

Irrawaddy dolphin demography in the Mekong River: an application of mark–resight models

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Abstract. Riverine Irrawaddy dolphin populations are critically endangered and much uncertainty exists over the population status in the Mekong River of northeast Cambodia and southern Lao People's Democratic Republic (Lao PDR). We conducted 11 surveys over three years to estimate abundance at each survey as well as survival and the probability of individuals becoming unavailable for detection between surveys. We utilized novel mark–resight estimators to account for the detection process in estimating these parameters. Annual survival was 0.977 (0.040 SE) and movement in (0.060) and out (0.018) of an observable state was low. We estimated abundance at 84.5 (95% CI = 77.9–91.2) with little change over our surveys. We also estimated recruitment and population growth rate for the marked, and presumably older, individuals by estimating seniority using a reverse-time model. Seniority was estimated at 0.999 (0.028 SE), recruitment at 0.001 and population growth rate at 0.978. Although the population size appears to be stable, we believe this represents the slow disappearance of a long-lived animal with no recruitment. Along with the isolated nature of the population and reduced population size as compared to historical estimates, we believe this population is in serious threat of extirpation. We believe there may be as few as 7 or 8 animals in Lao PDR and that the species is at risk of extinction there in the short-term. Although recent management actions (e.g., outlawing of explosive fishing and some restriction on the use of gill-nets) have likely been beneficial we believe identifying population goals to work towards, identifying additional management actions to improve recruitment, and designing the survey methods to best estimate the success of these actions is needed.

Key words: aquatic mammal; Cambodia; conservation; freshwater; Lao PDR; Laos; mark–recapture; *Orcaella brevirostris*; photographic identification; robust design; threatened species.

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INTRODUCTION

River dolphins are highly threatened throughout the world (Braulik 2006, Smith et al. 2007,

Wang 2009, Bashir 2010, Trujillo et al. 2010). The recent extinction of the baiji, *Lipotes vexillifer*, in the Yangtze River (Turvey et al. 2007), and sensitivity of river dolphins to anthropogenic

disturbance and environmental degradation have prompted increasing momentum and focus on riverine dolphin conservation (e.g., Smith et al. 2007, Trujillo et al. 2010). Here we consider the facultative freshwater Irrawaddy dolphin, *Orcaella brevirostris*, which occurs patchily in coastal, brackish, and freshwater habitats in South and Southeast Asia (Smith and Jefferson 2002). Though some marine populations remain relatively abundant (Smith et al. 2008), freshwater populations are highly threatened, with all exclusively riverine populations, in the Mekong River in Cambodia and Lao People's Democratic Republic (Lao PDR), the Mahakam River in Indonesia and the Ayeyarwady River in Myanmar, considered critically endangered by IUCN criteria (Smith et al. 2007). These riverine populations are all isolated from the marine environment, and appear to represent distinct genetic lineages (Beasley et al. 2005). As charismatic mega-fauna, and the only representatives of the mammalian order Cetacea in these systems, these unique freshwater Irrawaddy dolphins are also an important umbrella species for wider conservation of the aquatic systems they inhabit.

Concern for the Mekong River population has grown in recent decades due to a number of very different anthropogenic threats. In the 1970s a large number of dolphins were slaughtered for oil (Smith and Jefferson 2002), and in the 1980s and 1990s, intensive fishing practices with gill nets and explosives emerged as the major threat (Baird and Mounsouphom 1994, 1997). Irrawaddy dolphins are now protected in both Cambodia and Lao PDR. Explosive fishing is outlawed and the use of gill nets has been restricted in some dolphin habitat areas. By-catch of dolphins now appears to have been reduced, but not eliminated (WWF, unpublished data). In recent years, a large number of unexplained deaths, particularly among calves, has implicated environmental contamination as a factor in mortality (Dove 2009). Concurrently, the rise of dolphin-watching tourism, where many boats may approach dolphins within close range, has engendered concerns as a stressor in some areas (Beasley et al. 2010), although we note that well-managed ecotourism has potential to provide benefits for the animals and local communities. The culmination of these threats is concern that

the Mekong River Irrawaddy dolphin population may be in ongoing decline.

Because of the conservation concerns for dolphins generally, much attention has been focused on estimating abundance. In the case of Mekong River Irrawaddy dolphins, there have been numerous contrasting estimates of population size and divergent opinions of trend, ranging from an estimate of 71 and threatened (Dove et al. 2008), to the opinion that the dolphin population is closer to 160 and growing (Kyodo News Service 2009). This discrepancy has greatly hindered consensus on dolphin conservation management in the Mekong River. Estimating abundance is difficult because dolphins are hard to locate, catch, mark, and handle. Consequently, some methods focus on observational data such as raw counts of individuals detected (e.g., Baird and Beasley 2005). However the realization that detection probabilities are often less than 1, has led to the use of mark-recapture estimators, such as the Lincoln-Petersen estimator, to correct for this error (e.g., Currey et al. 2008, Kelkar et al. 2010). These methods inevitably rely on naturally evolving marks such as those from scars or irregular fin shapes, which are not present at birth and are more likely gained as individuals age.

Correcting for a mean detection error is often not enough because heterogeneity in detection probability (Gowans and Whitehead 2001) will often lead to abundance estimates that are biased low. To help address heterogeneity in detection error, modeling approaches have included distance sampling (Smith et al. 2008), Burnham's Jackknife (i.e., model Mh in Program CAPTURE, e.g., Chivers and Corkeron 2003), the use of covariates (Smith et al. 2006), mixture models (Silva et al. 2009) and resighting rates of individuals (i.e., Bowden's estimator in Program NOREMARK, e.g., Oremus et al. 2007). One challenge in using Bowden's approach is that the total number of marked individuals must be known; a difficult assumption to meet when individual marks are natural (e.g., fin shapes vs. tags) and the total number of "marked" individuals is unclear. Thus most studies disregard multiple observations of the same animal in formal mark-recapture analyses.

However, multiple observations of marked and unmarked individuals, are often used in a

subsequent step to better estimate the entire population size, not only the population of potentially marked individuals (e.g., Williams et al. 1993). Many of the above studies correct mark–recapture abundance estimates by the proportion of unmarked individuals (or photographs of unmarked individuals) detected during surveys (e.g., Chilvers and Corkeron 2003, Dove et al. 2008).

Beyond estimating abundance for a single point in time, estimating transition rates such as survival over multiple time periods has also been attempted for bottlenose dolphins, *Tursiops truncatus* (Silva et al. 2009). Relying on a robust design model, Silva et al. (2009) were able to estimate survival and address the problems associated with “temporary emigration” (Kendall and Nichols 1995)—the possibility that some individuals may not be present in an observable state during some surveys. In our case, we define temporary emigration as applying to any movement from observable, and available to be detected, to unobservable, and not available for detection, states (and vice versa). For instance, some individuals that had been detected in a previous survey may be in a part of the river that is not searched, or under water (and not available for detection) when a survey boat passed by, in a future survey.

When multiple abundance surveys can be combined in a single analysis, the distinction between biological process variance and sampling variance becomes important (Link and Nichols 1994). Total variance across time can be decomposed into both sampling variance and biological process variance (i.e., total variance = process variance + sampling variance) components (e.g., Link and Nichols 1994). The biological process variance is the component that we are most interested in explaining. By factoring out sampling variance, more precise and accurate abundance estimates can be derived, especially when testing for time trends.

Only recently were all of these survey/modeling issues (e.g., detection < 1, individual heterogeneity in detection, using all resight data from marked and unmarked individuals, estimating survival and temporary emigration across time), incorporated in a single, formal framework (McClintock et al. 2006, McClintock and White 2009, McClintock et al. 2009) and

available in user-friendly software (i.e., Program MARK) that can also separate process variance from sampling variance. We used this analytical advancement with survey data collected for the Irrawaddy dolphin in the Mekong River (Cambodia and Lao PDR), and believe this approach can be applied to similar surveys to great effect as well. We then apply a reverse-time approach (Pradel 1996) to the mark–resight data to estimate seniority (i.e., the probability of an individual present at time t being present at time $t - 1$) and deriving estimates of recruitment and population trend for the marked individuals.

Using data collected over 3 years, our objective was to estimate Mekong River Irrawaddy dolphin abundance, transition rates (i.e., survival, temporary emigration, seniority), and derive estimates of recruitment and population trend while correcting for detection rates. We also conducted simulations and power analyses to inform future survey efforts.

METHODS

Study area

The Mekong River is a large seasonal floodplain river, including deep pool areas which are important dry season habitat for dolphins and many fish species (Poulsen et al. 2002) and a Ramsar wetland site that provides habitat for several globally threatened species (Bezuijen et al. 2008). The survey route is along the Mekong River’s main channel from Kratie Town, Kratie province, Cambodia, to below the Khone Falls complex in Champassak Province, Lao PDR, and back again; a distance each way of around 190 km (Fig. 1). Each survey took 9–11 days (Table 1). Previous extensive surveys suggest this area is the current extent of dolphin distribution in the Mekong River (Baird and Mounsouphom 1997, Beasley 2007), and Khone falls is thought to be a physical upper limit to the dolphin’s range; dolphins never having been recorded upstream in recent history (Baird et al. 1994). The short time period for each survey and that we surveyed the known area of dolphin distribution supports the assumption of demographic and geographic closure for abundance estimation.

Survey methods

Survey methods followed those previously

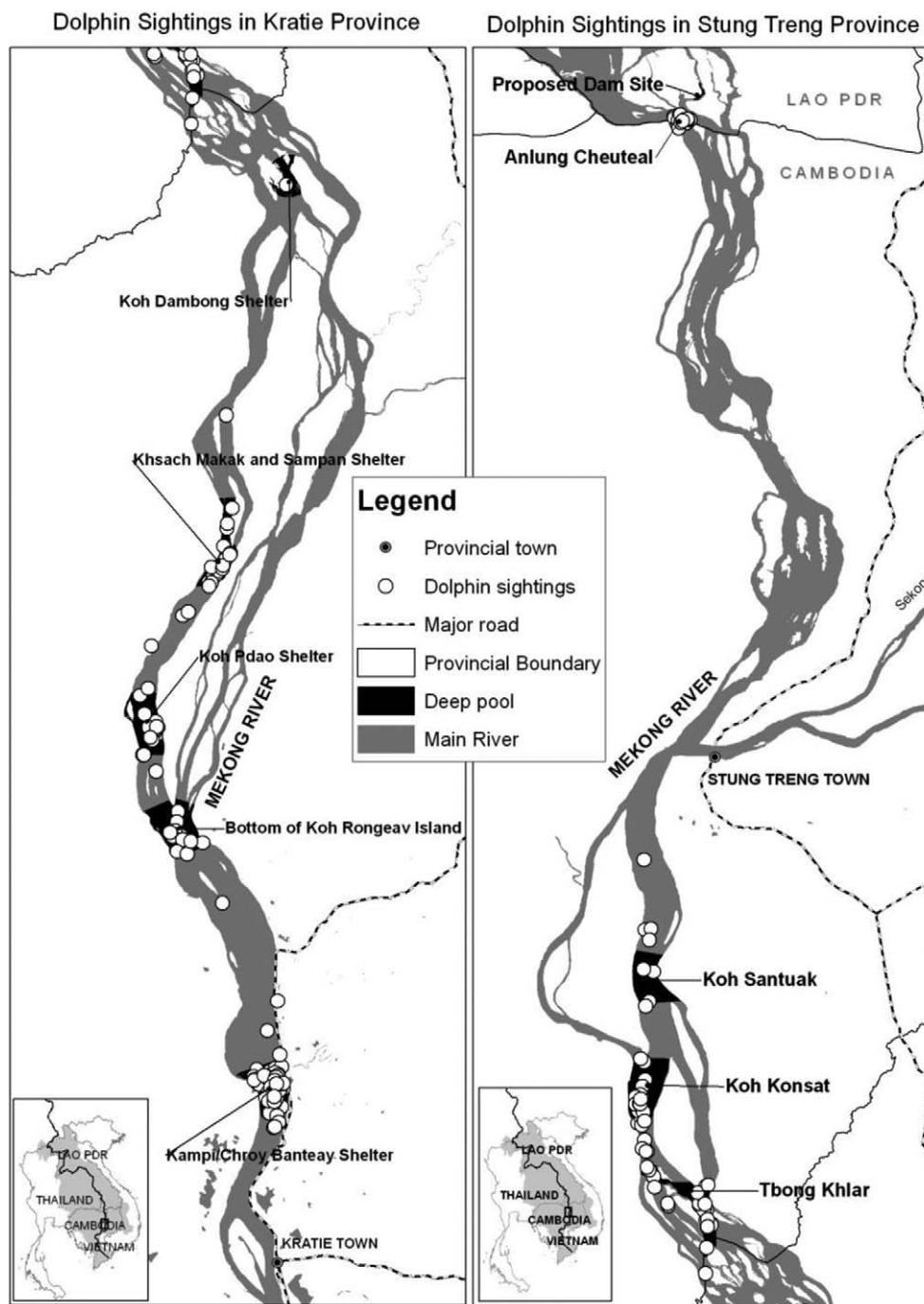


Fig. 1. Map of the lower (left) and upper (right) Cambodian Mekong River that we surveyed. Deep pools are designated by black and the dots represent dolphin groups we sighted. Inset: Lower Mekong Basin.

detailed by Dove et al. (2008). Surveys used a 9 m, narrow wooden boat with a long-tail out-board engine, and the route followed a system of

concrete channel-markers installed by the former French colonial government, though these markers were only visible in the low water season

Table 1. Survey dates, survey length (days), number of days between midpoints of surveys (interval), cumulative time since first survey, the number of unique individuals identified each survey, the cumulative number of unique individuals identified, and the proportion of individuals uniquely identified for Irrawaddy dolphin surveys in the Mekong River. The camera and lens combination(s) used are designated in footnotes.

Survey dates	Survey length (days)	Interval length (days)	Cumulative time since first survey (months)	No. individuals identified	Cumulative no. individuals identified	Proportion of individuals identified
17–25 April 2007†	9	-	-	62	62	0.93
21–29 May 2007‡	9	34	1.1	61	76	0.95
29 Oct–8 Nov 2007‡	11	162	6.4	41	76	0.93
18–27 Feb 2008‡	10	111.5	10.1	60	78	0.95
21 Apr–1 May 2008‡	11	63.5	12.2	48	79	0.96
25 May–3 Jun 2008‡	10	33.5	13.3	40	80	0.93
30 Nov–9 Dec 2008§	10	189	19.5	38	83	0.96
13 Mar–22 Mar 2009§,¶	10	103	22.9	69	85	0.93
21–30 Apr 2009§,¶	10	39	24.2	64	87	0.91
2–10 Mar 2010#,	9	314.5	34.5	63	88	0.95
31 Mar–9 Apr 2010#,	10	29.5	35.5	62	88	0.91

† Nikon D200/Nikkor 70–400 mm; ‡ Canon EOS 350D/Sigma 170–500 mm; § Canon EOS 350D/Canon 100–400 mm; ¶ Canon EOS 450D/Sigma 170–500 mm; # Canon EOS 450D/Canon 100–400 mm; || Canon EOS 50D/Canon 100–400 mm.

(December–May; Starr 2003). Eleven surveys were conducted from April 2007 to April 2010 (Table 1), generally during low water when the river covers a much smaller area, and dolphins are more easily found. The boat travelled at ~ 5 – 10 km h^{-1} , and where the river was wider than $\sim 500 \text{ m}$, a zigzag course was traveled from bank to bank to more effectively cover the whole area. In addition to the driver, at least six active observers were present, with two on the bow looking forward, and two in the center looking behind, and two toward the stern looking to either side.

When dolphins were sighted the engine was stopped and, by oar, we approached cautiously to within $\sim 100 \text{ m}$. To further avoid disturbing the animals, we approached in parallel to the dolphin groups, rather than head directly towards them, usually stopping upstream. Where the current was strong, repeatedly motoring upstream of the group and drifting past was necessary. Dolphins were photographed by one or two photographers using a digital camera with a large zoom lens (Table 1), from a bow platform raised $\sim 25 \text{ cm}$ above the water. Dolphin groups were photographed for sessions that were a minimum 30 minutes and a maximum of 2 hours long. We thought this amount of time allowed for good photographs of all animals present. The upper time limit ensured that an inordinate amount of time (and vessel disturbance) was not applied to any one group and

that survey effort was allocated throughout the study area. These sessions formed the base of our resightings. Generally tens of fast-action photos would be taken of each dolphin as it surfaced and these photos were used to identify individuals for each session (see *Photograph identification* below). Survey days were constrained by light, and observations finished $\sim 16:00$. Each day the boat began in the place it ended the afternoon before, incrementally working up-, and then down-stream within the study area.

In addition to these surveys, a carcass reporting network is fostered among local communities in dolphin habitat areas. Records are maintained of reported deaths, and confirmation, where possible, is obtained by project staff or from photographs.

Photograph identification

Surveys took large numbers of photographs of which only a small number of high quality shots were retained. Only those photographs where the dorsal fin was close to perpendicular to the camera, in clear focus, entirely in the shot, and otherwise of sufficient size and quality that subtle markings could be identified, were kept. Individuals were identified based on the profile shape of the fin, supplemented by deformities, pigmentation, scarring and lesions, and compared with a developing base catalogue (Dove et al. 2008). High quality photographs of unmarked animals were also kept and recorded in a similar

way to marked animals. Although insufficiently distinct for confident re-identification over a long period of time (i.e., across sessions), subtle distinctions occur among all fins such that we were able to differentiate unmarked animals within the same group/session (a short period of time). Given the small group sizes (mean 5.62, SD 3.95) and a low proportion of unmarked animals, we believe this is a reliable method.

As marks are naturally occurring in this population and acquired over time, calves are not born with markings and we believe that most unmarked animals are of a young age. Further, we believe that young calves (<1 year) are more boat shy than older animals, and therefore more difficult to resight and the main assumption of our main modeling efforts (below) is that the marked individuals are representative of the whole population in terms of sighting probabilities. For this reason unmarked photographs thought to be calves (by size) were excluded from further analysis, as per similar studies (Silva et al. 2009).

Analytical methods

We applied the recent developments of McClintock et al. (2009) and McClintock and White (2009), specifically the (zero-truncated) Poisson log-normal estimator (ZPNE) as available in Program MARK, (White and Burnham 1999) to our dolphin data. For each survey ($n = 11$) we summed the number of sessions each identifiable dolphin was observed. We also summed the number of unidentifiable dolphins observed during sessions for each survey period. Using these data we estimated the number of unmarked individuals in the population during each primary survey period (U_i), the mean resighting probability for each primary period (α_i) on the log-scale, additional variance in resighting due to individual heterogeneity (σ_i^2) on the log-scale, apparent survival between primary survey periods (ϕ_i), the probability of transitioning from an observable to unobservable state between primary survey periods given an individual was present to be observed (γ''_i), and the probability of remaining in an unobservable state (i.e., $1 -$ the probability of returning to an observable state) given an individual was not present to be observed (γ'_i) and derived the overall mean resighting rate for each primary

survey period as well as the population size (N_i) at each primary period.

We modeled U as a function of survey, i.e., we assumed there would be a different number of unmarked individuals for each survey so that we would not enforce a situation where changes in population size would only come from the marked population. We modeled the resighting probability as a constant across surveys (α) as well as a function of survey (α_i). We modeled the individual heterogeneity as a constant (σ^2), as function of survey (σ_i^2), as well as equal to zero ($\sigma_{=0}^2$). We modeled survival as a constant (ϕ) and as a function of survey (ϕ_i). Because surveys were spaced from 1 to 10 months apart we chose to standardize the estimation (and presentation) of transition rate (i.e., ϕ_i , γ''_i , γ'_i) estimates as annual rates rather than as monthly rates. Thus a 3 month interval was considered 3/12, or 0.25, of a year. Some monthly rates (e.g., survival) were expected to be very close to the upper boundary of 1 since dolphins are long-lived, and therefore these rates would be hard to estimate and hard for the reader to interpret. Estimating and presenting transitional rates on an annual scale helped address these issues. Because of the limited sample size and our primary interest in estimating other parameters, we chose to estimate γ'' and γ' as constants and either separate from each other or equal to each other (i.e., $\gamma'' = \gamma'$) to avoid confounding the model by over-parameterization. We modeled all combinations of these parameters for a total set of 24 models. For comparative purposes we also constructed an additional model in which all parameters were considered to vary with survey. We used Akaike's Information Criterion with a small sample size correction factor (AICc) to rank and compare models (Burnham and Anderson 2002). We were especially interested in estimating dolphin abundance over time and took a variance components approach with our abundance estimates. For investigating and explaining biological process variance, the sampling variance should be factored out of the analysis (e.g., Link and Nichols 1994), and thus our focus on a variance components approach. We used the variance component option (Burnham and White 2002) available in Program MARK and constructed, and compared, a means (i.e., no change in abundance over time) and a trend (i.e., change in

abundance over time) variance components model.

We were also interested in recruitment rate. We had raw counts of calves detected, but since these animals were unmarked, estimating reproductive rates, as well as recruitment into the breeding population, with these data was difficult. Instead we used a reverse-time approach (Pradel 1996, Nichols et al. 2000) to estimate seniority (ρ); the probability that an individual present at time t was present at $t - 1$. This can be done by reversing the data order in a survival model and has been used, and well developed, with other mark-recapture data types, but not with mark-resight data. Since this reverse-time approach has not been applied to mark-resight data and the joint forward-reverse model has not yet been developed, we used the top model from our first analysis and used the reversed time series of data to obtain our estimate of ρ . An estimate of recruitment (f) can then be derived as

$$f_t = \phi_t \left(\frac{1 - \rho_{t+1}}{\rho_{t+1}} \right).$$

An estimate of population growth rate (λ) for the age classes represented by the encounter histories can also be derived as

$$\lambda_t = \frac{\phi_t}{\rho_{t+1}}.$$

The associated variances of these terms, from the delta method, are

$$\begin{aligned} \text{var}(f) = & \left[\rho_{t+1}^2 (1 - \rho_{t+1})^2 \text{var}(\phi_t) + \phi_t^2 \text{var}(\rho_{t+1}) \right. \\ & \left. - 2\phi_t \rho_{t+1} (1 - \rho_{t+1}) \text{cov}(\phi_t, \rho_{t+1}) \right] \\ & \div \rho_{t+1}^4 \end{aligned}$$

and

$$\begin{aligned} \text{var}(\lambda) = & \left(\frac{1}{\rho_{t+1}} \right)^2 \text{var}(\phi_t) + \left(\frac{\phi_t}{\rho_{t+1}^2} \right)^2 \text{var}(\rho_{t+1}) \\ & + 2 \left(\frac{1}{\rho_{t+1}} \right) \left(-\frac{\phi_t}{\rho_{t+1}^2} \right) \text{cov}(\phi_t, \rho_{t+1}) \end{aligned}$$

respectively. Since the joint forward/reverse model has not been developed, the covariance terms for these equations are currently unavailable, so we set those terms = 0. However, from a standard robust-design Pradel model that ig-

nores multiple observations of individuals within a survey, as well as any observations of unmarked individuals, we estimated the $\text{cov}(\phi_t, \rho)$ to be 0.11, which is low and we doubt the covariance of the mark-resight data (with multiple observations and observations of unmarked individuals) would be much different, and probably not in terms of the direction (+) of the covariance. By leaving out this covariance term our estimates will be conservative in the sense that our confidence intervals will most likely be slightly larger than they should be.

Finally we wished to inform future survey efforts through a power analysis. Using our results as a basis we simulated a population of 85 dolphins, of which 5 were unmarked, with zero recruitment and temporary emigration, undergoing a 3%, 5%, or 10% annual decline for 3 years. The study design features we can influence in the field are the resighting rate (by increased effort per survey) and the number of surveys per year. We simulated a resighting rate of 1.5 (the average resighting rate for the last 3 surveys) as well as a doubling of the rate to 3. We also simulated 1, 2, and 3 surveys a year. We simulated each combination of population decline, resighting rate, and number of surveys per year 100 times using the ZPNE mark-resight model and the simulation capabilities of Program MARK. For each simulation we calculated a likelihood ratio test (probability of type 1 error = 0.15), between a ZPNE mark-resight model that modeled a decline, and one that did not model a decline. We used the proportion of the 100 simulations in which the likelihood ratio test indicated a decline as our power statistic.

RESULTS

The 11 surveys were conducted over a 3-year period with each survey being conducted over 9–11 days and intervals between surveys (defined as the time from the midpoint of one survey to the next) ranging from 33.5 to 314.5 days (Table 1). Two hundred and eighteen groups (defined as 1 or >1 dolphins congregated together) were sighted over all surveys, ranging from 13–32 groups seen per survey. Sightings were primarily concentrated around 8 deep pool areas (Fig. 1). The number of marked individuals observed over the 11 survey periods ranged from 34–69,

and a total of 88 individuals were identified over the whole period (Fig. 2); 6 of which are known to have died during the survey period (and 2 since). The proportion of individuals that could be uniquely identified ranged from 0.91–0.96 (Table 1). We also sighted calves 44 times over the 11 surveys. Mean group size from photographs was 5.62 (SD 3.95), ranging from 1–19, and the modal group size was 3. We note however, that this is likely to be a slight underestimate as it is unlikely that all animals present were photographed in every session.

Model selection results

Our top model indicated that the mean resighting probability varied by survey (α_t), that there was no additional variation in the resighting rate beyond that associated with a Poisson process ($\sigma^2_{=0}$), that the number of unmarked individuals varied by survey period (U_t) apparent survival was constant (ϕ) and that the probability of transitioning to an unobservable state between surveys (γ'') was different than the probability of remaining unobservable (γ ; Table 2). The second-best model was identical to the top model except the σ^2 was allowed to be estimated versus being fixed to zero, thus an additional parameter was estimated in this second model. The $-2\log(L)$ for both of these models is identical and the actual estimate of σ^2 , is $0.4 \times 10^{-4} \pm 0.02736$; which is essentially zero. Thus the first and second model can be considered identical except that the σ is being fixed to zero in one model and estimated at zero in the other. Otherwise the parameter estimates are essentially identical. This relationship between models in which σ is fixed to zero, or estimated at zero occurs multiple times within our model set (Table 2).

Resighting rates

Strong evidence existed for resighting rates varying across surveys as models with ranked highly (Table 2). However there was no evidence that additional variance beyond the variance associated with a Poisson distribution was needed to model heterogeneity in resighting rates, as σ^2 was estimated at nearly zero and models in which σ^2 was fixed to zero ranked highly (Table 2). The average number of times an individual was resighted was 1.23 with much

variability across the surveys (Fig. 3). Resighting rates increased for the last four surveys as compared to prior surveys.

Transition rates

Apparent survival of marked individuals was best estimated as a constant across our survey periods. We estimated annual apparent survival as 0.977 (0.040 SE). The probability of marked individuals transitioning to an unobservable state between primary survey periods (γ'') was 0.018 (0.013 SE), and the probability of transitioning to an observable state, given a marked individual was unobservable was 0.060 (0.062 SE). We present estimates of seniority below (see *Recruitment rate and population growth*).

Abundance

We assumed that the number of unmarked animals would vary over time and we estimated the number of unmarked individuals between 2.2 and 7.2 (Fig. 4). To obtain our best estimates of total abundance and associated variance we focused on the process variation only. We did this for estimates from the top model as well from the fully time-dependent model ($\Delta AIC_c = 65.96$). Results were similar and we focus on the estimates from our top model. There was no evidence of any clear + or – trend across time in dolphin abundance as the slope was estimated as 0.120 with a SE of 0.167 (a coefficient of variance of 139%). Thus our best variance components model estimated an average of 84.5 (95% CI = 77.9–91.2) dolphins over our surveys with survey specific estimates presented in Fig. 5.

Recruitment rate and population growth

By relying on a reverse time approach we estimated seniority, the probability that an individual in the population at time t was in the population at time $t - 1$, as 0.999 (0.028 SE). Seniority can also be interpreted as the sensitivity of population growth to adult survival and in this case, in a long-lived species with a low birth rate, adult survival is very influential in terms of defining the population change. We derived a population growth rate of 0.978 (95% CI 0.883–1.074) and a recruitment rate of 0.001 (95% CI –0.053–0.055). The recruitment and population growth rate apply only to the marked individuals.

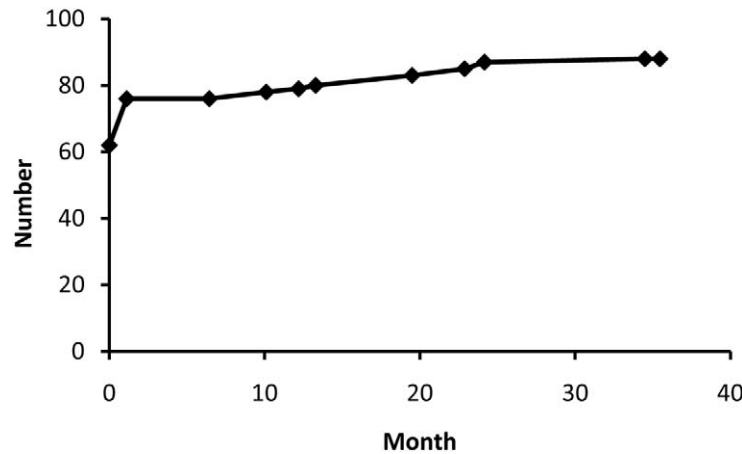


Fig. 2. The cumulative number of marked Irrawaddy dolphins detected in the Mekong River (Cambodia/Lao PDR) across 11 surveys. The first survey (month 0) was in April 2007 and the x axis is relative to that start date.

Power analysis

Our power analysis indicated that the current survey effort of 2–4 surveys per year is probably adequate to detect declines of 3% or higher. Effort that is less than 2 surveys a year has little power to detect a decline. Although increasing the resighting rate results in an increase in power,

increasing the number of surveys has a much larger effect (Fig. 6).

DISCUSSION

The transition rates into and out-of an unobservable state were low, and we note that individuals were 3× as likely to move into an observable state as move out. This result helps support the idea that our survey area is a fairly complete representation of the dolphin's dry season range in the Mekong River, and that minor side channels probably do not represent important habitat. We also note that this section of the Mekong River is populated and we believe that, through historic surveys (Baird and Moun-souphom 1997, Beasley 2007) and ongoing communication with the local people, we have a good understanding of where dolphins are likely and unlikely to be located. The high probability of staying unobservable once an individual dolphin becomes unobservable might indicate that some dolphins are especially boat-shy or cryptic.

As expected, annual survival was high for this long-lived species, though the number of dead animals estimated over the survey period (~6) is a little lower than the number of known dead marked animals recorded by the carcass recovery program in that period (9). However, we note that information for estimating survival in this model only comes from the marked individuals (versus abundance that includes both marked

Table 2. Model selection results for the Irrawaddy dolphin mark–resight analysis. We estimated the number of unmarked individuals in the population (U), the mean resighting probability (α) on the log scale, addition variance in resighting due to individual heterogeneity on the log-scale (σ^2), apparent survival between surveys (ϕ) the probability of transitioning to an unobservable state between primary survey periods (γ'') given an individual was observable, and the probability of remaining unobservable (i.e., $1 -$ the probability of returning to the survey area) given an individual was unobservable (γ'). These parameters were estimated as a constant (\cdot), for each survey period (t) or set equal to zero ($=0$). The minimum AICc was 2277.20. We only show models with $\Delta\text{AICc} < 20$.

Model	ΔAICc	AICc weights	No. parameters	$-2\log(L)$
$\alpha_t \sigma_{=0}^2 U_t \phi_t \gamma''_t \gamma'_t$	0.00	0.56	25	2225.01
$\alpha_t \sigma_{=0}^2 U_t \phi_t \gamma''_t \gamma'_t$	2.18	0.19	26	2225.01
$\alpha_t \sigma_{=0}^2 U_t \phi_t \gamma''_t \gamma'_t = \gamma'_t$	2.22	0.19	24	2229.40
$\alpha_t \sigma_{=0}^2 U_t \phi_t \gamma''_t \gamma'_t = \gamma'_t$	4.40	0.06	25	2229.40
$\alpha_t \sigma_{=0}^2 U_t \phi_t \gamma''_t \gamma'_t$	16.98	0.00	34	2222.10
$\alpha_t \sigma_{=0}^2 U_t \phi_t \gamma''_t \gamma'_t = \gamma'_t$	17.65	0.00	33	2225.01

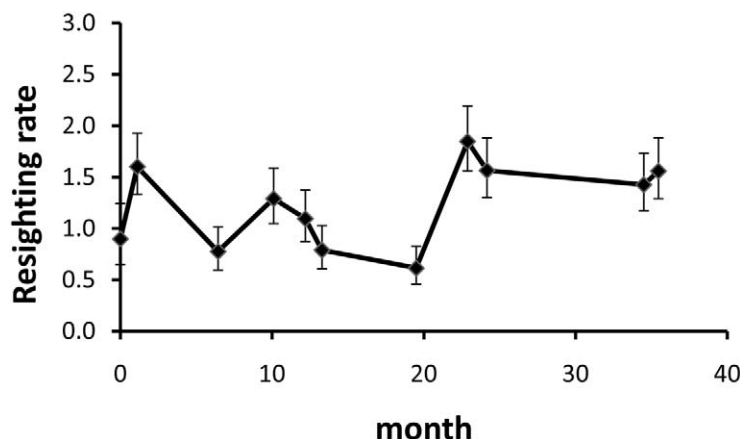


Fig. 3. Resighting rates of Irrawaddy dolphins in the Mekong River (Cambodia/Lao PDR) across 11 surveys. The first survey (month 0) was in April 2007 and the x axis is relative to that start date. Error bars are 95% confidence intervals.

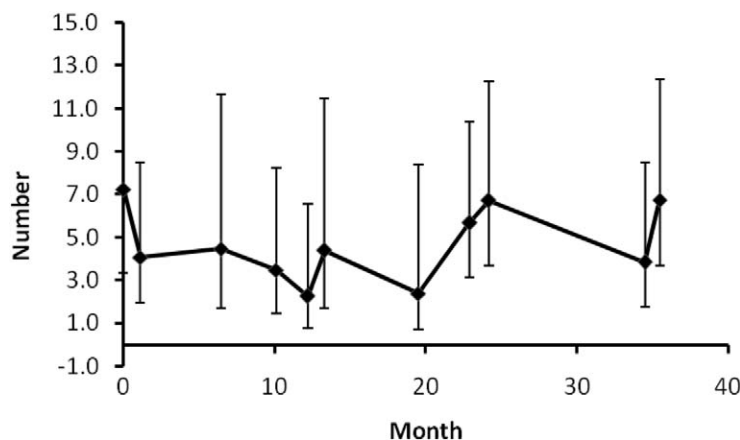


Fig. 4. The estimated number of unmarked dolphins photographed during the surveys for Irrawaddy dolphin in the Mekong River (Cambodia/Lao PDR). The first survey (month 0) was in April 2007 and the x axis is relative to that start date. Error bars are 95% confidence intervals.

and unmarked individuals). If the marked individuals are not representative of the unmarked, then this survival rate should be viewed with caution. Because individuals have naturally evolving marks, we believe that an age structure in our data is an important consideration. If marks are only gained later in life, then our survival and transition estimates only apply to older animals.

Resighting rates were variable, but notably higher in the last four surveys. We believe that the use of two photographers from 2009, and significantly improved equipment in 2009 and

2010 (Table 1) probably accounted for much of this variation. We also note that our modeling assumes that marked and unmarked animals have similar sightability. We believe we met this assumption well as photographs were not taken in relation to whether an individual was marked or not. In fact, taking photos was a fast reactive activity in which individual identifiers were only noted after examining the photos. Further, photographs of young calves, which may differ in sightability from older animals, were excluded from the analyses.

Our best estimates of abundance indicate a

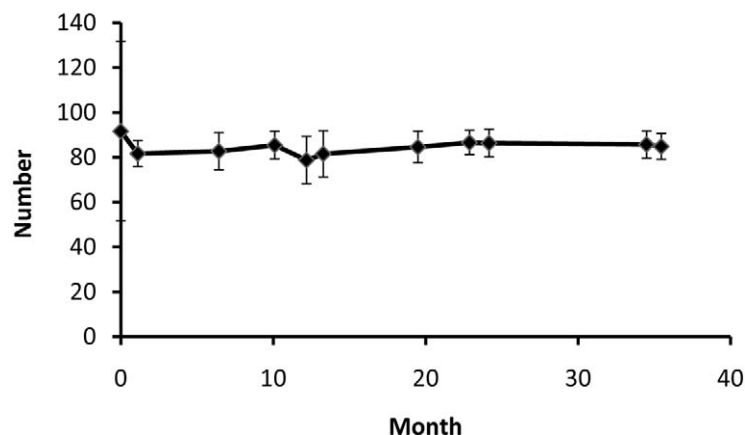


Fig. 5. Estimated number of Irrawaddy dolphins in the Mekong River (Cambodia/Lao PDR) across the 11 surveys. The first survey (month 0) was in April 2007 and the x axis is relative to that start date. Error bars are 95% confidence intervals of process variance only.

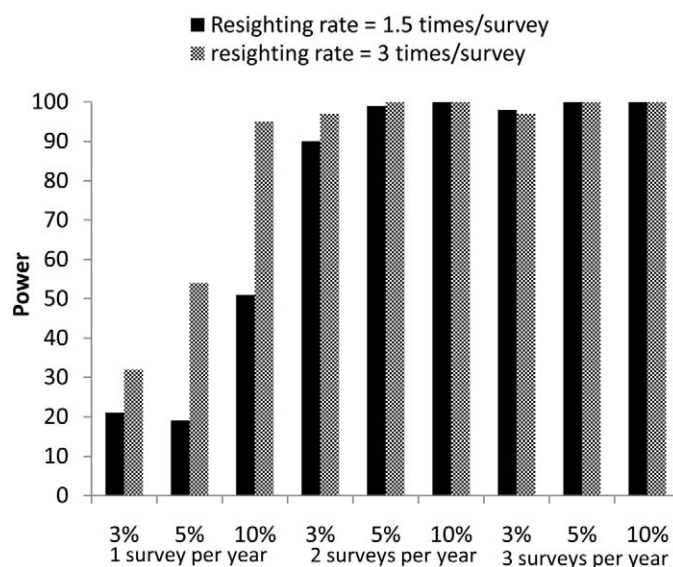


Fig. 6. The power to detect a 3%, 5%, or 10% average annual decline over 3 years of data collection given a starting population of 85 dolphins, 1, 2 or 3 surveys per year and with an individual animal resighting rate of 1.5 or 3 times per survey.

stable number of dolphins over the last three years of about 85 animals which includes both marked and unmarked animals. While current management actions seem to be preventing a detectable short-term decline of dolphins, there is no evidence that the population is growing. We believe that as individuals age, they are more likely to become naturally marked. Thus our marked population tends to be older, or adult,

animals. Our derived estimate of population growth, λ (0.978), does not indicate a positive trajectory, although the uncertainty around this estimate is great and this estimate applies to marked animals only. With long-lived animals this pattern probably means that adult animals (and ones more likely to be marked) are surviving, but few new animals are recruiting into the adult population (i.e., the marked

population), as is also indicated by our seniority estimate of 0.999. This corroborates concerns of the unsustainably high calf mortality rate documented through the carcass reporting program in Cambodia (Gilbert and Beasley 2006, Dove 2009). We note that the 44 calf sightings over the 11 surveys, excluded from the analyses, are approximately half that of the sighting of unmarked adult animals (74). If we assume that calves have the same resighting rate as adults and use a ratio estimator that equates the ratio of resightings of adults:actual adults to the ratio of resightings of calves:calves, then we would estimate ~5 calves on average. If in fact calves have lower resighting rates (and why calf resightings were excluded from analysis), then the number of calves would be higher. Dove (2009) reported roughly 9 calf deaths per year from 2003–2008, and we doubt all dead calves are recovered. Our derived estimate of recruitment (0.001) was also very low, and though we note this represents recruitment into the marked population, we detected no apparent increase in the estimated unmarked population either. These three pieces of information suggest that many, if not all, calves are dying and that recruitment to maturity may be close to zero. We believe this is a serious concern. With the ongoing threat of by-catch, the increasing threat from poorly managed tourism (Beasley et al. 2010), the looming threat of hydropower dam construction in and around dolphin habitat (Bezuijen et al. 2007, ICEM 2010), possible environmental contamination (Dove 2009), and the still unexplained mortality in many calves (WWF, *unpublished data*) the Mekong River's Irrawaddy dolphin population is at risk of extirpation. We believe that additional actions are needed to manage these threats.

Dove et al. (2008) focused on the data from the first two surveys in our analysis. Our abundance estimates are higher than their estimate of 71 (95% CI 66–86) although the confidence intervals of each study overlap. This difference is probably best explained by a much larger dataset and a difference in analysis methodologies. We were able to employ analytical methods not available to Dove et al., and we were able to use all the data, including resightings of unmarked animals, to better model heterogeneity and transition rates. Taking these methodological advances into account, we would have less biased estimates

that we expect in this case slightly higher.

Beasley (2007) estimated >115 dolphins during 2004 and 2005 relying on older analysis methods. In comparing Beasley's and our estimates, a >25% decline in population size is apparent from 2005 to 2007. We note that Beasley had 90 individuals identified in 2004–2005, and 99 between 2001 and 2005, which when accounting for the known deaths of ~6 adults per year in that period (Dove 2009), compares more favorably to our raw count of identified individuals (88; Fig. 2). We suggest that Beasley's study (and analysis methods) may have confounded temporary emigration with detection rates. Such a situation could have detection rates biased low, and abundance rates biased high, and this may account for some of the apparent decline over time. We were able to account for temporary emigration formally in our modeling. Without accounting for this transition probability, detection probabilities will be lower, which would result in higher estimates of abundance. We think that collating the previous survey data of Beasley's with ours would be useful to better estimate temporary emigration across all the survey efforts and better estimate the magnitude and shape of this population decline.

Although our adult population appears stable over the last 3 years, the current core range is greatly reduced from the historical range that included the Sekong River, from Cambodia into Lao PDR, the Tonle Sap, or Great Lake in Cambodia, and far downstream in the Mekong River into Viet Nam (Baird and Mounsouphom 1997, Smith and Jefferson 2002). In addition to a reduced range, the population in our survey area is also greatly reduced from presumed historical levels which, on consideration of reported hunting levels the latter half of the 20th century (Smith and Jefferson 2002, Beasley 2007), may have been an order of magnitude larger than it is today. We note that small, isolated populations such as this are at risk from demographic stochastic events, random catastrophes, and the longer-term issue of genetic drift. Of special concern is that we only noted 6 individually identifiable dolphins and probably 1 or 2 unmarked animals at the trans-boundary pool between Cambodia and Lao PDR (Fig. 1). These animals probably represent most, if not all, the dolphins in Lao PDR because of the waterfall

boundary upstream. With so few animals at this site, and the additional pressure of frequent disturbance from tourism activities (Beasley et al. 2010), we believe that the population is at considerable risk of extirpation in Lao PDR in the short-term. As the only cetacean species present in Lao PDR, we believe that future Irrawaddy dolphin conservation efforts there should be a high priority.

Our analysis strategy, based on the advances presented by McClintock et al., was able to address many issues with abundance estimation and use all of the adult survey data collected. Our power analysis also indicates that our current survey effort is adequate to detect declines of 3% or greater. We believe the application of mark–resight models would be useful to other researchers who have similar data to ours, and in particular to produce robust and efficient estimates for small, identifiable populations of conservation concern. In future developments we look towards the formalized incorporation of counts of unmarked calves. Identifying offspring when present with their mother is one potential avenue (e.g., Lukacs et al. 2004), though as the calves mature, they behave individually, and the association with the mother is lost. A formalized method of judging age class is needed to determine the age structure of marked and unmarked animals. Developments in laser photogrammetry to measure body size (Currey et al. 2008, McGuire et al. 2009) are one option we believe may be worth pursuing. Another source of data that may be incorporated into future developments in mark–resight modeling are dead recoveries, which with the carcass recovery program implemented in the Mekong River could provide additional precision and power. If a method of marking, or identifying individuals (e.g., DNA biopsies), could be safely employed with these dolphins, a more representative sample of individuals could be followed. However, the dolphins have proven to be susceptible to disturbance and such marking is still a challenge. Finally formalizing a reverse-time model for mark–resight data and making it available in user-friendly software would also be beneficial.

While national governments and conservation organizations recognize, and are attempting to deal with a number of threats to dolphins (MAFF

2005), we believe an important step is to designate a desired population size and distribution, against which conservation and management actions can be benchmarked. Such a step should involve wide stakeholder consultation and may involve heuristic risk-assessment and modeling tools such as a population viability analysis approach (Burgman et al. 1993). Without planning and actions to ameliorate identified threats, we believe that the Irrawaddy dolphin will be extirpated from the Mekong River.

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LITERATURE CITED

- Baird, I. G. and I. L. Beasley. 2005. Irrawaddy dolphin *Orcaella brevirostris* in the Cambodian Mekong River: an initial survey. *Oryx* 39:301–310.
- Baird, I. G. and B. Mounsouphom. 1994. Irrawaddy dolphins (*Orcaella brevirostris*) in Southern Lao PDR and Northeastern Cambodia. *Natural History Bulletin of the Siam Society* 42:159–175.
- Baird, I. G. and B. Mounsouphom. 1997. Distribution, mortality, diet and conservaiton of Irrawaddy dolphins (*Orcaella brevirostris* Gray) in Lao PDR. *Asian Marine Biology* 14:41–48.
- Baird, I. G., B. Mounsouphom, and P. J. Stacey. 1994.

- Preliminary surveys of Irrawaddy dolphins (*Orcaella brevirostris*) in Lao PDR and Northeastern Cambodia. Reports of the International Whaling Commission 44:SC/45/SM48:367–369.
- Bashir, T. 2010. Ganges River dolphin (*Platanista gangetica*) seeks help. *Current Science* 98:287–288.
- Beasley, I., L. Bejder, and H. Marsh. 2010. Dolphin-watching tourism in the Mekong River, Cambodia: a case study of economic interests influencing conservation. Report to the International Whaling Commission SC/62/WW4.
- Beasley, I., K. M. Robertson, and P. Arnold. 2005. Description of a new dolphin, the Australian Snubfin dolphin *Orcaella heinsohni* Sp N. (Cetacea, Delphinidae). *Marine Mammal Science* 21:365–400.
- Beasley, I. L. 2007. Conservation of the Irrawaddy Dolphin *Orcaella brevirostris* (Owen in Gray, 1866) in the Mekong River: Biological and Social Considerations Influencing Management. James Cook University, Townsville, Australia.
- Bezuijnen, M. R., R. Timmins, and T. Seng, editors. 2008. Biological surveys of the Mekong River between Kratie and Stung Treng towns, northeast Cambodia, 2006–2007. WWF Greater Mekong—Cambodia Country Programme, Cambodia Fisheries Administration, and Cambodia Forestry Administration, Phnom Penh.
- Bezuijnen, M. R., R. Zanre, and M. Goichot. 2007. The Don Sahong dam and the Irrawaddy dolphin. A science brief from WWF. WWF Greater Mekong Programme, Vientiane.
- Braulik, G. T. 2006. Status assessment of the Indus River dolphin, *Platanista gangetica minor*, March–April 2001. *Biological Conservation* 129:579–590.
- Burgman, M. A., S. Ferson, and H. R. Akçakaya. 1993. Risk assessment in conservation biology. Cambridge University Press, Cambridge, UK.
- Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.
- Burnham, K. P. and G. C. White. 2002. Evaluation of some random effects methodology applicable to bird ringing data. *Journal of Applied Statistics* 29:245–264.
- Chilvers, B. L. and P. J. Corkeron. 2003. Abundance of Indo-Pacific bottlenose dolphins, *Tursiops aduncus*, off point lookout, Queensland, Australia. *Marine Mammal Science* 19:85–95.
- Currey, R. J. C., L. E. Rowe, S. M. Dawson, and E. Slooten. 2008. Abundance and demography of bottlenose dolphins in Dusky Sound, New Zealand, inferred from dorsal fin photographs. *New Zealand Journal of Marine and Freshwater Research* 42:439–449.
- Dove, V. 2009. Mortality investigation of the Mekong Irrawaddy River dolphin (*Orcaella brevirostris*) in Cambodia based on necropsy sample analysis. WWF Cambodia Technical Report.
- Dove, V., D. Dove, F. Trujillo, and R. Zarne. 2008. Abundance estimation of the Mekong Irrawaddy dolphin *Orcaella brevirostris* based on mark and recapture analysis of photo-identified individuals. WWF Cambodia Technical Report.
- Gilbert, M. and I. Beasley. 2006. Mekong River Irrawaddy dolphin stranding and mortality summary. January 2001–December 2005. Wildlife Conservation Society.
- Gowans, S. and H. Whitehead. 2001. Photographic identification of northern bottlenose whales (*Hyperoodon ampullatus*): Sources of heterogeneity from natural marks. *Marine Mammal Science* 17:76–93.
- ICEM. 2010. MRC SEA for hydropower on the Mekong Mainstream: Impacts assessment (opportunities and risks). Discussion draft 14 May 2010. International Centre for Environmental Management.
- Kelkar, N., J. Krishnaswamy, S. Choudhary, and D. Sutaria. 2010. Coexistence of fisheries with river dolphin conservation. *Conservation Biology* 24:1130–1140.
- Kendall, W. L. and J. D. Nichols. 1995. On the use of secondary capture-recapture samples to estimate temporary emigration and breeding proportions. *Journal of Applied Statistics* 22:751–762.
- Kyodo News Service. 2009. Kyodo News Service, “Cambodia rejects report of Mekong River dolphins near extinction,” BBC Worldwide Monitoring, 20 Jun 2009. (<http://www.lexisnexis.com/hottopics/lnacademic>) [27 September 2010].
- Link, W. A. and J. D. Nichols. 1994. On the importance of sampling variance to investigations of temporal variation in animal population-size. *Oikos* 69:539–544.
- Lukacs, P. M., V. J. Dreitz, F. L. Knopf, and K. P. Burnham. 2004. Estimating survival probabilities of unmarked dependent young when detection is imperfect. *Condor* 106:926–931.
- MAFF. 2005. Cambodian Mekong dolphin strategy. Ministry of Agriculture, Forestry and Fisheries, Phnom Penh, Cambodia.
- McClintock, B. T. and G. C. White. 2009. A less field-intensive robust design for estimating demographic parameters with mark-resight data. *Ecology* 90:313–320.
- McClintock, B. T., G. C. White, M. F. Antolin, and D. W. Tripp. 2009. Estimating abundance using mark-resight when sampling is with replacement or the number of marked individuals is unknown. *Biometrics* 65:237–246.
- McClintock, B. T., G. C. White, and K. P. Burnham. 2006. A robust design mark-resight abundance estimator allowing heterogeneity in resighting probabilities. *Journal of Agricultural Biological and Environmental Statistics* 11:231–248.

- McGuire, T. L., C. C. Kaplan, and M. K. Blees. 2009. Photo-identification of beluga whales in Upper Cook Inlet, Alaska. Final report of belugas resighted in 2008. Report prepared by LGL Alaska Research Associates, Inc., Anchorage, AK, for National Fish and Wildlife Foundation, Chevron and ConocoPhillips Alaska Inc.
- Nichols, J. D., J. E. Hines, J. D. Lebreton, and R. Pradel. 2000. Estimation of contributions to population growth: A reverse-time capture-recapture approach. *Ecology* 81:3362–3376.
- Oremus, M., M. M. Poole, D. Steel, and C. S. Baker. 2007. Isolation and interchange among insular spinner dolphin communities in the South Pacific revealed by individual identification and genetic diversity. *Marine Ecology-Progress Series* 336:275–289.
- Poulsen, A., O. Poeu, S. Viravong, and N. T. Tung. 2002. Deep pools as dry season fish habitats in the Mekong Basin. MRC Technical Paper. No. 4:1683–1489 Mekong River Commission, Phnom Penh, Cambodia.
- Pradel, R. 1996. Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics* 52:703–709.
- Silva, M. A., S. Magalhaes, R. Prieto, R. S. Santos, and P. S. Hammond. 2009. Estimating survival and abundance in a bottlenose dolphin population taking into account transience and temporary emigration. *Marine Ecology-Progress Series* 392:263–276.
- Smith, B. D., B. Ahmed, R. M. Mowgli, and S. Strindberg. 2008. Species occurrence and distributional ecology of nearshore cetaceans in the Bay of Bengal, Bangladesh, with abundance estimates for Irrawaddy dolphins *Orcaella brevirostris* and finless porpoises *Neophocaena phocaenoides*. *Journal of Cetacean Research and Management* 10:45–58.
- Smith, B. D., G. Braulik, S. Strindberg, B. Ahmed, and R. Mansur. 2006. Abundance of irrawaddy dolphins (*Orcaella brevirostris*) and ganges river dolphins (*Platanista gangetica gangetica*) estimated using concurrent counts made by independent teams in waterways of the Sundarbans mangrove forest in Bangladesh. *Marine Mammal Science* 22:527–547.
- Smith, B. D. and T. A. Jefferson. 2002. Status and conservation of facultative freshwater cetaceans in Asia. *Raffles Bulletin of Zoology* 173–187.
- Smith, B. D., R. G. Shore, and A. Lopez. 2007. Status and conservation of freshwater populations of Irrawaddy dolphins. *Wildlife Conservation Society* 31:1530–4426.
- Starr, P. 2003. The people's highway: past, present and future transport on the Mekong River system. Mekong Development Series No. 3. Mekong River Commission, Phnom Penh, Cambodia.
- Trujillo, F., E. Crespo, P. A. van Damme, and J. S. Usma. 2010. The action plan for South American river dolphins 2010-2020. WWF, Fundacion Omacha, WCS, WDCS, Solamac, Bogota, D.C., Colombia.
- Turvey, S. T., R. L. Pitman, B. L. Taylor, J. Barlow, T. Akamatsu, L. A. Barrett, X. J. Zhao, R. R. Reeves, B. S. Stewart, K. X. Wang, Z. Wei, X. F. Zhang, L. T. Pusser, M. Richlen, J. R. Brandon, and D. Wang. 2007. First human-caused extinction of a cetacean species? *Biology Letters* 3:537–540.
- Wang, D. 2009. Population status, threats and conservation of the Yangtze finless porpoise. *Chinese Science Bulletin* 54:3473–3484.
- White, G. C. and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:120–139.
- Williams, J. A., S. M. Dawson, and E. Slooten. 1993. The abundance and distribution of bottle-nosed dolphins (*Tursiops truncatus*) in Doubtful Sound, New Zealand. *Canadian Journal of Zoology* 71:2080–2088.