# KEMP'S RIDLEY SEA TURTLE POPULATION DYNAMICS IN THE GULF OF

# MEXICO: EVALUATION OF POST-2010 TRENDS AND HYPOTHESES USING AN

# AGE-STRUCTURED SIMULATION MODEL

## A Thesis

by

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#### ABSTRACT

Kemp's ridley sea turtle (*Lepidochelys kempii*) is a critically-endangered species endemic to the Gulf of Mexico. Prior to 2010, based on nest counts at the primary nesting beach, the population appeared to be recovering. Since the lowest point in 1985, the population had exhibited an estimated annual growth rate of 19%. However, following a large mortality event between the 2009 and 2010 nesting seasons, population levels began to fluctuate. The present work describes development and use of an age-structured population simulation model to investigate plausibility of three hypothesized cause-effect relationships between the 2010 mortality event and subsequent population fluctuations.

The baseline model was parameterized based on published Kemp's ridley life history data and calibrated by adjusting the natural mortality rate of post-hatchlings (*nph*) such that simulated annual rate of population increase ( $\lambda$ ) was within 2% of the observed  $\lambda$ based on nest counts from 1985 to 2009. Sensitivity analysis indicated  $\lambda$  was most sensitive to changes in *nph*. The calibrated model was modified to incorporate each of the three hypothesized effects of the 2010 mortality event: (1) a single year "pulse" effect increasing Kemp's ridley mortality, (2) a multiple year "press" effect increasing Kemp's ridley mortality, and (3) a density-dependent effect decreasing recruitment due to a lengthened remigration interval. Scenarios representing various versions of each of these hypotheses were simulated and tested based on four criteria which characterized the population fluctuations observed from 2010 to 2014. None of the scenarios representing the "pulse" or "press" hypotheses satisfied all four hypothesis-testing criteria. Two scenarios representing the "density-dependent remigration" hypothesis satisfied all four criteria: (1) an exponential and (2) an inverse logistic relationship between remigration rate and number of reproductive individuals. Only the inverse logistic relationship was tentatively validated via comparison of population projections to an independent dataset consisting of nest counts at the primary nesting beach from 2015 to 2017. Population projections to 2035 using the inverse logistic version suggested down-listing criteria may be achieved as early as 2019. The model was the first of its kind to test these hypotheses and should prove useful to management professionals considering conservation strategies for Kemp's ridley sea turtles.

# DEDICATION

To my loving husband, Matthew

And my supportive family

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#### CHAPTER I

#### INTRODUCTION AND LITERATURE REVIEW

The Kemp's ridley sea turtle (*Lepidochelys kempii*) is a highly charismatic, critically-endangered species endemic to the Gulf of Mexico (Marine Turtle Specialist Group, 1996; Caillouet *et al.*, 2016). Their most major decline from 1947 to 1985 was due to a number of causes: a small geographic range (the smallest of all sea turtle species, Zug *et al.*, 1997), natural and anthropogenic predation (Cornelius *et al.*, 2007; Texas Parks and Wildlife Department [TPWD], 2017), life history characteristics (such as high hatchling mortality and a late maturity schedule, National Marine Fisheries Service [NMFS] *et al.*, 2011), commercial fisheries' bycatch (Caillouet, 2010), and potentially oil spills (Gallaway *et al.*, 2016b). While a number of conservation projects have been developed since the 1960s (Heppell *et al.*, 2007) and continue to contribute to species recovery, they alone do not account for the recent population trends seen in the historical nesting data, particularly the significant decrease in 2010 and subsequent fluctuations as evidenced by Gallaway *et al.* (2016a) and Gallaway *et al.* (2016b).

In this chapter, the Kemp's ridley distribution, life history, and conservation efforts that led to the current study are discussed. The rationale and objectives given were formulated based on an extensive scientific literature review, the results of which also provided the basis for the creation of an age-based population model. The model was used to assess the post-2010 Kemp's ridley sea turtle population dynamics and to describe potential underlying causes. The goal was to develop a model that will enable researchers to fill gaps in the current knowledge of the species to refine future management strategies.

#### Kemp's Ridley Distribution and Life History

As outlined below, Kemp's ridleys have the most restricted geographic range of all sea turtles (Zug *et al.*, 1997). Part of this restriction is due to some unique life history characteristics and/or competition that prevent individuals from migrating too far from their natal beach (Morreale *et al.*, 2007; Shaver *et al.*, 2013). In this section, the key features of Kemp's ridley life history and their geographic distribution are discussed.

#### Distribution

The Kemp's ridley sea turtle has the most restricted geographic range amongst all sea turtle species (Zug *et al.*, 1997). While some adolescents make their way to the Atlantic coast or are swept over to Europe (Carreras *et al.*, 2014; Insacco and Spadola, 2010; Tomas *et al.*, 2003), adults primarily forage and almost exclusively breed in the Gulf of Mexico (Zug *et al.*, 1997). It is reported that 90% of the Kemp's ridley population nest along the beaches of Rancho Nuevo (Burchfield, 2016). The 60-km area from Barra Ostionales-Tepehuajes to Playa Dos-Barra Del Tordo (Figure 1) is collectively referred to as the index beach from which the majority of population survival and mortality estimates stem (Caillouet *et al.*, 2016; Renaud *et al.*, 1996). The species has also been recorded to nest along the Texas coast (Shaver, 2005) and in Veracruz, Mexico (Carr and Caldwell, 1958;

Shaver et al., 2017), and a very limited number of nests have been recorded in Florida

(Shaver et al., 2016).





It is known that adult females migrate to foraging grounds when they are not nesting (Shaver *et al.*, 2013). An early study showed the most popular foraging areas for adults and sub-adults alike were the coastal waters from Port Aransas, Texas to Cedar Key, Florida (Ogren, 1989). Much later, Lohmann et al. (2013) found that Kemp's ridleys also travel south from Rancho Nuevo to forage around the Yucatan peninsula. Shaver *et al.* (2013) tracked post-nesting females from PAIS and Rancho Nuevo, Tamaulipas, Mexico using satellite telemetry and found more precise foraging "hotspots" in the northern Gulf of Mexico, particularly within the nearshore zones of Louisiana. In addition, Coleman *et al.* (2017) demonstrated that the Mississippi Sound is crucial habitat for developmental stages of Kemp's ridleys.

Renaud *et al.* (1996) used satellite telemetry to track the movements of a female Kemp's ridley released in August 1994 off the Louisiana coast and followed to Rancho Nuevo, where she successfully nested in April and May of 1995. Shaver *et al.* (2016) conducted a similar study on a larger scale and were able to track two individuals who each made a complete remigration to and from their natal beach. This study also established the importance of nearshore migratory corridors for female Kemp's ridleys in the Gulf of Mexico (which vary temporally) and is supported by a subsequent analysis on inter-nesting habitat and home ranges of post-nesting females (Shaver *et al.*, 2017).

### Life History, Diet, and Reproduction

Kemp's ridley adult females lay an average of 2.5 clutches of approximately 97 eggs during the daytime hours of each participatory nesting season (NMFS *et al.*, 2011; Gallaway *et al.*, 2013). The nesting season typically ranges from April to June of the same calendar year at the index beach, but some females nest as early as March (United States Fish and Wildlife Service [USFWS], 2006; Burchfield, 2016). Those participating typically congregate in near-shore waters before coming to shore in massive "arribadas," or "huge simultaneous nesting aggregations" (Pritchard, 1969). This synchronization of reproduction makes the *Lepidochelys* genus unique and is only observed at a handful of beaches worldwide (Bernardo and Plotkin, 2007). Kemp's ridley arribadas are particularly unique since they are always observed as diurnal (Pritchard, 2007), though this may promote easier access of predators to nests or nesting females. Females dig a hole in the sand with their rear flippers, lay eggs in the hole, and cover them up before returning to the ocean. After the eggs incubate for 50-55 days, the hatchlings emerge and make their way to the ocean (TPWD, 2017). Many hatchlings do not survive this journey to the water due to natural predators such as coyotes, ghost crabs, and shore birds (National Park Service, 2017; TPWD, 2017). Those individuals that reach the water, called pelagic post-hatchlings, may also face aquatic predators, such as sharks or large predatory fish (TPWD, 2017).

The typical pelagic post-hatchling individual that makes it to open water seeks out invertebrates living in or around floating *Sargassum* sp. to sustain the first few years of their life (Witherington *et al.*, 2012). It was long thought that post-hatchlings were pelagic "drifters," meaning they did not actively swim nor choose their own course at sea; they simply were pushed and pulled by the ocean's currents as the method of dispersal from the nesting beach (Witherington *et al.*, 2012). However, recent investigations completed by Putman and Mansfield (2015) found evidence contrary to this notion. Once the hatchlings reach the juvenile classification, they begin consuming benthic-dwelling invertebrates in coastal regions of the Gulf of Mexico and continue to do so for another three to four years

of their life (NMFS *et al.*, 2011; Schmid and Witzell, 1997). This may include blue crab (*Callinectes sapidus*) (Shaver, 1991; Werner, 1994) and benthic tunicates (Witzell and Schmid, 2005). As sub-adults and adults, blue crabs become their primary prey item, followed by mollusks and fish (TPWD, 2017; Shaver and Wibbels, 2007). The fish component of the diet may be discards from shrimp trawl bycatch (Gallaway *et al.*, 2016a; Gallaway *et al.*, 2016b).

The Kemp's ridley prey availability most likely plays a huge role in reproductive capacity and/or remigration (National Academies of Sciences, Engineering, and Medicine, 2017; Gallaway *et al.*, 2016b). It is thought that without enough foraging time or organisms to forage on, a female will not make the journey back to the nesting beach that year, therefore foregoing reproduction altogether until the following nesting season (Gallaway *et al.*, 2016b; Hays, 2000); however, more explicit testing is needed to support this claim. This delay of reproduction gave rise to the density-dependent nature of the remigration rate hypothesis discussed later in this chapter (Caillouet *et al., in press;* Gallaway *et al.*, 2016b). Still, the energetics relating female body size and/or weight to amount of food intake have yet to be determined.

#### Kemp's Ridley Conservation

In 1966, Mexico's Instituto Nacional de Investigaciones Biologico-Pesqueras began surveys in Rancho Nuevo to protect the Kemp's ridley from egg exploitation (Heppell *et al.*, 2007). It was the first conservation effort reported for this species; however, the population continued to decline. It was not until 1977 that bi-national conservation efforts came to fruition (Heppell *et al.*, 2007). An informal Kemp's Ridley Working Group formed to create a recovery plan, and in 1978, the first fenced corrals were placed in Rancho Nuevo (Heppell *et al.*, 2007).

Shortly following the implementation of this strategy, it became clear a policy change was needed for fishing and shrimping operations conducted offshore during the nesting season (Heppell *et al.*, 2007). This led researchers to develop Turtle Excluder Devices (TEDs) and policies were written to enforce this strategy (Register, 1987). Lastly, the experimental practice of imprinting and headstarting hatchlings was set in motion at the Padre Island National Seashore (PAIS) in 1978 to promote the establishment potential for a second nesting population (Shaver and Wibbels, 2007).

In 1992, a down-listing criterion was set at 10,000 nesting females for the Kemp's ridley (Heppell *et al.*, 2005). More recently, new criteria have been established which require the annual release of 300,000 hatchlings and 25,000 nests laid annually at the index beach (NMFS *et al.*, 2011; Caillouet *et al.*, 2016). The 25,000 nest requirement can be converted to a 10,000 nesting female requirement by dividing the number of nests by the number of clutches laid per nesting season per female (2.5) (Caillouet *et al.*, 2016). Caillouet *et al.* (2016) demonstrated that conservation efforts have produced the required number of hatchlings, but the population has not yet reached the requirement for number of nesting females. Some speculate the lasting effects that oil spills have had on coastal ecosystems can account for struggling populations (Crowder and Heppell, 2011), while

others believe there could be more to the picture.

In this section, the successes of various conservation programs and hardships the Kemp's ridley has experienced throughout the past 40 years are discussed.

## **Nesting Beaches**

The index beach, which extends from Barra Ostionales-Tepehuajes to Playa Dos-Barra Del Tordo in Tamaulipas, Mexico (Figure 1), is where the vast majority of the Kemp's ridley population nests (Burchfield, 2016; Caillouet *et al.*, 2016). As early as 1947, the Herrera film documented a massive, single-day arribada for the first time on film, from which Dr. Henry H. Hildebrand estimated around 40,000 nesting females were present (Bevan *et al.*, 2016; Shaver and Wibbels, 2007). However, Bevan *et al.* (2016) evaluated the accuracy of this estimation and found it was overestimated. The group estimated closer to a mean of 26,916 nesting females came to nest at the index beach during that single day. This translates to a total nesting female population of about 48,607 and a total nesting season nest count of 121,517 for 1947. Compared to the 1985 nest count of 702 (Gallaway *et al.*, 2013), the Kemp's ridley population underwent a severe decline in those 38 years, nearly to the point of extinction.

## **Head Start Program**

In 1978, the United States of America and Mexico teamed up to form the Kemp's Ridley Sea Turtle Head Start Experiment in a last-ditch effort to save the species from extinction (Shaver and Wibbels, 2007). One of the general ideas to support this species was to provide a second nesting beach to establish a second nesting colony at the PAIS (Shaver and Wibbels, 2007; Woody, 1989). The idea had been attempted before in Texas, but at a much smaller scale (Woody, 1989). Coupled with the Head Start Program's objective to raise hatchlings in captivity, the efforts aimed to alleviate the high post-hatchling mortality rate during the first year of life and to enhance species survival in the event a disaster struck the primary nesting beach in Mexico (Klima and McVey, 1982; Shaver and Wibbels, 2007; Woody, 1989).

Experimental by its very nature, there were and perhaps still are many criticisms of the program. The biggest criticisms stem from the idea of jeopardizing an already critically endangered species by using it to test a new protocol, not to mention doubts concerning whether or not captive-reared turtles would survive well in the wild (Allen, 1981; Shaver and Wibbels, 2007). It is also very costly to foster hatchlings for months at a time (Woody, 1981). The original plan included anywhere from 9-11 months of raising hatchlings in captivity, but it was intended to increase the likelihood of survival of the post-hatchling life stage to the juvenile stage which experiences significantly less mortality due to larger body size (Shaver and Wibbels, 2007). These notions, however, may simply have been provided to delay experimental action from being taken. When faced with dire circumstances, management officials more often must act on behalf of saving a species from extinction before a scientific consensus is achieved (Krebs, 2009).

Supporters of the Head Start Program contended that the Kemp's ridley had already

declined to the point whereby natural recovery was no longer possible, otherwise known as the Allee effect (Klima and McVey, 1982; Krebs, 2009). Early Kemp's ridley advocates such as Dr. Archie Carr were some of the first to suggest that young sea turtles can imprint on their natal beach and subsequently return there to nest when they reach sexual maturity (Carr, 1967). Though at the time there was limited evidence to support this claim, other advocates supported the program to acquire this knowledge (Klima and McVey, 1982).

After developing an age-structured matrix model for the Kemp's ridley population, Heppell *et al.* (1996) discussed the impact of the program on the overall population. The authors comment on how these types of recovery programs cannot be evaluated until data exist on the survival and growth rates of both wild and headstarted groups (Heppell *et al.*, 1996; Shaver and Wibbels, 2007). Similarly, Heppell and Crowder (1998) contended that the Head Start Program successes were minimal compared to TEDs. Even today, forty years later, the program is still being evaluated, albeit owing some of its delay to the late sexual maturation that characterizes Kemp's ridleys. At the very least, Caillouet *et al.* (2015) states clearly that the program provided a way to tag and subsequently identify nearly all individuals the program released, especially with respect to identifying which individuals are returning to their natal beaches.

### **At-Sea Mortality**

Pelagic post-hatchlings withstand the highest mortality rates of all age classes in the population (NMFS *et al.*, 2011). This is likely due to their small size; however, the

estimation of this parameter is not backed by much direct evidence since it is nearly impossible to monitor these individuals once they reach the open ocean (NMFS *et al.*, 2011; Burchfield and Pena, 2015). After reaching the juvenile stage, most Kemp's ridleys stay close to the coast or continental shelf in the Gulf of Mexico. Unfortunately, this means the turtles suffer additional mortality from high incidental capture in commercial fishing, especially shrimping operations (Frazier *et al.*, 2007). As concern for this added mortality mounted, National Research Council (1990) conducted a study that concluded sea turtle bycatch in shrimp trawls killed more individuals than all other human activities combined. Their statement supported the development and eventual mandatory use of Turtle Excluder Devices (TED) in all commercial fishery operations from the United States (Frazier *et al.*, 2007).

A TED consists of a barred metal ring that fits inside a commercial fishing or trawling net (National Oceanic and Atmospheric Administration [NOAA], 2017). The bars are spaced precisely such that organisms larger than the target species are not able to continue through into the net. Over the years, this device has been perfected to nearly a 97% success rate for a sea turtle to escape (NOAA, 2017). Not only do TEDs help prevent sea turtle bycatch mortality, but other species are also excluded from the landed catch. These include but are not limited to sharks, stingrays, and non-target fishes (NOAA, 2017).

TEDs made their first appearance in 1983 as voluntarily installations in commercial shrimp trawling nets (Register, 1987). Five years later, enough scientific evidence on TEDs had been gathered to require seasonal use of TEDs on all shrimping vessels operating in

offshore waters, and by the end of 1994, NMFS extended the mandate to include TED use on operating vessels at all times and in all waters (nearshore and offshore) (Register, 1987, 1992). More recently in December 2016, NOAA proposed that all skimmer trawls, pusherhead trawls, and wing net vessels should be required to have TEDs in their nets designed to enable smaller sea turtles to escape (Register, 2016). Although public comments were accepted as late as February 2017, the results of this proposition are still forthcoming.

#### **Deepwater Horizon Oil Spill**

The Deepwater Horizon oil spill was arguably the largest marine oil spill in the history of the United States, and quite possibly the largest within the entire petroleum industry (Deepwater Horizon Natural Resource Damage Assessment Trustees [DHNRDAT], 2016). Due to this incident, 11 workers were killed and an additional 17 were injured (National Commission on the B.P. Deepwater Horizon Oil Spill, 2010). Despite several capping attempts, oil and natural gas continuously and uncontrollably spewed into the Gulf of Mexico for 87 consecutive days beginning April 20, 2010, releasing an unprecedented 134 million gallons of oil into the Gulf of Mexico (DHNRDAT, 2016). The cumulative extent of the oil can be seen in Figure 2, which covers part of the Kemp's ridley's foraging grounds. Data were downloaded from the Environmental Response Management Application (2018) developed by NOAA.



**Figure 2.** Cumulative extent of the Deepwater Horizon oil spill in the Gulf of Mexico. Yellow mark indicates wellhead location.

Of the estimated 200 million gallons of oil that flowed from the wellhead, roughly 3-5% (6-10 million gallons) has settled to the seafloor while approximately 11-25% (22-50 million gallons) is still unaccounted for (Sea Grant, 2018). This has created extensive damage to marine and wildlife habitats, recreational and commercial fishing, and tourism industries, but long-term effects are still being monitored (DHNRDAT, 2016). The event was documented to have interacted directly and indirectly with sea turtles, including the Kemp's ridley (Gallaway *et al.*, 2016b).

#### Study Rationale and Objectives

Prior to 2010, the recovery of the Kemp's ridley population looked promising. Since the lowest point in 1985, the nest count at the index beach depicted an exponential annual population growth rate increase of 19% per year, largely due to the aforementioned conservation efforts (NMFS et al., 2011). However, between 2009 and 2010 nesting seasons, a mortality event occurred followed by subsequent population fluctuations. While unconfirmed in the literature, the Deepwater Horizon oil spill, which occurred during this time frame, may have been directly responsible for the unprecedented increase in sea turtle strandings as well as the 35% reduction in nesting success along the index beach in 2010 (Gallaway et al., 2013; Gallaway et al., 2016b). This reduction in nesting success is significantly larger than previous reductions observed historically in 2001 and 2004 ( $\approx$ 15% and  $\approx$  17%, respectively; see Figure 3). Annual nest counts at the primary nesting beach in Tamaulipas, Mexico are considered the best index of the Kemp's ridley sea turtle population dynamics (Figure 3). Dotted lines in Figure 3 indicate the partitioning of these nest count data for use in the present study: (A) data from 1986-2009 were used for model calibration, (B) data from 2010-2014 were used for hypothesis testing, and (C) data from 2015-2017 were used for model validation (these data were not available during model development and still are considered preliminary at the present time).

**Figure 3.** Annual nest counts from the Kemp's ridley primary nesting beach in Mexico, 1985-2017 (Gallaway, 2017; Gallaway *et al.*, 2013; Gallaway *et al.*, 2016b). Dotted lines indicate the partitioning of these data in the present study for (A) model calibration, (B) hypothesis testing, and (C) model validation. See text for details.



Several cause-effect relationships between the 2010 mortality event and the subsequent population fluctuations have been hypothesized. These include, but are not limited to:

- A single year "pulse" effect increasing Kemp's ridley mortality (Caillouet, 2011; Crowder and Heppell, 2011; Gallaway *et al.*, 2016b)
- A multiple year "press" effect increasing Kemp's ridley mortality (Caillouet, 2011; Crowder and Heppell, 2011; Gallaway *et al.*, 2016b)
- 3. A density-dependent negative feedback decreasing Kemp's ridley hatchling recruitment due to a lengthened remigration interval (Caillouet, 2011; Caillouet

et al., in press; Gallaway et al., 2016a; Gallaway et al., 2016b)

A diagram of how these hypotheses were tested can be seen in Figure 4.

**Figure 4.** Experimental design to test the proposed hypotheses explaining the post-2010 population dynamics of Kemp's ridley sea turtles in the Gulf of Mexico. See text for details.



### Rationale

The rationale behind the first two hypotheses is that in 2010 and 2011 an unprecedented number of Kemp's ridleys were found stranded and/or dead in the Gulf of Mexico (Gallaway *et al.*, 2016a). Additionally, Caillouet (2011) noted that nest counts made at the index beach were coincidentally no longer increasing exponentially, but rather had decreased in 2010 about 35% (Gallaway *et al.*, 2013; Gallaway *et al.*, 2016b). From this evidence, it was hypothesized that a single, significant mortality event occurred in 2010 which caused subsequent population fluctuations (hypothesis 1) (Gallaway *et al.*, 2016a; Gallaway *et al.*, 2016b). It also was hypothesized that this large mortality event in 2010 was followed by increased mortality over an extended period of time which caused subsequent population fluctuations (hypothesis 2) (Gallaway *et al.*, 2016a; Gallaway *et al.*, 2016b). Implicit in both of these hypotheses is that the mortality might be age-specific. Caillouet (2011) suggested that such age-specific mortality would have altered the population age structure and could have had a long-lasting effect on population dynamics.

The rationale behind the third hypothesis is that a large mortality event in 2010 was accompanied by a decrease in food, such as the blue crab, in the foraging grounds of the northern Gulf of Mexico which increased the length of time necessary for adult females to regain a sufficient body condition to migrate back to the nesting beach (Gallaway *et al.*, 2016b). Thus, the remigration interval lengthened, yielding an overall reduction of the annual number of adult females actually nesting in a given nesting season and decreasing recruitment of individuals into the population, thereby slowing population growth. Feeding

conditions vary from year to year and have been shown to affect the remigration rate of sea turtles (Gallaway *et al.*, 2016b; Hays, 2000), hence the number of turtles nesting in different years also changes. The blue crab stock has been reduced substantially since the mid-1990s (VanderKooy, 2013), and the shrimping effort has dropped and remained low since 2005 (Gallaway *et al.*, 2016a), generating less bycatch fish products which also have been an important food item for Kemp's ridleys (Cannon, 1998). Thus, food availability may have been approaching a critical level prior to 2010 (Caillouet *et al.*, *in press*).

To investigate the plausibility of these hypothesized cause-effect relationships between the 2010 mortality event and subsequent Kemp's ridley population fluctuations, an age-structured population simulation model was developed. Such models are often used in representing population dynamics of endangered species and have been used to simulate population trends in sea turtles, where life history information is sparse (i.e. Heppell *et al.* (2000) and Crouse *et al.* (1987)). This modeling approach helps identify and quantify cause-effect relationships between components that are thought to affect a population and quantify the uncertainty associated with model output via sensitivity analyses (Grant and Swannack, 2008).

#### **Objectives**

- Develop an age-structured model to simulate population dynamics of the Kemp's ridley in the Gulf of Mexico
- 2. Conduct a sensitivity analysis of the baseline version of the model to identify the

parameters that most affect the annual rate of population growth

- Modify the model to incorporate and to test each of three cause-effect relationships hypothesized to explain Kemp's ridley population dynamics following the 2010 mortality event
  - a. A single year "pulse" effect increasing Kemp's ridley mortality
  - b. A multiple year "press" effect increasing Kemp's ridley mortality
  - c. A density-dependent negative feedback decreasing Kemp's ridley hatchling recruitment due to a lengthened remigration interval
- Tentatively validate versions of the model not rejected during hypothesis-testing and use validated versions to project Kemp's ridley population dynamics through the year 2035

#### CHAPTER II

#### POPULATION MODEL

NMFS *et al.* (2011) and Gallaway *et al.* (2016a) are considered the most up-to-date stock assessments/population models for investigating Kemp's ridley population dynamics. These assessments include the best estimates for various population parameters related to survival and reproduction given the life history of the species, so they were drawn heavily upon to form the model. This chapter includes the specific data used and the specific processes by which the hypothesized causes of the post-2010 population fluctuations of the Kemp's ridley sea turtle were tested.

#### Model Overview and Description

The model is an age-structured compartment model based on difference equations with a 1-year time step, which is programmed in Stella Professional (Version 1.4.1; Isee Systems, Inc., 2017) for Windows. The basic output of the model is the simulated annual Kemp's ridley nest count on the index beach. Nest counts collected from the index beach are considered the best indicator of the status of the species because there is currently no way to estimate population size directly (Coyne, 2000; Gallaway *et al.*, 2016a).

The fundamental processes represented in the model are age-specific reproduction and mortality, similar to the model of Gallaway *et al.* (2016a) (Figure 5). Definitions of each component in the model can be seen in Table 1, the functional forms of each can be found in Table 2, and a complete list of the values and sources for each parameter can be seen in Table 3. For the purposes of this paper, the terms verification, calibration, validation, and corroboration were defined following Turner *et al.* (2001) (Table 4).



Figure 5. Conceptual model for the Kemp's ridley sea turtle population.

<b>Table 1.</b> Definitions of components in the Kemp's ridley population me
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Component	Definition
Post-Hatchling	Age classes 0 through 1; SCL less than 20 cm; Feed on pelagic seaweed and associated invertebrates
Juvenile	Age classes 2 through 5; SCL between 20 and 50 cm; Feed on near-shore benthic organisms
Sub-Adult	Age classes 6 through 11; SCL between 50 and 60 cm; Feed on near-shore benthic organisms
Adult	Age classes 12+; SCL greater than 60; Feed on near-shore benthic organisms; Reproductively mature
Recruit	Number of hatchlings entering the first age class annually
Mortality	Number of individuals dying from each age class annually
Reproductive Individuals	Sexually matured individuals in the population capable of reproduction
Maturation Rate	Rate at which individuals sexually mature from sub-adult to adult
Number of Nests	Number of nests laid annually on the index beach
Proportion Female	Percentage of females within the adult population
Remigration Rate	Length of time elapsed between a post-breeding female's migration from the nesting grounds to foraging grounds and back to nesting grounds the following nesting season
Clutch Frequency	Number of clutches laid in a nesting season
Total Eggs	Sum of all eggs laid in a nesting season
Clutch Size	Number of eggs laid per clutch
<b>Proportion</b>	Percentage of corral nests versus <i>in situ</i> nests on the index
Corrals/in situ	Deacn
Corrals/in situ	<i>in situ</i> on the index beach

Component	Functional Form	Symbol	
Recruits $\Sigma$ (Total Eggs * Proportion of Eggs * Hatch Rate) of <i>in situ</i> and corral nests			
Transition to			
(Growth) N(t) - (N(t) * Age Class Mortality Kate)		G	
Mortality in			
a Given Age Class	N(t) * Age Class Mortality Rate	Μ	
Individuals			
in a Given	N(t) = N(t-1) + N-1(t) - M - G	Ν	
Age Class			
Total Eggs	Remigration Rate * Proportion Female * Clutch Frequency * Reproductive Individuals * Clutch Size		
Number of Nests (Model Nests)Remigration Rate * Proportion Female * Clutch Frequency * Reproductive Individuals			
Reproductive Individuals	<b>ve</b> $\Sigma$ (N(t) * Age Class Maturation Rate) for age classes 9-14+		
Proportion Female	<b>Proportion</b> $\Sigma$ (Proportion of Eggs * Proportion Female) of <i>in situ</i> and <b>Female</b> corral nests		
**Note: Any age class can be substituted for N			

**Table 2.** Equations associated with components in the Kemp's ridley population model.

Parameter:	Value:	Source:
Clutch Frequency	2.5	NMFS <i>et al.</i> (2011) and
		Gallaway et al. (2016a)
Proportion Female	0.64	NMFS <i>et al.</i> (2011) and
in situ		Gallaway et al. (2016a)
<b>Proportion Female in</b>	0.74	Gallaway et al. (2016a)
corrals/boxes		
Clutch Size	97	NMFS et al. (2011)
Hatch Rate in situ	0.5	NMFS et al. (2011)
Hatch Rate	0.678	NMFS et al. (2011)
Corrals/Boxes		
Proportion Eggs	0.1035*	Gallaway et al. (2016a)
Hatched in situ		
Proportion Eggs	0.8965*	Gallaway et al. (2016a)
Hatched in		
Corrals/Boxes		
<b>Remigration Rate</b>	0.5	NMFS <i>et al.</i> (2011) and
		Gallaway et al. (2016a)
Age of Maturity	12	NMFS <i>et al.</i> (2011) and
(in years)		Gallaway <i>et al.</i> (2016a)
Post Hatchling	0.682 (0.7502**)	NMFS et al. (2011)
Mortality		
Juvenile Mortality	0.185	NMFS et al. (2011)
Sub-Adult Mortality	0.065	NMFS et al. (2011)
Adult Mortality	0.065	NMFS et al. (2011)
2010 Additive	0.312	Gallaway et al. (2016b)
Mortality Effect		
*Averaged value of years 2004-2012		
**Calibrated value, see section below titled Calibration of the Baseline Model.		

**Table 3.** Parameter values and sources of information for each component in the Kemp's ridley population model.
Table 4. Definitions of modeling terms (Turner et al., 2001).

Term	Definition
Verification	Process of checking the model for consistency and accuracy in its representation of model equations or relationships
Calibration	Process of changing model parameters to obtain an improved fit of the model output to empirical data
Validation	Process of evaluating model behavior by comparing it with empirical data

# **Age Class Determination**

The model contains thirteen age classes defined on an annual basis. Multiple age classes make up overarching life stages: pelagic post-hatchling, juvenile, sub-adult, or adult. These stages were determined in Ogren (1989) and Heppell *et al.* (2005) to be life stages where significant changes occur with regard to straight carapace length (SCL), per-capita mortality, their location of preferred feeding activity, and sexual maturity. Hatchlings are defined as individuals who just hatched and survive long enough to reach the ocean. Since this length of time is less than one day, these individuals are represented implicitly in the annual recruitment to the first post-hatchling stage. Hatchlings ranged from about 4.2 to 4.8 cm SCL (Burchfield and Pena, 2015).

Pelagic post-hatchlings (age classes 0 and 1 years) are individuals who survive long enough after hatching to enter the ocean. Individuals remain as pelagic post-hatchlings until they reach 20 cm SCL (NMFS *et al.*, 2011; Heppell *et al.*, 2005). They feed on floating *Sargassum* sp. seaweed and its associated invertebrates (Witherington *et al.*, 2012). Juveniles (age classes 2 through 5 years) are individuals between 20 and 50 cm SCL and feed in the benthic and neritic zones of the ocean floor (NMFS *et al.*, 2011; Heppell *et al.*, 2005; Schmid and Witzell, 1997). These individuals are far from reaching sexual maturity and suffer from higher per-capita mortality than their subsequent stages. Sub-adults (age classes 6 through 11 years) are individuals between 50 and 60 cm SCL and feed on benthic, neritic-dwelling organisms (NMFS *et al.*, 2011; Heppell *et al.*, 2005). Sub-adults have undergone sexual development but are not yet capable of reproduction (Coyne, 2000). Adults (age classes 12 through 14+ years) are individuals greater than 60 cm SCL, feed on near-shore, benthic-dwelling organisms, and have reached sexual maturity (NMFS *et al.*, 2011; Heppell *et al.*, 2005; Ogren, 1989).

# **Per-Capita Mortality Rates**

The Kemp's ridley population suffers from high mortality rates during most of its life stages (Zug *et al.*, 1997). The model follows the guidelines from NMFS *et al.* (2011) to determine stage-class mortality, and these mortality rates affect all age classes within a given stage equally. Pelagic post-hatchlings incur the highest per-capita mortality rates while sub-adults and adults incur the least.

The second edition of the bi-national Kemp's ridley recovery plan states that hatch rates (in terms of successes) are greater for corral or boxed hatchlings than they are for hatchlings left *in situ* (NMFS *et al.*, 2011). The proportions of successful hatchlings estimated for corral/box hatchlings versus *in situ* hatchlings averaged 0.8965 and 0.1035,

respectively (Gallaway *et al.*, 2016a). There was no significant difference between using the time-series data versus using an averaged value in the model, so the averaged value is used in the model.

# **Per-Capita Reproduction Rates**

Per capita reproduction rates used in the model are estimated based on clutch size, number of clutches per year, and age of first reproduction. Although various estimates of clutch size have been reported in the literature, the estimate of 97 eggs per clutch is used in the model, as it was in NMFS *et al.* (2011) and Gallaway *et al.* (2016a). It is not likely to fluctuate much from this value if the reproductive population is in a stable age distribution (Coyne, 2000).

Female Kemp's ridleys often lay multiple clutches in a single nesting season. The clutch frequency is estimated as the average number of clutches laid by a nesting female each nesting season. The value used in Gallaway *et al.* (2016a) was 2.5 clutches per nesting season. This value has been used in several other population models (Caillouet *et al.*, 2016; Heppell *et al.*, 2005), and is used in the current model.

Estimates of age of sexual maturity range from 10-17 years (Snover *et al.*, 2007). A "knife-edge" estimate of 12 years has been supported by skeletochronological data (NMFS *et al.*, 2011), although use of this estimate in modeling has been questioned (Caillouet, 2010). Gallaway *et al.* (2013) and Gallaway *et al.* (2016a) tested both "knife-edge" and "gradual" maturity schedules in which the proportions of sexually mature females increased gradually after a given age. The latter found that only an age of maturity at 11, 12, or 13 years yielded reasonable parameter estimation for their model. The current model uses a "knife-edge" estimate of 12 years, but various versions of both "knife-edge" and "gradual" maturity schedules are examined via sensitivity analysis.

## Initialization and Verification of the Baseline Model

The model was initialized such that the simulated population was in the stable ageclass distribution and produced the number of nests recorded at the index beach in 1985 (702, Gallaway *et al.*, 2016b). The nest count output was calculated as the number of reproductive individuals multiplied by the remigration rate, clutch frequency, and proportion female in the population. It was verified that the simulated population maintained the stable age-class distribution and grew exponentially, as indicated by the rate of increase in simulated nest counts, between 1985 and 2009.

## Sensitivity Analysis of the Baseline Model

A sensitivity analysis was conducted to identify the model parameters that most affected the rate of population growth ( $\lambda$ ), as indicated by the rate of change in simulated nest counts over the period from 1985 to 2009. For each simulation, the model was initialized such that the simulated population was in the stable age-class distribution and produced 702 nests for the year 1985. Parameters included in the analysis are listed in Tables 5 and 6. For parameters representing the maturity schedule (Table 5), both "knifeedge" and continuous representations of the schedule were tested. For "knife-edge" representations, the age at first reproduction was changed and all females classified as old as, or older, than the specified age were considered reproductively capable whereas all females younger than the specified age were considered incapable of reproduction. For continuous representations ("gradual" maturity), different proportions of the females in the various age classes were classified as reproductively capable, as suggested by Caillouet (2010) and demonstrated by Gallaway *et al.* 2013 (Table 5). For those parameters listed in Table 6, each parameter's value was altered by a percentage relative to its baseline value.

**Table 5.** Experimental design for sensitivity analysis of the maturity schedule of the Kemp's ridley population model. Scenarios 1-6 represent "knife-edge" maturity, whereas scenarios 7-11 represent continuous maturity, following Gallaway *et al.* (2013). Values indicate the proportion of reproductively capable females in the indicated age classes that contribute to reproduction. SA = Sub-Adult; A = Adult.

	Proportion Contributing to Reproduction:					
Scenario:	SA, Age 9	SA, Age 10	SA, Age 11	A, Age 12	A, Age 13	A, Age 14+
1 - Baseline	0	0	0	1	1	1
2	0	0	1	1	1	1
3	0	1	1	1	1	1
4	1	1	1	1	1	1
5	0	0	0	0	1	1
6	0	0	0	0	0	1
7	0.1	0.25	0.5	0.75	0.9	1
8	0.2	0.35	0.6	0.85	1	1
9	0	0.15	0.4	0.65	0.8	1
10	0.3	0.45	0.7	0.95	1	1
11	0	0.05	0.3	0.55	0.7	1

	Percent Change:						
Parameter:	-30	-20	-10	Baseline	+10	+20	+30
Clutch Frequency	1.75	2	2.25	2.5	2.75	3	3.25
Clutch Size	67.9	77.6	87.3	97	106.7	116.4	126.1
Proportion Eggs Hatched <i>in situ</i> *	0.07245	0.0828	0.09315	0.1035	0.11385	0.1242	0.13455
Hatch Rate in situ	0.35	0.4	0.45	0.5	0.55	0.6	0.65
Hatch Rate in corrals/boxes	0.4746	0.5424	0.6102	0.678	0.7458	0.8136	0.8814
Proportion Female <i>in situ</i>	0.448	0.512	0.576	0.64	0.704	0.768	0.832
Proportion Female in corrals/boxes	0.518	0.592	0.666	0.74	0.814	0.888	0.962
Remigration Rate	0.35	0.4	0.45	0.5	0.55	0.6	0.65
Post-Hatchling Mortality	0.4774	0.5456	0.6138	0.682	0.7502	0.8184	0.8866
Juvenile Mortality	0.1295	0.148	0.1665	0.185	0.2035	0.222	0.2405
Sub-Adult Mortality	0.0455	0.052	0.0585	0.065	0.0715	0.078	0.0845
Adult Mortality	0.0455	0.052	0.0585	0.065	0.0715	0.078	0.0845
*Proportion eggs hatched in corrals/boxes = 1 – proportion eggs hatched <i>in situ</i>							

**Table 6.** Experimental design for sensitivity analysis of parameter values of the Kemp's ridley population model. Values represent the indicated percentage change relative to the baseline value.

Results of the sensitivity analysis indicated that  $\lambda$  was affected by relatively small changes in post-hatchling mortality, but was relatively unaffected by changes in the other parameters tested (Tables 7 and 8).

**Table 7.** Results of sensitivity analysis of maturity schedules of the Kemp's ridley population model. Scenarios 1-6 represent "knife-edge" maturity whereas scenarios 7-11 represent continuous maturity, following Gallaway *et al.* (2013). Scenarios indicate the proportion of reproductively capable individuals in the indicated age classes that contribute to reproduction (see Table 5). Values represent  $\lambda$  (percent change in  $\lambda$  from baseline) for the simulated period from 1985-2009. Shaded cells represent a negative value in percent change; unshaded cells represent a positive value in percent change.

Scenario:	$\lambda$ (% Change from Baseline)
1 - Baseline	1.1785 (0%)
2	1.1954 (1.4%)
3	1.2162 (3.2%)
4	1.2407 (5.3%)
5	1.1625 (1.4%)
6	1.1510 (2.3%)
7	1.1909 (1.0%)
8	1.1999 (1.8%)
9	1.1817 (< 1%)
10	1.2077 (2.5%)
11	1.1748 (< 1%)

**Table 8.** Results of sensitivity analysis of parameter values of the Kemp's ridley population model. Values represent  $\lambda$  (percent change in  $\lambda$  from baseline) for the simulated period from 1985-2009. Shaded cells represent a negative value in percent change; unshaded cells represent a positive value in percent change.

	Percent Change:						
Parameter:	-30	-20	-10	Baseline	+10	+20	+30
Clutch	1.1539	1.1630	1.1711	1.1785	1.1853	1.1916	1.1974
Frequency	(2.1%)	(1.3%)	(< 1%)	(0%)	(< 1%)	(1.1%)	(1.6%)
Clutch	1.1539	1.1630	1.1711	1.1785	1.1853	1.1916	1.1974
Size	(2.1%)	(1.3%)	(< 1%)	(0%)	(< 1%)	(1.1%)	(1.6%)
Proportion	1 170/	1 1701	1 1700	1 1 7 9 5	1 1702	1 1770	1 1776
Eggs Hatched	1.1794 (< 1%)	(< 1%)	1.1700 (< 1%)	(0%)	1.1782 (< 1%)	(< 1%)	1.1770 (< 1%)
in situ*	(< 170)	(< 170)	(< 170)	(070)	(< 170)	(< 170)	(< 170)
Hatch Rate	1.1768	1.1774	1.1780	1.1785	1.1791	1.1796	1.1802
in situ	(< 1%)	(< 1%)	(< 1%)	(0%)	(< 1%)	(< 1%)	(< 1%)
Hatch Rate in	1.1561	1.1643	1.1717	1.1785	1.1848	1.1906	1.1961
corrals/boxes	(1.9%)	(1.2%)	(< 1%)	(0%)	(< 1%)	(1.0%)	(1.5%)
Proportion	1.1766	1.1772	1.1779	1.1785	1.1792	1.1798	1.1804
Female <i>in situ</i>	(< 1%)	(< 1%)	(< 1%)	(0%)	(< 1%)	(< 1%)	(< 1%)
Proportion	1 1 5 6 5	1 16/5	1 1710	1 1 705	1 10/7	1 1005	1 1050
Female in	(1.0%)	(1 2%)	1.1/10	1.1785	1.1047	(1.0%)	1.1939
corrals/boxes	(1.9%)	(1.270)	(< 1/0)	(070)	(< 1/0)	(1.070)	(1.5%)
Remigration	1.1539	1.1630	1.1711	1.1785	1.1853	1.1916	1.1974
Rate	(2.1%)	(1.3%)	(< 1%)	(0%)	(< 1%)	(1.1%)	(1.6%)
<b>Post-Hatchling</b>	1.2533	1.2314	1.2068	1.1785	1.1455	1.1054	1.0534
Mortality	(6.4%)	(4.5%)	(2.4%)	(0%)	(2.8%)	(6.2%)	(10.6%)
Juvenile	1.1975	1.1913	1.1849	1.1785	1.1721	1.1655	1.1589
Mortality	(1.6%)	(1.1%)	(< 1%)	(0%)	(< 1%)	(1.1%)	(1.7%)
Sub-Adult	1.1874	1.1844	1.1815	1.1785	1.1756	1.1726	1.1696
Mortality	(< 1%)	(< 1%)	(< 1%)	(0%)	(< 1%)	(< 1%)	(< 1%)
Adult	1.1841	1.1822	1.1803	1.1785	1.1767	1.1750	1.1733
Mortality	(< 1%)	(< 1%)	(< 1%)	(0%)	(< 1%)	(< 1%)	(< 1%)
*Proportion eggs hatched in corrals/boxes = $1 - proportion eggs hatched in situ$							

# Calibration of the Baseline Model

The model was calibrated such that the simulated nest count approximated the nest count observed from 1985 to 2009 by increasing the post-hatchling natural mortality rate to 110% of the original estimate. This parameter was selected for calibration since the simulated  $\lambda$  was most sensitive to changes in this parameter. The simulated nests produced by the calibrated model increased at an average annual rate ( $\lambda = 1.1455$ ) within 2% of the actual average annual rate ( $\lambda = 1.1653$ ) from 1985 to 2009, and the simulated nest count in 2009 was within 5% of the actual nest count in 2009 (n = 18289 vs. n = 19163, simulated vs. actual, respectively) (Figure 6).

**Figure 6.** Simulated nests produced by the calibrated baseline model (post-hatchling mortality increased by 110% of the original estimate) (green diamonds) compared to the historical nest counts from the Kemp's ridley primary nesting beach in Mexico, 1985-2009 (Gallaway *et al.*, 2013; Gallaway *et al.*, 2016b) (blue squares).



## Simulation of Post-2010 Population Dynamics

## **Experimental Design for Hypothesis-testing Simulations**

The baseline model was modified to incorporate and to test each of three causeeffect relationships that have been hypothesized to explain Kemp's ridley population dynamics following the 2010 mortality event: (1) a single year "pulse" effect increasing mortality, (2) a multiple year "press" effect increasing mortality, and (3) a densitydependent negative feedback decreasing recruitment due to a lengthened remigration interval (Figure 4). Scenarios representing various versions of these three hypotheses were simulated and the hypotheses were tested based on four criteria which characterized the post-2010 historical nest-count trends at the index beach:

- 1. The simulated 2010 index beach nest count decreased to within 15% of the historical 2010 index beach nest count (12,377 nests)
- The simulated 2011 count increased to within 15% of the historical 2011 count (18,215 nests)
- The simulated 2012 count remained within 10% of the simulated 2011 count (i.e., the simulated 2011 and 2012 counts "plateaued" as did the historical counts)
- The simulated counts decreased in 2013 and decreased further in 2014 (i.e., the simulated 2013 and 2014 counts continued to decline as did the historical counts)

The hypothesis-testing procedure was sequential, with 63 scenarios representing the "pulse" hypothesis being simulated first. Then the "press" versions of the "pulse" scenarios that had not been rejected were simulated. Finally, the "density-dependent remigration rate" versions of the pulse and press scenarios that had not been rejected were simulated. Details of the hypothesis-testing procedure are described below.

The single year "pulse" hypothesis was represented by increasing mortality during the year 2010, assuming the 2010 mortality was additive to natural mortality:

(1) IF 
$$Y = Y_E$$
 THEN  $A_E + M_X$  ELSE  $M_X$ 

where Y represents year,  $Y_E$  represents the year of the mortality event,  $A_E$  represents the additive mortality from the event, and  $M_X$  represents natural mortality of age x.

There were 63 scenarios tested for the "pulse" hypothesis (Appendix A). Scenarios representing seven versions of a universal pulse effect affecting all age classes were simulated assuming that the additional mortality was (1) equal to the estimate (0.312) of Gallaway *et al.* (2016b), (2) 10, (3) 20, and (4) 30% less than their estimate, and (5) 10, (6) 20, and (7) 30% greater than their estimate, respectively. Scenarios representing an additional 56 versions of the pulse effect were simulated assuming that the additional mortality affected only specific sets of age classes (except post-hatchlings, which were not subjected to the additional mortality in these scenarios; see Appendix A for details).

For each of the "pulse" scenarios that had not been rejected, the multiple year

"press" effect was represented by extending the increased mortality past the year 2010, assuming that the magnitude of the additive mortality diminished over time either abruptly or gradually:

(2) IF 
$$Y \ge Y_E$$
 AND  $Y < (Y_E + L_E)$  THEN  $A_E$  ELSE  $M_X$   
(3) IF  $Y \ge Y_E$  AND  $Y \le (Y_E + L_E)$  THEN  $A_E * EXP (-S_E * (Y - Y_E))$  ELSE  $M_X$ 

where  $L_E$  represents the number of years over which the increased mortality from the 2010 event was extended and  $S_E$  represents the slope of an exponential decay curve.  $L_E$  was assigned values of two, three, four, or five years, and the  $S_E$  associated with each  $L_E$  was assigned a value such that the total mortality rate decreased from the 2010 rate (pre-2010 natural mortality rate + 2010-event-related mortality rate) to the pre-2010 natural mortality rate in  $L_E$  years (Figure 7).





There were 88 scenarios tested for the "press" hypothesis (Appendix B). Eight scenarios represented the version of a universal press effect in which the additional mortality was equal to the estimate (0.312) of Gallaway *et al.* (2016b). In four of these scenarios, the total mortality rate declined abruptly to the pre-2010 natural mortality rate after  $L_E$  years. In the other four scenarios, the total mortality rate declined exponentially to the pre-2010 natural mortality rate over the course of  $L_E$  years (i.e. with  $L_E = 2$ , 3, 4, and 5 years, respectively). The remaining 80 scenarios represented an additional 10 versions of the press effect, each of which was simulated in the manner just described, except that the additional mortality affected only specific sets of age classes (see Appendix B for details).

For each of the "pulse" and "press" scenarios that had not been rejected, the density-dependent lengthening of the remigration interval was represented by replacing the remigration rate constant (R = 0.5, which represents a nesting female returning to nest at the index beach every 2 years) with three versions of each of the following four functional relationships:

(4)	$R = -\beta_1 R_S + \beta_0$	Linear Decrease
(5)	$\mathbf{R} = \boldsymbol{e}^{(-\beta_1 \mathbf{R}_S)}$	Exponential Decrease
(6)	$R = -\beta_2 {R_S}^2 + \beta_1 R_S + \beta_0$	Second-Order Polynomial
(7)	$R = \beta_0 + \frac{(\beta_1 * e^{\beta_2 - \beta_3 R})}{(1 + e^{\beta_2 - \beta_3 R})}$	Inverse Logistic Decrease

where R represents the remigration rate,  $R_S$  represents the number of reproductively capable individuals in the stock, and  $\beta_x$  represents associated coefficients (see Appendix C for coefficient values associated with each version of these equations). Each equation listed in Appendix C contains an upper and lower limit for the remigration rate to extend. These limits were influenced by an analysis by Hays (2000) where the author found evidence to suggest the remigration rate for sea turtles is not as frequent as every year (rate = 1) but not rarer than roughly 5 years (rate = 0.2). It was assumed the decreases in R governed by these equations occurred over the range 20,000  $\leq R_S \leq 40,000$ . That is, it was assumed the density-dependent effect was negligible below  $R_S = 20,000$  and was not intensified beyond  $R_S = 40,000$ .

There were 36 scenarios tested for the "density-dependent remigration rate" hypothesis (Appendix C). The scenarios tested represented 12 versions of each of three pulse or press scenarios: the universal pulse scenario U4, the age-specific pulse scenario AS10 (see Appendix A for scenario descriptions), and the age-specific press scenario AS106 (see Appendix B for scenario description). The 12 versions of each included three linear, three exponential, three second-order polynomial, and three inverse logistic rates of decrease in the remigration rate (R) (Figure 8, see Appendix C for details).

**Figure 8.** Graphical representation of the 12 equations representing the relationship between the remigration rate and the number of reproductive individuals in the stock which were used to test the "density-dependent remigration rate" hypothesis: (A) linear, (B) exponential, (C) second-order polynomial, and (D) inverse logistic. Blue lines represent lower limits of equations tested (i.e. L1, Appendix C), red lines represent median equations tested (i.e. L2, Appendix C), and green lines represent upper limits of equations tested (i.e. L3, Appendix C).



#### **Results of Hypothesis-Testing Simulations**

Results of the pulse analysis indicated that none of the 63 scenarios representing the "pulse" hypothesis satisfied all of the four hypothesis-testing criteria. However, 11 scenarios satisfied the first two criteria (scenarios U4 and AS1-AS10, see Appendix A). The two scenarios that best satisfied these criteria were U4 (a universal pulse effect affecting all age classes assuming the additional event-related mortality was equal to the estimate (0.312) of Gallaway *et al.*, 2016b) (Figure 9), and AS10 (an age-specific pulse effect affecting only the last sub-adult and all adult age classes assuming the additional event-related mortality was equal to the estimate (0.312) of Gallaway *et al.*, 2016b) (Figure 10). These two scenarios produced simulated 2010 nest counts within  $\approx$  13% of the nest count reported at the index beach in 2010 (criterion 1), and within  $\approx$  12% and  $\approx$  4%, respectively, of the nest count reported at the index beach in 2010 (criterion 2).

**Figure 9.** (**A**) Simulated nests produced by the "pulse" hypothesis Scenario U4 (a universal pulse effect affecting all age classes assuming the additional event-related mortality was equal to the estimate (0.312) of Gallaway *et al.*, 2016b) (green diamonds) compared to historical nest counts at the index beach, 1985-2014 (blue squares). (**B**) Scenario U4 compared to historical nest counts in relation to hypothesis-testing criteria, 2009-2014. Red arrow indicates inconsistency with criteria.



**Figure 10.** (A) Simulated nests produced by the "pulse" hypothesis Scenario AS10 (an age-specific pulse effect affecting only the last sub-adult and all adult age classes assuming the additional event-related mortality was equal to the estimate (0.312) of Gallaway *et al.*, 2016b) (green diamonds) compared to historical nest counts at the index beach, 1985-2014 (blue squares). (B) Scenario AS10 compared to historical nest counts in relation to hypothesis-testing criteria, 2009-2014. Red arrow indicates inconsistency with criteria.



Results of the press analysis indicated that none of the 88 scenarios representing the "press" hypothesis satisfied all of the four hypothesis-testing criteria. However, Scenario AS106 (an age-specific press effect affecting only the last sub-adult and all adult age classes, assuming an initial event-related mortality equal to the value (0.312) estimated by Gallaway *et al.* (2016b) which decreased gradually over the course of two years) satisfied the first two criteria (Figure 11). This scenario produced simulated 2010 nest counts within  $\approx 13\%$  of the nest count reported at the index beach in 2010 (criterion 1), and within  $\approx 14\%$  of the nest count reported at the index beach in 2011 (criterion 2).

**Figure 11.** (A) Simulated nests produced by the "press" hypothesis Scenario AS106 (an age-specific press effect affecting only the last sub-adult and all adult age classes, assuming an initial event-related mortality equal to the value (0.312) estimated by Gallaway *et al.* (2016b) which decreased gradually over the course of two years) (green diamonds) compared to historical nest counts at the index beach, 1985-2014 (blue squares). (B) Scenario AS106 compared to historical nest counts in relation to hypothesis-testing criteria, 2009-2014. Red arrow indicates inconsistency with criteria.



Results of the "density-dependent remigration rate" analysis indicated that, among the 36 scenarios representing the "density-dependent remigration rate" hypothesis, all of the four hypothesis-testing criteria were satisfied by Scenario E4 (an exponential decrease in the remigration rate superimposed on an age-specific pulse effect affecting only the last sub-adult and all adult age classes assuming the additional event-related mortality was equal to the estimate (0.312) of Gallaway et al., 2016b, see Appendix C for the equation governing rate of decrease) (Figure 12) and Scenario I4 (an inverse logistic decrease in the remigration rate superimposed on an age-specific pulse effect affecting only the last subadult and all adult age classes assuming the additional event-related mortality was equal to the estimate (0.312) of Gallaway et al., 2016b, see Appendix C for the equation governing rate of decrease) (Figure 13). Scenario E4 produced simulated 2010 nest counts within  $\approx$ 13% of the nest count reported at the index beach in 2010 (criterion 1) and within  $\approx 4\%$  of the nest count reported at the index beach in 2011 (criterion 2), as well as simulated nest counts within  $\approx 5\%$  of each other in 2011 and 2012 (criterion 3) and simulated nest counts that decreased in both 2013 and 2014 (criterion 4). Scenario I4 produced simulated 2010 nest counts within  $\approx 12\%$  of the nest count reported at the index beach in 2010 (criterion 1) and within  $\approx 8\%$  of the nest count reported at the index beach in 2011 (criterion 2), as well as simulated nest counts within  $\approx 6\%$  of each other in 2011 and 2012 (criterion 3), and simulated nest counts that decreased in both 2013 and 2014 (criterion 4).

**Figure 12.** (A) Simulated nests produced by the "density-dependent remigration rate" hypothesis Scenario E4 (an exponential decrease in the remigration rate superimposed on an age-specific pulse effect affecting only the last sub-adult and all adult age classes assuming the additional event-related mortality was equal to the estimate (0.312) of Gallaway *et al.*, 2016b, see Appendix C for the equation governing rate of decrease) (green diamonds) compared to historical nest counts at the index beach, 1985-2014 (blue squares). (B) Scenario E4 compared to historical nest counts in relation to hypothesis-testing criteria, 2009-2014.



**Figure 13.** (A) Simulated nests produced by the "density-dependent remigration rate" hypothesis Scenario I4 (an inverse logistic decrease in the remigration rate superimposed on an age-specific pulse effect affecting only the last sub-adult and all adult age classes assuming the additional event-related mortality was equal to the estimate (0.312) of Gallaway *et al.*, 2016b, see Appendix C for the equation governing rate of decrease) (green diamonds) compared to historical nest counts at the index beach, 1985-2014 (blue squares). (B) Scenario I4 compared to historical nest counts in relation to hypothesis-testing criteria, 2009-2014.



Additionally, Scenario L4 (a linear decrease in the remigration rate superimposed on an age-specific pulse effect affecting only the last sub-adult and all adult age classes assuming the additional event-related mortality was equal to the estimate (0.312) of Gallaway *et al.*, 2016b, see Appendix C for the equation governing rate of decrease) (Figure 14), passed three of the four criteria. Scenario L4 produced simulated 2010 nest counts within  $\approx$  13% of the nest count reported at the index beach in 2010 (criterion 1) and within  $\approx$  4% of the nest count reported at the index beach in 2011 (criterion 2), and simulated nest counts within  $\approx$  10% of each other in 2011 and 2012 (criterion 3), but it continued increasing in 2013 before decreasing in 2014, thus failing criterion 4. **Figure 14.** (A) Simulated nests produced by the "density-dependent remigration rate" hypothesis Scenario L4 (a linear decrease in the remigration rate superimposed on an age-specific pulse effect affecting only the last sub-adult and all adult age classes assuming the additional event-related mortality was equal to the estimate (0.312) of Gallaway *et al.*, 2016b, see Appendix C for the equation governing rate of decrease) (green diamonds) compared to historical nest counts at the index beach, 1985-2014 (blue squares). (B) Scenario L4 compared to historical nest counts in relation to hypothesis-testing criteria, 2009-2014. Red arrow indicates inconsistency with criteria.



## **Model Validation**

The two versions of the model that were not rejected during the hypothesis-testing procedure (those representing Scenarios E4 and I4) were used to project population dynamics through the year 2017 and were validated by comparing simulated 2015-2017 nest counts to 2015-2017 nest counts at the index beach. Recall that the 2015-2017 nest counts were not available during model development (Figure 3). These counts still are considered preliminary at present, thus validation is tentative.

Scenario I4 was validated in the sense that it produced the observed trend of increasingly higher nest counts in 2015, 2016, and 2017 (Figure 15b), whereas Scenario E4 was invalidated in the sense that it failed to produce the observed increase in nest counts in 2015, although simulated nest counts did increase in 2016 and 2017 (Figure 15a). Based on these results, Scenario I4 was used to project Kemp's ridley population dynamics (based on simulated nest counts) through the year 2035 (Figure 16) in terms of the estimated number of nests we can expect nesting females to lay at the index beach. Figure 17 is presented to compare failed scenario projections with the Scenario I4 projection to 2035.

**Figure 15.** (A) Simulated nests produced by the "density-dependent remigration rate" hypothesis Scenario E4 (green diamonds), and (B) simulated nests produced by the "density-dependent remigration rate" hypothesis Scenario I4 (green diamonds) compared to historical nest counts at the index beach, 1985-2017 (blue squares). The red arrow indicates the decrease or increase in simulated nests for 2015 for Scenarios E4 and I4, respectively.



**Figure 16.** Simulated nests produced by the "density-dependent remigration rate" hypothesis Scenario I4 (see Appendix C for the equation governing rate of remigration) projected through 2035 (green diamonds). Historical nest counts at the index beach from 1985-2017 also are shown (blue squares).



**Figure 17.** Projections of selected scenarios presented for comparison of model behavior through 2035. (A) Simulated nests produced by Scenario U4 (purple triangles), Scenario AS10 (green circles), and Scenario AS106 (red diamonds). (B) Simulated nests produced by Scenario L4 (purple triangles), Scenario E4 (green circles), and Scenario I4 (red diamonds). Historical nest counts at the index beach from 2009-2017 are also shown in each (blue squares).



## **Discussion of Model Performance**

#### **Model Assumptions**

*The model is deterministic.* This means there is one outcome for every simulation run. Some variation may exist in the parameters that were held constant. As such, the single outcome of the model should be referred to as the mean simulated population response. The current model does not include random events, such as tropical storms or other natural disasters, nor does it include variation in natural mortality or recruitment rates which are expected to vary over time and/or between cohorts. No other outside factors acted on the population other than those specified in the model description.

*Annual time step for growth and transfer into the next age class for any individual.* With the exception of the last class in the model (adults aged 14+ years, of which per-capita mortality and reproductive rates remain constant until death of the individual), the current model indicates all individuals in a given age class are subject to the same age-specific factors. The duration of 1 year was assumed to be accurate for modeling purposes. *All mortality is density-independent.* Per-capita mortality (and reproductive rates) are age-specific, affect all individuals in the age class equally, and are constant through time. This density-independent characteristic yielded an exponentially increasing projection to 2035 after the time-lag passed in 2027 (Figure 16); however, there are limits to population growth, and we would expect density-dependent mortality (via intraspecific competition for food sources) at large population sizes to be the primary limiting factor. *TED effect on mortality was not incorporated.* Data support that TED implementation

decreased age-specific mortality in ages 2+ in 1988 and again in 1996 (NMFS *et al.*, 2011). While age-specific mortality was not changed pre- and post-1988 or pre-1996, it was simpler to assume the post-1996 mortality estimates were suitable for the duration of the simulations to achieve an exponential growth curve from 1985-2009.

*Life expectancy is not accounted for explicitly.* The last age class (adults aged 14+ years) accumulates surviving individuals, but annual per-capita mortality rates are still in effect, implying a life expectancy will be reached at some point for this age class. The model could be improved to include a life expectancy estimate but is not included since that estimate is currently unknown (NMFS, 2005).

*Remigration rate is an annual occurrence.* The nesting season falls within a calendar year, therefore it was assumed the remigration rate occurred on an annual basis.

Population was in stable age distribution in 1985 and was maintained until 2009. Stable age distribution indicates that the proportion of individuals in a given age class remains constant through time, therefore allowing the annual population growth rate ( $\lambda$ ) to be constant as well. The observed population growth from 1985 to 2009 was represented well by a constant  $\lambda$  (1.1455 vs. 1.1653, simulated vs. actual average  $\lambda$ , respectively). The model system was perturbed out of stable age distribution by the 2010 mortality event and the subsequent effects on simulated nest counts were observed. Of course, the population almost surely does not maintain a stable age distribution, thus the specific age-class distribution resulting from the 2010 mortality event is unknown. The consequences of simulating the various versions of the 2010 mortality event assuming different 2009 ageclass distributions as a starting point would be interesting but computationally intensive. The effect of different starting points could be explored via approximate Bayesian computation (Siren *et al.*, 2018), but this is beyond the scope of the present work. *Observed number of nests reported every year for the index beach is accurate.* The historical nesting data for the index beach is considered the best indicator for evaluating Kemp's ridley population dynamics since there is currently no way to estimate population size directly (Coyne, 2000; Gallaway *et al.*, 2016a); however, the data do not account for annual variation in effort of locating nests (Gallaway *et al.*, 2013).

*Kemp's ridleys nest only at the index beach.* In actuality, the 2015 season estimated over 90% of the total nesting female population nested at the index beach while others nest elsewhere (Burchfield and Pena, 2015).

*Entire species is represented by a closed population residing completely in Gulf of Mexico.* For the sake of simplicity, it is assumed that individuals in Atlantic waters and European waters never return to the Gulf of Mexico and do not contribute to population growth. Those individuals were assumed to not have a significant impact on Gulf of Mexico population dynamics. In actuality, these individuals may return to the Gulf of Mexico when mature and contribute to population growth (Ogren, 1989).

*Entire population was modeled.* As opposed to modeling "female only" where males are not limiting population growth (Gallaway *et al.*, 2013; Coyne 2000, among others), the current model assumed the entire reproductive population was responsible for the density-dependent negative feedback on the remigration interval lengthening or shortening. This

was done to include all individuals supposedly competing for the same resources at the foraging grounds, although it is unclear if males actually journey to foraging grounds. Although sample size was small (n=11), Shaver *et al.* (2005) suggests a significant proportion of males occupy near-shore habitat near their natal nesting beaches year-round. Males were not a limiting factor in the current model.

*Highly sensitive density-dependent relationships were tested with a small range.* The relationships listed in Appendix C for the "density-dependent remigration rate" hypothesis are by no means an exhaustive list. Many other simulations were run, but each relationship proved to be highly sensitive to small changes in range.

## **Sensitivity Analysis**

Testing sensitivity of model parameters allows for comparison of model projections to what is known about sea turtle population dynamics and the effects of different management strategies currently in place for a species. Crouse *et al.* (1987) demonstrated with a sensitivity analysis how the management practice for loggerhead sea turtles at the time was focusing on the least responsive population parameters. While other models should be consulted for similar results before changing a conservation plan, the Crouse *et al.* (1987) model illustrates the importance of conducting these analyses for both practical and theoretical applications.

The most sensitive parameter found in this analysis, post-hatchling natural mortality rate, was also found to be the most sensitive parameter by Coyne (2000).

Interestingly enough, this parameter has had no direct measurements for estimation and is therefore surrounded by much uncertainty. One would expect post-hatchling mortality to be a sensitive parameter since it is directly affected by recruitment rates. Due to the model's assumptions and limitations, however, other similar models may suggest otherwise.

The sensitivity of a "knife edge" maturity schedule suggested it was a sensitive parameter (i.e. Scenario 4), but it was difficult to compare it to the parameters that were changed by a fixed amount (i.e. 10%). Therefore, additional investigation of this parameter may be needed for more accurate model projections. Since all other parameters tested suggested very little sensitivity in the model, the uncertainty surrounding those parameter estimates does not contribute greatly to the uncertainty of model projections.

# **Pulse Dynamics**

Although the "pulse" hypothesis was rejected, it nonetheless provided some insight to the integrity of the current mortality estimate of the 2010 mortality event. The results of the pulse analysis support that the Gallaway *et al.* (2016b) estimate of 0.312 for the 2010 mortality event is relatively accurate regardless if the event affected the Kemp's ridley population in a universal or age-specific form. However, the age-specific scenario AS10 produced simulated nests closer to the historical nest counts than did the universal scenario U4, suggesting the 2010 mortality event affected ages 11+ (last sub-adult class through all adult classes). The outcome of the simulation could be expected in the actual population

since adults contribute directly to reproduction and recruitment into the population while the last sub-adult stage is preparing to become reproductively active in the following year.

If the Deepwater Horizon oil spill was the source of the 2010 mortality event, the Kemp's ridley life history characteristics and the results of the age-specific pulse analysis support the timing of the event (April 2010) for sub-adults, but not necessarily that of adults. The nesting season would have already commenced, therefore we would have expected adults to have left the foraging areas that overlap with the oil spill site (Gallaway *et al.* 2016b). However, 2010 winter water temperatures were exceptionally cold and could have delayed the nesting season overall (Gallaway *et al.* 2016b). More investigation of this association is needed to make these claims certain.

## **Press Dynamics**

Although the "press" hypothesis was rejected, it nonetheless provided some insight to the universal vs. age-specific nature of the 2010 mortality event. The results suggest that if the 2010 mortality event was age-specific, it likely did not last more than two years (and conversely, if the event lasted 2 years, it had an age-specific effect). Only one of the simulations tested (AS106; 2010 mortality event length of two years, declining gradually) came as close to the historical data as did the pulse simulations. Similar to Scenario AS10, Scenario AS106 represented affected age classes 11+ (last sub-adult class through all adult classes). The universal counterpart of the same gradually declining, two-year 2010 mortality event (Scenario U12) did not meet the same criteria that AS106 met. In conjunction with the pulse results, this evidence further suggests that the 2010 mortality event had an age-specific effect on ages 11+ of the population instead of a universal effect.

When comparing Scenario AS106 as a gradually declining effect to its abruptly declining counterpart, Scenario AS66, the results support that if the 2010 mortality event lasted as long as two years, the effect diminished over these years as it returned to the natural mortality rate of the age class instead of persisting at the full effect. If the 2010 mortality event was caused by the Deepwater Horizon incident, the results suggest the event's effect diminished over a 2-year period. This is potentially due to oil removal efforts and natural evaporation/dispersion, which account for the removal of approximately 65-85% (130-170 million gallons) of the total oil released from the wellhead (Sea Grant, 2018).

# **Density-Dependent Remigration Rate Dynamics**

Two scenarios of the "density-dependent remigration rate" hypothesis met all criteria; therefore, this hypothesis is not rejected. The results suggest that an inverse logistic relationship (Equation 7, Scenario I4) between the remigration rate and reproductive individuals is likely, and that the 2010 mortality event had a single-year, agespecific effect on ages 11+ of the population. This outcome, visualized in Figures 13, 15b, and 16, provides a plausible explanation for the Kemp's ridley population dynamics historically observed from 2010-2014. The data from years 2015-2017, although preliminary, validate this outcome and suggest a density-dependent, inverse logistic relationship is present between the remigration rate and the number of reproductive individuals in the population. This is a potential cause for the fluctuations observed in the historical nest counts at the index beach during those years and why the population did not resume its previously exponential growth curve after the 2010 mortality event.

The outcome can be interpreted as though the population has a threshold of increased reproductive population density that it is able to withstand without affecting the remigration interval of those individuals. That is, it can be expected that some increase in density of reproductive individuals would not affect the remigration rate much (i.e. an increase in density from 20,000 to 25,000 yields a small decrease in the remigration rate overall), but at higher densities past this threshold (i.e. greater than 35,000), the remigration rate would decrease substantially to a lower value (longer remigration interval).

If the described relationship is present, the model can be used to estimate at what point in time the population may reach the down-listing criteria for Kemp's ridleys offered by Caillouet *et al.* (2016) and NMFS *et al.* (2011), particularly that of the number of nesting females existing in the population is greater than 10,000 (corresponding to 25,000 nests laid annually at the index beach). Using the inverse logistic density-dependent relationship (I4), the model projects that these numbers will be reached in the year 2019 (n = 10,732 nesting females and n = 26,831 nests), allowing for the Kemp's ridley to be down-listed to threatened status at that time. This projection is sooner than the more conservative estimate suggested by the Turtle Expert Working Group (TEWG, 1998) in
which the goal would be reached in the year 2020. However, Coyne (2000) contends that the TEWG (1998) model did not account for density-dependent factors and imposed a limit on the number of nests that could be protected in theory (n = 5,000 nests). Needless to say, the historical nesting data greatly exceeds this limit as early as the year 2002 (Gallaway *et al.*, 2013; Gallaway *et al.*, 2016b).

The exponential function (Equation 5, Scenario E4) using the same age-specific scenario AS10 met all criteria presented for evaluation but was not validated with the current model. It may have been a plausible explanation for the Kemp's ridley population dynamics historically observed from 2010-2014, but it appears the simulation contains a time-lag following the second depression in comparison to the 2015-2017 preliminary data (Figure 15a). Therefore, model projections made using the exponential function would not be as accurate as the inverse logistic function projection. The linear function (Equation 4, Scenario L4), again using the same age-specific scenario AS10, demonstrated a time-lag as well, leading to an increase in simulated nests in 2013 (Figure 14), hence the reason for this scenario failing criterion 4. Subsequent analyses may be needed to determine the underlying cause of these time-lags before completely disregarding them as possible density-dependent functional relationships. It is possible that the criteria presented could have been too restrictive, especially regarding criterion 3, therefore allowing the exclusion of a potentially valid relationship. The inverse logistic scenario I1 was just outside the 10% limit of criterion 3 to be considered for subsequent analysis. This scenario could have potentially suggested the 2010 mortality event had a universal effect instead of an agespecific effect. Further statistical investigation of the validity of the criterion presented may be necessary to reduce this uncertainty.

A density-dependent remigration rate may exist in the Kemp's ridley population because the length of the remigration interval is thought to be affected by per-capita food availability. Gallaway *et al.* (2016b) provided data supporting that a decline in two major food sources for Kemp's ridleys (blue crabs and discarded bycatch from shrimping operations) may have resulted in a longer length of time necessary for nesting females to gain enough energy for migration, hence a longer remigration interval. Hays (2000) demonstrated this notion using a model system, showing that variability in food availability could prevent the laying of more than one clutch and/or prevent remigration entirely when body nourishment is below a certain threshold at the time of migration. The current model has the ability to be used in subsequent analyses regarding food source variability given the appropriate time-series data.

### **Management Implications**

The model was the first of its kind to test these hypotheses and should prove useful to management professionals considering conservation strategies for Kemp's ridley sea turtles. Although this study does not solidify the link between the 2010 mortality event seen in the Kemp's ridley population and the 2010 Deepwater Horizon oil spill, the events were correlated in space and time (Crowder and Heppell, 2011). Some turtles were found to be visibly and heavily oiled and/or stranded as a result of the event, not to mention the

indirect effects of oil that are still being monitored and investigated, such as degradation and contamination within the food web (Crowder and Heppell, 2011; Gallaway *et al.*, 2016b). Regarding possible effects on remigration, it is expected that nesting females would have left the foraging area that overlaps with the oil spill before the spill occurred in April. However, seawater temperatures were unusually cold that year and could have possibly delayed the nesting season (Gallaway *et al.*, 2016b). If nesting was delayed, it is probable that more reproductive females would have been exposed to the oil. Since the model is already set up for density-dependent analyses for the remigration rate, it would be easy to investigate different density-dependent relationships of the remigration rate and segments of the population other than reproductive individuals (i.e. all foraging individuals based on age or female-only analyses).

While we may never know if remigration was delayed or not in 2010, we can prepare for the future by improving our current knowledge of the Kemp's ridley life history parameter estimates. Specifically, since this study has provided more evidence for the density-dependent nature of the remigration rate, satellite telemetry is recommended for subsequent studies to track migrating individuals in space and time to refine this parameter estimate. Spatial studies are crucial to understand potential differences in life history parameters that may exist between nesting and foraging grounds. Some information does exist on the whereabouts of individuals during different seasons via satellite telemetry (Shaver *et al.*, 2017, among others); however, more emphasis on this management approach is recommended. The results of the sensitivity analysis, consistent with Coyne (2000), imply that the post-hatchling life stage would be the most responsive stage upon which to focus conservation efforts and promote species recovery. Since it is unrealistic and extremely difficult to reduce at-sea mortality for such small individuals (SCL < 20 cm) during the first two years of their life, the Head Start Program historically offered the most practical solution since it fostered hatchlings for the first year of life until the program's termination in 1992 (Shaver and Wibbels, 2007). Further recommendations based on this analysis may be to reinstate the program and extend the foster period to two years to allow for more individual growth, cost-permitting, or to instead focus on obtaining more accurate parameter estimates (i.e. natural mortality) for the post-hatchling life stage. Additionally, Crowder and Heppell (2011) argue that the program may have been the key to the population's resilience and recovery from significant mortality events such as the one in 2010.

Although we do not currently have an estimate of the carrying capacity of the Gulf of Mexico for the Kemp's ridley, density-dependent age-specific natural mortality should be incorporated in future versions of the model. This might come in the form of a markrecapture study or by an energetics study regarding the declines in food sources (i.e. blue crab and/or shrimp bycatch discards, Gallaway *et al.*, 2016b). There are also speculations that Atlantic-dwelling individuals may actually have a larger impact on population dynamics than previously thought, either in the form of returning to the Gulf, reproducing, and contributing to population growth, or in the form of not returning and therefore not contributing to population growth (perhaps instead to the detriment of the population). The current model could be used for these studies given the time and resources to continue. Additionally, by integrating the effort of locating nests associated with the annual nest count data at the index beach, model simulation results could be better weighed against the historical observations.

All model projections should be analyzed with a degree of caution. Future projections imply that under the existing conditions and relationships established for the model system from the available scientific literature, the simulated outcome is what might be expected. Rather, future projections should not be taken as factual, but instead as possibilities. Refining each life history parameter with the most up-to-date information for estimation is vital to prepare for inevitable disasters, such as oil spills and hurricanes. Since the model is deterministic, it does not account for random events (i.e. mortality events or otherwise) that might affect the population in the near or far future. Therefore, the development of a stochastic model would be useful to investigate the likelihood of such events and their effect on the population. Future management strategies should embrace uncertainties of both natural and anthropogenic disasters in both space and time to anticipate population response and its ability to recover from these disasters.

#### CHAPTER III

#### SUMMARY AND CONCLUSIONS

This study investigated three hypotheses to explain the post-2010 fluctuations observed in the index beach nesting data of the Kemp's ridley sea turtle. An age-specific population model was created and parameterized using the best available estimates from peer-reviewed literature. The two most recent population models created for the Kemp's ridley sea turtle, NMFS *et al.* (2011) and Gallaway *et al.* (2016a), provided a majority of the parameter estimates and generated a baseline model. A sensitivity analysis was conducted on the baseline version of the model to identify the parameters that most affected the annual rate of population growth ( $\lambda$ ). The model was modified to test three cause-effect relationships hypothesized to explain Kemp's ridley population dynamics following the 2010 mortality event: a single year "pulse" effect increasing Kemp's ridley mortality, and a density-dependent negative feedback decreasing Kemp's ridley recruitment due to a lengthened remigration interval ("density-dependent remigration rate").

The "pulse" analysis yielded two potential scenarios and the "press" analysis yielded one potential scenario to describe the observed data, but these two hypotheses ultimately failed the hypothesis-testing criteria for further analysis. Two scenarios of the "density-dependent remigration rate" analysis met all hypothesis-testing criteria, but ultimately one scenario (Scenario I4) was tentatively validated by an independent dataset of preliminary nest counts from 2015-2017 (Figure 15b). Scenario I4 was then used to project Kemp's ridley population dynamics (based on simulated nest counts) through the year 2035 (Figure 16) in terms of the estimated number of nests we can expect nesting females to lay at the index beach. Results of the model simulation suggest that down-listing the species to threatened status may be achieved as early as 2019.

This study has provided sufficient evidence to support the plausibility of an agespecific, inverse logistic density-dependent relationship existing between the remigration rate and the number of reproductive Kemp's ridley sea turtles in the Gulf of Mexico population. The 2010 mortality event most likely lasted a single year and affected the ageclass distribution of reproductively mature individuals, which altered the remigration rate of those individuals (and subsequently recruitment of young into the population), causing fluctuations to occur in index beach nesting records. The 2010 mortality event may have been caused by the Deepwater Horizon oil spill, and the density-dependent relationship may be due to changes in primary food-item availability, but more investigation is needed to support these claims.

Future examinations of Kemp's ridley density-dependent negative feedback mechanisms, population carrying capacity, and similar stochastic events are needed to minimize uncertainty and integrate the model's use into a management framework. These improvements can aid management professionals to plan or modify current conservation strategies for tentative down-listing of the Kemp's ridley sea turtle.

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## APPENDIX A

## EXPERIMENTAL DESIGN FOR "PULSE" SIMULATIONS

Below is the experimental design for "pulse" simulations of post-2010 dynamics of the Kemp's ridley population. Values indicate the additive mortality due to the 2010 mortality event (AE) in the indicated age class/life stage. U = Universal Scenario; AS = Age-Specific Scenario; PH = Post-Hatchling; J = Juvenile; SA = Sub-Adult; A = Adult.

Scenario:	PH,	PH,	J,	J,	J,	J,	SA,	SA,	SA,	SA,	SA,	SA,	А,	А,	А,
	Age														
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14+
U1	0.2184	0.2184	0.2184	0.2184	0.2184	0.2184	0.2184	0.2184	0.2184	0.2184	0.2184	0.2184	0.2184	0.2184	0.2184
U2	0.2496	0.2496	0.2496	0.2496	0.2496	0.2496	0.2496	0.2496	0.2496	0.2496	0.2496	0.2496	0.2496	0.2496	0.2496
U3	0.2808	0.2808	0.2808	0.2808	0.2808	0.2808	0.2808	0.2808	0.2808	0.2808	0.2808	0.2808	0.2808	0.2808	0.2808
U4	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
U5	0.3432	0.3432	0.3432	0.3432	0.3432	0.3432	0.3432	0.3432	0.3432	0.3432	0.3432	0.3432	0.3432	0.3432	0.3432
U6	0.3744	0.3744	0.3744	0.3744	0.3744	0.3744	0.3744	0.3744	0.3744	0.3744	0.3744	0.3744	0.3744	0.3744	0.3744
U7	0.4056	0.4056	0.4056	0.4056	0.4056	0.4056	0.4056	0.4056	0.4056	0.4056	0.4056	0.4056	0.4056	0.4056	0.4056
AS1	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS2	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS3	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS4	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS5	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312

Scenario:	PH, Age	PH, Age	J, Age	J, Age	J, Age	J, Age	SA, Age	SA, Age	SA, Age	SA, Age	SA, Age	SA, Age	A, Age	A, Age	A, Age
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14+
AS6	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS7	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS8	0	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312
AS9	0	0	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312
AS10	0	0	0	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312
AS11	0	0	0	0	0	0	0	0	0	0	0	0	0.312	0.312	0.312
AS12	0	0	0	0	0	0	0	0	0	0	0	0	0	0.312	0.312
AS13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.312
AS14	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0	0	0
AS15	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0	0	0
AS16	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0	0	0
AS17	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0	0	0
AS18	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0	0	0
AS19	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0	0	0
AS20	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0	0	0
AS21	0	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0	0	0
AS22	0	0	0	0	0	0	0	0	0	0	0.312	0.312	0	0	0
AS23	0	0	0	0	0	0	0	0	0	0	0	0.312	0	0	0
AS24	0	0	0.312	0.312	0.312	0.312	0	0	0	0	0	0	0	0	0
AS25	0	0	0	0.312	0.312	0.312	0	0	0	0	0	0	0	0	0
AS26	0	0	0	0	0.312	0.312	0	0	0	0	0	0	0	0	0
AS27	0	0	0	0	0	0.312	0	0	0	0	0	0	0	0	0
AS28	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0

Scenario:	PH, Age	PH, Age	J, Age	J, Age	J, Age	J, Age	SA, Age	SA, Age	SA, Age	SA, Age	SA, Age	SA, Age	A, Age	A, Age	A, Age
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14+
AS29	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0	0
AS30	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0	0	0
AS31	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0	0	0	0
AS32	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0	0	0	0	0
AS33	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0	0	0	0	0	0
AS34	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0	0	0	0	0	0	0
AS35	0	0	0.312	0.312	0.312	0.312	0.312	0	0	0	0	0	0	0	0
AS36*	0	0	0.312	0.312	0.312	0.312	0	0	0	0	0	0	0	0	0
AS37	0	0	0.312	0.312	0.312	0	0	0	0	0	0	0	0	0	0
AS38	0	0	0.312	0.312	0	0	0	0	0	0	0	0	0	0	0
AS39	0	0	0.312	0	0	0	0	0	0	0	0	0	0	0	0
AS40	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0
AS41	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0	0
AS42*	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0	0	0
AS43	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0	0	0	0
AS44	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0	0	0	0	0
AS45	0	0	0	0	0	0	0.312	0.312	0.312	0	0	0	0	0	0
AS46	0	0	0	0	0	0	0.312	0.312	0	0	0	0	0	0	0
AS47	0	0	0	0	0	0	0.312	0	0	0	0	0	0	0	0
AS48	0	0	0	0	0	0	0	0	0	0	0	0	0.312	0.312	0
AS49	0	0	0	0	0	0	0	0	0	0	0	0	0.312	0	0
AS50	0	0	0	0.312	0	0	0	0	0	0	0	0	0	0	0
AS51	0	0	0	0	0.312	0	0	0	0	0	0	0	0	0	0

Scenario:	PH,	PH,	J,	J,	J,	J,	SA,	SA,	SA,	SA,	SA,	SA,	А,	А,	А,
	Age	Age	Age	Age	Age	Age	Age	Age	Age	Age	Age	Age	Age	Age	Age
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14 +
AS52	0	0	0	0	0	0	0	0.312	0	0	0	0	0	0	0
AS53	0	0	0	0	0	0	0	0	0.312	0	0	0	0	0	0
AS54	0	0	0	0	0	0	0	0	0	0.312	0	0	0	0	0
AS55	0	0	0	0	0	0	0	0	0	0	0.312	0	0	0	0
AS56	0	0	0	0	0	0	0	0	0	0	0	0	0	0.312	0
*Scenarios	s AS36 an	d AS42 aı	re repeats	of Scenari	os AS24 a	and AS18,	respective	ely, but ar	e included	l for the sa	ke of sim	plicity.			

## APPENDIX B

## EXPERIMENTAL DESIGN FOR "PRESS" SIMULATIONS

Below is the experimental design for "press" simulations of post-2010 dynamics of the Kemp's ridley population. Values indicate the additive mortality due to the 2010 2010 event ( $A_E$ ) in the indicated age class/life stage. U = Universal Scenario; AS = Age-Specific Scenario; PH = Post-Hatchling; J = Juvenile; SA = Sub-Adult; A = Adult.

Scenario:	Decay	Decay	PH,	PH,	J,	J,	J,	J,	SA,	SA,	SA,	SA,	SA,	SA,	А,	А,	А,
	Type:	Period	Age														
		(years)	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14+
		$(L_E)$															
U8	Abrupt	2	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
U9	Abrupt	3	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
U10	Abrupt	4	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
U11	Abrupt	5	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
U12	Gradual	2	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
U13	Gradual	3	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
U14	Gradual	4	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
U15	Gradual	5	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS57	Abrupt	2	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS58	Abrupt	2	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS59	Abrupt	2	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS60	Abrupt	2	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312

Scenario:	Decay Type:	Decay Period (years) (L <sub>E</sub> )	PH, Age 0	PH, Age 1	J, Age 2	J, Age 3	J, Age 4	J, Age 5	SA, Age 6	SA, Age 7	SA, Age 8	SA, Age 9	SA, Age 10	SA, Age 11	A, Age 12	A, Age 13	A, Age 14+
AS61	Abrupt	2	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS62	Abrupt	2	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS63	Abrupt	2	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS64	Abrupt	2	0	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312
AS65	Abrupt	2	0	0	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312
AS66	Abrupt	2	0	0	0	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312
AS67	Abrupt	3	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS68	Abrupt	3	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS69	Abrupt	3	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS70	Abrupt	3	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS71	Abrupt	3	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS72	Abrupt	3	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS73	Abrupt	3	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS74	Abrupt	3	0	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312
AS75	Abrupt	3	0	0	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312
AS76	Abrupt	3	0	0	0	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312
AS77	Abrupt	4	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS78	Abrupt	4	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS79	Abrupt	4	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS80	Abrupt	4	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS81	Abrupt	4	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS82	Abrupt	4	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312

Scenario:	Decay Type:	Decay Period (years) (L <sub>E</sub> )	PH, Age 0	PH, Age 1	J, Age 2	J, Age 3	J, Age 4	J, Age 5	SA, Age 6	SA, Age 7	SA, Age 8	SA, Age 9	SA, Age 10	SA, Age 11	A, Age 12	A, Age 13	A, Age 14+
AS83	Abrupt	4	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS84	Abrupt	4	0	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312
AS85	Abrupt	4	0	0	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312
AS86	Abrupt	4	0	0	0	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312
AS87	Abrupt	5	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS88	Abrupt	5	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS89	Abrupt	5	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS90	Abrupt	5	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS91	Abrupt	5	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS92	Abrupt	5	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS93	Abrupt	5	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS94	Abrupt	5	0	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312
AS95	Abrupt	5	0	0	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312
AS96	Abrupt	5	0	0	0	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312
AS97	Gradual	2	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS98	Gradual	2	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS99	Gradual	2	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS100	Gradual	2	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS101	Gradual	2	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS102	Gradual	2	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS103	Gradual	2	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS104	Gradual	2	0	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312

Scenario:	Decay Type:	Decay Period (years) (L <sub>E</sub> )	PH, Age 0	PH, Age 1	J, Age 2	J, Age 3	J, Age 4	J, Age 5	SA, Age 6	SA, Age 7	SA, Age 8	SA, Age 9	SA, Age 10	SA, Age 11	A, Age 12	A, Age 13	A, Age 14+
AS105	Gradual	2	0	0	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312
AS106	Gradual	2	0	0	0	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312
AS107	Gradual	3	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS108	Gradual	3	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS109	Gradual	3	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS110	Gradual	3	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS111	Gradual	3	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS112	Gradual	3	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS113	Gradual	3	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS114	Gradual	3	0	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312
AS115	Gradual	3	0	0	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312
AS116	Gradual	3	0	0	0	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312
AS117	Gradual	4	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS118	Gradual	4	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS119	Gradual	4	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS120	Gradual	4	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS121	Gradual	4	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS122	Gradual	4	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS123	Gradual	4	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS124	Gradual	4	0	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312
AS125	Gradual	4	0	0	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312
AS126	Gradual	4	0	0	0	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312

Scenario:	Decay Type:	Decay Period	PH, Age	PH, Age	J, Age	J, Age	J, Age	J, Age	SA, Age	SA, Age	SA, Age	SA, Age	SA, Age	SA, Age	A, Age	A, Age	A, Age
		(years) (L <sub>E</sub> )	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14+
AS127	Gradual	5	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS128	Gradual	5	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS129	Gradual	5	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS130	Gradual	5	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS131	Gradual	5	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS132	Gradual	5	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS133	Gradual	5	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312	0.312
AS134	Gradual	5	0	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312	0.312
AS135	Gradual	5	0	0	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312	0.312
AS136	Gradual	5	0	0	0	0	0	0	0	0	0	0	0	0.312	0.312	0.312	0.312

#### APPENDIX C

# EXPERIMENTAL DESIGN FOR "DENSITY-DEPENDENT REMIGRATION RATE" SIMULATIONS

Below is the experimental design for "density-dependent remigration rate"

simulations of post-2010 dynamics of the Kemp's ridley population. L = Linear Function;

E = Exponential Function; P = Second-Order Polynomial Function; I = Inverse Logistic

Function; R = Remigration Rate;  $R_S = Reproductive Individuals in Stock$ ;

U = Universal Scenario; AS = Age-Specific Scenario.

Remigration	Pulse/Press	Equation:
Scenario:	Scenario:	
L1	U4	$R = -0.3 * R_S + 0.8$
L2	U4	$R = -0.3496 * R_S + 0.9$
L3	U4	$R = -0.4 * R_S + 1$
L4	AS10	$R = -0.3 R_S + 0.8$
L5	AS10	$R = -0.3496 * R_{S} + 0.9$
L6	AS10	$R = -0.4 * R_S + 1$
L7	AS106	$R = -0.3 * R_S + 0.8$
L8	AS106	$R = -0.3496 * R_{S} + 0.9$
L9	AS106	$R = -0.4 * R_S + 1$
E1	U4	$R = 0.5007 * e^{(-0.1*R_{S})}$
E2	U4	$R = 0.5612 * e^{(-0.114 * R_S)}$
E3	U4	$R = 0.5814 * e^{(-0.119*R_S)}$
E4	AS10	$R = 0.5007 * e^{(-0.1 * R_{S})}$
E5	AS10	$R = 0.5612 * e^{(-0.114*R_S)}$
E6	AS10	$R = 0.5814 * e^{(-0.119*R_{S})}$

Remigration	Pulse/Press	Equation:
Scenario:	Scenario:	-
E7	AS106	$R = 0.5007 * e^{(-0.1*R_{\rm S})}$
E8	AS106	$R = 0.5612 * e^{(-0.114 * R_S)}$
Е9	AS106	$R = 0.5814 * e^{(-0.119*R_{S})}$
P1	U4	$R = -0.0038*R_{S}^{2} - 0.0092*R_{S} + 0.4884$
P2	U4	$R = -0.0027*R_{S}^{2} - 0.0076*R_{S} + 0.5563$
Р3	U4	$R = -0.004 * R_S^2 - 0.0007 * R_S + 0.6014$
P4	AS10	$R = -0.0038*R_S^2 - 0.0092*R_S + 0.4884$
Р5	AS10	$R = -0.0027 * R_S^2 - 0.0076 R_S + 0.5563$
P6	AS10	$R = -0.004 * R_S^2 - 0.0007 * R_S + 0.6014$
P7	AS106	$R = -0.0038*R_{S}^{2} - 0.0092*R_{S} + 0.4884$
P8	AS106	$R = -0.0027 * R_S^2 - 0.0076 R_S + 0.5563$
Р9	AS106	$R = -0.004*R_{S}^{2} - 0.0007*R_{S} + 0.6014$
I1	U4	$R = 0.2 + \frac{(0.3 * e^{9.69 - 0.0003737855*R}s)}{(1 + e^{9.69 - 0.0003737855*R}s)}$
12	U4	$R = 0.2 + \underbrace{(0.35^*e^{9.69-0.0003737855^*R}_{S})}_{(1 + e^{9.69-0.0003737855^*R}_{S})}$
13	U4	$R = 0.2 + (0.4 * e^{9.69 - 0.0003737855 * R} s)$
I4	AS10	$R = 0.2 + (0.3 * e^{9.69 - 0.0003737855 * R} s)$ (1 + e^{9.69 - 0.0003737855 * R} s)
15	AS10	$R = 0.2 + (0.35 * e^{9.69 - 0.0003737855 * R}) (1 + e^{9.69 - 0.0003737855 * R})$
I6	AS10	$R = 0.2 + (0.4 * e^{9.69 - 0.0003737855 * R} s)$
I7	AS106	$R = 0.2 + (0.3 * e^{9.69 - 0.0003737855 * R} s)$
18	AS106	$R = 0.2 + \frac{(0.35 * e^{9.69 - 0.0003737855 * R})}{(1 + e^{9.69 - 0.0003737855 * R})}$
19	AS106	$R = 0.2 + \frac{(0.4 * e^{9.69 - 0.0003737855 * R}_{S})}{(1 + e^{9.69 - 0.0003737855 * R}_{S})}$