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Spatiotemporal variations and driving factors of fine-scale habitat use by the Yangtze finless porpoise population in the Yangtze River

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Abstract

Background The Yangtze finless porpoise (*Neophocaena asiaeorientalis asiaeorientalis*) is critically endangered and has suffered from extensive habitat loss and fragmentation. Knowledge of its habitat preference could assist the conservation of the species and associated ecosystem. In the present study, spatiotemporal variations and driving factors of habitat use of a Yangtze finless porpoise population were studied in a 30-km section of the Yangtze mainstream. Seasonal variation in porpoise occurrences was observed based on visual surveys conducted from 2022 to 2023, with five surveys during the dry season and seven surveys during the wet season. Biological and environmental factors were synchronously sampled in both seasons. The maximum entropy model (MaxEnt) was applied to get the effects of biological and environmental variables on porpoise habitat preference.

Results Within the study area, high-suitability habitats of the finless porpoises accounted for 19.0% and 15.4% of the area during the dry and wet seasons, respectively. The high-suitability habitat shifted from the mainstream in the dry season to the sandbar head and tributary area in the wet season. In the dry season, variables influencing the distribution were phytoplankton biomass, water velocity, and zooplankton biomass, which contributed 97.05% variation in the MaxEnt modeling. In the wet season, water depth, surface water temperature, and zooplankton biomass accounted for 97.69% variation of the distribution. Above results highlight that food availability plays an important role in porpoises distribution regardless of seasons, particularly in the dry season. This is because plankton is the primary food source for filter-feeding and omnivorous fish, especially those in the upper-middle layer which are frequently preyed on by finless porpoises.

Conclusion Suitable areas for finless porpoises, particularly those with high suitability, differed significantly across seasons at a fine-scale in the Yangtze mainstream. Seasonal variations in habitat were driven by different factors. But food availability plays an important role in porpoises distribution regardless of seasons, particularly in the dry season. These results suggest prioritizing conservation of the finless porpoise in the dry season when fish resources are relatively scarce. Measures including monitoring and evaluating prey resources should be considered. More attention should also be paid on management of shipping in the dry season given that the high-suitability habitat of the finless porpoises shifts to the mainstream.

Keywords Yangtze finless porpoise, Habitat suitability, Habitat selection, Freshwater cetacean conservation

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Background

Understanding how animals use their habitats and how environmental and ecological factors influence animal distribution is one of the most fundamental aspects of ecology and critical for conservation of threatened species [1–5]. This is especially important for cetaceans living in freshwater ecosystems that are closely connected to human activities because almost all freshwater cetacean populations suffer from habitat loss [6–8]. Habitat loss is one of the primary causes for extinction of freshwater cetacean populations (e.g., Baiji (*Lipotes vexillifer*) [7]) and for critically endangering species (e.g., Irrawaddy dolphins (*Orcaella brevirostris*), Ganges River dolphins (*Platanista gangetica*) [8–10], and Yangtze finless porpoises (*Neophocaena asiaeorientalis asiaeorientalis*) [11–15]). Cetaceans are highly selective in habitat utilization which is influenced by a variety of factors, including water depth, flow velocity, eddies, water surface temperature, and prey availability [3, 9, 16]. Research on habitat use and the underlying impact factors on freshwater cetacean populations would provide a more comprehensive understanding of habitat distribution and help prioritize conservation efforts [9, 17, 18].

The Yangtze finless porpoise is a small critically endangered species endemic to the Yangtze River drainage, which is primarily restricted to the middle-lower Yangtze mainstream and two large appended lakes [19, 20]. The population size has suffered a remarkable decline due to the heavy impact of human activities, including overfishing of prey species, water development projects that cause habitat loss and degradation, water pollution, and accidental deaths [11]. Further, the finless porpoise's habitat loss is expected to worsen in the future because of channel improvement, shipping development, and coastal engineering [14, 15, 21]. Habitat conservation and restoration have emerged as critical components of finless porpoise conservation [13]. Previous findings regarding finless porpoises habitat utilization reveal that approximately 80% of Yangtze finless porpoises inhabit the near-bank stratum 300 m offshore [22, 23]. Finess porpoises stay away from the waters of artificial riverbanks and are mainly distributed in the nearshore waters of natural riverbanks [15, 24], with strong preferences for shallow and slow current waters, sandbar areas, and confluences [4, 22, 23]. While these studies were conducted on a large scale, fluvial aquatic species, including freshwater cetaceans, are frequently unevenly distributed and are primarily influenced by small-scale hydrological characteristics and prey availability [25]. This suggests that understanding fine-scale habitat selection can provide insights into the fundamental characteristics of habitat use [16, 26]. Quantitative studies on how finless porpoises exploit specific habitats in the Yangtze mainstream in different seasons, as well as driving forces are extremely limited. At present, this kind of research is only carried out in estuary areas and only fish resources have been considered the driving force [27–30]. Estuary areas are unique habitats for finless porpoise, and prey resource cannot completely explain cetacean distribution, particularly among relatively shallow diving cetaceans [26, 31]. For example, the Yangtze finless porpoises preferred to inhabit the head and tail water areas of the Qinjie Sandbar in the Yangtze mainstream [32], but no differences in fish resources were found between the head, sides, and tail waters of the sandbar [33]. Therefore, we addressed the following questions: Do porpoises display seasonal differences in habitat utilization in a certain section of the Yangtze main channel? What are the main factors causing seasonal differences?

The Taiziji section of the Yangtze mainstream is a hotspot for the Yangtze finless porpoise population [32]. In this study, porpoise numbers and sighting locations were collected during the dry and wet seasons to detect spatiotemporal variations in habitat use. Furthermore, biological and environmental factors were collected using uniform sampling for quantitative analysis of factors affecting finless porpoises habitat selection. Cetacean habitat utilization is influenced by a variety of factors including water depth, flow velocity, eddies, sea surface temperature, and prey availability [3, 9, 16]. In Poyang lake, the biggest lake habitat of the Yangtze finless porpoise, water depth is the most important environmental factor determining the distribution of finless porpoises across all seasons [5]. In an *ex situ* reserve, Mei [4] found that Yangtze finless porpoises preferred water areas with moderate water depth, flat benthic slope, and moderately high fish density. This study hypothesized that spatial distribution of finless porpoises in the Yangtze mainstream is influenced by some of the same factors as other cetaceans and the finless porpoise in static waters such as lake or *ex situ* reserve. As a result, we collected data on the depth and velocity of the flow, as well as plankton and phytoplankton biomass, and surface temperature. The habitat usage of animals can serve as an indicator of habitat suitability for species and individuals [34]. The goal of this study was to gain a better understanding of how porpoises use their habitats and provide information for management and conservation of finless porpoise habitats.

Materials and methods

Study area

The study area is located in the lower reaches of the mainstream of the Yangtze River, Zongyang, Tongling City, Anhui Province, with a length of approximately 30 km and a total water area of approximately 43 km^2 (Fig. 1). This section which is usually called Taiziji by local people is characterized by a large sandbar in the middle of the

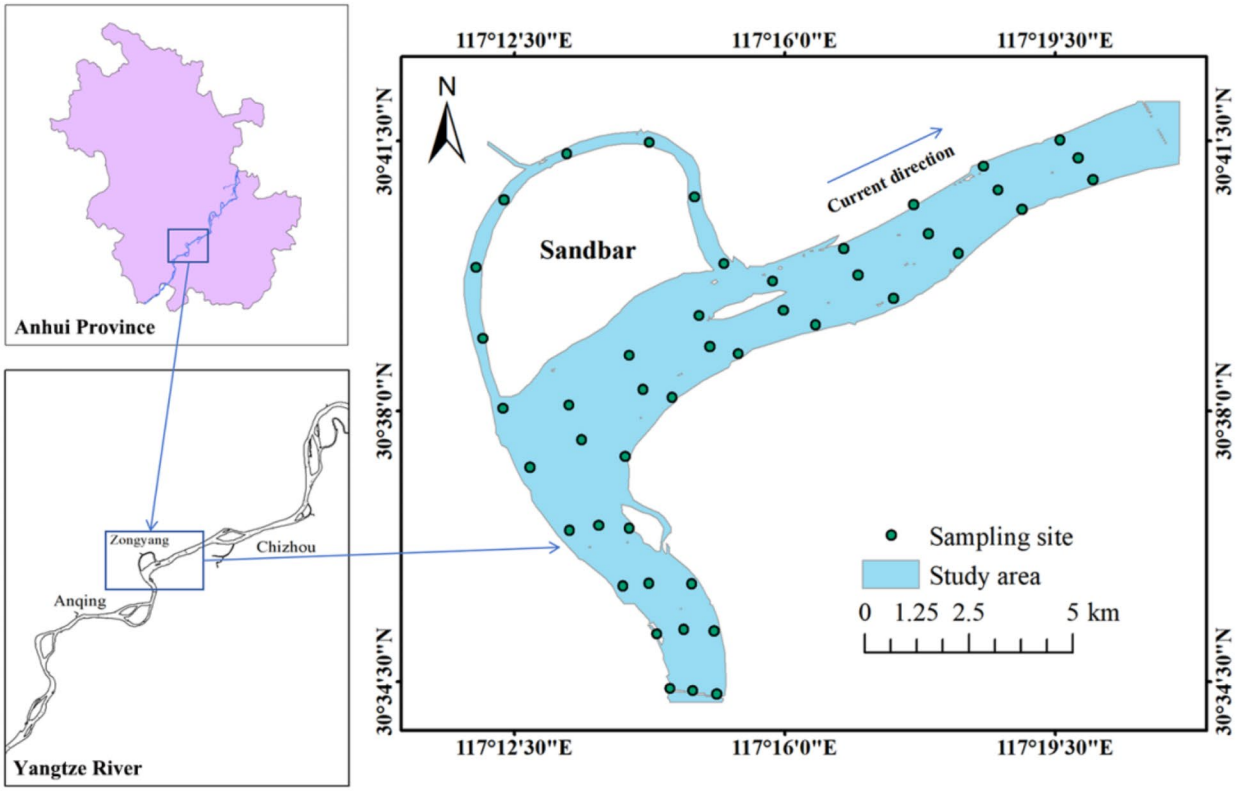

Fig. 1 Study area and sampling sites

river, which is a typical sandbar-type habitat of the finless porpoise in the lower reaches of the Yangtze River [32, 35]. This type of habitat is widespread in the lower reaches of the Yangtze River and is frequently inhabited by high concentrations of porpoises [35].

Field surveys

The group size and locations of the Yangtze finless porpoises were investigated through visual observations from two small boats. Twelve visual surveys were conducted, with five surveys completed during the dry season when water level and flow rate were both low (from November 2022 to March 2023) and seven surveys conducted during the wet season when water level was high and flow rate was fast (from June to August 2023). During each survey, boat speeds were maintained at 8–14 km h^{-1}, which is significantly faster than the swimming speed of porpoises (4.5 km h^{-1}) [36]. Surveys were conducted in sunny or cloudy conditions with winds below Level 3, because under these conditions, the sight was clear, the river surface was calm, and finless porpoises could be effectively observed. Sighting information regarding finless porpoises, including sighting time, GPS locations, group size, and distance from the sighting to the nearest river bank, were recorded. The survey routes ran parallel to the riverbanks, with three routes along the mainstream (left, middle, and right sides) and one route along the tributary. The small vessels provided effective visual coverage of approximately 300 m in width. The four survey routes covered the entire study area.

Biological and environmental factor data collection

Data were collected across two seasons: dry (December 2022) and wet (August 2023). Sampling sites were placed every 2 km along the visual survey routes, totaling 45 sampling sites (Fig. 1). Biological factors included zooplankton and phytoplankton biomass (mg/L), as well as environmental factors such as water depth (m), surface water temperature (°C), and flow velocity (m/s) were collected. Zooplankton collection and processing were performed as described by Shen [37]. Chen [38] detailed the methods for collecting and processing phytoplankton. Water depth was measured using a depth sounder (VA, USA), whereas surface water temperature and flow velocity were monitored using a Doppler flow meter (SonTek-M9; SonTek Inc., San Diego, CA, USA).

Data analysis

Mann-Whitney U-test was used to detect differences in porpoise abundance between seasons. Biological and environmental factors were processed using the Kriging interpolation method in ArcGIS 10.8 (Environmental

Systems Research Institute, Inc., Redlands, CA, USA). MaxEnt model has excellent predictive accuracy and can quantitatively characterize the habitat distribution of species and changes in biological and environmental factors through the screening of major ecological and environmental factors. MaxEnt model has been widely used in the evaluation of habitat suitability for cetaceans [39, 40]. An initial model was established by including Yangtze River finless porpoise distribution data and five environmental factors, with 75% of the distribution points set as the training set and 25% as the test set. The maximum number of background points was set to 10,000, the maximum number of iterations to 500, and the model was run 10 times with all other parameters remaining constant. The predictive accuracy of the model was evaluated using the average area under the receiver operating characteristic curve (AUC). The criteria were as follows: $0.5 \leq AUC < 0.6$, fail; $0.6 \leq AUC < 0.7$, poor; $0.7 \leq AUC < 0.8$, fair; $0.8 \leq AUC < 0.9$, good; $0.9 \leq AUC < 1.0$ [39]. The higher the AUC score, higher the accuracy of the model prediction and evaluation of potential habitats for the Yangtze finless porpoise. The Jackknife approach was used to examine the importance and contribution of environmental variables to the model prediction, and the responses of key variables were analyzed using the probability of the presence of the Yangtze finless porpoise. In ArcGIS 10.8, the habitat range of Yangtze finless porpoise was determined by the median of the cumulative results, and a cumulative probability of 5% was defined as a high suitability area, 5–35% as a medium suitability area, and >35% as a low suitability area [40].

Results

Porpoise number and distribution

A total of 36 sightings of 69 porpoises were recorded, with an average of 5.83 ± 2.98 individuals seen per survey. During the dry season, 18 sightings of 32 porpoises were documented, with an average of 6.40 ± 1.95 individuals observed per survey. During the wet season, there were 18 sightings of 37 porpoises, with an average of 5.29 ± 3.45 individuals seen per survey (Table 1). There was no significant change in the average number of finless porpoises seen between the two seasons (Mann-Whitney test, $Z = -0.828$, $P > 0.05$). In the wet season, finless porpoises were widely distributed in the water area of the sandbar head and tributaries, whereas in the dry season, they were densely distributed in the mainstream (Fig. 2).

Habitat suitability

The mean AUCs for the dry and wet seasons were 0.857 and 0.891, respectively. This shows that the habitat suitability prediction is highly accurate, stable, and reliable (Fig. 3). The predicted spatial distribution of the finless porpoise in the study area differed significantly between the dry and wet seasons. During the dry season, the upper section of the mainstream was highly suitable, the shoal waters at the head of the sandbar were moderately suitable, and the tributaries and lower sections of the mainstream were less suitable. During the wet season, highly suitable areas were in the water areas of the sandbar head and tributary, medium-suitable areas were in water areas outside of high-suitability areas, and some water areas along the riverbank and the main river channel of the Yangtze River were low-suitability areas (Fig. 4). During the dry season, the high-, moderate-, and low-suitability areas made up 19%, 32.6%, and 48.4% of the study area, respectively. During the wet season, these values were 15.4%, 26%, and 58.6%, respectively. The number of highly and moderately suitable areas during the wet season decreased by 19.53% compared with those in the dry season.

Table 1 Sightings, numbers, and group sizes from visual surveys in the dry and wet seasons

Survey period	Survey time	Sightings	Sighting rate (Sightings/km^2)	Number of finless porpoises	Largest group
Dry season	20,221,115	6	0.139	8	3
	20,221,124	3	0.070	9	3
	20,230,303	4	0.093	5	2
	20,230,328	3	0.070	5	2
	20,230,331	2	0.046	5	3
Mean ± SD		3.60 ± 1.52	0.08 ± 0.04	6.40 ± 1.95	2.60 ± 0.55
Wet season	20,230,627	4	0.093	12	5
	20,230,628	2	0.046	3	2
	20,230,712	3	0.070	5	3
	20,230,713	1	0.023	1	1
	20,230,805	2	0.046	4	2
	20,230,806	3	0.070	6	2
	20,230,813	3	0.070	6	2
Mean ± SD		2.57 ± 0.96	0.06 ± 0.02	5.29 ± 3.45	2.43 ± 1.27

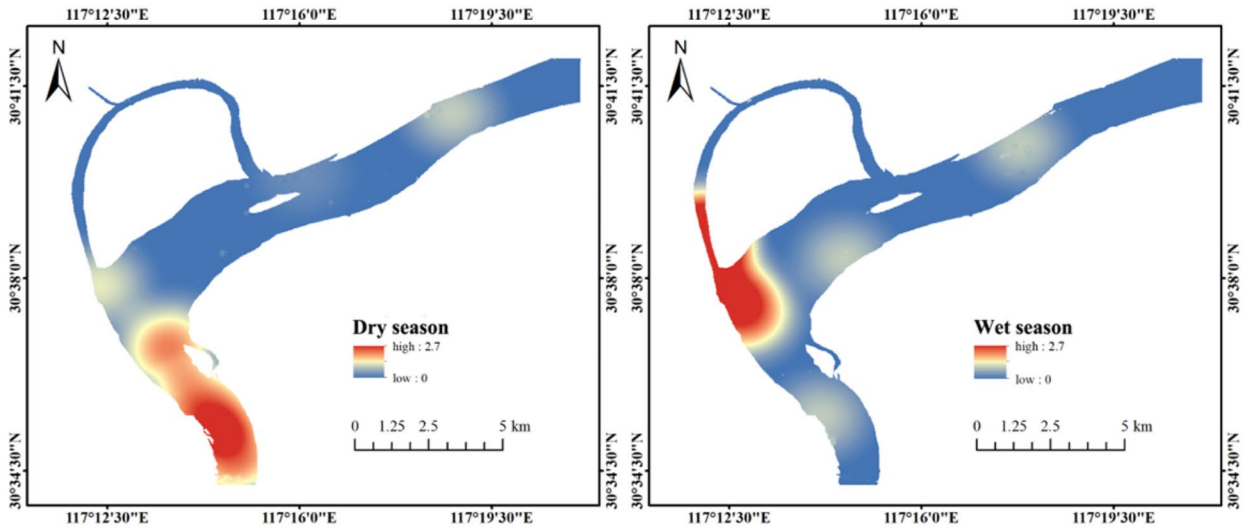

Fig. 2 The distribution density of finless porpoises

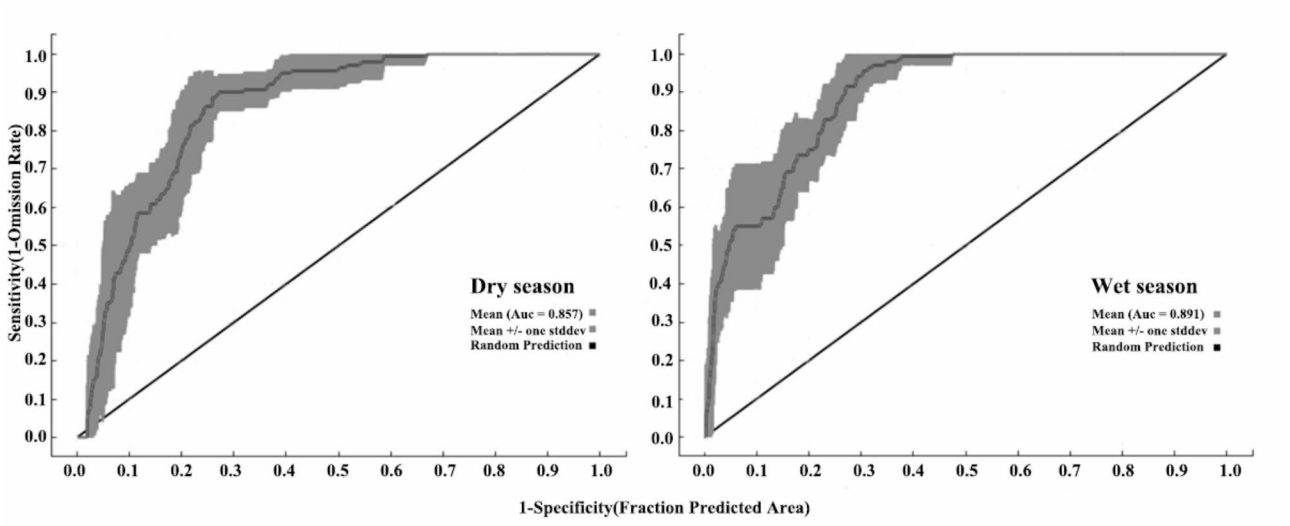

Fig. 3 MaxEnt model receiver operating characteristic (ROC) curves

Factors affecting habitat use of finless porpoises

In the dry season, the first three factors affecting the distribution of finless porpoise were phytoplankton biomass (57.23%), water velocity (30.04%), and zooplankton biomass (9.78%), with a cumulative contribution rate of 97.05% (Table 2). During the wet season, the first three factors affecting the distribution of finless porpoises were water depth (53.07%) and surface water temperature (35.38%), followed by zooplankton biomass (9.24%), with a cumulative contribution rate of 97.69% (Table 2). The Jackknife test findings showed that in the dry season, when this factor was absent, the first three factors influencing the regularized training gain were phytoplankton biomass, zooplankton biomass, and flow velocity (Fig. 5). During the wet season, the jackknife test showed that the first two factors influencing regularized training gain were water depth and surface water temperature (Fig. 5).

The dominant factors affecting the distribution of the Yangtze finless porpoise in the dry season were phytoplankton biomass (bio1), zooplankton biomass (bio2), and water velocity (bio3), whereas in the wet season the dominant factors were water depth (bio4), surface water temperature (bio5), and zooplankton biomass (bio2). In the dry season when the phytoplankton biomass exceeded 0.135 mg/L, the zooplankton biomass exceeded 0.125 mg/L, and the water flow velocity ranged between 0.34 and 0.45 m/s, the probability of finless porpoises occurrence was >0.5 (Fig. 6). In the wet season, when the

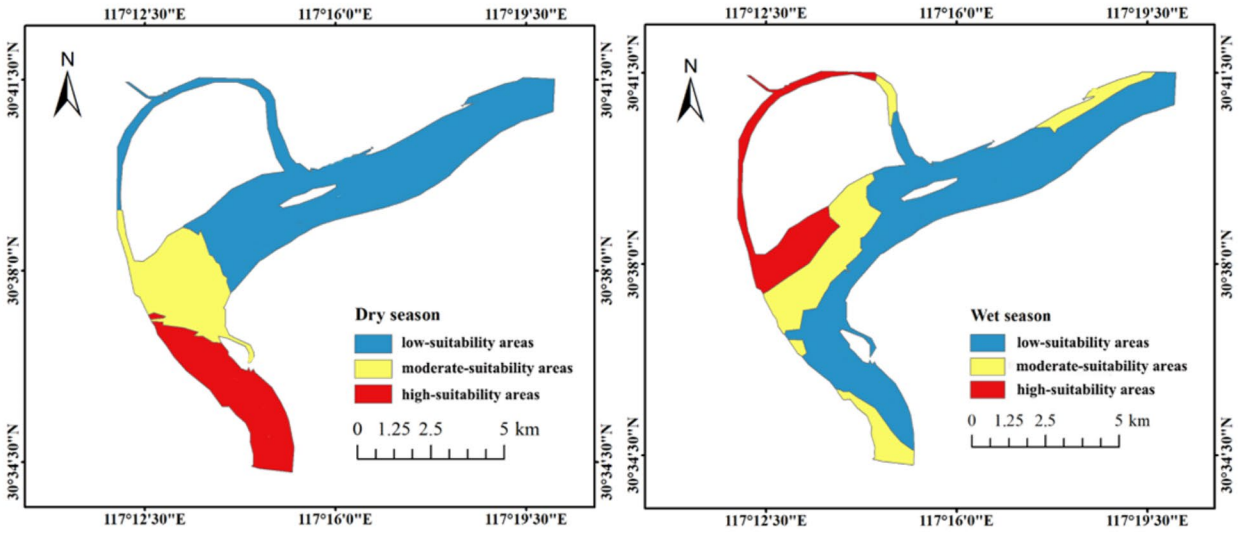

Fig. 4 Predicted habitat suitability for finless porpoises in the study area

Table 2 Factors and their contribution during the dry and wet seasons

Factor type	Factor code	Factors	Factor contribution in the dry season	Factor contribution in the wet season
Biological factors	bio1	Phytoplankton biomass (mg/L)	57.23%	1.43%
	bio2	Zooplankton biomass (mg/L)	9.78%	9.24%
Abiotic factors	bio3	Flow rate (m/s)	30.04%	0.87%
	bio4	Depth (m)	0.01%	53.07%
	bio5	Surface water temperature (℃)	2.94%	35.38%

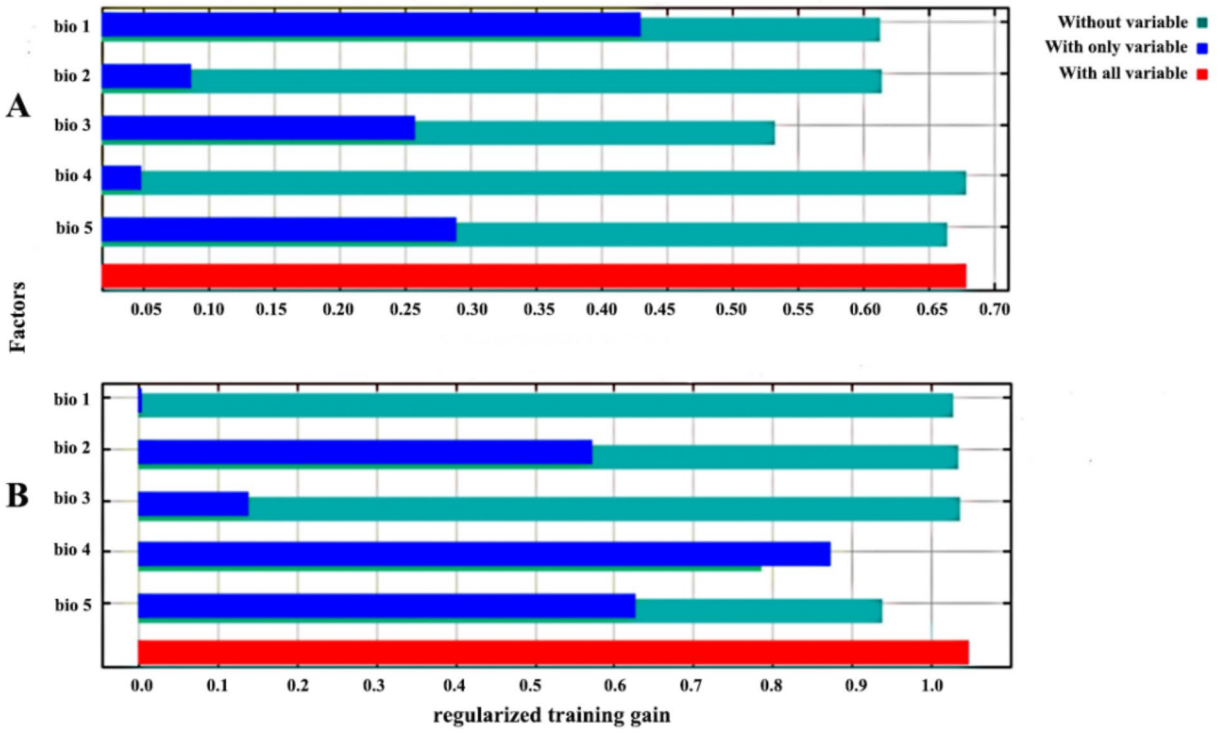

Fig. 5 Jackknife test showing the impact of biological and environmental factors on finless porpoise habitat selection (**A**: dry season; **B**: wet season)

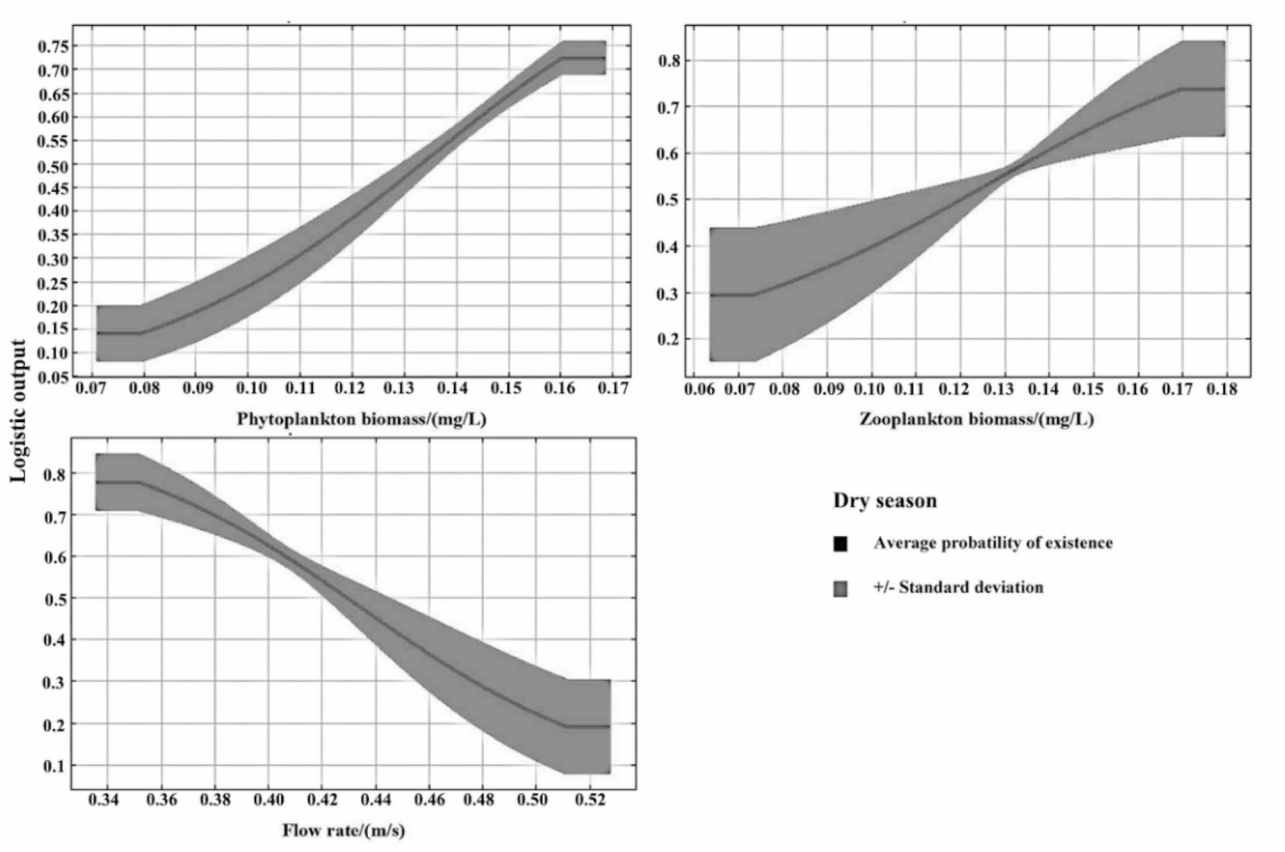

Fig. 6 Response curves of the key environmental variables during the dry season

water depth was between 7 and 11 m, the zooplankton biomass ranged from 1.50 to 3.25 mg/L, and the water temperature was between 23.7 °C and 24.7 °C, the probability of finless porpoises occurrence was >0.5 (Fig. 7).

Discussion

In this study, we found that finless porpoises congregated in specific fine-scale waters regardless of seasons. This is consistent with the findings of research on the habitat utilization of other freshwater porpoises and marine cetaceans [10, 41, 42]. However, in different seasons, the suitability of waters for the finless porpoise changed significantly across seasons. In the dry season, high- and moderately suitable waters were distributed throughout the Yangtze mainstream, whereas in the wet season, they were distributed around the sandbar and tributaries. Therefore, seasonally varying habitat utilization patterns also appeared in a certain section of Yangtze mainstream in addition to estuary areas [27–30].

By incorporating the changing contribution rates and training gains, it was found that the key determinants affecting the distribution of finless porpoises differed throughout the seasons. During the dry season, phytoplankton, water flow velocity, and zooplankton were the main environmental factors affecting the distribution of finless porpoises, with zooplankton and phytoplankton accounting for 67.01% of the total biomass, indicating that biotic factors played a dominant role. Although finless porpoises do not feed directly on plankton, it is the primary food source for filter-feeding and omnivorous fish, particularly those in the upper-middle layer [42]. Studies have shown that finless porpoises prey primarily on upper-middle-layer fish [43, 44]. Their main prey fish such as Beryx (*Hemiculter bleekeri*), silver carp (*Hypophthalmichthys molitrix*), bighead carp (*Hypophthalmchthys nobilis*), and coilia (*Coilia mystus*) [45–47] are all upper-middle layer filter-feeding or omnivorous fish. It is speculated that during the dry season, the most important factor affecting the distribution of finless porpoises is the distribution of prey fish resources. During the dry season, water flow velocity also significantly impacts the distribution of finless porpoises. Previous research found that the Yangtze finless porpoise prefers slow-current water areas along the Yangtze main stream [23], especially water velocity lower than 0.5 m/s [35]. This study revealed that although finless porpoise prefer slow current water area, they preferred water area within a certain range of water velocity in the dry season (0.34–0.45 m/s). The hydrodynamic environment is an important physical factor that drives the formation of aquatic

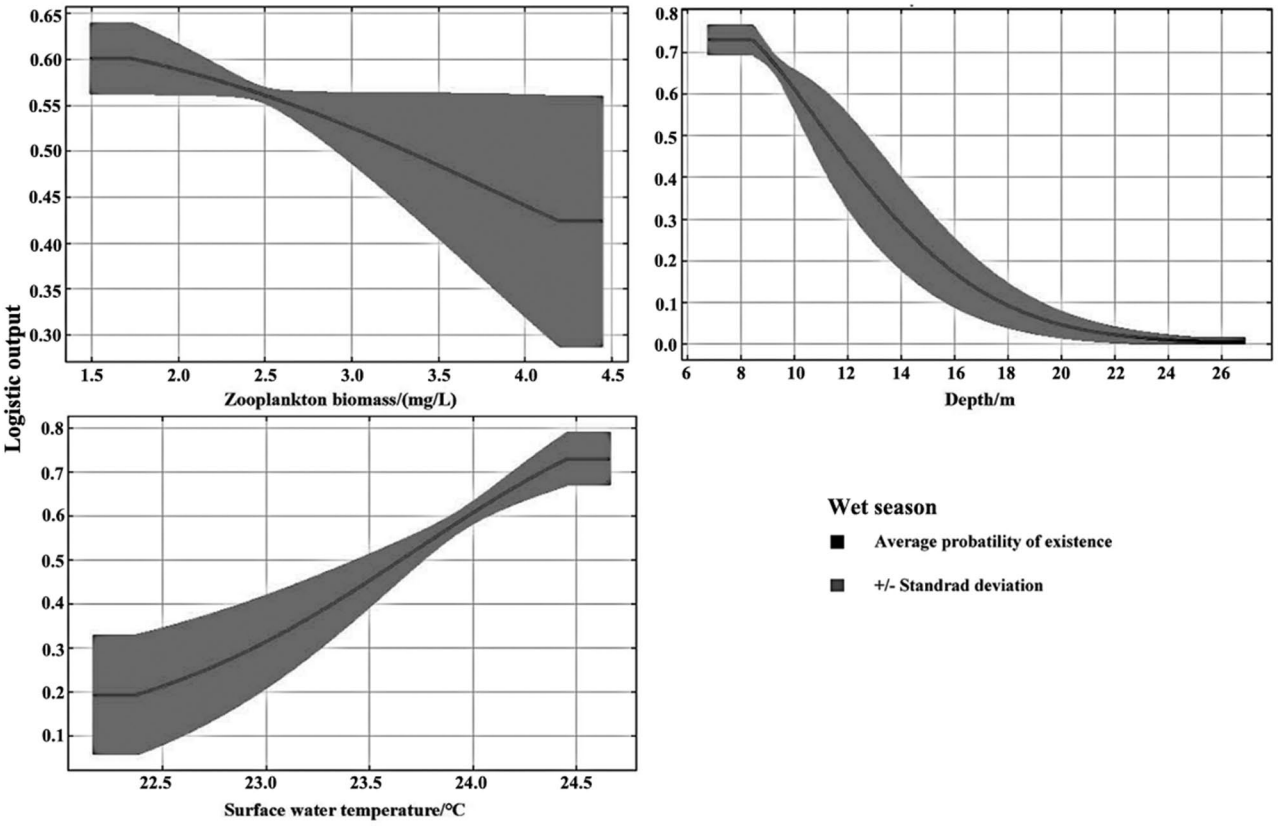

Fig. 7 Response curves of the key environmental variables during the wet season

animal habitat patches [48, 49]. The use of hydrodynamic environments has been shown to improve predation success rates in both marine and freshwater whales. Tidal currents, for example can increase the predation success rates in harbor porpoises [3]. Bottlenose dolphins (*Tursiops truncatus)* forage in small-scale frontal flow areas, which can increase their food encounter rates [41]. According to Ding [50], finless porpoises prefer to forage in a vortex environment near the confluence area of the Yangtze mainstream. Therefore, during the dry season, when the water flow slows, a particular flow condition may be critical for improving foraging success rates. In summary, food availability play the most important role in determining porpoises distribution in the dry season. Food shortage was considered one of the main factors that caused a rapid decline in the Yangtze finless porpoise population to a critically endangered state [11]. Although a 10-year fishing ban has been implemented in the Yangtze River [51], the fishery resources remain low [52]. Furthermore, in the dry season, winter of the Yangtze Basin, the activities of fish decrease and they enter the deep channel of the Yangtze River, or enter crevices for overwintering. This makes it difficult for finless porpoises to detect or capture fish. As a result, throughout the year, food availability for the porpoises is the lowest in the dry season.

During the wet season, the main environmental factors affecting the distribution of finless porpoises were water depth, surface water temperature, and zooplankton, with abiotic factors being the most important. Evidently, compared to the dry season, the degree of influence of food resources in the wet season is reduced. The wet season of the Yangtze River is the period during which fish breed, when they are active and form large groups [53]. During this season, finless porpoises have easier access to food resources than in the dry season. Therefore, although zooplankton, which reflect the distribution features of the upper-middle-layer fish, also plays a major role in the wet season, it was in a secondary dominant position. During the wet season, water depth was the dominant factor, accounting for 53.07% of the total. When the water depth ranged from 7 to 11 m, the probability of finless porpoises occurring was greater than 0.5. Previous research has revealed that finless porpoises are mainly found in waters 7–12 m deep in an *ex-situ* reserve [4], whereas in Poyang Lake, finless porpoises are mainly found in waters 7–20 m deep during the wet season [5]. Therefore, regardless of habitat types, finless porpoises require similar water depths. In studies on other freshwater dolphins, water depth is indeed a key factor affecting dolphins distribution. However, it is generally a limiting factor in the dry season. For example, during low river discharge,

Ganges River dolphins tend to occupy most of the deeper areas to ensure their survival [9]. The Irrawaddy dolphins were found in concentrated groups in several deep pools in the dry season [54, 55]. This may be related to the minimum average water depth and limited depth areas in the Ganges River [9] and the Mekong River in Cambodia during the dry season [54]. Contrasting this, in the Yangtze River, sites with suitable water depths are available in the dry season which may be causing low restrictive influence on porpoises distribution compared to food availability. In the wet season, the reason as to why finless porpoise prefer waters of certain depths has not been investigated. Finless porpoises prey on upper-middle-layer fish. In the wet season, the water level is high and the water flow is more complex. A moderate water depth may balance the energy expenditure for predation with surfacing for breathing. During the wet season, surface water temperature had a significant impact on the distribution of finless porpoises. The wet season of the Yangtze River occurs in the summer when surface water temperatures are high. Tang [56] found that the food intake of finless porpoises was affected by water temperature. When the water temperature was less than 19 °C, finless porpoises' food intake was positively correlated with the water temperature. However, it is negatively correlated when the water temperature exceeds 19 °C. As a result, excessively high or low water surface temperatures are detrimental to the survival of finless porpoises.

Conclusions

In conclusion therefore, this study found that suitable areas for finless porpoises, particularly those with high suitability, differed significantly across seasons at a fine-scale in the Yangtze mainstream. Further investigation found that seasonal variations in habitat were driven by different factors. Food availability plays an important role in determining porpoises distribution regardless of seasons, especially in the dry season. Although a 10-year fishing ban has been implemented in the Yangtze River and fish stocks initially recovered, the fishery resources of the Yangtze River remain low [52]. Therefore, the extent of prey resource recovery for finless porpoises remains unknown and is of significant concern. According to this study, available food resources may still be scarce in the dry season, but this situation is alleviated in the wet season. From the perspective of habitat management and protection, this study suggests strengthening the monitoring and evaluation of food resources of the species in the dry season. In addition, areas highly suitable for finless porpoises shifted from tributaries to the mainstream in the dry season. This may be a common phenomenon in river sections containing sandbars. The mainstream is more narrow and the shipping density is higher in the dry season than in the wet season; therefore, we recommend improving the shipping route management in the dry season. Slowing the speed of ships is also necessary to avoid encounters with porpoises when they approach key habitats. Finally, although biological and environmental factors were considered in this study, shipping was not included in the present study. Shipping could also affect the distribution of finless porpoise [15]. Although it is difficult to quantify underwater noise caused by shipping, the impact of shipping on finless porpoise habitat selection should be considered in future studies. In this study, during the dry season, the finless porpoise were mainly distributed in the mainstream with few occurrence in the sandbar head or tributary where ships are largely absent. This may indicate that the impact of shipping on porpoise distribution in the study waters is limited, or at least that it is not the main factor. Previous studies have shown that the distribution of finless porpoises in the Yangtze mainstream significantly overlaps with ship movement routes [15]. Finless porpoises avoided the ship during its movement, but can re-occupy their habitat after the movement [57].

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Author contributions
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Data availability
The datasets used and/or analysed during the current study are available from the corresponding author on request.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

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