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Condition of larval Spanish mackerel *Scomberomorus maculatus* in relation to the *Deepwater Horizon* oil spill

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ABSTRACT: 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 directly through toxicity or indirectly through 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, USA, in a region impacted by the DWHOS, the abundance and condition of larval Spanish mackerel *Scomberomorus maculatus* were compared during summer months in years before (2007–2009), during (2010) and after (2011) the DWHOS. Changes in larval quality were examined using morphometric and weight-based body condition indices, whereas potential trophic impacts were quantified using stable C and N isotopes. Larval abundance did not differ across years. However, larvae were in better body condition during the DWHOS period relative to before the spill. Larvae had generally similar isotopic values through time. Thus, larval Spanish mackerel body condition was largely resilient to the harmful effects of the DWHOS. Responses to the DWHOS are likely taxon-specific, as the resiliency of larval Spanish mackerel starkly contrast the response of another managed species (red snapper) during the same period.

KEY WORDS: *Deepwater Horizon* · Gulf of Mexico · Spanish mackerel · Larval condition

INTRODUCTION

The *Deepwater Horizon* oil spill (DWHOS) released 700 000 metric tons of oil into the northern Gulf of Mexico (nGOM) during the summer of 2010 (Adcroft et al. 2010, McNutt et al. 2012), making it the largest accidental oil spill in US history (Oil Spill Commission 2011). To accelerate weathering and biological degradation of the oil, chemical dispersants were also added to the water column. The complex mixture of released hydrocarbons likely had important consequences for fish eggs and larvae in the water column at the time of the event, because these early life stages are planktonic and highly sensitive to environmental conditions (Fodrie et al. 2014, Hernandez et al. 2016). In turn, the strength of larval recruitment to reproductive adults can have long-lasting impacts on fisheries yields and hence management strategies. Several studies have demonstrated the acute toxic effects of oil and dispersant to larval fishes (e.g. Hemmer et al. 2011, Goodbody-Gringley et al. 2013), and some found that dispersants increase toxicity of the oil as compared to exposure to oil alone (Almeda et al. 2013, Rico-Martínez et al. 2013). However, it is unclear how laboratory tests of larval fish exposure to oil and/or

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dispersants translate to those effects on larvae in the highly dynamic nGOM. Although direct exposure to oil could increase mortality rates, other indirect effects, such as changes in prey availability, may have latent impacts on the survival and growth of larval fishes (Carassou et al. 2014).

DWHOS impacts on the lower (pelagic) food web in the nGOM were varied and complex. For example, Redmond & Valentine (2012) found that the DWHOS may have stimulated heterotrophic production in the nGOM. The oil and methane released from the wellhead provided food for oil-degrading microbes, in turn enhancing the microbial loop and secondary productivity. Graham et al. (2010) and Chanton et al. (2012) used stable and radioactive carbon isotopes, respectively, to show that oil-derived carbon was integrated into the planktonic food web during summer 2010. In the eastern Gulf of Mexico, modelled trajectories of surface and subsurface oil corresponded with an anomalous phytoplankton bloom during August 2010 (Hu et al. 2011). Similar blooms have been documented during previous oil spills and could be related to increased phytoplankton production or release from grazing pressure due to zooplankton mortality (Johansson et al. 1980). Off the coast of Alabama, USA, 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 taxon-specific responses to the oil spill. Larval fishes are often selective feeders; therefore, impacts at lower trophic levels that affect their planktonic prey abundance, distribution, or quality could have implications for larval feeding, growth and survival (Peck et al. 2012).

The goal of this study was to examine the effects of the DWHOS on the condition of larval Spanish mackerel *Scomberomorus maculatus*, a commercially and recreationally important species with early life stages that were at risk during the DWHOS (Hernandez et al. 2010). Larvae were collected in our long-term surveys at sampling stations which were impacted by the DWHOS off the coast of Dauphin Island, Alabama, during years before (2007, 2009), during (2010) and after (2011) the DWHOS. Changes in larval quality were examined using morphometric and weight-based body condition indices, and whole-body stable carbon (C) and nitrogen (N) isotopes were measured to test whether oil-derived carbon supported larval growth or impacted larval trophic position (i.e. feeding habits) relative to the oil spill.

MATERIALS AND METHODS

Ichthyoplankton surveys

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. (2011) and Carassou et al. (2012). Briefly, plankton samples were collected monthly during May through August in 2007, 2008, 2009, and 2011, and twice monthly during 2010 at 3 sites located on the 10, 20, and 35 m depth contours south of Dauphin Island, Alabama (Fig. 1). These sampling locations were impacted by oil during the DWHOS

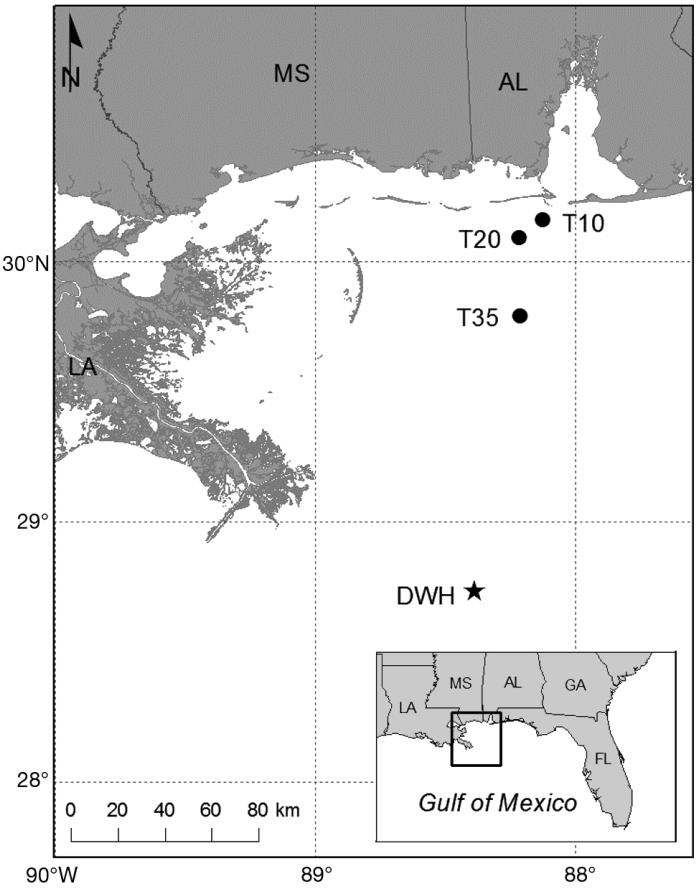

Fig. 1. Ichthyoplankton sampling stations (T10, T20, and T35) off the coast of Alabama, USA, and the *Deepwater Horizon* (DWH) blowout site in the northern Gulf of Mexico. Star: DWH wellhead

and were the same locations sampled by Graham et al. (2010) to document the uptake of oil-derived carbon into the planktonic food web. At each site, depth-discrete plankton samples were collected using a Bedford Institute of Oceanography Net Environmental Sampling System (BIONESS) with a 0.25 m^2 mouth opening fitted with 0.333 and 0.202 mm mesh nets. Samples were preserved at sea in 4% formalin and transferred to 95% ethanol after 48 h. 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), the Dauphin Island Sea Lab, and the University of Southern Mississippi.

Spanish mackerel was chosen as a target species to assess the effects of the DWHOS on larval fish condition, diet, and growth for several reasons. First, Spanish mackerel are prized by recreational fishermen in the nGOM and also support a commercial fishery (SEDAR 2012). Second, Spanish mackerel spawn on the inner continental shelf in 12–35 m of water in the nGOM (McEachran et al. 1980, Powell 1975), and larvae were present in the water column during the peak months of the oil spill (May–August) in abundances suitable for statistical comparisons among months and years. Third, they represent the response to the DWHOS of a high trophic-level species with specialized early-life piscivory and share a similar early life history as other species in the family Scombridae (e.g. king mackerel, tuna species). Finally, larval Spanish mackerel are relatively easy to identify to species, as opposed to many other taxa in the region; therefore, grouping larvae at a higher taxonomic level (e.g. genus or family) was not required.

Abundance and condition analyses

Areal abundance (larvae per 10 m^2) of larval Spanish mackerel collected in our ichthyoplankton surveys was compared across years (2007–2011) using an independent-sample Kruskal-Wallis test. Areal abundance data were unavailable for June and July 2011.

Individual larvae were imaged using a digital camera mounted on a dissecting microscope and measured using iSolution-Lite image analysis software. To determine differences in larval Spanish mackerel body condition among years before (2007–2009), during (2010), and after (2011) the DWHOS, we analyzed larval morphology using 7 measurements: notochord length (NL), depth at pectoral fin (DPF), depth at anus (DA), head length (HL), head height (HH), eye diameter (ED), and lower jaw length (LJL). Relationships among body measurements, particularly those associated with body depth and head size (e.g. DPF, HH), 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). In general, deeper-bodied and heavier larvae at a given length are in better body condition than their skinnier counterparts. Only specimens with the full suite of morphometric measurements were used in the analysis of body condition. 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 during collection and preservation (Suthers 1998). We did not correct for shrinkage because of the relatively narrow size range (1.7–5.0 mm) of the study specimens, similar handling time, and preservation methods (Theilacker 1986). To eliminate the influence of length on body shape, we standardized each body measurement to NL by using residual differences between the observed body dimension length (e.g. DPF) at a given NL relative to the predicted length.

Nonmetric multidimensional scaling (NMS) was used to ordinate fish according to body shape to investigate changes in body condition among years (Kruskal 1964, Mather 1976). A multivariate approach was selected for the morphometric analyses because of the lack of independence among the various body dimensions. 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). Because the distance measure we selected cannot calculate distances for negative integers, a nominal value of 1 was added to all residuals to generate all positive values. Kruskal-Wallis tests were used to explore differences in body shape among years and months. NMS axes may be interpreted and tested separately because they are orthogonal. Differences were considered significant at $\alpha \leq 0.05$.

Larval body condition was also quantified using the length–dry weight relationship. Individual fish were dried at 60°C for ≥16 h and weighed to the nearest microgram (µg) using a Mettler-Toledo XP26 microbalance. Relative condition factor (K_n) was calculated as:

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

where W is the dried weight of each larva, and W_{pred} is the predicted weight of each larva from a common

length–dry weight relationship (Le Cren 1951). Larval fish dry weight and notochord length were $\log_{10}$-transformed, and a linear regression was fitted to the data to calculate the W_{pred} values. Kruskal-Wallis tests were used to test differences in K_n among months and years.

Stable isotope analysis

Stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) were used to determine whether oil carbon was assimilated into larval tissue and assess changes in diet sources of larval Spanish mackerel, respectively. Oil from the DWHOS was more depleted in ^{13}C relative to natural levels in marine zooplankton in the nGOM. $\delta^{13}C$ 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:

$$\delta X = [(R_{sample} / R_{standard}) - 1] \times 1000 \quad (2)$$

where X represents the isotope of interest (^{13}C and ^{15}N) and R is the ratio of heavy to light isotopes ($^{13}C/^{12}C$ or $^{15}N/^{14}N$) for the sample being analyzed. $\delta^{13}C$ and $\delta^{15}N$ values of larvae were compared by month between 2010 and the other sampling years using Mann-Whitney U-tests.

Isotope values were not corrected for lipid content. Typically, $\delta^{13}C$ values are corrected for samples with C:N > 3.5 (Post et al. 2007); however, only 4 of the 120 samples had a C:N > 3.5 with a maximum 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 larval Spanish mackerel were considered negligible. Chemical preservation can also affect $\delta^{13}C$ and $\delta^{15}N$ values of larvae (Barrow et al. 2008). All larvae collected in this study were preserved using the same protocol of formalin and ethanol. Thus, any systemic effect of chemical preservation did not influence statistical comparisons of isotope values by month among years.

RESULTS

Larval abundance

In total, 768 Spanish mackerel larvae were collected during the study period (2007: n = 159; 2008: n = 8; 2009: n = 177; 2010: n = 264; and 2011: n = 160). Due to decreased sampling effort in 2008, the few larvae collected in that year were removed from all analyses. Larvae ranged in size from 1.3 to 11.37 mm NL (mean = 3.1 ± 1.2 SD mm). Larval abundance did not differ across years (independent-samples Kruskal-Wallis test, p = 0.49).

Condition analysis

Among the larvae collected, 348 larvae met our criteria for the morphometric condition analyses (Table 1). The NMS procedure settled on a 2-dimensional solution with a final stress of 13.2 and instability <0.00001 after 88 iterations of real data. The 2 resulting axes explained 93.4% of the variation in the larval morphometric measurements (Axis 1 = 75.4% and Axis 2 = 18.0%). Axis 1 was most strongly correlated with HH, HL, LJL, and DA, whereas Axis 2 was most strongly correlated with DPF (Table 2). Because Axis 1 explained most variation in body shape and Axis 1 scores were strongly and positively correlated with body dimensions (i.e. head size, body depth), these scores provided a suitable proxy for larval body condition. Axis 1 scores differed among years and months (Fig. 2). Larvae collected in 2010 had higher Axis 1 scores, and hence were in better body condition, as compared to those collected in 2007 and 2009 (independent-samples Kruskal-Wallis test, p < 0.001). Larval condition also varied by month; larvae collected in May had the lowest Axis 1 scores, whereas those collected in July had the highest Axis 1 scores (independent-samples Kruskal-Wallis test, p < 0.001).

Among the larvae collected, 361 larvae were available for the relative condition (K_n) analysis (Table 1).

Table 1. Number of samples by month and year used for the morphometric, dry weight (relative condition, K_n) and stable isotope analyses. Individual larvae were used for morphometric and dry weight analyses. Because of the small size of most larvae, multiple individuals (range from 1 to 10) were combined to achieve the minimum dry weight required (0.3–0.5 mg) for each stable isotope sample. Dashes (–) denote no available samples

Year	Month				Total
	May	Jun	Jul	Aug	
Morphometric analysis					
2007	10	37	–	27	**74**
2009	24	1	4	49	**78**
2010	13	26	93	1	**133**
2011	28	16	1	18	**63**
Total	**75**	**80**	**98**	**95**	**348**
Dry weight analysis					
2007	13	38	–	27	**78**
2009	26	1	4	51	**82**
2010	13	26	96	1	**136**
2011	29	16	1	19	**65**
Total	**81**	**81**	**101**	**98**	**361**
Stable isotope analysis					
2007	4	17	–	4	**25**
2009	4	3	–	6	**13**
2010	7	8	38	2	**55**
2011	17	2	–	9	**28**
Total	**32**	**30**	**38**	**21**	**121**

Table 2. Nonmetric multidimensional scaling (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). Axes 1 and 2 explained 75.4 and 18.0% of the variation in body size among *Scomberomorus maculatus* larvae, respectively

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

Larvae collected in 2007 and 2010 had higher K_n values as compared to those collected in 2009 (independent-samples Kruskal-Wallis test, $p < 0.001$; Fig. 3). However, larvae collected in 2011 did not differ significantly from any other year. Similar to the morphometric condition analysis, larvae collected in May had lower K_n values than larvae collected in July and August (independent-samples Kruskal-Wallis test, $p < 0.001$), while June larvae were not significantly

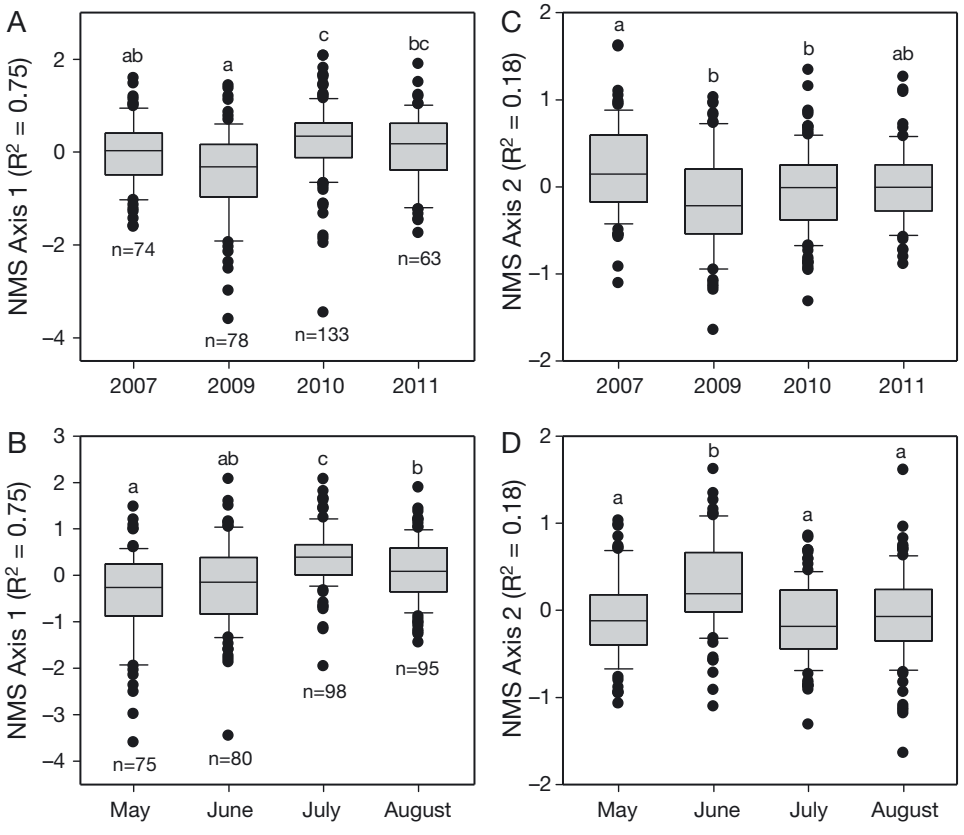

Fig. 2. Comparisons of morphometric nonmetric multidimensional scaling (NMS) Axis 1 (A,B) and Axis 2 (C,D) scores for larvae grouped by (A,C) year and (B,D) month. Boxes: interquartile ranges with medians; whiskers: 10th and 90th percentiles; circles: larvae with more extreme values. Different letters represent significant pairwise difference between groups after independent sample Kruskal-Wallis tests, adjusted for multiple comparisons

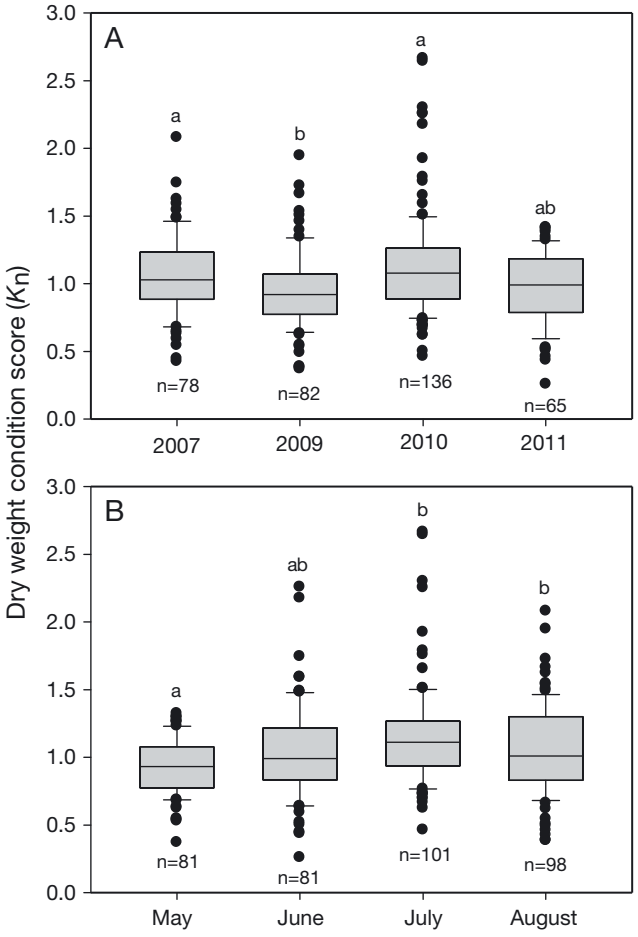

Fig. 3. Comparison of dry weight condition scores of larvae among (A) years and (B) months. Boxes: interquartile ranges with medians; whiskers 10th and 90th percentiles; circles: larvae with more extreme values. Different letters represent significant pairwise difference between groups after independent sample Kruskal-Wallis tests, adjusted for multiple comparisons. K_n: relative condition factor

different than any other month. Because the K_n values and NMS Axis 1 and 2 scores for larvae were not correlated with NL ($|r| < 0.01$, $p > 0.9$), the changes in body shape and relative weight we observed were not caused by allometric growth during this window of early development.

Stable isotope analysis

In total, 121 samples of multiple larvae were separately combusted for $\delta^{13}C$ and $\delta^{15}N$ measurements (Table 1). Samples consisted of 1 to 10 larvae, depending on size and mass, with a median value of 4 larvae per sample (520 larvae were combusted). $\delta^{13}C$ values ranged from −21.88 to −15.50‰ and $\delta^{15}N$ values ranged from 10.73 to 14.33 ‰ (Table 3).

Table 3. Number of samples (n) and mean $\delta^{13}C$ and $\delta^{15}N$ values (‰ ± 1SD) for Spanish mackerel larvae collected during ichthyoplankton surveys off the coast of Alabama, USA (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	55	−18.6 ± 0.7	12.1 ± 0.5
2011	28	−19.3 ± 0.7	12.7 ± 0.9

To test the effects of the oil spill on larval $\delta^{13}C$ and $\delta^{15}N$ values, samples were compared by month between 2010 and all other years combined (2007, 2009, 2011). Ideally, months of each year would be tested separately. However, low sample numbers necessitated combining non-oil spill years. (Increased sampling effort in 2010 resulted in twice as many samples for isotope measurements as compared to any other year.) Although there was an intriguing U-shaped pattern of depleted larval $\delta^{13}C$ values within 2010 during the peak of the oil spill, only August values differed from other years (Mann-Whitney *U*-test, $p = 0.01$; Fig. 4). Likewise, only larvae collected in May and August had different $\delta^{15}N$ values as compared to other years (Mann-Whitney *U*-tests, $p \leq 0.01$).

DISCUSSION

Morphometric and dry-weight condition indices revealed that Spanish mackerel larvae collected in 2010 were in better condition relative to similarly sized larvae collected before (2007, 2009) the DWHOS. By month, larval body condition was poorest in May and peaked in July. This monthly pattern was also observed in 2010 despite peak oil coverage in late June and July at the sampling stations used in this study (Graham et al. 2010). Based on length-at-age relationships generated from otoliths of larvae collected in this study (Ransom 2015), all larvae were less than 7 d old and thus were likely exposed to the released hydrocarbons.

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 variation in the physical environment in 2010 was within the range of that observed

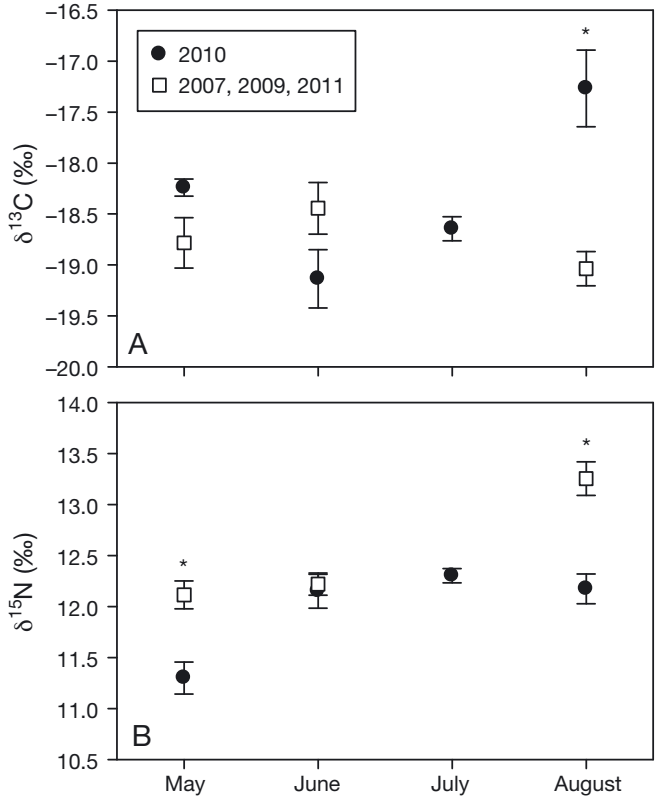

Fig. 4. Comparisons of monthly (A) $\delta^{13}C$ and (B) $\delta^{15}N$ values (mean ± SE) for larvae collected in 2010 and those collected in 2007, 2009, and 2011, combined. There were too few fish collected in July of 2007, 2009 and 2011 to perform isotope measurements. Mann-Whitney *U*-tests were used to compare isotope values by month between 2010 and the other years; significant differences denoted by (*)

during 2007–2009, with the exception of minor differences between July 2010 and historical July values. Thus, changes in zooplankton communities may be associated with the DWHOS and not changes in environmental conditions. Although, larval Spanish mackerel are mainly piscivorous (Finucane et al. 1990), increased zooplankton abundances would benefit planktivorous larval fishes (e.g. clupeids, carangids, engraulids), which are known prey items for Spanish mackerel (Finucane et al. 1990). Additionally, Ransom (2015) found that the diets of early larvae included other planktonic prey items (e.g. copepods, eggs) as opposed to older larvae and juveniles, which feed almost exclusively on ichthyoplankton (Finucane et al. 1990).

The monthly pattern of larval $\delta^{13}C$ values in summer 2010 was similar to the pattern observed in mesoplankton collected at the same stations by Graham et al. (2010). Especially intriguing is the depletion in larval $\delta^{13}C$ values during June, when oil coverage peaked at the coastal sampling sites used in this study. The magnitude of $\delta^{13}C$ depletion was substantially less in larval fish tissue (–0.4 to –2.2‰) as compared to mesozooplankton (–1 to –4‰; Graham et al. 2010). Moreover, $\delta^{13}C$ values of larvae collected in May 2010 did not differ from those values observed for larvae collected in May of the other sampling years before and after the DWHOS.

If oil carbon was assimilated into the tissue of larval Spanish mackerel, the isotopic signal could be reduced relative to that observed in mesozooplankton for several reasons. First, signals from isotope tracers are generally dampened through the successive trophic transfers and because of slower growth and longer generation times in higher trophic level organisms (Fry 2006). Second, differences in $\delta^{13}C$ values between oil and marine plankton are 4–8‰, making changes in source contributions extremely difficult to detect, especially considering the dynamic nature of carbon cycling on the continental shelf. Third, the timing of isotopic changes in marine organisms caused by addition of an isotopically unique source may have differed from the sampling schedule used in this study. Graham et al. (2010) found that isotopic values in mesozooplankton recovered within 2–4 wk after the oil spill. However, larvae in the present study were combined by month, and hence short-term changes in $\delta^{13}C$ values may have been masked by our longer sampling intervals and pooling of sampled larvae. To conclude, it is yet unclear whether oil carbon was assimilated by larval Spanish mackerel via bottom-up trophic transfers. Patterns of larval $\delta^{15}N$ values were also in the range of values observed for other years and did not suggest a change in feeding patterns by trophic level in summer 2010 as compared to the other years.

It is possible that other factors not examined in this study may have contributed to the observed annual and monthly variability observed in our condition metrics. By choice, we constrained our analyses to larvae within a relatively small size range (1.7–5.0 mm) to eliminate potential effects related to allometric growth. Because all larvae were less than 7 d old, it is possible that maternal effects may have contributed to some of the observed variability in condition (Green 2008). We were unable to account for the possible influence of maternal effects, but our analyses did not include yolk sac stages, and larvae as small as 3 mm were feeding, often, on other larval fishes (Ransom 2015). Previous laboratory studies have demonstrated the utility of our morphometric approach in quantifying larval condition relative to variable feeding (Powell & Chester 1985, Gisbert et

al. 2004). Given that larval Spanish mackerel are precocious, piscivorous feeders, we feel that dietary and environmental impacts likely had a substantial effect on these larvae, even at relatively small sizes. On a monthly scale, it is possible that the observed pattern of relatively high condition in larvae that were collected later in the summer may be related to environmental factors, such as temperature. Although growth rates of marine fish larvae are positively correlated with temperature (Houde 2008), early stage larvae are likely more limited by food availability. For example, variability in growth rates of larval Atlantic mackerel *Scomber scombrus* was related to densities of preferred prey for smaller size classes (<7 mm) and linearly related to temperature for larger (>7 mm) larvae (Robert et al. 2009). Further, DeVries et al. (1990) did not find a significant impact of month (May vs. September) for growth rates of larval and early juvenile Spanish mackerel (range of 2.8–22.0 mm) collected in the nGOM. It may be that for the relatively warm waters of the nGOM, the variability in temperature encountered during our sampling season (generally <5°C; Hernandez et al. 2010) may play less of a role in growth relative to prey availability.

Other factors besides the DWHOS may have also impacted larval fishes during the summer of 2010. During the oil spill, federal waters in the nGOM were closed to commercial and recreational fishing, which at its peak included an area approximately 229 270 km^2 in size (NOAA Fisheries 2010) and lasted much of the spawning period (May through September) for Spanish mackerel. 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 & 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 5 yr survey. Also, 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 (Filbrun et al. 2014). If fish eggs and larvae were more abundant in 2010, larval Spanish mackerel would have more available prey during the DWHOS. However, there is not strong evidence that zooplankton biomass or fish larvae abundances increased due to the release of adults from fishing pressure.

It is difficult to directly link changes in larval Spanish mackerel condition with the DWHOS because of the natural variability in the environmental conditions in the region. Although environmental conditions were not substantially different in 2010 as 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 relatively 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. For example, although larval Spanish mackerel showed resiliency during the summer of 2010, there is evidence that the effects of the DWHOS of larval fishes varied by taxon. Hernandez et al. (2016) found that larval red snapper *Lutjanus campechanus* were in poorer condition during and after the DWHOS (2010–2013) when compared to the period before the spill (2007–2009). Although these authors found that larval condition was negatively correlated to Mobile Bay, Alabama, discharge, red snapper larvae were in relatively poor condition in 2010, 2011 and 2013, even after accounting for river discharge and other environmental variables. Similarly, this study did not provide direct evidence to attribute observed patterns to the release of oil and dispersants during the DWHOS, but the findings do suggest that some combination of conditions related to DWHOS negatively impacted larval red snapper condition.

The results from our study suggest that larval Spanish mackerel body condition was resilient to the anticipated harmful effects of the DWHOS. It is possible that more subtle metrics of physiological health could provide different insights into short-term resiliency, whereas indices of annual recruitment could provide a better long-term picture of population-level health. Nevertheless, larvae were abundant in the water column in 2010 and were in better body condition than the other years surveyed in this study (i.e. 2007, 2009, 2011). These results, coupled with those of 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 DWHOS and in some cases even had increased productivity during summer 2010. Although these results are promising for the plank-

ton communities of the neritic zone in the nGOM, future analyses of long-term fisheries yields will provide better clues regarding the lasting impacts of the DWHOS on the nGOM coastal ecosystem.

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