

# Maintaining shallow waters to maximize the potential of saltpans as foraging habitat for migratory shorebirds along an endangered flyway

Weipan Lei<sup>a,b</sup>, José A. Masero<sup>c</sup>, Ziwen Chai<sup>a</sup>, Bing-Run Zhu<sup>a,d,e</sup>, Tong Mu<sup>f</sup>, He-Bo Peng<sup>d,g,\*</sup>, Zhengwang Zhang<sup>a,\*\*</sup>, Theunis Piersma<sup>d,h,i</sup>

<sup>a</sup> Key Laboratory for Biodiversity Science and Ecological Engineering, College of Life Sciences, Beijing Normal University, Beijing 100875, China

<sup>b</sup> Demonstration Center for Experimental Life Sciences & Biotechnology Education, College of Life Sciences, Beijing Normal University, Beijing 100875, China

<sup>c</sup> Ecology in the Anthropocene, Associated Unit CSIC-UEX, Zoology, Faculty of Sciences, University of Extremadura, Badajoz, Spain

<sup>d</sup> BirdEyes, Centre for Global Ecological Change at the Faculties of Science & Engineering and Campus Fryslân, University of Groningen, Wirdumerdijk 34, 8911 CE Leeuwarden, the Netherlands

<sup>e</sup> Hunan Global Messenger Technology Co., Ltd., Changsha, Hunan 410205, China

<sup>f</sup> Princeton School of Public and International Affairs, Princeton University, Princeton, NJ, USA

<sup>g</sup> Guangdong Basic Research Center of Excellence for Ecological Security and Green Development, Guangdong Provincial Key Laboratory of Water Quality Improvement and Ecological Restoration for Watersheds, Guangdong University of Technology, Guangzhou, 510006, China

<sup>h</sup> Department of Coastal Systems, NIOZ Royal Netherlands Institute for Sea Research, PO Box 59, 1790 AB, Den Burg, Texel, the Netherlands

<sup>i</sup> Rudi Drent Chair in Global Flyway Ecology, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, PO Box 11103, 9700 CC Groningen, the Netherlands

## ARTICLE INFO

### Keywords:

Artificial wetlands  
China's coast  
Food supply  
Habitat management  
Saltpans  
Shorebirds  
Water depth

## ABSTRACT

The global expansion of human activities has led to a dramatic reduction in natural wetlands. While effectively managed artificial wetlands hold the potential to counteract this decline, there is often a lack of knowledge regarding how to enhance their value for wildlife. To bridge this gap, we studied one of the world's largest saltworks in the Yellow Sea, China. This region has experienced significant natural wetland losses, resulting in marked declines in waterbird populations across the East Asian-Australasian Flyway (EAAF). Our research examined the impact of biotic factors such as prey abundance, and abiotic factors including water depth and management practices of saltpans, on the distribution of foraging shorebirds, as well as other waterbirds. Findings reveal that shorebirds, accounting for 95% of all waterbirds, heavily utilize saltpan evaporation ponds. Although various factors affect the distribution of shorebirds and other waterbirds, water depth and abandoned ponds (with low water depth) emerged as the primary factors. Notably, prey biomass (and abundance) did not exhibit a significant correlation with bird distribution across all shorebirds and other waterbirds, indicating that prey accessibility is more crucial than biomass in determining habitat suitability in these saltpans. Based on these insights, we propose tailored management strategies for the Yellow Sea saltpans that enhance conditions for shorebirds without impeding salt production, including lowering water levels through modifications to pond structures and reducing the volume of water evaporated during each stage of production. These straightforward, bird-friendly strategies provide practical solutions for adapting artificial wetlands to support migratory waterbirds in the EAAF and offer valuable insights for global waterbird conservation.

## 1. Introduction

With the expansion of global human activities, natural habitats are increasingly declining, significantly threatening biodiversity and ecosystem stability (Díaz et al., 2019; Fluet-Chouinard et al., 2023). This

loss is especially severe in densely populated coastal regions, where human expansion has led to the widespread loss of natural wetlands (O'Hara et al., 2021). Over the past 20 years, nearly 20% of natural tidal wetlands have been lost globally, mainly transformed into urban areas, industrial zones and artificial habitats (Murray et al., 2022). These

\* Correspondence to: H.-B. Peng, Guangdong Basic Research Center of Excellence for Ecological Security and Green Development, Guangdong Provincial Key Laboratory of Water Quality Improvement and Ecological Restoration for Watersheds, Guangdong University of Technology, Guangzhou 510006, China.

\*\* Corresponding author.

E-mail addresses: [hebo.peng@gdut.edu.cn](mailto:hebo.peng@gdut.edu.cn) (H.-B. Peng), [zzw@bnu.edu.cn](mailto:zzw@bnu.edu.cn) (Z. Zhang).

<https://doi.org/10.1016/j.biocon.2025.111100>

Received 18 November 2024; Received in revised form 12 March 2025; Accepted 17 March 2025

Available online 31 March 2025

0006-3207/© 2025 Elsevier Ltd. All rights are reserved, including those for text and data mining, AI training, and similar technologies.

changes have negatively impacted wildlife, particularly species that rely on tidal wetlands for refueling and breeding (Piersma et al., 2016; Studds et al., 2017; Li et al., 2018). Consequently, artificial wetlands have become increasingly important alternative habitats, serving as one of the most crucial refuges for lots of wildlife (Cheng et al., 2022).

Despite an increase in the availability and extensive coverage of man-made wetlands (Davidson et al., 2018), artificial wetlands often do not necessarily fully substitute all the ecological functions of the natural habitats which they replace (Bellio et al., 2009; Cheng et al., 2022). This underutilization may be because artificial wetlands are often designed primarily to meet human needs, lacking some functions that natural wetlands can provide (Bellio et al., 2009; Fan et al., 2021). Therefore, effective management of artificial wetlands is critical for wildlife conservation (Velasquez, 1992). As a key supplement to wetland restoration, proper management of artificial habitats can create more suitable environments for wildlife at a lower cost and on a larger scale (Seaman, 2007; Jackson et al., 2020). This approach aligns with the Ramsar Convention's wise-use principles, which advocate for sustainable wetland management (Ramsar Convention Secretariat, 2010). Although restoring natural wetlands to their original state is ideal, managing artificial wetlands specifically for conservation purposes provides a more practical and scalable solution, underscoring the importance of these efforts (Liu and Ma, 2024).

Saltpans, which are widely distributed artificial wetlands in coastal regions, serve as particularly important alternative habitats for migratory shorebirds (Warnock et al., 2002; Jackson et al., 2020; Green et al., 2015). The wildlife benefits of these habitats, primarily used for salt production, generally do not conflict with human financial interests, making them 'easy' substitutes for rapidly diminishing natural coastal wetlands (Masero, 2003; Sripanomyom et al., 2011; Lei et al., 2018; Barnagaud et al., 2019; Jackson et al., 2020; Lei et al., 2021). This is especially relevant in the East Asian-Australasian Flyway (EAAF), where waterbird (especially shorebird) populations have experienced dramatic declines due to extensive habitat loss in the Yellow Sea, the key refueling area of the EAAF (Piersma et al., 2016; Studds et al., 2017). More than 65% of natural coastal wetlands were converted into artificial landscapes in the past 60 years (Murray et al., 2014; Wang et al., 2021). Despite the extensive size and high abundance of brine fly, brine shrimp and chironomid larvae which are high quality food for shorebirds (Lei et al., 2018), they still primarily forage on natural mudflats where food abundance is limited (Jackson et al., 2020; Peng, 2024). Understanding what factors limit shorebird use of saltpans in the Yellow Sea is necessary for science-based conservation efforts.

Previous studies indicate water depth emerged as the most critical factor influencing shorebird distribution in the saltpans (Sripanomyom et al., 2011; Green et al., 2015). Unlike natural tidal wetlands, which experience regular tidal fluctuations that periodically expose food resources for foraging shorebirds (Velasquez, 1992; Bellio et al., 2009), artificial wetlands often maintain high water levels to support aquaculture or water storage (Cheng et al., 2022). Although deeper water may offer greater food biomass, most shorebirds are unable to swim, and even those that can are generally reluctant to feed while swimming, preferring to avoid deeper waters (Ntiemoa-Baidu et al., 1998). However, the effects of both water depth and food biomass on shorebirds' foraging in saltpans have never been examined together, and our understanding of their roles remains limited.

Here, we examined how biotic and abiotic factors affected the use of Nanpu Saltpans by shorebirds and other waterbirds. Situated in the Yellow Sea, China, it is one of the world's largest coastal saltworks (Lei et al., 2018). Factors included prey abundance - the most basic need for survival (Piersma, 2012), salinity, saltpan management practices and water depth, which influence the food accessibility for shorebirds (Velasquez, 1992). This research aims to provide essential insights into management practices that could enhance the ecological value of saltpans for refueling shorebirds in the Yellow Sea. The outcomes of this study will contribute to a broader understanding of how artificial

wetlands can be optimized to support wildlife populations and will offer practical recommendations for integrating artificial wetland management into global wetland restoration and conservation strategies.

## 2. Methods

### 2.1. Study area

The Nanpu Saltpans, covering an area of 290 km<sup>2</sup>, are located in northern Bohai Bay (39°3'–12°N, 118°8'–28°E), beside the Caofeidan Wetland Natural Reserve. This wetland system also includes adjacent tidal flats, which cover an additional 57 km<sup>2</sup>, as well as other anthropogenic supratidal habitats, such as aquaculture ponds used for shrimp and fish production (Fig. 1). Our research covered a small part of the saltworks, an area of 33.4 km<sup>2</sup> (Fig. 1). Similar to other industrial salt-pans, the Nanpu Saltpans consist of interconnected shallow pans of varying sizes, separated by dikes and categorized into three types: (1) storage ponds, (2) evaporation ponds and (3) crystallization ponds. Seawater is initially drawn into the storage ponds during the rising tide, then circulated through a series of evaporation ponds via water pumps until it reaches numerous small crystallization ponds (Masero, 2003). As the water moves from the storage ponds to the crystallization ponds, its salinity progressively increases, following a southeast to northwest gradient according to the layout designed for salt production (Fig. 1). Storage ponds typically hold large volumes of seawater for subsequent processing, while crystallization ponds, due to their extreme salinity, are inhospitable to most organisms. Evaporation ponds, on the other hand, with their shallower water and higher biomass, are frequently utilized by waterbirds (Lei et al., 2018). This study focuses specifically on the ecological role of evaporation ponds.

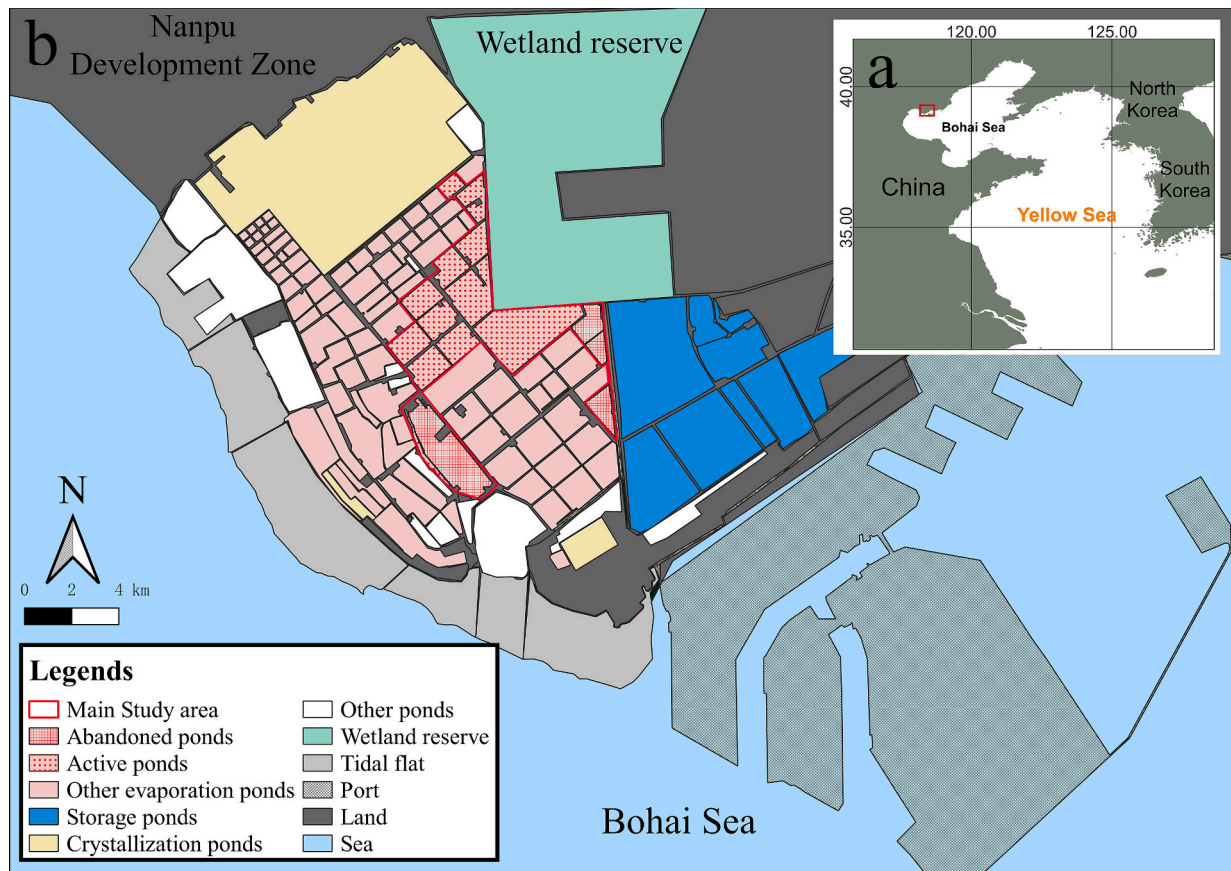
We assessed waterbirds distribution across two types of evaporation ponds, categorized by their management practices: (1) active ponds ( $n = 14$ ), with water depths ranging from 15 to 60 cm, used for salt production typically have a deeper water level; and (2) temporarily abandoned ponds ( $n = 4$ ), with water depths <20 cm (range from 0 to 20), consistently providing shorelines for shorebirds, except when completely dry. Temporarily abandoned ponds comprised approximately 24% of the total area examined in this study.

### 2.2. Waterbird surveys

From early April to early June 2014–2016 we conducted daytime counts of waterbirds during both low and high tide periods. Foraging and roosting individuals were differentiated, with roosting birds excluded from the numbers used for analysis in this study (Lei et al., 2021). High tide counts were typically performed within one or two days following the low tide counts. In total, 60 bird surveys were completed, with 32 occurring during high tide and 28 during low tide. Each survey was conducted using the accessible network of unpaved roads, either by car or on foot (for further details, see Lei et al., 2021). Counting commenced three hours before the respective tide (high or low) and was completed within six hours. During the survey, we recorded bird movements between ponds, and when finalizing the bird count, we removed these repeat data. The maximum number of waterbirds recorded in saltpans during northward migration were 96,000, with 23 waterbird species surpassing 1% of their estimated flyway populations (Lei et al., 2018). Most birds that foraged on the intertidal mudflats at low tide and roosted on pond banks during high tide (Hassell et al., 2013) were excluded from the analysis.

### 2.3. Biotic and abiotic variables

In parallel with waterbird counts, macroinvertebrates were sampled within the same ponds, albeit with a lower frequency. Each pond was sampled between one to three times from early April to early June. The ponds varied in size, ranging from 0.3 to 7.6 km<sup>2</sup>, and depending on the



**Fig. 1.** Study site of Nanpu Salt pans. (a) The location (red rectangle) of Nanpu Salt pans in the Yellow Sea. (b) Map of the Nanpu Salt pans. Waterbirds and macrobenthos were surveyed in abandoned ponds and active ponds of evaporation ponds in the main study area (bright red polygon). Green area presents the Caoifeidian wetland natural reserve, light yellow areas represent crystallization ponds, dark blue areas represent storage ponds, light red areas represent evaporation ponds. (For interpretation of the colour references in this figure legend, please refer to the web version of this article.)

pond's size, 4 to 12 sampling locations were established. At each sampling site, three cores were extracted using a PVC cylindrical corer with a 10.4 cm diameter, spaced 2 to 30 m apart. The precise locations of these cores were recorded with a handheld GPS device (Garmin 62 s, Garmin Ltd.).

Each core contained both the sediment core and the overlying water column. The height of the water column depended on the water depth of the sampling site, and therefore, there was no water column when the water depth was zero. Sediment cores were extracted to a maximum depth of 20 cm, corresponding to the deepest foraging reach of large shorebirds (Zwarts and Wanink, 1993). In areas with harder sediment, the sediment core depth was occasionally reduced. The sediment was sieved through a 0.5 mm mesh to retain macroinvertebrates. The overlying water column was separately sieved through a 150- $\mu$ m mesh to estimate brine shrimp abundance. All invertebrates were preserved in 75% ethanol for subsequent identification and biomass measurement. Following sampling, water depth and salinity were recorded; water depth was measured to the nearest centimeter with a long ruler, and salinity was determined using a refractometer (range 0–30, accuracy 0.2%).

All individual invertebrates were identified to the genus level, and their body lengths were measured. Intact invertebrates (brine shrimp, chironomid larvae, and brine fly larvae) were selected to build the equation between length and dry mass and ash-free dry mass (AFDM). In each length range (1 cm), 3–10 samples (each containing 1–30 individuals) were used. Before drying the sample, the aluminum foil cups were dried in a 500 °C muffle furnace for 3 h to avoid the influence of high temperature on cup weight. Samples were then dried at 60 °C for 12 h to obtain their dry weight, and burned at 500 °C muffle furnace for

3 h to obtain their ash weight. AFDM was obtained by subtracting the ash weight from the dry weight. A linear equation was built between the log of length (L) (in mm) and log of AFDM (in mg),  $\log(\text{AFDM}) = a + b \times \log(L)$  (where  $a$  is the mean intercept, and  $b$  is the mean slope). In each experiment, an empty cup was filled with water as a blank control. Brine fly pupa, with small variations of body length (4.2–10.2 mm) were only given their mean weight, with each sample containing 1–5 individuals. Biomass equations (ash-free dry mass, AFDM) were developed for brine shrimp (*Artemia* sp.), chironomid larvae (*Chironomus* sp.), and brine fly larvae (*Ephydra* sp.). Brine fly pupae were averaged to determine biomass. These four prey categories accounted for 99% of the prey items. The abundance of invertebrates was expressed as biomass density ( $\text{mg}/\text{m}^2$ ).

#### 2.4. Data analysis

Independent  $t$ -test was used to analyze whether there are differences in water depth among the salt pans with two different management methods. Since water depth may influence prey biomass, linear regression was used to separately analyze how the potential food biomass (Y-axis) varied with water depth (X-axis) in each of the two types of ponds.

To elucidate the potential biotic and abiotic factors influencing habitat utilization by shorebirds, and because many species have low abundances, the distribution of these rare species may affect the model's analysis and interpretation, we classified bird species into six distinct categories based on body size, feeding style, swimming ability, and other ecological traits (Ntiamoa-Baidu et al., 1998; Lei et al., 2021): 1) Tactile surface-foraging shorebirds use their bills to probe for prey in the mud or sand, such as Curlew Sandpiper; 2) Visual surface-foraging shorebirds

rely on their sight to capture visible prey on the surface, such as Kentish Plover; 3) Pelagic-foraging shorebirds hunt over open water, using both visual and tactile cues to capture prey, such as Pied Avocet; 4) Small shorebirds ( $\leq 20$  cm in body length) are agile and often forage for small invertebrates in coastal habitats, such as Red-necked Stint; 5) medium-large shorebirds ( $> 20$  cm) are better suited to foraging in more challenging environments due to their larger size, such as Black-tailed Godwit; 6) Swimming waterbirds, forage by swimming in water, using visual and tactile senses to detect prey like fish and crustaceans, such as Ducks (Table S1).

To explore the relationship between bird abundance and environmental variables, we employed a Generalized Linear Mixed Model (GLMM) with a negative binomial distribution and a log link function to account for overdispersion in the data. In our analysis, the bird density response variable originates from aggregated count data. Specifically, bird counts were summed across survey units and subsequently rounded to the nearest integer, effectively maintaining the discrete nature of the data. Considering the significant overdispersion and the prevalence of zero counts (23% of total counts) within our dataset, the negative binomial distribution proves particularly suitable. Given that the survey ponds are geographically adjacent, we incorporated spatial autocorrelation into the GLMM using the 'sdmTMB' package (Anderson et al., 2024), which is specifically designed for spatio-temporal models with the inclusion of spatial random effects.

Before constructing the model, numeric explanatory variables were centered and scaled to standardize their influence. Collinearity among covariates was assessed using the 'pairs' function in R, and variance inflation factors (VIF) were calculated with the 'corvif' function from the 'HighstatLibV4.R' file (Zuur et al., 2013). The centroid coordinates of each pond were converted to UTM format (km) for the evaluation of spatial autocorrelation in the model.

In the 'sdmTMB' models, we defined the mesh for the spatial model with a cutoff distance of 1 km. The response variable was bird density, analyzed for all shorebirds, total species richness, and six categories separately. Covariates included water depth (cm), salinity (%), pond size ( $\text{km}^2$ ), and food density. Fixed effects were management method (two levels: temporarily abandoned, active ponds) and tidal phase (high tide vs. low tide). Random effects included pond ID and year, while daily average temperature was treated as a smooth term (detailed descriptions of fixed and random effects are provided in Table 1). For food density, we separately modeled the effects of food abundance and food biomass as response variables, recognizing that these may have distinct effects on bird distribution.

Full models were constructed and reported for all waterbirds, total

species richness, and the six categories separately. If a model failed to converge, predictors were removed based on recommendations from the 'sanity' function in the 'sdmTMB'. Predictor variables with 95% confidence intervals (CIs) that did not include zero were considered biologically significant (Grueber et al., 2011).

All statistical analyses were conducted using RStudio (v1.4.1106) and R (v4.4.2; RStudio Team, 2022), with mapping performed in QGIS for Windows (v3.20.3).

### 3. Results

Over 60 surveys between 10 April and 4 June 2014–2016, a total of 441,690 waterbirds were recorded, 95% of which were shorebirds. The mean density of all waterbirds was  $1095 \text{ ind}/\text{km}^2$  (range: 0–27,710), tactile surface-foraging shorebirds was  $650 \text{ ind}/\text{km}^2$  (range: 0–27,641), visual surface-foraging shorebirds  $30 \text{ ind}/\text{km}^2$  (range: 0–2481), pelagic-foraging shorebirds  $309 \text{ ind}/\text{km}^2$  (range: 0–9642), small shorebirds  $216 \text{ ind}/\text{km}^2$  (range: 0–5338), medium-large shorebirds  $776 \text{ ind}/\text{km}^2$  (range: 0–22,372), and swimming waterbirds  $90 \text{ ind}/\text{km}^2$  (range: 0–2898).

Based on all the 782 samples collected (744 with both water column and sediment, 38 with only sediment), there were 17,544 invertebrates, in which, brine shrimp accounted for 28.3%, chironomid larvae for 28.0%, brine fly pupae for 26.2%, brine fly larvae for 16.7%, brine fly adult for 0.3%, and other invertebrates for 0.5% respectively. Excluding the latter, the different prey categories made the following contribution to total AFDM: brine shrimp 8.2%, chironomid larvae 8.7%, brine fly larvae 16.4%, brine fly pupae 66.0 %, and brine fly adults 0.7% (Fig. 2a). Considerable variation in abundance density and biomass density was observed among ponds, with a mean abundance density of  $3114 \pm 3659 \text{ ind.}/\text{m}^2$ , ranging from 52 to 15,115  $\text{ind.}/\text{m}^2$ , biomass density of  $1799 \pm 3686 \text{ mg AFDM}/\text{m}^2$ , ranging from 1.3 to 19,220  $\text{mg}/\text{m}^2$ .

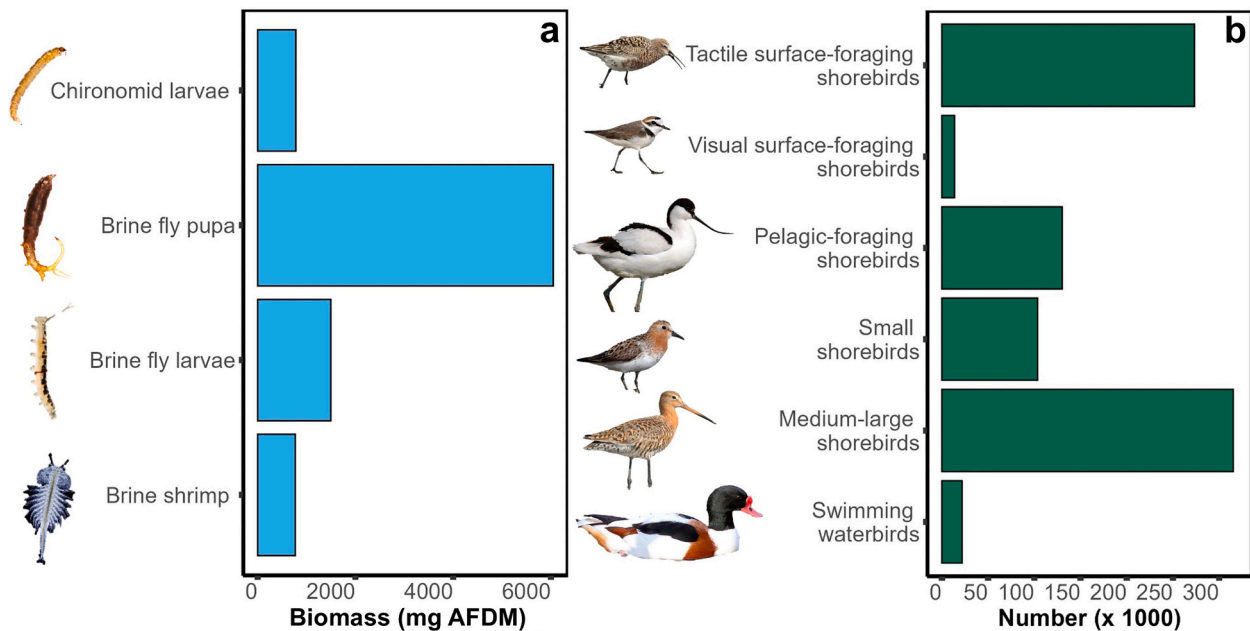
There were significant differences in water depth among the two types of pond management: temporarily abandoned ponds < active ponds (Fig. 3a). The water depth in temporarily abandoned ponds was  $< 15 \text{ cm}$  ( $6.9 \pm 5.7 \text{ cm}$ ), whereas the average depth in the active ponds exceeds 20 cm. The prey biomass increased significantly with increasing water depth across all types of ponds (Fig. 3b).

Overall, GLMM models indicated that water depth and management strategy emerged as the most influential factors affecting total waterbird density, species richness, and bird density of six categories, especially for all shorebird categories (Fig. 4; marginal  $R^2$  of models range from 0.26 to 0.54, conditional  $R^2$  of models range from 0.356 to 0.690, see Table 2 for detailed). In contrast, food biomass had no significant effect on the density or species richness of any category. Bird densities and species richness across all categories decreased with increasing water depth, with the exception of swimming waterbirds (which showed no significant trend). All bird categories, except for swimming waterbirds, were more likely to select abandoned ponds over active ponds, although tactile surface-foraging shorebirds, and medium-large shorebirds did not show a significant preference. Waterbirds exhibited a marked preference for foraging in evaporation ponds with lower salinity, although several categories (visual surface-foraging shorebirds, small shorebirds) showed no significant trend. Larger pond areas were associated with lower bird densities but higher species richness (not significant). Additionally, bird density and species richness were significantly higher at high tide than low tide for total waterbird density, visual surface-foraging shorebirds, and swimming waterbirds, while no significant differences were observed for other categories. When food biomass density was replaced by food abundance density as an independent variable, the results remained consistent: water depth and management strategy continued to be the dominant factors influencing waterbird densities and species richness, while food abundance had no significant effect on all categories (Fig. S1; marginal  $R^2$  of models range from 0.26 to 0.53, conditional  $R^2$  of models range from 0.36 to 0.69, see Table 2 for detailed).

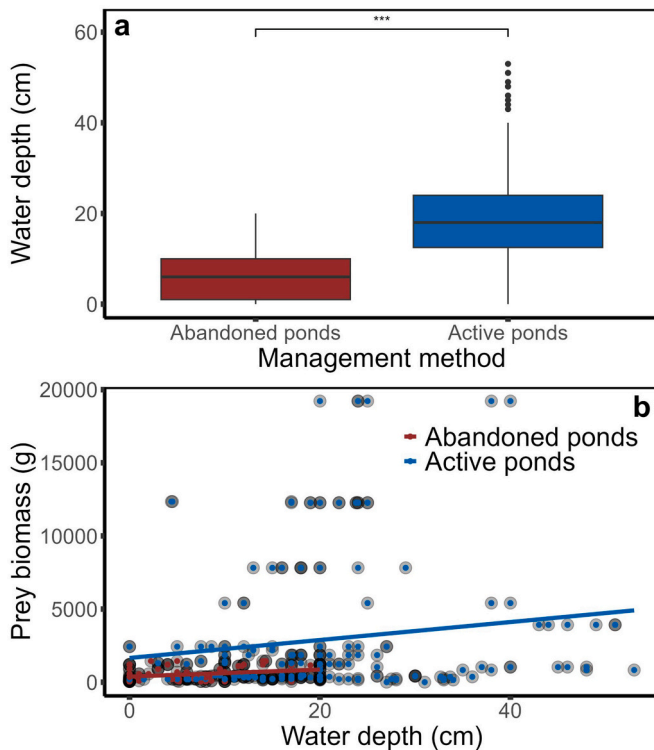
**Table 1**

Description of response variables in models predicting waterbirds density or species richness.

| Variables                                   | Description                               | Mean $\pm$ sd   | Range                                             |
|---------------------------------------------|-------------------------------------------|-----------------|---------------------------------------------------|
| Salinity (%)                                | Water salinity of pond                    | $9.5 \pm 3.8$   | 4.4–26.0                                          |
| Water depth (cm)                            | Water depth of pond                       | $15.4 \pm 11.4$ | 0–53.0                                            |
| Pond size ( $\text{km}^2$ )                 | Area of pond surface                      | $1.95 \pm 1.89$ | 0.29–7.60                                         |
| Biomass density ( $\text{mg}/\text{m}^2$ )  | Mean biomass density of prey in each pond | $1799 \pm 3686$ | 1–19,220                                          |
| Food abundance ( $\text{ind.}/\text{m}^2$ ) | Mean density of prey in each pond         | $3114 \pm 3659$ | 52–15,115                                         |
| Year                                        | Research year                             | –               | 2014, 2015, 2016                                  |
| Temperature ( $^{\circ}\text{C}$ )          | Daily average temperature                 | $18.4 \pm 4.1$  | 10.4–26.1                                         |
| Pond ID                                     | Name of 18 ponds                          | –               | –                                                 |
| Management method                           | Saltpans operation methods                | –               | Active ponds (14), Temporarily abandoned pond (4) |



**Fig. 2.** The total abundance of birds and prey in Nanpu Salt pans. (a) the total biomass of four prey types collected in Nanpu Salt pans. (b) The total numbers of six bird categories recorded in Nanpu Salt pans.



**Fig. 3.** The relationship between water depth and other biotic and abiotic factors. (a) Water depth in abandoned ponds and active ponds. (b) The relationship between prey biomass and water depth. “\*\*\*” in panel (a) represents  $p < 0.001$ , solid lines in panel (b) represent  $p < 0.001$ .

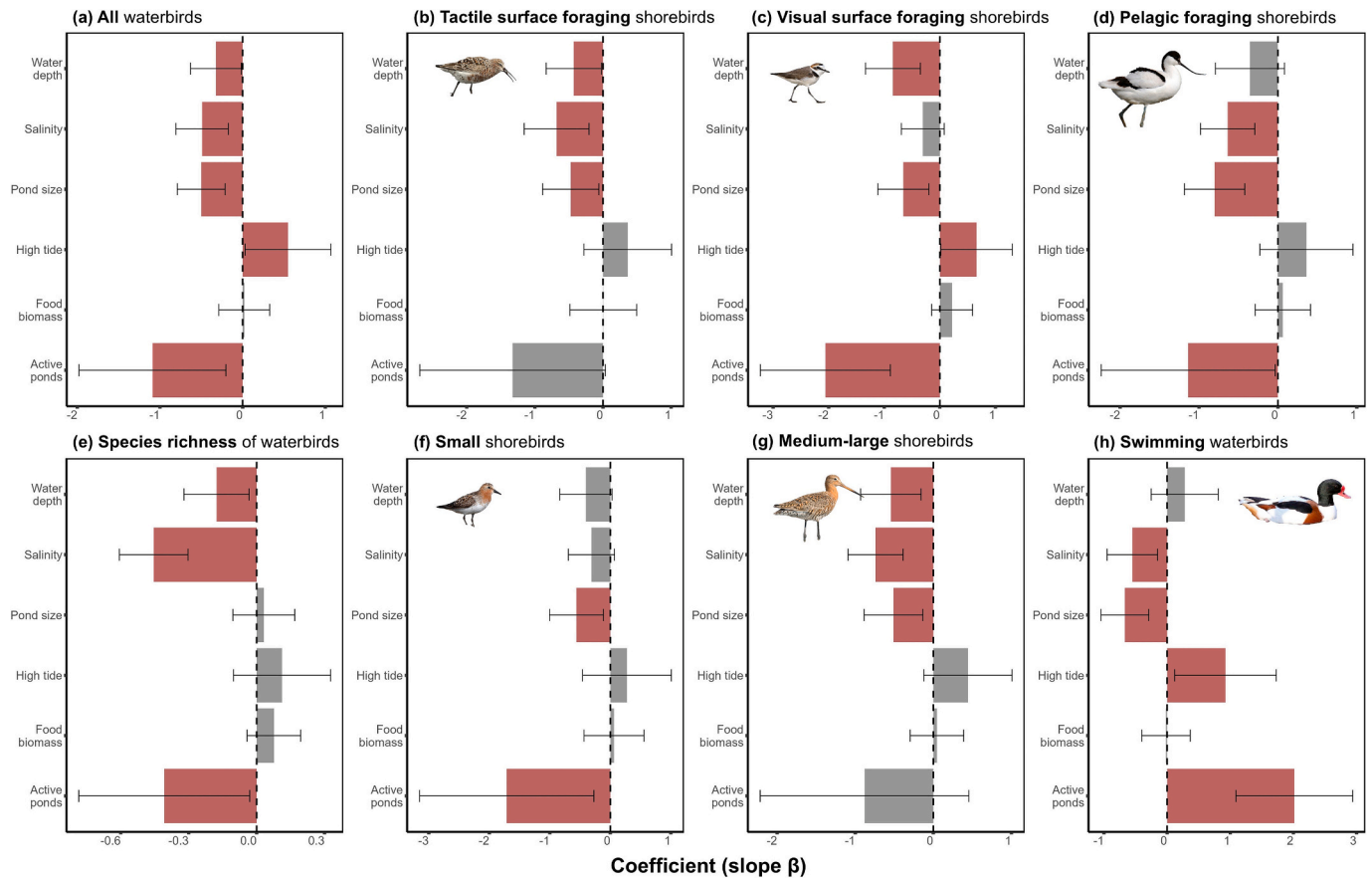
#### 4. Discussion

Our study reveals that shorebirds comprise most of the recorded waterbirds within the saltworks. To our surprise, the distribution of foraging shorebirds was not correlated with prey abundance but mainly correlated with abiotic factors that affect prey accessibility, particularly

water depth. Prey abundance is undoubtedly a key factor in determining habitat suitability (White, 2008; Piersma, 2012), a relationship well-established in studies on natural mudflats. In these environments, prey abundance—often closely aligned with the availability of harvestable prey—typically emerges as the primary factor correlated with shorebird habitat use (e.g., Piersma, 2012; Duijns et al., 2015; Zhang et al., 2019; Cai et al., 2024). However, our results indicate that in Nanpu Salt pans where most ponds were covered by deep water, water depth limits shorebirds’ ability to access abundant prey. Consequently, prey accessibility, rather than mere abundance, emerges as the key determinant of shorebird distribution within these artificial wetlands in the Yellow Sea.

In natural wetlands, conservation efforts often focus on enhancing food abundance and biomass to provide more resources for birds, primarily due to the ongoing decline in biomass in the Yellow Sea region’s wetlands, rather than limitations on birds’ access to food on mudflats (Zhang et al., 2018; Peng et al., 2024). In contrast, our study found that while food abundance and biomass are high at Nanpu Salt pans, the deep water in the ponds prevents birds from accessing the available food resources. Thus, improving the accessibility of existing food in salt pans is a more pressing priority than increasing food abundance. To optimize the conservation value of artificial salt pans, management practices should maintain water levels suitable for migratory shorebirds. Shallow water habitats within salt pans can significantly enhance their utility as foraging grounds. However, effective management must balance these ecological considerations with the operational requirements of salt production (Green et al., 2015). Given the relatively flat topography of salt pans, maintaining excessively low water levels can reduce total water volume, potentially disrupting salt production and hampering the growth of brine shrimp, a critical food source for shorebirds.

Here, we propose two potential management schemes that do not interfere with normal salt production efficiency, while keeping lower water levels throughout the production cycle in evaporation ponds, based on the design and management strategies outlined by Rehfsch (1994) for lagoons, and taking into account the operational needs of the Nanpu Salt pans. First, we recommend restructuring the salt pans by creating evaporation ponds with gradient depths (a sloped or terraced bottom) to ensure the presence of shallow areas (<15 cm) throughout the evaporation process (Fig. 5a, Management Scheme 1). This scheme can reduce the long-term costs of water depth management by ensuring



**Fig. 4.** Effects of food biomass and abiotic factors on the density distribution of different waterbird categories. (a) All waterbirds; (b) Tactile-surface foraging shorebirds; (c) Visual-surface foraging shorebirds; (d) Pelagic-foraging shorebirds; (e) Species richness of waterbirds; (f) Small shorebirds; (g) Medium-large shorebirds; (h) Swimming waterbirds. 95% Confidence Interval of coefficient (slope  $\beta$ ) is estimated from GLMM models. Significance is indicated by estimates not crossing zero. The red bars indicate the significant influence of the variable, grey bars indicate non-significant. (For interpretation of the colour references in this figure legend, please refer to the web version of this article.)

**Table 2**  
marginal  $R^2$  and conditional  $R^2$  of model result.

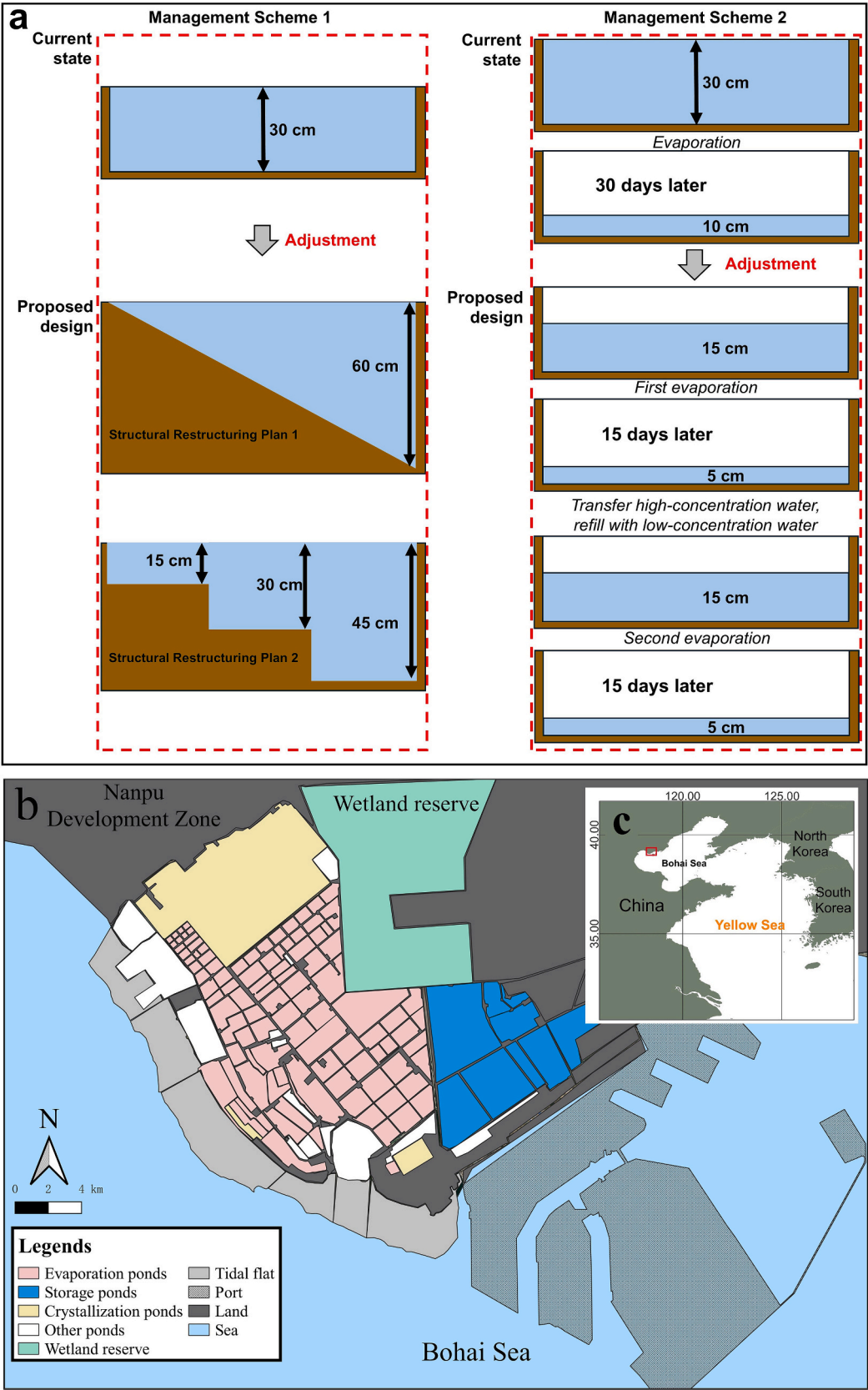
| Model                               | Food biomass density as fixed factor |                   | Food abundance as fixed factor |                   |
|-------------------------------------|--------------------------------------|-------------------|--------------------------------|-------------------|
|                                     | marginal $R^2$                       | conditional $R^2$ | marginal $R^2$                 | conditional $R^2$ |
| Total bird density                  | 0.31                                 | 0.36              | 0.31                           | 0.36              |
| Species richness                    | 0.26                                 | 0.36              | 0.26                           | 0.36              |
| Tactile surface-foraging shorebirds | 0.30                                 | 0.40              | 0.30                           | 0.40              |
| Visual surface-foraging shorebirds  | 0.54                                 | 0.69              | 0.53                           | 0.69              |
| Pelagic-foraging shorebirds         | 0.39                                 | 0.45              | 0.37                           | 0.44              |
| Small shorebirds                    | 0.32                                 | 0.44              | 0.31                           | 0.47              |
| Medium-large shorebirds             | 0.33                                 | 0.43              | 0.33                           | 0.43              |
| Swimming waterbirds                 | 0.52                                 | 0.52              | 0.53                           | 0.53              |

that there are always areas available for shorebird use in the pond, but it requires a high initial investment for restructuring. Second, we suggest dividing one current evaporation cycle into multiple sub-cycles, reducing the volume of water evaporated at each evaporation cycle to maintain water depths accessible to shorebirds, while still supporting salt production (see Fig. 5a Management Scheme 2). This scheme saves the cost for pond restructuring, but increase in routine operations by introducing additional water channeling operations. These approaches

keep the overall water volume and surface area in the evaporation process, ensuring evaporation at a similar rate while creating essential shallow foraging zones and preserving access to abundant food resources for shorebirds. In the Nanpu Saltpans, since other pond types do not provide adequate food for shorebirds, these management schemes will mainly focus on the evaporation ponds (pink areas in Fig. 5b). With a total of 153 km<sup>2</sup> of evaporation ponds available (accounting for 52% of the total area of Nanpu Saltpans), effective management could provide foraging habitats that far exceed the natural mudflat area (57 km<sup>2</sup>) currently available to shorebirds.

Moreover, temporarily abandoned ponds, which naturally feature lower water levels during migration, have proven crucial for tactile surface-foraging species such as Curlew Sandpipers and Red-necked Stints (this study, Lei et al., 2021). These ponds were abandoned by producers due to disturbances from local residents during our study, but this abandonment, which adversely affected salt production, meant they did not persist for long. We recommend that if any abandoned salt ponds remain, it is essential to maintain consistently low water levels to prevent them from drying out, as dry ponds would no longer provide food for the birds.

In regions like the East Asian-Australasian Flyway, where extensive natural habitat loss calls for coordinated strategies, integrating saltpan management into broader wetland conservation efforts become essential (Wang et al., 2021). By prioritizing water level regulation, reducing human interference, and improving habitat structures, artificial wetlands can be transformed into critical refuges that significantly contribute to global conservation efforts. This approach not only



(caption on next page)

**Fig. 5.** Proposed changes to saltpan design and water management to enhance the use of saltpans by foraging shorebirds without compromising salt production. (a) Suggested management schemes for saltpans. Management Scheme 1: modify the structure of saltpans. Transform the current flat-bottom design (30 cm depth) into a gradient bottom (plan 1: a sloped bottom with depth 0–60 cm; plan 2 a terraced bottom with depth 15 cm, 30 cm, and 45 cm). These approaches keep the necessary water volume for evaporation, while ensuring that, as evaporation progresses, sufficient areas with a water depth of <15 cm remain available to serve as foraging habitats for shorebirds. Management Scheme 2: Adjust the amount and duration of water evaporation. Currently, with a water depth of 30 cm, it takes 30 days to evaporate down to a depth of 10 cm, achieving the desired salinity. By dividing the evaporation process into two (or three) cycles and reducing the initial water depth to 15 cm per evaporation cycle, it will take only 15 days to reach the required concentration (corresponding to a depth of 5 cm). This adjustment guarantees that shorebirds have adequate foraging areas (water depth < 15 cm) throughout the entire evaporation process, while ensuring that the salt production over the 30-day period remains unchanged. (b) Suggested design across the entire Nanpu Saltpans. Different types of ponds and land are marked with different colors, pink areas represent the evaporation ponds, which can be managed to support foraging by shorebirds. (c) The location of Nanpu in the Yellow and Bohai Sea. (For interpretation of the colour references in this figure legend, please refer to the web version of this article.)

complements traditional wetland restoration but also provides a scalable, cost-effective solution to the ongoing loss of wetlands worldwide, aligning with sustainable wetland management principles.

#### CRediT authorship contribution statement

**Weipan Lei:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **José A. Masero:** Writing – review & editing, Supervision, Conceptualization. **Ziwen Chai:** Investigation. **Bing-Run Zhu:** Investigation. **Tong Mu:** Writing – review & editing, Investigation. **He-Bo Peng:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Formal analysis. **Zhengwang Zhang:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization. **Theunis Piersma:** Writing – review & editing, Supervision.

#### Author statement

All the required declarations are included in the title page.

#### Funding sources

This research was supported by National Key Research and Development Program of China (2022YFF0802400), National Natural Science Foundation of China (32470491 32270518). H.-B-P was supported by Young Scientist Fund of the National Science Foundation of China (32401458) and China Postdoctoral Science Foundation (2024 M760580).

#### Declaration of competing interest

The authors declare no conflict of interest.

#### Acknowledgments

We thank the dedicated volunteers and colleagues—Katarzyna Kucharska, Jian Zhao, Yinong Liu, Hong-yan Yang, Jin Liu, Ginny Chan, Hongru Lin, Peter Crighton, Janson Loghry, and Katherine Leung—as well as friends from the GSWJ Birding Group (Xin Zhang, Yanfei Jin, Ming Xiong, and Lei Zhu) and colleagues from the Global Flyway Network (Chris Hassel, Adrian Boyle, Matthew Slaymaker, and Bob Loos) for their invaluable help with the bird surveys and benthos sampling. We are grateful to Prof. Xinhua Wang (Nankai University), Prof. Ding Yang, and Dr. Liang Wang (China Agricultural University) for their assistance in invertebrate identification, and to Xiaoyue Wang, Yiwen Geng, and my wife, Yuting Wang, for their help in measuring the invertebrates. We also thank Yang Liu and his father for local logistical support. Finally, we appreciate the valuable and insightful comments from the editor Prof. Xingfeng Si, and two anonymous reviewers, which greatly improved the manuscript.

#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2025.111100>.

#### Data availability

Data will be made available on request.

#### References

- Anderson, S. C., Ward, E. J., English, P. A., Barnett, L. A. K., & Thorson, J. T. (2024). sdmTMB: an R package for fast, flexible, and user-friendly generalized linear mixed effects models with spatial and spatiotemporal random fields (p. 2022.03.24.485545). *bioRxiv*. doi:<https://doi.org/10.1101/2022.03.24.485545>.
- Barnagaud, J.-Y., Papaix, J., Audevard, A., Lascève, M., Wroza, S., Geoffroy, D., 2019. Interspecific variations in shorebird responses to management practices on protected Mediterranean saltpans. *Biol. Conserv.* 237, 470–479. <https://doi.org/10.1016/j.biocon.2019.07.035>.
- Bellio, M.G., Kingsford, R.T., Kotagama, S.W., 2009. Natural versus artificial wetlands and their waterbirds in Sri Lanka. *Biol. Conserv.* 142, 3076–3085.
- Cai, S., Mu, T., Peng, H.-B., Ma, Z., Wilcove, D.S., 2024. Importance of habitat heterogeneity in tidal flats to the conservation of migratory shorebirds. *Conserv. Biol.* 38 (1), e14153. <https://doi.org/10.1111/cobi.14153>.
- Cheng, C., Liu, J., Ma, Z., 2022. Effects of aquaculture on the maintenance of waterbird populations. *Conserv. Biol.* 36 (5), e13913. <https://doi.org/10.1111/cobi.13913>.
- Davidson, N.C., Fluet-Chouinard, E., Finlayson, C.M., 2018. Global extent and distribution of wetlands: trends and issues. *Mar. Freshw. Res.* 69, 620–627. <https://doi.org/10.1071/MF17019>.
- Díaz, S., Settele, J., Brondizio, E.S., Ngo, H.T., Agard, J., Arneth, A., Balvanera, P., Brauman, K.A., Butchart, S.H.M., Chan, K.M.A., Garibaldi, L.A., Ichii, K., Liu, J., Subramanian, S.M., Midgley, G.F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., Polasky, S., Purvis, A., Razzaque, J., Reyers, B., Roy Chowdhury, R., Shin, Y.J., Visconti, P., Willis, K., Zayas, C.N., 2019. Pervasive human-driven decline of life on earth points to the need for transformative change. *Science* 366, eaax3100. <https://doi.org/10.1126/science.aax3100>.
- Duijns, S., Knot, I.E., Piersma, T., van Gils, J.A., 2015. Field measurements give biased estimates of functional response parameters, but help explain foraging distributions. *J. Anim. Ecol.* 84, 565–575. <https://doi.org/10.1111/1365-2656.12309>.
- Fan, J., Wang, X., Wu, W., Chen, W., Ma, Q., Ma, Z., 2021. Function of restored wetlands for waterbird conservation in the Yellow Sea coast. *Sci. Total Environ.* 756, 144061. <https://doi.org/10.1016/j.scitotenv.2020.144061>.
- Fluet-Chouinard, E., Stocker, B.D., Zhang, Z., Malhotra, A., Melton, J.R., Poulter, B., Kaplan, J.O., Goldewijk, K.K., Siebert, S., Minayeva, T., Hugelius, G., Joosten, H., Barthelmes, A., Prigent, C., Aires, F., Hoyt, A.M., Davidson, N., Finlayson, C.M., Lehner, B., Moore, P., McIntyre, P.B., 2023. Extensive global wetland loss over the past three centuries. *Nature* 614, 281–286. <https://doi.org/10.1038/s41586-022-05572-6>.
- Green, J.M.H., Sripaomyom, S., Giam, X., Wilcove, D.S., 2015. The ecology and economics of shorebird conservation in a tropical human-modified landscape. *J. Appl. Ecol.* 52, 1483–1491. <https://doi.org/10.1111/1365-2664.12508>.
- Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. *J. Evol. Biol.* 24, 699–711. <https://doi.org/10.1111/j.1420-9101.2010.02210.x>.
- Hassel, C., Boyle, A., Slaymaker, M., Chan, Y.C., Piersma, T., 2013. Red Knot Northward Migration through Bohai Bay, China, Field Trip Report April & May 2013. Global Flyway Network, Broome.
- Jackson, M.V., Choi, C.-Y., Amano, T., Estrella, S.M., Lei, W., Moores, N., Mundkur, T., Rogers, D.I., Fuller, R.A., 2020. Navigating coasts of concrete: pervasive use of artificial habitats by shorebirds in the Asia-Pacific. *Biol. Conserv.* 247, 108591. <https://doi.org/10.1016/j.biocon.2020.108591>.
- Lei, W., Masero, J.A., Piersma, T., Zhu, B., Yang, H.-Y., Zhang, Z., 2018. Alternative habitat: the importance of the Nanpu saltpans for migratory waterbirds in the Chinese Yellow Sea. *Bird Conserv. Int.* 28, 549–566. <https://doi.org/10.1017/S0959270917000508>.
- Lei, W., Masero, J.A., Dingle, C., Liu, Y., Chai, Z., Zhu, B., Peng, H., Zhang, Z., Piersma, T., 2021. The value of coastal saltpans for migratory shorebirds:

- conservation insights from a stable isotope approach based on feeding guild and body size. *Anim. Conserv.* 24, 1071–1083. <https://doi.org/10.1111/acv.12717>.
- Li, X., Bellerby, R., Craft, C., Widney, S.E., 2018. Coastal wetland loss, consequences, and challenges for restoration. *Anthr. Coasts* 1, 1–15. <https://doi.org/10.1139/anc-2017-0001>.
- Liu, N., Ma, Z., 2024. Ecological restoration of coastal wetlands in China: current status and suggestions. *Biol. Conserv.* 291, 110513. <https://doi.org/10.1016/j.biocon.2024.110513>.
- Masero, J.A., 2003. Assessing alternative anthropogenic habitats for conserving waterbirds: Salinas as buffer areas against the impact of natural habitat loss for shorebirds. *Biodivers. Conserv.* 12, 1157–1173. <https://doi.org/10/dcb4g7>.
- Murray, N.J., Clemens, R.S., Phinn, S.R., Possingham, H.P., Fuller, R.A., 2014. Tracking the rapid loss of tidal wetlands in the Yellow Sea. *Front. Ecol. Environ.* 12, 267–272. <https://doi.org/10/f56b6z>.
- Murray, N.J., Worthington, T.A., Bunting, P., Duce, S., Hagger, V., Lovelock, C.E., Lucas, R., Saunders, M.I., Sheaves, M., Spalding, M., Waltham, N.J., Lyons, M.B., 2022. High-resolution mapping of losses and gains of Earth's tidal wetlands. *Science* 376, 744–749. <https://doi.org/10.1126/science.abm9583>.
- Ntiama-Baidu, Y.A.A., Piersma, T., Wiersma, P., Poot, M., Battley, P., Gordon, C., 1998. Water depth selection, daily feeding routines and diets of waterbirds in coastal lagoons in Ghana. *Ibis* 140, 89–103. <https://doi.org/10.1111/j.1474-919x.1998.tb04545.x>.
- O'Hara, C.C., Frazier, M., Halpern, B.S., 2021. At-risk marine biodiversity faces extensive, expanding, and intensifying human impacts. *Science* 372, 84–87. <https://doi.org/10.1126/science.abe6731>.
- Peng, H.-B. 2024. Listening to the mud: exploring shorebird conservation from on and in the mud. [thesis fully internal (DIV), University of Groningen]. University of Groningen. <https://doi.org/10.33612/diss.875545013>.
- Peng, H.B., Chan, Y.C., Huang, Y., Choi, C.Y., Zhang, S.D., Ren, S., Hassell, C.J., Zhu, Z., Melville, D.S., Ma, Z., Lei, G., Piersma, T., 2024. Intraseasonal movements between staging sites by migrating great knots: longer distances to alternatives decrease the probability of such moves. *Biol. Conserv.* 292, 110547. <https://doi.org/10.1016/j.biocon.2024.110547>.
- Piersma, T., 2012. What is habitat quality? Dissecting a research portfolio on shorebirds. In: Fuller, R.J. (Ed.), *Birds and Habitat: Relationships in Changing Landscapes*. Cambridge University Press, Cambridge.
- Piersma, T., Lok, T., Chen, Y., Hassell, C.J., Yang, H.-Y., Boyle, A., Slaymaker, M., Chan, Y.-C., Melville, D.S., Zhang, Z.-W., Ma, Z., 2016. Simultaneous declines in summer survival of three shorebird species signals a flyway at risk. *J. Appl. Ecol.* 53, 479–490. <https://doi.org/10/f8b8rn>.
- Ramsar Convention Secretariat, 2010. Wise Use of Wetlands: Concepts and Approaches for the Wise Use of Wetlands. In: *Ramsar Handbooks for the Wise Use of Wetlands*, 4th edition 1. Ramsar Convention Secretariat, Gland, Switzerland.
- Rehfsch, M.M., 1994. Man-made lagoons and how their attractiveness to waders might be increased by manipulating the biomass of an insect benthos. *J. Appl. Ecol.* 31, 383–401. <https://doi.org/10.2307/2404552>.
- RStudio Team, 2022. RStudio: Integrated Development for R. RStudio, PBC, Boston, MA. URL <http://www.rstudio.com/>.
- Seaman, W., 2007. Artificial habitats and the restoration of degraded marine ecosystems and fisheries. In: Relini, G., Ryland, J. (Eds.), *Biodiversity in Enclosed Seas and Artificial Marine Habitats*. Springer, Netherlands, pp. 143–155. [https://doi.org/10.1007/978-1-4020-6156-1\\_13](https://doi.org/10.1007/978-1-4020-6156-1_13).
- Sripanomyom, S., Round, P.D., Savini, T., Trisurat, Y., Gale, G.A., 2011. Traditional salt-pans hold major concentrations of overwintering shorebirds in Southeast Asia. *Biol. Conserv.* 144, 526–537.
- Studds, C.E., Kendall, B.E., Murray, N.J., Wilson, H.B., Rogers, D.I., Clemens, R.S., Gosbell, K., Hassell, C.J., Jessop, R., Melville, D.S., Milton, D.A., Minton, C.D.T., Possingham, H.P., Riegen, A.C., Straw, P., Woehler, E.J., Fuller, R.A., 2017. Rapid population decline in migratory shorebirds relying on Yellow Sea tidal mudflats as stopover sites. *Nat. Commun.* 8, 14895. <https://doi.org/10.1038/ncomms14895>.
- Velasquez, C.R., 1992. Managing artificial salt-pans as a waterbird habitat: Species' responses to water level manipulation. *Colon. Waterbirds* 15, 43–55. <https://doi.org/10.2307/1521353>.
- Wang, X., Xiao, X., Xu, X., Zou, Z., Chen, B., Qin, Y., Zhang, X., Dong, J., Liu, D., Pan, L., Li, B., 2021. Rebound in China's coastal wetlands following conservation and restoration. *Nat. Sustain.* 4, 1076–1083. <https://doi.org/10.1038/s41893-021-00793-5>.
- Warnock, N., Page, G.W., Ruhlen, T.D., Nur, N., Takekawa, J.Y., Hanson, J.T., 2002. Management and conservation of San Francisco Bay salt ponds: effects of pond salinity, area, tide, and season on Pacific flyway waterbirds. *Waterbirds* 25, 79–92. <https://doi.org/10.2307/1522454>.
- White, T.C.R., 2008. The role of food, weather and climate in limiting the abundance of animals. *Biol. Rev.* 83, 227–248. <https://doi.org/10.1111/j.1469-185X.2008.00041.x>.
- Zhang, S.-D., Ma, Z., Choi, C.-Y., Peng, H.-B., Bai, Q.-Q., Liu, W.-L., Tan, K., Melville, D. S., He, P., Chan, Y.-C., Gils, J. a. V., Piersma, T., 2018. Persistent use of a shorebird staging site in the Yellow Sea despite severe declines in food resources implies a lack of alternatives. *Bird Conserv. Int.* 28, 534–548. <https://doi.org/10.1017/S0959270917000430>.
- Zhang, S.-D., Ma, Z., Peng, C.-C., Melville, D.S., van Gils, J.A., Piersma, T., 2019. Individual diet differences in a molluscivore shorebird are associated with the size of body instruments for internal processing rather than for feeding. *J. Avian Biol.* 50, e02255. <https://doi.org/10.1111/jav.02255>.
- Zuur, A.F., Hilbe, J.M., Ieno, E.N., 2013. *A Beginner's Guide to GLM and GLMM with R: A Frequentist and Bayesian Perspective for Ecologists*. Highland Statistics Limited, Newburgh, UK.
- Zwarts, L., Wanink, J.H., 1993. How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. *Neth. J. Sea Res.* 31, 441–476. <https://doi.org/10/fk8spc>.