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Seasonal distribution and nature reserve planning of Indo-Pacific humpback dolphins in the Pearl River estuary from South China Sea

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ABSTRACT

Understanding habitat use patterns and assessing diffusion status are essential for effective conservation of cetaceans, particularly the Indo-Pacific humpback dolphins (*Sousa chinensis*) in the Pearl River Estuary (PRE), where habitat decline is contributing to demographic decline. This study provides a seasonal evaluation of habitat suitability and distribution for PRE humpback dolphins using five years of boat-based field survey data from 2019 to 2023. Our results indicate significant seasonal variations in dolphin habitat. The core habitat in eastern PRE increased from 738 km^2 in the dry season to 822 km^2 in the wet season, while the middle PRE core habitat decreased from 408 km^2 to 213 km^2. During the dry season, dolphin habitats are more dispersed and closer to the estuary's interior, whereas they become more concentrated in the wet season. This dynamic spatial redistribution reflects responses to seasonal changes in water quality and prey availability. Key environmental factors influencing habitat distribution include salinity, chlorophyll a concentration, water depth, and dissolved oxygen, with varying impacts across seasons. Additionally, precipitation and monsoons play significant roles in predicting dolphin habitats throughout the year. We recommend establishing dynamic protection zones in areas with seasonal changes in dolphin presence to enable adaptive management strategies. This study underscores the need for ongoing research and monitoring to clarify the interactions between climatic variables and the ecological integrity of marine habitats.

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1. Introduction

Marine mammals are crucial indicator species in marine ecosystems (Plön et al., 2024). Their presence, population size, and behavioral changes provide intuitive insights into the health and environmental quality of these ecosystems (van Weelden et al., 2021). However, many marine mammals worldwide face significant threats, including habitat loss, human activity interference, and environmental pollution (La Manna et al., 2020; Yang et al., 2020; Luo et al., 2024b). Habitat degradation, in particular, profoundly affects the health and viability of marine animal populations. A 30 % reduction in core habitats can drastically diminish a population's survival capacity, pushing it to a critically unsustainable threshold (Huang et al., 2022).

Habitats, as the immediate environment on which organisms depend for survival, are fundamental to conservation efforts. Effective identification of species' habitat distribution is a prerequisite for designing scientifically sound conservation strategies and delineating the boundaries of marine protected areas (Huang et al., 2018). Currently, nearly one-quarter of small cetacean species are threatened with extinction (Temple et al., 2024). Despite numerous conservation measures by the international community, including the establishment of Marine Protected Areas (MPAs), the effectiveness of these efforts in protecting cetacean habitats remains inadequate. This is particularly evident in nearshore waters, where human interference renders the habitats of nearshore marine mammals more vulnerable to degradation (Davidson et al., 2012; Temple et al., 2024).

Coastal cetaceans often exhibit species-specific habitat preferences driven by complex interactions among environmental variables and anthropogenic stressors. Observations of common dolphins (*Delphinus delphis*) in Portugal suggest that higher chlorophyll-a levels, indicative of primary productivity can effectively reflect prey abundance. plays a key role in shaping their distribution patterns (Moura et al., 2012). Parallel findings emerge from ecological niche modeling of Stenella species in the Caribbean, where environmental heterogeneity drives spatial segregation among sympatric dolphin populations (Barragán-Barrera et al., 2019). The Indian Ocean humpback dolphin (*Sousa plumbea*), a congener of *Sousa chinensis*, exhibits preferential use of nearshore habitats (1–2 km from shore) characterized by intermediate water depths and enhanced chlorophyll-α concentrations, these parameters likely associated with optimal foraging conditions and favorable water quality (Hemami et al., 2018). Despite these advances, contemporary cetacean habitat studies frequently neglect seasonal variability, potentially compromising our understanding of spatiotemporal distribution.

The Indo-Pacific humpback dolphin (*Sousa chinensis*) is a typical nearshore marine mammal, mainly found in coastal waters of tropical and subtropical regions, including estuaries, bays, and shallow waters (Jefferson and Smith, 2016), According to the assessment of IUCN, the humpback dolphin is at a Vulnerable level (VU), however, several studies suggest that the population status of humpback dolphins in the PRE, the largest known population with about 2000 individuals (Chen et al., 2010), may have reached Endangered (EN) or even Critically Endangered (CR) levels (Huang et al., 2012). Research indicates that the population of humpback dolphins in the Lingdingyang Bay of the PREis declining at a rate of 5.9 % (Lin et al., 2024). Previous studies indicate that the distribution of Indo-Pacific humpback dolphins is influenced by various environmental factors, including water depth, salinity, chlorophyll-a concentration, and dissolved oxygen levels (Wu et al., 2017; Lin et al., 2021a; Lu et al., 2023). Long-term monitoring in Hong Kong waters has revealed significant alterations in habitat suitability and movement ecology of humpback dolphins, primarily driven by shifting salinity regimes and extensive coastal reclamation activities (Jefferson et al., 2023). More recently, large-scale analyses using MaxEnt modeling have demonstrated that sea surface temperature, proximity to coastline, and anthropogenic pressures such as demersal fishing and pollution are the major drivers of habitat loss and fragmentation for Indo-Pacific humpback dolphins, especially under future climate change scenarios (Lu et al., 2023). These dolphins typically prefer shallow waters, likely due to better prey availability (Lin et al., 2021b). They thrive in salinity levels ranging from 15 ‰ to 25 ‰ (Dares et al., 2014) and are often found in areas with higher chlorophyll-a concentrations (Guo et al., 2022). Despite these established ecological preferences, existing studies have yet to adequately address two critical dimensions: seasonal fluctuations in environmental variables, and the broader impacts of climate variability on habitat suitability. This knowledge gap hinders a comprehensive understanding of the underlying mechanisms shaping their distribution patterns

Most studies have focused on static habitat assessments, often overlooking seasonal variations in habitat distribution. With the intensification of climate change and human activities, the dynamic nature of habitats has become increasingly prominent, yet these changes remain underexplored. Seasonal shifts in environmental factors likely affect the distribution and core habitat of humpback dolphins, but systematic research quantifying these effects is limited. Addressing this gap is crucial to understanding the seasonal changes in ecological factors and habitat distribution of nearshore toothed cetaceans.

Species Distribution Models (SDMs) are invaluable for analyzing species-environment relationships, such as abundance and occurrence, alongside environmental variables that influence species distribution. These models provide a robust framework for identifying and assessing habitat suitability (Guisan and Thuiller, 2005) and have seen increasing application in conservation biology and biodiversity assessment (Passadore et al., 2018; Araújo et al., 2019). This study employs SDMs, integrating several seasonal environmental factors, to: 1) examine the distribution and variation of the humpback dolphin's core habitats in the PRE during the dry and wet seasons, based on five years (2019–2023) of boat-based field observations; and 2) identify the primary preferences and driving factors for habitat distribution in these seasons. The findings aim to provide a scientific basis for effective monitoring programs, conservation strategies, and marine spatial planning for humpback dolphins.

2. Materials and methods

2.1. Study area

The Pearl River Estuary (PRE), located between 21°30′-23°30′ N and 112°30′-114°30′ E, ranks among the most urbanized areas

globally, surrounded by prominent cities such as Hong Kong, Shenzhen, Zhuhai, and Macau (Fig. 1). The Pearl River, which feeds into this estuary, is the largest river in southern China and ranks 13th globally in terms of freshwater discharge. Annually, the Pearl River discharges approximately 3.26×10^{11} m^3 of water, with around 80 % occurring during the wet season from May to October (Zhou et al., 2006). This substantial influx of freshwater during the summer months significantly reduces seawater salinity (from 24.43 ‰ to 9.95 ‰). Therefore, based on previous studies, we define the period from November to April as the dry season and May to October as the wet season (Chan and Karczmarski, 2017). The depth of the PRE varies between 2 and 30 m, with most areas being relatively shallow, primarily ranging from 2 to 10 m. Furthermore, multiple quantitative assessments indicate that the dolphin population in the PRE comprises three socially distinct and discrete units (Chan, 2019). To enhance the understanding of local differences, we have further divided the PRE into two independent units: the Eastern Pearl River Estuary (EPRE) and the Middle Pearl River Estuary (MPRE) (Fig. 1).

2.2. Data collection

The largest global population of Indo-Pacific humpback dolphins is found in the PRE, underscoring its significance as a critical habitat for this species. Specifically, approximately 900 individuals inhabit the eastern waters of the PRE (Lin et al., 2024). Between 2019 and 2023, information on the distribution of humpback dolphins in the PRE was gathered through boat-based observational surveys. Each survey followed a predetermined sailing route, with historical transect lines preloaded into handheld GPS devices to maximize spatial coverage of previously unsurveyed areas. Collectively, these efforts encompassed all known humpback dolphin distribution zones within the EPRE. Standardized survey protocols—including field sampling methodologies follow established procedures as described in (Guo et al., 2022). Fig. 1 presents the complete survey tracks alongside geographic coordinates of humpback dolphin sightings. Surveys were conducted continuously throughout the year, with each offshore expedition preceded by rigorous weather assessments. Departure was authorized only when wind speeds remained below Beaufort scale 3, a precautionary measure to

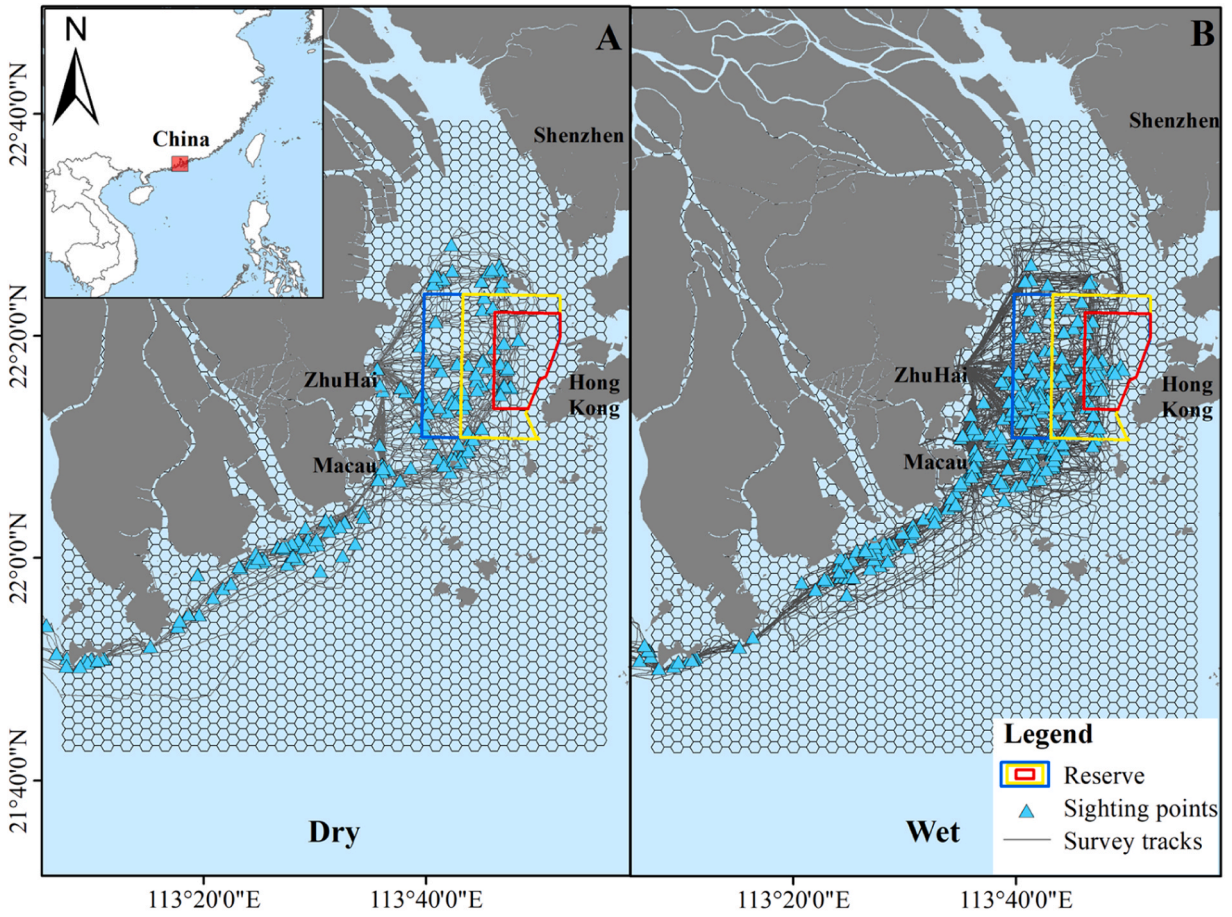


Fig. 1. (A) The survey tracks during the dry season and (B) wet season from 2019 to 2023. The colored polygon represents the national humpback dolphin reserve area, the blue triangles indicate the sighting points of dolphin groups, the gray lines depict the survey trajectories, and the hexagonal grid represents the statistical unit. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

both minimize environmental interference and ensure observational reliability of humpback dolphin detections

To analyze the habitat use of humpback dolphins, we collected a comprehensive array of environmental data. This included Chla, sea surface temperature (SST), offshore distance (OD), and water depth, as well as several water quality parameters sourced from the Department of Ecology and Environment of Guangdong Province, China (http://gdee.gd.gov.cn/jhszl/index.html). The water quality parameters included total inorganic nitrogen (TIN), DO, active phosphate (PO_4^{3-}), salinity (SAL), suspended solids (SS), and chemical oxygen demand (COD). To assess the impact of current policies on the PRE waters, we visualized the marine functional zoning for our analysis (http://www.gd.gov.cn/zwgk/gongbao/2012/14/content/post_3363568.html).

2.3. Data analyses

To address the uneven nature of the survey tracks and the inherent limitations of traditional ship-based surveys in fully covering all regions, we employed kernel density analysis to identify the core habitat distribution of humpback dolphins across the two seasons. We plotted hexagonal grids with a side length of 1 km on the map (Fig. 1), a methodology previously utilized in studies (Birch et al., 2007), compared to traditional square grid-based statistical analysis, hexagonal grids have equal distances between their centers, with a closer perimeter-area ratio to a circle, which could potentially reduce the edge effect (Giralt Paradell et al., 2019). To eliminate differences in survey effort across different areas, we calculated the sighting rate per unit survey transect within each grid cell to standardize the effort, we used the spatial join tool in ArcMap v10.2 toolbox to calculate the total number of sightings within each grid cell, divided by the total number of survey transects, to obtain the average sighting rate for each grid.

Spatial analysis was then conducted based on the sighting locations using the kernel density function available in the ArcMap v10.2 toolbox. In this analysis, the population parameter was represented by the sighting rate, with a search radius of 5 km applied. The geographic coordinate system utilized was WGS 1984, with the projected coordinate system being WGS 1984 UTM Zone 49 N.

Layered data, including chlorophyll-a and sea surface temperature, were categorized into distinct layers for the dry and wet seasons based on established seasonal definitions. Within the study area, we selected 47 monitoring sites from government marine water quality reports. Utilizing the distribution of these sites, we applied Inverse Distance Weighting (IDW) interpolation to derive the overall spatial values of water quality parameters (Li and Heap, 2008). Following the construction of environmental layers in ArcGIS, we exported these data layers as TIFF files for subsequent habitat modeling. Prior to analysis, we assessed multicollinearity among environmental variables, with detailed correlation results presented in Figure S7. The analysis revealed significant correlations between salinity (SAL) and reactive phosphate (PO_4^{3-}) and other environmental variables. Despite these correlations, we retained both parameters in our models due to their established ecological relevance for humpback dolphin habitat selection. As coastal cetaceans, humpback dolphins are particularly sensitive to the spatially heterogeneous salinity gradients characteristic of the Pearl River Estuary, which directly influence their physiological tolerance thresholds and prey distribution patterns (Fu et al., 2021). Similarly, PO_4^{3-} serves as a crucial biogeochemical indicator of primary productivity (Niu et al., 2020), ultimately shaping the trophic dynamics supporting dolphin populations. The inclusion of these variables, notwithstanding their correlations with other parameters, ensures our models capture essential ecological drivers that might otherwise be overlooked. This approach enables a comprehensive evaluation of how spatial variability in environmental conditions structures humpback dolphin habitat use patterns.

To model the presence-absence of humpback dolphins in relation to various explanatory variables, this research utilized the Biomod2 package (Thuiller et al., 2016) within the R programming environment (R Development Core Team, 2024). The Biomod2 model include the generalized linear model (GLM), generalized additive model (GAM), classification tree analysis (CTA), generalized boosting model (GBM), artificial neural network (ANN), surface range envelope (SRE), flexible discriminant analysis (FDA), multiple adaptive regression splines (MARS), random forest (RF), and eXtreme Gradient Boosting (XGBoost). Given the limited availability of genuine absence records, we randomly generated 1000 pseudo-absence points under environmental conditions that contrasted with those of the actual presence points (Antoine et al., 2024). The predictive accuracy of the models was evaluated using a fivefold cross-validation technique with ten repetitions. In this method, 80 % of the dataset was randomly selected for model calibration and testing, while the remaining 20 % was reserved for evaluating the models' predictive performance. The predictive performance of each model was evaluated using two metrics: the True Skill Statistic (TSS) and the Receiver Operating Characteristic curve (ROC). To ensure adequate predictive precision, only models with a mean TSS value exceeding 0.70 and an ROC value exceeding 0.85 were retained for further analysis (Zhang et al., 2019; Jinbo et al., 2021). Based on the cutoff values for the TSS and the Area Under the Curve (AUC), two ensemble models were constructed: EMca (Ensemble Mean with Committee Averaging) and EMmean (Ensemble Mean) to predict the distribution of humpback dolphins under current environmental conditions.

Studies have indicated that the southwest monsoon during the wet season induces upwelling, which increases nutrient levels in nearshore estuary waters and enhances net primary productivity (Lu et al., 2010). To analyze the specific impacts of monsoons and precipitation on humpback dolphin habitats, we calculated the core habitat area of the dolphins for each year. We obtained annual precipitation data for the Pearl River Basin from the "Guangdong Province Water Resources Bulletin" (http://slt.gd.gov.cn/szygb/) and sourced wind direction data from the ECMWF Reanalysis Dataset (https://www.ecmwf.int/en/forecasts/datasets) for the PRE area. During the dry season, northeast winds predominantly influence precipitation patterns, while southwest winds prevail during the wet season. To quantify the effect of these winds, we defined the sum of all wind vector components directed southwest throughout the year as the annual cumulative impact intensity of the southwest wind. This measure allows us to assess the influence of wind patterns on the habitat and distribution of humpback dolphins in relation to environmental conditions. The calculation formula is as follows (Miao et al., 2018):

$$SW\ Wind\ vector\ component = \sum_{i=1}^{n} \left(\frac{5}{4}\pi - \theta \frac{\pi}{180} \right) \times V$$

N represents the number of wind direction and wind speed data points in a year, θ represents the wind direction angle, and V represents the wind speed.

3. Results and discussion

3.1. Spatial distribution of the humpback dolphins in the PRE

Over a total of 198 boat-based surveys conducted from 2019 to 2023, we recorded 625 sightings of humpback dolphins (Table S1). Given the extensive distribution of dolphin populations, it is expected that field surveys will exhibit varying levels of survey effort across different regions (Félix et al., 2022). In this study, we optimize the methodologies by standardizing the sighting rate per grid. This method significantly mitigates the impact of uneven survey efforts on the seasonal kernel density results for the five-year period. The sighting rate during the dry season was 3.43 groups per survey, while during the wet season, it was 3.02 groups per survey. This seasonal variation in sighting rates can be attributed to adverse weather conditions in the Pearl River Delta during the winter months. During the dry season, humpback dolphins were found to inhabit an average depth of −4.98 m, whereas in the wet season, this average depth was −4.77 m. Additionally, the average sighting distance from the shore was 4.06 km in the dry season and 4.12 km in the wet season, with no significant differences observed between the two seasons. According to previous research, surveys from 2011 to 2015 calculated that in the EPRE the core habitat area of humpback dolphins is approximately 641.32 km^2 (Carmen Or, 2017). Surveys from

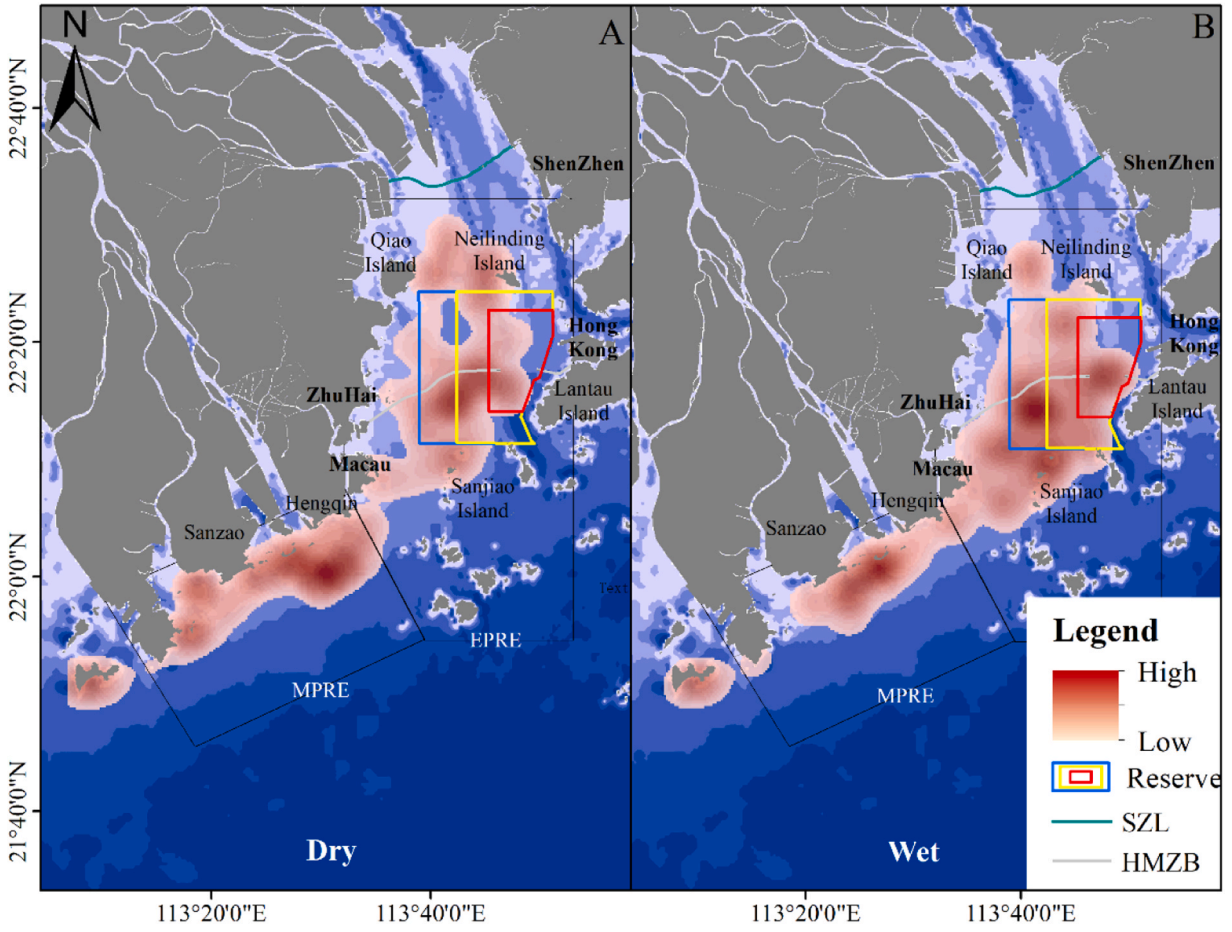


Fig. 2. The kernel density estimation of humpback dolphin sighting rates, showing the habitat distribution of humpback dolphins in the PRE from 2019 to 2023. Distribution of humpback dolphins during the dry (A) and wet (B) season. Dark red represents the high sighting rates of humpback dolphins, light red represents the low sighting rates of humpback dolphins, colored polygon represents national humpback dolphin reserve area. SZL represents Shenzhen-Zhongshan Link, HMZB represents Hong Kong-Macao-Zhuhai Bridge, MPRE stands for the Middle Pearl River Estuary, EPRE stands for the Eastern Pearl River Estuary. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2015 to 2021 obtained that in the entire PRE, the humpback dolphin core habitat area is 3204 km^2 (Guo et al., 2022). Based on our kernel density analysis, the core habitat range of the humpback dolphins in the PRE was determined to be 1170 km^2 for the dry season and 1293 km^2 for the wet season.

In this study, we identified the most recent hotspot for humpback dolphins in the EPRE primarily located on the southern side of the Hong Kong-Macao-Zhuhai Bridge. Meanwhile, the hotspot in the MPRE remains in the Sanzao waters (Fig. 2). Compared to previous research, there has been a noticeable shift in the distribution of relative hotspots. Notably, between 2005 and 2008, humpback dolphins were observed throughout the EPRE, with the northernmost sighting recorded at Humen (Chen et al., 2010). From 2015–2021, the distribution hotspots of dolphins were concentrated around Neilingding Island, the western artificial island of the Hong Kong-Macao-Zhuhai Bridge, and Sanjiao Island (Guo et al., 2022). However, sightings of dolphins around Neilingding Island and Qiao Island have decreased, indicating a potential southward shift in dolphin distribution.

Anthropogenic activities, particularly marine transportation and coastal development, generate persistent underwater noise

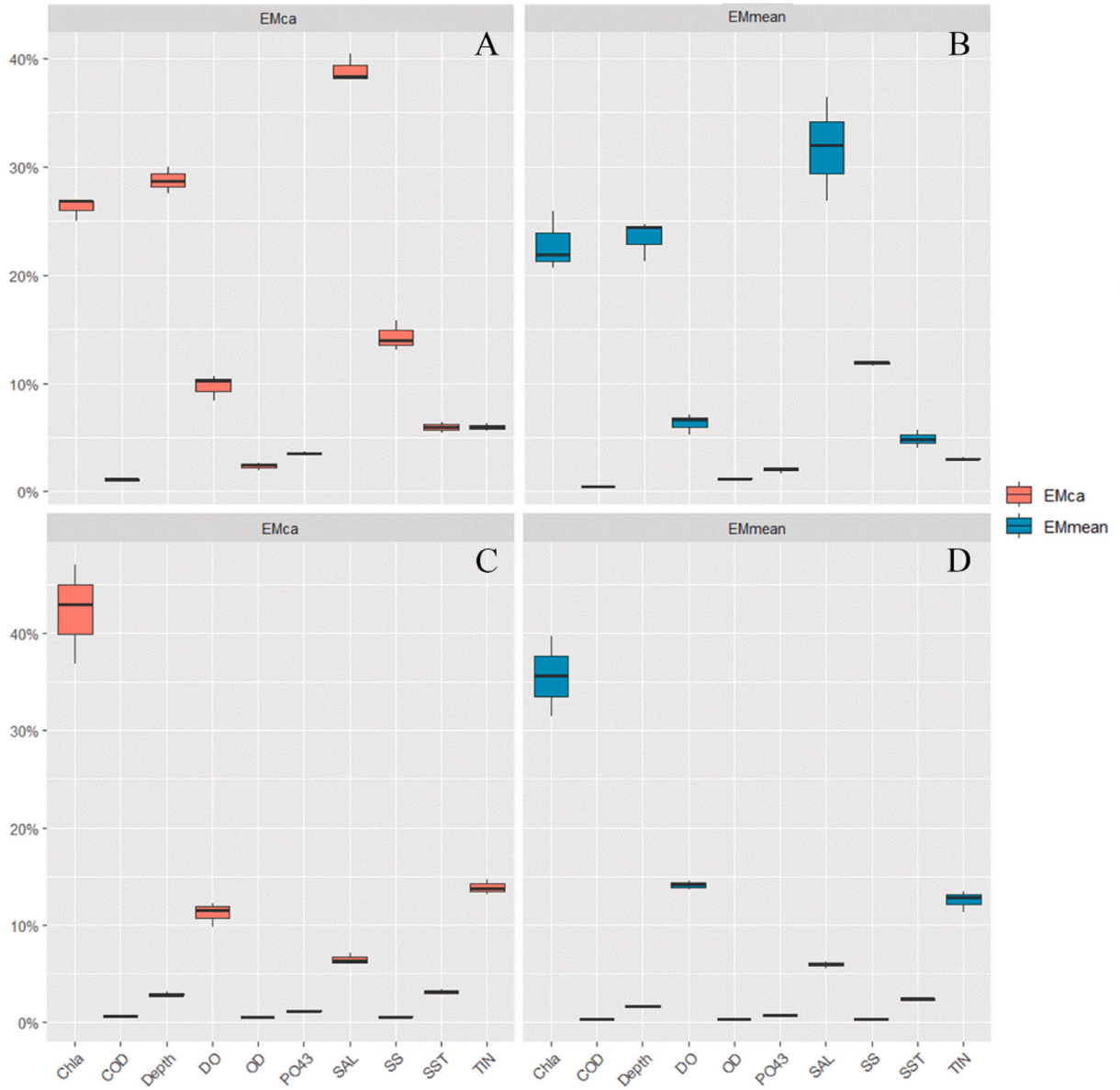


Fig. 3. The significance of ten environmental factors in the habitat models for the dry and wet seasons. (A) The Ensemble Mean with Committee Averaging (EMca) model for the dry season. (B) The Ensemble Mean model (EMmean) for the dry season. (C) The Ensemble Mean with Committee Averaging model for the wet season. (D) The Ensemble Mean model (EMmean) for the wet season. The water quality parameters used are total inorganic nitrogen (TIN), dissolved oxygen (DO), active phosphate (PO43-), salinity (SAL), suspended solids (SS), and chemical oxygen demand (COD). The environment factors used are chlorophyll a (Chla), water depth (Depth), sea surface temperature (SST), salinity (SAL).

pollution that significantly influences dolphin spatial ecology (Piwetz et al., 2021). The PRE, as one of the most heavily trafficked maritime zones in China, exhibits vessel densities capable of fragmenting critical dolphin habitats. Our findings reveal distinct seasonal distribution patterns: humpback dolphins demonstrated stronger coastal affinity during the dry season, while wet season observations documented range expansions into offshore areas. These spatiotemporal patterns appear driven by both natural hydrographic variability and behavioral adaptations to acoustic disturbance (Bridge et al., 2023). Emerging research confirms that vessel-generated noise imposes substantial physiological and ecological costs on coastal cetaceans (López et al., 2019), include chronic stress responses, compromised foraging success, and diminished reproductive performance (Díaz López and Methion, 2024). The PRE's escalating maritime traffic likely constitutes a primary driver of these distributional shifts. We recommend future studies incorporate Automatic Identification System (AIS) data to quantitatively evaluate vessel-dolphin interaction dynamics and their consequences for habitat

The Shenzhen-Zhongshan Link (SZL), representing the second major cross-estuary infrastructure project in the PRE, underwent construction from December 28, 2016 to November 28, 2023. This large-scale marine engineering project involved intensive operations in the central estuary, including high-impact activities such as percussive piling, dredging operations, extensive land reclamation, vessel anchorage, and heavy machinery deployment. These anthropogenic disturbances generated persistent underwater noise pollution, significantly elevated turbidity levels through sediment resuspension, and potentially modified benthic prey distributions (Pirotta et al., 2013), while concurrently altering physicochemical water parameters (Piwetz et al., 2021; Chan and Karczmarski, 2024). Given the ecological sensitivity of Indo-Pacific humpback dolphins and their reliance on acoustic cues for navigation, foraging, and communication (Wang et al., 2019; Song et al., 2024), such disturbances may have had direct behavioral impacts (e.g., avoidance, stress) or indirect effects through habitat degradation and prey displacement.

3.2. *The influence of ecological factors on the difference of seasonal distribution*

While there is a foundational body of research on the distribution of humpback dolphins in the PRE (Chen et al., 2010; Guo et al., 2022), there remains a need for more refined exploration of their habitat dynamics. Our results indicate that the distribution of humpback dolphins exhibits seasonal variations (Fig. 2). During the dry season, the core habitat range in the EPRE becomes discontinuous and reduced, with the upper boundary shifting slightly further north. In contrast, the habitat range in the MPRE is larger; however, the southwestern part of Macau experiences a discontinuity in its habitat. Conversely, in the wet season, the habitat range south of Hengqin Island decreases (Fig. 2), while the habitat range in the EPRE expands and shifts southward. This seasonal pattern aligns with findings from previous studies (Lin et al., 2015; Wang et al., 2016). Quantitatively, the habitat area in the EPRE increased from 738 km^2 in the dry season to 822 km^2 in the wet season, representing a gain of 84 km^2. In contrast, the habitat area in the MPRE decreased significantly, from 408 km^2 to 213 km^2, resulting in a loss of 195 km^2.

During the dry season, all models demonstrated satisfactory predictive performance, with the exception of the SRE and ANN models, which exhibited poor results. Following the exclusion of these two models, ensemble models were developed, specifically the EMca and EMmean models. These ensemble models achieved TSS and ROC values of 0.83 and 0.97 for EMca, and 0.79 and 0.96 for EMmean, respectively. In both the EMca and EMmean models, the top three most important environmental variables influencing humpback dolphin distribution were identified as salinity, depth, and Chla concentration (Fig. 3). In the wet season, the ANN model again demonstrated poor predictive performance, while the other models performed effectively. After excluding the ANN model, ensemble models were created, resulting in the EMca and EMmean models achieving higher TSS and ROC values of 0.97 and 0.99 for EMca, and 0.95 and 0.99 for EMmean, respectively. The top three most important environmental variables during the wet season were Chla concentration, total inorganic nitrogen, and dissolved oxygen content (Fig. 3). Notably, the concentration of Chla was recognized as an important factor in both seasonal models, indicating its critical role in influencing the habitat preferences of humpback dolphins throughout the year. These findings emphasize the significance of environmental variables in predicting dolphin distribution and highlight the effectiveness of ensemble modeling approaches in ecological studies.

Food resources are widely recognized as the most direct factor affecting dolphin distribution (Lin et al., 2021a; Sun et al., 2022). The seasonal spatial distribution differences of humpback dolphins may be closely linked to fishery resources and various ecological factors. The observed reduction in the habitat area of humpback dolphins in the MPRE during the wet season may be associated with the migration of food resources due to fish spawning. Specifically, the prey fish that humpback dolphins target spawn near the shore in spring (Shanshan et al., 2018), resulting in a richer food supply for the dolphins during the dry season. Research indicates that Indo-Pacific humpback dolphins tend to prefer feeding on benthic fish (Lin et al., 2021b). Furthermore, studies have shown that the distribution of cetaceans in tropical waters is influenced by dissolved oxygen levels (Mannocci et al., 2015). The PRE is particularly susceptible to seasonal hypoxic events (Liu et al., 2020), which may further impact cetacean distribution in this region. Sighting rates of humpback dolphins in hypoxic areas are consistently lower than in non-hypoxic regions (Guo et al., 2022). Hypoxia typically affects the survival of benthic fish, which in turn indirectly impacts dolphin populations. This relationship may help explain the influence of dissolved oxygen on dolphin distribution during the wet season. Additionally, studies have demonstrated that in the PRE, a decline in dissolved oxygen levels is often associated with an increase in dissolved inorganic nitrogen (DIN) concentrations (Qian et al., 2018). This phenomenon is largely attributed to the eutrophication of water bodies, recognized as a significant contributing factor to these changes. During the wet season, elevated DIN concentrations lead to eutrophication in coastal waters, promoting phytoplankton growth and thereby increasing biological resources in the area (Ke et al., 2022). Fishery resource surveys conducted in the PRE indicate that hypoxic conditions frequently occur in the bottom waters of the MPRE during the wet season (Lai et al., 2024). Under these hypoxic conditions, the abundance of key fish species that constitute the primary diet of humpback dolphins, such as *Coilia mystus* and *Collichthys lucidus* (Ning et al., 2020; Lai et al., 2024), significantly decreases. This decline in prey availability is likely a direct factor

contributing to the lower sighting rates of humpback dolphins in these regions. Understanding these ecological dynamics is crucial for conservation efforts aimed at protecting the habitat and food resources essential for the survival of humpback dolphins in the PRE.

Depth is a significant factor influencing the distribution of humpback dolphins during the dry season, with a response curve indicating an optimal distribution range of 0–20 m. Shallower waters enhance the feeding efficiency of humpback dolphins, as they can more easily access benthic prey (Huang et al., 2019). This depth-related distribution pattern may be explained by the availability of food resources in these shallower areas (Pitchford et al., 2016). During the dry season, lower concentrations of Chla can lead to scarcer food resources, further impacting the habitat preferences of humpback dolphins. As small coastal cetaceans, humpback dolphins typically inhabit estuarine environments, where salinity levels can range from fresh water to sea water (Dares et al., 2014). While salinity itself may not directly affect the distribution of humpback dolphins, it can indirectly influence the Chla content, which is crucial for the availability of their prey. Additionally, low salinity often indicates significant fresh water input into the estuary. This influx can lead to increased turbidity, which may have several ecological consequences (Liu et al., 2016). Increased turbidity can reduce light penetration, adversely affecting phytoplankton growth and, consequently, the overall productivity of the ecosystem. This chain of effects can further influence the distribution and abundance of prey species, ultimately impacting the foraging success of humpback dolphins.

The results of this study suggest that the seasonal distribution of Indo-Pacific humpback dolphins is influenced by both passive responses to prey availability and active habitat selection based on environmental preferences. During the wet season, factors such as chlorophyll-a and dissolved oxygen play a major role in shaping habitat use, as increased primary productivity enhances prey abundance, leading to dolphin aggregations in productive areas (Huang et al., 2019). Conversely, during the dry season, physical environmental factors such as salinity and water depth appear to be more dominant, potentially due to their direct physiological effects on dolphin survival and foraging behavior (Serres et al., 2024). This dual selection mechanism indicates that dolphins do not solely track prey movements but also actively seek optimal environmental conditions, as a small odontocete species inhabiting dynamic coastal and estuarine environments, Indo-Pacific humpback dolphins have likely evolved specialized physiological and behavioral adaptations to cope with fluctuations in salinity and water quality (J. Parra et al., 2006). Despite interannual environmental variations, our study found that their core habitat areas remained relatively stable, indicating that habitat selection is driven by a combination of environmental suitability and prey availability rather than short-term fluctuations in food resources alone.

In summary, bathymetry and chlorophyll-a concentrations emerge as key determinants of humpback dolphin distribution during the dry season, while salinity exerts multifaceted influences through its role in shaping estuarine ecosystem dynamics. These findings

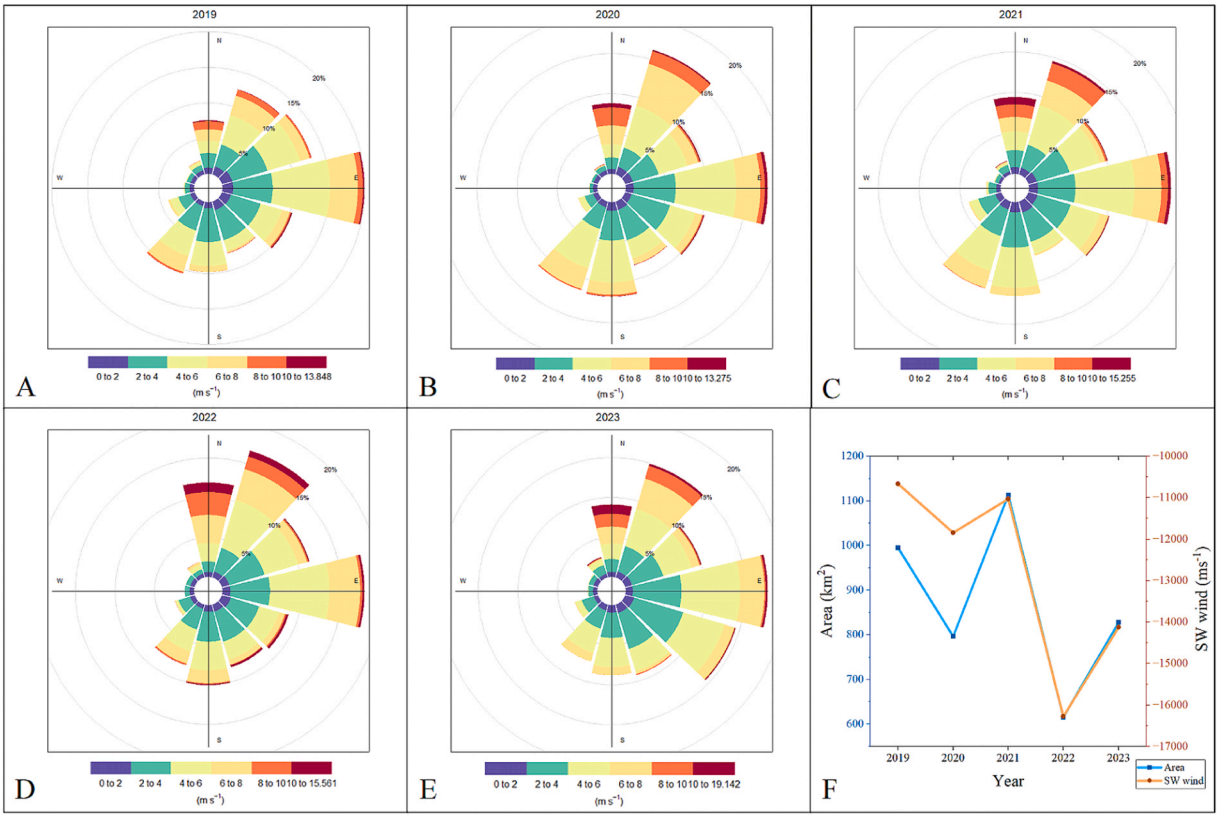


Fig. 4. Wind rose diagram for the year (A) 2019. (B) 2020. (C) 2021. (D) 2022. (E) 2023. (F) Annual southwesterly wind vector component and the trend of changes in the core habitat area of the Indo-Pacific humpback dolphin, SW represents Southwest.

underscore the importance of considering both direct habitat requirements and indirect ecological interactions when developing conservation strategies. A comprehensive understanding of these complex habitat relationships is crucial for implementing effective management measures to ensure the long-term viability of humpback dolphin populations in the Pearl River Estuary ecosystem.

3.3. The influence of climate factors on the difference of seasonal distribution

This study suggests that precipitation and monsoons play a significant role in evaluating and predicting humpback dolphin habitats across different seasonal periods. To better understand these influences, annual average wind rose diagrams for the PRE region were meticulously constructed to delineate the predominant wind patterns (Fig. 4 A-E). The prevailing wind directions in the PRE are characterized by northeasterly, easterly, and southwesterly winds, with minimal influence from the northwesterly direction. An analysis of the correlation between the annual core habitat area of the humpback dolphin and the aggregate impact intensity of the southwest monsoon reveals a striking congruence in their respective trends (Fig. 4 F). The southwest monsoon, which prevails during the wet season, pushes seawater in the eastern part of the PRE toward the open sea and generates upwelling (Wang and Yin, 2021). This upwelling enriches the eastern waters of the PRE with nutrients, thereby enhancing the net primary productivity of the area. As a result, there is a broader distribution of benthic fish in this region (Li et al., 2023), which may explain the observed expansion of humpback dolphin habitats in the eastern part of the estuary (Lai et al., 2022). Although the temporal scope of this study is limited, which restricts the statistical power to detect significant correlations between these variables, a compelling association is still evident. Given the increasing impacts of anthropogenic climate change, characterized by extreme weather events and alterations in monsoonal patterns, it is hypothesized that years with reduced cumulative southwest wind intensity may correlate with a decrease in the core habitat area of humpback dolphins. This potential relationship underscores the importance of understanding how climate variability and changing weather patterns can influence marine ecosystems and the species that inhabit them. Future research with a longer temporal scope may provide deeper insights into these dynamics and help inform conservation strategies for humpback dolphins in the context of a changing climate.

An examination of the habitat distribution area of humpback dolphins and annual precipitation in the Pearl River Basin from 2019

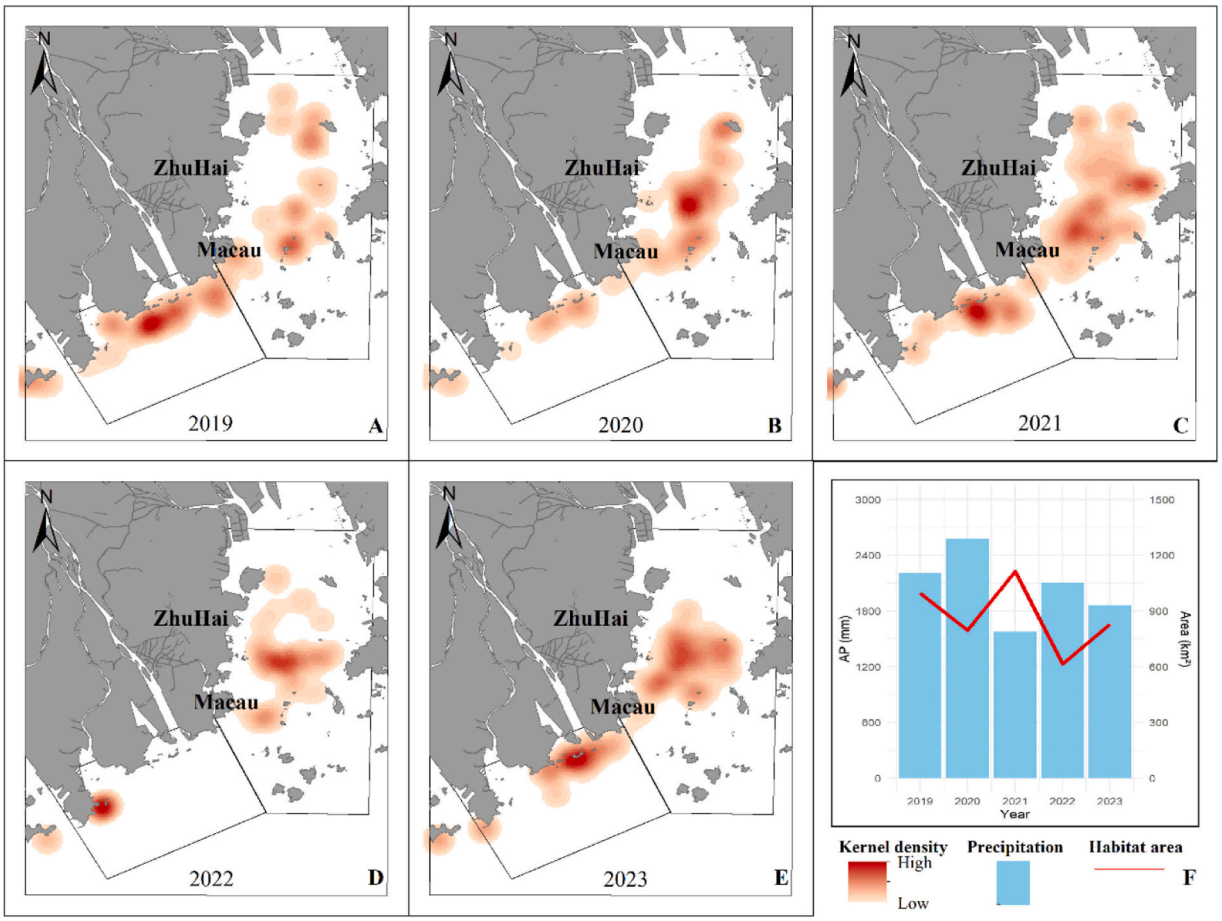


Fig. 5. Distribution of the Indo-Pacific humpback dolphin's core habitat in (A) 2019. (B) 2020. (C) 2021. (C) 2022. (E) 2023. (F) Trend chart of the annual average precipitation in the PRE and the annual change in the core habitat area of humpback dolphins, AP represents annual precipitation.

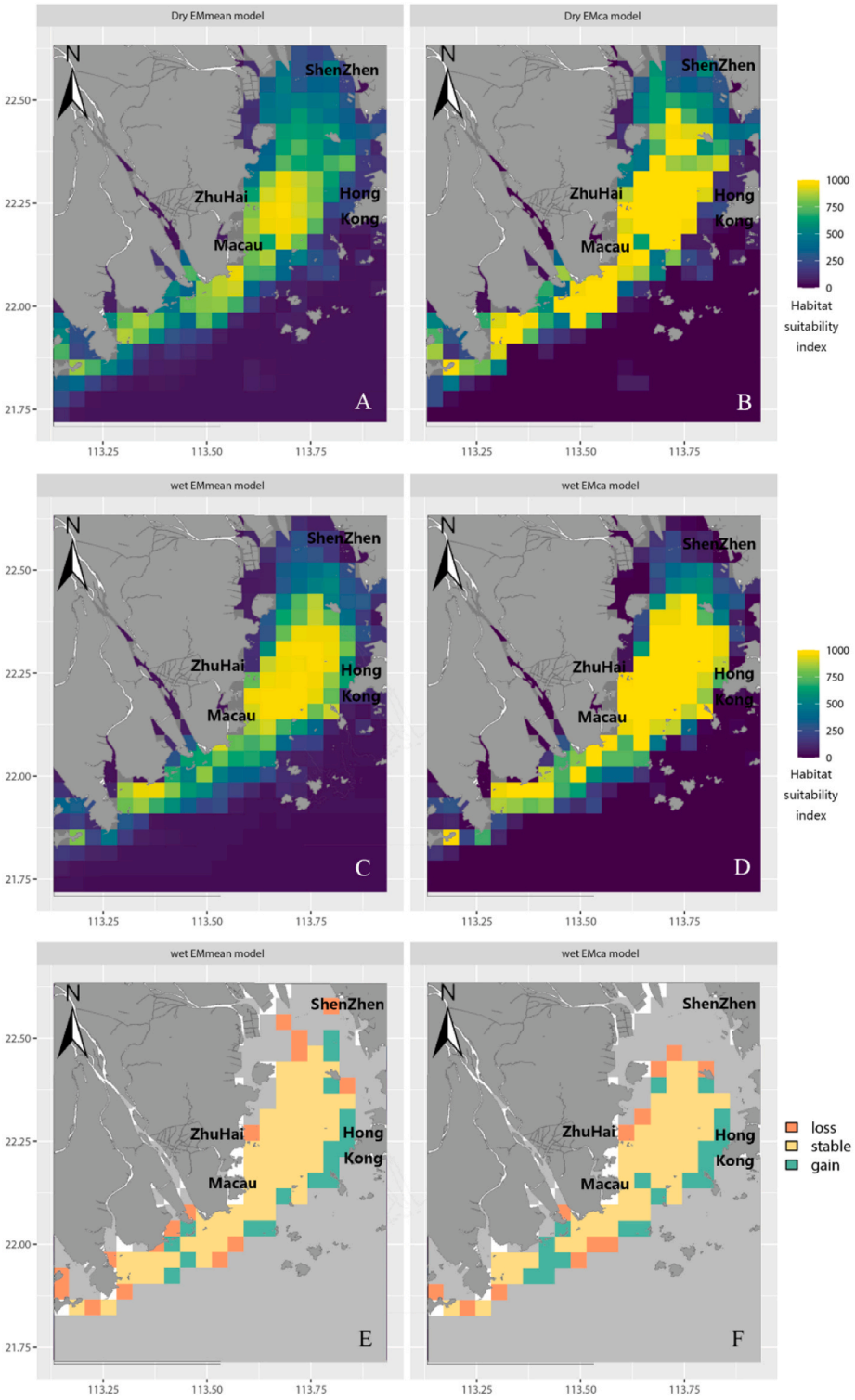


Fig. 6. The predicted habitat suitability indices provided by two ensemble models under dry and wet season conditions, with the range spanning from 0 to 1000. (A) Habitat predictions given by the Ensemble Mean (EMmean) model and (B) the Ensemble Mean with Committee Averaging (EMca) model in the dry season. (C) Habitat predictions given by the Ensemble Mean (EMmean) model and the (D) Ensemble Mean with Committee Averaging (EMca) model in the wet season. (E) Habitat changes calculated by the Ensemble Mean (EMmean) model and (F) the Ensemble Mean with Committee Averaging (EMca) model.

to 2023 revealed an inverse relationship between precipitation levels and habitat size (Fig. 5). Following heavy rainfall, increased river flow can significantly alter water quality, affecting important parameters such as turbidity and salinity. Such temporary fluctuations in water quality may affect the physiological health of dolphins and interfere with the distribution and movement of their prey (Fury and Harrison, 2011). Previous studies have suggested that a substantial influx of estuarine freshwater can lead to an increase in organic matter (Wu et al., 2024), thereby might enhance the productivity of the estuary and increasing the food sources for humpback dolphins. However, excessive freshwater flow in the PRE can also lead to a dilution effect, resulting in reduced Chla concentrations. Increased turbidity can further diminish photosynthetic rates and overall primary productivity (Shen et al., 2022). While it is commonly accepted that coastal upwelling brings nutrients from deeper waters to the surface, the presence of buoyancy layers—such as estuarine plumes and river outflows—can inhibit the Ekman effect (Wang and Yin, 2021). This suppression of the Ekman effect limits upwelling and reduces nutrient transport within the PRE, ultimately affecting the availability of food resources for humpback dolphins.

In summary, while increased precipitation may initially enhance ecosystem productivity through organic matter input, the concomitant alterations in water quality parameters can negatively impact dolphin habitat suitability. The intricate interactions between freshwater discharge, suspended sediment loads, and nutrient cycling underscore the ecological challenges confronting humpback dolphins in the Pearl River Basin. These challenges are particularly pronounced given current climate variability and projected shifts in precipitation regimes. A thorough understanding of these ecosystem dynamics is paramount for formulating science-based conservation strategies that safeguard critical habitat features and trophic resources necessary for the persistence of humpback dolphin populations in this region.

3.4. *Protected area planning strategy of the humpback dolphins in the PRE*

Based on the constructed models for the dry and wet seasons, an assessment and prediction of the potential habitat of humpback dolphins in the PRE were conducted (Fig. 6). During the dry season, the habitat of humpback dolphins is more dispersed and located closer to the interior of the PRE. In contrast, during the wet season, their habitat becomes more concentrated, particularly in the EPRE.

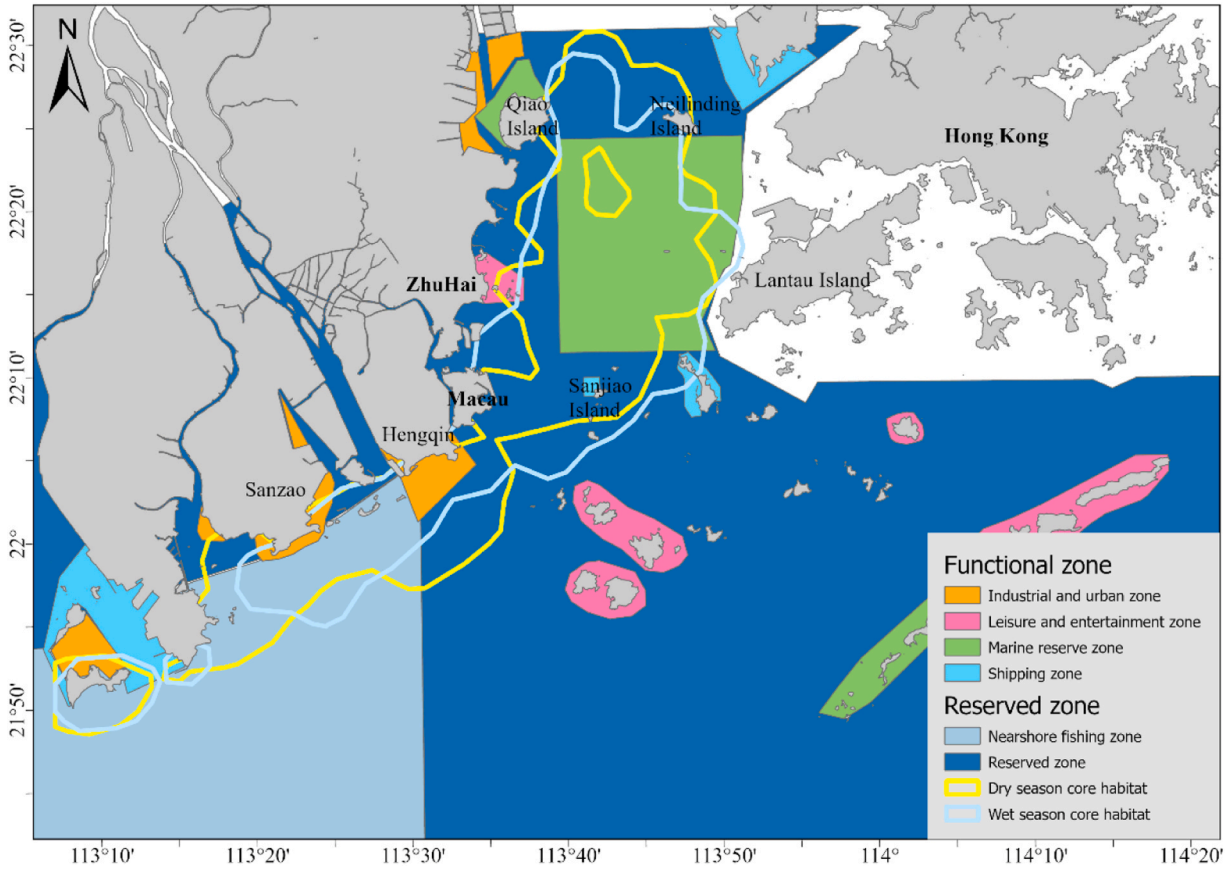


Fig. 7. The distribution range of the core habitat of the humpback dolphins in two seasons and the sea use plan of Zhuhai City. Among them, the different color lines represent the habitat range of the humpback dolphin in the two seasons, and the different color blocks represent the four artificially planned marine functional zones. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Notably, the suitability of the humpback dolphin's habitat in the MPRE appears to decline during the dry season. The EMca model indicates that in the wet season, the boundary of the humpback dolphin's habitat in the EPRE extends further eastward, bringing their habitat range closer to the waters of Hong Kong. The migration pattern is consistent with the previous study, which demonstrated that the movement is primarily driven by fish resources (Chan and Karczmarski, 2017). This shift suggests that seasonal changes significantly influence the distribution patterns of humpback dolphins in the PRE. Furthermore, we analyzed the TSS values provided by each grid from both models to calculate the increase and disappearance of humpback dolphin habitat grids from the dry season to the wet season (Fig. 6). According to the results constructed by the EMmean model, there was an increase of 1.29 % in the habitat area from the dry season to the wet season. In contrast, the EMca model indicated a more substantial increase of 11.11 % in the habitat area during the same period. Spatially, it can be observed that the habitat in the EPRE shows a trend of moving eastward and southward. In the MPRE, during the wet season, the habitat is found closer to the land, and its range becomes narrower (Fig. 6). This spatial redistribution highlights the dynamic nature of humpback dolphin habitats in response to seasonal changes in environmental conditions, such as water quality and prey availability. Overall, these findings underscore the importance of understanding the seasonal dynamics of humpback dolphin habitats in the PRE, which can inform conservation efforts and management strategies aimed at protecting this vulnerable species in the face of environmental changes. By recognizing the factors that influence habitat suitability, stakeholders can better address the needs of humpback dolphins and ensure their continued survival in this critical estuarine ecosystem.

Identifying the core habitats of wildlife populations is essential for developing effective conservation strategies (Fahrig, 2013). The Humpback Dolphin National Reserve in the PRE was established in 1999, covering an area of 460 km^2. Despite this protection, the population of humpback dolphins in the PRE continues to decline (Huang et al., 2012; Luo et al., 2024a), indicating that current conservation actions require significant improvement. The coverage of the existing PRE Indo-Pacific Humpback Dolphin National Nature Reserve is quite limited in relation to the core habitats of these dolphins. During the dry season, 363 km^2 of the reserve overlaps with the humpback dolphin's core habitat, which accounts for 78.91 % of the total area of the reserve. In contrast, during the wet season, the habitat area within the reserve increases to 395 km^2, representing 85.86 % of the total reserve area. These highlight the importance of reassessing the boundaries and management strategies of the existing reserve to better align with the seasonal distribution patterns of humpback dolphins. Given the significant portion of their core habitat that falls within the reserve, enhancing conservation efforts in these areas could be vital for the survival of the species. It is essential to consider factors such as habitat quality, prey availability, and environmental changes when planning conservation actions. By focusing on the critical habitats identified through this research, conservationists can implement more targeted measures to protect humpback dolphins and address the ongoing threats they face in the PRE. Enhanced protection and management of these core habitats will be essential for reversing the declining trends in humpback dolphin populations and ensuring their long-term survival in this ecologically important region.

The marine functional zoning analysis indicates a significant lack of policy protection for humpback dolphins in the MPRE area (Fig. 6). Notably, the planned industrial urban zone in the southern part of Hengqin Island overlaps extensively with the habitat range of humpback dolphins in both the dry and wet seasons. This overlap raises concerns that excessive human activities in this region, if conducted under the current policy framework, could weaken the population connectivity between the EPRE and MPRE. To address these challenges, we propose that the areas where humpback dolphins are present in both seasons be formally included in the protection scope designated for this species. Additionally, we recommend that areas experiencing seasonal changes in dolphin presence be designated as dynamic protection zones. This approach would allow for adaptive management strategies that respond to the seasonal fluctuations in dolphin habitat use.

3.5. Description of limitations

This study employed environmental variables with reliable, continuous spatial and temporal coverage to model seasonal distribution patterns of Indo-Pacific humpback dolphins in the Pearl River Estuary. However, critical anthropogenic variables including vessel traffic density, acoustic disturbance levels, and fisheries interactions could not be incorporated due to insufficient standardized, high-resolution, and temporally consistent datasets. This limitation underscores the importance of developing integrated monitoring programs to facilitate future incorporation of human activity metrics into cetacean habitat models, enabling more comprehensive assessments of cumulative environmental and anthropogenic impacts on dolphin spatial ecology.

While our survey methodology prioritized individual identification and movement tracking in this challenging estuarine environment over strict line-transect protocols, we acknowledge this approach precluded absolute density estimation. Instead, we utilized standardized sighting frequencies per sampling grid as an index of relative habitat preference—a well-established proxy measure in similar complex coastal systems. When combined with systematic multi-year sampling effort and photo-identification validation, this methodology provides robust, ecologically meaningful data on spatiotemporal distribution patterns despite its inherent limitations for population density estimation.

4. Conclusion

Understanding habitat use patterns and assessing diffusion status are essential for effective conservation of cetaceans. This study conducted a seasonal investigation of the currently known largest habitat of the humpback dolphins. Our results indicate significant seasonal variations in dolphin habitat, we also explored the impact of environmental factors and climate factors on the humpback dolphin habitats. This research enhances our understanding of how environmental factors influence dolphin distribution and habitat use. Additionally, the findings of this study are instrumental for relevant authorities in making timely adjustments to spatial planning and management strategies for conservation areas. The insights gained from this research can help inform decision-makers about the

critical habitats that require enhanced protection and the potential impacts of human activities on dolphin populations. Moreover, this study underscores the urgent need for ongoing research and monitoring to clarify the complex interactions between climatic variables and the ecological integrity of habitats for marine species. Understanding these dynamics is essential for developing adaptive management practices that can respond effectively to environmental changes and ensure the long-term survival of humpback dolphins in the Pearl River Estuary. Continuous research efforts will not only contribute to the conservation of this vulnerable species but also support broader marine ecosystem health and resilience in the face of climate change and human pressures.

CRediT authorship contribution statement

Xikai Tang: Investigation, Methodology, Formal analysis, Writing – original draft. **Dingyu Luo:** Investigation, Methodology, Formal analysis, Writing – original draft. **Xian Sun:** Conceptualization, Supervision, Writing – review & editing. **Bin Sun:** Investigation. **Lang Guo:** Investigation. **Hongri Wang:** Investigation. **Nuoyan Huang:** Investigation. **Yifei Liu:** Investigation. **Zhiwei Liu:** Writing – review & editing. **Nan Wang:** Formal analysis. **Yuping Wu:** Conceptualization, Supervision.

Ethical statement

The authors declare that the research conducted in this study complies with all relevant ethical guidelines and regulations. No human participants were involved in the study. For studies involving animals, all fieldwork and data collection were conducted in accordance with local wildlife protection laws and guidelines, and any necessary permits were obtained from the appropriate authorities. No endangered or protected species were harmed during the course of this research.

Declaration of Competing Interest

No potential conflict of interest was reported by the authors

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03639.

Data availability

Data will be made available on request.

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