


RESEARCH ARTICLE

Habitat configuration for an obligate shallow-water delphinid: The Indo-Pacific humpback dolphin, *Sousa chinensis*, in the Beibu Gulf (Gulf of Tonkin)

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Abstract

1. Habitat configuration is an important baseline to delineate protected area design, refine impact mitigation measures and define habitat protection plans for threatened species. For coastal delphinids, outlining their habitat configuration becomes a real challenge when faced with large distribution ranges that straddle international borders, leaving broad information gaps in uninvestigated areas.
2. This study projected likely habitats of Indo-Pacific humpback dolphins, *Sousa chinensis*, in the Beibu Gulf (Gulf of Tonkin) based on occurrence data and remotely sensed oceanographic characteristics. Net primary productivity was derived to measure the ecosystem service of humpback dolphin habitats.
3. Bathymetry and chlorophyll-*a* concentration are major variables contributing to humpback dolphin habitat configuration, which is characterized by shallow water depth and high primary productivity. Three major, likely habitats were identified in the northern Beibu Gulf from western Leizhou Peninsula to the China-Vietnam border, western Gulf of Tonkin from the Red River estuary to the central coast of Vietnam, and south-western Hainan Island. Less than 9% of likely habitats are currently protected by marine protected areas.
4. Affinity to high primary productivity and shallow depths implies that prey abundance and foraging efficiency influence habitat selection by Indo-Pacific humpback dolphins. Anthropogenic activities potentially altering oceanographic characteristics may impact regional marine ecosystem functions, and hence habitat configuration.
5. Habitat protection actions for Indo-Pacific humpback dolphins include implementing coordinated and systematic surveys in major habitats, associating core habitat protection with protected area networks and maritime function zoning, ensuring ecosystem function integrity within major habitats, and reducing both explicit lethal impacts and implicit anthropogenic impacts from activities that change oceanographic features. The habitat protection plan should not only consider marine habitats, but also adjacent coastal landscapes and river catchments.

This requires coordination, collaboration and information sharing between scientific research teams, government policy representatives, non-governmental organizations, local communities and other interested stakeholders.

KEYWORDS

ecosystem services, habitat configuration, habitat protection actions, Maxent modelling, net primary productivity, oceanographic characteristics, *Sousa chinensis*

1 | INTRODUCTION

When planning habitat protection actions (HPAs) for threatened animals, habitat configuration is an important baseline to delineate protected area design, refine impact mitigation measures and define protection scope (Huang, Wang, & Yao, 2018; Ross et al., 2010; Stralberg et al., 2011; Wu, Xu et al., 2017). For many marine megafauna species, their habitat configuration baselines are incomplete because their distribution ranges are often too wide to be comprehensively investigated, leaving information gaps throughout the species' range (Amaral, Smith, Mansur, Brownell, & Rosenbaum, 2017; Huang et al., 2018; Jefferson & Smith, 2016; Wu, Wang, Ding, Miao, & Zhu, 2014; Wu, Xu, et al., 2017). HPAs designed upon those incomplete baselines may not be able to provide sufficient protection, and hence hinder conservation efficacy (Devillers et al., 2015; Zhao, Wang, Turvey, Taylor, & Akamatsu, 2013). The need to bridge information gaps in habitat configuration to consolidate HPA planning has imposed serious challenges within habitat protection campaigns. This challenge is particularly emphasized for marine species living near intense anthropogenic activities (Chen, Huang, & Han, 2014; Huang et al., 2018; Ross et al., 2010).

Among marine species, dolphins and porpoises inhabiting coastal and estuarine waters are particularly vulnerable to anthropogenic activities (Balmer et al., 2013; Karczmarski et al., 2017; Ross et al., 2010). The Indo-Pacific humpback dolphin (*Sousa chinensis*) may be among the most vulnerable species, due to its high affinity for shallow and highly productive waters (Chen et al., 2016; Huang et al., 2018; Jefferson, 2000; Jutapruet, Intongcome, Wang, Kittiwattanawong, & Huang, 2017; Wu, Jefferson et al., 2017). HPAs for Indo-Pacific humpback dolphins frequently call for actions to protect vital habitats (Chen, Zheng, Yang, Xu, & Zhou, 2009; Huang et al., 2018; Jefferson, Hung, & Würsig, 2009; Ross et al., 2010; Wu, Jefferson, et al., 2017; Wu, Xu, et al., 2017). Conservation measures for Indo-Pacific humpback dolphins, however, sometimes fail to refer to vital habitat baselines. One of the typical conditions is that a protected area no longer protects core habitats of the humpback dolphin (Wang, Wu, Zhu, & Huang, 2017). In practice, vital habitat baselines are often derived from occurrence data from field surveys, such as the kernel density estimates or minimal convex polygon (Chen et al., 2016; Jutapruet et al., 2017; Wang et al., 2017; Wu, Jefferson, et al., 2017; Xu et al., 2015). These measurements seldom associate vital habitats with oceanographic features and ecosystem functions, and also restrict the scope of the vital habitat baselines to the survey area.

HPAs based on these vital habitat baselines are therefore subject to insufficient scope, thus superficially protecting known habitats but ignoring uninvestigated regions (Devillers et al., 2015; Huang et al., 2018).

In Chinese waters, occurrence of Indo-Pacific humpback dolphins is reported from several 'discontinuous' habitats (Chen et al., 2016; Chen, Hung, Qiu, Jia, & Jefferson, 2010; Jefferson, 2000; Li et al., 2016; Wang, Yang, Hung, & Jefferson, 2007; Wu, Jefferson, et al., 2017; Wu, Xu, et al., 2017; Xu et al., 2015). This 'discontinuity', however, sometimes comes from the lack of systematic surveys rather than true habitat configuration, and thus should not be regarded as habitat configuration baselines (Jefferson & Hung, 2004; Jefferson & Smith, 2016; Wu, Xu, et al., 2017). To bridge those information gaps, species distribution modelling based on systematically surveyed data has been shown to be a valid tool, and used with several cetacean species (Carlucci et al., 2016; Garaffo et al., 2011; Gerrodette & Eguchi, 2011; Pitchford et al., 2016), including the Indo-Pacific humpback dolphin in Taiwanese waters (Huang et al., 2018). The use of remote-sensing data provides a tool to access environmental variables over wide spatial scales (Huang et al., 2018; West et al., 2016; Wu, Jefferson, et al., 2017). Approaches combining the power of species distribution modelling and the scale of remote-sensing variables may provide a tool to map likely habitat configuration of humpback dolphins over a macroscopic spatial scale. These techniques can concurrently associate habitat configuration of target animals with habitat characteristics and ecosystem functions (Huang et al., 2018).

In the Beibu Gulf (as it is called in China), or Gulf of Tonkin (as it is referred to in Vietnam), occurrence of Indo-Pacific humpback dolphins is systematically surveyed at Hepu Dugon Reserves (Chen et al., 2016) and the Dafengjiang River estuary and its adjacent waters (Chen et al., 2016; Wu, Jefferson, et al., 2017; Wu, Xu, et al., 2017). Besides these two sites, sporadic reports of humpback dolphin occurrence include the Red River estuary in Vietnam (Smith et al., 2003) and south-western Hainan Island in China (Li et al., 2016). Information gaps in humpback dolphin habitat configuration are evident and need to be filled. This study used the Maxent model (Merow, Smith, & Silander Jr, 2013; Phillips, Anderson, & Schapire, 2006; Phillips, Dudík, & Schapire, 2017), a species distribution model with high prediction accuracy and comprehensive uses (Elith et al., 2011; Pitchford et al., 2016), to configure likely habitats for humpback dolphins in the Beibu Gulf. Predicted results substantially enlarge the current scope of humpback dolphin habitat baselines in the Beibu Gulf. Ecosystem

significance of humpback dolphin habitats is addressed in this study. Based on these results, HPA scopes for Indo-Pacific humpback dolphins are recommended.

2 | MATERIALS AND METHODS

2.1 | Data collection and preparation

The study region included the inshore and offshore waters of the Beibu Gulf (Gulf of Tonkin) from the western Leizhou Peninsula to central coast of Vietnam (18.00–21.94°N, 105.61–110.08°E, Figure 1). Presence data on humpback dolphins were referenced to the latest sighting records based on systematically designed surveys between 2013 and 2016 in the Dafengjiang River estuary and adjacent waters (Wu, Jefferson, et al., 2017), with equally stratified sampling effort within the survey area. Field surveys were conducted using a 7.5 m long boat cruising at 10–15 km/hr under a sea state condition of Beaufort 3 or less. The survey routes adopted a zigzag-line design starting at different points opportunistically on each survey trip, to ensure even coverage over the study region. When dolphins were sighted, the GPS position was recorded first. Then, the survey boat slowed down and followed the dolphin group by moving alongside it for approximately 30 min to take lateral photographs for photo-identification (photo-ID) analyses. When photographic sampling was finished, the field survey restarted at the point of departure from the line. All GPS records of sightings (in dd.dddd unit system) were seasonally aligned.

Environmental layers used for mapping likely habitats of humpback dolphins, including bathymetry, chlorophyll-*a* (chl_a) concentration

and sea-surface temperature (SST), were prepared by accessing public web databases (Table 1). For the bathymetry layer (Figure 2a), the data between 0 and –300 m of the ETOPO 1 Global Relief Model (<https://www.ngdc.noaa.gov/mgg/global/>, Amante & Eakins, 2009) over the study region were extracted, because humpback dolphins exclusively occur in coastal and shallow (up to –30 m depth) waters across the species' distribution range (Jefferson, 2000; Jutapruet et al., 2017; Wu, Jefferson, et al., 2017). For both chl_a (Figure 2b) and SST (Figure 2c) layers, level-3 seasonal climatology of the Visible Infrared Imaging Radiometer (VIIRS; NASA Goddard Space Flight Center, Ocean Biology Processing Group) data were downloaded from the oceancolor database (<https://oceancolor.gsfc.nasa.gov/>). The bathymetry layer was resampled to 4 km grid size, the grid size of VIIRS composites. All layers were then transformed into ASCII files with unified spatial extent for running Maxent exercises.

TABLE 1 Remotely-sensed habitat characteristics used for predicting likely habitats for Indo-Pacific humpback dolphins in the Beibu Gulf

Variable	Characteristics	Spatial resolution
Bathymetry	ETOPO 1 (https://www.ngdc.noaa.gov/mgg/global/)	1 arc-min
Chlorophyll- <i>a</i> concentration	Level 3 seasonal climatology (https://oceancolor.gsfc.nasa.gov/cgi/l3)	4 km
Sea-surface temperature	Level 3 seasonal climatology (https://oceancolor.gsfc.nasa.gov/cgi/l3)	4 km

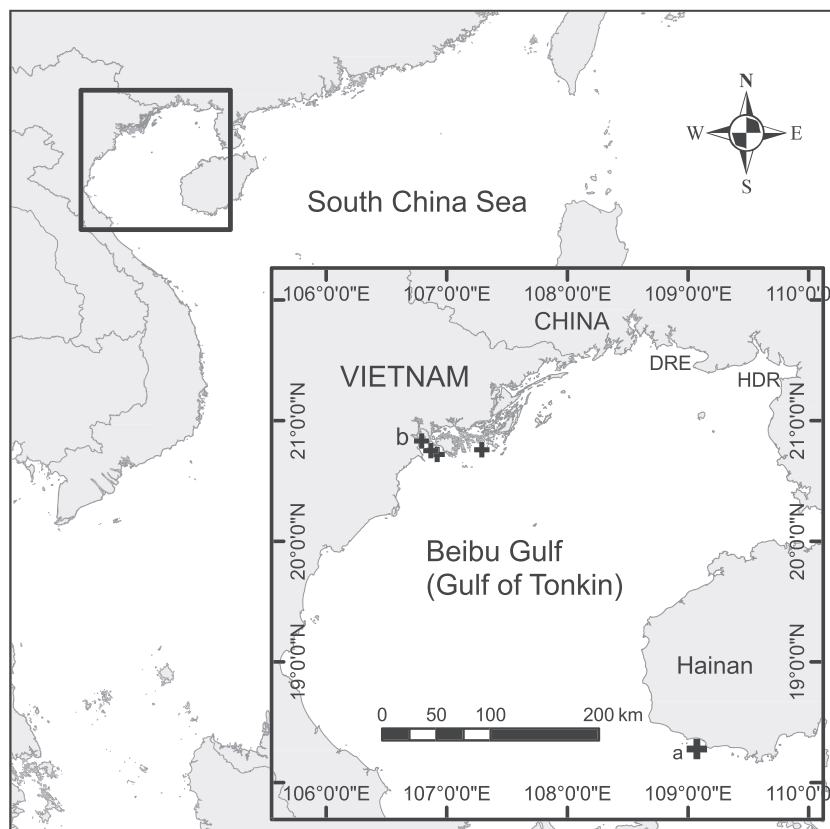


FIGURE 1 The Beibu Gulf study area, which is surrounded by China and Vietnam. Distribution of the Indo-Pacific humpback dolphin has been reported in the Red River estuary (RRE) in Vietnam and Dafengjiang River estuary (DRE), Hepu Dugong Reserve (HDR) and southern-west of Hainan in China. Black crosses indicate humpback dolphin sightings from opportunistic surveys in Hainan (a) and Vietnam (b) (Li et al., 2016; Smith et al., 2003) that were not used in the Maxent modelling

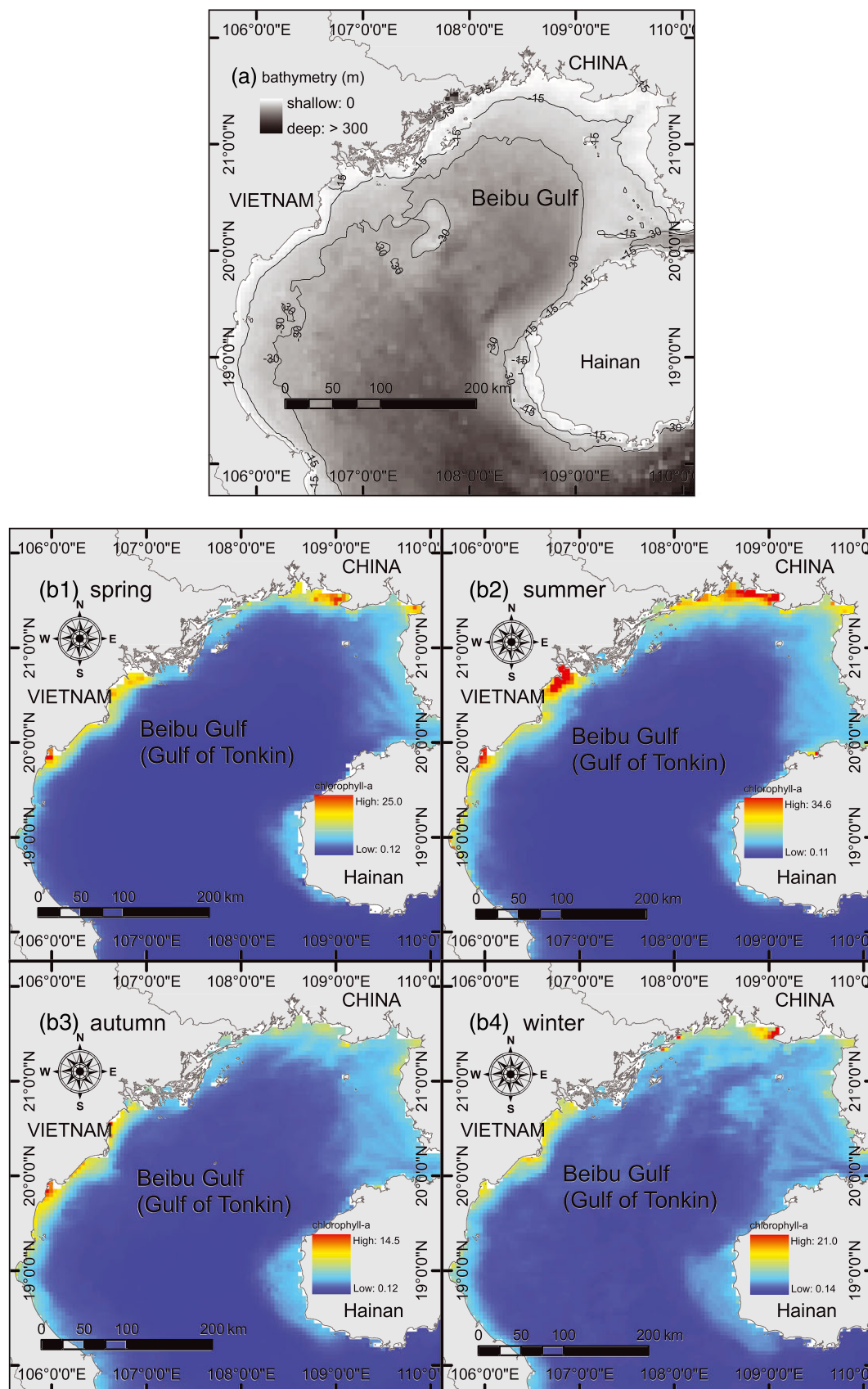


FIGURE 2 Environmental layers over the Beibu Gulf. (a) Bathymetry layer with data between 0 and ~300 m deep. Remotely-sensed chlorophyll-*a* (mg m^{-3}) concentration in spring (b1), summer (b2), autumn (b3) and winter (b4). Sea-surface temperature ($^{\circ}\text{C}$) in spring (c1), summer (c2), autumn (c3) and winter (c4). Net primary productivity ($\text{mg C m}^{-2} \text{day}^{-1}$) in (d.1) spring (d1), summer (d2), autumn (d3) and winter (d4). Colour hue was adjusted to unify scales and the contrast calibrated to highlight regional peaks

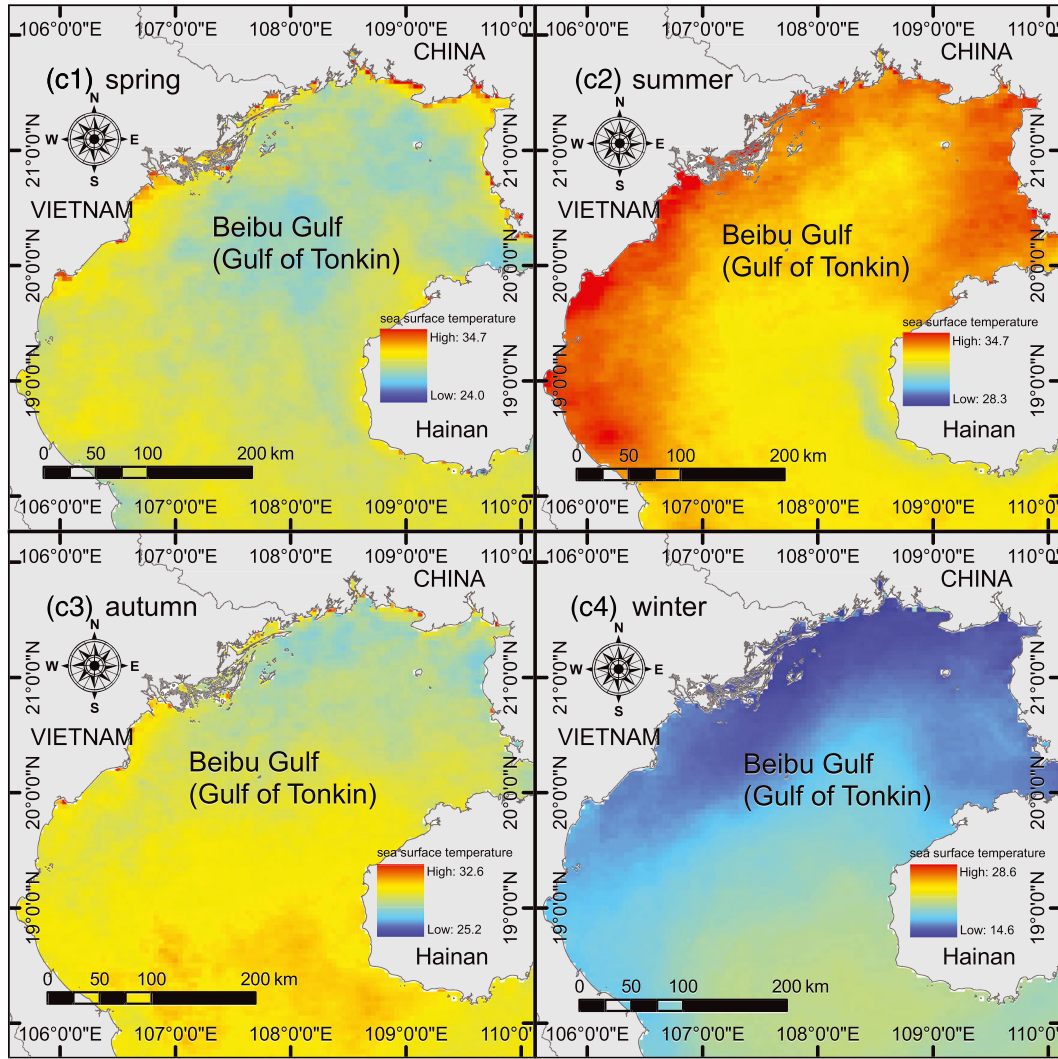


FIGURE 2 Continued.

2.2 | Net primary productivity and carbon absorption

Net primary productivity (NPP, $\text{mg C m}^{-2} \text{ day}^{-1}$) for each season in the Beibu Gulf (Figure 2d) was derived by the Eppley vertically generalized production model (Eppley, 1972; Morel, 1991; <http://www.science.oregonstate.edu/ocean.productivity/>) by:

$$\text{NPP} = \text{chl}_a \times \text{pb_opt}(\text{SST}_s) \times f(\text{PAR}_s) \times \text{Ze}_s \times D_s, \quad (1)$$

Eppley, 1972; Morel, 1991:

$$\text{pb_opt}(\text{SST}_s) = 1.54 \times 10^{0.0275 \times \text{SST}_s - 0.07}, \quad (2)$$

and Behrenfeld & Falkowski, 1997; Platt & Sathyendranath, 1993:

$$f(\text{PAR}_s) = 0.66125 \times \frac{\text{PAR}_s}{\text{PAR}_s + 4.1}, \quad (3)$$

where PAR, Ze and D are the seasonal photosynthetically available radiation, euphotic depth and daylight length respectively. PAR and Ze were referenced to level-3 seasonal climatology composites of VIIRS data and downloaded from the oceancolor database. To

measure ecosystem service, NPP values were further derived into carbon dioxide (CO_2) absorption (CS, $\text{kt CO}_2 \text{ km}^{-2} \text{ year}^{-1}$) by:

$$\text{CS} = \sum \text{NPP}_s \times \text{LH}_s \times D_s \times 3.667, \quad (4)$$

where NPP_s , LH_s and D_s are the sum of NPP, the area of either likely core habitat (LCH) or likely habitat maximum (LHM), and number of days during season s (s = spring, summer, autumn, winter) respectively (<http://www.science.oregonstate.edu/ocean.productivity/>). The coefficient 3.667 is derived from CO_2 equivalence ($44 \text{ g CO}_2 / 12 \text{ g C}$).

2.3 | Likely habitat mapping and habitat characteristics

Maxent software (Phillips et al., 2017, https://biodiversityinformatics.amnh.org/open_source/maxent/) was used to project likely habitats of the Indo-Pacific humpback dolphin in the Beibu Gulf. The Maxent exercises were run by adopting 30% randomly selected sightings data for testing points, running 250 bootstrapping replicates, while each replicate ran 5,000 iterations, and writing cumulative results (Huang

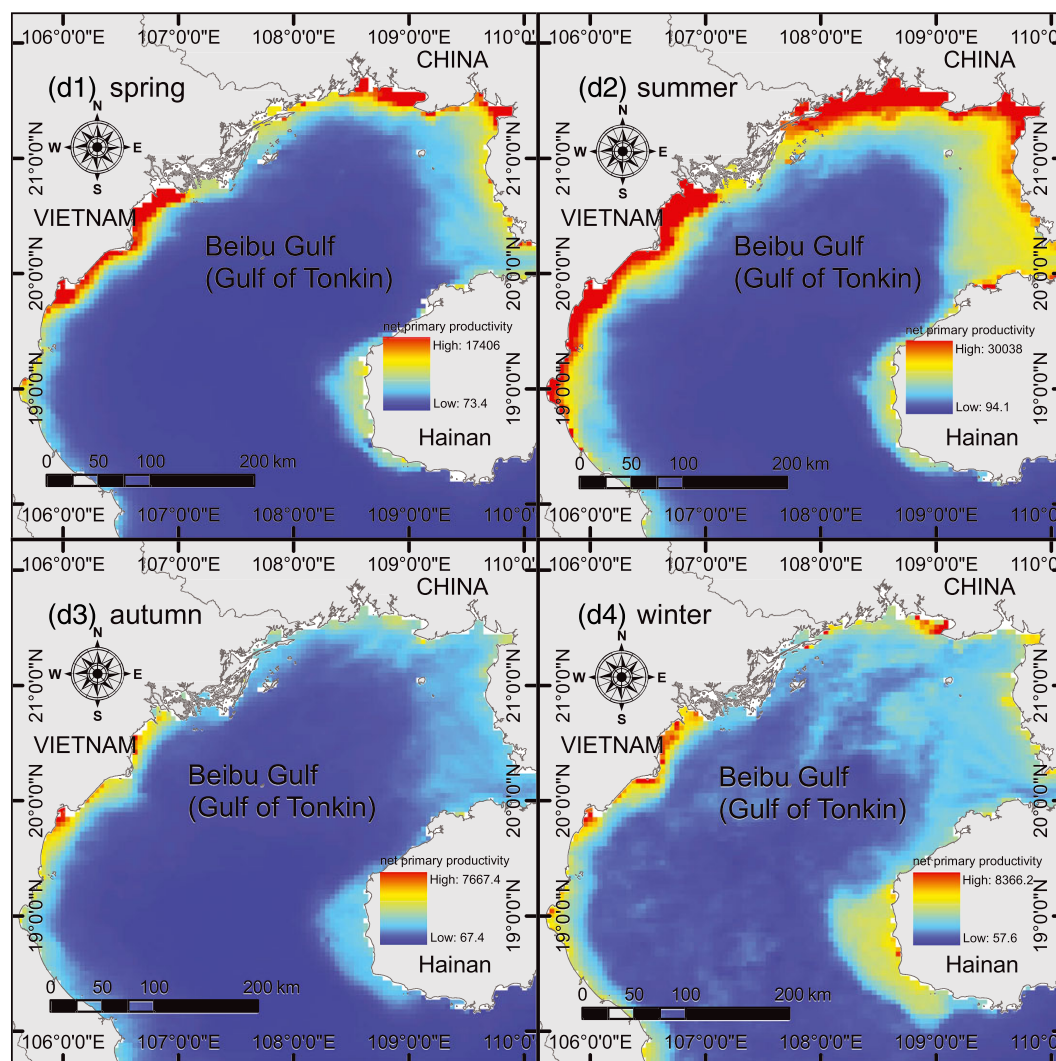


FIGURE 2 Continued.

et al., 2018). Sightings in each season were fitted to seasonal environmental layers, generating seasonal outputs. Likely habitats of humpback dolphins were identified by the median of all cumulative results, with areas enclosing 35% or higher cumulative probabilities identified as LCHs, and areas within 5–35% cumulative probabilities as LHM (Huang et al., 2018). Polygons outlining likely habitat configuration of humpback dolphins were projected onto a UTM49N coordinate system. Areas of LCH and LHM of each season were calculated by ArcMap 9.3. Finally, LCH and LHM were further superimposed to current (UNEP-WCMC, 2017; <https://protectedplanet.net/>) and ongoing protected areas (Dr Haipin Wu, unpublished data) to show the current percentage of habitat protection.

Variable (bathtmetry, chl_a and SST) contributions were used to measure the relative significance of environmental layers in likely habitat configuration of Indo-Pacific humpback dolphins. A two-sample *t*-test was used to test the differences of variable contributions between variables and between seasons. Habitat characteristics were summarized by zonal statistics in ArcMap 9.3. Differences of chl_a and SST between various habitat extents and among different seasons in the same habitat extents (either LCH or LHM) were tested by two-sample *t*-test.

3 | RESULTS

From August 2013 to June 2016, 82 field surveys were conducted over a 620 km² area, which recorded 194 humpback dolphin sightings (Figure 3a). Based on these sighting records, likely habitats of Indo-Pacific humpback dolphins in the Beibu Gulf were projected for spring (Figure 3b), summer (Figure 3c), autumn (Figure 3d) and winter (Figure 3e). The likely habitats were smallest during spring (885.2 and 4,136.29 km² for LCH and LHM respectively) and the largest in winter (2801.25 and 9,537.50 km² for LCH and LHM respectively) (Table 2). Combining all seasonal predictions, three major habitats of Indo-Pacific humpback dolphins were identified in the Beibu Gulf, including the northern Beibu Gulf from the western Leizhou Peninsula to the northern Vietnamese coast near the China–Vietnam border, the western Beibu Gulf from the Red River estuary to the central Vietnamese coast, and the habitat along the south-western coast of Hainan Island (Figure 3f). Among those likely habitats, 13.1% of LCHs and 6.8% of LHMs, or total 8.6% of likely habitats, were protected by marine protected areas (Figure 3f). Table 2 summarizes areas and habitat characteristics of humpback dolphin likely habitats by season.

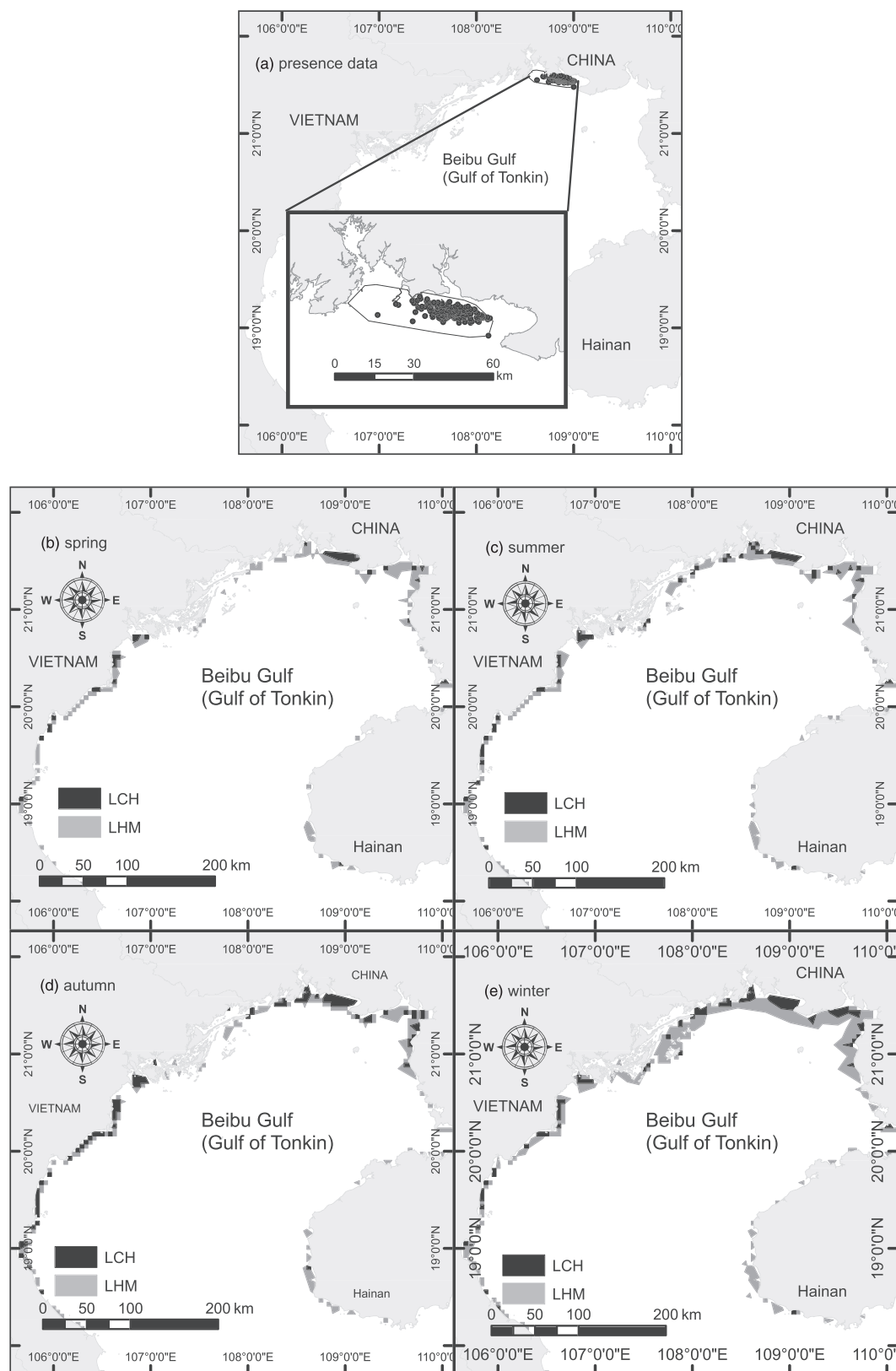


FIGURE 3 Presence data used for running Maxent modelling (a) and likely habitats of Indo-Pacific humpbacks dolphin in spring (b), summer (c), autumn (d) and winter (e), including likely core habitats (LCH) and likely habitat maxima (LHM). Merged likely habitats (f) were further superimposed with marine protected areas in the Beibu Gulf

Bathymetry, chl_a and SST contributed to humpback dolphin distribution differently in different seasons (Figure 4). Bathymetry had the highest influence in summer (62.09%, SD = ±4.22%), and its

contribution gradually declined from autumn (50.95%, SD = ±3.39%), through winter (44.02%, SD = ±16.11%) to spring (37.04%, SD = ±4.06%). Chl_a contributions were high in spring (55.58%,

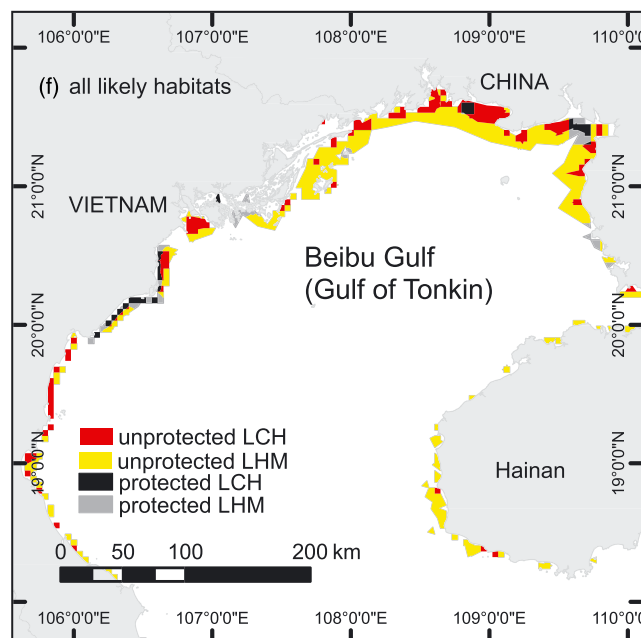


FIGURE 3 Continued.

SD = $\pm 5.27\%$) and autumn (48.68%, SD = $\pm 3.27\%$) and became the lowest in winter (28.02%, SD = $\pm 8.41\%$). SST did not show a significant contribution from spring to autumn, until winter (27.96%, SD = $\pm 22.38\%$), which is comparable to chl a importance (two-sample t -test, $t = 0.045$, $P = 0.96$).

In the LCHs, both chl a (Figure 5a) and NPP (Figure 5c) were significantly higher than the surrounding LHM ($t = 11.78$ and 10.376 respectively, $P < 0.001$) and background waters ($t = 20.83$ and 21.59 respectively, $P < 0.001$). Chl a and NPP in LHM were significantly higher than in adjacent background waters as well ($t = 27.27$ and 18.16 respectively, $P < 0.001$). SST generally ranged between 26 and 31°C from spring to autumn, but it dropped substantially to 19–23°C in winter (Figure 5b). The highest NPP occurred in summer (Figure 5c), 8039.8 (SD = ± 5232.6) mg C m $^{-2}$ day $^{-1}$ in the LCHs and 4549.2 (SD = ± 2504.6) mg C m $^{-2}$ day $^{-1}$ in the LHM, and was lowest during winter, 869.4 (SD = ± 419.6) mg C m $^{-2}$ day $^{-1}$ in the LCHs and 613.8 (SD = ± 220.3) mg C m $^{-2}$ day $^{-1}$ in the LHM (Figure 5c). Applying to likely habitat areas (Table 2) and seasonal lengths, carbon

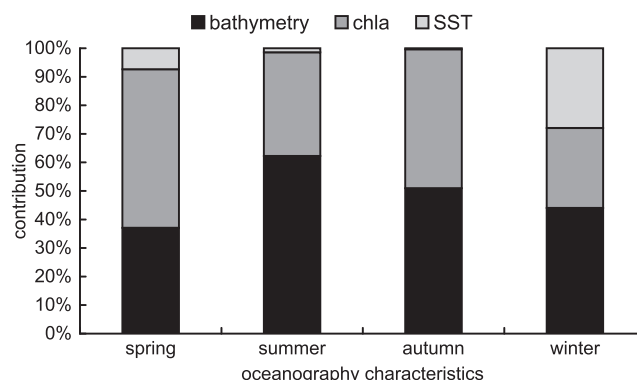


FIGURE 4 Contributions of bathymetry, chlorophyll- a (chl a) and sea-surface temperature (SST) to humpback dolphin distributions in the Beibu Gulf, modelled by Maxent model

absorption was 4.27 kt CO $_2$ km $^{-2}$ year $^{-1}$ in likely habitats (both LCH and LHM) of Indo-Pacific humpback dolphins in the Beibu Gulf.

4 | DISCUSSION

4.1 | Habitat configuration: Uniqueness and importance of humpback dolphin habitats

This study examined three major habitats for Indo-Pacific humpback dolphins in the Beibu Gulf, including the northern Beibu Gulf, the western Beibu Gulf, and the south-western coast of Hainan Island. In these three major habitats, systematic surveys are regularly conducted in the Dafengjiang River estuary and Hepu Dugon Reserve, as well as their adjacent waters (Chen et al., 2016; Wu, Jefferson, et al., 2017). In habitats other than at these two sites, empirical baselines of humpback dolphin distribution and habitat use are still not available, even though systematic surveys have been recently conducted in the south-western Hainan habitat (Li et al., 2016). These information gaps require immediate survey efforts to fill and concurrently verify model predictions. Until this is done, we recommended treating predictions of this study as a precautionary HPA baseline (Gerrodette & Eguchi, 2011; Huang et al., 2018).

Core habitats support critical behavioural and ecological functions, including feeding, socializing and calving (Hartman, Fernandez,

TABLE 2 Summary of the habitat characteristics area A, chlorophyll- a concentration (chl a), sea-surface temperature (SST) and net primary productivity (NPP) in likely core habitats (LCH) and likely habitat maxima (LHMs) of humpback dolphins in the Beibu Gulf

Season	A (km 2)	Chl a (mg m $^{-3}$)	SST (°C)	NPP (mg C m $^{-2}$ day $^{-1}$)
LCH				
Spring	885.2	6.90 (SD = 2.71)	29.09 (SD = 0.80)	4717.48 (SD = 1557.07)
Summer	1567.1	8.58 (SD = 5.91)	31.00 (SD = 0.68)	8039.80 (SD = 5232.58)
Autumn	2426.7	4.85 (SD = 1.05)	27.19 (SD = 0.65)	2473.86 (SD = 612.72)
Winter	2801.3	5.29 (SD = 2.75)	19.08 (SD = 1.61)	869.39 (SD = 419.61)
LHM				
Spring	4136.3	4.44 (SD = 1.88)	27.97 (SD = 0.96)	2711.22 (SD = 1215.16)
Summer	5004.0	4.96 (SD = 2.54)	30.61 (SD = 0.73)	4549.20 (SD = 2504.62)
Autumn	4604.7	3.81 (SD = 1.11)	26.95 (SD = 0.68)	1877.11 (SD = 564.6)
Winter	9537.5	3.46 (SD = 1.17)	19.47 (SD = 1.30)	613.79 (SD = 220.34)

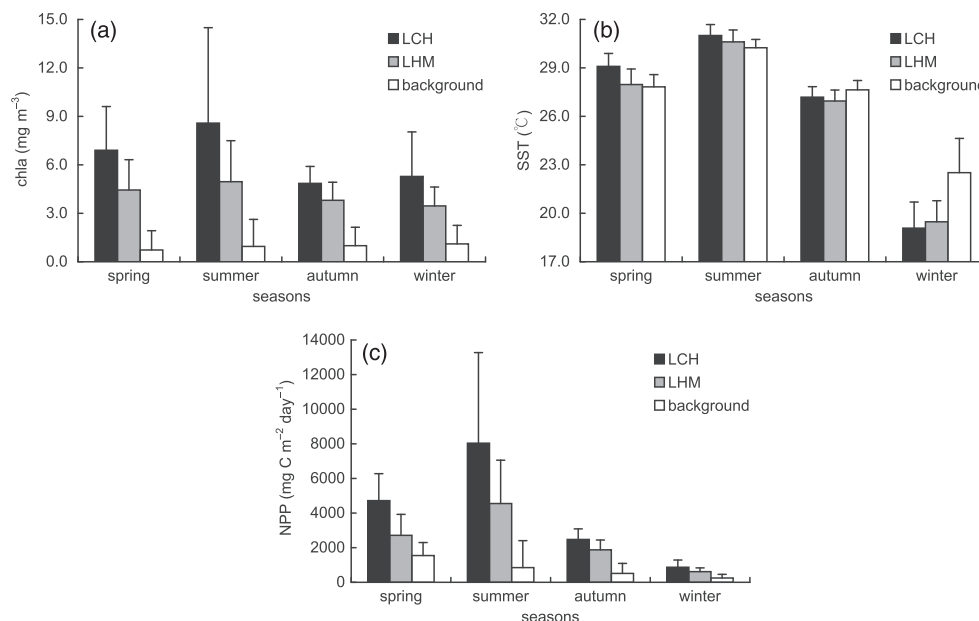


FIGURE 5 Habitat characteristics (mean + SD). (a) Chlorophyll-*a* (chl *a*) concentration, (b) sea-surface temperature (SST) and (c) net primary productivity (NPP), in different spatial extents and in different seasons. LCH: likely core habitat; LHM: likely habitat maximum; background: waters inside the 50 m contour

& Azevedo, 2014; Hastie, Wilson, Wilson, Parsons, & Thompson, 2004; Tyne, Johnston, Rankin, Loneragan, & Bejder, 2015; Wang, Wu, Turvey, Rosso, & Zhu, 2016). Wu, Jefferson, et al. (2017) proposed two major functions of the Dafengjiang River estuary core habitat, presenting abundant prey resources (by significant correlation with chl *a*) and facilitating foraging efficiency (by significant tendency toward shallow water depth) for the Indo-Pacific humpback dolphin. Feeding ecology of humpback dolphins in the Beibu Gulf has not been investigated yet, but as in other habitats, they very likely feed on species like herrings, sardines and croakers (Barros, Jefferson, & Parsons, 2004; Parra & Jedensjö, 2014) that are also abundant in this region (Froese & Pauly, 2018; Zhu, 2012). Generally, pelagic-neritic herrings, shads, sardines and menhadens (family Clupeidae) become abundant from late spring to early autumn, seeking shallow estuaries and brackish waters with high chl *a* contents for spawning (Froese & Pauly, 2018). Bathymetry has the highest contribution affecting humpback dolphin distribution in summer, which gradually decreases through autumn and winter. When the herrings, shads, sardines and menhadens become abundant throughout the Dafengjiang River estuary and its adjacent waters in summer (Dr Haiping Wu, unpublished data; Froese & Pauly, 2018; Zhu, 2012), the habitat where foraging efficiency is high (associated with shallow water depth) could be more attractive than other sites to humpback dolphins. On the other hand, SST becomes important in affecting humpback dolphin distribution in winter. SST has been known as an important factor in defining distribution of fish prey (Froese & Pauly, 2018) such as mullet (family Mugilidae) and croakers (family Sciaenidae), which are also important prey species of humpback dolphins (Barros et al., 2004) and more abundant than pelagic prey during winter in this region (Froese & Pauly, 2018; Zhu, 2012). This evidence thus implies that humpback dolphin distribution associates with their feeding ecology, and that it is in concert with prey resource seasonality (Barros et al., 2004; Froese & Pauly, 2018; Parra & Jedensjö, 2014; Wang, Wu, Turvey, et al., 2016).

Besides the features of high chl *a* and shallow water depth, humpback dolphin habitats are also characterized by high NPP. In coastal and estuarine environments, habitats with high NPP generally have high biomass and biodiversity (Barendregt, Whigham, Meire, Baldwin, & Van Damme, 2006). These habitats provide multiple ecosystem functions and ecosystem services (Barbier et al., 2011), from spawning and nursery waters for both local and pelagic species (Ramos, Amorim, Elliott, Cabral, & Bordalo, 2012; Ray, 2005), nutrient transportation between ecosystems (Deegan, 1993), and capability to retain nutrients and trace metals (Jickells, Andrews, & Parkes, 2015), to feeding sites for marine apex predators (Espinoza, Farrugia, & Lowe, 2011; Wu, Jefferson, et al., 2017). The LCHs of humpback dolphins across the Beibu Gulf may represent regional ecosystem centres with high biodiversity and multiple ecosystem functions. Protection of these LCHs thus provides greater prospects for preserving regional ecosystem services in addition to facilitating population viability for humpback dolphins. In this context, anthropogenic activities that likely change oceanographic characteristics, such as coastal alterations with land reclamation, embankment and construction of harbours, may compromise regional ecosystem integrity (França et al., 2012; Huang et al., 2018; Karczmarski et al., 2017), which, in turn, shifts habitat-use patterns of the Indo-Pacific humpback dolphin around those disturbed habitats (Dares, Araújo-Wang, Yang, & Wang, 2017; Karczmarski et al., 2017; Wang et al., 2017). This concern is not exclusive to the northern Beibu Gulf (Wu, Xu, et al., 2017), but may apply across the species' range.

4.2 | HPA scope: Ensuring connectivity and ecosystem integrity

In the Beibu Gulf, the projected likely habitats (Figure 3f) are much wider than the area covered in the current investigation (Chen et al.,

2016; Li et al., 2016; Wu, Jefferson, et al., 2017; Wu, Xu, et al., 2017). Similar information gaps also happen in population estimates, including population size, vital statistics and life histories. This information scarcity calls for the urgent need to conduct coordinated and systematic surveys and data collection processes. This demand, however, does not necessarily mean there is a need to investigate the entire Beibu Gulf frequently. The systematically designed surveys can be implemented in likely habitats where population baselines are still deficient; that is, the western Gulf of Tonkin (Beibu Gulf) around Red River estuary in Vietnam and south-western Hainan Island in China. While the field surveys are conducted, systematic surveys are more important than extending survey range or conducting more survey effort (Huang et al., 2018). In this manner, the field surveys need to consider regular visits across the survey area and adopt an equally stratified transect design (as Chen et al., 2010), but avoid designs targeting distribution hot zones that superficially increase encounter rates and collect 'more' photo-ID records (Boria, Olson, Goodman, & Anderson, 2014; Kramer-Schadt et al., 2013; Syfert, Smith, & Coomes, 2013). Ecological variables should be simultaneously recorded with (presence) and without (absence) the occurrence of humpback dolphins (as Wu, Jefferson, et al., 2017), so the habitat preferences of humpback dolphin can be measured and compared between habitats (Chen et al., 2016; Jutapruet et al., 2017; Wu, Jefferson, et al., 2017).

The likely habitat configuration shows discontinuous fragments of core habitats in the major habitats, which highlights an explicit information gap in population connectivity. Though Chen et al. (2016) suggested some 'social isolation' for humpback dolphins between Dafengjiang River estuary and Hepu Dugon Reserves, both oceanographic characteristics and likely habitat configuration present different results. Analogous information gaps may happen between major habitats, and therefore influence HPA scopes. Approaches to solve population connectivity include genetic analyses (Alves et al., 2013; Lowe & Allendorf, 2010; Parra et al., 2018) and cross-matching of individual photo-ID records (Guttridge et al., 2017; Wang, Wu, Chang et al., 2016). A collaborative network system that shares stranding information, carcass samples and photo-ID catalogues between research teams is recommended. This information-sharing network can include habitat and population baseline surveys, which should be integrated into current HPA projects.

Many HPA discussions seek to establish protected areas over key habitats to protect humpback dolphins from diverse anthropogenic impacts (Chen et al., 2009; Huang et al., 2018; Ross et al., 2010; Wu, Xu, et al., 2017). In the Beibu Gulf, less than 9% of likely habitats are currently protected by marine protected areas. This low protection percentage highlights the need to broaden protected area coverage immediately. Creating more protected areas seems an obvious solution, such as the ongoing Dafengjiang River Estuary Protected Area programme (Dr Haiping Wu, personal communication). This tactic, however, could be complicated by restrictive resource availability (Bottrill et al., 2008; McDonald-Madden, Chadès, McCarthy, Linkie, & Possingham, 2011), and the difficulties to protect animals outside the protected areas. The HPA scope thus needs to adopt integrative networks that associate protected areas targeting multiple species (Cicin-Sain & Belfiore, 2005; Green et al., 2011; Qiu, Wang, Jones, & Axmacher, 2009) with regional maritime function zoning to facilitate

preserving habitat connectivity (Green et al., 2011; Pendoley, Schofield, Whittock, Ierodiakonou, & Hays, 2014).

Simply maintaining spatial connectivity of the humpback dolphin population may not ensure long-term population persistence. The HPA scope needs to consider ecosystem properties such as habitat quality, ecosystem functions and ecosystem services (International Union for Conservation of Nature [IUCN], 2016). In this context, the biggest challenge to HPA planning may come from intense coastal alteration activities, including land reclamation, harbour construction and embankment, in the past decades (Wu, Xu, et al., 2017). In other habitats, these coastal alteration activities are responsible for changes in underwater features (Karczmarski et al., 2017), reduced ocean productivity (Huang et al., 2018), changes in humpback dolphin distribution and habitat use (Huang et al., 2018; Jefferson, 2018; Wang et al., 2017) and in population social structure (Wang et al., 2015). In the northern Beibu Gulf, the massive reclamation and embankment activities in the eastern Qinzhou Bay have compromised interchange between seawater and inland discharges, decreasing regional productivity and facilitating SST increase (Wu et al., unpublished data). These changes can further impact local ecosystem regimes, including accumulating inland pollutants (Dr Bing Gong, personal communication), forming a hypoxic region on warm-weather days (Dr Haiping Wu, unpublished data), and gradual shift in prey composition (Leitão, Maharaj, Vieira, Teodósio, & Cheung, 2018; Potts et al., 2014). HPA planning needs to consider measures mitigating ecosystem deterioration or, more proactively, restoring damaged habitat.

Present humpback dolphin HPAs often neglect the fluid and dynamic nature of coastal and marine environments (Cicin-Sain & Belfiore, 2005; Huang et al., 2018) and seldom consider anthropogenic impacts from nearby landscapes changing native oceanographic conditions (Huang et al., 2018; Karczmarski et al., 2017; Wang et al., 2017). HPAs under this scope often pay more attention to 'paper-protection' rather than solid conservation actions, such as those in western Taiwan (Wang, Riehl et al., 2016). In coastal and estuarine environments, primary productivity is highly associated with inland nutrient runoff (Brodie, De'ath, Devlin, Furnas, & Wright, 2007; Zheng & Tang, 2007). Activities associated with land reclamation, embankment and harbour construction can interrupt inland discharges, change local sediment processes, reshape bathymetry structure (Karczmarski et al., 2017) and likely alter chl *a* distribution and concentration (Huang et al., 2018). These impacts further influence regional ecosystem regimes and hence compromise ecosystem functions. Also, intense coastal alteration activities are commonly associated with rapid urbanization and industrialization processes (Chen et al., 2014; Karczmarski et al., 2017; Wang et al., 2017; Wu, Xu, et al., 2017). Nearby these densely populated areas, high levels of persistent pollutants are often reported in aquatic environments and in humpback dolphin tissues (Gui et al., 2014, 2017), imposing high risks to dolphin and ecosystem health.

Sound HPAs for humpback dolphins thus demand measures not only regulating and mitigating anthropogenic activities in marine habitats, but also management in nearby coastal landscapes and connected catchments (Huang et al., 2018; Jefferson et al., 2009; Karczmarski et al., 2017; Wang et al., 2017; Wu, Xu, et al., 2017). Sound HPA plans should include environmental baselines in both

coastal landscapes and seascapes, mitigating land-based pollutant discharges from connected landscapes (Kroon, Thorburn, Schaffelke, & Whitten, 2016), restoring degraded riverine runoffs, and hence nursery habitats for aquatic biota (Elliott et al., 2016), and recovering estuarine-coastal connectivity (Weinstein & Litvin, 2016). Long-term or irreversible coastal alterations in dolphin habitat, particularly from large-scale land reclamations, should be avoided, or strictly scrutinized in environmental impact assessments (Jefferson et al., 2009; Karczmarski et al., 2017; Wu, Xu, et al., 2017) by factoring in likely losses of NPP and ecosystem services. As the NPP in coastal and estuarine waters is primarily obtained from photosynthesis and the fixation of CO₂, the NPP values thus can be converted into amounts of CO₂ fixed ($1 \text{ mg C m}^{-2} \text{ day}^{-1} = 365 \text{ kg C km}^{-2} \text{ year}^{-1}$, C : CO₂ = 12 : 44), which is equal to 4.27 kt CO₂ km⁻² in the LCHs in the Beibu Gulf. We recommend using this value as a baseline measuring the ecosystem service losses from coastal alterations. The reason for this is that, in general, reclamations in humpback dolphin habitats are more frequently constructed for industrial parks (as in Karczmarski et al., 2017; Wang et al., 2017; Wu, Xu, et al., 2017) or airport/port expansions (as in Jefferson, 2018) that are not only reducing the original CO₂ absorption capability, but also emitting more CO₂. By using the methods to understand likely habitat configuration presented in this study, loss of ecosystem functions in those habitats can be evaluated, and hence the status of the overall ecosystem can be better understood (IUCN, 2016).

Thus, HPA scope for humpback dolphins in the Beibu Gulf should involve the following aspects: implementing coordinated and systematic surveys in major habitats, associating core habitat protection with protected area networks and maritime function zoning, ensuring ecosystem function integrity within and between major habitats, and inhibiting both explicit lethal impacts and implicit anthropogenic activities that change oceanographic features. HPA scopes for humpback dolphins should consider marine habitats, adjacent coastal landscapes and river catchments. As the likely habitat configuration in our study includes both Chinese and Vietnamese waters, cross-national collaboration in field surveys, protected area enactment and HPA campaigns will play an essential role. HPA planning and implementation will require effective and comprehensive coordination and collaboration between various sectors, including scientific research teams, government policy representatives, nongovernmental/nonprofit organizations, and various stakeholder groups (Arkema et al., 2015; Keeley et al., 2018; Spalding et al., 2016).

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