

On the importance of estimating detection probabilities from at-sea surveys of flying seabirds

Christophe Barbraud and Jean-Baptiste Thiebot

C. Barbraud (correspondence) and J.-B. Thiebot, Centre d'Etudes Biol. de Chizé, CNRS UPR 1934, 79360 Villiers en Bois, France. E-mail: barbraud@cebc.cnrs.fr

The primary and accepted method used to estimate seabird densities at sea from ships is the strip transect method, designed to correct for the effect of random directional bird movement relative to that of the ship. However, this method relies on the critical assumption that all of the birds within the survey strip are detected. We used the distance sampling method from line-transects to estimate detection probability of a number of species of flying seabirds, and to test whether distance from the ship and bird body size affected detectability. Detection probability decreased from 0.987 (SE = 0.029) to 0.269 (SE = 0.035) with increasing strip half-width from 100 to 1400 m. Detection probability also varied between size-groups of species with strip half-width. For all size-groups, this probability was close to 1 for strip half-width of 100 m, but was 0.869 (SE = 0.115), 0.725 (SE = 0.096) and 0.693 (SE = 0.091) for strip half-width of 300 m, a typical strip width used in seabird surveys, for respectively large, medium and small size flying seabirds. For larger strip half-width, detection probability was higher for large sized species, intermediate for medium sized species and lower for smaller sized species. For strip half-width larger than 100 m we suggest that more attention should be paid to testing the assumption of perfect detectability, because abundance estimates may be underestimated when this assumption is violated. Finally, the effect of the speed of travel of flying seabird on the detection probability was estimated in a simulation study, which suggests that detection probability was underestimated with increasing flying speed.

During the last twenty years research effort has increased to refine survey methods assessing seabird densities at sea. Currently, the most refined and commonly used of these methods are the vector method (Gaston and Smith 1984, Spear et al. 1992), and the snapshot method (Tasker et al. 1984, van Franeker 1994). Both methods are based on strip transects and rely on count statistics which include the number of birds that are stationary (i.e. sitting on water) and flying, but the methods differ in the way the count of flying birds is obtained. In the vector method, the observer counts all transiting birds and adjusts those counts for the effect of the ship's movement, while the snapshot method partitions the strip into contiguous segments, which are each surveyed only once for transiting birds by using instantaneous counts. These methods rely on two critical assumptions 1) that the designated survey strip width is accurately maintained, and 2) that all of the birds within the survey strip are detected (van Franeker 1994). The first assumption can be (and is often) tested and validated by calibrating strip width using radar fixes on floating objects (Heinemann 1981, Gordon 2001). However, since bird abundance at time and location i (\hat{N}_i) can be estimated using the relationship $\hat{N}_i = \frac{C_i}{\hat{p}_i}$, where C_i is the count statistic and \hat{p}_i is the detection probability (Williams et al.

2002), both the vector and snapshot methods assume that the probability to detect a bird within the survey strip, given it is present in the survey strip, is one. However, several authors stress that the assumption $p_i = 1$ within the survey strip might be unrealistic. Many factors may affect the detection probability of seabirds at sea from vessel or aerial based surveys including the size, colour and behaviour of birds, the weather and the observer ability (Tasker et al. 1984, van Der Meer and Camphuysen 1996). Although the assumption of perfect detectability is crucial for accurate abundance estimates and inferences based on these estimates, hardly any studies have estimated detection probability of seabirds during at-sea surveys. To our knowledge, exceptions are marbled murrelet *Brachyramphus marmoratus* (Strong et al. 1995, Becker et al. 1997) and Kittlitz's murrelet *B. brevirostris* (Kissling et al. 2007), which suggest that $p_i < 1$. In addition, small boats with a low point of view were used to survey murrelets, which would exacerbate problems with detectability. We do not claim that inferences emerging from past analyses of data from at-sea surveys of seabirds necessarily are wrong, but rather warn against an untested assumption. Terrestrial bird surveys increasingly use methods that allow to estimate detection probability (Thompson 2002), and marine mammal surveys commonly use methods that account for incomplete

delectability of individuals (Buckland et al. 2001). Here, we estimated the detection probability of flying seabirds during at-sea surveys using line-transects. Instead of using strip-transects where all birds are counted within the pre-defined transect width, we measured the distance from the vessel to detected flying seabirds and used the distance data to estimate detection rates. This method is based on the assumption that the probability of detecting an object decreases as a function of distance from the line, and uses the distance from the line to the object to correct for visibility bias. As did some authors (Dixon 1977, Briggs et al. 1985), we noted, from our own experience, the difficulties of detecting seabirds at sea at increasing distances. We also hypothesised that body size affects the detectability of birds and predicted a positive relationship between body size and detection probabilities.

Materials and methods

Study area

Data were collected during four cruises in November 2005, January 2006, December 2007, and January 2008 (Fig. 1). The first, third and fourth cruises were between the La Réunion (21° 06'S, 55° 6'E), Crozet (46° 30'S, 51° 00'E), and Kerguelen (49° 30'S, 69° 30'E) islands. The second cruise was between Kerguelen islands and Hobart (42° 52'S, 147° 19'E), Tasmania. Although these cruise tracks crossed sub-tropical and sub-Antarctic waters, we only surveyed the sub-Antarctic waters.

Survey protocol

We conducted line-transects (Buckland et al. 2001) to survey seabirds during daylight hours whenever the ship was underway. Both of us carried out observations and had previous experience identifying seabirds from the southern Indian Ocean by sight. Counts were not done simultaneously. All line-transects were made from the R.V. Marion Dufresne, while the vessel cruised at speeds between 10 and 16 knots (18.5–29.6 km h⁻¹). Line-transects were all conducted in fine weather conditions with no precipitation, Beaufort sea state ≤ 3, and visibility to horizon. At the beginning of each transect, we recorded ship speed and direction, latitude and longitude using the ship's global positioning system (GPS). The length of each transect was measured using the GPS, resulting in 267 km of line

transect. Birds were observed from the bridge (eye height: 17 m from the sea surface) on one forequarter of the ship's bow. The side without glare was chosen for each line-transect. Detection of birds was done with unaided eye, and binoculars (7 × 50) were used for confirmation of species identification. Observers measured a bird's line-of-sight distance (radial distance) with reticle binoculars. The observer recorded the number of marks down from the horizon to the bird. This number was then transformed to a distance using equation 7.39 in Buckland et al. (2001, pp. 256–258). The sighting angle from the transect line was measured with an angle board mounted on ship railings. During our surveys, all seabirds for which distances were measured were observed in flight and were not feeding. This is a problem for distance measurements since the equation in Buckland et al. (2001) used to calculate distances does not hold when the detected object is above water. Therefore, when a bird was detected it was followed using the reticle binoculars until it skimmed over the surface of the sea when the reticle and angle readings were recorded. Consequently, distances and angles could not be measured for all flying seabirds detected since some individuals never came close to the sea surface, and no measurement was taken for birds above the horizon. To limit the distance bias due to the time elapsed between first detection of a flying bird and its distance measurement, we only used data where this time was lower than 5 s.

Distance and angle measurement error are critical for the success of distance sampling (Buckland et al. 2001). Height above water, wave height and rolling or heeling may bias distance measurements (Gordon 2001). In our survey, height above water was known with precision, all distances were measured with low wave heights (typically less than 1 m) making boat rolling or heeling negligible, and angles were measured to the nearest degree with angle boards from the ship, which are very stable. Therefore, based on the results of Gordon (2001), we assumed that the resulting measurement errors were not significant. Distance can also be measured very accurately (typically ± 1 m) with laser range-finding binoculars provided a large clear target is 'hit' by the laser. However, we performed several trials with a laser range finder but could not obtain any distance measurement, probably because flying seabirds represent a too small target for the laser.

Statistical analyses

Data were analysed using program Distance 5.0 (Thomas et al. 2005). This program uses the perpendicular distance of each bird from the transect line to generate a histogram of the number of detections by distance. A monotonic, decreasing key function (half-normal, hazard, or uniform) with possible cosine or polynomial adjustment terms was used to model the detection function. Model fit was assessed by a chi-square goodness-of-fit test and by verifying that coefficient of variation of the detection probability did not exceed 20% (Buckland et al. 2001). Akaike's information criterion (AIC; Burnham and Anderson 2002) was used to select the model that best described the data with the lowest number of parameters. By modelling the detection function, an estimate of p , the

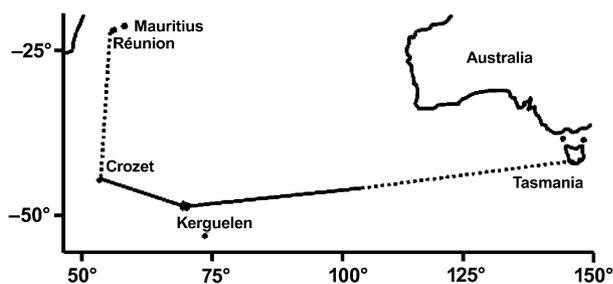


Figure 1. Map of the study area with the ship course (dotted line). The continuous (unbroken) line indicates where the distance sampling method was conducted.

proportion of individuals detected up to a given distance, was obtained. Right truncation of the distance data was set following identification of outliers from box plots (outliers were values higher than 1.5 box-lengths from the 75th percentile). Heaping was assessed from histograms, and data were grouped where necessary (Buckland et al. 2001).

Because seabird surveys based on strip-transects use different strip widths, there was an interest in determining how detection probability varied according to strip half-width. We thus right truncated observation data every 100 m from 100 to 800 m and at 1000 and 1200 m, and examined how detection probability varied within these strip half-widths. We used bootstrap estimates to calculate 95% confidence intervals (CI) for those estimated probabilities (Buckland et al. 2001). To investigate the effect of body size on detectability we grouped species within three body size classes (Appendix 1): albatrosses and giant petrels (2000–11 000 g), medium size petrels (500–1 500 g), and small size petrels (less than 500 g). Size-group was entered as a factor covariate in our models and detection probabilities were estimated using the truncation distances defined. For each truncation distance, models with or without a group effect were compared using AIC to test for an effect of body size on detection probability. Models were fitted with the multiple covariate distance sampling engine in Distance 5.0 (Buckland et al. 2004).

Flying seabirds can be considered as fast-moving objects relative to the ship speed. For example air speed in Procellariiformes varies from ~ 7 to 19 ms^{-1} (Pennycuik 1989), and ship speed during our survey was $\sim 7 \text{ ms}^{-1}$. This has long been recognized as an important problem for distance sampling methods, which assumes that the movement of objects should be slow relative to speed of the observer (Buckland et al. 2001). Animal movement (either random or in response to the observer) may bias density estimates (Granholt 1983), and methods taking into account animal movement when estimating density have been proposed (Tasker et al. 1984, Spear et al. 1992, Watson et al. 1995, Trenkel 2003). However, the effect of animal speed on the detection probability is less well understood, but can be expected to lead to underestimation of the true probability of detection. Mack et al. (2002) used an adaptable detection probability function to examine the effect of several factors on the probability of detection from a series of trials on marbled murrelets. We chose such a direct approach to simulate the effect of animal speed on the probability of detection using the following adaptable detection probability function:

$$g(x, S, F) = \frac{e^{\frac{S}{F}}}{1 - e^{\frac{S}{F}}} \left(1 - e^{-\left(\frac{x}{e^{\frac{S}{F}}}\right)^{-b}} \right), \text{ for } F > 0$$

where x is the perpendicular distance between line transect and animal, S is ship speed, F is flying seabird speed, b is a shape parameter. The first term in the equation adjusts the magnitude of detection probability equally for all distances. If $x = 0$ (i.e., observation is on the line transect), the second

term is unity (i.e., $\lim_{x \rightarrow 0} g(x, S, F) = \frac{e^{\frac{S}{F}}}{1 - e^{\frac{S}{F}}}$), and the

first term of the equation is the probability of detecting a moving animal on the line. If both x and F tend towards 0 the function tends towards 1 ($g(0) = 1$). The second term in

the equation can be expressed as $1 - e^{-\left(\frac{x}{\sigma}\right)^{-b}}$, which is the equivalent to a hazard-rate detection function (Buckland et al. 2001), except that σ , the scale parameter, is not constant and is a function of the speed of the animal relative to the observer speed. The inclusion of the animal speed in the second term in the equation permits to modify the effect of distance on detection probability. We estimated $g(x)$ for

various $\frac{S}{F}$ ratios (0.1, 0.3, 0.5, 0.7, 1, 1.5, 2, 5), and

estimated the detection probability as $\int_0^w g(x) dx$ with $w = 1$ for simplicity (Buckland et al. 2001).

Results

Overall we measured the radial distance and angle for 168 flying seabirds. The greatest distance at which flying seabirds were detected was 2693 m. We were able to fit detection functions to our data (GOF tests, $P > 0.121$, Table 1). Overall detection probability for all species combined was 0.552 (SE = 0.028) with a truncation distance of 554 m (Table 1). For a strip half-width of 100 m the detection probability was 0.987 (SE = 0.029, 95% CI: 0.929–0.990; Fig. 2). However, for larger strip half-width the detection probability was lower than 1 and decreased with increasing strip half-width (Fig. 2).

There was evidence that detection probability varied between size-groups of species for increasing strip half-width (Table 2). For strip half-width > 400 m models with size-group of species as a covariate had lower AICs than

Table 1. Selected models of detection functions of flying seabirds for different size-groups and estimated probability of detection. Group indicates the size-group, T the truncation distance.

Group	T (m)	Model selected	Goodness of fit			AIC	\hat{p}	CV	95% CI
			χ^2	df	P				
Large	755	Half-normal	4.62	5	0.464	474.84	0.50	0.11	0.40–0.63
Medium	787	Uniform + cosine	7.91	7	0.340	623.30	0.56	0.07	0.48–0.64
Small	412	Uniform + simple	8.71	5	0.121	572.49	0.55	0.06	0.49–0.62
All	554	Uniform + cosine	0.91	3	0.824	341.45	0.55	0.05	0.50–0.61

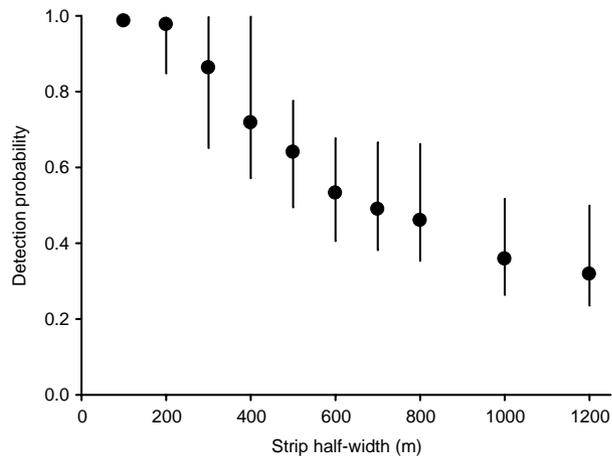


Figure 2. Detection probability estimates for all species for varying strip half-width. Errors bars indicate 95% CI.

models without covariate (Table 2). For all size-groups, detection probability was close to 1 for strip half-width of 100 m, although for smaller flying seabirds there was slight evidence that detection probability was < 1.0 in that case (Fig. 3). For larger strip half-width, detection probability varied according to the size-group, and was higher for large sized species, intermediate for medium sized species and lower for small sized ones (Fig. 3). For strip half-width of 300 m, larger flying seabirds had a mean detection probability of 0.869 (SE = 0.115), medium size flying seabirds of 0.725 (SE = 0.096), and smaller sized flying seabirds of 0.693 (SE = 0.091). The decline in detection probability appeared to occur at closer distances to the transect line for smaller species than for large and medium sized species (Fig. 3).

Our simulations suggest that, using this detection probability function, detection probability decreased non-linearly when the speed of flying seabirds increased. Simulation results indicate that when the $\frac{S}{F}$ ratio varied from 0.3 to 1, which corresponds to realistic values in the field, detection probability was negatively biased from 69% to 36%, respectively (Fig. 4). Bias became relatively small ($< 5\%$) when the ship speed was ~ 3 times higher than the flying speed of seabirds.

Table 2. Modelling the effect of body size on detection probabilities of flying seabird. The group effect indicates whether or not size-group is used as a covariate of detection probability. ΔAIC indicates the difference in AIC between the model with covariate and the model without covariate.

Strip half-width (m)	Model	Group effect	AIC	ΔAIC
100	Half	Yes	309.28	4.00
	Half	No	305.28	
200	Half	Yes	766.82	2.59
	Half	No	764.24	
300	Half	Yes	1051.78	3.06
	Half	No	1048.71	
400	Half	Yes	1244.94	-0.35
	Half	No	1245.29	
600	Half	Yes	1475.18	-1.51
	Half	No	1476.69	
1200	Half	Yes	1788.41	-3.05
	Half	No	1791.46	

Discussion

Many at-sea seabirds surveys used count as an index to assess abundance, and the typical survey method used is fixed-width transects with a range of strip width generally between 300 and 600 m (van Franeker 1994, Clarke et al. 2003, Spear et al. 2004), which assumes that all birds are detected within the strip-width. Although our findings suggest that detection probability was very close to 1 for strip half-width of 100 m, there was evidence that detection probabilities might be significantly lower than 1 for greater strip half-width. At 300 m detection probabilities were clearly lower than 1, suggesting that overall $\sim 14\%$ of birds were missed. As predicted, there was some evidence that detection probabilities declined faster for smaller sized species than for larger sized ones along distance for the transects line, although our sample sizes were small. For smaller species, the proportion of individuals missed at 300 m was $\sim 30\%$. This bias might even be higher for smallest species such as storm petrels (Hydrobatidae), since our small sized species group was heterogeneous and included species larger than storm petrels such as prions, blue petrels and soft plumaged petrels. In a study combining the vector and snapshot methods with multiple observers, Spear et al. (2004) also concluded that larger flying seabirds were more easily detected. Our results also compare with those from found for terrestrial surveys of grassland birds using distance sampling (Diefenbach et al. 2003). Diefenbach et al. (2003) also detected differences among observers in the proportion of birds detected. We did not examine observer effect on detection probabilities but previous studies on seabirds from at sea surveys suggest they might be important (Spear et al. 2004).

In our study we were not able to test directly the four key assumptions of distance sampling, that: 1) objects on the transect-line are detected with certainty ($g(0) = 1$), 2) objects are detected at their initial location, 3) measurements are exact, and 4) detections are independent events. The first assumption may be violated because of two main issues, which are detectability and availability. For flying seabirds, we believe that these issues are unlikely to be a

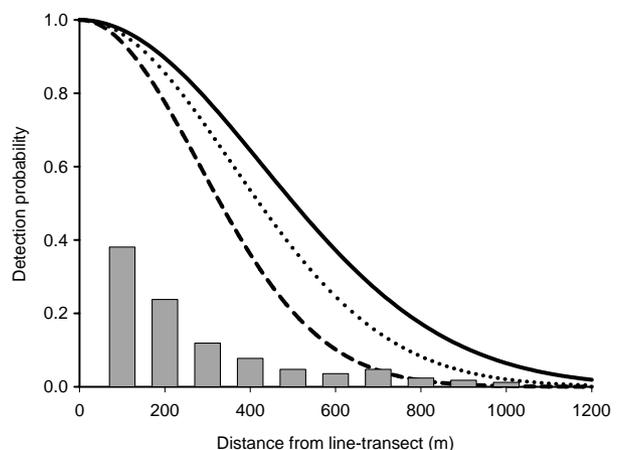


Figure 3. Detection probability function for a strip half-width of 1200 m for large sized species (plain line), medium sized species (dotted line) and small sized species (dashed line). Bars indicate the proportion of the total number of flying seabirds detected.

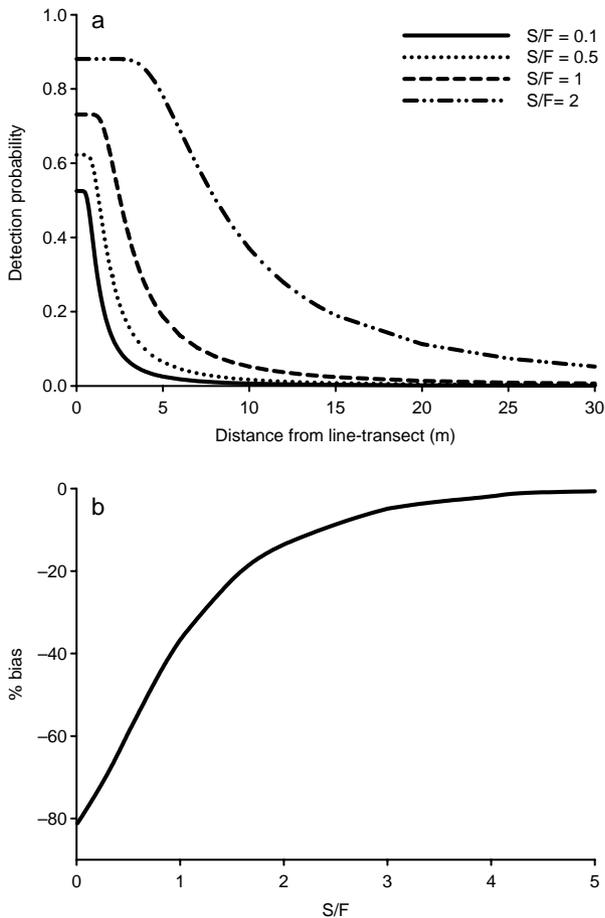


Figure 4. a) Detection probability function for varying distances from line-transect and ship speed/flying seabird speed ratios (S/F). b) Percent bias is detection probability as a function of increasing ship speed relative to flying seabird speed. The value of the parameter b was fixed to 2 for all simulations.

problem. Contrary to diving species, there is no reason to suspect that the probability of availability is lower than 1. We carried out our observations during calm sea conditions and flying seabirds are relatively conspicuous in such conditions at close distances. However, multiple observers could be used to estimate the proportion of birds missed by one observer on the transect line (Nichols et al. 2000), and that estimate and its variance can be incorporated into the distance sampling estimates (Buckland et al. 2004). The second assumption is more problematic due to movements of flying seabirds before detection. The movement problem can be viewed as two non exclusive components: random (or non-responsive) movement and responsive movement. Responsive movement of flying seabirds refers to individuals altering their behaviour (attraction or avoidance) in the presence of the ship, so that the density in the survey area is no longer representative of the wider habitat (Tasker et al. 1984, Spear et al. 1992, Buckland et al. 2001). Although we did not use the vector method (Spear et al. 1992), we do not think that responsive movement affected our results since our aim was not to estimate densities but detection probabilities as a function of distance. However, we recognise that the problem of species attracted by or avoiding the ships remains unsolved by our method

(see Borberg et al. 2005). Random movement is also problematic for estimating density since animal can enter the survey area during the survey, but might also be problematic for the estimation of detection probability since a fast flying individual is more likely to be missed by an observer than a slow flying individual. Our basic simulation suggests that detection probability is affected by the relative speed of the animals relative to the observer speed. The speed of travel of the animals may affect the distance at which animal are detected and the detection on the line transect ($g(0)$). When the travel speed of the animals increased the bias in detection probability increased faster at closer distances than at further distances. This suggest that when the travel speed of animals is high relative to the observer speed, $g(0)$ may be highly biased and need to be estimated using independent observers or other appropriate methods (Laake and Borchers 2004). Further empirical and theoretical studies aiming at estimating the influence of the travel speed of the animals on the detection probability are needed. Third, distance measurements were performed using reticle binoculars, which are commonly used in at-sea surveys of marine mammals. As explained in the Methods section, we believe that bias due to inaccuracy in distance measurements was small. The fourth assumption could be violated if aggregates of flying seabirds, either mono- or multi-specific, are detected while foraging on a particular patch, and distances are measured. However, this was not the case during our survey because behaviour of each bird was recorded and we thus believe this assumption was not violated, and departures from the fourth assumption do not seem to be too problematic (Buckland et al. 2001).

Our results suggest paying more attention to methods that incorporate probabilities of detection, such as distance sampling, when estimating abundance of seabirds at sea, particularly for small sized species. For large sized species surveying strip width of up to 200–300 m should allow fulfilling the assumption of complete detectability in vector and snapshot methods in fine observation conditions. For larger strip-width and/or small sized species we would suggest estimating detection probability to avoid obtaining biased estimates of abundance. However, if detectability is to be taken into account in a survey, it must be estimated during the survey for a given strip-width since search effort (and eventually detection probability) may vary according to the strip-width. Since detection probability is probably underestimated due to the fast movements of flying seabirds, we would recommend estimating detection probability for a range of strip widths and use a strip width for which detection probability is high. Further research on whether assumptions of distance sampling can be met is needed. Integrating estimation of detection probability and the vector method commonly used in seabird surveys (Spear et al. 1992), which takes into account seabird movements relative to the survey ship remains a challenge, would permit to improve estimates of abundance and densities of seabirds at sea. This would probably necessitate multiple observers, with some observers dedicated to the vector method allowing estimation of abundance, and other observers conducting distance sampling on species specific samples of individuals that would permit to estimate detection probability and correct counts obtained by the vector method.

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Appendix 1. List of species, number of individuals for which distance measurements were taken, and size-group in which species were assigned.

Species	No. observed	Size-group
Wandering albatross <i>Diomedea exulans</i>	8	Large
Black-browed albatross <i>Thalassarche melanophris</i>	20	Large
Grey headed albatross <i>Thalassarche chrysostoma</i>	6	Large
Sooty albatross <i>Phoebetria fusca</i>	1	Large
Light mantled sooty albatross <i>Phoebetria palpebrata</i>	2	Large
Northern giant petrel <i>Macronectes halli</i>	1	Large
Giant petrel spp. <i>Macronectes</i> spp.	4	Large
Cape petrel <i>Daption capense</i>	4	Small
Blue petrel <i>Halobaena caerulea</i>	2	Small
Prion spp. <i>Pachyptila</i> spp.	37	Small
White-chinned petrel <i>Procellaria aequinoctialis</i>	67	Medium
Soft plumaged petrel <i>Pterodroma mollis</i>	2	Small
White-headed petrel <i>Pterodroma lessonii</i>	1	Medium
Grey backed storm petrel <i>Garodia nereis</i>	4	Small
Black bellied storm petrel <i>Fregetta tropica</i>	7	Small
White bellied storm petrel <i>Fregetta grallaria</i>	1	Small
Diving petrel spp. <i>Pelecanoides</i> spp.	1	Small