Intra-Population Variability in Group Size of Indo-Pacific Humpback Dolphins (*Sousa chinensis*)

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Group size is a key social trait influencing population dynamics of group-living animals. The Indo-Pacific humpback dolphins (IPHDs), *Sousa chinensis*, a shallow water delphinid species, display a fission-fusion social system. Yet little is known about how social organization of this species vary with temporal scales and behavioral state. In this study, we sampled group size estimates from the world's second largest population of humpback dolphins (*Sousa* spp.), which inhabit the eastern waters of Zhanjiang, China. IPHD group sizes changed seasonally and inter-annually, but not with tidal phases. Group sizes also changed with behavioral state of IPHD groups and with number of mother-calf pairs present. IPHDs formed larger groups in the autumn than in other seasons, which might be related to seasonal changes in food availability and reproductive cycle. Of the groups observed, we recorded the presence of mother-calf pair in 85 groups (i.e., nursery groups: 47 ones with one pair, 25 ones with two pairs, and others with three pairs). Notably, nursery groups were about 2–4 times larger than non-nursery groups. In addition, group sizes greatly increased with the number of mother-calf pairs. Living in relatively large groups, more protection, food, and resources might be available for IPHD mothers and calves, and such social strategy provide higher reproduction efficiency and survival success for this species. During our observations, feeding (45.5%) and traveling (25.2%) represented the majority of IPHD's behavioral budget, while socializing (8.4%) and resting/milling (6.8%) were not frequently observed. Resting/milling groups were approximately 50% smaller than feeding, traveling, or socializing groups, while the latter three types had a similar mean group size. Large groups when IPHDs foraged, traveled, or socialized, might provide more added group benefits. For the first time, our findings clearly revealed intra-population variability in IPHD group sizes across different behavioral and temporal variables, and provided a better understanding of IPHDs' adaptations to various biological processes and ecological constraints.

Keywords: sociality, humpback dolphin, group size, social dynamics, season, mother-calf pairs, behavior

INTRODUCTION

For social animals, group-living is an important behavioral strategy, and their social interactions are usually variable and dynamic (Silk, 2007). Living in a group, social relationships of group members are generally considered a product of trade-offs between energetic costs and benefits (Parrish and Edelstein-Keshet, 1999; Lusseau, 2003). In dolphin societies, the energetic trade-offs are typically associated with food (Heithaus and Dill, 2002), safety (Lima and Dill, 1990), reproduction (Mann et al., 2000), and resources. Consequently, group-living strategy of dolphin species offers a foundation to build more complex social relationships, such as cooperation or competition that have the scope to increase survival and reproduction (Benoit-Bird and Au, 2003; Orbach et al., 2014), and therefore, ultimately affect population dynamics (Lusseau and Newman, 2004).

Almost all dolphins were described with fission-fusion societies (Kent et al., 2008), but there is large intra- and inter-specific variability in social organization depending on ecological landscape in which the dolphin species reside (Gygax, 2002a; Lusseau et al., 2003; Gowans et al., 2007). Group size is among the main characteristics of social organization of dolphin populations (Lusseau et al., 2006; Cantor et al., 2012; Kappeler, 2019). Changes in group size over time and space can reflect fission-fusion dynamics of dolphins, thus are essential to represent the variability of social interactions (Connor, 2000; Gygax, 2002b; Lusseau et al., 2003). Dolphins can vary their group sizes at spatial scales (Bouveroux et al., 2018; Liu et al., 2020b), and at temporal scales (e.g., year, season, month, and day; Koper et al., 2016; Wang et al., 2016; Sarabia et al., 2018).

The Indo-Pacific humpback dolphin (*Sousa chinensis* Osbeck, 1765), hereafter referred as IPHD, is a shallow water delphinid species (Jefferson and Curry, 2015; Jefferson and Smith, 2016). Its habitat preference of shallow and near-shore waters has been widely documented in most of the known IPHD populations, as well as in the other three recognized relative species of *Sousa* spp. (Jefferson and Rosenbaum, 2014). The IPHD was assessed "Vulnerable" by the IUCN Red List of Threatened Species (Jefferson et al., 2017). Our socio-behavioral knowledge on humpback dolphins (*Sousa* spp.) mainly came from studies on IPHDs in the Chinese waters (Chen et al., 2011; Dungan et al., 2012, 2016; Wang et al., 2015), Australian humpback dolphins (*S. sahulensis*) in the Australian waters (Parra et al., 2011; Hunt et al., 2019; Hawkins et al., 2020), and Indian Ocean humpback dolphins (*S. plumbea*) in the South Africa waters (Karczmarski, 1999; Koper et al., 2016; Bouveroux et al., 2019). Some studied populations were documented to display fission-fusion dynamics with some long-lasting social relationships. Typically, the IPHDs live in groups of less than 10 individuals (Parsons, 2004; Chen et al., 2011; Würsig et al., 2016), and their societies include both stable (i.e., preferred companionships) and fluid (i.e., casual acquaintances) social interactions (Dungan et al., 2012, 2016; Wang et al., 2015).

Intra-specific variability in IPHD group sizes is not fully investigated, although some previous studies have basically described social characteristics of humpback dolphins. Previous studies suggested dolphin group sizes and composition may

be associated with species characteristics, habitat structure, and social-environmental aspects of populations (Baird and Dill, 1996; Gibson and Mann, 2008b; Degrati et al., 2019). Changes in humpback dolphin group size, such as annual (Koper et al., 2016), seasonal (Chen et al., 2011; Wang et al., 2016), and behavioral variations (Würsig et al., 2016), are often habitat-specific and affected by a series of environmental variables at a regional scale. For instance, the mean group size observed for the Indian Ocean humpback dolphins in the Algoa Bay, South Africa, decreased from 7 individuals in 1990s to only 3 in 2010s (Karczmarski, 1999; Koper et al., 2016), whilst such a sharp decline has not been observed in other regions. In several known humpback dolphin populations, it has been reported that feeding groups, especially those groups following fishing trawlers (Parsons, 2004; Würsig et al., 2016), and breeding groups (Baldwin et al., 2004; Liu et al., 2020b), were much larger than those groups engaged in other behaviors, indicating a potential influence of behavioral states on group size.

A few studies have reported group size variations in the IPHDs. For example, the IPHDs in the Xiamen Bay, China, showed seasonal variations in their group sizes, with larger groups formed during the winter and spring when compared to summer and autumn (Wang et al., 2016). In the eastern Taiwan Strait, Dungan et al. (2016) revealed that IPHD groups were larger when contained calves, suggesting the importance of nursery behavior on IPHDs' sociality. However, we still lack an understanding of temporal and behavioral factors associated with intra-population variability in the IPHD group sizes. Thus, we know little about how the IPHDs vary their group sizes to adapt to various habitats.

In this study, we showed the variability in IPHD group sizes recorded in the eastern waters of Zhanjiang, China. We assessed whether IPHD group sizes varied at three temporal scales (year, season, and tide) and across two behavioral domains (number of mother-calf pairs, and behavioral state). We expect that IPHD group sizes vary with some of the above factors. This study aims to provide a better understanding of social characteristics of IPHDs at a population level, and to reveal potential factors important for the social dynamics of this population specifically, and IPHDs more generally.

MATERIALS AND METHODS

Study Area

Our survey area is the near-shore, eastern waters of Zhanjiang, China (**Figure 1**), covering an area of approximately 1,000 km^2. This area is a shallow-water embayment (water depth range: 2–40 m) with a sandy/muddy seafloor (Zhou et al., 2007; Xu et al., 2015; Liu et al., 2017a). The population of IPHDs residing in this area was first reported by Zhou et al. (2007). To provide protection for this population, the local Zhanjiang government established a protected area i.e., Zhanjiang Leizhou Bay Municipal Humpback Dolphin Nature Reserve (110° 26′−110° 29′ E, 20° 44′ −20° 46′ N; Area: 21-km^2; **Figure1**) in 2007 (Xu et al., 2015; Liu et al., 2020a). Based on local rainfalls and climate characteristics, we defined four season phases for the study
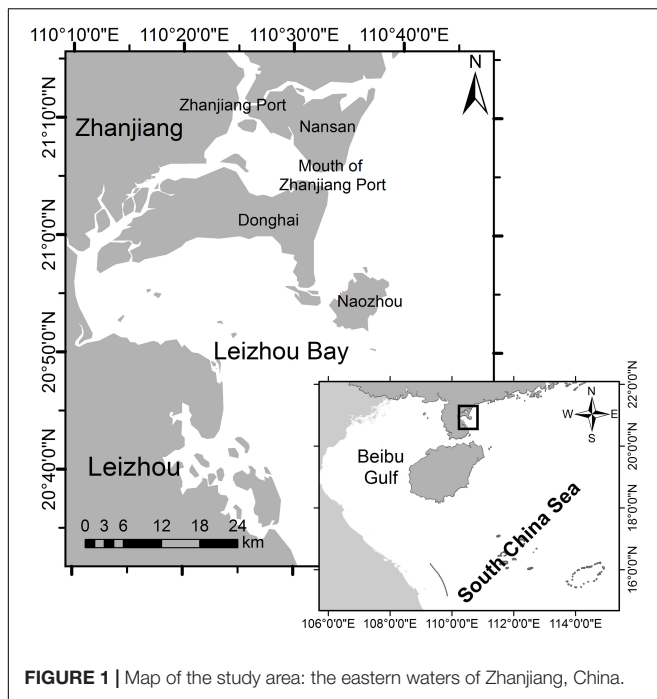
FIGURE 1 | Map of the study area: the eastern waters of Zhanjiang, China.

area: spring (March–May), summer (June–August), autumn (September–November), and winter (December–February) (Liu et al., 2017b). We divided tidal condition of a day into four consecutive phases: high, ebb, low, and flood (Liu et al., 2021).

Data Collection

To conduct field surveys, we used either a 12-m-length wooden fishing boat (60 HP outboard engine) or a 7-m-length fiberglass speed boat (75 HP outboard engine). We carried out surveys during October-November of 2013, and quarterly from January 2015 to May 2018. During our surveys, at least two experienced observers scanned the front 180° of sea surface, and searched IPHDs with the naked eyes and/or 7 × 50 binoculars (Li et al., 2016; Liu et al., 2020a). We performed the surveys only during the daytime and good visual conditions without rain or fog, and only under satisfied sea states of Beaufort scale ≤ 3.

In this study, we used the term "group" to define one or more dolphins observed with spatial co-occurrence (each member within 200 m of any other members) or social associations (all individuals within a unit in a similar behavioral state) (Wang et al., 2016; Liu et al., 2020b, 2021). Once a IPHD group was sighted, we approached and observed the group with 10−50 m between our boat and the group, unless the group actively approach us. During each observation, we recorded date, time, GPS location, group size, group composition based on age classes, number of mother-calf pairs (absence as 0), and primary behavioral state.

We used a hand-held Garmin 78 s GPS receiver (Garmin, Taiwan, China) to obtain information on date, time, and GPS location. For each group, we used the method of multiple-counts (minimum/best/maximum) to generate observer-based group size estimates (Gerrodette et al., 2002). We determined

the group composition based on IPHD coloration patterns along with age classes (Jefferson et al., 2012). We determined the presence/absence of mother-calf pair and number of mother-calf pairs by observing and counting how many individuals are poorly marked, obviously dark-gray, small (i.e., ∼1m length, less than half of adult body length), and at consistent echelon positions with an adult. We determined the behaviors of IPHDs using five recognizable behavioral states: feeding, traveling, socializing, resting, and milling (Parsons, 2004; Stockin et al., 2009; Würsig et al., 2016). See behavioral definitions in **Table 1**. Raw group size data (observer-based best estimates) were later verified with photographs taken during each sighting: if the observer-based best count was smaller than the number of individuals photographically identified for a group, the group size was modified as the latter (López et al., 2018).

Data Analysis

To test whether variability in IPHD group sizes was associated with temporal and/or behavioral variables, we constructed univariate generalized linear models (GLMs) with multivariate analysis of variance. We included five factors into our models, including three temporal factors i.e., year (2013, 2015, 2016, 2017, and 2018), season (spring, summer, autumn, and winter), and tide (high, ebb, low, and flood), and two behavioral factors i.e., number of mother-calf pairs (0, 1, 2, and 3) and behavioral state (feeding, traveling, socializing, and resting/milling) (**Table 2**). Not only resting and milling represented a small percentage in the behavioral budget of the dolphins, but these behavioral states are also similar in low activity rate (**Table 1**). Thus, we integrated resting and milling into one single behavioral state for analysis.

In total, we built five main effects and ten pairwise interaction terms into the GLMs. Our null hypothesis was that there was no difference in the IPHD group sizes across different years, seasons, tidal phases, number of mother-calf pairs, and behavioral states. Once a significant effect was found for either main factor, we performed the Kruskal-Wallis tests to make *post hoc* pairwise multiple comparisons using Tukey's HSD (equal variances, $p > 0.05$) or Tamhane's T2 method (unequal variances, $p < 0.05$). We also built and pruned a classification and regression tree (CART), in order to determine which variable is predominant in affecting the IPHD group sizes (De'ath and Fabricius, 2000; Liu et al., 2019). Results on IPHD group sizes are reported as mean ± standard deviation (SD) unless otherwise stated. We conducted all statistical analyses in the IBM SPSS 19.0 (SPSS Inc., Chicago, Illinois), and defined a significance level of $P < 0.05$.

RESULTS

Over 5 years (2013 and 2015–2018), we carried out 174-day boat-based surveys in the study area (**Table 2**). In total, we achieved 11,676 km survey effort (**Figure 2A**) and sighted 253 IPHD groups (**Figure 2B**). Throughout the survey period, group encounter rate was 2.17 sightings per 100 km (**Table 2**). Of the 253 groups, we sampled 229 (90.5%) with available group size estimates, generating a mean group size of 10.9 ± 8.8 individuals (range: 1–48). Of the 229 sampled groups, 227 (99.1%), 225

TABLE 1 | Summary of behavioral definitions and observations of Indo-Pacific humpback dolphins in the eastern waters of Zhanjiang, China.

Behavioral state	Behavioral characteristics	Number of groups (% out of the total groups)
Feeding	• Move in various directions without an obvious pattern, dive frequently and steeply downwards (often preceded by fluke up or peduncle arches), with extended submersion times. • Rapid accelerations and erratic movement at the surface, sometimes with indicative behaviors on chasing fish, such as directly pursuing a fish (fish jumping at surface), or with fish in their mouth, or following the fishing boats (especially trawlers), or sea birds in attendance for prey.	76 (30.0%)
Traveling	• Move persistently and directionally with a regular pattern of surfacing and diving, and are not underwater for extended lengths of time. • Dive angles are shallow, and dive intervals are short but relatively consistent.	79 (31.2%)
Socializing	• Dolphins are in close proximity, with showing high levels of interaction (chasing, rolling, rubbing, and other body contacts). • Fins and flukes often break the surface of the water, and aerial or acrobatic behavior occasionally occurs such as leaps or flips. • Dive direction is unpredictable, and dive intervals vary.	38 (15.0%)
Resting	• Almost statically float on the surface. • Dolphins swim in close proximity, but without interaction; Dolphins surface in a synchronized manner and most of the time is spent at the water surface; Dive angles are shallow. • No aerial behavior and activity levels are low.	8 (3.2%)
Milling	• Dolphins circle in a small area at low speed with no apparent direction and net movement. Dive intervals vary, and the activity levels are low. • Milling may indicate a transitory phase between other functional behaviors i.e., feeding, traveling, socializing, and resting.	9 (3.6%)
Undetermined	• Within one encounter, the observers have insufficient observation time window to determine the primary behavioral state. • Undetermined to be any categories above.	43 (17.0%)

TABLE 2 | Annual survey effort, sighting information, and group size of Indo-Pacific humpback dolphins in the eastern waters of Zhanjiang, China, in 2013, and 2015–2018.

Year	No. of survey days	Survey distance (kms)	No. of dolphin sightings	Group encounter rate (No. of groups per 100 kms)	Group size (mean ± SD)
2013	4	220	4	1.82	18.8 ± 11.4
2015	55	3,638	91	2.50	8.2 ± 6.3
2016	59	3,692	66	1.79	10.1 ± 8.1
2017	46	3,546	78	2.20	9.5 ± 8.8
2018	10	580	14	2.41	13.1 ± 11.0
Total	174	11,676	253	2.17	10.9 ± 8.8

(98.3%), 195 (85.2%), and 134 (58.5%) were comprised of less than 40, 30, 20, and 10 individuals, respectively (**Figure 3**). In addition, 24 groups (9.2%) consisted of single individual, and 17 (7.4%) were observed in a pair of individuals.

We recorded the presence of mother-calf pair in 85 groups (33.6%), where 47 had one pair of mother-calf (18.6%), 25 had two pairs (9.9%), and the other 13 had three pairs (5.1%) (**Figure 4A**). Feeding (30.0%) and traveling (31.2%) represented the great majority of behavioral states recorded in the study area (**Figure 4B**). Furthermore, we recorded 38 socializing groups (8.4%), 8 resting groups (3.2%), and 9 milling groups (3.6%), while 43 groups (17.0%) could not be determined with identifiable behavioral state (**Table 1**). IPHD group size was highest in 2013 (18.8 ± 11.4) and lowest in 2015 (8.2 ± 6.3) (**Table 2**). Although mean values of group sizes varied across years, there was no variation in group sizes among different years (Kruskal-Wallis test, $\chi^2 = 8.8$, $P = 0.168$). Our GLMs showed that variations in group sizes were associated with the season

($F = 1.0$, df = 3, $P = 0.002$), number of mother-calf pairs ($F = 9.0$, df = 3, $p << 0.001$), behavioral state ($F = 0.9$, df = 3, $P = 0.033$), year × season ($F = 4.9$, df = 12, $P = 0.04$), year × number of mother-calf pairs ($F = 5.1$, df = 12, $P = 0.001$), year × behavioral state ($F = 3.3$, df = 12, $P = 0.014$), and season × behavioral state ($F = 2.8$, df = 9, $P = 0.031$), but were not associated with other factors or interaction terms (**Table 3**).

IPHD group sizes varied among seasons (Kruskal-Wallis test, $\chi^2 = 2.6$, $P = 0.045$). Group size in the autumn (14.1 ± 9.4) was larger than those in the spring (9.0 ± 6.9), summer (9.0 ± 6.6) and winter (7.8 ± 6.0) (Tukey's HSD tests, $P_{autumn\ vs.\ spring} = 0.022$, $P_{autumn\ vs.\ summer} = 0.018$, and $P_{autumn\ vs.\ winter} = 0.007$), while there was no variation in group sizes across spring, summer, and winter (**Figure 5A**). In addition, there was no variation in group sizes with tidal phases (Kruskal-Wallis test, $\chi^2 = 1.343$, $P = 0.719$) (**Figure 5B**).

IPHD group sizes varied with the presence of mother-calf pair, as nursery groups (16.8 ± 5.2) were about 2–4
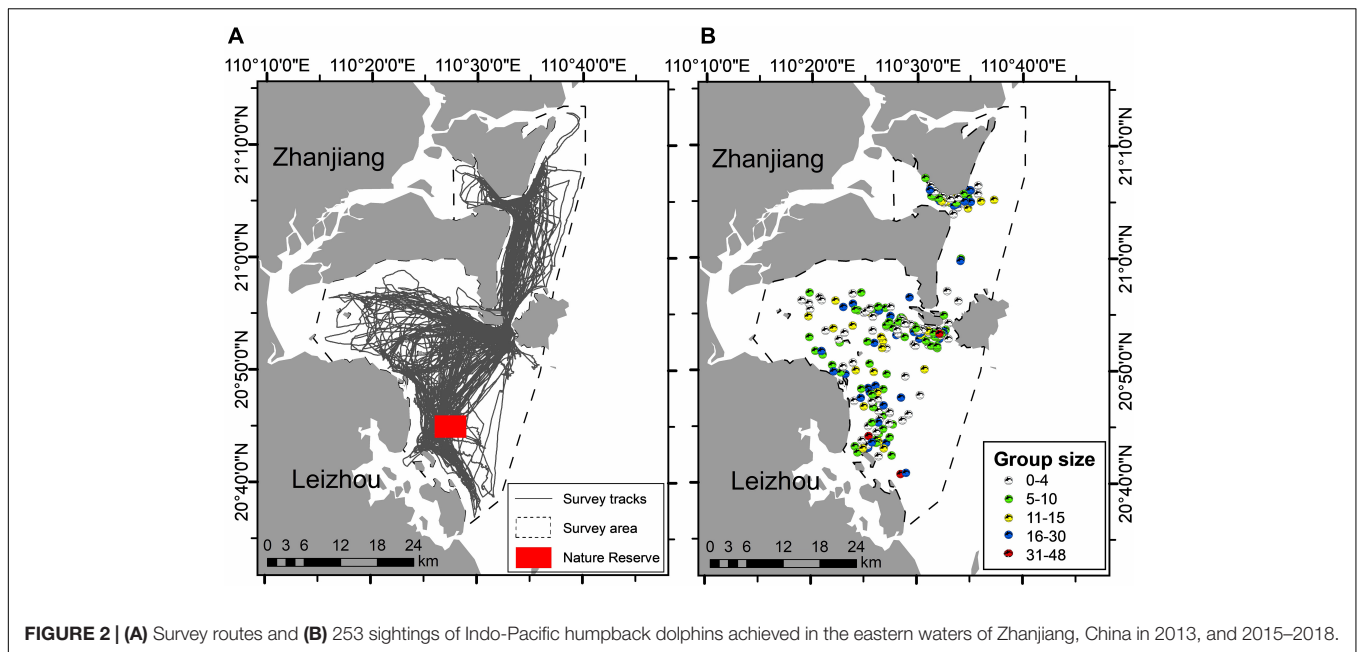
FIGURE 2 | (A) Survey routes and **(B)** 253 sightings of Indo-Pacific humpback dolphins achieved in the eastern waters of Zhanjiang, China in 2013, and 2015–2018.

times larger than non-nursery groups (i.e., groups without mother-calf pair, 6.8 ± 6.3). Group sizes also varied with the number of mother-calf pair (Kruskal-Wallis test, χ^2 = 76.417, P < 0.001). We found a positive influence of the number of mother-calf pairs on IPHD group sizes: group sizes with one pair of mother-calf, two pairs, and three pairs were 10.2 ± 6.2, 17.4 ± 5.4, and 24.9 ± 9.6, respectively (**Figure 5C**).

We detected variation in IPHD group sizes across different behavioral states (Kruskal-Wallis test, χ^2 = 14.1, P = 0.003). Resting/milling group size (5.5 ± 3.9) was smaller than feeding (12.1 ± 8.7), traveling (10.1 ± 8.1), and socializing group size (12.3 ± 6.5) ($P_{feeding\ vs.\ resting/milling}$ = 0.002, $P_{traveling\ vs.\ resting/milling}$ = 0.012, and $P_{socializing\ vs.\ resting/milling}$ = 0.003; **Figure 5D**). However, group

size was similar among feeding, traveling, and socializing behaviors (**Figure 5D**).

We built a CART with six leaves (**Figure 6**), including only three final explanatory variables i.e., number of mother-calf pairs, season, and behavioral state. We excluded the other two variables, i.e., year and tide, because they were insignificant in our GLMs (**Table 3**). In total, 68.1% of the variances in IPHD group sizes could be explained by the CART. The first split of CART was based on the number of mother-calf pairs, with ≤ 1 in the left branch [group size ≤ 10) and > 1 in the right branch (group size > 10)]. Then, these two branches were continuously divided into autumn in the left (group size > 8 or 15), spring, summer, and winter in the right (group size ≤ 8 or 15). The final splitting process was repeated for the two right seasonal branches, separating behavioral states into resting/milling in the next left (group size ≤ 5 or 10), and feeding, traveling, and socializing in the next right (group size > 5 or 10).
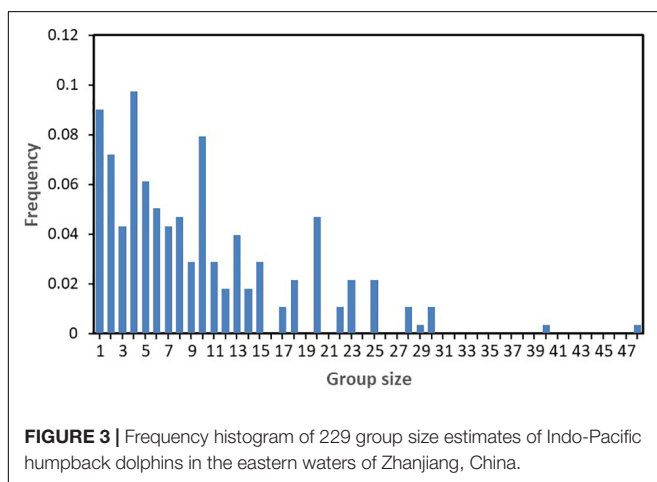
DISCUSSION

Our study yielded several critical findings. First, we demonstrated that IPHD group sizes in the Zhanjiang waters were influenced by the season, number of mother-calf pairs, behavioral state, and the interaction between these factors. Second, our results showed that IPHD group size was larger in the autumn (September-November) compared to the other seasons. Third, we observed a positive relation of nursery behavior in IPHD group sizes, as nursery groups were 2−4 times larger than those non-nursery groups, and group sizes increased with the number of mother-calf pairs. Lastly, we displayed variations in IPHD group sizes across various behavioral states:
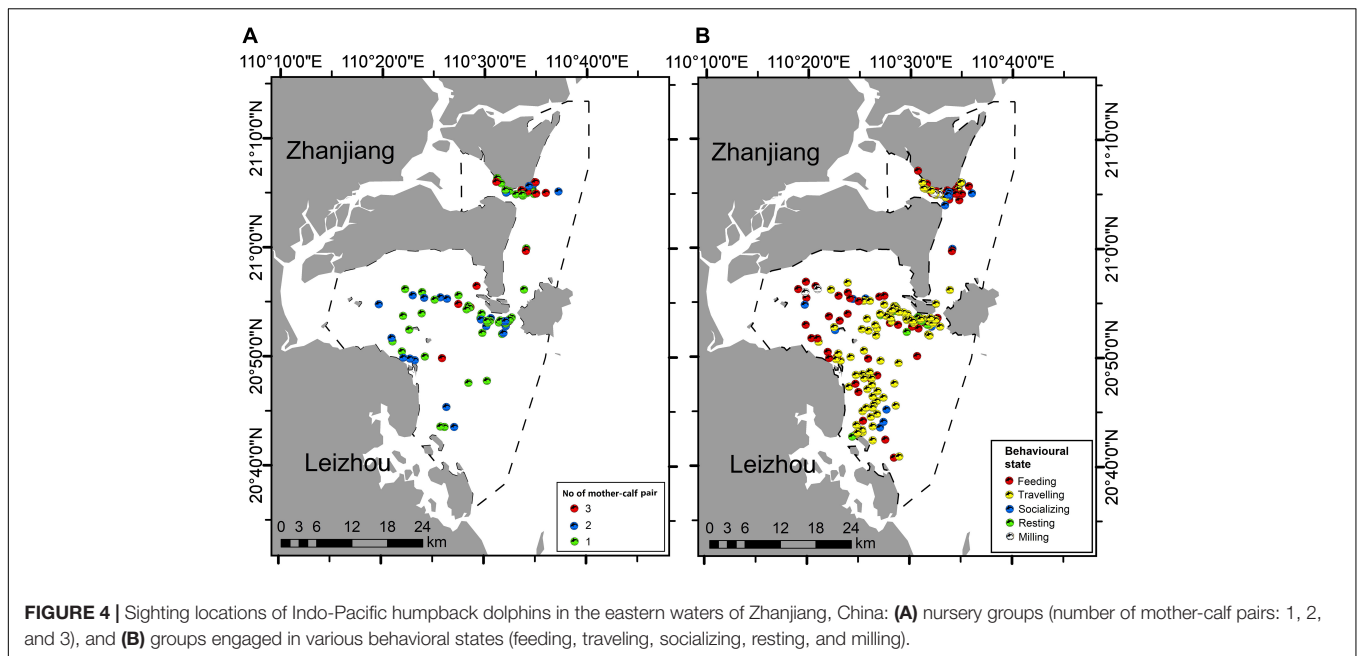

FIGURE 3 | Frequency histogram of 229 group size estimates of Indo-Pacific humpback dolphins in the eastern waters of Zhanjiang, China.

FIGURE 4 | Sighting locations of Indo-Pacific humpback dolphins in the eastern waters of Zhanjiang, China: **(A)** nursery groups (number of mother-calf pairs: 1, 2, and 3), and **(B)** groups engaged in various behavioral states (feeding, traveling, socializing, resting, and milling).

TABLE 3 | Generalized linear models (GLMs) built to determine potential temporal (year, season, and tide) and/or behavioral effects (number of mother-calf pairs, and behavioral state) on group sizes of Indo-Pacific humpback dolphins in the eastern waters of Zhanjiang, China.
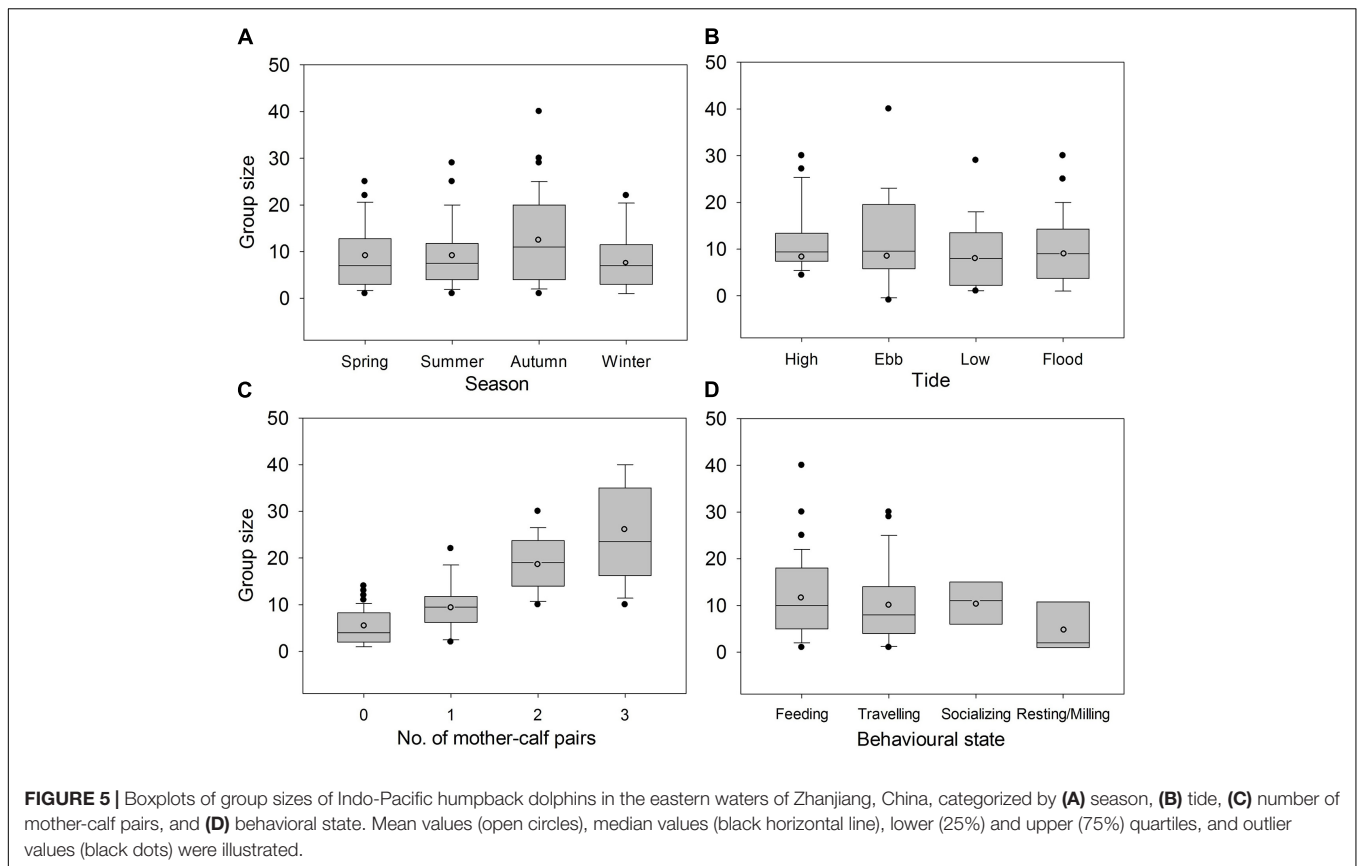
Source of variation	Type III sum of squares	df	Mean square	F	P
Corrected model	10,287.9	125	82.3	2.3	**<0.001***
Intercept	11,541.3	1	11,541.3	323.6	**<0.001***
Year	374.7	4	124.9	3.5	0.395
Season	107.7	3	35.9	1.0	**0.002***
Tide	334.1	3	111.4	3.1	0.131
Number of mother-calf pairs	964.2	3	321.4	9.0	**<0.001***
Behavioral state	99.0	3	33.0	0.9	**0.033***
Year × Season	693.3	12	173.3	4.9	**0.04***
Year × Tide	579.8	12	96.6	2.7	0.228
Year × Number of mother-calf pairs	729.4	12	182.4	5.1	**0.001***
Year × Behavioral state	477.6	12	119.4	3.3	**0.014***
Season × Tide	270.1	9	30.0	0.8	0.581
Season × Number of mother-calf pairs	184.5	9	36.9	1.0	0.404
Season × Behavioral state	403.3	9	100.8	2.8	**0.031***
Tide × Number of mother-calf pairs	85.3	9	14.2	0.4	0.178
Tide × Behavioral state	412.7	9	68.8	1.9	0.088
Number of mother-calf pairs × Behavioral state	131.8	9	26.4	0.7	0.597
Error	2,532.3	71	35.7		
Total	33,934.8	197			
Corrected total	12,820.2	196			

Asterisks represent statistical significance level of P < 0.05 (in bold). Five main interactions and ten pairwise interactions were included into the models.
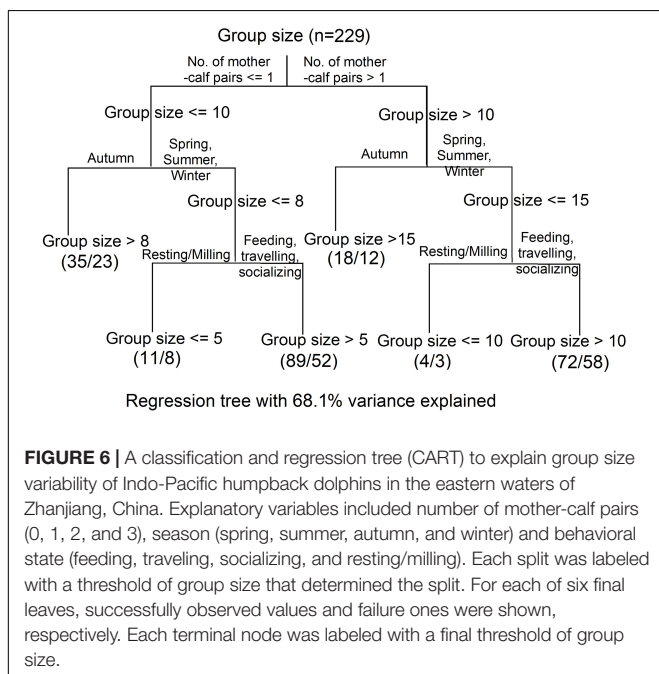
resting/milling groups were approximately 50% smaller than feeding, traveling, or socializing groups, but the latter three had a similar size.

We observed a mean group size larger for the IPHDs in the Zhanjiang waters when compared to other estimates reported in this are by previous studies, including 8 (median) documented by Zhou et al. (2007), 7.5 ± 5.45 by Xu et al. (2012), and 8.12 ± 5.85 by Xu et al. (2015). These differences among studies can be related

to different methodologies, as the previous studies only applied photo-identification technique to estimate the group size, while we used observer-based best counts complemented with photo-identification estimates. Photo-identification approach often generates an underestimated group size for each IPHD group (Liu et al., 2020b), which is based on the natural markings of each identifiable dolphin. However, some individuals within one group might be not photographically captured, and some

FIGURE 5 | Boxplots of group sizes of Indo-Pacific humpback dolphins in the eastern waters of Zhanjiang, China, categorized by **(A)** season, **(B)** tide, **(C)** number of mother-calf pairs, and **(D)** behavioral state. Mean values (open circles), median values (black horizontal line), lower (25%) and upper (75%) quartiles, and outlier values (black dots) were illustrated.

young individuals and especially claves, are poorly marked or unmarked, both of which would lead to an underestimation of IPHD group size (Gerrodette et al., 2002; López et al., 2018).

FIGURE 6 | A classification and regression tree (CART) to explain group size variability of Indo-Pacific humpback dolphins in the eastern waters of Zhanjiang, China. Explanatory variables included number of mother-calf pairs (0, 1, 2, and 3), season (spring, summer, autumn, and winter) and behavioral state (feeding, traveling, socializing, and resting/milling). Each split was labeled with a threshold of group size that determined the split. For each of six final leaves, successfully observed values and failure ones were shown, respectively. Each terminal node was labeled with a final threshold of group size.

Thus, IPHD group size data used in this study are more methodologically credible.

We observed annual fluctuations of the IPHD group sizes, while there was no statistical difference in group sizes across different years. The inter-annual fluctuations of group sizes were obvious, with the largest value in 2013 (18.8 ± 11.4) and the smallest in 2015 (8.2 ± 6.3), which might be due to the small sample size in 2013 ($n = 4$). Additionally, we observed that IPHD group sizes were relatively stable with a mean of ∼8–9 individuals across different tidal phases, indicating scant tidal fluctuations of group sizes.

Within a certain population, temporal and behavioral variations in social characteristics were generally attributed to environmental adaptations of dolphins to various biological requirements and ecological constraints, such as food availability (Heithaus and Dill, 2002), mating opportunities (Orbach et al., 2014), predation risk (Kelley et al., 2011), or nurturing offspring (Mann et al., 2000). Compared to oceanic dolphin species, most IPHD populations are subject to relatively low predation risk from sharks or killer whales (Gowans et al., 2007; Würsig et al., 2016). Therefore, the intra-population variability in IPHD group sizes illustrated by our GLMs and CART might be primarily explained by food availability and reproductive processes, which were considered to vary temporally and by behaviors (Wang et al., 2016; Liu et al., 2020b).

Since 1998, the Chinese government designated a mandatory summer-fishing-ban-season (from May 1 to August 16 per

year) in the territorial waters of South China Sea, aiming to preserve fisheries resources especially those reproduction-driven fish aggregations. Consequently, fisheries resources during and after the fishing ban season could be more abundant than before the season. Such seasonal variations in IPHD food resources might be a main driver leading to larger feeding groups in the autumn. Besides, previous studies in the study area indicated that the newborn IPHD calves peaked at the period between July and October (Zhou et al., 2007; Xu et al., 2012, 2015). Consequently, seasonal variations in IPHD group sizes can be related to their tendency to form larger breeding/mating aggregation during the autumn to improve mating opportunities and reproductive success (Baldwin et al., 2004; Orbach et al., 2014). However, seasonal variations in IPHD group sizes in the study area was different from that observed in the Xiamen Bay, China, where the mean group size of IPHDs during the winter-spring (7.2 individuals) were larger than those during the summer-autumn (mean: 4.4 individuals) (Wang et al., 2016). Such regional difference suggested that the variability in IPHD group sizes might vary across various habitats, as an adaptation to different ecological constraints in different geographical regions (Liu et al., 2021).

As demonstrated by our data, more mother-calf pairs were recorded in IPHD groups, the group size would be larger. More importantly, our CART clearly indicated that IPHD group sizes were primarily determined by the number of mother-calf pairs. Such positive impact of nursery behavior on enlarging group size has not only been reported for the IPHDs in the eastern Taiwan Strait (Dungan et al., 2016), and also for other dolphin species such as bottlenose dolphins (*Tursiops* spp.) (Gibson and Mann, 2008b), dusky dolphins (*Lagenorhynchus obscurus* Gray, 1828) (Degrati et al., 2019), and Guiana dolphins (*Sotalia guianensis*) (Azevedo et al., 2005; Santos and Rosso, 2007; Emin-Lima et al., 2010). This social strategy i.e., dolphin group became larger when calves were present, could bring a variety of added benefits such as enhanced calf-assistance, cooperative calf-caring, reduced maternal investments, and increased calf-protection (against predators or intraspecific aggression) (Mann et al., 2000; Gibson and Mann, 2008a; Kent et al., 2008).

Our data indicated that IPHD groups were mainly engaged in feeding and traveling behaviors, while socializing and resting/milling were less frequently observed. Such a behavioral budget was consistent with the patterns documented for humpback dolphins in the Hong Kong waters (Parsons, 2004; Würsig et al., 2016), in the Algoa Bay, South Africa (Karczmarski, 1999), and in the Cleveland Bay, Australia (Parra et al., 2011). Our results showed that resting/milling IPHD groups were smaller than feeding, traveling, or socializing groups, while the latter three group types had a similar group size. This increase in feeding, traveling, or socializing group size has been reported for the bottlenose dolphins (Heithaus and Dill, 2002), common dolphins (*Delphinus* spp.) (Neumann, 2001; Stockin et al., 2009), and dusky dolphins (Degrati et al., 2019). IPHDs tended to form large, temporary, and functional gathering of different social units when they were not resting or milling (Würsig et al., 2016), which might help strengthen group added benefits (Baird and Dill, 1996; Neumann, 2001; Yeater et al., 2013).

To conclude, our data are essential to show temporal and behavioral variations in IPHD group sizes in the Zhanjiang waters. Our findings suggested that the intra-population variability of IPHD group sizes was potentially associated with some environmental cycles and behavioral changes, and could be influenced by the food availability and reproductive process of IPHDs. To better protect the IPHDs in the Zhanjiang waters, we highlight the importance of protecting nursery groups/activities of IPHDs. According to our findings, we empathize that breeding season is an important period in the annual cycle of IPHDs, and in the study area, particular conservation effort is required during the autumn. The IPHDs in the study area also tended to form larger groups when they were engaged in feeding behavior and when food resources are more abundant (e.g., summer-fishing-ban-season), which indicated that social dynamics of IPHDs could be greatly influenced food availability. Therefore, protecting food resources from overfishing should be one of the most important actions to maintain social dynamics of IPHDs and to conserve this species. Compared to previous studies, we found that the intra-population variations in IPHD group sizes might vary among different habitats. Therefore, more data on IPHD mating strategies, reproductive fitness, prey resources, fisheries-dolphin conflicts, and how these factors may influence social dynamics of IPHDs are interesting venues of future research.

DATA AVAILABILITY STATEMENT

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

ETHICS STATEMENT

The animal study was reviewed and approved by IDSSE-SYLL-MMMBL-01.

AUTHOR CONTRIBUTIONS

MLiu and MLin: data collection. MLiu: formal analysis and writing—original draft. SL and MLin: 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.

FUNDING

ACKNOWLEDGMENTS

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