Received: 29 October 2018 | Revised: 2 December 2019 | Accepted: 2 December 2019

DOI: 10.1111/mms.12663

ARTICLE

Marine Mammal Science

Abundance and residency dynamics of the Indo-Pacific humpback dolphin, *Sousa chinensis*, in the Dafengjiang River Estuary, China

Chongwei Peng[1,2] | Haiping Wu[1,2] | Xianyan Wang[3] | Qian Zhu[4] | Thomas A. Jefferson[5] | Chun-Chieh Wang[1,6] | Youhou Xu[1,2] | Jian Li[1,2] | Hu Huang[1,2] | Mo Chen[6] | Shiang-Lin Huang[1,6]

[1]Guangxi Key Laboratory of Beibu Gulf Marine Biodiversity Conservation, Beibu Gulf University, Qinzhou, China

[2]Department of Marine Science, College of Ocean, Beibu Gulf University, Qinzhou, China

[3]Laboratory of Marine Biology and Ecology, Third Institute of Oceanography, Ministry of Natural Resources, Xiamen, China

[4]Ocean College, Shandong University (Weihai), Weihai, China

[5]Clymene Enterprises, Yerba Valley, Lakeside, California

[6]Guangxi Beibu Gulf Marine Research Center, Guangxi Academy of Sciences, Nanning, China

Correspondence
Dr. Xianyan Wang, Laboratory of Marine Biology and Ecology, Third Institute of Oceanography, Ministry of Natural Resources, 178 Daxue Road, Xiamen, Fujian, 361005 China.
Email: wangxianyan@tio.org.cn
Dr. Shiang-Lin Huang, Guangxi Beibu Gulf Marine Research Center, Guangxi Academy of Sciences, 98 Dalin Road, Nanning, Guangxi, 530000 China.
Email: shianglinhuang@gxas.cn

Funding information
Guangxi Key Laboratory of Beibu Gulf Marine Biodiversity Conservation, Grant/Award Number: 2017KA02; Ocean Park Conservation Foundation Hong Kong, Grant/Award Numbers: AW02.1718, MM01.1516

Abstract

Robust population size estimates are essential for informing population conservation status. Residency dynamics show population habitat use through time. Population size of Indo-Pacific humpback dolphins (*Sousa chinensis*) has been extensively investigated in Chinese waters, but their residency dynamics are rarely known. Mark-recapture analysis based on photo-identification records was applied to humpback dolphins in the Dafengjiang River Estuary habitat, one of the key habitats in the northern Beibu Gulf, China. Movement analyses based on lagged identification rate indicated the humpback dolphins spent, on average, 78.5 days inside and 46.9 days outside the survey area. Within the study area, the humpback dolphin abundance was 83 identifiable dolphins. A total of 353–430 humpback dolphins, estimated by POPAN modeling, were involved in this fluid habitat-use dynamic. Robust Design analysis showed strong seasonality

Chongwei Peng and Haiping Wu contributed equally to this article.

in humpback dolphin abundance and emigration probability, implying a movement- and habitat-use pattern likely associated with spatiotemporal distribution of oceanographic characteristics and prey occurrences. Population surveys and conservation measures currently conducted in Chinese waters seldom consider seasonality in movements between habitat patches, which can be addressed by genetic analyses across habitats and cross-matching photo-identification records among neighboring habitats.

KEYWORDS
age-class structure, Markovian emigration, photo-identification, POPAN, Robust Design

1 | INTRODUCTION

Robust estimates of population size are the key to accurately assessing extinction risks and informing population status in conservation of threatened species and populations (Huang, Chang, & Karczmarski, 2014; Huang et al., 2012; IUCN, 2001; Wang, Yang, Hung, & Jefferson, 2007). In cetaceans, techniques currently used for abundance estimation include distance sampling, most notably line transect analysis (Buckland, Anderson, Burnham, & Laake, 1993; Thomas et al., 2010; Wang et al., 2007; Zhao et al., 2008) and mark-recapture studies based on individual photo-identification histories (Chen et al., 2016, 2018; Jutapruet et al., 2015; Tyne, Pollock, Johnston, & Bejder, 2014; Wang, Yang, Fruet, Daura-Jorge, & Secchi, 2012; Xu et al., 2015). Distance sampling surveys estimate population density and then apply that density to a particular area chosen by the researcher, thereby producing abundance estimates (Buckland et al., 1993; Thomas et al., 2010). Surveys using distance sampling techniques concurrently provide information on animal distribution and habitat-use patterns (Chen, Hung, Qiu, Jia, & Jefferson, 2010; Parra, Schick, & Corkeron, 2006; Wu et al., 2017a) and offer representative data for mapping habitat configuration over a wide spatial scale (Bao et al., 2019; Huang, Wang, & Yao, 2018; Huang et al., 2019). Mark-recapture surveys, on the other hand, do not produce density estimates, but instead estimate the size of the pool (or subpool) of animals that use the study area as a part of their habitats (Arnason & Schwarz, 1999; Schwarz & Arnason, 1996). Mark-recapture exercises can provide additional information on reproductive and demographic parameters (Chang, Karczmarski, Huang, Gailey, & Chou, 2016; Chen et al., 2018; Tyne et al., 2014; Wang et al., 2012) and social relationships (Alves et al., 2013; Chen et al., 2016; Wang et al., 2015; Whitehead, 2009). When applied to the same population, distance-sampling surveys and mark-recapture studies sometimes report quite different abundance estimates (as those between Chen, Zheng, Yang, Xu, & Zhou, 2009 and Chen et al., 2016) as these two methods do not calculate the same parameters, and the resulting estimates are not directly comparable unless a very specific set of requirements is satisfied. Such differences might associate with residency patterns of animals, particularly for animals with wide distribution ranges. In cetacean studies, the field surveys are often conducted on a subarea of a population range (Bao et al., 2019; Huang et al., 2018, 2019) where edge effects, transients, and emigration-reimmigration make census results from different survey designs incomparable (Arnason & Schwarz, 1999). Failure to take account of these differences may lead to inappropriate interpretation of survey results (as in Pan, 2013), and hence bias population baselines and management strategies. This issue is seldom discussed in cetacean studies, even in frequently investigated species, such as the Indo-Pacific humpback dolphin (*Sousa chinensis*).

In Chinese waters (including western Taiwan and Hong Kong), the Indo-Pacific humpback dolphin is locally known as the Chinese White Dolphin. Current knowledge has shown there are eight investigated populations (or subpopulations) along the coast of these waters (Chen et al., 2009; Jefferson & Hung, 2004; Jefferson & Smith, 2016; Xu et al., 2015), though there is still some uncertainty about possible groups in some unstudied areas and questions about the distinctness of these putative populations (Bao et al., 2019; Huang et al., 2019; Jefferson & Smith, 2016; Wang et al., 2016; Wu, Wang, Ding, Miao, & Zhu, 2014; Wu et al., 2017b). Abundance estimates of these dolphin subpopulations range from approximately 2,500–2,550 dolphins in the Pearl River Estuary (Chen et al., 2010), through several hundred in the northern Beibu Gulf (Chen et al., 2016), to several dozen in Xiamen (Chen et al., 2018; Wang et al., 2015) and western Taiwan (Wang et al., 2007, 2012). These estimates generally lack information on residency dynamics associated with habitat use. These shortcomings can lead to inappropriate conservation targeting that focuses on local residents, but neglects regular visitors and transients (Alves et al., 2013; Guissamulo & Cockcroft, 2004; Karczmarski, 1999).

Among the eight known humpback dolphin subpopulations, the one in the Dafengjiang River Estuary in the northern Beibu Gulf has been broadly investigated, with population baselines and distribution patterns (Chen et al., 2016; Wu et al., 2017a), habitat configuration (Huang et al., 2019; Wu et al., 2017b), abundance estimates (Chen et al., 2009, 2016; Pan, 2013), and social structure (Chen et al., 2016) studied. These studies present sometimes contradictory information on abundance estimates and humpback dolphin status in the Dafengjiang River Estuary. Pan (2013) claimed that humpback dolphin abundance “increased” from <100 dolphins to approximately 180 dolphins in <10 years based on the “increase” of numbers of photographically identified dolphins, an inappropriate interpretation of photo-identification records, which contradicted long-term changes in distribution gradient and habitat structure of these dolphins in the northern Beibu Gulf (Wu et al., 2017b). Chen et al. (2016) estimated 250 humpback dolphins in the Dafengjiang River Estuary using mark-recapture models, and concluded that these dolphins are socially isolated from humpback dolphins in the Hepu Dugong Reserve, even though there seems no major oceanographic or geographic barrier partitioning these two habitats (Huang et al., 2019; Wu et al., 2017b). Age structure of humpback dolphins in the Dafengjiang River has not been reported, though Pan (2013) reported younger dolphins made up a high proportion and claimed an “increasing” population trend based on this structure and increasing numbers of identified dolphins. None of these studies reported residency patterns for humpback dolphins in the Dafengjiang River Estuary. Such deficiencies happen across most of the humpback dolphin habitats, and are not restricted to the Dafengjiang River Estuary, and they require feasible approaches to resolve them.

In humpback dolphins, mark-recapture studies based on photo-identification records have been used to estimate population size (Chen et al., 2016, 2018; Guissamulo & Cockcroft, 2004; Jutapruet et al., 2015; Parra et al., 2006; Wang et al., 2012), survival rate (Chen et al., 2018; Wang et al., 2012), site fidelity (Chen et al., 2016; Guissamulo & Cockcroft 2004; Karczmarski, 1999; Parra et al., 2006), and ranging patterns (Chen et al., 2011; Hung & Jefferson 2004; Xu et al., 2015). As the pattern of color in the body of these dolphins is highly associated with age-class in the Indo-Pacific humpback dolphin (Jefferson, 2000; Jefferson, Hung, Robertson, & Archer, 2012), photographs used for photo-identification analyses can concurrently provide information on population age-class structure. This makes age-class-specific estimates of abundance (Jutapruet et al., 2015), survival rates, and residency dynamics (Hung & Jefferson, 2004) more feasible. In this study, we estimated abundance, annual survival rates, residency, and emigration probabilities for the humpback dolphins in the Dafengjiang River Estuary in the northern Beibu Gulf, China, based on photo-identification records to help improve our understanding of temporal habitat use patterns.

2 | METHODS

2.1 | Field surveys

Systematically designed field surveys were conducted over the Dafengjiang River Estuary and adjacent waters (Huang et al., 2019; Wu et al., 2017a), including the eastern part of the Qinzhou Bay, Sanniang Bay, and the water

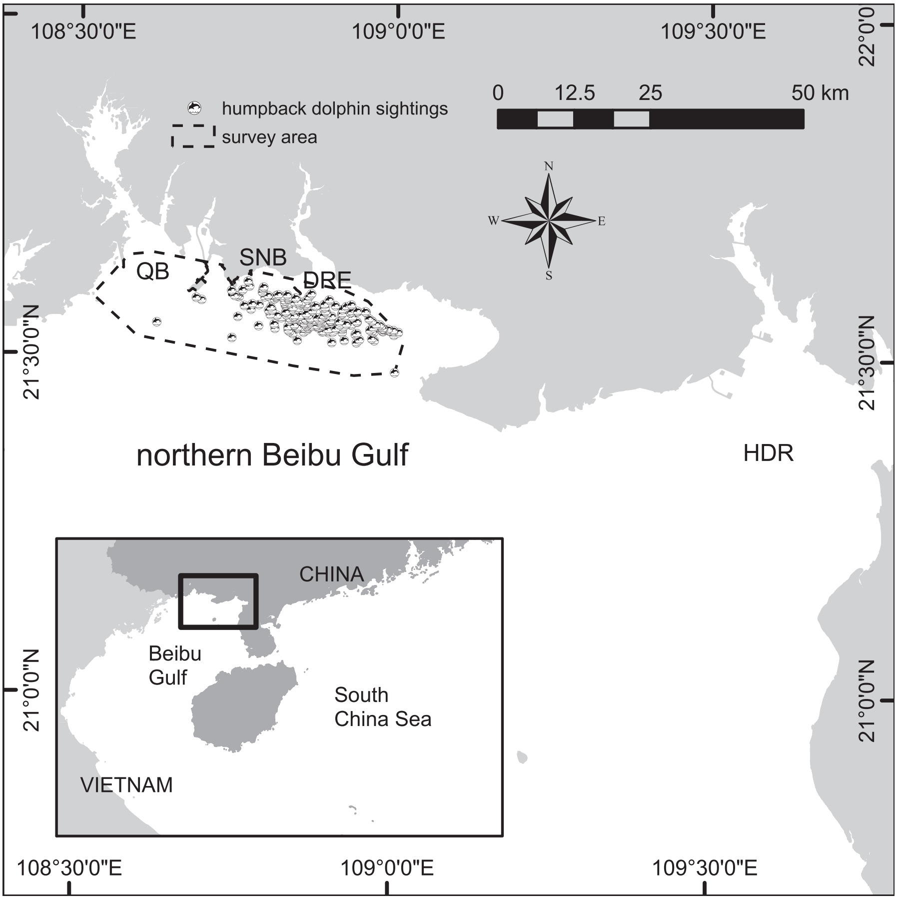

FIGURE 1 Study site: the waters encompassing the Sanniang Bay (SNB), Dafengjiang River Estuary (DRE), and eastern Qinzhou Bay (QB). The actual study area is enclosed by a dashed polygon. Humpback dolphin sightings are labeled.

east to the Dafengjiang River Estuary (Figure 1), 3–6 days per month from August 2013 to March 2016 based on budget/manpower limitations and availability on good weather using a 7.5-m-long fishing boat, powered by one 120HP 4-stroke outboard engine, cruising at approximately 10–15 km/hr under sea state conditions of Beaufort 3 or less. The survey routes adopted a zigzag line design starting at different points opportunistically at each survey trip, to ensure even coverage over the study region (Huang et al., 2019; Wu et al., 2017a). When dolphins were sighted, the survey boat slowed down and followed the dolphin group by moving alongside it for approximately 30 min to take lateral photographs. Distance between dolphins and the survey boat during photographic sampling was kept to at least 30 m in order to reduce potential behavioral disturbances to minimize the "animal sampling effect" that positively or negatively biases results (Urian et al., 2015). During sampling, all dolphins were photographed regardless of their color patterns or markings on the dorsal fin. When photographic sampling was finished, the field survey restarted at the point of departure.

2.2 | Image quality assessment and individual identification

Before conducting photo-identification tasks, image quality of each photograph was assessed and scored between 0 and 100 using five criteria: exposure, size, focus, perpendicularity, and contrast (Urian et al., 2015) of the dolphin image in a photograph (see Supplementary Material for details). Photographs scored under 60 were not used for photo-identification tasks to avoid false positive/negative matches (Urian et al., 2015). Dolphin images were first categorized into UA (unspotted adults), SA/SS (spotted/speckled adults), and SY (mottled and young subadults) age categories (by referencing Jefferson, 2000; Jefferson et al., 2012; Jutapruet et al., 2015). Then, individuals were identified by primary (notches and permanent scars on the dorsal fin) and secondary (shape and position of spots/speckles on dorsal fin and upper body) characteristics. Rake marks were not used as either primary or secondary characters for individual identification, because of their generally short duration, though they can be used to identify different young humpback dolphins in each sighting. For the same individual, the left and right side photographs were associated by matching primary characteristics. All image comparison and individual identification tasks were conducted by one senior researcher to ensure consistent character definition and matching.

For each sighting (i), the number of unidentifiable dolphins, u_i, including calves and young juveniles that seldom carry persistent distinguishable characteristics (Jefferson, 2000), was calculated by the number of mother-calf pairs ($u_{c,i}$) and young unidentifiable juveniles ($u_{j,i}$), $u_i = u_{c,i} + u_{j,i}$. The young unidentifiable juveniles were distinguished by temporary characters (such as rake marks). Then, the ratio of the identifiable dolphins in the ith sighting, θ_i, was calculated by

$$\theta_\iota = \frac{g_i}{g_i + u_i},$$

where g_i is the number of identified dolphins in the ith sighting. A matrix of individual sighting histories was then prepared for following analyses.

2.3 | Modeling exercises: Residency, abundance, and emigration-reimmigration

Capture-mark-recapture exercises based on photo-identification records were applied to understand residency pattern, emigration-reimmigration dynamics, and abundance estimates (Chan & Karczmarski, 2017; Chen et al., 2018). Program SOCPROG (version 2.7; Whitehead, 2009) and program MARK (version 8.2; White & Burnham, 1999) were used to conduct the above analyses. For running program MARK, encounter records of identified dolphins throughout the survey duration were integrated by month (total 32 months). For months without encounter records (either no dolphin encounter, or unable to photograph dolphins due to low accessibility within a survey of 3–6 days), 0 was assigned to the encounter of those months. In the following sections, the term “survey effort” refers to the number of days that encountered humpback dolphins. The term “population” was defined as the dolphins using the study area as a part of their habitats during the study period (Chan & Karczmarski, 2017; Chen et al., 2018). The term “abundance” refers to the number of humpback dolphins in the study area exposed to sampling within a given duration. The terms “emigration” and “reimmigration” refer to the condition when a dolphin moved from the study area to other likely habitats, noted as γ'' (for emigration), and then returned to the study area, noted as $1 - \gamma'$ (Kendall, Nichols, & Hines, 1997).

2.3.1 | Residency

Residency of the humpback dolphins was explored by calculating lagged identification rate (LIR) using Program SOCPROG (Whitehead, 2009). Model performance was evaluated by Akaike information criterion, AIC (Whitehead, 2007). The model with the lowest AIC was selected as the best-fitted model. Standard error (*SE*) and 95% confidence interval (95% CI) of the movement models and derived parameters were estimated by bootstrap method (Chan & Karczmarski, 2017; Whitehead, 2009).

2.3.2 | Abundance of the humpback dolphin

Because the study region is a part of humpback dolphin habitat in the northern Beibu Gulf (Huang et al., 2019; Wu et al., 2017b) and newborn recruitments were frequently observed during the survey period, the humpback dolphin population we observed was thus likely open to demographic (birth) and ecological/behavioral (emigration-reimmigration) events. Accordingly, POPAN modeling in program MARK was used to estimate the humpback dolphin abundance ($\overline{N}$) exposed to sampling during the entire study period (Chan & Karczmarski, 2017; Chen et al., 2018; Jutapruet et al., 2015; Schwarz & Arnason, 1996; Tyne et al., 2014; White & Burnham, 1999). A goodness-of-fit test by program RELEASE GOF in program MARK was applied to test the model suitability (Chen et al., 2018). Candidate models were built with effects on survival (ϕ) and capture (*p*) probabilities, including temporal dependency (*t*), group (age-classes) variation (*g*), and constant over occasions (.). The model with the lowest AIC value and estimable *SE* of parameters was selected as the best-fitted model. Models with ΔAIC < 5 were selected as the plausible models (Chan & Karczmarski, 2017).

Age classes (SY, SA/SS, and UA) were assigned to estimate $\overline{N}$ by age classes ($\overline{N_{SY}}$, $\overline{N_{SA/SS}}$, and $\overline{N_{UA}}$). Number of identifiable dolphins, $\overline{N_M}$, was calculated by sum of $\overline{N_{SY}}$, $\overline{N_{SA/SS}}$, and $\overline{N_{UA}}$. $\overline{N}$ and *SE* of $\overline{N}$ were estimated by

$$\overline{N} = \frac{\overline{N_M}}{\overline{\theta}}$$

and

$$SE(\overline{N}) = \sqrt{\overline{N}^2 \left(\frac{SE(\overline{N_M})^2}{\overline{N_M}^2} + \frac{\mathrm{var}(\theta_i)}{\overline{\theta}^2} \right)},$$

where $\overline{\theta}$ was the mean of θ_i for all sightings (Urian et al., 2015; Chan & Karczmarski, 2017). Log-normal 95% confidence intervals of $\overline{N}$ was calculated by $\overline{N_L} = \overline{N}/C$ as the lower limit and $\overline{N_U} = \overline{N} \times C$ as the upper limit (Burnham, Anderson, White, Brownie, & Pollock, 1987; Santostasi, Bonizzoni, Bearzi, Eddy, & Gimenez, 2016; Tyne et al., 2014), where

$$C = \exp\left\{ 1.96 \sqrt{\ln\left[1 + \left(\frac{SE(\overline{N})}{\overline{N}} \right)^2 \right]} \right\}.$$

2.3.3 | Emigration/reimmigration

We applied a set of capture-mark-recapture models, including program CAPTURE, Cormack-Jolly-Seber model, and Robust Design model, to explore the survival rate and emigration-reimmigration of the humpback dolphins. Program CAPTURE in MARK software was used to test the type of data heterogeneity. Goodness-of-fit TEST 3 and TEST 2 were applied to Cormack-Jolly-Seber model to test the significance of transient effect on survival probabilities and trap-dependence effect on capture probability (Chan & Karczmarski, 2017). Variance inflation factor (c-hat) was measured by bootstrap GOF and median c-hat methods in program MARK, which was further used to adjust the AIC of following Robust Design exercises. Robust Design model were used to measure emigration-reimmigration probabilities (γ'' and $1 - \gamma'$) and abundance fluctuation within study period (Chan & Karczmarski, 2017; Santostasi et al., 2016) because preliminary analyses using SOCPROG indicated a residency pattern with temporary emigration and reimmigration.

The Robust Design analysis (Kendall et al., 1997) allowed a combination of open (emigration/immigration + birth/mortality) condition between primary periods and closed condition within each primary period. Length of the primary period was defined bimonthly to ensure the closed condition is met within the primary period because preliminary movement analysis using SOCPROG estimated 60–80 days of residency inside the study area for this population. Within the primary period, the secondary samples used monthly encounters. Within the primary period, Closed Capture Model (full likelihood heterogeneity *pi*, *p*, and *c*) was selected. To simplify the model parameterization, we tested the combinations of $\phi()$, $\gamma''()$, and $\gamma'()$ with (.), (*g*) or (*t*) combinations, and set other variables (*pi*, *p*, *c*, *f*0) constantly between age classes (.). In addition, we tested the validity of movement patterns other than defaulted Markovian movement ($\gamma'' \neq \gamma'$), including no-movement ($\gamma'' = 0$, $\gamma' = 1$), random movement ($\gamma'' = \gamma'$) and even-movement ($\gamma'' = 1 - \gamma'$) (Chan & Karczmarski, 2017). The model with the lowest c-hat-adjusted AIC value was selected as the best-fitted model and models with $\Delta AIC \leq 5$ were selected as the plausible models. We adopted the c-hat value from Cormack-Jolly-Seber exercises, because no goodness-of-fit test was available for the Robust Design exercises in the program MARK (Chan & Karczmarski, 2017). Pearson correlation was applied to test the significance of correlation between bimonthly abundance and survey efforts. Here, the survey efforts refer to the number of days that encountered humpback dolphins in a month. Differences of temporary emigration (γ'' and γ') and survival rates between age classes were tested by *t*-tests.

3 | RESULTS

From August 2013 to March 2016, 76 field surveys were conducted over 3,009 km of survey effort. In these surveys, 172 groups of humpback dolphins were sighted (Figure 1) and 164 groups were photographed. The number of

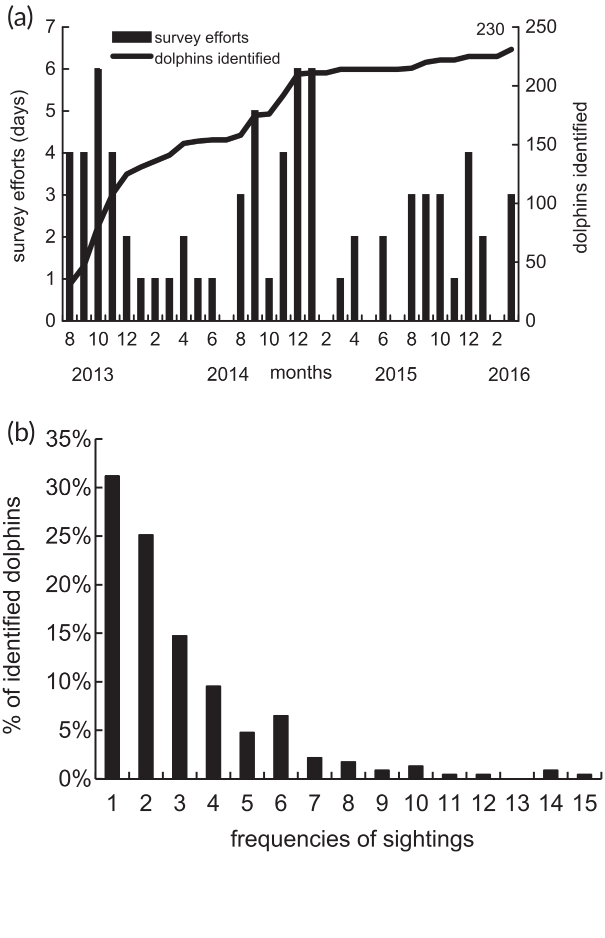

FIGURE 2 Cumulative photo-identified humpback dolphins (a), and frequencies of humpback dolphin sightings (b) throughout the entire survey duration. The survey efforts here referred to the number of days that encountered humpback dolphins.

humpback dolphins per photographed group ranged from 1 to 22 dolphins, on average 6.39 (±*SD* 4.43) dolphins per group. In total, 230 dolphins were identified from more than 30,000 high-quality (image quality scoring >60) photographs (Figure 2a), including 39 UA, 85 SA/SS, and 106 SY dolphins. Among them, 35 mother-calf pairs were recognized. The ϕ estimate was on average 0.840 (±*SD* 0.163) and ranged between 0.333 and 1. For the 230 identified dolphins, 68.83% of dolphins were sighted twice or more (Figure 2b), and eight dolphins were sighted more than 10 times on a monthly basis.

3.1 | Residency

Movement analyses based on LIR revealed a continuous decline throughout the 970 day lag projection and the fastest LIR decline happened between day 80 and day 90 (Figure 3). The movement model "abundance + residency inside + residency outside" was the best-fitted with the lowest AIC value (AIC = 18,319.8). The next candidate model (Emigration/Mortality) was not selected (ΔAIC > 5). In the model "abundance + residency inside + residency outside," the parameter estimates were 83 (*SE* 10.7, 95% CI [66.6, 107.7]) identifiable dolphins (abundance) that spent 78.5 days (*SE* 78.7, 95% CI [35.8, 330.0]) inside and 46.9 days (*SE* 159.32, 95% CI [21.0, 269.1]) outside the survey area.

3.2 | Abundance of the humpback dolphin

Tests of program RELEASE GOF were not significant (TEST 3 + TEST 2, χ^2 = 29.1, 65.3, and 34.4, *df* = 55, 56, and 47, *p* = .99, .19, and .91 for the SY, SA/SS, and UA dolphins, respectively), which suggests a low probability to detect transience or capture heterogeneity effect further. This result suggested the POPAN model fitted the data. The best-fitted model {ϕ(.) *p*(.) pent(.) *N*(*g*)} estimated 149 (*SE* = 8.8, 95% CI [132, 167]) SY dolphins, 121 (*SE* = 7.9, 95% CI [105, 136]) SA/SS dolphins, and 57 (*SE* = 5.4, 95% CI [46, 67) UA dolphins, which gave $\overline{N}$= 389 (*SE* = 19.6, 95% CI [353, 430]) humpback dolphins (Table 1). Based on these estimates, age structure of humpback dolphins in the Dafengjiang River Estuary (Figure 4) was significantly different from that directly calculated from sighting records (χ^2 = 36.8, *p* < .001).

3.3 | Emigration of humpback dolphins within study period

For the data heterogeneity, program CAPTURE adopted the Darroch M(t) model for SY and SA/SS dolphins and the Chao's M(th) model for UA dolphins (Table 2). For the Cormack-Jolly-Seber model, results of goodness-of-fit failed

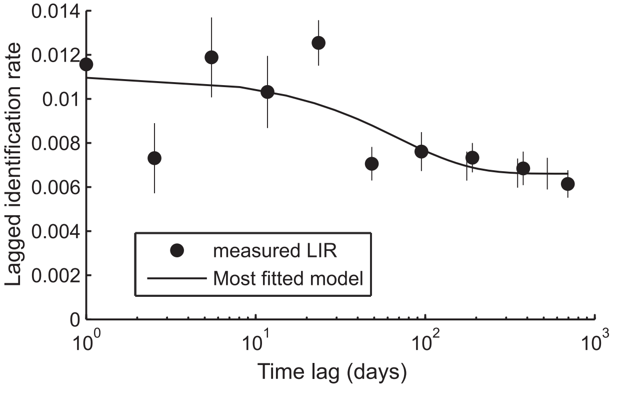

FIGURE 3 Lagged identification rates (LIR) of humpback dolphins in the Dafengjiang River Estuary. The best fitted model (AIC = 18,319.8), "abundance + residency inside + residency outside," indicated the estimated residencies were 78.5 days (*SE* 78.7, 95% CI [35.8, 330.0]) for "residency inside," and 46.9 days (*SE* 159.32, 95% CI [21.0, 269.1]) for "residency outside." Within the study area, the abundance was 83 (SE 10.7, 95% CI [66.6, 107.7]) identifiable dolphins.

TABLE 1 Population abundance ($\overline{N}$) estimates (*SE*, 95% CI) from POPAN modeling, including number of $\overline{N_{SY}}$ (mottled juveniles and young subadults), $\overline{N_{SA/SS}}$ (spotted/speckled adults), and $\overline{N_{UA}}$ (unspotted adults) of Indo-Pacific humpback dolphins in the Dafengjiang River Estuary under various model applications and parameter combinations. $\overline{N_M}$: number of identifiable humpback dolphins, calculated by $\overline{N_M} = \overline{N_{SY}} + \overline{N_{SA/SS}} + \overline{N_{UA}}$. $\overline{N}$ was calculated by $\overline{N} = \frac{\overline{N_M}}{\overline{\theta}}$ where $\overline{\theta}$ is average of percentage of dolphins with identifiable characteristics.

Models	$\overline{N_{SY}}$	$\overline{N_{SA/SS}}$	$\overline{N_{UA}}$	$\overline{N_M}$	$\overline{N}$
$\phi(.)\ p(.)$ pent(.) $N(g)$ QAICc = 52,816.1[a] QAIC weight = 1.00	149 (*SE* 8.8, 95% CI [132, 167])	121 (*SE* 7.9, 95% CI [109, 138])	57 (*SE* 5.4, 95% CI [49, 70])	327 (*SE* 12.9, 95% CI [303, 353])	389 (*SE* 19.6, 95% CI [353, 430])
$\phi(g)\ p(.)$ pent(g) $N(g)$ QAICc = 93,803.1[b] QAIC weight = 0					

Note: Both QAIC and variations were corrected by c-hat (1.186) from Cormack-Jolly-Seber model.
[a]best-fitted model,
[b]not used, $\overline{\theta} = 0.840$.

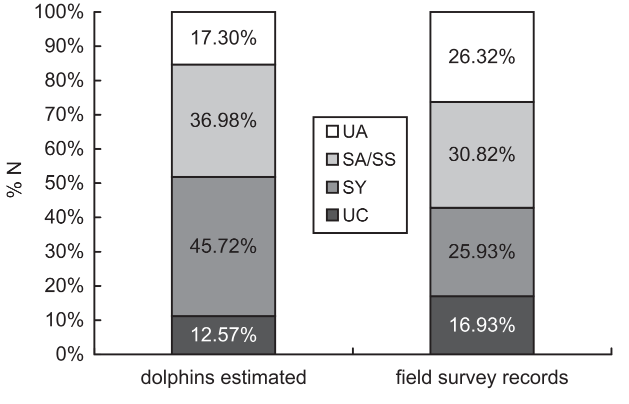

FIGURE 4 Age class compositions derived from abundance estimates based on mark-recapture analyses and from field photo-identification records. UA = unspotted adults, SA/SS = spotted/speckled adults, SY = mottled and young adults, and UC = mother-calf pairs.

TABLE 2 Program CAPTURE results showing the models describing the data heterogeneity in encounter histories.

Age- classes	M(o)	M(h)	M(b)	M(bh)	M(t)	M(th)	M(tb)	M(tbh)	Model suggested
SY	0.16	0	0.49	0	1	0.74	0.36	0.48	Darroch M(t)
SA/SS	0.2	0	0.84	0.02	1	0.93	0.73	0.74	Darroch M(t)
UA	0.12	0.04	0.32	0	0.75	1	0.16	0.45	Chao's M(th)

to find transience effects (TEST 3, χ^2 = 27.8, *df* = 67, *p* = 1.00), nor a trap-dependence effect on capture probability (TEST 2, χ^2 = 100.96, *df* = 91, *p* = .229). The median c-hat was 1.186, which was further used to correct the degree of overdispersion in model selection in following Robust Design exercises.

The best fitted model in Robust Design exercise was the $\{\phi(g)\gamma''(t)\gamma'(t)\ldots\}$ model (QAICc = 725.92, QAICc weight = 0.999), which indicated a significant difference of ϕ estimates between age-classes and temporally dependent emigration probabilities (Table 3). Movement models of no-movement (γ'' = 0, γ' = 1), random movement ($\gamma'' = \gamma'$), and even-movement ($\gamma'' = 1 - \gamma'$) effects poorly fit the data (ΔQAICc > 50) and hence were not used to describe the emigration-reimmigration of the humpback dolphins. The annual survival estimates ϕ were 0.894 (*SE* = 0.017, 95% CI [0.855, 0.924]), 0.971 (*SE* = 0.010, 95% CI [0.941, 0.985]), and 0.976 (*SE* = 0.013, 95% CI [0.935, 0.991]) for the SY, SA/SS, and UA dolphins, respectively. Different ϕ estimates were significant between SY and SA/SS

TABLE 3 Performances of Robust Design exercises arranged in QAICc values. ϕ: annual survival probability, γ″ and γ′: emigration probabilities, c-hat = 1.186, (.): constant throughout occasions, (*t*): time dependent, (*g*): group (age-classes) variation. To simplify the modeling exercises, other variables (probability of heterogeneity mixture: *pi*, capture probability: *p*, recapture probability: *c*) were set constant over time and between groups.

Parameterization	QAICc	ΔQAICCc	QAIc weight	Model likelihood	No. of parameters	Deviance
{ϕ(*g*)γ″(*t*)γ′(*t*)… }	725.92	0.00	1	1	58	987.7
{ϕ(.)γ″(*t*)γ′(*t*)… }	749.13	23.22	0	0	57	1,013
even flow {ϕ(*g*)γ″(*t*) = 1 − γ′(*t*)… }	781.76	55.84	0	0	52	1,058
random movement {ϕ(*g*)γ″(*t*) = γ′(*t*)… }	829.62	103.70	0	0	56	1,096
no movement {ϕ(*g*)γ″(*t*) = 0γ′(*t*) = 1… }	911.86	185.94	0	0	45	1,204

Note: Models of unlisted combinations [ϕ(.), ϕ(*g*)]; [γ″(.), γ″(*g*), γ″(*t*)]; and [γ′(.), γ′(*g*), γ′(*t*)] are not shown due to poor fit (ΔQAICc > 30).

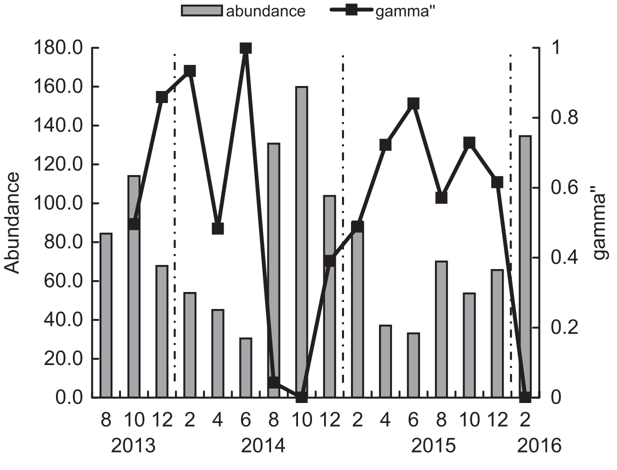

FIGURE 5 Bimonthly abundance estimates and emigration probabilities (gamma″) of humpback dolphins, estimated by Robust Design analysis. A significant negative correlation between abundance and emigration probability (gamma″) was observed (Pearson $r = -0.938$, $\chi^2 = 26.6$, $p < .001$).

(*t*-test = 3.766, $p < .01$) and between SY and UA (*t*-test = 3.810, $p < .01$) but we found no significant difference between SA/SS and UA (*t*-test = 0.318, $p = .38$).

Within the study period from August 2013 to March 2016, bimonthly humpback dolphin abundances fluctuated between 22 and 160 dolphins (Figure 5). We found no significant correlation between bimonthly abundance estimates and the number of days with dolphin encounters (Pearson $r = 0.40$, $\chi^2 = 2.40$, $p = .12$). Abundance estimates were negatively correlated with γ″(*t*) (Pearson $r = -0.938$, $\chi^2 = 26.6$, $p < .001$), but not the γ′(*t*) (Pearson $r = -0.304$, $\chi^2 = 1.02$, $p = .312$).

4 | DISCUSSION

In this study, we estimated the abundance of humpback dolphins exposed to the 3-year survey ranged between 353 and 430 (mean = 389). This number cannot and should not be interpreted literally into a population size estimate, though POPAN modeling is frequently used to report population size (Chan & Karczmarski, 2017; Chen et al., 2016, 2018; Xu et al., 2015). Chen et al. (2016) reported about 250 humpback dolphins in the Dafengjiang River Estuary, about 150 humpback dolphins in nearby Hepu Dugong Reserve habitat and, accordingly, concluded the population size is approximately 400 humpback dolphins in the northern Beibu Gulf. This study, however, showed the true population size estimate is very likely much higher than this value, making the northern Beibu Gulf (and perhaps the entire Beibu Gulf) the habitat of the third-largest known humpback dolphin population in the world, following the Pearl River Estuary (Chen et al., 2010) and eastern Leizuou Peninsula (Xu et al., 2015) habitats. The accurate population size estimate for the humpback dolphin in the northern Beibu Gulf habitat is thought to have explicit gaps in population distinctiveness (or population connectivity) between habitat patches and lacks humpback dolphin baselines in the habitats west of the Dafengjiang River Estuary.

In the Dafengjiang River Estuary, reported humpback dolphin abundance estimates ranged from 98 by photo-ID surveys in the early 2000s (Pan, 2013), 114 by line-transect surveys in the early 2000s (Chen et al., 2009), approximately 250 by photo-ID surveys from the early 2000s to the early 2010s (Chen et al., 2016), to 389 (95% CI [353, 430]) by photo-ID between 2013 and 2016 (this study). These numbers indicate influences of different survey protocols on abundance estimates that include survey ranges, survey frequencies, survey seasons, and survey and analysis methods. In Pan (2013), the abundance was simply the number of photographically identified dolphins and cannot be interpreted as a population estimate. The population increase indeed is the increase of identified dolphins, i.e., the discovery curve (as in Figure 2a). In Chen et al. (2009), the abundance estimate was based on distance sampling surveys, which represents the number of dolphins occurring in the survey region in the given time and does not factor in the number of dolphins outside the survey area. Both Chen et al. (2016) and this study estimated abundance by capture-mark-recapture methods, but reported somewhat different results. With fewer dolphins identified (155 dolphins in Chen et al., 2016 vs. 230 dolphins in this study) and a relatively narrower survey area in the Dafengjiang River Estuary (compared to Wu et al., 2017a), different abundance estimates between these two studies suggest that some dolphins occurring in the uninvestigated region were not sampled in Chen et al. (2016). The other plausible explanation for different abundance estimates between this study and Chen et al. (2016) may arise from increasing use of the Dafengjiang River Estuary habitat in the past decades that is highly associated with the coastal development histories (Wu et al., 2017b). It is our concern that this difference implies a dolphin aggregation from disturbing/disturbed habitats to a lightly disturbed habitat, which has been reported in western Taiwan (Dares, Araújo-Wang, Yang, & Wang, 2017; Karczmarski et al., 2017b) and Xiamen (Wang, Wu, Zhu, & Huang, 2017).

The differences in age structures between calculation methods raise concern about the current population age-structure description for the humpback dolphin in Chinese waters. For convenience, the age class percentages are frequently calculated from sighting records or photographs and used to represent the population age structure (Hung & Jefferson, 2004; Pan, 2013; Xu et al., 2015). This study, however, indicated that this calculation can be substantially biased by underestimating SY but overestimating UA percentages. The biased age class structure description may compromise the baselines of population trends and status classification for the humpback dolphin in Chinese waters. In some reports, the population age structures are arbitrarily connected with population trend and status by claiming "more young dolphins representing a [healthy] population with increasing trends" (Pan, 2013). In practice, the population trend and status classification need to be concluded by demography or trend analyses based on life table and/or survival rate estimates (Huang et al., 2012, 2014). In the Pearl River Estuary, the humpback dolphin population that was estimated to be declining at around 2.5% per year had a high SY percentage (Huang et al., 2012). In western Taiwan, this endemic subspecies had a high SY percentage too, but the estimated rate of decline was even greater than the Pearl River Estuary population (Huang et al., 2014). The results of these analyses show the risk of understating population status when the population trend is arbitrarily connected with the percentage of young dolphins, particularly when the SY dolphins account for a higher percentage in sighting records.

To know the population trend and status, survival and reproductive rates, as well as life history parameters of the population are required (Huang et al., 2012, 2014; Karczmarski, Huang, & Chan, 2017a), which can be obtained from life table (as in Huang et al., 2012) and mark-recapture (Chang et al., 2016; Chen et al., 2018; Wang et al., 2012) data. This study provided abundance and survival rate estimates for the SY, SA/SS, and UA dolphins. However, as the study period was relatively short, compared to Chen et al. (2016), and approximate 30% of the dolphins were sighted only once, using the survival rate estimates of this study to project population trends and viability may be still too premature. Information gaps in reproductive parameters (reproductive rate, calving interval, age at maturity, and lifespan) as well as robust age class-specific survival rate estimates require an additional year's survey to approximate.

4.1 | Fluid habitat-use dynamics

Recent studies indicated the Dafengjiang River Estuary is one of the core habitats for humpback dolphins in the northern Beibu Gulf (Chen et al., 2016; Huang et al., 2019; Wu et al., 2017b). The movement analysis based on LIR values presented a fluid habitat-use dynamics. The humpback dolphins repeatedly moved between the Dafengjiang River Estuary habitat study area and other likely habitats by spending 78.5 days inside and 46.9 days outside the study area. A total of 353–430 humpback dolphins were involved in this fluid habitat use dynamics. An analogous condition may also occur with humpback dolphins in other habitats, which highlights an explicit information gap of population distinctiveness and connectivity that needs to be addressed soon (Huang et al., 2018, 2019).

Results from robust design analysis revealed seasonal changes in humpback dolphin abundances, becoming high in late autumn and winter and low in later spring and summer. This change is not associated with different survey effort since correlation between abundance estimates and monthly survey effort was low. Significant negative correlation between humpback dolphin abundances and emigration probabilities (γ'') strongly indicated a seasonal movement and habitat use pattern. In summer season, when the emigration probability was high, the humpback dolphin might tend to leave the study area and spend a relatively longer duration in other likely habitats. In winter season, in contrast, the humpback dolphin had a stronger tendency to stay within the study area.

Similar seasonality is also reported in the Pearl River Estuary (Chen et al., 2010), which is in concert with regional environmental seasonality (Chen et al., 2010). Recent analysis indicated the habitat configuration and habitat preferences are strongly associated with seasonal patterns of marine primary productivity (indexed by chlorophyll-a concentration) in the northern Beibu Gulf (Huang et al., 2019). In the northern Beibu Gulf, pelagic-neritic herrings, shads, sardines, and menhadens (family Clupeidae) are abundant (Froese & Pauly, 2019; Zhu, 2012). These fish generally seek shallow estuaries and brackish waters with high primary productivity for spawning and nursery sites, which presents strong seasonality in autumn and winter (Froese & Pauly, 2019). They are the primary prey species for humpback dolphins (Barros, Jefferson, & Parsons, 2004; Parra & Jedensjö, 2014). One of the major functions of the Dafengjiang River Estuary habitat is to provide abundant prey resources and foraging feasibility for humpback dolphins (Wu et al., 2017a). The seasonality in abundance and emigration probability is likely associated with spatiotemporal dynamics in prey distribution in the northern Beibu Gulf and this merits further exploration.

Besides the Dafengjiang River Estuary, the Hepu Dugon Reserve is another core humpback dolphin habitat in the northern Beibu Gulf (Chen et al., 2016; Huang et al., 2019; Wu et al., 2017b). Recent studies report different results between distribution gradients (Huang et al., 2019; Wu et al., 2017b) and interhabitat communications (Chen et al., 2016). A cross-matching of photo-ID databases between the Dafengjiang River Estuary and Hepu Dugong Reserve study areas (Chen et al., 2016; Wang et al., 2016) and genetic comparison based on stranded carcasses (Alves et al., 2013; Parra et al., 2018), would help to clarify the above inferences. Clearly, transient dolphins between habitats are important elements in maintaining the (meta)population genetic diversity. Upon these inferences, population surveys currently implemented in Chinese waters may present incomplete population baselines in both distribution and population size estimates (Bao et al., 2019; Huang et al., 2019; Jefferson & Hung, 2004; Jefferson & Smith, 2016; Wu et al., 2017b). Those reported populations or, more precisely, subpopulations, may be comprised of resident dolphin groups inhabiting known habitats. Between these groups, there may be some unidentified groups and habitats. Capture-mark-recapture analyses based on multistate model exercises can provide information on transition probabilities between habitat patches (Brownie, Hines, Nichols, Pollock, & Hestbeck, 1993; Buchanan & Skalski, 2010). Genetic analyses across known habitats (Alves et al., 2013; Lowe & Allendorf, 2010; Parra et al., 2018), cross-matching of individual photo-ID records between neighboring habitats (Chen et al., 2016; Wang et al., 2016), and application of species distribution modeling (Bao et al., 2019; Huang et al., 2018, 2019) will help to clarify the population connectivity in Chinese waters and should be considered in future population baseline investigations.

ACKNOWLEDGMENTS

This study was supported by Ocean Park Conservation Foundation Hong Kong grants (MM01.1516 funding to Dr. S.-L. Huang, and AW02.1718 funding to Dr. H. Wu) and Guangxi Key Laboratory of Beibu Gulf Marine Biodiversity Conservation (No. 2017KA02 to Dr. S.-L. Huang). We sincerely thank anonymous reviewers for providing valuable comments and providing editorial improvements. We also sincerely thank the collaborative efforts from Wen Su, Chao Wang, Jixian Ma, Chunyan Wang, Yijian Fu, and numerous volunteers for participating in field surveys, and Captain Shihe Sun for helping us implement on-board surveys. The authors declare that they have no conflict of interests.

ETHICS STATEMENT

Data collection involved individual photo-identification of free-ranging animals from boats was conducted based on research permits issued by the Office of Chinese White Dolphin Conservation and Protection, Qinzhou City, in compliance with legal and ethical principles of animal welfare. Data collection entailed no handling of animals, no harm caused to animals, and no harassment of animals. Research permits issued by the Office of Chinese White Dolphin Conservation and Protection, Qinzhou City do not require further assessment by an animal ethics committee, and the benign research conducted in the context of this study does not raise ethical issues.

ORCID

Chun-Chieh Wang https://orcid.org/0000-0001-7398-5638
Shiang-Lin Huang https://orcid.org/0000-0002-6133-4851

REFERENCES

Alves, F., Quérouil, S., Dinis, A., Nicolau, C., Ribeiro, C., Freitas, L., … Fortuna, C. (2013). Population structure of short-finned pilot whales in the oceanic archipelago of Madeira based on photo-identification and genetic analyses: Implications for conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *23*, 758–776.

Arnason, A. N., & Schwarz, C. J. (1999). Using POPAN-5 to analyse banding data. *Bird Study*, *46*, S157–S168.

Bao, M., Wang, X., Liu, W., Chen, H. L., Li, Y., Wu, F., … Huang, S.-L. (2019). Habitat protection actions for coastal delphinids in a disturbed environment with explicit information gaps. *Ocean and Coastal Management*, *169*, 147–156.

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*, 179–188.

Brownie, C., Hines, J. E., Nichols, J. D., Pollock, K. H., & Hestbeck, J. B. (1993). Capture-recapture studies for multiple strata including non-Markovian transitions. *Biometrics*, *49*, 1173–1187.

Buchanan, R. A., & Skalski, J. R. (2010). Using multistate mark-recapture methods to model adult salmonid migration in an industrialized river. *Ecological Modelling*, *221*, 582–589.

Buckland, S. T., Anderson, D. R., Burnham, K. P., & Laake, J. L. (1993). *Distance sampling: Estimating abundance of biological populations*. London, UK: Chapman and Hall.

Burnham, K. P., Anderson, D. R., White, G. C., Brownie, C., & Pollock, K. H. (1987). Design and analysis of fish survival experiments based on release-recapture data. *American Fisheries Society Monograph*, 5.

Chan, S. C., & Karczmarski, L. (2017). Indo-Pacific humpback dolphins (*Sousa chinensis*) in Hong Kong: Modelling demographic parameters with mark-recapture techniques. *PLoS ONE*, *12*(3), e0174029.

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.

Chen, B., Xu, X., Jefferson, T. A., Olson, P. A., Qin, Q., Zhang, H., … Yang, G. (2016). Conservation status of the Indo-Pacific humpback dolphin (*Sousa chinensis*) in the northern Beibu Gulf, China. *Advances in Marine Biology*, *73*, 19–139.

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*, 240–247.

Chen, B. Y., Gao, H., Jefferson, T. A., Lu, Y., Wang, L., Li, S., … Yang, G. (2018). Survival rate and population size of Indo Pacific humpback dolphins (*Sousa chinensis*) in Xiamen Bay, China. *Marine Mammal Science*, *34*, 1018–1033.

Chen, B. Y., Zheng, D. M., Ju, J. F., Xu, X. R., Zhou, K. Y., & 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*, 751–762.

Chen, T., Hung, S. K., Qiu, Y., Jia, X., & Jefferson, T. A. (2010). Distribution, abundance, and individual movements of Indo-Pacific humpback dolphins (*Sousa chinensis*) in the Pearl River Estuary, China. *Mammalia*, *74*, 117–125.

Dares, L. E., Araújo-Wang, C., Yang, S. C., & Wang, J. Y. (2017). Spatiotemporal heterogeneity in densities of the Taiwanese humpback dolphin (*Sousa chinensis taiwanensis*). *Estuarine, Coastal and Shelf Science*, *187*, 110–117.

Froese, R., & Pauly, D. (2019). *FishBase* version (08/2019). Retrieved from http://www.fishbase.org

Guissamulo, A., & Cockcroft, V. G. (2004). Ecology and population estimates of Indo-Pacific humpback dolphins (*Sousa chinensis*) in Maputo Bay, Mozambique. *Aquatic Mammals*, *30*, 94–102.

Huang, S.-L., Chang, W.-L., & Karczmarski, L. (2014). Population trends and vulnerability of humpback dolphins *Sousa chinensis* off the west coast of Taiwan. *Endangered Species Research*, *26*, 147–159.

Huang, S.-L., Karczmarski, L., Chen, J., Zhou, R., Lin, W., Zhang, H., … Wu, Y. (2012). Demography and population trends of the largest population of Indo-Pacific humpback dolphins. *Biological Conservation*, *147*, 234–242.

Huang, S.-L., Peng, C., Chen, M., Wang, X., Jefferson, T. A., Xu, Y., … Wu, H. (2019). Habitat configuration for an obligate shallow-water delphinid: The Indo-Pacific humpback dolphin, *Sousa chinensis*, in the Beibu Gulf (Gulf of Tonkin). *Aquatic Conservation: Marine and Freshwater Ecosystems*, *29*, 472–485.

Huang, S.-L., Wang, C.-C., & Yao, C.-J. (2018). Habitat protection actions for the Indo-Pacific humpback dolphin: Baseline gaps, scopes and resolutions for the Taiwanese subspecies. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *28*, 733–743.

Hung, S. K., & Jefferson, T. A. (2004). Ranging patterns of Indo-Pacific humpback dolphins (*Sousa chinensis*) in the Pearl River Estuary, People's Republic of China. *Aquatic Mammals*, *30*, 159–174.

IUCN (International Union for Conservation of Nature) (2001). *Red List categories and criteria* version 3.1. IUCN Species Survival Commission, Gland, Switzerland.

Jefferson, T. A. (2000). Population biology of the Indo-Pacific hump-backed dolphin in Hong Kong waters. *Wildlife Monographs*, *144*, 1–65.

Jefferson, T. A., & Hung, S. K. (2004). A review of the status of the Indo-Pacific humpback dolphin (*Sousa chinensis*) in Chinese waters. *Aquatic Mammals*, *30*, 149–158.

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.

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*, 84–104.

Jutapruet, S., Huang, S.-L., Li, S., Lin, M., Kittiwattanawong, K., & Pradit, S. (2015). Population size and habitat characteristics of the Indo-Pacific humpback dolphin (*Sousa chinensis*) off Donsak, Surat Thani, Thailand. *Aquatic Mammals*, *41*, 129–142.

Karczmarski, L. (1999). Group dynamics of humpback dolphins (*Sousa chinensis*) in the Algoa Bay region, South Africa. *Journal of Zoology*, *249*, 283–293.

Karczmarski, L., Huang, S.-L., & Chan, S. C. Y. (2017a). Threshold of long-term survival of a coastal delphinid in anthropogenically degraded environment: Indo-Pacific humpback dolphins in Pearl River Delta. *Scientific Reports*, *7*, 42900.

Karczmarski, L., Huang, S.-L., Wong, W.-H., Chang, W.-L., Chan, S. C. Y., & Keith, M. (2017b). Distribution of a coastal delphinid under the impact of long-term habitat loss: Indo-Pacific humpback dolphins off Taiwan's west coast. *Estuaries and Coasts*, *40*, 594–603.

Kendall, W. L., Nichols, J. D., & Hines, J. E. (1997). Estimating temporary emigration using capture–recapture data with Pollock's robust design. *Ecology*, *78*, 563–578.

Lowe, W. H., & Allendorf, F. W. (2010). What can genetics tell us about population connectivity? *Molecular Ecology*, *19*, 3038–3051.

Pan, W. S. (2013). *The white dolphins* (Sousa chinensis) *of Qinzhou*. Beijing, China: Peking University Press.

Parra, G. J., & Jedensjö, M. (2014). Stomach contents of Australian snubfin (*Orcaella heinsohni*) and Indo-Pacific humpback dolphins (*Sousa chinensis*). *Marine Mammal Science*, *30*, 1184–1198.

Parra, G. J., Cagnazzi, D., Jedensjö, M., Ackermann, C., Frere, C., Seddon, J., … Krützen, M. (2018). Low genetic diversity, limited gene flow and widespread genetic bottleneck effects in a threatened dolphin species, the Australian humpback dolphin. *Biological Conservation*, *220*, 192–200.

Parra, G. J., Schick, R., & Corkeron, P. J. (2006). Spatial distribution and environmental correlates of Australian snubfin and Indo-Pacific humpback dolphins. *Ecography*, *29*, 396–406.

Santostasi, N. L., Bonizzoni, S., Bearzi, G., Eddy, L., & Gimenez, O. (2016). A robust design capture-recapture analysis of abundance, survival and temporary emigration of three odontocete species in the Gulf of Corinth, Greece. *PLoS ONE*, *11* (12), e0166650.

Schwarz, C. J., & Arnason, A. N. (1996). A general methodology for the analysis of capture-recapture experiments in open populations. *Biometrics*, *52*, 860–873.

Thomas, L., Buckland, S. T., Rexstad, E. A., Laake, J. L., Strindberg, S., Hedley, S. L., … Burnham, K. P. (2010). Distance software: Design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology*, *47*, 5–14.

Tyne, J. A., Pollock, K. H., Johnston, D. W., & Bejder, L. (2014). Abundance and survival rates of the Hawai'i Island associated spinner dolphin (*Stenella longirostris*) stock. *PLoS ONE*, *9*(1), e86132.

Urian, K., Gorgone, A., Read, A., Balmer, B., Wells, R. S., Berggren, P., … Hammond, P. S. (2015). Recommendations for photo-identification methods used in capture-recapture models with cetaceans. *Marine Mammal Science*, *31*, 298–321.

Wang, J. Y., Yang, S. C., Fruet, P. F., Daura-Jorge, F. G., & Secchi, E. R. (2012). Mark-recapture analysis of the critically endangered Eastern Taiwan Strait population of Indo-Pacific humpback dolphins (*Sousa chinensis*): Implications for conservation. *Bulletin of Marine Science*, *88*, 885–902.

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*, 157–165.

Wang, X., Wu, F., Chang, W.-L., Hou, W., Chou, L.-S., & Zhu, Q. (2016). 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*, 390–399.

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*, 964–971.

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*, 643–652.

White, G. C., & Burnham, K. P. (1999). Program MARK: Survival estimation from populations of marked animals. *Bird Study*, *46*, S120–S139.

Whitehead, H. (2007). Selection of models of lagged identification rates and lagged association rates using AIC and QAIC. *Communications in Statistics - Simulation and Computation*, *36*, 1233–1246.

Whitehead, H. (2009). SOCPROG programs: Analysing animal social structures. *Behavioral Ecology and Sociobiology*, *63*, 765–778.

Wu, F., Wang, X., Ding, X., Miao, X., & Zhu, Q. (2014). Distribution pattern of Indo-Pacific humpback dolphins (*Sousa chinensis*) along coastal waters of Fujian Province, China. *Aquatic Mammals*, *40*, 341–349.

Wu, H., Jefferson, T. A., Peng, C., Liao, Y., Huang, H., Lin, M., … Huang, S.-L. (2017a). Distribution and habitat characteristics of the Indo-Pacific humpback dolphin (*Sousa chinensis*) in the northern Beibu Gulf, China. *Aquatic Mammals*, *43*, 219–228.

Wu, H., Xu, Y., Peng, C., Liao, Y., Wang, X., Jefferson, T. A., … Huang, S.-L. (2017b). Long-term habitat loss in a lightly-disturbed population of the Indo-Pacific humpback dolphin, *Sousa chinensis*. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *27*, 1198–1208.

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*, 1–9.

Zhao, X., Barlow, J., Taylor, B. L., Pitman, R. L., Wang, K., Wei, Z., … Wang, D. (2008). Abundance and conservation status of the Yangtze finless porpoise in the Yangtze River, China. *Biological Conservation*, *141*, 3006–3018.

Zhu, Q. (2012). *Research of habitat environment of Indo-Pacific humpback dolphin*, Sousa chinensis, *in Sanniang Bay*, *Qinzhou City*, *Guanxi Province*, *China*. Xiamen, China: The Third Institute of Oceanography, State Oceanic Administration.

How to cite this article: Peng C, Wu H, Wang X, et al. Abundance and residency dynamics of the Indo-Pacific humpback dolphin, *Sousa chinensis*, in the Dafengjiang River Estuary, China. *Mar Mam Sci*. 2020;36:623–637. https://doi.org/10.1111/mms.12663