

Article

Thermal Preference May Facilitate Spatial Coexistence of Two Invasive Fish Species in Lake Bosten, China

Dan Song^{1,2,3} , Yinzhe Zhang^{1,2}, Junfeng Li^{1,2}, Puze Wang^{1,2}, Shaowen Ye¹ , Tanglin Zhang¹, Wei Li¹ , Chuansong Liao¹, Chuanbo Guo¹ and Jiashou Liu^{1,*}

- ¹ State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, China; songdan@ihb.ac.cn (D.S.); zhangyinzhe@ihb.ac.cn (Y.Z.); ljfkysss@163.com (J.L.); wpz2139@163.com (P.W.); yeshw@ihb.ac.cn (S.Y.); tlzhang@ihb.ac.cn (T.Z.); liwei@ihb.ac.cn (W.L.); liaocs@ihb.ac.cn (C.L.); guocb@ihb.ac.cn (C.G.)
- ² University of Chinese Academy of Sciences, Beijing 100049, China
- ³ Key Laboratory of Aquatic Organism Protection and Ecological Restoration in Cold Waters, Heilongjiang River Fisheries Research Institute, Chinese Academy of Fishery Sciences, Harbin 150010, China
- * Correspondence: jslu@ihb.ac.cn

Abstract: As aquaculture food production is expected to increase, introduced aquaculture species play an important role in meeting the rising demand for aquatic food products and contributing to great societal benefits. Species introduction forces sympatric species to coexist within the same ecosystem by niche segregation. Japanese smelt *Hypomesus nipponensis* and sharpbelly *Hemiculter leucisculus* are ecologically similar species and were introduced to Lake Bosten, the largest inland lake in Northwest China, accounting for more than 60% of the total production. We predicted that the coexistence of the two invasive species is mediated by habitat segregation. We analyzed spatiotemporal patterns of Japanese smelt and sharpbelly abundance in Lake Bosten to determine the patterns of spatial segregation between the two dominant fish species. Our results showed that, in Lake Bosten, sharpbelly are typically littoral dwellers when the surface temperature increases in spring and summer, while Japanese smelt often prefer pelagic waters, especially during summer and autumn when the surface temperature rises. Japanese smelt showed an affinity for deeper waters, using median depths 1.7 m deeper than those of sharpbelly, irrespective of the sampling season. Water temperature was the main underlying driver of such spatial segregation and coexistence of these two closely related species in Lake Bosten. Spawning, food resources, and fishing were also important possible factors affecting spatial segregation between the two species. Our results provide new information on niche partitioning patterns as strategies for the coexistence of the two dominant non-native fish in Lake Bosten, supporting the idea that ecologically similar species can avoid resource competition through spatial habitat segregation.

Keywords: Japanese smelt; sharpbelly; depth use; habitat selection; water temperature



Citation: Song, D.; Zhang, Y.; Li, J.; Wang, P.; Ye, S.; Zhang, T.; Li, W.; Liao, C.; Guo, C.; Liu, J. Thermal Preference May Facilitate Spatial Coexistence of Two Invasive Fish Species in Lake Bosten, China. *Sustainability* **2023**, *15*, 7592. <https://doi.org/10.3390/su15097592>

Academic Editor: George P. Kraemer

Received: 2 April 2023

Revised: 2 May 2023

Accepted: 3 May 2023

Published: 5 May 2023



Copyright: © 2023 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Globally, about 50% of farmed fish supplies came from inland aquaculture production in 2020, contributing a significant role in providing food and nutrition for the future [1]. As aquaculture food production is expected to increase by 15% by 2030, introducing aquaculture species is critical to meet the rising demand for aquatic food products [2,3]. Some countries rely on non-native fish species for aquaculture, especially Africa and Asia [4,5]; for example, in China, more than 110 non-native fish species for aquaculture exceed 25% of the total harvest [6,7]. Although the introduction of non-native fish species contributes to great societal benefits [8], it can be responsible for substantial biodiversity declines through competition, predation, disease transmission, the alteration of habitat, and genetic effects, as well as negative economic impacts [9–12]. The introduction of species forces sympatry among species that have not evolved together, which may result

in coexistence [13,14] or competitive exclusion [15], thereby altering community structure and ecosystems.

In many cases, multiple species of fish coexist within the same ecosystem by partitioning resources or occupying different ecological niches [16–18] to avoid competition. There are several ways in which resource partitioning can occur in fish. One common way is through the partitioning of their feeding strategies. For example, fish use a variety of feeding strategies, including herbivory, detritivory, insectivory, and piscivory, and the diversity of feeding strategies allows fish to avoid competition for resources [19]. Fish may also partition resources based on the type of prey they consume. Major ontogenetic dietary shifts are observed in many fish species [20,21], likely to provide them with a competitive advantage. Some species may be more active at night, while others may be more active during the day. These differences in feeding habits can allow multiple fish species to coexist in the same ecosystem without directly competing with each other for the same food resources [22]. In addition to feeding strategies, fish may also partition resources based on other ecological requirements, such as habitat use or reproductive strategies. Different fish species have different habitat requirements, and these requirements can vary depending on factors such as water temperature, dissolved oxygen, water depth, macrophyte coverage, or other physical structures [23–25], which can lead to habitat segregation. For example, Vendace *Coregonus albula* and Fontane cisco *Coregonus fontanae* occupy different water depths, thus reflecting their differing physiological temperature optima [26]. Additionally, within different zones of a lake, virile and rusty crayfish display spatial habitat segregation based on a trade-off between ideal habitat conditions and the density of a competing species [27]. Moreover, species can simultaneously take different adaptation mechanisms to coexist; for example, two closely related cyprinid fishes (*Hemiculter bleekeri* and *Hemiculter leucisculus*) show both spatial and trophic niche segregation [28]. The mechanisms of segregation reduce niche overlap, promote the partitioning of resources, and facilitate stable coexistence among ecologically similar species.

Smelt *Hypomesus* are among the most commonly introduced cold-water fish in China [29–31] and have become successfully established because of their broad trophic regime [32], considerable adaptability [33], and aggressive behavior [34] when introduced in new waterbodies (such as reservoirs and lakes). Although it was previously believed that the introduced fish species was the pond smelt (*Hypomesus olidus* Brevoort, 1856), both morphological comparisons and COI gene sequences have confirmed that the widely introduced fish species in China was the Japanese smelt (*Hypomesus nipponensis* McAllister, 1963) [35,36]. Japanese smelt, locally called the wakasagi, is a small freshwater fish that is native to Japan and other parts of East Asia and was introduced into Lake Bosten, the largest inland freshwater lake in China, in 1991 for commercial fisheries, where it was able to establish self-sustaining populations. It makes up the majority of the commercial fishery [29,34]. Japanese smelt is the only aquatic product exported from Lake Bosten, and it has been continuously exported to Japan, Korea, and other places. Currently, the Japanese smelt from Lake Bosten accounts for 70% of the market share in the Japanese smelt market [37]. Although the introduction of Japanese smelt increased the overall fish production in Lake Bosten, many studies have demonstrated significant negative impacts on aquatic ecosystems [38–41]. For example, in California's Sacramento–San Joaquin estuary, the introduced Japanese smelt may have negatively affected native delta smelt (*Hypomesus transpacificus*) through competition for food and space, predation on larval delta smelt, and hybridization [38]. Moreover, there was a significant shift in native fish assemblages in Lake Erhai, a subtropical plateau lake in southwestern China, after a Japanese smelt invasion [41]. Sharpbelly (*Hemiculter leucisculus*) is also a small freshwater fish similar to Japanese smelt in terms of diet and the occupied water layers and was introduced into Lake Bosten accidentally. Previous studies have shown the negative ecological consequences of Japanese smelt invasion in Lake Bosten through predation and competition [32,34,42], leading to the biodiversity loss of native fish species. Historical records indicate that the Lake Bosten fish community was formed by four native species: Big-head Schizothoracin

(*Aspiorhynchus laticeps*), Tarim Schizothoracin (*Schizothorax biddulphi*), slender stone loach (*Triplophysa tenuis*), and Kashgarian loach (*Triplophysa yarkandensis*) [29,34]. With the development of fisheries, a total of 38 fish species, including Japanese smelt and sharpbelly, have been introduced into Lake Bosten intentionally or accidentally [29]. However, in 2020, the survey on the fish community in Lake Bosten showed that a significant fish assemblage shift was found and there was only one native fish species, Big-head Schizothoracin, and this species is considered to be critically endangered, owing to a combination of factors, including climate change, overfishing, habitat loss and degradation, the introduction of non-native species, and pollution [43–45]. The annual yield of the two ecologically similar species, Japanese smelt and sharpbelly, accounts for more than 60% of the total production. They are ecologically similar in diet, and their diet typically consists of zooplankton, aquatic insects, algae, and the eggs and larvae of other small fish [30,34]. They mainly stay in the upper water column and have a high reproductive capacity and adhesive eggs [28,34,46]. Despite that, in theory, for species to co-occur in Lake Bosten, a certain degree of competition among the two ecologically similar species must be expected, no studies have revealed the niche segregation between Japanese smelt and sharpbelly.

This study investigated habitat segregation between the two dominant non-native species in Lake Bosten, Japanese smelt *Hypomesus nipponensis* and sharpbelly *Hemiculter leucisculus*. We hypothesized that the two species in Lake Bosten show the ability to adapt their behavior (i.e., habitat segregation) to seasonal thermal variation. The purposes of this study were (1) to understand spatiotemporal patterns of Japanese smelt and sharpbelly abundance and (2) to determine seasonal spatial segregation between the two fish species. Thus, this work provides new information on niche partitioning patterns as strategies for two dominant non-native fish coexistence in Lake Bosten.

2. Materials and Methods

2.1. Study Area

Lake Bosten is a large freshwater lake located in the Xinjiang Uygur Autonomous Region in China (Figure 1). With a surface area of approximately 1000 km², it is the largest lake in Xinjiang and the largest inland lake in China. The Kaidu River is the largest tributary of Lake Bosten and originates in the eastern Tian Shan Mountains before flowing into the lake from the southeast. The lake and its surrounding area are an essential part of Tarim Basin, one of the largest inland basins in the world. The climate of Lake Bosten is characterized as arid and semi-arid, with significant temperature variations throughout the year. Summers are long, hot, and dry, with temperatures often exceeding 35 °C in July and August. Winters are cold and dry, with temperatures occasionally dropping below freezing. The frozen period of Lake Bosten typically lasts from December to March [47].

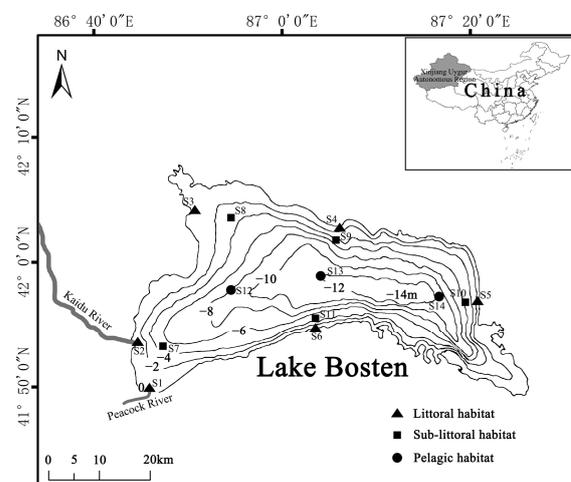


Figure 1. Geographical position and sampling sites of Lake Bosten.

2.2. Sampling Protocol

In 2020, Japanese smelt *Hypomesus nipponensis* and sharpbelly *Hemiculter leucisculus* in the lake were sampled seasonally: spring (April), summer (July), and autumn (October). A total of 14 sampling sites (S1–S14) were set from the shallow littoral habitat to the pelagic zone, covering three distinct depths, classified as (1) littoral (<2 m deep), (2) sub-littoral (ca. 5 m), and pelagic (ca. 10 m) (Figure 1). Fish were sampled using multi-mesh gill nets. Each gillnet used was 2 m (for the littoral area) or 5 m (for sub-littoral and pelagic areas) deep and 30 m long and consisted of twelve units of 2.5 m with different mesh sizes placed in random order (8.5, 4.0, 12.5, 2.0, 11.0, 1.6, 2.5, 4.8, 3.1, 1.0, 7.5, and 6.0 cm). At each sampling site, both floating and sinking gillnets were set in the late afternoon and retrieved the following afternoon (ca. 24 h). We used a YSI EXO3 profiling sonde to collect water temperature along the depth of the water column.

The captured fish were identified at the species level, measured to the nearest millimeter (total length, TL), and weight to the nearest gram (body weight) within 24 h. We also recorded the distances of each individual from the vertical position of captured fish to the headrope for the floating net (D1) and the footrope for the sinking net (D2). Thus, the depth used for the captured fish in the water column was D1 for the floating nets, and the water depth was minus D2 for the sinking nets.

The catch per unit effort (CPUE; the number of fish net⁻¹ day⁻¹) was estimated for each fish species caught on each sampling occasion from the littoral, sub-littoral, and pelagic habitats. The gillnet used in the sub-littoral and pelagic areas was 3 m deeper than that used in the littoral area; thus, the surface area of the net used in sub-littoral and pelagic areas was 1.5 times larger than that used in the littoral area. To account for this difference, catches in the sub-littoral and pelagic areas were normalized by dividing the total values by 2.5.

2.3. Statistical Analysis

Data were first tested for homoscedasticity (Levene's test for ANOVA) and normality (Shapiro–Wilk test), and, if necessary, data were subjected to an appropriate transformation. In this study, the data on the abundance of *Hypomesus nipponensis* and *Hemiculter leucisculus* were heteroscedastic, even after transformation. Therefore, differences in the abundance of *H. nipponensis* and *H. leucisculus* between season and habitat and the interaction between those two factors were tested using the Scheirer–Ray–Hare extension of the Kruskal–Wallis test [48], followed by pair-wise comparisons using the Mann–Whitney *U*-test. The Kruskal–Wallis test was used to test the differences in depth use between the two species, followed by pair-wise comparisons using the Mann–Whitney *U* test.

All statistical analyses were performed using R software [49], using the package *rcompanion* (version 2.4.21) [50] through the *scheirerRayHare* function for the Scheirer–Ray–Hare extension of the Kruskal–Wallis test.

3. Results

Our analysis indicated the main effects of habitat and season on the abundance of sharpbelly *Hemiculter leucisculus* (the Scheirer–Ray–Hare extension of the Kruskal–Wallis test, d.f. = 2, $H = 20.18$, $p < 0.001$; the Scheirer–Ray–Hare extension of the Kruskal–Wallis test, d.f. = 2, $H = 73.36$, $p < 0.001$; respectively), and interactions between habitat and season (the Scheirer–Ray–Hare extension of the Kruskal–Wallis test, d.f. = 4, $H = 11.01$, $p < 0.001$; Table 1). During spring and summer, the abundance was significantly higher in the littoral habitats and decreased with increasing water depth (Figure 2A). Sharpbelly was evenly distributed between the littoral and pelagic habitats in autumn ($p > 0.05$).

Table 1. Scheirer–Ray–Hare extension of the Kruskal–Wallis test on the ranks of the abundance of sharpbelly *Hemiculter leucisculus* and Japanese smelt *Hypomesus nipponensis* between habitat and season in Lake Bosten.

Species	Factors	d.f.	H	p
<i>Hemiculter leucisculus</i>	Habitat	2	20.18	<0.001
	Season	2	73.36	<0.001
	Habitat:Season	4	11.01	0.026
	Residuals	117		
<i>Hypomesus nipponensis</i>	Habitat	2	7.39	0.02
	Season	2	24.88	<0.001
	Habitat:Season	4	40.61	<0.001
	Residuals	117		

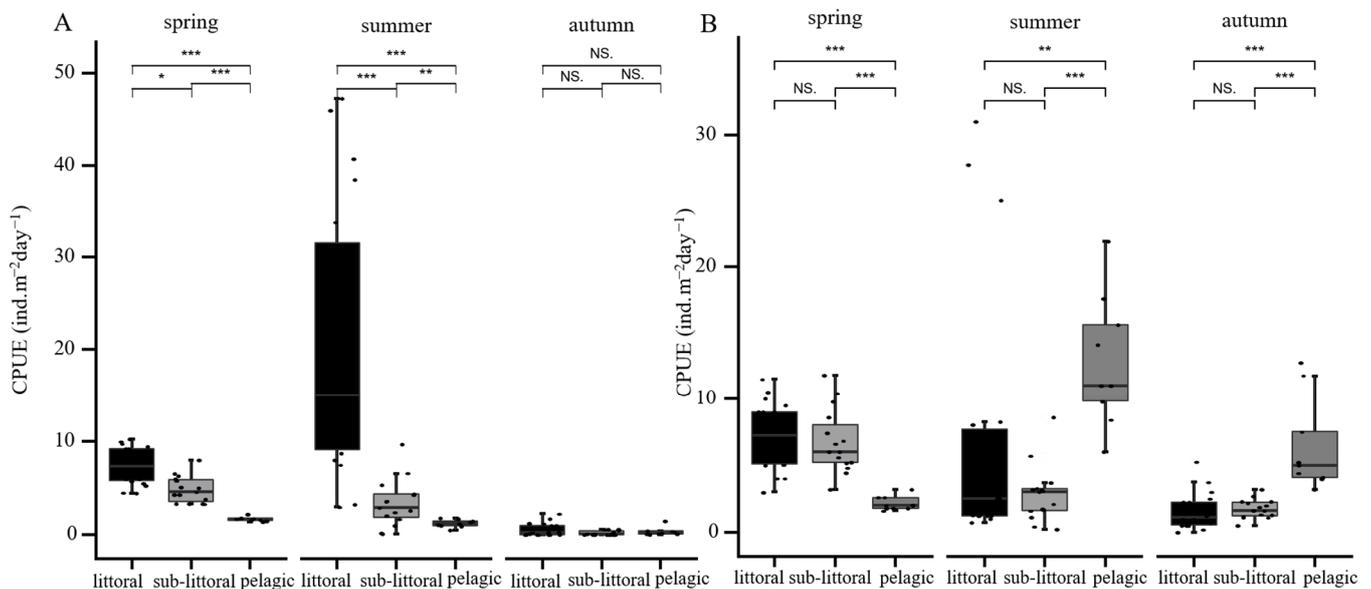


Figure 2. Boxplots with error bars indicate the abundance of sharpbelly *H. leucisculus* (A) and Japanese smelt *H. nipponensis* (B) in littoral, sub-littoral, and pelagic habitats during three seasons in Lake Bosten. Significances between habitats were computed with Mann–Whitney *U* test, with the symbol “*”, “**”, “***”, and “NS” representing $p < 0.05$, $p < 0.01$, $p < 0.001$, and non-significant, respectively.

Our analysis indicated that the abundance of Japanese smelt *Hypomesus nipponensis* did differ among habitat and seasons, and there was a significant interaction between habitat and season (the Scheirer–Ray–Hare extension of the Kruskal–Wallis test, d.f. = 2, $H = 7.39$, $p = 0.02$; the Scheirer–Ray–Hare extension of the Kruskal–Wallis test, d.f. = 2, $H = 24.88$, $p < 0.001$; the Scheirer–Ray–Hare test, d.f. = 4, $H = 40.61$, $p < 0.001$; respectively; Table 1). Japanese smelt used littoral and sub-littoral habitats in spring ($p < 0.05$) but behaved oppositely in summer and autumn (Figure 2B).

The gillnet survey revealed pronounced differences in the vertical distributions between Japanese smelt and sharpbelly ($p < 0.05$; Figure 3A). Japanese smelt and sharpbelly were detected from the surface to a maximum depth of 11.29 m and 7.95 m, respectively. Overall, Japanese smelt showed affinity to deeper waters, using median depths 1.7 m deeper than sharpbelly (Figure 3A), irrespective of the sampling season (Figure 4). There were no significant differences in the vertical distribution of sharpbelly among seasons ($p > 0.05$; Figure 3B). Sharpbelly were mainly caught in shallow waters in the littoral habitat, where the water temperature was relatively high (Figure A1). Japanese smelt, in opposite, used deeper waters (median depth = 3.40 m) when surface temperature increased, especially in summer, occupying shallower areas when the surface temperature dropped (Figure 3C).

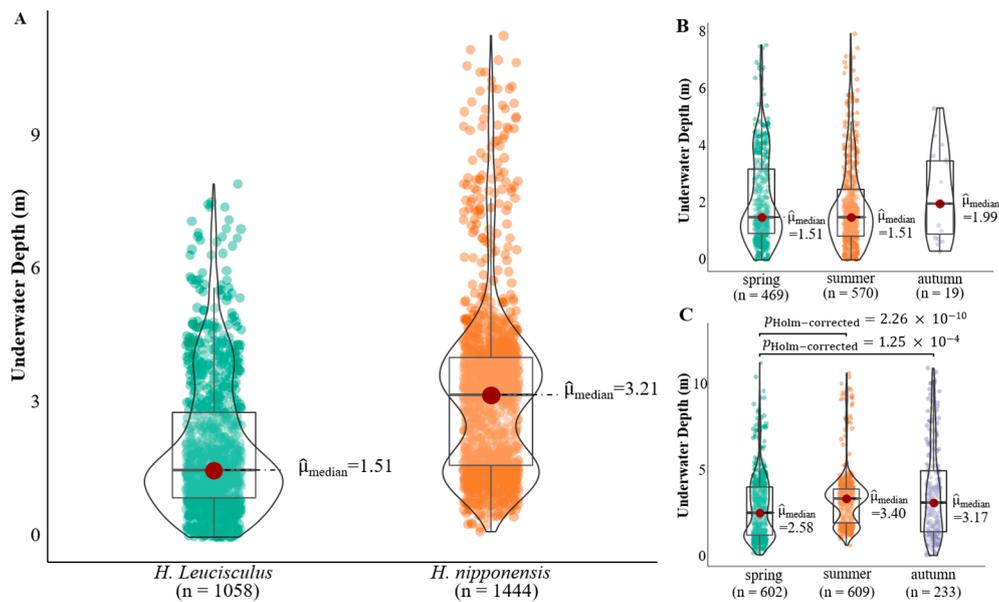


Figure 3. The violin plots, including boxplots and jittered dots, indicate the vertical distributions of sharpbelly *H. leucisculus* and Japanese smelt *H. nipponensis* in Lake Bosten (A) and the differences in the vertical distributions of *H. leucisculus* (B) and *H. nipponensis* (C) among three seasons.

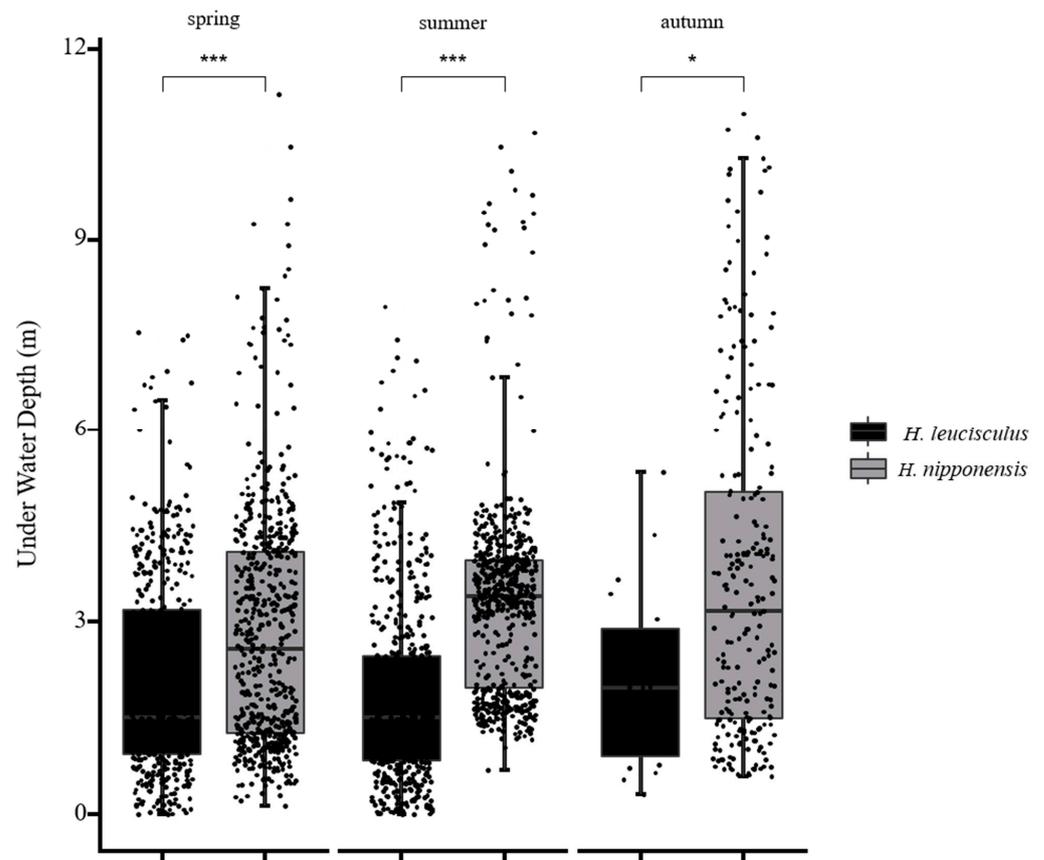


Figure 4. Boxplots with error bars indicate the vertical distributions of sharpbelly *H. leucisculus* and Japanese smelt *H. nipponensis* among seasons in Lake Bosten. Significances between species were computed with Mann–Whitney *U* test, with the symbol “*” and “***” representing $p < 0.05$ and $p < 0.001$, respectively.

4. Discussion

This study highlights spatial segregation and the differences in depth use by two closely related fish species facilitating coexistence in a freshwater lake ecosystem. As hypothesized, in Lake Bosten, there was significant spatial segregation between the two species. Specifically, sharpbelly *Hemiculter leucisculus* were typically littoral dwellers, especially when the surface temperature increased in spring and summer, while Japanese smelt *Hypomesus nipponensis* often preferred the pelagic waters, especially during summer and autumn when the surface temperature rose. There were also significant differences in vertical depth use among the two species. Japanese smelt occupied median depths 1.7 m deeper than those of sharpbelly, irrespective of the sampling season.

Over an evolutionary time scale, sympatric species, especially those closely related or ecologically similar, may prevent competitive exclusion by separating their spatiotemporal habitat utilization and/or food [13,51]. There was horizontal segregation in habitat use between Japanese smelt and sharpbelly. Segregation in habitat use by fish was modified by a very large number of possible factors, such as water temperature [52], spawning [53], food availability [54], predation risk [55], and other factors [56]. Fish movement and distribution across habitats are driven by the fact that fish can optimize their use of resources and promote their survival and reproduction in these habitats [23]. Several studies have suggested that the adaptability of fish species through behavioral plasticity may assist them in dealing with unfavorable environmental conditions, enabling them to maintain their functional roles in the ecosystems [23,57,58]. For example, when food resources are shared, the coexistence of the two species, Arctic charr *Salvelinus alpinus* and whitefish *Coregonus lavaretus*, may depend on the option for differential use of space. Therefore, Arctic charr mainly use the deeper water layers, and whitefish mainly occupy the littoral and upper pelagic habitats [59]. In this study, sharpbelly demonstrated a strong fidelity for warmer water layers, selecting shallower and warmer littoral habitats, especially during spring and summer. Sharpbelly mainly stay in the upper water column and spawn adhesive eggs between June and July [29]. In Lake Bosten, the littoral habitats, which are mainly composed of three species of submerged macrophytes (i.e., *Hydrilla verticillata*, *Ceratophyllum demersum*, and *Potamogeton pectinatus*) and two species of emergent macrophytes (i.e., *Phragmites australis* and *Typha orientalis*) [34], can provide a favorable spawning environment for fish, as macrophytes may offer shelter and protection for eggs and young fish [60]. Moreover, the dense foliage of macrophytes can create a complex habitat structure that can provide refuge for fish from predators [61]. Thus, sharpbelly move to shallower waters, where they can take advantage of the spawning grounds in spring and summer. Sharpbelly mainly feed on aquatic insects, Oligochaeta, Cladocera, and Copepod Crustacea [28]. High prey availability in the littoral habitats, coupled with a preference for complex habitats in shallow waters, likely provides thriving conditions for the growth of this species during spring and summer. Decreasing the preference for littoral habitats in autumn can indicate fluctuations of the abundance caused by differences in habitat selection, but a matching increase did not take place in the pelagic habitat. Such a pattern was probably induced by the low activity of fish caused by low littoral temperatures in autumn.

Japanese smelt, on the other hand, often occupy deeper and pelagic waters. Japanese smelt typically spawn in shallow, weedy areas from the end of February to the beginning of May, and the eggs are adhesive and attach to the surface of gravel or leaves of macrophytes [29]. This spawning behavior or its physical requirements for spawning determine the species to occupy shallower areas and exhibit site preference during spawning before moving to deeper areas. In addition, as the ice thaws and the water temperature begins to rise, a large number of nutrients and organic matters are carried into Lake Bosten by the Kaidu River, the largest tributary of Lake Bosten, which can stimulate the growth of aquatic plants and animals [62], providing a rich food source for fish. Thus, the two species appeared to show less horizontal habitat segregation in spring when food was abundant. Additionally, in spring, significant differences in the average depth use ($p < 0.05$) by the two species facilitated their coexistence in littoral habitats. Japanese smelt selected pelagic

habitats in summer and autumn, which probably were less profitable in terms of food but more thermally favorable. As the water temperature continues to rise in summer, Japanese smelt move to the pelagic zones, where the water is cooler and darker, contributing to obvious horizontal habitat segregation among the two species. A previous study showed that Japanese smelt prefer cold pelagic waters, avoid light, and swim in darker environments [33]. Japanese smelt are extremely sensitive to changes in light intensity. One reason for this behavior may be that Japanese smelt have a well-developed visual system, i.e., a high density of ganglion cells and the presence of area retinae temporalis [63], that support its highly visual behavior and adapt to low light levels, which allows them to detect and capture prey and avoid predators more effectively in darker waters [64]. Another possible reason is that the avoidance of light helps Japanese smelt conserve energy by reducing the need for constant swimming and maneuvering to avoid predators [65,66]. Additionally, fishing pressure may cause Japanese smelt to change their behavior, such as by avoiding areas where fishing is common [67]. This can result in changes in habitat use patterns, as fish may avoid areas where they perceive a higher risk of encountering fish gear or where they have previously been caught. As one of the most important commercial species for fisheries in Lake Bosten, Japanese smelt are typically caught using fyke nets that are typically set in shallow waters of the lake during the autumn months [29], which drives the species to migrate from littoral to pelagic habitats.

It has been suggested that the water temperature modifies the vertical distribution of fish through differences in physiological tolerance and thus may contribute to the coexistence of species [68,69]. As water temperature changes, fish will often adjust their vertical distribution in the water column in search of more favorable conditions [23]. Therefore, species are known to actively seek out and compete for thermal habitats that are optimal for their metabolism and behavior, where their performance can be at its peak [70]. In Lake Stechlin in Germany, for example, vendace (*Coregonus albula*) and Fontane cisco (*Coregonus fontanae*) segregate vertically with energetically optimum temperatures, choosing the water layers of about 6.5–9 °C and 4–6 °C during stratification, respectively [25]. Our study showed that during spring and summer, when water temperature decreased with water depth, Japanese smelt and sharpbelly showed significant differences in depth distribution, which further suggested that thermal preference promotes the coexistence of the two species. Japanese smelt selected relatively colder water conditions compared with sharpbelly and occupied significantly deeper water layers when surface temperature increased in summer. As a cold-water species, Japanese smelt have adapted to a relatively narrow temperature range and typically inhabit cool, well-oxygenated waters. Previous studies have shown a low-temperature affinity of Japanese smelt, generally using deeper water layers with the optimum temperature for development ranging between 7 and 19 °C in summer [33,71], and that the fish are relatively scarce in areas with temperatures above 20 °C [72]. Another study conducted in Lake Kasumigaura in Japan also found that Japanese smelt showed a preference for cold water and that water temperature resulted in inferior growth in summer [73]. Sharpbelly always occupied the warmest available water layers among seasons. Considering its wide distribution range in various freshwater, such as lakes, rivers, and reservoirs, and relatively high optimal temperature for growth, it was unsurprising that there existed an affinity for warm water [74]. In this study, the ability to adapt their behavior to seasonal thermal variation in species with both warm-water and cold-water affinities indicated that behavioral plasticity is an important determinant of the resilience of fish species to changing environmental conditions and the coexistence of species with similar resource requirements. Habitat segregation may help the coexistence of species with similar resource requirements to reduce the negative impacts of competition. Japanese smelt in Lake Bosten mainly feed on zooplankton [32] and may, therefore, overlap their diet with sharpbelly, which have an omnivorous diet [28]. On the other hand, significant differences in vertical distribution between the two species during autumn, when water temperatures were similar throughout the water column,

corroborated that diet and habitat specialization may also drive spatial patterns of vertical fish distribution.

5. Conclusions

In summary, spatial segregation occurs between two non-native species in Lake Bosten, Japanese smelt *Hypomesus nipponensis* and sharpbelly *Hemiculter leucisculus*. Water temperature was the main underlying driver of such spatial differences in their abundance distributions. Additionally, spawning, food resources, and fishing pressure were also important possible factors affecting spatial segregation between the two species. Further studies are needed to better understand the ecological pattern of habitat use, diet, and distribution for both fish species under sympatric conditions to monitor temporal and spatial habitat shifts responding to environmental changes and to determine the extent to which behavioral plasticity may allow species to cope with environmental variability.

Author Contributions: D.S.: conceptualization, methodology, investigation, formal analysis, writing—original draft, writing—review & editing. Y.Z.: investigation. J.L. (Junfeng Li): investigation. P.W.: investigation. S.Y.: investigation, formal analysis, writing—review & editing. T.Z.: writing—review & editing. W.L.: writing—review & editing. C.L.: investigation. C.G.: writing—review & editing. J.L. (Jiashou Liu): writing—review & editing, funding acquisition. All authors have read and agreed to the published version of the manuscript.

Funding: This work was financially supported by the National Key Research and Development Program of China (2019YFD0900601) and the Finance Special Fund of the Ministry of Agriculture and Rural Affairs (Fisheries Resources and Environment Survey in the Key Water Areas of North-west China).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: The raw data supporting the conclusions of this article will be made available by the authors without undue reservation.

Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

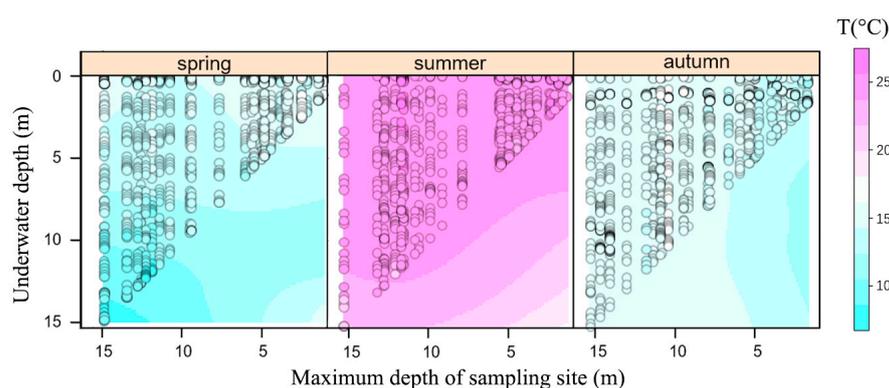


Figure A1. Vertical variations in the water temperature in Lake Bosten.

References

1. FAO. *The State of World Fisheries and Aquaculture*; FAO: Rome, Italy, 2022.
2. Shelton, W.L.; Rothbard, S. Exotic species in global aquaculture—A review. *Isr. J. Aquacult. Bamid*. **2006**, *58*, 3–28.
3. Subasinghe, R.; Soto, D.; Jia, J. Global aquaculture and its role in sustainable development. *Rev. Aquacult.* **2009**, *1*, 2–9. [[CrossRef](#)]
4. Casal, C.M.V. Global Documentation of Fish Introductions: The Growing Crisis and Recommendations for Action. *Biol. Invasions* **2006**, *8*, 3–11. [[CrossRef](#)]

5. Witt, A.B.R. Use of Non-Native Species for Poverty Alleviation in Developing Economies. In *Impact of Biological Invasions on Ecosystem Services*; Vilà, M., Hulme, P., Eds.; Invading Nature—Springer Series in Invasion Ecology; Springer: Cham, Switzerland, 2017; Volume 12.
6. Lin, Y.; Gao, Z.; Zhan, A. Introduction and use of non-native species for aquaculture in China: Status, risks and management solutions. *Rev. Aquacult.* **2015**, *7*, 28–58. [[CrossRef](#)]
7. Kang, B.; Vitule, J.R.S.; Li, S.; Shuai, F.; Huang, L.; Huang, X.; Huang, X.; Fang, J.; Shi, X.; Zhu, Y.; et al. Introduction of non-native fish for aquaculture in China: A systematic review. *Rev. Aquacult.* **2022**, *15*, 676–703. [[CrossRef](#)]
8. Gozlan, R.E. Introduction of non-native freshwater fish: Is it all bad? *Fish Fish.* **2008**, *9*, 106–115. [[CrossRef](#)]
9. Manchester, S.J.; Bullock, J.M. The impacts of non-native species on UK biodiversity and the effectiveness of control. *J. Appl. Ecol.* **2000**, *37*, 845–864. [[CrossRef](#)]
10. Simberloff, D.; Martin, J.-L.; Genovesi, P.; Maris, V.; Wardle, D.A.; Aronson, J.; Courchamp, F.; Galil, B.; García-Berthou, E.; Pascal, M.; et al. Impacts of biological invasions: What's what and the way forward. *Trends Ecol. Evol.* **2013**, *28*, 58–66. [[CrossRef](#)]
11. Haubrock, P.J.; Pilotto, F.; Innocenti, G.; Cianfanelli, S.; Haase, P. Two centuries for an almost complete community turnover from native to non-native species in a riverine ecosystem. *Glob. Chang. Biol.* **2021**, *27*, 606–623. [[CrossRef](#)]
12. Diagne, C.; Leroy, B.; Vaissière, A.C.; Gozlan, R.E.; Roiz, D.; Jarić, I.; Salles, J.M.; Bradshaw, C.J.; Courchamp, F. High and rising economic costs of biological invasions worldwide. *Nature* **2021**, *592*, 571–576. [[CrossRef](#)]
13. Ohlberger, J.; Mehner, T.; Staaks, G.; Hölker, F. Temperature-related physiological adaptations promote ecological divergence in a sympatric species pair of temperate freshwater fish, *Coregonus* spp. *Funct. Ecol.* **2008**, *22*, 501–508. [[CrossRef](#)]
14. Henkanaththegedara, S.M.; Stockwell, C.A. Intraguild predation may facilitate coexistence of native and non-native fish. *J. Appl. Ecol.* **2014**, *51*, 1057–1065. [[CrossRef](#)]
15. Böhn, T.; Amundsen, P.A.; Sparrow, A. Competitive exclusion after invasion? *Biol. Invasions* **2008**, *10*, 359–368. [[CrossRef](#)]
16. Garrison, L.P. Spatial and dietary overlap in the Georges Bank ground fish community. *Can. J. Fish Aquat. Sci.* **2000**, *57*, 1679–1691. [[CrossRef](#)]
17. Juncos, R.; Milano, D.; Macchi, P.J.; Vigliano, P.H. Niche segregation facilitates coexistence between native and introduced fishes in a deep Patagonian lake. *Hydrobiologia* **2015**, *747*, 53–67. [[CrossRef](#)]
18. Westrelin, S.; Balzani, P.; Haubrock, P.J.; Santoul, F. Interannual variability in the trophic niche of young-of-year fish belonging to four piscivorous species coexisting in a natural lake. *Freshwater Biol.* **2023**, *68*, 487–501. [[CrossRef](#)]
19. Winemiller, K.O. Spatial and Temporal Variation in Tropical Fish Trophic Networks. *Ecol. Monogr.* **1990**, *60*, 331–367. [[CrossRef](#)]
20. Araújo, M.S.; Bolnick, D.I.; Layman, C.A. The ecological causes of individual specialisation. *Ecol. Lett.* **2011**, *14*, 948–958. [[CrossRef](#)]
21. Sánchez-Hernández, J.; Nunn, A.D.; Adams, C.E.; Amundsen, P.-A. Causes and consequences of ontogenetic dietary shifts: A global synthesis using fish models. *Biol. Rev.* **2019**, *94*, 539–554. [[CrossRef](#)]
22. Westrelin, S.; Cucherousset, J.; Roy, R.; Tissot, L.; Santoul, F.; Argillier, C. Habitat partitioning among three predatory fish in a temperate reservoir. *Ecol. Freshw. Fish* **2021**, *31*, 129–142. [[CrossRef](#)]
23. Chrétien, E.; Chapman, L.J. Habitat heterogeneity facilitates coexistence of native fishes with an introduced predator: The resilience of a fish community 5 decades after the introduction of Nile perch. *Biol. Invasions* **2016**, *18*, 3449–3464. [[CrossRef](#)]
24. Freitas, C.; Villegas-Ríos, D.; Moland, E.; Olsen, E.M. Sea temperature effects on depth use and habitat selection in a marine fish community. *J. Anim. Ecol.* **2021**, *90*, 1787–1800. [[CrossRef](#)] [[PubMed](#)]
25. Dias, R.M.; Tófoli, R.M.; da Silva, J.C.B.; Gomes, L.C.; Agostinho, A.A. Effects of habitat complexity on trophic interactions of three congeneric fish species. *Aquat. Ecol.* **2022**, *56*, 877–889. [[CrossRef](#)]
26. Mehner, T.; Busch, S.; Helland, I.P.; Emmrich, M.; Freyhof, J. Temperature-related nocturnal vertical segregation of coexisting coregonids. *Ecol. Freshw. Fish* **2010**, *19*, 408–419. [[CrossRef](#)]
27. Perales, K.M.; Hansen, G.J.A.; Hein, C.L.; Mrnak, J.T.; Roth, B.M.; Walsh, J.R.; Vander Zanden, M.J. Spatial and temporal patterns in native and invasive crayfishes during a 19-year whole-lake invasive crayfish removal experiment. *Freshw. Biol.* **2021**, *66*, 2105–2117. [[CrossRef](#)]
28. Li, W.J.; Gao, X.; Liu, H.Z.; Cao, W.X. Coexistence of Two Closely Related Cyprinid Fishes (*Hemiculter bleekeri* and *Hemiculter leucisculus*) in the Upper Yangtze River, China. *Diversity* **2020**, *12*, 284. [[CrossRef](#)]
29. Guo, Y.; Zhang, R.; Cai, L. *Fish Resources and Fishery in Lake Bosten*; Xinjiang Science and Technology Press: Urumqi, China, 2005.
30. Jiang, X.; Wang, J.; Tang, W.; Sun, Z.; Pan, B. Non-native freshwater fish species in the Yellow River Basin: Origin, distribution and potential risk. *Environ. Biol. Fish.* **2021**, *104*, 253–264. [[CrossRef](#)]
31. Ji, F.; Ma, X.; Qiu, L.; Kang, Z.; Shen, J. Quantifying the effects of introduced Bighead Carp (Cyprinidae; *Aristichthys nobilis*) stocking on dominant fish species in the Ulungur Lake, China. *Biol. Invasions* **2022**, *24*, 1253–1265. [[CrossRef](#)]
32. Lai, Y. The Relationship between the Disappearance of Calanoida Population and the Introduction of *Hypomesus olidus* in Lake Bosten. *J. Hydroecol.* **2009**, *2*, 136–139, (In Chinese with English abstract).
33. Xie, Y.; Li, B. Behaviors of pond smelt (*Hypomesus olidus*) and the changes in its population structure in two reservoirs. *Acta Ecol. Sin.* **1991**, *11*, 37–43, (In Chinese with English abstract).
34. Chen, P.; Ma, Y.; Xie, C.; Qi, F. Preliminary study on community structure of fishes in Bositeng Lake. *Freshw. Fish.* **2014**, *44*, 36–42, (In Chinese with English abstract).
35. Cao, X.; Dong, S.; Yang, Z.; Gong, S. Species of genus *Hypomesus* for transplantation. *Hebei Fish.* **2009**, *6*, 10–12. (In Chinese)

36. Gong, X.; Wu, Y.; Cui, Z.; Bao, B. Molecular identification of transplanted *Hypomesus* species in seven places. *J. Fish. China* **2012**, *12*, 1802–1808. (In Chinese with English abstract) [[CrossRef](#)]
37. Xu, Y. The production of Lake Bosten's pond smelt exceeds 1700 tons. *Mod. Fisheries Inf.* **2010**, *25*, 3. (In Chinese)
38. Swanson, C.; Reid, T.; Young, P.S.; Cech, J.J. Comparative environmental tolerances of threatened delta smelt (*Hypomesus transpacificus*) and introduced wakasagi (*H. nipponensis*) in an altered California estuary. *Oecologia* **2000**, *123*, 384–390. [[CrossRef](#)]
39. Zhou, X.; Hu, Z.; Liu, Q.; Yang, L.; Wang, Y. Feeding ecology of the non-indigenous fish *Hypomesus nipponensis* in Lake Ulungur, China: Insight into the relationship between its introduction and the collapse of the native Eurasian perch population. *Mar. Freshw. Res.* **2013**, *64*, 549–557. [[CrossRef](#)]
40. Sakamoto, D.; Nemoto, T.; Sunoh, N.; Iwasaki, J.; Niwa, S.; Arayama, K.; Suzuki, N.; Takagi, K.; Sakuramoto, K. Population size estimation of the pond smelt *Hypomesus nipponensis* in Lake Kasumigaura and Lake Kitaura, Japan. *Fish. Sci.* **2014**, *80*, 907–914. [[CrossRef](#)]
41. Yin, C.; Chen, Y.; Guo, L.; Ni, L. Fish Assemblage Shift after Japanese Smelt (*Hypomesus nipponensis* McAllister, 1963) Invasion in Lake Erhai, a Subtropical Plateau Lake in China. *Water* **2021**, *13*, 1800. [[CrossRef](#)]
42. Zhang, T.; Yu, X.; Xian, Y.; Song, M.; Li, X.; Cai, L.; Niu, J. Appraisal and suggestions on fishery resources effectiveness evaluation of breeder releasing in Lake Bosten and Ulungur Lake. *Chin. Fish. Econ.* **2020**, *38*, 93–99. (In Chinese with English abstract)
43. Cao, G. Rediscovery of Bigstrachtery resources effectiveness. *Sci. Fish Farm.* **1999**, *1*, 40. (In Chinese)
44. Ren, B.; Ren, M.; Guo, Y.; Zhang, R.; Ma, Y.; Liu, Y.; Aizezi; Tuersun; Abudu. Studies on the biological characteristics of *Aspiorhynchus laticeps* (Day). *Chin. J. Fish.* **2006**, *2*, 9–22. (In Chinese)
45. Ma, Y.; Zhang, R.; Li, H.; Tuersun, G.Y. Research of Habitat and Community Conservation Biology of *Aspiorhynchus laticeps*. *J. Hydroecol.* **2010**, *31*, 38–42. (In Chinese)
46. Xie, Y.; Li, B. Observation on the embryonic development of pond smelt. *J. Fish. China* **1987**, *11*, 307–314.
47. Wang, S.; Dou, H. *Lake Records of China*; Science Press: Beijing, China, 1989.
48. Dytham, C. *Choosing and Using Statistics: A Biologist's Guide*, 3rd ed.; Wiley-Blackwell Publishing Ltd.: Oxford, UK, 2011.
49. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2020; Available online: <https://www.R-project.org/> (accessed on 6 March 2023).
50. Mangiafico, S. *rcompanion: Functions to Support Extension Education Program Evaluation*, R Package Version 2.4.21; R Foundation for Statistical Computing: Vienna, Austria, 2023. Available online: <https://CRAN.R-project.org/package=rcompanion>(accessed on 6 March 2023).
51. Carbia, P.S.; Brown, C.; Park, J.M.; Gaston, T.F.; Raoult, V.; Williamson, J.E. Seasonal and developmental diet shifts in sympatric and allopatric intertidal gobies determined by stomach content and stable isotope analysis. *J. Fish Biol.* **2020**, *97*, 1051–1062. [[CrossRef](#)] [[PubMed](#)]
52. Ivanova, S.V.; Johnson, T.B.; Metcalfe, B.; Fisk, A.T. Spatial distribution of lake trout (*Salvelinus namaycush*) across seasonal thermal cycles in a large lake. *Freshw. Biol.* **2021**, *66*, 615–627. [[CrossRef](#)]
53. Hunter, E.; Metcalfe, J.D.; Reynolds, J.D. Migration route and spawning area fidelity by North Sea plaice. *Proc. R. Soc. B.* **2003**, *270*, 2097–2103. [[CrossRef](#)]
54. Carassou, L.; Whitfield, A.K.; Moyo, S.; Richoux, N.B. Dietary tracers and stomach contents reveal pronounced alimentary flexibility in the freshwater mullet (*Myxus capensis*, Mugilidae) concomitant with ontogenetic shifts in habitat use and seasonal food availability. *Hydrobiologia* **2017**, *799*, 327–348. [[CrossRef](#)]
55. Heithaus, R.M.; Dill, M.L. Does tiger shark predation risk influence foraging habitat use by bottlenose dolphins at multiple spatial scales? *Oikos* **2006**, *114*, 257–264. [[CrossRef](#)]
56. Heggenes, J.; Bagliniere, J.L.; Cunjak, R.A. Spatial niche variability for young Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) in heterogeneous streams. *Ecol. Freshw. Fish* **1999**, *8*, 1–21. [[CrossRef](#)]
57. Day, T.; McPhail, J.D. The effect of behavioural and morphological plasticity on foraging efficiency in the threespine stickleback (*Gasterosteus* sp.). *Oecologia* **1996**, *108*, 380–388. [[CrossRef](#)]
58. Jolles, J.W.; Briggs, H.D.; Araya-Ajoy, Y.G.; Boogert, N.J. Personality, plasticity and predictability in sticklebacks: Bold fish are less plastic and more predictable than shy fish. *Anim. Behav.* **2019**, *154*, 193–202. [[CrossRef](#)]
59. Sandlund, O.T.; Museth, J.; Naesje, T.F.; Rognerud, S.; Saksgard, R.; Hesthagen, T.; Borgstrom, R. Habitat use and diet of sympatric Arctic charr (*Salvelinus alpinus*) and whitefish (*Coregonus lavaretus*) in five lakes in southern Norway: Not only interspecific population dominance? *Hydrobiologia* **2010**, *650*, 27–41. [[CrossRef](#)]
60. Ye, S.; Li, Z.; Lek-Ang, S.; Feng, G.; Lek, S.; Cao, W. Community structure of small fishes in a shallow macrophytic lake (Niushan Lake) along the middle reach of the Yangtze River, China. *Aquat. Living Resour.* **2006**, *19*, 349–359. [[CrossRef](#)]
61. Warfe, D.M.; Barmuta, L.A. Habitat structural complexity mediates the foraging success of multiple predator species. *Oecologia* **2004**, *141*, 171–178. [[CrossRef](#)] [[PubMed](#)]
62. Ba, W.; Du, P.; Liu, T.; Bao, A.; Chen, X.; Liu, J.; Qin, C. Impacts of climate change and agricultural activities on water quality in the Lower Kaidu River Basin, China. *J. Geogr. Sci.* **2020**, *30*, 164–176, (In Chinese with English abstract). [[CrossRef](#)]
63. Pushchin, I.; Kondrashev, S.; Kamenev, Y. Retinal ganglion cell topography and spatial resolution in the Japanese smelt *Hypomesus nipponensis* (McAllister, 1963). *J. Anat.* **2021**, *238*, 905–916. [[CrossRef](#)]
64. Fritsches, K.A.; Marshall, N.; Justin, W.E.J. Retinal specializations in the blue marlin: Eyes designed for sensitivity to low light levels. *Mar. Freshwater Res.* **2003**, *54*, 333–341. [[CrossRef](#)]

65. Mehner, T. Diel vertical migration of freshwater fishes—Proximate triggers, ultimate causes and research perspectives. *Freshwater Biol.* **2012**, *57*, 1342–1359. [[CrossRef](#)]
66. Andrzejaczek, S.; Gleiss, A.C.; Pattiaratchi, C.B.; Meekan, M.G. Patterns and drivers of vertical movements of the large fishes of the epipelagic. *Rev. Fish Biol. Fish.* **2019**, *29*, 335–354. [[CrossRef](#)]
67. Yang, T.; Sun, J.; Wang, Z.; Qiu, Z.; Du, L.; Zhang, P. Investigation on the habitats of the pond smelt in the Chaihe Reservoir. *Reserv. Fish.* **1998**, *6*, 31–32. (In Chinese)
68. Hilton, Z.; Wellenreuther, M.; Clements, K.D. Physiology underpins habitat partitioning in a sympatric sister-species pair of intertidal fishes. *Funct. Ecol.* **2008**, *22*, 1108–1117. [[CrossRef](#)]
69. Busch, S.; Kirillin, G.; Mehner, T. Plasticity in habitat use determines metabolic response of fish to global warming in stratified lakes. *Oecologia* **2012**, *170*, 275–287. [[CrossRef](#)] [[PubMed](#)]
70. Hayden, B.; Harrod, C.; Kahilainen, K.K. Lake morphometry and resource polymorphism determine niche segregation between cool- and cold-water adapted fish. *Ecology* **2014**, *95*, 538–552. [[CrossRef](#)]
71. Yamada, J. The normal developmental stages of the pond smelt, *Hypomesus olidus* (Pallas). *Bull. Fac. Fish. Hokkaido Univ.* **1963**, *14*, 121–126.
72. Hiroki, A. Early life ecology of Japanese smelt (*Hypomesus nipponensis*) in Lake Abashiri, a brackish water, eastern Hokkaido, Japan. *Sci. Rep. Hokkaido Fish. Exp. Stn.* **2004**, *67*, 1–79.
73. Kudo, T.; Mizuguchi, K. Growth of large and small forms of pond smelt *Hypomesus nipponensis* in Lake Kasumigaura, Japan. *Fish. Sci.* **2000**, *66*, 432–441. [[CrossRef](#)]
74. Chen, W.; Zhong, Z.; Dai, W.; Fan, Q.; He, S. Phylogeographic structure, cryptic speciation and demographic history of the sharp-belly (*Hemiculter leucisculus*), a freshwater habitat generalist from southern China. *BMC Evol. Biol.* **2017**, *17*, 216. [[CrossRef](#)] [[PubMed](#)]

Disclaimer/Publisher’s Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.