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Taxonomy, Diversity, and Distribution Patterns of Portunid Crab Megalopae in the Northern Gulf of Mexico During Fall of 2003

Carley Rain Knight
University of Southern Mississippi

The University of Southern Mississippi

TAXONOMY, DIVERSITY, AND DISTRIBUTION PATTERNS OF PORTUNID CRAB MEGALOPAE IN THE NORTHERN GULF OF MEXICO DURING FALL OF 2003

by

Carley Rain Knight

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Approved:

Chet Rakocinski
Director

Sara LeCroy

Wei Wu

Joanne Lyczkowski-Schultz

Maureen Ryan
Dean of the Graduate School

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ABSTRACT

TAXONOMY, DIVERSITY, AND DISTRIBUTION PATTERNS OF PORTUNID CRAB MEGALOPAE IN THE NORTHERN GULF OF MEXICO DURING FALL OF 2003.

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The field of zooplankton biology contributes to more accurate stock assessments as well as to a greater understanding of the marine food web. However, adequate information for the invertebrate component of zooplankton is lacking compared to the ichthyoplankton component. In this thesis, identification of Portunidae (Crustacea: Decapoda) megalopae collected during the fall of 2003 from a NOAA SEAMAP cruise revealed 7 species and 11 morphs with 90% of the total density comprised of *Callinectes sapidus, Achelous gibbesii, Callinectes similis, Achelous spinicarpus,* and *Achelous* sp.I. Keys and detailed descriptions are provided along with photographs and morphological drawings for each morph to use for future identification. Spatially explicit maps and non-metric multi-dimensional scaling (NMDS) depicted geographic distributions and community structure during the study period. Mapping of NMDS coordinates illustrated distribution patterns for four community types of portunid megalopae as mainly distinguished by the differences in relative abundances of the most dominate morphs. This showed *Callinectes* species were predominantly located in the western GOM while *Achelous* species dominated the eastern GOM. Spatial representation of station locations and assemblages at station locations was illustrated through the maps generated by Geographic Information System (GIS) software. Examination of environmental data

associated with the plankton samples was accomplished via visual inspection of spatial maps to identify any clear spatial coherence and/or linkages relative to the density or presence of portunid crab larvae. Time of day of sampling and currents, including the Loop Current, had the most visible effect on larval densities and distributions.

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CHAPTER I

INTRODUCTION

Fisheries and Plankton

Many countries rely heavily on fisheries to support their economy (Adams, Hernandez, and Cato, 2004; Bailey, 1988; FAO, 2012; Jiddawi & Öhman, 2002). In 2010 global fisheries production was reported to be 148.5 million tons (FAO, 2012). These fisheries place immense pressure on populations of economically important species, exacerbating the effects of existing pressures from food trophic interactions, environmental variability, climate change, and habitat loss. Management of these fisheries aims to maintain sustainability of the stock and prevent population collapse (Botsford, Castilla, and Peterson, 1997). A major factor to consider in the assessment of fisheries stocks is the recruitment of the juveniles into the adult population. The recruitment of juveniles can bolster the stability of the population and the recovery of overfished populations. Supporting the recruitment of juveniles is the supply of earlier stage larvae produced by the adult population (Boylan and Wenner, 1993). Such dependent fisheries populations are termed recruitment limited (Victor, 1986). The supply of larvae can also be affected by other factors external to the population, including predation pressure and environmental effects (Queiroga, 1995). Early larvae of many marine and estuarine species are not retained within the adult habitat, but instead are planktonic and entrained within the open water zooplankton community, from which they must recruit at the appropriate time.

Planktonic Life Stages

Numerous estuarine and marine species including fishes and invertebrates have multipartite life histories involving planktonic larval stages. Pelagic life stages are advantageous for dispersal, high survival due to stable environmental conditions, minimal resource competition, and high gene flow (Gaines and Lafferty, 1995; Jablonski and Lutz, 1983; Jackson, 1986; Pralon et.al., 2012). Drawbacks of pelagic early stages include high predation pressure, the risk of starvation (cf., match-mismatch hypothesis), the risk of being transported too far from settlement grounds, and fitness costs for adults taxed with the production of numerous small eggs (Hart, 1995; Jackson and Strathmann, 1981). Breeding adults typically broadcast gametes or offspring into the water column based on lunar phases, tidal cycles, diel cycles, or environmental cues (Forward, 1987).

Environmental variables, including salinity, sea surface temperature, wind, currents, and chlorophyll-a, may affect the distribution of planktonic larvae by controlling its growth, feeding and behavior throughout the Gulf of Mexico (GOM). Depending on the life stage of the larvae, different combinations of environmental variables may be more or less suitable (e.g. salinity and temperature) (Pechenik, 1999). Wind and currents transport spawned eggs and larvae away from adult spawning habitats and can either retain the early stages near nursery habitats or sweep them further out into open waters (Anger, 2001). Sea surface temperature and salinity may correlate with the presence of larvae (Anger, 1991; Costlow and Bookhout, 1959). They have strong effects on the duration of life stages and mortality of laboratory reared decapod larvae (Anger, 1991; Costlow and Bookhout, 1959). Temperature also governs vital rates like mortality and metamorphosis (Anger, 1991). Changes in environmental conditions can

alter the number and duration of decapod larval stages, as well as determine when larvae settle out of the plankton into nursery habitats (Anger, 2001; Pralon et.al., 2012).

Zooplankton has been studied for decades in the GOM and Atlantic, with a majority of those studies focusing primarily on ichthyoplankton and/or a few commercially important invertebrate taxa (Dransfeld et al., 2009; Dudley and Judy, 1971; Kurata, 1970). The vast majority of planktonic stages of invertebrate species remain poorly known due to the lack of proper descriptions of their larval stages, as well as substantial changes in the accepted taxonomy of some genera. Moreover, the lack of knowledge required for matching larval and adult stages often leaves identified larval specimens nameless and the adult counterpart without a full life history description (Morgan et al., 1985; Rice and Kristensen, 1982). Research is especially lacking on decapod crustacean larvae. As a result, decapod studies tend to focus on the adult stage (Fransozo and Negreiros-Fransozo, 1987) or on better known commercially important species, such as the blue crab, *Callinectes sapidus* (Andryszak, 1979; Kordos and Burton, 1993; Nichols and Keney, 1963; Stuck and Perry, 1981). Historically, the study of larval decapods has been restricted to certain groups, such as dendrobrachiate shrimps (Cook, 1966; Heegaard, 1966), carideans (Haynes, 1985; Williamson, 1962), anomurans (Gore, 1973; Hart, 1937), and lobsters (Lewis et al., 1952; Robertson 1968). Although the adult stage for species within commercially important brachyuran family Portunidae are well known, very little is known about the larval stages in the GOM (Costlow and Bookhout, 1966; Fransozo and Negreiros-Fransozo, 1987; Negreiros-Fransozo et al., 2007). The lack of information pertaining to early stages of many portunid crabs underscores the need for larval descriptions, as well as information on stage durations over the entire developmental series.

Because of their worldwide distribution and high abundance, portunid crabs form the base of a globally important fishery and are commercially exploited in several regions throughout Europe, Asia, and the Americas (Junior, Negreiros-Fransozo, and Fransozo 2008). Portunid fisheries exploit both wild caught specimens and crabs produced via aquaculture for the rapidly increasing soft shell crab market (Freeman and Perry, 1987; Perry et al., 1990). One of the most heavily fished species is the blue crab, *Callinectes sapidus*, which sustains various fisheries across the Atlantic and GOM coasts of the United States, with the Chesapeake Bay fishery being one of the largest (CapLog, 2011). The economic value and need for sustainable management practices for portunids make it important to study the early life histories of its component species, as well as factors influencing the distribution and abundance of the larvae, both of which are for more-informed efficient management of the portunid fishery.

Crabs within the family Portunidae are known as the "swimming" crabs, a name referring to their ability to swim up into the water column assisted by the paddle-shaped terminal segment of the fifth leg. Portunid crabs are ubiquitous around the world and comprise 27 extant genera containing hundreds of species, the majority of which are present in the Pacific and Indian Oceans. Only 11 genera and 29 species of portunids are recorded from the GOM (Felder and Camp, 2009). Adult habitats range from near shore estuarine to offshore open water and deep benthic environments. Most portunid species inhabit inshore habitats as adults and move to more offshore areas such as mouths of inlets and open waters to spawn (Smyth, 1980). Spawning for the family as a whole can occur year round, but each species spawns within certain months. For portunid species occurring in the GOM, peak spawning typically occurs between May and September

(Williams, 1984), and the resultant pulses of larvae are critical for commercially important populations.

Planktonic early stages typically undergo a series of transformations and metamorphoses while in the water column as they grow and progress towards the stage adapted for settlement into a suitable nursery habitat. Brachyuran crabs progress through a definitive series of larval stages, including several zoeal and one megalopal stage. The timing of molting between zoeal stages is determined by environmental cues such as salinity, temperature, and light cycle (Anger, 2001). The megalopal stage is typically reached 31-49 days after hatching, depending on species and environmental factors. Megalopae undergo only one molt, although this molt involves several physiological and behavioral phases in preparation for metamorphosis into the first crab stage. Within the family Portunidae, early crabs may remain in the stage for approximately 20-40 days (Sulkin and Van Heukelem, 1986), with the stage duration ultimately determined by environmental cues that can either accelerate or delay metamorphosis until conditions are suitable (Anger, 1991, Gebauer et al, 2003; Pralon et al, 2012). Once the first crab stage is reached, the crab settles out of the plankton into suitable benthic nursery habitats, after which it may move to more optimal conditions (Rakocinski et al., 2003; Rakocinski and McCall, 2005).

Environmental variables provide triggers and controls on the molting process and growth of portunid crab larvae and ultimately determine the overall quality and length of the planktonic life cycle (Gebauer et al., 1999). In particular, environmental cues signal the timing of ecdysis of stages up through the first crab stage, and initiate settlement out of the plankton for the megalopa stage. Thus, better understanding of environmental

variables and cues in relation to early stages should facilitate understanding the drivers on the composition of a given meroplankton community at a particular time and place.

As Gorsky et al. (2010) state, "the limited resolution of zooplankton data sets reduces our ability to understand processes controlling pelagic ecosystems dynamics on multiple time and space scales." The species composition of larval portunids and their abundances are not known well enough to fully delineate distribution patterns representing this family in the GOM. Broad spatial and temporal community patterns are likely driven by many environmental factors influencing when and where early stages of constituent species occur (Forward et al., 1997; Hines, 1986; Ong and Costlow, 1970; Tankersly et al., 1995). In addition, knowledge of larval distribution patterns for key species facilitates more-informed fisheries management and conservation efforts in the GOM. For the family Portunidae, larvae of component species should occur within an explicit subregion for each species as characterized by specific environmental conditions; and together the subregions for all portunid species should encompass the entire geographic region within which suitable conditions for the growth of early stages of portunid crabs exist. Yet within the family Portunidae, very little is known about how environmental variables influence larval development (Costlow, 1967).

Planktonic Invertebrate Taxonomy

Delineating distribution patterns for decapod larvae is problematic because it entails distinguishing between morphologically similar taxa. Many problems arise when we try to identify larval specimens of decapods collected from GOM because many specimens do not match existing taxonomic keys or morphological descriptions (Truesdale and Andryszak, 1983). Although some complete descriptions of portunid life histories exist, these are mainly limited to Pacific species, Western Atlantic species, and

some South American species. Further, the majority of existing larval descriptions originate from laboratory rearing of early stages produced from gravid females (e.g. Bookhout and Costlow, 1974; Bookhout and Costlow, 1977; Costlow and Bookhout, 1959; Meyer et al., 2006; Negreiros-Fransozo et al., 2007; Stuck et al., 2009). This approach can further exacerbate the difficulty of identifying decapods in the GOM due to undocumented regional variation in larval morphology, especially where larval descriptions are based on specimens from the east coast of the U.S. Thus many unidentifiable specimens are contained within any given plankton sample after the relatively few identifiable specimens have been removed.

According to Negreiros-Fransozo et al. (2007), of the 22 species of Portunidae that are known to occur along the southeast Atlantic Coast of the United States and in the GOM, only five have been completely described in terms of their larval development: *Ovalipes ocellatus* by Costlow and Bookhout (1966), *Arenaeus cribrarius* by Stuck and Truesdale (1988) and Sandifer (1972), *Portunus* (=*Achelous*) *spinicarpus* by Bookhout and Costlow (1974), *Callinectes similis* by Bookhout and Costlow (1977), and *Callinectes sapidus* by Costlow and Bookhout (1959) (additional *C. sapidus* descriptions have been published by Churchill, 1942; Costlow, 1965; Costlow et al, 1959; Robertson, 1938; Perry and Stuck, 1982; Stuck et al., 2009). Larval stages of *Portunus sensu stricto* crabs are even less well known since the recent revision of the genus which reassigned eight species, including several for which the larval development is known, to the genus *Achelous* (Mantelatto et al., 2009). Partial descriptions exist for the larvae of *Cronius ruber* (Fransozo et al., 2002), *Portunus* (=*Achelous*) *spinimanus* (Lebour, 1950; Negreiros-Fransozo et al., 2007), *Portunus* (=*Achelous*) *gibbesii* (Kurata, 1970; Negreiros-Fransozo et al., 2007), *Portunus anceps* (Lebour, 1944), *Portunus*

depressifrons (Lebour, 1944), *Portunus sayi* (Lebour, 1944; Kurata, 1970), and *Charybdis hellerii* (Dineen et al., 2001). No early stages of the remaining 11 portunid species have been described to date.

Southeastern Monitoring and Assessment Program (SEAMAP)

Although larval decapod research has been especially lacking for the GOM, recent attention has turned toward examination of spatial and temporal occurrence of invertebrate zooplankton in the GOM and Middle Atlantic Bight (Stuck and Perry, 1981; Smyth, 1980). Monitoring and assessment of zooplankton in the GOM has been taken on in part by the National Oceanographic and Atmospheric Administration (NOAA) for many years as part of the ongoing Southeastern Monitoring and Assessment Program (SEAMAP). SEAMAP is an established fisheries survey program supported by NOAA through various partners, including the National Marine Fisheries Service (NMFS), the Gulf States Marine Fisheries Commission, and state level marine resource departments in Texas, Louisiana, Mississippi, and Alabama. The SEAMAP surveys were designed to collect data on the occurrence, abundance, and distribution of marine organisms and their habitats and physical environment. SEAMAP consists of three independently operating units, with the Gulf of Mexico unit (SEAMAP-GOM) being the first formed. Initial surveys began in 1977 as part of the Marine Resources Monitoring Assessment and Prediction program, or MARMAP (Richards, 1987; Sherman et al., 1983). The SEAMAP-GOM initiative started in 1981 and included plankton surveys conducted by NMFS. Sampling targets of the various SEAMAP cruises include zooplankton, sharks, shrimp and ground fish, and marine mammals. Zooplankton cruises within the GOM range geographically from Florida to Texas and extend from the US coastline out past the 200m isobath. SEAMAP stations are arranged in a fixed systematic grid consisting of

300+ stations across the U.S. Exclusive Economic Zone (EEZ). Each survey samples a selected subset of the stations depending on the time of year and the goal of the survey. Extensive plankton cruises ensue in the spring and fall seasons in conjunction with peak spawning periods for targeted species, with moderate plankton sampling occurring on ground fish cruises in the summer and late fall. The goal of spring plankton survey is to sample beyond the shelf targeting the majority of the deep water sites. In contrast, the fall plankton survey collects samples at shallower stations within the 200 m isobath, plus a few deeper stations. The analysis of data from those surveys has mainly focused on ichthyoplankton, or on broad-scale invertebrate communities (Lyczkowski-Shultz and Hanisko, 2008; Marancik et.al, 2010; Millett, 2010). Recently, the SEAMAP focus has expanded to include larval decapods because of the importance of decapod crustaceans in the economy of the Gulf region and their importance as both predators and prey within the pelagic ecosystem.

Objectives

A preliminary project funded by the Northern Gulf Institute (NGI) through a collaboration of many institutions sought to expand the larval indices already in place to incorporate larval decapods as well as to further analyze environmental influences on the zooplankton community. Starting in 2009, the project launched the first in-depth analysis of available SEAMAP invertebrate data and linkages to the known ichthyoplankton data. Along with corresponding environmental data, this project contributed to a more holistic view of GOM planktonic assemblages (Hernandez et al., 2012). A foundation for this thesis comes from a follow-up NGI project dedicated to developing a working larval ichthyoplankton database incorporating all taxonomic and environmental information from the cruises. Additional studies utilizing the zooplankton and fish egg components

completed prior to the present project at Louisiana State University and Dauphin Island Sea Laboratory provided additional support. The goal of the NGI project was to obtain a more holistic view of the invertebrate zooplankton community in the GOM through identification of larvae, genetic applications, digital imagery analysis of sample biomass, and relating environmental variables to community structure (Lyczkowski-Shultz et al., 2008).

This project aims to address the need for taxonomic data and environmental linkages for portunid crab larvae by updating and developing identification guidance and adopting a macroecological approach to characterize distribution and abundance patterns for the portunid megalopa taxocene as revealed in an extensive 2003 SEAMAP Fall Plankton Survey. The entire northern GOM was surveyed within the 200m isobath shortly after a peak spawning period for portunid crabs. Relevant environmental factors of portunid megalopae recovered from neuston samples taken during the cruise are displayed within a spatially explicit framework using a combination of geospatial and multivariate analyses. An overarching goal of this study is to contribute to the developing picture of spatially-explicit assemblage patterns of early stages of portunid crabs in the northern GOM. Knowledge of these spatial patterns provides information for the proper management of portunid stocks in the face of major environmental challenges including climate change, hurricanes, or oil spills, as well as in fisheries management, directly in terms crab fisheries and indirectly in terms of the larvae serving as prey.

CHAPTER II

MATERIALS AND METHODS

Field Protocols and Sample Collection

Samples analyzed for this study came from the SEAMAP Fall Plankton Survey conducted in 2003 (Figure 1). This particular cruise was selected because of the combination of its spatial extent, seasonal timing relative to portunid abundances, and the lack of tropical weather effects (e.g. hurricanes, tropical storms, etc.). Samples were taken aboard the NOAA Ship *Gordon Gunter* throughout the northern GOM from off of Brownsville, TX to the Florida Keys. The cruise was completed in two legs over a period of 29 days. The first leg, covering the western end of the northern GOM, departed Pascagoula, MS on August 28th and returned on September 11th 2003. The second leg, covering the eastern end of the northern GOM, spanned from September 16th to September 29th 2003.

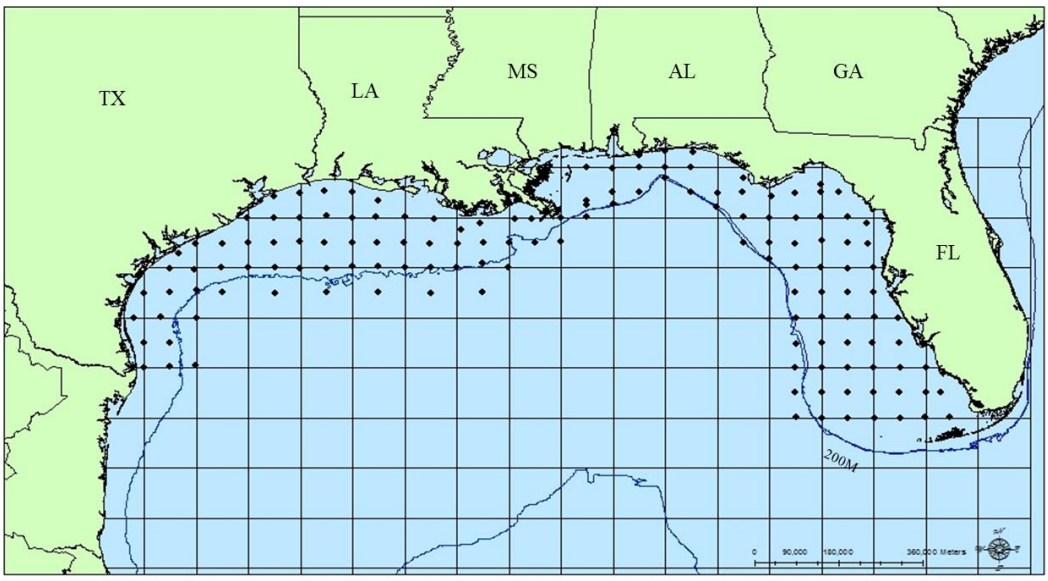

Figure 1. Stations Sampled During the Fall 2003 SEAMAP Plankton Cruise.

Standard SEAMAP plankton nets were used to collect samples at each station. A 61cm bongo frame fitted with two 0.335 mm mesh nets and a 1x2 m neuston frame fitted with a 0.947 mm (0.950 mm) mesh net (Figure 2). A SBE 19 Seacat profiler attached to the bongo collected real time temperature, salinity, and depth information. Water column physical data were collected with a Seabird SBE 9/11 Plus CTD (Conductivity, Temperature, and Depth) outfitted with a dual suite of sensors (Lyczkowski-Shultz and Hanisko, 2008) including temperature, salinity, dissolved oxygen, and transmissivity. During each cast the CTD generated a water column profile and water samples were taken with three mounted Nisken bottles at three levels in the water column: bottom (to a maximum depth of 200m), midwater or chlorophyll max, and surface. In instances where the chlorophyll max occurred at the surface or bottom, only bottom and surface samples were collected. Water samples were processed to measure the level of chlorophyll-a on board using bench top fluorometry. Wind direction, speed, barometric pressure, sea surface temperature, air temperature, water depth, as well as ship position, speed, and heading were recorded via the shipboard sensors and were accessed through the Scientific Computer System (SCS) software. The volume of *Sargassum* spp. collected in the nets was recorded at every station.

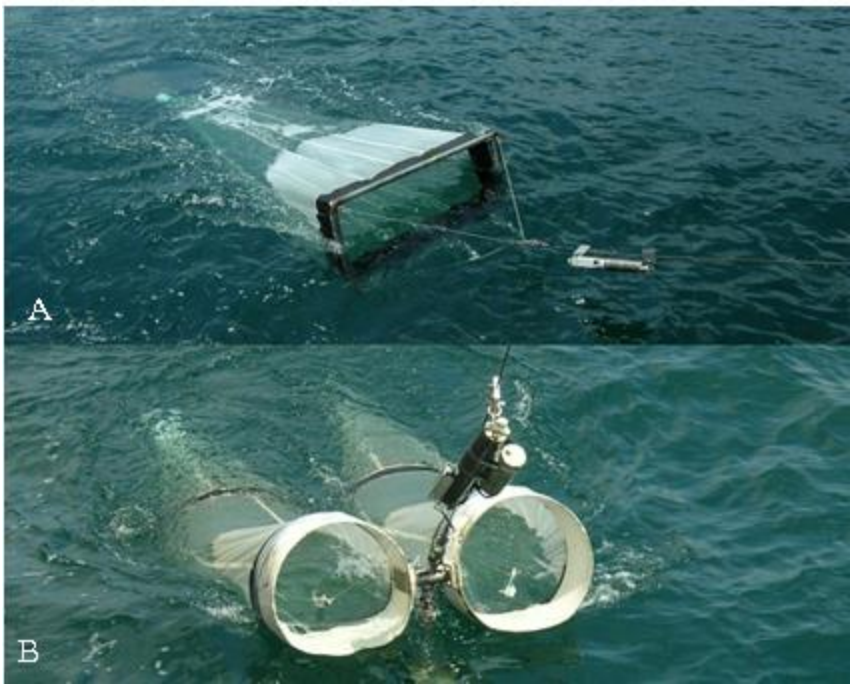

Figure 2. Photographs of the Neuston and Bongo Nets. Top panel (A) shows the Neuston net during a tow, displaying amount of net submerged. Bottom panel (B) shows the bongo nets at the end of a tow.

The bongo nets were fished in a double oblique tow at a wire angle of ~45 degrees to ensure a uniform sampling of the water column. The length of time of the bongo tow depended on the depth of the station but ranged from 2.5 to 35.6 minutes. Neuston tows ran for 10 minutes at a ship speed of ~2kts with the frame half submerged (0.5m) below the water. Upon net retrieval, nets were rinsed to condense the sample into the attached cod ends. Cod ends were removed and the sample poured through a .333 mm mesh sieve before being transferred into the appropriate size jar (pint or quart) and being labelled with station information and gear type. Neuston and right bongo samples were preserved in 10% formalin while left bongo samples were preserved in 95% ethanol. Ethanol samples were transferred into fresh ethanol 24 hours after initial preservation and formalin samples were transferred into 95% ethanol after 48 hours.

Sample and Taxonomic Analysis

Upon return the land, the collect samples are split up and sent to different locations. The left bongo samples are sent to the University of Southern Mississippi Gulf Coast Research Laboratory (USM-GCRL) for archiving. The right bongo and neuston samples were sent to the Sea Fisheries Institute, Plankton Sorting and Identification Center (ZSIOP), in Gdynia and Szczecin, Poland, for sorting and identification of icthyoplankton and select invertebrate zooplankton and decapod larvae. All sorting and initial identification to family level (and larval stages where applicable) of decapod larvae were conducted at ZSIOP following the protocols established by Dr. Ken Stuck (Appendix A). Aliquoting was preformed prior to sorting out the decapods and the final aliquot to be sorted was based on the original displacement of the sample. Samples representing each gear type are sorted in reference to a list of pre-selected target taxa. All decapods not removed during processing, as well as other invertebrates that were not removed, were retained in the original field sample and held at ZSIOP.

Displacement volume was measured for all samples at the time of ichthyoplankton sorting (for samples where no ichthyoplankton was removed, the displacement volume was measured before removing the invertebrates) using the appropriate graduated cylinder for the size of the sample and volume rounded off to the nearest milliliter. After displacement volume was measured, each sample was sorted according to the prescribed procedure for the gear type (Appendix A). Upon completion of the sorting, all of the identified taxon vials for the samples were shipped back to the United States and the invertebrate component was delivered to the SEAMAP Invertebrate Plankton Archive Center (SIPAC) at USM-GCRL for archiving in the GCRL Museum.

Once samples were received, all vials labeled as Portunidae megalopae were selected and set aside for further taxonomic identification during the present study.

Specimens were removed from each vial and placed into a Pyrex glass sorting dish filled with enough 70% ETOH to completely cover the specimens to prevent desiccation. Specimens were examined using an Olympus SZH-ILLD stereomicroscope, and identified based on key morphological features, including the segmentation and setation of the antennae; length, curvature, and thickness of the rostrum; the presence or absence and location of spines on the cheliped; the presence or absence of coxal spines on pereopods 2-5; length and shape sternal spines; the presence of a paddle like dactyl on the 5^{th} (swimming) leg, as well as the number of stiff hooked setae on the dactyl; presence or absence of lateral spines on the 5^{th} abdominal segment; shape of the telson; and the number of setae on the uropod (Figure 3).

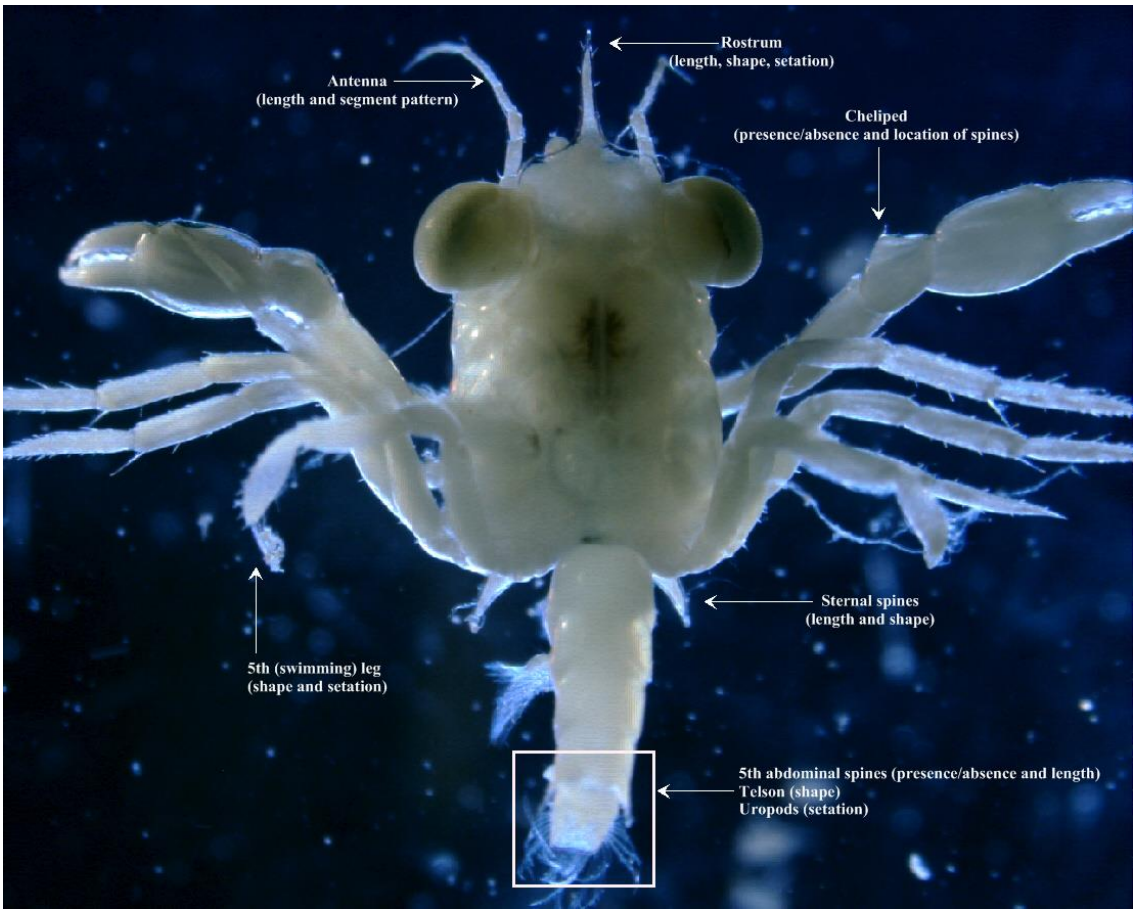

Figure 3. Diagram of the Morphological Features Used for Identifications.

The importance of these morphological features for genus and species level identification was confirmed using the taxonomic literature. When consistent similarities between unrecognized types of portunid megalopae were observed, the specimens were assigned to the genus or family level followed by a unique letter code for each type (e.g. *Achelous* sp. A). Letter codes started with 'A' and continued alphabetically until all types had been accommodated within the assigned taxonomic level. Each letter-code morph was defined by a diagnostic drawing illustrating the key characters that made it a distinctive taxonomic unit. Reference specimens representing each morph were also photographed. When there were a sufficient number of specimens for a particular morph,

a reference specimen was selected from which antennae, mouth parts, and other appendages (when present) could be removed and slide mounted.

These appendages were later removed under a Wild M8 dissecting microscope and mounted in CMC10 mounting medium stained with lignen pink. Based on all features used for identification, a key to identified morphs was created and detailed descriptions of the morphs were prepared after all samples were processed.

Counts for identified taxa were obtained for each station and gear type. In many cases, the original SEAMAP sample had been aliquoted due to the initial displacement volume of the sample (Appendix A). Therefore, in order to estimate abundances of taxa for a specific sample, counts were multiplied by the appropriate aliquot coefficient. Neuston catches of individual taxa were standardized to number of larvae per 10 minute tow time following the formula "total catch × (10/tow time)." Bongo catches of individual taxa were standardized to number of larvae under 10 m^2 of water according to the formula "total catch × ((max depth/volume filtered) × 10)." The resulting neuston catch per unit effort (CPUE) and bongo abundances were entered into a master MS Access database that included all station and corresponding environmental data taken at the time of sampling.

Data Analysis

Geospatial analysis

The neuston and right bongo data were uploaded into the Arc Desktop 10 suite of software (ESRI Corporation). Shape files of stations and environmental data were created in Arc Catalog using the actual starting latitude and longitude of each station to compensate for moving any of the stations due to obstructions at the time of sampling. The base map of the Gulf of Mexico which all data was mapped onto was a composite of

various other layers from different sources. The layer "states high" came from the NOAA website at http://www.ncddc.noaa.gov /interactivemaps, representing the states that border the GOM. The "depth_200m isobath" layer was extracted from a bathymetry GIS layer obtained from Betsy Gardner, the GIS coordinator at the Stennis Space Center. The layer "longitude_latitude_grid" was obtained from Christina Schobernd, a biologist with JHT, Inc, to display the fixed grid system of the SEAMAP stations. All shape files were imported into a new data frame in ArcMap and georeferenced to WGS 1984 to stay in compliance with other maps produced using SEAMAP data (David Hanisko, NOAA, personal communication).

All taxon data layers were generated within ArcMap from the gear type shape files by selecting each taxon as a layer file. Once each taxon was mapped as its own individual layer, the symbology was changed to display a density scale for those described taxon occurred five or more times. For these taxa, density, i.e. CPUE in neuston samples and abundance in bongo samples, was displayed via graduated symbols using a Jenks Natural Breaks model with no normalization. The maximum number of density classes selected was five. For all taxa with fewer than five occurrences, symbology was left at the default symbol simply indicating where specimens were found. Finally, spatially explicit maps were made per taxon for both gear types, as applicable.

Maps were also generated to illustrate spatial patterns of major environmental variables measured *in situ*, as well as derived averages from satellite data for the month of September 2003. *In situ* environmental variables included sea surface temperature, salinity, surface oxygen, *Sargassum* spp. abundance, time of day, and concentration of chlorophyll-a. Information on all variables was taken from the neuston shape file for consistency, though the same information was present in both the right bongo and

neuston shape files. Symbology was set to multiple features using a color ramp and Jenks Natural Breaks model classification for temperature, salinity, oxygen, and chlorophyll-a. *Sargassum* spp. abundances were classified using graduated symbols based on the generalized volumetric measurement scale used in 2003. The legend of the map for *Sargassum* spp. does not display the actual scale (A-D), but rather the volumetric description of each letter as this communicates the data more clearly. Day and night assignments were based on a combination of the date, time, and location of each sample following the methods provided by Seidelmann (1992). Nautical twilight delineated transitions between day and night, resulting in 4 categories: day, day twilight (sunrise ± 1 hour), evening twilight (sunset ± 1 hour), and night (Lyczkowski-Shultz and Hanisko, 2008).

Satellite derived data were incorporated into the GIS maps analysis to fill in data gaps and for comparison with *in situ* data at broader spatio-temporal scales. Satellite data was obtained via the BloomWatch 180 website hosted by the west coast node of NOAA's CoastWatch (http://coastwatch.pfel. noaa.gov /coastwatch/CWBrowserWW180.jsp). Max and min x/y coordinates were used to restrict the search window to the Gulf of Mexico (x = -98, X = -80, y = 18, Y = 31). Grid data was chosen so that all output files would be in raster form and meters was selected for display output where applicable. The September 2003 monthly averages were obtained from BloomWatch 180 for geostrophic currents (Current, Geostrophic, Aviso .25 degrees, Global, Zonal; Current, Geostrophic, Aviso, .25 degrees, Global, Meridional), sea surface temperature (SST,NOAA,GOES Imager, Day and Night, .05 degrees, Western Hemisphere; SST, Aqua MODIS, NPP, 0.05 degrees, Global, Daytime, Science Quality), and chlorophyll-a (Chlorophyll-a, Aqua MODIS, NPP, 0.05 degrees, Global, Science Quality). Sea surface height data (Sea

Surface Height, Absolute, Aviso .25 degrees, Science quality) was downloaded for weekly intervals. All data was exported as ESRI ASCII files for ease of importing into ArcMap.

Chlorophyll-a data was combined from multiple sources of data to obtain the most comprehensive dataset. *In situ* data collected using the CTD and bench top fluorometry produced an insufficient dataset for complete depiction of surface concentrations due to equipment failure during the 2003 survey. Thus, satellite data was used to fill in the gaps. Satellite values were checked against known *in situ* values to ensure that values were comparable. Using the Marine Geospatial Estimate Tools (MGET) toolbox, the monthly average and 8 day averages of chlorophyll-a data were downloaded from the SEAWIFS archive and were automatically added as fields to a database containing station number, dates, and coordinates. Values from the monthly average chlorophyll-a layer imported from BloomWatch 180 were added to the table via extraction. Station points were overlaid on the raster file and the chlorophyll-a values present at the station points were extracted via the extract tool. "Holes" or areas with no data values were numerous in the 8 day average available during the time frame of the cruise due to cloud cover preventing satellite imagery from being taken. Thus, the September 2003 monthly average was chosen to compare with chlorophyll-a concentrations measured during the time of sampling.

After importing the downloaded raster files into the ArcMap workspace, the symbology was modified to display the data clearly. Maps were generated with this data in a form that most closely matched the maps generated for the identified portunid species and morphs. An additional map of geostrophic currents displayed as vector data

was downloaded from the BloomWatch 180 site, and thus was not in the same format as the maps generated from ArcMap, but was used in the visual analysis.

Community analysis

The community analysis of species composition was accomplished via non-metric multidimensional scaling (NMDS) using R statistical software (R version 2.15.3 (2013-03-01)). Execution of the NMDS analysis was carried out using the R package Vegan, a package containing tools built for descriptive community ecology (Oksanen et al., 2013). Only the data from neuston samples were used, as right bongo samples were not as comprehensive for analyzing portunid community structure. Pre-processing of the data removed the taxa *Achelous* sp., *Callinectes* sp., and Unidentified from data because these categories lumped specimens that were too damaged to attribute to lower taxonomic levels. A total of 18 recognized taxa were included after these categories were removed.

Preparation of the data within R occurred in two steps. First, taxa occurring in two or fewer samples were excluded from analysis; this step eliminated five taxa from the analysis (*Cronius ruber,* Portunidae sp. C, Portunidae sp. E, *Achelous* sp. A, and *Achelous* sp. E). Next, stations with zero specimens for all remaining taxa were removed from the data set. These included both stations for which no taxa were present at the time of sampling or stations that had no remaining specimens after the previous step was executed. This step excluded 14 of 143 neuston samples, leaving 129 samples for the NMDS analysis. Once this step was completed, the NMDS was executed using metaMDS within Vegan. The default setting of Bray-Curtis dissimilarity was used with election of the options trymax=500 iterations, and noshare=0.1. A square root transformation was used and the option for a Wisconsin double standardization was applied to the data. The NMDS converged in 24 runs and the two dimensional solutions had a final stress score of

0.216. By default, a procrustes Principal Components rotation of the NMDS axes was performed in Vegan to maximize variation explained by successive NMDS axes.

NMDS generated both taxon scores (species and morphs) and sample scores, which were plotted together as a bi-plot in 2D NMDS space. Species codes were labeled in the resulting plot to illustrate concordances between samples and species' centers of abundance. NMDS coordinates were imported into Quantum GIS (QGIS) 1.8.0-Lisboa in order to be displayed spatially. NMDS coordinates were plotted so that each axis was represented by different symbology, i.e., symbol color and size. All classification breaks were based on a Jenks Natural Breaks model. NMDS1 was assigned a color ramp symbology and NMDS2 was attributed to symbol size (Table 1).

Table 1

Breakdown of NMDS Scores and Assigned Symbology

NMDS1	NMDS2
-1.8286 ± -0.9879 (white)	-1.3368 ± -0.8320 (extra small)
-0.9879 ± -0.2636 (beige)	-0.8320 ± -0.1925 (small)
-0.2636 ± 0.4029 (orange)	-0.1925 ± 0.2936 (medium)
0.4029 ± 1.2708 (red brown)	0.2936 ± 1.2150 (large)

In this manner, four symbol types were generated (White, xsmall; Orange, small; Beige, medium; Red brown; large), reflecting dominant and subdominant constituents as well as relative abundances of subdominant taxa, and whether samples represented relatively low vs. high densities of megalopae.

CHAPTER III

RESULTS: TAXONOMIC ANALYSIS

A total of 24,877 portunid megalopae from 260 samples were identified to the family level by the Polish sorting center. Of these, 24,549 were identifiable beyond family level, with the rest being too damaged to identify further. Out of 143 stations sampled with both gear types, portunid megalopae were present in 132 neuston and 128 bongo samples. From these samples 22,847 megalopae were recovered from neuston samples and 2,030 were recovered from bongo samples. Seven species and 11 morphs were identified; some specimens were too damaged to identify past genus (e.g. *Callinectes* sp. and *Achelous* sp.) (Table 3). Original numbers reported from Poland indicated that 24,660 megalopae were identified to family; however, inaccurate counts in some vials underestimated the actual number of megalopae present.

Table 2

Taxonomic Breakdown Showing the Number of Samples and Stations at which Each Taxon was Present

Taxon	No. Identified	No. Samples Present	No. Neuston samples	No. Bongo samples	No. Stations present
Achelous gibbesii	3705	139	101	38	110
Achelous spinimanus	549	68	51	17	58
Achelous spinicarpus	1788	110	62	48	87
Arenaeus cribrarius	137	30	25	5	26
Callinectes sapidus	13610	217	118	99	131
Callinectes similis	2162	145	87	58	109
Cronius ruber	2	1	1	0	1

Table 2 (continued).

Taxon	No. Identified	No. Samples Present	No. Neuston samples	No. Bongo samples	No. Stations present
Achelous sp. B	210	50	46	4	47
Achelous sp. C	850	84	57	27	68
Achelous sp. E	4	2	2	0	2
Achelous sp. F	10	6	5	1	6
Achelous sp. I	1253	74	39	35	59
Portunidae sp. A	69	21	15	6	20
Portunidae sp. C	4	4	2	2	4
Portunidae sp. D	7	5	5	0	5
Portunidae sp. E	1	1	1	0	1
Portunidae sp. G	132	17	16	1	16
Portunus sp. A	16	12	12	0	12
Achelous sp.	38	8	6	2	8
Callinectes sp.	25	11	11	0	11
Unidentified	305	64	57	7	63

Table 3

Morphological Features Used to Assign Specimens to Genera

Taxon	Number of antenna flagellum segments	Coxal spine(s) present	Carpal spine present	Basi-ischial spine present
Callinectes	8	No	No	Yes
Arenaeus	8	Yes	Yes	Yes
Achelous	7	Yes	Yes	No
Portunus	7	No?	No?	Yes?
Other (left as Portunidae)	6-8	Yes and no	Yes and no	Yes and no

Diagnoses, Descriptions, and Distributions of Morphs and Species

The descriptions of 18 morphs identified in this study are provided; they cover only morphological features used to identify specimens in this study and are not comprehensive descriptions of all characters. A generic key including morphs left at the family level, along with a key to Achelous species and morphs are included at the end of this document (Appendix B; Appendix C).

Family Portunidae (Rafinesque, 1815)

All megalopae within the family Portunidae were identified according to the following set of morphological characters: Single rostrum; carapace lacking lateral spines; seventh thoracic segment with one pair of spines ("sternal spines") projecting posteriorly; and fifth pereopod, dactyl flattened and paddle-like, with elongate terminal or subterminal hooked setae. Five genera and 22 morphs (Tables 3 and 4) were identified from the fall 2003 SEAMAP plankton samples, including six morphs that could not be assigned to a genus either because of the lack of appendages necessary for identification or from a lack of conformity with known generic descriptions. These are described below, followed by the taxa that were identified to a lower taxonomic level.

Portunidae sp. A (Figures 4 & 5)

Diagnostic description. Carapace and pereopods: Carapace rectangular, lacking a dorsal spine; rostrum 50% length of antenna, with 3 medium and 1 small pair of lateral setae and 1 medium pair of ventral setae, nearly horizontal; pair of spines extending from posterior margin of seventh thoracic segment posteriorly to anterior margin of third abdominal segment. Eyestalks lacking pigment spots. Cheliped lacking disto-medial carpal spine and basi-ischial spine; pereopod 2 with ventral spine on coxa; pereopods 3-5 lacking ventral spine on coxa; dactyl of pereopod 5 paddle like, bearing 8 hooked setae.

Antenna: Consisting of 10 segments, flagellum of 7 segments, relative segment length pattern for segments 1-4 of short-medium-medium-long, as shown (Figure 3).

Abdomen and pleopods: Abdomen, second segment humped in lateral view, fifth segment lacking posterolateral spines; telson almost square, distal margin transverse. Pleopods present on abdominal segments 2-6; pleopod 5 (uropod) lacking endopod, bearing 1 plumose seta on basal segment and 13 plumose setae on exopod.

Remarks. The most unique feature of this megalopa was the lack of lateral spines on the 5th abdominal somite. While this feature is typically seen as a family characteristic, it appears that it may not hold. Several of these specimens were found so it is not believed to be a mutation. The lack of spines on the cheliped also makes it difficult to assign or even speculate which genus this megalopa belongs to. The presence of the spine on the coxa of the second pereopod indicates that the megalopa may be a species of *Achelous* or *Portunus*, though undescribed genera are also possibilities. CL= 1.99 mm.

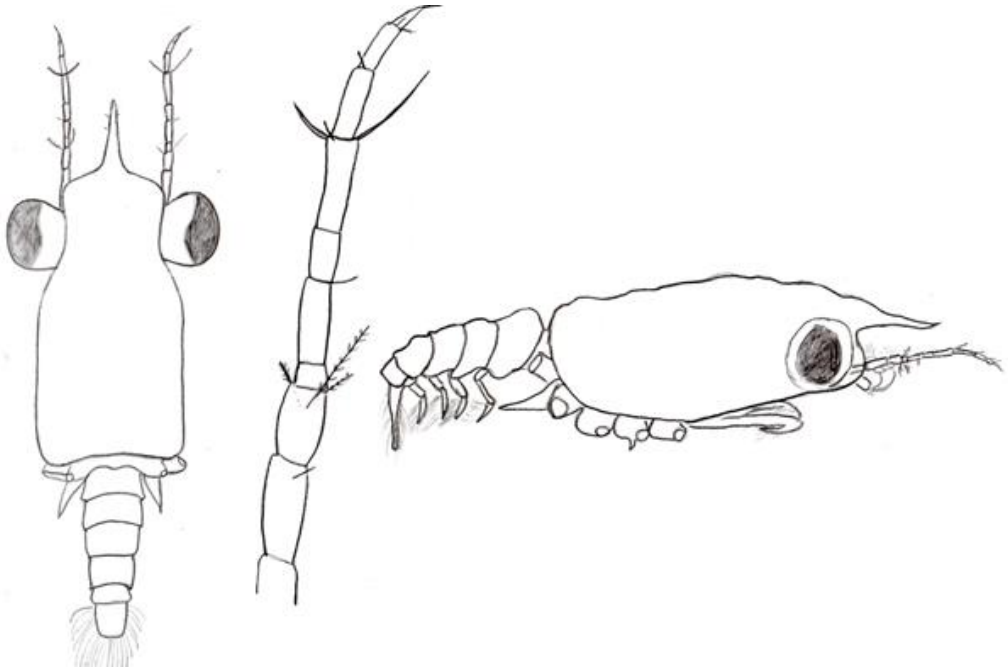

Figure 4. Drawings of Portunidae sp. A Megalopa. Full dorsal view, pereopods omitted (left); antenna, dorsal view (center); full lateral view, pereopods omitted (right).

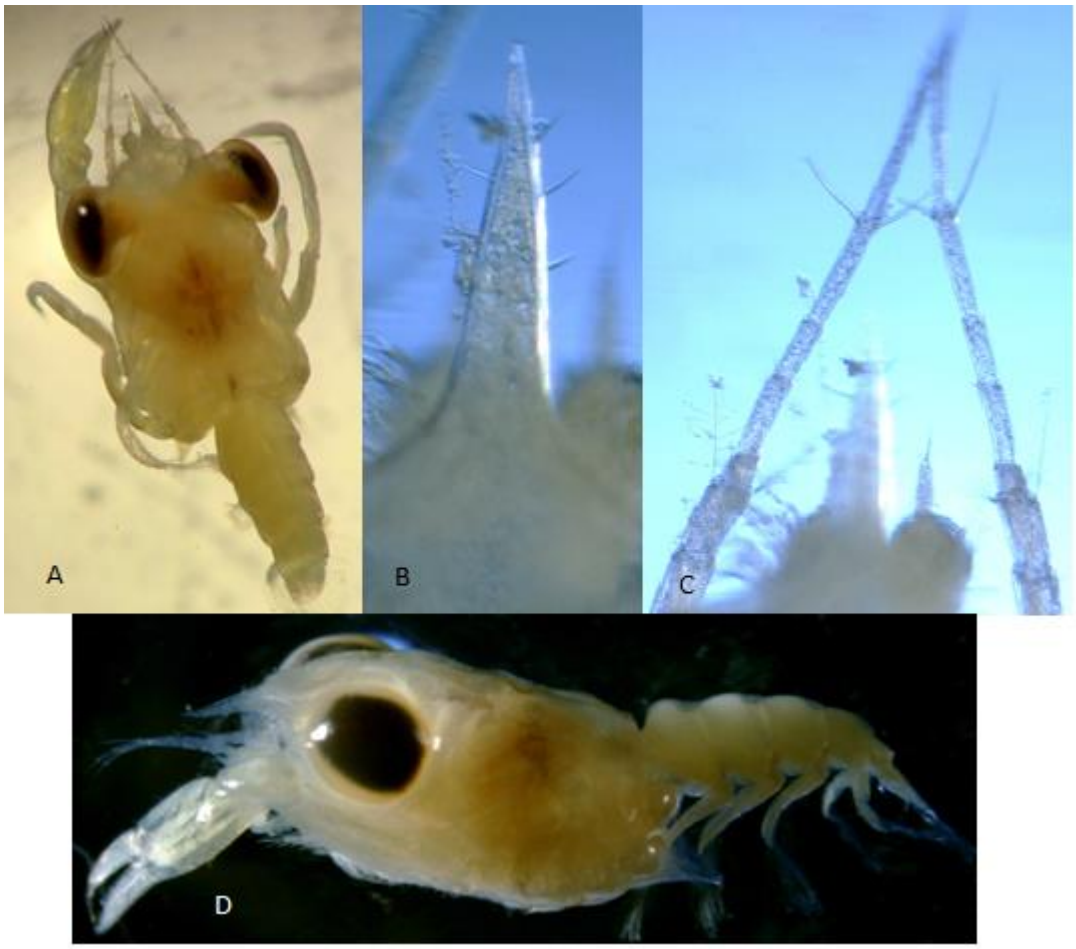

Figure 5. Photographs of Portunidae sp. A Megalopa. Full dorsal view (A); rostrum, dorsal view (B); antennae, ventral view (C); full lateral view (D).

Distribution. Portunidae sp. A occurred mostly on the shelf off the coast of Louisiana, with a few occurrences from off the coast of Florida (Figure 6). Most occurrences happened at mid to deep water stations.

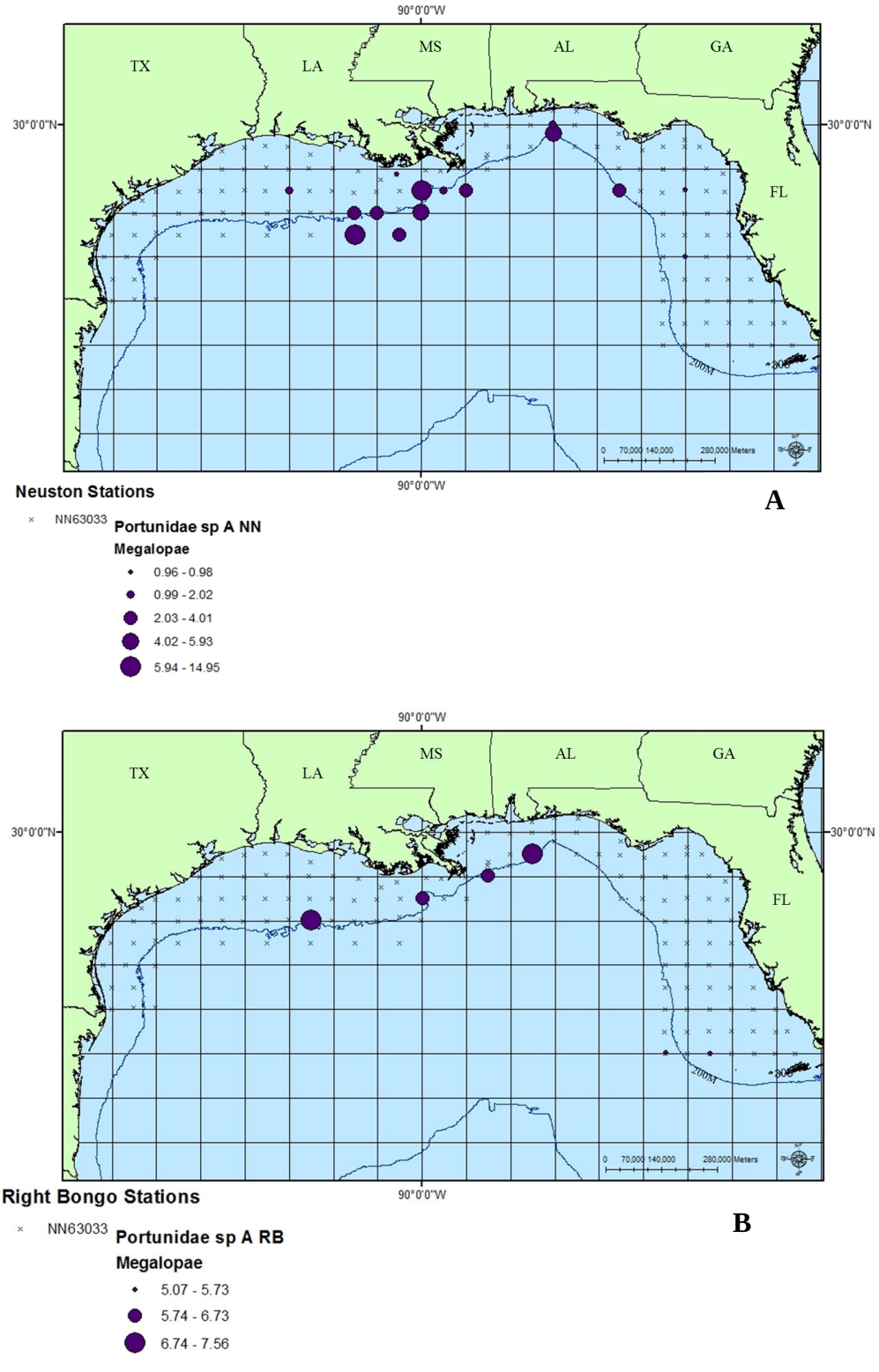

Figure 6. Maps of the Distributions and CPUE of Portunidae sp. A in Neuston (A) and Bongo (B) Samples.

Portunidae sp. C (Figures 7 & 8)

Diagnostic description. Carapace and pereopods: Carapace rectangular, lacking a dorsal spine; rostrum 80% length of antenna, bearing several pairs of setae along lateral margins and one pair of ventrolateral setae near tip, angling slightly downward before curving upward at tip; strong pair of spines extending from posterior margin of seventh thoracic segment posteriorly to anterior margin of fourth abdominal segment. Eyestalks each with pigment spot on dorsal surface (seen in freshly preserved specimens). Cheliped lacking disto-medial carpal spine, with large hooked basi-ischial spine; pereopods 2-5 lacking ventral coxal spine; dactyl of pereopod 5 paddle-like, bearing 11 hooked setae.

Antenna: Consisting of 11 segments, flagellum of 8 segments, relative segment length pattern for segments 1-5 of short-medium-medium-medium, long, as shown (Figure 7).

Abdomen and pleopods: Abdomen, second segment humped in lateral view, fifth segment with large posterolateral spines that extend well past posterior margin of sixth abdominal segment; telson with slightly rounded distal margin, with 3 pairs of setae running down the median dorsal surface. Pleopods present on abdominal segments 2-6; pleopod 5 (uropod) lacking endopod, bearing 1 plumose seta on basal segment and 14 plumose setae on exopod.

Remarks. While only a few of these megalopae were seen in the samples, it is believed that this megalopa might be *Portunus sayi* based off of the heavy presence seen in *Sargassum* samples taken for a different project. It is also possible that it may be another species *Callinectes*. The presence of 8 antennal flagellum segments and a basi-ischal spine on the cheliped while lacking carpal and coxal spines would place the

megalopa in this category, but the long rostrum and antennae coupled with the strong sternal spines suggest this may not be the case. CL= 2.48 ± 0.04 mm.

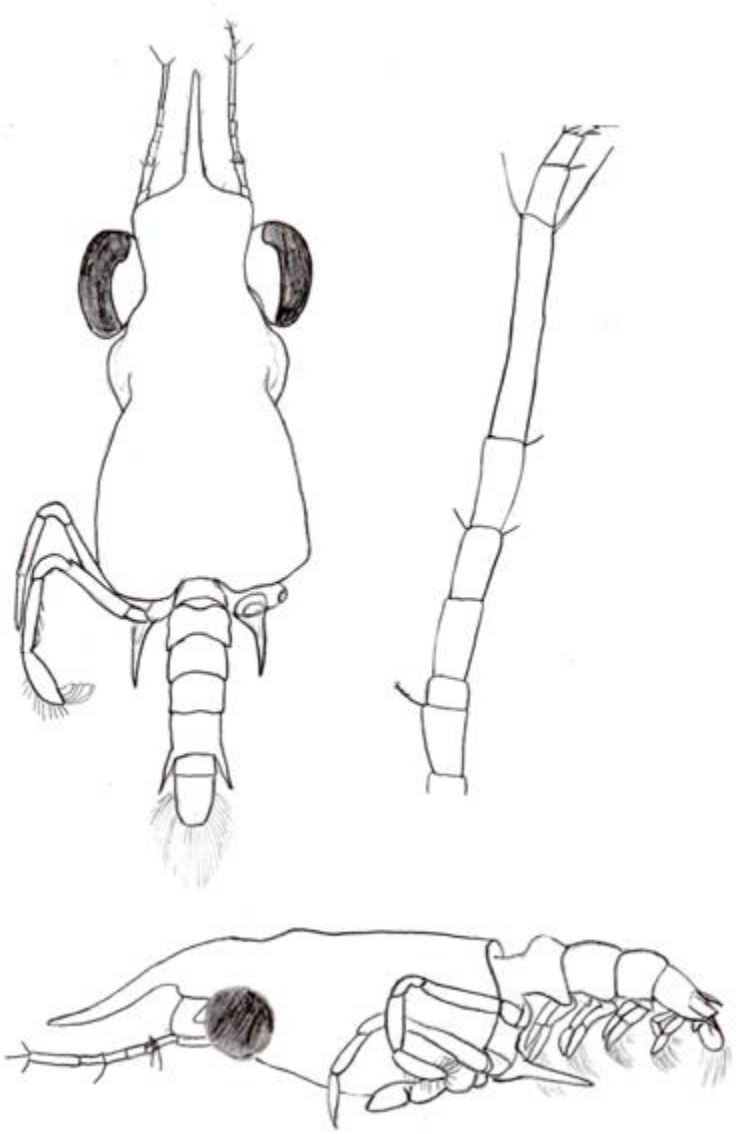

Figure 7. Drawings of Portunidae sp. C Megalopa. Full dorsal view, pereopods 1-3 omitted (top left); antenna, dorsal view (top right); full lateral view, pereopods 1-3 omitted (bottom).

Figure 8. Photographs of Portunidae sp. C Megalopa. Full dorsal view (A); rostrum and antenna, dorsal view (B); full lateral view (C).

Distribution. Portunidae sp. C only occurred at 4 stations, two off the coast of Louisiana, both relatively nearshore and two off the coast of Florida around the Tampa Bay area (Figure 9).

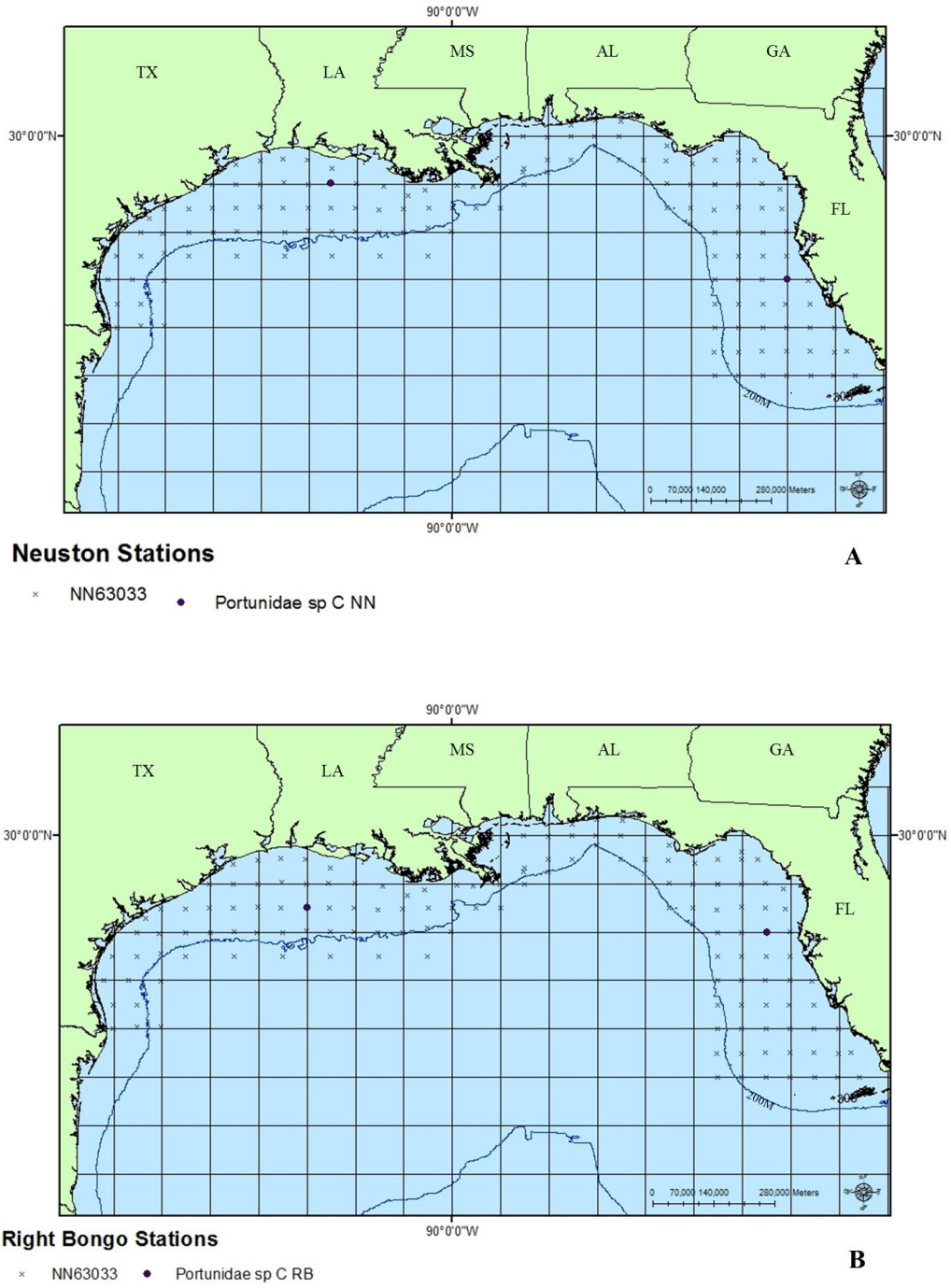

Figure 9. Maps of the Distribution of Portunidae sp. C Megalopae in Neuston (A) and Bongo (B) Samples.

Portunidae sp. D (Figures 10 & 11)

Diagnostic description. Carapace and pereopods: Carapace rectangular, lacking a dorsal spine; rostrum 70% length of antenna, without lateral or ventral setae, angled slightly downward; pair of spines extending from posterior margin of the seventh thoracic segment posteriorly to posterior margin of second abdominal segment. Eyestalks lacking pigment spots. Cheliped, spination unknown; pereopod 2 bearing coxal spine; pereopods 3-5 lacking coxal spine; dactyl of pereopod 5 paddle-like, number of hooked setae unknown.

Antenna: Consisting of 11 segments, flagellum of 8 segments, relative segment length pattern for segments 1-5 of short-short-short-short-medium, as shown (Figure 10).

Abdomen and pleopods: Abdomen, second segment humped in lateral view, fifth segment with posterolateral spines that extend slightly past posterior margin of sixth abdominal segment; telson with slightly squared distolateral margin, distal margin slightly rounded, bearing 2 pairs of setae on medial dorsal surface. Pleopods present on abdominal segments 2-6; pleopod 5 (uropod) lacking endopod, bearing 1 plumose seta on basal segment and 11 plumose setae on exopod.

Remarks. This megalopa is thought to possibly be *Charybdis helleri* based on brief characters mentioned by Kurata (1975) such as the overall size, 8 antennal flagellum segments, and the small sternal spines, though other possibilities abound. The antennal flagellum segment count and pattern resemble that of *Callinectes*, but the sternal spines are significantly smaller than those seen on identified species of *Callinectes* megalopae and *Callinectes* are supposed to lack a coxal spine on pereopod 2. Without knowledge of the spination of the cheliped, attributing this megalopa to a genus is difficult. CL= 1.64mm

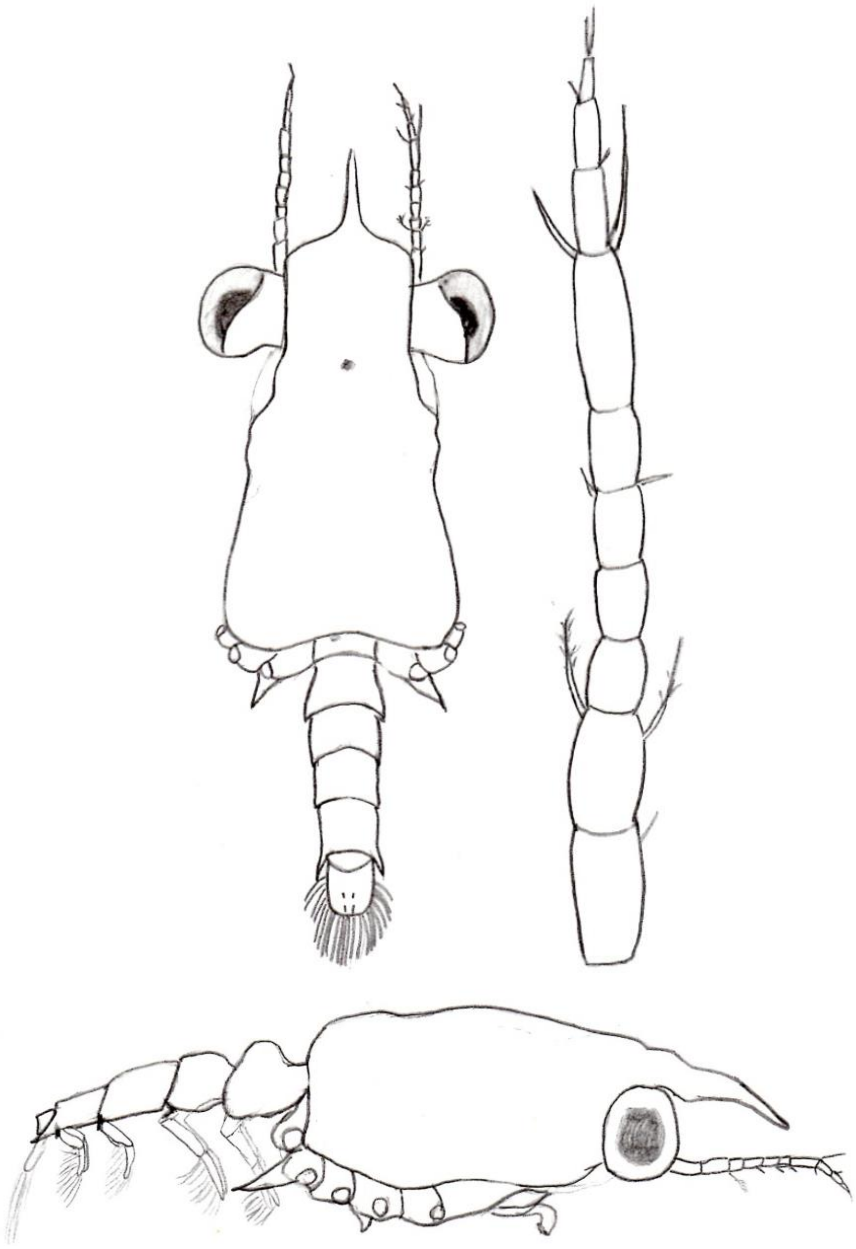

Figure 10. Drawings of Portunidae sp. D Megalopa. Full dorsal view, pereopods omitted (top left); antenna, dorsal view (top right); full lateral view, pereopods omitted (bottom).

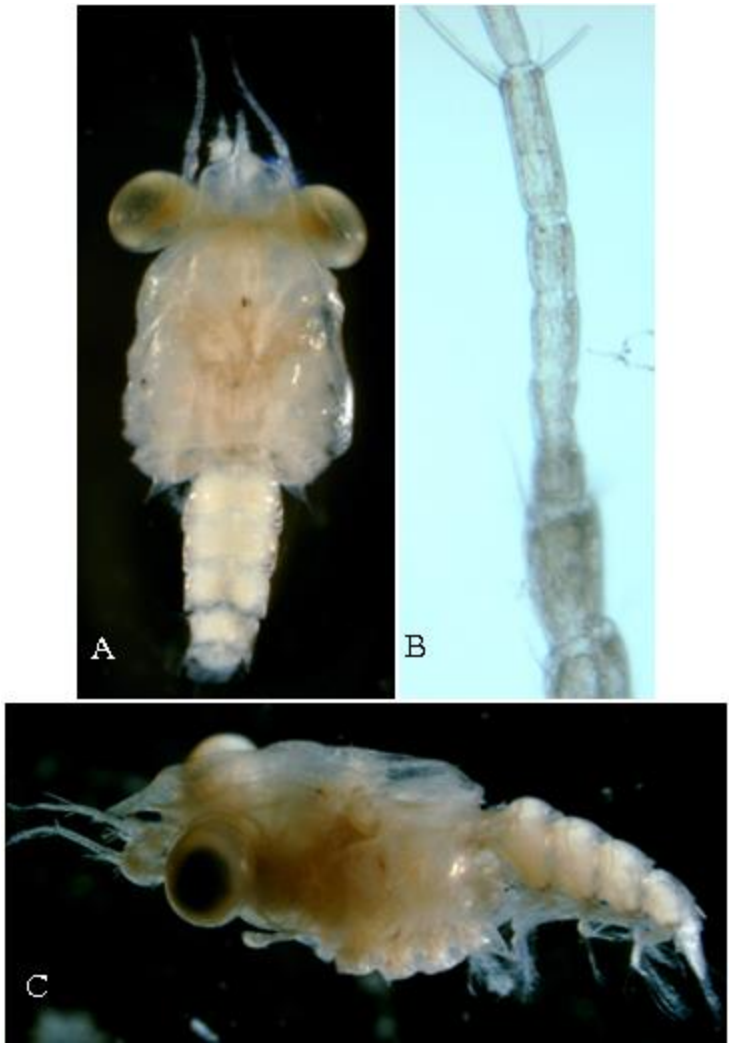

Figure 11. Photographs of Portunidae sp. D Megalopa. Full dorsal view (A); antenna, ventral view (B); full lateral view (C).

Distribution. Portunidae sp. D was only found in neuston samples across the GOM, ranging from inshore to offshore but not occurring below the 28 degree line of latitude (Figure 12).

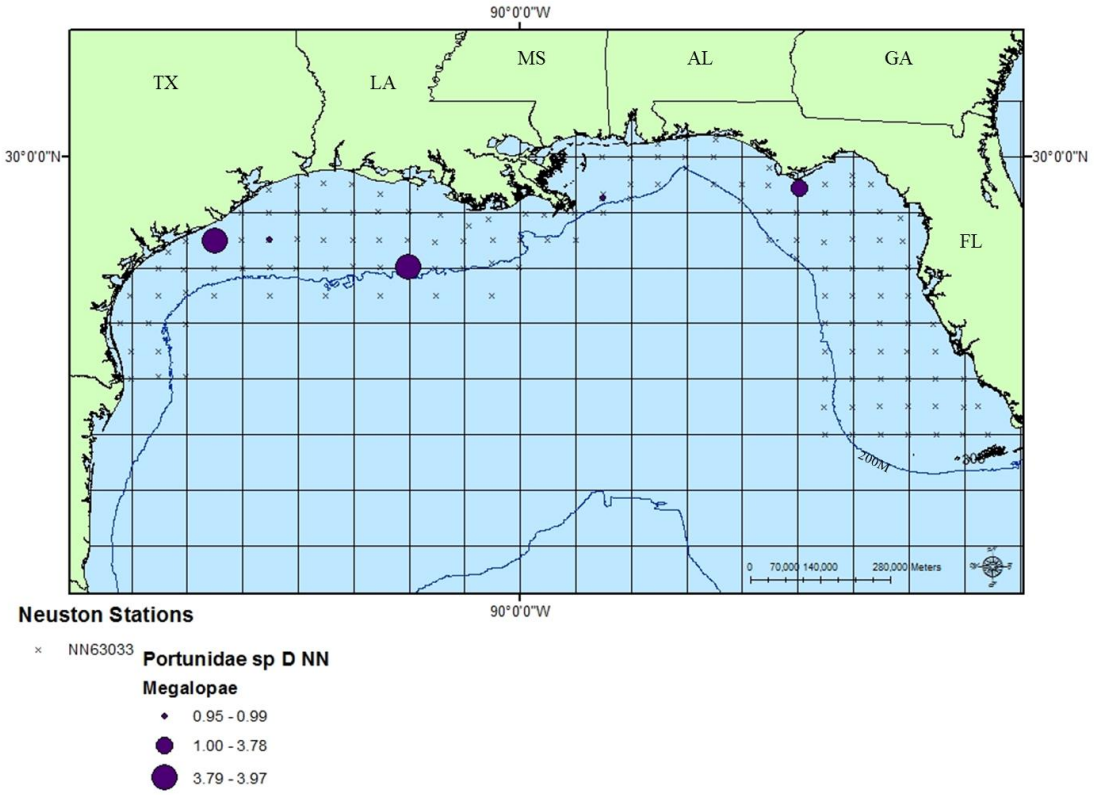

Figure 12. Map of the Distribution and CPUE of Portunidae sp. D Megalopae in Neuston Samples.

Portunidae sp. E (Figures 13 & 14)

Diagnostic description. Carapace and pereopods: Carapace rectangular, lacking a dorsal spine, with dip at base of rostral plate; rostrum 95% length of antenna, bearing one pair of ventral setae at tip, nearly horizontal; strong pair of spines extending from posterior margin of seventh thoracic segment posteriorly to midline of third abdominal segment. Eyestalks lacking pigment spots. Cheliped, spination unknown; pereopods 2-5 lacking spine; dactyl of pereopod 5 paddle-like, number of hooked setae unknown.

Antenna: Consisting of 9 segments, flagellum of 6 segments, relative segment length pattern for segments1-3 of short-short-medium, as shown (Figure 13).

Abdomen and pleopods: Abdomen, second segment smooth in lateral view, fifth segment with large posterolateral spines that extend past posterior margin of sixth abdominal segment; telson with slight medial point on distal margin, bearing one pair of setae on distomedial dorsal surface. Pleopods present on abdominal segments 2-6; pleopod 5 (uropod) lacking endopod, bearing 1 plumose seta on basal segment and 10 plumose setae on exopod.

Remarks. This morph did not match a known genera based on the presence of only 6 antennae flagellum segments. No known generic or species description for portunid taxa present in the GOM has this feature. CL= 1.49mm.

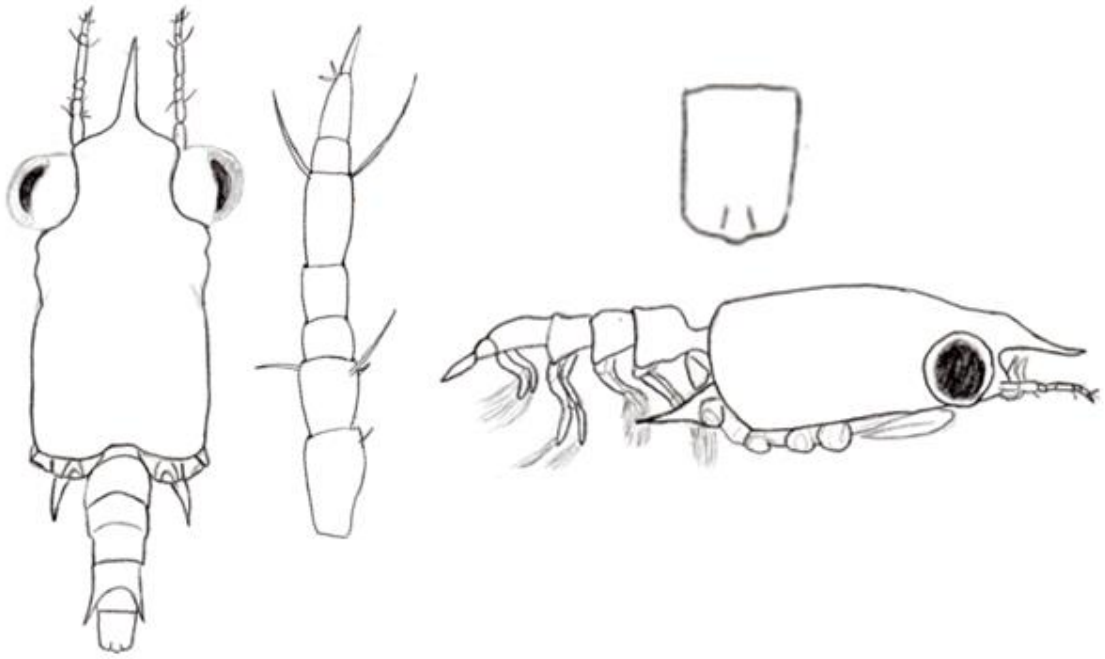

Figure 13. Drawings of Portunidae sp. E Megalopa. Full dorsal view, pereopods omitted (left): antenna, dorsal view (center); telson, dorsal view (top right): full lateral view, pereopods omitted (bottom right).

Figure 14. Photographs of Portunidae sp. E Megalopa. Full dorsal view (A); telson, dorsal view (B); antenna, ventral view (C); full lateral view (D).

Distribution. Portunidae sp. E was only found in one neuston sample at a station out past the shelf margin off the coast of southern Texas (Figure 15).

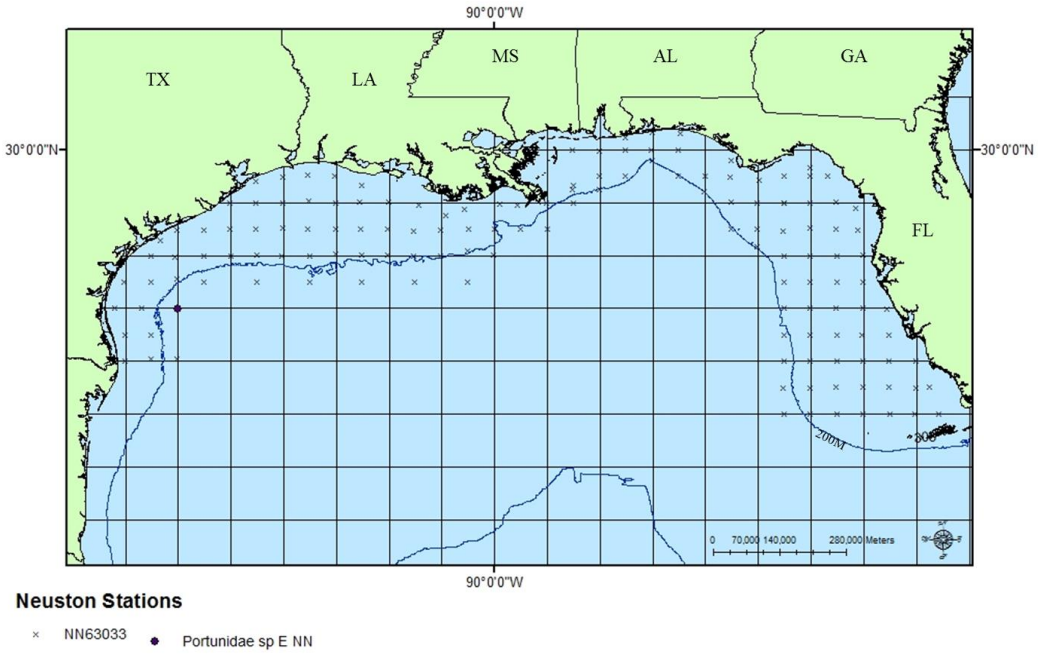

Figure 15. Map of the Distribution of Portunidae sp. E in Neuston Samples.

Portunidae sp. G (Figures 16 & 17)

Diagnostic description. *Carapace and pereopods*: Carapace rectangular, lacking a dorsal spine, with 3 small plumose setae on lateral edge of rostral plate above eyestalk; rostrum 90% length of antenna, bearing several pairs of setae along lateral margins without ventral setae, angling slightly downward before curving upward at tip; strong pair of spines extending from posterior margin of seventh thoracic segment posteriorly to anterior margin of third abdominal segment. Eyestalks lacking pigment spots. Cheliped, lacking disto-medial carpal spine, with large hooked basi-ischial spine; pereopod 2 bearing coxal spine; pereopods 3-5 lacking coxal spine; dactyl of pereopod 5 paddle like, number of hooked setae unknown.

Antenna: Consisting of 11 segments, flagellum of 8 segments, relative segment length pattern for segments 1-5 of short-medium-short-long-long, as shown (Figure 16).

Abdomen and pleopods: Abdomen, segments 2 and 3 mildly humped in lateral view, fifth segment with large posterolateral spines that extend past posterior margin of sixth abdominal segment; telson with flat distal margin, with 4 median terminal setae and 3 pairs of setae on dorsal surface, arrangement as shown. Pleopods present on abdominal segments 2-6; pleopod 5 (uropod) lacking endopod, bearing 1 plumose seta on basal segment and 16 plumose setae on exopod.

Remarks. This megalopa was the second largest identified in the samples (CL= 2.94 ± 0.03mm). Though visually similar to *Arenaeus cribrarius,* this megalopa lacked a carpal spine on the cheliped. Genetic analysis on this specimen yielded no match to sequences available for known GOM Portunids. The location of the samples in which this morph was found suggests that the morph may have been transported to the GOM via the Loop Current.

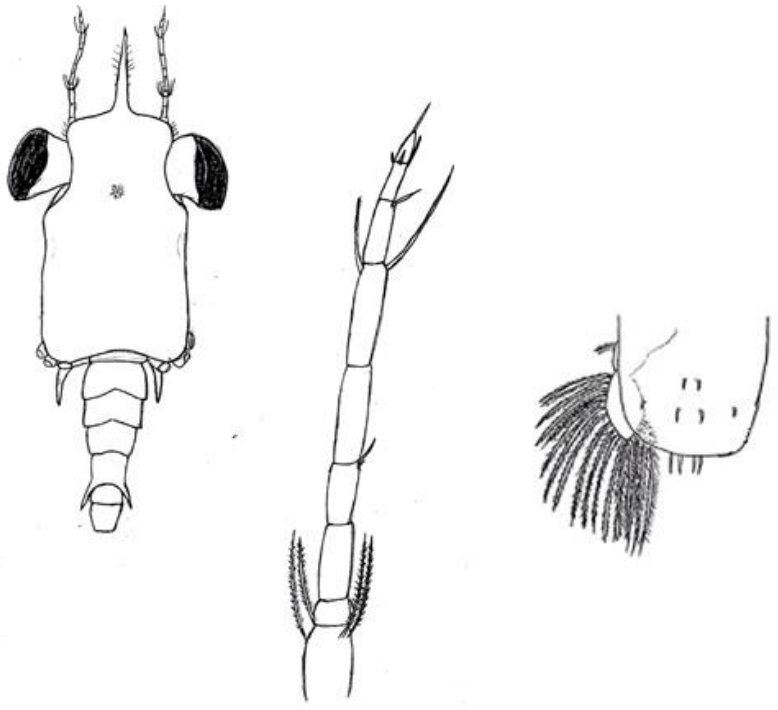

Figure 16. Drawings of Portunidae sp. G Megalopa. Full dorsal view, pereopods omitted (left); antenna, dorsal view (center); Telson, dorsal view with left uropod (right).

Figure 17. Photographs of Portunidae sp. G Megalopa. Full dorsal view (A); rostrum and antennae, dorsal view (B); full lateral (C).

Distribution. Portunidae sp. G was aggregated off the coast of Louisiana, both on and offshore, between the Atchafalaya river basin and the Mississippi river delta, with sparse occurrences off the coast of Florida (Figure 18).

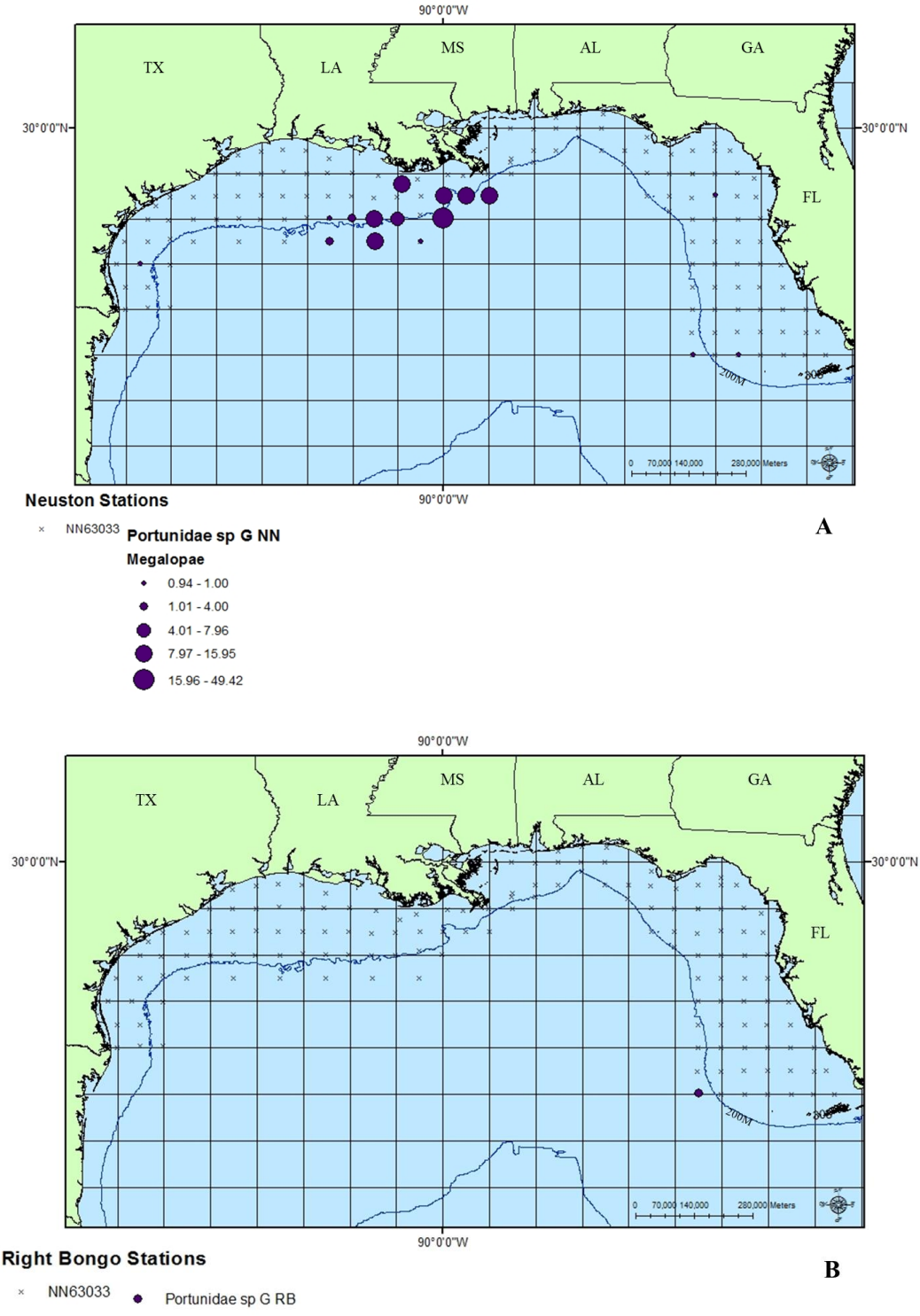

Figure 18. Maps of the Distribution and CPUE of Portunidae sp. G in Neuston (A) and Bongo (B) Samples.

Genus *Achelous* (DeHann, 1833)

Originally proposed by DeHann in 1833, this genus has been resurrected based on recent genetic work reclassifying several *Portunus* species (Mantelatto et al., 2009). All megalopae classified as *Achelous* possess 7 flagellum segments in the antennae, a distomedial carpal spine on the cheliped, and a ventral spine on the coxa of pereopod 2. All also lack a basi-ischial spine on the cheliped. Larval descriptions exist for *Achelous spinicarpus* (Bookhout and Costlow, 1974), *Achelous spinimanus* (Negrieros-Fransozo et al., 2007), and *Achelous gibbesii* (Negrieros-Fransozo et al., 2007), though all are described under the genus *Portunus*. The GOM harbors five additional species in this genus (*A. asper, A. binoculus, A.depressifrons, A. ordwayi*, and *A. sebae*) for which there are no larval descriptions available. In this study, specimens identified as *Achelous* but not fitting the available descriptions were assigned letter codes. Notes were made about their appearance and distinguishing characteristics in order to easily separate them. The first initial pass through the samples resulted in the identification of nine *Achelous* morphs, but after a second examination, some letter codes were consolidated, resulting in five remaining morphs.

Achelous gibbesii (Stimpson 1859) (Figures 19-24) (Modified from Negreiros-Fransozo et al., 2007)

Diagnostic description. Carapace and pereopods: Carapace rectangular, lacking a dorsal spine; rostrum short, approximately 70% length of antenna, slightly downturned; pair of spines extending from posterior margin of seventh thoracic segment posteriorly no further than the anterior portion of the second abdominal segment, not visible in dorsal view if pereopod 5 is present. Eyestalks bearing a pair of small pigment spots on either

the dorsal or anterior surface. Cheliped with disto-medial carpal spine present, lacking basi-ischial spine; pereopod 2 with ventral coxal spine; pereopods 3-5 lacking ventral coxal spine; dactyl of pereopod 5 paddle-like, with 6 hooked setae.

Antenna: Consisting of 10 segments, flagellum of 7 segments, relative segment length pattern for segments 1-4 of short-medium-short- medium, as shown (Figure 19).

Abdomen and pleopods: Abdomen, second segment humped in lateral view, fifth segment with large posterolateral spines that extend past posterior margin of sixth abdominal segment; telson square with slightly rounded distal margin with few fine setae. Pleopods present on abdominal segments 2-6; pleopod 5 (uropod) lacking endopod, bearing 1 plumose seta on basal segment and 10-11 plumose setae on exopod.

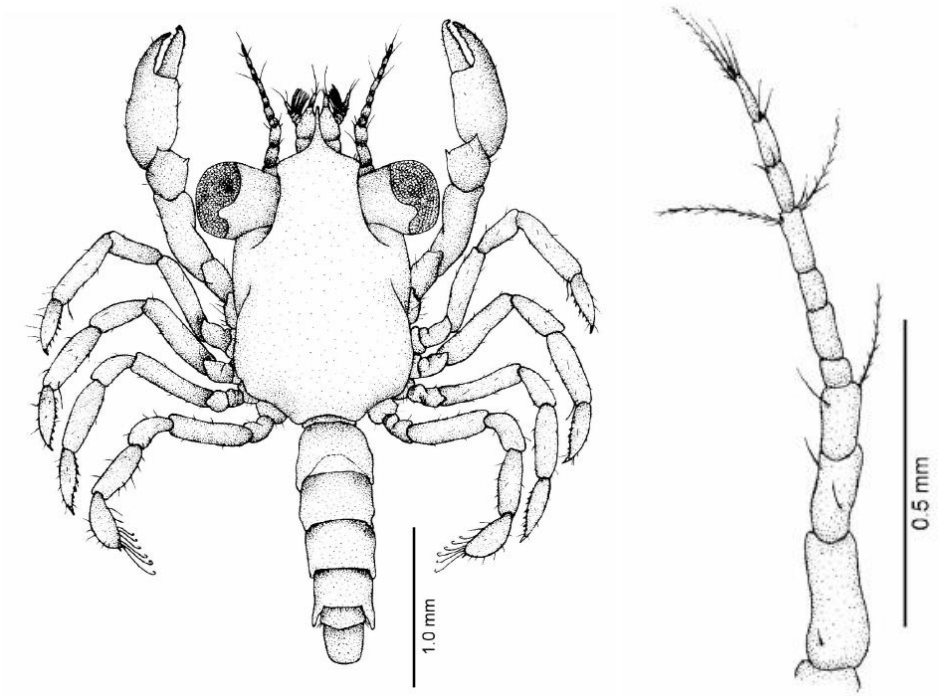

Figure 19. Drawings of *Achelous gibbesii* Megalopa. Full dorsal view (left); antenna, orientation unknown (right). From Negreiros-Fransozo et al. (2007) (as *Portunus gibbesii*).

Remarks. In the original description of the megalopa of *Portunus* (=*Achelous*) *gibbesii*), the authors noted the lack of a ventral spine on the coxa of pereopod 2.

However, to confirm identifications, the molts of specimens used by Negreiros-Fransozo et al. (2007) were examined and found to bear this spine. The spine was very small and tucked up against the sternum making it difficult to see. This pereopod 2 coxal spine was also seen in all GOM specimens. In addition, eyespots were not mentioned in the original description of the megalopa of *A. gibbesii*, and the presence or absence of pigmentation was not possible to determine from the molts. Eyespots were present in all GOM specimens, either on the dorsal or anterior surface of the eyestalk. This may be an actual variation in location or the eyes may have been rotated at time of preservation.

Three morphological variants of *A. gibbesii* occurred in the SEAMAP samples, originally identified as *Achelous* sp. A., *Achelous* sp. G., and *Achelous* sp. H and referred to herein as variants A, G and H. (Figures 20-22). The main differences between the variants were seen in the length and shape of the sternal spines, as well as in the length and angle of the rostrum and the amount of pigment present on the carapace and abdomen. In the original description, the sternal spines are noted to be small and not visible in dorsal view. Because the majority of specimens in this study lacked the fifth pereopods, the spines were visible. Spines across all variations were small, never extending past the posterior margin of the second abdominal segment. Sternal spine shape ranged from being v-shaped and extending posteriorly adjacent to the abdomen (variants A and G) to being more conical and flaring out from the abdomen (variant H). The short and stout rostrum varies from slightly (variant G) to strongly (variant A and H) angled downward. One variant, H, is highly covered in tiny pigment spots all over the dorsal surface of the carapace. Standard pigment placements noted across all variants include one spot on the dorsal surface of the carapace located medially behind the eyes,

one ventral spot on the coxa of pereopod 2, one to three spots located at the posterodorsal midline of the carapace, and spots above each pleopod along the ventral surface of the abdomen.

Negreiros-Fransozo et al. (2007) published a CL= 1.83 ± 0.17mm. The megalopae from this study that matched the morphological description provided by Negreiros-Fransozo et al. (2007) were much smaller than the published size (CL= 1.38 ± 0.09 mm). The 3 variants, however, were closer to the published length (variant A, CL= 1.70mm, variant G, 1.84mm, variant H, 1.46 ± 0.06mm).

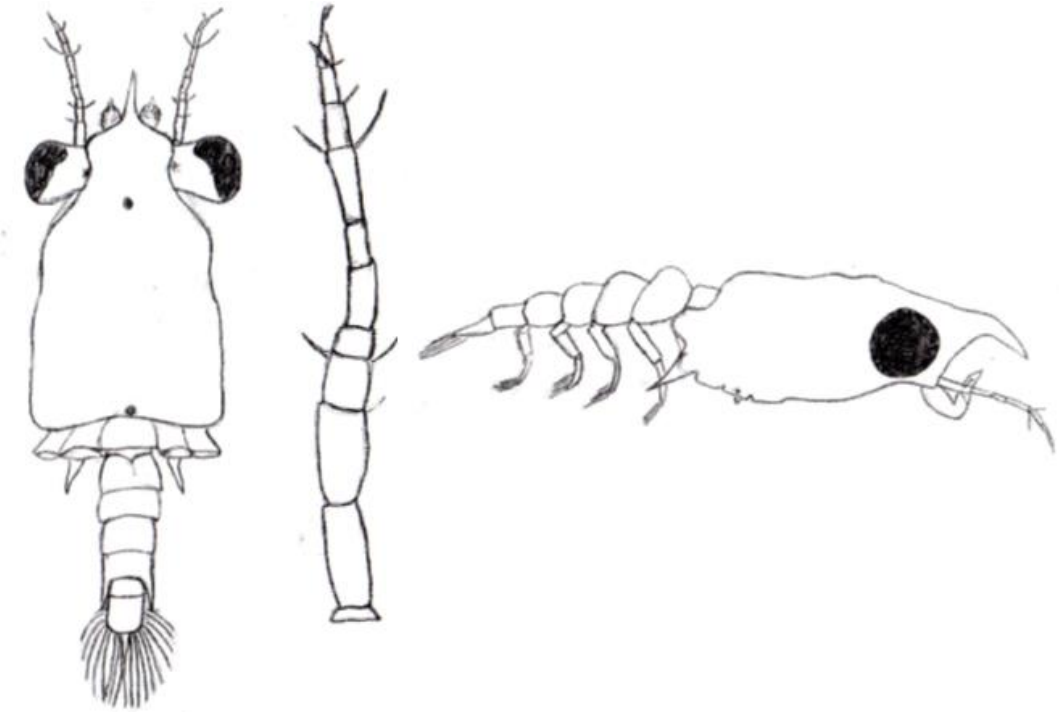

Figure 20. Drawings of *Achelous gibbesii* Megalopa (sp. A Variation). Full dorsal view (left); anteanna, dorsal view (center); full lateral view (right).

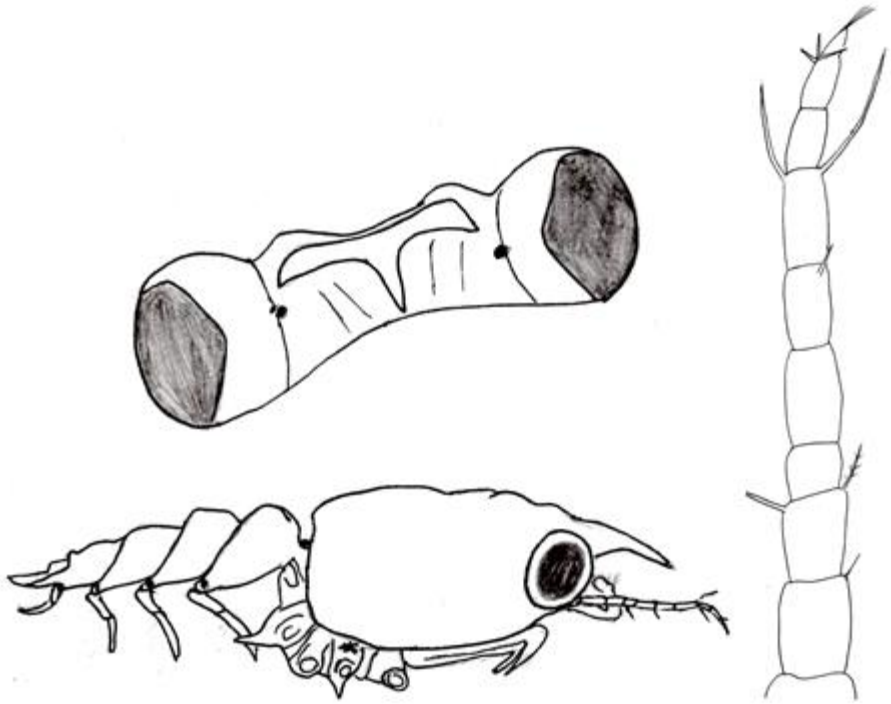

Figure 21. Drawings of *Achelous gibbesii* Megalopa (sp. G Variation). Eyes, showing placement of eye spots, anterior view (top left); full lateral view (bottom left); antenna, dorsal view (right).

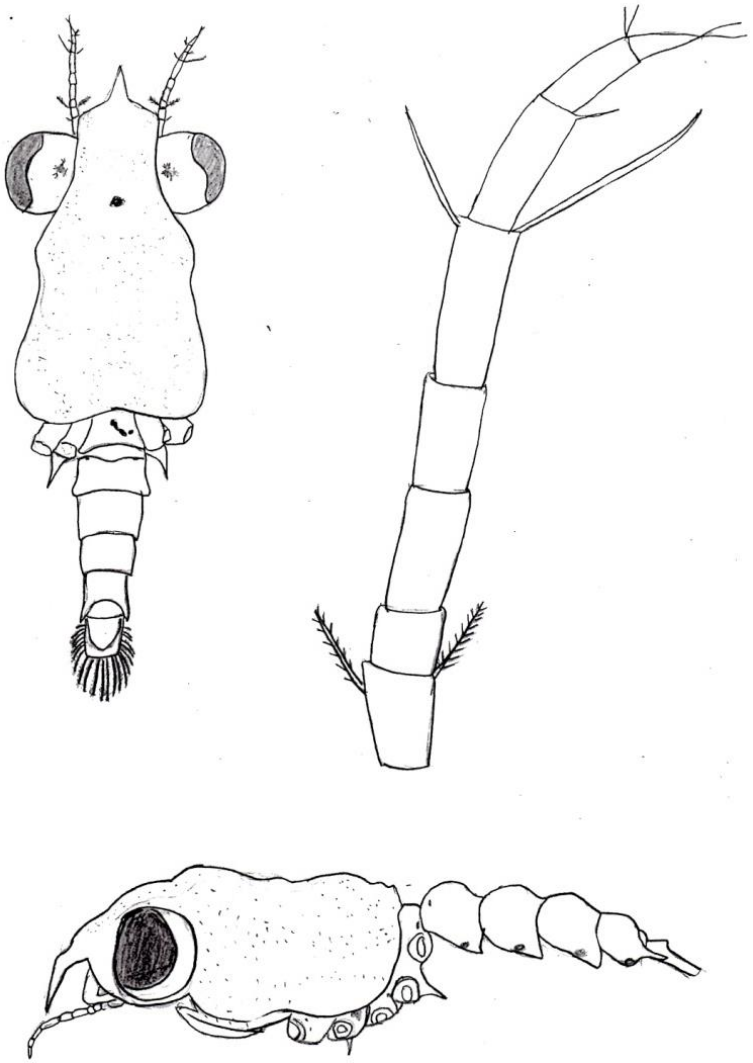

Figure 22. Drawings of *Achelous gibbesii* Megalopa (sp. H Variation): Full dorsal view (top left), antenna, dorsal view (top right); full lateral view (bottom).

Figure 23. Photographs of the Three Variations of *A. gibbesii* Megalopae Found in Samples. Variant A. (A); variant G. (B); variant H. (C).

Distribution. *Achelous gibbesii* was found on the continental shelf throughout the northern GOM, with larger densities generally occurring at shallower water depths (Figure 30).

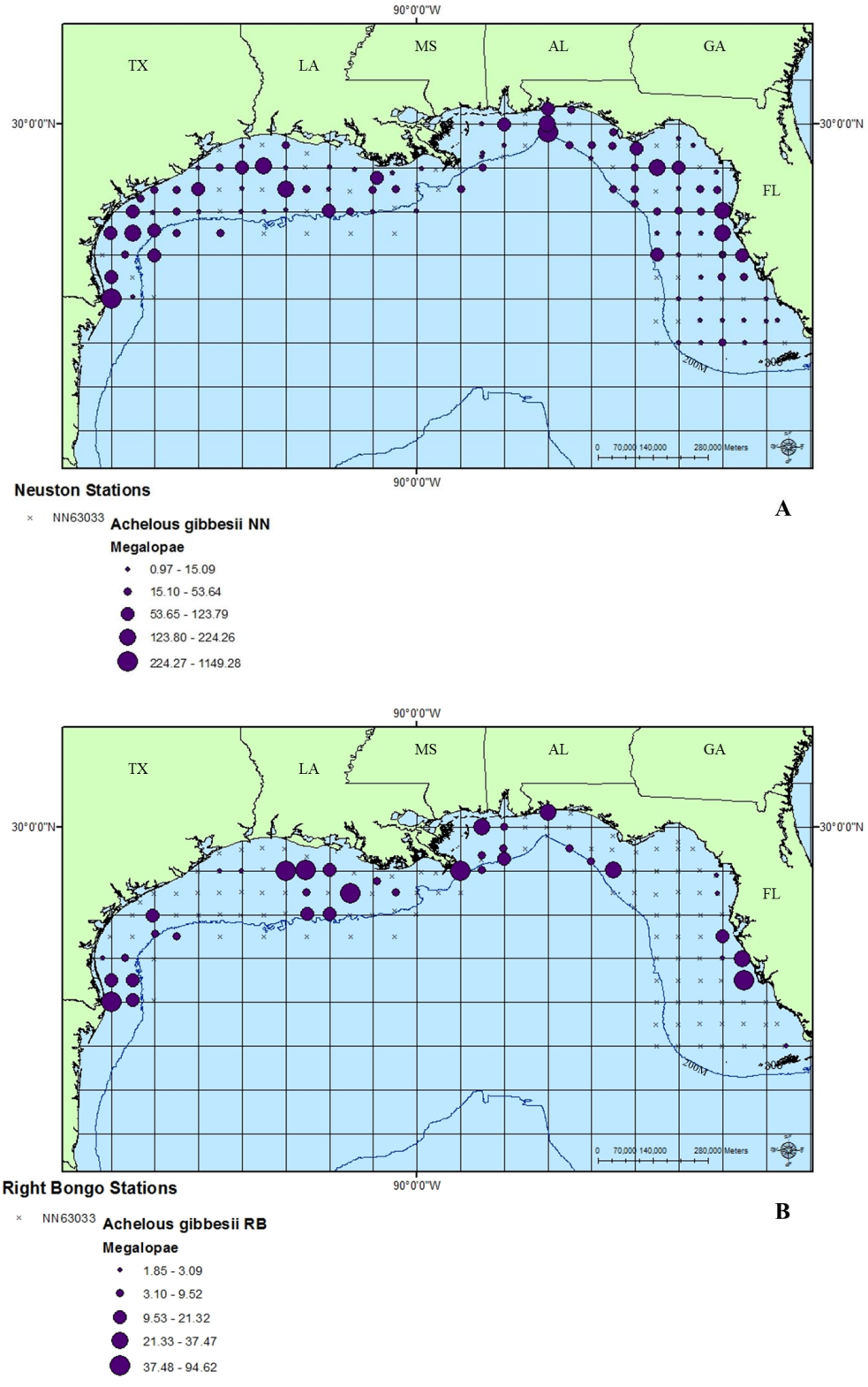

Figure 24. Maps of the Distribution and CPUE of *Achelous gibbesii* in Neuston (A) and Bongo (B) Samples.

Achelous spinicarpus (Stimpson, 1871) (Figures 25 & 26) (Modified from Bookhout and Costlow, 1974)

Diagnostic description. *Carapace and pereopods*: Carapace rectangular, lacking a dorsal spine; rostrum 50% length of antenna, horizontal to angled slightly downward, 50% the length of antenna; pair of spines extending from posterior margin of seventh thoracic segment posteriorly not reaching past the midline of second abdominal segment. Eyestalks lacking pigment spots. Cheliped with strong disto-medial carpal spine present, lacking basi-ischial spine; pereopod 2 with ventral coxal spine; pereopods 3-5 lacking ventral coxal spine; dactyl of pereopod 5 paddle-like, with 6-7 hooked setae.

Antenna: Consisting of 10 segments, flagellum of 7 segments, relative segment length pattern for segments 1-4 of short-medium-short-long, as shown (Figure 25).

Abdomen and pleopods: Abdomen, second segment humped in lateral view, fifth segment with large posterolateral spines that extend past posterior margin of sixth abdominal segment; telson with slightly rounded distal margin, lacking spines or setae. Pleopods present on abdominal segments 2-6; pleopod 5 (uropod) lacking endopod, bearing 1 plumose seta on basal segment and 11 plumose setae on exopod.

Remarks. Megalopa identified as *A.spinicarpus* match the published description (Bookhout and Costlow 1974) closely. Sizes of identified megalopae were comparable to those published. CL= 1.82 ± 0.10mm (Bookhout and Costlow, 1974; Stuck and Truesdale, 1988).

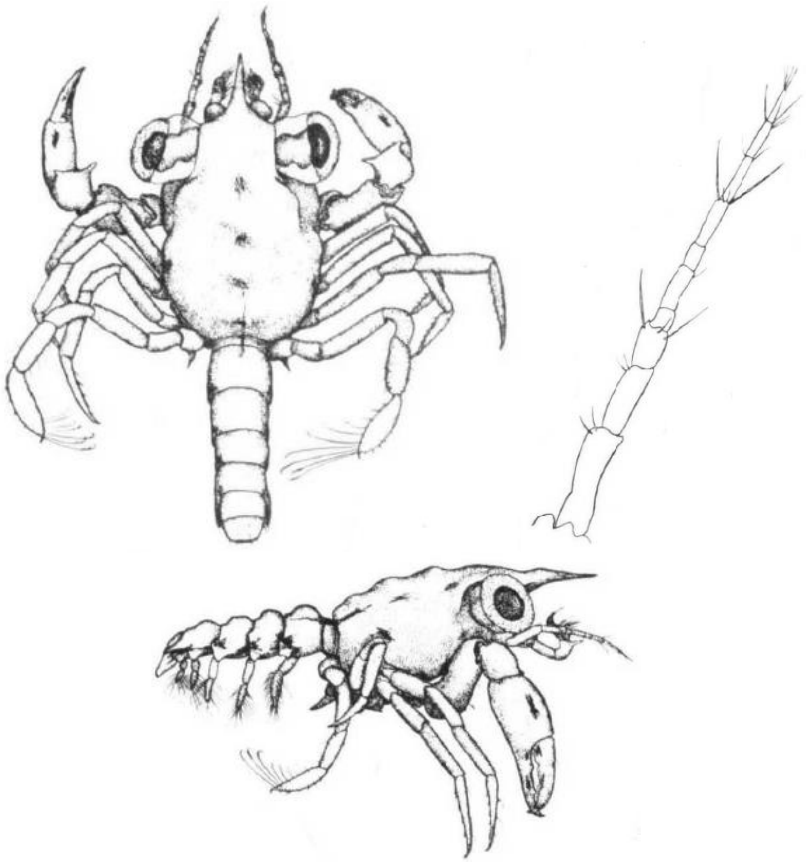

Figure 25. Drawings of *Achelous spinicarpus* Megalopa. Full dorsal view (top left); antenna, dorsal view (top right); full lateral view (bottom left) (from Bookhout and Costlow, 1974, as *Portunus spinicarpus*).

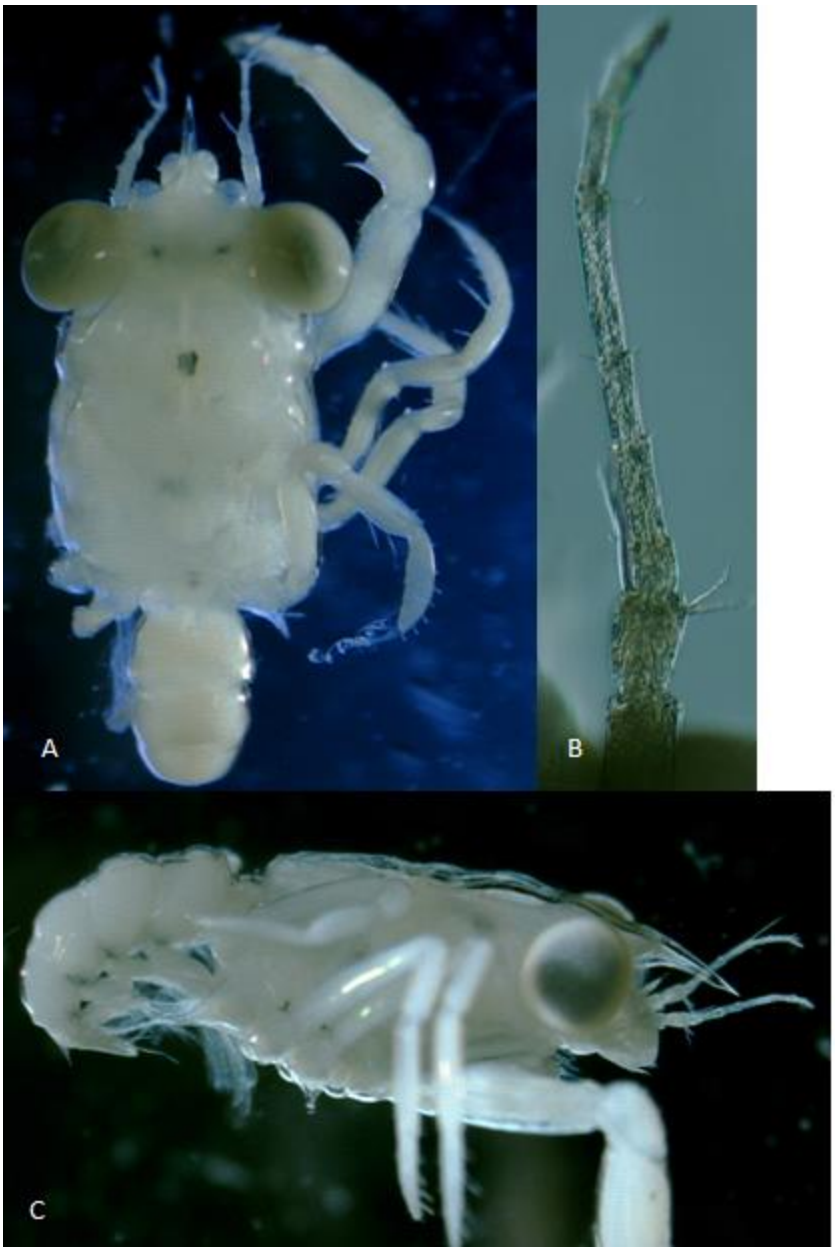

Figure 26. Photographs of *Achelous spinicarpus* Megalopa. Full dorsal view (A); antenna, dorsal view (B); full lateral view (C).

Distribution. *Achelous spinicarpus* was found throughout the GOM, ranging from onshore to offshore with the largest concentrations occurring off the coast of Florida (Figure 27).

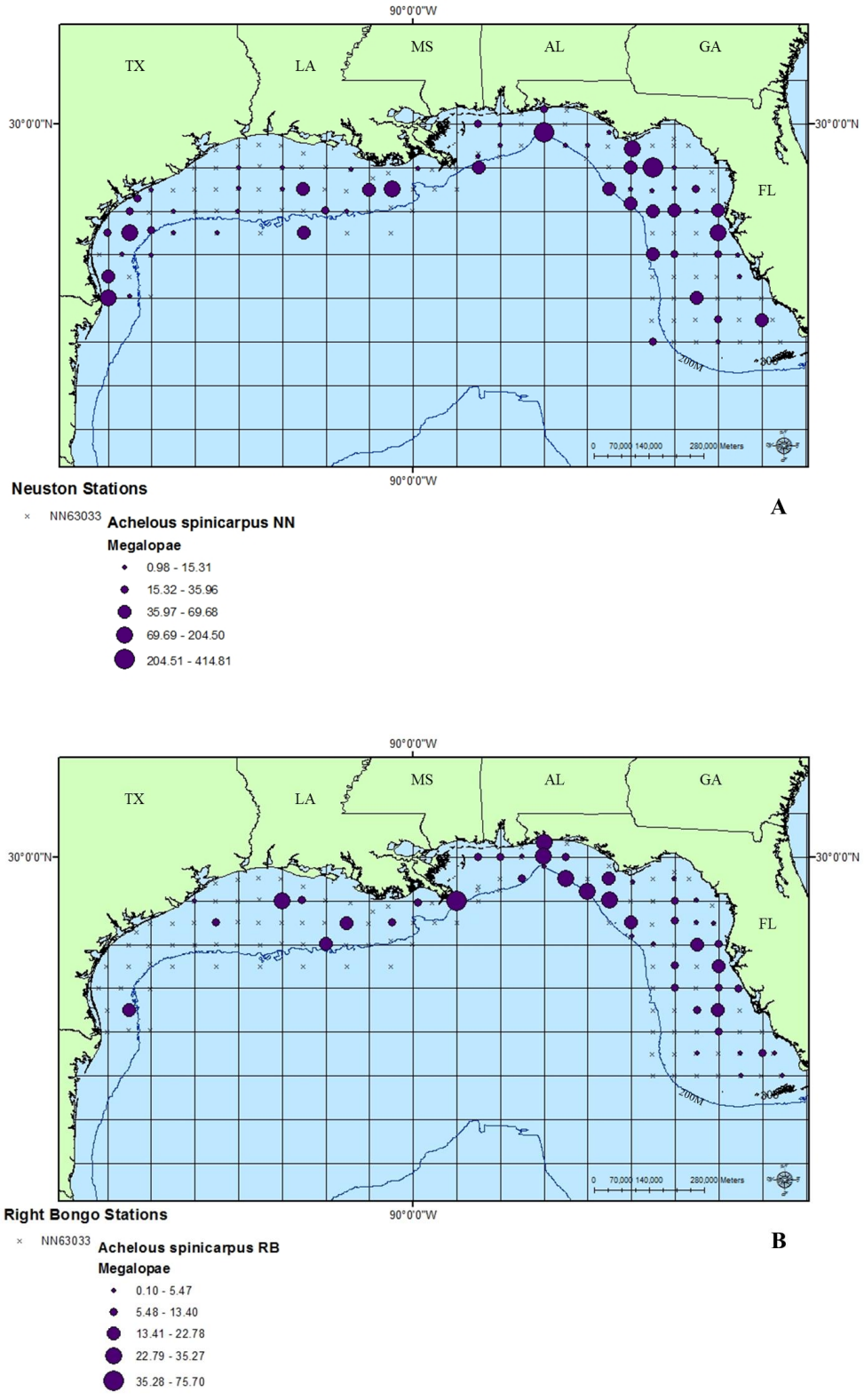

Figure 27. Maps of the Distribution and CPUE of *Achelous spinicarpus* in Neuston (A) and Bongo (B) Samples.

Achelous spinimanus (Latreille 1819) (Figures 28 & 29) (Modified from Negreiros-Fransozo et al., 2007)

Diagnostic description. *Carapace and pereopods*: Carapace rectangular, lacking a dorsal spine; rostrum 70% length of antenna, horizontal; pair of spines extending from posterior margin of seventh thoracic segment posteriorly no further than anterior portion of the second abdominal segment, not visible when pereopod 5 is present. Eyestalks lacking pigment spots. Cheliped with disto-medial carpal spine present, lacking basi-ischial spine; pereopod 2 with ventral coxal spine; pereopods 3-5 lacking ventral coxal spine; dactyl of pereopod 5 paddle-like, with 6-7 hooked setae.

Antenna: Consisting of 10 segments, flagellum of 7 segments, relative segment length pattern for segments 1-4 of short-medium-medium-long, as shown (Figure 22).

Abdomen and pleopods: Abdomen, second segment humped in lateral view, fifth segment with large posterolateral spines that extend past posterior margin of sixth abdominal segment; telson square with slightly rounded distal margin with few fine setae. Pleopods present on abdominal segments 2-6; pleopod 5 (uropod) lacking endopod, bearing 1 plumose seta on basal segment and 12 plumose setae on exopod.

Remarks. The published description of this megalopa (Negriros-Fransozo et al., 2007) was from specimens collected off the east coast of South Carolina. These specimens were much larger than what were identified in this study (CL= 20.9 ± 0.13mm (Negriros-Fransozo et al., 2007); 1.70 ± 0.02mm GOM specimens). All other morphological features seemed to hold true to the description of the megalopa.

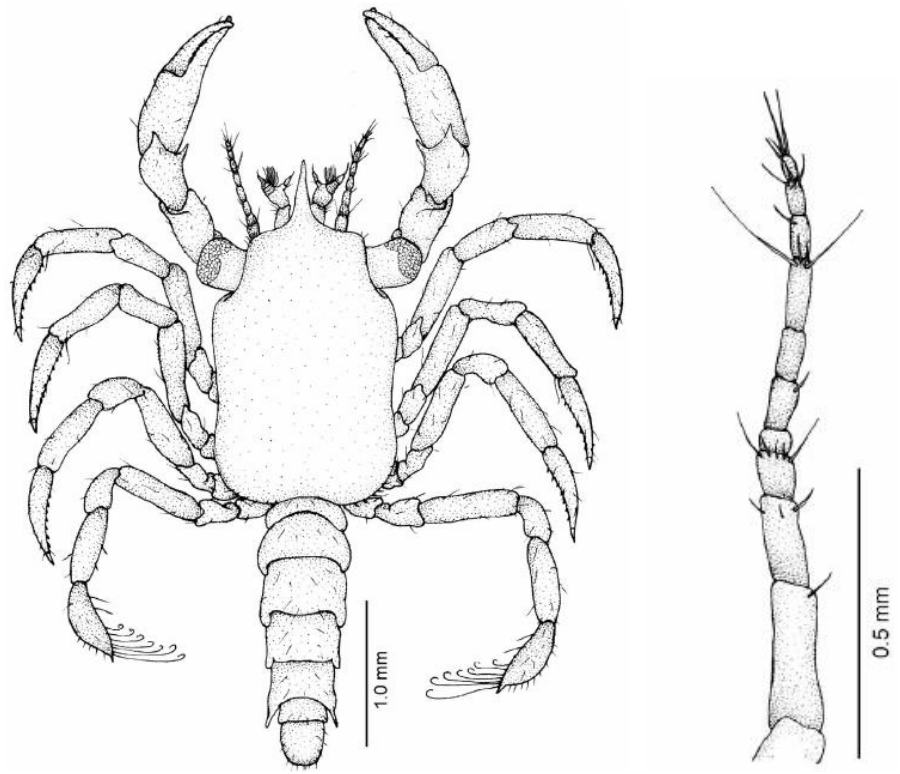

Figure 28. Drawings of *Achelous spinimanus* Megalopa. full dorsal view (left); antenna, orientation unknown (right). (from Negreiros-Fransozo et al., 2007, as *Portunus spinimanus*).

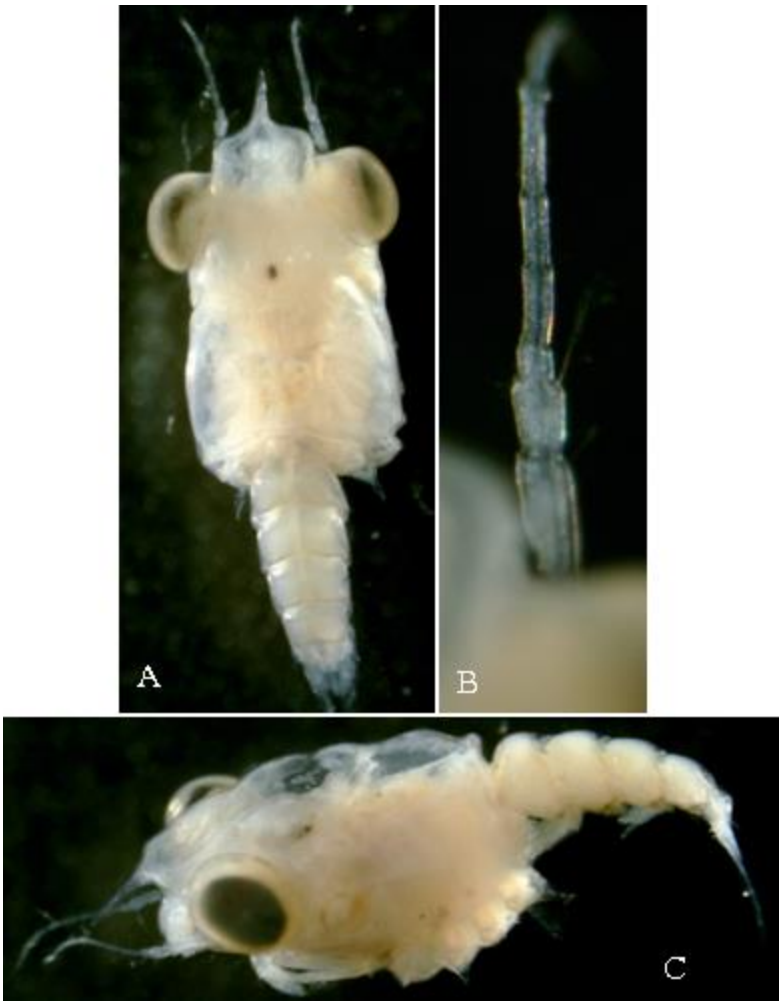

Figure 29. Photographs of *Achelous spinimanus* Megalopa. Full dorsal view (A); antenna, dorsal view (B); Full lateral view (C).

Distribution. *Achelous spinimanus* was found throughout the northern GOM,from shallow nearshore waters out to just beyond the shelf break with highest concentrations occuring off the coast of Florida (Figure 24).

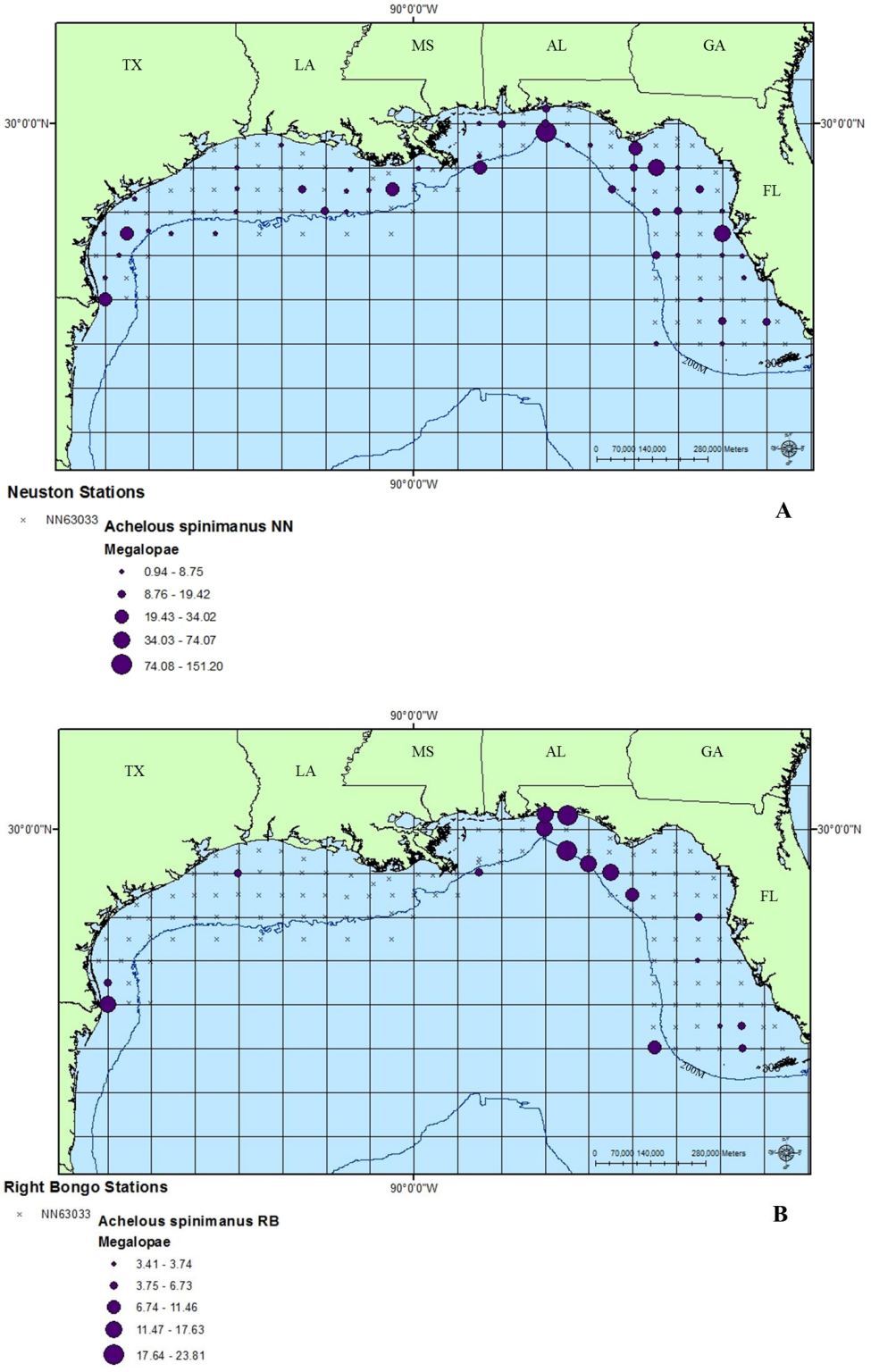

Figure 30. Maps of the Distribution and CPUE of *Achelous spinimanus* in Neuston (A) and Bongo (B) Samples.

Achelous sp. B (Figures 31 & 32)

Diagnostic description. Carapace and pereopods: Carapace rectangular, lacking a dorsal spine; rostrum long, 70% the length of antenna, horizontal; pair of spines extending from posterior margin of seventh thoracic segment posteriorly to anterior margin of third abdominal segment. Eyestalks lacking pigment spots. Cheliped bearing disto-medial carpal spine, lacking basi-ischial spine; pereopod 2 bearing strong ventral coxal spine; pereopods 3-5 lacking ventral coxal spine; dactyl of pereopod 5 paddle-like, number of hooked setae unknown.

Antenna: Consisting of 10 segments, flagellum of 7 segments, relative segment length pattern for segments 1-4 of short-medium-medium-long, as shown (Figure 31).

Abdomen and pleopods: Abdomen, second segment humped in lateral view, fifth segment with posterolateral spines that extend past posterior margin of sixth abdominal segment; telson squared, distal margin transverse, lacking spines or setae. Pleopods present on abdominal segments 2-6; pleopod 5 (uropod) lacking endopod, bearing 1 plumose seta on basal segment and 12-13 plumose setae on exopod.

Remarks. This megalopae was the largest *Achelous* morph seen (CL= 2.15mm). Morphologically it most closely matched *A. spinicarpus*, and may possibly be a variant. The antennal flagellum segment pattern more closely matched *A. spinimanus*, though the antennae were much larger in size than appears to be true in Negreiros-Fransozo et al.'s (2007) description. Based on the size of this megalopa it is possible it may also be a variant of *A. spinimanus*.

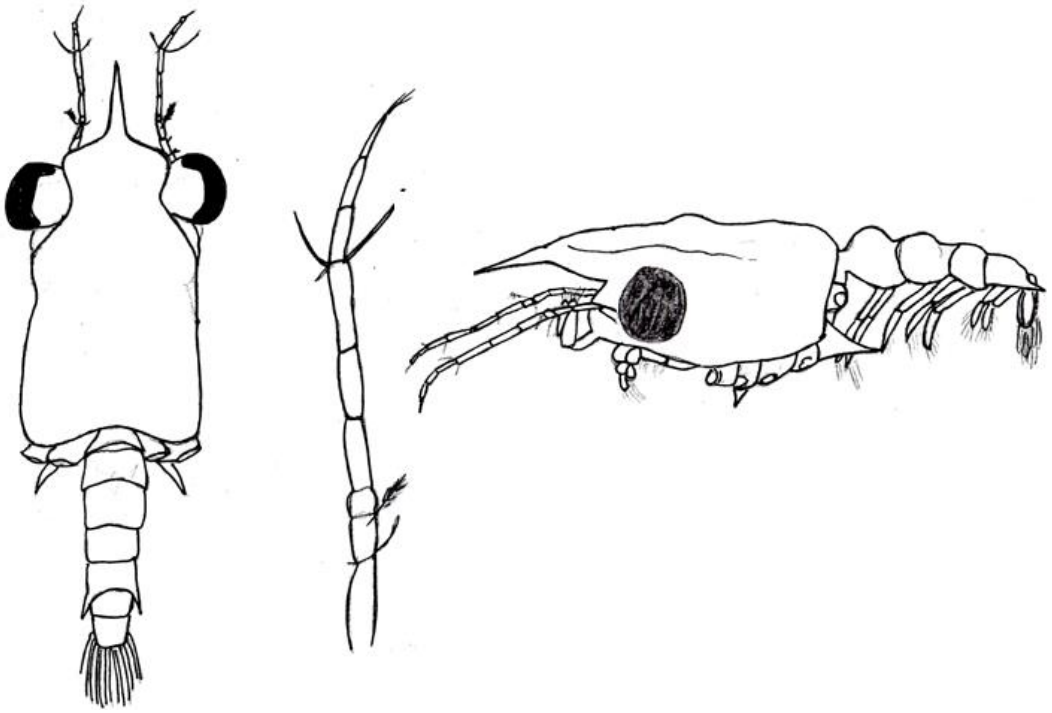

Figure 31. Drawing of *Achelous* sp. B Megalopa. Full dorsal view (left); antenna, dorsal view (center); full lateral view (right).

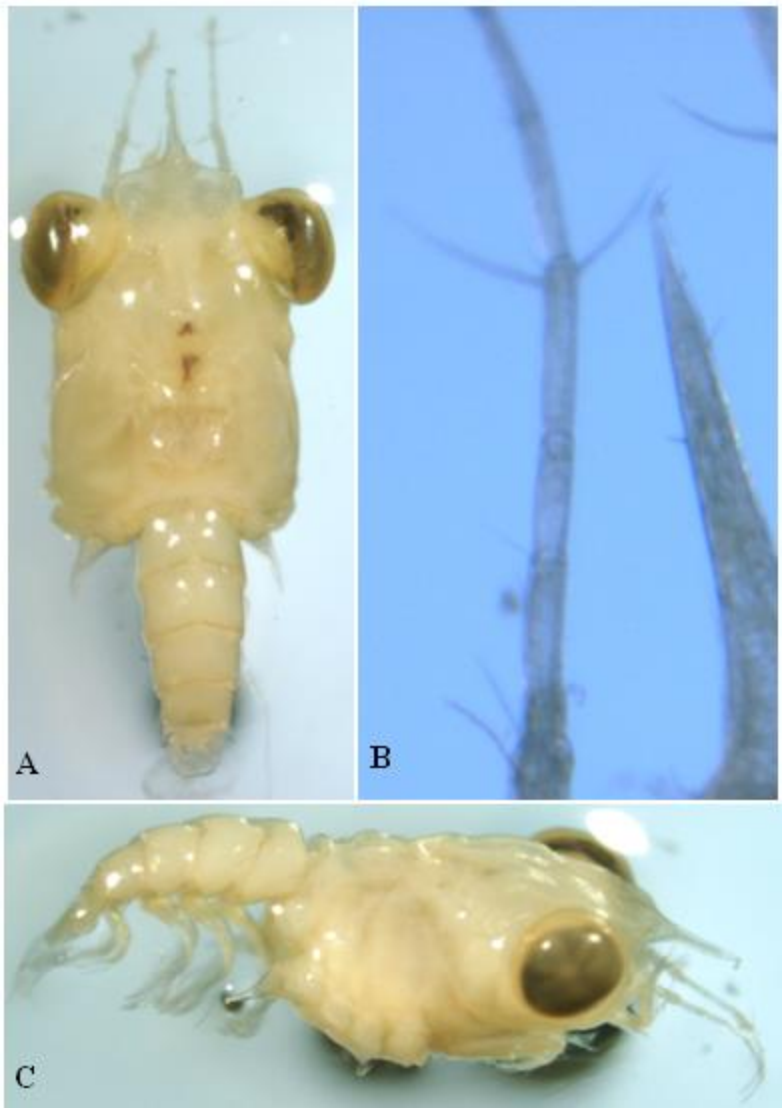

Figure 32. Photographs of *Achelous* sp. B Megalopa. Full dorsal view (A); antenna, dorsal view (B); full lateral view (C).

Distribution. *Achelous* sp. B was found in samples across the GOM, with the majority of the samples being from off the coast of Florida. Highest concentrations tended to lie near the shelf break (Figure 33).

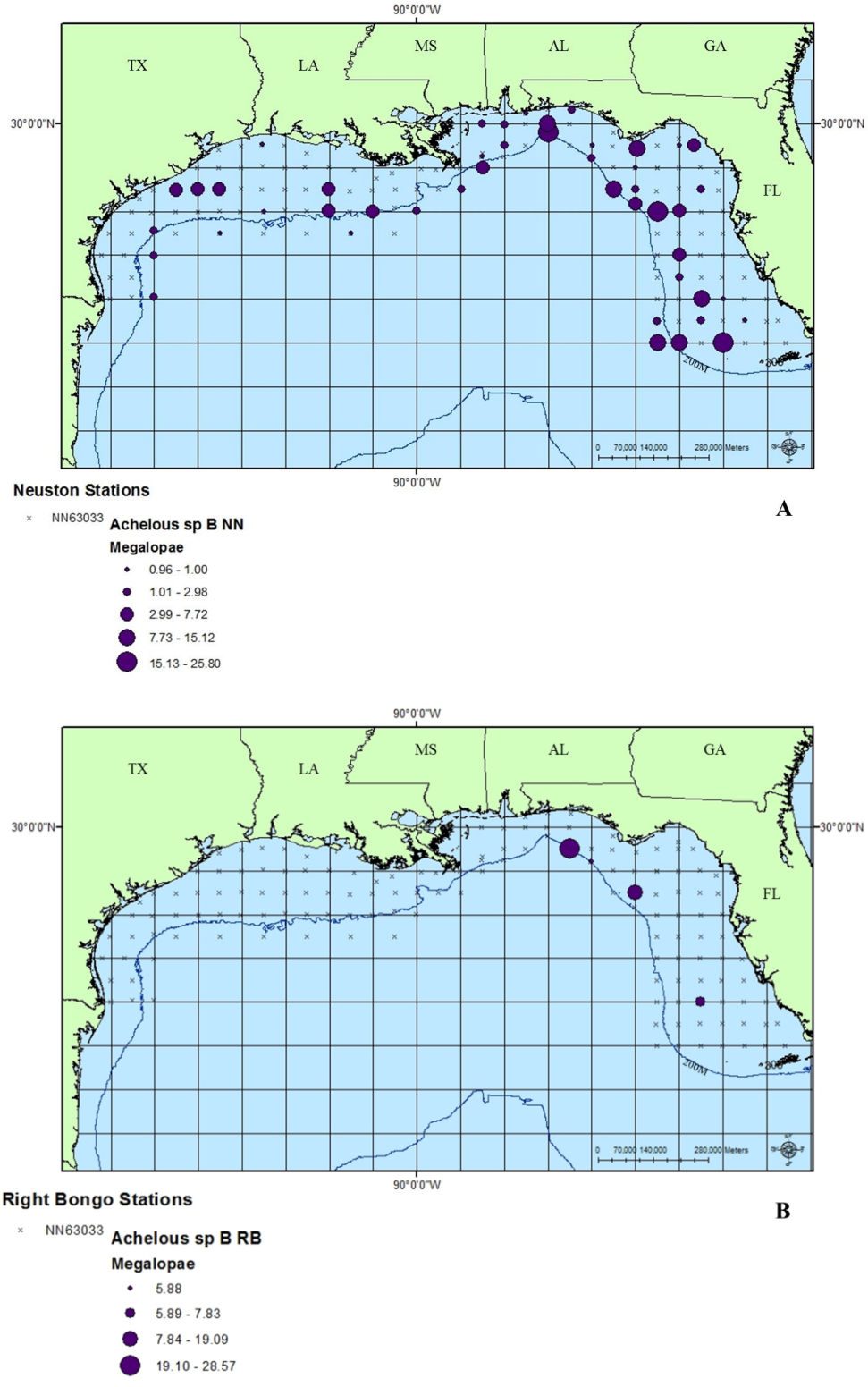

Figure 33. Maps of the Distribution and CPUE of *Achelous* sp. B in Neuston (A) and Bongo (B) Samples.

Achelous sp. C (Figures 34 & 35)

Diagnostic description. Carapace and pereopods: Carapace rectangular, lacking a dorsal spine; rostrum 80% the length of antenna, angled slightly downward; small pair of spines extending from posterior margin of seventh thoracic segment posteriorly to middle of second abdominal segment. Eyestalks lacking pigment spots. Cheliped bearing disto-medial carpal spine, lacking basi-ischial spine; pereopod 2 bearing small ventral coxal spine angled toward center of thorax; pereopods 3-5 lacking ventral coxal spine; dactyl of pereopod 5 paddle-like, number of hooked setae unknown.

Antenna: Consisting of 10 segments, flagellum of 7 segments, relative segment length pattern for segments 1-4 of short-long-short-long, as shown (Figure 34).

Abdomen and pleopods: Abdomen, second segment humped in lateral view, fifth segment with large posterolateral spines that extend past posterior margin of sixth abdominal segment; telson subquadrate with low, broad medial protrusion on distal margin, lacking spines or setae. Pleopods present on abdominal segments 2-6; pleopod 5 (uropod) lacking endopod, bearing 1 plumose seta on basal segment and 11 plumose setae on exopod.

Remarks. The two most unique features of this megalopa are the long second antennal flagellum segment and the medial protuberance on the distal margin of the telson. This megalopa also possesses a small spine on the posterior margin of the 4th thoracic segment. The small sternal spine size is similar to both *A. gibbesii* and *A. spinimanus* but the antennal segment pattern differs from both of these species. CL= 1.49mm.

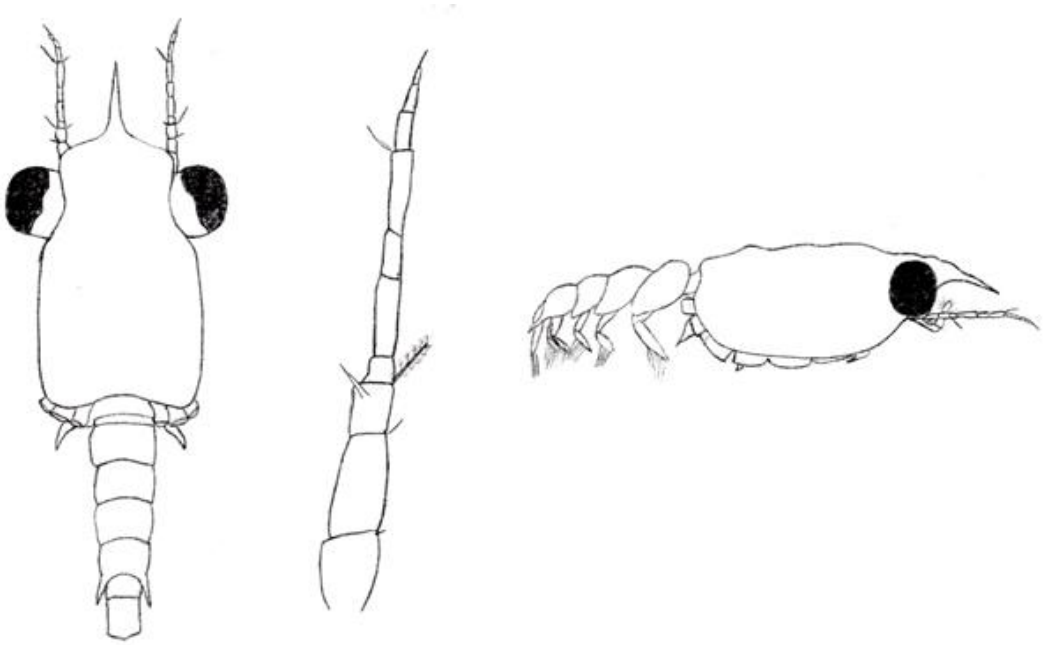

Figure 34. Drawings of *Achelous* sp. C Megalopa. Full dorsal view (left); antenna, dorsal view (center); full lateral view (right).

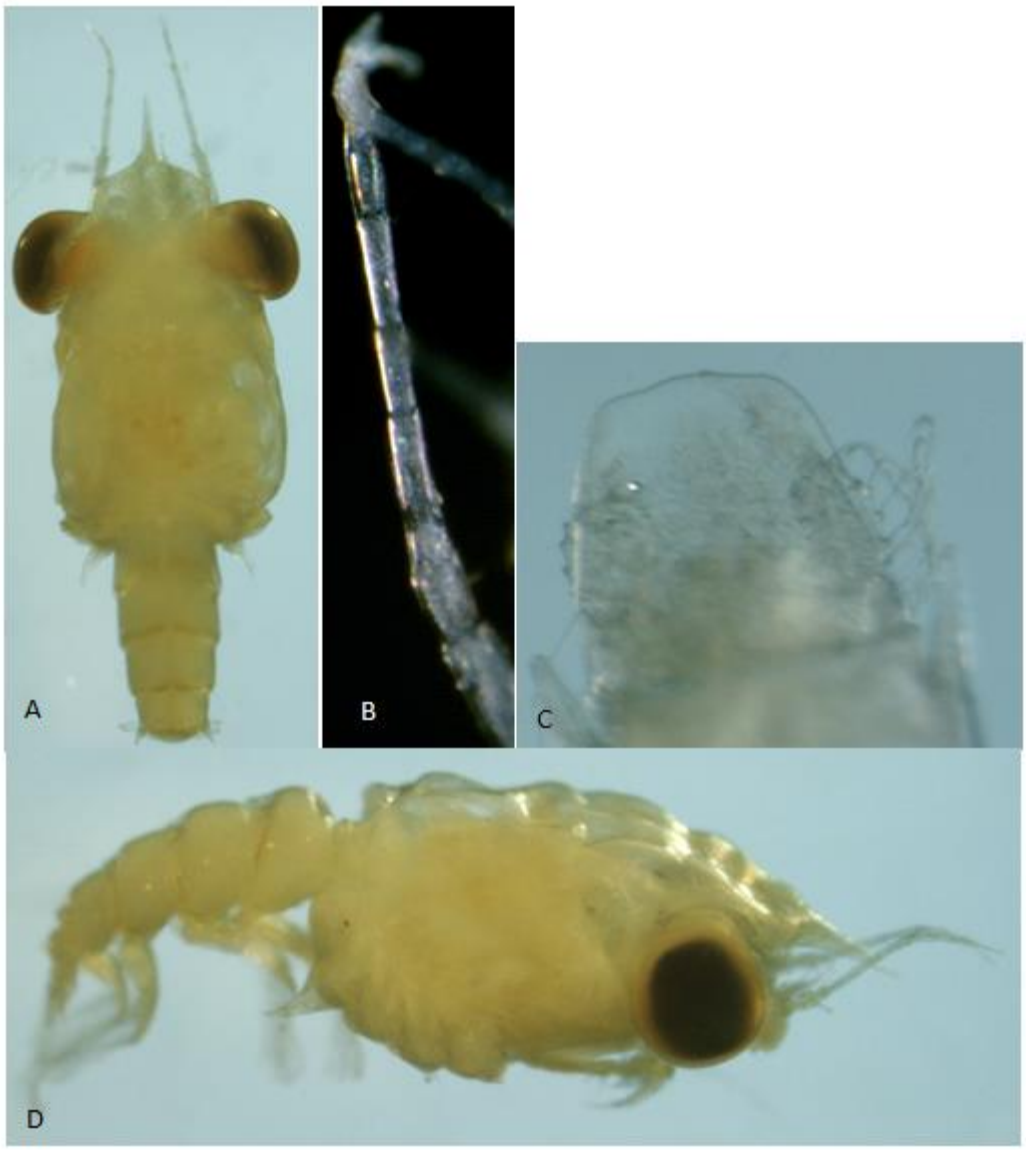

Figure 35. Photographs of *Achelous* sp. C Megalopa. Full dorsal view (A), antenna; ventral view (B); telson, dorsal view (C); full lateral view (D).

Distribution: *Achelous* sp. C occurred in samples ranging predominantly from the coast of Louisiana to the coast of Florida and occurred mostly offshore. (Figure 36).

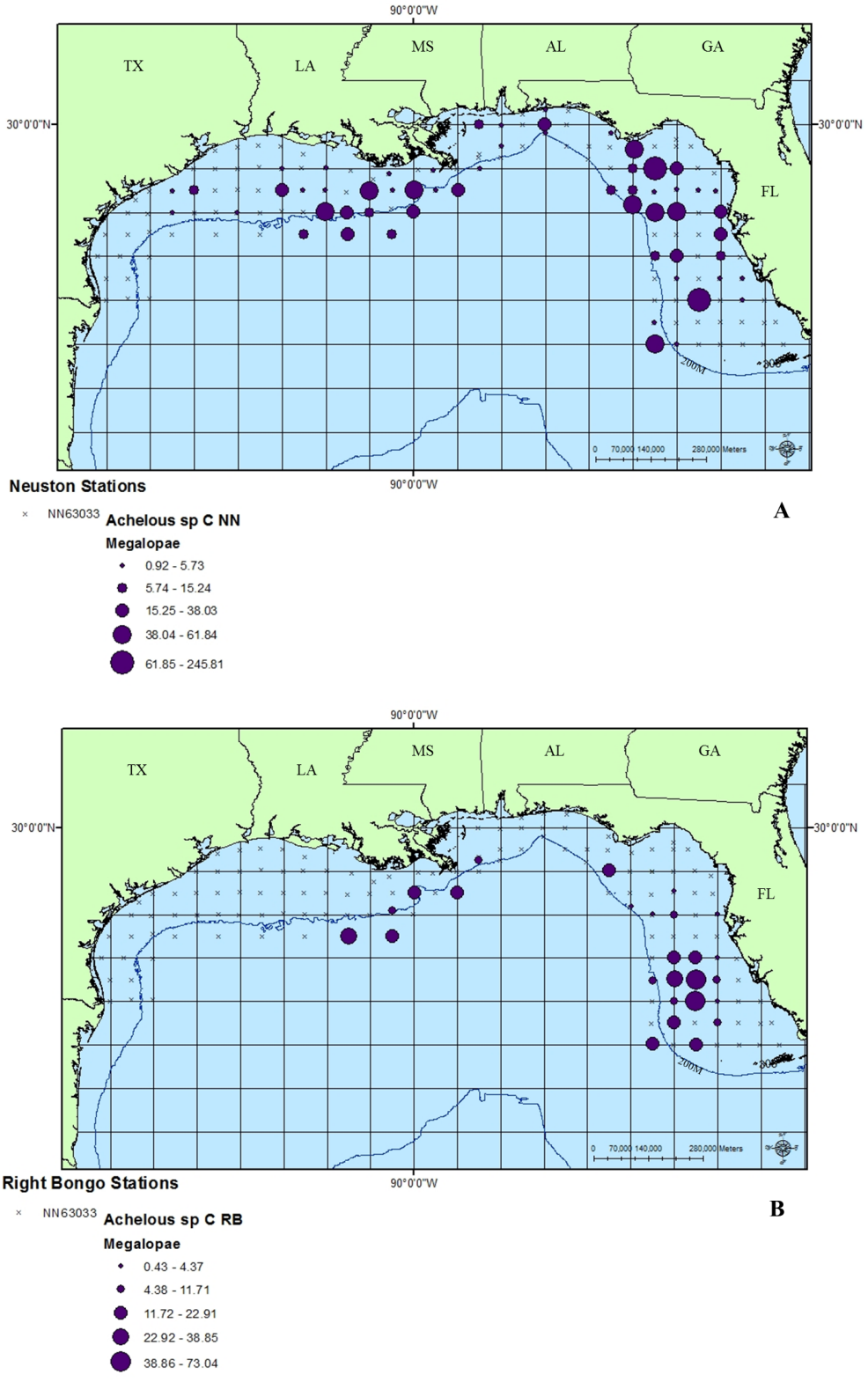

Figure 36. Maps of Distribution and CPUE of *Achelous* sp. C in Neuston (A) and Bongo (B) Samples.

Achelous sp. E (Figures 37 & 38)

Diagnostic description. Carapace and pereopods: Carapace rectangular, lacking a dorsal spine; rostrum 70% length of antenna; pair of spines extending from posterior margin of seventh thoracic segment posteriorly to just beyond the anterior margin of second abdominal segment. Eyestalks lacking pigment spots. Cheliped, supination unknown; pereopod 2 bearing small ventral spine on coxa; pereopods 3-5 lacking ventral spine on coxa; dactyl of pereopod 5 paddle-like, number of hooked setae unknown.

Antenna: Consisting of 10 segments, flagellum of 7 segments, relative segment length pattern for segments 1-4 of short-long-long-long, as shown (Figure 37).

Abdomen and pleopods: Abdomen, second segment humped in lateral view, fifth segment with large posterolateral spines that extend past posterior margin of sixth abdominal segment; telson subquadrate with small medial protrusion on distal margin , lacking spines or setae. Pleopods present on abdominal segments 2-6; pleopod 5 (uropod) lacking endopod, bearing 1 plumose seta on basal segment and 10 plumose setae on exopod.

Remarks. This megalopa is strikingly similar to morph C, with the exception of a much longer and more horizontal rostrum. The sternal spines on this morph were the smallest seen next to those on *Cronius ruber*. CL= 1.82 mm.

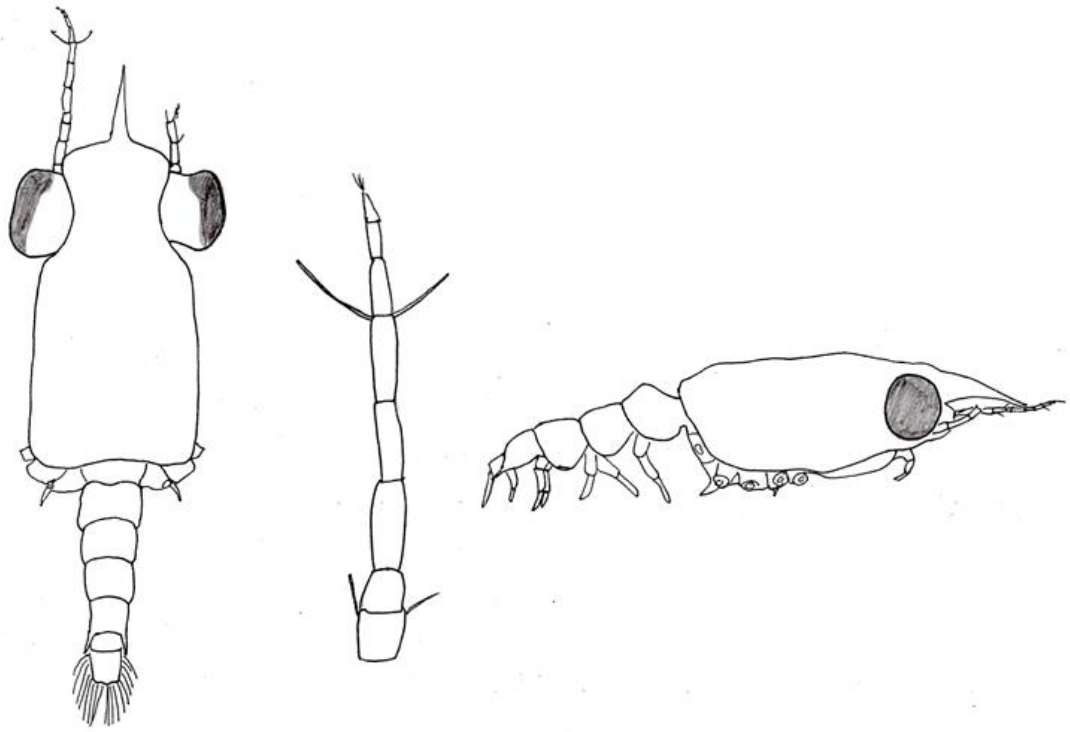

Figure 37. Drawings of *Achelous* sp. E Megalopa. Full dorsal view (left); antenna, dorsal view (center); full lateral view (right).

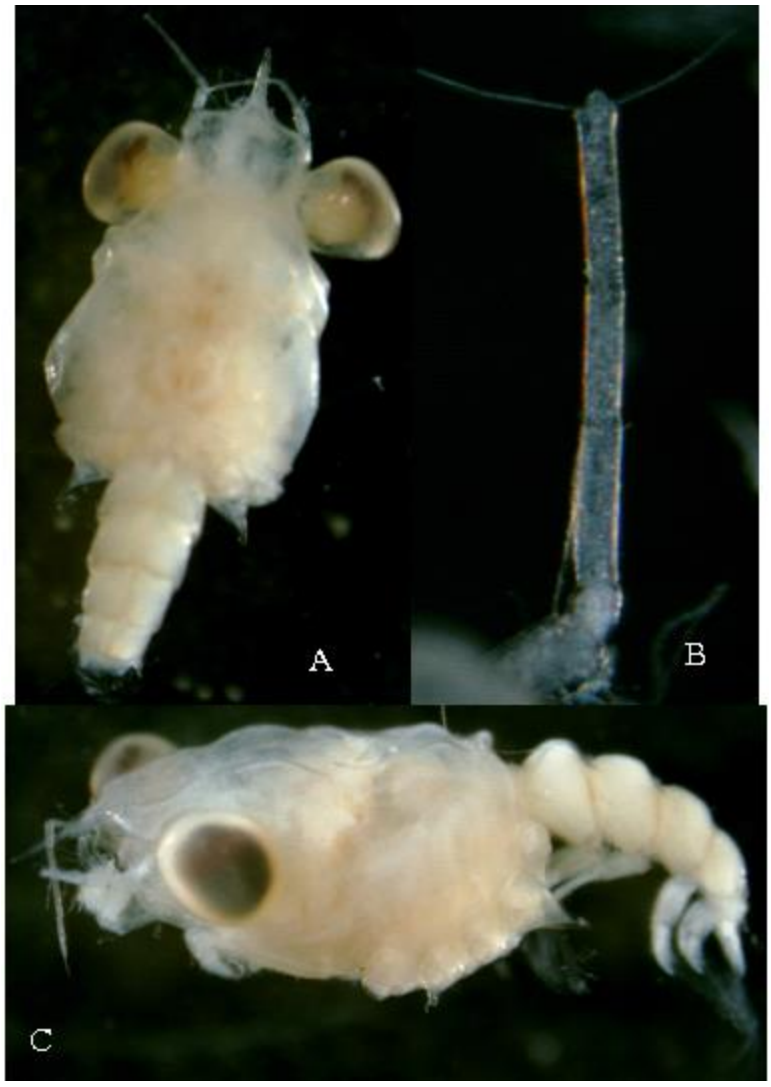

Figure 38. Photographs of *Achelous* sp. E Megalopa. Full dorsal view (A); antenna, dorsal view (B); full lateral view (C).

Distribution. *Achelous* sp. E was found in two neuston samples, both off the coast of Louisiana near the Mississippi river delta. Both of the stations lie out at the shelf break (Figure 39).

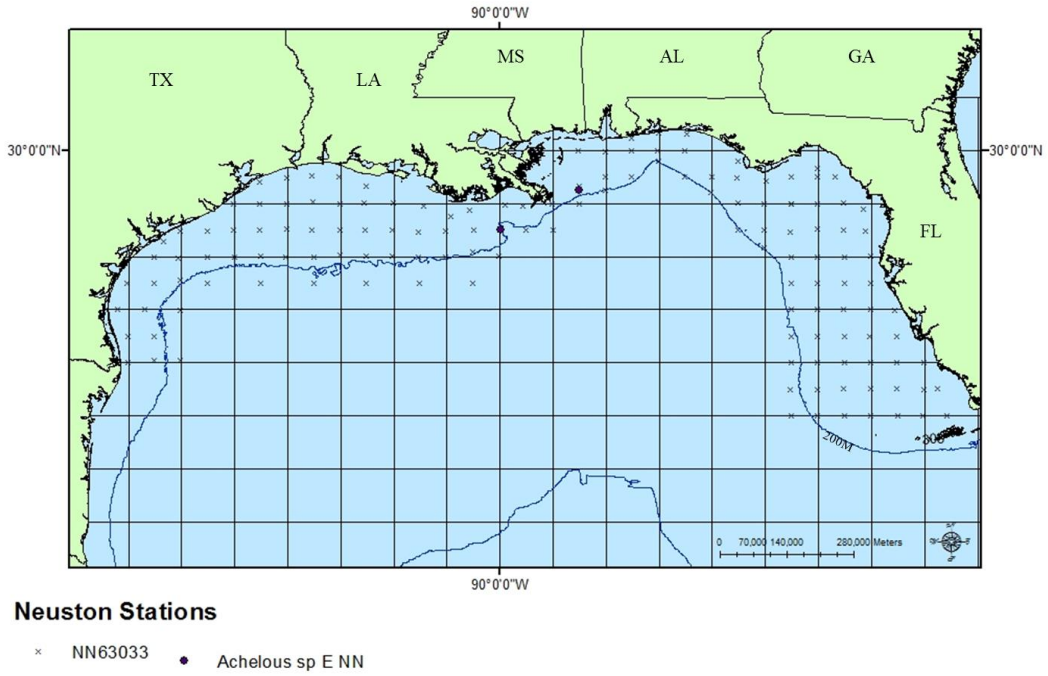

Figure 39. Map of the Distribution of *Achelous* sp. E in Neuston Samples.

Achelous sp. F (Figures 40 & 41)

Diagnostic description. Carapace and pereopods: Carapace rectangular, lacking a dorsal spine; rostrum stout, horizontal, 60% length of antenna ; small pair of spines extending from posterior margin of seventh thoracic segment posteriorly just past anterior margin of second abdominal segment. Eyestalks lacking pigment spots. Cheliped bearing disto-medial carpal spine, lacking basi-ischial spine; pereopod 2 bearing small ventral coxal spine; pereopods 3-5 lacking ventral coxal spine; dactyl of pereopod 5 paddle-like, number of hooked setae unknown.

Antenna: Consisting of 10 segments, flagellum of 7 segments, relative segment length pattern for segments 1-4 of short-long-medium-long, as shown (Figure 40).

Abdomen and pleopods: Abdomen, second segment humped in lateral view, fifth segment with large posterolateral spines that extend past posterior margin of abdominal

segment; telson subquadrate, with small medial protrusion on distal margin. Pleopods present on abdominal segments 2-6; pleopod 5 (uropod) lacking endopod, bearing 1 simple seta on basal segment and 12-13 plumose setae on exopod.

Remarks. This megalopa resembles morph E in antennal segment size and pattern as well as in sternal spine size, but possesses a blunt rostrum compared to those of other *Achelous* species and morphs. CL = 1.70 mm.

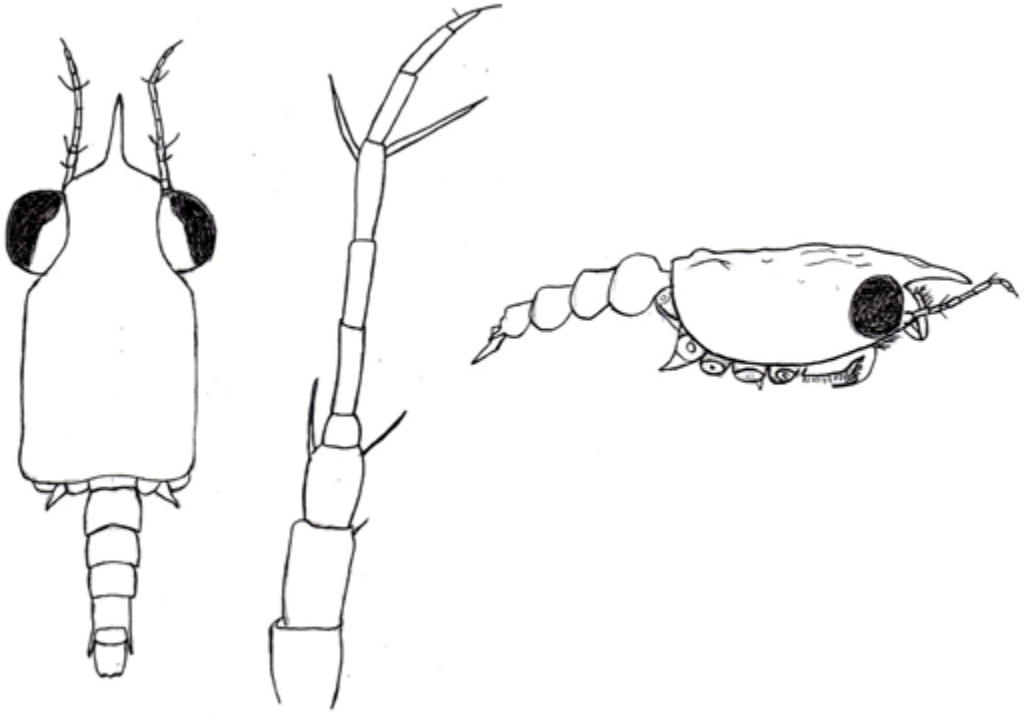

Figure 40. Drawing of Achelous sp. F Megalopa. Full dorsal view (left); antenna (center), dorsal view; full lateral view (right).

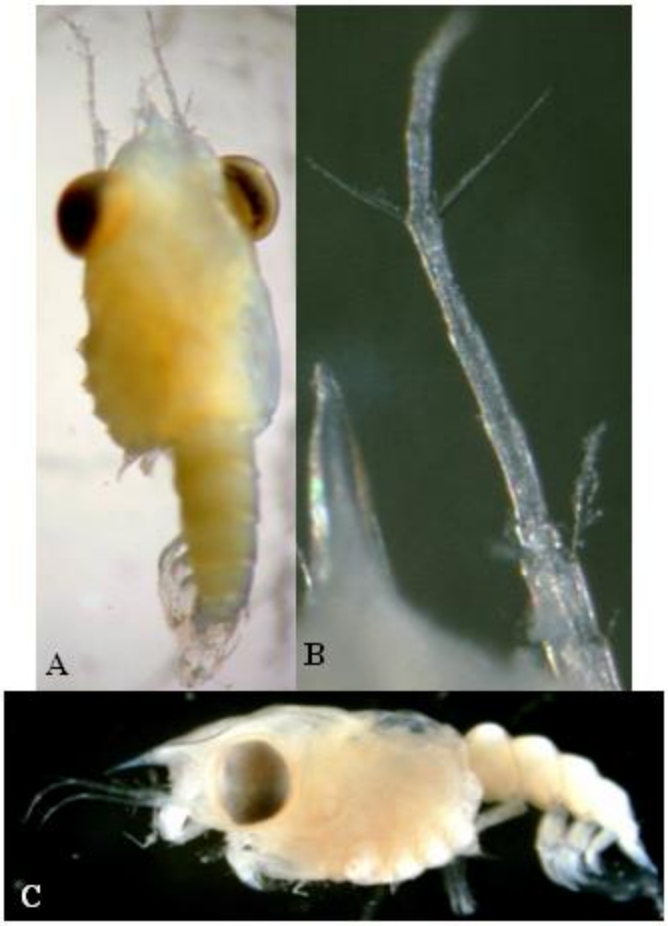

Figure 41. Photographs of *Achelous* sp. F Megalopa. Full dorsal view (A); and antenna, dorsal view (B); full lateral view (C).

Distribution. *Achelous* sp. F was collected off the coasts of Louisiana and Florida in mid-shelf to shelf break waters, with the greatest concentrations being near the bend of Florida (Figure 42).

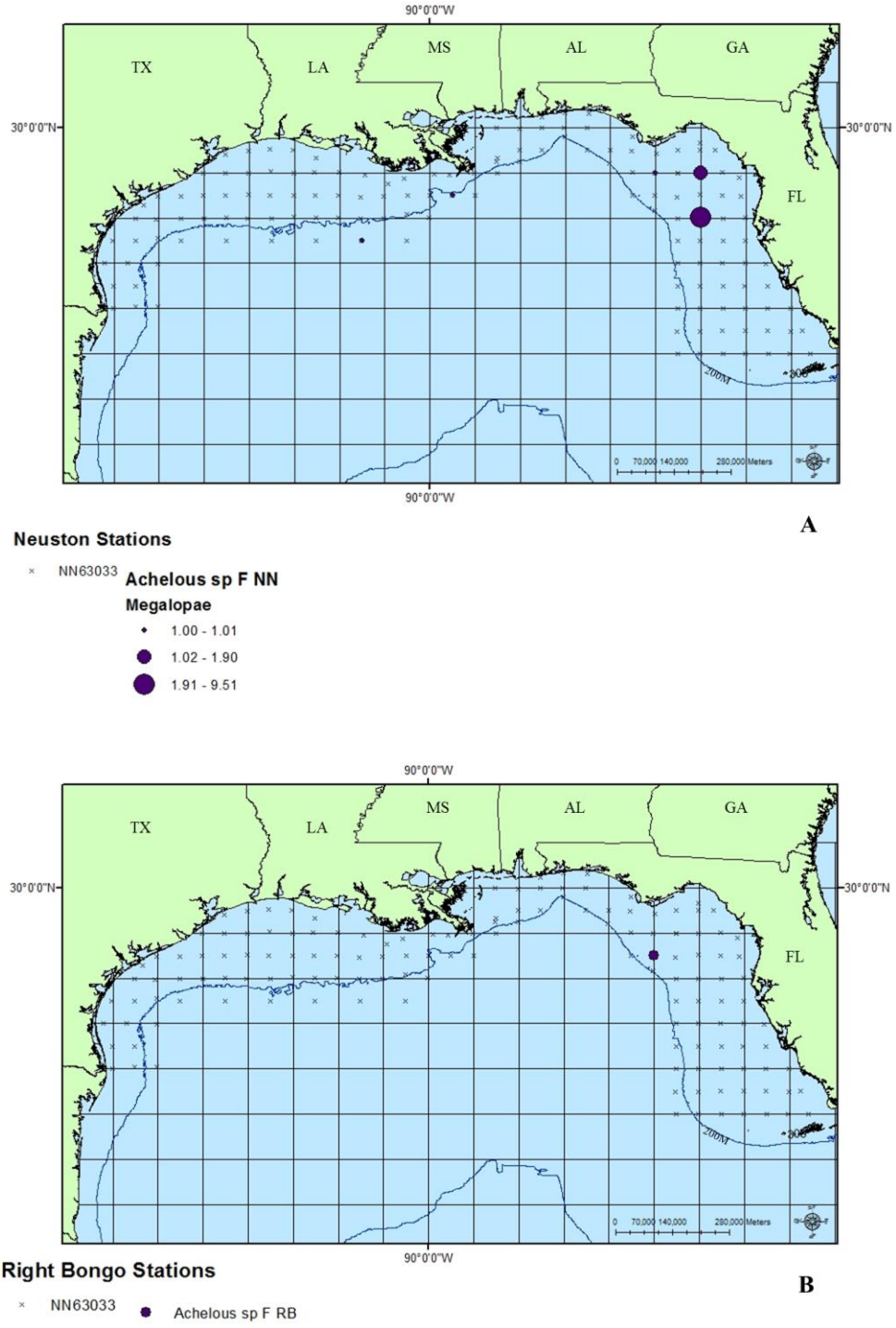

Figure 42. Maps of Distribution and CPUE of *Achelous* sp. F in Neuston (A) and Bongo (B) Samples.

Achelous sp. I (Figures 43 & 44)

Diagnostic description. Carapace and pereopods: Carapace rectangular, lacking a dorsal spine; rostrum horizontal, 80% length of antenna ; small pair of spines extending from posterior margin of seventh thoracic segment posteriorly, not reaching past posterior margin of second abdominal segment. Eyestalks lacking pigment spots. Cheliped bearing a disto-medial carpal spine, lacking basi-ischial spine; pereopod 2 bearing a small ventral coxal spine; pereopods 3-5 lacking ventral coxal spine; dactyl of pereopod 5 paddle-like, bearing 7 hooked setae.

Antenna: Consisting of 10 segments, flagellum of seven segments, relative segment length pattern for segments 1-4 of short-long-medium-long, as shown (Figure 43).

Abdomen and pleopods : Abdomen, second segment humped in lateral view, fifth segment with large posterolateral spines that extend past posterior margin of sixth abdominal segment; telson subquadrate, distal margin transverse; Pleopods present on abdominal segments 2-6; pleopod 5 (uropod) lacking endopod, bearing 1 plumose seta on basal segment and 11-12 plumose setae on exopod.

Remarks: This megalopa may be a possible variant of *A. spinicarpus* based on antenna flagellum segment pattern and length, length and horizontal direction of the rostrum, and sternal spine size. If this is a variant of *A. spinicarpus*, it is on the smaller end of the size range (CL= 1.74 ± 0.08).

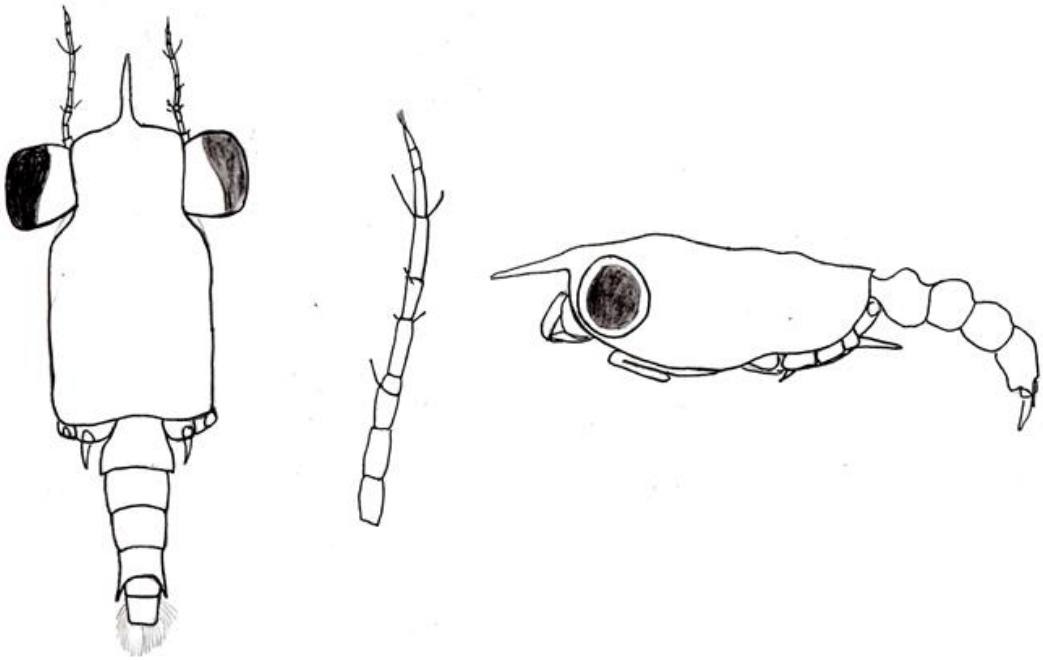

Figure 43. Drawings of *Achelous* sp. I Megalopa. Full dorsal view (left); antenna, dorsal view (center); full lateral view (right).

Figure 44. Photographs of *Achelous* sp. I Megalopa. Full dorsal view (A); antenna, dorsal view (B); full lateral view (C).

Distribution. *Achelous* sp. I was found throughout the northern GOM with the majority of the occurrences located off the coast of Florida. In the bongo samples, collections aggregated near the shelf break (Figure 45). This pattern was less evident in the neuston samples.

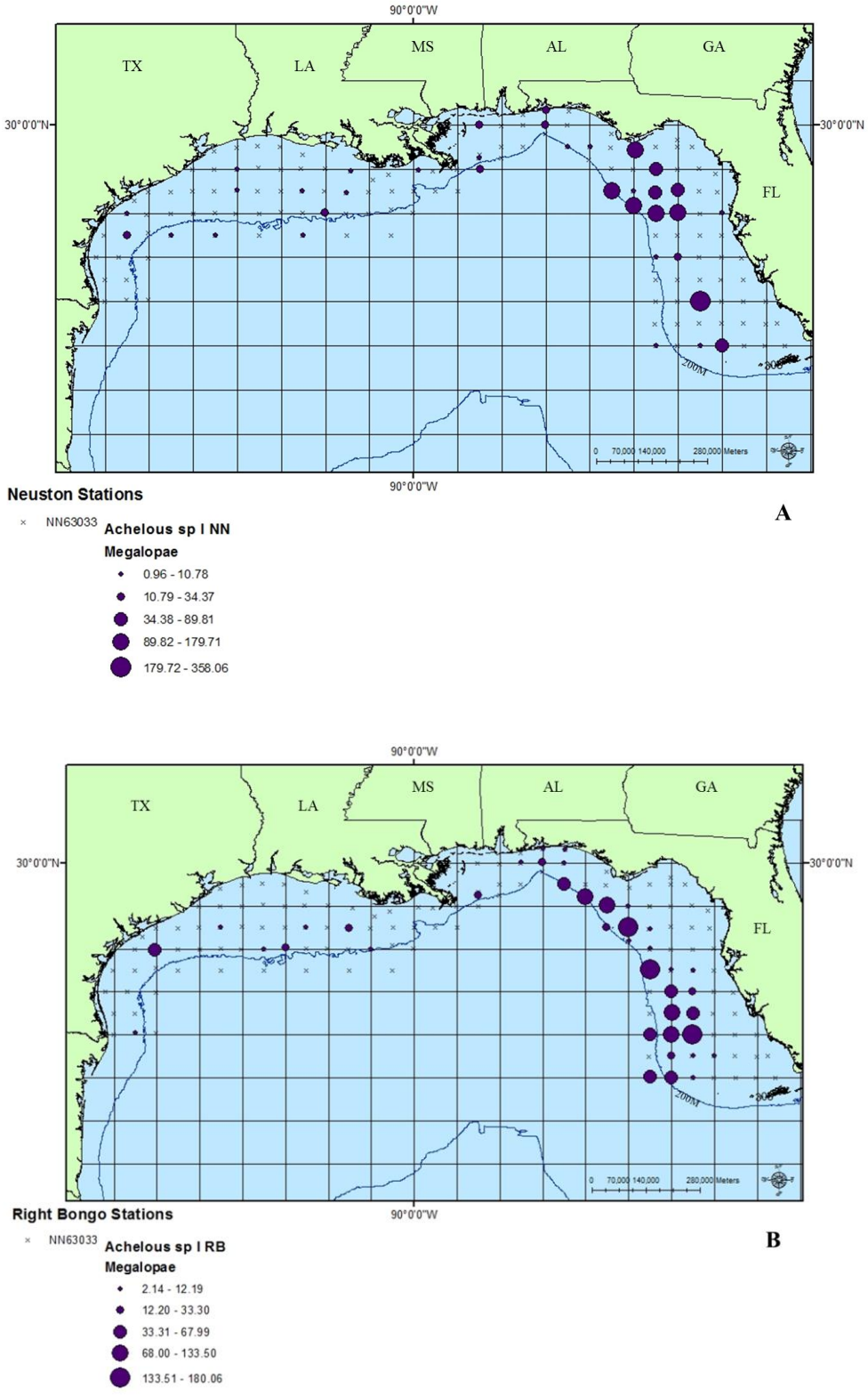

Figure 45. Maps of the Distribution and CPUE of *Achelous* sp. I in Neuston (A) and Bongo (B) Samples.

Genus *Arenaeus* (Dana, 1851)

Arenaeus cribrarius (Lamarck 1818) (Figures 46 & 47)

The only member of its genus, *Arenaeus cribrarius* is one of the larger megalopae in the family Portunidae. The megalopa stage is distinguished from those of other genera by having eight segments in the antennal flagellum, spines present on the carpus and basi-ischium of the cheliped, a ventral spine on the coxa of the second pereopod, and large sternal spines. Specimens were identified using the diagnosis and description of Stuck and Truesdale (1988).

Diagnostic description (modified from Stuck and Truesdale, 1988). *Carapace and pereopods*: Carapace rectangular, lacking a dorsal spine; rostrum horizontal, slightly upturned at tip, 80% length of antenna; strong pair of spines extending from posterior margin of seventh thoracic segment posteriorly to anterior margin of third abdominal segment. Eyestalks with proximal pigment spot on dorsal surface. Cheliped bearing strong medial carpal spine, with large hooked basi-ischial spine; pereopod 2 with ventral spine on coxa; pereopods 3-5 lacking ventral spine on coxa; dactyl of pereopod 5 paddle-like, bearing 10 hooked setae.

Antenna: Consisting of 11 segments, flagellum of 8 segments, relative segment length pattern for segments 1-5 of short-medium-short-medium-long, as shown (Figure 46).

Abdomen and pleopods: Abdomen, second segment humped in lateral view, fifth segment with large posterolateral spines that extend past posterior margin of sixth abdominal segment; telson with slightly rounded distal margin, lacking spines or setae. Pleopods present on abdominal segments 2-6; pleopod 5 (uropod) lacking endopod, bearing 1 simple seta on basal segment and 12-13 plumose setae on exopod.

Remarks. Stuck and Truesdale (1988) noted pigment placement proximodorsally on the eyestalk and on the ventral body surface in live or freshly preserved specimens. However, there was no further description of where this ventral pigment was located. The pigment appears to last at least two years into preservation when preserved in 95% EToH, with the pigments on the eyestalk lasting the longest. Additional pigment locations are as follows:

- Base of antennules.
- Base of mouthparts extending down sternum to base of coxa of Cheliped.
- Cheliped: on ischium proximal to basi-ischial spine; 2-3 spots along the merus; one pair of spots on the ventral surface of the carpus; large spot at base of palm that is visible from both dorsal and ventral surfaces, as well as a spot near the base of the moveable finger on the ventral surface of the palm; one spot on each interior surface of each finger near the base.
- Abdomen and pleopods: 2 pairs of ventral spots are present on segments 1-5. One pair at the anteroventral margin of the segment and the other pair on the posteroventral margin of the abdominal segment at the base of the pleopods. The sixth segment and telson lack pigment.

  CL = 2.03 mm (Stuck and Truesdale, 1988).

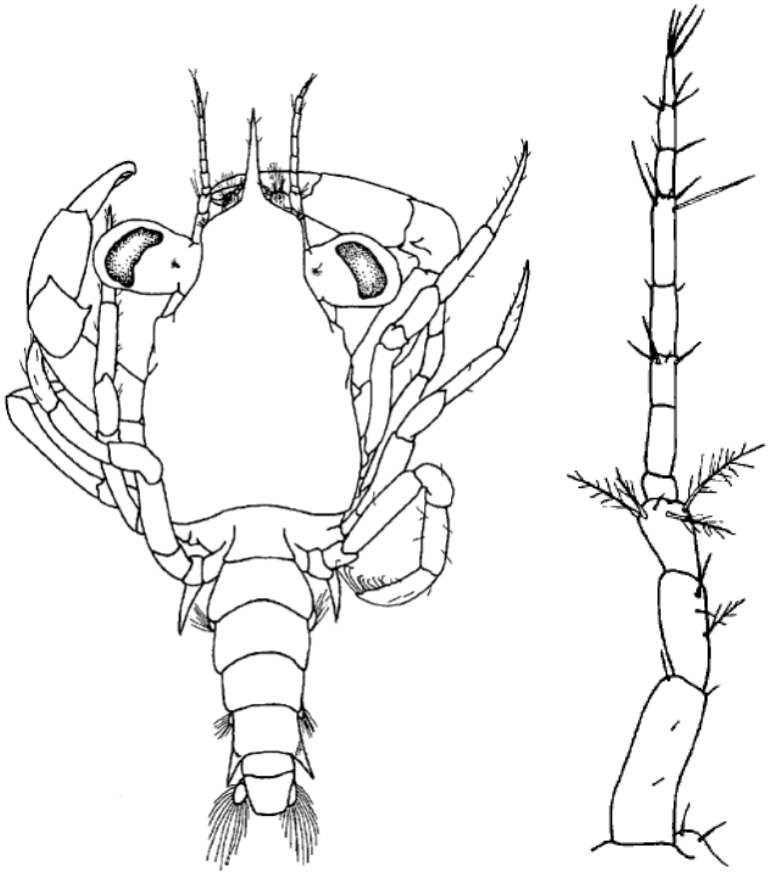

Figure 46. Drawings of *Arenaeus cribrarius* Megalopa. Full dorsal view (left); antenna, orientation unknown (right) (modified from Stuck and Truesdale, 1988).

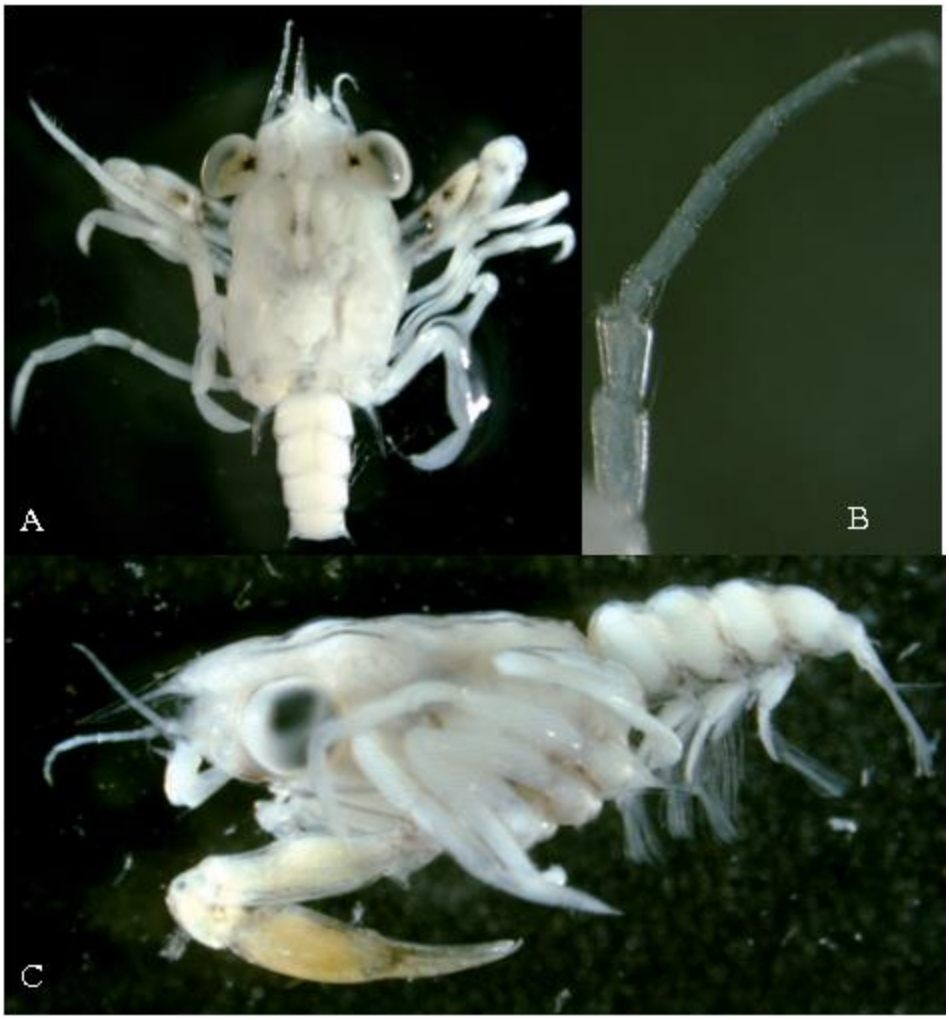

Figure 47. Photographs of *Arenaeus cribrarius* Megalopa. Full dorsal view (A); antenna, dorsal view (B); full lateral view (C).

Distribution. Though the range for the species includes the entire northern GOM, megalopa specimens present in GU 033 samples were concentrated at stations off the coast of Texas and Louisiana, from nearshore out to the shelf, with scattered occurrences on or just off the shelf along the Florida coast (Figure 48).

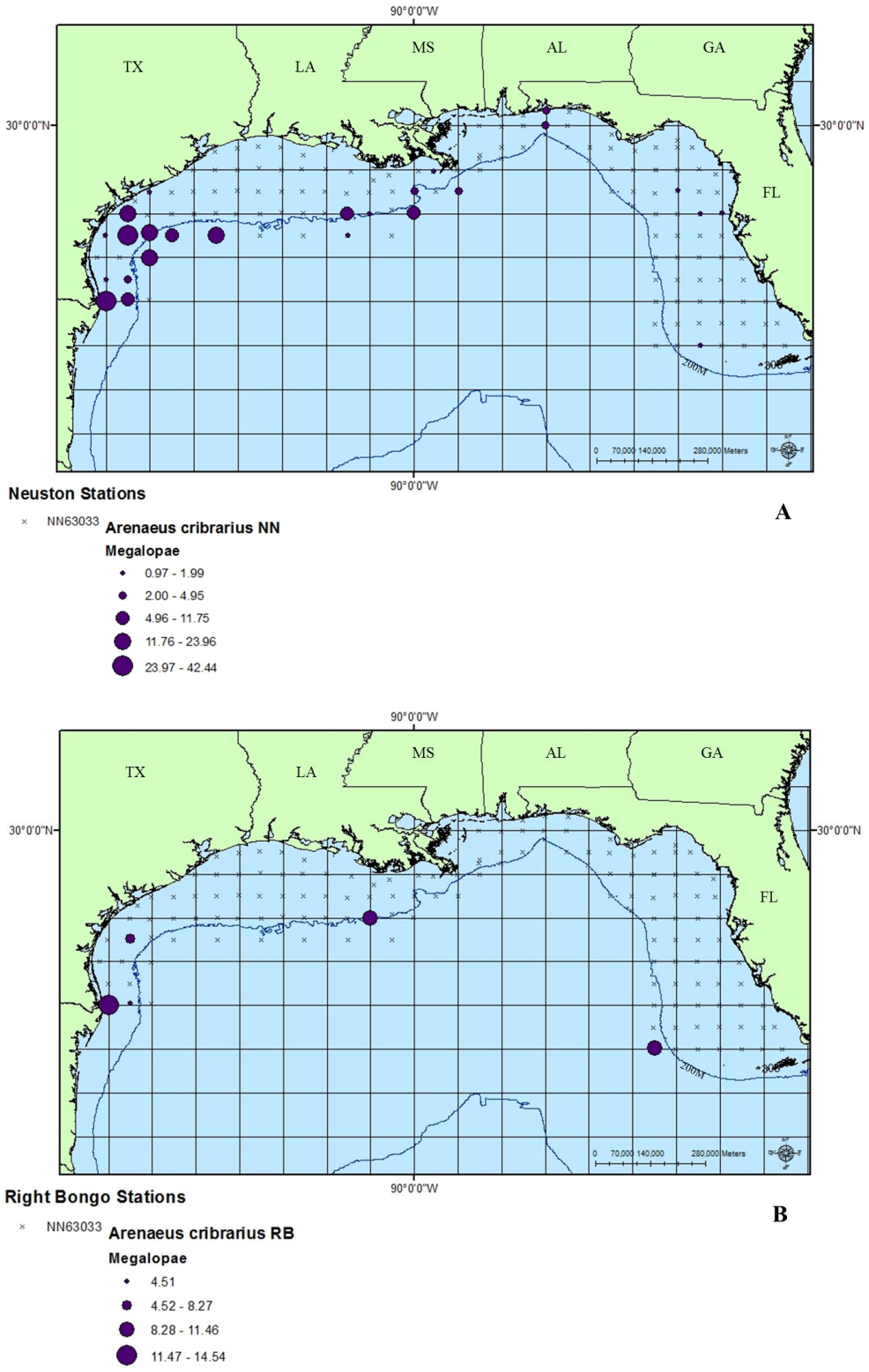

Figure 48. Maps of Distribution and CPUE of *Arenaeus cribrarius* in Neuston (A) and Bongo (B) Samples.

Genus *Callinectes* (Stimpson, 1860)

The genus *Callinectes* contains the most economically important portunid crab in the Gulf of Mexico, the blue crab (*Callinectes sapidus*). Although the Gulf of Mexico is home to eight species of *Callinectes*, the megalopae have been described for only two, *C. sapidus and C. similis*. By far the most abundant species in the northern GOM, these were the only members of the genus *Callinectes* identified to species in the GU 033 samples. None of the specimens examined were strikingly different from the descriptions provided by Costlow and Bookhout (1959, *C. sapidus*), Bookhout and Costlow (1977, *C. similis*), or by Stuck et al. (2009, *C. sapidus*). It should be noted that not all specimens match perfectly in the lengths of antenna flagellum segments and/or rostrum length to antenna ratio. These differences, however, are believed to be natural or seasonal variation among individuals across the gulf. It is possible, however, that other members in the genus with undescribed megalopae that may have a close resemblance to those of *C. sapidus* or *C. similis* were identified as those species in this study. Key features of the genus *Callinectes* are 8 antennae flagellum segments, the lack of a carpal spine and the presence of a basi-ishical spine on the cheliped, and a lack of coxal spines. These megalopae also have a strong pair of sternal spines compared to those seen in the *Achelous* species.

Callinectes sapidus (Rathbun, 1896) (Figures 49 & 50) (Modified from Costlow and Bookhout, 1959)

Diagnostic description. Carapace and pereopods: Carapace rectangular, lacking a dorsal spine; rostrum 70% the length of antenna, horizontal; strong pair of spines extending from posterior margin of seventh thoracic segment posteriorly to midline of second abdominal segment. Eyestalks lacking pigment spot. Cheliped lacking disto-

medial carpal spine, with hooked basi-ischial spine; pereopods 2-5 lacking ventral coxal spine; dactyl of pereopod 5 paddle-like, bearing 7-8 hooked setae.

Antenna: Consisting of 11 segments, flagellum of 8 segments, relative segment length pattern for segments 1-5 of short-short-short-medium-long, as shown (Figure 49).

Abdomen and pleopods: Abdomen, segments smooth in lateral view, fifth segment with large posterolateral spines that extend past posterior margin of sixth abdominal segment; telson with slightly rounded distal margin, 6 to 8 short spines on terminal border. Pleopods present on abdominal segments 2-6; pleopod 5 (uropod) lacking endopod, bearing 1 simple seta on basal segment and 11-12 simple setae on exopod.

Remarks. Variation was seen in antennal flagellum segment lengths but not strikingly enough to suggest multiple species of *Callinectes* being observed. This could be natural variation, regional variation across the GOM, or seasonal variation from the published descriptions. CL = 1.65mm (Bookhout and Costlow, 1977; Costlow and Bookhout, 1959).

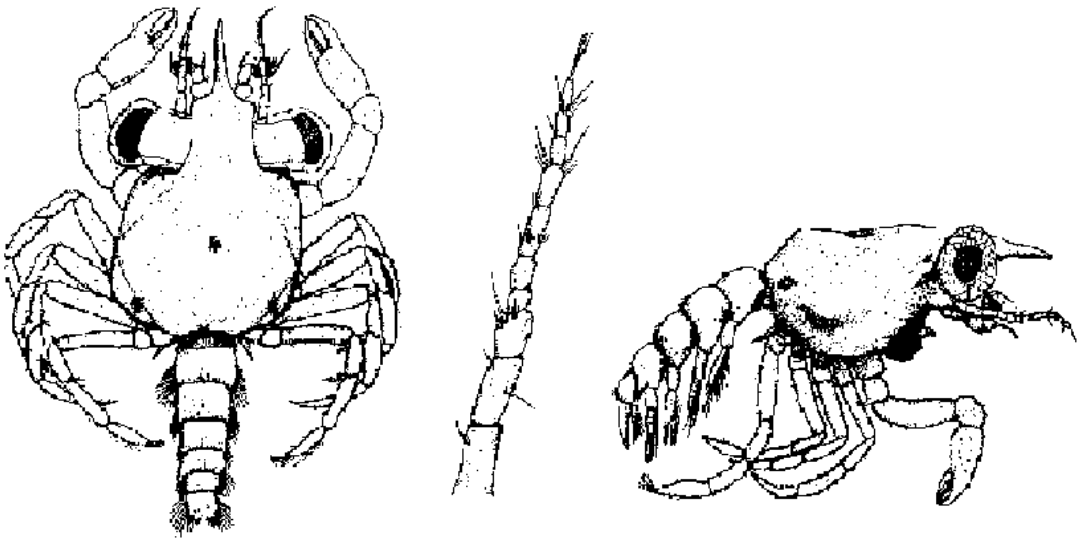

Figure 49. Drawings of *Callinectes sapidus* Megalopa. Full dorsal view (left); antenna, orientation unknown (center); full lateral view (right) (modified from Costlow and Bookhout, 1959).

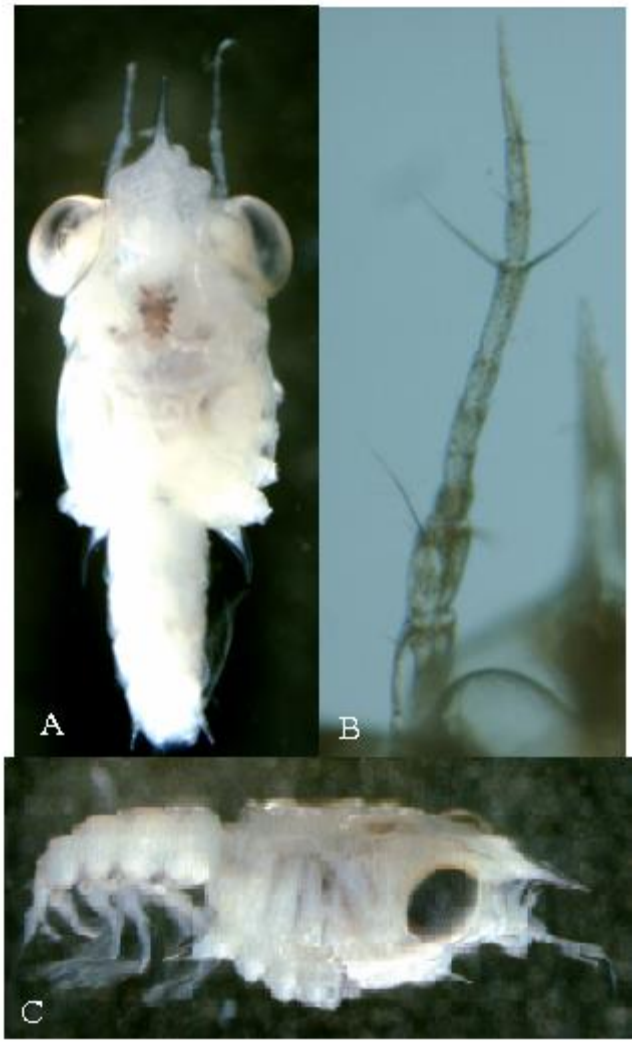

Figure 50. Photographs of *Callinectes sapidus* Megalopa. Full dorsal view (A); antenna, ventral view (B); full lateral view (C).

Distribution: *Callinectes sapidus* were present all across the northern GOM ranging from nearshore to offshore, with the largest concentrations occurring off the southern coast of Texas (Figure 51).

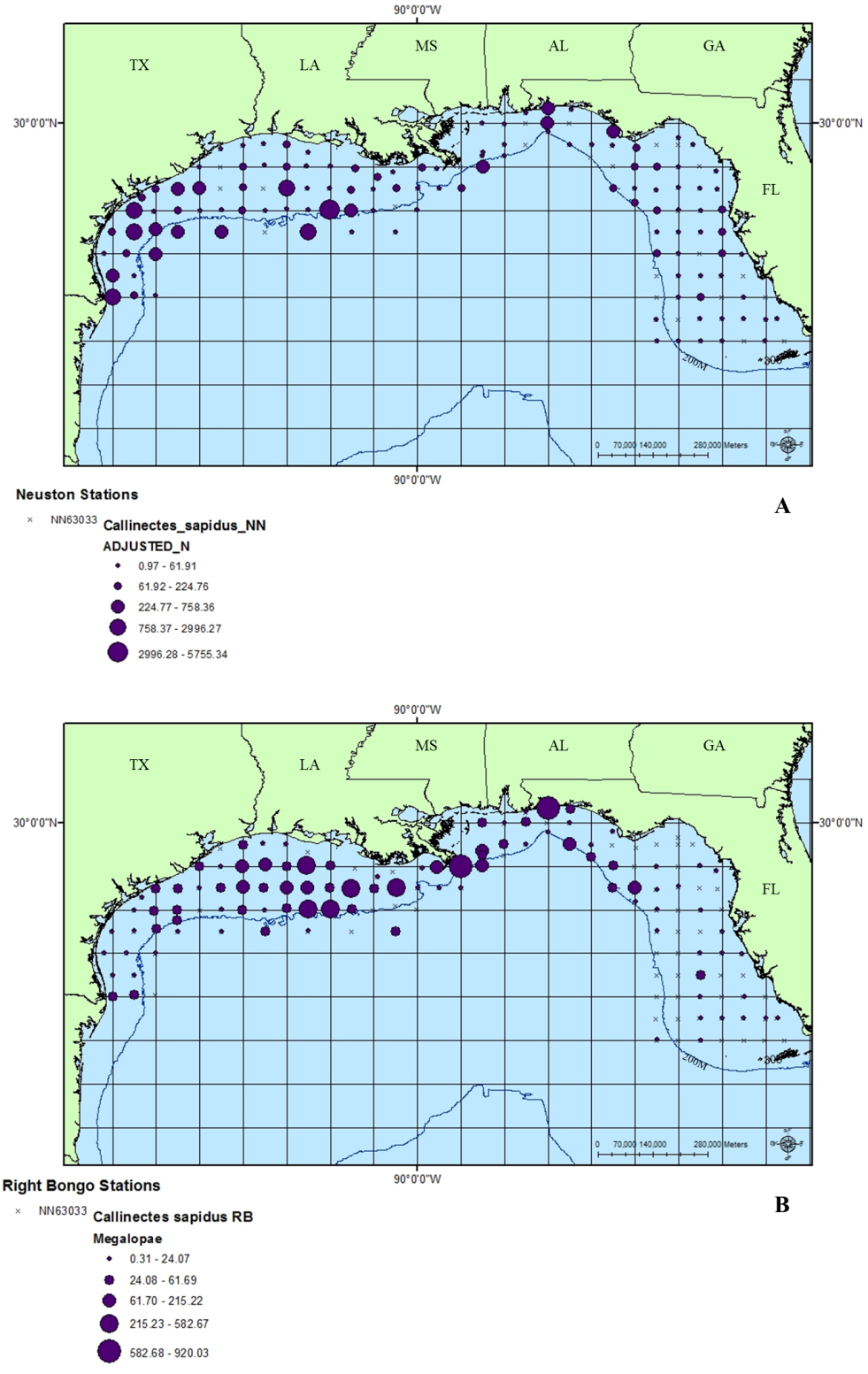

Figure 51. Maps of Distribution and CPUE of *Callinectes sapidus* in Neuston (A) and Bongo (B) Samples.

Callinectes similis (Williams, 1966) (Figures 52 and 53) (Modified from Bookhout and Costlow, 1977)

Diagnostic description. Carapace and pereopods: Carapace rectangular, lacking a dorsal spine; rostrum 50% the length of antenna, horizontal, bearing several pairs of setae along lateral margins; strong pair of spines extending from posterior margin of seventh thoracic segment posteriorly almost to posterior margin of second abdominal segment. Eyestalks lacking pigment spots. Cheliped lacking disto-medial carpal spine, with hooked basi-ischial spine; pereopods 2-5 lacking ventral coxal spine; dactyl of pereopod 5 paddle-like, bearing 8 hooked setae.

Antenna: Consisting of 11 segments, flagellum of 8 segments, relative segment length pattern for segments 1-5 of short-short-short-long-long, as shown (Figure 52).

Abdomen and pleopods: Abdomen, fifth segment with large posterolateral spines that extend past posterior margin of sixth abdominal segment; telson with slightly rounded distal margin, lacking spines or setae. Pleopods present on abdominal segments 2-6; pleopod 5 (uropod) lacking endopod, bearing 1 simple seta on basal segment and 11 plumose setae on exopod.

Remarks: *C. similis* megalopae identified in this sample very closely matched the published description of the megalopa from Bookhout and Costlow (1977). There was a minute amount of variation in the length of the rostrum compared to the length of the antennae, but this could be either natural or seasonal variation or subjective interpretation of the published drawings for this species. CL= 1.30mm (Bookhout and Costlow, 1977).

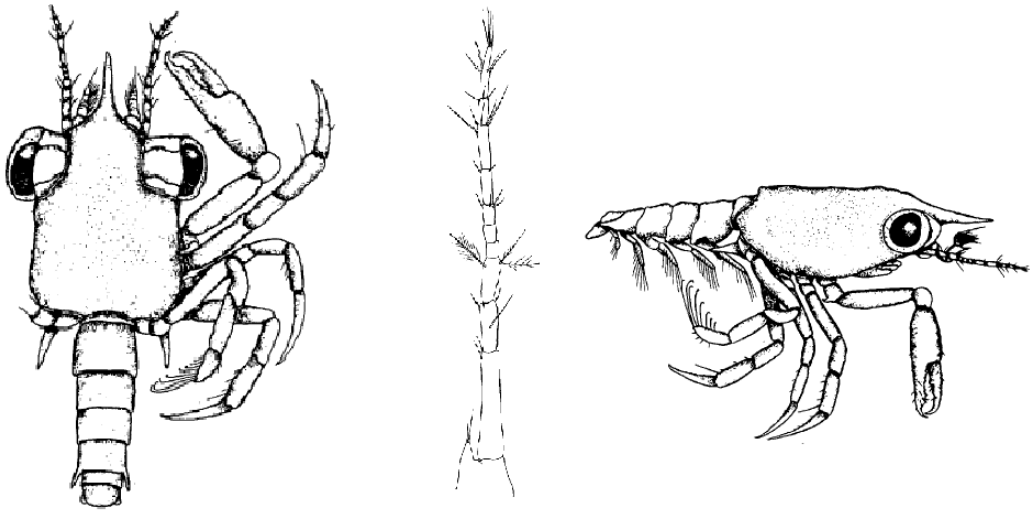

Figure 52. Drawings of *Callinectes similis* Megalopa. Full dorsal view (left); antenna, orientation unknown (center); full lateral view (right) (modified from Bookhout and Costlow, 1977).

Figure 53. Photographs of *Callinectes similis* Megalopa. Full dorsal view (A); antenna, dorsal view (B); full lateral view (C).

Distribution. *Callinectes similis* was less prevalent than its congener *C.sapidus* but was present in the same areas gulf wide, with larger concentrations tending to be toward the shelf break (Figure 54).

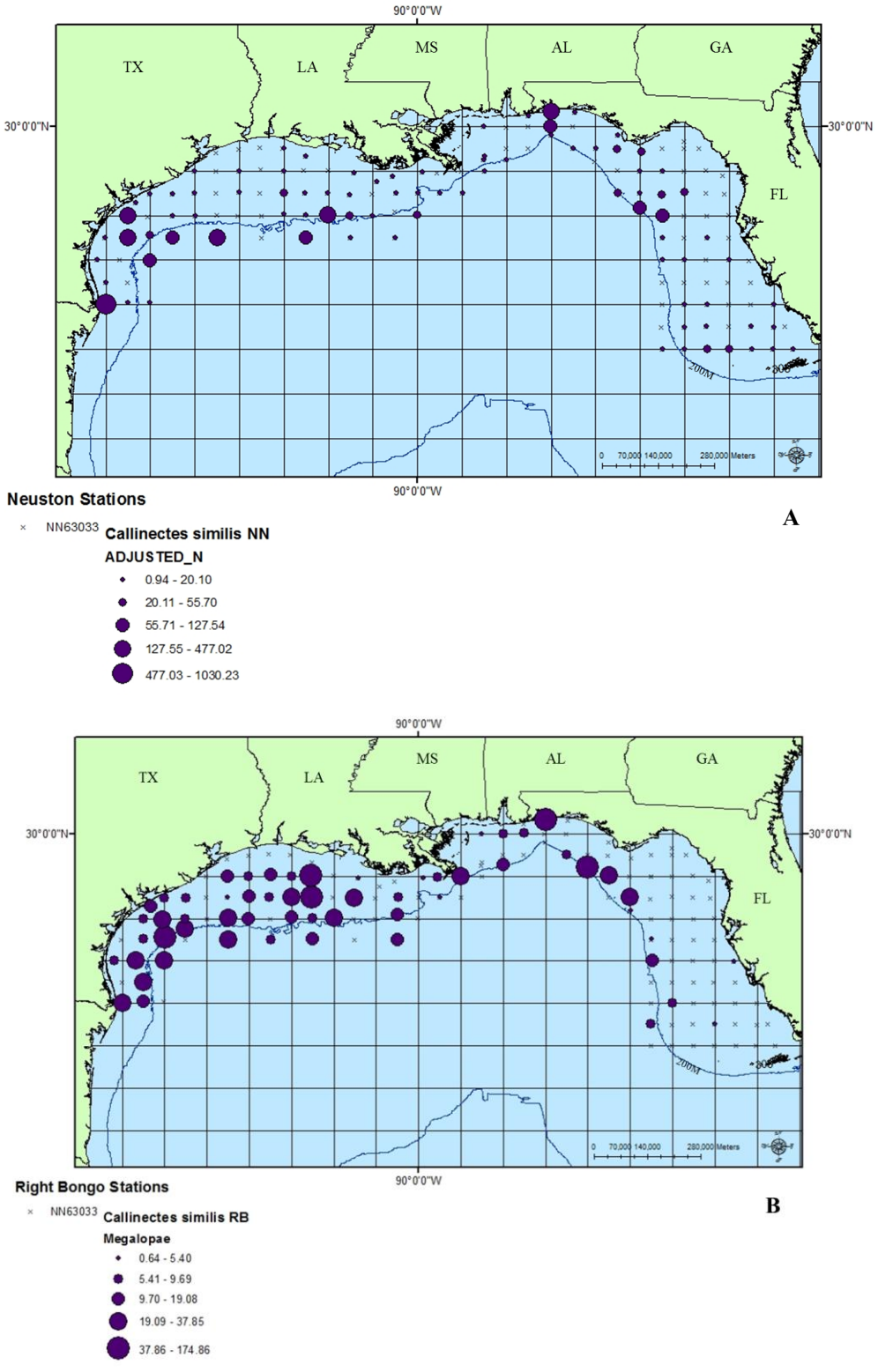

Figure 54. Maps of the Distribution and CPUE of *Callinectes similis* in Neuston (A) and Bongo (B) Samples.

Genus *Cronius* (Stimpson, 1860)

The last remaining member of the genus after the reassignment of *Cronius tumidulus* to the genus *Achelous* (Mantelatto et al., 2009), *Cronius ruber* larvae have never been formally described. Rice and Kristensen (1982) described a megalopa that was seen swarming off the coast of Curacao, but the authors were unable to identify the species. Genetic identification of a megalopa matching their description enabled this name. The diagnosis of the megalopa of genus is based solely on *C. ruber* and is distinguishable by overall size (it is by far the largest Portunidae megalopa seen in the Gulf of Mexico) and by having a rostrum with two blunt protrusions on either side of the rostral shield.

Cronius ruber (Lamarck, 1818) (Figures 55 & 56) (Modified from Rice and Kristensen, 1982)

Diagnostic description. Carapace and pereopods: Carapace rectangular, lacking a dorsal spine; rostrum horizontal, approximately 70% the length of antenna flanked by 2 small blunt "horns" on the anterolateral margins and fine setae on the lateral margins of the rostral plate; small pair of spines extending from the posterior margin of the seventh thoracic segment posteriorly to the posterior margin of second abdominal segment. Eyestalks lacking pigment spot. Cheliped lacking disto-medial carpal spine, with small, blunt basi-ischial spine; pereopods 2-5 bearing a small ventral coxal spine; dactyl of pereopod 5 paddle-like, bearing 13 hooked setae.

Antenna: Consisting of 11 segments, flagellum of 8 segments, relative segment length pattern for segments 1-5 of short-long-medium-medium-medium, as shown (Figure 55).

Abdomen and pleopods: Abdomen with second segment smooth in lateral view, fifth segment with large posterolateral spines that extend past posterior margin of sixth abdominal segment; telson with slightly rounded distal margin, lacking spines or setae. Pleopods present on abdominal segments 2-6; pleopod 5 (uropod) lacking endopod, bearing 1 plumose seta on basal segment and 22 plumose setae on exopod.

Remarks: The megalopa was the largest observed, with a carapace length of 6.0 ±0.03 mm. The unique rostrum is unlike that seen in any other known Portunid megalopa. Genetically identified material was obtained via a contact from Puerto Rico. No pigmentation was noted on either the GOM or Puerto Rico specimens.

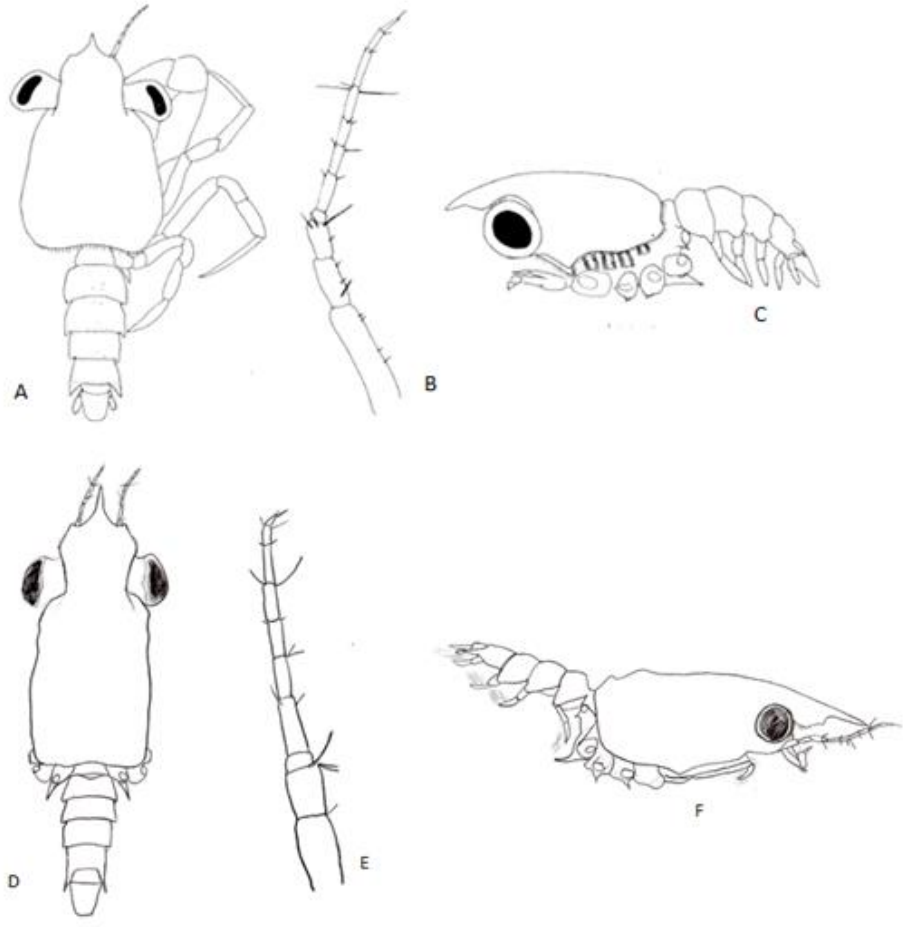

Figure 55. Drawings of *Cronius ruber* Megalopa. Full dorsal view (A, D); antenna, dorsal view (B,E); full lateral view (C, F).)(A-C from Rice and Kristensen, 1982).

Figure 56. Photographs of *Cronius ruber* Megalopa. Full dorsal view (A); rostrum (B); antenna, dorsal view (C); full lateral view (D).

Distribution: *Cronius ruber* occurred in only one neuston sample from just beyond the shelf break off the coast of Louisiana (Figure 57).

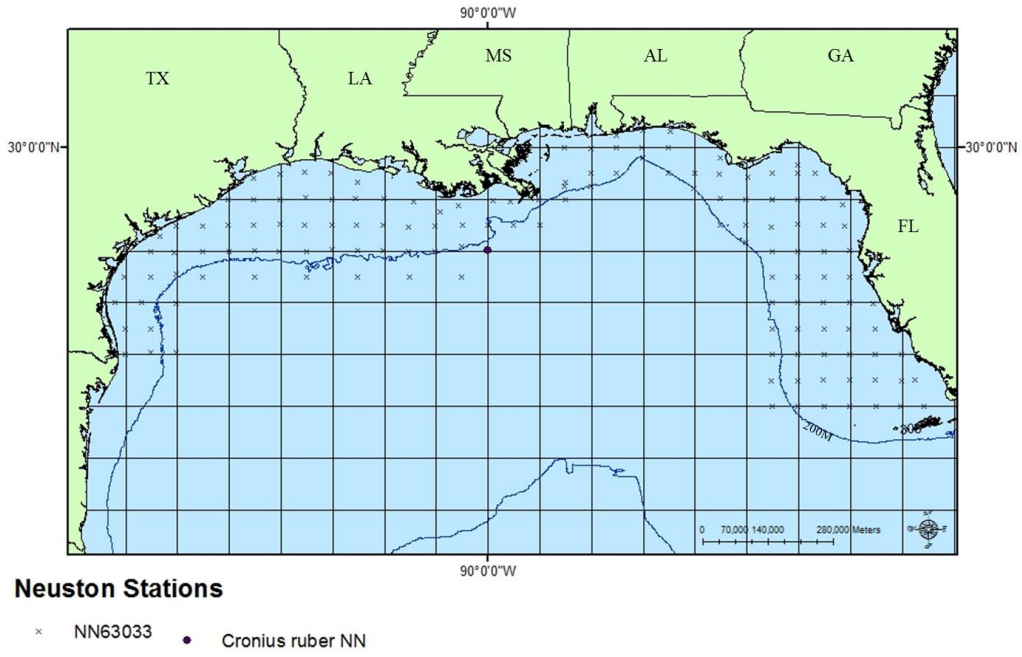

Figure 57. Map of the Distribution of *Cronius ruber* in Neuston Samples.

Genus *Portunus* (Weber, 1795)

Recent reassignment of some portunid species to the genus *Achelous* (Mantelatto et al., 2009) resulted in a greatly reduced number of species of *Portunus* occurring in the Gulf of Mexico. Currently, five species from the GOM remain in this genus: *P. sayi, P. floridanus, P.anceps, P. ventralis,* and *P. vossi.* Of these five, the megalopa is described only for *P.anceps* (Lebour 1944). A diagnosis for the genus is available in Kurata (1975), but it is unclear if this applies exclusively for Pacific species. The diagnosis is based on the holotype *P.pelagicus*. The GOM species previously in this genus did not match the diagnosis given by Kurata. In this study, *Portunus* from the Gulf of Mexico have a 7-segmented antennal flagellum, a basi-ischial spine on Cheliped, and no ventral coxal spines on pereopods 2-5. These characters differ from Kurata's (1975) in having only 7 antennal flagellum segments present (Kurata states 8 flagellum segments present in the

antennae) and the lack of carpal and coxal spines. Only one *Portunus* morph was identified from the fall 2003 plankton samples.

Portunus sp. A (Figures 58 & 59)

Diagnostic description. *Carapace and pereopods* : Carapace rectangular, lacking a dorsal spine; rostrum 80% length of antennae, with 1 small pair of lateral setae distally; pair of spines extending from posterior margin of seventh thoracic segment posteriorly to anterior margin of third abdominal segment. Eyestalks lacking pigment spots. Cheliped lacking disto-medial carpal spine, bearing large hooked basi-ischial spine; pereopods 2-5 lacking ventral spine on coxa; dactyl of pereopod 5 paddle-like, number of hooked setae unknown.

Antenna: Consisting of 10 segments, flagellum of 7 segments, relative segment length pattern for segments 1-4 of short-short-medium-long, as shown (Figure 58).

Abdomen and pleopods: Abdomen, mildly humped in lateral view, fifth segment with large posterolateral spines that extend past posterior margin of sixth abdominal segment; telson with rounded distal margin. Pleopods present on abdominal segments 2-6; pleopod 5 (uropod) lacking endopod, bearing 1 plumose seta on basal segment and 11 plumose setae on exopod.

Remarks: The identification of this morph to this genus was based on a combination of features from previous members of the genus from the GOM as well as the publish generic diagnosis by Kurata (1975). This morph is similar in size to *Callinectes sapidus* (CL = 1.40 mm). This is smaller than the noted sizes of the holotype for this genus *Portunus pelagicus* (CL= 2.9 -1.69mm (Kurata, 1975; Kurata and Midorikawa, 1975; Yatsuzuka and Sakai, 1980)).

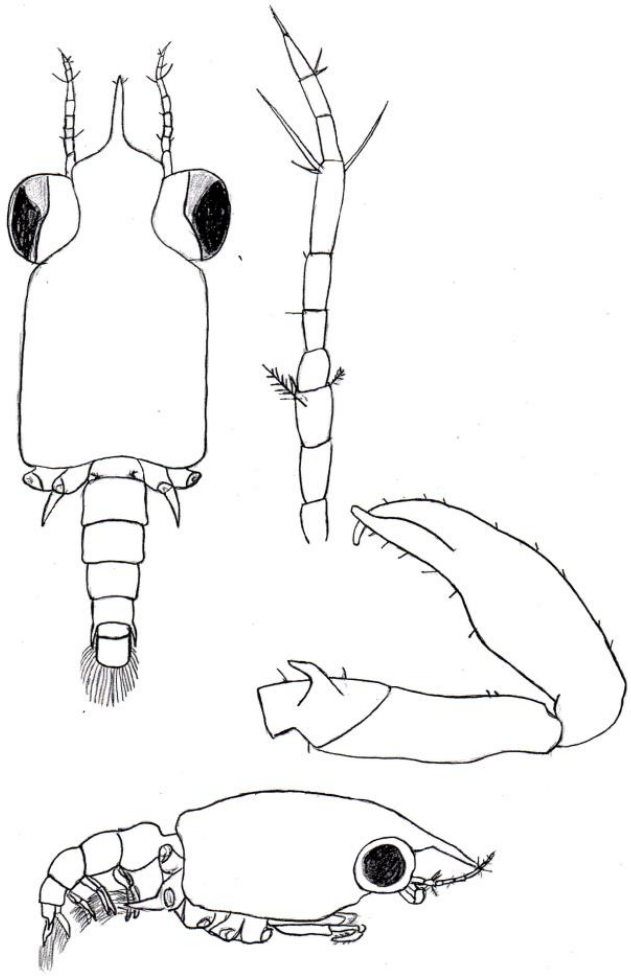

Figure 58. Drawing of *Portunus* sp. A Megalopa. Full dorsal view (top left); antenna, dorsal view (top right), cheliped, ventral view (center); full lateral view (bottom).

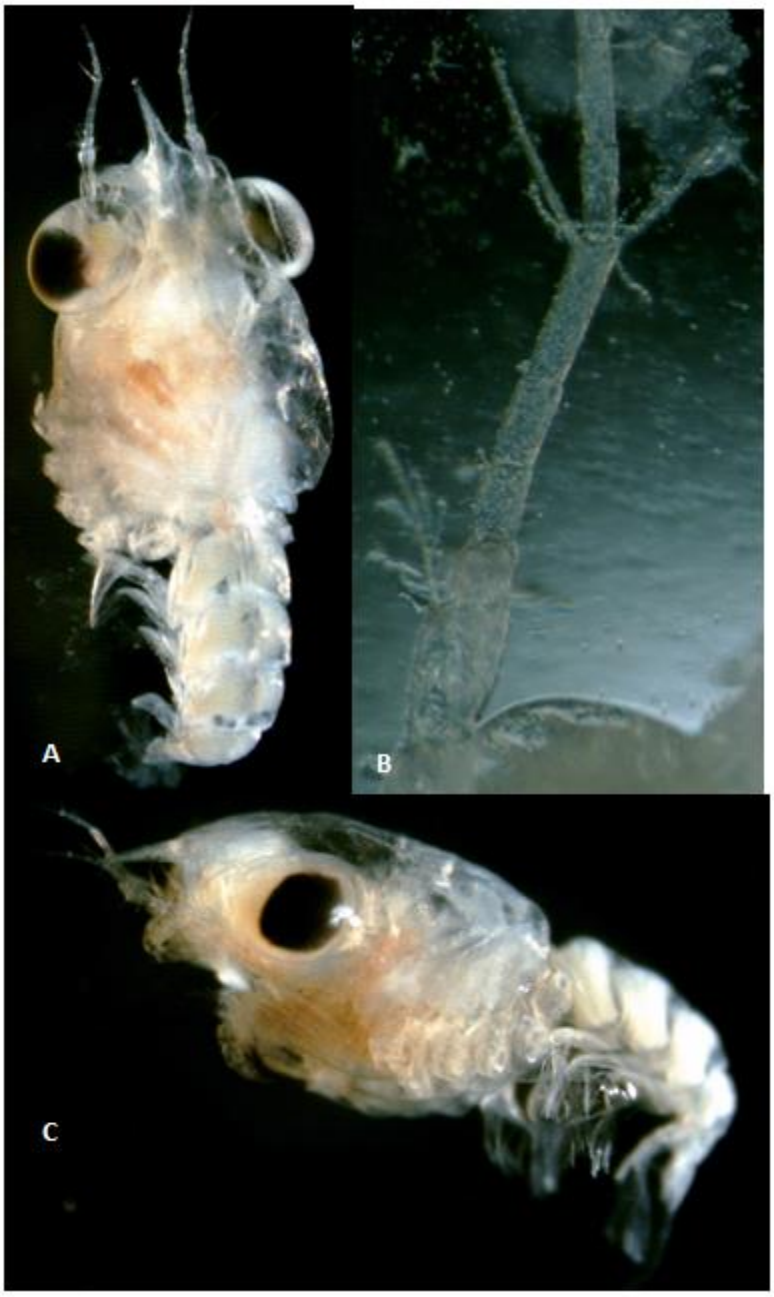

Figure 59. Photographs of *Portunus* sp. A Megalopa. Full dorsal view (A); antenna, dorsal view (B); full lateral view (C).

Distribution. *Portunus* sp. A occurred sparsely across the northern GOM, with the majority of occurrences off the coasts of Texas and Louisiana. *Portunus* sp. A was only present in neuston samples (Figure 60).

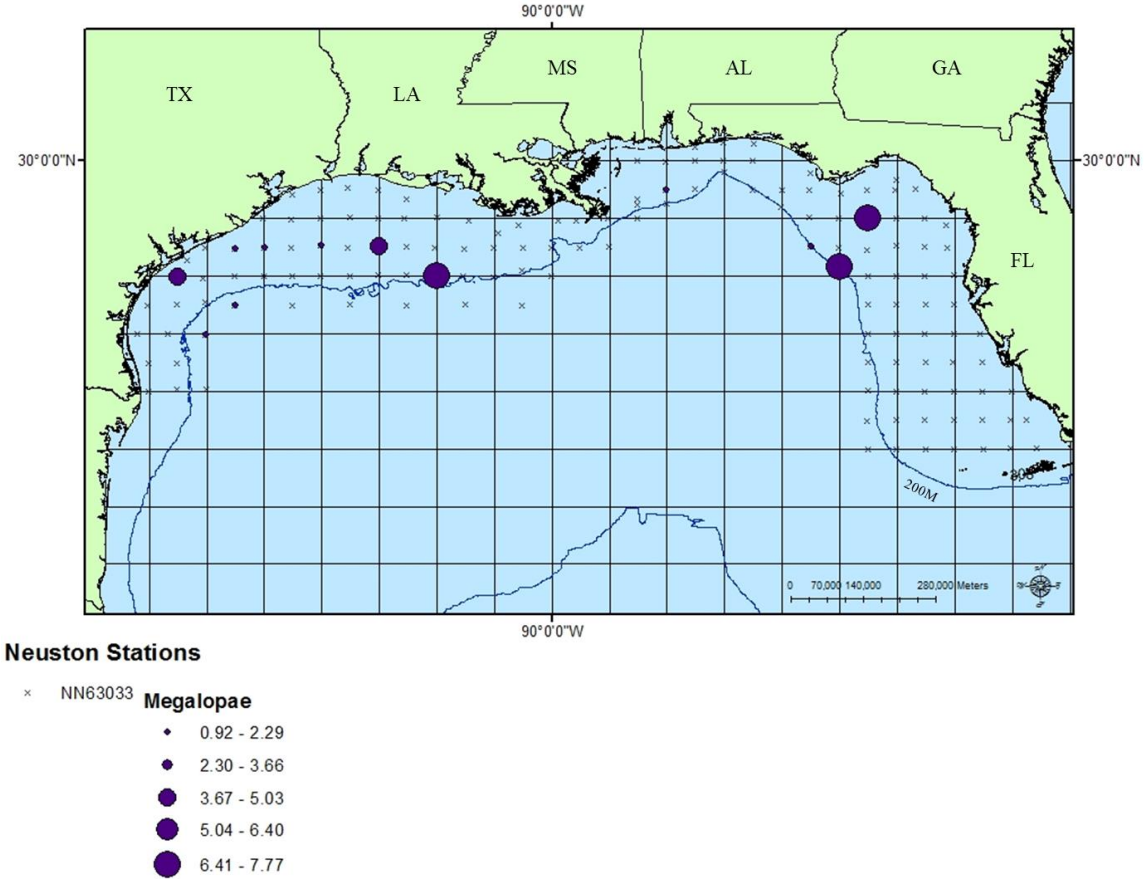

Figure 60. Map of Distribution and CPUE of *Portunus* sp. A in Neuston Samples.

CHAPTER IV

RESULTS: ENVIRONMENTAL AND COMMUNITY ANALYSIS

In this chapter, spatially explicit maps for various environmental variables at the time of sampling are presented, including those for sea surface temperature, chlorophyll-a concentrations, current vectors, and volume of *Sargassum* spp. collected during tows. Patterns in megalopa assemblage structure are presented, including diurnal abundances, abundance predictions for unsampled areas in the northern GOM, and results of NMDS multivariate analysis.

Environmental Data

Chlorophyll-a concentrations were typically higher for samples closer to shore presumably due to increased nutrient influx into these waters. However there were no strong peaks of chlorophyll-a seen in the sampling area and levels stayed fairly consistent for the duration of the cruise. The average chlorophyll-a concentration was 1.14 mg m^{-3}, and concentrations ranged from a minimum of 0.09 mg m^{-3} to a maximum of 12.31 mg m^{-3} (Figure 61).

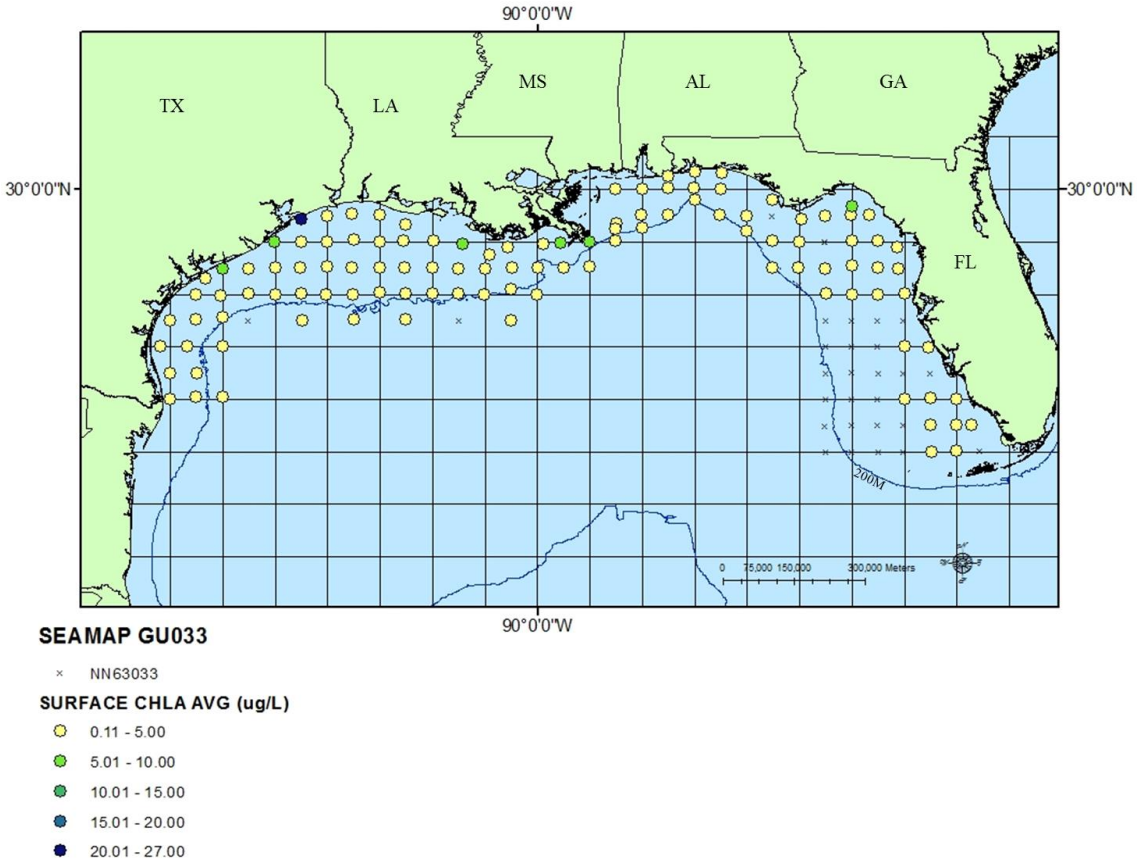

Figure 61. Average *In Situ* Surface Chlorophyll-a by Station Taken During the SEAMAP Fall Plankton Survey, Cruise GU033. Small grey x's indicate stations with no data recorded.

Sea surface temperature strongly affects the distribution and mortality of decapod larvae (Anger, 1991; Anger, 2001). Sea surface temperatures varied across the Gulf with the lowest temperatures occurring off the coast of Florida. The average temperature was 29.07° C +/- .052, ranging from a low of 27.85° C to a maximum of 30.35° C (Figure 62).

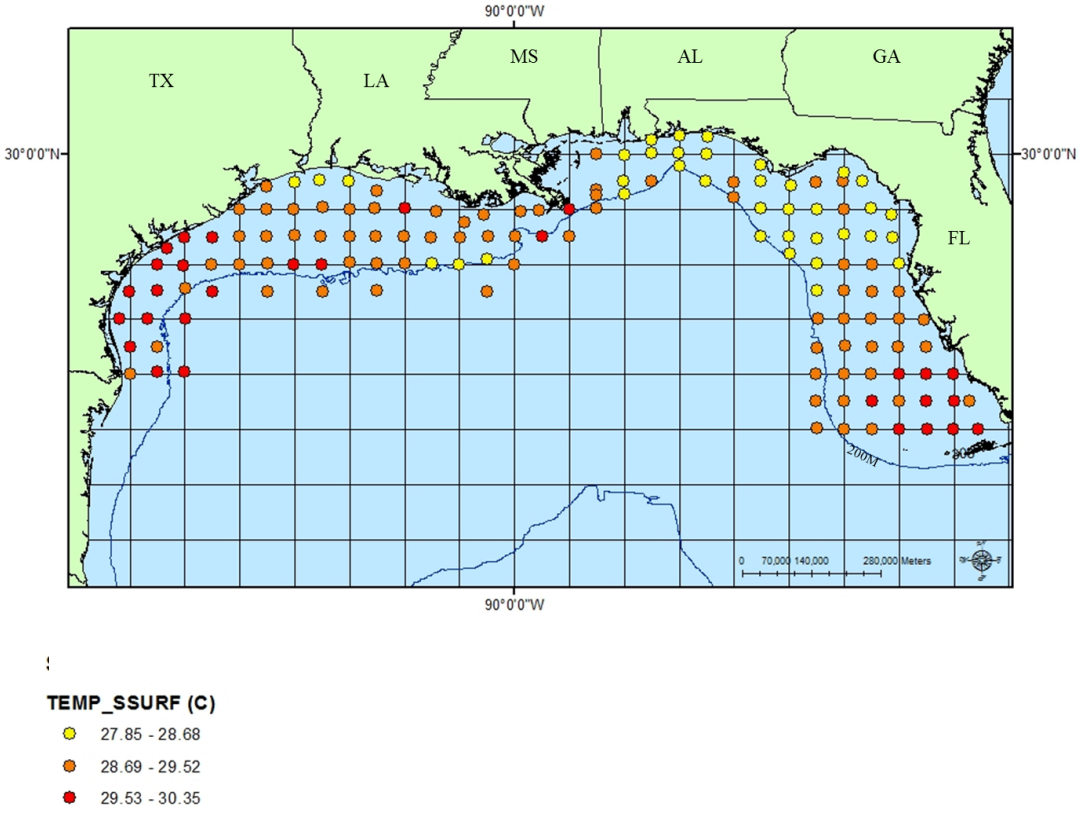

Figure 62. *In situ* Sea Surface Temperature Taken During the SEAMAP Fall Plankton Survey, Cruise GU033.

Plankton, including portunid larvae, are often concentrated in surface waters, and sea surface oxygen levels were fairly constant during sampling (Figure 63). Lower oxygen levels were seen near the southern tip of Florida, whereas higher oxygen levels were seen in near shore areas where freshwater inputs are present.

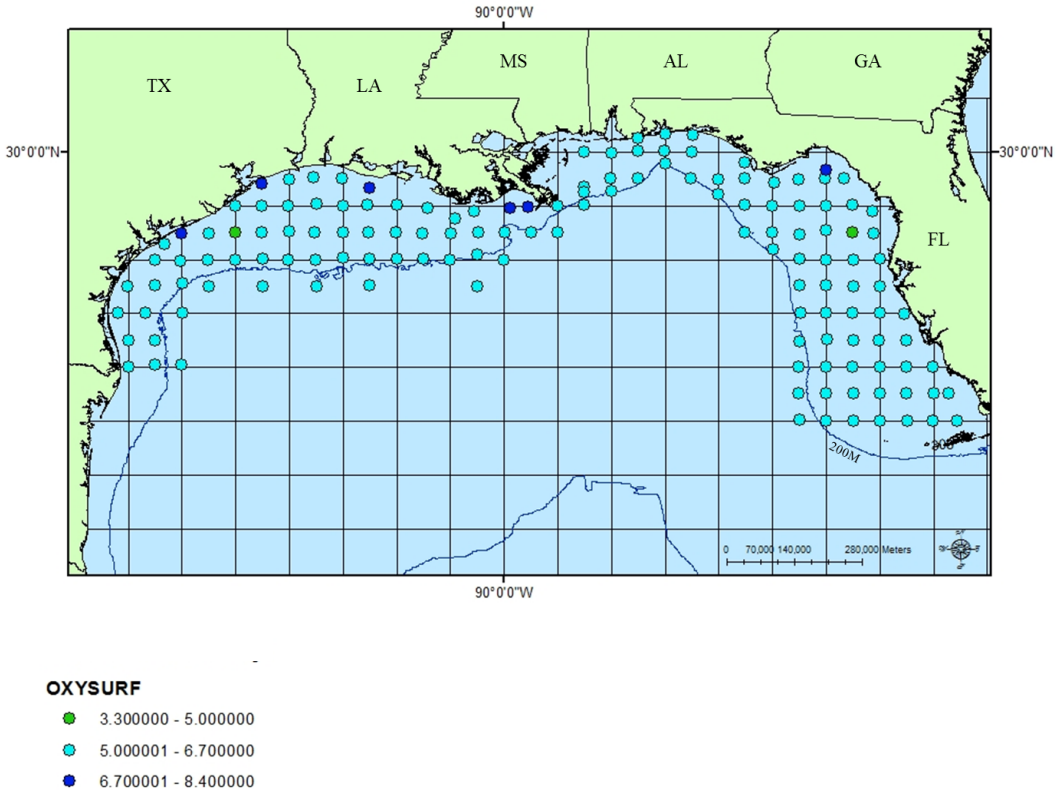

Figure 63. In situ Surface Oxygen Levels Taken During the SEAMAP Fall Plankton Survey, Cruise GU033.

The sea surface salinity was high at a majority of stations sampled, except near areas where there were strong sources of fresh water input (Figure 64). Surface salinity ranged from 22.17 ppt to 36.74 ppt, with the average salinity being 33.50 ppt. Lowest salinities were found off the northeastern coast of Texas and around Louisiana. The highest salinities were found out on the shelf break near Texas and Louisiana and along the western coast of Florida past the panhandle area. Records from three stations were dropped from consideration because of equipment failure noted in the database.

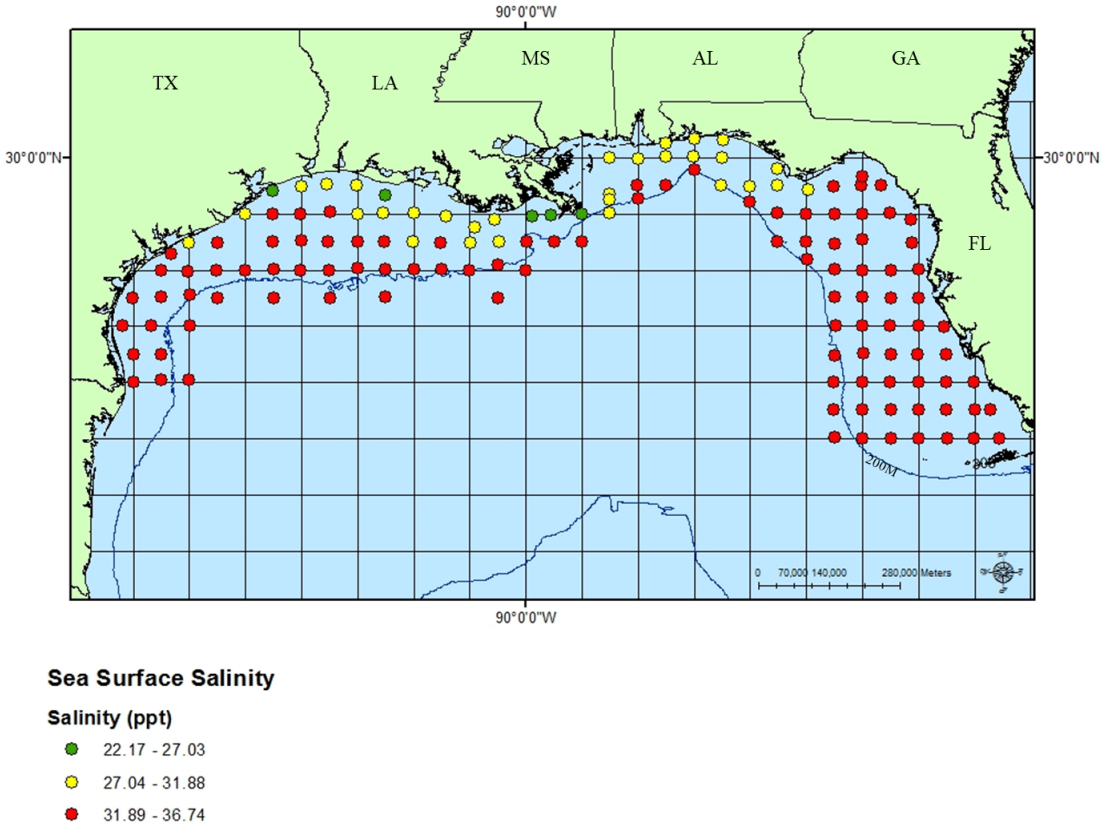

Figure 64. *In situ* Sea Surface Salinity Taken During the SEAMAP Fall Plankton Survey, Cruise GU033.

The strongest currents were associated with the Loop Current coming into the northern GOM and with resulting eddies separating from the Loop Current (Figure 65, Figure 66). As the largest and most powerful current to enter the GOM, the Loop Current fluctuates seasonally as well as annually in intensity and in intrusion depth (Huh et al., 1981; Hurlburt and Thompson, 1980; Molinari et. al., 1977; Molinari et. al., 1978). It can provide a source of larval transport both for bringing larvae in from the Caribbean as well for transporting early stages of native species around the gulf. Intrusion height of the Loop Current (e.g. how far into the GOM the current penetrates) and the shedding of eddies off of the current affect the distribution of larvae (Shulman and Bermingham,

1995). Sea surface height was chosen to display the position of the loop current throughout the cruise period. Sea surface height was aggregated into one week intervals resulting in five images representing the duration of the cruise. The first and last images are displayed in Figure 67, showing the breakdown of the loop current over the course of the cruise. The loop current sat low in the GOM at the time sampling started, with a strong eddy present off the coast of Louisiana and two weaker eddies in the southern GOM. By the end of the cruise the loop current barely penetrates the GOM, leaving behind a large and strong eddy near the southern portion of the eastern GOM.

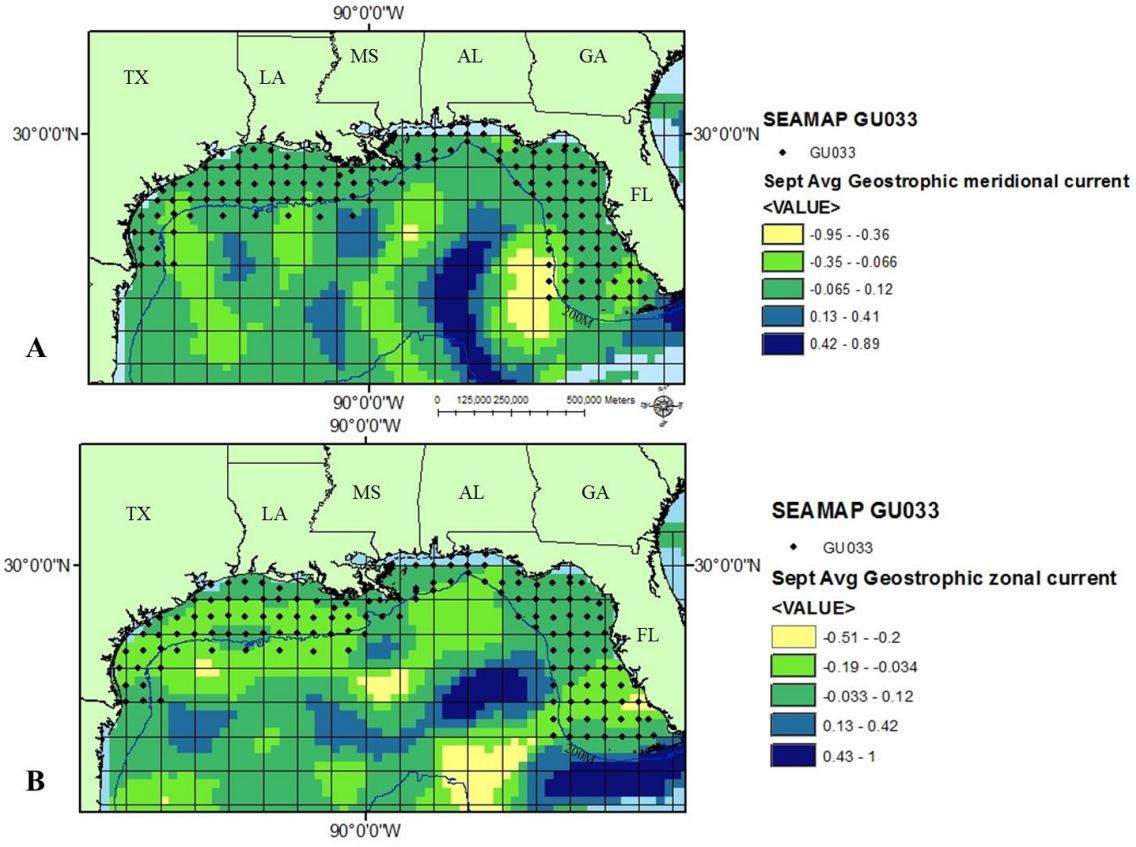

Figure 65. Average Meridonial (A) and Zonal (B) Currents for the Month of September Compiled From Satellite Imagery.

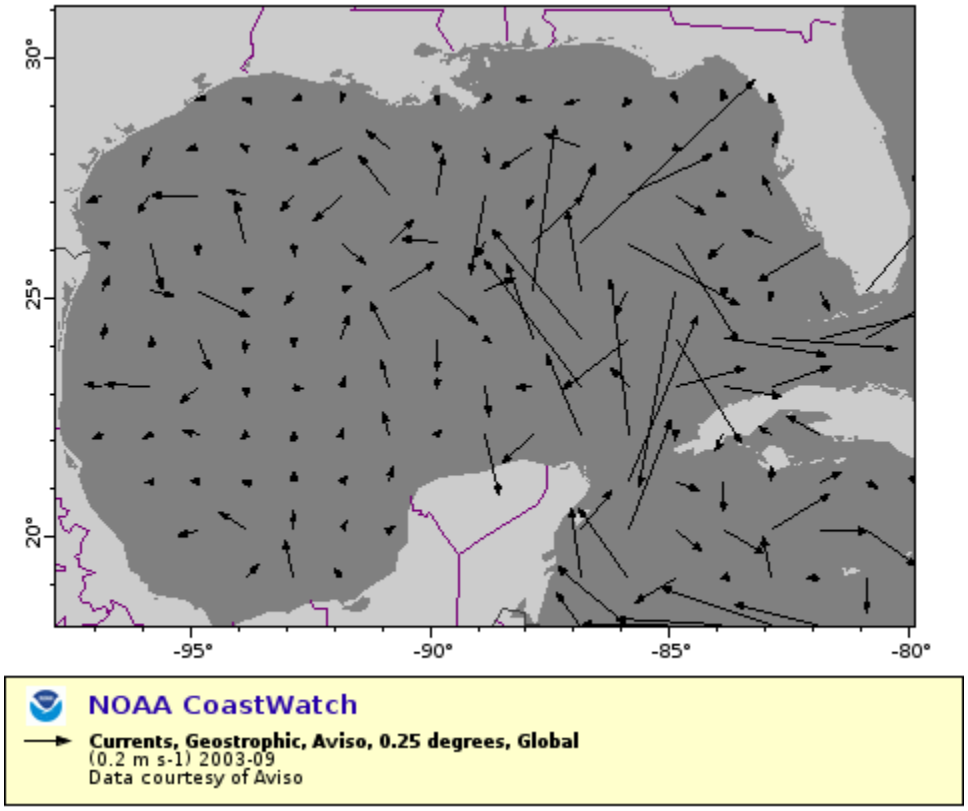

Figure 66. Map Generated from BloomWatch 180 Website Displaying the Average Currents for the Month of September in Vector Form as Compiled from Satellite Imagery.

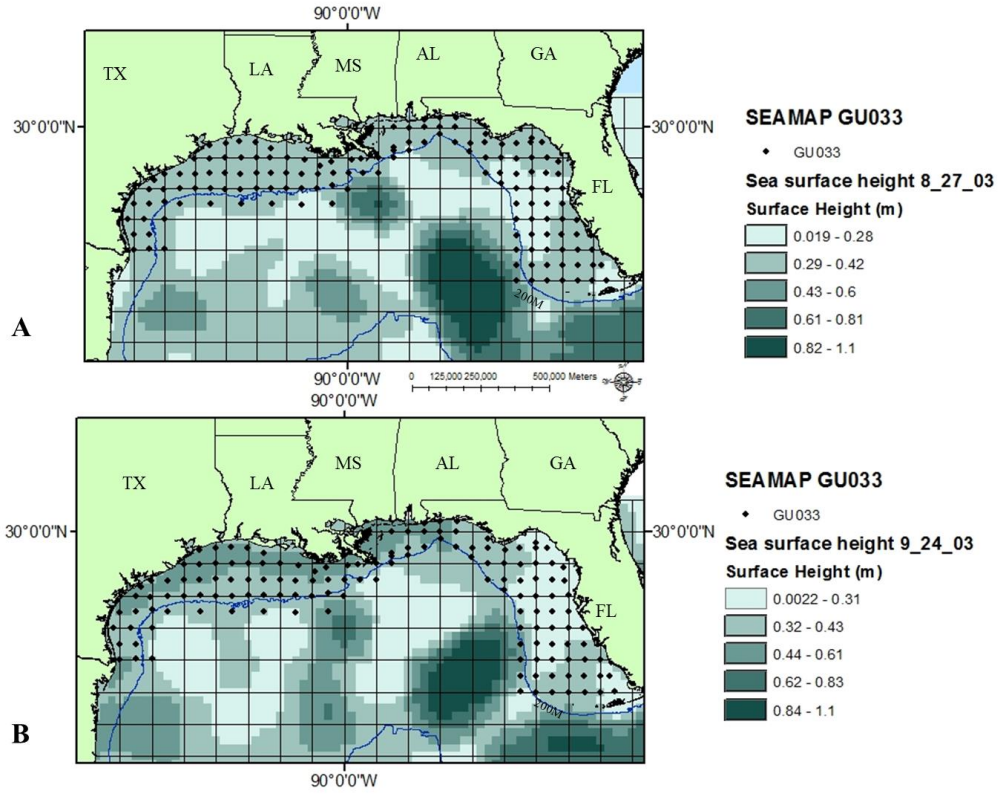

Figure 67. Sea Surface Height Near the Beginning (A) and End (B) of the Cruise as Derived From Satellite Imagery.

Sargassum serves as floating habitat for many organisms including portunid megalopae, in particular *Portunus sayi*, the sargassum crab. Currents transport *Sargassum* from the Caribbean and GOM through the Florida Straits and into the Atlantic Ocean and Sargasso Sea (Gower and King, 2011). Currents and wind also are responsible for clumping *Sargassum* mats together and can ultimately push them ashore where they desiccate along with entrained fauna (Jobe and Brooks, 2009). Occurrences of the large mats are greater in the fall, though *in situ* data from this cruise seem to suggest few large mats were encountered during the time of sampling (Figure 68). Regional patterns of *Sargassum spp.* distribution vary annually, though it appears that there is no discernible pattern within the GOM (Gower and King, 2011; Glenn Zapfe, personal communication).

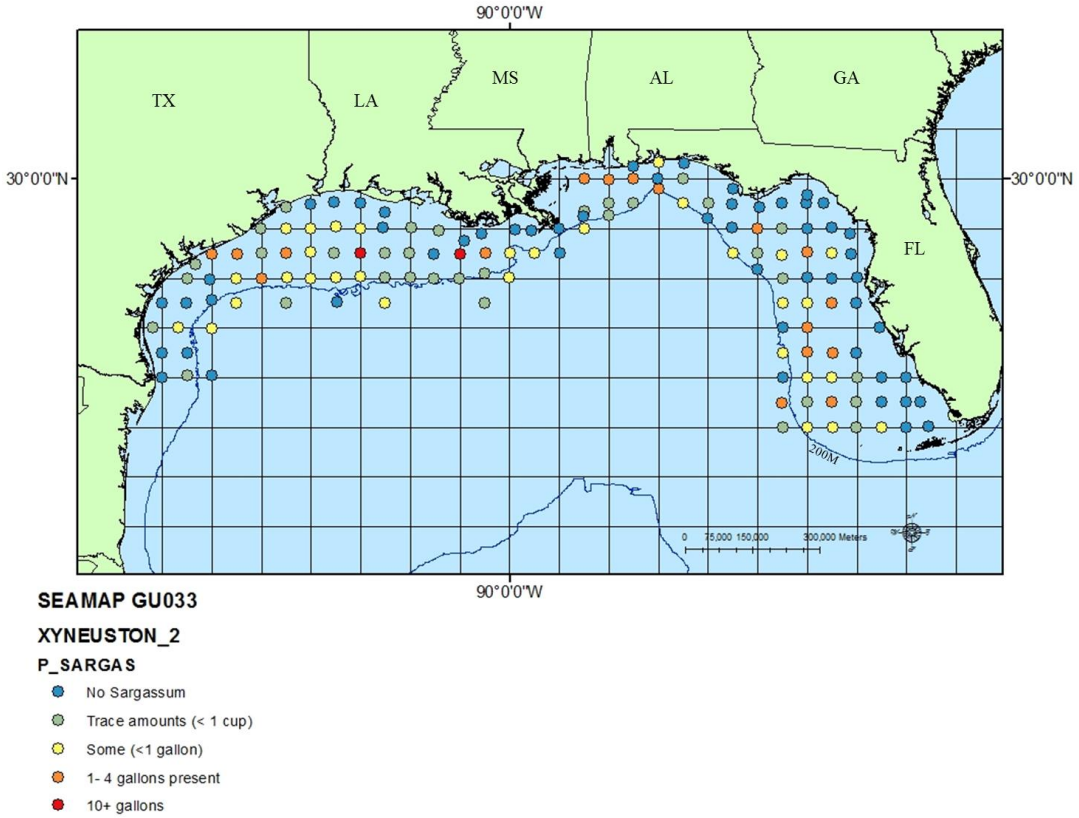

Figure 68. Volume of *Sargassum* Present in Neuston Tows Taken During the SEAMAP Fall Plankton Survey, Cruise GU033.

Sampling occurred around the clock during the cruise; thus, samples fall into different diel periods. Four different diel classifications are recognized. There were 63 day samples, 64 night samples, 11 day twilight samples (sunrise ± 1 hour), and three evening twilight samples (sunset ± 1 hour) (Figure 69). Samples representing different times of day were interspersed throughout the study region. Because portunid larvae migrate vertically, the time of day can help explain abundance patterns.

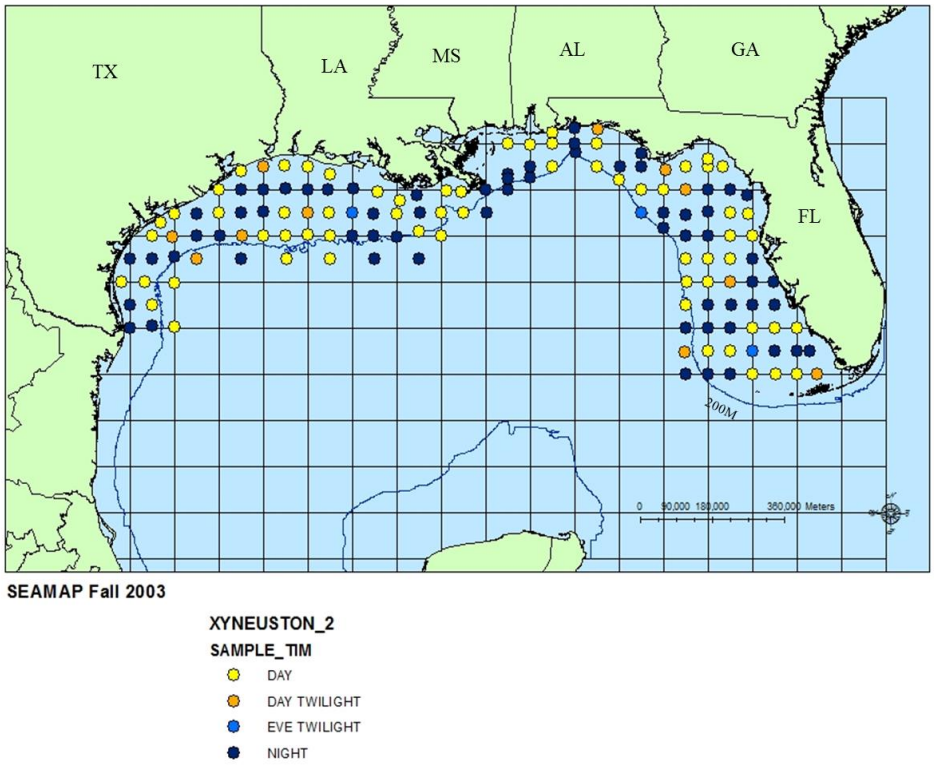

Figure 69. Time-of-Day for GU033 Stations.

Community Analysis

The neuston samples were chosen for community analysis because they contributed the highest densities (CPUE). CPUE for the first leg of the cruise was 37,728 individuals/min and 17,646 individuals/min for the second leg of the cruise. The generated scores from NMDS analysis were plotted in a NMDS biplot. This biplot illustrated correlations between the stations (points) and the taxa observed in the samples (text) (Figure 70). The NMDS spatial display of the Portunidae megalopa taxocene shows that each station was characterized by a combination of characteristic taxa and density levels (Table 4). The first two NMDS axes, NMDS1 and NMDS2, each represented 52.14% and 35.73% of the variance in community structure, respectively. Four assemblage types occurred across the northern gulf during the survey, including two high

density assemblages and two low density assemblages (Table 4). Density levels of each assemblage also corresponded with the taxon richness of that assemblage. Although none of the four assemblage types occurred exclusively within any region of the northern GOM, in the western gulf, the high density *Callinectes* dominant assemblage (small orange) was the most prevalent, whereas the high density *Achelous* dominant assemblage (medium beige) was more prevalent in the eastern gulf (Figure 71). The lower density *Callinectes* dominant (large red) and *Achelous* dominant (small white) communities were more evenly distributed across the northern gulf.

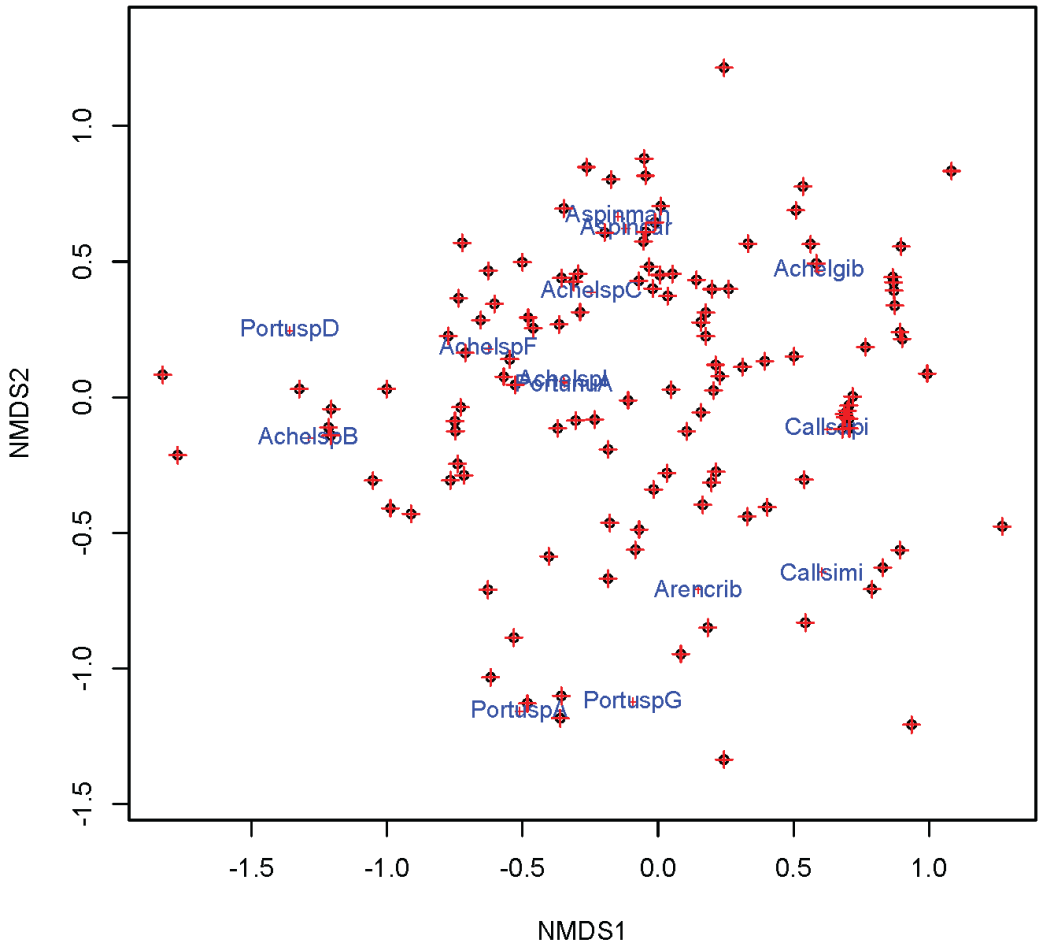

Figure 70. NMDS Biplot of Scores Generated by NMDS Analysis. Red points represent stations and blue text displays analyzed taxa.

Table 4

Characterization of Four NMDS Assemblages in Terms of Relative Composition of Member Taxa. Symbol designations explicitly mapped in Figure 71.

Taxon	small white	small orange	med beige	large red
Achelous spp.	0.570000342	0.10353835	0.27370276	0.018735123
Achelous gibbesii	0.103112146	0.170343894	0.141918302	0.334767048
Achelous spinicarpus	0	0.12574387	0.085713707	0.003341409
Achelous spinimanus	0	0.056034946	0.049211596	0.001413723
Arenaeus cribrarius	0	0.031396653	0.012860221	0.004725466
Callinectes sapidus	0.249497633	0.396331065	0.229687266	0.394295936
Callinectes similis	0.038762756	0.100675905	0.123358767	0.221878751
Portunidae spp.	0.038627123	0.012528842	0.076874597	0.020842545
Portunus sp. A	0	0.003406476	0.005152172	0
density	low	high	high	low
num collections	10	47	35	36
taxa richness	6	16	16	9
Community composition	*Achelous* dominant *Callinectes* subdominant rel low Csim/Csap ratio rel highest *Achelous* spp. rel average *A. gibbesii* no *A. spinicarpus* no *A. spinimanus* rel less *Arenaeus* rel more Portunidae spp. *Portunus* sp. A absent	*Callinectes* dominant *Achelous* subdominant rel low Csim/Csap ratio rel low *Achelous* spp. rel average *A. gibbesii* rel more *A. spinicarpus* rel more *A. spinimanus* rel more *Arenaeus* rel less Portunidae spp. *Portunus* sp. A present	*Achelous* dominant *Callinectes* subdominant rel high Csim/Csap ratio rel moderate *Achelous* spp. rel average *A. gibbesii* rel more *A. spinicarpus* rel more *A. spinimanus* rel more *Arenaeus* rel more Portunidae spp. *Portunus* sp. A present	*Callinectes* dominant *Achelous* subdominant rel high Csim/Csap ratio rel lowest *Achelous* spp. rel more *A. gibbesii* rel less *A. spinicarpus* rel less *A. spinimanus* rel less *Arenaeus* rel less Portunidae spp. *Portunus* sp. A absent

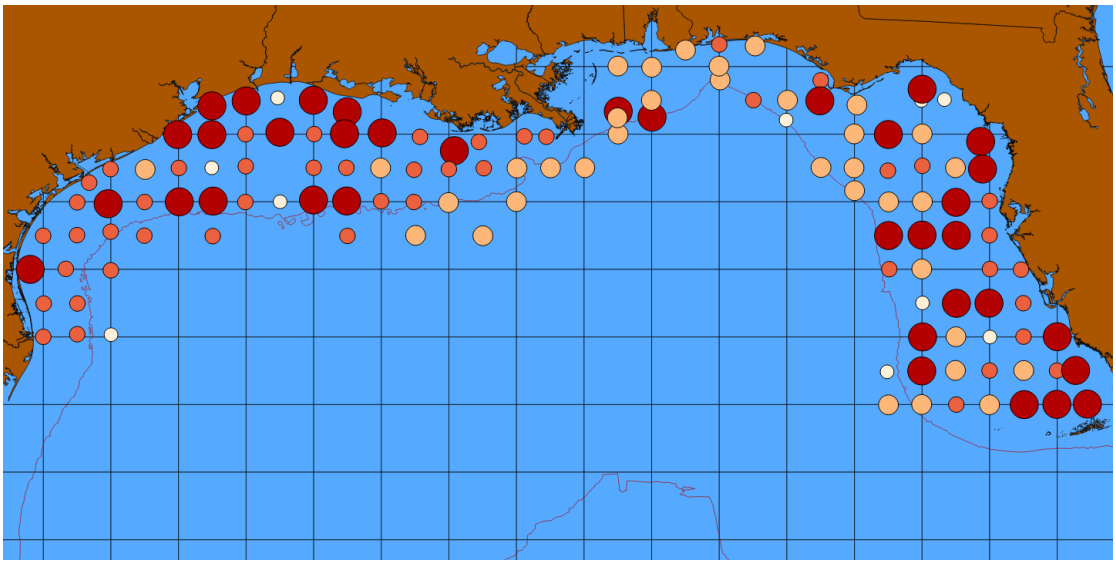

Figure 71. GIS Map of Four Portunid Megalopae Assemblage Types Identified Through NMDS. See Table 4 for taxonomic differences.

CHAPTER V

DISCUSSION

The goal of this project was to examine the diversity and community structure of portunid megalopae in the northern GOM by identifying specimens to the lowest taxonomic level possible and by examining environmental associations in conjunction with megalopa assemblage structure. Taxonomic identification led to the recognition of 18 taxa encompassing five genera and five unique morphs that could only be attributed to the family Portunidae. Spatial analysis of the locations of catches displayed geographic patterns describing where these taxa and morphs occurred during the 2003 fall cruise. An overview of the Portunidae megalopa taxocene in the fall of 2003 in the northern GOM using a multivariate analysis approach showed that four assemblage types occurred in the northern gulf. The interpretation of the composition of the assemblages was based on summaries of the densities and types of megalopae present in the samples characterizing each type of assemblage. Visual analysis of environmental data collected during the survey yielded little correlation between distribution of taxa and the assemblages and the environmental variables examined. Only currents and the time of day of sampling appeared to have an effect on the distributions of the taxa.

Taxonomic analysis

Identifications

The examination of Portunidae megalopae revealed 18 morphs, seven of which were identified to the species level. Of the 18 morphs occurring within the neuston, 13 were also caught in the bongo nets. Because megalopae predominantly frequent the surface waters, it is not unexpected that more morphs occurred in neuston (i.e. surface)

samples, which come from surface waters. Those found in the bongo (i.e. integrated water column) samples could have been caught at depth or at the surface upon net retrieval. In the GOM, 29 different species of swimming crabs occur; however, while it is possible that each of the 18 morphs collected represents a single species that is not necessarily the case. Rather, some of the morphs recognized in this study may represent variations of the same taxon, as was seen with *Achelous gibbesii*.

Portunid species of the GOM are represented by three subfamilies: Polybiinae, Portuniinae, and Thalamitinae. Of the three subfamilies, the Portuniinae contains the most species, and all specimens in this project identified to genus or below appear to fall solely within this subfamily. However, specimens that were identified to the family level may also represent other subfamilies, which make further discussion of their characteristics relevant.

The subfamily Polybiinae contains species of swimming crabs in which the megalopae lack sternal spines and posterolateral spines on the fifth abdominal segment. There is some disagreement on the classification of this group as a subfamily and some recognize it as a family of its own, distinct from Portunidae, despite the presence of a fifth pereopod modified for swimming. (Schubart and Reuschel, 2009). In the GOM, one of the best known members is *Ovalipes floridanus,* for which there is no description of the megalopa published in the primary literature but for which the megalopae are easily identified by their square carapace shape and large dorsal spine (Stuck et al., unpublished ms). However, these larvae were not seen in this study. All GOM genera within this subfamily include at least one species for which the megalopa stage has been described, though not all of these species occur in the gulf. The exception to this is *Raymanninus schmitti* (formerly in the genus *Benthochaceon*), a representative of a monotypic genus

for which the larvae have not been described. Based on existing descriptions of members of the polybiiinae, it is unlikely that any of the unidentified Portunidae morphs in this study belong to this subfamily.

The subfamily Thalamitinae contains only one species that is known to occur in the GOM, the introduced Indo-Pacific species *Charybdis hellerii* (Felder and Camp, 2009). Dineen et al. (2001) described the larval stages of *C. hellerii* but failed to describe any details of the megalopal stage and accurate morphological characteristics cannot be discerned from the image of a specimen provided. Kurata (1975) provides descriptions of other *Charybdis* species, as well as develops a brief diagnosis for the genus. According to Kurata (1975), *Charybdis* megalopae lack a carpal spine, possess a basi-ischial spine and a coxal spine on pereopod 2, have eight flagellum segments in the antenna, and have smaller sternal spines than those present on *Portunus* (*sensu lato*). If this description applies to *C. hellerii*, then it is possible that Portunidae sp. D could be the megalopa of this species.

Within the subfamily Portuniinae, the megalopae of only eight of the 25 species present in the GOM have been previously described, with varying degrees of detail. All eight of these species, belonging to five genera (*Arenaeus*, *Callinectes*, *Portunus*, *Cronius*, *Achelous*) were identified in this study. Of these, *Arenaeus*, represented by *Arenaeus cribrarius*, was the only genus without problematic or incomplete taxonomic descriptions and identified specimens closely matched the description by Stuck and Truesdale (1988). The identification of species in the remaining genera was often problematic, as discussed below.

For the GOM members of the genus *Callinectes*, only the commercially important species, *C. sapidus*, and the smaller *C. similis*, are represented by descriptions of the

megalopal stage. As there are eight species of *Callinectes* that have been recorded in the GOM, this leaves six other species of *Callinectes* lacking megalopal descriptions. Although half of the *Callinectes* species from the GOM are known to occur within the region of the gulf that was sampled by cruise GU033, only *C. sapidus* and *C. similis*, the two most abundant species in the gulf, were identified in this study. Megalopae identified as *Callinectes similis* in this study agreed well with the description provided by Bookhout and Costlow (1977). Megalopae identified as *Callinectes sapidus*, however, exhibited a wider range of variation in the study samples than was specified in the original description (Costlow and Bookhout, 1959). This variation was mostly seen in the antennal segment lengths. However, the overall antennal segment length pattern agreed with that shown in the description. This variation in length may reflect naturally occurring variation or may indicate the presence of multiple species, although little additional variation was noted. The original description of this megalopa was from the Beaufort Inlet, NC (Costlow and Bookhout, 1959). Variation could be attributed to differences in location differences in the samples collected (e.g. Atlantic Ocean vs. GOM). Seasonal variation has also been recorded in the literature for this species (Stuck et al., 2009), but variation in these samples due to seasonality is unlikely as they were all collected in the fall. Despite observed antennal variation, specimens were all identified as one of the two species for which the megalopae are known. Further work on identifying the megalopae of the various species of *Callinectes* is still needed.

Another genus whose larvae in the GOM are poorly described is *Portunus*. For GOM species, the only one for which a description of the megalopa exists is *Portunus anceps* (Lebour, 1944). However, the description provided by Lebour (1944) was based on material from Bermuda and is lacking in detail. In addition, it was done based on a

megalopa obtained from the plankton and verification of its identity was lacking. All other descriptions of *Portunus* megalopae represent Indo-Pacific species, which at least include the description of the megalopa for the type species of the genus, *Portunus pelagicus* (Linnaeus, 1758). For the GOM, problems arise with regard to the recent revision of the genus and the subsequent reassignment of many of the species to the genus *Achelous* (Mantelatto et al., 2009). This revision left the genus *Portunus* as a paraphyletic group, separating *P. sayi* and the type species, *P. pelagicus*, from most of the remaining gulf species (*P. anceps*, *P. floridanus*, *P. ventralis*). *Portunus vossi*, also a GOM species, was not included in that study. Kurata (1975) provided a megalopal diagnosis for the genus, but it is not clear if the diagnosis applies to both clades within the genus, as it was based on two Pacific species (*P. pelagicus* and *P. trituberculatus*) within the same clade. Megalopae of members of the other clade have not been fully described.

If Kurata's (1975) description is valid for all *Portunus* species, then none of the specimens identified in this study fits are likely to belong in the genus *Portunus*. The morph *Portunidae* sp. C may be *Portunus sayi*, based on the occurrence of these megalopae in Gulf *Sargassum* samples taken in another study. *Portunus sayi* is a strictly pelagic species that uses floating mats of *Sargassum* as habitat. Portunidae *sp.* C, however, lacks the carpal spine on the cheliped, as well as the pereopod 2 ventral coxal spine noted in the diagnosis of the genus.

The specimens identified in this study as *Portunus* sp. A also does not quite fit Kurata's (1975) diagnosis of *Portunus*. *Portunus* sp. A has only seven flagellum segments in the antennae as opposed to the eight called for in the diagnosis, as well as lacking the carpal spine on the cheliped. The provisional assignment of these specimens to the genus *Portunus* was done based on a combination of other characters noted in the

diagnosis of the genus, in addition to several characters common to species in the genus *Achelous* (7 antenna flagellum segments, basi-ischial spine present on cheliped).

It is possible that the megalopae of some GOM *Portunus* species, especially those in the clade that does not contain *P. pelagicus*, the type species of the genus (see Mantellato et al., 2009, Figure 1), could have a combination of characters found in the *P. pelagicus* clade and those found in the *Achelous* clade. Based on the genetic work done by Mantelatto et.al (2009), it is assumed that *P. sayi* would fit Kurata's (1975) diagnosis of the genus as this species falls into the same clade as the type species and does not seem to share a recent common ancestor with those species moved into the genus *Achelous*. Except for *P. vossi*, which was not included in the Mantellato et al. (2009) study, the remaining *Portunus* species (*P. floridanus, P.anceps, and P. ventralis*) fall into the second *Portunus* clade of Mantellato et al. (2009), and it is unknown what combination of morphological characters they possess. Based on the partial description and drawings of the megalopa and first crab of *Portunus anceps* given by Lebour (1944), it appears that *P. anceps* has seven flagellum segments in the antennae, no carpal spine as either a megalopa or first crab, sternal spines extending to the posterior border of abdominal somite two, and rather large posterolateral spines on abdominal somite five. However, it is unclear from the description and drawings whether or not this megalopa has basi-ischial or coxal spines. Of all the portunid genera found in this study, *Portunus* lacks the most definitive descriptive information, and further studies into the early life history of this genus are much needed.

One morph identified in the samples, Portunidae sp. G, appeared to be in agreement with Lebour's (1944) description of the megalopa of *Portunus anceps*, but it did not match the description well enough to be assigned to this species with certainty. As

part of a collaborative effort, fellow graduate student Luca Antoni conducted a genetic analysis of 16s mitochondrial DNA (mtDNA) on this morph in order to get an accurate identification. However, the genetic analysis failed to produce a 100% match with any known GOM species sequences within the GenBank nucleotide database (Benson et.al. 2012). The closest genetic match for Portunidae sp. G was *P.anceps*, at 92% (Luca Antoni, personal communication); however, that is not close enough to assign it to that species. The genetic analysis eliminated all known GOM portunid species with the exception of *Raymanninus schmitti*, for which no genetic sequence was available for comparison. Because *Raymanninus schmitti* is in the subfamily polybiinae, it is unlikely that this is the identity of this morph as the morph does not exhibit characters normally seen in this subfamily. Further genetic analysis of GOM species, as well as those from the Caribbean and south Atlantic, will be needed before a species name can be assigned to this morph.

In the case of *Cronius ruber*, the megalopae were successfully identified genetically with a 100% genetic match (Knight et al., in prep). The megalopa is very distinctive morphologically, as noted by Rice and Kristensen (1982) in their description of an unknown megalopa from the coast of Curaçao. These megalopae clearly stood out because of their extremely large size compared to other megalopae in the samples. Indeed, this species had the largest megalopa seen in this study, with a carapace length of approximately six mm. It is also distinguished by its unique rostrum, featuring a single rostral spine flanked by two smaller protrusions. Rice and Kristensen (1982) speculated that *Cronius* could be the genus of the Curaçao megalopa by ruling out other known species based on descriptions of their megalopae at either the genus or species level, but they were not able to demonstrate this conclusively.

The newly revised genus, *Achelous*, now contains eight species that occur in the GOM, all of which are known to occur in the SEAMAP survey area (Felder and Camp, 2009, as *Portunus*). In this study, three species and five morphs were identified in this genus, although it is unlikely that all morphs belonged to different species due to some species being southern GOM species. Much like *Callinectes*, the megalopae of only a few species (*A. gibbesii, A. spinicarpus, A. spinimanus*) have been described. One problem with the identification of these three species, despite the availability of larval descriptions, is that they are very similar to each other morphologically. Another problem with the identification of the specimens available for this study is that most of them lacked pereopods, in particular the first and fifth pereopods. Both of these appendages are crucial for identifying the megalopae to species. The number of hooked setae on the fifth pereopod dactyl is one of the best characters to use for distinguishing the *Achelous* species without having to examine their mouthparts as they are visible and present in all species. These setae were used whenever possible; however, body size, antennal flagellum segment length patterns, rostrum length and curvature, and sternal spine size provided the main diagnostic criteria for distinguishing between the three species and five GOM morphs of *Achelous.*

One additional diagnostic character seen on several of the *Achelous* morphs was the presence of a thoracic spine, which was very small and varied from a bump to a definite small hooked spine (Figure 72). This spine lies on what appears to be the posterior border of the fourth thoracic segment, and when viewed by looking at a specimen laterally, falls slightly anterior to the line of sight between the pair of coxal spines on the second pereopod. Not all of the *Achelous* morphs had this spine, so it may

provide a way to define groups within the genus. The spine was also not seen on specimens outside of the genus so may be a useful character to use for separating genera.

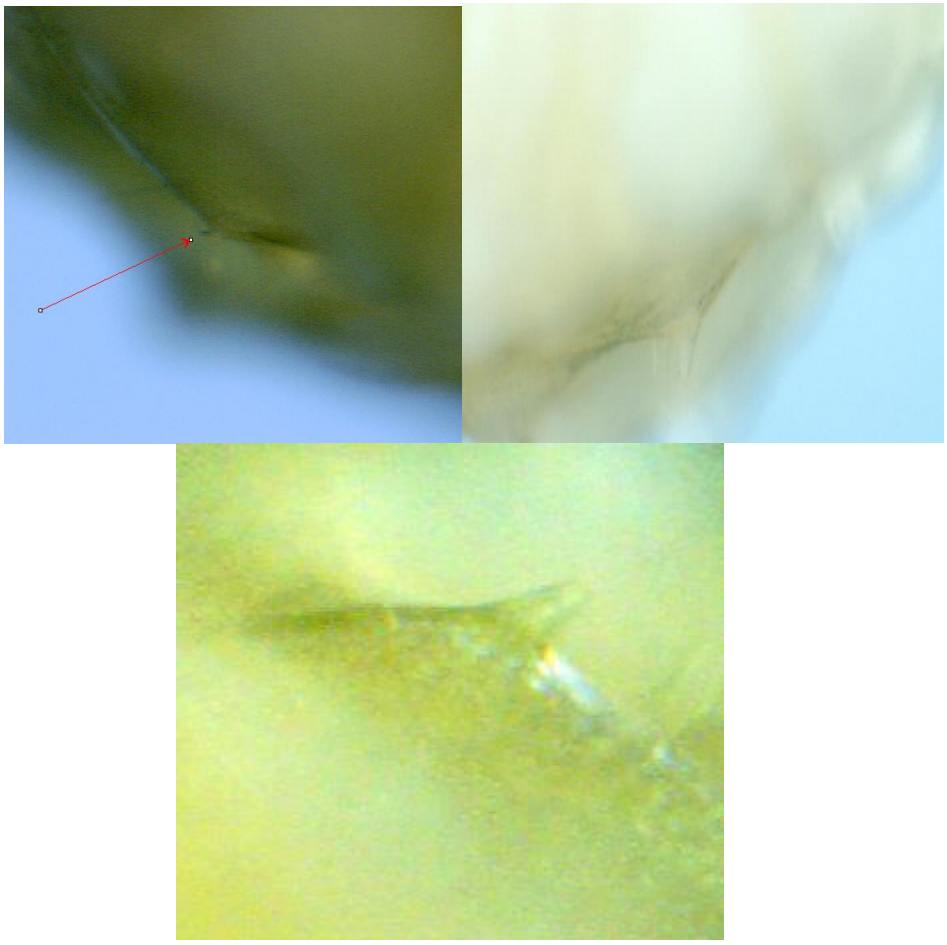

Figure 72. Thoracic Spine on an *Achelous* Megalopa. Difference between bump form (top left) and true spine (top right). Close up of the spine (bottom). Anterior is to the right in the two top Photographs and to the left in the bottom photo.

Another diagnostic character for *Achelous* was the distinctive distal border of the telson. Previous larval descriptions (Costlow and Bookhout, 1977; Negreiros-Fransozo et al., 2007) noted that the distal border of the telson for *Achelous* was flat to slightly convex, as opposed to the distally rounded, tongue-like telson of *Callinectes similis*. Among the identified morphs of *Achelous* from this study, some also displayed a telson with a slight medial protrusion on the distal margin. This character may also help to

define subgroups within *Achelous*, as not all morphs had this feature. Images and drawings of the telson characters are presented within the individual taxon descriptions in Chapter III.

Distribution

Knowledge of megalopal distributions aids in understanding their ecology and can be used as an additional tool in the identification of specimens. In the list of species provided by Felder and Camp (2009), each species is accompanied by a list of regions of the GOM where the adults are found. While larvae are not necessarily restricted to the same regions as are adults because of movement via currents, etc., matching the distributions of adults and early stages helps to rule out some species when identifying larvae. Thus, distribution maps for each identified species and morph of megalopa were included with their descriptions and the general distribution patterns encountered are discussed below.

Callinectes sapidus, C. similis, and Achelous gibbesii were the most abundant species of portunid megalopae found in the GU033 samples and were distributed widely across the northern gulf (Figure 24, Figure 51, Figure 54). These three taxa were also the most abundant species present in Stuck and Perry's (1981) study of megalopae in the Mississippi Sound. In this study, both species of Callinectes exhibited highest abundances and CPUE near the southern tip of Texas, which tapered off as the cruise moved east towards Florida. High densities of Callinectes at the 200m isobath are also not unusual; C. sapidus megalopae have previously been reported in offshore shelf waters (Dudley and Judy 1971; Nichols and Keney 1963). Williams (1974) noted that the spawning season for C. sapidus ranged from December to October in this area, with peak spawning occurring in June and early July. This spawning period agrees well with

megalopal data from the present study. Based on the estimated duration of 31-49 days from the time of spawning for early stages of portunids to reach the megalopal stage (Williams, 1974), the expected time of peak occurrence for megalopae of C. sapidus could have begun as early as late July. Because cruise sampling along the shelf break from Mississippi to the coast of Texas during the 2003 fall plankton survey took place early in September, observed densities likely represented crabs originating from near the end of the peak spawning season, and collected specimens were probably nearing time to settle into the adult habitat. The low observed abundance and CPUE off the coast of Florida may partly reflect the later sampling date. The later arrival of the cruise to the coast of Florida (September 16^{th}-29^{th}) may have missed the time window within which the highest densities would have occurred.

The opposite distribution pattern was seen for the majority of the Achelous species, which displayed relatively low abundance and CPUE off the coast of Texas and increased as sampling progressed eastward into coastal Florida waters (Figures 21, 24, 33, 36, 39, 42, 44). The exception to this is Achelous gibbesii, which occurred at a fairly uniform density across the northern gulf, with some patchy aggregations off the coast of Texas from Brownsville to Corpus Christi and off the Florida coast near Pensacola and Tampa Bay (Figure 30). Adults of Achelous gibbesii and A. spinimanus have been reported to be common on shrimping grounds of Campeche Bank but are rare on the Texas coast (Hildebrand, 1954), and these two species have also been noted to be closely associated with each another (Williams, 1984). However, the distribution of the megalopae of these two species in this study contradicted previously noted distributions for the adults, in that both A. gibbesii and A. spinimanus occurred off the coast of Texas, where A. gibbesii was present in relatively higher abundances than A. spinimanus. In

contrast, A. spinimanus was relatively more abundant in the eastern gulf, where it was more closely associated with A. spinicarpus than with A. gibbesii, contrary to the pattern noted for the adults by Williams (1984).

Arenaeus cribrarius occurrences were concentrated off the coast of Texas, with a few occurrences off the coast of Louisiana and Florida (Figure 48). This distribution pattern concurs with known distribution for the adults (Williams, 1984). Though this species is noted to occur throughout the GOM (Felder and Camp, 2009), adults have been reported to occur primarily from shrimping grounds off the coasts of Texas and Florida (Hildebrand, 1954; Siebenaler, 1952). Portunus sp. A had a similar distribution pattern, only more inshore than Arenaeus cribrarius.

Megalopae for Cronius ruber were only seen at one station, from which only two individuals were recovered from the sample (Figure 57). These two larvae were probably transported into the vicinity of this station via an eddy that split off from the loop current (Figure 67). Moreover, C. ruber is considered to be a Caribbean species, although adult populations do occur in the GOM (Felder and Camp, 2009). Previous studies report megalopae of this species to occur in Bermuda (Lebour, 1944), Curaçao (Rice and Kristensen, 1982) and Puerto Rico (Knight et al., in prep). The occurrence of Cronius ruber megalopae in this study corresponds with the reported spawning times for this species in Cuba, Jamaica, and Curaçao (Williams, 1965).

Megalopae of the morphs Portunidae sp. A and Portunidae sp. G could also have been brought into the north central gulf by the loop current, either from the Caribbean or from further offshore in the GOM. The occurrences of these morphs were concentrated off the coast of Louisiana near the shelf break (Figure 6, Figure 18). The loop current did extend well up into the gulf in the fall of 2003 and an eddy broke off and moved

northwestward into Louisiana shelf waters (Figure 67). Stuck and Perry (1981) noted, however, that some megalopae in their Mississippi Sound samples may have been what is recognized in the present study as Portunidae sp. G in the present study. A full description for these megalopae was not provided, but the general morphological features noted, such as size and a brief comparison to known species, alludes to a specimen similar to those seen in this study. In the event that these megalopae are the same, then Portunidae sp. G, and possibly Portunidae sp. A as well, could be local species that may occur only in the Louisiana/Mississippi region of the northern GOM. The sparse occurrences observed at the shelf break off the southern tip of Florida could then be attributed to larvae being transported by the Loop Current to that location.

The remaining identified Portunidae morphs (C, D, and E) occurred at low frequencies and were sporadically distributed throughout the northern GOM (Figures 9, 12, 15). It is possible that these morphs occur more commonly in a different area within the GOM than the area sampled in the fall of 2003 (e.g. out past the shelf break or possibly in the southern GOM) or that they were residual seasonal occurrences of taxa that had peak spawning periods outside of the sample period window.

Due to the typical peak in spawning for these crabs and given the length of time megalopae are expected to be present in this life stage, the area surveyed later in the cruise (i.e. the eastern GOM) might not yield as many megalopae. This is simply because they may have already settled out of the plankton. This effect confounded comparison of the distribution patterns over a wide region, such as the GOM. While berried females can be found at any time of year, several species share peak spawning periods (Williams, 1965). For most portunid crabs, the time between hatching and reaching the megalopal stage is 31-49 days (Williams, 1965), depending on the number of zoeal stages that a

particular species will pass through, as well as environmental conditions and cues. The megalopal stage itself lasts on average another 20-40 days (Williams, 1965), depending on environmental conditions and cues. Differences in the densities of portunid megalopae in the northern gulf as revealed by the fall 2003 plankton cruise might be partly explained by considering the date when the samples were taken. The first leg of the cruise, which was conducted primarily off the coast of Texas and Louisiana, was sampled within the 31-49 day range following the time at which peak spawning of portunids has been reported to occur (Williams, 1984), and their megalopae could be expected to be abundant in the plankton. As the cruise progressed on to the second leg in western Florida waters, the date window in which megalopae were sampled had shifted, falling outside of that 31-49 day post-spawning window. This may partially explain why total abundances of portunid megalopae were lower off the coast of Florida.

Environmental differences between the eastern and western parts of the northern GOM may also play a role in determining distribution patterns of megalopae. The western region has higher volume fresh water input sources, which provide the coastal areas with lower salinity waters and higher nutrient levels. The eastern gulf lacks the numerous fresh water inputs seen in the west, resulting in higher salinities. However, the intrusion of the Loop Current into this area provides a source of nutrients not generated by riverine influence and upwelling events that have been documented off the Florida coast (Weisburg et al., 2000) also deliver nutrients to surface waters.

The high levels of nutrient loading in the northern GOM near Louisiana and Mississippi have been shown to increase densities of some fish species (Courtney et al., 2013) and the increased primary productivity in the surface waters also provides increased food availability for mesoplankton. However, this high nutrient loading also

leads to the formation of a large hypoxic zone, which appears off the coast of Louisiana annually (Rabalais et al., 2002). The bottom water hypoxia leads to high epibenthic die-off in the affected areas, which can decimate the adults of these epibenthic species. High hypoxia sensitivity has been shown in Callinectes sapidus and Callinectes similis juveniles, with death occurring within a week of exposure (Das and Stickle, 1993). Larvae such as megalopae have been shown to reside in the surface waters near the oxycline while delaying metamorphosis until conditions become more suitable for settlement (Rabalais et al., 2002). Salinity differences may also be the cause of delayed settlement, as different species of portunids prefer different salinity levels, both as larvae and as adults (Williams, 1974; 1984; Das and Stickle, 1993).

Community Analysis

Although the community structure of early fall zooplankton communities has been examined with respect to the effects of jellyfish predation (Millett 2010), in the present study, community analysis focused strictly on the portunid megalopal taxocene. Smyth (1980) noted that megalopae are more numerous in neuston collections than in bongo collections and data from this study supports this finding. Collections of megalopae from bongo tows through the water column were less than half of those from surface towed neuston samples. This result is not unexpected since subsurface waters are where this life stage spends the majority of its time. For the neuston samples, the total estimated density of portunid megalopae for the first leg samples was 37,728 individuals/min, and for the second leg of the cruise, total estimated density was 17,646 individuals/min. Thus, the neuston samples were chosen for community analysis because they contributed the highest densities.

Data from the present study indicated the presence of identified four distinct portunid megalopal assemblages, labeled as species dominance patterns (Table 4, Figure 71); similar results were obtained by Millett (2010) for zooplankton communities within the study region. Two of the portunid assemblages were dominated by the genus Callinectes, whereas two others were dominated by the genus Achelous. Each pair of assemblages (i.e., Callinectes dominant vs. Achelous dominant) could be further subdivided into high and low density assemblage types. The high density Callinectes dominated assemblage (small orange circles, Figure 71) occurred at 47 stations included 16 taxa, and was most prominent in the western Gulf, while still showing a strong presence in the eastern Gulf as well. The ratio of Callinectes similis to Callinectes sapidus was low in this assemblage, with C. sapidus being relatively more abundant. The assemblage pattern also mirrored the individual distribution patterns for both C. sapidus and C. similis. The high density Callinectes assemblage was further distinguished by the presence of Portunus sp. A and relatively high densities of Achelous spinimanus and Achelous spinicarpus. Low densities of Achelous morphs in this assemblage matched the individual distribution patterns of these morphs, especially off the coast of Texas. In contrast to the high density Callinectes assemblage, the low density Callinectes dominant assemblage (large red circles, Figure 71) showed a higher ratio of C. similis to C. sapidus. This assemblage was found predominately off the northern coast of Texas and down the west coast of Florida. The low density Callinectes assemblage occurred at 36 stations and comprised only nine taxa. Achelous gibbesii was the dominant Achelous species in this assemblage, and densities of A. spinicarpus and A. spinimanus were low. Consequently, this assemblage had the least Achelous morph influence of the two

Callinectes dominated assemblages. Portunus sp. A was lacking in this assemblage. In both of the Callinectes dominated assemblages, influence from Portunidae morphs was minimal.

The two Achelous dominant assemblages had similar taxa, but different compositions compared to the Callinectes assemblages. In the high density Achelous assemblage (medium beige circles, Figure 71), 16 different morphs were present, and this assemblage was represented by 35 stations, ranging from off the coast of Louisiana and down the Florida west coastline. Achelous gibbesii densities were average in this assemblage, while Achelous spinicarpus and Achelous spinimanus densities were relatively high. Also, the ratio of Callinectes similis to Callinectes sapidus was high. Strong influences were also apparent from Arenaeus cribrarius, Portunus sp. A, and the Portunidae morphs. This assemblage was most prevalent around the 200m isobath, matching the overall distribution pattern seen for Achelous megalopae in general. The low density Achelous dominant assemblage (extra small white circles, Figure 71) was by far represented by the lowest number of stations in northern GOM in the early fall of 2003. This assemblage comprised 6 taxa and only characterized 10 stations restricted to the western and eastern GOM coastlines. Neither Achelous spinimanus nor Achelous spinicarpus occurred in this assemblage; instead, Achelous dominance was mostly driven by letter coded morphs and Achelous gibbesii, which was represented by its highest densities in this assemblage. The Callinectes species also had a low influence on this assemblage structure. While Portunus sp. A was absent from this assemblage, the Portunidae morphs were represented by high abundance and CPUE.

Using SEAMAP data, Millett (2010) showed distinct eastern and western zooplankton communities in the GOM, with the dividing line near Mobile Bay, Alabama.

This geographic interpretation is further supported by the location of the Mobile Bay area in the middle of a marine suture-zone (Remington, 1968), which is defined as an area of geographic overlap of major assemblages in the GOM (Portnoy and Gold, 2012). In addition, related NGI project work revealed 3 ecosystem sub-units in the GOM based on an analysis of zooplankton community structure (Hernandez et al., 2012; Millett, 2010). The community spatial pattern from the NGI study was similar to that found in the present study, in that there was a distinctive split between the western and eastern gulf. In the present study, the western gulf is Callinectes dominated with Achelous sub dominance mostly represented by A. gibbesii. In contrast, the eastern gulf appears to be equally represented by assemblages dominated by Callinectes or Achelous species. The Achelous dominated assemblages characterized the shelf break and over areas of deeper water while the Callinectes dominated assemblages were concentrated more inshore. Morphs of Achelous as well as the co-occurrence of A. spinimanus and A. spinicarpus characterized these deeper water Achelous assemblages. The coastal areas of Louisiana near the Mississippi River delta, as well as areas off Mississippi and Alabama, formed a transition zone between the western and eastern Gulf dominant assemblages. Although this taxonomic changeover was more gradual over a wider area than could be defined as a marine suture-zone, it is interesting that the suture zone is located within the same general area as the transitional zone for portunid megalopal assemblages. Millett (2010) notes that differences in salinity variation between these two sides of the gulf likely play a large role in determining the taxocenes on each side.

Although the patterns shown by the community analysis in this study may not apply to the portunid megalopa taxocene variation throughout the year, they do provide insights into possibly conveys what the taxocene pattern might be in early fall of years

with little to no weather anomalies such as hurricanes. This information can be useful in the management of crab fisheries as well as restoration ecology as it provides insights into the status of recruitment stocks as well as a means for knowing which species might be impacted due to weather anomalies or anthropogenic catastrophes (e.g. oil spills). Additional studies of fall samples from other years or further consideration of the spring and summer seasons from 2003 would broaden the perspective and provide further insights into how the portunid megalopa taxocene can vary over time or seasonally.

Exploratory Look at Environmental Data

Zooplankton communities are a consistent feature in all ocean waters and can be used as indicators of ocean health. Hays et al. (2005) state that planktonic assemblages are useful as environmental indicators for four reasons: 1) lack of commercial exploitation during the plankton stage; 2) tight coupling between plankton dynamics and changes in the environment due to short life histories and reduced influence from previous generations; 3) expansion and contraction of ranges in response to changes in temperature and currents; and 4) the non-linear responses of the communities are very sensitive to perturbations in the environment and thus are better indicators than the environmental variables themselves. However, Hays et al. (2005) also noted that a lack of long standing times-series of plankton communities leaves a gap in the knowledge of ocean biota and environmental linkages. Although the present study, which uses data and specimens collected from the SEAMAP time-series, did not aim to address environmental influence on Portunidae megalopae directly, an examination was undertaken as a basis for future research efforts.

Although temperature has been noted to have an effect on the distribution of planktonic larvae, it did not seem to have a strong effect on the distribution or abundance

of portunid megalopae in this study. Most of the stations sampled fell within areas where the surface temperature averaged 30° C or somewhat lower. Only about 10 stations were located in areas of relatively high sea surface temperature. Temperature variations over the course of a typical SEAMAP cruise are not likely to be substantial (Muller-Karger et al., 1991), so this result is not surprising. Sea surface salinity also seemed to have little bearing on the overall abundances of portunid megalopae. Smyth (1980) noted that salinity had the highest correlation with the abundance of Callinectes spp. larvae in his neuston samples. The same pattern was not seen in the samples from this study, which may be due to a seasonal difference or a geographic difference, as Smyth (1980) sampled the Mid Atlantic Bight once each season for two years.

Currents do appear to have affected the distribution of the megalopae. Overall, densities were higher to the west where currents were of small magnitude and direction (Figure 66). The lower current effect possibly facilitated high densities of megalopae to be spread out across the region instead of being concentrated within patches of unaffected or lightly affected waters. In the eastern Gulf, currents were of far greater magnitude and direction than in the western Gulf, mostly due to the intrusion of the Loop Current (Figure 68) in these waters. The low density Achelous dominant assemblage occurred in areas affected by the Loop Current. Localized areas along the western Florida coastline experienced less current effects than other nearby areas (Figure 67), and these areas also contained higher concentrations of megalopae, in particular the low density Callinectes dominant assemblage.

The most surprising outcome from the environmental map visualization is that chlorophyll concentrations seem to have had little to do with overall abundances or assemblage patterns. Most sampling occurred further offshore than where the highest

levels of chlorophyll-a occurred, according to the remotely sensed data. The only area where there seems to be a possible correlation between the chlorophyll concentration and megalopal abundance is off the coast of Louisiana near the Atchafalaya river basin, where 3 stations had measured chlorophyll-a concentrations greater than 5.00 μg/L. Abundance and CPUE of multiple species seemed to increase in this general area, but nothing points to it being due largely in part to the higher chlorophyll levels, as similar densities were also seen in areas of lower chlorophyll concentration. Millett (2010) noted that fluorescence levels and water depth (distance from shore) jointly drove the breakdowns of the different zooplankton communities present in early fall in the GOM. Chlorophyll-a concentrations in the GOM would need to be examined on a smaller spatial scale as Millett (2010) did to ascertain whether concentrations are playing a concerted role in driving the densities of individual species, or in certain areas of the gulf.

One variable that appeared to have a marked effect on the abundance and CPUE of the collected portunid taxa was the time of day a station was sampled. Since decapod larvae, particularly crab larvae, are known to vertically migrate over the diel cycle, it can be expected that abundances at the surface would fluctuate as well. Most vertical migration occurs during the dawn/dusk hours, with larvae moving to surface waters at night and back down into the water column during the day (Russell, 1928). Overall the highest densities in all taxa were seen in samples taken at night. There was also a diel shift in densities by gear type as well. The change in density relative to gear type on this temporal scale reflects the diel vertical migrations that these larvae undergo daily. For neuston nets, which fish at the surface, tow densities were generally higher in night samples, while those for bongo nets, which fish lower in the water column, were higher during the day. This was especially evident for Callinectes sapidus. Williams (1974)

noted that C. sapidus megalopae were more active at night than during the day. Densities for the Nevertheless, the overall assemblages of portunids were not affected by time of sampling. The only notable exception was for the low density Achelous dominant assemblage (small white circles, Figure 71), which characterized day samples more often than night samples. The remaining assemblages were fairly equally distributed between day and night samples. All assemblages characterized day twilight samples, but only the high density Achelous dominant and the high density Callinectes dominant assemblages characterized evening twilight samples.

Environmental cues undoubtedly drive brachyuran megalopae to initiate settlement to the benthos prior to metamorphosing into juvenile and ultimately adult stages. These cues can be physical, such as substrate or salinity, or chemical, for example chemical detection of conspecifics. The lack of such cues potentially delays molting from one stage to more advanced larval stages. Some species of mobile crabs have the ability to postpone metamorphosis (Pralon et al, 2012). Because the megalopa stage is the last larval stage before settlement occurs, megalopae occur in 1 of 3 possible phases: the post-molt phase (from zoea to megalopa), the intermolt phase, and the premolt phase (from megalopa to first crab). During the intermolt and premolt stages, megalopae are deemed "competent" to be able to respond to the environmental cues that drive metamorphosis. The average time spent in the megalopa phase for a portunid ranges from 10 to12 days, though this period may be shortened or lengthened depending on the presence or absence of proper environmental cues. Portunid larvae do not respond to just one cue, but rather to combinations of various stimuli (Gebauer et al., 2003). Also, megalopae must complete a certain percentage of the life stage in order to reach metamorphic competency. Correspondingly, the stimuli that induce molting must be present for a

threshold length of time, which also varies for each environmental cue. According to Gebauer et al. (2003), megalopae are most receptive to environmental cues at 30-50% of the life stage duration (intermolt) and at 45-76% development (premolt). These are the time points at which molting hormone secretion increases and where only a particular cue may be needed to increase production of the hormone (Anger, 1987; Anger, 2001).

Lengthening of the megalopa stage carries both advantages and disadvantages. The greatest advantage is that it allows time for suitable habitat to be found or for environmental cues to be perceived or to reach the proper duration of the megalopa stage for the molting process to begin. However, a prolonged presettlement duration for megalopae can also increase overall mortality in this stage as well as in later early juvenile stages after molting has occurred because these juveniles are often smaller (Anger, 1991; Gebauer et al, 2003). For the family Portunidae, the only genus that has been extensively studied in this regard is Callinectes, due to its abundance and commercial importance.

The phase that the megalopae examined in this study were in was not known, because there were no known morphological features that would indicate a change in phase. The only physical feature noted that may have signaled a phase change was the presence of soft, translucent megalopae in some samples. Many of the same megalopae were not identified as they were too damaged, but these megalopae could have been in the post-molt phase following the last zoeal stage. Some may also have been leftover molts of megalopae which metamorphosed into the first crab stage. In future studies it may be a viable option to do tissue extraction at time of collection to get an idea of what phases of megalopae are being collected. This could yield valuable information as to

which megalopae are preparing to settle and could establish distance from shore ranges for each phase, which could be helpful in fisheries management.

Future Research

Despite the larval descriptions provided in this study along preexisting information, there are still many gaps in knowledge of portunid about portunid life histories and larval descriptions. Additional descriptions are still needed, especially for species in the GOM. The capacity to identify megalopae from a plankton sample not only allows for the expansion of invertebrate larval indices and better fisheries management by being able to focus on the locations and abundances of commercially important species, but it also helps to better define zooplankton community structure within a region of interest, like the GOM.

As was seen by the successful genetic identification of one species, genetic analysis can serve as a useful tool for identifying wild caught specimens. Sequences from known adults are needed in order to allow for successful identification through matches with earlier stages. The identification of these adults is a far easier task than identification of their larvae, but taxonomic changes and undocumented regional differences in naming can hinder this process (Mantelatto et. al., 2009). While genetic identification will work for the megalopal stage, it may be less successful for the zoeal stages as zoeae occur in multiple stages (4-8 for portunids), and numerous zoeae would be needed to generate enough tissue for RNA extraction. Laboratory rearing provides another viable option for the identification of zoeae, as well as megalopae and early crab instars, provided reared specimens survive to these stages. Use of this age-old technique requires far more space and time than genetic analysis, but the results can be just as accurate and yield specimens that can be identified and described using traditional morphological techniques.

To get a true sense of variation in the community structure of portunid megalopae taxocene in the GOM, data representing several years would need to be compared. SEAMAP has an extensive time series of samples, starting from 2003, from which the Portunidae larvae have yet to be examined. This includes two to three gulf-wide cruises per year and an additional two cruises where supplemental plankton samples are taken. Comparing samples taken at the same time across multiple years, or even at different times within the same year, would provide added insights into spatio-temporal variation of the megalopal species composition in the gulf and better abundance indices of early juveniles available for early recruitment. Additionally, distribution data for megalopae is useful in discerning spatial patterns of settlement and can aid in explaining the distribution patterns for the corresponding adult crab populations (Pralon et al., 2012). The SEAMAP project generates adult and juvenile catch data from ground fish and pelagic trawl surveys that have been accompanied by or have followed shortly after a plankton survey. A comparison of the distribution of known species, as well as life stages of larvae and sizes of captured later stages of juveniles/adults could indicate when and where the larvae are settling and recruiting into the population.

The NGI project from which this study originated set out to examine the effect of climate change on zooplankton populations. As sensitive indicators of environmental change, understanding the linkages between the environment and the zooplankton community is crucial for an overall understanding of the health of fisheries and ecosystems (Hays et al., 2005). Though time-series are often best for determining links between the environment and zooplankton communities, looking at particular taxa or particular time frames can be beneficial as well. An understanding of the community structure present at a particular time across a broad region can also aid in understanding

the effects of environmental variability. Environmental data from the present Fall 2003 study (GU033) can be compared with environmental data from other years, including the Fall 2002 and Fall 2004 plankton cruises to check how well these annual regimes agreed and whether there were any environmental anomalies operating at the time of sampling in 2003, such as El Nino/La Nina or storm influences. Further analyses may reveal correlations between the occurrences and abundance patterns of taxa and eco-geographical variables and thus give some indication of which factors constitute suitable habitats, influence densities of portunid taxa, and contribute to the consistent occurrence of specific portunid assemblages within certain regions of the GOM.

APPENDIX A

SEAMAP SOUTHEAST FISHERIES SCIENCE CENTER ZOOPLANKTON SORTING PROTOCOLS

SUBMITTED BY: Joanne Lyczkowski-Shultz

REVISION DATE: October 2007

The primary objective of SEAMAP/SEFSC zooplankton analyses is to build a database on the abundance of commercially important decapod crustacean larvae in the Gulf of Mexico. This work was initiated by SEAMAP/SEFSC under the guidance of Dr. Ken Stuck of the Gulf Coast Research Laboratory in the late 1980's. A secondary objective of these analyses is to identify and count the other major zooplankton components of SEAMAP samples. Separate data sheets, one for the decapods and the other for the remaining zooplankton taxa are to be filled out.

Protocol A: DECAPOD CRUSTACEAN - BONGO SAMPLES

Taxa to be sorted from BONGO samples:

1. Lobster phyllosoma (all species)
2. Penaeidae postlarvae
3. Portunidae megalopae
4. Sicyoniidae postlarvae
5. *Menippe* megalopae
6. Geryonidae megalopae
7. Penaeidae larvae
8. Portunidae zoeae
9. Sicyoniidae larvae
10. Geryonidae zoeae

11. *Menippe* zoeae

12. Other Decapods (adults and larvae)

    12A. Sergestidae

    12B. Lucifer spp.

13. Miscellaneous unusual or rare decapods (qualitative)

Sorting Procedure for BONGO samples:

1. Measure displacement volume of the sample OR use the previous measurement of displacement volume when the sample was sorted for ichthyoplankton. This previous measurement can be found on the ISR sheet or data file. Record the required sample collection information and the displacement volume on SEAMAP/SEFSC Decapod Crustacean Larvae Data Sheet 1.

2. The sample should be split using a Folsom or comparable plankton splitter until an aliquot containing approximately 200 to 400 decapod larvae is obtained. When splitting the sample each split should be placed in individual beakers. In most cases, samples should be split to obtain a final aliquot size of 1/64. If the total number of larvae of taxa 7-12A&B (from above list) removed from the smallest aliquot (one of the final pair) is less than 200, the remaining aliquot from the final pair should also be sorted. If necessary, additional aliquots should be sorted until a minimum of 200 larvae of taxa 7-12 have been obtained.

3. Larvae of all taxa (1-12A&B in list above) should be removed from these aliquots and placed in individually labeled vials containing 70% ethanol.

4. When a minimum of 200 larvae have been obtained, those vials containing taxa 7-

12 A&B should be individually labeled and sealed. The number of specimens sorted of taxa 7-12A&B should be recorded on the data sheet together with the final aliquot sorted for each taxon. The final aliquot size sorted for each taxon should be calculated by the addition of all the sample fractions sorted. For example: if both 1/64 fractions and the 1/32 fraction were sorted to obtain the minimum of 200 larvae then the final aliquot recorded on the data sheet should be 1/16.

5. If displacement volume of the sample is 20 ml or less, the (entire) remainder of the sample should be sorted for taxa 1-6 and 13 (from above list). If the displacement volume is greater than 20 ml, the portion of the sample to be sorted for taxa 1-6 and 13 should be determined using the following schedule:

Displacement volume	Aliquot to be sorted
21-40 ml	1/2
41-80 ml	1/4
81 ml or greater	1/8

The maximum number of "Miscellaneous decapods" (taxon 13 from above list) to be removed from the sample is 50. These specimens will be used only to note the presence of rare or unusual larvae not found in the smaller aliquots.

6. When the required portion of the sample is sorted for larvae of taxa 1-6 and 13 the vials containing those taxa should be individually labeled and sealed. The number of specimens sorted should be recorded on the data sheet together with the final aliquot (portion) sorted for each taxon. All specimens are to be placed in vials containing 70% ethanol.

Protocol B: DECAPOD CRUSTACEAN - NEUSTON SAMPLES

Taxa to be sorted from NEUSTON samples:

1. Lobster phyllosoma (all species).
2. Penaeidae postlarvae
3. Portunidae megalopae
4. Sicyoniidae postlarvae
5. *Menippe* megalopae
6. Geryonidae megalopae

13. Miscellaneous unusual or rare decapods

Sorting Procedure for NEUSTON samples:

1. Measure displacement volume of the sample after removing debris, *Sargassum* etc. Record the required sample collection information and the displacement volume on SEAMAP/SEFSC Decapod Crustacean Larvae Data Sheet 1.
2. If displacement volume of the neuston sample is 30 ml or less, the entire sample should be sorted for taxa 1-6 and 13 (from above list) only. If displacement volume is greater than 30 ml, the portion of the sample to be sorted should be determined using the following schedule:

Displacement volume	Aliquot to be sorted
31-60 ml	1/2
61-120 ml	1/4
121-240 ml	1/8
241 ml or greater	1/16

If a large portion of the sample consists of *Sargassum* or coelenterates, a

larger aliquot should be sorted. The maximum number of "Miscellaneous decapods" (taxon 13 from above list) to be removed is 50. These specimens will be used only to note the presence of rare or unusual larvae not found in the smaller aliquots.

3. When the required portion of the sample is sorted for larvae of taxa 1-6 and 13 the vials containing those taxa should be individually labeled and sealed. The number of specimens sorted should be recorded on the data sheet together with the final aliquot (portion) sorted for each taxon. All specimens are to be placed in vials containing 70% ethanol.

APPENDIX B

GENERIC KEY TO THE KNOWN PORTUNID MEGALOPAE OF THE GULF OF MEXICO

1 Sternal spines present; peraeopods 3-4, coxal spines absent 2

Sternal spines absent; peraeopods 3-4, coxal spines present ..... (Polybiinae) 13

2 Fifth abdominal segment, posterolateral spines present ..... (Portuninae, Thalamitinae) 3

Fifth abdominal segment, posterolateral spines absent..... .Portunidae sp. A

3 Carapace subtriangular, lateral margins diverging posteriorly, interocular region with lateral margins strongly concave ..... *Charybdis**

Carapace subrectangular, lateral margins subparallel, interocular region with lateral margins straight to weakly concave 4

4 Antenna, flagellum with 6 articles ..... Portunidae sp. E

Antenna, flagellum with > 6 articles 5

5 Antenna, flagellum with 7 articles 6

Antenna, flagellum with 8 articles 7

6 Cheliped without basi-ischial spine, carpus with distomedial spine; pereiopods 2-3, dactyl with stout setae along anterior margin, setae subequal to width of dactyl in length; abdomen, dorsal margin with segments humped in lateral view .....*Achelous*

Cheliped with basi-ischial spine, carpus without distomedial spine; pereiopods 2-3, dactyl with slender setae along anterior margin, setae distinctly less than width of dactyl in length; abdomen, dorsal margin with segments smooth in lateral view .....*Portunus*

7 Rostrum short; sternal spines small 8

Rostrum long; sternal spines large 9

8 Pereiopod 5, dactyl with 11-12 long, hooked setae; exopods of uropods with 20-22 marginal setae; telson without median apical setae; large (TL = 11 mm) ..... *Cronius*

Pereiopod 5, dactyl with 4 long, hooked setae; exopods of uropods with 11 marginal setae; telson with 1-2 median apical setae; small (TL = 3mm) ..... *Thalamita* *[*]

9 Rostrum slender with few to no setae, extending anteriorly beyond antennule; cheliped with basi-ischial spine..... 10

Rostrum stout with many setae, extending anteriorly well beyond antennules; cheliped without basi-ischial spine..... Portunidae sp. G

10 Eyestalk with dorsal pigment spot (typically); carapace length > 2.3mm 11

Eyestalk without dorsal pigment spot; carapace length < 2.3mm 12

11 Cheliped, basi-ischial spine small, carpus with distomedial spine; peraeopod 2, coxal spine present; abdomen, dorsal margin with segments humped in lateral view .... *Arenaeus*

Cheliped, basi-ischial spine large, carpus without distomedial spine; peraeopod 2, coxal spine absent; abdomen, dorsal margin with segments slightly humped in lateral view..... .....Portunidae sp. C

12 Eyestalks without dorsal pigment spot; maxilla, endopod with 3 marginal setae; small, carapace length < 2.3mm; cheliped, basi-ischial spine large, carpus without distomedial spine; peraeopod 2, coxal spine absent; abdomen, dorsal margin with segments smooth in lateral view..... *Callinectes*

Eyestalk usually without pigment spot; small, carapace length < 2mm; peraeopod 2, coxal spine present; abdomen, dorsal margin with segments humped in lateral view .... Portunidae sp. D

13 Antenna, fourth article from tip with longest pair of distal setae elongate, reaching or extending beyond tip of terminal article; eyestalks with dorsal pigment spot; maxilla, endopod with apical setae; carapace subquadrate, dorsal spine present, dorsal pigment spots present.....*Ovalipes**

Antenna, fourth article from tip with longest pair of distal setae short to moderately long,

not reaching more than slightly beyond distal margin of penultimate article; eyestalks without dorsal pigment spot; maxilla, endopod without apical setae; carapace subrectangular or subtriangular, dorsal spine absent, dorsal pigment spots absent 14

14 Maxilla, endopod without setae; rostrum angled slightly downwards; carapace subrectangular, lateral margins subparallel; cheliped, basi-ischial spine present ....*Bathynectes**

Maxilla, endopod with marginal setae; rostrum angled strongly downwards; carapace subtriangular, lateral margins diverging posteriorly; cheliped, basi-ischial spine absent .....*Liocarcinus* *[*]

"*" These genera were not encountered in the samples from Cruise GU033.

[*] Genera reported as occurring in the South Atlantic Bight by Negreiros-Fransozo et al (2007) therefore potentially in Gulf of Mexico, but not reported from Gulf to date.

NOTE: Some of the morphological information used in the above key is based on descriptions of megalopae for species that do not occur in the Gulf of Mexico because that is the only information available. Other genera of portunids reported from the Gulf include *Laleonectes, Lupella* and *Raymanninus* (= *Benthochascon*); however, megalopae have not been described for members of these genera.

APPENDIX C

KEY TO THE KNOWN PORTUNID MEGALOPAE OF THE GENUS *ACHELOUS* IN THE GULF OF MEXICO

1 Sternal spines small, not extending beyond midline of second abdominal segment 2

Sternal spines medium to large, extending beyond posterior margin of second abdominal segment 6

2 Antenna, flagellum segment 2 longer than or equal to segment 4; pereopod 2, small ventral spine present on coxa 3

Antenna, flagellum segment 2 shorter than segment 4; Pereopod 2, small/medium spine present on coxa 4

3 Antenna, flagellum segment 2 longer than segment 3; telson, medial protuberance broad .....*Achelous* sp. C

Antenna, flagellum segment 2 equal or subequal to segment 3; telson, medial protuberance small and narrow .....*Achelous* sp. E

4 Antenna, flagellum segment 2 longer than segment 3; rostrum angled downward ~30°; Eyestalk, pigment spot present..... .*Achelous gibbesii*

Antenna, flagellum segments 2 and 3 equal in length; rostrum horizontal; eyestalk lacking pigment spot 5

5 Telson, distal margin with slight medial point.....*Achelous* sp. F

Telson, distal margin transverse or slightly convex.....*Achelous spinimanus*

6 Antenna, flagellum segment 2 subequal to segment 3; sternal spines large, extending just beyond anterior margin of third abdominal segment ....*Achelous* sp. B

Antenna, flagellum segment 2 noticeably longer than segment 3; sternal spines medium, extending to posterior margin of second abdominal segment 7

7 Antenna, flagellum segment 2 twice as large as segment3; sternal spines stout, diverging posteriolaterally; telson, distal margin with slightly convex terminal border .....*Achelous spinicarpus*

Antenna, flagellum segment 2 similar in size to segment 3 but still larger; sternal spines slender, directed posteriorly; telson, distal margin transverse.....

.....*Achelous* sp. I

REFERENCES

Adams, C. M., Hernandez, E., & Cato, J. C. 2004. The economic significance of the Gulf of Mexico related to population, income, employment, minerals, fisheries and shipping. *Ocean & coastal management*, *47*(11), 565-580.

Andryszak, B. L. 1979. Abundance, distribution, and partial descriptions of reptant decapod crustacean larvae collected from neritic Louisiana waters in July, 1976. Doctoral dissertation, Louisiana State University, Baton Rouge.

Anger, K. 1987. The D_0 Threshold: A Critical Point in the Larval Development of Decapod Crustaceans. Journal of Experimental Marine Biology and Ecology 108: 15-30.

--- 1991. Effects of Temperature and Salinity on the Larval Development of the Chinese Mitten Crab *Eriocheir sinensis* (Decapoda: Grapsidae). Marine Ecology Progress Series. 72: 103-110

--- 2001. The Biology of Decapod Crustacean Larvae. In: Vonk, R. (ed) Crustacean Issues 14. A.A. Balkema Publishers, Lisse, The Netherlands. 405 pp.

Bailey, C. 1988. The political economy of marine fisheries development in Indonesia. *Indonesia*, 25-38.

Benson, D. A., Karsch-Mizrachi, I., Clark, K., Lipman, D. J., Ostell, J., & Sayers, E. W. 2012. GenBank. Nucleic acids research, 40(D1), D48-D53.

Bookhout, C.G., &. Costlow Jr, J.D. 1974. Larval Development of *Portunus spinicarpus* Reared in the Laboratory. Bulletin of Marine Science 24(1): 20-51.

--- 1977. Larval Development of *Callinectes similis* Reared in the Laboratory. Bulletin of Marine Science 27(4): 704-728.

Botsford, L. W., Castilla, J. C., & Peterson, C. H. 1997. The management of fisheries and marine ecosystems. Science, *277*(5325), 509-515.

Boylan, J. M., & Wenner, E. L. 1993. Settlement of brachyuran megalopae in a South Carolina, USA, estuary. Marine ecology progress series. Oldendorf, 97(3), 237-246.

CapLog. 2011. CapLog Reports-Overview of the Maryland Commercial Blue Crab Fishery. http://watermenway.com/wp-content/uploads/2011/07/Overview-of-the-Maryland-Commercial-Blue-Crab-Fishery-Final-May-24.pdf

Churchill, E.P. 1942. The Zoeal Stages of the Blue Crab, *Callinectes sapidus* Rathbun. Chesapeake Biological Laboratory, Publication No. 49.

Cook, H. L. 1966. A generic key to the protozoean, mysis, and postlarval stages of the littoral Penaeidae of the northwestern Gulf of México.

Costlow Jr., J.D. 1965. Variability in Larval Stages of the Blue Crab, *Callinectes sapidus*. Biological Bulletin 128: 58-66.

--- 1967. The effect of salinity and temperature on survival and metamorphosis of megalops of the blue crab *Callinectes sapidus*. Helgoland Marine Research, 15(1), 84-97.

Costlow Jr., J.D., & Bookhout, C.G.. 1959. The Larval Development of *Callinectes sapidus* Rathbun, Reared in the Laboratory. Biological Bulletin 116(3): 373-396.

--- 1966. The larval development of *Ovalipes ocellatus* (Herbst) under laboratory conditions. Journal of the Elisha Mitchell Scientific Society, 82(2), 160-171.

Costlow Jr., J.D., Rees, G., & Bookhout, C.G.. 1959. A Preliminary Note on the Complete Larval Development of *Callinectes sapidus* Rathbun Reared in the Laboratory. Limnology and Oceanography 4(2): 222-223.

Courtney, J. M., Courtney, A. C., & Courtney, M. W. 2013. Nutrient Loading Increases Red Snapper Production in the Gulf of Mexico. Hypotheses in the Life Sciences, 3(1), 7-14.

Das, T., & Stickle, W. B. 1993. Sensitivity of crabs *Callinectes sapidus* and *C. similis* and the gastropod *Stramonita haemastoma* to hypoxia and anoxia. Marine Ecology-Progress Series, 98, 263-263.

Dineen, J. F., Clark, P. F,. Hines, A. H, Reed, S. A., & Walton, H. P.. 2001. Life History, Larval Description, and Natural History of *Charybdis hellerii* (Decapoda, Brachyura, Portunidae), an Invasive Crab in the Western Atlantic. Journal of Crustacean Biology 21(3): 774-805.

Dransfeld, L., Dwane, O., & Zurr, A.F.. 2009. Distribution Patterns of Ichthyoplankton Communities in Different Ecosystems of the Northeast Atlantic. Fisheries Oceanography, 18:6 470-475.

Dudley, D.L., & Judy, M.H.. 1971. Occurrence of Larval, Juvenile, and Mature Crabs in the Vicinity of Beaufort Inlet, North Carolina. NOAA Technical Report NMFS SSRF-637.

FAO, F. 2012. Yearbook 2010: Fishery and Aquaculture Statistics. Food and Agriculture Organisation of the United Nations, Rome, 78.

Felder, D.L. & Camp, D.K. (eds.). 2009. Gulf of Mexico–Origins, Waters, and Biota. Biodiversity. Texas A&M Press, College Station, Texas.

Forward, R. B. 1987. Larval release rhythms of decapods crustaceans: an overview. Bulletin of Marine Science 41(2): 165-176.

Forward, R.B., Swanson, J., Tankersely, R.A., & Welch, J.M. 1997. Endogenous Swimming Rhythms of Blue Crab, *Callinectes sapidus*, Megalopae: Effects of Offshore and Estuarine Cues. Marine Biology. 127: 621-628

Fransozo, A., & Negreiros-Fransozo, M.L.. 1987. Morfologia dos primeiros estagios jevenis de *Eriphia gonagra* (Fabricius) e *Eurypanopeus abbreviatus* (Stimpson, 1860) (Crustacea, Decapoda, Xanthidae), obtidos em laboratorio. Papeis Avulsos de Zoologia 36(22): 257-277

Fransozo, A., Mantelatto, F. L, & Bertini, G.. 2002. The first zoeal stage of the genus *Cronius* (Brachyura, Portunidae) from the Brazilian coast, hatched in a laboratory. Journal of plankton research 24(11): 1237-1244.

Freeman, J. A., & Perry, H. M. 1987. Recent Progress in the Production of the Soft Shell Blue Crab, Callinectes Sapidus. University of South Alabama.

Gaines, S. D., & Lafferty, K. D. 1995. Modeling the dynamics of marine species: the importance of incorporating larval dispersal. CRC Marine Science Series, 6.

Gebauer, P., Paschke, K., & Anger, K.. 1999. Costs of delayed metamorphosis: reduced growth and survival in early juveniles of an estuarine grapsid crab, *Chasmagnathus granulata*. Journal of Experimental Marine Biology and Ecology, 238(2), 271-281.

--- 2003. Delayed Metamorphosis in Decapod Crustaceans: Evidence and Consequences. Revista Chilena de Historia Natural 76: 169-175.

Gore, R. H. 1973. *Pachycheles monilifer* (Dana, 1852): The Development in the Laboratory of Larvae from an Atlantic Specimen with a Discussion of Some Larval Characters in the Genus (Crustacea: Decapoda; Anomura. The Biological Bulletin, 144(1), 132-150.

Gorsky, G., Ohman, M. D., Picheral, M., Gasparini, S., Stemmann, L., Romagnan, J. B., Cawood, A., Pesant, S., Garcia-Comas, C., Prejger, F. 2010. Digital zooplankton image analysis using the ZooScan integrated system. Journal of Plankton Research, 32(3), 285-303.

Gower, J. F. R., & King, S. A. 2011. Distribution of floating Sargassum in the Gulf of Mexico and the Atlantic Ocean mapped using MERIS. International Journal of Remote Sensing, 32(7), 1917-1929.

Hart, J. F. 1937. Larval and adult stages of British Columbia Anomura. Canadian Journal of Research, 15(10), 179-220.

Hart, M. W. 1995. What are the costs of small egg size for a marine invertebrate with feeding planktonic larvae? Am. Nat. 146: 415–426.

Haynes, E. B. 1985. Morphological development, identification, and biology of larvae of Pandalidae, Hippolytidae, and Crangonidae (Crustacea, Decapoda) of the northern north Pacific Ocean. Fishery Bulletin, 83(3), 253-288.

Hays, G. C., Richardson, A. J., & Robinson, C. 2005. Climate change and marine plankton. Trends in Ecology & Evolution, 20(6), 337-344.

Heegaard, P. 1966. Larvae of decapod Crustacea: The oceanic penaeids Solenocera-Cerataspis-Cerataspides. Dana Report, 67, 1-82.

Hernandez, F., LeCroy, S.E., & Sutor, M. 2012. Identifying linkages between zooplankton dynamics, fishery resources and climate change in the Northern Gulf of Mexico. Final Report, Contract No. NGI-09-11, National Oceanographic and Atmospheric Administration (NOAA), Northern Gulf Institute (NGI), 5 pp.

Hildebrand, H. H. 1954. A study of the pink shrimp (*Penaeus duorarum* Burkenroad) grounds in the Gulf of Campeche. Publications of the Institute of Marine Science, University of Texas, 4, 169-232

Hines, A.H. 1986. Larval patterns in the life histories of brachyuran crabs (Crustacea, Decapoda, Brachyura.) Bulletin of Marine Science, Volume 39, Number 2, September 1986, pp. 444-466(23)

Huh, O. K., Wiseman, W. J., & Rouse, L. J. 1981. Intrusion of Loop Current waters onto the west Florida continental shelf. Journal of Geophysical Research: Oceans (1978–2012), 86(C5), 4186-4192.

Hurlburt, H. E., & Thompson, J. D. 1980. A numerical study of Loop Current intrusions and eddy shedding. Journal of Physical Oceanography, 10(10), 1611-1651.

Jablonski, D., & Lutz, R. A. 1983. Larval ecology of marine benthic invertebrates: paleobiological implications. Biological Reviews, 58(1), 21-89.

Jackson, G. A., & Strathmann, R. R. 1981. Larval mortality from offshore mixing as a link between precompetent and competent periods of development.*American Naturalist*, 16-26.

Jackson, J. B. C. 1986. Modes of dispersal of clonal benthic invertebrates: consequences for species' distributions and genetic structure of local populations. Bulletin of Marine Science, 39(2), 588-606.

Jiddawi, N. S., & Öhman, M. C. 2002. Marine fisheries in Tanzania. Ambio: a journal of the Human Environment, 31(7), 518-527.

Jobe, C. F., & Brooks, W. R. 2009. Habitat selection and host location by symbiotic shrimps associated with Sargassum communities: The role of chemical and visual cues. Symbiosis, 49(2), 77-85.

Junior, E. A. B., Negreiros-Fransozo, M. L., & Fransozo, A. 2008. Juvenile development of *Callinectes ornatus* Ordway, 1863 (Crustacea: Decapoda: Portunidae), from megalopae obtained in the neuston. Zootaxa, 1(20).

Knight, C.R., Franks, J, & Salliant, E. In prep. The genetic identification of the megalopa of *Cronius ruber.*

Kordos, L.M., & Burton, R.S. 1993. Genetic Differentiation of Texas Gulf Coast Populations of the Blue Crab *Callinectes sapidus*. Marine Biology 117, 227-233.

Kurata, H. 1970. Studies on the life histories of decapod Crustacea of Georgia. Unpublished manuscript, Marine Institute, University of Georgia, Sapelo Island, Georgia.

Kurata, H. 1975. Larvae of decapoda brachyura of Arasaki, Sagami Bay [Japan], 5: The swimming crabs of subfamily Portuninae. Bulletin of the Nansei Regional Fisheries Research Laboratory.

Kurata, H., & Midorikawa, T. 1975. The larval stages of the swimming crabs, Portunus pelagicus and P. sanguinolentus reared in the laboratory. Bulletin of the Nansei Regional Fisheries Research Laboratory.

Lebour, M. V. 1944. Larval crabs from Bermuda. Zoologica, 29(3), 113-128.

--- 1950. Notes on some larval decapods (Crustacea) from Bermuda. Proceedings of the Zoological Society of London 120: 369-379

Lewis, J. B., Moore, H. B., & Babis, W. 1952. The post-larval stages of the spiny lobster Panulirus argus. Bulletin of Marine Science, 2(1), 324-337.

Linnaeus C., 1758. Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Edition 10, 1: i-iii, 1–824.

Lyczkowski-Shultz, J., & Hanisko, D.S. 2008 A time series of observations of red snapper larvae from SEAMAP surveys 1982-2003: seasonal occurrence, distribution, abundance and size. Pages 3-23 in W.F. Patterson, III, J.H. Cowan, Jr., G.R. Fitzhugh, and D.L. Nieland, editors. Red snapper ecology and fisheries in the U.S. Gulf of Mexico. American Fisheries Society, Symposium 60, Bethesda, Maryland.

Lyczkowski-Schultz, J., LeCroy, S.E., Sutor, M., Graham, W.M., Perry, H., Benfield, M., Hernandez, F.. 2008. Identifying linkages between zooplankton dynamics, fishery resources and climate change in the Northern Gulf of Mexico. Project Proposal, Contract No. NGI-09-11, National Oceanographic and Atmospheric Administration (NOAA), Northern Gulf Institute (NGI), 27 pp.

Mantelatto, F. L., Robles, R., Schubart, C. D., & Felder, D. L. 2009. Molecular phylogeny of the genus Cronius Stimpson, 1860, with reassignment of C. tumidulus and several American species of Portunus to the genus Achelous De Haan, 1833 (Brachyura: Portunidae). *Crustacean Issues: Decapod Crustacean Phylogenetics*. 554-567

Marancik, K. E., Richardson, D. E., Lyczkowski-Shultz, J., Konieczna, M., & Cowen, R. K. 2010. Evaluation of morphological characters to identify grouper (Serranidae: Epinephelini) larvae in the Gulf of Mexico using genetically identified specimens. Bulletin of Marine Science, 86(3), 571-624.

Meyer, R., Wehrtmann, I. S., & Melzer, R. R. 2006. Morphology of the first zoeal stage of *Portunus acuminatus*, Stimpson, 1871 (Decapoda: Portunidae: Portuninae) reared in the laboratory. Scientia Marina, 70(2), 261-270.

Millett, A. 2010. Zooplankton community structure in the northern Gulf of Mexico: Implications for ecosystem management (Master's Thesis). University of South Alabama, Mobile, AL.

Molinari, R. L., Baig, S., Behringer, D. W., Maul, G. A., & Legeckis, R. 1977. Winter intrusions of the Loop Current. Science, 198(4316), 505-507.

Molinari, R. L., Festa, J. F., & Behringer, D. W. 1978. The circulation in the Gulf of Mexico derived from estimated dynamic height fields. Journal of physical Oceanography, 8(6), 987-996.

Morgan, S.G., Manooch III, C.S., Mason, D.L., &. Goy, J.W. 1985. Pelagic Fish Predation on *Cerataspis*, A Rare Larval Genus of Oceanic Penaeoids. Bulletin of Marine Science. 36(2): 249-259

Müller-Karger, F. E., Walsh, J. J., Evans, R. H., & Meyers, M. B. 1991. On the seasonal phytoplankton concentration and sea surface temperature cycles of the Gulf of Mexico as determined by satellites. *Journal of Geophysical Research: Oceans (1978–2012)*, *96*(C7), 12645-12665.

Negrieros-Fransozo, M.L., Meyers, N., Fransozo, V., & Thorton-De Victor, S. 2007. The Megalopa Stage of *Portunus spinimanus* Latreille, 1819 and *Portunus gibbesii* (Stimpson, 1859) (Decapoda, Brachyura, Portunidae) from the Southeastern Atlantic Coast of the United States. Zootaxa 1638: 21-37.

Nichols, P. R., & Keney, P. M., 1963. Crab larvae (*Callinectes*), in plankton collections from cruises of M/V Theodore N. Gill, South Atlantic Coast of the United States, 1953-54. US Fish and Wildlife Service.

Oksanen, J., Blanchet, F. G., Kindt, R., Oksanen, M. J., & Suggests, M. A. S. S. 2013. Package 'vegan'. *Community ecology package Version*, *2*, 0-0.

Ong, K.S., & Costlow Jr., J.D., 1970. The effect of salinity and temperature on the larval development of the stone crab, *Menippe mercenaria* (Say), reared in the laboratory. Chesapeake Science 11, 16–29.

Pechenik, J. A. 1999. On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles. Marine Ecology Progress Series, 177, 269-297.

Perry, H.M., & Stuck, K.C.. 1982. The Life History of the Blue Crab in Mississippi with Notes on Larval Distribution. *In* H.M. Perry and W.A. Van Engel (editors), Proceedings Blue Crab Colloquium, October 18-19, 1979. 17-22

Perry, H. M., Ogle, J. T., & Nicholson, L. C. 1990. The Fishery of Soft Crabs: With Emphasis on the Development of a Closed Recirculating Seawater System for Shedding Crabs. Southeastern Region Marine Advisory Service Network (SEMAS).

Pralon, B.G.N., Hirose, G.L., & Negreiros-Fransozo, M.L. 2012. Horizontal distribution of megalopae of Brachyura (Crustacea, Decapoda) in a South American tropical estuary. Marine Biology Research 8(8): 715-726.

Queiroga, H. J. D. B. B. 1995. Processos de dispersão e recrutamento das larvas do caranguejo Carcinus maenas (L.) na Ria de Aveiro.

Rabalais, N. N., Turner, R. E., & Wiseman Jr, W. J. 2002. Gulf of Mexico hypoxia, AKA" The dead zone". Annual Review of Ecology and Systematics, 235-263.

Rakocinski, C. F., & McCall, D. D. 2005. Early blue crab recruitment to alternative nursery habitats in Mississippi, USA. Journal of Shellfish Research, 24(1), 253-259.

Rakocinski, C. F., Perry, H. M., Abney, M. A., & Larsen, K. M. 2003. Soft-sediment recruitment dynamics of early blue crab stages in Mississippi Sound. Bulletin of Marine Science, 72(2), 393-408.

Remington, C. L. 1968. Suture-zones of hybrid interaction between recently joined biotas. In Evolutionary biology (pp. 321-428). Springer US.

Rice, A.L., & Kristensen, I. 1982. Surface Swarms of Swimming Crab Megalopae at Curacao (Decapoda, Brachyura). Crustaceana 42:1-3, 233-240

Richards, W. J. 1987. MEXUS-Gulf Ichthyoplankton Research, 1977-84.Marine Fisheries Review, 49(1), 39-41.

Robertson, R. L. 1938. Observations on the Growth Stages in the Common Blue Crab, *Callinectes sapidus* Rathbun, with Special Reference to Post-larval Development. Doctoral dissertation, University of Maryland, College Park.

Robertson, P. B. 1968. The complete larval development of the sand lobster, Scyllarus americanus (Smith), (Decapoda, Scyllaridae) in the laboratory, with notes on larvae from the plankton. Bulletin of Marine Science, 18(2), 294-342.

Russell, F. S. 1928. The vertical distribution of marine macroplankton. VI. Further observations on diurnal changes. Journal of the Marine Biological Association of the United Kingdom (New Series), 15(01), 81-99.

Sandifer, P. A. 1972. Morphology and ecology of Chesapeake Bay decapod crustacean larvae. Doctoral dissertation, University of Virginia.

Schubart, C. D., & Reuschel, S. 2009. A proposal for a new classification of Portunoidea and Cancroidea (Brachyura: Heterotremata) based on two independent molecular phylogenies. Crustacean Issues, 18.

Seidelmann, P.K. 1992. Explanatory Supplement to the Astronomical Almanac. University Science Books, New York.

Sherman, K., R. Lasker, W. Richards, and A. W. Kendall, Jr. 1983. Ichthyoplankton and fish recruitment studies in large marine ecosystems. Marine Fisheries Review 45(10-12):1-25.

Shulman, M. J., & Bermingham, E. 1995. Early life histories, ocean currents, and the population genetics of Caribbean reef fishes. Evolution, 897-910.

Siebenaler, J. B. 1952. Studies of ‘‘trash’’ caught by shrimp trawlers in Florida. In Proc. Gulf Carrib. Fish. Inst (Vol. 4, pp. 94-99).

Smyth, P.O. 1980 *Callinectes* (Decapoda: Portunidae) Larvae in the Middle Atlantic Bight, 1975-77. Fisheries Bulletin US 78: 251-265

Stuck, K.C., Wang, S.Y., Heard, R.W. Identification of Portunidae Megalopae and Early Juvenile Stage Crabs from Mississippi Coastal Waters. Unpublished Manuscript.

Stuck, K.C., & Perry, H.M. 1981. Observations on the Distribution and Seasonality of Portunid Megalopae in Mississippi Coastal Waters. Gulf Research Reports Vol. 7, no. 1, pp. 93-95.

Stuck, K.C., & Truesdale, F.M. 1988. Larval Development of the Speckled Swimming Crab *Arenaeus cribrarius* (Decapoda: Brachyura: Portunidae) Reared in the Laboratory. Bulletin of Marine Science 42(1): 101-132.

Stuck, K.C., Perry, H., Graham, D., & Heard, R. 2009. Morphological Characteristics of Early Life History Stages of the Blue Crab, *Callinectes sapidus* Rathburn, From the Northern Gulf of Mexico with a Comparison of Studies From the Atlantic Seaboard. Gulf and Caribbean Research 21: 37-55.

Sulkin, S. D., & Van Heukelem, W. F. 1986. Variability in the length of the megalopal stage and its consequence to dispersal and recruitment in the portunid crab Callinectes sapidus Rathbun. *Bulletin of Marine Science*, *39*(2), 269-278.

Tankersley, R.A., McKelvey, L.M., & Forward Jr, R.B. 1995. Responses of Estuarine Crab Megalopae to Pressure, Salinity and Light: Implications for Flood-Tide Transport. Marine Biology. 122: 391-400.

Truesdale, F. M., & Andryszak, B. L. 1983. Occurrence and distribution of reptant decapod crustacean larvae in neritic Louisiana waters: July 1976. Contributions in Marine Science 26:37-53.

Victor, B. C. 1986. Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. Ecological Monographs, 145-160.

Weisberg, R. H., Black, B. D., & Li, Z. 2000. An upwelling case study on Florida's west coast. Journal of Geophysical Research: Oceans (1978–2012),105(C5), 11459-11469.

Williams, A. B. 1965. Marine decapod crustaceans of the Carolinas. US Department of the Interior, Fish and Wildlife Service, Bureau of Commercial Fisheries.

--- 1974. The swimming crabs of the genus Callinectes. Fish Bull. 72:685-798.

--- 1984. Shrimps, Lobsters and Crabs of the Atlantic Coast of the Eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, D.C., 550 pp.

Williamson, D. I. 1962. Crustacea Decapoda: Larvae III. Caridea, Families Oplophoridae, Nematocarcinidae and Pasiphaeidae. Conseil Internat. pour l'Exploration de la Mer.

Yatsuzuka, K., & Sakai, K. 1980. The larvae and juvenile crabs of Japanese Portunidae (Crustacea, Brachyura), 1: *Portunus* (*Portunus*) *pelagicus* (Linnaeus). Reports of the Usa Marine Biological Institute-Kochi University.