The Effect of Localized Oil Spills on the Atlantic Loggerhead Turtle Population Dynamics

My Huynh[1], Margaret-Rose Leung[2], Melissa Marchand[3], Samantha Stykel[4], Leon Arriola[5], José Flores[6]

[1]Arizona State University, Tempe, Arizona
[2]Oregon State University, Corvallis, Oregon
[3]California State University Bakersfield, Bakersfield, California
[4]Luther College, Decorah, Iowa
[5]University of Wisconsin – Whitewater, Whitewater, Wisconsin
[6]The University of South Dakota, Vermillion, South Dakota

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Abstract

The loggerhead sea turtle (*Caretta caretta*) is an endangered species with significantly different haplotype frequencies in the regional nesting populations of the Gulf of Mexico and the western North Atlantic Ocean. In this work, we analyze the population dynamics of loggerhead turtles affected by localized oil spill catastrophes. We develop a spatial, stage-classified matrix model and apply it to the three primary nesting regions in the area. Oil spills are simulated deterministically in each nesting region, with oil-induced mortality ranging from 25% to 100% and affecting stage classes either proportionally or equally. We then vary the fecundity and survival parameters uniformly, and use Latin Hypercube Sampling to run stochastic simulations for each nesting region. The results of this study are intended to provide insights into the population dynamics of the Atlantic loggerhead turtles and suggest conservation techniques appropriate in each oil spill case.

1 Introduction

The loggerhead turtle (*Caretta caretta*) is one of six endangered sea turtles in the Atlantic Ocean [19]. This situation has been caused primarily by human activities [19]. The most recent disturbance to the species occurred in late April 2010 with the explosion of the Deepwater Horizon oil rig. Historically, the majority of oil spills between 1992 and 2001 have occurred in the Gulf of Mexico or along the Florida peninsula [19]. Thus, the effect of oil spills on loggerhead population dynamics is of critical importance for the preservation of the species. However, data regarding the susceptibility of turtles to oil are sparse, although the physiological effects are understood [13]. Furthermore, studies on the weathering of oil have examined only specific compounds rather than their overall toxicity to sea turtles [1, 17].

Most existing models of loggerhead turtles have focused on determining the stage classes to which asymptotic population growth is most sensitive. Crouse et al. published one of the first models in 1987 [6]: a Lefkovitch stage-classified matrix parametrized with data collected by Frazer in 1983 [9]. In 1994, Crowder et al. developed a model to analyze the impact of turtle excluder devices (TEDs) [7]. In 2003, Heppell et al. used newer data to create two Lefkovitch models in hopes of bounding the true values for survival parameters and stage durations. One model used lower parameter estimates while the other used higher estimates [11].

Loggerhead population models that account for oil spills are difficult to find in the research literature. However, after the 1989 Exxon Valdez catastrophe, scientific interest in the ecological consequences of oil spills increased. This led to several studies on the effects of oil spills on other species, including sea otters [10], bald eagles [4], brown bears [18], and harlequin ducks [8]. In particular, Reed et al. spatially modelled oil's effect on migrating fur seals [16]. Due to lack of data, they examined heuristic oil-induced mortality rates ranging from 25–100%.

Our research is motivated by the potential impact of the Deepwater Horizon oil spill in the Gulf of Mexico. We intend to utilize previous work on loggerhead turtles and oil spills to enhance our understanding of the consequences of this disaster on the turtle population. We develop a system of stage-classified, spatial matrix models whose survival parameters can be easily modified to simulate a variety of oil spills. We do this by creating separate models for the three primary nesting regions of the Atlantic loggerhead turtle population. These models overlap geographically, as juvenile turtles disperse to forage beyond their nesting region. Therefore, oil spills may affect sea turtles from any of the three nesting regions, making the spatial component crucial to our method.

The remainder of this paper is organized as follows. In Section 2, we develop a stage-structured model of turtles in the absence of oil. A discussion of our parameter values is given in Section 2.1. We run deterministic (fixed parameters) and stochastic (varying parameters) simulations in Sections 2.2 and 2.3 and analyze asymptotic and transient sensitivities in Section 2.4. In Section 3, we consider oil spills both deterministically and stochastically and again conduct a transient sensitivity analysis. We discuss the implications of our findings in Section 4, and topics for future study in Section 5. Appendices A–D provide numerical results of our investigation.

2 Population Model without Oil Spill

We first model the Atlantic loggerhead population without the impact of an oil spill. Since a negligible proportion of loggerhead turtles nest away from their hatching region [2], we create multiple matrix models to describe separate nesting regions. Each matrix classifies turtles by their stage class and current location.

There are five primary nesting regions in the western North Atlantic Ocean [15]; we focus our study on the three most relevant. The North (region N) is defined as the northeastern corner of Florida through southern Virginia. Peninsular Florida (region F) is the main Florida peninsula, extending from the northeast through Pinellas County in the west (not including the Florida islands).

The North Gulf of Mexico (region G) includes the western panhandle of Florida through the Texas-Mexico border [15]. Figure 1 provides a map with G, F, N and S labelled accordingly.

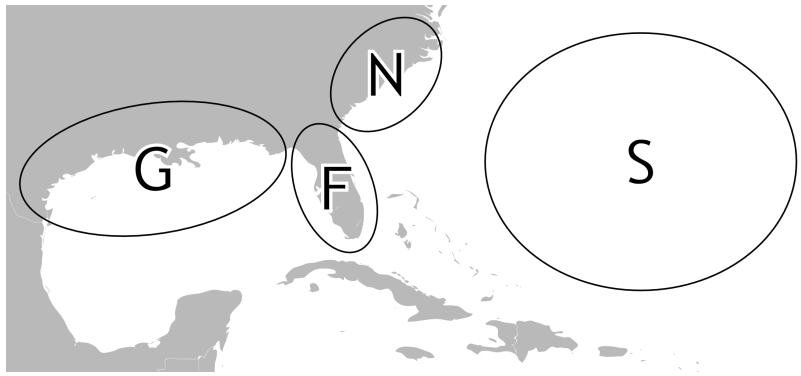

Figure 1: The four locations in our model.

We use stage classes corresponding to the five major life phases of the loggerhead turtle [11]. All turtles spend their first year as eggs/hatchlings (B) in their hatching region. In the second year, they become oceanic immatures (Y) and migrate to the Sargasso Sea (location S) in the North Atlantic Ocean. After 9 years, turtles disperse to any of the three coastal/nesting regions (G, F, N) [3], where they spend a total of 19 years as first small (I) and then large (L) neritic immatures [11]. After sexual maturation, turtles become adults (A) and return to their hatching region, where we assume they remain indefinitely. Although dispersal during non-breeding years has been suggested [3], the current data are inconclusive.

The life cycle graph for a population of turtles breeding in region j (for $j = G$ (Gulf), F (Florida), or N (North)), is provided in Figure 2. The first subscript of the state variable indicates region of origin; the second, current location (e.g. L_{FG} are large neritic immatures hatched in Florida but currently in the Gulf). Our parameters include fecundity (ζ), retention rates (σ), and four maturation rates ($\gamma, \delta, \alpha, \epsilon$) for hatchlings, oceanic immatures, small neritic immatures, and large neritic immatures respectively.

Based on this life cycle, we develop a projection matrix $\mathbf{M}_j$ to model the flow of turtles between stage and spatial classes. If the population at time n is $\mathbf{P}(n)$, then the formula $\mathbf{P}(n+1) = \mathbf{M}_j\mathbf{P}(n)$ describes populations at time $n+1$:

$$\begin{bmatrix} B_{jj}(n+1) \\ Y_{jS}(n+1) \\ I_{jG}(n+1) \\ I_{jF}(n+1) \\ I_{jN}(n+1) \\ L_{jG}(n+1) \\ L_{jF}(n+1) \\ L_{jN}(n+1) \\ A_{jj}(n+1) \end{bmatrix} = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \zeta_j \\ \gamma_j & \sigma_{Y_{jS}} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \delta_{jG} & \sigma_{I_{jG}} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \delta_{jF} & 0 & \sigma_{I_{jF}} & 0 & 0 & 0 & 0 & 0 \\ 0 & \delta_{jN} & 0 & 0 & \sigma_{I_{jN}} & 0 & 0 & 0 & 0 \\ 0 & 0 & \alpha_{jG} & 0 & 0 & \sigma_{L_{jG}} & 0 & 0 & 0 \\ 0 & 0 & 0 & \alpha_{jF} & 0 & 0 & \sigma_{L_{jF}} & 0 & 0 \\ 0 & 0 & 0 & 0 & \alpha_{jN} & 0 & 0 & \sigma_{L_{jN}} & 0 \\ 0 & 0 & 0 & 0 & 0 & \epsilon_{jG} & \epsilon_{jF} & \epsilon_{jN} & \sigma_{A_{jj}} \end{bmatrix} \begin{bmatrix} B_{jj}(n) \\ Y_{jS}(n) \\ I_{jG}(n) \\ I_{jF}(n) \\ I_{jN}(n) \\ L_{jG}(n) \\ L_{jF}(n) \\ L_{jN}(n) \\ A_{jj}(n) \end{bmatrix}.$$

2.1 Parameter Estimation

The fecundity of adults hatched in region j is ζ_j, which depends on the number of eggs laid annually per adult female and the proportion of eggs resulting in female hatchlings. When breeding, an adult female lays 3–5.5 (mean 4.25) clutches each containing 100–126 (mean 113) eggs [15]. On average, females breed approximately once every 2.8 years [14], giving an annual total of $4.25(113)/2.8 \approx 174$

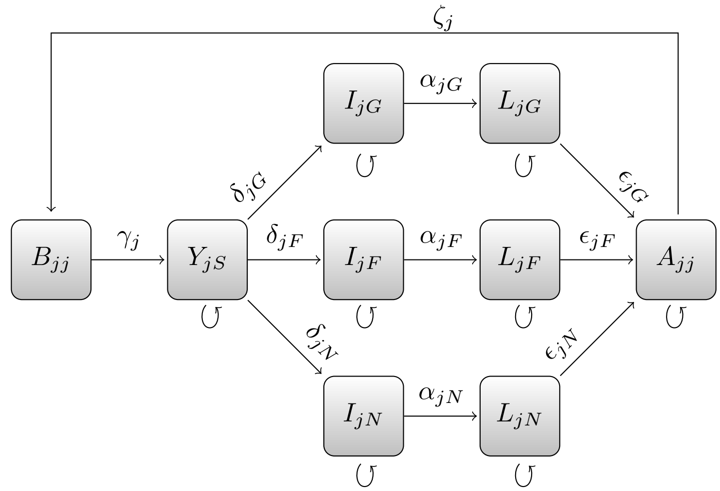

Figure 2: Diagram of turtle populations native to region $j = G, F, N$. Loops represent retention proportions (σ); arrows represent fecundity (ζ_j) and maturation proportions ($\gamma_j, \delta_j, \alpha_j, \epsilon_j$).

eggs per female. However, only 45–70% (mean 57.5%) of eggs survive to hatch [15], and the number of female hatchlings varies by region. The proportion of female hatchlings in Florida 0.88 and averaging the data for states in region N yields a proportion of 0.62 [20]. We estimate a proportion of 0.8 for region G because hatchling sex is determined by temperature and G is located closer to F than to N.

There are five survival proportions in our model: γ (hatchling), ω_Y (oceanic immature), ω_I (small neritic immature), ω_L (large neritic immature), and ω_A (adult). The survival (and maturation) proportion of hatchlings is 70% [15]; thus $\gamma = 0.7$. The annual adult survival proportion is 0.8091–0.85, with mean $\omega_A = 0.82955$. For stage classes with duration $k > 1$ years, Crouse et al. provide formulas for the retention (σ) and maturation (δ, α, ϵ) proportions [6] which depend on the survival proportion. If a proportion p of class members survive each year (cf. Table 1), then a proportion of p^k members are alive on the k^{th} year, making total abundance $1 + p + \cdots + p^{k-1}$. Of this total, $p\big(1 + p + \cdots + p^{k-2}\big)$ survive and remain in the class the next year; $p\big(p^{k-1}\big)$ survive and mature. Thus:

$$\text{Retention proportion: } \frac{p(1+p+\cdots+p^{k-2})}{1+p+\cdots+p^{k-1}} = \frac{p(1-p^{k-1})}{1-p^k}$$

$$\text{Maturation proportion: } \frac{p(p^{k-1})}{1+p+\cdots+p^{k-1}} = \frac{p^k(1-p)}{1-p^k}$$

Class		Age Range	Duration	Annual Survivorship
B	Egg/hatchling	0–1 years	1 years	70.0%
Y	Oceanic immature	1–10 years	9 years	74.5–87.5%
I	Small neritic immature	10–18.5 years	8.5 years	67.6–70.0%
L	Large neritic immature	18.5–29 years	10.5 years	74.3–80.0%
A	Adult	29+ years	—	80.9–85.0%

Table 1: Stage class durations and survival proportions [11].

Population censuses of loggerheads are limited to annual nest counts, which can be used to estimate the number of adult females breeding that year. In order to approximate the populations of the other classes, we assume that the population has reached its stable state distribution. We then scale the eigenvectors associated with the dominant eigenvalues of our parametrized matrices such that their adult population component matches the most recent data from 2007 [15]. This yields the initial population vectors based on Table 2.

Region	$j = G$	$j = F$	$j = N$
B_{jj}	34415	2774337	169419
Y_{jS}	174861	13781286	912354
I_{jG}	7157	644518	29060
I_{jF}	2136	105612	3733
I_{jN}	15171	1152786	99119
L_{jG}	610	53840	2603
L_{jF}	182	8822	334
L_{jN}	1292	96298	8879
A_{jj}	394	28974	2460
Total	236218	18646473	1227961

Table 2: Initial populations for each region.

2.2 Deterministic Simulations (Fixed Parameters)

By using the averages calculated in Table 3, we create deterministic simulations of our population model. Figure 3 displays populations over a 20-year period. All populations decay exponentially since their dominant eigenvalues are less than 1 (0.9142 for Gulf, 0.9174 for Florida, 0.9064 for North). Table 8 in Appendix A provides the percent decrease in total population by years 5 and 20. We expect the North's population to decrease the most in relation to its initial population, with a 5-year decline of 32.7% and a 20-year decline of 84.7%.

2.3 Stochastic Simulations (Varying Parameters)

Of the six independent parameters (fecundity and survival proportions), our sources provide ranges for all but γ (cf. Table 4). We run 1000 simulations for every combination of oil spill region, toxicity, and turtle susceptibility. In our simulations, we use a random sample of parameters from uniform distributions supported on ranges found in the literature [11,15]. Parameters are sampled every year for 20 years. Latin Hypercube Sampling is used to generate the 20000 sets of parameters used in each oil spill case.

The means, standard deviations, and quartiles of our resulting populations are provided in Appendix B. The results of our simulations show an average percent decrease from the initial population by year 5 of 30.1% (Gulf), 29.1% (Florida), and 32.7% (North) and an average percent decrease from the initial population by year 20 of 81.6% (Gulf), 80.3% (Florida), and 84.5% (North). Standard deviations are generally higher for younger classes and decrease throughout the simulation.

We show a histogram of the simulated populations at year 20 without an oil spill in Figure 4. A normal curve is fitted to our results to illustrate that total populations approach a normal distribution over time.

2.4 Sensitivity Analysis

Sensitivity indices quantify the proportional change in the output of a model with respect to a proportional change in its inputs. We use sensitivity analysis to determine the parameters with the

Parameter	Symbol	Value by Region		
		$j = G$	$j = F$	$j = N$
Fecundity	ζ_j	79.8546	87.8400	61.8873
Maturation rates				
Hatchling	γ_j	0.7	0.7	0.7
Oceanic immature, Gulf origin	δ_{Gj}	0.0098	0.0029	0.0208
Oceanic immature, Florida origin	δ_{Fj}	0.0114	0.0019	0.0203
Oceanic immature, North origin	δ_{Nj}	0.0074	0.0009	0.0252
Small neritic immature	α_j	0.0135	0.0135	0.0135
Large neritic immature	ϵ_j	0.0160	0.0160	0.0160
Retention rates				
Oceanic immature	$\sigma_{Y_{jS}}$	0.7764	0.7764	0.7764
Small neritic immature	$\sigma_{I_{j*}}$	0.6744	0.6744	0.6744
Large neritic immature	$\sigma_{L_{j*}}$	0.7552	0.7552	0.7552
Adult	$\sigma_{A_{jj}}$	0.8296	0.8296	0.8296

Table 3: Parameters of deterministic model as calculated in Section 2.1. Asterisks indicate that the retention rate for neritic immatures in regions G, F and N is assumed to be the same.

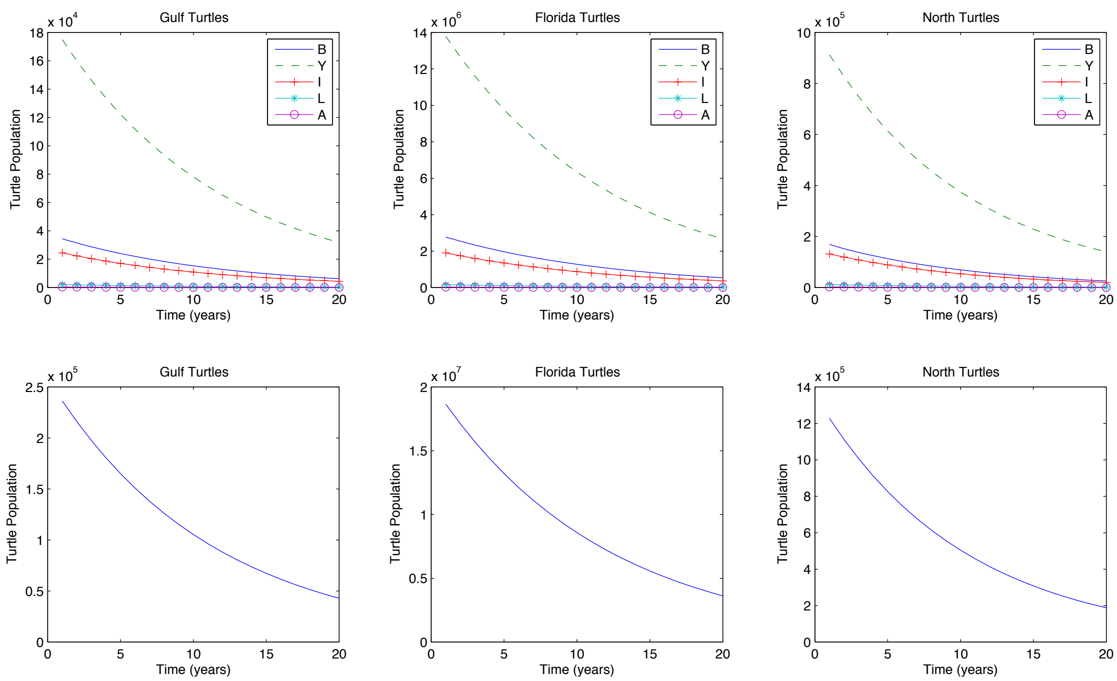

Figure 3: Deterministic simulation without oil spill. Above: populations by class. Below: total populations.

most influence on the population growth rate. In order to gain insight into the population's long- and short-term dynamics, we study asymptotic and transient sensitivity indices. In both cases, we

Parameter	Range
ζ	U$(100, 126)$ U$(3, 5.5)$ U$(0.45, 0.7)$ / 2.766467
ω_Y	U$(0.745, 0.875)$
ω_I	U$(0.6758, 0.7)$
ω_L	U$(0.7425, 0.8)$
ω_A	U$(0.8091, 0.85)$

Table 4: Parameter ranges we modeled via uniform distributions obtained from our sources [11,15]. U(a, b) signifies a continuous uniform random variable with support $[a, b]$.

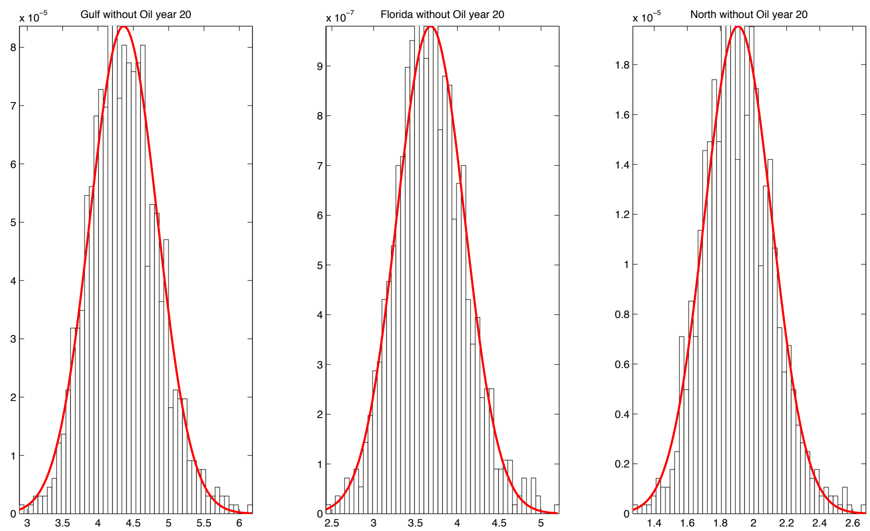

Figure 4: Histograms of populations at year 20 without an oil spill.

compare population growth rates to the survival proportion and fecundity parameters.

2.4.1 Asymptotic Sensitivity Indices

The asymptotic sensitivity indices describe the change in the asymptotic growth rate with respect to the change in the independent parameters $(\zeta, \gamma, \omega_Y, \omega_I, \omega_L, \omega_A)$. In order to calculate the asymptotic sensitivity indices, we follow the process outlined by Caswell [5]. Let ρ be an independent parameter corresponding to nesting region j. The sensitivity index SI_ρ of the dominant eigenvalue λ, which gives the asymptotic growth rate of matrix $\mathbf{M}_j$, to the parameter ρ is

$$SI_\rho = \frac{\rho}{\lambda}\frac{\partial \lambda}{\partial \rho}.$$

In $\mathbf{M}_j$, consider the entries a_{ik} which depend on ρ. The chain rule yields

$$SI_\rho = \frac{\rho}{\lambda}\sum_{ik}\frac{\partial \lambda}{\partial a_{ik}}\frac{\partial a_{ik}}{\partial \rho}.$$

For our parameters, we have:

$$SI_\zeta = \frac{\zeta}{\lambda_j}\frac{\partial\lambda_j}{\partial\zeta},$$
$$SI_\gamma = \frac{\gamma}{\lambda_j}\frac{\partial\lambda_j}{\partial\gamma},$$
$$SI_{\omega_Y} = \frac{\omega_Y}{\lambda_j}\left(\frac{\partial\lambda_j}{\partial\delta_{jG}}\frac{\partial\delta_{jG}}{\partial\omega_Y} + \frac{\partial\lambda_j}{\partial\delta_{jF}}\frac{\partial\delta_{jF}}{\partial\omega_Y} + \frac{\partial\lambda_j}{\partial\delta_{jN}}\frac{\partial\delta_{jN}}{\partial\omega_Y} + \frac{\partial\lambda_j}{\partial\sigma_{Y_{jS}}}\frac{\partial\sigma_{Y_{jS}}}{\partial\omega_Y}\right),$$
$$SI_{\omega_I} = \frac{\omega_I}{\lambda_j}\left(\frac{\partial\lambda_j}{\partial\alpha_{jG}}\frac{\partial\alpha_{jG}}{\partial\omega_I} + \frac{\partial\lambda_j}{\partial\alpha_{jF}}\frac{\partial\alpha_{jF}}{\partial\omega_I} + \frac{\partial\lambda_j}{\partial\alpha_{jN}}\frac{\partial\alpha_{jN}}{\partial\omega_I} + \frac{\partial\lambda_j}{\partial\sigma_{I_{jG}}}\frac{\partial\sigma_{I_{jG}}}{\partial\omega_I} + \frac{\partial\lambda_j}{\partial\sigma_{I_{jF}}}\frac{\partial\sigma_{I_{jF}}}{\partial\omega_I} + \frac{\partial\lambda_j}{\partial\sigma_{I_{jN}}}\frac{\partial\sigma_{I_{jN}}}{\partial\omega_I}\right),$$
$$SI_{\omega_L} = \frac{\omega_L}{\lambda_j}\left(\frac{\partial\lambda_j}{\partial\epsilon_{jG}}\frac{\partial\epsilon_{jG}}{\partial\omega_L} + \frac{\partial\lambda_j}{\partial\epsilon_{jF}}\frac{\partial\epsilon_{jF}}{\partial\omega_L} + \frac{\partial\lambda_j}{\partial\epsilon_{jN}}\frac{\partial\epsilon_{jN}}{\partial\omega_L} + \frac{\partial\lambda_j}{\partial\sigma_{L_{jG}}}\frac{\partial\sigma_{L_{jG}}}{\partial\omega_L} + \frac{\partial\lambda_j}{\partial\sigma_{L_{jF}}}\frac{\partial\sigma_{L_{jF}}}{\partial\omega_L} + \frac{\partial\lambda_j}{\partial\sigma_{L_{jN}}}\frac{\partial\sigma_{L_{jN}}}{\partial\omega_L}\right),$$
$$SI_{\omega_A} = \frac{\sigma_{A_{jj}}}{\lambda_j}\frac{\partial\lambda_j}{\partial\sigma_{A_{jj}}}.$$

The numerical sensitivity indices for each region are given in Table 5. The oceanic immature survival proportion is the most sensitive, with indices of 0.8328 (Gulf), 0.8477 (Florida), and 0.7805 (North). Thus, a one percent change in this proportion results in approximately a 0.8328 percent in the Gulf growth rate, 0.8477 in Florida, and 0.7805 in the North. The next most sensitive parameters are the small and large neritic immature and the adult survival proportion, while fecundity is the least sensitive.

Region	ζ	γ	ω_Y	ω_I	ω_L	ω_A
G	0.0357	0.0357	0.8328	0.3271	0.4259	0.3500
F	0.0365	0.0365	0.8477	0.3331	0.4324	0.3449
N	0.0334	0.0337	0.7805	0.3115	0.4090	0.3637

Table 5: Sensitivity indices of parameters relative to the asymptotic growth rate without an oil spill.

2.4.2 Transient Sensitivity Indices

The transient sensitivity indices describe the change in the transient growth rate with respect to the change in the independent parameters $(\zeta, \gamma, \omega_Y, \omega_I, \omega_L, \omega_A)$. We determine the transient sensitivity indices for the first five years of our simulation. In order to calculate the transient sensitivity indices, we follow the process outlined by Koons et al. [12]. Let $\mathbf{P}(n)$ be the population vector at time n. The transient growth rate $\mathbf{GR}(n)$ describes the ratio of the current total population to the population one time step earlier:

$$\mathbf{GR}(n) = \frac{||\mathbf{P}(n)||_1}{||\mathbf{P}(n-1)||_1}.$$

For an entry a_{ij} of the $m \times m$ projection matrix $\mathbf{M}$, the transient sensitivity describes the rate of change in transient growth rate with respect to a_{ij}:

$$TS_{ij} = \frac{\partial \mathbf{GR}(n)}{\partial a_{ij}}.$$

Let $\mathbf{e}$ be the $1 \times m$ identity vector, where all entries are 1. Let Δ_{ij} be an $m \times m$ matrix with all entries 0 except for a 1 in the (i, j) position. Then the transient sensitivity is:

$$TS_{ij}(n) = \begin{cases} \frac{\mathbf{e}\Delta_{ij}\mathbf{P}(0)}{\mathbf{e}\mathbf{P}(0)} & \text{for } n = 1, \\ \frac{\left[\sum_{l=0}^{n-2} \mathbf{e}\mathbf{M}^l\Delta_{ij}\mathbf{M}^{n-l-2}\left(\mathbf{M}\mathbf{P}(0)\mathbf{e} - \mathbf{P}(0)\mathbf{e}\mathbf{M}\right)\mathbf{M}^{n-1}\mathbf{P}(0)\right] + \mathbf{e}\mathbf{M}^{n-1}\Delta_{ij}\mathbf{P}(0)\mathbf{e}\mathbf{M}^{n-1}\mathbf{P}(0)}{(\mathbf{e}\mathbf{M}^{n-1}\mathbf{P}(0))^2} & \text{for } n > 1. \end{cases}$$

If the entries of $\mathbf{M}$ are constant over time, then the transient sensitivity index ($TSI(n)$) can be determined explicitly:

$$TSI_{ij}(n) = \frac{a_{ij}}{\mathbf{GR}(n)} \frac{\partial \mathbf{GR}(n)}{\partial a_{ij}}.$$

If a_{ij} is a function of a parameter ρ, then the transient sensitivity index becomes

$$TSI_{\rho}(n) = \frac{\rho}{\mathbf{GR}(n)} \sum_{i,j} \frac{\partial \mathbf{GR}_n}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial \rho}.$$

Therefore, the transient sensitivity indices of our parameters are:

$$\begin{aligned}
TSI_{\zeta}(n) &= \frac{\zeta}{\mathbf{GR}_j(n)} \frac{\partial \mathbf{GR}_j(n)}{\partial \zeta}, \\
TSI_{\gamma}(n) &= \frac{\gamma}{\mathbf{GR}_j(n)} \frac{\partial \mathbf{GR}_j(n)}{\partial \gamma}, \\
TSI_{\omega_Y}(n) &= \frac{\omega_Y}{\mathbf{GR}_j(n)} \left(\frac{\partial \mathbf{GR}_j(n)}{\partial \delta_{jG}} \frac{\partial \delta_{jG}}{\partial \omega_Y} + \frac{\partial \mathbf{GR}_j(n)}{\partial \delta_{jF}} \frac{\partial \delta_{jF}}{\partial \omega_Y} + \frac{\partial \mathbf{GR}_j(n)}{\partial \delta_{jN}} \frac{\partial \delta_{jN}}{\partial \omega_Y} + \frac{\partial \mathbf{GR}_j(n)}{\partial \sigma_{Y_{jS}}} \frac{\partial \sigma_{Y_{jS}}}{\partial \omega_Y} \right), \\
TSI_{\omega_I}(n) &= \frac{\omega_I}{\mathbf{GR}_j(n)} \left(\frac{\partial \mathbf{GR}_j(n)}{\partial \alpha_{jG}} \frac{\partial \alpha_{jG}}{\partial \omega_I} + \frac{\partial \mathbf{GR}_j(n)}{\partial \alpha_{jF}} \frac{\partial \alpha_{jF}}{\partial \omega_I} + \frac{\partial \mathbf{GR}_j(n)}{\partial \alpha_{jN}} \frac{\partial \alpha_{jN}}{\partial \omega_I} + \frac{\partial \mathbf{GR}_j(n)}{\partial \sigma_{I_{jG}}} \frac{\partial \sigma_{I_{jG}}}{\partial \omega_I} \right. \\
&\quad \left. + \frac{\partial \mathbf{GR}_j(n)}{\partial \sigma_{I_{jF}}} \frac{\partial \sigma_{I_{jF}}}{\partial \omega_I} + \frac{\partial \mathbf{GR}_j(n)}{\partial \sigma_{I_{jN}}} \frac{\partial \sigma_{I_{jN}}}{\partial \omega_I} \right), \\
TSI_{\omega_L}(n) &= \frac{\omega_L}{\mathbf{GR}_j(n)} \left(\frac{\partial \mathbf{GR}_j(n)}{\partial \epsilon_{jG}} \frac{\partial \epsilon_{jG}}{\partial \omega_L} + \frac{\partial \mathbf{GR}_j(n)}{\partial \epsilon_{jF}} \frac{\partial \epsilon_{jF}}{\partial \omega_L} + \frac{\partial \mathbf{GR}_j(n)}{\partial \epsilon_{jN}} \frac{\partial \epsilon_{jN}}{\partial \omega_L} + \frac{\partial \mathbf{GR}_j(n)}{\partial \sigma_{L_{jG}}} \frac{\partial \sigma_{L_{jG}}}{\partial \omega_L} \right. \\
&\quad \left. + \frac{\partial \mathbf{GR}_j(n)}{\partial \sigma_{L_{jF}}} \frac{\partial \sigma_{L_{jF}}}{\partial \omega_L} + \frac{\partial \mathbf{GR}_j(n)}{\partial \sigma_{L_{jN}}} \frac{\partial \sigma_{L_{jN}}}{\partial \omega_L} \right), \\
TSI_{\omega_A}(n) &= \frac{\omega_{A_{jj}}}{\mathbf{GR}_j(n)} \frac{\partial \mathbf{GR}_j(n)}{\partial \omega_{A_{jj}}}.
\end{aligned}$$

Consider the transient dynamics of the population changes in the Gulf region (cf. Table 6). In year 2, oceanic immatures are the most sensitive class. A one percent change in the survival proportion causes approximately a 0.7751 percent change in the population growth. In year 3, large neritic immature survival proportion is now the most sensitive (index 0.9180). This parameter continues to be most sensitive for years 4 through 6. The trends of the Gulf region are shared by Florida and the North (cf. Table 6).

There exist additional trends in all three regions. First, sensitivity indices for parameters associated with younger classes — fecundity (ζ) and survival proportions of hatchlings (γ) and oceanic immatures (ω_Y) — generally decrease over time. Second, the sensitivities indices associated with older classes — survival proportions of small (ω_I) and large neritic immatures (ω_L) and adults (ω_A) — generally increase.

3 Population Model with Oil Spill

To analyze the effects of an oil spill on the three populations, we introduce a spill into each of the three nesting regions. We did not trigger an oil spill in the Sargasso Sea because we are only considering offshore drilling. Thus, oceanic immature turtles, which live in the Sargasso Sea, are not affected by the oil.

Due to the lack of data on oil's toxicity to sea turtles, we use methodology similar to that of Reed et al. [16] and examine heuristic oil toxicities $\theta = 25, 50, 75,$ and 100%. In addition, we assume

Region	Year	ζ	γ	ω_Y	ω_I	ω_L	ω_A
G	2	0.1116	0.0988	0.7751	0.0648	0.5507	0.1336
	3	0.0988	0.0870	0.6039	0.1576	0.9180	0.2224
	4	0.0870	0.0762	0.4915	0.3042	1.2050	0.2915
	5	0.0762	0.0666	0.4328	0.4799	1.4220	0.3435
	6	0.0666	0.0582	0.4194	0.6662	1.5791	0.3808
F	2	0.1135	0.1002	0.7686	0.0634	0.5807	0.1358
	3	0.1002	0.0880	0.5967	0.1638	0.9652	0.2255
	4	0.0880	0.0768	0.4858	0.3209	1.2628	0.2945
	5	0.0768	0.0669	0.4307	0.5076	1.4852	0.3459
	6	0.0669	0.0583	0.4224	0.7042	1.6438	0.3822
N	2	0.1056	0.0952	0.7914	0.0684	0.4793	0.1279
	3	0.0944	0.0846	0.6218	0.1437	0.8045	0.2146
	4	0.0838	0.0747	0.5062	0.2659	1.0645	0.2835
	5	0.0741	0.0658	0.4394	0.4151	1.2666	0.3369
	6	0.0652	0.0579	0.4142	0.5762	1.4184	0.3767

Table 6: Transient sensitivity indices without an oil spill.

the toxicity decays with a half-life of one year. Thus, for years $n \geq 1$, oil-induced turtle mortality occurs at rate $\mu = (\theta)\left(2^{1-n}\right)$. Although it has been suggested that oil has greater effect on younger individuals [19], this is sufficiently inconclusive so as to require two scenarios.

Our first case is proportional toxicity: only eggs and hatchlings suffer the full impact of the oil. Fecundity is reduced to $\zeta_j(1-\mu)$. After spending one year in oil, the proportion of surviving hatchlings is $\gamma_j(1-\mu)$. For the remaining stage classes affected by oil, we assume the proportion of surviving turtles is

$$\left(1 - \frac{\mu}{[\text{mean age in class}]}\right) \cdot [\text{annual survival proportion in class}]$$

where the mean age in class is given in Table 7. For example, we suppose that 43 hatchlings die from oil exposure for every adult turtle that does.

Class		Age Range	Mean
Y	Oceanic immature	1–10 years	5.5 years
I	Small neritic immature	10–18.5 years	14.25 years
L	Large neritic immature	18.5–29 years	23.75 years
A	Adult	29–57 years	43 years

Table 7: Mean of class age range. Adult turtles are assumed to have a maximum lifespan of 57 years [15].

Our second case is equal toxicity: all stage classes (with the exception of oceanic immatures) are equally affected by oil. In this case, each annual survival proportion is reduced by a factor of $(1-\mu)$.

3.1 Deterministic Simulations with Oil Spill

We first introduce an oil spill into the deterministic population model (Section 2.2) in order to gain insights into the basic trends of the population dynamics. To observe the long-term impacts of an oil spill we run simulations over 20 years, using the fixed parameters taken from Table 3. The results of these simulations are found in Appendix A.

The introduction of an oil spill generally accelerates population decline. Without oil, the Gulf, Florida, and North populations decrease by 81.8%, 80.1%, and 84.7% respectively by year 20 (cf. Section 2.2). When we introduce a Florida oil spill with 100% toxicity and equal susceptibility, the Gulf, Florida, and North populations decrease by 82.4%, 97.2%, and 84.8% respectively by year 20 (cf. Table 11). North populations at 20 years are not substantially affected by a Florida oil spill for both equal and proportional susceptibilities at any toxicity level (cf. Tables 10 and 11). After introducing an oil spill in the North region with 100% toxicity and equal susceptibility (see Figure 5), 20-year populations in the Gulf, Florida, and North decrease by 86.3%, 85.4%, and 97.8% respectively (cf. Table 13). This case represents the largest difference between oiled and unoiled predictions for a non-local population in any simulated oil spills. Oil spills in the Gulf have a lesser effect on both Florida and North populations (cf. Tables 8 and 9).

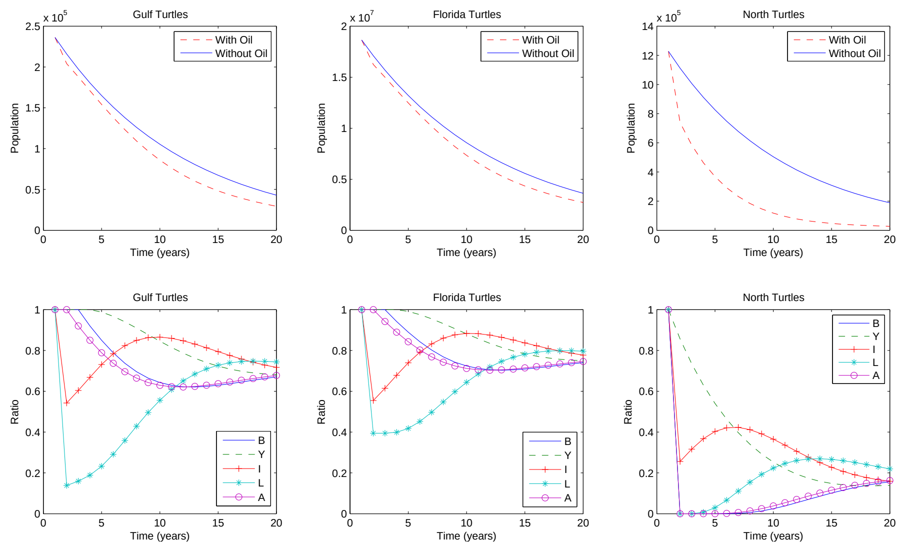

Figure 5: Deterministic simulation with 100% toxicity oil spill in North region with equal susceptibility.

3.2 Stochastic Simulations with Oil Spill

Next, we introduce an oil spill into our population model with varying parameters, which is described in Section 2.3. This allows us to better understand the range of possible population sizes. As described before, we use Latin Hypercube Sampling to select parameters from uniform distributions (cf. Table 4) annually during the 20-year simulations.

We introduce an oil spill into each nesting region and run 1000 simulations for each oil spill case (cf. Appendix C). Without oil, the mean Gulf, Florida, and North populations decrease by 81.6%, 80.3%, and 84.5% respectively by year 20 (cf. Section 2.3). When we introduce a 100% toxicity in a Florida oil spill with equal susceptibility, the mean Gulf, Florida, and North populations decrease by 82.2%, 97.2%, and 84.7% respectively by year 20 (cf. Table 18). This case represents the largest percent decrease in oiled population when compared to unoiled. By year 20, mean North populations are not substantially affected by a Florida oil spill at any toxicity or susceptibility (cf. Tables 17 and 18). In the case of a North oil spill with 100% toxicity affecting turtles equally (see Figure 6), the mean Gulf, Florida, and North populations decrease by 86.2%, 85.2%, and 97.8% respectively by year 20 (cf. Table 20). This case represents the largest difference between oiled and unoiled predictions for a non-local population in any of our simulated oil spills.

We consider the cases of varying turtle susceptibility, oil spill toxicity, and region. In all cases,

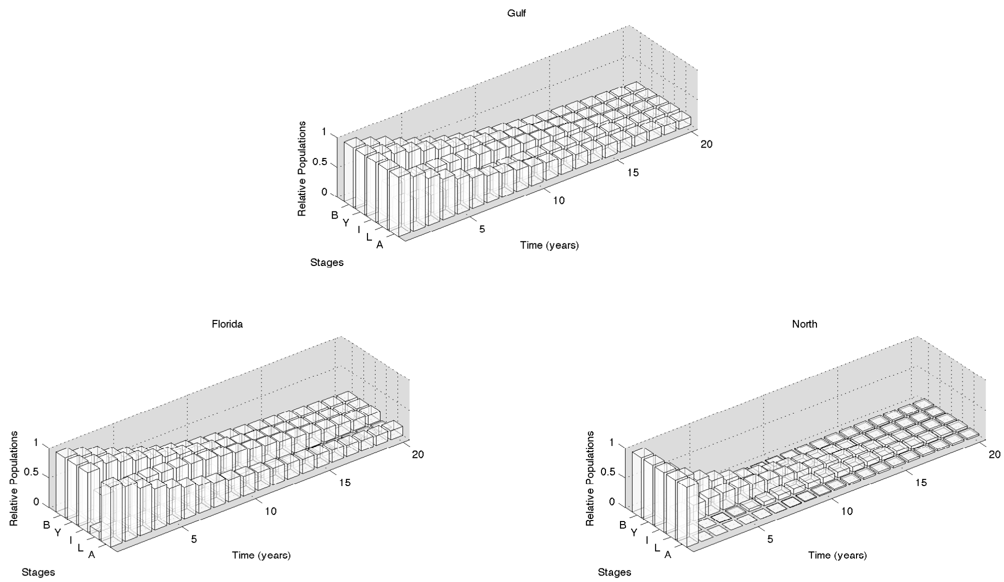

Figure 6: Stochastic simulation with 100% toxicity oil spill in North region and equal susceptibility.

equal susceptibility of turtles to oil toxicity has a greater effect on population means than proportional susceptibility, and the population that nests in the region of the oil spill has the greatest reduction in population mean. However, with the exception of the Florida spill's effect on the North, the remaining two populations experience a noticeable reduction in population mean.

The standard deviations of the 1000 simulations show the spread of the data. Due to the stochasticity of the parameters, the range of possible population sizes is visible. Furthermore, in all simulations, the variance of the data decreases over time. For example, for a 50% toxicity oil spill in the Gulf with equal susceptibility, the standard deviation at year 5 is 7148, whereas at year 20, it is 1914. This shows that simulated population sizes tend towards the mean population size rather than becoming more variable.

3.3 Transient Sensitivity Analysis with Oil Spill

We analyze transient sensitivity in order to examine the short-term effects of an oil spill on population dynamics. To extend our transient sensitivity analysis without oil (Section 2.4.2) to the case of an oil spill, we include the oil toxicity parameter θ. The decay of toxicity implies time-dependence of the projection matrix $\mathbf{M}(n)$. The population vector and transient growth rate can be written as follows:

$$\mathbf{P}(n) = \mathbf{e}\mathbf{M}(n-1)\mathbf{M}(n-2)\ldots\mathbf{M}(1)\mathbf{P}(1),$$

$$\mathbf{GR}(n) = \frac{\mathbf{e}\mathbf{M}(n-1)\mathbf{M}(n-2)\ldots\mathbf{M}(1)\mathbf{P}(1)}{\mathbf{e}\mathbf{M}(n-2)\mathbf{M}(n-3)\ldots\mathbf{M}(1)\mathbf{P}(1)} = \frac{||\mathbf{P}(n)||_1}{||\mathbf{P}(n-1)||_1}.$$

Thus, the transient sensitivity index with respect to parameter ρ is

$$\mathbf{TSI}_\rho(n) = \frac{\rho}{\mathbf{GR}(n)}\frac{\partial \mathbf{GR}(n)}{\partial \rho}.$$

It is not efficient to analytically derive $\dfrac{\partial \mathbf{GR}(n)}{\partial \rho}$; however, it may be numerically calculated. Appendix D provides TSI_ρ tables for each toxicity, region, and susceptibility to oil.

We first consider the transient sensitivity indices in the case that oil affects turtles proportionally. Our results are given in Table 21 of Appendix D. We found that growth rate is consistently the most sensitive to the oceanic immature survival proportion (ω_Y). The second most sensitive class switches from fecundity (ζ) to large neritic immature survival proportion (ω_L) in years 3–6. As before, sensitivity indices associated with the youngest classes — fecundity (ζ), hatchling survival proportion (γ) and oceanic immature (ω_Y) survival proportions — tend to decrease, while those associated with the oldest classes — large neritic immature (ω_I) and adult (ω_A) survival proportions — tend to increase. The small neritic immature survival proportion (ω_L) sensitivity index decreases for 1–2 years, then increases through year 6. The sensitivity index of oil toxicity (θ) is negative (as it is inversely related to growth rate) and relatively small, with decreasing magnitude over time.

We then consider the transient sensitivity indices in the case that oil affects turtles equally. Our results are given in Table 22 of Appendix D. As before, growth rate is most sensitive to changes in oceanic immature survival proportion (ω). In years 2–3, it is the next most sensitive to changes in fecundity (ζ); however, in years 4–6, it switches to large neritic immature survival proportion (ω_L). As in the case of proportional susceptibility, there is a general respective decrease and increase in sensitivity to the youngest and oldest classes with the exception of the sensitivities to small neritic immature survival proportion (ω_I). For the toxicities of 50%, 75%, and 100%, ω_I behaves the same; however, at $\theta = 25\%$, the magnitude of the sensitivity index increases in years 2–3.

An example of the transient sensitivity indices is shown in Figure 7, for an oil spill in the Gulf with oil toxicity $\theta = 0.5$.

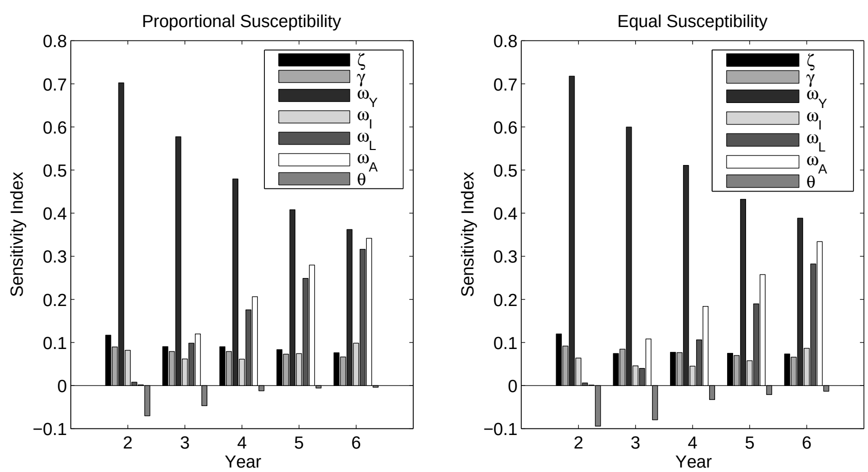

Figure 7: Transient sensitivity indices of the Gulf projection matrix with proportional (left) and equal (right) susceptibility to oil toxicity $\theta = 0.5$.

4 Discussion

A comparison of the deterministic and stochastic simulations shows similar trends in percentage change for both (cf. Appendices A–C). We conclude that an oil spill which equally affects the stages of the sea turtle would be more detrimental to the overall population than one which affects the stages proportionally. However, the analysis of our spatial results shows that an oil spill in the North with equal toxic susceptibility would have the greatest impact on other populations. Oil spills in the Gulf and Florida have minimal to almost non-existent impact on other populations.

While our deterministic and stochastic simulations display similar trends in percent change in population, the latter provides more information about potential population sizes. For example, in the case of a Gulf oil spill with 50% toxicity and equal susceptibility, the deterministic simulation gives a 5-year population of 100469, while the stochastic simulation gives a mean population of 100391 and a standard deviation of 7148. At 20 years, the deterministic population size is 15139, while the stochastic mean population is 15408 with a standard deviation of 1914. Although the deterministic population and stochastic mean population are similar, the stochastic simulations reveal more information about population trends. Potential populations are more variable in year 5, and at year 20 tend towards the mean population size.

To validate our model, we analyze the asymptotic sensitivity to verify that the behavior is comparable to previous loggerhead turtle models. We find oceanic immatures to be most sensitive with respect to asymptotic growth rate, with neritic immatures and adults moderately sensitive. Crouse et al. found that small immatures, large immatures, and subadults had the highest sensitivity [6]; these results were duplicated by Crowder et al. [7]. Heppell et al. also indicated that oceanic, small neritic, and large neritic immatures were the most sensitive stage classes [11]. Since our findings are similar, this supports the validity of our model.

To analyze the effects of an oil spill on the loggerhead population, we consider our model's transient sensitivity indices. Since toxicity is assumed to decay relatively quickly, transient dynamics are more relevant than long-term. The analysis of transient sensitivities after an oil spill shows that the growth rate is the most sensitive to the survival of oceanic immatures; however, since they are found exclusively in the Sargasso Sea, it is unnecessary to protect them (unless oil enters the central Atlantic Ocean). Instead, immediate efforts to preserve the population should focus on maintaining fecundity and hatchling survival by protecting breeding females and nests (e.g. relocating nests to beaches away from the spill). In later years (3–6), efforts should focus on increasing large neritic immature and adult survival (e.g. strictly enforcing the removal of turtles from oil burn zones).

5 Future Research

Our model is limited by the amount of quantitative data on the loggerhead sea turtle and would be improved by further research into the species. Since our model only includes female turtles, more research into sex ratios (particularly in the Gulf) or sex-specific differences in vital rates would be beneficial. Data on adult foraging migrations away from breeding grounds — similar to the study by Bowen [3] — would allow us to include this behavior in our model. Knowledge of the current populations of Atlantic loggerheads, of how oil changes turtle fecundity rates and the survival rates of each stage class, and of how this effect decays over time would strengthen our model.

Future research into the effects of an oil spill on the Atlantic loggerhead population might account for factors such as the spread of oil over time, hurricanes, and artificial cleanup methods such as oil dispersants and burning of oil slicks. Also, future models could simulate the effects of certain conservation methods such as nest relocation or stricter enforcement of the use of turtle excluding devices.

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A Deterministic Simulations

For our deterministic simulations with and without oil (oil toxicity 0), we provide six tables, differing by spill location (Gulf, Florida, or North) and turtle susceptibility to oil (equal or proportional). Each table provides the total population at 5 and 20 years; and the percent decrease in population (relative to the initial population).

		Population			Percent Decrease	
Region	Percent Toxicity	Year 1	Year 5	Year 20	Year 5	Year 20
G	0	236218	165008	42976	30.1	81.8
	25	236218	150209	40623	36.4	82.8
	50	236218	136859	38456	42.1	83.7
	75	236218	124933	36469	47.1	84.5
	100	236218	114403	34657	51.6	85.3
F	0	18646473	13205760	3621501	29.2	80.1
	25	18646473	13193813	3602934	29.2	80.7
	50	18646473	13182297	3585238	29.3	80.8
	75	18646473	13171194	3568370	29.4	80.9
	100	18646473	13160486	3552289	29.4	80.9
N	0	1227961	825911	188212	32.7	84.7
	25	1227961	825442	187629	32.8	84.7
	50	1227961	824989	187073	32.8	84.8
	75	1227961	824550	186543	32.9	84.8
	100	1227961	824126	186037	32.9	84.8

Table 8: Gulf oil spill with proportional susceptibility.

		Population			Percent Decrease	
Region	Percent Toxicity	Year 1	Year 5	Year 20	Year 5	Year 20
G	0	236218	165008	42976	30.1	81.8
	25	236218	125383	24705	46.9	89.5
	50	236218	100469	15139	57.5	93.6
	75	236218	82794	9464	65.0	96.0
	100	236218	70472	6151	70.2	97.4
F	0	18646473	13205760	3621501	29.2	80.1
	25	18646473	13052261	3392007	30.0	81.8
	50	18646473	12945934	3260040	30.6	82.5
	75	18646473	12864647	3174862	31.0	83.0
	100	18646473	12801086	3117902	31.3	83.3
N	0	1227961	825911	188212	32.7	84.7
	25	1227961	819825	180928	33.2	85.3
	50	1227961	815519	176707	33.6	85.6
	75	1227961	812248	173978	33.9	85.8
	100	1227961	809737	172160	34.1	86.0

Table 9: Gulf oil spill with equal susceptibility.

Region	Percent Toxicity	Population			Percent Decrease	
		Year 1	Year 5	Year 20	Year 5	Year 20
G	0	236218	165008	42976	30.1	81.8
	25	236218	164970	42921	30.2	81.8
	50	236218	164934	42867	30.2	81.9
	75	236218	164898	42817	30.2	81.9
	100	236218	164864	42768	30.2	81.9
F	0	18646473	13205760	3621501	29.2	80.1
	25	18646473	12005376	3419390	35.6	81.7
	50	18646473	10922939	3233419	41.4	82.7
	75	18646473	9956133	3063044	46.6	83.6
	100	18646473	9102811	2907751	51.2	84.4
N	0	1227961	825911	188212	32.7	84.7
	25	1227961	825851	188137	32.7	84.7
	50	1227961	825792	188066	32.8	84.7
	75	1227961	825736	187998	32.8	84.7
	100	1227961	825682	187933	32.8	84.7

Table 10: Florida oil spill with proportional susceptibility.

Region	Percent Toxicity	Population			Percent Decrease	
		Year 1	Year 5	Year 20	Year 5	Year 20
G	0	236218	165008	42976	30.1	81.8
	25	236218	164518	42285	30.4	82.1
	50	236218	164177	41887	30.5	82.3
	75	236218	163916	41630	30.6	82.4
	100	236218	163713	41458	30.7	82.4
F	0	18646473	13205760	3621501	29.2	80.1
	25	18646473	9982199	2077592	46.5	88.9
	50	18646473	7970845	1273274	57.3	93.2
	75	18646473	6546515	796636	64.9	95.7
	100	18646473	5554025	518143	70.2	97.2
N	0	1227961	825911	188212	32.7	84.7
	25	1227961	825129	187277	32.8	84.7
	50	1227961	824576	186735	32.9	84.8
	75	1227961	824156	186384	32.9	84.8
	100	1227961	823834	186151	32.9	84.8

Table 11: Florida oil spill with equal susceptibility.

Region	Percent Toxicity	Population			Percent Decrease	
		Year 1	Year 5	Year 20	Year 5	Year 20
G	0	236218	165008	42976	30.1	81.8
	25	236218	164738	42580	30.3	82.0
	50	236218	164478	42203	30.4	82.1
	75	236218	164226	41844	30.5	82.3
	100	236218	163983	41501	30.6	82.4
F	0	18646473	13205760	3621501	29.2	80.1
	25	18646473	13184391	3588292	29.3	80.8
	50	18646473	13163794	3556641	29.4	80.9
	75	18646473	13143936	3526472	29.5	81.1
	100	18646473	13124782	3497710	29.6	81.2
N	0	1227961	825911	188212	32.7	84.7
	25	1227961	754608	178404	38.5	85.5
	50	1227961	690233	169358	43.8	86.2
	75	1227961	632663	161048	48.5	86.9
	100	1227961	581783	153451	52.6	87.5

Table 12: North oil spill with proportional susceptibility.

Region	Percent Toxicity	Population			Percent Decrease	
		Year 1	Year 5	Year 20	Year 5	Year 20
G	0	236218	165008	42976	30.1	81.8
	25	236218	161528	38071	31.6	83.8
	50	236218	159102	35244	32.6	85.1
	75	236218	157250	33420	33.4	85.9
	100	236218	155809	32201	34.0	86.3
F	0	18646473	13205760	3621501	29.2	80.1
	25	18646473	12931211	3211048	30.7	82.8
	50	18646473	12741035	2975056	31.7	84.0
	75	18646473	12595645	2822766	32.5	84.9
	100	18646473	12481960	2720960	33.1	85.4
N	0	1227961	825911	188212	32.7	84.7
	25	1227961	636344	108864	48.2	91.1
	50	1227961	514828	66781	58.1	94.6
	75	1227961	428193	41718	65.1	96.6
	100	1227961	367690	27120	70.1	97.8

Table 13: North oil spill with equal susceptibility.

B Stochastic Simulations without Oil Spill

Table 14 is organized by nesting region and is subdivided by stage class and year (5 or 20). We record the mean populations of 1000 simulations and their standard deviation (STD) and quartiles (Q_1,Q_2, Q_3).

Region	Stage	Year	Mean	STD	Q_1	Q_2	Q_3
Gulf	Hatchling	5	24111	5443	20046	23563	27697
		20	6410	1536	5258	6260	7421
	Oceanic	5	121848	8618	115833	121591	127677
		20	32059	3467	29682	31902	34299
	Small neritic	5	17424	2143	15880	17295	18847
		20	4595	734	4066	4551	5069
	Large neritic	5	1464	73	1412	1461	1513
		20	390	48	355	387	420
	Adult	5	276	11	269	276	284
		20	73	7	69	73	78
	Total	5	165123	11787	156987	164799	172947
		20	43527	4740	40206	43308	46571
Florida	Hatchling	5	1967696	446848	1632260	1927212	2267061
		20	553635	133542	453599	540860	639804
	Oceanic	5	9734429	701620	9248681	9710971	10206964
		20	2705505	295284	2499021	2691998	2892107
	Small neritic	5	1375582	170949	1252443	1365902	1491190
		20	382793	61737	338964	378723	422553
	Large neritic	5	113379	5710	109315	113178	117223
		20	31798	3940	29063	31551	34335
	Adult	5	20620	807	20058	20610	21159
		20	5780	533	5416	5753	6123
	Total	5	13211706	955843	12540594	13183023	13856805
		20	3679511	404817	3400169	3655975	3941851
North	Hatchling	5	113557	25324	94490	111620	130639
		20	26457	6411	21653	25725	30644
	Oceanic	5	612189	42085	583053	611526	640531
		20	140731	15018	130219	139998	150406
	Small neritic	5	90837	11028	82910	90164	98372
		20	20863	3319	18476	20649	22981
	Large neritic	5	8022	382	7755	8007	8278
		20	1866	224	1708	1853	2009
	Adult	5	1666	62	1622	1664	1707
		20	389	34	365	387	411
	Total	5	826270	56758	786881	825463	863842
		20	190305	20419	175981	189370	203202

Table 14: Mean, standard deviation (STD), and quartiles (Q) of turtle populations during stochastic simulations without an oil spill.

C Stochastic Simulations with Oil Spill

We provide six tables, differing by oil spill location (Gulf, Florida, or North) and turtle susceptibility to oil (equal or proportional). Each table provides the mean population from the Gulf, Florida, or the North after 1000 simulations over 0, 5, and 20 years, in addition to the standard deviations (STD) and the percent decrease at 5 and 20 years.

		Population Mean			STD		Percent Decrease	
Region	Percent Toxicity	Year 1	Year 5	Year 20	Year 5	Year 20	Year 5	Year 20
G	0	236218	165123	43527	0	0	30.1	81.6
	25	236218	150402	41202	10521	4441	36.3	82.6
	50	236218	136984	38988	9607	4130	42.0	83.5
	75	236218	125006	36889	8833	3927	47.1	84.4
	100	236218	114458	35087	8204	3726	51.5	85.1
F	0	18646473	13211706	3679511	0	0	29.1	80.3
	25	18646473	13210814	3657311	941295	400505	29.2	80.4
	50	18646473	13198110	3639960	947012	39400	29.2	80.5
	75	18646473	13182887	3615907	947936	395120	29.3	80.6
	100	18646473	13170910	3602988	946752	393328	29.4	80.7
N	0	1227961	826270	190305	0	0	32.7	84.5
	25	1227961	826367	190001	57699	20166	32.7	84.5
	50	1227961	825800	189425	58108	19913	32.8	84.6
	75	1227961	825155	188503	58264	19984	32.8	84.6
	100	1227961	824646	188229	58164	19966	32.8	84.7

Table 15: Gulf oil spill: proportional susceptibility

		Population Mean			STD		Percent Decrease	
Region	Percent Toxicity	Year 1	Year 5	Year 20	Year 5	Year 20	Year 5	Year 20
G	0	236218	165123	43527	0	0	30.1	81.6
	25	236218	125485	25123	8644	2828	46.9	89.4
	50	236218	100391	15408	7148	1914	57.5	93.5
	75	236218	82711	9629	6361	1368	65.0	95.9
	100	236218	70342	6264	5759	1037	70.2	97.3
F	0	18646473	13211706	3679511	0	0	29.1	80.3
	25	18646473	13071829	3447665	931181	373361	29.9	81.5
	50	18646473	12951169	3309537	943043	362211	30.5	82.3
	75	18646473	12876672	3215872	929362	354560	30.9	82.8
	100	18646473	12808985	3159218	924221	346445	31.3	83.1
N	0	1227961	826270	190305	0	0	32.7	84.5
	25	1227961	820967	183430	57480	19256	33.1	85.1
	50	1227961	815775	178924	58197	18940	33.6	85.4
	75	1227961	812895	175797	57655	18741	33.8	85.7
	100	1227961	810163	174030	57328	18483	34.0	85.8

Table 16: Gulf oil spill: equal susceptibility

		Population Mean			STD		Percent Decrease	
Region	Percent Toxicity	Year 1	Year 5	Year 20	Year 5	Year 20	Year 5	Year 20
G	0	236218	165123	43527	0	0	30.1	81.6
	25	236218	164992	43396	11759	4764	30.2	81.6
	50	236218	164913	43493	11756	4720	30.2	81.6
	75	236218	164901	43412	11757	4797	30.2	81.6
	100	236218	164842	43274	11762	4739	30.2	81.7
F	0	18646473	13211706	3679511	0	0	29.1	80.3
	25	18646473	12007411	3458591	849096	380441	35.6	81.5
	50	18646473	10922728	3281228	770338	354579	41.4	82.4
	75	18646473	9957716	3105873	704734	340190	46.6	83.3
	100	18646473	9100669	2941383	650684	318229	51.2	84.2
N	0	1227961	826270	190305	0	0	32.7	84.5
	25	1227961	825952	189880	57951	20396	32.7	84.5
	50	1227961	825596	190451	57996	20247	32.8	84.5
	75	1227961	825683	190309	58114	20587	32.8	84.5
	100	1227961	825423	189854	58080	20355	32.8	84.5

Table 17: Florida oil spill: proportional susceptibility

		Population Mean			STD		Percent Decrease	
Region	Percent Toxicity	Year 1	Year 5	Year 20	Year 5	Year 20	Year 5	Year 20
G	0	236218	165123	43527	0	0	30.1	81.6
	25	236218	164515	42784	11762	4674	30.4	81.9
	50	236218	164128	42407	189139	20188	30.5	82.0
	75	236218	164091	42146	56811	729106	30.5	82.2
	100	236218	163621	41995	11741	4563	30.7	82.2
F	0	18646473	13211706	3679511	0	0	29.1	80.3
	25	18646473	9975827	2106030	690930	243897	46.5	88.7
	50	18646473	7956468	1293243	11494	4621	57.3	93.1
	75	18646473	6539535	811443	500236	116201	64.9	95.6
	100	18646473	5540621	529216	456121	89001	70.3	97.2
N	0	1227961	826270	190305	0	0	32.7	84.5
	25	1227961	825029	189139	825029	58147	32.8	84.6
	50	1227961	824182	188742	558161	163042	32.9	84.6
	75	1227961	824951	188362	58368	19999	32.8	84.7
	100	1227961	823317	188234	58143	20023	33.0	84.7

Table 18: Florida oil spill: equal susceptibility

Region	Percent Toxicity	Population Mean			STD		Percent Decrease	
		Year 1	Year 5	Year 20	Year 5	Year 20	Year 5	Year 20
G	0	236218	165123	43527	0	0	30.1	81.6
	25	236218	164770	43165	11558	4668	30.2	81.7
	50	236218	164372	42701	11604	4629	30.4	81.9
	75	236218	164139	42373	11486	4599	30.5	82.1
	100	236218	164090	42082	11681	4603	30.5	82.2
F	0	18646473	13211706	3679511	0	0	29.1	80.3
	25	18646473	13187036	3640509	929462	397332	29.3	80.5
	50	18646473	13156972	3601033	935096	394473	29.4	80.7
	75	18646473	13137790	3573065	924091	391512	29.5	80.8
	100	18646473	13134142	3549882	939773	391601	29.6	81.0
N	0	1227961	826270	190305	0	0	32.7	84.5
	25	1227961	754684	180507	51661	18991	38.5	85.3
	50	1227961	689784	170980	47439	17973	43.8	86.1
	75	1227961	632107	162681	43203	17049	48.5	86.8
	100	1227961	581980	155209	41249	16308	52.6	87.4

Table 19: North oil spill: proportional susceptibility

Region	Percent Toxicity	Population Mean			STD		Percent Decrease	
		Year 1	Year 5	Year 20	Year 5	Year 20	Year 5	Year 20
G	0	236218	165123	43527	0	0	30.1	81.6
	25	236218	161496	38592	11485	4167	31.6	83.7
	50	236218	159060	35654	11401	3896	32.7	84.9
	75	236218	157246	33852	11330	3727	33.4	85.7
	100	236218	155718	32605	11275	3612	34.1	86.2
F	0	18646473	13211706	3679511	0	0	29.1	80.3
	25	18646473	12931420	3257462	92458	354922	30.6	82.5
	50	18646473	12737792	3011968	916817	331843	31.7	83.8
	75	18646473	12595849	2861364	910789	318220	32.4	84.7
	100	18646473	12474065	2757396	907316	308216	33.1	85.2
N	0	1227961	826270	190305	0	0	32.7	84.5
	25	1227961	635932	110292	43590	12119	48.2	91.0
	50	1227961	514383	67660	36850	8154	58.1	94.5
	75	1227961	427241	42365	32642	5844	65.2	96.5
	100	1227961	366905	27619	30263	4512	70.1	97.8

Table 20: North oil spill: equal susceptibility

D Transient Sensitivity Indices with Oil Spill

The transient sensitivity indices are reported in two tables varying by the turtle susceptibility to oil (equal or proportional). Each table contains the toxicities and the corresponding nesting locations affected for years 2–6. The transient sensitivities are reported for the fecundity (ζ), survival proportions (γ, ω_Y, ω_I, ω_L, ω_A), and toxicity (θ).

Toxicity	Region	Year	ζ	γ	ω_Y	ω_I	ω_L	ω_A	θ
		2	0.1318	0.1009	0.6781	0.0799	0.0077	0.0016	-0.0340
		3	0.1008	0.0887	0.5680	0.0607	0.1054	0.1268	-0.0257
	G	4	0.0945	0.0829	0.4771	0.0612	0.1839	0.2142	-0.0063
		5	0.0853	0.0746	0.4081	0.0749	0.2550	0.2855	-0.0029
		6	0.0761	0.0665	0.3597	0.0986	0.3178	0.3426	-0.0027
		2	0.1347	0.1028	0.6752	0.0785	0.0074	0.0014	-0.0347
		3	0.0841	0.0900	0.5633	0.0594	0.1107	0.1290	-0.0261
0.25	F	4	0.0959	0.0838	0.4714	0.0611	0.1930	0.2171	-0.0063
		5	0.0862	0.0751	0.4022	0.0766	0.2669	0.2885	-0.0029
		6	0.0767	0.0667	0.3542	0.1024	0.3317	0.3450	-0.0027
		2	0.1237	0.0963	0.6861	0.0835	0.0084	0.0019	-0.0322
		3	0.0956	0.0849	0.5812	0.0641	0.0924	0.1207	-0.0245
	N	4	0.0906	0.0801	0.4930	0.0618	0.1439	0.2055	-0.0060
		5	0.0826	0.0728	0.4245	0.0712	0.2252	0.2765	-0.0028
		6	0.0745	0.0655	0.3749	0.0899	0.2828	0.3348	-0.0026
		2	0.1170	0.0896	0.7021	0.0819	0.0079	0.0016	-0.0703
		3	0.0903	0.0789	0.5771	0.0617	0.0983	0.1198	-0.0468
	G	4	0.0902	0.0789	0.4792	0.0611	0.1756	0.2060	-0.0123
		5	0.0835	0.0729	0.4079	0.0740	0.2486	0.2796	-0.0057
		6	0.0761	0.0663	0.3619	0.0984	0.3161	0.3417	-0.0041
		2	0.1196	0.0913	0.6995	0.0806	0.0076	0.0015	-0.0718
		3	0.0920	0.0801	0.5725	0.0605	0.1032	0.1219	-0.0476
0.5	F	4	0.0915	0.0798	0.4735	0.0610	0.1842	0.2089	-0.0125
		5	0.0844	0.0735	0.4019	0.0757	0.2602	0.2825	-0.0058
		6	0.0766	0.0666	0.3564	0.1021	0.3300	0.3442	-0.0027
		2	0.1095	0.0853	0.7090	0.0855	0.0087	0.0019	-0.0666
		3	0.0856	0.0754	0.5900	0.0651	0.0863	0.1139	-0.0444
	N	4	0.0864	0.0762	0.4934	0.0618	0.1541	0.1976	-0.0118
		5	0.0809	0.0712	0.4244	0.0705	0.2195	0.2707	-0.0055
		6	0.0744	0.0653	0.3772	0.0898	0.2812	0.3338	-0.0026
		2	0.1010	0.0774	0.7277	0.0842	0.0081	0.0017	-0.1094
		3	0.0801	0.0694	0.5854	0.0627	0.0913	0.1125	-0.0625
	G	4	0.0859	0.0748	0.4815	0.0609	0.1493	0.1979	-0.0181
		5	0.0818	0.0713	0.4077	0.0731	0.2422	0.2737	-0.0084
		6	0.0759	0.0662	0.3641	0.0981	0.3144	0.3407	-0.0041
		2	0.1033	0.0789	0.7255	0.0828	0.0078	0.0015	-0.1117
		3	0.0817	0.0705	0.5809	0.0614	0.0958	0.1144	-0.0636
0.75	F	4	0.0872	0.0757	0.4757	0.0608	0.1756	0.2007	-0.0184
		5	0.0827	0.0718	0.4017	0.0747	0.2535	0.2766	-0.0086
		6	0.0766	0.0665	0.3586	0.1019	0.3283	0.3433	-0.0041
		2	0.0944	0.0736	0.7334	0.0877	0.0089	0.0020	-0.1033
		3	0.0758	0.0663	0.5980	0.0660	0.0802	0.1070	-0.0592
	N	4	0.0822	0.0722	0.4974	0.0618	0.1469	0.1898	-0.0174
		5	0.0792	0.0695	0.4243	0.0698	0.2139	0.2650	-0.0083
		6	0.0742	0.0652	0.3795	0.0896	0.2796	0.3327	-0.0040
		2	0.0839	0.0642	0.7552	0.0866	0.0084	0.0017	-0.1515
		3	0.0703	0.0603	0.5927	0.0635	0.0842	0.1049	-0.0719
	G	4	0.0816	0.0709	0.4838	0.0608	0.1594	0.1899	-0.0237
		5	0.0800	0.0696	0.4076	0.0723	0.2360	0.2678	-0.0113
		6	0.0758	0.0660	0.3664	0.0979	0.3128	0.3398	-0.0055
		2	0.0859	0.0656	0.7536	0.0853	0.0081	0.0016	-0.1547
		3	0.0717	0.0613	0.5882	0.0623	0.0883	0.1067	-0.0734
1	F	4	0.0829	0.0717	0.4780	0.0606	0.2367	0.1926	-0.0241
		5	0.0809	0.0702	0.4016	0.0738	0.2470	0.2707	-0.0114
		6	0.0764	0.0664	0.3609	0.1016	0.3266	0.3424	-0.0055
		2	0.0782	0.0609	0.7596	0.0900	0.0092	0.0021	-0.1433
		3	0.0664	0.0576	0.6052	0.0668	0.0740	0.0997	-0.0680
	N	4	0.0781	0.0684	0.4998	0.0617	0.1400	0.1820	-0.0227
		5	0.0774	0.0679	0.4243	0.0691	0.2084	0.2593	-0.0109
		6	0.0741	0.0650	0.3819	0.0894	0.2780	0.3316	-0.0053

Table 21: Transient sensitivity for the oil model with proportional susceptibility.

Toxicity	Region	Year	ζ	γ	ω_Y	ω_I	ω_L	ω_A	θ
0.25	G	2	0.1332	0.1020	0.6854	0.0713	0.0068	0.0014	-0.0449
		3	0.0920	0.0920	0.5809	0.0528	0.0691	0.1208	-0.0502
		4	0.0874	0.0816	0.4940	0.0522	0.1442	0.2026	-0.0183
		5	0.0808	0.0729	0.4206	0.0660	0.2231	0.2740	-0.0114
		6	0.0748	0.0663	0.3729	0.0925	0.3005	0.3390	-0.0138
	F	2	0.1361	0.1039	0.6822	0.0700	0.0066	0.0013	-0.0454
		3	0.0766	0.0934	0.5767	0.0518	0.0725	0.1230	-0.0509
		4	0.0886	0.0826	0.4888	0.0520	0.1514	0.2054	-0.0187
		5	0.0816	0.0734	0.4150	0.0673	0.2336	0.2769	-0.0116
		6	0.0754	0.0666	0.3676	0.0960	0.3139	0.3415	-0.0140
	N	2	0.1251	0.0974	0.6938	0.0745	0.0075	0.0017	-0.0437
		3	0.0875	0.0878	0.5933	0.0557	0.0608	0.1149	-0.0480
		4	0.0840	0.0789	0.5086	0.0532	0.1266	0.1942	-0.0173
		5	0.0784	0.0711	0.4363	0.0632	0.1970	0.2653	-0.0107
		6	0.0732	0.0653	0.3878	0.0845	0.2671	0.3309	-0.0129
0.5	G	2	0.1196	0.0915	0.7176	0.0639	0.0061	0.0012	-0.0941
		3	0.0744	0.0844	0.5996	0.0458	0.0398	0.1080	-0.0794
		4	0.0771	0.0764	0.5106	0.0449	0.1061	0.1837	-0.0325
		5	0.0750	0.0697	0.4322	0.0577	0.1895	0.2574	-0.0209
		6	0.0734	0.0659	0.3882	0.0865	0.2820	0.3339	-0.0134
	F	2	0.1222	0.0932	0.7147	0.0629	0.0059	0.0012	-0.0951
		3	0.0756	0.0858	0.5957	0.0450	0.0417	0.1100	-0.0805
		4	0.0781	0.0773	0.5058	0.0445	0.1113	0.1863	-0.0332
		5	0.0758	0.0702	0.4268	0.0587	0.1984	0.2602	-0.0214
		6	0.0739	0.0662	0.3830	0.0897	0.2947	0.3367	-0.0137
	N	2	0.1121	0.0873	0.7255	0.0668	0.0067	0.0015	-0.0915
		3	0.0708	0.0804	0.6110	0.0481	0.0353	0.1025	-0.0763
		4	0.0741	0.0737	0.5242	0.0461	0.0931	0.1760	-0.0309
		5	0.0728	0.0680	0.4473	0.0558	0.1672	0.2490	-0.0198
		6	0.0717	0.0648	0.4028	0.0793	0.2502	0.3255	-0.0126
0.75	G	2	0.1045	0.0801	0.7531	0.0559	0.0053	0.0011	-0.1482
		3	0.0583	0.0763	0.6144	0.0387	0.0215	0.0952	-0.0922
		4	0.0678	0.0713	0.5252	0.0388	0.0682	0.1658	-0.0435
		5	0.0697	0.0666	0.4432	0.0507	0.1601	0.2415	-0.0289
		6	0.0718	0.0654	0.4032	0.0809	0.2639	0.3285	-0.0195
	F	2	0.1069	0.0816	0.7503	0.0550	0.0052	0.0010	-0.1498
		3	0.0593	0.0776	0.6107	0.0380	0.0225	0.0969	-0.0935
		4	0.0686	0.0722	0.5207	0.0384	0.0802	0.1682	-0.0442
		5	0.0704	0.0671	0.4380	0.0514	0.1677	0.2442	-0.0301
		6	0.0724	0.0658	0.3981	0.0837	0.2759	0.3231	-0.0194
	N	2	0.0979	0.0763	0.7603	0.0583	0.0059	0.0013	-0.1438
		3	0.0556	0.0726	0.6250	0.0405	0.0193	0.0902	-0.0884
		4	0.0652	0.0688	0.5379	0.0401	0.0671	0.1587	-0.0414
		5	0.0677	0.0649	0.4578	0.0495	0.1412	0.2336	-0.0274
		6	0.0701	0.0642	0.4175	0.0744	0.2337	0.3197	-0.0183
1	G	2	0.0880	0.0674	0.7922	0.0471	0.0045	0.0009	-0.2078
		3	0.0438	0.0680	0.6253	0.0317	0.0110	0.0826	-0.0858
		4	0.0593	0.0664	0.5378	0.0337	0.0539	0.1488	-0.0517
		5	0.0647	0.0636	0.4536	0.0448	0.1346	0.2264	-0.0356
		6	0.0702	0.0648	0.4180	0.0756	0.2463	0.3226	-0.0251
	F	2	0.0900	0.0687	0.7898	0.0463	0.0043	0.0009	-0.2102
		3	0.0445	0.0691	0.6218	0.0312	0.0114	0.0841	-0.0873
		4	0.0600	0.0672	0.5336	0.0333	0.0807	0.1510	-0.0526
		5	0.0653	0.0642	0.4486	0.0452	0.1410	0.2290	-0.0363
		6	0.0708	0.0652	0.4130	0.0781	0.2577	0.3139	-0.0257
	N	2	0.0823	0.0641	0.7986	0.0490	0.0049	0.0011	-0.2014
		3	0.0418	0.0646	0.6354	0.0331	0.0101	0.0782	-0.0816
		4	0.0571	0.0639	0.5499	0.0349	0.0474	0.1424	-0.0494
		5	0.0628	0.0620	0.4677	0.0441	0.1186	0.2188	-0.0338
		6	0.0685	0.0636	0.4320	0.0697	0.2178	0.3135	-0.0236

Table 22: Transient sensitivity for the oil model with equal susceptibility.