

2012

**Function and diversity of the Ship, Trinity, and Tiger Shoal  
Complex, with emphasis on macrofauna and spawning blue crabs  
(*Callinectes sapidus*)**

Carey George Gelpi Jr.  
*Louisiana State University and Agricultural and Mechanical College*

Follow this and additional works at: [https://digitalcommons.lsu.edu/gradschool\\_dissertations](https://digitalcommons.lsu.edu/gradschool_dissertations)



Part of the [Oceanography and Atmospheric Sciences and Meteorology Commons](#)

---

**Recommended Citation**

Gelpi Jr., Carey George, "Function and diversity of the Ship, Trinity, and Tiger Shoal Complex, with emphasis on macrofauna and spawning blue crabs (*Callinectes sapidus*)" (2012). *LSU Doctoral Dissertations*. 937.

[https://digitalcommons.lsu.edu/gradschool\\_dissertations/937](https://digitalcommons.lsu.edu/gradschool_dissertations/937)

This Dissertation is brought to you for free and open access by the Graduate School at LSU Digital Commons. It has been accepted for inclusion in LSU Doctoral Dissertations by an authorized graduate school editor of LSU Digital Commons. For more information, please contact [gradetd@lsu.edu](mailto:gradetd@lsu.edu).

FUNCTION AND DIVERSITY OF THE SHIP, TRINITY, AND TIGER SHOAL COMPLEX,  
WITH EMPHASIS ON MACROFAUNA AND SPAWNING BLUE CRABS  
(*CALLINECTES SAPIDUS*)

A Dissertation

Submitted to the Graduate Faculty of the  
Louisiana State University and  
Agricultural and Mechanical College  
in partial fulfillment of the  
requirements for the degree of  
Doctor of Philosophy

in

The Department of Oceanography and Coastal Sciences

by

Carey Gelpi

B.A. Louisiana State University and Agricultural and Mechanical College, 1996

B.S. Louisiana State University and Agricultural and Mechanical College, 2005

May 2012

## ACKNOWLEDGMENTS

This study was jointly funded by the U.S. Department of Interior Minerals Management Services (contract number 1435-01-04-CA-35162) and by the Louisiana Department of Natural Resources (contract number 2513-04-02/613082). I would first like to thank Dr. Richard Condrey who provided valuable insight as my advisor and who shared in my excitement during many discoveries. I would also like to thank Drs. John Fleeger and Kevin Carman for serving on my committee and providing me with a solid knowledge base in the study of benthic ecology, and giving me my first student worker job sorting meiofauna. In addition, I would like to thank Dr. Stanislas Dubois, particularly for his help in polychaete identification and for being a great host during my time in Brest, France; Dr. Mark Grippo, Ms. Marjo Alavillamo, Ms. Heather Drucker, Mr. Jerry George and the crews of the LUMCON research vessels Acadiana and Pelican for help collecting samples and Dr. Nancy Rabalais for lending us her GoMEX box corer. Drs. Melissa Baustian and Darryl Felder, and Ms. Sarah Arndt, Lisa Appelbaum, and Sara LeCroy for help in species identification. I appreciate the collaboration with MMS contract managers Barry Drucker, Roger Amato, and Colleen Finnegan. Thanks to my buds Dr. Matthew Moerschbaecher and Mr. Mathew Kupchik whose conversations and friendship contributed to this work. Thanks also to Dr. Brian Fry, whose collaboration greatly improved my isotope chapter, and Drs. Robert Gambrell and Zhimin Xu for generously agreeing to serve on my committee. Thanks to Dr. Greg Stone, he was always interested in the critters that inhabited the sediment he loved. Thank you Azure Bevington, for everything! Finally I would like to thank my parents Carey and Billie Gelpi, who instilled in me a love of the ocean and who encouraged me during this journey.

## TABLE OF CONTENTS

ACKNOWLEDGMENTS.....	ii
ABSTRACT.....	v
CHAPTER 1: INTRODUCTION.....	1
GENESIS AND BACKGROUND OF THIS STUDY.....	4
LITERATURE CITED.....	6
CHAPTER 2: DIVERSITY AND COMPOSITION OF MACROBENTHIC COMMUNITY ASSOCIATED WITH SANDY SHOALS OF THE LOUISIANA CONTINENTAL SHELF.....	9
INTRODUCTION.....	10
MATERIALS AND METHODS.....	12
RESULTS.....	17
DISCUSSION.....	28
CONCLUSION.....	39
LITERATURE CITED.....	40
CHAPTER 3: BENTHIC ECOLOGY OF THE SHIP, TRINITY, AND TIGER SANDY SHOALS AND SURROUNDING MUDDY OFF SHOAL HABITATS OF THE LOUISIANA CONTINENTAL SHELF IN THE NORTHERN GULF OF MEXICO.....	47
INTRODUCTION.....	48
MATERIALS AND METHODS.....	51
RESULTS.....	56
DISCUSSION.....	84
LITERATURE CITED.....	100
CHAPTER 4: DISCOVERY, EVALUATION AND IMPLICATIONS OF BLUE CRAB, <i>CALLINectes Sapidus</i> , SPAWNING, HATCHING, AND FORAGING GROUNDS IN FEDERAL (US) WATERS OFFSHORE OF LOUISIANA.....	107
INTRODUCTION.....	108
MATERIALS AND METHODS.....	110
RESULTS.....	118
DISCUSSION.....	131
LITERATURE CITED.....	138
CHAPTER 5: ISOTOPIC EVIDENCE OF AN ESTUARINE-OFFSHORE CONNECTION FOR THE LOUISIANA BLUE CRAB SPAWNING STOCK.....	143
INTRODUCTION.....	144
MATERIALS AND METHODS.....	147
RESULTS.....	156
DISCUSSION.....	164
CONCLUSION.....	170
LITERATURE CITED.....	172

CHAPTER 6: SUMMARY AND MANAGEMENT IMPLICATIONS.....	177
SUMMARY.....	178
SAND MINING IMPLICATIONS.....	186
POST DEEPWATER HORIZON OIL SPILL CONSIDERATIONS.....	189
LITERATURE CITED.....	190
APPENDIX A: FAMILIES AND SPECIES IDENTIFIED FROM THE GOMEX BOX CORE SAMPLES TAKEN FROM SHIP SHIOAL IN 2006.....	194
APPENDIX B: SPECIES SAND PERCENTAGE FROM THE STTSC IN 2007.....	199
APPENDIX C: RESULTS OF CALLINECTES SAPIDUS GUT CONTENT ANALYSIS.....	209
APPENDIX D: COPY OF PERMISSION LETTER TO PUBLISH CHAPTER 2.....	216
APPENDIX E: COPY OF PERMISSION LETTER TO PUBLISH CHAPTER 4.....	221
VITA.....	223

## ABSTRACT

The ecological and economic value of sandy shoals off the Louisiana coast is not well understood. During three years of comprehensive benthic sampling and environmental measurements I studied the Ship, Trinity, Tiger Shoal Complex (STTSC), which comprises changing and discrete benthic habitats including high relief sandy shoals, and muddier, mostly deeper off-shoal areas, prone to hypoxia. Benthic macrofaunal assemblages of shoals included endemic species, and shoal communities were significantly different from each other and the muddier offshoal habitat, contributing to northern Gulf of Mexico (GoM) regional biodiversity. Sand percentage was the most influential environmental parameter shaping macrofaunal community composition across the region. My study revealed several more potential shoal-based functions such as providing a conduit for GoM sandy-habitat metapopulations, serving as an oxygenated benthic refuge from seasonal bottom water hypoxia, and functioning as offshore blue crab (*Callinectes sapidus*) spawning grounds. I discovered unexpectedly high concentrations of spawning female blue crabs, greatly expanding what was previously understood about blue crab reproductive migrations. Blue crab abundances were significantly higher on Ship and Trinity Shoals than the surrounding muddier and deeper seafloor. STTSC blue crabs compared favorably with those from nationally recognized spawning grounds in terms of condition factor (an index of health), abundance, and fecundity. This work is the first to use an ecological field study to predict the number of days (~21) between successive spawns for blue crabs, suggesting STTSC blue crabs produce at least seven broods per spawning season (~April–October). My morphometric predictors of crab weight were 12 to 16% better than the traditionally used method. In addition, I used natural abundance isotopes ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) to link blue crabs from the STTSC to the inshore blue crab fishery. I analyzed isotopic variations in crab

muscle and ovary tissue and found relationships with salinity and proximity to the Atchafalaya River, indicating that crabs predominately migrate directly offshore from their home estuary, including from low salinity environments. Isotopic analysis also suggests that crabs utilize offshore prey resources and do not re-enter inshore estuaries during the spawning season but rather remain offshore for the season, continually spawning and hatching their eggs.

## **CHAPTER 1: INTRODUCTION**



My study area, the Ship, Trinity, and Tiger Shoal Complex (STTSC; Fig. 1.1), is located within the north-central Gulf of Mexico on the Louisiana continental shelf. The STTSC is composed of Ship, Trinity, and Tiger Shoals and the surrounding off shoal area. This region is influenced by fresh water and associated fluvial inputs from the Mississippi and Atchafalaya Rivers, including suspended sediment, organic matter, and nutrients (Wiseman et al. 1997; Allison et al. 2000). High nutrient input contributes to hypoxia in bottom water that has been consistently reported west of the Mississippi River along the Louisiana and Texas continental shelf during the spring and summer (Rabalais et al. 2001a). Prevailing coastal currents within the STTSC are wind driven and in a westward direction for most of the year (Oey 1995; Walker et al. 2005).

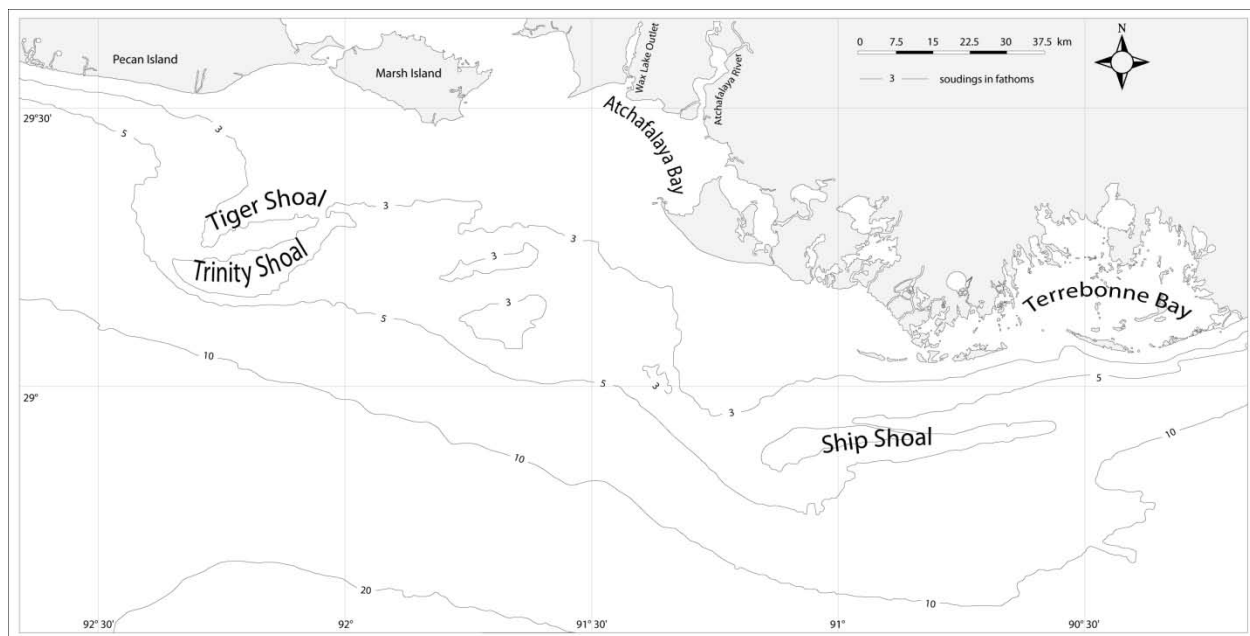


Figure 1.1 Station locations of 2007 benthic study within the Ship, Trinity, and Tiger Shoal Complex (STTSC).

Ship, Trinity, and Tiger Shoals are shallow, high-relief, sandy structures on the Louisiana continental shelf, located between the Mississippi River Bird's Foot Delta and the Sabine River. Ship, Trinity, and Tiger Shoals are remnants of past deltas (Roberts 1997) and are now

subaqueous concentrations of sand within the otherwise muddy depositional plain of the Mississippi River.

Ship Shoal (Ship) is a shore-parallel sand body located ~25 km offshore. It extends from southwest of Terrebonne Bay approximately 50 km westward and is 5-12 km wide. Depth on Ship ranges from 3-9 m with 3-6 m relief relative to the immediately surrounding seafloor (Penland et al. 1986). Ship broadens and shallows east to west ranging from approximately 5-10 km wide; it is separated from the coast by a trough that is 2-4 m deeper than the shoal base. Ship is situated approximately 200 km to the southwest of the Mississippi River Bird's foot delta and approximately 100 km from the Atchafalaya River delta and, thus it receives less deposition of riverine suspended silts and clays compared to Trinity and Tiger Shoals. Due to Ship's relatively shallow depth range, it is also subject to currents and wave action that winnow away fluvially-derived fine-grain particles or those deposited after resuspension from the surrounding muddier offshoal area (Kobashi 2007). Surface sediment of the shoal front and shoal crest of Ship is 90-100% fine to medium sand with a low silt-clay content (Penland et al. 1986).

Trinity and Tiger Shoals (TTS) represent the westernmost members of the Louisiana shelf shoals. They lie ~100 km to the northwest of Ship Shoal and directly seaward of Pecan and Marsh Islands. They are lunate-shaped sand bodies, several 10's of km long (east/west), and generally less than 10 km wide (north/south). Tiger Shoal extends from the coast to ~30 km offshore, while Trinity Shoal is located directly south of Tiger Shoal extending ~48 km from the coast. Depth on TTS ranges from 3-6 m with 2 to 4 m of relief relative to the immediately surrounding seafloor. They are situated directly southwest of the mouth of the Atchafalaya River and Wax Lake Outlet, which contribute suspended sediment that ultimately settles on the continental shelf. The surface sediment of TTS consists of 75 to 100% very fine sand (Frazier

1974) with mud content that is generally higher than Ship Shoal but less than surrounding muddy off shoal areas.

Off shoal areas (Off) sampled in our study were located both seaward and landward of Ship and TTS with depth generally increasing with distance from shore. This area is characterized by high concentrations of silts and clays (Krawiec 1966) with the potential of high interannual variability in sediment composition (e.g. Baustian and Rabalais 2009). The offshoal area surrounding Ship, Trinity, and Tiger Shoals lies within a large seasonally hypoxic area (Rabalais et al. 2001b). The dead zone is fueled by excessive riverine inputs of nutrients that increase phytoplankton primary production, ultimately leading to microbial respiration of phytodetritus in the lower layers of a stratified water column where re-oxygenation through mixing is prohibited.

## GENESIS AND BACKGROUND OF THIS STUDY

The majority of Louisiana's coast is experiencing extremely high rates of coastal erosion and subsidence due to storm impacts, relative sea level rise, and anthropogenic influences (e.g., Penland and Ramsey 1990; Stone 2000). Federal agencies such as the Mineral Management Service (MMS) were addressing the demand for long-term use of U.S. continental shelf sand resources for coastal erosion management, a critical challenge to Louisiana's ecosystems and economies (e.g., MMS 2008). Louisiana considers barrier island restoration as a promising way to combat wetland loss, with sand mined from Ship, Trinity, and Tiger Shoals as the most feasible sediment source (CPRA 2012). Sand mining is known to adversely affect the existing benthic communities (Newell et al. 1998; Palmer 2008) and to result in altered communities for an unknown period of time. The review by Newell et al. (1998) suggests that sand-based communities will take longer to recover from mining disturbance than mud-based communities, with recovery defined as the ability to maintain 80% of pre-mining diversity and biomass. As

such sand-mining related alterations in benthic communities may result in decreases in prey resources that are needed to support ecologically and/or economically important species that preferentially utilize shoals. The present study was initiated to assess the potential impact of sand mining on Ship, Trinity, and Tiger Shoals because ecological studies of offshore sandbanks in the north central Gulf of Mexico are almost entirely lacking.

Our original (2005-2006) intention was to study how the feeding ecology of three recreationally, commercially, and ecologically important species, white shrimp (*Litopenaeus setiferus*), spotted seatrout (*Cynoscion nebulosus*), and brown shrimp (*Farfantepenaeus aztecus*), might be affected by sand mining on Ship. However, during the initial phase of this project, we found little evidence for direct, persistent use of Ship by white or brown shrimp or regular use of Ship Shoal by recreational fishers. However, we did discover unexpectedly high abundances of spawning female blue crabs (*Calinectes sapidus*) on Ship. No previous studies emphasizing the potential importance of offshore blue crab spawning grounds existed in the literature. This finding was punctuated by periodic nighttime observations of gravid female blue crabs swimming in the water column and apparently feeding on small prey attracted to illumination from our research vessel.

As part of our 2005 and 2006 Ship study, we quantified the abundance, composition, and seasonality of Ship's macrobenthic community and how that community is influenced by existing physical and chemical conditions. Benthic macrofauna was defined as animals retained on a 0.5-mm mesh sieve. This work serves as the basis for Chapter 2 in my dissertation and suggested that large, shallow sand deposits surrounded by deeper, muddy sediments, support a unique community and may serve biological roles not provided by the surrounding and usually deeper soft-bottom habitats. This chapter has been published (Dubois et al., 2009).

In 2007 our study area was expanded beyond Ship Shoal to the STTSC, allowing us to compare the benthic ecology of Ship to that of TTS as well as surrounding Off. In Chapter 3 I focus on identifying the macrobenthic communities of the STTSC and their apparent ecological functions. In Chapter 4 I focus on STTSC blue crab abundance, fecundity, and condition factor. This chapter has been published (Gelpi et al., 2009). In chapter 5 I use stable isotopes to address blue crab migration and residence within the STTSC, seeking an understanding of their connection with the inshore blue crab fishery. My overall goal was to inform decision makers about the potential contributions of these shoals to the biological services and overall system integrity of the northern Gulf of Mexico, a goal which has become even more relevant in wake of the Deepwater Horizon Oil Spill, Chapter 6.

#### LITERATURE CITED

- Allison, M.A., G.C. Kineke, E.S. Gordon, M.A. Goñi. 2000. Development and reworking of a seasonal flood deposit on the inner continental shelf off the Atchafalaya River. *Continental Shelf Research*. 20:2267-2294.
- Baustian M, N. Rabalais. 2009. Seasonal composition of benthic macroinfauna exposed to hypoxia in the northern Gulf of Mexico. *Estuaries and Coasts*. 32: 975-983.
- CPRA. 2012. Louisiana's comprehensive master plan for a sustainable coast. Coastal Protection and Restoration Authority of Louisiana. Baton Rouge, LA.
- Dubois, S., C.G. Gelpi, R.E. Condrey, M.A. Grippo, J.W. Fleeger. 2009. Diversity and composition of macrobenthic community associated with sandy shoals of the Louisiana continental shelf. *Biodiversity and Conservation*. 18:3759-3784.

- Frazier, D.E. 1974. Depositional episodes, their relationship to the Quaternary stratigraphic framework in the northwestern portion of the Gulf basin: Austin, University of Texas, Bureau of Economic Geology, Geology circular 74-1, 28p.
- Gelpi, C.G., R.E. Condrey, J.W. Fleeger, S.F. Dubois. 2009. Discovery, evaluation, and implications of blue crab, *Callinectes sapidus*, spawning, hatching, and foraging grounds in federal (US) waters offshore of Louisiana. *Bulletin of Marine Science*. 85:203-222.
- Kobashi, D., F. Jose, G.W. Stone. 2007. Impacts of fluvial fine sediments and winter storms on a transgressive shoal, off south-central Louisiana, USA. Proceedings of the 9th international coastal symposium. *Journal of Coastal Research*. Gold Coast, Australia, pp 858–862.
- Krawiec, W. 1966. Recent sediments of the Louisiana inner continental shelf. Dissertation. Rice University.
- MMS. 2008. Louisiana-Sand Management Working Group. Minerals Management Service, U.S. Department of Interior. Internet website:  
<http://www.mms.gov/sandandgravel/RegionalSandManagementWorkingGroups.htm>.  
 Accessed April 25, 2008.
- Newell, R.C., L.J. Seiderer, D.R. Hitchcock. 1998. The impact of dredging works in coastal waters: a review of the sensitivity to disturbance and subsequent recovery of biological resources on the seabed. *Oceanography and Marine Biology Annual Review*. 36:127-178.
- Oey L.-I. 1995. Eddy- and wind-forced shelf circulation. *Journal of Geophysical Research*. 100:8621-8637.
- Palmer, T.A., P.A. Montagna, R.B. Nairn. 2008. The effects of a dredge excavation pit on benthic macrofauna in offshore Louisiana. *Environmental Management*. 41:573–583.
- Penland, S., J.R. Suter, T.F. Moslow. 1986. Inner-shelf shoal sedimentary facies and sequences: Ship Shoal, northern Gulf of Mexico, SEPM Core Workshop No.9, Modern and Ancient Shelf Clastics 73-123.
- Penland, S., K. Ramsey. 1990. Relative sea level rise in Louisiana and the Gulf of Mexico: 1908-1988. *Journal of Coastal Research*. 6:323-342.
- Rabalais N.N., R.E. Turner, W.J. Wiseman. 2001a. Hypoxia in the Gulf of Mexico. *Journal of Environmental Quality*. 30: 320-329.

- Rabalais, N.N., L.E. Smith, D.E. Harper Jr., D. Justic. 2001b. Effects of seasonal hypoxia on continental shelf benthos. In: Rabalais NN and Turner RE (eds) Coastal hypoxia: consequences for living resources and ecosystems, coastal and estuarine studies, American Geophysical Union, Washington D.C., pp211-240.
- Roberts, H.H. 1997. Dynamic changes of the Holocene Mississippi River delta plain: The delta cycle. *Journal of Coastal Research*. 13:605-627.
- Stone, G. W. 2000. Wave climate and bottom boundary layer dynamics with implications for offshore sand mining and barrier island replenishment in south-central Louisiana. OCS Study MMS 2000-053. U.S. Dept. of the Interior, Minerals Mgmt. Service, Gulf of Mexico OCS Region, New Orleans, La. 90 pp.
- Walker, N. D., W. J. Wiseman, L. J. Rouse, A. Babin. 2005. Effects of river discharge, wind stress, and slope eddies on circulation and the satellite-observed structure of the Mississippi River plume. *Journal of Coastal Research*. 21: 1228–1244.
- Wiseman, W.J., N.N. Rabalais, R.E. Turner, S.P. Dinnel, A. MacNaughton. 1997. Seasonal and interannual variability within the Louisiana coastal current: stratification and hypoxia. *Journal of Marine Systems*. 12:237-248.

## **CHAPTER 2: DIVERSITY AND COMPOSITION OF MACROBENTHIC COMMUNITY ASSOCIATED WITH SANDY SHOALS OF THE LOUISIANA CONTINENTAL SHELF\***

---

\*Dubois et al. (2009) reprinted with permission and modification of table and figure numbers from the journal *Biodiversity and Conservation*.

Literature cited: Dubois, S., C.G. Gelpi Jr., R.E. Condrey, M.A. Grippo, J.W. Fleeger. 2009. Diversity and composition of macrobenthic community associated with sandy shoals of the Louisiana continental shelf. *Biodiversity and Conservation*. 18:3759-3784.



## INTRODUCTION

Recently, sandy shoals of the US continental shelf have received increased attention because they have been identified as potential exploitable sand deposits (Drucker et al. 2004). This is especially true for the Louisiana coast where a single shoal (Ship Shoal) is considered one of the largest sand sources in the Gulf of Mexico (Drucker et al. 2004), containing 1.6 billion cubic yards of fine sand being considered for beach reinforcement and coastal stabilization projects designed to prevent coastal erosion due to storm damages and prevent wetland loss due to anthropogenic disturbances that induce sea-level rise (Michel et al. 2001). This increased interest in shoals highlights the observation that the benthic and nektonic composition of shoals is less well studied than other continental shelf environments (Brooks et al. 2006). Faunal composition may be important to predicting recovery after sand mining and to understanding ecological relationships on shoals. For example, benthic invertebrates are directly related to the sediment they inhabit (Gray 1974; Snelgrove and Butman 1994), and any sand mining activity or associated human-related change in sediment features may negatively affect the resident community and consequently impact trophic relationships within these communities. It is thus of primary importance to identify and characterize macroinfaunal benthic assemblages associated with potential sand mining sites.

The macrobenthos of some Louisiana – Texas shoals (i.e. Sabine and Healds Shoals) have been recently investigated (Cheung et al. 2006) but these studies and a recent macrobenthic survey of Louisiana in-shore and off-shore waters (Baustian 2005) did not include Ship Shoal (Ship), partly because its shallow depth has discouraged access by larger research vessels. A habitat specific survey of the epifauna and fish fauna of several sandbanks off the Welsh coast (UK) revealed that sandbanks were characterized by a unique (although low diverse) epifauna and fish assemblages (Kaiser et al. 2004). But the authors also stated that sandbanks are difficult

habitats to sample and may have been overlooked by biologists. Ship's benthic species assemblages might be used as a food source for numerous fishes or large crustaceans that permanently or temporarily forage on this shoal, as suggested by Thouzeau et al. (1991) for the Georges Bank, northeast coast of the United States. In addition, because of its location in the north central Gulf of Mexico, and unlike the west Florida shelf, Ship is surrounded by muddy soft-bottoms affected by seasonally hypoxia events that causes drastic decreases in abundances of benthic species inhabiting this "dead zone" (Rabalais et al. 1994; Justić et al. 1996). It is unknown whether benthic populations living on Ship are affected by hypoxic events. It is possible that Ship may serve as a hypoxia refuge for benthic populations or as a faunal reserve from which larvae, juveniles, and/or adults may disperse and recolonize the surrounding hypoxic area when normoxia returns.

The overall objectives for this study are thus to better understand the potential role Ship Shoal is likely to play in the Louisiana's coastal ecosystem, and to address the potential effects of sand mining on the benthic community. Our approach was to describe spatial and seasonal variations in diversity and structure of macrobenthic assemblages associated with Ship Shoal over a relatively fine-scale latitudinal and longitudinal gradient and to link community patterns with variation in environmental parameters.

On a broader scale, there is an increasing awareness of the ecological implications of sand and gravel mining from land, river, and coastal-ocean systems (i.e., Peckenhams et al. 2009; Pempel and Church 2009; Zeppelini et al. 2009). Though sand mining has historically been associated with road and building construction, it has become one of the preferred approaches in beach nourishment projects, despite the likelihood of broad ecological impacts on both the extracted and receiving sites and the ephemeral beach-restoration expectations (Defeo et al. 2009). Demands on coastal-ocean sand supplies are likely to increase as human occupation of the

coastal zone and sea level continue to rise, and land-based sand supplies decline. Lessons learned from careful studies of the impacts of current coastal-ocean sand mining operations could prove valuable as extractions of other marine minerals begin and increase (e.g., Rona 2008).

## MATERIALS AND METHODS

### Study Site

Samples were taken from 21 stations on Ship, located in the north central part of the Gulf of Mexico approximately 20 km off-shore from Terrebonne Bay and Isles Dernieres, Louisiana (28°54.092' N, 91°00.989' W). The shape of this shoal is elongated, parallel to the shore. It spans a 50 km distance along the east-west dimension and 1 to 10 km along the north-south dimension (Fig. 2.1). Based on depth contours available on existing sea charts, stations were chosen according to an east-west distribution with three main north-south transects, one in the east (stations 15-16-17), one in the west (stations 23-22-21), and one in the middle (stations 24-25-26). Other stations were distributed along the spine of this sandy shoal in three main groups: east stations from station 18 to station 13, central stations from station 12 to station 09 and 10, and west stations from stations 07 and 08 to station 01 and 19. The general bathymetry of the shoal is related to east-west and north-south gradients: the western region is the shallowest (ca. 4 m) and the depth increase toward the east (ca. 10 m). A north-south transect across the shoal shows that the northern edge is well-defined with a sharp slope while the slope of the southern edge is more gentle with depth increasing slightly from the spine, i.e. middle, of the shoal toward the south, making the definition of the southern edge difficult to discern.

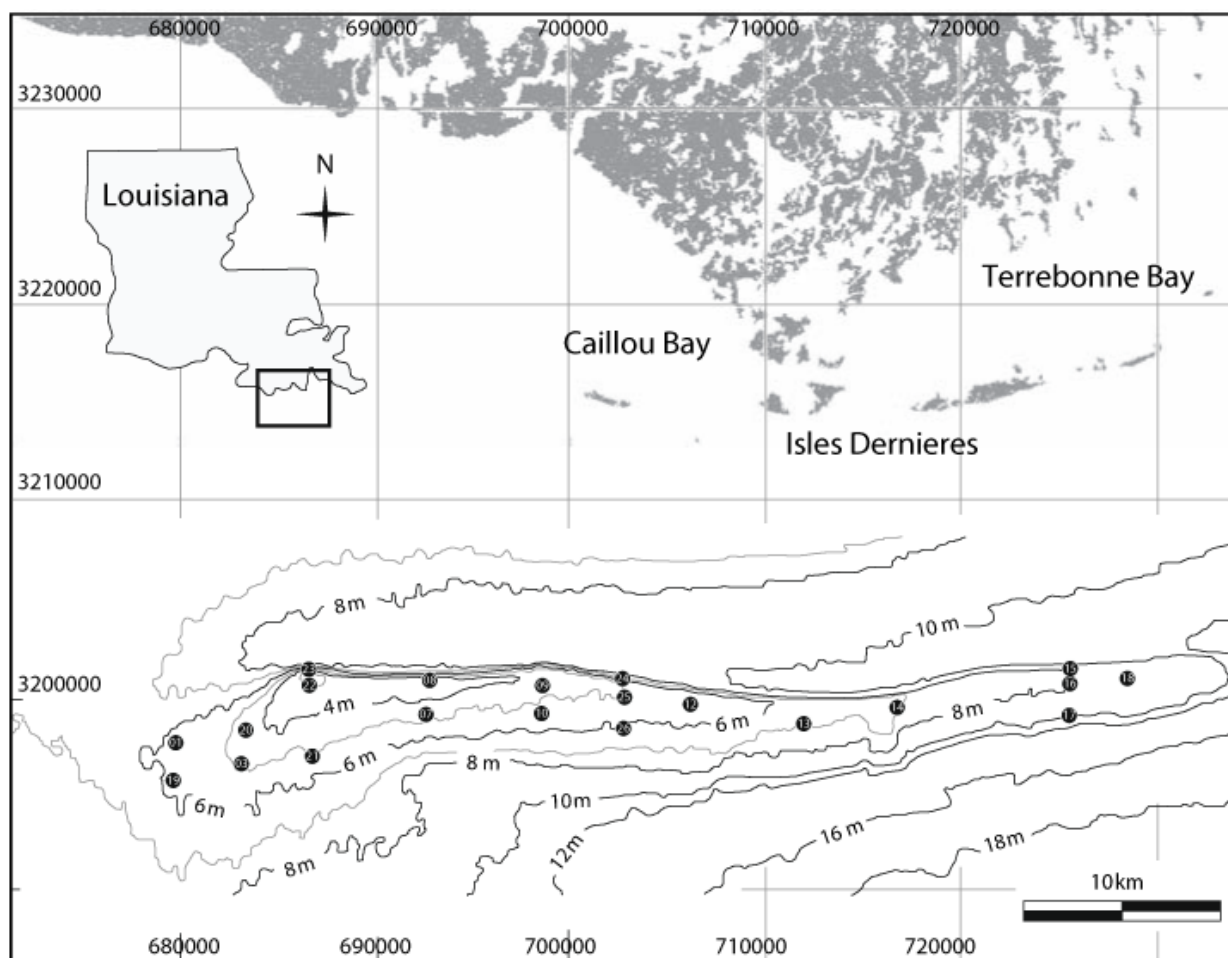


Figure 2.1 Geographic positions of the 21 sampling stations on Ship Shoal, off Louisiana. Detailed bathymetry outlining the shoal and surrounding area is given. Depths in meters (m). Coordinates in NTF (system) Lambert (projection). Data for the bathymetry provided by Divins D.L. and Metzger D., National Geophysical Data Center (NOAA). <http://www.ngdc.noaa.gov/mgg/coastal/coastal.html>

## Field Sampling

Samples were collected during three cruises in 2006 using the Louisiana Universities Marine Consortium (LUMCON) Research Vessel “ACADIANA”: May 21<sup>st</sup> to 24<sup>th</sup> (spring), August 19<sup>th</sup> to 21<sup>st</sup> (summer) and October 30<sup>th</sup> to November the 1<sup>st</sup> (autumn). Because of inclement weather, only 16 stations were sampled in October. Benthic macrofauna were collected using a GOMEX box corer which has been shown to efficiently sample muddy and very fine to fine sandy sediments (Boland and Rowe 1991). Three replicates of 900 cm<sup>2</sup> (30 x 30 cm) were taken at each station, for each of the three cruises. Subsamples for sediment analysis and chlorophyll *a* sediment content were extracted from each box core with a 3 cm diameter cylinder over ca. 5 cm depth. Sediment samples were frozen until ready for analysis. Water characteristics (temperature, salinity, dissolved oxygen = DO) were monitored ca. 1 m above the bottom.

Box core samples were sieved at sea on a 500 µm sieve using seawater. Retained organisms, including sediment, were fixed and preserved in 5% buffered formalin and returned to the laboratory.

## Laboratory Analysis

In the laboratory, macroinvertebrates were sorted to major taxon (i.e. polychaetes, mollusks and others) and transferred to 70% ethanol. Bivalve and gastropod shells were examined for the presence of tissue. Wet weight of each group (shells included for mollusks) was taken before all individuals were sorted, identified to the species level (or the lowest taxonomic level possible) and enumerated. Species were classified into five feeding-guilds: (1) suspension-feeders, (2) surface deposit-feeders, (3) interface feeders (i.e. species which can switch from suspension-feeding to surface deposit-feeding), (4) sub-surface deposit-feeders, (5) predators or

scavengers/detritivores, based on taxonomic affiliation of families after Fauchald and Jumars (1979) for polychaetes, Yonge and Thompson (1976) for mollusks, Lecroy (2000) for amphipod crustaceans and Pechenik (2005) for other taxonomic groups. Some nematodes and planktonic copepods were retained but were excluded from analysis following Rzeznik-Orignac et al. (2004).

Sediment particle size analysis was conducted for each station. Sediment samples were washed with distilled water through a 63  $\mu\text{m}$  sieve to separate sand from silt and clay and to dissolve NaCl particles that may agglomerate smaller particles. The fraction <63  $\mu\text{m}$  was collected in a bowl with water and allowed to settle for 72 hours. The water was then siphoned and the silt/clay fraction dried to constant weight in an oven at 60°C, then weighed. The sand fraction was dried to constant weight in an oven at 60°C, and placed on a Ro-Tap sieve shaker for 3 min (21 sieves from 2 mm to 63  $\mu\text{m}$  mesh size with  $\frac{1}{2} \Phi$  intervals). The fraction retained on a 2 mm mesh size is the gravel fraction (consisting mostly of shell debris). The average particle size and the sorting index  $\sigma$  were determined using the Folk and Ward (1957) method. Results were processed by the Gradistat software (Blott and Pye 2001).

#### Statistical Analysis

Data were analyzed using univariate and multivariate methods. Macrofauna species diversity was estimated using species richness and Hill's (1973) heterogeneity of diversity indices:  $N1 = \exp(H')$ , where  $H'$  is Shannon-Wiener diversity ( $\log_e$  - Shannon 1948); and  $N2 = 1/SI$ , where  $SI$  is Simpson's index (Simpson 1949);  $N1$  is sensitive to the number of medium-density species whereas  $N2$  is sensitive to the number of very abundant species (Whittaker 1972). Species richness, i.e. the number of different species, is also called  $N0$ , consistently with  $N1$  and  $N2$  indices. These indices are well suited to the analysis of diversity of benthic

macrofauna communities and, together with the equitability index  $J'$  (Sheldon 1969), are recommended by Gray (2000) to measure heterogeneity of marine coastal diversity.

One-way ANOVA was used to test for geographic and seasonal trends in species richness, diversity indices, and species abundances. Cochran's test was used to determine homogeneity of variances and, if necessary, data were  $\log_e (x+1)$  transformed. When parametric ANOVA testing was acceptable, the Student-Newman-Keuls (SNK) test was used for multiple comparisons. As recommended by Hsu (1996), post-hoc comparisons were performed using Tukey HSD tests. A significance level of  $p < 0.05$  was used in all tests.

Differences in the composition of the macrofaunal assemblages between sites were determined using non-metric multidimensional scaling (nMDS) and cluster analysis (group average mode), followed methods of Clarke and Warwick (1994), using the Primer package (Clarke and Gorley 2001). Unstandardized multivariate data were  $\log_e (1+x)$  transformed to down-weight the importance of the very abundant species, and similarity matrices were calculated with the Bray-Curtis similarity index. The statistical significance of differences among sites was assessed using analysis of similarities (ANOSIM), a non-metric method based on randomization of rank-similarities among all samples (Clarke 1993), as well as multiple pairwise comparisons. To build the matrix, species occurring in less than 5% of the samples, with only one individual, were excluded. To identify within two different sample groups which species primarily accounted for the observed assemblage differences, SIMPER (similarity percentage) routines were performed using a decomposition of Bray-Curtis dissimilarity on  $\log_e (x+1)$  transformed abundance data. Species were listed in decreasing order of their importance in discriminating the two sets of samples (Clarke and Gorley 2001).

Two approaches were used to link environmental parameters, i.e. depth (m), sediment grain size (mean grain-size, sorting index), silt/clay and gravel (%) content, bottom DO ( $\text{mg L}^{-1}$ ) and chlorophyll *a* ( $\text{mg Chl } a \text{ g sediment}^{-1}$ ) sediment content, with the Ship macrobenthic community: (1) pair-wise regressions were used between environmental parameters and descriptors of benthic community (N0, N1, N2, taxonomic biomass or mean species abundances) to explore if the variation in one environmental parameter followed the variation in species richness and (2) multivariate BIOENV procedures (see Clarke and Ainsworth 1993 for details) were used to determine how spatial patterns in multivariate invertebrate community structure were related to spatial patterns in multivariate environmental structure, i.e., to what extent observed biological patterns fits with variations environmental parameters.

## RESULTS

### General Description

A total of 29,331 macrofaunal individuals in 161 species were collected from Ship Shoal during the three cruises (see Appendix A). Polychaetes represented 45% (72 species) of the total species number, following by crustaceans (28%, 46 species) and mollusks (17%, 27 species). Other taxa (nemerteans, sipunculids, anthozoans etc.) represented 10% (16 species). Global species richness exhibited a sharp decrease from spring to autumn, together with the mean species richness ( $p < 10^{-5}$ ). Except for a significant difference between N1 in autumn and N1 in spring or summer ( $p < 0.003$ ), heterogeneity indices and equitability did not exhibit seasonal variation (Table 2.1). In terms of abundances, polychaetes and crustaceans predominated the Ship community with mean abundances between 2000 and 2500 individuals  $\text{m}^{-2}$  in spring (Fig. 2.2). Within these two taxonomic groups, spionids and amphipods were respectively the largest component, representing more than 50% of individual polychaetes and 80% of the crustaceans. *Amphioxus* *Branchistoma floridae* (Cephalochordata) abundance peaked in summer.



Community mean biomass (wet weight) followed the same pattern, from  $40.55 \text{ g m}^{-2}$  (SE = 5.22) in spring to  $21.77 \text{ g m}^{-2}$  (SE = 2.88) in summer and  $15.44 \text{ g m}^{-2}$  (SE = 3.22) in autumn (Figure 2.3). While this decrease in biomass occurred throughout the year for polychaetes, it was not significant between summer and autumn for mollusks or between spring and summer for other taxa.

Table 2.1 Species richness and heterogeneity of diversity and equitability (mean  $\pm$  SE) for each season. Core cross-sectional area =  $0.09 \text{ m}^2$ . Results of one-way ANOVA for each measurement, where same letters indicate non-significant differences at  $p$ -level = 0.05.

	Seasonal global species richness	Species Richness	Heterogeneity of diversity N1 = exp (H')	Heterogeneity of diversity N2 = 1/SI	Equitability J'
Spring	134	$33.19 \pm 1.53^a$	$13.90 \pm 1.15^a$	$8.67 \pm 0.86$	$0.72 \pm 0.10$
Summer	118	$23.71 \pm 1.05^b$	$12.40 \pm 0.96^a$	$8.19 \pm 0.73$	$0.77 \pm 0.08$
Autumn	91	$13.54 \pm 1.01^c$	$8.38 \pm 0.80^b$	$6.08 \pm 0.58$	$0.78 \pm 0.11$

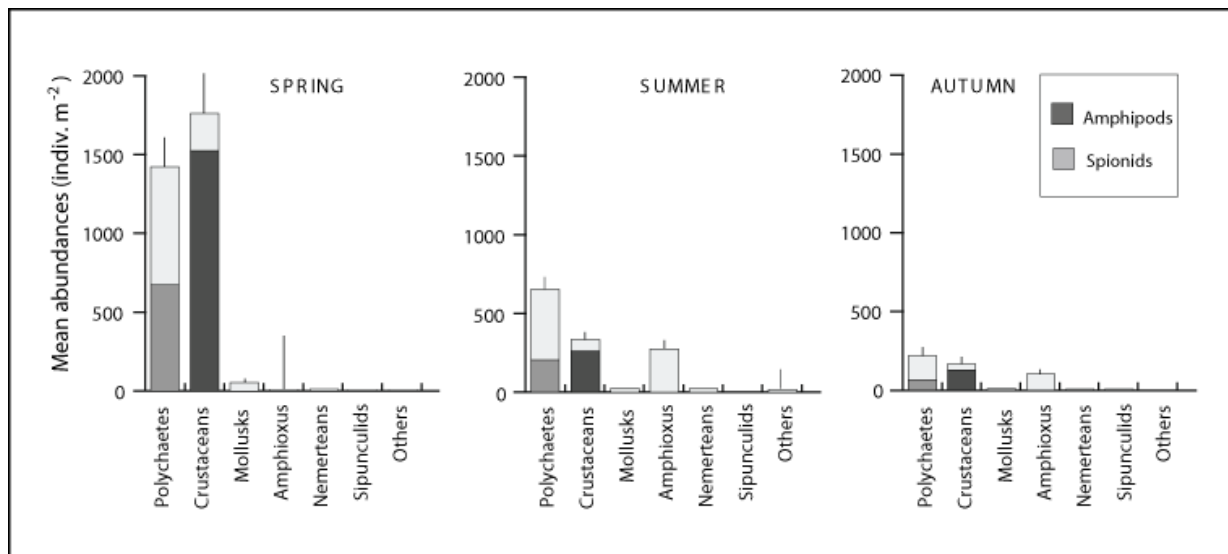


Figure 2.2 Seasonal variations in abundances (individuals  $\text{m}^{-2}$ ; mean  $\pm$  SE) of main taxonomic groups, with emphasis on spionids and amphipods. Core cross-sectional area =  $0.09 \text{ m}^2$ .

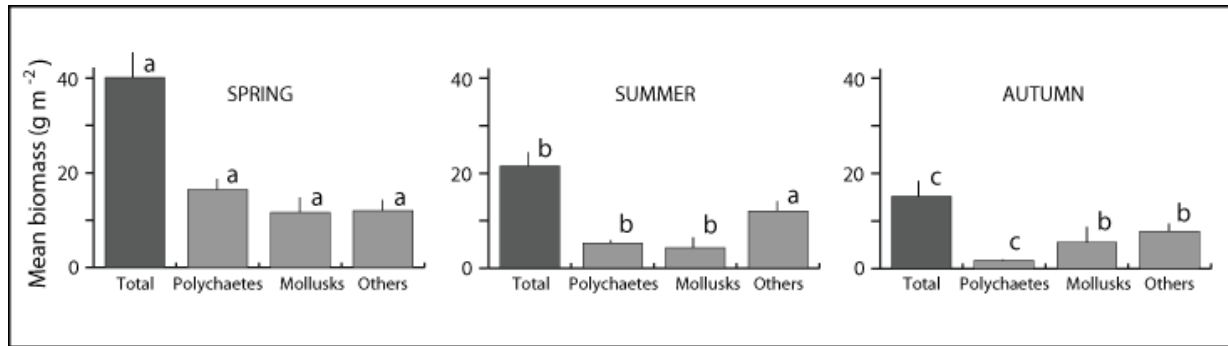


Figure 2.3 Mean biomass (wet weight;  $\text{g m}^{-2}$ ; mean  $\pm$  SE) of polychaetes, mollusks (including shells) and other taxonomic groups according to seasonality. Core cross-sectional area =  $0.09 \text{ m}^2$ . Letters a, b and c refers to statistical differences between the 3 seasons for total biomass, polychaetes, mollusks and others.

In terms of the measured environmental parameters, Ship Shoal constituted a relatively homogenous sandy habitat (Table 2.2). Sediment analysis revealed that all 21 stations were well or very well sorted unimodal. Sediment was classified sand or slightly gravelly sand for the most eastern stations (stations 14 to 18). Silt/clay (i.e. particles  $< 63 \mu\text{m}$ ) and gravel (i.e. particles  $> 2 \text{ mm}$  - primarily shell fragments) were very low at each station. Mean grain size, smaller in the west part of the shoal and larger in the east, was significantly negatively correlated in spring with  $N_0$  ( $r = 0.722$ ;  $p < 0.001$ ),  $N_1$  ( $r = 0.477$ ;  $p < 0.05$ ),  $N_2$  ( $r = 0.421$ ;  $p < 0.05$ ) and species abundances ( $r = 0.601$ ;  $p < 0.01$ ). The DO at the sediment surface was positively correlated with  $N_0$  ( $r = 0.596$ ;  $p < 0.01$ ) and species abundances ( $r = 0.670$ ;  $p < 0.01$ ) in spring. Dissolved oxygen and sediment grain size were autocorrelated ( $r = 0.569$ ;  $p < 0.01$ ). No significant relation was found between environmental parameters and any diversity indices in summer or autumn.

Table 2.2 Seasonal variations in monitored environmental parameters over Ship Shoal.

	Spring		Summer		Autumn	
	min - max	mean $\pm$ sd	min - max	mean $\pm$ sd	min - max	mean $\pm$ sd
Depth (m)	4.2 - 10.2	6.9 $\pm$ 1.6	4.2 - 9.4	6.4 $\pm$ 1.5	4.9 - 10.5	7.2 $\pm$ 1.7
Mean grain size ( $\mu\text{m}$ )	127.7 - 198.1	159.9 $\pm$ 20.6	118.1 - 323.3	170.0 $\pm$ 39.5	115.6 - 320.6	174.3 $\pm$ 46.2
Silt/clay content (%)	0.3 - 3.4	1.4 $\pm$ 1.0	0.3 - 4.5	1.4 $\pm$ 1.1	0.3 - 18.1	1.9 $\pm$ 4.2
Gravel content (%)	0.0 - 3.7	0.5 $\pm$ 1.0	0.1 - 11	1.2 $\pm$ 2.6	0.1 - 11.8	1.4 $\pm$ 3.1
Sorting index	1.2 - 1.7	1.2 $\pm$ 0.1	1.2 - 2.5	1.3 $\pm$ 0.3	1.3 - 2.4	1.3 $\pm$ 0.3
Chlorophyl <i>a</i> ( $\text{mg m}^{-2}$ )	12.0 - 120.1	41.8 $\pm$ 27.4	2.7 - 122.0	37.0 $\pm$ 31.5	1.8 - 94.0	30.2 $\pm$ 21.8
Dissolved oxygen ( $\text{mg L}^{-1}$ )	2.0 - 8.4	6.1 $\pm$ 1.5	4.5 - 8.3	6.3 $\pm$ 1.1	6.3 - 7.2	6.9 $\pm$ 0.3

Significant differences in diversity and abundances between western, middle and eastern stations of Ship Shoal, as well as between northern and southern stations (ANOVA; Table 2.3) were observed. More precisely, species richness was significantly higher in the southernmost stations of the shoal in spring ( $p = 0.032$ ), summer ( $p = 0.002$ ) and autumn ( $p = 0.030$ ) than in the middle or in the northernmost stations. Spring variations in global SR (i.e., total number of species for one station) and mean SR within the three transects across the shoal showed that both global and mean SR were higher at the southernmost stations (i.e., 17, 26 and 21) (Fig. 2.4). The same pattern was indicated in summer and autumn.

Mean species abundances were significantly higher in the southern edge in spring ( $p = 0.018$ ), summer ( $p < 10^{-6}$ ) and autumn ( $p < 1.16 \cdot 10^{-4}$ ) but were also significantly higher in the western region in spring ( $p = 0.004$ ), summer ( $p < 10^{-6}$ ) and autumn ( $p = 1.13 \cdot 10^{-4}$ ) than in the central or in the eastern region of the shoal. N1 and N2 indices exhibited more seasonal differences; in spring, both indices were significantly higher toward the west (N1,  $p = 7.2 \cdot 10^{-5}$ ; N2,  $p = 4.0 \cdot 10^{-4}$ ) and the southern edge (N1,  $p = 0.012$ ; N2,  $p = 0.029$ ) but both indices only exhibited a significant north-south gradient in summer (N1,  $p = 6 \cdot 10^{-4}$ ; N2,  $p = 4.4 \cdot 10^{-6}$ ) and no significant variation in autumn. While total biomass showed no significant variation, polychaete biomass was significantly higher in the west and south in spring ( $p = 0.013$  and  $p < 10^{-7}$ , respectively) and in summer ( $p = 0.026$  and  $p = 3 \cdot 10^{-4}$ , respectively) (Table 2.3).

### Macrofaunal Benthic Assemblages

Cluster analysis of the macrofauna abundance data showed a strong seasonal effect in sample composition (Fig. 2.5), supported by ANOSIM results (global  $R = 0.684$ ;  $p < 0.001$ ; Table 4). SIMPER results (Table 2.4) comparing seasons showed that a small number of species contributed most to the dissimilarity among seasons: the amphipods *Acanthohaustorius* sp.A and *Protohaustorius bousfieldi*, the polychaetes *Spiophanes bombyx* and *Dispio uncinata*, and the

amphioxus *Branchiostoma floridae*. These species had a very high frequency of occurrence in samples each season but exhibited strong decreases in abundances, especially between spring and summer, with the exception of the amphioxus *B. floridae* which was more abundant in summer. Many species contributed to a smaller extent to the discrimination between spring and other seasons because they had low abundances and high frequency of occurrence in spring but occurred only in a few stations in summer and autumn. This was mainly the case for polychaetes such as *Scolecopsis texana*, *S. squamata*, *Paraprionospio pinnata*, *Spiochaetopterus costarum*, *Phyllodoce mucosa*. In addition to *B. floridae*, a few species with a high frequency of occurrence were more abundant in summer, such as the polychaetes *Thalenessa spinosa* and *Eupolymnia nebulosa* or the nemertean *Micrura leidy*. The polychaete *Paramphimone* sp.B and the shrimp *Acetes americanus* mostly occurred in autumn. A few species, the polychaetes *Neanthes micromma* and *Nephtys simoni*, the gastropod *Oliva sayana*, the hermit crab *Pagurus annulipes* or the mole crab *Albunea paretii*, did not vary through the spring, summer or autumn with a high frequency of occurrence throughout.

#### Spatial Distribution in Spring, Summer, and Autumn

Cluster analyses also showed a clear difference in species assemblages between samples from the same season (Fig. 2.6). SIMPER analyses revealed that in spring (global  $R = 0.564$ ;  $p < 0.001$ ) and summer (global  $R = 0.323$ ;  $p < 0.001$ ), samples from east, middle and west Ship Shoal region differed from each other mainly because of changes in species abundances. SIMPER also showed that discrepancies in species composition were predominately found between the eastern and the rest of the shoal, as the middle and western regions were similar in species composition.

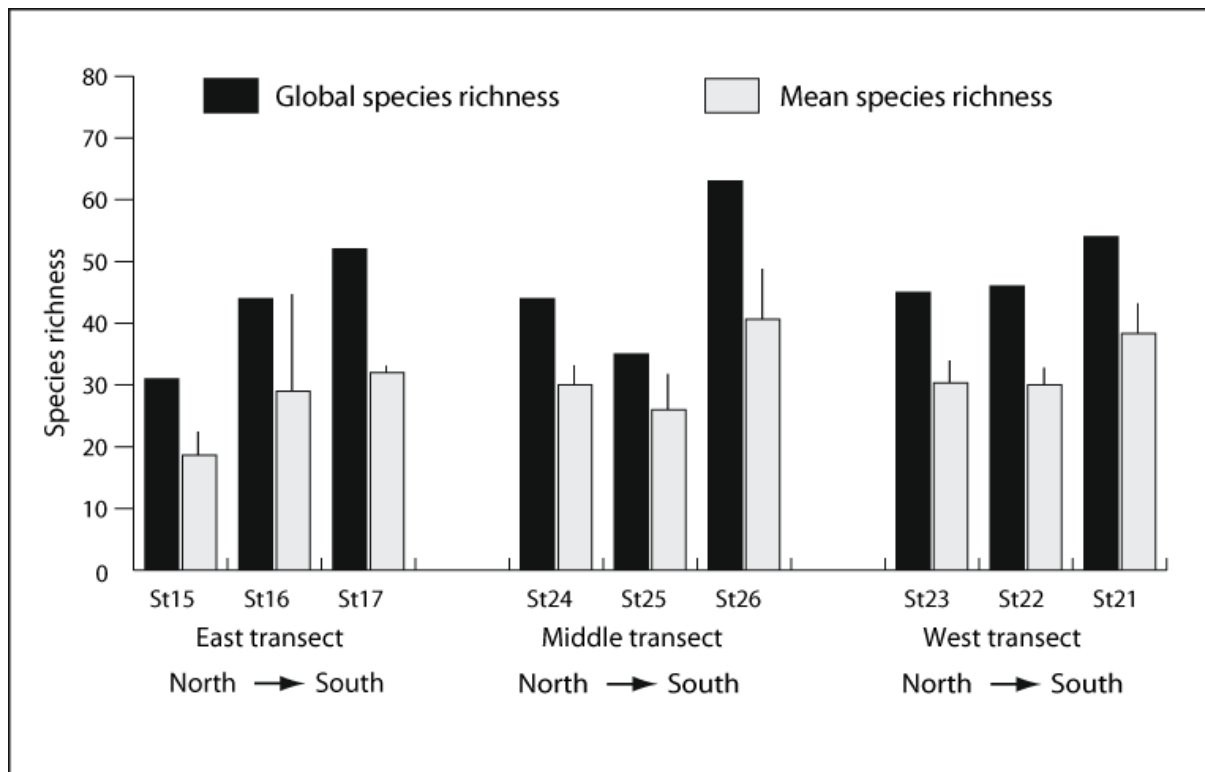


Figure 2.4 Global and mean ( $\pm$ SE) species richness in spring on Ship Shoal within the east, middle and west transects on the Ship Shoal. Core cross-sectional area =  $0.09 \text{ m}^2$ . See Fig. 2.1 for precise location of the stations.

Table 2.3 Results of ANOVA tests showing east-west gradient and north-south gradient within Ship Shoal area according to diversity indices, species abundance and biomass for each season. SR = species richness (N0), N1 and N2 = heterogeneity of diversity. Post-hoc columns indicated results of post-hoc comparisons between E (east), M (middle) and W (west) or between N (north), M (middle) and S (south), with “ = ” indicating non-significant difference and “ < ” indicating significant difference at  $p$ -level = 0.05.

Spring	east - west gradient			north - south gradient		
	F	p-level	post-hoc	F	p-level	post-hoc
SR	2.91	NS	-	4.27	0.032	N = M < S
N1	18.35	$7.2 \cdot 10^{-5}$	E < M < W	5.91	0.012	N < M < S
N2	13.05	$4.0 \cdot 10^{-4}$	E < M < W	4.41	0.029	N < M = S
abundances	13.06	$4.0 \cdot 10^{-3}$	E = M < W	5.19	0.018	N < M = S
total biomass	1.07	NS	-	2.09	NS	-
polychaete biomass	5.77	0.013	E < M = W	39.29	$1.0 \cdot 10^{-7}$	N = M < S

Summer	east - west gradient			north - south gradient		
	F	p-level	post-hoc	F	p-level	post-hoc
SR	2.85	NS	-	8.83	0.002	N < M < S
N1	1.52	NS	-	11.40	$6 \cdot 10^{-4}$	N = M < S
N2	3.17	NS	-	15.04	$4.4 \cdot 10^{-6}$	N = M < S
abundances	58.82	$1 \cdot 10^{-6}$	E < M < W	37.42	$1 \cdot 10^{-6}$	N < M < S
total biomass	2.13	NS	-	0.15	NS	-
polychaete biomass	4.47	0.026	E = M < W	13.15	$3 \cdot 10^{-4}$	N = M < S

Autumn	east - west gradient			north - south gradient		
	F	p-level	post-hoc	F	p-level	post-hoc
SR	11.32	$6.54 \cdot 10^{-4}$	E = M < W	4.26	0.030	N = M < S
N1	2.80	NS	-	1.93	NS	-
N2	1.11	NS	-	1.16	NS	-
abundances	15.71	$1.13 \cdot 10^{-4}$	E < M < W	9.39	$1.16 \cdot 10^{-4}$	N < M < S
total biomass	0.47	NS	-	1.15	NS	-
polychaete biomass	0.06	NS	-	0.06	NS	-

Table 2.4 ANOSIM and SIMPER results comparing species composition according to seasons. Core cross-sectional area = 0.09 m<sup>2</sup>. SIMPER cumulative dissimilarity cut-off = 50%. See Fig. 2.6 for nMDS plots.

	Spring	Summer	Spring	Autumn
R statistic	0.733		0.861	
p-value	0.001		0.001	
Similarity (%)	38.34	33.97	38.34	28.55
Bray-Curtis dissimilarity (%)	81.38		88.35	
Contribution to dissimilarity (%)	<i>Acanthohaustorius</i> sp. A	14.85	<i>Acanthohaustorius</i> sp. A	18.69
	<i>Protohaustorius bousfieldi</i>	8.41	<i>Spiophanes bombyx</i>	8.83
	<i>Branchiostoma floridae</i>	7.66	<i>Protohaustorius bousfieldi</i>	8.26
	<i>Spiophanes bombyx</i>	7.04	<i>Dispia uncinata</i>	4.44
	<i>Dispia uncinata</i>	3.84	<i>Microprotopus raneyi</i>	3.83
	<i>Prionospio pygmaea</i>	3.74	<i>Ampelisca</i> sp. C	3.70
	<i>Microprotopus raneyi</i>	3.41	<i>Branchiostoma floridae</i>	3.41
	<i>Ampelisca</i> sp. C	3.34		
	Summer	Autumn		
R statistic	0.459			
p-value	0.001			
Similarity (%)	33.97	28.55		
Bray-Curtis dissimilarity (%)	76.70			
Contribution to dissimilarity (%)	<i>Branchiostoma floridae</i>	16.12		
	<i>Acanthohaustorius</i> sp. A	10.51		
	<i>Prionospio pygmaea</i>	9.18		
	<i>Protohaustorius bousfieldi</i>	6.37		
	<i>Scoloplos</i> sp. B	3.82		
	<i>Mediomastus californiensis</i>	2.86		
	<i>Magelona</i> sp. A	2.64		

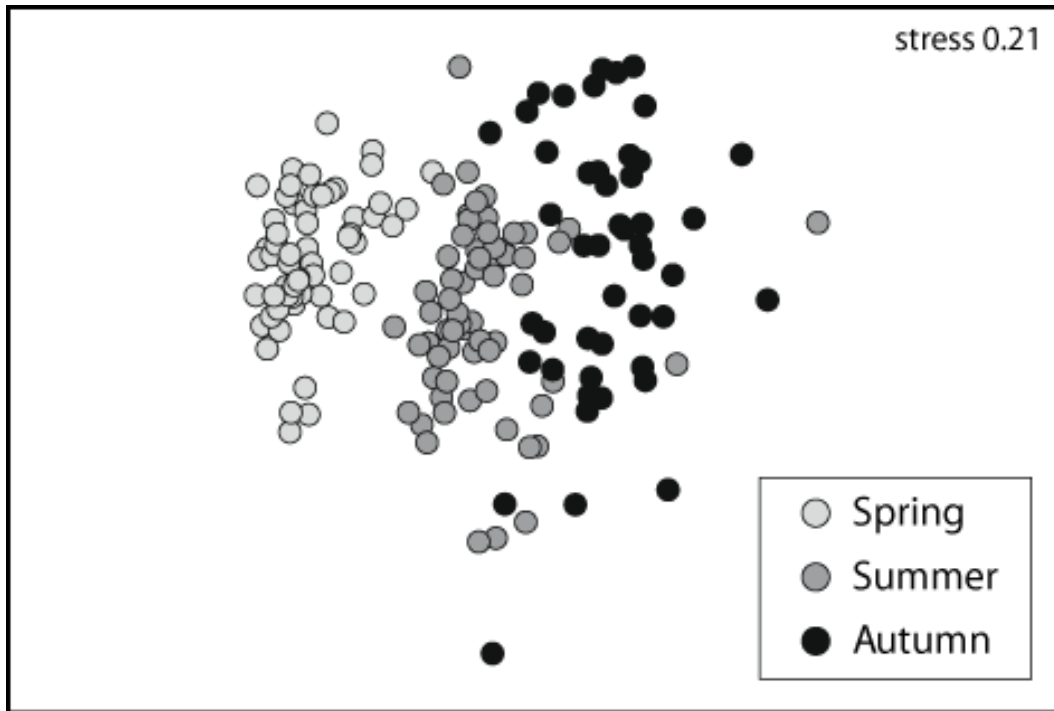


Figure 2.5 Multi-dimensional scaling ordination diagram of all samples of all stations showing seasonal changes in species composition and assemblages. Ordination was based on unstandardized log-transformed abundances matrix.

In spring, the amphipod *Acanthohautorius* sp. A and spionids *Spiophanes bombyx* and *Dispio uncinata* contributed most to the dissimilarity between regions but also most to the similarity within each region. Amphipod species contributed the most to changes in species composition across the whole of the study area: *P. bousfieldi* occurred almost only in the western stations, while *Hartmanodes ranyei*, *Microprotopus ranyei* and *Ampelisca* sp.C were more abundant in the middle and western stations.

In summer, the lancelet *B. floridae*, the amphipod *Acanthohautorius* sp. A and the polychaete *Prionospio* (*Apoprionospio*) *pygmaea* contributed mostly to the dissimilarity between regions but also mostly to the similarity within each region. Polychaete species contributed most to the discrimination between groups: *Euploymnia nebulosa*, *Scoloplos* sp.B, *Tharyx annulosus*



dominated abundances in the west stations, *Thalenessa spinosa* was more abundant in the middle region and *Nereis falsa*, *N. micromma* and *Travisia hobsonae* in the eastern region.

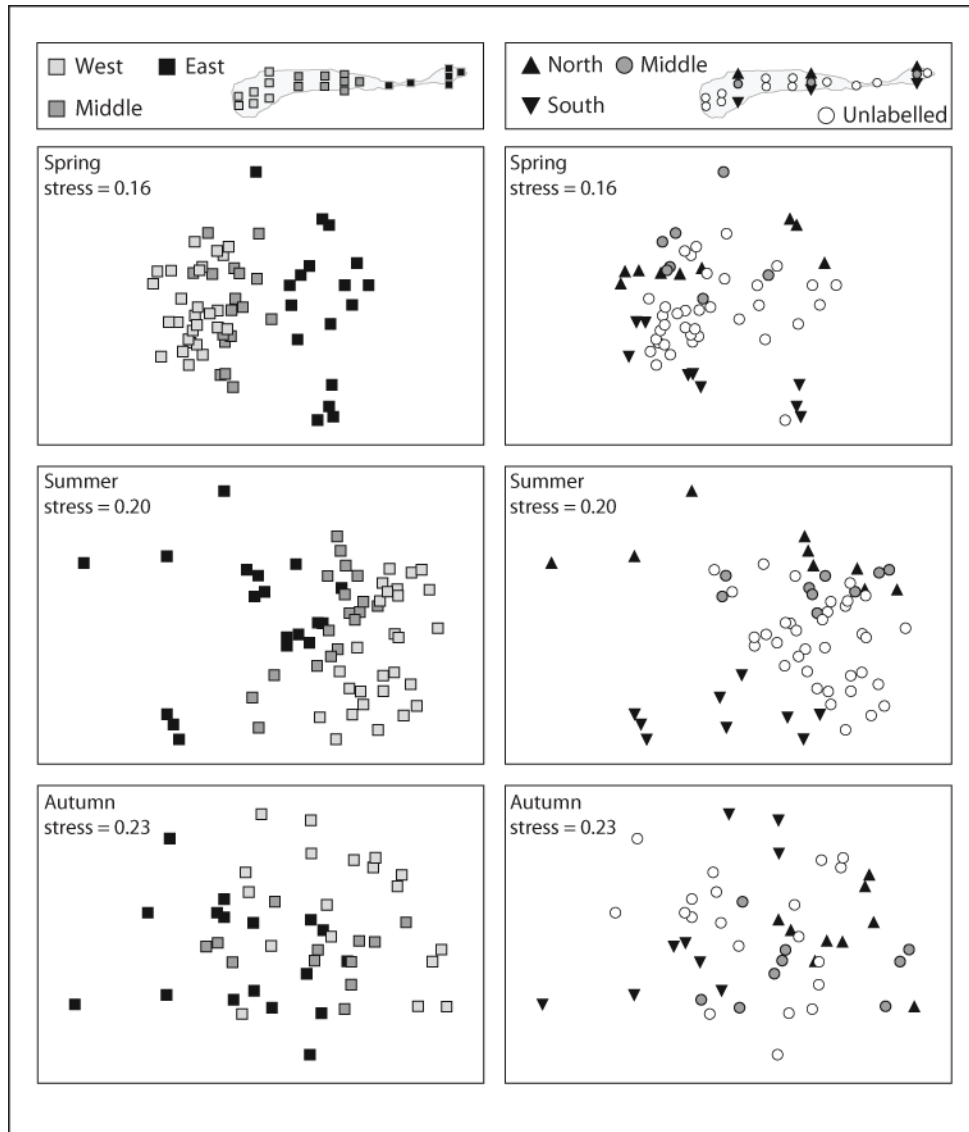


Figure 2.6 Multi-dimensional scaling ordination diagrams showing, for spring (top), summer (middle) and autumn (bottom) samples east-west variations (left panels) or north-south variations (right panels). A schematic of the shoal is provided to illustrate the position of the stations on the east-west and north-south transects (see Fig. 2.1 and description of study site for details). Ordination was based on unstandardized log-transformed abundances matrix.

In autumn, similarity indices decreased, as revealed by the greater scatter in the MDS plots of stations (Fig. 2.6). This is due to larger discrepancies between species composition of the samples between and within stations. As in summer, the lancelet *B. floridae* and the amphipod *Acanthohautorius* sp. A were the two structuring species. Also, *P. bousfieldi* occurred mostly in the western stations, and the polychaetes *Magelona* sp. A and *Magelona* sp. H occurred mostly in the northern and in the southern stations, respectively.

Though east-west changes were found, a high similarity threshold was also found between all northern and all southern stations from the three transects (46.33, 36.77% and 29.84, 34.14% for spring and summer respectively Fig. 2.6). While this result was supported by diversity indices, this was also due to species that exhibited higher abundances in the southern stations, such as the polychaetes *Owenia fusiformis*, *M. californiensis*, *T. annulosus*, *Magelona* sp. H, *S. bombyx*, *Scoloplos* sp. B., *P. pinnata* or higher abundances in the north stations such as the polychaetes *N. simoni* and *Magelona* sp. A or the cumaceans *Oxyurostylis smithi* and *C. varians*.

BIOENV procedures showed that variations in macrobenthic assemblages were best matched by a combination of three or four environmental variables in spring, that were depth / grain size / % gravel (Spearman correlation = 0.687) or depth / grain size / % gravel / DO (Spearman correlation = 0.682). In summer, depth provided the best match (Spearman correlation = 0.505). No significant correlations were found in autumn.

### Feeding Guilds

Species that are able to switch between suspension-feeding and surface deposit-feeding dominated the trophic guild in spring (47%), and exhibited a decrease in summer (31%) and autumn (30%) (Fig. 2.7). True suspension-feeders almost disappeared in autumn while the

dominance of species relying on deposit-feeding varied but did not decrease. Only the dominance of predators/scavengers increased with seasons, from 8% in spring to 30% in autumn. In spring, abundance of sub-surface deposit-feeders was positively correlated with water depth ( $r = 0.545$ ;  $p < 0.01$ ) and % silt/clay ( $r = 0.524$ ;  $p < 0.01$ ) but negatively correlated with sediment mean grain size ( $r = 0.471$ ;  $p < 0.05$ ). On the contrary, abundance of surface deposit-feeders was negatively correlated with water depth ( $r = 0.747$ ;  $p < 0.001$ ) and % silt/clay ( $r = 0.538$ ;  $p < 0.01$ ). In summer, abundance in sub-surface deposit-feeders was positively correlated with water depth ( $r = 0.451$ ;  $p < 0.05$ ) and abundance in surface deposit-feeders was negatively correlated with depth ( $r = 0.427$ ;  $p < 0.05$ ). Abundance in suspension-feeders or interface-feeders was positively correlated with chlorophyll *a* sediment content ( $r = 0.523$ ;  $p < 0.05$ ).

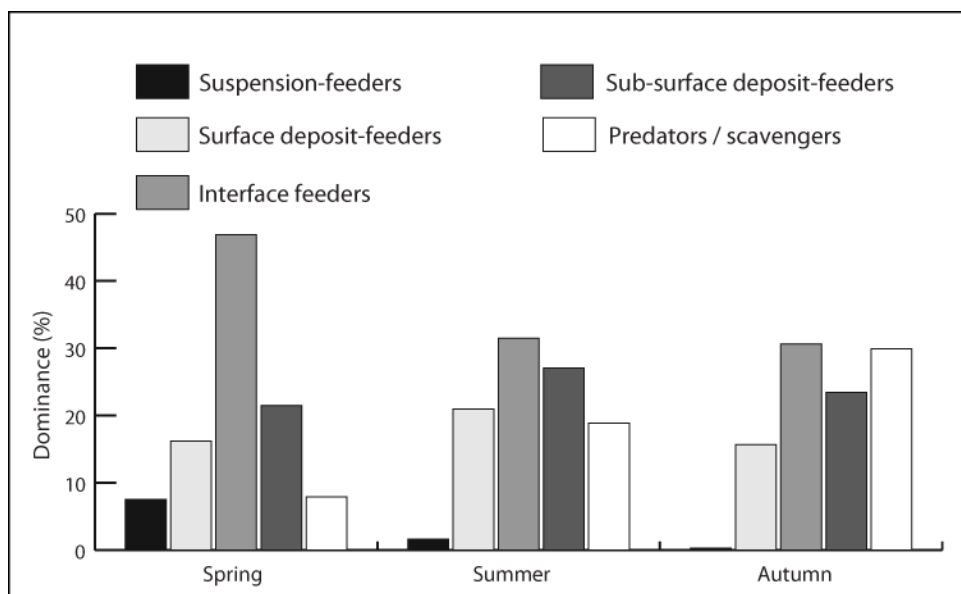


Figure 2.7 Seasonal variations in dominance (%) of the five feeding guilds. Interface feeders are species which can switch between suspension-feeding and surface deposit-feeding.

## DISCUSSION

Sandbanks and sandy shoals occur on continental shelves, in coastal embayments and in estuaries throughout the world. Their associated mineral deposits represent potentially valuable resources to help mitigate coastal erosion and to supply the raw material for beach reinforcement

and coastal stabilization projects (Michel et al. 2001). Demands on coastal ocean sand supplies are likely to increase as both human occupation of the coastal zone and sea level continues to rise, and as land-based sand-supplies decline. Although a large number of studies have examined sandbank formation, modeled sediment transport, and evaluated the importance of shoals to local hydrodynamic conditions (e.g., Berthot and Pattiaratchi 2004), few ecological studies have examined the functional value of these high-relief structures in their ecosystems, especially in terms of biodiversity and associated ecological services. Even so, there is a growing awareness of the potential impact of sand and gravel mining, to both the extracted and receiving sites, in coastal-ocean systems (i.e., Defeo et al. 2009; Peckenhams et al. 2009; Pempel and Church 2009; Zeppelini et al. 2009), and more studies are needed to aid policy decisions. Finally, lessons learned from careful studies of the impacts of current coastal-ocean sand mining operations could prove valuable as extractions of other marine minerals begin and increase (e.g., Rona 2008).

### The Ship Shoal Macrobenthic Assemblage

Ship is a large, discrete formation composed of fine to very fine sand (ca. 150  $\mu\text{m}$  diameter) about 25 km offshore from the Louisiana coast. Environmental gradients of water depth (increasing depth toward the east) and granulometry (increasing mean grain size toward the east) characterize the shoal. In terms of benthic macroinvertebrates, our results suggest that Ship represents a faunally distinct habitat type in a transition between in-shore and off-shore habitats. Species composition revealed differences between east and west areas, along with differences between northern and southern edges of the shoal. Ship hosted a unique combination of macroinfauna composed of species commonly found typically in the swash zone of sandy beach communities associated with the Mississippi and northwest Florida seashore (e.g., *Leitoscoloplos fragilis*, *Scolecopsis squamata*, *D. uncinata*) (Rakocinski et al. 1998), or abundant in shallow

enclosed bays of the northern Gulf of Mexico (e.g., *P. pinnata*, *Gyptis vittata*, *Notomastus latericeus*, *Mulinia lateralis*) (Mannino and Montagna 1997; Montagna and Ritter 2006), as well as species typically found in muddy off-shore environments south of Terrebonne Bay, Louisiana (e.g., *Armandia maculata*, *Magelona* sp. H, *Tellina versicolor*, *Nassarius acutus*) (Baustian et al. 2009). More generally, shoals exhibit a unique physical regime, leading to special hydrodynamic and sedimentary patterns and to distinct species assemblages. But the extent to which associated fauna is distinct from surrounding environments is poorly known (Kaiser et al. 2004).

A significant number of species not reported previously for the Louisiana continental shelf were found on Ship Shoal. Uebelacker and Johnson (1984) provided a distribution range of polychaete species occurring on a large portion of the outer continental shelf of the northern Gulf of Mexico, e.g., south Texas (Texas), central Louisiana (Louisiana) and Mississippi–Alabama–west Florida (Florida) outer shelves. Based on that comprehensive work, we report that 50% of the polychaete species found on Ship (35 species) were recorded either from the Florida continental shelf only (23 species) or from both the Texas and Florida continental shelves (12 species). Thus half of the Ship Shoal polychaete species had not been recorded for the Louisiana continental shelf. While most of these polychaete species had a low density and widely scattered distribution on Ship Shoal (e.g., *Streptosyllis pettiboneae*, *Myriowenia* sp. A, *Anaitides groenlandica*), a few species (*P. mucosa*, *T. spinosa*, *N. falsa* or *N. simoni*) exhibited high frequency of occurrence with low density (ca. 10 individual m<sup>-2</sup>).

The Ship Shoal community appears to be a melange of species. Among species found throughout the year, with a high frequency of occurrence, mole crabs *Albunea paretii* and amphioxus *B. floridae* best typified the very fine-sand shoal community and comprised most of the biomass. In this *Albunea-Brachyostoma* community, defined based on the two ubiquitous

species which constitute the majority of the biomass on the shoal, we typically found the polychaetes *Nephtys simoni*, *N. micromma*, *D. uncinata* and *Magelona* sp. A, the amphipod *Acanthohautorius* sp. A and the burrowing shrimp *Ogyrides alphaerostris*. They constituted the basis of the sandy shoal community, which exhibited variation according to seasons or according to on-shore or off-shore influences. As expected, the shoal community is typified by species that are adapted to changes in hydrography and are able to re-burrow rapidly when washed out of the sediment during a storm event. Moreover, nephtyid or magelonid polychaetes distinguish the fauna of sandbanks in the North-Sea (Vanosmael et al. 1982).

The occurrence of amphioxus (*B. floridae*) has been reported in sandy-shore macrobenthic community of barrier islands to the west of the Mississippi river (Hefley and Shoemaker 1952; Rakocinski et al. 1998), but this is the first report of high abundances of amphioxus (up to 1250 individuals m<sup>-2</sup>) off the Louisiana coast. In the spring, most individuals were large ovigerous females. In the summer, many juveniles were present, suggesting Ship Shoal is a locally important habitat for reproduction and early summer recruitment. The findings presented here strongly suggest that Ship Shoal in particular and Louisiana sandy shoals in general play an important role in the marine landscape ecology of the northern Gulf of Mexico, by aiding dispersal and gene flow of benthic species over large spatial scales. The sediment characteristics of Ship are similar to that of the Florida shelf (Posey et al. 1998). In addition, a recent large-scale study of current circulation in the northern Gulf of Mexico (Ohlmann and Niiler 2005) found a strong interregional connectivity, especially during passage of tropical storms that allowed particles to cross the Florida–Louisiana shelf-break and the Mississippi river outflow. Thus, Ship represents a suitable area along the Louisiana coast for larvae to settle and for a diverse group of species adapted to life in fine sand to survive and develop.

More locally, Ship Shoal may serve as a source pool for recruitment of benthic invertebrate larvae and adults to surrounding areas affected by seasonal hypoxia. Powilleit and Kube (1999) found rapid recolonization by adult benthic macrofauna from an undisturbed shallow coastal area with high macrofauna density to an area moderately affected by hypoxia in the Pomeranian Bay in the Southern Baltic Sea. Ship may provide the same function as abundances of benthic invertebrates on the hypoxia affected areas of the Louisiana shelf increase after hypoxia ends (Rabalais et al. 2001). In addition, a study designed to study hyperbenthic (=suprabenthic) species assemblages of subtidal sandbanks in the North Sea, Dewicke et al. (2003) hypothesized that sandbanks might also sustain nursery areas for several fish and crustacean species. Molecular tools would be of primary interest in testing hypotheses regarding gene flow and dispersal.

#### Is Ship Shoal a Diversity Hotspot?

Few authors have focused specifically on sandbanks, employing multiple collections with quantitative sampling devices (Kaiser et al. 2004). In the present study, the overall species richness of macrobenthos on Ship totaled 161 species (with a mean per sample of  $23.71 \pm 1.05$ ). Benthic assemblages over a large sampling area off the central coast of Louisiana surrounding Ship Shoal showed that the mean species richness for summer was  $19.1 \pm 2.3$  (Baustian et al. 2009). This investigation covered a much broader area (ca.  $4,000 \text{ km}^2$ ) than the present study (ca.  $200 \text{ km}^2$ ) and encountered a greater habitat variety (muddy substrata through gravelly soft-bottoms). One would thus expect the off-shoal species richness to be comparatively much higher than Ship Shoal for a similar number of stations (Rosenzweig 1995). A comparable study was conducted on the Kwinte Bank in the Belgian coastal waters on the area where the sediment is composed of coarse to fine grained sand (Vanosmael et al. 1982). The Kwinte Bank was found to

be more speciose than the surrounding habitat composed of finer grained sediment and considered a “biogeographical island” located within the transition zone between the coastal zone and open sea.

In addition, Baustian (2005) studied seasonal variation in a macrobenthic community at one particular site that typifies muddy soft-bottom environments surrounding Ship Shoal (ca. 10 km off Ship Shoal). This seasonal survey provides a relevant comparison of seasonal patterns with the present study. It showed a similar decrease in species richness and abundances from spring to autumn: mean SR ranged from 14 to 4 species between May and October, while the range was 33–13 species for the same months in Ship Shoal sediments. Thus, Ship appears to maintain a higher number of species than nearby locations on the Louisiana shelf. Biodiversity in benthic communities is often linked with many environmental factors, of which sediment characteristic is of primary importance (Gray 1974). Traditionally, infaunal species richness is lower in muddy communities than in sandy community but heterogeneous sands have typically more species than well-sorted mobile sands, which are characterized by dominance of polychaetes and amphipods (e.g., Van Hoey et al. 2004), as found in Ship Shoal.

Significant variation in species diversity occurred over a small latitudinal gradient (less than 10 km) between the northern and southern edges of Ship (biodiversity in southern stations was higher). This north-south gradient is characterized by the higher abundances of large tube-building polychaete species at stations close to the southern edge in deepening water. For example, average abundances for the main tube-building onuphid species *Diopatra cuprea* and *Onuphis eremita occulata* and Oweniidae *O. fusiformis* were  $6.17 \pm 6.17$ ,  $74.03 \pm 20.38$  and  $513.67 \pm 482.31$  individuals  $m^{-2}$  for the southern edge, versus  $0, 4.90 \pm 3.23$  and  $54.33 \pm 54.33$  individuals  $m^{-2}$  for the northern edge, respectively. These tube-builders contribute to the high



diversity on Ship compared to nearby non-shoal habitats. Tubes that protrude several cm above the sediment surface are known to increase surface heterogeneity and provide habitat for other small invertebrates (Zuhlke 2001; Dubois et al. 2002), as well as settlement surface for larval and postlarval benthic organisms (Qian and Chia 1991). This last hypothesis was supported by high densities of spionid and oweniid juveniles in southern samples (e.g., up to  $1478 \pm 475$  juveniles  $m^{-2}$  of *O. fusiformis* in the station 21, Fig. 2.1).

Baustian's (2005) seasonal study off Ship Shoal showed that, while polychaetes dominated (ca. 50%) throughout the year, mollusks were the second most important taxonomic group (24% in May, 45% in August and 38% in October). *Nuculana acuta*, *Natica pusilla* and *Abra aequalis* were particularly abundant in Baustian's study but were found on Ship Shoal in very low abundances (less than 3 individuals  $m^{-2}$ ). We found that mollusks represented < 3% of the macroinfauna on Ship, but that crustaceans, and especially amphipods, were almost as abundant as polychaetes (even more abundant in spring), while it is traditionally assumed that polychaetes are the most diverse and dominant taxonomic group in most marine and estuarine environments (e.g., Hutchings 1998).

#### Is Ship Shoal a Local Refuge From Seasonal Hypoxia?

Ship Shoal is situated within one of the largest hypoxic areas in the world (Rabalais et al. 2001). Mid-summer surveys from 1993 to 2000 revealed severe and persistent hypoxia (i.e., DO < 2 mg  $l^{-1}$ ) on the inner-to mid-Louisiana continental shelf (Rabalais et al. 2001). Yet, our estimates of bottom DO concentrations over the entire shoal were fairly high and constant in spring ( $6.1 \pm 1.5$  mg  $l^{-1}$ ), summer ( $6.3 \pm 1.1$  mg  $l^{-1}$ ) and autumn ( $6.9 \pm 0.3$  mg  $l^{-1}$ ), with only one spring sample reaching 2.0 mg  $l^{-1}$ . Amphipods occurred in very high abundance and diversity

over Ship, with a total of 20 species identified. *Acanthohaustorius* sp. A, *P. bousfieldi*, *Ampelisca* sp. C and *Hartmanodes nyei* were highly-ranked among the benthic assemblages throughout the year. In contrast, complete and long lasting (one or more years) disappearance of amphipod communities was recorded at stations in an area of severe oxygen depletion in the Pomeranian Bay of the Southern Baltic Sea (Powilleit and Kube 1999). More locally, Baustian (2005) confirmed that crustaceans in general and amphipods in particular are absent from muddy areas surrounding Ship in summer and autumn. Because amphipods are known to be affected by low oxygen (Gaston 1985; Wu and Or 2005), together these results support the hypothesis that Ship Shoal is a hypoxia refuge for benthic species.

Irregular bottom topography in shallow waters such as sand banks and shoals is known to influence coastal hydrodynamics and bottom boundary layer dynamics (Pepper and Stone 2004). For instance, such bathymetric elevated areas act as submerged breakwaters, mitigating wave energy, flow patterns, and consequently increase DO concentrations (e.g., Kobashi et al. 2007) and the shoal is too shallow to facilitate local stratification (Grippo et al. 2009). Moreover, biogenic activity exemplified by the high density of tubicolous polychaetes (e.g., spionids, representing between 30 and 50% of polychaete density, as well as *O. fusiformis*, or *Onuphis eremita occulata*) may enhance oxygen flux in sediment surface layer (Jorgensen et al. 2005). Together, these factors may contribute to Ship Shoals high DO concentrations.

Species abundances exhibited a steady but large rate of decline between spring, summer and autumn, affecting amphipods as well as all other taxonomic groups (except amphioxus). The magnitude and extent of these declines suggest an increase in the rate of mortality that is most likely not due to a short life-span. The most abundant structuring amphipod species, *Acanthohaustorius* sp. A exhibit a lifespan of 1.5 years (Sainte-Marie 1991) and the most abundant polychaete family, spionids, exhibit a mean life-span of 1.8 years (McHugh and Fong

2002). As indicated by our DO measurements (ca.  $6 \text{ mg l}^{-1}$ ), a hypoxia event is not likely the cause for such a decrease in species abundances on Ship Shoal. Sedimentation in the form of an ephemeral fluiditic flood layer has been reported to have a dramatic effect on benthic species abundances on the US Pacific Northwest coast (e.g., Wheatcroft and Sommerfield 2005). However, a 2006 survey done by US Army Corps of Engineers (data available at [www.mvn.usace.army.mil/eng/edhd/watercon](http://www.mvn.usace.army.mil/eng/edhd/watercon)) did not reveal summer and/or autumn flooding of the Atchafalaya and Mississippi Rivers on the adjacent Louisiana continental shelf that could lead to a large-scale mud-layer deposition. Furthermore, our sediment analyses over the entire Ship Shoal area found that silt and clay was always  $< 2\%$  of the total sediment. Flooding events are most likely to affect Ship Shoal in the winter and spring when continental cold fronts occur and when river flow is high (Allison et al. 2005). Recent modeling investigations showed that ephemeral and patchy fluiditic mud may occur in spring on Ship (Kobashi et al. 2007). While we did not find evidence of this in our seasonal survey, it may have had adversely affected the benthic populations on a small-scale. Lastly, a seasonal influx of benthic predators may strongly affect benthic populations (e.g., Langlois et al. 2005). In Chapter 4 we discuss unexpectedly high concentrations of spawning/hatching blue crabs *Callinectes sapidus* in summer 2006 on Ship Shoal, but not in spring trawls. Stable isotopes (Chapter 5) and gut content data showed that these blue crabs actively fed on Ship Shoal. *C. sapidus* is known to be an important benthic predator which may have a strong influence on polychaete and bivalve populations (Bell et al. 2003). We suggest here that seasonal blue crab predation (perhaps supplemented by other predators such as white, brown shrimp and croaker) on Ship may contribute to the observed seasonal decline in the macroinfaunal community.

## Are Ship Shoal Macrofauna Sensitive to Sand Mining Disturbance?

Ship Shoal has been identified as perhaps the most significant sand resource (ca. 1.6 billion cubic yards of fine sand) in the northern Gulf of Mexico (Drucker et al. 2004). Dredged sand may be used to supply beach reinforcement and coastal stabilization projects and mitigate Louisiana coastal erosion and wetland loss (Michel et al. 2001). Much previous research suggests that dredging and mining activities negatively affect, at least temporarily, shoal benthic communities (Newell et al. 1998). Our study provides baseline information to better understand the ecological services provided by Ship Shoal and to predict its sensitivity to human disturbances in general and sand-mining disturbances in particular. Given the size of Ship, it is likely that mining would remove only a fraction of the available sand but localized effects may be strong and similar to responses experienced by sandbanks worldwide.

Newell et al. (1998) estimated that the rate of recovery for sandy environments after sediment extraction is much longer (2–3 years) than the rate for muddy environments (6–8 months), and may be even longer depending on the amount of sand removed, the proportion of slow-growing species and the intensity of environmental disturbance. Palmer et al. (2008) found that macrofauna off the western coast of Louisiana were not fully recovered 3 years after dredging a sand excavation pit. The macrofauna assemblage of Ship Shoal is species-rich with strongly contrasting life history characteristics compared to the surrounding off-shoal community (Palmer et al. 2008; Baustian et al. 2009). Many of Ship Shoal's more abundant species (including *B. floridae*, *Scoloplos* sp., *Sabellides* sp., *Terebellides* sp. and *Dosinia* sp., *Tellina* sp., *Ensis* sp.) have been designated "equilibrium species" (K-strategists) (Newell et al. 1998) because they are relatively large in body size, have a slow reproduction rate and a long life-cycle. These species, and the amphipod fauna as a whole, are considered sensitive species (Gesteira and Dauvin 2000), and are probably controlled by biological interactions rather than extreme changes

in environmental conditions on Ship. Large species accounted for most of the biomass on Ship, which is high ( $37.3 \text{ g wet weight m}^{-2}$ ) compared to other areas of similar water depth (Pinn and Robertson 2003; Thouzeau et al. 1991). These observations suggest that Ship's macrofauna will be strongly affected by and slow to recover from sand extraction. We predict that sand extraction on Ship Shoal and other sandbanks will cause a shift in dominance to small, rapidly-growing species including spionid polychaetes. These "disturbance specialists" or "opportunistic species" (r-selected species, Pianka 1970) are found throughout the world. They have a rapid rate of reproduction and body growth which facilitates colonization of disturbed habitats (e.g. Dubois et al. 2002; Palmer et al. 2008), and are less sensitive to sand mining. The resulting reduction in macrofaunal biomass may elicit indirect effects at higher trophic levels, for example on fishes and crustaceans using Ship as a foraging ground.

Sand mining will also impact physical factors that have direct and indirect effects on ecological services. Variation in water depth and mean particle size was closely associated with changes in benthic communities across Ship. Excavation of sand will lead to localized increases in water depth and turbidity (due to the overflow of fine particles). Even small changes in water depth may influence primary production on Ship. Grippo et al. (2009) found that benthic microalgae may have higher biomass than phytoplankton integrated through the water column on Ship, suggesting benthic primary production contributes significantly to the shoal's food web. For example, the high macrofaunal biomass we observed may be attributed to high levels of in situ primary production (e.g., our observed correlation between chl a and benthic interface feeders). Changes in primary production and a finer particle size will likely influence the benthic community by reducing community biomass and altering community composition. Higher trophic levels may be influenced by resulting bottom-up effects induced by changes in the biomass or community composition of macrofauna.

## CONCLUSION

Sandy shoals appear to provide key ecological services at multiple trophic levels from all localities studied so far. For example, Vanaverbeke et al. (2007) showed that sand extraction affected the nematode community at the base of the food web from the Kwinte sandbank (Southern Bight of the North Sea). Kaiser et al. (2004) showed that sandbanks on the Welsh coastline (United Kingdom) hosted distinct fish assemblages foraging on benthic species colonizing the sandbanks. McGuire and Winemiller (1998) demonstrated that the presence of sandbanks in the Cinaruco estuary (Venezuela) was associated with a greater frequency of dolphin sightings. Our work suggests that larvae spawned by benthic invertebrates living on Ship Shoal contribute to the recolonization of a nearby seasonally hypoxic “dead zone” and that this sandy habitat is a species richness hotspot that hosts a unique macrobenthic community that contrasts strongly with the surrounding deeper muddy community. Ship offers a hypoxia refuge for benthic species, as well as a settlement area for postlarvae and juveniles, enhancing the survival probability for newly settled species. Ship might also be an important foraging ground for fishes or large crustaceans preying upon benthic invertebrates, especially when nearby severe hypoxia reduces essential habitat.

The effects of sand-mining on Ship Shoal benthos would likely last for months to years and effects may extend to shoal-dependent nekton by food web interactions. In general, human interventions to combat coastal erosion and shoreline retreat have been shown to cause local ecological impacts and a loss of biodiversity that may have cumulative large-scale consequences (Schlacher et al. 2007). Because of the scale of this problem, the continued existence of sandy shoals—the main sand resource all over the world—as functional ecosystems is likely to depend on direct conservation efforts. Our work, although not a before-after study, suggests that shoals are more than mineral resources and that sand mining activities should be carried out with caution,

especially where sandy shoals differ markedly from surrounding benthic habitats.

#### LITERATURE CITED

- Allison, M.A., A. Sheremet, M.A. Goni, G.W. Stone. 2005. Storm layer deposition on the Mississippi-Atchafalaya subaqueous delta generated by Hurricane Lili in 2002. *Continental Shelf Research*. 25:2213-2232.
- Baustian, M.M. 2005. Benthic communities in the northern Gulf of Mexico hypoxic area: potential prey for demersal fish. Master Thesis, Louisiana State University.
- Baustian, M.M., J.K. Craig, N.N. Rabalais. 2009. Effects of summer 2003 hypoxia on macrobenthos and Atlantic croaker foraging selectivity in the northern Gulf of Mexico. *Journal of Experimental Marine Biology and Ecology*. 381:S31-S37.
- Berthot, A, C. Pattiaratchi. 2004. Maintenance of headland-associated linear sandbanks: modelling the secondary flows and sediment transport. 12th International Biennial Conference on Physics of Estuaries and Coastal Seas. Springer, Heidelberg, Merida, Mexico, pp 526–540.
- Bell, G.W., D.B. Eggleston, T.G Wolcott. 2003. Behavioral responses of free-ranging blue crabs to episodic hypoxia. II. Feeding. *Marine Ecological Progress Series*. 259:227-235.
- Blott, S.J., K. Pye. 2001. GRADISTAT: a grain size distribution and statistics package for the analysis of unconsolidated sediments. *Earth Surface Processes and Landforms*. 26:1237-1248.
- Boland, G.S., G.T. Rowe. 1991. Deep-Sea Benthic Sampling with the Gomex Box Corer. *Limnology and Oceanography*. 36:1015-1020.
- Brooks, R.A., C.N. Purdy, S.S. Bell, K.J. Sulak. 2006. The benthic community of the eastern US continental shelf: A literature synopsis of benthic faunal resources. *Continental Shelf Research*. 26:804-818.
- Cheung, M.M., R.A. Brooks, K.J. Sulak. 2006. Benthic polychaete assemblages on Sabine and Heald sand banks, northern Gulf of Mexico: a pre-disturbance study on a sand extraction site, USGS Outer Continental Shelf Ecosystem Studies Program Report, Gainesville, FL

- Clarke, K.R. 1993. Nonparametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*. 18:117-143.
- Clarke, K.R., M. Ainsworth. 1993. A method of linking multivariate community structure to environmental variables. *Marine Ecological Progress Series*. 92:205-219.
- Clarke, K.R., R.N. Gorley. 2001. PRIMER v5 : User Manual/Tutorial. PRIMER-E Ltd, Plymouth.
- Clarke, K.R., R.M. Warwick. 1994. Change in marine communities: an approach to statistical analysis and interpretation. Report No. 144, Plymouth Marine Laboratory, Plymouth.
- Drucker, B.S., W. Waskes, M.R. Byrnes. 2004. The US minerals management service outer continental shelf sand and gravel program: Environmental studies to assess the potential effects of offshore dredging operations in federal waters. *Journal of Coastal Research*. 20:1-5.
- Defeo, O.A. McLachlan, D.S. Schoeman, T.A. Schlacher, J. Dugan, A. Jones, M. Lastra, F. Scapini. 2009. Threats to sandy beach ecosystems: a review. *Estuarine Coastal Shelf Science*. 81:1-12.
- Dewicke, A., A. Cattrijsse, J. Mees, M. Vincx. 2003. Spatial patterns of the hyperbenthos of subtidal sandbanks in the southern North Sea. *Journal of Sea Research*. 49:27-45.
- Dubois, S., C. Retiere. F. Olivier. 2002. Biodiversity associated with *Sabellaria alveolata* (Polychaeta : Sabellariidae) reefs: effects of human disturbances. *Journal of the Marine Biological Association of the United Kingdom*. 82:817-826.
- Fauchald, K., P.A. Jumars. 1979. The diet of worms: A study of polychaete feeding guilds. *Oceanography and Marine Biology Annual Review*. 17:193-284.
- Folk, R.L., W.C. Ward. 1957. Brazos River bar: a study in the significance of grain size parameters. *Journal of Sediment Petrology*. 27:3-26.
- Gaston, G.R. 1985. Effects of Hypoxia on macrobenthos of the inner shelf off Cameron, Louisiana. *Estuarine, Coastal and Shelf Science*. 20:603-613.
- Gesteira, J.L.G., J.C. Dauvin. 2000. Amphipods are good bioindicators of the impact of oil spills on soft-bottom macrobenthic communities. *Marine Pollution Bulletin*. 40:1017-1027.



- Gray, J.S. 1974. Animal-sediment relationships. *Oceanography and Marine Biology*. 12:223-261.
- Gray, J.S. 2000. The measurement of marine species diversity, with an application to the benthic fauna of the Norwegian continental shelf. *Journal of Experimental Marine Biology and Ecology*. 250:23-49.
- Grippo, M. A., J. W. Fleeger, R. E. Condrey, K. R. Carman. 2009. High biomass of benthic microalgae found on Ship Shoal, north-central Gulf of Mexico. *Bulletin of Marine Science*. 84: 237-256.
- Hefley, H.M., H. Shoemaker. 1952. The occurrence of *Branchiostoma* (Amphioxus) in Mississippi and Louisiana. *Science*. 115:48.
- Hill, M.O. 1973. Diversity and evenness: a unifying notation and its consequence. *Ecology*. 54:427-432.
- Hsu, J. 1996. Multiple comparisons: theory and methods. Chapman and Hall, London.
- Hutchings, P.A. 1998. Biodiversity and functioning of polychaetes in benthic sediments. *Biodiversity and Conservation*. 7:1133-1145.
- Jorgensen, B.B., R.N. Glud, O. Holby. 2005. Oxygen distribution and bioirrigation in Arctic fjord sediments (Svalbard, Barents Sea). *Marine Ecological Progress Series*. 292:85-95.
- Justic, D., N.N. Rabalais, R.E. Turner. 1996. Effects of climate change on hypoxia in coastal waters: A doubled CO<sub>2</sub> scenario for the northern Gulf of Mexico. *Limnology and Oceanography*. 41:992-1003.
- Kaiser, M.J., M. Bergmann, H. Hinz, M. Galanidi, R. Shucksmith, E.I.S. Rees, T. Darbyshire, K. Ramsay. 2004. Demersal fish and epifauna associated with sandbank habitats. *Estuarine Coastal Shelf Science*. 60:445-456.
- Kobashi, D., F. Jose, G.W. Stone. 2007. Impacts of fluvial fine sediments and winter storms on a transgressive shoal, off south-central Louisiana, U.S.A. Proceedings of the 9th International Coastal Symposium. *Journal of Coastal Research*. Gold Coast, Australia, p 858-862.
- Langlois, T.J., M.J. Anderson, R.C. Babcock. 2005. Reef-associated predators influence adjacent soft-sediment communities. *Ecology*. 86:1508-1519.

- Lecroy, S. 2000. An illustrated identification guide to the nearshore marine and estuarine Gammaridean Amphipoda of Florida, vol 1. Families Gammaridae, Hadziidae, Isaeidae, Melitidae and Oedicerotidae. Tallahassee. Florida Department of Environmental Protection, Florida.
- Mannino, A., P.A. Montagna. 1997. Small-scale spatial variation of macrobenthic community structure. *Estuaries*. 20:159-173.
- McGuire, T.L., K.O. Winemiller. 1998. Occurrence patterns, habitat associations, and potential prey of the river dolphin, *Inia geoffrensis*, in the Cinaruco river, Venezuela. *Biotropica*. 30:625-638.
- McHugh, D, P.P. Fong. 2002. Do life history traits account for diversity of polychaete annelids? *Invertebrate Biology*. 121:325–338.
- Michel, J., R. Nairn, J.A. Johnson, D. Hardin. 2001. Development and design of biological and physical monitoring protocols to evaluate the long-term impacts of offshore dredging operations on the marine environment, U.S. Department of the Interior, Mineral Management Service, International Activities and Marine Minerals Division (INTERMAR), Herndon, VA.
- Montagna, P.A., C. Ritter. 2006. Direct and indirect effects of hypoxia on benthos in Corpus Christi Bay, Texas, USA. *Journal of Experimental Marine Biology and Ecology*. 330:119-131.
- Newell, R.C., L.J. Seiderer, D.R. Hitchcock. 1998. The impact of dredging works in coastal waters: a review of the sensitivity to disturbance and subsequent recovery of biological resources on the seabed. *Oceanography and Marine Biology Annual Review*. 36:127-178.
- Ohlmann, J.C., P.P. Niiler. 2005. Circulation over the continental shelf in the northern Gulf of Mexico. *Progress in Oceanography*. 64:45-81.
- Palmer, T.A., P.A. Montagna, R.B. Nairn. 2008. The effects of a dredge excavation pit on benthic macrofauna in offshore Louisiana. *Environmental Management*. 41:573-583.
- Pechenik, J.A. 2005. Biology of the invertebrates, McGraw-Hill, New York.
- Peckenham, J.M., T. Thornton, W.B. Whalen. 2009. Sand and gravel mining: effects on ground water resources in Hancock County, Maine, USA. *Environmental Geology*. 56:1103-1114.

- Pempel, L.L., M. Church. 2009. Physical and ecological response to disturbance by gravel mining in a large alluvial river. *Canadian Journal of Fisheries and Aquatic Science*. 66:52-71.
- Pepper, D.A., G.W. Stone. 2004. Hydrodynamic and sedimentary responses to two contrasting winter storms on the inner shelf of the northern Gulf of Mexico. *Marine Geology*. 210:43-62.
- Pianka, E.R. 1970. R-Selection and K-Selection. *American Naturalist*. 104:592-597.
- Pinn, E.H., M.R. Robertson. 2003. Macro-infaunal biodiversity and analysis of associated feeding guilds in the Greater Minch area, Scottish west coast. *Journal of the Marine Biological Association of the United Kingdom*. 83:433-443.
- Posey, M.H., T.D. Alphin, S. Banner, F. Vose, W. Lindberg. 1998. Temporal variability, diversity and guild structure of a benthic community in the northeastern Gulf of Mexico. *Bulletin of Marine Science*. 63:143-155.
- Powilleit, M., J. Kube. 1999. Effects of severe oxygen depletion on macrobenthos in the Pomeranian Bay (southern Baltic Sea): a case study in a shallow, sublittoral habitat characterised by low species richness. *Journal of Sea Research*. 42:221-234.
- Qian, P.Y., F.S. Chia. 1991. Effects of food concentration on larval growth and development of two polychaete worms, *Capitella capitata* (Fabricius) and *Polydora ligni* (Webster). *Bulletin of Marine Science*. 48:477-484.
- Rabalais, N.N., W.J. Wiseman, R.E. Turner. 1994. Comparison of continuous records of near-bottom dissolved oxygen from the hypoxia zone along the Louisiana coast. *Estuaries*. 17:850-861.
- Rabalais, N.N., L.E. Smith, D.E. Harper Jr., D. Justic. 2001. Effects of seasonal hypoxia on continental shelf benthos. In: Rabalais NN and Turner RE (eds) Coastal hypoxia: consequences for living resources and ecosystems, coastal and estuarine studies, American Geophysical Union, Washington D.C., pp211-240.
- Rakocinski, C.F., S.E. LeCroy, J.A. McLelland, R.W. Heard. 1998. Nested spatiotemporal scales of variation in sandy-shore macrobenthic community structure. *Bulletin of Marine Science*. 63:343-362.
- Rosenzweig, M.L. 1995. Species diversity in space and time, Cambridge University Press, Cambridge.

- Rona, P.A. 2008. The changing vision of marine minerals. *Ore Geology Reviews* 33:618-666.
- Rzeznik-Orignac, J., D. Fichet, G. Boucher. 2004. Extracting massive numbers of nematodes from muddy marine deposits: efficiency and selectivity. *Nematology*. 6:605-616.
- Sainte-Marie, B. 1991. A review of the reproductive bionomics of aquatic gammaridean amphipods. Variation of life-history traits with latitude, depth, salinity and superfamily. 7th international colloquium on Amphipoda. Walpole, Me, pp 189–227.
- Schlacher, T.A., J. Dugan, D.S. Schoeman, M. Lastra, A. Jones, F. Scapini, A. McLachlan, O. Defeo. 2007. Sandy beaches at the brink. *Diversity and Distribution*. 13:556-560.
- Shannon, C.E. 1948. A mathematical theory of communications. *Bell Systems Technical Journal*. 27:379-423.
- Sheldon, A.L. 1969. Equitability indices: dependence on the species count. *Ecology*. 50:466-467.
- Simpson, E.H. 1949. Measurement of diversity. *Nature*. 163:688.
- Snelgrove, P.V.R., C.A. Butman. 1994. Animal-sediment relationships revisited: cause versus effect. *Oceanography and Marine Biology Annual Review*. 32:111-177.
- Thouzeau, G., G. Robert, R. Ugarte. 1991. Faunal assemblages of benthic megainvertebrates inhabiting sea scallop grounds from eastern Georges Bank, in relation to environmental factors. *Marine Ecological Progress Series*. 74:61-82.
- Uebelacker, J.M., P.G. Johnson. 1984. Taxonomic guide to the polychaetes of the northern Gulf of Mexico, Vol.1-7 Barry A. Vittor & Associates, Inc., Mobile, Alabama.
- Van Hoey, G., S. Degraer, M. Vincx. 2004. Macrobenthic community structure of soft-bottom sediments at the Belgian continental shelf. *Estuarine, Coastal and Shelf Science*. 59:599-613.
- Vanaverbeke, J., T. Deprez, M. Vincx. 2007. Changes site in nematode communities at the long-term sand extraction of the Kwintebank (Southern Bight of the North Sea). *Marine Pollution Bulletin*. 54:1351-1360.

- Vanosmael, C., K.A. Willems, D. Claeys, M. Vincx, C. Heip. 1982. Macrobenthos of a sublittoral sandbank in the southern Bight of the North Sea. *Journal of the Marine Biological Association of the United Kingdom*. 62:521-534.
- Wheatcroft, R.A., C.K. Sommerfield. 2005. River sediment flux and shelf sediment accumulation rates on the Pacific Northwest margin. *Continental Shelf Research*. 25:311-332.
- Whittaker, R.H. 1972. Evolution and measurement of species diversity. *Taxon*. 21:213-251.
- Wu, R.S.S., Y.Y. Or. 2005. Bioenergetics, growth and reproduction of amphipods are affected by moderately low oxygen regimes. *Marine Ecological Progress Series*. 297:215-223.
- Yonge, C.M., T.E. Thompson. 1976. Living marine molluscs, Collins, St James Place, London.
- Zeppelini, D., B.C. Bellini, A.J. Creado-Duarte. 2009. Collembola as bioindicators of restoration in mined sand dunes of Northeastern Brazil. *Biodiversity and Conservation*. 18:1161-1170.
- Zühlke, R. 2001. Polychaete tubes create ephemeral community patterns: *Lanice conchilega* (Pallas, 1766) associations studied over six years. *Journal of Sea Research*. 46:261-272.

**CHAPTER 3: BENTHIC ECOLOGY OF THE SHIP, TRINITY, AND TIGER SANDY  
SHOALS AND SURROUNDING MUDDY OFF SHOAL HABITAT OF THE  
LOUISIANA CONTINENTAL SHELF IN THE NORTHERN GULF OF MEXICO**

## INTRODUCTION

A substantial portion of the Earth's biota can be found in soft-sediment benthic landscapes or "benthoscapes" (Zajac 2008a). In coastal regions, benthoscapes are important foci of resource extraction (e.g. oil and gas, sand mining, fishing) and subject to other, varied human disturbances. Most soft-sediment habitats are defined by their two- and three-dimensional geomorphological structure, which is mainly based on sediment characteristics and geomorphological/topographic features. In most cases benthic landscape structure is physically defined rather than based on biological attributes. One component of assessing benthoscape structure in soft-sediments is the interaction between the physical structure defining the benthoscape and its biota (Zajac 2008a). It has been shown that sedimentary environments are heterogeneous and spatially complex and those areas that perhaps at first do not appear unique may be critical to regional environmental dynamics and human use of these systems (Hewitt et al. 2004).

Studies of biodiversity patterns in soft-sediment systems suggest that habitat heterogeneity contributes to high species richness and biodiversity (Ellingsen 2002; Ellingsen and Gray 2002; Hewitt et al. 2005). Because species may differ in their life history strategies they may be adapted to specific sediment characteristics such as sediment composition (e.g. medium sand, coarse sand, gravel etc.; Thouzeau et al. 1991), particle size (Rhoads and Young 1970) and variables associated with particle size such as sediment porosity, permeability, and oxygen content (Grey 1974 and references within). For example, Craig and Jones (1966) found a mix of mud and sand promoted a higher number of species than mud or sand alone. In addition, recent studies have found that transitions between marine benthic habitat types of differing sediment composition, such as from mud to sand, promote greater species richness along a benthic landscape (Zajac et al. 2003, Zajac 2008a,b). Thus, benthic landscape heterogeneity may

be a critical determinant of sea floor biodiversity. One possible example of benthoscape heterogeneity can be seen in the distinct sedimentary habitats that occur along the gradient from shallow sandy shoals to deeper muddy habitats along the Louisiana coast of the Northern Gulf of Mexico.

Globally, shoals are underexplored areas on the continental shelf benthoscape that are difficult to sample and may represent areas that are overlooked by marine ecologists (Kaiser et al. 2004; Dubois et al. 2009). Ship, Trinity, and Tiger Shoals are large, high-relief stands of sandy sediment rising some 10 m above the muddy sediments of the Mississippi River depositional plain off the Louisiana coast. These shoals are the sediment relics of past Mississippi River deltas (Maringouin and Teche 7,500 to 3,800 years BP; Roberts 1997) that formed when sea-level rose over the continental shelf. Ship Shoal (Ship) and Trinity/Tiger Shoals (TTS) and the surrounding off shoal areas (Off) comprise the Ship, Trinity, Tiger Shoal Complex (STTSC; Fig. 3.1). The STTSC benthos is exposed to disturbances from oil and gas industry, hypoxia, hurricanes, trawling, and sediment deposition from re-suspension and fluvial processes. In addition Ship and TTS are also presently being targeted for sand mining (i.e., Sutor et al. 1989; Stone et al. 2004), a consideration that has prompted our recent studies.

Benthic invertebrates are directly related to the sediment they inhabit (e.g. some species are adapted to specific sediment types and associated habitat characteristics; Gray 1974; Snelgrove and Butman 1994; Fleeger et al. 2011) and anthropogenic changes in sediment features may disrupt the resident benthic community and/or impact associated shoal-function. In an initial study limited to Ship (Chapter 2), we found it contained a unique benthic macrofauna consisting of high biomass and diversity, including species never before reported from the Louisiana continental shelf. In a follow-up study of the entire STTSC, the sediment of sandy shoals was found to contain a higher abundance of benthic microalgae (BMA) than settled



phytoplankton (Grippo et al. 2009), suggesting that BMA may represent the foundation, or at least an integral component of a shoal-based food web (Grippo et al. 2010; Grippo et al., 2011). In contrast, the Off food webs were found to be based more heavily on settled phytoplankton (Grippo et al. 2011). In addition, large numbers of female blue crabs (*Callinectes sapidus*) were sampled on and around Ship and TT (Chapter 4). These crabs were actively spawning, feeding, and hatching their eggs, providing strong evidence that these shoals (located > 25km offshore) were used as spawning grounds. Due to their shallow depths and possible oxygen contribution from resident BMA, the shoals may also act as a hypoxia refuge (Chapter 2; Chapter 4; DiMarco et al. 2010), within the seasonal dead zone which occurs from the mouth of the Mississippi River to the Texas continental shelf (Rabalais et al 1994, 2001a, 2002).

The questions we seek to address in this study:

- a. Are there differences and/or similarities in macrofaunal species assemblages between Ship, TTS and Off?
- b. Do sandy shoals enhance the regional biodiversity of the continental shelf?

In addition we use data generated to address the potential of shoals to provide a refuge to hypoxia, resupply surrounding hypoxia-affected areas with larvae, act as east-west northern Gulf of Mexico stepping stones for sandy sediment species, and/or serve as important blue crab spawning grounds.

## MATERIALS AND METHODS

### Site Description

Our study was located in the north-central Gulf of Mexico on the Louisiana continental shelf (Fig. 3.1). Samples were collected on Ship, Trinity, and Tiger Shoals and surrounding off shoal areas. Ship is located ~25 km offshore and is 5-12 km wide, 50 km long, and separated from the coast by a trough. TTS is located ~100 km to the northwest of Ship. Comprised within TTS, Tiger Shoal extends from the coast to ~30km seaward, while Trinity Shoal is located directly south of Tiger Shoal extending ~48 km from the coast. Depth ranged on the shoals from 3 to 9 m while Off station depths ranged from 3 to 19 m. All three shoals were composed mostly ( $\geq 77\%$ ) of sand. Stations on Ship typically contained higher sand concentrations than TTS. The Off stations were a mix of different sized particles with high inter-seasonal variation in sediment composition, and were typically much muddier than the shoals (see Table 1 Grippo et al. 2009; Appendix B). The region is heavily influenced by fluvial input from the Mississippi and Atchafalaya Rivers, which contribute nutrients and freshwater along the continental shelf resulting in large phytoplankton blooms, which ultimately sink and decompose and result in a large expanse of seasonal bottom water hypoxia (Rabalais et al 1994, 2001a, 2002).

### Field Sampling

Samples were collected during three cruises in 2007 aboard the Research Vessel “Pelican”: spring (April 1-5) 21 stations, summer (August 16-19) 18 stations, and fall (October 5-7) 11 stations. Due to inclement weather, total sampling effort was reduced in the summer and fall, however all areas were sampled with the exception of Tiger Shoal in fall. At each station depth, salinity, temperature, and dissolved oxygen (DO) were measured continuously for the entire water column with a Seabird CTD system. Macrofauna were sampled with a 0.09 m<sup>2</sup> (30 x

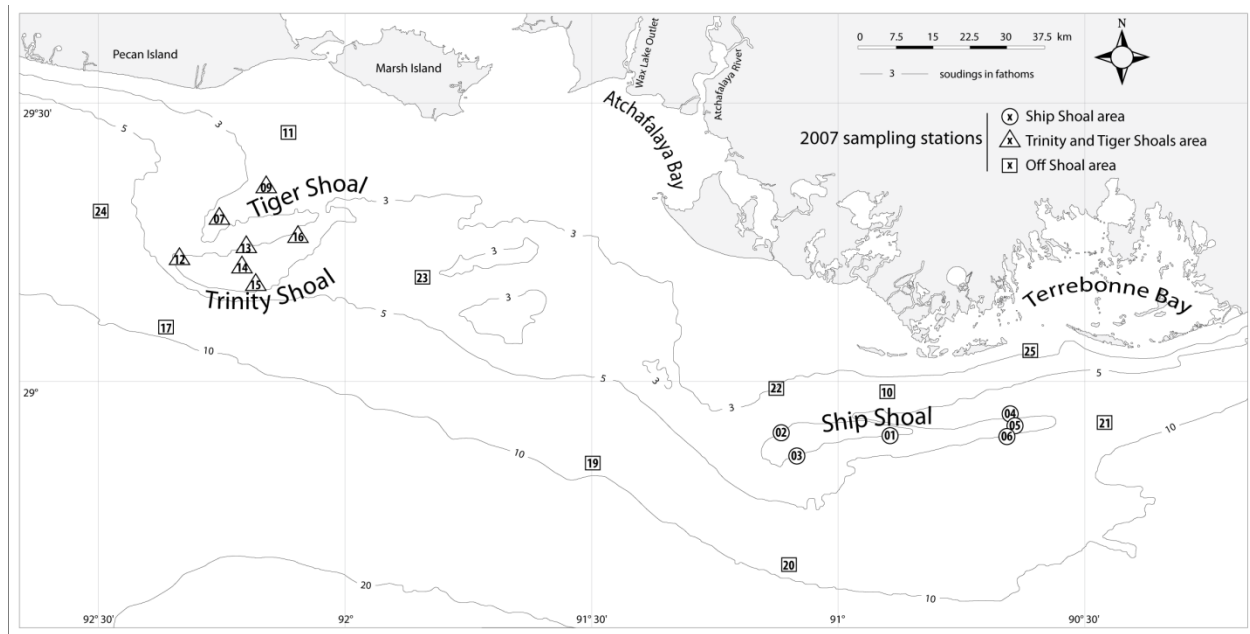


Figure. 3.1. Study area and station locations of 2007 benthic study

30 cm) GOMEX box corer. Three replicates were taken at each station during each of the three cruises. Macrofauna were sieved at sea on a 500- $\mu$ m sieve using seawater. Retained animals and remaining hash were preserved in a 70% buffered formalin solution. Sediment subsamples were extracted from each box core with a 2.5 cm diameter cylindrical syringe ca. 5 cm depth for particle size, carbon/nitrogen ratio (C/N), and chlorophyll a, and phaeopigment analyses.

### Laboratory Analysis

In the laboratory, macrofauna were separated from remaining sediment and sorted to three major taxonomic groups: polychaetes, mollusks, and others. Mollusks were examined for the presence of tissue. Wet weight of each group (shells included for crustaceans and mollusks) was measured with a OHAUS model balance to the nearest 1 mg before all individuals were sorted and identified to the lowest possible taxonomic level (species in most cases) and enumerated using Uebelacker and Johnson (1984) for polychaetes, Lecroy (2007) for amphipods, and Emerson and Jacobson (1976) for Mollusks.

Sediment particle size analysis was done for each station. Sediment samples were washed with distilled water through a 63  $\mu\text{m}$  sieve to separate sand from silt and clay and to remove NaCl that may cause smaller sediment particles to agglomerate. The <63  $\mu\text{m}$  fraction was collected in a bowl and allowed to settle for 72 hours. The overlying water was then slowly removed with a small siphon and the remaining silt/clay dried in an oven at 60 C, then weighed. The sand fraction was also dried in an oven at 60 C and placed on a Ro-Tap sieve shaker for three minutes (21 sieves from 2 mm - 63  $\mu\text{m}$  mesh size with  $\frac{1}{2} \Phi$  intervals). Results were processed with Gradistat software (Blott and Pye 2001). Phaeopigment, C/N, and chlorophyll a data from the same stations were obtained from (Grippo et al., 2010).

#### Statistical Groupings

Stations were originally grouped based on the designation of shoal areas on nautical charts. However, station 23 (Fig. 3.1) was shallow (5 m) and was found to contain a sand content characteristic of sandy shoals. Therefore, station 23 was included in all analysis when area was not a statistical factor (i.e. MDS and BEST), but was excluded when it would have been designated as an Off station in the analysis. Final station groupings consisted of two shoal areas, TTS and Ship with a total of 13 stations, and one Off (which did not include station 23, for a total of 9 stations).

#### Community Assemblages

Spatial and temporal differences in the composition of the macrofaunal assemblages were determined using cluster analysis (group average mode) and non-parametric multidimensional scaling on  $\log_e(x+1)$  transformed abundances and ranked Bray-Curtis similarities among samples following methods of Clarke and Warwick (1994) using the Primer software package (Clarke and Gorley 2001). To build the matrix, species occurring in less than 5% of the samples with overall abundances of < 10 individuals were excluded from the analysis. Analysis of

similarities (ANOSIM; Clarke and Warwick, 2001) established variation in communities among sites (significance was set at 0.05). Species similarity percentage (SIMPER) analysis (Clarke and Warwick, 2001) was used to rank species contributions to dissimilarities between areas and similarity within areas.

Macrofauna species diversity was estimated using Hill's (1973) heterogeneity of diversity indices:  $N1 = \exp(H0)$ , where  $H0$  is Shannon–Wiener diversity ( $\log_e$ —Shannon 1948); and  $N2 = 1/SI$ , where  $SI$  is Simpson's index (Simpson 1949);  $N1$  is sensitive to the number of medium-density species whereas  $N2$  is sensitive to the number of very abundant species (Whittaker 1972). Rarefaction index (ES 50), which estimated the expected number of species from 50 randomly selected individuals was also calculated. In addition, total benthic macrofaunal species abundances ( $N$ ), biomass, species richness ( $S$ ) and taxonomic distinctness ( $\Delta^*$ ), were calculated for each area/season combination. Taxonomic distinctiveness accounts for phylogenetic distance between species and was weighted according to Clarke and Warwick (1999). Two-way ANOVAs tested for significant effects of season and area on abundance, species richness, biomass, and environmental variables. Cochran's test was used to determine homogeneity of variance and if necessary data were  $\log_e (x + 1)$  transformed. Post-hoc tests were made using Tukey HSD. Area based K-dominance curves were plotted for the three seasons and the most dominant species and their feeding types were designated using Uebelacker and Johnson (1984) for polychaetes, Lecroy (2007 and references within) for amphipods, and Riisgard and Svane (1999) for amphioxus. Gamma diversity (Whittaker 1972) was calculated for the entire STTSC by season and across all seasons. Beta diversity was calculated for area comparisons within each season.

## Environmental Correlations and Analysis

Spearman correlations were used in Primer's BEST procedure (Clarke and Gorley, 2001) to isolate the best combination of measured environmental variables that match patterns of species assemblages. Simple linear regression was used in a preliminary exploration of area-based relationships of the environmental variables chosen by the BEST procedure. Species abundances within sand percentage intervals are provided as a means of viewing the distribution of all species within sediment type for our study area (Appendix B). This provided a visual assessment of sediment preference by species.

Using ANCOVA, we also tested the effect of water depth on near-bottom water DO with month and area as class variables. Area and season variations in bottom water DO were examined with ANOVA. Amphipod presence and abundance was also used as an indicator of hypoxia disturbance because crustaceans and amphipods in particular are highly sensitive to low bottom-water dissolved oxygen (Gaston 1985, Wu and Or 2005) and their presence is consistent with oxygenated conditions.

Uebelacker and Johnson (1984) provide the only comprehensive study of the distribution of polychaetes in the northern Gulf of Mexico. However, species preferring sandy habitat may have been underrepresented in Uebelacker and Johnson's (1984) sampling design, which did not include Louisiana shoals (except for one possible sampling location). We examined the species distribution of polychaetes within our study area in relation to those provided by Uebelacker and Johnson (1984) for the Florida shelf (defined here as the continental shelf from southern tip of Florida to the Alabama/Mississippi border), Louisiana shelf, and Texas shelf. Based on their nomenclature we classified 23 of 30 sediments as sandy, five as silty, and two as clayey (Their Tables 2-6). Based on this classification sandy stations made up 95%, 40%, and 71% of total sampling for the Florida, Louisiana, and Texas shelves, respectively. In order to address the role

of sand in facilitating connectivity between similar sandy habitats we used regression analysis to examine the relationship between sediment sand % and the abundance and richness of total, previously reported, and newly reported polychaete species from our study using the species distributions and taxonomic guides from Uebelacker and Johnson (1984).

## RESULTS

### General Description

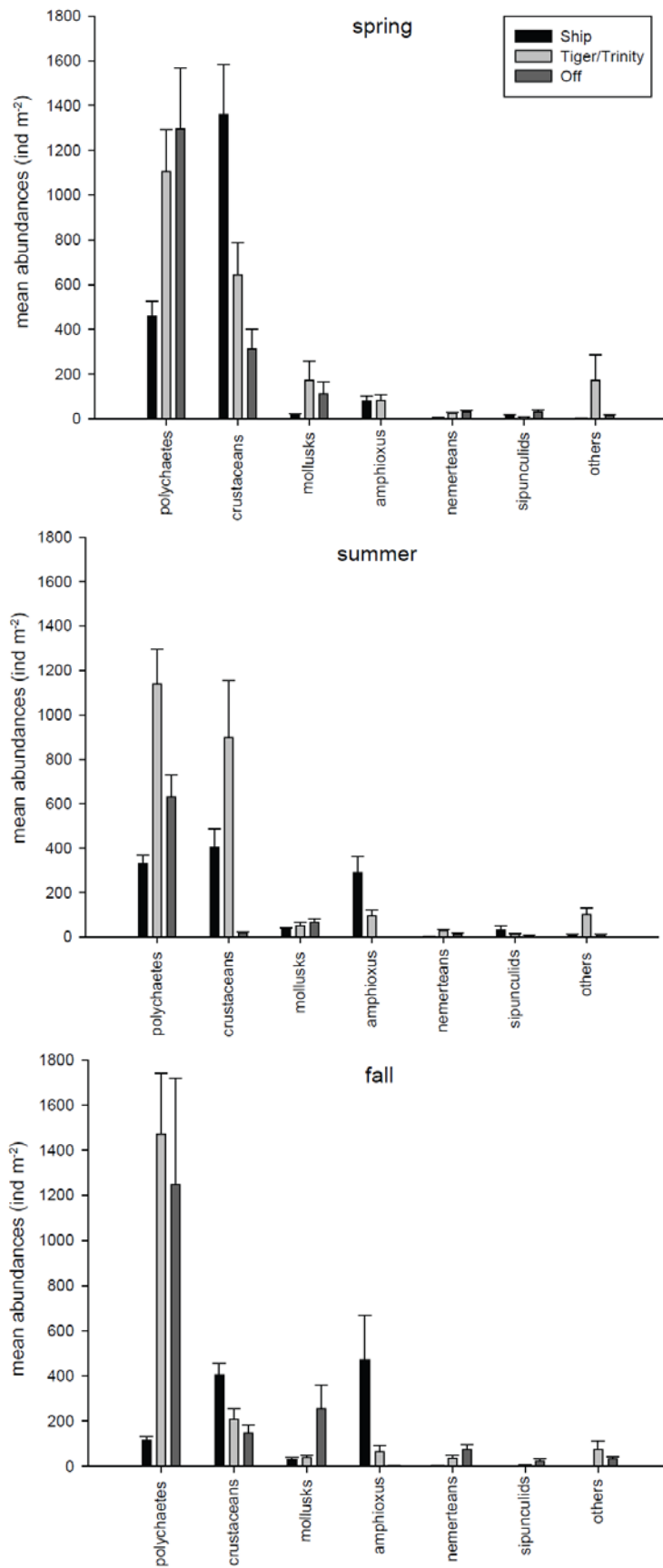
We collected a total of 22,170 individuals comprising 254 species (Appendix B) from Ship (111), TTS (170), and Off (201) during three cruises in 2007. Percentages of species that were shared by all three areas during spring, summer, and fall was 23, 18 and 16% respectively. Crustaceans dominated Ship with a mean of 814 ind m<sup>-2</sup> over the year. Ninety-seven percent of these were amphipods. Ship crustacean abundance was greatest in spring ( $\bar{x}$  = 1361 ind m<sup>-2</sup>) and decreased in summer and fall ( $\bar{x}$  = 403 and 404 ind m<sup>-2</sup>). Ship's second most abundant taxon was polychaetes ( $\bar{x}$  = 338 ind m<sup>-2</sup>). Fifty-three percent of these were spionids. Ship was also characterized by high abundances of the amphioxus *Branchiostoma floridae*, and density increased from spring to fall ( $\bar{x}$  = 79 to 472 ind m<sup>-2</sup>) when it was the most abundant species sampled on Ship (Fig. 3.2). TTS was characterized by polychaetes ( $\bar{x}$  = 1200 ind m<sup>-2</sup>) whose numbers increased each season from spring to fall ( $\bar{x}$  = 1106 to 1472 ind m<sup>-2</sup>). Thirty one percent of these were spionids. TTS was also characterized by high numbers of crustaceans ( $\bar{x}$  = 621 ind m<sup>-2</sup>), and 87% were amphipods. TTS crustacean abundances increased from spring to summer and then decreased in the fall ( $\bar{x}$  = 642, 897, and 209 ind m<sup>-2</sup>). TTS also had moderate numbers of amphioxus that remained steady over all seasons ( $\bar{x}$  = 82 ind m<sup>-2</sup>), as well as the highest abundances of taxa designated as others ( $\bar{x}$  = 164 ind m<sup>-2</sup>) composed mostly of ophurids, anemones, nemerteans, and sipunculids (Fig. 3.2). Off had a high interseasonal variation where all taxonomic groups decreased during summer, then subsequently increased in fall (Fig. 3.2).

Off was characterized by polychaetes during spring, summer, and fall ( $\bar{x} = 1297, 629, \text{ and } 1247$  ind  $\text{m}^{-2}$ , respectively), and 39% were spionids. Off had comparatively lower abundances of crustaceans ( $\bar{x} = 312, 18, \text{ and } 146$  ind  $\text{m}^{-2}$ , spring, summer, and fall, respectively). Fifty-one percent were cumaceans and 25 percent were amphipods.

Sixty-eight of the 121 polychaetes species sampled during 2007 were not previously reported by Uebelacker and Johnson (1984) as being distributed within the Louisiana continental shelf. Of the polychaete species we sampled from our study area, 107 had been found on the Florida shelf and 77 on the Texas shelf.



Figure.3.2. Seasonal and spatial variations in abundances (individuals m<sup>-2</sup>; mean  $\pm$  SE) of main taxonomic groups.



## Comparisons of STTSC Community Assemblages

Two-factor ANOSIM revealed significant effects of area and season on species similarities among stations. The MDS plot of macrofaunal species composition and abundances across all seasons (Fig. 3.3a) illustrates a significant area effect (global  $R = 0.691$ ; pairwise  $R = 0.804, 0.711, \text{ and } 0.556$  for Ship vs. Off, TTS vs. Off, and Ship vs. TTS, respectively). In general the shoals, both Ship and TTS, grouped separately from Off. Ship and Off separation was the most distinct, while TTS occupied an intermediate position with some overlap of both Ship and Off samples. The overlap between Ship and TTS occurred primarily with stations 9 and 14. Examination of environmental data showed that these stations were the shallowest and sandiest on TTS. Overlap between TTS and Off was due primarily to the station 23, which as noted, was the sandiest station sampled and was initially classified as Off. Seasonal effects across all areas were also significant (global  $R = 0.310$ ; pairwise  $R = 0.324, 0.402, 0.206$  for spring vs. summer, spring vs. fall, and summer vs. fall, respectively).

Seasonal one-factor ANOSIMs revealed significant area effects. Ordination of macroinfaunal species composition and abundances (Fig. 3.3b-d) revealed a general pattern of temporally increasing separation (global  $R = 0.664, 0.675, 0.857$  for spring, summer, and fall, respectively). Overlap in the spring MDS plot between Ship and TTS was again primarily due to sandy sites on TTS, stations 14 and 9, while the overlap between TTS and Off was due to the sandy Off station 23 (Fig. 3b). Pairwise area comparisons for spring -- Ship vs. Off, TTS vs. Off, and Ship vs. TTS -- were all significant ( $R = 0.897, 0.677, \text{ and } 0.403$ , respectively; Table 3.1a-c). The summer MDS (Fig. 3.3c) shows no overlap between Ship and TTS stations, while Off station 23 again grouped close to TTS. However, Ship exhibited a greater spread in summer than spring and a slight overlap with Off due to Ship station 3 which was characterized as the muddiest on Ship. As in the spring, pairwise area comparisons for summer were all significant

( $R = 0.659, 0.788, 0.651$ , respectively; Table 3.1a-c). By fall, the MDS showed Ship and TTS were each tightly grouped and completely separated (Fig. 3.3d). In contrast the fall spread of Off was comparatively greater with sandy Off station 23 again grouping close to TTS. The spring and summer trend for pairwise comparisons continued for fall, as all fall pairwise comparisons were significant ( $R = 0.981, 0.567$ , and  $1.0$ , respectively; Table 3.1a-c).

### Species Contributing to Area Differences

Seasonal SIMPER results suggest that a few abundant and ubiquitous species contributed the most to dissimilarities between areas. In spring, the amphipod *Acanthohaustorius* sp. A and polychaete *Mediomastus californiensis* accounted for the most dissimilarity between Ship and TTS while the polychaete *Chone americana* became the most important contributor in summer and fall (Table 3.1a).

Species contributing most to dissimilarity between Ship and Off in the spring were *Acanthohaustorius* sp. A, and the polychaetes *Spiophanes bombyx*, *Magelona* sp. H, and *Paraprionospio pinnata*. Summer and fall dissimilarities were due to the same species except *S. bombyx*, which was replaced by *B. floridae* (Table 3.1b).

Species contributing most to dissimilarity between TTS and Off in the spring included many polychaetes such as *S. bombyx*, *M. californiensis*, and *P. pinnata*. *B. floridae* contributed more to dissimilarity in summer in addition to *C. americana* which remained the top contributor through fall (Table 3.1c).

Figure 3.3. Temporal variation in multi-dimensional scaling ordination diagrams of species assemblages for Ship Shoal (triangle), Tiger/Trinity Shoal (x), Off Shoal (square) for a) spring, b) summer, c) fall, and d) all seasons.

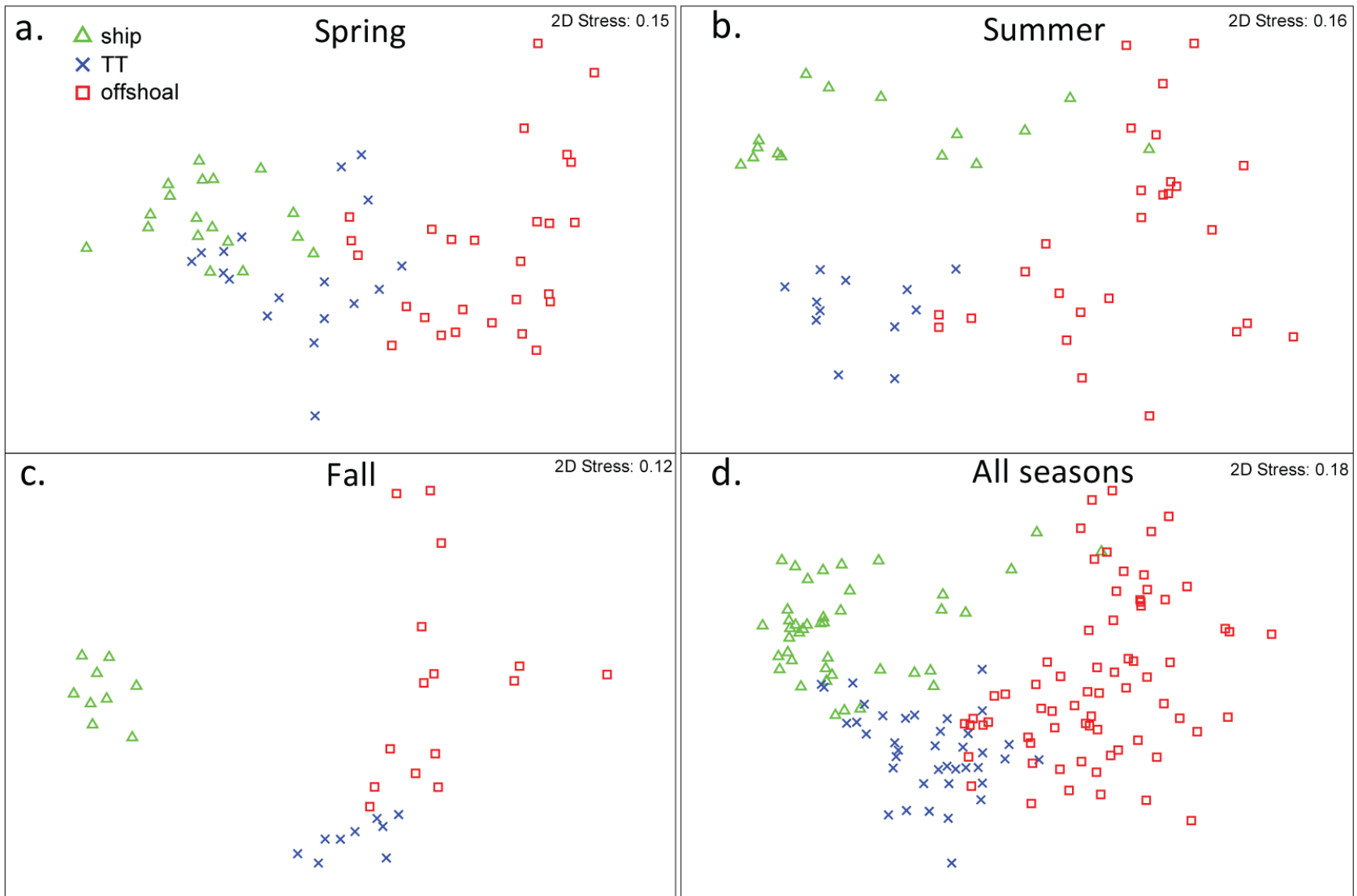


Table 3.1a ANOSIM and SIMPER results comparing species composition between a) Ship Shoal and Tiger/Trinity Shoal, b) Ship Shoal and Off shoal, and c) Tiger/Trinity Shoal and Off shoal by season.

Spring					
<i>R</i> statistic	0.403	Individual species	Dissimilarity (%)	Ship similarity (%)	Tiger/Trinity similarity (%)
<i>P</i> value	0.001				
Dissimilarity (%)	68.47	<i>Acanthohaustorius</i> sp. A	7.07	29.05	4.54
Ship Similarity (%)	46.26	<i>Mediomastus californiensis</i>	5.04	4.2	16.44
Tiger/Trinity Similarity (%)	37.03	<i>Protohaustorius bousfieldi</i>	4.5	5.17	3.21
		<i>Branchiostoma floridae</i>	3.6	8.47	4.24
		<i>Mulinia lateralis</i>	3.2	0.08	3.42
		<i>Magelona</i> sp.A	3.06	10.16	5.7
		<i>Spiophanes bombyx</i>	3.03	15.34	17.24
		<i>Magelona</i> sp.H	2.76	0.37	3.79
Summer					
<i>R</i> statistic	0.651	Individual species	Dissimilarity (%)	Ship similarity (%)	Tiger/Trinity similarity (%)
<i>P</i> value	0.001				
Dissimilarity (%)	77.71	<i>Chone americana</i>	6.58	-	12.51
Ship Similarity (%)	38.34	<i>Acanthohaustorius</i> sp. A	5.40	28.52	1.43
Tiger/Trinity Similarity (%)	44.93	<i>Metharpinia floridana</i>	3.58	-	5.01
		<i>Protohaustorius bousfieldi</i>	3.57	2.20	2.31
		<i>Spiophanes bombyx</i>	3.56	-	5.17
		<i>Mediomastus californiensis</i>	3.50	1.77	6.41
		<i>Branchiostoma floridae</i>	3.28	24.76	7.83
		<i>Magelona</i> sp.H	3.05	5.80	3.71
Fall					
<i>R</i> statistic	1.0	Individual species	Dissimilarity (%)	Ship similarity (%)	Tiger/Trinity similarity (%)
<i>P</i> value	0.001				
Dissimilarity (%)	86.42	<i>Chone americana</i>	7.95	-	17.88
Ship Similarity (%)	52.46	<i>Acanthohaustorius</i> sp. A	7.03	37.74	-
Tiger/Trinity Similarity (%)	48.28	<i>Metharpinia floridana</i>	3.58	-	2.22
		<i>Branchiostoma floridae</i>	4.72	27.0	2.16
		<i>Mediomastus californiensis</i>	3.75	2.86	8.94
		<i>Notomastus latericeus</i>	3.13	-	6.18
		<i>Magelona</i> sp.H	2.95	-	3.91
		<i>Paramphinome</i> sp.B	2.85	-	4.88

(Table 3.1 cont.)

Table 3.1b

<i>R</i> statistic	0.897	Individual species	Dissimilarity (%)	Ship similarity (%)	Off similarity (%)
<i>P</i> value	0.001				
Dissimilarity (%)	89.3	<i>Acanthohaustorius</i> sp. A	8.79	29.05	-
Ship Similarity (%)	46.26	<i>Spiophanes bombyx</i>	4.46	15.34	1.1
Off Similarity (%)	32.6	<i>Paraprionospio pinnata</i>	4.37	-	15.3
		<i>Magelona</i> sp.H	3.88	0.37	16.47
		<i>Protohaustorius bousfieldi</i>	3.49	5.17	-
		<i>Magelona</i> sp.A	3.45	10.16	-
		<i>Branchiostoma floridae</i>	3.45	8.47	-
Summer					
<i>R</i> statistic	0.659	Individual species	Dissimilarity (%)	Ship similarity (%)	Off similarity (%)
<i>P</i> value	0.001				
Dissimilarity (%)	86.52	<i>Acanthohaustorius</i> sp. A	9.98	28.52	-
Ship Similarity (%)	38.34	<i>Branchiostoma floridae</i>	9.30	24.76	-
Off Similarity (%)	31.94	<i>Paraprionospio pinnata</i>	6.89	3.02	34.17
		<i>Magelona</i> sp.H	5.86	5.80	36.01
Fall					
<i>R</i> statistic	0.981	Individual species	Dissimilarity (%)	Ship similarity (%)	Off similarity (%)
<i>P</i> value	0.001				
Dissimilarity (%)	94.1	<i>Acanthohaustorius</i> sp. A	7.46	37.74	-
Ship Similarity (%)	52.46	<i>Branchiostoma floridae</i>	6.86	27.0	-
Off Similarity (%)	32.67	<i>Paraprionospio pinnata</i>	5.42	-	18.12
		<i>Magelona</i> sp.H	3.83	-	8.39
		<i>Mediomastus californiensis</i>	3.05	2.86	5.76
		<i>Protohaustorius bousfieldi</i>	2.83	5.79	-
		<i>Oxyurostylis smithi</i>	2.83	-	6.0

(Table 3.1 cont.)



Table 3.1c

<i>R</i> statistic	0.677	Individual species	Dissimilarity (%)	Tiger/Trinity similarity (%)	Off similarity (%)
<i>P</i> value	0.001				
Dissimilarity (%)	82.06	<i>Spiophanes bombyx</i>	4.81	17.24	1.1
Tiger/Trinity Similarity (%)	37.03	<i>Mediomastus californiensis</i>	3.82	16.44	8.13
Off Similarity (%)	32.6	<i>Paraprionospio pinnata</i>	3.68	0.61	15.3
		<i>Acanthohaustorius</i> sp. A	3.35	4.54	-
		<i>Ampharete</i> sp. A	3.17	-	8.32
		<i>Magelona</i> sp. A	2.95	5.7	-
		<i>Magelona</i> sp. H	2.89	3.79	16.47
		<i>Mulinia lateralis</i>	2.78	4.42	0.49
		<i>Branchiostoma floridae</i>	2.64	4.24	-
		<i>Oxyurostylis smithi</i>	2.57	3.38	5.08
Summer					
<i>R</i> statistic	0.788	Individual species	Dissimilarity (%)	Tiger/Trinity similarity (%)	Off similarity (%)
<i>P</i> value	0.001				
Dissimilarity (%)	87.44	<i>Chone americana</i>	6.32	12.51	-
Tiger/Trinity Similarity (%)	44.93	<i>Paraprionospio pinnata</i>	4.63	0.62	34.17
Off Similarity (%)	31.94	<i>Branchiostoma floridae</i>	4.06	7.83	-
		<i>Mediomastus californiensis</i>	3.74	6.41	1.76
		<i>Spiophanes bombyx</i>	3.47	5.17	-
		<i>Metharpinia floridana</i>	3.46	5.01	-
		<i>Magelona</i> sp. H	3.11	3.71	36.01
		<i>Prionospio pygmaea</i>	2.96	4.92	-
Fall					
<i>R</i> statistic	0.567	Individual species	Dissimilarity (%)	Tiger/Trinity similarity (%)	Off similarity (%)
<i>P</i> value	0.001				
Dissimilarity (%)	77.81	<i>Chone americana</i>	5.77	17.88	1.06
Tiger/Trinity Similarity (%)	48.28	<i>Paraprionospio pinnata</i>	3.97	0.3	18.12
Off Similarity (%)	32.67	<i>Mediomastus californiensis</i>	3.14	8.94	5.76
		<i>Magelona</i> sp. H	2.77	3.91	8.39
		<i>Onuphis eremite oculata</i>	2.37	4.57	0.5
		<i>Ampelisca</i> sp. C	2.35	4.25	-
		<i>Paramphinoe</i> sp. B	2.3	4.88	0.15
		<i>Notomastus latericeus</i>	2.23	6.18	0.88

Seasonal K-dominance curves (Fig. 3.4a-c) suggest that all areas were dominated by a few high-abundance species, especially Ship in spring and fall. On Ship, the two most abundant species (composed of *Acanthohaustorius* sp. A, *Protohaustorius bousfieldi*, or *B. floridae*) comprised greater than 50% of the total individuals each season. The shape of the Ship K-dominance curve fluctuated from spring, to summer, to fall, mirroring the shift in numerical dominance from the amphipods *Acanthohaustorius* sp. A and *Protohaustorius bousfieldi*, to the amphioxus *B. floridae*. These species constituted the largest proportion of the dominant feeding guilds of suspension feeders and surface deposit feeders, for Ship (Table 3.2). In addition, several species that contributed to area similarity were found frequently but in lower concentrations. Examples were *S. bombyx* in spring; and *P. bousfieldi*, the mole crab *Albunea paretii*, and polychaetes *Magelona* spp. A and H, *Nereis micromma*, and *Nephtys simoni* during summer and fall.

The shape and position of the TTS K-dominance curve (Fig. 3.4a-c) indicates that there was a more equitable distribution of species abundances on TTS than on Ship. Several species on TTS such as *M. californiensis* and *B. floridae* were both abundant and ubiquitous each season while others increased in abundance and similarity percent each season such as *Owenia fusiformis*, and particularly *C. americana*, which was the species that characterized TTS beginning in summer. Other species decreased in abundance and similarity percentage spring to fall such as *Acanthohaustorius* sp. A, *P. bousfieldi*, *S. bombyx*, and particularly *M. lateralis*, which dropped from the fifth most abundant species in spring to zero abundance in subsequent seasons. There were also species such as the anemone *Parianthus raptiformis* that were found in patchy distributions making them numerically important without a large contribution to the area similarity percentage. The pattern that emerged for TTS when comparing the K-dominance curve

with Table 3.2, was the suggestion of a temporal shift in feeding guilds from a mix (suspension, surface deposit, sub-surface deposit feeders, and carnivores in spring), to suspension feeders (most notably *C. americana*) in summer, and back to spring-like mix in the fall.

Off was characterized by species that dominated in spring and then decreased substantially during the summer, such as the crustacean *Oxyurostylis smithi* and polychaete *Diopatra cuprea*, or completely disappeared such as the polychaete *Ampharete* sp. A (Fig. 3.4a-c, Table 3.2). Otherwise Off was numerically dominated by two species of polychaetes (*P. pinnata*, *Magelona* sp. H) that were found consistently in high numbers within the offshoal, and a species more ubiquitously distributed within the STTSC (*Mediomastus californiensis*). The most abundant species for Off were members of an unchanging mix of feeding guilds with a predominance of surface deposit, sub-surface deposit, and suspension feeders on all three sampling seasons.

#### Environmental Relationships

The BEST procedure found percent sand to be the most highly correlated (Spearman correlation = 0.606) single environmental variable with macrofaunal assemblages. The next best single variable was phaeopigment (Spearman correlation = 0.578, Table 3.3). The BEST procedure found that the combination of the four most highly ranked individual environmental variables (depth, percent sand, particle size, and phaeopigment produced the highest correlation (Spearman correlation = 0.669) for a four variable model.

Preliminary regression analysis between water depth versus the three other variables chosen by BEST were as follows: negative relationships with sand on Ship, TTS, and Off ( $P = 0.09$ ,  $0.11$ , and  $0.03$ ); negative relationships with particle size on TTS and Off ( $P = 0.1$  and  $0.12$ ),

but a positive relationship on Ship ( $P = 0.11$ ); and positive relationships with phaeopigment on Ship, TTS, and Off, though with a generally low significance ( $P = 0.45, 0.19$ , and  $0.65$ ).

Table 3.2 First four dominant species from K-dominance curves (Fig. 3.3. a-c) and feeding type (1-suspension, 2-surface deposit, 3-sub-surface deposit, 4-carnivore) for each area and season.

Spring	Type	Summer	Type	Fall	Type
Ship Shoal					
<i>Acanthohaustorius</i> sp. A	1,2	<i>Acanthohaustorius</i> sp. A	1,2	<i>Brachiostoma floridae</i>	1
<i>Protohaustorius bousfieldi</i>	1,2	<i>Brachiostoma floridae</i>	1	<i>Acanthohaustorius</i> sp. A	1,2
<i>Spiophanes bombyx</i>	1,2	<i>Protohaustorius bousfieldi</i>	1,2	<i>Protohaustorius bousfieldi</i>	1,2
<i>Brachiostoma floridae</i>	1	<i>Magelona</i> sp. H	2,3	<i>Magelona</i> sp. H	2,3
Tiger/Trinity Shoal					
<i>Mediomastus californiensis</i>	2,3	<i>Chone americana</i>	1	<i>Chone americana</i>	1
<i>Acanthohaustorius</i> sp. A	1,2	<i>Protohaustorius bousfieldi</i>	1,2	<i>Mediomastus californiensis</i>	2,3
<i>Spiophanes bombyx</i>	1,2	<i>Acanthohaustorius</i> sp. A	1,2	<i>Owenia fusiformis</i>	1,2
<i>Paranthus raptiformis</i>	4	<i>Metharpinia floridana</i>	1	<i>Magelona</i> sp. H	2,3
Off shoal					
<i>Ampharete</i> sp. A	2	<i>Paraprionospio pinnata</i>	1,2	<i>Mediomastus californiensis</i>	2,3
<i>Oxyurostylis smithi</i>	1,2	<i>Magelona</i> sp. H	2,3	<i>Paraprionospio pinnata</i>	1,2
<i>Diopatra cuprea</i>	4	<i>Mediomastus californiensis</i>	2,3	<i>Magelona</i> sp. H	2,3
<i>Magelona</i> sp. H	2,3	<i>Nereis micromma</i>	4	<i>Nuculana concentrica</i>	2

The model testing the effect of depth and month on bottom-water DO was significant (ANCOVA,  $P < 0.001$ ,  $R^2 = 0.77$ ) with a significant interaction of month and depth (Fig. 3.5). Negative linear trends (where slopes and intercepts vary by month) existed between DO and water depth for the three months studied. The steepest slope (which accounts for most of the significance of the overall model) occurred in August ( $-0.35 \text{ mg l}^{-1} / \text{m}$ ), followed by April ( $-0.15 \text{ mg l}^{-1} / \text{m}$ ). The shallow October slope ( $-0.01 \text{ mg l}^{-1} / \text{m}$ ) would not be significant in a single regression approach. The results suggest that hypoxic conditions were becoming established in April, reached a peak by at least August, and were largely dissipated by October.

Figure.3.4. K-dominance plots of ranked species abundances for Ship Shoal (triangle), Tiger/Trinity Shoal (x), Off Shoal (square) for a) spring, b) summer, and c) fall.

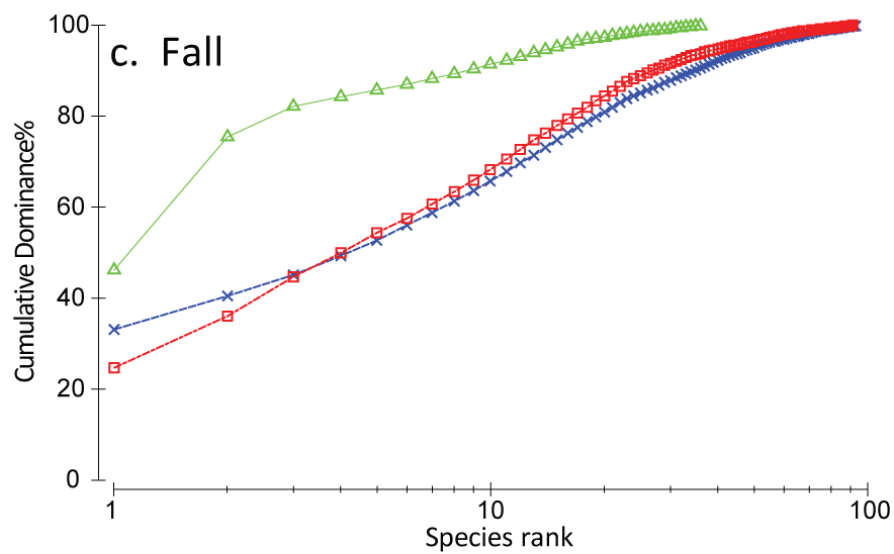
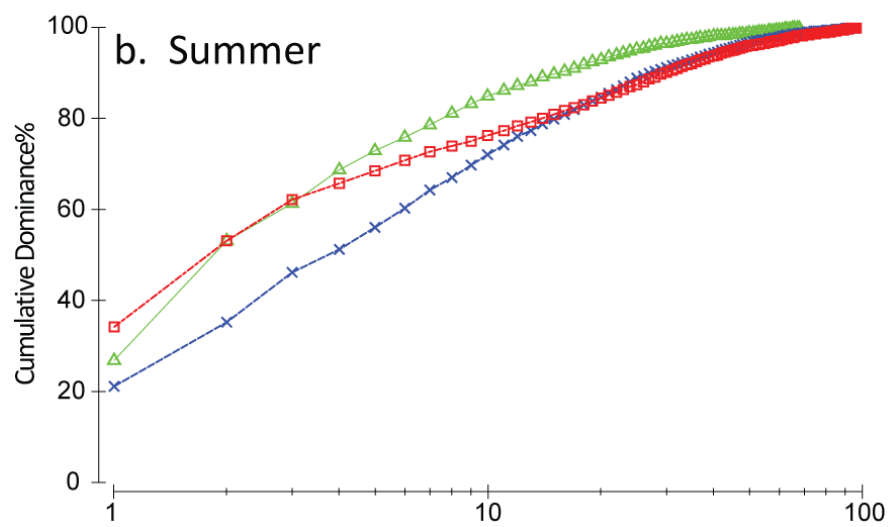
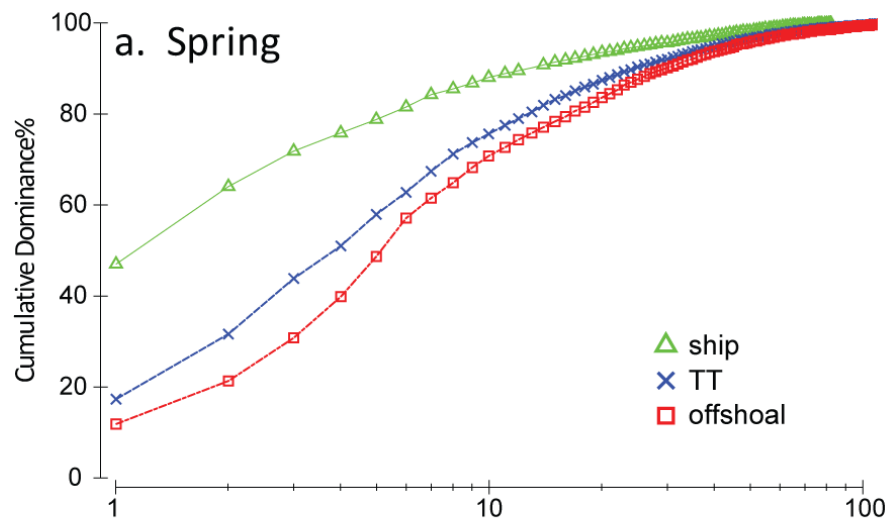


Table 3.3 Results of BEST analysis for correlation of environmental factors with species assemblages, as well as mean, minimum, and maximum of each geographical grouping for the four most highly correlated variables

Correlation	Variables			
0.606	sand (%)			
0.578	phaeopigment (mg m <sup>-2</sup> )			
0.554	particle size(μm)			
0.364	depth (m)			
0.233	Salinity			
0.206	dissolved oxygen (mg l <sup>-1</sup> )			
0.175	C/N ratio			
0.124	chlorophyll a (mg m <sup>-2</sup> )			
0.11	temperature (°C)			
-0.065	gravel (%)			
0.643	sand (%), particle size (μm)			
0.662	sand (%), particle size (μm), phaeopigment (mg m <sup>-2</sup> )			
0.669	depth (m), sand (%), particle size (μm), phaeopigment (mg m <sup>-2</sup> )			

	Depth	Sand	Particle size	Phaeopigment
Ship Shoal				
mean	5.7	97.6	165.2	11.8
min	3.3	90.4	132.9	5.2
max	8.9	99.7	283.9	28.5
Tiger/Trinity Shoal				
mean	4.7	90.3	116.4	13.6
min	2.8	76.7	88.6	5.23
max	6.0	97.0	142.1	22.7
Off Shoal				
mean	10.1	47.0	77.4	39.2
min	2.9	7.1	57.9	12.9
max	19.2	93.1	122.4	93.7

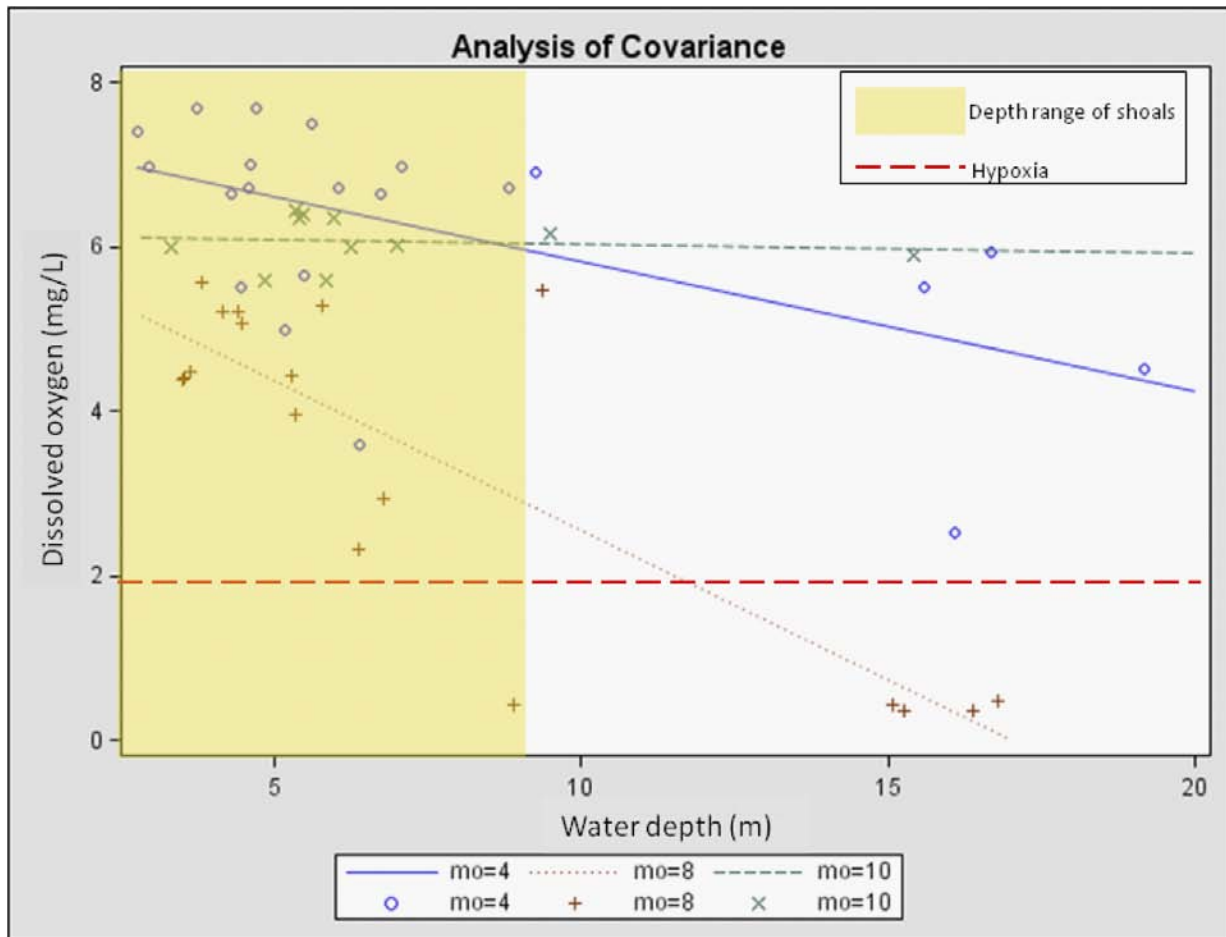


Figure. 3.5. Results of ANCOVA comparing dissolved oxygen (DO) and depth (m) with month as a class variable where April = o, August = +, and October = x.

The effects of area and month on bottom water DO were significant ( $F_{2,132} = 10.6$ ,  $P < 0.001$  and  $F_{2,132} = 39.7$ ,  $P < 0.001$ , respectively). Means and standard deviations for Ship, TTS, and Off were  $5.4 \pm 1.9$ ,  $6 \pm 1.1$ , and  $4.5 \pm 2.3$ . Seasonal means and standard deviations for April, August, and October were  $6.2 \pm 1.3$ ,  $3.4 \pm 2.0$ ,  $6.1 \pm 0.3$ . There was also a significant interaction between area and month ( $F_{2,132} = 2.8$ ,  $P < 0.03$ ) post hoc comparisons found TTS significantly greater than Off in summer. During summer sampling four Off stations (17, 19, 20, 21) and the deepest Ship station (6) were hypoxic.



## Shoal's Contributions to Regional Biodiversity

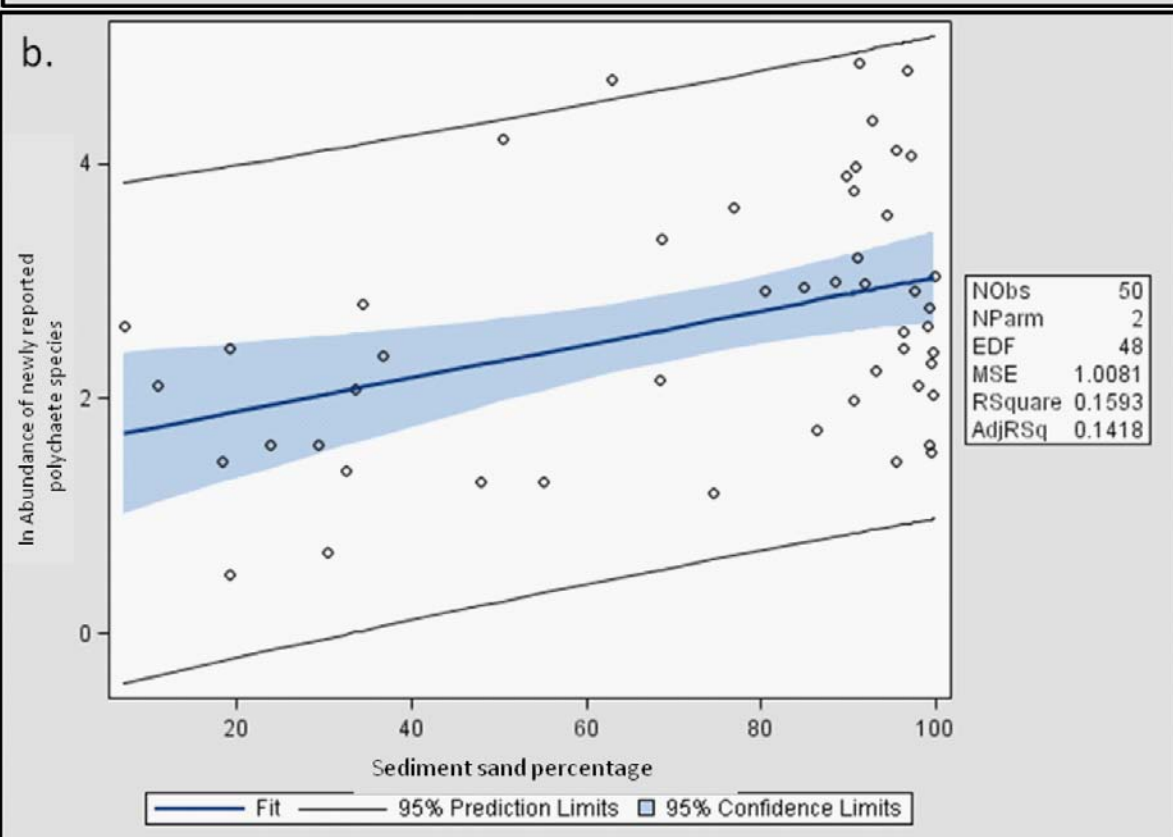
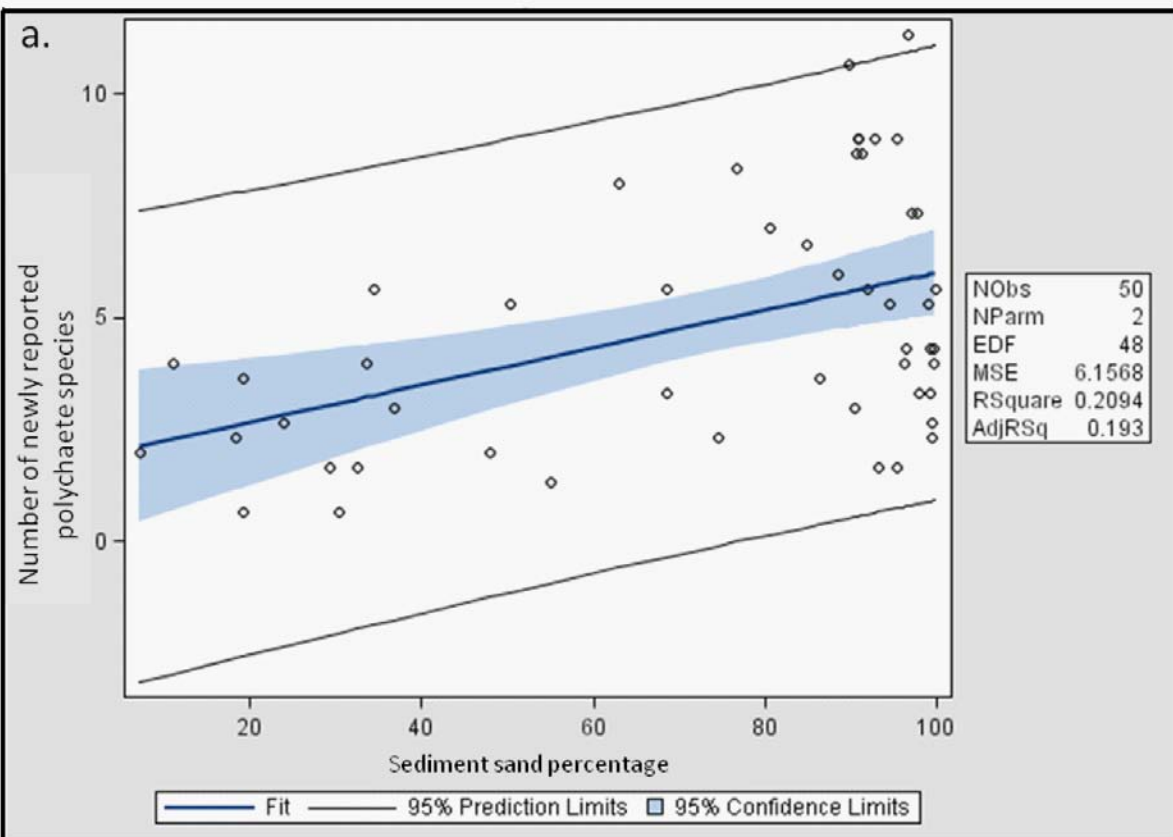
Seventy-nine species were found only in sediment with a sand composition of  $\geq 70\%$  representing 31% of all the species found during our study. In contrast, 24 species were found only in sediment with a mud composition of  $\geq 50\%$  representing 9% of all sampled species. Appendix B illustrates the important role sand plays particularly for certain species which are found primarily in the very high (70-100%) sand percentage interval range (e.g., *Branchiostoma floridae*, *Acanthohaustorius* sp.A, *Protohaustorius bousfieldi*, *Metatiron triocellatus*, *Metatiron tropakis*, *Ampelisca* sp. A, *Eudevenopus honduranus*, *Metharpinia floridana*, *Pagurus* sp., *Paranthus raptiformis*, *Magelona* sp A, *Leitoscoloplos fragilis*.

We found significant correlations between the percent sand and newly reported polychaetes from the Louisiana continental shelf for both species richness ( $P < 0.001$ ,  $R^2 = 0.21$ ) and total abundance ( $P < 0.01$ ,  $R^2 = 0.16$ , Fig. 3.6a,b). Significant correlations with sand percentage were not found for previously reported polychaete species richness or abundance, and total polychaete species richness or abundance, because increasing trends were not found at stations with a very high percent sand.

## Area and Seasonal Variation in Biological Parameters and Indices

Species abundance of total benthic invertebrates (Fig. 3.7a) showed a significant area ( $F_{2,132} = 8.68$ ,  $P < 0.001$ ) and month ( $F_{2,132} = 4.95$ ,  $P = 0.01$ ) effect with significant interaction ( $F_{4,132} = 3.14$ ,  $P < 0.02$ ). The main effects showed that benthic invertebrates were more abundant in spring than summer, and TTS significantly greater than Ship and Off. Post-hoc comparisons showed TTS was greater than Off in summer (Table 3.4).

Figure. 3.6 Regressions comparing the relationships between sand percentage and both a) species richness of newly reported polychaete species, and b)  $\ln(\text{abundance} + 1)$  of newly reported polychaete species.



Species richness (Fig. 3.7b) showed a significant area ( $F_{2,132} = 33.80$ ,  $P < 0.001$ ) and month ( $F_{2,132} = 5.51$ ,  $P < 0.001$ ) effect with significant interaction ( $F_{4,132} = 4.132$ ,  $P < 0.001$ ). The main effects showed spring significantly greater than summer and TTS significantly greater than Off, which was significantly greater than Ship. Post-hoc comparisons showed that TTS species richness was significantly greater than both Ship and Off in summer, while TTS and Off were significantly greater than Ship in fall (Table 3.4).

Taxonomic distinctiveness (Fig. 3.7c) showed a significant area effect ( $F_{2,132} = 18.92$ ,  $P < 0.001$ ) as well as area x month interaction ( $F_{2,132} = 7.15$ ,  $P < 0.001$ ). The main effect showed Ship and TTS significantly greater than Off. Post-hoc comparisons showed Ship and TTS significantly greater than Off in summer (Table 3.4).

Total benthic biomass (Fig. 3.7d) showed a significant main effect of area ( $F_{2,132} = 11.53$ ,  $P < 0.001$ ) with both shoals significantly greater than Off, but not a significant month or area x month interaction (Table 3.4).

N1 (Fig. 3.7e) showed a significant area ( $F_{2,132} = 24.2$ ,  $P < 0.001$ ) effect with significant interaction ( $F_{4,132} = 6.9$ ,  $P < 0.001$ ). The main effects showed TTS significantly greater than Off, which was significantly greater than Ship. Post-hoc comparisons showed Off was significantly greater than Ship in spring, while TTS was significantly greater than Ship and Off in summer, while both TTS and Off were significantly greater than Ship in fall (Table 3.4).

N2 (Fig. 3.7f) showed a significant area ( $F_{2,132} = 14.7$ ,  $P < 0.001$ ) effect with significant interaction ( $F_{4,132} = 5.6$ ,  $P < 0.001$ ). The main effects showed TTS and Off were significantly greater than Ship. Post-hoc comparisons showed Off was significantly greater than Ship in

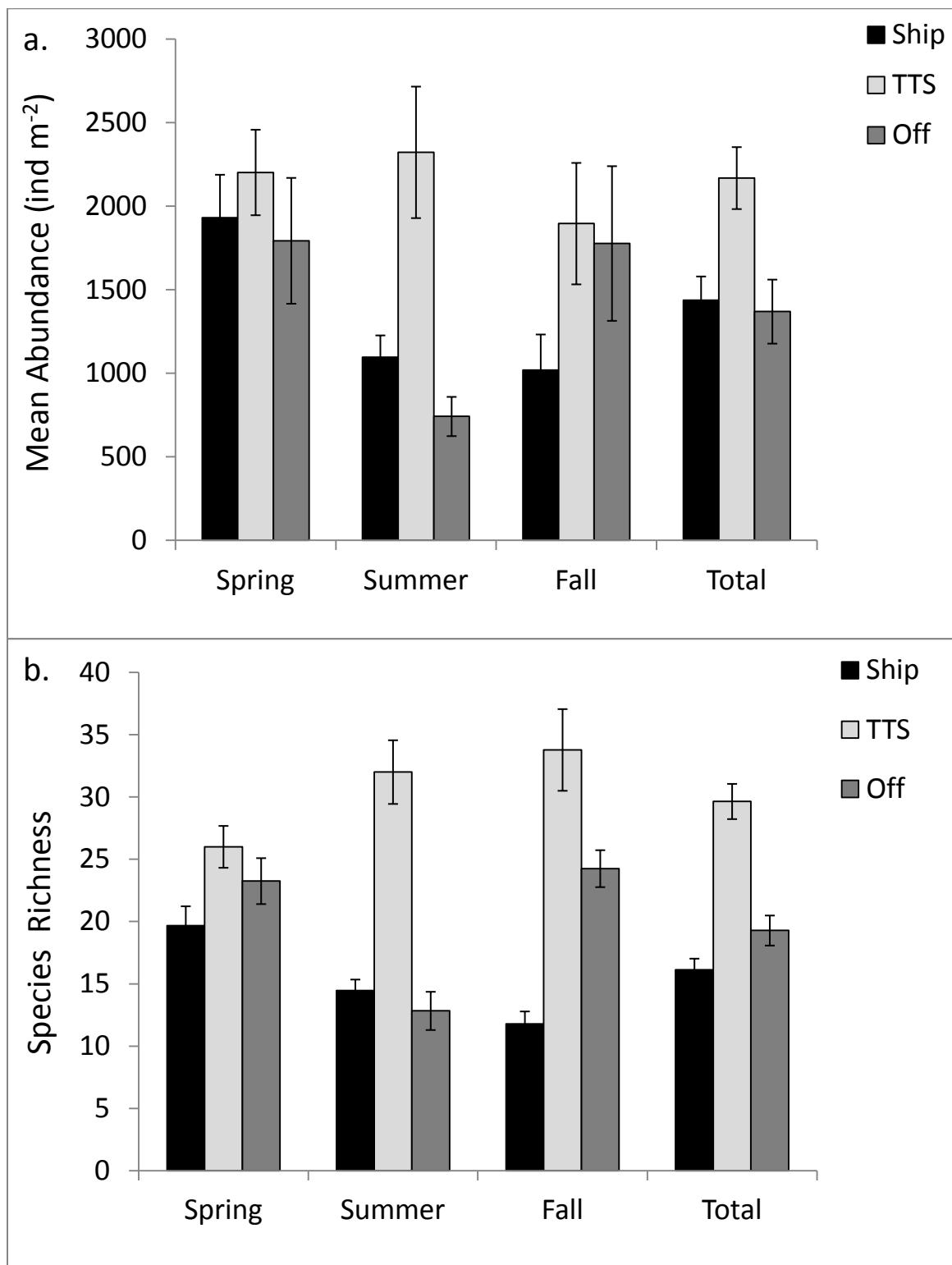
spring, while TTS was significantly greater than Off in summer, while both TTS and Off were significantly greater than Ship in fall (Table 3.4)

Rarefaction (Fig. 3.7g) showed a significant area ( $F_{2,132}=26$ ,  $P < 0.001$ ) effect with significant interaction ( $F_{4,132} = 8.2$ ,  $P < 0.001$ ). The main effects showed TTS was significantly greater than Off, which was significantly greater than Ship. Post-hoc comparisons showed TTS was significantly greater than Ship and Off in summer, while TTS and Off were significantly greater than Ship in fall (Table 3.4)

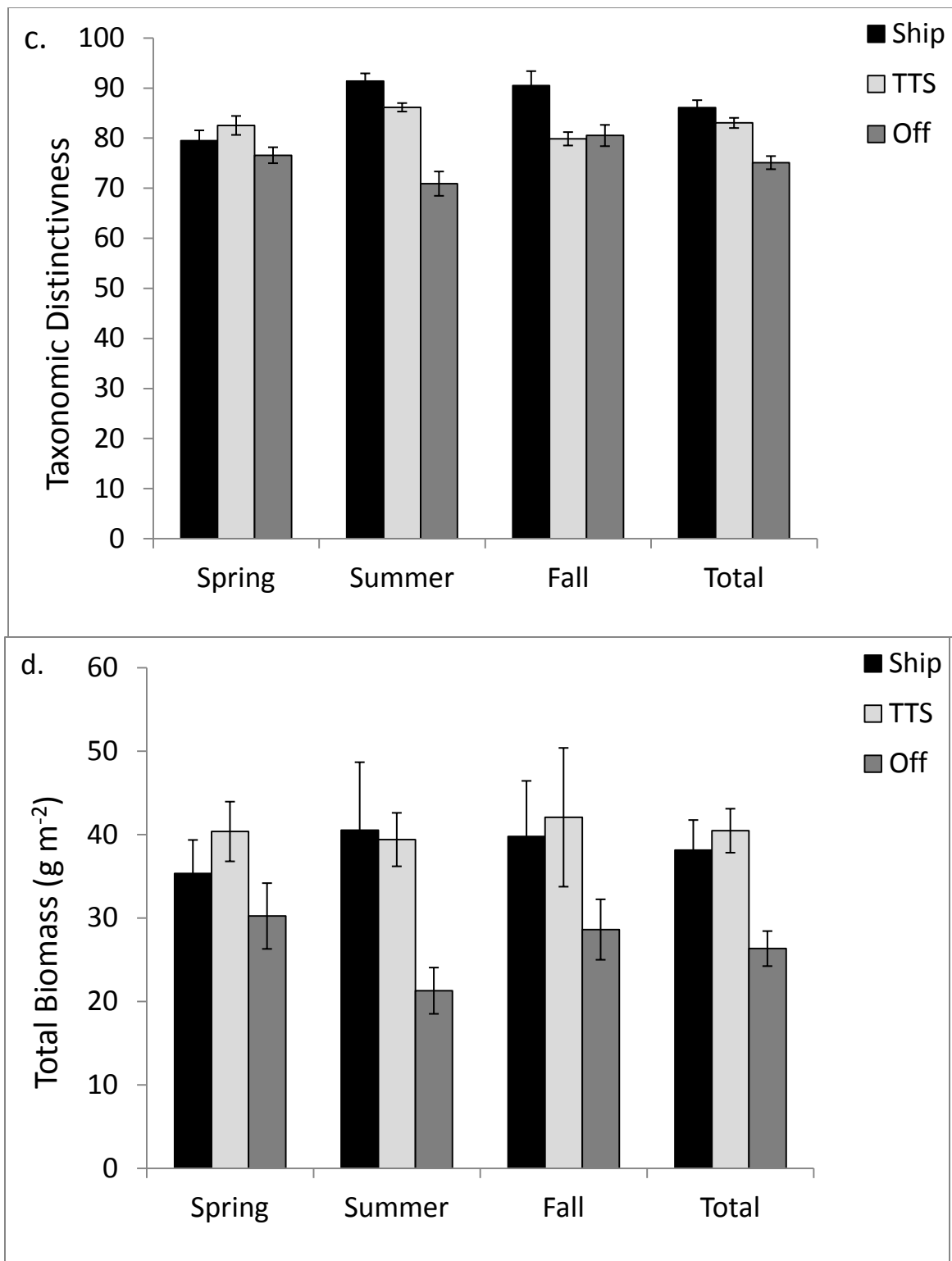
Table 3.4 Results of ANOVA for area and seasonal comparisons of diversity indices and environmental parameters.

	Area	Season	Interaction
Depth	Off > Ship, TTS	n.s.	n.s.
Salinity	n.s.	n.s.	n.s.
Dissolved oxygen	n.s.	April, Oct > Aug	n.s.
Chlorophyll a	Ship > TTS	n.s.	n.s.
Phaeopigment	Off > Ship, TTS	Aug > April, Oct	n.s.
C/N	Off > Ship, TTS	n.s.	n.s.
Particle size	Ship > TTS > Off	n.s.	n.s.
% Gravel	n.s.	n.s.	n.s.
% Mud	Off > TTS > Ship	n.s.	n.s.
% Sand	Ship, TTS > Off	n.s.	n.s.
S	TTS > Off > Ship	April > Aug	Summer: TTS > Ship, Off; Fall: TTS > Ship, Off
N	TTS > Ship, Off	April > Aug	Summer: TTS > Off
N1	TTS > Off > Ship	n.s.	Spring: Off > Ship; Summer: TTS > Off > Ship; Fall: TTS, Off > Ship
N2	TTS, Off > Ship	n.s.	Spring: Off > Ship; Summer: TTS > Off; Fall: TTS, Off > Ship
Rarefaction ES(50)	TTS > Off > Ship	n.s.	Summer: TTS > Ship, Off; Fall: TTS, Off > Ship
Taxonomic distinctivness	Ship, TTS > Off	n.s.	Summer: Ship, TTS > Off
Biomass total	Ship, TTS > Off	n.s.	n.s.
Biomass polychaete	TTS, Off > Ship	n.s.	n.s.
Biomass mollusk	TTS, Off > Ship	n.s.	n.s.
Biomass others	Ship, TTS > Off	n.s.	Spring: TTS > Off; Summer: Ship, TTS > Off; Fall: Ship > Off

Figure. 3.7. Comparisons of mean area values by season, and over all seasons (bars indicate SE) for a) abundance, b) species richness, c) taxonomic distinctiveness, d) total biomass, e) N1(exponentiated Shannon index), f) N2 (1/Simpsons index), and g) rarefaction.

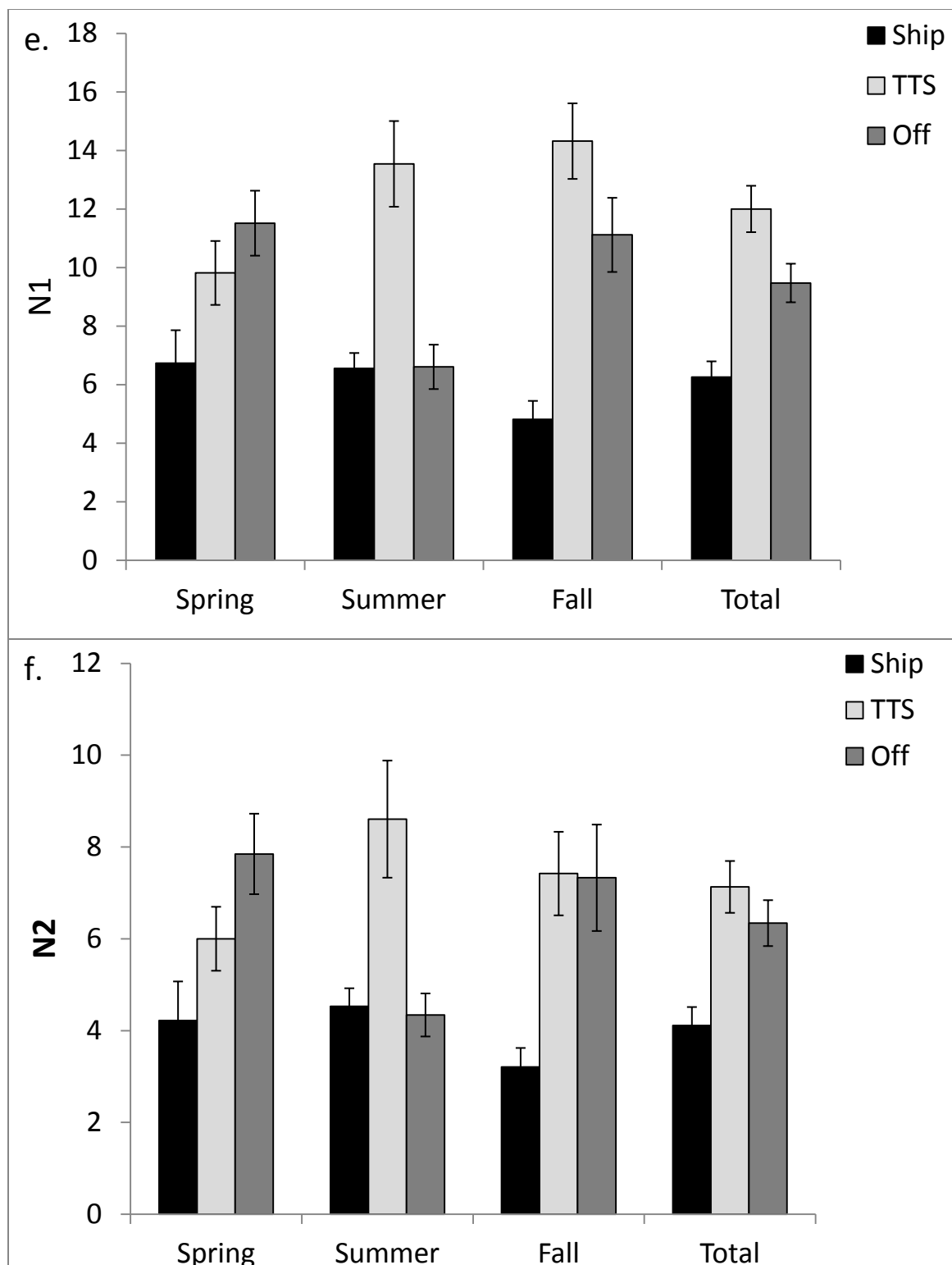


(Fig. 3.7 cont.)



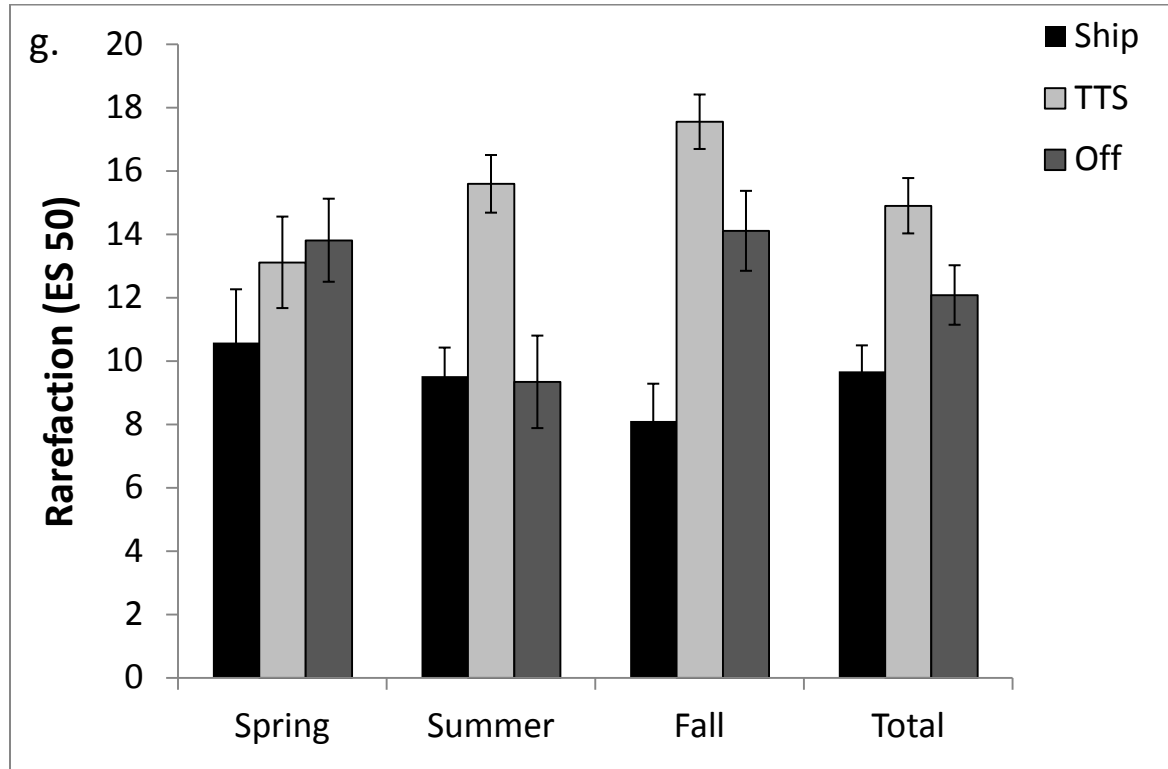
(Fig. 3.7 cont.)





(Fig. 3.7 cont.)

(Fig 3.7 cont.)



Gamma diversity decreased each season from 178, 158, 135 for spring, summer, and fall respectively (Fig. 3.8). Shoal areas Ship/TTS had the lowest beta diversity in spring (72) versus Ship/Off (99) and TTS/Off (103). This pattern held true for beta diversity in the summer Ship/TTS (77) versus Ship/Off (92) and TTS/Off (89). In the fall the pattern evened out with Ship/TTS (77), Ship/Off (77), TTS/Off (74).

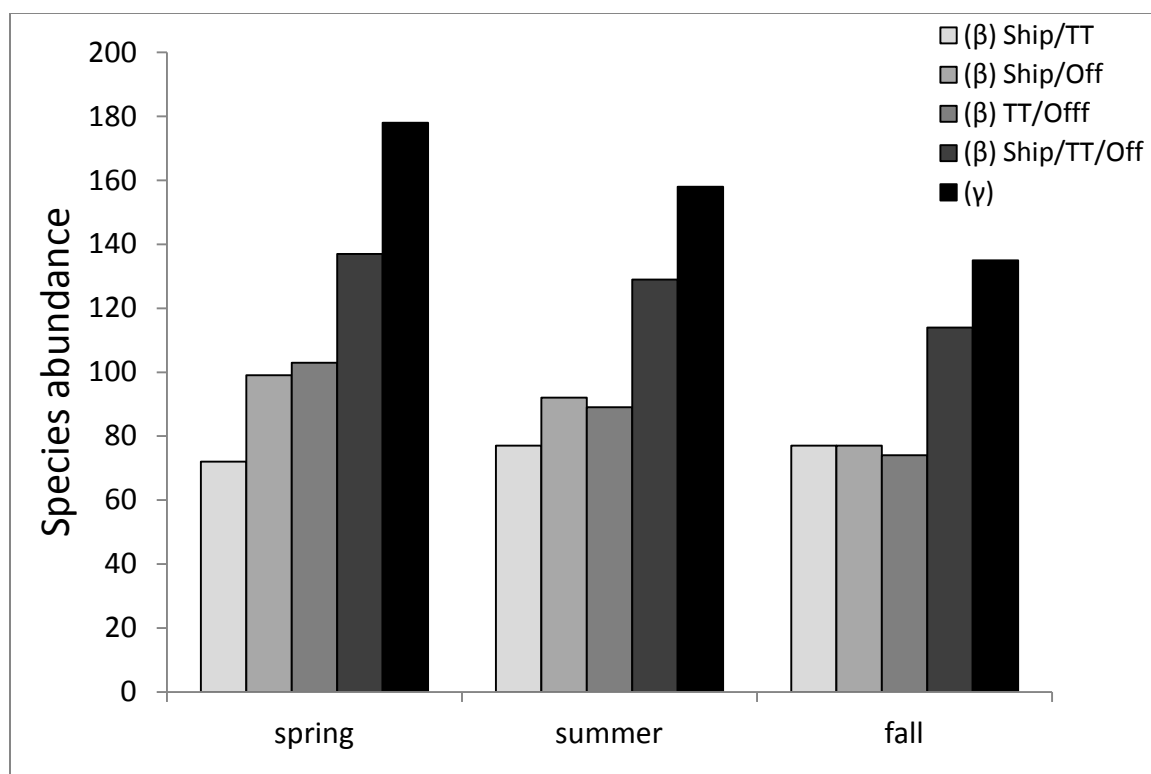


Figure. 3.8. Seasonal comparisons of gamma and beta diversity for the STTSC.

## DISCUSSION

### Factors Affecting Ship, Tiger/Trinity, and Offshoal Community Composition

The results of our study provide evidence that the STTSC is a biologically diverse area with changing and discrete benthic habitats each supporting different types of communities that contribute to the regional biodiversity of the northern Gulf of Mexico. Within the STTSC, we found that shoals support distinct communities that differ significantly, not only from the surrounding off-shoal habitat, but also from each other (Table 3.1). Sediment composition is the dominant environmental parameter determining the make-up of macrofaunal species assemblages (Table 3.3). Specifically, the macrofaunal species distributions were most heavily influenced by the sand/mud ratio of the sediment, which supports the review by Gray (1974) detailing the importance of sediment characteristics in determining macrofaunal species

assemblages and a recent investigation by Fleege et al. (2011) within the STTSC that showed sediment composition had significant effects on nematode communities in terms of nematode body shape. Our findings indicate that, in addition to sediment composition, other interrelated factors, including proximity to fluvial input, depth, disturbance, and biological interactions, also influence the character of STTSC communities. These points are elaborated below.

### Tiger/Trinity Shoals

TTS is located approximately 60 km directly southwest of the Atchafalaya River outlets. During periods of high river discharge, usually occurring during the spring, large volumes of Atchafalaya River water rich in suspended sediment and inorganic nutrients inundate the local continental shelf, and generally flow in a westerly direction (Allison et al 2000; Wiseman et al. 1997). Deposition from suspended sediment contributes fine-grained material to the benthic environment of TTS (Allison et al. 2000). TTS is a very shallow (3 to 6 m), high-relief structure compared to its immediately surrounding area. Therefore TTS is subjected to increased effects of wave action and coastal currents, and has greater capacity to winnow away fine-grain particles (Wright et al. 2002). A combination of frequent sediment input, and shallow depth-related increases in hydrologic energy at the benthic boundary layer are likely responsible for the greater range in sand percentage on TTS versus Ship (Table 3.3). These conditions are reflected in the dominant species that represent 4 different functional groups utilizing predation, interface, suspension, and surface/subsurface deposit feeding methods (Table 3.2). TTS's most abundant species have a greater range of feeding types from spring to summer (Table 3.2) than Ship or Off, which is likely a function of its more dynamic environment and greater range of sand to mud ratio. TTS did not have a core group of species that remained abundant across all seasons. Although *M. californiensis*, *Acanthohaustorius* sp. A, and *C. americana* were each among the

top four most abundant species in two of the three seasons, the most abundant species shifted each season representing a shift of the dominant feeding type from a mix of interface feeders (able to switch between suspension and surface deposit feeding), surface/subsurface deposit feeders, and carnivores in spring; to all suspension or interface feeders in summer; and to a mix of suspension, interface, and surface/subsurface deposit feeders in fall (Table 3.2). During the summer the discharge of fresh water and suspended sediment typically decreases in the STTSC (Wiseman et al. 1997, Allison et al. 2000) resulting in a greater capacity for filter and/or interface feeders to thrive due to high food availability and a lessened threat of burial or clogging of feeding structures. The increase in animals that suspension feed in summer is concurrent with an increase in summertime TTS chlorophyll a levels (Grippo et al. 2010), which is a proxy for phytoplankton concentration.

Patterns of species diversity on TTS could also be influenced by the intensity or frequency of disturbance from periodic deposition of fluvial (e.g. spring floods) or resuspended sediment (e.g. storm events). Intermediate levels of disturbance have been shown to increase diversity in many communities (Connell 1978; Sousa 1979). A community in dynamic equilibrium as defined by Huston (1979) has just enough disturbance to maintain high levels of species diversity through reductions in competition and by allowing new colonization while not disturbing the environment to a level that would decrease diversity. The high and stable levels of richness, abundance, diversity and biomass on TTS (Fig. 3.7a-f) are consistent with those outlined in Huston (1979) for a system that is in dynamic equilibrium.

### Ship Shoal

Ship is located approximately 200 km to the southwest of the Mississippi River Bird's foot delta and approximately 100 km from the Atchafalaya River delta. Thus, Ship receives less

deposition of riverine suspended silts and clays than TTS. Due to Ship's relatively shallow depth range (3 to 9 m), it is also subject to currents and wave action that winnow away fluvially-derived fine-grain particles or those deposited after resuspension from the surrounding muddier offshoal area (Kobashi 2007). These factors contribute to a sediment of a comparatively larger particle size (Table 3.3) composed of relatively homogeneous particles in the range of sand (Appendix B). A larger particle size provides greater interstitial space increasing porosity and permeability of sediments and in turn promotes oxygen flux from overlying water (Grey 1974 and references within). Grippo et al. (2010) found a greater percentage of surface light was able to reach the sediment on Ship than TTS or Off. The combination of shallow depth, greater light penetration, and relatively homogeneous sand creates an environment that more efficiently stimulates benthic photosynthesis, resulting in high BMA concentrations (Grippo 2009). Our findings suggest higher concentrations of BMA, less sediment deposition and, to a lesser extent, phytoplankton and phytodetritus, such as is found on Ship, favor the survivorship of surface deposit and suspension feeders over sub-surface deposit feeders (Table 3.2). This pattern was observed in the feeding types of the structuring species within the Ship benthic community. Examples include a high degree of numerical dominance by suspension and interface feeders such as amphipods, particularly *Acanthohaustorius* sp. A; the amphioxus *B. floridae*, which dominates both numerically and in terms of biomass; as well as to the mole crab *A. paretti*, which was less abundant but was a major contributor to the biomass on Ship.

The shallow depth of Ship makes it susceptible to disturbance by storm events and species found there must be adapted to changes in hydrography with the ability to re-borrow rapidly following such disturbance (Chapter 2). The habitat on Ship is uniquely suited to the requirements of the amphioxus population; in fact it was characterized as the *Albunea*

*paretti/Branchiostoma floridae* community in Chapter 2. Qualitative comparisons of amphioxus within the STTSC showed that those from Ship had full gonads in spring, and in the summer large numbers of juveniles were present, while TTS amphioxus did not appear to be as reproductively developed during spring and concentrations of juveniles were not as great in summer. Amphioxus-dominated communities, similar to Ship, have been reported globally. For example, in the Mediterranean Sea there are sediment types known as “amphioxus sands” (Antoniadou et al. 2004).

In both 2006 and 2007, a seasonal pattern of increasing dominance of amphioxus and concurrent decrease in virtually every other species was observed on Ship, suggesting that biological interactions, in addition to the physical environment, play a major role in shaping the community assemblage. Interspecific competition for space and food resources likely contributes to the patterns observed in the community parameters on Ship, such as seasonal decreases in mean species richness, abundance, and diversity, while maintaining a consistently high biomass (Fig. 3.7a,f); this is consistent with competitive displacement (Huston 1979). It was hypothesized in Chapter 2 that the springtime influx of spawning blue crabs to Ship may have contributed to the decrease in macrofaunal species abundance and richness observed for Ship Shoal in 2006. However, in this 2007 study we found similar concentrations of blue crabs on TTS without a decrease in the biological parameters of its macrofaunal community as we observed on Ship. Amphioxus made up 70% of all the individuals sampled from Ship in fall, which suggests they were present in high enough relative abundance to exert pressure on surrounding species through competition for available food or space, as well as inhibiting other species by re-burrowing into the sediment consistent with soft-sediment species interactions discussed in Wilson (1990). Blue crabs are voracious predators that likely also influence

community composition through predation. Preliminary examination of blue crab gut contents revealed that they feed on resident macrofauna (Gelpi unpublished). Therefore our findings are in agreement with Menge and Sutherland (1987) whose model outlines the importance of physical factors (e.g. sediment composition), predation (e.g. blue crabs), and competition (e.g. dominant amphioxus population) in shaping community composition in marine benthic habitats along a gradient of environmental stress (e.g. hydrologic energy due to shallow depth) on Ship.

#### Off Shoal

Off covered a much greater area than either Ship or TTS (Fig. 3.1). Off is characterized as a comparatively muddy sedimentary environment consisting of a varying mix of mud and sand (Table 3.3, Appendix B). There was a high interseasonal variation in sediment composition (Table 1 in Grippo et al. 2010), suggesting a changing seafloor environment likely due to resuspension events, fluvial deposition, and/or redistribution of sediment from sand sources such as Ship and TTS. The mix of feeding types of the most abundant species was characterized by a predominance of surface deposit, sub-surface deposit and interface feeders, with only one suspension feeder within the top four most abundant species over all three seasons (Table 3.2). This grouping of feeding types is consistent with an unstable benthic environment that is dominated by finer-grained sediments, and supportive of the results from Rhoads and Young (1970) that link feeding type with sediment characteristics (specifically, that deposit feeders increase in relative abundance while suspension feeders decrease in relative abundance with increasing mud content). In addition, Off was generally deeper than shoal stations, particularly the more southerly Off stations (i.e., 21, 20, 19, 17; 15 to 19 m) making them especially susceptible to bottom water hypoxia (Fig. 3.5). Despite the changing mix of sedimentary types and susceptibility to low DO in the bottom water, the Off stations maintained a relatively high



mean species richness in the spring that was higher than Ship, though not as high as TTS. This was followed by a catastrophic decline in all biological parameters (e.g. richness, abundance, biomass, taxonomic distinctiveness, and diversity, Fig. 3.7a-f) during the summer, consistent with hypoxia-related mass mortality (Harper et al. 1981; Gaston 1985; Rabalais et al. 2001b). In fall all biological parameters subsequently increased, consistent with rapid recolonization by opportunistic species as well as potential recruitment from surrounding areas not affected by hypoxia.

Off areas exhibited a core group of species, with *M. californiensis* among the four most abundant species in all three seasons, and *P. pinnata* and *Magelona* sp. H within the four most abundant species during summer and fall. These three species are known to be largely unaffected by hypoxia disturbance and are often found in high concentrations in areas suffering from low oxygen bottom water ([Santos and Simon 1980, *M. californiensis*] [Diaz and Rosenberg 1995; Baustian and Rabalais 2009, *P. pinnata*, *Magelona* sp. H]). The polychaete *Ampharete* sp. A, and cumacean *O. smithi*, both structuring species in spring, underwent strong seasonal population fluctuations. *Ampharete* sp. A was not found in Off samples taken during the summer or fall, despite a ubiquitous springtime distribution (present at every station) when it was also the most abundant Off species (Table 3.2). This was unexpected because *Ampharete* sp. A is reportedly tolerant to low DO (Rabalais et al. 2002). *O. smithi* was also ubiquitously distributed in the spring (present at all but one station) when it was the second most abundant offshoal species (Table 3.2), but nearly disappeared in summer, then rebounded somewhat in the fall. This pattern may be linked to its mobility (Alldredge and King 1980) which would enable it to flee encroaching hypoxia and then return to affected areas following a hypoxic event.

There are many factors that potentially affect macrofaunal community composition in the STTSC, including food sources such as organic matter, sediment/phytodetritus, phytoplankton, and benthic microalgae; biological interactions such as competition, amensalism, facilitation, and predation; depth-associated hydrodynamics such as, wave action, and currents (Snelgrove and Butman 1994); environmental changes such as hypoxia and fluvial deposition; direct anthropogenic disturbance such as oil spills and trawling. Of the factors that were measured during our study, sediment structure in terms of sand percentage seems to be the most fundamental driving variable determining macrofaunal community composition (Table 3.3). Further evidence of this is supported by MDS plots (Fig. 3.3) as they exhibit a general pattern of decreasing sand percentage from left to right. Overlap between Ship and TTS was mainly confined to the sandiest TTS stations 9 and 14. Overlap between TTS and Off occurred with sandy Off station 23, which we now realize, is a part of the remnant shoal system (Krawiec 1966) that is diminished in size compared to Ship and TTS.

Sand percentage likely contributes to the makeup of different habitat patches and may constitute niches that are differentially taken advantage of depending on the species. The temporal diversity patterns (spring to fall) we found for Ship, TTS and Off are consistent with an overarching source sink dynamic (Levin 1974; Pulliam 1988; Mouquet and Loreau 2003). Within this framework of diversity maintenance we would expect large numbers of planktonic larvae in the spring to blanket the STTSC and settle in many habitat types including areas of high sand percentages such as shoals and low sand percentages such as off shoal. Not all of these species would be suited for the areas they settle and over time would likely die from inability to feed, be outcompeted, or be killed off due to environmental disturbance. In addition, a sink habitat for one species may be a source for other species (Pulliam 1988) and thus a community

within Ship, TTS or Off may be a mixture of populations, some of which are self-maintaining and some of which are not.

### Shoal Implications to Biodiversity of the Northern Gulf of Mexico

Maintaining regional-scale benthic heterogeneity helps support regional biodiversity (Zajac 2008b). Our study is consistent with this idea as evidence from the STTSC indicates that large sandy shoals promote increased biodiversity across the northern Gulf of Mexico continental shelf. Supporting evidence is provided by our analyses of beta diversity as highest values were found between shoal and offshoal areas (Fig. 3.8). Many species have been shown to have habitat preferences related to sediment type (Gray 1974), and this likely contributes to the uniqueness of species assemblages between dissimilar benthic habitats in the STTSC (Table 3.1, Fig 3.2). Particle size has been shown to be an important component of sediment structure. For example, Thorson (1955, 1957) found geographical differences in species distributions that were restricted within particle size ranges. Within the STTSC we found 67 species that were only found on shoal areas and 57 species that were only found within the off shoal. The relative lack of sand on the Louisiana continental shelf therefore suggests that sandy shoals are ecologically valuable because they may represent benthic habitat that supports a well adapted community. For example, 79 species we sampled from the STTSC were restricted to sediment composed of relatively high sand percentages (>70%, Appendix B), representing 31% of all species sampled. In contrast only 24 species were restricted to the muddiest stations (< 50%, Appendix B), representing 9% of all species sampled.

Habitat complexity has been shown to increase diversity in marine systems (Gray 1974). For instance, Craig and Jones (1966) found that muddy sand had a higher number of species of macrofauna than more uniform mud or pure sand. On a regional scale, increased diversity has

been shown along transition zones between different types of habitat patches within a benthoscape (Zajac 2008b). Within our study area, the shoals (which are eroding and moving shoreward [Penland et al. 1986]) are most likely major sources of surface sands for off shoal areas potentially increasing both habitat complexity and transition zones. Through these mechanisms, shoals may promote greater species diversity within STTSC benthic habitats.

Differing species assemblages also occur between similar habitat types. One example is station 23, an area that is not directly connected to Ship or TTS but had a shoal-like benthic habitat with a sediment composition of 88% sand. Station 23 had nine species that were not found anywhere else during our study. In addition, the species assemblages of Ship and TTS grew increasingly different from each other as the season's advanced from spring to fall. By fall, they had an R value of 1 (Table 3.1a), indicating complete dissimilarity (i.e. no station within either area was more similar to any station within the other area) and also supporting a source-sink method (Levin 1974; Pulliam 1988; Mouquet and Loreau 2003) for diversity within the STTSC.

Biodiversity has been shown to be important for several reasons including: increased resiliency to disturbance and resistance to invasive species (Stachowicz et al. 2002); services to humans in the form of chemical compounds used for medicine (Chivian 2001); increased biomass and greater food resources for fisheries (Worm et al. 2006); as well as biodiversity for its own sake (Ehrlich and Wilson 1991; Cardinale et al. 2006). The results of our study suggest at least four important biodiversity enhancing functions for high sand concentrations found on shoals within the Louisiana continental shelf. These shoals have high localized abundances of unique species found only in sandy sediment, and have a more varied community phylogeny (i.e. taxonomic distinctiveness; Fig. 3.7c). Large concentrations of sand contribute to the regional

benthic heterogeneity and provide recruitment areas for larvae of species which may be adapted to sandy habitat. In addition, sand redistributed from shoals to the surrounding muddier non-shoal areas helps promote local patch complexity making the benthoscape of the STTSC more varied and potentially able to support greater biodiversity.

#### Are Shoals Hypoxia Refuge and Larval Sources for the Dead Zone?

Hypoxia in the northern Gulf of Mexico, termed the dead zone, is a major environmental hazard to many species. The STTSC is typically afflicted with late spring and summer bottom water DO values of  $< 2 \text{ mg l}^{-1}$  that define hypoxic conditions in the Gulf of Mexico (Rabalais et al. 2001a). Recent studies have hypothesized that Louisiana shoals function as hypoxia refuges (Chapters, 2, 4)). Our results confirm and expand upon this hypothesis and the results of Grippo et al. (2009, 2010) and DiMarco et al. (2010) by examining the seasonal relationship of depth and bottom water DO, as well as through seasonal comparisons of biological parameters between Ship, TTS and Off. Our seasonal analysis of depth and DO (Fig. 3.5) indicates that areas below 9 m are more susceptible to hypoxia. This is in general agreement with analyses from Rabalais et al (2001a) on the extent of hypoxia, and provides evidence supporting the hypoxia refuge function of shoals. The shoal-based hydrodynamic influence on the dead zone has recently been addressed by DiMarco et al. (2010) where they showed that shoals are better oxygenated than surrounding areas, and hypoxia is “phase-locked” with shoal geographic configuration thus influencing hypoxia distribution on the continental shelf. Shallow areas in general interact with surface currents and waves, and shoals in particular have an increased energy regime due to irregular bottom water topography (Wright et al. 2002; Pepper and Stone 2004) that discourages stratification and bottom water hypoxia. In addition, local production of BMA and phytoplankton below the pycnocline may also provide oxygen through photosynthesis (Grippo et

al. 2009; 2010). Our area comparisons between shoals and off shoal amphipod abundances also provide evidence that the shoals are less affected by hypoxia than surrounding areas.

Amphipods are known to be indicator organisms that are highly sensitive to low DO (Gaston 1985, Wu and Or 2005). During the summer there was a catastrophic decline in amphipod abundances for off shoal stations, while amphipod distribution on shoal stations remained relatively ubiquitous.

Mobile animals may migrate in order to escape hypoxia while less mobile or sessile species are often directly affected, resulting in large scale mortality (Diaz and Rosenberg 1995). This has been previously reported in the northern Gulf of Mexico dead zone (Harper et al. 1981; Gaston 1985; Rabalais et al. 2001b) and during 2007 we also found substantial summer decreases in all Off taxonomic groups and community parameters (Fig. 3.7a-d). However, there was a substantial rebound in Off taxonomic groups as well as species abundance and richness in the fall. Since hypoxia is more prevalent in stratified deeper water on the continental shelf, shallow areas within the dead zone, including shoals, may function as sources of larvae or adults to re-establish macrofaunal populations within surrounding areas that have been affected by hypoxia. We found evidence that shoals are potential larval source for surrounding areas following hypoxia disturbance. In support of this re-seeding hypothesis we found the 29 Off species (out of 91 total for Off in fall) that increased in mean abundance following summer time hypoxia all occurred on TTS or Ship.

#### Are Shoals Larval Stepping Stones?

Specific size ranges are necessary for recruitment of some benthic species and/or their larva. For example, there are some species whose larvae will delay metamorphosis until suitable types of sediment are found; with some able to actively select an appropriate substratum (Gray

1974). Our findings suggest that sandy areas have the potential to enhance across-shelf connectivity for species with a habitat preference for a high sand composition and therefore contribute to northern Gulf of Mexico metapopulations. For example we detected positive relationships between sand percentage and total polychaete species richness and abundance, and significant positive relationships for those polychaete species that were newly reported (Fig. 3.6 a, b) from the Louisiana continental shelf (i.e. not found in Ubelacker and Johnson 1984). Sandy habitats have therefore been underrepresented in previous surveys of Louisiana continental shelf biodiversity. The presence of sandy shoals may facilitate recruitment for the larvae of ‘sandy species’ and help maintain populations between the sandier Florida and Texas continental shelves. Therefore, the potential for genetic exchange across the northern Gulf of Mexico due to connectivity between localized populations with planktonic larvae or mobile adults is likely improved by such accessible pockets of sand.

#### Are Shoals Preferential Habitat for Spawning Blue Crab?

Shallower areas within the STTSC, particularly Ship and Trinity shoals, support high concentrations of spawning blue crabs that are an integral component of the Louisiana inshore fishery and whose larvae may recruit to estuaries all along the northern Gulf of Mexico (Chapter 4, 5). Our results suggest that deeper offshoal areas are less hospitable and less productive for blue crab reproduction possibly due to hypoxia. Crab avoidance of low DO has been reported by Pihl et al. (1991) and hypoxia refuge is likely an important feature of shallow shoals in areas affected by low DO. The highest concentrations of blue crabs within the STTSC were found during summer on Ship and Trinity Shoals (Chapter 4). In addition, hypoxia disturbance likely contributes to a decreased macrofaunal biomass for Off stations. Biomass comparisons between Ship, TTS and Off (Fig. 3.7d, Table 3.4) indicate that there are area differences in the available

foraging potential for spawning blue crabs because food resources are greater on the shoals. This finding is further supported by preliminary examination of crab stomachs where chi square analysis of empty versus non-empty stomachs suggests a higher incidence of empty crab stomachs from off shoal versus shoals in August (Gelpi unpublished, Appendix C Table C.1) when the highest concentrations of blue crabs were found in the STTSC (Chapter 4). In addition, prey group composition of gut contents (Gelpi unpublished) was consistent with area macroinfauna reported in Chapters 2 and 3. In my preliminary gut content analyses some area differences were also noted in the prey items found in guts. For example Ship guts contained a higher Prey Point value for gastropods and TTS guts contained a higher Prey Point value for shrimp, suggesting that shoal blue crab prey affinities or availabilities may differ between shoals (Appendix C Table C.3). A hypoxia related decrease in blue crab prey resources could inhibit the females' ability to produce eggs and decrease overall brood production. Therefore, our results and preliminary analyses suggest that STTSC shoals are more valuable blue crab spawning grounds than surrounding, deeper off shoal areas.

#### Sand Mining Threats to System Integrity

Shoals on the Louisiana coast are considered prime locations for sand mining, with Ship Shoal alone comprising 1.6 billion cubic yards of fine sand (Drucker et al. 2004). These marine sand concentrations have been identified as potential sand sources for various coastal projects, including barrier island restoration and beach reinforcement to protect against storm surge and combat wetland loss (Nairn et al. 2004; Michel 2004; Stone et al. 2004). As a prime component of these proposals, a 30' (9.14 m) depth x 1000' (304.8 m) width extraction zone (with an unspecified length), was proposed for Ship Shoal following the Deepwater Horizon Oil Spill (DWHOS) for use in emergency berm construction (CPRA 2010). In light of our analyses of



depth and DO (Fig. 3.5), if this extraction exceeded a depth of 9 m it would be expected to become hypoxic every August.

The unique shoal-based benthic communities that contribute to the biodiversity of the region would be threatened by extensive sand mining. Ship Shoal has been characterized as possessing many K-selected species (Chapter 2), and TTS is similar in that both areas support structuring species that are larger, relatively long-lived, and with a slow reproduction rate, such as *A. paretti* and *B. floridae*, and others described in Newell et al. (1998) as equilibrium species (e.g., *Scoloplos* sp., *Tellina* sp., *Abra* sp., *Dosinia* sp. on both Ship and TTS; *Nephtys* sp. on Ship; *Sabellides* sp. on TTS). The review by Newell et al. (1998) estimated post-dredging recovery of a benthic community from a sandy habitat would take two to three years versus six to eight months for muddy habitat with “recovery” defined as a community able to “maintain itself” after 80% of the species diversity and biomass have been restored to pre-dredging levels. However, previous studies documenting sand mining disturbance have focused on changing sediment composition, depth, and bottom currents. None of these studies have addressed an area’s increased susceptibility to hypoxia following sand mining–related depth increases, nor the changes in benthic community that would likely follow.

Due to the likely synergistic effects of altered sediment composition and increased depth (i.e., greater vulnerability to hypoxia), sand mining would likely alter existing shoal community structure and “recovery” as defined by Newell et al. (1998) would be slowed, diminished, or precluded. Additional STTSC ecosystem services that our studies suggest are provided by sandy shoals would be lost or diminished as a result of sand mining. These include: larval connectivity for species that have a preference for sandy habitat; ability of the surrounding region to recover following hypoxia; sand sources that redistribute to surrounding areas and increase local habitat

heterogeneity and transition zones; landscape scale differences in benthic habitat complexity; and spawning grounds for blue crab. In addition, altering depth and sediment type would likely influence bottom-up changes in shoal food webs especially in areas in which BMA is a major constituent of primary production. One possible negative trophic cascade could result by decreased prey biomass for spawning blue crabs, which are the most preferred prey for federally protected Kemp's ridley sea turtles (Liner 1954; Schaver 1991).

Finally, the STTSC shoal benthic community has not to our knowledge been evaluated following the Deepwater Horizon Oil Spill (DWHOS) despite the unprecedented use of dispersants and satellite evidence that the sheen of oil from the DWHOS extended over much, if not all, of the STTSC. This lack of a post-impact study of the STTSC is a disservice to those wishing to understand the spill's full impact for at least three reasons. First, the adsorbing properties of oil hydrocarbons are different depending on organic matter content (Pezeshki et al. 2000). Because STTSC shoals are sandy and low in organic content compared to the muddier off shoal (Grippo 2010), we would expect different interactions between sediment and deposited oil on the shoals as opposed to off the shoals. Second, our pre-DWHOS shoals supported high concentrations of macrofaunal bioindicators that are sensitive to the impact of oil spills. (e.g., amphipods, Gesteira and Dauvin 2000). Third, we have developed unique, quantitative, pre-impact indicators of blue crab condition factor/ecosystem health (Gelpi et al. 2009, Dubois et al. 2009; Grippo et al 2009, 2010) that should be compared with post-DWHOS-impact on blue crabs and their offshore ecosystems. Within the STTSC (shoals and off shoal), we therefore have a unique assortment of pre-impact statistical models with which post-DWHOS impacts could be compared. However, without an appraisal of the DWHOS shoal impacts, it would be

statistically unlikely that a benthic study could distinguish between effects of the oil and/or dispersant and sand mining.

#### LITERATURE CITED

Allredge, A.L., J.M. King. 1980. Effects of moonlight on the vertical migration patterns of demersal zooplankton. *Journal of Experimental Marine Biology and Ecology*. 44:133-156.

Allison, M.A., G.C. Kineke, E.S. Gordon, M.A. Goñi. 2000. Development and reworking of a seasonal flood deposit on the inner continental shelf off the Atchafalaya River. *Continental Shelf Research*. 20:2267-2294.

Antoniadou, C., Y. Krestenitis, C. Chintiroglou. 2004. Structure of the “Amphioxus sand” community in Thermaikos bay (Eastern Mediterranean). *Fresenius Environmental Bulletin*. 13:1122-1128.

Baustian, M., Rabalais N. 2009. Seasonal Composition of Benthic Macroinfauna Exposed to Hypoxia in the Northern Gulf of Mexico. *Estuaries and Coasts* 32: 975-983.

Blott, S.J., K. Pye. 2001. GRADISTAT: a grain size distribution and statistics package for the analysis of unconsolidated sediments. *Earth Surface Processes and Landforms*. 26:1237-1248.

Cardinale, B.J., D.S. Srivastava, J.E. Duffy, J.P. Wright, A.L. Downing, M. Sankaran, C. Jouseau. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature*. 443:989-992.

Chivian, E. 2001. Environment and Health 7: Species loss and ecosystem disruption-the implications for human health. *Canadian Medical Association Journal*. 164:66-69.

Clarke, K.R., R.M. Warwick. 1994. Change in marine communities: an approach to statistical analysis and interpretation. Report No. 144. Plymouth Marine Laboratory, Plymouth.

Clarke, K.R., R.N. Gorley. 2001. PRIMER v5: user manual/tutorial. PRIMER-E Ltd, Plymouth

Clarke, K.R., R.M. Warwick. 1999. *Marine Ecology-Progress*. 184:21-29.

- CPRA (Coastal Protection and Restoration Authority). 2010. Application to U.S. Army Corps of Engineers for emergency authorization for barrier island sand berm construction. May 11, 2010. Baton Rouge, Louisiana.
- Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science*. 199:1302-1310.
- Craig G.Y., N.S. Jones. 1966. Marine benthos, substrate and palaeoecology. *Paleontology*. 9:30-38.
- Diaz, R.J., R. Rosenberg. 1995. Marine benthic hypoxia: A review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanography and Marine Biology: An Annual Review*. 33:245-303.
- DiMarco, S.F., P. Chapman, N. Walker, R.D. Hetland. 2010. Does local topography control hypoxia on the eastern Texas–Louisiana shelf? *Journal of Marine Systems*. 80:25-35.
- Drucker, B.S., W. Waskes, M.R. Byrnes. 2004. The U.S. Minerals Management Service outer continental shelf sand and gravel program: environmental studies to assess the potential effects of offshore dredging operations in federal waters. *Journal of Coastal Research*. 20:1-5.
- Dubois, S., C.G. Gelpi, R.E. Condrey, M.A. Grippo, J.W. Fleeger. 2009. Diversity and composition of macrobenthic community associated with sandy shoals of the Louisiana continental shelf. *Biodiversity and Conservation*. 18:3759-3784.
- Ehrlich, P.R., E.O. Wilson. 1991. Biodiversity studies: science and policy. *Science*. 16:758-762.
- Ellingsen, K.E. 2002. Soft-sediment benthic biodiversity on the continental shelf in relation to environmental variability. *Marine Ecology-Progress Series*. 232:15-27.
- Ellingsen, K.E., J.S. Gray. 2002. Spatial patterns of benthic diversity: is there a latitudinal gradient along the Norwegian continental shelf? *Journal of Animal Ecology*. 71:373-389.
- Emerson, W.K., M.K. Jacobson. 1976. The American Museum of Natural History guide to shells--land, freshwater, and marine, from Nova Scotia to Florida, Knopf.
- Fleeger, J.W., M.A. Grippo, S.T. Pastorick. 2011. What is the relative importance of sediment granulometry and vertical gradients to nematode morphometrics? *Marine Biology Research*. 7:122-134.

- Gaston, G.R. 1985. Effects of hypoxia on macrobenthos of the inner shelf off Cameron, Louisiana. *Estuarine, Coastal and Shelf Science*. 20:603-613.
- Gelpi, C.G., R.E. Condrey, J.W. Fleeger, S.F. Dubois. 2009. Discovery, evaluation, and implications of blue crab, *Callinectes sapidus*, spawning, hatching, and foraging grounds in federal (US) waters offshore of Louisiana. *Bulletin of Marine Science*. 85:203-222.
- Gesteira, J.L.G., J.C. Dauvin. 2000. Amphipods are good bioindicators of the impact of oil spills on soft-bottom macrobenthic communities. *Marine Pollution Bulletin*. 40:1017-1027.
- Gray, J.S. 1974. Animal-Sediment relationships. *Oceanography and Marine Biology Annual Review*. 12:223-261.
- Grippo, M., J.W. Fleeger, R. Condrey, K.R. Carman. 2009. High benthic microalgal biomass found on Ship Shoal, north-central Gulf of Mexico. *Bulletin of Marine Science*. 84:237-256.
- Grippo, M.A., J.W. Fleeger, N.N. Rabalais, R. Condrey, K.R. Carman. 2010. Contribution of phytoplankton and benthic microalgae to inner shelf sediments of the north-central Gulf of Mexico. *Continental Shelf Research*. 30:456-466.
- Grippo, M.A., Fleeger J.W., Dubois S.F., Condrey R. 2011. Spatial variation in basal resources supporting benthic food webs revealed for the inner continental shelf. *Limnology and Oceanography*. 56:841-856.
- Harper, Jr., D.E., L.D. McKinney, R.R. Salzer, R.J. Case. 1981. The occurrence of hypoxic bottom water off the upper Texas coast and its effects on the benthic biota. *Contribution in Marine Science*. 24:53-79.
- Hewitt, J.E., S.E. Thrush, P. Legendre, G.A. Funnell, J. Ellis, M. Morrison. 2004. Mapping of marine soft-sediment communities: Integrated sampling for ecological interpretation. *Ecological Applications*. 14:1203-1216.
- Hewitt, J.E., S.E. Thrush, J. Halliday, C. Duffy. 2005. The importance of small-scale habitat structure for maintaining beta diversity. *Ecology*. 86:1619-1626.
- Hill, M.O. 1973. Diversity and evenness: a unifying notation and its consequence. *Ecology* 54:427-432.

- Huston, M. 1979. A General Hypothesis of Species Diversity. *The American Naturalist*. 113:81-101.
- Kaiser, M.J., M. Bergmann, H. Hinz, M. Galanidi, R. Shucksmith, E.I.S. Rees, T. Darbyshire, K. Ramsay. 2004. Demersal fish and epifauna associated with sandbank habitats. *Estuarine Coastal and Shelf Science*. 60:445-456.
- Kobashi, D., F. Jose, G.W. Stone. 2007. Impacts of fluvial fine sediments and winter storms on a transgressive shoal, off south-central Louisiana, USA. Proceedings of the 9th international coastal symposium. *Journal of Coastal Research*. Gold Coast, Australia, pp 858–862.
- Krawiec, W. 1966. Recent sediments of the Louisiana inner continental shelf. Dissertation. Rice University.
- Lecroy, S. 2007. An illustrated identification guide to the nearshore marine and estuarine Gammaridean Amphipoda of Florida, vol 1- 4 Florida Department of Environmental Protection, Florida
- Levin, A.S. 1974. Dispersion and population interactions: *The American Naturalist*. 108: 207-228.
- Liner, E. A. 1954. The herpetofauna of Lafayette, Terrebonne and Vermilion Parishes, Louisiana. *Proceedings Louisiana Academy of Sciences*. 17:65-85.
- Menge, B.A., J.P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *The American Naturalist*. 130:730-757.
- Michel, J. 2004. Regional management strategies for federal offshore borrow areas, U.S. East and Gulf of Mexico Coasts. *Journal of Coastal Research*. 20:149-154.
- Mouquet, N., M. Loreau. 2003. Community patterns in source-sink metacommunities. *The American Naturalist*. 62: 544-557.
- Nairn, R., J.A. Johnson, D. Hardin, J. Michel. 2004. A biological and physical monitoring program to evaluate long-term impacts from sand dredging operations in the United States Outer Continental Shelf. *Journal of Coastal Research*. 20:126-137.

- Newell, R.C., L.J. Seiderer, D.R. Hitchcock. 1998. The impact of dredging works in coastal waters: a review of the sensitivity to disturbance and subsequent recovery of biological resources on the seabed. *Oceanography and Marine Biology – An Annual Review*. 36:127-178.
- Penland, S., J.R. Suter, T.F. Moslow. 1986. Inner-shelf shoal sedimentary facies and sequences: Ship Shoal, Northern Gulf of Mexico, SEPM Core Workshop No.9, Modern and Ancient Shelf Clastics. 73-123.
- Pepper, D.A., G.W. Stone. 2004. Hydrodynamic and sedimentary responses to two contrasting winter storms on the inner shelf of the northern Gulf of Mexico. *Marine Geology*. 210:43-62.
- Pihl, L., S.P. Baden, R.J. Diaz. 1991. Effects of periodic hypoxia on distribution of demersal fish and crustaceans. *Marine Biology*. 108:349-360.
- Pezeshki, S.R., M.W. Hester, Q. Lin, J.A. Nyman. 2000. The effects of oil spill and clean-up on dominant US Gulf coast marsh macrophytes: a review. *Environmental Pollution*. 108:129-139.
- Pulliam, H.R. 1988. Sources, sinks, and population regulation: The American Naturalist. 132: 652-661.
- Rabalais, N., W. Wiseman, R. Turner. 1994. Comparison of continuous records of near-bottom dissolved oxygen from the hypoxia zone along the Louisiana coast. *Estuaries and Coasts*. 17:850-861.
- Rabalais, N.N., R.E. Turner, W.J. Wiseman. 2001a. Hypoxia in the Gulf of Mexico. *Journal of Environmental Quality*. 30:320-329.
- Rabalais, N.N., L.E. Smith, D.E. Harper Jr., D. Justić. 2001b. Effects of seasonal hypoxia on continental shelf benthos. In Coastal hypoxia: Consequences for living resources and ecosystems, Coastal and Estuarine Studies 58, ed. N.N. Rabalais and R. E. Turner, 211-240. Washington, DC: American Geophysical Union.
- Rabalais, N.N., R.E. Turner, W.J. Wiseman Jr. 2002. Gulf of Mexico Hypoxia, a.k.a. "The Dead Zone". *Annual Review of Ecology and Systematics*. 33:235-263.
- Rhoads, D.C., D.K. Young. 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. *Journal of Marine Research* 28:150-178.

- Riisgård, H.U., I. Svane. 1999. Filter Feeding in Lancelets (Amphioxus), *Branchiostoma lanceolatum*. *Invertebrate Biology*. 118:423-432.
- Roberts, H.H. 1997. Dynamic changes of the Holocene Mississippi River delta plain: The delta cycle. *Journal of Coastal Research*. 13:605-627.
- Santos, S.L., J.S. Simon. 1980. Response of softbottom benthos to annual catastrophic disturbance in a south Florida estuary. *Marine Ecology Progress Series*. 3:347-355.
- Shannon, C.E. 1948. A mathematical theory of communications. *Bell Systems Technical Journal*. 27:379-423.
- Shaver, D. J. 1991. Feeding ecology of wild and head-started Kemp's ridley in South Texas waters. *Journal of Herpetology*. 25:327-334.
- Simpson, E.H. 1949. Measurement of diversity. *Nature*. 163:688.
- Snelgrove, P.V.R., C.A. Butman. 1994. Animal sediment relationships revisited – cause versus effect. *Oceanography and Marine Biology*. 32:111-177.
- Sousa, W.P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology*. 60:1225-1239.
- Stachowicz, J.J., H. Fried, R.W. Osman, R.B. Whitlatch. 2002. Biodiversity, invasion resistance, and marine ecosystem function: Reconciling pattern and process. *Ecology*. 83:2575-2590.
- Stone, G.W., D.A. Pepper, J. Xu, X. Zhang. 2004. Ship Shoal as a prospective borrow site for barrier island restoration, coastal south-central Louisiana, USA: numerical wave modeling and field measurements of hydrodynamics and sediment transport. *Journal of Coastal Research*. 20:70-88.
- Suter, J.R., J. Mossa, S. Penland. 1989. Preliminary assessments of the occurrence and effects of utilization of sand and aggregate resources of the Louisiana inner shelf. *Marine Geology*. 90:31-37.
- Thorson, G. 1955. Modern aspects of marine level-bottom communities. *Journal of Marine Research*. 14: 387-397.



- Thorson, G. 1957. Bottom communities. *Geological Society of America*. 67:461-534.
- Thouzeau, G., G. Robert, R. Ugarte. 1991. Faunal assemblages of benthic megainvertebrates inhabiting sea scallop grounds from eastern Georges Bank, in relation to environmental factors. *Marine Ecology Progress Series*. 74: 61-82.
- Uebelacker, J.M., P.G. Johnson. 1984. Taxonomic guide to the polychaetes of the northern Gulf of Mexico, Vol. 1–7 Barry A. Vittor & Associates, Inc, Mobile.
- Whittaker, R.H. 1972. Evolution and measurement of species diversity. *Taxon*, 21, 213-251
- Wilson, W.H. 1990. Competition and Predation in Marine Soft-Sediment Communities. *Annual Review of Ecology and Systematics* 21: 221-241.
- Wiseman, W.J., Rabalais N.N., Turner R.E., Dinnel S.P., MacNaughton A. 1997. Seasonal and interannual variability within the Louisiana coastal current: stratification and hypoxia. *Journal of Marine Systems*. 12:237-248.
- Worm, B., E.B. Barbier, N. Beaumont, J.E. Duffy, C. Folke, B.S. Halpern, J.B.C. Jackson, H.K. Lotze, F. Micheli, S.R. Palumbi, E. Sala, K.A. Selkoe, J.J. Stachowicz, R. Watson. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science*. 314:787-790.
- Wright, J., A. Colling, D. Park. 2002. Waves, tides, and shallow-water processes: Oxford, UK; Boston, MA; Milton Keynes, England, Butterworth-Heinemann; In Association with the Open University.
- Wu, R.S.S., Y.Y. Or. 2005. Bioenergetics, growth and reproduction of amphipods are affected by moderately low oxygen regimes. *Marine ecology Progress Series*. 297:215-223.
- Zajac, R.N. 2008a. Challenges in marine, soft-sediment benthoscape ecology. *Landscape Ecology*. 23:7-18.
- Zajac, R.N. 2008b. Macrobenthic biodiversity and sea floor landscape structure. *Journal of Experimental Marine Biology and Ecology*. 366:198-203.
- Zajac, R.N., R.S. Lewis, L.J. Poppe, D.C. Twichell, J. Vozarik, M.L. DiGiacomo-Cohen. 2003. Responses of infaunal populations to benthoscape structure and the potential importance of transition zones. *Limnology and Oceanography*. 48:829-842.

**CHAPTER 4: DISCOVERY, EVALUATION, AND IMPLICATIONS OF BLUE CRAB,  
*CALLINECTES SAPIDUS*, SPAWNING, HATCHING, AND FORAGING GROUNDS IN  
FEDERAL (US) WATERS OFFSHORE OF LOUISIANA\***

---

\* Reprinted with permission and modifications from the journal *Bulletin of Marine Science*. Literature cited: Gelpi Jr., C.G., R.E. Condrey, J.W. Fleeger, S.F. Dubois. 2009. Discovery, evaluation, and implications of blue crab, *Callinectes sapidus*, spawning, hatching, and foraging grounds in federal (US) waters offshore of Louisiana. *Bulletin of Marine Science*. 85:203-222.

## INTRODUCTION

Blue crabs, *Callinectes sapidus* (Rathbun, 1896), are an ecologically and economically important crustacean, historically common along the US Atlantic and Gulf of Mexico coasts. Blue crabs support the most valuable crab fishery in the world (Eggleson et al., 2008). The US fishery accounted for 87% of the world blue crab catch in 1999 (UN, 2008). Louisiana leads all other US states in recent (1997-2006) hard-shelled landings (26% of the US total), followed by North Carolina (22%), the Chesapeake Bay states of Maryland (16%) and Virginia (15%), and each of the remaining thirteen blue-crab producing states (Rhode Island to Texas, 21%, combined) (NOAA, 2007).

Louisiana's leading position in US blue crab landings is largely attributable to recent 1) increases in Louisiana's yield and 2) declines in the blue crab fisheries of Chesapeake Bay (Maryland and Virginia), and North Carolina (NOAA, 2007). Chesapeake Bay and North Carolina declines are attributed to overfishing and/or habitat degradation (e.g. Zohar et al., 2008). As a result, managers in these areas are implementing methods of increasing spawning stock biomass through regulations, i.e., migration corridors and spawning sanctuaries (Lipcius et al., 2003), augmented by an experimental release of hatchery-raised juveniles (Aguilar et al., 2008; Eggleson et al., 2008).

During a pre-impact sand-mining study, we discovered unexpected abundances of female blue crabs in federal waters off the Louisiana coast (~ 20 and 40 km), first on Ship Shoal in 2005 and 2006, and then on the Ship, Trinity, Tiger Shoal Complex when our study area was expanded in 2007 (hereafter STTSC, Fig. 4.1). While suggestions that the offshore plays a role in the adult blue crab life cycle may be found in the literature (e.g., Van Engel, 1958; Dudley and

Judy, 1971; Adkins, 1972; and Perry, 1975), no study has demonstrated or quantitatively explored the offshore environment as an important adult blue crab habitat.

This paper provides information about underexplored offshore areas of importance to blue crabs that are vulnerable to fishery exploitation and sand-mining disturbance. Currently, the accepted paradigm of the female blue crab life cycle includes 1) a single, lifetime mating event; 2) a salinity-associated separation of the sexes following mating; 3) spawning in estuarine waters; 4) post-fertilization brooding of attached eggs (a.k.a. sponge); 5) hatching in lower estuarine and coastal waters; 6) offshore larval development; and 7) estuarine development of juveniles (e.g. Churchill, 1919; Van Engel, 1958).

In this paper, we use analyses of condition factor, reproductive condition, and abundance to examine the following four null hypotheses relating to the use of the STTSC as an important spawning, hatching, and foraging ground for mature female blue crabs:

- (1) Condition factor, fecundity, and abundance of STTSC crabs do not differ from those of nationally recognized spawning grounds;
- (2) STTSC crabs do not undergo a continuous spawning/hatching cycle from April to October;
- (3) Morphometric indicators of individual weight are equivalent and not affected by symbionts or reproductive state;
- (4) Crab abundance is uniform over space and time across the STTSC.

In addition, we examine the ecological, sand mining, and fishery management implications of our findings.

## MATERIALS AND METHODS

### Study Site and Field Collection

The STTSC (Fig. 4.1) is located in the northern Gulf of Mexico south of Louisiana, within a region where annual bottom-water hypoxia occurs (Rabalais et al., 2002). Ship, Trinity, and Tiger Shoals are relic barrier islands (Roberts, 1997) composed mostly of fine grain sand; the surrounding off-shoal areas are typically much muddier. The depths of these shoals ranged between ~3 and 4 m in our most shallow sampling areas. The stations immediately north of Ship Shoal (but several kilometers seaward of land), designated in Fig. 4.1 as inshore, ranged in depth from ~4 to 6.5 m. All other non-shoal stations, designated in Fig. 4.1 as offshore, ranged in depth from ~4.5 to 19 m.

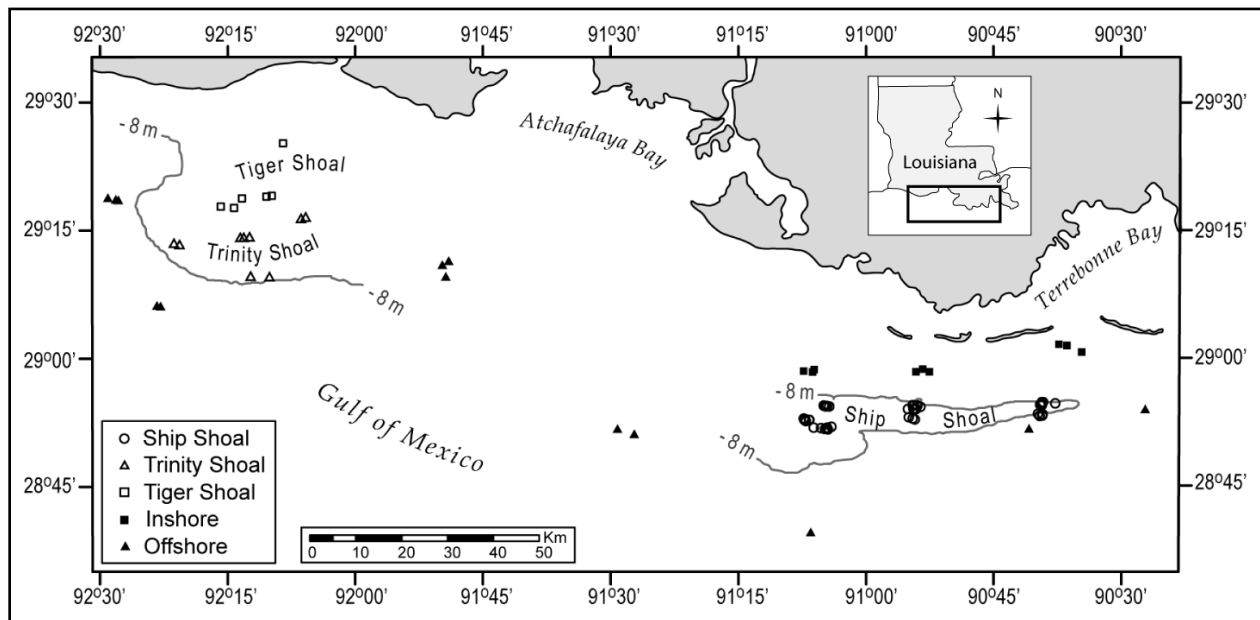


Figure 4.1 Ship, Trinity, Tiger Shoal Complex (STTSC) and trawl station locations for 2005-07. Areas within the STTSC are divided into five groups (see legend). Ship, Trinity, and Tiger Shoals are partly outlined by the 8 m contour associated with each shoal (based on Braud, 1999).

We attempted three collection trips per year: spring, summer, and fall. The spring cruise occurred in June, May, and April for 2005-2007 respectively; the summer and fall, in August and October each year. In 2005 and 2006 we concentrated on Ship Shoal, completing nine nighttime trawls per trip, except in June 2005 (exploratory efforts not reported) and October 2005 (one trawl lost). During each cruise in 2005-06 three replicate trawls were pulled on the western, middle, and eastern portions of the shoal, respectively, using a 7.3 m balloon net with 5.08 cm mesh from the R/V *Acadiana*. In 2007 we sampled the five STTSC areas completing 13-21 nighttime trawls per trip using a 12.8 m balloon net with 5.08 cm mesh from the R/V *Pelican*. Sampling effort in all years was 30 minutes per trawl. After enumerating the catch by sex per trawl, all crabs were immediately frozen until laboratory analysis.

Bottom-water salinity, temperature, dissolved oxygen (DO), and depth were measured for each station. Water samples were collected ~1 m from the bottom using a 5-L Niskin bottle. Temperature, salinity, and DO were measured with a YSI 85 handheld multimeter and Winkler titrations during 2005-06 and using a CTD probe in 2007. Environmental data were taken during daytime benthic sampling prior to nighttime trawl sampling.

## Measurements

Blue crabs were thawed in the laboratory before examination. During initial exploratory analysis we recorded basic morphometric measurements and made exploratory measurements of the reproductive states and symbionts of the female blue crabs taken during the August 2005 cruise. Based on these insights we developed a procedure (outlined in Table 4.1) for making detailed measurements of the 2006 and 2007 blue crabs.

Table 4.1 Definitions of variable abbreviations. All weights are in g; all linear measurements, in cm.

WHOLE CRAB MEASUREMENTS	
BB	carapace width between the bases of the lateral spines
H	carapace height
L	carapace length
TT	carapace width between the tips of the lateral spines
V	crab volume ( $L * BB * H$ )
W	crab weight without acorn barnacles, ( <i>Chelonibia patula</i> , <i>Balanus</i> spp.)
REPRODUCTION	
AW	weight of the abdomen
d	average age (days) of the embryos in a sponge
E	number of eggs (in millions) in a crab sponge
O	fullness of the ovary (ranked from 1 to 3 as inconspicuous, intermediate, or large)
P	presence/absence of a sponge
SC	sponge color (bright orange = 1, dark orange = 2, brown = 3, dark brown = 4, black = 5, and no sponge = 6)
SYMBIONTS	
BC	acorn barnacle ( <i>Chelonibia patula</i> , <i>Balanus</i> spp.) coverage of the exoskeleton (10% intervals)
BW	weight of acorn barnacles ( <i>Chelonibia patula</i> , <i>Balanus</i> spp.) removed from the exoskeleton
D	diameter of the largest acorn barnacle ( <i>Chelonibia patula</i> , <i>Balanus</i> spp.) on the exoskeleton
G	gooseneck barnacle ( <i>Octolasmis muelleri</i> ) intensity on the gills (based on a six point scale approximating 0, 10, 25, 50, 100, or more than 200)
GN	nemertean ( <i>Carcinonemertes carcinophila</i> , presence/absence) on the gills; gill nemerteans
SN	nemertean abundance ( <i>Carcinonemertes carcinophila</i> ) on a sponge (measured within a 1.6 cm diameter subsection and ranked from 0 to 3 as 0, 1-3, 4-6, or > 7 individuals)
OTHER VARIABLES	
A	area (Ship, Trinity, Tiger, inshore, offshore)
M	month (April, May, August, October)
PC	average peak monthly catch rate of mature female blue crabs (n/mo-30 min)
t	time ( $t_1 = 1988-91$ and $t_2 = 1992-2000$ )
TW	trawl width (m)

Linear measurements of the carapace were based on Williams (1974). They were carapace width from tip to tip of the lateral spines (TT), carapace width from base to base of the lateral spines (BB), length (L), and height (H). We estimated crab volume (V) as  $L * H * BB$ . We used a dial caliper for all linear measurements with the exception of TT where a measuring board was used. All linear measurements were made to the precision of  $\pm 1$  mm.

We recorded sex, stage of sexual maturity, and (for mature females) weighed the entire crab with ( $W_b$ ), and without (W), acorn barnacles *Chelonibia patula* (Ranzani, 1818) and *Balanus* spp. Missing legs were noted and the opposing leg, if present, was removed, weighed, and its weight added to the total. We removed and weighed the abdomen (AW) of all mature females. All wet weights were recorded to the precision of  $\pm 0.01$  g.

We took three measurements of acorn barnacles: percent barnacle coverage (BC) in 10% intervals; diameter (D) of the largest; and weight ( $BW = W_b - W$ ). We took two measurements of nemerteans *Carcinonemertes carcinophila* (Kölliker, 1845): nemertean presence/absence on the gills (GN) as 0 or 1 and sponge nemertean intensity (SN) within a 1.6 cm diameter subsection of the sponge as 0, 1-3, 4-6, or  $> 7$  individuals. Gooseneck barnacle (G) *Octolasmis muelleri* (Coker, 1902) abundance was ranked on a six point scale approximating 0, 10, 25, 50, 100, or more than 200 barnacles on the gills.

We recorded presence/absence of a sponge (P) and of hatched egg casings on the abdominal hairs of non-ovigerous crabs. We classified sponge color (SC) of ovigerous females as bright orange = 1, dark orange = 2, brown = 3, dark brown = 4, and black = 5 and used Jivoff et al. (2007) to estimate development time. We assigned non-ovigerous females with hatched egg casings a value of 6.



We determined egg abundance (E) per sponge from a subsample of twenty crabs stratified by length and month (ten from May and ten from August 2006) using a modification of Prager et al.'s (1990) dry weight technique. Here we generated an error term to test for outliers by using the average dry weight of three replicates of 200 eggs/sponge and did not extrapolate from our subsample to the entire sample of ovigerous crabs.

We established three readily apparent categories of ovarian development (O) after Hard (1945, p.8-9): inconspicuous, intermediate, and large. Inconspicuous was consistent with both Hard's stage 1 (ovary "small, inconspicuous, white in color") and his stage 5 (ovary "collapsed, grey or brownish in color"). Large was consistent with both Hard's stage 3 (ovary "preceding first ovulation...bright orange and of large size") and stage 4 (ovary "between ovulations...orange in color and of large size"). Intermediate was consistent with Hard's stage 2 ovary (ovaries yellow or light orange, and of intermediate size). For statistical analysis, inconspicuous, intermediate, and large were designated as one, two, and three respectively.

#### Statistical Framework

Statistical tests involved the use of simple regression analysis, ANCOVA, ANOVA, and stepwise multiple regression techniques (Freund and Wilson, 2003). SAS® version 9.1.3 (SAS Institute Inc., 2004) was used for all statistical analyses. PROC GLM was used for all tests with the exception of PROC GLMSELECT (factors affecting condition) and PROC MIXED (analysis of STTSC spatiotemporal patterns of abundance). PROC GLMSELECT allows the user to treat each level of a class variable as an independent effect using the 'split' statement. PROC MIXED adjusts for an unbalanced design, accounts for heterogeneous variance, and is relatively robust to small departures from normality. Analysis results were examined for significant interactions when necessary and appropriate *post-hoc* tests applied.

All size and weight data were  $\log_{10}$ -transformed with the exception of the national comparison of fecundity where E and TT (cm) were ln-transformed to conform to Prager et al. (1990). All statistical effects were considered significant at  $\alpha = 0.05$ . As the aggregate catch data we used from previously published literature were untransformed before the published means were computed, with the possible partial exception of Eggleston et al. (North Carolina State University, unpubl. data), we did not transform our catch data. Specific details for individual tests are provided in the descriptions of analyses that follow.

#### National Comparison of Condition Factor

The condition factor is the ratio of a fish's weight  $W$  to a linear estimate ( $X$ ) of its volume  $V$ . It is normally used to compare differing populations under the assumption that the heavier fish (per unit of volume) are healthier (e.g. Ricker, 1975). When  $W$  and  $X$  are measured over a range of sizes in at least two different populations, differences in the condition factor are normally tested using a linear form of the general size/weight relationship:

$$\log W = \log a + b * \log X. \quad (\text{Eq 1})$$

When raw data are available, an ANCOVA may be used to test differences between populations. When, as with blue crabs, only population-specific equations are available from the literature one can examine plots of the intercepts ( $\log a$ ) against the respective slopes ( $b$ ) for apparent conformity to, or deviation from, a single relationship which would apply for a homogenous population,

$$\log a = a' + b' * b \quad (\text{Eq 2})$$

where  $\log a$  and  $b$  are as in Eq 1, and  $a'$  and  $b'$  are constants.

With blue crabs, it is the convention when fitting Eq 1 to eliminate ovigerous females and use TT as a measure of X (e.g. Olmi and Bishop, 1983). Therefore, to compare the condition factor of STTSC crabs with those from nationally recognized spawning grounds we used our measures of W and TT for non-ovigerous STTSC blue crabs in Eq 1 and then employed the intercept and slope of the resulting ‘STTSC’ equation in Eq 2 to compare these parameters with those reported in the literature for other spawning areas where wet weights were used (i.e., Newcombe et al., 1949; Pullen and Trent, 1970; Olmi and Bishop, 1983; Rothschild et al., 1992; modified from Perry in Guillory et al., 2001; and Lipcius and Stockhausen, 2002).

#### National Comparison of Fecundity

To compare egg abundance E from our area and Chesapeake Bay we manually extracted the 1986 data from Prager et al.’s Fig. 3. These data represent the time period before recent declines in blue crab fecundity (Lipcius and Stockhausen, 2002). In an ANCOVA we regressed E versus TT, with area as a class variable.

#### National Comparison of Spawning Grounds

Fishery independent catch rates of mature female blue crabs in areas recognized as blue crab spawning grounds were reported by More (1969) for Galveston Bay, TX; Adkins (1972) for Terrebonne Bay, LA; Archambault et al. (1990) for Charleston Harbor, SC; Lipcius and Stockhausen (2002) for Chesapeake Bay, VA; and Eggleston et al. (North Carolina State University, unpubl. data) for Pamlico Sound, NC. Size and duration of the trawling efforts varied across these studies, as did number of areas sampled, duration and timing of study, and temporal aggregation of the published data. Most of the published studies represent at least two years of sampling and report data in monthly averages by area. Lipcius and Stockhausen (2002) divided

their catches into two time periods (t) based on abundance: high, pre-1992 ( $t_1$ ) and low, post-1991 ( $t_2$ ). No study statistically compared catch rates among years with different times and trawl dimensions with another study.

To compare catch rates we calculated the area and trawl width specific average untransformed peak monthly catch rates (PC) of mature female blue crabs and adjusted it for 30 min trawls for each of the above studies and for our study. Using ANCOVA we regressed PC versus trawl width (TW) and included Lipcius and Stockhausen's division of time as a class variable.

#### Continuous Spawning / Hatching Cycle

To estimate the recovery time for an ovary between successive sponge productions, we regressed the average ovarian condition of ovigerous females per sponge color against the respective embryo age in days (d, where  $d = 0$  at spawning) assuming that each successive sponge color represented three days of embryo development time (based on Jivoff et al., 2007). Then using the resulting regression equation, an average ovarian condition value for inter-brood females was predicted.

#### Best Morphometric Indicator of Weight

To find the best morphometric model, we first examined the relationship between crab weight W and four measurements of size: carapace width including TT, and excluding BB, the lateral spines; length L; and height H. Then we used the best indicator of carapace width along with the measurements of L and H to calculate an estimated volume V for each crab. Five ANCOVAs were run testing the relationship of these morphological variables and W with sponge present/absent as a class variable.

## Effects of Symbionts, Ovarian/Embryonic Development, Month, and Area on Weight

The variables included in the GLMSELECT procedure were estimated volume V, sponge presence/absence P, sponge color SC, ovarian development O, gill nemertean intensity GN, sponge nemertean intensity SN, gill barnacle intensity G, acorn barnacle weight BW, percent coverage of acorn barnacles BC, acorn barnacle diameter D, month (M), and area (A). A split statement was used to treat each level of month and area as an independent effect.

To test for an effect of M on weight of the abdomen AW with eggs, we ran an ANCOVA in which we regressed AW on V with M as a class variable. The data limited us to a consideration of ovigerous crabs with well developed embryos (sponge color > 3).

To test for an effect of embryonic development on the abdominal weight of the ovigerous crabs, we ran an ANCOVA in which we regressed AW on V with SC as a class variable.

## STTSC Spacio-Temporal Patterns of Abundance

We used PROC MIXED in an ANOVA to test for the effects of month (April, August, and October) and area (Ship, Trinity, Tiger, inshore, and offshore in Fig. 4.1) on blue crab abundance (crabs / 30 min. trawl) for 2007. Interactions were examined and *post-hoc* pairwise comparisons were made using a Tukey-Kramer adjustment.

## RESULTS

### General Description

During three years of seasonal sampling, 505 blue crabs were caught within the STTSC (Table 4.2). Overall, 99% were mature females of which 49% were ovigerous. Sponge colors of ovigerous crabs indicated an approximately equal distribution of embryonic developmental

stages from spawning to hatching with a slightly higher percentage possessing late stage eggs (Fig. 4.2a). Most of the non-ovigerous crabs possessed a large ovary (Fig. 4.2b) and showed evidence of a previous spawn in the form of hatched egg casings on their abdominal hairs (Fig. 4.2c). In addition, more than 25% of ovigerous females with late stage eggs also had a large ovary. One soft-shelled female was newly mated as evidenced by an enlarged and hardened spermathecae, and two hard-shelled females had recently mated as evidenced by an enlarged but softening spermathecae corresponding to Wolcott et al. (2005) scale's 1 and 2 respectively. The most common symbionts and their relative frequencies of occurrence were acorn barnacles *C. patula* and *Balanus* spp., 63%; gooseneck barnacles *O. muelleri*, 63%; nemerteans *C. carcinophila* on the gills, 24%, and nemerteans in sponges, 34%.

Table 4.2 Total number of female blue crabs sampled on Ship Shoal during 2005–06 and within the Ship, Trinity, Tiger Shoal Complex during 2007 as well as the percentage of the total that were ovigerous for 2006–2007.

	2005	2006		2007	
	number	number	% ovigerous	number	% ovigerous
Ship	98	178	53	101	35
Trinity	-	-	-	72	46
inshore	-	-	-	31	68
offshore	-	-	-	15	67
Tiger	-	-	-	8	75

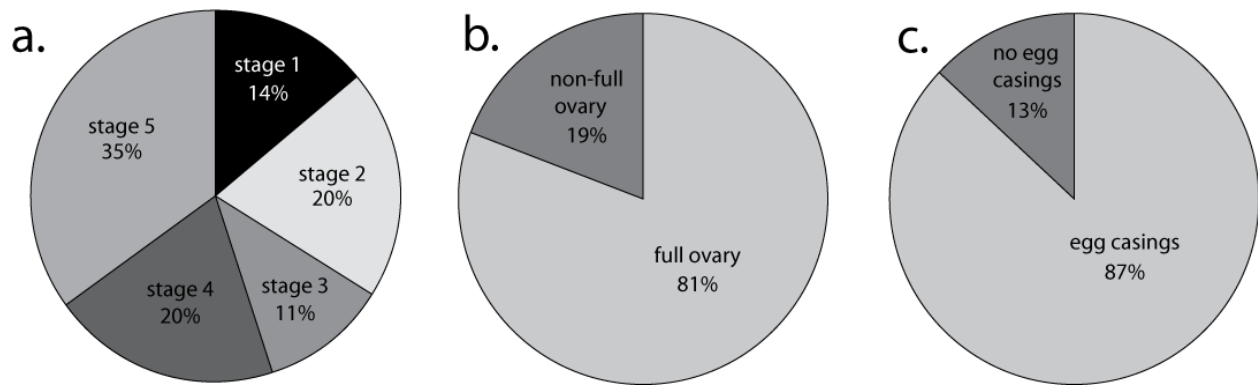


Figure 4.2 Percentages of: (a) different sponge colors (stage 1 to stage 5) for ovigerous STTSC blue crabs 2006-2007, (b) non-ovigerous females with and without a full ovary, (c) non-ovigerous females with and without evidence of a previous spawn (hatched egg casings on abdominal hairs).

#### Environmental Measurements

No seasonal trend was observed for salinity variation within the STTSC for 2007 (Table 4.3). Salinity ranged from 25.4 to 34.8 and was generally lower for the stations closer to shore (e.g. inshore and Tiger Shoal) during all sampling cruises. There was a seasonal trend observed for temperature: the lowest recorded April temperature was 20.4°C followed by a peak of 31.4°C in August, and a decrease to a low of 27.6°C in October. There was also a seasonal trend for dissolved oxygen. Highest dissolved oxygen values were recorded in April and October with lowest values for all areas recorded in August. Bottom water oxygen values below 2 mg/L (i.e., hypoxia) occurred only at deeper offshore trawling locations in August 2007. No hypoxic bottom water was found at stations shallower than 8 m. We observed one hypoxic reading at our deepest Ship Shoal station (no trawl), though shallower Ship Shoal stations remained free of hypoxia consistent with other shoal stations.

Table 4.3 Mean (range), salinity (Sal), temperature (Temp), and dissolved oxygen (DO) for 2007 trawl stations by area and month.

		Ship	Trinity	Tiger	inshore	offshore
Sal (ppt)	April	32.6	29.8	26.5	27.4	34.8
		(27.2 - 35.4)	(27.8 - 32.5)	(24.1 - 28.3)	(25.4 - 29.5)	(33.3 - 36.3)
	Aug	27	29.5	28.1	25.4	33.3
		(25.3 - 29.1)	(28.9 - 29.9)	(27.7 - 28.6)	(23.8 - 26.8)	(30.1 - 36.1)
	Oct	31.4	31.1	30.4	29.6	30.2
		(30.1 - 33.3)	(31 - 31.1)	(30.4)	(29 - 30.1)	(30.1 - 30.2)
Temp (°C)	April	22.2	22.9	23.3	22.2	21.4
		(21.6 - 22.8)	(22.1 - 23.4)	(23.1 - 23.5)	(22.1 - 22.3)	(20.4 - 22.1)
	Aug	30.8	31	30.9	31.1	29.3
		(30.6 - 31.1)	(30.7 - 31.3)	(30.8 - 30.9)	(30.9 - 31.4)	(27.5 - 31.2)
	Oct	28.1	27.8	27.6	27.9	27.9
		(28.1 - 28.2)	(27.8)	(27.6)	(27.8 - 27.9)	(27.7 - 28)
DO (mg/L)	April	6.8	7.1	7.1	4.3	5.5
		(5.5 - 7.7)	(6.7 - 7.7)	(7.0 - 7.4)	(3.6 - 5)	(2.5 - 6.9)
	Aug	4.1	4.7	4.5	4.4	3.7
		(2.9 - 5.2)	(4.4 - 5.2)	(4.4 - 4.5)	(2.3 - 5.6)	(0.5 - 5.5)
	Oct	5.9	6.4	6.2	5.8	6.1
		(5.6 - 6)	(6.3 - 6.4)	(6.2)	(5.6 - 6)	(5.9 - 6.3)

#### National Comparison of Condition Factor

The transformed STTSC data for non-ovigerous females provided the following significant fit to the linear form of the general size/weight relationship (Eq 1):

$$\log W = -3.0743 + 2.3966 * \log TT \quad (\text{Eq 3})$$

( $P < 0.0001$ ,  $R^2 = 0.80$ ). Use of all the available and comparable estimates of the constants  $\log a$  and  $b$  in Eq 2 generated a single significant regression of the form:

$$\log a = 1.9066 - 2.0603 * b \quad (\text{Eq 4})$$



( $P < 0.0001$ ,  $R^2 = 0.99$ , Fig. 4.3). The condition factor comparison (Eq 4 and Fig. 4.3) suggests a single width-weight relationship applies to all female blue crab populations reported in the literature despite wide geographical and temporal differences (Chesapeake Bay to Texas coasts, 1966-2007).

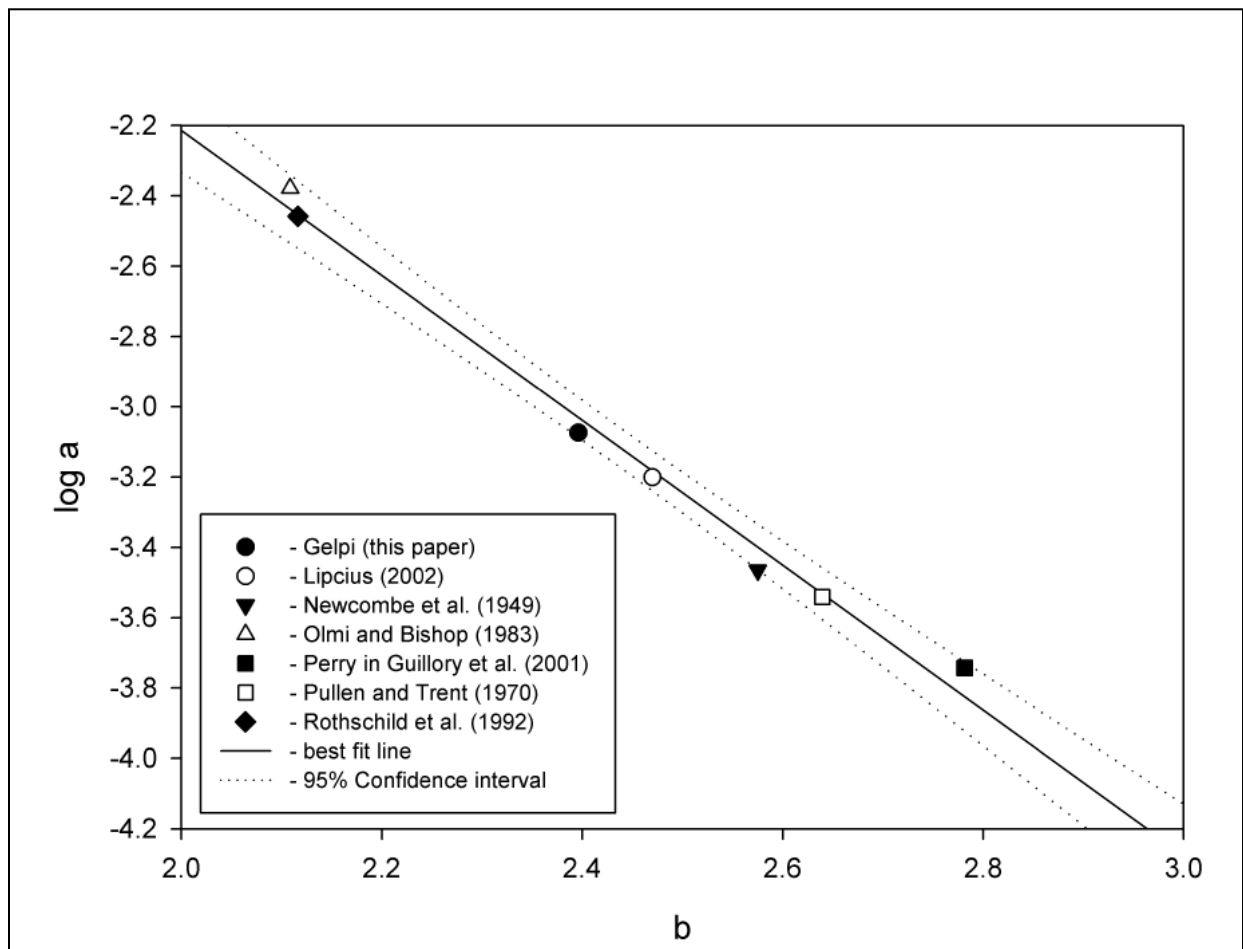


Figure 4.3 Results of an ANCOVA demonstrating the conformity of all published carapace width (TT, mm) – weight (W, g wet wt) relationships of non-ovigerous female blue crabs,  $\log W = \log a + b * \log TT$ , where TT = carapace width including the lateral spines.

## National Comparison of Fecundity

The ANCOVA comparing the fecundity of Chesapeake Bay and STTSC crabs found no significant interaction or class effect and generated the following single significant equation:

$$\ln E = -4.8453 + 2.1151 * \ln TT \quad (\text{Eq 5})$$

( $P < 0.0001$ ,  $R^2 = 0.31$ , Fig. 4.4). Eq 5 predicts a linear increase in E with increasing TT and finds no significant difference in the E versus TT relationship of ovigerous blue crabs from the two areas/time periods.

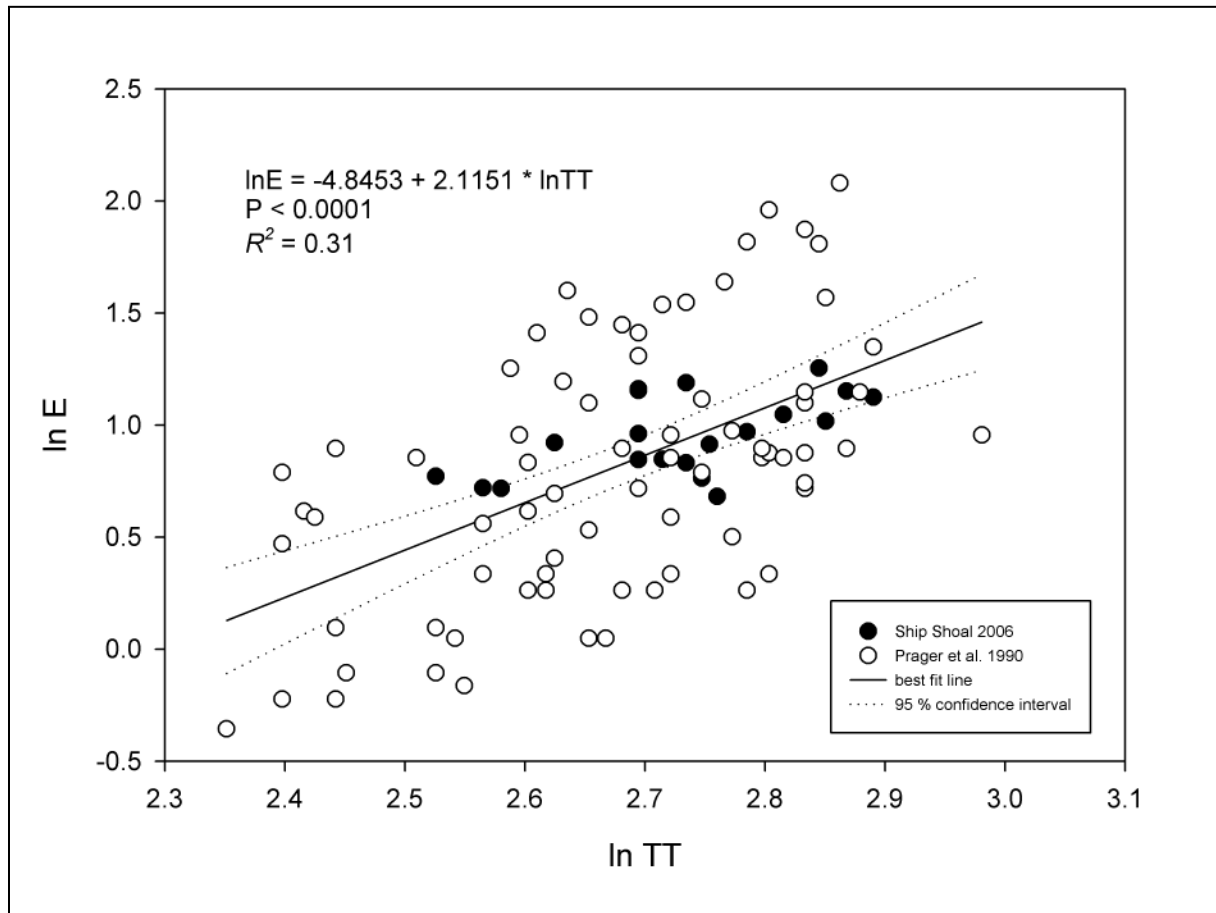


Figure 4.4 Results of ANCOVA comparing egg abundance in millions (E) vs. carapace width (TT, cm) including the lateral spines for mature female blue crabs from the Chesapeake Bay, VA (Prager et al., 1990) and Ship Shoal, LA, 2006.

## National Comparison of Spawning Grounds

In the ANCOVA run to compare abundance across known spawning grounds, the class variable  $t$  was significant ( $P = 0.0073$ ), but not TW ( $P = 0.8058$ ). The mean observed PCs for  $t_1$  and  $t_2$  were 35.5 and 8.3 crabs/30 min trawl respectively, representing a 76% decline in the mean peak monthly catch rates between these two time periods. As such, peak monthly catch rates for all areas within the STTSC are comparable to other known spawning grounds within the current time period ( $t_2$ , Table 4.4).

Table 4.4 Trawl width (TW) and peak catch rates (PC) of mature female blue crabs (adjusted for 30 min of trawl time) for studies of blue crab spawning grounds.

Author	TW (m)	Years of study	Area of study	PC
More (1969)	3	1966-1977	Galveston Bay, TX	44
Adkins (1972)	4.9	1969-1972	surf zone off Galveston Bay, TX	46
			lower Terrebonne Bay, LA	31.5
			mid Terrebonne Bay, LA	30.0
Archambault et al., (1990)	6	1979-1987	Charleston Harbor, SC	15.7
Lipcius and Stockhausen (2002)	9.1	1988-1991	Chesapeake Bay, VA	45.8
Eggleston et al., (unpublished data)	6.7	1992-2000		8.8
		2002	Pamlico Sound, NC	4.8
Present study	7.3	2005-2006	Ship Shoal	13
	12.8	2007		15.3
			Trinity Shoal	15
			Inshore STTSC	6
			Offshore STTSC	2
			Tiger Shoal	1.7

## Continuous Spawning / Hatching Cycle

The regression of  $O$  versus  $d$  was significant,

$$O = 0.9908 + 0.0971 * d \quad (\text{Eq 5})$$

( $P = 0.0023$ ,  $R^2 = 0.97$ ), and predicts that the ovary of non-ovigerous crabs will fully recover ( $O = 3$ ) 21 days after hatching. At the midpoint of the predicted inter-brood period (18 d) the predicted ovarian condition,  $O = 2.74$ , is remarkably similar to the observed average ovarian condition of non-ovigerous STTSC crabs where  $O = 2.73$  (Fig 4.5). This suggests a linear increase in ovarian development between successive spawns of STTSC crabs and that the STTSC crabs were in a continuous cycle of spawning, hatching, and ovarian replenishment from April through October.

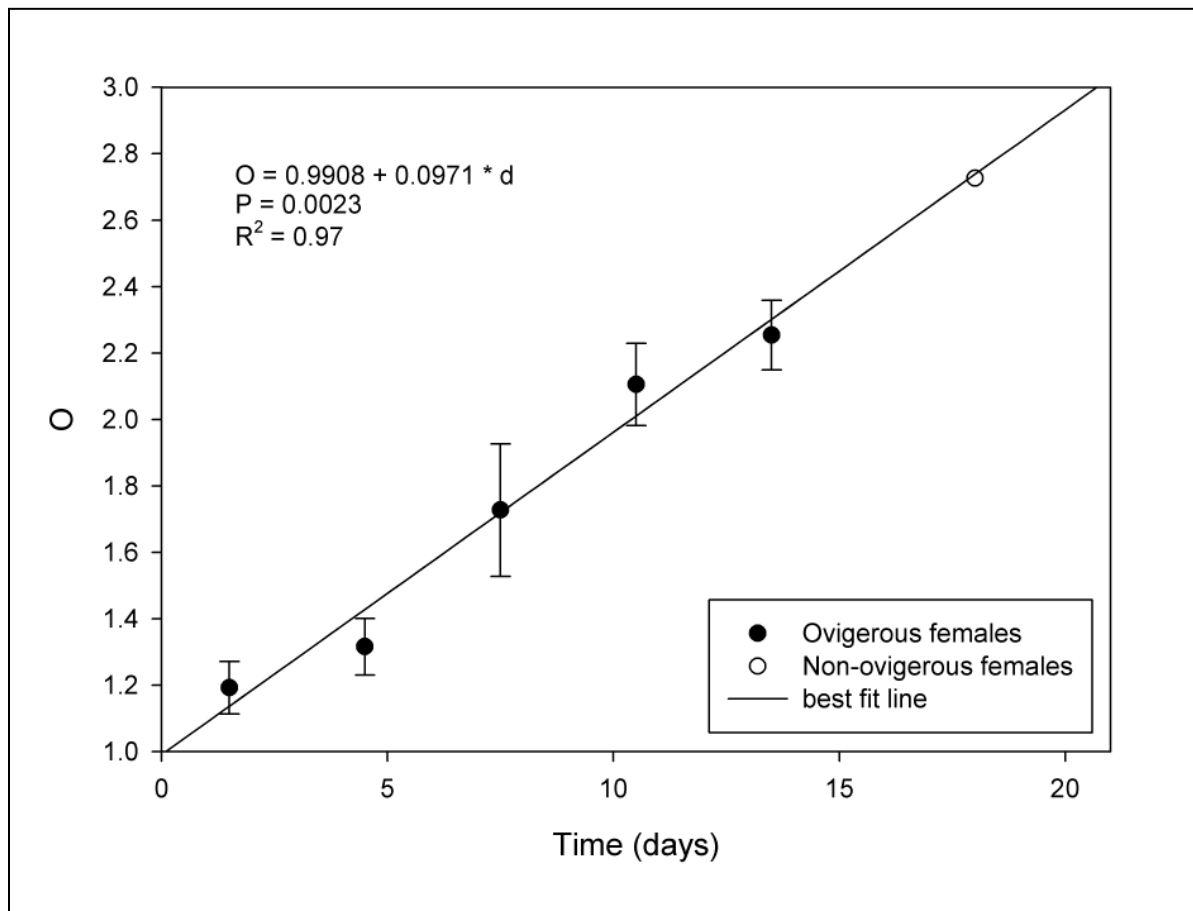


Figure 4.5 Average ovarian development ( $O$ ) for mature female blue crabs vs. estimated embryo development time in days, based on respective sequential egg color as follows: orange, dark orange, light brown, dark brown, and black. The regression was fit to our data for ovigerous crabs and then used to predict a time for the recovery implicit in the average ovarian condition of non-ovigerous crabs.

## Best Morphometric Indicator of Weight

In the comparison of estimators of weight derived from linear measurements, the volumetric estimator,  $V = L * H * BB$ , provided a slightly better predictor of  $W$  ( $R^2 = 0.966$ ) than all single linear measurements (Table 4.5). Of the single linear estimators,  $L$  was the best estimator of  $W$  ( $R^2 = 0.961$ ), though it was followed closely by  $BB$  and  $H$ . The traditionally used  $TT$  was the poorest estimator ( $R^2 = 0.806$ ).

Table 4.5 Comparison of size ( $X$ ) vs weight ( $W$ ) relationships,  $\log W = \log a + b (\log X)$ , for mature female blue crabs from the Ship, Trinity, Tiger Shoal Complex. Length equals  $L$ ; height,  $H$ ; carapace width including lateral spines,  $TT$ ; carapace width excluding lateral spines,  $BB$ . Solutions are results of ANCOVAs testing the effect of ovigery, where  $X$  is varied as in column one. Base equation is for ovigerous females. Weights of the non-ovigerous females were obtained by adding  $c$  to  $\log(a)$  and  $d$  to  $b$  (where  $a$  and  $b$  are the intercept and slope for ovigerous crabs and  $c$  and  $d$  are the adjustments for non-ovigerous crabs). When  $d = 0$ , the ANCOVA's interaction term was not significant and the equations reflect parallel slopes.

X estimator	$R^2$	$\log(a)$	$b$	$c$	$d$
L	0.961	-2.8452	2.8651	-0.5165	0.2424
H	0.925	-1.977	2.7446	-0.4573	0.2445
BB	0.942	-3.7103	2.9111	-0.0887	0
TT	0.806	-2.3349	2.1025	-0.7394	0.2942
$L*H*BB$	0.966	-2.9455	0.9682	-0.4627	0.0706

## Effects of Symbionts, Ovarian/Embryonic Development, Month, and Area on Weight

The stepwise procedure chose  $V$ ,  $P$ ,  $O$ ,  $M_{(August)}$ , and  $GN$  as the most predictive combination of variables:

$$\log W = -3.0894 + 0.9743 * \log V + 0.0960 * P + 0.0104 * O + 0.0081 * GN - 0.0105 * M_{(August)} \quad (\text{Eq 6})$$

( $P < 0.0001$ ,  $R^2 = 0.9715$ ). However, a more parsimonious model included only  $V$  and  $P$ ,

$$\log W = -3.2462 + 1.0085 * \log V + 0.0838 * P \quad (\text{Eq 7})$$

( $P < 0.0001$ ,  $R^2 = 0.9654$ ) with a slight 0.006 decrease in  $R^2$ .

Eq 6 predicted the weight of a crab where  $P$  and  $GN = 0$ ,  $M = 8$ ,  $O = 3$ , and  $V = 229.6 \text{ cm}^3$  was 142.8 g. For this case, when  $O = 1$ , predicted weight declined by 4.7%; when  $GN = 1$ , predicted weight increased by 1.9%; and when  $M = \text{April, May, and October}$ , predicted weight increased by 2.4%.

The ANCOVA run using abdominal weights with black/brown sponges found a significant main effect of month on the relationship between  $V$  and  $AW$ , but no significant interaction of  $M$  and  $AW$ . The resulting equation,

$$\log AW = a + 0.7151 * \log V,$$

where  $a = -0.0159$  for April,

$= -0.0522$  for May,

$= -0.0815$  for August, and

$= -0.0907$  for October (Eq 8)

( $P < 0.0001$ ,  $R^2 = 0.61$ ) suggests that the observed weight of black/brown sponges for a given length interval of STTSC crabs declined from April to October (Fig. 4.6).

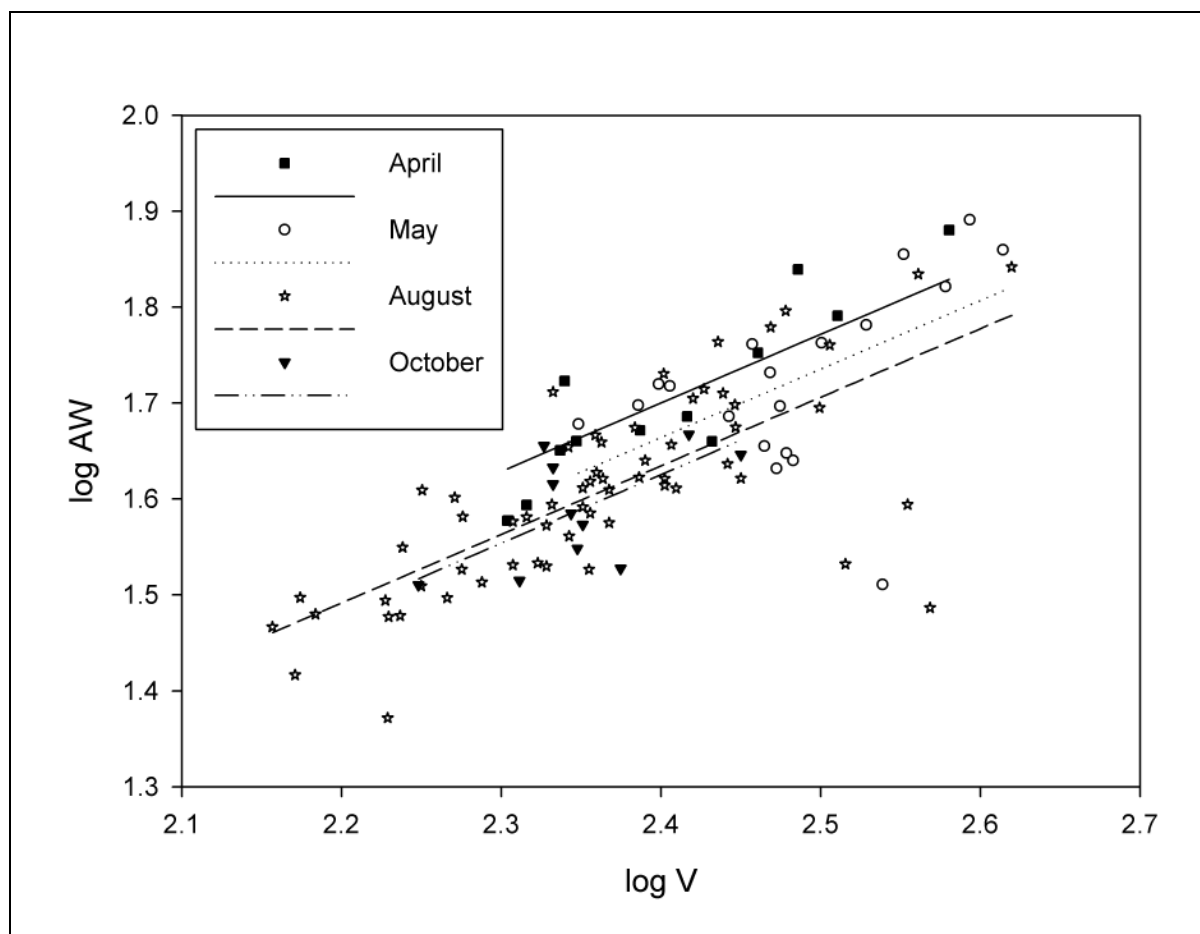


Figure 4.6 Results of ANCOVA testing the effect of month (M) on the logarithmic relationship between abdomen-sponge weight (AW) of ovigerous crabs with well developed embryos and estimated volume (V). Lines fit to the data are the solution to:  $\log AW = a + 0.7151 * \log V$ ; where  $a = -0.0159$  for April,  $-0.0522$  for May,  $-0.0815$  for August, and  $-0.0907$  for October ( $P < 0.0001$ ,  $R^2 = 0.61$ ). V is estimated as  $L * H * BB$ ; where L = length, H = height, and BB = carapace width excluding lateral spines.

The analysis of an effect of embryo development as evidenced by sponge color SC on the relationship between V and AW found a significant relationship,

$$\log AW = a + 0.7802 * \log V,$$

where  $a = -0.2748$  when  $SC = 1$ ,

$= -0.2678$  when  $SC = 2$ ,

$= -0.2479$  when  $SC = 3$ ,

$= -0.2158$  when  $SC = 4$ , and

$= -0.2301$  when  $SC = 5$  (Eq 9)

( $P < 0.0001$ ,  $R^2 = 0.60$ ), which indicates an approximate 10% increase in wet weight from stage 1 to stage 5, and suggests a fairly sudden increase in the wet weight of the sponge as SC increases above 2 (Fig. 4.7).

#### STTSC Spacio-Temporal Patterns of Abundance

The ANOVA found a significant area effect ( $F_{4,36} = 5.57$ ,  $P < 0.01$ ) and month effect ( $F_{2,36} = 10.71$ ,  $P < 0.01$ ) as well as a significant area by month interaction ( $F_{8,36} = 2.62$ ,  $P = 0.02$ ) on female blue crab abundance in the STTSC for 2007. Pairwise comparisons found that mean area catch rates for Ship and Trinity Shoals in August were significantly greater than those from the STTSC offshore area and Tiger Shoal for all months (Fig. 4.8; Tukey-Kramer;  $P < 0.05$ ). In addition, Ship Shoal had significantly greater mean area catch rates across all months than the STTSC offshore area and Tiger Shoal, while Trinity Shoal had significantly greater mean area catch rates across all months than Tiger Shoal (Tukey-Kramer;  $P < 0.05$ ). Mean monthly catch rates across all areas were significantly higher in August than April and October (Tukey-Kramer;  $P < 0.01$ ).



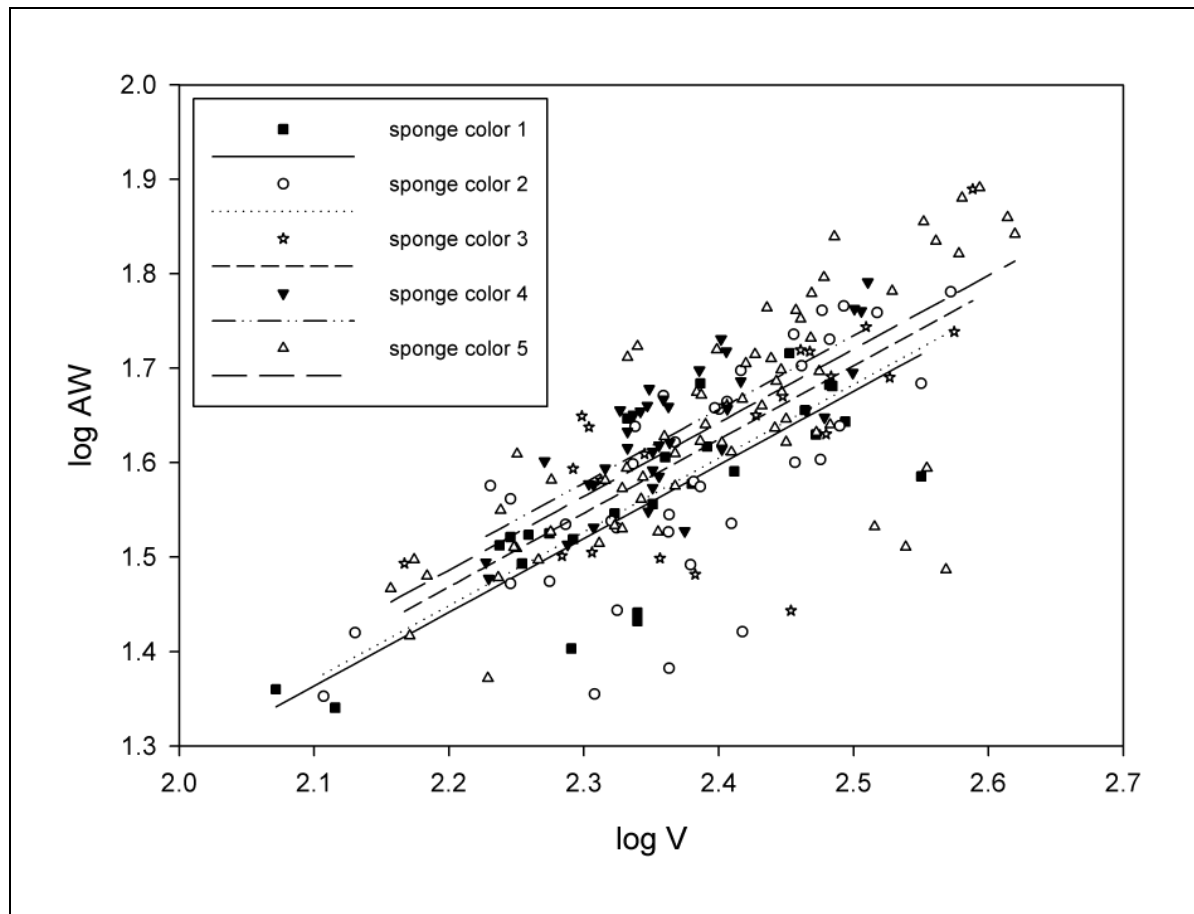


Figure 4.7 Results of ANCOVA testing the effect of the embryo development stage on the relationship between abdomen-sponge weight (AW) of ovigerous crabs and estimated volume (V). Lines fit to the data are the solution to  $\log T = a + 0.7802 * \log V$ , where  $a = -0.2748$  when  $SC = 1$ ,  $-0.2678$  when  $SC = 2$ ,  $-0.2479$  when  $SC = 3$ ,  $-0.2158$  when  $SC = 4$ , and  $-0.2301$  when  $SC = 5$  ( $P < 0.0001$ ,  $R^2 = 0.60$ ). V is estimated as  $L * H * BB$ ; where L = length, H = height, and BB = carapace width excluding lateral spines.

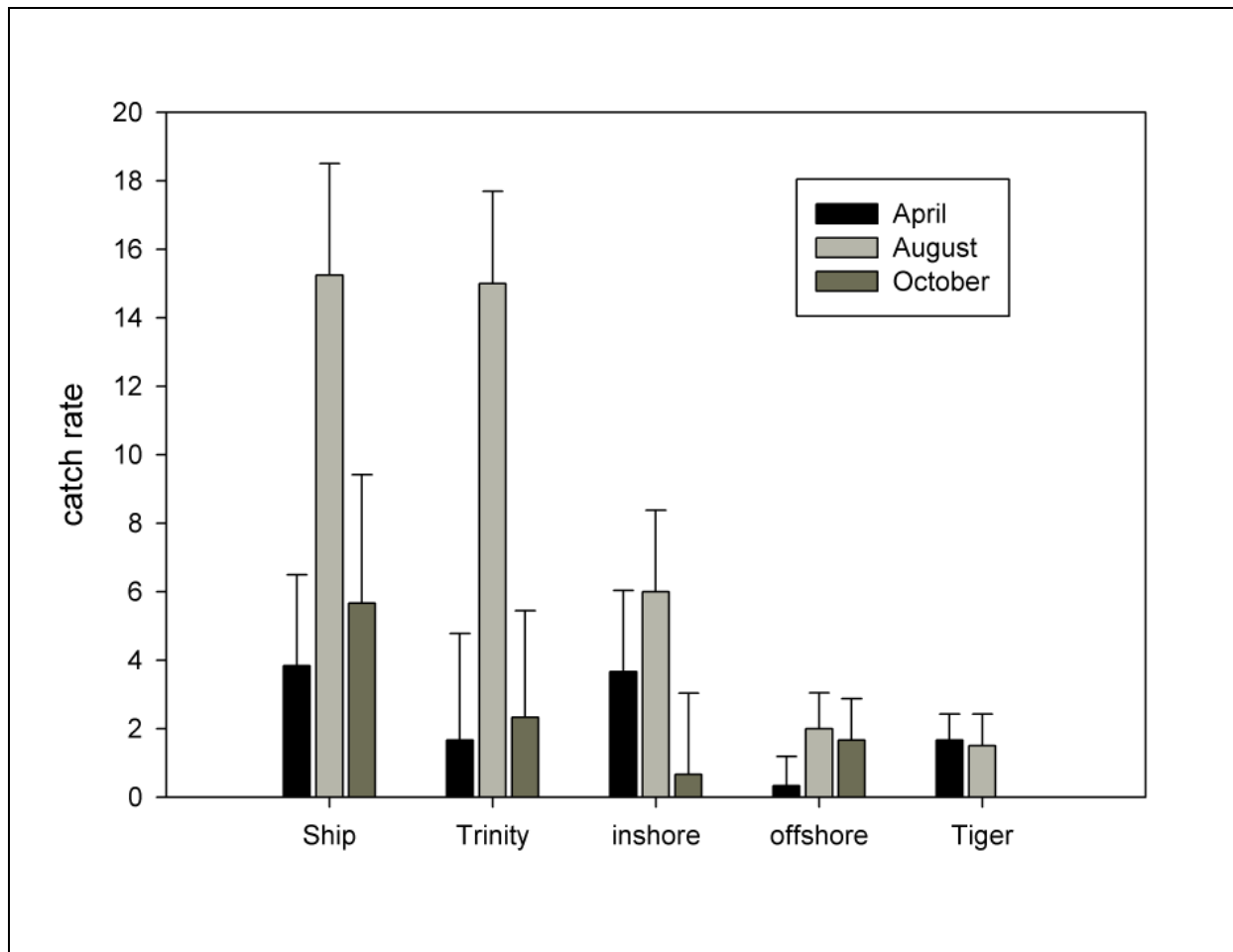


Figure 4.8 Comparison of mean monthly catch rates of mature female blue crabs in the Ship, Trinity, Tiger Shoal Complex, April-October 2007.

## DISCUSSION

All of our statistical tests support the argument that STTSC female blue crabs compare favorably to those from other recognized spawning grounds in terms of condition factor (Fig. 4.3), fecundity (Fig. 4.4) and abundance (Table 4.4). Actively spawning, hatching, and foraging blue crabs were present from at least April through October within the STTSC with highest abundances occurring in August on Ship and Trinity Shoals (Fig. 4.8). These results strongly suggest that Ship Shoal and Trinity Shoal, within the STTSC, are locally important, though

unprotected, offshore blue crab spawning, hatching, and foraging grounds which may have national significance for the blue crab fishery.

Blue crab catch rates for STTSC inshore areas were highest during April and August but declined in October toward the end of the spawning season. STTSC offshore areas had their highest catch rates in August and October suggesting an increased utilization of the offshore later in the spawning season while high concentrations were sampled on Ship and Trinity Shoals throughout the spawning season. These patterns may reflect a continued seaward migration to the offshore region including Ship and Trinity Shoals. A continued seaward migration of our ovigerous female blue crabs is consistent with behavioral experiments and field observations in Bogue Sound, North Carolina (Hench et al., 2004), where the authors found that females with late-stage eggs and post-release females used ebb-tide-transport and suggested that crabs may continue a seaward migration to release subsequent clutches.

Based on our analysis of ovarian replenishment (Fig. 4.5), STTSC blue crabs are capable of producing at least seven broods in a spawning season. This is consistent with the *in situ* findings of Hines et al. (2003) and Dickenson et al. (2006) that documented the production of up to seven broods by mature female crabs in Indian River Lagoon, Florida, and Beaufort, North Carolina, respectively. In these studies female blue crabs were fed daily, which suggests that a consistent food source such as that found on Ship and Trinity Shoals (Chapter 2) is beneficial to sustain successive brood production. There was no significant difference in egg abundance between STTSC crabs and those from Chesapeake Bay (Fig. 4.4) using data from that area before recent declines in abundance of spawning females. There was also a 20% decrease in the sponge wet weight (for at least females with broods close to hatching) from April to October for STTSC crabs (Fig. 4.6). This may be due to the seasonal decrease in macrofaunal prey as was

noted by Dubois et al. in press for Ship Shoal in 2006 and a subsequent reduction in available energy for egg production or to some effect of age of the female (i.e., Dickenson et al., 2006), a decline in the number of viable sperm in subsequent fertilization events (i.e., Hines et al., 2003), or changes in environmental gradients (i.e., Jivoff et al., 2007).

We speculate that abundant prey resources for crabs contribute to high crab abundance on Ship and Trinity Shoals as we have found 2007 STTSC macroinfaunal biomass higher on the shoals than off the shoals (Chapter 3). In turn, macroinfaunal biomass on Ship Shoal may be more dependent upon benthic microalgae than phytoplankton, while the inverse may be true for Trinity and Tiger Shoal's macroinfauna (Grippio 2009). Seitz et al. (2003) found blue crab and bivalve *Macoma balthica* (Linnaeus, 1758) densities were positively correlated on sandy substrate within the York River of Lower Chesapeake Bay. In 2006, macrofaunal biomass declined on Ship Shoal (Dubois et al. 2009) concurrent to the influx of spawning blue crabs, which is consistent with blue crab predator/prey responses in the Chesapeake Bay (Hines et al., 1990; Eggleston et al., 1992). Tiger Shoal catch rates were lower than those on Ship or Trinity Shoals and possibly an artifact of lower sampling frequency or suggestive of differences in environmental quality, fishing pressure, predation pressure, or recruitment rates that may exist among shoals. More study is needed to determine if such differences among shoals exist.

STTSC's high-relief shoals may provide other ecological services that enhance blue crab fitness. Principally, shoals may also be acting as hypoxia refuges. They are located within an area of seasonal bottom-water hypoxia (Rabalais et al., 2002). Bottom water on the Shoals was not hypoxic (i.e.  $DO < 2$  mg/L) during our cruises with the exception of the deepest shoal station during the August 2007 sampling when many of the deeper off-shoal stations were also hypoxic. It is possible that blue crabs avoid local low oxygen conditions by seeking refuge on the shoals.

This observation would be consistent with Pihl et al. (1991) who concluded that blue crabs were “shown to migrate from deeper hypoxic to shallower normoxic areas in Chesapeake Bay.”

In higher latitude estuaries around Chesapeake Bay female blue crabs are known to concentrate in polyhaline areas before brood production, while “at lower latitudes, mature and ovigerous females also aggregate in high salinity zones” (Hines, 2007). Salinity ranged from 23.8 to 36.3 for our trawl areas within the STTSC, though the salinity in areas further from shore (e.g. Ship, Trinity, offshore) was generally higher (Table 4.3). The offshore location of the shoals may benefit blue crab larvae compared with larval release locations in lower estuarine areas or those offshore areas close to the shore. High salinities, like those on the shoals, are necessary to prevent osmotic stress (Sandoz and Rogers, 1944). Larval mortality may be reduced in offshore waters through avoidance of estuarine predators (Morgan, 1990). The offshore location of the shoals may provide a broader dispersal range thus reducing density-dependent mortality (Eggleston et al. 1992), decreasing the likelihood of passive transport into the estuary before the zoeal larval stages are completed, and benefiting the genetic diversity of a northern Gulf metapopulation. Cochrane and Kelly (1986) and Walker et al. (2005) describe a westward coastal current off central/western Louisiana and eastward return flow along this portion of the Louisiana shelf. This should move larvae west along the coast yet retain them on the Louisiana-Texas shelf (Cowan et al., 2008). Perry et al. (2003) found wind patterns in the northern Gulf of Mexico aid in recruitment by returning megalope to the nearshore within the Mississippi Bight. Thus, previous studies suggest that blue crab larvae hatched in STTSC also have access to coastal marshes and that juveniles will enter the marsh populations.

With the possible exception of Perry (1975), blue crab mating is reported to occur in the lower salinity waters of upper estuaries. Although rare in our sampling, we found evidence of

blue crabs mating on Trinity and Ship Shoals suggesting that mating pairs are not strictly confined to the upper estuary. This finding suggests blue crab populations have the potential to successfully mate in the open ocean; a potential which could conceivably prove advantageous given the current threat of estuarine habitat loss exacerbated by sea-level increases associated with global climate change.

### Management Implications

Accurately predicting blue crab weight from a linear measure of crab size is an important tool in assessing blue crab stocks and health. Most previous blue crab studies incorporating size measured carapace width including the lateral spines TT. However the lateral spines introduce variability due to broken tips and differences in spine morphology (Olmi and Bishop, 1983). The finding that estimated volume ( $V = L * H * BB$ ) is the best predictor of crab weight (Table 5) has implications for future research in the blue crab fishery and the fisheries of other heavily exploited swimming crab species such as *Portunus trituberculatus* (Miers, 1876) and *P. pelagicus* (Linnaeus, 1758). Measurement of V, although slightly more time consuming, is a much better predictor than TT and may be more forgiving of small measurement errors than any one of the single linear estimators of which it is composed. We suggest future studies phase out the use of TT and replace it with V. In addition, we encourage the measurement of crab weight and volume for ovigerous as well as non-ovigerous crabs.

Ship and Trinity Shoals potentially support an important component of the Gulf of Mexico spawning stock. Ship and Trinity Shoals' blue crab spawning grounds have a combined area of  $\sim 1000 \text{ km}^2$ , none of which is protected. By comparison, the historical blue crab spawning sanctuary in lower Chesapeake Bay apparently encompassed  $\sim 775 \text{ km}^2$  (Fig. 1 in Lipcius et al., 2003). Amid decreasing spawning stocks, this protected area has since been expanded to include

a migration corridor of post-mated females (Lipcius et al., 2003). North Carolina has established five Pamlico Sound spawning sanctuaries which total ~120 km<sup>2</sup>. Eggleston et al. (North Carolina State University, unpubl. data) present evidence that these “spawning sanctuaries are too small to protect the spawning stock in North Carolina”.

Presently, there does not appear to be a directed fishery currently operating on female blue crabs within the STTSC. The current social norm in Louisiana, Gulf of Mexico, and the nation seems to favor a protection of ovigerous females. In contrast, there is a national/international market for non-ovigerous female blue crabs with ‘full ovaries’, a condition characteristic of at least our ‘sponge color = 6’ females, (Fig. 4.5). The current lack of a directed fishery on the reproductively active STTSC crabs, particularly on Ship and Trinity Shoals, likely enhances the stability of Louisiana and the Gulf’s traditional inshore blue crab fishery. A conservative management would help maintain the stability of the current inshore blue crab fishery by protecting Ship and Trinity Shoals, as well as all other STTSC blue crabs, from a directed harvest of STTSC blue crabs until their contribution to the health of the current inshore fishery can be assessed.

There is an increasing need to understand the potential impact of sand and gravel mining in coastal-ocean systems to aid in policy decisions. Few ecological studies have examined the functional value of high-relief sandy shoals in their ecosystems, especially in terms of biodiversity and associated ecological services. Within our study area, sand mining may have negative impacts on spawning blue crabs given the possibility that fecundity of blue crabs on Ship Shoal becomes seasonally limited by prey abundance (Chapter 2) under prevailing natural conditions. Palmer et al. (2008) reported significant sand-mining related declines in macrofaunal abundance, biomass, and diversity within coastal Louisiana. It is likely that sand-mining

disturbance and subsequent reduction in available macrofauna prey would result in negative effects on spawning blue crab health and fecundity. Sand mining may also alter the sediment composition from that preferred by STTSC females. Schaffner and Diaz (1988) found that overwintering females in the Lower Chesapeake spawning grounds preferred certain sediment types with high concentrations of sand. Other studies (Ryan, 1967b; Kuris, 1991) have suggested that sediment is necessary for the successful spawning and egg adherence to the hairs of the pleopods. In addition, the threat of hypoxia would increase if the depth on the shoals were increased to a point where wave action could no longer keep the bottom water well oxygenated (Kobashi et al., 2007).

Management should act now to create a blue crab spawning sanctuary in the STTSC. National efforts to restore the Chesapeake Bay and North Carolina populations have found no inexpensive “quick fixes”. For example, Chesapeake Bay stock enhancement scientists “expect the production cost of blue crab juveniles will be in the range of US \$0.15 – 0.30/juvenile” and that there will be a “10% survival of cultured females until spawning in the sanctuary” (Zohar et al., 2008). Under this scenario, the production costs associated with the arrival of mature female blue crabs from a hatchery to the STTSC spawning grounds would be \$18 to \$36/dozen, or approximately the current retail price of blue crabs in the Louisiana market. In light of the blue crab crisis on the east coast and the extensive efforts under way to restore the east coast spawning stock, it makes financial and ecological sense to protect these natural, though previously unknown, blue crab spawning, hatching, and foraging areas in the offshore federal waters of the STTSC.



## LITERATURE CITED

- Adkins, G. 1972. A study of the blue crab fishery in Louisiana. Tech. Bull. 3. Louisiana Wildlife and Fisheries Commission, Oysters, Water Bottoms and Seafoods Division, New Orleans. 57 p.
- Aguilar, R., E. G. Johnson, A. H. Hines, M. A. Kramer, M. R. Goodison. 2008. Importance of blue crab life history for stock enhancement and spatial management of the fishery in Chesapeake Bay. *Reviews in Fisheries Science*. 16:117-124.
- Archambault, J. A., E. L. Wenner, J. D. Whitaker. 1990. Life history and abundance of blue crab, *Callinectes sapidus* Rathbun, at Charleston Harbor, South Carolina. *Bulletin of Marine Science*. 46:145-158.
- Braud, D. 1999. Louisiana GIS CD: a digital map of the state. Version 2.0. Louisiana State University, Department of Geography and Anthropology. Baton Rouge.
- Churchill, E. P., Jr. 1919. Life history of the blue crab. *Bulletin of the Bureau of Fisheries*. 36: 91-128.
- Cochrane, J. D., F. J. Kelly. 1986. Low-frequency circulation on the Texas-Louisiana continental shelf. *Journal of Geophysical Research Oceans*. 91:645-659.
- Cowan, J. H., C. B. Grimes, R. F. Shaw. 2008. Life history, history, hysteresis, and habitat changes in Louisiana's coastal ecosystem. *Bulletin of Marine Science*. 83:197-215.
- Dickinson, G. H., D. Rittschof, C. Latanich. 2006. Spawning biology of the blue crab, *Callinectes sapidus*, in North Carolina. *Bulletin of Marine Science*. 79:273-285.
- Dubois, S. F., C. G. Gelpi, Jr., R. E. Condrey, J. W. Fleeger. 2009. Diversity and composition of macrobenthic community associated with sandy shoals of the Louisiana continental shelf. *Biodiversity Conservation*. 18:3759-3784.
- Dudley, D. L., M. H. Judy. 1971. Occurrence of larval, juvenile, and mature crabs in the vicinity of Beaufort Inlet, North Carolina. U.S. Dept. Commer. NOAA Tech. Rep. NMFS SSRF-637. 10 p.

- Eggleston, D. B., R. N. Lipcius, A. H. Hines. 1992. Density-dependent predation by blue crabs upon infaunal clam species with contrasting distribution and abundance patterns. *Marine Ecological Progress Series*. 85:55-68.
- Eggleston, D. B., E. G. Johnson, G. T. Kellison, G. R. Plaia, C. L. Huggett. 2008. Pilot evaluation of early juvenile blue crab stock enhancement using a replicated BACI design. *Review of Fisheries Science*. 6:91-100.
- Freund, R. J., W. J. Wilson, 2003. Statistical methods. Academic Press, San Diego, California. 673 p.
- Grippo, M. A., J. W. Fleeger, R. E. Condrey, K. R. Carman. 2009. High biomass of benthic microalgae found on Ship Shoal, north-central Gulf of Mexico. *Bulletin of Marine Science*. 84:237-256.
- Guillory, V., H. Perry, S. Vanderkooy. 2001. width-weight Relationships. 3-35 to 3-36. in The blue crab fishery of the Gulf of Mexico, United States: A regional management plan. Gulf States Marine Fisheries Commission, Oceans Springs, Mississippi.
- Hard, W. L. 1945. Ovarian growth and ovulation in the mature blue crab, *Callinectes sapidus* Rathbun. *Chesapeake Biological Laboratory* (Solomons, Maryland) *Contribution*. 46:3-17.
- Hench, J. L., R. B. Forward, Jr., S. D. Carr, D. Rittschof, R. A. Luettich, Jr. 2004. Testing a selective tidal-stream transport model: Observations of female blue crab (*Callinectes sapidus*) vertical migration during the spawning season. *Limnology and Oceanography*. 49:1857-1870.
- Hines, A. P. 2007. Ecology of juvenile and adult crabs. 565-654 in V.S. Kennedy and L. E. Cronin, ed. The blue crab *Callinectes sapidus*. Maryland Sea Grant College, College Park, Maryland.
- Hines, A. P., A. M. Haddon, L. A. Wiechert. 1990. Guild structure and foraging impact of blue crabs and epibenthic fish in a subestuary of Chesapeake Bay. *Marine Ecology Progress Series*. 62:105-126.
- Hines, A. P., P. R. Jivoff, P. J. Bushmann, J. van Montfrans, S. A. Reed, D. L. Wolcott, T. G. Wolcott. 2003. Evidence for sperm limitation in the blue crab, *Callinectes sapidus*. *Bulletin of Marine Science*. 72:287-310.

- Jivoff, P., A. H. Hines, L. S. Quackenbush. 2007. Reproductive biology and embryonic development. 255-286 in V.S. Kennedy and L. E. Cronin, eds. The blue crab *Callinectes sapidus*. Maryland Sea Grant College, College Park, Maryland.
- Kobashi, D., F. Jose, G. W. Stone. 2007. Impacts of fluvial fine sediments and winter storms on a transgressive shoal, off South-Central Louisiana, U.S.A. Proceedings of the 9th International Coastal Symposium. *Journal of Coastal Research*. Gold Coast, Australia, (SI 50): 858-862.
- Kuris, A. M. 1991. A review of patterns and causes of crustacean brood mortality. 117 – 141 in A. Wenner and A. Kuris, eds. Crustacean Issues 7: Crustacean egg production. A. A. Balkema, Rotterdam.
- Lipcius, R. N., W. T. Stockhausen. 2002. Concurrent decline of the spawning stock, recruitment, larval abundance, and size of the blue crab *Callinectes sapidus* in Chesapeake Bay. *Marine Ecology Progress Series*. 226:45-61.
- Lipcius, R. N., W. T. Stockhausen, R. D. Seitz, and P. J. Geer. 2003. Spatial dynamics and value of a marine protected area and corridor for the blue crab spawning stock in Chesapeake Bay. *Bulletin of Marine Science*. 72:453-469.
- More, W. R. 1969. A contribution to the biology of the blue crab *Callinectes sapidus* Rathbun in Texas, with a description of the fishery. Tech. Ser. 1. Texas Parks and Wildlife Department, Seabrook, Texas. 31 p.
- Morgan, S. G. 1990. Impact of planktivorous fishes on dispersal, hatching, and morphology of estuarine crab larvae. *Ecology*. 71:1639-1652.
- Newcombe, C. L., F. Campbell, A. M. Eckstine. 1949. A study of the form and growth of the blue crab *Callinectes sapidus* Rathbun. *Growth*. 13:71-96.
- NOAA. 2007. Annual commercial landing statistics. National Oceanographic and Atmospheric Administration, National Marine Fisheries Service, Office of Science & Technology, Commercial Fisheries. 1315 East-West Highway, Silver Spring, MD 20910: August 6, 2007. Available from: [http://www.st.nmfs.noaa.gov/st1/commercial/landings/annual\\_landings.html](http://www.st.nmfs.noaa.gov/st1/commercial/landings/annual_landings.html).
- Olmi, E. J., J. M. Bishop. 1983. Variations in total width-weight relationships of blue crabs, *Callinectes sapidus*, in relation to sex, maturity, molt stage, and carapace form. *Journal of Crustacean Biology*. 3:575-581.

- Palmer, T. A., P. A. Montagna, R. B. Nairn. 2008. The effects of a dredge excavation pit on benthic macrofauna in offshore Louisiana. *Environmental Management*. 41:573-583.
- Perry, H. M. 1975. The blue crab fishery in Mississippi. *Gulf Research Reports*. 5: 39-57.
- Perry, H. M, D. R. Johnson, K. Larsen, C. Trigg, F. Vukovich. 2003. Blue crab larval dispersion and retention in the Mississippi Bight: Testing the hypothesis. *Bulletin of Marine Science*. 72:331-346.
- Pihl, L., S. P. Baden, R. J. Diaz. 1991. Effects of periodic hypoxia on distribution of demersal fish and crustaceans. *Marine Bioogy*. 108:349-360.
- Prager, M. H., J. R. McConaugha, C. M. Jones, P. J. Geer. 1990. Fecundity of blue crab, *Callinectes sapidus*, in Chesapeake Bay: Biological, statistical and management considerations. *Bulletin of Marine Science*. 46:170-179.
- Pullen, E. J., W. L. Trent. 1970. Carapace width-total weight relation of blue crabs from Galveston Bay, Texas. *Transactions of the American Fisheries Society*. 99:795-798.
- Rabalais, N. N., R. E. Turner, W. J. Wiseman. 2002. Gulf of Mexico hypoxia, aka "The Dead Zone". *Annual Review Ecology and Systematics*. 33:235-263.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada*. 191:382 p.
- Roberts, H. H. 1997. Dynamic changes of the Holocene Mississippi River delta plain: The delta cycle. *Journal of Coastal Research*. 13:605-627.
- Rothschild, B. J., J. S. Ault, E. V. Patrick, S. G. Smith, H. Li, T. Maurer, B. Daugherty, G. Davis, C. I. Zhang, R. N. McGarvey. 1992. Weight-width relationship. 136-138. *in* Assessment of the Chesapeake Bay blue crab stock. Chesapeake Biological Laboratory. University of Maryland, Center for Environmental and Estuarine Studies. Solomons, Maryland.
- Ryan, E. P. 1967b. Structure and function of the reproductive system of the crab *Portunus sanguinolentus* (Herbst) (Brachyura: Portunidae) II. The female system. 522-544. *in* Proceedings of the symposium on crustaceans. Marine Biological Association of India.

- Sandoz, M., R. Rogers. 1944. The effect of environmental factors on hatching, moulting, and survival of zoea larvae of the blue crab *Callinectes sapidus* Rathbun. *Ecology*. 25:216-228.
- Schaffner, L. C., R. J. Diaz. 1988. Distribution and abundance of overwintering blue crabs, *Callinectes sapidus*, in the Lower Chesapeake Bay. *Estuaries*. 11:68-72.
- SAS Institute Inc. 2004. SAS OnlineDoc® 9.1.3. Cary, NC.
- Seitz, R. D., R. N. Lipcius, W. T. Stockhausen, K. A. Delano, M. S. Seebo, P. D. Gerdes. 2003. Potential bottom-up control of blue crab distribution at various spatial scales. *Bulletin of Marine Science*. 72:471-490.
- UN. 2008. UN atlas of the oceans. 2008. FAO Fisheries Global Information System (FIGIS) – Species. Species of major importance to fisheries: under blue crab. 2008. Available from: <http://www.fao.org/fishery/species/2632>.
- Van Engel, W. A. 1958. The blue crab and its fishery in Chesapeake Bay. *Commercial Fisheries Review*. 20:1-17.
- Walker, N. D., W. J. Wiseman, L. J. Rouse, A. Babin. 2005. Effects of river discharge, wind stress, and slope eddies on circulation and the satellite-observed structure of the Mississippi River plume. *Journal of Coastal Research*.. 21:1228-1244.
- Williams, A. B. 1974. Swimming crabs of genus *Callinectes* (Decapoda-Portunidae). *Fishery Bulletin*. 72:685-798.
- Wolcott, D. L., C. W. B. Hopkins, T. G. Wolcott. 2005. Early events in seminal fluid and sperm storage in the female blue crab *Callinectes sapidus* Rathbun: Effects of male mating history, male size, and season. *Journal of Experimental Marine Biology and Ecology*. 319:43-55.
- Zohar, Y., A. H. Hines, O. Zmora, E. G. Johnson, R. N. Lipcius, R. D. Seitz, D. B. Eggleston, A. R. Place, E. J. Schott, J. D. Stubblefield, J. S. Chung. 2008. The Chesapeake Bay blue crab (*Callinectes sapidus*): a multidisciplinary approach to responsible stock replenishment. *Reviews in Fisheries Science*. 16:24-34.

**CHAPTER 5: ISOTOPIC EVIDENCE OF AN ESTUARINE-OFFSHORE  
CONNECTION FOR THE LOUISIANA BLUE CRAB SPAWNING STOCK**

## INTRODUCTION

Globally, sandy shoals are under-explored areas on the continental shelf that are difficult to sample and are too frequently overlooked by biologists. Examples within the north-central Gulf of Mexico are Ship, Trinity, and Tiger Shoals (Fig. 5.1). Located 25 to 40 km offshore, they are high-relief (water depth 3 to 10 m), subaqueous stands of mostly sandy sediment within the otherwise muddy Mississippi/Atchafalaya River depositional plain (water depth 4 to 19 m). These shoals and their surrounding muddy bottoms constitute the Ship, Trinity, Tiger Shoal Complex (STTSC; Fig. 5.1). The STTSC is heavily influenced by nutrients, freshwater, and sediments associated with the Mississippi and Atchafalaya Rivers which contribute to large phytoplankton blooms and an extensive expanse of seasonal bottom-water hypoxia (Rabalais et al. 2002). Despite growing recognition of their ecological importance (e.g., Gelpi et al. 2009; Dubois et al. 2009; Grippo et al. 2010), Ship and Trinity Shoals are targeted for sand mining for coastal restoration projects including barrier island restoration and berm construction.

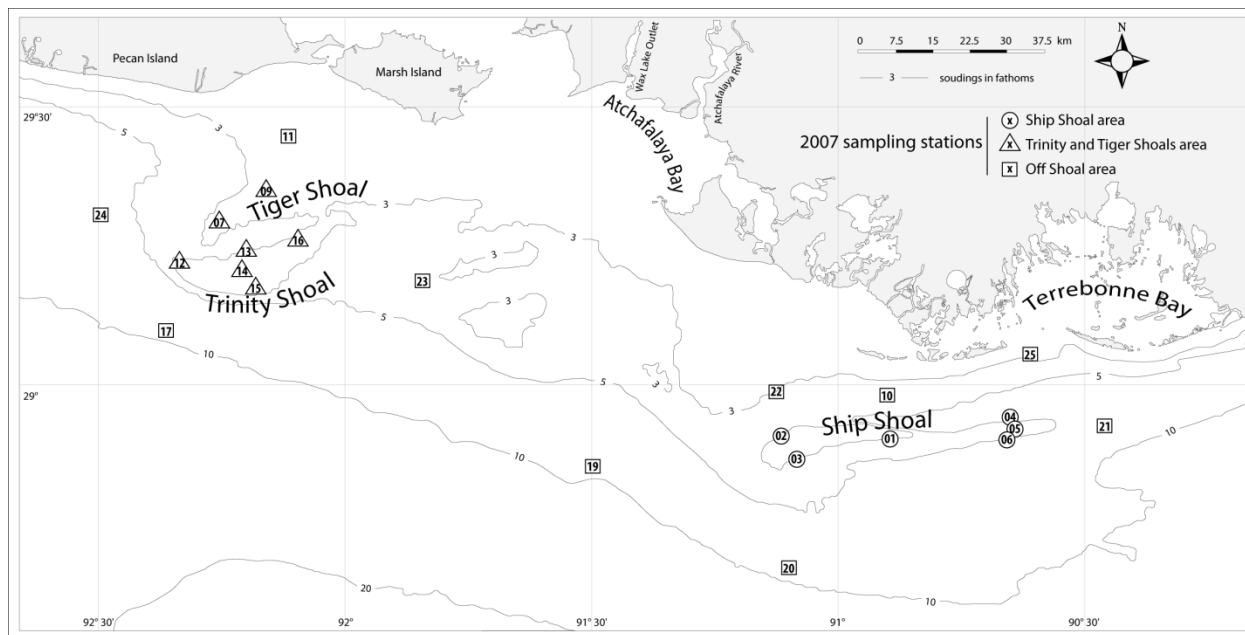


Figure 5.1 Station locations within our study area, the Ship, Trinity, Tiger Shoal Complex (STTSC), located off the south-central Louisiana coast.

Recently, I in collaboration with several colleagues discovered large concentrations of spawning blue crabs, *Callinectes sapidus*, within the STTSC, with the highest concentrations on sandy shoals (Chapter 4). The generally accepted paradigm for blue crab reproductive behavior (e.g., developed in the Chesapeake Bay) includes a two phase migratory pattern; first to lower estuarine regions to spawn, and then to tidal inlets, bay mouths, and barrier islands to hatch their eggs. My findings greatly expanded what was known about blue crab reproductive biology because offshore spawning grounds at such a distance had not previously been reported. The crabs from my study area were 99% female, almost all were carrying eggs or were about to spawn, and in some instances females with late stage eggs also had full ovaries, indicating a constant state of spawning and ovarian replenishment. Internal examination and subsequent analysis suggested that they were in good condition, that their health was not affected by the presence of epibiotic acorn barnacles, and that they were forming and releasing a new spawn approximately every 21 days. However, the origin and life history of this newly discovered blue crab spawning stock remain unclear. In an effort to determine if blue crabs located on the federal STTSC are an important component of the spawning biomass of Louisiana's inshore blue crab fishery, and to expand the knowledge of blue crab ecology and migratory dynamics, this study aims at investigating whether spawning female blue crabs taken from the STTSC were part of a long-term resident offshore population or newly recruited from an inshore, estuarine source.

Stable isotopes have proven to be an invaluable tool to understand trophic linkages and contribution of food sources to an organism's diet (e.g. Fry, 2006). They are also increasingly used as a valuable tool to discover migratory routes and understand migratory patterns (Hobson 1999; Rubenstein and Hobson 2004; Newsome et al. 2007; Fry 2011). They have been successfully employed within or across systems where isotopic composition of autotrophs (end



members) is sufficiently different to distinguish basal food sources and therefore feeding sites. The Louisiana shoal complex (i.e. STTSC) and its adjacent estuaries consists of the interface of a near marine environment with coastal salt, brackish and fresh marshes influenced by both high and low amounts of riverine input, making it a likely candidate for an isotopic study. Specifically, if STTSC crabs were migrating from various inshore source areas, their carbon and nitrogen isotopic signals should reflect their migratory and feeding histories.

The main objective in this study is to determine the source of spawning blue crabs on the STTSC. If migrated from Louisiana's inshore nursery grounds, STTSC blue crabs will prove to be an important component of the spawning stock biomass of Louisiana's inshore blue crab fishery. If not, STTSC blue crabs may be considered a federal-only fishery resource, available for foreign exploitation. Here I test the null hypothesis that crabs do not migrate from inshore estuaries to the STTSC. To test this hypothesis, I examine the isotopic composition of *C. sapidus* tissues, and compare it with an offshore resident crab, *Callinectes similis* isotope composition, and to body size of *C. sapidus* epibiotic barnacles. I will reject this  $H_0$  if the muscles of STTSC *C. sapidus* are less enriched in  $^{13}\text{C}$  than the ovaries and both tissues do not fall within offshore  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  residency boxes and around our proxy for offshore residence (*C. similis*); and if growth of epibiotic barnacles is correlated with convergence of crab tissue  $\delta^{13}\text{C}$  towards a known offshore range (-14 to -19). If the first null hypothesis is rejected then I test a second null hypothesis that blue crabs are not migrating directly offshore from their home estuary by examination of  $^{15}\text{N}$  enrichment relative to riverine influenced estuaries. I will reject the second  $H_0$  if there is no distinction in  $^{15}\text{N}$  between crabs caught westward and eastward of  $91^\circ 30' \text{ W}$  (Fig 5.1).

## MATERIALS AND METHODS

To address STTSC blue crab migratory dynamics I have developed the following isotopic framework.

(1) Although commonly used to evaluate trophic position (Minagawa and Wada 1984; Post 2002),  $\delta^{15}\text{N}$  has also been shown to be a useful tool in estuarine migratory studies where source areas differ in the amount of freshwater input (Fry 2011). Mississippi/Atchafalaya River waters have elevated nitrate and dissolved inorganic carbon concentrations that are high in  $\delta^{15}\text{N}$  (8‰; Fry and Allen 2003), and low in  $\delta^{13}\text{C}$ . This results in  $^{15}\text{N}$ -enriched and  $^{13}\text{C}$ -depleted food webs for river-influenced estuaries. Within the STTSC (Fig. 5.1), marked differences between blue crabs that are migrating from areas of high freshwater input (e.g. Mississippi or Atchafalaya River deltas) and areas that no longer have a direct riverine connection and therefore have relatively little freshwater input (e.g. Barataria and Terrebonne Bays) would therefore be expected. Given the configuration of the Louisiana coast and the dominant westerly direction of the longshore current in our study area, I expect that crabs caught west of  $91^{\circ} 30' \text{ W}$  will have a higher  $\delta^{15}\text{N}$  signal and lower  $\delta^{13}\text{C}$  signal than crabs caught east of this longitude (Fig. 5.1).

(2) A relative  $\delta^{13}\text{C}$  depletion occurs at lower salinities (Deegan and Garritt 1997; Fry 2011), and the  $\delta^{13}\text{C}$  signal should become relatively enriched if crabs moved seaward from inshore estuaries, converging to an offshore range of approximately -14 to -19‰ (Fry 1981, 1983, 1988, 2011; Fry and Sherr 1984; Fry et al. 1984, 2003; Sherwood and Rose 2005), due to high  $\delta^{13}\text{C}$  contribution of marine phytoplankton. We therefore expect that an association of the STTSC crabs with the open waters of the Gulf of Mexico will increase their  $\delta^{13}\text{C}$  values, while their association with Louisiana's inshore estuaries will deplete this signal.

(3) Benthic microalgae (BMA) have recently been found to be an important component of the offshore autotrophic community of the STTSC, predominately on Ship Shoal (Grippo et al. 2009, 2010, 2011). BMA usually are 3 to 5‰ enriched in  $\delta^{13}\text{C}$  versus phytoplankton (France 1995) therefore I expect the  $\delta^{13}\text{C}$  signal will be enriched on Ship Shoal.

(4) Muscle is typically used as a slow turnover tissue and representative of an animal's long-term diet and migratory history (Logan et al. 2006). I therefore assume that turnover of muscle will reflect basal metabolism and that the isotopic composition of the muscle will represent an integration of 'long-term' migratory history. Growth in width does not occur in post-copulation female *C. sapidus* and muscle tissue turnover may be long when growth is slow. In contrast, STTSC crabs replenish their ovary every 21 days (Chapter 4), so I expect that the blue crab ovary will be an indicator of recent diet and migratory history (< 21 days). Residency designation for crabs found on the STTSC would thus be indicated if the ovarian and muscle isotopic signals are equilibrated with each other and are within an offshore isotopic range (i.e., Fry et al. 2003). Conversely, if the ovarian and muscle isotopic signals differ, and at least one lies outside the range for offshore residents, then migratory history to the STTSC can be approximated. For crabs which are newly recruited to the STTSC from an inshore source, I expect a seasonal convergence in their isotopic carbon signal from an inshore range generally less than -19 (Deegan and Garritt 1997; Fry 2011) to an offshore (and STTSC) isotopic range of approximately -19 to -14 as they become resident. I expect that this convergence will be seen first in the ovary, and then in the muscle.

(5) Because larvae of the epibiotic acorn barnacle *C. patula* requires salinities > 25 ppt for survival (Crisp and Costlow 1963) I expect larval settlement to begin shortly after inshore crabs

have entered high salinity water, and a correlation between the isotopic composition of the ovary and muscle of STTSC crabs with body size of their acorn barnacles.

(6) The lesser blue crab, *Callinectes similis*, taken from the STTSC are used here as a proxy for shoal-resident blue crab (*C. sapidus*). *C. similis* is known to occupy high salinity water on the continental shelf (Williams 1974) and has been found to feed on similar prey types to those consumed by *C. sapidus* (Hsueh 1992). If recently migrated to the STTSC, muscle to ovary convergence of *C. sapidus* isotopic values towards that of *C. similis* is expected.

#### Sample Collection and Laboratory Preparation

Two hundred and twenty nine (Table 5.2) blue crabs, *C. sapidus* were collected from the STTSC (Fig. 5.1) during three cruises in spring, summer and fall as outlined in Gelpi et al. (2009) and used for isotope analysis. A total of 48 lesser blue crabs, *C. similis* were taken from Trinity Shoal in summer and Ship Shoal in summer and fall and muscle analyzed for isotopic content. The gut contents of 31 *C. sapidus* taken from Ship Shoal and off shoal stations immediately north were also analyzed for  $\delta^{15}\text{C}$  and  $\delta^{15}\text{N}$ . Raw isotopic data on potential food web contributors (i.e., sediment, phytoplankton, BMA, and resident macroinfauna) were obtained from recent work in the STTSC by Grippo et al. (2011).

Forceps were used to extract muscle tissue from *C. sapidus* and *C. similis* claws and ovary tissue from the interior of the *C. sapidus* cephalothorax. Each tissue sample was washed with fresh deionized water and frozen. All tissues were freeze-dried, ground to a fine powder, and then weighed in tin caps. Isotope analyses were performed by the University of California Davis Stable Isotope Facility. Nitrogen and carbon isotope values were determined using a PDZ

Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon). The  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values were calculated using the formula:

$$X = [(R_{\text{SAMPLE}} / R_{\text{STANDARD}}) - 1] * 1000,$$

where  $X = \delta^{15}\text{N}$  or  $\delta^{13}\text{C}$ , and  $R$  is the ratio of the heavy isotope to the light isotope. Vienna Pee Dee Belemnite and atmospheric  $\text{N}_2$  were used as standards for carbon and nitrogen, respectively. Because *C. sapidus* ovary tissue exhibited a higher lipid content than muscle, measured C/N ratios were used to provide a lipid-free basis for ovary using the following mass balance equation based on Fry et al. (2003):

$$\delta_p = \delta_o + 6 - (6 * 3.2)/R_o$$

$\delta_p$  is the  $\delta^{13}\text{C}$  value of lipid-free protein (i.e. the ovary value after correction),  $\delta_o$  is the  $\delta^{13}\text{C}$  value of the ovary, 6 refers to a 6‰ depletion in lipid C isotopic composition versus muscle, 3.2 is the average C/N ratio of blue crab muscle and used here as a proxy for lipid-free protein, and  $R_o$  is the C/N ratio of the ovary. On average, ovary  $\delta^{13}\text{C}$  values were corrected by 1.9‰ due to lipid content. Preliminary tests with other correcting models (Kiljunen et al. 2006; Bodin et al. 2007) were not significantly different.

Stomach contents were also freeze dried and ground to a fine powder for carbon and nitrogen isotopic analysis. A portion of each stomach sample was acidified to remove inorganic carbon for  $\delta^{13}\text{C}$  analysis.

### Inshore Boxes

In order to evaluate blue crab migratory history within the STTSC I define six ‘isotopic boxes’ (four ‘inshore’ and two ‘offshore’ boxes). Each box should delineate the range of  $\delta^{15}\text{N}$

and  $\delta^{13}\text{C}$  values indicative of a resident which is trophically comparable to spawning female blue crabs.

The environmental framework of the four inshore boxes I use to determine estuarine isotopic ranges are: Low salinity with riverine influence (LSR), low salinity without riverine influence (LS), high salinity with riverine influence (HSR), and high salinity without riverine influence (HS) (Fig. 5.2). My requirements were that the studies involved Louisiana estuarine areas west of the Mississippi River, and contained sufficient data to define at least one of our inshore boxes within a  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  bi-plot. I chose the simplest geometric configuration (i.e. rectangle) which I felt described each set of values. Two studies with sufficient data were used to construct the four inshore boxes (Table 5.1). I used data on benthic, generalist-feeding finfish from the fresh marsh (salinity < 1) environment of the Atchafalaya Basin (Fry et al. 2002) for the LSR box. For the LS box I used data on benthic, generalist-feeding finfish from an oligohaline marsh (salinity < 3) in upper Barataria Bay (Fry 2002). For the HSR box, I used brown shrimp associated with a meso/polyhaline environment (salinity 20-30) near the Mississippi River Bird's Foot Delta (Fry 2011). And for the HS box I used brown shrimp associated with the meso/polyhaline estuaries (salinity 20-30) of Barataria and Terrebonne Bays (Fry 2011).

#### Offshore Boxes

To construct our offshore boxes I plotted the carbon and nitrogen isotopes for all benthic macrofauna available from a 2007 study in STTSC (e.g. Grippo et al. 2011) by area and season (Fig. 5.3a-c). Preliminary examination of STTSC blue crab stomachs revealed an STTSC-based macroinfauna diet (Gelpi unpublished data). As an initial check on our boxes, I plotted the isotopic composition of sediment, phytoplankton, and BMA from Grippo et al. (2011) and examined the pattern for consistency with expected trophic relationships. These bi-plots were

examined by area and season. Using the inshore box procedure I chose the simplest geometric configuration which described the bi-plots for Ship Shoal, Trinity and Tiger Shoal, and all off shoal stations (Fig. 5.3a-c). I collapsed the Trinity/Tiger Shoal and the off shoal boxes into a single box (TTS/Off) due to their similarity. These groupings of two summary boxes: 1) Ship Shoal, and 2) TTS/Off are in agreement with the results of Grippo (2009). I then applied trophic enrichment factors of 1 and 2.5‰ for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  respectively (Fig 5.3d), based on Fry and Sherr (1984); Vanderklift and Ponsard (2003); and McCutchan et al. (2003). Finally, as an additional check on the offshore boxes, I plotted mean isotopic values for *C. similis* muscle (Ship Shoal summer mean  $\delta^{13}\text{C}$  = -16.6 and  $\delta^{15}\text{N}$  = 12.7; Ship Shoal fall mean  $\delta^{13}\text{C}$  = -17.8 and  $\delta^{15}\text{N}$  = 11.5; Trinity Shoal summer mean  $\delta^{13}\text{C}$  = -15.9 and  $\delta^{15}\text{N}$  = 11.7) which was used as a proxy for an offshore resident *C. sapidus*.

## Convergence

The orientation and spacing of muscle to ovary isotopes was used to determine convergence patterns for STTSC crabs. Spacing was calculated as the (‰) hypotenuse in two dimensional isotopic space created from tissue differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  biplots using the Pythagorean Theorem. Based on known salinity-associated changes in  $\delta^{13}\text{C}$  from fresh to marine systems, I tested the assumption that blue crabs in offshore in high salinity water are converging on an offshore/shoal based  $\delta^{13}\text{C}$  isotopic range, and a proxy value for offshore blue crabs (i.e., *C. similis* muscle). The acorn barnacle, *Chelonibia patula*, is a filter feeder with larvae that require high salinity water, between 25 and 30, to develop (Crisp and Costlow 1963). When present, the diameter of the largest adult *Chelonibia patula* for each crab was used here as an indication of time spent offshore and plotted against crab  $\delta^{13}\text{C}$  values for ovary and muscle tissues.

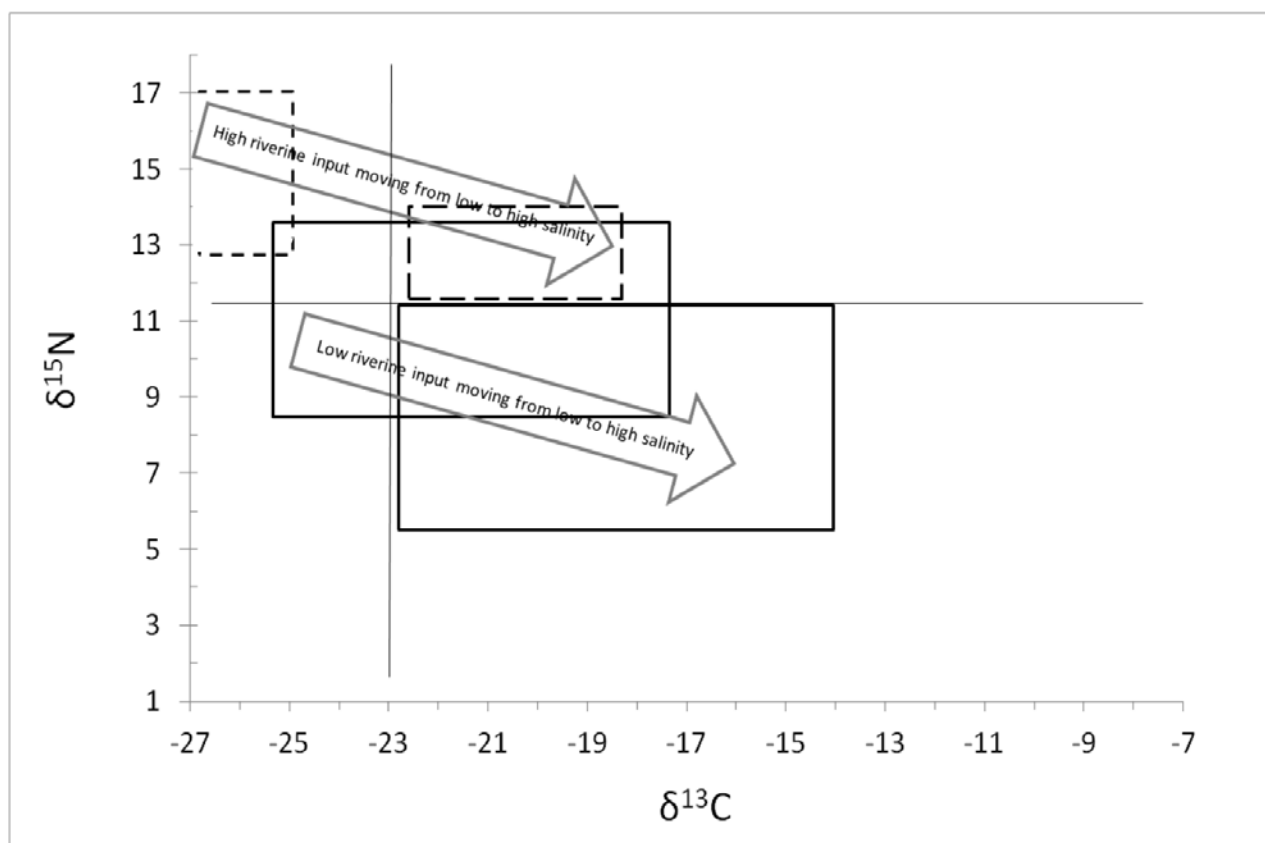


Figure 5.2 Inshore boxes (based on Fry 2002, 2011, see methods) with conceptual model for changing isotopes based on riverine and salinity influences.

### Statistical analysis

Two station groupings within the STTSC were outlined in proximity to the Atchafalaya River as those west and east of  $91^{\circ} 30' W$  (Fig. 5.1). Mean values of isotopes were given with standard error of the mean (SEM) unless otherwise stated. Statistical analysis was performed on  $\delta^{13}C$  and  $\delta^{15}N$  isotope values using linear regression and two-way analysis of variance (ANOVA), with the main effects of area and season and area x season interactions, using Statistical Application Software (SAS). Data were transformed when required in order to approximate the assumptions of normality and equal variance.



Table 5.1 Proxy carbon and nitrogen isotope ranges of source regions for blue crab migration.

Area designation	Sampling region	Species sampled	Salinity	$\delta^{13}\text{C}$ range	$\delta^{15}\text{N}$ range	Source
Low salinity with riverine influence (LSR)	Atchafalaya River (AR)	<i>Aplodinotus grunniens</i> <i>Ictiobus bubalus</i> <i>Ictalurus furcatus</i> <i>Ictalurus punctatus</i> <i>Pylodictis olivaris</i>	< 1	-32.6 to -25	12.8 to 17	Fry 2002, appendix
Low salinity without riverine influence (LS)	Barataria Bay (BB)	<i>I. furcatus</i> <i>I. punctatus</i>	< 3	-25.3 to -17.4	8.5 to 13.6	Fry 2002, appendix
High salinity with riverine influence (HSR)	Riverine shrimp from the Bird's Foot Delta	<i>Farfantepenaeus aztecus</i>	20 to 33	-22.8 to -18.4	11.6 to 14	Fry 2011, Figure 5 and pages 3,11
High salinity without riverine influence (HS)	Bay shrimp from Barataria & Terrebonne Bay	<i>F. aztecus</i>	20 to 33	-22.8 to -14.1	5.5 to 11.5	Fry 2011, Figure 5 and pages 3,11

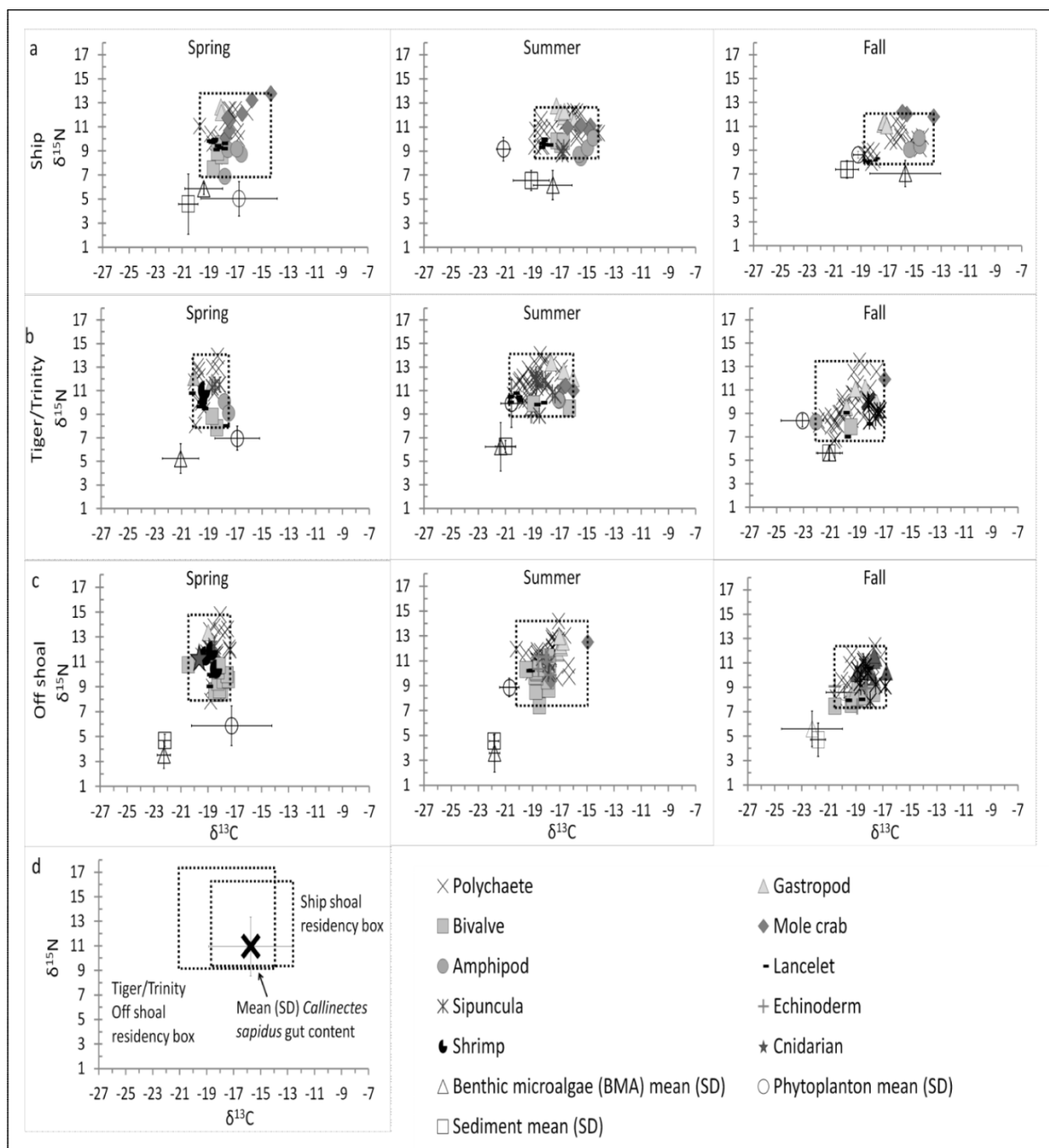


Figure 5.3 Carbon and nitrogen isotopes for macrofauna and mean ( $\pm$  SD) of potential contributors to the base of the food web from spring, summer and fall from Ship (a), Tiger/Trinity (b), Off shoal (c). Offshore composite boxes, shown in (d), represent offshore blue crab residency based on macrofauna from: Trinity/Tiger/Off shoal areas, left box (combined from b and c), and the Ship Shoal area, right box (combined from a). Both composite residency boxes and mean *Callinectes sapidus* gut contents (X) from east area have a +1 and 2.5‰ trophic enrichment factor applied for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  respectively.

## RESULTS

### General Pattern

There was a broad range of isotopic values for STTSC blue crab tissue including both muscle  $\delta^{13}\text{C}$  (-25.3 to -14.7‰),  $\delta^{15}\text{N}$  (7.2 to 15.1‰), and ovary  $\delta^{13}\text{C}$  (-23.6 to -15.1‰),  $\delta^{15}\text{N}$  (7.2 to 14.7‰) with widest seasonal range for each tissue occurring in summer. ANOVA tested for effects of the Atchafalaya River, Gulf, and BMA on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of crab tissues and revealed substantial geographic and seasonal patterning of isotope composition (Table 5.2). There was a general enrichment of  $\delta^{15}\text{N}$  for the west station group which was significantly greater than the east station group for muscle and ovary for nearly every season. Conversely,  $\delta^{13}\text{C}$  was more enriched in the east station group with differences significantly greater in the muscle tissue in spring and over all seasons (Table 5.2), and ovary values for both groups slightly converged towards a narrower offshore range (Fig. 5.4).

Table 5.2. Mean  $\pm$ SEM seasonal and spatial carbon and nitrogen isotope values for the muscle and ovary tissue of spawning female blue crabs from the Ship, Tiger, and Trinity Shoal Complex (STTSC) in 2007. East and west station groupings are delineated by stations 19 and 23 (Fig. 5.1) respectively. Parentheses denote number of observations. If Analysis of Variance (ANOVA) interactions were significant then pairwise significance is indicated by lettering.

Season	Location	Muscle $\delta^{13}\text{C}$	Ovary $\delta^{13}\text{C}$	Muscle $\delta^{15}\text{N}$	Ovary $\delta^{15}\text{N}$
spring	east	-19.5 $\pm$ 0.3(35) A	-18.5 $\pm$ 0.2(35)	10.1 $\pm$ 0.2(35) D	9.9 $\pm$ 0.2(35) D
	west	-21.8 $\pm$ 0.4(11) B	-20.2 $\pm$ 0.6(10)	13.8 $\pm$ 0.3(11) A	13.4 $\pm$ 0.2(10) A
summer	east	-19.8 $\pm$ 0.3(79) AB	-18.0 $\pm$ 0.2(79)	11.0 $\pm$ 0.2(79) C	11.3 $\pm$ 0.1(79) B
	west	-19.9 $\pm$ 0.3(73) AB	-18.3 $\pm$ 0.2(70)	12.6 $\pm$ 0.2(73) B	12.8 $\pm$ 0.1(70) A
fall	east	-18.7 $\pm$ 0.4(23) A	-18.4 $\pm$ 0.3(23)	10.0 $\pm$ 0.2(23) D	10.5 $\pm$ 0.2(23) CD
	west	-19.9 $\pm$ .5(8) AB	-18.2 $\pm$ 0.4(8)	12.7 $\pm$ 0.3(8) AB	11.4 $\pm$ 0.3(8) BC
interaction	area x season	p<0.05	ns	p<0.01	p<0.01
fixed	area	east>west	ns	west>east	west>east
	season	Ns	summer>spring	Ns	summer, spring>fall

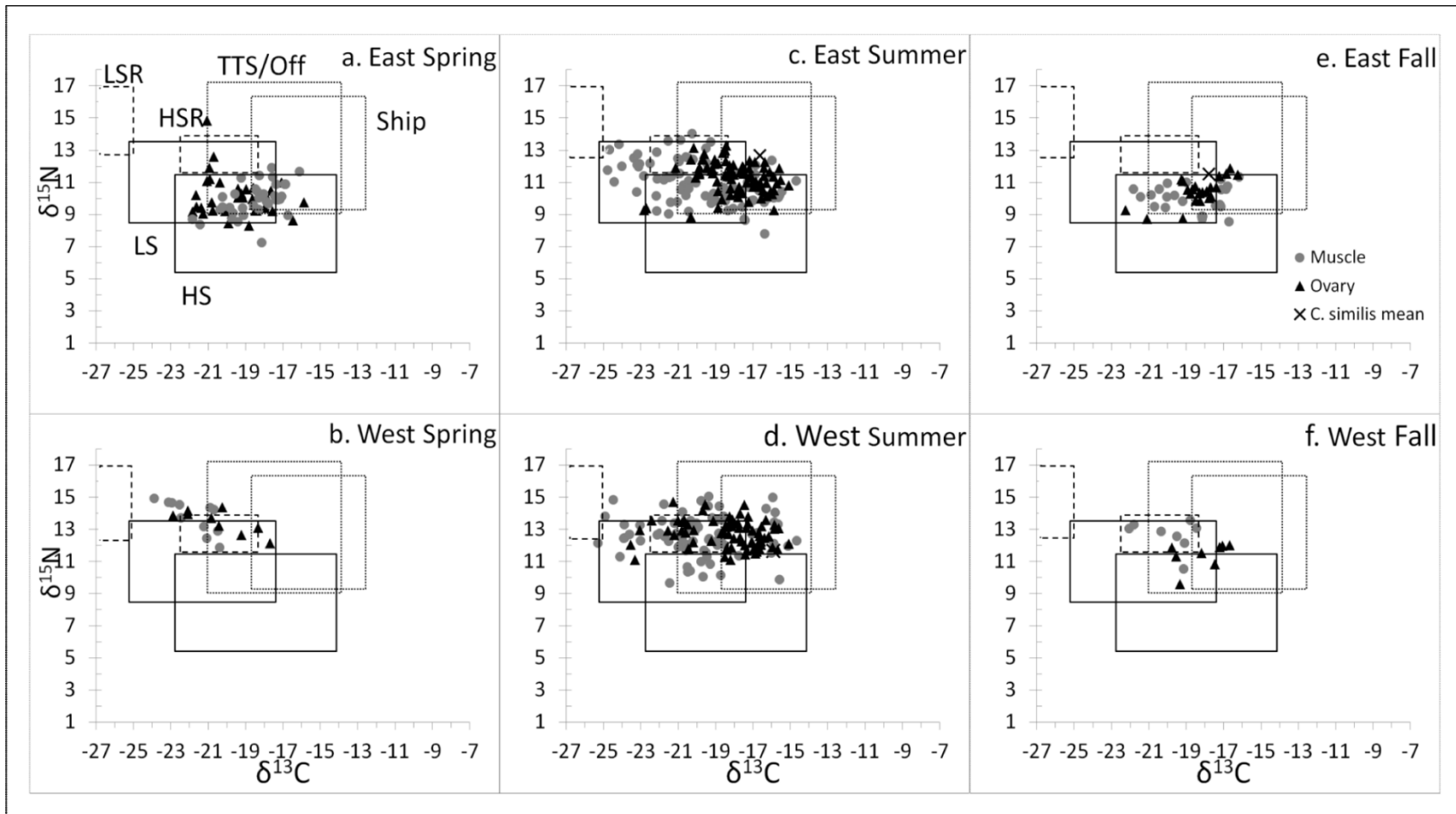


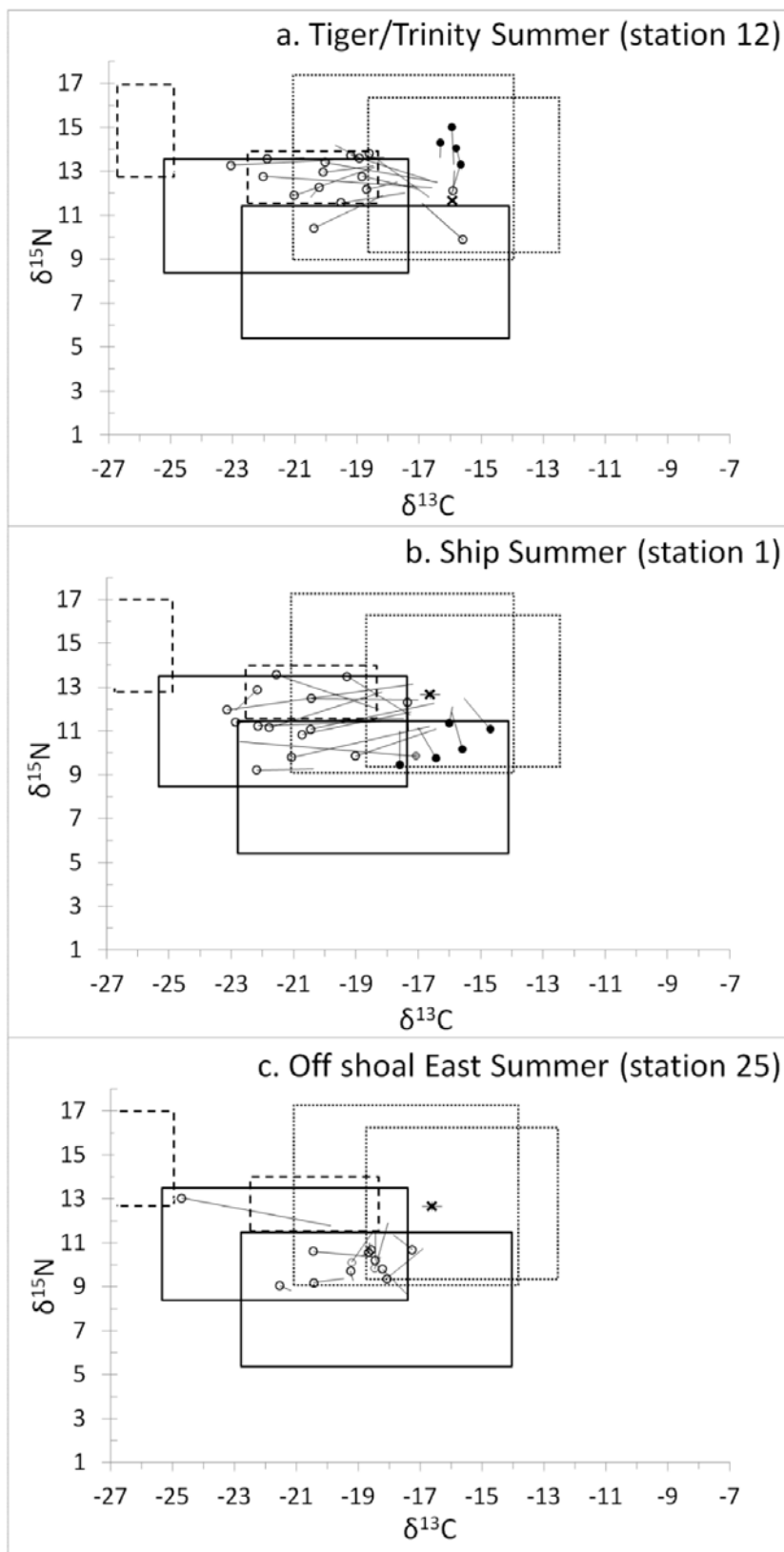
Figure 5.4 Seasonal (spring, summer, fall presented from left to right) and spatial plots of carbon and nitrogen isotopes from blue crab muscle (circles) and ovary (triangles). East (a,c,e) and west (b,d,f) station groupings are delineated by stations 19 and 23 (Figure 5.1) respectively. The two boxes in the upper right within each figure represents residency ranges for Ship Shoal and Tiger/Trinity/Off shoal based on resident macrofauna +1 and 2.5 for trophic enrichment for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  respectively. The four boxes from the bottom center to the upper left within each figure represents potential source area ranges for higher salinity without river influence (HS), lower salinity without river influence (LS), higher salinity with river influenced (HSR), and lower salinity with river influence (LSR), respectively, based on values from Fry (2011, 2003, see methods for details). Mean *Callinectes similis* (x) is plotted when available as a proxy for offshore, resident *Callinectes sapidus*.

Using studies by Fry (2002 Appendix; 2011 Fig. 5) involving trophically comparable species from extreme ends of both riverine and salinity influences, I outlined a conceptual isotopic gradient for migratory species estuarine source locations. The gradient represented by the four inshore boxes is oriented from the upper left to lower right on a  $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$  bi-plot as follows: LSR to HSR and LS to HS (Fig. 5.2).

#### Inshore to Offshore Convergence

There was a consistent pattern of greater ovary  $^{13}\text{C}$  enrichment relative to muscle when tissues were examined on a per crab basis. Seventy-five percent of crabs taken from the STTSC had ovary  $\delta^{13}\text{C}$  values greater than those of muscle. There was also an area-based difference in the ovary muscle spacing for shoal areas ( $2.4\text{‰} \pm 0.1$ ) compared to off shoal ( $1.7\text{‰} \pm 0.2$ ) over all seasons ( $F_{1,216} = 10.5$ ;  $p < 0.01$ ), suggesting that shoal and off shoal migratory dynamics differ. I also found non-significant trends in seasonal differences in isotope spacing when comparing the mean spring ( $1.8\text{‰} \pm 0.2$ ) summer ( $2.6\text{‰} \pm 0.1$ ) and fall ( $1.6\text{‰} \pm 0.1$ ) values, consistent with migration. In addition, there were some unusual cases of paired muscle ovary values, such as an apparent vertical convergence (black circles Fig. 5.5a,b) on isotopic targets (i.e. *C. similis*) within the residency boxes that highlights differences between the east station group, which generally converge from below, versus the west station group, which generally converge from above (Fig. 5.5a,b).

Figure 5.5 Plots of *Callinectes sapidus* muscle (circles) and ovary (tip of line) isotopes for representative stations from summer for Ship Shoal, Off shoal east, and Tiger/Trinity Shoals. Mean *Callinectes similis* ( $x \pm \text{SEM}$ ) is plotted when available. The two boxes in the upper right within each figure represents residency ranges for Ship Shoal and Tiger/Trinity/Off Shoal based on resident macrofauna +1 and 2.5 for trophic enrichment for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  respectively. The three boxes from the bottom center to the upper left within each figure represents potential source area ranges for poly/mesohaline, oligohaline, and river influenced areas, respectively, based on values from Fry 2010, 2003 (see methods for details).



A generally consistent pattern was found in the  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  bi-plots of east/west grouping in which crab values fall to the lower left for the east station grouping and to the upper left for the west station groupings i.e.,  $\delta^{15}\text{N}$  was higher in the west (Fig. 5.4). This pattern is especially evident in the spring and fall, with an increase in the spread of points (especially muscle values) in the summer. A more specific illustration of these two patterns is found in the relationship between muscle and ovary of individuals (e.g. Fig. 5.5), in which crab isotopes appear to converge toward isotopic target values (i.e. mean *C. similis* signature).

The  $\delta^{13}\text{C}$  of blue crab ovary tissue was significantly positively related to barnacle diameter (linear regression,  $F_{1,222} = 10.02$ ;  $p < 0.01$ ). A similar analysis with muscle tissue was not significant ( $F_{1,224} = 1.7$ ;  $p = 0.19$ ), though the same general convergence trend occurred between  $\delta^{13}\text{C}$  of both tissues and barnacle diameter (Fig. 5.6 a,b). Plots of  $\delta^{13}\text{C}$  versus barnacle diameter revealed slightly different convergence trends based on proximity to the Atchafalaya River. The  $\delta^{13}\text{C}$  values from east area crabs with largest barnacle diameter of 1 mm or greater fell within a range of -19.6 to -15.1‰ with a mean of -17.5‰, and values for west area crabs fell within a range of -20.7 to -15.9‰ with a mean of -17.8‰. The means of both areas were similar to values consistently found for offshore benthic invertebrates in marine systems (Fry 1984, 1988; Sherwood and Rose 2005).

#### STTSC blue crab migratory dynamics

Over all seasons, the east station group had 77% of muscle values fell below the  $\delta^{15}\text{N}$  value of 11.6‰; in contrast 87% of western crabs were above 11.6‰ (Fig. 5.4); this is the nitrogen isotopic value that Fry (2011) used to delineate shrimp migrants from estuaries without direct riverine influence versus estuaries receiving direct riverine influence (Fry 2011).



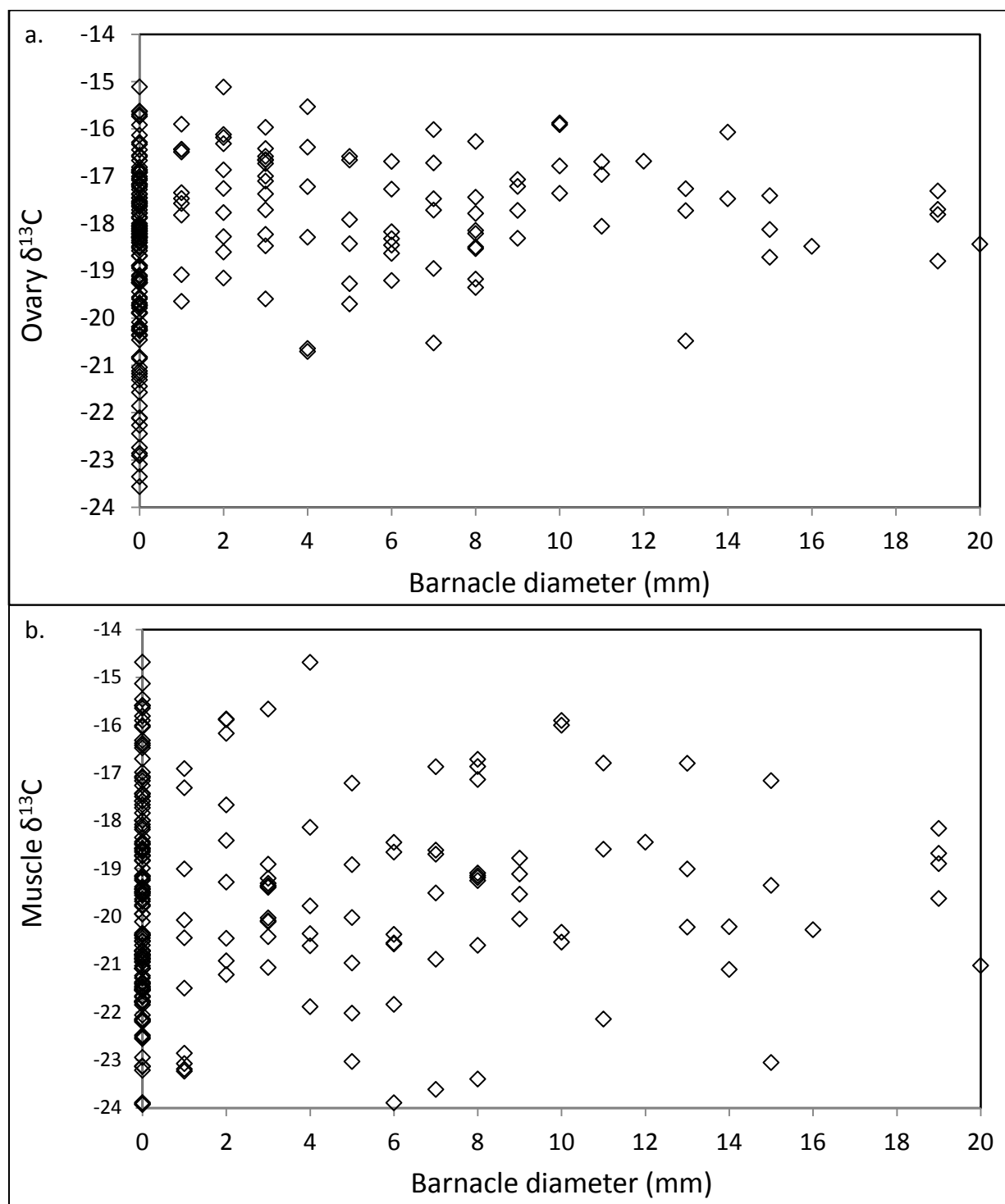


Figure 5.6 Relationship of Ship, Tiger, Trinity Shoal Complex (STTSC) blue crab  $\delta^{13}\text{C}$  ovary (a) and muscle (b) with growth of the epibiont acorn barnacle, *Chenobla patula*

Carbon/nitrogen bi-plots indicate that many blue crabs were residing within or near the offshore region with 70% of Tiger/Trinity and off shoal individuals having both muscle and ovary values within the TTS/Off box, although there is some overlap with the TTS/Off box and inshore boxes (Fig. 5.4) likely due to TTS proximity to the Atchafalaya river. We found 23% of isotope values for Ship Shoal crabs' muscle and ovary tissue fell within the offshore Ship Shoal box, which is probably a better estimator of an offshore residency range (i.e.  $\delta^{13}\text{C}$  of approximately -19 to -14) than the TTS/Off box because of a reduced riverine isotopic influence. Though the largest concentration of crabs in the STTSC was found in summer, there was a seasonal increase in proportion of Ship Shoal crabs that fell within the Ship Shoal range with 13, 25 and 30% of crabs for spring, summer, and fall respectively and a seasonal increase of 59, 71, and 79%, respectively for Tiger/Trinity/Off Shoal crabs that fell within the TTS/Off range.

Carbon isotope values provide evidence that some crabs from both the east and west station groupings moved offshore directly from areas with depleted  $\delta^{13}\text{C}$  (i.e. low salinity reaches of estuaries). Because isotopic gradients occur in relation to changing salinity, I was able to estimate the percentage of crabs from high versus low salinity estuarine areas. The distinction between salinity regimes was especially apparent in the muscle tissue (slower turnover) where a portion (15%) of summer-caught crabs had muscle  $\delta^{13}\text{C}$  values indicative of low salinity marsh outside the range of the meso-polyhaline estuaries delineated here by  $\delta^{13}\text{C}$  values  $< -22.8\text{‰}$  (Fig. 5.4). The presence of STTSC crabs within this range provides evidence that some blue crabs are migrating from inshore areas with little saltwater influence to offshore areas to spawn and doing so rapidly enough to retain their distinct inshore isotopic composition from low salinity areas.

## DISCUSSION

### Source Region Designation: An Estuary-Specific Offshore Connection to An Inshore Blue Crab Fishery

I was able to reject the first null hypothesis that inshore crabs do not migrate to STTSC. I base this conclusion on three observations, (1) blue crab isotope tissue composition converged on that of an offshore resident with similar diet, (2) correlations between body size of an epibiotic barnacle that recruits to the crab carapace only offshore and crab isotope composition, and (3) variation in slow and rapid turnover tissues that suggest values change with increasing time on the shoals. Therefore a direct link is noted between the inshore blue crab fishery and the offshore spawning grounds, particularly shoals, where the highest concentrations of spawning blue crabs were located. I was able to reject the second null hypothesis that blue crabs are not migrating directly offshore from their home estuary. I base this on the general consistency in crab tissue isotopic composition with that of estuaries closest in proximity to their place of capture.

My analyses of blue crab  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  reveal a changing east-west isoscape from Barataria Bay to areas west of the Atchafalaya delta (Table 5.2), likely reflecting estuarine source migratory areas with differing amounts of freshwater input. These spatial differences provide evidence that the tissues of female blue crabs respond to a shift in the “isoscape” (West et al. 2010) along the south-central Louisiana coast based on proximity to freshwater influence from the Atchafalaya River. The western grouping of STTSC stations is directly southwest of the Atchafalaya Basin, which, due to high inflow of freshwater with an elevated nitrate and dissolved inorganic carbon concentration, would promote higher  $\delta^{15}\text{N}$  and lower  $\delta^{13}\text{C}$  (Fry and Allen 2003; Fry 2011). The eastern grouping (Fig. 5.1) is directly south of Terrebonne and

Barataria Bays, which currently has no direct connection to Mississippi River freshwater input and as a result has lower  $\delta^{15}\text{N}$  and higher  $\delta^{13}\text{C}$ . The shifting pattern detected in the dual carbon and nitrogen isotopic labels is similar to that observed for brown shrimp sampled from the Mississippi River Bird's foot delta to Terrebonne Bay (Fry 2011).

In addition to low  $\delta^{13}\text{C}$  from terrestrial freshwater sources, carbon from primary producers in lower salinity portions of estuaries are also sources of low  $\delta^{13}\text{C}$  providing a natural isotopic label in comparison to typical marine values. Many blue crabs from the STTSC had depleted  $\delta^{13}\text{C}$ , particularly in the slower turn-over muscle tissue (Table 5.2; Fig. 5.4), suggesting that their migration originated from mid-salinity bay environments (Deegan and Garritt 1997) as well as inshore low salinity marsh and/or coastal areas near freshwater input (Fry 2002, 2011). This provides evidence that females undergo a rapid spawning seaward migration occurring on the order of days, from fresher inshore estuaries. This is within their migratory capability, based on an average movement estimate of  $5.4 \text{ km day}^{-1}$  for females prior to hatching their eggs (Carr et al. 2004). A rapid spawning migration from fresh inshore marsh for Louisiana female *C. sapidus* is in contrast to migratory behavior from higher latitude estuaries such as Delaware and Chesapeake Bays, where females overwinter in high concentrations in polyhaline zones (Hines 2007 and refs within). Thus, our results call into question whether or not seasonally separated Phase I (i.e. movement from mating locations to the lower estuary before brood production), and Phase II (i.e. movement to the mouth of, or seaward from the estuary; Tankersley et al. 1998) migratory patterns of the central Atlantic be extrapolated to Gulf of Mexico blue crabs.

In addition to inorganic carbon, freshwater from terrestrial runoff is high in nitrate and this fertilizer imparts a bottom-up higher  $\delta^{15}\text{N}$  signal for food webs. Crabs taken from west station groupings were higher than east station groupings in muscle and ovary  $\delta^{15}\text{N}$  (Table 5.2), a

pattern seen in the  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  bi-plot of both tissues (Fig. 5.4). Most STTSC blue crab carbon and nitrogen isotopes are consistent with expected isotopic patterns of the estuary nearest to their place of capture, which suggests that STTSC blue crabs are generally moving in a seaward direction and minimize the east-west migratory distance away from source estuaries. This is in contrast to tagging studies from east of the Apalachee Bay where crabs migrated, long distances in some cases, northwest along the Florida coast (Oesterling 1976; Steele 1987).

There was an increase in the spread of isotopic values (especially muscle values) in the summer (Fig. 5.4), which appears to be a prime migration period to shoals within the STTSC, and when crab abundance in the offshore waters was highest. Lower flow of the Mississippi/Atchafalaya Rivers in summer may allow source areas to diverge more in their isotopic signals. Increased flow of the Mississippi River in the spring may be responsible for making all areas ‘fresher’ while decreased flow after spring likely accounts for a seasonally shifting isotopic landscape or ‘isoscape’ (West et al. 2010). Thus, increased variation in summer crab tissues could reflect changes in isotopic values that occur over small geographic scales, such as those between estuarine ponds, channels, and bays (Fry et al. 2003). Another explanation in greater summertime isotopic heterogeneity is an increase in cross-shelf exchange of crabs from source locations to offshore spawning grounds, possibly because crabs are seeking Shoals as a hypoxia refuge.

This use of isotopes is a novel approach to assess blue crab population dynamics. Migratory studies of blue crabs have traditionally relied on tagging studies which are dependent on commercial and recreational fishers finding and accurately reporting the necessary information, often resulting in a low return of tagged individuals (Cronin 1949). In addition other factors must be taken into account when using tagging methodology in migratory studies

such as mortality, loss of tags, assumptions that crabs will move and mix naturally with the existing local population, and that tagged animals are as susceptible to fishing as untagged ones (Ricker 1948; Cronin 1949). This new approach has allowed me to demonstrate a facet of blue crab life history that has been overlooked for years, and sheds light on the potential importance of offshore shoal-based blue crab spawning grounds to the inshore blue crab fishery for the norther Gulf of Mexico.

#### Isotopic Convergence and Crab Residency

The more rapid turnover ovarian tissue of STTSC crabs was typically enriched in  $^{13}\text{C}$  compared to the slower turnover muscle. A muscle to ovary convergence pattern is evident (Fig. 5.4) and typically trends towards the isotopic proxy for offshore residence (i.e. *C. similis*) that lies within the offshore residency boxes (Fig. 5.5a,b). This suggests a net inshore to offshore movement of female blue crabs based on previously established patterns of tissue enrichment for other migratory species such as brown shrimp (Fry et al. 2003; Fry 2011).

The average muscle to ovary isotopic spacing is greatest for the summer season and may represent wave of newly arrived blue crabs that have recently left source areas from inshore estuaries. Previous studies have described two waves of spawning females in the Gulf estuaries (Jaworski 1972; More 1969) and Atlantic estuaries (Van Engle 1958; Tagatz 1968), though connections to preferential offshore spawning grounds such as Ship and Trinity Shoals have not been made. Feeding studies which seek to quantify muscle and ovary turnover rates for spawning blue crabs would be an important tool that could be used to model the timing of migrating females.

My barnacle analysis revealed a correlation between barnacle presence and size with a reduction in the  $\delta^{13}\text{C}$  range of crab tissue (Fig 5.5a,b), providing corroborating evidence that convergence to offshore isotopic values occurs for blue crabs. This suggests that convergence of crab carbon isotopes to an offshore range begins in the higher salinity offshore environment where a crab would have a higher probability of encountering viable barnacle larvae. A similar offshore convergence pattern for carbon isotopes has been reported between  $\delta^{13}\text{C}$  and migrating brown shrimp (Fry 2011), where tissue convergence to an offshore carbon range was correlated with shrimp growth. However, a positive relationship between crab growth and  $\delta^{13}\text{C}$  would not be expected for spawning blue crabs because a female's size does not increase following her terminal molt. Because barnacle larvae require a higher salinity for survival, barnacles provide a good proxy for offshore habitation by female blue crabs. Therefore, using their presence and growth in correlation with crab carbon isotopes I infer that STTSC blue crabs initiate movement to the offshore in spring and gradually incorporate the offshore isotopic signal.

My findings add insight to what is known about blue crab spawning behavior, which includes the assumption that females would often re-enter inshore estuaries after spawning. (Daugherty 1952; Adkins 1972; Tagatz 1968; Oesterling 1976; Steele 1987; Tankersley 1998). A generally consistent convergence pattern reflecting offshore migration without re-entry is evident for the majority of crabs taken from offshore shoal stations (Fig. 5.5a,b). However, crabs from some inshore stations did not conform to the general pattern of convergence seen within the STTSC (e.g. Station 25, Fig. 5.5c). It is possible that re-entry to the estuary is a behavioral variate in crabs that remain close inshore, and differs from that of crabs taken from areas such as STTSC shoals, which lie approximately 25-40 km offshore. The variation in muscle to ovary tissue isotopic patterns, such as seen from station 25 crabs, could be due to movement in and out

of tidal passes and thus reflects changes in isotopic values that occur over small geographic scales. Although there is a generally consistent convergence pattern reflecting offshore migration for the majority of crabs taken from offshore shoal stations (Fig. 5a,b), exceptions were found. One such exception (e.g. Fig 5.5a, station 1, grey symbol) was an individual from Ship Shoal with a high muscle and low ovary  $\delta^{13}\text{C}$ . This pattern is consistent with a crab that migrated to the offshore and remained long enough for the slower turnover muscle tissue to equilibrate with offshore isotopic values, then returned to an inshore estuary long enough for the ovary but not muscle to equilibrate, and then migrated to the offshore again.

These data on crab isotopes and epibionts suggest that the blue crabs we sampled from the STTSC are not composed of a resident offshore population that had persisted from a previous spawning season, but rather represent a new class of spawning females recently migrated from inshore estuaries. If the crabs taken from our study area were part of a long-term (on the order of many months) resident population then they theoretically would have had very similar ovary and muscle  $\delta^{13}\text{C}$ , which probably would not have a consistent convergence pattern, and both tissues would be centered near the offshore values of -17 to -18‰. It is possible that because STTSC blue crabs were actively spawning, newly acquired energy was allocated more towards ovarian replenishment and less to muscle maintenance. Because female blue crabs do not grow following their terminal molt (Churchill 1919), energy allocation is only to maintenance of muscle tissue and not growth. If true, the muscle may incorporate the offshore  $\delta^{13}\text{C}$  signal more slowly, and offshore residence could be masked, isotopically speaking. Feeding studies that would elucidate tissue turnover rates would be useful to answer such questions. However, isotopic evidence suggesting the STTSC crabs are relatively new arrivals to the offshore is congruent with epibiont data. Only one crab from our spring collections had acorn barnacles attached to the carapace;



heavy fouling by epibionts would be expected if crabs had spent much time in a high salinity environment such as the STTSC.

## STTSC Importance to the Gulf of Mexico Blue Crab Fishery and Use of Isotopes in Management

Beginning around 1991 the Chesapeake Bay blue crab fishery began a period of historically low yields. This decline was highlighted by an 84% decline in mature females (Lipcius and Stockhausen 2002). The recent recovery in the Chesapeake's blue crab fishery was correlated with a decreased fishing effort that targeted migrating females, an end to the winter blue crab dredge fishery targeting females, and greater protection of the Chesapeake Bay blue crab spawning grounds through an expansion of the lower bay spawning sanctuary. Estimates of the number of females actually residing within the blue crab spawning sanctuary are between 2 and 11% of the total Chesapeake Bay adult female population, however, despite the low percentage, they "form the core of the Chesapeake reproductive stock" (Hines 2007). Our studies within the STTSC have shown Ship, Trinity, and Tiger shoals peak catch rates are comparable with other well-studied blue crab spawning grounds and as in the Chesapeake Bay, may also provide a disproportionate amount of larvae that are needed to resupply the inshore fisheries. More studies are needed to resolve the extent that females from the STTSC, and shoal areas in particular, are supplying larvae that benefit to the inshore fisheries along the northern Gulf of Mexico coast.

## CONCLUSION

Isotopic analysis suggests that there is a direct estuarine-offshore link between STTSC spawning blue crabs and the Louisiana inshore blue crab spawning stock, which may be needed

to sustain Louisiana's blue crab fishery valued at approximately 35 million dollars a year (NOAA, 2009). Based on Louisiana coastal areal extent with salinities  $> 20$  (Barrett 1971), and the known salinity threshold for proper blue crab zoeal development of  $> 25$  (Sandoz and Rodgers 1944; Costlow and Bookhout 1959), I estimate that shoal areas within the STTSC comprise at least 20% of the known blue crab spawning grounds west of the Mississippi River.

Using nitrogen and carbon natural abundance isotopes I was able to identify a coastal east-west isoscape based on proximity to the Atchafalaya River, which suggests that females are generally migrating in a southerly direction from source estuaries and concentrating on shoals nearest to those estuaries. Once female blue crabs have migrated to the STTSC they generally do not continue in a back and forth migratory pattern during the spawning season, but rather remain in the offshore environment in a continuous cycle of spawning and hatching. Offshore spawning within the STTSC likely provides a large amount of viable larvae due to the advantageous environmental conditions potentially benefitting the Louisiana blue crab fishery as well as neighboring coastal states such as Texas, Mississippi, Alabama, and Florida.

These findings add to recent work within the STTSC that has begun to document its ecological and economic importance (e.g., Chapters 2-4; Grippo et al. 2009, 2010, 2011) and vulnerability to anthropomorphic impacts. The discovery of large concentrations of spawning blue crabs, *C. sapidus*, within the STTSC has not yet resulted in the protection of this largely unexploited population, despite the likelihood that it is a substantial component of the current fishery's spawning biomass, adversely impacted by the Deepwater Horizon Oil Spill, and a target for sand mining operations.

## LITERATURE CITED

- Adkins, G. 1972. A study of the blue crab fishery in Louisiana. Tech. Bull. 3. Louisiana Wildlife and Fisheries Commission, Oysters, Water Bottoms and Seafoods Division, New Orleans. 57 p.
- Barrett, B.B., J.W. Tarver, W.R. Latapie, J.F. Pollard, W.R. Mock, G.B. Adkins, W.J. Gaidry, C.J. White, J.S. Mathis. 1971. Cooperative Gulf of Mexico Estuarine Inventory and Study, Louisiana: Phase II, Hydrology. Louisiana Wild Life and Fisheries Commission in Cooperation with the U.S. Department of Commerce, National Marine Fisheries Service.
- Bodin, N., F. Le Loc'h, C. Hily. 2007. Effect of lipid removal on carbon and nitrogen stable isotope ratios in crustacean tissues. *Journal of Experimental Marine Biology and Ecology*. 341:168-175.
- Carr, S.D., R.A. Tankersley, J.L. Hench, R.B. Forward Jr, R.A. Luettich Jr. 2004. Movement patterns and trajectories of ovigerous blue crabs *Callinectes sapidus* during the spawning migration. *Estuarine, Coastal and Shelf Science*. 60:567-579.
- Churchill, E.P., Jr. 1919. Life history of the blue crab. *Bulletin U.S. Bureau of Fisheries*. 36:91-128.
- Costlow, J.D., Bookhout C.G. 1959. The larval development of *Callinectes sapidus* Rathbun reared in the laboratory. *Biological Bulletin*. 116:373-396.
- Crisp, D.J., J.D. Costlow Jnr. 1963. The tolerance of developing cirripede embryos to salinity and temperature. *Oikos*. 14:22-34.
- Cronin, L.E. 1949. Comparison of methods of tagging the blue crab. *Ecology*. 30:390-394.
- Daugherty, F. M. 1952. The blue crab investigation. *Texas Journal of Science*. 4:77-84.
- Deegan, L.A., R.H. Garritt. 1997. Evidence for spatial variability in estuarine food webs. *Marine Ecology Progress Series*. 147:31-47.

- Dubois, S., C.G. Gelpi Jr., R.E. Condrey, M.A. Grippo, J.W. Fleeger. 2009. Diversity and composition of macrobenthic community associated with sandy shoals of the Louisiana continental shelf. *Biodiversity and Conservation*. 18:3759-3784.
- France, R.L. 1995. Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. *Marine Ecology Progress Series*. 124:307-312.
- Fry, B. 1981. Natural stable carbon isotope tag traces Texas shrimp migrations. *Fishery Bulletin*. 79:337-345.
- Fry, B. 1983. Fish and shrimp migrations in the Northern Gulf of Mexico analyzed using stable C, N, and S isotope ratios. *Fishery Bulletin*. 81:789-801.
- Fry, B. 1988. Food web structure on Georges Bank from stable C, N, and S isotopic compositions. *Limnology and Oceanography*. 33:1182-1190.
- Fry, B. 2002. Stable isotopic indicators of habitat use by Mississippi River fish. *Journal of the North American Benthological Society*. 21:676-685.
- Fry, B., 2006. Stable isotope ecology. Springer, Heidelberg, 308 pp.
- Fry, B., D.M., Baltz, M.C., Benfield, J.W. Fleeger, A. Gace, H.L. Haas, Z.J. Quinones-Rivera. 2003. Stable isotope indicators of movement and residency for brown shrimp (*Farfantepenaeus aztecus*) in coastal Louisiana marshscapes. *Estuaries*. 26:82-97
- Fry, B. 2011. Mississippi River sustenance of brown shrimp (*Farfantepenaeus aztecus*) in Louisiana coastal waters. *Fishery Bulletin*. 109:147-161.
- Fry, B., E.B. Sherr. 1984.  $\delta^{13}\text{C}$  Measurements as indicators of carbon flow in marine and freshwater ecosystems. *Contributions in Marine Science*. 27:13-47.
- Fry, B., R.K. Anderson, L. Entzeroth, J.L. Bird, P.L. Parker. 1984.  $^{13}\text{C}$  Enrichment and oceanic food web structure in the Northwestern Gulf of Mexico. *Contributions in Marine Science*. 27:49-63.
- Fry, B., Y.C. Allen. 2003. Stable isotopes in zebra mussels as bioindicators of river-watershed linkages. *River Research and Applications*. 19:683-696.

- Gelpi, C.G., Jr., R.E. Condrey, J.W. Fleeger, S.F. Dubois. 2009. Discovery, evaluation, and implications of blue crab, *Callinectes sapidus*, spawning, hatching, and foraging grounds in federal (US) waters offshore of Louisiana. *Bulletin of Marine Science*. 85:203-222.
- Grippo, M.A. 2009. Benthic microalgae on the Louisiana inner continental shelf: biomass, distribution, and contribution to benthic food-webs. Ph.D .Dissertation. Louisiana State University.
- Grippo, M.A., J.W. Fleeger, R. Condrey, K.R. Carman. 2009. High benthic microalgal biomass found on Ship Shoal, North-Central Gulf of Mexico: *Bulletin of Marine Science*. 84:237-256.
- Grippo, M.A., J.W. Fleeger, N.N. Rabalais, R. Condrey, K.R. Carman. 2010. Contribution of phytoplankton and benthic microalgae to inner shelf sediments of the north-central Gulf of Mexico. *Continental Shelf Research*. 30:456-466.
- Grippo, M.A., J.W. Fleeger, S. Dubois, R. Condrey . 2011. Spatial variation in basal resources supporting benthic food webs revealed on the inner continental shelf. *Limnology and Oceanography*. 56:841-856.
- Hines, A.P. 2007. Ecology of juvenile and adult crabs. Pages 572-573, 578 in V. S. Kennedy and L. E. Cronin, eds. The blue crab *Callinectes sapidus*. Maryland Sea Grant College, College Park.
- Hobson, K..A. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia*. 120:314-326.
- Hsueh, P.W., J.B. McClintock, T.S. Hopkins. 1992. Comparative study of the diets of the blue crabs *Callinectes similis* and *C. Sapidus* from a mud bottom habitat in Mobile Bay, Alabama. *Journal of Crustacean Biology*. 12:615-619.
- Jaworski, E. 1972. The blue crab fishery, Barrataria estuary, Louisiana. L.S.U. Ph.D. Dissertation.
- Kiljunen, M., J. Grey, T. Sinisalo, C. Harrod, H. Immonen, R.I. Jones. 2006. A revised model for lipid-normalizing delta C-13 values from aquatic organisms, with implications for isotope mixing models. *Journal of Applied Ecology*. 43:1213-1222.

- Lipcius, R.N., W.T. Stockhausen. 2002. Concurrent decline of the spawning stock, recruitment, larval abundance, and size of the blue crab *Callinectes sapidus* in Chesapeake Bay. *Marine Ecology Progress Series*. 226:45-61.
- Logan J., H. Haas, L. Deegan, E. Gaines. 2006. Turnover rates of nitrogen stable isotopes in the salt marsh mummichog, *Fundulus heteroclitus*, following a laboratory diet switch. *Oecologia* 147:391-395.
- McCutchan, J.H., W.M. Lewis, C. Kendall, C.C. McGrath. 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos*. 102:378-390.
- McCutchan, J.H., Jr., W.M. Lewis, Jr. 2002. Relative importance of carbon sources for macroinvertebrates in a Rocky Mountain stream. *Limnology and Oceanography*. 47:742-752.
- More, W.R. 1969. A contribution to the biology of the blue crab *Callinectes sapidus* Rathbun in Texas, with a description of the fishery. Tech. Ser. 1. Texas Parks and Wildlife Department, Seabrook, Texas. 31 p.
- Newsome, S.D., C.M. del Rio, S. Bearhop, D.L. Phillips. 2007. A niche for isotopic ecology, *Frontiers in Ecology and the Environment*. 5:429-436.
- NOAA. 2009. Annual commercial landing statistics. National Oceanographic and Atmospheric Administration, National Marine Fisheries Service, Office of Science & Technology, Commercial Fisheries. 1315 East-West Highway, Silver Spring, MD 20910. Available from:  
<[http://www.st.nmfs.noaa.gov/st1/commercial/landings/annual\\_landings.html](http://www.st.nmfs.noaa.gov/st1/commercial/landings/annual_landings.html)>
- Oesterling, M.J. 1976. Reproduction, growth, and migration of blue crabs along Florida's Gulf Coast. A marine advisory bulletin in cooperation with the school of forest resources and conservation. Resource Management Systems Program School of Forest Resources and Conservation. University of Florida.
- Rabalais, N.N., R.E. Turner, W.J. Wiseman Jr. 2002. Gulf of Mexico hypoxia, a.k.a. "The Dead Zone". *Annual Review of Ecology and Systematics*. 33:235-263.
- Ricker, W.E. 1948. Methods of estimating vital statistics of fish populations. Indiana University. Publication. Science Series. 15:1-101.

- Rubenstein, D.R., K.A. Hobson. 2004. From birds to butterflies: animal movement patterns and stable isotopes: *Trends in Ecology & Evolution*. 19:256-263.
- Sandoz, M., R. Rogers. 1944. The effect of environmental factors on hatching, moulting, and survival of zoea larvae of the blue crab *Callinectes sapidus* Rathbun. *Ecology*. 25:216-228.
- Sherwood, G.D., G.A. Rose. 2005. Stable isotope analysis of some representative fish and invertebrates of the Newfoundland and Labrador continental shelf food web. *Estuarine, Coastal and Shelf Science*. 63:537-549.
- Steele, P. 1987. Population dynamics and migration of the blue crab, *Callinectes sapidus* (Rathbun), in the Eastern Gulf of Mexico. Proceedings of the 40<sup>th</sup> Gilt of Mexico and Caribbean Fisheries Institute. Florida Department of Natural Resources Bureau of Marine Research. St. Petersburg Florida.
- Tagatz, M.E. 1968. Biology of the blue crab, *Callinectes sapidus* Rathbun, in the St. Johns River, Florida. *Fishery Bulletin*. 67:17-33.
- Tankersley, R. A., M.G. Wieber, M.A. Sigala, K.A. Kachurak. 1998. Migratory behavior of ovigerous blue crabs *Callinectes sapidus*: Evidence for selective tidal-stream transport. *Biological Bulletin*. 195:168-173.
- Van Engel, W.A. 1958. The blue crab and its fishery in Chesapeake Bay. *Commercial Fisheries Review*. 20:1-17.
- Vanderklift, M.A., S. Ponsard. 2003. Sources of variation in consumer-diet  $\delta^{15}\text{N}$  enrichment: a meta-analysis. *Oecologia*. 136:169-182.
- West, J. B., G. J. Bowen, T. E. Dawson, K. P. Tu, eds. 2010. Isoscapes: Understanding movement, pattern, and process on Earth through isotope mapping, 487p. Springer Science+Business Media B.V., New York and Dordrecht, The Netherlands.
- Williams, A.B. 1974. The swimming crabs of the genus *Callinectes* (Decapoda: Portunidae). *Fishery Bulletin*. 72:685-789.

## **CHAPTER 6: SUMMARY AND MANAGEMENT IMPLICATIONS**



## SUMMARY

Sandbanks and sandy shoals occur on continental shelves, in coastal embayments, and in estuaries throughout the world. Their associated mineral deposits represent potentially valuable resources to help mitigate coastal erosion and to supply the raw material for beach reinforcement and coastal stabilization projects (Michel et al. 2001). Demands on coastal-ocean sand supplies are likely to increase as both human occupation of the coastal zone and sea level continues to rise, and as land-based sand-supplies decline. Although a large number of studies have examined sandbank formation, modeled sediment transport, and evaluated the importance of shoals to local hydrodynamic conditions (e.g., Berthot and Pattiaratchi 2004), few ecological studies have examined the functional value of these high-relief structures in their ecosystems, especially in terms of biodiversity and associated ecological services. This study began with the need to examine the biological value of Ship Shoal, a high-relief sandy shoal within the seasonal Dead Zone of the northern Gulf of Mexico as part of a pre-sand mining assessment of the area. In this dissertation I focused on potential ecological services of three sandy shoals off the Louisiana coast with emphasis on macrobenthic communities and offshore spawning blue crabs, *Callinectes sapidus*.

In our 2006 study of Ship Shoal's benthic macrofauna (Chapter 2), I found it characterized by high biomass (averaging  $26.7 \text{ g m}^{-2}$ ) and high diversity (161 species), suggesting that Ship Shoal was a diversity hotspot. In contrast to hypoxic conditions reported for the area surrounding Ship Shoal, we found it was generally not characterized by hypoxia, but by well oxygenated waters and high concentrations of amphipods. These observations led us to suggest that the shoal may serve as a hypoxia refuge, a valuable ecological service that would facilitate other potential Ship Shoal functions. Detailed analysis of the benthic macrofauna

revealed that several species known to inhabit sandy sediment formed the basis of the Ship Shoal faunal assemblage. We named this assemblage the *Albunea paretii*-*Branchiostoma floridae* community after the mole crab and amphioxus that are ubiquitous on Ship Shoal and compose much of its biomass. This study represented the first report of high abundances of *B. floridae* (amphioxus) off the Louisiana coast. In addition, nearly half of the polychaete species (35 of 72) we found on Ship Shoal were not reported for the Louisiana continental shelf in Ubelacker and Johnson's (1984) comprehensive work cataloging known polychaete distributions for the northern Gulf of Mexico. Since these polychaete species had been reported in Ubelacker and Johnson (1984) for the Florida and/or Texas continental shelf, our findings indicated that Ship Shoal may facilitate, through larval transport, connectivity of macroinfaunal metapopulations occupying sandy habitats across the northern Gulf of Mexico.

During our 2005-2006 trawl surveys on Ship Shoal (Chapter 4), we discovered high and fairly consistent concentrations of spawning and hatching blue crabs, *Callinectes sapidus*. This was the first report of spawning grounds >25 km offshore and suggested that Ship Shoal might be an important spawning ground for the inshore blue crab fishery of the northern Gulf of Mexico.

In 2007, we expanded our sampling design to encompass the Ship, Trinity Tiger Shoal Complex (STTSC), composed of Ship Shoal (Ship), Trinity/Tiger Shoals (TTS), and the surrounding off shoal area (Off). This enabled us to compare our findings from Ship's relatively homogenous sandy habitat, to other similar and dissimilar habitats within the Northern Gulf of Mexico and test our hypotheses concerning Ship's diversity and functions.

As a whole, we found the STTSC to be a biologically diverse area with three dynamic benthic habitats (Ship, TTS, and Off) each supporting distinctly different benthic macrofaunal

communities that contribute to the regional biodiversity of the northern Gulf of Mexico (Fig.3.2, Table 3.1); this supports the argument that maintaining regional-scale benthic heterogeneity helps support regional biodiversity (Zajac 2008).

My analyses indicated that sediment composition is the dominant environmental parameter determining the make-up of macrofaunal species assemblages (Table 3.3). Specifically, our macrofaunal species distributions are most heavily influenced by the sand percentage of the sediment (Table 3.3). Shallow shoals are subjected to increased effects of wave action and coastal currents, and have greater capacity to winnow away fine-grain particles (Wright et al. 2002). This along with proximity to fluvial input likely influences sediment composition and associated levels of disturbance, which our analyses suggest is also a contributing factor controlling community composition within the STTSC. In addition a source sink framework (Levin 1974; Pulliam 1988; Mouquet and Loreau 2003) fits well with the various mechanisms (e.g. disturbance, competition, habitat heterogeneity) that my study suggests contribute to the community patterns within the STTSC.

TTS is located nearer the Atchafalaya River than Ship and is generally shallower than Off. The high and stable levels of richness, abundance, diversity and biomass we found on TTS (Fig. 3.7a-f) are consistent with Huston's (1979) definition of a system that is in dynamic equilibrium. Furthermore, TTS is characterized by a seasonal shift in predominant feeding types, possibly a result of its dynamic environment such as high levels of river input and suspended sediment in the spring. Examples include high abundances of surface/subsurface deposit feeders (e.g. the polychaete *Mediomastus californiensis*) in the spring, and a greater predominance of suspension feeders (e.g. *Chone americana*) in the summer (Table 3.2).

Ship is located further from sources of riverine input than TTS. As such its surface is expected to receive less deposition of riverine suspended silts and clays, an expectation reflected in our measurements of surface sediments composed of homogeneous sand with a low mud content. In general Ship is characterized by suspension and interface feeding types (e.g. the amphipods *Acanthohaustorius* sp. A, *Protohaustorius bousfieldi*, and the polychaete *Spiophanes bombyx*), which are known to thrive in this type of benthic environment (Rhoads and Young 1970). Comparisons between Ship and TTS suggest that the habitat on Ship is uniquely suited to the requirements of its amphioxus population and may be similar to habitats classified by Antoniadou et al. (2004) as “amphioxus sands”. The concurrent patterns of decreasing mean species richness, abundance, and diversity, with a steady biomass (Fig. 3.7a-f) revealed that Ship is consistent with Huston’s (1979) description of a competition influenced community structure, in addition to possible synergistic effects due to predation pressure.

Off was characterized as a comparatively muddy sedimentary environment consisting of a varying mix of mud and sand (Table 3.3) with a high interseasonal variation in sediment composition (Baustian and Rabalais 2009; Grippo et al. 2010). Feeding types of the most abundant species were surface deposit, sub-surface deposit and interface feeders. This is consistent with Rhoads and Young’s (1970) description of an unstable benthic environment that is dominated by finer-grained sediments. Off stations had relatively high mean species richness in the spring that was higher than Ship and less than TTS. This was followed by a catastrophic decline in all biological parameters (e.g. richness, abundance, diversity, biomass and taxonomic distinctiveness (Figs 3.7 a-f) during the summer, consistent with hypoxia-related mass mortality (Harper et al. 1981; Gaston 1985; Rabalais et al. 2001a). In fall, Off appeared to exhibit a resilience following hypoxia. All our measured biological parameters, and community

composition were consistent with a system undergoing rapid recolonization by opportunistic species that are resistant to low dissolved oxygen conditions (e.g. *Mediomastus californiensis*, *Paraprionospio pinnata*, and *Magelona* sp. H).

Many macrofaunal species have been shown to have habitat preferences relating to sediment type, and specific size ranges of sediment are necessary for recruitment of some benthic species and/or their larva (Gray 1974). Our findings suggest that sandy areas within the STTSC have the potential to enhance across-shelf connectivity for species with a habitat preference for a high sand composition and may therefore facilitate the connectivity of northern Gulf of Mexico metapopulations. For example, we found significant positive relationships (Fig. 3.6 a,b) between sand percentage and polychaete species that were not reported in Ubelacker and Johnson (1984) from the Louisiana continental shelf. This suggests that the potential for genetic exchange across the northern Gulf of Mexico due to connectivity between localized populations with planktonic larvae or mobile adults is improved by accessible sandy habitats, such as those on Ship and TTS.

Our STTSC-wide analyses of the seasonal relationships between depth and DO suggests that shallow areas (< 9 m) are less susceptible to hypoxia and may function both as hypoxia refuge within the Dead Zone and as sources of larvae or adults to re-establish benthic macrofaunal populations within surrounding areas that have been affected by hypoxia. Our results indicate that areas below 9 m are expected to become hypoxic during the summer (Fig. 3.5). Shallow areas such as shoals are more likely to be impacted by the turbulence associated with surface currents and waves (Wright et al. 2002; Pepper and Stone 2004), which discourages stratification and bottom water hypoxia. In addition, local production of BMA on shoals may also provide oxygen through photosynthesis (Grippo et al. 2009; 2010). Our area comparisons

between shoals and off shoal amphipod abundances, which are highly sensitive to low DO (Gaston 1985, Wu and Or 2005), also provide evidence that the shoals are less affected by hypoxia than surrounding areas. During the summer there was a catastrophic decline in amphipod abundances for Off, while on Ship and TTS they remained present April to October. Spawning blue crabs may also benefit from more oxygenated bottom water found in shallower areas of the STTSC, particularly shoals. Blue crabs actively avoid low DO (Phil et al. 1991) and likely benefit from the greater prey biomass found on both Ship and TTS (Fig. 3.7d; Table 3.4), which may also be a function of a more consistently oxygenated benthic environment.

Although blue crabs are ecologically important predators and support the world's most valuable crab fishery, little was known about their spawning and hatching migrations beyond the estuary. We discovered unexpectedly high concentrations of female blue crabs actively spawning, hatching their eggs, and foraging in federal waters within the STTSC (Chapter 4). During our 2007 investigation, blue crab abundances were significantly higher on Ship and Trinity Shoals than the surrounding muddy and deeper seafloor (Fig.4.8), supporting our 2005-2006 prediction that shoals represented preferential spawning habitat.

Using the female blue crabs taken during our 2005-2007 cruises, we developed the first suite of comprehensive statistical examinations of blue crab population dynamics across geographical areas. Crabs from the STTSC compared favorably with those from nationally recognized spawning grounds in terms of condition factor (an index of health). The condition factor comparison (Eq 4.4; Fig.4.3) suggests a single width-weight relationship applies to all female blue crab populations reported in the literature despite wide geographical and temporal differences (Chesapeake Bay through Texas, 1966-2007). Crabs from the STTSC also compared favorably with those from nationally recognized spawning grounds in terms of

abundance (Table 4.4) and fecundity (Eq 4.5; Fig.4.4). Almost all STTSC female blue crabs possessed a sponge, large ovary, or both. Eighty-seven percent of non-ovigerous females showed evidence of a previous hatching. Using our analysis of ovarian and sponge development we were the first to use an ecological field study to predict the number of days (~21) between successive spawns for blue crabs (Fig.4.5), suggesting that at least seven broods were produced per spawning season (~April– October).

Our morphometric analysis indicates that the traditional linear predictor of blue crab weight, carapace width measured from tip to tip of the lateral spines (TT), is not the most accurate method. We found three other easily obtainable linear measurements [carapace length (L), carapace width excluding the lateral spines (BB), carapace height (H), and/or estimated crab volume ( $L*BB*H$ )] were more predictive, increasing the  $R^2$  by a factor of 0.12 to 0.16 and allowing for a statistical evaluation of the effect of ovigery on the size-weight relationship (Table 4.5).

Thus, these analyses indicate that STTSC shoals are important spawning grounds that likely provide benefit to inshore populations through larval input. The importance of spawning ground protection has recently been highlighted on the east coast with the rebound of the Chesapeake Bay blue crab stock and spawning biomass just a few years after expansion of its spawning sanctuary, and ending a winter dredge fishery that targeted overwintering females at the mouth of Chesapeake Bay (Pala 2010).

In chapter 5 we used natural abundance isotopes to test the overall hypothesis that the mature female blue crabs we captured on the STTSC had recently migrated from inshore nursery grounds and were becoming resident on its shoals (Ship and TTS). Central to our approach was

the different turnover rates we expected from the ovary (i.e. rapid turnover) and muscle (i.e. longer turnover) tissues and established trends related to  $^{13}\text{C}$  (i.e. positive correlation with salinity) and  $^{15}\text{N}$  (i.e. positive correlation with proximity to riverine input). I found several consistent and informative trends. One was an east-west relationship of decreasing  $\delta^{13}\text{C}$  and increasing  $\delta^{15}\text{N}$  for both tissues (muscle and ovary) with a closer proximity of capture to the Atchafalaya River. Here the results indicated that crabs predominately migrate directly offshore from their home estuary rather than long distances alongshore (Table 5.2; Fig.5.4). We also found that many  $\delta^{13}\text{C}$  values for offshore crab tissue, especially muscle, were depleted relative to typical lower estuary salt marsh values, indicating that some female blue crabs migrate directly offshore from low salinity regions of their home estuary. Here the results suggest geographic differences in migratory behavior from areas like Chesapeake Bay where females are known to undergo seasonally separated migrations and typically overwinter in high salinity regions of the estuary before spawning their eggs (Tankersley et al. 1998; Hines 2007 and refs within).

Muscle and ovary isotope orientation and spacing converged towards our proxy for offshore residence (i.e. mean values for *Callinectes similis*; Fig.5.5) suggesting that migrating *C. sapidus* utilize offshore prey resources. This finding is corroborated with positive correlations between crab  $\delta^{13}\text{C}$  and diameter of an epibiotic barnacle, *C. patula* (Fig. 5.6) whose larvae requires salinities > 25 ppt for survival (Crisp and Costlow 1963) and thus likely preferentially recruits to the crab carapace off shore. These results indicate that STTSC females do not typically re-enter inshore estuaries during the spawning season. Thus our study provides evidence that once female blue crabs migrate to the STTSC they generally do not continue in a back and forth migratory pattern, but rather remain in the offshore environment in a continuous cycle of spawning and hatching from at least April to October. As these results directly link our



offshore STTSC spawning female blue crabs to the inshore blue crab fishery they have important management implications. Based on our estimates STTSC shoals support at least 20% of the known Louisiana blue crab spawning stock west of the Mississippi River (Chapter 5 Discussion) and though these crabs do not yet appear to be the subject of a directed fishery, they are also not protected by federal management.

My use of isotopes is a new approach to assess blue crab migratory dynamics. Migratory studies of blue crabs have traditionally relied on tagging studies which are dependent on a vast array of assumptions and conditions including under and over reporting, differing fishing gears and pressures, tag induced mortality and tag shedding (Ricker 1948; Cronin 1949).

#### SAND MINING IMPLICATIONS

Following the Deepwater Horizon Oil Spill (DWHOS), Louisiana State Coastal Protection Restoration Authority (CPRA) pressed for an extraction of Ship Shoal sand resources for use in emergency barrier island sand berm construction. In this request for sand removal an extraction zone 9.14 m deep by 304.8 m with an unspecified third dimension was proposed (CPRA 2010); this portion of the application was denied. However, use of these sand resources and the active search for borrow areas on other shoals, particularly Tiger and Trinity Shoals continue (Khalil et al. 2010), despite the potential ecological consequences of such activity, outlined in our study.

Our results strongly suggest that extensive sand mining of the Ship, Trinity, or Tiger Shoals will have adverse ecological impacts. The extent and nature of these impacts are largely dependent upon the amount of surface area involved, and depth of the shoal surface below the water/air interface following sand mining. There are currently a number of proposed locations of

sand mining within the STTSC as well as elsewhere along the Louisiana continental shelf (Khalil et al. 2010; Khalil and Finkl 2010). On Ship Shoal the three identified sand extraction polygons are centered along the shallow shoal crest. Based on volumetric and surface area data from Khalil et al. (2010) and CPRA (2010) these extraction polygons compose a total area of 75.55 km<sup>2</sup>, accounting for at least 15% of the total surface area of Ship Shoal. The proposed depth of available sediment removal from the Western Ship Shoal borrow area is 4 m (Khalil et al. 2010) though a greater maximum extraction depth of 9.14 m was proposed in CPRA (2010) for Ship Shoal Blocks 88 and 89 as well as for South Pelto Blocks 12 and 13. If 15% of the surface area of Ship Shoal is mined, the results of my biological analyses as well as the high likelihood that the mined area will fill with muddy sediment (Palmer et al. 2008) strongly suggest that a dramatic change in benthic functions will occur. Potential changes include a likely reduction in the sand mined area's contribution to regional biodiversity, larval connectivity of species that have a preference for sandy habitat, regional benthic resiliency following hypoxia, BMA-based benthic food web production, benthic macrofaunal biomass, and blue crab carrying capacity. Moreover, any sand removal from the crest of Ship Shoal which results in a benthic surface 9 m or more below the water/air interface will likely result in the incursion of hypoxic bottom water, reducing the biological use of this important blue crab foraging and spawning ground during the summer months, the period of highest blue crab spawning concentrations. All three of the proposed sand extraction polygons lie at or below the 4 m contour (Khalil et al. 2010). At the currently and previously proposed sand removal depths of 4 m and 9.14 m (Khalil 2010; CPRA 2010, respectively) the polygon extraction sites would all fall within a depth range where hypoxia encroachment is likely, as suggested by Figure 3.5. In addition, analysis by Rabalais et

al. (2001b) has shown hypoxia encroachment at even shallower depths of approximately 4 m in off shoal areas.

We have found that Ship and TTS macrobenthos are characterized by many K-selected species that are larger, relatively long-lived, and with a slow reproduction rate. The review by Newell et al. (1998), published before my study began, estimated post-dredging recovery of a sandy benthic community would take two to three years with “recovery” defined as a community able to “maintain itself” after 80% of the species diversity and biomass have been restored to pre-dredging levels. However, my study suggests that within the STTSC there is a greater susceptibility to hypoxia resulting from sand mining–related depth increases. In such cases recovery of the benthic community would be further hindered. Thus, sand mining related changes in sediment such as a finer particle size (Palmer et al. 2008), and altered bottom water oxygen dynamics would likely lead to fundamental changes in the structure of STTSC communities typified by declines in blue crab use and increases in opportunistic macroinfaunal species such as *M. californiensis*, *P. pinnata*, and *Magelona* sp. H (Table 3.1b,c; Table 3.2), which are found throughout the muddier, hypoxia-prone offshoal habitat.

Given our overall findings, it is difficult to recommend sand mining of the Shoals comparable to that outlined in our understanding of BOEM (2010) and Khalil et al. (2010). However, if sand mining of Ship, Trinity, or Tiger Shoals proceeds, one might suggest based on Figure 3.5 that the sediment surface following sand mining have a 2m buffer above my 9 m projected depth of susceptibility to hypoxia. However, this suggestion would ignore Rabalais (2001b) finding that hypoxia may encroach in depths as shallow as 4 m in off shoal areas associated with the Dead Zone. Regardless of the depth of any sand mining operation in the STTSC I highly recommend that a BACI-ANCOVA sampling design be implemented to assess

the effects of sand mining by using previously identified bioindicators such as benthic macrofaunal groups that are sensitive to environmental disturbance (e.g. amphipods), as well as analyses established in this study for the health and fecundity of blue crabs.

## POST DEEPWATER HORIZON OIL SPILL CONSIDERATIONS

The STTSC shoal benthic community has not to our knowledge been evaluated following the DWHOS, despite the unprecedented use of dispersants (Kujawinski et al. 2011) and satellite evidence that the sheen of oil from the DWHOS extended over much, if not all, of the STTSC (Times-Picayune 2010). Though a post-DWHOS study of the STTSC is needed for a comprehensive understanding of the impact of the spill on all habitats within the Louisiana continental shelf, the unique characteristics of STTSC shoal ecosystems make it imperative that they are included in post spill assessment. For example, adsorbing properties of oil hydrocarbons are different depending on organic matter content (Pezeshki et al. 2000); because STTSC shoals are sandy and low in organic content compared to the muddier off shoal (Grippio 2010), we would expect different interactions between sediment and deposited oil on the shoals as opposed to off the shoals. We have developed unique, quantitative, pre-DWHOS biological indicators of ecosystem health (Chapter 2,3; Grippo et al. 2009, 2010) such as baseline data on amphipod community, which are known to be adversely affected by oil (Gesteira and Dauvin 2000). In addition we have detailed baseline analyses of blue crab condition factor and fecundity (Chapter 4). These readily available pre-DWHOS studies should be used to assess any post-DWHOS changes in benthic community, blue crab data, and STTSC ecosystems. Specific tests could include reductions or disappearance of bioindicator macrofaunal species, changes in morphometric relationship of blue crab body and/or sponge weight, changes in relationship between blue crab ovarian and egg development, changes in fecundity as measured by egg

number per sponge, altered blue crab embryo morphology, and reductions in abundance of blue crabs. However, if sand mining were to occur on STTSC shoals before an appraisal is made of the DWHOS impacts, it seems likely that a statistical distinction between these two effects would, at best, be compromised.

#### LITERATURE CITED

- Antoniadou, C., Y. Krestenitis, C. Chintiroglou. 2004. Structure of the “Amphioxus sand” community in Thermaikos bay (Eastern Mediterranean). *Fresenius Environmental Bulletin*. 13:1122-1128.
- Baustian, M., Rabalais N. 2009. Seasonal Composition of Benthic Macroinfauna Exposed to Hypoxia in the Northern Gulf of Mexico. *Estuaries and Coasts* 32: 975-983.
- BOEM, 2010. OCS sand and gravel mining. U.S. Department of Interior, Bureau of Ocean Energy Management, Washington D.C.  
<http://www.gomr.boemre.gov/homepg/offshore/sandgrvl.html>; last updated 9/21/2010; text moved to <http://www.boem.gov/Non-Energy-Minerals/Sand-and-Gravel/Sand-Grvl.aspx> accessed 3/16/2012.
- Berthot, A., C. Pattiaratchi. 2004. Maintenance of headland-associated linear sandbanks: modelling the secondary flsec and sediment transport. 12th International Biennial Conference on Physics of Estuaries and Coastal Seas. Springer, Heidelberg, Merida, Mexico, pp 526–540.
- Coastal Protection and Restoration Authority (CPRA). 2010. Application to U.S. Army Corps of Engineers for emergency authorization for barrier island sand berm construction. May 11, 2010. Baton Rouge, Louisiana.
- Crisp, D.J., J.D. Costlow Jr. 1963. The tolerance of developing cirripede embryos to salinity and temperature. *Oikos*. 14:22-34.
- Cronin, L.E. 1949. Comparison of Methods of Tagging the Blue Crab. *Ecology* 30:390-394.

- Gaston, G.R. 1985. Effects of hypoxia on macrobenthos of the inner shelf off Cameron, Louisiana. *Estuarine, Coastal and Shelf Science*. 20:603-613.
- Gesteira, J.L.G., J.C. Dauvin. 2000. Amphipods are good bioindicators of the impact of oil spills on soft-bottom macrobenthic communities. *Marine Pollution Bulletin*. 40:1017-1027.
- Gray, J.S. 1974. Animal-Sediment relationships. *Oceanography and Marine Biology Annual Review*. 12:223-261.
- Grippo, M., J.W. Fleeger, R. Condrey, K.R. Carman. 2009. High benthic microalgal biomass found on Ship Shoal, north-central Gulf of Mexico. *Bulletin of Marine Science*. 84:237-256.
- Grippo, M.A., J.W. Fleeger, N.N. Rabalais, R. Condrey, K.R. Carman. 2010. Contribution of phytoplankton and benthic microalgae to inner shelf sediments of the north-central Gulf of Mexico. *Continental Shelf Research*. 30:456-466.
- Harper, D.E. Jr., L.D. McKinney, R.R. Salzer, R.J. Case. 1981. The occurrence of hypoxic bottom water off the upper Texas coast and its effects on the benthic biota. *Contribution in Marine Science*. 24:53-79.
- Hines, A. P. 2007. Ecology of juvenile and adult crabs. Pages 572-573, 578 in V. S. Kennedy and L. E. Cronin, eds. The blue crab *Callinectes sapidus*. Maryland Sea Grant College, College Park.
- Huston, M. 1979. A General Hypothesis of Species Diversity. *The American Naturalist*. 113:81-101.
- Khalil, S. M. C.W. Finkl, H. H. Roberts, R. C. Raynie. 2010. New Approaches to Sediment Management on the Inner Continental Shelf Offshore Coastal Louisiana. *Journal of Coastal Research*. 26:591-604.
- Khalil, S. M., C. W. Finkl. 2010. An Overview of Sedimentary Resources for Coastal Restoration and Protection in Louisiana. *Proceedings of the June 2010 State of the Coast Meeting*. Baton Rouge Louisiana.
- Kujawinski, E.B., M.C.K. Soule, D.L. Valentine, A.K. Boysen, K. Longnecker, M.C. Redmond. 2011. Fate of dispersants associated with the Deepwater Horizon Oil Spill. *Environmental Science & Technology*. 110126010225058 DOI: [10.1021/es103838p](https://doi.org/10.1021/es103838p).

- Levin, A.S. 1974. Dispersion and population interactions. *The American Naturalist*. 108:207-228.
- Lipcius, R. N., W. T. Stockhausen. 2002. Concurrent decline of the spawning stock, recruitment, larval abundance, and size of the blue crab *Callinectes sapidus* in Chesapeake Bay. *Marine Ecology Progress Series*. 226:45-61.
- Michel, J., R. Nairn, J.A. Johnson, D. Hardin. 2001. Development and design of biological and physical monitoring protocols to evaluate the long-term impacts of offshore dredging operations on the marine environment. US Department of the Interior, Mineral Management Service, International Activities and Marine Minerals Division (INTERMAR), Herndon.
- Mouquet, N., M. Loreau. 2003. Community patterns in source-sink metacommunities. *The American Naturalist*. 162:544-557.
- Newell, R.C., L.J. Seiderer, D.R. Hitchcock. 1998. The impact of dredging works in coastal waters: a review of the sensitivity to disturbance and subsequent recovery of biological resources on the seabed. *Oceanography and Marine Biology – An Annual Review*. 36:127-178.
- Pala, C. 2010. Chesapeake crabs: engineering a rebound. *Science*. 330:1474.
- Palmer, T.A., P.A. Montagna, R.B. Nairn. 2008. The effects of a dredge excavation pit on benthic macrofauna in offshore Louisiana. *Environmental Management*. 41:573–583.
- Pepper, D.A., G.W. Stone. 2004. Hydrodynamic and sedimentary responses to two contrasting winter storms on the inner shelf of the northern Gulf of Mexico. *Marine Geology*. 210:43-62.
- Pezeshki, S.R., M.W. Hester, Q. Lin, J.A. Nyman. 2000. The effects of oil spill and clean-up on dominant US Gulf coast marsh macrophytes: a review. *Environmental Pollution*. 108:129-139.
- Pihl, L., S.P. Baden, R.J. Diaz. 1991. Effects of periodic hypoxia on distribution of demersal fish and crustaceans. *Marine Biology*. 108:349-360.
- Pulliam, H.R. 1988. Sources, sinks, and population regulation. *The American Naturalist*. 132:652-661.

- Rabalais, N.N., L.E. Smith, D.E. Harper Jr., D. Justić. 2001a. Effects of seasonal hypoxia on continental shelf benthos. In *Coastal hypoxia: Consequences for living resources and ecosystems*, Coastal and Estuarine Studies 58, ed. N.N. Rabalais and R. E. Turner, 211-240. Washington, DC: American Geophysical Union.
- Rabalais, N.N., R.E. Turner, W.J. Wiseman. 2001b. Hypoxia in the Gulf of Mexico. *Journal of Environmental Quality*. 30:320-329.
- Rhoads, D.C., D.K. Young. 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. *Journal of Marine Research* 28:150-178.
- Ricker, W.E. 1948. Methods of estimating vital statistics of fish populations. Indiana University Publications, Science Series No. 15, Contribution No. 352 from the Department of Zoology, pp. 1-101.
- Tankersley, R. A., M.G. Wieber, M.A. Sigala, K.A. Kachurak. 1998. Migratory behavior of ovigerous blue crabs *Callinectes sapidus*: Evidence for selective tidal-stream transport. *Biological Bulletin*. 195:168-173.
- Times-Picayune. 2010. First 100 days of the Gulf of Mexico oil spill: An animated timeline of events. [http://www.nola.com/news/gulf-oil-spill/index.ssf/2010/05/gulf\\_of\\_mexico\\_oil\\_spill\\_anima.html](http://www.nola.com/news/gulf-oil-spill/index.ssf/2010/05/gulf_of_mexico_oil_spill_anima.html)
- Uebelacker, J.M., P.G. Johnson. 1984. Taxonomic guide to the polychaetes of the northern Gulf of Mexico, Vol. 1–7 Barry A. Vittor & Associates, Inc, Mobile.
- Wright, J., A. Colling, D. Park. 2002. Waves, tides, and shallow-water processes: Oxford, UK; Boston, MA; Milton Keynes, England, Butterworth-Heinemann; In Association with the Open University.
- Wu, R.S.S., Y.Y. Or. 2005. Bioenergetics, growth and reproduction of amphipods are affected by moderately low oxygen regimes. *Marine ecology Progress Series*. 297:215-223.
- Zajac, R.N. 2008. Macrobenthic biodiversity and sea floor landscape structure. *Journal of Experimental Marine Biology and Ecology*. 366:198-203.



**APPENDIX A: FAMILIES AND SPECIES IDENTIFIED FROM THE GOMEX BOX  
CORE SAMPLES TAKEN FROM SHIP SHIOAL IN 2006**

Core cross-sectional area = 0.09 m<sup>2</sup>. Mesh size 500 µm.

Phyla	Family	Species
Plathelminthes	-	<i>Probusa veneris</i>
	Plehnidae	<i>Discocelides ellipsoides</i>
Cnidaria	Actinostolidae	<i>Paranthus rapiformis</i> <i>burrowing Anemone</i> sp. 2 <i>burrowing Anemone</i> sp. 3
Nemertea	Lineidae	<i>Micrura leidy</i>
	-	<i>Nemertea</i> sp. 1
	-	<i>Nemertea</i> sp. 2
	-	<i>Nemertea</i> sp. 3
Polychaeta	Orbiniidae	<i>Leitoscoloplos fragilis</i> <i>Scoloplos rubra</i> <i>Scoloplos</i> sp. B <i>Phylo felix</i>
	Paraonidae	<i>Cirrophorus forticirratus</i> <i>Aricidea fragilis</i> <i>Aricidea suecica</i> <i>Aricidea alisdairi</i> <i>Aricidea quadrilobata</i> <i>Paraonis pygoenigmatica</i>
	Spionidae	<i>Spiophanes bombyx</i> <i>Boccardiella</i> sp. A <i>Polydora ligni</i> <i>Polydora socialis</i> <i>Dispio uncinata</i> <i>Aonides paucibranchiata</i> <i>Scoelepis texana</i> <i>Scoelepis squamata</i> <i>Paraprionospio pinnata</i> <i>Prionospio cristata</i> <i>Prionospio pygmaea</i> <i>Prionospio cirrobranchiata</i> <i>Spio pettibonea</i> <i>Microspio pigmentata</i>
	Magelonidae	<i>Magelona</i> sp. A <i>Magelona</i> sp. H
	Poecilochaetidae	<i>Poecilochaetus johnsoni</i>
	Chaetopteridae	<i>Spiochaetopterus costarum</i> <i>Mesochaetopterus capensis</i>
	Cirratulidae	<i>Tharyx annulosus</i>

	<i>Chaetozone</i> sp. A
	<i>Cirriformia</i> sp. B
Capitellidae	<i>Mediomastus californiensis</i>
	<i>Mastobranchus</i> sp. A
	<i>Notomastus latericeus</i>
Arenicolidae	<i>Arenicola</i> sp.
Opheliidae	<i>Armandia maculata</i>
	<i>Travisia hobsonae</i>
Phyllodocidae	<i>Phyllodoce mucosa</i>
	<i>Anaitides groenlandica</i>
Polynoidae	<i>Malmgreniella</i> sp. C
	<i>Lepidonotus sublevis</i>
	<i>Perolepis</i> sp. A
	<i>Polynoidae</i> sp.
Eulepethidae	<i>Grubeulepis</i> sp. A
Sigalionidae	<i>Thalenessa</i> cf. <i>spinosa</i>
	<i>Fimbriosthenelais minor</i>
Hesionidae	<i>Podarke</i> sp. A
	<i>Gyptis brevipalpa</i>
Pilargiidae	<i>Sigambra tentaculata</i>
	<i>Synelmis klatti</i>
Syllidae	<i>Streptosyllis pettiboneae</i>
Nereidae	<i>Neanthes micromma</i>
	<i>Nereis falsa</i>
	<i>Websterinereis tridentata</i>
Glyceridae	<i>Glycera americana</i>
	<i>Glycera abbranchiata</i>
Goniadidae	<i>Goniada littorea</i>
Nephtyidae	<i>Nephtys simoni</i>
	<i>Aglaophamus verrilli</i>
Amphinomidae	<i>Paramphinome</i> sp. B
Onuphidae	<i>Diopatra cuprea</i>
	<i>Onuphis emerita oculata</i>
Lumbrineridae	<i>Lumbrineris latreilli</i>
	<i>Lumbrineris tenuis</i>
Oweniidae	<i>Owenia fusiformis</i>
	<i>Myriowenia</i> sp. A
Ampharetidae	<i>Sabellides</i> sp. A
	<i>Ampharete</i> sp. A
Terebellidae	<i>Loimia viridis</i>
	<i>Eupolymnia nebulosa</i>
Sabellidae	<i>Chone americana</i>
Mollusca	
Olividae	<i>Oliva sayana</i>
	<i>Olivella mutica</i>
Nassariidae	<i>Nassarius acutus</i>

	Fasciariidae	<i>Latirus distinctus</i>
	Columbellidae	<i>Anachis obesa</i>
	Naticidae	<i>Polinices duplicatus</i>
		<i>Natica pusilla</i>
		<i>Simun maculatum</i>
	Litiopinae	<i>Epitonium multistriatum</i>
	Calyptraeidae	<i>Crepidula plana</i>
	Cyclostremellinae	<i>Cyclostremella humilis</i>
	Tellinidae	<i>Strigilla pisiformis</i>
		<i>Tellina iris</i>
		<i>Tellina versicolor</i>
		<i>Macoma pulleyi</i>
	Mactridae	<i>Mulinia lateralis</i>
		<i>Raeta plicatella</i>
	Cardiidae	<i>Americardia media</i>
	Solecurtidae	<i>Abra aequalis</i>
	Ungulinidae	<i>Diplodonta soror</i>
	Lucinidae	<i>Parvilucina multilineata</i>
		<i>Linga amiantus</i>
	Veneridae	<i>Chione clenchi</i>
	Solenoidae	<i>Solen viridis</i>
	Dosiniinae	<i>Dosinia discus</i>
	Pandoridae	<i>Pandora trilineata</i>
	Arcidae	<i>Anadara transversa</i>
Crustacea		
	Haustoriidae	<i>Acanthohaustorius</i> sp. A
		<i>Protohaustorius bousfieldi</i>
		<i>Pseudohaustorius americanus</i>
	Synopiidae	<i>Metatiron triocellatus</i>
		<i>Metatiron tropakis</i>
	Liljeborgiidae	<i>Listriella barnardi</i>
	Isaeidae	<i>Microprotopus raneyi</i>
	Corophiidae	<i>Monoconophium</i> sp. A
		<i>Monocorophium tuberculatum</i>
	Ampelisca	<i>Ampelisca</i> sp. C
	Oedicerotidae	<i>Hartmanodes nyei</i>
		<i>Americhelidium americanum</i>
	Ischyroceridae	<i>Ericthonius brasiliensis</i>
		<i>Cerapus tubularis</i>
	Argissidae	<i>Argissa hamtipes</i>
	Stenothoidae	<i>Parametopella cypris</i>
	Caprellidae	<i>Deutella</i> sp.
	Platyschnopidae	<i>Eudevanopus honduranus</i>
	Phoxocephalidae	<i>Trichophoxus</i> sp.
	-	unknown Amphipod
	Portunidae	<i>Portunus gibbesii</i>

		<i>Ovalipes floridanus</i>
		<i>Callinectes similis</i>
		<i>Portunidae</i> sp
	Pinnotheridae	<i>Pinnixia chacei</i>
		<i>Pinnixia sayana</i>
	Xanthidae	<i>Xanthidae</i> sp.
	Majidae	<i>Libinia dubia</i>
		<i>Mithrax acuticormis</i>
	Paguridae	<i>Pagurus annulipes</i>
	Albuneidae	<i>Albunea paretii</i>
		<i>Lepidopa benedicti</i>
	Porcellanidae	<i>Euceramus praelongus</i>
	-	<i>Thalassinidean</i> sp.
	Callianassidae	<i>Glypturus</i> nr. <i>acanthochirus</i>
	Pasiphaeidae	<i>Leptochela serratorbita</i>
	Processidae	<i>Processa hemphilli</i>
	Hippolytidae	<i>Latreutes parvulus</i>
	Panaeidae	<i>Solenocera vioscai</i>
	Sergestidae	<i>Lucifer faxoni</i>
		<i>Acetes americanus</i>
	Ogyrididae	<i>Ogyrides alphaerostris</i>
	Nannosquillidae	<i>Coronis scolopendra</i>
		<i>Squilla</i> sp. A
	Diastylidae	<i>Oxyurostylis smithi</i>
	Bodotriidae	<i>Cyclaspis varians</i>
Echinodermata		
	Amphiuridae	<i>Amphipholis squamata</i>
Sipuncula		
	Golfingiidae	<i>Phascolion strombi</i>
		<i>Golfingia tenuissima</i>
	Sipunculidae	<i>Sipunculus</i> sp.
Echiura		
	Echiuridae	<i>Thalassema</i> sp.
Phoronida		
	Phoronidae	<i>Phoronis architecta</i>
Chordata		
	Branchiostomatidae	<i>Branchiostoma floridae</i>

---

## **APPENDIX B: SPECIES SAND PERCENTAGE FROM THE STTSC IN 2007**

Mean species abundances per sand percentage intervals across all seasons and sampling locations. Symbols represent number of individuals (· < 1, ♦ 1-5, ◆ 6-10, ◆ 11-50, ◆ 51-210 individuals). \* = newly reported polychaete species (see methods Chapter 3)

			Range of sand percentage occurrence among sampling locations									
			I-----Ship Shoal ---I									
			I-----Tiger/Trinity Shoal -I									
Phyla are listed in alphapetical order			I-----Offshoal -----I									
Phylum	Family	Species	0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	90-100
Annelida	Acoetidae	<i>Polyodontes</i> sp. A*									·	·
Annelida	Acoetidae	<i>Polyodontes lupina</i> *								·		
Annelida	Ampharetidae	<i>Ampharete</i> sp. A*	◆	♦				◆	◆			·
Annelida	Ampharetidae	<i>Isolda pulchella</i> *								·		·
Annelida	Ampharetidae	<i>Lysippe</i> sp.*									·	
Annelida	Ampharetidae	<i>Melinna maculata</i> *									·	
Annelida	Ampharetidae	<i>Sabellides</i> sp. A							·	·	·	·
Annelida	Ampharetidae	<i>Amphicteis gunneri</i>			·	·						
Annelida	Amphinomidae	<i>Eurythoe</i> sp.*				·			·		·	·
Annelida	Amphinomidae	<i>Paramphinome</i> sp. B	◆			·		·	♦	♦	♦	♦
Annelida	Aphroditidae	<i>Aphroditidae</i> sp.			·							
Annelida	Capitellidae	<i>Mediomastus californiensis</i>	♦	◆	♦	◆	♦	◆	◆	◆	◆	◆
Annelida	Capitellidae	<i>Notomastus latericeus</i> *		♦	♦	♦			◆	♦	◆	♦
Annelida	Chaetopteridae	<i>Mesochaetopterus capensis</i> *										·
Annelida	Chaetopteridae	<i>Spiochaetopterus costarum</i>				·	·	·	·	♦		·
Annelida	Chrysopetalidae	<i>Paleanotus heteroseta</i>		·				·	·			
Annelida	Cirratulidae	<i>Caulleriella</i> sp.*		·	·	·			·			
Annelida	Cirratulidae	<i>Chaetozone</i> sp. A*								·		·
Annelida	Cirratulidae	<i>Cirriformia</i> sp.*									·	·
Annelida	Cirratulidae	<i>Cirriformia</i> sp. A*										·
Annelida	Cirratulidae	<i>Tharyx annulosus</i>				·			·	♦	·	♦
Annelida	Cossuridae	<i>Cossura delta</i>	·	◆		◆	·	·	♦	·	·	
Annelida	Dorvilleidae	<i>Protodorvillea kefersteini</i> *		·								
Annelida	Eulepethidae	<i>Grubeulepis</i> sp. A*							·		♦	♦

Phylum	Family	Species	0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	90-100
Annelida	Flabelligeridae	<i>Piromis roberti</i> *					•	◆	•			
Annelida	Glyceridae	<i>Glycera abranchiata</i> *										•
Annelida	Glyceridae	<i>Glycera</i> sp. C*		•		•			◆		•	•
Annelida	Glyceridae	<i>Glycera dibranchiata</i> *								•		
Annelida	Glyceridae	<i>Glycera americana</i>	◆	•		◆		•	•		•	•
Annelida	Goniadidae	<i>Goniadides carolinae</i> *		◆		•		◆	◆			
Annelida	Goniadidae	<i>Goniada littorea</i>				•	•		◆	◆	•	•
Annelida	Hesionidae	<i>Podarkeopsis brevipalpa</i>		•	•	•		•		•	•	•
Annelida	Hesionidae	<i>Ophiodromus</i> sp. A			•	•		•				
Annelida	Lumbrineridae	<i>Lumbrineris</i> sp. A*										•
Annelida	Lumbrineridae	<i>Lumbrineris latreilli</i> *			◆	•				•	◆	◆
Annelida	Lumbrineridae	<i>Lumbrineris tenuis</i> *				•					•	•
Annelida	Lumbrineridae	<i>Ninoe</i> sp. A*			•							
Annelida	Lumbrineridae	<i>Lumbrineris coccinea</i>				•						•
Annelida	Lumbrineridae	<i>Lumbrineris verrilli</i>		◆		◆		◆	◆	•	◆	•
Annelida	Lumbrineridae	<i>Lumbrineris ernesti</i>		•		•			•		◆	•
Annelida	Lumbrineridae	<i>Ninoe</i> sp. B		•	◆	◆				•		
Annelida	Magelonidae	<i>Magelona</i> sp. A*								•	•	◆
Annelida	Magelonidae	<i>Magelona</i> sp. H	◆	◆	◆	◆	◆	◆	◆	◆	◆	◆
Annelida	Maldanidae	<i>Euclymene</i> sp. A*			◆	•						
Annelida	Maldanidae	<i>Asychis elongata</i>	◆	◆	◆	•		•				
Annelida	Maldanidae	<i>Clymenella torquata</i>		◆	◆	•			◆			
Annelida	Nephtyidae	<i>Micronephthys minuta</i> *						◆	◆		•	◆
Annelida	Nephtyidae	<i>Nephtys simoni</i> *										◆
Annelida	Nephtyidae	<i>Nephtys squamosa</i> *										•
Annelida	Nephtyidae	<i>Nephtys incisa</i>		◆	◆	•			•			
Annelida	Nephtyidae	<i>Aglaophamus verrilli</i>			•	◆			•	◆	◆	◆
Annelida	Nereididae	<i>Nereis falsa</i> *				•		•	◆	•		•
Annelida	Nereididae	<i>Nereis micromma</i>		◆	•	◆		•	◆	◆	◆	◆
Annelida	Nereididae	<i>Nereis grayi</i>										•



Phylum	Family	Species	0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	90-100
Annelida	Nereididae	<i>Ceratocephale oculata</i>							•			
Annelida	Oeononidae	<i>Drilonereis longa</i> *										•
Annelida	Oeononidae	<i>Drilonereis debilis</i>										•
Annelida	Onuphidae	<i>Onuphid</i> sp.*									•	
Annelida	Onuphidae	<i>Diopatra cuprea</i>	◆	•	•	•	•	◆	◆		•	•
Annelida	Onuphidae	<i>Onuphis eremita oculata</i>							◆	•	•	•
Annelida	Opheliidae	<i>Armandia agilis</i> *				◆	•					•
Annelida	Opheliidae	<i>Travisia hobsonae</i> *										•
Annelida	Opheliidae	<i>Ophelina acuminata</i> *										•
Annelida	Opheliidae	<i>Ophelina cylindricaudata</i> *									•	
Annelida	Opheliidae	<i>Armandia maculata</i>		•		•			•		•	•
Annelida	Orbiniidae	<i>Scoloplos acmeceps</i> *										•
Annelida	Orbiniidae	<i>Scoloplos</i> sp. B*							•	•	•	•
Annelida	Orbiniidae	<i>Leitoscoloplos fragilis</i>								•	•	•
Annelida	Orbiniidae	<i>Scoloplos rubra</i>									•	•
Annelida	Oweniidae	<i>Owenia fusiformis</i>		•		•	◆		◆	◆	•	◆
Annelida	Oweniidae	<i>Myriowenia</i> sp. A				•	•	•	•	•	•	•
Annelida	Paraonidae	<i>Aricidea pseudoarticulata</i> *									•	•
Annelida	Paraonidae	<i>Aricidea fragilis</i> *				•			•			•
Annelida	Paraonidae	<i>Aricidea suecica</i> *							•		•	◆
Annelida	Paraonidae	<i>Aricidea quadrilobata</i> *	•									
Annelida	Paraonidae	<i>Aricidea</i> sp.*										•
Annelida	Paraonidae	<i>Aricidea</i> sp. C*										•
Annelida	Paraonidae	<i>Paraonis fulgens</i> *			•							
Annelida	Paraonidae	<i>Cirrophorus forticirratus</i>			•			•				•
Annelida	Paraonidae	<i>Acmira finitima</i>					•					
Annelida	Paraonidae	<i>Aricidea alisdairi</i>							•	•	•	•
Annelida	Pectinariidae	<i>Amphictene</i> sp. A*								•		•
Annelida	Pectinariidae	<i>Pectinaria</i> sp.						•	•			
Annelida	Phyllodocidae	<i>Anaitides mucosa</i> *		•		•	•	◆	◆	◆	◆	•

Phylum	Family	Species	0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	90-100
Annelida	Phyllodocidae	<i>Eulalia viridis</i> *		•				•			•	
Annelida	Phyllodocidae	<i>Anaitides maculata</i>										•
Annelida	Phyllodocidae	<i>Gyptis vittata</i>										•
Annelida	Pilargidae	<i>Synelmis klatti</i> *									•	•
Annelida	Pilargidae	<i>Ancistrosyllis carolinensis</i> *		♦		•		♦	♦			•
Annelida	Pilargidae	<i>Ancistrosyllis</i> sp. B*		•		♦					•	•
Annelida	Pilargidae	<i>Sigambra tentaculata</i>		◆	♦	♦	♦	♦	◆	♦	♦	♦
Annelida	Pilargidae	<i>Sigambra wassi</i>		•		•	♦		•	•		
Annelida	Pilargidae	<i>Ancistrosyllis jonesi</i>									•	
Annelida	Poecilochaetidae	<i>Poecilochaetus johnsoni</i>		•		•						
Annelida	Polynoidae	<i>Harmothoe</i> sp. C*									•	
Annelida	Polynoidae	<i>Malmgreniella</i> sp. B*							•	♦	♦	•
Annelida	Polynoidae	<i>Malmgreniella</i> sp. A*								•		•
Annelida	Polynoidae	<i>Lepidonotus</i> sp.*										•
Annelida	Polynoidae	<i>Lepidasthenia</i> sp. A		•		♦	•			♦		•
Annelida	Polynoidae	<i>Lepidonotus sublevis</i>		•	♦	•		•				•
Annelida	Sabellidae	<i>Chone americana</i> *				•		•	◆	◆	♦	◆
Annelida	Sigalionidae	<i>Thalenessa</i> cf. <i>spinosa</i> *				♦					•	♦
Annelida	Sigalionidae	<i>Sthenelais</i> sp.*		♦		♦			♦		•	•
Annelida	Spionidae	<i>Spiophanes missionensis</i> *				•						
Annelida	Spionidae	<i>Polydora aggregata</i> *										•
Annelida	Spionidae	<i>Scolecipis texana</i> *							♦		•	•
Annelida	Spionidae	<i>Scolecipis squamata</i> *					•				•	•
Annelida	Spionidae	<i>Prionospio pygmaea</i> *	•			♦		•	♦	♦	◆	◆
Annelida	Spionidae	<i>Prionospio cirrobranchiata</i> *									♦	•
Annelida	Spionidae	<i>Prionospio</i> sp. A*							♦	♦	•	•
Annelida	Spionidae	<i>Malacoceros vanderhorsti</i> *			•							
Annelida	Spionidae	<i>Spiophanes bombyx</i>				◆		♦	◆	◆	◇	◆
Annelida	Spionidae	<i>Polydora ligni</i>						•			•	
Annelida	Spionidae	<i>Polydora socialis</i>							•			•

Phylum	Family	Species	0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	90-100
Annelida	Spionidae	<i>Dispio uncinata</i>										•
Annelida	Spionidae	<i>Paraprionospio pinnata</i>	◆	◆	◆	◆	◆	◆	◆	◆	◆	•
Annelida	Spionidae	<i>Prionospio cristata</i>		•					•		•	
Annelida	Spionidae	<i>Microspio pigmentata</i>										•
Annelida	Terebellidae	<i>Neoamphitrite edwardsi</i> *									•	
Annelida	Terebellidae	<i>Eupolymnia nebulosa</i> *								•	◆	•
Annelida	Terebellidae	<i>Loimia viridis</i>			•					•		•
Arthropoda	Albuneidae	<i>Albunea paretii</i>				•			•	•		•
Arthropoda	Alpheidae	<i>Automate evermanni</i>								•		•
Arthropoda	Alpheidae	<i>Automate</i> sp.								•		
Arthropoda	Ampeliscidae	<i>Ampelisca</i> sp. A		◆	•	•			◆			
Arthropoda	Ampeliscidae	<i>Ampelisca</i> sp. C								•	◆	•
Arthropoda	Ampeliscidae	<i>Ampelisca vadorum</i>			•							
Arthropoda	Argissidae	<i>Argissa hamatipes</i>		•		•					•	•
Arthropoda	Bateidae	<i>Batea catharinensis</i>						•	◆		•	•
Arthropoda	Bodotriidae	<i>Cyclaspis varians</i>							•		•	•
Arthropoda	Calappidae	<i>Calappa</i> sp.									•	
Arthropoda	Callianassidae	<i>Glypturus acanthochirus</i>								•	•	
Arthropoda	Callianassidae	<i>Callichirus</i> sp.			•							•
Arthropoda	Corophiidae	<i>Monocorophium</i> sp. A						•			•	•
Arthropoda	Corophiidae	<i>Monocorophium tuberculatum</i>		•				•	•		◆	•
Arthropoda	Diastylidae	<i>Oxyurostylis smithi</i>	•	•		•	◆	◆	◆	◆	◆	•
Arthropoda	Haustoriidae	<i>Acanthohaustorius</i> sp. A							•		•	◆
Arthropoda	Haustoriidae	<i>Protohaustorius bousfieldi</i>									•	◆
Arthropoda	Haustoriidae	<i>Pseudohaustorius americanus</i>										•
Arthropoda	Hepatidae	<i>Hepatus</i> sp.				•				•		•
Arthropoda	Hippidae	<i>Emerita</i> sp.									•	
Arthropoda	Isaeidae	<i>Microprotopus raneyi</i>	•			•		◆	◆		•	•
Arthropoda	Isaeidae	<i>Photis macromana</i>							◆			
Arthropoda	Ischyroceridae	<i>Erichthonius brasiliensis</i>						•	•			•

Phylum	Family	Species	0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	90-100
Arthropoda	Leucosiidae	<i>Persephona punctata</i>										.
Arthropoda	Liljeborgiidae	<i>Listriella barnardi</i>	.	.				.	♦	♦	♦	♦
Arthropoda	Liljeborgiidae	<i>Listriella</i> sp.							.			
Arthropoda	Mithracidae	<i>Nemausa acuticornis</i>		.								
Arthropoda	Munnidae	<i>Munna</i> sp.						♦				
Arthropoda	Mysidae	<i>Americamysis</i> sp.		.								
Arthropoda	Mysidae	<i>Americamysis stucki</i>				.			♦			.
Arthropoda	Mysidae	<i>Americamysis alleni</i>					♦	♦			.	.
Arthropoda	Mysidae	<i>Americamysis bahia</i>						♦				.
Arthropoda	Mysidae	<i>Bowmaniella floridana</i>							.			.
Arthropoda	Oedicerotidae	<i>Hartmanodes nyei</i>						.	.		♦	.
Arthropoda	Oedicerotidae	<i>Americhelidium americanum</i>							♦		♦	♦
Arthropoda	Ogyrididae	<i>Ogyrides alphaerostris</i>				.					♦	.
Arthropoda	Paguridae	<i>Pagurus pollicaris</i>										.
Arthropoda	Paguridae	<i>Pagurus</i> sp.				.		.	.	♦	♦	♦
Arthropoda	Panopeidae	<i>Panopeus herbstii</i>							.			
Arthropoda	Pariambidae	<i>Paracaprella tenuis</i>									.	
Arthropoda	Pasiphaeidae	<i>Leptochela serratorbita</i>							.			.
Arthropoda	Penaeidae	<i>Rimapenaeus constrictus</i>							.			
Arthropoda	Penaeidae	<i>Rimapenaeus similis</i>										.
Arthropoda	Phoxocephalidae	<i>Metharpinia floridana</i>								.	♦	♦
Arthropoda	Pinnotheridae	<i>Austinixa chacei</i>		♦		♦			.	♦	.	.
Arthropoda	Pinnotheridae	<i>Pinnixa retinens</i>	.	♦		.			♦		.	.
Arthropoda	Pinnotheridae	<i>Austinixa cristata</i>										.
Arthropoda	Platyischnopidae	<i>Eudevenopus honduranus</i>									♦	♦
Arthropoda	Porcellanidae	<i>Euceramus praelongus</i>				.						.
Arthropoda	Portunidae	<i>Portunus gibbesii</i>		.		.		.				.
Arthropoda	Portunidae	<i>Portunus ordwayi</i>										.
Arthropoda	Portunidae	<i>Portunid</i> sp.				.			.		♦	.
Arthropoda	Portunidae	<i>Ovalipes ocellatus</i>										.

Phylum	Family	Species	0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	90-100
Arthropoda	Portunidae	<i>Ovalipes floridanus</i>									•	
Arthropoda	Portunidae	<i>Callinectes similis</i>						•			•	
Arthropoda	Raninidae	<i>Raninoides</i> sp.							•			
Arthropoda	Solenoceridae	<i>Solenocera vioscai</i>										•
Arthropoda	Solenoceridae	<i>Solenocera necopina</i>					•				•	
Arthropoda	Squillidae	<i>Squilla</i> sp. A										•
Arthropoda	Stenothoidae	<i>Parametopella cypris</i>						♦	•			•
Arthropoda	Synopiidae	<i>Metatiron triocellatus</i>								•	•	•
Arthropoda	Synopiidae	<i>Metatiron tropakis</i>								♦	♦	♦
Arthropoda	Xanthidae	<i>Speocarcinus lobatus</i>		•								
Arthropoda	Xanthidae	<i>Xanthid</i> sp.					•			•		
Arthropoda	~	<i>Decapoda</i> sp.		•								
Chordata	Branchiostomatidae	<i>Branchiostoma floridae</i>							•	♦	♦	♦
Chordata	~	<i>Tunicate</i> sp.		•					•			
Cnidaria	Actinostolidae	<i>Paranthus rapiformis</i>		•				•	•	♦	♦	♦
Cnidaria	Actinostolidae	burrowing anemone sp. 1								•		•
Cnidaria	Actinostolidae	burrowing anemone sp. 2				•	•		♦		•	•
Cnidaria	Actinostolidae	burrowing anemone sp. 3							•			
Cnidaria	Actinostolidae	burrowing anemone sp. 4			•							
Cnidaria	Actinostolidae	burrowing anemone sp. 5									•	
Cnidaria	Actinostolidae	burrowing anemone sp. 6		•								•
Cnidaria	~	non-burrowing anemone										•
Echinodermata	Amphiuridae	<i>Ophiophragmus moorei</i>									♦	♦
Echinodermata	Amphiuridae	<i>Amphiodia planispina</i>		•		•				♦	♦	♦
Echinodermata	Amphiuridae	<i>Amphioplus coniertodes</i>			♦	•						•
Echinodermata	Amphiuridae	<i>Ophiostigma isacanthum</i>						•				
Echinodermata	Ophiactidae	<i>Hemipholis elongata</i>		•	♦	♦	♦		♦	♦	♦	♦
Echinodermata	Synaptidae	<i>Protankyra</i> sp.				•						
Echinodermata	~	<i>Ophiurid</i> sp.	•									
Mollusca	Arcidae	<i>Anadara transversa</i>		•		•	•	•	•		•	•

Phylum	Family	Species	0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	90-100
Mollusca	Arcidae	<i>Anadara brasiliiana</i>									•	•
Mollusca	Arcidae	<i>Arcidae</i> sp.							•			
Mollusca	Cardiidae	<i>Trigoniocardia antillarum</i>										•
Mollusca	Cerithiidae	<i>Bittium varium</i>				•				•		•
Mollusca	Columbellidae	<i>Anachis obesa</i>				•		•	•			
Mollusca	Corbulidae	<i>Corbula chittyana</i>										•
Mollusca	Corbulidae	<i>Corbula swiftiana</i>									•	
Mollusca	Epitoniidae	<i>Epitonium angulatum</i>										•
Mollusca	Lucinidae	<i>Parvilucina multilineata</i>										•
Mollusca	Lucinidae	<i>Linga amiantus</i>				•						•
Mollusca	Mactridae	<i>Mulinia lateralis</i>				♦	♦	♦	◆	•	◆	♦
Mollusca	Mactridae	<i>Raeta plicatella</i>							•			•
Mollusca	Nassariidae	<i>Nassarius acutus</i>				♦		♦	♦	♦	♦	♦
Mollusca	Naticidae	<i>Polinices duplicatus</i>										•
Mollusca	Naticidae	<i>Natica pusilla</i>				•	•	•	•	♦	•	•
Mollusca	Naticidae	<i>Sigatica semisulcata</i>									•	
Mollusca	Nuculanidae	<i>Nuculana concentrica</i>	•	♦	•	◆		•	•	♦	•	
Mollusca	Olividae	<i>Oliva sayana</i>		•	•	•			•			•
Mollusca	Pandoridae	<i>Pandora trilineata</i>				•	•					•
Mollusca	Periplomatidae	<i>Periploma margaritaceum</i>									•	•
Mollusca	Pholadidae	<i>Pholadidae</i> sp.					•	•				
Mollusca	Pyramidellidae	<i>Cyclostremella humilis</i>					•					
Mollusca	Semelidae	<i>Abra aequalis</i>		•	•	•	♦		♦	♦	♦	•
Mollusca	Solenidae	<i>Solen viridis</i>				•			•		•	•
Mollusca	Tellinidae	<i>Strigilla pisiformis</i>									•	•
Mollusca	Tellinidae	<i>Tellina iris</i>				•		•			•	♦
Mollusca	Tellinidae	<i>Tellina versicolor</i>	•	•	♦	◆		♦	◆	◆	♦	•
Mollusca	Tellinidae	<i>Tellina alternata</i>									•	•
Mollusca	Tellinidae	<i>Macoma pulleyi</i>									•	•
Mollusca	Tellinidae	<i>Macoma tenta</i>							•			•

Phylum	Family	Species	0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	90-100
Mollusca	Terebridae	<i>Terebra dislocata</i>				.						
Mollusca	Ungulinidae	<i>Diplodonta soror</i>							.		.	.
Mollusca	Veneridae	<i>Lirophora clenchi</i>										.
Mollusca	Veneridae	<i>Lirophora latilirata</i>					.	.				
Mollusca	Veneridae	<i>Dosinia discus</i>				.	.		.	♦	.	♦
Mollusca	Vitrinellidae	<i>Solariorbis blakei</i>			♦	◆						.
Mollusca	Vitrinellidae	<i>Parviturboidea interruptus</i>				.						
Nemertea	~	Nemertea sp. 1		.	.	.	.		♦	♦	♦	.
Nemertea	~	Nemertea sp. 2	♦	♦	♦	.	♦	◆	♦	◆	♦	♦
Nemertea	~	Nemertea sp. 3		.			◆	◆	◆	♦	♦	.
Nemertea	~	Nemertea sp. 4				♦	♦		.			.
Phoronida	~	<i>Phoronis psammophila</i>							.			
Phoronida	~	<i>Phoronis</i> sp.					♦				.	.
Platyhelminthes	Uteriporidae	<i>Turbellaria</i> sp. 1										.
Platyhelminthes	Uteriporidae	<i>Turbellaria</i> sp. 2		.								.
Sipuncula	Aspidosiphonidae	<i>Aspidosiphon</i> sp.				.	.	.	.			.
Sipuncula	Golfingiidae	<i>Nephasoma minutum</i>										.
Sipuncula	Phascoliidae	<i>Phascolion strombi</i>			.	♦	♦	♦	♦	♦	♦	.
Sipuncula	Phascolosomatidae	<i>Apionsoma misakianum</i>			.	.	◆	◆	◆	.	♦	♦
Sipuncula	Sipunculidae	<i>Sipunculus</i> sp.						.				

## **APPENDIX C: RESULTS OF CALLINECTES SAPIDUS GUT CONTENT ANALYSIS**



Table C.1. *Callinectes sapidus* stomach fullness by area and season for 2007. Stomachs were ranked for fullness on a scale from 0 to 5 following Wear and Haddon (1987): 0 = nothing; 1 = > 0%, < 5%; 2 = 5% to 35%; 3 = 36% to 65%; 4 = 66% to 95%; and 5 = > 95% full.

Stomach rankings 0-5	Number of stomachs by ranking by area		
Spring	Ship	TTS	Off
0	0	0	1
1	1	1	1
2	2	3	4
3	3	0	2
4	2	1	1
5	5	0	5
Total	13	5	14
Weighted average	2.6	1.2	2.2
Summer			
0	9	11	16
1	21	10	3
2	12	14	5
3	8	10	2
4	8	7	0
5	3	11	1
Total	61	63	27
Weighted average	1.0	1.6	0.4
Fall			
0	2	3	1
1	5	0	1
2	6	2	2
3	2	1	2
4	0	1	0
5	2	0	0
Total	17	7	6
Weighted average	1.1	1.0	1.0

Table C.2. Mean prey group proportion by area and season for STTSC *Callinectes sapidus* gut contents in 2007. Individual stomachs were emptied into a Petri dish with a bottom that was divided into 36 squares. Proportions were calculated based on the total number of squares in which a specific food item was found divided by the total number of squares in which any food item was found for each stomach. Procedure modified from Wear and Haddon (1987).

Spring	Ship	TTS	Off
Bivalve	0.11	0.06	0.15
Gastropod	0.04	0.12	0.12
Crab	0.37	0.43	0.26
Shrimp	0.17	0.20	0.15
Polychaete	0.00	0.00	0.00
Fish	0.25	0.20	0.18
Nemertine	0.00	0.00	0.00
Squid	0.06	0.00	0.00
Nematode	0.00	0.00	0.00
Summer			
Bivalve	0.19	0.23	0.13
Gastropod	0.32	0.12	0.05
Crab	0.24	0.19	0.08
Shrimp	0.01	0.20	0.00
Polychaete	0.01	0.03	0.00
Fish	0.07	0.06	0.04
Nemertine	0.00	0.00	0.00
Squid	0.01	0.01	0.00
Nematode	0.00	0.00	0.00
Fall			
Bivalve	0.09	0.25	0.19
Gastropod	0.43	0.01	0.27
Crab	0.14	0.23	0.18
Shrimp	0.12	0.07	0.00
Polychaete	0.00	0.02	0.00
Fish	0.10	0.00	0.18
Nemertine	0.00	0.00	0.00
Squid	0.00	0.00	0.02
Nematode	0.00	0.00	0.00

Table C.3. Mean Prey Point calculations derived from the product values based on *Callinectes sapidus* weighted gut fullness (Table C.1) and prey group proportion (Table C.2) during 2007 sampling in the STTSC. Specifically Prey Points were derived as follows: a stomach with fullness of 0 was weighted as 0; fullness of 1 was weighted as .02; fullness of 2 was weighted as .25; fullness of 3 was weighted as .5; fullness of 4 was weighted as .75; fullness of 5 was weighted as 1. Gut fullness weights were multiplied by prey group proportion point values assigned as follows: 0% = 0 points; 0.1% to 4% = 2.5 points; 5% to 34% = 25 points; 35 to 64% = 50 points; 65 to 94% = 75 points; and >94% = 100 points. Procedure modified from Wear and Haddon (1987).

Spring	Ship	TTS	Off
Bivalve	10.10	1.25	8.32
Gastropod	5.19	3.75	8.48
Crab	21.30	10.00	18.04
Shrimp	18.27	15.00	11.61
Polychaete	0.00	0.00	0.00
Fish	12.17	0.40	11.33
Nemertine	0.00	0.00	0.00
Squid	7.69	0.00	0.00
Nematode	0.00	0.00	0.00
Summer			
Bivalve	6.30	6.84	4.28
Gastropod	7.71	3.77	0.35
Crab	11.25	9.79	4.17
Shrimp	0.02	15.77	0.00
Polychaete	0.41	0.69	0.00
Fish	2.42	3.29	0.96
Nemertine	0.01	0.00	0.00
Squid	0.86	0.60	0.00
Nematode	0.00	0.00	0.00
Fall			
Bivalve	3.68	6.52	6.25
Gastropod	6.38	0.89	10.42
Crab	5.60	13.39	8.33
Shrimp	4.41	5.36	0.00
Polychaete	0.00	0.98	0.00
Fish	6.99	0.00	2.42
Nemertine	0.00	0.00	0.00
Squid	0.00	0.00	2.08
Nematode	0.00	0.00	0.00

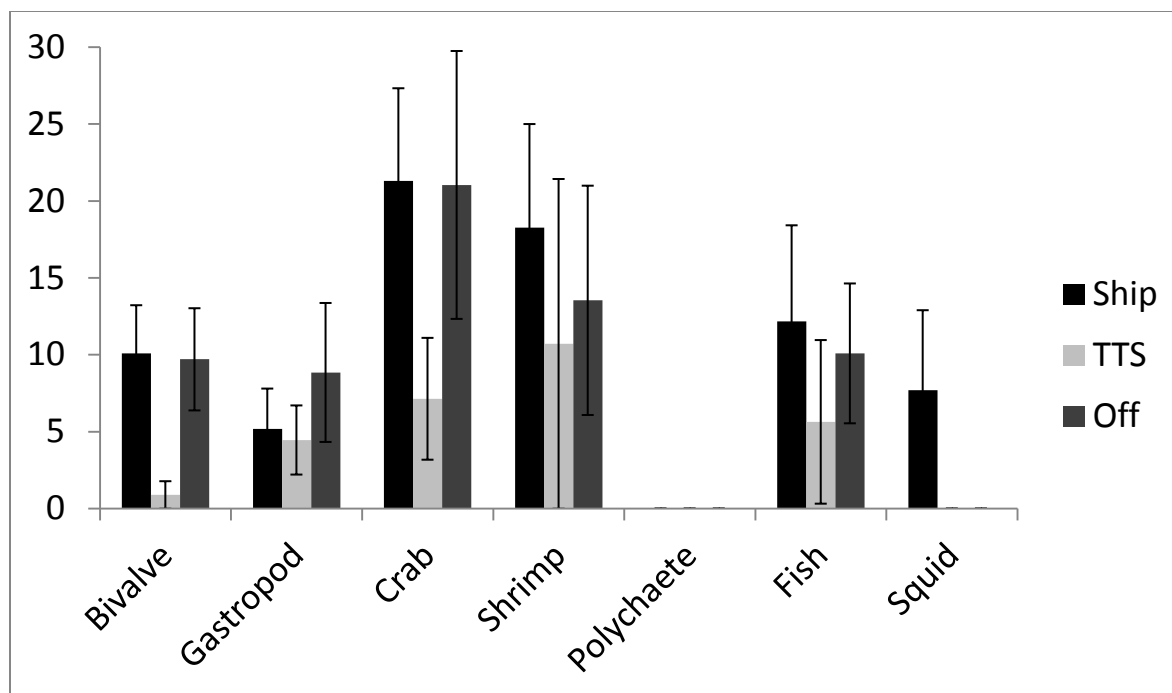


Figure C.1 Mean prey point calculations derived from a weighted combination of *Callinectes sapidus* gut fullness (Table C.1) and percentage occurrence of prey items (Table C.2) during spring 2007 sampling in the STTSC.

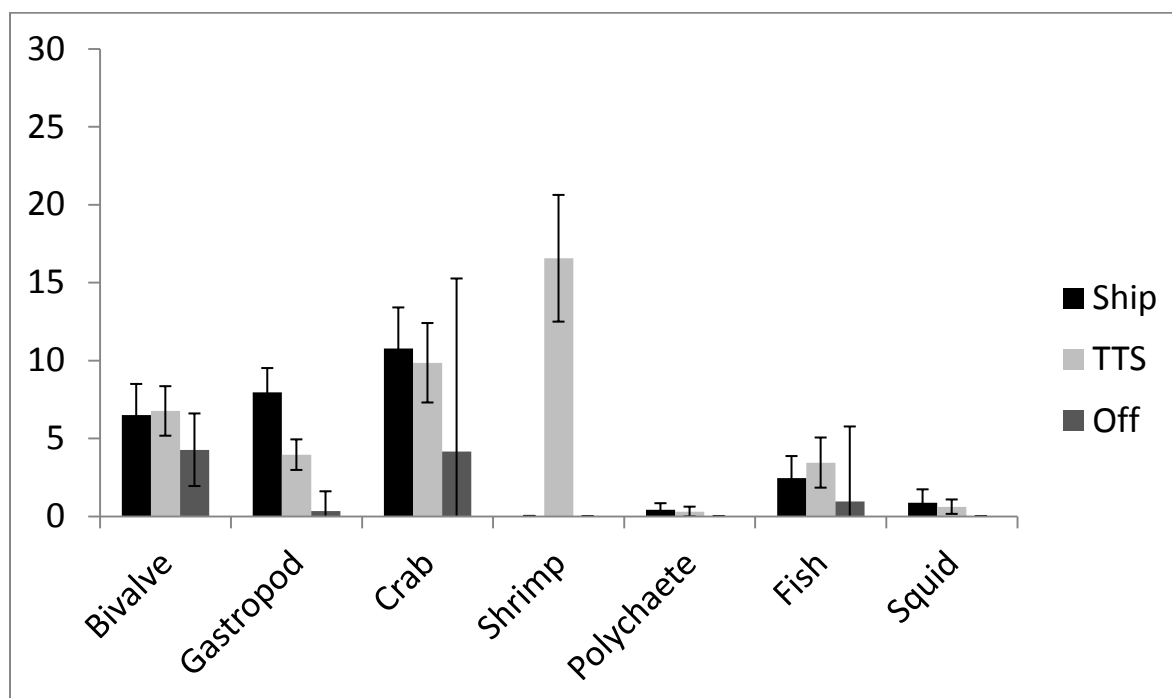


Figure C.2 Mean prey point calculations derived from a weighted combination of *Callinectes sapidus* gut fullness (Table C.1) and percentage occurrence of prey items (Table C.2) during summer 2007 sampling in the STTSC.

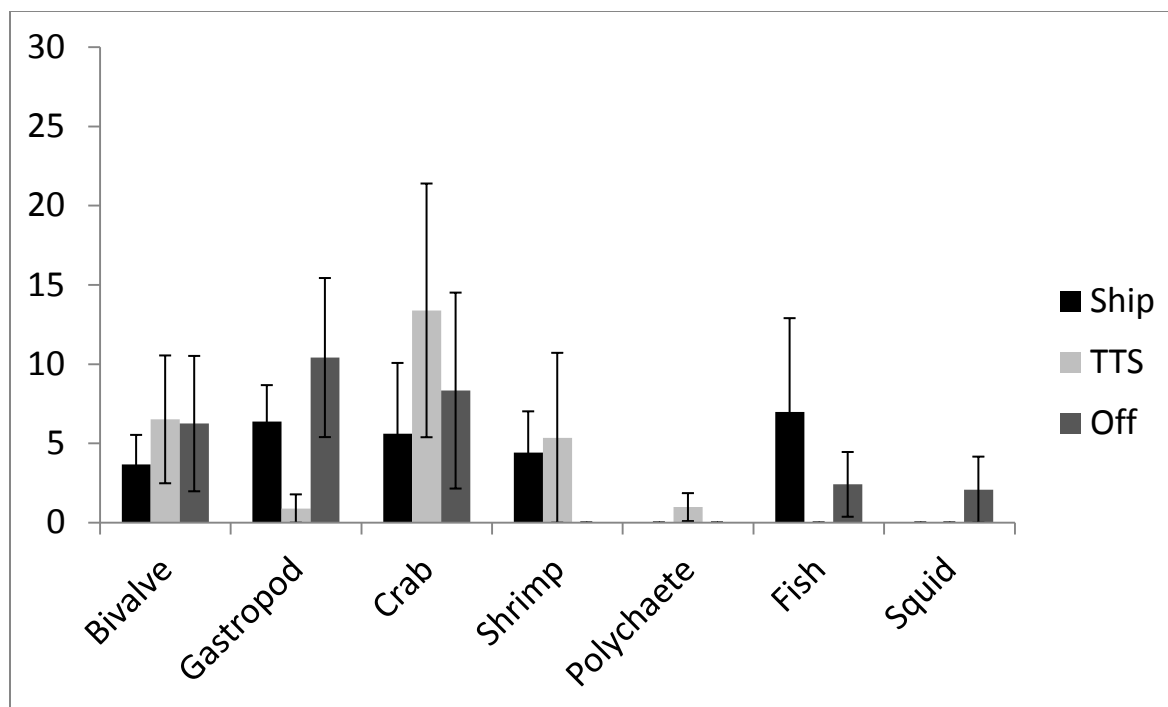


Figure C.3 Mean prey point calculations derived from a weighted combination of *Callinectes sapidus* gut fullness (Table C.1) and percentage occurrence of prey items (Table C.2) during fall 2007 sampling in the STTSC.

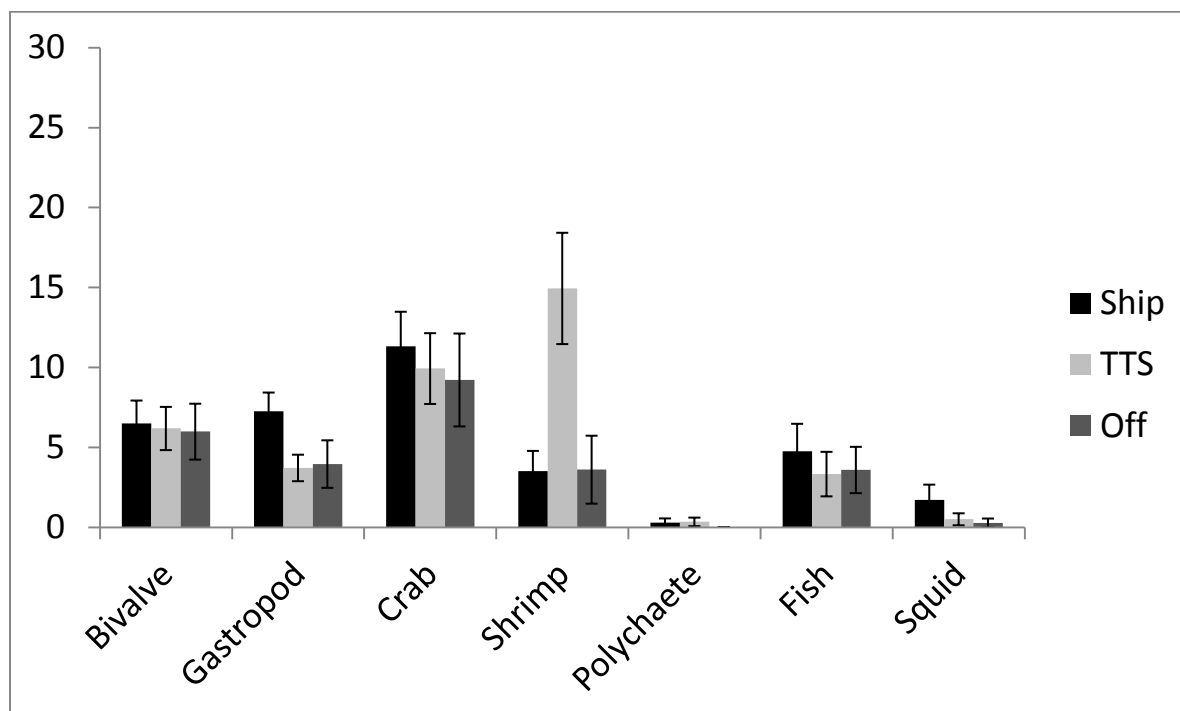


Figure C.4 Mean prey point calculations derived from a weighted combination of *Callinectes sapidus* gut fullness (Table C.1) and percentage occurrence of prey items (Table C.2) for all seasons in 2007 in the STTSC.

## LITERATUR CITED

Haddon, M., R.G. Wear. 1987. Biology of feeding in the New Zealand paddle crab *Ovalipes catharus* (Crustacea, Portunidae). *New Zealand Journal of Marine and Freshwater Research*. 21:55-64.

## **APPENDIX D: COPY OF PERMISSION LETTER TO PUBLISH CHAPTER 2**

---

tel [+91 44 42197752](tel:+914442197752)

fax [+ 91 44 42197763](tel:+914442197763)

[Rameshbabu.Rathinam@springer.com](mailto:Rameshbabu.Rathinam@springer.com)

---

[www.springer.com](http://www.springer.com)

---

**From:** Carey Gelpi [mailto:[cgelpi1@tigers.lsu.edu](mailto:cgelpi1@tigers.lsu.edu)]  
**Sent:** Thursday, January 19, 2012 9:19 PM  
**To:** Rathinam, Rameshbabu  
**Subject:** permission request to use article in dissertation

Dear Rameshbabu Rathinam,

I am writing to request permission to use our article,

Diversity and composition of macrobenthic community associated with sandy shoals of the Louisiana continental shelf. *Biodiversity and Conservation*. 2009. 18:3759-3784

as a chapter in my dissertation.

Please let me know what information you may need in order to grant permission.

Sincerely,  
Carey Gelpi

--

PhD Candidate  
Louisiana State University  
Department of Oceanography & Coastal Sciences  
phone # [\(225\) 578-6507](tel:(225)578-6507)

----- Forwarded message -----

From: "Carey Gelpi" <[cgelpi1@tigers.lsu.edu](mailto:cgelpi1@tigers.lsu.edu)>  
To: "Rathinam, Rameshbabu" <[Rameshbabu.Rathinam@springer.com](mailto:Rameshbabu.Rathinam@springer.com)>  
Cc:  
Date: Mon, 30 Jan 2012 20:03:55 +0100  
Subject: Request Permission to Use Publication in Dissertation  
Dear Rameshbabu Rathinam,

I am writing to request permission to use our article,

Diversity and composition of macrobenthic community associated with sandy shoals of the Louisiana continental shelf. *Biodiversity and Conservation*. 2009. 18:3759-3784

as a chapter in my dissertation.

Please let me know what information you may need in order to grant permission.

Sincerely,  
Carey Gelpi

--

PhD Candidate  
Louisiana State University  
Department of Oceanography & Coastal Sciences  
phone # [\(225\) 578-6507](tel:(225)578-6507)

---

Permissions Europe/NL <[Permissions.Dordrecht@springer.com](mailto:Permissions.Dordrecht@springer.com)>

Tue, Jan 31, 2012 at 8:28 AM



To: "cgelpi1@tigers.lsu.edu" <cgelpi1@tigers.lsu.edu>

---

Dear Sir/Madam,

Thank you for your message.

Springer is pleased to announce our partnership with Copyright Clearance Center to meet your licensing needs.

With Copyright Clearance Center's Rightslink® service it's faster and easier than ever before to secure permission from Springer journal titles to be republished in a secure intranet site, restricted internet site, CD-ROM/DVD, journal (print/online), book (hardcopy or electronic), coursepack, e-reserve, doctoral thesis, research project, magazine, newsletter, directory, newspaper, brochure/pamphlet, presentation, or photocopies/handouts.

Simply visit: <http://www.springerlink.com> and locate your desired content.

Go to the article's abstract and click on "Obtain Permission and Reprints" on the right to open the following page:

1. Select the way you would like to reuse the content
2. Create an account if you haven't already
3. Accept the terms and conditions and you're done!

For questions about using the Rightslink service, please contact Customer Support via phone [877/622-5543](tel:8776225543) (toll free) or [978/777-9929](tel:9787779929), or email [customercare@copyright.com](mailto:customercare@copyright.com)

Best wishes,

—  
**Maike Duine**  
Springer

Rights and Permissions

—  
Van Godewijckstraat 30 | 3311 GX  
P.O. Box 17 | 3300 AA  
Dordrecht | The Netherlands  
tel [+31 \(0\) 78 657 6537](tel:+3120786576537)  
fax [+31 \(0\) 78 657 6377](tel:+3120786576377)

[maiike.duine@springer.com](mailto:maiike.duine@springer.com)  
—

**From:** Carey Gelpi [mailto:[cgelpi1@tigers.lsu.edu](mailto:cgelpi1@tigers.lsu.edu)]  
**Sent:** Thursday, January 19, 2012 9:19 PM  
**To:** Rathinam, Rameshbabu  
**Subject:** permission request to use article in dissertation

Dear Rameshbabu Rathinam,

I am writing to request permission to use our article,

Diversity and composition of macrobenthic community associated with sandy shoals of the Louisiana continental shelf. *Biodiversity and Conservation*. 2009. 18:3759-3784

as a chapter in my dissertation.

Please let me know what information you may need in order to grant permission.

Sincerely,  
Carey Gelpi

--

PhD Candidate  
Louisiana State University  
Department of Oceanography & Coastal Sciences  
phone # [\(225\) 578-6507](tel:(225)578-6507)

---

Permissions Europe/NL <[Permissions.Dordrecht@springer.com](mailto:Permissions.Dordrecht@springer.com)>  
To: "cgelpi1@tigers.lsu.edu" <[cgelpi1@tigers.lsu.edu](mailto:cgelpi1@tigers.lsu.edu)>

Wed, Feb 1, 2012 at 9:35 AM

Dear Sir,

With reference to your request (copy herewith) to reprint material on which Springer Science and Business Media controls the copyright, our permission is granted, free of charge, for the use indicated in your enquiry.

This permission

- allows you non-exclusive reproduction rights throughout the World.
- permission includes use in an electronic form, provided that content is
  - \* password protected;
  - \* at intranet;
- excludes use in any other electronic form. Should you have a specific project in mind, please reapply for permission.
- requires a full credit (Springer/Kluwer Academic Publishers book/journal title, volume, year of publication, page, chapter/article title, name(s) of author(s), figure number(s), original copyright notice) to the publication in which the material was originally published, by adding: with kind permission of Springer Science and Business Media.

The material can only be used for the purpose of defending your dissertation, and with a maximum of 100 extra copies in paper.

Permission free of charge on this occasion does not prejudice any rights we might have to charge for reproduction of our copyrighted material in the future.

Kind regards,

Nel van der Werf (Ms)

Rights and Permissions/Springer

Van Godewijckstraat 30 | P.O. Box 17  
3300 AA Dordrecht | The Netherlands  
tel [+31 \(0\) 78 6576 298](tel:+31(0)786576298)  
fax [+31 \(0\)78 65 76-377](tel:+31(0)786576377)

[Nel.vanderwerf@springer.com](mailto:Nel.vanderwerf@springer.com)  
[www.springer.com](http://www.springer.com)

---

**From:** Rathinam, Rameshbabu  
**Sent:** Tuesday, January 31, 2012 02:06 PM  
**To:** Permissions Europe/NL  
**Cc:** [cgelpi1@tigers.lsu.edu](mailto:cgelpi1@tigers.lsu.edu)  
**Subject:** RE: BIOC1696R2- Permission request to use article in dissertation...

[Quoted text hidden]

---

## **APPENDIX E: COPY OF PERMISSION LETTER TO PUBLISH CHAPTER 4**

Carey Gelpi <[cgelpi1@tigers.lsu.edu](mailto:cgelpi1@tigers.lsu.edu)>

---

**Permission to use publication in dissertation**

2 messages

---

**Carey Gelpi** <[cgelpi1@tigers.lsu.edu](mailto:cgelpi1@tigers.lsu.edu)>  
To: [bms@rsmas.miami.edu](mailto:bms@rsmas.miami.edu)

Mon, Jan 16, 2012 at 12:59 PM

Dear Dr. Sponaugle,

I am writing to request permission to use my article,

Discovery, evaluation, and implications of blue crab, *Callinectes sapidus*, spawning, hatching, and foraging grounds in federal (US) waters offshore of Louisiana. *Bulletin of Marine Science*. 2009. 85:203-222.

as a chapter in my dissertation.

Please let me know what information you may need in order to grant permission.

Sincerely,  
Carey Gelpi—  
PhD Candidate  
Louisiana State University  
Department of Oceanography & Coastal Sciences  
phone # [\(225\) 578-6507](tel:(225)578-6507)

---

**Geoffrey Shideler** [*Bulletin of Marine Science*] <[bmsassistant@rsmas.miami.edu](mailto:bmsassistant@rsmas.miami.edu)>  
To: Carey Gelpi <[cgelpi1@tigers.lsu.edu](mailto:cgelpi1@tigers.lsu.edu)>

Tue, Jan 17, 2012 at 12:15 PM

Ms Gelpi,

Thank you for your request. We permit you to use this article as a chapter of your dissertation.

Best regards,

Geoffrey Shideler  
Editorial Assistant  
Bulletin of Marine Science  
Rosenstiel School of Marine and Atmospheric Science  
University of Miami  
4600 Rickenbacker Causeway  
Miami, Florida 33149-1098  
Phone: [305-421-4624](tel:305-421-4624)  
Fax: [305-421-4600](tel:305-421-4600)  
Email: <[bmsassistant@rsmas.miami.edu](mailto:bmsassistant@rsmas.miami.edu)><http://www.rsmas.miami.edu/bms>

[Quoted text hidden]

## VITA

Carey George Gelpi Jr. was born in 1973 in Baton Rouge, Louisiana. In fall 1979 he moved with his family to Watson, Louisiana, where he grew up. Carey graduated from Live Oak High School in 1991. He completed a Bachelor of Arts in psychology from Louisiana State University in fall 1996. He then pursued other interests until returning to LSU in 2002 to study biology. During this time he worked as an undergraduate researcher in Dr. Kevin Carman's meiofauna lab, where he got a firsthand introduction to the wonders of benthic ecology. In the spring of 2005 he completed his Bachelor of Science degree in biology with a marine concentration. The summer of 2005 he worked as an intern at Louisiana Universities Marine Consortium, in Cocodrie, Louisiana, and also officially became a graduate student in the Department of Oceanography and Coastal Sciences, initially intending to complete a master's degree with Dr. Richard Condrey. During this time he also participated in the first research cruises of his graduate career and was lucky enough to help recognize the discovery of offshore spawning blue crabs concentrating on his study site, Ship Shoal, which became the focus of his study. In 2007 after it became apparent that his research project on Ship Shoal would be expanded to include Trinity Shoal and Tiger Shoal and surrounding areas on the continental shelf, he decided to pursue a doctoral degree. In 2009 he spent seven months working in Brest, France, at the French Institute for Exploitation of the Sea; during which time he identified benthic macrofauna from the Louisiana continental shelf with "Dr. Polychaete" himself Stanislas Dubois. After returning to LSU in the fall of 2008, he continued work on his dissertation and will be receiving his Doctor of Philosophy degree from the Department of Oceanography and Coastal Sciences on May 18, 2012.