Monitoring seabirds population in marine ecosystem: The use of strip-transect aerial surveys

Grégoire Certain [a,b,*], Vincent Bretagnolle [b]

[a] CRELA, Université de La Rochelle, 23 avenue Albert Einstein, 17071 La Rochelle Cedex 9, France
[b] Centre d'Études Biologiques de Chizé, CNRS, 79360 Beauvoir sur Niort, France

ABSTRACT

In the case of marine systems, monitoring seabird populations at sea require adequate, low cost protocols that maximize data resolution, accuracy and survey effort. This paper examines bias associated with pelagic aerial strip-transects, an easily designed and low cost survey method, to validate its use for monitoring and mapping seabird populations at sea at a very large scale. We used data collected on the entire seabird community between October 2001 and March 2002 in the Bay of Biscay ($100\,000$ km^2 on the French Atlantic coast, Northeast Atlantic) to determine whether aerial strip-transect seabird survey were subject to temporal (i.e. variations of detection probability during the survey) or distance (i.e. variations of detection probability across the strip) bias. To detect these biases, two seabird taxa were contrasted, the highly conspicuous northern gannet versus three cryptic species of auks pooled as one taxonomic group. We reported that the only temporal bias was attributable to sun glare. By contrast, distance bias did not occur in a strip of 150 m for both species, and the effect of distance up to 230 m was very weak. We conclude that visibility bias have a limited effect on pelagic aerial surveys for most seabird species. Particular attention should be paid to the constant record of sun glare, while altitude and speed can be fixed in a relatively wide range (140–180 m, 150–200 km/h) without affecting detection probability. Since distance bias did not occur across a 150 m strip, there is no need to add complexity to survey protocol by using line-transect method. This method takes distance effects into account but requires distance estimates between the bird and the transect line for every sightings. These estimates are usually easily collected in the case of marine mammals but become problematic in the case of flying animals such seabirds, sometimes encountered in very high density and aggregated into groups of several hundred individuals.

© 2008 Elsevier Inc. All rights reserved.

1. Introduction

Collecting seabird data at sea can be achieved by several methods. Basically, two types of counting platforms are available, ship and aircraft (Camphuysen et al., 2002). Sampling schemes are mainly composed of transects either randomly or regularly distributed (Buckland et al., 2001). Seabird sightings may be collected either by strip (Eberhardt 1978; Tasker et al., 1984) or line-transect (Burnham et al., 1980) methods. Line-transect methods assume that all objects directly on the transect line are detected (i.e. seen and recorded by observers) and allow for objects off the line to be missed, but perpendicular distance from the trackline to all objects must be measured. Strip-transect methods assume all objects within the strip (typically a few hundred meters) are detected (Fig. 1a), does not allow for objects to be missed, but does not required estimates of distance to be made. Typically, line-transect methods are assumed to be state of the art for marine mammals (Hammond et al., 2002), whereas strip-transect methods are that for seabirds (Tasker et al., 1984).

Three kinds of bias can be distinguished, namely homogenous, temporal and distance (Fig. 1). Homogeneous bias (Fig. 1b) results in a detection probability constant but inferior to one and is attributable to constant parameters of the survey (for example observer performance, or targets randomly diving). As a consequence, animals are randomly missed and abundances are underestimated. Temporal bias (Fig. 1c) results in variations of the detection probability along the transect line and is attributable to varying parameters during the survey (for example deteriorations of weather conditions at a particular time). As a consequence, the detection probability is reduced in some parts of the transect and abundances are locally underestimated. Distance bias (Fig. 1d) results from a decrease in the detection probability with an increase in the lateral distance between the observations and the transect line. As a consequence, sightings located far away from the observer are more likely to be missed. The distance bias is problematic for the strip-transect method because it assumes a constant detection probability across the strip, but is not for line-transect method where distance data are collected and used as

* Corresponding author. CRELA, Université de La Rochelle, 23 avenue Albert Einstein, 17071 La Rochelle Cedex 9, France.
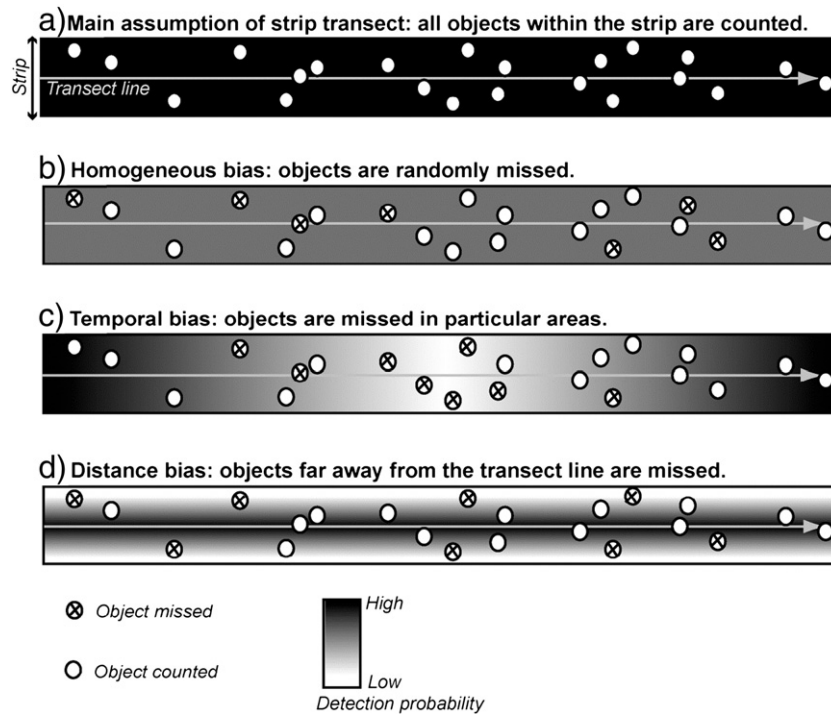E-mail address: gregoirecertain@hotmail.com (G. Certain).

Fig. 1. Schematic representation of strip-transects with the detection probability (grey level) within the strip. (a) shows the main assumption of strip-transect methods. (b), (c) and (d) shows the three kind of bias associated: b) homogeneous bias; c) temporal bias and d) distance bias. Biases are differentiated on the basis of the kind of variations in detection probability.

covariates to model the decrease of detection probability (Buckland et al., 2001).

Whether or not observations are subject to distance bias at short distances (typically within the strip) is a criterium to choose between line- and strip-transect methods. By contrast, line- and strip-transect methods are affected in the same way by homogeneous and temporal bias that requires analogous sampling and analytical procedure to be corrected (Borchers et al., 1998; Pollock et al., 2006). Routine monitoring protocols for seabirds at sea should reach a compromise between accuracy of the data collected, feasibility and economic cost. The choice is not straightforward, because it also depends on the size and location of the study area (e.g., the use of an aircraft is limited to a few hundred kilometres off the coastline, typically continental shelves areas), on the target species and on the aim of the study.

During winter 2001–2002, we collected seabird data in the Bay of Biscay (100 000 km^2 of continental shelf on the French Atlantic coast, see Bretagnolle et al., 2004) using aerial strip-transect method (Briggs et al., 1985a,b). The goal of the research programme was to provide, for management purpose, distribution maps and abundance estimates of the seabird community. We used an aircraft because it can survey a greater distance in a shorter period of time than a ship, so the cost per unit effort is lower. This allows for increased survey effort and replicated surveys to better capture the variability inherent to natural population of birds at sea. Furthermore, aerial surveys are less constrained by adverse weather conditions since the decision of carrying a survey can be taken with prior knowledge of meteorological forecasts: in poor weather, aerial surveys can be stopped while ship-based surveys cannot. Recently, Camphuysen et al. (2002) recommend aerial or ship-based line-transect, while most surveys on seabirds have used strip-transect methodology from ship-based counts (e.g., Ainley et al., 2005; Davoren et al., 2003; Spear et al., 2003). We used strip-transect rather than line-transect because distance estimates are time consuming and, therefore, are problematic when density of survey targets is high. However, the robustness of the aerial strip-transect method to the different sources of bias must be evaluated,

especially for the distance bias which cannot be corrected when distance data are not recorded.

The aim of this paper was to validate the use of aerials strip-transects to carry routine monitoring of seabirds at sea. In a first step we carefully examine the biases that could have affected our survey. We focused in particular on (1) temporal bias and on (2) distance bias. We did not used double platform methods, required to directly measure the effect of homogeneous bias (Borchers et al., 1998; Pollock
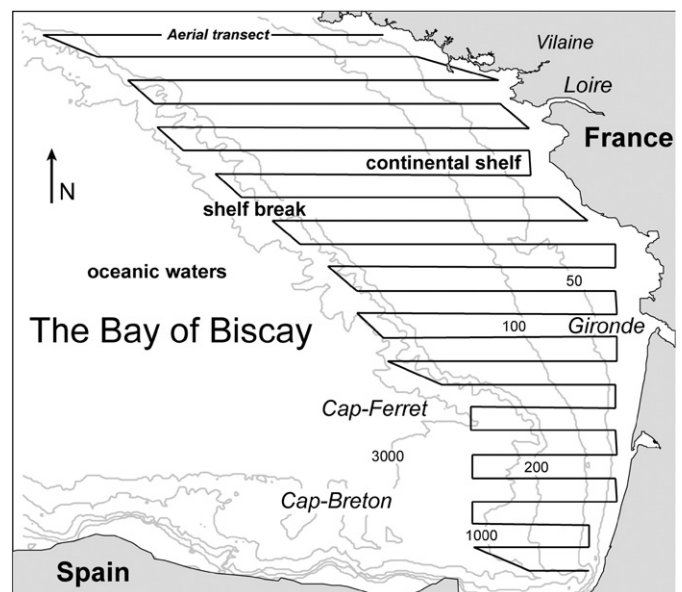

Fig. 2. Sampling scheme ROMER ("Recherche sur les Oiseaux Marins en MER") used during the study, composed of 24 transects (totalling c. 5000 km) over the continental shelf (100 000 km^2) of the Bay of Biscay.
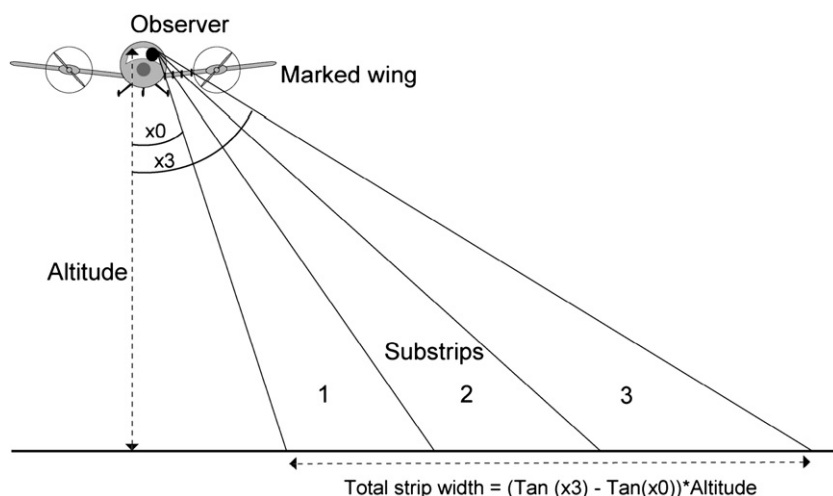
Fig. 3. Observation protocol. Observers (each side of the plane) scan a 230 m strip located by marks on the wing. From Jan to March 2002, strip was subdivided in three substrips.

et al., 2006). To investigate temporal bias, we tested if the detection probability varied along transects (i.e. during the survey) together with survey or environmental parameters. To investigate distance bias, we tested if the detection probability varied across the strip. We used the density of seabird sighting as a proxy for detection probability. In a second step, we analyse the data collected and we take into account the detected bias, in order to provide unbiased species richness and log abundance maps for the seabird community. Both indexes can be understood as primary tools of an integrated environmental management.

2. Methods

2.1. Study area and survey design

Aerial surveys were conducted during winter 2001–2002 in the Bay of Biscay, on the French Atlantic coast. The survey occurred two years after an important oil spill (the "Erika") on the french coast, in order to sample seabirds populations after an important mortality event (Bretagnolle et al., 2004; Cadiou et al., 2004). We sampled the Bay of Biscay (i.e. shelf area, 100 000 km²) on a monthly basis. Six surveys were carried out between October 2001 and March 2002. Each was composed of 5000 km of aerial transects that were designed under a systematic sampling scheme (Fig. 2).

A complete coverage of the study area was achieved in six days (a similar coverage by a ship would need more than 30 days). The sampling days were consecutive when the meteorological conditions allowed it. Our aircraft was a twin engine PA 34 Seneca, with low wings (i.e. wings are located beneath the observers and mask the sea except for observers located in the rear seats of the plane) although upper-wings are usually recommended (Buckland et al., 2001; Camphuysen et al., 2002). However no high winged aircraft was available in France at the time surveys started. Low wings permitted putting marks on the wing as a visual guide for observations into specified substrips (see below).

Flights were carried out all day long, usually between 09:00h and 17:00h. Flight duration ranged from 150 to 180 min, and generally two flights were carried out per day. Preliminary surveys were conducted in February 2001 in order to determine the optimal speed and altitude. 150 km/h at 150 m above sea level (asl) were estimated as the best trade-off between time window, good visibility and safety needs. Briggs et al. (1985a) and Camphuysen et al. (2002) recommend 80 m asl, but under French legislation, planes are not allowed to fly over the sea at less than 150 m. Moreover, we found difficult to identify and count seabirds at 80 m asl, simply because the time during which birds

can be seen by the observers is about 2 s in a plane with lower wings (instead of 4–7 s, depending on the location of the animals across the strip, at 150 m asl). Despite the attention paid during flight, our survey had variations in speed (from 150 to 200 km/h) and altitude (from 140 to 180 m). Weather conditions were carefully examined before take off and flights only started when weather conditions were equivalent or better to: sea state < Beaufort 3, absence of rain or fog, visibility >10 km.

2.2. Counting method

As did Briggs et al. (1985a,b) and Pollock et al. (2006), we used aerial strip-transect method. We used a narrow strip (Briggs et al., 1985a) to ensure an equal detection rate. The strip was indicated by permanent marks on the wings, and was on average 230 m wide on each side. However, with varying altitude (and lateral inclination of the plane), the strip width ranged between 200 and 300 m (Fig. 3). A "blind" strip (i.e. hidden to observers) of 180 m was below the plane (Fig. 3). Such a blind strip may be problematic when using a line-transect methodology (Alldredge and Gates, 1985; Quang and Lanctot, 1991) but is less so for the strip-transect method, provided that distance bias across the strip does not exist.

In order to check for the distance bias, we recorded the position of seabirds within the strip during three monthly surveys from January to March 2002 (on one side only). To this end, the strip was subdivided in three substrips (respectively of 70, 75 and 85 m; see Fig. 3). Two observers, experienced in seabird observation (always the same) were placed on each side of the plane. The plane had three seats on each side, and observers sat on the rear seats which were c.1.5 m behind wings, allowing the use of marks on the wing to visualize the strip and

Table 1
Taxonomic groups used to calculate a spatial index of the specific richness of the seabird community within the Bay of Biscay

Taxonomic group	Species composition
Large gulls	40% *Larus argentatus*; 50% *Larus fuscus*; 10% *Larus marinus*
Kittiwakes	90% *Rissa Tridactyla*; 10% *Larus melanocephalus*
Auks	85% *Uria aalge*; 10% *Alca torda*; 5% *Fratercula arctica*
Terns	85% *Sterna sandvicensis*; 15% *Sterna hirundo*
Puffins	90% *Puffinus puffinus*; 10% *Calonectris diomedea*
Gannets	100% *Sula bassana*
Skuas	97% *Catharacta skua*; 2% *Stercorarius longicaudus*; 1% *Stercorarius parasiticus*

Species composition has been calculated on the basis of aerial sightings identified to the species level.

to quickly allocate sightings to a given substrip. Each observer had a GPS (Garmin 12) connected to a laptop computer and record every seabird species seen. At each new sighting, observers recorded the GPS position, the number of birds, the species composition of the seabird group, if any, and the time of observation to the nearest second. Species were identified at the species level as far as possible, and when not they were nonetheless identified as belonging to one of the seven taxa listed in Table 1. Speed and altitude (using an altimeter) were given by the pilot and recorded every 10 min by observers on paper sheets (together with time), as well as cloud cover and sea state. We did not record a glare index during surveys, but we assumed that orientation side of the plane was an indirect measure of glare effect. Due to the East–West orientation of transects, only southward oriented observations were potentially affected by sun glare (see also Yoshida et al., 1998 for a similar situation). The two observers switched their position at each new flight to avoid getting a stiff neck.

2.3. Description of the sources of biases and of their consequences

Two categories of factors may affect the probability of detecting an animal from a plane, namely visibility and availability bias (Caughley, 1974). This designation refers to the cause of the bias, while our designation (homogeneous, temporal and distance bias, see introduction) refers to the consequence of the bias (i.e. the way the detection probability varies in the strip).

Visibility bias (also called perception bias, Pollock et al., 2006) occurs when targets should be recorded but are not (animals are present, visible but are missed by observers). The effect of visibility bias had already been demonstrated for terrestrial aerial surveys (Redfern et al., 2002). During at-sea surveys, the weather conditions (waves, cloud-cover and sun glare) can affect the visibility (Holt and Cologne, 1987) and may result in temporal bias. Object detection by the human eye at sea relies mainly on movements (flying or flushing) and/or color contrasts with the ocean (see Tasker et al., 1984). Cryptic species such seabirds with dark dorsal plumage may be randomly missed by observers, resulting in homogeneous bias. Training, skills or tiredness of observers, type of engine, time of day, specific equipment (binoculars, sun glasses) and many other factors can affect visibility (Barlow et al., 2001; Pollock & Kendall, 1987). Some of these factors can fortunately be controlled during the surveys (training, type of engine, equipment, weather conditions before take-off).

Availability bias occurs when the animals are present but cannot be detected, or are counted when they should not. A first example of such bias is the diving behaviour of auks which, in its simplest form (assuming that birds dive randomly and independently), corresponds to an homogeneous bias that requires specific protocols to be estimated (Borchers et al., 1998; Hiby & Lovell, 1998; Okamura, 2003; Pollock et al., 2006). Other, more complex availability bias results from target movements: attraction or repulsion to the survey platform, random or directional displacement. Spear et al. (2004) provide a complete overview of such biases and Trenkel (2003) presents similar developments applied to fish schools. These situations may lead to serious bias when the speed of the survey platform (e.g. a ship) is similar to the speed of birds (Garthe & Huppop, 1999) and specific methods based on the record of behaviours have been developed to correct for these effects (Spear et al., 1992; Hyrenbach, 2001; Spear et al., 2004). Fortunately, the problem of target movements is greatly minimized when the speed of the counting platform far exceeds the speed of the targets (Southwell, 1994) and we assume that our aerial survey was not subject to movement bias since our reference speed, 150 km/h, was near 5 times greater than bird speed (around 30 km/h depending on species, Spear et al., 2004).

2.4. Temporal bias evaluation

Our first aim is to evaluate whether or not some parameters may introduce temporal bias during seabird strip-transect aerial surveys. More precisely, we focus on "survey parameters" and "environmental parameters". Survey parameters refer to speed (km/h), altitude (m), observer (1 or 2), and tiredness (measured by the elapsed time from departure). Environmental parameters refers to orientation (N or S, proxy for sun glare), cloud cover (from 0 to 4), sea state (Beaufort), and time of the day (h).

Transects were sliced into 'bins' of equal length. Bin length was fixed at 20 km, according to the frequency at which the survey and environmental parameters were recorded. Each side of the plane produced one bin, to conserve observer and orientation information. These bins are the statistical unit of our analyses. Ideally, the response variable should be the detection probability, but without double platform, it can't be estimated. We then used the number of bird detection (regardless of group size) or "sightings" per bin as a proxy for detection probability. However, the use of such a proxy for detection probability can be subject to several confounding factors.

The first confounding factor is the group size, which is known to increase the detection probability (Quang, 1991). Hence, large seabird aggregations are not relevant from the detection process and do not provide information on the variations of the detection probability. Then, the sightings containing more than five individuals (<1% of the dataset) were removed before the analysis.
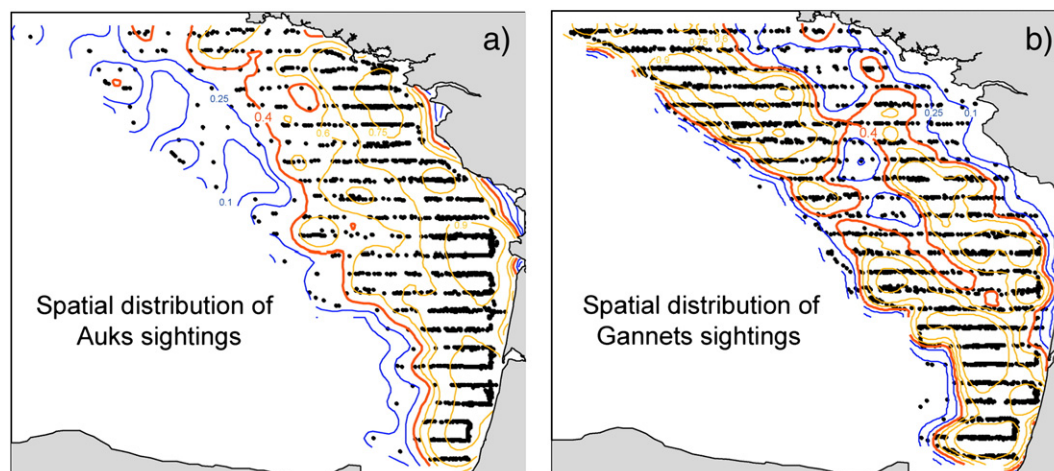

Fig. 4. Geographical position of observations (black dots), collected during the six monthly surveys, from October 2001 to March 2002. The red contour lines delineate the areas used for testing temporal and distance bias for auks and gannets. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Second, sightings density is likely to vary within the study area together with bird density, which constitutes a problem to disentangle a decrease in the number of sightings due to a true decrease in detection probability and a decrease in the number of sightings attributable to a decrease in bird density. To circumvent this problem, we contrasted two seabird taxa. One taxa is highly conspicuous (adult northern gannet *Sula bassana*: white plumage, 3 kg mass; 165–180 cm wingspan, 90 cm length) and the other is cryptic (auks *Uria aalgae* (85%), *Alca torda* (10%) *Fratercula arctica* (5%), all with a dark dorsal plumage, 800–900 g mass, 60–70 cm wingspan, 38–45 cm length). We worked under the assumption that gannets detection is not biased. In other word, gannets sightings are considered as a control. Hence, biases will be detected relatively by the comparison between both taxa.

A third confounding factor could be the simple absence of birds in the data collected outside bird's habitat. In fact, data collected out of gannets or auks habitat are useless, because whatever the survey conditions, they will not contain any sightings and will not provide any information on detection probability. Core areas of seabird presence were defined (Fig. 4) using an approximation of the ordinary kernel density estimate (Bailey & Gatrell, 1995) to ensure that the statistical analyses were performed in high density area. For both species, we then selected the areas containing 90% of observations.

The statistical analyses only consider bins located within these core areas.

Data collected from October 2001 to March 2002 were used to test for temporal bias. We obtained 2652 bins, 1304 for the auk and 1348 for the adult gannets. Each bin contains one response variable, the number of sightings, a set of covariates of interest (the environmental and survey parameters), and a ninth covariate specifying the taxa. To detect and quantify effects of environmental and survey parameters, we used Generalized Linear Models (Mc Cullagh & Nelder, 1989).

To specify the model family, the statistical distribution of the response has to be known. We used a negative binomial distribution (widely used in animal counts, White & Bennetts, 1996). To check whether or not this statistical distribution is appropriate, we searched for the descriptive parameters of the distribution with the log-likelihood function. We then compared observed distribution and theoretical distributions with a parametric bootstrap.

To model the effects of survey and environmental parameters, we used Generalised Linear Model with a negative binomial error distribution and a log link function (Venables & Ripley, 2002). The most parsimonious model was selected through a stepwise algorithm, based on the *Bayesian Information Criterion* (BIC, Schwarz, 1978), which is usually recommended for prediction when datasets are large, and when assuming that the "true model" exists and is one of the
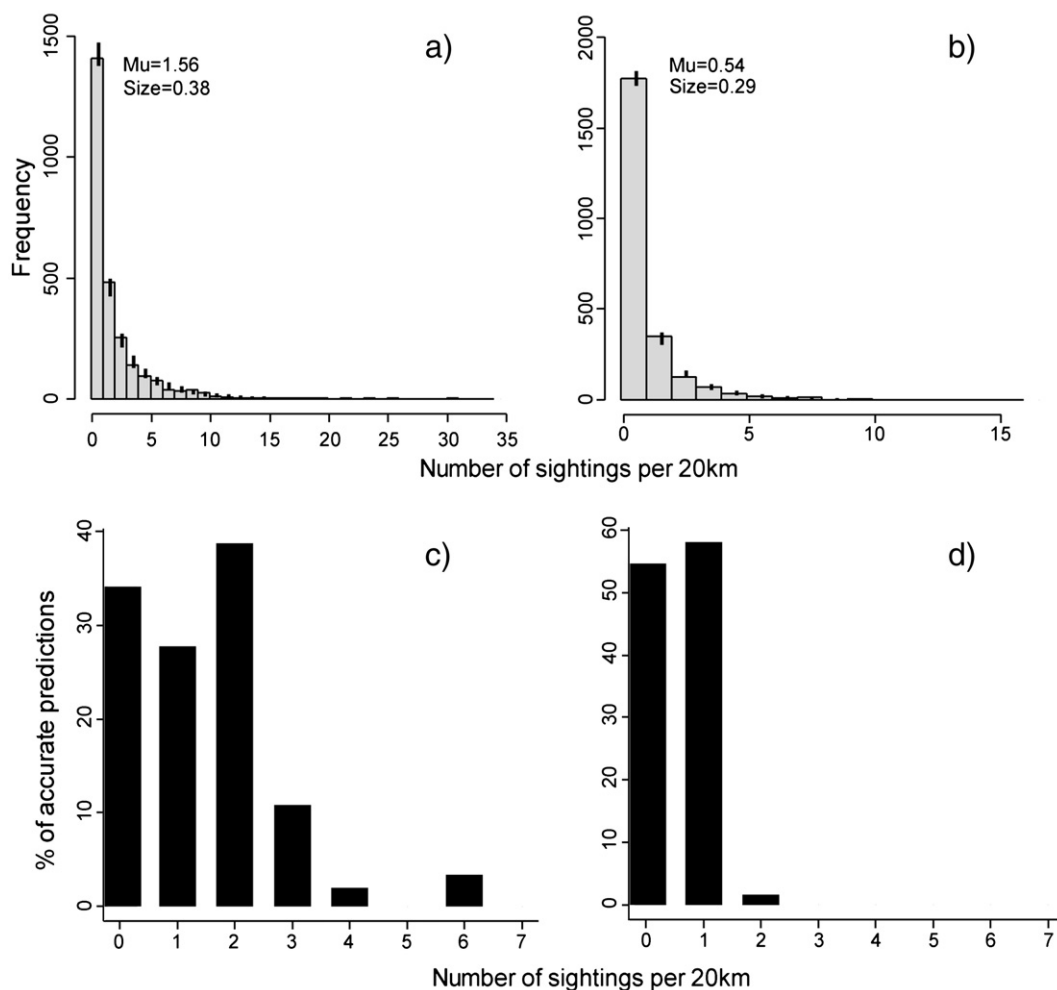

Fig. 5. Graphs checking for validity and performance of our models. a) shows the statistical distribution of the response (number of sightings per bin of 20 km) of the model testing for temporal bias. Black bars represent 95% confidence intervals of a negative binomial distribution fitted to the data whose parameters are reported on the graph. Confidence intervals are extracted from 999 simulations. b) Same thing as a) but for the model testing for distance bias. c) Accuracy of the model testing for temporal bias, calculated as the percentage of good predictions obtained by the model when applied to the 50% of the data not used to build the model. The percentage of good prediction had been calculated for every value of the response. d) Same thing as c) but for the model testing for distance bias.

Table 2
Final model evaluating effects of visibility biases along the transect

Effect (modality)	P value	% Expl. deviance	GLM coefficient	Coef. std. error
Orientation (S)	<0.001	4.465	−2.202	0.209
Taxa (Gannets)	0.59	1.731	−0.067	0.127
Speed	<0.001	0.0224	0.064	0.019
Cloud cover	0.032	0.003	−0.087	0.041
Sea state	<0.001	2.482	−0.373	0.066
Time of day	<0.001	0.117	0.74	0.219
Orientation:Taxa	<0.001	4.008	1.515	0.200
Orientation:Cloud cover	<0.001	0.758	0.216	0.064
Speed:Time of day	<0.001	0.837	−0.004	0.001

Significance levels, effect size (% deviance explained by each covariates), value of the GLM coefficient and its associated standard error are reported. Covariates were selected by a backward stepwise selection procedure based on the BIC. In cases of factors, the modality (the class used as a reference to measure the effect) is put between brackets.

candidate models being considered (Burnham & Anderson, 2002). BIC is furthermore a "dimension-consistent" criterion which selects amongst a subset of identical models (in terms of information) for the model with smallest dimension. The procedure started from a model incorporating all 9 simple effects (all covariates), and all possible second order interactions (36), and moved backward.

Our data are potentially subject to spatial autocorrelation. To reduce autocorrelation, only half of the dataset was used (50% of bins were randomly selected) to run the model. Once the most parsimonious model was identified by the BIC, the other half of the dataset was then compared to the predictions obtained by the final model, to check its performance.

2.5. Distance bias evaluation

We further examined if the number of sightings observed varied across the strip (among substrips) using data gathered between January and March 2002. Each substrip produced one bin, so that every 20 km, three bins were available (3 substrips on one side of the plane). We obtained N=2403 such bins. A second GLM was run, incorporating distance effects (i.e. distance class of 70, 75 and 85 m), taxa (as a control), and the principal covariates identified in the first model. For a more comprehensive representation, average densities of sightings for the time period between January and March were calculated for each substrip and were associated to confidence intervals obtained from a non-parametric bootstrap in the bins. Density calculation took into account substrip width variation due to altitude variation (see Fig. 3). All Statistical computing were made with freeware R 2.0.1 (R development core team, 2005).

2.6. Species richness and abundance of the seabird community

Once biases were evaluated, we selected unbiased bins (according to the covariates identified as a source of bias in the previous models). We then computed species richness and log abundance maps for the seabird community. We used the 7 seabird taxa listed in Table 1, because they correspond to the identification level at which all sightings were at least identified. From a plane it can be difficult to discriminate between similar species, so we rather grouped species with similar aspects and ecological characteristics. The species composition of these taxa is listed in Table 1.

These data were then analysed as follows: for every 20 km bins, we calculated the total number of taxa per bin and the log of the total number of seabirds counted per bin. We used log abundance of birds rather than simple abundance because important bird aggregations (i.e. >100 individuals) creates outlier in the data with important weights during interpolation. These outliers mask the global pattern of bird distribution and are not relevant from the process under study: the large-scale spatial distribution of birds. In fact, these aggregations

correspond to a local and very dynamic process that can be encountered anywhere in areas of high bird density.

Binned data were then interpolated with geostatistics (Cressie, 1993). First, a variogram model is fitted to the experimental variogram calculated on the data, then this model (which reflects the spatial structure of the variance of the data) is used to calculate appropriate weights for the interpolation (the prediction of the value at a given spatial location is a weighted average of neighbouring points). The interpolation procedure provides a spatial measure of species richness (approximated by the total number of ecological taxa) and of seabird log abundance during the studied period (winter 2001–2002). Interpolation was carried out on a 5*5 km grid.

3. Results

3.1. Temporal bias evaluation

The statistical distribution of our response variable lay well in the confidence intervals of a theoric negative binomial distribution (Fig. 5) and thus the use of negative binomial GLMs was appropriate. After running the stepwise analysis, three interactive terms (orientation and taxa, orientation and cloud cover, and speed and time of day) and six simple effects (orientation, taxa, cloud cover, sea-state, speed and time of day) were retained in the final model (Table 2). However, the model explained only 14.4% of the variation in the data. When the model was applied to the other half of our data, we found that, for a given number of sighting per bin, the percentage of predictions equal to the observed data was around 30% and for the bins containing 2 sightings or less, but decreased quickly to 0% for the bins containing more than 4 sightings (Fig. 5c).

A clear temporal bias was due to sun glare, as we observed an important interaction between orientation and taxa coupled to an important effect of sun glare (Table 2). Both explained 8.8% of the deviance in the data (out of the 14.4% explained by the model) and suggest that auk's detection was more affected by sun glare than gannet's detection, as expected by the comparison between a cryptic and an easily detectable target. The effect size of covariate "Sea-state" was weaker (2.5%) and furthermore no interactions were found between sea state and taxa, which indicates that sightings density decreased under high sea state conditions in the same way for both species. Other significant effects were associated to very small GLM coefficient and effect size (Table 2).

3.2. Distance bias evaluation

Given that orientation affected the detection probability along transect, we kept this effect as a covariate in addition to distance (the covariate of interest) and taxa. We also incorporated sea state, especially to investigate the interaction with distance: animals located at the external border of the strip may be more frequently masked by the waves. In other words, the distance bias, if it exists, could be reinforced under high sea state. Hence the second model incorporated

Table 3
Final model evaluating effects of visibility biases across the strip

Effect (modality)	P value	% Expl. Deviance	GLM coefficient	Coef. std. error
Distance	0.692	0.231	0.001	0.003
Orientation (S)	0.006	7.538	−0.868	0.315
Sea-state	0.209	2.503	−0.270	0.215
Taxa (Gannets)	0.063	0.049	−0.571	0.308
Distance:Orientation	0.471	0.006	−0.001	0.002
Distance:Sea-state	0.464	0.0474	−0.001	0.001
Distance:Taxa	0.019	0.592	0.004	0.002

Covariates have been chosen according to the results obtained in the previous model (see Table 2).
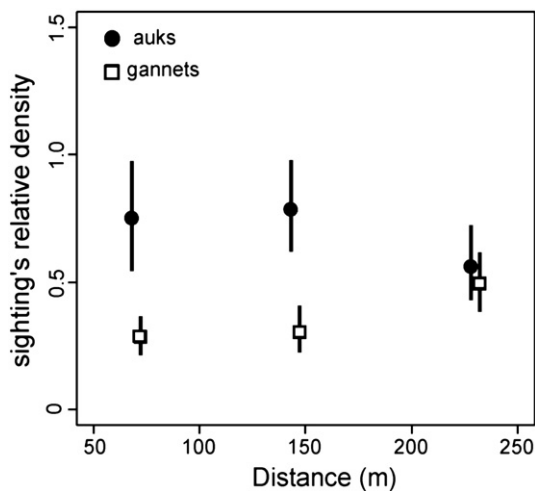
Fig. 6. Gannets and auks sightings density (N/km^2) among our three substrips (0–70 m; 70–145 m; 145–230 m). Bars represent confidence intervals obtained from 999 non-parametric bootstrap samples. Average density was calculated using data collected in January, February and March 2002.

sea state, orientation, taxa and distance effects plus all interactions involving distance and other covariates (Table 3).

Except orientation (whose effect had been already presented in the previous section), we found a significant interaction between distance and taxa, but without significant effect of distance alone. This suggests that the number of sightings of gannets and auks evolve perhaps differently with distance, but that overall distance effect is not significant. Non significant interactions between distance and other covariates suggested that effects of sun glare and sea state were homogeneous across the strip. Model predictive power is shown in Fig. 5d: we obtained more than 50% of correct predictions only for bins containing 0 or 1 sighting. This latter model only accounted for 10.9% of the total deviance.

Sightings density among substrip for both species (Fig. 5) showed that density was constant up to c.150 m. In the third substrip (between 150 m and 230 m), we observed contrasting variations for auks and gannets that can be related to the significant interaction observed in the model: sightings density slightly decreased for auks and slightly increased for gannets. These variations were considered as non significant because (1) distance effect was not significant in the model and (2) confidence intervals of densities in the last substrip were not

disjoint from those of substrips 1 and 2 (Fig. 6). However, this result indicates that 230 m is clearly an upper limit for strip width.

We then conclude that the distance bias was inexistent in the two first substrip and furthermore that neither environmental nor survey parameters interacted with distance effects. Further aerial surveys should reduce the strip to 150 m each side of the plane if one would avoid the variability detected in the last substrip.

3.3. Species richness and abundance of the top seabird community

On the basis of biases analyses, we choose to take sun glare effect into account, but not sea state effect. To take sun glare into account, only data collected with the northward oriented observer (i.e. not affected by glare) were used to achieve the spatial interpolation of seabird specific richness and log abundance.

Both maps are shown in Fig. 7 and highlight the most interesting areas in the Bay of Biscay, in terms of seabirds. Both maps are similar: log abundances and species richness are important in a coastal band located between the 20 m and 100 m isobath, and near the shelf break. Some local differences should nonetheless be noted in the north of the Bay: nears the shelf break, seabirds are abundant but a local decrease in species richness is reported. By contrast, at the same latitude but in the middle of the shelf, log abundance is low and species richness is high.

4. Discussion

4.1. Effect of survey parameters

Under the range of speed and altitude we used, the survey parameters did not affect the number of sightings and thus were not identified as sources of temporal biases during our surveys. Therefore, a relatively large range of speed (150–200 km/h) and altitude (140–180 m) can be used without detectable impacts on the detection probability. However, our study concerned species with 40 cm–1 m of body length and our results should not be extrapolated to smaller species. Briggs et al. (1985a) used similar speed (165–185 km/h) but different altitude (30–60 m), probably adapted to very cryptic species such phalaropes or auklets. They did not report any altitude effect, as in our surveys. Recommendations given in Camphuysen et al. (2002), 80 m and 220 km/h, concerns upper-winged airplanes (with larger and longer visibility windows) and in general, different birds (mainly seaducks and divers). Together with our results, these two examples show that the choice of speed and altitude can be relatively flexible and mainly depends on the kind of plane and of targets. There are no
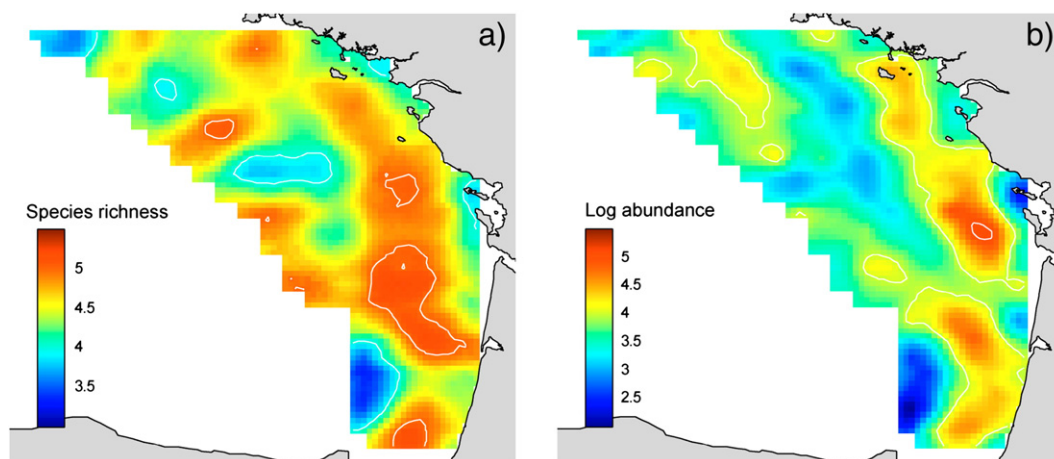

Fig. 7. Spatial representation of the specific richness (the mean number of different species recorded during a 20 km transect) and of the log abundance of seabirds (log number of seabirds counted within a 20 km bin) of the seabird community in the Bay of Biscay.

universal rules concerning speed and altitude, and instead we recommend the implementation of experiental trials before running routine surveys, in order to choose speed and altitude according to survey's aim and conditions. Furthermore, tiredness effect was not consistent even after 3 h of continuous observations, suggesting that relatively long flight times are feasible.

4.2. Effects of the environmental parameters

One environmental parameter, sun glare, had a significant effect on the detection of auks, even if it was slightly modulated by the cloud coverage. Glare should then be considered as a source of temporal bias for seabird strip-transect aerial survey. The strip-transect methodology is particularly sensitive to glare, which can make part or the whole strip unobservable, especially when using narrow strips (Briggs et al., 1985a). To take account for glare effect, glare conditions should be continuously and accurately recorded (intensity and angle, and/or the proportion of strip affected). In addition, the record of sightings on both sides of the plane provides a reference side, because the sun glare is not likely to affect in the same time the both sides of the plane. Also, the use of specific equipment, such as polarised glasses, could improve observer's sight under glare conditions.

The effect of sea state was not easy to interpret, because it appears to affect in the same way both auks and gannets densities. Even if sea state is known to affect cetacean detection, either from ship (DeMaster et al., 2001) or plane (Pollock et al., 2006), the effect we found in the present study was unexpected with two contrasted targets in terms of detectability. Since the densities of both auks and gannets are affected in the same way by sea state, it is not clear weather sea state affected equally the detection of both taxa, or if both taxa simply selected areas with low sea state. In the first case, a correction is required, but in the second case, a correction should not be used. In the present study, we cannot distinguish between both cases, but we consider the second case as the most probable: gannets spent most of their time flying and are thus not masked behind waves. Their detection should not be affected by sea state, at least not in the same way than Auks. Furthermore, hypotheses can be formulated to explain why birds would avoid high sea state areas. Since gannets detect their preys visually, their foraging success may be increased under calm sea because preys would be more easily detected. Auks, that spent most of their time swimming, may increase their energetic expanse under agitated sea and would then select calm areas to reduce energetic loss. To be prudent, we have not applied any correction under high sea state. However, to clearly conclude about the effect of sea state on seabird detection, double platform counts that can measure directly the detection probability are required.

4.3. Correcting for bias

To correct for detection bias during aerial surveys, methods have been developed in the field of marine mammal surveys. Aerial strip-transect surveys of marine mammals are subject to both an homogeneous bias due to diving animals, and a temporal bias due to environmental parameters (mainly glare, sea state and water turbidity). Methods to take account for these biases are described in Marsh and Sinclair (1989) and in Pollock et al. (2006). These methods are particularly useful to estimate temporal bias on diving birds, because the detection process is expressed as the combination of two terms. The first is the probability that the animal is available to the observer, estimated from diving rates obtained from loggers and from experimental surveys carried out under various environmental conditions and targeting animal models placed on the transect line. The second is the probability that the animal is detected, given that it is available to the observer. It could be estimated from the double counts method. Such experiments are clearly the next challenge for seabird surveys that focus on diving birds such as auks.

In the field of seabird surveys, methods of bias correction that have been developed mainly concerning seabird movements and must be applied to ship-based surveys (Spear et al., 2004). In this paper, we assumed that the high speed of the survey platform prevented the effects of seabird movement. We believe that in the case of a plane this assumption is robust. However this general question could be addressed with an individual-based model where birds are moving according to a common rule (random or directional movements, attraction or repulsion to the platform) and where a platform records observations at varying speed. Such a model would contain two parameters, the behaviour of birds and the speed of the platform, and would measure how much the platform speed must be greater than the target speed in order to avoid bias due to target movement. It would provide general recommendations for all kinds of transect survey.

4.4. Aerial survey methodology for seabirds

Although we recognised glare as a temporal bias during strip-transect aerial survey, our results demonstrated that temporal bias remained fairly limited (they explain only 14% of data deviance). Concerning the distance bias, we found that a 230 m strip should be slightly reduced to avoid any distance effect in the strip with certainty. The assumption that detection does not vary in a strip of 150 m is therefore a robust assumption either for highly detectable species such as gannets, or cryptic ones such as auks. Any further reduction in strip width might not be necessary. These findings contrast with previous results given in Briggs et al. (1985a) who compared seabird density estimated using 50, 100 and 200 m strip and reported that seabird density was underestimated even with a strip 100 m wide. Their reference altitude (30 and 60 m asl), lower than our surveys, might explain these differences: to cover the same strip, an observer located 60 m asl must scan a larger angle and has less time for recording species than if located at higher altitude. The use of higher altitude may prevent this effect and is more secure. Grier et al. (1981) experienced a crash and gave important recommendations concerning low-altitude aerial surveys.

To conclude, since bird detection does not vary across a strip of 150 m, strip-transect aerial surveys appears to be a promising tool to survey seabird populations at sea. Three important questions should now concentrate the effort of the scientific community working on the sampling of seabird populations at sea: the effect of bird movement, the effect of sea state and the direct estimate of the detection probability in the case of diving birds. These questions should constitute the focus of future works on seabirds strip-transect aerial surveys.

References

Ainley, D. G., Spear, L. B., Tynan, C. T., Barth, J. A., Pierce, S. D., Ford, R. G., et al. (2005). Physical and biological variables affecting seabird distributions during the upwelling season of the northern California Current. *Deep-Sea Research II*, *52*, 123–143.

Alldredge, J. R., & Gates, C. E. (1985). Line transect estimators for left truncated distributions. *Biometrics, 41,* 273–280.

Bailey, T. C., & Gatrell, A. C. (1995). *Interactive Spatial Data Analysis* (pp. 1–434). New York: Wiley Inter-Science.

Barlow, J., Gerrodette, T., & Forcada, J. (2001). Factors affecting perpendicular sighting distances on shipboard line-transect surveys for cetaceans. *Journal of Cetacean Resource Management, 3,* 201–212.

Borchers, D. L., Zucchini, W., & Fewster, R. M. (1998). Mark-recapture models for line transect surveys. *Biometrics, 54,* 1207–1220.

Bretagnolle, V., Certain, G., Houte, S., & Métais, M. (2004). Distribution maps and minimum abundance estimates for wintering auks in the Bay of Biscay, based on aerial survey. *Aquatic Living Resource, 17,* 353–360.

Briggs, K. T., Tyler, W. B., & Lewis, D. B. (1985a). Aerial survey for seabirds: Methodological experiment. *Journal of Wildlife Management, 49,* 412–417.

Briggs, K. T., Tyler, W. B., & Lewis, D. B. (1985b). Comparison of ship and aerial surveys of bird at sea. *Journal of Wildlife Management, 49,* 405–411.

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L., & Thomas, L. (2001). *Introduction to distance sampling: Estimating abundance of biological populations.* New York: Oxford University Press.

Burnham, K. P., & Anderson, D. R. (2002). *Model Selection and Multimodel Inference. A Practical Information-Theoretic Approach* (pp. 1–488). New York: Springer-Verlag.

Burnham, K. P., Anderson, D. R., & Laake, J. L. (1980). Estimation of density from line transect sampling of biological populations. *Wildlife Monographs, 72,* 1–202.

Cadiou, B., Riffaut, L., McCoy, K. D., Cabelguen, J., Fortin, M., Gélinaud, G., et al. (2004). Ecological impact of the "Erika" oil spill: Determination of the geographic origin of affected common guillemots. *Aquatic Living Resource, 17,* 369–378.

Camphuysen, C. J., Fox, A. D., Leopold, M. F., & Petersen, I. K. (2002). Towards standardised seabirds at sea census techniques in connection with environmental impact assessments for offshore wind farms in the U.K. *Southampton: Cowrie report 02 2002* (pp. 1–38).

Caughley, G. (1974). Bias in aerial survey. *Journal of Wildlife Management, 38,* 921–933.

Cressie, N. A. C. (1993). *Statistics for Spatial Data* (pp. 1–900). New York: Wiley inter-science.

Davoren, G. K., Montevecchi, W. A., & Anderson, J. T. (2003). Distributional patterns of a marine bird and its prey: Habitat selection based on prey and conspecific behaviour. *Marine Ecological Progress Series, 256,* 229–242.

DeMaster, D. P., Lowry, L. F., Frost, K. J., & Bengtson, R. A. (2001). The effect of sea state on estimates of abundance for beluga whales (*Delphinapterus leucas*) in Norton Sound, Alaska. *Fishery Bulletin, 99,* 197–201.

Eberhardt, L. L. (1978). Transect Methods for population studies. *Journal of Wildlife Management, 42,* 1–31.

Garthe, S., & Huppop, O. (1999). Effect of ship speed on seabird counts in areas supporting commercial fisheries. *Journal of Field Ornithology, 70,* 28–32.

Grier, J. W., Gerrard, J. M., Hamilton, J. D., & Gray, P. A. (1981). Aerial-visibility bias and survey techniques for nesting bald eagles in Northwestern Ontario. *Journal of Wildlife Managements, 45*(1), 83–92.

Hammond, P. S., Berggren, P., Benke, H., Borchers, D. L., Collet, A., Heide-Jorgensen, M. P., et al. (2002). Abundance of harbour porpoise and other cetaceans in the North Sea and adjacent waters. *Journal of Applied Ecology, 39*(2), 361–376.

Hiby, L., & Lovell, P. (1998). Using aircraft in tandem formation to estimate abundance of harbour porpoise. *Biometrics, 54,* 1280–1289.

Holt, R. S., & Cologne, J. (1987). Factors affecting line transect estimates of dolphin school density. *Journal of Wildlife Management, 51,* 836–843.

Hyrenbach, K. D. (2001). Albatross response to survey vessels: Implications for studies of the distribution, abundance, and prey consumption of seabird populations. *Marine Ecology Progress Series, 212,* 283–295.

Marsh, H., & Sinclair, D. F. (1989). Correcting for visibility bias in strip transect aerial surveys of aquatic fauna. *Journal of Wildlife Management, 53,* 1017–1024.

Mc Cullagh, P., & Nelder, J. A. (1989). *Generalized Linear Models.* London: Chapman and Hall.

Okamura, H. (2003). A line transect method to estimate abundance of long-diving animals. *Fisheries Science, 69,* 1176–1181.

Pollock, K. H., & Kendall, W. L. (1987). Visibility bias in aerial survey: A review of estimation procedures. *Journal of Wildlife Management, 51,* 502–510.

Pollock, K. H., Marsh, H. D., Lawler, I. R., & Alldredge, M. W. (2006). Estimating animal abundance in heterogeneous environments: An application to aerial surveys for dugongs. *Journal of Wildlife Management, 70,* 255–262.

Quang, P. X. (1991). A non-parametric approach to size-biased line transect sampling. *Biometrics, 47,* 269–279.

Quang, P. X., & Lanctot, R. B. (1991). A line transect model for aerial surveys. *Biometrics, 47,* 1089–1102.

R Development Core Team (2005). *R: A language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing ISBN 3-900051-07-0, URL: http://www.R-project.org

Redfern, J. V., Viljoen, P. C., Kruger, J. M., & Getz, W. M. (2002). Biases in estimating population size from an aerial census: A case study in the Kruger National Park, South Africa. *South African Journal of Science, 98,* 455–461.

Schwarz, G. (1978). Estimating the dimension of a model. *The Annals of Statistics, 6,* 461–464.

Southwell, C. (1994). Evaluation of walked line transect counts for estimating macropod density. *Journal of Wildlife Management, 58,* 348–356.

Spear, L., Nur, N., & Ainley, D. G. (1992). Estimating absolute densities of flying seabirds using analyses of relative movement. *The Auk, 109,* 385–389.

Spear, L. B., Ainley, D. G., Hadesty, B. D., Howell, S. N. G., & Webb, S. W. (2004). Reducing biases affecting at-sea surveys of seabirds: Use of multiple observer teams. *Marine Ornithology, 32,* 147–157.

Spear, L. B., Ainley, D. G., & Webb, S. W. (2003). Distribution, abundance and behaviour of Buller's, Chatman Island and Salvin's Albatrosses off Chile and Peru. *Ibis, 145,* 253–269.

Tasker, M. L., Jones, P. H., Dixon, T. J., & Blake, B. F. (1984). Counting seabirds at sea from ships: A review of methods employed and a suggestion for a standardized approach. *The Auk, 101,* 567–577.

Trenkel, V. M. (2003). Density estimator for strip transects when animals show directional movement and observation speed is slow. *Computational statistics & Data Analysis, 44,* 305–312.

Venables, W. N., & Ripley, B. D. (2002). *Modern Applied Statistics with S* (pp. 1–496). Springer-Verlag.

White, G., & Bennetts, R. (1996). Analysis of frequency count data using the negative binomial distribution. *Ecology, 77*(8), 2249–2257.

Yoshida, H., Shirakihara, K., Kishino, H., & Takemura, A. (1998). Finless porpoise abundance in Omura Bay, Japan: Estimation from aerial sighting surveys. *Journal of Wildlife Management, 62,* 286–291.