Aquatic Mammals 2021, *47*(1), 43-52, DOI 10.1578/AM.47.1.2021.43

Preliminary Study on the Reproductive Ecology of a Threatened Indo-Pacific Humpback Dolphin (*Sousa chinensis*) Population in Xiamen Bay, China

Qianhui Zeng,[1, 2, 3] Xianyan Wang,[2, 3] and Qian Zhu[1]

[1]*Ocean College, Shandong University, Weihai 264209, People's Republic of China*
E-mail: qianzhu@sdu.edu.cn
[2]*Laboratory of Marine Biology and Ecology, Third Institute of Oceanography, Ministry of Natural Resources, Xiamen 361005, People's Republic of China*
[3]*Fujian Provincial Key Laboratory of Marine Ecological Conservation and Restoration, Xiamen 361005, People's Republic of China*
E-mail: wangxianyan@tio.org.cn

Abstract

Reproductive data can provide important information for the conservation and management of threatened animals. The small resident Indo-Pacific humpback dolphin (*Sousa chinensis*) population in Xiamen Bay is threatened by frequent exposure to anthropogenic activities, and its reproductive ecology is still unknown. Based on photo-identification data collected from August 2010 to August 2015, the present study tracked 13 reproductive females and 19 of their calves and estimated the reproductive data. Births occurred all year round but were mainly concentrated in spring and summer; the annual crude birth rate was 0.053 ± 0.025, and the annual recruitment rate was 0.028 ± 0.024; the calf survival rate to 1 year old was 0.600 ± 0.392; and females had a long inter-birth interval (4.27 ± 1.06 y). All these factors may be due to intense extrinsic anthropogenic disturbances (such as busy vessel traffic and coastal construction). In addition to these substantial extrinsic pressures, the low birth rate, low calf survival rate, and long inter-birth interval of humpback dolphins would further intrinsically preclude the sustainable survival of this population.

Key Words: Indo-Pacific humpback dolphin, *Sousa chinensis*, calf survival, calving seasonality, crude birth rate, inter-birth interval, photo-identification

Introduction

Assessing the population dynamics and viability of threatened mammals is essential as it provides the fundamental knowledge required to set up frameworks for conservation management. Estimating and analyzing demographic parameters for these assessments, including reproductive data, require studies based on the identification and observation of individual animals. However, reproductive studies based on individual animals are challenging to conduct on wild dolphins as these animals are wide-ranging, deep diving, and fast moving (Mann & Karniski, 2017). It is also difficult to observe female dolphins giving birth in field surveys. To obtain accurate reproductive data, extended periods of systematic fieldwork should be undertaken. These require extensive investment of time, effort, and finances (Hayes & Schradin, 2017). Given the above conditions, most researchers tend to study reproductive details only on resident dolphin populations in a certain area where data are either collected from stranded or bycaught carcasses (Addink et al., 1997; Calzada et al., 2010), through photo-identification sampling (Herzing, 1997; Steiner & Bossley, 2008), or by using both methods over the same period (McFee et al., 2014; Chivers et al., 2016).

The Indo-Pacific humpback dolphin (*Sousa chinensis*; hereafter referred as "humpback dolphin") is widely distributed in coastal and inshore waters ranging from the eastern Indian Ocean to the western Pacific Ocean (Jefferson & Smith, 2016). In China, this species occurs along the southeastern coast in locations such as Xiamen Bay (Liu & Huang, 2000), the eastern Taiwan Strait (Wang et al., 2007), Shantou waters (Chen et al., 2009), the Pearl River Estuary (including Hong Kong waters) (Jefferson, 2000; Karczmarski et al., 2016), Zhanjiang waters (Xu et al., 2015), the Beibu Gulf (Chen et al., 2016), and the southwestern Hainan coastal waters (Li et al., 2016). Humpback dolphins prefer inshore habitats with a water depth shallower than 30 m and, therefore, are often exposed to intense human activity (Jefferson & Smith, 2016).

The humpback dolphin population in Xiamen Bay is known to be a small resident population, isolated from neighboring populations along the eastern Taiwan Strait (Wang et al., 2016b) and in Shantou waters (unpub. data). The Xiamen Bay humpback dolphin population size was reported as 72 individuals between 2007 and 2010 (Chen et al., 2018), while it was estimated as 64 individuals by a mark-recapture analysis based on a photo-identification catalog collected between 2010 and 2015 (Zeng et al., 2020). Apart from population size estimation, studies have also been carried out to explore the echolocation characteristics (Niu et al., 2012), social organization (Wang et al., 2015), seasonal group size (Wang et al., 2016a), and habitat use (Wang et al., 2017) of this population. Nevertheless, the reproductive details of this threatened dolphin population are still not well understood.

The present study reports several reproductive details for this population, including inter-birth interval, calving seasonality, crude birth rate, recruitment rate, and calf survival rate, using the same photo-identification data collected through boat-based surveys between 2010 and 2015. Additionally, stranded carcass records were collected along the coast of the entire Xiamen Bay over the same period as supporting data. Assessment of these data will facilitate a better understanding of the reproductive ecology of this population and emphasize the urgency of effective conservation and management measures to protect this population.

Methods

Study Area

The study area covered the entire Xiamen Bay, including waters inside the Kinmen–Tatan–Wuyu island chain, with a total area of 750 km^2 (Figure 1). To ensure our survey effort was evenly distributed, the study area was further divided into four subregions—West Harbor–Jiulong River Estuary subregion, Wuyu subregion, Dadeng subregion, and Tongan Bay subregion—and survey routes were standardized in each subregion (Figure 1); each route could be covered by the survey boat within one day. Seasons were distinguished based on local climate characteristics as follows: spring (March to May), summer (June

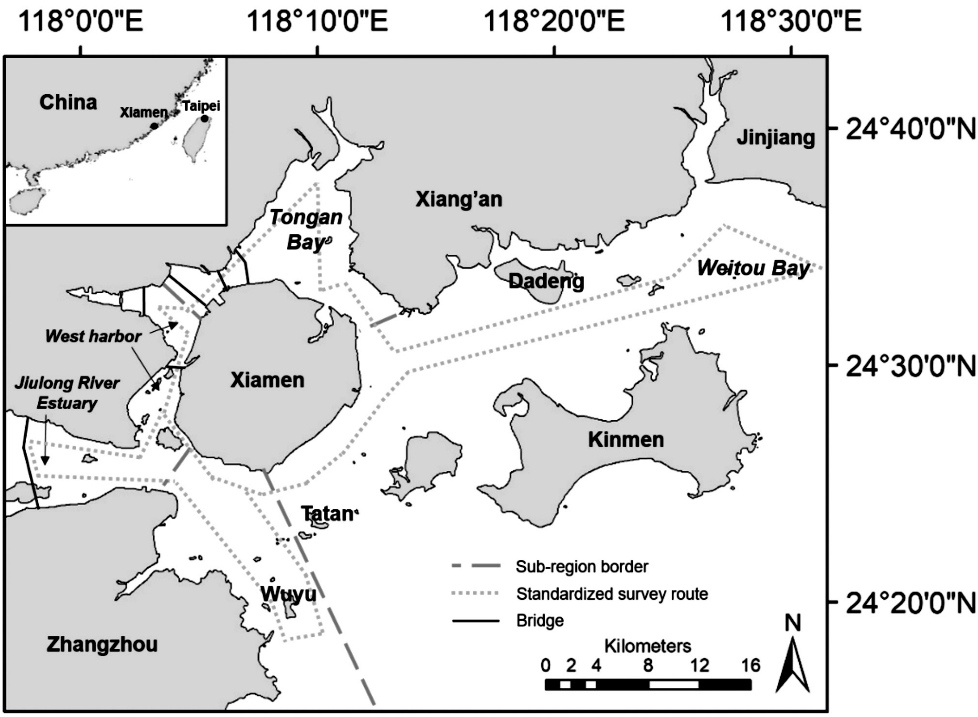

Figure 1. Map of Xiamen Bay. Gray broken lines show the borders of the four subregions, and dotted lines show the standardized survey routes.

to August), autumn (September to November), and winter (December to February) (Wang et al., 2016a).

Field Data Collection

Monthly boat-based surveys were conducted from August 2010 to August 2015. During the study period, each subregion was covered in at least one day's effort every month in principle. The surveys were conducted on days with a Beaufort Sea state ≤ 3, using a 13-m wooden boat powered by a 50-hp speed (10 to 15 kts) following standardized routes. Searches for dolphins were made using the unaided eye and with 7 × 50 binoculars. Two observers, standing on each side of the boat, were assigned to search for dolphins, and a data recorder, sitting in the middle of the boat, was assigned to record data. Detailed survey procedures are described in Wang et al. (2015).

Once a dolphin or dolphin group was sighted, the sighting location was recorded. Then, the boat approached the dolphin(s) from the side at a speed of less than 5 kts. Photographs of each dolphin's dorsal fin and upper body were taken by the observers with at least two cameras equipped with 100-400 mm lenses. The recorded data included the time, location, water depth, dolphin group size, and behavior. Each dolphin or dolphin group encountered was tracked for a minimum of 20 min to ensure both sides of all individuals were photographed for identification. When photographic sampling was finished, the boat continued the survey route from the point of encounter and patrolled until the route in the subregion was fully covered.

Photo-Identification Analysis

All collected images were processed and cataloged using the photo-identification data management software *Discovery* (Gailey & Karczmarski, 2012). Images were scored from 0 to 100 according to quality, including exposure, focus, and the angle of the dolphin to the camera. Only images with scores above 60 were used for identification. Individuals were identified according to distinctive and permanent characteristics on their dorsal fin region such as notches and pigmentation (Würsig & Würsig, 1977; Würsig & Jefferson, 1990). Juvenile humpback dolphins that were young and thus did not bear permanent characteristics were identified according to temporary marks on their dorsal fin region such as tooth rakes, notches, or unusual pigmentation.

Individually identified adults who were observed to accompany a calf during two or more subsequent and independent encounters were assumed to be mothers (Bezamat et al., 2019). Calves were defined as small and black or gray dolphins (see relevant body length and color descriptions in Table 1) closely associated with an adult, regardless of the calf's age (Wells & Scott, 1990; Chang et al., 2016). Neonates were very small (approximately 1 m—1/3 of adult body length), newly born (less than 1 mo old) calves and were identified by the presence of apparent fetal folds and their characteristic head-out swimming style (Cockcroft & Ross, 1990; Jefferson et al., 2012). As calves rarely exhibited persistent marks, and because they lacked spots, they were tracked by their consistent association with a particular adult (the presumed mother). Temporary marks on the calves' dorsal fin regions also assisted in re-identification. A mother–calf pair was defined as two dolphins, a presumed mother and a calf, swimming in close proximity to each other in the echelon position during each survey (Grellier et al., 2003; Noren & Edwards, 2011).

The birth month of each calf was estimated retrospectively based on the external appearance of the calf and its inferred age at its first sighting. To infer the age of each calf at its first sighting, characteristics of body size, coloration, and the presence of fetal folds were considered (Table 1). The last sighting date of the mother without a calf was also considered to narrow the inferred age range.

Table 1. Definitions of Indo-Pacific humpback dolphin (*Sousa chinensis*) calf age classes less than ~1 y old in the present study (based on experience during field observations and descriptions in Jefferson et al. [2012], modified from Table 2 in Chang et al. [2016])

Age class of calf	Description
< 1 mo, neonate	Approximately 1/3 of adult body length, dark gray or black in color, with clear fetal folds, a clearly discernible cranium, and with characteristic head-out swimming style
1-2 mo	Approximately 2/5 of adult body length, dark gray in color, with obvious fetal-fold marks, and a slightly wrinkled body shape posterior to the blowhole
3-5 mo	Approximately 1/2 of adult body length, dark gray in color, with weak fetal-fold marks
6-10 mo	More than 1/2 but less than 2/3 of adult body length, grayish in color, without obvious fetal-fold marks
~1 y	At least 3/4 of adult body length, light gray in color, with dorsal ridge not yet well defined

When analyzing calving seasonality, only calves which were first sighted at less than 6 mo old were included.

The minimum age of humpback dolphins at weaning was 3 y according to Guo et al. (2020); therefore, if a presumed mother was sighted without her calf before the calf had reached 3 y on two or more subsequent independent encounters, the calf was assumed to be deceased. Furthermore, calf carcasses found along the coasts of Xiamen Bay were recorded, and only those that were considered not to be calves from the identified mothers, based on mother–calf pair tracking records and the date carcasses were found, and that were estimated as less than 6 mo old when they died, were included in the subsequent analysis.

Reproductive Data Analysis

The reproductive details of the Xiamen Bay humpback dolphin population estimated in the present study were defined as follows:

(a) The *inter-birth interval* was defined as the period between the estimated birth months of two successive calves of an identified female. In the present study, only mothers that had two calves and where both calves were first sighted at less than 1 y of age were included in the inter-birth interval analysis.

(b) The *annual crude birth rate (CBR)* was defined as the proportion of neonate calves in the total population in year *t* (Wells & Scott, 1990; Kogi et al., 2004):

$$CBR(t) = T_{n,t} / (T_{c,t} + T_{i,t})$$

where $T_{n,t}$ referred to the total number of neonates in year *t*, $T_{c,t}$ referred to the total number of calves (equal to the number of mother–calf pairs, including $T_{n,t}$) in year *t*, and $T_{i,t}$ referred to the total number of noncalves in year *t*.

(c) The *annual recruitment rate (RR)* was calculated as follows (Wells & Scott, 1990; Kogi et al., 2004):

$$RR(t) = T_{n1,t} / (T_{c,t} + T_{i,t} - T_{n,t})$$

where $T_{n1,t}$ referred to the number of calves that were born in year *t* and survived to at least 1 y old after birth.

(d) The *calf survival rate* to the age of 1 ($l_{1,t}$) was calculated as follows:

$$l_{1,t} = T_{n1,t} / T_{n,t}$$

Statistical analyses were carried out using *SPSS*, Version 13.0, software. The parameters (b), (c), and (d) are presented as weighted means ± standard deviation (SD), and other data are represented as means ± SD.

Results

Data for the photo-identification analysis were collected on 252 d through boat-based surveys from August 2010 to August 2015, and survey days were nearly evenly distributed between each month (Table 4). The number of newly identified individuals increased greatly in the first year and gradually slowed down in the second year, suggesting that the photo-identification effort did not cover the whole resident population at the beginning of the study. Nevertheless, most of the presumed mothers were sighted and identified before 2012, with the exception of individual XM063, which was first sighted in the middle of 2012 (Table 2).

Throughout the study period, a total of 166 humpback dolphin sightings were recorded, with an average group size of 5.45 ± 3.32 dolphins (range = 1 to 16). Seventy-five (45.2%) sightings contained at least one mother–calf pair, with an average of 1.31 ± 1.28 pairs per group (range = 1 to 6). A total of 13 mothers were reliably identified, while 19 calves from these 13 mothers were also identified (Table 2). Of those 13 identified mothers, six (46.2%) were sighted with their second calf, and four (cataloged as XM006, XM018, XM034, and XM037) were sighted with both of their calves individually when each calf was less than 1 y old; the inter-birth intervals for these four mothers were 5.83, 4.00, 3.50, and 3.75 y, respectively, with an average interval of 4.27 ± 1.06 y.

Of the 19 calves observed, seven (36.8%) were born before the beginning of the study period, and 12 (63.2%) were born during the study period (Table 3). Of these 19 calves, two were assumed to have died before they reached their second year, and another calf's fate remains unknown: this calf was first sighted at approximately 3 y old in 2012 but was not subsequently sighted alone or with its mother (XM063) (Table 3). Apart from the 19 calves which were sighted and tracked in the field surveys, four neonate carcasses were recorded and considered not to be calves from the 13 identified mothers, based on analysis of mother–calf pair tracking records and the date carcasses were found between 2010 and 2015 (Table 3). Based on the analysis of 11 calves observed with reliable birth month estimates and four neonate carcasses from unknown mothers, we found that calving took place throughout all seasons, but the

Table 2. Sightings of reproductive humpback dolphin females (ID# = individual photo-identification catalog number) and their calves from August 2010 to August 2015 in Xiamen Bay, including sightings of females without a calf (marked with a "--") and their first (C1) or second (C2) calves

ID#	2010	2011	2012	2013	2014	2015
XM001	--	C1	C1	C1	C1	--
XM006	C1	C1	C1	C1	--	C2
XM013	--	--	--	--	--	C1
XM014	C1	C1	C1	C1	C2	--
XM018	--	C1	C1	C1	C1	C2
XM021	--	--	C1	C1	C1	C1
XM025	--	--	--	C1	--	--
XM026	C1	C1	C1	C1	C1	C1
XM031	C1	C1	C1	C1	--	--
XM034	C1	C1	--	C2	C2	C2
XM037	--	C1	C1	C1	--	C2
XM043		C1	C1	C1 + C2	C2	C2
XM063			C1	--	--	*

*The female cataloged as XM063 was found dead in March 2015 while pregnant.

Table 3. The birth circumstances and fates of all observed and recorded humpback dolphin calves until the end of the present study (August 2015) in Xiamen Bay

Calf's circumstances	Number of total calves	Still with mother	Weaned	Assumed or confirmed dead	Fate unknown
Calves from known mothers born before January 2010	5	0	4	0	1
Calves from known mothers born between January 2010 and July 2010	2	1	1	0	0
Calves from known mothers born between August 2010 and August 2015	12	7	3	2	0
Calves from unknown mothers born between January 2010 and August 2015 (based on carcass records)	4	0	0	4	0

majority of births (73.3%) occurred during spring and summer (Figure 2).

The number of calves born per year ranged from one to five (Table 4), with an average of at least 3.00 ± 1.41 calves born per year (n = 6 y). The mean annual crude birth rate (CBR) from 2010 to 2015 was 0.057 ± 0.026 (n = 6 y). Since we only carried out surveys for 4 mo in 2010, and the incomplete coverage of the dolphin population in 2010 may lead to biased results, the estimates of 2010 were excluded from the following calculations. Therefore, the population had a mean annual CBR of 0.053 ± 0.025 (n = 5 y). As the calves born in 2015 had not reached 1 y of age at the end of the study, the recruitment rate (RR) and the calf survival rate to age 1 for 2015 could not be calculated. The mean annual RR from 2011 to 2014 was 0.028 ± 0.024 (n = 4 y), with a range from 0 to 0.064 (Table 4). The mean calf survival rate to age 1 from 2011 to 2014 was 0.600 ± 0.392 (n = 4 y).

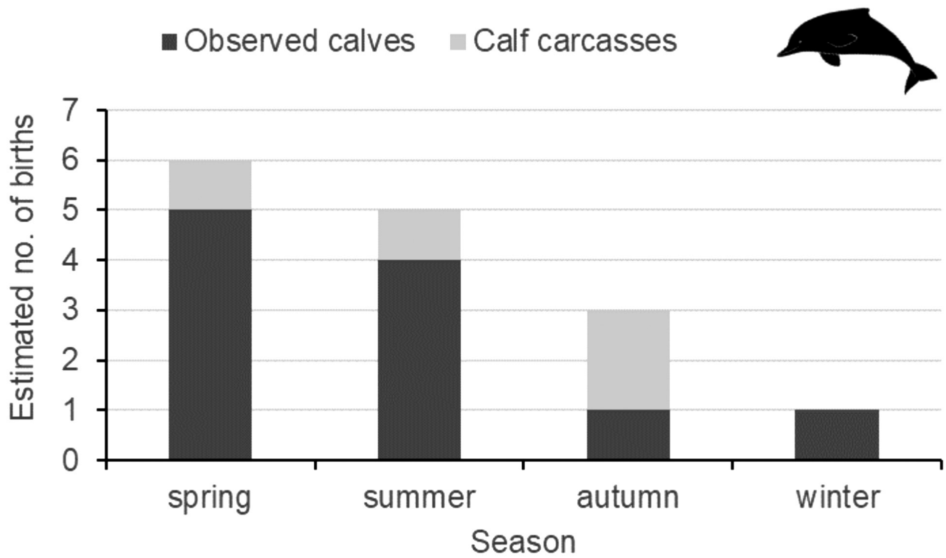

Figure 2. Estimated number of births in different seasons of 15 Indo-Pacific humpback dolphin (*Sousa chinensis*) calves between 2010 and 2015 (including 11 calves from known mothers and four calf carcasses from unknown mothers)

Table 4. Annual reproductive data of the humpback dolphin from 2010 to 2015 in Xiamen Bay. The number of photographic sampling survey days is indicated for each year.

Parameters	2010	2011	2012	2013	2014	2015
Number of neonates, $T_{n,t}$	3[a]	4[a]	2	3[a]	1	5[a]
Number of calves that survive to age 1, $T_{n1,t}$	2	3	2	1	0	≤ 4[b]
Number of noncalves, $T_{i,t}$	28	41	46	47	50	51
Number of calves (mother–calf pairs), $T_{c,t}$	5	9	10	11	7	8
Number of total individuals, $T_{i,t} + T_{c,t}$	34[a]	51[a]	56	59[a]	57	60[a]
Crude birth rate, $CBR(t)$, $T_{n,t} / (T_{i,t} + T_{c,t})$	0.088	0.078	0.036	0.051	0.018	0.083
Recruitment rate, $RR(t)$, $T_{n1,t} / (T_{i,t} + T_{c,t} - T_{n,t})$	0.065	0.064	0.037	0.018	0.000	NA[b]
Calf survival rate to age 1, $T_{n1,t} / T_{n,t}$	0.667	0.750	1.000	0.333	0	NA[b]
Survey days	22	49	52	51	45	33

[a]We included one neonate from an unknown mother found dead in the study area.
[b]Needs further investigation.

Discussion

To the best of our knowledge, the present study is the first preliminary study into the reproductive ecology of the Xiamen Bay humpback dolphin. The reproductive histories established in the present study suggest that the Xiamen Bay humpback dolphin has distinct reproductive characteristics such as apparent seasonality, long inter-birth interval, and long maternal care period. Our results indicate that calving occurred throughout the year in the Xiamen Bay population, but most births occurred in spring and summer (from March to August). This is consistent with the results of Liu & Huang (2000) in which stranded neonates were mainly found from April to September in Xiamen Bay, and similar to humpback dolphin calving in Hong Kong waters (Jefferson, 2000). Our results do differ from Xu et al. (2012), however, as humpback dolphins in Zhanjiang waters mainly gave birth between August and October.

Calving seasonality in dolphins is mainly influenced by sea surface temperature (Henderson et al., 2014), shifts in food resources related to oceanic productivity or animal migration (Barros et al., 2004; Romero et al., 2012), and predation pressure (Fearnbach et al., 2012). Since there were no predators of humpback dolphins in Xiamen Bay, it can be concluded that calving seasonality mainly resulted from the dynamics of both sea surface temperature and changes in food resources. Female dolphins tend to give birth when the water temperature is thermally efficient for calves in order to increase calf survival (Henderson et al., 2014; Bezamat et al., 2019). Meanwhile, a seasonal increase in sea surface temperature triggers high oceanic productivity and the migration of prey animals, making food resources more accessible (Barros et al., 2004; Romero et al., 2012; Chang et al., 2016). In Xiamen Bay, fishes such as *Collichthys lucidus*, *Coilia mystus*, and *Johnius belangerii* are known prey for humpback dolphins. These species spawn nearshore in spring and shift southward and eastward into deeper waters in summer (Huang et al., 2010), thus providing ample food for humpback dolphins. Easy access to food resources helps females to meet the energetic requirements of lactation (Lockyer, 2007; Rechsteiner et al., 2013). As such, exact seasonal timing is important for calving in humpback dolphins.

Reproductive female humpback dolphins in Xiamen Bay had a longer inter-birth interval (mean = 4.27 ± 1.06 y) when compared to humpback dolphins in the eastern Taiwan Strait (3.26 y; Chang et al., 2016) and to Indian Ocean humpback dolphins (*Sousa plumbea*) in Algoa Bay, South Africa (~3 y; Karczmarski, 1999), but shorter than that of humpback dolphins in Hong Kong waters (~5 y; Jefferson et al., 2012). Since only four females were included when calculating the mean inter-birth interval in the present study, the sample size might not be large enough to represent all reproductive females. However, females which were observed to give birth to only one calf during this 5-y study had a long maternal care period, mostly longer than 4 y. In the future, an investigation including more samples might result in a longer inter-birth interval than the current result. Giving birth and subsequent calf-caring are high-energy costs; long inter-birth intervals and long maternal care periods might suggest that dolphin mothers put more effort into reproductive output (Altmann & Samuels, 1992; Miketa et al., 2018) or that mothers are too old to have continuous and frequent births (Robinson et al., 2017). Among the 13 mothers tracked in the present study, 11 were young adults with spotting at the speckled stage and, thus, likely between 10 and 20 y old based on the descriptions of Jefferson et al. (2012) and Guo et al. (2020). Therefore, the long inter-birth intervals and maternal care periods likely resulted from these females putting more effort into their reproductive output. Xiamen and Hong Kong are both well-developed port cities, with neighboring waters often disturbed by fishing, shipping, dredging, and other human activities (Jefferson et al., 2012). It is possible that dolphin mothers in Xiamen Bay and Hong Kong waters have to invest more energy to avoid potential dangers from human activities during nursing. They may also have to give more care to their calves because of impacts from these activities and, therefore, have extended their inter-birth intervals and maternal care periods to protect their offspring.

The annual CBR of the Xiamen Bay population fluctuated widely, which could either be a result of births that may have gone unnoticed or could reflect the true reproductive characteristics. To minimize bias from unrecorded and missing calves, the calf carcasses from unknown mothers were recorded and included as supporting data. As the Xiamen government conducted extensive public education for humpback dolphin protection in local communities and established a well-developed stranding monitoring network along Xiamen Bay, most stranding events, either dead or alive, should be located and could offer reliable stranding records. Although the annual CBR varied widely (0.018 to 0.083), the mean estimate (0.053 ± 0.025) was slightly higher than that of humpback dolphins in the eastern Taiwan Strait (0.046; Chang et al., 2016). However, the means of the annual CBR from Xiamen Bay and the eastern Taiwan Strait were both lower than the CBRs of bottlenose dolphins (*Tursiops aduncus*) that reside in Adelaide, Australia (Steiner & Bossley, 2008); Shannon Bay, Ireland (Baker et al., 2017); and Laguna, Brazil (Bezamat et al., 2019). The annual RR varied widely in the Xiamen Bay population compared to that in the eastern Taiwan Strait (Chang et al., 2016) or that in Algoa Bay (Karczmarski, 1999), which may be related to our short study period and limited samplings. As such, investigations with extended periods and more study effort are required in the future.

The mean calf survival rate to age 1 of the Xiamen Bay population (0.600 ± 0.392) was slightly lower than that of the Hong Kong population (0.61; Jefferson et al., 2012) and that of the population in the eastern Taiwan Strait (0.667; Chang et al., 2016). Calf survival of the Xiamen Bay humpback dolphins is mainly affected by birth timing, the mother's reproductive output, and human activities. As mentioned above, a proper seasonal birth timing and higher maternal reproductive output will increase calf survival. Anthropogenic influence is another major concern that affects calf survival. Humpback dolphins in Xiamen Bay face anthropogenic threats from underwater noise (Wang et al., 2003), busy vessel traffic (Chen et al., 2011), habitat degradation (Wang et al., 2017), and fishing entanglement (Wang et al., 2018). The above human activities would either cause direct trauma to the calves (e.g., one calf carcass recorded during the study period had a broken jaw that could have been caused by a ship collision) or they could affect calves through the constant exposure to negative stressors (e.g., noise disturbance from a series of coastal constructions as noise disturbance may be more detrimental to young animals).

The Xiamen Bay humpback dolphins are highly threatened. As an isolated population containing fewer than 100 individuals, it is extremely vulnerable to extinction (Thompson et al., 2000; Traill et al., 2007). Furthermore, anthropogenic threats represent substantial extrinsic pressures on this dolphin population (Liu & Huang, 2000; Chen et al., 2011). Our findings indicate that the current reproductive characteristics of these Xiamen Bay humpback dolphins, such as low birth rate, low calf survival rate, and long inter-birth interval, would further intrinsically preclude the sustainable survival of this population. To increase calf survival and reduce the energetic costs of dolphin mothers in Xiamen Bay, we suggest that (1) vessel traffic and fishing activities should be strictly managed during the major calving season (spring and summer); (2) intensity of coastal construction and relevant underwater blasting activities should be reduced to the minimum during the major calving season; and (3) if construction projects must be implemented during the major calving season, the environmental impacts of each coastal construction project should be carefully assessed and more effort should be made to deter dolphins from construction areas.

Acknowledgments

The authors would like to give their sincere thanks to the captain of our survey vessel, S. Ke, for his splendid boat driving skills; F. Wu, X. Miao, C. Tao, X. Ding, M. Xu, and J. Mou of the Third Institute of Oceanography, Ministry of Natural Resources, for their dedication during the field surveys; and C. Gsottbauer for her generous help on polishing the manuscript. This work was financially supported by the National Natural Science Foundation of China (42076159), the China-ASEAN Maritime Cooperation Fund (HX01-190701), the Third Institute of Oceanography, Ministry of Natural Resources of China (HE01-190505 and TIO2015023), and the Ocean Park Conservation Foundation, Hong Kong (MM03_1617). The field surveys were approved by the Management Office of the Xiamen Indo-Pacific Humpback Dolphin National Natural Reserve.

Literature Cited

Addink, M., Garcia Hartmann, M., & Couperus, B. (1997). A note on life-history parameters of the Atlantic white-sided dolphin (*Lagenorhynchus acutus*) from animals bycaught in the northeastern Atlantic. *Reports of the International Whaling Commission*, *47*, 637-639.

Altmann, J., & Samuels, A. (1992). Costs of maternal care: Infant-carrying in baboons. *Behavioral Ecology & Sociobiology*, *29*(6), 391-398. https://doi.org/10.1007/BF00170168

Baker, I., O'Brien, J., McHugh, K., & Berrow, S. (2017). Female reproductive parameters and population demographics of bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland. *Marine Biology*, *165*(1), 15-34. https://doi.org/10.1007/s00227-017-3265-z

Barros, N. B., Jefferson, T. A., & Parsons, E. C. M. (2004). Feeding habits of Indo-Pacific humpback dolphins (*Sousa chinensis*) stranded in Hong Kong. *Aquatic Mammals*, *30*(1), 179-188. https://doi.org/10.1578/AM.30.1.2004.179

Bezamat, C., Castilho, P. V., Simões-Lopes, P. C., Ingram, S. N., & Daura-Jorge, F. G. (2019). Reproductive parameters and factors influencing calf survival of bottlenose dolphins that engage in a unique foraging cooperation with fishermen. *Marine Biology*, *167*(1), 5-17. https://doi.org/10.1007/s00227-019-3611-4

Calzada, N., Aguilar, A., Sørensen, T. B., & Lockyer, C. (2010). Reproductive biology of female striped dolphin (*Stenella coeruleoalba*) from the western Mediterranean. *Proceedings of the Zoological Society of London*, *240*(3), 581-591. https://doi.org/10.1111/j.1469-7998.1996.tb05308.x

Chang, W-L., Karczmarski, L., Huang, S-L., Gailey, G., & Chou, L-S. (2016). Reproductive parameters of the Taiwanese humpback dolphin (*Sousa chinensis taiwanensis*). *Regional Studies in Marine Science*, *8*, 459-465. https://doi.org/10.1016/j.rsma.2016.08.001

Chen, B., Zheng, D., Yang, G., Xu, X., & Zhou, K. (2009). Distribution and conservation of the Indo-Pacific humpback dolphin in China. *Integrative Zoology*, *4*(2), 240-247. https://doi.org/10.1111/j.1749-4877.2009.00160.x

Chen, B., Zheng, D., Ju, J., Xu, X., Zhou, K., & Yang, G. (2011). Range patterns of resident Indo-Pacific humpback dolphins (*Sousa chinensis*, Osbeck 1765) in Xiamen, China: Implications for conservation and management. *Zoological Studies*, *50*(6), 751-762.

Chen, B., Xu, X., Jefferson, T. A., Olson, P. A., Qin, Q., Zhang, H., He, L., & Yang, G. (2016). Conservation status of the Indo-Pacific humpback dolphin (*Sousa chinensis*) in the northern Beibu Gulf, China. *Advances in Marine Biology*, *73*, 119-139. https://doi.org/10.1016/bs.amb.2015.10.001

Chen, B., Gao, H., Jefferson, T. A., Lu, Y., Wang, L., Li, S., Wang, H., Xu, X., & Yang, G. (2018). Survival rate and population size of Indo-Pacific humpback dolphins (*Sousa chinensis*) in Xiamen Bay, China. *Marine Mammal Science*, *34*(4), 1018-1033. https://doi.org/10.1111/mms.12510

Chivers, S. J., Perryman, W. L., Lynn, M. S., Gerrodette, T., Archer, F. I., Danil, K., Berman-Kowalewski, M., & Dines, J. P. (2016). Comparison of reproductive parameters for populations of eastern North Pacific common dolphins: *Delphinus capensis* and *D. delphis*. *Marine Mammal Science*, *32*(1), 57-85. https://doi.org/10.1111/mms.12244

Cockcroft, V. G., & Ross, G. J. B. (1990). Observations on the early development of a captive bottlenose dolphin calf. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 461-478). Academic Press. https://doi.org/10.1016/B978-0-12-440280-5.50031-7

Fearnbach, H., Durban, J., Parsons, K., & Claridge, D. (2012). Seasonality of calving and predation risk in bottlenose dolphins on Little Bahama Bank. *Marine Mammal Science*, *28*(2), 402-411. https://doi.org/10.1111/j.1748-7692.2011.00481.x

Gailey, G., & Karczmarski, L. (2012). *DISCOVERY: Photo-identification data-management system for individually recognizable animals*. www.cetaecoresearch.com/research-software-discovery.html

Grellier, K., Hammond, P. S., Wilson, B., Sanders-Reed, C. A., & Thompson, P. M. (2003). Use of photo-identification data to quantify mother-calf association patterns in bottlenose dolphins. *Canadian Journal of Zoology*, *81*(8), 1421-1427. https://doi.org/10.1139/z03-132

Guo, L., Lin, W., Zeng, C., Luo, D., & Wu, Y. (2020). Investigating the age composition of Indo-Pacific humpback dolphins in the Pearl River Estuary based on their pigmentation pattern. *Marine Biology*, *167*(4), 50-62. https://doi.org/10.1007/s00227-020-3650-x

Hayes, L. D., & Schradin, C. (2017). Long-term field studies of mammals: What the short-term study cannot tell us. *Journal of Mammalogy*, *98*(3), 600-602. https://doi.org/10.1093/jmammal/gyx027

Henderson, S. D., Dawson, S. M., Currey, R. J. C., Lusseau, D., & Schneider, K. (2014). Reproduction, birth seasonality, and calf survival of bottlenose dolphins in Doubtful Sound, New Zealand. *Marine Mammal Science*, *30*(3), 1067-1080. https://doi.org/10.1111/mms.12109

Herzing, D. L. (1997). The life history of free-ranging Atlantic spotted dolphins (*Stenella frontalis*): Age classes, color phases, and female reproduction. *Marine Mammal Science*, *13*(4), 576-595. https://doi.org/10.1111/j.1748-7692.1997.tb00085.x

Huang, L., Xie, Y., Zhang, Y., Li, J., & Liu, Q. (2010). Current fisheries resources assessment in Xiamen coastal waters. *Journal of Jimei University*, *15*, 81-86. [In Chinese]

Jefferson, T. A. (2000). Population biology of the Indo-Pacific hump-backed dolphin in Hong Kong waters. *Wildlife Monographs* (No. 144). 65 pp.

Jefferson, T. A., & Smith, B. D. (2016). Re-assessment of the conservation status of the Indo-Pacific humpback dolphin (*Sousa chinensis*) using the IUCN *red list* criteria. *Advances in Marine Biology*, *73*, 1-26. https://doi.org/10.1016/bs.amb.2015.04.002

Jefferson, T. A., Hung, S. K., Robertson, K. M., & Archer, F. I. (2012). Life history of the Indo-Pacific humpback dolphin in the Pearl River Estuary, southern China. *Marine Mammal Science*, *28*(1), 84-104. https://doi.org/10.1111/j.1748-7692.2010.00462.x

Karczmarski, L. (1999). Group dynamics of humpback dolphins (*Sousa chinensis*) in the Algoa Bay region, South Africa. *Journal of Zoology*, *249*(3), 283-293. https://doi.org/10.1111/j.1469-7998.1999.tb00765.x

Karczmarski, L., Huang, S-L., Or, C. K. M., Gui, D., Chan, S. C., Lin, W., Porter, L., Wong, W-H., Zheng, R., Ho, Y. W., Chui, S. Y., Tiongson, A. J., Mo, Y., Chang, W-L., Kwok, J. H., Tang, R. W., Lee, A. T., Yiu, S-W., Keith, M., Gailey, G., & Wu, Y. (2016). Humpback dolphins in Hong Kong and the Pearl River Delta: Status, threats and conservation challenges. *Advances in Marine Biology*, *73*, 27-64. https://doi.org/10.1016/bs.amb.2015.09.003

Kogi, K., Hishii, T., Imamura, A., Iwatani, T., & Dudzinski, K. M. (2004). Demographic parameters of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) around Mikura Island, Japan. *Marine Mammal Science*, *20*(3), 510-526. https://doi.org/10.1111/j.1748-7692.2004.tb01176.x

Li, S., Lin, M., Xu, X., Xing, L., Zhang, P., Gozlan, R. E., Huang, S-L., & Wang, D. (2016). First record of the Indo-Pacific humpback dolphins (*Sousa chinensis*) southwest of Hainan Island, China. *Marine Biodiversity Records*, *9*(1), 3. https://doi.org/10.1186/s41200-016-0005-x

Liu, W., & Huang, Z. (2000). Distribution and abundance of Chinese white dolphins (*Sousa chinensis*) in Xiamen. *Acta Oceanologica Sinica*, *22*, 95-101. [In Chinese]

Lockyer, C. (2007). All creatures great and smaller: A study in cetacean life history energetics. *Journal of the Marine Biological Association of the United Kingdom*, *87*(4), 1035-1045. https://doi.org/10.1017/S0025315407054720

Mann, J., & Karniski, C. (2017). Diving beneath the surface: Long-term studies of dolphins and whales. *Journal of Mammalogy*, *98*(3), 621-630. https://doi.org/10.1093/jmammal/gyx036

McFee, W. E., Speakman, T. R., Balthis, L., Adams, J. D., & Zolman, E. S. (2014). Reproductive seasonality of a recently designated bottlenose dolphin stock near Charleston, South Carolina, U.S.A. *Marine Mammal Science*, *30*(2), 528-543. https://doi.org/10.1111/mms.12055

Miketa, M. L., Patterson, E. M., Krzyszczyk, E., Foroughirad, V., & Mann, J. (2018). Calf age and sex affect maternal diving behaviour in Shark Bay bottlenose dolphins. *Animal Behaviour*, *137*, 107-117. https://doi.org/10.1016/j.anbehav.2017.12.023

Niu, F., Yang, Y., Xu, X., Wen, H., & Liu, Z. (2012). Study on the characteristics of echolocation clicks from Indo-Pacific humpback dolphins (*Sousa chinensis*) in Xiamen. *Journal of Xiamen University*, *5*, 151-154. [In Chinese]

Noren, S. R., & Edwards, E. F. (2011). Infant position in mother-calf dolphin pairs: Formation locomotion with hydrodynamic benefits. *Marine Ecology Progress Series*, *424*, 229-236. https://doi.org/10.3354/meps08986

Rechsteiner, E. U., Rosen, D. A. S., & Trites, A. W. (2013). Energy requirements of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) as predicted by a bioenergetic model. *Journal of Mammalogy*, *94*(4), 820-832. https://doi.org/10.1644/12-MAMM-A-206.1

Robinson, K. P., Sim, T. M. C., Culloch, R. M., Bean, T. S., Aguilar, I. C., Eisfeld, S. M., Filan, M., Haskins, G. N., Williams, G., & Pierce, G. J. (2017). Female reproductive success and calf survival in a North Sea coastal bottlenose dolphin (*Tursiops truncatus*) population. *PLOS ONE*, *12*(9), e0185000. https://doi.org/10.1371/journal.pone.0185000

Romero, M. A. A., Dans, S. L., García, N., Svendsen, G. M., González, R., & Crespo, E. A. (2012). Feeding habits of two sympatric dolphin species off North Patagonia, Argentina. *Marine Mammal Science*, *28*(2), 364-377. https://doi.org/10.1111/j.1748-7692.2011.00477.x

Steiner, A., & Bossley, M. (2008). Some reproductive parameters of an estuarine population of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). *Aquatic Mammals*, *34*(1), 84-92. https://doi.org/10.1578/AM.34.1.2008.84

Thompson, P. M., Wilson, B., Grellier, K., & Hammond, P. S. (2000). Combining power analysis and population viability analysis to compare traditional and precautionary approaches to conservation of coastal cetaceans. *Conservation Biology*, *14*(5), 1253-1263. https://doi.org/10.1046/j.1523-1739.2000.00099-410.x

Traill, L. W., Bradshaw, C. J. A., & Brook, B. W. (2007). Minimum viable population size: A meta-analysis of 30 years of published estimates. *Biological Conservation*, *139*(1-2), 159-166. https://doi.org/10.1016/j.biocon.2007.06.011

Wang, D., Liu, R., Zhao, Q., Yang, G., Xu, X., Huang, Z., Xin, J., & Chen, B. (2003). Pathological anatomy and analysis of death causes for a Chinese white dolphin. *Acta Theriologica Sinica*, *23*(2), 183-184.

Wang, J. Y., Yang, S. C., Hung, S. K., & Jefferson, T. A. (2007). Distribution, abundance and conservation status of the eastern Taiwan Strait population of Indo-Pacific humpback dolphins, *Sousa chinensis*. *Mammalia*, *71*(4), 157-165. https://doi.org/10.1515/MAMM.2007.032

Wang, X., Wu, F., Zhu, Q., & Huang, S-L. (2017). Long-term changes in the distribution and core habitat use of a coastal delphinid in response to anthropogenic coastal alterations. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *27*(3), 643-652. https://doi.org/10.1002/aqc.2720

Wang, X., Wu, F., Turvey, S. T., Rosso, M., & Zhu, Q. (2016a). Seasonal group characteristics and occurrence patterns of Indo-Pacific humpback dolphins (*Sousa chinensis*) in Xiamen Bay, Fujian Province, China. *Journal of Mammalogy*, *97*(4), 1026-1032. https://doi.org/10.1093/jmammal/gyw002

Wang, X., Jutapruet, S., Huang, S-L., Turvey, S. T., Wu, F., & Zhu, Q. (2018). External injuries of Indo-Pacific humpback dolphins (*Sousa chinensis*) in Xiamen, China, and its adjacent waters as an indicator of potential fishery interactions. *Aquatic Mammals*, *44*(3), 285-292. https://doi.org/10.1578/AM.44.3.2018.285

Wang, X., Wu, F., Chang, W-L., Hou, W., Chou, L-S., & Zhu, Q. (2016b). Two separated populations of the Indo-Pacific humpback dolphin (*Sousa chinensis*) on opposite sides of the Taiwan Strait: Evidence from a larger-scale photo-identification comparison. *Marine Mammal Science*, *32*(1), 390-399. https://doi.org/10.1111/mms.12257

Wang, X., Wu, F., Turvey, S. T., Rosso, M., Tao, C., Ding, X., & Zhu, Q. (2015). Social organization and distribution patterns inform conservation management of a threatened Indo-Pacific humpback dolphin population. *Journal of Mammalogy*, *96*(5), 964-971. https://doi.org/10.1093/jmammal/gyv097

Wells, R., & Scott, M. (1990). Estimating bottlenose dolphin parameters from individual identification and capture-release techniques. *Reports of the International Whaling Commission*, Special Issue 12, 407-415.

Würsig, B., & Jefferson, T. A. (1990). Methods of photo-identification for small cetaceans. *Reports of the International Whaling Commission*, Special Issue 12, 43-52.

Würsig, B., & Würsig, M. (1977). The photographic determination of group size, composition and stability of coastal porpoises. *Science*, *198*(4318), 755-756. https://doi.org/10.1126/science.198.4318.755

Xu, X., Song, J., Zhang, Z., Li, P., Yang, G., & Zhou, K. (2015). The world's second largest population of humpback dolphins in the waters of Zhanjiang deserves the highest conservation priority. *Scientific Reports*, *5*, 8147. https://doi.org/10.1038/srep08147

Xu, X., Zhang, Z., Ma, L., Peng, L., Yang, G., & Zhou, K. (2012). Site fidelity and association patterns of Indo-Pacific humpback dolphins off the east coast of Zhanjiang, China. *Acta Theriologica*, *57*(2), 99-109. https://doi.org/10.1007/s13364-011-0058-5

Zeng, Q., Lin, W., Dai, Y., Zhong, M., Wang, X., & Zhu, Q. (2020). Modeling demographic parameters of an edge-of-range population of Indo-Pacific humpback dolphin in Xiamen Bay, China. *Regional Studies in Marine Science*, *40*, 101462. https://doi.org/10.1016/j.rsma.2020.101462