



# Assessing *Karenia brevis* red tide as a mortality factor of sea turtles in Florida, USA

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**ABSTRACT:** Data on *Karenia brevis* red tides ( $\geq 10^5$  cells  $l^{-1}$ ) and on dead or debilitated (i.e. stranded) Kemp's ridleys *Lepidochelys kempii*, loggerheads *Caretta caretta*, green turtles *Chelonia mydas*, hawksbills *Eretmochelys imbricata*, and leatherbacks *Dermochelys coriacea* documented in Florida during 1986–2013 were evaluated to assess red tides as a sea turtle mortality factor. Unusually large numbers of stranded sea turtles were found coincident with red tides primarily along Florida's Gulf coast but also along a portion of Florida's Atlantic coast. These strandings were mainly adult and large immature loggerheads and Kemp's ridleys, and small immature green turtles and hawksbills. Unusually large numbers of stranded leatherbacks never coincided with red tide. For the 3 most common species, results of stranding data modeling, and of investigations that included determining brevetoxin concentrations in samples collected from stranded turtles, all indicated that red tides were associated with greater and more frequent increases in the numbers of stranded loggerheads and Kemp's ridleys than in the number of stranded green turtles. The mean annual number of stranded sea turtles attributed to *K. brevis* red tide was 80 (SE = 21.6, range = 2–338). Considering typical stranding probabilities, the overall mortality was probably 5–10 times greater. Red tide accounted for a substantial portion of all stranded loggerheads (7.1%) and Kemp's ridleys (17.7%), and a smaller portion of all stranded green turtles (1.6%). Even though *K. brevis* red tides occur naturally, the mortality they cause needs to be considered when managing these threatened and endangered species.

**KEY WORDS:** Sea turtles · *Karenia brevis* · Mortality · Brevetoxin · Red tide · Florida

## 1. INTRODUCTION

The term 'red tide' generally describes a harmful algal bloom (HAB). In the Gulf of Mexico, it refers specifically to a bloom of the toxic dinoflagellate *Karenia brevis*, which can appear as a reddish discoloration of the water (Tester & Steidinger 1997). *K. brevis* regularly occurs in background concentrations ( $\leq 10^3$  cells  $l^{-1}$ ) throughout the Gulf of Mexico and the South Atlantic Bight (Tester & Steidinger 1997). Blooms are characterized by any cell concentrations above that background level (Steidinger 2009).

The initiation of a *K. brevis* bloom is a complex process that begins in oligotrophic waters of the Gulf of Mexico from 18 to 74 km offshore (Tester & Steidinger 1997, Walsh & Steidinger 2001, Walsh et al. 2006, Vargo et al. 2008, Weisberg et al. 2016). Blooms of *K. brevis* usually develop along Florida's Gulf coast (Tester & Steidinger 1997), but the Florida Current and Gulf Stream can transport these blooms to Florida's Atlantic coast and occasionally into the rest of the South Atlantic Bight (Murphy et al. 1975, Tester et al. 1991). These red tides are natural phenomena that have occurred in the Gulf of Mexico for at least several hundred years (Tester & Steidinger 1997, Steidinger 2009). If a red tide is transported to a nearshore area, nutrient inputs from coastal pollution might help maintain and intensify it, but pollution does not appear to influence the initiation of these blooms (Steidinger & Ingle 1972, Weisberg et al. 2016).

*K. brevis* produces potent neurotoxins known as brevetoxins (Baden 1989, Landsberg 2002). Marine animal mortalities associated with *K. brevis* red tides have been well documented since 1844 (reviewed by Landsberg 2002), but the causative dinoflagellate was not identified until more than a century later (Davis 1948). It was another 20 yr before the brevetoxins were first characterized (McFarren et al. 1965). Fish are most commonly killed during these red tides (reviewed by Landsberg 2002), but substantial mortality has often been documented in higher vertebrates such as sea turtles (cheloniids; Fauquier et al. 2013a), birds (waterfowl, seabirds, and shorebirds; Forrester et al. 1977, Kreuder et al. 2002, van Deventer et al. 2012, Fauquier et al. 2013b), and marine mammals (bottlenose dolphins *Tursiops truncatus* and Florida manatees *Trichechus manatus latirostris*; O'Shea et al. 1991, Bossart et al. 1998, Flewelling et al. 2005, Twiner et al. 2012). Mortality of higher vertebrates due to red tide is anticipated when concentrations of *K. brevis* are  $\geq 10^5$  cells  $l^{-1}$  (Kreuder et al.

2002, Landsberg et al. 2009, Twiner et al. 2011, Fauquier et al. 2013a,b).

Higher vertebrates can inhale aerosolized brevetoxin, but ingesting food containing brevetoxin appears to be the most significant means of exposure (Landsberg et al. 2009). Clinical signs of brevetoxicosis among higher vertebrates include lethargy, weakness, lack of coordination (i.e. the inability to stay upright, or swimming in circles), and unusual muscular activity (e.g. generalized twitching, spasms, head bobbing, seizures) (Quick & Henderson 1975, Bossart et al. 1998, Castle et al. 2013, Fauquier et al. 2013a,b). Necropsies of these animals typically reveal no specific gross or pathologic abnormalities related to brevetoxicosis (Kreuder et al. 2002, Twiner et al. 2012, Fauquier et al. 2013a).

The role of *K. brevis* red tides in marine animal mortalities is not always straightforward. For example, in some mortality events involving Florida manatees and bottlenose dolphins, carcasses had relatively high concentrations of brevetoxin in collected samples even though the mortalities did not coincide with a red tide. In such cases, brevetoxin vectors (e.g. fish) or brevetoxin reservoirs (e.g. seagrass) resulted in either remote or delayed exposure (Flewelling et al. 2005). Thus, identifying a red tide as the cause of a mortality event may depend entirely on being able to determine the significance of any brevetoxin found in carcasses.

The effects of brevetoxin are dose-dependent, and not every exposure is lethal (Cocilova & Milton 2016). Higher marine vertebrates living in areas where *K. brevis* occurs can test positive for brevetoxin when not associated with a large-scale mortality event (Fire et al. 2007, Atwood 2008), when not suspected to have died from brevetoxicosis (Flewelling 2008, Capper et al. 2013), or when alive and found to be behaving normally (Twiner et al. 2011, Perrault et al. 2014, 2016). The brevetoxin concentrations documented under these circumstances are the best available representatives of baseline (i.e. probable subclinical) exposure, and higher concentrations documented during large-scale mortality events coincident with red tides probably indicate the amounts of brevetoxin necessary to cause acute mortality (Fire et al. 2007, Landsberg et al. 2009, Twiner et al. 2011).

Research on the mortality of higher vertebrates associated with *K. brevis* red tides has typically focused on 1 or 2 individual mortality events over relatively short periods (2 mo to 2 yr; Forrester et al. 1977, Geraci 1989, O'Shea et al. 1991, Bossart et al. 1998, Flewelling et al. 2005, van Deventer et al. 2012, Fauquier et al. 2013a,b). In one longer-term study,

Twiner et al. (2012) examined mortality of bottlenose dolphins related to red tides over an 8 yr period along a 300 km stretch of the northern Gulf coast of Florida. We are not aware of any similar, long-term assessments of sea turtle mortality associated with red tides. For threatened and endangered species such as sea turtles, thoroughly characterizing threats like red tides and regularly quantifying the mortality they cause is essential for successful recovery planning (Clark et al. 2002, Lawler et al. 2002).

The Florida Fish and Wildlife Conservation Commission coordinates many long-term state-wide monitoring programs. Among these are the Florida Sea Turtle Stranding and Salvage Network (FLSTSSN) and HAB monitoring. Dead, sick, and injured sea turtles (i.e. stranded sea turtles) have been documented in some areas of Florida since 1980, and a consistent effort statewide began in 1986. Six species of sea turtles have been documented in Florida as strandings and include loggerheads *Caretta caretta*, green turtles *Chelonia mydas*, Kemp's ridleys *Lepidochelys kempii*, hawksbills *Eretmochelys imbricata*, leatherbacks *Derموchelys coriacea*, and olive ridleys *L. olivacea*. The HAB monitoring program has been documenting *K. brevis* red tides in Florida since 1954, and more regular monitoring (especially along the southern Gulf coast of Florida) began in the mid-1990s (Steidinger 2009). Our objective was to assess *K. brevis* red tides as a mortality factor of sea turtles by species in Florida during 1986–2013 using data from these 2 monitoring programs. We evaluated these data to determine if numbers of stranded sea turtles (as an index of sea turtle mortality) increased coincident with red tide and during which months and in what areas of Florida this occurred. We also measured brevetoxin concentrations in samples taken from strandings to determine baseline exposure and to characterize concentrations suspected of causing acute mortality. Finally, we used this information to estimate the number of stranded sea turtles and the likely overall sea turtle mortality in Florida that could be attributed to red tide.

## 2. MATERIALS AND METHODS

### 2.1. Collection of data on stranded sea turtles and red tides

For the period of 1986–2013, we used data collected on stranded sea turtles by the FLSTSSN (methodology described by Foley et al. 2005) and data on cell concentrations of *Karenia brevis* in seawater samples col-

lected by the HAB monitoring program (methodology described by Steidinger 2009). For the purposes of the present study, we defined a red tide as a *K. brevis* bloom with a concentration of  $\geq 10^5$  cells  $l^{-1}$ . The discovery locations of stranded sea turtles and of red tides were grouped by zone (Fig. 1), and the dates on which they were documented were grouped by month.

### 2.2. Data analysis

To determine if numbers of stranded sea turtles in Florida were significantly elevated during red tides while accounting for other factors that could influence stranding numbers, we first constructed Poisson regressions relating numbers of strandings (per month per zone) to various predictor variables (including red tide) over a 28 yr period (1986–2013). This was done for each of the 3 most common species (loggerheads, green turtles, and Kemp's ridleys). The less common species (hawksbills, leatherbacks, and olive ridleys) were not modeled because they accounted for relatively few strandings (mean of  $< 25$   $yr^{-1}$  by species), especially those coincident with red tide (mean of  $< 2$   $yr^{-1}$  by species).

The predictor variables included in the regressions were month, zone, lag count (LCT: the number of stranded turtles found in the same zone during the previous month), ongoing red tide (ORT: whether red tide was found in the same zone and during the same month as stranded turtles), and lag red tide (LRT: whether red tide was found in the same zone as stranded turtles but during the previous month and not during the same month). Month and zone were included because numbers of stranded turtles varied consistently by both, with the highest numbers of strandings occurring during the spring and the lowest occurring during the fall, and with some zones always having more strandings than other zones. LCT was included because high (or low) stranding numbers in a zone for a given month could be related to high (or low) stranding numbers in the same zone during the previous month. ORT was included to account for the effect of an ongoing red tide on stranding numbers. LRT was included to account for any effects of red tide on the numbers of stranded turtles that may have continued for 1 mo after the red tide dissipated (delayed mortality).

The 2 simplest Poisson regression models included effects of month, zone, ORT, and LRT, with and without an interaction between month and ORT. The simple models were then enhanced to include LCT with different combinations of interactions between

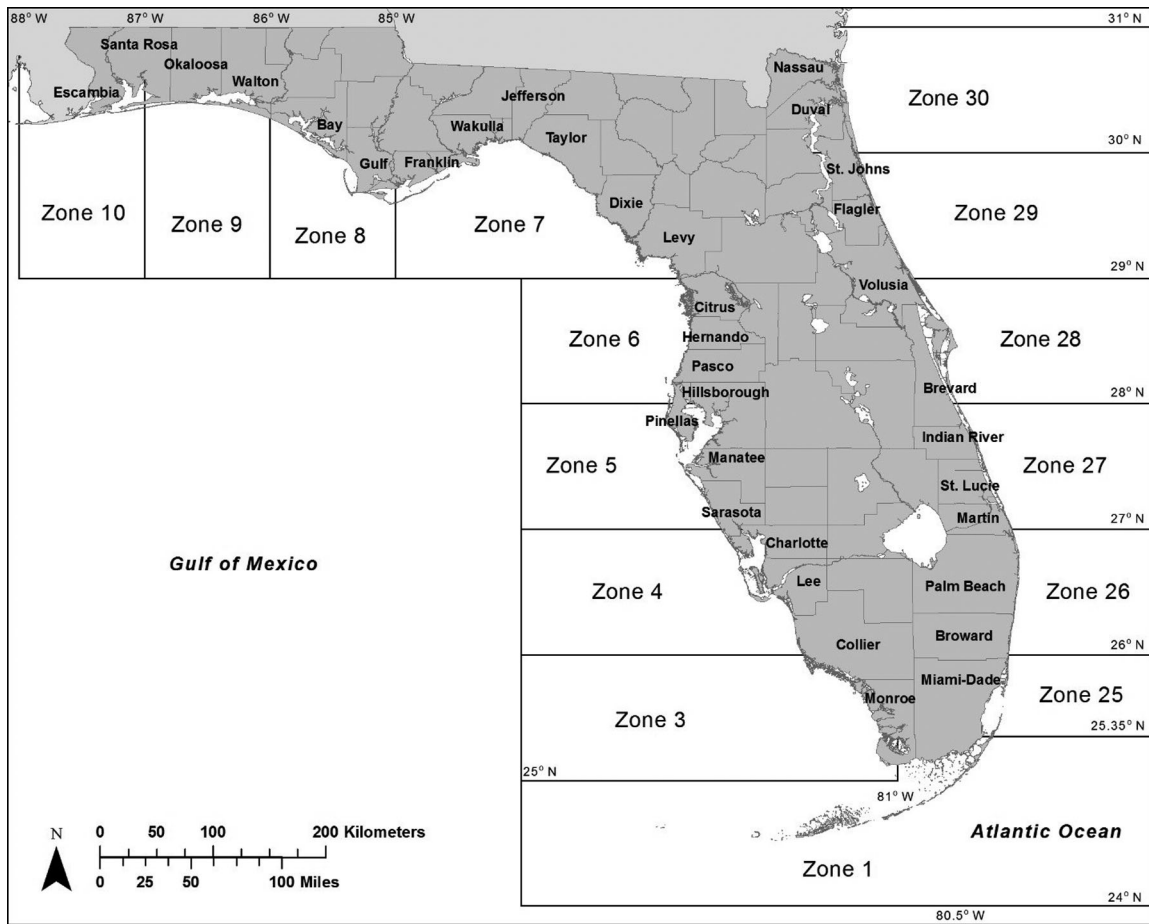


Fig. 1. Modified National Marine Fisheries Service Statistical Zones and coastal counties in Florida. For this study, the original Zones 1, 2, and 24, and the southern portion of Zone 25 were combined to create a modified Zone 1. The original Zone 25 was reduced (southern boundary at 25.35° N instead of 25.00° N). In Zones 10 and 30, only stranded sea turtles found in Florida are reported here

month, ORT, and LRT. All regression models were fit in R (R Development Core Team 2008), and Akaike’s information criterion (AIC; Akaike 1973) was used to determine the most plausible model. The Poisson regression outputs are displayed in Table 1.

The Poisson regressions exhibited overdispersion and temporally autocorrelated residuals. To account for this, we constructed a Bayesian overdispersed Poisson regression for each species. We included all predictor variables and interactions in the Bayesian models because the corresponding Poisson regression carried substantial AIC weight (see Table 1). However, in the Bayesian model, the effect of zone was treated as a random effect. The Bayesian models also included an occasion-specific random effect (unique for the month and year within each zone) that was multivariate-normally distributed with means of 0 and an autoregressive covariance matrix estimated from the data. Consequently, a random effect term for

each count could be estimated that accounted for both overdispersion and temporal autocorrelation (Kéry & Schaub 2010). This model was expressed as follows:

$$\begin{aligned}
 y_{z,y,m} &\sim Poi(\lambda_i) \\
 \log(\lambda_i) &= X\beta_j + \epsilon_{zone} + \epsilon_{occ} \\
 \epsilon_{zone} &\sim Norm(0, \sigma_{zone}) \\
 \epsilon_{occ} &\sim MVNorm(0, \Sigma_{occ(AR)})
 \end{aligned}$$

$$\Sigma_{occ(AR)} = \sigma_{z,occ}^2 \times \begin{bmatrix} 1 & \rho & \rho^2 & \dots & \rho^{n-1} \\ \rho & 1 & \rho & \dots & \rho^{n-2} \\ \rho^2 & \rho & 1 & \dots & \rho^{n-3} \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ \rho^{n-1} & \rho^{n-2} & \rho^{n-3} & \dots & 1 \end{bmatrix}$$

where  $y_{z,y,m}$  is the number of strandings in a given zone, year, and month;  $\lambda_i$  is the mean number of expected strandings for a particular count;  $X$  is a

Table 1. Output of regression models constructed to investigate the relationship between numbers of dead or debilitated (i.e. stranded) sea turtles by species and *Karenia brevis* red tides in Florida during 1986–2013. The response variable was the number of stranded sea turtles per month per zone. Predictor variables were month (M), zone (Z), lag count (LCT, the number of stranded turtles found in the same zone during the previous month), ongoing red tide (ORT, whether red tide was present in the same zone and during the same month as stranded turtles), and lag red tide (LRT, whether red tide was present in the same zone as stranded turtles but during the previous month and not during the same month). We defined a red tide as a *K. brevis* bloom with a concentration of  $\geq 10^5$  cells  $l^{-1}$ . Model outputs were Pearson's correlation coefficient (r), root mean square error (RMSE), Akaike's information criterion score (AIC), and AIC weights (AIC<sub>w</sub>). na: not applicable

Regression model	Loggerhead				Green turtle				Kemp's ridley				
	r	RMSE	AIC	AIC <sub>w</sub>	r	RMSE	AIC	AIC <sub>w</sub>	r	RMSE	AIC	AIC <sub>w</sub>	
Standard Poisson	M+Z+ORT+LRT+LCT+(M×ORT)+(M×LRT)	0.70	4.03	23290.50	0.72	0.65	3.02	17716.60	0.63	0.51	1.20	8656.60	0.71
	M+Z+ORT+LRT+LCT+(M×ORT)+ (M×LRT)+(LRT×ORT)	0.70	4.03	23292.40	0.28	0.65	3.02	17717.60	0.37	0.51	1.20	8658.40	0.29
	M+Z+ORT+LRT+LCT+(M×ORT)+(LRT×ORT)	0.69	4.05	23310.50	0.00	0.65	3.05	17767.40	0.00	0.50	1.20	8671.40	0.00
Bayesian Poisson	M+Z+ORT+LRT+LCT+(LRT×ORT)	0.69	4.07	23361.20	0.00	0.64	3.07	17800.00	0.00	0.44	1.25	8781.00	0.00
	M+Z+ORT+LRT+LCT+(M×ORT)	0.69	4.05	23310.20	0.00	0.65	3.05	17766.40	0.00	0.50	1.20	8670.00	0.00
	M+Z+ORT+LRT+LCT	0.69	4.07	23360.50	0.00	0.64	3.07	17798.50	0.00	0.44	1.25	8779.10	0.00
	M+Z+ORT+LRT+(M×ORT)	0.66	4.20	24599.10	0.00	0.61	3.10	19324.50	0.00	0.48	1.20	9002.50	0.00
	M+Z+ORT+LRT+(M×ORT)+ (M×LRT)+(LRT×ORT)	0.66	4.22	24666.10	0.00	0.61	3.11	19365.70	0.00	0.43	1.23	9146.70	0.00

design matrix;  $\beta_j$  is a vector of unknown regression parameters;  $\epsilon_{zone}$  is the random effect of zone;  $\epsilon_{occ}$  is the occasion-specific temporal random effect; and  $\Sigma_{occ(AR)}$  is the autoregressive covariance matrix of the occasion-specific temporal random effect, which included parameters for the zone-specific standard deviation of the random effect  $\sigma_{z,occ}$  and the correlation among occasions  $\rho$ .

The Bayesian Poisson regressions were fit using Markov Chain Monte Carlo (MCMC) in program JAGS (Plummer 2003). All parameters were given diffuse priors. For all regression parameters, a normal prior distribution with a mean of 0 and a standard deviation of 100 was used. For all standard deviations, a uniform prior distribution from 0 to 20 was used. For the correlation parameter  $\rho$  of the occasion-specific random effect covariance matrix, a uniform distribution from -1 to 1 was used. For the MCMC chains, we ran an adaptive phase of 20 000 iterations, after which we discarded a burn-in period of 10 000 iterations, and then followed that with a sampling of 20 000 iterations. Convergence of the chains to the stationary distribution was determined by using  $\hat{R}$  (Gelman & Rubin 1992). Once values of  $\hat{R}$  were <1.1 for all parameters, we considered the model as converged. For all estimated parameters, 95% credible intervals were based on the 2.5 and 97.5 percentiles of the posterior distribution. The outputs of the Bayesian Poisson regressions are also shown in Table 1.

To assess their significance, we used exponentiation to convert the parameter estimates of the Bayesian Poisson regressions to multiplicative effects on numbers of stranded sea turtles (Gelman & Hill 2007). We also determined the combined multiplicative effects of ORT and LRT (both [ORT + LRT + ORT×LRT] and [ORT + LRT]) on the numbers of stranded turtles to assess the significance of at least 2 consecutive months of red tide (CRT). The predicted effects of ORT, LRT, and CRT were modeled monthly, while the predicted effects of LCT and all other parameters were modeled annually. We considered any multiplicative effects with 95% credible intervals that did not overlap 1 as significant.

### 2.3. Necropsies and brevetoxin analysis

Necropsies were conducted on a subset of stranded sea turtles following the guidance of Wolke & George (1981). Samples collected for brevetoxin testing included 1 or more of the following: liver, lung, kidney, contents of the upper gastrointestinal tract (esophagus, stomach, or small intestine), and contents of

the lower gastrointestinal tract including feces. From live-stranded sea turtles, fecal samples were collected opportunistically, and blood was collected as described by Owens & Ruiz (1980). All samples were stored frozen at  $-20^{\circ}\text{C}$ .

Samples for brevetoxin testing were processed as described by Whitney et al. (1997) (prior to 1998) or by Fauquier et al. (2013a). Brevetoxin-3 (PbTx-3)-concentrations were measured by competitive ELISA (Naar et al. 2002) with modifications described by Flewelling (2008). We report values as ng PbTx-3 eq.  $\text{g}^{-1}$  for all samples except for blood and plasma, for which we report values as ng PbTx-3 eq.  $\text{ml}^{-1}$ . The lower brevetoxin concentration detection limits for Steuthe assays were 5 ng  $\text{g}^{-1}$  for tissue samples, gut contents, and feces, and 1 ng  $\text{ml}^{-1}$  for blood and plasma. For statistical analyses, we considered a result below the detection limit as a 0.

Samples were grouped according to the red tide status where the stranded turtle was found. These groups were (1) samples from stranded turtles found in a zone during a month without a red tide and without a red tide during the previous 3 mo (i.e. the no red tide group), (2) samples from stranded turtles found in a zone during a month without a red tide but where a red tide had occurred during at least 1 of the previous 3 mo (i.e. the recent red tide group), and (3) samples from stranded turtles found in a zone during a month with red tide (i.e. the red tide group). We chose the no red tide sample group to characterize baseline concentrations of brevetoxin (if it was represented by at least 5 samples). We separated the recent red tide sample group from the no red tide sample group (both were from stranded turtles found when there was no red tide) because brevetoxins are known to persist for up to 3 mo in diet items of sea turtles (benthic invertebrates and seagrasses; Dickey et al. 1999 and Flewelling et al. 2005, respectively). We chose the red tide sample group to identify concentrations of brevetoxin suspected of causing acute mortality.

Brevetoxin concentrations were compared to detect any differences among the samples from different groups for each species. Only groups with at least 5 samples were used in the comparisons. None of the groups had brevetoxin concentrations that were normally distributed (as determined by Shapiro-Wilk normality tests), so non-parametric analyses were used. First, a Wilcoxon rank sum test was used to compare brevetoxin concentrations in the red tide group to those in the recent red tide group. If there was no difference ( $p \geq 0.05$ ), these 2 groups were combined, and then the brevetoxin concentrations in that combined group were compared to those in the

no red tide group using the same test (differences considered significant at  $p < 0.01$ ). If there was a difference in the brevetoxin concentrations between the red tide group and the recent red tide group ( $p < 0.05$ ), then a Kruskal-Wallis rank sum test was used to compare the concentrations among all 3 groups. If there was a significant difference in a 3-group comparison ( $p < 0.05$ ), Dunn's test was used to make pairwise comparisons (differences considered significant at  $p < 0.01$ ).

#### 2.4. Estimation of strandings and overall mortality attributable to red tide

We identified a zone in which red tide was likely a sea turtle mortality factor by determining if an unusually large monthly number of stranded sea turtles ( $>10$  yr mean number of stranded turtles for that month plus 2 standard deviations) ever coincided with red tide and if the brevetoxin concentrations in samples taken from any of those stranded turtles exceeded baseline concentrations (i.e. exceeded the maximum concentration in the corresponding no red tide group). This evaluation was conducted for 1996–2013 because 1996 was the first year that 10 yr monthly mean numbers of stranded turtles could be calculated.

We estimated the number of stranded sea turtles by species that could be attributed to red tide for 1996–2013 by first determining the total number of strandings that were found during a red tide in a zone where we identified red tide as a sea turtle mortality factor. To determine the fraction of those strandings attributable to red tide, we then multiplied these totals by the overall percentage of sampled turtles by species found in 1 of these zones during a red tide that had a brevetoxin concentration above the baseline. Finally, we estimated the range of overall sea turtle mortality that could be attributed to red tide by multiplying the number of stranded sea turtles that we attributed to red tide by 5 to estimate the minimum mortality and by 10 to estimate the maximum mortality (assuming stranding probabilities of 10–20%; see Epperly et al. 1996 and Hart et al. 2006).

### 3. RESULTS

#### 3.1. Strandings, red tides, and regression models

The number of stranded sea turtles by species and zone, and the number of months of red tide by zone

in Florida during 1986–2013 are given in Table 2. Unusually large monthly numbers of stranded sea turtles were found coincident with red tide in 10 of the 15 zones (Zones 1, 3–9, 28, and 29). Of the months of red tide combined for these 10 zones during 1996–2013 ( $N = 261$ ), unusually large numbers of stranded sea turtles were found coincident with red tide during 32% ( $N = 83$ ) of those months. About 94% of these stranded turtles were either dead when found or died soon thereafter. The rest were found alive and then rehabilitated and released. Overall, these stranding numbers exceeded the 10 yr monthly means by a total of 1009 (589 loggerheads, 234 Kemp's ridleys, 175 green turtles, and 11 hawksbills). Stranded leatherbacks were never found in unusually large numbers during a red tide. The stranded loggerheads and Kemp's ridleys found during these times were primarily adults and large immature turtles (mean  $\pm$  SD curved carapace length [CCL]: loggerhead =  $88.3 \pm 12.9$  cm, Kemp's ridley =  $43.2 \pm 11.5$  cm). The stranded green turtles and hawksbills were primarily small immature turtles (green turtle =  $40.9 \pm 13.5$  cm, hawksbill =  $40.7 \pm 17.3$  cm). For all species, the CCLs of stranded sea turtles found in unusually large numbers during a red tide were not different from those of stranded turtles found in the same areas when there was no red tide (Wilcoxon rank sum tests,  $p \geq 0.05$ ). Groups of stranded sea tur-

tles found in unusually large numbers during a red tide typically had a lower percentage occurrence of external anomalies that indicated another possible cause of death (other than brevetoxicosis) than did similar groups found when there was no red tide (Fig. 2).

The Bayesian Poisson regressions predicted that an ongoing red tide (ORT), a red tide that dissipated during the previous month (LRT), and at least 2 consecutive months of red tide (CRT) would all be associated with significant increases in the numbers of stranded loggerheads and Kemp's ridleys during some months but that only CRT would be associated with significant increases in the number of stranded green turtles during some months (Fig. 3). The effect of LCT, all random effect standard deviations, and the temporal random effect correlation parameters are provided in Table 3.

### 3.2. Necropsies and brevetoxin

Necropsies that included sampling for determination of brevetoxin concentration were conducted on 304 sea turtles (119 Kemp's ridleys, 110 loggerheads, 74 green turtles, and 1 hawksbill). Fauquier et al. (2013a) previously reported the results of some of these necropsies and the findings of the remainder

Table 2. Numbers of months of *Karenia brevis* red tide and the total number of dead or debilitated (i.e. stranded) sea turtles documented in each of 15 zones in Florida (anticlockwise, west to [north] east; see Fig. 1) during 1986–2013 (excluding strandings of olive ridleys,  $N = 4$ , and those not identified to species,  $N = 1045$ ). We defined a red tide as a *K. brevis* bloom with a concentration of  $\geq 10^5$  cells  $l^{-1}$ . The subset of stranded turtles found during a red tide is given in parentheses

Zone	Number of months of red tide	Number of stranded sea turtles						Total	Found during red tide (%)
		Loggerheads	Green turtles	Kemp's ridleys	Hawksbills	Leatherbacks			
10	6	173 (10)	45 (0)	115 (2)	0 (0)	21 (1)	354 (13)	3.7	
9	12	340 (25)	59 (1)	137 (2)	1 (0)	36 (0)	573 (28)	4.9	
8	24	563 (46)	144 (7)	302 (47)	4 (0)	12 (0)	1025 (100)	9.8	
7	11	184 (18)	54 (1)	128 (10)	6 (0)	4 (0)	376 (29)	7.7	
6	15	169 (22)	393 (12)	108 (10)	20 (0)	10 (0)	700 (44)	6.3	
5	93	1787 (645)	733 (223)	519 (244)	60 (22)	10 (4)	3109 (1138)	36.6	
4	100	1685 (533)	340 (111)	463 (215)	23 (10)	8 (4)	2519 (873)	34.7	
3	37	230 (42)	45 (3)	81 (49)	2 (0)	0 (0)	358 (94)	26.3	
1	18	1416 (143)	1403 (106)	34 (1)	158 (7)	33 (7)	3044 (264)	8.7	
25	1	514 (2)	617 (1)	11 (0)	93 (0)	13 (0)	1248 (3)	0.2	
26	0	1165 (0)	1699 (0)	26 (0)	165 (0)	71 (0)	3126 (0)	0.0	
27	4	2243 (12)	2797 (19)	35 (0)	49 (0)	56 (1)	5180 (32)	0.6	
28	7	3255 (68)	1313 (76)	112 (4)	19 (0)	54 (2)	4753 (150)	3.2	
29	6	2656 (59)	871 (15)	201 (3)	21 (0)	167 (1)	3916 (78)	2.0	
30	4	2256 (45)	339 (3)	272 (5)	3 (0)	115 (0)	2985 (53)	1.8	
All	338	18636 (1670)	10852 (578)	2544 (592)	624 (39)	610 (20)	33266 (2899)	8.7	
Found during red tide (%)		9.0	5.3	23.3	6.3	3.3	8.7		

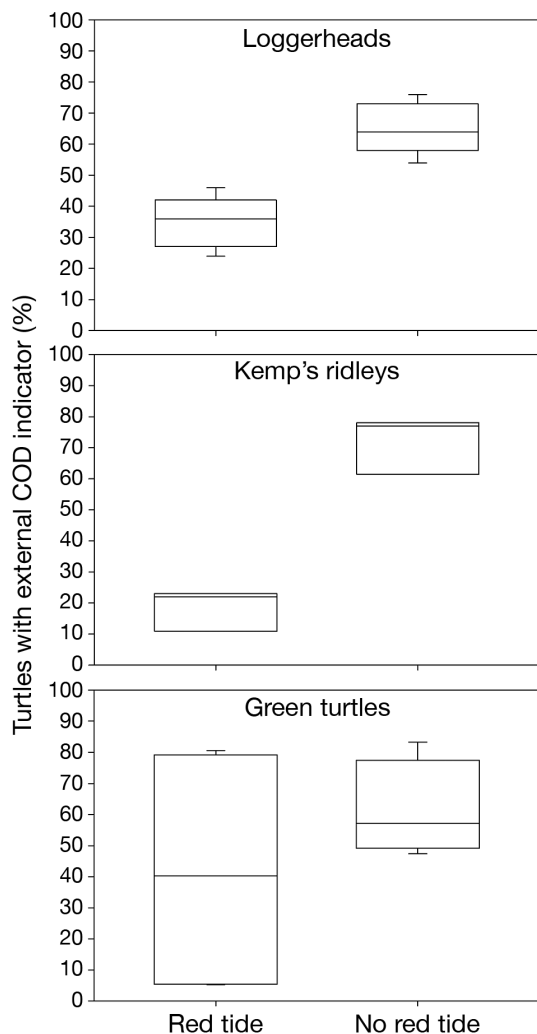


Fig. 2. Percentages of dead-stranded sea turtles with external evidence of a possible cause of death (COD) for groups found in unusually large monthly numbers ( $>10$  yr monthly mean + 2 SD) during a red tide (*Karenia brevis* bloom with a concentration of  $\geq 10^5$  cells  $l^{-1}$ ) and for paired groups found in the same zone and during the same months but when there was no red tide (i.e. the latter were found in different years). Five paired groups of stranded loggerheads, 3 paired groups of stranded Kemp's ridleys, and 4 paired groups of stranded green turtles were used. Externally apparent possible CODs included major injury (e.g. vessel-strike injury or shark-bite injury), entanglement, and indications of disease (e.g. tumors, lesions, or diminished nutritional condition). Paired *t*-tests showed a difference between the 2 categories for loggerheads and Kemp's ridleys ( $p = 0.015$  and  $p < 0.001$ , respectively) but not for green turtles ( $p \geq 0.05$ ). Bar: median; box: interquartile range; whiskers: minimum and maximum

conducted for this study were consistent with those. A dead-stranded sea turtle with suspected brevetoxicosis was typically an animal in fair to good nutritional condition found during a red tide and without gross or histological evidence of primary systemic

disease or major injury. Blood or fecal samples (or both) were collected from another 50 live-stranded sea turtles (26 loggerheads, 22 green turtles, and 2 Kemp's ridleys) that were eventually rehabilitated and released.

Brevetoxin concentrations in samples by species (except for the hawksbill and the 1 Kemp's ridley specified below) are summarized in Tables 4–6. Fauquier et al. (2013a) previously reported the results of brevetoxin testing for 28% of these turtles ( $N = 99$ ) but they are incorporated here to provide a larger context. The hawksbill was found in Zone 5 during a red tide. It was lethargic with poorly coordinated movements and died shortly after discovery. A necropsy revealed no significant findings. Brevetoxin concentrations in samples from this turtle were as follows: liver, 234  $ng\ g^{-1}$ ; kidney, 85  $ng\ g^{-1}$ ; lung, 47  $ng\ g^{-1}$ ; and contents of the upper gastrointestinal tract, 471  $ng\ g^{-1}$ . The 1 Kemp's ridley excluded from Table 5 was found in Zone 1, where red tide had not been documented for more than a year. However, it was found only 15 km south of Zone 3, where red tide was present at that time. The brevetoxin concentration in samples taken from this turtle were well above those in all other samples taken from turtles found when there was not a red tide or a recent red tide (liver, 1777  $ng\ g^{-1}$ ; contents of the upper gastrointestinal tract, 6333  $ng\ g^{-1}$ ).

### 3.3. Strandings and mortality attributable to red tide

Of the 10 zones where unusually large numbers of stranded sea turtles were found coincident with red tides, brevetoxin concentrations above the baseline were documented in samples from stranded turtles associated with red tide in every zone except for Zone 1. Samples taken from 17 stranded loggerheads found during periods of red tide in Zone 1 during 2001, 2003, 2005, and 2006 all tested either negative for brevetoxin or had a concentration within the range of the baseline. In the remaining 9 zones (Zones 3–9, 28, and 29, where we identified red tide as a likely sea turtle mortality factor), a total of 2273 stranded turtles were found coincident with a red tide during 1996–2013 (1298 loggerheads, 505 Kemp's ridleys, 431 green turtles, 32 hawksbills, and 11 leatherbacks). Of these strandings, 189 were sampled to determine brevetoxin concentration (51 loggerheads, 83 Kemp's ridleys, and 55 green turtles). The percentages of these turtles having a sample with a brevetoxin concentration above the baseline



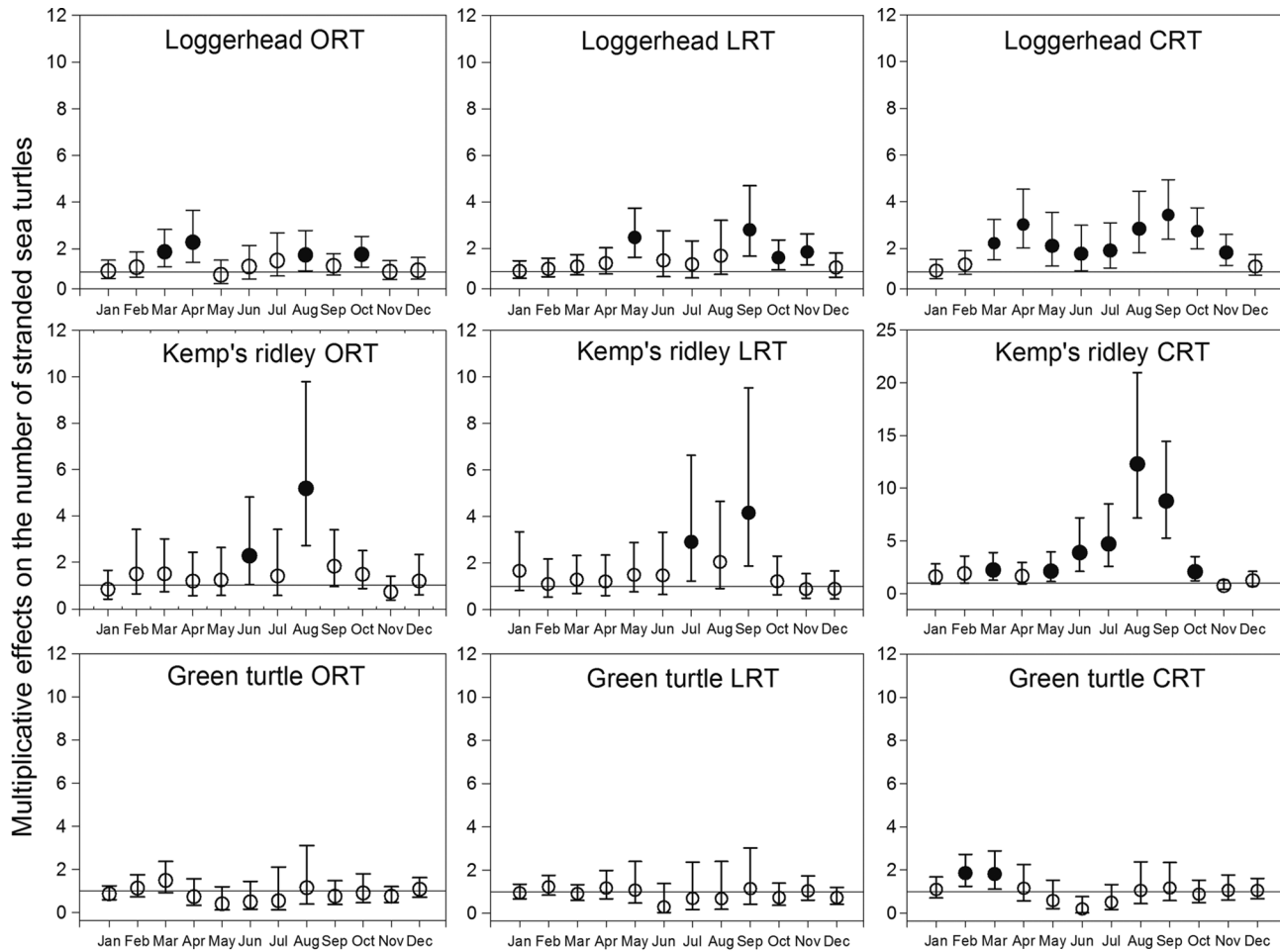


Fig. 3. Predicted multiplicative effects of red tide on the numbers of dead or debilitated (i.e. stranded) loggerheads, Kemp's ridleys, and green turtles by month according to Bayesian Poisson regression models. ORT: ongoing red tide (whether red tide was present in the same zone and during the same month as stranded turtles); LRT: lag red tide (whether red tide was present in the same zone as stranded turtles but during the previous month and not during the same month); CRT: consecutive red tide (whether red tide was present in the same zone as stranded turtles during both the previous month and the same month). A red tide was defined as a *Karenia brevis* bloom with a concentration of  $\geq 10^5$  cells  $l^{-1}$ . Circles indicate the mean effect on stranding numbers and error bars represent the upper and lower 95% credible intervals. Significant increases are denoted by the solid circles (credible interval does not overlap 1, which is shown as a horizontal line on the graph)

were 73.5% for Kemp's ridleys, 72.5% for loggerheads, and 32.4% for green turtles. The annual number of stranded sea turtles by species attributed to red tide, the percentage of strandings statewide these represented, and the estimated overall mortality from red tide are shown in Table 7.

## 4. DISCUSSION

### 4.1. Red tide as a sea turtle mortality factor and species-specific effects

Stranded sea turtles found during a *Karenia brevis* red tide were regularly investigated to identify a pos-

sible cause of death. Even though brevetoxicosis was never the likely cause of every stranding during these periods, it appeared to be a predominant cause. Necropsies did not reveal any alternative mortality factor that might regularly account for unusually large numbers of strandings found coincident with red tide. Live strandings found during these periods often presented with clinical signs of brevetoxicosis, and relatively few of the dead strandings had an external anomaly that indicated another possible cause of death. Additionally, the brevetoxin concentrations in samples from these strandings were up to 2 or 3 orders of magnitude greater than the baseline and were often equal to or greater than the concentrations found in tissue samples (e.g. liver, kidney,

Table 3. Parameter estimates from Bayesian Poisson regressions relating numbers of dead or debilitated (i.e. stranded) sea turtles by species in Florida during 1986–2013 to predictor variables. The parameters shown here include LCT (lag count, i.e. the number of stranded turtles found in the same zone during the previous month), the standard deviation (SD) of the random effect of zone, the temporal correlation of counts estimated from the autoregressive random effect, and the zone-specific (see Fig. 1) temporal SD from the occasion-specific, autoregressive random effect. LCI and UCI are the lower and upper 95% credible intervals

Parameter	Loggerhead			Green turtle			Kemp's ridley		
	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI
LCT	0.992	0.987	0.998	0.982	0.975	0.989	0.987	0.963	1.011
SD zone random effect	1.891	0.810	4.250	3.787	1.574	8.659	1.536	0.566	3.779
Temporal correlation	0.698	0.655	0.740	0.894	0.865	0.917	0.858	0.795	0.918
SD temporal random effect									
Zone 1	0.835	0.722	0.960	0.759	0.595	0.948	0.671	0.174	1.390
Zone 3	0.738	0.490	1.016	1.179	0.757	1.789	1.095	0.807	1.454
Zone 4	0.607	0.470	0.755	0.842	0.619	1.110	0.913	0.074	2.000
Zone 5	0.552	0.447	0.662	0.785	0.612	0.988	0.885	0.144	1.736
Zone 6	0.549	0.461	0.641	0.755	0.617	0.914	0.385	0.060	0.915
Zone 7	0.648	0.562	0.745	1.140	0.956	1.356	1.285	0.917	1.728
Zone 8	0.827	0.722	0.943	1.353	1.121	1.626	1.588	1.153	2.188
Zone 9	0.903	0.675	1.176	0.671	0.247	1.213	2.177	1.505	3.129
Zone 10	1.088	0.949	1.242	1.092	0.838	1.389	1.503	1.115	2.024
Zone 25	0.740	0.633	0.854	1.385	1.082	1.757	1.323	1.018	1.733
Zone 26	0.725	0.620	0.845	1.703	1.358	2.093	0.755	0.564	0.986
Zone 27	0.811	0.581	1.064	1.311	1.012	1.689	0.868	0.560	1.253
Zone 28	0.838	0.601	1.109	1.202	0.751	1.737	1.130	0.770	1.575
Zone 29	0.759	0.585	0.964	1.706	1.236	2.298	1.166	0.864	1.554
Zone 30	0.793	0.582	1.023	1.718	1.198	2.357	1.412	1.033	1.886

and lung) and in gut contents (e.g. stomach contents and feces) of other higher vertebrates suspected of having died from brevetoxicosis (manatees and dolphins: Flewelling et al. 2005, Twiner et al. 2012; canids: Castle et al. 2013; birds: Fauquier et al. 2013b).

The Bayesian Poisson regression models predicted that red tides would be associated with greater and more frequent increases in the numbers of stranded loggerheads and Kemp's ridleys than in the number of stranded green turtles. This was consistent with other results from the present study. For example, a higher percentage of stranded loggerheads and Kemp's ridleys were found during a red tide than stranded green turtles (9.0 and 23.3% vs. 5.3%, respectively). Also, relatively few of the stranded loggerheads and Kemp's ridleys found during a red tide had an external anomaly that indicated another possible cause of death. This was sometimes true for stranded green turtles but not as consistently. Brevetoxin concentrations in samples taken from stranded loggerheads and Kemp's ridleys found during a red tide were significantly higher than in those taken from strandings found when there had not been a recent red tide. This was not the case for stranded green turtles. Brevetoxin concentrations in samples taken from almost three-quarters of the stranded log-

gerheads and Kemp's ridleys found during a red tide had a brevetoxin concentration that exceeded the range of the baseline, but this was only true for about a third of the stranded green turtles.

Overall, green turtles might tend to be exposed to less brevetoxin than loggerheads or Kemp's ridleys because of their diet or their local distribution (or both). Along the southern Gulf coast of Florida, where most of the red tides occurred, green turtles feed primarily on seagrasses (A. M. Foley pers. obs.) and Kemp's ridleys and loggerheads feed primarily on benthic invertebrates (Dodd 1988, Witzell & Schmid 2005). These diet items can vary considerably in their accumulation of brevetoxin (see Flewelling et al. 2005, Bricelj et al. 2012), and this could account for differences in exposure to brevetoxin among these sea turtle species. Alternatively (or additionally), there may have been differences in local distributions that led to loggerheads and Kemp's ridleys more frequently overlapping with red tide. At a study site along the Gulf coast of Florida, Schmid (1998) documented spatial separation between the herbivorous green turtles and the carnivorous loggerheads and Kemp's ridleys based on apparent differences in foraging habitat preferences. In southwest Florida, green turtles may tend to prefer coastal inland waters, where most of the seagrasses

Table 4. Brevetoxin concentrations (ng PbTx-3 eq. g<sup>-1</sup> or PbTx-3 eq. ml<sup>-1</sup>) in samples taken from 136 dead or debilitated (i.e. stranded) loggerheads found in Florida during 1995–2013. Lower detection limits were about 5 ng g<sup>-1</sup> and 1 ng ml<sup>-1</sup>, respectively, but any negative result was counted as 0. UGI: upper gastrointestinal contents (from esophagus, stomach, or small intestine); LGI: lower gastrointestinal contents including feces. A red tide was defined as a *Karenia brevis* bloom with a concentration of ≥10<sup>5</sup> cells l<sup>-1</sup>. NRT: no red tide group includes stranded turtles found in a zone during a month without red tide and without red tide during the previous 3 mo. RRT: recent red tide group includes stranded turtles found in a zone during a month without red tide but where red tide had occurred during 1 of the previous 3 mo. ORT: ongoing red tide group includes stranded turtles found in a zone during a month with red tide. Concentrations in samples from the liver, UGI, lung, and kidney of the ORT and the RRT groups were not different (p ≥ 0.05), and concentrations in samples of these 2 groups combined were greater than those of the NRT groups (p ≤ 0.003). Concentrations in samples from the LGI and the plasma/blood of the ORT groups were greater than those of the NRT groups (p < 0.001)

Group	N	Liver		UGI		Lung		Kidney		LGI		Plasma/blood	
		n	Brevetoxin conc. Range	n	Brevetoxin conc. Range	n	Brevetoxin conc. Range	n	Brevetoxin conc. Range	n	Brevetoxin conc. Range	n	Brevetoxin conc. Range
NRT	58	38	0–91	26	0–65	23	0–0	31	0–30	16	0–48	12	0–2
RRT	14	14	0–462	7	0–12449	8	0–94	9	0–134	3	107–1739	684	(205)
ORT	64	39	0–888	33	0–11804	27	0–109	27	0–1045	30	0–61078	3450	(110) 27 0–89 23 (8)

Table 5. Brevetoxin concentrations (ng PbTx-3 eq. g<sup>-1</sup> or PbTx-3 eq. ml<sup>-1</sup>) in samples taken from 121 dead or debilitated (i.e. stranded) Kemp's ridleys found in Florida during 1995–2013. Other details as in Table 4. Concentrations in samples from the liver and UGI of the ORT and the RRT groups were not different (p ≥ 0.05), and concentrations in samples of these 2 groups combined were greater than those of the NRT groups (p < 0.001). Concentrations in samples from the lung, kidney, and UGI of the ORT groups were greater than in those of the NRT groups (p < 0.001)

Group	N	Liver		UGI		Lung		Kidney		LGI		Plasma/blood	
		n	Brevetoxin conc. Range	n	Brevetoxin conc. Range	n	Brevetoxin conc. Range	n	Brevetoxin conc. Range	n	Brevetoxin conc. Range	n	Brevetoxin conc. Range
NRT	29	28	0–160	20	0–306	11	0–57	13	0–91	14	0–306	33	(8) 1 1
RRT	9	7	9–918	310	(23)	8	0–6438	2	0–0	1	12	5	0–19 4 (0) 0
ORT	83	74	0–4421	565	(320)	57	0–45589	4633	(410)	16	0–1014	217	(133) 57 0–955 284 (142) 5 0–82 47 (74)

Table 6. Brevetoxin concentrations (ng PbTx-3 eq. g<sup>-1</sup> or PbTx-3 eq. ml<sup>-1</sup>) in samples taken from 96 dead or debilitated (i.e. stranded) green turtles found in Florida during 1996–2013. Other details as in Table 4. Concentrations in samples from the liver, UGI, and LGI of the ORT and the RRT groups were not different (p ≥ 0.05), and concentrations in samples of these 2 groups combined were not different from those of the NRT groups (p ≥ 0.05)

Group	N	Liver		UGI		Lung		Kidney		LGI		Plasma/blood	
		n	Brevetoxin conc. Range	n	Brevetoxin conc. Range	n	Brevetoxin conc. Range	n	Brevetoxin conc. Range	n	Brevetoxin conc. Range	n	Brevetoxin conc. Range
NRT	33	31	0–33	10	(10)	17	0–190	16	0–7	0.4	(0)	19	0–19 8 (9) 8 0–23 4 (0) 2 0–0
RRT	8	8	0–75	24	(20)	7	0–1650	301	(12)	1	0	2	13–14 5 0–1142 444 (0) 0
ORT	55	31	0–942	46	(8)	32	0–7187	340	(0)	3	0–0	3	0–21 7 (0) 24 0–1126 199 (0) 21 0–10 2 (2)

occur (Dawes et al. 2004). Kemp's ridleys and loggerheads occur in coastal inland waters and in shelf waters along the Gulf coast of Florida (Schmid & Witzell 2006, Hardy et al. 2014, Perrault et al. 2014) but could have a stronger preference for shelf waters than green turtles do. Because of patterns of red tide bloom initiation and transport, and the salinity preferences of *K. brevis*, blooms are more frequent in shelf waters than in coastal inland waters (Steidinger & Ingle 1972, Tester & Steidinger 1997, Steidinger 2009). Furthermore, the Bayesian regression model predicted that significant increases in the numbers of stranded green turtles would be associated with red tide only during the late winter and early spring. This was also the time of year when manatees (also herbivorous) living in the coastal inland waters along the southern Gulf coast of Florida experienced periodic large-scale die-offs attributable to red tide (Landsberg et al. 2009). For loggerheads and Kemp's ridleys, the Bayesian regression models predicted that some significant increases in the numbers of stranded turtles would be associated with red tide during the late winter and early spring but that the greatest effects on the stranding numbers for these species would occur during the late summer and fall, which is when red tide blooms are most likely found in shelf waters (Tester & Steidinger 1997).

#### 4.2. Distribution of mortality and delayed mortality

This study investigated sea turtle mortality associated with *K. brevis* red tides over a large spatio-temporal scale (coastal Florida over a 28 yr period) using data that were grouped by zone and month. Mortality was represented by data on sea turtles that were found dead or debilitated (i.e. stranded). Because carcasses or debilitated turtles may drift tens of kilometers and for periods of up to a week or so before being discovered (see Nero et al. 2013), these data only approximated the location and timing of that mortality or debilitation. Some of the stranded turtles may have been found in a different zone than where the mortality or debilitation occurred or during a different month than when the mortality or debilitation occurred. The presence and extent of a *K. brevis* red tide ( $\geq 10^5$  cells  $l^{-1}$ ) were generally represented by opportunistic water sampling over large areas. When we determined that a red tide was present in a zone during a certain month, it may not have been present in all areas of that zone or in that zone during the entire month. It was also possible that a red tide was present in some zones during some

months without being detected by water sampling. Consequently, some associations between sea turtle mortality and red tides could have been obscured by the limitations of these data.

On the scale of the zones used in the present study, the results of brevetoxin testing appeared to represent the expected spatiotemporal aspects of brevetoxin exposure related to *K. brevis* red tides. Brevetoxin concentrations in samples taken from stranded sea turtles found in zones with a red tide were consistently higher and spiked up to 2 or 3 orders of magnitude greater than concentrations in samples taken from stranded turtles found in a zone without a recent red tide. The only exception was relatively high brevetoxin concentrations in samples from 1 stranded Kemp's ridley that was found in a zone without a recent red tide. This carcass likely originated in the adjacent zone (the border of which was only 15 km from the stranding location) where a red tide was ongoing.

Because high concentrations of brevetoxin may persist in diet items of sea turtles for a few months after a red tide dissipates (in benthic invertebrates and seagrasses; Dickey et al. 1999 and Flewelling et al. 2005, respectively), some delayed mortality related to red tide would not have been unexpected. The Bayesian Poisson regression models predicted that significantly elevated numbers of stranded loggerheads and Kemp's ridleys could continue for 1 mo after a red tide dissipated, and brevetoxin concentrations in samples from strandings of these species found 1–3 mo after a red tide were as high as those from strandings found during a red tide. However, it was possible in these cases that a red tide continued to occur in some portion of a zone for 1 or 2 mo longer than was detected by water sampling. Consequently, some of the stranded turtles categorized as being found shortly after a red tide could have been found during a red tide. In either case, the numbers of stranded loggerheads and Kemp's ridleys that were attributed to red tide in the present study (and the total mortality estimated due to red tide) should be considered a minimum because none of the stranded sea turtles that were found 1–3 mo after a red tide were included in these estimates.

Red tides were almost always located along the Gulf coast of Florida and most of the months of red tide by zone (68.0%) and most of the stranded sea turtles documented during a red tide (72.6%) were in Zones 3, 4, or 5. One quarter to a little over a third of the stranded sea turtles documented in one of these zones were found during a red tide. Only 6.5% of the months of red tide by zone were located along the

Table 7. Number of dead or debilitated (i.e. stranded) sea turtles by species, attributable to *Karenia brevis* red tide (red tide attributable [RTA] strandings), the percentage of strandings statewide these represented, and the estimated overall mortality from red tide in Florida each year during 1996–2013. RTA strandings were those found during a red tide in Zones 3–9, 28, or 29, multiplied by the percentage of sampled turtles found in 1 of those zones during a red tide that had a brevetoxin concentration above the baseline (72.5% for loggerheads, 73.5% for Kemp's ridleys, and 32.4% for green turtles). Mortality was estimated using stranding probabilities of 10–20%. A red tide was defined as a *K. brevis* bloom with a concentration of  $\geq 10^5$  cells l<sup>-1</sup>

Year	Loggerheads			Kemp's ridleys			Green turtles		
	RTA strandings	Statewide %	Total estimated mortality	RTA strandings	Statewide %	Total estimated mortality	RTA strandings	Statewide %	Total estimated mortality
1996	56	9.0	280–560	33	35.5	165–330	22	5.0	110–220
1997	7	1.3	35–70	2	2.9	10–20	2	0.7	10–20
1998	7	1.3	35–70	5	6.6	25–50	0	0.0	0
1999	30	6.0	150–300	19	19.8	95–190	3	1.2	15–30
2000	34	5.1	170–340	21	18.8	105–210	2	0.6	10–20
2001	28	4.0	140–280	14	11.6	70–140	2	0.5	10–20
2002	57	8.6	285–570	15	14.0	75–150	7	1.9	35–70
2003	159	15.0	795–1590	56	47.1	280–560	10	1.8	50–100
2004	8	1.1	40–80	2	3.2	10–20	5	1.5	25–50
2005	226	26.1	1130–2260	90	55.6	450–900	22	6.3	110–220
2006	167	14.2	835–1670	28	24.6	140–280	10	2.7	50–100
2007	103	11.3	515–1030	9	12.3	45–90	21	5.2	105–210
2008	4	0.6	20–40	1	1.3	5–10	1	0.2	5–10
2009	1	0.1	5–10	1	0.9	5–10	0	0.0	0
2010	9	1.2	45–90	1	0.8	5–10	1	0.1	5–10
2011	13	1.6	65–130	11	5.6	55–110	10	1.1	50–100
2012	8	1.3	40–80	30	18.6	150–300	11	1.8	55–110
2013	23	3.0	115–230	32	14.3	160–320	9	1.1	45–90
Annual mean	52	7.1	260–520	21	17.7	105–210	8	1.6	40–80
Total	940	7.1	4700–9400	370	17.7	1850–3700	138	1.6	690–1380

Atlantic coast. Nevertheless, unusually large numbers of stranded loggerheads and green turtles ( $n = 34$  and  $51$ , respectively) were documented along the Atlantic coast of Florida coincident with a red tide. This occurred in Zones 28 and 29 during October–December 2007. A mass mortality event of bottlenose dolphins and manatees was also attributed to that red tide (Fire et al. 2015).

#### 4.3. Overall mortality from red tide and management considerations

*K. brevis* red tides in Florida were a periodically significant mortality factor of loggerheads, Kemp's ridleys, and green turtles along the Gulf coast of Florida, particularly along the southern part of that coast. A few hawksbill mortalities were also likely related to red tides in this area, but there were no indications from strandings that red tides caused mortality of any leatherbacks. However, strandings of leatherbacks were rare where most of the red tides occurred and may have been a particularly poor representation of mortality. During 1996–2013, red tide

likely caused considerable sea turtle mortality over relatively short periods (months to a year), and in 1 year (2005) it probably accounted for about a quarter of all strandings statewide. Over the entire 18 yr period, red tide appeared to account for a substantial portion of stranded loggerheads and Kemp's ridleys (7.1 and 17.7%, respectively), but only a small portion of the stranded green turtles (1.6%).

Landsberg et al. (2009) identified a combination of environmental, geographical, and biological conditions apparently necessary for a *K. brevis* red tide to cause substantial manatee mortality in Florida. This was used to explain why this degree of mortality did not always occur when red tide was present. A similar situation is likely required for red tide to cause substantial mortality of sea turtles in Florida. Unusually large numbers of stranded sea turtles were not documented during about two-thirds of the months of red tide by zone. However, we did attribute some sea turtle mortality to red tide even when it was not associated with unusually high stranding numbers because brevetoxin concentrations in samples from stranded turtles found during any red tide were often greater than the baseline.

Preventing or controlling *K. brevis* red tides is challenging because of the large spatial scale of blooms or bloom initiation areas, the excessive costs and difficult logistics of any treatment applications, and the desire to avoid unintended adverse biological or ecological consequences (Steidinger 2009). Current management of *K. brevis* red tides primarily involves monitoring, regulation, and education to limit the risk of brevetoxin exposure for people (Steidinger 2009). As a part of the recovery efforts for threatened or endangered species such as sea turtles, direct management of *K. brevis* red tides is not a viable option, but quantifying and monitoring mortality from this source allows a more complete accounting of natural mortality factors and their overall effects.

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