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Bird mortality from the *Deepwater Horizon* oil spill. I. Exposure probability in the offshore Gulf of Mexico

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ABSTRACT: Following the 2010 *Deepwater Horizon* MC 252 blowout in the Gulf of Mexico, most surface oil remained more than 40 km offshore, precluding reliable estimation of offshore avian mortality based on shoreline counts. Using an exposure probability model as an alternative approach, we estimated that between 36 000 to 670 000 birds died in the offshore Gulf of Mexico as result of exposure to oil from the *Deepwater Horizon*, with the most likely number near 200 000. Our exposure probability model is a technique for estimating this offshore component of avian mortality as the product of the oil slick area, the density of the birds above the oil slick, and the proportionate mortality of birds that could be exposed to oil during an assumed exposure period. The duration of the exposure period is treated as an estimated parameter to account for oil slick movement, exposure of birds immigrating to the oil-contaminated area, and re-exposure of birds that survived prior vulnerability to exposure. Total avian mortality is determined as the sum of mortalities from each exposure period. Exposure probability may be the only method available to estimate bird mortality from large, remote oil spills in the open ocean where carcasses are unlikely to ever reach shore. In the case of the *Deepwater Horizon*, the uncertainty interval is quite large because several parameters could not be well estimated. Historically sparse survey coverage effectively led to an under-appreciation of the effects of this spill on marine birds.

KEY WORDS: Avian mortality · Exposure probability · Oil spill · *Deepwater Horizon* · Gulf of Mexico · Offshore habitat · Marine birds

INTRODUCTION

Following large oil spills at sea, seabirds are particularly sensitive to both internal and external oil exposure (Leighton 1993), and their foraging habits, preening behavior, and resting requirements lead to frequent contact with surface oil. Whereas proximate exposure, cause-of-death, and pathologies for individual birds can be directly examined (Balseiro et al. 2005), population-level effects must be approximated indirectly (Wilhelm et al. 2007).

Bird mortality resulting from oil spills has usually been estimated by tallying recovered carcasses, assessing the probability of recovery, and using an assumed expansion factor to statistically extrapolate the carcass tally to an estimate of total mortality (Wiese & Robertson 2004, Haney et al. 2014, this volume). However, when mortality occurs far offshore, winds and currents, scavenging by consumer species, and sinking from loss of buoyancy during decomposition combine to greatly diminish carcass recoveries (Wiese 2003, Munilla et al. 2011).

The *Deepwater Horizon* blowout began on 20 April 2010 and discharged liquid and gaseous hydrocarbons continuously into the Gulf of Mexico over the next 86 d. Before the seafloor wellhead was

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capped on 15 July 2010, the *Deepwater Horizon* had discharged about 6.7×10^8 l of liquid petroleum into the Gulf, of which about 3.3×10^8 l reached the sea surface (McNutt et al. 2012), equivalent to about 8 *Exxon Valdez* spills. Extensive satellite and other reconnaissance detected a massive surface oil slick in the north central Gulf of Mexico (Fig. 1) that spread over the outer continental shelf, continental slope, and abyssal plain. Frontal eddies of the Loop Current (Vukovich 1995) entrained some oil from the well towards southwestern Florida (Liu et al. 2011), with smaller, isolated patches of surface oil advected toward the Yucatan coast of Mexico (NOAA 2013).

Climatic and oceanographic conditions during the *Deepwater Horizon* blowout acted to suppress shoreline deposition of bird carcasses along the coastline (Haney et al. 2014). Outflow by the Mississippi River impeded surface oil and other drifting objects from reaching shorelines during the early phase of oil discharge (Kourafalou & Androulidakis 2013). Other surface oil was advected by Loop Current frontal eddies even further away from the coast (Liu et al. 2011). Wind-driven transport of oil toward the shoreline was negligible except near the immediate coast (Huntley et al. 2011). Because more than 80% of the cumulative oil slick occurred 40 km or more offshore, an alternative to carcass recovery is needed to estimate avian mortality in most of the spill zone.

We applied different methods to estimate seabird mortality from the blowout, depending on distance from the shoreline, for several reasons. The offshore seabird community consists almost entirely of aerial foragers, whereas the community closer to shore includes surface foraging seabirds. Average aerial seabird densities are lower offshore (Tasker & Mustoe 2003), but increase substantially approaching the coast within 40 km (McFarlane & Lester 2005), so the average density of the offshore community may be considered nearly isotropic with respect to horizontal direction, but the community within 40 km of the shore may not. Finally, in the northern Gulf of Mexico, seabird mortality within 40 km of the shore may be estimated based on recoveries of oiled carcasses from shorelines, whereas seabirds killed more than 40 km offshore have negligible probability of reaching the coastline (Haney et al. 2014), and hence a different approach must be used.

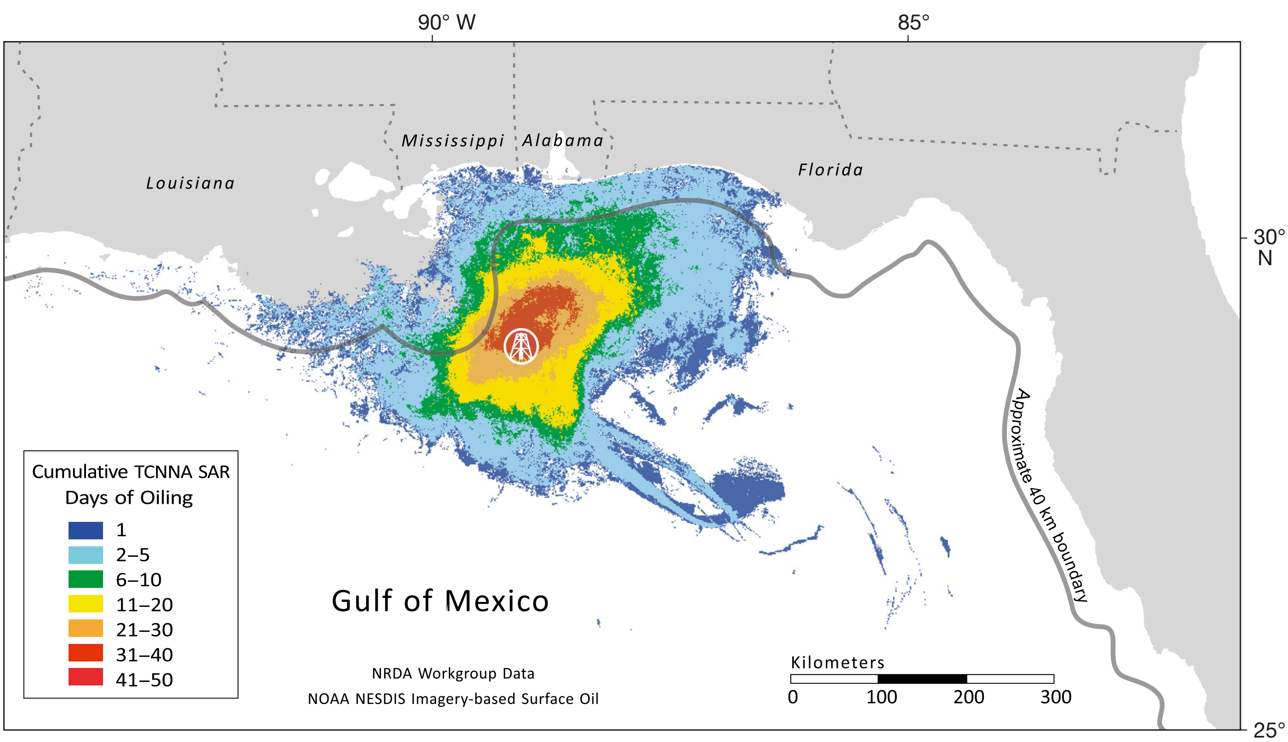

Fig. 1. Total duration of surface oil from the 2010 *Deepwater Horizon* MC 252 blowout in the northern Gulf of Mexico. Duration indicates the number of days that oil slicks were detectable by satellites. Duration does not necessarily imply continuous oil presence at any location. Oil presence was analyzed with the Textural Classifier Neural Network Algorithm (TCNNA) for synthetic aperture radar (SAR; see also 'Data sources for surface oil' and 'Oil surface area measurement' in Supplement at www.int-res.com/articles/suppl/m513p225_supp.pdf) from NOAA (2013)

Here we develop an estimate of the offshore bird mortality caused by the blowout, along with the associated uncertainty using an exposure probability model. This model is based on 3 parameters (oil slick size, bird density, and proportionate mortality) combined with a temporal expansion factor for the effective duration of exposure for a cohort of exposed birds. We estimate uncertainty by assigning probability distributions to the parameters to reflect alternative assumptions about the parameter values. We then use Monte Carlo simulation to assess the consequences of these assumptions. The resulting framework provides an alternative approach for estimating seabird mortality at remote, open ocean oil spills.

METHODS

Study area and modeling domain

We considered the acute mortality phase to last 103 d, from 20 April until 31 July 2010, to account for bird mortality from contact with lingering surface oil after the wellhead was capped on 15 July (Aeppli et al. 2012). Oil slicks were detectable by satellite sensors beginning 22 April 2010 (Tables S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m513p225_supp.pdf), but seabirds were exposed to oil as soon as it surfaced above the wellhead. Avian mortality clearly continued after the well was capped based on Wildlife Collection Reports that revealed an increasing ratio of dead-to-live bird recoveries through late July 2010 (Belanger et al. 2010). In the present paper, we limit the scope of investigation to waters 40 km or more offshore (Fig. 1).

Exposure probability model

We assumed that the number of birds killed, denoted as N, can be approximated as the product of 3 factors: oil slick surface area (A), seabird density above the slick (D), and a proportionate mortality (M):

$$N_I = ADM \quad (1)$$

where N_I is the initial or conceptual approximation, prior to accounting for the temporal dynamics of the spilled oil. Eq. (1) is based on the fundamental assumption that all birds over an oil slick during a sufficient period of time (i.e. exposure period) would eventually be exposed to oil (Fifield et al. 2009), and that birds flying above the uncontaminated sea surface in the same period of time will remain unaffected. Furthermore, we assume that some proportion M of the birds that would be exposed during this period will die as a result of oil contact (Wilhelm et al. 2007).

To estimate total mortality resulting from a protracted oil discharge event such as the *Deepwater Horizon*, we partitioned the assumed 103 d duration of the oil slick, denoted here as T, into a series of consecutive exposure periods, denoted as P, and apply Eq. (1) to each period. We treat the exposure period P as an adjustable parameter to account for the time required to replenish birds killed by oil, either by slick movement to areas not previously oiled or not recently oiled, or by birds that immigrate into oiled areas. Birds that immigrate into oiled areas may include previously un-exposed birds and birds that survived past vulnerability to exposure in immediately adjacent areas currently un-oiled, or birds that arrive to the region through longer-distance seasonal migrations. We use the notation P to denote a variable describing an interval of time. We use $\hat{P}$ to denote a specific number of days for a particular exposure period. Symbolically there are T/P total periods and we index these with $p = 1, 2, \ldots T/P$. Parameters may vary by period, so that A_p denotes the oil slick surface area during period p. Then, using Eq. (1) for each individual period, the second approximation (denoted with the II subscript) of total number of birds killed by the oil spill can be found with summation:

$$N_{II} = \sum_{p=1}^{T/P} N_p = \sum_{p=1}^{T/P} A_p D_p M_p \quad (2)$$

We have assumed that the population exposed within an exposure period declines by proportion M_p by the end of the period, after which the population is restored to a new density of birds, D_{p+1}, exposed during the succeeding period as a result of slick movement, bird immigration and survival. Varying the exposure period duration P then allows us to assess alternative assumptions regarding the time necessary to replenish the density of birds above the oil slick.

The next simplifying assumptions we make are that the exposure periods have equal durations P, that the proportionate mortality M is the same for each period, and that the initial seabird density D averaged over the oiled area for exposure period p is approximately constant for all exposure periods as a result of slick movement and bird immigration to oiled areas over the duration of the exposure period. If M and D are assumed constant, they may be factored out of the summation in Eq. (2) to give

$$N_{III} = \sum_{p=1}^{T/P} DMA_p = DM\sum_{p=1}^{T/P} A_p \quad (3)$$

If we denote the average spatial extent of the oil slick as

$$\bar{A} = \frac{P}{T}\sum_{p=1}^{T/P} A_p \quad (4)$$

then the number of bird deaths is found as the product of 3 parameters to describe the average deaths per period and the number of exposure periods:

$$N = (\bar{A}DM)\left(\frac{T}{P}\right) \quad (5)$$

Each parameter ($\bar{A}$, D, M, and P) can be thought of as an unknown random variable (i.e. in the Bayesian sense), and each random variable could be given a probability distribution to represent alternative assumptions about values of the parameter. At other times we will view the problem in a sampling context (i.e. in the sampling sense the parameters are fixed and data realizations are thought of as random), denoting the parameter's specific fixed numerical estimates as $\hat{\bar{A}}$, $\hat{D}$, $\hat{M}$, and $\hat{P}^{-1}$. In this latter case, we will multiply the estimates together to develop a single estimate of bird mortality. When we think of the parameters as random, we mean that we will assign probability distributions to each parameter in order to explore the alternative values of N that would have come about as the result of alternative assumptions about the values of the individual parameters (Silver 2012).

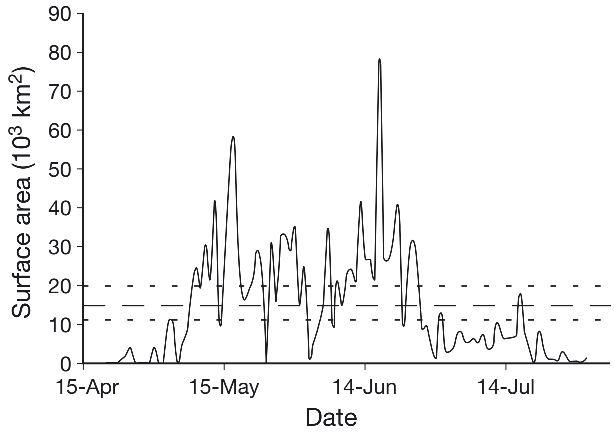

Fig. 2. Solid line: extent (in km^2) of the surface oil slick (waters ≥40 km offshore) in the northern Gulf of Mexico oiled zone during the *Deepwater Horizon* MC 252 blowout (includes days with no satellite coverage); dashed line: average slick size used in the model; dotted lines: 2.5th and 97.5th percentiles of a probability distribution for this average. Satellite measurements of slick extent were augmented with oil spill trajectory models and other ancillary data. See Table S2 in the Supplement for details

Parameter estimates and probability distributions

Several estimates of oil slick area over time are available for the *Deepwater Horizon* blowout (e.g. Hu et al. 2011). Based on a synthesis of this information (Fig. 2; see also Tables S1 & S2 in the Supplement), the estimated average slick size, $\hat{\bar{A}}$, is 15 000 km^2. For the purpose of assessing uncertainty, we assigned this parameter a gamma probability distribution with mean 15 000 and SD 2300 km; 2 SD are approximately 30 % of the mean slick size, which reflects classification errors associated with remote sensing estimates of oil extent (Garcia-Pineda et al. 2009). A gamma distribution was assigned because it has an inherent lower bound of zero but is otherwise similar to the normal distribution with the parameter values chosen.

Because direct measurements of bird density above the oil slick were not made contemporaneously during the spill, we used estimates of bird density reported from prior surveys of the northern Gulf of Mexico during spring and summer. While actual density is highly variable on small spatial or temporal scales, the variability of averages across large spatial and temporal scales would be considerably less. Tasker & Mustoe (2003) covered a total survey distance of 1903 km in the same season, along the outer continental shelf and continental slope near the *Deepwater Horizon* well, and observed a total of 912 birds from 23 species (all aerial foragers). Multiplied by a transect width of 300 m (Tasker et al. 1984), spatial coverage was therefore 570.9 km^2, resulting in an estimated density of 1.6 birds km^{-2} (unadjusted for detectability; e.g. Barbraud & Thiebot 2009). In a different Gulf survey in the oiled area from the 1990s, Hess & Ribic (2000) recorded 769 birds in August within a strip transect 300 m wide by 1592 km long (= 477.6 km^2) for an identical value of 1.6 birds km^{-2}. The estimated density of birds, $\hat{D}$, was therefore assumed to be 1.6 birds km^{-2}. Assuming that the true average density of birds must have been substantially lower than the observed average density in coastal areas (3.6–9.4 birds km^{-2}; McFarlane & Lester 2005), and assuming that the true average density should have a very low probability of being more than twice the 1.6 birds km^{-2} reported by Tasker & Mustoe (2003) or Hess & Ribic (2000), this density parameter was assigned a gamma distribution with a mean of 1.6 and SD of 0.61 birds km^{-2}.

In some previous studies of offshore spill mortality to seabirds, all diving birds on the ocean surface inside the perimeter of an oil slick were assumed to have died (Wilhelm et al. 2007), or if bird flight vectors intersected the slick within a 24 h period, all such flying birds were also assumed to have died (Fifield et al. 2009). Seabird vulnerability to surface oil, however, can vary as a function of the species' time spent on the sea surface (Williams et al. 1995). Although we assumed all birds over the oil slick could have been exposed, we considered only some proportion of these birds, *M*, as having had contact sufficient to lead to death from oil exposure (whether via ingestion, respiration, or plumage contamination).

Because many of the bird species affected were storm-petrels, frigatebirds, tropicbirds, and pelagic terns, all of which spend a high proportion of time in the air (Table 1), we reasoned that oiling mortality rates would be lower for these birds than it would be for species that spent more of their time resting on the sea surface. Published estimates of oiling mortality rates for all seabird species, regardless of foraging styles and from all locations, range from 5 to 100% (Camphuysen & Heubeck 2001, Williams et al. 1995). However, when restricted to those seabirds with aerial foraging styles, the range narrows to 22–89% (Camphuysen & Heubeck 2001), including birds whose deaths in northern climates would be proximately caused by thermal stress. Assuming that thermal stress would be lower and that highly aerial seabirds spend less time in surface contact in the Gulf of Mexico, we chose a value of 0.33 as a reasonable estimate of proportionate mortality, *M*, for offshore birds affected by the blowout. To represent uncertainty, *M* was assigned a beta distribution with a mean of 0.33 and SD of 0.15 so that *M* would rarely exceed 0.65 in simulation.

Based on oil slick movement, local bird movements, long-distance migrations, and weather changes (see the Supplement: Migration and replacement of seabirds over the spill zone), we estimated time to restore density following the loss of birds due to mortality as likely between 1 and 7 d. We further assumed density of birds returned to the initial level of *D*

Table 1. Species composition, breeding origin, and relative abundances (total numbers observed) of marine birds characteristic of May, June, and August in the offshore Gulf of Mexico within the oiled zone; H&R: Hess & Ribic (2000); T&M: Tasker & Mustoe (2003). Breeding origins — ONWA: outside the northwest Atlantic Ocean; NWA: northwest Atlantic Ocean; WI/C/B: West Indies, Caribbean Sea, or Bahamas; NGOM: northern Gulf of Mexico (in or near spill zone); SGOM: southern Gulf of Mexico (outside the spill zone). Totals in H&R included birds tallied both inside and outside the 300 m strip transect used to derive a density estimate. Aerial foraging behavior characterized birds that rely extensively on flight between exploited feeding patches (e.g. shearwaters) or that use aerial feeding techniques (Nelson 1979), including surface plunging (e.g. boobies, some terns), aerial dipping (e.g. some terns), aerial pursuit (e.g. frigatebirds), skimming and hydroplaning (e.g. gulls, storm-petrels). Surface foraging behavior characterized birds that use prolonged pursuit diving (e.g. loons, sea ducks) and surface seizing (e.g. phalaropes). Taxonomy after American Ornithologists' Union checklist of North American birds (http://checklist.aou.org/taxa/; accessed 29 June 2014)

Species	Common name	Breeding origin	Abundance H&R	Abundance T&M
Calonectris diomedea	Cory's shearwater	ONWA	10	1
Puffinus gravis	Great shearwater[a]	ONWA	3	0
Puffinus griseus	Sooty shearwater	ONWA	1	0
Puffinus puffinus	Manx shearwater[a]	ONWA	5	0
Puffinus lherminieri	Audubon's shearwater[a]	WI/C/B	154	14
Calonectris or *Puffinus*	Shearwater species[a]	WI/C/B	21	14
Oceanites oceanicus	Wilson's storm-petrel	ONWA	10	50
Oceanodroma leucorhoa	Leach's storm-petrel[a]	NWA	1	4
Oceanodroma castro	Band-rumped storm-petrel	ONWA	250	189
Oceanodroma or *Oceanites*	Storm-petrel species	ONWA	62	208
Phaethon aethereus	Red-billed tropicbird	WI/C/B	2	0
Phaethon spp.	Tropicbird species	WI/C/B	0	2
Fregata magnificens	Magnificent frigatebird[a]	NGOM	4	13
Fregata spp.	Frigatebird species[a]	NGOM	174	0
Sula dactylatra	Masked booby[a]	SGOM	4	11
Sula spp.	Sulid species	SGOM	0	3
Pelecanus occidentalis	Brown pelican[a]	NGOM	0	2
Phalaropus spp.	Phalarope species	ONWA	22	0
Leucophaeus atricilla	Laughing gull[a]	NGOM	38	31
Leucophaeus pipixcan	Franklin's gull	ONWA	0	1
Larus delawarensis	Ring-billed gull[a]	NWA	0	1
Larus fuscus	Lesser black-backed gull[a]	NWA	0	1
Larus spp.	Gull species[a]	NGOM	2	0
Anous stolidus	Brown noddy	SGOM	0	16
Onychoprion fuscatus	Sooty tern[a]	SGOM	111	2
Onychoprion anaethetus	Bridled tern	WI/C/B	70	75
Sternula antillarum	Least tern[a]	NGOM	1	0
Chlidonias niger	Black tern[a]	ONWA	1119	174
Sterna dougallii	Roseate tern	SGOM	0	1
Sterna hirundo	Common tern[a]	NGOM	4	6
Sterna paradisaea	Arctic tern	ONWA	2	0
Sterna forsteri	Forster's tern[a]	NGOM	0	1
Thalasseus maximus	Royal tern[a]	NGOM	19	14
Thalasseus sandvicensis	Sandwich tern[a]	NGOM	24	15
Onychoprion and *Sterna* spp.	Tern species[a]	NGOM	179	59
Stercorarius pomarinus	Pomarine jaeger	ONWA	14	3
Stercorarius parasiticus	Parasitic jaeger	ONWA	1	0
Stercorarius longicaudus	Long-tailed jaeger	ONWA	2	0
Stercorarius spp.	Jaeger species	ONWA	1	1
Total individuals			2310	912
Percent aerial foragers			99.1	100
Percent breeding outside northern Gulf of Mexico			81.5	84.5
Percent breeding outside entire Gulf of Mexico			76.8	80.9

[a]Species documented as visibly oiled during the *Deepwater Horizon* blowout

every 4 d, on average. These assumptions are supported by Kinlan et al. (2012, p. 50), who reported on offshore surveys of Atlantic birds and concluded that '… bird abundance de-correlates rapidly with time in this region, supporting our assumption that repeat surveys are approximately independent as long as they are separated by a few days or longer.' Uncertainty in P was then assessed by assigning this parameter a uniform distribution on the interval 2 to 6 d (SD approximately 1.15 d).

After assigning probability distributions to the parameters, we drew 1 million random numbers from the assigned distributions (Table 2), and then we repeatedly used Eq. (5) to compute bird deaths. This gave a Monte Carlo probability distribution for the number of bird deaths (rounded to no more than 2 significant digits). From this distribution we constructed what we call an 'uncertainty interval' or 'Monte Carlo simulation interval'. Our intervals are not confidence intervals, because our simulations are not an attempt to estimate a sampling distribution. We have chosen not to call them 'credible intervals' to stress that they were constructed from the prior distribution of the parameters — and not from a posterior distribution.

To examine sensitivity of the overall uncertainty to contributions to the variability of each individual parameter, each parameter in sequence was replaced with its 2.5th and 97.5th percentile, while the other 3 parameters were fixed at their mean values. Although we call this a sensitivity analysis, the traditional notion of sensitivity is intertwined with the probability distribution for each parameter. The deviation, expressed as a range that we will call the 'deviation range', is the result. The 'cumulative deviation range' was computed as the sum of the individual deviation ranges for each parameter. Sensitivity of the overall mortality estimate to each parameter was expressed as a proportion of this cumulative deviation range, computed as the ratio of each parameter's deviation range and the cumulative deviation range. Taken together, these ratios indicate where new information could be most helpful in improving the mortality estimate.

Table 2. Probability distributions used to simulate the number of offshore bird deaths caused by the *Deepwater Horizon* blowout. $\bar{A}$: average oil slick area (km^2); D: average bird density (birds km^{-2}); M: proportionate mortality for birds; P: exposure period needed for the bird density over the oiled water to return to the initial value of D

Parameter	Assigned distribution	Mean	SD	2.5th quantile	97.5th quantile
$\bar{A}$	gamma	15000	2300	11000	20000
D	gamma	1.6	0.606	0.64	2.99
M	beta	0.33	0.15	0.09	0.65
P	uniform	4	1.15	2.1	5.9

RESULTS

Mortality estimate with exposure probability

Regardless of the exposure period duration $\hat{P}$ chosen, the estimated average number of birds killed is given by the product of $\hat{\bar{A}}$, $\hat{D}$, and $\hat{M}$ (= 15 000 km^2 × 1.6 birds km^{-2} × 0.33), or approximately 7900 birds period^{-1}. For any period of length $\hat{P}$ days over the 103 d duration of the slick, the estimated number of bird deaths would be approximately 7900 × 103/$\hat{P}$ (= 820 000/$\hat{P}$), such that N = 410 000 for $\hat{P}$ = 2, N = 270 000 for $\hat{P}$ = 3, etc. Focusing on the value of $\hat{P}$ that we consider is most likely to represent the time to replenish the bird density above the oil slicks to D (i.e. 4 d), the estimated number of bird deaths would be approximately 200 000, after rounding to 2 significant figures to reflect the inherent overall imprecision of this estimate.

Using the named probability distributions to assess the effect of alternative parameter assumptions (Table 2), the central 95 % of the probability was over the interval 36 000 to 670 000 bird deaths, whereas the central 80 % of the simulated probability covered the interval from 68 000 to 440 000 deaths. The probability that bird deaths exceeded 97 000 is approximately 80 %, and the probability that this mortality exceeded 120 000 is approximately 70 %. The mean and median of the distribution were 230 000 and 180 000, indicating a probability distribution skewed toward larger values (Fig. 3).

Model sensitivity to parameters

The estimates of total bird deaths in the offshore Gulf of Mexico were most sensitive to the proportionate mortality, M (34.2 % of cumulative deviation range; Fig. 4). Similarly, the final mortality estimates were sensitive to assumptions about the parameter values for bird density (29.3 % of cumulative deviation range) and exposure period (24.5 %). The mortality estimate was least sensitive to the parameter that was measured during the spill, the average oil slick area, $\bar{A}$ (12.0 %).

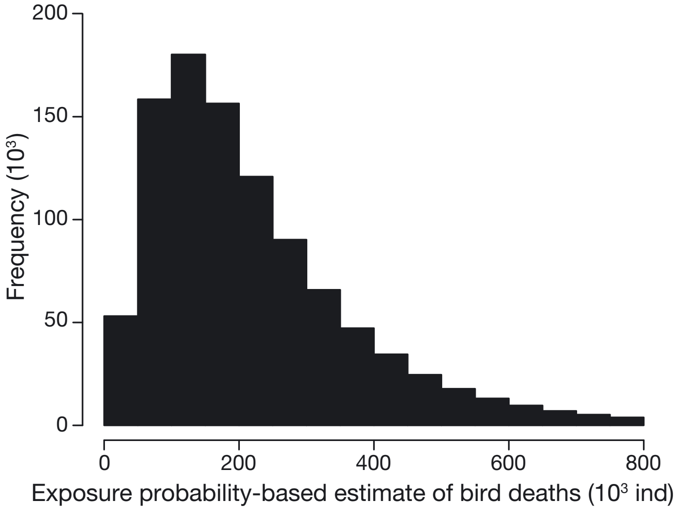

Fig. 3. Monte Carlo distribution (1 million trials) for the bird mortality in the offshore Gulf of Mexico derived from an exposure probability model

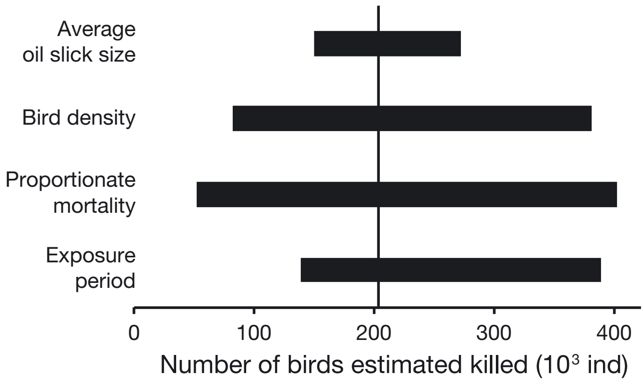

Fig. 4. Changes in estimates of bird mortality from the *Deepwater Horizon* blowout when each of 4 parameters — average daily oil slick size ($\bar{A}$), bird density (D), proportionate mortality (M), and exposure period (P) — is replaced by the 2.5th and 97.5th percentiles of the distribution for that parameter, while the other parameters are held at their mean values

DISCUSSION

Based on our simulation, we found a very high probability that between 36 000 and 670 000 birds died in the offshore waters of the Gulf of Mexico due to the *Deepwater Horizon* blowout. A number of 200 000 is the most reasonable single estimate for this offshore area. This estimate applies only to the acute discharge phase of the blowout, which extended for 103 d. Additional bird mortality not considered in our estimates continued to be reported months after the well was capped (Belanger et al. 2010).

Loss of 200 000 birds appears reasonable in comparison with the number of birds in the region. The cumulative area of the oil slick more than 40 km offshore was ≥100 000 km^2 (NOAA 2013; see also Table S2 in the Supplement). With a density of 1.6 birds km^{-2}, there would have been more than 160 000 birds in total above the cumulative oil slick footprint, implying aggregated mortality of essentially all of these birds plus others supplied by migration. The upper bound of our uncertainty interval (670 000 birds) implies the death of all birds above the cumulative oil slick area more than 4 times over, requiring replacement of killed birds through immigration at rates that approach implausibility. Conversely, our lower bound (36 000 birds) represents loss of less than 25 % of birds projected over a large slick during a particularly long-lasting discharge, which also approaches implausibility.

Given breeding population sizes at the species' nearest origin, loss of 200 000 offshore birds (<10 % of source breeding populations; Table 3) during the *Deepwater Horizon* spill duration also appears plausible. Breeding numbers represent only a minimum source size as they do not account for the non-breeding fraction of the population that could be present in the offshore Gulf of Mexico. Seabird abundance in the offshore Gulf can increase 17 % (Peake 1996) over months in which this oil discharge occurred, and storm-petrels, shearwaters, and some terns may become 4 to 5 times more abundant (Hess & Ribic 2000).

In fewer than 10 oil spills worldwide has the total estimated bird mortality exceeded 10^5 birds (e.g. *Exxon Valdez*, 1.0–6.9 × 10^5: Piatt & Ford 1996; *Selendang Ayu*, 1.4 × 10^5: Munilla et al. 2011; *Prestige*, 2.0 × 10^5: Munilla et al. 2011; *Tricolor*, 1.0 × 10^5: Camphuysen & Leopold 2004; *Stylis*, 2.0–3.0 × 10^5, and *Erika*, 1.2–3.0 × 10^5: Camphuysen et al. 2005). The estimate that we report here pertains only to the offshore birds — a value lower than the estimate of ~7 × 10^5 for coastal birds (Haney et al. 2014). Combining both estimates, the resulting number of bird deaths from this oil spill reaches approximately 9 × 10^5. However, even this value does not represent a total bird mortality estimate for the *Deepwater Horizon* spill because acute bird deaths from estuarine oiling have not yet been estimated or reported, and we have not considered delayed effects that may decrease lifespans of oil-exposed birds (Peterson et al. 2003). These additional mortalities might plausibly increase total mortality to above 1 million birds.

Table 3. Breeding populations of offshore seabirds found affected by the 2010 *Deepwater Horizon* blowout. Total population sizes are higher as a result of uncounted sub-adults, non-breeding adults, and adult breeders absent from the colony due to year-round nesting (e.g. Tunnell & Chapman 2000). Unless stated otherwise, population size refers only to estimated breeders from the source population(s) within or closest to the Gulf of Mexico (origin abbreviations as in Table 1)

Species	Breeding origin	Pop. size (10^3 ind.)	Notes	Reference(s)
Calonectris diomedea Cory's shearwater	ONWA	600–1200	Entire Atlantic Ocean population	Brooke (2004), BirdLife International (2014)
Puffinus gravis Great shearwater	ONWA	15000	Entire Atlantic Ocean population	Brooke (2004)
Puffinus lherminieri Audubon's shearwater	WI/C/B	60	Bahamas and West Indian populations only	Mackin (2013)
Oceanodroma leucorhoa Leach's storm-petrel	NWA	400	Saint-Pierre and Miquelon, largest North American breeding colony	Lormée et al. (2012)
Sula dactylatra Masked booby	SGOM	9	Campeche Bank, southern Gulf of Mexico only	Tunnell & Chapman (2000)
Leucophaeus atricilla Laughing gull	NGOM	730	Estimated Gulf of Mexico population of breeders, non-breeding adults, and sub-adults	Haney et al. (2014)
Onychoprion fuscatus Sooty tern	SGOM	96	Southwest Florida and Campeche Bank populations only	Tunnell & Chapman (2000), Mackin & Lee (2014)
	WI/C/B	576	Campeche Bank, USA, Bahamas, and West Indian populations	Tunnell & Chapman (2000), Mackin & Lee (2014)
Chlidonias niger Black tern	ONWA	100–500	Total North American continental breeding population	Heath et al. (2009)

Assumptions for exposure probability

Proportionate mortality of affected birds (M) contributed the most uncertainty to the overall mortality estimate (Fig. 4). This parameter is also closely associated with the assumed period length (P) that corresponds to the time it takes for the density of birds above the oil slick to return to the assumed initial value through oil slick movement, local bird movement, and regional bird immigration. In both cases, these parameters were chosen without direct measurement from this oil spill, and had to be inferred from literature on bird migration, previous oil spills, and avian physiology.

We estimated bird density, D, with the value of 1.6 birds km^{-2} derived from observations across the offshore Gulf of Mexico 7 yr or longer before the blowout. In the *Terra Nova* spill off southeastern Canada, bird density values collected at different times or spatial scales did not greatly influence the mortality estimates (cf. Fifield et al. 2009, Wilhelm et al. 2007). The value for D that we used is below bird densities typically found in similar oligotrophic waters elsewhere (Haney 1986). Except for local aggregation, bird density is characteristically low off the southeastern USA. Additionally, our estimate was derived without adjustments for detection probability, a correction that when measured can raise apparent density of birds surveyed by ~5 to 30% (Barbraud & Thiebot 2009).

The exposure probability method requires a reasonable estimate of the average extent of the oil slick, $\bar{A}$. Yet measurements with satellite imagery may have consistently under-estimated the surface extent of oil. Estimates of spatial extent depend on sensitivity of the particular satellite platform, influence of cloud cover, and other factors related to the sensor's spatial coverage. Estimates also varied with the algorithms used to infer oil presence, thickness, or concentration (e.g. Leifer et al. 2012, Lindsley & Long 2012). Dissolved hydrocarbons were invisible in surface waters (<5 cm deep; Liu et al. 2014), with the visible fractions less detectable by satellite platforms early and late during the incident (Lindsley & Long 2012). Other platforms could not discriminate thicker (>100 µm) from thinner (to 0.1 µm) oil sheens (Leifer et al. 2012). Underestimating oil slick size would lead directly to an underestimate of the number of bird deaths using Eq. (5).

By using assigned probability distributions for each parameter, we were able to logically organize, weight, and present alternative assumptions (Figs. 3 & 4). In each case, we considered a range of reasonable assumptions about the parameter's value. Substantially different assumptions about parameter values will lead to mortality estimates that are either so low or so high as to approach implausibility (cf. Fig. 3, Table 3).

The exposure probability approach is attractive because of its simplicity, which it achieves through broad assumptions. For example, we assumed that birds were neither attracted to nor repelled by surface oil. Birds are unlikely to avoid altogether an oil slick the size of the *Deepwater Horizon* (Fig. 1). Although some species may avoid small spills (Lorentsen & Anker-Nilssen 1993), observations elsewhere indicate no consistent spill avoidance behavior in seabirds (French McCay & Rowe 2004). In 2 studies during the 2009 *Montara* blowout in the Timor Sea off northern Australia, seabirds were more abundant over oil slicks than in oil-free waters nearby (Mustoe 2009, Watson et al. 2009). At smaller spatial scales birds could be attracted to surface slicks if buoyant, dark oil attracts seabird prey (see Watson et al. 2009), if weathered oil particles resemble small prey (Mustoe 2009), or if thin oil sheens mimic convergence slicks that attract dense foraging aggregations of marine birds.

Deepwater Horizon oil also presented 2 novel hazards to seabirds. Audubon's shearwater and several other offshore Gulf seabirds are *Sargassum*-foraging specialists (Haney 1986, Moser & Lee 2012). Therefore, risk to these seabirds increases at floating *Sargassum* when algal mats were coalesced by surface processes that aggregate oil concurrently (cf. Carmichael et al. 2012, Powers et al. 2013). Also, flames from *in situ* oil burning (FISG 2010) increased mortality risk because storm-petrels and other nocturnal-feeding pelagic seabirds may be attracted to the light (Le Corre et al. 2002, Montevecchi 2006) and may then die in the flames, smoke, or residual oil.

We further assumed that proportionate mortality was independent of bird density. This assumption may not hold if seabirds are curious about oil-debilitated birds and approach them. In such cases, probability of oil exposure is greater than assumed, implying that we underestimated offshore bird mortality. Because patterns of local seabird aggregation (e.g. Beauchamp 2011) as well as small-scale spatial processes that govern individual oil slicks (Christensen & Terrile 2009) likely influenced the relationship between D and M in ways not captured by our exposure probability model, we recommend future research aimed at clarifying the key assumption of independence between D and M in exposure probability models. This could be done by characterizing seabird behavior around individual oil patches during particularly large or long-lasting spills.

Probable fate of bird carcasses

An obvious question is, where did 200 000 carcasses go if that many birds died? Carcasses were not systematically surveyed in the offshore Gulf of Mexico; fewer than 30 carcasses were retrieved >40 km from land, and all of these carcasses were recovered incidentally (Dead Bird Map for week of 14 December 2010, Bird Recovery Map Archive, Bird Impact Data, www.fws.gov/home/dhoilspill/collectionreports.html; accessed 25 Feb 2013).

Few carcasses could have persisted long in warm waters at these latitudes because decomposition leads to loss of carcass buoyancy and subsequent sinking. Decomposition in the Gulf of Mexico is likely to be more rapid than the 5 to 10 d in cooler seas (Wood 1996, Wiese 2003). Carcasses also would have disappeared quickly from opportunistic scavenging by other marine consumers (Lowe et al. 1996) such as tiger sharks *Galeocerdo cuvier* (Kaufman 2012). Even partial scavenging accelerates carcass sinking (Wiese 2003).

Carcasses were also destroyed by widespread *in situ* burning of surface oil from early May to mid July 2010, which totaled 4.2×10^7 l, equivalent to one *Exxon Valdez* spill (FISG 2010). Most burns took place along current- and wind-driven convergence lines where buoyant oil was sufficiently concentrated for ignition (FISG 2010). Such convergences are likely to also aggregate and sink floating carcasses (Barstow 1983). Additional bird carcasses may have disappeared from oil skimming operations.

It may seem unlikely that blowout responders would overlook large numbers of bird carcasses, but birds were not exposed simultaneously and so did not die all at once or in one place. Aerially foraging birds typical of the offshore Gulf (Table 1) likely dispersed from points of initial exposure. Deaths of birds from crude petroleum and weathered by-products can be delayed (Nevins & Carter 2003). Following the *Exxon Valdez* spill, >80% of dead birds were recovered outside the immediate spill zone (Piatt et al. 1990).

Even had all mortality occurred instantaneously, carcasses would be dispersed across an area greater than the surface area of Portugal at an average density of about 2 dead birds km^{-2}. Individual birds would be exceedingly difficult to observe on the ocean surface at appreciable distance (but see Hyrenbach et al. 2001). Furthermore, marine birds in this offshore region comprise species that are small, dark-plumaged, and very difficult to discern from a moving ship even when alive and active. Dark storm-petrels and black terns account for nearly 60% of survey observations for the offshore Gulf (Table 1).

Alternatives for estimating avian mortality at marine spills

In our companion article (Haney et al. 2014), we estimated bird mortality caused by the *Deepwater Horizon* in the coastal waters of the northern Gulf of Mexico using both the exposure probability model and a carcass deposition model. Results of these 2 modeling approaches produced broadly overlapping estimates, with largely independent data sources. Furthermore, a ~60% decrease of the northern Gulf of Mexico population of the laughing gull *Leucophaeus atricilla* was evident in National Audubon Society Christmas Bird Counts (NAS 2010), in broad agreement with the 36% decline of this species projected on the basis of a carcass deposition model (Haney et al. 2014). This supports the exposure probability approach we applied offshore.

Prior to the *Deepwater Horizon* blowout, an exposure probability approach had been applied to a much shorter, smaller spill (~1.7×10^5 l), the *Terra Nova* incident, covering 793 km^2 over 6 d on the Grand Banks of eastern Canada (Wilhelm et al. 2007); avian mortality estimated by exposure probability gave similar results to an estimate interpolated from a regression of bird mortality on spill volume. Moreover, this estimate was confirmed when some of the initial assumptions in the exposure probability model were validated by measuring seabird movements (Fifield et al. 2009).

In contrast to the exposure probability model, carcass sampling requires extensive field effort (Wiese 2003, Byrd et al. 2009). With less data-collection cost and effort, exposure probability models could provide estimates of comparable accuracy and precision to carcass sampling, but only if comprehensive surface maps of oil slick area and seabird density estimates are available from survey coverage of adequate resolution (e.g. Begg et al. 1997).

Alternatively, measuring differences between pre- and post-spill colony attendance in coastal bird populations (Piatt & Ford 1996) can be used to infer mortality after large marine oil spills. This approach is not feasible for estimating avian mortality in offshore systems such as the Gulf of Mexico because virtually all bird species breed in highly dispersed colonies far outside the spill zone (Tables 1 & 3; see also Fig. 3 in the Supplement). In summary, for large, offshore, deep-water oil spills, an exposure probability approach is the only feasible method currently available for estimating bird mortality.

Spill mortality in warm seas

With increases anticipated in offshore, deep-water oil exploration (Pettingill & Weimer 2002), massive oil discharges such as the *Deepwater Horizon* spill are likely to recur. The effects of offshore oil discharges on ocean biota can easily go undetected (Williams et al. 2011) due to remoteness, unfavorable environmental conditions, and logistical constraints on researchers imposed by spill response.

Except for the Gulf of Mexico's 1979 *Ixtoc I* (Jernelöv & Lindén 1981) and the Australian 2009 *Montara* blowouts (Watson et al. 2009), no other large oil discharges have affected warm-ocean assemblages of marine birds. Most post-spill assessments to date have been for avifauna in cool temperate seas (Balseiro et al. 2005, Oppel et al. 2009). Despite their aerial foraging habits, shearwaters, storm-petrels, boobies, and tropical terns (the same taxa found in the Gulf of Mexico; Table 1) were frequently observed resting on and feeding over weathered oil and sheen in the Timor Sea after the *Montara* blowout (Mustoe 2009). These birds and their prey were more closely associated with contaminated waters than with oil-free waters, with more than 80% of all encounters for some species occurring over oil sheen (cf. Watson et al. 2009, O'Hara & Morandin 2010). Among birds exposed to oil and recovered, the proportionate mortality reached 58 to 76% (Brassington & King 2010, Short 2011).

Despite protracted oil pollution in the Gulf of Mexico (Burgherr 2007), we know little about how either chronic or acute oiling affect the region's aerially foraging seabird assemblage. Given the extent of the hydrocarbon industry's operations in the Gulf of Mexico (>4000 offshore oil production platforms; Dismukes 2010), the absence of region-wide, baseline seabird surveys prior to the *Deepwater Horizon* spill is of grave concern. Indeed, in no other region of the USA has the marine avifauna been so ineffectually studied in conjunction with exploration and development of offshore energy.

Our ability to estimate bird mortality was limited by the resolution of seabird surveys and a lack of direct measurements of the mortality processes. These limitations are reflected in our large measures of uncertainty (Figs. 3 & 4). In order to reduce uncertainty and improve assessment of avian mortality from future spills, we strongly recommend (1) surveys that accurately and precisely measure seabird density and seasonal occurrence across the entire Gulf of Mexico, and (2) applied research on avian behavior at oil patches, lethal dosages, and physiological responses (including effects of hydrocarbon inhalation).

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