Abundance of freshwater Irrawaddy dolphins in the Mahakam River in East Kalimantan, Indonesia, based on mark-recapture analysis of photo-identified individuals

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ABSTRACT

From February 1999 to August 2002 *ca* 9,000km (840 hours) of search effort and 549 hours of observation on Irrawaddy dolphins (*Orcaella brevirostris*) were conducted by boat in the Mahakam River in East Kalimantan, Indonesia. An abundance estimate based on mark-recapture analysis of individuals photographed during separate surveys is presented here. Petersen and Jolly-Seber analysis methods were employed and compared along with earlier estimates derived from strip-transect analysis and direct counts. These comparisons serve to evaluate the biases of each method and assess the reliability of the abundance estimates. The feasibility of video-identification is also assessed. Total population size calculated by Petersen and Jolly-Seber mark-recapture analyses, was estimated to be 55 (95% CL=44-76; CV=6%) and 48 individuals (95% CL=33-63; CV=15%) respectively. Estimates based on strip-transect and direct count analysis for one sampling period, which was also included in the mark-recapture analysis, were within the confidence limits of the Jolly-Seber estimate (N_{count} = 35 and N_{strip} = 43). Calculated potential maximum biases appeared to be small, i.e. 2% of *N* for Petersen and 10% of *N* for the Jolly-Seber method, which are lower than the associated CVs. In addition, a high re-sight probability was calculated for both methods varying between 65% and 67%. Video images were considered a valuable, supplementary tool to still photography in the identification of individual dolphins in this study. For future monitoring of trends in abundance using mark/recapture analyses, a time interval is recommended between the two sampling periods that is short enough to minimise the introduction of errors due to gains and losses. Also, survey area coverage during photo-identification should be similar to avoid violation of the assumption of equal capture probabilities. The alarmingly low abundance estimates presented underline the need for immediate and strong action to preserve Indonesia's only known freshwater dolphin population.

KEYWORDS: ABUNDANCE ESTIMATE; CONSERVATION; MARK RECAPTURE; IRRAWADDY DOLPHIN; PHOTO-ID; ASIA

INTRODUCTION

Since 1970, photo-identification has proved to be a valuable tool in the assessment of population dynamics, social organisation, distribution and movement patterns for many species of cetaceans (e.g. Hammond *et al.*, 1990; Whitehead *et al.*, 2000). The technique involves collecting and cataloguing photographs of the dorsal fins, flukes and bodies of cetaceans with distinctive marks that allow for identification of individuals. However, the ease of getting good photo-identification results varies among species depending on uniqueness of the marks and behaviour of the species. Easily identifiable cetaceans with nearly complete photo-identification databases for certain populations include killer whales, *Orcinus orca* (Baird, 2000) and humpback whales, *Megaptera novaeangliae* (Clapham, 2000). For most other species, e.g. Indo-Pacific hump-backed dolphins, *Sousa chinensis* (Jefferson and Leatherwood, 1997; Jefferson, 2000); Pacific white-sided dolphins, *Lagenorhynchus obliquidens* (Morton, 2000) and northern bottlenose whales, *Hyperoodon ampullatus* (Gowans and Whitehead, 2001) only a proportion of the population can be reliably identified. Another factor limiting such studies is the elusive behaviour of some species. Photo-identification of Irrawaddy dolphins, commonly described as elusive (Lloze, 1973; Dhandapani, 1992; Kreb, 1999), requires greater effort, but was shown to be feasible for coastal populations in Australia (Parra and Corkeron, 2001). Freshwater populations of Irrawaddy dolphins that are known to occur in only three major river systems, i.e. the Mahakam River in Kalimantan, the Mekong River in Vietnam, Laos and Cambodia and the Ayeyarwady River in Myanmar (Burma) have been reported to be visually identifiable, but only an opportunistic photo-identification effort had been undertaken until recently (Stacey, 1996; Smith *et al.*, 1997; Krebs, 1999). Since freshwater dolphin populations often live in a closed system with no exchange with coastal populations, photo-identification and subsequent mark-recapture analysis to determine total population size might be feasible. This study reports on photo-identification studies of a population of Irrawaddy dolphins in the Mahakam River, Indonesia and represents the first attempt to obtain a catalogue in which most individuals of an entire freshwater Irrawaddy dolphin population are identified.

The Irrawaddy dolphin is a facultative freshwater dolphin, occurring both in shallow coastal waters and large river systems in tropical South East Asia and sub-tropical India (Stacey and Arnold, 1999). Irrawaddy dolphins in Indonesia occur along several coastlines and in one river in East Kalimantan, the Mahakam, where they are commonly referred to as *pesut* (Kreb, 1999). The species has been fully protected by law in Indonesia since 1990 and is the adopted symbol of East Kalimantan Province. Their IUCN status was raised from 'Data Deficient' to 'Critically Endangered' based on data related to abundance collected from 1999 until 2000 (Hylton-Taylor, 2000; Kreb, 2002).

This study presents estimates of total population size based on photo-identification using different mark-recapture methods and compares these with earlier estimates of abundance from strip-transects and direct counts (Kreb, 2002). The feasibility of using digital video recordings as a tool to identify dolphins is also evaluated. This photo-identification study is part of a long-term conservation and research project begun in 1999 to provide a framework to protect the freshwater Irrawaddy dolphin population in the Mahakam River in East Kalimantan, Indonesia.

SURVEY METHODS

During the study period (February 1999 – August 2002), 12 surveys were conducted. Six extensive monitoring surveys (mean duration 20 days; standard deviation (SD) = 4 days) covered the entire range and six focussed surveys (mean duration 12 days; SD = 3 days) were conducted in areas of high dolphin density (Fig. 1). Extensive surveys were conducted with 12-16m long motorised vessels (between 12 and 21hp), travelling at an average speed of 10km hr^{-1}. The average observation time and photographic effort during the extensive monitoring surveys was one hour per sighting. The focussed surveys involved attempts to follow one group for an entire day, with daily alternation of groups and using a small, motorised canoe with a 5hp outboard engine. Photographic effort was spread out over the observation time (average duration 7 hours; range 1.5-13 hours).

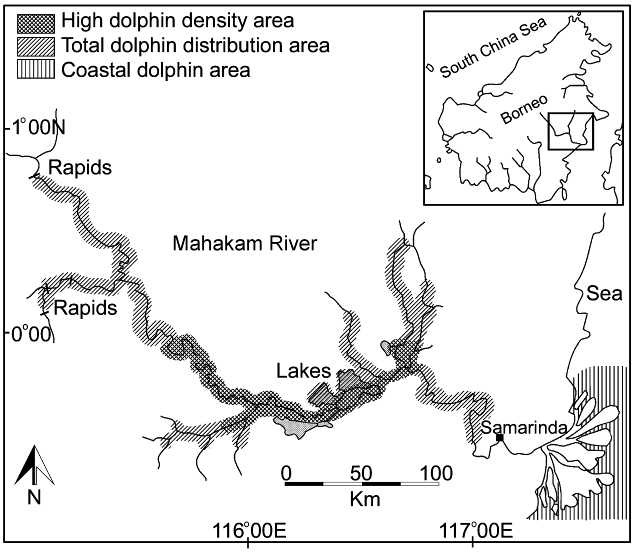

Fig. 1. Study area.

Upon sighting, a group was approached to a minimum distance of 30m in order to take photographs and video images. Effort was made to take these photos from similar angles, i.e. perpendicularly to the dolphins' dorsal fin region. In addition, identification marks were recorded on datasheets. For each sighting, the duration, location, group behaviour, group size, group composition and environmental data were collected. Four age classes were defined: (1) 'neonates' – animals of less than 1/2 the average length of an adult, which spent all their time in close proximity to an adult and exhibited an awkward manner of swimming and surfacing; (2) 'calves' – animals between 1/2 and 3/4 the average length of an adult and which still spent most of their time in close proximity to an adult; (3) 'juveniles' – animals of 3/4 the average length of an adult and which swam independently; and (4) 'adults' – animals larger than an estimated 2m in length.

Photographs were taken using a *Canon* EOS 650 camera body with a *Sigma* 300mm/f4.0 lens, occasionally attaching a 1.4 teleconverter, effectively making it a 420mm/f5.6 lens. Manual focus was always used with shutter speeds of 1/250 to 1/1500 of a second. About 75% of the photo-id images were taken using slide films (*Sensia Fujichrome* 100 ISO) the rest using print films (*Fuji Superia* 200 ISO). Effort was made to photograph every individual within the group irrespective of whether they appeared to have distinct dorsal fin markings.

Additionally, drawings of dorsal fins (made by aid of binoculars) were made by observers who did not take photographs. Dolphin age classes were also noted for each drawing. Direct observations and drawings were matched with a field photo-identification catalogue and assigned an existing or new identification code.

One field-assistant was assigned to the task of taking simultaneous video footage using a *Sony* VX 1000 digital camcorder with 10x optical and 20x digital zoom. In the majority of cases only the 10x optical zoom was employed to ensure better image quality. The auto-focus option was usually preferred since manual focusing proved more difficult with the camcorder than with the photo-camera.

Information on the number and occurrence of dead dolphins during the entire study period and in particular between the two sampling periods, was obtained through our own observations and from local, reliable reporters.

ANALYSIS

Photographs and slides were selected by aid of an 8x loupe for their good image quality (i.e. focus, glare, photographic angle, dorsal fin size coverage in image) and catalogued on the basis of identifiable features. Distinctive features noted included distinct fin shapes and notches, scars and cuts on the dorsal fin. Pigmentation patterns were only secondarily considered if they could be linked to a distinct fin shape. Pigment spots or areas do not occur symmetrically on both sides of the dorsal fin. In addition, it was found that pigmentation patterns on the bodies of dolphins and therefore likely also on dorsal fins, were not stable during the study period. Each photograph in the photo-identification catalogue corresponded to an identified individual and held information on the date, time and location at which the picture was taken as well as data on group size and composition. Photographs with distinctive features such as scars, cuts and humps on the dolphins' bodies were also selected, but catalogued under a separate identification code. Photographs with distinctive body features alone were only used for mark-recapture analysis if they could be linked to an individual, which was already identified based on its dorsal fin. Identifications that were obtained through direct observation and drawings were kept in a separate database to the photo-identified dolphins. These identifications were not used for the mark-recapture analysis.

For analysis of recorded video-images, each dorsal fin image was played in slow motion and paused. Again, only images of good photographic quality were selected. The selected images were then compared with individuals from the photo-identification catalogue, given an identification code and put into a video-identification catalogue together with related sightings data.

Two estimates of total population size (*N*) were calculated based on two different mark-recapture analysis methods. Only sampling periods with extensive area coverage were selected. The first estimate utilised the Petersen method for closed populations, involving one session of catching and marking and one recapture session and Bailey's modified estimator (Hammond, 1986) was applied for sampling with replacement (Equations 1.1-1.3).

Sample periods May/June 2000 and August 2001 were chosen because the photographic efforts (i.e. area coverage) were similar in those periods (Table 1).

The second method to estimate total abundance was the Jolly-Seber method for open populations, allowing for gains and losses within the sampling periods (Equations 2.1-2.4).

Table 1

Photo-identification success rate and discovery rate of new individuals.

Year	Survey period	Survey area coverage	No. dolphin photographs	No. identified dorsal fins	No. different individuals (n_i)	No. of new individuals
1999	Feb/Mar	E	25	3	2	2
	Apr/May	E	25	7	5	5
	Oct	E	49	28	16	13
2000	May/Jun	E	206	90	33	21
	Aug	I	157	83	24	4
	Nov	I	65	23	16	1
2001	Jan/Feb	E	175	82	29	6
	Jun/Jul	I	267	127	37	1
	Aug	E	178	90	34	3
	Oct/Nov	I	89	36	23	1
2002	Apr	I	181	102	28	1
	Aug	I	82	54	23	1
Total	12 periods		1,499	728		59

E = extensive monitoring survey in entire dolphin distribution area; I = intensive monitoring survey in high dolphin density areas.

$$N = n_1 \frac{(n_2+1)}{(m_2+1)(1-p)} \text{(Petersen method)} \qquad (1.1)$$

$$CV(N) = N^{-1}\sqrt{\frac{n_1^2(n_2+1)(n_2-m_2)}{(m_2+1)^2(m_2+2)} + \frac{\text{var}(1-p)}{(1-p)^2}} \qquad (1.2)$$

where:

n_1 = number identified on the first occasion;
n_2 = total number identified on the second occasion;
m_2 = number of identified dolphins found on the second occasion;
p = proportion of unidentifiable individuals.

$$N_i = \frac{M_i(n_i+1)}{(m_i+1)(1-p)} \text{(Jolly-Seber method)} \qquad (2.1)$$

$$M_i = \frac{m_i + (R_i+1)z_i}{(r_i+1)} \qquad (2.2)$$

$$\Phi_i = \frac{M_i+1}{(M_i - m_i + R_i)} \qquad (2.3)$$

$$CV(N_i) = \sqrt{x_i} \bullet \frac{\sqrt{\left(\frac{M_i - m_i + R_i + 1}{M_i+1}\right)\left(\frac{1}{(r_i+1)} - \frac{1}{(R_i+1)}\right) + \frac{1}{m_i+1} - \frac{1}{n_i+1} + \frac{\text{var}(1-p)}{(1-p)^2}}}{\log_e N_i + 0.5\log_e\left(\frac{0.5-3n_i}{8N_i}\right)} \qquad (2.4)$$

where:

N_i = population size at the time of the ith sample;
M_i = number of marked animals in the population when the ith sample is taken (excluding animals newly marked in the ith sample);
n_i = total number of animals caught in the ith sample;
R_i = number of animals that are released after the ith sample;
m_i = number of animals in the ith sample that carry marks from previous captures;
z_i = number of animals caught both before and after the ith sample but not in the ith sample itself;
r_i = number of animals that were released from the ith and were subsequently recaptured;
x_i = number of samples;
Φ_i = proportion of the population surviving from the ith to the $(i + 1)^{th}$ sampling occasion.

Capture histories of each identifiable individual are needed since the method requires both knowledge of the number of animals in each sample that were previously marked and information on the most recent previous sample in which each of them was last trapped. The number of marked individuals in four sampling periods, i.e. October 1999, May/June 2000, January/February 2001 and August 2001, with extensive area coverage, were higher than the minimum sample size of 10 marked individuals recommended to overcome the imprecision of abundance estimates (Sutherland, 1996). Prior to the calculation of an abundance estimate, a goodness-of-fit test was applied (Sutherland, 1996) to test if animals differed in capture-probabilities, which may cause a serious bias of the estimate. After testing, three sampling periods were chosen to be appropriate for abundance estimation (see results).

According to the Jolly-Seber method, no estimates of abundance can be calculated for the first and last sampling periods and thus only one estimate is derived from the second sampling period (Equation 2.1). For this last method, it was also possible to calculate the proportion of the population surviving (Φ) from the 1st to the 2nd sampling occasion (Equation 2.3).

A correction factor was applied to the population estimates from both methods to correct for the proportion (p) of dolphins that are not identifiable (Jefferson and Leatherwood, 1997). These were neonates and calves which could not be photographed effectively because their mothers protected them from the boat and from a good camera angle, and because calves often surface very suddenly (high arch dives). The averages of the proportion of neonates and calves encountered during two (Petersen) and three (Jolly-Seber) sampling periods are 10% and 8% respectively, which represent the proportion of unidentifiable dolphins (p).

For the Petersen method, binomial 95% confidence intervals were calculated for the fraction of marked individuals (m_2+1) / (n_2+1), which were then applied to Equation 1.1 to obtain the 95% confidence limits for population size (Krebs, 1999). Jolly-Seber confidence limits were calculated using the formula provided by Manly (1971). Coefficients of variation were calculated for both methods according to the formulae in Equations 1.2 and 2.4. Estimated resighting probabilities for the Petersen estimator are given by m_2/n_2 and $p_2=m_2/n_1$ and for Jolly-Seber by n_i/N_i, in which N_i is (only here) the uncorrected abundance estimate for the proportion of identifiable dolphins.

Finally, maximum biases that may affect population size estimates for each method were calculated. A maximum bias using Petersen's method, which assumes no losses, was calculated by adding the number of dead dolphins (3) inbetween the two sampling periods, to the number of 'recaptured' animals during the second sampling period ($m_{2bias}=m_2+3$). This number was also added to the total number caught on the second occasion ($n_{2bias}=n_2+3$). When addressing this bias it is assumed that these dolphins would have been 'marked' during the first session and also assumes that they would have been 'recaptured' if they had not died.

A 'maximum' bias using the Jolly-Seber method can be obtained from the fact that one area was not surveyed during the second sampling period of the three sampling periods in total. This area, which is an area inbetween two rapids and known to be the home of a group of six dolphins, was surveyed only during the first and last sampling period. Two and three new individuals were marked during the first and last sampling period, respectively, without any recaptures. The largest deviation from the abundance estimate would apply for a situation in which it is assumed that this area would have been surveyed during the second sampling period, where four new individuals would be captured and marked and three of these would be recaptured during the third sampling period. This maximum deviation of the estimate is calculated following Equation 2 by adding three individuals to r_2 (number of marked dolphins in the 2nd sample, which were recaptured in the 3rd sample) and four individuals to n_2 and R_2 (total number caught and released in the 2nd sample). Variable z_2 is not affected by the missing survey effort during the second sampling period because the individuals marked in that area were not similar during the first and last sampling period. This 'maximum' bias holds only if the following assumptions are true: neither of the two individuals marked during the first sampling period would be recaptured if the 'missed' area was surveyed during the second sampling period. Four individuals would be marked during the second sampling period so that $r_{2bias} = r_2 + 3$, $n_{2bias} = n_2 + 4$ and $R_{2bias} = R_2 + 4$. To assess the minimum annual birth rates the total number of newborns were counted during five separate surveys between November 2000 and November 2001, with an average gap of 2.5 months between surveys. Newborns were assumed to be different from those encountered in any earlier survey.

RESULTS

Estimates of abundance based on photo-identification mark-recapture analysis

During the entire study period from February 1999 until August 2002, a total of 2,074 photographs were taken during 83 days of which 1,499 (partially) portrayed dolphins and 558 (27%) completely failed, showing merely circles in the water (Table 1). Of the dolphin photographs, 753 photographs (50%) were selected for photo-identification because of good image quality. Some 728 photographs showed identifiable features on dorsal fins, sometimes in combination with other characteristic traits on the dolphins' bodies, producing an average of almost nine identifiable dorsal fin photographs per day. An additional 25 photographs only showed identifiable features on the dolphins' bodies. As such, a total of 59 individual dolphins were catalogued based on dorsal fin identification. Four individuals are shown in Fig. 2.

Within the four initially chosen sampling periods for the Jolly-Seber method, animals appeared to differ significantly in capture-probabilities (G=10.06; d.f.=2; P<0.01), meaning that the underlying assumptions (see discussion) of the method were violated. The bias was consequently rendered insignificant by only using sampling periods which include a high proportion (i.e. over 50%) of the population. Therefore, the October 1999 sampling period was removed from analysis, which included only 31% of the Petersen population estimate. Another G-test for the remaining periods revealed that this time no assumptions were violated (G=1.8; d.f.=1; P=0.17).

The number of dolphins identified by photograph for each sampling period (n_i) are presented in Table 1. For the Petersen method the number of dolphins that were identified in the first period (May/June 2000) and recaptured by photograph during the second period (m_2) (August 2001) is 22 individuals. For the Jolly-Seber method m_2 is 14 individuals (using periods May/June 2000 and January/February 2001). The estimated resighting probabilities for the Petersen method are either 65% or 67%; 66% for the Jolly-Seber method. The number of dolphins that were recaptured by photograph in the third sampling occasion (Jolly-Seber) and identified during earlier occasions (m_3) is 28 individuals, illustrating the high resighting probability over more than two sampling periods.

The estimate of total population size using the Petersen two-sample mark-recapture method was 55 individual dolphins (95% CL=44-76; CV=6%). Calculating a potential maximum bias due to loss of individuals between the sample periods, lowers the estimate to 54 individuals (95% CL=44-76; CV=10%), which is 2% lower than the population size estimate above. During the 3.5 year study period at least 17 dolphins have died but the specific dolphin identities were not available and thus could not be traced back to the photo-identification catalogue. An estimate of population size using the Jolly-Seber method arrives at 48 individual dolphins (95% CL=33-63; CV=15%). The proportion of the population surviving from the 1st to the 2nd sampling occasion is 66%. The reported number of dead dolphins between these two sampling periods is two individuals (4% of N_2). An estimate was also calculated including a maximum bias due to lack of survey effort during one of the sampling periods in one 'closed' area that is inhabited by a group of six dolphins. The corrected estimate is 53 individuals (95% CL=36-64; CV=19%), which is 10% greater than the unbiased population size estimate of 48.

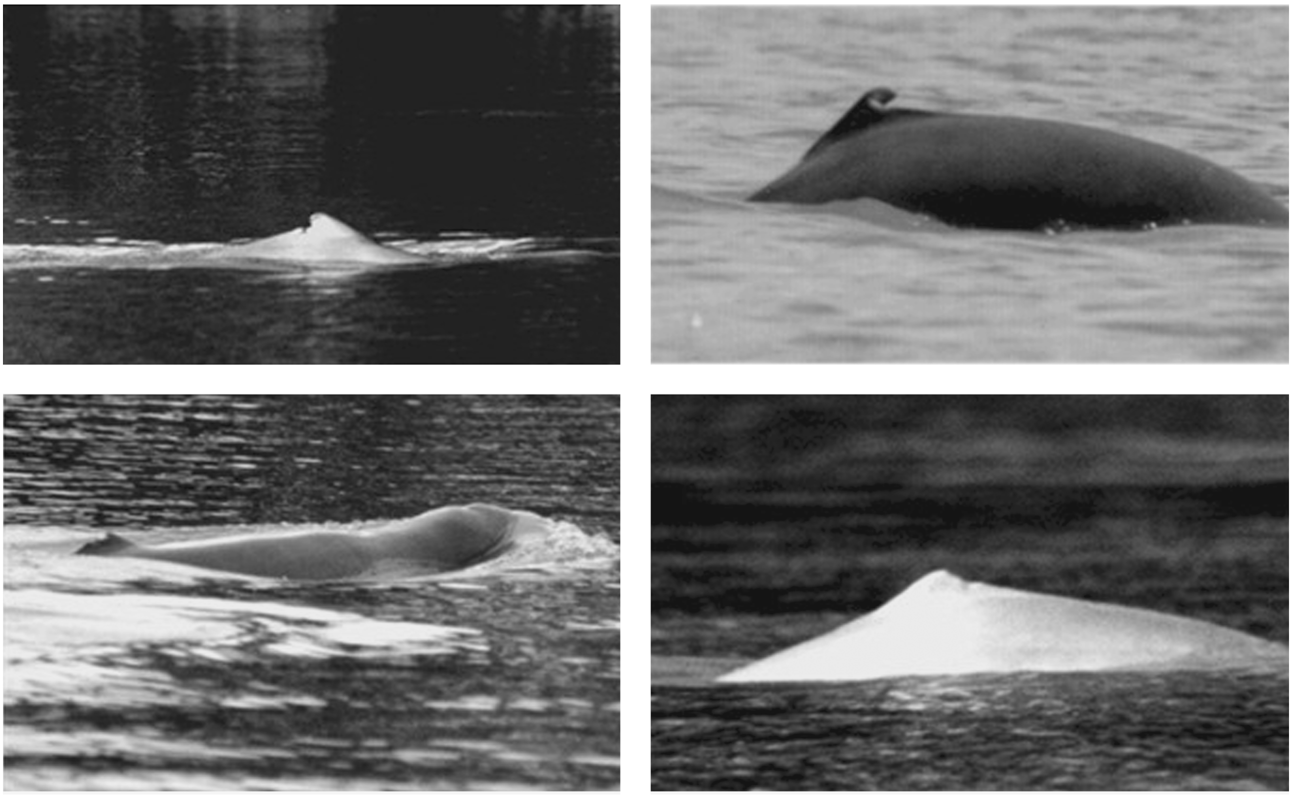

Fig. 2. Left above = PM 2; Right above = PM 1; Left below = PM 8; Right below = PM 3.

Fig. 3 shows the cumulative number of new individuals identified in different survey periods in combination with photographic success in obtaining identifiable pictures of dorsal fins for each sub-period. The cumulative frequency curve begins to level off after the August 2001 survey period and during the next three survey periods only one individual was added each time (Table 1). Some 95% of the individuals of the photo-identification catalogue are identified in the period March 1999 until August 2001. After that date a plateau in the number of new identifications is more or less reached, with only a yearly 5% increase of new identifications (three individuals) of the total photo-identification catalogue. With an estimated annual birth rate of 10.5% of the total population, this yearly 5% increase is within this birth rate range and may therefore be attributed to possible neonates. It should however be noted that these

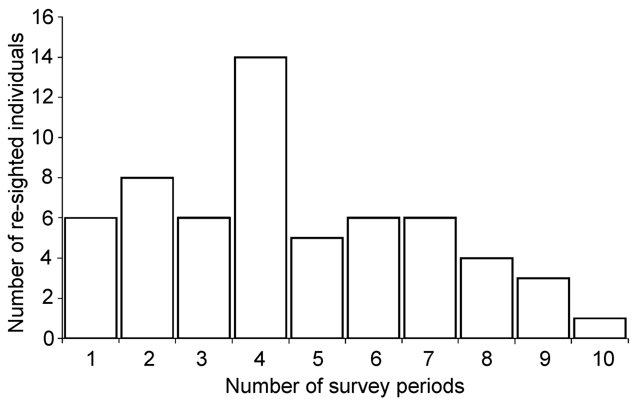

Fig. 4. The number of re-sighted individuals during a number of survey periods, e.g. 14 individuals were re-sighted during four different survey periods.

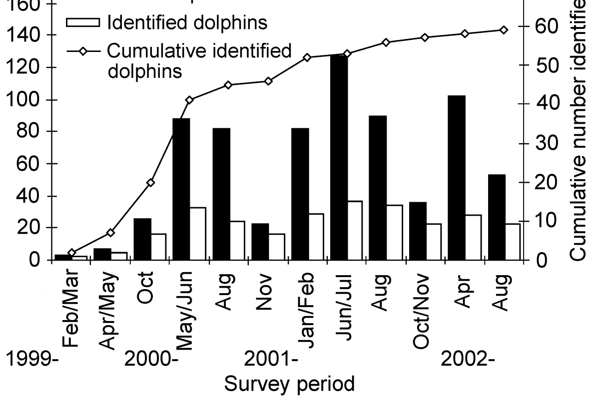

Fig. 3. Discovery rate of new individuals and number of identified dolphins per survey period in relation to the number of selected pictures.

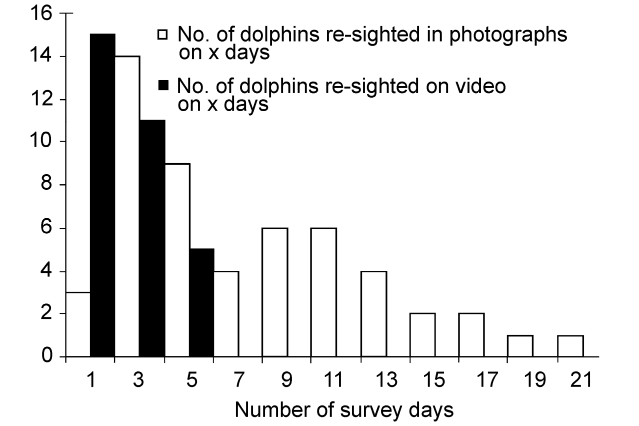

Fig. 5. The number of re-sighted dolphins on photograph and video over a maximum of 21 days, e.g. 14 and 11 dolphins were re-sighted on photograph and video respectively during periods of 2 and 3 days.

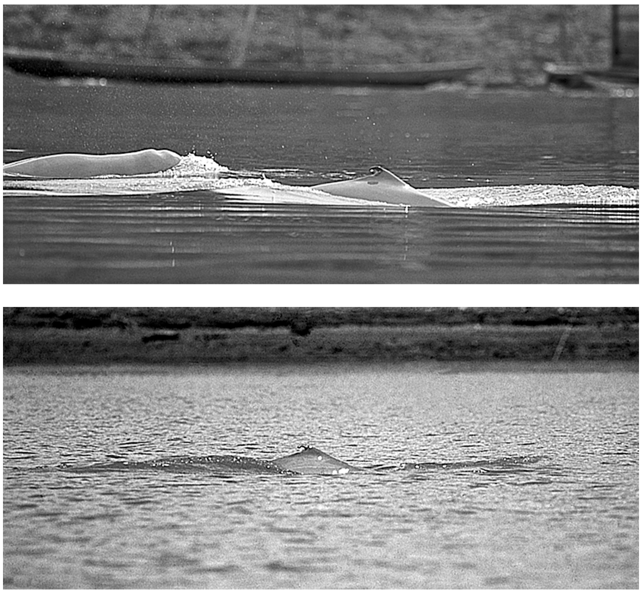

Fig. 6. Example of a low quality photograph (small dorsal fin image), in which dolphin PM01 can still be identified over larger distances due to the distinctiveness of its mark. Dolphin PM01 was photographed during 21 different survey days, on 41 pictures and photographed here on 23 August 2000 (upper picture) and 2 July 2001 (lower picture).

neonates can be identified only when they are over one-year of age, since they are otherwise difficult to photograph. Thus, new identifications within any one year may include last year's neonates, i.e. one-year old calves. The plateau was not a result of low photographic effort, since the number of new individuals added to the catalogue is not correlated with the number of identifiable photographs (r=0.06; d.f.=10).

Some 98% of the identified dolphins were recaptured by photograph on at least two different days and 90% were recaptured during at least two different survey periods (Figs 4 and 5). Individual dolphins were recaptured on a mean of 7.0 different survey days (± SD=4.7) and 4.5 survey periods (± SD=2.4). Individual dolphins were recaptured on a maximum of 21 days and 10 survey periods (Fig. 6).

Feasibility of video-identification

Video recordings were made during seven different survey periods and 21 days. The total recording effort was 8.8 hours. Identifiable dorsal fins of surfacing dolphins were recorded on 79 video-images, from which 31 different individuals could be identified. On average, nine identification images per hour and four images per day recording were produced. Four individuals were identified based on body marks alone. Fifty-two percent of the individuals were encountered on more than one day (mean=2.1; ± SD 1.4; range=1-5) (Fig. 5).

DISCUSSION

Estimates of abundance based on photo-identification mark-recapture analysis

Violated assumptions and biases

Two methods for analysing mark-recapture results of photo-identified dolphins were used in this study, the Petersen two-sample method and the Jolly-Seber method. The former method was found to be appropriate to obtain an estimate of total population since during two of the 12 survey-periods photographic 'trapping' effort was equally spread over the entire dolphin distributional range. This ensured that all animals had the same probability of being identified (assumption 2, see below). Most other survey periods involved intensive monitoring surveys in only areas of high dolphin density. Also, one area in between two rapids was not surveyed during the other extensive monitoring surveys due to bad weather conditions. The second method (Jolly-Seber) was applied because it allows for gains and losses between sampling periods. The disadvantages of using these methods are that they rely on underlying assumptions, which, if violated, produce serious biases in the results. For the Petersen method, these assumptions are: (1) the population is closed; (2) all animals have the same probability of being caught; (3) marking does not affect the catchability of an animal; (4) the second sample is a simple random sample; (5) animals do not lose their marks; and (6) all marks are reported on recovery. For the Jolly-Seber method, assumptions 2 and 5 from Petersen are also applicable. Additionally it is assumed that: (7) every marked animal has the same probability of surviving from the ith to the (i+1)th sample; (8) every animal caught in the ith sample has the same probability of being returned to the population; (9) all samples are instantaneous (Hammond, 1986).

The first and second assumptions are violated in this study by the Petersen and Jolly-Seber methods, respectively, and the effects are discussed below. The first assumption of the Petersen method was violated as three dolphins (identity unknown) died and four dolphins were born between the sampling periods. Mortality is unlikely to have influenced n_2 (total number caught on the second occasion), since during each sampling period only 55-57% of the total photo-identification catalogue was captured on film. However, m_2 (number of 'marked' animals recaptured on the second occasion) may have been affected since the number of 'recaptured' animals was not equal (only 64-66%) to the total number of individuals caught on the first and second occasions. Therefore, these dead dolphins of unknown identity may not have been 'marked' on the first occasion or, if they were, had not been recaptured. However, the three dead dolphins may have produced a biased estimate and therefore a correction was calculated for this bias, which decreased the estimate at the most by two individuals. This bias only applies if we assume that these three dolphins were 'marked' on the first occasion and presumably would have been caught on the second occasion if they had not died. In that case, the abundance estimate would be 54 individuals, which is clearly within the confidence limits of the abundance estimate of 55 individuals as described in the Results section. This small difference may be a result of the fact that a high proportion of the estimated population was captured during each sampling period (65-67%). Catching over 50% of the population limits biases that may arise through violations of assumptions (Sutherland, 1996).

As for mortality, recruitment (dolphins born between two sampling periods) is unlikely to have influenced the overall number of dolphins caught on the second occasion (n_2). Furthermore, neonates will not have influenced the number of 'marked' animals found on the second occasion (m_2), since they were born after the first sampling period and were thus not recorded. Neonates and calves have a low chance of being identified since they surface very irregularly and briefly during their first few months and are hard to photograph as they swim very close to the mother. Consequently, neonates encountered during the first sampling period are unlikely to have been 'marked' and so did not affect any of the variables of the Petersen formula.

Violations of the second assumption due to heterogeneity in catchability between dolphins and 'trap responses' were tested with a goodness-of-fit test for three sampling periods used within both analysis methods. This revealed no differences in capture probabilities except for the neonates and calves, for which a correction factor is applied to calculate abundance estimates (see analysis). This is in contrast to most other cetacean photo-identification studies in which unequal capture probabilities are often the case, due to variations in individual behaviour, such as wariness of boats or fluking behaviour, that affect the probability of obtaining good photographs (Whitehead *et al.*, 2000). Capture probabilities are more likely to vary for bow-riding dolphins, whereas the dolphins in this study were all photographed some distance from the boat. Thus, boat-shyness or attraction probably did not play a major role. Since photo-identification is in principal a non-invasive technique, any issues of trap responses are not relevant here. In spite of the fact that in theory dolphins had equal probabilities of being photographed, differences in distinctiveness of marks and in survey area may have caused capture probabilities (obtaining identifiable images) to vary among individuals and caused a bias of the population size estimate (Gowans and Whitehead, 2001). Although all photographs of good image quality yielded identifiable marks, photographs of lower quality (smaller images) were only identifiable for those individuals with very distinct marks (Fig. 6). Other markings needed to fill a significant part of the frame for identification and therefore more slides were discarded for use in connection with these features. Another bias in capture probability was related to differences in area coverage for each sampling period. However, the *G*-test result and the high percentage of re-sightings over different survey days and periods (95% and 90% of total identified individuals were re-sighted over two days and periods or more, respectively), indicate that the bias is not large, possibly due to the fact that a large part of the population was caught during both samples, as stated earlier. Nevertheless, a maximum bias was calculated that could affect the Jolly-Seber estimate for the difference in area coverage. This bias produced an estimate that only differed from three individuals from the Jolly-Seber estimate. Finally, dolphins in this study were only identified using natural marks, which would be stable over long sampling intervals (such as notches, cuts, scars and fin shapes) to prevent biases when marks are lost (such as pigmentation patterns) as suggested by Gowans and Whitehead (2001). Furthermore, other underlying assumptions of both methods did not seem problematic in this study.

The difference between the total number of dolphins identified (59) and the estimated total population size (N=48-55), may be explained by the fact that the first number was derived from a 3.5 year study period, during which 17 dolphins died. The total number of dolphins identified therefore does not represent an abundance estimate.

The proportion of the population surviving from the 1st to the 2nd sampling occasion was estimated to be 66% based on the Jolly-Seber equation, whereas the proportion surviving based on the reported number of dead dolphins between these two sampling periods is 96%. The difference may be explained by the fact that the probability of survival using the Jolly-Seber equation is determined by sampling the marked population only and variations in the size of this population may occur between two sampling periods for reasons other than mortality and emigration. For example, photographs are not always successful for all sightings within each sampling period due to the dolphins' group behaviour at that specific moment, which may vary through time for the same group. In this way, some groups may be missed from identification during one period but identified during another.

Identifiability

As stated above, from all photographs of good image quality of dorsal fins, individual dolphins could be identified. This agrees with a photo-identification study on coastal Irrawaddy dolphins in North Queensland, Australia, although juveniles were reported to lack any distinctive features that allow identification (Parra and Corkeron, 2001). In addition, as in the Australian study, no standardised identification measure (e.g. the Dorsal Fin Ratio; Defran *et al.*, 1990) could be used to identify Irrawaddy dolphins in the Mahakam River, since fins lacked clearly distinct top and bottom points. Irrawaddy dolphins in this study and those of others could also be identified based on the variation of dorsal fin shapes (Stacey, 1996; Parra and Corkeron, 2001). With regard to possible false matches, only three dolphins with more uniform, smooth dorsal fin shapes were found (although not similar compared to each other). However, each of these dolphins was only re-sighted on 5, 7 and 11 different survey days, i.e. within one standard deviation of the mean number of days on which all dolphins were re-sighted (mean=7 days, SD=4.7). So, the probability that other dolphins were identified as one of these three is low and otherwise the number of sighting days for these dolphins would be expected to be higher. In addition, fins were still identifiable on the basis of overall shape, even though characteristic notches were missing.

With regards to identification of calves and juveniles, Irrawaddy dolphins in the Mahakam River had identifiable features on their dorsal fins. This stands in contrast to work by Parra and Corkeron (2001), who conducted a photo-identification study of coastal Irrawaddy dolphins in Australia and found that calves and juveniles had no distinctive features to allow identification. During each of the extensive sampling periods (covering entire dolphin distribution range), one group of animals consisting of some six juveniles without adults was encountered. Unfortunately, only drawings of dorsal fins, (made by aid of binoculars) and one photograph showing distinctive marks on the juvenile's body were taken for this group due to their elusive surfacing behaviour. Juveniles in mixed groups were on the other hand much less shy, in fact they often surfaced near the boat. Since no record was kept in the field of the dolphin age classes of each photograph, it is not possible to trace which identified dolphin is a juvenile and which is an adult on the basis of the picture alone. However, occasionally, when drawings were made during the study of several characteristic dorsal fins, age class was also noted and these included both juveniles and calves.

The high percentage of individuals that were re-sighted on more than one occasion (98% of 59 identified dolphins) is an indication of the closeness of the Mahakam dolphin population. Percentages of re-sightings were similar (97% and 100%) for resident populations of marine tucuxis, *Sotalia fluviatilis* in Southern Brazil and of 21 identified bottlenose dolphins, *Tursiops truncatus*, in the Stono River estuary in South Carolina (Flores, 1999; Zolman, 2002). Resightings of seasonally occurring groups are typically lower; varying percentages of 32%, 50% and 57% were found for 675 identified individual Pacific white-sided dolphins in the Broughton Archipelago, Canada, 35 identified Irrawaddy dolphins in Cleveland and Bowling Green Bay in North Queensland, Australia and 213 identified Indo-Pacific hump-backed dolphins in Hong Kong waters, respectively (Jefferson, 2000; Morton, 2000; Parra and Corkeron, 2001).

Comparison of different techniques to estimate population abundance

The estimates of population size based on two different methods are similar and each is within the confidence limits of the other (combined between 33 and 76). Although the Petersen estimate (N=55) is somewhat higher than the Jolly-Seber estimate (N=48), the CV is smaller for the first estimate (CV=6% and 15%). The latter estimate is close to the estimate derived from direct counts and strip-transects in May/June 2000 (N_{count}=35 and N_{strip}=43) by Kreb (2002), with both estimates within the confidence limits of the Jolly-Seber estimate. Because the low estimates calculated here represent the total population size of dolphins in the Mahakam, immediate conservation measures are required to reduce the high minimum mortality rate of 10.5% dolphins of total population per year. It also shows that intended live-captures of dolphins for display in a local oceanarium should not be allowed for this small population.

In order to monitor future trends in abundance, photo-identification may be a valuable tool. However, to increase precision and prevent biases due to gains and losses of individuals it is recommended that photographs be taken during two extensive monitoring surveys in sequence covering the entire dolphin distribution range with a minimum time interval. Conclusively, since the results of the mark-recapture studies and direct count and strip-transect studies are very similar, future surveys to monitor trends in abundance of the latter type are feasible, if one needs to be cost efficient. However, surveys in combination with photo-identification are preferable in order to obtain data on long-term social systems and migration patterns.

Feasibility of video-identification

The number of identifiable video-images per hour recording in this study (9 images hr^{-1}), was much lower than those recorded in the video-identification study of bottlenose dolphins in South Carolina (Zolman, 2002), which yielded 31 images per hour recording time. This may be a result of the fact that in the latter study only a video was used for identification of dolphins, which may increase the drive to make good quality recordings. Another reason is that it may be more difficult to record dorsal fins of Irrawaddy dolphins because of their shy and irregular surfacing pattern (Kreb, 1999). The number of identifiable video images per day (4) was much lower than for still photography (9) in this study.

Nevertheless, although the yield of identifiable images may be less than in other studies and in comparison to still photography, video-identification has some advantages as an additional tool. Firstly, in most cases the entire movement of the dolphin is visible during playback, including all the different angles from which a dorsal fin can be seen. This was particularly useful in cases when there were any doubts within the photo-identification catalogue about whether two assumedly different identified dorsal fins belonged in fact to one and the same individual. Although dorsal fin pictures were always attempted to be taken perpendicularly to the dolphin's body axis close to the dorsal fin region, small deviations from this angle could in some cases cause confusion in the identification. Secondly, this technique can link body characteristics to individuals, which are initially identified based on dorsal fins alone. Thirdly, for other purposes, such as study of social structure, video recordings make it possible to record the physical position of individual dolphins with regard to each other.

However, disadvantages in the use of a video camera were experienced in connection with the slow adjustment between wide-angle and zoom modes. Despite attempts to use a fixed zoom length and estimation of where the dolphins would surface, the poor manoeuvrability of the video camera in comparison with the photo-camera limited the quality of the results obtained. In addition, the quality of video images for which a digital zoom was used often did not allow accurate identification. Since the images were analysed by using the slow motion, or pause mode, the quality of still video images decreased significantly as a consequence, as did images recorded with the optical zoom.

No mark-recapture analyses were performed using video images, since the images were not recorded systematically throughout the study period. The quality of the still video images was found to be low in comparison with the photographs. Therefore, identifications were not directly based on the video images, but were first traced back to the photo-identification catalogue. However, overall video-identification in combination with photo-identification appears to be useful for individual dolphin identification.

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