LINE TRANSECT ESTIMATES OF SHORT-TAILED SHEARWATER *PUFFINUS TENUIROSTRIS* MORTALITY IN THE SOUTH-EASTERN BERING SEA, 1997–1999

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SUMMARY

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During 1997, hundreds of thousands of Short-tailed Shearwaters *Puffinus tenuirostris* starved to death in the Bering Sea. We surveyed the distribution and abundance of floating carcasses during a cruise between 27 August–12 September, and estimated that over 95 000 carcasses were afloat within three survey grids covering approximately 52 400 km^2. We repeatedly surveyed the same areas during two subsequent cruises in 1998 and 1999, and used standard population sampling techniques to evaluate the background levels of shearwater mortality during additional years when a die-off did not occur. The mortality event we observed in 1997 was unusual due to its extent and magnitude. During the die-off, dead shearwaters were sighted within all three survey grids. Conversely, we only encountered carcasses at one of these sites in 1998. Moreover, carcass densities in 1997 were at least one order of magnitude higher than those recorded during the following year. Surveys of seabird mortality at sea can account for floating carcasses before they are lost through advection and scavenging. Therefore, vessel-based surveys are likely to improve the accuracy of seabird mortality estimates based solely on counts of beach-cast carcasses. Here we describe the use of line transects to estimate seabird mortality at sea, and offer suggestions to standardize future surveys. Standardized surveys will improve our ability to compare the frequency, extent, and magnitude of seabird die-offs over time.

Key words: Short-tailed Shearwater, *Puffinus tenuirostris*, Bering Sea, distance sampling, line transects, seabird die-offs, seabird mortality estimates, seabird population monitoring

INTRODUCTION

Ornithologists survey marine birds to determine patterns of distribution and abundance, and to estimate the size of their populations (Spear *et al*. 1995, Hunt *et al*. 1996a). Additionally, wildlife biologists survey beach-cast seabirds systematically, and whenever large die-offs occur (Stenzel *et al*. 1988, Piatt *et al*. 1990, Piatt & Van Pelt 1997). Estimating baseline mortality rates is particularly useful because it places unusually large seabird die-offs in perspective, and facilitates the comparison of natural and anthropogenic impacts on seabird populations (Piatt *et al*. 1990, Bodkin & Jameson 1991, Piatt & Van Pelt 1997). During the fall of 1997, an estimated 600 000 Short-tailed Shearwaters *Puffinus tenuirostris* starved to death in the Bering Sea. Carcasses were sighted across a vast geographical area spanning from Cape Anadyr, Russia and the Aleutian Islands as far west as Adak, eastwards to Bristol Bay (Mendenhall 1997, Vance *et al*. 1998, Baduini *et al*. 2001). We used standard population sampling techniques to estimate the number of floating carcasses within three survey grids during and after the 1997 die-off. In this paper, we compare the extent and magnitude of the die-off with background mortality levels during subsequent years (1998 and 1999) when no die-off was detected (Baduini *et al*. 2001, V.M. Mendenhall pers. comm.).

Traditionally, wildlife biologists count beach-cast carcasses to estimate the magnitude of seabird die-offs. However, a large number of carcasses are scavenged, sink, or drift away before they are counted on the beaches, and an unknown proportion of the birds that die wash ashore (Piatt *et al*. 1990, Piatt & Ford 1996). Carcass drift experiments have revealed that relatively few (0–59%) birds that die at sea ever reach shores where they can be counted (Bibby & Lloyd 1977, Bibby 1981). Furthermore, attempts to model the rate at which carcasses disappear due to sinking and

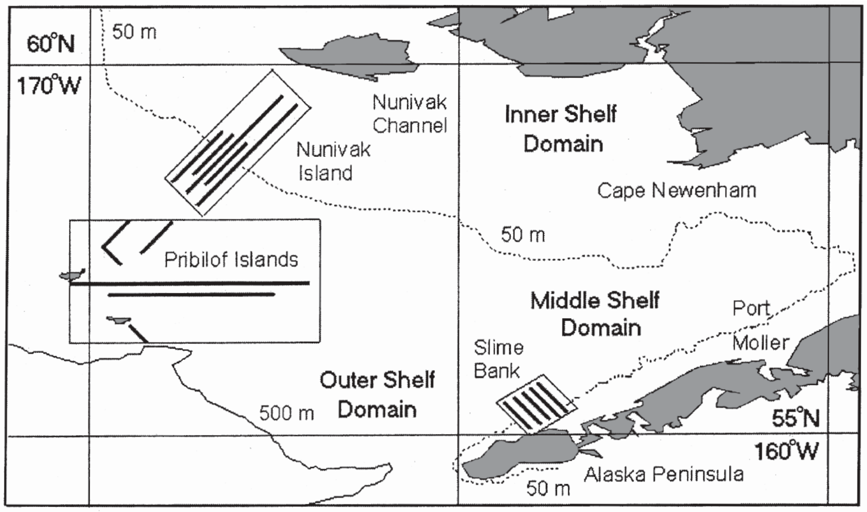

Fig. 1. *The study area in the south-eastern Bering Sea. The thick lines depict the tracks repeatedly surveyed each year and the thin rectangles portray the three grids used to estimate total carcass abundance.*

advection have shown that wind and currents largely determine the proportion of carcasses deposited on beaches (Piatt *et al*. 1990, Piatt & Ford 1996). Therefore, even if standardized techniques are used to survey beach-cast carcasses repeatedly, the comparison of mortality events through time is often inhibited by varying environmental conditions during die-offs (Piatt *et al.* 1990, Piatt & Van Pelt 1997).

Shipboard cruises can provide platforms to survey the extent and the magnitude of seabird die-offs (Tasker 1983 unpubl. rep., this study). In particular, vessel-based surveys can improve overall mortality estimates derived from beach counts because they can account for dead birds before they are lost at sea. These improved estimates are vital to compare the frequency and magnitude of seabird die-offs over time. Seabirds are good indicators of changing marine ecosystems because they are numerous, upper-level predators sensitive to shifts in ocean productivity, prey abundance, and ecosystem structure (Hunt *et al*. 1996b, Veit *et al*. 1996, Baduini *et al*. 2001). Thus, the incidence and magnitude of seabird die-offs may provide useful insights into the ability of marine ecosystems to support top predator populations. Here, we describe the use of line transects to survey a large Short-tailed Shearwater *Puffinus tenuirostris* die-off in the south-eastern Bering Sea during 1997, and offer suggestions to standardize future vessel-based surveys of seabird mortality.

METHODS

Carcass surveys

We employed standard population surveying techniques to assess the distribution and abundance of floating Short-tailed Shearwater carcasses during three cruises to the south-eastern Bering Sea in August–September 1997–1999. Two observers standing in the wheelhouse (eye height approximately 7.7 m above the sea surface) counted every floating carcass observed forward of the cruising vessel, within a 180-degree arc extending from beam to beam. Seabirds were recorded continuously during all daylight hours when visibility was at least 300 m and the vessel was cruising at speeds between 7 and 10 knots. Most counts were made with the unaided eye, and binoculars were used primarily to confirm identification. Seabird observations were recorded in a microcomputer with a temporal resolution of 0.1 minutes.

Observers estimated the perpendicular distance from the trackline to carcasses when they were abeam of the ship using hand-held range-finders (Heinemann 1981). This information was used to estimate the effective strip width (ESW) over which carcasses were accurately surveyed (Buckland *et al*. 1993a). We sighted a total of 164 dead shearwaters and obtained 132 perpendicular range measurements during shipboard surveys. Fifty-three carcasses occurred within the three survey grids, and the remainder originated from areas that were not surveyed systematically in all three years (Table 1). Specifically, dead shearwaters were sighted in Nunivak Channel and between the Pribilof Islands and Slime Bank in 1997, and in the Port Moller region during the spring of 1999. To establish the effective strips widths surveyed in clear and dark water, we employed all the available perpendicular range data, regardless of their origin.

Estimation of the detection function

The detection function *f*(0) describes how the ability to sight targets depends on their perpendicular distance from the track, and is used to determine the area effectively searched during wildlife surveys (Buckland *et al*. 1993a). Estimating this function is complicated by the fact that the probability of detection depends on a myriad of endogenous (e.g. target size and colour) and exogenous (e.g. environmental conditions during surveys) factors known to affect sightability (Forney & Barlow 1993). Therefore, we stratified our surveys by two factors likely to affect the observers' ability to detect floating carcasses: Beaufort sea state and water colour. In particular, we were concerned that dark shearwater carcasses would be more conspicuous in waters turned milky green by the presence of a coccolithophore bloom, than in dark blue waters outside of the bloom (Vance *et al*. 1998, Napp & Hunt 2001). We compared the distributions of perpendicular ranges for different sea state and water colour conditions using Kolmogorov-Smirnov tests (Zar 1984), and pooled those that did not differ significantly (Forney & Barlow 1993).

Perpendicular distance truncation

Truncation of the most distant 5–10% of the line transect observations is recommended because distant sightings often bias density estimates (Barlow 1995) and their removal facilitates model fitting (Buckland *et al*. 1993a). We truncated the distributions of perpendicular ranges at 120 m from the track and removed the seven (7.3%) and four (11.1%) most distant sightings in light and dark water. This threshold was selected by visually inspecting the data for breaks in the distributions of perpendicular ranges (Buckland *et al*. 1993a).

Model fitting

We did not impose any preconceived assumptions on the shape of the detection function because seabird carcasses are 'neutral' targets neither attracted nor repulsed by the vessel (Buckland 1985). Therefore, we fitted half-normal, hazard rate and uniform models to the distributions of perpendicular sighting distances using the Distance 2.1 software (Laake *et al.* 1994).

Carcass densities

Before we could compare the density of dead shearwaters across time and space, we had to determine whether carcass counts were autocorrelated, and whether there was a statistically significant tendency for carcasses to occur in the vicinity of each other. Autocorrelation inhibits the statistical analysis of count data, since samples that are too closely spaced are not independent (Schneider 1990). The lack of sample independence biases population statistics and enhances the likelihood of falsely rejecting the null hypothesis (type I error) (Zar 1984). We averaged carcass counts into three-km bins (10 minutes at a cruising speed of 10 knots), and calculated the autocorrelation function (ACF) of carcass densities for lags between one to three bins (3–9 km) using the Systat 7.0 software package (Wilkinson 1997). We restricted the autocorrelation analyses to transects with a length of at least 18 km (six bins) and found that shearwater carcasses were not autocorrelated at any lag. Out of 50 transects and a total of 150 possible pair-wise comparisons (50 transects and up to a three-bin lag), we detected no instances where carcass densities were significantly autocorrelated. Once we had determined that carcass counts were not autocorrelated, we used a two-way extension of the Kruskal-Wallis test to assess whether carcass densities differed across years (1997, 1998, 1999) and sites (Nunivak Island, Pribilof Islands, and Slime Bank).

Estimates of carcass abundance

According to line-transect theory (Buckland *et al*. 1993a), the basic equation for estimating abundance (N_T) is given by:

$$D_i = \frac{n_{i,k}\, S_{i,k}\, f_k(0)}{2\, L_i\, g_k(0)} \qquad (1)$$

$$N_T = \Sigma\,(A_i * D_i) \qquad (2)$$

Where:
N_T = estimated total abundance (birds) of a given species within a study area made up of *i* survey grids. In this case *i* = 3.
N_i = estimated total abundance within survey grid *i*.
A_i = the size of survey grid *i* (km^2).
D_i = estimated density (birds km^{-2}) of a given species within survey grid *i*.
$S_{i,k}$ = the average size for group-size category *k* in grid *i*. In this case, $S_{i,k} = 1$.
L_i = length of trackline surveyed within grid *i* (km). See Table 1.

TABLE 1

Vessel-based surveys in the south-eastern Bering Sea during August–September, 1997–1999

Survey grid	**Year**	**Survey effort (no. 3-km bins)**	**Number of carcasses sighted**	**Carcass density (Mean ± S.E.)**	**Estimate of carcass abundance**
Nunivak Island	1997	197	22	0.773 ± 0.180	7419
	1998	164	1	0.048 ± 0.048	465
	1999	166	0	0	0
Pribilof Island	1997	97	28	2.182 ± 0.445	87 270
	1998	103	0	0	0
	1999	68	0	0	0
Slime Bank	1997	70	2	0.227 ± 0.159	636
	1998	71	0	0	0
	1999	72	0	0	0
Totals	**1997**	**364**	**52**	**–**	**95 325**
	1998	**338**	**1**	**–**	**465**
	1999	**306**	**0**	**–**	**0**

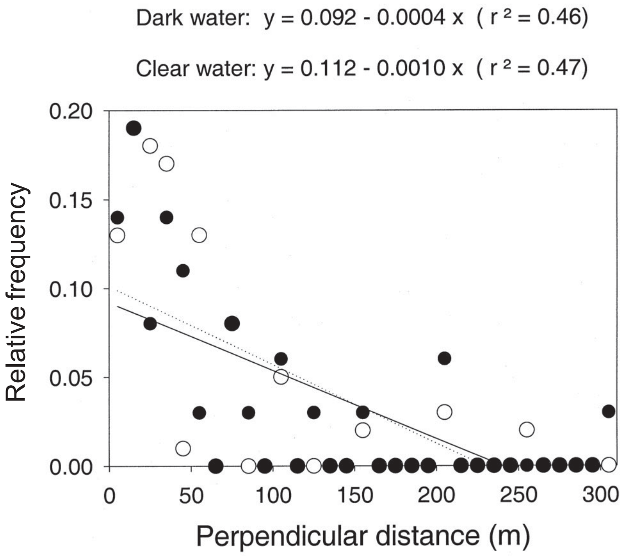

Fig. 2. *Relative frequency of Short-tailed Shearwater carcasses as a function of perpendicular distance from the trackline in dark (solid circles and continuous line) and light (open circles and hatched line) water within a coccolithophore bloom.*

$n_{i,k}$ = the number of group-size category k sightings in grid i.
$f_k(0)$ = the sighting probability density function for group-size category k evaluated at the trackline.
$g_k(0)$ = the probability of detecting a target of group-size category k directly on the trackline.

We assumed the probability of detecting a carcass directly on the trackline was certain ($g(0) = 1$). This is a standard assumption of line transect methods (Buckland *et al*. 1993b), particularly appropriate when surveying 'neutral' targets neither attracted to nor repulsed by the vessel (Thompson *et al*. 1999). We derived $f(0)$ and the effective strip width ESW = $1 / f(0)$ from the integral of the detection function using the Distance 2.1 software (Buckland *et al.* 1993a, Laake *et al.* 1994) as follows:

$$\frac{1}{f(0)} = \int_0^w g(x)dx \qquad (3)$$

We stratified our survey effort into three grids selected on the basis of hydrographic domains known to influence Short-tailed Shearwater distributions (e.g. Eppley *et al.* 1982, Schneider *et al.* 1986, Hunt *et al*. 1996a). The Nunivak Island (NI) and Slime Bank (SB) grids encompassed waters of the inner and middle domains, on both sides of the inner front and the 50 m isobath. The Pribilof Islands (PI) grid extended across the middle and outer domains over waters between 50- and 200-m depth. We estimated shearwater mortality within these three grids separately because carcass densities during the 1997 die-off differed significantly across sites (Kruskal-Wallis Test, $H = 14.87$, df = 2, n = 364, $P = 0.00059$; Table 1).

Within each grid, we estimated carcass densities using the same methods employed to survey historical seabird distributions in the south-eastern Bering Sea (Eppley *et al*. 1982). We divided the survey trackline into contiguous 3-km transects and calculated the density of carcasses within each of these bins by dividing the number of dead shearwaters sighted (N) by the area surveyed (3 km × ESW), where ESW was not the standard 300-m strip, but the effective strip width estimate for light or dark water. We calculated carcass densities on a grid-specific basis and estimated the number of carcasses afloat within each survey area by multiplying those densities by each grid's area as described in formula 2 (Buckland *et al*. 1993a). We calculated the total number of shearwater carcasses afloat in our study area by adding the estimates from the three survey grids (Table 1). Additionally, to illustrate the disparity between the line and strip methodologies, we estimated carcass abundance using fixed-width 100-m and 300-m strip transects.

RESULTS

Carcass surveys

Floating carcasses were sighted over a broad range of distances ranging from zero to 300 m from the trackline. Nevertheless, the probability of detecting a carcass decreased significantly as the distance from the trackline increased (Fig. 2) for observations in both light (Simple Linear Regression, $F = 20.98$, $P = 0.0001$, n = 31), and dark water (Simple Linear Regression, $F = 2624.76$, $P = 0.00002$, n = 31). Since the assumption of perfect detectability required to use strip transects was not met, we counted shearwater carcasses using distance sampling techniques.

The following hazard rate model best fits the truncated distributions of perpendicular sighting distances to carcasses:

$$k(x) = 1 - \exp[-(x / \alpha)]^{-\beta} \qquad (4)$$

where x is the perpendicular distance from the trackline, and $k(x)$ is the probability of detection.

The hazard rate model is characterized by a shoulder, over which the probability of detection is flat or independent of distance, close to the trackline. Beyond that shoulder, the probability of detection precipitously decreases with increasing distance (Buckland 1985). The best fitting hazard rate models yielded effective strip widths (ESWs) of 54.79 m in light water and 41.94 m in dark water (Table 2).

Estimates of carcass abundance

In 1997, shearwater carcasses were widespread across the south-eastern Bering Sea. Overall, we estimated that over 95 000 carcasses were afloat in the three grids we surveyed. Conversely, during 1998 and 1999 we encountered only one carcass at Nunivak Island (Table 1). A two-way non-parametric analysis of variance revealed that the density of Short-tailed Shearwater carcasses varied significantly between years. On the other hand, we detected no significant differences across sites, and no interaction term between site and year (Table 3).

DISCUSSION

We used standardized survey methods to estimate the abundance of Short-tailed Shearwater carcasses in the south-eastern Bering Sea during three consecutive years. Our observations suggest that

TABLE 2

Parameters used to estimate Short-tailed Shearwater carcass abundance in dark and light water. See equation 4 for definitions of the variables

Water colour	Max. distance (m)	Sample size	$\alpha \pm$ S.E.	$\beta \pm$ S.E.	Effective strip width (ESW ± S.E.) (m)
Dark	250	36	22.93 ± 16.19	1.47 ± 0.69	41.94 ± 15.31
Light	300	96	42.37 ± 6.72	3.13 ± 0.73	54.79 ± 6.92

a significant mortality event occurred during the fall of 1997, when we estimated that over 95 000 carcasses were afloat within our survey grids. Our estimates of floating Short-tailed Shearwater carcasses probably underestimated the magnitude of the 1997 die-off, due to the mismatch between the timing and scope of our surveys and the duration and scale of the mortality event. The first reports of dead shearwaters in the south-eastern Bering Sea occurred on 1 August, almost four weeks before the start of our surveys on 28 August (Baduini *et al*. 2001). Even though the persistence of seabird carcasses in the Bering Sea is not known accurately, it probably ranges from 10 to 20 days (G. Ford pers. comm.). Therefore, a substantial proportion of the floating carcasses may have disappeared due to sinking, scavenging, and deposition on beaches by the time our surveys began. Overall, during the summer–fall period of 1997, an estimated 400 000 Short-tailed Shearwaters were deposited on beaches across a vast geographical area spanning from Cape Anadyr (Russia) and Adak Island (Aleutians) eastwards to Bristol Bay (south-eastern Bering Sea) (Mendenhall 1997). This figure more than doubles our overall at-sea mortality estimates within the south-eastern Bering Sea during August–September 1997 (Baduini *et al*. 2001).

A two-way analysis of variance revealed significant differences in at-sea carcass abundance between years, but not across sites, suggesting that 1997 was indeed a remarkable year of pervasive mortality. In other words, higher mortality occurred at all sites during 1997, whereas we detected no consistent grid-specific differences in the incidence of shearwater carcasses across years.

Line transects are a special case of strip transects, where W (the width of the survey transect) is determined by the ability to detect the targets being surveyed. Although line transects are regularly employed to survey seabirds (Hamer *et al*. 1999, Thompson *et al*. 1999), to our knowledge, this is the first time this technique has been used to estimate bird mortality at sea. However, carcasses have been previously surveyed from vessels, though previous studies did not estimate the strip width effectively searched during surveys. Instead, observers recorded the total numbers of dead birds encountered (Piatt *et al.* 1990, Piatt & Van Pelt 1997), or estimated their density using standard fixed-width strip transects (Tasker 1983 unpubl. rep.). Line transects consistently produced the highest carcass density estimates, when compared to the abundance estimated using fixed-width strip transects (Table 4). It is likely that strip transects underestimated carcass densities because the width of the standard survey transect (100 m or 300 m) was broader than the shoulder of the sightability function (Fig. 3). In other words, observers using standard 300-m (Tasker *et al*. 1984) and modified 100-m (Tasker 1983 unpubl. rep.) strip transects would have undercounted dead birds along the periphery of the transect. Therefore, strip transect surveys would have underestimated the density of shearwater carcasses and the magnitude of the die-off.

A variety of factors including the size and behaviour of the species being surveyed (e.g. small alcids sitting on the water versus flying gulls), visibility conditions during surveys (e.g. fog, glare, sea state), characteristics of the observation platform (e.g. observer height above the water and vessel cruising speed), and overall seabird abundance influence the selection of the appropriate seabird survey protocols (Tasker *et al*. 1984, Spear *et al*. 1992, Van Franeker 1994). Line transects are effort-intensive, and should be employed only when seabirds are sparse and non-mobile, and enough observers are available to estimate the perpendicular ranges to sightings and to monitor birds directly on the track. On the other hand, fixed-width transects are less effort-intensive because they do not require the estimation of perpen-

TABLE 3

Spatial and temporal differences in the density of Short-tailed Shearwater carcasses observed in the south-eastern Bering Sea during August–September, 1997–1999. Results of non-parametric two-way analyses of variance. Independent variables: year (1997, 1998, 1999); location (Nunivak Island, Pribilof Islands, Slime Bank). Dependent variable: carcass density (carcasses km^{-2})

Source	Sum of squares	DF	Total MS	H	Chi-square critical value	Probability	Result
Cells	$46\,419.2 \times 10^{5}$	8	95 319				
Year × Site	7.5×10^{5}	2		7.92	5.991	$0.005 < P < 0.001$	Signif.
Site	1.6×10^{5}	2		1.69	5.991	$0.5 < P < 0.25$	N.S.
Year site	3.3×10^{5}	4		3.47	9.488	$0.75 < P < 0.50$	N.S.

TABLE 4

Estimates of overall Short-tailed Shearwater carcass abundance within three survey grids in the south-eastern Bering Sea (Fig. 1). Mean carcass abundance was calculated using line transects (ESWs from Table 2) and strip transects (w = fixed strip width)

Year	Mean carcass abundance (ESW)	Mean carcass abundance (w = 100 m)	Mean carcass abundance (w = 300 m)	Relative magnitude
1997	95325	40442	13480	1 / 0.42 / 0.14
1998	465	195	65	1 / 0.42 / 0.14
1999	0	0	0	–

dicular ranges. Therefore, strip transects are particularly suited to survey birds that are too numerous and too mobile for the use of line transects. Commonly, 300-m strip transects are used to survey seabird distributions in temperate and polar seas, although the strip width is ultimately determined by the observers' ability to detect every bird within the survey transect. Given this understanding, we offer some recommendations for standardizing surveys of seabird mortality at sea:

1) Line transect methods are preferable to fixed-width strip transects when estimating the abundance of seabird carcasses at sea. The use of an empirically derived optimum detection function will yield more accurate abundance estimates, and will minimize the inaccuracies caused by the under-detection of carcasses at increasing distances from the trackline. Moreover, line transect methods can account for changes in carcass detectability due to differences in platform characteristics, environmental conditions during surveys, and differences in observer ability. These effects are initially quantified when estimating the effective strip widths for varying survey conditions, and can be incorporated into the statistical analysis of carcass densities as co-factors. Therefore, we advocate the use of line transect methods to estimate the abundance of seabird carcasses at sea. However, because line transect methods are effort-intensive and require multiple observers, they may not always prove feasible.

2) Strip transects may be employed to estimate bird mortality at sea in instances where carcasses are too numerous, or when not enough observers are available to conduct line transect surveys. Before fixed-width transects can be employed, however, it is imperative to test whether the underlying assumption of perfect detectability within the survey strip is met. Observers should determine whether the ability to detect carcasses decreases significantly with increasing distance from the track. That is, whether the slope of the detectability function is significantly different from zero (Fig. 2).

3) We recommend that observers estimate the perpendicular distances to carcasses as they float by at a 90-degree angle to the track using a range-finder (Heinemann 1981). We discourage measuring headings and radial distances because small errors in the angle estimates can lead to large errors in the estimated perpendicular distances (Weins *et al.* 1978, Barlow 1995).

4) Accurate mortality estimates require that every carcass close to the track be counted. An independent observer may be specifically devoted to ensure the perfect detectability of targets on the trackline ($g(0) = 1$) (Hamer *et al*. 1999).

5) Exogenous factors such as sea state and differences in observer ability influence target detectability during vessel-based surveys (Buckland *et al*. 1993a, Vandermeer & Camphuysen 1996). The distributions of perpendicular ranges for different survey conditions and observers must be compared statistically before the sightings of a given species are pooled and used to estimate the effective strip width. In this study, the colour of the water affected the distance over which carcasses were effectively detected (Table 2, Fig. 3). Conversely, we detected no significant differences in the perpendicular range distributions across observers and during different sea states. Therefore, we combined observations gathered by different observers during Beaufort 4 and 5 sea states, and estimated effective strip widths separately for light and dark water.

6) We also recommend stratifying sightings by target size (e.g. individual carcasses versus aggregations), whenever targets of varying detectability are encountered. Once more, we suggest comparing the perpendicular range distributions for different size categories, and pooling those that do not differ statistically (Forney & Barlow 1993). The presence of different sized targets would require calculating average group sizes ($S_{i,k}$ in formula 1) and estimating effective strip widths for each target size class separately. Total density estimates would be obtained by adding the estimates from the various target size classes.

7) Once the pooling within species has been accomplished, small sample sizes may require pooling the distributions of similar species based on considerations of colouration and body size. Taxa with statistically indistinguishable perpendicular range distributions are commonly pooled to increase the sample sizes before the effective strip widths are estimated (Forney & Barlow 1993, Barlow 1995).

8) Additionally, we recommend stratifying the study area into survey grids based of distinct habitats known to affect the abundance of live birds (e.g. hydrography, distance from shore) and the distribution of floating carcasses (e.g. current systems, frontal zones, areas of convergence and divergence). We suggest calculating separate density estimates for each survey grid and combining these estimates to obtain a total abundance estimate for the entire study area (Forney & Barlow 1993, Barlow 1995).

9) Finally, to enable the standardization of mortality estimates, it

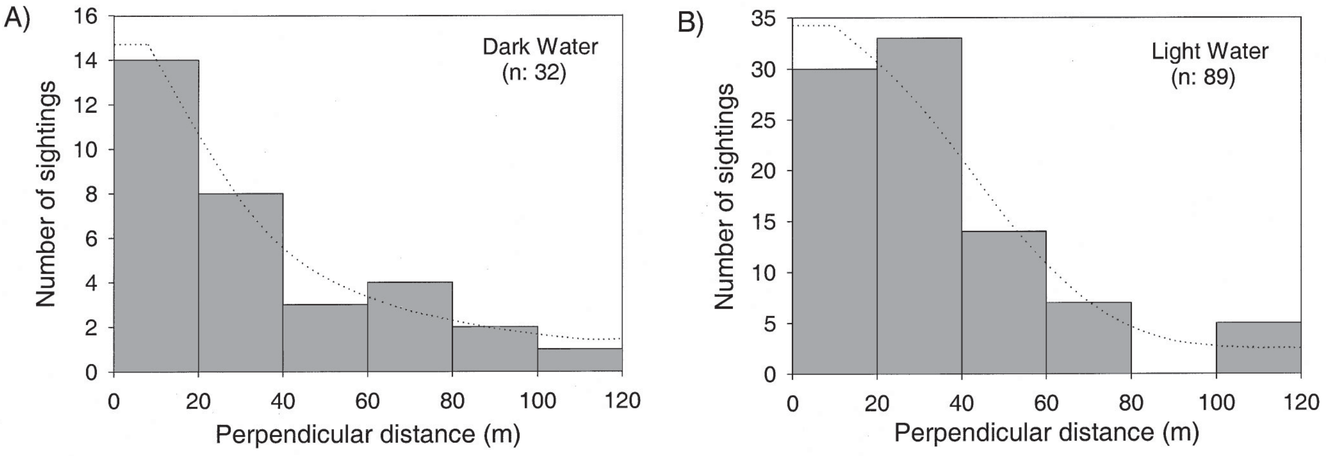

***Fig. 3**. Distribution of perpendicular sighting distances (histograms) and best-fit Hazard model (dotted line) for Short-tailed Shearwater carcasses sighted during sea states of Beaufort 4–5 in (A) dark and (B) light water within a coccolithophore bloom.*

is important that vessel-based surveys be carefully planned to coincide with large-scale mortality events. Substantial delays in the onset of at-sea surveys would lead to the under-estimation of seabird mortality due to the loss of floating carcasses before they could be counted. A dual monitoring programme of 'background' and 'intensive' surveys could ensure the accurate sampling of seabird die-offs. First, regularly scheduled surveys, designed to overlap temporally with important life-history periods characterized by high energetic requirements (e.g. moulting, chick fledging), could target known areas of seabird aggregation (e.g. frontal regions, areas surrounding breeding colonies). These surveys would estimate the background levels of species-specific mortality on a regional and seasonal basis, and would help detect the onset of large-scale seabird die-offs. Evidence of unusual mortality levels would trigger an 'intensive' programme of carefully timed surveys at sea and along beaches, designed to determine the areal extent and the magnitude of the die-off.

An understanding of marine bird distributions, and the physical mechanisms supporting ocean productivity and prey aggregation, will help design monitoring programmes to estimate the magnitude of marine bird die-offs (Hunt *et al*. 1996a, Huettmann & Diamond 2000). In the same way that the standardization of seabird counting protocols (Tasker *et al*. 1984) has facilitated long-term studies of marine bird distribution and abundance (Veit *et al*. 1996), standardized mortality estimates will enable the comparison of seabird die-offs over time.

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REFERENCES

BADUINI, C.L., HYRENBACH, K.D., COYLE, K.O., PINCHUK, A., MENDENHALL, V.M. & HUNT Jr, G.L. 2001. Mass mortality of Short-tailed Shearwaters in the southeastern Bering Sea during summer 1997. *Fisheries Oceanography* 10: 117–130.

BARLOW, J. 1995. The abundance of cetaceans in California waters. Part I: ship surveys in summer and fall 1991. *Fisheries Bulletin* 93: 1–14.

BIBBY, C.J. 1981. An experiment on the recovery of dead birds from the North Sea. *Ornis Scandinavica* 12: 261–265.

BIBBY, C.J. & LLOYD, C.S. 1977. Experiments to determine the fate of dead birds at sea. *Biological Conservation* 12: 295–309.

BODKIN, J.L. & JAMESON, R.J. 1991. Patterns of seabird and marine mammal carcass deposition along the central California coast, 1980–1986. *Canadian Journal of Zoology* 69: 1149–1155.

BUCKLAND, S.T. 1985. Perpendicular distance models for line transect sampling. *Biometrics* 41: 177–195.

BUCKLAND, S.T., ANDERSON, D.R., BURNHAM, K.P. & LAAKE, J.L. 1993a. Distance sampling: estimating abundance of biological populations. London: Chapman & Hall.

BUCKLAND, S.T., CATTANACH, K.L. & HOBBS, R.C. 1993b. Abundance estimates of Pacific White-side Dolphin, Dall's Porpoise and Northern Fur Seal in the North Pacific, 1987–1990. *International North Pacific Fisheries Commission Bulletin* 53: 387–408.

EPPLEY, Z.A., HUNT, Jr, G.L. & BUTOWSKI, N. 1982. Pelagic distribution of marine birds of the north Aleutian shelf and analysis of encounter probability. U.S. Department of Commerce, NOAA, OCSEAP Final Report 45 (1986): 1–120.

FORNEY, K.A. & BARLOW, J. 1993. Preliminary winter abundance estimates for cetaceans along the California coast based on a 1991 aerial survey. *Reports of the International Whaling Commission* 43: 407–415.

HAMER, T.E., THOMPSON, C., BRENNAN, K. & BEISSINGER, S. 1999. Testing assumptions of the line transect sampling method used to estimate murrelet densities at sea. *Pacific Seabirds* 26: 36.

HEINEMANN, D. 1981. A range-finder for pelagic bird censusing. *Journal of Wildlife Management* 45: 489–493.

HUETTMANN, F. & DIAMOND, A.W. 2000. Seabird migration in the Canadian northwest Atlantic Ocean: moulting locations and movement patterns of immature birds. *Canadian Journal of Zoology* 78: 624–647.

HUNT Jr, G.L., COYLE, K.O., HOFFMAN, S., DECKER, M.B. & FLINT, E.N. 1996a. Foraging ecology of Short-tailed Shearwaters near the Pribilof Islands, Bering Sea. *Marine Ecology Progress Series* 141: 1–11.

HUNT Jr, G.L., DECKER, M.B. & KITAYSKY, A. 1996b. Fluctuations in the Bering Sea ecosystem as reflected in the reproductive ecology and diets of kittiwakes on the Pribilof Islands, 1975 to 1991. In: Greenstreet, S.P.R. & Tasker, M.L. (Eds). Aquatic predators and their prey. Oxford: Fishing News Book. pp. 142–153.

LAAKE, J.L., BUCKLAND, S.T., ANDERSON, D.R. & BURNHAM, K.P. 1994. Distance. User's Guide V 2.1. Fort Collins: Colorado Cooperative Fish and Wildlife Research Unit.

MENDENHALL, V.M. 1997. Preliminary report on the 1997 Alaska seabird die-off. U.S. Fish and Wildlife Service. 3 pp.

NAPP, J.M. & HUNT Jr, G.L. 2001. Anomalous conditions in the southeastern Bering Sea, 1997: linkages among climate, weather, ocean and biology. *Fisheries Oceanography* 10: 61–68.

PIATT, J.F. & FORD, R.G. 1996. How many seabirds were killed by the Exxon Valdez oil spill? In: Rice, S.D., Spies, R.B., Wolfe, D.A. & Wright, B.A. (Eds). Exxon Valdez Oil Spill Symposium Proceedings. *American Fisheries Symposium* 18: 712–719.

PIATT, J.F., LENSINK, C.J., BUTLER, W., KENDZIOREK, M. & NYSEWANDER, D.R. 1990. Immediate impact of the 'Exxon Valdez' oil spill on marine birds. *Auk* 107: 387–397.

PIATT, J.F. & VAN PELT, T.I. 1997. Mass-mortality of Guillemots (*Uria aalge*) in the Gulf of Alaska in 1993. *Marine Pollution Bulletin* 34: 656–662.

SCHNEIDER, D.C. 1990. Spatial autocorrelation in marine birds. *Polar Biology* 8: 89–97.

SCHNEIDER, D.C., HUNT Jr, G.L. & HARRISON, N.M. 1986. Mass and energy transfer to seabirds in the southeastern Bering Sea. *Continental Shelf Research* 5: 241–257.

SPEAR, L.B., AINLEY, D.G., NUR, N. & HOWELL, S.N.G. 1995. Population size and factors affecting the at-sea distributions of four endangered procellariids in the tropical Pacific. *Condor* 97: 613–638.

SPEAR, L.B., NUR, N. & AINLEY, D.G. 1992. Estimating absolute densities of flying seabirds using analyses of relative movement. *Auk* 109: 385–389.

STENZEL, L.E., PAGE, G.W., CARTER, H.R. & AINLEY, D.G. 1988. Seabird mortality as witnessed through 14 years of beached bird censuses. Point Reyes Bird Observatory report for the Gulf of the Farallones Marine Sanctuary.

TASKER, M.L., HOPE JONES, P., DIXON, T. & BLAKE, B.F. 1984. Counting seabirds from ships: a review of methods employed and a suggestion for a standardized approach. *Auk* 101: 567–577.

THOMPSON, C.W., BRENNAN, K., HAMER, T. & STRONG, C. 1999. Behavior of marbled murrelets in response to survey vessels during at-sea surveys: implications for use of line transects. *Pacific Seabirds* 26: 47.

VANCE, T.C., SCHUMACHER, J.D., STABENO, P.J., BAIER, C.T., WYLLIE-ECHEVERRIA, T., TYNAN, C.T., BRODEUR, R.D., NAPP, J.M., COYLE, K.O., DECKER, M.B., HUNT Jr, G.L., STOCKWELL, D., WHITLEDGE, T., JUMP, M. & ZEEMAN, S. 1998. Aquamarine waters recorded for the first time in eastern Bering Sea. *EOS Transactions, American Geophysical Union* 79(10): 121, 126.

VANDERMEER, J. & CAMPHUYSEN, C.J. 1996. Effect of observer differences on abundance estimates of seabirds from ship-based strip transect surveys. *Ibis* 138: 433–437.

VAN FRANEKER, J.A. 1994. A comparison of methods for counting seabirds at sea in the Southern Ocean. *Journal of Field Ornithology* 65: 96–108.

VEIT, R.R., PYLE, P. & MCGOWAN, J.A. 1996. Ocean warming and long-term change in pelagic bird abundance within the California Current system. *Marine Ecology Progress Series* 139: 11–18.

WEINS, J.A., HEINEMANN, D. & HOFFMAN, W. 1978. Community structure, distribution, and interrelations of marine birds in the Gulf of Alaska. U.S. Department of Commerce NOAA, OCSEAP Final Report 3: 1–178.

WILKINSON, L. 1997. SYSTAT: The system for statistics. Evanston: Systat Inc.

ZAR, J.H. 1984. Biostatistical analysis. Englewood Cliffs: Prentice-Hall.