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# Group Size of Indo-Pacific Humpback Dolphins (*Sousa chinensis*): An Examination of Methodological and Biogeographical Variances

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Observer-based counts and photo-identification are two well-established methods with an extensive use in cetacean studies. Using these two methods, group size has been widely reported, especially for small dolphins. Both methods may come with potential errors in estimating the group size, yet there is still a lack of comparison between both methods over a broad range of group size. Particularly, biogeographical variances in group size estimates were often mixed with methodological variances, making it difficult to compare estimates from different geographic regions. Here, group size estimates of a small, shallow-water, and near-shore delphinid species, Indo-Pacific humpback dolphins (*Sousa chinensis*), were simultaneously sampled using observer-based counts and photo-identification at three regions in the northern South China Sea. Data showed that dolphin group size from two methods were highly variable and associated with sampling regions. Generalized linear mixed models (GLMMs) indicated that dolphin group size significantly differed among regions. Statistical examinations further demonstrated dolphin group size could be affected by a complex combination of methodological and biogeographical variances. A common hurdle to examine potential factors influencing the estimation process is the inability to know the true group size at each sample. Therefore, other methods that could generate comparable estimates to represent true group size are warranted in future studies. To conclude, our findings present a better understanding of methodological and biogeographical variances in group size estimates of humpback dolphins, and help yield more robust abundance and density estimation for these vulnerable animals.

**Keywords:** humpback dolphins, group size, observer-based counts, photo-identification, methodology, biogeography

## INTRODUCTION

Groups are a fundamental unit of gregarious animal species (Casari and Tagliapietra, 2018). Thus, the estimation of group size is crucial for research in animal ecology and behavior (Peña and Nöldeke, 2018; Kappeler, 2019). For example, in standard distance sampling protocols, a reliable estimate of animal abundance is highly dependent on whether group size of detected animals could be estimated as accurately as possible (Buckland et al., 1993; Barlow et al., 1998). Group size is also a prominent trait to indicate social characteristics for a wide range of animal taxa (Parrish and Edelman-Keshet, 1999; Kappeler et al., 2019). However, it is difficult to generate accurate group size estimates for wild animals, since the estimation process may be affected by diverse factors (Walsh et al., 2009; Clement et al., 2017).

A fundamental approach to estimate group size of free-ranging dolphins is on-site counts by observers from vessels (Mann, 1999). However, dolphins are highly mobile, spend prolonged periods underwater, and are partially visible from the sea surface, all of which pose substantial difficulties to estimate group size (Gerrodette et al., 2002). Furthermore, social dynamics may differ among dolphin species (Gowans et al., 2007), which can greatly affect the estimation process of group size. Consequently, group size estimates from observer counts are often variable, especially for extremely large groups (referred to as “schools” in some studies), with non-trivial between-observer variance as well as within-observer between sample variance (Erwin, 1982; Gerrodette and Perrin, 1991; Bouveroux et al., 2018). Although observers’ experience can be improved through training and practice, it is still hard to remove potential bias from observer-based counts (Gerrodette and Perrin, 1991; Clement et al., 2017), and the bias may increase with the group size (Gerrodette et al., 2019).

The photo-identification technique can be available in estimating the group size of those naturally marked cetacean species (Würsig and Würsig, 1977). Many delphinid species have distinctive natural markings on/around the dorsal fin, which allows the identification of individuals from photographs and further provides a mechanism for estimating their group size (Urian et al., 2015; Pawley et al., 2018). However, the use of photo-identification may bring potential errors due to misidentification. Dolphin group size may be underestimated, because no guarantee can ensure that all marked individuals present within an encounter could be captured, and some individuals, particularly younger ones, are often poorly marked or unmarked (Hupman et al., 2018; Wickman et al., 2021). Furthermore, photo-identification cannot always generate accurate group size estimates, as some dolphin species have poor nick/notch markings for matching the left and right sides of the same individuals (Auger-Méthé et al., 2010; Hupman et al., 2018).

In dolphin societies, group size, social structures, and dynamics differ among species, which is known as interspecific variability of sociality (Gygax, 2002b; Gowans et al., 2007). Additionally, a specific dolphin species can build different sizes of groups at various spatial and temporal scales (Gygax, 2002a;

Liu et al., 2021a,b), which is so-called biogeographical or inter-population variability of sociality (Liu et al., 2021c). Although both observer-based counts and photo-identification have been widely applied in dolphin sociality studies, little attention, if anything at all, has been paid to compare the performance of these two methods in estimating group size. Intraspecific variability in dolphin group size is often confusing, since variances from methodology and biogeography were mixed in many studies, leading to substantial difficulties in comparing the estimates from different systems (Gygax, 2002a,b; Liu et al., 2020b, 2021c).

Thus far, it is well known that both observer-based counts and photo-identification might come with potential errors in estimating dolphin group size. However, scant is known at which bias in group size estimates might occur and how these methods have potential influences. A common hurdle to examine potential factors influencing the estimation process is the inability to know the true group size at each sample (Walsh et al., 2009; Hamilton et al., 2018). Moreover, the potential bias and variance in group size estimates might be of species specificity, and thus bias correction factors estimated in different ocean basins and for different species cannot guarantee to apply for all studies.

The Indo-Pacific humpback dolphins (*Sousa chinensis* Osbeck, 1765), hereafter referred to as “humpback dolphins,” are small delphinid species inhabiting shallow and near-shore waters of the eastern Indian and western Pacific Oceans (Jefferson and Smith, 2016; Li, 2020). Group size estimates have been widely reported for this species across many known populations, and all studies have used either observer-based counts (Chen et al., 2010; Wang et al., 2015) or photo-identification (Chen et al., 2016; Wang et al., 2016). Humpback dolphins are often observed or photographically captured in groups with variable sizes (Würsig et al., 2016), from a single animal to small groups (mostly about ten or fewer), and sometimes to large aggregations (several tens or low hundred; Parsons, 2004; Liu et al., 2021c). Reducing errors in estimating group size is crucial to density and abundance estimate for this species (Marsh and Sinclair, 1989; Chen et al., 2010), but there is no a good grasp of how well traditional estimation methods (i.e., observer-based counts, and photo-identification) applied to this species.

In this study, observer-based counts and photo-identification were simultaneously used to sample group size estimates of three geographically isolated humpback dolphin populations in the northern South China Sea. Both methodological and biogeographical variances in group size estimates of humpback dolphins were assessed. This study aims (1) to better understand the bias and variance in group size estimates of humpback dolphins and (2) to reveal the intra- and inter-population variability in group size of this species.

## MATERIALS AND METHODS

### Sampling Regions

Three areas along the northern coast of the South China Sea were selected as sampling regions: the waters southwest off Hainan Island (SWH; Li et al., 2016; Liu et al., 2020b), Sanniang Bay

(SNB; Chen et al., 2016; Wu et al., 2017; Peng et al., 2020), and Leizhou Bay, China (LZB; Xu et al., 2012, 2015; Liu et al., 2021a,b; **Figures 1A,B**). All these regions have been well known to support critical habitats with resident humpback dolphins. In this manuscript, sampling regions were always depicted in the order of SWH, SNB, and LZB, unless otherwise stated. Based on line-transect sampling design, boat-based surveys were performed in each sampling region by evenly-spaced zigzag transects (Buckland et al., 1993; Dawson et al., 2008). Given that humpback dolphins strongly preferred inhabiting shallow and near-shore waters (Jefferson and Smith, 2016), similar fishing or speed boats (~7-15 m in length) were used to investigate the waters at depth  $\leq 30$  m and offshore  $\leq 20$  km. Boat-based surveys were only conducted under satisfactory visual conditions (no rain/fog) and sea states ( $\leq 4$  on the Beaufort scale; Li et al., 2016; Liu et al., 2020a,b, 2021a).

## Observer-Based Counts

During the boat-based surveys, a minimum of two trained observers visually scanned  $180^\circ$  of the sea surface to search humpback dolphins, with naked eyes and/or  $7 \times 50$  binoculars (Li et al., 2016; Liu et al., 2020a,b, 2021a). All observers were experienced with basic knowledge on humpback dolphin behavior, and had received observation training over than 30 days at sea prior to this study. To keep consistency, two primary observers were maintained throughout the survey period and across different sampling regions. Within an encounter, one primary observer would count the number of dolphins and the other would take photos (Liu et al., 2021b). In this study, the term “group” was referred to any aggregation of humpback dolphins (including solitary individual) in the observers’ effective field of view, generally either socially (i.e., engaged in similar behaviors) or spatially associated (e.g., within 200 m of each other; Karczmarski, 1999; Jefferson, 2000). Once a group was encountered, the group was approached at a slow sailing speed ( $< 8$  km/h) and kept an appropriate distance (10–50 m) behind or off to the side of the group. To ensure the independence of each group sample, our data collection procedures referred to the protocols described by Kinzey et al. (2000).

For each group, multiple counts were repeated several times to estimate the group size whenever possible (Karczmarski, 1999; Jefferson, 2000). Typically, the group size was recorded in the form of minimum/maximum/best counts on the standardized datasheet (e.g. 5/10/7; Kinzey et al., 2000). Sometimes, only one individual or a pair of individuals were observed, the group size was thus recorded as absolute best values (1 or 2). In some other cases, only a low estimate (e.g.,  $\geq 10$ ) was possible to be recorded as a best count. Besides, the group size might also be recorded in the form of a range (e.g., 10-20), thus the best count was averaged by the upper and lower limits (e.g., 15 was average by 10 and 20). For the further analysis, only the best counts were used to indicate observer-based counts, i.e.,  $G_{\text{observer}}$  (Gerrodette et al., 2002).

## Photo-Identification

Once a group was encountered, high-quality digital photos were taken, using a Canon 7D Mark II camera (Canon, Tokyo, Japan) fitted with 100-400 mm lens and an Olympus EM-1

camera (Olympus, Fujifilm, Japan) with 150- or 300-mm lens ( $1.5 \times$  amplifier). Whenever possible, both the right and left lateral sides of dolphin dorsal fins would be photographed (Tang et al., 2021). For each group, a scoring system was used to assess all original photos based on the visibility, size, focus, direction, and contrast (Liu et al., 2020b; Tang et al., 2021). Each of the five aspects accounted for 20 at most, and the total scores range from 20 to 100 on a 100-point scale. All original photos were classified into three classes: poor  $< 60$ ,  $60 \leq \text{good} < 80$ , and excellent  $\geq 80$  (Fearnbach et al., 2012). Only qualified photos (i.e., good, and excellent) were used for establishing the photo-identification dataset. Dolphin individuals were manually identified according to natural or non-natural markings on/around their dorsal fin. Several identifiable features like nicks, notches, pigmentation, and/or permanent scars, were included for identification and cross-matching (Wang et al., 2015; Methion and López, 2018). Whenever possible, body color, dorsal fin shape, nicks, notches, and sometimes permanent scars would be used to match two lateral sides of an individual (López et al., 2018; Liu et al., 2020b).

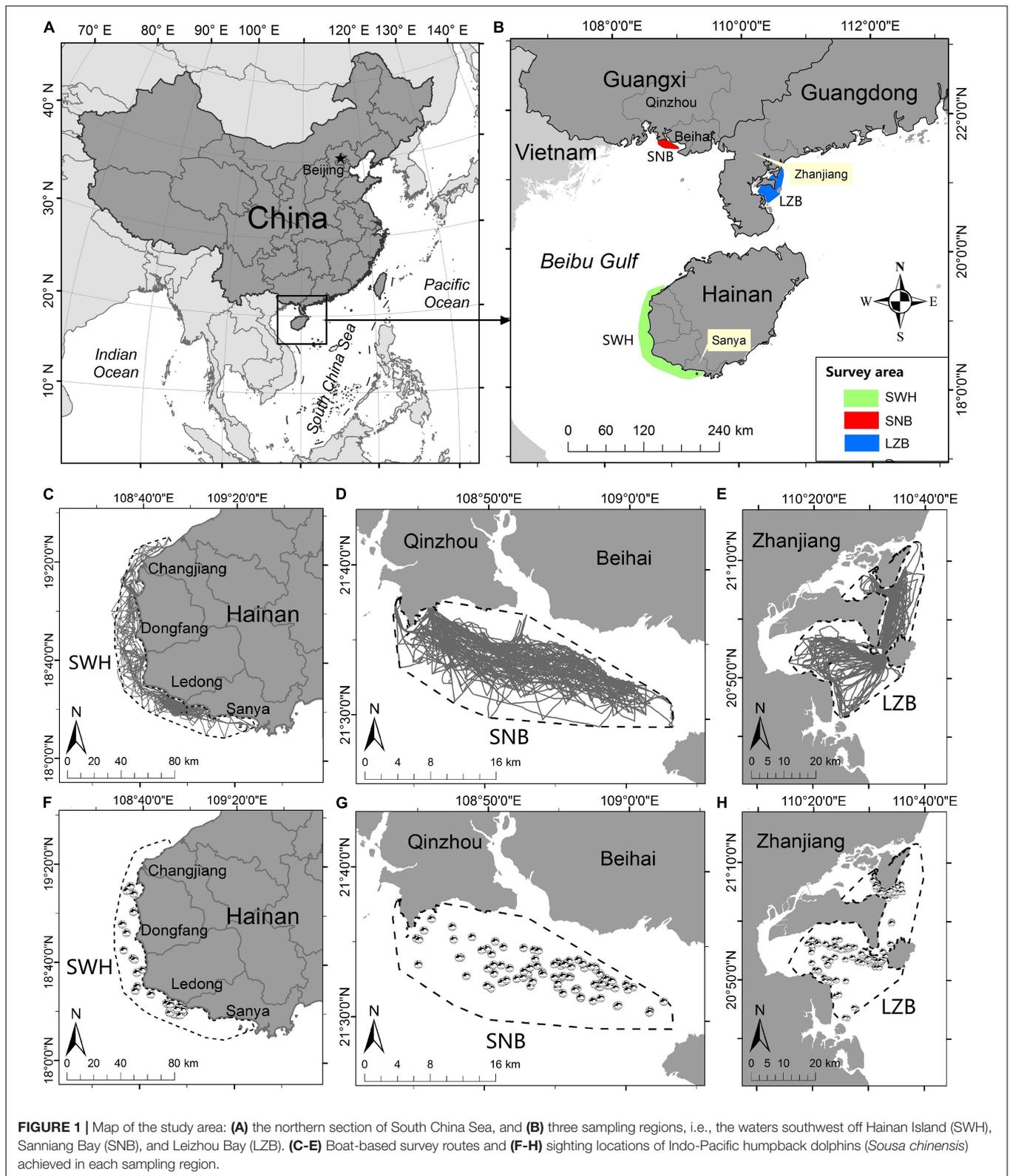
In this study, three classes of individual distinctiveness were defined: highly distinctive (D1), medium distinctive (D2), and non-distinctive (D3) (Friday et al., 2000; Zanardo et al., 2016). For each group, the marked individuals included D1 and D2 individuals, while the unmarked individuals only consisted of D3 individuals. All dolphin groups were classified into three types: almost all captured (AAC), not all captured (NAC), or all not captured (ANC). Group size estimates were only generated for AAC or NAC groups while excluding ANC because of no available photos. A group was considered as AAC when  $G_{\text{observer}} \leq 10$  individuals, indicating that all or almost all individuals were captured in the group (Tyne et al., 2014; Hupman et al., 2018). A threshold, i.e., 10 was selected because humpback dolphins were often observed in small groups with  $\leq 10$  individuals (Parsons, 2004; Würsig et al., 2016; Liu et al., 2021c). For AC groups, we calculated the photo-identification group size  $G_{\text{photo}}$  by counting the number of D1, D2, and D3 individuals present. We defined a group with  $G_{\text{observer}} > 10$  individuals as NAC group. For NAC groups, the photo-identification group size  $G_{\text{photo}}$  were estimated as using the formula:

$$G_{\text{photo}} = \frac{n_{(\text{marked}, i)}}{\theta} = n_{\text{marked}, i} \cdot \frac{N_{(\text{marked} + \text{unmarked}, i)}}{N_{(\text{marked}, i)}}$$

where  $n_{(\text{marked}, i)}$  is number of marked individuals in the group  $i$ . The mark rate ( $\theta$ ) was calculated from the proportion of randomly selected photos that contained identifiable dolphins (Williams et al., 1993; López et al., 2018). Among given randomly selected photos,  $N_{(\text{marked} + \text{unmarked}, i)}$  and  $N_{(\text{marked}, i)}$  is number of photos with marked and unmarked individuals, number of photos with marked individuals (Tyne et al., 2014; Hupman et al., 2018).

## Data Analysis

Using the ArcGIS 10.1 (ESRI, Redlands, CA, United States), all boat-based survey routes and sighting locations of humpback dolphin achieved in each sampling region were mapped. A matrix



heatmap was illustrated to show the number of boat-based survey days and humpback dolphin sightings per month from 2013 to 2019 in three survey regions. Frequency histograms were

illustrated to display group size patterns obtained from various methods in different regions (Bouveroux et al., 2018; Liu et al., 2021b). The skewness, kurtosis, and median value of group

size data were calculated for each subset (Doane and Seward, 2011). For paired group size estimates, all groups were presented in a scatter plot to illustrate the ratio of  $G_{\text{observer}}$  to  $G_{\text{photo}}$  (i.e.,  $R_{\text{observer/photo}}$ ) on a log-log scale with 1:1 reference line (Scott et al., 1985).

Generalized linear mixed models (GLMMs) were built to examine variances in group size of humpback dolphins, including fixed and random effects. In this study, the fixed effects were predicted by method ( $G_{\text{observer}}$  or  $G_{\text{photo}}$ ) and region (SWH, SNB, or LZB), and the random effects by year (2013–2019) and season (spring: March–May, summer: June–August; autumn: September–November; or winter: December–February; Liu et al., 2021b). In the R 4.0.5 (R Development Core Team, 2021), the package “lme4” was used (Bates et al., 2015) to construct GLMMs with a Poisson family and logit link function (Vargas-Fonseca et al., 2018; Dorning and Harris, 2019). According to Akaike’s Information Criterion (AIC), the GLMMs were simplified sequentially to remove non-significant fixed and random effects. Once a significant effect was found, *Post hoc* Scheffe tests or Wilcoxon paired tests were used to compare mean values of estimated group size in different levels.

Based on relevant published literature (Zhou et al., 2007; Chen et al., 2009; Xu et al., 2012, 2015; Wang et al., 2013; Li et al., 2016; Liu et al., 2020a,b, 2021a; Peng et al., 2020), mean or median values of humpback dolphins previously collected in the sampling region were extracted from previous studies. Then, non-parametric one sample sign tests were used to compare the group size estimates in each sampling region collected from the present study and from the previous studies. All statistical analyses were conducted in the R 4.0.5, with a defined significance level of  $p < 0.05$ . All descriptive statistics were shown as mean  $\pm$  SD, unless otherwise stated.

## RESULTS

From 2013 to 2019, a total of 231, 58, and 101 surveys were carried out in the SWH, SNB, and LZB, respectively (Figure 2). In these three waters, boat-based surveys covered a survey area of 3,319, 329, and 939 km<sup>2</sup>, respectively (Figures 1C–E). In total, 1,540, 299, and 714 h of survey effort (6.67, 5.16, and 7.07 h per survey day on average) were achieved, resulting in 15,548, 4,246, and 6,089 km of survey distance in each survey area. During these boat-based surveys, 47, 136, and 143 humpback dolphin groups were encountered (Figures 1F–H). The encounter rate (i.e., number of groups per 100 km) was 0.30, 3.20, and 2.35, respectively (Table 1). In each survey region, observer-based counts ( $G_{\text{observer}}$ ) were recorded for 45, 117, and 139 dolphin groups, respectively (Figure 2). In addition, 11,354 (32.8% out of 34,615), 11,056 (42.4% out of 26,076), and 15,779 (34.5% out of 45,739) qualified photos were available for the photo-identification in each region (Table 1). The process of photo-identification generated group size estimates ( $G_{\text{photo}}$ ) for 30, 123, and 113 dolphin groups in the SWH, SNB, and LZB, respectively (Table 1).

Histograms of group size estimates were skewed with a long tail to the right (Figures 3A–F), since most groups (80–90% of the

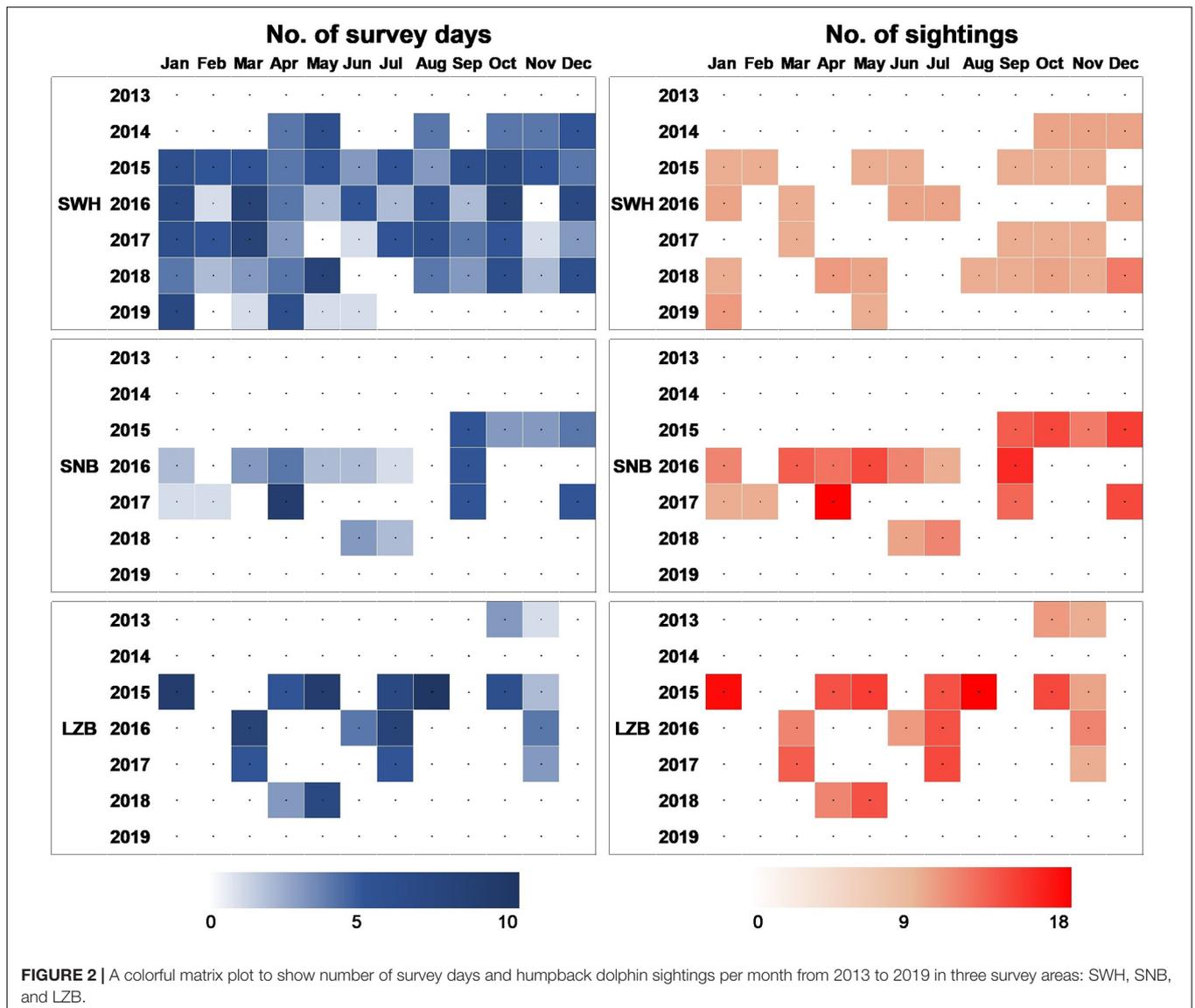
total observation) consisted of fewer than 20 members and only a few groups (<5%) were large with >30 members. The skewness and kurtosis of histograms varied between estimation methods, and also differed among sampling regions (Figures 3A–F). The median values of  $G_{\text{observer}}$  were 10, 5, and 9 in the SWH, SNB, and LZB, respectively. The median values of  $G_{\text{photo}}$  were 12, 5, and 8 in each sampling region (Figures 3A–F). The scatter plot of  $R_{\text{observer/photo}}$  i.e., the ratio of  $G_{\text{observer}}$  to  $G_{\text{photo}}$ , showed that values of  $R_{\text{observer/photo}}$  were randomly distributed on and near the 1:1 line (Figure 4).

The GLMM indicated that variances in dolphin group size were primarily affected by sampling region ( $p < 0.001$ ) and interaction of region  $\times$  method ( $p = 0.035$ ; Table 2). In addition, the interaction of year  $\times$  season had a significant random effect on influencing dolphin group size ( $p < 0.001$ ). The interaction of method  $\times$  year  $\times$  season had a significant mixed effect on influencing dolphin group size ( $p = 0.022$ ). *Post-hoc* Scheffe tests showed that  $G_{\text{observer}}$  in the SWH were significantly larger than  $G_{\text{observer}}$  in the SNB ( $p < 0.001$ ), or LZB ( $p < 0.001$ ), while  $G_{\text{observer}}$  in the SNB were smaller than  $G_{\text{observer}}$  in the LZB ( $p < 0.001$ ; Figure 5).  $G_{\text{photo}}$  in the SWH were significantly larger than  $G_{\text{photo}}$  in the SNB ( $p < 0.001$ ), or LZB ( $p = 0.009$ ), but  $G_{\text{photo}}$  in the SNB were not statistically different from  $G_{\text{photo}}$  in the LZB ( $p = 0.129$ ; Figure 5). Wilcoxon paired comparisons indicated that group size in the SWH ( $p = 0.023$ ) and LZB ( $p = 0.038$ ) varied between two estimation methods, but group size in the SNB ( $p = 0.177$ ) did not vary between methods.

In total, 10 relevant publications were obtained with documenting group size estimates of humpback dolphins in the SWH ( $n = 2$ ), SNB ( $n = 3$ ), and LZB ( $n = 5$ ; Table 3). In the SWH, statistical comparisons indicated significant differences between  $G_{\text{observer}}$  or  $G_{\text{photo}}$  in this study and the mean group size estimated from Li et al. (2016):  $G_{\text{observer}}$  vs. 21.6 ( $p = 0.036$ ),  $G_{\text{photo}}$  vs. 21.6 ( $p = 0.004$ ). In the SNB, there was no significant differences between  $G_{\text{observer}}$  or  $G_{\text{photo}}$  in this study and the mean group size of 6.39 (Peng et al., 2020) or 5.63 (Chen et al., 2009):  $G_{\text{observer}}$  vs. 6.39 ( $p = 0.141$ ),  $G_{\text{photo}}$  vs. 6.39 ( $p = 0.062$ ),  $G_{\text{observer}}$  vs. 5.63 ( $p = 0.922$ ), and  $G_{\text{photo}}$  vs. 5.63 ( $p = 0.378$ ). In the LZB, no significant differences were detected between  $G_{\text{observer}}$  or  $G_{\text{photo}}$  in this study and the median group size of 8 estimated from Zhou et al. (2007) or the mean group size of 8.12 estimated from Xu et al. (2015):  $G_{\text{observer}}$  vs. 8.12 ( $p = 0.087$ ),  $G_{\text{photo}}$  vs. 8.12 ( $p = 0.057$ ),  $G_{\text{observer}}$  vs. 8 ( $p = 0.159$ ),  $G_{\text{photo}}$  vs. 8 ( $p = 0.088$ ). However, significant differences were detected between our data and the mean or median group size of estimated from Xu et al. (2012, 2015):  $G_{\text{observer}}$  vs. 7 ( $p = 0.013$ ),  $G_{\text{photo}}$  vs. 7 ( $p = 0.043$ ),  $G_{\text{observer}}$  vs. 7.5 ( $p = 0.013$ ),  $G_{\text{observer}}$  vs. 6 ( $p < 0.001$ ),  $G_{\text{photo}}$  vs. 7.5 ( $p = 0.045$ ), and  $G_{\text{photo}}$  vs. 6 ( $p = 0.036$ ).

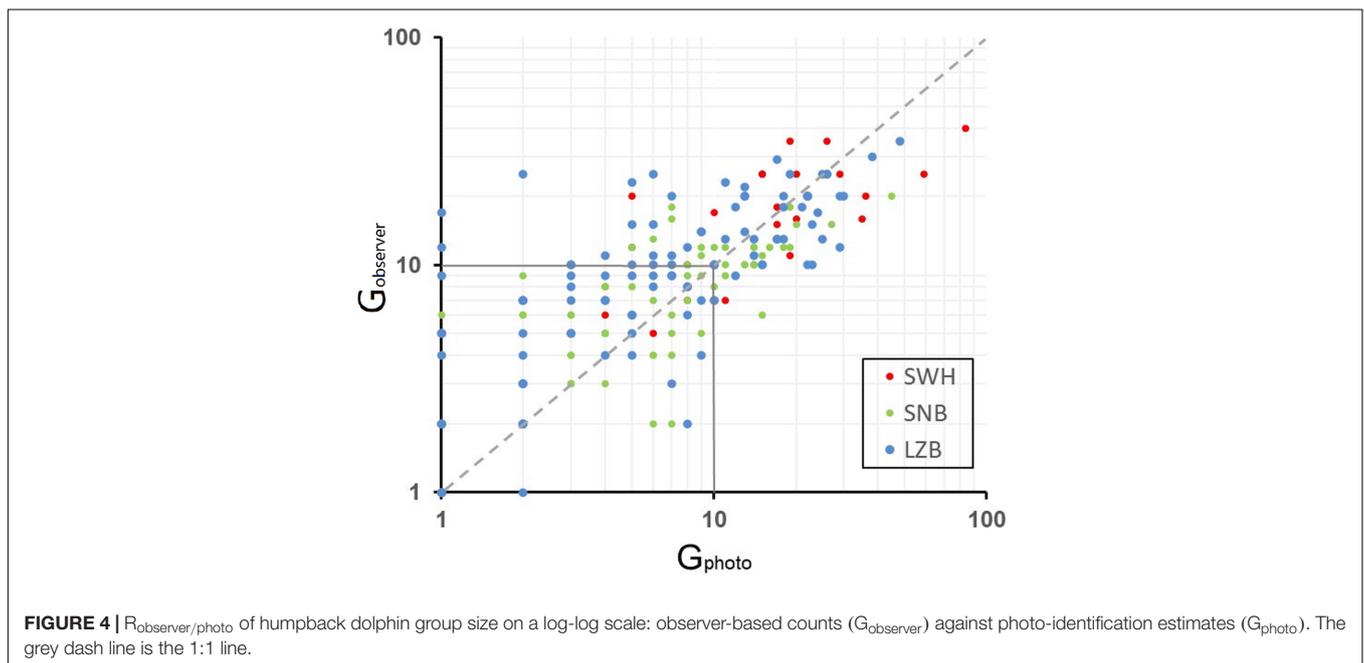
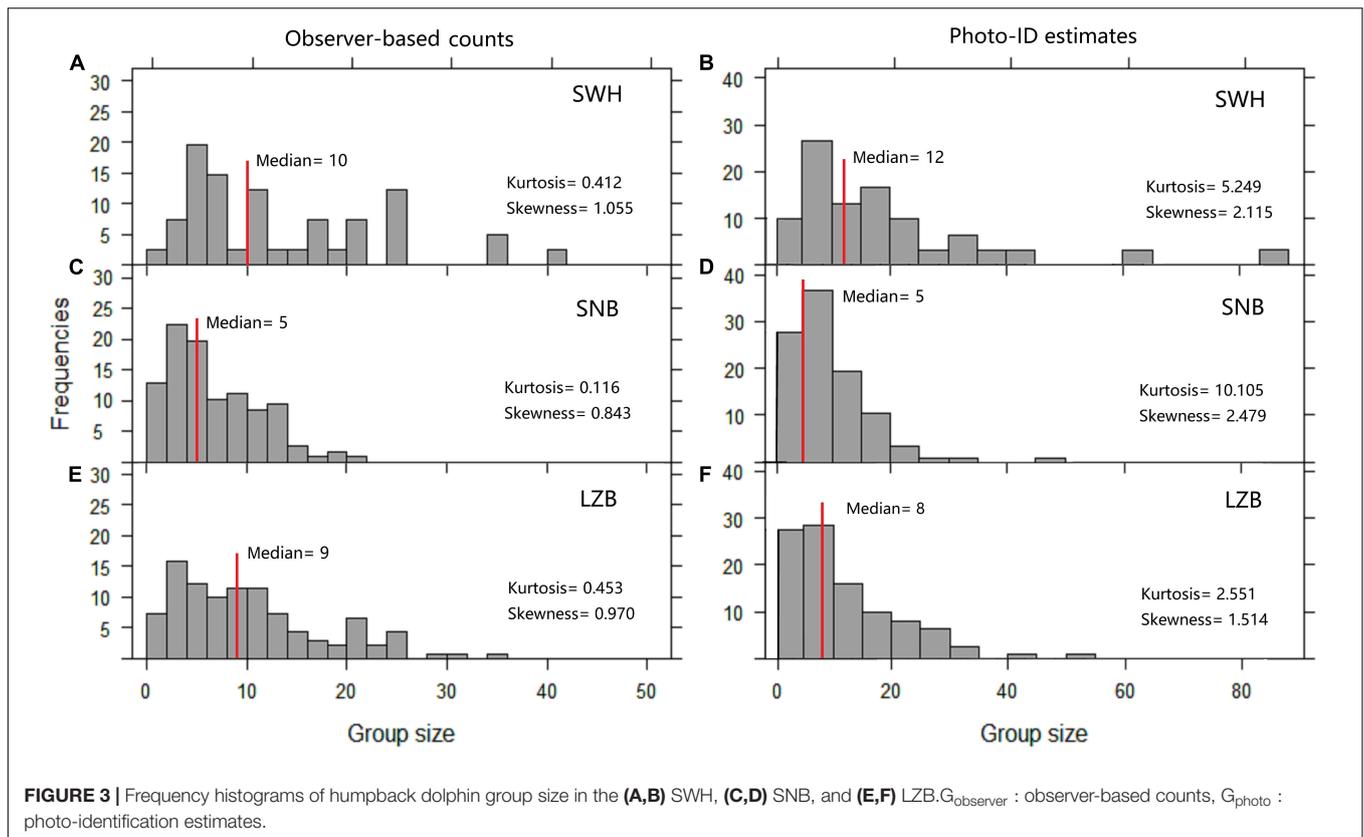
## DISCUSSION

In this study, several key findings were obtained. First, this study clearly illustrated that traditional estimation methods, i.e., observer-based counts and photo-identification could generate variable group size estimates for humpback dolphins. Second, this study demonstrated that group size of humpback dolphins



**TABLE 1 |** Summary of survey information on Indo-Pacific humpback dolphins (*Sousa chinensis*) in the waters southwest off Hainan Island (SWH), Sanniang Bay (SNB), and Leizhou Bay (LZB).

Metrics	Sampling region			Total
	SWH	SNB	LZB	
Survey area (km <sup>2</sup> )	3,319	329	939	4,587
No. of survey days	231	58	101	390
Survey hours	1,540	299	714	2,553
Survey effort (km)	15,548	4,246	6,089	25,883
No. of groups	47	136	143	326
Encounter rate (groups/100 km)	0.30	3.20	2.35	1.26
No. of observer-based counts	45	117	139	297
No. of dolphin photos	34,615	26,076	45,739	106,430
Observer-based counts ( $G_{\text{observer}}$ , mean $\pm$ SD)	12.9 $\pm$ 10.1	6.1 $\pm$ 4.4	9.4 $\pm$ 7.4	9.73 $\pm$ 7.5
No. of photo-identification group size estimates	30	123	113	266
Photo-identification estimates ( $G_{\text{photo}}$ , mean $\pm$ SD)	17.2 $\pm$ 18.2	7.0 $\pm$ 6.4	10.1 $\pm$ 8.1	9.32 $\pm$ 10.2



was significantly different among three sampling regions. Third, methodological variances in dolphin group size were found in some sampling regions, revealed by statistical comparisons between data in this study and in previous studies. These findings are beneficial to the use of different methods in

estimating group size for humpback dolphins, and help clarify potential methodological and biogeographical variances in group size estimates.

This study made the first attempt to sample comparable group size of humpback dolphins from different geographic regions

**TABLE 2** | A Poisson generalized linear mixed model (GLMM) investigating the fixed effects of method (observer-based counts and photo-identification) and region (SWH, SNB, and LZB), the random effects of survey year (2013-2019) and season (spring, summer, autumn, and winter), and the mixed effects of their interactions on group size of humpback dolphins.

Model parameter	Coefficient	Standard error (SE)	Z-value	P-value
Intercept	2.91	0.22	9.25	<b>&lt;0.001</b>
Region	0.87	0.39	6.14	<b>&lt;0.001</b>
Method × Region	0.62	0.13	5.68	<b>0.035</b>
Year × Season	-0.24	0.04	-4.18	<b>&lt;0.001</b>
Method × Year × Season	-0.38	0.16	-6.98	<b>0.022</b>

Significant *P* values (<0.05) are shown in bold. The GLMM was simplified based on minimizing the value of Akaike's Information Criterion (AIC).

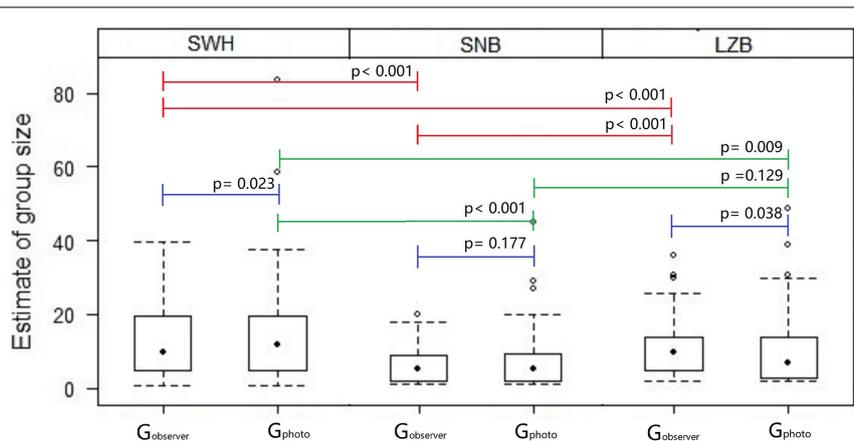
by using two methods simultaneously. Our data clearly revealed that dolphin group size across three sampling regions, no matter from observer-based counts or photo-identification, were highly variable, typically including single individual, small pairs, and rarely middle-to-large aggregations of several tens (Parsons, 2004; Würsig et al., 2016; Liu et al., 2021c). Notably, small groups with  $\leq 10$  members were the most frequently encountered (80-90%), while only a small proportion (<5%) were large groups with > 30 members. Such grouping pattern (i.e., living in small groups) has been considered a general social strategy of near-shore delphinid species inhabiting shallow and/or estuarine waters (Gygax, 2002a,b; Gowans et al., 2007), where the availability of prey is often predictable in space and time. Additionally, near-shore dolphins might prefer hosting small groups due to relatively low predation pressure compared with oceanic species (Bouveroux et al., 2018; Liu et al., 2021c).

This study confirmed that the inter-population variability of humpback dolphin group size was primarily explained by biogeographical differences. Dolphin group size manifested skewed distribution patterns with only a few groups much larger than the median, but the skewness and kurtosis of histograms

varied among regions and between methods. This finding suggested possible biogeographical and methodological variances in group size estimates of humpback dolphins, which was further demonstrated by the GLMM and statistical comparisons. The GLMM indicated that variances in group size of humpback dolphins were primarily explained by the sampling region. Besides humpback dolphins, several other delphinid species, such as bottlenose dolphins *Tursiops* spp. (Connor, 2000; Bouveroux et al., 2018), Guiana dolphins *Sotalia guianensis* (Moura et al., 2019), and some river dolphins *Inia geoffrensis* and *Sotalia fluviatilis* (Gomez-Salazar et al., 2012), have been found to form different sizes of groups in various geographic habitats. Such inter-population variability in dolphin group size might reflect the adaptations of dolphin populations to different ecological constraints in fine-scale environments (Gygax, 2002a,b; Gowans et al., 2007; Peña and Nöldeke, 2018).

This study revealed that both inter- and intra-population variability of humpback dolphin group size might be influenced by different methods. Using either observer-based counts or photo-identification, group size data have been previously documented in the SWH (Li et al., 2016), SNB (Chen et al., 2009; Wang et al., 2013; Peng et al., 2020), LZB (Zhou et al., 2007; Xu et al., 2012, 2015), and elsewhere (Parsons, 2004; Würsig et al., 2016; Liu et al., 2021c). However, previous studies rarely provided comparable estimates that were simultaneously collected with these two methods, making it hard to compare estimates achieved in different study systems. Statistical comparisons between different studies clearly showed that the use of observer-based counts or photo-identification might result in complex variances in group size estimates of humpback dolphins (Liu et al., 2020b, 2021c). Furthermore, dolphin group size might also be influenced by sample size (Gerrodette et al., 2019; Liu et al., 2020b), survey period (Koper et al., 2016), observer experience (Boyd et al., 2019), and/or the process of photo-identification (Auger-Méthé et al., 2010; Hupman et al., 2018) to varying degrees.

Both experienced observers and photo-identification might give underestimated, overestimated, or unbiased group size for



**FIGURE 5** | Boxplot of humpback dolphin group size obtained from observer-based counts ( $G_{\text{observer}}$ ) and photo-identification estimates ( $G_{\text{photo}}$ ) in the SWH, SNB, and LZB. The median (black dots), lower (25%) and upper (75%) quartiles, and outlier values (black circles) are illustrated. *P*-values were indicated for the paired comparisons of group size between methods and geographic comparisons of group size between regions, with a significance level of <0.05.

**TABLE 3** | Comparisons of humpback dolphin group size obtained from different studies in three sampling regions, i.e., SWH, SNB, and LZB.

Sampling region	Group size estimates					References	Comparison with means of $G_{\text{observer}}$ or $G_{\text{photo}}$ in this study ( $P$ value)
	Mean $\pm$ SD	Median	No. of sampling groups	Range	Method <sup>#</sup>		
SWH	12.9 $\pm$ 10.1	NA	45	1-40	$G_{\text{observer}}$	Liu et al., 2020b	FSD
SWH	17.8 $\pm$ 18.2	NA	30	1-84	$G_{\text{photo}}$	Liu et al., 2020b	FSD
SWH	21.6 $\pm$ 8.8	NA	6	12-40	$G_{\text{observer}}$	Li et al., 2016	$G_{\text{observer}}$ vs. 21.6 ( $p = 0.036^*$ ) $G_{\text{photo}}$ vs. 21.6 ( $p = 0.004^*$ )
SNB	6.39 $\pm$ 4.43	NA	164	1-22	$G_{\text{photo}}$	Peng et al., 2020	$G_{\text{observer}}$ vs. 6.39 ( $p = 0.141$ ) $G_{\text{photo}}$ vs. 6.39 ( $p = 0.062$ )
SNB	NA	NA	13	2-15	$G_{\text{observer}}$	Wang et al., 2013	NA
SNB	5.63	NA	19	NA	$G_{\text{photo}}$	Chen et al., 2009	$G_{\text{observer}}$ vs. 5.63 ( $p = 0.922$ ) $G_{\text{photo}}$ vs. 5.63 ( $p = 0.378$ )
LZB	9.4 $\pm$ 7.2	NA	253	1-48	$G_{\text{observer}}$	Liu et al., 2020a, 2021a	FSD
LZB	8.12 $\pm$ 5.85	7	611	1-35	$G_{\text{photo}}$	Xu et al., 2015	$G_{\text{observer}}$ vs. 8.12 ( $p = 0.087$ ) $G_{\text{observer}}$ vs. 7 ( $p = 0.013^*$ ) $G_{\text{photo}}$ vs. 8.12 ( $p = 0.057$ ) $G_{\text{photo}}$ vs. 7 ( $p = 0.043^*$ )
LZB	7.5 $\pm$ 5.45	6	118	1-23	$G_{\text{photo}}$	Xu et al., 2012	$G_{\text{observer}}$ vs. 7.5 ( $p = 0.013^*$ ) $G_{\text{observer}}$ vs. 6 ( $p < 0.001^*$ ) $G_{\text{photo}}$ vs. 7.5 ( $p = 0.045^*$ ) $G_{\text{photo}}$ vs. 6 ( $p = 0.036^*$ )
LZB	NA	8	96	1-27	$G_{\text{photo}}$	Zhou et al., 2007	$G_{\text{observer}}$ vs. 8 ( $p = 0.159$ ) $G_{\text{photo}}$ vs. 8 ( $p = 0.088$ )

NA, Not available; FSD, From the same dataset.

<sup>#</sup> $G_{\text{observer}}$ : observer-based counts;  $G_{\text{photo}}$ : photo-identification estimation.

\*Statistically significant difference ( $<0.05$ ) shown in bold.

humpback dolphins, while the potential bias and variance in  $G_{\text{observer}}$  and  $G_{\text{photo}}$  became unpredictable as the true group size was unknown for each sample (Scott et al., 1985; Gerrodette et al., 2002). Although primary observers in this study were experienced, there was still a high risk of underestimating group size due to various factors including visual conditions (i.e., sea state, sun glare; Barlow et al., 1998), dolphin behaviors (aerial behavior, underwater foraging, or boat-avoiding; Walsh et al., 2009), observers' perception (Erwin, 1982; Binda et al., 2011), and group dispersal (Clement et al., 2017; Hamilton et al., 2018).

Humpback dolphins typically have higher mark rates than other cetacean species (Pawley et al., 2018), and within an encounter, most often, all photographically captured individuals can be identified at least temporarily (i.e., within the encounter) including young individuals sometimes (Liu et al., 2020b; Tang et al., 2021). Photo-identification is less likely to overestimate group size for a given group, since each individual is often identified by comparable markings, unless repeated counts or mismatch between two lateral sides happen (Stevick et al., 2001; Urian et al., 2015). Thus, the comparisons between  $G_{\text{observer}}$  and  $G_{\text{photo}}$  in this study is a classic problem, in which there is a relatively accurate method, i.e., photo-identification to obtain conservative measurements (Scott et al., 1985; Gerrodette and Perrin, 1991), while another method, i.e., observer-based counts, to generate measurements without knowing the potential bias and variance (Gerrodette et al., 2002, 2019).

Across all three sampling regions, photo-identification, i.e.,  $G_{\text{photo}}$  appeared to generate larger values of mean group size

than observer-based counts, i.e.,  $G_{\text{observer}}$ , suggesting a high risk of underestimation of  $G_{\text{observer}}$ . This finding was consistent with previous studies: even experienced observers still tend to underestimate dolphin group size (Scott et al., 1985), and such trend increased with the group size (Gerrodette et al., 2019). However, photo-identification could not always give larger values of median group size. This was mainly because that the mean group size could be enlarged by rare large groups (Gerrodette et al., 2002, 2019), while the median group size was less likely affected by large values (Doane and Seward, 2011; Meropi et al., 2018). For example, large groups with up to 84 members have been identified through photo-identification in the SWH (Liu et al., 2020b), which greatly contributed to enlarge the mean group size 17.2, but would not influence the median group size 12.

The Indo-Pacific humpback dolphin is currently listed as a "Vulnerable" (VU) species by the Red List of International Union for Conservation of Nature (Jefferson et al., 2017), with an inferred decrease in abundance but no global abundance estimates (Jefferson and Smith, 2016; Li, 2020). The findings in this study are essential to yield more accurate abundance and density estimation for this species. Nevertheless, the true size of dolphin group in the wild is often uncertain, no matter in this study or in previous studies. Consequently, the potential bias and variance in dolphin group size estimated from observer-based counts or photo-identification could not be removed. The main challenge is to compare these traditional methods with a third one on that could better represent the true group size (Boyd et al., 2019). Therefore, other methods, such as drones-based

aerial photographic counts (Hartman et al., 2020; Giles et al., 2021) and acoustic estimation (Van Parijs et al., 2002; Wang et al., 2005), are warranted to be employed in future research for a wider comparison and calibration.

## DATA AVAILABILITY STATEMENT

The raw data supporting the conclusion of this article will be made available by the authors, without undue reservation.

## ETHICS STATEMENT

This animal study was reviewed and approved by the Chinese Academy of Sciences under an Ethics Statement with the number of IDSSE-SYLL-MMMBL-01.

## AUTHOR CONTRIBUTIONS

MLiu, MLin, XT, LD, and PZ: data collection. MLiu, MLin, and XT: photographic catalogue establishment. MLiu: formal analysis and writing—original draft. SL, ML, and MLiu: funding acquisition. MLiu, MLin, DL, and SL: methodology. MLin, DL,

and SL: writing—review and editing. All authors contributed to the article and approved the submitted version.

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