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Deepwater Horizon Impacts on the Diet, Growth, and Condition of Larval Spanish Mackerel (*Scomberomerus maculatus*)

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DEEPWATER HORIZON IMPACTS ON THE DIET, GROWTH, AND CONDITION OF LARVAL SPANISH MACKEREL (*SCOMBEROMORUS MACULATUS*)

by

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ABSTRACT

DEEPWATER HORIZON IMPACTS ON THE DIET, GROWTH, AND CONDITION OF LARVAL SPANISH MACKEREL (*SCOMBEROMORUS MACULATUS*)

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The Deepwater Horizon oil spill (DWHOS) coincided with the pelagic larval stages of many valued commercial and recreational fishes in the northern Gulf of Mexico. Larval fish survival and eventual recruitment into adult populations may have been impacted by changes in the planktonic food web caused by the release of oil and chemical dispersants during the DWHOS event. Using samples from a long-term ichthyoplankton survey off the coast of Alabama, I sought to resolve the effects of the DWHOS on larval fishes. I compared the condition, growth, and diet of larval Spanish Mackerel (*Scomberomorus maculatus*), collected during summer months in years before (2007–2009), during (2010) and after (2011) the DWHOS. Comparisons of condition using morphometric analyses and length-weight relationships revealed that larvae were deeper-bodied and heavier during the DWHOS period relative to before and after spill periods. The most abundant prey items of larval *S. maculatus* were larval fishes, copepods, and ostracods. Diet composition did not differ significantly among the three time periods. Also, daily growth did not differ between larvae collected during and after the DWHOS (no otoliths were available to estimate growth before 2010). Overall, larval *S. maculatus* were resilient to harmful effects of the DWHOS. These findings will help fisheries managers better understand the impacts of the DWHOS on fisheries in the northern Gulf of Mexico.

DEDICATION

Dedicated to Ruthy, for all of her love and support

ACKNOWLEDGMENTS

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LIST OF ABBREVIATIONS

nGOM	northern Gulf of Mexico
DWHOS	Deepwater Horizon oil spill
PAHs	polycyclic aromatic hydrocarbons
NL	notochord length
NMS	nonmetric multidimensional scaling
C	carbon
N	nitrogen

CHAPTER I

INTRODUCTION

On April 20, 2010 British Petroleum's Deepwater Horizon oil rig exploded and two days later sank on site at a location approximately 150 km south-southwest of Dauphin Island, Alabama. During the following 87 days, the wellhead released about 4.1 million barrels of crude oil and 205,000 mT of methane and other gases into the northern Gulf of Mexico (nGOM; Adcroft et al. 2010, McNutt et al. 2011). At its peak, the surface oil slick covered 180,000 km^2 and oiling was reported on over 950 miles of coastline from Texas to Florida during the summer of 2010 (Norse & Amos 2010, National Ocean Service NOAA 2011). The Deepwater Horizon oil spill (DWHOS) is now the largest accidental oil spill in history (National Commission 2011), and the resiliency of the nGOM ecosystem to the oil spill and application of chemical dispersant remain largely unknown. Large petroleum spills can have both direct and indirect impacts on marine organisms. Direct effects include physical actions (e.g., loss of light, smothering; Albers 2003), and exposure to toxic compounds (e.g., death, mutations; Mitra et al. 2012) which can be lethal for marine organisms. Indirect impacts include habitat alterations (Silliman et al. 2012, Powers et al. 2013) and food web alterations (Abbriano et al. 2011), which may have chronic sub-lethal effects.

In addition to the released crude oil, methane, and other gases, chemical dispersants were used extensively during the DWHOS to accelerate weathering and biological consumption of the oil. Despite the presumed benefits of dispersants, numerous studies show that they increase toxicity of the oil by 2–3 times as compared to the exposures to oil alone, and they increase the contact between oil and marine

organisms by enabling oil to mix throughout the water column (Hemmer et al. 2011, Almeda et al. 2013, Goodbody-Gringley et al. 2013, Rico-Martínez et al. 2013). The use of dispersants during the oil spill complicated the assessment of the exposure pathways and effects of the released oil on marine organisms.

An important consideration for both short-term and lasting effects of the DWHOS is the response of the biota. Natural oil seeps have long been documented in the nGOM (MacDonald et al. 1993). These seep areas have chemosynthetic communities (e.g., tube worms, methanotrophic mussels) that are dependent on the bacterially-mediated hydrocarbons from the released oil (Sassen et al. 1999). Thus, at the time of the DWHOS these microbial communities (e.g., oil-degrading bacteria; Hunter et al. 2006) were present and may have mitigated the effects of oil on higher tropic levels. Evidence shows that during the oil spill there was an increase in the abundance of oil and methane degrading bacteria in the nGOM (Hazen et al. 2010). Almeda et al. (2013) observed the dinoflagellate *Oxyrrhis marina* removed oil from the water column, thereby reducing the sub-lethal effects and bio-accumulation of toxic polycyclic aromatic hydrocarbons (PAHs) in copepods *Acartia tonsa* in the same area. However, they also found increasing accumulation of PAHs with increased exposure to oil in many other mesozooplantkon (< 2 mm) and metazooplankton (> 2 mm) taxa.

Despite potentially harmful effects, the oil spill may have stimulated heterotrophic production in the nGOM (Redmond & Valentine 2012). The oil and methane released from the wellhead provided food for oil-degrading microbes, in turn enhancing the microbial loop and secondary production. Graham et al. (2010) and Chanton et al. (2012) traced oil carbon into the planktonic food web using carbon

isotopes. Both studies showed that oil and methane entered the lower food web during the summer 2010. Additionally, Carassou et al. (2014) found that many zooplankton taxa increased in abundance during the summer of 2010 at stations on the inner and mid continental shelf as compared to previous years. However, some taxa were found in lower abundances during 2010, which suggests differential responses of different taxa to the oil spill.

The effects of the DWHOS on the marine organisms are important to understand because the nGOM is home to many highly valued marine fisheries species. The temperate waters of the nGOM support economically important species such as Bluefin Tuna (*Thynnus thunnus*), Red Snapper (*Lutjanus campechanus*), Gulf Menhaden (*Brevoortia patronus*), Blue crab (*Callinectes sapidus*), Eastern oysters (*Crassostrea virginica*), and various shrimp species (Felder & Camp 2009). The species diversity of the region is attributable to its varied marine habitats including estuaries, coastal wetlands, river plumes, seagrass beds, barrier islands, reefs, and pelagic zones. These habitats are essential for spawning, refuge, and feeding of these species, many of which support the region's multi-million dollar fishing industry (NMFS 2011). In 2011, commercial fishery landings in the Gulf of Mexico were valued at over $797 million, making up 19% of the total United State domestic landings (National Ocean Service NOAA 2012). Also, in 2011 recreational anglers took over 21 million fishing trips and spent $9.8 billion on fishing related equipment (NOAA 2012).

Fish eggs and larvae are the most vulnerable life stages of marine fishes with natural mortality rates approaching 100% (Houde 1987, Leis 1991). These early life stages are largely planktonic, and thus were vulnerable to the effects of the DWHOS

because of their limited mobility and the impacts of the oil on their planktonic prey. Although direct exposure to oil could increase mortality rates, changes in prey availability may have longer lasting impacts on the survival and growth of larval fishes. The larvae of many fish species in the nGOM were vulnerable to the effects of the DWHOS because of their high spatial and temporal overlap with the spill, including, Spanish Mackerel (*S. maculatus*), Red Snapper (*L. campechanus)*, King Mackerel (*S. cavalla*), Yellowfin Tuna (*Thunnus albacares)*, and Little Tunny (*Euthynnus alletteratus*), among others (Hernandez et al. 2010).

Variations in the vital rates (e.g., growth, survival) of marine fish eggs and larvae have long been hypothesized to drive fluctuations in recruitment (Hjort 1914, 1926). Many of the hypotheses used to explain fisheries recruitment focus on a specific fish stock (e.g., Cod *Gadus morhua*, Atlantic Herring *Clupea harengus*) or physical feature (e.g., upwelling zones, river plumes), and most relate physical and biological conditions to the feeding success, growth, and predation on larval fishes as the main drivers of survival and eventual recruitment (Cushing 1990, Leggett & Deblois 1994, Houde 2008). Further, many studies have shown that larval fish growth and size at age are strongly correlated with survival (Cushing 1975, Houde 2008). For instance, the "bigger is better" and size-duration hypotheses argue that cohorts of faster growing larvae reach their juvenile stage and escape predation pressure from gape limited predators during the larval stage sooner than slower growing cohorts thus resulting in better recruitment into adult populations (Anderson 1988). Studies have also shown that faster growing larvae within a cohort, independent of size, are less vulnerable to predation (Takasuka et al. 2004) and larger larvae are less susceptible to pelagic predators than their slower-growing

counterparts (Miller et at. 1988). There is a large body of evidence suggesting that small changes in the conditions that affect growth rates can produce large fluctuations in larval fish survival.

Availability of suitable prey has long been considered one of the predominate factors influencing larval fish growth and survival (Hjort 1914, Cushing 1975, 1990). One of the most prominent fisheries recruitment hypotheses, Cushing's "match-mismatch" hypothesis, states that larval growth and survival is dependent on the extent of the spatial-temporal overlap of larval fish with abundant, suitable prey (e.g., spring and fall plankton blooms; Cushing 1975, 1990). Cohorts that exhibit a strong match with their planktonic prey will grow faster, avoid starvation, and outgrow the mouth gape of their pelagic predators, thereby increasing larval survival and eventual recruitment to adult populations. Although planktonic prey abundance is usually driven by physical and climatic events (e.g., upwelling, spring turnover), large anthropogenic disturbances may affect primary production in marine ecosystems thus affecting prey availability to larval fishes (Vitousek et al. 1997, Elser et al. 2007).

Spanish Mackerel (*S. maculatus*) is a commercially and recreationally important species with early life stages that were at risk during the DWHOS. Spawning occurs on the inner continental shelf in 12–35 m of water from May through September in the nGOM (McEachran et al. 1980, Powell 1975), when water temperatures reach 25° C and within a salinity range from 30 to 36 ppt (Beaumariage 1970). Female *S. maculatus* are highly fecund batch spawners; each female produces 190,000–1,500,000 eggs per spawning season with individual fecundity increasing with size (Powell 1975). Eggs are planktonic, hatching 25 hours after fertilization at 26° C; size at hatching is

approximately 2 mm and transformation to the juvenile stage occurs around 13 mm (Smith 1907: Powell 1975).

Study Objectives

The objectives of this study were to determine the effects of the DWHOS on the condition, diet, and growth of larval *S. maculatus*. If the DWHOS had an effect on larval *S. maculatus*, I predict 1) poorer condition in 2010 due to sub-lethal effects of oil and changes in the prey field; 2) a shift in diet in 2010 reflecting a shift in zooplankton communities; and 3) a reduced growth rate in 2010 due to sub-lethal effects of oil and changes in prey field.

CHAPTER II

MATERIALS AND METHODS

Larvae Collection

Larval fishes were collected during the Fisheries Oceanography of Coastal Alabama (FOCAL) and Gulf of Mexico Research Initiative (GoMRI) ichthyoplankton surveys during 2007–2011. Ichthyoplankton collections followed methods described in detail by Hernandez et al. (2010). Briefly, ichthyoplankton samples were collected monthly (May–August, though twice monthly during 2010) in the nGOM at three sites located on the 10 m, 20 m, and 35 m depth contours south of Dauphin Island, Alabama (Figure 1). At each site, depth-discrete samples were collected at 3-m depth bins from one meter below the surface to one meter above the bottom using a 0.25-m^2 mouth opening, Bedford Institute of Oceanography Net Environmental Sampling System (BIONESS) sampler fitted with 0.333-mm and 0.202-mm mesh nets. Additional surface samples were collected using a 1 x 0.5 m neuston net (0.505 mm mesh). Samples were sorted and fish larvae were identified to the lowest taxonomic level possible by taxonomists at the Plankton Sorting and Identification Center (Szczecin, Poland), Dauphin Island Sea Lab, and The University of Southern Mississippi.

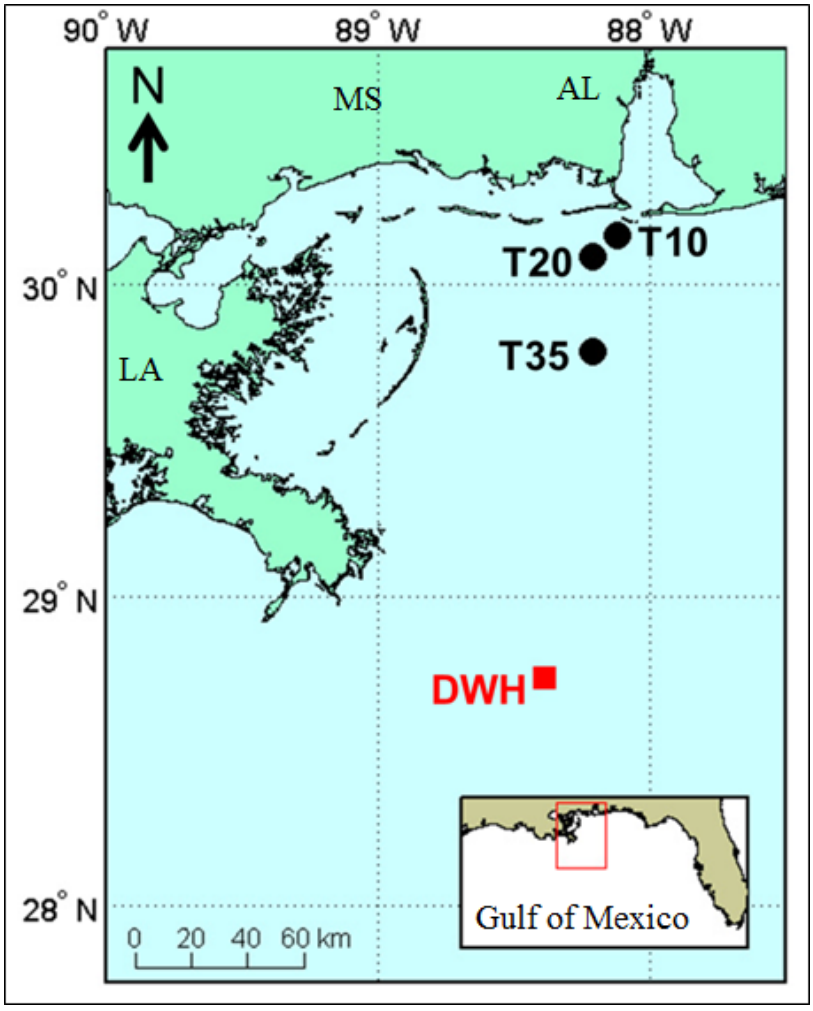

Figure 1. Map showing ichthyoplankton sampling sites (black dots: T10 = 10 m, T20 = 20 m, T35 = 35 m depth contour) and the Deepwater Horizon oil spill location (DWHOS red square).

Among the species collected over the course of the surveys, *S. maculatus* was selected to assess effects of the DWHOS on larval fish for several reasons. Spanish Mackerel are prized by recreational fishermen in the nGOM, and also support a commercial fishery. Larvae were present in the water column during the peak months of the oil spill (May–August), and were collected in relatively high numbers suitable for statistical comparisons among baseline, impact, and recovery periods. Further, they represent the response of a high trophic-level species with specialized early-life piscivory

to the oil spill event and share a similar early life history as other highly-regulated species in the family Scombridae (e.g., *S. Cavalla*, tunas). Lastly, larval Spanish Mackerel are relatively easy to identify to species, as opposed to many other taxa in the region.

Condition

Morphometric Analysis

To determine differences in larval *S. maculatus* body condition among baseline (2007–2009), impact (2010), and recovery (2011) periods, I analyzed potential changes in morphology using seven measurements: notochord length (NL), depth at pectoral fin, depth at anus, head length, head height, eye diameter, and lower jaw length. Relationships among body measurements, particularly those associated with body depth and head size (e.g., depth at pectoral fin, head height), have been found to be useful metrics in assessing larval condition and deriving indices of starvation (Ehrlich et al. 1976, Neilson et al. 1986, Lochmann & Ludwig 2003). Only specimens with the full suite of morphometric measurements were used in the analysis of body condition (e.g., eye diameter could not be measured on a larvae with missing eyes). Additionally, larvae > 5 mm NL (n = 30) were removed from analysis to avoid compounding effects of ontogenetic changes in body shape during or after flexion, changes in allometric growth, and effects of shrinkage (Suthers 1998). I did not correct for shrinkage because of the relatively narrow size range (1.69–5.0mm) of the study specimens, similar handling time, and preservation methods (Theilacker 1986). Individual larvae were imaged using a digital camera mounted on a dissecting microscope and measured using iSolution-Lite image analysis software. To eliminate the influence of length on body shape, I standardized each measurement to NL.

Nonmetric multidimensional scaling (NMS) was used to ordinate fish according to body shape in order to investigate changes in body condition among time periods (Kruskal 1964, Mather 1976). The final NMS ordination was run using the "slow and thorough" autopilot mode with the Sorensen (Bray-Curtis) distance measure and random starting configuration in the PC-ORD version 6.0 software (McCune et al. 2002). To determine significant grouping of larvae on different temporal scales (e.g., month; baseline, impact and recovery periods), I used multiple response permutation procedure (MRPP; Mielke & Berry 2001), a non-parametric procedure for testing differences among two or more predesignated groups (e.g., baseline, impact, recovery periods). Groups failed normality (Shapiro-Wilks test) and equal variance assumptions, so a Kruskal-Wallis non-parametric analysis of variance (ANOVA) of ranks on axes scores was used to test differences of median values among months and time period (e.g., baseline, impact, and recovery). All statistical analyses were considered significant at $\alpha \leq 0.05$.

Relative Condition Factor K_n

A second, independent measure of body condition was calculated using dry weight-length relationships. Relative condition factor was used to assess changes in condition across time periods and validate our morphometric condition index. To compare condition indices, the same larvae were used for both the morphometric and relative condition analyses. Individual fish were dried at 60°C for $\geq$ 16 hours and weighed to the nearest microgram (µg) using a Mettler-Toledo XP26 microbalance. Relative condition factor (K_n) is defined as:

(1) $$K_n = W/W_{pred}$$

where W is the dried weight, and W_{pred} is the predicted weight from a weight-length relationship (LeCren 1951). Larval fish dry weight and notochord length were $\log_{10}$ transformed and a linear regression was fitted to the data. A Kruskal-Wallis one-way ANOVA was used to test differences in relative condition among months and time periods.

Diets

Gut Content Analysis

I analyzed gut contents of individual *S. maculatus* following methods of Llopiz and Cowen (2008) and Carassou et al. (2009). I removed entire alimentary canals and placed them in glycerin under a stereomicroscope. Once gut canals were opened, all visible prey items were removed, imaged, counted, and identified to coarse taxonomic groups (e.g., larval fish, copepods). Comparisons of feeding incidences (prey per fish) were made across time periods and differences were tested using a Kruskal-Wallis one-way ANOVA. I used percent frequency of occurrence of each prey item (%FO defined by the percentage of all fish examined for a given year) and percent of total number (%N defined by the percentage of all prey items for a given year) of prey ingested to compare diets across years. Schoener's index (1970) was used to measure diet similarity among years using the equation:

(2) $$\alpha = 100[\,1 - 0.5\ \textstyle\sum_{i=1}^{n} / P_{xi}\ -\ P_{yi} / \,]$$

where P_{xi} is the proportion of prey items (percent of total prey items) in category *i* in the diet of *S. maculatus* larvae in year x; P_{yi} is the proportion (percent of total prey items) of food category *i* in the diet of larvae in year y; and n is the number of prey categories. Values range from 0 (no overlap) to 100 (complete overlap) with values over 60 considered biologically meaningful (Wallace 1981). Schoener's index is typically used as a measure of diet overlap between species or size classes within a species (interspecific and intraspecific overlap, respectively) collected during the same time period (Laroche 1982, Deus & Petrere-Junior 2003). However, in this study it is used as index of similarity of diets of a single species among years because it is considered one of the most suitable indices when resource-availability data is not considered (Wallace 1981).

Stable Isotope Analysis

Stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) were used to assess changes in diets sources and trophic position (respectively) of larval *S. maculatus* and to determine whether oil carbon was assimilated into larval tissue. Oil from the DWHOS was more depleted in ^{13}C relative to natural levels in marine zooplankton. $\delta^{13}C$ values for fresh and weathered oil are -27.23 ± 0.03‰ and -27.34 ± 0.34‰, respectively (Graham et al. 2010), as compared to $\delta^{13}C$ values of marine zooplankton that range from -20 to -24‰ (Moncreiff & Sullivan 2001, Fry 2006).

After larvae were dried and weighed, whole fish (excluding the alimentary canal and otoliths) were combined into the lowest possible grouping (by year, then month, then individual sampling event) to obtain a minimum tissue weight of 0.3–0.5 mg for stable isotope analysis. All samples were analyzed using continuous flow stable isotope ratio mass spectrometry (CF-IRMS) with a Costech Elemental Analyzer coupled to a Thermo-

Fisher Scientific Delta V Advantage Isotope Ratio Mass Spectrometer at the Gulf Coast Research Laboratory's stable isotope facility. Isotope values are reported relative to established standards (Vienna PeeDee Belemnite limestone carbon and atmospheric nitrogen) for each element and expressed in standard δ notation from the equation below:

$$\delta X = [(R_{sample} / R_{standard}) - 1] \times 1000 \quad (3)$$

where X represents the isotope of interest (^{13}C and ^{15}N) and R is the ratio of heavy to light isotopes ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) for the sample being analyzed.

To assess changes in diets of *S. maculatus* across months and years, I compared median $\delta^{13}C$ and $\delta^{15}N$ isotopic values using a Kruskal-Wallis ANOVA. Pairwise comparisons of median isotopic values among time periods were tested posteriori using Dunn's methods (Dunn-Rankin & King 1969). Additionally, I tracked changes in $\delta^{13}C$ and $\delta^{15}N$ isotopic values across months in 2010 larval *S. maculatus* to test the hypothesis that oil carbon was assimilated into larval fish tissue. Monthly patterns of C and N isotopic signatures were graphically compared between 2010 and all other years and differences among monthly mean values were tested using the Kruskal-Wallis ANOVA.

I did not correct isotopic values for lipid content. Typically, $\delta^{13}C$ values are corrected for samples with C:N > 3.5 (Post et al. 2007), however only four of the 120 samples had a C:N > 3.5 with a max value of 3.82. Because of the low number of samples needing correction and the small difference between corrected $\delta^{13}C$ values and original $\delta^{13}C$ values (0.39 ± 0.1 ‰) the effects of lipids on stable isotope values of larvae *S. maculatus* were deemed negligible.

Two different ichthyoplankton preservation methods were used during the duration of this study. Most samples were initially fixed with 10% formalin (24–48 hours) then placed in ethanol for long-term storage (2–6 years). Starting in 2010, some samples were initially placed in 95% ethanol (24–48 hours) and then transferred to 85% ethanol for long-term storage (2–3 years). Preserving samples in carbon-rich ethanol or formalin has the potential to alter $\delta^{13}C$ and $\delta^{15}N$ signatures, but many studies have shown that preservation effects on isotopic signatures are relatively minor and predictable (Mullin et al. 1984, Arrington & Winemiller 2002, Edwards et al. 2002, Sarakinos et al. 2002, Barrow et al. 2008). I looked for differences in C and N isotopic values for larvae using different preservation methods collected during the same sampling event (i.e. collected during the same year and month at the same sampling station: this occurred on three separate occasions). Differences in $\delta^{13}C$ values were not significant between preservation methods. Nitrogen isotope values were only significantly different at one of three sampling occurrences ($p = 0.05$; Appendix A). Therefore, I did not correct isotopic values based on preservation methods because the effects were largely negligible (Appendix A).

Growth

Differences in growth rates of larval *S. maculatus* collected during (2010) and after the DWHOS (2011) were determined using otolith increment analysis. Daily periodicity in increment deposition has not been validated for larval *S. maculatus* however; it has been validated for other scombrids (e.g., *T. Thynnus*; Brothers et al. 1983). Also, DeVries et al. (1990) found strong correlations between standard length and otolith radius in *S. maculatus* larvae suggesting a relationship between otolith radial

growth and larval somatic growth. Otoliths were extracted and analyzed following standard methods (Secor et al. 1990). Sagittal otoliths were removed using dissecting pins, mounted on glass slides using Crystal Bond and imaged using Canon EOS Rebel T3i digital camera attached to compound light microscope. The otolith radius was measured and increments were counted and measured along the longest axis from the center of the core to the outer edge using iSolution lite software. If the longest radius axis did not correspond with the radius along which increments were most clearly visible for counting and measuring, resulting measurements were proportionally adjusted to match the length of the maximum radius. Increments were counted and measured by two observers. The number of increments was taken to represent the age in days post hatch. If there was disagreement in increment count between observers; both observers re-examined the otolith until age was agreed upon. If agreement in age was reached with the initial readings of both observers, the measurements used for final analysis was selected by a random number generator (either 1 for the first observer or 2 for the second observer). To ensure that otolith deposition rates can be used as a proxy for somatic larval growth, I used a standard least squares regression to examine the relationship between age in days and NL and between NL and otolith radius (Hare & Cowen 1995).

Samples from FOCAL collected during the baseline period (2007–2009) where briefly stored in formalin prior to long-term storage which oxidizes to create formic acid which lowered the pH of the ethanol preserved and dissolved the calcium carbonate structure of the otoliths. Thus, I could not compare the baseline larval growth rates to impact and recovery period larvae.

A Student's t-test was used to compare daily otolith increment growth rates (μm/day) between impact and recovery periods growth rates of larval *S. maculatus*. I also tested for differences in the slopes and intercepts of the linear regressions of age and NL and NL and otolith radius between 2010 and 2011 larvae using Student's t-tests of each parameter.

CHAPTER III

RESULTS

Larvae Collection

A total of 768 *S. maculatus* larvae were collected from 2007–2011 (May–August). Larvae were collected in all years (2007: n = 159; 2008: n = 8; 2009: n = 177; 2010: n = 264; and 2011: n = 160). Because relatively few larvae were collected in 2008, these larvae were removed from all analyses. Larvae ranged in size from 1.3–11.37 mm NL (mean = 3.1 ± 1.2 SD mm).

Condition

Morphometric Analysis

A total of 348 larvae were used for condition analysis. The NMS procedure settled on a two dimensional solution with a final stress of 13.2 and instability < 0.00001 after 88 iterations of real data. The two resulting axes explained 93.4% of the variation of the larval morphometric measurements (Axis 1 = 75.4% and Axis 2 = 18.0%). Axis 1 was strongly correlated with head height, head length, and depth at anus and Axis 2 was most correlated with depth at pectoral fin (Table 1). Axis 1 scores were strongly and positively correlated with body dimensions, so it provided a metric of larval body condition. Axis 1 scores differed by month, year, and time period (Figures 2 and 3). Larval *S. maculatus* had significantly higher Axis 1 scores during the impact period than larvae captured during the baseline and recovery periods (Kruskal-Wallis $p < 0.001$ H = 31.1, degrees of freedom df = 2); larvae captured in the recovery period were not significantly different than baseline or impact larvae (Kruskal-Wallis $p > 0.05$). Additionally, larval condition differed among months; larvae in May had significantly

lower Axis 1 scores than larvae collected in all other months and July larvae had significantly greater Axis 1 scores (Kruskal-Wallis $p < 0.001$, $H = 45.0$, $df = 3$).

Table 1

NMS correlations between axes and larval morphometric measurements (depth at pectoral fin DPF, depth at anus DA, head length HL, head height HH, eye diameter ED, lower jaw length LJL). Axis 1 explained 75.4% and axis 2 explained 18.0% of the variation in body size among S. maculatus larvae.

Body measurement	Axis 1		Axis 2	
	r	*P*	r	*P*
DPF	0.512	< 0.001	0.737	< 0.001
DA	0.668	< 0.001	0.097	0.678
HL	0.788	< 0.001	-0.475	< 0.001
HH	0.816	< 0.001	0.388	< 0.001
ED	0.261	< 0.001	0.397	< 0.001
LJL	0.751	< 0.001	-0.363	< 0.001

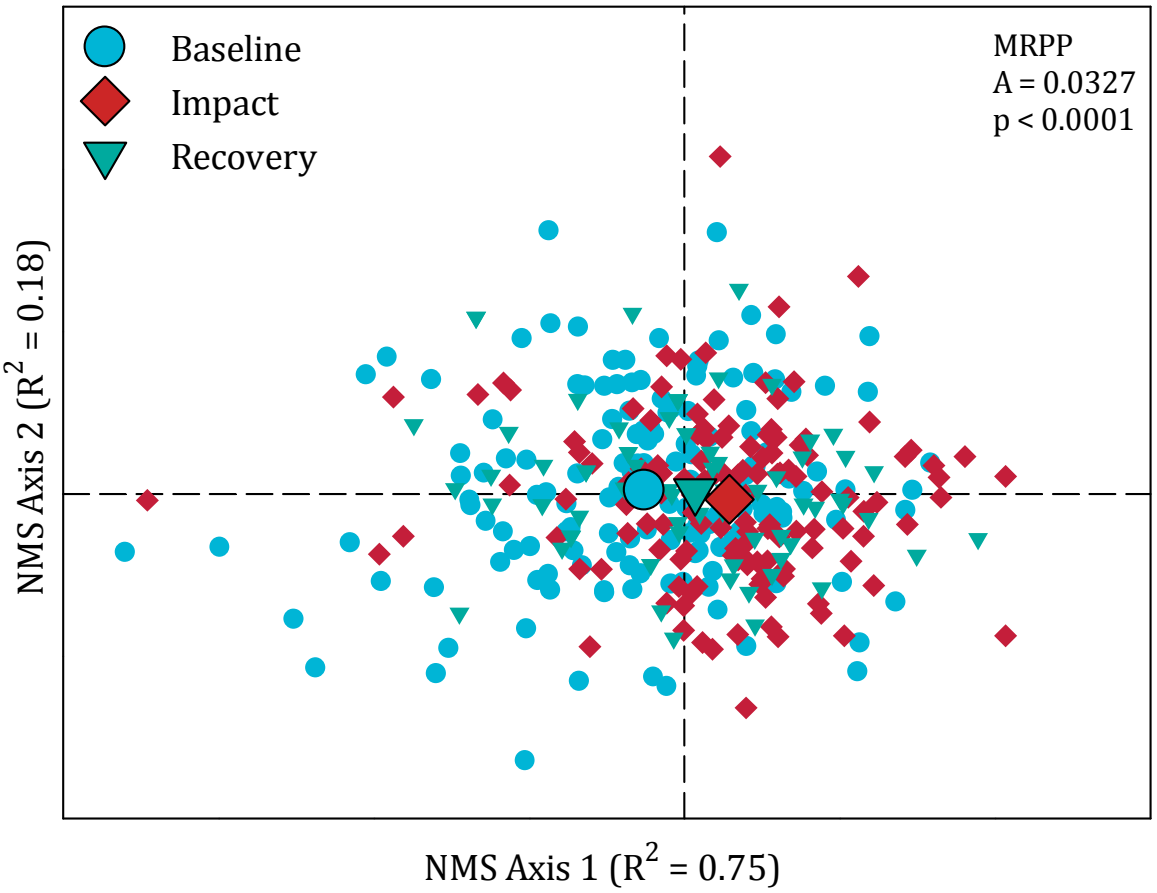

Figure 2. NMS scores of larvae grouped by time periods. Smaller shapes represent individual larvae and larger shapes represent mean values of larvae collected during baseline, impact, and recover periods. Dashed lines are the mean values of each axis.

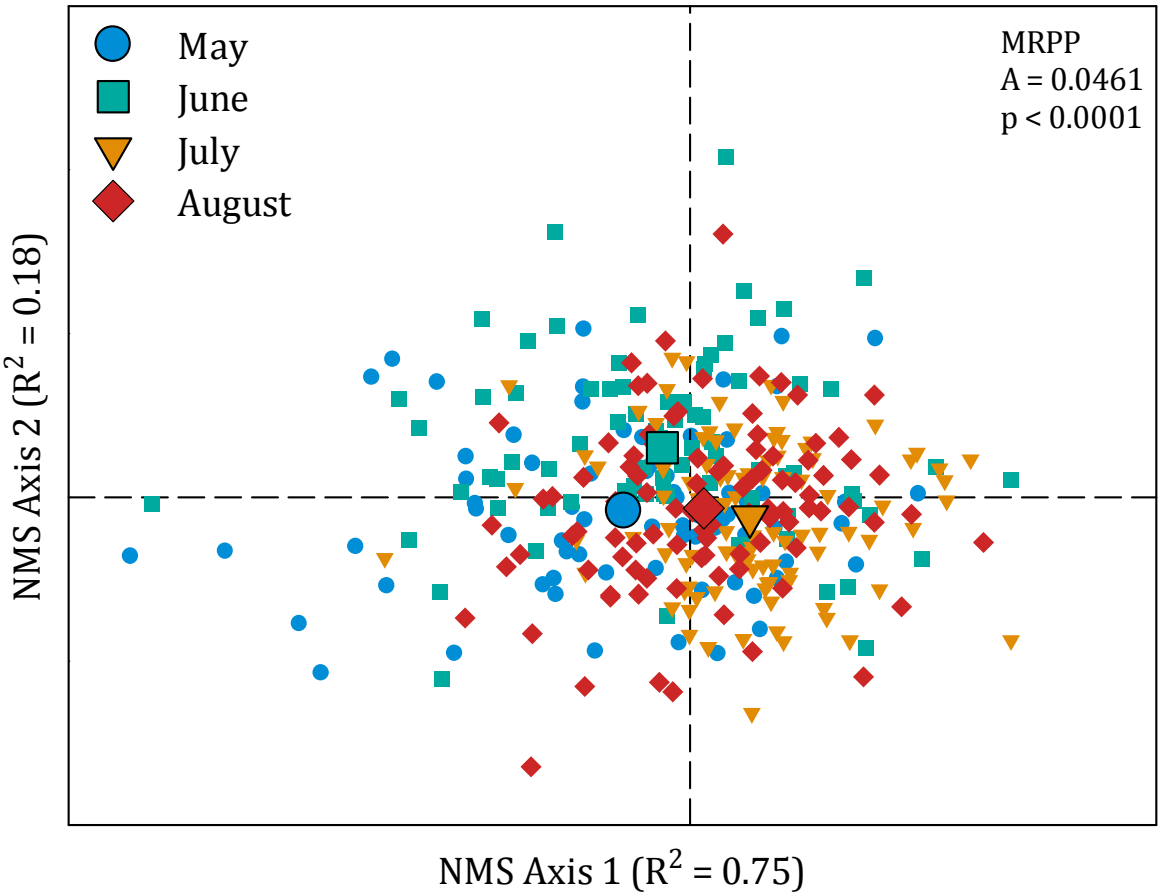

Figure 3. NMS grouped by months. Smaller shapes represent individual larvae and larger shapes represent mean values of larvae by month. Dashed lines are the mean values of each axis.

Relative Condition Factor

Larvae collected during the impact period had significantly higher K_n values (n = 136) than baseline (n = 160) and recovery (n = 65) period larvae (Figure 4: Shapiro-Wilks $p < 0.05$, Kruskal-Wallis $p = 0.004$, H = 11.25, df = 2). Larvae collected in May were in poorer condition than larvae collected in July and August (Kruskal-Wallis $p < 0.001$, H = 21.88, df = 3), while June larvae were not significantly different than any other month. Predicted weights were calculated using the regression equation from the $\log_{10}$ transformed dry weight and length values ($W_{pred} = 2.5003 \times \text{length} - 2.4721$, $r^2 = 0.8326$, $p < 0.0001$).

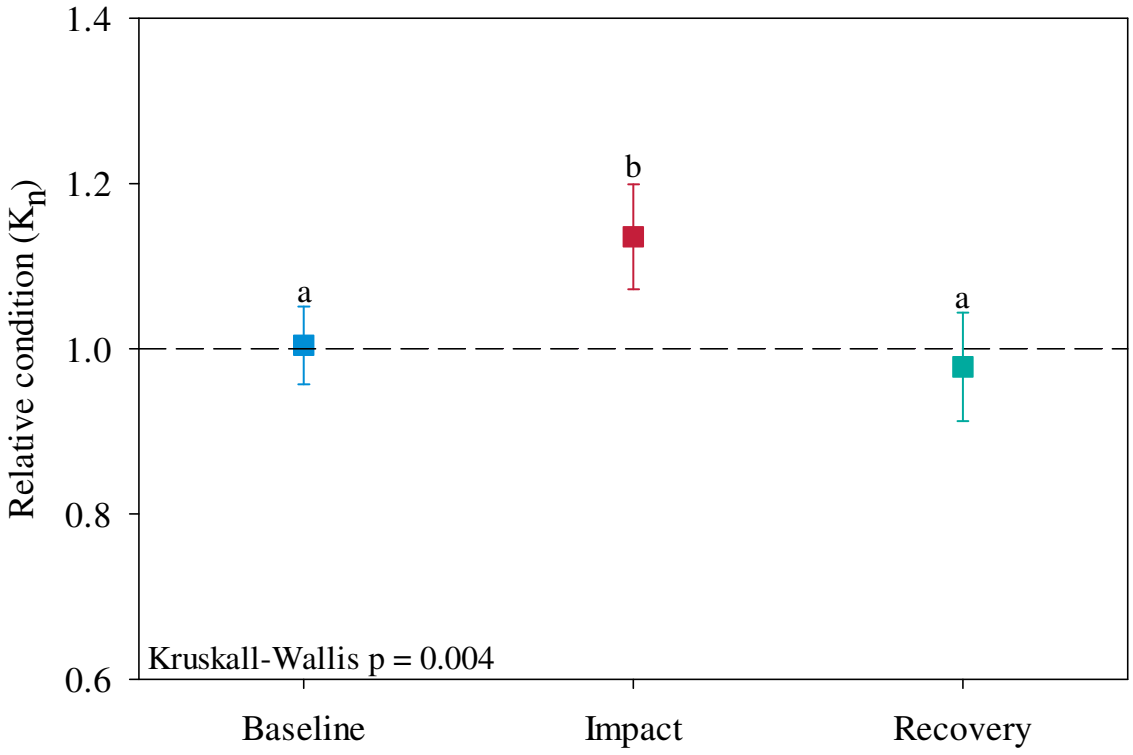

Figure 4. Relative condition factor of larval *S. maculatus* by time period. Squares are mean values (error bars = 95% CI) of larvae collected during each time period. Letters above error bars denote statistical differences (p = 0.05). The dashed line represents mean relative condition.

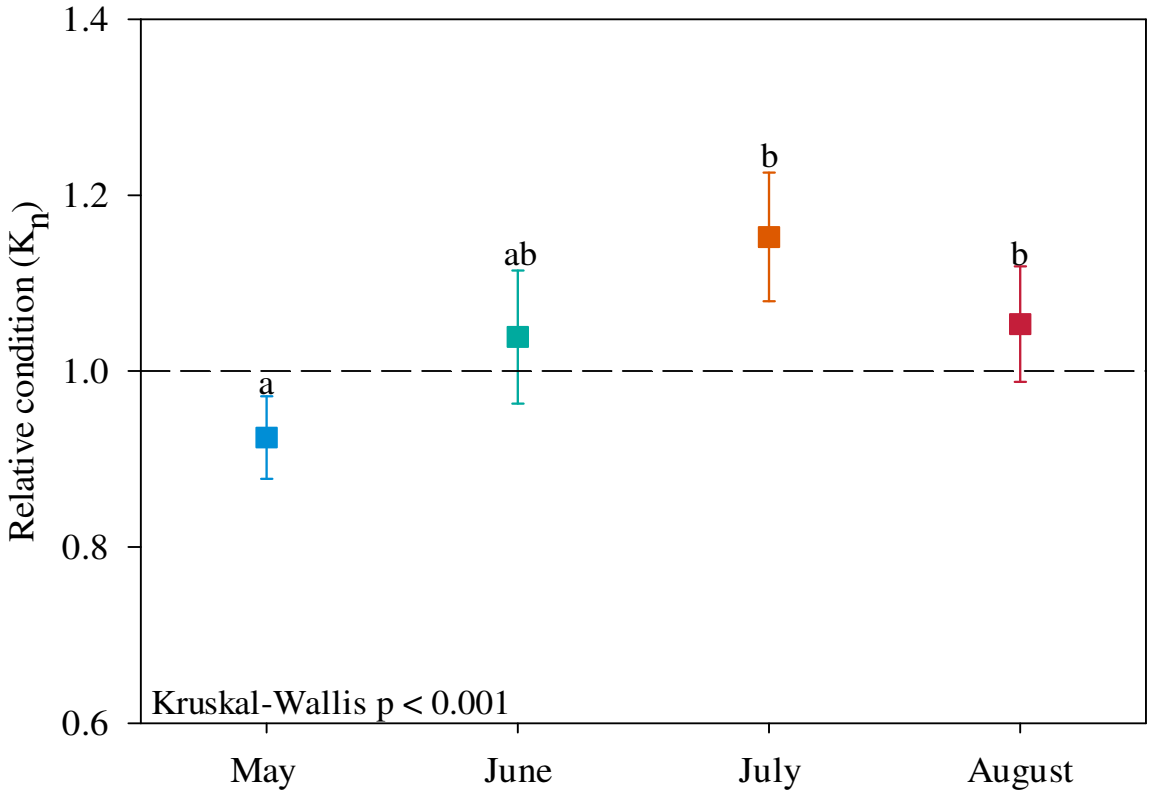

Figure 5. Monthly mean (error bars = 95% CI) relative condition factor values of larval *S. maculatus* collected from 2007–2011. Letters a and b represent groups that are significantly different ($p \leq 0.05$). Dashed line represents mean relative condition.

Diets

Gut Content Analysis

A total of 50 different prey items were found in the stomachs of 234 larval *S. maculatus*. The most common prey item was larval fish (n = 17) followed by invertebrate eggs (n = 4), copepods, cladocerans, and fish eggs (n = 3 each: Table 2). Feeding incidences (prey items / fish) were not significantly different between time periods (mean ± SE: baseline 0.16 ± 0.03, impact 0.22 ± 0.7, recovery 0.30 ± 0.09, Kruskal-Wallis p = 0.257, H = 2.78, df = 2).

Table 2

Results of gut content analysis of 234 larval S. maculatus collected May–August off the coast of Alabama. %N = percent of the total prey items (N) found in that year: FO = frequency of occurrence; %FO = percent frequency of occurrence among larvae containing food; n = the total number in each category.

	Year															
	2007				**2009**				**2010**				**2011**			
Prey Items	n	%N	FO	%FO	n	%N	FO	%FO	n	%N	FO	%FO	n	%N	FO	%FO
larval fish	4	50.0	4	6.2	2	15.4	2	2.8	5	31.3	5	8.2	6	46.2	5	13.9
cladoceran	-				1	7.7	1	1.4	-				2	15.4	2	5.6
copepod	1	12.5	1	1.5	-				1	6.3	1	1.6	1	7.7	1	2.8
ostracod	1	12.5	1	1.5	-				-				-			
fish egg	-				2	15.4	2	2.8	1	6.3	1	1.6	-			
invert. egg	-				2	15.4	2	2.8	-				2	15.4	1	2.8
diatom	-				2	15.4	2	2.8	-				-			
unidentified	2	25.0	1	3.1	4	44.4	3	4.2	9	56.3	5	8.2	2	18.2	2	5.6
total prey	8				13				16				13			
# fish larvae	65				72				61				36			
# empty guts	58				62				50				25			

Larval fish were the dominate prey item in the stomachs of *S. maculatus* larvae across all years except 2009, when fish larvae were equally as common as fish eggs (n = 2 each). Larval fish %FO was greatest in 2011 followed by 2010, 2007, and 2009 (Table 2). Larval fish also had the highest %N value in 2007 at 50.0% of prey items found followed by 2011, 2010, and 2009 (Table 2).

Schoener's index of diet overlap was greatest between 2007 and 2010 with the least overlap occurring between 2007 and 2009 (Table 3). Overlap between 2010 and all other years were relatively high, with 2007 being the most similar.

Table 3

Matrix for Schoener index (1970) values measuring the percent diet overlap of S. maculatus *larvae among years.*

Year	Schoener's Index value		
2009	43.3		
2010	78.1	65.1	
2011	74.0	61.5	73.3
Year	2007	2009	2010

Stable Isotope Analysis

A total of 120 *S. maculatus* larvae samples were measured for stable isotope values of carbon and nitrogen. Values ranged from -21.88 to -15.50 ‰ for $\delta^{13}C$ and 10.73 to 14.33 ‰ for $\delta^{15}N$. Mean $\delta^{13}C$ were significantly different among years, however 2010 larvae were not depleted in $\delta^{13}C$ compared to other years (Table 5 and 6: Kruskal-Wallis $p < 0.001$, $H = 27.948$, $df = 3$). Mean $\delta^{15}N$ values differed slightly among years (Kruskal-

Wallis p = 0.044, H = 8.115, df = 3), although pairwise comparisons were not significant between any years (Table 5).

Although ^{13}C was not depleted in 2010 compared to other years, within 2010, $\delta^{13}C$ values were most depleted in June and July corresponding to the peak of the oil spill. Also, $\delta^{15}N$ were significantly lower in May as compared to all other months in 2010, suggesting that the ^{13}C depletion was not related to a change trophic position (Figure 6 A and B). There were no differences among months when $\delta^{13}C$ values baseline and recovery periods were considered together. Additionally, $\delta^{15}N$ values were significantly higher in August as compared to May and June when baseline and recovery periods were combined (Figure 6 C and D). Thus, the monthly isotopic patterns in 2010 were not typical of isotopic patterns when baseline and recovery period larvae were combined.

Table 4

Number of samples (n) and mean $\delta^{13}C$ and $\delta^{15}N$ (‰ ± 1SD) of S. maculatus *larvae collected during ichthyoplankton surveys off the coast of Alabama from 2007–2011.*

Year	N	$\delta^{13}C$	$\delta^{15}N$
2007	25	-18.0 ± 0.8	12.2 ± 0.6
2009	13	-18.9 ± 1.5	12.6 ± 0.8
2010	54	-18.6 ± 0.7	12.1 ± 0.5
2011	28	-19.3 ± 0.7	12.7 ± 0.9

Table 5

Multiple pairwise comparisons of ranks (Dunn's method) of $\delta^{13}C$ values for larval S. maculatus.

Comparison	Diff of Ranks	Q	P < 0.05
2007 vs 2011	50.35	5.22	Yes
2007 vs 2009	31.49	2.63	No
2007 vs 2010	22.93	2.71	Did not test
2010 vs 2011	27.42	3.37	Yes
2010 vs 2009	8.57	0.79	Did not test
2009 vs 2011	18.85	1.60	No

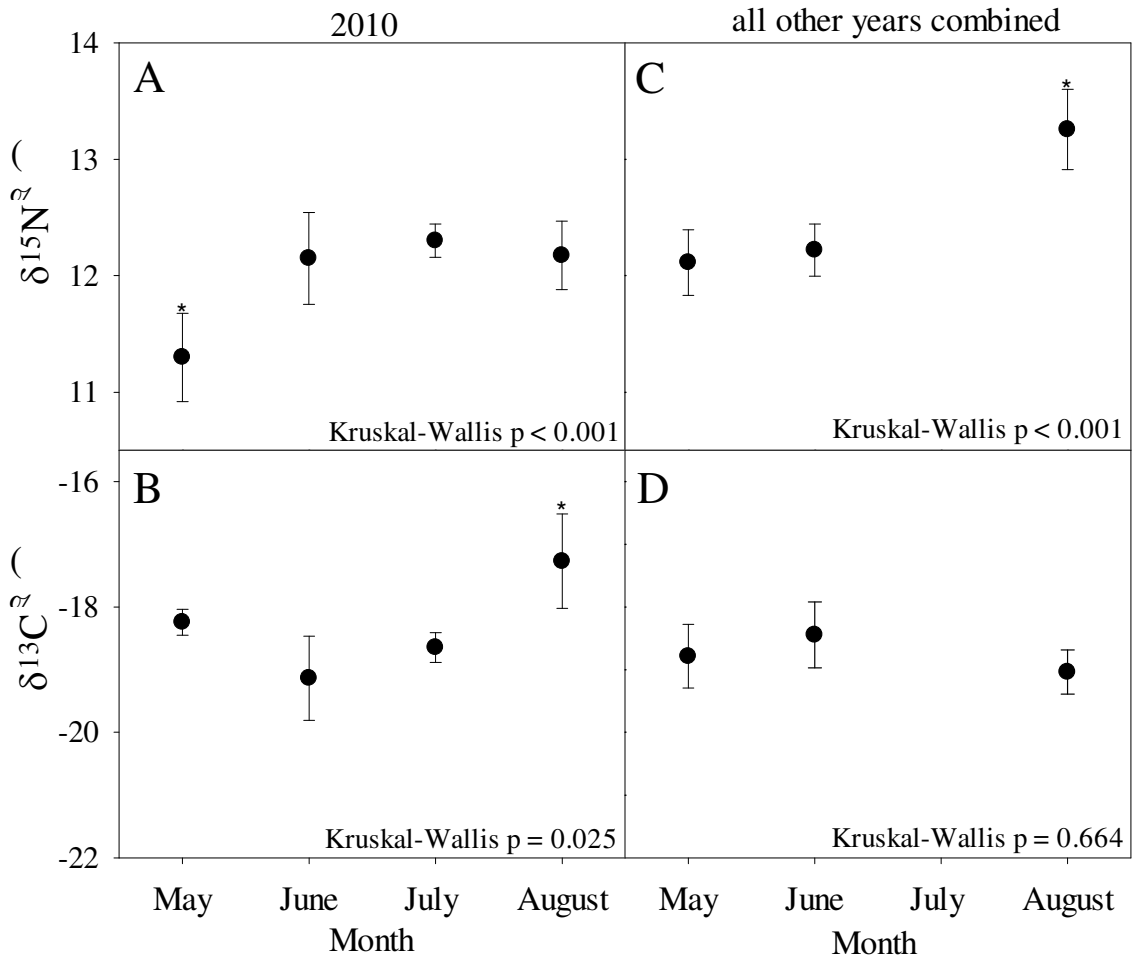

Figure 6. Monthly comparisons of mean (error bars = 95% CI) stable isotope values for larval *S. maculatus* collected in 2010 (A) and(B) and monthly comparisons for larvae collected in 2007, 2009, and 2011 combined (C) and (D). No stable isotope samples were available for July 2007, 2009 and 2011 because combined dry weight < 0.3 mg for those years. (*represents mean values that are significantly different than all other months).

Growth

Otolith radius of larval *S. maculatus* was positively and significantly correlated somatic growth (Figure 7). I found no significant difference between 2010 and 2011 larvae in the slope or intercept of the following least squares regression equations of age (in days) and NL (Figure 7a: $t_{0.05\ (2),\ (49)} = 0.093$, $p > 0.05$).

2010: NL = 0.551 (age) + 1.793, n = 8

2011: NL = 0.531 (age) + 1.432, n = 43

Daily otolith increment growth did not differ between impact (3.95 µm/day ± 1.25, n = 8) and recovery (4.11 µm/day ± 1.09, n = 31) period larvae ($t_{0.05, (2) (37)} = 0.360$, p = 0.721). Because of the unequal number of samples between periods the power of the test (0.064) was below the desired power of 0.800. Less than desired power indicates that the test is less likely to detect a difference when one actually exists.

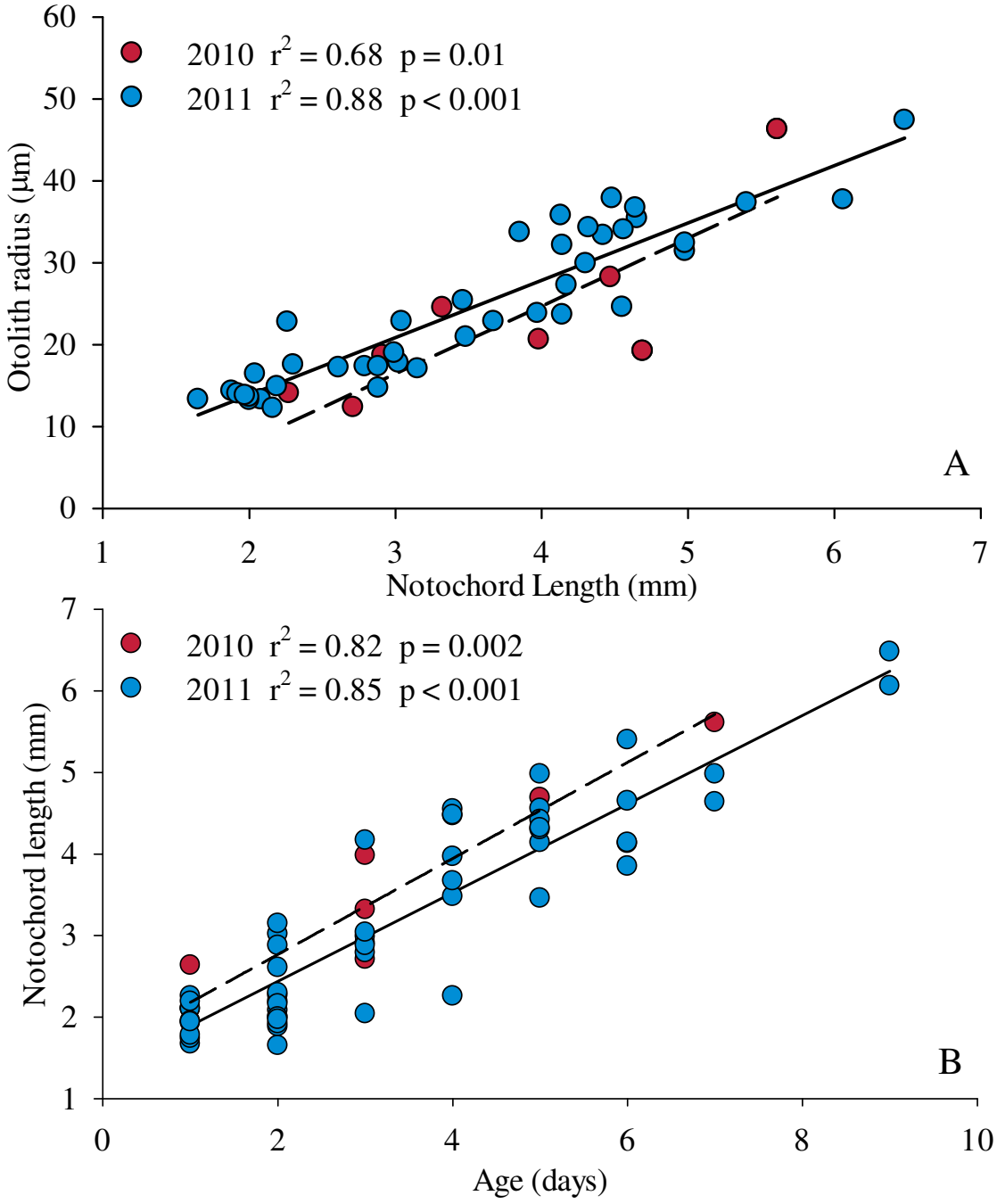

Figure 7. Relationship between notochord length and otolith radius (A) and age (as determined from otolith daily increments) and notochord length (B) for *S. maculatus* larvae collected in 2010 and 2011 off the coast Alabama. Dashed and solid lines are least squares regression of 2010 and 2011 larvae respectively.

CHAPTER IV

DISCUSSION

Condition, Feeding and Growth During the DWHOS

Morphometric analysis of body shape and relative condition factor revealed that body condition of larval *S. maculatus* was better in 2010 relative to baseline (2007, 2009) and recovery (2011) periods. Morphometric analysis and relative condition showed similar patterns across years and months, which supports the conclusion that *S. maculatus* larvae were deeper bodied and heavier in 2010 compared to similarly sized larvae collected during baseline and recovery periods. Also, larval *S. maculatus* were in significantly better condition in July compared to all other months when all years were combined. This was also true in 2010 despite peak oil coverage in late June and July in our sampling area (Graham et al. 2010). However, larval morphometric indices (e.g., dry weights and body depth) are considered to be insensitive to short-term events (less than a week: Ferron & Leggett 1994). Based on length-at-age relationships larvae in the condition analyses were less than seven days old and would have been subjected to the direct influence of the DWHOS.

The diets of *S. maculatus* larvae did not changed as a result of the DHWOS. Larval fish were the most important prey item across all years. Schoener's index of diet overlap was consistently high when comparing diets in 2010 to other years. Additionally, 2010 fell within the annual ranges of the isotopic values for both carbon and nitrogen. Typically, as organisms increase trophic position they become more enriched in heavy isotopes $\delta^{15}N$ (3.4‰ 1 SD = 1.0 ‰) and $\delta^{13}C$ (0.4‰ 1 SD = 1.3‰: Post 2002). Although stable isotope values of $\delta^{13}C$ and $\delta^{15}N$ of larval *S. maculatus* were significantly different

among years, mean values only ranged 1.3‰ and 0.6‰ respectively, which is less than one trophic level (Post 2002).

Larval *S. maculatus* displayed similar patterns of $\delta^{13}C$ depleted in the summer of 2010 as compared to mesoplankton found by Graham et al. (2010). Trophic transfer of the depleted carbon was tracked into the mesoplankton (presumably 2–3 trophic levels above raw oil) at the same stations used in the current study (Graham et al. 2010). $\delta^{13}C$ mean values in *S. maculatus* tissue in 2010 were lowest in June and July but were not significantly different than May. This correlates with peak oil coverage during June and July at our sampling sites. However, the magnitude of carbon isotopic depletion was less in larval fish tissue (-0.4‰ to -2.2‰) than plankton (-1‰ to -4‰; Graham et al. 2010).

If oil was assimilated into the tissue of larval *S. maculatus*, the isotopic signal could be reduced for several reasons. First, signals from isotopic tracers can be dampened through the trophic transfer of isotopes (Fry 2006). For example, in ^{13}C addition experiments in freshwater lakes, the magnitude of the ^{13}C signal is greater in planktivorous young of year Largemouth Bass (*Micropterus salmonides*) than in juveniles that fed at a higher trophic level (Carpenter et al. 2005). Also, in isotope addition experiments, differences between tracer ^{13}C values and natural values are ~ 1000‰, but differences between oil ^{13}C and marine plankton are 4–8‰, making differences much harder to detect. Oil-degrading microbes and plankton grazers would have a greater and faster response reflecting the oil carbon signal due to their more rapid carbon turnover rate and growth as compared to larval fish (Herzka & Holt 2000, Bolsey et al. 2002). Also, Graham et al. (2010) found that isotopic values in mesoplankton recovered within 2–4 weeks. However, larvae in this study were combined by month and

short-term changes in $\delta^{13}C$ values may have been masked by our coarse sampling intervals and pooling of sampled larvae.

This study also revealed that early *S. maculatus* larvae may rely on zooplankton prey more than previously shown. Finucane et al. (1990) found that 96% of the prey items found larval *S. maculatus* stomachs were other larval fish as opposed to just 38% in the current study. However, this difference may be related to differences in the size of larvae examined in each study ($\overline{x}$ = 3.1 mm NL in current study; $\overline{x}$ = 10 mm SL in Finucane et al. 1990). Although *S. maculatus* larvae were still found to be piscivorous, pre-flexion larvae are presumably poorer swimmers and may also feed on more abundant zooplankton prey.

Larval *S. maculatus* growth rates, as determined by daily otoliths increments, did not change between impact and recovery periods. Growth rates in larval fish have been linked to survival because faster growing larvae reduce their larval duration, thus decreasing their vulnerability to starvation and pelagic predators (Houde 1987, Suthers 1998). Although, faster growth in the 2010 larvae is supported in the morphometric and relative condition results, statistical power in determining differences in growth was limited because there were few otoliths analyzed from 2010.

Growth rates as predicted by the slope of the regression equation age in days × NL (2010 = 0.551 mm × d^{-1} and 2011 = 0.531 mm × d^{-1}) were lower than previously found in the literature for *S. maculatus* (1.31 mm × d^{-1}; DeVries et al. 1990). However, this difference in growth rate is expected because of the size difference between the larvae used in the two studies (range: 1.65–6.48 mm NL in current study; 2.8–22 mm SL in DeVries et al. 1990). Growth rates increase with size for early life stages of fishes.

Additionally, DeVries et al. (1990) found a positive relationship between growth and larval size suggesting the rate of growth for *S. maculatus* larvae increases with size.

Changes in larval condition in relation to the DWHOS could be a result of the effect the oil spill had on the planktonic food web. Carassou et al. (2014) found that many zooplankton taxa were present in higher abundances in the summer of 2010 compared to previous years (2004–2009). They also found that monthly environmental conditions in 2010 were within the range of historical observations (2007–2009) with the exception of minor differences between July 2010 and historical July values. Thus, changes in zooplankton communities may be caused by the DWHOS and not changes in environmental conditions. Although, larval *S. maculatus* are piscivorous (Finucane et al. 1990, current study), I have shown that early larvae may depend on a variety of planktonic prey items (e.g., copepods, eggs). Also, increased zooplankton abundances would benefit planktivorous larval fishes (e.g., Clupeids, Carangids, Engraulids) which are known prey items for *S. maculatus* (Finucane et al. 1990).

In addition to the DWHOS, other factors may have impacted larval fishes during the summer of 2010. During the oil spill, federal waters in the nGOM were closed to commercial and recreational fishing (NOAA Fisheries 2010). These closures could have increased abundances of pelagic piscivores leading to cascading effects for the lower food web. Previous studies, in smaller enclosed systems, have shown that increases in piscivores can decrease abundances of planktivorous fishes through predation, in turn releasing zooplankton populations from predation and increasing zooplankton biomass (Lathrop et al. 2002). Additionally, the fishing closures could have increased the biomass of spawning fishes thus increasing the number of larval fish and eggs that were present in

2010. Fodrie and Heck (2011) found that juvenile fishes of 12 of the 20 most common seagrass-associated species in the nGOM had significantly higher catch per unit effort in 2010 during a five year survey. Additionally, initial findings from the ichthyoplankton surveys used in this study show that larval fish abundances were similar or greater in 2010 compared with previous years (unpublished data). If fish eggs and larvae were more abundant in 2010, larval *S. maculatus* would have more available prey during the DWHOS. However, evidence that zooplankton biomass or fish larvae abundances increased due to the release of fishing pressure is lacking and relationships between fishing and the lower marine food web in a large open marine ecosystem like the nGOM are still unknown.

The DWHOS could have indirectly impacted larval fish by disrupting the distributions of zooplankton in the nGOM. There is evidence that zooplankton actively avoid hydrocarbon-contaminated water (Seuront 2010). If zooplankton were avoiding oil-contaminated water during the DWHOS event, oil slicks could have acted as a physical front concentrating plankton both horizontally and vertically (e.g., throughout the water column) increasing the patchiness of plankton distributions. Plankton patchiness increases encounter rates between larval fish and their prey and can be advantageous for larval fish feeding success and growth (Lasker 1978, Letcher & Rice 1997). Again, little evidence exists that the oil-contaminated water caused increased plankton patchiness during the DWHOS.

It is difficult to directly link the changes larval *S. maculatus* condition with the DWHOS because of the natural variability in the environmental conditions in the region. Although evidence shows that environmental conditions were not significantly different

in 2010 compared to years before the spill (Carassou et al. 2014), variability in larval fish vital rates and recruitment may occur within normal environmental windows. Even if plankton and fish populations were stable during 2010 (Fodrie & Heck 2011, Carassou et al. 2014), fisheries recruitment success depends on many complex processes (Houde 2008) which may have been directly or indirectly impacted by the DWHOS.

Future Research

I have shown through the analysis of the condition, diets, and growth that larval *S. maculatus* may have been resilient to the perceived harmful effects of the DWHOS. These results coupled with other studies (Fodrie & Heck 2011, Carassou et al. 2014) provide a growing body of evidence that the planktonic communities in the nGOM were resilient to the oil spill and in some cases populations thrived during the summer 2010. Although these results are promising for the recovery of the nGOM, further analysis of ecosystem and long-term impacts should be investigated.

Spanish Mackerel provided a good model species for the impacts of the DWHOS on pelagic larval fishes because of their potential interaction with the oil, however species-specific effects should still be considered. One way the oil spill may have impacted larval fishes is by changing the planktonic community structure. Larval fishes exhibit a variety of feeding habits and may be affected differently by changes in the planktonic communities in 2010. Differences in feeding strategies could have major implication on how the DWHOS affected larval fish.

Analysis of body morphometrics and dry weights appear to be sensitive to monthly and annual variations in larval condition. This sensitivity to changes in condition is vital to understanding how quickly larvae are impacted and recover from disturbances

like the DWHOS. However, species-level laboratory validation for such metrics is important to interpret results.

Lastly, to fully understand the long-term impacts of the DWHOS, fluctuations of adult populations should be assessed to determine recruitment variability. Although, studying the vital rates of early life stages of fishes can be a powerful tool in predicting changes in fish populations, the DWHOS may have stage-specific or latent impacts that could uncouple larval fish survival and recruitment. Future analyses of fish population dynamics (e.g., larval and adult abundances, growth rates) need to be investigated before the effects of the DWHOS are fully elucidated.

APPENDIX A

COMPARISON OF PRESERVATION METHODS ON ISOTOPIC VALUES

Due to the variable isotopic response of long-term ethanol storage and the lack of studies comparing differences between ethanol only and formalin-EtOH preservation, I compared differences between non-corrected and corrected (based on literature values) isotopic values of larval *S. maculatus*. Larvae preserved using both methods were collected during three separate sampling events (i.e. collected during the same year and month at the same sampling station). Based on literature values, stable C isotope ratios were corrected by adding 1‰ for formalin-EtOH preserved samples (Arrington & Winemiller 2002) and stable N isotope values were corrected by adding 0.37‰ for EtOH only preserved samples (Sarakinos et al. 2002). A t-test was used to compare mean isotopic values between preservation methods of larvae collected during the same sampling event.

*Comparison of mean isotopic values of larval S. maculatus preserved using both formalin fixation – ethanol storage and ethanol only preservation. Isotopic corrections were based on literature values. (*significant difference between preservation methods using t-test)*

Sample (month, year, station)	δ Isotope (‰)	EtOH	Form-EtOH	p
		non-corrected		
July 2010, T20	C	-18.3	-18.5	0.50
	N	12.1	12.5	0.05*
May 2011, T35	C	-18.5	-19.6	0.11
	N	12.4	12.1	0.50
August 2011, T20	C	-19.0	-19.4	0.07
	N	13.8	14.0	0.53
		corrected		
July 2010, T20	C	-18.3	-17.5	0.01*
	N	11.8	12.5	0.0005*
May 2011, T35	C	-18.5	-18.6	0.95
	N	12.0	12.1	0.71
August 2011, T20	C	-19.0	-18.4	0.03*
	N	13.4	14.0	0.07

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