Did the *Deepwater Horizon* oil spill affect growth of Red Snapper in the Gulf of Mexico?

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ABSTRACT

The explosion of the *Deepwater Horizon* (*DWH*) oil platform in 2010 released more than 200 million gallons of crude oil into the northern Gulf of Mexico (GoM). Elevated levels of carcinogenic polycyclic aromatic hydrocarbons (PAHs) were abundant in the upper water column throughout the event. Previous research suggests that PAHs may have negatively affected fishes in the northern GoM. Our objective was to test whether crude oil contamination from the *DWH* oil spill was correlated with changes in growth rates in adult Red Snapper, *Lutjanus campechanus*. We fit von Bertalanffy growth curves and back-calculated length-at-age using data collected from 2011–2013 during long-line surveys in the northern GoM and on the West Florida Shelf. No significant variation in von Bertalanffy growth parameters existed among the catch years; a combined-years model gave L_∞, k, and t_0 values of 82.91, 0.20, and 0.43, respectively. No significant difference existed between pre- (back-calculated) and post-*DWH* growth curves. However, annual widths of the fourth, fifth, and sixth increments (the dominant cohorts in the population) declined significantly post-*DWH* (2010–2012) by 13%, 15%, and 22%, respectively, and were significantly smaller than the mean width of each respective increment in pre-spill years (2006–2009). While the *DWH* event was related temporally to growth declines in the dominant adult age groups, other environmental factors (winds, temperature, and river discharge) may also affect growth. Accordingly, meridional (V) and zonal (U) winds, sea level height anomalies (a proxy for water temperature variation), and Mississippi River discharge were compared to increment widths but none of the factors were strongly correlated with variation in age-specific growth increments (maximum Pearson's $r = 0.47$). Therefore, we are unable to reject the hypothesis that the *DWH* resulted in growth rate declines as opposed to climatic variation.

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1. Introduction

Red Snapper, *Lutjanus campechanus,* is an economically important, relatively long-lived reef fish (Patterson et al., 2001a; Wilson and Nieland 2001) supporting both commercial and recreational fisheries in the Gulf of Mexico (GoM; Gold and Saillant, 2007). Although Red Snapper was both overfished (depleted) and experienced overfishing (Goodyear, 1988), conservation efforts under the Gulf of Mexico Fishery Management Council's Reef Fish Fishery Management Plan have resulted in an improved population status (Fischer, 2007; GMFMC, 1981; Strelcheck and Hood, 2007). Red Snapper enter the directed hook and line fishery between the ages of 2–4 years old (Szedlmayer and Shipp, 1994). They tend to associate with artificial reefs, reef pinnacles, rock ledges, and shelf-banks (Gallaway et al., 2009). In the western GoM, where natural reef structures are less common, they often associate with shallow water oil infrastructure (Gitschlag et al., 2003; Stanley, 1994), where they are potentially vulnerable to crude oil contamination. Notably, while Red Snapper exhibit high site fidelity in the eastern GoM (east of the Mississippi River), site fidelity to individual man-made structures is less than 1% per year in the western GoM (Patterson and Cowan, 2003).

During the 2010 *Deepwater Horizon* (*DWH*) oil spill, polycyclic aromatic hydrocarbons (PAHs), an abundant class of carcinogenic compounds in crude oil (Eisler, 1987; Short, 2003), were found at elevated levels in the upper 100 m of the water column (McNutt et al., 2012; Watson, 2014). Consequently, fishes in the northern GoM may have been contaminated by PAHs through ingestion of PAH-laden food or water (Mackay, 1991; McKim, 1994), direct contact via gills, or by transdermal exposure to contaminated sediment (Murawski et al., 2014). Overwhelming evidence from laboratory studies of larval and juvenile life-stages indicates that PAH contamination can result in developmental and morphological abnormalities, reduced survival, growth declines, mutagenic

effects, disrupted cardiac function, reproductive impairment, and increased mortality (Carls et al., 1999; Heintz et al., 2000; Incardona et al., 2014, 2011; Marty et al., 1997; Reynaud and Deschaux, 2006; Roy et al., 1999). Additionally, several studies have demonstrated that metabolism, somatic growth, and otolith growth are also highly sensitive to crude oil contamination (Brown-Peterson et al., 2015; Kerambrun et al., 2012; Moles and Norcross, 1998; Morales-Nin et al., 2007). Results of a 1995 study showed that Chinook salmon exposed to PAHs in an urban estuary had significantly altered concentrations of regulatory growth hormones suggesting that PAH exposure, through habitat or diet, affects growth by interfering with metabolic pathways (Casillas et al., 1995; Meador et al., 2006).

Field studies after the *DWH* on adult fish in the GoM found increased concentrations of *DWH*-associated PAHs in the bile of demersal fishes, increased prevalence of external skin lesions in northern GoM fishes, and aberrant protein expression in gill tissue of juvenile and adult estuarine fish (Murawski et al., 2014; Snyder et al., 2015; Whitehead et al., 2012). However none, to date, have evaluated growth effects. Evaluating the effects of PAH contamination on somatic growth of adult fishes is especially important as growth declines might lead to increased susceptibility to predation, decreased ability to find food and resources, and may be associated with reproductive impairment (Kime, 1995; Morales-Nin, 2000). Growth effects and reproductive impairment of the English sole have been found to co-occur at threshold levels of PAH contamination (Johnson et al., 2008). Moreover, reduced reproductive output may have significant implications for overall population productivity as Heintz et al. (2000) and Geiger et al. (1996) observed with pink salmon populations exposed to PAHs from the *Exxon Valdez* oil spill.

Red Snapper are a fishery management priority in the Gulf of Mexico, and evaluating the effects of potential oil contamination on population-level growth of adults is important to inform rebuilding strategies (GMFMC, 2013). The objective of this study was to determine whether growth rates in Red Snapper changed during the three years post-*DWH* using annual growth increment data and fitted von Bertalanffy growth functions (VBGFs). Using sclerochronology techniques (Jones, 1983) and increment width analysis (Campana and Thorrold, 2001), we estimated age-specific, annual growth variation in Red Snapper among years 2006–2009 (pre-oil spill) and 2010–2012 (post-oil spill). This provided direct comparison of age-specific growth rates pre- and post- oil spill as well as back-calculated length data necessary to estimate a VBGF applicable to the length-at-age relationship in Red Snapper immediately before the event. Because exogenous environmental variables can also affect growth in fishes, we tested the relative influences of meridional (north-south) and zonal (east-west) winds in the Gulf of Mexico (Black et al., 2011), temperature, and the influence of river outflow (a proxy for nutrient enrichment), in comparison to the timing of the *DWH* oil spill on annual growth in Red Snapper.

2. Materials and methods

2.1. Field sampling procedures

Demersal long-line sampling was conducted during the summers of 2011–2013 along pre-defined transects on the shelf and shelf edge of the northern GoM and the west Florida shelf (WFS). Sampling in 2011 occurred from June-August aboard chartered commercial fishing vessels following methods described in Murawski et al. (2014). Sampling in 2012 consisted of two sampling cruises, one occurring from June-July aboard a commercial, long-line fishing vessel (F/V *Pisces*) and the other in August aboard the
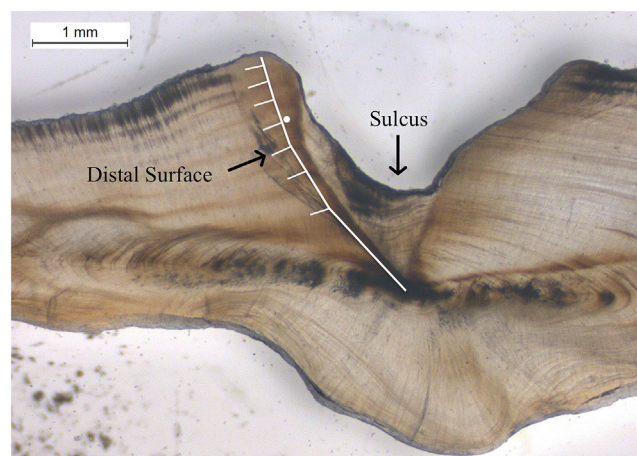

Fig. 1. Dorsal half of a thin-sectioned Gulf of Mexico Red Snapper sagittal otolith as viewed under transmitted light. The axis of measurement is shown along with increment width boundaries indicated by the horizontal white dash marks. The month of June 2010 is shown as a single white dot. Catch date was August 2013.

R/V *Weatherbird II*. Sampling in 2013 occurred in August also aboard R/V *Weatherbird II*. Sampling occurred within the distribution of the surface oil contamination from the *DWH* as well as west of the Mississippi River mouth. Red Snapper have the potential to move great distances (>100 km; Patterson et al., 2001b) so it is possible that Red Snapper collected west of the Mississippi River had originated from more oiled areas. Otoliths from the WFS were included in this analysis because there is evidence that hydrocarbons from the *DWH* were present on the west Florida continental shelf in June of 2010 (Weisberg et al., 2014).

Morphometric data including fork length and standard length (nearest cm), as well as weights (g), were obtained from all captured samples using a Marel® motion-compensated scale or a hand scale for animals larger than the measurement range of the Marel (6 kg). Left and right sagittal otoliths were excised and cleaned of the endolymphatic fluid and placed in individual envelopes.

2.2. Otolith aging

A total of 822 Red Snapper sagittal otoliths were used for age analysis. Of these, 327 otoliths were collected across 84 sampling stations in 2011, 387 otoliths were collected across 34 sampling stations in 2012, and 108 otoliths were collected across 16 sampling stations in 2013. Left otoliths were thinly sectioned (0.4 mm) along the transverse plane using a Buehler Isomet® low speed saw equipped with four, 10 centimeter impregnated diamond cutting blades (VanderKooy and Guindon-Tisdel, 2009). Left otoliths were chosen to be consistent with aging methods followed by Florida Fish and Wildlife Research Institute's (FWRI) Age and Growth Lab (J. Carroll, pers comm.). Right otoliths were only used if the left otoliths were incomplete, unavailable, or deformed as alternating between left and right otoliths can potentially cause discrepancies in the ageing process (VanderKooy and Guindon-Tisdel, 2009). The three resulting cross sections were mounted on glass slides with Flo-Texx®, a permanent toluene-based mounting medium, and viewed under transmitted light at 10X magnification with a SZ61 Olympus® dissection microscope.

Age analyses were performed using the cross-sections containing the primordial core by counting annuli along the dorsal axis from the primordial core to the otolith margin (Fig. 1). If annuli were not clear along any part of the otolith cross-section, they were viewed under reflected light because some annuli appeared more distinct under different light conditions. The width of the marginal increment was defined following a four-level, ordinal coding sys-

tem (VanderKooy and Guindon-Tisdel 2009). The final assigned age of the animal was based on the number of observed annuli, an *a priori* birthdate, the code assigned to the marginal increment and the catch date (VanderKooy and Guindon-Tisdel, 2009). The *a priori* birthdate assigned to Red Snapper in the northern GoM was assumed to be July 1, based on the demonstrated peak of their spawning season in the region (Goodyear, 1995). Therefore, to keep individuals in their true age classes (VanderKooy and Guindon-Tisdel, 2009), samples with catch dates prior to June 30th and a margin that was between two-thirds to fully complete (i.e. margin code = "4"), the age (in years) of the otolith was calculated as the number of observed annuli plus one. If samples had a margin code of "3" or less, the age of the otolith was calculated solely based on the number of observed annuli. For example, an otolith collected between January 1 and June 30th with six observable annuli and a "4" margin code would be assigned an age of seven. Likewise, for all samples collected after June 30th, the age was determined based only on the number of observed annuli along the described axis regardless of the observed margin code.

Quality assurance and control was performed on the data by the Age and Growth Lab at (FWRI) in St. Petersburg, Florida. Our annulus counts and margin codes were compared with those obtained by an independent, experienced otolith reader at FWRI who aged the otoliths under similar lighting conditions. If the reader assigned an age in disagreement with our previously determined age, discrepancies were resolved in favor of the FWRI reader. Most of the discrepancies in age occurred when determining the presence of an annulus on the edge and timing of the first annulus. Between-reader ageing precision was evaluated with the Coefficient of Variation (CV) and Average Percent Error (APE; Beamish and McFarlane, 1983).

Growth functions were fitted to fork-length-at-age data via non-linear least-squares using the *stats* package in R version 3.0.3 (R Core Team, 2014). The growth functions were fitted separately to data from each catch year. Non-parametric bootstrap resampling was performed using the *nlstools* package in R to obtain parameter estimates and the 95% confidence intervals (Baty and Delignette-Muller, 2013) of L_∞, K, and t_0. Likelihood ratio testing and residual sums of squares analysis (ARSS) was performed following methods described by Kimura (1980) and Ogle (2016) to test for differences among year-specific von Bertalanffy growth curves. Nested models were also compared with likelihood ratio testing to test for differences in the individual growth parameters among years.

2.3. Increment width analysis

A total of 190 otoliths were selected for increment width analysis representing a subset of the 822 otoliths used for the age and growth analysis. Seventy-four of these were from those collected in 2011, 89 were collected in 2012, and 27 were collected in 2013. Only otoliths with clearly defined annuli and margins along the dorsal axis of the sulcal groove were chosen for this analysis because of the clarity of their observed annuli banding patterns. As a result, otoliths no older than nine years were chosen for this analysis due to limited clarity of older samples and the small number of otoliths in ages 10+ (Fig. 3). Between-reader agreement of these otoliths was 100%.

Annual growth increments were measured continuously from the dorsal distal margin to the primordial core along the sulcal groove following an axis perpendicular to increment growth using a microscope-mounted camera and the Lumenera Infinity Analyze® software (Fig. 1). Annual growth increments were measured from the distal side of one opaque zone to the distal side of the previous year's opaque zone. Measurements were obtained three times on each otolith to estimate measurement variability. Measurements were then averaged and individual increment widths were summed to obtain an average "chord" length per otolith. The averaged increments were categorized by the fish age and growth year in order to make annual comparisons of average increment width by age.

Validation processes have determined opaque zone completion occurs in May (Patterson et al., 2001b) so the distal side of each opaque zone aligns with a June date. Thus, otolith increment formation was defined as between successive Junes. For example, increments that were assigned a formation year of 2010 started forming a translucent zone (when viewed under transmitted light) in June of that year. So, although the *DWH* oil spill occurred in April–July 2010 (McNutt et al., 2012), all increments assigned a 2010 formation year accreted post- *DWH.* Likewise, increments with a formation year 2009 would only have overlapped with the oil spill by ~1 month, as it began April 20, 2010. This measuring convention was necessary in order to make direct comparisons of complete increments formed before and after the oil spill. We chose age-specific increments three through seven to use for further analysis because they represented the dominant age classes in the survey catch (Fig. 3) and because rapid ontogenetic changes during the first and second year of life caused distortion of the first two increments (Matta et al., 2010). Also, the standard deviations of the first and second increment (0.10 and 0.06, respectively) were three and two times larger than the standard deviation of all other increments (0.03). Furthermore, sample size for increments eight and older were low.

2.4. Data analysis

Otolith increment width analysis was performed using 678 growth increments measured from 175 otoliths collected in the northern GoM and 15 collected from the WFS. Of the 175 from the northern GoM, 68 were collected west of the mouth of the Mississippi River but still within the distribution of surface oil. Regression analysis with Bonferroni adjusted alpha levels was performed using two contrast-coding schemes to compare age-specific increment widths formed among years before (n = 361) and after the *DWH* event (n = 317). We used forward-difference contrast-coding (R Core Team, 2011), which compared the mean width of each age-specific increment to the same age in adjacent years. We also used reverse helmert coding (R Core Team, 2011) to compare the mean width of each age-specific increment formed after the *DWH* event to the mean width of that same age-specific increment in all years previous to the event. Both coding schemes were used to analyze the widths of each age-specific increment (three thru six). These contrasts were evaluated within the context of linear mixed-effects models that included width measurements of age-specific increments, the year of formation for each individual, and fish identification number as a random effect.

To evaluate exogenous factors that could potentially account for variability in growth and thus increment width, we fitted linear mixed-effects models with environmental variables as fixed factors. The diagnostic plots of the linear mixed-effects models (see Herdter, 2014 for results) suggested poor model fits so we opted in favor of correlation analyses. Pearson correlations (*r*) were fitted between each age-specific increment width series and five environmental variables. North-south winds (V winds) and east-west winds (U winds) were considered due to their potential influence on currents and upwelling along shelf edges (Bakun, 1990; Black et al., 2011). Vector V and U wind data were obtained from the NCEP/NCAR Reanalysis[1] available at a 2.5° × 2.5° spatial resolution and a pressure level of 1000 mb. Mississippi River discharge data

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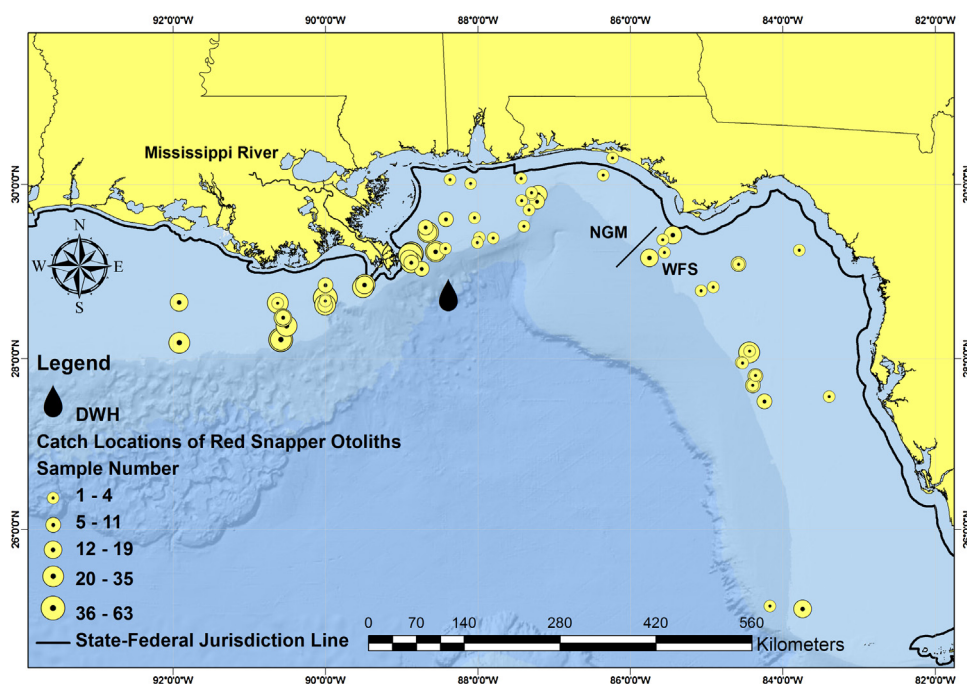[1] http://www.esrl.noaa.gov/psd/data/gridded/data.ncep.reanalysis.pressure.html

Fig. 2. Location of sampling stations and the number of Red Snapper sagittal otoliths extracted per station visited aboard commercial and research vessels along the West Florida Shelf (WFS) and northern Gulf of Mexico (NGM) during May–August 2011, June–August 2012 and August 2013.

measured at Tarbert Landing, MS (gage 01100) were included as an indicator of nutrient input (Black et al., 2011) and were obtained through the United States Army Corp of Engineers.[2] Finally, sea level height anomaly, an indicator of heat storage in the upper ocean (Chambers et al., 1998), was also included. Sea level height anomaly (SLA) data were obtained from the daily Ssalto/Duacs-Delayed Time MSLA data set[3] available at a $0.25° \times 0.25°$ grid.

We calculated monthly averages (June–May) of each environmental variable during formation year of each individual increment width. We also included monthly averages of each environmental variable for five months prior to otolith increment formation (January–May), to assess potential lag relationships that may have existed between climate and growth (Black et al., 2011). Each variable was extracted from the grid square containing the catch location of the otolith. We assumed catch location did not deviate significantly from the location in their adult years post-settlement since Red Snapper have relatively high site fidelity in the eastern GoM (Patterson and Cowan, 2003). Increment-width measurements and environmental variables were normalized to zero mean and unit variance to attain a common scale among all data sets. Correlations were performed using normalized age-specific increment widths and environmental variables using the *cor.test* function in R (Rizopoulos, 2006).

2.5. Deriving growth curves using back-calculated length

We used the Biological Intercept equation (1; Campana, 1990; Campana and Neilson, 1985) to back-calculate fish length (Morita and Matsuishi, 2001; Wilson et al., 2009):

$$L_i = L_{cpt} + (L_{cpt} - L_{0p}) * [(R_i - R_{cpt})/(R_{cpt} - R_{0p})] \tag{1}$$

L_i, fish length at age; L_{cpt}, fish length at capture;
    L_{0p}, fish length at biological intercept;

R_i, otolith radius at age;
R_{cpt}, otolith radius at capture;
R_{0p}, otolith radius at biological intercept.

Fish length at biological intercept and otolith radius at biological intercept were set to 0.2 cm and 0.001 cm, respectively (Richards, 2004). VBGF growth parameters were estimated using back-calculated length-at-age data before and after the *DWH* event; likelihood ratio testing following Kimura (1980) was performed to test for differences between the two growth curves.

3. Results

3.1. Age and growth

The age distribution of fish captured across long-line sampling stations from 2011 to 2013 (Fig. 2) was dominated by 4–6 year olds and smaller numbers of 7+ fish (Fig. 3). Ages ranged from 2 to 40 in 2011 with a mean of 5.76 ± 0.19 SE and median of 5, 3–24 in 2012 with a mean age of 6.43 ± 0.12 SE and median of 6, and 4–15 in 2013 with a mean age of 6.95 ± 0.15 SE and median of 7 (Fig. 3). No age 0 or 1 fish were sampled primarily because they are not available to offshore sampling gears. The oldest Red Snapper aged was 40 years, caught in 2011. Age 10 and older Red Snapper represented only 2% of the samples. Notably, 2010 and 2011 cohorts (those originating from spawning following the *DWH* event) were missing from the survey catches. Age 2 Red Snapper were absent in 2012 and 2013 survey catches as were age 3 Red Snapper in 2013. Between-reader APE was $1.74\% \pm 0.001$ SE and the CV was $2.47\% \pm 0.002$ SE. The VBGF curves calculated from fish sampled in each catch year were:

2011:	Fork Length = $84.93(1 - e^{-0.22[t-0.86]})$
2012:	Fork Length = $81.12(1 - e^{-0.23[t-0.04]})$
2013:	Fork Length = $80.11(1 - e^{-0.23[t-1.15]})$

Growth curve parameters were not significantly different among years (Table 1). Additionally, overall VBGFs were not significantly different among catch years so all data were combined and one global growth equation was estimated for the complete set (Table 1; Fig. 4). The VBGF model for all fish was: Fork
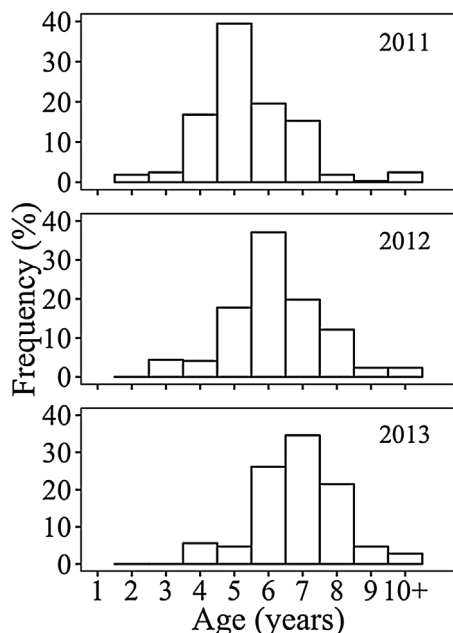
Fig. 3. Age frequency histograms of northern Gulf of Mexico and West Florida Shelf Red Snapper collected in 2011, 2012 and 2013.

Length = 82.91(1-e$^{-0.20[t-0.43]}$). Bootstrapped 95% confidence estimates were

L_∞ = 80.13 to 86.14, K = 0.17 to 0.23, and t_0 = 0.00 to 0.81.

3.2. Age specific annual growth

We measured the width of third increments formed in years 2006–2011, fourth increments formed in years 2007–2012, fifth increments formed in years 2008–2012, sixth increments formed in years 2009–2012, and seventh increments formed in years 2010–2012 (Table 2). Results from the forward-difference contrast-coding indicated a significant ($t = 4.37$, $p < 0.001$) 13% decline in growth at age 3 between 2007 and 2008 (Table 3). Moreover,

Table 1
Summary statistics comparing vonBertalanffy parameters estimates for Gulf of Mexico and West Florida Shelf Red Snapper collected during 2011–2013. Results of likelihood ratio tests and residual sums of squares analyses (RSS) comparing overall yearly growth models are presented next to the years. Additional statistics represent the results of likelihood ratio tests used to determine whether individual growth curve parameters were significantly different between years.

Hypothesis	χ^2	P
2011 vs. 2012: RSS: $F_{(608)} = 2.23$, $p = 0.08$	6.72	0.08
H$_0$ = L_∞	0.40	0.52
H$_0$ = k	0.02	0.86
H$_0$ = t_0	3.69	0.05
2011 vs. 2013: RSS: $F_{(407)} = 2.09$, $p = 0.09$	6.34	0.09
H$_0$ = L_∞	0.50	0.47
H$_0$ = k	0.24	0.62
H$_0$ = t_0	0.28	0.59
2012 vs. 2013: RSS: $F_{(408)} = 1.26$, $p = 0.28$	3.82	0.28
H$_0$ = L_∞	0.10	0.74
H$_0$ = k	0.41	0.52
H$_0$ = t_0	1.21	0.27
Pre- DWH vs. Post- DWH: RSS: $F_{(1250)} = 26.554$, $p < 0.001$	77.59	0.001
H$_0$ = L_∞	0.003	0.95
H$_0$ = k	0.54	0.45
H$_0$ = t_0	10.91	<0.001

there were significant declines in age-specific growth of fishes in age classes 4, 5, and 6 in 2010 (i.e., post- DWH) compared to growth in those age classes in the previous year (2009; Table 3). The mean width of the fourth increment declined by 13% ($t = 4.41$, p < 0.001), the width of the fifth increment declined by 15% ($t = 4.61$, $p < 0.001$), and the width of the sixth increment declined by 22% ($t = 3.82$, $p < 0.001$; Table 3). In contrast, results from the reverse helmert coding indicated no difference between growth at age 3 following the DWH compared to mean growth at age 3 in all previous years measured (2006–2009; $t = 1.61$, $p = 0.53$). However, there was a significant difference in age-specific growth at age 4 following the DWH compared to growth at age 4 in all previous years (2007–2009; $t = -4.58$, $p < 0.001$). Similarly, age-specific growth of ages 5 and 6 following the DWH (fifth and sixth increments formed in 2010) was significantly different than the mean age-specific growth of these ages in all previous years (fifth and sixth increments formed during 2008–2009; $t = -3.98$, $t = -3.82$, $p < 0.001$; Table 3). Although the sample sizes of the contrasts were
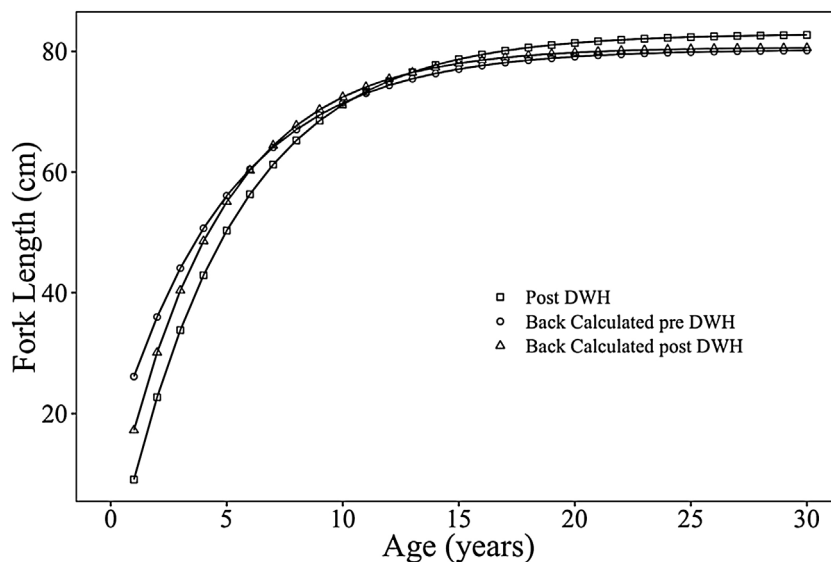

Fig. 4. Comparative vonBertalanffy growth curves estimated for northern Gulf of Mexico and West Florida Shelf Red Snapper. The diamonds represent the curve estimated using age data obtained from otoliths collected post-DWH and the upside-down triangles and hashed squares represent growth curves estimated via back-calculation techniques.

Table 2

Mean (SD) of otolith increment width measurements (mm) of age-specific increments three through seven in formation years 2006–2012 for Gulf of Mexico and West Florida Shelf Red Snapper. Sample sizes are reported as bold values. Note: *DWH* occurred in formation year 2010.

Age					
Year	3	4	5	6	7
2006	0.27(0.05), **20**	–	–	–	–
2007	0.28(0.03), **32**	0.23(0.04), **20**	–	–	–
2008	0.24(0.04), **71**	0.22(0.03), **32**	0.20(0.03), **20**	–	–
2009	0.24(0.03), **43**	0.23(0.04), **71**	0.21(0.03), **32**	0.19(0.03), **20**	–
2010	0.27(0.04), **17**	0.19(0.04), **43**	0.18(0.04), **71**	0.16(0.02), **32**	0.15(0.04), **20**
2011	0.29(0.04), **6**	0.21(0.05), **12**	0.18(0.03), **31**	0.16(0.03), **43**	0.14(0.02), **17**
2012	–	0.23(0.05), **3**	0.20(0.01), **2**	0.14(0.03), **10**	0.14(0.03), **10**

Table 3

Forward-difference and reverse-helmert contrast coding schemes used to assess differences in the mean values of third, fourth, fifth, and sixth otolith increments of Gulf of Mexico and West Florida Shelf Red Snapper formed before and after the *Deepwater Horizon* blowout. Asterisks and dots indicate p-values of <0.001 for the forward-difference and reverse-helmert schemes, respectively. Pre-DWH encompasses years 2009 and earlier.

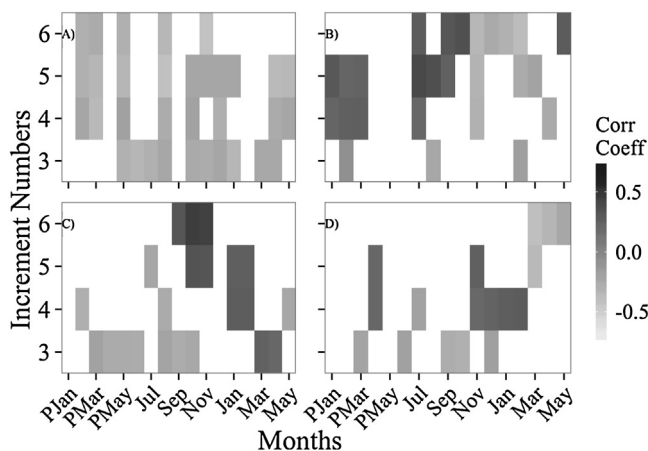| Age					
Forward-Difference	3	4	5	6	Reverse-Helmert
2006					–
2007					2007 vs. 2006
2008		*			2008 vs. '07, '06
2009					2009 vs.'08, '07, '06
2010		*,●	*,●	*,●	2010 vs. '09,'08,'07,'06
2011					2011 vs. pre-DWH
–					2012 vs. pre-DWH

Fig. 5. Correlation plots of age-specific otolith increment widths of Gulf of Mexico and West Florida Shelf Red Snapper and monthly averages of A) U vector winds, B) V vector winds, C) Mississippi River discharge, and D) sea level height anomaly in the Gulf of Mexico. Non-colored spaces indicate non-significant correlations at α = 0.01. Months preceded with a "P" indicate those previous to otolith increment formation.

unequal, the results of the reverse-helmert coding corroborate with those from the forward-difference coding. By applying back-calculation techniques to the increment width data, we obtained back-calculated lengths and used them to estimate a VBGF for years pre- *DWH* (2004–2009) and post- *DWH* (2010–2012) where: Pre-*DWH* Fork Length = 80.30 $(1-e^{-0.20[t-(-0.96)]})$ and post-*DWH* Fork Length = 80.64$(1-e^{-0.23[t-(-0.06)]})$ (Fig. 4). Likelihood testing between this model and the estimated model post-*DWH* indicated that L_∞ and k were not significantly different, although t_0 was significantly different (Table 1).

About one-third (37%) of the 272 Pearson correlations between age-specific increments and monthly averages of U and V winds, Mississippi River discharge, and sea level height anomaly resulted in significant correlation coefficients ($\alpha = 0.01$); (Figs. 5 and 6). The annual mean width of third increments was mostly nega-
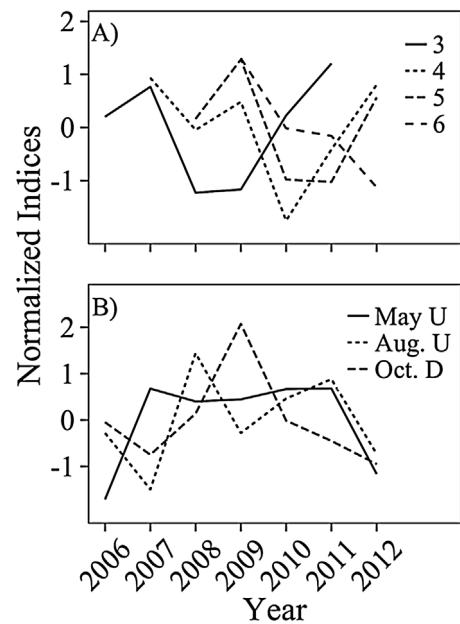
Fig. 6. Normalized indices of (A) the third, fourth, fifth, and sixth annual otolith growth increments of West Florida Shelf and Gulf of Mexico Red Snapper and (B) mean values of May and August U vector (May U, Aug. U) winds and October Mississippi River Discharge (Oct. D) in the Gulf of Mexico.

tively correlated with monthly averages of U winds, Mississippi River discharge, and sea level anomaly; however, none of the correlation coefficients were larger in magnitude than r = 0.34. The annual mean width of fourth increments displayed largest correlations with prior March U winds (r = 0.36). Likewise, fifth increments displayed largest correlations with prior March (r = −0.33) and August (r = −0.41) U winds as well as November V winds (r = −0.31) and October river discharge rates (r = 0.34). Sixth increments displayed largest correlations with August (r = −0.34) and November (r = −0.42) U winds, October (r = 0.36) and November (r = −0.34) V winds, October (r = 0.47) and November river discharge (r = 0.45), and March sea level anomaly (r = −0.40). However, none of the statistically significant correlation coefficients described more than 22% of variance (r = 0.47) in fish growth (Fig. 6).

4. Discussion

We performed increment width analysis on Red Snapper sagittal otoliths collected via scientific, demersal long-line sampling conducted during three years post-*DWH* (2011–2013). We found that average age-specific growth of the dominant age groups (4, 5, and 6) declined significantly post-*DWH* compared to growth at age in pre-spill years. Pearson correlation analysis between age-specific increments and monthly averages of wind, river discharge, and sea-level height resulted in no significantly compelling correlations. As such, these environmental variables are unlikely to explain growth

declines in Red Snapper that occurred in years coincident with the *DWH*. We are thus unable to reject the hypothesis that crude oil contamination from the *DWH* event was associated with the significant declines in growth observed for the dominant age groups sampled. Given the fact that otolith growth is, in general, proportional to somatic growth (Campana and Neilson, 1985; Neilson and Geen, 1985; Mossegard et al., 1988) and somatic growth is positively related egg production (Helfman et al., 2009; Hixon et al., 2014), the observed growth declines could potentially result in lowered egg production and stock productivity of northern GoM Red Snapper compared to years pre-*DWH* (Geiger et al., 1996; Hixon et al., 2014).

4.1. Age analyses

Our results from age analyses are consistent with previous studies on Red Snapper in the northern Gulf of Mexico (Patterson et al., 2001b; Wilson and Nieland, 2001). Low numbers of fish older than 7 years old were most likely due to strong year classes produced in the early 2000s, and depletion of the older age groups due to previous overfishing (Wilson and Nieland, 2001). A GoM-wide survey of age and growth of Red Snapper found fish older than 10 years represented less than 1% of the 1800 Red Snapper sampled which corroborates our findings (Saari et al., 2014). Additionally, recent stock assessments indicated a paucity of animals greater than 8 years old in any of the Red Snapper fisheries in the GoM population (SEDAR, 2013). The strong 2006 cohort observed during 2011–2013 as well as the lack of post-*DWH* cohorts are consistent with recent stock assessments indicating strong 2006 year classes and reduced recruitment of the eastern GoM sub-stock in years after the *DWH* oil spill (SEDAR, 2013). The role of this spill contributing to reduced cohort abundance is unclear, but cannot be eliminated as a cause.

4.2. Growth analyses

We did not detect differences in the VBGFs estimated for the three years post-*DWH*. Our final estimated growth function was similar to those from previous studies (Manooch and Potts, 1997; Nelson and Manooch, 1982; Patterson et al., 2001b; Szedlmayer and Shipp, 1994; Wilson and Nieland, 2001). The same fast growth is observed in young ages, followed by a decline in growth reaching an estimated asymptote between 82.8 cm (current study) and 96.7 cm (Szedlymayer and Shipp, 1994). There was a significant difference between VBGFs fitted with pre- and post-*DWH* data most likely due to the difference in estimated t_0 but this value does not have much biological significance as a fish of length zero does not exist (Ogle, 2016). Therefore, we conclude there is no real biological difference between pre- and post-*DWH* growth curves. However, because back-calculation procedures depend on measurements of otolith radius-at-age (R_i, Eq. (1)), which is a summation of all increment widths, differences in widths of age-specific increments among ages are smoothed by fitting an overall growth curve. Also, these growth functions were calculated with length data only for ages 3 through 6 (pre-*DWH*) and 3 through 7 (post-*DWH*), so our estimates of maximum length may have been biased. Furthermore, VBGFs provide estimates only for a growth rate constant between an extended age-range but do not capture the high-resolution variability in age-specific growth achieved by increment analysis.

4.3. Increment width analyses

There were significant declines in age-specific growth of the dominant age groups coincident with the *DWH*. A number of exogenous factors can affect growth in fishes (Helfman et al., 2009), including temperature variation, food and nutrient availability, photoperiods, oxygen levels, salinity, predator density, social interactions, and pollutants (reviewed by Wootton, 1990). Likewise, endogenous factors can affect growth (Berkeley et al., 2004; Chambers and Miller, 1995; Fischer, 2007), so we expected some annual variation in growth. High-frequency variation in growth chronologies has been observed in other GoM *Lutjanus* species (Black et al., 2011). There were contrasting patterns of growth following the *DWH* event between age 3 fish (increment width did not differ from pre-*DWH* values) and fish ages 4 through 6. As age 3 Red Snapper occupy similar habitat and exhibit similar behavioral and movement patterns as those aged 4, 5, and 6 (Gallaway et al., 2009; Patterson and Cowen, 2003), they could potentially be exposed to the same toxic constituents present in the water column. However, a possible explanation for contrasting growth patterns is that during the time of the third increment formation, rapid growth distorted third increments along the sulcal groove (Matta et al., 2010). Also, it is possible that different food resources of juvenile and adult Red Snapper were disproportionately influenced by oil contamination. Romero et al. (2015) found that there was increased deposition of hydrocarbons to the northern Gulf of Mexico seafloor in 2010 via hydrocarbon-contaminated marine snow following the *DWH*. As adult Red Snapper are more dependent on mud and sand associated organisms than are juvenile and pre-adult fish (Wells et al., 2008), they may have been consuming more contaminated prey items due to the disproportionate abundance of hydrocarbons in the sediment.

We correlated year- and age-specific growth increments with four potential environmental parameters. Although there was a negative growth anomaly in 2010, we saw no such environmental anomaly. While our results indicated several weak but significant correlations these were most likely due to the limited time series and subject to cross correlations among climate variables. Because the changes in growth pre- and post-*DWH* were much greater than can be explained by these data, we concluded that none of the environmental parameters explained the systematic reduction in age-specific growth between ages 4 and 6 post-*DWH*. It is worth noting that Black et al. (2011) found V and U vectors winds were significantly correlated with Red Snapper growth. However, they used growth chronologies that extended more than 15 years. Perhaps a larger sample size of increment width measurements and a longer time series would resolve the relative roles of environmental parameters and *DWH* on declines in growth of Red Snapper. Such data would also complement the Black et al. (2011) chronology study of northern GoM Red Snapper, which only accounted for trends pre-2006.

Previous studies of the effects of oil exposure on wild fish growth have primarily been limited to larval and juvenile life stages (Carls et al., 1999; Heintz et al., 2000; Kerambrun et al., 2012; Short, 2003), generally because most past oil spills did not occur over wide spatial extents commensurate with population-level effects as well as logistical constraints on studying larger, older individuals. Because the *DWH* spill was prolonged (~3 months) and widespread (McNutt et al., 2012), it provided an opportunity for evaluating growth effects on demersal fish populations with limited migration potential. Our results of age-specific growth indicated significant declines in otolith widths following the *DWH* event that were primarily related to a year effect (2010) but only weakly correlated with exogenous environmental variation. Longer time series may be useful in assessing these variables, but with the available data no compelling alternative hypothesis explaining significant growth declines can be supported.

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