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Evaluation of the Status of the Kemp's Ridley Sea Turtle After the 2010 Deepwater Horizon Oil Spill

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Coincident with the 2010 Deepwater Horizon oil spill, unprecedented numbers of Kemp's ridley sea turtles (*Lepidochelys kempii*) stranded on northern Gulf of Mexico beaches and the number of nests recorded on the primary nesting beaches plummeted far below expected levels. High levels of strandings have continued since 2010 and the number of nests recovered to approximately 2009 levels in 2011, and improved slightly in 2012. A stock assessment conducted in 2012 indicated that a mortality event occurred in 2010, and that the number of nests should once more exhibit an increasing trend from 2013 and beyond. This has not happened; rather, the number of nests declined sharply in 2013. We conducted a new stock assessment to evaluate additional scenarios, including 1) three stock-recruitment options; 2) the potential that a new source of ongoing mortality is present; and 3) the potential that the number of nests-per-adult-female is dependent on the size of the age-2+ benthic population. The latter model provided the best fit to the data. Further, the preliminary estimate of actual nesting in 2014 is consistent with model projections. The reduction in reproductive output could be due to the combination of a large population and reduced prey levels. Together these may have increased the remigration interval or reduced the number of nests per female. However, research is needed to evaluate this and other plausible hypotheses. Nesting may be highly variable in the future depending on feeding conditions on the foraging grounds.

Introduction

Before 2010, the outlook for the endangered Kemp's ridley (*Lepidochelys kempii*) recovery was promising, due in large part to the conservation efforts of 1) Mexico's Instituto Nacional de Investigaciones Biologico-Pesqueras and Instituto Nacional de Pesca during 1966–77 and 2) the efforts of the Mexico–U.S. Kemp's Ridley Restoration and Enhancement Program from 1978 to the present. In 1966, the Kemp's ridley was near extinction, but by 1986 additions to the population began to exceed losses, and population growth ensued. The Bi-National Recovery Plan for the Kemp's ridley sea turtle (NMFS et al., 2011) predicted that the population would grow during 2010–20 at a rate of 19% per year, assuming survival rates of all life stages remained constant. NMFS et al. (2011) also projected that the down-listing criteria of 10,000 nesting females in a single season would be attained by 2011, and that the delisting criteria might be attained by 2024. However, survival rates did not remain constant and the number of nests declined by 35% in 2010.

The Deepwater Horizon (DWH) oil spill, beginning on 20 April 2010, was documented to have interacted with Kemp's ridley as well as other sea turtles. The 2010 spill also corresponded with an unprecedented surge in sea-turtle strandings in the northern Gulf of Mexico, especially in Alabama, Mississippi, and Louisiana—the areas most affected by the spill (Crowder and Heppell, 2011; Caillouet, 2014). In addition, nesting at the key Kemp's ridley index nesting beaches in Tamaulipas, Mexico, where over 95% of the nesting of this species occurs (e.g., Marquez-M., 1994), dropped approximately 35% in 2010 as compared with 2009 (Caillouet, 2010, 2014; Crowder and Heppell, 2011; Gallaway et al., 2016). These were disturbing developments for the Kemp's ridley sea turtle.

The concern about the 2010 decline, the increased levels of strandings that have occurred since 2010, and the uncertainty regarding the causal factors of these events (i.e., shrimp trawling mortality was also suggested as a potential cause along with the spill and remedial responses to the spill) motivated the development of a Kemp's Ridley stock assessment model (KRSAM) to predict annual, postpelagic female population size and mortality in the Gulf of Mexico (Gallaway et al., 2016). The KRSAM is a population dynamics synthesis model that integrates historical Kemp's ridley data from multi-

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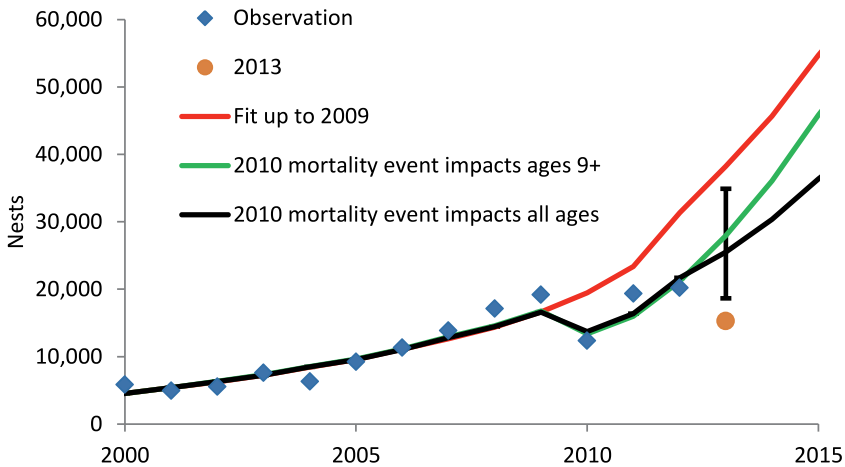


Fig. 1. Initial model of Kemp's ridley sea turtle nests (prompting a revised assessment model). Observed (points) and predicted (lines) nests based on three hypothetical scenarios with projections to 2015. The line for the scenario "Fit up to 2009" used estimated 2009 terminal mortalities and population sizes by age to make the 2010 through 2015 projections. The remaining scenarios used estimated 2012 terminal mortalities and population sizes by age to make the 2013 through 2015 projections. The 2013 nest index (not used to estimate trends) and the 95% confidence interval for the 2013 projection using the 2010 mortality event that impacts all ages are also plotted. Source: Gallaway et al. (2016).

ple sources, including shrimp trawl effort to provide estimates of shrimp trawl mortality. The KRSAM was able to obtain excellent fits to the nest index data available for 1966 through 2012. The predicted trend was an exponential increase, with the exception of a 2010 mortality event. Projections for 2013 through 2015 reflect a continued increase in the number of nests (Fig. 1). However, the actual number of nests observed in 2013 fell below the 95% confidence interval for the predicted value (calculated following Morris and Doak, 2003), even for the projection scenario having the smallest rate of increase (Fig. 1). The KRSAM is not consistent with either the actual 2013 observation or the preliminary observation for 2014 (Peña, 2014). These observations led us to evaluate other hypotheses that might produce more realistic model behavior. In particular, density-dependent mechanisms for 1) turtles entering the benthic life-history stage and 2) the number of nests per adult female were explored along with a model adjusted to include a new mortality factor. In this paper, we describe some alternative models that were fit to the 1966 through 2013 data including 1) the current KRSAM or base model, 2) the KRSAM modified with an additional density-independent mortality factor for all life stages from 2010 through 2013, 3) the KRSAM with Beverton–Holt recruitment to the benthic stage, 4) the KRSAM with a hockey-stick recruitment to the benthic stage, 5) the KRSAM with a Ricker recruitment to the benthic stage, and 6) the KRSAM modified with the number of nests per adult female dependent on the size of the benthic population.

Methods

The conventional annual nest index (number of nests observed at Rancho Nuevo, Tepehaujes and Playa Dos at Barra del Tordo beaches combined) and subsequent hatchlings produced are listed in Table 1 for 1966 through 2014. The 2014 nest index was a preliminary estimate as of 5 August 2014, and hatchling data were not available for 2013 and 2014. The penaeid shrimp effort data (nominal net days fished) and habitat-weighted net days scaled to the historical mean in U.S. waters in the Gulf of Mexico for 1966 through 2013 are listed in Table 2. The methodology for weighting the effort for habitat importance to the Kemp's ridley turtle is given by Gallaway et al. (2016). New observations for strandings or mark–recapture of Kemp's ridleys were not available.

Since the 2014 nesting index was a preliminary estimate and the 2014 shrimp effort data were not yet available, we mostly confined the analysis to data for 1966 through 2013. We follow the KRSAM specification and notation provided by Gallaway et al. (2016) and, in this paper, only

Table 1. Annual conventional index (nests) and hatchlings released. Data provided by La Comision Nacional de Areas Naturales Protegidas as reported in Gallaway et al. (2016).

		Hatchlings		
Year	Nests	Corral and box	in situ	Total
1966	5,991	29,100	—	29,100
1967	5,519	24,100	—	24,100
1968	5,117	15,000	—	15,000
1969	4,018	28,400	—	28,400
1970	3,017	31,400	—	31,400
1971	2,012	13,100	—	13,100
1972	1,824	14,600	—	14,600
1973	1,643	23,500	—	23,500
1974	1,466	23,500	—	23,500
1975	1,266	11,100	—	11,100
1976	1,110	36,100	—	36,100
1977	1,036	30,100	—	30,100
1978	924	48,009	—	48,009
1979	954	63,996	—	63,996
1980	868	37,378	—	37,378
1981	897	53,282	—	53,282
1982	750	48,007	—	48,007
1983	746	32,921	—	32,921
1984	798	58,124	—	58,124
1985	702	51,033	—	51,033
1986	744	48,818	—	48,818
1987	737	44,634	—	44,634
1988	842	62,218	—	62,218
1989	828	66,802	—	66,802
1990	992	74,339	—	74,339
1991	1,178	79,749	—	79,749
1992	1,275	92,116	—	92,116
1993	1,241	84,605	—	84,605
1994	1,562	107,687	—	107,687
1995	1,930	120,038	—	120,038
1996	1,981	114,842	—	114,842
1997	2,221	141,770	—	141,770
1998	3,482	167,168	—	167,168
1999	3,369	211,355	—	211,355
2000	5,834	365,479	—	365,479
2001	4,927	291,268	—	291,268
2002	5,525	357,313	—	357,313
2003	7,604	433,719	—	433,719
2004	6,309	413,761	7,923	421,684
2005	9,236	555,884	14,079	569,963
2006	11,322	688,755	26,247	715,002
2007	13,849	709,619	192,671	902,290
2008	17,131	731,383	74,696	806,079
2009	19,163	767,633	257,394	1,025,027
2010	12,377	644,665	18,949	663,614
2011	19,361	637,923	4,384	642,307
2012	20,197	769,660	268,638	1,038,298
2013	15,284	—	—	—
2014[a]	10,504	—	—	—

[a] Preliminary estimate as of 5 August 2014.

Table 2. Days fished of annual shrimp trawling effort by the U.S. fleet in the Gulf of Mexico, 1966–2013. The scaled shrimping effort in the right-most column was used to estimate annual shrimping-related mortality. (Source: James M. Nance, NOAA Fisheries, Galveston Laboratory)

Year	Nominal days	Net days	Habitat-weighted net days	Scaled net days
1966	178,216	263,346	247,193	0.4918
1967	192,476	285,749	265,580	0.5284
1968	219,162	323,257	315,615	0.6280
1969	225,818	332,975	320,770	0.6382
1970	198,257	291,446	272,047	0.5413
1971	202,676	300,385	290,341	0.5777
1972	244,116	426,874	432,641	0.8608
1973	236,858	409,418	393,083	0.7821
1974	235,123	408,155	405,629	0.8071
1975	211,921	365,580	347,090	0.6906
1976	214,511	387,548	373,140	0.7424
1977	221,056	430,345	434,549	0.8646
1978	244,816	516,235	564,141	1.1224
1979	297,851	633,067	671,339	1.3357
1980	202,820	437,906	483,878	0.9627
1981	232,012	510,827	525,895	1.0463
1982	238,511	517,650	529,336	1.0532
1983	247,968	518,723	538,029	1.0705
1984	267,381	568,146	575,625	1.1453
1985	259,213	560,834	581,933	1.1578
1986	313,757	666,327	674,846	1.3427
1987	337,347	735,871	776,815	1.5456
1988	309,053	662,644	664,454	1.3220
1989	304,309	677,785	714,335	1.4213
1990	306,825	681,453	724,163	1.4408
1991	299,845	719,953	758,175	1.5085
1992	319,928	718,855	720,750	1.4340
1993	289,164	659,845	667,917	1.3289
1994	299,161	659,219	673,018	1.3391
1995	250,950	603,026	603,017	1.1998
1996	253,462	647,114	641,251	1.2759
1997	291,655	724,807	714,581	1.4218
1998	280,634	700,904	698,055	1.3889
1999	270,475	694,062	727,534	1.4475
2000	260,103	669,441	696,023	1.3848
2001	277,889	701,250	711,548	1.4157
2002	304,639	779,201	739,281	1.4709
2003	254,598	645,433	616,096	1.2258
2004	214,644	552,768	479,638	0.9543
2005	150,019	386,585	314,322	0.6254
2006	139,078	355,148	330,662	0.6579
2007	125,368	315,572	297,657	0.5922
2008	106,886	259,903	257,319	0.5120
2009	132,902	319,287	311,808	0.6204
2010	108,403	255,898	236,861	0.4713
2011	121,668	286,772	267,872	0.5330
2012	117,085	287,521	286,633	0.5703
2013	111,344	269,724	252,347	0.5021
Mean	231,707	502,601	502,601	1.0000

detail the equations that were altered to generate the alternative models.

We first fit the KRSAM without any model alterations for comparison with the density-dependent scenarios. Next, for comparative purposes, we replaced the 2010 mortality event by an additional density-independent instantaneous mortality (M_{add}) from 2010 through 2013; thus, Equation 16 in Gallaway et al. (2016) was altered:

$$Z_{ya} = \begin{cases} Z_{\mathrm{P}}, & a \leq 1 \\ M_a + F_{ya}, & a > 1 \text{ and } y < y_{\mathrm{TED}} \\ M_a + F_{ya} X_{\mathrm{TED}}, & a > 1 \text{ and } y_{\mathrm{TED}} \leq y < 45 \\ M_a + F_{ya} X_{\mathrm{TED}} + M_{\mathrm{add}}, & y \geq 45 \end{cases} \tag{16}$$

where all terms in Equation 16 are instantaneous, Z_{ya} is the total mortality during year y for age a turtles, Z_{p} is total mortality for the pelagic stage (ages 0 and 1), M_a is natural mortality, F_{ya} is incidental fishing mortality from shrimp trawls, and X_{TED} is a multiplier ($\leq$1.0) representing the impact of turtle exclusion devices (TEDs) commencing in year y_{TED}. Note that $y \geq 45$ references 2010 and later.

The current KRSAM assumes that any density-dependent mechanisms occur before the hatchlings enter the water. In other words, any density-dependent mortality would be subsumed in the hatchling estimates. Density-dependent mechanisms posthatching might also occur during the pelagic stage where mortality (Z_{p} in Eq. 16) and the number of age-0 turtles entering the population are replaced with a stock recruitment function with the number of turtles recruited to the benthic stage (end of age 1) as a function of hatchlings 2 yr earlier. Equation 17 was replaced with three alternative stock-recruitment functions:

$$N_{y1} = \begin{cases} \dfrac{\alpha_{\mathrm{BH}} \tilde{H}_{y-2}}{1 + \beta_{\mathrm{BH}} \tilde{H}_{y-2}}, \text{ or} & \text{Beverton-Holt} \\ \text{if } \tilde{H}_{y-2} < H^* \text{ then } \alpha_{\mathrm{HS}} \tilde{H}_{y-2} \\ \quad \text{otherwise } \alpha_{\mathrm{HS}} H^*, \text{ or} & \text{hockey stick} \\ \alpha_{\mathrm{R}} \exp(-\beta_{\mathrm{R}} \tilde{H}_{y-2}), & \text{Ricker} \end{cases} \tag{17}$$

where,

$$\tilde{H}_y = \tilde{H}_{\mathrm{C}y} r_{\mathrm{C}} + \tilde{H}_{\mathrm{I}y} r_{\mathrm{I}},$$

and where $\tilde{H}_y$ is the number of female hatchings produced in year y, $\tilde{H}_{\mathrm{C}y}$, and $\tilde{H}_{\mathrm{I}y}$ are the annual numbers of corral-plus-box and in situ hatchlings entering the water each year, and r_{C} and r_{I} are annual proportions of hatchlings that are females, respectively. Each of the recruitment functions has two associated fundamental parameters: α_{BH} and β_{BH} for Beverton–Holt; α_{HS} and H^* for hockey stick; and α_{R} and β_{R} for Ricker. The Beverton–Holt curve assumes that the rate of natural mortality for all age classes is a linear function of density (hatchlings). The hockey-stick function assumes density-independent mortality but with limited available habitat space for individuals. The Ricker curve exhibits decreased recruitment at high hatchling levels (overcompensation) possibly caused by disease transmission, habitat destruction, predation response, or competition between juveniles (e.g., age 0 vs age 1).

Density-dependent mortality for benthic-stage Kemp's ridley sea turtles is considered unlikely because they have broad spatial distribution, they have few predators, and they are opportunistic feeders. Marquez-M. (1994) notes that Kemp's ridley turtles have the ability to fast for long periods of time, and that a juvenile refused food for 150 d before dying. However, food resources can affect the remigration interval and the number of nests laid by a breeding female (Hayes, 2000). KRSAM currently represents the number of nests per adult female (ratio of nests laid per breeding female and remigration interval) as a known constant set at 1.25. Here, we portray the number of nests per adult female produced in year y, $n_{\mathrm{M}y}$, as dependent on the size of the benthic population through a logistic decay function. We replaced Equation 22 in Gallaway et al. (2016) with two equations:

$$n_{My} = n_M \left[1 - \frac{1}{1 + \exp\left(\dfrac{r_{50} - \sum_{a=2}^{A} N_{ya}}{r_{\mathrm{sl}}} \right)} \right], \tag{22a}$$

where n_M is the assumed known mean number of nests per adult female (a constant set at 1.25), r_{50} is the number of hatchlings when n_{My} is 50% of maximum, and r_{sl} is the slope at r_{50} (r_{50} and r_{sl} are fundamental parameters that were estimated). We then calculated the number of mature females in the population by year, P_y, as the sum of the products of the population size and proportion mature by age, i.e.,

TABLE 3. Evaluation of six modifications of the base Kemp's ridley stock assessment model based on Akaike's information criterion adjusted for sample size (QAIC). All models include a 2010 mortality event. S/R = stock/recruit

Model	Parameters	QAIC	ΔQAIC	QAIC weight	Model likelihood
Density-dependent nests per female	13	3,204.4	0.0	0.789	1.000
Mortality post-2009	11	3,207.1	2.7	0.205	0.260
Ricker S/R	12	3,214.2	9.8	0.006	0.007
Hockey-stick S/R	12	3,240.0	35.6	0.000	0.000
No modifications	11	3,241.0	36.7	0.000	0.000
Beverton–Holt S/R	12	3,245.5	41.2	0.000	0.000

$$P_y = n_{My} \sum_a N_{ya} G_a, \tag{22b}$$

where G_a is the assumed known proportion mature by age a.

We fit the six alternative models to the data following Gallaway et al. (2016). All of the models included a 2010 mortality event as part of the base model. We used Akaike's information criterion adjusted for sample size (QAIC) to evaluate model fit following Burnham and Anderson (2002). We assumed an effective sample size of 36 from the nest years (1978–2013) used to fit the model. Because additional data (length frequency of strandings and growth data) were used (see Gallaway et al., 2016), the assumed effective sample size was conservative, with the consequence that inferences of differences between models were conservative.

We report the parameter estimates for the model with the best fit in this paper along with associated standard errors, total annual deaths, annual deaths from shrimp trawling, annual population estimates by age class, predicted annual instantaneous mortality from shrimp trawling, predicted annual instantaneous total mortality, and terminal (2013) population estimates with 95% confidence intervals. We also use this model to make projections for 2014 through 2016. Hatchlings for 2013 and 2014 (required for the 2015 and 2016 projections) were estimated from the number of observed nests using the maximum number of nests to be protected in corrals, number of eggs per nest, and survival rates adopted by NMFS et al. (2011) for the purpose of making projections.

RESULTS

The best-fitting model was the density-dependent nests per adult female, with 79% of the total QAIC weight, followed by the model with additional mortality post-2009 [21% of total QAIC weight (Table 3)]. The remaining four models were very distant on the basis of QAIC. Only the results for the best-fitting model are discussed further.

Predictions for the density-dependent nests-per-adult-female model compared with the observed number of nests along with the log residuals vs the predicted number of nests (residual plot) are shown in Figure 2. Residuals were homogeneous and there did not appear to be a readily apparent trend consistent with the assumed log-normal sampling distribution. The predicted logistic decay curve is shown in Figure 3. Note that only the last 2 yr (2012 and 2013) affected the number of nests per adult female.

The parameter and terminal 2013 population estimates with the associated standard errors for the density-dependent nests-per-adult-female model are listed in Table 4. Instantaneous fishing mortality by year for ages 2 to 4 and ages 5+ is shown by Figure 4, panel A. A significant mortality drop occurred in 1990 when the TED multiplier was applied. Panel B of Figure 4 plots instantaneous total mortality by year for age 2, age 5, and age-class 14+. Each age has a different mortality profile because natural mortality is a monotonically decreasing function of age. Mortalities summed over ages 2+ and 5+ assigned to shrimp trawls and from all sources are plotted in Figure 4, panels C and D, respectively. The increasing trend in mortalities over time was caused by the increasing population. The mortalities assigned to shrimp trawls in comparison with total mortalities for the period 1980 to 2013 are listed in Table 5. The major factors that influence the percent mortality from shrimp trawls were directed shrimping effort, TEDs commencing in 1990, and the 2010 mortality event. In 2010, there was a total estimate of 61,330 deaths. Of these, 2,945 can be attributed to shrimp trawl mortality and 11,744 were due to natural mortality. The balance, 46,642, is attributable to anthropogenic causes other than

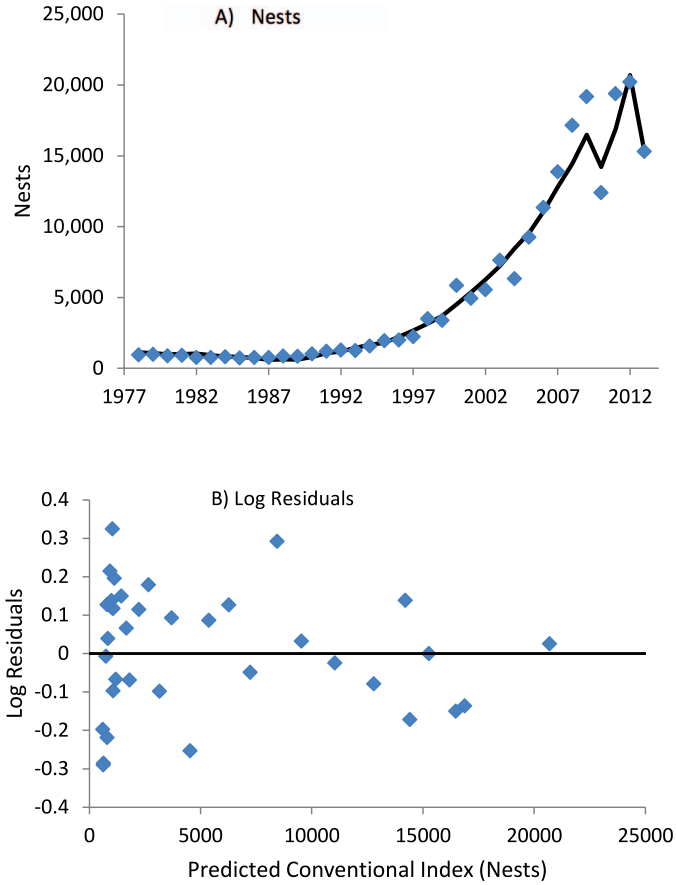


Fig. 2. Model results of Panel A shows observed (points) and predicted (line) nests from 1978 through 2013 based on the model with density-dependent nests-per-adult-female and a 2010 mortality event. Panel B shows log residuals (observed ? predicted) versus predicted conventional index (Nests), 1978-2013.

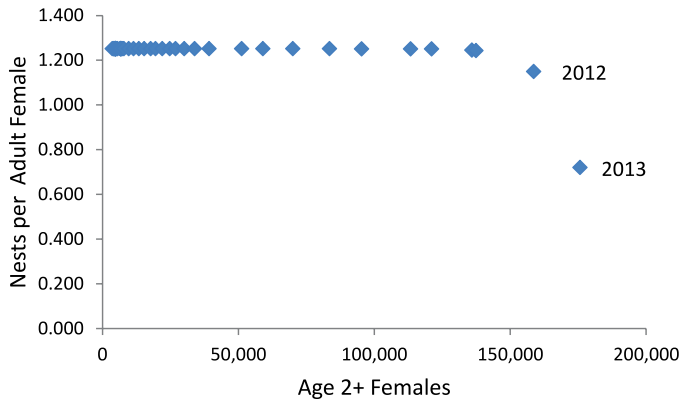


Fig. 3. Predicted nests-per-adult female as a function the number of age 2+ females. The last two years are labelled.

TABLE 4. Fundamental parameters and terminal (i.e., 2013) postpelagic female population size estimates with standard deviations (SD).

Parameter	Notation	Estimate	SD
Density-dependent nests per female:			
Number of age 2+ when at 50% of max.	r_{50}	179,950	31,272
Slope	r_{sl}	8,163	6,991
Mortality:			
Instantaneous mortality (ages 0 and 1 yr)	M_P	1.321	0.115
Instantaneous mortality 2010 event	F_{2010}	0.312	0.134
Catchability (ages 2–4)	q_1	0.196	0.039
Catchability (ages 5+)	q_2	0.155	0.014
Turtle excluder device (TED) effect multiplier	X_{TED}	0.242	0.067
Growth:			
Straight carapace length (SCL) (cm) at age 1	μ_1	17.2	0.51
SCL (cm) at age 10	μ_2	58.0	0.63
von Bertalanffy growth coefficient	K	0.232	0.013
Individual length variation (SD)	σ_L	9.37	0.56
Selectivity:			
Age when selectivity at 50%	a_{50}	1.75	0.22
Slope	a_{sl}	0.555	0.072
Terminal population size (2013)			
Ages 2–4		83,244	16,704
Ages 2+		177,540	31,852
Ages 5+		94,294	15,830
Ages 9+		35,209	4,845

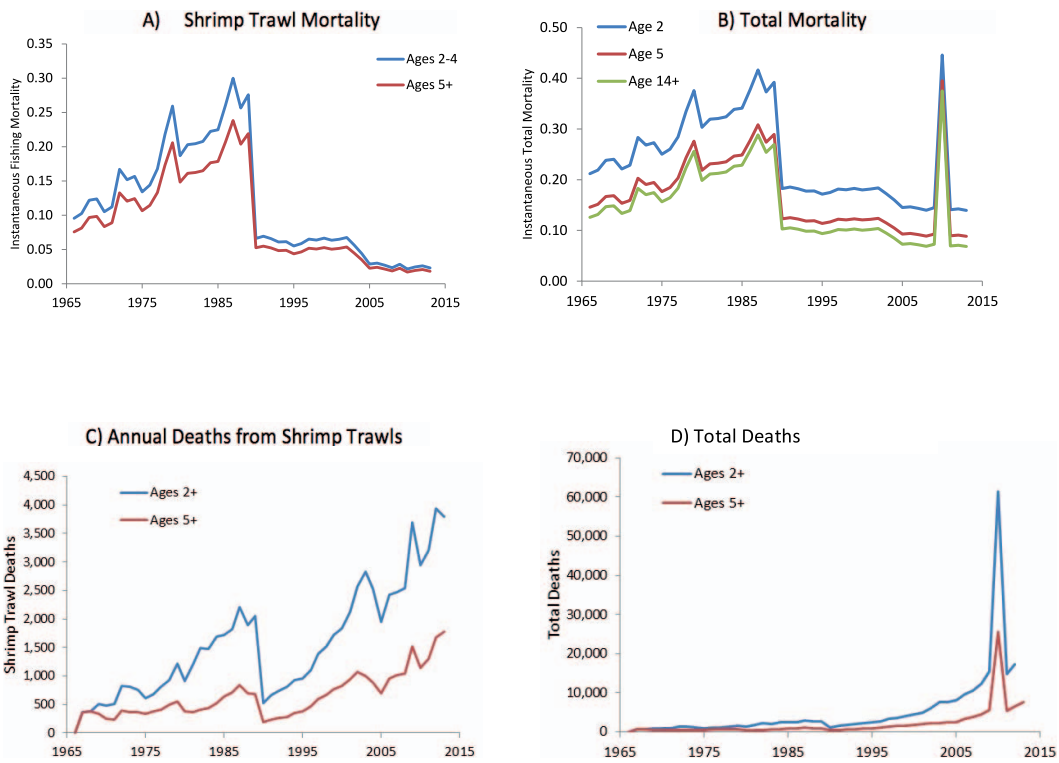


Fig. 4. Model estimates of mortality. Panel A show predicted instantaneous rate of mortality attributed to incidental capture in shrimp trawls by the U.S. fleet by year and ages 2-4 and 5+; Panel B shows predicted instantaneous rate of total mortality by year and ages 2, 5, and14+; Panel C shows predicted annual deaths by year and ages 2+ and 5+, attributed to incidental capture in shrimp trawls by the U.S. fleet; Panel D shows predicted annual total deaths by year and ages 2+ and 5+.

TABLE 5. Estimated total annual deaths for ages susceptible to shrimp trawling (ages 2+ yr).

Year	Shrimp trawl	Total	Percent
1980	907	1,346	67.4
1981	1,201	1,751	68.6
1982	1,492	2,190	68.2
1983	1,479	2,124	69.6
1984	1,693	2,394	70.7
1985	1,719	2,424	70.9
1986	1,821	2,442	74.6
1987	2,215	2,901	76.4
1988	1,899	2,584	73.5
1989	2,043	2,720	75.1
1990	516	1,227	42.1
1991	664	1,550	42.8
1992	746	1,785	41.8
1993	806	2,009	40.1
1994	925	2,286	40.5
1995	952	2,512	37.9
1996	1,103	2,775	39.7
1997	1,386	3,280	42.3
1998	1,519	3,647	41.7
1999	1,719	3,994	43.0
2000	1,835	4,387	41.8
2001	2,122	5,027	42.2
2002	2,571	5,985	43.0
2003	2,832	7,513	37.7
2004	2,523	7,722	32.7
2005	1,947	8,036	24.2
2006	2,418	9,677	25.0
2007	2,473	10,576	23.4
2008	2,538	12,231	20.8
2009	3,696	15,432	24.0
2010	2,945	61,330	4.8
2011	3,204	14,816	21.6
2012	3,946	17,322	22.8
2013	3,797	18,223	20.8

shrimping. In the absence of other information, we believe this constitutes the best estimate of the impact of the DWH oil spill on the Kemp's ridley sea turtle in 2010. The population sizes by year and age class are shown in Figure 5, partitioned into two panels (ages 2 to 8 and ages 9 to 14+) because of the substantial difference in population scale over the age classes. Terminal (2013) population estimates summed over ages 2 to 4 and ages 2+, 5+, and 9+ with the associated 95% confidence intervals are plotted in Figure 6 (also see Table 4).

The density-dependent nests-per-adult-female model (see Table 4) projections for 2014 through 2016 are displayed in Figure 7. The preliminary 2014 nest index is also plotted for reference. Note that the density-dependent model projection captured the 2014 decline in the nest index.

DISCUSSION

The best model included estimates of shrimp trawl mortality, a "mortality event" in 2010, and a density-dependent factor where nests per adult female was a function of the age-2+ total population size. Although the timing of the mortality event corresponds with the occurrence of the DWH oil spill, the spill did not start until 20 April 2010. Typically, most of the reproductively active female Kemp's ridleys in the area of the spill would have already migrated out of the area by the time the spill occurred. However, winter/spring seawater temperatures for 2010 in the northern Gulf Kemp's ridley foraging grounds were among the coldest on record (Fig. 8, panel A). The cold winter/spring of 2010 was associated with a delay in the nesting season (Fig. 8, panel B), and long-term analyses of nesting trends show a significant correlation of the timing of the start of the nesting season with ambient temperatures in the foraging area (Elizabeth Bevan, unpubl. data). A plausible explanation resulting from these observations is that the cold temperature in the Kemp's ridley foraging grounds in 2010 caused a delay in that year's migration to nesting beaches in Texas and Mexico and resulted in exposure to the DWH oil spill and a mortality event.

The occurrence of a large mortality event in 2010 cannot capture the sudden decline of Kemp's ridley nests that was estimated in 2013. However, the 2013 decline in nest numbers and further decline in 2014 are coincidental with the predicted increase in the benthic population. A possible explanation is that the nests-per-female-per-year index is decreasing because the age-2+ population size has reached a threshold where it now takes a longer time to acquire sufficient energy reserves to support new egg production and nesting migrations than was typical at smaller population levels. This increase in remigration interval would be expected to continue to increase until some equilibrium level is reached.

The concept that variation in remigration intervals of female turtles may lead to interannual changes in the numbers of females nesting is not new, dating from Carr and Carr (1970). This concept was also addressed by Carr (1975), Carr et al. (1978), and Bjorndal et al. (1999). Hayes (2000) demonstrated that interannual variability in feeding conditions changed the remigration rate of individuals, and dramatically affects the number of turtles nesting in different

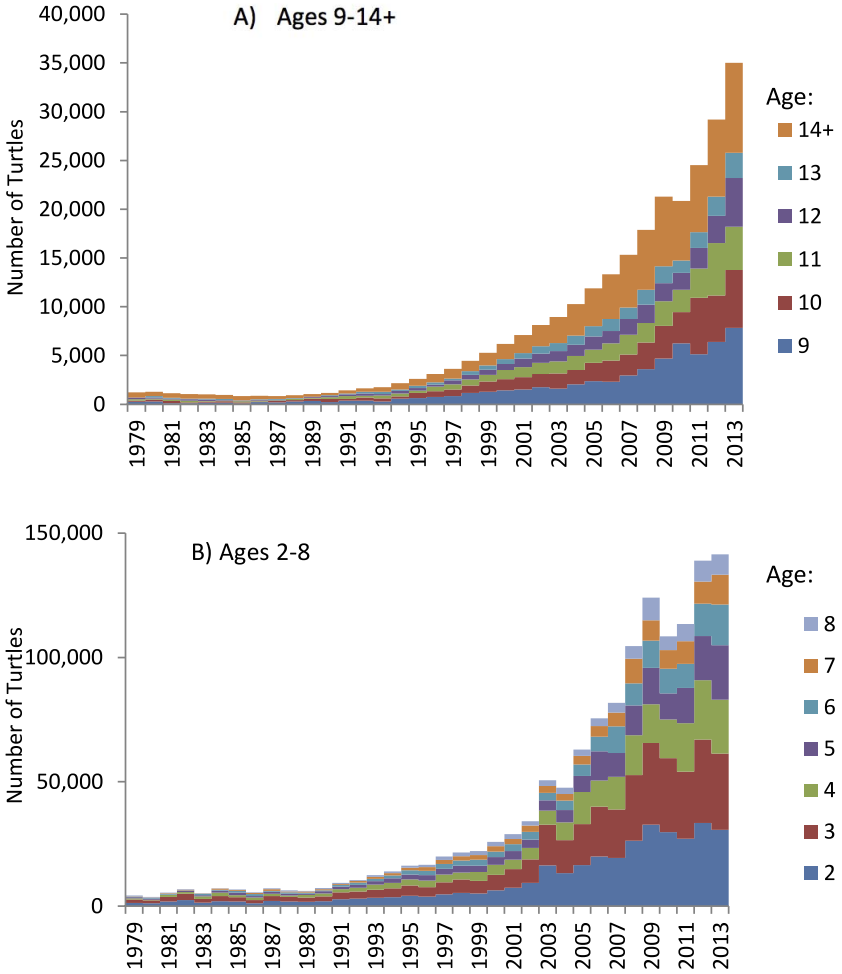


Fig. 5. Predicted population size by year and age class. Panel A shows ages 9 to 14+. Panel B shows ages 2 to 8.

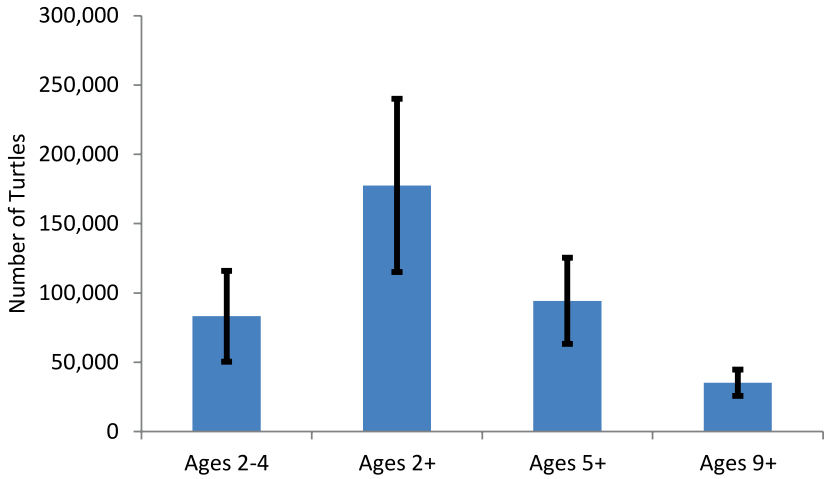


Fig. 6. Terminal (2013) population estimates with the 95% confidence interval for ages 2-4, ages 2+, ages 5+ and ages 9+ (see Table 3).

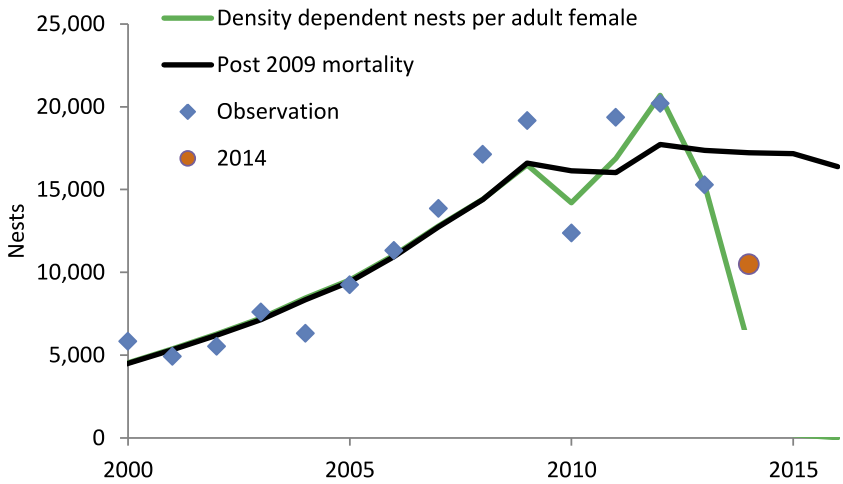
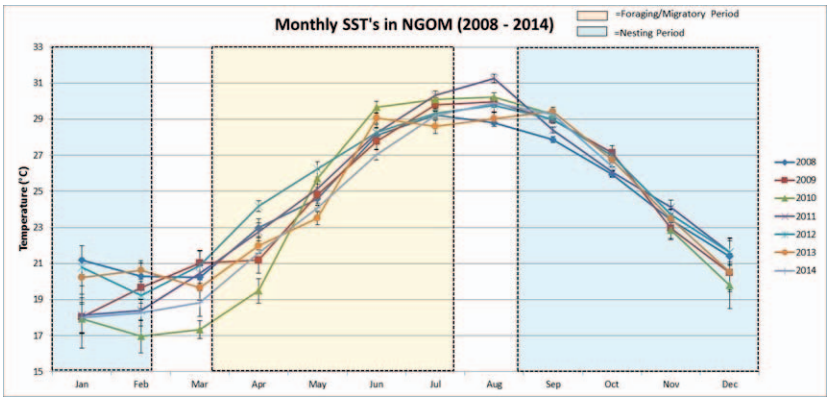


Fig. 7. Observed (points) and predicted (lines) nests based on two hypothetical scenarios fit to 1978 through 2013 with subsequent projections from 2014 through 2016. The scenario "Density-dependent nests-per-adult-female" assumes the number of nests-per-adult-female depends on the number of age 2+ females in the population; and, the "Post 2009 mortality" scenario assumes an additional mortality post 2009. The preliminary 2014 nest index is also plotted for reference.

A) Monthly SST's in NGOM (2008-2014)



B) Nesting chronology and average Jan-Mar SSTs

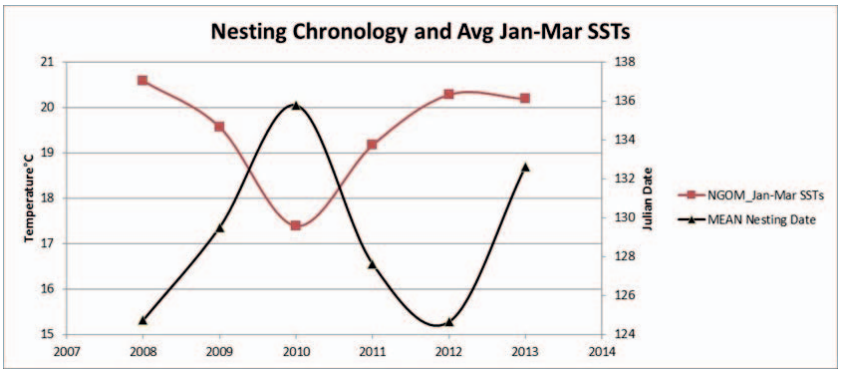


Fig. 8. Seawater temperatures on the northern Gulf foraging grounds in the spring of 2010 (Panel A) and nesting chronology and average temperature (January – March) on the northern Gulf of Mexico foraging grounds (Panel B) (Elizabeth Bevan, unpublished data).

years. Remigration intervals of several years suggest that sea turtles must attain some threshold body condition before migration. As noted by Hayes (2000): "Short of this threshold, turtles might not migrate either (a) because they have insufficient energy reserves to complete the migration or (b) they have insufficient energy reserves to lay several clutches and hence their transport costs per clutch will be high." He observed that body condition of individuals on the feeding grounds might be viewed as ranging from 0 (a turtle that has just completed its nesting migration) to 1 (the threshold above which the turtle migrates to nest). Under this concept, the body condition will increase between these levels while the individual is on the feeding grounds, and the rate of increase over time will determine the remigration interval. When the increase in body condition is more gradual, the remigration interval will be longer (Hayes 2000). Unfortunately, there are no data on Kemp's ridley female condition on foraging grounds, and remigration intervals have not been calculated in Mexico since the early 1990s. Additional research is needed to evaluate the hypothesis of a reduction in reproductive output and its causes.

We suggest that there has been a recent change in the ability of Kemp's ridley to attain a body condition necessary for remigration and reproduction due to a combination of reduced food supply and an increasing population of neritic-stage sea turtles in the northern Gulf of Mexico feeding grounds. The estimated increase in neritic-stage female Kemp's ridleys from a few thousand in 1979 to over 177,000 in 2013 (see Fig. 5, Table 4), and many other sources of information, leaves little doubt that the population has substantially increased. As outlined below, we believe it is equally clear that prey resources have declined.

It is generally accepted that the Kemp's ridley feeds primarily on an array of crab species, especially portunid crabs. Dobie et al. (1961) observed that the primary prey of the Kemp's ridleys was portunid crabs, and both Hildebrand (1981) and Ogren (1989) pointed out that the distribution of the Kemp's ridley was frequently correlated with areas having high abundance of crabs. Shaver (1991) provided a comprehensive analysis of the diets of both wild and head-started Kemp's ridleys. For neritic-stage, wild subadult, and adult Kemp's ridleys, she observed that crabs had been consumed by over 75% of the turtles examined and that crabs comprised over 90% of the dry weight of the gut contents. NMFS et al. (2011) summed up the importance of crabs in the Kemp's ridley diet, stating, "Nearly every Kemp's ridley stomach and fecal sample examined to date from the U.S. Atlantic and Gulf of Mexico has included crabs. Therefore, crabs constitute the bulk of their diet."

Owens (unpubl. data) reported that Kemp's ridleys also appeared to feed on shrimp trawl bycatch on the basis of finding fish and the gastropod scavenger, *Nassarius* sp., which feeds on dead fish, in the guts of the Kemp's ridleys he necropsied. His opinion was that Kemp's ridleys could not normally catch fish, and that the turtles were feeding on shrimp trawl discards. Shaver (1991) also noted that wild, subadult, and adult Kemp's ridleys fed on fish and shrimp in addition to crabs. She noted that both the fish and shrimp were likely dead when eaten and were probably shrimp trawl discards. Manzella and Williams (1992) observed that fish, crabs, and the gastropod scavenger *Nassarius* sp. were the most frequent food items found in the guts of 49 stranded Kemp's ridleys necropsied during 1986–89. Cannon (1998) confirmed that fish were an important part of the Kemp's ridley diet on the basis of necropsy results obtained in 1994. She also believed the fish were dead when consumed, and that they were likely shrimp trawl discards. Additionally, she cited a 1993 personal communication from James Carpenter (NMFS Galveston Laboratory) that Kemp's ridleys had been observed following shrimp boats and feeding on discarded bycatch. Shrimp trawl bycatch, mostly fish discarded at sea, appear to have become an important part of the diet of Kemp's ridleys in the northern Gulf of Mexico feeding grounds.

Above, we have made the case that crabs and fish discards from shrimp trawling are important food sources for neritic-stage Kemp's ridleys. One of the important crab species in the diet of Kemp's ridleys is the blue crab, *Callinectes sapidus*. This species supports an important nearshore fishery throughout the Gulf and was the subject of a recent stock assessment (VanderKooy 2013). Two stocks are represented in the Gulf, a western stock occurring from central Texas to Apalachicola Bay and centered in Louisiana and an eastern stock extending from South Florida to Apalochee and centered in Tampa Bay. Of these, the western stock corresponds to the major Kemp's ridley feeding grounds in the northern Gulf. Each of these stocks is also divided into juvenile and adult stock components. Juveniles

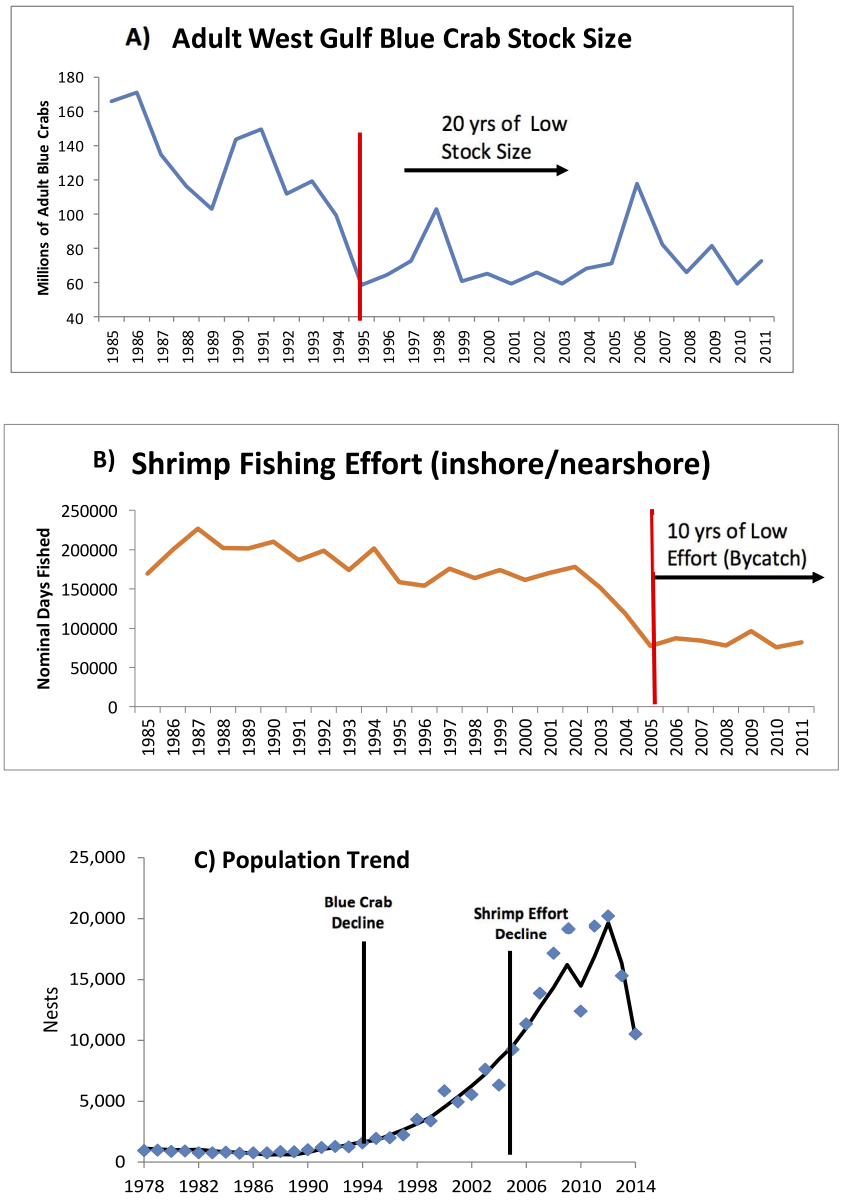


Fig. 9. Declines of Kemp's ridley food resources, blue crabs (Panel A) and bycatch index (effort, Panel B). Population trend of Kemps ridley versus starting of prey reductions is shown by Panel C.

are classified as specimens collected from October to March that are ≤80 mm carapace width (CW). Adults are defined as specimens ≥125 mm CW collected during April–September. As defined, adult crabs are the stock component of most importance as a food of Kemp's ridleys.

The western stock of adult blue crab underwent a pronounced decline from the mid-1980s to about 1995, and the stock has been relatively stable at low levels since the mid-1990s. (VanderKooy 2013; Fig. 9 panel A). The causes of the decline in adult blue crab abundance are unclear. The stock is not presently overfished or undergoing overfishing, although it is in a depressed state. Potential causes of the blue crab decline include reductions in freshwater inflow, coastal wetland losses in the Gulf of Mexico (Stedman and Dahl, 2008), and step increases in the spatial extent of the hypoxic zone, dating from the mid-1990s. Whatever the cause, the western blue crab stock has been depressed since the mid-1990s.

Shrimp fishing effort in the inshore zone and the 0- to 10-fathom-deep nearshore zone (an index to shrimp trawl bycatch discards in prime Kemp's ridley feeding grounds in the northern Gulf of Mexico) remained high until about 2000, when it began to decline. By 2005, nearshore shrimp effort had bottomed out at a much reduced level (Fig. 9, panel B). Since 2005, shrimp effort (and presumably discards) has remained low. Therefore, two important food sources of the Kemp's ridley have been greatly reduced since 2005.

The Kemp's ridley sea turtle was steadily increasing from the mid-1980s to the early to-mid-2000s, but the rate of population increase accelerated greatly from that point (Fig. 9, panel C). During this later period of population increase, blue crab and shrimp trawl bycatch (indexed by effort levels) had both dropped to low levels. We believe it is reasonable to infer that these reduced prey resources coupled with an increase in the number of Kemp's ridleys might be sufficient to change the remigration interval or the number of nests or eggs produced within a year. This provides a possible explanation for the recent (2013 and 2014) reductions in the number of nests, which have been far below what was predicted. The number of Kemp's ridley nests may be highly variable in the future, with large nesting events following good feeding conditions on the foraging grounds. On average, it may take longer for turtles to reach a body condition threshold enabling migration and reproduction than has been the case in the recent past.

Empirical data enabling an assessment of potential changes in the remigration interval are available from mark–recapture studies conducted on Kemp's ridleys that nest in Texas (Shaver et al., 2016, this issue). Over the period 2008 to 2014, mean annual remigration of Kemp's ridleys on North Padre Island increased steadily from 1.9 yr in 2008 to 3.3 yr in 2014 (Shaver et al., 2016). Subsequent data for 2015 suggest a mean remigration interval of 3.5 yr (Donna Shaver, pers. comm.). Additionally, Donna Shaver (pers. comm.) has recently verified that a female Kemp's ridley that nested in 2011 and was monitored since that time by satellite telemetry has remained in the foraging grounds for more than 4 yr and has yet to return to the nesting grounds. Similar observations have been made on South Padre Island. Thirteen Kemp's ridleys were tagged in 2010. Of these, seven were observed nesting again on South Padre Island, six in 2012 (2-yr remigration interval) and 1 in 2014 (4-yr remigration interval) (Jeff George, pers. comm.). In 2011, 15 nesting Kemp's ridleys were tagged on South Padre Island and five of these have been observed nesting again, all in 2015, which reflects a 4-yr remigration interval (Jeff George, pers. comm.). These available estimates of the remigration interval for Kemp's ridleys are all subject to a potential bias that might result from individuals nesting outside the study area or not observed during some years. If this occurred, it would result in inflated estimates of the remigration interval. Despite the potential bias, these data do support the premise that there has been a recent increase in the remigration interval, at least for some of the Kemp's ridleys that nest in Texas.

Caillouet (2014) has provided another explanation for the post-2010 decline in the number of Kemp's ridley nests—the DWH oil spill or some other factor resulted in a fundamental reduction in numbers of subadults and adults between the end of the nesting seasons in 2009 and 2010, and this reduction had profound effects on the number of nesting Kemp's ridleys, nests, eggs, and hatchlings in 2010 and beyond. He believes that losses of adults and subadults are a more likely explanation for the recent decline in the number of nests.

To resolve these issues will require a continuation of the index nesting beach studies (which have not been funded for 2016 and beyond) and additional in-water research to verify population levels and age structure, body condition of female Kemp's ridley sea turtles, remigration interval, and nesting frequency. Fitness of females in the post-oil spill era is a question of major concern and can be influenced by factors other than prey resources.

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Literature Cited

Bjorndal, K. A., J. A. Wetherall, A. B. Bolton, and J. A. Mortimer. 1999. Twenty-six years of green turtle nesting at Tortuguero, Costa Rica: an encouraging trend. Conserv. Biol. 13:126–134.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. 2d ed. Springer-Verlag, New York.

Caillouet, C. W., Jr. 2010. Editorial: demographic modeling and threats analysis in the draft 2d revision of the binational recovery plan for the Kemp's ridley sea turtle (*Lepidochelys kempii*). Mar. Turtle Newsl. 128:1–6 (http://www.seaturtle.org/mtn/archives/mtn128/mtn128p1.shtml).

———. 2011. Guest editorial: did the BP–Deepwater Horizon–Macondo oil spill change the age structure of the Kemp's ridley population? Mar. Turtle Newsl. 130:1–2 (http://www.seaturtle.org/mtn/archive/mtn130/mtn130pl.shtml).

Caillouet, C. W., Jr. 2014. Guest editorial: interruption of the Kemp's ridley populations pre-2010 exponential growth in the Gulf of Mexico and its aftermath: one hypothesis. Mar. Turtle Newsl. 143:1–7.

Cannon, A.C. 1998. Gross necropsy results of sea turtles stranded on the upper Texas and western Louisiana coasts, 1 January–31 December 1994. *In:* Characteristics and causes of Texas marine strandings. R. Zimmerman (ed.). NOAA Technical Report, NMFS 143, Silver Spring, MD.:85 p.

Carr, A. 1975. The Ascension Island green turtle colony. Copeia 1975:547–555.

———, and M. H. Carr. 1970. Modulated reproductive periodicity in *Chelonia*. Ecology 51:335–337.

———, ———, and A. B. Meylan. 1978. The ecology and migrations of sea turtles, 7. The West Carribean green turtle colony. Bull. Am. Mus. Nat. Hist. 162:1–146.

Crowder, L., and S. Heppell. 2011. The decline and rise of a sea turtle: how Kemp's ridleys are recovering in the Gulf of Mexico. Solutions 2:67–73.

Dobie, J. L., L. H. Ogren, and J. Fitzpatrick. 1961. Food notes and records of the Atlantic ridley turtle (*Lepidochelys kempii*) from Louisiana. Copeia 1961(1):109–110.

Gallaway, B. J., et al.. 2016. Development of a Kemp's ridley sea turtle stock assessment model. Gulf Mex. Sci. 33. In press.

Hayes, G. C. 2000. The implications of variable remigration intervals for the assessment of population size in marine turtles. J. Theoret. Biol. 206:221–227.

Hildebrand, H. H. 1981. A historical review of the status of sea turtle populations in the western Gulf of Mexico, p. 447–453. *In:* Biology and conservation of sea turtles. K. A. Bjorndal (ed.). Smithsonian Institution Press, Washington, DC.

Manzella, S. A., and J. A. Williams. 1992. The distribution of Kemp's ridley sea turtles (*Lepidochelys kempii*) along the Texas coast: an Atlas. NOAA Technical Report 110. 52 p.

Marquez-M., R. 1994. Synopsis of biological data on the Kemp's ridley turtle, *Lepidochelys kempii* (Garman, 1980). NOAA Technical Memorandum NMFS-SEFSC-343. 91 p.

Morris, W. F., and D. F. Doak. 2003. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Sunderland, MA.

National Marine Fisheries Service, U.S. Fish and Wildlife Service, and Secretaria de Medio Ambiente y Recursos Naturales (NMFS, USFWS, and SEMARNAT). 2011. Binational recovery plan for the Kemp's ridley sea turtle (*Lepidochelys kempii*). 2nd rev. National Marine Fisheries Service, Silver Spring, MD. 156 p.+ appendices.

National Oceanic and Atmospheric Administration (NOAA) Fisheries. 2014. 2010 Gulf of Mexico oil spill: sea turtles, dolphins and whales. http://www.NMFS.NOAA.gov/pr/health/oil spill/gulf2010.htm. Updated October 10, 2014. Visited 27 February 2015.

Ogren, L. J. H. 1989. Distribution of juvenile and subadult Kemp's ridley turtles: preliminary results from the 1984–1987 surveys, p. 116–123. *In:* C. W. Caillouet, Jr. and A. M. Landry (eds.). Proceedings of the 1st international symposium on Kemp's ridley sea turtle biology, conservation and management, October 1–4, 1985, Galveston, TX.

Peña, J. 2014. 2013 report on the Mexico/United States of America population restoration project for the Kemp's ridley sea turtle, *Lepidochelys kempii* on the coast of Tamaulipas, Mexico. Programa Binacional de la Tortuga Lora. Gladys Porter Zoo, Brownsville, TX.

Shaver, D. S. 1991. Feeding ecology of wild and head-started Kemp's ridley sea turtles in south Texas waters. J. Herpetol. 25(3):327–334.

Shaver, D. S., C. Rubio, J. S. Walker, J. George, A. F. Amos, K. Reich, C. Jones, and T. Shearer. 2016. Kemp's ridley (*Lepidochelys kempii*) nesting on the Texas coast: geographic, temporal, and demographic trends through 2014. Gulf Mex. Sci. 33. In press.

Stedman, S., and T. E. Dahl. 2008. Status and trends of wetlands in the coastal watersheds of the eastern United States 1998 to 2004. National Oceanic and Atmospheric Administration, National Marine Fisheries Service and the U.S. Department of the Interior, Fish and Wildlife Service. 32 p.

VanderKooy, S. (ed). 2013. Stock assessment report GDAR 01: Gulf of Mexico blue Crab. GSMFC (number 215. Gulf Data, Assessment and Review, Gulf States Marine Fisheries Commission, Ocean Springs, MS. 291 p.

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