MARINE MAMMAL SCIENCE, 22(3): 527–547 (July 2006)
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DOI: 10.1111/j.1748-7692.2006.00041.x

ABUNDANCE OF IRRAWADDY DOLPHINS (*ORCAELLA BREVIROSTRIS*) AND GANGES RIVER DOLPHINS (*PLATANISTA GANGETICA GANGETICA*) ESTIMATED USING CONCURRENT COUNTS MADE BY INDEPENDENT TEAMS IN WATERWAYS OF THE SUNDARBANS MANGROVE FOREST IN BANGLADESH

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ABSTRACT

Independent observer teams made concurrent counts of Irrawaddy dolphins *Orcaella brevirostris* and Ganges River dolphins *Platanista gangetica gangetica* in mangrove channels of the Sundarbans Delta in Bangladesh. These counts were corrected for

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missed groups using mark-recapture models. For Irrawaddy dolphins, a stratified Lincoln-Petersen model, which incorporated group size and sighting conditions as covariates, and a Huggins conditional likelihood model, which averaged models that individually incorporated group size, sighting conditions, and channel width as covariates, generated abundance estimates of 397 individuals (CV = 10.2%) and 451 individuals (CV = 9.6%), respectively. For Ganges River dolphins, a stratified Lincoln-Petersen model, which incorporated group size as a covariate, and a Huggins conditional likelihood model, which averaged the same models described above, generated abundance estimates of 196 individuals (CV = 12.7%) and 225 individuals (CV = 12.6%), respectively. Although the estimates for both models were relatively close, the analytical advantages of the Huggins models probably outweigh those of the Lincoln-Petersen models. However, the latter should be considered appropriate when simplicity is a priority. This study found that waterways of the Sundarbans support significant numbers of Irrawaddy and Ganges River dolphins, especially compared to other areas where the species have been surveyed.

Key words: Irrawaddy dolphins, *Orcaella brevirostris*, Ganges River dolphins, *Platanista gangetica*, abundance estimation, Chapman's modified Lincoln-Petersen mark-recapture estimator, Huggins conditional likelihood model, correction factors, independent concurrent counts, Sundarbans, mangroves, Bangladesh.

Freshwater dolphins in Asia are among the world's most endangered mammals and there is an urgent need to establish conservation priorities based on scientifically credible abundance estimates (Perrin and Brownell 1989, Smith and Reeves 2000*a*, IWC 2001, Smith and Jefferson 2002). The value of existing population estimates has been limited, however, by logistical and analytical difficulties that generally do not apply to cetaceans in marine environments (Smith and Reeves 2000*b*). The complex geomorphology of freshwater (and estuarine) systems tends to concentrate the distribution of cetaceans in counter-currents associated with confluences, meanders and mid-channel islands (see Hua *et al.* 1989; Smith 1993; Smith *et al.* 1997, 1998). This generally prevents vessel-based surveys from following transect lines placed randomly relative to the animals' distribution which violates a primary assumption of sampling theory. Past population assessments have therefore generally employed relatively simple direct counts in an attempt to enumerate the total number of animals present in a given area. These counts have probably been biased downward because under most circumstances some unknown proportion of the population has not been observed. Sighting biases are related to dolphin availability (most animals are underwater at any given time, and, when they are at the surface they generally show little of their body) and observer perception (all surfacings are not necessarily recorded because observers may be distracted, fatigued, or focused elsewhere, or they may not recognize a quiescent surfacing as a cetacean detection, especially during poor sighting conditions) (see Marsh and Sinclair 1989, Smith and Reeves 2000*b*).

Ganges River dolphins, *Platanista gangetica gangetica*, are found in the Ganges-Brahmaputra-Meghna and Karnaphuli-Sangu river systems of Nepal, India, Bangladesh, and possibly Bhutan (Mohan *et al.* 1997, Sinha *et al.* 2000, Smith *et al.* 2001). There is no credible estimate of range-wide abundance, but the subspecies was listed as "endangered" in the 2004 IUCN Red List due to a reduction in its historical range and projected declines in population size due to increasing threats (IUCN 2004).

Irrawaddy dolphins, *Orcaella brevirostris*, are patchily distributed in primarily estuarine, tropical, and subtropical waters of the Indo-Pacific, from northeastern India

east to the Philippines (Dolar *et al.* 2002) and south to northern Australia (Stacey and Leatherwood 1997, Stacey and Arnold 1999). Freshwater populations occur in two lagoons or lakes: Chilka in India and Songkhla in Thailand, and in three river systems: the Mahakam of Indonesia, the Ayeyarwady (formerly Irrawaddy) of Myanmar (formerly Burma), and the Mekong of Laos, Cambodia, and Vietnam. Although the species is classified in the IUCN Red List as "data deficient," the three riverine populations and ones in Songkhla Lake and Malampaya Sound, Philippines, have been Red Listed as "critically endangered" (IUCN 2004).

Prior to this survey no information was available on the status of these dolphins in the estuarine waterways of the Sundarbans mangrove forest, except for reports of species occurrence in Anderson (1879), Mörzer Bruyns (1966), Kasuya and Haque (1972), Khan (1982), and (Sarkar and Sarkar 1988). This was despite indications of increasing threats to cetaceans in the area from incidental killing in gill-net fisheries, destruction of fish-spawning habitat through mangrove deforestation, toxic contamination from large human population centers located upstream (*e.g.*, Dhaka and Calcutta), non-selective catch of fish fingerlings and crustacean larvae in small mesh "mosquito nets" and increased vessel traffic (see Rahman 2000, Islam 2003). An additional threat to the dolphins and other biodiversity, such as the threatened Indo-Pacific crocodile *Crocodylus porosus*, is declining freshwater flows. This problem will undoubtedly worsen if India proceeds with a series of planned, inter-river basin water transfer projects, which will involve large-scale dam construction and diversion of water from rivers that provide freshwater input to the Sundarbans. Although no final decision has been taken to proceed with construction, feasibility studies are scheduled to be completed in December 2005 and detailed project reports in 2006. It was anticipated in 2004 that, if built, the entire project would be finished by 2016. Declining freshwater supplies and the predicted sea level rise from global warming may profoundly affect the viability of dolphin populations in the Sundarbans and reinforce the need to establish baseline abundance estimates necessary for detecting long-term trends. These considerations led to an initiative to assess populations of Irrawaddy and Ganges River dolphins in the Sundarbans being included as one of 57 priority projects described in the IUCN 2002–2010 Conservation Action Plan for the World's Cetaceans (Reeves *et al.* 2003).

The Sundarbans are among the largest contiguous mangrove forests, encompassing about 577,000 ha, of which approximately 175,600 are inundated by a complex network of tidal and fluvial waterways, ranging from a few meters to a few kilometers wide (Hussain and Karim 1994). Large rivers enter the forest from the north and flow south, and are connected laterally by numerous smaller channels. From west to east the largest rivers in the Bangladesh Sundarbans are the Raimangal, Bal, Sibsa, Passur, Sela Gang, and Baleswar. The western rivers diverge from the Ganges but dry season flow in these waterways have been significantly reduced by construction of the Farakka Barrage (a low, gated diversion dam) located just upstream of the India-Bangladesh border (Mirza 1998). Three wildlife sanctuaries in the Bangladesh portion of the Sundarbans, covering a total of 32,386 ha, were designated as World Heritage sites in 1997 and were the subject of numerous ecological studies (*e.g.*, Seidensticker and Hai 1983, Khan 1986, Alcon and Johnson 1989, UNDP/FAO 1998) focusing mainly on the Bengal tiger, *Panthera tigris*, with scant attention paid to aquatic fauna.

The present paper reports on mark-recapture analyses of double concurrent counts made by independent teams used to estimate the abundance of Irrawaddy and Ganges River dolphins in the waterways of the Sundarbans mangrove forest in Bangladesh. These analyses corrected for perception bias but did not address availability bias.

METHODS

Field Survey

During 4–24 March 2002, a group of 18 scientists and conservationists, mostly from Bangladesh and India, conducted a visual vessel-based survey for dolphins in almost all navigable channels (wider and deeper than the beam and draft of our vessel: 6.5 and 1.8 m, respectively) of the Bangladesh portion of the Sundarbans mangrove forest (Fig. 1). Based on the geographically extensive field experience of R. Mansur, who has worked as a nature guide in the Sundarbans for the last 12 yr, and observations during casual surveys conducted by most of the other authors using small paddle boats, dolphins never occur in channels less than 15-m wide. We therefore assumed that our visual coverage of dolphin habitat was virtually complete.

Two independent observer teams were used to obtain concurrent records of dolphin sightings. A primary observer team was stationed on the upper deck (4.4 m above the waterline) and a secondary team was stationed on the lower deck (2.3 m above the waterline). The teams were not in visual contact and observers were instructed to avoid alerting the other team about dolphin sightings. The survey protocol was the same for both teams. Three observers stood watch at all times while "on-effort" (*i.e.*, actively searching for dolphins along the transect line and recording effort and sighting data), one stationed on each the port and starboard sides, searching with handheld 7 × 50 binoculars and naked eye from the beam to about 10° past the bow, and one in the center searching by naked eye in about a 20° cone in front of the

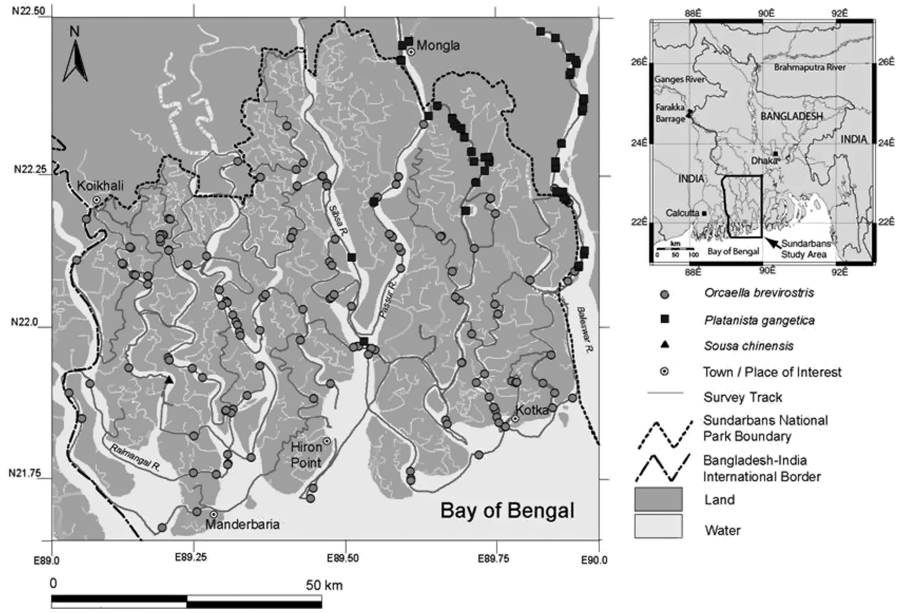


Figure 1. Map of the inner Sundarbans Delta showing the March 2002 survey trackline and the locations of dolphin sightings, and a side map showing the location of the study area in Bangladesh. Note that the Sundarbans image was derived from satellite imagery. It therefore shows numerous channels that do not contain water during the dry season and others that are too small to support dolphins.

bow. The center observer also served as the data recorder. Observers rotated through the three different positions every 30 min followed by at least an hour of rest before switching teams.

For logistical reasons we sometimes had to transit channels more than once. Although we generally maintained search effort on these occasions, only data from the first time the channel was surveyed were used for calculating abundance estimates. To increase sample size for estimating perception bias we did, however, include sightings made during duplicate search coverage in the mark-recapture analysis (see below). Whenever there was sufficient depth, channels wider than about 2 km were surveyed on both sides. We considered this to be non-duplicate effort but did not include groups detected on the opposite side of the estimated midpoint of the channel cross section in our abundance estimates.

Every 30 min, at the location of dolphin sightings, or when there was a significant change in sighting conditions we recorded our position with a Global Positioning System (GPS) and information on sighting conditions, human activities, channel width, and the distance covered along the transect line. Channel width was recorded according to the sum of distance measurements to the right and left banks using a laser range finder (Bushnell Yardage Pro 1000), if less than 500 m, or the sum of estimates made by naked eye, if greater. Wind, glare, or rain/fog conditions were given codes of 0, 1, or 2, corresponding to good (no effect on sighting conditions), fair (small effect on sighting conditions), and poor (large effect on sighting conditions), respectively. More specifically, for wind, code 0 meant that the water surface was glassy or had only small ripples; code 1 was small waves but no white caps; code 2 was larger waves with whitecaps. For glare, code 0 was no glare, code 1 was severe glare (view completely obscured) covering less than 10% of the field of view or slight glare (view only partially obscured) covering less than 50% of the field of view, code 2 was severe glare covering more than 10% of the field of view or slight glare covering more than 50% of the field of view. For rain/fog, code 0 was no fog or rain, code 1 was fog or rain obscuring no more than 10% of the field of view or partially obscuring no more than 50% of the field of view, and code 2 was fog or rain obscuring more than 10% of the field of view or partially obscuring more than 50% of the field of view. Overall sighting conditions were considered good when the sum of the codes for all three parameters was 0–1, fair 2, and poor ≥ 3, unless any one parameter was given a code of 2, whereupon overall sighting conditions were considered poor.

When dolphins were sighted we identified the species and recorded information on the time, radial distance to the first dolphin sighted, the location (according to the GPS reading) of the estimated position where the dolphins were located when first observed (or as close as the vessel came to this position while continuing along the transect line) and group sizes (according to best, high and low estimates). All sighting data were recorded while in "passing mode" (*i.e.*, the vessel did not turn toward the dolphin group) so that the other team was not alerted to the dolphin detection. The low group size estimate was considered a minimum count and the high estimate a maximum count. For some sightings, a low estimate of zero was used to reflect the possibility of double counting. Estimates of the total number of individuals for each species and of group size were calculated from the "best" estimates of group size, while the high and low estimates were used to evaluate the uncertainty of the observers about the accuracy of their best estimates.

The criterion for defining dolphin groups was the number of animals occupying a channel reach, defined as a relatively homogeneous stretch of channel located between obvious breaks in side slopes or tributary confluences. In a meandering channel this

was analogous to the distance from the outer edge of a bend on one bank to the outer edge of a bend on the opposite bank (*i.e.*, one half of the meander wavelength). This criterion was appropriate because, except for mother-young pairs, the motivation for individual Ganges River dolphins to form "groups" appears to be the common use of habitat, defined by hydraulic and geomorphic features, rather than obvious social affiliations (Smith 1993; Smith *et al.* 1998, 2001). Irrawaddy dolphins are more socially cohesive than Ganges River dolphins, but often exhibit fission-fusion activity, meaning that during only a few surfacings (*i.e.*, before a reliable count can be made), the animals split into multiple groups and then coalesce into a single group (or *vice versa*), and then split apart again into some other configuration. Although using habitat to define groups involved some unavoidable subjectivity, it provided a more reliable mechanism for determining whether groups were detected by both primary and secondary observer teams or by only one of them, and it helped us to estimate their size in a more consistent manner than using a more ill-defined social definition (see Smith and Reeves 2000*b*).

Analyses

We calculated a cumulative frequency distribution of sighting distances, and determined that 95% of the Irrawaddy dolphin groups were observed at a radial distance 800 m or less and that 95% of Ganges River dolphin groups were observed at a radial distance of 500 m or less. We assumed that dolphin groups separated by distances greater than these (*i.e.*, 800 m for Irrawaddy dolphins and 500 m for Ganges River dolphins) were different, and then used two different methods to evaluate whether a sighting was made by both teams or if they were unique to either the primary or secondary team.

The "geographic method" was based on the linear distance between the GPS positions (D_g) recorded at the approximate location along the trackline perpendicular to where the dolphin group was initially sighted. A potential problem of this method was that in the field it was often difficult to pinpoint the exact position where the animals were located at the initial time of detection, especially if the animals were traveling or diving for long durations. We were able to partially mitigate for these difficulties by using shoreline and hydraulic features for visual orientation.

The "time method" used the time difference between sightings made by the primary and secondary teams multiplied by the mean vessel speed and then adjusted for the estimated sighting distance. For this method the estimated distance between sightings D_t was calculated according to

$$D_t = |(T_p - T_s)\,\mathrm{VS}| + |D_s - D_p|$$

where, T_p is the time of sighting made by primary observer team, T_s is the time of sighting made by secondary observer team, VS is the mean vessel speed, D_s is the estimated distance to dolphin group for sighting made by primary observer team, and D_p is the estimated distance to dolphin group for sighting made by secondary observer team.

When D_g or D_t was less than 500 m for Ganges River dolphin and 800 m for Irrawaddy dolphins, the sightings were considered to be a match (or recapture), and if greater than these values the sightings were assumed to be unique. Because a failure to recognize matched sightings detected by both the primary and secondary teams (analogous to a "tag loss" in mark-recapture terminology) would result in a positive bias in the mark-recapture estimators (see below), we erred on the conservative side by

choosing the method (based on time or distance) that resulted in the most sightings that were considered the same (*i.e.*, matches).

One problem with the "time method" was that D_p and D_s were radial distances estimated at an unknown angle relative to the survey direction, whereas an implicit assumption of this method is that the dolphin groups were located directly in front of the vessel. The severity of this problem was mitigated, however, by the fact that a large portion of survey effort was conducted in relatively narrow channels (see below) such that the sighting angle relative to the survey direction was usually quite small. During future surveys it would be advisable to collect data on sighting angles so that a more accurate model could be developed that takes into account the actual distance to the dolphin group along the vessel transect. During this survey, however, we did consider it important not to overwhelm a relatively inexperienced observer team with too many data collection tasks during dolphin sightings.

We used two different analytical methods for estimating perception bias. The first was a modification of the double counting method employed by Marsh and Sinclair (1989) for aerial surveys of dugongs, *Dugong dugon*, and Rugh *et al.* (1993) for shore-based counts of gray whales, *Eschrichtius robustus*, which estimated the corrected number of groups G_c using a Chapman's modified Lincoln-Petersen mark-recapture estimator (Chapman 1951):

$$G_c = \frac{(n_p + 1)(n_s + 1)}{(m_{ps} + 1)} - 1;$$

with associated variance V_c (Seber 1970):

$$V_c = \frac{(n_p + 1)(n_s + 1)(n_p - m_{ps})(n_s - m_{ps})}{(m_{ps} + 1)^2(m_{ps} + 2)};$$

and coefficient of variation CV_c:

$$\mathrm{CV}_c = \sqrt{V_c}\,/\,G_c$$

where n_p is the the total number of groups detected by the primary observer team, n_s is the the total number of groups detected by the secondary observer team, and m_{ps} is the the total number of groups detected by both teams (matches or recaptures).

This estimator was used because it has a lower bias compared to the unmodified Lincoln-Petersen estimator and is unbiased for $n_p + n_s \geq G_c$. The correction factor for groups missed by the primary team was then G_c/n_p, and the corrected estimate of the total number of groups was calculated by multiplying this parameter by the total number of on-effort sightings made by the primary team while surveying non-duplicate transects. This number was then multiplied by the mean group size for estimating the abundance of individuals in the survey area A_i. The variance and coefficient of variation of A_i were approximated using the delta method (Seber 1982), with estimation components from the mark-recapture estimate of the corrected number of dolphin groups (V_c and CV_c—see above) and the best group size estimates of the primary observers. The upper and lower ranges of the 95% confidence interval were then calculated as $A_i \pm 1.96\sqrt{\mathrm{VAR}(A_i)}$.

Because mark-recapture analyses assume homogeneity of capture (or in our case sighting) probabilities, a condition that may have been violated by extraneous variations, we also conducted a stratified analysis using sighting covariates. Based

on our field experience we hypothesized three potential covariates that may have affected within stratum sighting probabilities: group size, sighting conditions, and channel width. We then investigated whether or not there was a statistical relationship between an individual covariate x and a sightability response y, such that the conditional distribution of y given x had a smaller variance than the distribution of y alone (see Williams *et al.* 2001). The intention was to strike a balance between including covariates that would reduce bias in the resultant correction factor while not including those that did not significantly affect sighting probabilities but would reduce precision if included *ad hoc*.

Sighting probabilities were plotted for individual covariates to identify natural groupings and the number of dolphins groups detected by each team was stratified according to combinations that affected sighting probabilities. A Chapman's modified Lincoln-Petersen mark-recapture estimator (see above) was used to calculate the corrected number of dolphin groups available for detection by the observers in each stratum G_{ci}, where i denotes the stratum, and these were then summed to determine the total estimated number of corrected groups G_{cst}. The same procedure that was used for calculating the non-stratified correction factor (see above) was then used to calculate the stratified correction factor and the total corrected number of on-effort sightings made by the primary team while surveying non-duplicate transects. Variability in group size estimates were also calculated for each stratum and incorporated into the upper and lower bounds of the 95% confidence interval for estimates of animal abundance.

The second approach used conditional likelihood methods developed by Huggins (1989, 1991) and implemented in the program MARK (White and Burnham 1999). These methods provide a flexible framework for modeling capture probabilities according to explanatory variables and use the capture-recapture histories corresponding to each observation rather that just the results aggregated by observer team.

The same covariates were considered during this analysis, namely group size, sighting conditions, and channel width. For group size the largest "best" estimate of the primary or secondary observer team was used. The raw values for channel width ranged from 124 to 5,000 m and the option to "Standardize Individual Covariates" was selected as suggested by Cooch and White (2004) to ensure optimization of the numerical algorithm for finding correct parameter estimates. We also considered whether there may have been a difference between the capture probabilities p_p and p_s corresponding to the primary and secondary observer teams, respectively, or a difference between these and the recapture probability c for those sightings detected by both observer teams.

Using the Huggins method capture probabilities were modeled as follows:

$$\text{logit}(p_{ik}) = \ln\left(\frac{p_{ik}}{1 - p_{ik}}\right) = \beta_0 + \sum_j \beta_j x_{jk}$$

where "logit" indicates the type of link function, $i = \{p, s\}$ denotes the primary or secondary observer team, k denotes the dolphin sighting, β_0 is the intercept, and β_j the slope parameter for the covariate value x_j. A type of Horvitz-Thomson estimator was then used to obtain the abundance estimate $\hat{N}$:

$$\hat{N} = \sum_k \frac{1}{1 - (1 - p_{pk})(1 - p_{sk})}.$$

We selected among models using Akaike's Information Criterion (AIC) values produced by MARK that were adjusted to take into account differences in effective sample size and lack of fit (Akaike 1973). Likelihood ratio tests were used to compare the deviance of nested models (where one model differs from another by the elimination of one or more model terms). We then attempted to follow Burnham and Anderson's (2002) recommendation for selecting among models, based on differences in AIC. According to their rules of thumb, when the difference in AIC between 2 models is (1) less than 2, it is reasonable to assume that both models have approximately equal weight in the data, (2) more than 2 and less than 7, then there is considerable support for a real difference between the models, and (3) more than 7, then there is strong evidence to support the conclusion of differences between the models. We thus focused on the top ranked model with the smallest AIC value and those models whose AIC values differ from this top model by less than 2.

RESULTS

During 1,510.4 km of non-duplicate search effort (Fig. 1) conducted at a mean vessel speed of 10.2 km/h the primary observer team detected 89 Irrawaddy dolphin groups for a total of 208 individuals (mean group size = 2.30, SD = 1.36, range = 1–6), including at least seven calves, and 55 sightings of Ganges River dolphin groups for a total of 135 individuals (mean group size of 2.45, SD = 2.25, range = 1–13), including at least nine calves (Fig. 1). Encounter rates within the extent of occurrence (see IUCN 2001) of each species were 0.19 dolphins/linear km and 0.47 dolphins/linear km for Irrawaddy and Ganges River dolphins, respectively. We also had a single sighting of four Indo-Pacific humpback dolphins, *Sousa chinensis*, and 11 sightings of cetaceans that could not be identified to species. The survey trackline was covered during sighting conditions rated good, fair, and poor during 71%, 19%, and 10% of the total "on-effort" distance searched, respectively.

All sightings made by the primary and secondary teams during duplicate and non-duplicate searching effort (see above) were evaluated using the "geographic" and "time" methods to determine whether sightings were matched (*i.e.*, recaptures) or unique. A total of 219 Irrawaddy dolphin sightings and 127 Ganges River dolphin sightings were evaluated. Both methods resulted in the same classifications for 92.8% of Irrawaddy dolphin sightings and 93.7% of Ganges River dolphin sightings. Although the differences between the two methods were insignificant (chi-square $P < 0.05$), we selected the "geographic" method because it resulted in a greater number of matches and it is the easiest to use during future surveys.

Using the "geographic" method for Irrawaddy dolphins, both teams detected 55 groups (matches) and the primary and secondary teams detected 65 and 44 unique groups, respectively, during both duplicate and non-duplicate searching effort. Using the Chapman estimator with these unstratified data, we estimated that the primary team detected 55.8% (CV = 6.5%) of all groups with a correction factor of 1.80. Applying this factor to the 89 groups detected by the primary team during non-duplicate effort resulted in estimates of 160 groups or 367 individuals (CV = 8.4%; 95% CI = 286–449), calculated using the mean group size estimate of the primary observer team (2.30). Using the same method for Ganges River dolphins, both teams detected 44 groups, and the primary and secondary teams detected 20 and 19 unique groups, respectively. Using the Chapman estimator with these unstratified data, we

estimated that the primary team detected 69.6% (CV = 4.5%) of all groups with a correction factor of 1.44. Applying this factor to the 55 Ganges River dolphin groups detected during non-duplicate effort resulted in estimates of 79 groups or 194 individuals (CV = 12.4%; 95% CI = 138–247) detected by the primary team during non-duplicate effort, calculated using the mean of best group size estimates of primary observer team (2.45).

We then tested for homogeneity of covariances (group sizes, sighting conditions and channel widths) between matched and unique sightings using a Box's *M* test, and investigated for equality among individual variables using a Bartlett's univariate test (α probability level = 0.05). For Irrawaddy dolphins the null hypothesis of no significant difference for all three variables combined was rejected ($P = 0.0262$; df = 6), and explained by significant differences in group sizes ($P = 0.0458$, df = 1) and sighting conditions ($P = 0.0488$, df = 1). However, because these differences could also be explained by significant departures from normality in the data ($P < 0.05$), we also tested each variable individually using a non-parametric Mann-Whitney *U* test. Group sizes were significantly larger ($P = 0.0022$) and sighting conditions were close to significantly better ($P = 0.1118$) for matched sightings. Due to the broad agreement among the more powerful Barlett's test for equality of covariances (albeit one that assumes a normally distributed data set), the Mann-Whitney *U* tests, and graphs of the effects of the three covariates on the percentages of unique sightings (Fig. 2), we limited the variables considered in our stratified Chapman's modified Lincoln-Petersen mark-recapture analysis of Irrawaddy dolphin sightings to group size and sighting conditions. After examining covariate plots of group sizes and sighting conditions for natural groupings and considering sample sizes within these, we settled on four covariate groups to use in the analysis: (1) dolphin group sizes of one or two detected during sighting conditions coded one or two, (2) dolphin group sizes of one or two detected during sighting conditions coded three, (3) dolphin group sizes greater than three detected during sighting conditions coded one or two, and (4) dolphin group sizes of greater than three detected during sighting conditions coded three. The sum of the four stratified abundance estimates (Table 1) for duplicate and non-duplicate searching effort combined indicated that the primary team detected 51.5% (CV = 8.7%) of all groups with a correction factor of 1.94. Applying this factor to the number of groups detected by the primary team during non-duplicate effort (89) resulted in a total estimate of 173 groups or 397 individuals (CV = 10.2%; 95% CI = 290–505).

For Ganges River dolphins, we failed to reject the null hypothesis of no significant difference for all three variables combined. The covariance closest to being rejected was group size at $P = 0.19962$ (df = 1) as being larger for matched sightings. Similarly, Mann-Whitney *U* tests of individual variables were non-significant, although group size was close to being significantly larger for matched sightings at $P = 0.06895$. We therefore used only a single covariate for the stratified Chapman's modified Lincoln-Petersen mark-recapture analysis of Ganges River dolphin sightings. After examining covariate plots of group sizes, we settled on two covariate groups to use in the analysis: (1) group sizes one or two, and (2) group sizes greater than three. The sum of the two stratified abundance estimates (Table 1) for duplicate and non-duplicate searching effort combined indicated that the primary team detected 69.0% (CV = 5.3%) of all groups with a correction factor of 1.45. Applying this factor to the number of groups detected by the primary team during non-duplicate effort (55) resulted in a total estimate of 80 dolphin groups or 196 individuals (CV = 12.7%; 95% CI = 139–253).

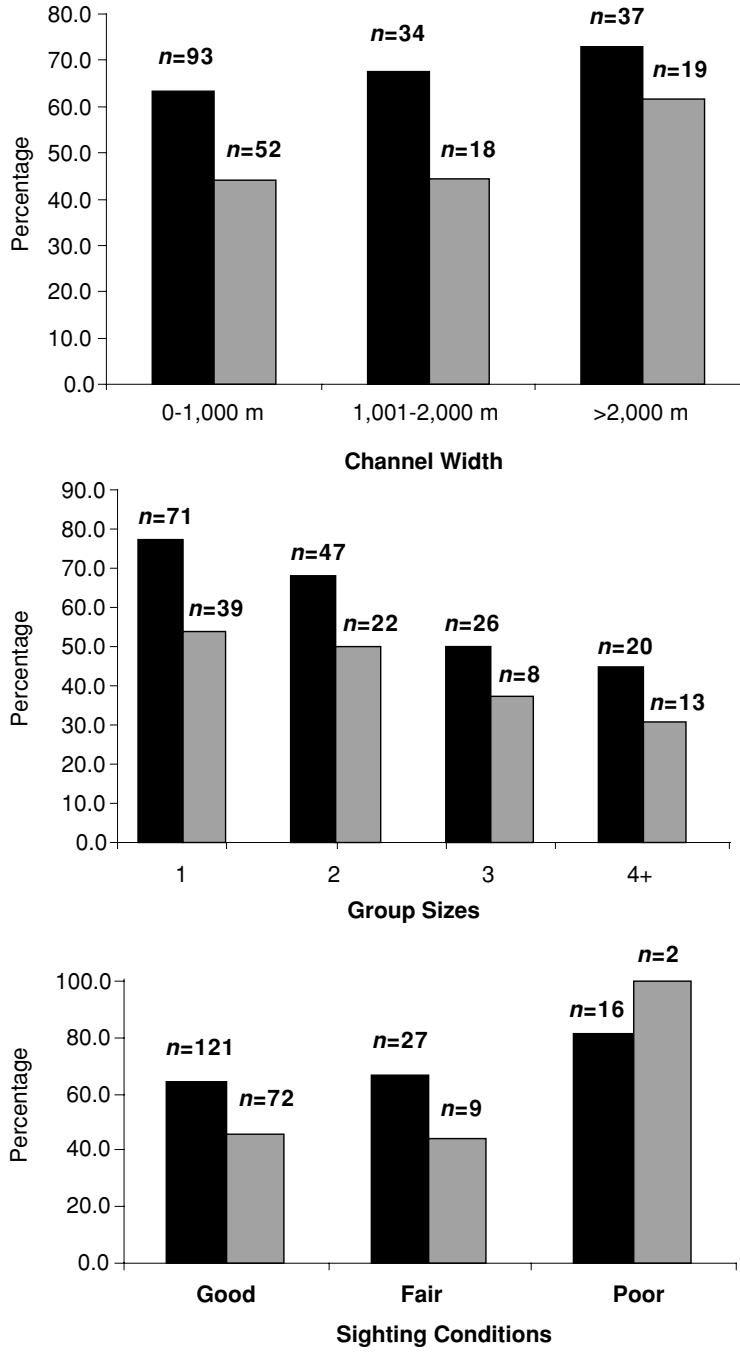


Figure 2. Percentage of missed sightings (unique to primary or secondary observer team) for Irrawaddy dolphins (black) and Ganges River dolphins (gray) according to channel widths, group sizes, and sighting conditions.

Table 1. The stratified number of Irrawaddy and Ganges River dolphin groups detected by the primary and secondary observer teams during duplicate and non-duplicate search effort, and the number of corrected groups and their associated CVs calculated from the Chapman's modified Lincoln-Petersen mark-recapture estimator. GS: group size and SC: sighting conditions.

	Number of sightings detected by primary team (n_p)	Number of sightings detected by secondary team (n_s)	Number of sightings detected by both teams (mp_s)	Corrected groups (G_c)	Coefficient of variation (CV_c) (%)
Irrawaddy dolphins					
GS = 1–2; SC = 1–2	72	58	27	153	10.6
GS = 1–2; SC = 3	7	6	1	27	43.8
GS > 3; SC = 1–2	38	32	25	49	5.2
GS > 3; SC = 3	3	3	2	4	15.3
Ganges River dolphins					
GS = 1–2	42	42	26	67	7.1
GS > 3	22	21	18	26	3.6

By conducting a mark-recapture analysis using the Huggins conditional likelihood model we found the parameter values and abundance estimates for the top ranked models that best explained the variation according to their adjusted AIC values for Irrawaddy and Ganges River dolphins, respectively. For all of the top ranked models, the capture probabilities for the two observer teams were modeled as a single parameter and the recapture probability as an additional parameter. We did, however, consider models where the capture probabilities p_p and p_s for the primary and secondary observer teams, respectively, and the recapture probability c were estimated as separate parameters or models where all three were estimated as a single parameter. All models supported the hypothesis that there is heterogeneity in Irrawaddy dolphin capture probabilities due to the group size and the second and third models suggest that this heterogeneity could be further explained by sighting conditions and channel width, respectively (Table 2). The first model for Ganges River dolphins supported the hypothesis that there was heterogeneity in capture probabilities due to group size but, according to Burnham and Anderson's rule-of-thumb (see above), support for this model was not substantially more than for a model without any covariates (Table 3). The third model indicated that group size and channel width were appropriate explanatory variables, whereas the last model with only sighting conditions as a covariable received the least support.

By applying the Likelihood ratio tests to the top ranked nested models we considered the difference in deviance between the candidate models that were distributed as a chi-square statistic (the difference in the number of estimable parameters between the two models determines the degrees of freedom). The results for all the different nested model combinations for Irrawaddy and Ganges River dolphins indicated that none of the auxiliary variables were statistically significant.

Specifically for Irrawaddy dolphins, we considered the first two models and found that the difference of fit was not significant ($\chi^2 = 1.498$; df = 1; $P = 0.2210$). We therefore concluded there was no evidence that the capture or recapture probabilities were influenced by sighting conditions, because the model with just the group size

Table 2. All of the top ranked Huggins closed capture models for estimating Irrawaddy dolphin abundance had the same capture probability for the primary and secondary team, but a different recapture probability for those observations by both teams ($p_p = p_s \neq c$). For each model its adjusted AIC, the difference in AIC values between the top ranked model and other models (Delta AIC) and the weight of the model given its AIC value (AIC weight) is shown along with the estimates of abundance (with their standard errors and 95% confidence intervals) and the capture and recapture estimates (with their standard errors and 95% confidence intervals).

Model covariates	AIC	Delta AIC	AIC weight	$\hat{N}$	SE ($\hat{N}$)	95% CI $\hat{N}$	$\hat{p}$ $\hat{c}$	SE ($\hat{p}$) SE ($\hat{c}$)	95% CI $\hat{p}$ 95% CI $\hat{c}$
Group size	347.01	0.00	0.25	195	14.37	177–238	0.65	0.07	0.51–0.76
							0.46	0.05	0.37–0.55
Sighting conditions + group size	347.56	0.55	0.19	197	16.07	178–246	0.64	0.07	0.50–0.76
							0.46	0.05	0.37–0.55
Group size + channel width	348.50	1.49	0.12	195	14.43	177–238	0.65	0.07	0.51–0.76
							0.46	0.05	0.37–0.55
Group size[a]	348.83	1.82	0.10	198	17.22	177–251	0.65	0.07	0.50–0.77
							0.46	0.05	0.37–0.55
Weighted average				196	15.40	166–226	0.64	0.07	0.51–0.76
							0.46	0.05	0.37–0.55

[a] This model differs from the first one in the table as the group size covariate was assumed to vary independently for the capture and recapture probabilities, whereas for the first model in Table 2 and the remaining models in Table 2 and 3 the covariates were assumed to vary in the same way for both capture and recapture probabilities.

Table 3. All of the top ranked Huggins models for estimating Ganges River dolphin abundance had the same capture probability for the primary and secondary team, as well as the same recapture probability for those observations by both teams ($p_p = p_s = c$). For each model its adjusted AIC, the difference in AIC values between the top ranked model and other models (Delta AIC) and the weight of the model given its AIC value (AIC weight) is shown along with the estimates of abundance (with their standard errors and 95% confidence intervals) and the capture/recapture estimates (with their standard errors and 95% confidence intervals).

Model covariates	AICc	Delta AICc	AICc weight	$\hat{N}$	SE ($\hat{N}$)	95% CI $\hat{N}$	$\hat{p}$	SE ($\hat{p}$)	95% CI $\hat{p}$
Group size	170.30	0.00	0.37	92	4.62	87–106	0.70	0.05	0.60-0.78
None	170.85	0.53	0.29	92	4.24	86–104	0.69	0.05	0.60-0.78
Group size + channel width	171.87	1.54	0.17	93	4.84	87–104	0.70	0.05	0.60-0.78
Sighting conditions	171.93	1.61	0.17	92	4.67	87–107	0.69	0.05	0.59-0.78
Weighted average				92	4.58	83–101	0.70	0.05	0.60-0.78

covariable fitted equally well. For either of the top ranked models (according to the adjusted AIC values) the estimates of the capture probabilities and abundance were very similar.

Specifically for Ganges River dolphins, we considered the first two models and found that the difference of fit was not significant ($\chi^2 = 2.576$; df = 1; $P = 0.1085$). We therefore concluded there was no evidence that the capture or recapture probabilities were influenced by group size, because the model without the group size

covariable fitted equally well. Again, for the top ranked models (according to the adjusted AIC values) the estimates of the capture probabilities and abundance were very similar.

Given that there were a number of models with very similar adjusted AIC values we dealt with the uncertainty in model selection by using model averaging. The MARK Program weighted models in a way that reflects the support for each model in the data. The average value for parameter θ was calculated as $\sum_i w_i \hat{\theta}_i$, where w_i denotes the AIC weight and $\hat{\theta}_i$ the parameter estimate for model i (Buckland *et al.* 1997). This model averaging resulted in total estimates of 196 Irrawaddy dolphin groups (CV = 7.9%; 95% CI = 166–226; variation attributable to model variation was 1.2%) or 451 individuals (CV=9.6%; 95% CI = 337–565) and 92 Ganges River dolphin groups (CV = 5.0%; 95% CI = 83–101; variation attributable to model variation was 1.0%) or 225 individuals (CV=12.6%; 95% CI = 160–290).

DISCUSSION

Distribution and Encounter Rates

Encounter rates in the Sundarbans for Ganges River dolphins were greater than has been recorded in some waterways but less than in others, while for Irrawaddy dolphins encounter rates were apparently higher (Table 4). These comparisons should be considered judiciously, however, because vessel speed, sighting conditions, platform

Table 4. Comparisons of encounter rates (ER; dolphins/linear km) among waterways of the Sundarbans mangrove forest and other river channels where Irrawaddy and Ganges River dolphins have been surveyed. CL: channel length; VS: mean vessel speed in km/h.

Species	Study area	CL	VS	ER	Reference
Irrawaddy dolphins					
	Sundarbans, Bangladesh	960	10.2	0.19	This study
	Ayeyarwady River, Myanmar	360	13.0	0.16	Smith and Hobbs (2002)
	Mahakam River (mainstem), Indonesia	432	?	0.06	Kreb (1999)
	Mahakam River (tributaries)	78	?	0.09	Kreb (1999)
	Mekong, Sekong and Sesan Rivers, Cambodia	350	?	0.11	Baird and Beasley (2005)
Ganges River dolphins					
	Sundarbans	196	10.2	0.47	This study
	Chambal River, India[a]	425	?	0.27	Sharma *et al.* (1995)
	Bhagirathi River, India[a]	323	?	0.37	Sinha (1997)
	Sangu River, Bangladesh	44	9.9	1.36	Smith *et al.* (2001)
	Karnaphuli River, Bangladesh	70.8	8.7	0.47	Smith *et al.* (2001)
	Middle Ganges River, India[b]	60	5.0	1.8	Choudhary *et al.* (in press)

[a] Calculated from raw data presented in the paper.

[b] Mean based on the counts from eight surveys conducted in an upstream direction.

height, and the number and ability of observers can dramatically affect visual detection rates of small cetaceans (see Palka 1996, Barlow *et al.* 2001).

Encounter rates for both species varied dramatically according to area in the delta, with Irrawaddy dolphins generally occurring in the western, high-salinity portion and Ganges River dolphins generally in the eastern, low-salinity portion, especially in upstream segments receiving freshwater inputs from the Passur, Sela Gang, and Baleswar rivers (Fig. 1). There were distributional outliers for Ganges River dolphins and a distinct zone of overlap where, on six occasions, both species were observed surfacing within a few meters of each other. Both species were observed to have an affinity for counter-currents and deep pools, located in and adjacent to channel convergences and divergences, and downstream (direction dependent upon the tide) of sharp meanders, where the dolphins find refuge from hydraulic forces and where biological productivity is generally concentrated. It is not surprising that these areas also tended to be where gill-net fishing was most often concentrated. Martin *et al.* (2004) reported similar observations of an overlap between areas of high gill-net deployment and the occurrence of botos, *Inia geoffrensis*, and tucuxis, *Sotalia fluviatilis*, in the Amazon River. Within the Sundarbans National Park, a relatively high density of Ganges River dolphins was documented in the upper reaches of the Mrigamari distributary of the Passur River. The reasons for distributional clumping in this area are unclear but may be related to its relatively pristine conditions and moderate channel width, which has an optimal shoreline-to-water surface ratio that encourages the formation of the large, deep pools where the animals were generally found. In addition, its close proximity to the Passur River, a movement corridor for riverine fishes as evidenced by the large number of gillnets deployed there during the survey, may be a contributing factor. No abundance hotspots were identified for Irrawaddy dolphins, except possibly the upper reaches of the Sibsa River, and portions of the mainstem influenced by confluences.

Concurrent Counts from Independent Teams

This study advanced the methodology for surveying freshwater and estuarine cetaceans, especially in geomorphically and hydraulically complex riverine and estuarine channels where distance sampling methods are generally inappropriate (see above). Using concurrent counts made by independent teams we estimated perception biases and their associated variances, and applied scientifically defensible correction factors to direct counts of Irrawaddy and Ganges River dolphins. We also evaluated statistically the effects of extrinsic factors (group size, sighting conditions, and channel width) on the detection rates of both species.

Stratification using sighting covariates had only minor effects on the Chapman's modified Lincoln-Petersen abundance estimate for Ganges River dolphins but a comparatively greater effect on the abundance estimate for Irrawaddy dolphins. This implied that perception biases when searching for Ganges River dolphins were probably related to the ability of the observers to consistently maintain vigilance and recognize visual cues of animal presence. For Irrawaddy dolphins, sighting probabilities were affected by the same intrinsic factors but also by extrinsic ones related to sighting conditions and group sizes. This meant that the stratified mark-recapture estimate for this species was less biased compared to the non-stratified estimate. However, the precision of the stratified estimate was also less, caused almost certainly by the small sample sizes available for the individual strata.

Evaluation of Potential Biases Associated with the Availability of Groups

The mark-recapture analysis of double concurrent counts estimated perception bias associated with group detection but did not address availability (see above). Ignoring this issue means that we obtained an abundance estimate that reflects only the available component of the population (*i.e.*, groups on the surface), which may have been only a small portion of its overall size (see Pollock *et al*. 2004). A rough, preliminary evaluation was made on whether availability bias could have resulted in an underestimation of abundance for both species by using group dive time information (*i.e.*, the time intervals when no individuals of the group were available on the surface) collected from the survey vessel and the distance estimates made to dolphin groups at the time of detection. During the survey mean dive times of 15.2 s ($n = 264$, SD = 17.8, range = 1–97) and 22.7 s ($n = 102$, SD = 23.0, range = 1–140) were recorded for three Irrawaddy dolphin groups and two Ganges River dolphin groups, respectively. According to distance estimation data from the primary team, a decline in sighting frequencies occurs past 200 m and 75 m for Irrawaddy and Ganges River dolphins, respectively. The mean vessel speed during our survey was 10.4 km/h or 2.88 m/s. This meant that on average it took 69.4 s and 26.0 s to cover the distance where it could be assumed that Irrawaddy and Ganges River dolphin groups available on the water surface, respectively, would have a high probability of being detected. A cumulative frequency distribution of group dive times for Irrawaddy dolphins indicated that while surveying along 200 m of trackline 97.0% of the groups would be available for detection at least once and on average during 4–5 surfacings. Irrawaddy dolphins would also be available during the same number of times within the second distance increment (201–400 m) where the proportion of detected animals on the surface was still relatively high (76.4%). A cumulative frequency distribution of dive times for Ganges River dolphins indicated that while surveying along 75 m of trackline 72.5% of the groups would be available for detection at least once and on average for 1–2 surfacings. Ganges River dolphins would also be available during the same number of times within the second distance increment (76–150 m) where the proportion of detected animals on the surface was also relatively high (72.4%). Although these analyses indicated that availability was probably not a significant source of negative bias in our abundance estimates, particularly for Irrawaddy dolphins, we caution that the evaluations were made on the basis of very limited data, especially on dive times. Another problem was that the method assumed all dolphins were positioned directly in front of the vessel at the time of detection, whereas their actual positions were oriented at various radial angles determined by random chance, the availability of suitable habitat, channel width, and detection distances. For evaluating availability bias associated with group detection we recommend that data on the relative angle in relation to the bow of detected groups be collected during future surveys and that a more sophisticated approach be developed, which takes into account differential periods of visual coverage across variable channel widths.

Evaluation of Potential Biases Associated with Estimating Group Sizes

An implicit assumption of our concurrent count technique was that group sizes were estimated without error. For our abundance calculation we incorporated the variability associated with sampling error (as well as any biological heterogeneity that may select for different size groups according to sex and age and/or environmental variables) in the CV and 95% CI (see above). This was justified because, although this

was an "enumeration" survey, we made no assumption that individual animals (or groups) were counted only once. Instead we assumed that the probability of double counting was balanced by the probability that animals were missed altogether while we were not actively searching (*i.e.*, "off-effort") due to movements in the opposite direction. This means that there was an element of "sampling" involved in our direct counts. However, group size estimation is also affected by availability and perception biases, similar to those discussed above for group detection. The potential for these biases to affect abundance estimates was not explicitly addressed and may have been accentuated by our practice of estimating group sizes while in "passing mode" (to avoid alerting the other team about a detected group) rather than stopping to spend more time to obtain a better estimate. An initial attempt was made to incorporate the variability associated with matched sightings detected by both the primary and secondary observer teams, which would have addressed the issue of perception but not availability. However, group size estimates made by the primary team were significantly greater than those made by the secondary team for matched sightings (paired t-test $P = 0.02982$ for Irrawaddy dolphins and $P = 0.0106$ for Ganges River dolphins—a difference almost certainly explained by the greater height of the observation platform used by the primary team). This meant that using these data would introduce a source of error unrelated to the internal bias of the group size estimates made by the primary team. We also considered using information from the best, high, and low estimates made by the primary team but these data were not strictly independent, and using them would therefore violate a primary assumption of statistical theory. However, the mean percent differences in the best *vs.* high, and best *vs.* low group size estimates (26% and 8% for Irrawaddy dolphins, respectively, and 17% and 3% for Ganges River dolphins, respectively) implied that the best estimates of the primary team may have been imprecise but probably not to the extent that it significantly invalidated our abundance estimates. Future surveys would benefit from group size estimation experiments using independent teams stationed at the same height. Two different scenarios could be attempted. One would involve both teams spending the same amount of time observing the animals, to estimate perception bias, and the other would involve the two teams spending different amounts of time observing the animals to separate out the availability component.

Comparison of Lincoln-Petersen and Huggins Conditional Likelihood Models

The results from the tests for homogeneity of covariance and the Huggins models were in broad agreement as to the covariates that produce heterogeneity in the capture probabilities. However, the abundance estimates produced by the Huggins models were slightly greater than those obtained by means of the Chapman's modified Lincoln-Petersen mark-recapture estimator. The Huggins models have the advantage of incorporating covariates directly into the modeling process by maintaining the link between individual capture histories and their respective covariate values, which the other estimation method does not. Although the Huggins modeling procedures make better use of the capture-recapture information for integrating covariates, a drawback is that it is not possible to assess goodness-of-fit with these types of models and the methods can be positively biased if less than 60% of the population is captured (White 2002) (or visually detected)—a situation that, according to the percentage of corrected *vs.* uncorrected counts, applied to Irrawaddy dolphins (42.3%) and was close for Ganges River dolphins (65.2%). Another drawback is that these modeling

procedures require specialized computer skills and a more in-depth knowledge of population sampling theory.

Application of the Chapman's modified Lincoln-Peterson estimator was relatively straight forward as compared to the Huggins models and the 95% CIs for the abundance estimates overlapped for both methods. Ultimately the analytical advantages of the Huggins models probably outweigh those of the Chapman's modified Lincoln-Petersen estimator, but the latter should be considered appropriate when simplicity is a priority (*e.g.*, when population assessments are carried out by nonspecialists) and reliable data on explanatory variables are not available.

Conservation and Research Recommendations

Regardless of the analytical model used and the potential for availability and group size estimation biases, our investigation indicated that waterways of the Sundarbans mangrove forest in Bangladesh support significant numbers of Irrawaddy and Ganges River dolphins, especially compared to other areas where these species have been surveyed. Ganges River dolphins inhabiting the Sundarbans are the downstream boundary of a much larger population in the Ganges-Brahmaputra-Meghna system (see references above). Conversely, Irrawaddy dolphins are the inland extent of a much larger population that extends to the shallow and more saline waters of the outer delta (Smith *et al*. 2005). The boundary between the ranges of both species migrates along a southwest and northeast axis according to seasonal freshwater discharge. The tonal character of this ecological boundary, which apparently follows salinity and turbidity gradients, implies that long-term monitoring of dolphin distribution patterns may prove insightful into the impacts of declining freshwater flows on other aquatic biota. Future research in the Sundarbans should focus on identifying "hotspots" where the two species occur in relatively high densities (especially together) during various stages of the seasonal freshwater flood cycle. Once these areas are identified, it may be possible to improve protection of both the dolphins and their habitat. A program for long-term monitoring and identifying seasonal hotspots for dolphins in the eastern portion of the Sundarbans was established shortly after the survey reported in this paper. This program uses sightings logged by the captains of three nature tourism vessels from The Guide Tours Ltd. One advantage of this program is that data collection activities are virtually self sufficient. There is a vital need to conduct a similar status assessment of dolphins in the Indian portion of the Sundarbans.

ACKNOWLEDGMENTS

We gratefully acknowledge the enthusiastic and conscientious efforts of our observer team including Bashir Ahmed, Rashiduzzaman Ahmed, Mohammad Abdul Hannan, Alia Islam, Tajul Islam, M. Zahirul Islam, Ummay Habiba Khatun, Rubiayat Mansur, Ilana Sara Meallem, Razia Quadir, Albert P. Reichert, Mohammad Abu Saeed, K.P Srinivasakumar, Dipani Sutaria, R. Thangaraja, and Khondoker Zakaria. Funds for this project were provided by the U.S. World Wildlife Fund, Whale and Dolphin Conservation Society, Ocean Park Conservation Foundation, and Wildlife Conservation Society. From these organizations, we would particularly like to thank Karen Baragona, Alison Wood, Jessica Wong, and Liz Lauck for their strong support. We gratefully acknowledge IUCN Bangladesh for providing the venue for the pre-survey training course and for helping us to obtain the research permit. The assistance of S.M. Munjurul Hannan Khan was also very helpful in obtaining the permit. We also appreciate the help of Mr. Mohammad Osman Gani which allowed us to conduct our work inside the

Sundarbans National Park. Special appreciation is given to Hasan Mansur from The Guide Tours for providing an ideal research vessel. The captain and crew of the MV *Chutti* also deserve great appreciation for their hard work and extraordinarily good cheer which made our survey a success. The Ministry of Environment and Forests, Government of the People's Republic of Bangladesh provided the research permit. Comments from two anonymous reviewers were helpful for improving the manuscript.

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Received: 12 April 2005
Accepted: 2 November 2005