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Seasonal, Lunar and Tidal Influences on Habitat Use of Indo-Pacific Humpback Dolphins in Beibu Gulf, China

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Shanshan Li, Huili Gao, Xiuqing Hao, Lin Zhu, Ting Li, Hongke Zhang, Yi Zhou, Xinrong Xu, Guang Yang, and Bingyao Chen (2018) Cetacean habitat use based on different environmental phases varies between species and geographies, and little is known about Pacific humpback dolphin habitat use in the Beibu Gulf. Here we aimed to identify seasonal, lunar and tidal influences on the spatial use of Beibu humpback dolphins based on two parameters: water depth and distance to an estuary. The ANOVA test indicated that habitat use was influenced by seasons and tidal phases, but not lunar phases. The humpback dolphins utilized shallow areas near an estuary throughout the wet season and high tides, and moved toward deeper water during the dry season and low tides. This habitat preference is likely synchronized with prey seasonal and tidal movements. The wet season and high tides bring abundant prey resources and increase accessibility to inshore shallow waters for humpback dolphins. The present study provides new information on regular habitat use by Indo-Pacific humpback dolphins, which is crucial for developing effective conservation strategies.

Key words: Beibu Gulf, Habitat use, Indo-Pacific humpback dolphins, Seasonal distribution, Tidal influence.

BACKGROUND

Marine mammal species occurring in coastal areas are the most likely to display tidal and seasonal variations in their habitat use patterns (Abrantes et al. 2015; Lin et al. 2015). The seasonal and tidal changes in the water quality and levels can dictate the spatiotemporal changes in prey resources and thus shape the distribution gradient of cetaceans (Lin et al. 2015). Along with tidal and seasonal changes (Benjamins et al. 2015; Taylor et al. 2016), some other environmental factors such as temperature (Neumann 2001), salinity (Tynan et al. 2005), depth (Fazioli et al. 2006; Hastie et al. 2006), distance to shore or bank (Fazioli et al. 2006; Parra et al. 2006), habitat type (Kimura et al. 2012; Martin et al. 2004), etc., were also thought to have an impact on habitat use of cetaceans. These cetaceans included Belugas (*Delphinapterus leucas*) (Stafford et al. 2013), Franciscana dolphins (*Pontoporia blainvillei*) (Bordino 2002), harbour porpoises (*Phocoena phocoena*) (Wilson et al. 2013), bottlenose dolphins (*Tursiops truncatus*/*T. aduncus*) (Fury and Harrison 2011), humpback dolphins (*Sousa* spp.) (Lin et al. 2015; Wang et al. 2015b), Risso's dolphins (*Grampus griseus*) (Jefferson et al. 2014), killer whales (*Orcinus orca*) (Dahlheim et al. 2008), gray whales (*Eschrichtius robustus*) (Barrett-Lennard et al. 2011), Commerson's dolphins (*Cephalorhynchus*

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commersonii) (Rocio et al. 2013), and North Atlantic right whales (*Eubalaena glacialis*) (Pike 2008).

The Indo-Pacific humpback dolphin (*Sousa chinensis*) is a strictly coastal species, and those in Taiwan are considered a new subspecies (*S. c. taiwanensis*) (Wang et al. 2015a). The estuary is the reported core habitat of Indo-Pacific humpback dolphins (Parsons 2004). Seasonal changes in Indo-Pacific humpback dolphin distribution were also observed in the Pearl River Estuary (Chen et al. 2010; Wang et al. 2015b), Xiamen Bay/Jiulong River Estuary (Chen et al. 2008) and XinWuwei River Estuary/Taiwan (Lin et al. 2015). Dolphins also show preference for particular tidal states; for example, the acoustic encounter rate of humpback dolphins is lowest during ebb tides in Eastern Taiwan Strait (Lin et al. 2013), and the echolocation detection probability of humpback dolphins is significantly higher at high tide than that at flood tide in the Pearl River Estuary (Wang et al. 2015b). The current studies on how tide influences dolphin distribution were conducted in Taiwan (Lin et al. 2013 2015) and Pearl River Estuary (Wang et al. 2015b), and little is known about other populations off Chinese waters.

The present study aims to provide a better understanding of the seasonal, lunar and tidal influences on Indo-Pacific humpback dolphins' spatial use in Beibu Gulf, China.

MATERIALS AND METHODS

Study area and population introduction

This study was conducted in the Beibu Gulf (21°25'-37'N, 108°40'-109°05'E), located in the northwestern South China Sea. The Beibu Gulf is characterized by an open area with a semi enclosed bay and smooth shoreline (Fig. 1); it normally has a diurnal tide with the largest tidal range of 7 m. The study area contains the Dafengjiang and Nanliujiang Rivers, which inject a combined annual 7.91 billion m^3 of freshwater into the gulf. There are an estimated 248-282 humpback dolphins in the Dafengjiang and Nanliujiang areas (Chen et al. 2016).

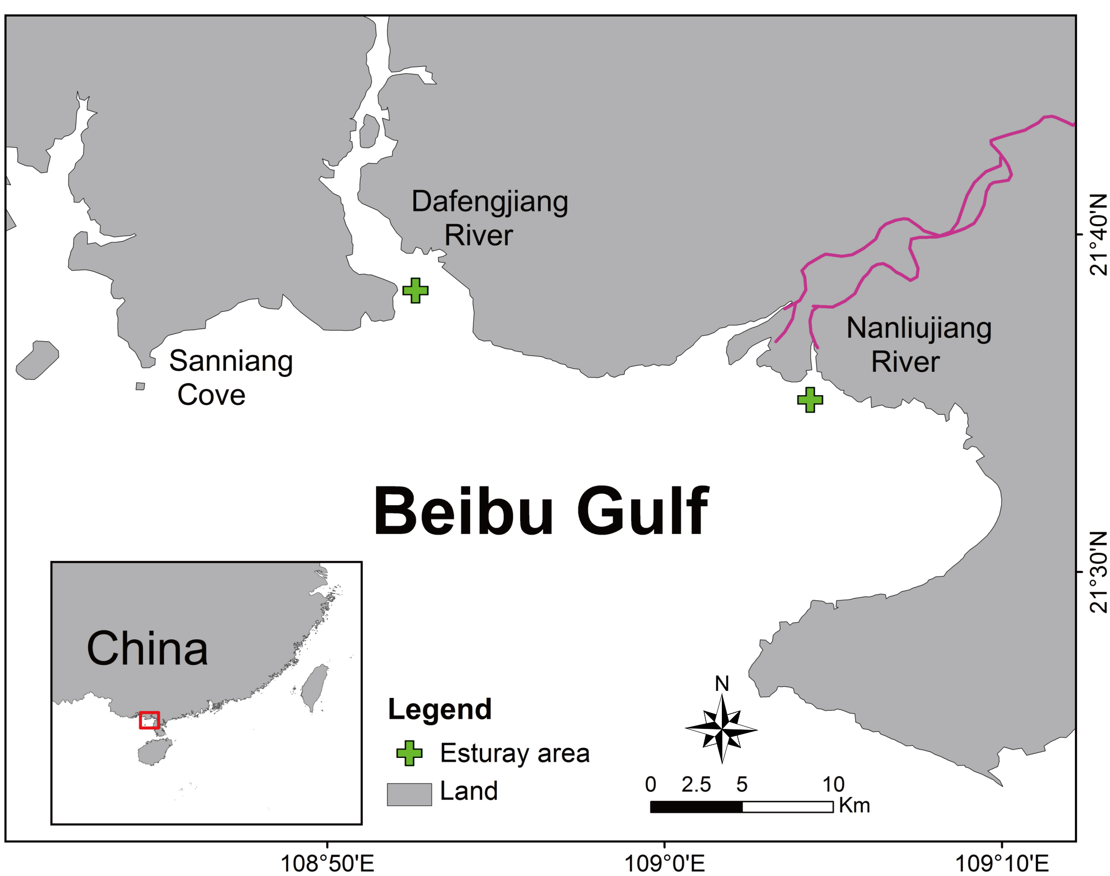

Fig. 1. Map of the study site: the Beibu Gulf, China.

Vessel-based field survey

The daytime vessel-based surveys were carried out weather permitting (Beaufort Sea state ≤ 3). The vessels were 10-18 m in length, powered by 100-150 hp diesel engines, and sailed at a steady speed of 9-14 km/h. A minimum of two observers searched for dolphins with the naked eye. Once dolphins were sighted, the vessel would approach them slowly. The time, water depth and location of longitude and latitude (using a Garmin GPS, Etrex Venture, and MAP 60CSx) were recorded.

Boat-based surveys were undertaken for six years from October 2011 to August 2016. A total of 152 groups of dolphins were recorded during this study.

Definitions and data analysis

We analyzed the influences of season, lunar phases and tide on the distribution gradients of humpback dolphins by categorizing dry and wet seasons, spring and neap tides, and tidal phases.

October-April and May-September were defined respectively as dry and wet seasons based on rainfall.

In the lunar calendar (29.54 day), two spring tides and neap tides occur twice a month. Spring tides occur when the moon is either new or full and the sun, moon, and earth are aligned; the difference between high and low tide is the greatest during this period. Neap tides occur when the sun and moon are at right angles to the earth; the difference between high and low tide is the least during this period. Using the tide-generating software WXTIDE32 version 4.7 (http://www.wxtide32.com/), we defined the spring and neap tide ranges based on the continuous running tidal curve, with each period lasting seven days.

The Beibu Gulf normally has a diurnal tide. The 24-hour tidal phase period was divided into two observational periods - high tide, low tide (Fig. 2) - each 12 hours long. High tide period included the hours of high tide plus hours before and after it and low tide period included the hours of low tide plus hours before and after it.

Indo-Pacific humpback dolphins have a preference for freshwater estuaries (Jefferson 2000) and the estuary has been reported as their core habitat (Parsons 2004). The Dafengjiang and Nanliujiang Rivers flow into the study area in the Beibu Gulf, and the estuaries were defined as the areas with high concentrations of humpback dolphins. We therefore used distance from reference sites of two estuaries - instead of distance offshore - and water depth to test how dolphin spatial distribution differs with the seasons and lunar and tidal phases. Water depth was directly recorded using a fish detector (HONDEX HE-670) in the vessel fieldwork. The distance from the dolphin sighting location to two reference sites in both estuaries (Dafengjiang Estuary point: 21°38'0"N, 108°52'0"E; Nanliujiang Estuary point: 21°35'0"N, 109°04'0"E) were measured using a proximity analysis tools module in the ARCGIS (ESRI, version 9.3). Only the closest distance was recorded and tested.

With regard to the habitat use of Indo-Pacific humpback dolphins, distance from the estuary and water depth were recorded in table 1 based on tidal and lunar phase and the season they were recorded in. Differences between the groups were determined using a three-way ANOVA (two seasons, two lunar phases, two tidal phases) with distance from estuary and water depth. Statistical analyses were conducted using SigmaPlot 14.0. Values were statistically significant when $P \leq 0.05$.

RESULTS

Humpback dolphin sightings during different seasons and lunar and tidal phases are shown in figures 3 and 4. The distance to estuary data (DE) failed the equal variance test ($P < 0.05$), but passed the normality test after reciprocal transformation. Therefore, one-way ANOVA was

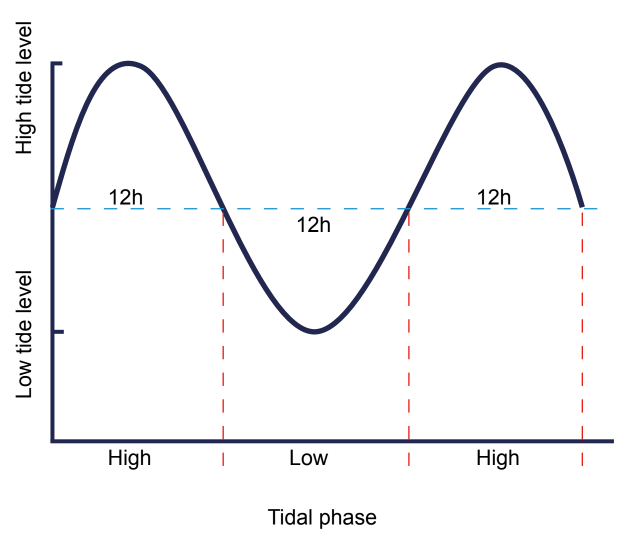

Fig. 2. Definitions for high and low tidal phases in the Beibu Gulf, China, as used in the present study.

used to test the differences in DE among seasons, lunar phases and tidal phases separately (Table 2). Most of the humpback dolphins were significantly closer to the estuary during the wet season (Fig. 3a, mean = 10.88 ± 1.67 km) than the dry season (11.51 ± 2.29 km) (Fig. 4c) (ANOVA, *d.f.* = 1, Dunn's method, Q = 4.385, $P < 0.001$). The dolphins' spatial distribution was not significantly determined by lunar phases (Fig. 3b) (spring tide 11.22 ± SD 2.24, neap tide 11.14 ± 1.19 km, ANOVA, *d.f.* = 1, $P = 0.167$). The distance to the estuary is statistically insignificant between tides (ANOVA, $F = 3.312$, *d.f.* = 1, $P = 0.079$), although figure 3c suggests that dolphins move closer to the estuary during high tides (high tides: 10.38 ± 1.28 km, low tide: 11.87 ± 2.25).

Water depth data (WD) of humpback dolphin sightings passed the normality test (Shapiro-Wilk, $P = 0.260$) and equal variance test (Brown-Forsythe, $P = 0.376$) after reciprocal transformation; it was then analyzed using three-way ANOVA to test the differences among seasons, lunar phases and tidal phases (Table 3). The result showed that the WD of dolphins' sightings was not determined by lunar phases but by seasons, tidal phases, and the interaction between seasons and tidal phases (Table 3, Fig. 4d). Because interaction between tidal phases and seasons exist, we then conducted the Student-Newman-Keuls to test them separately. The results showed that the humpback dolphins significantly preferred shallow waters in low tides (wet 2.84 ± 0.97 m, dry 4.28 ± 1.44 m) to high tides (wet 3.87 ± 1.3 m, dry 5.4 ± 2.37) in both the wet season (Q = 6.881, $P < 0.001$) and dry season (Q = 3.243, $P < 0.05$). Significant seasonal difference was found during low tide (Q = 7.695, $P < 0.001$), but not high tides (Q = 2.297, $P = 0.107$).

DISCUSSION

The Indo-Pacific humpback dolphins in the Beibu Gulf used shallow inshore waters during the wet season and moved out to deeper water during dry season. This habitat selection preference is likely synchronized with prey movements. Most fish species, including humpback dolphin prey such as *Sardinella nymphaes*, *Clupanodon punctatus*, *Ilisha elongage*, *Seipinna taty*, *Coilia grayi*, *Collichthys lucida* (Barros et al. 2004), were observed to enter the shallow inshore waters during the rainy, hot season and move into the deep sea during autumn and winter/dry season (Jia 2003; Zhao et al. 2007). The spatial distribution of Beibu humpback dolphins seems contrary to that of

Table 1. The number of sightings of Indo-Pacific humpback dolphins during different seasons and lunar and tidal phases at northern Beibu Gulf, China

Seasonal phases	Lunar phases	Tidal phases	Number of sightings	Period
Wet season	Spring tide	High	7	2012-2014
		Low	17	2013-2015
	Neap tide	High	21	2012-2016
		Low	26	2012-2013
Dry season	Spring tide	High	29	2011-2015
		Low	11	2013-2014
	Neap tide	High	25	2011-2015
		Low	16	2013-2015

Table 2. One-way ANOVA testing the null hypothesis that there is no difference in the distance dolphins were sighted at from an estuary across the different seasons, lunar phases and tidal phases separately

Parameter	Source of Variation	DF	Normality Test	Equal Variance Test	Method	MS	*F*	*P*
Distance to Estuary	Season	1	0.858	< 0.050	Dunn's	-	Q = 4.385	< 0.001
	Lunar	1	0.134	0.846	Default	< 0.001	< 0.001	0.977
	Tidal	1	0.164	0.241	Default	< 0.001	3.132	0.079

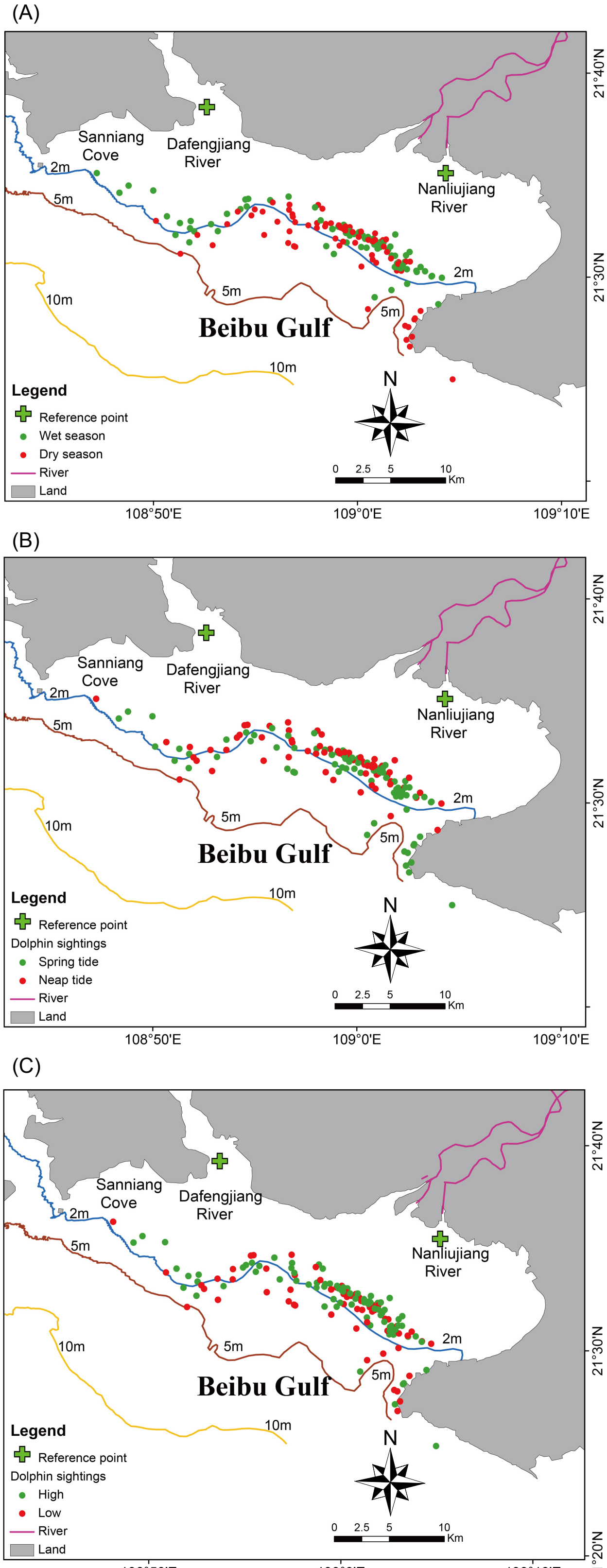

Fig. 3. Map of humpback dolphin sightings based on (a) dry and wet seasons, (b) lunar phases and (c) tidal phases for the humpback dolphins in northern Beibu Gulf.

Taiwan humpback dolphins as the latter frequently inhabit area near the river mouth during dry seasons, but move seaward during wet seasons (Lin et al. 2015). Even so, Taiwan humpback dolphins' habitat selection is also closely related to prey movements, i.e. snapping shrimp mainly stay near to the river mouth during dry seasons and move seaward during rainy seasons (Lin et al. 2015). We thereby agree with Wang et al. (2003) and Hastie et al. (2004) that the distribution of prey is a direct factor in determining the movement patterns of Indo-Pacific humpback dolphins.

During the dry season, Beibu humpback dolphins tend to enter inshore waters during high tide (P = 0.079, close to significance). The influence of tide on dolphins' habitat use was widely attributed to their relationship with prey: higher prey availability means humpback dolphins need lower energy expenditure on obtaining them (Kimura et al. 2012; Lin et al. 2013; Taylor et al. 2016; Vermeulen et al. 2015). Extensive shallow inshore waters exist in the Beibu Gulf, and their ebb and flow can significantly influence the local environment. In general, fishes migrate between subtidal resting grounds and intertidal feeding grounds (Forward and Tankersley 2001; Gibson 2003). Although no clear tidal presence patterns of their benthic prey have been reported in the Beibu Gulf, the epipelagic prey of humpback dolphins - including anchovies and mullets - have been observed to ride high tides into the intertidal zone and stay until low tide brings them back (Lin et al. 2013). Accordingly, Beibu humpback dolphins move into inshore waters and forage during high tide. Moreover, another reason could be that inshore waters become more accessible during high tide and so the dolphins travel inshore during that time; this behavior was reported in bottlenose dolphins in the Clarence River estuary, Australia (Fury and Harrison 2011).

As is well known, dolphins require a particular salinity to maintain physiological health fitness and may die if exposed to freshwater for too long (Manton 1986). The Beibu Gulf has a smooth shoreline and the exchange of freshwater and seawater is fast. Although large amounts of imported fresh water leads to dramatic decrease in salinity during the rainy/wet seasons, the salinity of Dafengjiang and Nanliujiang River Estuaries can maintain a certain salinity ranging from 15.7‰ to 35.8‰. The salinity there probably meets the humpback dolphins' basic needs, making it possible for these animals to move into nearshore waters without suffering from low salinity.

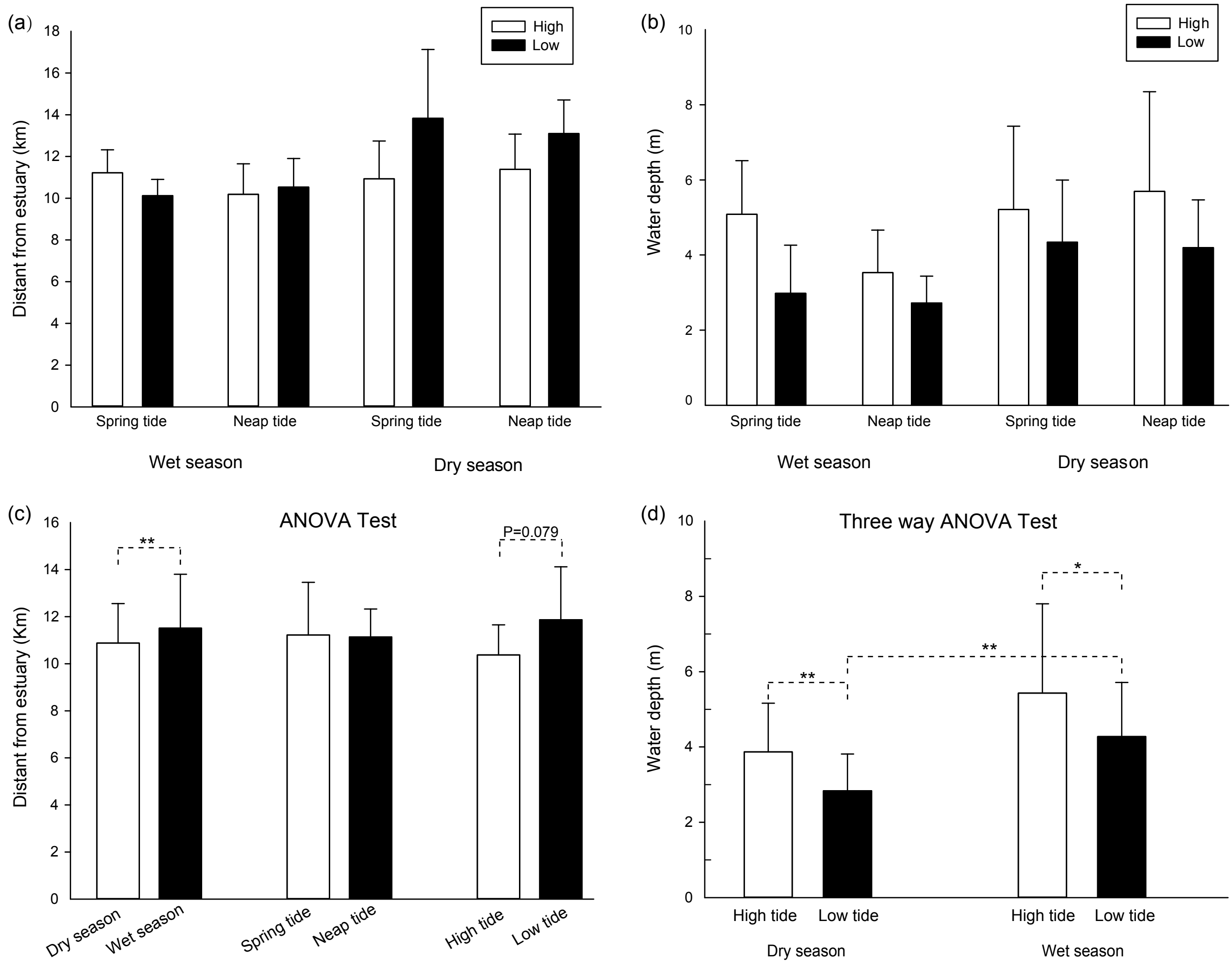

Fig. 4. The profile of distance from estuary (a) and water depth (b) of humpback dolphin sightings in northern Beibu Gulf among different seasons, lunar phases and tidal phases, and significance tests (c, d). Note: "*" indicates a significance at $P < 0.05$, "**" indicates a significance at $P < 0.01$.

Table 3. Three-way ANOVA testing the null hypothesis that there is no difference in the water depth dolphins were sighted at across the different seasons, lunar phases and tidal phases. SNK: Student-New-Keuls was used. Normality Test (Shapiro-Wilk, $P = 0.260$), and Equal Variance Test (Brown-Forsythe, $P = 0.376$) were passed

Source of Variation	DF	MS	F	*P*
Season	1	0.142	21.409	< 0.001
Lunar	1	0.0128	1.938	0.167
Tidal	1	0.175	26.478	< 0.001
Season × Lunar	1	0.0189	2.853	0.094
Season × Tidal	1	0.0283	4.267	0.041
Lunar × Tidal	1	0.00677	1.022	0.314
Season × Lunar × Tidal	1	0.0115	1.733	0.191
Residual	105	0.00663		

Most humpback dolphins in the Beibu Gulf were distributed within 5m bathymetry (Fig. 3). The Beibu Gulf is a semi-enclosed area; the seafloor is basically plain, slowly descending from the coastline to the middle (Liu and Yu 1980). The shallow water area is extensive and the area within 5 m bathymetry could provide enough spatial area for humpback dolphins. Following the increase of rainfall during the wet season, the stranding risk of dolphins gets lower and the inshore waters' accessibility is higher for humpback dolphins. This could partly explain the significant seasonal distribution shifts.

In addition, the temporary changes in temperature, turbidity, and chlorophyll in seawater after rains might affect the physiological health conditions of the dolphins or reshape the distribution and movement of prey resources (Fury and Harrison 2011; Fury and Reif 2012); these ideas need further research.

CONCLUSIONS

In conclusion, our results suggest that Beibu Indo-Pacific humpback dolphins' habitat use pattern showed regular changes in response to seasonal and tidal cycles. The distribution pattern of local prey fish may be a direct factor in determining the movement of these dolphins. The increased accessibility to shallow waters during the wet season and high tide may be another factor.

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Authors' contributions: BC and GY conceived and designed the research. BC, XX, HZ and YZ performed the field work. SL, HG, BC, LZ, and TL performed the statistical analyses. SL, BC, XH, and GY wrote the paper.

Competing interests: SL, HG, XH, LZ, TL, HZ, YZ, XX, BC and GY declare that they have no conflict of interest.

Availability of data and materials: We do not want to open up our data.

Consent for publication: Not applicable.

Ethics approval consent to participate: Data were collected with approval from the Animal Research Ethics Committee of Nanjing Normal University.

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