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Length–Weight Relationship and Spatiotemporal Distribution Pattern of Three Schizothoracinae Fishes Along the Nujiang River in the Qinghai–Tibetan Plateau, China

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Abstract: The Qinghai–Tibet Plateau (QTP) is a unique ecological area that has faced issues like diminishing ecosystem stability and increasing pressures on resources and the environment. These issues have arisen as a result of the combined impact of global warming and human activities in recent times. The study of the growth and distribution patterns of schizothoracinae fishes can support guiding policy decisions about the conservation of aquatic species and ecological habitats in the QTP. The investigation on fish resources was carried out in the QTP section of the Nujiang River during the spring and autumn seasons of 2017, 2018, and 2019. A total of seven sampling sites were established based on variations in elevation. According to length–weight relationship (LWR) analysis, *Schizothorax nukiangensis* mainly displayed a negative allometric growth while *Ptychobarbus kaznakovi* and *Schizopygopsis thermalis* mainly showed near isometric growth or positive allometric growth in the QTP section of the Nujiang River. Due to temperature and food abundance, the three schizothoracinae fishes showed better growth performance in autumn than spring. Spatial heterogeneity exhibited a greater influence on the LWR of *S. nukiangensis* and *P. kaznakovi* than seasonal variation. In contrast, seasonal variation on *S. thermalis* showed greater influence than spatial heterogeneity. According to the linear mixed effect model (LMM), both spatial factors and seasons had influence on fish growth in the QTP. *Schizothorax nukiangensis* was identified as the predominant species from CWL to BS, spanning an altitude range of 1800 to 2700 m. *Ptychobarbus kaznakovi* was identified as the main species at LL, BB, and BR, occupying an altitude range of 2700 to 3800 m. *Schizopygopsis thermalis* is primarily distributed at altitudes beyond 4000 m and along the tributary river Yuqu. Principal coordinates analysis (PCOA) and nonmetric multidimensional scaling (NMDS) divided schizothoracinae fish populations into three clusters by spatial differences. Redundancy analysis (RDA) and Monte Carlo Permutation analysis revealed that habitat elevation and water temperature had a significant impact on schizothoracinae fish distribution. This article enhances our understanding of the distribution and environmental adaptation of indigenous fish in the Qinghai–Tibet Plateau.

Keywords: *Schizothorax nukiangensis*; *Ptychobarbus kaznakovi*; *Schizopygopsis thermalis*; habitat environment; linear mixed effect model; redundancy analysis

Key Contribution: 1. Assessing the length–weight relationship in three schizothoracinae fishes with varying specialized grades in different sites and seasons along the Nujiang River in the Qinghai–Tibetan Plateau. 2. The schizothoracinae fish populations along the Nujiang River were mainly separated into three clusters based on spatial variations. 3. The populations of schizothoracinae fish are significantly influenced by their habitat elevation and the water temperature.

1. Introduction

The Nujiang River, often referred to as the Upper Salween, originates at the southern base of the Tanggula Mountains on the Qinghai–Tibet Plateau (QTP). It flows over the Qinghai–Tibet Autonomous Region and Yunnan Province in China. As an important region in terms of global biodiversity and protection for ecological landscape, the Nujiang River basin has various and changeable climate types and is ecologically essential to China for its role as the vital ecological corridor of both the southwest of the country and southeast Asia [1]. Both the upper and part of the middle reaches of the Nujiang River are included in the QTP. It is in the plateau climate zone and features cold, dryness, and scant rainfall. The water mostly comes from the melting snow of the high mountains and has fairly low temperatures [2]. The fish faunas of the Nujiang River in the QTP are primarily composed of species that are able to withstand the extreme cold conditions. These species notably include schizothoracinae fishes and triplophysa fishes.

Schizothoracinae fishes are within the family Cyprinidae, exclusively inhabiting the highlands of central Asia, particularly around the Qinghai–Tibet Plateau and adjacent regions. Schizothoracinae fishes have successfully adapted to the extreme conditions of the Qinghai–Tibet Plateau, making them valuable subjects for investigating fish adaption to high-altitude environment [3]. According to morphological characters such as scales, pharyngeal teeth, and barbels, the schizothoracine fishes can be divided into three specialized grades: primitive, specialized, and highly specialized grades [3,4]. Some studies have found that the distribution of schizothoracinae fishes distribution pattern was mainly caused by periodic uplift of the Qinghai–Tibet Plateau [5]. The schizothoracinae fish in the Qinghai–Tibet Plateau and adjacent regions represent the largest and most varied species group in the Nujiang, holding significant commercial and ecological importance [6].

The dominant indigenous species in this region were *Schizothorax nukiangensis*, *Ptychobarbus kaznakovi*, and *Schizopygopsis thermalis* according to our investigation. Moreover, *S. nukiangensis* is classified as a primitive grade species, *P. kaznakovi* is classified as a specialized grade species, and *S. thermalis* is classified as a highly specialized grade species. In addition, *S. nukiangensis* is only distributed in the Nujiang River, and *P. kaznakovi* is a vulnerable species listed in the China Red Data Book of Endangered Animals. The existing studies on fish in the Nujiang River are mostly on examining the morphology, identifying new species, and analyzing the genetic structure of various species [4,7–9]. There has been a limited amount of research conducted on the population structure of fish in the Nujiang River. Therefore, the research targeting the distribution pattern of three schizothoracinae fishes of different specialized grades in the Nujiang River is representative. The results can provide a decision-making reference for the protection of three schizothoracinae fishes in the Nujiang River and in the QTP.

The length–weight relationship (LWR) is crucial for effectively exploiting and managing fish species populations [10]. The collection of these data is essential for the estimation of growth rates, length, and other factors related to the dynamics of fish populations [11]. Moreover, the LWR in fishes holds significant importance in the assessment of fish stocks [12], as it receives variations in response to factors such as food, the fluctuation of environmental conditions over the seasons, the level of salinity, the temperature of the water, as well as geographical differences [13–15]. Estimations of the LWR enable fisheries scientists to determine fish condition, as well as compare the life history and morphological characteristics of populations in different regions [16,17]. This study aimed to investigate the growth performance and spatiotemporal distribution pattern of schizothoracinae fishes along the Nujiang River in the QTP and their temporal and spatial variations. Furthermore, the investigation of the impact of environmental factors on the distribution of schizothoracinae fishes in the QTP sections of the Nujiang River was conducted using cluster analysis and redundancy analysis (RDA). This study provides a scientific foundation for the conservation and sustainable utilization of fish resources in the Nujiang River.

2. Materials and Methods

2.1. Sampling Sites and Material Collection

The selection of sampling sites was based on multiple factors including the characteristics of the river habitat, the presence of tributary inflows, and the impact of human activity. Typical river transverse sections and sample regions were selected according to longitudinal distance gradients and elevation differences in the river. A total of seven sampling sites were established along the portion of the Nujiang River located in the Qinghai–Tibet Plateau (QTP). These sites were Chawalong Township (CWL), Basu County (BS), Luolong County (LL), Bianba County (BB), Biru County (BR), Naqu City (NQ), and Zuogong County (ZG). The ZG sampling site is situated in the central portion of the Yuqu River, which is a tributary to the Nujiang River, while the remaining six sampling sites are positioned along the main stream of the Nujiang River. The sampling points are shown in Figure 1 and Table 1. Schizothoracinae fishes were obtained using gill nets with consistent effort at each sampling site during the spring and autumn of 2017–2019, totaling six occasions. Specimens were caught with gill nets, using nylon with different mesh sizes, 2.3 cm (1 inch) and 10.0 cm (4 inches). At each sampling site, 1.5 m tall, 100 m long gill nets with 1-inch mesh and 1.5 m tall and 100 m long gill nets with 4-inch mesh were used for 48 h to ensure the equivalent effort to compare the number and biomass of schizothoracinae fishes. The CPUE was calculated according to the formula: CPUE = $N/(T \times S)$, in which N was fish biomass (g), T was the investigation time (hour), S was the area of all gill nets.

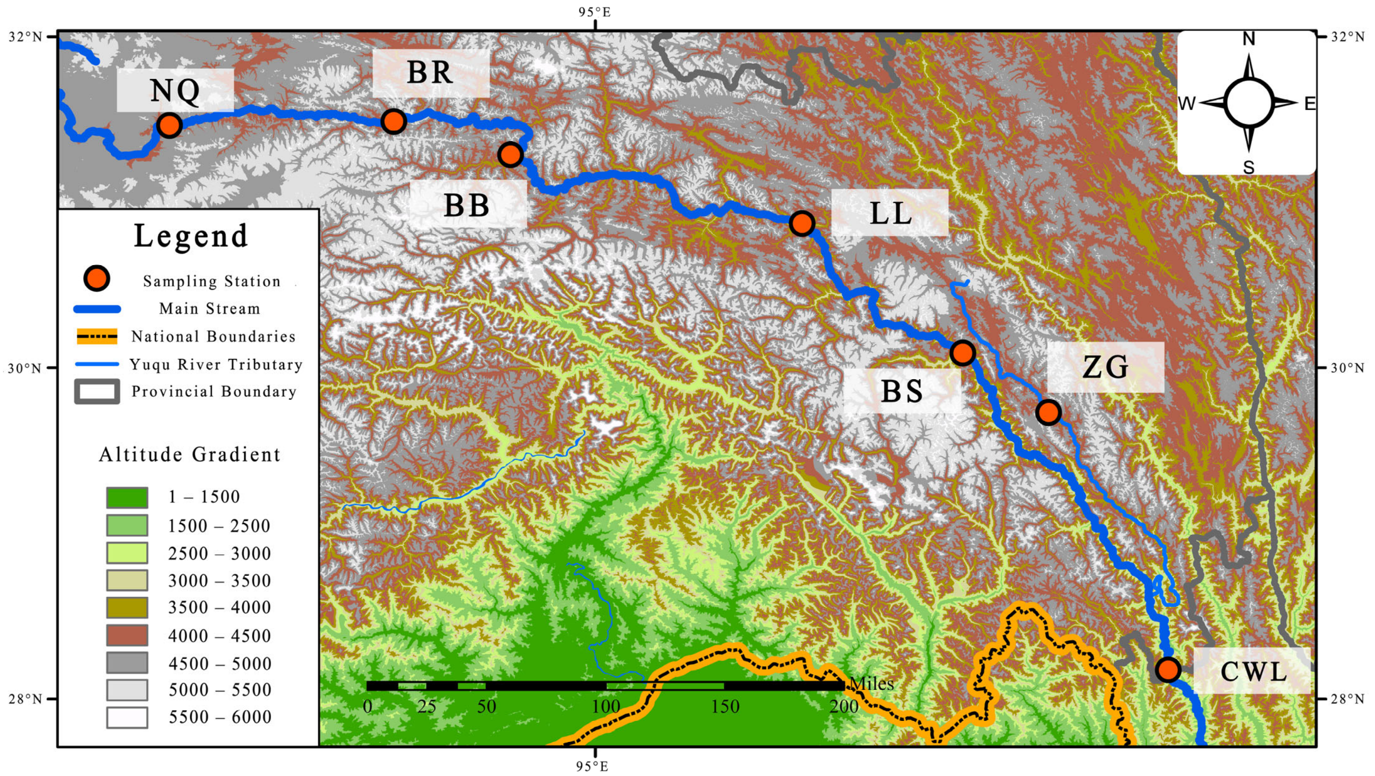

Figure 1. Nujiang River and distribution of sampling sites.

The schizothoracinae fish were collected, followed by identification and measurement of their standard length (mm) and body weight (g). Standard length and body weight were obtained by rulers, fish plates (accurate to 0.1 cm), and electronic scale (accurate to 0.1 g).

Table 1. List of name, location, elevation, and river morphology of sampling stations.

Abbreviation	Sampling Sites	Longitude and Latitude		Elevation (m)	River Morphology
		°N	°E		
CWL	Chawalong Township	28.44818	98.46026	1749	Broad valley
BS	Basu County	30.09977	97.23578	2664	Broad valley
LL	Luolong County	30.81108	96.32362	3100	Canyon in mountains
BB	Bianba County	31.28114	94.47794	3632	Canyon in mountains
BR	Biru County	31.4878	93.77231	3836	Canyon in mountains
NQ	Naqu City	31.45665	92.35575	4375	Shallow valleys in plateau
ZG	Zuogong County	29.73331	97.75565	3816	Canyon in mountains

2.2. Environmental Factors

During every investigation in 2017–2019 spring and autumn, temperature, pH, and dissolved oxygen levels were measured at each of the seven sampling sites using portable meters (YSI ProPlus, YSI Inc., Yellow Springs, OH, USA). The flow velocity was measured using a rotary cup velocimeter (LS45A, Chongqing Hydrological Apparatus Manufacture of the Hydraulic Ministry, China). Altitude and coordinates were assessed using GPS. Water samples were obtained using a 2 L water collector positioned at a depth of 0.5 m beneath the water surface of each sampling location. These samples were afterwards preserved and sent to the laboratory for analysis. Measuring total nitrogen, total phosphorus, nitrate, ammonium, phosphate and permanganate index (CODMn), and chemical oxygen demand (COD) were followed by standard procedures [18].

2.3. Data Analysis

2.3.1. LWR

The LWR ($W = a \times L^b$) was adopted to fit the standard length and body weight of the sampled fish, where W stands for the weight of individual samples (g), L represents fish standard length (mm), and "a" and "b" are the regression parameters. Parameter b represents the heterogeneity in the growth and development of fish, and its value is influenced by both the environment of the fish and the biological productivity of fish habitats. Data of allometric growth were obtained by comparing the relationship between the b value and 3 via a one-sample t test.

Moreover, in consideration of the random effects of different regions and different seasons, the linear mixed model (LMM) was adopted to explore the impacts of different regions and seasons on the LWR of the three schizothoracinae fishes. In a mixed effects model, parameters are classified as either fixed effects or random effects. Fixed effects capture the average growth characteristics of species, while random effects are employed to analyze the heterogeneity arising from various data sources [19]. To facilitate the application of the LMM for calculation, the equation underwent a logarithm transformation and was rewritten as $\mathrm{Log}_{10}(W) = \mathrm{Log}_{10}(a) + b\mathrm{Log}_{10}(L)$. The LMM incorporates the effects of sampling sites and seasons as random effects for parameters a and b, in order to elucidate the spatiotemporal variation in the relationship between body length and body weight. Then, the root mean square error (RMSE) was applied to determine the optimal model. A lower value of RMSE suggests a smaller discrepancy between the predicted value and the actual value, indicating a higher level of accuracy in the fitting process.

2.3.2. PCOA, NMDS, and ANOSIM Analysis

The recorded data on the number and biomass of the three schizothoracinae fishes collected at each sampling site were used to perform a principal coordinates analysis (PCOA) and nonmetric multidimensional scaling (NMDS) analysis to investigate the fish communities. Additionally, a clustering analysis, based on the Bray–Curtis similarity, was performed, and the resulting clustering patterns were displayed using a heatmap.

Furthermore, an analysis of similarities (ANOSIM) was employed to assess the significance of differences across groups. The aforementioned analysis and charting were conducted using the vegan and the ggplot2 packages in R.

2.3.3. RDA

Based on the findings of a detrended correspondence analysis (DCA) conducted on the species data, it was seen that the highest gradient of the ordination axis was 2.5, which falls below the threshold of 3. Consequently, an RDA was selected for subsequent study because RDAs can help in understanding the complicated relationships between presence and abundance of species in different areas and the environmental factors that affect them [12]. The spatial distribution of fish communities was investigated by conducting a redundancy analysis (RDA) to examine the influence of environmental factors. The aim was to identify the most significant environmental factors that had an effect on the distribution patterns of fish populations. The use of an RDA allows for the integration and examination of several environmental aspects simultaneously. This analytical approach includes an important amount of information and presents the results in a clear and detectable manner. Consequently, an RDA provides a more accurate analysis of the interconnections between species groups and their surrounding environments.

3. Results

3.1. Length–Weight Relationship

The findings presented in Table 2 and Figure 2 indicate that *S. nukiangensis* exhibited the highest a value at the BS sampling site, followed by BB, CWL, and BR. Conversely, the LL sampling site had the lowest a value. The allometric growth factor, denoted as the b value, had the largest value at LL. Subsequently, BR, CWL, and BB displayed gradually decreasing b values. The minimum b value was measured at BS, with all recorded b values being significantly lower than 3. The a value in autumn had a slightly greater value compared with spring, which aligns with the observed comparison of the b value. Across sampling sites, *S. nukiangensis* showed variations in the a value and b value, measured at 1.988×10^{-4} and 0.435, respectively. In contrast, the difference in the a value and the b value was 1.354×10^{-6} and 0.307, respectively, across the seasons. These findings suggested that there were greater variations among sampling sites compared with variations among the seasons in the growth model of this fish. Otherwise, the b values at all the sampling sites along the QTP section of the Nujiang River were lower than 3, with the lowest value measured at BS. In this study, *S. nukiangensis* was found to have a negative allometric growth, indicating a suppressed growth of this fish in the QTP section of the Nujiang River (Figure 3).

In the case of *P. kaznakovi*, the highest value for value a was observed in ZG, with LL, BS, BB, NQ, and BR following in descending order. In contrast, BR displayed the highest value for value b, followed by NQ, BB, BS, LL, and ZG. When comparing the seasons, it was observed that the a value in autumn exhibited a slightly higher magnitude compared with spring, whilst the b value in spring had a slightly greater magnitude than in autumn. *P. kaznakovi* exhibited a difference in the significance of the a value and the b value in the sampling sites, with a scope of 2.126×10^{-5} and 0.267, respectively. In contrast, the difference in scope for these values in seasons was 1.354×10^{-6} and 0.030, respectively. These findings suggest that the influence of the sampling sites on *P. kaznakovi* growth is significantly greater than that of seasons.

In the case of *S. thermalis*, comparative analysis yielded the following results: LL exhibited the highest value for the parameter a, followed by NQ, ZG, and BR. Conversely, for parameter b, ZG displayed the highest value, followed by BR, NQ, and LL. Of the four sampling sites, only LL revealed a negative allometric growth significantly lower than 3 ($p < 0.05$), while the other three high elevation sampling sites all indicated near isometric growth of *S. thermalis* (Figure 3).

Table 2. Parameters of three schizothoracine fishes' length–weight relationships.

Sampling Sites	*a*		*b*			Adj. R^2	Sample Size (n)
	Value	Std	Value	Std	Sig.		
			S. nukiangensis				
CWL	3.627×10^{-5}	1.182×10^{-5}	2.821	0.061	**	0.97350	75
BS	2.166×10^{-4}	7.352×10^{-5}	2.479	0.063	**	0.93400	142
LL	1.781×10^{-5}	2.427×10^{-6}	2.914	0.024	**	0.98632	107
BB	5.793×10^{-5}	2.552×10^{-5}	2.761	0.076	**	0.98845	28
BR	3.529×10^{-5}	1.290×10^{-5}	2.845	0.062	**	0.98440	51
Spring	9.529×10^{-5}	2.455×10^{-5}	2.672	0.044	**	0.98988	51
Autumn	1.554×10^{-5}	3.423×10^{-6}	2.979	0.038		0.96288	319
			P. kaznakovi				
BS	1.287×10^{-5}	1.479×10^{-5}	2.983	0.214	**	0.95056	25
LL	1.806×10^{-5}	2.338×10^{-6}	2.912	0.023	**	0.98506	124
BB	1.113×10^{-5}	2.440×10^{-6}	3.004	0.040		0.97842	145
BR	6.000×10^{-6}	8.349×10^{-7}	3.110	0.025	**	0.97788	318
NQ	8.175×10^{-6}	5.340×10^{-6}	3.055	0.110		0.95361	38
ZG	2.726×10^{-5}	9.762×10^{-6}	2.843	0.066	**	0.98107	56
Spring	8.545×10^{-6}	7.119×10^{-7}	3.051	0.015	**	0.99240	238
Autumn	9.899×10^{-6}	1.111×10^{-6}	3.021	0.019		0.98504	413
			S. thermalis				
LL	3.481×10^{-5}	1.968×10^{-5}	2.809	0.113	**	0.97658	32
BR	1.293×10^{-5}	4.953×10^{-6}	2.990	0.071		0.97305	98
NQ	1.548×10^{-5}	3.189×10^{-6}	2.971	0.038		0.97327	454
ZG	1.39×10^{-5}	1.068×10^{-6}	2.992	0.014		0.98819	349
Spring	7.810×10^{-5}	2.189×10^{-5}	2.674	0.049	**	0.93502	398
Autumn	1.833×10^{-5}	4.502×10^{-6}	2.942	0.043		0.96318	460

Note: Sig. means significance level of one-sample *t*-test between *b* value and 3, "**" means $p < 0.01$.

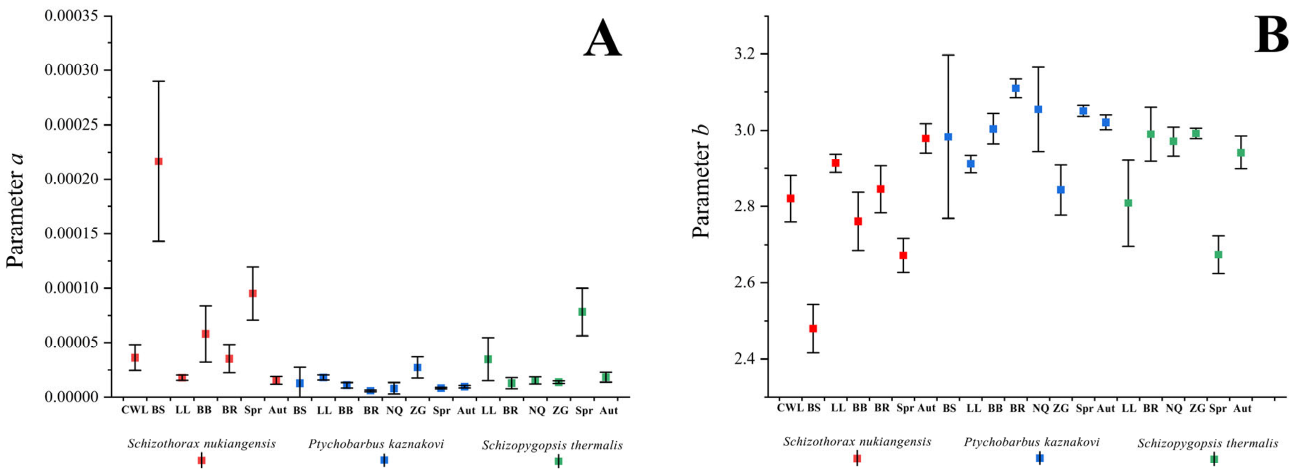

Figure 2. Parameter *a* (**A**) and parameter *b* (**B**) in the length–weight relationships of three schizothoracinae fishes in different sampling sites and different seasons. Spr is the abbreviation of the season of spring. Aut is the abbreviation of the season of autumn.

In terms of seasonal variations, the magnitude of the a parameter was greater during the spring season compared with the autumn season, whereas parameter *b* had a higher value during autumn as compared with spring. *S. thermalis* exhibited variations in the parameters *a* and *b*, with a difference of 2.188×10^{-5} and 0.183, respectively, observed across the sample sites. However, when considering seasons, the difference in parameters *a* and *b* were 5.977×10^{-5} and 0.268, respectively. These results suggested that seasons have a more severe influence on the LWR of *S. thermalis* compared with geographic differences.

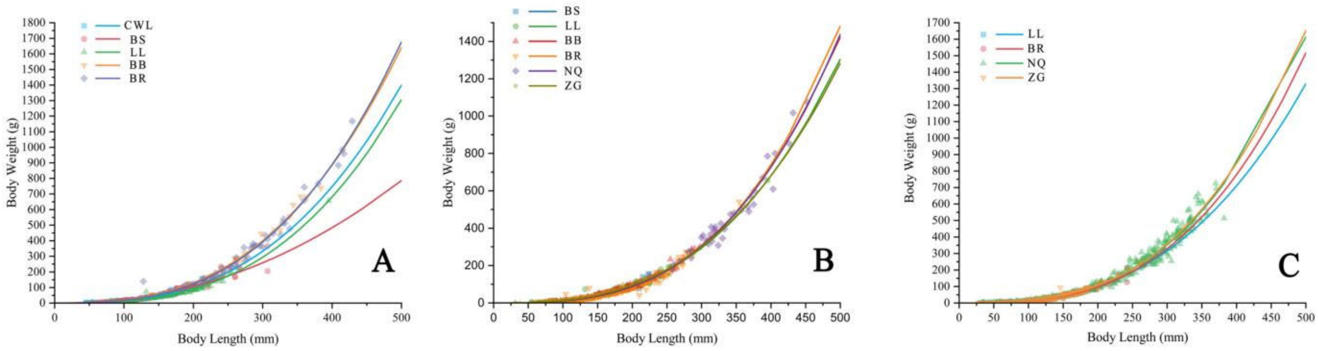

Figure 3. Fitting curves of the length–weight relationships of *S. nukiangensis* (**A**), *P. kaznakovi* (**B**), and *S. thermalis* (**C**) in different sampling sites.

3.2. LMM Analysis

We investigated the random effects of the parameter *a* and the allometric growth factor (*b* value) under the effects of various sample locations and seasons. Based on RMSE results, the results showed that the LMM suited the random effects based on sampling site differences better than the model fit the random effects based on seasonal changes in all three schizothoracinae fish species (Table 3). Furthermore, it was discovered that the random effect model's fitting degree, which took into account sampling sites and seasons, was better than that of regular generalized linear models. This suggested that the growth curves of all three schizothoracinae fish species exhibit random effects resulting from variations in regions and seasons (Table 3).

Table 3. Fitting models for length–weight relationships of three types of schizothoracinae fish based on LMM and root mean square error value (RMSE).

Model Abbreviation	Model (Log10-Transformed)	Random Effect	*S. nukiangensis*	*P. kaznakovi*	*S. thermalis*
WLR	W = a × L^b ln(W) = ln(a) + b × ln(L)	None	0.0999641	0.0520337	0.0655127
I.R	W = (a × exp(ReR.I)) × L^b ln(W) = (ln(a) + ReR.I) + b × ln(L)	Region	0.0977282	0.0492677	0.0639772
I.S	W = (a × exp(ReS.I)) × L^b ln(W) = (ln(a) + ReS.I) + b × ln(L)	Season	0.0991763	0.0518604	0.0655127
I.R&S	W = (a × exp(ReR.I)) × exp(ReS.I) × L^b ln(W) = (ln(a) + ReR.I + ReS.I) + b × ln(L)	Region + Season	0.0975144	0.0492253	0.0637690
S.R	W = a × L^(b + exp(ReR.S)) ln(W) = ln(a) + (b + ReR.S) × ln(L)	Region	0.0991154	0.0493031	0.0639683
S.S	W = a × L^(b + exp(ReS.S)) ln(W) = ln(a) + (b + ReS.S) × ln(L)	Season	0.0991154	0.0518821	0.0655127
S.R&S	W = a × L^(b + exp(ReR.S) + exp(ReS.S)) ln(W) = ln(a) + (b + ReR.S + ReS.S) × ln(L)	Region + Season	0.0973583	0.0492933	0.0637777
I&S.R	W = (a × exp(ReR.I)) × L^(b + exp(ReR.S)) ln(W) = (ln(a) + ReR.I) + (b + ReR.S) × ln(L)	Region	0.0971276	0.0478646	0.0630079
I&S.S	W = (a × exp(ReS.I)) × L^(b + exp(ReS.S)) ln(W) = (ln(a) + ReS.I) + (b + ReS.S) × ln(L)	Season	0.0990382	0.0517763	0.0654740
I&S.R&S	W = (a × exp(ReR.I)) × exp(ReS.I) × L^(b + exp(ReR.S) + exp(ReS.S)) ln(W) = (ln(a) + ReR.I + ReS.I) + (b + ReR.S + ReS.S) × ln(L)	Region + Season	0.0968849	0.0477507	0.0629002

Note: the first column shows the abbreviations of models detailed in the second column. L: standard length in millimeters; W: whole weight in grams; I.R: random effects on intercept (ln(a)) of regions (CWL, BS, ZG, LL, BB, BR, NQ); I.S: random effects on intercept (ln(a)) of seasons (spring, autumn); I.R&S: random effects on intercept (ln(a)) of regions and seasons; S.R: random effects on slope (b) of regions; S.S: random effects on slope (b) of seasons; S.R&S: random effects on slope (b) of regions and seasons; I&S.R: random effects on intercept (ln(a)) and slope (b) of regions; I&S.S: random effects on intercept (ln(a)) and slope (b) of seasons; I&S.R&S: random effects on intercept (ln(a)) and slope (b) of regions and seasons; RMSE means the root mean square error.

In addition, the fitting degree of the LMM for the random effects based on differences among the sampling sites was found superior to that of the model for the random effects based on differences among seasons in the three schizothoracinae fishes, indicating that geographical differences have a greater impact on the length–weight relationship of the three schizothoracinae fishes than seasonal changes.

3.3. Distribution Analysis

According to a comparison of the abundance of schizothoracinae fishes collected at each sampling site under the same catching intensity (Table 4 and Figure 4), *S. nukiangensis*, *P. kaznakovi*, and *S. thermalis* were found as the dominant species one after another as the elevation of the sampling sites gradually rose. All three fishes could be collected at the sampling sites except for CWL (the lowest in elevation among all the sampling sites) where only *S. nukiangensis* was collected. At NQ, the highest elevation site, no *S. nukiangensis* was found. In the main stream of the Nujiang River, *S. nukiangensis* was found at elevations below 4000 m, but *S. thermalis* and *P. kaznakovi* were present at elevations over 1800 m, and they were mainly distributed at LL, BR, NQ, and ZG.

S. nukiangensis, distributed along the QTP section of the Nujiang River from CWL to BR, displayed a tendency to decrease in quantity as the elevation of the sampling sites rose but an opposite trend in terms of biomass, which was ascribed to a larger size of *S. nukiangensis* at high-elevation sampling sites. Both the quantity and biomass of *P. kaznakovi* showed a tendency to rise as the elevation of the sampling sites climbed, reaching the maximum value at NQ. *S. thermalis*, mainly concentrated at ZG and NQ with a high elevation, had a limited distribution at other sampling sites. All these results revealed that *P. kaznakovi* and *S. thermalis* were more adaptable to high elevation environments than *S. nukiangensis*.

A heatmap and cluster analysis was conducted on the schizothoracinae species sampled along the QTP section of the Nujiang River, as depicted in Figures 5 and 6. Based on the findings of the clustering analysis, it was observed that the sample sites throughout the spring and autumn seasons exhibited a division into two distinct groups, characterized by a similarity threshold of around 20% in relation to abundance. NQ and ZG were classified into the same group. The other sampling sites were classified based on a similarity of 26%. The data from multiple seasons of CWL and BS were combined, while the data from BB, LL, and BR were grouped together. The clustering outcomes for biomass at each sampling site throughout the spring and fall seasons exhibited similarities to the clustering analysis results for quantity. These similarities mostly involved the presence of an NQ and ZG cluster, CWL and BS cluster, and BB, LL, and BR cluster. In conclusion, the examination of both the quantity and biomass data of schizothoracinae fishes revealed that the clustering results mostly emphasized the grouping of sampling sites. This indicates that the sampling sites played a significant role in affecting the degree of clustering observed.

According to the heatmap and cluster result, in the NQ and ZG cluster, *S. nukiangensis* had a limited distribution while *S. thermalis* enjoyed an advantage as the dominant species. In the CWL and BS cluster, both *P. kaznakovi* and *S. thermalis* were narrowly distributed, with *S. nukiangensis* as the dominant species. In the BB, LL, and BR cluster, all three schizothoracinae fishes had their distribution regions with *P. kaznakovi* as the dominant species.

The results of the heatmap indicated that *S. thermalis* was the prevailing species in the NQ and ZG cluster, which was situated at a high elevation. In contrast, *S. nukiangensis* was found infrequently in these clusters. *P. kaznakovi* and *S. thermalis* exhibited restricted distribution within CWL and BS cluster, whereas *S. nukiangensis* emerged as the prevailing species. Schizothoracinae fishes were observed in the BB, LL, and BR region, with *P. kaznakovi* being the predominant species.

Table 4. The amount, biomass, CPUE, and average weight of the three species of schizothoracine fishes at each sampling station.

Sampling Sites	*S. nukiangensis*				*P. kaznakovi*				*S. thermalis*			
	Amount (ind)	Biomass (g)	CPUE (g/(h × m^2))	Average Weight (g)	Amount (ind)	Biomass (g)	CPUE (g/(h × m^2))	Average Weight (g)	Amount (ind)	Biomass (g)	CPUE (g/(h × m^2))	Average Weight (g)
CWL	393	9718.7	0.1125	24.73	NA	NA	NA	NA	NA	NA	NA	NA
BS	340	34,304.7	0.3970	100.896	75	6020.5	0.0697	80.274	48	962.5	0.0111	20.053
LL	164	13,522.1	0.1565	82.452	199	13,784	0.1595	69.267	53	3063.8	0.0355	57.808
BB	42	13,828.7	0.1601	329.256	257	22,002.8	0.2547	85.614	37	547.1	0.0063	78.159
BR	78	29,001.2	0.3357	371.81	547	27,478.5	0.3180	50.235	130	6173.9	0.0715	47.492
NQ	NA	NA	NA	NA	57	29,666.4	0.3434	520.464	578	91,139.5	1.0549	157.681
ZG	13	97.77	0.0011	7.521	142	8405	0.0973	59.19	697	23,217.3	0.2687	33.31

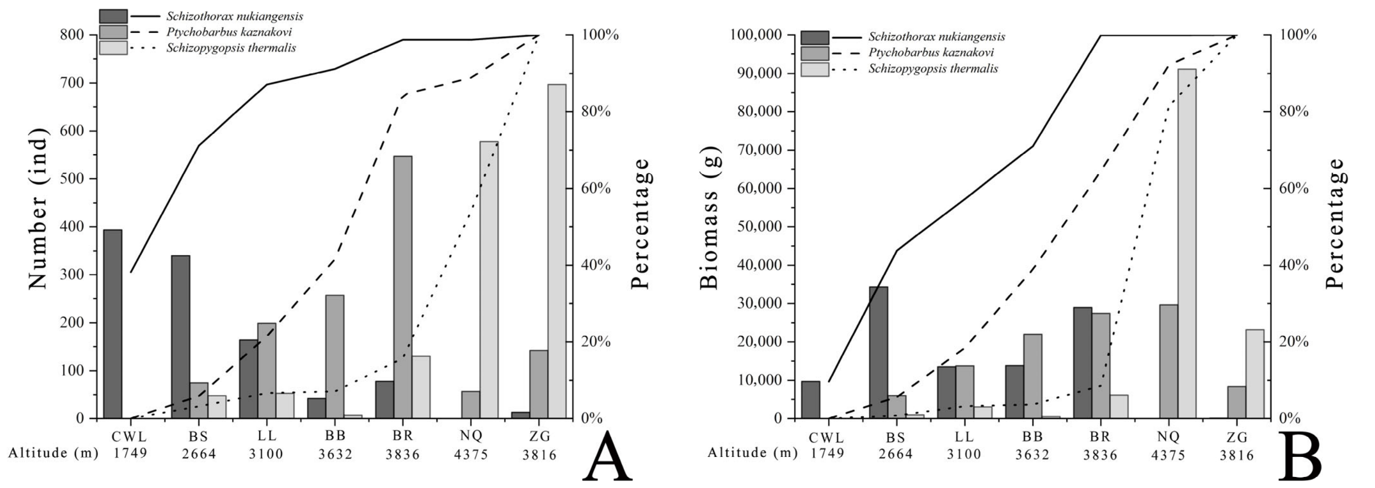

Figure 4. Amount (**A**), biomass (**B**), and cumulative proportion of three schizothoracine fishes at each sampling site along the Nujiang River in the QTP.

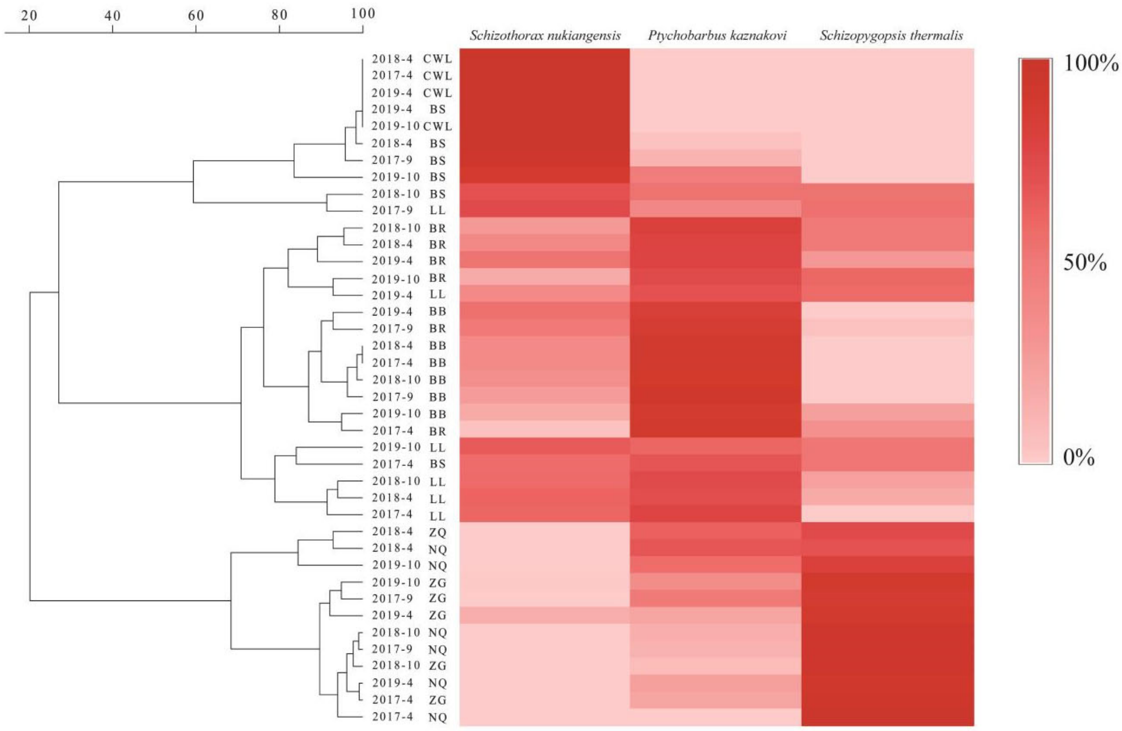

Figure 5. Cluster analysis based on the Bray–Curtis similarity and heatmap of three schizothoracine fishes amount at each sampling site along the Nujiang River in the QTP.

Seasons had a lesser impact on the variations in quantity and biomass of the three schizothoracinae fishes living the QTP section of the Nujiang River compared with geographical differences, as demonstrated by the outcomes of clustering analyses employing Bray–Curtis similarity coefficients (Figures 7 and 8). In the PCOA, the combined interpretation of the two coordinates exceeded 90%, showing a positive degree of interpretation. The two-dimensional analysis of NMDS revealed that both stress coefficients were less than 0.1, with respective values of 0.0077 and 0.0095, which denote that the NMDS graph plays a significant role in the interpretation of the similarity of the population structure. The results of the PCOA and NMDS provided evidence that validated the schizothoracinae fish population are grouped mainly by area, not season. ZG and NQ, which were grouped together for analysis, are geographically different from the remaining sampling sites over the seasons. The ANOSIM analysis (Table 5) indicated that there were no statistically significant differences in schizothoracinae fishes between ZG and NQ. However, there were substantial differences seen between these two sites and the remaining sample sites. Among the remaining five sampling sites, it was observed that CWL exhibited no statistically significant changes when compared to BS. However, CWL showed significant differences when compared with LL and BR. The analysis revealed no significant differences among LL, BB, and BR. All in all, the findings of the PCOA were corroborated by the results of the ANOSIM analysis: schizothoracine fishes in BS and CWL were significantly different compared with the other populations.

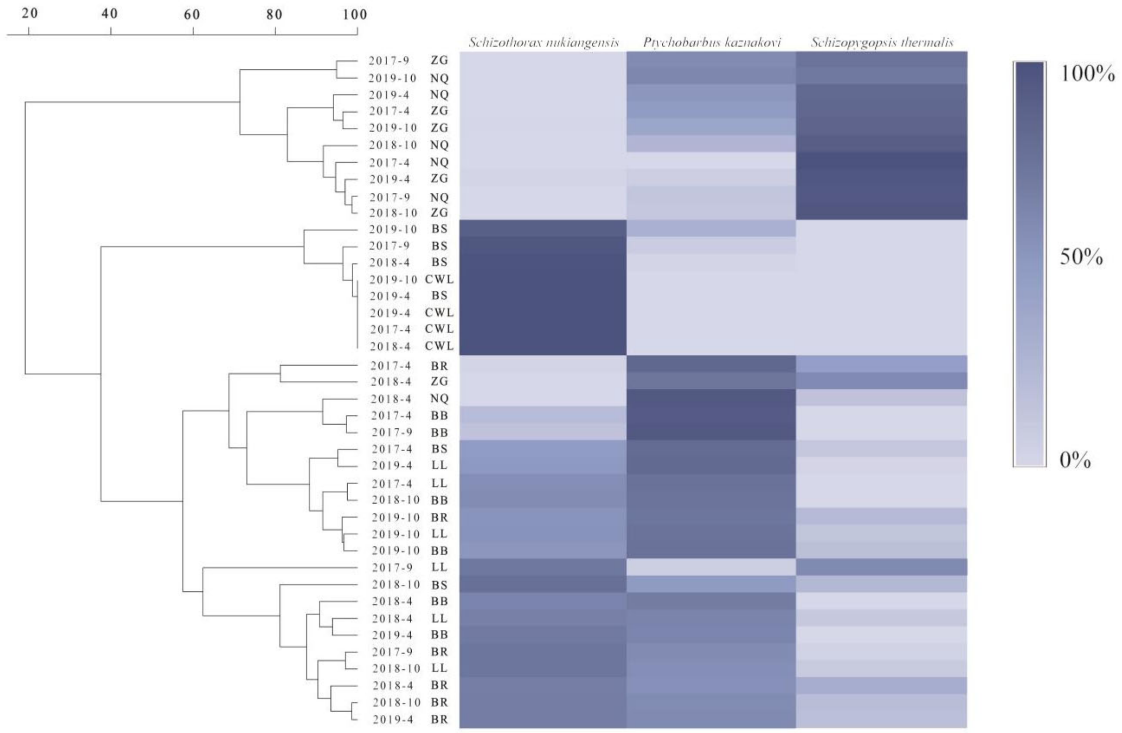

Figure 6. Cluster analysis based on the Bray–Curtis similarity and heatmap of three schizothoracine fishes biomasses at each sampling station along the Nujiang River in the QTP.

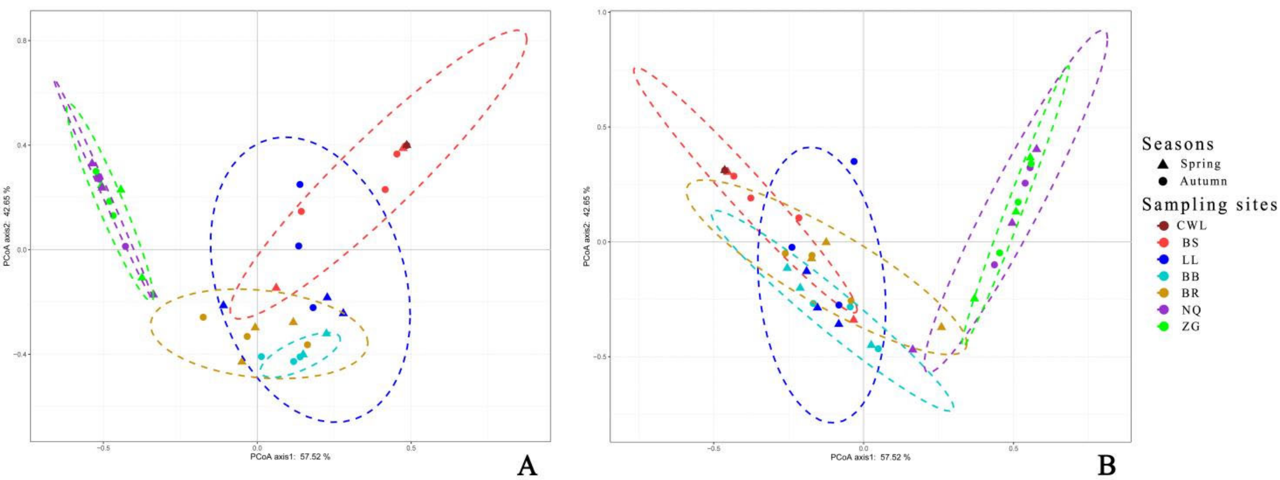

Figure 7. PCOA based on three schizothoracine fishes amount (**A**) and biomass (**B**) at each sampling site.

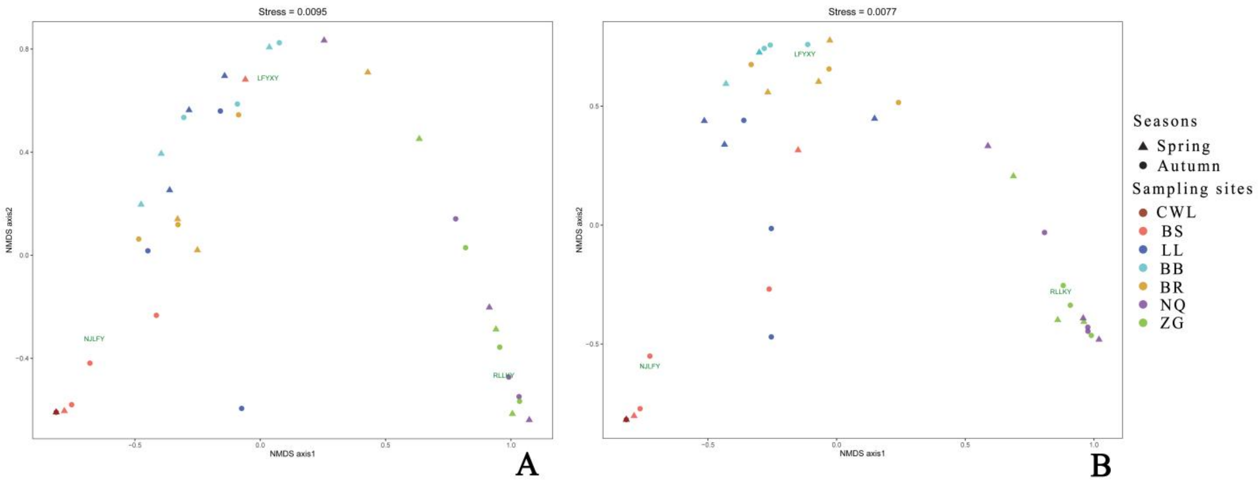

Figure 8. NMDS based on the Bray–Curtis similarity of three schizothoracine fishes amount (**A**) and biomass (**B**) at each sampling station.

Table 5. Using analysis of similarity (ANOSIM) to compare the differences between population of schizothoracine fishes at each sampling site based on the amount and biomass data (Global R = 0.76. Relative p = 0.001).

Sampling Sites	CWL	BS	LL	BB	BR	NQ	ZG
CWL		0.294	0.369 *	0.177	0.065	0.802 **	0.679 **
BS	0.012		0.470 *	−0.130	0.356 *	0.580 **	0.606 *
LL	0.266	−0.056		0.463 **	0.328 *	0.620 *	0.720 **
BB	−0.147	0.75 **	0.468 *		0.133	0.630 **	0.520 ***
BR	0.339 *	−0.156	0.222	0.598 **		0.717 **	0.681 **
NQ	0.598 *	0.220 *	0.280 *	0.689 **	0.565 **		−0.017
ZG	0.139	0.507 **	0.402 **	0.809 **	0.633 **	0.191	

Note: the upper triangular is the result of the amount, and the lower triangular is the result of the biomass. "***" means $p < 0.001$, "**" means $p < 0.01$, "*" means $p < 0.05$.

3.4. Relations Between Schizothoracine Fishes Populations and Environmental Factors

According to the results of the RDA study, it was shown that axis 1 and axis 2 accounted for 57.4% explanatory degree of the variance in population quantity and 51.28% explanatory degree of the variance in population biomass (Figure 9). According to the Monte Carlo Permutation analysis conducted on environmental parameters, it was found that elevation and temperature had a significant influence on changes in population quantity ($p < 0.05$). Additionally, the analysis revealed that elevation, conductivity, and COD had significant influences on changes in population biomass (Table 6). The elevation of the sampling locations had a highly significant influence on the populations of schizothoracinae fishes, both in terms of their abundance and biomass ($p < 0.001$). This relationship was supported by strong correlations of 0.8996 and 0.7805, respectively. Moreover, temperature also influenced the quantity of schizothoracinae fishes in an extremely significant manner ($p < 0.01$), with a correlation of 0.6165. In addition, it was observed that temperature exhibited a negative association with the first ordination axis in terms of both population quantity and biomass. Similarly, elevation showed a positive correlation with the first ordination axis in regard to population quantity and biomass. A negative association was seen between conductivity and the second ordination axis in the population biomass, whereas COD exhibited a positive correlation with the first ordination axis in the population biomass.

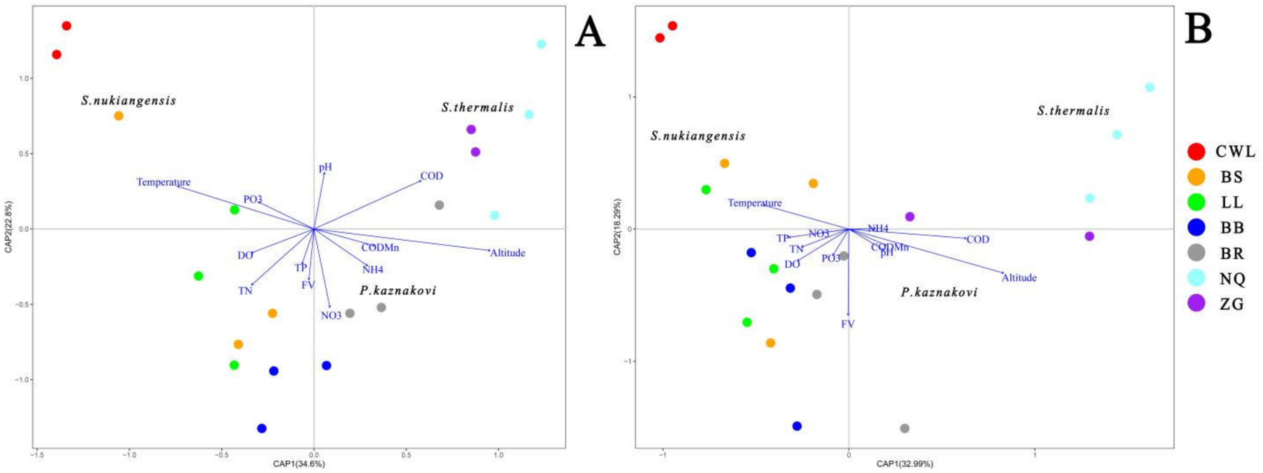

Figure 9. Relativity of fish community amount (**A**) and biomass (**B**) and environmental factors analyzed by RDA at each sampling site.

Table 6. Correlation and significance test of environmental factors and fish communities in RDA.

Environmental Factors	Name in Figure 8	Fish Amount		Fish Biomass	
		Correlation with Species Distribution (R^2)	Sig. (P)	Correlation with Species Distribution (R^2)	Sig. (P)
Altitude	Altitude	0.8996	0.001 ***	0.7805	0.001 ***
Water temperature	Temperature	0.6165	0.001 ***	0.2375	0.126
Dissolved oxygen	DO	0.1273	0.348	0.1186	0.367
Flow velocity	FV	0.1042	0.409	0.3838	0.016 *
pH	pH	0.1306	0.326	0.0582	0.626
Total nitrogen	TN	0.2250	0.123	0.0752	0.543
Total phosphorus	TP	0.0526	0.663	0.1004	0.454
Permanganate index	CODMn	0.1163	0.374	0.0541	0.633
Nitrate	NO3	0.2601	0.077	0.0203	0.857
Phosphate	PO3	0.1204	0.369	0.0414	0.711
Ammonium	NH4	0.1417	0.287	0.0193	0.872
Chemical oxygen demand	COD	0.3998	0.022	0.3851	0.019 *

Note: "***" means $p < 0.001$, "*" means $p < 0.05$.

4. Discussion

4.1. Growth Characteristics of the Three Schizothoracinae Fishes and Environmental Impacts

Knowledge of the LWR is useful for the fish population stock assessment [19]. The parameters a and b in the LWR are of special significance in fish ecology, because a is correlated to the environment in which the fish live, and b is related to the growth pattern of the fish [20]. A number of factors (e.g., sex, seasons, environmental conditions, stress, availability of food) also affect the parameter a of fish growth [21,22]. The variation in value b can suggest differences in their growth [23]. In addition to a general scope of b values between 2.5 and 3, the fish was revealed to have near isometric growth when $b = 3$. Moreover, the fish showed a decelerating growth rate when $b < 3$, denoting the weight of the fish, which was suppressed in growth, as "thin and weak", decreased with the increase in standard length. The fish grew at a faster rate when $b > 3$, indicating increased body weight in proportion to increased standard length as well as a "short and fat" or "round" shape of the fish [24]. The LWR of *S. nukiangensis* revealed that the value b was significantly below 3 in various regions and throughout spring. This indicated that *S. nukiangensis* exhibited negative allometric growth in the Qinghai–Tibet Plateau. The extent and direction of the deviation of value b was mainly influenced by the productivity of the habitat environment, as highly productive regions tend to promote positive allometric growth, while low productive regions such as the deep sea zone encourage negative allometric growth [25,26]. *Schizothorax nukiangensis* in the QTP showed low *b* value, particularly the lowest *b* value in BS, mainly due to considerable elevation variation, rapid water flow, and a gravel riverbed in Basu. These conditions increase energy consumption and decrease food availability. So, the Nujiang River in the Qinghai–Tibet Plateau is characterized by low productivity for *S. nukiangensis*.

Additionally, there have been reports on the investigation of the LWR in *P. kaznakovi*. Li et al. [27] determined the value *a* of *P. kaznakovi* in the Zengqu River, a tributary of the upper Jinsha River, China, to be 2×10^{-5}, and the value *b* to be 2.864. These results fell within the scope of the *a* value and the *b* value of *P. kaznakovi* in this study. When comparing allometric growth across various sampling sites, the b values at ZG and BS were found to be significantly lower than 3, indicating a negative allometric growth. On the other hand, the *b* values at BB and NQ showed no significant differences from the value of 3, suggesting a near isometric growth of *P. kaznakovi*. However, the value *b* at BR was markedly greater than 3, indicating a favorable allometric growth of *P. kaznakovi.* Consequently, *P. kaznakovi* had better growth performance in regions with elevations ranging from 3000 m to 4000 m at BB and BR. Otherwise, we found that *S. thermalis* mainly distributed in high elevation regions showed negative allometric growth in LL. On the other hand, the growth of *S. thermalis* was mostly influenced by seasonal variations.

He et al. [28] found that the value *b* was 2.74 for *S. nukiangensis* and 2.54 for *S. thermalis* in the headwater of the Nujiang River. This outcome validated our findings in *S. nukiangensis*; however, it was comparatively lower than the findings in *S. thermalis*. One potential explanation for this could be that the findings of He et al. [28] were obtained between 2001 and 2004, a considerable time prior to the present study. The main factors that affect biodiversity on the QTP include climate, geography, and human disturbances, which can have both direct and indirect impacts [29]. In the past two decades, there have been significant changes in global climate, and the QTP is one of the most sensitive areas to global climate change [30]. The findings presented infer that global change could potentially impact the growth of *S. thermalis*. Consequently, we plan to conduct further research to investigate the influence of climate change on fish growth in the QTP.

Allometric growth factors for the three schizothoracinae fishes were found to be significantly below 3 in the spring, but in the fall, they exhibited nearly isometric growth patterns. This suggested that schizothoracinae fishes will have a "thin and long" shape in spring rather than in autumn. Wang et al. [31] discovered that *S. nukiangensis* and *P. kaznakovi* are omnivorous. They have a preference for animals and mainly consume aquatic insects. On the other hand, *S. thermalis* is an omnivore that primarily consumes algae and phytoplankton. Moreover, within an appropriate range of temperature, the metabolic activity of fish will enhance as temperature rises, promoting their growth as well [32]. During the summer, the schizothoracinae fishes will experience increased metabolic activity and increased appetite due to the rise in temperature and abundance of food. For example, chironomid serves as the primary food source for *S. nukiangensis* and *P. kaznakovi*. The biggest amount of variation in the chironomid assemblages was accounted for by air temperature among several other environmental factors [33]. As temperatures rise in summer, the availability of food increases for fish, leading to weight gain and increased fatness. Therefore, in contrast to their negative allometric growth in spring, they showed better growth in autumn. This discovery provides substantial support for the research conducted by Kaylor et al. [34], who demonstrated, by coupling longitudinal patterns of fish density and growth, that the majority (60%) of fish production occurs during the summer when fish were concentrated in the headwaters of the river. In summary, the better growth performance of three schizothoracinae fishes in high elevation area may be attributed to enhanced nutrition in summer.

Multiple studies have identified that various factors, including regional, seasonal, and environmental conditions, have an impact on the estimations of variables *a* and *b* in the LWR [23,35]. It makes more sense to use a generalized linear mixed model to include all the spatial and temporal impacts in a single model rather than building many models to reflect different conditions. Mixed effects models enable the researcher to concurrently analyze all elements that may contribute to understanding the structure of the data [36]. Many researchers tend to employ the LMM for its convenience of analyzing diversified statistics in a way that includes fixed effects and random effects simultaneously to build models of the random effects of the LWR and then conduct further analysis [37]. The LMM has been widely used in population resource characteristics and resource assessments of *Thunnus obesus* [38], *Larimichthys polyactis* [39], and *Lophius litulon* [40]. The linear mixed effect model, which incorporates effects from both regions and seasons on parameters *a* and *b*, was determined to be the most favorable model based on RMSE. The suggested model aligns with prior research indicating that the LWR varies among areas and seasons based on the prevailing habitat conditions [16,35]. In this research, the mixed effects model incorporated the random effects for regions and seasons in a single model, providing a more convenient and reasonable approach to estimate geographical and temporal variations, which accords with previous study [35,41]. The variance in physical conditions across landscapes, known as spatial heterogeneity, interacts with the temporal variation caused by climate [42] and temperature fluctuations [43]. As elevation increases, temperature decreases. This decrease in temperature leads to adaptive changes in the growth, development, and physiological mechanisms of organisms in the QTP [44]. This study demonstrates that schizothoracinae fish exhibit the ability to adapt to various elevation environments by modulating their growth performance. Fernandes and McMeans [45] offered a fresh viewpoint on the physiological reactions to seasonality and the varying restrictions faced by freshwater fish, and they implied that energy gained during warm months is generally significant for fish overwintering survival and reproduction. It seems possible that fish in the QTP gain weight in autumn for overwinter survival and reproduction in the next year's spring.

4.2. Three Schizothoracinae Fishes Spatiotemporal Distribution Pattern Under Environmental Stress in QTP

The distribution of a species among a specific location is determined by its biological characteristics like temperature tolerance, nutrient field, environmental conditions (temperature, salinity, and dissolved oxygen), biological interaction (habitats and food supply), biogeographic history, and random events (extinction and dispersion) [46,47]. *S. nukiangensis*, *P. kaznakovi*, and *S. thermalis* were found to be the dominant species one after another as the elevation of the sampling area gradually rose. This could be the result of ecological niche differentiation, which occurs through natural selection and interspecific competition [48]. According to Wang et al. [31], *S. nukiangensis* and *P. kaznakovi* have a similar diet. However, *S. nukiangensis* was the most common species at the CWL and BS sampling sites. As the elevation increased, *P. kaznakovi* became the dominant species and replaced *S. nukiangensis*. These results suggest that *P. kaznakovi* and *S. nukiangensis* may possess different temperature tolerances, indicating that *P. kaznakovi* has better adaptability to high elevation environments compared with *S. nukiangensis*. The high-elevated regions, NQ and ZG, exhibited a diminished productivity and aquatic insects due to a decrease in temperature. This circumstance reduced the food source availability for *P. kaznakovi*, which prefers to feed on animals. Under these conditions, *S. thermalis*, which prefers to feed on vegetation and is adapted to cold water, became the dominant species. Similar conclusions have also been reported in studies on the Lancang River, in which species group substitution is found among *Cyprinidae* fish as the elevation rises [49]. Based on the findings of the clustering analysis, PCOA, and NMDS, it was found that seasonal variations do not significantly contribute to the changes in distribution of schizothoracinae fishes.

To examine previous hypotheses regarding the influence of temperature on the distributions of species, this study employed RDA, taking into account a multitude of environmental factors including elevation, temperature, and water quality. Elevation was revealed as an extremely significant influential factor for spatial distribution of schizothoracinae fishes populations, according to the RDA results and the Monte Carlo Permutation for variables. Fish have the ability to distribute themselves across this gradient, but they have a preference for habitats that are best suited to their biology and specific requirements [50]. This study supports evidence from previous observations of the sequential replacement of species from upstream to downstream along the longitudinal gradient within European freshwater ecosystems [51]. Temperature indicated an extremely significant impact on the quantity of schizothoracinae fish along the QTP section of the Nujiang River as well. In terms of organisms, changes in temperature affect physiological processes (e.g., oxygen consumption) within the isotherm [52]. If such changes do not cause the death of species, they do alter the energy consumption of organisms [53]. Therefore, organisms tend to live within regions where the temperature varies within an appropriate scope to reduce energy consumption and dramatic fluctuations of physiological processes [54]. The results further support the idea of temperature as a key component that influences the spatial distribution of stream fish [55,56]. The QTP is one of the most sensitive areas to global climate change and exhibits an early warning signal of global warming [30,57]. Extending the time of monitoring should be adopted to evaluate the climatic change impact on the spatial–temporal growth and distribution pattern of schizothoracinae fishes in the QTP.

5. Conclusions

According to this study, *S. nukiangensis* mainly showed a negative allometric growth while *P. kaznakovi* and *S. thermalis* mainly showed near isometric growth or positive allometric growth in the QTP section of the Nujiang River. Due to factors like temperature and food abundance, the three schizothoracinae fishes exhibited better growth performance in autumn than spring, which may benefit overwinter survival and reproduction in the next year's spring. Spatial heterogeneity has a greater impact on the LWR of the two schizothoracinae fishes, *S. nukiangensis* and *P. kaznakovi*, than seasonal factors. According to the LMM, both regions and seasons had influence on fish growth. *Schizothorax nukiangensis* was identified as the predominant species from CWL to BS, spanning an elevation range of 1800 to 2700 m. *Ptychobarbus kaznakovi* was identified as the main species at LL, BB, and BR, occupying an altitude range of 2700 to 3800 m. *Schizopygopsis thermalis* is primarily distributed at elevation beyond 4000 m and along the tributary river Yuqu. PCOA and NMDS divided schizothoracinae fish populations into three clusters mainly by spatial differences. The RDA and Monte Carlo Permutation analysis revealed that elevation and water temperature had a significant impact on the quantity of schizothoracinae fish populations. The spatial distribution of schizothoracinae fishes in the QTP segment of the Nujiang River varied due to the major influences of elevation, water temperature, and spatial variations. Considering the aforementioned results, it is important to implement in situ conservation strategies, create large, protected areas, and closely monitor the effects of seasonal and climate variations on schizothoracine fishes populations, as they are important conservation measures. This research is constrained by the incomplete investigation into the causes of forming distribution patterns and the impact of temperature and elevation on schizothoracine fishes and their adaptations. Our findings support the management and preservation of fish along the Nujiang River in the QTP. Additional efforts should be undertaken to assess the influence of climate change on the geographical and temporal patterns of growth and distribution of schizothoracinae fish populations. It would take additional research to determine how their morphology, physiology, genetics, and other characteristics contribute to their adaptation to high-elevation environments.

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Institutional Review Board Statement: "Guidelines for Experimental Animals" of the Ministry of Science and Technology (Beijing, China) and Yangtze River Fisheries Research Institute, Chinese Academy of Fishery Sciences on animal welfare and animal ethics were compiled during the experimental period. The Tab of Animal Experimental Ethical Inspection of Laboratory Animal Centre of Yangtze River Fisheries Research Institute, Chinese Academy of Fishery Sciences had approved our study. All efforts were made to minimize the suffering of sampled fish (ID = YFI2023XWT01).

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Data Availability Statement: The original contributions presented in the study are included in the article, further inquiries can be directed to the corresponding author.

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