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Source: Chelonian Conservation and Biology, 17(1) : 123-133

Published By: Chelonian Research Foundation and Turtle Conservancy

URL: https://doi.org/10.2744/CCB-1283.1

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Chelonian Conservation and Biology, 2018, 17(1): 123–133
doi:10.2744/CCB-1283.1

Did Declining Carrying Capacity for the Kemp's Ridley Sea Turtle Population Within the Gulf of Mexico Contribute to the Nesting Setback in 2010–2017?

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ABSTRACT. – **The Kemp's ridley (*Lepidochelys kempii*) is the most endangered sea turtle species. During 1966–2017, an annual count of nests (i.e., clutches of eggs laid) has served as an annual index of Kemp's ridley nesting female abundance on the Gulf of Mexico (GoM) index beach in Tamaulipas, Mexico. This index was increasing exponentially at 19% per year in 2009, but it dropped unexpectedly by more than a third in 2010 and through 2017 remained well below levels predicted. We hypothesize that pre-2010 declining carrying capacity for the Kemp's ridley population within the GoM contributed to this nesting setback. We discuss pre-2010 factors that may have caused carrying capacity to decline, including degradation of the GoM ecosystem, the exponentially increasing Kemp's ridley population, and declining per capita availability of neritic (i.e., postpelagic) Kemp's ridley food, including natural prey and scavenged discarded bycatch from shrimp trawling. We encourage evaluations (especially those within a robust modeling framework) of this hypothesis and others put forth to explain the nesting setback to provide information needed to guide restoration of the population's progress toward recovery.**

KEY WORDS. – **Reptilia; Testudines; Cheloniidae; *Lepidochelys kempii*; Tamaulipas; Mexico; nesting female abundance index; regression models; Gulf of Mexico; carrying capacity; ecosystem degradation; per capita food availability; Deepwater Horizon oil spill; shrimp trawling**

The Kemp's ridley (*Lepidochelys kempii*) remains the most endangered sea turtle species, despite more than half a century of cumulative regulatory actions, conservation efforts, and research applied toward its recovery (Gallaway et al. 2013, 2016a, 2016b; Márquez-Millán et al. 2014; Caillouet et al. 2015b, 2016). Beginning in 1966, Mexico's federal government began protecting Kemp's ridley nesting females, nests (i.e., clutches of eggs laid), and hatchlings released on the species' primary nesting beach near Rancho Nuevo on the Gulf of Mexico (GoM) coast of Tamaulipas, Mexico (Pritchard and Márquez M. 1973; Márquez-M. et al. 1982; Márquez Millan et al. 1989; Marquez-M. 1994; Márquez M. 2001; Márquez-Millán et al. 2014; Peña 2017; see Caillouet et al. 2016, fig. 1). Mexico's federal government also initiated annual counts of nests, eggs, and hatchlings released at Rancho Nuevo in 1966. As nesting spread along the Tamaulipas coast, these protections and counts were incrementally extended from Rancho Nuevo southward to Barra del Tordo and northward to Tepehuajes (see Márquez-Millán et al. 2014, table 2; Caillouet et al. 2016, fig. 1). During 1966–2017, the annual count of nests has served as an annual index of abundance of nesting females and is referred to hereinafter as the index.

The binational recovery plan for Kemp's ridley turtles (National Marine Fisheries Service [NMFS] et al. 2011) estimated that the index was increasing exponentially at 19% per year in 2009. This high rate of increase resulted from cumulative beneficial effects of regulatory actions, conservation efforts, spatiotemporal closures to shrimp

trawling, and diminishing shrimp trawling effort that, in combination, restored and increased annual inputs of hatchlings into the western GoM and reduced at-sea mortality of neritic (i.e., postpelagic) Kemp's ridleys (reviewed by Gallaway et al. 2013, 2016a, 2016b; Caillouet et al. 2015b, 2016; Keithly and Roberts 2017). Natural factors, such as climate change or shifts in predator and/or prey populations, may also have contributed to the exponential increase (Heppell et al. 2007). Based on the simple concepts that population growth occurs when births (measured as annual hatchlings released, sexes combined) exceed deaths and that immigration and emigration can be ignored (Heppell et al. 2007), the pre-2010 exponential increase in the index could not have occurred unless additions of female hatchlings to the population overwhelmed all losses of females from natural and anthropogenic causes combined (Caillouet et al. 2016).

NMFS et al. (2011) predicted that by 2011, the Kemp's ridley population would become large enough to support 10,000 females nesting in a season (equivalent to 25,000 clutches divided by 2.5 clutches per nesting female), which is 1 of 2 criteria established for downlisting this species from endangered to threatened status. The other criterion for downlisting is a minimum annual release of 300,000 hatchlings from the index beach, which has been exceeded for more than a decade. However, instead of continuing to increase exponentially, the index dropped unexpectedly by more than a third in 2010 (Caillouet 2010, 2011, 2014; Crowder and Heppell 2011; Gallaway et al. 2013) and remained well below levels predicted by NMFS et al. (2011) through 2017 (Caillouet et al. 2015b, 2016; Dixon and Heppell 2015; Gallaway et al. 2016a, 2016b; Peña 2017).

The 87-d Deepwater Horizon (DWH) oil spill (which began on 20 April 2010; Lubchenco et al. 2012; Wallace et al. 2017; Ylitalo et al. 2017), remedial responses to this oil spill (Lubchenco et al. 2012; Wallace et al. 2017; Ylitalo et al. 2017), and incidental capture in shrimp trawls within the northern GoM were initially hypothesized to have caused the Kemp's ridley nesting setback (Caillouet 2010, 2011, 2014; Crowder and Heppell 2011; Gallaway et al. 2013, 2016a, 2016b). Incidental capture in shrimp trawls was suspected because it was characterized in 1990 as the most important human-associated source of sea turtle mortality (National Research Council [NRC] 1990) and continues to be associated with at-sea mortality of neritic Kemp's ridleys, albeit to a diminishing extent (Gallaway et al. 2013, 2016a, 2016b). Additional anthropogenic and natural causes of the nesting setback were also hypothesized (Caillouet 2010, 2011, 2014; Crowder and Heppell 2011; Gallaway et al. 2016a, 2016b; Shaver et al. 2016b; Avens et al. 2017). So far, evaluations of hypothesized causes of the nesting setback have been inconclusive (NMFS and US Fish and Wildlife Service [US FWS] 2015; Caillouet et al. 2016; Deepwater Horizon Natural Resource Damage Assessment Trustees [DWH NRDA Trustees] 2016; Gallaway et al. 2016a, 2016b). We recognize that various natural and anthropogenic causes could have contributed to the nesting setback either separately or synergistically.

We hypothesize that pre-2010 declining carrying capacity for the Kemp's ridley population within the GoM contributed to the observed downward departures of the index during 2010–2017 compared with levels predicted by NMFS et al. (2011). For our purposes, carrying capacity for the Kemp's ridley population within the GoM is assumed to be the annual maximum population size (including both sexes and all life stages combined) that the GoM ecosystem and adjoining nesting beaches can support. Kemp's ridleys nest beyond the index beach, so we do not consider availability of nesting space to have limited the index's rate of increase (Caillouet et al. 2016). Carr (1967) stated that Kemp's ridley nesting females were not squeezed mechanically into diminishing nesting space and suggested other possible causes for their characteristic aggregated (i.e., *arribada*) nesting behavior. We recognize that annual survival rates of oceanic (surface-pelagic) life stage Kemp's ridleys are likely very low and variable (Heppell 1997; Putman et al. 2013, 2015). Therefore, our focus is on factors that may have caused carrying capacity within the GoM to decline, including pre-2010 degradation of the GoM ecosystem, the exponentially increasing Kemp's ridley population, and declining per capita availability of neritic Kemp's ridley food, including natural prey and scavenged discarded bycatch from shrimp trawling. We also applied an exponential regression model to the 1966–2009 time series of the index and a logistic regression model to the 1966–2017 time series of the index, assuming multiplicative error.

EARLY THREATS AND REMEDIES

The Rancho Nuevo nesting beach was discovered on 18 June 1947 by Andrés Herrera, who filmed the largest-ever-recorded *arribada* of Kemp's ridley nesting females (Carr 1963, 1967; Hildebrand 1963; Bernardo and Plotkin 2007; Pritchard 2007; Wibbels and Bevan 2014, 2016). Hildebrand (1963) estimated there were 40,000 nesting females in that *arribada* (see also Wibbels and Bevan 2016). Hildebrand (1963) gave early warnings that natural predation and human overexploitation were serious threats that could lead to Kemp's ridley extinction and recommended that conservation measures be promulgated to prevent it. Eleven years after Mexico's federal government initiated conservation efforts at Rancho Nuevo, Carr (1977) added the warning that shrimp trawling was wiping out the species (see also Pritchard and Márquez M. 1973).

Regulatory actions were initiated during 1956–1977 by Mexico's federal government to reduce harvest of sea turtles and their eggs (Márquez-M. et al. 1982; Márquez Millan et al. 1989). Although covered by all of these

actions, the Kemp's ridley was not mentioned specifically in such regulatory actions until 1965 (Márquez Millan et al. 1989). In 1966, Mexico's federal government initiated its program of Kemp's ridley protection, conservation, monitoring, and research at Rancho Nuevo (Chavez et al. 1968; Pritchard and Márquez M. 1973; Márquez-M. et al. 1982; Márquez Millan et al. 1989; Marquez-M. 1994; Márquez M. 2001; Márquez-Millán et al. 2014). In 1977, Mexico's federal government declared the Rancho Nuevo beach a natural reserve, prohibiting trawling offshore of the beach between Barra del Tordo and Barra de Ostionales during the nesting season (Márquez-M. et al. 1982; Márquez Millan et al. 1989; Márquez M. 2001; Márquez-Millán et al. 2014).

In 1978, federal governments of Mexico and the United States launched the Kemp's Ridley Restoration and Enhancement Program aimed at reintroducing Kemp's ridley nesting to Padre Island National Seashore near Corpus Christi, Texas, and increasing protection, conservation, monitoring, and research efforts in Tamaulipas (Márquez-M. et al. 1982; Marquez-M. 1994; Márquez-Millán et al. 2014; Caillouet et al. 2015b; Shaver and Caillouet 2015). Despite these efforts, the index continued declining to its lowest level in 1985 (Byles 1993; Caillouet 2006; Caillouet et al. 2016).

Incidental capture in shrimp trawls also contributed to the Kemp's ridley population's post-1947 decline (Pritchard and Márquez M. 1973; Carr 1977; NRC 1990; NMFS et al. 2011; NMFS and US FWS 2015; Caillouet et al. 2016). In the mid-1940s, the GoM shrimp fishery underwent a major expansion (Condrey and Fuller 1992; Iversen et al. 1993). American shrimpers started trawling off Mexico's GoM coast in 1945 (Iversen et al. 1993), and in 1946 US registries of at least 48 vessels were transferred to Mexico, which allowed them to fish legally in Mexico's waters (Condrey and Fuller 1992). One of the 3 major areas fished in Mexico's waters by these vessels was along the coast of Tamaulipas (Iversen et al. 1993). Shrimp trawling by the US fleet in Mexico's GoM waters was phased out during 1976–1979, under a US–Mexico treaty (Iversen et al. 1993). At-sea mortality of neritic Kemp's ridleys was also reduced by spatiotemporal closures to shrimp trawling, development and use of turtle excluder devices in shrimp trawls, and declining shrimp trawling effort (Heppell 1997; Turtle Expert Working Group [TEWG] 1998, 2000; Lewison et al. 2003, 2013; Gallaway et al. 2013, 2016a, 2016b; Caillouet et al. 2016).

UTILITY AND LIMITATIONS OF THE INDEX

Utility of the index has been demonstrated by its incorporation into demographic models (Márquez-M. et al. 1982; TEWG 1998, 2000; Heppell et al. 2005, 2007; Crowder and Heppell 2011; NMFS et al. 2011; NMFS and US FWS 2015), stock assessment models (Gallaway et al. 2013, 2016a, 2016b), regression models (Dixon and Heppell 2015), and novel analyses of the time-lagged index and cumulative hatchlings released (Caillouet et al. 2016). However, the annual number of multiaged adult females is a relatively small and unknown proportion of the Kemp's ridley population, and those that nest constitute a smaller proportion that influences the index (Bjorndal et al. 2011; Crowder and Heppell 2011; NMFS et al. 2011; NMFS and US FWS 2015; Caillouet et al. 2016). The Committee on Sea Turtle Population Assessment Methods (CSTPAM 2010) questioned the use of such an index in the absence of estimates of breeding probability and recruitment of new turtles to the breeding population and suggested that assessment of population trends on the basis of nesting beach data is highly tenuous (see also Seminoff and Shanker 2008). Only intermittent estimates of adult female Kemp's ridley recruitment and breeding probability exist (Heppell et al. 2005, 2007; Witzell et al. 2005; Crowder and Heppell 2011; NMFS et al. 2011; NMFS and US FWS 2015; Shaver et al. 2016b). However, comparable 1966–2017 time series of actual abundance of neophyte nesting females (those nesting for the first time), remigrant nesting females (those that nested in 1 or more previous nesting seasons), adult females in the population, and total population size (all life stages and both sexes combined) do not exist, so it is impossible to evaluate their expected correlations with the index or with each other. Logically, they should all be correlated to some extent. The proportion of the annual total population made up of Kemp's ridley males varies, and it is smaller than that of females because overall sex ratios have generally been dominated by females (reviewed by NMFS and US FWS 2015). We assume that all clutches found annually on the index beach have been documented, whether translocated to protective corrals or left in situ (NMFS and US FWS 2015).

PRE-2010 DENSITY DEPENDENCE OF THE INDEX

The hypothesis that pre-2010 declining carrying capacity for the Kemp's ridley population within the GoM contributed to the nesting setback requires evidence of pre-2010 development of density dependence in the index. Peter C.H. Pritchard suggested that the inflection point in Kemp's ridley population growth would be reached at a much higher population level than would have occurred naturally because protection and incubation of clutches in beach corral hatcheries produce much higher numbers of hatchlings than do clutches left in situ and natural limitations on population growth would be imposed by carrying capacity (Caillouet 2014). Heppell et al. (2007) suggested that carrying capacity for the Kemp's ridley population can be decreased by a restriction in the amount of available nesting habitat, degradation of high-quality foraging habitat in the northern GoM, and reduction in abundance of prey by competition with fisheries or interspecific competition with loggerhead sea

Table 1. Parameter estimates for the exponential (1966–2009 time series of the index) and logistic (1966–2017 time series of the index) models.

		Exponential			Logistic		
Parameter	Description	Before t_A	At t_A	After t_A	Before t_A	At t_A	After t_A
t_A	Calendar year when $N_t = A$ during the time series	—	1984.5	—	—	1985.0	—
N_0	N_t when $t - t_A = 0$ and $A = 0$	—	149.3	—	—	—	—
A	Lower asymptote	—	522.1	—	—	703.8	—
r	Instantaneous growth rate	−0.192	—	0.201	−0.297	—	0.289
K	Upper asymptote	—	—	—	24,306.5	—	17,433.6
I	Year when point of inflection occurred	—	—	—	1962.4	—	2004.3

turtles (*Caretta caretta*). Heppell et al. (2007) noted that annual numbers of hatchlings had been increasing less rapidly than numbers of nests for many years and attributed this to gradual reductions in average nest survival or fecundity (see Márquez M. 2001; Caillouet 2014).

Because of expectations that there eventually would not be enough resources to find, translocate, and protect increasing numbers of clutches in beach corrals in Tamaulipas as nesting increased, TEWG (1998, 2000) used demographic models to simulate effects of leaving various numbers of clutches in situ (Crowder and Heppell 2011; NMFS et al. 2011; Bevan et al. 2014). Hatching success in clutches left in situ is lower than that in beach corral hatcheries (TEWG 2000; Heppell et al. 2005, 2007; Crowder and Heppell 2011; Bevan et al. 2014; NMFS and US FWS 2015). In addition, Caillouet (2014) showed that average number of hatchlings released per nest increased to a peak in 1989 and thereafter declined. Many factors that affect survival between the egg and hatchling life stages and during the hatchlings' crawl to the surf could have contributed to the post-1989 decline in average number of hatchlings released per nest (Bevan et al. 2014; Caillouet 2014; Caillouet et al. 2016). Caillouet et al. (2016) plotted upward trends in cumulative hatchlings released from the index beach as well as trends in 2 novel metrics derived from the 1986–2014 time series of the index and the 1976–2004 time series of cumulative hatchlings released. All plots exhibited sigmoid shapes through 2009, suggesting that density dependence affecting the index began developing prior to 2010 (Caillouet et al. 2016). Because annual hatchlings released at the index beach depend to a large extent on the magnitude of the index, slowing of the rate of increase in cumulative hatchlings released from the index beach reflects, to a large extent, a slowing in the rate of increase in the index (see Heppell et al. 2007).

For Kemp's ridleys nesting in Texas, Shaver et al. (2016b) reported a pre-2010 trend of increase in the remigration interval for experienced nesting females (i.e., remigrants) as well as a trend of decline in the annual proportion of apparent neophyte (i.e., first time) nesting females. Avens et al. (2017) reported pre-2010 slowing of the growth rate of individual Kemp's ridleys in the GoM. Such trends would be expected from development of density dependence prior to 2010.

Because of the aforementioned evidence that density dependence began developing in the index before 2010, we parameterized and applied 2 regression models to selected time series of the index. An exponential model was applied to the index's (N_t) 1966–2009 time series:

$$N_t = A + N_0 e^{r \cdot (t - t_A)} \quad [1]$$

where A = lower asymptote, t = calendar year, t_A = calendar year when $N_t = A$, N_0 = index when $t - t_A = 0$, and r = instantaneous growth rate. A logistic model was applied to the index's 1966–2017 time series:

$$N_t = A + \frac{K - A}{1 + e^{-r \cdot (t - (t_A - I))}} \quad [2]$$

where K = upper asymptotes and I = calendar years in which points of inflection occurred (one for the decline in the index and another for its increase). Error was assumed to be multiplicative for fitting both models (see Dixon and Heppell 2015). Two sets of parameters were required for each model (Table 1): one to fit the decline in the index from 1966 to the mid-1980s and the other to fit the subsequent increase in the index from the mid-1980s to the ends of the respective time series. Fitting 2 sets of parameters for each model allowed estimation of the year in which the lower asymptote (A) of the index occurred. The logistic model also estimated years in which the maximum rates of decline and increase in the index occurred and therefore the intervals of years during which density-independent and density-dependent declines and increases occurred. Parameters A and N_0 were assumed to be equal for the decline and increase phases of the logistic model.

Both models estimated the year in which the lower asymptote (A) occurred to be around 1985 (Table 1), which is consistent with previous views that the index reached its lowest level in 1985 (Byles 1993; Caillouet 2014; Bevan et al. 2016; Caillouet et al. 2016). Both models were used to extrapolate N_t backward from 1966 to 1945 and forward from 2009 to 2017. The exponential model fit the index during 1966–2009 more closely than did the logistic model (Fig. 1A). Also, the exponential model estimated the rate of decline in the index (i.e.,

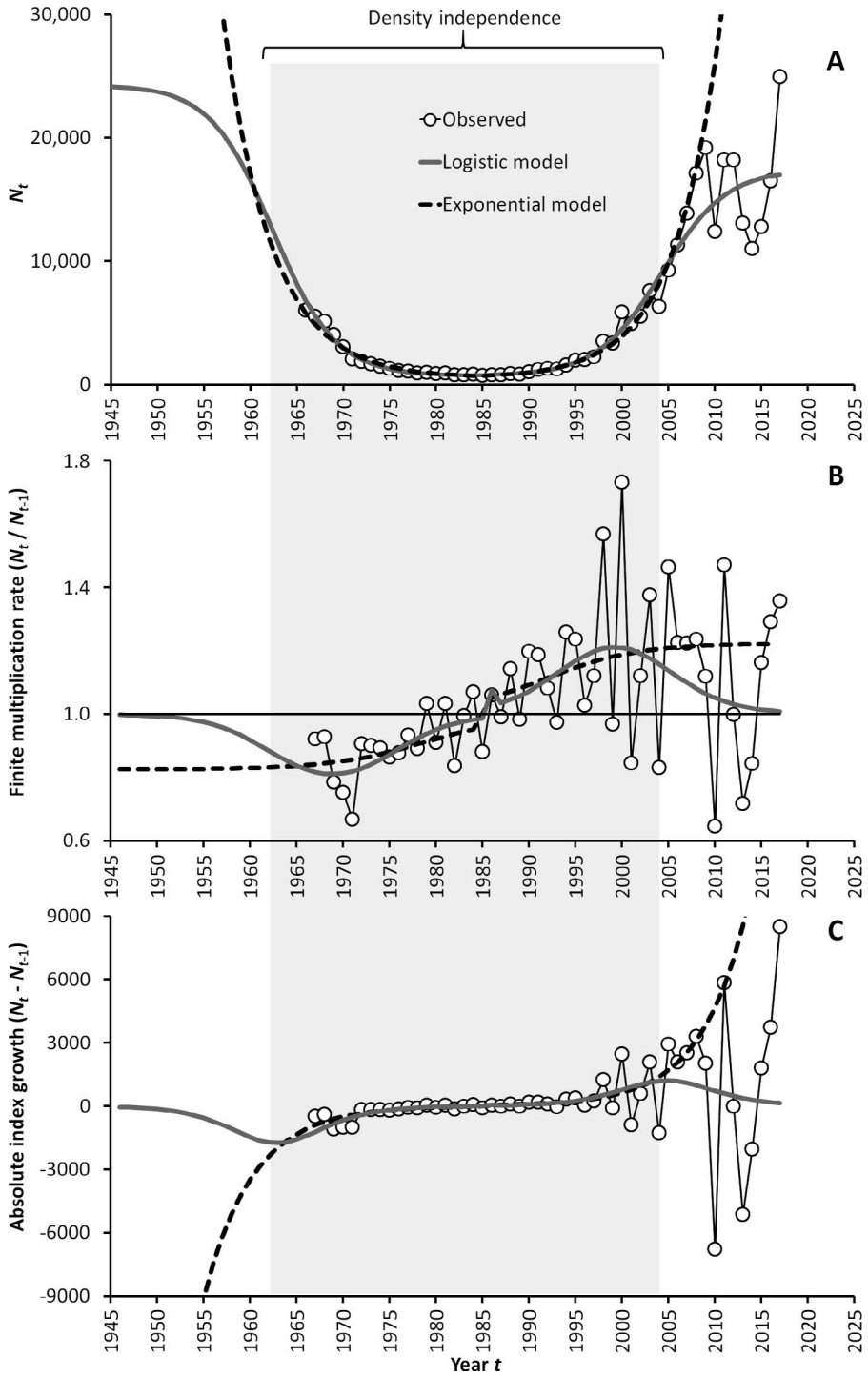

Figure 1. Graphs of time series of (A) observed index N_t, showing lines fitted by the exponential and logistic models; (B) corresponding finite multiplication rate estimated for both models; and (C) absolute growth estimated for both models. The shaded area represents the span of years between the 2 inflection points estimated by the logistic model, that is, the estimated period of years during which the index experienced density-independent decline and growth.

$100[e^r - 1]$) during 1966–1985 at –17% per year and the rate of increase (also ($100[e^r - 1]$) thereafter through 2009 at 22% per year (Table 1), the latter of which is higher than the 19% per year rate estimated by the demographic model applied by NMFS et al. (2011). All levels of the index during years 2010–2017 were well below those predicted (extrapolated) by the exponential model (Fig. 1A).

The logistic model's main advantage over the exponential model was its better fit to the index during years 2010–2017. During 2010–2017, the index fluctuated widely around the line predicted by the logistic model, which is consistent with multiplicative error. The 2 upper asymptotes (K) estimated by the logistic model (Table 1) were 24,306 (before the pre-1986 decline) and

17,434 (after the 1986–2009 increase) (Fig. 1A; Table 1). Interestingly, the upper asymptote preceding the decline was near the 25,000-nest level that is assumed equivalent to the Kemp's ridley downlisting criterion of 10,000 females nesting in a season (NMFS et al. 2011). This asymptote (K) was also the same order of magnitude as the number of nests estimated by Bevan et al. (2016) for the 1947 *arribada*, namely, approximately 26,916. Density-dependent periods estimated by the logistic model occurred before 1962 and after 2004 (Fig. 1). After reaching its minimum around 1969 (Fig. 1B), the finite multiplication rate increased to its maximum around 1999 and then declined through 2017. The estimated index was 3612 in 1969 and 3675 in 1999 (Fig. 1A). Starting around the late 1990s, annual fluctuations in the finite multiplication rate increased considerably. Absolute index growth (Fig. 1C) reached its minimum around 1962 and maximum around 2004, the years that marked the 2 points of inflection (Table 1) in the fitted logistic curve (Fig. 1A). We infer from this result that density-independent decline and growth of the index occurred during 1962–2004; corresponding index levels estimated for 1962 and 2004 were 13,170 and 8695, respectively (Fig. 1A).

POSSIBLE CAUSES OF CARRYING CAPACITY DECLINE

Although the details are outside the scope of this article, there is widespread evidence of long-term alteration and degradation of the GoM ecosystem prior to 2010 (Peterson et al. 2011; Walker et al. 2012; Yasuhara et al. 2012; Karnauskas et al. 2013; Shepard et al. 2013; Benitez et al. 2014; Davis 2017; Hu et al. 2017; Scavia et al. 2017; Ward 2017). In addition, exponentially increasing numbers of neritic Kemp's ridleys (both sexes combined) may have contributed to a reduction in per capita availability of Kemp's ridley natural prey and scavenged discarded bycatch from shrimp trawling prior to 2010 (Gallaway et al. 2016b; Shaver et al. 2016b). Would-be nesting females require energy reserves for migration from foraging grounds to nesting beaches and for reproduction (Morreale et al. 2007; Caillouet 2014; Caillouet et al. 2016; Gallaway et al. 2016b; Rees et al. 2016). Sea turtle populations that have access to ample high-quality food exhibit somatic growth rates, body condition, and clutch frequency that are higher and interbreeding intervals that are shorter than populations that have poor food resources or are approaching carrying capacity at which competition for food is high (CSTPAM 2010). The National Academies of Sciences, Engineering, and Medicine (2017) recognized that monitoring prey (such as blue crab [*Callinectes* sp.] stocks) can help explain sea turtle response to restoration along with turtle-specific monitoring practices.

GoM diets of neritic Kemp's ridleys include organisms that are natural prey (particularly crabs, dominated by the blue crab, *C. sapidus*), scavenged discarded bycatch from shrimp trawling, or organisms that feed on such bycatch (Pritchard and Márquez M. 1973; Rebel 1974; Shaver 1991; Marquez-M. 1994; Cannon 1998; Shaver et al. 2013, 2016a, 2016b; Servis et al. 2015; Metz and Landry 2016; Seney 2016; Valverde and Holzwart 2017). Increasing numbers of neritic Kemp's ridleys (both sexes) may have reduced per capita availability of their prey and scavenged discarded bycatch. Neritic Kemp's ridleys also compete with loggerheads, numerous other marine species, and crab fisheries, all of which can reduce abundance of their food (Guillory et al. 2001; Bourgeois et al. 2014; Perry and VanderKooy 2015; Servis et al. 2015; Metz and Landry 2016; Seney 2016; Shaver 2016a, 2016b). Declining shrimp trawling effort and use of bycatch reduction devices have reduced amounts of shrimp trawling bycatch (Shaver et al. 2013; Gallaway et al. 2016b). Abundance of blue crabs has also been reduced by GoM ecosystem degradation (Bourgeois et al. 2014; Perry and VanderKooy 2015). Belskis et al. (2016) hypothesized that neritic juvenile Kemp's ridleys congregate to feed on discarded fisheries bycatch, thereby becoming vulnerable to incidental capture by recreational hook and line fisheries and commercial trawl fisheries. Recent increases in reported incidental hook-and-line interactions with Kemp's ridleys by recreational fishers (Coleman et al. 2016; Seney 2016) may be evidence of reduced per capita availability for prey and discarded scavenged bycatch.

DISCUSSION

GoM carrying capacity for the Kemp's ridley population likely was very high for decades prior to 1947 (Pritchard 2007; Wibbels and Bevan 2016), thus allowing accumulation of adult females sufficient to support the 1947 *arribada* and additional nesting during that season (Caillouet 2006; Wibbels and Bevan 2016). However, Andrés Herrera's film suggested that survival of clutches was reduced by human harvest of eggs and predation by coyotes (*Canis latrans*), the latter because some *arribada* nesting females dug up and exposed large numbers of eggs from previously laid clutches (Carr 1963, 1967; Hildebrand 1963; Pritchard and Márquez M. 1973). The loss of emergent hatchlings to predators (Hildebrand 1963; Pritchard and Márquez M. 1973) during their crawl to the surf also likely was high. Even though anthropogenic threats had emerged on the Rancho Nuevo beach and at sea by 1947 and natural mortality of eggs and hatchlings was apparently high, adult females apparently were very abundant in the Kemp's ridley population at that time. If age structure of the 1947 population could be estimated by modeling, assuming that it was stable at that time, it could serve as one of the goals to be achieved through restoration efforts. We recommend that stock assessment modeling be applied to estimate age structures of the annual population in each year 1947 and 1966–2017. Changes in estimated annual age structure during

1966–2009 could provide information on the effects of population recovery actions and factors that reduced the impacts of shrimp trawling before 2010, and changes in estimated annual age structure during 2010–2017 could provide information related to the nesting setback (see Caillouet 2014).

If declining carrying capacity is later proved to have contributed significantly to the Kemp's ridley nesting setback during 2010–2017, this would not exonerate other possible contributors. For example, DWH NRDA Trustees (2016) concluded the following:

1) DWH oil did not arrive on the continental shelf of the northern GoM until late May or early June 2010. By that time, adult Kemp's ridleys that were going to breed in 2010 would likely have already departed the northern GoM for breeding and nesting areas in the western GoM.
2) DWH oil was unlikely to have had a direct impact on Kemp's ridley nesting in 2010. However, DWH oil could have contributed to reduced numbers of nests in 2011–2014 through direct and indirect pathways. For example, adult females that were not nesting in 2010, as well as subadults that would have recruited to the adult female portion of the population in 2011–2014, were among the Kemp's ridleys present on the continental shelf in 2010 and potentially killed by DWH oil exposure. Loss of these adult and subadult females would have affected the overall Kemp's ridley turtle nesting trajectory in subsequent years.

Moreover, studies of exposure of Kemp's ridley to DWH oil and dispersants focused on small, surface-pelagic juveniles collected or sighted in the oceanic zone during boat-based rescue operations (McDonald et al. 2017; Wallace et al. 2017), whereas exposure status of larger, neritic juveniles and adults was estimated from aircraft-based aerial surveys over the continental shelf (Wallace et al. 2017). It is possible that heavily oiled neritic turtles were more difficult for plane-based observers to see, particularly if dark-colored, oiled turtles surfaced in or near a dark-colored oil slick (Wallace et al. 2017). Some of the larger, neritic juveniles and adults observed were not identified to species; thus, the probability of heavy oiling was not estimated for each species separately (Wallace et al. 2017). NMFS et al. (2011) recognized that sublethal effects are likely inherent in any threat where mortality also occurs, and such effects are likely to affect individual fitness (e.g., somatic growth, egg production, and hatchling production). There is concern that Kemp's ridley delisting criteria established by NMFS et al. (2011) may no longer be achievable (Wibbels and Bevan 2016). Caillouet et al. (2015a) proposed that the Kemp's ridley recovery plan (NMFS et al. 2011) be updated and modified because of new findings and changes in this species' status after 2009. In addition, future changes in the index might serve as one measure of efficacy of GoM ecosystem restoration (Gulf Coast Ecosystem Restoration Council 2016; DWH NRDA Trustees 2017; National Academies of Sciences, Engineering, and Medicine 2017).

Annual numbers of Kemp's ridley nests in Mexico and Texas are highly correlated (Shaver et al. 2016b). Encouragingly, the index reached a post-1965 record high in 2017 (Peña 2017), and the same was true for Texas (D.J. Shaver, *pers. comm.,* August 2017). However, the index (22,415 nests) in 2017 was less than half of that predicted by NMFS et al. (2011). Perhaps it simply represents another wide, post-2009 fluctuation. Alternatively, because the lowest post-2009 index occurred in 2014 and the index increased incrementally in 2015, 2016, and 2017, this upward trend (Fig. 1A) may represent a delayed return to an exponentially increasing population growth phase (see Caillouet 2014).

As consequences of the nesting setback, annual numbers of hatchlings released from the index beach during 2010–2017 also were reduced well below expectations (Caillouet et al. 2016; Peña 2017). These reductions likely will reduce numbers of year-class 2010–2017 females that survive to maturity and nest in future years. Thereby, their time-lagged effects on future levels of the index should be detectable (Caillouet 2011) and could serve as metrics of partial losses of GoM ecosystem services (NRC 2013). Therefore, we recommend that all hypotheses put forward to explain the nesting setback be subjected to robust evaluations. Achievement of Kemp's ridley recovery goals (NMFS et al. 2011) may depend on a better understanding of the natural and anthropogenic environmental influences (both biotic and abiotic) and demographic processes that initiated the nesting setback (Bjorndal et al. 2011). This will require acquisition and synthesis of essential data on Kemp's ridley demography and abundance and environmental influences as well as evaluations within a robust modeling framework (Bjorndal et al. 2011; Putman et al. 2013, 2015). Such an approach can provide valuable information needed to guide restoration of the population's progress toward recovery.

ACKNOWLEDGMENTS

We are grateful to all federal, state, and local agencies, organizations, and individuals in Mexico and the United States that contributed to planning, funding, execution, oversight, and evaluation of Kemp's ridley population recovery actions and efforts, monitoring, and research as well as monitoring shrimp trawling effort (see Caillouet et al. 2015b, 2016). The source of the index's 1966–2014 time series was Mexico's Comisión Nacional de Áreas Naturales Protegidas (CONANP) via NMFS and US FWS (2015); the sources of index levels for 2015, 2016, and 2017 were also CONANP via Peña et al. (2015), Burchfield (2016), and Peña (2017), respectively. Nathan F. Putman and Katherine L. Mansfield acknowledge funding from the Gulf Research Program of the National Academy of Sciences under award number 2000006434 and also from a Florida RESTORE

Act Centers of Excellence Grant through the Florida Institute of Oceanography under sub-agreement no. 4710-1126-00-H. We are grateful to Selina S. Heppell, Erin E. Seney, and R. Bruce Bury for offering many helpful comments and suggestions on early versions of the manuscript. We also thank the peer reviewers for their thoughtful and substantive reviews. The senior author dedicates his contribution to this article to his wife, Nancy Laird Caillouet, and children, Suzanne R. Caillouet, Theresa E. Caillouet, Michelle M.C. Bailey, and C. Christopher Caillouet.

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Received: 27 September 2017
Revised and Accepted: 31 January 2018
Published Online: 23 May 2018
Handling Editor: Jeffrey A. Seminoff