EARLY LIFE HISTORY AND RESURGENCE OF SNOOK (FAMILY

CENTROPOMIDAE) IN TEXAS

A Thesis

by

CHRISTOPHER JACOB CHAPA

Submitted to the Office of Graduate Studies of Texas A&M University in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

May 2012

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

Chair of Committee: Andre M. Landry, Jr. Committee Members: Jaime R. Alvarado-Bremer William H. Neill Jay R. Rooker Head of Department: John B. Carey

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ABSTRACT

Early Life History and Resurgence of Snook (Family Centropomidae) in Texas. (May 2012)

Christopher Jacob Chapa, B.S., Texas A&M University Chair of Advisory Committee: Dr. Andre M. Landry, Jr.

The resurgence of Texas' snook (Family Centropomidae) recreational fishery is coupled with an uncertainty as to what species occur in State waters, a limited understanding of life history, and habitat needs of its constituents. This study described species composition and early life history aspects of juvenile (< 100 mm SL) centropomids taken in bag seine collections in estuarine and freshwater habitats along the upper, middle, and lower coast of Texas during 2006 to 2010. *Centropomus* specimens (n = 548) captured from 41 locations across the Texas coast as well as congeners from Mexico (n = 24), Florida (n = 7), and Costa Rica (n = 3) were used in a genetics- and meristic-based determination of species composition, growth rates, range of hatching dates, geographic distribution, and habitat association.

Genetic analyses of the mitochondrial DNA 16s ribosomal RNA gene and the mitochondrial control region (D – loop) validated the presence of smallscale fat snook (*C. parallelus* Poey, 1860, n = 333), common snook (*C. undecimalis* Bloch 1792, n = 212) and Mexican snook (*C. poeyi* Chavez, 1961, n = 3) in Texas, with the last of these validations representing the first known record of this species in Texas. AMOVA of 16s

and D – loop sequences failed to detect genetic differentiation within Texas for *C*. *parallelus* and *C. undecimalis*. However, AMOVA for 16s and D – loop *C. undecimalis* sequences did yield significant genetic differences between Texas and Mexico against those from Florida and Costa Rica.

Juvenile centropomids (< 100 mm SL) in Texas occupied backwater habitats with dissipated currents similar to those of Florida congeners (tidal sloughs, freshwater habitats, and structured shorelines). Coastal ranges of these species differed with *C. parallelus* taken from the Rio Grande to West Galveston Bay, whereas *C. undecimalis* was captured from the Rio Grande northward near Palacios. Three *C. poeyi* were captured at only two locations (Laguna Vista and Port Aransas). Daily growth rates varied between species and capture years, with these ranging from 0.22 to 0.97 mm d⁻¹. Analyses of hatch-date distribution suggest centropomids in Texas begin spawning in August and continue it through late September into mid-November.

DEDICATION

To my parents.

ACKNOWLEDGEMENTS

I would like to thank my committee chair, Dr. Landry, and my committee members, Drs. Alvarado-Bremer, Neill, and Rooker, for their help and guidance throughout the course of this research.

Thanks also go to my colleagues in Dr. Landry's Sea Turtle and Fisheries Ecology Research Laboratory, Drs. Tasha Metz and Kim Reich, and Bill Dailey, and Josh Parks for their assistance. My appreciation also goes out to Dr. Rooker's Fisheries Ecology Lab, Dr. Brinkmeyer's and Dr. Schwarz's Coastal Health and Estuarine Microbiology Lab and Seafood Safety Lab. Additionally, I would like to thank the entire staff of the Perry R. Bass Marine Fisheries Research Center for their genetics help and guidance and Dr. Juan Carlos Perez from El Colegio de la Frontera Sur for his hospitality and fish finding skills in Campeche, Mexico. In particular I would like to thank Joel Anderson, Bill Karel, Britt Bumguardner, Rudy Salazar, Dustin Roberts, Ryan Schloesser, Luke Murphy, Shane Cantrell, The Snook Foundation, Fishing Guide Ernest Cisneros, Dr. Jim Ditty, and Randy Blankinship for their help either in the field or laboratory. I also want to extend my gratitude to the Southeast Texas Sportfishing Association, McDaniel Charitable Foundation, Texas A&M at Galveston Marine Biology Department and Graduate Office for their financial support and to the students who were willing to go into the field with me.

Finally, thanks to my mom and pop for their encouragement and to Katrina for her patience and love.

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NOMENCLATURE

| ‰ | parts per thousand |
|-------|-------------------------------------|
| AMOVA | Analysis of molecular variance |
| ANOVA | Analysis of variance |
| d | days |
| GOM | Gulf of Mexico |
| LLM | Lower Laguna Madre |
| mtDNA | mitochondrial DNA |
| NJ | neighbor joining |
| PCR | polymerase chain reaction |
| SL | standard length |
| TAMUG | Texas A&M University at Galveston |
| TL | total length |
| TPWD | Texas Parks and Wildlife Department |

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CHAPTER I

INTRODUCTION

Snook are a monogenetic group of fishes (genus *Centropomus*) comprising the Family Centropomidae (Nelson 2006). Twelve constituent species occur in tropical and subtropical coastal waters of the American Atlantic and Pacific; none occur in both oceans (Rivas 1986, Aliaume et al. 1997, Tringali et al. 1999b, Orrell 2003). Centropomids are distributed in the American Atlantic from Florida (Atlantic and Gulf coasts), Greater and Lesser Antilles, southern coast of the Gulf of Mexico (GOM), continental Caribbean coast southward to Brazil (Shafland & Foote 1983, Rivas 1986, Howells et al. 1990, Pope et al. 2006). Although *Centropomus* species have been reported from Cape Hatteras, North Carolina and Port Aransas, Texas, their distribution in northern latitudes is limited by thermal intolerance, with few fish occurring in water cooler than 7 to 12 °C (Cooley 1974, Shafland & Foote 1983, Matlock & Osburn 1987, Howells et al. 1990). Nearly all descriptions of juvenile and adult centropomid life history demonstrate constituent species' use of brackish and freshwater tidal sloughs as nurseries for feeding, protection, growth, and overwintering (Volpe 1951, Marshall 1958, Martin & Shipp 1971, Fore & Schmidt 1973, McMichael et al. 1989, Blewett et al. 2006).

Largescale fat snook (Centropomus mexicanus Bocourt, 1886), smallscale fat

This thesis follows the style of Bulletin of Marine Science.

snook (*C. parallelus* Poey, 1860), and common snook (*C. undecimalis* Bloch, 1792) are the only known representatives of six centropomid species with an Atlantic distribution assumed to inhabit Texas coastal waters (Mark Fisher & Randy Blankenship, TPWD, pers. comm., Martin & King 1991). *Centropomus undecimalis* exhibits the widest geographical range of all species in the genus and is the model for centropomid distribution (Figure 1.1). Swordspine snook (*C. enserferus* Poey, 1860), tarpon snook (*C. pectinatus* Poey, 1860), and Mexican snook (*C. poeyi* Chavez, 1961) exhibit a more restricted distribution and are not known from Texas, possibly as a result of their inability to tolerate variable environmental conditions (Rivas 1986, Tringali et al. 1999a, Tringali et al. 1999b).

Centropomid populations supported a commercial fishery in Texas during the early 20th century (Marshall 1958, Matlock & Osburn 1987, Alvarez-Lajonchère & Taylor 2003). Annual commercial landings in Texas peaked at 104,451 kg in 1928 followed by steady declines through 1961 (113 kg), after which no landings were reported (Matlock & Osburn 1987). Texas Parks and Wildlife Department prohibited the commercial capture and sale of centropomids in 1987 and set bag and size restrictions that were subsequently modified in 1991 and 1996. Current fisheries regulations in Texas for all *Centropomus* species include a one-fish bag limit per day and a slot limit of 61.0 to 71.1 cm (24 to 28 inches).

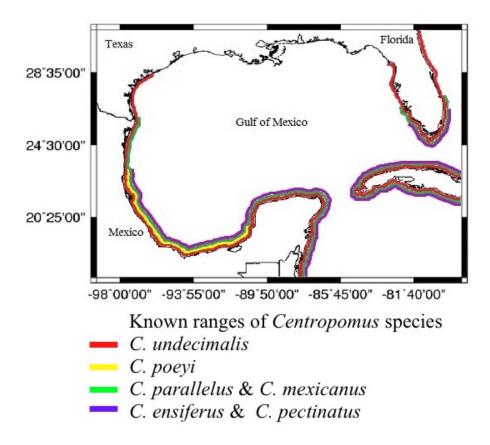


Figure 1.1. Distribution of the six recognized *Centropomus* species in the western Atlantic (Rivas 1986).

Centropomid Life History

Centropomus undecimalis and *C. parallelus* exhibit relatively similar life histories (Volpe 1951, Alvarez-Lajonchère et al. 2002a, Temple et al. 2004, da Silva Rocha et al. 2005, Tsuzuki et al. 2007a, Tsuzuki et al. 2007b), whereas comparable documentation for other centropomids is lacking. These species are estuarinedependent, protandric hermaphrodites, maturing first as males within one year of age and later converting to females 2.5 - 3.5 years old (McMichael et al. 1989, Taylor et al. 2000, Muller & Taylor 2006, Alvarez-Lajonchère & Tsuzuki 2008). All female centropomids are considered sexually mature on the assumption they have developed directly from males that have previously participated in spawning events (Taylor et al. 2000). Females migrate to high salinity regions at the mouths of passes, canals, and ocean inlets just offshore during the spring and summer to spawn (Volpe 1951, Marshall 1958, Tucker & Campbell 1988, Peters et al. 1998b, Taylor et al. 1998), with this activity influenced by water temperature, salinity, tidal current and moon phase (Table 1.1, Taylor et al. 1998, Yanes-Roca et al. 2009). The biogenic need to spawn near tidal passes was confirmed by (Ager et al. 1976) who reported that C. undecimalis requires saltwater for sperm activation, after which fertilized eggs depend on salinities of 28 ‰ or greater for buoyancy that ensures optimal developmental conditions (Chapman 1987, Peters et al. 1998a). The necessity for higher salinities during spawning has also been confirmed for C. parallelus (Alvarez-Lajonchère et al. 2002b, Alves et al. 2006, Alvarez-Lajonchère & Tsuzuki 2008, Cerqueira & Tsuzuki 2009) and C. poeyi (Carvajal 1975).

| Species | Spawning Season | Location | Citation |
|-------------------------|------------------|---------------------|--------------------------|
| Centropomus ensiferus | NA | NA | - |
| Centropomus mexicanus | NA | NA | - |
| Centropomus parallelus | June – August | Veracruz | (Chavez 1963) |
| | Spring - Summer | Brazil | (Santos et al. 2009) |
| Centropomus pectinatus | NA | NA | - |
| Centropomus poeyi | July – August | Veracruz & Campeche | (Carvajal 1975) |
| Centropomus undecimalis | June – July | SW Florida | (Volpe 1951) |
| | June – November | SW Florida | (Marshall 1958) |
| | July – October | SE Florida | (Tucker & Campbell 1988) |
| | April – December | SW Florida | (McMichael et al. 1989) |
| | April – October | SE & SW Florida | (Taylor et al. 1998) |

Table 1.1. Status of information on spawning dynamics of Atlantic Centropomus species.

NA, no information currently available

Centropomid larvae occur mainly in open waters near spawning locations but are eventually transported by tidal flow and currents to nursery habitats (Peters et al. 1998a). Settlement-sized centropomids (6 to 7 mm SL) spend their first months of life utilizing freshwater and marine marshes, seagrasses, and mangrove prop-root habitats (Tolley et al. 1987, Aliaume et al. 1997, Alvarez-Lajonchère & Tsuzuki 2008), primarily feeding on crustaceans (Fore & Schmidt 1973, Gilmore et al. 1983, Muller & Taylor 2006). Spatial distribution of these new recruits depends on circulation patterns and habitat suitability of each estuary. (Peters et al. 1998b) suggested that the low salinity requirement for newly settled C. undecimalis is misleading, by observing settlement sized (> 6 mm SL) C. undecimalis in polyhaline waters (18 to 30 ‰). Like their larval counterparts, juvenile centropomids prefer low-energy habitats and sporadically occur under overhanging vegetation and within submerged structure of freshwater tributaries and estuaries (Peters et al. 1998a, Peters et al. 1998b, Stevens et al. 2007). With growth, *Centropomus* species move from shallow riparian habitats to seagrass meadows, mangrove fringe, and deeper estuarine waters such as passes, nearshore reefs, jetties, and beachfronts (Muller & Taylor 2006).

Study Justification

The Texas centropomid fishery vanished 50 years ago; however, reopening of the Rio Grande and recent occurrence of milder winters may have facilitated a resurgence of populations of one or more *Centropomus* species from Mexico into Texas waters where they occupy the northern limit of their range in the western GOM. Increasing reports of centropomids taken by anglers, TPWD fisheries-independent and fisheries-dependent

surveys, and Texas A&M University at Galveston Field Ichthyology (MARB 312) classes confirm this reappearance. Fisheries-independent surveys conducted by TPWD since 1975 have yielded only a small number of centropomids tentatively identified as three species that are at the northern limit of their range in the western GOM (C. undecimalis n = 532, C. mexicanus n = 111, and C. parallelus n = 48; Mark Fisher, TPWD, pers. comm.). All published studies on the genus *Centropomus* in Texas refer only to C. undecimalis and are limited to ecologically-related articles that describe freeze related mortalities (Gunter 1941, 1951, Moore 1976, Holt & Holt 1983), sporadic occurrence (Springer & Pirson 1958, Moore 1975), and surveys of the LLM (Breuer 1962), Baffin Bay (Breuer 1957), South Bay (Hook 1991), and the Rio Grande (Breuer 1970, Edwards & Contreras-Balderas 1991). These studies coupled with TPWD data provide little information on the species composition, recruitment patterns, or habitat requirements that sustain constituent species. Lack of the aforementioned information and the need to manage an emerging fishery prompt the study described herein to identify species composition, extent of the spawning season, and age structure and growth characteristics.

Research Objectives

Research described herein characterized early life history and ecology of the Family Centropomidae in Texas, with specific objectives to:

- determine species composition in Texas waters;
- identify early recruitment habitats into which initial settlement occurs;
- determine age, growth and hatch-date distribution of juvenile centropomids recruiting to Texas waters.

CHAPTER II

GENETIC ANALYSIS OF *CENTROPOMUS* SPECIES IN TEXAS COASTAL WATERS

Introduction

Systematic reviews and revisions have classified *Centropomus* on the basis of morphology (Greenfield 1975, Rivas 1986, Orrell 2003); however, misidentification of species is common among researchers and field technicians unfamiliar with constituents of the Family Centropomidae. Rivas' (1986) thorough evaluation of centropomid classification examined multiple meristic and morphological characteristics differentiating these species. Although complete, Rivas' identification key lacks the ability to correctly identify centropomids < 100 mm SL due to unstable characteristics found within constituent life history stages. Since many *Centropomus* species co-occur over the range of the genus it is necessary to correctly identify juveniles to ensure that systematically valid studies of early life history, recruitment, and growth are conducted (Tringali et al. 1999a). Determination of molecular genetic data supporting morphological classification of centropomids provided by Rivas has been accomplished through allozyme electrophoresis and sequencing of the mitochondrial DNA 16s ribosomal RNA (rRNA) gene (Tringali et al. 1999a).

Currently, TPWD has identified *C. mexicanus*, *C. parallelus*, and *C. undecimalis* occurring in Texas bay systems through routine fisheries-dependent and fisheriesindependent sampling efforts. The three *Centropomus* species occurring in Texas waters look similar and are difficult to distinguish from one another. Confirmation of two Centropomus species' presence in Texas coastal waters has been verified through genetics (C. parallelus; Martin & King 1991) and historical data (C. undecimalis; Moore 1975, Holt & Holt 1983, Matlock & Osburn 1987, Pope et al. 2006). However, the occurrence of C. mexicanus in Texas waters is questionable, as no taxonomic investigation has been conducted to confirm such a presence. Additionally, mere mention of C. mexicanus in the scientific literature is restricted to Rivas' (1986) centropomid identification key, a report of this species' feeding habits in Brazil by (Sazima 2002) and genetic investigations conducted by (Tringali et al. 1999a) & (Seyoum et al. 2005). Based on mtDNA data, (Tringali et al. 1999a) identified C. *mexicanus* and *C. parallelus* as sister species, differing by only 1% divergence. Morphological analysis conducted by (Rivas 1986) separates these two species through overlapping scale counts (Table 2.1). Possible reasons for limited information on C. mexicanus could stem from the smaller sizes attained by this species (maximum 43 cm, common to 18 cm TL; Rivas 1986), cryptic behavior and associated capture difficulty within its habitat or misidentification as another species.

Centropomus parallelus is a commercially valuable species in Central and South America due to characteristics (robustness, resistance to disease, tolerance to high stocking densities, and euryhalinity) that foster culture success (Ribeiro & Tsuzuki 2010). Despite this commercial importance, limited genetic investigations involving *C. parallelus* have been conducted (Martin & King 1991, Tringali et al. 1999a, Prodocimo et al. 2008). Conversely, the recreationally popular *C. undecimalis* has been extensively studied, with numerous genetic assessments characterizing restrictive gene flow (Donaldson & Wilson 1999, Tringali & Leber 1999, Seyoum et al. 2005), divergence rate (Donaldson et al. 1993), and genetic markers (Wilson et al. 1997); however, all of these were limited to Florida's centropomid fishery.

| Quantitative Characters | Centropomus mexicanus | Centropomus parallelus |
|-----------------------------------|-----------------------|------------------------|
| Ray count | | |
| First dorsal | VIII | VIII |
| Second dorsal | I + 10 | I + 10 |
| Anal fin | III + 6 | III + 6 |
| Pectoral fin | 15 | 15 |
| Scale count | | |
| Lateral line | 68 – 79 | 79 - 92 |
| Second dorsal fin to lateral line | 10 - 16 | 10 - 16 |
| Anal fin to lateral line | 12 - 16 | 13 – 18 |
| Scales around caudal peduncle | 24 - 28 | 26 - 31 |
| Gill raker count | | |
| Lower limb | 11 - 12 | 11 - 12 |

 Table 2.1. Morphological comparison between Centropomus mexicanus and Centropomus parallelus derived from Rivas (1986).

Although TPWD has developed and implemented a sound sampling program to assess the health of Texas' marine fisheries, considerable portions of the state's estuary systems go uninvestigated due to sampling difficulties in constituent habitats. Ecologically important groups such as the Family Centropomidae whose various life history stages use habitats not sampled by TPWD are poorly known from both a taxonomic and natural history perspective. Such a lack of information is problematic for strategic management of Texas' centropomid stocks and the fisheries that may harvest these stocks. Additionally, implementation of a regional management plan for spotted seatrout (*Cynoscion nebulosus* Cuvier, 1830) in the LLM (lowering bag and possession limits from ten to five) may redirect recreational fishing pressure toward the developing centropomid fishery in Texas. The possibility of misidentification of unknown *Centropomus* species occurring in Texas justifies the necessity for genetic analyses of constituent species. A common perception is that two or more *Centropomus* species are utilizing Texas estuaries. Effective, long-term management of Texas' centropomid populations will depend upon an understanding of the species' constituency and their genetic structure. This chapter assesses species composition of centropomids in Texas, with specific attention to:

- species identity of juvenile centropomids found in Texas waters;
- genetic diversity of each species;
- morphological characteristics that aid in field identification of centropomids.

Materials and Methods

Study Areas

Juvenile centropomids were collected at spatially restricted wetland sloughs, boat ramps, and other tidal- and freshwater- influenced habitats from Carancahua Bay (Palacios, Texas) to the Rio Grande (US – Mexico border). Selection of each collection site was based on historical data generated by TPWD and TAMUG as well as published (Breuer 1962, 1970, Pezold & Edwards 1983, Contreras-Balderas et al. 2002, Pope et al. 2006) and anecdotal reports of larval and juvenile centropomid occurrence. Collection sites were classified according to regions along the upper (Galveston to Matagorda Bay), middle (San Antonio Bay to Corpus Christi), and lower Texas coast (Port Mansfield to Boca Chica) that are divided into two major climatological zones (temperate and subtropical). The only temperate climate collection site was located in the upper coast region, within the upper reaches of Carancahua Bay south of Palacios. The remaining study areas were located within the Aransas and LLM estuaries that exhibited subtropical climates. The Aransas estuary housed the middle coast collection sites that included Goose Island State Park (Rockport), Redfish Bay (at two locations along SH 361, Stedman Island), and a drainage ditch located in the city of Aransas Pass on SH 35. Lower coast collections were conducted from the southernmost portion of the LLM and included the Arroyo Colorado (and surrounding drainages), Laguna Vista, San Martin boat ramp and channel, Mexiquita Flats, Padre Island Coast Guard Station (northwest of the Brazos Santiago Pass) and Boca Chica (Rio Grande and surrounding sloughs).

Sampling Protocol

Bag seine tows were conducted biweekly at the aforementioned study sites from April to November 2006, September 2007 to January 2008, and September 2009 to January 2010 to increase sample size for genetic and age-growth analysis. Standardized and randomized tows of a 9.1 m long by 1.2 m deep bag seine with 0.6 cm bar mesh wings and a 0.3 cm bar mesh $1.2 \times 1.2 \times 1.2 m$ bag were used to sample juvenile centropomids. Three (15.2 m long x 6.0 m wide) standardized tows were conducted at each collection site to generate CPUE data on spatial and temporal occurrence. This sampling protocol was complemented by randomized bag seine sampling that took two forms: 1) a minimum of 30 minutes of non-standardized effort with the aforementioned bag seine at each collection site to characterize centropomid occurrence in any habitat type not sampled during standardized sampling and to capture additional centropomids for age growth analysis; and 2) non-standardized effort conducted at sites and habitats other than those described previously in response to additional information on possible centropomid settlement grounds that was received during the study. Fin clippings from centropomids from Jacksonville, Florida; Barra del Colorado, Costa Rica; Campeche, Campeche, Mexico; and Frontera, Tabasco, Mexico were used as sources of additional DNA material for genetic analysis. Additional samples were obtained through hook and line sampling from LLM guides and local anglers. Subsequently, in January 2010, coldkilled centropomids from the upper Texas coast also were obtained for genetic analysis.

All centropomids captured were kept on ice for transport to the laboratory where they were processed immediately or frozen for subsequent analysis. Species identification to the lowest possible taxon relied on keys by (Greenfield 1975), (Rivas 1986), (McEachran & Fechhelm 1998), and (Orrell 2003). Each specimen was enumerated SL and TL were measured to the nearest millimeter, and with meristic counts recorded as follows: Spines and soft rays in the first and second dorsal and anal fins were counted. Scale counts followed Rivas' (1986) protocol wherein lateral line, second dorsal to lateral line, and anal fin to lateral line scale counts were recorded. These morphological characteristics were examined for potential differences to aid in identification of centropomid species found in Texas.

DNA Isolation

Genetic identification of centropomids to the species level was performed in collaboration with TPWD's Perry R. Bass Marine Fisheries Research Center in Palacios following the protocols of (Tringali et al. 1999a) and (Anderson & Karel 2009). A single eyeball was removed from each centropomid to isolate DNA using Qiagen DNeasy Blood and Tissue Kit (Qiagen Inc., Valencia, California, USA) and PUREGENE DNA Isolation Kit (Gentra Systems Inc., Minneapolis, Minnesota, USA), following the manufacturers' protocols, with final rehydration values between 75 and 100 μ L. Determination of quantity and purity of DNA was analyzed through spectrophotometry using a NanoDrop 1000 (NanoDrop Tech., Wilmington, Delaware, USA). Isolated DNA samples were stored at -20 °C.

PCR Reactions

PCR primers specific to the 16s rRNA (16s) region were designed using sequence data from previously published studies to investigate genetic identification in centropomids. The mitochondrial DNA control region (D – loop) was also characterized; data from the D – loop sequences, because of the substantially higher levels of variation, and thus resolution, compared to 16s data, were used to test a subsample of centropomids to identify any cryptic speciation and finer phylogeographic partitioning. Sequencing of 16s and D – loop was conducted according to protocols developed by(Tringali et al. 1999a) and (Anderson & Karel 2009). Amplifications of template DNA were conducted via PCR under a modified touchdown protocol by using Ready-To-Go PCR beads (GE Healthcare, Piscataway, New Jersey, USA) on a Techne Genius thermocycler (Techne Inc., Princeton, New Jersey, USA). Reactions consisted of 1 μ L of template DNA (50 ng/ μ L), one Ready-To-Go bead, and 24 μ L of forward and reverse primer cocktail (0.4 μ M standard concentration of each primer), for a total of 25 μ L. The touchdown PCR protocol utilized for all reactions consisted of the following: an initial single denaturation period of 2 minutes at 95 °C, 10 cycles of initial amplification (95 °C for 30 seconds; 55 °C for 30 seconds, lowering 1 °C each cycle; and 72 °C for 1 minute), 20 cycles of primary product amplification (95 °C for 30 seconds; 55 °C for 30 seconds; and 72 °C for 1 minute, adding 3 seconds of extension per cycle), and a final extension period of 7 minutes at 72 °C. The primer sequences used for 16s PCR were: 16Sar (5'-CGCCTCTTTATCAAAAAC-3') and 16Sbr (5'-CCGGTCTGAACTCAGATCACG-3') (Palumbi 1994, Tringali et al. 1999a). The primer sequences used for D – loop PCR were: L15990 snk (5'-

TACCGTCAACTCCCAAAGCTA-3') and CRSNOOK4H (5'-

CTGCCCTCTGGAAATAATGCTRGGC-3').

PCR products were purified using ExoSAP-IT (USB, Cleveland, Ohio, USA) to free DNA of excess primers and nucleotides. Following the manufacturer's recommendations, 5 μ L of PCR product were mixed with 2 μ L of enzyme and placed on a thermocycler for 15 minutes at 37 °C, followed by an inactivation step for 30 minutes at 80 °C.

Sequencing Reactions

Sequencing reactions were carried out according to (Anderson & Karel 2009) using 10 µL volumes by means of Genomelab Quick Start Master Mix DTCS (Beckman Coulter Inc., Fullerton, California, USA). Primers for sequencing were the same as those used in PCR. Cycle sequencing parameters consisted of 30 cycles of denaturing at 96 °C for 20 seconds, annealing at 50 °C for 20 seconds, and extension at 60 °C for 4 minutes. Sequencing reactions were precipitated by adding 1/20 volume of a cocktail containing 2 µL sodium acetate (3M), 2 µL EDTA (100mM) and 1 µL glycogen, followed by 2 volumes of 95% ethanol, and centrifuged at 3,700 rpm for 30 minutes to form pellets. Resulting pellets were then rinsed twice with a 70% ethanol, dried, and rehydrated by using a formamide sample loading solution (Beckman Coulter, Fullerton, California, USA). Finally, sequences were separated and analyzed on a Beckman CEQ8000 capillary sequencer (Beckman Coulter, Fullerton, California, USA) using default sequencing module parameters. Examination of raw sequences for base-calling errors was trimmed manually. Forward and reverse traces for each sequence were aligned using Sequencher version 4.2 (Gene Codes Corp., Ann Arbor, Michigan, USA), and haplotypes were characterized only for those sequences that contained overlapping forward and reverse reads.

Genetic Analysis

Positive identification of centropomid species was confirmed via BLAST searches through GenBank (GenBank accession numbers: U85008, U85012, U85014, U85016, U85017, U85018; Tringali & Leber 1999) coupled with gene trees reconstructed in MEGA 5.0 (Tamura et al. 2011). Gene tree structure was determined via NJ based on Tamura-Nei distances, as well as Maximum Likelihood (ML) distances among haplotypes. Statistical support for branching patterns was tested by bootstrap consensus. DnaSP v5.10 (Librado & Rozas 2009) was used to obtain genetic diversity estimates, including haplotype diversity (h), nucleotide diversity (π), number of pairwise nucleotide differences (k), number of haplotypes (m), and segregating sites (S) for all centropomid species identified. Parsimony-based haplotype networks were constructed from the data using MEGA 5.0 (Tamura et al. 2011). Nested Clade Analysis was performed using the TCS program and statistical parsimony (v1.13; Clement et al. 2000) and to subsequent phylogeographic inference. The degree of genetic variation among samples of each centropomid species identified was measured with analysis of molecular variance (AMOVA) using Arlequin 3.5.1.2 (Excoffier & Lischer 2010). Estimates of gene flow and genetic differentiation among sampling areas were based on Wright's F_{ST} using Arlequin.

Results

Identification of Centropomids

Overall, 580 centropomid specimens were examined for genetic analyses and meristic comparisons. Distribution of samples collected for genetic analysis is listed in Tables 2.2, 2.3 and Figure 2.1. Centropomids identified included *Centropomus parallelus*, *C. poeyi*, and *C. undecimalis*. Meristic comparisons were not useful in distinguishing among juveniles (< 100 mm SL) due to lateral line scale counts that were difficult to determine due to incomplete and/or missing scales. However, anal fin to lateral line and second dorsal to lateral line counts were relatively easy to perform but did not accurately separate species due to overlapping values. Physical characteristics described by (Greenfield 1975), pelvic fins reaching past the anus in *C. parallelus* and not reaching past the anus in *C. poeyi* and *C. undecimalis*, was useful.

Nucleotide sequences of 16s ranged from 621 bp for *C. parallelus*, 609 bp for *C. poeyi*, and 628 bp for *C. undecimalis*; sequences were aligned and trimmed to 475, 535, and 483 bp, respectively. Sequence submissions to GenBank (using BLAST) revealed matches with three species: *C. parallelus*, *C. poeyi*, and *C. undecimalis*. Consensus sequences for each species identified (*C. parallelus* n = 337, *C. poeyi* n = 4, and *C. undecimalis* n = 239) were generated and aligned against the six recognized Atlantic centropomid representatives from GenBank (Figure 2.2; Tringali et al. 1999a) to assure positive genetic identification.

| Site # | County | Location | Latitude N | Longitude W | C. parallelus (n) | C. poeyi (n) | C. undecimalis (n) |
|--------|-----------|-------------------------------|---------------|----------------|----------------------|-----------------|-----------------------|
| 1 | Galveston | Hitchcock Diversionary Canal | 29 20.134 | 95 01.417 | 1 | - | - |
| 4 | Brazoria | Bastrop Bayou | 29 05.598 | 95 16.940 | 4 | - | - |
| 7 | Brazoria | Oyster Creek | 29 00.059 | 95 18.070 | 1 | - | - |
| 8 | Brazoria | Intracoastal waterway | 28 57.850 | 95 17.533 | 1 | - | - |
| 9 | Brazoria | Brazos River | 28 52.803 | 95 22.780 | 1 | - | - |
| 13 | Jackson | Carancahua Bay | 28 44.252 | 96 24.121 | 10 | - | 1 |
| 14 | Matagorda | Matagorda Bay | 28 43.593 | 95 47.124 | 2 | - | - |
| 21 | Nueces | Redfish Bay | 27 53.637 | 97 07.676 | 10 | - | - |
| 22 | Nueces | Redfish Bay at Stedman Island | 27 53.341 | 97 07.063 | 9 | - | 3 |
| 23 | Nueces | Aransas Pass | 27 53.566 | 97 09.188 | 37 | 1 | 8 |
| 28 | Willacy | Port Mansfield | 26 33.822 | 97 16.590 | 2 | - | - |
| 30 | Cameron | Arroyo Colorado | 26 20.998 | 97 23.483 | 94 | - | 25 |
| 32 | Cameron | Laguna Vista | 26 05.705 | 97 17.024 | 88 | 2 | 79 |
| 33 | Cameron | Lower Laguna Madre | 26 04.461 | 97 12.878 | 3 | - | - |
| 34 | Cameron | Lower Laguna Madre | 26 04.356 | 97 09.994 | 5 | - | - |
| 35 | Cameron | Mexiquita Flats | 26 04.044 | 97 11.659 | 3 | - | 1 |
| 36 | Cameron | South Bay | 26 01.529 | 97 10.272 | 20 | - | 22 |
| 38 | Cameron | Lake San Martin | 26 00.125 | 97 17.913 | 17 | - | 12 |
| 40 | Cameron | Rio Grande (6 km from mouth) | 25 57.613 | 97 11.116 | 28 | - | - |
| 41 | Cameron | Rio Grande (mouth) | 25 57.556 | 97 08.810 | 3 | - | 55 |

Table 2.2. Catch distribution of Texas centropomids.

| Locality | Collector | Capture date | Latitude N | Longitude W | C. parallelus (n) | C. poeyi (n) | C. undecimalis (n) | |
|-----------|--------------------------------|--------------|---------------|----------------|----------------------|-----------------|-----------------------|--|
| Barra del | Barra del Colorado, Costa Rica | | | | | | | |
| | A. Landry | January 2006 | 10 46.170 | 83 35.566 | - | - | 3 | |
| Jacksonvi | lle, Florida | | | | | | | |
| | M. Hanke | October 2008 | 30 28.801 | 81 28.841 | - | - | 7 | |
| Frontera, | Tabasco, M | exico | | | | | | |
| | C. Chapa | January 2010 | 18 31.773 | 92 39.224 | 4 | - | 7 | |
| San Pedro | o, Tabasco, I | Mexico | | | | | | |
| | C. Chapa | January 2010 | 18 30.646 | 92 39.034 | - | 1 | - | |
| Campech | e, Campecho | e, Mexico | | | | | | |
| | C. Chapa | January 2010 | 19 50.506 | 90 32.039 | - | - | 12 | |

Table 2.3. Locations of *Centropomus* species captured outside of Texas.

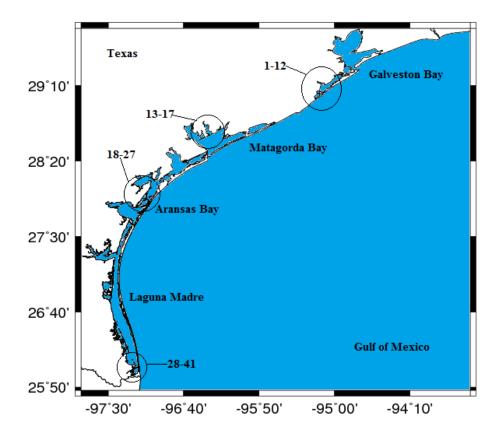


Figure 2.1. Map of the Texas Gulf coast, illustrating study site locations (numbered) within major bay systems. Refer to Table 2.3 to identify numbered sites.

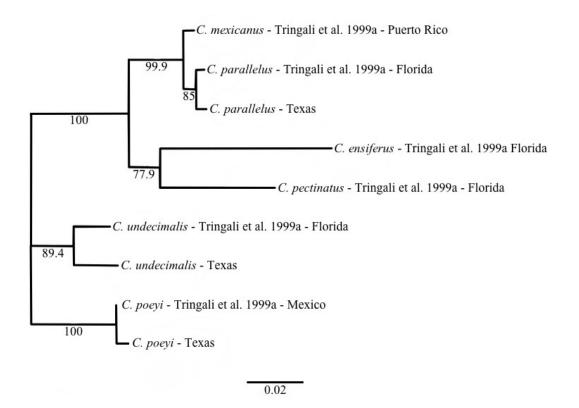


Figure 2.2. NJ tree, using the Maximum Composite Likelihood method, identifying Texas captured *Centropomus parallelus, Centropomus poeyi*, and *Centropomus undecimalis* 16s mtDNA consensus sequences with 16s mtDNA sequences from (Tringali et al. 1999a). Bootstrap values above 50% are shown.

Patterns of Variation in the mtDNA 16s Gene

The 475 bp region of the 16s gene for 337 assayed *C. parallelus* identified six variable positions, seven haplotypes, and six polymorphic sites; of which two were parsimoniously informative that corresponded to six transitions and zero transversions. Base frequencies of the 16s region for *C. parallelus* were 28.6% for A, 24.8% for C, 21.7% for G, and 24.8% for T. One haplotype (par – 1) was widely distributed throughout Texas and Mexico and represented 97% of all samples taken (Table 2.4, Figure 2.3). The remaining six haplotypes (par – 2 through par – 7) were restricted to Texas' LLM, with low overall haplotype diversity (h = 0.053) and nucleotide diversity ($\pi = 0.000$) differing by less than one substitution event. The absence of genetic differentiation among all localities of *C. parallelus* 16s is result of a dominant haplotype found throughout, thus a regional AMOVA was not executed.

| Haplotype | Texas | | | Mexico | Total | Polymorphic Sites | | | | | |
|-----------|---------------|--------|---------|-------------------------|---------|-------------------|---|---|---|---|---|
| | Upper | Middle | Lower | Mexico | Total | | 1 | 1 | 2 | 3 | 4 |
| | <i>n</i> = 18 | n = 52 | n = 263 | <i>n</i> = 4 <i>n</i> = | n = 337 | 3 | 4 | 9 | 6 | 8 | 2 |
| | <i>n</i> – 10 | n - 52 | n - 203 | | n - 337 | 8 | 1 | 2 | 7 | 8 | 4 |
| par – 1 | 1.000 | 1.000 | 0.966 | 1 | 0.973 | Α | G | G | G | С | Т |
| par – 2 | 0 | 0 | 0.004 | 0 | 0.003 | | | | Α | | |
| par – 3 | 0 | 0 | 0.004 | 0 | 0.009 | | | | | Т | |
| par – 4 | 0 | 0 | 0.004 | 0 | 0.003 | | | | | | С |
| par – 5 | 0 | 0 | 0.008 | 0 | 0.003 | G | | | | | |
| par – 6 | 0 | 0 | 0.004 | 0 | 0.006 | | Α | | | | |
| par - 7 | 0 | 0 | 0.011 | 0 | 0.003 | | | Α | | | |

Table 2.4. Haplotype relative frequency, distribution, and polymorphic sites contained within the475bp segment of the 16s gene among *Centropomus parallelus* collected from Texas and Mexico.Identical bases (.) are shown.

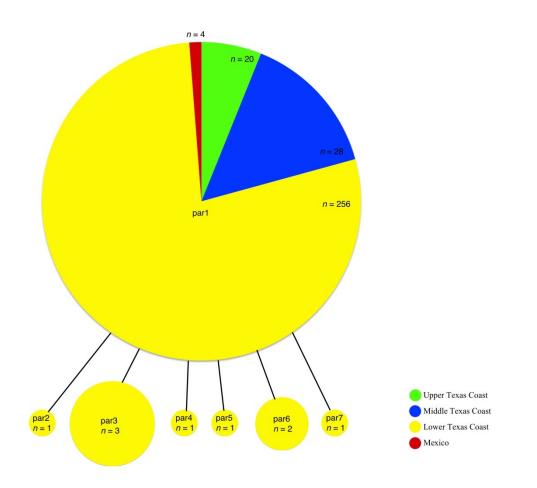


Figure 2.3. TCS network of the seven *Centropomus parallelus* 16s mtDNA haplotype sequences.

The 535 bp region of 16s sequenced from four *C. poeyi* specimens revealed three haplotypes and two variable sites corresponding to two transitions. Base frequencies for the four *C. poeyi* were: A = 28.5%, C = 26.9%, G = 22.1%, and T = 22.4%. Haplotype diversity was high (h = 0.833); distribution and frequency of *C. poeyi* haplotypes are shown in Table 2.5. Low nucleotide diversity for *C. poeyi* ($\pi = 0.001$) was similar to that for all centropomids sampled, possibly due to the reduced number of substitution events. AMOVA was not conducted on *C. poeyi* 16s data due to small sample size (n = 4).

Of the three species identified using 16s sequences, the 483 bp region of *C*. *undecimalis* was the most variable. A total of 12 variable sites, corresponding to 12 transitions and one transversion, generated 15 haplotypes (Table 2.6). The base frequencies were 29.7% for A, 26.1% for C, 20.4% for G, and 23.8% for T. Two haplotypes were most common (und – 1 and und – 2), each with frequencies greater than 0.05% that accounted for 90.3% of all *C. undecimalis* sampled. The remaining 13 haplotypes occurred at a frequency lower than 1%. Basic haplotype diversity estimates for each species and region sampled are provided in Table 2.7.

| | Tex | kas | | | Polymor | phic Sites |
|-----------|--------------|--------------|--------------|--------------|---------|------------|
| Haulatana | Middle | Lower | Mexico | Total | 5 | 5 |
| Haplotype | | | | | 4 | 5 |
| | <i>n</i> = 1 | <i>n</i> = 2 | <i>n</i> = 1 | <i>n</i> = 4 | 1 | 7 |
| poe – 1 | 0 | 0.500 | 0 | 0.250 | А | G |
| poe – 2 | 1.000 | 0 | 0 | 0.250 | G | А |
| poe – 3 | 0 | 0.500 | 1.000 | 0.500 | | А |

 Table 2.5. Haplotype relative frequency, distribution, and polymorphic sites contained within the 535bp segment of the 16s gene among *Centropomus poeyi* collected from Texas and Mexico. Identical bases (.) are shown.

| | . | omus unue | | | | | | | | | | | () | | | | | | |
|-----------|-------------|--------------|-------|-------------|--------------|---------------|-------|---|---|---|---|-----|------|--------|------|---|---|---|---|
| | | Texas | | Florida | Costa | Mexico | Total | | | | | Pol | ymor | phic s | ites | | | | |
| Haplotype | Upper | Middle | Lower | | Rica | | | | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 3 | 3 | 3 |
| парютуре | | | | - | 2 | 10 | 220 | 4 | 3 | 8 | 9 | 0 | 0 | 2 | 3 | 9 | 3 | 4 | 4 |
| | <i>n</i> =1 | <i>n</i> =17 | n=192 | <i>n</i> =7 | <i>n</i> = 3 | <i>n</i> = 19 | n=239 | 0 | 6 | 4 | 6 | 2 | 7 | 6 | 5 | 9 | 3 | 3 | 9 |
| und – 1 | 0 | 0.235 | 0.344 | 0.857 | 1.000 | 0.316 | 0.356 | Т | G | Α | G | Т | Α | Т | С | С | G | Α | G |
| und – 2 | 1.000 | 0.706 | 0.557 | 0.143 | 0 | 0.526 | 0.548 | | | • | | | | | | | • | | Α |
| und – 3 | 0 | 0 | 0.026 | 0 | 0 | 0 | 0.021 | | | G | | | | | | | | | Α |
| und – 4 | 0 | 0 | 0.005 | 0 | 0 | 0 | 0.004 | | | | | | | | | | | | С |
| und – 5 | 0 | 0 | 0.005 | 0 | 0 | 0 | 0.004 | | | | | | | | Т | | | | |
| und – 6 | 0 | 0 | 0.021 | 0 | 0 | 0.105 | 0.025 | | | | | | | | | | | G | |
| und – 7 | 0 | 0 | 0.005 | 0 | 0 | 0.053 | 0.008 | | Α | | | | | | | | | | Α |
| und – 8 | 0 | 0 | 0.005 | 0 | 0 | 0 | 0.004 | | | | А | | | | | | | | |
| und – 9 | 0 | 0 | 0.005 | 0 | 0 | 0 | 0.004 | | | | | | G | | | | | | Α |
| und – 10 | 0 | 0 | 0.005 | 0 | 0 | 0 | 0.004 | С | | | | | | | | | | | |
| und – 11 | 0 | 0 | 0.005 | 0 | 0 | 0 | 0.004 | | | | | | | | | Т | | | Α |
| und – 12 | 0 | 0 | 0.005 | 0 | 0 | 0 | 0.004 | | | | | | | С | | | | | |
| und – 13 | 0 | 0 | 0.005 | 0 | 0 | 0 | 0.004 | | | | | С | | | | | | | |
| und – 14 | 0 | 0 | 0.005 | 0 | 0 | 0 | 0.004 | | | | | | G | | | | | | |
| und – 15 | 0 | 0.059 | 0 | 0 | 0 | 0 | 0.004 | | | | | | | | | | А | | Α |

 Table 2.6. Haplotype relative frequency, distribution, and polymorphic sites contained within the 483bp segment of the 16s gene among *Centropomus undecimalis* collected from Texas, Florida, Costa Rica, and Mexico. Identical bases (.) are shown.

| Species | п | S | т | h | π | k |
|-------------------------|-----|----|----|-------|-------|-------|
| Centropomus parallelus | 337 | 6 | 7 | 0.053 | 0.000 | 0.053 |
| Texas – upper | 20 | 0 | 1 | 0 | 0 | 0 |
| Texas – middle | 50 | 0 | 1 | 0 | 0 | 0 |
| Texas – lower | 263 | 6 | 7 | 0.067 | 0.000 | 0.068 |
| Mexico | 4 | 0 | 1 | 0 | 0 | 0 |
| Centropomus poeyi | 4 | 2 | 3 | 0.833 | 0.002 | 0.002 |
| Texas – middle | 1 | 0 | 1 | 0 | 0 | 0 |
| Texas – lower | 2 | 1 | 2 | 1.000 | 0.002 | 1.000 |
| Mexico | 1 | 0 | 1 | 0 | 0 | 0 |
| Centropomus undecimalis | 239 | 12 | 15 | 0.574 | 0.001 | 0.668 |
| Texas – upper | 10 | 2 | 3 | 0.600 | 0.001 | 0.002 |
| Texas – middle | 8 | 1 | 2 | 0.250 | 0.000 | 0.250 |
| Texas – lower | 192 | 11 | 14 | 0.573 | 0.001 | 0.671 |
| Mexico | 19 | 3 | 4 | 0.643 | 0.002 | 0.795 |
| Florida | 7 | 1 | 2 | 0.286 | 0.000 | 0.286 |
| Costa Rica | 3 | 0 | 1 | 0 | 0 | 0 |

Table 2.7. Summary of haplotype diversity statistics of 16s for all *Centropomus* species including sample size (n), segregating sites (S), number of haplotypes (m), haplotype diversity (h), nucleotide diversity (π) and pairwise nucleotide differences (k).

AMOVA results for Texas *C. undecimalis* yielded no significant genetic differentiation for 16s between regions of capture (Table 2.8), most likely due to the shared haplotypes across regions. Virtually all variation (100%) is within the population (p = 0.36). An expanded AMOVA investigation across Gulf (Texas versus Costa Rica, Mexico, and Florida individually) identified differences between Florida/Costa Rica and Texas samples. The comparison of *C. undecimalis* from Texas and Florida yielded a significant (p = 0.01) proportion of variation between populations at 22.02%. Similarly, AMOVA revealed additional differences between Mexico and Florida populations (p =0.04, Variation = 21.91%). A haplotype network tree displaying the distribution of *C. undecimalis* haplotypes sampled in this study is found in Figure 2.4.

| Species | Source of variation | d.f. | Percentage of variation (p) |
|----------|---------------------|-------|------------------------------|
| Centropo | omus undecimalis | | |
| | | Texas | (upper vs. middle vs. lower) |
| | Between populations | 2 | -0.43 (0.36) |
| | Within populations | 207 | 100.43 |
| | | | Texas vs. Mexico |
| | Between populations | 1 | -1.29 (0.57) |
| | Within populations | 227 | 101.29 |
| | | | Texas vs. Florida |
| | Between populations | 1 | 22.02 (0.01) |
| | Within populations | 215 | 77.89 |
| | | | Mexico vs. Florida |
| | Between populations | 1 | 21.91 (0.04) |
| | Within populations | 14 | 78.09 |
| | | | Texas vs. Costa Rica |
| | Between populations | 1 | 29.89 (0.04) |
| | Within populations | 211 | 70.11 |
| | | | Costa Rica vs. Mexico |
| | Between populations | 1 | 27.73 (0.09) |
| | Within populations | 20 | 72.27 |

Table 2.8. Summary of AMOVA results of Centropomus undecimalis 16s mtDNA.

Bold items indicate significant difference

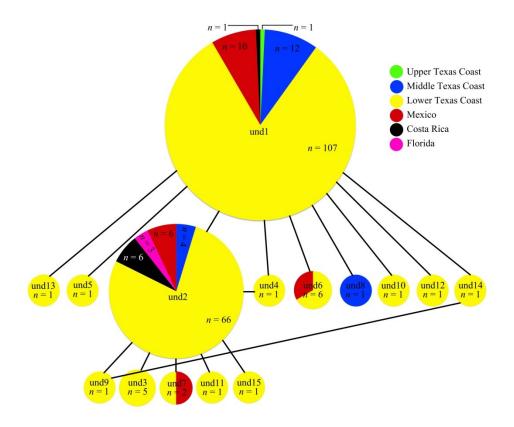


Figure 2.4. TCS network of the 15 Centropomus undecimalis 16s mtDNA haplotype sequences.

$\underline{D-loop}$

The length of the mitochondrial control region (D - loop) for both *C. parallelus* and *C. undecimalis* resulted in 500+ bp sequences with multiple (ten plus) tandem repeats for each species (Table 2.9) thus, sequences were aligned and edited manually, resulting in 181 bp and 152 bp sequences for *C. parallelus* and *C. undecimalis*, respectively.

 Table 2.9. Repeated sequences found in mitochondrial control region (D – loop) for Centropomus parallelus (41 bases) and C. undecimalis (39 bases)

| Species | Repeated Sequence |
|----------------|---|
| C. parallelus | TACATAAAGTGTATGCCCCTGACATACTATAATGGTGGTAA |
| C. undecimalis | GGTGATTATACATAGAATGTATAATTTATCATCATATAT |

Variation in the 181 bp segment of the mitochondrial control region (D – loop) was analyzed for 82 *C. parallelus*. Forty-eight polymorphic sites were found, with six transversions and 46 transitions. Haplotype diversity was high, as expected due to rapid evolution and divergence of the D – loop sequence (Table 2.10). A total of 47 haplotypes was observed, with the most common haplotype (Dpar – 1) accounting for 25.6% of the sample (Table 2.11). Specimens representing Dpar – 1 all came from the LLM and Aransas Pass collection sites. AMOVA results of *C. parallelus* D – loop sequences identified no significant differences among regions at any level (Table 2.13). The results of these AMOVAS (upper coast versus middle, upper versus lower, and middle versus lower) suggest a lack of regional genetic differentiation (Figure 2.5).

A segment 152 bp long of the D - loop was characterized for seventy-four *C*. *undecimalis*. The segment contained 27 polymorphic sites corresponding to four transversions and 28 transitions. Similar to the D-loop of *C. parallelus*, the D – loop of *C. undecimalis* is characterized by relatively low nucleotide diversity values within samples, indicating that haplotypes are closely related concurrent with high values of haplotype diversity (Table 2.10). There were 24 haplotypes with two haplotypes, Dund – 4 and Dund – 5, accounting for 38.2 and 14.9% of the sample, respectively (Table 2.12). The two most common *C. undecimalis* haplotypes (Dund - 1 and Dund - 2) consisted of samples largely from LLM and Aransas Pass collection sites. Frequencies of all other haplotypes for both species were less than 10%. Many *C. undecimalis* haplotypes were not detected in the GOM; for instance, Dune – (1,2,6,8, and 20) was restricted to Florida and Costa Rica, and these were highly divergent from the majority of haplotypes present in Texas and Mexico. The NJ tree developed for *C. undecimalis* D – loop haplotypes indicated divergence between Texas samples and those from Costa Rica and Florida (Figure 2.6). AMOVA for *C. undecimalis* revealed similar results for intrastate comparisons of D – loop analysis, with no significant variation (p = 0.06) between middle and lower coast populations, suggesting a lack of genetic population structure within Texas (Table 2.13). Comparisons between Texas *C. undecimalis* and Florida conspecifics illustrated significant difference among populations (p = 0.00), with 20.5% of the genetic variation among Texas and Florida. Lastly, a comparison of Texas *C. undecimalis* to Costa Rica conspecifics yielded similar significant difference results among groups (p = 0.00).

| Species | | n | S | т | h | π | k |
|-------------------------|----------------|----|----|----|-------|-------|-------|
| Centropomus parallelus | Texas | 82 | 48 | 47 | 0.929 | 0.023 | 4.154 |
| | Texas – upper | 2 | 6 | 2 | 1.000 | 0.034 | 6.000 |
| | Texas – middle | 8 | 13 | 6 | 0.928 | 0.025 | 4.392 |
| | Texas – lower | 72 | 47 | 44 | 0.928 | 0.023 | 4.095 |
| | | | | | | | |
| Centropomus undecimalis | Texas | 74 | 27 | 24 | 0.820 | 0.027 | 3.787 |
| | Texas – middle | 6 | 7 | 5 | 0.766 | 0.021 | 2.933 |
| | Texas – lower | 58 | 19 | 17 | 0.755 | 0.012 | 1.593 |
| | Florida | 7 | 13 | 4 | 0.714 | 0.028 | 3.905 |
| | Costa Rica | 3 | 3 | 2 | 0.667 | 0.014 | 3.905 |

Table 2.10. Summary of D - loop haplotype diversity statistics for 156 *Centropomus* specimens including sample size (n), segregating sites (S), number of haplotypes (m), haplotype diversity (h), nucleotide diversity (π) , and pairwise nucleotide differences (k).

| | | Texas | Ţ | Total |
|------------------|-------|--------------|---------------|---------------|
| Haplotype | Upper | Middle | Lower | |
| _ | n=2 | <i>n</i> = 8 | <i>n</i> = 72 | <i>n</i> = 82 |
| Dpar – 1 | 0 | 0.250 | 0.264 | 0.256 |
| Dpar – 2 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 3 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 4 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 5 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 6 | 0 | 0.125 | 0.014 | 0.024 |
| Dpar – 7 | 0 | 0.250 | 0.042 | 0.061 |
| Dpar – 8 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 9 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 10 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 11 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 12 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 13 | 0 | 0.125 | 0.014 | 0.024 |
| Dpar – 14 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 15 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 16 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 17 | 0 | 0 | 0.028 | 0.024 |
| Dpar – 18 | 0.50 | 0 | 0 | 0.012 |
| Dpar – 19 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 20 | 0 | 0.125 | 0.028 | 0.037 |
| Dpar – 21 | 0 | 0 | 0.028 | 0.024 |
| Dpar – 22 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 23 | 0 | 0 | 0.028 | 0.024 |
| Dpar – 24 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 25 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 26 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 27 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 28 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 29 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 30 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 31 | 0 | 0 | 0.056 | 0.049 |
| Dpar – 32 | 0 | 0 | 0.028 | 0.024 |
| Dpar – 33 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 34 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 35 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 36 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 37 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 38 | 0 | 0.125 | 0 | 0.012 |
| Dpar – 39 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 40 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 41 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 42 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 43 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 44 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 45 | 0 | 0 | 0.014 | 0.012 |
| Dpar – 46 | 0.50 | 0 | 0 | 0.012 |
| Dpar – 47 | 0 | 0 | 0.014 | 0.012 |

 Table 2.11. Haplotype distribution and frequency of Centropomus parallelus D - loop sequences.

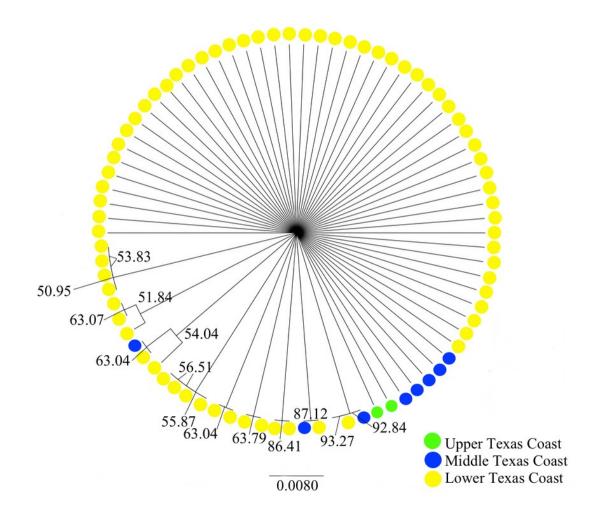


Figure 2.5. Unrooted NJ tree based on 47 *Centropomus parallelus* D - loop haplotypes from Texas using the Maximum Composite Likelihood method. Bootstrap values above 50% are shown by the nodes.

| | Tey | kas | Florido | Costa Diag | Total |
|------------------|--------------|---------------|--------------|--------------|---------------|
| Haplotype | Middle | Lower | Florida | Costa Rica | Total |
| | <i>n</i> = 6 | <i>n</i> = 58 | <i>n</i> = 7 | <i>n</i> = 3 | <i>n</i> = 74 |
| Dund – 1 | 0 | 0 | 0.571 | 0.667 | 0.081 |
| Dund – 2 | 0 | 0 | 0.143 | 0 | 0.014 |
| Dund – 3 | 0.167 | 0.034 | 0 | 0 | 0.041 |
| Dund – 4 | 0.333 | 0.466 | 0 | 0 | 0.392 |
| Dund – 5 | 0.167 | 0.172 | 0 | 0 | 0.149 |
| Dund – 6 | 0 | 0 | 0 | 0.333 | 0.014 |
| Dund – 7 | 0 | 0.017 | 0 | 0 | 0.014 |
| Dund – 8 | 0 | 0 | 0.143 | 0 | 0.014 |
| Dund – 9 | 0 | 0.017 | 0 | 0 | 0.014 |
| Dund – 10 | 0.167 | 0 | 0 | 0 | 0.014 |
| Dund – 11 | 0 | 0.069 | 0 | 0 | 0.054 |
| Dund – 12 | 0 | 0.034 | 0 | 0 | 0.027 |
| Dund – 13 | 0 | 0.017 | 0 | 0 | 0.014 |
| Dund – 14 | 0 | 0.034 | 0 | 0 | 0.027 |
| Dund – 15 | 0 | 0.017 | 0 | 0 | 0.014 |
| Dund – 16 | 0 | 0.017 | 0 | 0 | 0.014 |
| Dund – 17 | 0 | 0.017 | 0 | 0 | 0.014 |
| Dund – 18 | 0 | 0.017 | 0 | 0 | 0.014 |
| Dund – 19 | 0 | 0.017 | 0 | 0 | 0.014 |
| Dund – 20 | 0 | 0 | 0.143 | 0 | 0.014 |
| Dund – 21 | 0 | 0.017 | 0 | 0 | 0.014 |
| Dund – 22 | 0 | 0.017 | 0 | 0 | 0.014 |
| Dund – 23 | 0 | 0.017 | 0 | 0 | 0.014 |
| Dund – 24 | 0.167 | 0 | 0 | 0 | 0.014 |

 Table 2.12. Haplotype distribution and frequency of Centropomus undecimalis D - loop sequences.

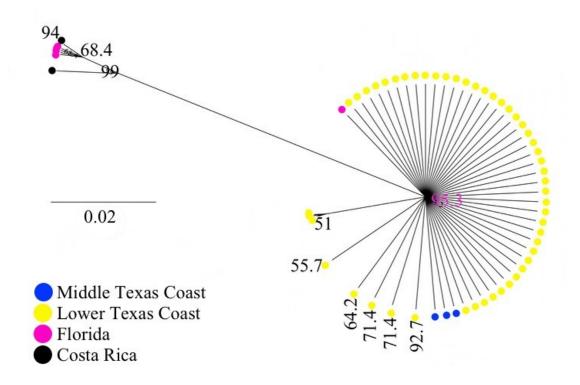


Figure 2.6. Twenty-four *Centropomus undecimalis* D – loop haplotypes displayed on an unrooted NJ tree using the Maximum Composite Likelihood method. Bootstrap values above 50% are shown by the nodes.

| Species | Source of variation | d.f. | Percentage of variation (p) |
|----------|---------------------|-------|------------------------------|
| Centropo | omus parallelus | | |
| | | Texas | (upper vs. middle vs. lower) |
| | Between populations | 2 | 0.83 (0.35) |
| | Within populations | 79 | 99.17 |
| Centropo | mus undecimalis | | |
| | | | Texas (middle vs. lower) |
| | Between populations | 1 | 11.19 (0.06) |
| | Within populations | 62 | 88.81 |
| | | | Texas vs. Florida |
| | Between populations | 1 | 79.26 (0.00) |
| | Within populations | 1 | 20.74 |
| | | | Texas vs. Costa Rica |
| | Between populations | 1 | 84.43 (0.00) |
| | Within populations | 1 | 15.57 |

Table 2.13. Summary of AMOVA results of *Centropomus* species D – loop sequences.

Bold items indicate significant difference

Morphological Identification

Using results of the aforementioned genetic identification, a subset of 20 randomly selected individuals from *C. parallelus* and *C. undecimalis* and all three *C. poeyi* (< 100 mm SL) was examined to produce identification aids. Meristic analysis yielded morphological differences between all three species as described by (Greenfield 1975), where pelvic fins (P₂) in *C. parallelus* reach past the anus but fail to reach the anus in *C. undecimalis* and *C. poeyi* (Figures 2.7) Separation of *C. undecimalis* and *C. poeyi* (an be differentiated by Rivas' (1986) use of first dorsal spine (D₁) counts, wherein *C. undecimalis* = 8 and *C. poeyi* = 7 (Figure 2.8).

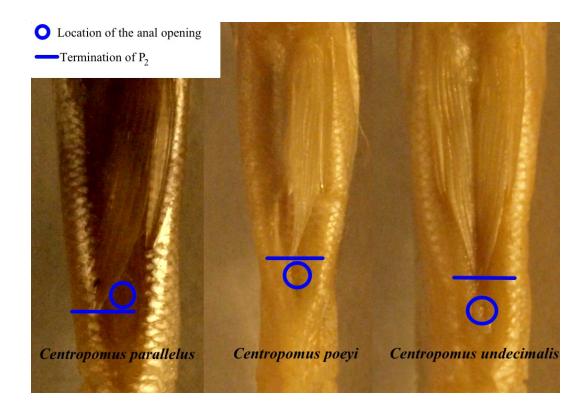


Figure 2.7. Ventral view of *Centropomus* species showing relationship of pelvic fin termination (P₂) to anal opening.

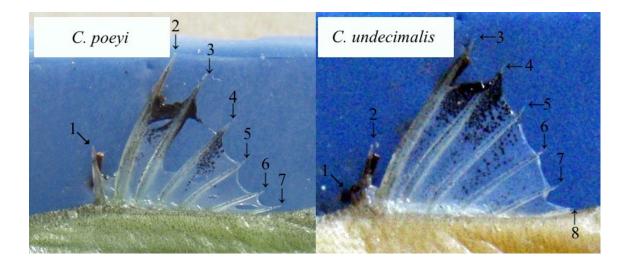


Figure 2.8. Images of dorsal fin spine counts for *Centropomus poeyi* and *Centropomus undecimalis* illustrating differences between species.

Discussion

Genetic analysis of the mtDNA16s gene from centropomids collected during this study yielded three species in Texas: C. parallelus, C. poeyi, and C. undecimalis. The presence of *C. mexicanus* could not be confirmed with mitochondrial data. The existence of C. parallelus in Texas waters was previously documented (Martin & King 1991). The occurrence of *C. undecimalis* in Texas is a presumption largely based on historical documentation and the common misconception that all centropomids in the state were C. undecimalis (Gunter 1941, 1951). The capture of only three C. poeyi in Texas 500 km from their closest established range (Carvajal 1975, Chavez 1981, Alvarez-Lajonchère & Tsuzuki 2008) provides little indication of a resident population in Texas. However, otolith microstructure analyses (Chapter 4) for two C. poevi captured in Laguna Vista, Texas indicate that these specimens were spawned 80 to 90 days prior to their capture. Possible reasons for this species' presence in Texas include: 1) successful transport of larvae from resident spawning grounds in Mexico via longshore currents, and 2) populations of C. poevi have migrated further north along the Mexican coast and have colonized Texas waters.

Warmer winters may have facilitated a northern advancement of other centropomids into Texas waters may have also facilitated *C. poeyi*'s migration beyond their normal range into northern localities with suitable habitats. However, the only information about the possibility of *C. poeyi* conducting large-scale migrations is based on a small scale tagging study in the Papaloapan River system south of Veracruz, Veracruz, Mexico. (Chavez 1981) identified migrations of *C. poeyi* between the Papaloapan and Grijalva River systems, where one specimen traveled 333 km south to the Grijalva River. The remaining *C. poeyi* that were recaptured in Chavez's study were found within the confines of the Papaloapan estuary, only migrating out of the river to the GOM during their reproductive season to spawn. The single *C. poeyi* found in the Grijalva River suggests that *C. poeyi* and possibly all centropomids are not limited to a single estuary and freely move from one estuary to another. Additionally, the migration patterns of Florida's Atlantic *C. undecimalis* are known to migrate up to 350 km along the Atlantic coast (Tringali & Bert 1996). Migration patterns identified by Chavez (1981) and Tringali & Bert (1996) indicate that settlement into new estuaries is possible if new habitats are adequate for establishment.

The low genetic diversity and shared haplotypes found within Texas' *C*. *parallelus* 16s suggest a lack of genetic population structure; most likely all Texas *C*. *parallelus* are from an expanding population originating from Mexico. Haplotype par – 1 accounted for 328 of the 337 (97.3%) *C. parallelus* examined in this study, and could be considered as the genetic hub from which all different *C. parallelus* haplotypes develop. Specimens from this haplotype ranged from the northernmost collection site of any centropomid captured in this study (Freeport, Texas) to the most southern collection site (Frontera, Tabasco, Mexico). The remaining haplotypes (par – 2 through par – 7) were represented by few individuals (less than two in most cases) and were only found in the LLM.

AMOVA results for 16s *C. undecimalis* specimens within Texas and Mexico region yielded no significant genetic variation; however, variation was found within

Texas and Florida/Costa Rica comparisons. These results suggest that centropomids from Texas are reproductively isolated from those in Florida and Costa Rica. The separation between populations utilizing of 16s mtDNA haplotypes is notable, since (Tringali & Bert 1996) found differences between Atlantic and Gulf populations of *C. undecimalis* in Florida utilizing the entire mtDNA nucleotide sequence. AMOVA for the 16s *C. poeyi* samples were not conducted due to small sample size (n = 4); however it is important to note that the single sample from Frontera, Tabasco, Mexico shared a haplotype with a specimen from Laguna Vista, Texas. The shared haplotype suggests a potential connection between Mexico and Texas populations. Size and age of *C. parallelus* and *C. undecimalis* (Chapter 4) captured in this study provide evidence that recruits found in Texas stem from a resident spawning population rather than from longrange dispersal that is strongly dependent on favorable long-shore currents.

D –loop sequences were perceived as a diagnostic tool to identify any potential hybridization or cryptic speciation within *C. parallelus* and the potential probability of the occurrence of *C. mexicanus*. However, the D – loop sequence analysis of *C. parallelus* stocks present in Texas revealed no genetic differentiation, suggesting that *C. parallelus* populations could be treated as a single genetic stock. *Centropomus undecimalis* exemplified the same lack of genetic differences among Texas populations; however, analysis of D – loop data revealed differences between the samples of Texas and Mexico against those from Florida and Costa Rica.

The absence of genetic population structure between both *C. parallelus* and *C. undecimalis* within Texas can be explained by the reproductive patterns of these species.

Spawning strategies documented for centropomids (spawning at the mouths of passes) allow for dispersion of these species, thus facilitating gene flow; however, a noticeable decrease in genetic differentiation is expected for new or invading populations.

Conclusion

This study successfully confirmed the identification of early juveniles of three centropomid species (C. parallelus, C. poeyi, and C. undecimalis) in Texas waters. The lack of population structure resolvable by 16s data most likely reflects the highly conserved nature of this mitochondrial gene. D – loop AMOVA of C. undecimalis indicated significant differences between Texas and Florida/Costa Rica populations, a finding supported by the separation shown on the NJ tree (Figure 2.6) and nucleotide diversity for each clade (Texas dominant clade $\pi = 0.012$ and Florida/Costa Rica clade π = 0.008). Along with these differences, the potential for differences between Texas and Mexico should be investigated for both C. parallelus and C. undecimalis using satellite markers. Genetic validation aided in morphological identification of species captured in Texas. Termination of P_2 in relation to the anal opening separates C. parallelus from C. *poevi* and *C. undecimalis*, and D_1 counts separated the latter two species from one another. This separation follows a combination of identification characteristics given in keys developed by (Greenfield 1975) and (Rivas 1986), and should assist fisheries biologists in correctly identifying similar looking centropomids.

Sources of centropomid recruits to Texas populations have yet to be determined and could originate from distant spawning grounds and not a contribution from resident populations. An assessment of sources and pathways of centropomid populations into Texas waters remains to be conducted. Otolith microstructure analyses (Chapter 4) insinuate a proximal spawning population, and additional otolith chemistry studies could also aid in determination of origins and possible separate populations. Further morphometric and molecular analyses are necessary to interpret population structure, relationships, origins, and possible morphological or genetic divergence of centropomids in Texas. Additionally, examination of a larger sample size of *Centropomus* species from ecologically- and geographically-diverse locations along the Texas coast, spanning multiple spawning seasons across several years, is necessary to clarify genetic diversity on a regional basis. Continued genetic analysis will elucidate the population structure of centropomids and assess the potential for additional species occurring in Texas waters.

CHAPTER III

DISTRIBUTION AND OCCURRENCE BY HABITAT OF *CENTROPOMUS* SPECIES IN TEXAS

Introduction

The Texas Gulf shoreline stretches 595 km from the Sabine River to the Rio Grande, and spans seven major and five minor estuaries covering one million hectares. These estuaries serve an important role by providing habitats, nurseries, food, and spawning grounds for estuarine dependent fishes (Blaber & Blaber 1980, Boesch & Turner 1984, Adams et al. 2006). Despite their importance, Texas estuaries are confronted with significant problems related to anthropogenic alterations of freshwater inflow (Longley 1994, Adams et al. 2009) and habitat loss (Bell et al. 1988, Rozas et al. 2007, Engle 2011) that impact fish assemblages. Additionally, the susceptibility of Texas estuaries to severe climatic impacts due to regional climate and coastal geology (Larkin & Bomar 1983, Montagna et al. 2011) can affect fish population structure.

Changes in global temperatures are occurring more rapidly (IPCC 2008), intensifying impact on sea surface temperature and subsequently affecting estuarine ecosystems. Population cycles, fish kills, and range expansions have been linked with fluctuations in water temperature (Gunter 1941, Matlock & Osburn 1987, Enfield et al. 2001, Hare & Able 2007). The eastern equatorial Pacific and Texas' Gulf coast represent excellent examples where temperature shifts have resulted in changes in fish community structure. Climatic variability along the Texas coast investigated by (Tolan & Fisher 2009) determined that the presence of gray snapper (*Lutjanus griseus* Linnaeus, 1758) in inshore waters of Texas is related to increased water temperatures. Additional studies support the interplay between estuarine biological expansions and climate change (Barber & Chavez 1983, Oviatt 2004, Preston 2004, Roessig et al. 2004, Winder et al. 2011).

Members of the Family Centropomidae are semicatadromous, stenothermic, euryhaline, and protandric hermaphroditic group of species represented by a single genus *Centropomus* (Tringali & Leber 1999) inhabiting subtropical and tropical waters of North and South America (Gilmore et al. 1983, Rivas 1986). Although one species (*C. undecimalis*) has been collected as far north as New York (Schaefer 1972), centropomids occur mostly from Florida south to Rio de Janeiro, Brazil along the Atlantic and throughout Mexico, and in Texas from Port Aransas southward to the US – Mexico border (Marshall 1958, Seaman & Collins 1983, Rivas 1986).

Centropomus undecimalis' intolerance of low water temperature has been historically cited for southern Texas being this species' northernmost limit in the western GOM (Tucker & Campbell 1988). Juvenile and adult *C. undecimalis* have been collected in 14.2 to 35.6 °C waters in Florida (Marshall 1958, Fore & Schmidt 1973, McMichael et al. 1989). Four reports have identified centropomids as unresponsive, stunned, or killed as a result of winter cold events throughout their distributional range in Texas waters (Gunter 1941, 1951, Moore 1976, Holt & Holt 1983). Temperature tolerances of all centropomids may vary throughout their range due to genetic composition, salinity, size, and diet (Shafland & Foote 1983, Howells et al. 1990). This chapter describes habitat and distribution of juvenile *Centropomus* species captured for the genetics and age growth portions of this study. The experimental design deployed during this study did not allow for analysis of CPUE due to sporadic sampling frequency and severely limited catch (<2%) in standardized tows prerequisite to determining CPUE. Specific objectives of this chapter were to:

- identify habitats used by settled centropomids;
- identify habitats utilized by juvenile centropomids.

Materials and Methods

Juvenile centropomids were collected at wetland sloughs, boat ramps, and other tidal- and freshwater- influenced habitats from Carancahua Bay (Palacios) to the Rio Grande (US – Mexico border). Selection of each collection site was based on historical data generated by TPWD and TAMUG as well as published and anecdotal reports of larval and juvenile centropomid occurrence (Martin & King 1991, Pope et al. 2006). Collection sites were classified according to upper, middle, and lower regions of the Texas coast and divided into two major climatological zones (temperate and subtropical; Figure 3.1). The temperate climate collection area was located in the upper coast region within the Galveston and Matagorda Estuary Systems. Upper coast collection sites included Caney Creek (south of Sargent), Tres Palacios River (at its intersection along FM 521), upper reaches of Carancahua Bay (near FM 35), and Lavaca Bay (near Port Lavaca).

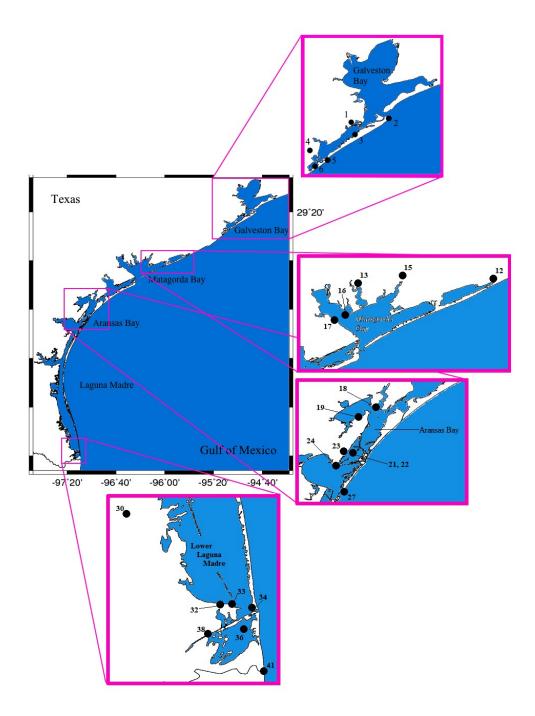


Figure 3.1 Texas sampling sites. Numbers correspond to sites labeled in Table 3.1.

Remaining study areas were located within the Aransas and LLM Estuary Systems that featured subtropical climates. The Aransas Estuary represented the middle coast collection site that included Goose Island State Park (Rockport), Redfish Bay (at two locations along SH 361, Stedman Island), and a drainage ditch located in the city of Aransas Pass on SH 35. Lower coast collections were conducted from the southernmost portions of the LLM Estuary System and included the Arroyo Colorado (and surrounding drainages), Laguna Vista, San Martin boat ramp and channel, Mexiquita Flats, Padre Island Coast Guard Station (northwest of the Brazos Santiago Pass), and Boca Chica (Rio Grande and surrounding sloughs). Complete information regarding all sample locations is listed in Table 3.1. Sampling protocol was the same as that described in Chapter 2.

Hydrographic data taken during each collection included: 1) dissolved oxygen content (mg/L) and water temperature (°C) using an YSI 550 DO meter (YSI Inc., Yellow Springs, OH, USA); 2) wind speed (meters per second) and air temperature (°C) using an EA-3010 anemometer (La Crosse Technology Ltd., La Crosse, WI, USA); 3) salinity (‰) using an SR6 Salinity Refractometer (Aquatic Ecosystems Inc., Apopka, FL, USA); and 4) turbidity (cm) using a 20 cm Secchi disk (Aquatic Ecosystems Inc., Apopka, FL, USA). Habitat characteristics including shoreline vegetation, submerged aquatic vegetation, bottom structures and obstructions were documented and photographed to aid in determination of settlement habitats of *Centropomus* species.

| Site # | County | Location | Region of the Texas coast | Latitude | Longitude |
|--------|--------------|------------------------------|---------------------------|-------------|-------------|
| 1* | Galveston | Diversionary Canal | Upper | 29 20.134 N | 95 01.417 W |
| 2 | Galveston | East Lagoon | Upper | 29 19.209 N | 94 45.489 W |
| 3 | Galveston | West Galveston Bay | Upper | 29 12.725 N | 94 57.409 W |
| 4* | Brazoria | Bastrop Bayou | Upper | 29 05.598 N | 95 16.940W |
| 5 | Brazoria | San Luis Pass | Upper | 29 04.728 N | 95 07.847 W |
| 6 | Brazoria | Christmas Bay | Upper | 29 02.928 N | 95 09.933 W |
| 7* | Brazoria | Oyster Creek | Upper | 29 00.059 N | 95 18.070 W |
| 8 | Brazoria | Intracoastal Waterway | Upper | 28 57.850 N | 95 17.533 W |
| 9 | Brazoria | Brazos River | Upper | 28 52.803 N | 95 22.780 W |
| 10 | Brazoria | San Bernard River | Upper | 28 52.586 N | 95 28.171 W |
| 11 | Matagorda | Tres Palacios River | Upper | 28 47.147 N | 96 08.977 W |
| 12 | Brazoria | Caney Creek | Upper | 28 46.329 N | 95 38.063 W |
| 13 | Jackson | Carancahua Bay | Upper | 28 44.252 N | 96 24.121 W |
| 14* | Matagorda | Matagorda Bay | Middle | 28 43.593N | 95 47.124W |
| 15 | Matagorda | Turtle Creek | Upper | 28 43.251 N | 96 16.417 W |
| 16 | Calhoun | Lavaca Bay | Upper | 28 39.898 N | 96 34.378 W |
| 17 | Calhoun | Lavaca Bay | Upper | 28 38.297 N | 96 36.659 W |
| 18 | Aransas | Aransas Bay | Middle | 28 07.677 N | 96 59.164 W |
| 19 | Aransas | Copano Bay | Middle | 28 05.747 N | 97 03.137 W |
| 20 | Aransas | Little Bay | Middle | 28 01.854 N | 97 02.341 W |
| 21 | Nueces | Redfish Bay | Middle | 27 53.637 N | 97 07.676 W |
| 22 | Nueces | Redfish Bay | Middle | 27 53.341 N | 97 07.063 W |
| 23 | Nueces | Aransas Bay | Middle | 27 53.566 N | 97 09.188 W |
| 24 | San Patricio | Nueces Bay | Middle | 27 51.515 N | 97 21.193 W |
| 25 | Nueces | Redfish Bay | Middle | 27 50.396 N | 97 07.734 W |
| 26 | Nueces | Corpus Christi Bay | Middle | 27 45.010 N | 97 09.003 W |
| 27 | Nueces | Packery Channel | Middle | 27 37.592 N | 97 12.987 W |
| 28** | Willacy | Lower Laguna Madre | Lower | 26 34.193 N | 97 25.637 W |
| 29 | Willacy | Creek West of Port Mansfield | Lower | 26 30.221 N | 97 29.320 W |
| 30 | Cameron | Arroyo Colorado | Lower | 26 20.998 N | 97 23.483 W |
| 31 | Cameron | Harlingen Shrimp Farm | Lower | 26 08.097 N | 97 18.017 W |
| 32 | Cameron | Laguna Vista | Lower | 26 05.705 N | 97 17.024 W |
| 33 | Cameron | Lower Laguna Madre | Lower | 26 04.461 N | 97 12.878 W |
| 34 | Cameron | Lower Laguna Madre | Lower | 26 04.356 N | 97 09.994 W |
| 35 | Cameron | Mexiquita Flats | Lower | 26 04.044 N | 97 11.659 W |
| 36 | Cameron | South Bay | Lower | 26 01.529 N | 97 10.272 W |
| 37 | Cameron | Bahia Grande | Lower | 26 00.826 N | 97 16.537 W |
| 38 | Cameron | Lake San Martin | Lower | 26 00.125 N | 97 17.913 W |
| 39 | Cameron | Port Brownsville | Lower | 25 57.795 N | 97 24.123 W |
| 40 | Cameron | Rio Grande (6 km upstream) | Lower | 25 57.613 N | 97 11.116 W |
| 41 | Cameron | Rio Grande (mouth) | Lower | 25 57.556 N | 97 08.810 W |

Table 3.1. Geographical information for all sites sampled.

* centropomids were collected at this location after January 2010 freeze event ** centropomids were collected at this location after October 2009 red tide event

Results

Environmental Conditions

Water temperature differed significantly with presence or absence of centropomids (p = 0.03) across all collections. Mean water temperature values at collection sites where centropomids were present was 23.3 °C and ranged from 12.5 to 33.1 °C (Table 3.2). Collection sites where centropomids were not captured displayed a slightly wider temperature range (10.9 to 32.4 °C) while averaging 25.1 °C. Water temperature varied seasonally, with mean readings highest in summer (29.2 °C) and declining steadily from 23.4 to 18.8 °C during fall and winter, respectively. Centropomid presence or absence was not related to salinity or DO levels, as attested by nonsignificant ANOVA results (salinity p = 0.10, DO p = 0.08). Mean salinity readings did not differ significantly among seasons or regions but displayed significant variation (p =0.007) among years 2006 (21.3 ‰, n = 16), 2007 (24.5 ‰, n = 23), 2008 (22.8 ‰, n = 16) 2), and 2009 (24.9 %, n = 3). Conforming to seasonal variability in water temperature, salinity averaged 22.4, 15.0 and 21.0 ‰ in winter, summer and fall, respectively. Regional salinity differences followed trends in the amount of freshwater inflow along the Texas coast, with mean salinities increasing from upper (16.5 ‰) to middle (19.6 ‰), and finally the lower coast (21.9 ‰). Dissolved oxygen concentrations, averaging 6.14 mg/L coast wide and ranging from 2.28 to 11.86 mg/L at collection sites, failed to exhibit significant differences between regions, seasons, years, and presence or absence of centropomids.

| - | | Up | per | |
|---------------------------------|------|---------------|------|---------------|
| |] | Present | | Absent |
| | | <i>n</i> = 4 | | <i>n</i> = 36 |
| | Mean | Min – Max | Mean | Min - Max |
| Temperature (°C) | 17.8 | 12.6 - 23.7 | 26.1 | 19.9 – 32.4 |
| Salinity (ppt) | 16.5 | 5.0 - 35.0 | 18.7 | 0.0 - 34.0 |
| Dissolved O ₂ (mg/L) | 5.81 | 4.46 - 6.43 | 6.55 | 2.75 - 9.89 |
| | | Mic | ldle | |
| |] | Present | | Absent |
| | | <i>n</i> = 11 | | <i>n</i> = 49 |
| | Mean | Min – Max | Mean | Min - Max |
| Temperature (°C) | 21.9 | 12.5 - 31.6 | 25.3 | 12.8 - 31.9 |
| Salinity (ppt) | 21.2 | 0.0 - 38.0 | 25.1 | 3.0 - 41.0 |
| Dissolved O ₂ (mg/L) | 6.60 | 3.04 - 10.38 | 7.04 | 2.75 - 11.86 |
| | | Lov | ver | |
| |] | Present | | Absent |
| | | <i>n</i> = 27 | | <i>n</i> = 31 |
| | Mean | Min – Max | Mean | Min - Max |
| Temperature (°C) | 24.8 | 18.4 - 33.1 | 25.3 | 10.9 - 30.6 |
| Salinity (ppt) | 21.9 | 3.3 - 40.0 | 28.8 | 0.0 - 50.0 |
| Dissolved O ₂ (mg/L) | 6.63 | 2.28 - 11.27 | 6.63 | 2.48 - 11.40 |
| | | Ove | rall | |
| |] | Present | | Absent |
| | | <i>n</i> = 42 | - | n = 116 |
| | Mean | Min – Max | Mean | Min - Max |
| Temperature (°C) | 23.5 | 12.5 - 33.1 | 25.1 | 10.9 - 32.4 |
| Salinity (ppt) | 21.3 | 0.0 - 40.0 | 24.2 | 0.0 - 50.0 |
| Dissolved O ₂ (mg/L) | 6.16 | 2.28 - 11.27 | 6.78 | 2.48 - 11.86 |

 Table 3.2. Summary for hydrographic parameters at sites sampled where centropomids were present or absent, arranged by region and overall.

Species Distribution

Centropomus parallelus captured during this study ranged from 10 to 411 mm SL (size mode: 27 mm SL), and *C. undecimalis* captured ranged from 12 to 271 mm SL (size mode: 27 mm SL; Table 3.3, 3.4). *Centropomus parallelus* was taken from the Freeport/Brazos River area to the Rio Grande. Distribution of *C. undecimalis* ranged from its northernmost capture site near Palacios south to the Rio Grande. Collections were dominated by *C. parallelus* at all sites except for those conducted at the Rio Grande. *Centropomus undecimalis* was found at the mouth of the Rio Grande whereas only *C. parallelus* was found up river; however, this observation was based on a single up river collection. Twenty-seven percent of collections with any centropomid contained at least two *Centropomus* species, revealing that Texas centropomids co-occur over their range during early life history. Additionally, the current study identified the occurrence of one new species, *Centropomus poeyi*, previously unknown from Texas. Three specimens of *C. poeyi* captured were 52, 55, and 62 mm SL. Two *C. poeyi* were captured at Laguna Vista on 10 November 2007 and the remaining conspecific was captured at the Aransas Pass ditch on 26 October 2007.

 Table 3.3. Percent composition of *Centropomus* species listed by region of capture along the Texas coast.

| | Upper | Middle | Lower |
|----------------|-------|--------|-------|
| C. parallelus | 95% | 74% | 57% |
| C. poeyi | 0% | 1% | 1% |
| C. undecimalis | 5% | 25% | 42% |

| Centropomus parallelus | n | Min | Max | Average |
|-------------------------|-----|-----|-----|---------|
| Upper | 20 | 20 | 376 | 150.4 |
| Middle | 50 | 16 | 160 | 63.6 |
| Lower | 243 | 10 | 411 | 37.6 |
| Centropomus poeyi | п | Min | Max | Average |
| Middle | 1 | - | - | 62 |
| Lower | 2 | 52 | 55 | 53.5 |
| Centropomus undecimalis | n | Min | Max | Average |
| Upper | 1 | - | - | 27 |
| Middle | 17 | 34 | 271 | 65.6 |
| Lower | 172 | 12 | 113 | 47.6 |

Table 3.4. Size distribution of all *Centropomus* species by region capture along the Texas coast.

Habitat Utilization

Ninety-four percent of the 506 Texas centropomids captured were < 100 mm SL(mean: 38.4 mm; mode: 21 mm; range: 10 to 100 mm SL; Table 3.5). Habitats utilized by these centropomids varied broadly, making the characterization of primary habitat use difficult. Smallest centropomids (5 to < 15 mm SL, 5.0% of the catch) were collected in shallow, sheltered riverine or drainage areas with mud substrates in the Arroyo Colorado and a sewage effluent ditch at Laguna Vista. The Arroyo is one of few freshwater tributaries to the LLM and serves to support riparian, freshwater wetland, and estuarine habitats. The Laguna Vista effluent ditch was primarily influenced from discharge of the Laguna Madre Water District and received additional influence from tidal exchange with the LLM during high tides. No submerged vegetation was found at either site; furthermore, constituent habitats were proximate to complex structures such as boat ramps, debris, and bulkheads. Scattered shoreline vegetation included black mangrove (Avicennia germinans), saltmeadow cordgrass (Spartina patens), and spike grass (Distichlis spicata). Each of these areas contained habitat described as early settlement sites for centropomids in Florida (Gilmore et al. 1983, McMichael et al. 1989, Peters et al. 1998a).

| C. parallelus | n | Range | Mode | Average |
|----------------|-----|----------|------|---------|
| Upper | 11 | 20 - 69 | 29 | 40.9 |
| Middle | 46 | 16 - 95 | 48 | 57.7 |
| Lower | 231 | 10 - 76 | 21 | 27.3 |
| C. poeyi | п | Range | Mode | Average |
| Middle | 1 | - | - | 62 |
| Lower | 2 | 52, 55 | - | 53.5 |
| C. undecimalis | п | Range | Mode | Average |
| Upper | 1 | - | - | 27 |
| Middle | 16 | 34 - 78 | 52 | 52.8 |
| Lower | 168 | 12 - 100 | 27 | 46.1 |

Table 3.5. Size distribution of *Centropomus* species < 100 mm SL by region along the Texas coast.

Post-settlement sized centropomids (>15 to 50 mm SL, 65.2% of the catch) occurred across three distinct habitats: predominantly freshwater, semi-isolated sloughs and ditches, and complex structure. Freshwater-influenced sites (Arroyo Colorado, Carancahua Bay, and a slough 6.5 km from the mouth of the Rio Grande) were protected backwater habitats with dissipated currents and a soft mud/silt substrate. Sites with semi-isolated ditch and slough habitats included Laguna Vista, Aransas Pass, and tidal sloughs near Redfish Bay and mouth of the Rio Grande. Laguna Vista and Aransas Pass sites were influenced primarily by storm drain discharge from surrounding communities and local sewage treatment plants. Each of these habitats was frequently isolated from their respective estuary during low tide and exhibited soft muddy substrates. The postsettlement size class was routinely captured in the vicinity of structure provided by shoreline vegetation such as prop roots and rhizomes of black mangroves, palms (Sabal and Serenoa spp) and man-made structures consisting of debris and culverts. Largest centropomids (50 mm SL and greater) were captured across multiple habitat types previously described for smaller size classes at Aransas Pass and Laguna Vista.

Discussion

Statistical support from CPUE data was lacking, three percent of all centropomids captured were the result of standardized sampling. However, habitats used by settlement-sized and early juvenile centropomids were identified. The tendency for settlement-sized *Centropomus* species to occupy backwater habitats with dissipated currents is similar to that observed for *C. undecimalis* in Florida (Peters et al. 1998a, Peters et al. 1998b). Texas juvenile centropomids were captured in habitats comparable to those of tidal sloughs described by (Fore & Schmidt 1973) and (McMichael et al. 1989), freshwater habitats identified by (Volpe 1951) and (Gilmore et al. 1983), and utilization of shoreline vegetation as protective structure described by (McMichael et al. 1989). Similarities found between Florida and Texas conspecifics during early life are noteworthy; however, there is little documentation to support that all phases of Texas centropomid life history are analogous to that observed elsewhere.

Two of the three centropomid species captured during this study (*C. parallelus* and *C. undecimalis*) dominated capture totals. The aforementioned dominance and expanded range exhibited by *C. parallelus* was unexpected, given the fact this species composed < 7% of TPWD's fisheries-independent centropomid catch data. Temperature tolerances for *C. parallelus* have yet to be determined; however, this species' wide geographical distribution across the Texas coast may imply it has greater tolerance of cooler water than does *C. undecimalis*. However, both *C. parallelus* and *C. undecimalis* were found in water temperatures as low as 12.6 °C, which has been documented as the upper boundary of *C. undecimalis*' lower lethal temperature (Shafland & Foote 1983,

Howells et al. 1990). The geographical range of *C. poeyi* has been reviewed by (Chavez 1961) and (Rivas 1986) and consists of a restricted distribution along the Mexican Gulf coast from Tampico, Tamaulipas to Campeche, Campeche, Mexico (Chavez 1961, 1981, Rivas 1986, Orrell 2003). The potentially similar spawning habits shared by all centropomids (Chavez 1963, Carvajal 1975, Taylor et al. 1998) could have aided in the widespread dispersion of *C. poeyi* larvae outside their native range through pelagic larvae dispersal.

Relatively mild winters were an additional factor that may have allowed for apparent northward expansion of centropomids captured in this study. Above-average winter temperature minima across Texas estuaries during the past decade (Tolan & Fisher 2009, Montagna et al. 2011) may have benefitted centropomids, allowing for increased settlement, survival, and growth rates. Other species that are sensitive to low winter temperatures (*Lutjanus griseus* and *Avicennia germinans*) are flourishing in Texas estuaries (Sherrod & McMillan 1981, Tolan & Fisher 2009). Several exogenous factors other than temperature per se may influence centropomid settlement in Texas waters, including reduced frequency of freeze events (Sherrod & McMillan 1981, Hare & Able 2007, Tolan & Fisher 2009, Montagna et al. 2011), genetic change (Tringali & Bert 1998, Tringali et al. 2008), essential habitat availability (Blaber & Blaber 1980, Aliaume et al. 1997, Peters et al. 1998a, Stevens et al. 2007), and freshwater sources (Volpe 1951, Fore & Schmidt 1973, Peters et al. 1998b).

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Conclusion

Although *C. parallelus* and *C. undecimalis* have been previously reported to inhabit Texas coastal waters (Moore 1975, Martin & King 1991), the present study is the first to document the geographical distribution and habitat types used by early life history constituents of these species. The geographical distributions of these two species overlap one another, although that of *C. parallelus* is broader. Lack of captures north of Palacios may indicate *C. undecimalis*' use of nursery grounds and developmental habitat in Texas is limited to that along the middle and lower coast. Lastly, this study's capture of multiple life history stages at various collection sites mandate that thorough investigations be conducted on the biology and ecology of *Centropomus* species in Texas to provide information prerequisite to developing successful management practices.

CHAPTER IV

AGE, GROWTH, AND HATCH-DATE DISTRIBUTION OF JUVENILE SMALLSCALE FAT SNOOK (*CENTROPOMUS PARALLELUS*) AND COMMON SNOOK (*CENTROPOMUS UNDECIMALIS*) IN TEXAS

Introduction

The Family Centropomidae consists of inshore tropical euryhaline species that are valued recreationally in Texas and Florida and support important food fisheries in Central and South America (Roberts et al. 1999, García-Galano et al. 2003, da Silva Rocha et al. 2005, Jackson & Ockelmann-Lobello 2006, Lemos et al. 2006). Increased abundance (TPWD fisheries-independent and fisheries-dependent collection data, Mark Fisher, TPWD, pers. comm.) and growing recreational popularity of centropomids in Texas have failed to motivate comprehensive examination of constituent species' life history, including age and growth analysis. Considerable life history data exist for centropomids in Florida; however, the majority of studies reported on the genus *Centropomus* in Texas are based on opportunistic capture (Martin & King 1991, Pope et al. 2006) and reflect sporadic occurrence of *C. undecimalis* (Springer & Pirson 1958, Moore 1975). Studies on growth and developmental biology of *Centropomus* species present in Texas are needed to effectively characterize and manage nursery areas utilized by constituent taxa.

Information on growth and development of *C. parallelus* is limited to aquaculture studies in Central and South America (Alvarez-Lajonchère et al. 2002a,

Temple et al. 2004, da Silva Rocha et al. 2005, Tsuzuki et al. 2007a, Tsuzuki et al. 2007b) that indicate its spawning parameters and embryonic development are similar to those of *C. undecimalis* (Alvarez-Lajonchère et al. 2002a, Cerqueira & Tsuzuki 2009). Summer spawning of *C. parallelus* has been reported by (Chavez 1963) in Veracruz, Veracruz, Mexico while comparable results were obtained via histological examination by (Santos et al. 2009) in Brazil (Table 4.1). Reported size at age data for *C. parallelus* are the result of aquaculture pilot studies and reflect little information on naturally occurring growth rates. A synopsis of these data is presented in Table 4.2.

| Species | Spawning season | Location | Citation |
|-------------------------|------------------|---------------------|--------------------------|
| Centropomus ensiferus | NA | NA | - |
| Centropomus mexicanus | NA | NA | - |
| Centropomus parallelus | June – August | Veracruz | (Chavez 1963) |
| | Spring - Summer | Brazil | (Santos et al. 2009) |
| Centropomus pectinatus | NA | NA | - |
| Centropomus poeyi | July – August | Veracruz & Campeche | (Carvajal 1975) |
| Centropomus undecimalis | June – July | SW Florida | (Volpe 1951) |
| _ | July - November | SW Florida | (Marshall 1958) |
| | July – October | SE Florida | (Tucker & Campbell 1988) |
| | April – December | SW Florida | (McMichael et al. 1989) |
| | April – October | SE & SW Florida | (Taylor et al. 1998) |

Table 4.1. Status of information on spawning dynamics of Atlantic Centropomus species.

NA denotes no information available

| Age | SL (SD) (mm) | TL (SD) (mm) | Citation |
|-----|--------------|--------------|-----------------------------------|
| 28 | 9.6 (1.4) | - | (Alves et al. 2006) |
| 48 | 14.2 (1.12) | - | (Alves et al. 2006) |
| 56 | - | 22.7 (NA) | (Corrêa & Cerqueira 2007) |
| 66 | 29.7 (2.53) | - | (Cerqueira et al. 1995) |
| 76 | 26.4 (0.3) | - | (Tsuzuki et al. 2007b) |
| 88 | 57.6 (0.1) | - | (Alvarez-Lajonchère et al. 2002b) |
| 90 | - | 52.4 (1.4) | (Alvarez-Lajonchère et al. 2004) |
| 106 | 32.1 (0.22) | - | (Tsuzuki et al. 2007b) |
| 126 | 38.2 (0.13) | - | (Tsuzuki et al. 2007b) |
| 156 | 70.0 (5.7) | - | (Tsuzuki et al. 2008) |
| 190 | - | 112.0 (1.4) | (Ribeiro & Tsuzuki 2010) |

 Table 4.2. Reported size (SL & TL) at age (days) for *Centropomus parallelus* from aquaculture studies in Mexico and Brazil.

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There are numerous studies involving spawning patterns (Taylor et al. 1998, Roberts et al. 1999, Taylor et al. 2000), early development (Lau & Shafland 1982), and growth of *C. undecimalis* (McMichael et al. 1989, Peters et al. 1998b, Aliaume et al. 2000, Taylor et al. 2000). The most comprehensive study on *C. undecimalis* spawning was conducted by (Taylor et al. 2000) who observed female oocyte maturation extending from April – October throughout Florida. Age determination of larval and early juvenile *C. undecimalis* (3.5 to 22.0 mm SL) was conducted under laboratory conditions by (Lau & Shafland 1982) who determined growth rates increase gradually with increasing size from 0.15 to 0.50 mm d⁻¹. Studies of juvenile *C. undecimalis* (15 to 150 mm SL) from southern Florida reported growth rates of 0.9 to 1.0 mm d⁻¹ (Fore & Schmidt 1973, Gilmore et al. 1983). Reported growth rates for juvenile C. undecimalis in the wild ranged from 0.5 to 1.0 mm d⁻¹ and 0.41 to 0.67 mm d⁻¹ for western Florida (McMichael et al. 1989) and Puerto Rico (Aliaume et al. 2000). Age, growth, and hatch-date distribution of juvenile *C. parallelus* and *C. undecimalis* from Texas as determined by otolith microstructure analysis are characterized in this chapter. Although general patterns of centropomid spawning and age growth characteristics are known (Taylor et al. 1998), no study has been conducted to determine these characteristics for *Centropomus* species in Texas waters. Specific objectives were to:

- estimate age and model age and growth of *C. parallelus* and *C. undecimalis*;
- assess spatial and temporal variation in growth of these species;
- determine hatch-date distribution of spawning centropomids;
- compare growth rates of Texas centropomids with those published for *C*. *undecimalis*.

Materials and Methods

Sample Processing

All *C. parallelus* and *C. undecimalis* were sampled, identified, and processed as described in Chapter II. Juvenile centropomids captured for otolith analysis were kept on ice for transport to the laboratory where they were processed immediately or frozen for subsequent analysis. Individual specimens were measured to the nearest 1.0 mm SL and, when possible, TL.

Otolith Microstructure Analysis

Sagittal otoliths were removed, cleaned and processed following protocols developed by (Secor et al. 2002), while those for age and growth analysis follow procedures developed by (Aliaume et al. 2000) for *C. undecimalis*. One sagitta from

each centropomid was randomly selected for age determination and mounted in Struer's Resin (EPOES/EPOAR; Struers Inc., Cleveland, Ohio, USA). Otoliths were then sectioned along a transverse plane, adjacent to the core, using a Buehler IsoMet 1000 Precision Saw (Buehler, Lake Bluff, Illinois, USA). Each otolith section containing the core was fixed to a 27 mm x 46 mm petrographic slide (Lakeside Microscope Accessories, Monee, Illinois, USA) with Crystal Bond (Armeco Products Inc., Ossining, New York, USA), sanded on Buehler CarbiMet paper discs (320, 400, 600 and 800 grit) and polished with Buehler 0.3 μm MicroPolish Alumina on a microcloth following techniques reported by (Rooker et al. 2004).

Sectioned and polished otoliths were examined through transmitted light on an Olympus BX41 compound microscope at 40X magnification. Image analysis software Image Pro Plus (version 4.5, Media Cybernetics Inc.) was utilized to enumerate daily growth increments, beginning at the core and counting along the sulcus to the otolith edge. Ages were based upon the average of two independent counts conducted by a single reader. In the event of a mean difference of counts greater than 10%, a third count was taken for age estimation. If the third count was within 10% of one of the prior readings, the mean of the two was used for analysis. If the third count differed by 10% or more, the otolith was not used for analysis. A random subsample of *C. parallelus* and *C. undecimalis* otoliths (n = 25) was read by a second independent reader to ensure quality control in ageing techniques. Validation of daily increment formation has been conducted for *C. undecimalis* in aquaculture and wild specimens (Tucker & Warlen

1986, McMichael et al. 1989, Joyeux et al. 2001) and, thus, was not performed in this study.

Age, Growth, and Hatch-date Analysis

Centropomus species greater than 100 mm SL were considered too large for effective sampling in this study, and therefore were not included in age and growth analysis. Growth of centropomids was determined by otolith-derived age estimates and length data (*C. parallelus n* = 168, *C. undecimalis n* = 113). Length-length conversion regression (SL & TL) relationships were calculated for comparison with other studies conducted on *C. undecimalis*. Length-frequency histograms for *C. parallelus* and *C. undecimalis* were generated by categorizing lengths into 5-mm increments to determine the size distribution of juvenile centropomids sampled by species.

Linear regression was applied to otolith-derived age data to determine growth rates (*C. parallelus* n = 171, *C. undecimalis* n = 114) using the following equation:

1. *Standard length* = *slope***age* (days) + *y*-*intercept*

To complete hatch-date distributions, ages were also predicted for individuals with unreadable otoliths (*C. parallelus n* = 119, *C. undecimalis n* = 72). Equations predicting age of individuals were developed for each year (Table 4.3). Daily instantaneous growth was estimated utilizing an exponential model:

2. $L_t = L_0 e^{gt}$

Where L_t = length (mm SL) at time t (days); L_0 = the estimated length at hatching; g = the daily instantaneous growth coefficient; and t = otolith-derived age in days.

| | п | Linear Equation | r^2 | | | | | |
|------------------------|--------|--|-------|--|--|--|--|--|
| Centropomus parallelus | | | | | | | | |
| 2006 | 24 | $Predicted \ age = 1.1593SL + 34.644$ | 0.95 | | | | | |
| 2007/2009 | 141 | $Predicted \ age = 1.3756SL + 29.262$ | 0.83 | | | | | |
| 2008 | 4 | $Predicted \ age = 1.687SL + 36.148$ | 0.62 | | | | | |
| Centropom | us und | ecimalis | | | | | | |
| 2006 | 79 | $Predicted \ age = 0.8506SL + 38.124$ | 0.73 | | | | | |
| 2007 | 17 | $Predicted \ age = 0.9234SL + 29.838$ | 0.90 | | | | | |
| 2009 | 16 | <i>Predicted age</i> = $0.9335SL + 60.759$ | 0.21 | | | | | |

Table 4.3. Equations for predicting age of individuals with unreadable otoliths.

All statistical analyses were preformed on SPSS 17.0 (IBM Corp., Somers, New York, USA), and significance was accepted at the $\alpha = 0.5$ level. Temporal and spatial variation in environmental parameters was analyzed across year, season, and region using one-way analysis of variance (ANOVA); however, these analyses were not used to evaluate variations in growth due to unequal sampling effort across 2006 – 2009. Analysis of covariance (ANCOVA) was used to assess intra- and inter-annual variability of growth by comparing growth of each species captured across years (covariate: age).

Results

Centropomid Otolith Structure and Age Determination

Sagittal otoliths of *C. parallelus* and *C. undecimalis* were similar in appearance: elliptical in shape and concavo-convex with a deep sulcus on the medial surface. Otoliths from both species exhibited a rounded rostrum differing along the margins of the antirostrum and dorsal surface and the path of the sulcus groove. Thin transverse cross-sections of each otolith revealed a singular central primordia, followed by alternating translucent and opaque zones (Figure 4.1) indicating the formation of daily growth increments. The counting path of transverse-sectioned otoliths consisted of a dorso-ventral path from the core to increments that were followed to the sulcus, continuing counts to the otolith edge.

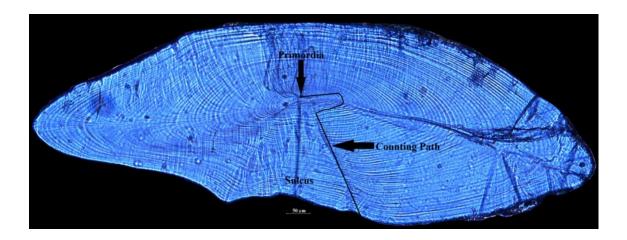


Figure 4.1. Transverse, polished section of Centropomus parallelus otolith (29 mm SL; 67 d).

Catch Composition

Juvenile centropomids collected from Texas coastal waters during 2006 - 2009 (n = 474) were used for age and growth analysis (Table 4.4). Only 284 otoliths (C. *parallelus n* = 169, C. *poeyi n* = 2, and C. *undecimalis n* = 113) were included in otolith microstructure analysis (Table 4.5). Seven otoliths were excluded from the analysis because of reader disagreement while the remaining otolith complement (n = 185) was either unreadable or destroyed during the polishing process. Quality control of reader accuracy indicated high reader agreement between the primary reader and the second independent reader based upon linear regression:

| | Upper | | | | | | | | |
|----------------|-------|---------|-----|----------|----|---------|------|---------|--|
| | 2 | 2006 | | 2007 | | 2008 | 2009 | | |
| | n | Range | п | Range | п | Range | п | Range | |
| C. parallelus | 5 | 27 - 32 | 0 | - | 0 | - | 6 | 20 - 69 | |
| C. undecimalis | 1 | 27 | 0 | - | 0 | - | 0 | - | |
| | | | | Midd | le | | | | |
| | 2006 | | | 2007 | | 2008 | 2009 | | |
| | n | Range | п | Range | п | Range | n | Range | |
| C. parallelus | 6 | 16 - 90 | 25 | 48 - 95 | 6 | 45 - 65 | 9 | 35 - 79 | |
| C. undecimalis | 9 | 34 - 61 | 0 | - | 0 | - | 7 | 49 – 78 | |
| | | | | Lowe | er | | | | |
| | 2 | 2006 | | 2007 | | 2008 | | 2009 | |
| | n | Range | п | Range | п | Range | п | Range | |
| C. parallelus | 24 | 12 - 47 | 207 | 10 - 76 | 0 | - | 0 | - | |
| C. poeyi | 0 | - | 2 | 52, 55 | 0 | - | 0 | - | |
| C. undecimalis | 112 | 14 - 87 | 34 | 12 - 100 | 0 | - | 21 | 48 - 94 | |

 Table 4.4. Number, size range, and capture year of all juvenile centropomids used in age structure and growth analysis. Size range given in millimeters of SL.

 Table 4.5. Number, size range, and capture year of the 284 otoliths used in age structure and growth analysis. Size range given in millimeters of SL.

| | Upper | | | | | | | | |
|----------------|-------|---------|-----|---------|-----|---------|------|---------|--|
| | | 2006 | 2 | 2007 | | 2008 | 2009 | | |
| | п | Range | n | Range | п | Range | n | Range | |
| C. parallelus | 3 | 27 - 32 | 0 | - | 0 | - | 5 | 20 - 69 | |
| C. undecimalis | 1 | 27 | 0 | - | 0 | - | 0 | - | |
| | | | | Mid | dle | | | | |
| | 2006 | | 2 | 2007 | | 2008 | 2009 | | |
| | n | Range | п | Range | n | Range | n | Range | |
| C. parallelus | 6 | 16 - 90 | 16 | 48 - 95 | 4 | 45 - 65 | 5 | 35 - 49 | |
| C. undecimalis | 6 | 70 - 90 | 0 | - | 0 | - | 4 | 49 - 61 | |
| | | | | Low | er | | | | |
| | | 2006 | 2 | 2007 | | 2008 | | 2009 | |
| | n | Range | п | Range | п | Range | n | Range | |
| C. parallelus | 15 | 13 - 47 | 115 | 10 - 76 | 0 | - | 0 | - | |
| C. poeyi | 0 | - | 2 | 52, 55 | 0 | - | 0 | - | |
| C. undecimalis | 72 | 14 - 72 | 17 | 12 - 83 | 0 | - | 12 | 48 – 91 | |

Centropomid Length and Age Distribution

Standard length of centropomids examined for age and growth (Figure 4.2) ranged from 10 to 100 mm (*C. parallelus*: 10 to 95 mm SL, mean 32.6, SD = 17.5; *C. undecimalis*: 12 to 100 mm SL, mean 46.6, SD = 20.1). Intra-annual differences in mean length of centropomids were observed across *C. parallelus* (ANOVA, p < 0.001) and *C. undecimalis* (ANOVA, p < 0.001); smallest mean lengths were observed in September for *C. parallelus* (24.4 mm SL, SD = 20.3) and October for *C. undecimalis* (39.3 mm SL, SD = 18.2). Largest individuals of both species were captured in March (*C. parallelus*: 66.5 mm SL, SD = 17.7; and *C. undecimalis*: 62.5 mm SL, SD = 11.0).

Centropomid ages ranged from 36 to 168 d (*C. parallelus* 36 to 168 d, mean = 74.6, SD = 26.0; *C. undecimalis* 37 to 164 d, mean = 80.2, SD = 24.5). Intra-annual differences in mean ages of centropomids were observed across species, *C. parallelus* (ANOVA, p < 0.001) and *C. undecimalis* (ANOVA, p < 0.001); youngest mean ages corresponded to length distributions (*C. parallelus*: 59.4 d, SD = 29.4, September; and for *C. undecimalis*: 67.6 d, SD = 14.7, October). Oldest centropomids for both species were captured in March (*C. parallelus*: 120.5 d, SD = 24.7; *C. undecimalis*: 119.3 d, SD = 17.4). The length-length regressions for *C. parallelus* and *C. undecimalis* were significantly different (ANCOVA, intercepts test, p < 0.001); relationships between SL and TL are presented in Table 4.6.

| | $\mathbf{Y} = \mathbf{a} + \mathbf{b}\mathbf{X}$ | | | | | | | | |
|----|--|-----|----------------|--------|-------|-------|--|--|--|
| Y | Х | n | Species | а | В | r^2 | | | |
| SL | TL | 277 | C. parallelus | -0.124 | 0.773 | 0.99 | | | |
| SL | TL | 188 | C. undecimalis | 0.277 | 0.776 | 0.99 | | | |
| TL | SL | 277 | C. parallelus | 0.379 | 1.288 | 0.99 | | | |
| TL | SL | 188 | C. undecimalis | 0.021 | 1.278 | 0.99 | | | |

Table 4.6. Relationship between SL and TL of Centropomus parallelus and Centropomus
undecimalis <100 mm SL.</th>

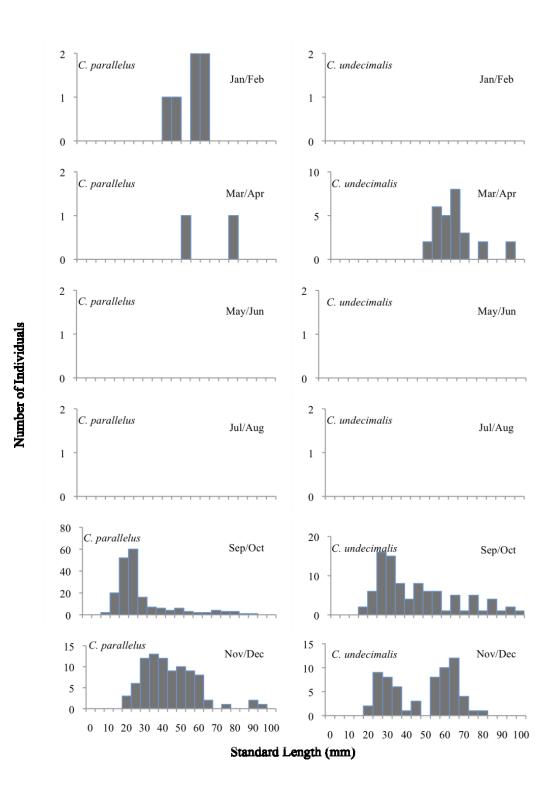


Figure 4.2. Bimonthly length frequency distribution of *Centropomus parallelus* and *Centropomus undecimalis* from 2006 through 2009.

Age and Growth

Centropomus parallelus growth rate was similar (0.61 mm d⁻¹, r^2 = 0.83) during 2007 (n = 131) and 2009 (n = 10; ANCOVA slopes p = 0.397, ANCOVA intercept p = 0.335). Inter-annual variation (Figure 4.3, 4.4) in *C. parallelus* growth was detected in 2006 (n = 24, 0.82 mm d⁻¹, r^2 = 0.95) and 2008 (n = 4, 0.37 mm d⁻¹, r^2 = 0.63). A linear growth equation was fitted to length-age data to produce an overall growth description for all years *C. parallelus* were captured:

4.
$$SL = 0.6026 * age - 12.277$$
 [$n = 169, r^2 = 0.84$]

Centropomus undecimalis displayed inter-annual variation in growth across all years sampled (ANCOVA slopes p < 0.001; Figure 4.5, 4.6). Growth of *C. undecimalis* in 2006, based on the largest number (n = 79) of otoliths examined, was 0.86 mm d⁻¹ ($r^2 = 0.73$). This species' highest growth rate occurred in 2007 ($n = 17, 0.97 \text{ mm d}^{-1}, r^2 = 0.90$) while 2009 yielded the lowest ($n = 16, 0.22 \text{ mm d}^{-1}, r^2 = 0.21$). Overall growth of juvenile *C. undecimalis* was described by the linear equation:

5.
$$SL = 0.6227 * age - 4.1629$$
 [$n = 112, r^2 = 0.70$]

Centropomus parallelus data from 2007/2009 were further analyzed to examine the influence of geographic location on growth from three different regions (upper, middle, lower coast). No significant differences were detected in 2007/2009 *C. parallelus* growth across these regions (ANCOVA slopes p = 0.150, ANCOVA intercept p = 0.636). Geographical influence on growth for 2006 *C. parallelus* was not detected among regions sampled (ANCOVA slopes p = 0.092, ANCOVA intercept p = 0.097). Collections in 2008 were all made at a single location (Aransas Pass); consequently, the

influence of geographical distribution could not be assessed. No geographic or intraannual effect was detected for *C. undecimalis* (ANCOVA slopes p = 0.081, ANCOVA intercept p = 0.069).

Hatch dates for both *Centropomus* species, based on otolith-based and predicted age, indicate centropomids captured in Texas are the result of spawning that occurs from late May to early December. A unimodial hatch-date distribution was observed for *C. parallelus*, represented by a single peak in late August (Figure 4.7). Alternatively a bimodial hatch-date distribution was observed for *C. undecimalis*, with a major peak in early September and a minor peak in mid-November.

Centropomus poeyi Age Characteristics

Three *Centropomus poeyi* were captured in two locations (Aransas Pass, n = 1; Laguna Vista, n = 2) in 2007. Specimen identification was based on genetic analysis of 16s mtDNA described in Chapter II. On October 26, a 62 mm SL *C. poeyi* was captured in Aransas Pass (San Patricio County). Age of this specimen was not determined due to destruction of both sagittal otoliths during the polishing process. Two other *C. poeyi* were captured in Laguna Vista (Cameron County) on November 10 that measured 52 and 55 mm SL (aged 90 and 79 d, respectively). Hatch dates for Laguna Vista specimens were August 12 and 23.

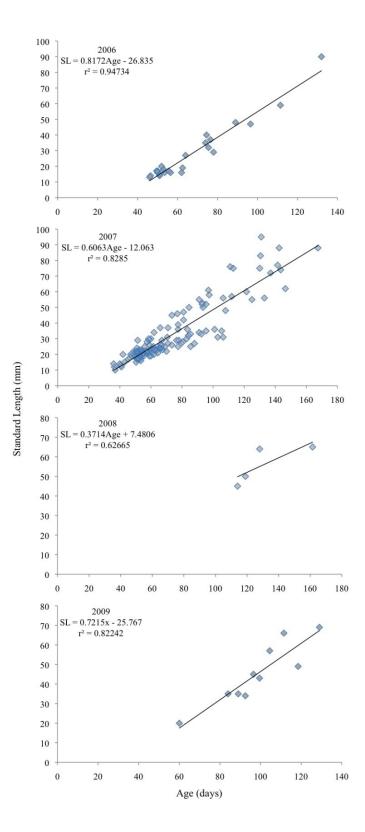


Figure 4.3. Size at age relationships by year for *Centropomus parallelus* (<100 mm SL) from Texas.

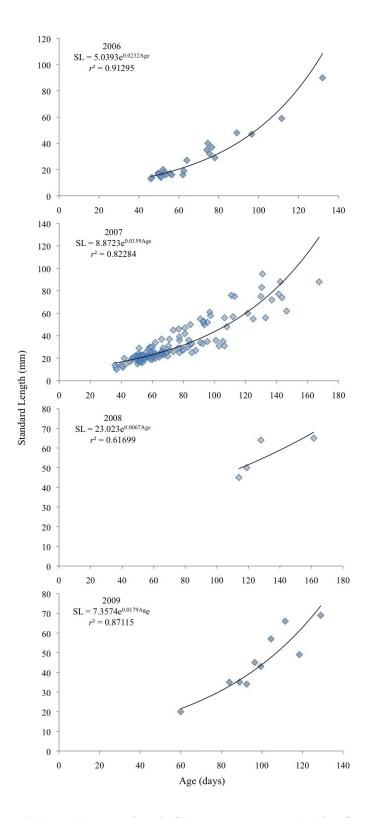


Figure 4.4. Exponential growth comparison in SL among years sampled for *C. undecimalis* (<100 mm SL) from Texas.

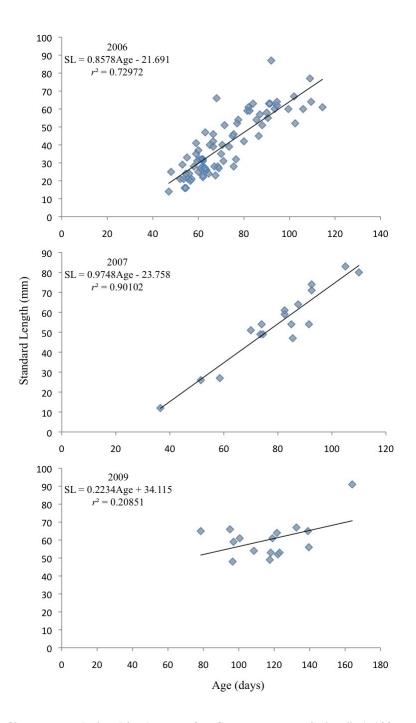


Figure 4.5. Size at age relationships by year for *Centropomus undecimalis* (<100 mm SL) from Texas.

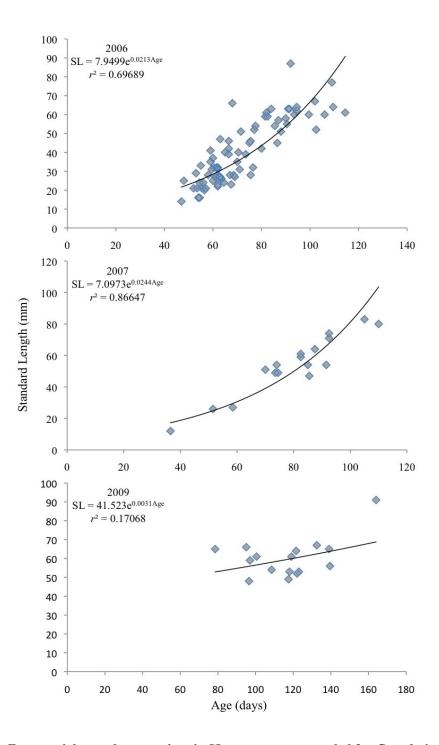


Figure 4.6. Exponential growth comparison in SL among years sampled for *C. undecimalis* (<100 mm SL) from Texas

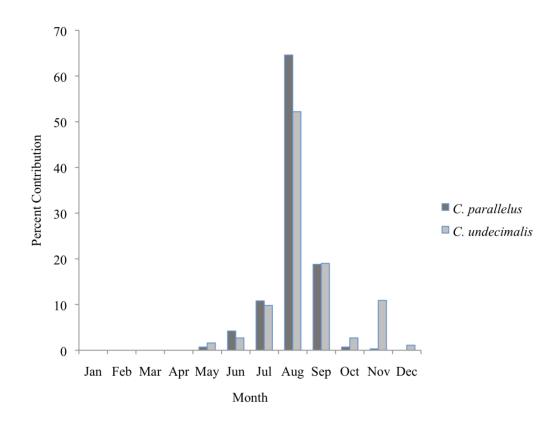


Figure 4.7. Monthly hatch-date distribution for *Centropomus* species from Texas coastal waters.

Discussion

All specimens in age and growth analysis were captured via unmethodical sampling conducted at opportunistic times of the year that would yield highest abundances. Mortality estimates based on age and abundance (i.e., catch curves) were not determined due to discontinuity in capture efforts. Most centropomids from upper and middle coast collection sites were captured via single-day sampling trips that allowed for repeated effort but resulted in low yield (upper n = 12, middle n = 62). Lower coast collection sites, not regularly sampled due to logistical limitations associated with the distance and time required to get to these sites, yielded the highest catch of centropomids (n = 399). Therefore, the ability for this study to quantify growth rates other than differences among years was limited. The finding that *C. parallelus* exhibited significantly higher growth in 2006 (n = 24) than it did in 2007 (n = 131) may be the result of a smaller sample size in 2006. However, differences in instantaneous growth rates for specimens of similar age (46 to 56 days) across 2006 and 2007 were negligible (0.06 mm d⁻¹). Additionally, comparison of overall growth rate for both species yielded similar slopes (ANCOVA, slopes, p = 0.832) yet different intercepts (ANCOVA, intercepts, p < 0.001).

The smallest specimens captured (10 to 15 mm SL) for both species in this study indicate that larvae and early juveniles along the Texas coast spend approximately the first 30 to 40 days in the plankton (planktonic larval duration) before settling into nursery grounds. This finding is not much different from that of (Gilmore et al. 1983), (McMichael et al. 1989), (Peters et al. 1998a), and (Adams & Wolfe 2006) who concluded that settlement sizes range from 13 to 25 mm SL for *C. undecimalis*. However, this study and that of the aforementioned studies were conducted years apart and on opposite sides of the GOM; additionally, differences observed could be accounted for by sampling gear, temperature regimes, and habitats. Spawning activity has been documented for higher salinity waters of inlets, mouths of coastal rivers, and secondary embayments in Florida (Tolley et al. 1987, Tucker & Campbell 1988, Taylor et al. 1998) and could support inshore spawning of centropomids in Texas. The hypersaline environment of Texas' LLM is a possible inshore spawning ground that could provide quick access to proximal settlement habitats for juvenile centropomids. The only major freshwater source for the LLM is the Arroyo Colorado, a distributary of the Rio Grande no longer connected to the river. The Arroyo Colorado serves as a major drainage of the Lower Rio Grande Agricultural District (Onuf 1996) and seemingly provides characteristic *C. undecimalis* habitat described by (McMichael et al. 1989) and (Fore & Schmidt 1973). Alternatively, it is anticipated that centropomids in Texas spawn near inlets such as the Mansfield Channel, Brazos Santiago Pass, or the Rio Grande, thus following Florida's centropomid spawning pattern.

Centropomus parallelus Growth

Determination of growth rate of smallest *C. parallelus* captured was relevant only for 2007 catches. Length-specific growth rate of the 2007 *C. parallelus* (36 to 46 days old ranging from 10 to 20 mm SL) averaged 0.27 mm d⁻¹. These *C. parallelus* were considered settlement sized according to (Peters et al. 1998a) who categorized settlement size for *C. undecimalis* as 15 mm SL. Although inter-annual differences in growth was observed, variability in seasonal growth was not observed for a single yearclass of centropomid. Nonetheless, four *C. parallelus* captured in January 2008 (winter) displayed a significantly lower growth rate (ANCOVA, slopes, P < 0.001; 0.37 mm d⁻¹) when compared to that of conspecifics sampled in other years. This estimate of winter growth rate, however, should be viewed with caution owing to the small sample size involved. However, this species' stenothermic nature (Marshall 1958) and determination of seasonally influenced growth rates of *C. undecimalis* (McMichael et al. 1989) render it plausible that all centropomids achieve faster growth over the summer. Although a literature review provided no estimates of growth rates in *C. parallelus*, eight aquaculture trials (Cerqueira et al. 1995, Alvarez-Lajonchère et al. 2002b, Alvarez-Lajonchère et al. 2004, Alves et al. 2006, Corrêa & Cerqueira 2007, Tsuzuki et al. 2007b, Tsuzuki et al. 2008, Ribeiro & Tsuzuki 2010) reported size at age data for *C. parallelus* (Table 4.2). Comparisons between findings of the current study and those from the eight trials show variable growth for certain age classes (Table 4.7). The apparent growth discrepancy between *C. parallelus* in Texas versus that recorded during aquaculture trials may be a result of several factors including wild versus laboratoryreared stock, genetic differentiation, water temperature, and food availability.

| Age (days) | Texas coast | | Aquaculture study |
|------------|-------------|-------|-----------------------------------|
| 48 | 16.6 | 14.2 | (Alves et al. 2006) |
| 56 | 21.5 | 22.7* | (Corrêa & Cerqueira 2007) |
| 66 | 27.5 | 29.7 | (Cerqueira et al. 1995) |
| 76 | 33.5 | 26.4 | (Tsuzuki et al. 2007b) |
| 88 | 40.8 | 57.6 | (Alvarez-Lajonchère et al. 2002b) |
| 90 | 42.0 | 52.4* | (Alvarez-Lajonchère et al. 2004) |
| 106 | 51.6 | 32.1 | (Tsuzuki et al. 2007b) |
| 126 | 63.7 | 38.2 | (Tsuzuki et al. 2007b) |
| 156 | 81.7 | 70.0 | (Tsuzuki et al. 2008) |

 Table 4.7. Comparison of size at age data from 2007/2009 and various aquaculture studies of *Centropomus parallelus* (size in mm SL).

* TL converted to SL from equations given in Table 4.5

Centropomus undecimalis Growth

Estimated growth of *C. undecimalis* along the Texas coast displayed variable rates across every year sampled. This could be due to small sample sizes during 2006, 2007, and 2009 (n = 76, 17, 16, respectively). Growth rate of smallest *C. undecimalis* (47 to 57 days, 14 to 29 mm SL) averaged 0.51 mm d⁻¹ and was well above the instantaneous growth rate for equally sized *C. parallelus* (0.32 mm d⁻¹ and 0.39 mm d⁻¹, respectively) for 2007 and 2006. This difference could be due to the larger size typically attained by *C. undecimalis* and an indication of faster growth (Rivas 1986, Tringali et al. 1999b). Failure to observe seasonal variation in growth in any year-class was probably due to lack of year-round capture. The winter capture of *C. undecimalis* in 2009 did not provide viable data to establish reduced growth rates ($r^2 = 0.21$); however, it could be assumed that slower growth rates occur during winter months.

Comparison of growth rates of *C. undecimalis* in this study with those of similar investigations revealed that estimated growth rates for 2006 constituents from Texas (0.85 mm d^{-1}) were similar to values reported in the literature. Faster growth rates were reported (through length frequency distribution analysis) for *C. undecimalis* for Ten Thousand Island, Florida (Fore & Schmidt 1973) and the Indian River Lagoon, Florida (Gilmore et al. 1983; 1.0 to 0.9 mm d⁻¹, respectively). Otolith-based estimates of SL growth for *C. undecimalis* from Tampa Bay, Florida (McMichael et al. 1989) varied between 0.5 and 1.0 mm d⁻¹.

Factors on Centropomid Growth

The habitat description for *C. undecimalis* by (McMichael et al. 1989) resembles that for habitats in which Texas centropomids were collected during this study. However, aside from inter-annual differences, this study did not detect differences in growth of centropomids among regions that could be temperature related. Upper and middle coast sites, when sampled, did not vary significantly in their temperature regimes (ANOVA, p = 0.551). However, comparison of lower coast water temperatures to the aforementioned regions (independently and combined) yielded statistical significance (ANOVA, p < 0.001). The impact of salinity on growth in this study was not assessed.

Temperature's influence on centropomid growth rates has been assessed under aquaculture trials for *C. parallelus* and *C. undecimalis* (Zarza-Meza et al. 2006) and with wild *C. undecimalis* (McMichael et al. 1989). These studies considered temperature a determinant factor in yielding growth variation (Neidig 2000, Alvarez-Lajonchère & Tsuzuki 2008, Cerqueira & Tsuzuki 2009), also observed in this study's capture of *C. parallelus* during 2008. However, this study's lack of year-round sampling and associated hydrographic data limits the ability to assess variability in growth across regions.

Hatch-date Distribution

The wide distribution of hatch dates for both species reflects a protracted spawning period. These species spawn earlier than Florida's *C. undecimalis* (Tucker & Campbell 1988, McMichael et al. 1989, Taylor et al. 1998) and Mexico's *C. parallelus* (Chavez 1963). Termination of spawning in Texas occurs in November and is similar to

that for Florida and Mexico conspecifics, and this implies that spawning behavior of *C*. *parallelus* and *C. undecimalis* throughout their North American range is generally similar. Initiation of spawning might be temperature dependent (Figure 4.8), when highest spawning peaks coincide with or near yearly maximum temperatures. However, (Chapman 1987), (Peters et al. 1998b), and (Yanes-Roca et al. 2009) reported that *C. undecimalis* in Florida spawned on either side of the new and full moon, correlating with stronger tides. This study found that spawning activity of 2007 *C. parallelus* and 2006 *C. undecimalis* corresponded with moon phase (Figure 4.9). Additionally, the bulk of the spawning during this period alternated between species, with the majority of C. *parallelus* hatched under a new moon whereas most *C. undecimalis* hatched under a full moon.

Conclusion

The present study has provided knowledge of centropomid growth and spawning periods in Texas that is considered prerequisite to strategic management of fisheries populations. Additionally, identification of growth characteristics is important to generate growth models that can be used to better understand population dynamics and facilitate effective management of these species. The findings of this study revealed that growth patterns for *C. parallelus* and *C. undecimalis* do not differ greatly from those of Florida *C. undecimalis* growth studies; however, further work is necessary to fully understand the settlement period of centropomids in Texas estuaries. Identifying spawning locations and the dynamics of spawning frequency of these species through acoustic telemetry tags and histological analysis should aid in discovery of other

proximal settlement habitats.

The comparisons made in this study of centropomid growth and hatch-date distributions should be further investigated due to the lack of year round sampling and the variations found among years sampled. Findings generated by the present study should be considered a starting point for TPWD to further pursue research on centropomid age growth characteristics. Even implementation of a small-scale mark and recapture project could aid TPWD in further understanding the growth, habitat use, and possible spawning characteristics of *Centropomus* species in Texas. Moreover, examination of young-of-the-year and juvenile mortality, linkages between spawning grounds, and additional larval recruitment locations should be the next step in the research.

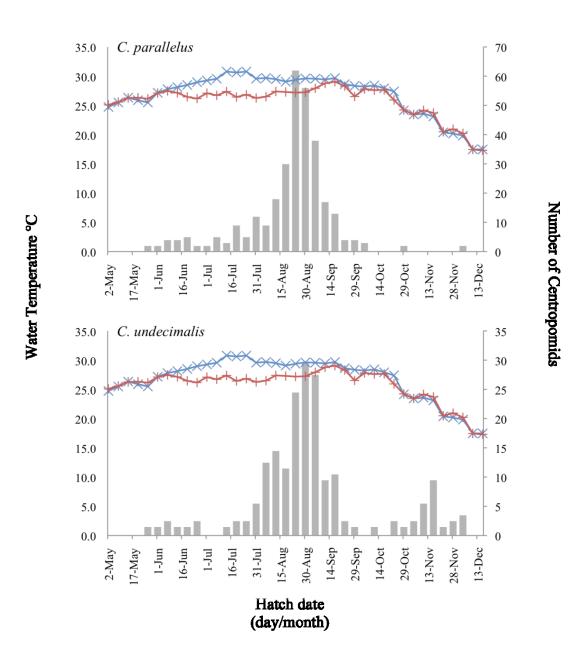


Figure 4.8. Weekly hatch-date distributions for *C. parallelus* and *C. undecimalis* in Texas. Comparisons shown are for mean weekly water temperatures from Aransas Pass (x) and South Padre Island (+) during 2006 - 2009.

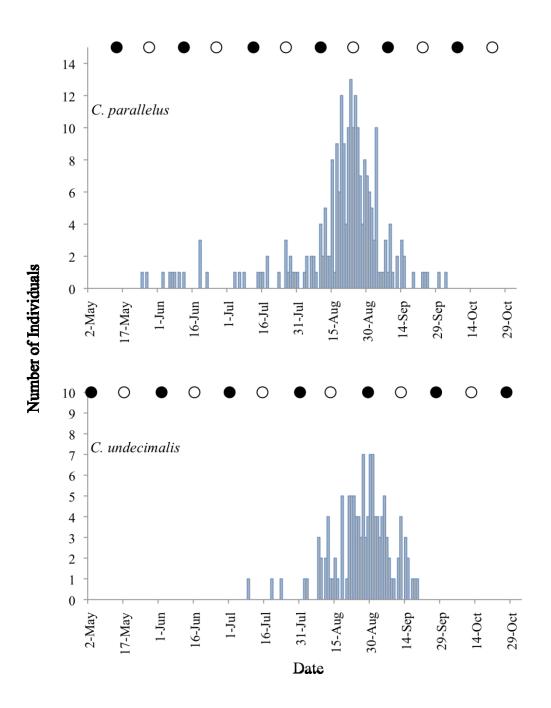


Figure 4.9. Daily hatch date distributions for *C. parallelus* (2007) and *C. undecimalis* (2006) collected from Texas coastal waters and moon phase (● = full moon; ○ = new moon) during their collection.

CHAPTER V

SUMMARY

- Genetic analyses of 548 Texas captured centropomids resulted in successful identification of *C. parallelus*, *C. poeyi*, and *C. undecimalis*.
- The capture of three *C. poeyi* is the first known occurrence of this species in Texas waters.
- AMOVA for D Loop sequences revealed significant differences between Texas and Florida/Costa Rica populations.
- Morphological identification key developed by this study should aid fisheries biologist in correctly identifying *Centropomus* species.
- Geographic distribution between the two dominant species varies with *C*.
 parallelus capture range extending from the Rio Grande to Galveston, whereas
 C. undecimalis ranged was limited from the Rio Grande to Palacios.
- Faster growth rates were observed for *C. undecimalis* versus *C. parallelus* in Texas, additionally growth rates for Texas and Florida *C. undecimalis* assemblages.
- Texas spawning season ranges from August to September for *C. parallelus* and from August to November for *C. undecimalis*.

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APPENDIX A

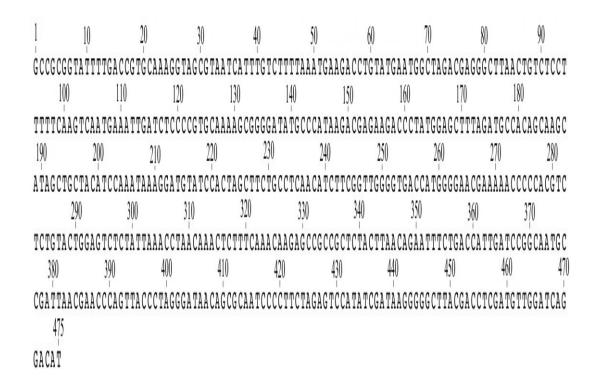


Figure A-1. Consensus sequence of the 475bp segment of Texas captured *Centropomus parallelus* 16s mtDNA gene.

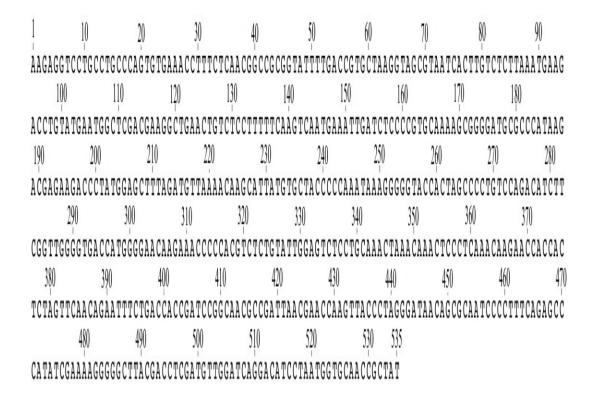


Figure A-2. Consensus sequence of the 535bp segment of Texas captured *Centropomus poeyi* 16s mtDNA gene.

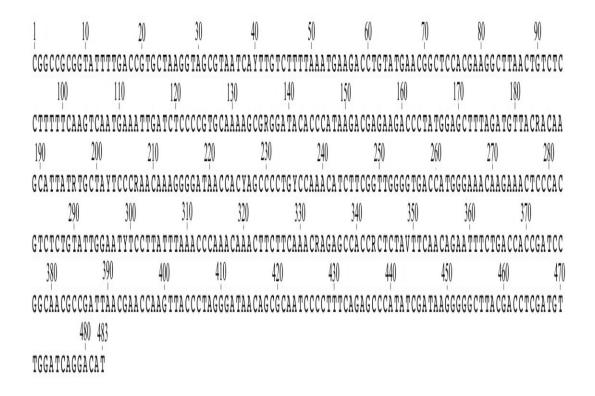


Figure A-3. Consensus sequence of the 483bp segment of Texas captured *Centropomus undecimalis* 16s mtDNA gene.

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| | 4 | ***** | | 2222222222 | 44444444 | 5555555556 | | 00000000000 | 0000000000 | - | **** | ********* | ********* | | ********* | | | |
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| 1LowerTexas | | | | | | | | | | | | | | | | GTATGCCCCT GA | | |
| 2LowerTexas | | ••••• | ••••• | ••••• | | ••••• | ••••• | ••••• | ••••• | ••••• | ••••• | •••- | G | ••••• | ••••• | | ••••• | |
| 3LowerTexas | C | | ••••• | | | ••••• | ••••• | | ••••• | | ••••• | C | ••••• | ••••• | ••••• | | | |
| 4LowerTexas | | | | | | | | | | | | | | | | | | |
| 5LowerTexas | T | | | | | | T | C | | | | T | | .G | | | | A |
| 6LowerTexas | | | | | | | T | | | | | | | .GT | | | | A |
| 7LowerTexas | | | | | T | | | | | | | | | | | | | |
| 8LowerTexas | | | | | | | | | | | | | | | | | | |
| 9LowerTexas | | | | | | | | | | | | | | | | | | |
| 10LowerTexas | | | | | | | T | C | | | C | | | .G | | G A. | | A |
| 11LowerTexas | T | | | | C | | T | C | | | | | | .G | | | | A |
| 12LowerTexas | | | | | | | | | | | | | | | | | | |
| 13LowerTexas | | | | | | | | | | | | | | | | | | |
| 14LowerTexas | | | | | | | | | | | | | | .G | | | | |
| 15LowerTexas | | | | | | | | | | | | | C. | | | | | |
| 16LowerTexas | | | | | | | T | | | | | | | .G | | | | Å |
| 17LowerTexas | | | | | | | T | | | | | | | .GT | | | | A |
| 18LowerTexas | | | | C | | | T | | | | | | | .GC.T | | | | A |
| 19LowerTexas | | | | | T | | C | | | | C | | | T | | | | |
| 20LowerTexas | T | | | | | | T | C. | | | C | | Τ | .G | | | | A |
| 21LowerTexas | | | | | | | | C | | | | •••- | | | | | | |
| 22LowerTexas | | | | | | | | | | C | | | | | | | | |
| 23LowerTexas | T | | | | | | | | | T | | | | | | | | |
| 24LowerTexas | | | | | | | | | | | | | | | | | | |
| 25LowerTexas | | | | | | | .A | | | | | | | | | | | |
| 26LowerTexas | | | Å | | | | AT.A | | | | | | | | | T | | A |
| 27LowerTexas | G | | | | | | T | | | | | | .0 | .G | | | | |
| 28LowerTexas | | | | | | | | | | | | | | | | | | |
| 29LowerTexas | | | | | | | T | C | | T | | C | | .GT | | | | A |
| 30LowerTexas | | | | | | | | | | | | | | | | | | |
| 31LowerTexas | ····T···· | | | | | | ·····T·· | C | | | C | | | .GT. | | | ····T··· ·· | Å |
| 32LowerTexas | | | ••••• | | | ••••• | | | | | | | | | | | | |
| 33LowerTexas | G | C. | | | | | | | | | | •••- | | | | | | |
| 34LowerTexas | ····T···· | | | | | | ·····T·· | C | | | | •••- | | .G | | | ····T··· ·· | Å |
| 35LowerTexas | C | | | | | | | | | | | | | T. | | | | |
| 36LowerTexas | | | | | | | | | | C | | | | | | | | |
| 37LowerTexas | | | | | | | | | | | | | | T | | | | |
| 38LowerTexas | ····T····· | | | | | | T | | | ····A····· | | | T | | | | | A |
| 39LowerTexas | ····T···· | | | | | | .AT | C | | | | ····T····· | | .6 | | | | A |
| 40LowerTexas | | | | | | | .A | | | | | | | | | | | |
| 41LowerTexas | | | | | | | | | | | | | .0 | | | | | |
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Figure A-4. Consensus alignment of 181bp long segment of the D – loop of 82 Centropomus parallelus.

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| | 1 | 1111111112 | 222222222223 | 3333333334 | 444444445 | 5555555556 | 6666666667 | 7777777778 | 888888888 | - | | | | | | | | 7777777778 8 |
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| 42LowerTexas | | | | | | | | | | | | | | | | | | |
| 43LowerTexas | | | | | | | | | | | | | | T. | | | | |
| 44LowerTexas | | | | | | | | | | | | | | | | | | |
| 45LowerTexas | | | | | | | | | | | | | | | | | | |
| 46LowerTexas | | | | | | | | | | | | | | T | | | | |
| 47LowerTexas | | | | | | | | | | | | | | | | | | |
| 48LowerTexas | | | | | | | | | | | | | | | | | | |
| 49LowerTexas | T | | | | | | | | | | | | | | | | | |
| 50LowerTexas | | | | | | | T | | | | | ····T····· | | .GT | | | | A |
| 51LowerTexas | | | | | | | | | | | ••••• | | | | | ••••• | | |
| 52LowerTexas | | | G | | | | | | | | | | | | | ••••• | | A |
| 53LowerTexas | | ••••• | ••••• | ••••• | | ••••• | | | | | | | | | ••••• | ••••• | ••••• | ••••• |
| 54LowerTexas | ·····T····· | ••••• | ••••• | ••••• | | | | | | | ••••• | ····T····· | | .6 | ••••• | ••••• | ••••• | |
| 55LowerTexas | ••••• | ••••• | ••••• | ••••• | | | | | | C | ••••• | •••- | | ••••• | | ••••• | ••••• | |
| 56LowerTexas | ••••• | ••••• | ••••• | | | ••••• | | | | | ••••• | •••• | t | ····· | | ••••• | ••••• | |
| 57LoverTexas | ••••• | ••••• | ••••• | A | | | | | | | ••••• | t | 1 | .6 | | ••••• | ••••• | A |
| 58LowerTexas 59LowerTexas | | | ••••• | | | | | | | | | | ••••• | і. с т | | ••••• | | |
| 59LowerTexas 60LowerTexas | | | ••••• | | | | | | | | | | | .0ا ۸ | | ••••• | ••••• | |
| 61LowerTexas | | ••••• | ••••• | | | | | | | | | | | A | | ••••• | ••••• | |
| 62LowerTexas | | | | | | | | | | | | | | | | ••••• | с | |
| 63LowerTexas | | | | | | | | | | | | | | | | | | |
| 64LowerTexas | | | | | | | | | | | | | г | т | | | | ····· · |
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| 66LowerTexas | | | | | | | | | | | | C | Τ | .G | | | | |
| 67LowerTexas | | | | | | | | | | | | | | | | | | |
| 68LowerTexas | | | | | | | | | | | | | | T | | | | |
| 69LowerTexas | T | | | | | | T | | | | | T | | .G | | | G. | |
| 70LowerTexas | | | | | | | | | | | | | | | | | | |
| 71LowerTexas | | | | | | | | | | | | | | | | | | |
| 72LowerTexas | | | | | | | T | | | | | | TA | .GT | | | | A |
| 73MiddleTexas | | | | | | | T | | | C | | | | .GT | | | | A |
| 74MiddleTexas | | | | | | | | | | | | | | | | | | |
| 75MiddleTexas | | | | | | | T | | | | | | | .GT | | | | A |
| 76MiddleTexas | | | | | | | | | | | | ···C | | | | | | |
| 77MiddleTexas | | | | | | | | | | | | | | | | | | |
| 78MiddleTexas | | | | | | | | | | | ••••• | ····T····· | | .G | | ••••• | | ····· |
| 79MiddleTexas | | | | | | | T | | | | | | | .GT | | ••••• | | A |
| 80MiddleTexas | | | ••••• | | | | | | | | | | | | | | | |
| 81UpperTexas | ••••• | ••••• | ••••• | | | | | | | | | | | | ••••• | ·····.T. | ••••• | A |
| 82UpperTexas | ••••• | ••••• | ••••• | ••••• | C | | ••••• | ••••• | ••••• | ••••• | ••••• | •••- | ••••• | ••••• | ••••• | ••••• | ••••• | ••••• |

Figure A-4. Continued.

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| 1234567890 1234567890 1234567890 1234567890 1234567890 123 | | | |
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| | G | | |
| | .A | | |
| | TGGA | G ATT A | CA |
| 6Florida | | | |
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| 8Florida | G | | |
| 9Florida | | | |
| | | | |
| | TG | | |
| | TG | | CA |
| | TGGA | G ATT A | TCAT TCA |
| 14LowerTexasTGCAA. | TG | CG ATT A | CA |
| 15LowerTexas | TG | TT A | |
| 16LowerTexasCTGCAA. | TG | TT A | CA |
| 17LowerTexas | TG | TT A | CA |
| 18LowerTexasTGCA | TG | G ATT A | CA |
| 19LowerTexasTGCAA. | TG | G ATT A | CA |
| 20LowerTexas | TG | | |
| 21LowerTexas | TG | TT A | CA |
| 22LowerTexas | TG | G ATT A | CA |
| 23LowerTexasC–T––GCA | TG | G ATT A | CA |
| 24LowerTexas | TG | | CA |
| 25LowerTexas | TG | G ATT A | CA |
| 26LowerTexas | TG | | CA |
| 27LowerTexas | TG | TT A | CA |
| 28LowerTexas | TG | G ATT A | CA |
| 29LowerTexas | TG | | CA |
| 30LowerTexas | TG | G ATT A | CA |
| 31LowerTexas | TG | | |
| 32LowerTexas | TG | GA ATT A | |
| 33LowerTexas | T | Т. А | CA |
| | T | | |
| | T | | TC TCA |
| | T | | |
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Figure A-5. Consensus alignment of 152bp long segment of the D – loop of 74 Centropomus undecimalis

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| 1 1111111112 222222223 3333333334 4444444445 5555555556 6666666666 | |
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| 38LowerTexas | |
| 39LowerTexas | |
| 40LowerTexas | |
| 41LowerTexas | |
| 42LowerTexas | |
| 43LowerTexasTGC | |
| 44LowerTexas | |
| 45LowerTexas | |
| 46LowerTexas | |
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| 49LowerTexas | |
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| 67LowerTexas | |
| 68LowerTexas | |
| 69MiddleTexas | |
| 70MiddleTexas | |
| 71MiddleTexas | |
| 72MiddleTexas | |
| 73MiddleTexas | |
| 74MiddleTexas | ATT ACA |
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Figure A-5. Continued.

VITA

Christopher Jacob Chapa

2809 Red Oak Lane Pearland, Texas 77584

texassnook@gmail.com

B.S., Marine Fisheries, Texas A&M University, 2007