USF Tampa Graduate Theses and Dissertations

USF Graduate Theses and Dissertations

1-1-2015

Population Dynamics of the Little Gulper Shark *(Centrophorus uyato)* and Community Analyses of Elasmobranch Species in the Northern Gulf of Mexico

Jacquelin Joye Hipes
University of South Florida, jhipes12@gmail.com

Follow this and additional works at: https://digitalcommons.usf.edu/etd

Part of the Biology Commons, Marine Biology Commons, and the Oceanography Commons

Population Dynamics of the Little Gulper Shark (*Centrophorus uyato*) and Community Analyses

of Elasmobranch Species in the Northern Gulf of Mexico

by

Jacquelin J. Hipes

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science
Department of Marine Science
College of Marine Science
University of South Florida

Major Professor: Steven A. Murawski, Ph.D.
Christopher D. Stallings, Ph.D.
José I. Castro, Ph.D.

Date of Approval:
January 22, 2015

Keywords: elasmobranch, population dynamics, gulper shark, community analysis

DEDICATION

First and foremost I would like to recognize my parents, Jackie Kirkham and Mark Hipes, for their illimitable support throughout my educational career. You have listened to and advised me at every step of my life, encouraging me to grow and seek happiness in all my endeavors. Mom: your care packages were always a pick-me-up, even when there were more treats for the rabbit than for me. Dad: you always found just the right comic at just the right time. To my first grade teacher, Ms. Cox, who assigned that fateful animal project, and to my unfortunate partner who had to suffer through reading about sharks instead of wolves: thank you both, no matter how trivial it might have seemed at the time. I have been blessed with an unreasonable number of talented, dedicated, and invested educators throughout my school years, all of whom I could not possibly list, so this brief mention of my gratitude must suffice. I have learned from all of you and will treasure that knowledge for the rest of my life. To Carly Bender and Madeline Lewis, my two best friends: it can be difficult for three girls with different careers and different ambitions to maintain so strong a friendship, but I hope you both know how fortunate I consider myself that we've done just that (although I'll likely have to tell you in person, as you are both far too busy making heaps of money in the business world to read a Master's thesis on sharks!). Lastly I would like to acknowledge the impact Dr. Eugenie Clark has had on my continued love of the marine sciences. You were the best role model a little girl who loved sharks could have ever wished for.

ACKNOWLEDGMENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

In chapter 1 I describe the population dynamics of an understudied species of gulper shark, *Centrophorus uyato* (common name, the Little Gulper), found in the Northern Gulf of Mexico. Sharks in the family Centrophoridae are mid-sized, demersal fish, with seven species identified in North American waters. These deepwater species can be difficult to study due to the extreme depths at which they occur. During four longlining cruises from 2012-2014, 593 sharks were landed, predominantly in the Mississippi Canyon off the Louisiana coast. Mean depth of capture was 290 m. Supplementing these data are catch records for *C. uyato* from a second series of cruises east of these stations. These data suggest the Little Gulper displays sexual dimorphism in its population size structure, similar to other elasmobranchs. Length frequency distributions, sex ratios by length, and length-weight curves were similar for both catch series, however females comprised a greater fraction of the catch from Mississippi Canyon stations compared to those further east. The high incidence of females in the region may indicate the use of Mississippi Canyon as a nursery for *C. uyato*, and the species' tendency to sexually segregate at some point in its life history. A high number of large, pregnant females, along with observations of recently delivered animals, was noted at the Mississippi Canyon sites.

Little Gulper sex ratios by length exhibited a characteristic "notch", indicative of a low female-to-male ratio at intermediate lengths, then a reversal to female dominance at the largest sizes captured. I modeled this curve under various assumptions of growth, mortality, and longevity for the species. The combination of the von Bertalanffy growth parameter, *K*, and the

total instantaneous mortality rate, Z, that best fit the data suggests a population of slow growing, long-lived animals with a differentially higher growth rate for males.

In chapter 2, I examine species associations among elasmobranchs in the Northern Gulf of Mexico in relation to depth of capture. From 2011-2014, 3609 sharks, comprising 31 species in 10 families, were landed on five long-lining cruises throughout the Northern Gulf and along the West Florida Shelf. Stations were grouped *a priori* according to depth into one of three categories, based on pre-existing divisions in the station data: 0-73 m (shallow), 110-146 m (intermediate), and 183 m or greater (deep). Using a non-parametric multivariate analysis of variance (NP-MANOVA) and a pairwise test found I found significant differences in species composition among all three depth groupings. Gulf Smoothhound (*Mustelus sinusmexicanus*) and Atlantic Sharpnose (*Rhizoprionodon terraenovae*) contributed most to the differences, and also accounted for over 65% of the total catch. A canonical analysis of principal coordinates (CAP) showed mid-water species such as the Scalloped Hammerhead (*Sphyrna lewini*) to be more indicative of intermediate depth stations, while the Little Gulper (*Centrophorus uyato*) and Shortspine Dogfish (*Squalus mitsukurii*) distinguished deepwater sites. A "leave-one-out cross-validation" (LOO-CV) procedure correctly re-classified 78% of the samples back into their *a priori* groupings; catches from the shallow and deep groups were never confused for one another, although there was moderate confusion with classifying catches from intermediate stations. Taking into consideration the potentially large movements undertaken by many shark species on both small and large time scales, as well as additional biological and physical drivers for range and location, it is unsurprising that these animals would be present in two or more depth groups, and thus more frequently misclassified.

I also performed a second analysis grouping the stations according to their location on the West Florida Shelf, or in the eastern or western quadrants of the Northern Gulf of Mexico. Again I found significant differences among the species composition of all three station groups, but the LOO-CV overall reclassification success rate was lower than when the stations were grouped according to depth. There was also a smaller interval between this reclassification success rate and one performed using random group allocation.

Both of these chapters provide data on previously poorly understood species and phenomena in the Northern Gulf of Mexico. These data are important in defining the potential susceptibility of shark species and communities to future threats, including by-catch in fisheries and contamination events such as shallow and deepwater oil spills.

CHAPTER ONE:

POPULATION DYNAMICS OF THE LITTLE GULPER SHARK, *CENTROPHORUS*

***UYATO*, IN THE NORTHERN GULF OF MEXICO**

Introduction

Chondrichthyan Life History Traits

Knowledge of the biology and ecology of chondrichthyans (cartilaginous fishes such as sharks and rays) varies greatly among species, although available data suggest that many are long-lived, late-maturing animals, with low fecundity (Caillet et al. 2005). For deepwater species, these life history features can be exaggerated, with even slower growth, later age of maturity, and longer life spans than their coastal or pelagic relatives (Garcia et al. 2008). All of these traits can make these fish differentially susceptible to the impacts of human activities including pollution events, exploitation in targeted fisheries, or as by-catch.

Additionally, many sharks are predators at or near the top of the marine food web, making them important to the overall structuring of marine communities (Rigby and Simpfendorfer 2013). Any changes in the health or composition of their populations then have the potential to affect prey species at lower trophic levels (Pauly 1998; Jackson et al. 2001). In regions subjected to intensive fishing efforts, many species of shark, including those of the *Centrophorus* genus, are affected as by-catch in directed fisheries (Stevens et al. 2000). These effects are difficult to quantify in many cases because of a lack of records regarding the content

of a fishery's by-catch, as well as inconsistencies in identification for many species of gulper shark.

Biology and Morphology of the Centrophoridae

Gulper sharks are small to mid-sized demersal elasmobranchs (some species reach a maximum length of 170 cm) with a global range (Compagno 2005). Seven species have been identified in North American waters, although recently a combination of morphometric and genetic sequencing techniques have been used with the goal of restructuring this genus (Castro 2011). The population biology and reproduction of some species, specifically the Leafscale Gulper (*Centrophorus squamosus*), are well described, though most data originate from the Eastern Atlantic (see: Clarke et al. 2001; Bañon et al. 2006; Figueiredo et al. 2008; Severino et al. 2009; White and Dharmandi 2010). Deepwater fishermen off the coasts of Portugal and the United Kingdom exploit *C. squamosus*, creating additional mortality due to fishing, as well as generating catch records for the species in that region. Unlike other gulper sharks, its distinctive leaf-patterened dermal denticles can make field identification of this species easier (Castro 2011).

Centrophoridae are also found throughout Tropical Western Atlantic, including the Gulf of Mexico, although the taxonomy of this genus remains poorly understood (Castro 2011). The Little Gulper, *Centrophorus uyato*, is one of these understudied species. Previously found in the Bahamas and Gulf of Mexico (Castro 2011), the limits to its distribution are still unknown due to lingering identification issues exacerbated by the limited sampling of deepwater habitats where these animals reside. This shark is described by Castro (2011) as one of the smaller species in the genus, earning its common name when there were only two known species along the East Coast, in order to differentiate from the "larger" species (*Centrophorus niaukang*, the Taiwan Gulper).

2

It reaches a maximum length of approximately 1 meter, with a long, free rear tip to the pectoral fins that reaches to about the midpoint of the first dorsal fin. Its coloration is described as "grayish brown" dorsally and "pale or whitish" on the sides and ventrally. There are "conspicuous" white corners to its mouth.

Other aspects of this species' biology remain poorly described or unknown. *C. uyato* is an aplacental viviparous shark with a brood size of two, females generally carrying one embryo in each uterus. Smaller females often carry only one young. That females have been caught carrying both developing ova and developing embryos, indicative of concurrent vitellogenesis and gestation, suggests a two year reproductive cycle. Oocytes may reach a diameter of 80-90 mm prior to ovulation (Castro 2011).

Sexual Segregation in Sharks

Sexual size dimorphism, where one sex reaches a maximum length at maturity that is different than the other, and monomorphism, where both sexes may reach the same maximum length or lengths at maturity, have both been recorded in chondrichthyans. Reproductive mode has been suggested as a possible driver for the observed differences in size according to sex, with females of placental and aplacental viviparous species found to be 10-16% larger than their male counterparts (Sims 2005).

Sexual segregation is considered a general attribute of both pelagic and demersal shark species (Springer 1967). The sexual segregation of Leafscale Gulpers, a sexually dimorphic species, has been described in the North Atlantic (Girard and Du Buit 1999). The distribution of males was uniform across sampled depths, while only immature females displayed a similar abundance across depth; pregnant females, as well as neonates and small juveniles, have never been recorded in the sampled fishing grounds, an area of the continental slope west of the British

3

Isles. Both bottom trawling and long-lining methods failed to catch smaller specimens or pregnant females within the study site. This phenomenon led the authors to suggest that parturition may take place in unobserved waters where the young then remain for protection from predators.

This segregating behavior is not limited to deepwater species; it has also been observed in large, open ocean species such as the Shortfin Mako (*Isurus oxrinchus*) and Scalloped Hammerhead (*Sphyrna lewini*); (Klimley 1987; Mucientes et al. 2009). These studies, however, could not identify a sole driver for the recorded segregation. Segregation of a population likely has several drivers which may change over the life of the animal, including environmental conditions, behavioral drivers related to migration or mating, and physiological differences that arise from sexual size dimorphism.

Monomorphic species, such as the oviparous Lesser Spotted Dogfish (*Scyliorhinus canicula*) are also observed to sexually segregate (Sims 2005). While the hypothesis of separate energetic requirements based on size differences would suggest that segregation would be weak or non-existent for monomorphic species, fine-scale differences in habitat selection by sex for *S. canicula* indicate that other drivers for sexual segregation may exist. Sims (2005) suggests that females may seek refuge from predators while males scavenge, or that they may instead be driven by thermal gradients, residing in warmer, shallower waters to increase egg production. Social behaviors, such as male aggression during mating, can also lead females to segregate. Data are insufficient to test these hypotheses, and thus factors affecting spatial segregation remain speculative (Wearmouth and Sims 2008).

Shark Nurseries

A shark nursery is a habitat where pregnant females and their young will separate from the general population for protections. According to Heupel et al. (2007), an area must meet three criteria with regards to newborn or young-of-the-year sharks to be considered a nursery: sharks are more commonly encountered in that area than others, sharks exhibit higher site fidelity for that area than others, and that area is repeatedly used across years, unlike others. Recent studies have suggested deepwater corals, including communities found in the Mississippi Canyon in the Gulf of Mexico, as potential nursery sites for benthic species such as Scyliorhinid catsharks (Etnoyer and Warrenchuk 2007; Henry et al. 2013).

Population Modeling

Predicting the growth or decline of a population aids both responsible fisheries and environmental management. Sex ratio at length for a species can be used to estimate species and sex-specific constants such as growth, K, mortality, Z, and t_0, a correction factor for when the animal's length would theoretically equal zero. Asymptotic length, L_∞, and length at birth, L_0, can be calculated from catch data which include the full length distribution of the species. The von Bertalanffy growth function (VBGF) uses K, L_∞, and t_0 to estimate length at age t, L_t: $L_t = L_\infty(1 - e^{-K(t-t_0)})$. The inverse of this function can be used to back-calculate age from length measurements, useful for data sets where age-at-length is not known: $t = -1/K * \ln(1-L_t/L_\infty) + t_0$ (Mackay and Moreau 1990).

Following the estimation of age from length measurements, numbers at age t, N_t, for a model population can be calculated with the following formula: $N_t = N_0 * e^{-zt}$, where N_0 is the initial population size. Once the numbers-at-age are calculated for each sex, a sex-ratio-at-length model can be manipulated by adjusting the growth, mortality, and t_0 constants to optimize its fit

to the observed data. Through this series of back-calculations, growth and mortality constants for species that are either untargeted by fisheries or difficult to study in a controlled lab environment can still be estimated.

Studies on age and growth for the Centrophoridae are limited. Aging via dorsal spines or vertebral centrae has been met with limited success in the genus, and it is still unknown what the maximum longevity of these animals might be. Results of studies done on related species are summarized in Table 1.

Study Aims

This study aims to describe the population dynamics of the Little Gulper in North American waters, including length distributions, sex ratios, and length-versus-weight curves. From sex-at-length and size-at-age data I model the differential sex ratios at length to exploit a characteristic "notch" in the sex ratio curve as a method to estimate mortality, growth, and longevity for the species in the absence of growth curves. I also examine the implications of increased mortality that may result from increased fishery by-catch or pollution-related effects on the lifetime pup production per female recruit. This has yet to be done for this poorly studied, deep-water species of shark. Through the comparison of two independent sampling schemes I was also able to describe a range of depths at which these fish may live, clarify their distribution range within the Northern Gulf of Mexico, and suggest a possible pupping ground for *C. uyato* off the Louisiana coast.

Table 1. Age and growth studies on *Centrophorus* relatives. *S. acanthias* is well-studied in this area, due to the use of dorsal fin spines for age validation. Some work has been done exploring the utility of fin spines from *Centrophorus* species, although radiometric dating has not been successful (Cotton et al. 2014). Note: the Birdbeak Dogfish, referred to as *Deania calceus* by Clarke et al. (2002*a*), is also referred to as *Deania calcea*, including in Castro (2011).

Species	Location	Sex	L_∞	K	t_0	Reference
Deania calceus	NE Atlantic	Female	119.303	0.077	-0.933	Clarke et al. (2002*a*)
Deania calceus	NE Atlantic	Male	93.516	0.135	0.165	Clarke et al. (2002*a*)
Squalus acanthias	NE Atlantic	Female	112	0.07	-3.37	Henderson et al. (2002)
Squalus acanthias	NE Atlantic	Male	79.5	0.15	-2.54	Henderson et al. (2002)
Squalus acanthias	NW Pacific	Female	152.9	0.036	-6.7	Bonham et al. (1949)
Squalus acanthias	NW Pacific	Male	101.8	0.071	-5.2	Bonham et al. (1949)
Squalus acanthias	NE Atlantic	Female	98.8	0.09	-1.57	Fahy (1989)
Squalus acanthias	NE Atlantic	Male	79.9	0.16	-1.69	Fahy (1989)
Squalus acanthias	North Sea	Female	101.4	0.11	-3.6	Holden and Meadows (1962)
Squalus acanthias	North Sea	Male	79.7	0.21	-2.0	Holden and Meadows (1962)
Squalus acanthias	Hecate Strait	Female	125.1	0.031	-10.6	Ketchen (1975)
Squalus acanthias	Hecate Strait	Male	89.7	0.092	-3.7	Ketchen (1975)
Squalus acanthias	Georgia Strait	Female	129.1	0.034	-7.3	Ketchen (1975)
Squalus acanthias	Georgia Strait	Male	96.1	0.067	-5.0	Ketchen (1975)
Squalus acanthias	NW Atlantic	Female	100.5	0.107	-2.9	Nammack et al. (1985)
Squalus acanthias	NW Atlantic	Male	82.5	0.148	-2.67	Nammack et al. (1985)

Methods

Study Site

Sampling for demersal fish species took place along the continental slope from off

Louisiana to the southern Gulf coast of Florida, from 2011-2014 (Figure 1). The West Florida

Slope sites were spread from west of Naples, along the slope to an area south of Pensacola. The

Northern Gulf sites ranged along the continental shelf and slope from an area south of New

Iberia, LA, to an area south of Mobile, AL. Both areas followed transects designed to sample a

gradient of near-shore, shallow waters into deepwater environments; depths for both areas

ranged from 17.1-859.5 m, although the sharks used in this study were captured in waters of 150-

705.5 m deep.
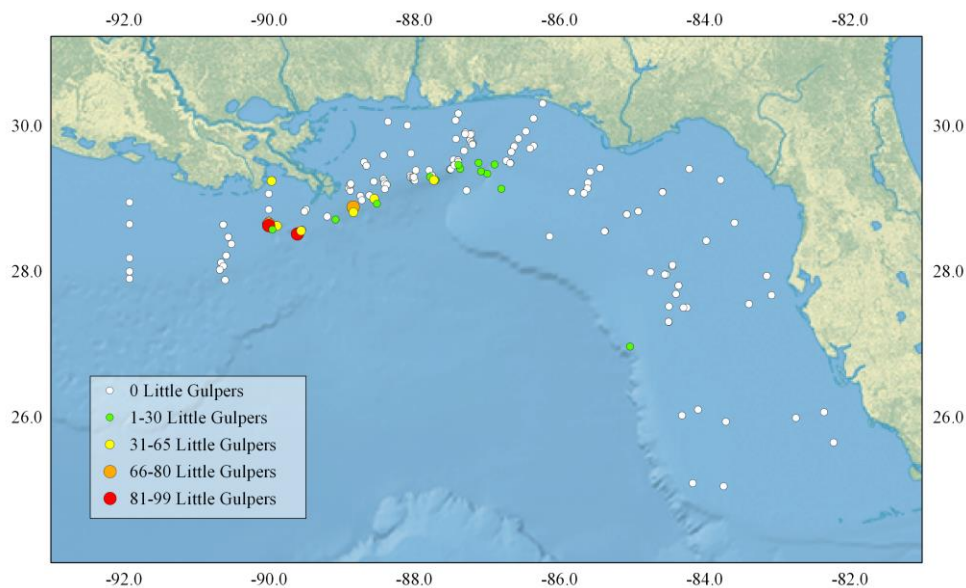
Figure 1. Sampling sites for *C. uyato*, 2012-2014. Catches predominantly came from
the Mississippi Canyon area, off the Louisiana coast. Some specimens were caught at
stations further east, off the Mississippi and Alabama coasts, using a second sampling
scheme.

Sampling Methods

Specimens were obtained during four demersal long-lining cruises in June 2012, August

2012, August 2013, and August 2014 aboard the C/V *Pisces* and R/V *Weatherbird II*. In total,

8

170 stations were sampled within the study region. At each station, five miles of 3.22 mm galvanized-steel main line was deployed, with 400-500 #13 circle hooks attached to 91-kg-test leaders, alternating cut herring or squid as bait. In 2013 and 2014, 1200-lb. monofilament main line was used. At the beginning and end of the main line, Star: Oddi CDST Centi temperature-time-depth recorders were deployed to record bottom temperature, depth fished, and actual bottom time. Latitude, longitude, depth from the vessel's depth finder, time, and local weather conditions were recorded at set-out and haul-back. Soak times ranged between 2-3 hours per set, dependent on transit time and surface conditions during haul-back. Catches were predominantly centered in the Mississippi Canyon, off the Louisiana coast (Figure 1). All specimens were initially weighted, and total length and sex recorded. Several individuals were frozen for later examination landside, and additional tissue samples (liver, gastrointestinal tract) were taken during the 2014 cruise.

The second set of catch data provided by Dr. Dean Grubbs and the Coastal and Marine Laboratory at Florida State University was collected according to the methods outlined in Churchill et al. (2014). These sites focused on deeper waters, ranging from 250-2500 m, although all the sharks used in this study were caught between 483-717 m (Figure 1). In total, 237 *Centrophorus* sp. were recorded in this additional data set.

Species Identification

Two female sharks were frozen at -40°C for landside dissection. Muscle tissue was taken from directly below the first dorsal fin for genetic sequencing. A skin sample was also taken from below the first dorsal fin for dermal denticle identification; because the size and shape of denticles can vary across an animal's body, this area was selected to match that chosen by Castro

(2011) for comparison to his representative photographs. The skin was pressed between two glass slides and dried overnight before viewing.

Data Analysis

Population Dynamics. Total length was calculated for specimens sampled at sea as the distance from snout tip to the posterior tip of the caudal fin. Measurements were recorded to the nearest centimeter; unless otherwise stated, all shark sizes given are for total length. Figures for length frequency distributions include measurements from all sampling years. Weight was calculated to the nearest gram; digital scales were used for smaller specimens (< 6 kg), while a hanging spring scale was used on the largest animals (centigram accuracy). Depth data from all sampling years was used to calculate the cumulative fraction of stations sampled by depth. The sex ratio by length was expressed as the proportion of females to the total number of specimens per 5-cm length class. Fitted growth curves were calculated by nonlinear regression for each sex individually, using the exponential relationship $W = aL^b$, where *W* equals specimen weight, *L* equals specimen length, and *a* and *b* are coefficients calculated by regression. All analyses were carried out using MATLAB R2012b and the Fathom Toolbox for MATLAB (Jones 2014).

Genetic Identification. Muscle samples taken from both individuals were used for extraction, polymerase chain reaction (PCR), and sequencing for comparison to other known *Centrophorus* spp. sequences. Two primers were used: the FishF2/R1 COI primer (Ward et al. 2005), and the 16Sar-L/br-H primer (Daley et al. 2012). A third universal fish primer set (Naylor et al. 2012) was tested, yet did not successfully amplify the samples. The PCR thermal routine consisted of an initial denaturation at 95°C for 2 minutes, followed by 35 amplification cycles of 0.5 minutes at 94°C, 0.5 minutes at 50°C, and 1 minute at 72°C, followed by a final extension at

72°C for 10 minutes. Following successful amplification, the PCR products were sent to Eurofins

Genomics (http://www.operon.com) for complete sequencing.

Population Modeling. Catch by sex data from both the Northern Gulf of Mexico and

Mississippi Canyon were used to construct a length and age-based simulation model for changes

in the sex ratio of *C. uyato* with length. The von Bertalanffy growth function (VBGF); (von

Bertalanffy 1934) was used to calculate length-at-age: $L_t = L_\infty(1 - e^{-K(t-t_0)})$, in which L_t is length at

age t, L_∞ is the asymptotic size, and K is a growth constant [Eqn. 1]. The inverse of the VBGF

(Mackay and Moreau 1990) was used to back calculate age-at-length for the midpoint values of 5

cm length classes: $t = -1/K * \ln(1-L_t/L_\infty) + t_0$ [Eqn. 2]. Numbers-at-age were calculated using the

following equation: $N_t = N_0 * e^{-Zt}$, in which N_0 is initial recruitment, and Z is mortality [Eqn. 3].

Initial recruitment for both males and females was set to 10,000 individuals. Plus groups were

added to the numbers-at-age for the final three length classes (males: 80 – 84 cm [midpoint = 82

cm], 85 – 89 cm [midpoint = 87 cm], and 90 – 94 cm [midpoint = 92 cm]; females: 95 – 99 cm

[midpoint = 97 cm], 100 – 104 cm [midpoint = 102 cm], and 105 – 109 cm [midpoint = 107 cm])

with the following formula: $1/(1 - e^{-K}) * N_{t-1}$, in which N_{t-1} is the number of individuals entering

the terminal size interval [Eqn. 4]. Using only one or two plus groups created a "notch" much

narrower than the one in the observed data, so the last three length classes were used to

accurately replicate the shape of the observed data curve.

Using the 99th percentile of recorded lengths by sex in this study as a proxy, L_∞ was

estimated as 94 cm for males and 112 cm for females. The growth parameter, K, was also

estimated for males and females independently, through a meta-analysis of existing population

and growth studies for related species (Table 1). There are currently no studies which define the

growth parameters of *Centrophorus uyato*. Thus, K was estimated to be 0.19 for males and 0.15

for females, so that a calculated L_0 for each sex (using Eqn. 1) would approximate the constant L_0 of 40 cm for both males and females, which was based on the minimum length captured. The value of t_0 was estimated as -3. Mortality was initially set to a value of 0.05. Both K and Z were adjusted to assess the model's sensitivity to each variable, ranging from values of 0.02 to 0.2, at intervals of 0.02.

In addition to the sex ratio model, lifetime pup production was estimated for *C. uyato* females by again creating a model population of females ages 1-50 using Eqn. 3 ($Z = 0.05$; $N_0 = 10,000$). Total pups produced for each age class were calculated using the following formula: $p_t = N_t * f * m$, in which N_t is the number of females at age t, f is fecundity, and m is the proportion of mature females at age t [Eqn. 5]. The female's ability to carry one embryo in each uterus results in a fecundity (f) value of 2. Castro (2011) suggests that gestation for this species is 2 years, similar to the Spiny Dogfish, meaning that an individual gives birth every other year, setting the proportion of mature females (m) equal to 0.5. This species is not born sexually mature, however; using the inverse VBGF [Eqn. 2], an age at maturity equal to 7 was calculated from the 85-89 cm length class. All ages below $t = 9$ had m values set to 0. The lifetime pup production of an individual female was calculated using the following formula: PPR = (Σ p_t) / N_0, in which p_t is the number of pups born to each age class, and $1 \leq t \leq 50$ [Eqn. 6]. A sensitivity analysis calculated how pups per recruit would change with increasing Z, from 0.02 – 0.2 at intervals of 0.02, and an increasing age at maturity of 7, 14, and 21 years respectively. Calculations were performed in Microsoft Excel 2013 and figures were drawn using MATLAB R2012b.

Results

Population Dynamics

Mississippi Canyon Catch (MCC). Of the 170 stations sampled, *Centrophorus uyato* was captured at seven. All of these stations were located either in the Mississippi Canyon or in nearby waters. A total of 593 individuals identified as *Centrophorus* sp. were caught: 145 were landed in June 2012, 131 were landed in August 2012, 193 were landed in August 2013, and 124 were landed in August 2014. Total lengths for the captured Little Gulper ranged from 38-113 cm (Figure 2). Some of the smallest specimens were individuals that pregnant females spontaneously aborted as they were brought on board. Length frequency distributions differed between the sexes: males ranged from 38-101 cm in length, while females ranged from 44-113 cm. Females comprised a greater fraction of the overall catch, accounting for 72% of all the Little Gulpers landed, and represented most of the specimens exceeding 100 cm in length (Figure 3).
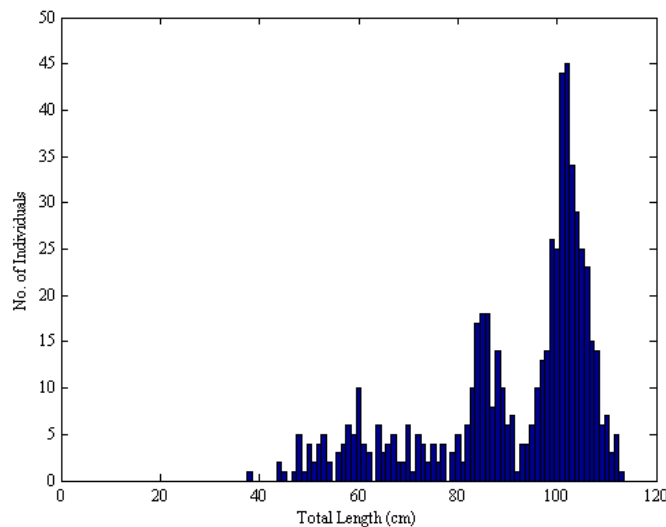
Figure 2. Total length frequency distribution of *C. uyato* in the MCC. Lengths ranged from 38-113 cm, with females predominating the largest length classes. Field notes indicate that many of the large females brought on board were pregnant, or spontaneously aborted their young on deck.

Figure 3. Catch composition and sex ratio by length of *C. uyato* in the MCC. Total sample size was 586 individuals: 422 females and 164 males, predominantly caught in and around the Mississippi Canyon off the Louisiana coast.

As expected for a deep-water species, no Little Gulpers were caught at the shallowest stations fished (Figure 4). Although stations as shallow as 17.1 m were fished, *C. uyato* specimens were only caught in waters from 150-705.5 m deep. Eighty percent of the Little Gulpers landed were taken from stations with an average depth between 200-500 m; 18% came from waters between 150-199 m deep, while the remaining 2% came from waters exceeding 500 m average depth. Across all sampling years, Little Gulpers were caught at an average depth of 290 m. The average depth of all stations fished during this time was 134 m, and 84% of stations had an average depth less than 200 m.
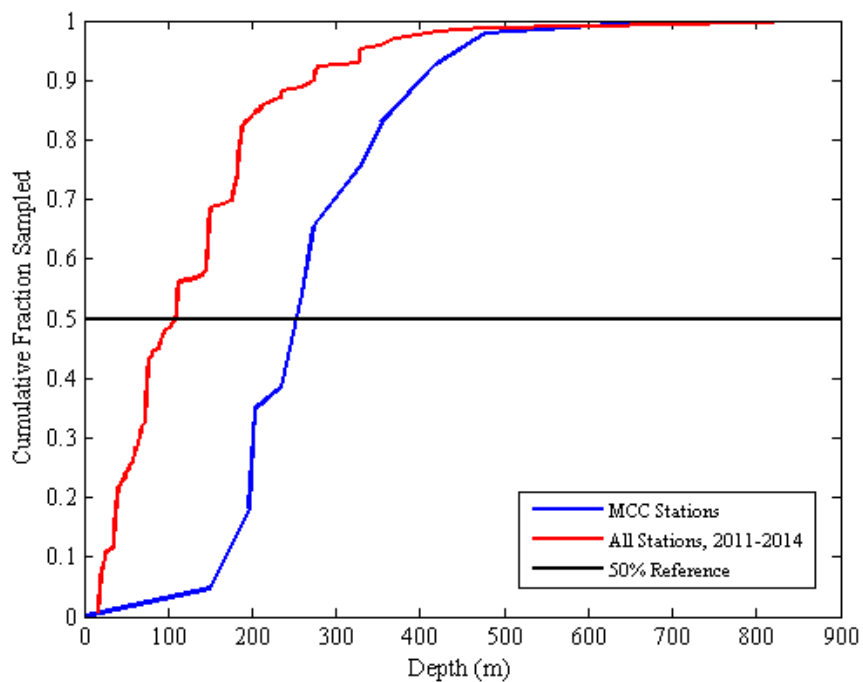
Figure 4. Catch by depth of *C. uyato* in the MCC. The fraction sampled for MCC stations was calculated as the cumulative number of Little Gulpers caught by depth. The fraction sampled for all fished stations was calculated at the cumulative number of stations sampled by depth.

The calculated sex ratio by length of females to males oscillated around an equal 1:1 ratio from the minimum recorded length (38 cm) until approximately 77 cm (Figure 3). Males comprised the majority of the sampled population from approximately 77-91 cm length; the ratio then climbed steeply above 1:1 for all lengths 92 cm and greater, indicating a female majority at the largest length classes. This phenomenon created a distinct "notch and rise" in the sex ratio by length plot.

The coefficients for the length-weight regressions were calculated separately for males and females (Figure 5). For males, $a = 6 \times 10^{-5}$ and $b = 2.4766$; for females, $a = 4 \times 10^{-6}$ and $b = 3.1043$.
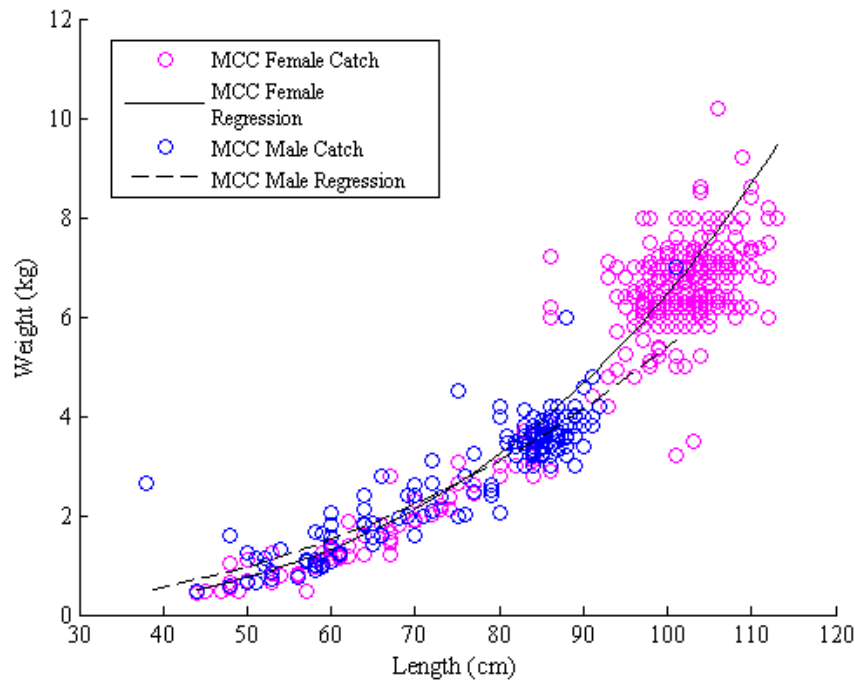
Figure 5. Length-weight regression curves by sex for *C. uyato* in the MCC. The lengths and weights of seven individuals for which no sex was recorded were excluded from this analysis. Female regression had an $r^2 = 0.93$. For the males, $r^2 = 0.81$.

Comparison to Northeastern Gulf of Mexico Catch (NEC). While the overall catch from the stations further east in the Northern Gulf of Mexico was smaller, with a total of 237 Little Gulpers landed, the length frequency distribution covered a similar range (44.5-120 cm) as that seen in the Mississippi Canyon data set (Figure 6). This seems to indicate a negligible difference in size selectivity between the two gear sets used. However, there was a notable difference in the sex composition of the two Little Gulper catches. Females comprised a smaller proportion of specimens landed in the NEC, accounting for only 34% of the total catch (Figure 7). Despite the differences in sex composition between the two data sets, the NEC sex ratio by length still exhibited the characteristic "notch and rise" of male predominance beginning near 75 cm length, then ascending to female predominance at 92 cm length and greater (Figure 8-9).

16
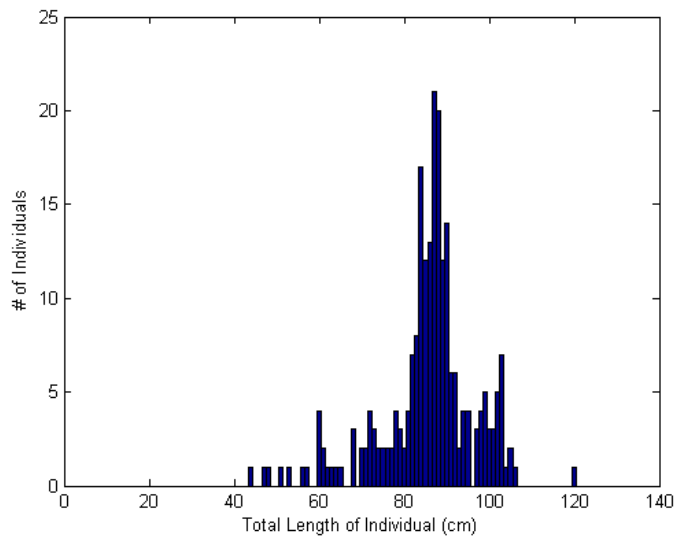
Figure 6. Total length frequency distribution of *C. uyato* in the NEC. Lengths ranged from 44.5-120 cm. Compared to the MCC, males predominated the overall catch, although females still accounted for the largest individuals landed. No pregnant females were noted at these stations.
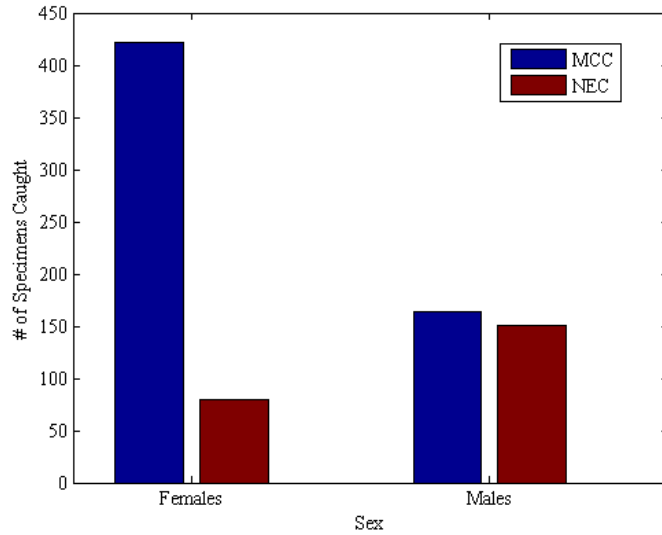
Figure 7. Catch count by sex of *C. uyato*, MCC and NEC. The preponderance of females at the MCC stations, many of them pregnant, suggests that this region may be used by the species as a nursery area.

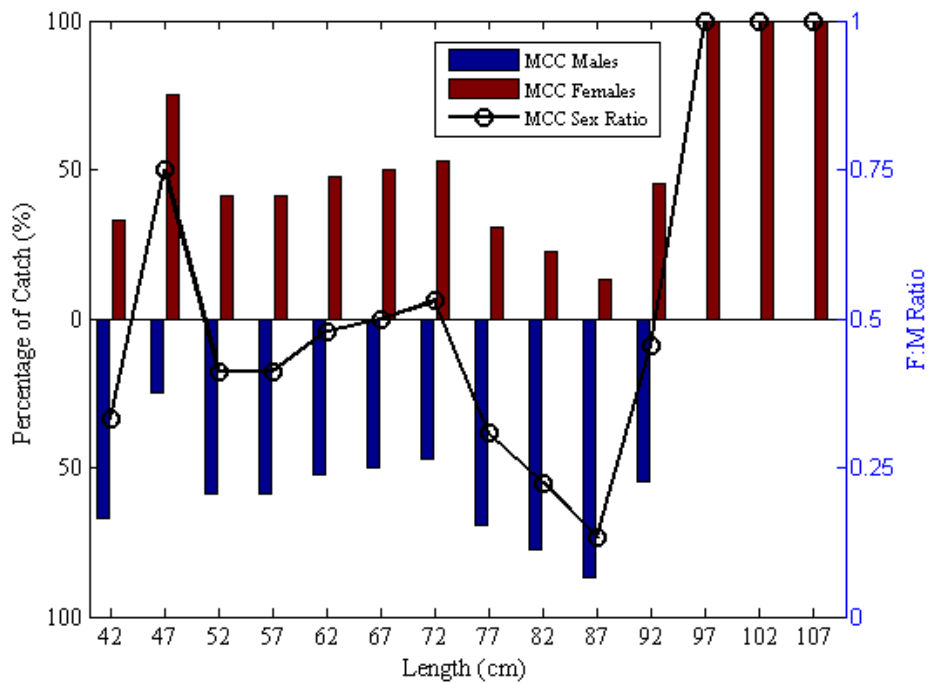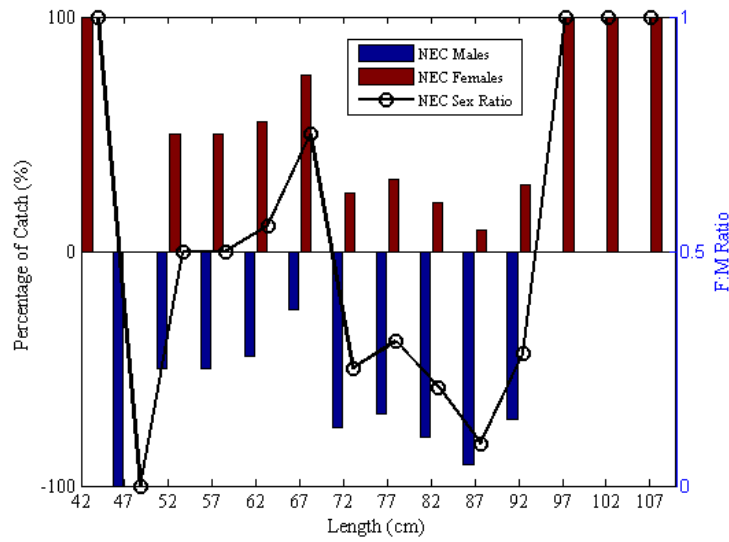**Figure 8**. Catch composition and sex ratio by length of *C. uyato* in the NEC. Total sample size was 231 individuals: 80 females and 151 males, caught in the waters off the Mississippi and Alabama coasts.
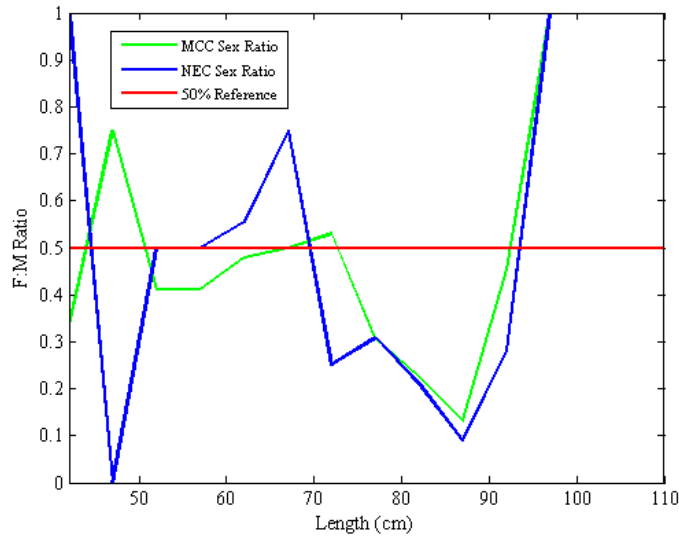
Figure 9. Comparison of sex ratios by length for *C. uyato*, MCC and NEC. Both curves have a characteristic "notch and rise" of male predominance beginning around a length of 75 cm, which then rises to female predominance of the largest length classes beginning around 92 cm. This feature was used to build a length and age-based simulation model of sex ratio at length for *C. uyato*.

18
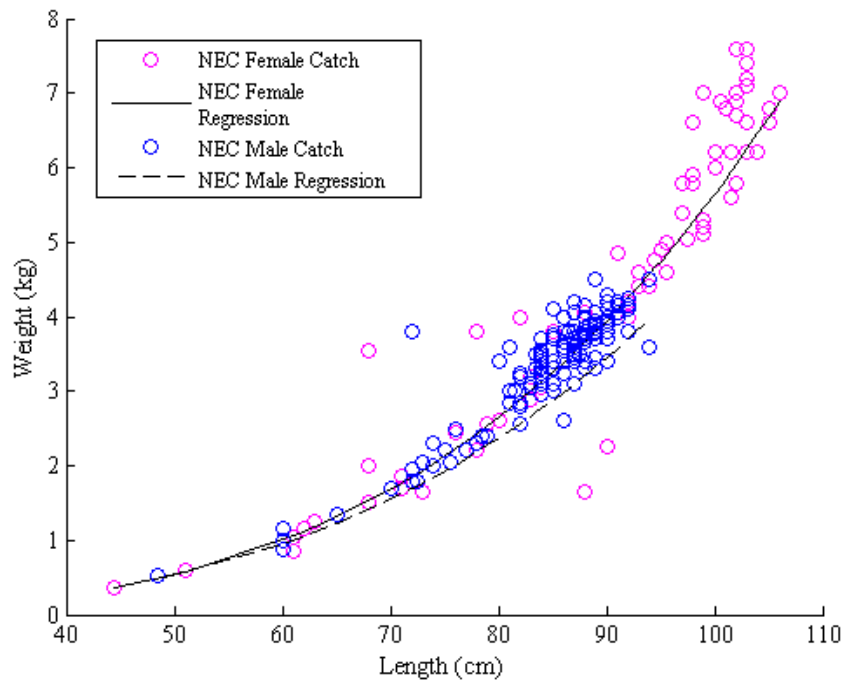
Figure 10. Length-weight regression curves by sex for *C. uyato* in the NEC. Female regression had an $r^2 = 0.91$. For the males, $r^2 = 0.89$.

The length-weight regressions for the NEC produced similar curves to that of the MCC. For males from the NEC set, $a = 2 \times 10^{-6}$ and $b = 3.1913$; for females from the NEC set, $a = 9 \times 10^{-7}$ and $b = 3.399$.

Genetic Identification

The initial genetic identification for both specimens from the MMC returned as *Centrophorus squamosus*, the Leafscale Gulper, with 97% certainty according to Eurofins Genomics. Morphological differences between the specimens landed during the course of this study and *C. squamosus*, most notably the dermal denticle pattern mentioned previously, contradicted this identification (Figure 11). The raw sequences were then input into a genetic tree with other samples from the Centrophoridae taken from waters throughout the North Atlantic and Gulf of Mexico, previously identified to species level. The resulting tree provided an

identification of *Centrophorus uyato*, the Little Gulper, with the most closely related sequences having been taken from *C. uyato* specimens in the northeastern stations data set and used in the current population analyses (Figures 12-13). Both trees are neighbor-joining, with 1,000 bootstrap replicates.
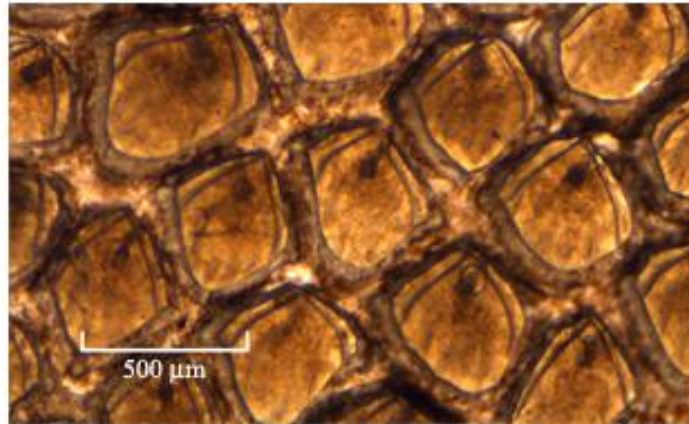
Figure 11. Dermal denticles of *C. uyato*. Note the ridges and rhomboidal shape of the denticles, now identified as *C. uyato*. *C. squamosu*s denticles are tear-shaped and overlapping, with a leaf-like appearance (Castro 2011).
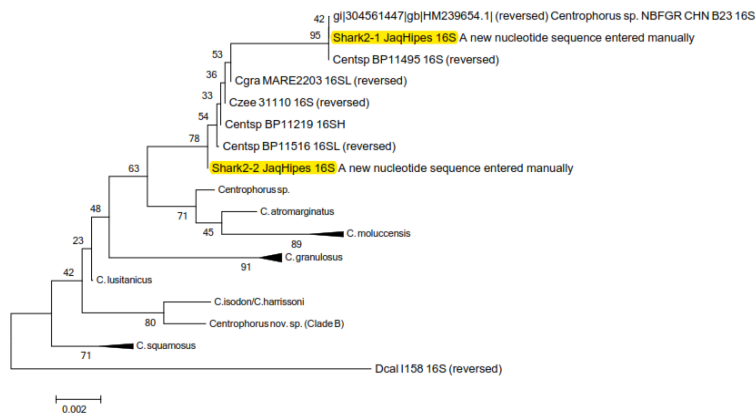
Figure 12. Tree containing Centrophoridae 16S sequences, courtesy of A. Verissimo. Author's sample sequences are highlighted. The species *C. zeehani* (coded "Czee" above) is an equivalent name for *C. uyato* used in some Australian publications.
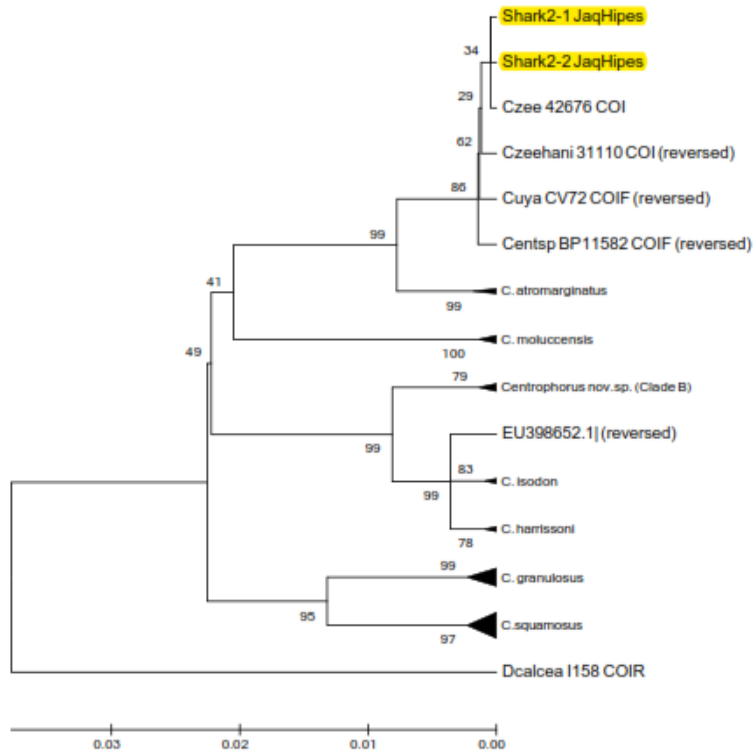
Figure 13. Tree containing Centrophoridae COI sequences, courtesy of A. Verissimo. Author's sample sequences are highlighted. The species *C. zeehani* (coded "Czee" above) is an equivalent name for *C. uyato* used in some Australian publications. Additional *C. uyato* sequences shown above are coded as "Cuya".

Population Modeling

The initial model successfully replicated the characteristic notch and rise in the sex ratio

by length of *C. uyato* (Figures 14-15). Calculating this curve provided the first estimates of *K*, *Z*,

and t_0 for this species as well. These calculations are given in Table 2. The sensitivity of these

results was assessed with regards to changes in both mortality and growth constants. Increasing

or decreasing mortality rate produced a distinct pattern (Figure 16). The lowest simulated value

of *Z* = 0.02 produced the deepest notch; as mortality increased by intervals of 0.02, this male-

predominated notch became shallower. For a *Z* = 0.02, the sex ratio at the 87 cm midpoint

equaled 0.157; for a *Z* = 0.2, this value increased to 0.265.

Growth rates for both sexes of 0.02-0.2, at intervals of 0.02, were input into the model and their corresponding R^2 value recorded. Mortality rate was assumed to equal 0.05, the same Z used in Figures 14-15. A contour plot shows the range of these values (Figure 17). The highest goodness-of-fit ($R^2 \geq 0.90$) of the model to the observed data occurred when $K_{male} \geq 0.16$ and $K_{female} \geq 0.08$; the estimates of this study fell within this range ($K_{male} = 0.19$, $K_{female} = 0.15$, $R^2 = 0.902$). At a low mortality rate (i.e., little or no pressure from fisheries or large-scale disturbances), males appear to grow at a faster rate than females although they reach a smaller maximum length.

Growth rates for both male and female *C. uyato* were high in comparison to studies of related species (Figure 18). No other estimate for K_{female} exceeded this study's estimate of $K_{female} = 0.15$ for *C. uyato*; only one study on *S. acanthias* (Holden and Meadows 1962) estimated a larger K_{male} than this study's estimate of $K_{male} = 0.19$ for *C. uyato*, with a value of $K_{male} = 0.21$. According to Castro (2011), *C. uyato* has the smallest maximum length of the three species (*S. acanthia*, *D. calceus*, and *C. uyato*), although catch records examined for this study did include specimens larger than the suggested 100 cm. For this reason, this study's data points fell closer to the center of the range of L_∞ values, rather than among the smallest values.

The model also reproduced a phenomenon initially attributed to random noise in the observed data. In the length class prior to the "notch" (75-79 cm, in the model), the sex ratio rose noticeably above 0.5, slightly favoring females; this can be observed in Figure 15, and is exaggerated with increasing Z in Figure 16. The magnitude of this increase grew with increasing mortality and is likely attributable to the differential growth between the sexes. According to this model, females have a slower growth rate, K, than males, but also reach a larger L_∞, so that at a given length, $t_{female} < t_{male}$ [Equn. 2]. Numbers at age [Equn. 3] decrease with increasing t (before

the addition of a plus group), meaning that as the age gap widens between males and females with increasing length, the number of males at a given length decreases and the sex ratio at length will increase above 0.5.

Values from the model were also used to estimate the total pup production over a female Little Gulper's lifetime. Age and growth studies have not yet been done for this species, meaning that maximum longevity and age at maturity remain estimates. Calculating up to 50 years of age, one female could produce as many as 13 pups in her lifetime; with a low mortality of $Z = 0.05$, one would expect to see the population grow over time. As Z increases, however, the pups per female recruit decreases exponentially (Figure 19). Lifetime reproductive capabilities are also sensitive to changes in age at maturity, with pups per recruit decreasing as age at maturity increases.
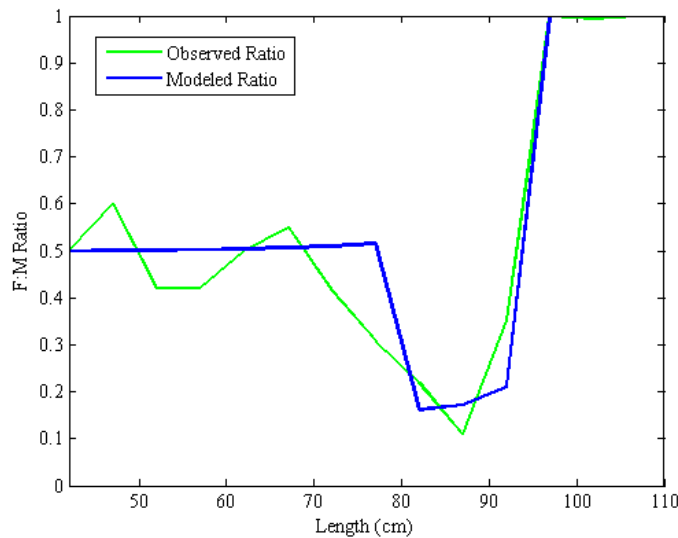
Figure 14. Modeled sex ratio by length of *C. uyato*. $R^2 = 0.902$. Model used the initial parameters outlined above: $K_{male} = 0.19$, $K_{female} = 0.15$, and $Z = 0.05$. Observed ratio included all sex and length data from both the MCC and NEC data sets.

23

Table 2. Sex ratio model calculations for *C. uyato* males and females. Length classes to which a plus group was added are in bold. These values were calculated with $L_0 = 40$, $t_0 = -3$, $L_{\infty M} = 94$, $L_{\infty F} = 112$, $K_{male} = 0.19$, $K_{female} = 0.15$, $Z = 0.05$, and $N_0 = 10000$. The results of this model are plotted in Figures 14 and 15.

Females					Males				
Length class (cm)	Mid-point (cm)	Calc. age (years)	No. at age	Percent of total pop.	Length class (cm)	Mid-point (cm)	Calc. age (years)	No. at age	Percent of total pop.
40-44	42	0.133358	9933.543	49.97838	40-44	42	0.116058	9942.139	50.0216
45-49	47	0.627411	9691.164	50.02592	45-49	47	0.648143	9681.123	49.9741
50-54	52	1.161029	9436.014	50.09888	50-54	52	1.240132	9398.767	49.9011
55-59	57	1.741105	9166.265	50.20768	55-59	57	1.907247	9090.435	49.7923
60-64	62	2.376506	8879.629	50.36856	60-64	62	2.671363	8749.679	49.6314
65-69	67	3.078909	8573.188	50.60829	65-69	67	3.565568	8367.095	49.3917
70-74	72	3.864129	8243.118	50.97401	70-74	72	4.643433	7928.1	49.026
75-79	77	4.754339	7884.258	51.55711	75-79	77	6.000429	7408.023	48.4429
80-84	82	5.78201	7489.369	16.08865	**80-84**	**82**	**7.833622**	**39061.27**	**83.9114**
85-89	87	6.997487	7047.766	17.21338	**85-89**	**87**	**10.67045**	**33895.77**	**82.7866**
90-94	92	8.485111	6542.567	21.16036	**90-94**	**92**	**17.26393**	**24376.41**	**78.8396**
95-99	**97**	**10.40299**	**42675.21**	**100**	95-99	97	0	0	0
100-104	**102**	**13.10609**	**37280.23**	**100**	100-104	102	0	0	0
105-109	**107**	**17.72707**	**29589.34**	**100**	105-109	107	0	0	0
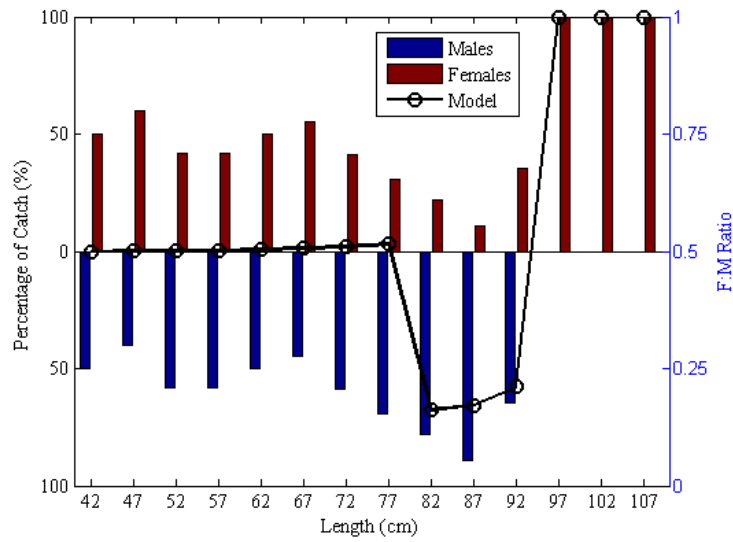
Figure 15. Sex ratio model and observed catch by sex. Model used the initial parameters outlined above: $K_{male} = 0.15$, $K_{female} = 0.19$, and $Z = 0.05$. Observed ratio included all sex and length data from both the MCC and NEC data sets.
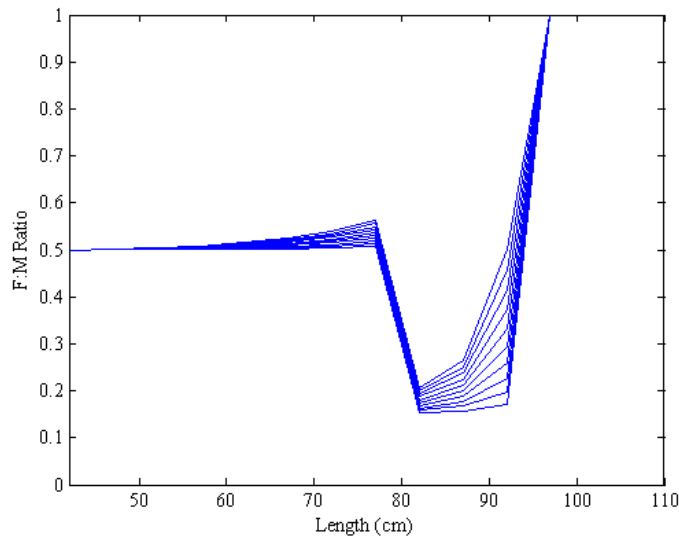
Figure 16. Sensitivity of sex ratio model to Z. Mortality values ranged from 0.02 to 0.2, at an interval of 0.02. As the value of Z increases, the notch at 82-92 cm becomes shallower, although males continue to predominate those length classes. The slight increase in females in the 75-79 cm length class increases in magnitude with increasing Z due to the differential growth between sexes.
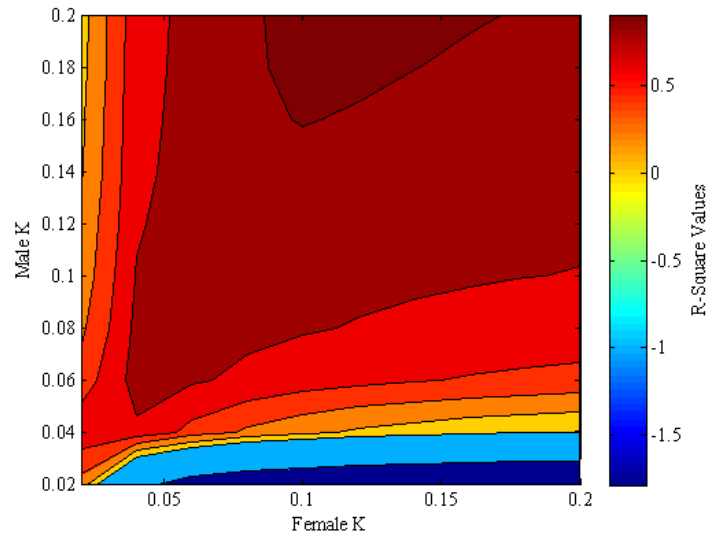
Figure 17. Sex ratio model goodness-of-fit with changes to male and female growth rates. The highest R^2 values (≥ 0.90) fall within the dark red shaded area at the top of the graph. This model best fit the observed data when $K_{male} > Kf_{emale}$; $K_{male} \geq 0.16$; and $K_{female} \geq 0.08$. Initial estimates of K used in this study fell within this range, with an R^2 value of 0.902.
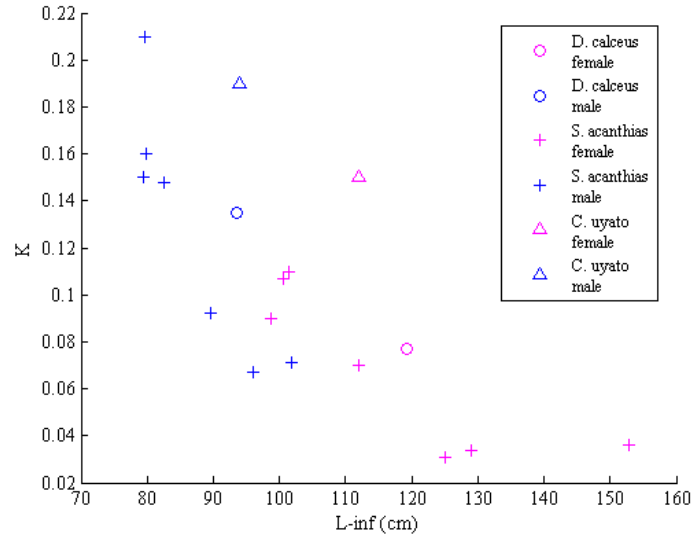
Figure 18. Comparison of modeled L_{∞} and K to additional studies. All values come from the studies cited in Table 1. Estimated female growth rate for *C. uyato* was higher than previously calculated values for *D. calceus* or *S. acanthias*. Only one estimate of male growth for *S. acanthias* was greater than the estimate for *C. uyato* males. Castro (2011) suggests a maximum length of 110 cm for *S. acanthias* males, and 130 cm for females; for *D. calceus* (referred to as *D. calcea* by Castro (2011)), maximum length is given as "at least" 120 cm.
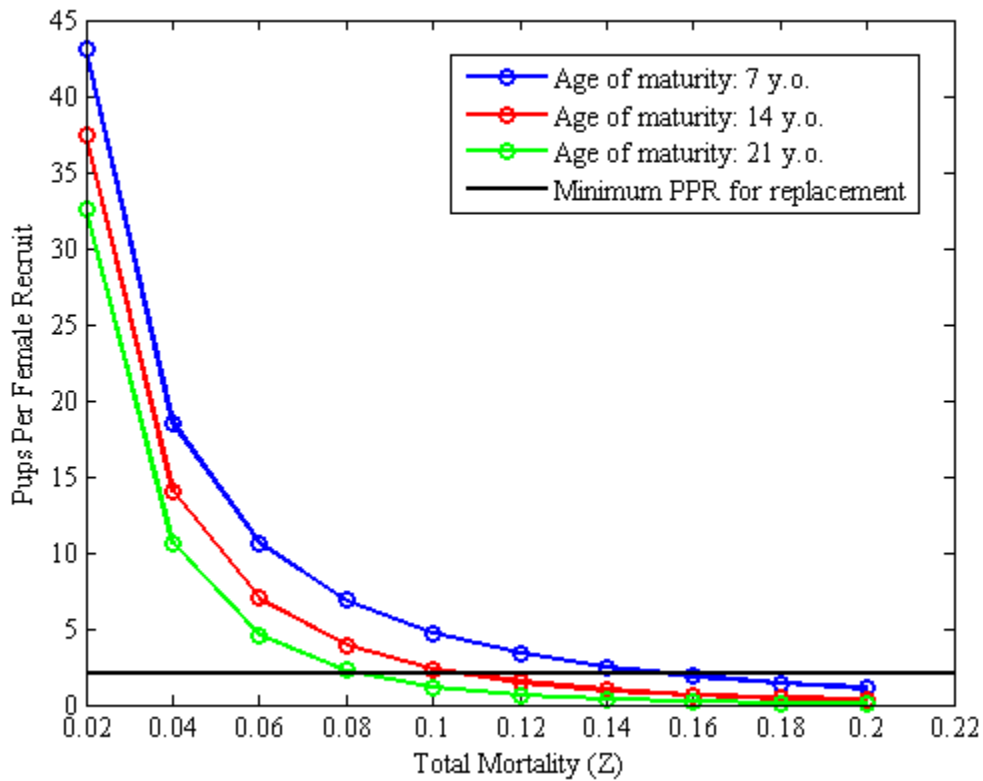
Figure 19: Sensitivity of pups per recruit to changes in both mortality (*Z*) and age at maturity. Here a higher age at maturity serves as a proxy for a decreased female growth rate (*K$_f$*), meaning that females will reach a sexually mature size at a later age. Pups per recruit decreases exponentially with increasing *Z*. The maximum Z allowable for the population to remain in equilibrium (i.e., with a PPR of 2 or greater), decreases as age at maturity increases.

Discussion

Length frequency distributions for the Little Gulper show the species can reach lengths exceeding the previously suggested maximum of about 100 cm. The landing and measurement of spontaneously aborted individuals at MCC stations suggests a length at birth of approximately 40 cm. Length at birth is bounded by a minimum size that can successfully compete and survive in the environment, and a maximum size that the female can hold within her body cavity; while

27

individuals could reach a length exceeding 40 cm at birth, the lack of recorded aborted young reaching sizes much greater suggests 40 cm may be approaching the upper bounds for what a female is capable of carrying to term.

Despite the small percentage of MCC specimens caught in waters exceeding 500 m depth, other evidence suggests that *C. uyato* can be found much deeper in the Gulf. Forty-eight percent of NEC specimens were taken in waters 510 m or deeper, with an average station depth of 514 m. Migratory excursions into waters shallower than 150 m or deeper than 778 m (the minimum and maximum depths at which *C. uyato* was caught, respectively) cannot be dismissed as a possibility, especially if they take place seasonally during a time of year when sampling did not occur. As a deepwater species, the Little Gulper may not be found in shallower water during the summer months due to increased water temperatures that would cause metabolic stress.

Due to a difference in sampling methods for the MCC and NEC, it is not possible to perform analyses which combine the animals' densities (i.e., catch per station). Differential selectivity by sampling method is a possibility, but the differences in overall sex ratio by sampling site argue that using the data sets individually would be biased.

The Little Gulper exhibits sexual size dimorphism like the cogeneric Leafscale Gulper (Gerard and Du Buit 1999), with a maximum female length 12% greater than the largest male landed (Figure 19). The average length of all females examined in this study was 18.6% greater than the average length of all males landed; at NEC stations, where large, pregnant individuals were not commonly encountered, the average female length was only 6% greater than that of males.
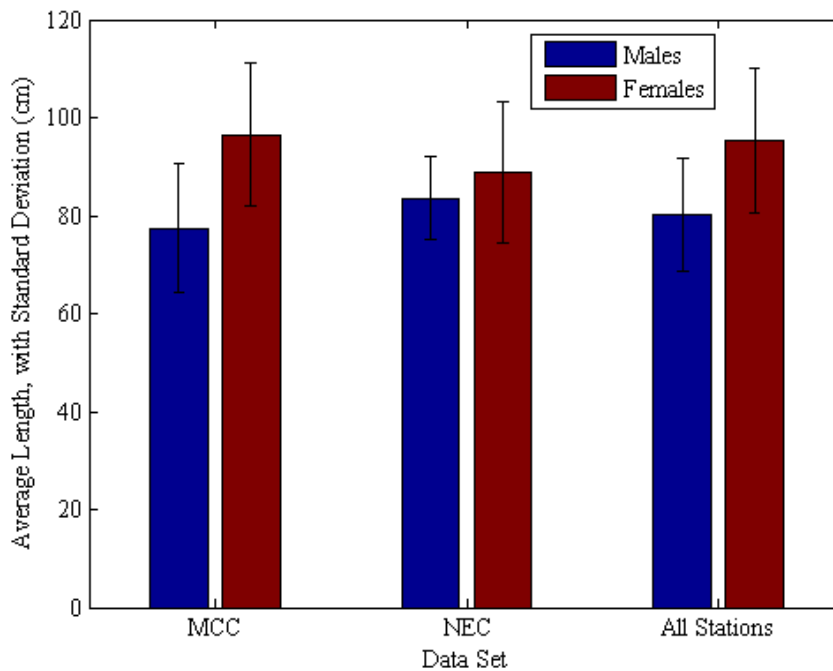
Figure 20. Average length and standard deviations of males and females landed; MCC, NEC, and total catch. There does not appear to be a significant difference in average female or male lengths between the two catch series. At both the MCC stations, as well as all stations combined, the maximum male length was less than the average female length. A reduced number of females, and lack of pregnant individuals, at NEC stations might be responsible for the more equivalent average lengths from those sites.

Size differences could reflect elasmobranch mating behaviors. In many species of shark, the male bites onto the pectoral fin of the female during mating. With the male now aligned slightly behind the female, a smaller body size is necessary for the male's claspers to properly align with the female's cloaca. Females also require a larger body cavity size in order to carry young which may reach up to 40 cm length before birth. The mating behaviors of *C. uyato* have not yet been described.

The Little Gulper appears to sexually segregate for some portion of its life cycle, a commonly observed behavior in elasmobranchs. The large fraction of pregnant females in the MCC, as well as the proximate location of stations where they were landed all within or near the

29

Mississippi Canyon, may indicate the area as a nursery for *C. uyato*. This female dominated catch was a localized phenomenon not seen at NEC stations. Current MCC data fulfills two of the three criteria set forth by Heupel et al. (2007). Late-term pregnant females have been caught in the area for three consecutive years, suggesting site fidelity, and *C. uyato* was more commonly encountered at the Mississippi Canyon stations than other sites fished. Since sampling has only taken place during the summer months, it is not currently known how long this congregation of pregnant females persists through time, or how their appearance may be seasonally linked. Extending the frequency of sampling to include additional seasons, as well as expanding the study area to westward to include waters off the Texas and Mexico coasts, and southward into waters further offshore, would help clarify the full range and migratory habits of this species in the Gulf of Mexico.

Males larger than the modeled maximum length of 94 cm could be found in waters not sampled by these expeditions, further to the west or south in the Gulf of Mexico. Although this paper describes a possible pupping or nursery ground for *C. uyato* in and around the Mississippi Canyon, congregations of very large, older males could leave the northern Gulf region during the summer months and return during an unsampled time of the year. Though current observations agree with general elasmobranch knowledge (sexual segregation during some or most of the year, females reaching a greater maximum size than the males), making the existence of such undescribed congregations unlikely, they can only be ruled out with a spatial and temporal expansion of the current sampling procedure.

The *Centrophorus* genus has been marked by unreliable morphological identifications and a lack of type specimens accompanying genetic studies. Initial difficulties in establishing a positive genetic identification for the specimens used in this study were due, in part, to such

misidentifications, likely made in the field and propagated through to the databank, or gaps in the available gene sequences for comparison. These difficulties highlight an inconsistency in the species record, which is still being addressed through the collection of type specimens and sequences. While a reconstruction of the genus is currently underway (Verissimo, in review), both the MCC and NEC specimens were identified as *C. uyato*, the Little Gulper. Due to such a small sample size, these results are not intended to address the population genetics of *C. uyato*, but taking into account the morphological similarities and geographic proximity of the two catch data sets they can be used as a species identification tool.

Life history parameters such as natural mortality, growth, and size-at-birth have never been before been estimated for *Centrophorus uyato*. This model provides a first look at the growth and longevity of this species in the absence of validated aging studies. Data on growth and mortality for other Centrophoridae are lacking, although the growth constants for males and females were both large in comparison to those estimated for other deep-water species of Squaliformes. The basic shape of the sex ratio by length curve for this species was reproduced by the model and its estimated constants, although the "notch" where males predominate occurs over a narrower range of lengths than in the observed data. Currently this model assumes equivalent values of t_0 and Z for this species; additional sampling may indicate sex-specific values for these constants is more appropriate, which could increase the goodness-of-fit to observed data. This modeling procedure could have further applications for other genera or species of shark for whom age-validated studies have not yet been done.

This characteristic, "notched" curve persists even with a doubling or quadrupling of mortality, estimated as $Z = 0.05$ in the initial model as natural mortality alone. Increases in mortality could come from increased fishing pressure, most likely in the form of by-catch, or

31

environmental disturbances such as an oil spill. While the general shape remains intact, males appear disproportionately affected as the mortality rate increases. The sex ratio rises above 1:1 and favor females at smaller lengths, and the male-predominated notch becomes shallower.

Lifetime pup production is dependent on several age and growth factors, many of which remain unknown. Maximum longevity and age at maturity are estimates until the species has a validated age model. These calculations also assume females immediately begin producing two pups per litter, though it has been noted that smaller individuals may only carry one embryo at a time (Castro 2011). These estimates, however, show that the Little Gulper, like other elasmobranchs, has a low fecundity. Such a low rate of replacement makes this species especially vulnerable to pressure from fisheries as a targeted species or as by-catch, as well as environmental disturbances like the 2010 Deepwater Horizon oil spill.

Although these sharks are not currently targeted by a commercial fishery, they remain an understudied component of the Gulf of Mexico ecosystem. The likelihood of *C. uyato* becoming the focus of a commercial fishery is low at this time, although there might be some value to their skin for leather goods, but this species is found in a highly active fishing region and could be susceptible as bycatch to other fisheries along the northern Gulf. Even basic information on the population structure, species range, and reproductive habits of the Little Gulper have gone undefined until recently, with many more aspects to their biology still in need of clarification. This study highlights an ongoing need for sampling throughout the Gulf, particularly in less accessible, deeper offshore waters, and at multiple time points throughout the year to assess seasonal components of a species' life history. As scientists continue to emphasize a regional or global perspective, particularly where conservation is concerned, the literature must strive to provide as much biological and behavioral information as possible on these understudied species,

regardless of the economic or recreational values that drove early topics of study. These data are a valuable foundation for defining the life history traits of the Little Gulper and will hopefully serve as a useful aid to future investigations into the species.

CHAPTER TWO:

MULTIVARIATE COMMUNITY ANALYSES OF ELASMOBRANCH SPECIES

IN THE GULF OF MEXICO

Introduction

Elasmobranch Diversity

While numerous habitat studies have included sharks in their examination of overall

species assemblages, relatively few consider the elasmobranch community and its species

associations alone. Several studies in the Mediterranean have investigated shark assemblages, the

most recent finding a difference in species assemblages with changing depth (Massuti and

Moranta 2003). In the nearshore waters of Shark Bay, Australia, White and Potter (2004)

described changes in elasmobranch species composition between habitats with varying degrees

of seagrass and mangrove vegetation. No similar studies have yet been conducted in the

Northern Gulf of Mexico.

Sharks in the Gulf of Mexico

Elasmobranch fauna are diverse in Gulf waters, although an exact count of species found

in the region is not known. The most recent Fisheries Management Plan for sharks set forth by

the National Marine Fisheries Service includes 39 species, the majority of which are coastal and

pelagic species (NMFS 2006). Grace and Henwood (1997) landed 17 species of sharks in the

Gulf of Mexico and along the eastern seaboard of the United States, describing an additional

eight species not caught, but known to occupy the region. In the southern waters of the Gulf, off the coast of Mexico, Bonfil (1997) described "at least" 34 species as residing in the area.

Comprehensive examinations of the composition and abundance of the elasmobranch community are rare, with most surveys focusing on species that are economically important or more easily captured for study. Some of the species most abundant in surveys of the Gulf region include the Atlantic Sharpnose (*Rhizoprionodon terraenovae*), the Blacktip (*Carcharinus limbatus*), and the Bonnethead (*Sphyrna tiburo*); (Carlson and Brusher 1999, Cortes 2002). Since they are not of interest to commercial or recreational fishermen, deepwater species of shark are often underrepresented in surveys compared to coastal and pelagic species, although some studies in Mediterranean waters have focused on demersal elasmobranch assemblages (Massuti and Moranta 2003).

Study Aims

In this chapter I examine species distributions by depth in the Northern Gulf of Mexico elasmobranch community. Multivariate statistical analysis methods were used to calculate differences among *a priori* groupings of sampling station catches according to depth and according to location, as well as determine which species most contribute to any differences found. While previous studies have focused on coastal communities, this study represents one of the first attempts in the region to define elasmobranch species associations across a broad range of environments, from nearshore waters along the shelf to deepwater stations on the continental slope.

Methods

Study Site

Sampling took place along the continental slope from off Louisiana to the southern Gulf coast of Florida (Figure 20). The West Florida Slope sites were spread from west of Naples northward along the slope to an area south of Pensacola. The Northern Gulf sites ranged along the continental shelf and slope from an area south of New Iberia, LA to an area south of Mobile Bay, AL. Both areas followed transects designed to sample a gradient of near-shore, shallow waters into deep-water environments, with a depth range of 17.1 m to 859.5 m.
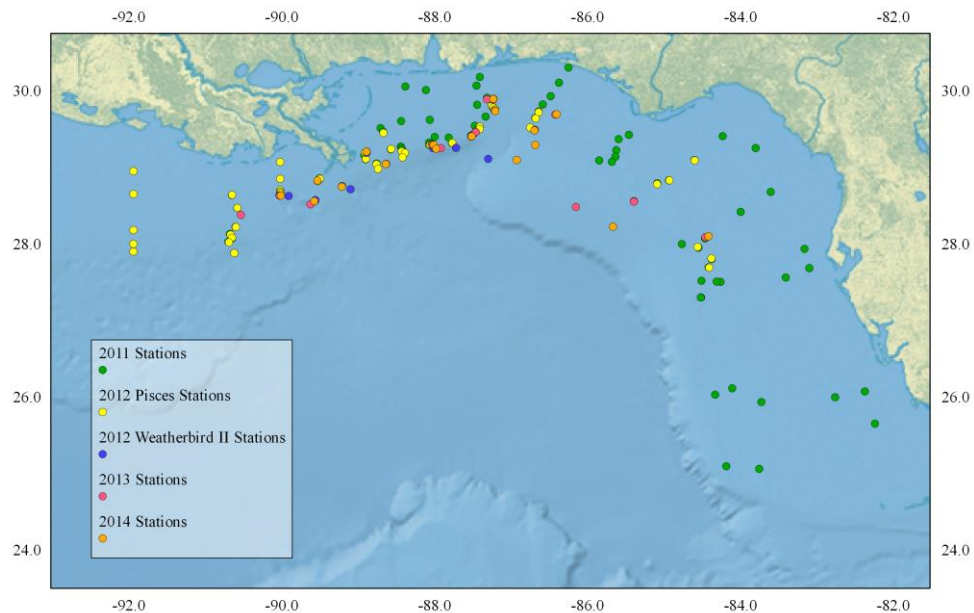
Figure 21. Elasmobranch sampling sites, 2011-2014. Sampling took place over four years on two vessels, targeting both bony fish and elasmobranchs. A total of 170 stations were sampled, with elasmobranchs recorded at 115.

Sampling Methods

Specimens were obtained during 5 demersal long-lining cruises in July/August 2011, June 2012, August 2012, August 2013, and August 2014 aboard the C/V *Pisces* and R/V

Weatherbird II. In total, 170 stations were sampled along the West Florida Slope and Northern Gulf; elasmobranchs were landed at 115 stations. At each station, 5 miles of 3.22 mm galvanized-steel main line with 400-500 #13 circle hooks attached to 91-kg-test leaders, alternating cut herring or squid as bait, was deployed. In 2013 and 2014, 1200-lb monofilament main line was used. At the beginning and end of the main line, Star: Oddi CDST Centi temperature-time-depth recorders were deployed to record bottom temperature, depth fished, and actual bottom time. Latitude, longitude, depth from the vessel's depth finder, time, and local weather conditions were recorded at set-out and haul-back. Soak times ranged between 2-3 hours per set, dependent on transit time and surface conditions during haul-back. A total of 3609 elasmobranchs, representing 31 species and 10 families were caught: 1318 were landed in July/August 2011, 1023 were landed in June 2012, 434 were landed in August 2012, 449 were landed in August 2013, and 385 were landed in August 2014 (Table 3). All specimens were initially weighted, and total length and sex recorded.

Multivariate Analyses

Stations were grouped *a priori* by average depth, calculated from CDST measurements, into three categories: shallow, 0-73 m (0-40 fathoms [ftm]); intermediate, 110-146 m (60-80 ftm); and deep, ≥ 183 m (100 ftm). These groups were formed according to divisions present in the station data; depth gaps between each group are representative of unsampled depth ranges in the data. Only stations where elasmobranchs were caught were included in the groupings. Bray-Curtis similarity coefficients were calculated based on the square-root transformed abundances of each species for each station in order to make community-level comparisons among depth categories. Non-parametric multivariate analysis of variance (NP-MANOVA) was used to calculate the among-group differences in community composition by depth. Then a pairwise test

37

was performed to determine which depth categories differed from one another. For all depth pairings with a statistically significant difference in community composition, similarity percentages (SIMPER) were calculated to determine which species contributed the most to differences among groups. Canonical analysis of principal coordinates (CAP) was then used to plot the differences calculated by the NP-MANOVA in two-dimensional space. Finally, a leave-one-out cross-validation (LOO-CV) procedure assessed through 1000 permutations how well the *a priori* group assignments represented the original data.

A second analysis routine, following the same procedure, was performed with the stations placed into *a priori* groups based on location. All stations on the West Florida Shelf (WFS), east of Cape San Blas, FL (29.84°, -85.30°), comprised Group 1; Group 2, the Eastern Gulf of Mexico (EGOM), contained all stations west of Cape San Blas and east of the Mississippi River mouth (30.17°, -89.65°); Group 3, the Western Gulf of Mexico (WGOM), contained all stations west of the Mississippi River mouth. All statistical differences were considered significant at $p <$ 0.05. All analyses were carried out using MATLAB R2012b and the Fathom Toolbox for MATLAB (Jones 2014).

Results

Station Groupings by Depth

Catch by depth for the ten most common species in the data set did not immediately reveal distinct groupings, however it was apparent that some species (Atlantic Sharpnose, Bignose, Blacknose, and Blacktip) were more prevalent in shallower waters, while others (Gulf Smoothhound, Little Gulper, and Shortspine Dogfish) were predominantly caught at the deeper

stations (Figure 21). Others, such as the Sandbar and Scalloped Hammerhead, were found across a wider range of depths.

Following verification that the data met the assumption of homogenous within-group variances, the among-group variation was found to be high (F=10.2) and significant (p=0.001) using an NP-MANOVA test. A pairwise test returned significance differences for the species compositions among all three *a priori* depth groupings (Table 4); a SIMPER analysis determined which species contributed the most to differences between each pair of depth groupings (Tables 6-8). Gulf Smoothhound and Atlantic Sharpnose were the predominant driving species in each test, although they also comprised 65.4% of the total catch (Figure 22).
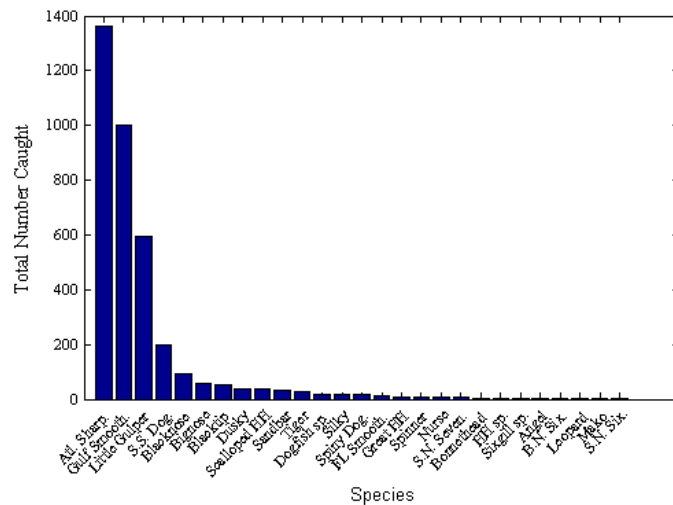
Figure 22. Catch by depth for the ten most commonly landed species, 2011-2014. Several species, including the Little Gulper and Shortspine Dogfish, were predominantly landed in deeper waters. Blacktip and Dusky were caught in some of the shallowest waters. Many species, however, were landed across a wider range of depths. The cumulative fraction of all depths sampled is given by the solid red line. No species were captured at 0 m depth because surface waters were not sampled. Horizontal steps at 73-110 m and 146-183 m result from no samples being taken at those depths and do not necessarily reflect an absence of elasmobranchs in those ranges.

Table 3. Elasmobranch species catch counts, common and scientific names. Atlantic Sharpnose and Gulf Smoothhound dominated the overall landings, together making up 65% of the total catch. The Little Gulper, though the third most captured species, was landed in a relatively small region of the study area in the Mississippi Canyon off the coast of Louisiana.

Species (Common name)	Species (Scientific name)	Total Number Caught
Atlantic Sharpnose	*Rhizoprionodon terraenovae*	1362
Gulf Smoothhound	*Mustelus sinusmexicanus*	1000
Little Gulper	*Centrophorus uyato*	594
Shortspine Dogfish	*Squalus mitsukurii*	197
Blacknose	*Carcharhinus acronotus*	94
Bignose	*Carcharhinus altimus*	57
Blacktip	*Carcharinus limbatus*	51
Dusky	*Carcharhinus obscurus*	37
Scalloped Hammerhead	*Sphyrna lewini*	36
Sandbar	*Carcharhinus plumbeus*	33
Tiger	*Galeocerdo cuvier*	29
Dogfish sp.	-	20
Silky	*Carcharhinus falciformis*	16
Spiny Dogfish	*Squalus acanthias*	16
Florida Smoothhound	*Mustelus norrisi*	13
Great Hammerhead	*Sphyrna mokarran*	9
Spinner	*Carcharhinus brevipinna*	9
Nurse	*Ginglymostoma cirratum*	8
Sharpnose Sevengill	*Heptranchias perlo*	7
Bonnethead	*Sphyrna tiburo*	5
Florida Dogfish	*Mustelus norrisi*	4
Hammerhead sp.	-	2
Sixgill sp.	-	2
Mustelus sp.	-	2
Angel	*Squatina squatina*	1
Bluntnose Sixgill	*Hexanchus griseus*	1
Leopard	*Triakis semifasciata*	1
Mako	*Isurus oxyrinchus*	1
Sharpnose Sixgill	?	1
Chain Dogfish	*Scyliorhinus retifer*	1
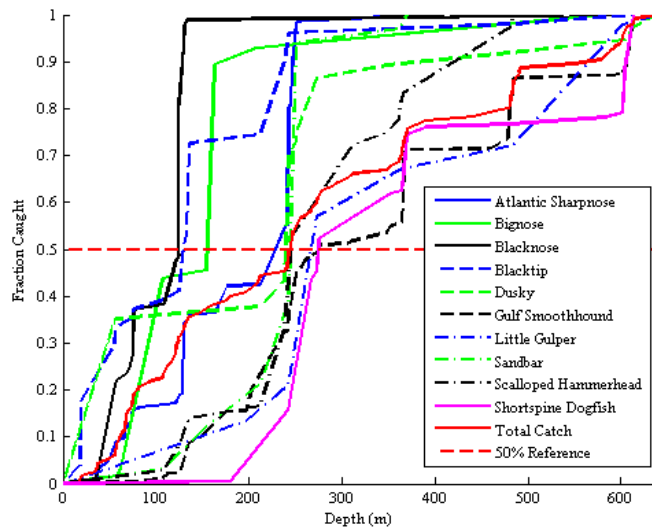
Figure 23. Total catch by species, 2011-2014. The top three species caught (Atlantic Sharpnose, Gulf Smoothhound, and Little Gulper) accounted for 82% of the total landings. Twenty-seven species comprised the remaining 18%. Five or fewer individuals were landed for 11 species.

A CAP was used to visualize the relationships between species composition and station groups, showing distinct clusters for the shallow, Group 1 stations and deepwater, Group 3 stations, with the intermediate, Group 2 stations spread throughout the space between them (Figure 23). Five axes were determined as optimal for the data, which explained 63% of the variation in species composition among the groups. Some of the most commonly caught species produced vectors with a magnitude indicative of the distinct station clusters (Figure 24). Many of the rarely caught species produced vectors of a small magnitude, resulting in a cluster of vectors around the origin; only the ten most frequently caught species were included in the published figure. Both the Little Gulper and Shortspine Dogfish distinguished deepwater, Group 3 stations, and the Atlantic Sharpnose, Blacktip, and Bignose indicated shallow, Group 1 stations. The Scalloped Hammerhead and Gulf Smoothhound species vectors distinguished the more broadly distributed cluster of intermediate, Group 2 stations, however *S. lewini* indicated those nearer or

41

intermixed with Group 1 stations, while *M. sinusmexicanus* indicated those nearer or intermixed

with Group 3 stations.

Table 4. Pairwise test results for species composition by depth grouping. The difference in species composition between all three pairs of depth groups was found to be statistically significant ($p < 0.05$). A SIMPER test was performed following these results, to determine what species were contributing to the differences between each depth group pair.

	t-statistic	Unadjusted *p*-value
Shallow vs. Intermediate	3.1478	0.0010
Shallow vs. Deep	3.7068	0.0010
Intermediate vs. Deep	2.1430	0.0010

The relationships observed in the CAP diagrams were also demonstrated by the LOO-CV

misclassification values (Table 5). Species caught at Group 1 stations had the largest percentage

of correct classifications, while Group 3 had the least. There was no misclassification between

Groups 1 and 3, however the intermediate, Group 2 catches were misidentified as belonging to

Group 1 18.2% of the time, and to Group 3 4.5% of the time. Overall, 77.8% of the catches were

correctly reassigned to their a priori groups (p=0.0010). This compares to a 38.2% classification

success using only random group allocation (p=0.0010).

Table 5. LOO-CV confusion matrix, depth groups. This table can be read along its diagonal, colored green, which gives the percentage of correct re-classification for each station group (i.e., the procedure correctly re-classified shallow stations into Group 1 86.3% of the time). Read from left to right along each row, the cells colored red give the misclassification error by group (i.e., the procedure incorrectly classified shallow stations as Group 2 13.7% of the time, and as Group 3 0.0% of the time).

Group	Shallow (1)	Intermediate (2)	Deep (3)
Shallow (1)	86.3%	13.7%	0.0%
Intermediate (2)	18.2%	77.3%	4.5%
Deep (3)	0.0%	38.5%	61.5%
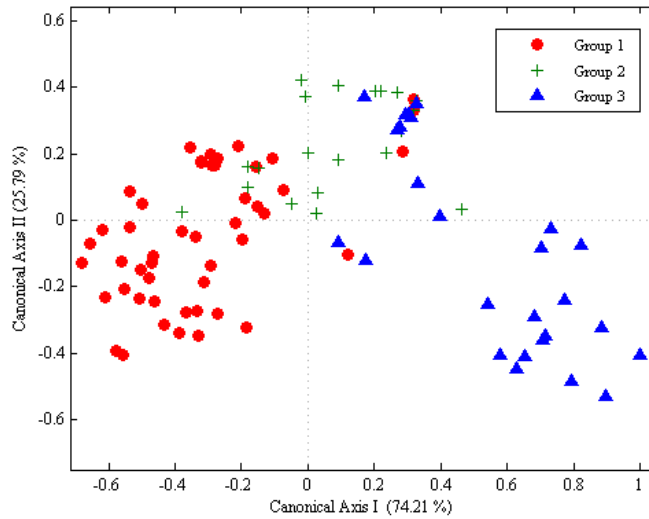
Figure 24. Canonical discriminate analysis ordination, depth groupings. While the shallow, Group 1 stations and deep, Group 3 stations both have independent, distinct clusters, the intermediate stations of Group 2 have a less distinct cluster that intermixes with the edges of the other two clusters as well.

Figure 25. Canonical discriminate analysis vector bi-plot, top ten catches, depth groupings. When viewed concurrently with Figure 21, species vector directions indicate which group of points each variable (species) is indicative of. Larger vectors show a greater influence. For example, the Little Gulper and Shortspine Dogfish vectors both point into the lower right quadrant of the graph, where a cluster of Group 3 stations is located in Figure 21. Both the Blacknose and Bignose vectors point towards a cluster of Group 1 stations, but the Blacknose vector is much larger, showing that species has a stronger effect on that cluster.

43

Station Groupings by Location

The differences between species compositions when stations were grouped by location were also found to be significant ($F = 2.765$, $p = 0.001$) using a second NP-MANOVA test. The pairwise test returned significant differences among all three possible pairs of *a priori* groups (Table 9) and a SIMPER analysis determined which species contributed the most to these differences (Tables 10-12). Nine axes were determined as optimal for the data, which explained 84% of the variation in species composition among the groups. Once again, Gulf Smoothhound and Atlantic Sharpnose were the predominant drivers of differences among the groups.

Table 9. Pairwise test results for species composition by location. The difference in species composition between all three pairs of station groups was found to be statistically significant ($p < 0.05$). A SIMPER test was performed following these results, to determine what species were contributing to the differences between each station group pair.

	t-statistic	Unadjusted *p*-value
WFS vs. EGOM	1.7573	0.0040
WFS vs. WGOM	1.8589	0.0010
EGOM vs. WGOM	1.4256	0.0280

The CAP ordination plot showed overlap with all three location groupings, despite the significant differences among them (Figure 25). Bignose distinguished the WFS, although species such as the Blacknose and Sandbar were also indicative of these stations (Figure 26). Several species distinguished the broad cluster of EGOM stations, including the Atlantic Sharpnose, Blacktip, Dusky, Little Gulper, and Scalloped Hammerhead. Gulf Smoothhound and Shortspine Dogfish were indicative of the WGOM stations. Again, due to a non-descriptive cluster of rarely landed species around the origin, only the ten most commonly landed species were included in the published figure.
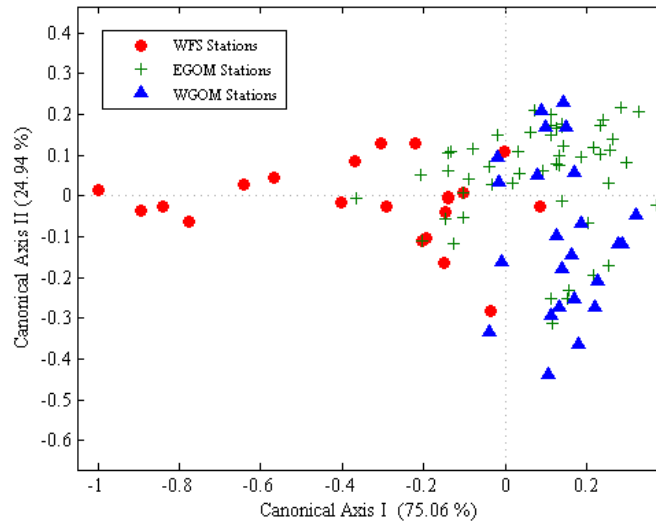
Figure 26. Canonical discriminate analysis ordination, by location. Note the much greater intermixing compared to the CAP for depth groups. Although a pairwise test returned significant differences in the species composition for all three possible group pairings, EGOM and WGOM stations plot together in one large cluster, along with several WFS stations. Only 6 WFS stations appear independent of the larger cluster.
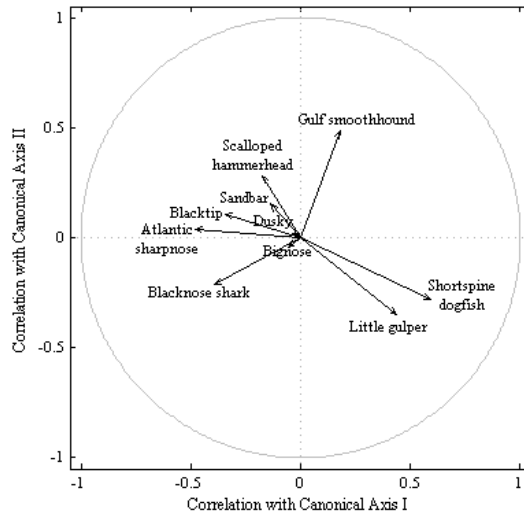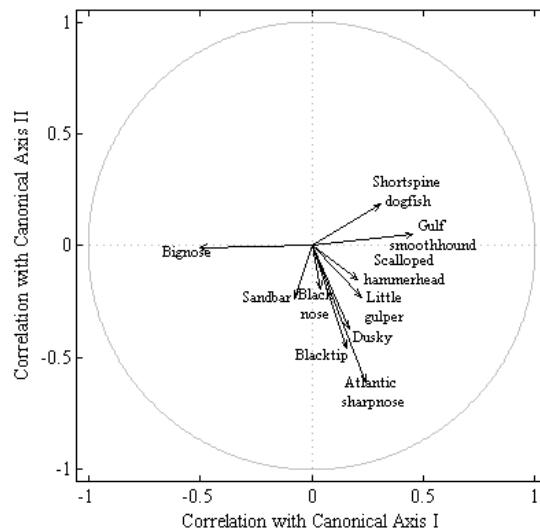

Figure 27. Canonical discriminate analysis vector bi-plot, top ten catches, by location. When viewed concurrently with Figure 23, species vector directions indicate which group of points each variable (species) is indicative of. Larger vectors show a greater influence. For example, the Bignose vector points to the left at a right angle, where small cluster of WFS stations is located in Figure 23. The Shortspine Dogfish and Gulf Smoothhound vectors point towards the upper right quadrant, where EGOM stations dominated the larger cluster, while several species vectors point to the lower left, which is comprised predominately of WGOM stations.

45

This overlap of station clusters was also demonstrated by the LOO-CV misclassification values (Table 13). Species caught on the WFS had the largest percentage of correct classifications, while species caught in the WGOM had the least. Catches in the EGOM were moderately confused with both the WFS (24.1%) and WGOM (16.7%), while the WGOM catches were predominantly confused with those in the EGOM (37.5%). Overall, 63.64% of the catches were correctly reassigned to their a priori groups ($p = 0.0010$). This compares to a 40.13% classification success using only random group allocation ($p = 0.0010$).

Table 13. LOO-CV confusion matrix, by location. This table can be read along its diagonal, colored green, which gives the percentage of correct re-classification for each station group (i.e., the procedure correctly re-classified WFS stations into Group 1 81.0% of the time). Read from left to right along each row, the cells colored red give the misclassification error by group (i.e., the procedure incorrectly classified WFS stations as Group 2 9.5% of the time, and as Group 3 9.5% of the time).

Group	WFS (1)	EGOM (2)	WGOM (3)
WFS (1)	81.0%	9.5%	9.5%
EGOM (2)	24.1%	59.3%	16.7%
WGOM (3)	4.2%	37.5%	58.3%

Discussion

Station Groupings by Depth

Elasmobranch species groups do appear to change with increasing depth. These associations were driven by a small number of frequently encountered species such as the Atlantic Sharpnose, Gulf Smoothhound, and Spiny Dogfish; some cosmopolitan species, such as the Scalloped Hammerhead and Sandbar, were captured across a broad range of depths, and less indicative of a particular depth grouping. As shown in the CAP ordination and vector bi-plot, each depth grouping was indicated by two to three species whose vectors had a large, positive magnitude towards each station group cluster.

A subdivision appears to exist within the Group 2 station cluster. Although this group had a species composition significantly different from the other two, the CAP ordination shows an overlap with both the Group 1 and Group 3 clusters. Group 2 points which plotted near or among Group 1 stations were indicated by the Scalloped Hammerhead species vector. The Gulf Smoothhound species vector extends towards Group 2 points which clustered near or among Group 3 stations. This division could be due in part to how stations were grouped. Average depth was calculated using measurements taken at set-out and haul-back, so if sampling took place over a depth gradient of tens or hundreds of meters, then the average depth may classify a station as Group 2 despite actually sampling waters in the shallow or deep categories as well. This was an infrequent occurrence, however: only 4 out of 115 stations sampled across depth groups. The more likely contributors to this observed overlap of depth groups were cosmopolitan species of shark that were recorded across two or more depth groupings.

These vectors clarify the percent contributions of species to the dissimilarities between each pair of depth groupings. Species whose vectors distinguished Groups 1 and 3 were also some of the largest contributors to the dissimilarity between those two groups. The same agreement occurs in the SIMPER results for Groups 1 and 2, and Groups 2 and 3, with the species with large contribution percentages to the dissimilarity also producing distinguishing species vectors.

The occurrence of these species as indicators for their respective depth groupings agrees with what is known about their biology. Atlantic Sharpnose, Blacktip, and Blacknose are all described as shallow water, coastal sharks, with the Blacktip also known to occupy surface waters offshore (Castro 2011). Adult Scalloped Hammerheads are found offshore, although they are also believed to be migratory and perform daily "yo-yo" movements within the water column

from the surface to depths exceeding 400 m (Klimley 1993). The habits of the Gulf Smoothhound, another indicator species for Group 2, are less well-known, but it has a reported depth range of 36-229 m in the Gulf of Mexico (Castro 2011). Both Group 3 indicator species, the Shortspine Dogfish and Little Gulper, are deepwater species of shark (Castro 2011).

Although the groups were all characterized by species naturally occurring within each depth range, that measure alone cannot predict the presence of a particular species or the general composition of the elasmobranch community. Stations were correctly classified into their *a priori* groups 77.8% of the time by a LOO-CV procedure ($p = 0.0010$), compared to a 38.2% success rate with random allocation ($p = 0.0010$). Correct assignments to Group 1 accounted for over two-thirds of the success of random group assignments; such a large proportion may be expected when Group 1 stations accounted for nearly half of all sampling locations. No one parameter can be used to fully predict the spatial-temporal occurrence of a species, although depth does appear to be a large influence.

The confusion in group assignment mostly concerns misclassification into or out of the intermediate depths comprising Group 2, reflective of the overlap of stations in that group with both the shallow and deepwater station clusters in the CAP ordination. While the issue of group assignment by average depth, addressed previously, could contribute to the misclassification error, a number of biological and environmental factors not quantified in this study could also influence an individual's location in the water column at time of capture. Migrations are common for many species of shark and they may traverse a wide depth range on a daily (in the case of the Scalloped Hammerhead) or seasonal basis (Speed et al. 2010). Similar behaviors on short timescales could make it possible to catch a species at multiple stations falling in two or

more of the depth categories, which can lead to overlap between the station groups when plotted according to community composition.

Station Groupings by Location

Visual inspection indicates a greater amount of overlap in the CAP scatterplot when stations are grouped according to geographic location rather than depth. There were, however, still statistically significant differences between the species compositions of each of the three groups. Since the results discussed above show depth to be a determining factor in the composition of elasmobranch communities in the Gulf, its effects might also help explain the patterns seen when stations are instead grouped according to geographic location.

The WGOM stations were predominantly indicated by pelagic shark species, with an average station depth of 200 m. The Little Gulper served as an exception, explained by the Mississippi Canyon sites located in this geographic region. EGOM sites had a greater average depth of 298 m and were instead distinguished by benthopelagic species. The WFS stations had the shallowest average depth, 183 m, and were indicated by the "bottom-dwelling" Bignose (Castro 2011). Although these stations were some of the shallowest, according to average depth, sampling transects on the WFS followed pipelines running along the shelf floor or other benthic features of interest, targeting species found at or near the bottom.

Stations in this analysis were most often confused with those in an adjacent region, i.e. WFS stations were most confused with EGOM stations. Located between the WFS and WGOM, EGOM stations were moderately confused with both neighboring areas. Given the movement and migration habits of many elasmobranch species, discussed above, a species' range might include two or more of the geographic regions sampled, contributing to the observed group overlap. While the LOO-CV procedure correctly re-classified 40.1% of stations into their *a*

priori groups using random assignments, both the WFS and WGOM stations were correctly re-classified by the LOO-CV less than 6% of the time. The EGOM stations made up 74% of the correct re-classifications and also comprised more than half of all the stations sampled.

All of the cruises included in this study took place during the summer months. Sampling during the fall or winter, when sea surface temperatures can drop below 24°C, compared to summertime highs of 28-30°C, could possibly show changes in the species assemblages (NOAA 2014). While a species may have a large distribution range within the Gulf, migratory behavior may cause seasonal restrictions to that range, leading to seasonal or annual shifts in assemblages. Species may also be more cosmopolitan with regards to geographic range compared to depth, which could explain the greater cluster overlap when stations were grouped according to location. Life history traits, such as ontogenetic habitat shifts and prey availability can also influence the prevalence of a species within its range. Segregation by sex and the utilization of nursery habitat may change the predominant age or sex of a species within an assemblage, an important consideration for management efforts seeking to reduce mortality for juveniles or sexually mature age classes.

Shark species may have similar responses to pressures such as increased mortality from fishery by-catch and pollution events. Identifying the occurrence and composition of elasmobranch communities throughout the Gulf of Mexico can help researchers predict and quantify the effects of these disturbances on individual species, along with the community as a whole. Should a species, or age or sex classes within a species, be differentially affected by a disturbance event this could manifest in changes to the assemblage composition.

The composition of the shark community in the Northern Gulf of Mexico varies with depth, as evidenced by the three significantly difference assemblages described here. These

patterns are driven by a few species that were caught with a high frequency, and may change across space or time. Other factors not addressed here, such as salinity, temperature, life history traits, or prey availability, can also influence patterns of occurrence in the elasmobranch community. The migratory nature of many species can lead to their capture in two or more pre-assigned depth categories, leading to some overlap between the groups as well. Year-round sampling to include the spring, fall, and winter months would be of great use and help build an understanding of how the elasmobranch community changes on annual or multi-year timescales. Knowledge of these species assemblages, and how they may change through space and time, is an important tool as we continue to work towards responsible ecosystem-level management and conservation in the Gulf of Mexico.

Table 6. SIMPER results, shallow versus intermediate depth groups. Shallow water and pelagic species were some of the highest contributors, by percent, to the differences between the two groups.

Species (Common name)	Percent contribution	Cumulative percent contribution
Gulf smoothhound	30.87%	30.87%
Atlantic sharpnose shark	25.80%	56.67%
Blacknose shark	7.34%	64.01%
Scalloped hammerhead	5.36%	69.37%
Tiger shark	5.04%	74.41%
Blacktip shark	4.35%	78.76%
Bignose shark	4.23%	83.00%
Sandbar shark	2.98%	85.98%
Silky shark	2.39%	88.37%
Nurse shark	2.23%	90.59%
Dusky shark	1.99%	92.58%
Dogfish sp.	1.24%	93.82%
Spinner shark	1.19%	95.01%
Great hammerhead	1.16%	96.18%
Shortspine dogfish	0.95%	97.13%
Spiny dogfish	0.70%	97.83%
Bonnethead shark	0.68%	98.51%
Florida smoothhound	0.37%	98.88%
Hammerhead shark sp.	0.31%	99.18%
Mako shark	0.25%	99.43%
Mustelus sp.	0.24%	99.68%
Sixgill sp.	0.23%	99.91%
Florida dogfish	0.09%	100.00%
Angel shark	0.00%	100.00%
Bluntnose sixgill	0.00%	100.00%
Leopard shark	0.00%	100.00%
Little gulper	0.00%	100.00%
Sharpnose sevengill	0.00%	100.00%
Sharpnose sixgill	0.00%	100.00%
Chain dogfish	0.00%	100.00%

Table 7. SIMPER results, shallow versus deep depth groups. Shallow and deep water species were some of the highest contributors, by percent, to the differences between the two groups.

Species (Common name)	Percent contribution	Cumulative percent contribution
Atlantic sharpnose shark	21.41%	21.41%
Gulf smoothhound	17.95%	39.36%
Little gulper	13.07%	52.43%
Shortspine dogfish	12.56%	65.00%
Blacknose shark	5.74%	70.74%
Tiger shark	3.43%	74.17%
Blacktip shark	3.28%	77.45%
Bignose shark	3.15%	80.60%
Spinner shark	2.68%	83.28%
Silky shark	2.38%	85.66%
Dusky shark	2.10%	87.76%
Sharpnose sevengill	1.85%	89.62%
Nurse shark	1.74%	91.36%
Spiny dogfish	1.39%	92.75%
Florida smoothhound	1.30%	94.05%
Sandbar shark	1.09%	95.14%
Dogfish sp.	0.99%	96.13%
Scalloped hammerhead	0.99%	97.12%
Florida dogfish	0.67%	97.79%
Bonnethead shark	0.55%	98.35%
Hammerhead shark sp.	0.25%	98.60%
Angel shark	0.25%	98.85%
Sixgill sp.	0.25%	99.09%
Mustelus sp.	0.20%	99.30%
Bluntnose sixgill	0.19%	99.49%
Leopard shark	0.15%	99.64%
Sharpnose sixgill	0.15%	99.78%
Chain dogfish	0.15%	99.93%
Great hammerhead	0.07%	100.00%
Mako shark	0.00%	100.00%

Table 8. SIMPER results, intermediate versus deep depth groups. Pelagic and deep water species were some of the highest contributors, by percent, to the differences between the two groups.

Species (Common name)	Percent contribution	Cumulative percent contribution
Gulf smoothhound	30.74%	30.74%
Shortspine dogfish	16.69%	47.43%
Little gulper	16.47%	63.90%
Scalloped hammerhead	5.11%	69.00%
Atlantic sharpnose shark	4.32%	73.32%
Silky shark	3.87%	77.20%
Spinner shark	3.22%	80.42%
Spiny dogfish	2.50%	82.92%
Sharpnose sevengill	2.49%	85.40%
Bignose shark	2.31%	87.71%
Sandbar shark	1.95%	89.67%
Dusky shark	1.84%	91.50%
Tiger shark	1.70%	93.20%
Florida smoothhound	1.31%	94.52%
Great hammerhead	1.15%	95.67%
Blacktip shark	0.97%	96.63%
Florida dogfish	0.83%	97.46%
Blacknose shark	0.64%	98.11%
Sixgill sp.	0.54%	98.65%
Angel shark	0.31%	98.96%
Mako shark	0.27%	99.23%
Bluntnose sixgill	0.24%	99.47%
Leopard shark	0.18%	99.64%
Sharpnose sixgill	0.18%	99.82%
Chain dogfish	0.18%	100.00%
Bonnethead shark	0.00%	100.00%
Dogfish sp.	0.00%	100.00%
Hammerhead shark sp.	0.00%	100.00%
Nurse shark	0.00%	100.00%
Mustelus sp.	0.00%	100.00%

Table 10. SIMPER results, WFS versus EGOM stations. The Bignose was the only species vector produced by the CAP routine to indicate an isolated cluster of WFS stations, agreeing with its SIMPER ranking as the third-highest contributor to differences between these two groups.

Species (Common name)	Percent contribution	Cumulative percent contribution
Gulf smoothhound	23.14%	23.14%
Atlantic sharpnose shark	16.64%	39.78%
Bignose shark	8.44%	48.22%
Blacknose shark	7.14%	55.36%
Tiger shark	6.59%	61.95%
Shortspine dogfish	6.04%	67.99%
Nurse shark	4.05%	72.04%
Sandbar shark	3.58%	75.63%
Scalloped hammerhead	2.91%	78.54%
Little gulper	2.78%	81.32%
Dogfish sp.	2.66%	83.98%
Blacktip shark	2.41%	86.39%
Silky shark	2.32%	88.71%
Dusky shark	2.23%	90.93%
Spinner shark	1.73%	92.66%
Bonnethead shark	1.48%	94.14%
Florida smoothound	1.19%	95.33%
Spiny dogfish	1.17%	96.50%
Sharpnose sevengill	0.89%	97.39%
Hammerhead shark sp.	0.53%	97.92%
Great hammerhead	0.50%	98.42%
Florida dogfish	0.48%	98.90%
Sixgill shark	0.25%	99.15%
Mustelus sp.	0.24%	99.39%
Angel shark	0.15%	99.54%
Mako shark	0.11%	99.65%
Bluntnose sixgill	0.11%	99.76%
Leopard shark	0.08%	99.84%
Sharpnose sixgill	0.08%	99.92%
Chain dogfish	0.08%	100.00%

Table 11. SIMPER results, WFS versus WGOM stations. The Little Gulper was such a large contributor to the differences between these two groups because of its isolated incidence at Mississippi Canyon stations located in the WGOM. The Bignose was also the only species vector produced by the CAP routine to indicate an isolated cluster of WFS stations.

Species (Common name)	Percent contribution	Cumulative percent contribution
Atlantic sharpnose shark	25.28%	25.28%
Gulf smoothhound	19.66%	44.93%
Little gulper	10.90%	55.83%
Bignose shark	6.26%	62.09%
Blacktip shark	5.87%	67.96%
Blacknose shark	4.90%	72.86%
Shortspine dogfish	4.67%	77.53%
Tiger shark	4.54%	82.07%
Nurse shark	2.80%	84.88%
Dusky shark	2.17%	87.05%
Sandbar shark	2.16%	89.20%
Dogfish sp.	2.06%	91.26%
Silky shark	2.01%	93.27%
Spinner shark	1.83%	95.09%
Scalloped hammerhead	1.61%	96.71%
Bonnethead shark	1.18%	97.88%
Florida smoothound	0.73%	98.62%
Sharpnose sevengill	0.66%	99.28%
Hammerhead shark sp.	0.54%	99.82%
Great hammerhead	0.18%	100.00%
Angel shark	0.00%	100.00%
Bluntnose sixgill	0.00%	100.00%
Leopard shark	0.00%	100.00%
Mako shark	0.00%	100.00%
Sharpnose sixgill	0.00%	100.00%
Sixgill shark	0.00%	100.00%
Spiny dogfish	0.00%	100.00%
Chain dogfish	0.00%	100.00%
Florida dogfish	0.00%	100.00%
Mustelus sp.	0.00%	100.00%

Table 12. SIMPER results, EGOM versus WGOM stations. The Little Gulper was such a large contributor to the differences between these two groups because of its isolated incidence at Mississippi Canyon stations located in the WGOM.

Species (Common name)	Percent contribution	Cumulative percent contribution
Atlantic sharpnose shark	26.36%	26.36%
Gulf smoothhound	22.95%	49.32%
Little gulper	12.60%	61.92%
Shortspine dogfish	8.28%	70.20%
Blacktip shark	5.66%	75.86%
Blacknose shark	5.22%	81.08%
Scalloped hammerhead	3.04%	84.12%
Silky shark	2.57%	86.69%
Spinner shark	2.55%	89.24%
Tiger shark	2.34%	91.58%
Dusky shark	2.20%	93.78%
Sharpnose sevengill	1.21%	94.99%
Spiny dogfish	0.92%	95.91%
Sandbar shark	0.72%	96.63%
Florida smoothound	0.70%	97.33%
Great hammerhead	0.58%	97.92%
Bignose shark	0.35%	98.26%
Florida dogfish	0.34%	98.60%
Nurse shark	0.31%	98.91%
Sixgill shark	0.21%	99.13%
Mustelus sp.	0.20%	99.32%
Hammerhead shark sp.	0.14%	99.46%
Angel shark	0.12%	99.58%
Mako shark	0.10%	99.68%
Bluntnose sixgill	0.10%	99.78%
Leopard shark	0.07%	99.85%
Sharpnose sixgill	0.07%	99.93%
Chain dogfish	0.07%	100.00%
Bonnethead shark	0.00%	100.00%
Dogfish sp.	0.00%	100.00%

LITERATURE CITED

Bañon, R., Pineiro, C., Casas, M. (2006). Biological aspects of deep-water sharks *Centroscymnus coelolepis* and *Centrophorus squamosus* in Galician waters (north-western Spain). J. Mar. Biol. Ass. U.K. 86: 843-846.

Bonfil, R. (1997). Status of shark resources in the Southern Gulf of Mexico and Caribbean: implications for management. Fish. Res. 29: 101-117. DOI: 10.1016/S0165-7836(96)00536-X.

Bonham, K., Sanford, F.B., Welden, B.A. (1949). Biological and vitamin A studies of dogfish landed in the State of Washington (*Squalus suckleyi*). Biological Report of Washington Department of Fisheries 49A:83-113.

Cailliet, G., Musick, J. A., Simpfendorfer, C. A., Stevens, J. D. (2005). Ecology and life history characteristics of chondrichthyan fish. Sharks, Rays and Chimeras: The Status of the Chondrichthyan Fishes. Status Survey. S. L. Fowler, Cavanagh, R.D., Camhi, M., Burgess, G.H., Fordham, S.V., Simpfendorfer, C.A., and Musick, J.A. Gland, Switzerland, IUCN/SSC Shark Specialist Group: 12-18.

Carlson, J. K., Brusher, J.H. (1999). An index of abundance for coastal species of juvenile sharks from the northeast Gulf of Mexico. Mar. Fish. Rev. 61(3): 37-25.

Castro, J. I. (2011). The Sharks of North America. New York, Oxford University Press.

Churchill, D. A., Heithaus, M. R., Vaudo, J. J., Grubbs, R. D., Gastrich, K., Castro, J. I. (2014). Trophic interactions of common elasmobranchs in deep-sea communities of the Gulf of Mexico revealed through stable isotope and stomach content analysis. Deep-Sea Res. Pt. II. In press. DOI: 10.1016/j.dsr2.2014.10.011.

Clarke, M. W., Connolly, P. L., Bracken, J. J. (2001). Aspects of reproduction of the deep water sharks *Centroscymnus coelolepis* and *Centrophorus squamosus* from west of Ireland and Scotland. J. Mar. Biol. Ass. U.K. 81: 1019-1029. DOI: 10.1017/S0025315401005008.

Clarke, M., Connolly, P.L., Bracken, J.J. (2002*b*). Age estimation of the exploited deepwater shark *Centrophorus squamosus* from the continental slopes of the Rockall Trough and Porcupine Bank. J. Fish Biol. 60(3): 501-514. DOI: 10.1006/jfbi.2001.1861.

Clarke, M., Connolly, P.L., Bracken, J.J. (2002*a*). Catch, discarding, age estimation, growth and maturity of the squalid shark *Deania calceus* west and north of Ireland. Fish. Res. 56: 139-153. DOI: 10.1016/S0165-7836(01)00419-2.

Compagno, L. J. V. (2005). Sharks of the World. Princeton, NJ, Princeton University Press.

Cortes, E. (2002). Stock Assessment of Small Coastal Sharks in the U.S. Atlantic and Gulf of Mexico. NOAA. 133 pp.

Cotton, C. F., Andrews, A. H., Cailliet, G. M., Grubbs, R. D., Irvine, S. B., Musick, J. A. (2014). Assessment of radiometric dating for age validation of deep-water dogfish (Order: Squaliformes) finspines. Fish. Res. 151: 107-113. DOI: 10.1016/j.fishres.2013.10.014.

Daley, R. K., Appleyard, S. A., Koopman, M. (2012). Genetic catch verification to support recovery plans for deepsea gulper sharks (genus *Centrophorus*, family Centrophoridae) - an Australian example using the 16S gene. Mar. Freshwater Res. 63(8): 708-714. DOI: 10.1071/MF11264.

Etnoyer, P., Warrenchuk, J. (2007). A catshark nursery in a deep gorgonian field in the Mississippi Canyon, Gulf of Mexico. B. Mar. Sci. 81(3): 553-559.

Fahy, E. (1989). The spurdog *Squalus acanthias* (L) fishery in south west Ireland. Irish Fisheries Investigations, Series B (Marine), No. 32. Dublin: Department of the Marine. 22 pp.

Figueiredo, I., Moura, T., Neves, A., Gordo, L. S. (2008). Reproductive strategy of leafscale gulper shark *Centrophorus squamosus* and the Portuguese dogfish *Centroscymnus coelolepis* on the Portuguese continental slope. J. Fish Biol. 73(1): 206-225.

Garcia, V. B., Lucifora, L. O., Myers, R. A. (2008). The importance of habitat and life history to extinction risk in sharks, skates, rays and chimaeras. Proc. Biol. Sci. 275(1630): 83-89. DOI: 10.1098/rspb.2007.1295.

Girard M., De Buit, M. H. (1999). Reproductive biology of two deep-water sharks from the British Isles, *Centroscymnus coelolepis* and *Centrophorus squamosus* (Chondrichthyes: Squalidae). J. Mar. Biol. Ass. U.K. 79: 923-931. DOI: 10.1017/S002531549800109X.

Grace, M., Henwood, T. (1997). Assessment of the distribution and abundance of coastal sharks in the US Gulf of Mexico and eastern seaboard, 1995 and 1996. Mar. Fish. Rev. 59(4): 23-32.

Henderson, A.C., Flannery, K., Dunne, J. (2002). Growth and Reproduction in Spiny Dogfish *Squalus acanthias* L. (Elasmobranchii: Squalidae), from the West Coast of Ireland. Sarsai. 87(5): 350-361. DOI: 10.1080/00364820210000155805

Henry, L.A., Navas, J. M., Hennige, S. J., Wicks, L. C., Vad, J., Roberts, J. M. (2013). Cold-water coral reef habitats benefit recreationally valuable sharks. Biol. Conserv. 161: 67-70. DOI: 10.1016/j.biocon.2013.03.002.

Heupel, M. R., Carlson, J.K., Simpfendorfer, C.A. (2007). Shark nursery areas: concepts, definition, characterization and assumptions. Mar. Ecol. Prog. Ser. 337: 287-297. DOI: 10.3354/meps337287.

Holden, M.J., Meadows, P.S. (1962). The structure of the spine of the spur dogfish (*Squalus acanthias* L.) and its use for age determination. J. Mar. Biol. Ass. U.K. 42(2): 179-197. DOI: 10.1017/S0025315400001302.

Jackson, J. B., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H., Cooke, R., Erlandson, J., Estes, J. A., Hughes, T. P., Kidwell, S., Lange, C. B., Lenihan, H. S., Pandolfi, J. M., Peterson, C. H., Steneck, R. S., Tegner, M. J., Warner, R. R. (2001). Historical overfishing and the recent collapse of coastal ecosystems. Science 293(5530): 629-637. DOI: 10.1126/science.1059199.

Jones, D. L. (2014). Fathom Toolbox for Matlab: software for multivariate ecological and oceanographic data analysis. College of Marine Science, University of South Florida, St. Petersburg, FL, USA. Available from: http://www.marine.usf.edu/user/djones/.

Ketchen, K.S. (1975). Age and growth of the dogfish (Squalus acanthias) in British Columbia waters. Journal of the Fisheries Research Board of Canada. 32:43-58.

Klimley, A. P. (1987). The determinants of sexual segregation in the scalloped hammerhead shark, *Sphyrna lewini*. Environ. Biol. Fish. 18(1): 27-40. DOI: 10.1007/BF00002325.

Klimley, A. P. (1993). Highly directional swimming by scalloped hammerhead sharks, *Sphyrna lewini*, and subsurface irradiance, temperature, bathymetry, and geomagnetic field. Mar. Biol. 117: 1-22. DOI: 10.1007/BF00346421.

Mackay, D., Moreau, J. (1990). A Note on the Inverse Function of the von Bertalanffy Growth Function. Algorithms. 36(7.75): 28-31.

Massutí, E., Moranta, J. (2003). Demersal assemblages and depth distribution of elasmobranchs from the continental shelf and slope off the Balearic Islands (western Mediterranean). ICES J. Mar. Sci. 60(4): 753-766. DOI: 10.1016/S1054-3139(03)00089-4.

Mucientes, G. R., Queiroz, N., Sousa, L. L., Tarroso, P., Sims, D. W. (2009). Sexual segregation of pelagic sharks and the potential threat from fisheries. Biol. Lett. 5(2): 156-159. DOI: 10.1098/rsbl.2008.0761.

Nammack, M.F., Musick, J.A., Colvocoresses, J.A. (1985). Life history of the spiny dogfish off the northeastern United States. T. Am. Fish. Soc. 114:367-376. DOI: 10.1577/1548-8659(1985)114%3C367:LHOSDO%3E2.0.CO;2.

National Oceanic and Atmospheric Administration (NOAA) (2014). Gulf of Mexico SST Time Series. <http://www.aoml.noaa.gov/phod/regsatprod/gom/sst_ts.php>

National Marine Fisheries Service (NMFS) (2006). Consolidated Atlantic Highly Migratory Species Fishery Management Plan. U.S. Department of Commerce. 1629 pp.

Naylor, G. J. P., Caira, J.N., Jensen, K., Rosansa, A. M., White, W. T., Last, P. R. (2012). A DNA Sequence–Based Approach to the Identification of Shark and Ray Species and Its Implications for Global Elasmobranch Diversity and Parasitology. B. Am. Mus. Nat. Hist. 367: 1-262. DOI: 10.1206/754.1.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres Jr., F. (1998). Fishing Down Marine Food Webs. Science 279(5352): 860-863. DOI: 10.1126/science.279.5352.860.

Rigby, C., Simpfendorfer, C. A. (2013). Patterns in life history traits of deep-water chondrichthyans. Deep-Sea Res. Pt. II. DOI: 10.1016/j.dsr2.2013.09.004.

Severino, R. B., Afonso-Dias, I., Delgado, J., Afonso-Dias, M. (2009). Aspects of the biology of the leaf-scale gulper shark *Centrophorus squamosus* (Bonnaterre, 1788) off Madeira archipelago. Arquipelago. Life and Marine Sciencs. 26: 57-61.

Sims, D. W. (2005). Differences in habitat selection and reproductive strategies of male and female sharks. In: Sexual segregation in vertebrates: ecology of the two sexes. Eds. Ruckstuhl, K. E., Neuhaus, P. Cambridge U.K., Cambridge University Press: 127-147.

Speed, C. W., Field, I. C., Meekan, M. G., Bradshaw, C. J. A. (2010). Complexities of coastal shark movements and their implications for management. Mar. Ecol. Prog. Ser. 408: 275-293. DOI: 10.3354/meps08581.

Springer, Stewart (1967). Social organization of shark populations. In: Sharks, skates and rays Eds. Gilbert, P. W., Mathewson, R. F., Rall, D. P. Baltimore, M.D., The Johns Hopkins Press : 149-174.

Stevens, J. D., Bonfil, R., Dulvy, N. K., Walker, P. A. (2000). The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. ICES J. Mar. Sci. 57(3): 476-494. DOI: 10.1006/jmsc.2000.0724.

von Bertalanffy, L. (1934). Untersuchungen über die Gesetzlichkeiten de Wachstums I. Allgemeine Grundlagen der Theorie, mathematische und physiologische Gesetzlichkeiten des Wachstum bei Wassertieren. Roux Arch. Entwicklungsmech 131:613-652.

Ward, R. D., Zemlak, T. S., Innes, B. H., Last, P. R., Hebert, P. D. N. (2005). DNA barcoding Australia's fish species. Philos. Trans. R. Soc. Lond. B. 360(1462): 1847-1857. DOI: 10.1098/rstb.2005.1716

Wearmouth, V. J., Sims, D. W. (2008). Sexual segregation in marine fish, reptiles, birds and mammals: behavior patterns, mechanisms, and conservation implications. Adv. Mar. Biol. 54: 107-170.

White, W. T., Dharmadi (2010). Aspects of maturation and reproduction in hexanchiform and squaliform sharks. J. Fish. Biol. 76(6): 1362-1378. DOI: 10.1111/j.1095-8649.2010.02560.x.

White, W. T., Potter, I. C. (2004). Habitat partitioning among four elasmobranch species in nearshore, shallow waters of a subtropical embayment in Western Australia. Mar. Biol. 145(5): 1023-1032. DOI: 10.1007/s00227-004-1386-7.