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MARK-RECAPTURE ANALYSIS OF THE CRITICALLY ENDANGERED EASTERN TAIWAN STRAIT POPULATION OF INDO-PACIFIC HUMPBACK DOLPHINS (*SOUSA CHINENSIS*): IMPLICATIONS FOR CONSERVATION

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ABSTRACT

Accurate and precise estimates of abundance and survival rates are important for assessing the conservation status of cetacean populations. Mark-recapture analysis of photo-identification data of the critically endangered eastern Taiwan Strait (ETS) population of Indo-Pacific humpback dolphin, *Sousa chinensis* (Osbeck, 1765), was conducted on data collected between 2007 and 2010 to refine a preliminary, and the only available, abundance estimate for this isolated population (n = 99; CV = 51.6%), as well as to provide survival rates. About 14,000 good quality photographs (about 2100–6300 yr^{-1}) were used to estimate both parameters for marked animals under Pollock's Robust Design model. The total population size (N_T) was determined by correcting for the proportion of the population possessing long-lasting marks ($\widehat{\theta}$). The annual point estimates were lower, varying from 54 to 74, and had much better precision (CV varied from 4% to 13%) than previous estimates, suggesting that mark-recapture is a suitable method for estimating abundance of this population. These estimates also further supported the precarious state of the ETS population under another criterion of the IUCN Red List of Threatened Species. As expected for long-lived mammals, annual apparent survival rate was high at 0.985 (95% CI = 0.832–0.998). Continuing to monitor the ETS population of humpback dolphins with such high precision and accuracy will allow examination of the population's trends over time and to better understand its future persistence.

The eastern Taiwan Strait (ETS) population of Indo-Pacific humpback dolphins, *Sousa chinensis* (Osbeck, 1765), appears to be distinct and isolated from conspecifics in adjacent waters (Wang et al. 2008). These dolphins are found only in a highly restricted stretch of shallow (<30 m), inshore waters off central-western Taiwan (<3 km from shore) and numbers <100 individuals (Wang et al. 2007a,b). These dolphins are exposed to numerous human activities that are known or suspected to be seriously harmful to cetaceans (e.g., habitat degradation and destruction due land reclamation, reduction of freshwater flow to estuaries, fisheries interactions, air and water pollution, underwater noise) and the intensity of these threats appear to be increasing (Wang et al. 2004a,b, 2007b, Ross et al. 2010, Dungan et al. 2012). Because the Indo-Pacific humpback dolphin is a coastal species with a fairly small home range (Hung 2000, Hung and Jefferson 2004) and often associated with estuaries (Jefferson 2000), where human activities tend to be concentrated, it is especially susceptible to anthropogenic threats. In August 2008, this population was included in the IUCN Red List of Threatened Species as "critically endangered," CR C2a(ii) (Reeves et al. 2008).

One of the most fundamental tasks for biologists studying endangered species is to obtain an accurate and precise estimate of abundance and other population parameters so that trends can be monitored and viability assessed. The first abundance estimate for this population of 99 dolphins (CV = 51.6%) was obtained using line-transect methodology (Wang et al. 2007a), but the limited amount of sighting data resulted in great uncertainty. Although this low precision estimate was adequate as a first approximation and for the assessment of the conservation status of this population, the difference between the extreme ends of the 95% CI (37–266) was sufficiently large that the urgency and level of precaution needed in mitigating harmful human activities were open to various interpretations and debates. Furthermore, with this imprecise estimate, the detection of even moderately steep trends in abundance over relatively short periods of a few years is not possible. With small highly endangered populations, the ability to detect shallow trends quickly is particularly important for assessing the effectiveness of management actions, if any, so improvements can be made, if needed, with minimal delay.

Mark-recapture analysis of photo-identification data is a proven method for estimating abundance and other relevant parameters such as recruitment and survival rates (Amstrup et al. 2005). It is particularly suited for small populations of distinctive individuals that are restricted in distribution, such as the ETS *S. chinensis*, which is usually found in small numbers, travels slowly, and often appears indifferent toward our research vessel when approached slowly (JY Wang, unpubl data). Mark-recapture has provided precise and accurate estimates of population abundance for several small dolphin populations (e.g., Wilson et al. 1999, Bejder and Dawson 2001, Currey et al. 2008, Fruet et al. 2011), as well as survival rates (e.g., Currey et al. 2009, Silva et al. 2009, Cantor et al. 2012). Precise abundance estimates also increase the likelihood of detecting trends in abundance over shorter time periods (e.g., Gerrodette 1987, Wilson et al. 1999, Gormley et al. 2005, Parra et al. 2006, Cantor et al. 2012). The main aim of the present study was to use mark-recapture methods for analyzing photo-identification data to provide better abundance estimates of the critically endangered ETS humpback dolphin population and with higher precision so that the population's trajectory, which is needed for evaluating the efficacy of conservation actions, can be better monitored. As a consequence of this analysis, the first estimates of survival rates were also generated for this population.

Materials and Methods

Survey Area, Design, and Methods.—Dolphin survey trips were conducted in most of the inshore (within approximately 3 km from shore) waters of western Taiwan between just north of Tongshiao, Miaoli County (approximately 24°30′N), and south of Taixi, Yunlin County (approximately 23°40′N), covering a linear distance of almost 110 km (Fig. 1). The study area represented about 65% of the entire known distribution and encompassed the primary distribution of the ETS population as described in Wang et al. (2007b). Twenty-four preset waypoints (12 inshore and 12 offshore) were established to form two wide, overlapping zig-zag tracks that alternated between inshore and offshore waypoints while avoiding hazards (e.g., protruding sandbars, newly reclaimed land, shallow water). Most surveys followed this zig-zag pattern. Inshore waypoints were located between 0.2 and 2.8 km from shore (note: "shore" is defined here as any solid land mass at low tide including sandbars and man-made structures), while initial offshore waypoints varied from 2.6 to 5.7 km from shore (excludes waypoint 20, which was only about 1 km from the tip of a long pier). After five initial trips in

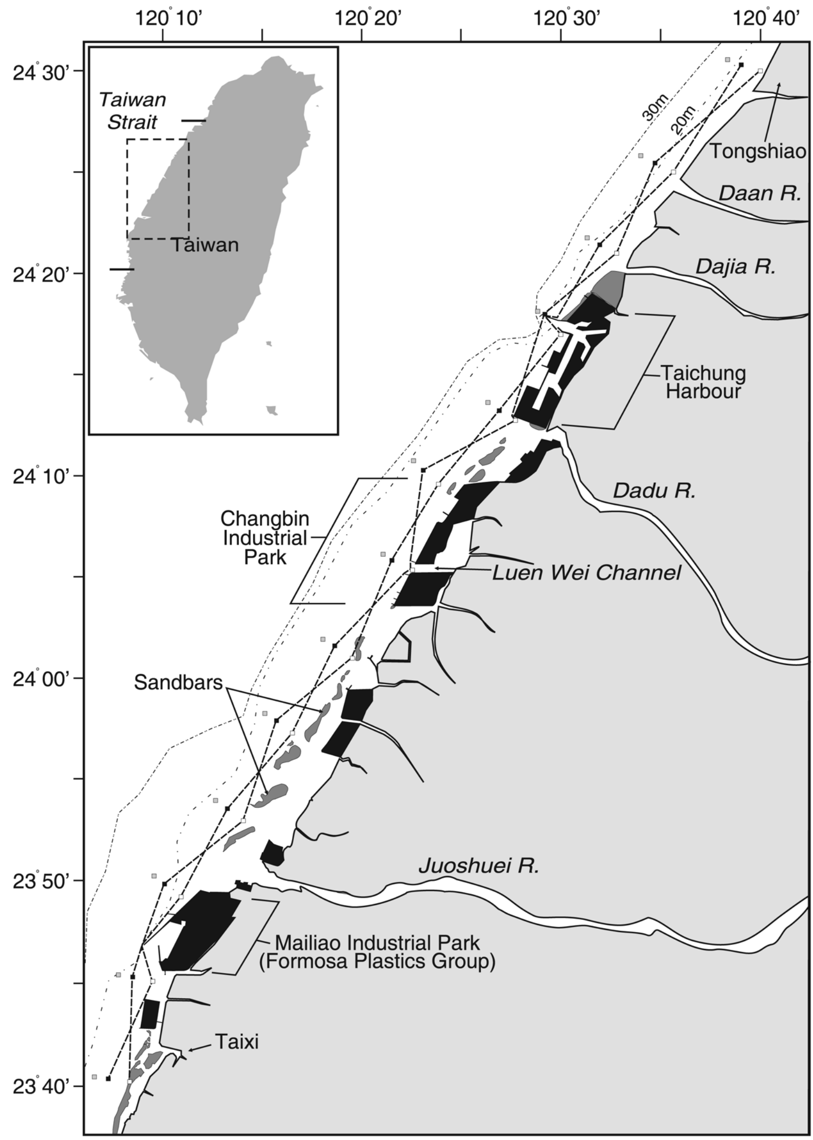

Figure 1. Map of the study area with preset waypoints and zig-zag tracks (thick broken lines) designed for surveying Indo-Pacific humpback dolphins (*Sousa chinensis*) of the eastern Taiwan Strait (ETS). Original offshore, adjusted offshore, and inshore waypoints are shown by gray, black, and open squares, respectively. Thin broken lines mark the 20 and 30 m depth contour and black polygons along the shoreline represent areas of considerable land reclamation. The study area along western Taiwan is shown in the inset map by a box with a broken outline and the short thick lines represent the extreme ends of the confirmed distribution of the ETS humpback dolphins.

2007, it was determined that too much effort was spent surveying waters where dolphins were unlikely to be found so offshore waypoints were moved inshore by 1.0–1.3 km. Water depths of the inshore waypoints were generally <10 m, whereas those of adjusted offshore waypoints were 10–30 m. The tidal difference can be up to 6 m in these waters and so waypoint depths can be very different from that reported, but regardless, the inshore waypoints were always considerably shallower than their offshore counterparts.

With the exception of one survey from a 19-m long fishing boat, all surveys were conducted from an inflatable boat (4.5 m in length) with a target boat speed of 18–25 km hr^{-1}. In general, about half of the study area (either north or south of the Luen Wei Channel) was covered during each survey trip day unless marine conditions shortened the survey period. The surveyed area (either north or south of the Luen Wei Channel) generally alternated but sometimes weather dictated the area that could be surveyed effectively. Due to marine and weather issues, surveys rarely could be conducted for more than three consecutive days. Attempts were made to survey the waters north and south of the channel as evenly as possible. Annual surveys were conducted for about 2 mo during the boreal summer (June–September) when weather conditions are generally most favorable and conducive to boat-based surveys along western Taiwan (Table 1).

Data Collection.—At preset waypoints and when dolphins were encountered, some standard data were recorded. The information included: date, time, geographic positions (determined using a handheld global positioning system—Garmin GPSMAP 76), group size, and number of mother-calf pairs with particular attention given to neonatal calves (defined as calves with prominent foetal creases, dark gray in color, noticeably smaller than their presumed mothers, and with obvious proportionately shorter beaks).

Approaching and Photographing Dolphins.—When dolphins were sighted, boat speed was reduced and the above data were collected before photographing the dolphins. Dolphins were approached at a constant slow speed (generally <5 km hr^{-1}) to avoid startling them and affecting their behavior as much as possible. Photographs were taken by two photographers using both traditional SLR (Nikon F100, only for 2007) and digital SLR (Canon 20D and Nikon D200) cameras with 80–200 mm f2.8, 300 mm f4.0, or 100–400 mm f4.5-5.6 IS lenses. For the film camera, Kodachrome 64 and Fujichrome Velvia 50 diapositive slide and Fujicolor 100 print films were used. Attempts were made to obtain high quality photographs of the dorsal fin and back, just below the dorsal fin, of each individual in the group (and both sides whenever possible). Photographs were taken randomly (i.e., without any intentional bias toward photographing certain individuals such as the most conspicuously "pink" individuals).

Scoring Photographs and Identifying Individuals.—The quality of all photographs of dolphins (Q_x) was scored on a scale of 1 to 4 (with 1 being the best) by two of the authors (JYW and PFF) based on sharpness, composition, and lighting. Aiming to minimize chances of false positives and false negatives, only Q_1 and Q_2 photographs were used in the analysis (e.g., Hammond et al. 1990). All photographs were also examined for identifiable or marked individuals by one author (JYW). The unique spotting patterns were the primary character for identifying individuals in the ETS population (Fig. 2). Unlike the humpback dolphins of the Pearl River and Jiulong River provisional populations, where the oldest dolphins lose all spotting on the body, the ETS population maintains some spotting throughout their lives (see Wang et al. 2008), so spotting patterns can be used for identifying all individual dolphins regardless of age (with the exception of very young, unspotted, or nearly so, calves) and do not appear to change greatly over several years (JY Wang, unpubl data). Furthermore, the unique spotting pattern is easily observable in photographs even if the orientation of dolphins is moderately oblique (Fig. 2). As a consequence of such clear, unique markings, the criteria for scoring photographic quality for the ETS dolphins was less stringent than scoring the quality of photographs taken of other species (i.e., bottlenose dolphins, *Tursiops* spp.), where nicks and scars on dorsal fins, being the usual principal features for individual identification, can be affected by the angle of the dolphins in the photographs (see Würsig and Jefferson 1990). The full reference catalog of the ETS humpback dolphins maintained since 2002 contained 76 individuals, but only 71 individuals had been seen within the last 5 yrs. Photographs of both sides of these 71 dolphins were available so photographs of either side could be used

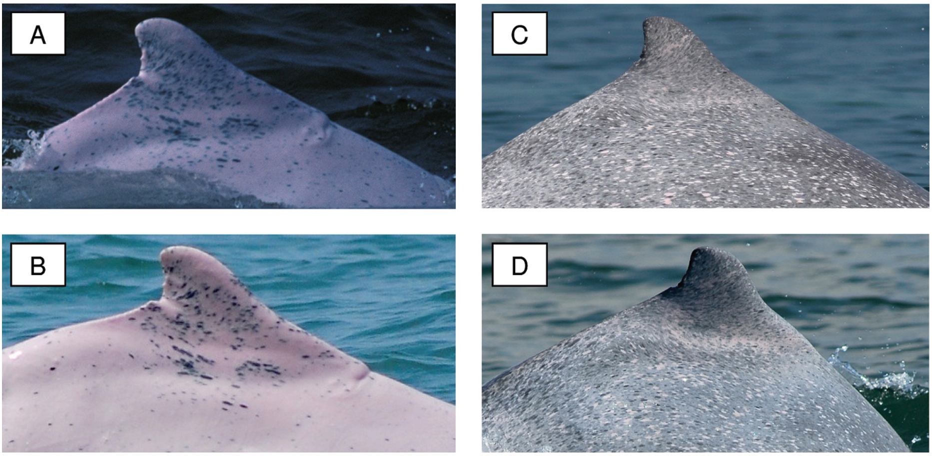

Figure 2. Examples of marked individuals in different color-classes from the eastern Taiwan Strait population of Indo-Pacific humpback dolphins (*Sousa chinensis*): TW-22, an older, mostly pink dolphin that was photographed in (A) 2004 and (B) 2010; TW-68, a younger, mostly gray dolphin that was photographed in (C) 2007 and (D) 2010. These photos show minimal changes in the dolphins' pigmentation patterns over several years and that pigmentation patterns are useful for individual identification even if photographs are not of the best quality [e.g., (A); but note that the original diapositive photograph quality is better than this scanned version] or if the dolphins in the photographs are slightly to moderately angled (D).

for individual identification. Permanent emigration is unlikely given that the population appears to be distinct and isolated from conspecifics found in waters along mainland China's coastline (Wang et al. 2008) and suitable habitat of this species appears to be highly restricted along western Taiwan (Wang et al. 2007b, Ross et al. 2010). If such an emigration event were to occur, it would be considered effectively as a potential death for the population.

Matches were made using the shapes, sizes, and relative positions of many spots, which were individually identifiable and fairly straightforward. Large, obvious scars were also a very useful, rapid, and nearly-independent means for confirming the identities of individuals that possessed such long-lasting marks. Small nicks and scars were also occasionally used for additional support of individual identification. Whenever a marked individual was detected in a photograph, it was compared to the reference catalog. Photographs of uniquely marked individuals that did not match any of those in the catalog were considered "new" individuals and were therefore added into the catalog and given new identification codes. Otherwise, they were considered "recaptures" (resightings in this case) of previous individuals. All individuals that were clearly not young calves possessed individually-distinct pigmentation patterns and were considered to be marked individuals. Unmarked calves included neonates, but older calves that had individually recognizable long-term spotting were included in the analyses as marked individuals. A mark-recapture matrix containing the sighting history of each marked individual was constructed.

Modelling Demographic Parameters.—The sighting history data of each marked animal was uploaded into the program MARK version 6.1 (White and Burnham 1999), which was used to perform all the mark-recapture analyses. Pollock's Robust Design (Pollock 1982), which combines open and close population models, was used to estimate a set of parameters such as survival, temporary emigration, capture probabilities, and abundance. Our sampling effort was organized into two hierarchical periods: the primary periods were composed of 4 yrs with 2 mo of effort each year; and the secondary periods were represented by several sampling occasions within each of the 2-mo periods.

A sampling occasion comprised 2 d of survey trips that were conducted alternately in the areas north and south of the Luen Wei Channel. This pooling was necessary to ensure adequate coverage of our study area and to reduce the effects of individual heterogeneity from differences in spatial distribution patterns of individuals (which, if present, did not appear to be obvious). To avoid pseudoreplication, data from consecutive surveys in the areas north or south of the Luen Wei Channel were omitted from the present analysis; in these cases, we excluded the surveys with fewer good quality photographs[1].

The following assumptions were made under the Pollock's Robust Design (Williams et al. 2002): (1) marks are not lost during the study period; (2) marked individuals are correctly recognized when recaptured; (3) individuals are instantly released after being marked; (4) intervals between sampling occasions are longer than the duration of the sampling; (5) all individuals observed during a given sampling occasion have the same probability of surviving to the next occasion; (6) study area does not vary; (7) marked and unmarked individuals have the same probability of being captured; (8) the population remains closed (i.e., events of births and deaths, immigration and emigration do not occur) within primary periods; and (9) the capture of an individual does not affect its subsequent recapture probability during the secondary period. Violations of these assumptions may cause overdispersion, or extra binomial variation (Williams et al. 2002), a common characteristic of cetacean data (Hammond et al. 1990). Unfortunately, a goodness-of-fit test to investigate this is not available for the robust design in MARK (see White and Burnham 1999). Therefore, the overall model fit could not be evaluated and the models were not adjusted for overdispersion. The effects of possible violations of assumptions in our data are discussed below, but because these dolphins are long-lived animals with a highly restricted distribution and the sampling period is short, we assumed that the population remained closed within the primary periods.

Our models contained the following parameters: ϕ_t = apparent survival probability between primary periods; p_{st} = the probability that an individual available for capture in period t would be captured in the secondary sample s of the primary period t; $\gamma''_t\, \gamma'_t$ = the probability that an individual would be unavailable for capture during primary period t, given that it was available or unavailable, respectively, for capture in period $t - 1$ (the probability of temporary emigration), and abundance (N) that was estimated using the Huggins's parameterization method (Huggins 1991), which is more stable with small sample sizes, and implemented in the program MARK. As there is no biological reason to expect obvious behavioral responses to "capture" by photographic identification (dolphins are not handled and there has been no obvious negative response to our approaches in subsequent photography of individuals), recapture probability (c) was set to be equal to capture probability (p) in all candidate models ($c_i = p_i$). We used Pledger's mixture models with two mixtures of capture probability ($2 - p_i$) to incorporate individual heterogeneity (Pledger 2000) only in models with no emigration since a full-likelihood estimator of temporary emigration for these models has not yet been developed (Kendall et al. 1997). Furthermore, heterogeneity was not included in the models with full time-dependence effect due to over-parameterization (non-identifiability of several parameters). We started our analyses by running a model that ignored temporary emigration (i.e., setting $\gamma'' = \gamma' = 0$) and aimed to investigate the effects of individual heterogeneity and time variation on capture probabilities (p) between (t) and within primary periods (s) and their interaction (st). After exploring the time-dependence effect on capture probability we explored the temporal effect on survival and then included random and Markovian emigration processes (Kendall et al. 1997), considering or not the time effect on these parameters.

Model Selection.—The most parsimonious models were selected using the Akaike Information Criterion corrected for small sample size (AICc; Burnham and Anderson 2002). Normalized AICc weights were used to evaluate the strength of evidence for a given model relative to the others. A model averaging approach was used to take into account uncertainty in model selection. Specific biological hypotheses between nested models were tested using the likelihood ratio tests (LRT) of Burnham and Anderson (2002).

1 Due to weather conditions, surveys were sometimes conducted in the same waters on consecutive days to maximize the collection of data that could be used for other studies.

Estimation of the Total Population Size.—The total population size ($\widehat{N}_T$) was estimated by correcting for the estimated proportion of the population possessing long-lasting marks ($\widehat{\theta}$), using the ratio $\widehat{N}_T/\widehat{\theta}$.
Theta was obtained by

$$\widehat{\theta}=\frac{\sum_{i=1}^{k}\frac{I_i}{T_i}}{k},$$

and its variance expressed as

$$\mathrm{var}(\widehat{\theta})=\left(\sum_{i=1}^{k}\frac{\theta_i(1-\theta_i)}{T_i}\right)\Big/k^2,$$

where I_i is the total number of dolphins with long-lasting marks photographed in the group i; T_i is the total number of dolphins photographed[2] in group i; k is the total number of groups sampled. Young unspotted (or nearly so) calves were considered as "unmarkable" dolphins and were incorporated in the calculation of $\widehat{\theta}$.

The coefficient of variation for the total population size, $CV(N_T)=\sqrt{(CV(\widehat{N})^2+CV(\widehat{\theta}))^2}$, was expressed as a combination of CVs of $\widehat{N}$ and $\widehat{\theta}$, while the 95% confidence interval was constructed assuming a lognormal approximation as recommended by Burnham et al. (1987) and calculated by $r=\exp\{1.96\sqrt{\ln(1+(CV(\widehat{N}_{CH}))^2)}\}$. The lower bound of the confidence interval was calculated as $\widehat{N}_L=\widehat{N}/r$ and the upper bound as $\widehat{N}_U=\widehat{N}\times r$, where $(1+(CV(\widehat{N}_T))^2)$ is an approximation of $\mathrm{var}(\ln\widehat{N}_T)$.

Results

Search Effort.—A total of 273.6 hrs were spent surveying 4891.0 km of water in the study area, which covered about 65% of the known distribution of the population (see inset in Fig. 1). Annual survey effort varied between 1138.4 km (and 61.2 hrs) and 1292.0 km (and 90.0 hrs) due to weather conditions and logistical issues (Table 1).

Sightings.—In total, 125 sightings were made during the study period. However, 30 (3 in 2007, 9 in 2008, 3 in 2009, and 15 in 2010) sightings were not included in the main analysis because poor marine conditions prevented the collection of photographs of adequate quality and data from some survey trips were excluded to avoid the potential issue of pseudoreplication. Dolphins were observed throughout the study area, including at the extreme ends, but most of the sightings (about 60%) were recorded near the mouths of the Dadu River and Luen Wei Channel, the latter being the convergence of freshwater discharge from several smaller creeks and sewage canals. Estimates of group size based on all sighting events varied from 1 to 31, but smaller groups were most commonly observed (median = 5; Table 1).

Photographs and Number of Individuals Photographed.—Combined, a total of 13,726 photographs in the two best categories of quality were used for estimating the marked population. In total, 72 marked individuals were photographed during the present study, but varied annually between 41 and 64 individuals (Table 1). Within primary periods, the discovery curves of the number of different individuals photographed did not reach an asymptote in 2007 to 2009 and just barely in 2010, while for all years combined, a clear asymptote was reached at slightly more than 70 individuals (Fig. 3). The distribution of the recapture frequencies for different

2 Almost all young calves were identifiable in the groups; some possessed long-lasting marks while most others possessed superficial marks that allowed temporary identification.

Table 1. Indices of annual research effort and coverage (duration of survey period; number of primary (1°) and secondary (2°) sampling periods; survey distance (km) and time (hrs); number of good quality photographs obtained; number of dolphin groups encountered; number of different individual dolphins photographed).

				Survey effort						
Year	Survey dates	1° (days)	2° (periods)	trips	km	hrs	Q_1 and Q_2 photos	Dolphin groups	Group size mean (SD)	Different individuals
2007	06/16–08/04	50	6	24	1,292	90.0	2,479	22	9.0 (7.12)	55
2008	08/05–09/25	52	6	20	1,199	59.7	2,102	19	4.5 (3.82)	48
2009	06/06–07/30	55	6	17	1,138	61.2	2,847	20	5.2 (4.91)	41
2010	07/10–08/29	51	12	28	1,262	62.7	6,298	34	8.4 (7.77)	64
Totals				89	4,891	273.6	13,726	95	7.0 (6.61)	72

Notes: Survey dates are shown as MM/DD–MM/DD; each 2° period represent the pooled sampling of two trips (not all trips were included in the analysis to avoid or at least reduce the possibility of pseudo-replication); Q_1 and Q_2 represent the two best quality photographs; the mean (SD) group size was based on all sightings (n = 125) that were made during the study period; total number of different individuals photographed during this study is not the simple sum of the individuals across years.

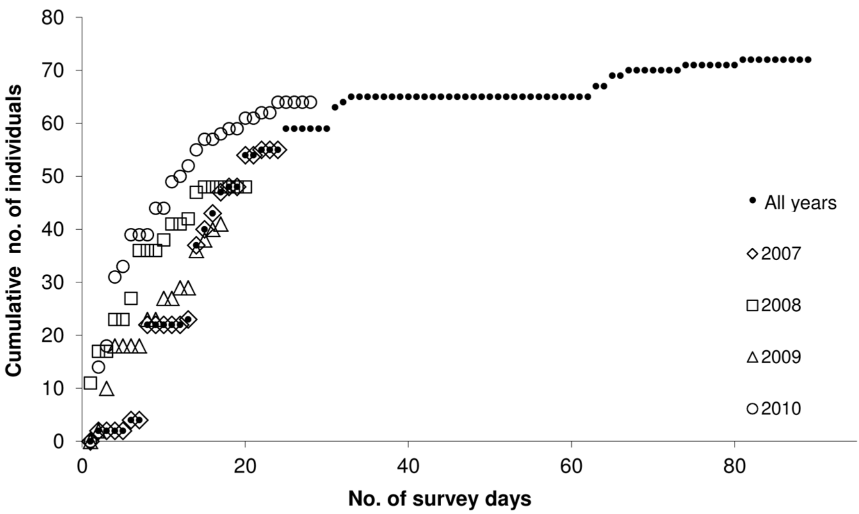

Figure 3. Discovery plot of the cumulative number of recognizable individual Indo-Pacific humpback dolphins (*Sousa chinensis*) of the eastern Taiwan Strait population vs the total number of survey days for 2007 (open diamonds), 2008 (open squares), 2009 (open triangles), 2010 (open circles), and all years combined (black points).

individual dolphins varied greatly across primary periods, but by 2010 almost all individuals had been photographed and fewer dolphins (<10%) were captured only once compared with previous years while for all years combined, only three of 72 individuals were captured once (Fig. 4).

Each year, there were a minimum of two to six young calves with little to no spotting; these were considered unmarked (i.e., did not bear clear, lasting, individually-unique marks). These calves included a minimum of one to three neonatal or near neonatal calves each year. The estimated proportion of marked animals in the population (θ) was high, but varied annually. On average, about 90% of the individuals from the population are distinguishable by consistent spotting patterns.

Model Selection.—Our first round modelling (Table 2), which disregarded the effects of temporary emigration, showed that the model considering full time-dependence in capture probability (model 5) fitted the data better than the constant model (model 9) or models that incorporated individual heterogeneity (models 6, 7, and 8). Starting from models with constant survivor probability {$\phi(.)$} and time-dependence in capture probabilities between and within primary periods {$p(st)$}, we tested the effects of emigration processes (both random and Markovian). Models taking these processes into account provided better support of our data (models 1–3) and were also confirmed by LRT that rejected models with no emigration when tested against models with random (χ^2 = 10.019, df = 1, P = 0.0016) and Markovian (χ^2 = 10.019, df = 2, P = 0.0067) emigration processes. Although the Markovian model also provided reasonable support (model 3), random emigration models provided the best description of the data (models 1 and 2). Specifically, the most parsimonious model assumed constant survivor probability, constant random temporary emigration, and full time-dependence in capture probabilities (model 1).

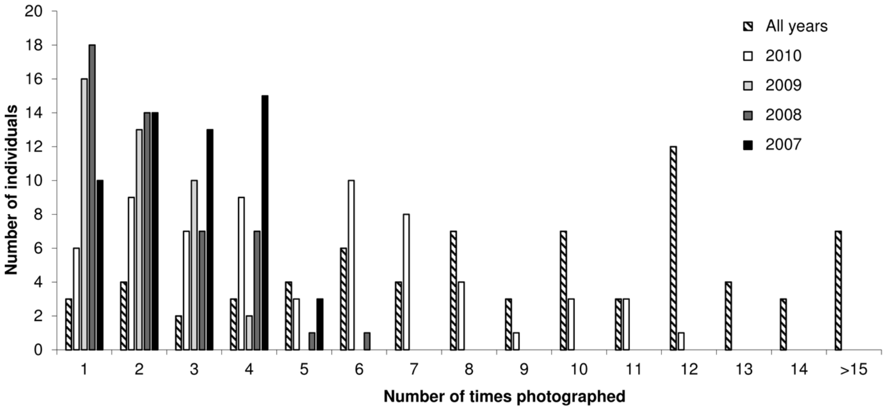

Figure 4. Frequency distribution of the number of sightings (i.e., number of times photographed) for individual eastern Taiwan Strait Indo-Pacific humpback dolphins (*Sousa chinensis*) for all years combined (hatched) and separately for 2010 (open), 2009 (light gray), 2008 (dark gray), and 2007 (black).

Survivorship and Capture Probability.—The averaged model estimated a constant high annual apparent survival rate for this population (0.985, SE 0.018, 95% CI = 0.832–0.998). Capture probability was generally low, but highly variable between sampling occasions (within primary periods), ranging from: 0.03 to 0.54 in 2007; 0.03 to 0.38 in 2008; 0.04 to 0.32 in 2009; and 0.05 to 0.57 in 2010. The mean capture probability for each primary period was also low (Table 3).

Temporary Emigration.—We estimated a relatively low probability of temporary emigration for individuals in the ETS humpback dolphin population. The random emigration model estimated an annual probability of 0.13 (95% CI = 0.06–0.26) for an individual to move out (γ'') or remain outside of the study area (γ'), regardless of their previous state (i.e., whether or not it was available in the sample area for capture in previous years). This means that dolphins that emigrated temporarily have the same probability of returning ($1 - \gamma'$) to the study area as dolphins that remained in the study area ($1 - \gamma''$) between sampling seasons ($1 - \gamma'' = 1 - \gamma' = 0.87$).

Abundance Estimates.—The mean number of marked dolphins in the population estimated by Pollock's Robust Design model was 58 for 2007; 54 for 2008; 51 for 2009; and 64 for 2010. Correcting for the proportion of marked dolphins in the population, the estimated total population size was: 65 in 2007; 58 in 2008; 54 in 2009; and 74 in 2010. The measures of uncertainty were low for all estimates, with CVs varying between 4% (2007 and 2010) and 13% (2009), while 2008's estimate had a CV of 6% (see Table 3). Even considering the highest of all upper confidence limits, the abundance of this population still did not exceed 80 dolphins.

Discussion

The abundance estimates of the ETS population in the present study using mark-recapture analysis of photo-identification data had much higher precision (four to 13 times) and were about 25%–45% lower than the initial line-transect abundance

Table 2. Pollock's Robust Design candidate models for 2007–2010 ETS humpback dolphins (*Sousa chinensis*) mark-recapture data of survival (f), capture (p), recapture (c) and temporary emigration (g) probabilities. Models are sorted in decreasing order of AICc values with the lowest AICc value representing the most parsimonious model. NPar denotes the number of parameters. Notation (following Kendall et al. 1997): $\gamma'' = \gamma' = 0$ = no emigration; $\gamma''(x) = \gamma'(x)$ = random emigration model; $\gamma''(x)\ \gamma'(x)$ = Markovian emigration model; (pi) mixture proportion; (.) constant parameter; (s,t) time-variant parameter and session-variant $p(x) = c(x)$ = no behavior effect.

	Model	AICc	Delta AICc	AICc weights	Model likelihood	NPar	Deviance
1	$\{\phi(.)\ \gamma''(.) = \gamma'(.)\ p(st) = c(st)\}$	2,203.83	0.00	0.446	1.00	32	2,779
2	$\{\phi(.)\ \gamma''(t) = \gamma'(\mathrm{t})\ p(st) = c(st)\}$	2,204.14	0.32	0.381	0.85	34	2,775
3	$\{\phi(.)\ \gamma''(.)\ \gamma'(.)\ p(st) = c(st)\}$	2,205.98	2.15	0.152	0.34	33	2,779
4	$\{\phi(.)\ \gamma'' = \gamma' = 0\ p(st) = c(st)\}$	2,210.26	6.43	0.018	0.04	31	2,778
5	$\{\phi(t)\ \gamma'' = \gamma' = 0\ p(st) = c(st)\}$	2,214.06	10.23	0.003	0.01	33	2,787
6	$\{\phi(t)\ \gamma'' = \gamma' = 0\ \mathrm{pi}(.)\ p(t)\}$	2,287.04	83.22	0.000	0.00	12	2,906
7	$\{\phi(t)\ \gamma'' = \gamma' = 0\ \mathrm{pi}(t)\ p(t)\}$	2,290.49	86.67	0.000	0.00	13	2,907
8	$\{\phi(t)\ \gamma'' = \gamma' = 0\ p(t) = c(t)\}$	2,315.50	111.68	0.000	0.00	7	2,945
9	$\{\phi(t)\ \gamma'' = \gamma' = 0\ p(.) = c(.)\}$	2,355.87	152.04	0.000	0.00	4	2,991

estimate of 99 individuals with a CV of 51.6% (Wang et al. 2007a). The results of our study showed that there are many fewer ETS dolphins than the previous point estimate indicated (although well within the 95% confidence interval of the initial estimate). However, possible dependence on capture probabilities (and individual capture probabilities increasing with sightings of associates) may have resulted in underestimation of the confidence intervals, but the high short-term fluidity of individual associations and the lack of modularity found in this population (Dungan 2011) potentially reduced this source of bias. Also, the present study had representative survey coverage of the population's distribution, including all of its primary distribution (see Wang et al. 2007b). A recent preliminary examination of the ranging patterns of catalogued individuals (including surveys that were conducted beyond the present study area) revealed that all individuals (except one) were observed around the Dadu Estuary (JY Wang, unpubl data), which is almost in the middle of the present study area, which means there is a good probability of capturing all animals. Moreover, even though more surveys were conducted in areas beyond the study area in 2011, preliminary analysis has revealed that no new individuals were observed (JY Wang, unpubl data). Therefore, the 2010 estimate is probably an accurate estimate of the abundance of this critically endangered population.

The ETS humpback dolphin population appears to be genetically and demographically isolated from other adjacent populations (Wang et al. 2008). As such, the main changes to the population within primary periods (assumption 8) would be births and deaths. The short annual survey seasons between 50 and 55 d (from the first to last sampling days each year) in 2007 to 2010, and the high survival rates estimated for this population reduced the probability of losing individuals to deaths between the "marking" and "recapturing" periods. Also, the chance for young animals to enter the marked population by gaining new, long-lasting, distinctive marks during a short sampling year is also low. Several years of photographic monitoring of several individuals showed that changes in pigmentation patterns are minimal over several years and none of the young animals with non-pigmentation marks (i.e., scars, nicks, etc.) that were observed in 2007 gained new long-lasting spots during the study period (JY Wang, unpubl data). These data, together with the resighting frequencies of

Table 3. Abundance estimates of marked individuals (*N*) in the ETS population of humpback dolphins based on the weighted averages of the five best robust design models corrected by the proportion of marked individuals in the population ($\hat{\theta}$) and the estimated total population size (N_T) from 2007 to 2010 photo-identification data. Mean capture probability (*P*) per sampling season and associated measures of uncertainty (standard error, SE; coefficient of variation, CV; 95% confidence interval, CI) are also shown for each estimate. The 95% CIs were determined assuming log-normal distributions.

Year	*P*	SE	*N*	CV (*N*)	95%CI	$\hat{\theta}$	CV($\hat{\theta}$)	N_T	CV (N_T)	95% CI
2007	0.22	0.16	57	0.033	54–61	0.89	0.03	65	0.04	60–70
2008	0.14	010	56	0.061	48–61	0.93	0.02	58	0.06	52–65
2009	0.14	0.11	48	0.089	42–60	0.94	0.02	54	0.13	42–70
2010	0.26	0.13	64	0.006	63–65	0.86	0.04	74	0.04	68–80

individuals, the area surveyed, the use of photographs for identifying individuals, and the fitting of the data to models accounting for temporary emigration are consistent with the population remaining closed within each of the sampling seasons and with the other assumptions of the mark-recapture model.

Is the Population Declining?—It would be of even greater concern if the abundance of this small, critically endangered population was declining. Although the point estimates of abundance varied annually, with the lowest being in 2009, it was largely an artifact of other factors affecting our data rather than a true decline in the population size. In 2010, for example, there were many non-calf individuals photographed that were not sighted in 2009. Possible explanation for such variation may be related to yearly shifts in the availability of dolphins for capture in the study area or to our inability to monitor the entire survey area in just one sampling period (weather and sighting many individuals to photograph can often reduce the area surveyed), resulting in low capture probabilities per sampling occasion (varying between 0.03 and 0.57). Although we have monitored a large part of the whole population distribution, environmental conditions (e.g., prey availability in some areas outside of our study site) or slight changes in survey effort can easily affect the availability of animals for capture at least once during a sampling season, especially if some animals are more mobile or transient (as evidenced by the number of animals captured only once during the 2007, 2008, and 2009 sampling seasons). This also can affect the overall likelihood of capture and increase individual heterogeneity. However, the robust design reduces the bias of abundance estimates that are caused by heterogeneity in capture probabilities (Pollock et al. 1990). Given the present data, it is unclear how comparable the data are across years because annual research effort, particularly sampling effort in sea conditions that are conducive to obtaining good quality photographs of dolphins from a small boat, appears to have varied. In 2007 and 2010, effort was the greatest due to overall calm conditions (few typhoons occurred and many days had a Beaufort sea state ≤2). The high survey effort in 2007 was also due to ongoing refinements of the methods and study area where considerable effort was allotted to waters in which the species is not known to occur (i.e., in waters deeper than 30 m). Furthermore, these early surveys were also conducted at a slower speed so many more hours were spent surveying almost the same amount of water as in 2010. Also in 2007, relatively fewer photographs were obtained because both digital and traditional SLR cameras were still being used while in other years, only digital SLR cameras were used. With such variation in survey and sampling effort and just four primary periods, presently it is not possible to determine the trajectory of the population with any level of certainty. The 2010 estimate was likely the most accurate because of the better sampling of the population (34 groups of dolphins were encountered and 64 different marked individuals were photographed) probably as a result of favorable weather conditions, resulting in the highest mean capture probabilities, abundance estimates, and precision. This estimate was also consistent with the cumulative discovery curve that appeared to reach asymptote, or nearly so, at about 72 marked individuals (a very few may have perished but would not be apparent on this plot). In 2011, good weather also resulted in similarly good sampling and data collection as well as a few additional surveys south of the present study area. However, preliminary analyses revealed that no new marked individual were sighted while a minimum of 61 different marked individuals were photographed. Continuing to monitor this population with at least the same level of sampling as in 2010 and 2011 is important for understanding the trajectory of the abundance of this population.

The present study showed that for this population, mark-recapture analysis is capable of producing accurate estimates and with a level of precision that may allow the detection of small changes over relatively short time periods of a few years. The power of detecting changes in abundance is directly related to the precision of the estimates (Gerrodette 1987), so future studies should strive to reduce uncertainty to the lowest level reasonable to improve detection of trends more rapidly, especially if abundance is changing very slightly each year. Long-term monitoring is also vital for quantifying and assessing the effectiveness of conservation actions (or lack thereof) and the impacts of threats on the population. Moreover, such longitudinal studies will further improve our understanding of many other biological parameters of the ETS population. Increasing sampling effort (and possibly geographical coverage of the distribution) should result in higher capture probabilities, reduced heterogeneity, and improved precision and accuracy of abundance estimation.

Survival Rates and Temporary Emigration.—To our knowledge, this study generated the first ever estimate of survival for this species or genus and the apparent survival rate was very high at 0.985 (95% CI = 0.832–0.998). This was comparable to but still noticeably higher than bottlenose dolphins, *Tursiops* spp., and other species (e.g., Currey et al. 2008, Silva et al. 2009, Cantor et al. 2012). The level of imprecision was quite large, which is likely in part due to inclusion of all age-classes of dolphins combined in the analysis. The point estimate of survival rate is as high as those observed for large baleen whales and higher than most odontocetes (e.g., Taylor et al. 2007). This probable overestimate is possibly a consequence of the short study period (some individuals may have perished but considered to have emigrated temporarily). However, the possibility of a survival rate higher than what would be expected for a small cetacean should not be excluded if a density-dependent response favored individual survival due to increased per capita food availability. Given the very low numbers in this isolated population, and therefore low recruitment, a high survival is the best chance for this population to persist.

The low estimates of temporary emigration compared to other species (e.g., Silva et al. 2009, Cantor et al. 2012) was not surprising because this population is small and isolated to a restricted distribution and the study area occupied about 65% of the central part of the population's known restricted range, including its primary distribution. With one exception, all known individuals that have been recorded from throughout the known distribution have been observed within the present study area and many individuals have large (>80%) ranges relative to the known distribution of the population (JY Wang, unpubl data). Even so, temporary emigration may still have been overestimated due to inadequate sampling (in terms of total survey effort and because survey effort decreases with increasing distance from the center of the study area, where most surveys began and ended).

Conservation.—The abundance estimates of the present study were all much lower than the estimate of Wang et al. (2007a) and further confirm the IUCN Red List assessment of the ETS humpback dolphin population as "critically endangered" (Reeves et al. 2008). With the largest total abundance estimate being 74 individuals and assuming that mature individuals comprised 60% of the total population (following Jefferson 2000), the ETS population would contain <45 mature individuals. As such, this population would also meet the "critically endangered" threshold under criterion D [i.e., <50 mature individuals—see IUCN (2001)]; this would be true even if the actual abundance was as high as the upper bound of the 95% CI for the largest point estimate. Thus, the IUCN Red List status for the ETS population should be revised to CR C2a(ii);D, i.e., Critically Endangered under the thresholds of subcriterion 2a(ii) of criterion C (fewer than 250 mature individuals, a decline is projected and at least 90% of the individuals occur in a single subpopulation; and criterion D (fewer than 50 mature individuals).

The low abundance and dire conservation status of this population is of great concern because this species is especially vulnerable to anthropogenic threats (e.g., Perrin 1989, Reeves and Leatherwood 1994, Leatherwood and Jefferson 1997, Reeves et al. 2003) being long-lived, with limited reproductive capacity, individuals having relatively small home ranges (Hung 2000, Hung and Jefferson 2004), and the entire population occurring within a restricted distribution of only about 600 km^2. Furthermore, these dolphins are found in coastal and estuarine waters adjacent to the shores of western Taiwan so there is great overlap between their distribution and human activities. Five major anthropogenic threats that have been identified include fisheries, pollution (air and water), habitat degradation and destruction as a result of land reclamation and coastal development for heavy industry, loss of fresh water to the river estuaries upon which the dolphins depend, and noise (Wang et al. 2007b, Ross et al. 2010, Dungan et al. 2012). Most of these threats are still increasing (Reeves et al. 2008) with more proposals for construction of massive petrochemical projects and related energy and water infrastructure projects to meet the needs of increased heavy industrial development. For example, two new thermal (coal-fired) power plants have been proposed for the region even though the existing coal-fired power plant at the mouth of the Dadu River (Taichung County) is already infamous as the world's highest CO_2-emitting power plant, producing 37 million metric tons per annum (Tollefson 2007). These thermal power plants have been or will be built on "reclaimed" land over water that once was or still is habitat for these dolphins. New water diversion projects will result in a further reduction of freshwater flow to productive estuaries that are important habitat of the ETS dolphins and their prey, which appear to be mainly estuarine-related or -dependent fishes (Barros et al. 2004). Along with such industry and energy infrastructure projects, there will also be an increase in local air and water pollution.

This unique population of Indo-Pacific humpback dolphins in Taiwanese waters is likely declining (Reeves et al. 2008) and faces “imminent extinction if measures are not taken to protect them and their habitat from a number of serious threats” (Wang et al. 2007b). And unless actions to conserve these dolphins are immediate and effective, the ETS population will continue toward the same fate as the baiji or Chinese river dolphin, *Lipotes vexillifer* (Miller, 1918), which once lived in the mighty Yangtze River but was driven to recent extinction by similar kinds of human activities (Turvey et al. 2007).

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