

# Trackline detection probability for long-diving whales

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**ABSTRACT:** Long-diving whales such as dwarf and pygmy sperm whales (*Kogia* spp.) and beaked whales (*Mesoplodon* spp., *Ziphius cavirostris*, and *Berardius bairdii*) are often missed on visual line-transect surveys because they do not always surface within an observer's field-of-view. I develop a simulation model to estimate the probability of detecting these species. This model differs from similar models in that it more completely considers parameter uncertainty. Search parameters are estimated from data that were collected on the behavior of observers using 25x binoculars during cetacean surveys. Whale dive times were estimated from visual observations. Conditional detection probabilities (given that a previously undetected animal is at the surface within an observer's field-of-view) were fitted to observed distributions of radial sighting distances. The probability of detecting a whale on the trackline,  $g_0$ , was estimated from the simulation model. For the given methods (>50 m ship, 25x binoculars, etc.), the estimates of  $g_0$  are 0.35 (CV=0.29) for *Kogia* spp., 0.45 (CV=0.23) for *Mesoplodon* spp., 0.23 (CV=0.35) for *Ziphius cavirostris*, and 0.96 (CV=0.23) for *Berardius bairdii*. These estimates are most sensitive to estimates of vessel speed and the duration of long dives.

**Key words:** abundance, beaked whale, *Berardius bairdii*, detection model, detection probability, diving model, dwarf sperm whale,  $g_0$ , *Kogia*, line transect, marine mammal, *Mesoplodon*, pygmy sperm whale, search model, survey, whale, *Ziphius cavirostris*.

## 1 INTRODUCTION

Line-transect survey methods require either that all animals directly on the transect line are seen or that the fraction seen can be estimated (Buckland et al. 1993). For whales that spend a large proportion of their time submerged, trackline animals can easily be missed as a survey platform (either aircraft or ship) passes over them. Many methods have been proposed and tested to estimate the fraction of trackline cetaceans seen, generally referred to as  $g_0$  (see review by Buckland et al. 1993). Recent estimates of  $g_0$  have been based on methods which use two independent teams of observers, either on the same survey platform or on different platforms (e.g. parallel ships). These independent observer methods can only estimate the probability of being seen given that the animals are available to be seen by at least one team. Independent observer methods cannot estimate the fraction missed for those animals that do not surface within the visual range of either team.

For species that dive for long periods, many individuals may not surface within the visual range of observers on a ship conducting line-transect surveys. This is of particular concern for species of small beaked whales (*Mesoplodon* spp. and *Ziphius cavirostris*) and dwarf and pygmy sperm whales (*Kogia simus* and *K. breviceps*) which cannot be seen at great distances (because they surface inconspicuously without a visible blow or splash) and which dive for relatively long periods. It is also true for larger beaked whales (*Berardius* spp. and *Hyperoodon* spp.) and sperm whales (*Physeter macrocephalus*) which are conspicuous at the surface but which can dive for

extraordinarily long periods (>60 minutes, Leatherwood et al. 1982a, Kasuya 1986, Hobson & Martin 1996). For such species, independent observer methods will underestimate the fraction missed.

A model-based approach of estimating  $g_0$  (Doi 1971) allows estimation of the fraction of animals that are seen even if some animals are never available to be seen. This approach is based on detailed analytical (Doi 1971, 1974) or simulation (Doi et al. 1982, 1983) models of: 1) the search behavior of the observers, 2) the probabilities of whale detection as a function of distance from the ship, and 3) the diving behavior of the whales. The model-based approach has been faulted and has fallen into disuse, largely because its results were sensitive to model assumptions (Best & Butterworth 1980, Doi et al. 1982, 1983, Buckland et al. 1993). This approach is, however, the only approach that has been used for long-diving whales such as beaked whales (Kasamatsu & Joyce 1995) and may be the only practical method for such species.

In this paper, I use simulation modeling to estimate  $g_0$  for long-diving whale species. My approach is similar to the simulation models of Doi et al. (1982, 1983). However, in past implementations of this approach, different assumptions lead to appreciably different results (Doi et al. 1982, 1983) and estimates of statistical precision for  $g_0$  did not incorporate these structural uncertainties in the model. I eliminate assumptions about the sighting process and recast them as parameters within the model. By doing so, I ensure that uncertainty about the structure of the model is reflected in the estimates of uncertainty for  $g_0$ . I use data collected on cetacean surveys to estimate parameters describing the search behavior of marine mammal observers using 25x binoculars. I develop a new approach to fit a conditional detection probability for long-diving whales as a function of sighting distance. Data on the duration of dive and surface periods for *Mesoplodon*, *Ziphius*, *Kogia*, and *Berardius* are used to formulate a model of diving behavior for the species in these genera. Finally, I use the simulation model to estimate  $g_0$  for these species and investigate the sensitivity of these results to a range of feasible parameters.

## 2 METHODS

### 2.1 Survey methods

The simulation model is based on the method of conducting visual sighting surveys for cetaceans which has been used by the Southwest Fisheries Science Center (SWFSC) since 1979 (Holt 1987, Wade & Gerrodette 1993, Barlow & Lee 1994, Barlow 1995) and which has been adopted for cetacean surveys by the Southeast Fisheries Science Center and Texas A&M University. This method (referred to here as the SWFSC Method) uses three observers located on the flying bridge deck of a >50 m research vessel. Two observers search with 25x pedestal-mounted binoculars and a data recorder searches with unaided eyes (and occasionally a 7x binocular). Searching in this mode continues until a marine mammal sighting is confirmed. At that time, the bearing to the animal(s) (relative to the bow) is measured using a calibrated collar on the 25x binoculars (or, rarely, "by eye" if not seen through a 25x binocular), and the distance to the animal(s) is estimated using a reticle scale in the oculars of both the 25x and 7x binoculars (Barlow & Lee 1994). Search effort is typically discontinued if the animal(s) is within 3 nmi of the trackline, and the vessel is directed towards the animal(s) to identify species and to estimate group size. After group size is estimated, the vessel typically resumes its course, and observers resume searching.

SWFSC observers have been given little guidance on how to conduct their search using 25x binoculars. They have been told that they are responsible for searching from  $10^\circ$  on the opposite side of the bow to just abeam of the ship on their side. [The region of overlap at the bow was to reduce the probability of missing trackline animals.] There has been no attempt to tell the observers at what speed they should swing the binoculars or whether they should swing the binoculars from the bow towards abeam or vice versa. New observers have, however, watched and picked up tips from the more experienced observers, and most observers have converged on a similar approach. Many observers search while swinging the binoculars from the bow towards abeam; when binoculars have swung to the abeam position (or just slightly aft of abeam), the observers swing the binoculars rapidly (without searching) to their starting position (Figure 1a). The observers who do not use this approach generally use the opposite (starting abeam and

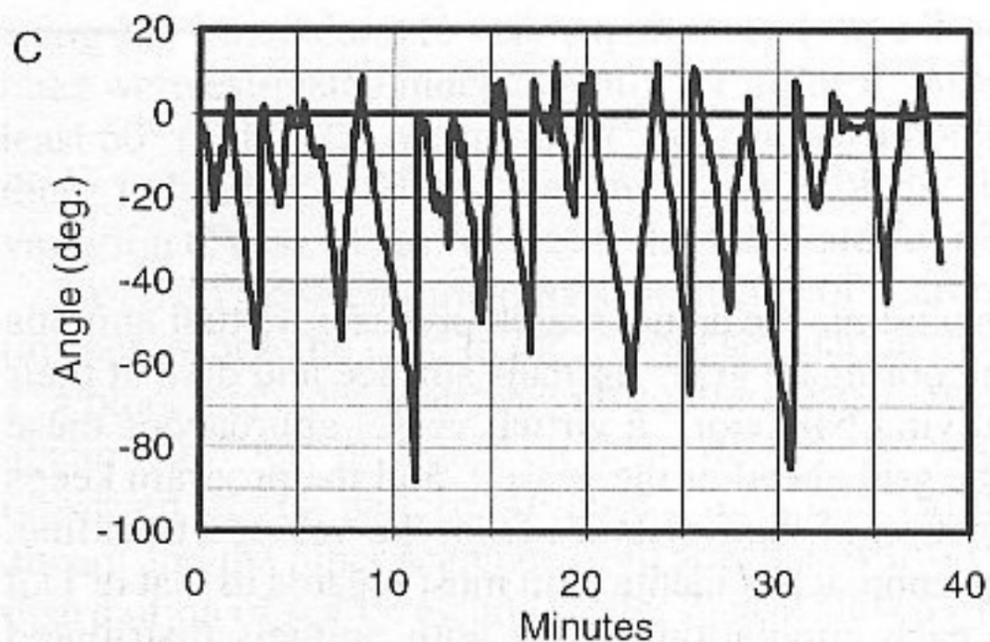
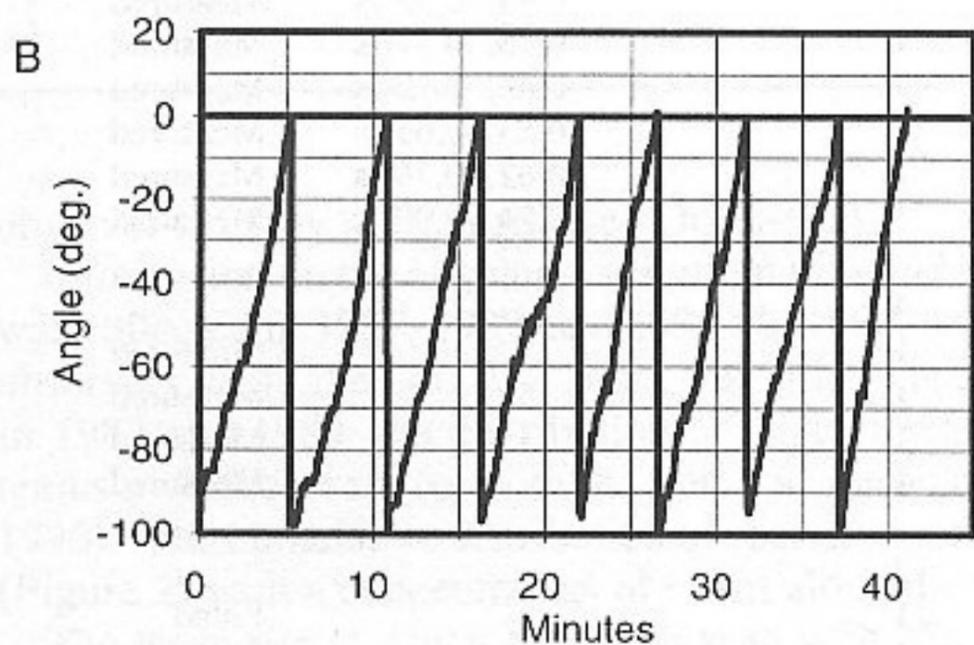
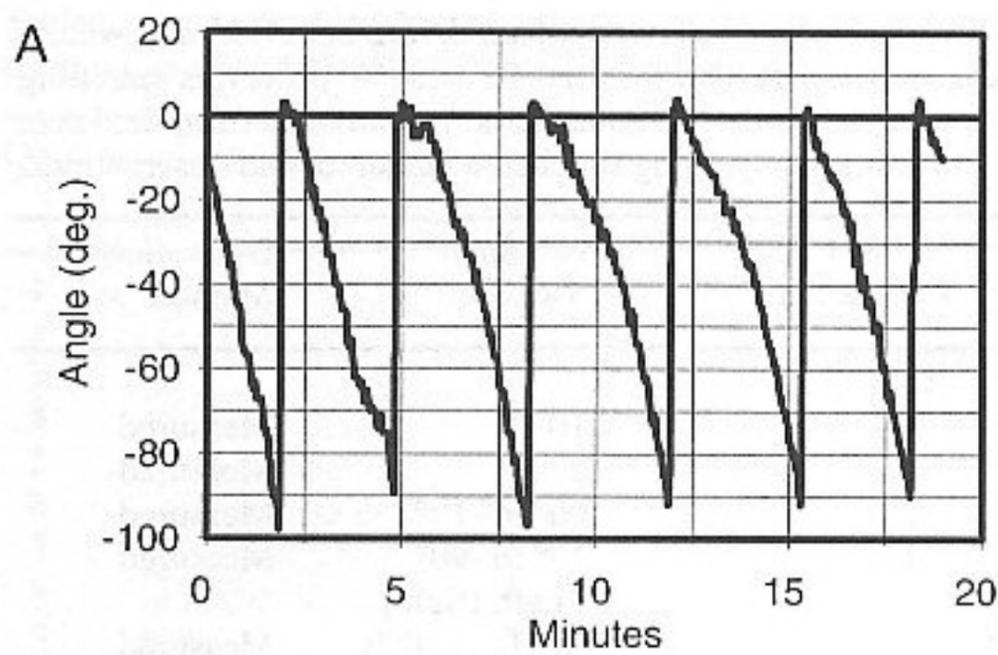


Figure 1. Typical search patterns for 3 observers using the 25X port binocular: A) sweeps from bow towards abeam, B) sweeps from abeam toward bow, and C) irregular sweeps in both directions. Negative angles are left of bow.

scanning forward only, Figure 1b). A few observers use a more random search pattern, scanning in both directions (Figure 1c).

The data recorder is instructed to search at shorter distances to ensure that animals which surface close to the ship (under the visual range of the 25x binoculars) are detected. Most searching by the data recorder is in the forward quadrant by unaided eyes; a 7x binocular is typically used only to verify objects seen by eye. In practice, the vast majority of sightings (>90%) are made by the observers using 25x binoculars.

Table 1. Parameters used in a model to simulate observer searching behavior, whale diving behavior, and whale-detection probabilities. Angles to the left of the bow are negative. The SWFSC Method uses two observers searching with 25x binoculars and one observer searching with unaided eyes. Measured parameters are estimated from field data independent of the simulation model. Fitted parameters are estimated by fitting simulation output to field observations.

Variables	Number of Parameters	Nominal Values	Estimation Method
Search Model	13		
Vessel speed	1	10 kts	Measured
25x Binocular field-of-view	1	2.5°	Measured
Right 25x Binocular search sector	1	90° to -10°	Measured
Left 25x Binocular search sector	1	10° to -90°	Measured
25x Binocular scan rates		(Left, Right)	
0-10°		-0.31, -0.38°/s	Measured
10-20°	1	-0.28, -0.35°/s	Measured
20-30°	1	-0.35, -0.43°/s	Measured
30-40°	1	-0.43, -0.52°/s	Measured
40-50°	1	-0.46, -0.57°/s	Measured
50-60°	1	-0.49, -0.59°/s	Measured
60-70°	1	-0.53, -0.65°/s	Measured
70-80°	1	-0.62, -0.76°/s	Measured
80-90°	1	-0.74, -0.90°/s	Measured
Diving Model	4		
Duration of long dives (min.)	1	"	Measured
Duration of surfacing series (sec.)	1	"	Measured
Number of surfacings per series	1	"	Measured
Duration of a surfacing event (sec.)	1	"	Measured
Detection Model	2		
$\sigma$ , 25x binocular	1	"	Fitted
$\alpha$ , 25x binocular	1	"	Fitted
TOTAL	19		

" All values are species-specific; see Table 3.

## 2.2 Overview of the simulation model

The simulation model was structured to closely mimic the actual search process: virtual animals are generated as fixed points on a Cartesian coordinate grid; animals surface and dive at their fixed points according to a model of their diving behavior; a virtual vessel approaches these animals while two virtual observers search the grid ahead of the vessel; and the program keeps track of which animals are detected as a function of their distance from the vessel's trackline. The time step of the model is one second. The approach is identical in most regards to that of Doi et al. (1982), but to save computer time, each simulation begins with animals distributed uniformly at trackline distances between 6 nmi (just over the horizon) and 12 nmi ahead of the vessel (instead of distributing the animals along a 120 nmi transect line). In reality, a "sighting" often represents a group of animals. For simplicity in the following description, I will use the term "group" to refer to either a group or an individual.

## 2.3 Search model

The "searching" component of the simulation model includes 13 parameters (Table 1) which determine changes in the location of the ship and the angles being scanned by the observers. The fields-of-view of each of the two observers are represented as two independently scanning sectors whose angular widths are equal to the field-of-view for binoculars (2.5° for 25x binoculars). Scan rates are allowed to vary between 10° strata. Insufficient information is available to quantify search behavior for the data recorder (who searched with unaided eyes). Because so few sightings are made by unaided eyes, the bias in estimating  $g_0$  caused by not including this

Table 2. Scan rates (degrees per sec) and standard deviations (S.D.) measured for 13 individuals. Sample size (n) is the number of completed scans used for this measurement.

Observer	n	Scan Rate	S.D.
1	15	0.65	0.10
2	13	0.53	0.13
3	7	0.30	0.04
4	8	0.25	0.04
5	2	0.15	0.04
6	12	0.24	0.04
7	2	0.23	0.01
8	3	0.68	0.07
9	8	0.36	0.04
10	7	0.95	0.13
11	10	0.51	0.06
12	13	0.51	0.09
13	8	0.35	0.07

observer is likely to be small (see Discussion).

Information on the angular distribution of searching effort for observers using 25x binoculars was collected in 1987, 1989, and 1996. In 1996, search angle was recorded every second for six observers using the port 25X binocular, allowing a detailed look at search behavior (Figure 1). In 1987 and 1989, the distribution of angular search effort in  $\sim 5^\circ$  bins was only recorded for teams of 3 observers for both the port and starboard 25X binoculars pooled (Barlow & Sexton 1996). The cumulative distribution of search angles for all three years showed a similar pattern (Figure 2) with a concentration of effort along the trackline.

The mean rate at which observers scan with 25x binoculars was measured on a 1996 dolphin survey in the Gulf of Mexico (R. Pitman, unpubl. data) and on a 1996 SWFSC survey off the U.S. west coast. The observers included a variety of experience levels from beginner (first survey using 25x binoculars) to very experienced (more than 20 years using 25x binoculars). Mean scan rates were estimated independently for thirteen individuals based on complete scans covering at least  $60^\circ$  (Table 2). Mean rates ( $^\circ/\text{sec}$ ) varied among individuals but were fairly constant within these individuals. Here I use the average of the thirteen individuals ( $0.438^\circ/\text{s}$ , coefficient of variation  $CV=0.14$ ) to represent the scan rate for observers using 25x binoculars.

Based on these empirical measurements of searching behavior, I create a simplified model of this behavior to be used in the overall simulation model. In this model I assume that, when using 25x binoculars, observers search continuously between  $10^\circ$  on the opposite side of the vessel and abeam ( $90^\circ$  left or right) on their side of the vessel. To simulate the two most commonly observed search patterns (Figure 1 a,b), one virtual observer searches from the bow towards abeam and the other searches from abeam towards the bow. The observed non-uniform angular distribution of search effort (Figure 2) is achieved by making scan rate a function of bearing angle (using scan rates that are constant within ten  $10^\circ$  bins but which vary between bins) (Table 1). The mean duration of a scan is estimated from the total number of degrees scanned ( $100^\circ$ ) divided by the mean scan rate ( $0.438^\circ/\text{s}$ ), or 228 s (3.8 min). To avoid the artificial situation caused by an exact synchronization of the two 25x binoculars, I use mean scan durations of -10% for one binocular (205 s) and +10% for the other (251 s).

#### 2.4 Whale diving model

A typical whale diving pattern consists of a long dive, followed by a period of frequent surfacings to breathe, followed by another long dive. Periods of submergence during a surfacing series are typically much shorter than those between surfacing series. I use four parameters to model this behavior: 1) the duration of a long dive, 2) the duration of a surfacing series, 3) the number of surfacings within a series, and 4) the time actually spent at the surface during one surfacing (Table 1). Surfacing are distributed uniformly within a surfacing series. In the model, the time

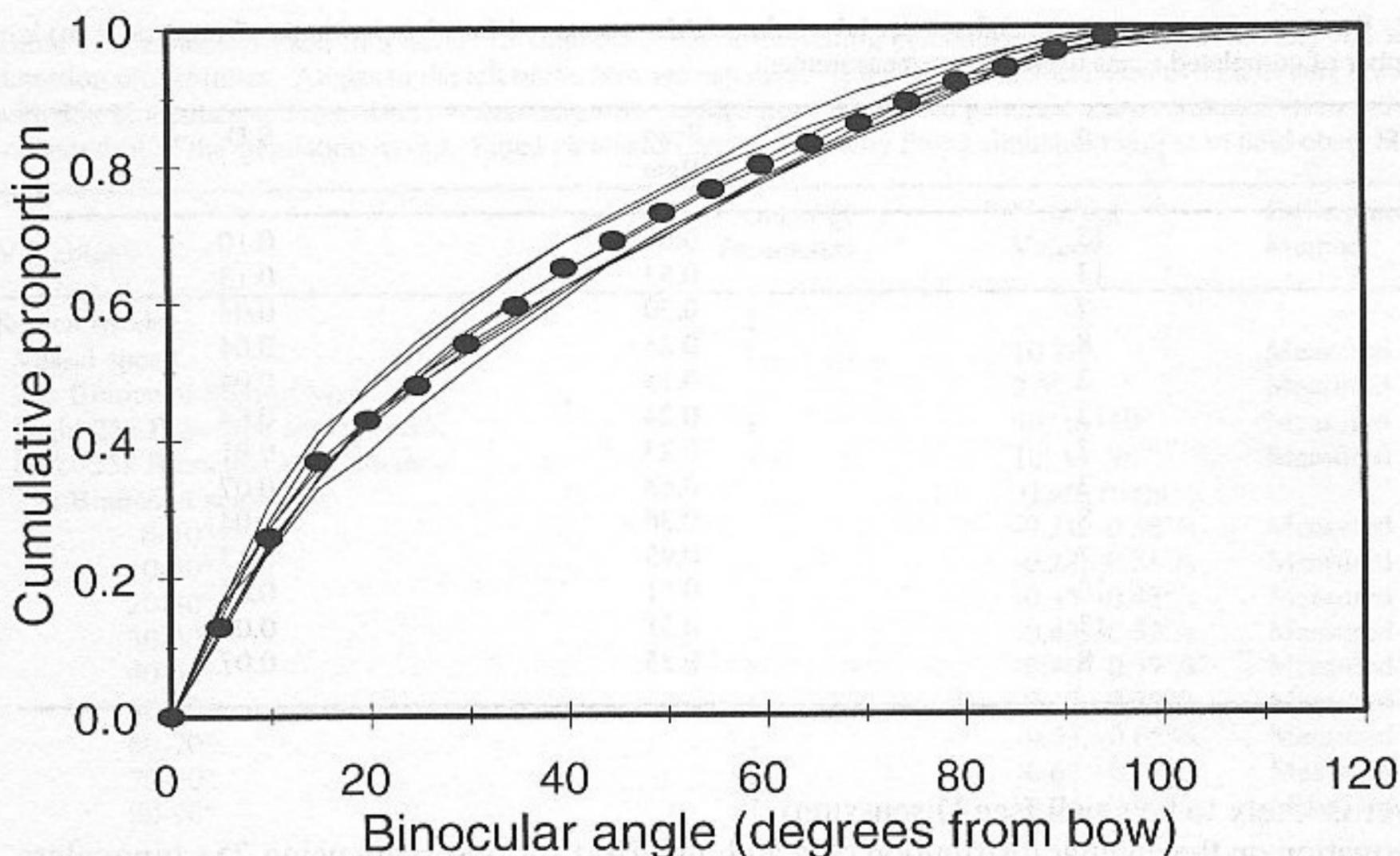


Figure 2. Cumulative proportion of angles searched using 25x binoculars on actual surveys (lines) and from the simulation model using parameters given in Table 1 (black dots). Survey data include eight observer teams in 1987/89 and six individual observers in 1996.

until the next surfacing is recorded for each group and is updated at each time step. All groups are assumed to have the same dive patterns, but their dive times are staggered by initializing each group at a random time in this dive cycle.

Very few quantitative observations of dive patterns have been recorded for beaked whales or dwarf and pygmy sperm whales. Most of the available data were collected during 1993 and 1995 SWFSC research cruises in the Gulf of California (Barlow et al. 1997) with a few additional observations in 1992 in the Gulf of Mexico (R. Pitman & K. Mullin, unpubl. data) and in 1993 and 1996 off California (Barlow 1997). In all cases, observations were made from a ship at distances of greater than 0.5 nmi to avoid affecting their behavior (see Barlow et al. 1997 for methods). Forty-two dive cycles (each including the duration of one surfacing series and one long dive) were recorded for *Ziphius cavirostris*, 59 cycles were recorded for *Kogia* spp. [most were identified as *Kogia simus* and the remainder could not be identified to species], 27 dive cycles were recorded for *Mesoplodon* spp. [species included *Mesoplodon peruvianus*, *Mesoplodon densirostris*, a yet unnamed *Mesoplodon* sp. (Pitman et al. 1987), and an unidentified *Mesoplodon* sp. (probably *Mesoplodon europaeus*)], and 23 dive cycles were recorded for *Berardius bairdii*. Dive cycles were measured for a mix of individuals and synchronously diving groups. Median durations of long dives (Table 3) are a better estimate of expected dive time than are mean dive times because medians are less affected by extreme outliers (that may represent errors). Observed dives include observations which are more than twice the median values (Figure 17 in Barlow et al. 1997) and may represent two dives with an unobserved surfacing between. Median durations of surfacing series (Table 3) are also likely to be less biased than mean surface times when outliers represent errors (in this case, because the first surfacings in a series may be missed).

For the vast majority of the surfacing series, the number of surfacings could not be counted (either because the swells were too high to reliably see every surfacing or because the animals occurred in groups and surfacing rates of individuals could not be discriminated). On two occasions, however, the number of surfacings per series were measured: once for a group of two *Ziphius cavirostris* and once for a group of three *Mesoplodon peruvianus*. For both species, the number of surfacings is strongly correlated with the length of the surfacing series. Based on these surfacing rates and the median lengths of surfacing series (2.1 min. and 2.5 min), Barlow & Sexton (1996) estimated that the expected numbers of surfacings are approximately 17 and 18

Table 3. Estimates of  $g_0$  and its precision based on given parameters used to simulate whale diving behavior and detection probabilities for *Kogia*, *Mesoplodon*, *Ziphius cavirostris*, and *Berardius bairdii*. Precision of parameters is represented as CVs and ranges. Surfacing series for *Kogia* and *Berardius* are modeled as one continuous period of time at the surface, hence the CV of the number of surfacings per series is not applicable (N/A). Parameters describing search behavior are given in Table 1. Estimates of  $g_0'$  are based on simulations with the binoculars fixed on the trackline.

Variables	<i>Kogia</i> spp.	<i>Mesoplodon</i> spp.	<i>Ziphius</i> <i>cavirostris</i>	<i>Berardius</i> <i>bairdii</i>
<b>Diving Model</b>				
Duration of long dives (min.)	10.9	20.4	28.6	15.5
(CV)	(0.19)	(0.08)	(0.07)	(0.13)
Duration of surfacing series (sec.)	78	150	126	210
(CV)	(0.12)	(0.11)	(0.07)	(0.10)
Number of surfacings per series	1	18	17	1
(CV)	(N/A)	(0.20)	(0.20)	(N/A)
Duration of a surfacing event (sec.)	78	3	3	210
(Range)	(N/A)	(2-4)	(2-4)	(N/A)
<b>Detection Model</b>				
$\alpha$ , 25x binocular	0.771	1.244	0.94	4.78
(CV)	(0.20)	(0.21)	(0.23)	(0.37)
$\sigma$ , 25x binocular	2.45	0.891	1.50	0.00129
(CV)	(0.13)	(0.11)	(0.22)	(0.56)
$g_0$	0.35	0.45	0.23	0.96
(CV)	(0.29)	(0.23)	(0.35)	(0.23)
95% C.I.	0.17-0.57	0.23-0.62	0.09-0.41	0.20-1.00
$g_0'$	0.99	0.98	0.75	1.00

(respectively, for *Ziphius* and *Mesoplodon*). I use these surfacing parameters in the simulation model for these beaked whales (Table 3). Typically, *Kogia* and *Berardius* are observed resting at the surface almost continuously during their surfacing series (Leatherwood et al. 1982b, Kasuya 1986). I modeled the diving pattern of these species as a long dive followed by a continuous surface period (1.2 min. for *Kogia* and 3.5 min. for *Berardius*) (Table 3).

The duration of a single surfacing event has not been measured for small beaked whales. For large whales, the time that an animal or its blow is visible to an observer has been measured to range from 2.7 sec for sperm whales to 5.1 sec for blue whales (Doi 1974). Because small beaked whales do not typically have a visible blow, the visible surface period of an individual will be less than these values. Roughly, I estimate that some part of the whale will be visible above water for approximately 2 sec. However, because small beaked whales are often found in cohesive, synchronously surfacing groups of 2-5 individuals and because surfacings are not precisely synchronous, I estimate that at least one member of a group will be visible for up to 4 sec. I use an estimate of 3 sec to model the duration of a single surfacing event for *Ziphius* and *Mesoplodon* (for a "typical" group of 1-5 individuals), but I consider the range of 2-4 sec to be as likely.

## 2.5 Detection model

A group can be detected only if, within a time step of the model, it falls within a sector being scanned by one of the observers and is at the surface. If these conditions are met, the probability that a group will be detected within one time step is calculated as a function of its distance from the ship:

$$Pr(seen) = e^{-\sigma \cdot d^\alpha} \quad (1)$$

where  $d$  = straight-line (radial) distance to the group. The probability of being seen is always

1.0 at zero distance. This is a generalization of the same hazard-rate formulation used by Doi et al. (1982, 1983) with  $\alpha=2$ . To simulate detection probability, a number is drawn randomly from a uniform distribution between 0 and 1, and the group is considered to be detected if the random number is less than  $Pr(Seen)$ . The Detection Model is specified by the parameters  $\alpha$  and  $\sigma$ .

The detection function (Eq. 1) represents the conditional probability that a group will be detected if it is within the visual line-of-sight of one observer for one time step of the model (1 sec). Previously, the parameters of the detection function were estimated by fitting the function to the cumulative distribution of radial sighting distances for groups that were seen close to the transect line (Doi et al. 1982, 1983; Kasamatsu & Joyce 1991). This ad-hoc approach is not appropriate to estimate parameters for my model because it ignores the time-dependence of these parameters. The probability of seeing a group is evaluated each time a group is within the field-of-view of an observer. A group may remain within an observer's field-of-view for several time steps of the model or may reappear on a later binocular sweep, and each time, the probability of detection will be evaluated. The realized distribution of radial sighting distances from the model will depend on the time step used, the scan rates, the duration of surfacing cues, etc. The detection parameters must be estimated within the context of the other parameters of the model. I estimated the detection parameters ( $\alpha$  and  $\sigma$ , Eq. 1) by finding the values that give the best fit of the predicted distribution of radial sighting distances from the simulation model to the observed distribution of radial sighting distances measured during actual surveys. To estimate the predicted distribution of radial sighting distances for a given  $\alpha$  and  $\sigma$ , I initialized a simulation with 10,000 groups distributed uniformly at perpendicular distances up to 6 nmi from the trackline. Values of  $\alpha$  and  $\sigma$  were varied, and the Simplex algorithm was used to find the values that gave the best fit to the observed distribution of radial sighting distances for a given species (Figure 3). When fitting Eq. 1, a transformation was used to reduce the correlation between the parameters and to improve the convergence to a stable solution (Barlow & Sexton 1996). A Kolmogorov/Smirnov 2-sample test statistic was used as a measure of similarity between the observed and predicted distributions of radial sighting distance. Radial sighting distances for observers searching with 25x binoculars were taken from two similar vessels (R/V *David Starr Jordan* and R/V *McArthur*) on SWFSC surveys in the eastern Pacific from 1986 to 1996. I limited observation to those sea state conditions that are considered to be "acceptable" for abundance estimation (Beaufort 0 to 2 for *Kogia*, *Mesoplodon*, and *Ziphius*; Beaufort 0-5 for *Berardius*). Observations included 124 sightings of *Kogia* spp., 55 sightings of *Mesoplodon* spp., 50 sightings of *Ziphius cavirostris*, and 12 sightings of *Berardius*.

## 2.6 $g_0$ estimation

I estimated  $g_0$  from the simulation model using my best estimates of the parameters of the Search Model, the Dive Model, and the Detection Model (Tables 1 & 3). I initialized a simulation with 10,000 groups directly on the trackline and estimated  $g_0$  as the fraction of those that were "seen". To estimate the fraction of groups that surface within the visual range of the observers, I fixed the binocular scan angles to continuously cover the trackline ( $-1^\circ$  to  $1^\circ$ ) and repeated the simulation with 10,000 trackline groups. I found that a sample size of 10,000 groups is sufficient to reduce the stochastic variation in repeated estimates of  $g_0$  so that its coefficient of variation is less than 1%.

## 2.7 Model sensitivity studies

The sensitivity of estimates of  $g_0$  to error in the input parameters was measured by varying the parameters (one at a time) and measuring the change in  $g_0$ . I used a quantity known as "elasticity" (Caswell 1984) to measure the proportional change in  $g_0$  caused by a proportional change in one of the input parameters:

$$Elasticity = \frac{\Delta g_0}{g_0} / \frac{\Delta p}{p} \quad (2)$$

where  $p$  is the parameter being changed. In sensitivity studies, I used  $\pm 20\%$  changes in the parameters given in Table 4. An elasticity value of 1.0 for dive time would indicate that a 20% change in dive time would cause a 20% change in  $g_0$ . Although the fit of the Detection Model is somewhat dependent on the other model parameters, I did not re-estimate the hazard-rate parameters  $\alpha$  and  $\sigma$  after the change in each parameter because, when the elasticity is small, the differences in  $g_0$  due to error in estimating these parameters was greater than the difference in  $g_0$  due to the change in parameter  $p$ . I averaged the elasticities estimated from positive and negative changes in each parameter.

## 2.8 Quantifying uncertainty

I used a non-parametric bootstrap to quantify uncertainty in estimating the hazard-rate parameters  $\alpha$  and  $\sigma$ . The coefficients of variation for these parameters were estimated by repeating the fitting process for 30 bootstrap iterations; prior to each iteration I drew a new distribution of radial sighting distances from the observed distribution (with replacement). [A bootstrap sample size of 30 is generally considered small, but due to the complexity of the fitting process, each bootstrap simulation took approximately 15 hours on a 90 MHz Pentium computer.]

I used a parametric bootstrap to estimate the effect of parameter uncertainty on the coefficients of variation for  $g_0$ . Each bootstrap estimate of  $g_0$  was obtained by initializing a simulation with different values for seven of the input parameters: 25x binocular scan rate, dive duration, surfacing series duration, number of surfacings per series, the hazard-rate parameters  $\alpha$  and  $\sigma$ , and the duration of a surfacing event. For the first six parameters, values were determined for each bootstrap simulation by adding a normally-distributed random number with a standard deviation equal to its standard error. The same normal random number was added to the scan rates of both 25x binoculars. For the duration of a surfacing event, I chose from three likely values (2 s, 3 s, and 4 s) with equal probability. I estimated the coefficient of variation and 95% confidence intervals of  $g_0$  from 1,000 bootstrap estimates.

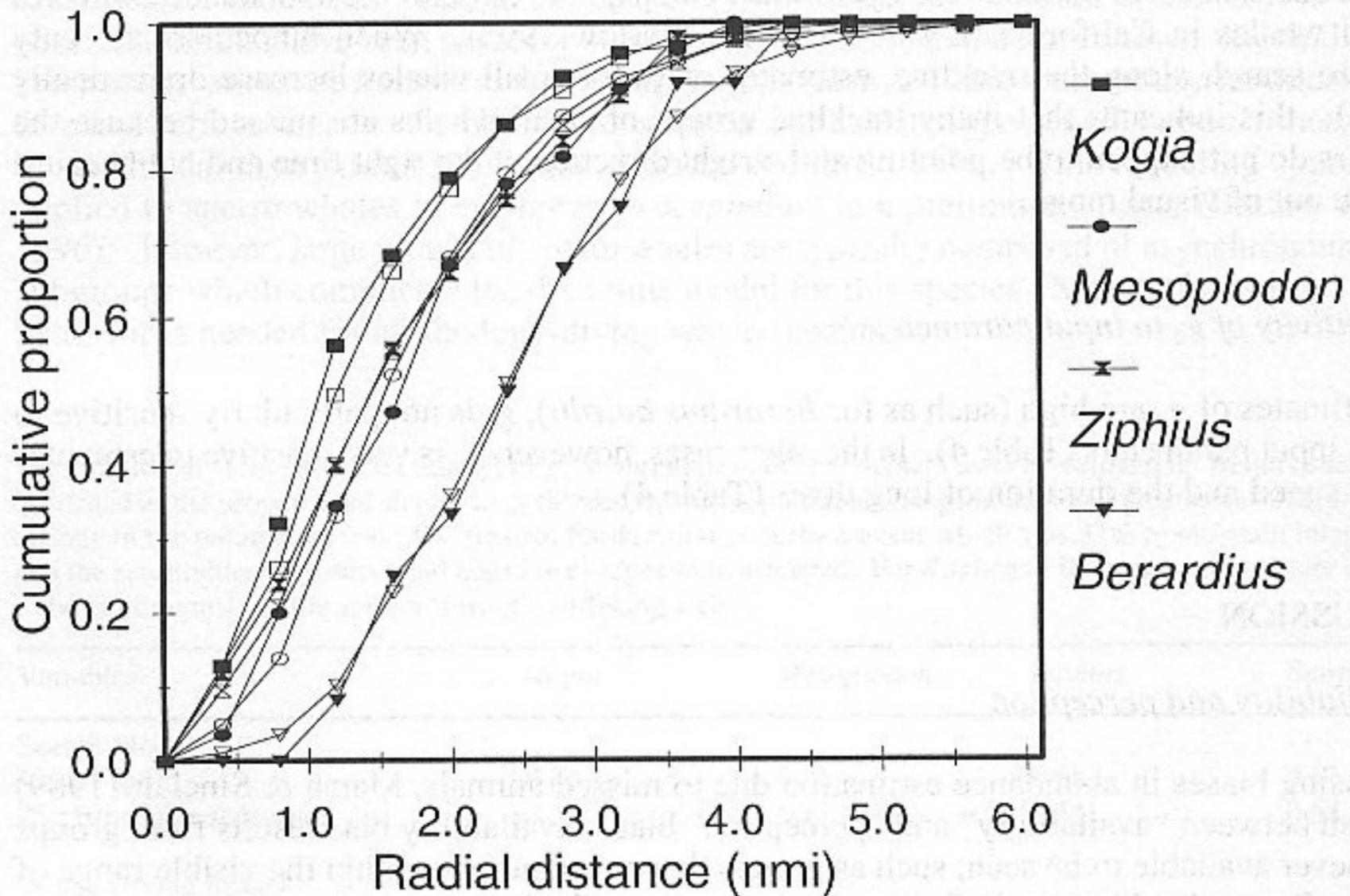


Figure 3. Cumulative distributions of radial distances of sightings made with 25x binoculars on surveys (solid symbols) and from the best-fit models (open symbols).

## 3 RESULTS

### 3.1 Comparison with previous models

To verify that the model was designed and programmed without significant errors, I tested the model using the same parameters as were used by previously by other authors (Doi et al. 1982, 1983; Kasamatsu & Joyce 1991). Some minor modifications of my model were necessary to facilitate this comparison; the actual parameters used and results are given by Barlow & Sexton (1996). Estimates of  $g_0$  from my model were not statistically different from values estimated by these other authors.

### 3.2 Fitting values to the detection model

When the value for one of the hazard-rate parameters,  $\alpha$ , is fixed and the other,  $\sigma$ , is fitted to the observed distribution of radial sighting distances, a wide range of values for the parameter  $\alpha$  provided adequate fits ( $p > 0.1$ ) of the predicted to the observed distributions of radial sighting distances. These ranges varied from  $\alpha = 0.5$  to 1.0 for *Kogia* and from  $\alpha = 0.5$  to 1.5 for small beaked whales. The best fit for the other detection parameter,  $\sigma$ , was highly correlated with  $\alpha$  (Barlow & Sexton 1996). Detection parameters were similar for two genera of beaked whale. The fitted distributions of radial distances from the simulations were very similar to those observed on surveys (Figure 3).

### 3.3 Estimates of $g_0$

Estimates of  $g_0$  from my simulation model (Table 3) indicate that the abundance of small long-diving whales is greatly underestimated by visual surveys using 25x binoculars. Abundance corrected for  $g_0$  would be approximately 2 to 4 times the uncorrected abundance estimates for *Kogia*, *Mesoplodon*, and *Ziphius* but would be only slightly greater for *Berardius bairdii*. The estimated coefficients of variation for  $g_0$  are small compared to those of the abundance estimates for small whales in California (CVs  $\approx 0.7$  to 1.0, Barlow 1995). When binoculars are only allowed to search along the trackline, estimates of  $g_0$  for small whales increase dramatically (Table 3); this indicates that many trackline groups of small whales are missed because the binoculars do not happen to be pointing at the right direction at the right time and not because they were out of visual range.

### 3.4 Sensitivity of $g_0$ to input parameters

When estimates of  $g_0$  are high (such as for *Berardius bairdii*),  $g_0$  is not particularly sensitive to any of its input parameters (Table 4). In the other cases, however,  $g_0$  is very sensitive to estimates of vessel speed and the duration of long dives (Table 4).

## 4 DISCUSSION

### 4.1 Availability and perception

In discussing biases in abundance estimation due to missed animals, Marsh & Sinclair (1989) distinguish between "availability" and "perception" bias. Availability bias results from groups that are never available to be seen, such as groups that never surface within the visible range of observers. Perception bias results from groups that are available but are not seen for some other reason. The distinction between these two sources of bias is not complete because the visual range of observers does not have a distinct edge. Nonetheless, this distinction is useful in understanding  $g_0$ .

Estimates of  $g_0$  for availability bias ( $g_0'$ ) are much higher than estimates of total  $g_0$  for small whales (Table 3). This indicates that trackline groups of small whales are available to be seen but are most frequently missed because they are not perceived. Because the surface times of small whales are so short (<3 min) compared to the scan rates of the binoculars ( $100^\circ$  in >3 min), it is not surprising that trackline groups are missed even at close range. The lower  $g_0'$  for *Ziphius* helps explain why the total  $g_0$  is so much less for *Ziphius* than for *Mesoplodon* or *Kogia*. Availability bias is small if dive times are less than 20 min because all groups are likely to surface at some time within the visual range of observers. Above this threshold,  $g_0'$  decreases sharply with increasing dive times.

#### 4.2 Previous estimates of $g_0$

Based on a 1991 SWFSC survey,  $g_0$  was estimated for the general categories of “small whales” (including *Ziphius* and *Mesoplodon*) and for “cryptic species” (including *Kogia*) (Barlow 1995). These estimates (0.79, 0.84, and 0.84 respectively for *Kogia*, *Mesoplodon*, and *Ziphius*) were based on data collected by independent observers who reported groups that were missed by the three primary observers. These values only account for perception bias; therefore, it is not surprising that they are larger than the values reported here (Table 3) which include both perception and availability bias.

#### 4.3 Diving behavior

Because most of the dive-time data come from a study in the Gulf of California, I do not know to what extent my models of diving behavior can be extrapolated to other areas or to other species of *Kogia* and *Mesoplodon* found in other areas. Most (if not all) of the dive times for *Kogia* were for *Kogia simus*. The other species in this genus (*Kogia breviceps*) is slightly larger and might have longer dive times (and, perhaps, longer surface times). For *Mesoplodon*, most of the dive times are for *Mesoplodon peruvianus* (the smallest species of the genus) and a yet-undescribed *Mesoplodon* sp. A (an average-sized, 5-5.5 m *Mesoplodon*, Pitman et al. 1987). The few observations that have been made for other species of *Mesoplodon* have shown similar dive times. Prior observations of *Berardius bairdii* off Japan (Kasuya 1986) were nearly identical in mean dive and surface times as the observations I used, but a related species (*B. arnuxii*) showed much longer modal dive times (35-60 min., Hobson & Martin 1996). This modeling approach was applied to sperm whales (*Physeter macrocephalus*) in a preliminary paper (Barlow & Sexton 1996); however, large groups of sperm whales are typically composed of asynchronously diving subgroups which complicate the dive time model for this species. More information on diving behavior is needed for all the long-diving whale species.

Table 4. Relative sensitivity (elasticity) of  $g_0$  to variation in the parameters used to estimate it. Relative sensitivity is estimated as the proportional change in  $g_0$  divided by the proportional change in the input parameter. The proportional change in the parameters was 20% (except for duration of surface event which was 33% to maintain integer values) and the sensitivities of positive and negative changes were averaged. For *Kogia* and *Berardius*, animals are considered to be continuously at the surface during a surfacing series.

Variables	<i>Kogia</i>	<i>Mesoplodon</i>	<i>Ziphius</i>	<i>Berardius</i>
Search Model				
Vessel speed	0.86	0.92	0.88	0.61
25x Binocular scan rates	0.55	0.31	0.34	0.63
Whale Diving Model				
Duration of long dives (min.)	0.80	0.92	0.90	0.39
Duration of surfacing series (sec.)	0.61	0.24	0.30	0.49
Number of surfacings per series	N/A	0.65	0.46	N/A
Duration of a surfacing event (sec.)	N/A	0.40	0.46	N/A

#### 4.4 Sightings made by observers not using 25x binoculars

The estimates of  $g_0$  made in this paper are based only on a model of search by two observers using 25x binoculars. SWFSC surveys also include a third observer (the data recorder) who searches by unaided eye and occasionally a 7x binocular. The data recorder does make some sightings (usually close to the vessel), and in the past, abundance estimates have been based on sightings made by all observers. Of all groups that were seen close to the trackline (<0.4 nmi), the fractions made by the data recorder were 14% for *Mesoplodon*, 31% for *Ziphius*, and 0% for *Kogia*. Because the sighting distances by unaided eye are so much less than by 25x binoculars, many (or even most) of the groups seen first by the data recorder would have quickly passed behind the vessel and would therefore have been “missed” by the observers using 25x binoculars. Given my estimates of  $g_0$ , it is not surprising that this number of groups would have been missed by the observers using 25x binoculars. However, these data indicate that the value of  $g_0$  for the entire team of three observers may be appreciably (10-30%) higher than the values of  $g_0$  estimated for two observers using 25x binoculars.

These data show the importance of considering the effect of sightings by the data recorder on estimates of  $g_0$ . Information about the behavior of observers searching by unaided eyes is unavailable and is likely to be much more difficult to gather than information about the search behavior of observers using binoculars. It is difficult to measure where the eyes are pointing and what the “effective” field-of-view (field-of-acuity) of the human eye might be for seeing marine mammals. Rather than developing a separate model for observers searching with unaided eyes, a better solution might be to ignore those sightings and to estimate abundance based only on sightings made with 25x binoculars. If that were done, the estimates of  $g_0$  presented here could be applied in a more straight-forward fashion.

#### 4.5 Generality of results

Although the simulation method presented here should be widely applicable, it is important to recognize that my estimates of  $g_0$  cannot be extrapolated to other survey methods. Using different binoculars or different observation heights would result in very different parameters for the Detection Model. The Detection Model also depends on sighting conditions so estimates of  $g_0$  should only be applied to estimates of abundance that were made for similar conditions (e.g. Beaufort sea state 0-2 for small whales or 0-5 for *Berardius*).

#### 4.6 Future directions

Although this paper makes some improvements in the simulation modeling approach to estimating  $g_0$ , it remains true that the simulation is based on a large number of measured and fitted parameters (approximately 20) and does not account for all statistical and biological uncertainties. I did not investigate the potential effect of animal movement; random movements are not likely to be a problem (because the ship travels 3-5 times faster than the animals), but directed movements may cause a significant bias. Group size almost certainly affects detection probabilities and estimates of  $g_0$ , a factor that could be investigated further. Perhaps the greatest challenge will be in reducing the number of measured parameters without introducing bias.

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