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Coexistence of Two Closely Related Cyprinid Fishes (*Hemiculter bleekeri* and *Hemiculter leucisculus*) in the Upper Yangtze River, China

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Abstract: Species coexistence is one of the most important concepts in ecology for understanding how biodiversity is shaped and changed. In this study, we investigated the mechanism by which two small cyprinid fishes (*H. leucisculus* and *H. bleekeri*) coexist by analyzing their niche segregation and morphological differences in the upper Yangtze River. Morphological analysis indicated that *H. leucisculus* has posteriorly located dorsal fins, whereas *H. bleekeri* has a more slender body, bigger eyes, longer anal fin base, and a higher head. Niche segregation analysis showed spatial and trophic niche segregation between these two species: on the spatial scale, *H. leucisculus* was more widely distributed than *H. bleekeri*, indicating that *H. leucisculus* is more of a generalist in the spatial dimension; on the trophic scale, *H. bleekeri* had a wider niche than *H. leucisculus*. Therefore, these two species adopt different adaptation mechanisms to coexist

Keywords: biodiversity; species coexistence; spatial niche segregation; trophic niche segregation; morphology

1. Introduction

Species coexistence is one of the most important concepts in ecology for understanding how biodiversity is shaped and changed [1,2]. The mechanism that enable species—especially closely related, ecologically similar species—to coexist remains of interest in community ecology [3]. Although similar species commonly coexist in nature, classical niche theory suggests that complete niche overlap is evolutionally impossible [4,5]. Niche segregation, a process by which competing species evolve different patterns of resource-use under evolutionary pressures, is widely used to explain how similar species coexist [6–8]. Variation in resource-use can generally be separated into three aspects: space, time and food [9,10]. However, competing species tend to be segregated by at least one niche dimension [8,10,11].

Studies across diverse taxa, including birds [12], invertebrates [3,13], microbes [14,15], plants [16,17], fishes [1,8,18,19], amphibians and reptiles [20,21], have found that niche segregation is the main mechanism promoting coexistence. Rossier [22] confirmed the fish undergo spatial and temporal separation by identifying the spatial (distance from the shore) and seasonal (summer-winter) distributions of the ichthyofauna in the littoral zones of Lake Geneva. Knickle and Rose [5] studied the spatial and temporal movement patterns of sympatric juvenile *Gadus morhua* and *Gadus ogac*, using high-resolution radio-acoustic positioning in a coastal area of Newfoundland. Carniatto et al. [1] confirmed two sympatric, morphologically similar species of *Moenkhausia* with segregated food

resources. Leray et al. [23] demonstrated that dietary partitioning promotes the coexistence of two species of damselfish that commonly co-occur in branching corals.

Ecomorphology is a branch of environmental science that studies the relationship between organisms' morphologies and ecologies [24–26]. Fish morphology is related to environmental factors like habitat, diet and predation risk [27–29]. Morphological variation in aquatic systems can promote resource partitioning among competitors, and facilitate coexistence among closely related fishes [30,31]. Therefore, morphological measurements may be a reliable methodology for predicting factors of a fish's niche, such as its habitat and diet preferences [25,27,32–34].

Hemiculter leucisculus and *Hemiculter bleekeri* are two ecologically similar species that are dominant in many bodies of water in China [35]. They are extremely similar in morphology and diet, and mainly stay in the upper water column [36]. Both are omnivores whose diets mainly consist of aquatic insects, algae, plant detritus, Oligochaeta, and the Cladocera and Copepod Crustacea [36]. *H. leucisculus* is a small resident fish that spawns between May and June. It has a high fecundity and adhesive eggs. *H. bleekeri* spawns between May and June, but has pelagic eggs. Congeneric and ecologically similar species may be considered as good models for studies on niche segregation among co-occurring species [7,37–39]. There have been some studies on species coexistence, but very few on the coexistence between two sympatric freshwater fish species that are widely distributed, ecologically similar, and phylogenetically closely related.

This study investigated niche segregation and morphological variation between the two small cyprinid fishes *H. leucisculus* and *H. bleekeri* in the Upper Yangtze River. The goals of the present study were to (i) identify the niche segregation between these fishes in the basin of the upper Yangtze River and use it to elucidate the mechanisms governing how these two closely related and widely distributed congeners coexist, and (ii) examine the morphological variation between *H. bleekeri* and *H. leucisculus*, to determine whether morphological features might be indicators of species niche [33].

2. Materials and Methods

2.1. Study Area and Fish Sampling

The upper Yangtze River is 4500 km long from its headwaters to Yichang in Hubei Province; it accounts for around 2/3 of the total length of the Yangtze River and has a drainage area of 1.0×10^{6} km² [40]. It exhibits significant habitat heterogeneity across its reaches as a result of its meteorological, hydrological, physiographical, and geological variations [41]. These reaches include large drops, deep gorges and rushing flows, and the main tributaries include the Yalong River, Min River, Tuo River, Jialing River and Wujiang River. This study covered the main stream of the Yangtze River from the Panzhihua to Yichang reaches, and their tributaries (Figure 1).

Surveys investigating the temporal niche of *H. leucisculus* and *H. bleekeri* were conducted twice (May–June and September–October) each year from 2012 to 2016 in three reaches in the upper Yangtze River: Yibin (28°41′23″ N, 104°32′01″ E), Hejiang (28°48′26″ N, 105°50′42″ E) and Mudong (29°34′42″ N, 106°50′26″ E) (Figure 2). Each survey was conducted for 15–20 days of each season, using at least two local fishing boats for each reach.

Fishes were collected using local fishing boats with stationary gill nets ($35 \text{ m} \log \times 5 \text{ m} \text{ high}$, with mesh size of 1.0 to 6.0 cm). Fishermen deployed the stationary gill nets at 06:00 a.m. and retrieved them at 06:00 a.m. the next day. The specimens were identified based on the description of Ding [42]. Each specimen was counted and weighed (to the nearest 0.1 g) and its body length was measured (to the nearest mm). First, a piece of dorsal muscle tissue was dissected from each specimen, oven-dried at 60 °C for more than 48 h, and powdered to prepare it for stable isotope analysis (SIA). Then, fishes were placed into 10% neutral buffered formaldehyde solution and transported to the laboratory for morphological measurement. The research followed the guidelines specified by the research permits from the Institute of Hydrobiology, Chinese Academy of Sciences (permit number Y216011001).



Figure 1. Six habitat types in the upper Yangtze River from Yichang to Panzhihua, and distribution of *H. leucisculus* and *H. bleekeri* in this region. + indicates *H. leucisculus* and × indicates *H. bleekeri*; 1—sinuous headwater; 2—sinuous tributary; 3—steep headwater; 4—middle and upper sinuous river; 5—low altitude sinuous river; 6—upstream river habitat.



Figure 2. Sampling sites along the upper Yangtze River, China.

2.2. Morphological Measurement

Samples of *H. leucisculus* and *H. bleekeri* for morphological measurements were collected from Mudong town in the upper Yangtze River during the period May–June 2016 (Figure 3). A total

of 58 specimens of these two species were measured (29 of each species), and 20 morphometric characteristics were measured for each specimen [43] (Figure 4). All measurements were taken by the same investigator to minimize artificial error, and morphometric characteristics were measured to the nearest 0.01 mm with a digital vernier caliper, except for body length, which was accurate to 1 mm.



Figure 3. Photos of the studied species, Hemiculter leucisculus (a) and Hemiculter bleekeri (b).



Figure 4. Morphometric parameters investigated for *H. leucisculus* and *H. bleekeri*. BL, Body length; BD, Body depth; ED, Eye diameter; HL, Head length; HD, Head depth; DprD, Predorsal fin distance; DPrP₁, Prepectoral fin distance—P₁ is an abbreviation for pectoral fin; LP₁, Pectoral fin length; DPrP₂, Prepelvic fin distance—P₂ is an abbreviation for pelvic fin; LP₂, Pelvic fin length; DPrA, Pre-anal fin distance; LD, Dorsal fin length; LA, Anal fin length; LAb, Anal fin base length; CPL, Caudal peduncle length; CPD, Caudal peduncle depth [43].

A previous study identified the different morphological traits between the two species by analyzing the morphometric data of the specimens collected from the different locations (Table S1) [44]. Those results coincided with the results of the present study, demonstrating that the two species evidently had different morphological traits no matter where the specimens were collected. Moreover, many studies

have performed morphometric analysis on fish using 22–32 specimens of a species [45–48]. Therefore, the number of specimens analyzed in the present study was enough for a robust morphometric analysis.

2.3. Spatial Niche

2.3.1. Data Sources

Our data consisted of a 1:250,000 drainage map and 90-m high-resolution Shuttle Radar Topography Mission (SRTM) Digital Elevation Models (DEM). The drainage map was provided by the National Geomatics Center of China and the SRTM DEM data were provided by the National Aeronautics and Space Administration (NASA) and the USGS National Imagery and Mapping Agency (NIMA) at 90-m resolution (http://srtm.csi.cgiar.org) [49]. These data provided information on the river, sub-catchment boundaries and altitude needed to calculate parameters. The information concerning the *H. leucisculus* and *H. bleekeri* distributions were obtained from surveys from our research group and other literature.

2.3.2. Technical Procedure for Classifying River Habitats

The habitat in this study was analyzed on the macro scale. The following habitat classification methods were used. First, appropriate classification indexes were chosen based on references. Second, the sub-catchment was generated on the ArcGIS platform based on the SRTM DEM data and the river drainage map. Then, the values of indexes within each sub-catchment were calculated with ArcGIS software, the indexes were analyzed by the cluster analysis method in R software, and the number of habitat types was determined according to the clustering results. Finally, each habitat type was named according to the dominant habitat factors.

2.3.3. Choice and Calculation of Habitat Classification Index

According to the scale characteristics of the habitats, the classification index should be able to reflect the medium- or large-scale characteristics of the river system, such as the physical form, water system structure, and scale. River slope, sinuosity, drainage density, stream order and altitude were selected as the classification indexes, based on a literature review [50] and the river characteristics.

Stream order [50] and altitude indexes were directly extracted from the 1:250,000 drainage map and SRTM DEM data in ArcGIS software.

The slope (m/km) of a reach was calculated using Equation (1) [51]:

$$Slope = \frac{The altitude difference between the up and downslope points}{Straightline downcalley distance}$$
(1)

The sinuosity of a reach was calculated using Equation (2) [52]:

$$Sinuosity = \frac{Channel distance}{Straightline downcalley distance}$$
(2)

Drainage density (km/km²) was calculated using Equation (3) [52]:

Drainage density =
$$\frac{\text{channel length}}{\text{drainage area}}$$
 (3)

The parameters, such as straightline downvalley distance, channel distance, channel length and drainage area, used in Equations (1)–(3), were directly extracted from the 1:250,000 drainage map and SRTM DEM data in ArcGIS software.

2.4. Trophic Niche

A total of 14 samples for each species were randomly selected from Mudong town in the upper Yangtze River, from May to June 2016 (Figure 2), for stable isotopes (δ^{13} C and δ^{15} N) analysis. Firstly,

we grouped all of the collected samples according to their standard body length, and randomly selected samples from each group. Thus, the average body length of the selected samples was approximately equal to the average body length of the population (Table S2). Our aim was to make the selected samples as representative of the population as possible. One dorsal muscle tissue (about 0.3 mg) was used for stable isotope analysis (SIA).

 δ^{13} C and δ^{15} N were measured with a Delta Plus (Finnigan, Bremen, Germany) continuous-flow isotope ratio mass spectrometer coupled to a Carlo Erba NA2500 elemental analyzer (Carlo Erba Reagenti, Milan, Italy) at the Institute of Hydrobiology, Chinese Academy of Sciences. Stable isotope ratios were expressed in δ , a deviation from the international standards of parts per thousand (‰) that was calculated according to the following equation: $\delta X = [(R_{sample}/R_{standard}) -1] \times 1000$, where δ is the measure of heavy to light; the standards are Vienna Pee Dee Belemnite for carbon and atmospheric N2 for nitrogen [53]; X is ¹³C or ¹⁵N; and R is the corresponding ratio ¹⁵N/¹⁴N or ¹³C/¹²C. Three working standards (USGS40, USGS41 and UREA-Thermo) were employed to calibrate the analyzer. The average standard errors of replicate measurements for δ^{13} C and δ^{15} N were both less than 0.3‰. After obtaining δ^{13} C and δ^{15} N, we corrected the values according to the fitting function obtained from the fitting of the measured and standard values of the three working standards.

2.5. Statistical Analysis

To eliminate any effect of size (length) on the dataset, the morphometric parameters were transformed according to Lahnsteiner and Jagsch [54]: Transformed morphometric parameter = $\left(\frac{\text{measured morphometric parameter}}{\text{standard body length or head length}} \times 100\right)$. One-way analysis of variance (ANOVA) was firstly used to test whether those traits significantly differed between two species. Then a principal component analysis (PCA) was used to reduce the dimensionality of the variables, transform interdependent variables into significant and independent components [43,55], clarify the greater part of the variation, and extract new composite variables [56]. According to Kaiser–Meyer–Olkin (KMO) measures of sampling adequacy, and Bartlett's test of sphericity (Yakubu and Okunsebor, 2011), the factor analysis of the transformed morphological data set was valid ($\chi^2 = 1028.608$; P < 0.01). To avoid super factorization, and to select variables that better represent morphology, only components with eigenvalue scores greater than 1.000 were considered, following the Kaiser–Guttman criteria [57]. The extracted principal components (PCs) were rotated using varimax rotation for simplifying factors, which could help interpret the factors or rotated PCs. Finally, an independent sample *t*-test was used to analyze traits comprising PC1, then the means of these traits were compared. The above procedures were all carried out using IBM SPSS Statistics (version 20.0, Armonk, New York, NY, USA).

In this study, catch per unit effort (CPUE) was expressed as $g \cdot boat^{-1} \cdot day^{-1}$ [58]. We investigated the CPUE of the two species based on the same sampling methods, using the same time for each location. Therefore, the CPUE results could be used to compare the population density of the two fish species in each location. The data for all five years were divided into spring and autumn seasons for each site, and then the CPUE data were compared between (a) different species from the same season and (b) different seasons in the same location.

One-way ANOVA was conducted to test whether there were significant differences in the δ^{13} C and δ^{15} N values between *H. leucisculus* and *H. bleekeri*. We also calculated the δ^{13} C range (CR), the δ^{15} N range (NR), the total area of the convex hull encompassing the data points (TA), and the corrected standard ellipse area (SEAc) for *H. leucisculus* and *H. bleekeri* [59–61], and then compared the trophic niches between these two species. All metrics were calculated using the R statistical computing package "siar" [62].

3. Results

3.1. Morphological Measurements

The results of the one-way ANOVA showed that, among the 21 morphometric parameters, the following 10 were significantly different between *H. leucisculus* and *H. bleekeri*: relative body depth (BD/BL), relative head depth (HD/HL), relative snout length (SnL/HL), ratio of snout length to eye diameter (SnL/ED), relative eye diameter (ED/HL), relative dorsal fin length (LD/HL), relative pelvic fin length (LP₂/BL), relative anal fin base length (LAb/BL), relative pre-dorsal fin distance (DPrD/BL) and relative pre-anal fin distance (DPrA/BL).

The principal component analysis of 21 morphometric parameters extracted six factors with eigenvalues > 1, explaining 75.59% of the variance (Table 1). The first principal component (PC1) accounted for 26.00% of the variation, and the following PCs (PC2–6) accounted for 18.31%, 10.68%, 7.76%, 7.41% and 5.41%. For parsimony, only those factors with loadings above 0.60 were considered significant in this study.

Comparison of the mean and standard deviations of morphological traits in PC1 (Table 1) showed that *H. leucisculus* had greater values than *H. bleekeri* for BD/BL and DPrD/BL, but had smaller values for the measurements HD/HL, ED/HL and LAb/BL. Therefore, *H. leucisculus* had posteriorly located dorsal fins, whereas *H. bleekeri* had a slender body, bigger eyes, a longer anal fin base and a higher head.

Variables	Principal Component 1	Principal Component 2	Principal Component 3	Principal Component 4	Principal Component 5	Principal Component 6	Mean	
							H. bleekeri	H. leucisculus
BD/BL	-0.802	-0.084	-0.289	-0.164	0.027	-0.117	0.202 ± 0.014	0.233 ± 0.015
BW/BL	-0.100	-0.105	-0.252	-0.743	-0.077	0.066	0.101 ± 0.012	0.100 ± 0.006
HL/BL	-0.205	0.445	-0.022	0.725	-0.017	0.268	0.212 ± 0.010	0.213 ± 0.008
HD/HL	0.687	0.128	-0.224	-0.472	0.063	0.092	0.689 ± 0.024	0.630 ± 0.034
SnL/HL	-0.274	0.006	0.746	-0.074	0.225	0.182	0.289 ± 0.016	0.302 ± 0.020
SnL/ED	-0.758	-0.109	0.496	-0.060	0.161	0.006	1.002 ± 0.192	1.192 ± 0.107
ED/HL	0.799	0.179	-0.114	0.032	-0.064	0.113	0.289 ± 0.020	0.254 ± 0.014
SnL/IDE	-0.141	0.038	0.939	0.205	-0.050	0.105	0.741 ± 0.081	0.779 ± 0.100
IDE/HL	-0.046	-0.003	-0.769	-0.308	0.215	0.020	0.392 ± 0.031	0.392 ± 0.048
CPL/BL	-0.168	-0.096	0.037	0.470	0.424	-0.511	0.176 ± 0.012	0.181 ± 0.012
CPD/BL	0.044	0.154	0.032	0.014	0.908	0.009	0.097 ± 0.025	0.095 ± 0.004
LD/BL	0.354	0.796	0.029	0.207	0.134	-0.074	0.181 ± 0.012	0.172 ± 0.008
LP_1/BL	-0.199	0.743	-0.006	-0.096	0.115	0.057	0.193 ± 0.008	0.195 ± 0.010
LP ₂ /BL	0.399	0.723	0.094	0.234	0.112	-0.129	0.147 ± 0.009	0.139 ± 0.007
LA/BL	0.245	0.690	-0.044	0.292	-0.007	-0.022	0.112 ± 0.009	0.109 ± 0.006
LAb/BL	0.792	0.252	-0.092	-0.055	0.106	-0.059	0.139 ± 0.009	0.119 ± 0.007
HBE/HL	-0.148	0.112	-0.069	0.048	0.918	0.120	0.471 ± 0.068	0.490 ± 0.022
DPrD/BL	-0.777	0.028	0.062	0.008	0.116	0.278	0.495 ± 0.012	0.524 ± 0.017
DPrP ₁ /BL	-0.088	0.210	0.132	0.702	0.008	0.346	0.224 ± 0.009	0.224 ± 0.008
DPrP ₂ /BL	0.068	0.033	0.089	0.175	0.176	0.855	0.464 ± 0.012	0.461 ± 0.013
DPrA/BL	-0.347	-0.239	0.173	0.119	-0.011	0.696	0.700 ± 0.013	0.710 ± 0.014
Eigenvalue	5.71	4.029	2.35	1.71	1.63	1.20		
Explained variability (%)	26.00	18.31	10.68	7.76	7.41	5.44		
Accumulative variability (%)	26.00	44.31	54.99	62.75	70.16	75.59		

Table 1. Percentage of explained variance and weights of 21 morphometric characteristics (corrected based on standard body/head length) in six principal components (PCs), and the mean and standard deviation of morphometric characteristics in PC1. See Figure 4 for abbreviations. Sample number (n) = 58.

3.2. Spatial Niche

We identified 521 stream segments, according to the rules of river habitats classification [63], with lengths ranging from 0.216 to 337.904 km. Some sections of the river were short because there were many river junctions and the segmentation points were close to each other; these were mainly distributed in areas with good water systems. On the contrary, some rivers were poorly developed with fewer river intersections, yielding a longer river section.

According to the clustering results and the comprehensive characteristics of rivers, the river habitats in the upper Yangtze River were divided into six categories (Figure 1), containing 59, 60, 36, 104, 163 and 99 stream segments, respectively. The results of one-way ANOVA showed that river slope, sinuosity, drainage density, stream order and altitude were all significant in the six categories (P < 0.01). The six habitat types were named according to the differences in their index characteristics: sinuous headwater habitat, sinuous tributary habitat, steep headwater habitat, middle and upper sinuous river habitat, low altitude sinuous river habitat and upstream river habitat (Table 2).

Habitat Type	Stream Order *	Altitude (m)	Slope (m/km)	Sinuosity	Drainage Density (km/km ²)
1	1(37), 2(16), 3(6)	1969.9 ± 199.8	14.1 ± 18.0	1.39 ± 0.24	0.04 ± 0.02
2	1(39), 2(13), 3(8)	1379.1 ± 158.3	15.2 ± 11.9	1.42 ± 0.23	0.03 ± 0.01
3	1(24), 2(8), 3(4)	3041.9 ± 398.7	15.9 ± 15.2	1.41 ± 0.20	0.02 ± 0.01
4	1(52), 2(19), 3(30), 4(2), 5(1)	476.3 ± 68.7	4.5 ± 6.3	1.55 ± 0.35	0.04 ± 0.02
5	1(67), 2(32), 3(22), 4(13), 5(29)	254.0 ± 83.5	2.9 ± 4.3	1.69 ± 0.36	0.04 ± 0.03
6	1(42), 2(34), 3(23)	853.4 ± 154.6	11.9 ± 32.7	1.49 ± 0.36	0.03 ± 0.01

Table 2. Characteristics of six habita	t types in	the upper	Yangtze Riv	ver from Yi	ichang to l	Panzhihua
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* Note: The numbers in front of the brackets represented the stream order and the numbers in the brackets were the numbers of stream segments belonging to each stream order category.

The habitat classification in the upper Yangtze River, from the Yichang to Panzhihua reaches, and the distribution of *H. leucisculus* and *H. bleekeri*, suggested that *H. leucisculus* was distributed in types 2, 4, 5 and 6, mainly in types 4 and 5, and *H. bleekeri* was distributed in types 4 and 5 (Figure 1).

3.3. Temporal Niche

Surveys over the entire sampling period, from 2012 to 2016, yielded 2460.2 g of *H. leucisculus* and 4870.6 g of *H. bleekeri* in total. The CPUE of *H. leucisculus* in the Mudong reach was 92.8 g·boat⁻¹·day⁻¹ in spring, and 137.7 g·boat⁻¹·day⁻¹ in autumn; the CPUE of *H. bleekeri* was 61.5 g·boat⁻¹·day⁻¹ in spring and 159.1 g·boat⁻¹·day⁻¹ in autumn. The CPUE of *H. leucisculus* in the Hejiang reach was 7.4 g·boat⁻¹·day⁻¹ in spring and 0.8 g·boat⁻¹·day⁻¹ in autumn; the CPUE of *H. bleekeri* was 58.9 g·boat⁻¹·day⁻¹ in spring and 34.8 g·boat⁻¹·day⁻¹ in autumn. The CPUE of *H. bleekeri* in autumn was 8.2 g·boat⁻¹·day⁻¹ in the Yibin reach. The stationary gill nets did not capture *H. leucisculus* or *H. bleekeri* in spring in the Yibin reach, or *H. leucisculus* in autumn in the Yibin reach.

The CPUE of *H. bleekeri* was higher than that of *H. leucisculus* in all reaches except the Mudong reach in spring. In the Mudong and Yibin reaches, the CPUEs of *H. leucisculus* and *H. bleekeri* in spring were lower than those in autumn (Figure 5).



Figure 5. CPUE of *H. leucisculus* and *H. bleekeri* in the Mudong, Hejiang, and Yibin reaches in spring (May–June) and autumn (September–October), 2012–2016 ((a): Mudong, (b): Hejiang, (c): Yibin). The blank square represents *H. leucisculus* and the solid square represents *H. bleekeri*.

3.4. Trophic Niche

According to the one-way ANOVA, the δ^{13} C and δ^{15} N values were all significantly different between the two species (δ^{13} C: F = 54.040, *P* < 0.001; δ^{15} N: F = 31.897, *P* < 0.001). The δ^{13} C range (CR), δ^{15} N range (NR), corrected standard ellipse area (SEAc), and total area of the convex hull encompassing

the data points (TA) of *H. leucisculus* and *H. bleekeri* at Mudong were all different (Table 3). The CRs of *H. leucisculus* and *H. bleekeri* were 2.280 and 3.882, respectively. The NRs of *H. leucisculus* and *H. bleekeri* were 1.223 and 3.444, respectively. The SEAcs of *H. leucisculus* and *H. bleekeri* were 0.789 and 2.999, respectively. The TAs of *H. leucisculus* and *H. bleekeri* were 1.905 and 7.064, respectively (Table 3).

Table 3. δ^{13} C range (CR), δ^{15} N range (NR), corrected standard ellipse area (SEAc), and total area of the convex hull encompassing the data points (TA) of *H. leucisculus* and *H. bleekeri* at the Mudong site.

Species	δ ¹³ C Range CR	δ ¹⁵ N Range NR	Corrected Standard Ellipse Area SEAc	Total Area of the Convex Hull Encompassing the Data Points TA
H. leucisculus	2.280	1.223	0.789	1.905
H. bleekeri	3.882	3.444	2.999	7.064

4. Discussion

4.1. Morphological Characteristics and Ecological Niches

Morphological characteristics provide evidence for important ecological characteristics, which might be indicators of life habits, resource utilization types or environmental adaptations of species [24,26,33,43]. Since recent studies have confirmed the close relationship between morphological features and ecological niches, it has proven useful to infer ecological information from morphological characteristics [25,26,33,34,43]. Morphological variations are tightly related to niche segregation.

First, body depth (BD) is related to swimming behavior. According to the hydrodynamic theory, fishes in lotic habitats have more slender bodies than those living in lentic habitats, as they reduce drag during steady swimming while searching for prey and during fast acceleration while attacking prey [54,64]. Generally, the location of the dorsal fin (DPrD) is associated with the fish's vertical position in the water. Fishes with posteriorly located dorsal fins adapt more easily to surface habitats in non-flowing water, and have the capacity to stabilize and brake when accelerating [56]. Eye diameter (ED) is assumed to be related to the visual sensitivity and foraging position of the fish in the water column [33]. Head depth (HD) is generally associated with food size, as fishes with larger heads always consume larger prey items [25,26,33]. Anal fin base length (LAb) is associated with maneuverability capacity and movement stabilization [65]. Fishes in lotic habitats usually have wider anal fins to improve their swimming and stability in a current [56].

In the present study, we found a clear morphological difference and strong relationship between morphology and ecology in these two species. The PCA results showed that *H. leucisculus* has a posteriorly located dorsal fin, whereas *H. bleekeri* has a more slender body, bigger eyes, a longer anal fin base, and a higher head than *H. leucisculus* (Table 2). Combining all of the above characters and their functions, we conclude that *H. bleekeri* can consume larger prey than *H. leucisculus*, and the former inhabits a part of the water column closer to the surface. Moreover, *H. bleekeri* swims better than *H. leucisculus*, and is better suited to living in a flowing water environment. As expected, morphological variation between these two species is indeed a reliable predictor of differences in their habitats and diet preferences [25,27,33,34].

4.2. Niche Segregation and Species Coexistence

Spatial niche segregation may be expressed in the form of habitat segregation [66]. A fish's habitat preference can be influenced by many factors: environment variables, like water temperature [67–69], salinity [69], depth [69,70], turbidity [71], altitude [70], current velocity [71], vegetation characteristic, pH and dissolved oxygen [67]; and biological variables like competition, food availability and predation [72,73].

In terms of the large distribution area, *H. leucisculus* and *H. bleekeri*, in the upper reaches of the Yangtze River, are only distributed in the lower and middle reaches of the main stream and tributaries at low altitudes, but it is difficult for them to live in the source and upper reaches. This may be related

to the following factors: (1) Body size. Both *H. leucisculus* and *H. bleekeri* are compressiform, and fish with this body shape mostly inhabit areas with slow currents [25]. However, the river source and upstream areas have fast currents, high altitudes and large slopes [74–76]. Fishes living here are mostly anguilliform (e.g., *Coreius guichenoti* and *Rhinogobio cylindricus*) or depressiform (e.g., *Homaloptera* and *Gastromyzon*) [76]. (2) Feeding mode. The eutrophication degree of the water in the source and upstream areas is low. Most of the phytoplankton are sessile diatoms [77], and most of the aquatic arthropods and crustaceans are benthic. Therefore, the fish in these areas can either stabilize their bodies in the water flow and search for crustaceans in the bottom sand with their snouts, like *Rhynchocypris* does, or develop scraping habits [74], like *Onychostoma* and *Schizothorax* do. Therefore, fish in source and upstream areas are mainly adapted to the rapid current and benthic life, while *H. leucisculus* and *H. bleekeri* are pelagic fishes that struggle in these areas.

In the current study, *H. bleekeri* was usually distributed in areas of the upper Yangtze River basin with low altitude and slope, like habitat types 4 and 5. *H. leucisculus*, however, was distributed in habitat types 2, 4, 5 and 6, including the low altitude and slope areas (types 4 and 5)—which *H. bleekeri* preferred—and the slightly higher altitude and slope areas (types 2 and 6), which were difficult for *H. bleekeri* to occupy. Therefore, *H. leucisculus* is more widely distributed than *H. bleekeri* in the Yangtze River. Yibin had the highest *H. leucisculus* and *H. bleekeri* biomass in spring and autumn, followed by Hejiang and Mudong. Yibin is more upstream in the upper Yangtze River, Mudong is more downstream, and Hejiang is in between the two. This also shows that *H. leucisculus* and *H. bleekeri* are more suited to living in the lower reaches, with a lower altitude and slope.

When they coexist in a specific place, *H. bleekeri* is significantly more abundant than *H. leucisculus*. The results of the trophic niche analyses at the Mudong site showed that the food source (CR), trophic level (NR) and trophic niche width (TA and SEAc) of *H. bleekeri* were all greater than those of *H. leucisculus*, which indicates that *H. bleekeri* uses more resources and is more competitive than *H. leucisculus* when the two are sympatric. Therefore, when *H. leucisculus* and *H. bleekeri* are sympatric, to reduce the disadvantage of competition, *H. leucisculus* is forced to move to regions without *H. bleekeri*. According to the literature, *H. leucisculus* can survive in various habitats, such as reservoirs, lakes and rivers, even in other countries [78–80]. Some studies have also shown that the spawning habits of *H. leucisculus* are different in different regions. For example, it spawns adhesive eggs in Erhai [81], Fenhe Reservoir [82] and Dalai Lake [83], but pelagic eggs in Heilongjiang [84] and Erlonghu Reservoir [85]. In addition, *H. leucisculus* is invasive in some places (e.g., Erhai) [81]. All the above factors indicate that *H. leucisculus* has a strong adaptability, and this explains why it is more widely distributed in the upper Yangtze River.

5. Conclusions

In summary, niche segregation occurs between *H. leucisculus* and *H. bleekeri* in the upper Yangtze River, and such niche segregation and partitioning likely allows these two closely related species to co-exist. Of the three important dimensions of niche partitioning—space, time and food—food and space are the principal mechanisms of niche segregation between *H. leucisculus* and *H. bleekeri* in the upper Yangtze River, whereas we found no robust evidence of temporal segregation. *H. bleekeri* is more competitive, while *H. leucisculus* is more adaptive. In addition, there are morphological variations between *H. leucisculus* and *H. bleekeri*, and morphological characteristics are good indicators of a species' niche.

Supplementary Materials: The following are available online at http://www.mdpi.com/1424-2818/12/7/284/s1, Table S1: Comparison of the range of morphometric characteristics between *H. leucisculus* and *H. bleekeri* from reference "Fauna Sinica – Osteichthyes Cyperiniformes II" and this study, Table S2: Sampling location and sample information (body length, body weight, and their mean values) that used in stable isotope analysis, and the mean of all samples.

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