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

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ABSTRACT

Independent concurrent counts were used to estimate the abundance of Ganges River dolphins *Platanista gangetica gangetica* and Irrawaddy dolphins *Orcaella brevirostris* in mangrove channels of the Sundarbans Delta in Bangladesh. For Irrawaddy dolphins, a stratified Lincoln-Petersen model, which incorporated group size and sighting conditions as covariables, and a Huggins conditional likelihood model, which incorporated group size as it varied independently for capture and recapture probabilities, generated abundance estimates of 397 individuals (CV=10.4%; 95% CI=290-505) and 449 individuals (CV=17.0%; 95% CI=384-514), respectively. For Ganges River dolphins, a stratified Lincoln-Petersen model, which incorporated group size as a covariate, and a Huggins conditional likelihood model, which incorporated no covariables, generated abundance estimates of 181 individuals (CV=11.1%; 95% CI=156-244) and 207 individuals (CV=10.8%; 95% CI=163-251), 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 and data on explanatory variables are not available. These abundance estimates indicate that waterways of the Sundarbans mangrove forest support potentially viable populations of both species, and that these dolphins deserve conservation attention due to favorable prospects for long-term survival if protected from human threats.

Key Words: *Orcaella brevirostris*, *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 2000a; 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 population assessments of cetaceans in marine environments (Smith and Reeves 2000b). The complex geomorphology of freshwater [and estuarine] systems tends to concentrate the distribution of cetaceans in areas with specific hydraulic characteristics (generally counter-currents at confluences or associated with meanders or mid-channel islands; see Hua *et al.* 1989; Smith 1993, Smith *et al.* 1998) and generally prevents vessel-based surveys from following transect lines placed randomly relative to the animals' distribution. These difficulties have resulted in population estimates (or counts) that generally lack measures of precision and are biased in unknown ways (Smith and Reeves 2000b). Suggestions in Perrin and Brownell (1989), Leatherwood (1996) and Vidal *et al.* (1997) for employing cue-counting and multi-platform survey techniques have rarely been followed. The present paper reports on a mark-recapture analysis of independent double concurrent counts used to estimate the abundance of two freshwater cetaceans: the Irrawaddy dolphin *Orcaella brevirostris* and Ganges River dolphin *Platanista gangetica gangetica*, in the waterways of the Sundarbans mangrove forest.

Ganges River dolphins are found in the Ganges-Brahmaputra-Megna 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. Irrawaddy dolphins 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 appended 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", all three riverine populations and ones in Songkhla Lake and Malampaya Sound, Palawan, Philippines have been listed as "critically endangered."

Prior to this survey no information was available on the status of these dolphins in the estuarine waterways the Sundarbans mangrove forest, except for reports of species occurrence in Anderson (1879), Mörzer Bruyns (1966) and Kasuya and Haque (1972). This was despite indications of increasing threats to cetaceans in the area from incidental killing in gillnet 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 (Reeves *et al.* 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 inhabited by the dolphins. Although no final decision has been taken to proceed with construction, feasibility studies are 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.

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 several 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 and Sela Gang. The western rivers diverge from the Ganges but dry season flows in these waterways have been significantly reduced by the construction of the Farakka Barrage (a low, gated diversion dam) located just upstream of the India-Bangladesh border (Fig. 1).

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 studies (e.g. Seidensticker and Hai 1983; Blower 1985; Khan 1986; Alcon and Johnson 1989; Tamang 1993; UNEP/FAO 1998) focusing mainly on the Bengal Tiger *Panthera tigris tigris* with scant attention paid to aquatic fauna.

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 of the Bangladesh portion of the Sundarbans mangrove forest (Fig. 1). Prior to the survey all observers participated in a two-day training course on cetacean survey techniques. Two observer teams were used to obtain independent concurrent records of 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 7x50 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 bow. The center observer also served as the data recorder. Observers rotated through the three different positions every 30 minutes followed by at least an hour of rest before switching teams.

For logistical reasons we often 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 abundance estimation. To increase our sample size we did, however, include sightings made during duplicate search coverage to estimate a correction factor for sightings missed due to perception bias (see below). Most channels wider than about two km, were surveyed on both sides. We considered this to be non-

duplicate effort, but did not include sightings that were judged to be on the opposite side of the estimated mid-point of the channel cross section.

Every 30 minutes, 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, the distance covered along the transect line, and environmental parameters (salinity, depth, temperature and turbidity – methods and results of these are reported in Smith (2003)). 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 almost completely 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 completely 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, group sizes (according to best, high and low estimates), the number of calves, and the location (according to the GPS reading) of the estimated position where the dolphins were located when first observed. The criterion for defining dolphin groups was the zone of hydrologic influence in the channel reach where the animals were initially seen. This criterion was appropriate because,

except for mother-young pairs, the attractive force of Ganges River dolphin 'groups' appears to be the common use of habitat, defined by hydraulic features, rather than obvious social affiliations (Smith 1993, Smith *et al.* 1998, Smith *et al.* 2001). Although this definition involved some unavoidable subjectivity, it provided a mechanism for determining whether groups were detected by both primary and secondary observer teams or one of them, and for reporting a range of estimates for the number of individuals, rather than attempting a direct census, which would not reflect the inherent uncertainty about the actual number present (see Smith and Reeves 2000b). Irrawaddy dolphins are more socially cohesive compared to Ganges River dolphins, but often exhibit constant 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. For this species, using a habitat definition of dolphin groups also helped us to estimate their size in a more consistent manner than an ill-defined social definition.

Double counts were avoided within each team by maintaining close communication. A zero was occasionally used for low and occasionally best group size estimates, if there was a possibility that the animals had already been counted (see Smith *et al.* 1994). We assumed that the probability of double counting groups, due to dolphins moving past our research vessel when we were stopped for the night, was balanced by the probability that groups were missed altogether, due to movements in the opposite direction.

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., 800m for Irrawaddy dolphins and 500m 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 recorded at the approximate location of dolphin sightings. 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 was calculated according to:

$$D = |(Tp - Ts) * VS| + |Ds - Dp|$$

where, T_p = time of sighting made by primary observer team,

T_s = time of sighting made by secondary observer team,

VS = mean vessel speed,

D_s = estimated distance to dolphin group for sighting made by primary observer team, and

D_p = estimated distance to dolphin group for sighting made by secondary observer team.

When D was less than 500m for Ganges River dolphin and 800m 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 using the method 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 dolphin 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:

$$CV_c = \sqrt{V_c} / G_c$$

where n_p = the total number of groups detected by the primary observer team,

n_s = the total number of groups detected by the secondary observer team,

and

m_{ps} = 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 +/- 1.96 * $\sqrt{VAR(A_i)}$.

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

compare the deviance of nested models (where one model differs from another by the elimination of one or more model terms). We then followed Burnham and Anderson's (2002) recommendation as to how one might select among models, based on differences in AIC. According to their rules of thumb, when the difference in AIC between 2 models is (a) less than 2, it is reasonable to assume that both models have approximately equal weight in the data, (b) more than 2 and less than 7, then there is considerable support for a real difference between the models, and (c) 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 1510.4 km of non-duplicate search effort (Fig. 1) the primary observer team detected 89 Irrawaddy dolphin groups for a total of 205 individuals (mean group size = 2.3, SD = 1.4, 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 2.3, SD = 1.7, range = 1-9; after eliminating an outlier of a single group of 13 individuals), including at least nine calves (Fig. 2). Estimates of the total number of individuals for each species and of group size were calculated from the best group size data. 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. Encounter rates were 5.9 groups/100 km or 13.6 individuals/100 km for Irrawaddy dolphins and 3.6 groups/100 km or 8.9 individuals/100 km for Ganges River dolphins. 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. The results of both methods concurred for 92.8% of Irrawaddy dolphin sightings and 93.7% of Ganges River dolphins sightings. Although the differences

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 covariables were considered during this analysis, namely group size, sighting conditions and channel width. Only the sighting conditions variable was coded as a categorical variable with values of 3 (Good), 2 (Fair) and 1 (Poor). 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 5000 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 Huggins method the capture probabilities were modelled 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 (LRT) were used to

between the two methods were insignificant (Chi-square $P < 0.05$) we selected the "geographic" method because it resulted in the greatest 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. Based on non-stratified data collected during both duplicate and non-duplicate searching effort a correction factor was calculated as 1.79 ($CV_c = 6.5\%$). This meant that the non-stratified corrected estimate of Irrawaddy dolphins groups detected by the primary observer team during non-duplicate effort was 160 groups or 367 individuals (CV = 8.4%; 95% CI = 286-449), calculated using the mean of the best group size estimates of the primary observer team (2.3). 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. A correction factor was calculated as 1.43 ($CV_c = 4.5\%$), resulting an estimate of 79 Ganges River dolphin groups or 178 individuals (CV = 10.8%; 95% CI = 155-238) detected by the primary team during non-duplicate effort, calculated using the mean of best group size estimates of primary observer team (2.3).

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 plots of the effects of the three covariates on unique versus matched sightings (Fig. 3), 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 for 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 resultant correction factor calculated from the sum of the four stratified abundance estimates (Table 1) for duplicate and non-duplicate searching effort combined was 1.94 (CV = 8.7%). Multiplying this figure by the number of sightings made by the primary team during non-duplicate effort resulted in a total estimate of 173 dolphin groups or 397 individuals (CV = 10.4%; 95% CI = 290-505).

For Ganges River dolphins, the null hypothesis of no significant difference was accepted for all three variables combined after deleting sightings that were two extreme outliers for group sizes of 12 and 13 individuals and two for the only groups detected during sighting conditions given a code 3. The null hypothesis for 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 for 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 resultant correction factor calculated from the sum of the two stratified abundance estimates (Table 1) for duplicate and non-duplicate searching effort was 1.45 (CV = 5.3%). Multiplying this figure by the number of sightings made by the primary team during non-duplicate effort resulted in a total estimate of 80 dolphin groups or 181 individuals (CV = 11.1%; 95% CI = 156-244).

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, although we did 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 of less than two in the adjusted AIC values (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 LRT to the top ranked nested models we considered the difference in deviance between the candidate models that were distributed as a χ_2 statistic (the difference in the number of estimable parameters between the two models determines the degrees of freedom). The results of the LRTs 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, since the model with just the group size 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.

Selecting the most parsimonious model that included group size as a covariate (also the top ranked model according to the adjusted AIC values) gave an estimate of 195 Irrawaddy dolphin groups (CV = 15.7%), which corresponded to 449 individuals (CV = 16.99%; 95% CI = 384-514) using the same group size estimate as before.

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, since 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. Selecting the most parsimonious model with no covariates gave an estimate of 92 Ganges River dolphin groups (CV = 4.6%), which corresponded to 207 individuals (CV = 10.82%; 95% CI = 163-251) using the same group size estimate as before.

DISCUSSION

Distribution and Abundance

Within the extent of occurrence of each species (determined by creating a polygon around all sightings with the exception of two extreme outliers for Ganges River dolphins) we recorded 0.194 sightings/km and 0.487 dolphins/km for Ganges River dolphins, and 0.076 sightings/km and 0.182 dolphins/km for Irrawaddy dolphins. Compared to other areas where Ganges river dolphins have been surveyed, encounter rates in the Sundarbans were greater than some but less than others. For example, 1.36 dolphins/km were recorded in 43.5 linear km of the lower Sangu River in January 1999 but only 0.47 dolphins/km in 70.8km of the neighboring Karnaphuli River during the same month (Smith *et al.* 2001). Comparisons for Irrawaddy dolphins show that encounter rates in the Sundarbans were apparently higher. For example, 0.16 dolphins/km were recorded in 360 linear km of the upper reaches of the Ayeyarwady River in January and February 1998 (Smith and Hobbs 2002) and 0.06 and 0.09 dolphins/km for 432 km and 78 km of the middle section and tributaries of the Mahakam River, respectively, during February through April 1997 (Kreb 1999). These comparisons should be considered judiciously, however, because vessel speed, sighting conditions, platform

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

Detection rates for each 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 the upstream segments receiving freshwater inputs from the Passur, Sela Gang and Baleswar Rivers (Fig. 3). There were distributional outliers for Ganges River dolphins and a distinct overlap zone 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 gillnet fishing was most often concentrated. Martin *et al.* (2004) reported similar observations of an overlap between areas of high gillnet deployment and the occurrence of botos *Inia geoffrensis* and tucuxis *Sotalia fluviatilis*. Within the Sundarbans National Park, a relatively high density of Ganges River dolphins was documented in the upper reaches of the Mrigamarikha 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 a optimal shoreline-to-water surface ratio that provides sufficient space for the formation of the large, deep pools where the animals are generally found (see Smith 1993; Smith *et al.* 1998), and its close proximity to the Passur River, a movement corridor for riverine fishes, as evidenced by the large number of gill nets deployed there during the survey. No abundance hotspots were identified for Irrawaddy dolphins, except possibly the upper reaches of the Sibsa River, the mouths of confluences and portions of the mainstem influenced by confluences.

Independent Concurrent Counts

This study advanced the methodology for surveying freshwater and estuarine cetaceans - especially in complex, alluvial channels where distance sampling methods are generally inappropriate due to the impossibility of following transects placed randomly relative to

dolphin distribution. In past studies abundance estimates for freshwater cetaceans in Asia have probably been biased downward, because under most circumstances some unknown proportion of the population has not been detected (Smith and Reeves 2000b). Sighting biases were 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). Using independent concurrent counts 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 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 maintain consistent vigilance and consistently 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. The 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, almost certainly caused by the small sample sizes available for the individual strata.

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 higher than those from the simple and stratified estimates obtained by means of the Chapman's modified Lincoln-Petersen mark-recapture estimator. The Huggins models

have the advantage of incorporating these covariates directly into the modeling process making use of the capture histories, and also maintaining the link between individual specific capture histories and the individual covariate values, which the other estimation method does not. Although the Huggins modeling procedures make better use of the capture-recapture information for integrating the 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 that 60% of the population is captured (White 2002) [or visually detected] – a situation that, according to the percentage of corrected versus 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 proved to be robust for both species, since the 95% CIs overlapped for both methods. Ultimately the analytical advantages of the Huggins models probably outweigh those of the Lincoln-Petersen Estimator, but the latter should be considered appropriate when simplicity is a priority (e.g., where population assessments are carried out by non-specialists) and reliable data on explanatory variables are not available.

Evaluation of Precision and Biases of Abundance Estimates

Although we incorporated variability associated with the estimation of group size when calculating the variance of our abundance estimates (see above), the results reflected potential sampling error (as well as biological heterogeneity that may select for different size groups according to sex and age class and/or environmental variables) and not potential biases related to the ability of observers to accurately estimate group sizes. An initial attempt was made to incorporate the mean percent difference between the group sizes estimated for matched sightings by the primary and secondary observer teams as a component of variability for our abundance estimates. However, group size estimates made by the primary team were significantly greater than those made by the secondary team (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 versus high, and best versus low group size estimates (17% and 41% for Irrawaddy dolphins, respectively, and 11% and 22% 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 would invalidate our abundance estimates. The larger difference in the numbers calculated for the best versus low compared to the best versus high group size estimates implied that the observers had greater confidence that their best estimates were unbiased in a positive compared to negative direction.

The mark-recapture analysis of double concurrent counts estimated perception bias but did not address availability bias (see above). A rough evaluation was made on whether availability bias may have resulted in an underestimation of abundance for both species by using group dive time information and the distance estimates made to dolphin groups at the time of detection. 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 groups of Irrawaddy dolphins and two groups of Ganges River dolphins. According to distance estimation data from the primary team, a decline in sighting frequencies occurs past 200m and 75m for Irrawaddy and Ganges River dolphins, respectively. The average 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 that while surveying along 200m 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 (201-400m) where the proportion of detected animals was still relatively high (76.4%). A cumulative frequency distribution of dive

times for Ganges River dolphins indicated that while surveying along 75m 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 (76-150m) where the proportion of detected animals 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 limited information, 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 the actual positions were oriented at various radial angles determined by random chance, the availability of suitable habitat, channel width and detection distances. We recommend that data on the relative angle of detected dolphins in relation to the bow be collected during future surveys, and that a more sophisticated approach, which takes into account differential periods of visual coverage across variable channel widths, be developed for evaluating availability bias.

Conservation and Research Recommendations

Regardless of the analytical model used, the results of our investigation indicate that waterways of the Sundarbans mangrove forest in Bangladesh support potentially viable populations of Ganges River and Irrawaddy dolphins. Ganges River dolphins inhabiting these channels are the downstream boundary of a much larger population in the Ganges-Brahmaputra-Megna system (see references above). Conversely, Irrawaddy dolphins are the inland extent of a larger population that extends to the shallow and more saline waters of the outer delta (Smith, B.D., unpublished data from a line-transect survey conducted in February 2004). The boundary between the ranges of both species migrates along a southwest and northeast axis according to the seasonal freshwater regime. 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 biological impacts of declining freshwater flows on other aquatic biota. Future research on these dolphins 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 strong 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. A survey was planned for February 2002, with many of the same members of the research team who conducted this survey, but the research permit was withdrawn by the West Bengal Forest Department, reportedly due to security concerns, the day before fieldwork was scheduled to begin.

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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.

	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					
GG=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%

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	347.0097	0.0000	0.24876	194.79	14.37	176.90-237.51	0.645 0.459	0.066 0.048	0.508-0.762 0.368-0.552
Sighting conditions + group size	347.5615	0.5518	0.18878	197.33	16.07	177.60-245.64	0.641 0.457	0.067 0.0478	0.501-0.761 0.366-0.551
Group size + channel width	348.4997	1.4900	0.11809	194.91	14.43	176.95-237.80	0.648 0.457	0.066 0.048	0.511-0.764 0.366-0.551
Group size[a]	348.8282	1.8185	0.10021	197.64	17.22	177.07-250.59	0.645 0.460	0.068 0.047	0.503-0.765 0.370-0.553

[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 Tables 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	170.3244	0.0000	0.37335	92.44	4.62	86.81-106.41	0.696	0.047	0.596-0.780
None	170.8509	0.5265	0.28694	91.64	4.24	86.48-104.49	0.693	0.047	0.595-0.776
Group size + channel width	171.8669	1.5425	0.17265	92.77	4.84	86.89-104.49	0.696	0.047	0.595-0.781
Sighting conditions	171.9326	1.6082	0.16707	92.22	4.67	86.61-106.54	0.693	0.047	0.594-0.777

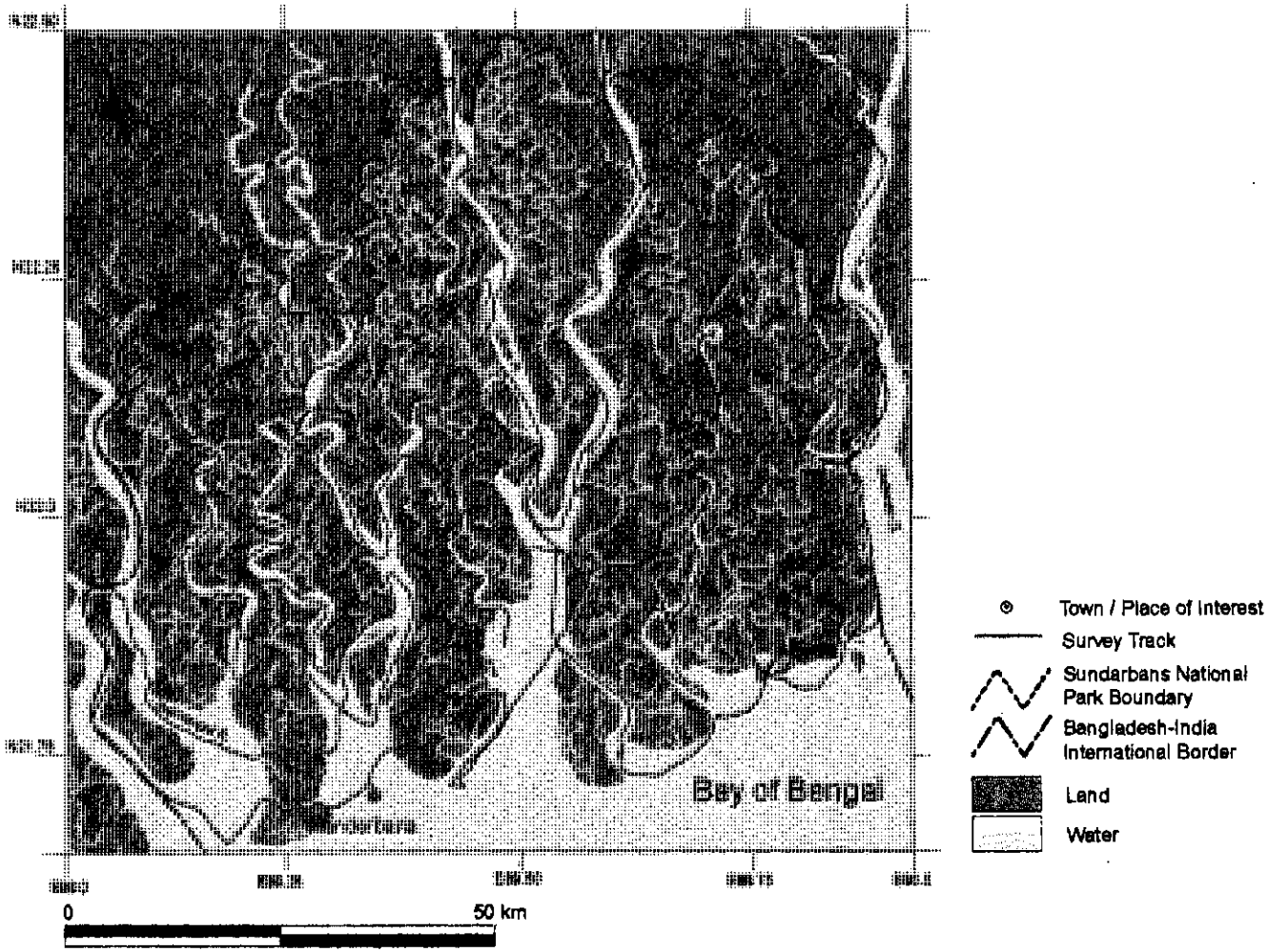

Figure 1. Map of the inner Sundarbans Delta in Bangladesh showing the March 2002 survey trackline.

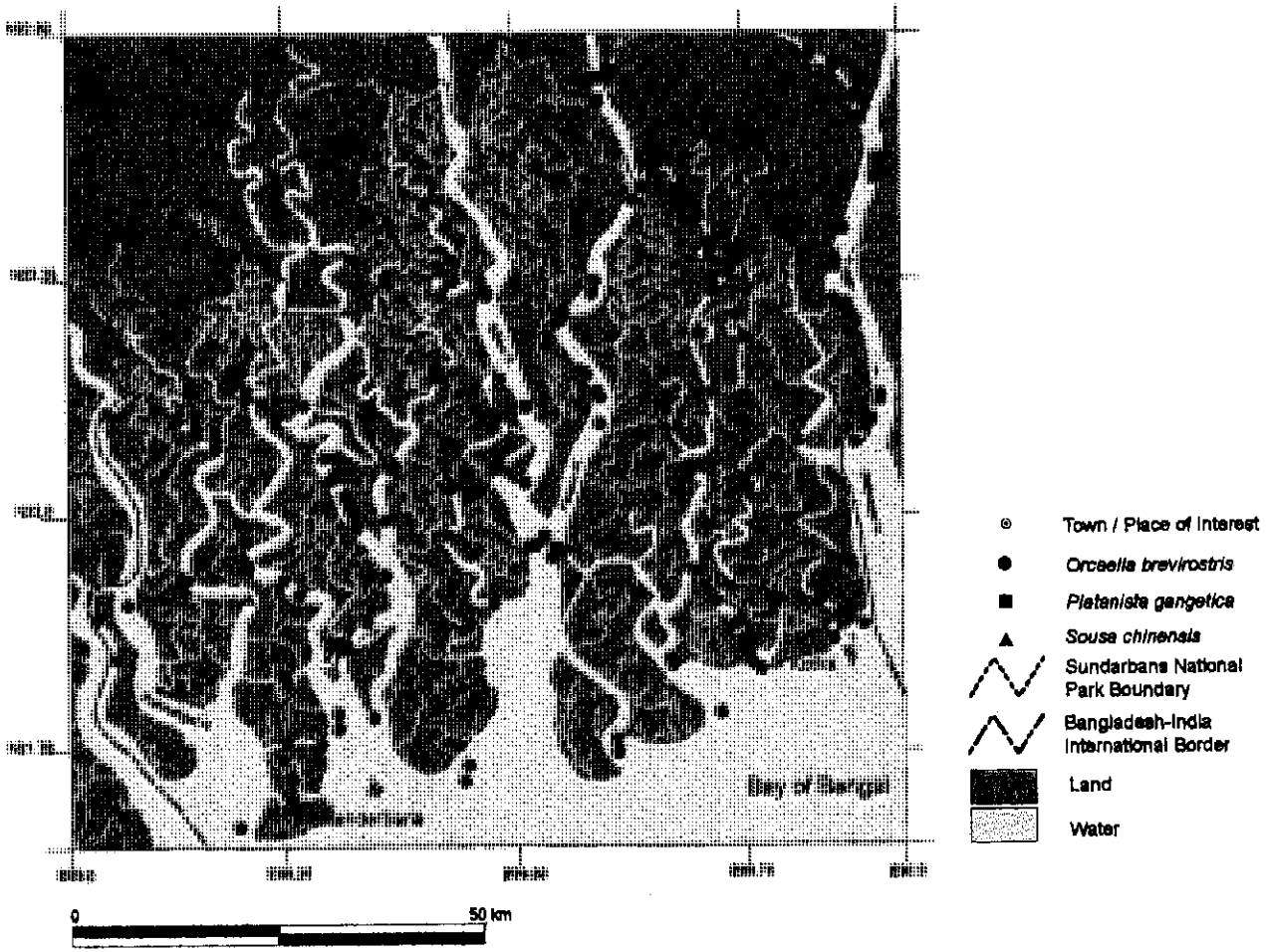

Figure 2. Map of the inner Sundarbans Delta in Bangladesh showing the locations of dolphin sightings recorded during a survey in March 2002.

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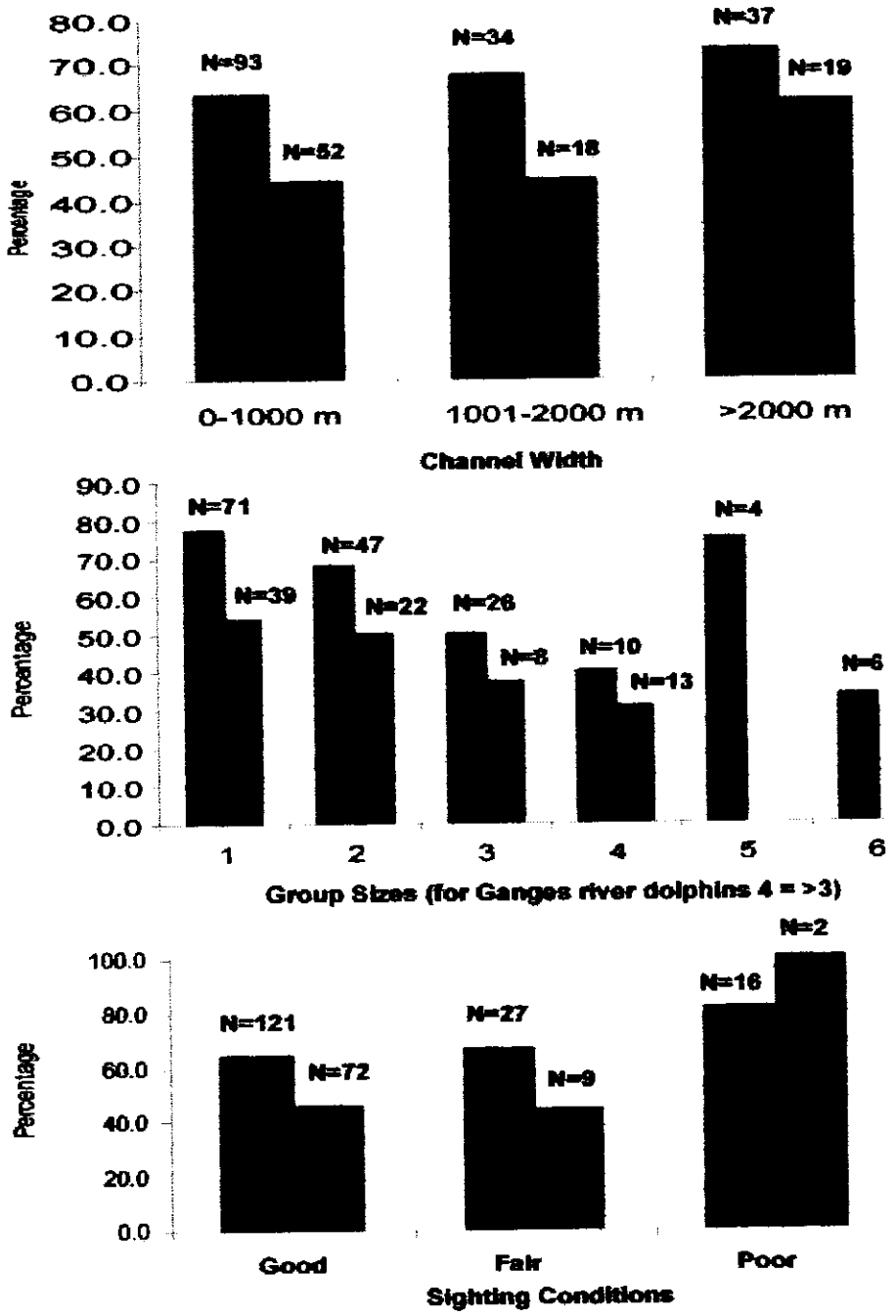

Figure 3. Percentage of missed sightings (unique to primary or secondary observer team) for Irrawaddy dolphins (black) and Ganges River dolphins (gray) according to channel widths, group sizes and sighting conditions.