Accounting for responsive movement in line transect estimates of abundance

D.L. Palka and P.S. Hammond

Abstract: A method is developed to account for effects of animal movement in response to sighting platforms in line transect density estimates using data on animal orientation. Models of expected distributions of animal orientation show that presence of responsive movement is determined by the ratio of animal sightings with angles of orientation in the third quadrant relative to the first quadrant. The distance at which response began is estimated using logistic generalized additive models of the relationship between radial distance and orientation. Density corrected for responsive movement is estimated by applying the Buckland and Turnock two-team analysis method to data poststratified into regions "close" to and "far" from (beyond the distance that responsive movement began) the observation platform instead of the original stratification by observation team. For data collected in the North Atlantic, white-sided dolphins, harbor porpoises, and minke whales responded by avoiding the survey ship, and white-beaked dolphins were attracted to the ship. For these populations, our method to correct for responsive movement gave significantly higher estimates, from 1.4 to 2.7 times the uncorrected estimates.

Résumé : On trouvera ici une méthode qui tient compte des déplacements des animaux en réaction à la présence de plates-formes d'observation dans les estimations de densité par transects linéaires basés sur des données sur l'orientation des animaux. Les modèles des distributions attendues des orientations des animaux indiquent que la présence de mouvements de réaction peut être déterminée par le rapport du nombre d'animaux aperçus avec un angle d'orientation dans le troisième quadrant par rapport au nombre dans le premier quadrant. La distance à partir de laquelle la réaction se fait sentir a pu être estimée à l'aide de modèles logistiques additifs généralisés de la relation entre la distance radiale et l'orientation. La densité, avec correction pour tenir compte du mouvement de réaction, est estimée par l'application de la méthode d'analyse à deux équipes de Buckland et Turnock; les données ont été stratifiées a posteriori en «proches» et «éloignées» (au delà de la distance où se manifeste le mouvement de réaction) de la plate-forme d'observation, au lieu de la stratification originale faite par les observateurs. Dans les cas de données récoltées dans l'Atlantique Nord, les Dauphins à flancs blancs, les Marsouins communs et les petits Rorquals réagissent en évitant le bateau d'observation, alors que les Dauphins à nez blanc sont attirés par le bateau. Chez ces populations, notre méthode de correction des mouvements de réaction donne des estimations significativement plus élevées, de 1,4 à 2,7 fois les estimations non corrigées.

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Introduction

Line transect estimators of animal density assume, among other things, that animals do not move. When animals move randomly, estimates of density are biased upward by a factor that depends on the speed of the animals relative to the speed of the survey platform and on the animal detection rate (Koopman 1980; Hiby 1982). The bias is small unless the ratio of animal speed to survey platform speed is around 0.5 or greater (Buckland et al. 1993).

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A potentially more serious violation occurs if animals move in response to the survey platform. If animals respond prior to detection by moving either towards (attraction) or away from (avoidance) the transect line, density will be over- or under-estimated, respectively. In recent years, line transect sampling has become a primary tool for estimating abundance of cetacean populations (Hiby and Hammond 1989; Buckland et al. 1993). Aircraft typically survey at speeds that are sufficiently high for animal movement not to be considered. However, cetaceans have a well-developed sense of hearing and are capable of responding to ships at distances far greater than those at which they may be detected by an observer on a ship. For example, Au and Perryman (1982) found that dolphin schools of three *Stenella* species started avoiding a survey ship while still 7–13 km away, and Barlow (1988) recorded a harbor porpoise (*Phocoena phocoena*) that drastically changed its swim direction to avoid a survey ship at a distance of 800 m. Thus, movement in response to a survey ship is potentially a source of substantial bias in line transect estimates of cetacean abundance.

There are a number of ways to investigate effects of responsive movement. Previously, tracks of animals resighted one or more times were examined (e.g., Borchers and Haw
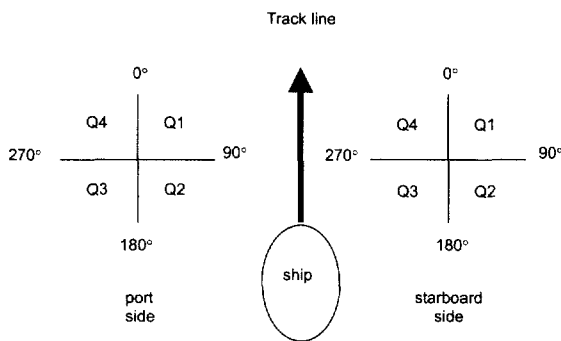
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Fig. 1. Illustration of definition of swimming directions and quadrants (Q1, Q2, Q3, and Q4).

1990; Hammond et al. 1995), and data on the swim direction of animals when initially detected were also examined (e.g., Leatherwood et al. 1982; Polacheck and Thorpe 1990). These studies indicated that some species might be responding before observers detected them, but results were inconclusive because of small sample sizes.

Buckland and Turnock (1992) developed an analytical method, which was an extension of Turnock and Quinn (1991), to estimate abundance corrected for the effects of responsive movement. This method required observers on a helicopter to follow a group of animals until the group was detected by observers on a survey ship. Borchers et al. (1998) extended this methodology to allow animals to be tracked by an independent team on the same ship as the primary search team. The tracker team searched further ahead than the primary team in an attempt to detect animals before they responded.

For the methods of Buckland and Turnock (1992) and Borchers et al. (1998) to take full account of responsive movement, it was assumed that animals detected by the tracker team had not yet reacted to the survey ship. If sightings from the tracker team are made within the average distance at which responsive movement occurs, then success of these methods will be incomplete. This situation is more likely to occur if the tracker team is a second independent team on a ship. In such cases, it is important to determine the distance from the survey ship at which responsive movement occurs so that the tracking methodology can be properly applied to fully account for responsive movement.

In this paper, we develop a method that uses animal orientation data collected on shipboard line transect surveys to determine whether, and at what distance, cetaceans are responding to the survey ship. We assume that the observed orientation of an animal at the surface is representative of the direction of travel. We present models to describe expected distributions of orientation when accounting for random movement, the angle at which the animal presents itself, and responsive movement. We describe how to determine whether responsive movement is occurring and to estimate the critical distance from the ship at which the effects of avoidance or attraction begin. Finally, we develop a modification of the Buckland and Turnock method in which the data are post-stratified into "close" and "far" regions relative to the estimated critical distance rather than by observation team.

These methods are applied to data from cetacean species collected on shipboard line transect surveys off the east coast of the United States (Palka 1995; D.L. Palka, unpublished

data) and in the waters of the Northeast Atlantic (Hammond et al. 1995; Øien 1996). In each case, we determine if there is a response to the survey ship and estimate the bias in estimates of density that result if responsive movement is not taken into account.

Materials and methods

Swim direction data

Swim directions are defined relative to the transect line and measured clockwise from 0 to 360°; 0° describes an animal swimming parallel to and in the same direction as the ship, and 90° describes an animal swimming perpendicular to the transect line and to the right (Fig. 1). It is assumed that observers scan from the track line to 90° on either side of the track line. Starboard sightings are animals seen initially at sighting angles 10–90° and port sightings as initially seen at 270–350°. Sightings 10° on either side of the transect line were excluded to simplify the parameterization of the models. Swim directions were pooled into quadrants where quadrant 1 represents swim directions 0–90°, quadrant 2 swim directions 90–180°, etc.

To depict expected distributions of swim directions as affected by various factors, the following conventions are followed. If the probability of detecting an animal group is independent of swim direction, an equal number of sightings would be expected in all quadrants. Let this be represented as unity in all quadrants. A factor causing an increase in the detection probability in a quadrant is represented by a number greater than 1. Conversely, a decrease is represented as a number less 1 one but greater than 0. The product of values in all quadrants is assumed to equal 1, and factors are assumed to be independent. In line transect sampling, factors affecting detection of animals are assumed to be the same on both sides of the platform; thus, we "fold over" starboard sightings onto the port side and henceforth only consider the port side.

Swim direction models

In the case when the sighting platform is not present, it is assumed that swim directions of the animal groups are randomly distributed (random model). In cases where the sighting platform is present, it is possible that the distribution of swim directions is influenced by two factors. One factor is that the probability of detecting a group may be dependent on the orientation of the animal's body with respect to the observer's line of sight (presentation angle model). The other factor is that animals may actively respond to the platform (responsive movement model). These models are described below.

Random model

Random movement of animals affects their encounter rate in two ways: movement along the ship's line of travel ("forwards–backwards") and movement across the line of travel ("left–right"). Concerning left–right movement, for animals detected on the port side, more will be encountered with swim directions in quadrants 1 and 2 than in quadrants 3 and 4 (see Appendix for more details). Concerning forward–backwards movement, more animals on the port side will be encountered with swim directions in quadrants 2 and 3 than in quadrants 1 and 4. Combining these two effects, for animals encountered on the port side, there is a peak in the expected distribution of swim directions in quadrant 2, with a corresponding trough in the opposite quadrant 4 (see Appendix). Hiby (1982) found that this is particularly true for species that surface only a few times within the area of detection, which is the common situation in cetacean sighting surveys.

If forwards–backwards and left–right movements were independent, then effects would be multiplicative and the ratio of relative encounter rates in quadrants 1 versus 3 would be 1. However, be-

cause both ship and animals are moving, the ratio of expected encounter rates in quadrants 1 versus 4 differs from the ratio in quadrants 2 versus 3. Thus, the ratio of relative encounter rates in quadrants 1 versus 3 deviates from 1 as the ratio of the animal speed to ship speed increases (see Appendix). However, deviations from 1 are small until the ratio of animal speed to ship speed is greater than about 0.5 (Fig. 2). Animal swim speed is typically much less than ship speed when a line transect survey is conducted. We assume that the ratio of animal speed to ship speed is small and therefore that the ratio of relative encounter rates in quadrants 1 versus 3 is 1 (Fig. 3a). Using simulations, Hiby (1982) reached similar conclusions. Specifically, he found that when search effort was equal at all angles between 0 and 60° on either side of the track line, increase in encounter rates due to fast swimming whales was insignificant even when whales' blow rates were high.

Presentation angle model

If presentation angle affects the probability of detection, more animals will be detected side-on to the observer than head-on or tail-on, relative to the line of sight between the observer and animal group. As a result, using the common framework for animal orientations defined as that with respect to the ship's track line, more animals on the port side will be detected with swim directions in quadrants 1 and 3 and fewer in quadrants 2 and 4 (Fig. 3b).

Responsive movement model

For animals on the port side, if they are attracted to the ship, they will tend to be detected with swim directions in quadrants 1 and 2 (Fig. 3c with $v < 1$). If animals are avoiding the ship, they will tend to be detected with swim directions in quadrants 3 and 4 (Fig. 3c with $v > 1$).

Estimates of model parameters

To estimate whether avoidance or attraction occurred during a survey, parameters for all the above models were fitted. This was done by modeling the number of sightings, n_i, detected with swim directions in quadrant i ($i = 1$–4) using a log-linear relationship for a two-way contingency table for multinomial factors. The factors were random movement, presentation angle, and responsive movement (either avoidance or attraction). Assuming a log-linear model (Agresti 1990) and that the factors are mutually independent, the log of expected counts in quadrant i, $m_i = \log (n_i)$, was modeled for each combination of factors. For example, the log-linear model for the random − presentation angle − responsive movement combination (Fig. 3f) is the product of the two-way tables representing the random model (Fig. 3a), presentation angle model (Fig. 3b), and responsive movement model (Fig. 3c):

$$(1) \quad m_1 = \mu + 0 + z' - v' \quad m_2 = \mu + y' - z' - v'$$

$$m_3 = \mu + 0 + z' + v' \quad m_4 = \mu - y' - z' + v'$$

where μ is the mean, $y' = \log(y)$, $z' = \log(z)$, $v' = \log(v)$, and y, z, and v are defined in Fig. 3. Assuming a multinomial sampling model, maximum likelihood estimates of the parameters (y, z, v) for all the model combinations were estimated (Table 1). Asymptotic standard errors (ASE) of the estimates can be found by the delta method, for example, $\text{ASE}(\hat{v}') = \frac{1}{2} \left(\frac{1}{n_1} + \frac{1}{n_3} \right)$ for the random − presentation angle − responsive movement combination model.

Relationships between model parameters

The aim of modeling swim direction data in this way is to identify a key quantity that indicates evidence of responsive movement, whether or not presentation angle affected the probability of detection. This was found by comparing parameter estimates between models with and without responsive movement. The key quantity

Fig. 2. Relationship between the ratio of animal speed to ship speed and the ratio of the relative encounter rates in quadrants 1 versus 3.
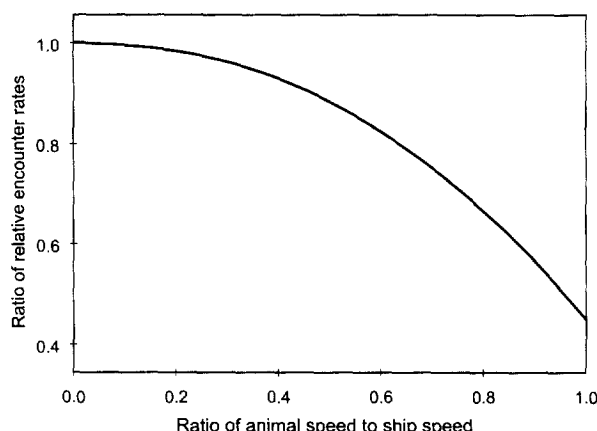

Fig. 3. Expected swim direction distributions for the (a) random model, (b) presentation angle model, (c) responsive movement model, (d) random − presentation angle model, (e) random − responsive movement model, and (f) random − presentation angle − responsive movement model. The four quadrants represent expected swim direction distributions of sightings detected on the port side of a survey ship. In Fig. 3a, $y > 1$ represents an increase in the probability of detection resulting from random movement, in Fig. 3b, $z > 1$ represents an increase in the probability of detection resulting from angle of presentation to the ship, and in Fig. 3c, v represents a change in the probability of detection resulting from responsive movement, where avoidance is $v > 1$ and attraction is $v < 1$.

that emerged was the ratio n_3/n_1. When the ratio n_3/n_1 was significantly greater than 1, avoidance was evident, and when the ratio n_3/n_1 was significantly less than 1, attraction was evident. A test for either avoidance or attraction is a one-sided test with H_0: $\pi_1 = 0.5$, where π_1 is the conditional probability of the number of swim directions falling in quadrant 1 (n_1) given that in quadrant 3 (n_3). When n_1 and n_3 were greater than 5, the chi-square test was used to evaluate H_0; otherwise, the exact binomial test was used.

Estimation of the critical distances

The expectation is that animals do not react to ships when sighted at sufficiently far distances (greater than a critical radial distance r_c), and so the ratio n_3/n_1 (when $r > r_c$) would not be significantly different from 1. At closer distances, if responsive movement occurs, the ratio n_3/n_1 (when $r < r_c$) would be either significantly greater than 1 (for avoidance) or significantly less than 1 (for attraction). If no responsive movement occurs, then the ratio n_3/n_1 would be 1 at all radial distances. This is illustrated by a plot of the cumulative sum of Y (ΣY_i) versus radial distance r_i, where $Y_i = n_{3i} -$

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Table 1. Maximum likelihood estimators of model parameters, where n_i are the positive number of sightings detected with swim directions in quadrant i ($i = 1$–4).

Model	Model parameter		
	y	z	v
Random	$\left(\dfrac{n_2}{n_4}\right)^{1/2}$	1	1
Random – presentation angle	$\left(\dfrac{n_2}{n_4}\right)^{1/2}$	$\left(\dfrac{n_1 n_3}{n_2 n_4}\right)^{1/4}$	1
Random – responsive movement	$\left(\dfrac{n_2 n_3}{n_1 n_4}\right)^{1/2}$	1	$\left(\dfrac{n_3}{n_1}\right)^{1/2}$
Random – presentation angle – responsive movement	$\left(\dfrac{n_2 n_3}{n_1 n_4}\right)^{1/2}$	$\left(\dfrac{n_1 n_3}{n_2 n_4}\right)^{1/4}$	$\left(\dfrac{n_3}{n_1}\right)^{1/2}$

Note: Model parameters y, z, and v are defined in Fig. 3.

n_{1i} for all i sightings with radial distances less than or equal to r_i. If animals avoid ships at distances closer than r_c, ΣY_i will tend to increase until $r = r_c$ and then approach an asymptote for $r > r_c$ where it would fluctuate around a constant level according to a symmetric random walk. If animals are attracted to ships at distances closer than r_c, then ΣY_i will decrease until r_c. If no responsive movement occurs, then the plot would be approximately horizontal fluctuating around a constant level.

Critical radial distances were found by modeling the relationship between swim direction and radial distance using logistic generalized additive models (GAMs). Only sightings with a swim direction in the first or third quadrant were considered. It was assumed that there were n sightings, each of which recorded a random variable, Q_i, that had a binomial (n_i, p_i) distribution. To account for the two ways in which swim directions have been recorded, there are two special cases. The first case is for data sets in which swim directions were recorded in degrees relative to the ship's heading. Thus, $Q_i = 1$ if the swim direction was in quadrant 3 and $Q_i = 0$ if in quadrant 1. In this case, $n_i = 1$ and Q can be consider a Bernoulli random distribution because the Bernoulli distribution is a nearly degenerate case of the binomial distribution (McCullagh and Nelder 1991). The second case is for data sets in which swim directions were recorded in quadrants relative to observer line of sight (head-on, tail-on, side-right, and side-left). In this case, it was not possible to determine with certainty swim direction quadrants relative to the ship's heading. Instead, the binomial variable Q_i was approximated by the probability that the true swim direction was in quadrant i. This probability was estimated using recorded swim directions with respect to observer line of sight (head-on, tail-on, side-right, and side-left) and angles at which sightings were detected. Note a sighting that had a nonzero probability of a swim direction in quadrant 3 has a zero probability of it being in quadrant 1, and vice versa. In either case, the explanatory variable in the logistic GAM of swim direction was radial distance r:

(2) $\text{logit}(p) = a + b \times f(r, x)$

where $f(r, x)$ was an estimated smoothing spline function (Venables and Ripley 1999) of radial distance r with x degrees of freedom that define the smoothness of the function, a was the intercept, and b was the slope of $f(r, x)$. Critical radial distance was defined as the radial distance where $\text{logit}(p) = 0$.

The sign of slope b indicates whether the response was avoidance (negative slope), attraction (positive slope), or no response ($b = 0$). Significance of b was evaluated in two ways. First, significance was estimated by the percentage of bootstrap estimates of b that were greater or less than 0. Second, the Wilcoxon one-sided

signed rank test was used on the bootstrapped estimates of b, where the null hypothesis H_0: $b = 0$ was rejected for H_A: $b < 0$ for avoidance and H_0 was rejected for H_A: $b > 0$ for attraction.

A compelling reason to use the logit model is that this model ensures that p_i lies between 0 and 1, without any constraints on the response predictor(s). A compelling reason to use GAMs is that this type of model automatically allows the data to suggest models with complex response shapes, if needed, rather than assuming a priori a model with a specified level of complexity.

In S-PLUS (Venables and Ripley 1999), the software used here, degrees of freedom in a GAM can vary from $x = 1$, a linear relationship, to $x \geq 2$, curves of increasing complexity. Degrees of freedom cannot be chosen a priori because this depends on the behavior of the animals being surveyed (as indicated by the data themselves). When $x \geq 2$, it is possible for the logit(p) to equal 0 at more than one radial distance. If there is no responsive movement, a linear model ($x = 1$) and a slope (b) of 0 are expected. If there is a simple on–off switch of responsive movement at one radial distance, a model with $x = 2$ is expected. If responsive movement begins at a distance greater than that observed during the survey, then a linear model ($x = 1$) and a slope (b) different from 0 could be expected. More complex animal behavior would require a more complex model ($x > 2$). For example, if critical distance for some animals in a population differs from that of other animals, or if animals avoid ships at some distances but are attracted at other distances, then, in essence, there is more than one r_c.

To choose the most representative model, the r_c from models with a range of x values were compared with the asymptote of the diagnostic plot of ΣY versus r. If responsive movement existed within the range of radial distances observed, the most representative model results in an r_c (r where logit(p) = 0) close to the start of the asymptote in the diagnostic plot and has the lowest possible Akaike information criterion (AIC) from a model where $x \geq 2$. In addition, other standard diagnostics were used, for example, inspection of plots of the fitted model along with standard error bands and partial residuals (as recommended in Hastie and Tibshirani (1991)), using the C_p criterion $\left(= \dfrac{\text{SSE}_p}{\hat{\sigma}^2} - (n - 2p),\ \text{where } p \text{ is the number of parameters}\right)$ to compare different models (Chambers and Hastie 1992), and comparing the number of correctly predicted Q_is (Venables and Ripley 1999). Especially in cases of complex animal behavior, it was helpful to jackknife the data to determine overly influential data points or to right (or left) truncate the radial distances to model the central tendency. As a check, n_3/n_1 for $r > r_c$ was evaluated to determine whether or not it was significantly different from 0.

Variances and confidence intervals (CIs) of critical radial distances

were estimated using bootstrap resampling techniques (Efron and Tibshirani 1993), where resampling units were sightings. Data were resampled with replacement 1000 times, and for each bootstrap data set, the model was fitted and critical radial distance evaluated. For simplicity, degrees of freedom for all resamples were set to the degrees of freedom of the most appropriate model from the original data. Standard errors of estimated critical radial distances were the standard deviation of the 1000 bootstrapped critical radial distances. The 95% CI was estimated using the bias-corrected accelerated percentile interval method, where the acceleration vector was estimated using jackknifing (default option in S-PLUS).

Estimation of density

Methods developed by Buckland and Turnock (1992) and Borchers et al. (1998) give asymptotically unbiased density estimates that account for both responsive movement and the probability of detection on the track line being less than unity. To fully account for responsive movement, it is assumed that sightings made by the team searching further ahead of the ship were initially detected beyond the distance at which responsive movement occurs. To ensure that this assumption is valid, we propose a modification of the Buckland and Turnock method. In our modification, data were not stratified into teams searching at different distances from the ship, as originally designed, but they were poststratified into sightings detected before animals responded (in the far region) and those detected after they responded (in the close region). This modified method fully accounts for responsive movement if there are sufficient numbers of sightings in the far region and sufficient numbers of duplicate sightings.

Initial sightings seen in the far region correspond to "secondary" sightings as defined by Buckland and Turnock (1992) and Buckland et al. (1993). Initial sightings seen in the close region correspond to their "primary" sightings. Duplicates are then defined as a pair of sightings where one sighting is in the far region and can be detected by either team and the other sighting is detected in the close region by the other team. For groups of animals that were detected by both teams within the same region (either close or far), only the first detection is used. Poststratifying data in this manner allows far sightings to be considered as confirming the position prior to responsive movement of a sample of animals, and then it is not necessary to assume that all animals were detected on the transect line within the close region.

Asymptotically unbiased density estimates that account for responsive movement and the probability that detection on the transect line was less than unity are D_u:

$$(3) \quad \hat{D}_u = \frac{n_c \hat{f}_c(0)}{2L \hat{g}_c(0)}$$

where

$$(4) \quad \hat{f}_c(0) = \frac{\hat{g}_c(0)}{\int_0^w \hat{g}_c(x')dx'}, \quad \hat{g}_c(x') = \frac{n_{cf} \hat{f}_{cf}(x')}{n_f \hat{f}_f(x')}$$

where n_c, n_f, and n_{cf} are the numbers of animal groups seen within the close region, far region, and by both teams (one team saw the group in the far region and the other team saw the same group in the close region), respectively. $f_c(x')$ is the probability density of perpendicular distances, prior to responsive movement, of animals subsequently detected within the close region, $f_f(x')$ is the probability density of perpendicular distances of groups seen in the far region, $f_{cf}(x')$ is the probability density of perpendicular distances of duplicate sightings, as recorded by the team that saw the sighting in the far region, L is the length of the transect line, and w is the maximum perpendicular distance.

As in the Buckland and Turnock method, probabilities $f_{cf}(x')$ and $f_f(x')$ were estimated using standard line transect methods and the assumptions were the same. In addition, the probabilities $f_{cf}(x')$ and $f_f(x')$ can incorporate covariates in any of the standard ways (Buckland et al. 1993; Borchers et al. 1998).

Survey data

The methods described above were applied to two-team shipboard line transect sightings data for Atlantic white-sided dolphins (*Lagenorhynchus acutus*), harbor porpoises, and minke whales (*Balaenoptera acutorostrata*) in the Gulf of Maine (GoM) (Palka 1995; D.L. Palka, unpublished data), minke whales in the Northeastern Atlantic (NEA) (Øien 1996; Schweder et al. 1999), and harbor porpoises, minke whales, and white-beaked dolphins (*Lagenorhynchus albirostris*) in the North Sea and adjacent waters (NS) (Hammond et al. 1995). For convenience, we subsequently refer to a species in a region as a population. In the GoM and NEA, both teams searched by naked eye. In the NS, the tracker team searched using 7 × 50 binoculars and the primary team searched by naked eye.

Results

Evidence of responsive movement

For all populations, there was evidence of responsive movement (Table 2). For NS white-beaked dolphins, H_0 was rejected for H_A: $b > 0$, demonstrating attraction close to the ship (more on results from this population below). For all other populations, H_0: $b = 0$ was rejected for H_A: $b < 0$, demonstrating avoidance. Estimated critical radial distances ranged from 279 m for NS white-beaked dolphins to about 1000 m for harbor porpoises from the GoM and NS (Table 2).

For most populations, there were large differences in the ratio n_3/n_1 between the close and far regions (Table 3). These differences are strongly indicative of substantial responsive movement that, if not accounted for, will lead to estimates of density that are seriously biased. The ratio n_3/n_1 in close regions were significantly different from 1 for all populations except GoM minke whales ($p = 0.069$) and NS white-beaked dolphins ($p = 0.944$). For GoM minke whales and especially NS white-beaked dolphins, evidence for responsive movement was weaker or included a combination of attraction and avoidance (see below).

For all populations, the ratio n_3/n_1 in the far region was not significantly different from 1 (Table 3), suggesting that critical distances were properly selected by the GAMs. To illustrate effects of model (animal behavior) complexity, three populations are examined in detail: GoM white-sided dolphins, GoM minke whales, and NS white-beaked dolphins.

For GoM white-sided dolphins, estimated critical distances (where logit(p) = 0) for $x = 1$, 2, 3, and 4 were 535, 592, 610, and 598 m, respectively. AICs were 120.9, 122.3, 124.0, and 125.4, respectively. The diagnostic plot (Fig. 4a) has an asymptote, so a GAM with $x \geq 2$ is appropriate. The asymptote begins at a radial distance of about 600 m, and there are no other inflection points in the plot. Thus, the GAM with $x = 2$ (Fig. 4b) was chosen and resulted in $r_c = 592$ m.

For GoM minke whales, estimated critical distances for GAMs with $x = 1$, 2, and 3 were 490, 407, and 346 m, respectively. For $x = 4$, logit(p) = 0 at 304, 550, and 717 m. AICs were 193.7, 194.8, 195.5, and 196.1 for $x = 1$, 2, 3, and 4, respectively. The diagnostic plot (Fig. 5a) indicates a major asymptote at radial distances greater than 700 m, but

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Table 2. Parameter values and CVs for the fitted GAM used to estimate the critical radial distance, r_c (metres).

Population (area)	x	a (CV)	b (CV)	$P(b < 0)$	r_c (CV)	95% CI of r
Harbor porpoise (GoM)	4	1.30 (9%)	-4.0×10^{-4} (71%)	0.914	1010 (20%)	733–1442
Harbor porpoise (NS)	3	–0.37 (42%)	-2.1×10^{-4} (75%)	0.914	1004 (22%)	625–1556
Minke whale (GoM)	4	0.98 (38%)	-8.5×10^{-4} (78%)	0.888	717 (24%)	580–1135
Minke whale (NS)	2	–0.32 (80%)	-1.2×10^{-3} (41%)	0.997	563 (23%)	306–819
Minke whale (NEA)	2	0.75 (30%)	-7.9×10^{-4} (37%)	0.993	695 (18%)	551–894
White-sided dolphin (GoM)	2	2.25 (23%)	-2.1×10^{-3} (34%)	0.999	592 (18%)	386–780
White-beaked dolphin (NS)[a]	2	–1.15 (45%)	8.6×10^{-4} (133%)	0.203	300 (43%)	16–440
White-beaked dolphin (NS)[b]	4	–0.73 (51%)	-2.9×10^{-4} (203%)	0.603	279 and 716	107–354 and 466–1443

Note: x is the degrees of freedom of $f(r, x)$, a is the intercept, b is the slope of $f(r, x)$, $P(b < 0)$ is the proportion of bootstrap estimates $b < 0$, and 95% CI of r is the 95% bias-corrected accelerated percentile CI of r_c.
[a]Using sightings data where radial distance is less than 800 m.
[b]Using sightings data where radial distance is less than 1600 m.

Table 3. Distribution of swim directions for sightings in the close and far strata as divided by the critical radial distances (Table 2).

Population (area)	Stratum	n_1	n_2	n_3	n_4	n_3/n_1	p
Harbor porpoise (GoM)	Close	541.0	1691.0	1743.0	476.0	3.2	<0.001
	Far	5.0	5.0	4.5	2.5	0.9	1.000
Harbor porpoise (NS)	Close	129.2	268.9	286.7	127.2	2.2	<0.001
	Far	32.7	57.4	47.9	24.0	1.5	0.089
Minke whale (GoM)	Close	42.5	63.5	61.0	40.0	1.4	0.069
	Far	18.5	22.5	15.0	9.0	0.8	0.543
Minke whale (NS)	Close	11.5	33.7	25.1	14.7	2.2	0.025
	Far	20.4	22.4	18.6	14.5	0.9	0.764
Minke whale (NEA)	Close	75.5	12.7	120.5	67.0	1.6	0.001
	Far	91.0	82.5	85.0	96.5	0.9	0.655
White-sided dolphin (GoM)	Close	8.5	45.0	61.0	23.5	7.2	<0.001
	Far	17.0	16.0	29.0	8.0	1.7	0.077
White-beaked dolphin (NS)[a]	<300 m	4.7	3.3	3.5	3.5	0.8	0.944
	≥300	10.2	9.5	9.7	6.6	1.0	0.920
White-beaked dolphin (NS)[b]	<279 m	3.8	2.4	2.3	3.5	0.6	0.840
	279–716 m	6	9.1	10.3	3.6	1.7	0.290
	>716 m	1.5	2	1.7	1.8	1.1	1.000

Note: Data are numbers of unique groups of animals that had a recorded swim direction. Also given is the p value for the null hypothesis H_0: $n_3 = n_1$ using the χ^2 test or, when $n_i \leq 5$, the exact binomial test. Note that the number of sightings in each quadrant can be a noninteger. For data sets from the NS, this was because the number in a quadrant is the sum of probabilities that swim directions were in that quadrant and each sighting could have a positive probability in two neighboring quadrants. For the other data sets, sightings that had swim directions recorded at the boundaries between quadrants (0, 90, 180, and 270°) were divided equally between adjacent quadrants.
[a]Using sightings data where radial distance is less than 800 m.
[b]Using sightings data where radial distance is less than 1600 m.

the plot is not smooth for $r < 700$ m. This variation could be due to complex animal behavior, influential covariates, random error, or some other reason. The GAM with $x = 4$ (Fig. 5b) models the variation and predicts 717 m as the radial distance at the start of the asymptote; thus, this was selected as the best estimate of critical distance. When these data were left-truncated at 300 m to remove the complexity close to the ship, the GAM with $x = 2$ resulted in one critical radial distance of 760 m, $n_3/n_1 = 0.9$ in the far region ($p = 0.863$ for χ^2 test of H_0: $n_3 = n_1$), and $n_3/n_1 = 1.5$ in the close region ($p = 0.030$ for χ^2 test of H_0: $n_3 = n_1$), confirming that a critical distance of approximately 700–800 m is appropriate.

For NS white-beaked dolphins, the diagnostic plot (Fig. 6a) shows a similar pattern to that for GoM minke whales but with much more structure. There may be no net responsive movement at distances less than 150 m, an indication of attraction at distances between 150 and 300 m, avoidance between about 300 and 700 m, and no net response beyond 700 m. Estimated critical distances were 522 m when $x = 1$, 252 and 833 m when $x = 2$, 252 and 781 m when $x = 3$, and 279 and 716 m when $x = 4$. AICs were 38.1, 39.1, 40.7, and 42.4 for $x = 1$, 2, 3, and 4, respectively. A GAM with $x \geq 4$ is required to model all of these inflection points, and the GAM with $x = 4$ does indeed model this complex behavior (Fig. 6b). There are few data beyond 800 m, as indicated by the rug plot in Fig. 6b. A rug plot is tick marks on the x-axis indicating the radial distance of sightings, where sightings with the same radial distance were "jittered" to break ties. If data beyond 800 m were deleted, a GAM with $x = 2$ was the most representative and resulted in one radial distance where logit(p) = 0 at $r = 300$ m. For comparison, results for this population are given for the GAM with $x = 4$ using all data and the GAM with $x = 2$ using truncated data (Tables 2 and 3). These results confirm the general interpretation of the diagnostic plot and also indicate that effects are not significant, perhaps because of small sample size.
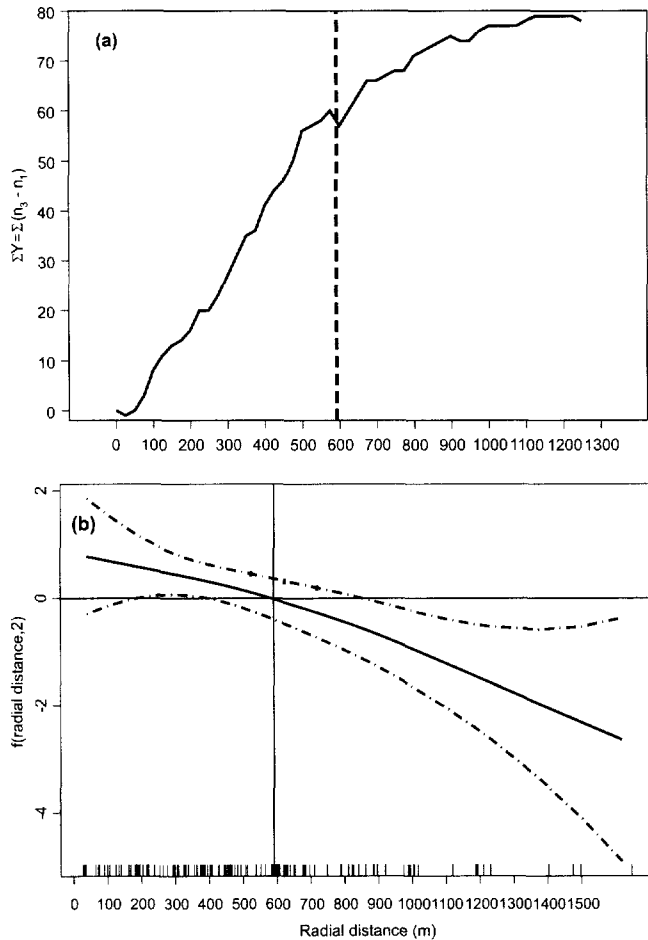
Fig 4. Plots used to estimate the critical radial distance (r_c) for the GoM white-sided dolphins. (*a*) Diagnostic plot of the radial distance (*r*) and the ΣY, where $Y = n_3 - n_1$ (solid line). The vertical reference line (dashed) is at $r = r_c$, as estimated from the GAM. (*b*) Plot of the GAM (thick solid line) with two standard error bands (dashed–dotted lines) and vertical and horizontal reference lines of logit(*p*) = 0 and r_c, respectively. The rug plot on the *x*-axis indicates radial distances of the data.

Fig 5. Plots used to estimate the critical radial distance (r_c) for the GoM minke whales. (*a*) Diagnostic plot of the radial distance (*r*) and the ΣY, where $Y = n_3 - n_1$ (solid line). The vertical reference line (dashed) is at $r = r_c$, as estimated from the GAM. (*b*) Plot of the GAM (thick solid line) with two standard error bands (dashed–dotted lines) and vertical and horizontal reference lines of logit(*p*) = 0 and r_c, respectively. The rug plot on the *x*-axis indicates radial distances of the data.
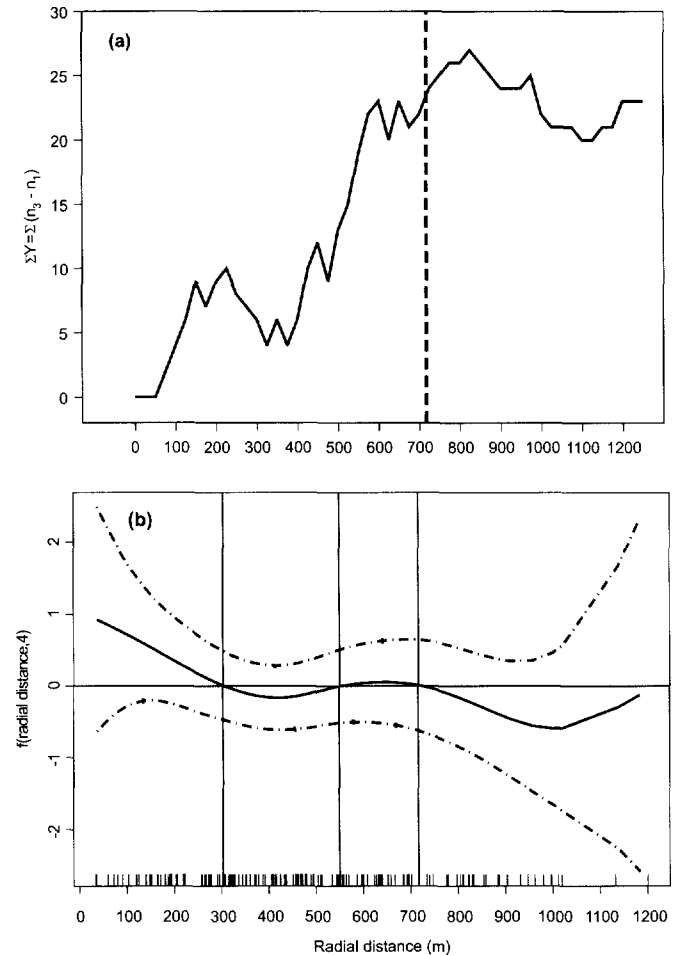
Corrected estimates of density

For all populations where sufficient sample sizes were available, density estimates using our method show that responsive movement has been accounted for to a greater extent than in the estimates from the unmodified Buckland and Turnock method (Table 4). The bias correction ranged from 1.4 for GoM minke whale and white-sided dolphins to 2.7 for NS minke whales. That these corrections are large is explained by the large differences in the ratio n_3/n_1 in close versus far regions. For all populations, differences between corrected and uncorrected density estimates were significant (Table 4).

It was not possible to estimate a corrected density for NEA minke whales because duplicate sightings data were not available or for GoM harbor porpoises and NS white-beaked dolphins because there were insufficient numbers of sightings. Coefficients of variation (CVs) estimated by our method were approximately the same as those estimated by

the unmodified Buckland and Turnock method. This is expected because the same equations are used; only the stratification scheme changed.

Discussion

Reliability and validity of swim direction observations

Our method relies on separating sightings into close and far regions using swim directions as recorded during line transect sighting surveys. Fundamental assumptions are that swim directions seen at the surface reflect the true direction of travel and that swim directions are measured without error at all distances from the ship. The first assumption is difficult to validate. However, for dolphins and porpoises, a typical dive pattern is that at least one animal in the group surfaces two to six times within a 0.5–1 min and then dives for 1–5 min (Westgate et al. 1995). This dive pattern provides the observer the opportunity to accurately determine the direction of travel and record it as the swim direction.

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Fig 6. Plots used to estimate the critical radial distance (r_c) for the NS white-beaked dolphins. (a) Diagnostic plot of the radial distance (r) and the ΣY, where $Y = n_3 - n_1$ (solid line). The vertical reference line (dashed) is at $r = r_c$, as estimated from the GAM. (b) Plot of the GAM (solid thick line) with two standard error bands (dashed–dotted lines) and vertical and horizontal reference lines of logit(p) = 0 and r_c, respectively. The rug plot on the x-axis indicates radial distances of the data.
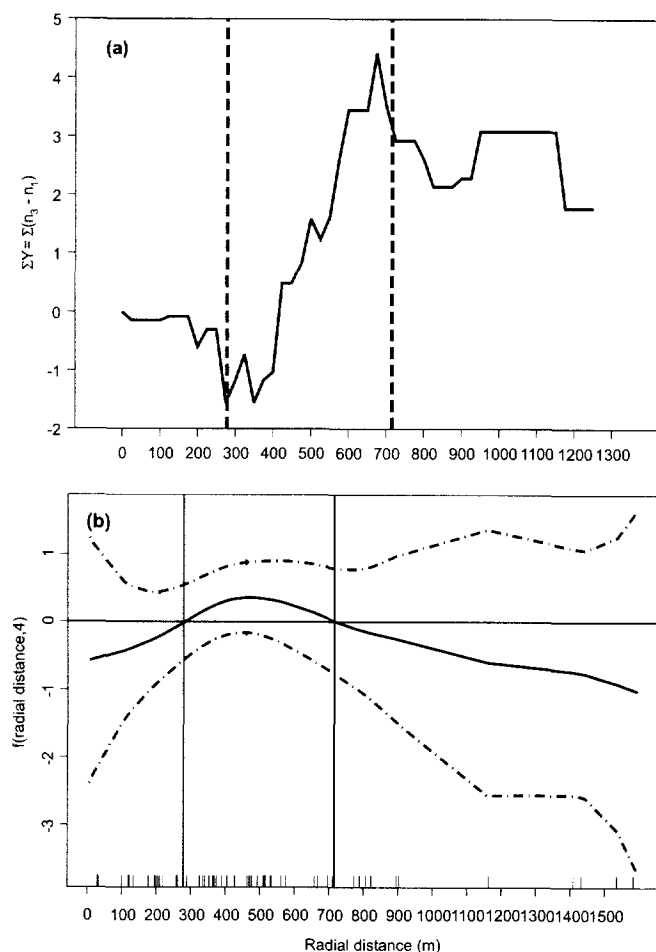
Minke whales are known to surface less frequently and are usually alone, so it is expected that swim directions recorded for minke whales would be less accurate than for the other species investigated in this paper.

The second assumption can be investigated by comparing swim directions of groups at various distances from the ship as recorded by both teams, particularly groups that were detected close in time to ensure that the same group was seen by both teams. If swim directions were accurate, then there should be a one-to-one relationship between swim directions of the same group as recorded by the two teams. GoM minke whale swim directions of sightings seen by both teams within 30 s of each other were consistent between the two teams (Fig. 7a). Using least trimmed squared robust regression on these duplicates, the multiple R^2 was 0.90 and the slope was 1.023. There were a few extreme points, but overall, the two teams recorded similar swim directions. At distances far from the ship (>525 m), the multiple R^2 decreased to 0.85 and the slope was 1.000. For GoM white-sided dolphins, the R^2 was 0.92 and the slope was 0.972 (Fig. 7b). For sightings de-

tected at greater than 650 m, the R^2 was still high (0.98) and the slope was 1.013. In conclusion, the two teams usually recorded similar swim directions for white-sided dolphin groups seen by both teams; however, it appears to be more difficult to estimate swim directions of minke whales, particularly at far distances.

Estimates of density

Differences between the unmodified Buckland and Turnock estimates and our corrected estimates were large and significant. GoM data were collected by two teams, neither of them being a tracker team (as required for the Buckland and Turnock method). Consequently, when the unmodified Buckland and Turnock method was applied, it was not expected that responsive movement would be fully accounted for. For the NS data, tracker teams were used, and if all assumptions were valid, Buckland and Turnock estimates should have accounted for responsive movement. However, differences between estimates from the unmodified Buckland and Turnock method and our method remain large. This could be because many tracker team sightings were not sufficiently far from the ship to ensure that no responsive movement had occurred. Alternatively, the differences could be because other sources of heterogeneity as a result of variation in survey ships, weather conditions, or school sizes were not accounted for in this study as was done in Borchers et al. (1998).

Sensitivity of results to ratio of animal speed to ship speed

Our method relies on separating sightings into close and far regions at the radial distance where the ratio n_3/n_1 differs from 1. When animals move at random, it is expected that this ratio differs from 1, albeit by a small amount, when average animal speeds are at least half that of the survey ship. Any bias from our method will be small if animals move slowly relative to the ship. However, if animals swim fast relative to the ship's speed, then densities from our method will be overestimated. In fact, standard line transect estimators will also be overestimated (Buckland et al. 1993).

Typical swim speeds of minke whales are 1.5–3.9 $km \cdot h^{-1}$ (Kasamatsu et al. 1995), of harbor porpoises are 2.1–2.3 $km \cdot h^{-1}$ (Westgate et al. 1995), and of bottlenose dolphins are 1.5–4.5 $km \cdot h^{-1}$ (Wells et al. 1999). The typical speed of a survey ship is 18.5 $km \cdot h^{-1}$ (10 kn). Using these figures, corrected n_3/n_1 ratios range from 0.985 to 0.998. However, Ridoux et al. (1997) gave a maximum swim speed of 17.3 $km \cdot h^{-1}$ for bottlenose dolphins, which equates to a corrected n_3/n_1 ratio of 0.741. If a target population as a whole exhibits this behavior during a survey, bias in any line transect method could be nontrivial. In this case, to avoid this bias, data on the swim speed of the animals could be used to determine the critical radial distances on the basis of a difference in the ratio n_3/n_1 from the expected value, not the value of 1.

Sensitivity of results to estimated critical distance

Our results are sensitive to estimated values of the critical radial distance. In general, the greater the critical distance, the greater the correction. However, our density estimates were fairly stable within a range of critical distances. For example, for NS harbor porpoises, doubling the critical distance from 1004 to 2008 m increased the estimated density

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Table 4. Number of sightings (n) within the close and far regions and the number of duplicates and estimates of density and their CVs using our method (PH) and the Buckland and Turnock method (BT).

Population (area)	n_c	n_f	n_d	PH density (CV)[a]	BT density (CV)[a]	Bias correction
Harbor porpoise (NS)	922	190	15	0.597 (39%)[b]	0.293 (32%)	2.0
Minke whale (GoM)	217	74	9	0.098 (21%)[b]	0.069 (36%)	1.4
Minke whale (NS)	87	80	11	0.043 (41%)[b]	0.016 (30%)	2.7
White-sided dolphin (GoM)	156	87	15	0.760 (14%)[b]	0.544 (14%)	1.4

Note: Bias correction is the proportional increase in PH density over BT density.

[a]Density of individuals for GoM species and density of groups for NS species.

[b]Significant difference ($p < 0.05$) between two density estimates using the Wilcoxon rank-sum test.

of groups by 10%, from 0.597 to 0.657. Factors influencing the estimated critical distance were the choice of the smoothing parameter in the logistic GAM and the underlying animal behavior. We chose models that had the lowest possible AIC that resulted in an r_c near the asymptote of the ΣY versus r plot. Using this approach, critical distances should not lead to a positively biased density estimate, although effects of responsive movement may not be fully taken into account.

Improvements in methodology

The method that we present to account for responsive movement in density estimates is just one step towards reducing bias in the estimates. As in all line transect analyses, assumptions should be validated and corrections incorporated. Effects of other assumptions are discussed below.

Measurements are without error

To ensure minimal measurement errors, observers should be trained, appropriate measuring equipment provided, and calibration experiments conducted. It is expected that measurement error will not bias density estimates from our method more than those from other methods utilizing two-team data. However, because measurement error cannot be eliminated, when using our method, corrections for measurement error should be incorporated.

Identification of duplicate sightings is without error

This is difficult, particularly when both teams do not see identical surfacings. Any density estimate utilizing data from two teams is sensitive to the number of duplicate sightings. In general, if too few duplicates are identified, then density estimates will be overestimated. Consequently, methods have been developed to decrease this error and incorporate the uncertainty into the density estimate. A protocol used to increase the accuracy of duplicate identification is tracking groups. For example, surveys in the NEA required both teams to record all surfacings of animal groups (Schweder et al. 1997), NS surveys required the tracker team to record as many surfacing as possible (Hammond et al. 1995), and GoM surveys required that "a couple" of surfacings of a group be recorded (Palka 1995). An analysis method used to incorporate the uncertainty in duplicate identification into the density estimate is to have multiple people determine the duplicates (Palka 1995) and classify duplicate sightings as definite, likely, or possible duplicates (Palka 1995; Borchers et al. 1998). In the future, additional methods to reduce duplicate identification error and incorporate this uncertainty into density estimates should be developed.

Fig 7. Scatter plot of swim directions as recorded by the upper and lower teams for sightings seen by both teams. Circles are sightings detected at distances less than the median radial distance, and triangles are sightings at distances greater than the median. The line fitted to points used least trimmed squares robust regression (solid line). The reference line depicts a one-to-one relationship (dotted line). (a) GoM minke whales; (b) GoM white-sided dolphins.
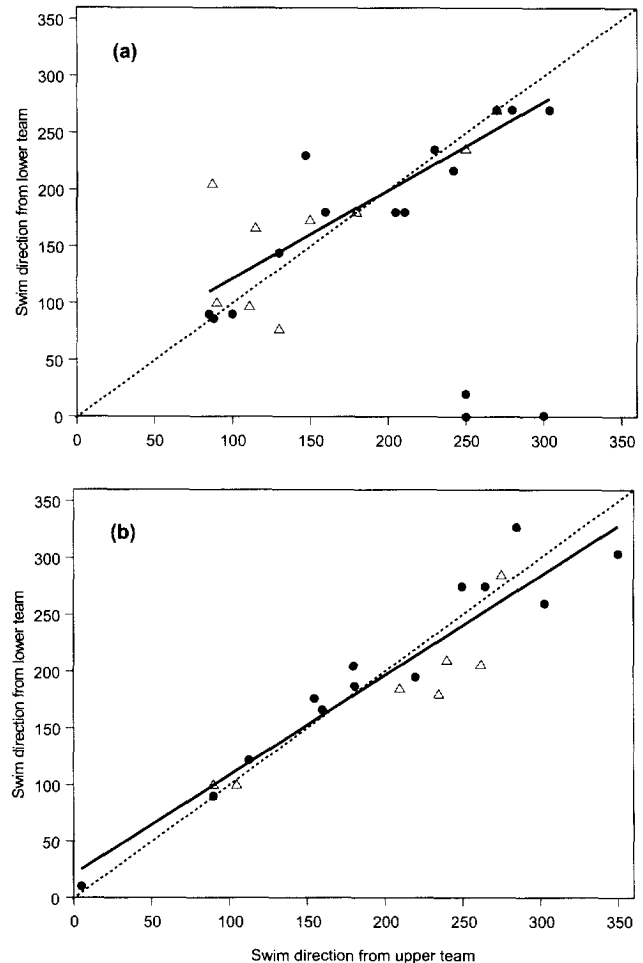
Detection is a function only of perpendicular distance

When estimating cetacean densities, Borchers et al. (1998) and Schweder et al. (1997, 1999) included other covariates that influenced the sighting detection function. Important covariates included sighting conditions (sea state as measured on the Beaufort scale), sighting team or platform (e.g.,

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if teams of observers were "good" or "bad" at collecting data), vessel (animals react differently to ships with different acoustic signatures), and group size. Our method can readily incorporate covariates. Indeed, school size was included as a covariate in the analysis of white-sided dolphin data.

In conclusion, although we developed this method specifically for shipboard surveys for cetaceans, it could be applied to any line transect survey where the species may respond to the sighting platform. Necessary requirements are two teams of observers searching simultaneously, at least some searching at distances at which responsive movement has not yet begun, determination of duplicate sightings, and data on headings. Using the methods presented in this paper, a less biased density can be estimated for species that respond to the sighting platform.

Acknowledgements

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Appendix. Effect of random animal movement on relative encounter rate as a function of animal swim direction and swim speed relative to the survey ship

Let a be animal speed, α animal swim direction, and b ship speed and, for simplicity, set the ship's direction at $0°$. Assume that all animals ahead of the ship are detected as soon as they cross a semicircle of constant radius with the ship at the center. The effect of the left–right component of swim directions in quadrant i ($i = 1$–4, where quadrant 1 is 0–$90°$, etc.) results in an effective angle at which animals are encountered by the ship, x_i, that is given by

$$(A1) \quad x_1 = \tan^{-1}\left(\frac{a\sin\alpha}{b - a\cos\alpha}\right) \quad x_2 = \tan^{-1}\left(\frac{a\cos\alpha}{b + a\sin\alpha}\right) \quad x_3 = \tan^{-1}\left(\frac{a\sin\alpha}{b + a\cos\alpha}\right) \quad x_4 = \tan^{-1}\left(\frac{a\cos\alpha}{b - a\sin\alpha}\right)$$

Relative encounter rates, r_i, of animals detected on the port side of the ship that have effective encounter angles, x_i, are equivalent to the length of a line perpendicular to the resultant vector that intersects with the semicircular detection threshold, where

$$(A2) \quad r_1 = \sin x_1 + \cos x_1 \quad r_2 = \sin x_2 + \cos x_2 \quad r_3 = 1 - \sin x_3 \quad r_4 = 1 - \sin x_4$$

This results in more animals being encountered that are moving in towards the track line (quadrants 1 and 2) than are moving away (quadrants 3 and 4). For example, using eqs. A1 and A2, a ship speed of 18.5 km·h^{-1}, and an animal speed of 3.7 km·h^{-1}, the ratio of relative encounter rates of groups with swim directions in quadrants 1 and 2 to those of groups with swim directions in quadrants 3 and 4 is 1.280.

Because both ship and animals are moving, effects of the forwards–backwards component results in animals swimming in the opposite direction to the ship (quadrants 2 and 3) being encountered more often per unit time than animals swimming in the same direction as the ship (quadrants 1 and 4). In the above example, the ratio of relative encounter rates of groups with swim directions in quadrants 2 and 3 to those of groups with swim directions in quadrants 1 and 4 is 1.004. To incorporate this effect, encounter rates in quadrants 2 and 3 are inflated by a correction factor, c, the ratio of the along-transect component of the resultant movement vectors from swim directions in quadrant 1 versus 2, averaged over the whole of each quadrant:

$$(A3) \quad c = \frac{\text{mean}(b + a\sin\alpha)}{\text{mean}(b - a\cos\alpha)}$$

When the correction factor is applied in the above example, the relative encounter rates of groups with swim directions in quadrants 1, 2, 3, and 4 are 1.13, 1.43, 1.15, and 0.86, respectively. These relative encounter rates vary depending on the ratio of animal speed to ship speed. If the animal speed tripled to 11.1 km·h^{-1} (60% of the ship's speed), corrected relative encounter rates of groups with swim directions in quadrants 1, 2, 3, and 4 change to 1.34, 2.76, 1.64, and 0.51, respectively.