



# Deposition and Persistence of Beachcast Seabird Carcasses

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Following a massive wreck of guillemots (*Uria aalge*) in late winter and spring of 1993, we monitored the deposition and subsequent disappearance of 398 beachcast guillemot carcasses on two beaches in Resurrection Bay, Alaska, during a 100 day period. Deposition of carcasses declined logarithmically with time after the original event. Since fresh carcasses were more likely to be removed between counts than older carcasses, persistence rates increased logarithmically over time. Scavenging appeared to be the primary cause of carcass removal, followed by burial in beach debris and sand. Along-shore transport was negligible. We present an equation which estimates the number of carcasses deposited at time zero from beach surveys conducted some time later, using non-linear persistence rates that are a function of time. We use deposition rates to model the accumulation of beached carcasses, accounting for further deposition subsequent to the original event. Finally, we present a general method for extrapolating from a single count the number of carcasses cumulatively deposited on surveyed beaches, and discuss how our results can be used to assess the magnitude of mass seabird mortality events from beach surveys.

and scavenging or physical processes that remove carcasses (Ford *et al.*, 1987; Piatt *et al.*, 1991). Variability in these parameters, particularly persistence rates (ECI, 1991), influence greatly the final estimate in any model of total mortality (Page & Carter, 1986). Many researchers have called for better estimates of persistence (Bodkin & Jameson, 1991; ECI, 1991; Piatt *et al.*, 1991; Burger, 1992a).

In late winter and spring of 1993, a minimum of 121 000 guillemots (*Uria aalge*) died *en masse* from starvation and more than 3500 washed ashore throughout the northern Gulf of Alaska (Piatt & Van Pelt, in prep.). This 'wreck' provided us with an opportunity to examine rates of carcass deposition and removal under natural conditions over a long period and with a large sample size. In this paper we present mathematical models of carcass deposition and persistence, and we propose a simplified method for extrapolating cumulative numbers of carcasses deposited on beaches which may have been surveyed only once. We demonstrate the practical application of this method, and discuss the implications for estimating total seabird mortality from beach surveys.

## Study Area and Methods

Beaches near the town of Seward (60°05'N, 149°25'W) in Resurrection Bay, Alaska, were surveyed repeatedly from 20 March to 28 June 1993. The waters of Resurrection Bay are protected from Pacific Ocean swells, and wave action on local beaches is light to moderate. We surveyed two disjunct beaches: Seward town (ST) beach and Lowell Point (LP) beach, which are separated by about 3 km of rocky shoreline. Both beaches were delineated by natural or man-made features. ST beach (*ca* 2 km in length) is narrow and straight, with a moderate aspect and a minimum of debris at the well-defined and continuous high tide line. LP beach (*ca* 2.5 km in length) includes Lowell Creek and its alluvial fan, which has created a broad, very low aspect plain characterized by a meandering high tide line and extensive debris accumulation. This plain comprises roughly half of LP beach's total area, with the remainder having features similar to ST beach. Because of the alluvium, LP beach has an intertidal area roughly twice that of ST beach.

Both beaches were surveyed on 20 March, 8 April, 21 April, 15 May and 28 June. In addition, ST beach

The toll of seabirds from both natural (e.g. food shortages, biotoxins) and anthropogenic (e.g. net entanglement, oil pollution) mortality events is usually extrapolated from numbers of carcasses found on beach surveys (Armstrong *et al.*, 1978; Stowe & Underwood, 1984; Piatt *et al.*, 1985; Page & Carter, 1986; Camphuysen, 1989; Piatt *et al.*, 1990; Bodkin & Jameson, 1991; Burger, 1992a; Camphuysen & van Franeker, 1992). In the last decade, a series of 10 significant oil spills (Burger & Fry, 1993) including the *Exxon Valdez* (Piatt *et al.*, 1990) has focused attention on the impact of oil pollution on seabird populations in the eastern North Pacific, and on methods used to assess the magnitude of oil mortality.

Using beached bird carcasses to estimate total mortality is an uncertain exercise because: 1. only a fraction of birds that die at sea ever wash ashore; 2. comprehensive or repetitive beach surveys are rarely logistically feasible; and 3. birds are cast up on and removed from surveyed beaches at variable rates over time and space because of changing deposition rates

was surveyed on 24 and 27 March. Van Pelt conducted all surveys using consistent search effort with assistance from one or two other persons. Guillemots found moribund on beaches were euthanized or removed for rehabilitation. Birds found freshly dead (< 8 h) were removed for necropsy and are therefore not included in our results. All guillemots found and estimated to be more than 8 h old were scored into three classes by age (time since death), spray-painted on the underside of a wing with a colour unique to the date of survey, and left where they were found. Subjective classes, based on our experience, were defined as follows: class 1, carcass 4 or fewer days old; class 2, carcass between 4 and 14 days old; class 3, carcass more than 2 weeks old. During all surveys, all 'captures' of unmarked birds were recorded and marked, and all 'recaptures' of marked birds were identified by colour cohort and recorded. We first surveyed beaches in Seward on 20 March, and for our purposes in this experiment we consider 20 March as the date of initial deposition of carcasses.

### Deposition

We quantified the rate of deposition by counting the number of captures per survey, and dividing by the number of days since the preceding survey. By plotting the deposition rates determined on each of six surveys at ST beach against time, we can calculate the deposition rate ( $D$ ) as a function of time ( $d$ ) using the regression equation:

$$D = b + (m \times \log[d]), \quad (1)$$

where  $b$  is a constant,  $m$  is the slope of the regression line, and  $d$  is the number of days past original deposition. Knowing that the sum of each day's deposition should equal the total number of carcasses deposited on the beach, we used a derived equation based on the deposition rate as a function of time (see the Appendix):

$$N_{\text{tot}} = 10^{(-b/m)}[-m/2.303], \quad (2)$$

to obtain an estimate of the total number of carcasses ( $N_{\text{tot}}$ ) deposited on the beach since the event origin.

### Persistence

Mortality models traditionally use the persistence coefficient  $s$  to estimate the number of carcasses ( $N_0$ ) that were originally beached on day zero using total carcasses ( $N_d$ ) found  $d$  days after the initial mortality event (Ford *et al.*, 1987; Page *et al.*, 1990). The persistence coefficient  $s$  is the inverse of the persistence rate, which is commonly expressed as the percentage of carcasses remaining from one day to the next. By noting how long the carcasses counted and marked on our original survey remained on the beach, we quantified the change in persistence over time. Assuming that significant deposition of carcasses does not occur after the original event, and that  $s$  remains constant, the relationship is described by the equation:

$$N_0 = N_d s^d. \quad (3)$$

We calculated  $s$  for each beach ( $n=2$ ) and survey date ( $n=6$  for ST beach;  $n=4$  for LP beach) by dividing the number of carcasses ( $N_0$ ) found at day zero by the number ( $N_d$ ) counted at day  $d$ , and raising this proportion to the inverse power of  $d$ :

$$s = (N_0/N_d)^{1/d}. \quad (4)$$

We found that the persistence coefficient  $s$  was not constant throughout the study period (100 days). We therefore averaged persistence coefficients from both beaches within each survey date and then used a linear regression equation:

$$s_t = b + (m \times \log(d)), \quad (5)$$

to calculate  $s_t$ , a persistence coefficient as a function of time, where  $b$  is a constant and  $m$  is the slope of the regression line.

Substituting  $s_t$  for  $s$  in equation (1) provides a more accurate equation for calculating  $N_0$  from known values of  $N_d$  and  $d$ :

$$N_0 = N_d (b + (m \times \log(d)))^d. \quad (6)$$

To test the sensitivity of initial mortality estimates to the fixed ( $s$ ) and time-dependent ( $s_t$ ) persistence coefficients, we calculated  $N_0$  from actual data collected on six surveys at ST and LP beaches using equation (3) with a fixed  $s$  value determined at 4, 18 and 100 days, and equation (6) with  $s_t$ .

### Cumulative total deposition based on ratio

We calculated the ratios of cumulative total deposition on ST beach over the entire 100-day study to the total number found from all cohorts on each survey date. Plotting those ratios against time and using exponential regression results in an equation which describes the changing ratio over time:

$$R = b \times 10^{m(d)}, \quad (7)$$

where  $b$  is the  $y$ -intercept,  $m$  is the slope of the exponential curve, and  $d$  the number of days since event origin. Multiplying the number of carcasses counted on any day following the origin ( $N_d$ ) by this time-sensitive ratio extrapolates to the cumulative total of carcasses deposited over the entire event duration ( $N_{\text{cum}}$ ):

$$N_{\text{cum}} = N_d (b \times 10^{m(d)}). \quad (8)$$

We applied this method to 1-day counts of beachcast carcasses made throughout the Gulf of Alaska over the duration of the wreck (Piatt & Van Pelt, in prep.), and compared the results to those extrapolations made using  $s_t$ .

## Results

Over the course of our study, beachcast guillemots were found in varying post-mortem physical condition. During the first few weeks, we found specimens that ranged from moribund or freshly-dead, to carcasses with only wings, feet and furculum remaining (Table 1). Between these extremes, carcasses ranged from very

fresh but thoroughly scavenged, to weeks-old and unscavenged. Almost all carcasses were eventually scavenged to some degree. Although fewer fresh carcasses were found as our study progressed, we consistently found a small number of new (unmarked) class 3 birds on each survey (Table 1). Due to increasingly long intervals between surveys, it was impossible to determine whether these newly discovered carcasses had been missed on previous surveys or had been deposited between surveys. Of those carcasses that were marked, many disappeared from beaches over time, while others decomposed *in situ* and were recaptured on subsequent surveys (Table 2).

Several factors contributed to the disappearance and decomposition of carcasses. During our surveys, we frequently observed bald eagles (*Haliaeetus leucocephalus*) and northern ravens (*Corvus corax*) scavenging from and carrying away guillemot carcasses. Telephone poles, pilings and moored barges in the vicinity of both beaches were strewn with scavenged guillemot carcasses. Glaucous-winged gulls (*Larus glaucescens*) also scavenged from guillemot carcasses, but did not appear to remove them from beaches. Concurrent with this study, river otters (*Lutra canadensis*) were observed scavenging from guillemot carcasses on beaches not far from Lowell Point, and wolverine (*Gulo gulo*) tracks were seen near guillemot carcasses. American black bears (*Ursus americanus*) are carrion eaters and are commonly seen on local

beaches (M. Tetreau, pers. comm.). Scavenging by animals was more likely at the forest-bordered LP beach than at ST beach, which borders the town of Seward. Conversely, tampering by humans was more likely to occur at the easily accessible ST beach than at the more remote LP beach. By notifying the public of our experiments, we minimized the effect that beach combers would have on the study by removing, covering or otherwise tampering with marked carcasses.

After the first week of the study, all carcasses were found at or above the high tide line. Given the right combination of high tides and waves, the removal of carcasses back into the sea was a possibility, and it was also apparent that many carcasses disappeared because they were eventually buried under sand, rocks, seaweed and other beach debris. Near the end of the study, many carcasses were visible only because their wing tips protruded above the sand or debris.

Beach-to-beach transport appeared to be minimal. None of the 48 birds painted on ST beach on 24 and 27 March with colours unique to ST beach were ever observed on LP beach, despite it being downcurrent from ST beach (J. Piatt, pers. obs.). Also, the distribution of carcasses on both beaches remained similar from survey to survey. By recognizing individual carcasses based on scavenging pattern, etc. we observed that carcasses, once deposited, tended to be static or to be removed altogether. Any new discoveries were typically buried and had only been recently exposed.

TABLE 1

Class-composition of cohorts of guillemot (*Uria aalge*) carcasses captured and marked during beach surveys in Resurrection Bay, Alaska, in 1993.

Survey date	Time interval (days)	No. found by class*							
		1		2		3		Total	
		STB†	LPB†	STB	LPB	STB	LPB	STB	LPB
20 March	0	16	21	30	80	14	34	60	136
24 March	4	1	ND	12	ND	24	ND	37	ND
27 March	3	1	ND	4	ND	6	ND	11	ND
8 April	11	4	1	23	9	18	41	45	51
21 April	13	1	0	7	0	13	9	21	9
15 May	24	0	0	2	0	7	2	9	2
28 June	44	0	0	0	0	13	4	13	4
Total		23	22	78	89	95	90	196	202

\*Classes (1-3) graded by age (time since death) and scavenging; see the Methods section.

†STB is Seward Town Beach, LPB is Lowell Point Beach; see the Methods section.

ND: No data.

TABLE 2

Recaptures (numbers found by class\*) of marked guillemot (*Uria aalge*) carcasses on two beaches in Resurrection Bay, Alaska, in 1993.

Date found	Seward Town Beach				Lowell Point Beach			
	1	2	3	Total	1	2	3	Total
20 March†	16	30	14	60	21	80	34	136
24 March	1	24	12	37	ND	ND	ND	ND
27 March	0	17	10	27	ND	ND	ND	ND
8 April	0	4	11	15	0	3	28	31
21 April	0	0	9	9	0	0	26	26
15 May	0	0	3	3	0	0	18	18
28 June	0	0	2	2	0	0	18	18

\*Classes (1-3) graded by age (time since death) and scavenging; see the Methods section.

†Initial capture date; subsequent dates are recaptures.

ND: No data.

On any given date of survey, the number of birds found on a beach reflected the two processes of deposition and persistence. For example (Table 3), of 67 carcasses found on ST beach on 27 March, 27 were recaptures from deposition of 60 birds on 20 March, 29 were recaptures from 37 deposited on 24 March, and 11 were captured on that day. The total cumulative number of carcasses that had been deposited on ST beach by that date was actually 108, meaning that a total of 41 birds had disappeared since the original survey on 20 March.

*Deposition of carcasses*

Carcass deposition declined logarithmically following the initial deposition (Table 4; Fig. 1,  $D=10.702 - 5.6709 \log(d)$ ;  $r^2=0.816$ ). The deposition rate measured on our second survey at ST beach, 4 days after the origin, was 9.25 carcasses deposited per day. One hundred days after the origin, the deposition rate was only 0.295 carcasses per day. No freshly dead birds (class 1) were deposited after about 30 days (Table 1), and 'deposition' after that time reflected the discovery of old carcasses that had not been detected previously (all class 3). There is an inverse relationship between deposition rate and the cumulative total of carcasses deposited (Fig. 1). Total cumulative carcass deposition ( $N_{tot}$ ) can therefore be determined by integrating the area under the deposition curve (Fig. 1; see the Appendix). After calculating the deposition rate as a function of time (equation (1)), the total cumulative deposition was calculated using equation (2) (see the Methods section).

*Persistence of carcasses*

The rate at which carcasses disappeared depended on their age and condition (Fig. 2). On ST beach, a carcass  $\leq 4$  days old (class 1) had only a 6% probability of being recounted 4 days later ( $N_d=20.683 - 24.687 \log(d)$ ;  $r^2=1.000$ ), whereas a carcass more than 2 weeks old (class 3) had an 86% probability of being recounted 4 days later ( $N_d=122.851 - 50.394 \log(d)$ ;  $r^2=0.767$ ). Persistence of 4-14 day-old carcasses (class 2;  $N_d=133.829 - 91.068 \log(d)$ ;  $r^2=0.993$ ) closely resembled the average persistence of all classes combined

(total;  $N_d=83.332 - 43.236 \log(d)$ ;  $r^2=0.967$ ). Persistence rates were most variable in class 3 carcasses. Persistence rates at LP beach (total of all classes expressed as percentage of initial numbers found:  $N_d=40.417 - 14.281 \log(d)$ ;  $r^2=0.891$ ) followed the same general pattern. Lacking critical data points from the second and third surveys, however, we used LP beach data only for determination of persistence coefficients.

Persistence coefficients (see the Methods section) were similar at ST and LP beaches, and decreased from a maximum of 1.13 to a minimum of 1.02 during the course of the study (Fig. 3), corresponding to mean daily persistence rates of 0.889 and 0.976, respectively (Table 5). Thus for ST and LP beaches the half-life of carcasses was about 8 and 9 days, respectively. Persistence coefficients were strongly correlated with date (Fig. 3) at both ST beach ( $s_t=1.172 - 0.070 \log(d)$ ;  $r^2=0.975$ ) and LP beach ( $s_t=1.181 - 0.082 \log(d)$ ;  $r^2=0.973$ ). Using the mean of persistence coefficients from both beaches ( $s_t=1.178 - 0.076 \log(d)$ ;  $r^2=0.986$ ), we derived a specific formula to calculate the number of carcasses originally deposited on a beach, based on the number found  $d$  days after the original deposition event (using equation (6); see the Methods section):

$$N_0 = N_d(1.178 - 0.076 \log(d))^d \quad (9)$$

To test the sensitivity of equation (3) (see the Methods section) which assumes that persistence rates are constant (Ford *et al.*, 1987; Page *et al.*, 1990), and our equation (equation (6)), which includes a time-dependent function for persistence, we calculated  $N_0$  from actual data collected on surveys at both ST and LP beaches (Fig. 4). All models provided reasonably accurate measures of  $N_0$ , the actual count at day zero, for back-calculations of up to 10 days from the initial deposition event. After 25 or more days, the estimates derived from equation (3) that use constant persistence coefficients ( $s$ ) determined from data collected over fixed time intervals (4-100 days), departed from the actual  $N_0$  by 1-4 orders of magnitude. Estimates made from our time-dependent equation remained similar to the actual  $N_0$  for up to 100 days past the initial deposition event.

TABLE 3

Deposition and recapture of colour-marked guillemot (*Uria aalge*) carcasses on Seward Town Beach (and Lowell Point Beach) in Resurrection Bay, Alaska, in 1993.

Survey date	Days*	Cohort							Daily total	Cumulative deposition total†
		Red	Blue	Orange	Yellow	Green	Purple	Plain		
20 March	0	60 (136)							60 (136)	60 (136)
24 March	4	37 (ND)	37 (ND)						74 (ND)	97 (ND)
27 March	7	27 (ND)	29 (ND)	11 (ND)					67 (ND)	108 (ND)
8 April	19	15 (31)	7 (ND)	4 (ND)	45 (51)				71 (82)	153 (187)
21 April	32	9 (26)	9 (ND)	2 (ND)	30 (26)	21 (9)			71 (61)	174 (196)
15 May	56	3 (18)	3 (ND)	0 (ND)	14 (17)	5 (1)	9 (2)		34 (38)	183 (198)
28 June	100	2 (18)	5 (ND)	1 (ND)	5 (11)	3 (0)	1 (1)	13 (4)	30 (34)	196 (202)

\*Number of days past original deposition.

†Total number of captures.

ND: No data.

TABLE 4

Deposition rates of new guillemot (*Uria aalge*) carcasses found on six surveys of Seward Town Beach, Resurrection Bay, Alaska, in 1993.

Survey date	Time interval (days)	Deposition rate by class*			
		1	2	3	Total
24 March	4	0.25	3.00	6.00	9.25
27 March	3	0.33	1.33	2.00	3.67
8 April	11	0.33	1.92	1.50	3.75
21 April	13	0.08	0.54	1.00	1.62
15 May	24	0	0.08	0.28	0.38
28 June	44	0	0	0.30	0.30

\*See the Methods section for definition.

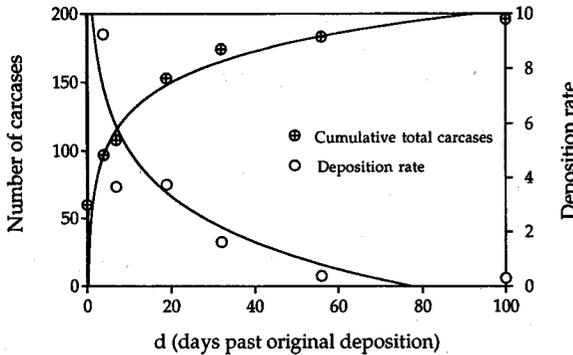


Fig. 1 The change in deposition rate (see the Methods section) over time, and the cumulative deposition of carcasses at Seward Town Beach.

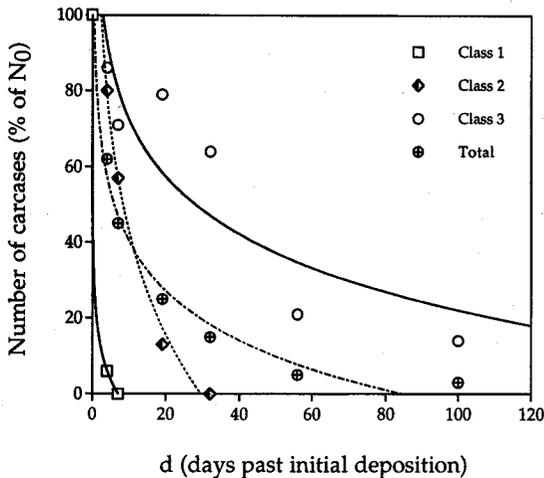


Fig. 2 Disappearance over time of carcasses at Seward Town Beach, graphed by class of initial state of decomposition (see the Methods section) and using all classes combined (Total).

Application of methods to the wreck

Extrapolating totals from the ratio of cumulative to daily recoveries. The ratio of cumulative total deposition on a beach to the total number of carcasses found on any given day was variable, but generally hovered around 3:1 during the first month (Table 3, Fig. 5). During the second and third months of the study, however, the ratio roughly doubled. We used the equation of the exponential regression curve ( $R=2.672 \times 10^{0.004(d)}$ ;  $r^2=0.771$ ) to estimate total cumulative number of carcasses deposited on all

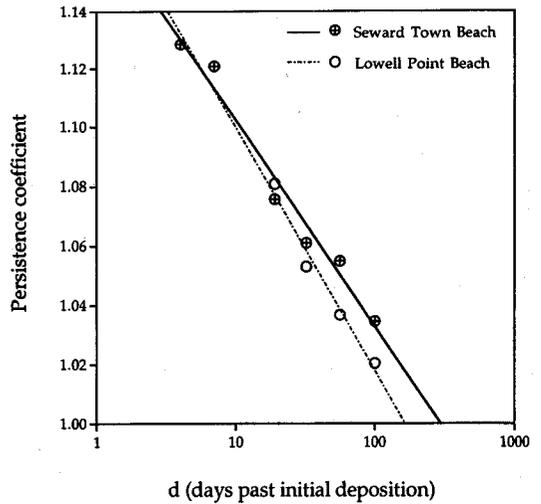


Fig. 3 The change in persistence coefficients over time at each of the two study beaches. Least-square regression lines are shown (see text for equations).

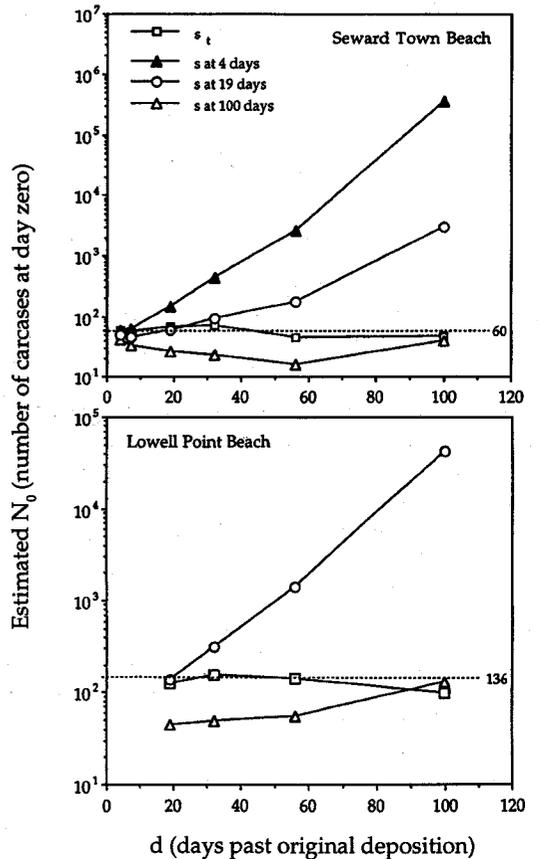


Fig. 4 Back-calculations of  $N_0$ , the number of carcasses at day zero, for each of the two study beaches (see text and the Methods section). Plotted points show the estimates of  $N_0$  that result when values of the persistence coefficient  $s$  (a constant determined over differing study time intervals; 4–100 days) or  $s_t$  (time-dependent  $s$ ) are used to back-calculate  $N_0$  at varying time intervals after the original event. For example, back-calculating  $N_0$  from the number of carcasses found on LP beach after 100 days by using a constant  $s$  calculated from a study of persistence conducted over 19 days would suggest that about 50 000 carcasses were initially deposited on the beach (the actual number being 136).

TABLE 5

Guillemot (*Uria aalge*) carcass persistence coefficients ( $s$ ) calculated from Resurrection Bay, Alaska, beach surveys in 1993.

Survey date	Persistence coefficients $s^*$			
	Days $^\dagger$	STB $^\ddagger$	LPB $^\ddagger$	Mean
24 March	4	1.128	ND	1.128
27 March	7	1.121	ND	1.121
8 April	19	1.076	1.081	1.078
21 April	32	1.061	1.053	1.057
15 May	56	1.055	1.037	1.046
28 June	100	1.035	1.020	1.028

\*See the Methods section for definition and calculation.

$^\dagger$ Number of days since origin of mortality.

$^\ddagger$ STB is Seward Town beach; LPB is Lowell Point beach.

ND: No data.

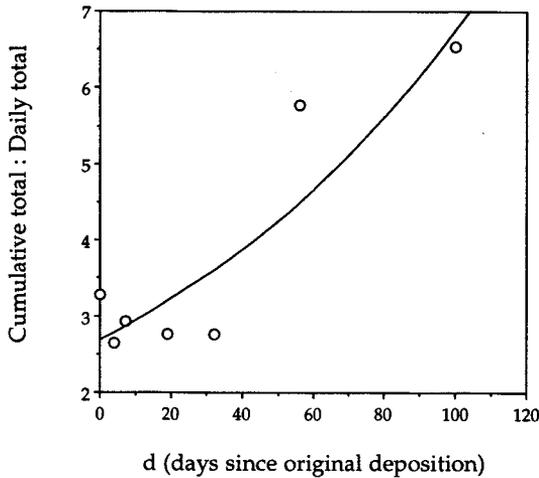


Fig. 5 The change over time in the ratio of cumulative total carcasses deposited on Seward Town Beach to the total number of carcasses counted on 1-day surveys. The best-fitting exponential regression line is shown (see the Results section for equation).

surveyed beaches over the entire area affected by the wreck (Piatt & Van Pelt, in prep.). Most of these beaches were visited only once. Knowing  $N$  the number of carcasses counted and  $d$  the number of days since the wreck origin (considering the wreck as a whole, we used 11 March, the date of peak mortality, as the 'origin' in calculations of cumulative mortality), we calculated that a cumulative total of 10 848 carcasses were deposited on surveyed beaches over the duration of the wreck, compared to a total number of 3504 carcasses actually counted on beaches in one-time surveys.

*Extrapolating  $N_0$  based on  $s_t$ .* We applied equation (9) which uses  $s_t$  as the basis for extrapolation of total number of carcasses present at the event origin. Again, we used 11 March as the 'origin', and counts of any carcasses found prior to 11 March were included in the total, but were not extrapolated. We calculated a total of 10 911 carcasses present on surveyed beaches at the origin of mortality.

## Discussion

### *Deposition of carcasses*

Although deposition rates in this case followed a logarithmic decline, our data did not capture the initial

stages of the wreck and so are not illustrative of the complete process. From a study of carcass deposition which began earlier in the wreck chronology (M. Tetreau, unpublished data; Piatt & Van Pelt, in prep.), we know that mortality in this wreck actually began with minimal deposition, then increased rapidly to a peak, before slowly tapering off to near-zero values. Apparent 'deposition' measured in the latter half of our study was likely to have been due to the discovery of carcasses which were deposited but not observed on preceding surveys (Camphuysen, 1989). This 'discovery' rate may introduce error into assessments of deposition rates, but given a consistent survey effort, deposition rates should still provide an accurate estimate of total cumulative mortality. Misidentification of recaptures was unlikely, since nearly all carcasses retained the painted wing attached to the furcula.

### *Persistence of carcasses*

We observed an inverse relationship between the persistence of beachcast guillemot carcasses and their degree of freshness. Scavenging appeared to be the dominant agent for removal of carcasses and fresh, intact carcasses were quickly removed by predators, especially bald eagles. Many carcasses were scavenged *in situ* and left on beaches where they persisted until covered by sand or debris, or washed back offshore. All class 3 birds were in various stages of mummification and most were heavily scavenged. The low variance observed in class 1 and 2 carcass persistence rates compared to the high variance in class 3 carcasses suggests that physical processes of removal are more variable than scavenging. Beach-to-beach transport appeared to be of minimal importance in removing carcasses. Camphuysen (1989) and Bodkin & Jameson (1991) noted a similar lack of alongshore transport. However, factors influencing carcass persistence may vary widely from beach to beach and season to season, depending on beach aspect, orientation, exposure and substrate, near-shore currents, wave intensity, tidal ranges, weather, and on the density and activity of scavengers (Bodkin & Jameson, 1991; Burger, 1992b, 1993a).

Despite their different physical characteristics and vulnerability to scavenging and human disturbance, we found that persistence rates on two beaches were similar. Persistence rates that have been determined in a variety of geographic areas (Table 6) vary considerably, but this variation may be attributable largely to differing experimental conditions and study durations. The latter factor appears to be most important in determining persistence rates. Our experiment clearly demonstrated that fresh carcasses disappear rapidly in the first few days of study. Therefore, it seems likely that the low persistence rates observed by Jones (1989), Page *et al.* (1990) and ECI (1991) are due to the short periods of time (2–8 days) that they conducted their studies (Table 6). Carcasses not removed rapidly by scavengers tend to decay or mummify until only inedible evidence of the mortality remains on beaches (Camphuysen, 1989). Thus, studies of longer duration report substantially higher persistence rates (Kuyken, 1978; Camphuysen, 1989; Bodkin & Jameson, 1991).

TABLE 6  
Seabird carcass persistence rates from various studies.

Location	Species used	Duration of study	No. of carcasses	Mean persistence rate (per day)	Reference
Resurrection Bay, Alaska	Guillemots	100 days	398	0.93 (range 0.89–0.98)	This study
Barren Islands, Alaska	Oiled seabirds, mostly guillemots	2 days	198	0.84	Jones (1989)
Prince William Sound, Alaska	Radio-tagged seabirds	8 days	9	0.80*	ECI (1991)
Prince William Sound, Alaska	Radio-tagged auklets	7 days	23	0.47*	ECI (1991)
Vancouver Island, British Columbia	Seabirds	4 days	12	0.54*	Burger in ECI (1991)
Washington	Guillemots, de-oiled	4–5 days	81	0.47–0.84*†	ECI (1991)
California	Oiled seabirds, mostly guillemots	3 days	235	0.38–0.72	Page <i>et al.</i> (1990)
California	Seabirds	11 months	71	0.96‡ (range 0.89–0.99)	Bodkin & Jameson (1991)
Belgium	Seabirds	No data	No data	0.93‡	Kuyken (1978)
The Netherlands	Alcids	5 months	44	0.98‡	Camphuysen (1989)

\*Calculated from data and graph provided in ECI (1991).

†Range of values for different placement on beaches, and different levels of scavenging.

‡Rate calculated from data provided as the average number of days a carcass remained on the beach.

### Extrapolations of total beachcast mortality

Persistence rates have traditionally been used to extrapolate total mortality from numbers of carcasses on beaches (Page & Carter, 1986; Ford *et al.*, 1987; Bodkin & Jameson, 1991; ECI, 1991). However, it is clear that averaged or single values used to represent persistence (Table 6) lead to inaccurate extrapolations because they do not account for the trend of increasing persistence over time. In back-calculating total mortality from carcasses found some time after initial deposition, it is critical that the persistence coefficient reflect the length of time that the carcasses have been exposed to scavenging and other removal processes. The ideal persistence coefficient ( $s_t$ ) would accurately reflect the change in persistence with time (see Fig. 4), but in the absence of the repeated surveys required to calculate  $s_t$ , constant persistence estimates should at least be calculated over the entire period of extrapolation. Our sensitivity analysis showed that  $s$  calculated over a 100-day period provided a within order-of-magnitude estimate of the original carcass count ( $N_0$ ) on beaches (Fig. 4).

Unknown error is introduced, however, when extrapolations of  $N_0$  based on persistence rates are used to estimate the total number of beached birds, because such extrapolations do not account directly for continued deposition following the origin or peak of mortality. Indeed, except for cases where deposition occurs all at once, this method is seriously flawed because it assumes that all carcasses found on any given day are those persisting from a single cohort deposited at day zero when in fact they are comprised of carcasses persisting from many different cohorts deposited over time.

When we back-calculated  $N_0$  to estimate the number of birds killed in the wreck, we were surprised to find that the estimate (10 911) was very close to the estimate determined by the more appropriate ratio method (10 848). This appears to be fortuitous, however, and deserves further investigation.

If deposition rates are measured directly over time, a model may be constructed which predicts total deposition based on results from an initial survey and

at least two subsequent surveys (equation (2)). This is the most accurate method for calculating total cumulative mortality. However, this technique is limited in application since an equation describing deposition rates must be determined individually for each surveyed beach. In the case of large die-offs or oil pollution events, it would be impossible to study all beaches in such detail.

Therefore, the most practical and cost-effective method for estimating total numbers of birds cast upon beaches is to: 1. study one or a few representative beaches in great detail using marked carcasses to establish the ratio of total cumulative carcasses beached to numbers observed on any given day, 2. conduct single-visit beach surveys on all possible beaches throughout the area affected, and 3. use the ratio method presented here to extrapolate from experimental beaches the total mortality on all beaches.

### Conclusions and Recommendations

The ratio method of extrapolating total mortality offers maximum utility and accuracy, because it effectively bypasses the problems involved in estimating mortality from either deposition or persistence rates. More research is needed to address questions about scavenging and the possible 'saturation effect' (local populations of scavengers being overwhelmed by carcass accumulation), the fate of individual carcasses (rather than cohorts of carcasses), and the variation in deposition and persistence due to differing weather conditions and physical characteristics of beaches.

We recommend that, following any mass mortality event, detailed carcass surveys be carried out on selected beaches throughout the mortality zone, preferably on a sample of representative beach types. Surveys should be at regular intervals of 1 week or less, and should continue for at least 100 days, or until deposition has ceased and most carcasses have been removed. Carcasses should be marked in some fashion allowing later determination of the date on which they were first censused. By noting all carcass captures and recaptures, workers would have sufficient data to

duplicate the analyses we have carried out here. Obviously, with more frequent surveys, more beach types surveyed, and longer survey durations, more accurate assessments of deposition and removal processes will be obtained.

In the eastern North Pacific alone, tens of thousands of seabirds have been found dead on beaches over the last few decades. A significant portion of those were killed by discrete events such as large-scale wrecks (Bailey & Davenport, 1972; Nysewander & Trapp, 1984; Hatch, 1987; Piatt *et al.*, 1990; Piatt & Van Pelt, in prep.) or oil pollution from the T/V *Puerto Rican*, T/V *Apex Houston*, T/V *Nestucca*, and the T/V *Exxon Valdez* (Ford *et al.*, 1987; Page *et al.*, 1990; Piatt *et al.*, 1990; ECI, 1991; Burger, 1993b). Many advances have been made in methods for calculating total seabird mortality from oil spills and wrecks since Vermeer & Vermeer (1975) noted that estimates of total mortality were little more than guesses. Here we have shown how site-specific processes of carcass deposition and removal can be quantified and used to extrapolate area-wide estimates of cumulative total carcass deposition. However, the number of birds that actually make it to shore (where they can be quantified on beach surveys) is still only a fraction of the total number killed, because a large proportion of carcasses sink at sea or drift offshore (Ford *et al.*, 1987). Additional studies of all these processes would further improve our ability to assess seabird and other marine mass-mortality events.

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## Appendix: Derivation of Equation Used to Calculate Total Deposition on Beach

The equation for the regression line describing deposition rates as a function of time, with values from the Results section and Fig. 4:

$$D = 10.702 - 5.6709 \log_{10}(x)$$

$$D = b + m \log_{10}(x),$$

where  $D$  are carcasses deposited per day;  $b$  is the  $y$ -intercept;  $m$  is the slope of line; and  $x$  are days since origin (d).

Using the logarithmic identity:

$$D = b + (m/2.303)\ln(x),$$

or

$$D = p - q \ln(x),$$

where  $p = 10.702$  and  $q = -m/2.303$ .

Solving for  $x$  intercept of the regression line, where  $D=0$ ;

$$0 = p - q \ln(x)$$

$$q \ln(x) = p$$

$$x = e^{p/q}$$

$$x = 77.1.$$

Let  $k = e^{p/q}$ .

Total number of birds deposited on beach =

$$N_{\text{tot}} = \int_0^k D(x) dx$$

$$N_{\text{tot}} = \int_0^k [p - q \ln(x)] dx$$

$$= \int_0^k p dx - q \int_0^k \ln x dx$$

$$= px \Big|_0^k - q[x \ln x - x]_0^k$$

$$= pk - q[(k \ln k - k) - (0(\ln(0)) - 0)]$$

$$\text{where } \lim_{x \rightarrow 0} x \ln x = 0$$

$$= pk - qk \ln k + qk$$

$$= k[p - q \ln k + q]$$

$$= e^{p/q}[p - q \ln(e^{p/q}) + q]$$

$$= e^{p/q}[p - p + q]$$

$$N_{\text{tot}} = e^{p/q}[q]$$

Or, as expressed using original variables  $b$  and  $m$  and their experimentally determined values:

$$N_{\text{tot}} = e^{b^m - m/2.303}[-m/2.303]$$

$$N_{\text{tot}} = e^{(2.303)(-bm)}[-m/2.303].$$

Since  $e^{2.303} = 10$ :

$$N_{\text{tot}} = 10^{(-bm)}[-m/2.303]$$

$$N_{\text{tot}} = 190,$$

where  $b = 10.702$  and  $m = -5.6709$ .