



The influence of hydrological variables, climatic variables and food availability on Anatidae in interconnected river-lake systems, the middle and lower reaches of the Yangtze River floodplain



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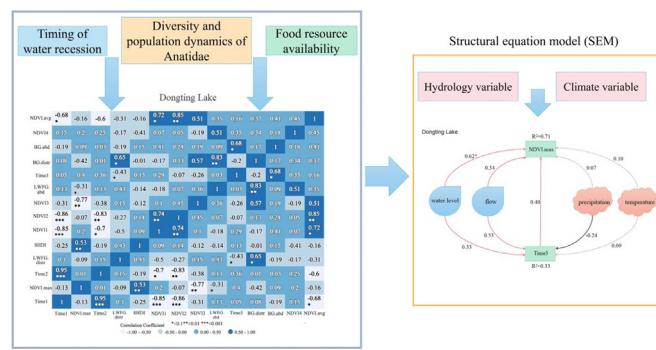
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HIGHLIGHTS

- Environmental impact on Anatidae was studied in an interconnected river-lake system.
- Variations in the timing of water recession influenced Anatidae diversity.
- Anatidae diversity were significantly correlated with vegetation cover (NDVI.max).
- Water level, flow and interval time of water recession explained 71% of NDVI.max.

GRAPHICAL ABSTRACT



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ABSTRACT

Hydrology-climate changes and food availability are expected to be the primary drivers that result in a loss of waterbird diversity. Non-biological factors are vital to food availability in interconnected river-lake systems, so in addition to identifying the ecological response to drivers, it is also important to analyze and quantify relationships between drivers. In order to explore the impacts of these drivers on the wintering waterbirds, we selected Dongting Lake (DTL) as a study area, which is a typical interconnected river-lake system in the middle and lower reaches of the Yangtze River Floodplain. The Anatidae species, most of which are herbivorous, were chosen as the representative waterfowl. The Pearson correlation coefficient was applied to select variables related to the timing of water recession and food availability, which have significant influences on the Anatidae. Then, the structural equation model (SEM) was carried out to quantify the relationships among the food availability, hydrological variables, and climatic variables. The results showed that unseasonably early or late water recession had a negative impact on the diversity of the Anatidae, and in particular affected population dynamics of the Lesser White-fronted goose *Anser erythropus*. Significant changes in Anatidae populations in DTL occurred in response to maximum NDVI ($r = 0.53, p < 0.01$) and the interval time of water recession ($r = -0.43, p < 0.1$). Water level, flow, and interval time of water recession explained 71% of maximum NDVI in DTL. In addition, hydraulic interactions between the mainstream and each lake jointly affected the inundation pattern and the vegetation

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growth stage of the lake after the flood season, thus affecting foraging suitability. Our findings suggest that water compensation should be carried out within an appropriate range of hydraulic gradient to optimize the time of water recession and improve the suitability of the habitat effectively.

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1. Introduction

Waterbirds, one of the most sensitive and vulnerable groups, are a key criterion for Ramsar-listing of wetlands (Kingsford et al., 2017) and also the most symbolic ecological indicators in assessing wetland quality (Zhang et al., 2016). Waterbirds are susceptible to hydrology-driven or climate-driven niche shifts (Liang et al., 2020; Liang et al., 2018c; Lopez-Ballesteros et al., 2020). Understanding related environmental factors that shape waterbird population dynamics is significant for their effective conservation (Jia et al., 2018). For example, reduction of large flows was predicted to decrease ibis breeding frequency by 170% in the Narran Lakes, which is one of the most important sites for birds to breed in Australia (Brandis et al., 2018). In European Union (EU) protected areas, *Mergellus albellus* are responding to climate change by changing their distributions (Pavón-Jordán et al., 2015). However, a comprehensive and in-depth understanding about the crucial environmental variables affecting overwintering waterbirds and relationships between these variables is rarely obtained.

The food resource availability of waterbirds is driven by hydrology and has strong habitat associations. Hydrological regimes such as water level fluctuation and inflow are important abiotic factors affecting the foraging and the perching of waterbirds (Zhang et al., 2016). The extent, timing, and duration of inundation are also critical for macrophytic growth as a food source of waterbirds (Wang et al., 2017). Therefore, the way in which food availability and inundation patterns influence waterbird populations is of worldwide concern. Environmental variables used in previous studies include the timing of water recession and Normalized Difference Vegetation Index (NDVI) (Zhang et al., 2018b; Zou et al., 2019). Moreover, most studies have suggested that uncertain and complex interactions occur among environmental factors (Guan et al., 2016b). For instance, generalized linear mixed models suggest that crane numbers in natural wetlands are positively related to tuber density and the interaction between dry season (October–March) water level and tuber density (Hou et al., 2020).

However, water regimes in wetlands are often modified by human activities, such as urbanization, agriculture, dam operations, and large-scale water transfer projects. These human-induced modifications have significant impacts on waterbird species (Liang et al., 2018b; Liang et al., 2021; Mei et al., 2015). The ecological status of lakes in many regions are reported to be affected by water conservancy projects, such as the Amur Basin (Jia et al., 2020), the semi-arid rivers in Colorado, USA (Diehl et al., 2020), and the Sudd wetland of South Sudan (Sosnowski et al., 2016). Dam constructions dramatically change hydrological regimes of global river systems. Water resource development has severe long-term ecological impact on prominent freshwater animals (Kingsford et al., 2017). These studies also provided the theoretic base regarding the relationships between hydrological regimes, climatic factor, food availability, and waterbirds.

To clarify the relationships among overwintering waterbirds, hydrology-climate regimes, and food availability, we examined the Dongting Lake (DTL), a Ramsar site, and the representative Yangtze-connected freshwater lake in the middle and lower reaches of the floodplain. As a typical case of interconnected river-lake system, the growth cycle of vegetation is closely related to the seasonal hydrological changes in DTL. The wetland is characterized by high water levels in summer and low water levels in autumn and winter, which progressively creates large areas of shallow water and exposed lake sediments, temporarily attracting tens of thousands of wintering waterbirds (Guan et al., 2016b). The impoundment or discharge of the Three-Gorges Dam

may lead to premature or late exposure of wetland meadows and mudflats in DTL (Zou et al., 2019). In addition, extreme hydrological conditions may induce alterations in ecological function of the wetland. Providing suitable habitat in a way that maintains or improves wetlands has become a crucial issue (Li et al., 2019).

The Structural Equation Models (SEM) are statistical procedures for testing measurement, functional, predictive, and causal hypotheses. The direct and indirect effects of dams, habitat, and fish biodiversity in lotic ecosystems were studied by using the SEM (Hitchman et al., 2018). Hence, it can be hypothesized that the SEM may facilitate our understanding of the driving mechanisms of hydrological (water level and flow) and climatic (temperature and precipitation) factors on the timing of water recession and food resource availability for the Anatidae in the interconnected river-lake systems. In our study, DTL was divided into three lake areas (the west, the south, and the east) to analyze the relationships among these drivers. It may reveal the main ways in which the input of environmental variables affects the ecological conditions of different lakes, provide in-depth insights of their internal relationships, and identify the dominant factors affecting the ecological status of wetlands (Zhang et al., 2020c).

The direct and indirect effects of habitat drivers have not been properly explored in relation to the structure (diversity and population dynamics) of waterbirds assemblages in DTL and more widely (Zhang et al., 2015). In this study, we identified crucial environmental variables for Anatidae populations utilising a 15 year time-series. We quantified relationships among a wide range of drivers by analyzing the relationship between hydrological factor, climatic factor, and food availability. The studied species were the Anatidae, including dominant species such as Bean goose *Anser fabalis* and the protected Lesser White-fronted goose *Anser erythropus*. We hypothesized that the diversity and population dynamics of Anatidae would be negatively affected by changes in the timing of water recession and food supply. Specifically, the main objectives of this paper were to (1) compare the variation of waterbird population in different conditions of water recession; (2) explore how food availability and the timing of water recession affect the diversity and population dynamics of Anatidae; and (3) analyze how hydrological and climatic factors influence food availability and the timing of water recession in wetlands.

2. Materials and methods

2.1. Study area and species

Our study (Fig. 1) focuses on Dongting Lake (28°30'–30°20'N, 111°40'–113°10'E), the second largest freshwater lake in China with a total area of approximately 2625 km² (Yuan et al., 2016). DTL, which consists of three regions - East Dongting Lake (EDL), South Dongting Lake (SDL), and West Dongting Lake (WDL), is a typical interconnected river-lake system. The area is characterized by subtropical monsoon climate (Yuan et al., 2015). The topography is high in the west and low in the east (Xie et al., 2015). The water from Yangtze River mainly enters the DTL through three inlets located in the northwest catchment, including the Songzi, Taiping, and Ouchi Rivers. In addition, DTL receives discharge from four major tributaries (Xiangjiang River, Zishui River, Yuanjiang River, and Lishui River). Finally, it discharges into the Yangtze River from Chenglingji, the only outlet of DTL (Zhang et al., 2016). DTL has typical seasonal characteristics (wet season and dry season) and plays a critical role in flood regulation in the Yangtze flood plain (Hu et al., 2015). With the change of water level, a wide range of habitat

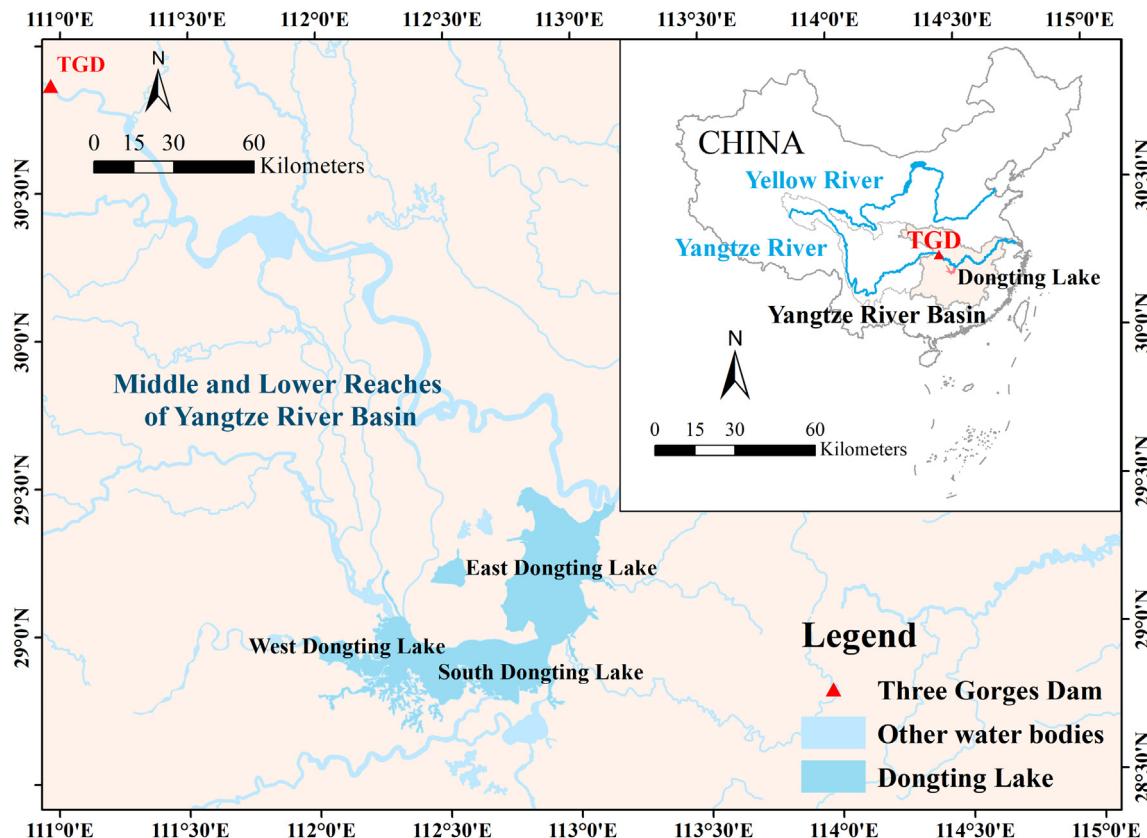


Fig. 1. The location of the Dongting Lake and the Three Gorges Dam in China.

types appeared in DTL, providing a main food resource for arriving waterbirds (Zou et al., 2016). DTL is the first large lake downstream of the Three Gorges Project (TGP) along with substantial changes identified in the hydrological regimes, water quality, and wetland environments since the TGP began operation in 2003. Changes in the water regime can result in significant change of vegetation which is the main food source for Anatidae in DTL.

Eastern China is one of the most important wintering areas for migratory birds, supporting more than 2 million waterbirds, and over 1 million of which are Anatidae within the group. Most of Anatidae are distributed in the middle and lower reaches of the Yangtze River, especially in DTL (Jia et al., 2019). Anatidae were selected because they are the most abundant and diverse species of waterbirds in the DTL. Moreover, we also explored the population dynamics of two representative species of Anatidae: Bean goose with the largest population and Lesser White-fronted goose a flagship species (Liang et al., 2018a).

2.2. Data source

According to lots of documents related to the diversity of waterbirds in DTL, as well as survey reports in some nature reserves, the data on the species of Anatidae in DTL was sorted out. In this paper, we obtained the data of the Anatidae population from 2000 to 2015 (data of 2001–2003, 2006 and 2011 was deficient) (see Tables A1, A2, A3, and A4).

Changes in water level and flow in DTL provide a good measure of hydrological status (Zhang et al., 2016). In this study, daily water level and flow data (at 8:00 AM) of DTL were obtained from the representative hydrological stations of the three lakes (Chenglingji Hydrological Station (EDL), Yuanjiang Hydrological Station (SDL), and Nanju Hydrological Station (WDL)). The water level data was obtained from the Hydrology Inquiry System of Hunan Province (<http://yzt.hnswkjc.com:9090/#/>). Similarly, the weather station data (precipitation and temperature) of the three lakes were used as the daily climate data for

the entire lake. The three representative weather stations were Yueyang Weather Station (EDL), Changde Weather Station (SDL), and Nanxian Weather Station (WDL). The climate data were obtained from the Chinese Meteorological Science Data Website (<https://data.cma.cn/>). We used the MODIS (moderate-resolution imaging spectroradiometer) 16-day composite NDVI time series data products (MOD13Q1) during 2000–2015, with a spatial resolution of 250 m, which were downloaded from NASA (National Aeronautics and Space Administration) (<https://search.earthdata.nasa.gov/search>).

2.3. Environmental variables

Six variables of food availability (NDVI1, NDVI2, NDVI3, NDVI4, NDVI.max, and NDVI.avg) and three variables of water recession time (Time1, Time2, and Time3) were chosen in the DTL to identify critical variables correlating with Anatidae diversity and the population dynamics of Bean goose and Lesser White-fronted goose (Table 1). Two hydrological variables (water level (m) and flow (m³/s)) and two climatic variables (temperature (°C) and precipitation (mm)) were assembled as explanatory variables to investigate the integrated effects on variables correlated with Anatidae diversity and the population dynamics of Bean goose and Lesser White-fronted goose. Details of all variables are provided in Table 1. The reference method of water recession was selected for migrating waterbirds in winter (Guan et al., 2016b). The method processing of NDVI time series data is detailed in Supplementary information.

2.4. Data analyses

According to previous research and relevant data, the normal water recession is between the end of September and the beginning of November (Guan et al., 2016b). Therefore, approximately the 255th to the 305th days of the year are regarded as the normal period of water

Table 1

The indices of the Anatidae species and description of the environmental variables.

Environmental variables	Description
SHDI	Shannon's Diversity Index of the Anatidae.
BG.abd	The abundance of Bean goose <i>Anser fabalis</i> .
BG.distr	The distribution of Bean goose <i>Anser fabalis</i> .
LWFG.abd	The abundance of Lesser White-fronted goose <i>Anser erythropus</i> .
LWFG.distr	The distribution of Lesser White-fronted goose <i>Anser erythropus</i> .
NDVI1	NDVI at the beginning time of water recession.
NDVI2	NDVI at the ending time of water recession.
NDVI3	NDVI when the Anatidae arrived.
NDVI4	NDVI at the time of bird survey.
NDVI.max	Maximum NDVI before bird survey based on MODIS data.
NDVI.avg	Average NDVI before bird survey based on MODIS data.
Time1	The beginning time of water recession.
Time2	The ending time of water recession.
Time3	The interval time of water recession.

receding before the arrival of Anatidae. The rest of periods belong to abnormal timing of water recession (too early or too late) for the arrival of Anatidae. To explore the impacts of water recession conditions on the dynamics of Anatidae, the independent sample *t*-test was performed to compare the significant difference between the two kinds of water recession conditions (normal water recession and abnormal water recession). We also divided DTL into three lake areas (the west, the south, and the east) to analyze. The statistical analysis was performed with the IBM SPSS Statistics 20 software. The Pearson correlation coefficient was used to investigate significant correlation between the water recession and food availability on Anatidae dynamics. We used R 3.5.2 to calculate the correlation among variables.

SEM is increasingly used in ecological research to explore complex relationships and causal relationships (Guan et al., 2016a). The model is based on the assumption that the previous layer has a direct influence on the subsequent layers, and all these layers will eventually have a joint impact on the crucial variable. In this study, we provided a framework to clarify the direct and indirect effects of hydrological (water level and flow) and climatic (temperature and precipitation) factors on the timing of water recession and food resource availability for the Anatidae based on previous research and ecological principals. For recognizing relationships among the factors in different lake areas, three lakes of DTL were also analyzed separately. The selected water recession index and NDVI index came from the correlation analysis results of each lake area in the previous step. The direct and indirect effects of exogenous variables on endogenous variables were expressed by the standard path coefficient (*r* value) (Zhang et al., 2020c). Goodness-of-fit of the model (Fisher's statistic) was accessed by using Shipley's test of d-separation, which evaluated the probability that none of the paths missing from the hypothesized causal network contain useful information. The final model had an adequate fit (*p*>0.05) and the AICc was computed (AIC (Akaike Information Criterion) corrected for small sample size) (Tang et al., 2020). We used R version 3.5.2 with the package 'piecewise SEM' (<https://github.com/jlslefche/piecewiseSEM>) (Zhang et al., 2019b).

3. Result and discussion

3.1. Variations of the timing of water recession

Fig. 2 showed that the timing of water recession in 2000 was late while the timing of water recession in 2009 was early. In 2013, the stage of water recession fluctuated greatly, and the water level rebounded largely during the period. Therefore, the timing of water recession in 2000, 2009, and 2013 belong to abnormal water recession (too early or too late) based on arrival of Anatidae, and the other years had normal water recession. Similar results were obtained by Wang (Wang et al., 2019). Next, we compared the water recession conditions

of EDL, SDL, and WDL (Fig. 3). The average beginning time of water recession was the 264th, the 271st, and the 283rd day of year in WDL, SDL, and EDL, respectively. The WDL began to recede earliest, followed by the SDL and the EDL. The beginning of water recession in DTL was approximately the 273rd day every year. The WDL was the first to end the water receding with the average ending time of the 282nd day. The Time2 of SDL and EDL was the 302nd day and the 301st day respectively, and they were later than the Time2 of WDL. The ending time of water recession in DTL was about the 295th day in each year. The SDL had the longest interval time of water recession with the average interval time of 30 days. The WDL and the EDL were nearly the same with an average interval time of about 18 days (see Tables A5, A6, A7, and A8).

3.2. Influence of the timing of water recession and food availability on Anatidae

Does the timing of water recession have any influence on Anatidae dynamics? According to the results of the *t*-test (Table 2), the diversity of Anatidae in DTL was significantly reduced by the different conditions of water recession (*p*<0.1). But there was no distinct difference in the distribution and abundance of Bean goose and Lesser White-fronted goose. The diversity of Anatidae in the three sub-lakes decreased to varying degrees. The difference in SDL and WDL was not obvious, however, there were significant differences on Anatidae diversity in the EDL (*p*<0.1). In particular, the LWFG.abd was significantly different (*p*<0.05).

How about the impact of water recession and food availability on the Anatidae diversity and population dynamics? Correlation analysis (Fig. 4) showed that diversity of Anatidae was positively correlated with NDVI.max (*r* = 0.53, *p*<0.01). The BG.abd was positively correlated with the Time3 (*r* = 0.68, *p*<0.1). The LWFG.abd and LWFG.distr were negatively correlated to NDVI.max (*r* = -0.31, *p*<0.1) and the Time3 (*r* = -0.43, *p*<0.1), respectively. The environmental drivers for each sub-lake area were also analyzed in this study to identify areas within DTL to carry out restoration work. In general, the diversity and population dynamics of Anatidae in EDL were correlated with the NDVI.max (Fig. S1), while the diversity and dynamics in SDL were related to the NDVI.avg and NDVI3 (Fig. S2). The relevant factors of Anatidae population dynamics and diversity in WDL were the NDVI2, Time1 and Time2 (Fig. S3).

After the operation of the TGP, the duration of inundation of vegetation was significantly shortened from July to November. As a result, Anatidae suffered from adverse habitat changes, as their seasonal arrival in early winter no longer coincided with high quantity and quality of foraging. The EDL supported nearly 90% of Lesser White-fronted goose living through the winter. The Lesser White-fronted goose were more sensitive to changes in habitat. Changes in timing of inundation have affected the extent of seasonally flooded grassland feeding for the Lesser White-fronted goose (Jia et al., 2018). Therefore, abnormal timing of water recession (too early or too late) had a significant influence on the abundance of Lesser White-fronted goose in the EDL. The Bean goose were one of the most abundant Anatidae species in DTL (Zhang et al., 2020b). After December, due to the overabundance of Anatidae and the shortage of food resources, the Bean goose left the grasslands and mudflats to search for food in the surrounding rice fields (which were artificial foraging habitats), indicating that the Bean goose are more flexible in responding to changes in food density (Zhu et al., 2020). Compared with the globally vulnerable Lesser White-fronted goose, the larger Bean goose appeared to be less susceptible to food shortages and showed a more stable response in winter (Zhang et al., 2020b). In addition, Bean goose were less sensitive to habitat changes, and there was no obvious temporal trend (Jia et al., 2019).

A higher NDVI may indicate the presence of better food availability (Wu et al., 2014). Similar to the findings by Pettorelli et al. (2005), the diversity of Anatidae was positively correlated with the NDVI.max in DTL. Due to proper light and heat conditions, water in the mudflat

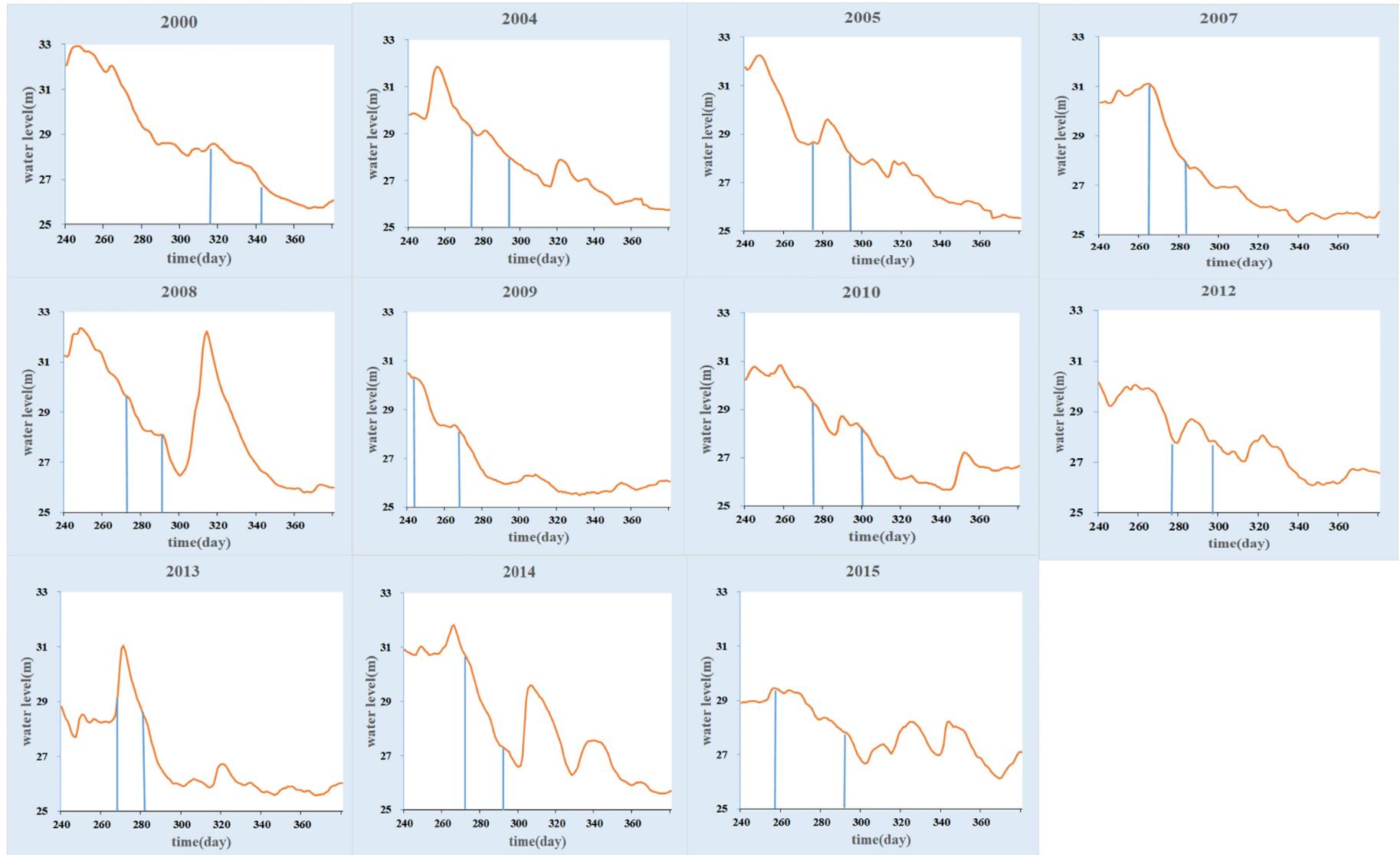


Fig. 2. Variations in water level and the timing of water recession during the study period. The two blue vertical lines represent the beginning and the ending time of water recession respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

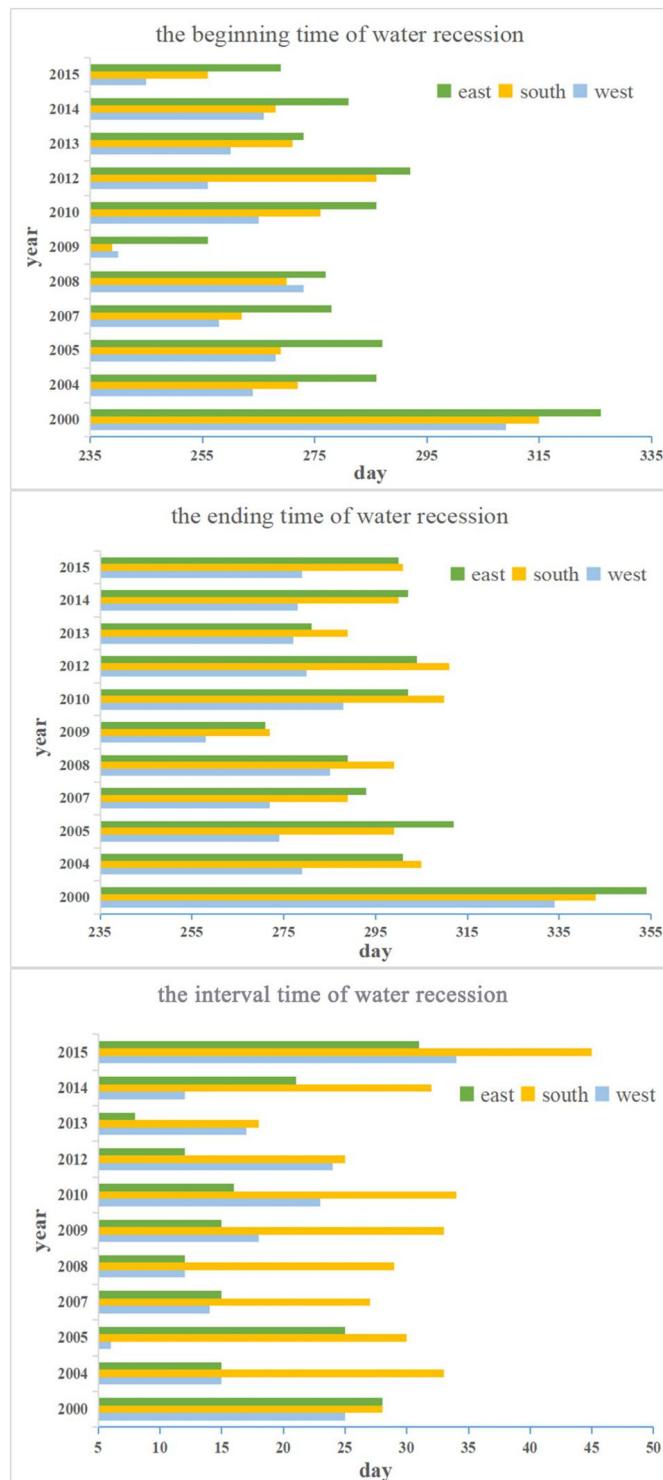


Fig. 3. The beginning time of water recession, the ending time of water recession and the interval time of water recession in three lakes (the East Dongting Lake, the South Dongting Lake and the West Dongting Lake).

evaporated, then the plant propagules sprouted and covered habitat rapidly. This period of plant growth in the mudflats occurred at the stage of water recession. If the mudflats appear for a short time, they cannot provide stable food resources for Anatidae. Therefore, an appropriate interval time of water recession could have a positive impact on the foraging of Anatidae. However, Lesser White-fronted goose showed a negative correlation with NDVI.max. A possible explanation was that the hydrological conditions were alternating (Xia et al., 2016). It might be the impact of impounding in autumn by

the TGP. The changes of hydrological rhythm influenced the biomass of plants, which affected the foraging suitability of Lesser White-fronted goose and the composition of food resource. In addition, Lesser White-fronted goose were highly dependent and sensitive to habitat changes. Contrary to a positive correlation between SHDI of Anatidae and NDVI.max, factors such as competition for forage with other Anatidae species might affect population dynamics of Lesser White-fronted goose, thus showing a negative correlation. In general, the habitat and food supply of Anatidae were largely

Table 2

Results from the independent sample *t*-test for the Anatidae in overwintering periods with two situations of water recession based on arrival time of waterbirds in the Dongting Lake and its three sub-lakes.

	Normal water recession (<i>n</i> = 8)	Abnormal (too early or too late) water recession (<i>n</i> = 3)	<i>p</i> -Value
Dongting Lake			
SHDI	1.77 ± 0.29	1.01 ± 1.00	0.064
BG.abd	17,480.38 ± 11,201.88	17,079.33 ± 5120.24	0.955
BG.distr	0.37 ± 0.40	0.39 ± 0.37	0.931
LWFG.abd	13,726.13 ± 13,150.84	18,198.67 ± 15,924.14	0.644
LWFG.distr	0.32 ± 0.45	0.43 ± 0.38	0.715
East Dongting Lake			
SHDI	1.74 ± 0.29	1.09 ± 0.72	0.053
BG.abd	14,283.63 ± 9858.89	9866.00 ± 7889.52	0.508
LWFG.abd	10,257.25 ± 7454.66	21,839.00 ± 5206.89	0.038
South Dongting Lake			
SHDI	1.28 ± 0.65	1.22 ± 0.32	0.893
BG.abd	2966.60 ± 4372.56	2308.33 ± 1211.09	0.813
LWFG.abd	4367.00 ± 3232.58	3338.67 ± 3123.63	0.690
West Dongting Lake			
SHDI	1.40 ± 0.56	1.39 ± 0.63	0.970
BG.abd	3443.14 ± 4122.24	6620.00 ± 7371.39	0.396
LWFG.abd	3968.75 ± 3211.53	8733.00 ± 377.59	0.120

affected by the hydrological system. The population dynamics of Anatidae in DTL were significantly correlated with Time3 and NDVI_{max}. It suggested that hydrological regimes and food availability might be the main non-biological and biological factors that determined the presence of Anatidae, which was consistent with the research view of Zhang et al., 2020b.

The indicators and correlations affecting the population dynamics of Anatidae in EDL were similar to DTL, indicating that the hydrological situation in EDL was roughly consistent with the hydrological situation in the whole lake. BG.abd was positively correlated with most of the NDVI in each period, reflecting the strong adaptability to the change of the habitat of Bean goose and their wide feeding range that were not limited to

Dongting Lake

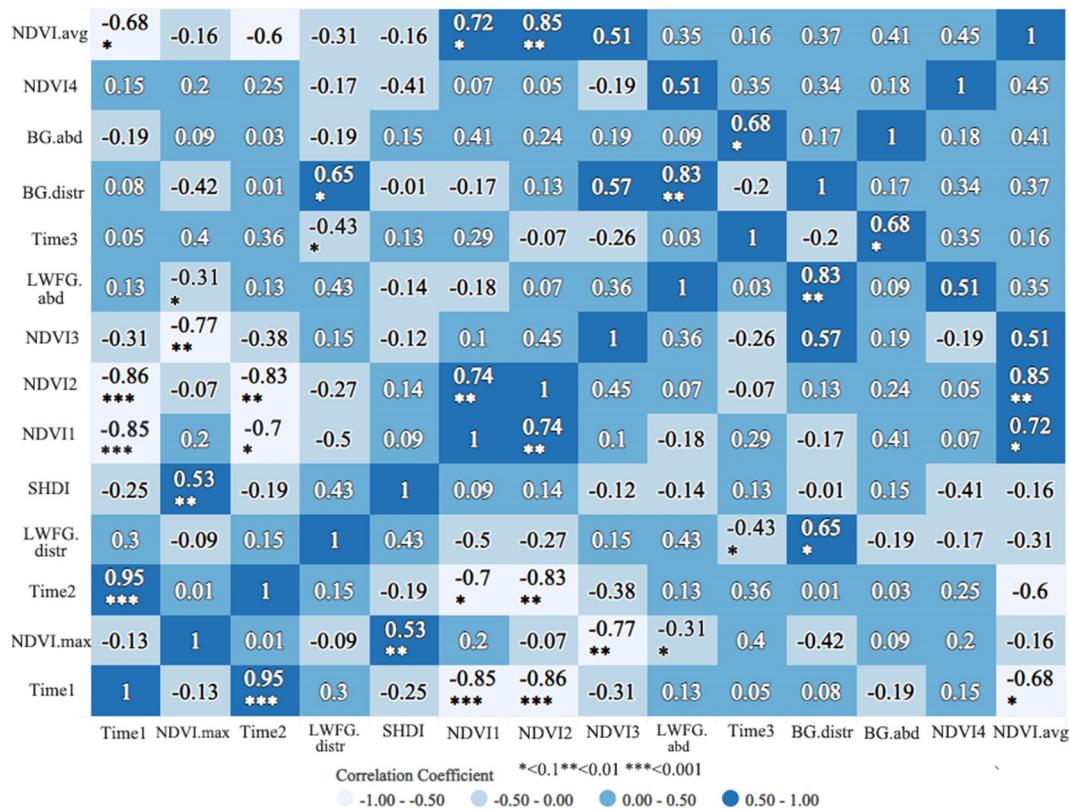


Fig. 4. Relationships of the timing of water recession and food availability on diversity and population dynamics of Anatidae species in the Dongting Lake. Pearson's correlation coefficient is used to test whether the factors exhibit significant correlation. BG.abd represents abundance of Bean goose *Anser fabalis*. BG.distr represents distribution of Bean goose *Anser fabalis*. LWFG.abd represents abundance of Lesser white-fronted goose *Anser erythropus*. LWFG.distr represents distribution of Lesser white-fronted goose *Anser erythropus*. The number in each square represents the correlation coefficient between the two corresponding variables. *** represented *p* < 0.1. ** represented *p* < 0.01. *** represented *p* < 0.001.

specific food resources. It also showed that there was an inevitable trend that the Bean goose could become one of the most dominant species in DTL. The SDL was an important water area connecting the EDL and the WDL with a bridge connecting the entire ecological corridor in DTL. It played a unique role in the original wetland ecosystem, biodiversity, and the intensity of the impact of the TGP (Yuan et al., 2016). The variable related to the dynamic changes of Anatidae in SDL was NDVI.avg, which measured the average vegetation productivity and biomass level of the lake area. It also reflected the transitional and buffering role of the SDL. From the perspective of hydrological spatial relationship, WDL, an important area for flood diversion, sedimentation, flood regulation, and storage retention, received many incoming water resources. Therefore, it had a great impact on the hydrological situation in DTL. After the flood season, the inflow of the Yangtze River decreased, directly affecting the water recession period in WDL, which was shown that the BG.abd and LWFG.abd were significantly positively correlated with the Time1 and Time2. Studies have shown the earlier the dry season came in DTL, the poorer the food quality of Anatidae got (Cheng et al., 2018). The water receding period in WDL was earlier than other lake areas, thus the beaches exposed earlier and vegetation grew earlier, which were not synchronized with the arrival of Anatidae. At this time, the population dynamics of Anatidae was negatively correlated with NDVI. The correlation results suggested that if the water receding node of WDL was delayed appropriately, Anatidae could potentially obtain more abundant foraging resources and potentially increase species diversity.

3.3. Quantitative relationships among the hydrology-climate variables, the timing of water recession, and food availability

SEM revealed the pathways in which the hydrological and climatic parameters affected the timing of water recession and food availability

in DTL. The model with Fisher's C statistic $p = 0.421 > 0.05$ and $AICc = 21.73$ was determined (Fig. 5). The results showed that the water level and flow of DTL had a positive and direct impact on NDVI.max, which was intermediated by Time3. Precipitation had a negative and direct impact on the Time3, but little indirect effect on NDVI.max. The explanation ratio of the variation of NDVI.max by water level, flow and the Time3 was 71%.

The results of model in the WDL showed that flow and temperature had a direct negative impact on Time1 and Time2, which indirectly had a positive impact on NDVI2. The explanation ratio of 78% indicated change in NDVI2 was best explained by water level, flow, temperature, Time1, and Time2. We estimated that it might be in a stage when the flow was dropping while the water level of the lake area was slowly rising. The complex effects of water level and flow on the Time1 reflected the unique regulation and storage effect of WDL, which might cause the water level of the lake to have a certain hysteresis effect in response to the inflow change. The results of the SEM in SDL explained that the water level and flow had a directly negative impact on NDVI3 and indirectly had a negative impact on NDVI.avg. Water level, flow, and NDVI3 accounted for 78% of the variation in the NDVI.avg. The results of the SEM in EDL suggested that water level and temperature had a positive and direct influence on NDVI.max. The explanation ratio of water level and temperature to the NDVI.max was 24%.

In general, among the four explanatory variables, water level and flow accounted for the most important proportion that affected the time of water recession and food availability, but the manifestation on each lake area was different. The results of the study agreed with previous research on habitat variables of DTL (Zhang et al., 2016). Some studies have shown that hydrological alteration index degree in different lake areas might cause varying degrees of impact in each lake area. The operation of the dam directly affected the hydrological conditions,

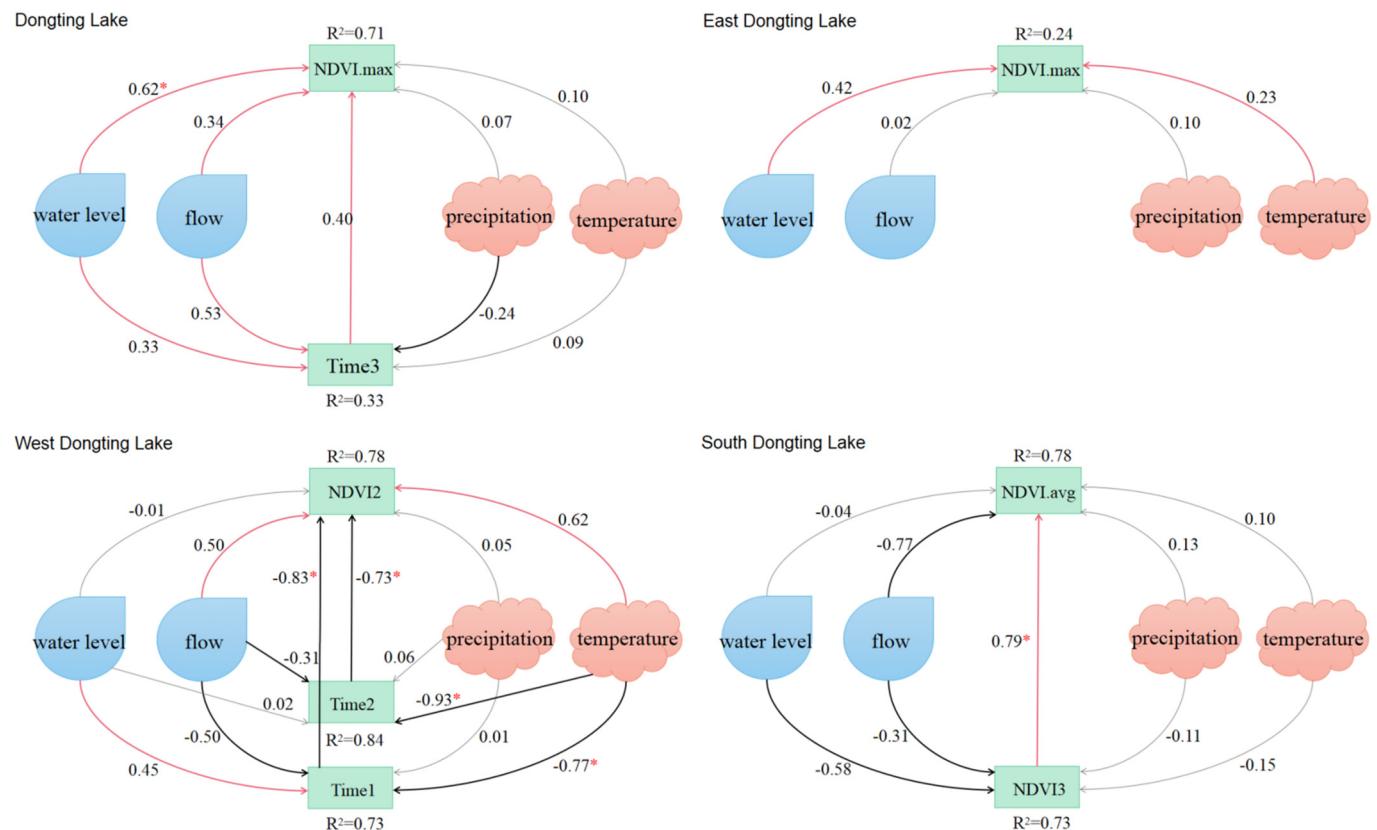


Fig. 5. Structural equation model is used to describe the direct and indirect effects of hydrological and climatic factors on the timing of water recession and food availability of the Anatidae. The strength of the causality is indicated by the size of the link. Black lines indicate negative impacts while red lines indicate positive effects. Grey lines indicate slight influence. * $p < 0.05$. The R^2 of the arrow is the explanatory ratio of the explanatory variable to the change of these endogenous variables. The entire path coefficient is the product of each direct path coefficient in the path. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

which may alter the topography of river channels and aquatic ecosystems (Cheng et al., 2018). DTL had evolved into a group of waterways connecting the EDL, the SDL, and the WDL. The distribution of water level had obvious spatial heterogeneity (Dai et al., 2020). There might be a kind of hydraulic interaction between the mainstream and the lake area (Zhang et al., 2020a). The reduction of the mainstream led to the drying of the inlet, which caused the reduction of river (Zhang et al., 2020c). It was estimated that water storage could reduce lake productivity by about 40% (Cheng et al., 2018). In WDL, hydrological variation directly affected Time1 and Time2, which explained 78% of the variation in NDVI2. Due to the drastic reduction of the mainstream inflow and the weak hydraulic relationship between the east and the west in the western lake area, the flow velocity had dropped (Zhang et al., 2019a). In SDL, the flow rate was slow and the vegetation was exposed late because of the intensified sedimentation. At the same time, Anatidae had begun to migrate and forage, which had a greater impact on the NDVI3. As a result, the NDVI.avg. of the entire dry season was affected. Finally, the mainstream flowed out from Chenglingji, EDL. When low water level occurred in the whole lake area, the upstream reservoir storage was considered to be a key driver, as it significantly altered the natural hydrological conditions between the downstream river and the lakes connected to the river (Bino et al., 2020). Higher NDVI values usually indeed indicate lower water levels (Wu et al., 2014). In that case, the NDVI.max became the main indicator affecting the diversity and population dynamics of Anatidae in EDL (Fig. S1).

Hydrological changes caused by the TGP posed a threat to the habitat and food quality of wetland on Anatidae (Guan et al., 2016b). The water exchange between the Yangtze River and DTL was mainly caused by the outflow of the TGP and the hydraulic gradient between the inlet and outlet of DTL (Zhang et al., 2018a). As the time of water recession in each lake area was different, the hydrological parameters created different ecological responses in each lake area, showing a progressive effect from west to east. It also reflected the impact of hydraulic gradient. There were inconsistent water vapor temperature and wind speed in the EDL, SDL, and WDL, making the exchange of water vapor energy flux different, so the temperature had different effects in each lake area (Ma et al., 2019). The temperature of the lake area was self-adjusted and allocated, so it was not prominent in the influencing variables of the whole lake. Changes in precipitation led to obvious changes in runoff, and the amount of water flowing into the lake that affected the exchange of water between lakes and rivers (Guo et al., 2020). The results of the SEM in DTL and each lake area also reflected the joint effects among regions. In view of the comprehensive effect of explanatory variables on the timing of water recession and the availability of food resources in each lake area, water level and flow were the dominant drivers of Time3 and NDVI.max in the entire lake area. Similar results were obtained from Zhang et al., 2016.

The quality and quantity of food might directly determine the physical condition of Anatidae, while the abundance and accessibility of food resources were highly vulnerable to fluctuations in water level and flow. High water levels put tubers beyond the waterbirds reach, and substrates were desiccated by too rapid water level recession, thus making food inaccessible. Under normal circumstances, the growth of meadows in DTL was synchronized with the arrival of overwintering birds (Gao et al., 2020). Meadows provided important wintering sites for Anatidae (Guan et al., 2014). The early water recession caused the NDVI to increase, and vegetation were high and withered, hindering the growth of new shoots. Hence, the food quality of the rich meadows declined after Anatidae arrived in the DTL. The food stress caused by the serious premature decline of the water could lead the Anatidae to be forced to choose other food strategies. Low feeding efficiency might further affect their spring migration and future reproduction (Zhang et al., 2020b). The richness and distribution of the Anatidae in winter habitats were driven by changes in water level and flow, and these drivers should be kept at a suitable level (Zhang et al., 2016). Stable hydrological conditions helped to stabilize the regional distribution of wetland vegetation

and improve productivity (Gao et al., 2020), becoming a high-quality foraging ground or habitat shelter for waterbirds.

3.4. Implications for conservation and future studies

In terms of the period of water recession and the time of vegetation exposure in each sub-lake area, we can better manage the growth of meadows by controlling the moisture in the meadows, which improves the feeding and digestibility of vegetation by Anatidae, increases the food supply, and makes up for the quantity and quality of food sources. Our results indicated that Lesser White-fronted goose had inverse correlations to habitat variables compared with other species of Anatidae, so all aspects of the water regime must be considered to protect Anatidae. For example, some artificial wetland management plans can be implemented. Managers need to increase the availability of rice grains in man-made habitats after the harvest such as marshes or rice fields (Gaget et al., 2020). Taking active measures on a large scale, like spreading and increasing the availability of foraging habitats, can avoid fierce inter-species competition with other waterbirds. It is also conducive to protection and survival of Anatidae. The protection of the ecological function of wetlands and rice fields should be taken into account, and relevant ecological restoration projects should be implemented. Zhang et al. (2020b) showed that there was a significant correlation between human disturbance and the abundance of waterbirds in the wetlands of the Yangtze River. Managers should strengthen regulatory measures to minimize the interference of harmful human factors on reserves, especially in winter when quality food resources are scarce. In view of the different responses of each lake region to environmental variables, adjustments can be made according to the characteristics of each lake area when adopting water resources management methods. It is suggested that hydrological regulation and intervention measures are used to restore the alternating pattern of dry and wet, optimize the time of receding water, and promote biodiversity (Liang et al., 2017). To promote the ecological restoration and the environmental improvement of the river and lake system, we should pay enough attention to the hydraulic gradient changes affecting the interaction between rivers and DTL. Water compensation within an appropriate range of hydraulic gradient can effectively improve the suitability of the habitat in DTL.

Climatic variables (such as temperature and rainfall) also play an important role in regulating Anatidae diversity and population dynamics. Although the hydrological explanatory variables of the SEM are greater than the climatic explanatory variables in this study, climatic factors cannot be ignored. Based on the results of this study, combined with historical and current hydrological data, it is possible to predict the time when the water level declines and better adjust the water level and flow. The impacts of hydrological changes mean that more attention should be paid to the lake ecosystem. Under the influence of the TGP, we should focus on these highly related factors to alleviate the rapid changes caused by TGP. However, these results are only based on statistical analysis, and the economic and ecological foundations need to be investigated in future research.

4. Conclusions

This study constructed an evaluation framework, which combined the timing of water recession, the availability of food resources and hydrology-climate variables to assess and explain the ecological status of different lake regions. Through the establishment of SEM, we quantified the relative contribution of hydrology-climate variables to water recession and food availability, and provided a way of revealing the driving mechanism of Anatidae diversity and population dynamics. The findings displayed that abnormal timing of water recession (too early or too late) could affect the diversity of Anatidae, and notably the abundance and distribution of the Lesser White-fronted goose. The diversity and population dynamics of Anatidae in DTL were significantly

correlated with NDVI.max ($r = 0.53, p < 0.01$) and the Time3 ($r = -0.43, p < 0.1$), respectively. In DTL, 71% of the variation in NDVI.max was explained by water level, flow, and Time3. However, lake regions were affected by hydraulic gradients, so the performance of each lake was different. The driving factors were multiple and complex. We recommend that adjustments should be made when adopting water resources management methods according to the different responses of each lake area to environmental variables. There might be an implicit hydraulic interaction between the main river channel and the lakes, which affect habitat changes synergistically. In order to promote the environmental improvement of dependent wetland ecosystems, more attention should be paid to hydraulic gradient changes affecting the interaction between rivers and DTL.

CRediT authorship contribution statement

Jie Liang: Writing – review & editing, Conceptualization, Methodology. **Qianfang Meng:** Writing – original draft, Software, Data curation. **Xin Li:** Writing – review & editing. **Yujie Yuan:** Data curation. **Yuhui Peng:** Data curation. **Xiaodong Li:** Data curation. **Shuai Li:** Data curation. **Ziqian Zhu:** Data curation. **Ming Yan:** Data curation.

Declaration of competing interest

There is no actual or potential conflict of interest including any financial, personal or other relationships with other people or organizations within five years of beginning the submitted work that could inappropriately influence, or be perceived to influence, their work.

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Appendix A. Supplementary data

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