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RESEARCH

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Effect of complex hydraulic variables and physicochemical factors on freshwater mussel density in the largest floodplain lake, China

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Abstract

Background Habitat degradation and flow regime alterations are two of the most prominent and common impact factors to freshwater mussel populations. Knowledge of the correlation between freshwater mussel distribution, density and habitat characteristics is important for maintaining and restoring their biodiversity and ecological functions. Information on predicting habitat suitability of freshwater mussels is lacking in China. Here, we aimed to analyze the correlation between freshwater mussel density and complex hydraulic and physicochemical variables to predict habitat suitability.

Results The results showed that four complex hydraulic variables (boundary Reynolds number, critical shear stress, bed roughness and mean sediment particle size) and four physicochemical variables (water temperature, chlorophyll-a, transparency and pH) were key factors for predicting habitat suitability of freshwater mussels. Freshwater mussel density was significantly correlated with Froude number, water temperature and chlorophyll-a.

Conclusions Our results confirmed that higher freshwater mussel density would be associated with areas that are stable in complex hydraulic and physicochemical variables. These results provide an important insight into the conservation of freshwater mussel diversity and their habitat restoration in China and globally.

Keywords Habitat suitability, Freshwater mussel, Complex hydraulic variable, Habitat degradation

Introduction

Freshwater mussels are among the most imperiled animal fauna globally (Bogan 2008; Lopes-Lima et al. 2017; Liu et al. 2022). Freshwater mussel population declines have been attributed to multiple anthropogenic pressures, including climate change, invasive species, and habitat degradation (e.g., water pollution, overexploitation, flow regime alterations, expansion of agricultural and urban landscapes) (Vörösmarty et al. 2010; Lopes-Lima et al. 2017; Böhm et al. 2021; Liu et al. 2022). Habitat degradation and flow regime alterations are two of the most prominent and common factors influencing freshwater mussel populations (Haag 2012). Freshwater mussels provide important ecosystem services including filtration, excretion of nutrients, and biodeposition (Geist 2010; Lummer et al. 2016; Vaughn 2018; Zieritz et al. 2019). Therefore, declines in their population will have negative

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impacts on the ecological function in freshwater ecosystems (Ilarri et al. 2018).

Freshwater mussels are benthic animals, and interact strongly with the water–sediment interface (Lummer et al. 2016; Vaughn 2018). As they live partly or wholly in the sediments of rivers and lakes, the substrate type has an impact on their assemblage structure (Strayer 2008). Some species can tolerate a wide range of sediments, while others can only occur in certain substrate types (Allen and Vaughn 2010; Colle and Callil 2012). Because they are sedentary, the dissolved oxygen-deprived habitat is particularly challenging for freshwater mussels. Dissolved oxygen for respiration may be the main habitat conditions for maintaining their populations, and habitats with low dissolved oxygen availability affect freshwater mussel survival (Strayer 2008). Flow is also an important driving factor of habitat heterogeneity and species distribution (Strayer 2008; Silva and Yalin 2017). At low flow, aquatic organisms can be exposed to lower dissolved oxygen concentrations, higher water temperatures, and dry environments, while increased flow and hydraulics can be equally harmful at high flow (Allen and Vaughn 2010; Stoeckl and Geist 2016). Distribution and density of freshwater mussels are also influenced by changes in flow conditions (Goodding et al. 2019; Stoeckl and Geist 2016). Therefore, knowledge of freshwater mussel habitat preferences is essential for their effective conservation and management (Ferreira-Rodrıguez et al. 2019).

Knowledge of the correlation between freshwater mussel distribution, density and habitat characteristics are important for maintaining and restoring their biodiversity and ecological functions (Haag and Williams 2014; Dobler et al. 2019; Smit and Kaeser 2016). Many studies have explored the response of freshwater mussel assemblage composition to human disturbances, such as flow alteration and habitat degradation (Cao et al. 2013; Daniel and Brown 2013; Johnson et al. 2014), which improved our knowledge of the effects of environmental change on freshwater mussel assemblage. Early studies have explored the correlation between freshwater mussel distribution, density and simple hydraulic variables (e.g., depth, current velocity, substrate type) to predict habitat suitability (Holland Bartels 1990; Strayer and Ralley 1993; Box et al. 2002). However, simple hydraulic variables did not reflect the effect of flow on the ecosystem for predicting habitat suitability (Allen and Vaughn 2010; Lopez and Vaughn 2021). Recently, some studies have provided evidence that freshwater mussel distribution and density was related to complex hydraulic variables (e.g., Froude and Reynolds numbers, shear stress and shear velocity) (Steuer et al. 2008; Allen and Vaughn 2010; Cao et al. 2015; Simeone et al. 2021). For example, low shear stress provides hydraulic refuges for freshwater mussels, while high shear stress may limit habitat suitability for them (Gangloff and Feminella 2007; Steuer et al. 2008; Stoeckl and Geist 2016). Complex hydraulic variables were related to flow conditions, which were more robust for predicting habitat suitability (Strayer 1999; Steuer et al. 2008; Simeone et al. 2021; Lopez and Vaughn 2021). Complex hydraulic variables have been used to predict habitat suitability in North America and Europe (Allen and Vaughn 2010; Steuer et al. 2008; Lopez and Vaughn 2021).

Information on predicting habitat suitability of freshwater mussels is lacking in China, and the correlation between freshwater mussel density and physicochemical factors have sometimes been reported (Sun et al. 2019). Furthermore, there are no studies from China that combine complex hydraulic variables and physicochemical variables to analyze the effect of these changes on mussel density. This is of great concern because the habitats of Chinese basins have been modified by multiple anthropogenic pressures, including climate change, habitat loss and degradation, water pollution, flow regime alterations, expansion of agricultural and urban landscapes (Liu et al. 2020; Böhm et al. 2021; Liu et al. 2022). Many freshwater mussel populations have been extirpated or greatly reduced because of these negative impacts on habitats (Shu et al. 2009; Liu et al. 2020, 2022). In addition, information on the correlation between freshwater mussel distribution, density and habitat characteristic has been developed on streams or rivers (Allen and Vaughn 2010; Steuer et al. 2008; Simeone et al. 2021; Lopez and Vaughn 2021), whereas floodplain lakes have received much less attention. Floodplain lakes are environmental and fluvial systems with variable properties that create complex habitat, which contain unique biota, including rare and highly specialized species with high conservation value, and provide important ecosystem services (Ward et al. 1999; Amoros and Bornette 2002; Schindler et al. 2014). Hydraulic and physicochemical conditions available to biota in floodplain lakes may be more diverse than smaller systems. For example, change of water level and water flow in floodplain lakes was more diverse than smaller systems (Li et al. 2019). Some freshwater mussels may track water levels closely, moving shoreward during high water elevation and retreating to deeper water as water levels recede (Allen and Vaughn 2010; Gough et al. 2012). This movement behavior may reduce mortality because it can allow mussels to avoid emersion during times of receding water levels (Allen and Vaughn 2010). Therefore, floodplain lakes are good community systems to study the correlation between community composition and environmental variables. Historically, they are more likely hydraulically and physiochemically stable than smaller systems, but these conditions have been altered in China by multiple anthropogenic pressures (Liu et al. 2022). Poyang Lake is the largest floodplain lakes with ~ 50% of the endemic freshwater mussel species in China (Wu et al. 2000; Shu et al. 2009; Xiong et al. 2012; Liu et al. 2020). Poyang Lake is also a dynamic wetland system, covering an expansive area in the rainy season and a low water level in the dry season, and has diverse hydraulic and physicochemical conditions (Li et al. 2019). Here, we aimed to analyze the correlation between freshwater mussel density and complex hydraulic and physicochemical variables to predict habitat suitability. We hypothesized that the freshwater mussel density would exhibit significant spatial differences, where they were correlated with Froude number, water temperature and chlorophyll-a, and higher freshwater mussel density would be associated with complex hydraulic and physicochemical variables. This study provides an important reference for the conservation of freshwater mussel diversity and restoration of freshwater ecosystem in China and globally.

Methods

Study area

Poyang Lake (28° 22′–29° 45′ N, 115° 47′–116° 45′ E), the largest floodplain lake in China, is located in the middle reach of the Yangtze River and northern Jiangxi Province with a total area of 162,200 km^2 and an average annual precipitation of 1350–2150 mm (Li et al. 2019; Fig. 1). Poyang Lake is interconnected river–lake–wetland system, fed by five rivers, including Gan River, Fu River, Xiu River, Xin River and Rao River. The fluctuations of water level in Poyang Lake exhibit significant seasonal change, which have the lowest surface area during dry season (146 km^2) and the highest surface area during wet season (2993 km^2; Wu et al. 2019; Li et al. 2019).

Sampling areas were selected in the Poyang Lake based on considering different geomorphic units, environmental conditions (complex hydraulic and physicochemical variables), spatial distribution and sampling processes (for details, see Tables 1, 2; Li et al. 2019; Simeone et al. 2021; Wang et al. 2021). A total of 17 sampling sites were established across four different sampling areas with unique habitat characteristics. There was a significant difference in complex hydraulic and physicochemical variables among different habitats (ANOVA, $p < 0.05$). Sampling areas were established as follows: (a) M1 included the lake outflow into the Yangtze River (3 sampling sites); (b) M2 included the connected river channel of Poyang Lake (3 sampling sites); (c) M3 included the main lake area of Poyang Lake (7 sampling sites); (d) M4 included the mouths of the rivers meeting Poyang Lake (4 sampling sites) (Fig. 1).

Sampling methods

Freshwater mussel surveys were mainly conducted in April, July, and October 2019 and January 2020 (Additional file 1: Table S1). Four replicate surveys were conducted of each site. We used homemade mussel rakes (60 cm wide, 20 mm mesh, rake tooth spacing 15 mm) to collect freshwater mussel samples across the survey site. The homemade mussel rakes were thrown into the water and dragged 50 m with slow uniform speed by a boat. The sampling area (30 m^2) was obtained by multiplying the mussel rake mouth width (15 mm) by the dragging distance (50 m). Freshwater mussel samples were poured into a white porcelain container then sorted. Freshwater mussel specimens were then identified and counted. Taxonomic levels of freshwater mussel were mainly based on Liu et al. (1979), He and Zhuang (2013), Liu et al. (2022), MolluscaBase (https://molluscabase.org/index.php) and Graf and Cummings (2022).

Measurement of hydraulic variables and physicochemical factors

The data set of physicochemical factors were obtained from Lu et al. (2021). The hydraulic variables and physicochemical factors were measured on the same day mussel surveys took place in April, July, and October 2019 and January 2020 (Additional file 1: Table S1). We calculated a number of lake descriptors for each sampling areas, including: dissolved oxygen (DO; mg/L), hydrogen ions (pH), salinity (Sal; mg/L), turbidity (TURB; NTU), and water temperature (T; °C), chlorophyll-a (Chl-a; mg/L), water velocity (V; m/s), water depth (WD; m), Total nitrogen (TN; mg/L) and total phosphorus (TP; mg/L) (Table 3). The substrate samples were collected using a modified Petersen grab (area of 1/16 m^2), which were then bagged and shipped to the laboratory. The substrate samples in the laboratory were first oven-dried at 105 °C for 24 h (Gordon et al. 2004). The substrate samples were sieved using mesh sieves and laser diffraction particle size analyzer (LS13320; for details see Table 1). The complex hydraulic variables were calculated according to the value of complex hydraulic variables in Table 2 and formula in Table 3.

Data analysis

To predict habitat suitability of freshwater mussels, a Random Forest Model (RMRF) was used to assess the correlation between density and complex hydraulic and physicochemical variables in the randomForest package (Liaw and Wiener 2002) in GNU R 4.0.1 (R Core Team 2020). The repeated measures random forest (RMRF) was used to consider the possible independence and potential pseudo-duplication of randomly selected

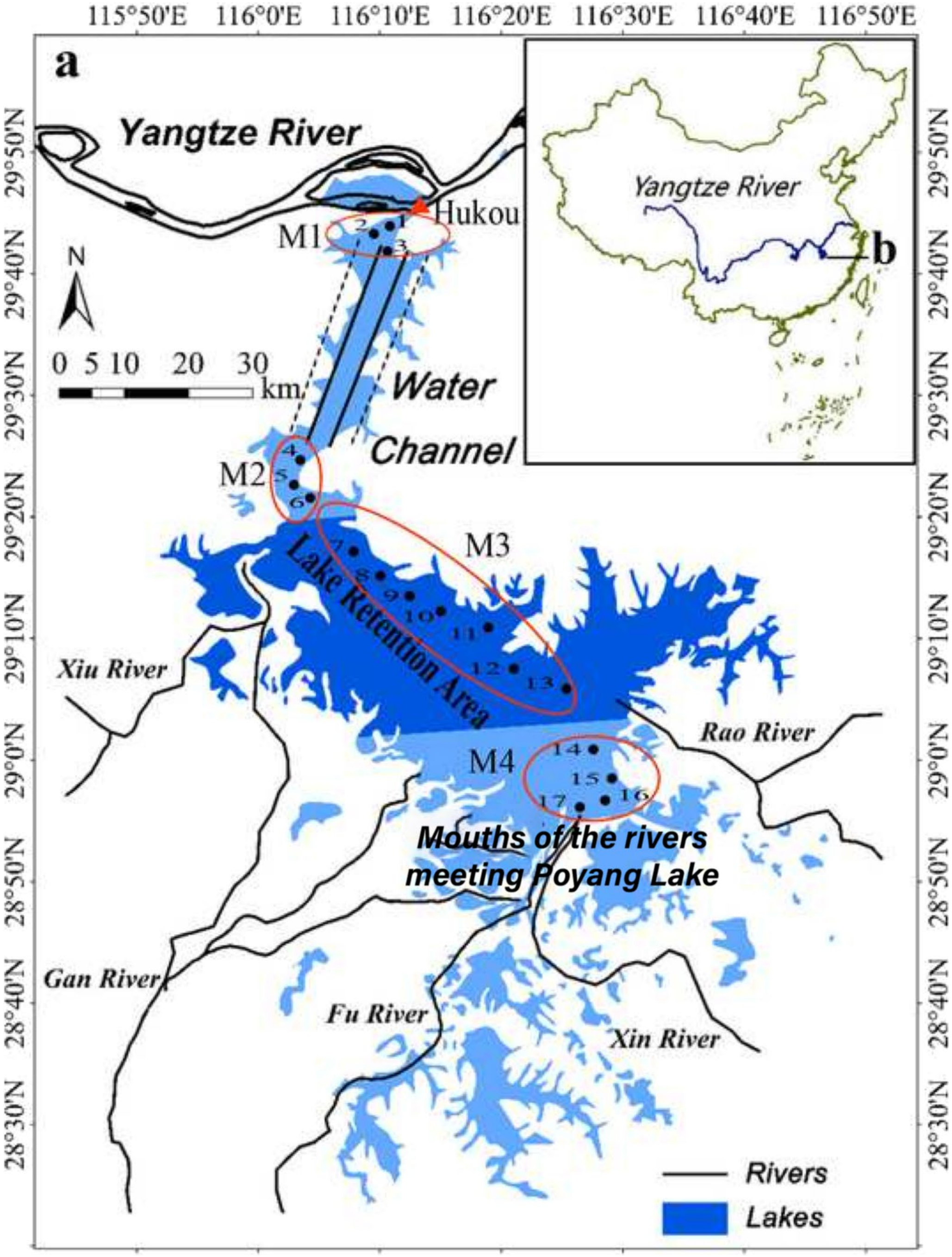


Fig. 1 Map showing the study area in Poyang Lake, China

replicates within each sampling areas (Calhoun et al. 2021). The raw data of freshwater mussel density was log transformed by log $(x+1)$ transformation (Simeone et al. 2021). We overtrained the model by guiding the selection of sub-samples from the entire data set by bootstrapping (Simeone et al. 2021). We then ran the training model step-by-step to increase the number of predictors used for group splitting (mtry functions; Liaw and Wiener 2002; Simeone et al. 2021). The following settings were tested: mtry = 1 to 8 for physicochemical variables and mtry = 1 to 9 for hydraulic variables. These models were ran five times using different random seeds (ntree function = 200, 400, 600, 800 and 1000) at each level of mtry. Observations not included in the bootstrap subsample

Table 1 Habitat stability, sediment composition, particle size and water flow velocity in four habitats, Poyang Lake

		Habitat stability	Sediment classification	Grain size range (mm)	Water flow velocity (m/s)
Poyang Lake outflow with Yangtze River	M1	Unstable	Clay to fine gravel	< 0.005, 0.005–10	0.36 ± 0.07
Connected river channel of Poyang Lake	M2	Stable	Clay to giant sand	< 0.005, 0.005–2	0.25 ± 0.03
Main lake area of Poyang Lake	M3	Stable	Clay to fine gravel	< 0.005, 0.005–10	0.20 ± 0.02
Mouths of the rivers meeting Poyang Lake	M4	Stable	Clay to fine gravel	< 0.005, 0.005–10	0.20 ± 0.03

Table 2 Mean value and the one-way analysis of variance (ANOVA) of complex hydraulic variables and physicochemical factors in four habitats, Poyang Lake

Complex hydraulic variables

	D (mm)	S_o	k_s (mm)	Fr	Re	Re$_*$	*V* (m/s)	T (N/m^2)	τ_c (N/m^2)
M1	0.053 ± 0.010	5.67 ± 0.04	0.089 ± 0.019	0.056 ± 0.014	160,156 ± 38,172	0.039 ± 0.007	0.009 ± 0.002	0.117 ± 0.043	0.027 ± 0.006
M2	0.023 ± 0.001	5.30 ± 0.11	0.030 ± 0.002	0.036 ± 0.006	160,037 ± 20,397	0.010 ± 0.002	0.005 ± 0.001	0.050 ± 0.010	0.009 ± 0.001
M3	0.048 ± 0.008	4.70 ± 0.16	0.090 ± 0.007	0.047 ± 0.007	75,131 ± 14,103	0.029 ± 0.004	0.006 ± 0.001	0.044 ± 0.011	0.027 ± 0.002
M4	0.290 ± 0.015	2.50 ± 0.13	0.515 ± 0.034	0.090 ± 0.033	101,029 ± 20,228	0.192 ± 0.030	0.006 ± 0.001	0.051 ± 0.013	0.153 ± 0.010
F	119.797	79.303	141.683	1.793	4.107	30.936	2.074	2.663	140.841
p	**0.000*****	**0.000*****	**0.000*****	0.157	**0.010****	**0.000*****	0.112	**0.050***	**0.000*****

Physicochemical factors

	WD (m)	SD (cm)	*T* (℃)	DO (mg/L)	Chl-a (mg/L)	pH	TN (mg/L)	TP (mg/L)
M1	9.4 ± 1.4	48.4 ± 6.2	19.3 ± 1.9	98.6 ± 1.6	7.3 ± 2.1	7.2 ± 0.1	2.01 ± 0.05	0.146 ± 0.023
M2	9.3 ± 0.8	48.9 ± 4.6	19.1 ± 1.9	98.8 ± 1.6	9.2 ± 2.7	7.0 ± 0.1	2.05 ± 0.06	0.165 ± 0.012
M3	6.8 ± 0.7	46.2 ± 3.4	20.0 ± 1.3	96.2 ± 3.4	8.5 ± 1.7	6.7 ± 0.1	1.87 ± 0.06	0.135 ± 0.006
M4	5.8 ± 1.1	52.8 ± 5.8	21.0 ± 1.9	100.7 ± 5.9	10.9 ± 2.6	7.1 ± 0.1	2.18 ± 0.07	0.161 ± 0.013
F	2.787	0.164	1.034	4.744	0.095	10.246	10.013	1.097
p	**0.048***	0.920	0.384	**0.005****	0.962	**0.000*****	**0.000*****	0.357

Significant results are in bold ($^{*}p < 0.05$; $^{**}p < 0.01$, $^{***}p < 0.001$)

Table 3 Calculation of complex hydraulic variables for four habitats in Poyang Lake

Complex hydraulic variables	Formula	Description
Substrate variables		
D (mm)	Laser diffraction particle size analyzer	Mean particle size
Sorting index (S_o, unitless)	$\frac{\varphi 84-\varphi 16}{2}$	Substrate heterogeneity
Bed roughness (k_s, mm)	$2 \times D50$	Topographical variation of river bed
Hydraulic variables		
Froude number (Fr, unitless)	$\sqrt{\frac{U^2}{gd}}$	Ratio of inertial to gravitational forces
Reynolds number (Re, unitless)	$\frac{ud}{v}$	Turbulence of free flow
Boundary Reynolds number (Re$_*$, unitless)	$\frac{Uk_s}{v}$	Near-bed turbulence
Shear velocity (*V*, m/s)	$\sqrt{\frac{\tau}{\rho}}$	Friction velocity
Shear stress (τ, N/m^2)	$\rho\ (u_*{}^2)$	Force of friction on substrate
Critical shear stress (τ_c, N/m^2)	$\theta_c g D_{50}\ (\rho_s-\rho)$	Shear stress required to initiate substrate motion

D = the substrate size in the sample (mm), *d* = water depth (m), φ = phi unit size of the substrate size ($\varphi = -\log_2 D$ [mm]); φx = percentage of substrate with particle size *x* in the sample, *U* = average velocity (m/s), *g* = acceleration of gravity (9.8 m/s), *v* = dynamic viscosity of water (0.0000176 m/s), ρ = density of water (996 kg/m^3, average temperature 28 ℃), ρs = density of substrate (2730 kg/s), θc = masking parameter (0.035) (Gordon et al. 2004) were defined as out-of-bag (oob) samples and used to create oob estimates for generalized errors in the model (Breiman 2001; Simeone et al. 2021). The optimal number of mtry was selected from the forest with the least generalized error for the final model (Breiman 2001; Liaw and Wiener 2002). We evaluated the relationship between the predictor and the response variable using the increase in mean standard error (MSE, Breiman 2001; Liaw and Wiener 2002).

One-way analysis of variance (ANOVA) performed by the SPSS 22.0 was used to test for significant differences (*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$) between density, complex hydraulic and physicochemical variables among each sampling site. The post hoc tests was used to make further comparisons, Tukey's honestly significant difference test was used to compare group means, but in cases of persistent heteroscedasticity we used Welch tests. Nonmetric multidimensional scaling (NMDS) ordination plots and the Bray–Curtis index were used to assess the variation in the freshwater mussel density among sampling sites. Permutational multivariate analysis of variance (PERMANOVA) was used to determine the significance of differences in the density of freshwater mussels among sampling sites. Heat map analysis was used to analyze the significance of the correlations between the freshwater mussel species density and complex hydraulic and physicochemical variables and *t* tests were used to analyze significant difference for these correlations. Redundancy analysis (RDA) was used to analyze the correlations between the freshwater mussel species density and complex hydraulic and physicochemical variables. The NMDS ordination plots, Bray–Curtis index, PERMANOVA and heat map analysis were performed in R 4.0.1 (R Core Team 2020) using the VEGAN (Oksanen et al. 2015). CANOCO Version 4.5 (ter Braak and Verdonschot 1995) were used to perform RDA.

Results

Freshwater mussel density in different habitats

There was a significant difference in freshwater mussel density among different sampling areas that contained unique habitat characteristics (ANOVA, $F_{df1,df2} = 3.481$, $p = 0.016$). The freshwater mussel density in M3 was the highest, followed by M2, the density in M4 was the lowest (Fig. 2a). The species with the highest density in M1 and M2 was *Lanceolaria lanceolata* (Fig. 2b). The species with the highest density in M3 and M4 was *Nodularia douglasiae* and *Lamprotula caveata*, respectively (Fig. 2b). The NMDS plot showed that there were two different groups of sites, and the structure of freshwater mussel community exhibited significantly spatial change based on the result of PERMANOVA test ($F = 2.098$, $p = 0.014 < 0.05$; Fig. 3).

Habitat suitability for freshwater mussels in Poyang Lake based on hydraulic and physicochemical variables

The final RMRF hydraulic and physicochemical model to predict suitable habitats explained 84% and 90% of the total variance for freshwater mussels, and the oob generalized error was 0.21 and 0.19, respectively (Table 4), which indicated predictive ability for these models. The first four predictors ranked were both the key predictors for hydraulic and physicochemical model of freshwater mussels (Table 4). There was a significant difference in *D*, sorting index, bed roughness, Reynolds number, boundary Reynolds number, shear stress, critical shear stress, water depth, dissolved oxygen, hydrogen ions, water temperature and total nitrogen among different habitats (Table 2). The boundary Reynolds number (Re*), bed roughness (k_s), water temperature, pH and transparency in different habitats ranged from 0.01 to 0.09, 0.1 to 0.5, 9 to 28, 5.2 to 8.0 and 20 to 100, respectively, and freshwater mussel density generally decreased for all of these variables (Fig. 4). The critical shear stress range (τ_c) ranged from 0.015 to 0.080, showing a bimodal trend, with the highest mussel density in 0.015–0.025 and 0.006–0.008 (Fig. 4). The mean sediment particle size (*D*) ranged from 0.025 to 0.25, showing a unimodal trend, with the highest density in 0.025–0.1 (Fig. 4). The chlorophyll-a ranged from 2.5 to 30.0, and freshwater mussel density generally increased for all of these variables (Fig. 4). Freshwater mussel species were absent in the habitats measured outside of these habitat measurement ranges.

The correlation between the density of each freshwater mussel species and complex hydraulic and physiochemical variables

For complex hydraulic variables, the freshwater mussel density was significantly correlated with Froude number based on heat map analysis (*t* tests, $p < 0.05$; Fig. 5a). In addition, *Sinosolenaia oleivora* was significantly negatively correlated with Reynolds number. *Lepidodesma languilati* and *Lanceolaria lanceolata* were both significantly positively correlated with substrate index (Fig. 5a). *Sinohyriopsis cumingii* was significantly negatively correlated with boundary Reynolds number and Froude number (Fig. 5a). For physicochemical variables, the freshwater mussel density was significantly positively correlated with chlorophyll-a and negatively correlated with water temperature and based on heat map analysis (Fig. 5c). *Lamprotula leaii* was also significantly correlated with water depth and total nitrogen (Fig. 5c). *Anemina arcaeformis* and *Sinohyriopsis cumingii* were also significantly correlated with total nitrogen (Fig. 5c).

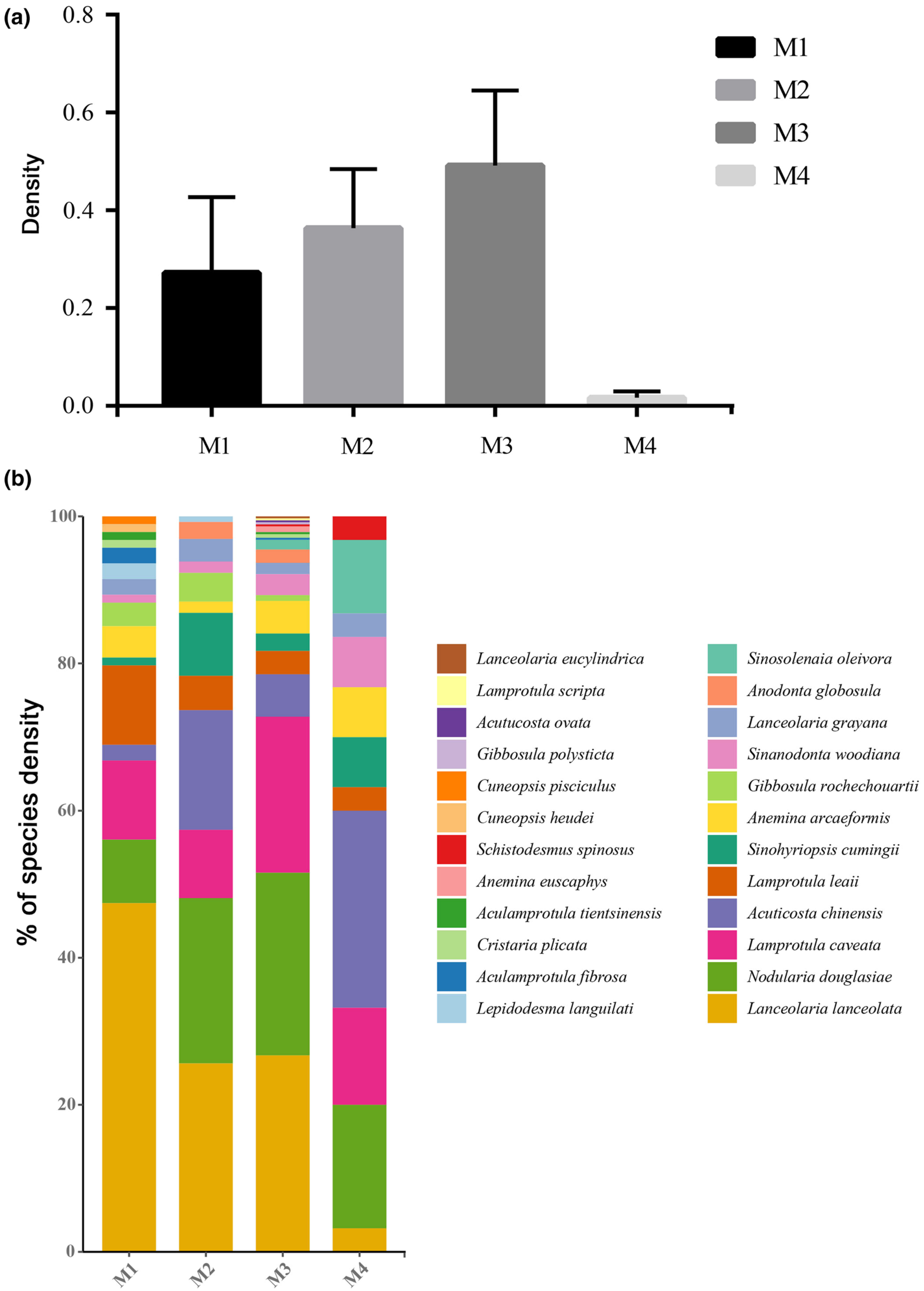


Fig. 2 Mean density of freshwater mussels (**a**) and species density (**b**) in different habitats, Poyang Lake

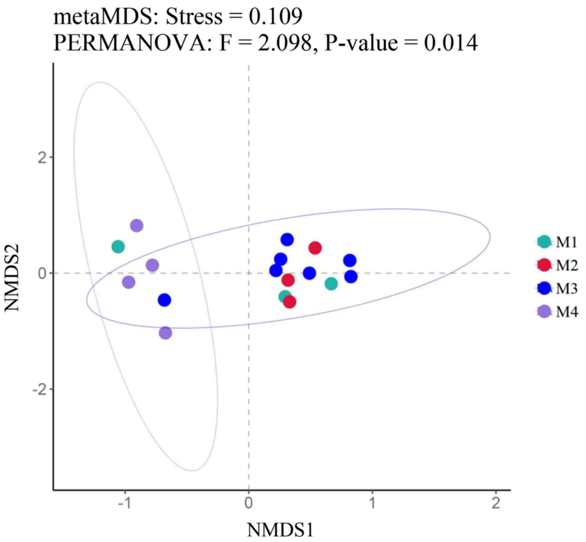


Fig. 3 Non-metric multidimensional scaling (NMDS) ordination for the community structure of freshwater mussels in Poyang Lake

Nodularia douglasiae and *Lanceolaria lanceolata* were also significantly correlated with water depth (Fig. 5c). *Sinosolenaia oleivora* was significantly correlated with transparency, total nitrogen and total phosphorus (Fig. 5c). The redundancy analysis (RDA) showed a similar pattern of correlation to the heat map analysis of complex hydraulic and physicochemical variables, with freshwater mussel density being significantly correlated with Froude number, sorting index, water temperature and chlorophyll-a (Fig. 5b, d).

Discussion

This study was one of the first to analyze the correlation between freshwater mussel density and complex hydraulic and physicochemical variables to predict habitat suitability in the floodplain lake, China. Our results clearly showed that freshwater mussel density would be associated with complex hydraulic and physicochemical variables.

Many previous studies estimated the relationship between hydraulic variables and freshwater mussel density, but the relationship between complex hydraulic variables and freshwater mussel density explained more community variability than did simple hydraulic variables (Steuer et al. 2008; Allen and Vaughn 2010; Simeone et al. 2021). Simple hydraulic variables, such as current velocity and substrate type, did not reflect the real impact on flow, so they produced weak predictions for the identification of these habitats (Hardison and Layzer 2001; Allen and Vaughn

Table 4 Random forest importance ranking of four habitat hydraulic variables and physicochemical factors on freshwater mussel density in Poyang Lake

Rank	Hydraulic predictors	% increase in MSE
1	Re_* (unitless)	8.5
2	τ_c (N/m^2)	6.5
3	k_s (mm)	6.0
4	D (mm)	6.0
5	Fr (unitless)	5.9
6	τ (N/m^2)	3.5
7	S_o (unitless)	3.3
8	V (m/s)	2.9
9	Re (unitless)	2.7
Rank	**Physicochemical factors**	**% increase in MSE**
1	T (℃)	8.2
2	Chl-a (mg/L)	5.4
3	SD (cm)	3.4
4	pH (unitless)	4.0
5	TN (mg/L)	1.6
6	DO (%)	1.6
7	TP (mg/L)	1.5
8	WD (m)	− 0.2

The ranking is based on the magnitude of MSE% value of freshwater mussel density

2010). Complex hydraulic conditions can be more important factors for the habitat suitability of freshwater mussels (Allen and Vaughn 2010), due to the fact they may change with flow conditions (Morales et al. 2006; Newton et al. 2008; Drew et al. 2018). Some studies have showed the upper limit of near-bed complex hydraulic conditions as an important predictor of mussel distribution (Steuer et al. 2008; Allen and Vaughn 2010; Simeone et al. 2021). Our results showed that four hydraulic variables (boundary Reynolds number, critical shear stress, bed roughness and mean sediment particle size) were key factors for predicting suitable habitats of freshwater mussels, which indicated habitats with low hydrodynamic energy were more suitable for many freshwater mussels. Freshwater mussel density was usually the highest in the low flow period, while those habitats with low hydrodynamic energy in the high flow period were more likely to provide shelter habitats for mussels (Simeone et al. 2021). The hydrodynamic conditions in this study area were different (Li et al. 2019). For example, M2 was located in the inside shoreline bend of the lake and maintained a lower hydrodynamic condition and substrate stability in the high flow period, which provided shelter habitat for the survival of freshwater mussels (Hegeman et al. 2014; Simeone et al. 2018; Quinlan et al. 2015). M3 was located in the lake area and had low hydrodynamic energy and substrate stability, which may increase the survival of many freshwater mussels.

Habitat stability was positively correlated with freshwater mussel density, confirming similar studies in rivers or streams (Zigler et al. 2008; Randklev et al. 2019; Steuer et al. 2008; Simeone et al. 2021). Habitats with stable substrates are more likely to provide shelter for many freshwater mussels (Wilson et al. 2011; Mansur and Pereira 2006), and our studies confirmed that this view is an important factor for the survival of freshwater mussels in Poyang Lake. The shear stress is strongly correlated with the habitat stability. Low shear stress may provide a hydraulic shelter for freshwater mussels, while high shear stress may limit the habitat suitability of them (Gangloff and Feminella 2007; Steuer et al. 2008; Stoeckl and Geist 2016). In addition, habitat stability was associated with Froude number and Reynolds number (Simeone et al. 2021), because Froude number and Reynolds number are good predictors of habitat stability and describe flow conditions (Gordon et al. 2004). Our results also confirmed that boundary Reynolds number and critical shear stress were key factors for predicting suitable habitats of freshwater mussels. At the same time, the freshwater mussel density was significantly correlated with Froude number in this study.

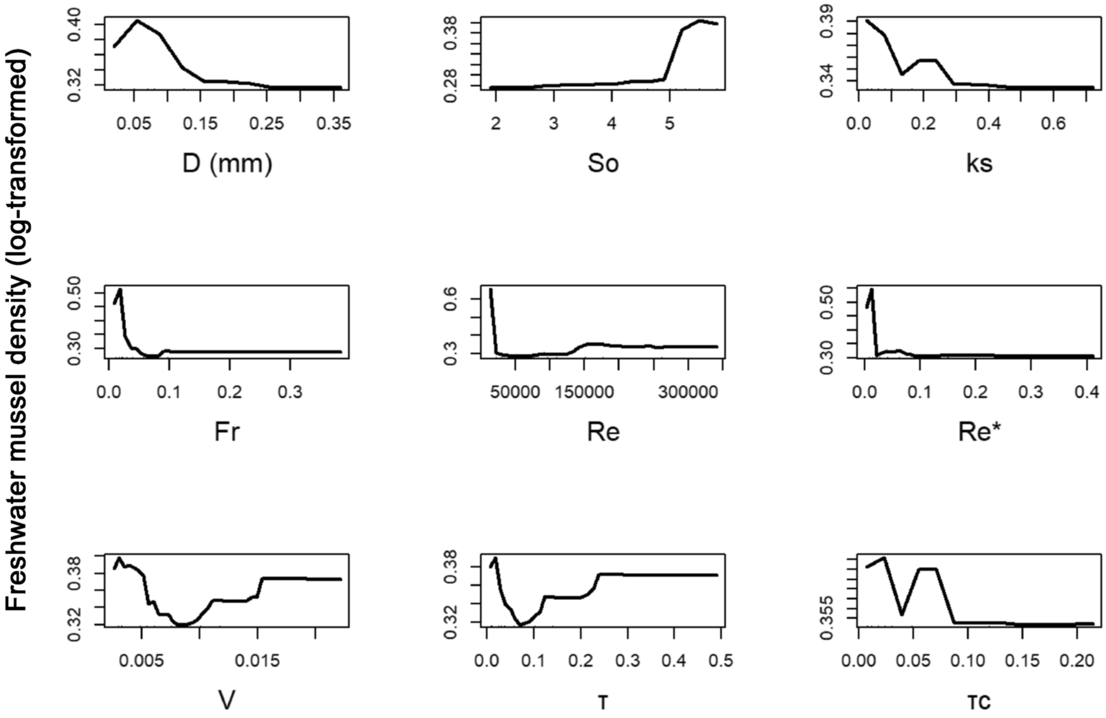
The spatial difference and the complexity of habitat characteristics affected the community structure of freshwater mussels (Haag 2012). Many studies showed that the complex habitat heterogeneity had higher diversity of freshwater mussels (Daniel and Brown 2014; Sun et al. 2019). This study showed that the community structure of freshwater mussels in Poyang Lake showed spatial differences. Freshwater mussels are sensitive to environmental change, and species with stronger adaptability to environmental change may become dominant (Bogan 2008; Vaughn 2018). Information on the correlation between freshwater mussels and habitat characteristics is considered as the key way to protect endangered freshwater mussels (Williams et al. 1993; Vaughn 2018; Lopez and Vaughn 2021), and we may apply that information to make decisions involving habitat management. The habitat characteristics of freshwater mussels are different (Vaughn 2018). For example, species within *Nodularia* and *Sinanodonta* have extensive habitats in lakes, rivers, reservoirs and ponds with mud substrates, while species within *Aculamprotula* and *Sinosolenaia* prefer habitats with rapid water flow, clear water and hard mud substrate (Liu et al. 2022). Some studies have also shown that habitat characteristics, such as physicochemical factors affected the survival of freshwater mussels, such as water depth, current velocity, pH, transparency, water temperature and chlorophyll-a (Strayer and Ralley 1993; Vaughn et al. 2004; Nakano et al. 2007; Zieritz et al. 2016; Simeone et al. 2018; Sun et al. 2019). For example, some studies showed that the survival and growth of freshwater mussels was significantly correlated with turbidity (Osterling et al. 2008; Sun et al. 2019). Water temperature is an important physical factor driving the change of freshwater mussel community structure, which affects growth and reproduction of mussels (Clarke 2010; Xiong et al. 2012; Su et al. 2014; Yang et al. 2011). In addition, some studies showed higher freshwater mussel density occurred in environments with lower pH (Simeone et al. 2018). Our results showed that four physicochemical variables (water temperature, chlorophyll-a, transparency and pH) were key factors for predicting suitable habitats of freshwater mussels. Freshwater mussel density was significantly correlated with water temperature and chlorophyll-a.

Habitat loss and fragmentation are usually considered one of the most important threats to freshwater mussels (Lopes-Lima et al. 2017; Böhm et al. 2021; Liu et al.

(See figure on next page.)

Fig. 4 Dependence plots based on Random Forest regression, showing the relationship of the hydraulic (**a**) and physicochemical (**b**) predictors, with freshwater mussel density, in Poyang Lake, China. Dissolved oxygen (DO; mg/L), hydrogen ions (pH), salinity (Sal; mg/L), turbidity (TURB; NTU), and water temperature (*T*; °C), chlorophyll-a (Chl-a; mg/L), water velocity (*V*; m/s), water depth (WD; m), Total nitrogen (TN; mg/L) and total phosphorus (TP; mg/L), *D* (mm), Sorting index (S_o, unitless), Bed roughness (k_s, mm), Froude number (Fr, unitless), Reynolds number (Re, unitless), Boundary Reynolds number (Re*, unitless), Shear velocity (*V*, m/s), Shear stress (τ, N/m^2). Critical shear stress (τ_c, N/m^2)

(a) Complex hydraulic variables



(b) Physicochemical factors

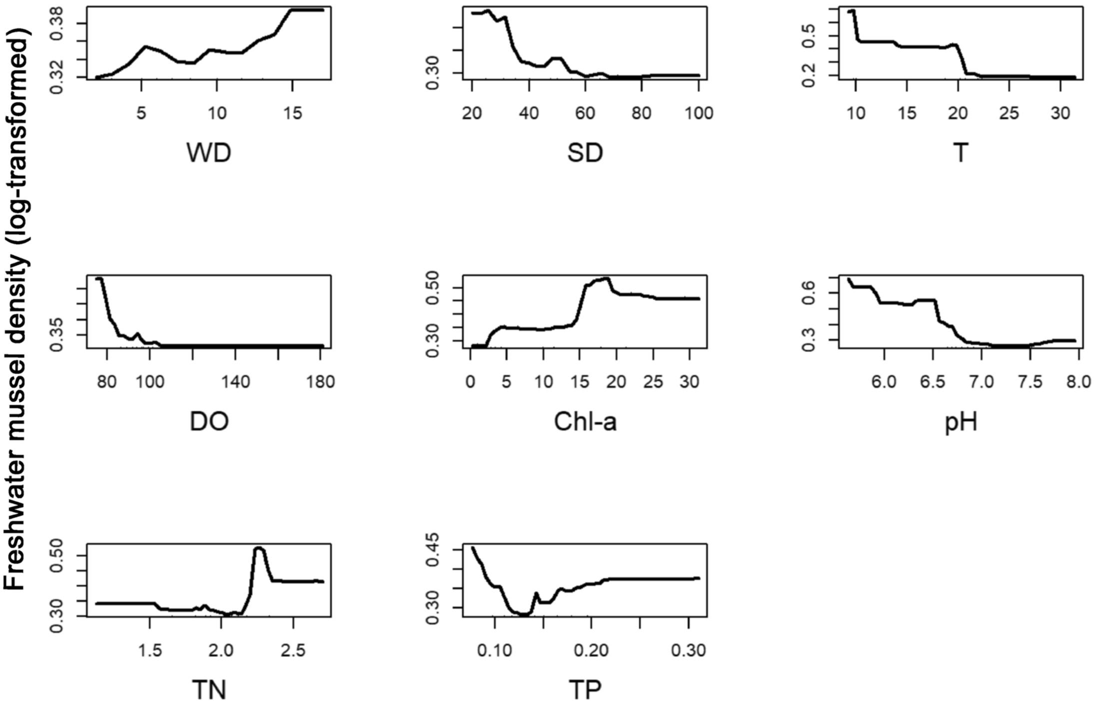


Fig. 4 (See legend on previous page.)

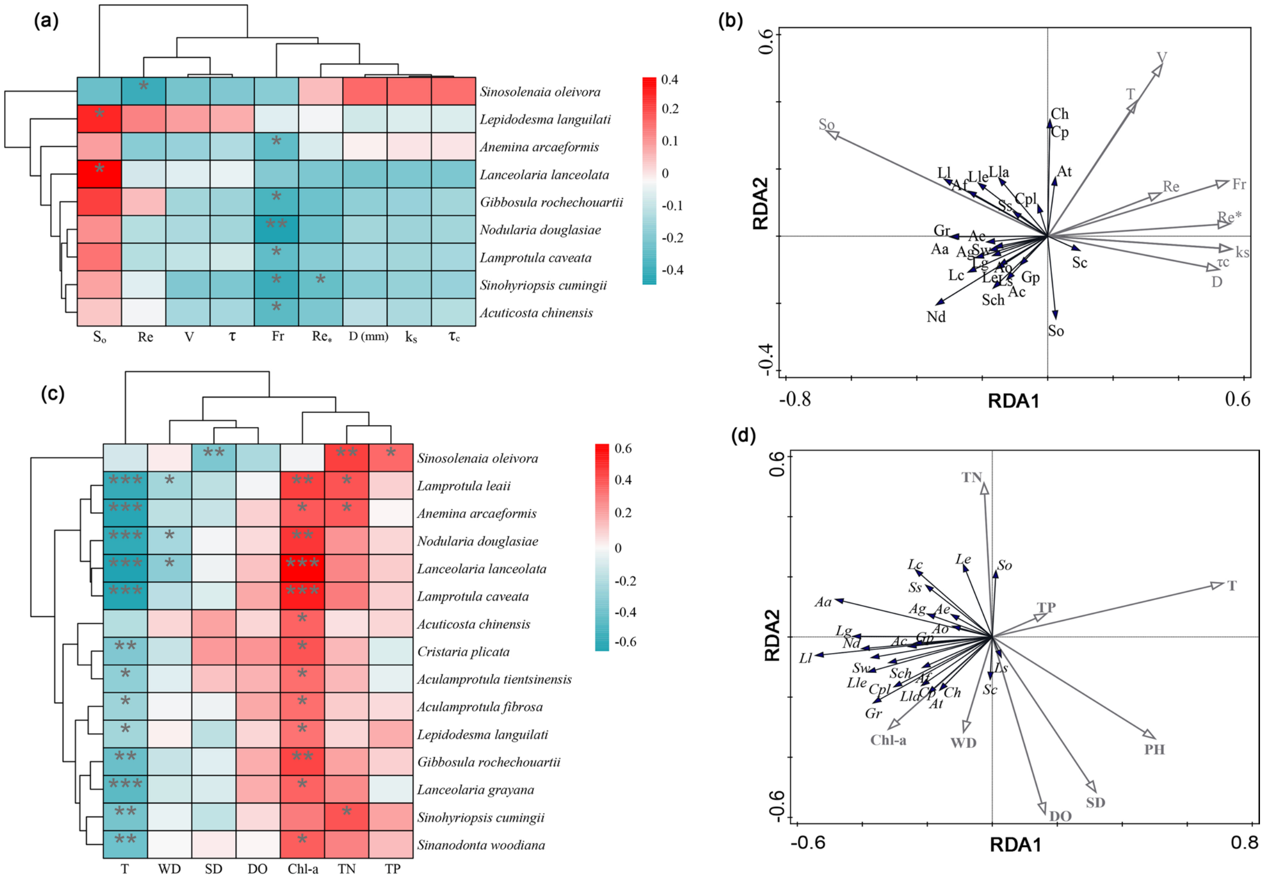


Fig. 5 Correlation between density of freshwater mussel species and hydraulic (**a**, **b**) and physicochemical variables (**c**, **d**) based on heat map analysis and redundancy analysis (RDA). The clustering dendrograms of heat maps including the distance metrics of density of freshwater mussel species, hydraulic and physicochemical variables used to produce it. Horizontal coordinates are hydraulic and physicochemical variables in heat map analysis, vertical coordinates are density of freshwater mussel species. Red shows positive correlation between density of freshwater mussel species and hydraulic and physicochemical variables. Blue shows negative correlation between density of freshwater mussel species and hydraulic and physicochemical variables. The color patch gradient is used to show the value of R^2. The clustering dendrograms on the left and top are the result of clustering of species density (left), hydraulic and physicochemical variables (top), respectively. Significant results are in * (*$p < 0.05$; **$p < 0.01$; *** $p < 0.001$). Dissolved oxygen (DO; mg/L), hydrogen ions (pH), salinity (Sal; mg/L), turbidity (TURB; NTU), and water temperature (*T*; °C), chlorophyll-a (Chl-a; mg/L), water velocity (*V*; m/s), water depth (WD; m), Total nitrogen (TN; mg/L) and total phosphorus (TP; mg/L), *D* (mm), Sorting index (S_o, unitless), Bed roughness (k_s, mm), Froude number (Fr, unitless), Reynolds number (Re, unitless), Boundary Reynolds number (Re*, unitless), Shear velocity (*V*, m/s), Shear stress (τ, N/m^2), Critical shear stress (τ_c, N/m^2). Code of freshwater mussel species see Additional file 2: Table S2

2022). When attempting to preserve declining freshwater mussel populations, habitat restoration and suitability is suggested as one of the most effective methods for increasing freshwater mussel diversity (Cope and Waller 2010). Direct physical habitat disturbance, such as dams and sand mining, resulting in alteration of flow regimes and habitat fragmentation of rivers or lakes, usually leads to mussel diversity and abundance decline (Mueller et al. 2011). Knowledge of the correlation between freshwater mussel distribution, density and hydraulic and physicochemical variables for predicting suitable habitats is important for maintaining and restoring their biodiversity and ecological functions (Haag and Williams 2014; Dobler et al. 2019; Smit and Kaeser 2016). Our results provide insights into habitat suitability of freshwater mussels for Poyang Lake correlated with four key hydraulic variables (boundary Reynolds number, critical shear stress, bed roughness and mean sediment particle size) and four key physicochemical variables (water temperature, chlorophyll-a, transparency and pH). These results showed that hydrodynamics habitat was important for maintaining freshwater mussel populations. Therefore, management plans should consider habitat diversity in terms of hydrodynamics types, which are important for freshwater mussels and other aquatic diversity. In addition, landscape design should give priority to the protection of shoreline buffer habitats to maintain the freshwater mussel populations and habitat quality.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13717-023-00427-y.

Additional file 1: Table S1. Surveys of freshwater mussel density and measurement of hydraulic variables and physicochemical factors in Poyang Lake.

Additional file 2: Table S2. Code of freshwater mussel species.

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Author contributions

JCC, LXJ, OYS and WXP conceived the study. All authors contributed to the study design and data collection. JCC and LXJ analyzed the data. JCC, LXJ, OYS and WXP led the writing of the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

All data will be available in the data center of Nanchang University (http://www.ncu.edu.cn/) after publication.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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