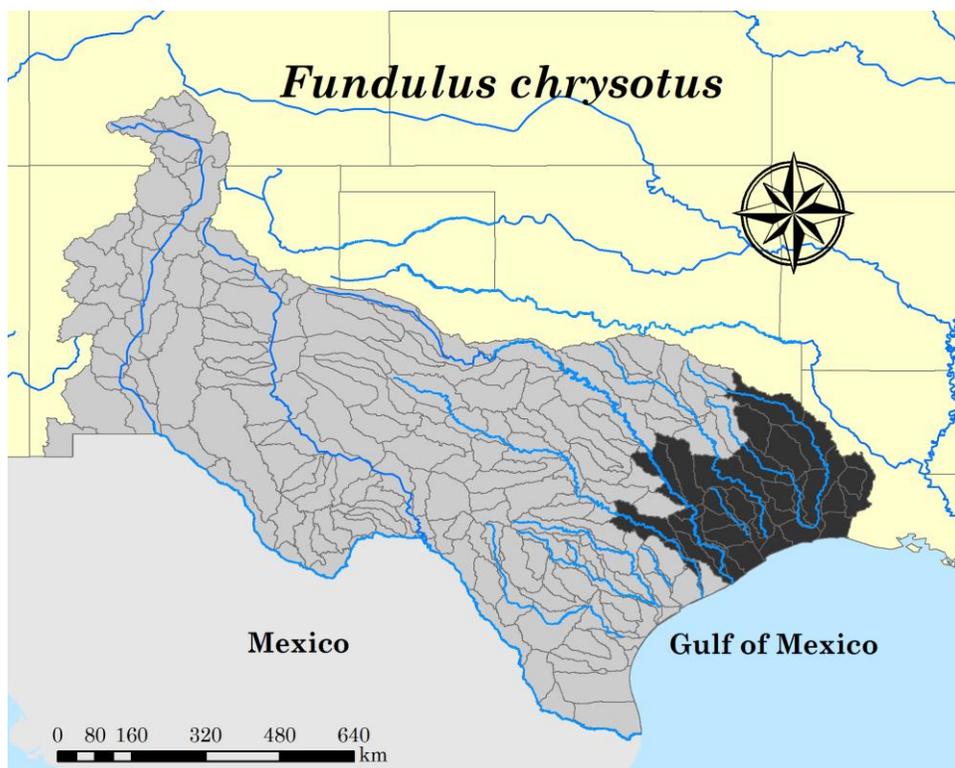
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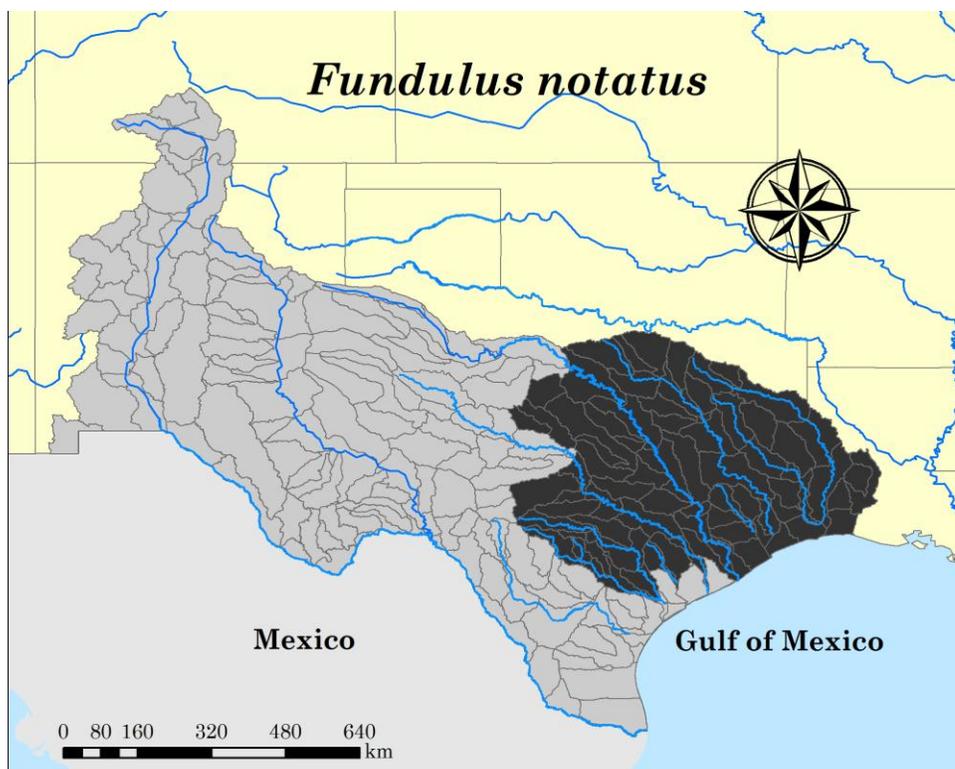




Fundulidae

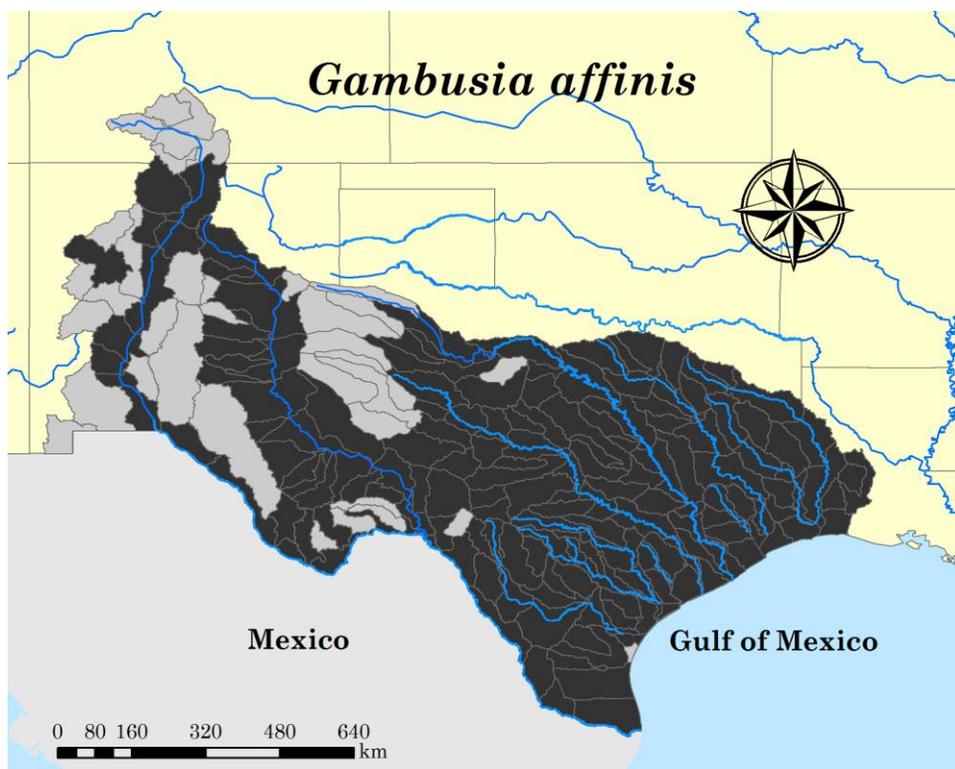


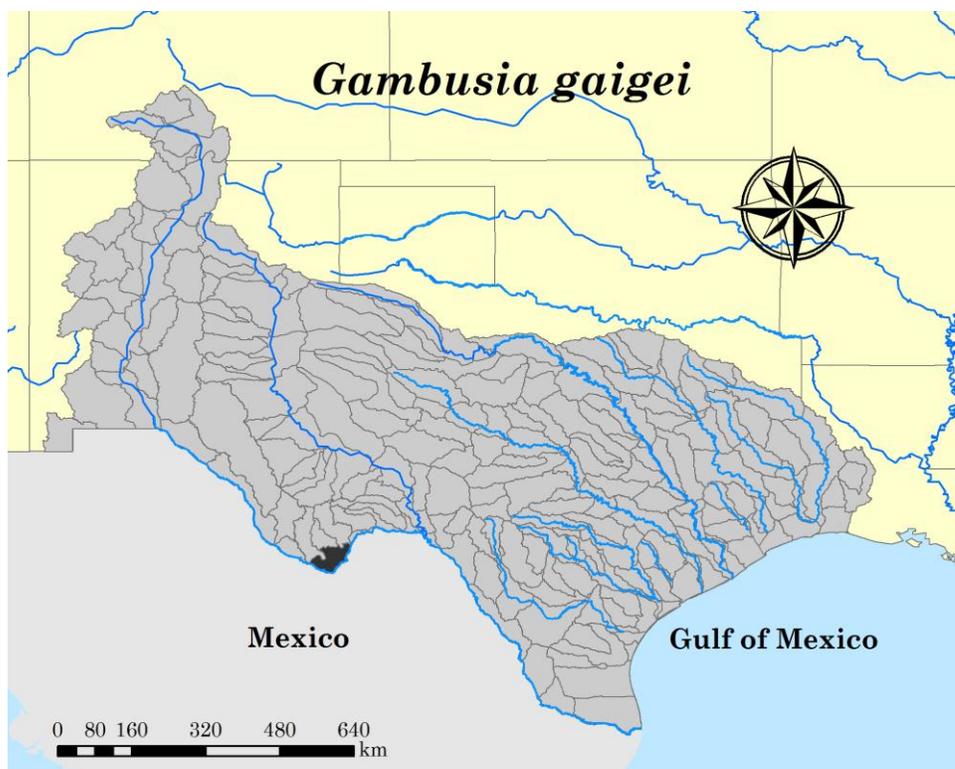






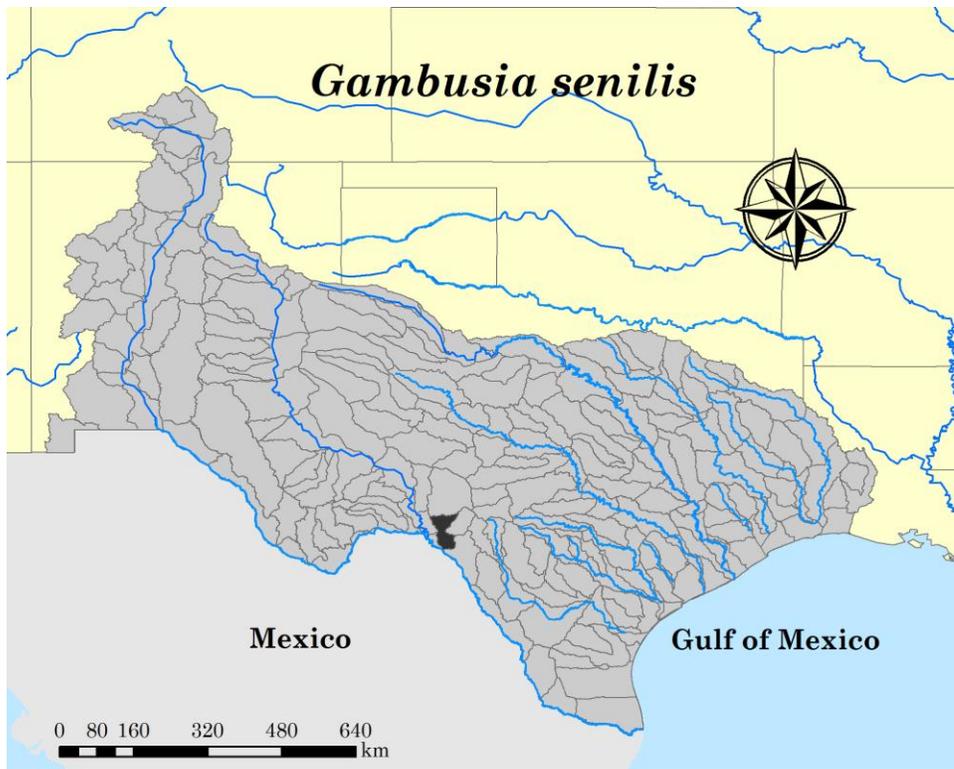
Poeciliidae

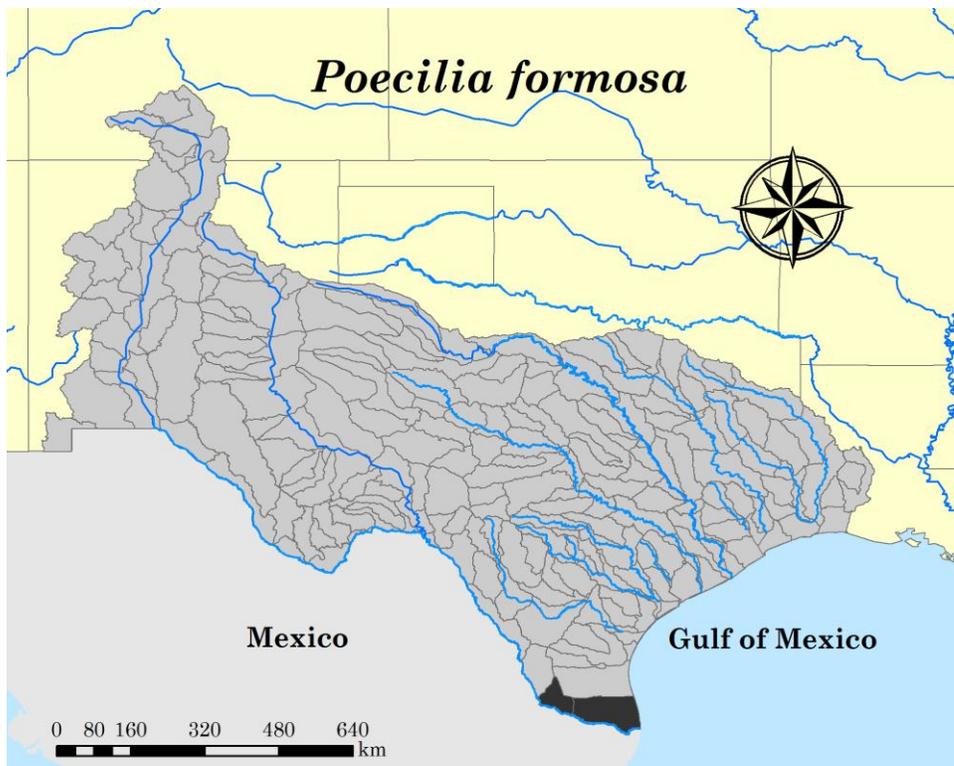






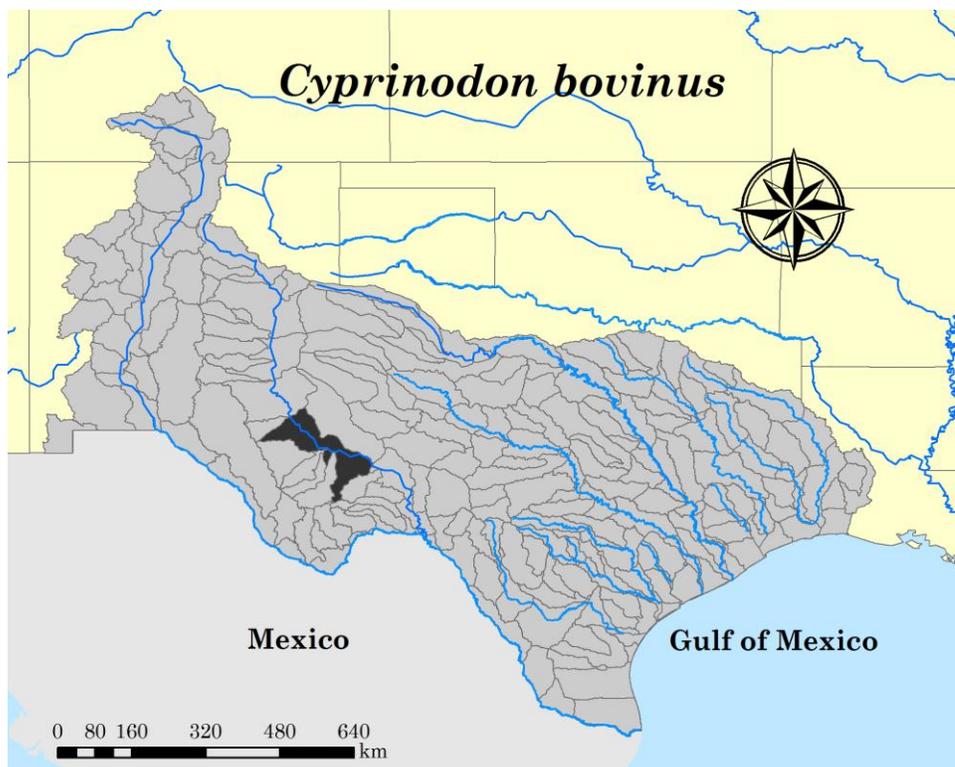


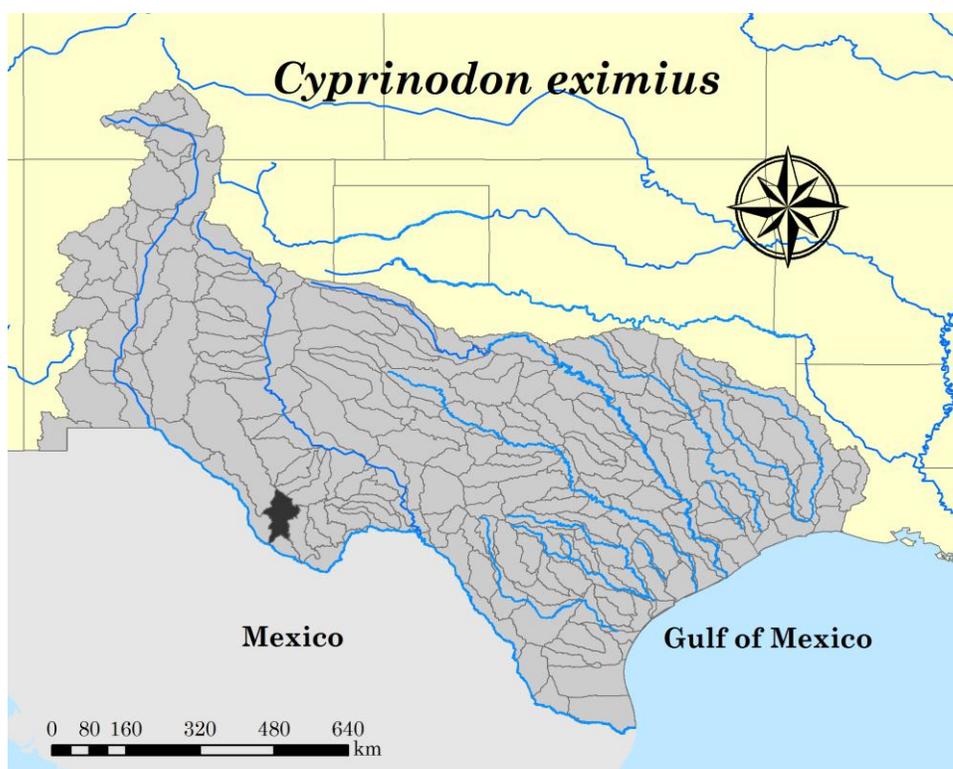
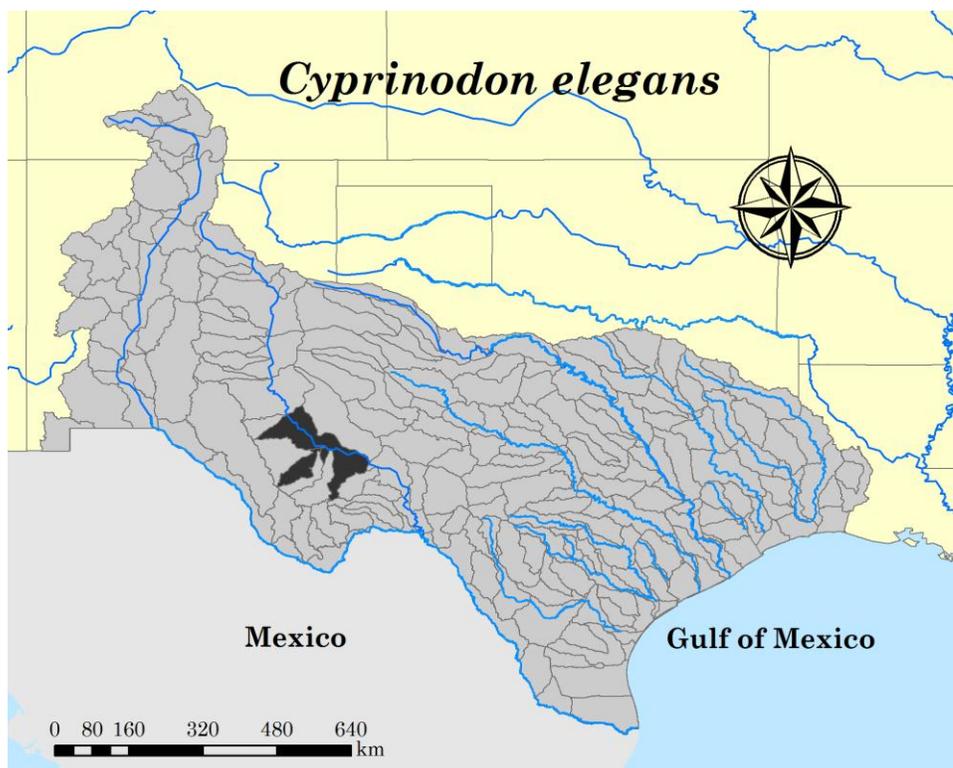


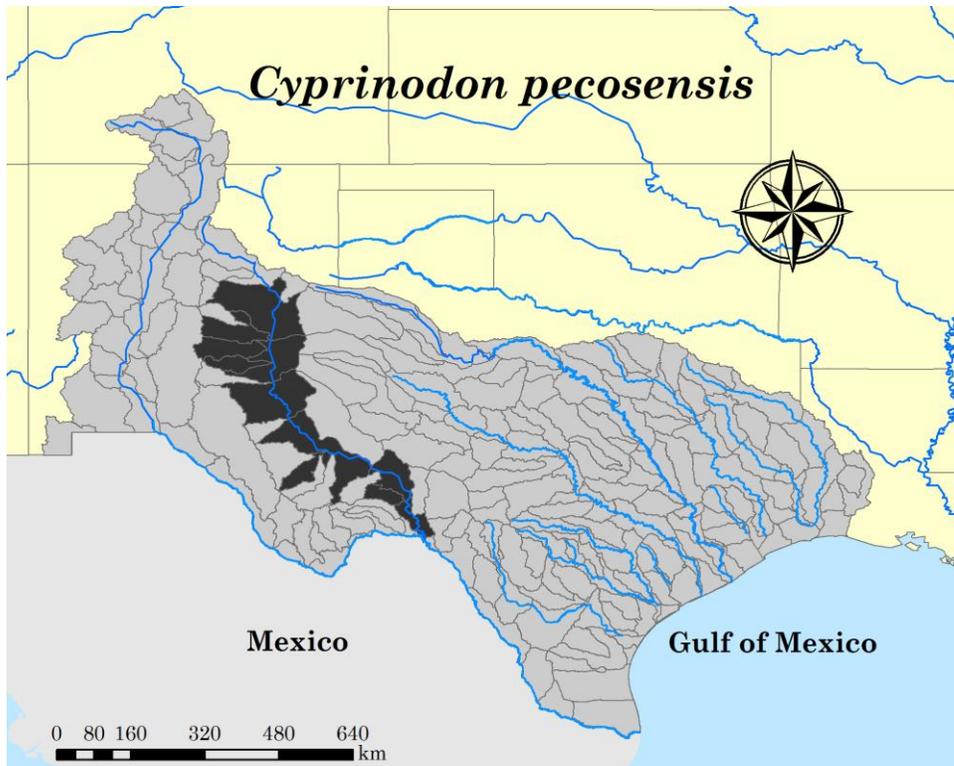
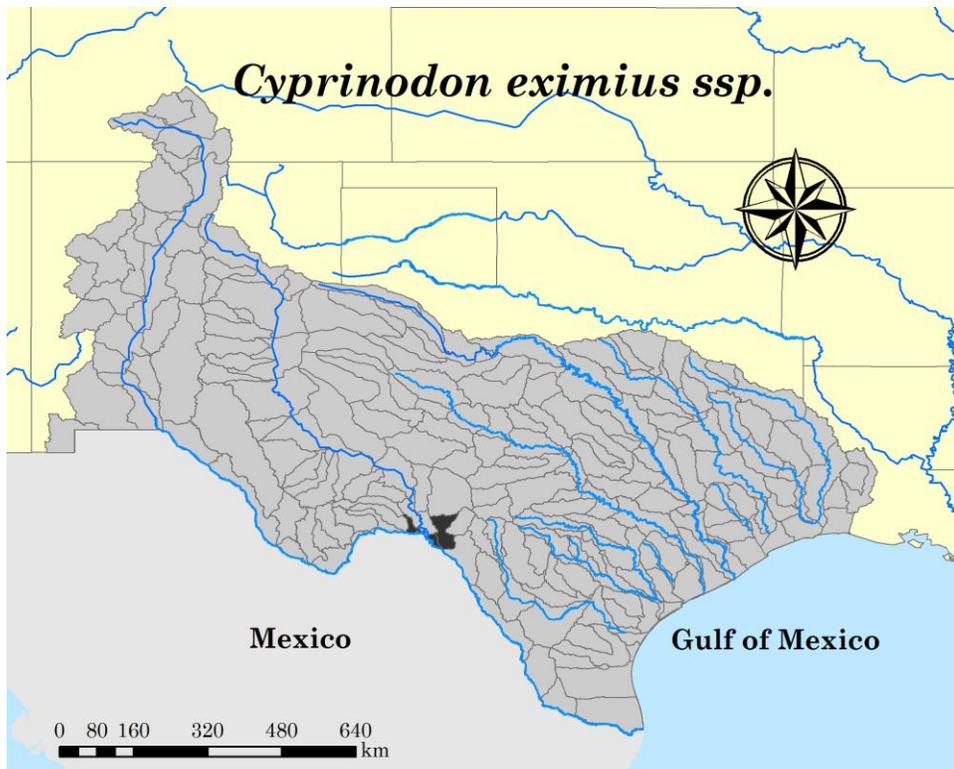


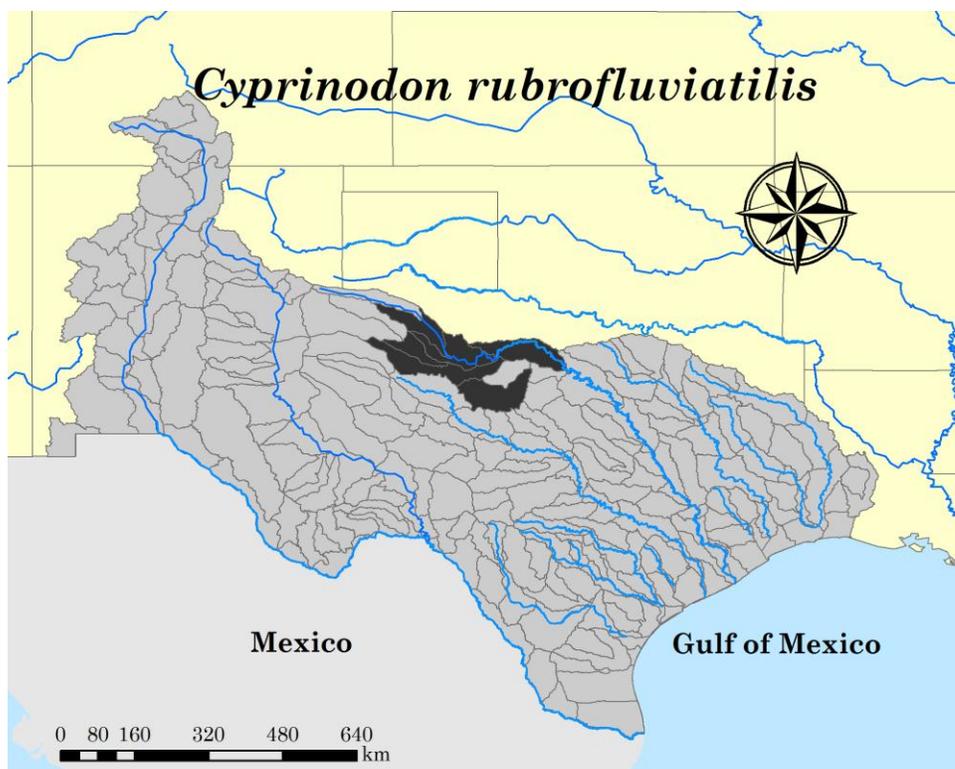


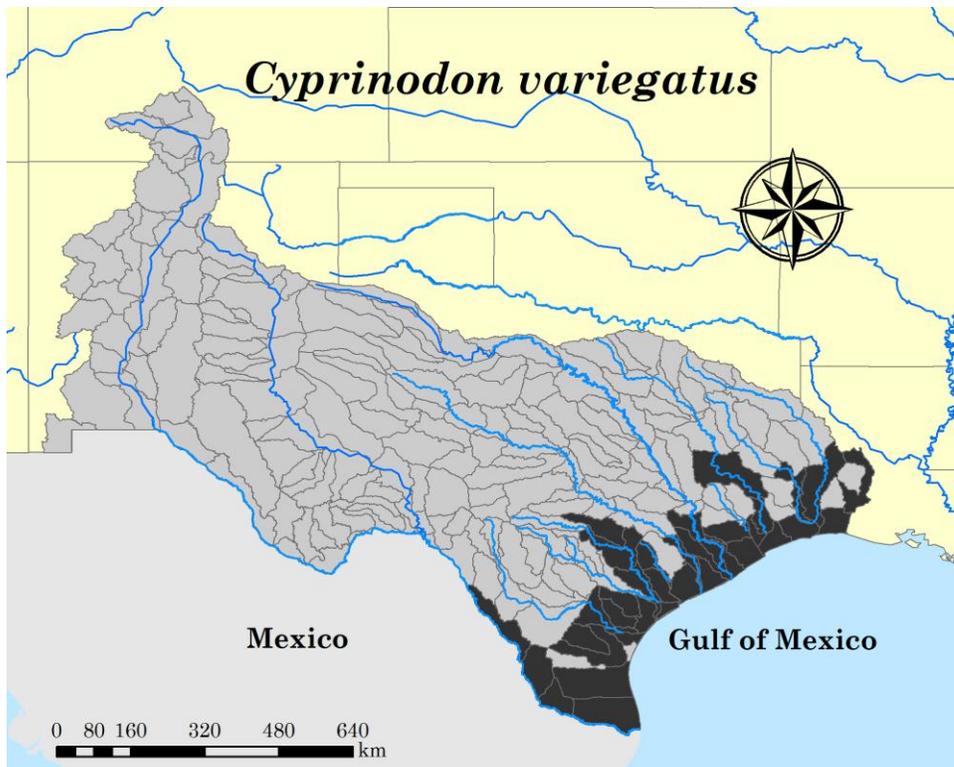
Cyprinodontidae







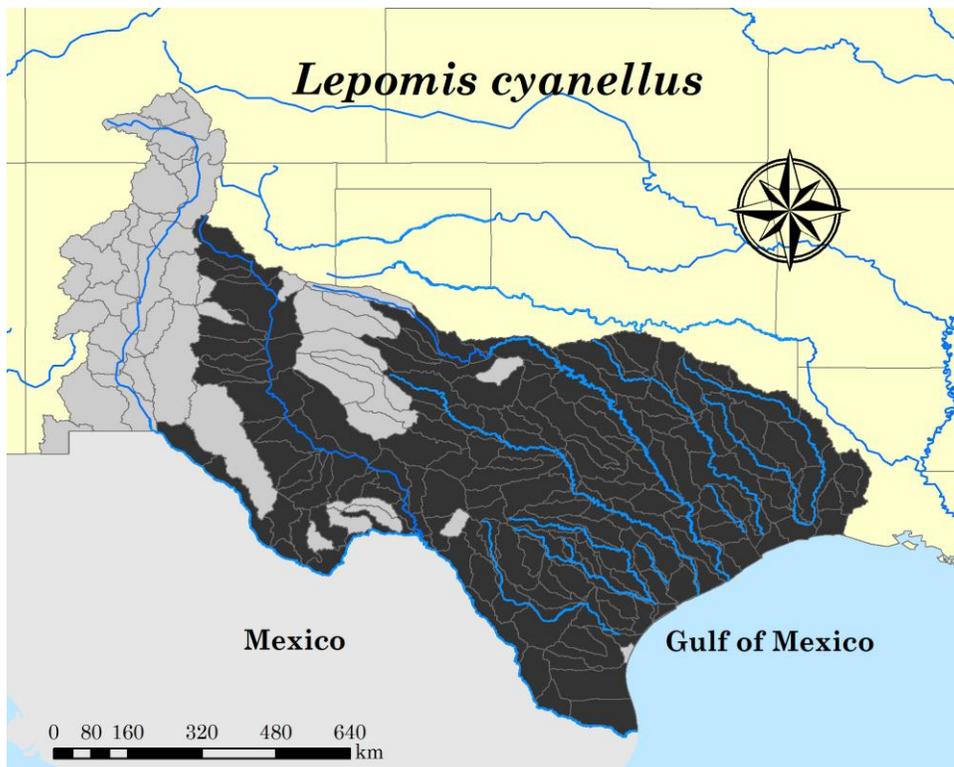


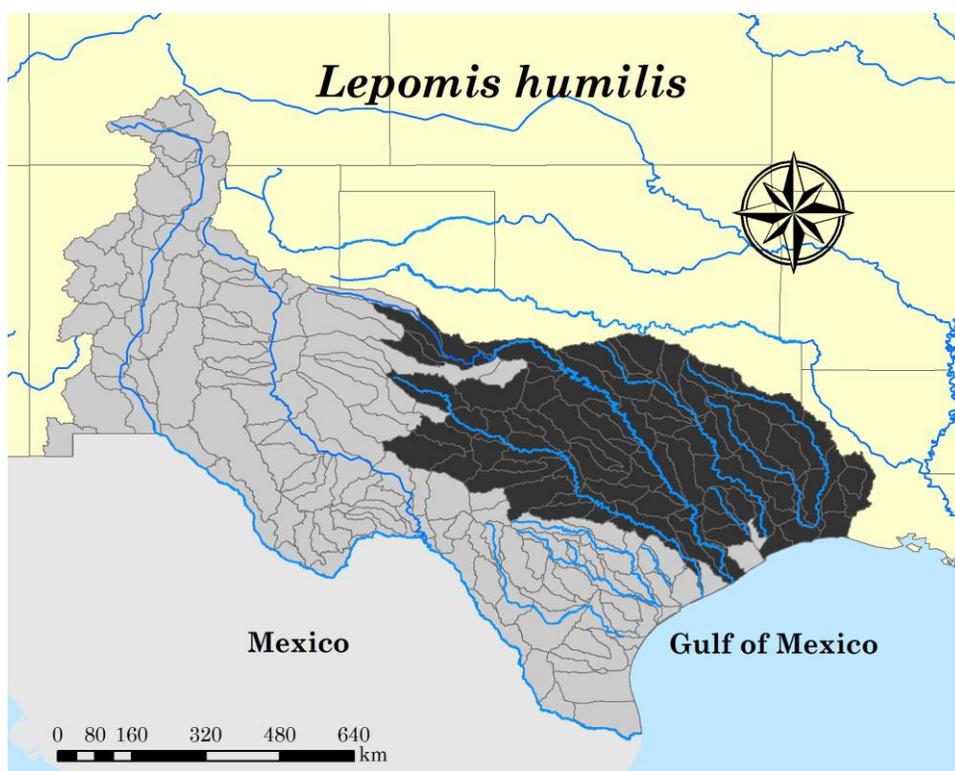
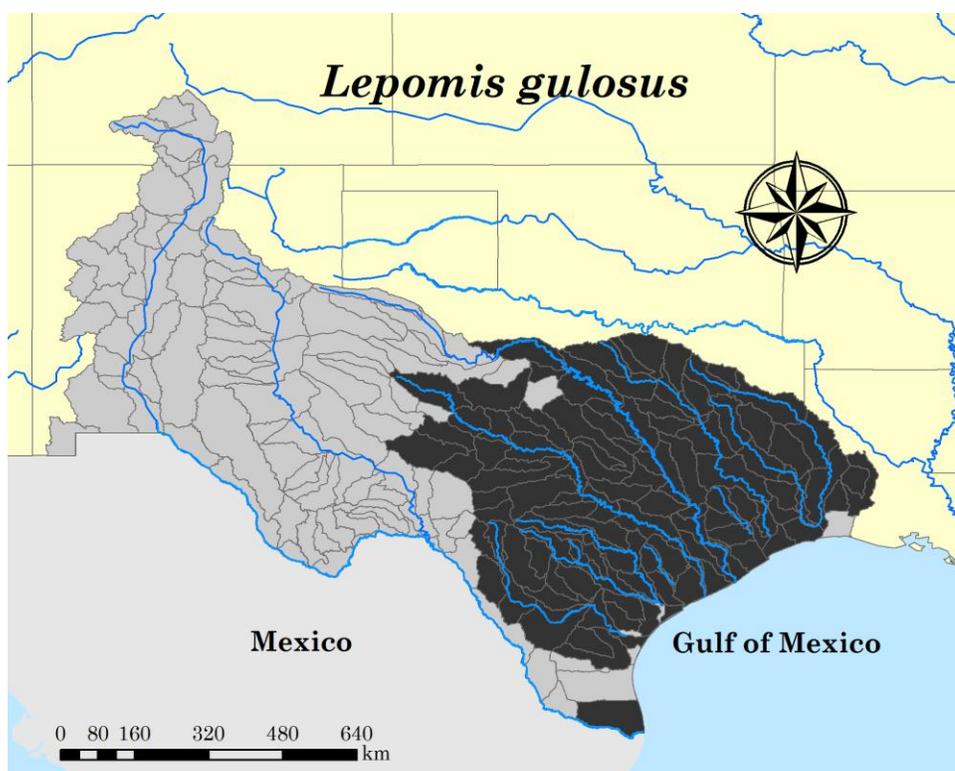


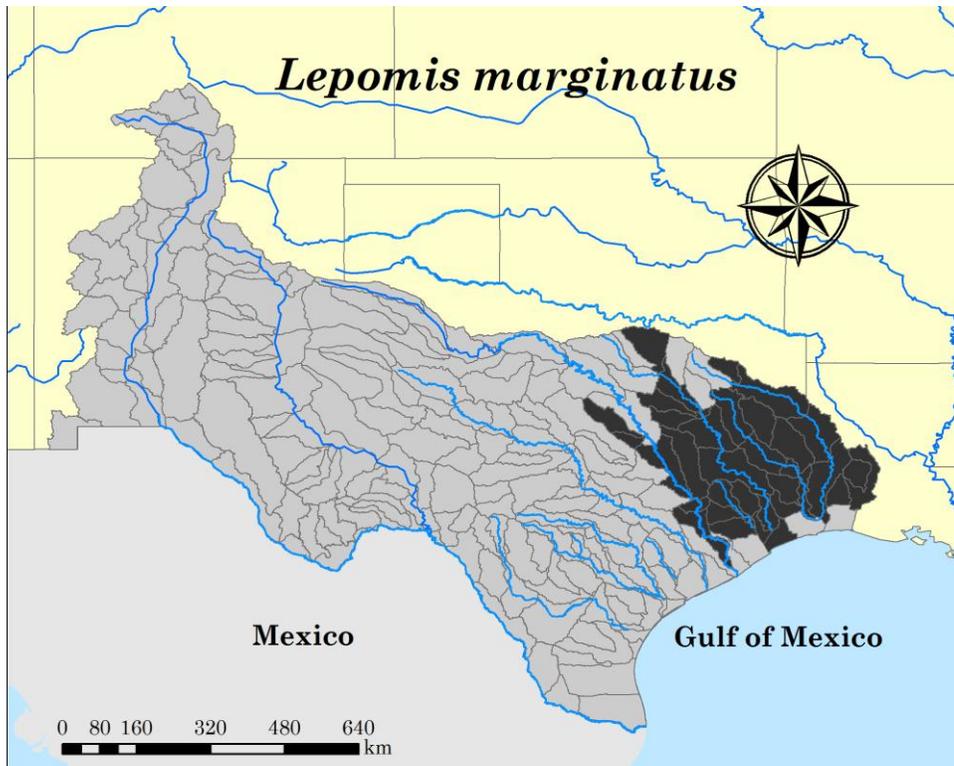
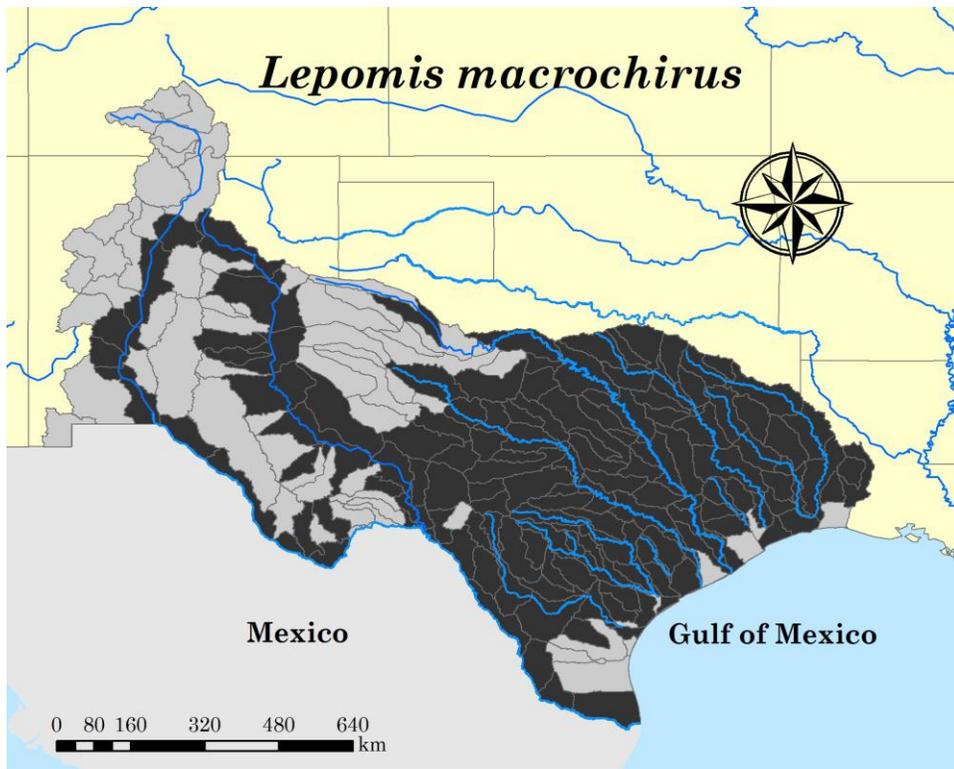
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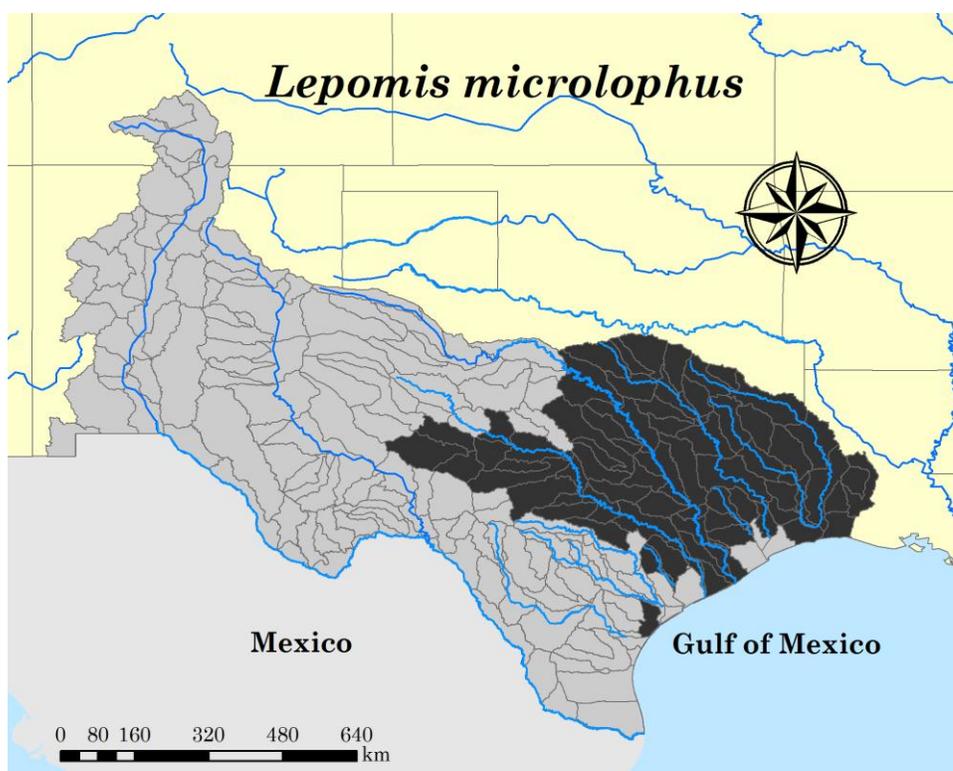
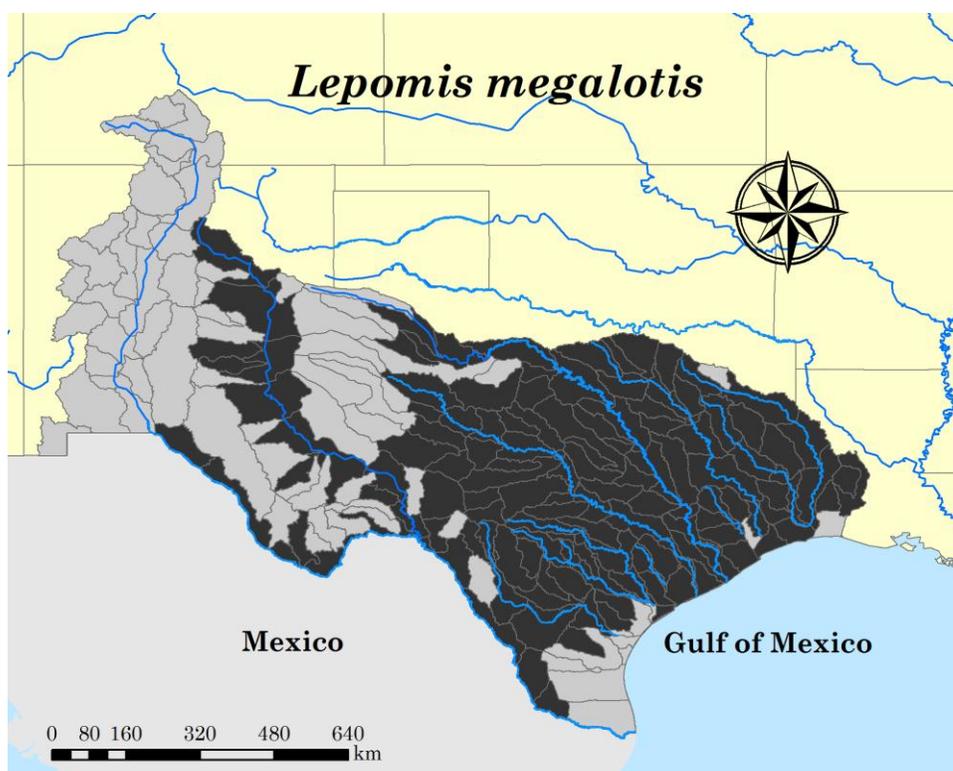


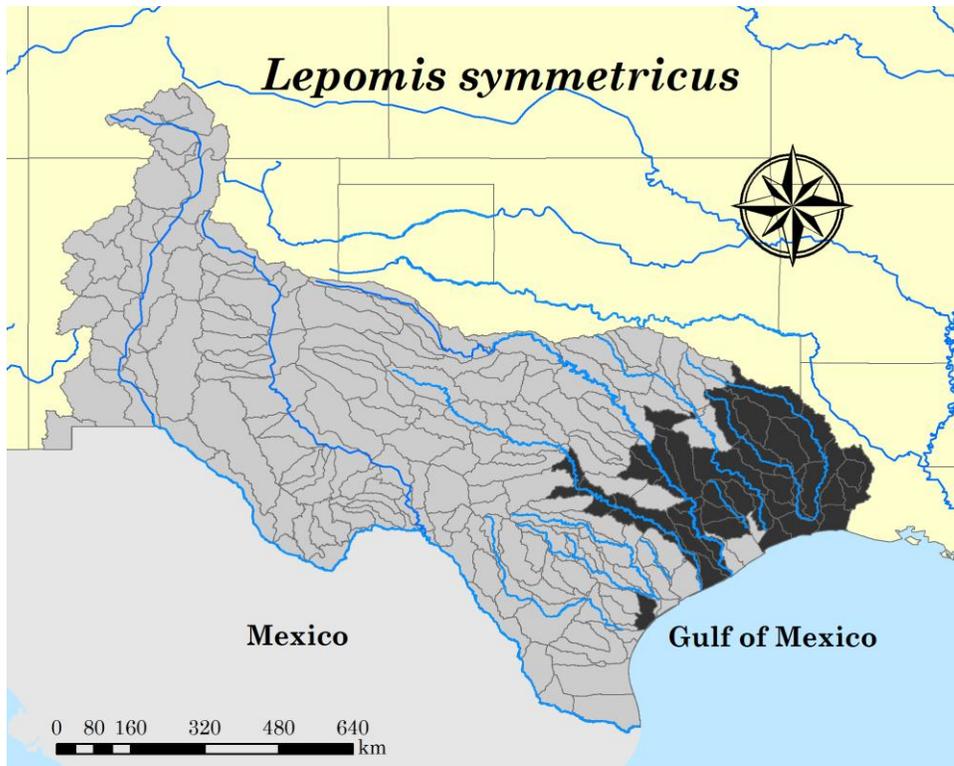
Centrarchidae

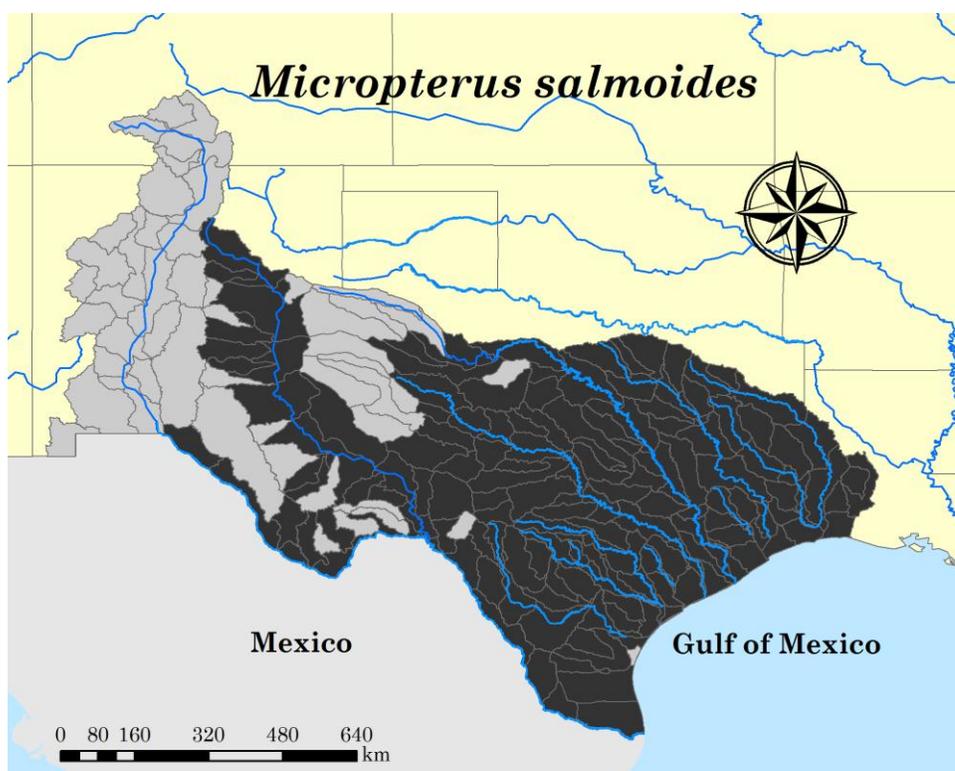
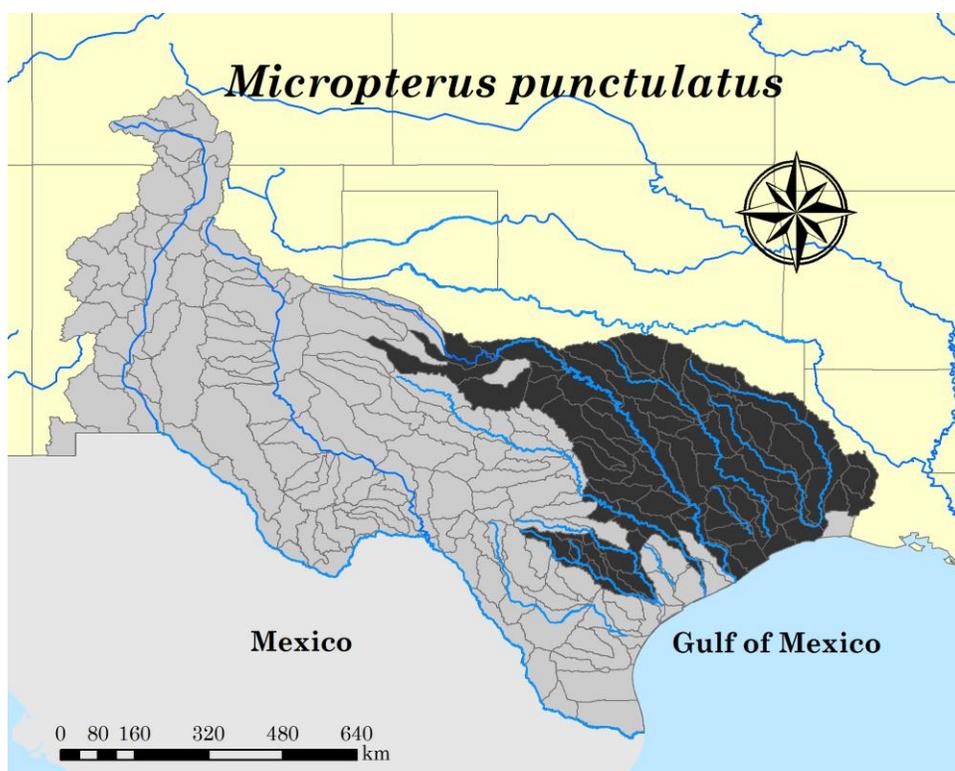


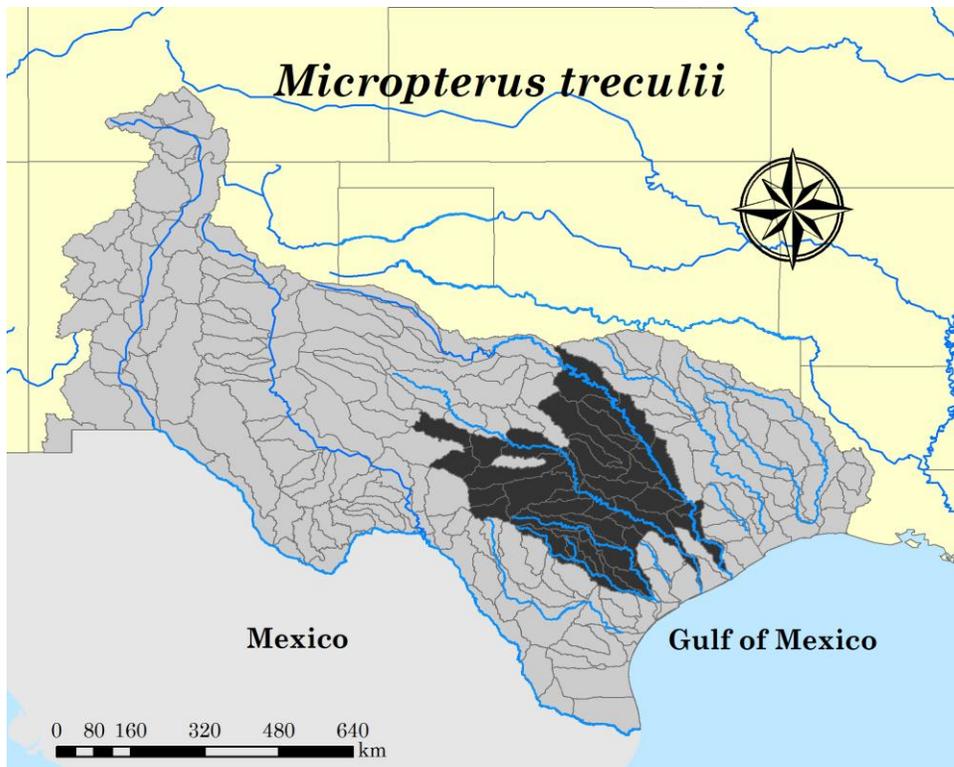






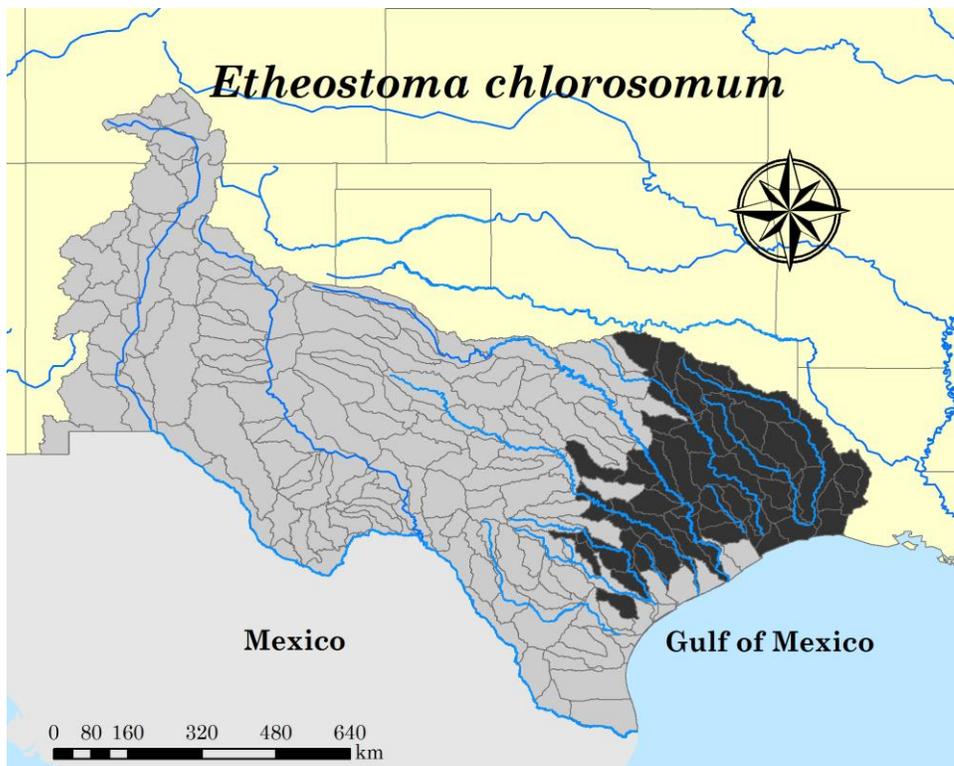


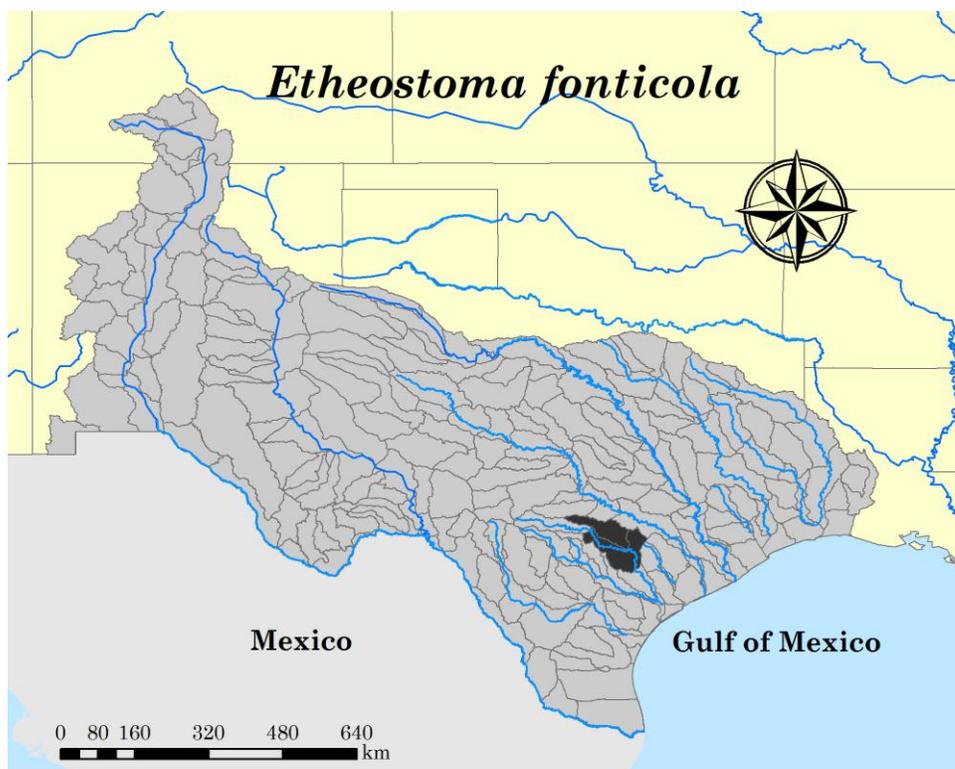


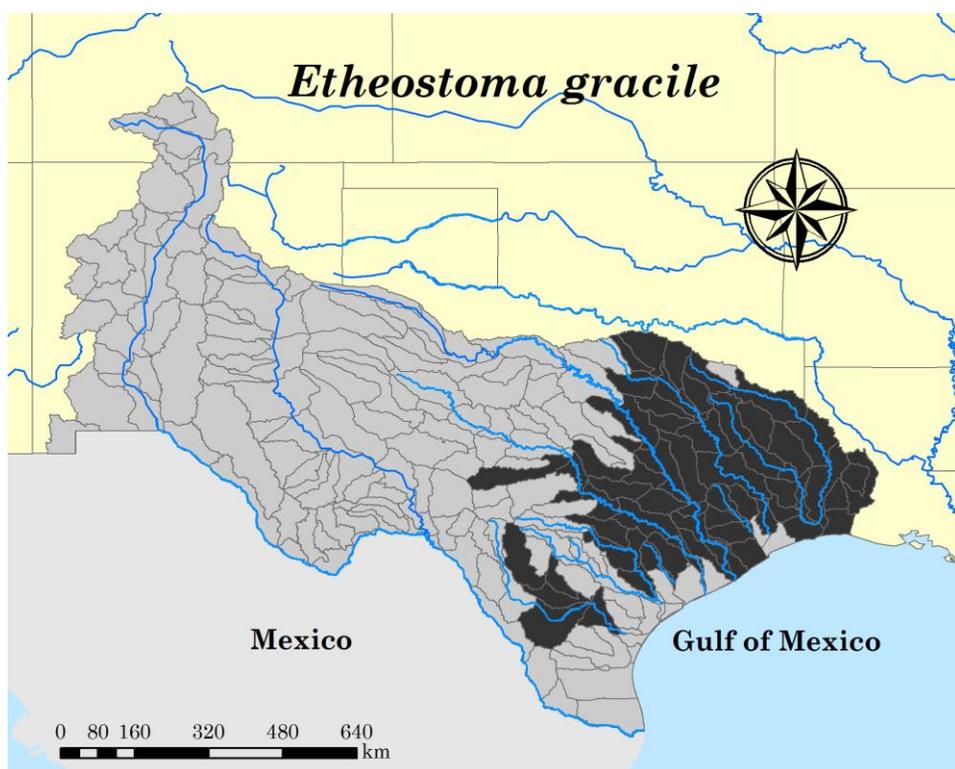
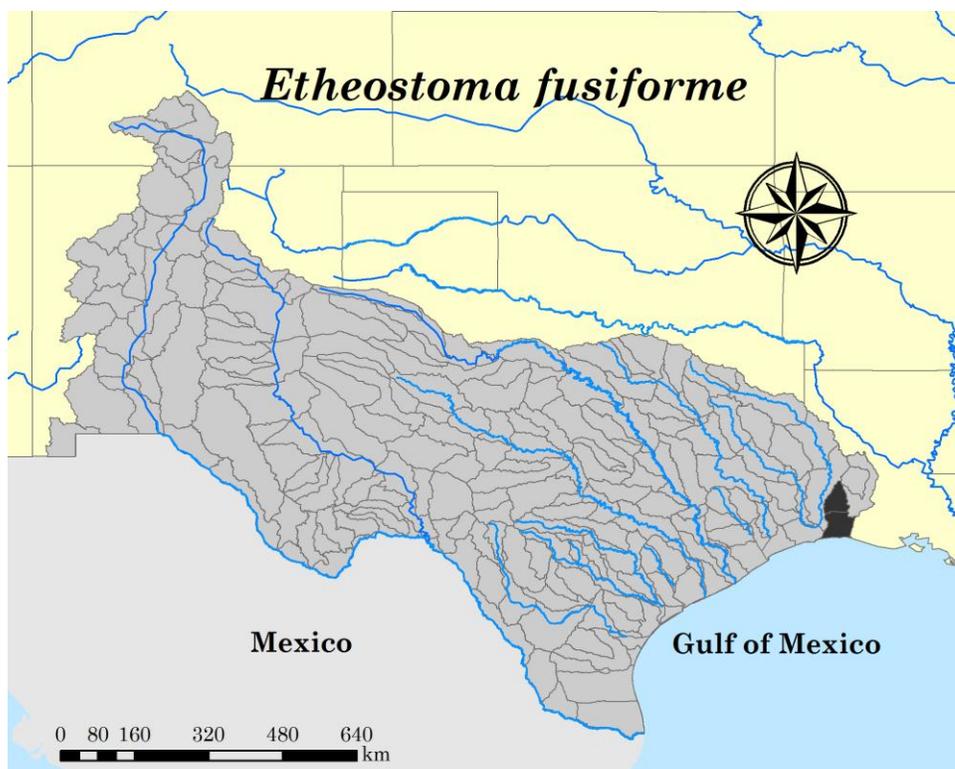


Percidae

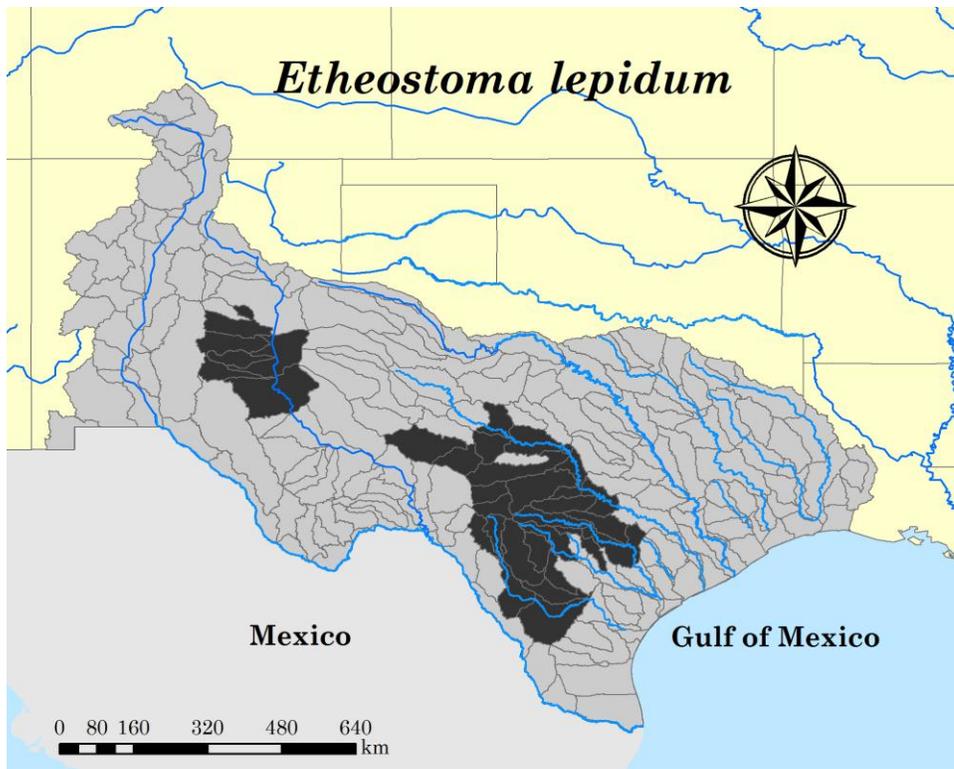


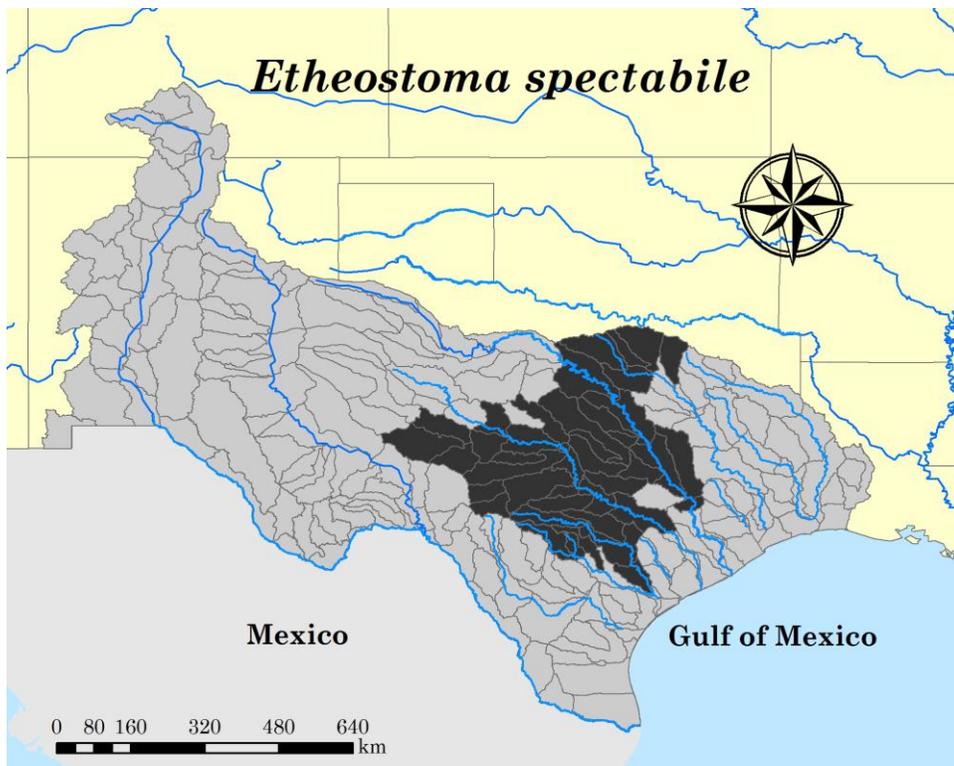
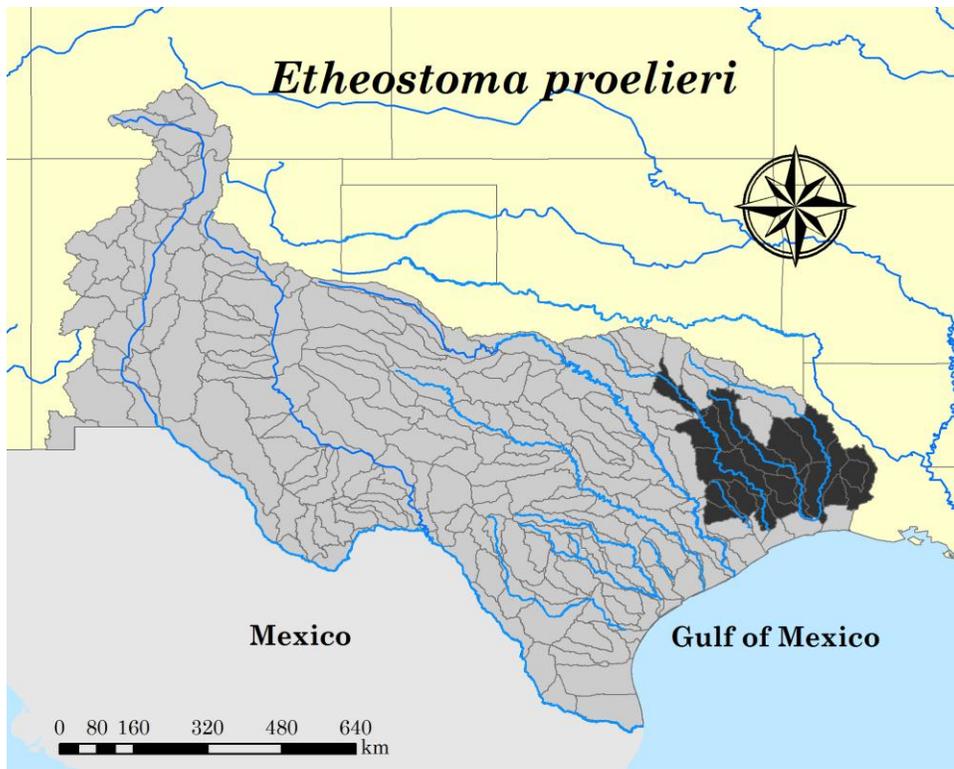


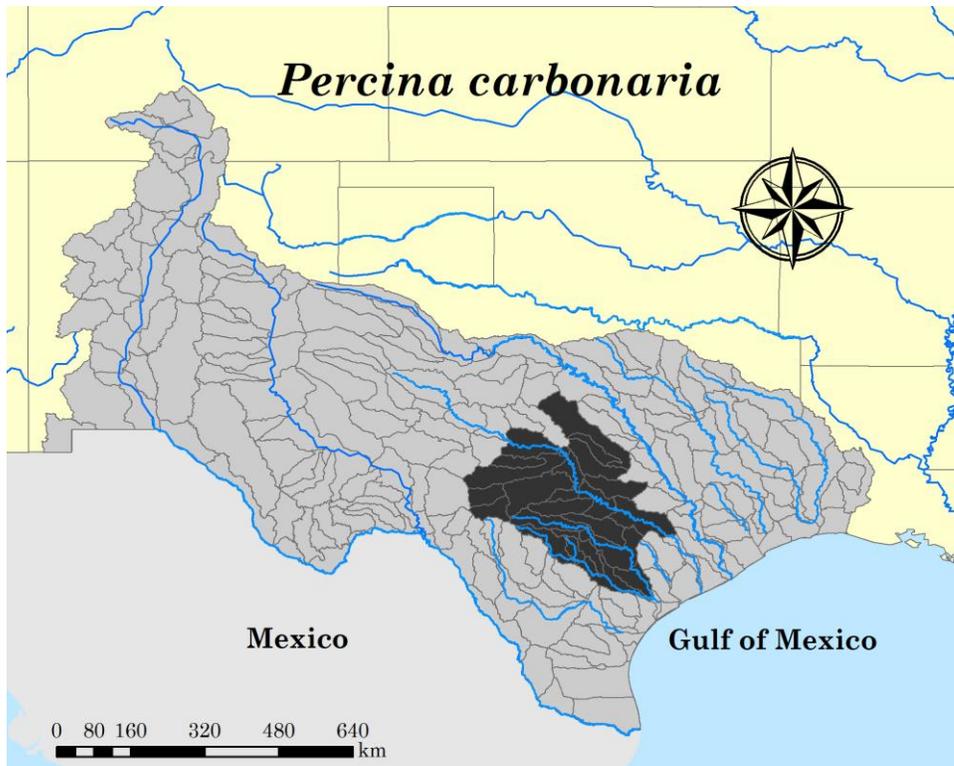
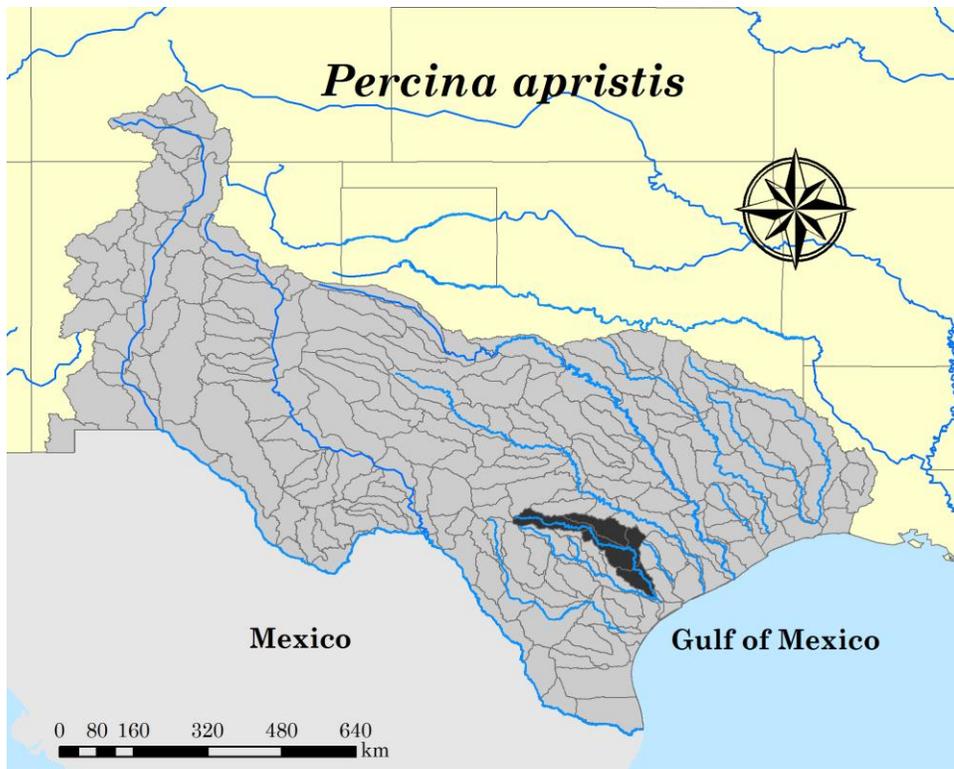


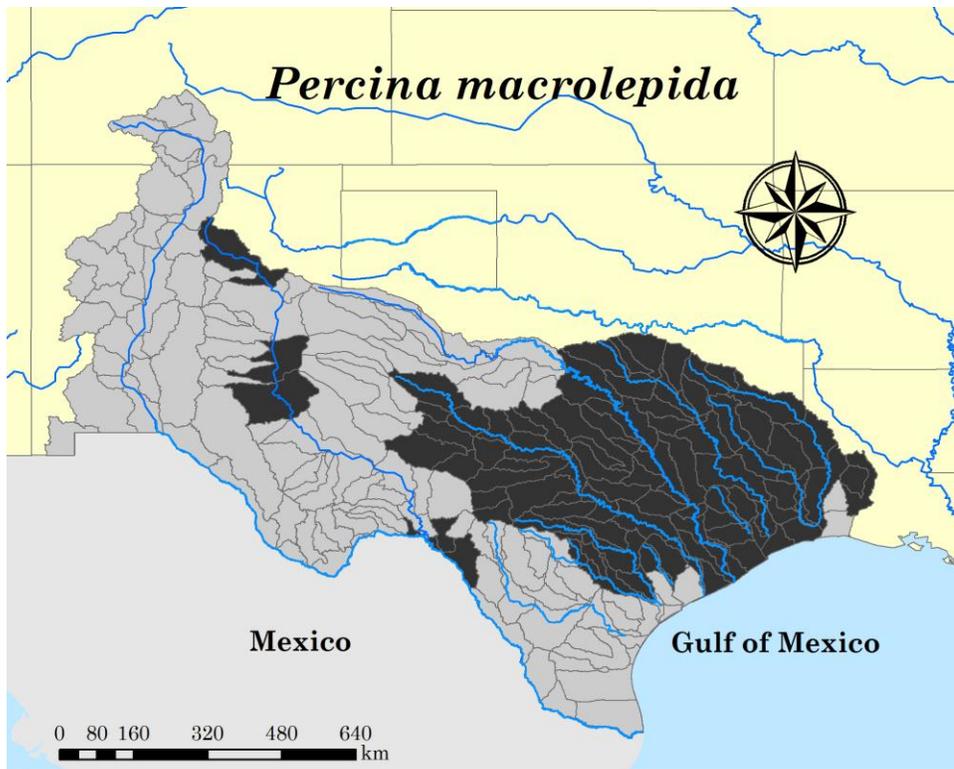


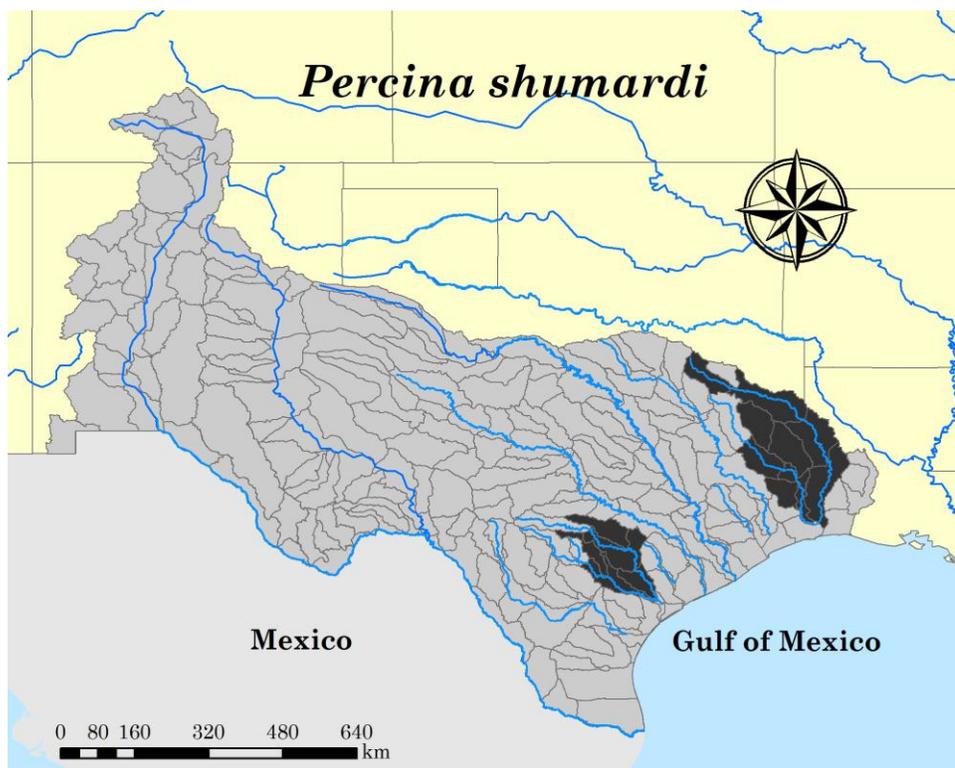
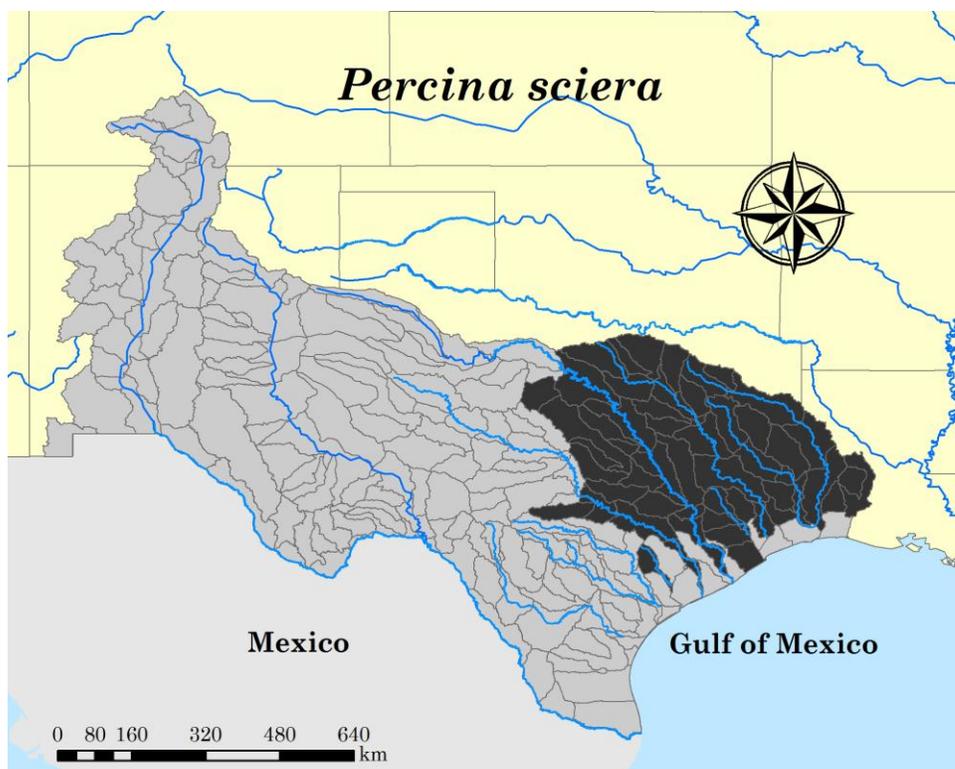












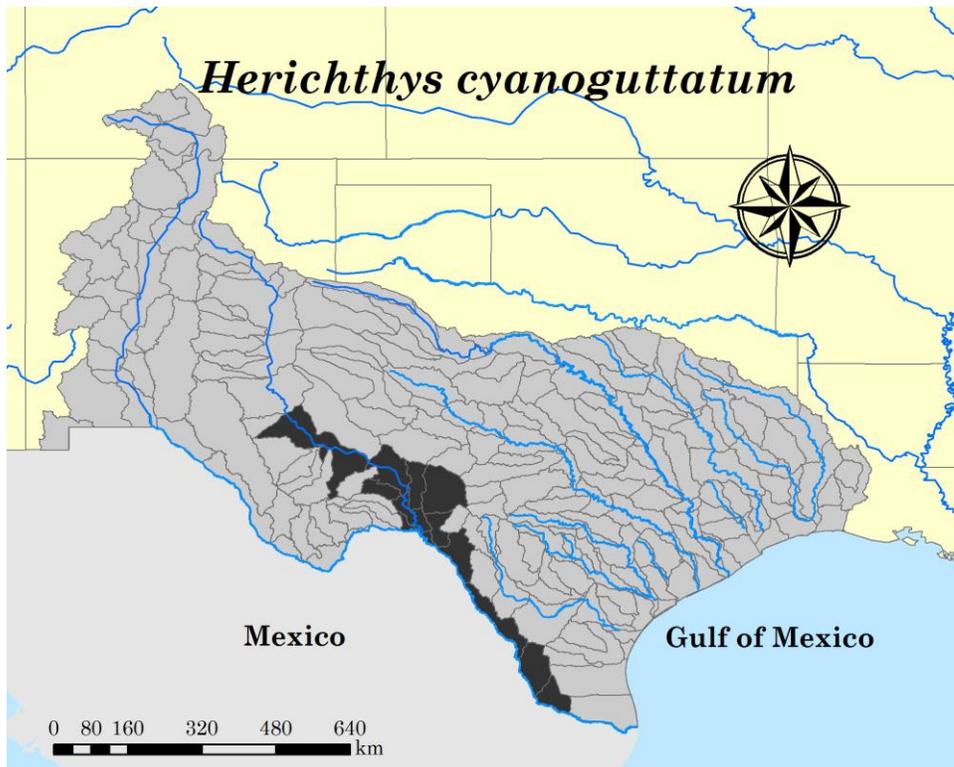
Sciaenidae



Elassomatidae



Cichlidae



APPENDIX II

RANGE MAPS LITERATURE CITED

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VITA

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