

A REANALYSIS OF THE CHANGE IN THE ABUNDANCE OF THE COASTAL MIGRATORY STOCK OF THE BOTTLENOSE DOLPHIN DURING THE 1987-1988 EPIZOOTIC

Introduction

From the 1970s through 1990s, the number of die-offs among marine mammals increased (Geraci et al. 1999). Causes of these die-offs included viral infections, parasitic infections, brevetoxin poisoning, oil spills, and environmental changes (such as El Niño). Although no populations were extirpated by these die-offs, the reported total mortality by population ranged from a few percent to greater than 50% (Geraci et al. 1999). Because the total population sizes often were unknown in these species, however, only the number of detected carcasses was reported for many of these die-offs. Long-term consequences of these die-offs, therefore, were difficult to evaluate.

The existing management regulations for marine mammals in the U.S. waters depend on the abundance of a population relative to its optimum sustainable population (OSP; Marine Mammal Protection Act, 1972, amended 1994). A population of a marine mammal species is defined “depleted” if the population is either “(i) ... below its optimum sustainable population or (ii) listed as an endangered or threatened species under the Endangered Species Act of 1973 (MMPA).” Consequently, if a die-off reduces a population below its OSP, the population should be declared as depleted. Without the knowledge of the abundance of the population before a die-off, however, the estimation of the population size after the die-off relative to its OSP is difficult.

An indicator of many die-offs is the increased number of carcasses found on beaches. In many U.S. coastal areas, stranded carcasses of marine mammals are reported to a regional stranding network. Each reported carcass is recorded in a stranding

database, which allows longitudinal records of the number of stranded carcasses in the region. By using these longitudinal stranding records, a die-off may be detected.

In this study, the stranding process of marine mammal carcasses was modeled for calculating the mortality rate during a die-off by using a longitudinal stranding database. The epizootic event during 1987 and 1988 of the coastal bottlenose dolphin (*Tursiops truncatus*) along the Atlantic coast of the United States was used as a numerical example.

Methods

The mortality during a die-off of a marine mammal population was calculated by modeling the stranding process of a carcass. The estimation was based on the number of carcasses found and reported to a stranding network. I defined relationships among the following parameters and variables: natural mortality, human-induced mortality, additional mortality during the die-off, probability of a carcass being stranded and reported, numbers of carcasses stranded and reported before, during, and after the die-off, abundance of the population, and the duration of the die-off (Table 3.1). In defining these relationships, I made the following assumptions:

- (1) The duration of the die-off was < 1 yr,
- (2) The additional instantaneous per capita mortality rate owing to the die-off was constant throughout the die-off,
- (3) The instantaneous per capita birth rate remained constant before, during, and after the die-off period (i.e., no density dependence on the birth rate was incorporated into the calculation) and the die-off had no direct effects on reproduction,
- (4) The instantaneous birth rate (yr^{-1}) equaled the sum of the natural mortality rate, exclusive of the die-off mortality, and human induced mortality rates (yr^{-1}),

- (5) The per capita instantaneous human induced mortality rate remained constant before, during, and after the die-off,
- (6) The instantaneous per capita natural mortality rate, exclusive of deaths due to the die-off, remained constant before, during, and after the die-off,
- (7) The population was at equilibrium before the die-off, and
- (8) No immigration or emigration occurred to the population.

Because the duration of the die-off was assumed to be short (< 1 yr) relative to life cycles of marine mammals, effects of density dependence were ignored in the model.

Table 3.1. List of notations.

Notation	Definition
b	Instantaneous per capita birth rate of the population (yr^{-1}), which was assumed to be equal to $\mu_0 + h$
f_0	The probability of a stranded carcass being sighted and reported before the die-off ($0 < f_0 < 1$)
f_1	The probability of a stranded carcass being sighted and reported during the die-off ($0 < f_1 < 1$)
f_2	The probability of a stranded carcass being sighted and reported after the die-off ($0 < f_2 < 1$)
μ_0	Instantaneous per capita base mortality rate of the population before the die-off (yr^{-1} ; $0 < \mu_0 < 1$)
μ_1	Additional instantaneous per capita mortality rate of the population caused by the die-off (yr^{-1} ; $0 < \mu_1 < 1$),
h	Instantaneous per capita human-induced mortality rate of the population (yr^{-1} ; $0 \leq h < 1$)
N_0	The constant abundance of the population before the die-off ($0 < N_0$)
N_t	The abundance of the population during the die-off at time = t , which was measured as time since the beginning of the die-off in years ($0 < N_t$; $0 \leq t \leq T$)
T	Duration of the die-off (yr; $0 < T < 1$),

The following three equations were written based on these assumptions. The total number of observed stranded carcasses per year before the die-off (D_0) was:

$$\begin{aligned} D_0 &= \int_0^1 N_0 (\mu_0 + h) f_0 dt \\ &= N_0 (\mu_0 + h) f_0 \end{aligned} \quad (3.1)$$

The total number of stranded carcasses during the die-off (D_1) was:

$$\begin{aligned} D_1 &= \int_0^T N_t (\mu_0 + h + \mu_1) f_1 dt \\ &= \int_0^T N_0 e^{(b-\mu_0-h-\mu_1)t} (\mu_0 + h + \mu_1) f_1 dt \\ &= N_0 (\mu_0 + h + \mu_1) f_1 \int_0^T e^{-\mu_1 t} dt \\ D_1 &= \frac{N_0 (\mu_0 + h + \mu_1) f_1 (1 - e^{-\mu_1 T})}{\mu_1} \end{aligned} \quad (3.2)$$

Finally, the total number of stranded dead animals during the first year after the die-off (D_2) was:

$$\begin{aligned} D_2 &= \int_0^1 N_0 e^{-\mu_1 T} (\mu_0 + h) f_2 dt \\ &= N_0 e^{-\mu_1 T} (\mu_0 + h) f_2 \end{aligned} \quad (3.3)$$

Calculating the mortality during the die-off

In these three equations, information often is available on T , D_0 , D_1 , and D_2 , whereas N_0 , f_0 , f_1 , f_2 and μ_1 are usually unknown. To simplify the algebra, the detection

probability after the die-off (f_2) is expressed as a simple function of the detection probability during the die-off (f_1):

$$f_2 = \alpha f_1, \quad (3.4)$$

where $0 < \alpha$. The multiplier α indicates the amount by which the detection probability changed from during the die-off to after the die-off. Equation (3), therefore, becomes:

$$D_2 = N_0 e^{-\mu_1 T} (\mu_0 + h) \alpha f_1. \quad (3.5)$$

Equations (3.2) and (3.5) involved 4 unknowns: α , f_1 , N_0 , and μ_1 . In these two equations, however, N_0 and f_1 only appeared as a product in both equations.

Consequently, this product was treated as a single unknown variable ($C = N_0 f_1$), allowing me to compute a solution for μ_1 . Solving equation (3.2) for C :

$$C = N_0 f_1 = \frac{D_1 \mu_1}{(\mu_0 + h + \mu_1)(1 - e^{-\mu_1 T})}. \quad (3.6)$$

Substituting equation (3.6) into equation (3.5):

$$\begin{aligned} D_2 &= N_0 e^{-\mu_1 T} (\mu_0 + h) \alpha f_1 = \alpha C e^{-\mu_1 T} (\mu_0 + h) \\ &= \frac{\alpha e^{-\mu_1 T} (\mu_0 + h) D_1 \mu_1}{(\mu_0 + h + \mu_1)(1 - e^{-\mu_1 T})} \end{aligned} \quad (3.7)$$

In equation (3.7), μ_1 and α were the only unknown parameters. Equation (3.7) was considered to be a function of μ_1 and rewritten as:

$$f(\mu_1) = D_2 - \frac{\alpha e^{-\mu_1 T} (\mu_0 + h) D_1 \mu_1}{(\mu_0 + h + \mu_1)(1 - e^{-\mu_1 T})} = 0. \quad (3.8)$$

Equation (3.8), then, was solved numerically for μ_1 . Because α was a positive value, equation (3.8) was a non-decreasing function with respect to μ_1 for all values of $(\mu_0 + h)$. Only one root (μ_1), therefore, was possible for a value of $\mu_0 + h$.

Calculating the change in abundance and detection probabilities

Under my assumptions, the population size changed without density dependence during the die-off. Consequently, the change in abundance during the die-off can be expressed as:

$$\frac{N_T}{N_0} = e^{-\mu_1 T}. \quad (3.9)$$

Equation (3.3) involved 2 unknowns ($N_0 \times f_2$ and μ_1), whereas, the product of N_0 and f_0 was the only unknown variable in equation (3.1). Therefore, the system can be solved for the ratio of detection probabilities before and after the die-off (f_2/f_0) as a function of μ_1 . To calculate the ratio of detection probabilities, equation (3.1) was solved for f_0 :

$$f_0 = \frac{D_0}{N_0(\mu_0 + h)}. \quad (3.10)$$

Equation (3.3) was solved for N_0 :

$$N_0 = \frac{D_2}{e^{-\mu_1 T}(\mu_0 + h)f_2}. \quad (3.11)$$

Equation (3.11), then, was substituted into (3.10) and was rearranged:

$$f_0 = \frac{D_0}{\left(\frac{D_2(\mu_0 + h)}{e^{-\mu_1 T}(\mu_0 + h)f_2} \right)} = \frac{D_0 e^{-\mu_1 T} f_2}{D_2} \quad (3.12)$$

$$\frac{f_2}{f_0} = \frac{D_2}{D_0 e^{-\mu_1 T}}. \quad (3.13)$$

Equation (3.13) calculates the amount by which the survey effort changed before and after the die-off.

Numerical example

A large number of bottlenose dolphins were found dead on beaches along the Atlantic coast of the United States during 1987 and 1988 (Scott et al. 1988). Later analyses on carcasses indicated that infection by morbilliviruses was the main cause of the mass mortality event (Scott et al. 1988, Lipscomb et al. 1994, Duignan et al. 1996). Assuming there was one coastal migratory stock of the species, Scott et al. (1988) reported more than 50% of the entire stock was killed by this epizootic.

To apply the model to the epizootic, I examined stranding records of bottlenose dolphins along the Atlantic coast of the United States between 1987 and 1997 (courtesy of Blair Mase¹ and Charles Potter²). I grouped all stranding records of bottlenose dolphins along the Atlantic coast by 30-day periods, starting from 1 January 1987 (Table 3.2). I defined the duration of the epizootic to be the number of 30-day periods between 1 June 1987 and 30 April 1988 (Scott et al. 1988), in which the number of stranded bottlenose dolphins was greater than the 95 percentile for the entire time series.

I calculated the additional instantaneous mortality rate during the epizootic (μ_1) by inserting numerical values for instantaneous mortality rates ($\mu_0 + h$), the multiplicative factor for the change in detection probability of a carcass (α), and the three known variables (T , D_1 , and D_2) into equation (3.8) and solving the equation. I considered a range of the sum of natural and anthropogenic mortality rates between 0.04 and 0.10,

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which was within the plausible mortality for dolphin populations (Reily and Barlow 1986). I considered a range of α between 0.1 and 2.0.

Table 3.2. The number of stranded bottlenose dolphins per 30 days along the Atlantic coast of the United States. The duration of the epizootic was defined as the time period in which the number of stranded carcasses was greater than the 95 percentile between 1/1/1987 and 12/03/1997 and indicated by bold face.

Start Date	End Date	Number per 30 days
19870101	19870130	0
19870131	19870301	0
19870302	19870331	1
19870401	19870430	2
19870501	19870530	6
19870531	19870629	19
19870630	19870729	83
19870730	19870828	234
19870829	19870927	110
19870928	19871027	48
19871028	19871126	38
19871127	19871226	58
19871227	19880125	69
19880126	19880224	62
19880225	19880325	21
19880326	19880424	30
19880425	19880524	23
19880525	19880623	11
19880624	19880723	15
19880724	19880822	19
19880823	19880921	11
19880922	19881021	15
19881022	19881120	12
19881121	19881220	7
19881221	19890119	16
19890120	19890218	19
19890219	19890320	17
19890321	19890419	16
...
19971104	19971203	23
Mean		24.6
SD		25.5
95%-ile		58

To estimate effects of errors in the estimated parameter ($\mu_0 + h$) and measured variables (D_1 and D_2) on the additional mortality (μ_1), sensitivity analyses were conducted. I calculated additional mortality (μ_1) as a function of the sum of natural and human-induced mortality rates ($\mu_0 + h$). To estimate effects of the number of undetected stranded carcasses on the computed additional mortality rates (μ_1), I considered errors in detecting stranded carcasses. The additional mortality rate (μ_1) was calculated when D_1 and D_2 in equation (3.8) was varied from 101% to 125% of the reported value. I also estimated the sensitivity of the solutions for (N_T/N_0) to uncertainties in estimates for ($\mu_0 + h$), D_1 , and D_2 . Equation (3.9) was evaluated under ranges of ($\mu_0 + h$), D_1 , and D_2 .

Results

During eight 30-day periods between 30 June 1987 and 24 February 1988 along the U. S. Atlantic coast, a total of 702 carcasses of bottlenose dolphins were reported to the stranding network (D_1 ; Table 3.2). Although there were two months during which the number of stranded carcasses was less than the 95 percentile, the duration of the epizootic was defined as 240 days, or eight months ($T = 8/12$). A total of 199 (D_2) carcasses were reported during the 1-yr period after the epizootic. An average of 73.3 ($D_0=73$) bottlenose dolphins was reported to the stranding network every year during the 3-yr period before the epizootic (Scott et al. 1988).

Under my assumptions, the computed additional mortality rate during the 8-mo epizootic ranged approximately from 0.16 to 0.37 (Table 3.3). By incorporating uncertainty in variables and parameters in the model, however, significant variability was found in the calculated additional mortality rate. There was a positive relationship between the sum of natural and anthropogenic mortality rates ($\mu_0 + h$) and computed

additional mortality rate during the epizootic (μ_1 ; Table 3.3). The calculated change in the population size ranged from 10% to >20% if the detection and reporting probability was the same during and after the epizootic (i.e., $\alpha = 1.0$; Table 3.3).

Table 3.3. Calculated instantaneous additional mortality rate (μ_1) during the epizootic, calculated change in the abundance of the stock (N_T/N_0), and calculated change in detection probabilities before and after the epizootic (f_2/f_0) as a function of the sum of natural and human-induced mortality rates ($\mu_0 + h$). The duration of the epizootic was assumed to be 8 mo. Equation (3.8) was used to calculate the additional mortality rate during the epizootic. Change in the abundance was calculated by using equation (3.9). Change in detection probability (f_2/f_0) was calculated by using equation (3.13). The probability of detecting and reporting a carcass during and after the epizootic was assumed to be the same (i.e., $\alpha = 1.0$).

	Natural and human-induced mortality ($\mu_0 + h$; yr ⁻¹)						
	0.04	0.05	0.06	0.07	0.08	0.09	0.10
μ_1	0.161	0.198	0.233	0.268	0.302	0.335	0.367
N_T/N_0	0.899	0.877	0.856	0.836	0.818	0.800	0.783
f_2/f_0	3.03	3.11	3.19	3.26	3.33	3.41	3.48

The sensitivity analysis indicated positive relationships between the proportion of undetected stranded carcasses during the epizootic (D_1) and the computed additional mortality rates during the epizootic (μ_1 ; Figure 3.1). The proportion of undetected stranded carcasses during the first year after the epizootic (D_2), however, indicated negative relationships with calculated additional mortality rates during the epizootic (μ_1 ; Figure 3.1). The proportion of undetected stranded carcasses had less effect on computed additional mortality rates during the epizootic (μ_1 ; Figure 3.1) than the uncertainty in natural and anthropogenic mortality rates.

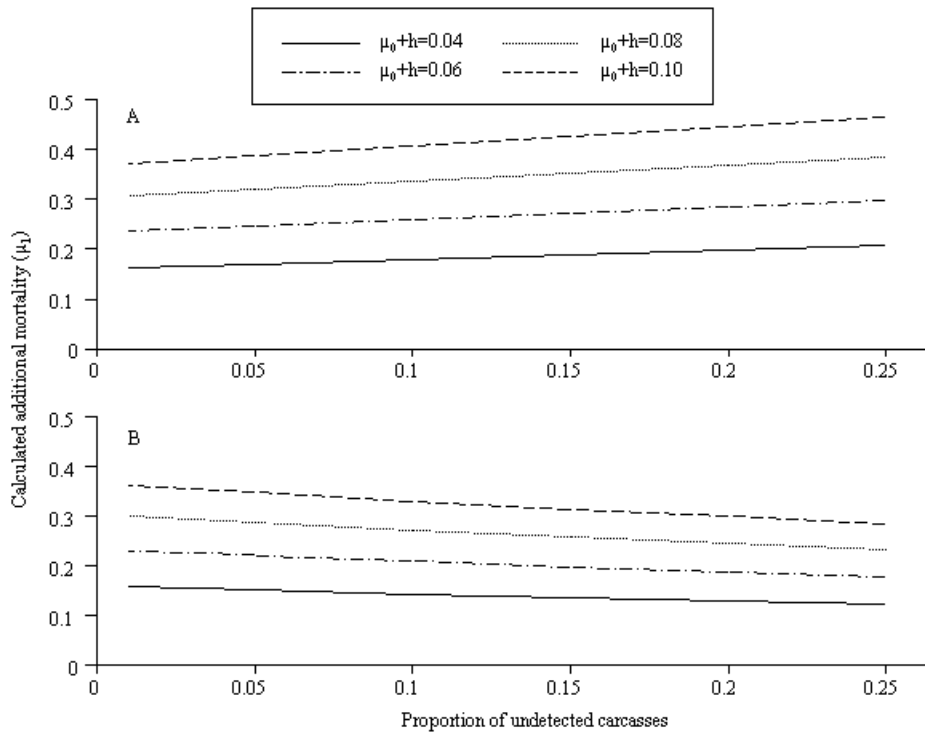


Figure 3.1. Effects of uncertainty in the proportion of undetected stranded carcasses and natural and human-induced mortality rates ($\mu_0 + h$) on calculated additional mortality rate (μ_1). The abscissa of the upper figure (A) indicates the proportion of undetected carcasses during the epizootic (D_1), whereas that of the lower figure (B) indicates the proportion of undetected carcasses during 1 yr after the epizootic (D_2). The duration of the epizootic (T) was assumed to be 8 mo ($T = 8/12$), the number of reported carcasses during the epizootic (D_1) was 702, and the number of stranded carcasses during 1 yr after the epizootic (D_2) was 199. Additional mortality rate (μ_1) was calculated as the solution for equation (3.8). The probability of detecting and reporting a carcass during and after the epizootic was assumed to be the same (i.e., $\alpha = 1.0$).

The sensitivity analysis also indicated positive relationships between the proportion of undetected stranded carcasses during the epizootic (D_1) and the change in the population size during the epizootic (μ_1 ; Figure 3.2). Negative relationships were found between the proportion of undetected stranded carcasses during the first year after the epizootic (D_2) and change in the population size during the epizootic (μ_1 ; Figure 3.2).

Uncertainty in D_1 and D_2 had less effect on the calculated rate of change in abundance during the epizootic (N_T/N_0) than the uncertainty in natural and anthropogenic mortality rates (Figure 3.2).

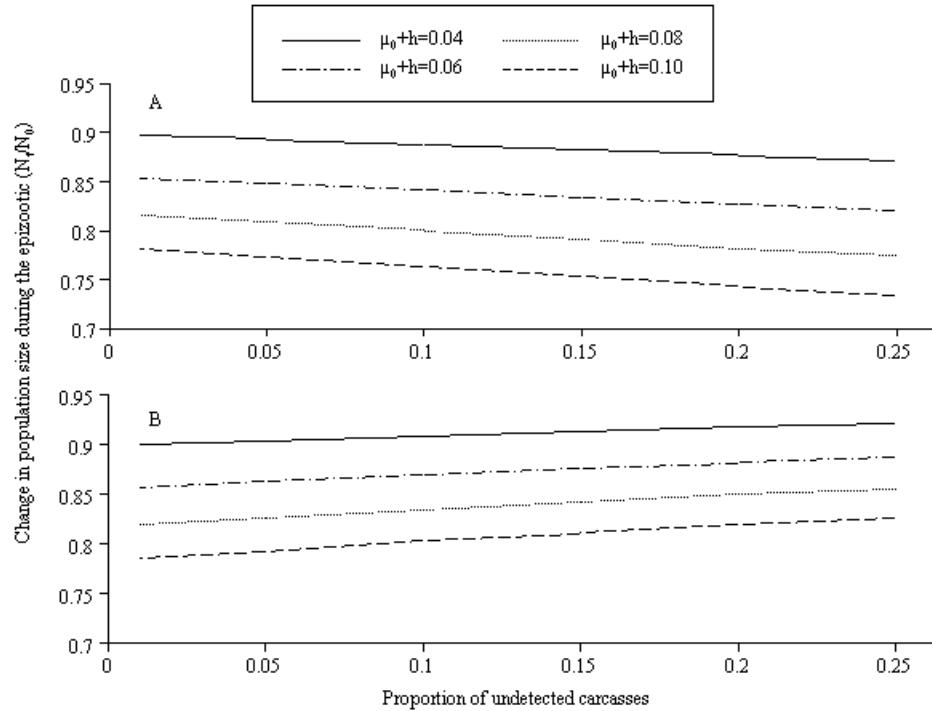


Figure 3.2. Effects of uncertainty in the proportion of undetected stranded carcasses on the calculated change in the abundance (N_T/N_0). The abscissa of the upper figure (A) indicates the proportion of undetected carcasses during the epizootic (D_1), whereas that of the lower figure (B) indicates the proportion of undetected carcasses during 1 yr after the epizootic (D_2). The duration of the epizootic (T) was assumed to be 8 mo ($T = 8/12$), the number of reported carcasses during the epizootic (D_1) was 702, and the number of reported carcasses during 1 yr after the epizootic (D_2) was 199. Change in abundance (N_T/N_0) was calculated by using equation (3.9). The probability of detecting and reporting a carcass during and after the epizootic was assumed to be the same (i.e., $\alpha = 1.0$).

For the range of natural and human-induced mortality rates under consideration, the calculated detection probability of carcasses was approximately 3 times greater after

the epizootic than before the epizootic ($f_2/f_0 \approx 3.0$; Table 3.3). The calculated additional mortality rate (μ_1) during the epizootic was greater if the detection probability of a carcass increased after the end of the epizootic (α ; Table 3.4). If the effort increased during the epizootic and the same effort continued after the epizootic (i.e., $\alpha \approx 1$), then the computed additional mortality rate during the epizootic ranged from approximately 0.17 to 0.4 (Table 3.4). If, however, the majority of increased effort was after the epizootic (i.e., $\alpha > 1$), the calculated additional mortality rates were much greater (Table 3.4).

Table 3.4. Effects of change in detection probabilities (α) between during and after the epizootic on calculated additional mortality rate during the epizootic (μ_1). Duration of the epizootic was assumed to be 8 mo ($T = 8/12$), the number of reported carcasses during the epizootic (D_1) was 702, and the number of reported carcasses during 1 yr after the epizootic (D_2) was 199. Additional mortality rate (μ_1) was calculated as the solution for equation (3.8).

Mortality ($\mu_0 + h$)	Rate of change in detection probability (α)					
	0.5	0.8	1.1	1.4	1.7	2.0
	Additional mortality during the epizootic (μ_1)					
0.04	0.064	0.123	0.179	0.234	0.287	0.338
0.06	0.094	0.179	0.260	0.337	0.409	0.479
0.08	0.123	0.233	0.336	0.432	0.522	0.607
0.10	0.151	0.284	0.407	0.520	0.625	0.724

Discussion

The deterministic model of stranding and reporting process was shown to be useful in calculating additional mortality during a die-off from longitudinal stranding records. The model incorporated the stranding and reporting process, enabling sensitivity analyses on unknown parameters and variables. The result of using this model for estimating additional mortality during a die-off, however, depended on precision of other parameters and variables.

Sensitivity analyses indicated that uncertainty in natural and anthropogenic mortality rates had significant effects on calculated additional mortality rates during the epizootic of bottlenose dolphins during 1987-1988. The proportion of undetected stranded carcasses during and after the epizootic also had significant effects on calculated additional mortality rates during the epizootic (Figure 3.1). I have shown that by varying the proportion of undetected carcasses from 1% to 25% of the reported number of carcasses, the calculated additional mortality during the epizootic ranged from 0.12 to 0.46 (Figure 3.1). Consequently, the calculated decline in the abundance of the coastal migratory stock during the epizootic ranged approximately from 10% to 27% (Figure 3.2). These sensitivity analyses indicated that uncertainty in the proportion of undetected carcasses should be incorporated when the stranding record was used in estimating the mortality rate. The proportion of undetected carcasses may be estimated indirectly by recording the longitudinal effort dedicated to detecting stranded carcasses.

The computed detection and reporting probability of carcasses increased by approximately a factor of three over the period of the epizootic. Without the information on how search and reporting effort changed over the duration of the epizootic, it is impossible to attribute when the change occurred. A great variability was found in

calculated additional mortality rates as a function of the rate of change in detection probability. This sensitivity analysis indicated that survey effort should be estimated for stranding data if these data are to be used for estimating the mortality during a die-off.

To obtain reliable mortality rates during a die-off, precise estimations of life history parameters, such as birth rate, natural mortality rate, and anthropogenic mortality rate, are critical. Without information on natural mortality and human-induced mortality rates, the calculated additional mortality rate during the die-off could be either insignificant to the population or significant enough to nearly exterminate the population. These results were not directly useful in making a decision for successful management of the population. The following information on the population should be collected prior to the onset of the die-off: (1) natural mortality rate, (2) anthropogenic mortality rate, (3) birth rate, and (4) trend of the population size.

Stranding data should be collected in a consistent manner and effort for establishing the baseline data. Survey areas should be predetermined and defined. Trained observers should collect stranding data periodically within these defined survey areas. These data should include but not be limited to: species, the number of animals, and location of stranding. Effort data (e.g., hours of survey) for each survey area should be recorded for non-die-off periods. Collected data, then, should be added to a database, which will enable a data analyst to detect the unusual number of stranded carcasses of a species if a die-off occurs. If a die-off is suspected, the survey effort should be continued but not necessarily increased. If more funding or volunteer workers are available, the change in survey effort should be measured. Data collection should continue after the die-off. These data will enable a reliable estimate of mortality rate during the die-off.

In conclusion, a mathematical modeling of stranding processes was shown to be useful for calculating the mortality during a die-off. For these analyses to be satisfactory,

however, baseline data should be collected on several factors prior to a potential die-off and continue after the die-off. In particular, search effort must be quantified.