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ARTICLE

Temporal and spatial patterns in population demography of Tilefish in the Gulf of Mexico

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Abstract

Objective: The objectives of this study were to compare population dynamics of Tilefish *Lopholatilus chamaeleonticeps* before and after the 2010 *Deepwater Horizon* (DWH) oil spill in the north-central Gulf of Mexico (GoM) as well as inside and outside the spill area in the western and southwestern GoM (off Mexico).

Methods: Due to the availability of prespill samples of Tilefish, we were able to evaluate growth, mortality, and condition factors during two time periods (2000–2009 versus 2011–2017). Samples were derived from commercial landings and research vessel surveys using demersal longline fishing gear.

Result: Although some von Bertalanffy growth parameters differed for fish caught before and after the spill within the spill area, confidence limits for predicted growth curves overlapped for ages >10, while predicted growth for ages <10 declined somewhat after the spill. Tilefish grew faster off Mexico than in the northern GoM. Total instantaneous mortality rates (Z), estimated from aggregate multi-year catch curves, were highest off Mexico (0.39 ± 0.05 SE), lowest in the western GoM outside the spill area (0.21 ± 0.03), and similar before and after the DWH spill within the spill zone (0.32 ± 0.02).

Conclusion: Although Z on the stock within the spill area apparently did not change, differences in fishing mortality may have compensated for changes in natural mortality. Because 90% of the fish that were aged after the spill were alive prior to the spill, their accumulated growth history may have masked postspill growth changes. As we are now 14+ years past the 2010 spill, comparisons of population dynamics from samples collected now and in the future may provide a clearer picture of the strength of incoming year-classes and the long-term implications of the spill on Tilefish populations.

KEYWORDS

Deepwater Horizon, *Lopholatilus chamaeleonticeps*, population dynamics, Tilefish

INTRODUCTION

The Tilefish *Lopholatilus chamaeleonticeps* is a demersal, nonmigratory species occurring throughout the Gulf of Mexico (GoM) and in the western Atlantic from Nova Scotia to Venezuela (Aiken et al. 2015). Typically slow growing and long-lived, the estimated maximum longevity is about 30 years, and age-10 and older (age-10+) adults are common (Palmer et al. 2004; Lombardi et al. 2010; Lombardi 2012; Lombardi-Carlson and Andrews 2015). The species is commercially fished; in the GoM, it is primarily fished in a small, directed demersal longline fishery (Scott-Denton et al. 2011) and is managed under the Reef Fish Fisheries Management Plan of the GoM Fishery Management Council. Fishery landings averaged 183 metric tons/year during 2000–2022 (Figure S1 available in the Supplementary Information separately online). Adult Tilefish maintain burrows in mud–clay habitats in water depths of up to 500 m (National Marine Fisheries Service [NMFS] 2019). Tilefish have high site fidelity; previous tagging studies indicate adult movements of no more than 2 km/year (Grimes et al. 1983). Because of their burrowing behavior and lack of extensive movements, Tilefish may be particularly susceptible to pollution events that result in contaminant accumulation in the benthos (Snyder et al. 2015).

The *Deepwater Horizon* (DWH) oil spill in the northern GoM (Lubchenco et al. 2012) overlapped Tilefish habitats, with much of the DWH oil eventually sequestered in sediments at the edge of the continental shelf and in the abyssal region (Brooks et al. 2015; Romero et al. 2015). Oil contamination from the DWH spill likely exposed Tilefish through ingestion of contaminated sediments via their burrow digging and maintenance and potentially through exposure to contaminated near-bottom waters (Snyder et al. 2015, 2019, 2020, 2023). Relatively high levels of polycyclic aromatic hydrocarbon (PAH) compounds and metabolites in Tilefish (Snyder et al. 2015; Pulster et al. 2020a, 2020b) were associated with a variety of sublethal health effects, including an increased incidence of skin lesions (Murawski et al. 2014, 2021), a series of liver abnormalities (Snyder et al. 2019, 2023), and progressive reductions in body condition and percent liver lipid content, both of which were negatively correlated with hepatic PAH concentrations (Snyder et al. 2019). A number of other GoM species exhibited changes in growth, feeding ecology, abundance trajectories, and other population traits after the DWH spill, including Red Snapper *Lutjanus campechanus* (Tarnecki and Patterson 2015; Herdter et al. 2017; Patterson et al. 2023) and other demersal and pelagic species (Patterson et al. 2023).

Given the above effects associated with elevated PAH exposure in Tilefish and other shelf species, we designed this study to evaluate whether exposure effects were sufficient to result in impaired rates of body growth and elevated total mortality of adults. Because of the broad spatial scale of sampling, particularly after the DWH spill, we were also able to conduct comprehensive evaluations of spatial demographics of Tilefish throughout the GoM. Our study benefited from extensive prespill baselines of fish growth rates that were estimated from data collected during 2000–2009, prior to the DWH spill in 2010 (Lombardi et al. 2010; Lombardi 2012; Lombardi-Carlson and Andrews 2015). Prespill data consisted primarily of length and weight measurements and otolith-based age estimates derived primarily from fishery-dependent port and observer sampling augmented by limited fishery-independent longline survey samples (Figure 1). Postspill information on Tilefish lengths and weights, otolith samples, and body condition factors were determined from Tilefish samples obtained from demersal longline surveys in areas within the DWH spill footprint, elsewhere in U.S. waters of the GoM (primarily off Texas and western Louisiana), and off Mexico (Figure 1B; Murawski et al. 2018; Pulster et al. 2020a).

Using the pre- and postspill data gathered from the sources outlined above, we evaluated three questions regarding Tilefish demographics in the GoM:

1. Are there differences in the demographics (age composition, growth, and estimated total instantaneous mortality rate Z) of Tilefish caught before and after the DWH spill within the area where the spill occurred?
2. Do the demographics of Tilefish caught from the areas within the spatial domain of the DWH oil spill differ from the demographics of fish caught elsewhere in the northern GoM?
3. Are there differences in adult Tilefish demographics between northern (U.S.) and southern (Mexican) GoM waters?

The first question provides a before–after test of the potential effects of the DWH spill on body growth and

Impact statement

Adult Gulf of Mexico Tilefish did not differ in growth or total mortality before versus after the 2010 *Deepwater Horizon* oil spill. Condition of postspill fish was lower than prespill. Mexican fish grew faster but had lower condition and higher mortality than U.S. fish. Postspill fish analyzed were predominantly born before the spill.

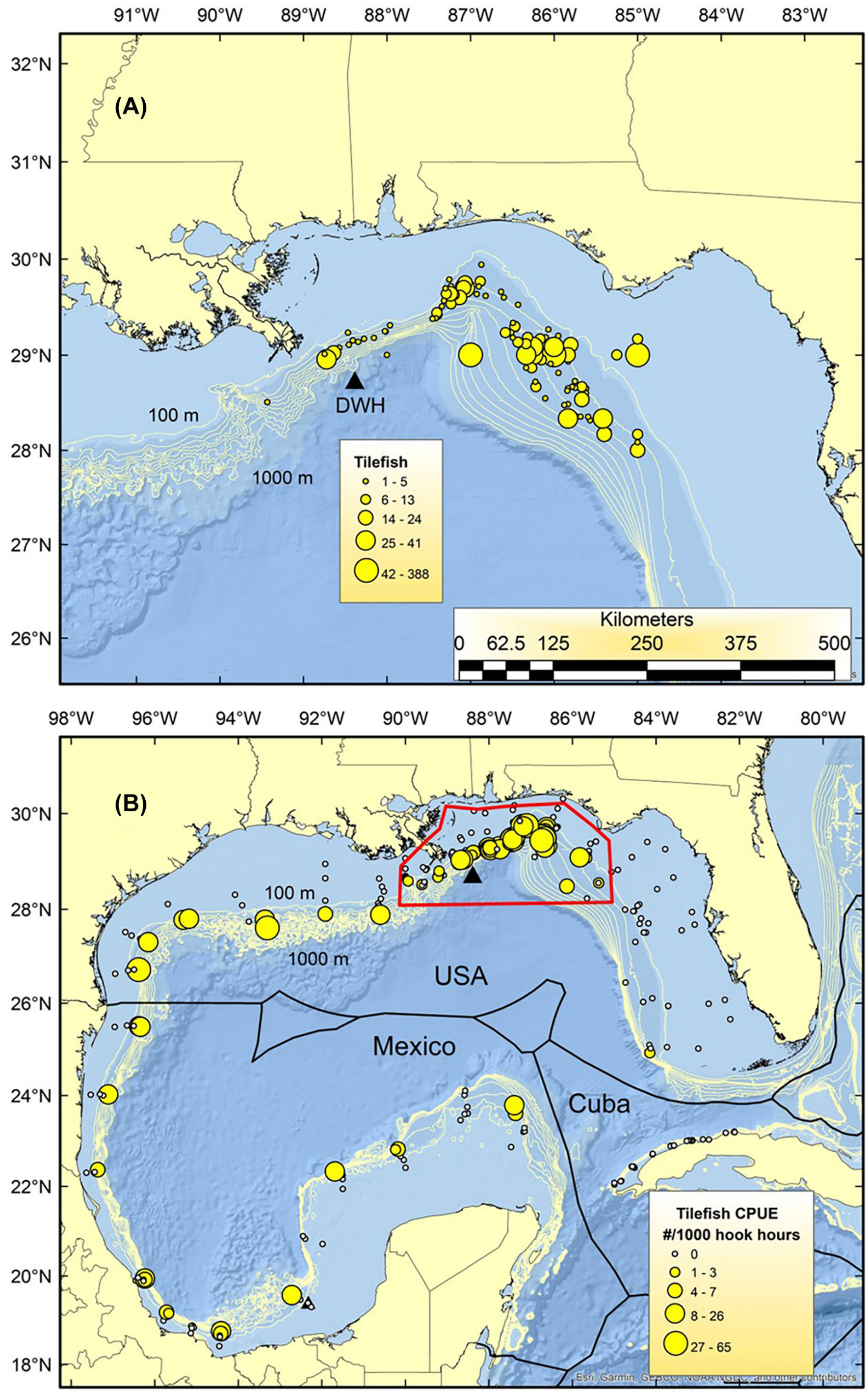

FIGURE 1 (A) Map of Gulf of Mexico sites sampled for Tilefish from 2000 to 2009, primarily from commercial fishery catches; and (B) demersal longline survey samples collected during 2011–2017 (CPUE = catch per unit effort). The black triangle in each panel denotes the site of the *Deepwater Horizon* (DWH) oil rig explosion. The red polygon in panel B represents the DWH spill footprint for this study.

mortality. The second question provides a test of a putative "control" area of relative ecological similarity to the area affected by the DWH spill. The second and third questions also provide baseline information not heretofore collected and analyzed, which may be useful for measuring impacts in the event of a future large-scale spill in the northwestern or southwestern GoM (Murawski et al. 2020).

METHODS

Sample collection

Pre-2010 Tilefish samples were collected by NMFS Southeast Fisheries Science Center sampling programs throughout the northern GoM (Lombardi 2012; Table 1;

TABLE 1 Number of Tilefish sampled and otoliths aged by year, country of capture (United States or Mexico), and location of U.S. samples relative to the *Deepwater Horizon* (DWH) oil spill footprint (Figure 1B).

	U.S. samples within the DWH footprint		U.S. samples outside of the DWH footprint		Mexican samples	
Year	Fish	Aged	Fish	Aged	Fish	Aged
2017	129	119	4	4		
2016	0	0	142	134	96	91
2015	180	168	0	0	44	39
2014	130	47	30	11		
2013	165	97	0	0		
2012	372	161	59	11		
2011	49	44	33	29		
2010 (DWH oil spill)						
2009	521	516				
2008	30	29				
2007	76	74				
2006	121	117				
2005	266	254				
2004	396	385				
2003	230	222				
2002	67	66				
2001	52	52				
2000	17	17				
Total	2801	2368	268	189	140	130

Figure 1A). Since most Tilefish that are landed by the commercial fishery are gutted at sea, Trip Interview Program port agents made special requests to willing commercial captains to collect whole fish for obtaining body weights in addition to sampling for fish lengths and otoliths for aging studies. At-sea observers that were onboard commercial longline vessels (Scott-Denton et al. 2011) also provided biological samples (otoliths in addition to individual fish lengths and weights). For consistency, only Tilefish sampled from longline gear catches were used in this analysis. All commercial fishery sites sampled north of 28°N latitude and east of 90°W longitude were included in our analysis (Figure 1A). Methodologies, including standardization procedures and age validation for that particular set of samples, are detailed by Lombardi et al. (2010).

Although most prespill fish were sampled from fishery catches, two fishery-independent survey series provided additional Tilefish biological samples for the prespill period. These longline surveys used a depth-stratified random sampling design (Lombardi 2012). The surveys were conducted by deploying a 1.85-km (1-nautical-mile) mainline consisting of 100 size-15/0 circle hooks baited with Atlantic Mackerel *Scomber scombrus* and soaking for 1 h prior to retrieval. Fish lengths for all commercial and survey data were recorded as fork length (FL) in millimeters, and whole fresh weights were recorded in grams (the values were converted to cm and kg, respectively).

Postspill Tilefish samples were obtained from a series of demersal longline surveys occurring from 2011 to 2017 around the GoM continental shelves (Figure 1B). Inshore to offshore transects were selected, with (usually) six stations per transect, sampling a range of depths from 37 to 274 m (Murawski et al. 2018). In 2011, surveys were conducted onboard chartered commercial fishing vessels. Most of the sampling in 2012 was done onboard chartered commercial fishing vessels, but some samples were also collected onboard the RV *Weatherbird II* in 2012. The RV *Weatherbird II* was the sole research vessel used in subsequent years. A series of six surveys (2011, 2012, 2013, 2014, 2015, and 2017) was conducted within the DWH impact area in the north-central GoM. Two surveys covered Mexican waters (2015 and 2016), one survey occurred off northwest Cuba (2017), and one survey occurred off Texas and western Louisiana (2016).

For the postspill longline surveys, the main line was 9.26 km (5 nautical miles); an average of 446 2.4-m leaders with size-13/0 circle hooks were set, and either Atlantic Mackerel or primarily Humboldt squid *Dosidicus gigas* wings were used as bait, mixed randomly along the set (Murawski et al. 2018). Soak time averaged

2.1 h. The FLs (cm), whole weights (kg), and liver weights (g) from Tilefish subsamples were recorded from these surveys (Table 1; Figure 1B). Sagittal otoliths were also collected from each subsampled Tilefish (Table 1) and were stored dry in scale envelopes until they were sectioned for aging.

Otolith analysis

One otolith from each Tilefish collected during both the pre- and post-DWH spill periods was sectioned using a Buehler Isomet low-speed saw (Vanderkooy and Guindon-Tisdel 2003). Four blades were used to extract three thin, transverse sections that were each approximately 0.3 mm thick. For consistency, the left otolith was sectioned if available; if not, the right otolith was used. Otolith cross sections were then mounted on a microscope slide using FloTexx epoxy and were examined under a microscope using transmitted light at 10× power to determine age.

Annual growth banding in Tilefish has been validated using lead–radium dating (Lombardi-Carlson and Andrews 2015). Annuli (consisting of pairs of opaque and translucent bands) were counted from the primordial core either along the ventral axis edge or the ventral sulcus edge depending on readability. After age was determined, age and corresponding length were used to estimate growth parameters (e.g., von Bertalanffy 1938) and to calculate the total mortality rate Z from catch-curve analysis using numbers sampled at age (e.g., Hilborn and Walters 1992).

Precision of age determinations

Two indices of aging precision (percent agreement [PA] and average percent error [APE]) were determined using methods outlined by Campana (2001). The primary reader for the pre-DWH spill samples was L.A.L.-C. For reading of the postspill samples, L.A.L.-C. trained G.J.H. in age estimation for Tilefish. Between the first and second age reads of postspill samples by the primary reader (G.J.H.), a subset of 100 otoliths was read by the more experienced L.A.L.-C., which clarified interpretations to be more consistent with previous aging. The second reads were considered more accurate and were used in further analyses. Age precision estimates were calculated between primary reader and secondary reader determinations as well as between the first and second readings of all samples by the primary reader (G.J.H.). Because there were only 100 samples independently aged by both readers, an age–bias plot was constructed only from the first and second reads accomplished by G.J.H. (Figure S2).

Group identification

To determine whether population demographics differed by potential exposure to DWH oil, putative DWH-affected fish were designated based on whether or not the station of capture was within the geographic distribution of the spill (Murawski et al. 2014; Figure 1B). All prespill age, length, and weight samples were selected to be within the zone designated as the DWH spill "footprint" area (Figure 1; Table 1; Brooks et al. 2015; Romero et al. 2015). Fish from those sites were also found to have declining condition factors during the years since the DWH oil spill, corresponding with an increase in PAH exposure (Snyder et al. 2023). All other Tilefish collected from transects within the U.S. Exclusive Economic Zone (EEZ) were designated as being from outside of the DWH spill footprint (Table 1).

Data analysis

Differences in length frequencies were tested using a Kolmogorov–Smirnov (K–S) test with 1000 bootstrap iterations to evaluate differences in size structure between groupings (e.g., pre- and post-DWH spill; Neumann and Allen 2007). Length–weight relationships were compared between the pre- and postspill periods, between central (spill footprint) and western GoM areas, and between U.S. and Mexican waters. Length–weight relationships were fitted as

$$W = \alpha L^{\beta},$$

where W is total (whole) weight (kg), L is FL (cm), and α and β are parameters.

To determine whether differences in parameters were statistically significant between groups (Table 2), the above equation was log transformed:

$$\log_{10}(W) = \log_{10}(\alpha) + \beta \log_{10}(L).$$

Analysis of covariance (ANCOVA) was used to test for differences in slope (β) between pairs of regression equations. Length and whole-weight measurements were also used to calculate indicators of Tilefish body condition. The most commonly used measure of condition is Fulton's condition factor (K_f; Bolger and Connolly 1989), which is given as

$$K_f = \left(W / L^3\right) \times 100,$$

where W is weight (g) and L is FL (cm).

We also calculated the Le Cren (1951) index, known as the relative condition factor (K_n), comparing the predicted weight at a given length to the actual weight of the fish, although it can only be used to compare groups of fish when

TABLE 2 Estimates of weight–length relationship parameters (α and β) for Tilefish caught from sites in the *Deepwater Horizon* (DWH) oil spill footprint before the spill (2000–2009) and after the spill (2011–2017), all U.S. and Mexican samples obtained during 2011–2017, and all U.S. samples obtained outside of the DWH footprint during 2011–2017. ***highly significant at $p < 0.001$. FL, fork length; SD, standard deviation; SE, standard error.

		FL (cm)		Weight (kg)							95% confidence limits	
Samples	*N*	Range	Mean (SD)	Range	Mean (SD)	Parameter	Estimate	SE	*t*	*p*	Lower	Upper
Before DWH spill	437	29–104	54.6 (11.4)	0.26–14.00	2.3 (1.7)	α	6.50×10^{-6}	7.0936×10^{-7}	9.1573	<0.001***	5.08×10^{-6}	7.91×10^{-6}
						β	3.1525	0.0257	122.8614	<0.001***	3.1011	3.2039
After DWH spill	979	34–106	57.0 (13.4)	0.35–15.80	2.5 (2.2)	α	7.39×10^{-6}	6.6875×10^{-7}	11.0515	<0.001***	6.05×10^{-6}	8.73×10^{-6}
						β	3.1079	0.0208	149.3436	<0.001***	3.0663	3.1495
All U.S. waters	1154	34–106	57.0 (13.5)	0.35–15.80	2.5 (2.2)	α	7.24×10^{-6}	5.9791×10^{-7}	12.1139	<0.001***	6.05×10^{-6}	8.44×10^{-6}
						β	3.1092	0.0189	164.0931	<0.001***	3.0714	3.147
Mexico	137	36–97	61.0 (12.7)	0.43–11.55	2.8 (2.1)	α	2.00×10^{-6}	6.6471×10^{-7}	3.0087	<0.001***	6.70×10^{-7}	3.33×10^{-6}
						β	3.3959	0.0764	44.4241	<0.001***	3.24	3.5487
All other U.S. sites	158	34–104	57.9 (13.4)	0.38–14.80	2.4 (2.1)	α	5.91×10^{-6}	1.0366×10^{-6}	5.7054	<0.001***	3.84×10^{-6}	7.99×10^{-6}
						β	3.1351	0.04	78.406	<0.001***	3.06	3.2151

β values in the length–weight relationships are not significantly different (Bolger and Connolly 1989). The index K_n is defined as

$$K_n = W / \widehat{W},$$

where W is the actual weight and $\widehat{W}$ is the predicted weight from the length–weight equation.

Mean K_f and K_n were compared between groups by using Welch's t-test; for K_n, we used a common length–weight equation when the parameters did not differ between the groups being compared (e.g., before versus after the DWH spill; United States versus Mexico; DWH footprint versus the rest of the U.S. sites).

Sex-aggregated growth curves for each Tilefish group were calculated using the von Bertalanffy (1938) equation,

$$L_t = L_\infty \times \left[1 - e^{-K \times (t - t_0)}\right],$$

where L_t is the length at time t; L_∞ is the asymptotic length; K is the growth coefficient; t is time (years); and t_0 is the theoretical age at a length of zero.

Growth curves were calculated for each group, and 95% confidence intervals were estimated via bootstrapping ($n = 1000$ iterations). Growth curves for each pair of groups (Table 3) were then compared using Kimura's likelihood ratio test (Tables S1–S3 available in the Supplementary Information separately online) to determine which parameters significantly differed between groups (Kimura 1980). Model selection procedures using Akaike's information criterion (AIC) and the Bayesian information criterion (BIC) determined the best model fits (Tables S4–S6; Burnham and Anderson 2002).

Estimates of Z were calculated and compared for each fish group (Table 4). Catch-at-age frequency was determined for the various fish groupings, $\log_e$ transformed, and plotted. The slope of the descending limb of presumed fully selected age-groups was calculated via least-squares linear regression to determine Z (Maceina and Bettoli 1998). Catch curves were calculated by aggregating ages from a series of annual data (Table 1). Additionally, mortality estimates from annual data were estimated for 2011–2017 (Table 1). Age ranges used in catch-at-age analyses were consistent between pairs of catch curves being compared. Differences in slopes between pairs of catch curves were tested with ANCOVA to determine whether the Z-estimates differed significantly by group.

All statistical analyses and graphics were developed in R (R Core Team 2019). Bootstrapping, growth model parameterization, and hypothesis testing were performed using the FSA package (Ogle et al. 2018).

RESULTS

Samples collected

Pre-DWH spill samples that we analyzed included 1776 total individuals, with ages determined for 1732 fish (Table 1). The majority of prespill samples aged were obtained in the years 2009, 2004, 2005, and 2003. In total, 1433 Tilefish were caught over the 7 years of postspill fishery-independent sampling, with 955 otoliths used in age determination (Table 1). The remaining sampled Tilefish were not aged because (1) the otoliths were never extracted in the field (e.g., station- and size-specific sampling quotas were met) or (2) the otoliths cracked and/or became unusable during the extraction and sectioning processes.

Age determination

Reader precision and PA estimates were calculated between the first and second readings by G.J.H. and between the primary and secondary readers. The APE between the first and second readings was 8.4%. The between-reader APE was 11%. Age uncertainty was highest for Tilefish older than 15 years, although only a small number of fish were aged by two different readers for ages 15+. Percent agreement within ±3 bands was 89% between the primary reader's first and second age determinations. The PA within ±3 bands was 77% between readers. Bias plots of the first and second readings by the primary reader indicated a slight overestimation for the first reading (~1 year) for ages younger than 11 years but no obvious bias for older fish (Figure S2).

Pre- and post-DWH spill comparisons

The dominant length-class was approximately 50 cm for Tilefish caught both before and after the DWH oil spill (Figure S3). The age frequency of Tilefish was also generally consistent between the pre- and postspill periods, with a slight age shift to older animals after the spill (Figure 2A). Although the length distributions analyzed via the bootstrapped K–S test were significantly different ($p = 0.012$), the empirical cumulative distribution function showed marginal differences in cumulative distributions between groupings, with postspill fish being slightly larger, on average, than prespill fish (Table 2; Figure S3).

Length–weight relationships were similar between pre- and postspill groupings, as evidenced by the estimated

TABLE 3 Estimated von Bertalanffy growth function parameters (L_∞, K, and t_0; defined in Methods) with bootstrapped ($n = 1000$) 95% confidence intervals for Tilefish caught from sites in the U.S. Exclusive Economic Zone (EEZ) before the *Deepwater Horizon* (DWH) oil spill (2000–2009; $n = 1732$) and after the spill (2011–2017; $n = 624$), from within the U.S. EEZ ($n = 816$) and the Mexican EEZ ($n = 125$) during 2011–2017, and from sites within the DWH oil spill area ($n = 624$) and all other sites in the U.S. EEZ ($n = 192$) during 2011–2017. ns, nonsignificant; *significant at $p < 0.05$; **highly significant at $p < 0.01$; ***highly significant at $p < 0.001$; SE, standard error.

						95% confidence limits	
Samples	**Parameter**	**Estimate**	**SE**	***t***	***p***	**Lower**	**Upper**
Before DWH spill	L_∞	85.147	3.568	23.867	<0.001***	79.911	94.612
	K	0.084	0.013	6.704	<0.001***	0.060	0.108
	t_0	−4.485	0.985	−4.552	<0.001***	−6.869	−2.882
After DWH spill	L_∞	92.960	6.955	13.366	<0.001***	82.353	114.161
	K	0.073	0.015	4.824	<0.001***	0.044	0.104
	t_0	−3.229	1.081	−2.988	0.003**	−6.039	−1.461
U.S. waters	L_∞	83.822	4.330	19.356	<0.001***	77.075	94.702
	K	0.090	0.015	5.813	<0.001***	0.062	0.122
	t_0	−2.838	0.957	−2.967	0.003**	−4.957	−1.227
Mexico	L_∞	87.382	7.678	11.381	<0.001***	76.405	112.993
	K	0.116	0.035	3.303	0.001**	0.051	0.199
	t_0	−1.380	1.412	−0.978	0.330 ns	−5.473	0.839
DWH footprint sites	L_∞	92.960	6.955	13.366	<0.001***	82.353	114.161
	K	0.073	0.015	4.824	<0.001***	0.044	0.104
	t_0	−3.229	1.081	−2.988	0.003**	−6.039	−1.461
All other U.S. sites	L_∞	70.431	4.383	16.069	<0.001***	64.513	88.680
	K	0.135	0.044	3.060	0.002**	0.053	0.228
	t_0	−1.987	1.968	−1.009	0.314 ns	−9.110	0.596

TABLE 4 Estimates of the instantaneous total mortality rate (Z) from catch-curve analysis, standard error (SE), test results for the significance of regression slopes, and 95% confidence intervals (CIs) for Tilefish based on various groups of pre- and post-*Deepwater Horizon* (DWH) aging data. The U.S. data set includes all fish caught in longline surveys within U.S. waters after the DWH oil spill. The Mexico data set includes all fish caught in surveys within Mexican waters after the spill. The "DWH footprint sites" data set includes fish caught at locations within the DWH spill footprint (Figure 1B). ***highly significant at $p < 0.001$.

Samples	***Z*-estimate**	**SE**	***t***	***p***	**95% CI**
Before DWH spill	0.31	0.02	13.29	<0.001***	0.26–0.36
After DWH spill	0.32	0.02	18.62	<0.001***	0.29–0.36
U.S. waters	0.26	0.03	8.86	<0.001***	0.19–0.33
Mexico	0.39	0.05	7.68	<0.001***	0.20–0.52
DWH footprint sites	0.32	0.02	18.62	<0.001***	0.29–0.36
Other U.S. sites	0.21	0.03	6.58	<0.001***	0.14–0.28

parameters and the plotted regression curves (Table 2; Figure 3A). The β parameters of the length–weight equations for Tilefish caught before and after the DWH oil spill were not significantly different, as indicated by ANCOVA ($p = 0.904$). Mean K_f and K_n were slightly but significantly lower after the spill relative to prespill values (Welch's t-tests: $p < 0.001$ for both K_f and K_n).

Estimates of the von Bertalanffy growth functions for fish caught before and after the DWH spill were also similar (Table 3). The predicted von Bertalanffy growth curves and bootstrapped 95% confidence intervals closely overlapped, but likelihood ratio tests indicated statistically significant differences in L_∞ and t_0 between the two groups (Table S1; Figure 4). The AIC model selection process identified the best fitting model as one in which L_∞ and t_0 differed, whereas BIC model selection identified the model in which only t_0 differed as the best fitting model. However, BIC model selection

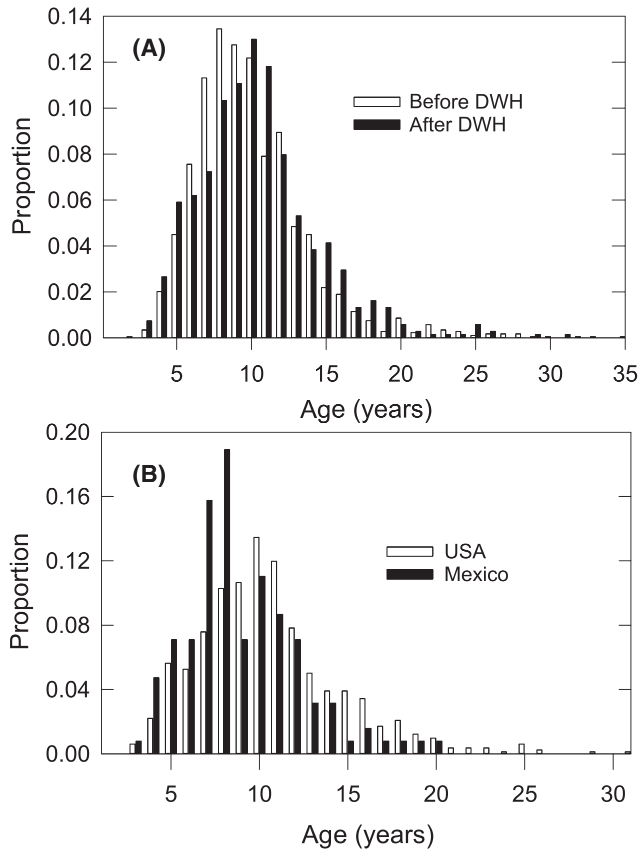

FIGURE 2 Age frequency distributions of (A) Tilefish sampled from sites in the U.S. Exclusive Economic Zone (EEZ) before the *Deepwater Horizon* (DWH) oil spill (2000–2009) and after the spill (2011–2017); and (B) Tilefish sampled within the U.S. and Mexican EEZs during 2011–2017.

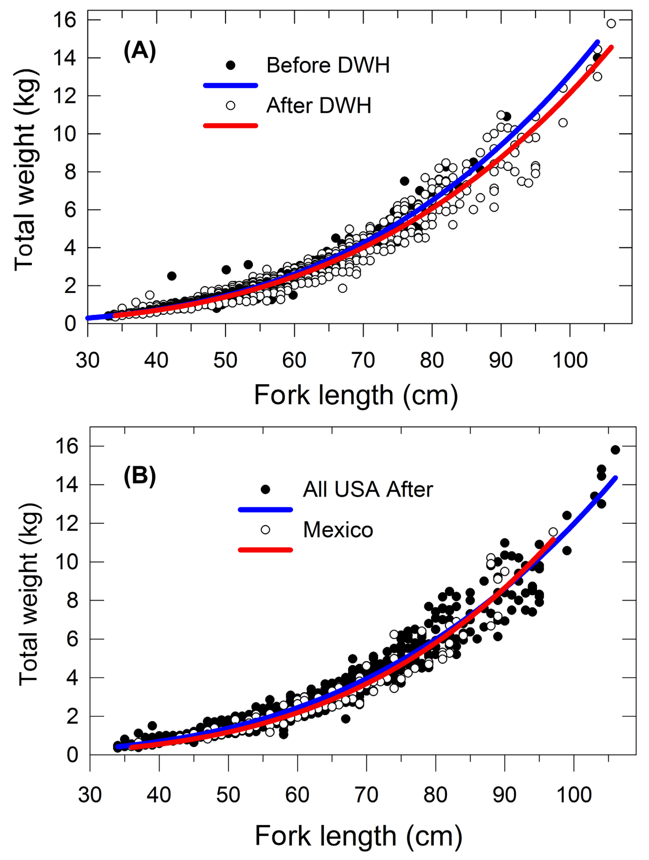

FIGURE 3 Fork length (cm) versus total weight (kg) of (A) Tilefish sampled from sites in the U.S. Exclusive Economic Zone (EEZ) before the *Deepwater Horizon* (DWH) oil spill (2000–2009) and after the spill (2011–2017); and (B) Tilefish sampled within the U.S. and Mexican EEZs during 2011–2017.

did not include a specific hypothesis test, whereas the likelihood tests clearly delineated some parameter differences (Table S4).

Values of Z for Tilefish caught before and after the DWH oil spill were nearly identical (prespill Z[mean ± SE] = 0.31 ± 0.02; postspill $Z=0.32 \pm 0.02$; Table 4; Figure 5). An ANCOVA of the descending limbs (linear slopes) of the catch curves indicated no statistically significant difference ($p=0.759$). Relative to aggregated Z-estimates, the annual estimates of Z (2011–2017) were lower, with a higher SE ($Z=0.22 \pm 0.049$) and lower average coefficient of determination (mean $R^2=0.74$).

Southern versus northern GoM comparisons

Both the K–S test and the bootstrapped K–S test with 1000 bootstrap iterations indicated that there were differences in length distributions between the U.S. and Mexican samples ($p=0.046$; bootstrap $p=0.028$; full sample statistic $=0.132$). The dominant size-group of Tilefish from both countries was approximately 50 cm (Figure S3A). However, there were fewer larger/older Tilefish found in Mexico compared to samples from the United States (Figure 2B).

Calculated parameters for the length–weight relationship were similar for Tilefish sampled from U.S. waters and Mexican waters (ANCOVA of the β parameter: $p=0.166$, $F=1.921$; Table 2). Predicted length–weight curves plotted over the raw data illustrated the lack of statistical difference in the length–weight relationships for Tilefish from the United States and those from Mexico (Figure 3B). Despite the similarity in length–weight relationship parameters, condition estimates differed significantly between fish caught from U.S. and Mexican waters. Mean estimates for both K_f and K_n were found to significantly differ between fish from the United States and those from Mexico (Welch's t-test: $p<0.001$).

The fitted von Bertalanffy growth curves predicted faster growth, on average, for Tilefish sampled off Mexico compared to those sampled off the United States, particularly for fish younger than about age 20; thereafter, the confidence intervals of predicted length at age overlapped (Figure 4B). Results from model selection based on Kimura's likelihood ratio test (Kimura 1980) indicated a significant difference

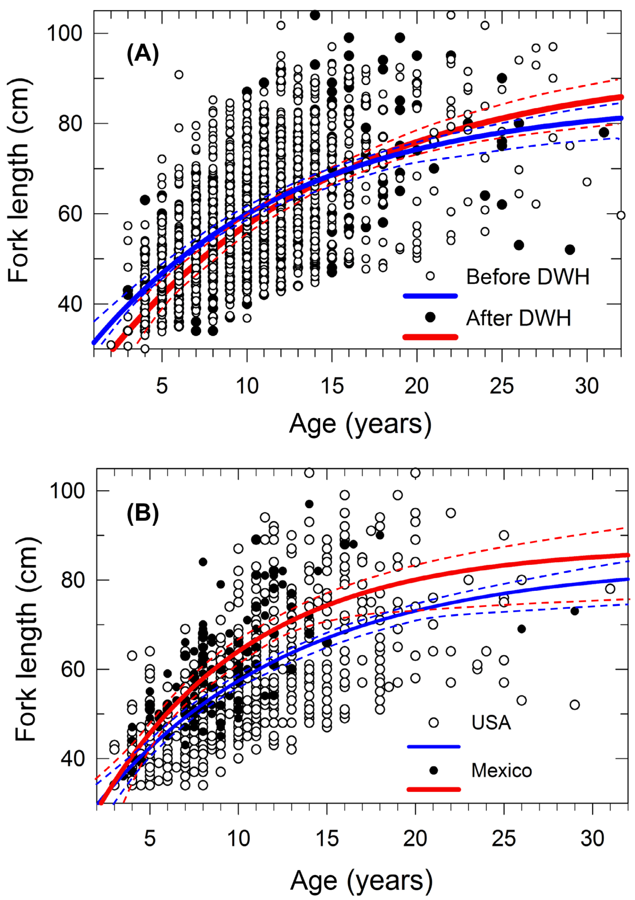

FIGURE 4 Von Bertalanffy growth curves (solid lines) for (A) Tilefish sampled from sites in the U.S. Exclusive Economic Zone (EEZ) before the *Deepwater Horizon* (DWH) oil spill (2000–2009) and after the spill (2011–2017); and (B) Tilefish sampled within the U.S. and Mexican EEZs during 2011–2017. Dashed lines represent the bootstrapped 95% confidence intervals; circles represent the observed lengths at age.

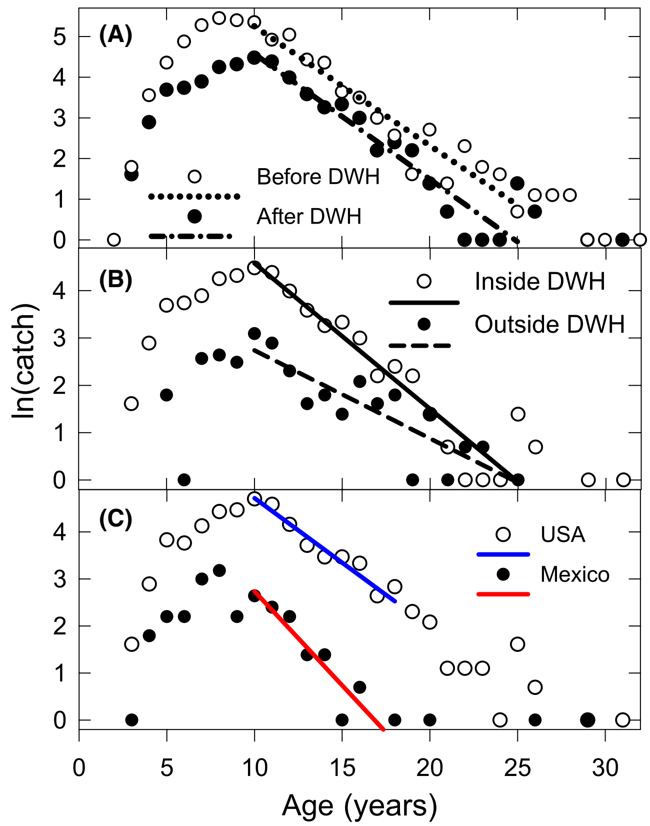

FIGURE 5 Catch curves for Tilefish sampled from (A) sites in the United States before the *Deepwater Horizon* (DWH) oil spill (2000–2009) and after the spill (2011–2017; sample ages 10–25 were used to compute the curves); (B) within the DWH spill area versus all other U.S. sites during 2011–2017 (sample ages 10–25 were used to compute the curves); and (C) Mexican waters versus U.S. waters during 2011–2017 (sample ages 10–18 were used to compute the curves).

in the K-parameter between the United States and Mexico (Table S2). The AIC and BIC model selection methods, however, suggested that the best model was the one in which only L_∞ differed between parameterizations.

The value of Z for all Tilefish from U.S. waters (Z [mean ± SE] = 0.26 ± 0.03) was 50% lower than that for fish from Mexico (Z = 0.39 ± 0.05; Table 4; Figure 5B) over the age range used for comparison (10–18 years). An ANCOVA comparing the slopes of the descending limbs revealed that the difference in Z between the United States and Mexico was statistically significant ($p = 0.017$), although the confidence intervals overlapped (Table 4).

Comparisons of the DWH spill area versus other U.S. areas

These tests compared data collected during the post-DWH spill period (2011–2017) from within the DWH spill area (i.e., footprint) with the postspill data for fish sampled in the remainder of the U.S. EEZ (Figure 1B). Although fish length distributions were similar between the DWH spill area and elsewhere in U.S. waters (Figure S5), the bootstrapped K–S test results indicated that they were statistically different ($p < 0.05$). Length–weight relationships were similar between the two groups (Table 2). The ANCOVA for β of the length–weight relationship for Tilefish from DWH spill footprint sites versus those from all other U.S. sites was not statistically significant ($p = 0.691$).

Both K_f and K_n were higher at DWH oil spill perimeter sites compared to all other U.S. sites. The Welch's t-test results for K_f and K_n between groups were statistically significant ($p < 0.001$ for both tests). The predicted von Bertalanffy growth curves were similar, although some of the individual parameters differed (Table 3). The likelihood ratio test suggested that the parameters L_∞ and K differed between postspill Tilefish caught from within the DWH spill area and those caught from all other U.S. waters (Table S3).

The estimated mean Z for fish from the DWH footprint was 52% higher than the estimate for fish elsewhere in the United States ($Z = 0.32 \pm 0.02$ versus 0.21 ± 0.03, respectively; Table 4; Figure 5C). The age range used for the comparison was 10–25 years. The descending limbs of the catch curves tested with ANCOVA were significantly different ($p = 0.030$).

DISCUSSION

We analyzed the population demographics of Tilefish in the GoM to investigate potential effects of the 2010 DWH oil spill and to establish temporal baselines of Tilefish demographics and compare rates of growth and mortality from areas in the northwestern and southwestern GoM unrelated to the spill. The Tilefish is an important candidate indicator species with which to assess site-specific environmental perturbations because Tilefish exhibit a high degree of site fidelity as adults (Grimes et al. 1983). The effect of the DWH spill on Tilefish is of particular interest due to (1) their burrow-digging behavior and association with fine, clay-bearing sediments (Able et al. 1982; NMFS 2019), in which much of the DWH oil was sequestered (Brooks et al. 2015; Romero et al. 2015); and (2) the documented sublethal health effects experienced by Tilefish in the spill area (Murawski et al. 2014; Snyder et al. 2015, 2019, 2020, 2023). Measures of growth, mortality, and body condition were tested for differences in population demographics based on locations sampled (e.g., within and outside of the oil spill perimeter) and to detect any impacts by substituting space for time (e.g., Damgaard 2019) using "control" areas that were adjacent to but unaffected by the spill. Unlike many DWH environmental impact studies, extensive prespill data on Tilefish demographics were available from areas impacted by the spill via sampling of commercial longline fishery catches (Lombardi 2012; Lombardi-Carlson and Andrews 2015) and elsewhere in U.S. waters of the GoM (Southeast Data, Assessment, and Review [SEDAR] 2011). Combining those data with extensive postspill survey collections using similar commercial-type longline fishing gear (Murawski et al. 2018) allowed us to assess in detail three salient questions: (1) "Were there differences in Tilefish demographics pre- and postspill for fish captured from within the DWH area (i.e., before–after comparisons)?"; (2) "Were there differences in Tilefish population dynamics in the northern (U.S.) and southern (Mexican) regions of the GoM?"; and (3) "Were there differences between Tilefish captured within the DWH spill area versus elsewhere in the U.S. EEZ (i.e., off western Louisiana and Texas)?" One question left unresolved is whether pre- and postspill demographics differed in the area beyond the spill region.

While the use of otolith banding structure results in generally valid ages for the species (Lombardi-Carlson and Andrews 2015), production aging of Tilefish can be difficult for a variety of reasons. As compared with other species, the range of ages for a given length varies widely (e.g., Figure 4). For example, a 60-cm fish can range in age from 5 to 25 years (Figure 4B). Additionally, banding in some Tilefish otoliths may appear nondistinct. Part of this may be due to the somewhat ambiguous opaque banding resulting from the lack of seasonal contrast in water temperatures occupied by the fish at the extreme depths in which Tilefish live (9–14°C; Grimes et al. 1986). Tilefish samples from our post-DWH spill surveys were derived from waters averaging 12.6°C off the United States and 13.5°C off Mexico at depths (averaging ~250 m; Murawski et al. 2018) where temperatures vary little seasonally (https://www.ncei.noaa.gov/maps/gulf-data-atlas/atlas.htm). Nevertheless, both first and second reading precision and multi-reader estimates proved to be relatively reliable (APE = 6–11%; PA within ±3 bands = 77%) and similar for ages used in previous assessments (SEDAR 2011). Although age estimates are inherently more variable for deepwater fish, indices of reader precision were consistent between this study and previously published studies of Tilefish population demographics (SEDAR 2011; Lombardi 2012); thus, growth and mortality estimates based on Tilefish ages should also be considered reliable. Apart from the reliability of individual ages, our sex-aggregated age estimates of von Bertalanffy parameters were highly variable, especially for older fish. Part of this variability may have been contributed by the sexually dimorphic growth that has previously been observed (Lombardi et al. 2010).

Calculation of Z from catch-curve analysis averaged over multiple years is subject to several rather severe assumptions, including stationarity in recruitment, natural mortality, fishing mortality, and the size selectivity of fishing gear. The 2011 stock assessment results (SEDAR 2011) are instructive in this regard, as are our comparative size and age compositions (Figures 4, 5, and S3–S5). Annual size compositions and age frequencies were remarkably stable over time for both the eastern and western population components of the Tilefish stock in U.S. waters prior to the spill (SEDAR 2011). Although there were some statistically significant K–S test differences in our size and age frequencies from before and after the spill, the size and age compositions were generally quite similar (e.g., Figures 2 and S3). With respect to the size selectivity of hook fishing gears influencing size compositions, the demersal longline fishery (Scott-Denton et al. 2011) also deployed primarily size-13/0 circle hooks (prespill), as did our postspill longline surveys (Murawski et al. 2018). Although the consistency in the gear used does not address the potential issue of dome-shaped selectivity of hook gear or spatial differences in demography, the fact that pre- and postspill sampling used similar gears allows for consistent estimation of relative Z-values between time periods (Table 4).

Before and after the DWH spill

Comparisons of pre- and postspill Tilefish population dynamics from within the area of the spill (Figure 1) were conducted to investigate whether changes in vital rates could be temporally associated with spill effects. Length distributions before and after the spill, although statistically distinct (Figure S3), only showed slight increases in average fish length after the spill, which is generally consistent with some progression in age at capture between the two time periods (Figure 2A). Some von Bertalanffy growth parameters differed for fish caught before and after the DWH spill within the spill area; however, confidence limits for predicted growth curves overlapped for ages greater than 10 years, whereas predicted growth for ages less than 10 declined somewhat after the spill (Figure 4A). Predicted weight at length declined only slightly (and nonsignificantly) between the two time periods. Apparent stability in growth rates during the pre- and postspill periods within the area influenced by the spill is seemingly incongruous with the range of sublethal health effects exhibited by Tilefish in the years after the spill (e.g., Murawski et al. 2014; Snyder et al. 2019). Similarity of growth curves is perhaps influenced by a number of factors. Importantly, about 90% of the postspill fish that we aged were alive prior to the DWH event; thus, depending on age, their accumulated growth history may have masked incremental growth impacts occurring after the spill. To address this "hangover" effect, Herdter et al. (2017) back-calculated growth increments at age for several cohorts to disentangle pre- and postspill growth effects in Red Snapper, illustrating growth depression in fish captured from within the spill area. However, given the large number of ages represented in the Tilefish population as well as the extreme range of lengths at age (Figure 4), such an approach was not feasible for the number of Tilefish that we sampled. More obvious health effects as well as increasing hepatic PAH concentrations emerged over time for Tilefish in the spill area (Snyder et al. 2019, 2020, 2023), so perhaps the full measure of growth impacts was not expressed, as the majority of our postspill samples were obtained in the first 3 years after the spill (Table 1). That said, the growth curve for postspill samples younger than age 10 did predict slower growth, which may indicate that cohorts that were spawned after the spill indeed exhibited growth depression, although sample sizes were too small to reliably compare individual sizes at age for the pre- and postspill periods. Future growth studies including more cohorts spawned after the spill may indeed be more revealing of potential growth impacts.

Both K_f and K_n were lower for Tilefish caught after the oil spill than for fish caught prior to the spill. Snyder et al. (2019) documented postspill declines in K_f, especially for samples taken in 2015 and 2017, as compared to those obtained earlier. These temporal declines in condition were correlated with elevated PAH metabolite concentrations in livers and with declines in liver lipid concentrations (Snyder et al. 2019). An important consideration in this regard is the timing of sampling in both studies, as total weight is influenced by the spawning condition of adults. About 54% of the pre-DWH spill samples were obtained from January to June, whereas only 2% of the postspill samples were obtained during the same months. Lombardi (2012) noted that all spawning-capable fish were observed in the first 6 months of the year and that the gonadosomatic index for Tilefish peaked in April, prior to any of the postspill sampling.

The use of K_f and other condition factors has been criticized based on the potential for varying slopes of the weight–length relationship among test groups relative to the assumption that β is equal to 3.0 in the index (Cone 1989). This bias would be especially important if the sizes of fish varied substantially between the samples being compared and if β was also substantially different among them. To evaluate this potential bias, we plotted K_f versus fish length for the Tilefish samples obtained from the spill area during the pre- and post-DWH spill periods (Figure S6). Linear regression models that were fitted to these relationships were parallel (i.e., equal slopes) and marginally significant. Because the mean fish lengths differed only slightly between prespill (54.6 cm) and postspill (57.0 cm) samples (Table 2) and because the β values for the length–weight relationships did not differ (3.15 versus 3.11; Table 2), we conclude that the use of K_f for assessing fish condition was appropriate in this case.

Estimates of Z were nearly identical between the two time periods (Table 4), indicating no appreciable excess mortality of Tilefish due to spill impacts, despite the plethora of sublethal symptomology associated with oil exposure (Murawski et al. 2014; Snyder et al. 2019, 2020). This conclusion should be tempered by the possibility of compensatory effects due to changing fishing mortality rates affecting Z-estimates, especially since effort in the spill area was temporarily displaced due to fishery closures in 2010 and early 2011. Thus, Tilefish present a paradox. The usual metrics of Tilefish population dynamics were largely unchanged after the spill despite the relatively high levels of PAH contamination from the DWH event (Pulster et al. 2020a) and despite the correlated sublethal health effects, possibility indicative of adaptation to a region where sustained oil contamination occurs. The DWH spill area (Figure 1B) has been subjected to oil and gas exploration, with resulting discharges, for decades (National Academies of Sciences, Engineering, and Medicine 2022). Likewise, oil that is transported into the northern GoM via river discharges and chronic oil from natural seeps and other well discharges (e.g., the Taylor Platform; Mason et al. 2019) have all conspired to elevate the ambient PAH levels there. Co-existing species, including the King Snake Eel *Ophichthus rex*, may similarly exhibit local adaptation to elevated PAH pollution in this region (Murawski and Gracia 2023).

USA–Mexico comparisons

Our data provide the first detailed population dynamics information yet published for Tilefish from Mexican waters. Size composition data indicated that fish collected off Mexico were larger, on average, than fish sampled from U.S. waters of the GoM (Figure S5), although the age structure for Tilefish off Mexico was truncated relative to the U.S. age structure (Figure 4B). Although length–weight relationships were similar between countries, both K_f and K_n were significantly higher off the United States. Growth curves indicated higher predicted length at age off Mexico, but the sample size and corresponding number of older fish were lower off Mexico than in U.S. waters (Table 1). Although the values of K and L_∞ for Tilefish from the United States and Mexico were significantly different according to Kimura's likelihood ratio test and AIC and BIC tests, respectively, there was substantial overlap in the 95% confidence intervals of each. Due to the low sample size of Tilefish from Mexico and the uncertain aging of Tilefish by otolith annuli (Lombardi 2012), there may not have been sufficient age data to definitively estimate differences in growth rates between countries, thus requiring caution in the interpretation of growth curve differences.

The value of Z from the catch-curve analysis was 50% higher off Mexico than in the United States (Table 4; Figure 5B), although confidence intervals on the slope of the regression also overlapped (Table 4). Whether higher mortality off Mexico is a result of natural or fishery effects cannot be evaluated with the data in hand.

Differences in size and age composition between areas (e.g., United States and Mexico in the GoM) can result from differential recruitment, Z, and fishing mortality as well as the size selectivity of fisheries and sampling gear (Neumann and Allen 2007). As noted above, since we used identical gear in postspill sampling, gear selectivity per se is not an issue in such comparisons, although differential distributions by size, age, and habitat type may exist. The predominant sediment type yielding Tilefish at sites in both Mexican and U.S. waters was mud (National Oceanic and Atmospheric Administration 2019), indicating coherence in habitat types sampled between areas. In addition, all otoliths were interpreted using the same methodologies. Size composition differences were likely due to recruitment and/or mortality variations between regions. Importantly, the lower condition factors may reflect differences in the productivity of ecosystems in the two areas (White and Fletcher 1985; Bolger and Connolly 1989). Weighted mean temperatures at capture were virtually identical, so the differences in condition were likely not due to temperature-dependent metabolic differences. The most likely contributing factor to the lower weights at length was the level of primary productivity, which has been calculated to be about 40% lower off Mexico compared with the northern GoM (Benway and Coble 2014).

Within versus outside of the DWH spill area

Population demographics differed in several ways between Tilefish within the DWH spill area and those outside of the region. The apparent lower Z-value for fish in U.S. waters outside of the DWH impact perimeter, as compared to within the DWH spill area (Table 4; Figure 5C), is consistent with lower fishing mortality rates there, as demersal longline effort off Texas and western Louisiana was low, especially prior to and just after the spill (Figures 1 and 2 of Scott-Denton et al. 2011), as compared to the region surrounding DWH (Figure 5C). The stock assessment conducted in 2011 (with data from prior to the DWH spill; SEDAR 2011) indicated low and declining fishing mortality trends on western GoM Tilefish, as compared to relatively high and increasing fishing mortality on the eastern GoM Tilefish component. Both commercial catch per unit effort (CPUE; Figure 8 of Scott-Denton et al. 2011) and our survey CPUE values (catch in numbers per 1000 hook-hours soaked) for Tilefish (Figure 1B) were relatively high outside of the DWH area, thus indicating relatively high Tilefish density combined with low fishing effort. Our estimates of Z did not differ in before–after comparisons of samples taken within the region of the DWH spill, indicating that fishing effort, although initially constrained by fishery closures during the last half of 2010 (Ylitalo et al. 2012), quickly returned to near prespill levels (Figure S1). The average annual landings of Tilefish from U.S. waters increased only marginally (10%) between the prespill (2000–2009) and postspill (2011–2017) time periods (Figure S1), suggesting that compensation of fishing for natural mortality rates was limited.

Length frequencies of the survey catches (Figure S5) were nearly identical, and length–weight relationships were indistinguishable between the two areas (Figure 3). Point estimates of the von Bertalanffy parameters L_∞ and K indicated a lower asymptotic length (L_∞) and faster growth rate (K) outside of the DWH spill impact region, but confidence intervals for all parameters overlapped (Table 3). Again, the limited sample size outside of the DWH area resulted in greater uncertainty in parameter estimates.

SUMMARY AND FUTURE RESEARCH

The aftermath of the DWH oil spill revealed substantial and important gaps in baseline information and contaminant data for many species of fish in the GoM—especially demersal, sedentary species, including Tilefish, in relatively deep waters of the continental shelf and especially in areas of active oil and gas exploration and production. This study, in combination with extensive investigations on contaminants in the species (see Snyder et al. 2023 for a summary), provides a comprehensive baseline of population demographics for Tilefish, not only within the area subject to the DWH spill, but also across the species' full distribution in the GoM. In the event of another large deepwater spill in the GoM, researchers will be able to compare both the contaminant levels and population demographics for the impacted spill area with our comprehensive results. However, there are several important caveats, both in drawing firm conclusions about the impacts of the DWH spill on Tilefish population dynamics and in contrasting dynamics by using before–after comparisons. A majority (89.6%) of the post-DWH collected fish that we examined were hatched prior to the DWH spill, as evidenced by the dominance of ages 7–20 in longline samples (Figure 2A). Thus, it is not possible to conclude from these data that recruitment dynamics were not negatively impacted by oil exposure from the DWH spill. As oil exposure may have more direct and detrimental effects on fish larvae and eggs (Moore and Dwyer 1974), there may have been elevated mortalities in early life stages that would not have been apparent given the selectivity of our fishing gear and the years over which postspill samples were collected. Our sampling occurred through 2017. Over 14 years have passed since the 2010 spill; thus, comparisons of population dynamics from samples collected now and in the future may provide a clearer picture of the strength of incoming year-classes that were potentially impacted due to DWH oil exposure. Likewise, growth comparisons between the pre- and post-spill periods suggest possible negative growth effects for young fish after the spill, but additional sampling now and in the future may help to resolve whether long-term growth was affected.

The use of catch-curve analysis for calculating Z is subject to a rather severe set of constraints that assume stationarity in processes, particularly when multiple years of data are aggregated. These assumptions include stable recruitment, growth, and selectivity by sampling gears. Some prespill samples were obtained with the larger size-15/0 circle hooks (~8%), but the vast majority of both pre- and postspill samples were caught with the same hook size (13/0); thus, gear selectivity characteristics were similar between time periods. The apparently consistent results of catch-curve analysis for pre- and postspill comparisons and for comparisons between regions indicate that the Tilefish may be one of the rare species for which such approaches are tenable. A more robust approach would be to develop long-term, spatially explicit stock assessments based on sufficient biological and fisheries data, including updating the 2011 stock assessment (SEDAR 2011), which will reveal how population dynamics of the species have changed over the long term since the DWH spill.

Condition factors (e.g., K_f and K_n), which measure the general well-being of fish by assuming that fish that are heavier for their length are better off, do not respond uniformly to oil exposure. Some studies have found lower condition factors in response to oil, whereas other studies have shown that condition factors are presumably unaffected by oil or, in fact, increase (Kiceniuk and Khan 1987; Tollefsen et al. 2011; Sundt et al. 2012; Brown-Peterson et al. 2016). Kiceniuk and Khan (1987) found that condition factors decreased in Atlantic Cod *Gadus morhua* in response to oil exposure, due to a significant reduction in food consumption by oil-exposed fish. However, the condition factor *increased* in the Southern Flounder *Paralichthys lethostigma*—a benthic species with a high sediment association like Tilefish—after exposure to DWH oil-contaminated sediments (Brown-Peterson et al. 2016). The increase was likely due to an increase in liver weight from PAH stress rather than being a positive response, as length and weight both decreased (Brown-Peterson et al. 2016). Both K_n and K_f were similarly lower in Tilefish that were sampled in the vicinity of the DWH spill site during the postspill period.

Finally, we and other investigators have focused on Tilefish as a sentinel species for monitoring the impacts of the DWH spill because of its abundance, its wide distribution within and outside of the spill area, the lack of migratory behavior as demersal juveniles and adults, and the extensive fishery and availability of considerable prespill data. A broader community of deepwater fishes is caught in association with Tilefish, including hakes, deepwater groupers, and snappers (Murawski et al. 2018), which can similarly be sampled for prespill baseline monitoring and which would provide important and potentially variable insights into the significance of various sources of contamination in the GoM (e.g., National Academies of Sciences, Engineering, and Medicine 2022) and the sensitivity of various populations to spills that will eventually occur. Prudent investment in such baselines would help to obviate the expensive and frustrating postspill scramble for samples obtained prior to contamination and the second-best substitution of space for time to conduct comparative evaluations of spill effects.

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CONFLICT OF INTEREST STATEMENT

The authors have no known conflicts of interest with regards to this study.

DATA AVAILABILITY STATEMENT

Data from the GoMRI-funded data collections are publically available through the GoMRI Information and Data Cooperative (https://data.gulfresearchinitiative.org; https://doi.org/10.7266/n7g73c4n).

ETHICS STATEMENT

Sampling was performed in accordance with Protocol IS00000515 approved by the Institutional Animal Care and Use Committee at the University of South Florida.

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