Distribution and Habitat Characteristics of the Indo-Pacific Humpback Dolphin (*Sousa chinensis*) in the Northern Beibu Gulf, China

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Abstract

Studies on the distribution and habitat characteristics of the Indo-Pacific humpback dolphin (*Sousa chinensis*) indicate a general preference toward estuarine environments. However, quantitative connections between this preference and estuarine characteristics are seldom investigated. Distribution of the humpback dolphin in the northern Beibu Gulf, China, was evaluated through systematically designed surveys and was compared to oceanographic characteristics from on-board measured and remotely sensed variables. The humpback dolphins' core distribution zone, measured by the 50% kernel density estimate (50% KDE), was confined to the Dafengjiang River Estuary in a 50.23 km² area, with a steep-edged underwater sand bar below and locally high chlorophyll-a concentration. The surface salinity distribution showed an eco-cline environment in which riverine runoff mixes with sea water in the 50% KDE. We found significant relationships between distribution probability and two oceanographic variables: (1) water depth and (2) chlorophyll-a concentration. This associates the distribution preference of humpback dolphins with regional productivity and biodiversity peaks that may facilitate prey aggregation. As humpback dolphins inhabit comparable environments in other locations throughout their range, the oceanographic features of the 50% KDE may help to provide proxies to identify other key habitats over a broader spatial scale.

Key Words: habitat characteristics, distribution, oceanography, bathymetry, chlorophyll-a, kernel density estimate, MODIS

Introduction

Studies on the distribution and habitat characteristics of animals identify the dynamic function of animal habitat use as it relates to the accessibility of prey, social interactions, predator-prey interactions, and inter-habitat-patch mobility (Wilson et al., 1997; Karczmarski et al., 2000; Heithaus, 2001; Davis et al., 2002; Braulik et al., 2012; Wang et al., 2015, 2016). Baselines for such data provide further insights into practical habitat protection and management planning (International Union for Conservation of Nature [IUCN], 2001; Wilson et al., 2004; Cañadas et al., 2005; Garaffo et al., 2011; Zhao et al., 2013; Wang et al., 2016). Relevant studies can be especially important in protecting key habitat for coastal cetacean species, such as the Indo-Pacific humpback dolphin (*Sousa chinensis*), which frequently interact with anthropogenic activities (Jefferson, 2000; Ross et al., 2010; Dungan et al., 2012; Würsig et al., 2016).

The Indo-Pacific humpback dolphin (known as the Chinese white dolphin in Chinese waters) is known to specifically rely primarily on coastal waters shallower than 20 m deep (Jefferson, 2000; Jefferson & Karczmarski, 2001; Hung, 2008; Ross et al., 2010; Jutapruet et al., 2015). The taxonomy of the humpback dolphins was recently revised, resulting in four species now recognized in the

genus (Jefferson & Rosenbaum, 2014). From a worldwide perspective, many studies on humpback dolphin distribution, not just the Indo-Pacific humpback species but also other *Sousa* species, reveal a general preference toward estuarine environments (e.g., Jefferson & Karczmarski, 2001; Jefferson & Hung, 2004; Sutaria & Jefferson, 2004; Chen et al., 2010; Jutapruet et al., 2015; Xu et al., 2015; Chen et al., 2016; Li et al., 2016). Quantitative connections between habitat preference and estuarine features, however, are still very rare for humpback dolphins (Jefferson, 2000). These kinds of studies are particularly essential and are urgently needed in developing areas like China and some other Southeast Asian countries where rapid economic growth, urbanization, and industrialization often accompany uncompensated changes in coastal and estuarine environments (Ross et al., 2010; MacKinnon et al., 2012; Chen et al., 2014; Karczmarski et al., 2016; Wang et al., in press).

In Chinese waters, the occurrence of the humpback dolphin has been reported in many coastal-estuarine waters in the southern and central part of the country (Jefferson, 2000; Jefferson & Hung, 2004; Wang et al., 2007; Xu et al., 2015; Chen et al., 2016; Li et al., 2016; Wang et al., 2016). While pioneering studies on the humpback dolphin started in Hong Kong and adjacent waters in the early 1990s (see Jefferson, 2000), many investigations have primarily focused on abundance estimates for various locations (e.g., Xu et al., 2015). Distribution and ranging patterns of humpback dolphins have been described in some populations (Hung & Jefferson, 2004; Hung, 2008; Wang et al., 2015, 2016; Xu et al., 2015; Chen et al., 2016), but few of them connected the distribution preferences with estuarine characteristics.

In the northern Beibu Gulf, People's Republic of China (PR China), occurrence of the humpback dolphin has been reported from Sanniang Bay (SNB, North & East), Dafengjiang River Estuary (DRE), and the Hepu Dugong Reserve (Chen et al., 2009, 2016). Frequent sightings of humpback dolphins in the SNB-DRE region attract high levels of public attention, and dolphin-watching tourism specifically targeting the humpback dolphin began in 2004. Intense land use/landscape change, however, has been occurring along the northern Beibu Gulf, following recent rapid economic development and industrialization activities (Huang & Karczmarski, 2015). In this study, the habitat preferences of the humpback dolphin in the SNB-DRE area were explored, based on data from systematically designed surveys, and were further compared to the estuarine features derived from on-board-measured and remotely sensed oceanographic variables. Defining an empirical connection between the humpback dolphins'

habitat preferences and estuarine environments provides further ecological insight to identifying critical habitats over a wider spatial range.

Methods

Study Site
The study site covered Sanniang Bay (SNB), the Dafengjiang River Estuary (DRE), and part of the adjacent Qinzhou Bay (QB) off the central coast of Guangxi Province, PR China (Figure 1). Habitat type in this region is primarily sandy/muddy seabed (Tong et al., 2012; Zhu, 2012). Principal fish fauna taxa include several types known to be humpback dolphin prey such as Clupeidae, Engraulidae, Sciaenidae, and *Leiognathus* (Zhu, 2012). Oceanographic measurements in this region are mainly from offshore regions rather than inshore sites (Tong et al., 2012).

Field Survey and Data Collection
Systematically designed field surveys were conducted from August 2013 to December 2015 using a 7.5-m-long fishing boat cruising at approximately 10 to 15 km/h under sea-state condition of Beaufort 3 or less. The survey routes adopted a zig-zag line design that started at different points opportunistically at each survey trip to ensure even coverage over the study site. During each survey, GPS position and oceanographic variables, including water depth, sea-surface temperature (SST, in °C), dissolved oxygen (DO, in mg/L), and surface salinity (SAL, in PSU), were measured every 4 to 5 km regularly. When humpback dolphins were sighted, GPS position and oceanographic variables were measured and recorded first. Then, the survey boat slowed down and followed the dolphin group by moving alongside it for at least 30 min to take lateral photos for photo-identification. Distance between the dolphins and the survey vessel during photographic sampling was kept to at least 30 m to reduce potential behavioral and acoustic disturbance to the animals. When photographic sampling was finished, the field survey restarted at the point of departure from the line. The photographs will be used for photo-identification analyses that estimate population size, residency patterns, and individual-based habitat use in the near future. In August, October, and December 2015, we collected a sample of 500 mL of water at each sampling site during the field survey and measured the chlorophyll-a concentrations (CHLA) at the lab of the Marine Environment Monitoring and Forecasting Centre, Qinzhou Municipal Oceanic Administration.
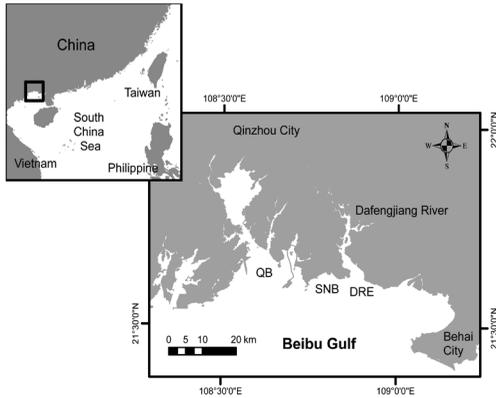
Figure 1. The study site, including Qinzhou Bay (QB), Sanniang Bay (SNB), and Dafengjiang River Estuary (DRE) in the northern Beibu Gulf, central coast of Guangxi Province, People's Republic of China

Distribution of the Humpback Dolphin
We used the minimum convex polygon (MCP) (IUCN, 2001) and 50% kernel density estimate (50% KDE) (Parra, 2006; Wang et al., 2015, 2016) to estimate the extent of occurrence and core distribution of humpback dolphins in the study site. The original GPS records of dolphin sightings in the WGS84 coordinate system were projected into the UTM49N coordinate system using *ArcMap*, Version 9.3. Then, polygons outlining MCP and 50% KDE of the humpback dolphin were plotted against the GPS positions of dolphin sightings. The coastline, offshore sand bars, and artificial structures (like land reclamations) that are inaccessible to dolphins were subtracted. Then, the areas of MCP and 50% KDE were calculated.

Oceanographic Features in the Study Site
The on-board-measured water-depth data (D) were calibrated to the tidal phases (D_T) by referencing to the tidal-height-per-hour-per-day (H_T) at Longmen Port (21.750 N, 104.550 E) in the Qinzhou Bay (Qinzhou Municipal Oceanic Administration):

$$D_T = D - \left(\frac{H_{T+1} - H_T}{60} \times m + H_T \right) \quad (1),$$

where T and m are the hour and minute of recordings. Then, the D_T values were interpolated using *ArcMap*, Version 9.3, with the Kriging method to show the bathymetric structure of the study site. We also interpolated the on-board measured salinity data by *ArcMap* to determine the pattern of surface salinity in the study site.

We applied a multi-variable linear regression to the on-board measured DO, SST, and CHLA data:

$$DO = k + a \times SST + b \times CHLA,$$

where k, a, and b are regression coefficients to be estimated as preliminary analyses indicated a significant correlation among these three variables (Table 1). The model-calculated DO was further compared to the on-board-measured DO to validate the application of the regression results. We finally applied the regression results to the MODIS AQUA-based SST and CHLA data.

We downloaded the annual composites of MODIS AQUA's SST and CHLA data between 2013 and 2015 from the Oceancolor Data website (http://oceandata.sci.gsfc.nasa.gov; OB.DAAC, 2015). We extracted the data layers over the northern Beibu Gulf via the *SeaDAS* program (http://seadas.gsfc.nasa.gov) and calculated the averages of SST and CHLA data from 2013 to 2015. Then, the regression equation of DO was applied to the averaged SST and CHLA layers to build DO layers over the study area. Differences of the oceanographic variables between the water inside and outside 50% KDE were tested using a two-sample *t* test. Distribution probabilities measured by KDEs inside the survey area were extracted, and then the relations between KDE and habitat variables were explored by least squared non-linear approaches.
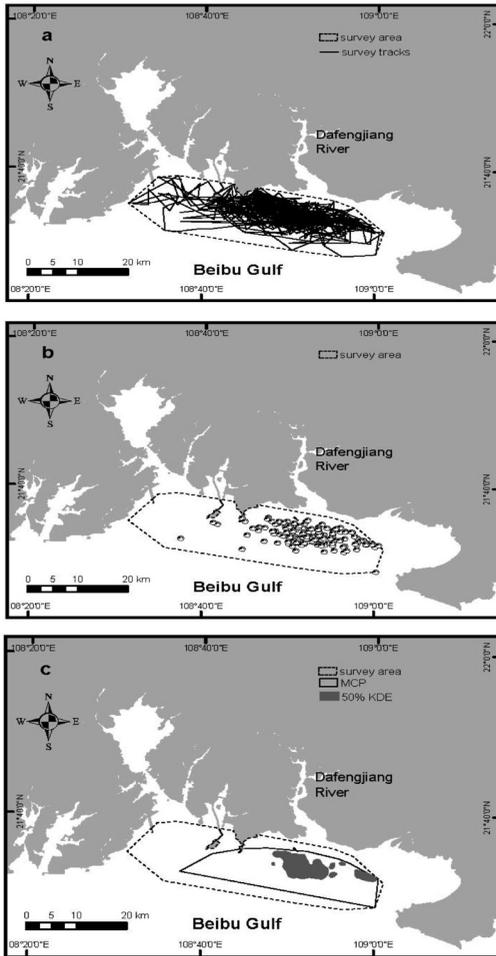
Table 1. Pairwise correlations between the four on-board-measured habitat characteristics: salinity (SAL), sea-surface temperature (SST), dissolved oxygen (DO), and chlorophyll-a concentration (CHLA)

	SAL	SST	DO
SST	-0.035		
DO	-0.002	-0.958**	
CHLA	0.049	-0.478**	0.581**

$*p < 0.05$, $**p < 0.001$

Results

From August 2013 to December 2015, a total of 55 surveys were conducted over a 619.85 km² area, with a total of 2,929.03 km of survey effort (Figure 2a). In these surveys, a total of 163 groups of humpback dolphins were sighted (Figure 2b). Regions enclosing the MCP (minimum convex polygon; 300.45 km²) and 50% KDE (kernel density estimate; 50.23 km²) were plotted against these sighting records (Figure 2c) and were used to present the extent of occurrence (MCP) and core distribution site (50% KDE) of the humpback dolphins within the study site.
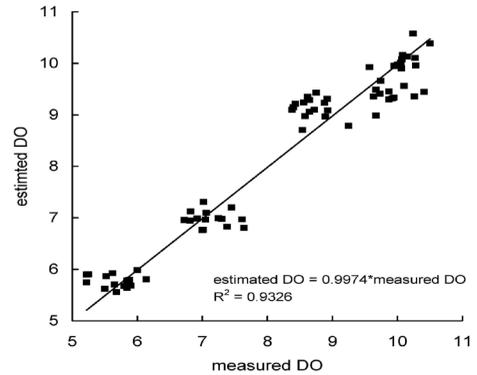
Figure 3. Comparison of on-board-measured DO to the model-estimated DO values

A significant regression was found between on-board-measured oceanographic variables, including dissolved oxygen (DO, in mg/L), sea-surface temperature (SST, in °C), and chlorophyll-a concentration (CHLA, in mg/m³) (Table 2):
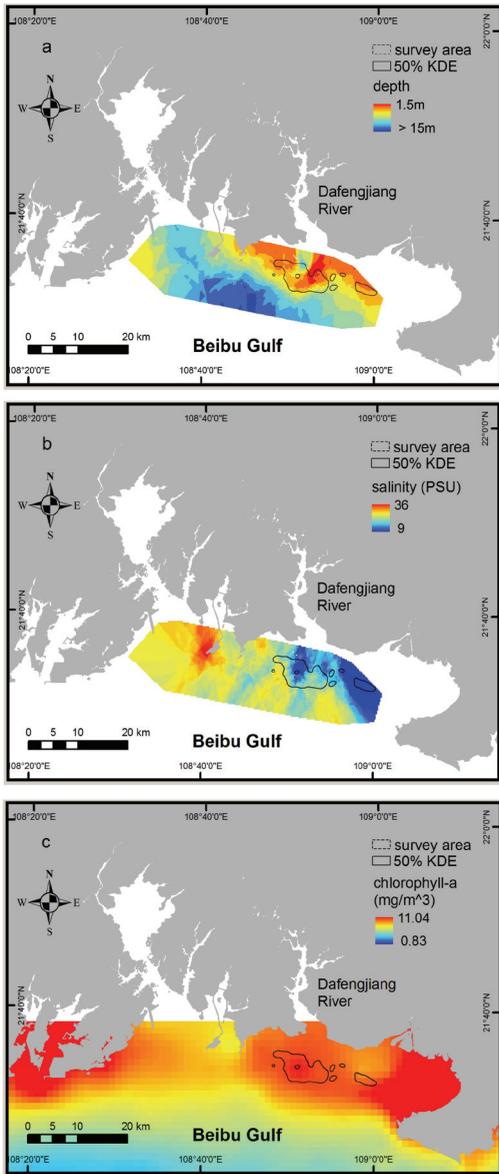
$$DO_e = 13.1134 - 0.2440 \times SST_e + 0.07314 \times CHLA_e, \quad R^2 = 0.935 \quad (2),$$

where *e* represents values from on-board measures. Since there was a good match between the measured and model-estimated DO values (Figure 3), we applied this regression to the remotely sensed SST and CHLA data from the

Table 2. Regression coefficient estimates (estimates, SE, and CI) of the model: $DO = k + a \times SST + b \times CHLA$, $R^2 = 0.935$
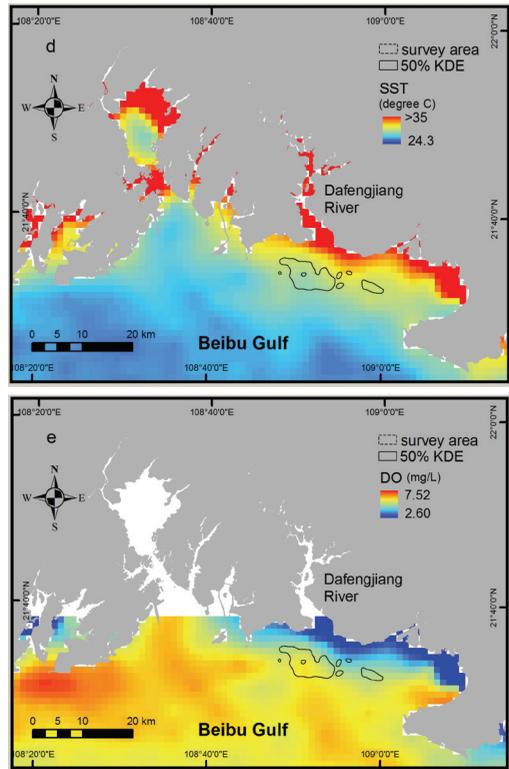
	Estimates	SE	CI	t test
k	13.1134	0.2672	12.5802 ~ 13.6465	49.08**
a	-0.2440	0.0096	-0.2632 ~ -0.2248	-25.36**
b	0.07314	0.0159	0.0415 ~ 0.1048	4.61*

*p < 0.05, **p < 0.001

Figure 2. (a) Survey area: 610.67 km² that enclosed all survey routes, totaling 2,317.80 km, from August 2013 to December 2015; (b) locations of Indo-Pacific humpback dolphin (*Sousa chinensis*) sightings over all surveys; and (c) the areas enclosing the minimum convex polygon (MCP) and 50% kernel density estimates (50% KDE).

Table 3. Summary of habitat features (mean SD and range), including water depth, surface salinity, MODIS-based chlorophyll-a concentration (CHLA), sea-surface temperature (SST), and dissolved oxygen (DO), for the study site. A two sample *t* test revealed that features inside the 50% KDE have significantly lower water depth (*t* = 21.88, *p* < 0.001) and salinity (*t* = 19.86, *p* < 0.001), and higher CHLA concentration (*t* = 10.17, *p* < 0.001) than features outside the 50% KDE.

Spatial range in the	Area (km²)	Depth (m)	Salinity (PSU)	CHLA[a] (mg/m³)	SST[a] (°C)	DO[b] (mg/L)
Study area	619.85	5.052.69	22.225.16	8.280.48	27.530.52	7.000.12
		0.97 - 13.35	9.38 - 31.14	6.56 - 8.98	26.27 - 29.28	6.59 - 7.24
MCP	300.45	5.062.69	22.225.17	8.280.48	27.530.51	7.000.12
		0.97 - 13.35	9.38 - 31.14	6.56 - 8.98	26.27 - 29.23	6.59 - 7.24
50% KDE	50.23	3.521.58	20.115.03	8.580.23	27.570.34	7.020.10
		0.97 - 10.0	9.38 - 29.44	7.63 - 8.98	26.98 - 28.79	6.70 - 7.16

[a]Based on the average of MODIS AQUA annual composites from 2013 to 2015
[b]Based on applying the regression model (equation 1) to the remotely sensed CHLA and SST data

Figure 4. Oceanographic features of the study site, including (a) water depth, (b) salinity, (c) CHLA, (d) SST, and (e) DO. Water depth and salinity are interpolated from on-board measurements. CHLA and SST were averages of the MODIS AQUA annual composites from 2013 to 2015. DO distribution was derived from applying the regression equation 2 to CHLA and SST data.

MODIS AQUA from 2013 to 2015 to extrapolate the DO distribution over the study site (see Figure 4e).

Figure 4 and Table 3 summarize the features of the humpback dolphin habitat, including bathymetry (in m), salinity (in PSU), CHLA concentration (in mg/m³), SST (in °C), and DO (in mg/L). Bathymetric structure in the study site revealed an underwater sand bar at the DRE (Figure 4a), which directly overlapped with the 50% KDE site for the dolphins. The surface salinity distribution indicated a mixing zone where riverine runoff mixes with sea water above the underwater sand bar (Figure 4b). At this site, the CHLA values were significantly higher than those of surrounding water (two-sample t test = 3.49, $p < 0.001$; Figure 4c). SST and DO inside the 50% KDE were not statistically different from those outside (two-sample t test = 1.22 and 0.75, $p = 0.22$ and 0.45, respectively; Figures 4d & 4e). Exponential relationships were found between the distribution probabilities (measured by the KDE) of the humpback dolphin and two habitat characteristics—(1) the water depth (Figure 5a) and (2) CHLA concentration (Figure 5b):

$$KDE = 0.0176 \times \exp(-0.4626 \times depth), \quad R^2 = 0.493 \quad (3),$$

$$KDE = 7.2995 \times 10^{-13} \times \exp(2.6010 \times CHLA_M), \quad R^2 = 0.503 \quad (4),$$

where M represents the average of MODIS AQUA data between 2013 and 2015. Though the KDE values were statistically correlated with

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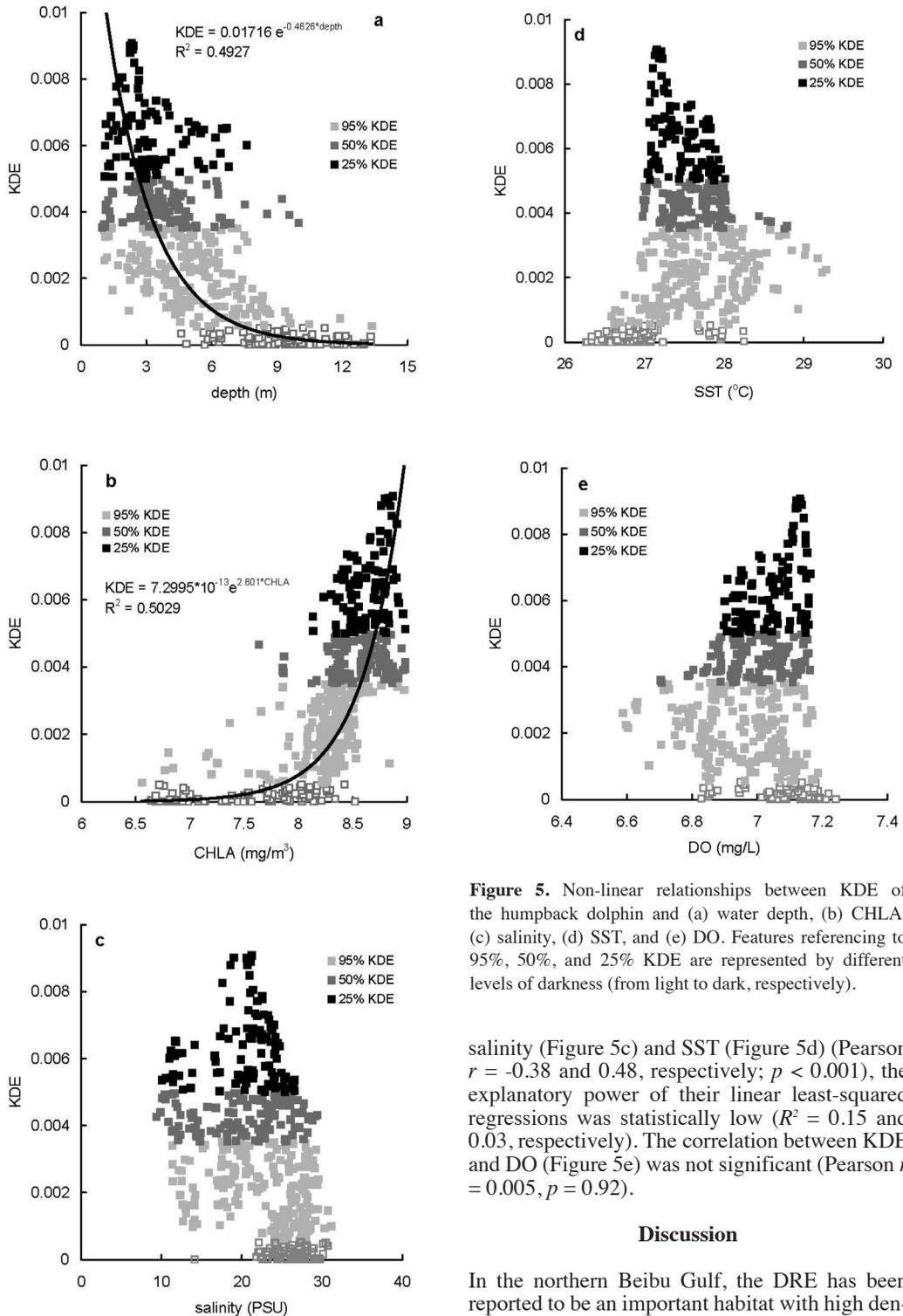
Figure 5. Non-linear relationships between KDE of the humpback dolphin and (a) water depth, (b) CHLA, (c) salinity, (d) SST, and (e) DO. Features referencing to 95%, 50%, and 25% KDE are represented by different levels of darkness (from light to dark, respectively).

salinity (Figure 5c) and SST (Figure 5d) (Pearson $r = -0.38$ and 0.48, respectively; $p < 0.001$), the explanatory power of their linear least-squared regressions was statistically low ($R^2 = 0.15$ and 0.03, respectively). The correlation between KDE and DO (Figure 5e) was not significant (Pearson $r = 0.005$, $p = 0.92$).

Discussion

In the northern Beibu Gulf, the DRE has been reported to be an important habitat with high densities and frequent feeding/socializing behaviors

of Indo-Pacific humpback dolphins (Zhu, 2012; Chen et al., 2016). In the current study, the bathymetric structure reveals a submerged sand bar with a steep edge at the DRE, which directly overlaps with the humpback dolphin core distribution site. This seabed conformation, along with the spatial distribution of surface salinity and CHLA, indicates an estuarine turbidity maximum (ETM) zone that has been frequently observed at many estuarine eco-clines (Burchard & Baumert, 1998). The ETM zone has been reported to have a regional productivity peak (Levin et al., 2001; Barendregt et al., 2006; Suzuki et al., 2013) and also represents important spawning and nursing areas for many marine organisms (Secor et al., 1998; Barendregt et al., 2006; Jaureguizar et al., 2008; Braverman et al., 2009; Zhu, 2012). Many pelagic-neritic fishes, like *Konosirus punctatus* (family Clupeidae) and *Thryssa* spp. (family Engraulidae), as well as benthic fishes, like croakers (family Sciaenidae) and *Arius maculates* (family Ariidae), have been reported aggregating in DRE water (Zhu, 2012). Most of these are important prey items for humpback dolphins (Barros & Cockcroft, 1991; Barros et al., 2004).

The bathymetric structure at the DRE may have further ecological and behavioral implications for humpback dolphin habitat use. The underwater sand bar at the estuary may provide more microhabitats for marine organisms and may enhance local nutrient cycling, concurrent with local tidal cycle. These implications can amplify the ecosystem function that aggregates prey resources further. As humpback dolphins have to dive deeper to pursue prey at the bottom, especially when neritic/surface prey become rare or absent, feeding near the underwater sand bar, where prey resources aggregate, can facilitate feeding efficiency.

Consequently, the 50% KDE area at the DRE may not only represent a core-distribution site behaviorally but also an ecologically valuable habitat with vital implications for feeding, and even calving and socializing (Zhu, 2012). Comparing our results to those of Chen et al. (2016), however, the exact site and shape of the 50% KDE identified in this study appears to be slightly different. Different methods and extent of spatial coverage of survey effort between the two studies may explain this discrepancy. As previous survey efforts (Chen et al., 2016) did not cover the inshore and shallow water as thoroughly as we did, the 50% KDE identified in this study helps to fill in missing information on distribution and habitat use of humpback dolphins in this area.

Occurrence of humpback dolphins has been reported at the eastern (Chen et al., 2016), central (Chen et al., 2009, 2016), and western (H. Wu,

unpub. data) parts of the northern Beibu Gulf. Chen et al. (2016) found that two groups of humpback dolphins in the eastern and central part of this area showed no photo-identification matches in their study. Accordingly, they suggest the chances the same individuals can be found across the entire Beibu Gulf, from Chinese to Vietnamese waters, are low. This argument, however, may still be under debate as there is no significant geographic or oceanographic barrier that partitions the northern Beibu Gulf environment. Some evidence suggests younger humpback dolphins have a wider range (Yeh, 2011) but may be seldom involved in photo-identification exercises primarily due to lack of long-lasting markings (see photographs in Jefferson, 2000, and Jutapruet et al., 2015). In this situation, the databases used for cross-matching might be incomplete. Until conclusive evidence, based on comprehensive photo-identification matching and/or genetic methods, elucidates the population structure of the humpback dolphins in the northern Beibu Gulf, we recommend treating the entire northern Beibu Gulf as one management unit. From this perspective, the MCP and 50% KDE parameters identified in this study, as well as earlier studies, should not be literally interpreted as the population's "home range." Instead, this site should be regarded as one of the critical habitats for the species in the northern Beibu Gulf, and it appears very likely that humpback dolphins visit this important habitat on a regular basis (H. Wu, unpub. data).

If there are other valuable habitats across the northern Beibu Gulf, determining their likely locations will have strong implications for forming effective habitat protection programmes. First, we could plan systematic surveys at sites where sighting probabilities of the humpback dolphin are high to validate our predictions and also to calibrate the predictive modeling process. Second, we could identify the likely sites to be protected on a precautionary basis when planning regional habitat-conservation programmes, especially for areas where baseline information is lacking or insufficient. Third, we could also work to adjust regional coastal zone management plans by examining whether current zoning plans properly address the critical habitats of humpback dolphins. Predictive extrapolation, based on species-distribution modeling (Faleiro et al., 2013; Merow et al., 2013; Pitchford et al., 2016), or applying the KDE relationships (as in equations 2 and 3) to oceanographic variable layers over the northern Beibu Gulf (e.g., the bathymetry and CHLA-concentration layers) may help to reach this objective. Currently, the major challenge may come from the lack of bathymetric information over the entire region. Traditional vessel-based bathymetry

surveys over the target area may provide a valid approach to solve this problem, but the limitations involved in accessing shallow (e.g., < 1.5 m deep) water by survey vessels need to be resolved by other available techniques. Besides, as non-linear relations between the distribution probabilities and habitat characteristics (Figure 5), and complex correlations between different habitat variables (Table 1), direct application of multivariate approaches (such as generalized linear model, generalized additive model, or ecological niche factor analysis) that base modeling exercises on the assumptions in linear response and non-colinearity might need additional caution to validate modeling results.

Similar preferences for estuarine environments have been reported for some other Chinese water regions (Jefferson, 2000; Hung, 2008; Wang et al., 2015, 2016; Xu et al., 2015; Chen et al., 2016; Li et al., 2016; Würsig et al., 2016) and also for the southwestern Gulf of Thailand (Jutapruet et al., 2015). These studies, in addition to the present study, imply two common proxies to identify valuable habitats for humpback dolphins: (1) the regional productivity peak and (2) regional bathymetric lift/slope. In addition, one implicit feature is that all these sites are located at the confluence region where oceanic currents meet bathymetric lift/slope, riverine runoff, or both. These characteristics correlate with a local eco-cline region where primary and secondary productivity and biodiversity can be high. If the above inference is valid, habitat protection programmes for the humpback dolphin, such as enacting relevant protected areas, should not merely protect and facilitate the long-term survival of the humpback dolphin but, more importantly, protect regional ecological hot spots for a variety of species. Since this is a key area for feeding and reproduction for many aquatic-pelagic organisms—not just humpback dolphins—protection of the area would facilitate biological and ecological resource conservation for multiple species.

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