



Bird mortality from the *Deepwater Horizon* oil spill. II. Carcass sampling and exposure probability in the coastal Gulf of Mexico

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ABSTRACT: Two separate approaches, a carcass sampling model and an exposure probability model, provided estimates of bird mortalities of 600 000 and 800 000, respectively, from the 2010 *Deepwater Horizon* MC 252 oil spill in coastal waters of the Gulf of Mexico. Monte Carlo simulation of parameter uncertainty led to respective 95 % uncertainty intervals of 320 000 to 1 200 000 and 160 000 to 1 900 000. Carcass sampling relied on expansion factors multiplied by counts of bird carcasses retrieved in shoreline surveys, whereas exposure probability estimated bird deaths as a product of estimated coastal bird density, average oil slick size, slick duration, and proportionate mortality due to oiling. The low proportion of small-sized carcasses recovered, compared with considerably higher proportions of small live birds in coastal Gulf habitats, indicate an especially low probability of recovery for small birds after oil spills at sea. Most mortality affected 4 species: laughing gull *Leucophaeus atricilla* (32 % of the northern Gulf of Mexico population killed), royal tern *Thalasseus maximus* (15 %), northern gannet *Morus bassanus* (8 %) and brown pelican *Pelecanus occidentalis* (12 %). Declines in laughing gulls were confirmed by ~60 % reductions in National Audubon Society Christmas Bird Count data for 2010–2013 along the Gulf coast. Population-level effects in apex predators of this magnitude likely had effects on prey populations that warrant careful assessment.

KEY WORDS: Avian mortality · Exposure probability · Carcass sampling · Oil spill · *Deepwater Horizon* · Gulf of Mexico · Coastal habitat · Christmas Bird Count · Monte Carlo simulation

INTRODUCTION

Large oil spills into the coastal ocean can kill hundreds of thousands of birds (Piatt & Ford 1996, Tan et al. 2008, Munilla et al. 2011). Petroleum exposure alters feather microstructure (Jenssen 1994, O'Hara & Morandin 2010), compressing plumage so that it loses its buoyancy, insulating function, and flight capability (Leighton 1993). Physiological health of birds is further impaired by oil-induced diseases (Briggs et al. 1996), including hemolytic anemia,

ulcerations, cachexia, and aspergillosis (Balseiro et al. 2005). Birds contaminated at sea thereby die due to drowning, hypothermia, starvation, or dehydration.

The largest accidental release of petroleum into marine waters in history (Camilli et al. 2012, McNutt et al. 2012), the *Deepwater Horizon* MC 252 blowout was an unprecedented perturbation to the northern Gulf of Mexico. The cumulative slick area exceeded 100 000 km² (Norse & Amos 2010, Garcia-Pineda et al. 2013). Oiling impacts extended from the pelagic ocean seaward of the continental slope, across the

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continental shelf, and into remote brackish estuaries along the Gulf coastline (Peterson et al. 2012, Michel et al. 2013).

Avian mortality is one direct, immediate measure of ecological impact caused by a marine oil spill. Because it is impossible to observe each seabird death from acute oil exposure, total mortality is usually inferred from shoreline carcass surveys and probability-based expansion factors to account for birds that are killed but not collected (e.g. an Oiled Seabird Mortality Model; Wiese & Robertson 2004). These factors account for birds that die but disappear before arriving on shore (Wiese 2003, Munilla et al. 2011) and those on shore that go undetected by spill responders (Van Pelt & Piatt 1995, Byrd et al. 2009). Alternatively, seabird mortality can be estimated from the numbers of birds present and vulnerable to lethal exposure (Wilhelm et al. 2007, Haney et al. 2014, this volume).

Our objective here is to estimate coastal seabird mortality from acute oil exposure during the *Deepwater Horizon* spill. We compare mortality estimates derived from both a carcass sampling model and an exposure probability model. The carcass sampling model includes expansion factors for lost, missed, and unobservable bird carcasses. The exposure probability model is based on surveys of aerial seabird densities above coastal waters of the northern Gulf of Mexico, estimates of the size of the *Deepwater Horizon* oil slick, and an estimate of the proportion of oiled seabirds that subsequently died. The 2 approaches are based on largely independent data, providing an unusual opportunity to compare alternative models of estimating avian mortality after a large marine oil spill.

MATERIALS AND METHODS

Study area and modeling domain

Spatially, we limited the scope of investigation to coastal waters within 40 km offshore of the Gulf coast (see Fig. 1 in Haney et al. 2014), thus delineating an effective catchment area (sensu Wiese & Robertson 2004). We chose 40 km as the likely maximum distance from shore inhabited routinely by coastal seabirds.

The *Deepwater Horizon* discharged oil into the Gulf from the day when the casing was breached on 20 April 2010 until the well was capped on 15 July 2010. Oil first appeared within 40 km of the coast on 28 April 2010. We thus considered the acute mortal-

ity phase to last for 95 d, until 31 July 2010, to account for bird mortality from contact with lingering surface oil (Aeppli et al. 2012). Avian mortality clearly continued after the well was capped (based on wildlife collection reports) because the ratio of dead-to-live bird recoveries increased in late July 2010 (Belanger et al. 2010, Antonio et al. 2011).

Bird carcass tallies by size category and location

We obtained carcass counts retrieved in all habitats during the *Deepwater Horizon* incident and archived by spill response authorities (www.fws.gov/home/dhoilspill/collectionreports.html, table dated 12 May 2011; accessed 22 March 2013). Using a total of 2121 carcasses identified as known oiled, we organized these counts by species and body size. Live moribund oiled birds were not counted as carcasses because they could reach shorelines independent of winds and currents (e.g. Stienen et al. 2004).

To account for variation in detectability with body size during spill response (Seys et al. 2001, Ford & Zafonte 2009), each bird species and all individual birds were assigned to one of 3 size categories: large (≥ 500 g), medium (300–499 g), or small (10–299 g). We excluded 92 bird carcasses not considered as coastal on the basis of primary habitat used by each species, life history traits, and migratory habits. Species of estuarine categorization included rails, gallinules, certain waders, and species that occur in terrestrial vegetation types.

Species that feed in the neritic zone and associated shorelines, including shorebirds and other seasonal migrants that rely upon beach or wide mudflats during the time of year of the spill, were broadly designated as coastal for purposes of oil exposure. Birds listed in the recovery archives as 'other' (a total of 31) and 'unknown' (a total of 51) were categorized as coastal and medium sized. Other birds tallied unknown to species were assigned to the same size category and habitat as the most commonly recovered species in that taxon (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m513p239_supp.pdf). Dead birds assigned to the coastal category but retrieved offshore (a total of 25 carcasses recovered before they reached shore; see www.fws.gov/home/dhoilspill/collectionreports.html), were also subtracted from the carcass tally. A total of 2004 bird carcasses constituted the observations that represented the recoveries of birds from the coastal habitat, comprising 128 small-, 1383 medium- and 493 large-bodied bird carcasses.

Carcass sampling model

From a sampling perspective, carcass counts can be thought of as the realization of repeated stochastic sampling steps, with each step reducing the number of carcasses ultimately available for recovery (e.g. Seys et al. 2001, Wiese & Robertson 2004). The unknown number of bird deaths in each body size category from the *Deepwater Horizon* spill was denoted as N_j , and the number of carcasses counted as x_j , with the index j indicating body size category (1: large; 2: medium; 3: small). Within each body size category, a series of 5 stochastic steps reduced the carcasses available to be recovered by some proportion.

We denote r as the probability that a carcass was transported and deposited on shore following a bird's death from oil, l the probability that a carcass persisted on shore until it could be found, h the proportion of habitat sampled for bird carcasses, k the proportion of the total carcass deposition period systematically sampled with a fixed interval between successive sampling events, and d the probability that a carcass would be detected by searchers. Parameters r , l , h , and k were assumed to be the same for all bird body size categories. Parameter d was assumed to vary by size category, with d_1 , d_2 , and d_3 the probabilities of detection that correspond to x_1 , x_2 , and x_3 . For convenience, we let p_j denote the combined probability that a bird from size category j that died as a result of oil spill exposure was eventually recovered. Also, we used the caret notation to indicate between an estimate (e.g. \hat{p}_j) of a parameter and we leave off the caret to denote either the true value or else the parameter as a random variable (in the Bayesian sense, e.g. p_j). Then, in a sampling context (Thompson 2002), the estimated number of total birds killed within size category j is

$$\hat{N}_j = \frac{x_j}{\hat{r}\hat{l}\hat{h}\hat{k}\hat{d}_j} = \frac{x_j}{\hat{p}_j} \quad (1)$$

The grand total number of birds estimated killed is the sum of each \hat{N}_j .

Parameter selection

Carcasses adrift will vary in their final destination as a consequence of daily changes in wind speed and direction. Shelf currents in the northern and eastern Gulf of Mexico are dominated by wind and freshwater driven flows (Barker 2011). Surface oil reached Gulf shorelines only during strong onshore winds (MacFadyen et al. 2011). We therefore estimated car-

carcass drift from wind data, because neritic currents from the Mississippi and Atchafalaya River discharges are primarily alongshore to the west in response to Coriolis forcing.

The probability r that a carcass was transported to shore depends on its initial position offshore, the carcass drift velocity towards a shoreline, and the probability of remaining afloat en route. We assumed the initial carcass position was proportional to the product of the relative area densities of seabirds and surface oil as a function of distance from shoreline, averaged over the 95 d when seabird carcasses were presumed present within 40 km of the shoreline. We assumed that coastal seabird density declined from a maximum at the shoreline to some negligibly low value 40 km offshore, proportional to $1 - z/40$, where z indicates the distance from shoreline in km. Daily oil slick size was calculated from shape files that were synthesized in the Experimental Marine Pollution Surveillance Daily Composite Products (www.ssd.noaa.gov/PS/MPS/deepwater.html; accessed 11 August 2013). Spatial depictions of the *Deepwater Horizon* oil slick in these products were based primarily on satellite sensors augmented with oil spill trajectory models and other ancillary data (see 'Parameter selection for exposure probability model' in the Supplement). The initial location of seabird carcasses was then assumed to be proportional to the product of the risk of oiling and the assumed seabird density of $1 - z/40$ (Table S2 in the Supplement).

We estimated shoreward carcass drift velocity from observations of wind velocities archived for Station BURL1, Southwest Pass, Louisiana, a C-MAN Station maintained by the National Data Buoy Center. We assumed a 2% coupling of wind and seabird carcass drift speeds (Seys et al. 2001, Castege et al. 2007), and a Coriolis deflection for seabird carcass drift of 18° to the east (Poulain et al. 2009). Shorelines where seabird carcasses were deposited were assumed to face either southward (80%) or eastward (20%). Seabird carcass drift speeds were computed as the respective northward and westward components of the drift velocity vector, and the average values of these velocities v_N and v_W were determined. The overall average drift velocity, \bar{v} , of 4.1 km d⁻¹ was computed as $\bar{v} = 0.8 \bar{v}_N + 0.2 \bar{v}_W$ (Table S3 in the Supplement).

We assumed carcasses lost buoyancy from decomposition at an instantaneous rate of 1.00 d⁻¹ (see 'Computation of transport probability to shorelines' in the Supplement), based on results reported by Ford et al. (1991) and Wiese (2003) after accounting for temperature differences and for likely effects of

scavengers that increase carcass decomposition rates. The probability that a carcass would remain afloat after a time t at sea was computed as $\exp[-(1.00 t)]$, where $t = z/4.1 \text{ km d}^{-1}$. The probability r that a carcass was transported to shore was computed as a numerical approximation of the integral of the product of this exponential function and the distribution of initial carcass positions at sea as described above (Table S4 in the Supplement).

Based on these assumptions regarding carcass losses at sea, <1% of the carcasses would remain available for shoreline deposition after 4 d. Integrating these time-dependent losses with the initial distribution of carcasses led to an estimated average proportion of carcasses reaching a shoreline of approximately $\hat{r} = 0.057$ (Table S4). Most of this transport probability arises from carcasses within 15 km of the shore, beyond which the average transport time of ~ 4 d or more leads to nearly complete removal of carcasses from the sea surface. The parameter r was assigned a beta probability distribution with the mean centered at 0.057 to model uncertainty in this parameter.

To estimate the probability of carcass persistence on a beach prior to search and recovery, l , we assumed that a carcass survey was conducted every 3 d, as was originally planned (USDOI 2011). We took the daily probability of carcass persistence to be 0.50 to account for removals by scavengers or burial by wind- or wave-driven sediment transport, a reasonable approximation based on other studies (Page et al. 1990, Seys et al. 2001). We assumed that the probability of a carcass persisting n days was 0.50^n ($n \leq 3$). Probability of carcass persistence, l , within this deposition interval was thus the average of 1/2, 1/4 and 1/8, or 0.292. We assigned this variable a beta distribution with a mean centered at 0.292 to model uncertainty.

We assumed that all Gulf shorelines exposed to neritic waters of the Gulf of Mexico and suitable for carcass deposition were searched, so $h = 1.00$. We also assumed that 90% of the shoreline surveys for carcasses were separated by intervals of 3 d so $k = 0.90$. We assigned this variable a beta distribution with the mean centered at 0.90 to model uncertainty.

Estimates of searcher efficiency (d_j) were based on Ford et al. (2013). We used a value of 0.424 ($= \hat{d}_1$) as the estimate of searcher efficiency for large bird carcasses. Using the average of the 2 values for searcher efficiency reported in Table 2 from Ford et al. (2013) for small bird carcasses, we assumed $\hat{d}_3 = 0.078$. Finally, we assumed the average of the values for small and large bird carcasses, $\hat{d}_2 = 0.251$, as the searcher efficiency for medium-sized carcasses. These

searcher efficiency parameters were also assigned beta distributions, with the means centered at the values listed above.

Parameter uncertainty

The beta probability distributions assigned to each unknown parameter represent our attempt to organize and display what we do and do not know about the parameter's location (Silver 2012), and to assess what would have happened had we used alternate assumptions about the parameter values. To explain how the variances of these distributions were derived, let q represent any of the carcass model parameters. Because these are beta distributions for parameters, the associated distribution for q has hyperparameters a_q and b_q . The mean of the beta distribution is given by $a_q/(a_q + b_q)$ and the variance is also a function of a_q and b_q (Casella & Berger 2002). We linked all of the beta distributions together, for all of the parameters, through a single common hyperparameter, u , such that $a_q = u\hat{q}$ and $b_q = u(1 - \hat{q})$, for \hat{q} representing the estimate of r , l , k , and each value of d_j . Without this step we would have had twelve individual hyperparameters to manipulate (2 hyperparameters for each beta distribution). Note that u can be factored out of both numerator and denominator of the mean, so the mean is independent of u . However, the variance is strongly affected by u : the larger the value of u , the smaller the variance of each parameter.

The value of hyperparameter u was chosen so that distributions of all 6 model parameters were as consistent as possible with uncertainty in parameters described in the literature and with estimates from this and other oil spills (Table 1). Rather than develop even more complexity to express the uncertainty in u , we simply set the value of u at 200 after acknowledging that the distribution of N is sensitive to this choice. We established the value of u at 200 by iterative fitting. That is, we varied u , examined the central 95% interval for each of the variables, and then readjusted u until all 6 probability intervals closely approximated the 95% interval for parameter values that we considered plausible for likely alternate parameter assumptions (Table 1). Later, we doubled and halved this value of u to assess the sensitivity of the analysis to our choice of u (and to the assumed variance of the beta distributions, which u controls).

After setting the value of u at 200, we evaluated the overall uncertainty in our estimates by making re-

peated random draws from the beta distributions of each carcass model parameter and then calculating N_j and summing over j . The Monte Carlo distribution for N was developed by taking 1 million random draws for each parameter (r , l , h , k , d_j), then developing 1 million values of N by the repeated use of Eq. (1) and summation over j .

Exposure probability model

Bird deaths from a spill can also be estimated using bird density (D), the proportionate mortality due to oiling (M), and the spatial extent of the oil (A). We assume that birds become contaminated with oil in direct proportion to the product of the spatial extent of oiling on the water and the density of seabirds within that spatial extent. The number of affected birds in contact with the oil multiplied by the proportionate mortality (bird deaths/oil-exposed bird) should then approximate N , the number of bird deaths, so $N = ADM$ (e.g. Wilhelm et al. 2007, Haney et al. 2014).

Estimating seabird mortality as the product of oil slick area, seabird density and proportionate mortality due to oiling presumes exposure population size equal to AD for an exposure period sufficient to result in proportionate mortality M . This simple relation for estimating mortality due to oil exposure must be modified to account for exposure of new populations of birds owing to oil slick movement and to replacement of birds killed by oil exposure through immigration to the slick area, especially given the ~3 mo persistence of the *Deepwater Horizon* oil slick.

To account for the total population of birds exposed to oil, we introduce an effective exposure renewal-period parameter, P , after which the population of birds exposed to oil is effectively renewed. Denoting the duration of the oil spill as T , there are T/P such exposure renewal periods. If the area of the oil slick during the i^{th} exposure renewal period is denoted as A_i , the number of birds killed during that period is $N_i = A_i D_i M_i$, where D_i and M_i are the bird density and proportionate mortality during that period. The total number of birds killed, N , is:

$$N = \sum_1^{T/P} A_i D_i M_i \quad (2)$$

Table 1. Key features for the probability distributions used to simulate the number of coastal bird deaths caused by the *Deepwater Horizon* oil spill. The following parameters constitute the random variables for the carcass sampling model: r : probability of a bird carcass transported to shore following death; l : probability of the bird carcass persisting between survey periods; k : temporal fraction of the spill that was sampled; d_j : probability of detection of a carcass ($j = 1, 2$ or 3 denoting large [≥ 500 g], medium [300–499 g] or small [10–299 g] carcasses, respectively). For the exposure probability model: \bar{A} : average oil slick size (km^2); D : bird density (birds km^{-2}); M : proportionate mortality for birds

Parameter	Assigned distribution	Mean of distribution	2.5 th –97.5 th quantiles	Median expansion factor
Carcass sampling model				
r	Beta	0.057	0.029–0.093	18
l	Beta	0.292	0.231–0.356	3.5
k	Beta	0.900	0.855–0.938	1.1
d_1	Beta	0.424	0.357–0.493	2.4
d_2	Beta	0.251	0.194–0.313	4
d_3	Beta	0.078	0.045–0.119	13
Exposure probability model				
\bar{A}	Gamma	3600	2520–4780	NA
D	Poisson	5.8	2–11	NA
M	Beta	0.4	0.177–0.659	NA

If D_i and M_i are assumed constant over the duration of the oil spill T , it can readily be shown that $\sum_1^{T/P} A_i$ reduces to $\bar{A}(T/P)$, where \bar{A} is the average oil slick area over the duration of the spill (Haney et al. 2014). Then the number of birds killed is simply:

$$N = \bar{A} D M \left(\frac{T}{P} \right) \quad (3)$$

Parameter selection

We set value of the period P to 1 d based in part on information from satellite imagery for oil spill persistence and recurrence in coastal waters (see the Supplement for more detailed justifications of parameter values). We estimated the average extent of the surface oil slick (\bar{A}) as 3600 km^2 for coastal waters of the northern Gulf of Mexico spill zone based on methods described above for the carcass sampling model. To simulate the uncertainty in \bar{A} , this parameter was treated as a random variable (in the Bayesian sense), and assigned a gamma distribution with shape parameter of 36 and a scale parameter of 100 (i.e. mean and standard deviation approx. 3600 and 600 $\text{km}^2 \text{d}^{-1}$, respectively). A gamma distribution was chosen because it has an inherent lower bound of zero but is otherwise similar to the normal distribution with the parameter values chosen. Two standard deviations constituted ca. 33% of the mean, which reflects uncertainty associated with the overestima-

tion from pixel distortion and analyst misclassification during satellite image assessment for oil presence (e.g. Haney et al. 2014).

We assumed that the mean density of birds, D , was 5.8 birds km⁻² based on McFarlane & Lester (2005), who gave a range of 3.6 to 9.4 birds km⁻². We assumed the density of seabirds in the coastal Gulf of Mexico remained at approximately this level because of several movement processes available for repopulating the spill zone. Birds in this area had flight speeds that facilitated influx to any part of the spill zone in less than 24 h. Also, aerial foragers (species that use surface plunging, aerial dipping, aerial pursuit, skimming and hydroplaning; Nelson 1979) accounted for 96% of all species in the coastal seabird community in the Gulf, whereas more sedentary divers and other primarily surface foragers (a group mutually exclusive from aerial foragers, and that included loons, sea ducks, and phalaropes) are a negligible fraction (Johnson 2011). Finally, new birds arrived continuously into the region during the incident period via ongoing seasonal migrations. Seabird abundance in the Gulf of Mexico increases 17% from spring to summer (Peake 1996), and certain taxa (e.g. storm-petrels, shearwaters, and some terns) become 4 to 5 times more abundant (Hess & Ribic 2000). This random variable D was assigned a Poisson distribution (see Clarke et al. 2003, Oppel et al. 2012) with mean and variance of 5.8 birds km² to reflect the observed range of seabird density in coastal waters (McFarlane & Lester 2005).

We selected a value of 0.40 (i.e. 40%) as an estimate of the proportionate mortality, M , in part based on the observed proportionate mortality in the oiled birds retrieved during the *Deepwater Horizon* (justification detailed in the Supplement). We also considered the proportionate mortality of aerial seabird species reported from other oil spills. Proportionate mortalities from 5% to near 90% from oil exposure are reported for marine birds, with rates of 22 to 89% (median 61%) listed for 13 aerially foraging seabird groups (Camphuysen & Heubeck 2001). This parameter was assigned a beta distribution with parameters $a = 6$ and $b = 9$ (mean of 0.40 and standard deviation of 0.12) so that most values in the distribution were below the median value of reported estimates noted above.

Parameter uncertainty

As in the carcass sampling approach, we used a Bayesian notion of probability to organize and weight

plausible assumptions about alternative parameter values and to reflect our knowledge of parameter location based on available literature and observations from the *Deepwater Horizon* spill. A Monte Carlo distribution for the unknown number of bird deaths estimated by the exposure probability model was then developed by taking 1 million replicates from the distribution of the parameters (Table 1), then generating 1 million values using Eq. (3).

RESULTS

Estimates of total bird deaths

The carcass sampling and exposure probability approaches produced similar estimates for the number of bird deaths. Dividing the number of recovered carcasses by the estimated expansion factors (Table 2) gave an estimated 600 000 bird deaths. Alternatively, assuming an average slick size of 3600 km², a proportionate mortality of 0.40 bird deaths per exposed bird, and a bird density of 5.8 birds km⁻², we estimated slightly over 8000 bird deaths d⁻¹, on average. Expanding for all 95 d having an observed oil slick within 40 km of the coast, the number of bird deaths was estimated as approx. 800 000.

Notably, with the carcass sampling approach, expansion factors ranged from slightly under 200 to over 800 unobserved carcasses per each recovered carcass (Table 2), depending on size category. The largest expansion factor was for birds with small body sizes, the size category with the fewest number of carcasses found (6.4% of all recoveries). Numbers of bird deaths in the small body size category were ultimately estimated to be slightly over 15% of the total.

The Monte Carlo distribution of the number of bird deaths from carcass sampling had a mean of 630 000 and a median of 590 000, indicating the distribution was skewed slightly toward larger values (Fig. 1). Approx. 95% of the simulated probability covers the interval from 320 000 to 1 200 000 bird deaths (shortest interval), whereas 80% of the simulated probability covers the interval from 390 000 to 910 000. The probability that the number of bird deaths exceeded 400 000 is approx. 89%, and the probability that the number of bird deaths exceeded 500 000 is approx. 69%, based on the carcass sampling probability model.

The Monte Carlo distribution for the carcass sampling distribution of bird deaths was sensitive to the

value of the hyperparameter ($u = 200$). A change to this hyperparameter changes the variances of all of the distributions of the parameters for the carcass survey together. Halving this hyperparameter to 100 increased the variance, flattened the distribution somewhat, and shifted the distribution toward larger values. This change raised the standard deviation of the r parameter from 0.016 to 0.023, the l parameter from 0.032 to 0.045, and the k parameter from 0.021 to 0.030. The standard deviation of the Monte Carlo distribution of bird deaths increased from approx. 220 000 to 400 000, the medians increased from 590 000 to 620 000, and the upper 97.5th percentile increased from 1.2 million to slightly over 1.8 million. Halving the hyperparameter again to 50 flattened the distribution of the total bird deaths even more, with the 97.5th percentile being greater than 3 million bird deaths. In contrast, doubling u to 400 reduced the standard deviation of the r parameter from 0.016 to 0.012, the l parameter from 0.032 to 0.023, the k parameter from 0.021 to 0.015, and the 97.5th percentile of the distribution to 920 000 — values that we judged to be too small to reflect the actual uncertainty in the parameter values. We concluded that $u = 200$ produced distributions of the parameters that were the most consistent with reasonable alternate assumptions about the parameter values.

The Monte Carlo distribution for the number of bird deaths using exposure probability was flatter, and centered over slightly higher values when compared to the distributions of estimates from the carcass sampling approach. The median of this distri-

Table 2. Estimates of the combined probability of final shoreline recovery for large-, medium-, and small-bodied seabirds (denoted \hat{p}_j) in a carcass-sampling model used to estimate mortality in coastal waters of the Gulf of Mexico during the *Deepwater Horizon* spill. The sampling-based expansion factor for the observed number of carcasses in the i^{th} size category is the multiplicative inverse ($1/\hat{p}_j$) of the probability of recovery for each size class. \hat{N}_j denotes a sampling-based estimate of the number of birds killed for body size j . Observed carcass counts were 493 for large birds ($j = 1$), 1383 for medium birds ($j = 2$), and 128 for small birds ($j = 3$). All estimates are rounded (mortality estimates do not necessarily sum exactly due to rounding)

Parameter	Large birds (≥500 g)	Medium birds (300–499 g)	Small birds (10–299 g)
\hat{p}_j	0.00635	0.00376	0.00117
$1/\hat{p}_j$	157	266	856
95 % uncertainty interval for $1/\hat{p}_j$	90–330	150–570	440–2100
\hat{N}_j	80000	400000	100000

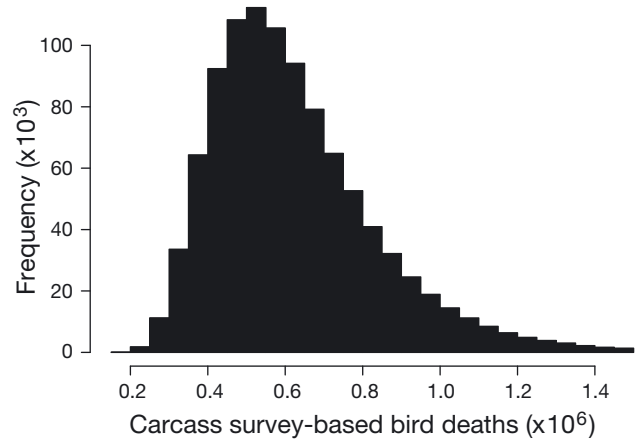


Fig. 1. Monte Carlo distribution (1 million simulation replicates) of the number of coastal bird deaths from the *Deepwater Horizon* oil spill based on a carcass survey approach to estimating total bird mortality. Median for the simulated distribution = 590 000 bird deaths; mean = 630 000

bution was approx. 700 000 whereas the mean was approx. 800000, again skewed toward larger values (Fig. 2). The 95 % uncertainty interval covers 160 000 to 1 900 000 bird deaths, while the 80 % interval covers 300 000 to 1 400 000. The probability that the number of bird deaths exceeded 400 000 is approx. 81 %, and the probability that the bird deaths exceeded 500 000 is approx. 72 %.

Influence of carcass size

Relative to their occurrence when surveyed while alive in coastal Gulf habitats, small-bodied carcasses were markedly under-represented in the tally of dead oiled birds found during the *Deepwater Horizon* spill (Fig. 3). As defined here, small-bodied birds account for about 34 % of the communities in coastal habitats (Johnson 2011). Conversely, both medium- and large-bodied birds made up a disproportionately large proportion of the carcass counts relative to their occurrence in coastal habitat.

By implementing a searcher parameter (d) specific to body size, the size distribution of bird-death estimates more closely matched the live proportions observed in the small-bodied bird category (Fig. 3). In addition, by using the size-group searcher efficiency parameters we eliminated entirely the disproportionately high representation of large-bodied birds in the carcass counts relative to their live occurrence in coastal Gulf habitats. However, the searcher efficiency adjustments did not reduce a similar discrepancy in representation seen for the medium size birds (Fig. 3).

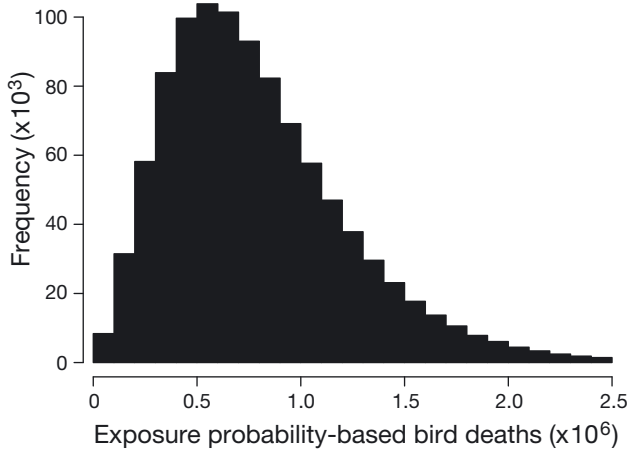


Fig. 2. Monte Carlo distribution (1 million simulation replicates) of the number of coastal bird deaths from the *Deepwater Horizon* oil spill based on an exposure probability model over 95 d. Median number of bird deaths \approx 700 000

DISCUSSION

Our results indicate that bird losses from the *Deepwater Horizon* oil spill almost certainly numbered into the hundreds of thousands in coastal waters of the northern Gulf of Mexico. Although each estimation approach was different conceptually—and used largely independent data—both showed that the most likely coastal bird mortality was approx. 700 000.

Carcass sampling model

Carcass sampling expanded approx. 2000 bird carcasses recovered from the coastal zone into an

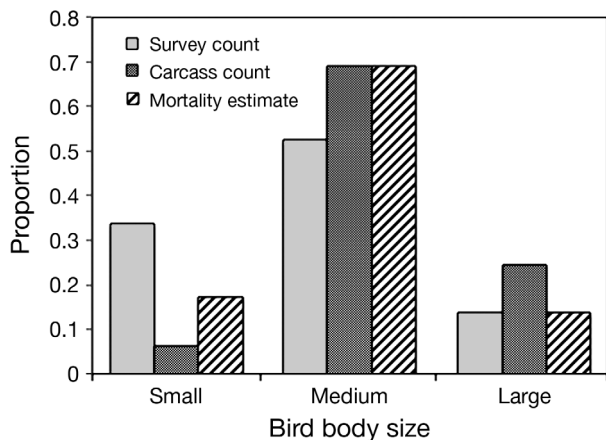


Fig. 3. Comparison of the proportions of birds that were surveyed live in coastal Gulf habitat (Johnson 2011) to the proportions recovered as carcasses and estimated killed during the *Deepwater Horizon* spill. Bird size categories: small: 10–299 g; medium: 300–499 g; large: \geq 500 g

estimate of nearly 600 000 bird deaths—a very large statistical extrapolation. Even so, those few observed carcasses constitute the actual, observable evidence analyzed in the conventional manner used for avian mortality assessments after oil spills (e.g. Castege et al. 2007, Munilla et al. 2011). What was less conventional was using probability to generate numerical results that include a probability distribution of alternate assumptions about how to statistically expand such carcass counts to account for realistic processes that reduced the numbers recovered from shoreline surveys.

The counts of recovered carcasses are usually far less than the number of birds killed by an oil spill (Seys et al. 2001, Ford 2006). Low carcass counts or small recovery probabilities alone do not necessarily lead to bias. However, in this case, because carcass recovery was low and expansion factors were large, any source of bias would be highly leveraged. For example, if some unmeasured process (e.g. carcass burning) removed even a small number of carcasses en route to shore, each missing carcass would create bias in our estimate proportional to the large expansion factors.

We have tried to understand and account for all recovery processes. On balance we suspect that we were more likely to have underestimated than to have overestimated bird mortality. Nevertheless, if birds tended to fly towards coastlines after exposure, and then later died near or on shore, then we would have underestimated r and overestimated mortality. If the actual decline of seabird density with distance from shore is better described as a negative exponential function, then our assumption of a linear decline also would lead to overestimation of mortality.

Cleanup tactics during spill response may have led to underestimation by intercepting and destroying carcasses before they could be retrieved. Between 28 April and 19 July 2010, 376 controlled burns at sea consumed 3.5 to 4.9×10^7 l of oil, a volume approximately equivalent to one *Exxon Valdez* spill. Although burns were avoided if live apex predators were present (Allen et al. 2011), floating carcasses would have been destroyed since ignitions took place where convergences had concentrated buoyant material (FISG 2010). Skimming operations removed half of the oil volume removed by burning (FISG 2010), which may also have removed carcasses.

Carcass loss at sea from biological factors also reduces shoreline deposition. Bird consumption by tiger sharks *Galeocerdo cuvier* or other higher trophic-level consumers (Kaufman 2012) in the Gulf exacerbates carcass loss (Wiese 2003). Such losses

lower the estimate of mortality if, as in this study, no correction is applied for *in toto* ingestion of seabird carcasses.

Our estimate of 5.7% probability for carcass transport to shorelines is lower than values reported in most previous studies. Piatt & Ford (1996) reported a probability of 12%. A summary by Munilla et al. (2011) gave a mean of 17.1% based on 37 experimental studies with 7040 combined block and carcass releases. Block recoveries overstate deposition as blocks do not decompose and weather like carcasses (Wiese & Jones 2001). Using a block-to-carcass correction provided by Munilla et al. (2011), the difference between values from the meta-analysis above and our study narrows to 11.2% versus 5.7%, respectively. Our estimate of carcass deposition was nevertheless higher than reported for another Atlantic Ocean oil spill (as low as 0.8% in the *Prestige* spill; Castege et al. 2007).

Although we describe the carcass movement with a simple model, the actual movement process was quite complex. Early in the spill, oil was steered away from the coast (Dietrich et al. 2012). Response authorities opened locks on Mississippi River canals to redirect the discharge and prevent or delay *Deepwater Horizon* oil from reaching the ecologically fragile coastal marshes. Under weak winds and effects of sea surface slope, high buoyancy-driven outflow (Falcini et al. 2012) blocked much of the surface oil from reaching most Gulf shorelines until late May 2010. Except along the immediate shoreline, wind forcing played a negligible role in large-scale oil transport (Huntley et al. 2011) until early July when Tropical Storm Alex transited the southern Gulf (Dietrich et al. 2012, Le Hénaff et al. 2012). Oil was then driven shoreward by the storm surge (Pugliese Carratelli et al. 2011). The extent of oiled shoreline subsequently tripled (Boufadel et al. 2014), and recovery of bird carcasses accelerated just before the well was capped (Belanger et al. 2010).

We assumed that all shorelines affected by this spill were searched (i.e. $h = 1.00$). Responders searched 6841 km of the Gulf's beach, wetland, and man-made shorelines during the *Deepwater Horizon* incident, and some oiling was observed on 1705 km (Owens et al. 2011a,b). If some shorelines were missed, or if they received less attention by searchers, both of which seem likely given the geographic extent of the *Deepwater Horizon* spill and the complexity of shorelines, then fewer carcasses would be recovered, ultimately leading to an underestimate of the bird losses.

Our assumed daily carcass persistence proportions of ~50% on beaches the first few days after deposi-

tion is similar to values reported from other oil spills. Nevertheless, as few as 10% of carcasses may remain 2 to 4 d after reaching shore (Ford 2006, Byrd et al. 2009, Ford & Zafonte 2009). Due to the Gulf's many scavengers (e.g. gulls, crows, raptors, raccoons, mink, crabs), shoreline persistence may have been even lower than we assumed. Given search intervals by *Deepwater Horizon* responders that ranged up to 12 d (USDOJ 2011), our assumed 3 d interval would, at least on some occasions, lead to an overestimate of carcass persistence, ultimately underestimating bird deaths. Carcass persistence was not derived *in situ*, however, so this parameter had to be approximated from values based on previous oil spills.

Exposure probability model

Despite a simpler conceptual approach and fewer parameters, the exposure probability model gave an even wider uncertainty interval for the bird deaths estimated in coastal waters (Fig. 2). Here again, we may have made incorrect assumptions about the values of the parameters that led to estimates that erred in either direction.

We assumed that 60% of coastal birds exposed to *Deepwater Horizon* oil avoided a lethal dosage. The lethal exposure proportion we used falls near the lower end of the interval of values used to characterize bird mortality from other oil spills (e.g. 23 to 100%; WIW 2001, Robertson et al. 2006, Wilhelm et al. 2007, Fifield et al. 2009). Assuming that warm Gulf waters may be less likely to induce thermoregulatory stress from exposure, we projected that all live oiled birds survived (e.g. see Selman et al. 2012). In cooler seas, live oiled birds are typically included in the tally of mortality (cf. Page et al. 1990, Castege et al. 2007, Munilla et al. 2011). To the extent that we underestimated the lethal dose, we would have underestimated the total bird deaths with the exposure probability approach. We could not, for example, consider all of the ways that oil could lead to mortality, such as via ingestion and inhalation. Any error in Eq. (3) would propagate linearly. If, for example, 60% of exposed birds died rather than our assumed 40%, then our estimate of total mortality would underestimate by a factor of 60/40 or 1.5.

We note that few large coastal spills have occurred in warm subtropical seas where the seabird communities comprise high proportions of aerially foraging species. Future study aimed at documenting seabird exposure and behavior around oil slicks in warm oceans are needed (e.g. see Watson et al. 2009).

Delayed mortality of oiled birds may have occurred at a higher rate than what we assumed.

We can think of several ways we could have overestimated the bird mortality through errors in measurement, incorrect assumptions, or oversimplification. The most obvious potential source for overestimate might be our assumption that the bird density returned to a baseline level of 5.8 birds km⁻² due to emigration and bird flux after a period of just 1 d (but see Fifield et al. 2009). Numbers of birds subject to risk at the time of a spill are often hard to quantify for assessments of spill mortality (e.g. French McCay & Rowe 2004). The bird density that we used for coastal Gulf waters was typical for seasons when the *Deepwater Horizon* incident occurred (McFarlane & Lester 2005), although it was derived from outside the immediate spill zone. We attempted to account for uncertainty in this parameter with an assigned probability distribution, but we have no way to assess our success at estimating the background density or the time it took after mortality for the density to return to the background level because there are no alternative estimates for bird density readily available.

Most importantly, due to limits imposed by image coverage or sensor sensitivity (Leifer et al. 2012, Lindsley & Long 2012) and high application of chemical dispersants (e.g. Allan et al. 2012), satellite delineation of the exposure risk presented to birds is incomplete (Haney et al. 2014). Underestimation of contamination risk on the water would also lead to underestimation bias in the bird mortality using the exposure probability approach.

Importance of body size

Our study is among very few to make substantial adjustments to mortality estimation based on carcass size following a large marine oil spill. An adjustment for bird body size was used in the relatively small MV *Kure* spill (1.7×10^4 l) in Humboldt Bay, California (Ford et al. 2013). Smaller birds are more difficult to detect under field conditions, whether alive (Barbraud & Thiebot 2009) or dead (Smallwood 2007). Such adjustments are necessary to account for the large disparity observed between relatively low proportions of small bodied carcasses recovered compared with live small birds detected in Gulf surveys (Fig. 3).

Proportionate mortalities from oil spills do vary by body size (Page et al. 1990), although differences among species are not well understood (Evans &

Keijl 1993). Exposures to very small oil dosages cause loss of plumage integrity (O'Hara & Morandin 2010), lowering insulation and raising mortality (Jenssen 1994). Because thermal conductance scales allometrically to body size (Aschoff 1981), insulation is more easily compromised in smaller-bodied species, and a greater representation of small birds might be expected in the tally of mortality. Instead, however, only 128 small-bodied carcasses were retrieved during the *Deepwater Horizon* spill (6.4% of the total), despite smaller birds making up a third of avian communities in the coastal Gulf (Johnson 2011).

Small-bodied birds may have beach persistence times only 5 to 13% those of large- and medium-bodied birds (Seys et al. 2001), as small birds are more readily carried off by scavengers (Ford & Zafonte 2009, Ponce et al. 2010), whereas large, heavy birds must usually be scavenged *in situ*. In addition, smaller bird carcasses can be scavenged by consumers having a wider range of body sizes, including small-bodied predators. Without correcting for body-size, especially where bird communities contain a large proportion of small-bodied birds as in the Gulf of Mexico (Johnson 2011), bird losses in marine oil spills could be substantially underestimated.

Ecological implications from spill mortality

We focused solely on near-term, acute mortality from the *Deepwater Horizon* spill, even though observations of oiled birds continued for at least 1 yr (Henkel et al. 2012). We did not include estimates for indirect (Velando et al. 2005) or chronic population effects (Irons et al. 2000), either of which can increase the avian mortality (Pérez et al. 2008). For example, oil cleanup and other response activities reduce bird survival (Burger & Tshipoura 1998).

Despite a focus here on near-term effects, high avian mortality in the *Deepwater Horizon* spill likely had population-level repercussions. We estimated mortality in 4 seabird species using the size-specific expansion factors ($1/p_i$ listed in Table 2) and numbers of carcasses found for that species (listed in Supplement 1). Projected losses reached or exceeded 24 000 birds in all 4 species and reached 232 000 for laughing gulls (*Leucophaeus atricilla*, Table 3). In 3 species, estimated losses reached or exceeded 12% of the total population estimated present in the northern Gulf of Mexico.

Mortality of laughing gulls was ~32% of the regional Gulf population (Table 3). National Audubon Society Christmas Bird Count (CBC) data from Florida, Ala-

Table 3. Estimated population size and mortality from the *Deepwater Horizon* oil spill for 4 coastal bird species. Breeding numbers refer to the US Gulf of Mexico only (except northern gannet, for which breeding numbers pertain to entire Canadian population; Chardine et al. 2013). Sub-adults are numbers in age classes prior to age at first breeding, estimated with life tables (e.g. Rattiste 2004) that accounted for longevity and age-specific survival (Belant & Dolbeer 1993a, Burger 1996, Buckley & Buckley 2002, Mowbray 2002, Shields 2002). Unless otherwise specified, non-breeders were assumed to constitute 50% of breeders (Votier et al. 2008), not including subadults. Total populations assumed to be vulnerable to the spill were adjusted for any non-residents and non-breeding adults (Dolbeer & Bernhardt 2003). Spill mortality was estimated using size-specific expansion factors (Table 2) applied to the carcass counts of each species (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m513p239_supp.pdf). Size categories: large: ≥ 500 g; medium: 300–499 g

Species	Size cat.	Population exposed ($\times 10^3$ ind.)				Estimated mortality ($\times 10^3$ ind.)	
		Sub-adults	Br.	Non-Br.	Total	%	
Northern gannet <i>Morus bassanus</i>	Large	170	234	32	436	35	8 ^a
Brown pelican <i>Pelecanus occidentalis</i>	Large	99	68 ^b	34	201	24	12
Laughing gull <i>Leucophaeus atricilla</i>	Medium	238	260	232 ^c	730	232	32
Royal tern <i>Thalasseus maximus</i>	Medium	81	79 ^d	40	200	26	13

^aApproximately 50% if considering only the fraction of North American gannets projected as over-wintering in the Gulf of Mexico (Montevecchi et al. 2012)

^bShields (2002), updated by Louisiana Department of Wildlife and Fisheries (www.wlf.louisiana.gov/news/29112; accessed 16 June 2013)

^cMinimum 40% of non-residents (all ages) estimated to be in the Gulf from northeastern USA (see Belant & Dolbeer 1993b)

^dBuckley & Buckley (2002), updated by Florida Fish and Wildlife Conservation Commission (www.myfwc.com/bba/; accessed 9 June 2013)

bama, Mississippi, Louisiana, and Texas (NAS 2010) corroborate this decline. CBC data reveal that after the *Deepwater Horizon* incident, laughing gulls in the Gulf region declined by 61 to 64% between winter 2010 and winters 2011, 2012, and 2013. Given adequate coverage and sample sizes (only for laughing gull did CBC survey effort exceed 10 birds h^{-1} among the 4 species examined), the NAS CBC could provide an alternative to evaluate population-level impacts from large marine oil spills in North America.

In addition to carcass sampling and exposure probability models, differences in breeding colony attendance before and after a spill are another means to corroborate avian mortality (e.g. Piatt & Ford 1996). Without due consideration of the population age class and vital rates affected (Votier et al. 2008), oil spill impacts to seabirds can be masked. We therefore encourage more research into the demographic consequences to the Gulf's coastal birds from this large marine spill.

Given both its chronic and acute characteristics, the *Deepwater Horizon* disaster was a major perturbation to the northern Gulf of Mexico (Peterson et al. 2012). Our estimates do not address delayed mortality from changes to ecosystem function (e.g. Peterson 2001) or consequences to food webs from reductions in marine predators caused by this oil spill. Both topics await further study.

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