# Using simultaneous counts by independent observers to correct for observer variability and missed sightings in a shore-based survey of bottlenose dolphins, *Tursiops truncatus*

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#### ABSTRACT

Simultaneous counts by independent shore-based observers have been used to generate revised population estimates for gray and bowhead whales, but no similar technique has been applied to shore-based dolphin surveys. Shore-based whale surveys generally rely on a single observation site from which migrating whales are counted as they pass in one direction over a period of weeks to months. Shore-based dolphin surveys, however, typically use multiple observation sites over a much shorter time period (hours) in order to avoid double counting individuals as they change direction. This paper reports on a new technique to correct for observer variability and missed sightings for coastal bottlenose dolphin surveys conducted at Myrtle Beach, South Carolina, USA. Comparisons were made between concurrent counts by 39 pairs of independent shore-based observer teams. A model was developed to revise observer estimates in which the number of observed dolphin groups was multiplied by a correction factor to estimate the true number of groups, and this number in turn was multiplied by the mean group size to determine the total number of dolphins. The true number of dolphin groups was estimated using a modified Petersen mark-recapture estimate, stratified by group-size category. The mean proportion of groups missed by observers was negatively correlated with reported group size: 32.7% for groups of 1-2 dolphins; 16.5% for groups of 3-4 dolphins; and 9.9% for groups of >4 dolphins. A variability factor was also calculated to determine a confidence interval for the average number of dolphins per group, based on the mean percent difference between paired observer teams, stratified by group size. The model was used to calculate revised estimates for shore-based bottlenose dolphin surveys conducted in South Carolina in 1994 and 1995. The original uncorrected abundance estimates were increased by a factor of 1.14 and 1.19 respectively, comparable to similar calculations from shore-based surveys of gray whales, However, the estimated confidence interval of ± 38% of the revised estimates is approximately four times the magnitude found in the gray whale studies. This difference is primarily due to the large observer variability for estimated dolphin group size and can be reduced using various revisions of survey design and methodology. Ideal conditions for this technique include elevated observer posts and accurate estimates of the proportion of the population within visual range of the coastline. This study demonstrates that shore-based dolphin surveys are a potentially efficient census technique and an attractive low cost alternative to aerial and boat surveys.

KEYWORDS: SURVEY - SHORE-BASED; TECHNIQUES; ABUNDANCE ESTIMATE; MARK-RECAPTURE; BOTTLENOSE DOLPHIN

## INTRODUCTION

When choosing census techniques for coastal cetaceans, shore-based population surveys are an attractive option. Data can be obtained at a low cost and with potential efficiency in waters where high turbidity may cause aerial observers to miss submerged animals. If conducted on a regular basis, shore-based surveys can be used to track local population trends over time. For species such as the Californian gray whale (*Eschrichtius robustus*), in which nearly the entire migratory population passes within sight of land near Granite Canyon in central California, shore-based census techniques have been used to estimate the entire population (Buckland *et al.*, 1993; Rugh *et al.*, 1993) and monitor trends in abundance over time (IWC, 1993).

There are few published shore-based surveys that focus on smaller cetaceans. Bottlenose dolphin (*Tursiops truncatus*) surveys have typically been conducted from boats (Wilson *et al.*, 1997), aircraft (Carretta *et al.*, 1998; Cockcroft *et al.*, 1992; Leatherwood, 1979), or some combination of both (Hansen, 1990; Kenney, 1990; Wells *et al.*, 1990). However, Hammond and Thompson (1991), used shore-based counts to estimate the minimum population of bottlenose dolphins in the Moray Firth, Scotland. Although not a population survey, Hanson and Defran (1993) systematically monitored 19 land-based observation points in California to identify dolphin groups for behavioural studies. Along the

southeastern coast of the United States, dolphin researchers in Virginia have conducted semi-regular shore-based surveys each year since 1993 and researchers in every state from New Jersey to Florida have conducted at least one shore-based survey during the 1990s (Swingle and Barco, pers. comm.).

The purpose of this study was to develop a technique to improve shore-based population estimates of bottlenose dolphins by examining observer variability in simultaneous counts by paired independent observers. Specifically, a double-count survey was conducted to generate a correction factor for the number of dolphin groups missed and an estimated confidence interval for the mean group size. These correction factors were applied to data from shore-based surveys conducted in 1994 and 1995 in South Carolina, USA. Similar double-count techniques have been used in aerial transect studies for both aquatic (Bayliss, 1986; Carretta et al., 1998; Marsh and Sinclair, 1989) and terrestrial animals (Grier et al., 1981; Caughley and Grice, 1982; Graham and Bell, 1989). In shore-based cetacean surveys, comparisons between independent observers have been used to revise estimates of bowhead whales (e.g. Krogman et al., 1989) and gray whales (Rugh, 1984; Rugh et al., 1990; 1993; Buckland et al., 1993). Coastal dolphins typically differ from migrating whales, because the entire population does not travel in a single consistent direction. Whereas the whale surveys rely on single observer stations

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counting whales as they pass in one direction over a period of weeks to months, the dolphin surveys avoid the double-counting of individuals by using simultaneous counts at multiple observation sites over a period of hours. To our knowledge, no one has examined observer variability in shore-based dolphin surveys.

## **METHODS**

## Survey location and techniques

Surveys were conducted from 0900 to 1100 hours during eight days between 19 October and 10 November 1996, along the coast of Myrtle Beach, South Carolina. This region is an almost linear stretch of shallow sloping coastline that extends for a length of approximately 55km from Little River Inlet to Murrells Inlet, South Carolina. This study was conducted during the fall migratory peak when observers were most likely to encounter dolphins. Between 1995 and 1998, we conducted boat transect surveys that indicate the local dolphin population increases by greater than an order of magnitude during this four week period (Young, unpublished data).

Observers worked in teams of two, with one observer and one observer/data recorder periodically switching roles to avoid fatigue. Data forms were simplified from a widely used protocol for dolphin shore counts in the Southeast USA, designed by a scientific advisory team lead by Mark Swingle of the Virginia Marine Science Museum. Observer training levels were designed with practical limitations in mind. For dolphin counts in South Carolina in 1994 and 1995, Young and Murphy (unpublished data) coordinated up to 200 volunteers per survey, with teams spaced every 3.2 km along the coast. Such a large number of participants means that many volunteers, although enthusiastic, are unspecialised in the field and are unable to participate in lengthy training sessions. Thus, in order to model realistic conditions and to maintain consistency with the 1994/1995 survey protocol, observers in this study had no prior experience and training sessions were limited to a maximum of 90 minutes. Even within this narrow time restriction, two different training levels were used to test the possibility that small differences in basic training techniques can improve observer performance. Observer teams receiving Training Level 1 (TL1) were instructed in a standardised survey technique, consisting of 45 minutes of instructions for recognising and counting dolphins and filling out data sheets. Training Level 2 (TL2) observer teams received the same training as the TL1 teams, but they also spent an additional 45 minutes of practice counts and discussion using videotape of dolphins shot from survey area beaches.

Four observer teams (two TL1 and two TL2 teams) were stationed at each survey site. This design allowed comparison between teams of each training level at each survey site, and it also allowed potential paired comparisons of all four teams, conditional upon a finding of no significant difference between TL1 and TL2 teams. Teams participated in the survey for only two consecutive days in order to restrict learning over the course of the study. Up to four survey sites, each with four observer teams, were used per day, depending on the availability of volunteers. In a few cases, only two teams (of the same training level) were stationed at a survey site on a given day due to the availability of volunteers. Survey sites were spaced approximately every 4km along the Myrtle Beach coast. The design of four different survey sites, each with only four observer teams, ensured close proximity between paired observer teams and guarded against the possibility that no dolphins would pass through a given site during the survey. At each survey site, the four observer teams were spaced approximately 20m apart and observed from the same elevation with seven-power binoculars (sitting on the berm of the beach, with their eyes approximately 2-4m above sea level, depending on the tide). Visual barriers were erected between teams, and each team was instructed not to verbally communicate with the others. The maximum dolphin sightings distance was estimated by the principle investigators to be approximately 500m from shore, but varied with elevation and sea surface conditions.

The number of dolphins and their direction of travel along the coast were recorded in five-minute intervals. Dolphins were counted as they crossed the observers' line of sight from either direction. The observers' sighting focus was on an imaginary line perpendicular to the shore. Individuals that were observed to turn around and re-cross the line were not recounted. Observers also made written notes for each five-minute period with dolphins present, indicating any distinctive dorsal fins, obvious behaviours and the timing and distribution of groupings. Maximum, minimum and best estimates of the numbers of dolphins were tallied by the observers at fifteen-minute intervals. Only best estimate values were used in the analysis. Beaufort Sea State was determined by the principle investigators.

### **Estimation strategy**

The strategy for calculating correction factors for shore-based counts was based on the conceptual model of Buckland *et al.* (1993) in which the number of groups observed was multiplied by a correction factor to estimate the true number of groups, and this number in turn was multiplied by the mean group size to determine a revised estimate of the total individuals. In our model, all correction factors were stratified by group size, based on the assumption that the ability of observers to detect groups changes with group size. A confidence interval was generated around the revised abundance estimate based on the 95% confidence interval for the number of groups and a variability factor for the mean group size.

## Determination of the number of groups

Definition of 'group' and 'match'

Due to the rapidly changing composition of perceived dolphin subgroups within a dolphin 'group', it is essentially impossible to identify specific individuals sighted by different observer teams. Therefore, only sightings of dolphin groups were compared for matches between observer teams at each survey site. Similar studies with gray whales have also compared sightings of groups rather than individuals (Rugh et al., 1990; 1993; Buckland et al., 1993). Although gray whale groups are defined as travelling together within a half body length of one another (Rugh et al., 1990), bottlenose dolphin groups are typically defined more loosely as all dolphins within a 100m radius of one another (Wells et al., 1980; 1987; Barco et al., 1999). Thus, a dolphin 'group' was defined in this study as all dolphins sighted within the same, or an adjacent five-minute interval. Based on subjective observations during the survey, this was judged to be a reasonable time frame for milling or slowly travelling dolphins to pass before all four observer teams at each site (a distance along the beach of up to 60m or more, assuming some error in spacing by the observer teams). This definition may cause some separate groups to be incorrectly identified as a single group and thus provides a conservative estimate of the number of missed group sightings between observer teams. As an example of group definition, if three

different clusters of four dolphins were observed travelling past an observer team in each of three consecutive five-minute intervals, they would be counted as a single group of twelve, but if two clusters of four dolphins were separated by an empty five-minute interval, they would be counted as two groups of four. A 'match' between two observer teams at the same survey site occurred if both teams sighted dolphins within the same or adjacent five-minute intervals. In rare cases when overlapping groups were clumped in one observer team's record but split in the other's, judgement was used to classify a sighting as a match based on timing and the observer's written comments. The latter is consistent with match criteria from similar gray whale studies (Rugh *et al.*, 1990; 1993; Buckland *et al.*, 1993).

#### Determination of stratified group size categories

In order to compare matches between paired observer teams, observations were stratified by dolphin group size. For each observer team, X, the total number of group sightings of a given estimated group size was compared to the number of matched sightings by the paired observer team, Y. Note that the group size was defined by the estimate of team X, and a group match occurred if team Y sighted dolphins during the same time interval, even if the estimates of group size did not agree between observer teams.

For each dolphin group-size category, s, the mean percent of missed sightings for all paired observer teams,  $MS_s$ , was calculated using the formula:

$$MS_{\rm s} = \frac{\sum_{X=1}^{k} (1 - \frac{m_{y}}{(n_{x})_{s}})100}{k}$$
 (1)

where:

 $(n_x)_s$  is the number of groups of size category s reported by observer team X;

 $m_y$  is the number of these same groups sighted (matched) by a paired observer team Y; and

k is the total number of observer teams, X, that reported dolphin groups of size s.

Matches of dolphin groups between the two teams did not have to agree in their estimates of group size. The MS, for all group size categories (s = 1 dolphin, 2, 3, 4, ...) were plotted to visually identify natural size category groupings. The data were then pooled by these natural groupings (for example, s=1-2 dolphins, 3-4 dolphins, ...) and the  $MS_s$  was recalculated for the revised size categories. Differences between MS<sub>s</sub> for all revised group-size categories were tested for significant difference using ANOVA and the Newman-Keuls and Scheffe post-hoc tests (STATISTICA for Windows, 5.1 software). In order to verify the statistical significance of the subjectively determined group-size categories, the process was repeated for alternative scenarios of group-size categories. This comparison ensured that the total data was subdivided into the largest number of significantly different group-size categories possible. These categories were then considered separately for all subsequent analyses.

A correction factor to determine the true number of dolphin groups

The true number of groups passing before each survey site was determined by a technique similar to that used by Rugh *et al.* (1990) for gray whale surveys. For each group-size category, *s*, simultaneous counts by paired independent observer teams were used to estimate the true number of

groups using Bailey's (1951) modification of the Petersen mark-recapture estimate as recommended in Hammond (1986):

$$N_s = \frac{(n_x)_s[(n_y)_s + 1]}{(m_{yy})_s + 1}$$
 (2)

where:

 $N_s$  is the true number of dolphin groups of size s passing before each survey site;

 $(n_x)_s$  is the number of groups classified as category s counted by observer team X;

 $(n_y)_s$  is the number of groups classified as category s counted by observer team Y; and

 $(m_{xy})_s$  is the number of matches between the two teams for groups classified as category s.

Since the true group size is unknown, dolphin groups were classified as category s if either of the teams reported the group size to be within category s.

Each observer team's count,  $(n_x)_s$ , was expressed as a proportion of the estimated true number of groups,  $N_s$ . With up to four observer teams per survey site, each team, X, could be paired with up to three different observer teams, Y. However, in a few cases only two or three teams were at a site. To ensure that all observer teams were equally weighted, the proportion  $(n_x)_s/N_s$  was first averaged for all paired observer team combinations for each observer team, X. The mean proportions from each observer team were then averaged to generate an overall estimate of the proportion of the estimated true number of groups,  $PN_s$ , sighted by observer teams for each dolphin group-size category, s. These calculations are summarised by the formula:

$$PN_s = \frac{\sum_{x=1}^{j} \left\{ \left[ \sum_{Y=1}^{i} \frac{(n_x)_s}{N_s} \right] / i \right\}}{j}$$
 (3)

where:

*i* is the total number of observer teams, *Y*, paired with observer team *X* for concurrent surveys (in most cases, three); and

is the total number of observer teams in which the team (X) or their paired observer team (Y) reported dolphin groups of size s.

The standard error, SE, for  $PN_s$  was determined by a non-parametric bootstrapping technique.

By allowing s to encompass all group sizes, the same formulae were used to calculate PN for the entire dataset (unstratified by group size). In order to assess the effect of training level, separate PN values were also calculated for TL1 and TL2 observer teams and were compared using an independent t-test. These comparisons were not stratified by group size due to the decreased sample size of observer team combinations. Separate PN values were also calculated for groups with milling dolphins (moving back and forth) and for groups with unidirectionally travelling dolphins, and these values were compared using an independent t-test. This was based on the assumption that milling dolphins might be more easily seen by observers, since they are within visual range for a longer period.

# Determination of mean group size

The mean group size, or number of dolphins per group, is easily calculated from the observer records, but the determination of a confidence interval around the mean is

less straightforward. Mark-recapture statistics cannot be used to estimate the true number of dolphins per group, because it is not possible to match sightings of individual dolphins within a group between paired observer teams. One possible method to account for errors in group size estimates would be to use the observers' maximum and minimum estimates to generate a range. This technique assumes that the true number of dolphins per group falls somewhere within this range. In this study, however, we observed a number of matched groups in which the maximum to minimum ranges estimated by paired observer teams did not overlap. This may be due to frequent splitting and merging of groups or to unsynchronised surfacing patterns by individuals within a group. Merely using the maximum and minimum estimates to define a range does not take advantage of the comparison between paired observer

Therefore, we developed a conservative estimate of the error in group size estimation based on the mean percent difference (as a percent of the larger estimate) between the group size estimates for matches between paired observer teams, X and Y. Consistent with the analysis of missed groups, these estimates were stratified by group-size category, s, as defined by the reported group size for each observer team. For each dolphin group-size category s, the mean percent difference between paired observer teams,  $D_s$ , was determined using the formula:

$$D_{s} = \frac{\sum_{x=1}^{k} \left\{ \left[ \sum_{m=1}^{n} \left( \frac{\left| g_{x} - g_{y} \right|}{g'} \right) 100 \right] / n \right\}}{k}$$
(4)

where:

 $g_x$  and  $g_y$  are the group sizes estimated by observer teams X and Y, respectively, for matched groups between the two teams;

g' is the larger of  $g_x$  or  $g_y$ ;

n is the number of matches, m, between teams X and Y in which team X reported a group size of s; and

k is the total number of observer teams, X, that reported dolphin groups of size s.

The maximum, and therefore most conservative, estimate for the mean percent difference between teams was calculated as  $D_s + 2$  SE<sub>Ds</sub> (the upper range of the 95% confidence interval). SE was determined by the standard statistical formula.

## Testing the estimation model

Using the correction factors and confidence intervals generated in this study, a model was constructed to revise estimates from general shore-based surveys that do not use paired observer teams. The surveys, of course, must follow the same methodology under similar conditions in order to be comparable.

A revised estimate,  $\hat{E}_{NGs}$ , of the number of groups of size s for any shore-based survey can be calculated using the formula:

$$\hat{E}_{NGs} = \frac{NG_s}{PN_s} \tag{5}$$

where  $NG_s$  is the observed number of groups of size category s. We have defined  $\hat{E}_{NGsU}$  and  $\hat{E}_{NGsL}$  as the upper and lower boundaries of the 95% confidence interval  $\hat{E}_{NGs} \pm 2SE_{\hat{E}_{NGs}}$ .

Since the  $PN_s$  term is a correction factor with an associated variance, the standard error for  $\hat{E}_{NGs}$  is estimated by the Delta method (Casella and Berger, 1990) in which:

$$SE_{\hat{E}_{NGs}} = NG_s (\frac{1}{PN_s})^2 SE_{PN_s}$$
 (6)

Using a variability factor of  $\pm$  the percent difference between observers for group size, defined as  $(D_s + 2 \text{SE}_{Ds})/100$ , we have constructed a conservative confidence interval,  $\hat{E}_{GSs}$ , around the mean group size for each group-size category s, using the formula:

$$\hat{E}_{GSs} = GS_s \left[ 1 \pm (\frac{D_s + 2SE_{Ds}}{100}) \right]$$
 (7)

where  $GS_s$  is the mean group size for all observed groups of size category s. We have defined  $\hat{E}_{GSsU}$  and  $\hat{E}_{GSsL}$  as the upper and lower boundaries of this interval.

The revised estimate,  $\hat{E}$ , of the total dolphins present is simply the sum, for each group-size category, of the revised estimate for the number of dolphin groups ( $\hat{E}_{NGs}$ ) times the mean group size ( $GS_s$ ):

$$\hat{E} = \sum_{s=1}^{t} (\hat{E}_{NGs} \cdot GS_s)$$
 (8)

where t is the total number of group-size categories, s. To determine the boundaries of a confidence interval around  $\hat{E}$ , we replaced  $\hat{E}_{NGs}$  and  $GS_s$  in the equation with  $\hat{E}_{NGsU}$  and  $\hat{E}_{GSsU}$  for the upper boundary and  $\hat{E}_{NGsL}$  and  $\hat{E}_{GSsL}$  for the lower boundary. Thus, the interval around  $\hat{E}$  is a conservative approximation based upon the 95% confidence interval for the number of groups and a variability factor for the mean group size. This interval is more conservative than the 95% confidence intervals calculated for corrected gray whale abundance which do not account for discrepancies in estimated group size between paired observers (Rugh et al., 1990).

The model was applied to data from two previous South Carolina shore-based surveys conducted by the principle investigators on 9 July 1994 and 1 July 1995. A revised estimate,  $\hat{E}$ , was generated for each, along with the confidence interval. Each survey utilised 30 observer teams spaced approximately every 3.2km between Little River Inlet and Winyah Bay, South Carolina (a distance of approximately 93km). The count was from 0900-1200 hours, and used identical methods to those described in this paper. Only data from the hour with the highest total estimate were used for analysis. This was based on the assumption that travelling dolphins might be counted at more than one site if more than one hour was used and that longer time intervals increase the possibility that dolphins might turn around beyond the sight of observers and be counted twice.

## **RESULTS**

A total of 19 TL1 and 22 TL2 observer teams were trained and participated in the count for a total of 168 observer team hours. However, dolphins were not observed on all days at all sites and only 32 observer teams were involved in surveys in which dolphins were sighted. The total comparison hours for all combinations of paired observer teams at sites where dolphins were present was 118 hours. This is comparable to the gray whale double counts by Rugh *et al.* (1990) in which 120 observer hours yielded 60 comparison hours between two observer groups.

Comparing the total data for only TL1 team and TL2 team comparisons, unstratified by group size, PN was 0.700 for TL1 teams (n=14) and 0.762 for TL2 teams (n=16). In other words, TL1 teams missed an average of 30.0% of the dolphin groups passing their station and TL2 teams missed an average of 23.8% of the groups. This difference was not significant, based on an independent t-test (p = 0.48). The two groups were further compared by calculating the percent difference between the total hourly estimates of the paired TL1 teams and the paired TL2 teams at each site, as a percentage of the larger estimate for each pair. Intervals in which only one of the two observer teams sighted dolphins were not included in this analysis. The mean percent differences were then compared between TL1 and TL2 teams using a dependent t-test. If minimal additional training improved observer accuracy, a lower percent difference would be expected between TL2 teams as they converge on the true number of dolphins. However, the average percent difference was high for both groups, 37% for TL1 teams (n=20) and 39% for TL2 teams (n=17) and did not differ significantly between training levels (dependent t-test, p = 0.69). Based on these analyses, no difference was assumed between TL1 and TL2 observer teams. Therefore each observer team was compared to the three other concurrent teams from their survey site in subsequent analyses, yielding 39 paired observer team combinations in which dolphins were sighted during their surveys.

After pooling the data from all observer team comparisons, matches were stratified by dolphin group size. The mean group size estimate was 6.16, with a median size of 3. Only four groups were estimated to be larger than 20 individuals, including the largest group which was estimated to contain from 54 to 89 dolphins, depending on observer team. The mean percent of missed sightings, MS<sub>s</sub> was first calculated for narrow group-size categories (s = 1 dolphin, 2, 3, 4, ...), and the results were plotted in an attempt to identify natural groupings (Fig. 1). Based on this figure, three potential natural size category groupings were identified: 1-2, 3-4 and >4. The  $MS_s$  was then recalculated for each of these three size categories, yielding percentages of 51.1, 27.1 and 8.2 for the size categories 1-2, 3-4 and >4, respectively. In other words, only about half of the small (1-2) dolphin groups were seen by both pairs of observer teams, while over 90% of the large (>4) groups were seen by both teams. An ANOVA of the MSs for the three categories identified a significant difference (p < 0.001), and a Newman-Keuls test indicated that all three categories were significantly different from one another (Table 1). The more conservative Scheffe test, however, found the 3-4 size category did not significantly differ from the >4 category, although the p value of 0.100 suggests a non-trivial difference in detectability. (Table 1). These three size categories were the only combination of group sizes that yielded three significantly different categories by either statistical test. Therefore, groupings of 1-2, 3-4 and >4 were identified as the three group-size categories, s, used for all subsequent analyses.

Although the complete data are not included, an example of the procedure for calculating  $PN_s$  is shown in Table 2 for group size 1-2. The mean  $PN_s$  and 95% confidence interval for each group size-category are presented in Table 3. The mean proportion of groups missed by observers (equal to 1- $PN_s$ ) was negatively correlated with group size: 0.327 (32.7%) for groups of 1-2 dolphins; 0.165 for groups of 3-4 dolphins; and 0.099 for groups of > 4 dolphins. The overall PN for all observations, unstratified by group size, was 0.741.

Milling groups made up 23.4% of all observed groups (as compared to 33.1% travelling unidirectionally, northeast along the coast and 43.5% travelling unidirectionally, southwest along the coast). A separate PN was calculated for all groups with milling dolphins and for all groups with unidirectionally swimming, or non-milling, dolphins. PN was significantly higher for milling dolphins (0.892 versus 0.725 for non-milling dolphins, p = 0.015, dependent t-test, n=24) suggesting an improved sightings frequency for milling dolphins. This is misleading, however, because most of the milling groups were in the >4 group-size category, which had a similar PN, of 0.902. As milling is generally associated with group feeding or social behaviour, the percent sightings with milling dolphins increases dramatically with group size, with 62.1% of the observed milling groups in the >4 category. Milling dolphins were observed in 5.1% of the sightings in the 1-2 group-size category, in 20.0% of the 3-4 category sightings, and in 39.1% of the >4 category sightings. Enough milling groups were present in the >4 category to compare the mean percent difference (as a percent of the larger estimate) in group size estimates between paired observers for all milling and non-milling groups. As in other calculations, observer team averages were computed first in order to weight all teams equally. If missed sightings were more common among non-milling dolphins, a higher percent difference would be expected for non-milling dolphins. The mean percent difference was 40.6% for groups with milling

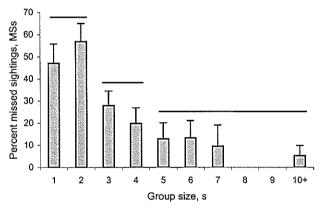


Fig. 1. Mean percentage of missed group sightings,  $MS_s$ , between paired independent observer teams, stratified by narrow categories of dolphin group size. Error bars represent 1 SE. Means are based on a sample size of 21, 19, 19, 13, 11, 9, 7, 3, 4 and 22 for group sizes of 1, 2, 3, 4, 5, 6, 7, 8, 9 and 10+, respectively. The absence of missed sightings for group sizes 8 and 9 is likely a function of the small sample size. Potential natural groupings (indicated by the overlying horizontal lines) were identified from this figure for further statistical analysis (see Table 1).

#### Table 1

Significance values for the statistical difference between percent missed sightings,  $MS_s$ , for comparisons between all dolphin group size categories (s = 1-2, 3-4 and >4). All comparisons are significantly different by the Newman-Keuls test, but the more conservative Scheffe test found one (\*) non-significant comparison. The sample size is respectively 29, 22 and 24 observer teams for each of the group size categories.

Group size comparison	Newman-Keuls significance level	Scheffe significance level	
(1 - 2) vs (3 - 4)	0.006	0.019	
(1 - 2) vs (>4)	< 0.001	< 0.001	
(3 - 4) vs (>4)	0.027	0.100*	

#### Table 2

Sample calculations for determining  $PN_s$ , using data from the s=3-4 group size category, modified from the example of Rugh  $et\ al.$  (1990). The letters A through L are arbitrary designations defining separate observer teams. The variables and calculations are described in the text. For all combinations of paired observer teams, the Petersen estimate,  $N_s$ , of the true number of groups was calculated, and the group count of team X was expressed as a proportion of  $N_s$ . In order to weight all teams equally, these values were averaged for all observer team combinations for each team X prior to the final calculation of  $PN_s$ . This table shows the calculation of only six of the 25 observer team averages used to calculate a  $PN_s$  of 0.835 for the group size 3-4. Average of mean proportion counted for each observer team X is  $PN_s$ .

Observer team X	Group count $(n_x)_s$	Observer team Y	Group count $(n_y)_s$	Matches (m <sub>xy</sub> ) <sub>s</sub>	Missed $(N_s - (n_x)_s)$	Total estimate <i>N</i> s	Proportion of groups counted $((n_x)_s/N_s)$	Mean proportion counted for each observer team X
Α	7	В	6	5	1.2	8.2	0.857	
Α	5	G	4	4	0.0	5.0	1.000	
Α	4	H	2	0	8.0	12.0	0.333	
A Average								0.730
В	6	Α	7	5	2.0	8.0	0.750	
В	4	G	6	4	1.6	5.6	0.714	
В	3	H	2	ı	1.5	4.5	0.667	
B Average								0.710
C	3	D	4	3	0.8	3.8	0.800	
С	3	I	4	3	0.8	3.8	0.800	
С	3	J	4	3	0.8	3.8	0.800	
C Average								0.800
D	4	C	3	3	0.0	4.0	1.000	
D	4	I	4	4	0.0	4.0	1.000	
D	3	J	2	2	0.0	3.0	1.000	
D Average								1.000
E	2	F	2	2	0.0	2.0	1,000	
E	2	K.	3	2	0.7	2.7	0.750	
E	1	L	2	1	0.5	1.5	0.667	
E Average								0.806
F	2	Е	2	2	0.0	2.0	1.000	
F	2	K	2	2	0.0	2.0	1.000	
F	1	L	2	1	0.5	1.5	0.667	
F Average							•	0.889
etc							***	***

Table 3

Mean  $PN_s \pm$  two standard errors (95% confidence interval), stratified by group size category, s.  $PN_s$  is the estimated proportion of the true number of dolphin groups actually seen by the observer teams. The sample size, n, reflects the number of observer teams reporting groups of size s.

Group size, s	Sample size, n	$PN_s$	SE	
1-2	32	0.673	0.035	
3-4	25	0.835	0.041	
>4	>4 30		0.034	

Table 4

The mean percent difference,  $D_s$ , between paired observer teams for the estimated number of dolphins per group, stratified by group size category, s. The maximum range of the 95% confidence interval is  $D_s + 2$  standard errors.

Group size	Sample size n	$D_s$	$2SE_{Ds}$	Maximum range of 95% C I $(D_s + 2SE_{Ds})$
1-2	23	28.2	7.5	35.7
3-4	21	29.0	6.1	35.1
>4	24	33.4	5.7	39.1

dolphins (n = 22 observer teams) and 39.6% for groups with non-milling dolphins (n = 14 observer teams). The number of observer teams in which milling and non-milling values could be compared was too small for a dependent t test, but the mean percent differences do not indicate a difference between the two groups. Thus, the greater PN for milling groups was apparently due primarily to an association between milling behaviour and the >4 group size category, and no correction factor was generated based on dolphin swimming direction.

Sea state is also likely to effect observer estimates. In this study, all survey days in which dolphins were sighted had mostly sunny skies and a Beaufort Sea State of 1-2, usually increasing from 1-2 over the course of the survey. This lack of variability in conditions effecting visibility prevented any statistical analysis of sea states. However, two of the eight survey days had sea states of level 4-5, and no dolphins were observed at any sites on either day, indicating an obvious upper limit for effective shore-based counts.

Table 4 shows the mean percent difference for estimated group size,  $D_s$ , for each group-size category, s. The mean plus two standard errors yields the maximum 95% confidence interval range. The  $D_s$  values ranged from 28.2% for group sizes of 1-2 to 33.4% for group sizes >4, with no significant difference between group sizes (ANOVA, p=0.457). Nonetheless, the specific  $D_s$  values for each group-size category were included in the estimation model, since group sizes were already treated separately when determining the number of groups.

Data from the 1994 and 1995 shore-based dolphin surveys were reanalysed, and revised estimates,  $\hat{E}$ , were calculated (Table 5). The original 1994 survey total of 153 dolphins was revised to 174 with an estimated confidence interval from 107-241. The 1995 survey estimate increased from 73-87 with a confidence interval from 54-120. These changes in 1994 and 1995 abundance estimates represent an increase by a factor of 1.14 and 1.19, respectively.

Table 5

Calculation of revised abundance estimates,  $\hat{E}$ , for 1994 and 1995 shore-based dolphin surveys. The number of observed groups for each size category,  $NG_s$ , and the mean reported group size for each size category,  $GS_s$ , were obtained from the original survey data. The revised estimate of the number of groups,  $\hat{E}_{NG_s}$ , its associated SE, and the variability factor for the mean group size,  $(D_s + 2SE_{D_s})/100$ , are from this study. The original uncorrected survey counts were 153 in 1994 and 73 in 1995. The revised estimates,  $\hat{E}$ , represent a positive correction factor of 1.14 and 1.19, respectively.

Group size category s	Number of groups NG <sub>s</sub>	$ ilde{E}_{NGs}$	SE of $\vec{E}_{NGs}$	Mean group size GS <sub>s</sub>	$\frac{D_s + 2SE_{Ds}}{100}$	Revised estimate $\hat{E}_s$	Upper and lower boundaries of interval around $\hat{E}_s$
1994 Survey							
1 to 2	5	7.43	0.382	1.60	0.357	11.9	7.6 - 16.1
3 to 4	4	4.79	0.236	3.50	0.351	16.8	10.9 - 22.7
>4	8	8.87	0.337	16.38	0.391	145.3	88.5 - 202.1
Total $(\hat{E})$						174.0	107.0 - 240.9
1995 Survey							
1 to 2	9	13.37	0.688	1.56	0.357	20.9	13.4 - 28.3
3 to 4	2	2.40	0.118	4.00	0.351	9.6	6.2 - 12.9
>4	4	4.43	0.168	12.75	0.391	56.5	34.4 - 78.6
Total ( $\hat{E}$ )						87.0	54.0 - 119.8

# DISCUSSION

The difference between the uncorrected totals and the revised estimates for the 1994 and 1995 South Carolina surveys was comparable to Rugh et al.'s (1993) correction factor for gray whales, in which the original totals were revised upward by a factor of 1.26. However, the range for the confidence interval, as a proportion of the population estimate,  $\hat{E}$ , was  $\pm 38\%$  in this study. This is approximately four times the magnitude of the 95% confidence intervals calculated by Buckland et al. (1993) for gray whale estimates from shore-based surveys. The larger confidence intervals from our model are a function of  $D_s$  and the variability factor for error in estimating group size. This error is reported but largely ignored in large whale studies comparing independent observers. Buckland et al. (1993) introduced a size-stratified correction factor for group size estimates based on comparisons with aerial surveys, but this correction did not include any measure of the discrepancy between the paired independent shore-based observers. Rugh et al. (1990) reported that 32% of the inter-observer count discrepancies were due to errors in estimating group size (as opposed to missed groups), however their model generated a correction factor for the number of groups missed and did not address group size estimates. Their average group size was two whales, as compared to an average group size of six dolphins in this study. The only marine mammal survey we are aware of in which the group size error is truly negligible is Estes and Jameson's (1988) double count shore-based survey of sea otters.

Corrections for errors in estimating group size between paired observers have been avoided in large whale studies for several reasons. It is impractical for paired observers to match individual whales or dolphins within a group, and therefore, mark-recapture statistics cannot be used to estimate the true number of individuals. Whales are visible to observers for a longer time period than dolphins when surfacing, the mean group size is smaller, and individuals in the group are, by definition, within half a body length of each other. Therefore, observer estimates of group size are more likely to be correct for whales, and in the absence of an estimate for the true number of individuals, these estimates are assumed to be correct in the models.

In tandem aerial surveys off California, Carretta et al. (1998) were unique in their ability to identify individual

bottlenose dolphins and subgroups within groups and were thus able to calculate a corrected estimate and variance for mean group size. These estimates were of widely dispersed groups, reducing the confusion created by splitting and merging adjacent groups. Group size estimates from aerial surveys are likely to be better than those from shore-based surveys, because the lateral spacing of dolphins within a group is more apparent from above, especially in low turbidity waters, and observers are able to circle and follow a group until satisfied with their count. We argue that the true number of dolphins in our study cannot be estimated from the shore-based survey data, and it is unlikely to be determined using any method. The high turbidity of coastal waters in the southeast US reduces the efficiency of near-shore aerial surveys, and although photo-ID of dorsal fins from small boats is effective, even this method may not define a single true number of individuals in large groups. It is possible to determine a variance for mean group size by bootstrapping the double count group size data, but this assumes that the observed mean group size approximates the true mean group size. Given the large percent differences between observer team estimates, we reject this assumption and suggest that the group size estimate is the largest source of error in shore-based dolphin surveys and is more significant than in shore-based surveys of large whales. Therefore, we have used the mean group size ± the mean percent difference between observer teams to account for errors in group size estimation. In the absence of an estimate for the true group size, we believe this is the best estimate upon which to base a conservative confidence interval.

Unlike group size, the overall correction for missed groups is comparable between this study and the shore-based surveys for large whales. The PN for all group sizes was 0.741, indicating that 26% of the dolphin groups were missed. Estimated missed sightings rates of 21% and 19% have been calculated for shore-based gray whale surveys in California (Rugh et al., 1990) and Alaska (Rugh, 1984); and Krogman et al. (1989) estimated 30% of the groups were missed in ice-based surveys of bowhead whales. The low observer elevations of the latter are more comparable to this study, although their paired observers were more widely spaced. The 26% missed sightings rate from this study is less than half that of published mark-recapture aerial surveys of bottlenose dolphins, which range from 69% for all groups (Cockcroft et al., 1992) to 53% for groups less than 10

individuals (Carretta *et al.*, 1998). Thus, shore-based surveys are less likely to miss groups within the survey area.

The similarity between observer sightings efficiency in this study and the whale studies is somewhat surprising. since the whale studies used experienced observers. However, the group sightings efficiency in this study may be exaggerated based on our definition of a match. The assumption that dolphin groups were a match if sighted by two observer teams within the same or an adjacent five-minute interval was necessary for analysis, but it was not ideal and almost certainly underestimated the number of missed groups. The similarities between observers' notes indicated several examples in which likely true matches for slow moving groups were separated by a full five minutes or more, but most matches were not as obvious. If at least some of the groups were moving at published travelling speeds of 5-6 km/hr for bottlenose dolphins in the southeast US (Shane, 1990), sightings could represent different groups (greater than 100m apart) if separated by as little as one minute. This error can be substantially improved, however, by clarifying the definition of a match using precise records of sightings time and location.

Although not demonstrated in this study, group size is likely to be overestimated for milling groups, because some individuals may be double counted. Since the proportion of milling groups increases with group size, this trend is impossible to identify without a measure of the true number of individuals per group. Since our model is stratified by group size, this potential error may be accounted for in the larger percent difference for the >4 group size category.

In our experience, sighting efficiency for shore-based dolphin surveys at or near sea level is strongly affected by Beaufort Sea States of three or more. Dolphin sightings went to zero in this study for sea states of 4-5. A much longer, similar study could potentially generate correction factors for a sea state of three. In our experience, however, once waves and chop begin to approximate the size of dorsal fins, sightings become much more difficult, and an upper sea state limit of two may be a reasonable requirement for a valid survey when observers are at or near sea level.

Estimates and confidence intervals can be potentially improved in several ways. This study was designed to correct for observer variability between inexperienced observers, based on the assumption that large scale shore-based dolphin counts can require hundreds of volunteers at a time and the expectation of experienced observers is often unrealistic. The population estimate from such a survey generates a wide confidence interval, and minor changes in the training procedure had no effect in this study. Therefore, extremely large-scale shore-based dolphin surveys are unlikely to improve the reliability of their estimates. However, such surveys can be quite effective for obtaining minimum population estimates over a large area and for identifying large population changes, such as those associated with migration or a significant die-off event. For localised habitat utilisation studies, discrepancies between paired observers can be decreased by using a smaller number of more experienced volunteers. Since smaller counts are more easily coordinated, they are more likely to be able to track local habitat usage patterns with frequent regular surveys. Experienced observers who conduct regular surveys can then be used in a paired independent observer study, such as this one. Greater agreement is likely to occur between experienced observers, thereby generating a smaller confidence interval for abundance estimates.

Stationing observers at a higher elevation above sea level can also substantially improve estimates, although all teams must be at comparable elevations if correction factors are to be applied to group data. Along developed coastlines, observers may be able to utilise beachfront buildings as elevated survey sites for substantial stretches of the coast. Elevated observers can see further offshore and can calculate distances to groups and between groups by measuring the sightings angle and compass bearing. This may enable a clearer definition of a match between paired observers for groups of dolphins, which would result in a more accurate estimate of the number of missed groups as well as improved estimates for group size. The wider field of view and ability to estimate distance would also enable observers to estimate dolphin swimming speeds (essential for avoiding double counts by an adjacent survey site at a later time) and to identify backtracking dolphins to avoid double

For population estimates (versus habitat utilisation studies), shore-based surveys are most useful when all animals occur within a narrow coastal strip, or they must at least be accompanied by some estimate of the proportion of the population that is within visual range of the coastline. In South Carolina, this has not been clearly established for bottlenose dolphins. Although an inshore stock and an offshore stock have been identified by both genetic (Curry and Smith, 1997; Hoelzel et al., 1998) and morphometric studies (Hersh and Duffield, 1990; Mead and Potter, 1994), no clear distinction has been determined in the distribution of dolphins across the continental shelf, with both stocks possibly intermixing to an unknown degree (Barco et al., 1999; Blaylock and Hoggard, 1994; Wang et al., 1994). North of Cape Hatteras, however, the distribution of the two stocks clearly diverges, with the inshore stock largely restricted to shallow coastal waters (Kenney, 1990). This distribution, therefore, is more suitable for the shore-based dolphin surveys regularly conducted in Virginia.

The effectiveness of shore-based dolphin surveys is largely dependent upon the behaviour and distribution of the species and the physical characteristics of the coastline. Under the proper conditions, shore-based surveys are potentially more efficient than boat or aerial surveys for near-shore populations of whales and dolphins. Cetaceans are likely to surface more times within range of shore-based observers as compared to observers on a moving platform and are therefore more likely to be seen. Although shore-based surveys are time and labour intensive, they are inexpensive and technologically simple and are thus accessible to essentially all researchers in all countries. They also employ numerous volunteers, and are therefore effective public awareness and educational tools. The technique developed in this study can be repeated to provide a site-specific corrected estimate and confidence interval for shore-based dolphin surveys in other areas. The correction factors can then be used for subsequent surveys, assuming similar conditions and observer abilities. It is applicable where species are going in both directions along the coast and short duration counts must be carried out using multiple observation sites to reduce double counting. It is most effective using experienced observers at observation posts well above sea level. Shore-based surveys of migrating cetaceans moving in one consistent direction along the coastline, however, are best conducted from a single survey site with paired independent observers (Buckland et al., 1993; Rugh et al., 1990; 1993).

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#### REFERENCES

- Bailey, N.T.J. 1951. On estimating the size of mobile populations from capture-recapture data. *Biometrika* 38:293-306.
- Barco, S.G., Swingle, W.M., McLellan, W.A., Harris, R.N. and Pabst, D.A. 1999. Local abundance and distribution of bottlenose dolphins (*Tursiops truncatus*) in the nearshore waters of Virginia Beach, Virginia. Mar. Manmal Sci. 15(2):394-408.
- Bayliss, P. 1986. Factors affecting aerial surveys of marine fauna, and their relationship to a census of dugongs in the coastal waters of northern Australia. Aust. Wildl. Res. 13:27-37.
- Blaylock, R.A. and Hoggard, W. 1994. Preliminary estimates of bottlenose dolphin abundance in southern US Atlantic and Gulf of Mexico continental shelf waters. NOAA Tech. Mem. NMFS-SEFSC-356:10pp.
- Buckland, S.T., Breiwick, J.M., Cattanach, K.L. and Laake, J.L. 1993.
  Estimated population size of the California gray whale. *Mar. Mammal Sci.* 9(3):235-49.
- Carretta, J.V., Forney, K.A. and Laake, J.L. 1998. Abundance of southern California coastal bottlenose dolphins estimated from tandem aerial surveys. *Mar. Mammal Sci.* 14(4):655-75.
- Casella, G. and Berger, R.L. 1990. Statistical Inference. Wadsworth and Brooks/Cole, Pacific Grove, CA. 650pp.
- Caughley, G. and Grice, D. 1982. A correction factor for counting emus from the air, and its application to counts in western Australia. Aust. Wildl. Res. 9:253-9.
- Cockcroft, V.G., Ross, G.J.B., Peddemors, V.M. and Borchers, D. 1992. Estimates of density and undercounting of bottlenose dolphins off northern Natal, South Africa. S. Afr. J. Wildl. Res. 22:102-9.
- Curry, B.E. and Smith, J. 1997. Phylogeographic structure of the bottlenose dolphin (*Tursiops truncatus*): stock identification and implications for management. pp. 227-47. *In:* A.E. Dizon, S.J. Chivers and W.F. Perrin (eds.) *Molecular Genetics of Marine Mammals*. The Society for Marine Mammalogy, Lawrence, KS.
- Estes, J.A. and Jameson, R.J. 1988. A double-survey estimate for sighting probability of sea otters in California. J. Wildl. Manage. 52:70-6.
- Graham, A. and Bell, R. 1989. Investigating observer bias in aerial survey by simultaneous double-counts. *J. Wildl. Manage*. 53(4):1009-16.
- Grier, J.W., Gerrard, J.M., Hamilton, G.D. and Gray, P.A. 1981. Aerial visibility bias and survey techniques for nesting bald eagles in northwestern Ontario. J. Wildl. Manage. 45:83-92.
- Hammond, P.S. 1986. Line transect sampling of dolphin populations. pp. 251-79. In: M.M. Bryden and R. Harrison (eds.) Research on Dolphins. Clarendon Press, Oxford. 478pp.

- Hammond, P.S. and Thompson, P.M. 1991. Minimum estimate of the number of bottlenose dolphins (*Tursiops truncatus*) in the Moray Firth. *Biol. Conserv.* 56(1):79-88.
- Hansen, L.J. 1990. California coastal bottlenose dolphins. pp. 403-20. In: S. Leatherwood and R.R. Reeves (eds.) The Bottlenose Dolphin. 1st. Edn. Academic Press, San Diego, California, xvii+653pp.
- Hanson, M.T. and Defran, R.H. 1993. The behavior and feeding ecology of the Pacific coast bottlenose dolphin, *Tursiops truncatus*. *Aquat. Mamm.* 19(3):127-42.
- Hersh, S.L. and Duffield, D.A. 1990. Distinction between northwest Atlantic offshore and coastal bottlenose dolphins based on hemoglobin profile and morphometry. pp. 129-39. *In:* S. Leatherwood and R.R. Reeves (eds.) *The Bottlenose Dolphin*. Academic Press, San Diego. 653pp.
- Hoelzel, A.R., Potter, C.W. and Best, P.B. 1998. Genetic differentiation between parapatric 'nearshore' and 'offshore' populations of the bottlenose dolphin, *Proc. R. Soc. Lond. Ser. B.* 265(1402):1177-83.
- International Whaling Commission. 1993. Report of the Special Meeting of the Scientific Committee on the Assessment of Gray Whales, Seattle, 23-27 April 1990. Rep. int. Whal. Commn 43: 241-59.
- Kenney, R.D. 1990. Bottlenose dolphins off the northeastern United States. pp. 369-86. *In:* S. Leatherwood and R.R. Reeves (eds.) *The Bottlenose Dolphin*. Academic Press, San Diego. 653pp.
- Krogman, B., Rugh, D., Sonntag, R., Zeh, J. and Ko, D. 1989. Ice-based census of bowhead whales migrating past Point Barrow, Alaska, 1978-1983. Mar. Manmal Sci. 5(2):116-38.
- Leatherwood, S. 1979. Aerial survey of the bottlenose dolphin *Tursiops truncatus* and the West Indian Manatee, *Trichechus manatus*, in the Indian and Banana Rivers, Florida, *Fish. Bull.* 77:47-59.
- Marsh, H. and Sinclair, D.F. 1989. Correcting for visibility bias in strip transect aerial surveys for aquatic fauna. *J. Wildl. Manage*. 53:1017-24.
- Mead, J.F. and Potter, C.W. 1994. Recognizing two populations of the bottlenose dolphin (*Turnsiops truncatus*) off the Atlantic coast of North America: morphologic and ecologic considerations. pp. 20-3. *In:* K.R. Wang, P.M. Payne and B.G. Thayer (eds.) Coastal stocks of Atlantic bottlenose dolphin: status review and management. NOAA Tech Mem. NMFS-OPR-4. 121pp.
- Rugh, D.J. 1984. Census of gray whales at Unimak Pass, Alaska, November-December 1977-1979. pp. 225-48. *In:* M.L. Jones, S.L. Swartz and S. Leatherwood (eds.) *The Gray Whale*, Eschrichtius robustus. Academic Press, Inc., Orlando, Florida, xxiv+600pp.
- Rugh, D.J., Ferrero, R.C. and Dahlheim, M.E. 1990. Inter-observer count discrepancies in a shore-based census of gray whales (Eschrichtius robustus). Mar. Mammal Sci. 6(2):109-20.
- Rugh, D.J., Breiwick, J.M., Dahlheim, M.E. and Boucher, G.C. 1993.
  A comparison of independent, concurrent sighting records from a shore-based count of gray whales. Wildl. Soc. Bull. 21(4):427-37.
- Shane, S.H. 1990. Behavior and ecology of the bottlenose dolphin at Sanibel Island, Florida. pp. 245-66. In: S. Leatherwood and R.R. Reeves (eds.) The Bottlenose Dolphin. Academic Press, San Diego. 653pp.
- Wang, K.R., Payne, P.M. and Thayer, B.G. 1994. Coastal stocks of Atlantic bottlenose dolphin: status review and management. NOAA Tech Mem, NMFS-OPR-4. 121pp.
- Wells, R.S., Irvine, A.B. and Scott, M.D. 1980. The social ecology of inshore odontocetes. pp. 263-317. *In:* L.M. Herman (ed.) *Cetacean Behaviour: Mechanisms and Functions*. John Wiley & Sons, New York. xiii+463pp.
- Wells, R.S., Scott, M.D. and Irvine, A.B. 1987. The social structure of free-ranging bottlenose dolphins. pp. 247-306. *In:* H. Genoways (ed.) Vol. 1. *Current Mammalogy*. Plenum Press, New York. 519pp.
- Wells, R.S., Hansen, L.J., Baldridge, A.B., Dohl, T.P., Kelly, D.L. and Defran, R.H. 1990. Northward extension of the ranges of bottlenose dolphins along the California coast. pp. 421-31. *In:* S. Leatherwood and R. Reeves (eds.) *The Bottlenose Dolphin*. Academic Press, San Diego, California. 653pp.
- Wilson, B., Thompson, P.M. and Hammond, P.S. 1997. Habitat use by bottlenose dolphins: seasonal distribution and stratified movement patterns in the Moray Firth, Scotland. J. Appl. Ecol. 34:1365-74.