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RETRACTED: Distribution Pattern and Brood Parasitism Characteristics of an Endangered Fish, *Pseudopungtungia nigra*, in the Geum River Basin, South Korea

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Abstract: *Pseudopungtungia nigra* is an endangered fish species endemic to South Korea with a narrow habitat range in the Geum River basin. Understanding their long-term distribution (25 years, 1997–2021) and breeding characteristics can contribute to the conservation and habitat management of endangered species in this area. We analyzed long-term data on environmental factors and fish in the Geum River and investigated the invading and spawning characteristics of *P. nigra* using underwater cameras. From the study results, *P. nigra* indicated no clear dispersion or decline trend in the Geum River. *P. nigra* exhibits brood parasitic behavior in the nest of *Coreoperca herzi*, another species found in the same region. *C. herzi* males protect their nests during the spawning period, and the eggs spawned by *P. nigra* in the nests of *C. herzi* are also protected by *C. herzi*. This high dependency of *P. nigra* on *C. herzi* possibly contributed to its distribution range in the Geum River basin. Habitat changes caused by anthropogenic interventions during the study period did not significantly affect the distribution of *P. nigra*. The results indicate that the distribution pattern of *P. nigra* is influenced by the distribution of sympatric fish species rather than environmental changes.

Keywords: long-term monitoring; dispersion; spawn; habitat conservation; endangered fish; restoration

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1. Introduction

Disturbances and environmental changes occurring in freshwater ecosystems undermine the unique characteristics of habitats and affect the distribution of aquatic organisms [1,2]. Various freshwater ecosystem types (e.g., wetlands, streams, ponds, and reservoirs) are clearly distinguished by differences in chemical factors, including dissolved oxygen and pH, and physical factors, such as water flow, depth, and morphology [3,4]. Each freshwater ecosystem's unique habitat characteristics lead to the distribution of different biological communities. Freshwater ecosystems are not only narrower in area than other ecosystems (e.g., oceans, terrestrial ecosystems) but are also subjected to habitat fragmentation, making them highly heterogeneous and unique, and vulnerable to changes in the environment [5]. Thus, freshwater organisms are sensitive to environmental changes, and drastic environmental changes could lead to population decline or extinction [6].

Currently, South Korea has designated 27 species of fish as endangered and has established a management strategy to preserve their habitats. However, long-term monitoring of their distribution range and decline/proliferation trends or recent data have not been updated due to difficulties in securing populations or a lack of continuous research. Identifying endless distribution patterns for endangered species is expected to contribute to national policies for ensuring biodiversity and providing basic information on developing management plans to preserve their habitats. The upstream parts of the Geum River have undergone various artificial habitat changes, such as the construction of Yongdam Dam (1997) and the river maintenance project (2012). Fish species distributed in the upstream parts of rivers and streams are highly sensitive to water flow and habitat changes [7]. Fish species such as *Rhynchocypris kumgangensis*, *Gobiobotia brevibarba*, and *Moroco lagowskii* are

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rarely found in freshwater ecosystems outside of the upper reaches because they prefer high dissolved oxygen and rapid water flow as habitats [8]. Owing to these distribution characteristics, 21 of 27 endangered species currently designated in South Korea are fish species that live specifically in the upstream area [9]. This suggests that continuous environmental changes in upstream areas may lead to a decline in the population or extinction of fish species distributed in the upstream areas.

Pseudopungtungia nigra, the target species of this study, is a Korean endemic and endangered species found exclusively in the upper reaches of the Geum River basin [10]. As breeding in *P. nigra* is unique, their distribution range is minimal. Previous studies reported that the spawning of *P. nigra* is caused by brood parasitism in the nest of *Coreoperca herzi* [11]. The *C. herzi* male protects the nests during spawning to prevent their eggs from being consumed by other fish [11]. By adopting brood parasitic behavior, *P. nigra* prevents its eggs from being consumed by other fish and increases its hatching rate as the *C. herzi* male protects its eggs. Owing to the spawning characteristics of *P. nigra*, its distribution pattern in the Geum River basin is closely related to the distribution pattern of *C. herzi* [10,11]. *P. nigra*, designated as an endangered species in 2012, was rarely investigated or analyzed in 2012. Its ecological characteristics have not been investigated apart from its brood parasitic behavior. As *P. nigra* is not only sensitive to environmental changes of habitat but also highly dependent on *C. herzi*, it is expected that various environmental disturbances in the upstream area of the Geum River have affected their distribution range. The combined use of environmental variables and underwater camera data of sympathetic species in a species distribution evaluation framework from freshwater ecosystems can help in more precise data acquisition. This can contribute to creating reliable data in identifying species' annual distribution patterns by providing additional information about their relationship with other organisms, not just species observations.

In this study, we aimed to elucidate: (1) the long-term distribution pattern of *P. nigra* in relation to environmental variables in the Geum River basin for approximately 25 years (1997–2021) through previous data and field surveys, and (2) the brood parasitism characteristics of *P. nigra* concerning the spawning of *C. herzi*. We hypothesized that owing to various disturbances and environmental changes occurring in this region, the distribution range of *P. nigra* was gradually affected. It may have been affected directly or gradually by a host fish species (i.e., *C. herzi*). This study identified the distribution range of *P. nigra* through long-term monitoring (25 years, 1997–2021) in the Geum River basin in South Korea. *P. nigra* has been identified, and its diffusion/decrease trend has been studied in this region. In addition, to understand the distribution pattern of *P. nigra*, their spawning and breeding characteristics were investigated. These findings help update recent information on the distribution and spawning characteristics of *P. nigra* in the Geum River basin and contribute to establishing a management strategy for preserving *P. nigra* in the future.

2. Materials and Methods

2.1. Study Site

The Geum River is one of South Korea's five major river basins (Han, Nakdong, Geum, Yeongsan, and Seomjin Rivers) and has the third longest flow path (394.79 km). Most of the upstream sections of Geum River are adjacent to forest areas, where the water quality and landscape are good, while the middle and lower sections penetrate downtown areas such as Daejeon, Gongju, Buyeo, and Gunsan, where the excessive inflow of nutrient and eutrophication are frequent [12]. In addition, the upstream section of the Geum River has a steep slope, and the water flow is diverse as the meandering sections exist in various channels. About 33 endemic fish species are distributed in the area, including endangered species such as *P. nigra*, *Liobagrus obesus*, and *Gobiobotia brevibarba*. However, the upstream region of Geum River has undergone physical habitat changes due to the construction of Yongdam Dam in 2001 and the activities associated with the river maintenance project in 2012; moreover, human disturbances such as fishing, marsh snail collection, and other recreational activities continue to date. In particular, the direct modification of the waterfront or the creation of waterways as part of the river maintenance project led to a large-scale habitat change in the upper stream of the Geum River [13].

Additionally, due to the river maintenance project in 2012, three large dams (Sejongbo, Gongjubo, and Baekjebo) were newly constructed in the middle and lower sections after Daecheong Dam, resulting in little water flow in this section. The distribution pattern of the target species (*P. nigra*) in the Geum River basin could be identified based on previous research data. Previous studies suggested that *P. nigra* was distributed in Uncheon Stream and Mangyeong River, including the upper reaches of the Geum River [11]. Figure 1 shows the basin range of Geum River to identify the distribution of *P. nigra*.

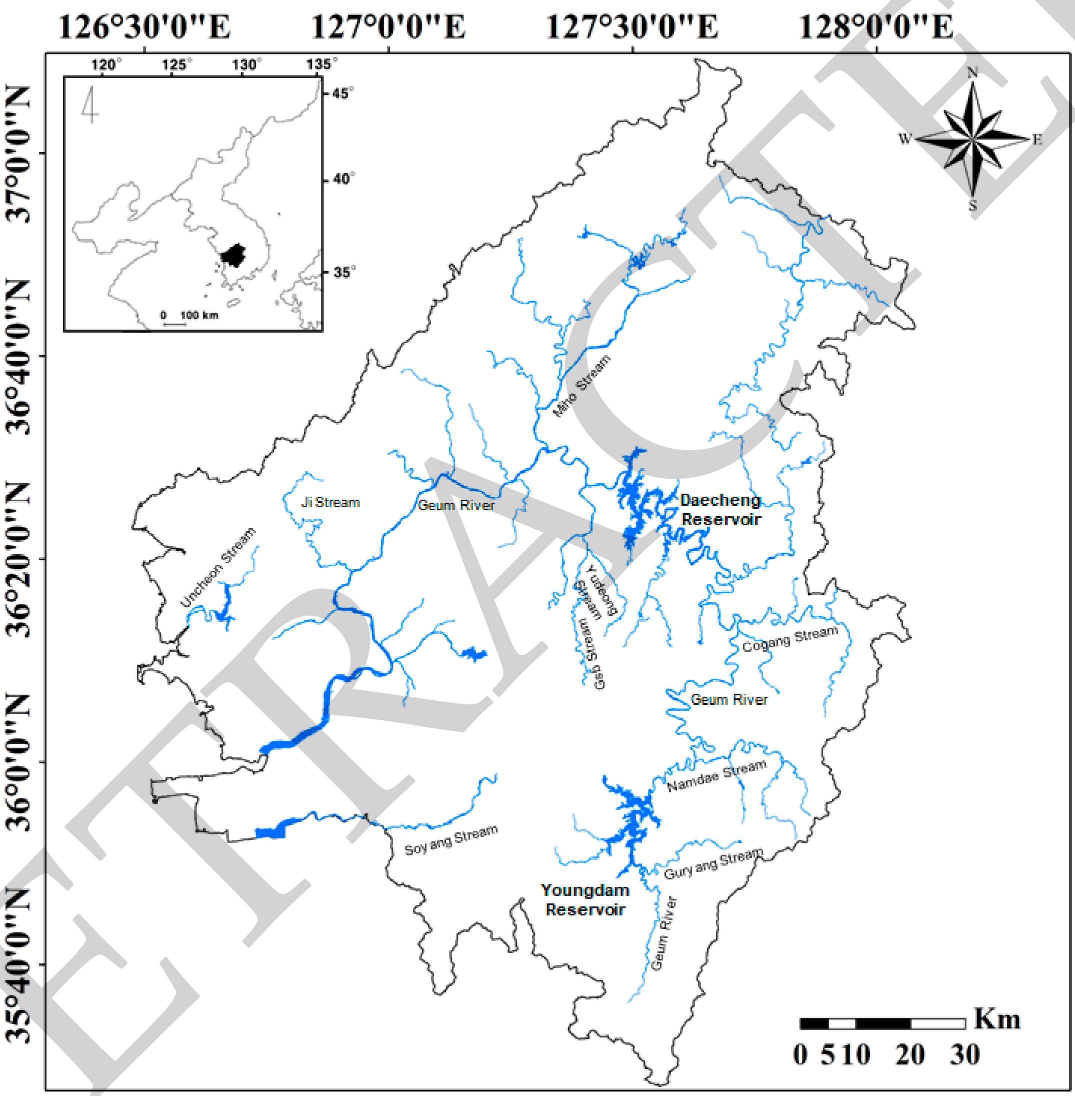

Figure 1. Map of the Geum River basin. The main river (Geum River), seven significant tributaries (Guyang, Namdae, Co, Gap, Yudeong, Miho, and Ji Streams), and two independent streams (Soyang and Uncheon Streams) constitute the study sites. The small map in the upper left corner shows the Korean peninsula.

2.2. Data Collection and Analysis

In Geum River basin, the distribution pattern of *P. nigra* was evaluated using fish data from the national ecosystem survey [14–17] and the stream/river ecosystem survey and health assessment [18]. All the study points identified in the distribution of *P. nigra* were extracted using previous data, which were further organized into a year-wise distribution pattern of *P. nigra*. Long-term distribution data of *P. nigra* spanning 25 years were retrieved, starting from the first record from the national ecosystem survey in 1997 to the last data in 2021. In this study, the survey period was divided into three sections based on the years where the distribution of *P. nigra* was newly identified: (1) 1997–2021, (2) 2011–2021, and (3) 2016–2021. To determine the environmental range in the distribution area of *P. nigra*, the data of eight environmental variables (water velocity, water temperature, dissolved oxygen, pH, conductivity, turbidity, total nitrogen, and total phosphorus) were obtained from WEIS (Water Environment Information System; https://water.nier.go.kr).

To explain the distribution pattern of *P. nigra*, their breeding characteristics were additionally investigated. The abundance and nest number of *C. herzi* were recorded based on previous reports, which indicated brood parasitism of *P. nigra* in the nest of *C. herzi* [10,11]. We investigated the abundance and nest number of *C. herzi* using snorkeling during the spawning period (April to July) of *C. herzi* for six years (2016~2021) in the upper reaches of Geum River. In addition, 10 nests of *C. herzi* were observed during the study period every year, and the invading and spawning rates of *P. nigra* were thus measured in a total of 60 nests. Underwater cameras were installed to observe the invading and spawning times of *P. nigra* in each nest of *C. herzi* for about 14 days during the spawning period of *C. herzi*, and the invading and spawning rates of *P. nigra* per day were determined using the recorded data. The invading (1) and spawning rates (2) were calculated as follows:

$$\text{Invading rate } (\%) = \frac{\text{No. of } C.\ herzi\ nests \text{ invaded by } P.nigra}{\text{60 nests of } C.\ herzi} \times 100 \quad (1)$$

$$\text{Spawning rate } (\%) = \frac{\text{No. of successful spawning of } P.nigra\ in\ C.\ herzi\ nest}{\text{No. of invading } P.\ nigra\ into\ the \text{ nest of } C.\ herzi} \times 100 \quad (2)$$

One-way analysis of variance (ANOVA) was used to examine the differences in eight environmental variables by year, an abundance of *C. herzi*, and the nest number of *C. herzi*. Tukey’s honestly significant difference (HSD) test was performed for additional post hoc comparison analysis to determine which of the differences were statistically significant. This statistical analysis method is suitable for identifying differences between values and has been addressed in various ecological studies. When applying statistical analysis, we used log-transformation to convert the data (i.e., eight environmental variables by year, an abundance of *C. herzi*, and the nest number of *C. herzi*). This measure minimizes differences in the range of values so as not to be hindered in identifying statistical differences. Statistical analyses were performed using SPSS ver. 20 (2011 release, IBM SPSS Statistics for Windows, Version 20.0. IBM Corp Armonk, NY, USA). Differences and relationships were considered significant at $p < 0.05$.

3. Results

3.1. Distribution Pattern of P. nigra

The distribution pattern of *P. nigra* remained the same for 25 years (1997–2021) in the upstream region of Geum River (Figure 2). During the study period (25 years, 1997–2021), *P. nigra* was consistently identified at 52 sampling points, mainly in the upper reaches of the Geum River (the section from Yongdam Dam to Daecheong Dam) and the main tributaries (Guryang Stream, Namdea Stream, Co Stream, Yudeung Stream, and Gab Stream) flowing into the region.

Of the 52 sampling points, 23 points were located in the main body of the Geum River, and the remaining 29 points were in the tributary streams. Since 2011, the distribution of *P. nigra* has been newly observed at five sampling points (indicated in orange or green in Figure 1), but the remaining points, except those in the Uncheon Stream, were adjacent to the existing *P. nigra* habitat and had high connectivity. In contrast, *P. nigra* was not observed in the main river section from Daecheong Dam to the estuary of the Geum River (the middle and lower reaches of Geum River) and the Jicheon Stream (e.g., Jicheon Stream, Mihocheon Stream, etc.) flowing into this section. Ultimately, in the Geum River basin, *P. nigra* was identified in 57 sampling points upstream of the Geum River.

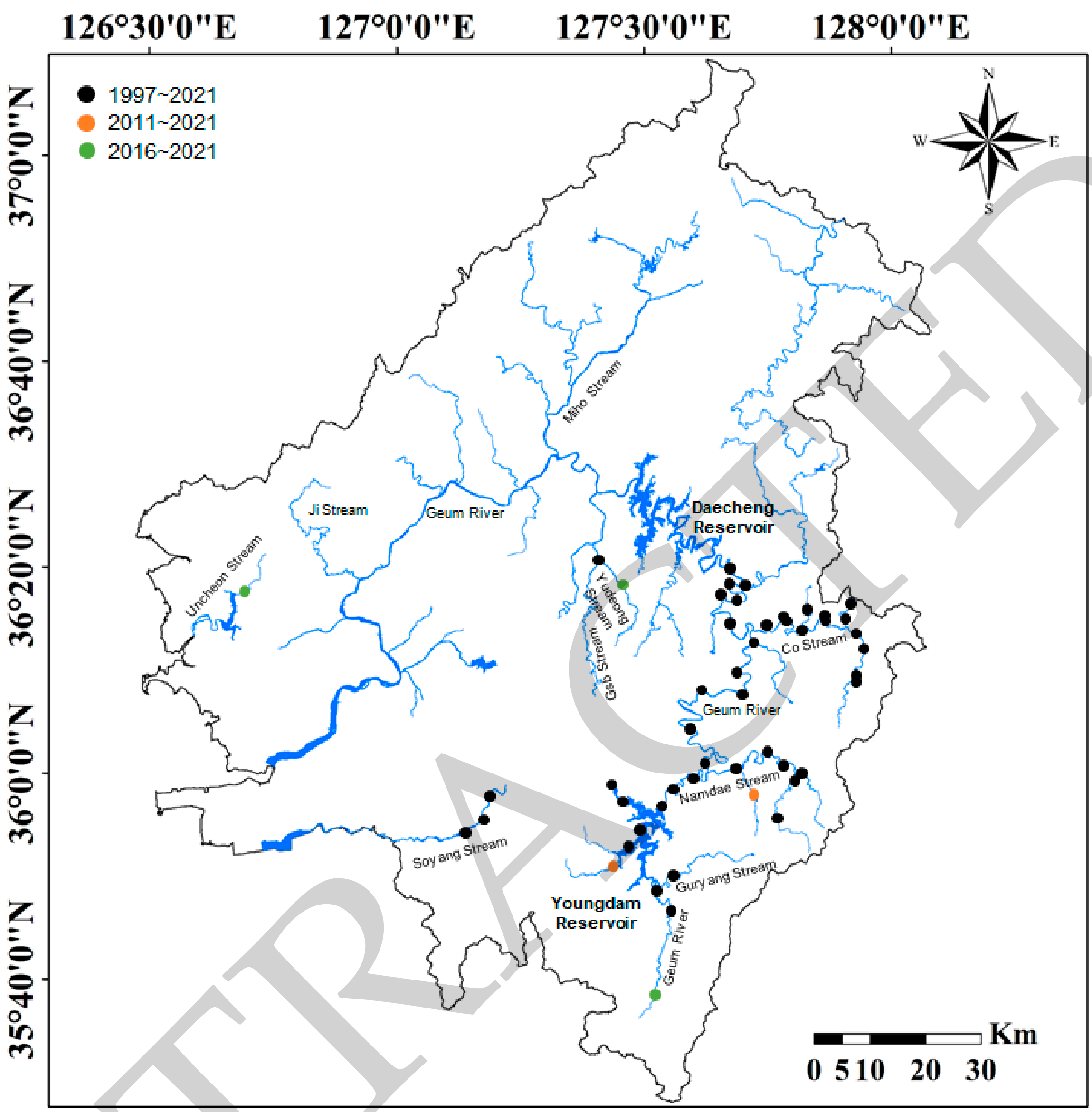

Figure 2. Distribution pattern of *Pseudopungtungia nigra* for 25 years in the Geum River basin. The study sites where *P. nigra* was observed indicated solid circles (black circles from 1997 to 2021, orange circles from 2011 to 2021, and green circles from 2016 to 2021). *P. nigra* was not found in the middle and lower reaches of the Geum River (the section after Daecheong Reservoir) and the two tributary streams (Ji Stream and Miho Stream).

About 7 to 22 fish species were distributed in the streams where *P. nigra* was observed (Table 1). Among them, *C. herzi* was found in all the distribution areas of *P. nigra*. However, each stream's distribution of the remaining fish species differed. Notably, *P. nigra* was absent in the Uncheon Stream from 1997 to 2017 but was observed for the first time in 2018.

Table 1. List of fish species in the Geum River basin during the study period (1997–2021). The circles and bars indicate the presence and absence of fish species, respectively.

Fish Species	Geum River [1]						Un [1]	So [1]
	M (*n* = 23)	Gur (*n* = 7)	Nam (*n* = 7)	Co (*n* = 14)	Yu (*n* = 1)	Gab (*n* = 1)	(*n* = 1)	(*n* = 3)
Cyprinidae								
Carassius auratus	O				O			
Rhodeus uyekii	O	O			O		O	O
Acheilognathus lanceolatus	O		O	O			O	O
Acheilognathus yamatsutae	O			O				O
Acheilognathus rhombeus	O		O					O
Pseudorasbora parva	O		O				O	O
Pseudopungtungia nigra	O	O	O	O	O	O	O	O
Pungtungia herzi	O	O	O	O	-	O	O	O
Coreoleuciscus splendidus	O	O				O		O
Squalidus gracilis majimae		O		O				O
Hemibarbus longirostris	O							
Rhynchocypris oxycephalus	O	O		O	O	O		O
Zacco koreanus	O	O	-	O	O	O	O	O
Zacco platypus	O	O	-	-	O	O	O	
Cobitidae								
Misgurnus anguillicaudatus	O					O	O	
Iksookimia koreensis	O	O					O	
Cobitis lutheri		O			O	O	O	
Centropomidae								
Coreoperca herzi	O	O	O	O	O	O		O
Coreoperca kawamebari	O							
Bagridae								
Pseudobagrus koreanus	O	O		O	O	O	O	O
Odontobutidae						O	O	O
Odontobutis interrupta	O	O						
Gobiidae								
Rhinogobius brunneus	O	O	O	O	O	O	O	O
Tridentiger brevispinis	O	O		O		O	O	O
Centrachidae								
Micropterus salmoides	O				O	O		

[1] M, main river; Gur, Guryang Stream; Nam, Namdea Stream; Co, Co Stream; Yu, Yudeong Stream; Gab, Gab Stream; Un, Uncheon Stream; So, Soyang Stream. *Pseudopungtungia nigra* was distributed in a total of 57 sampling points.

Figure 3 shows the range of eight environmental variables measured at the sampling points of *P. nigra*. Most distribution areas of *P. nigra* were located upstream, and the eight environmental variables were also supported by the typical characteristics of the upper reaches of rivers or streams. The average values of water velocity and dissolved oxygen (DO) were high at 1.24 m/s and 104.4%, respectively, and the maximum or minimum ranges were relatively narrow at 0.6 to 1.75 m/s and 94.2% to 105.4%, respectively. In contrast, the mean conductivity (98 µS/cm), turbidity (1.24 NTU), total nitrogen (1.28 mg/L), and total phosphorus (0.024 µg/L) were relatively low values, and the range of these variables was also narrow. In addition, since 2011, there has been little annual difference in each of the 8 environmental variables at 52 sampling points, except for the 5 newly observed points (Table 2).

3.2. *P. nigra as a Brood Parasite of C. herzi*

In an additional field survey, the abundance and nest numbers of *C. herzi* were continuously observed for six years (2016–2021) in the upper reaches of the Geum River (Figure 4). Here, 18 to 35 individuals of *C. herzi* were collected yearly, and the corresponding nest numbers were 8 to 17 each year. In the nests of *C. herzi*, the invading and spawning frequency (%) of *P. nigra* was 80% to 94% annually, and *P. nigra* eggs were not found anywhere else other than inside the *C. herzi* nest.

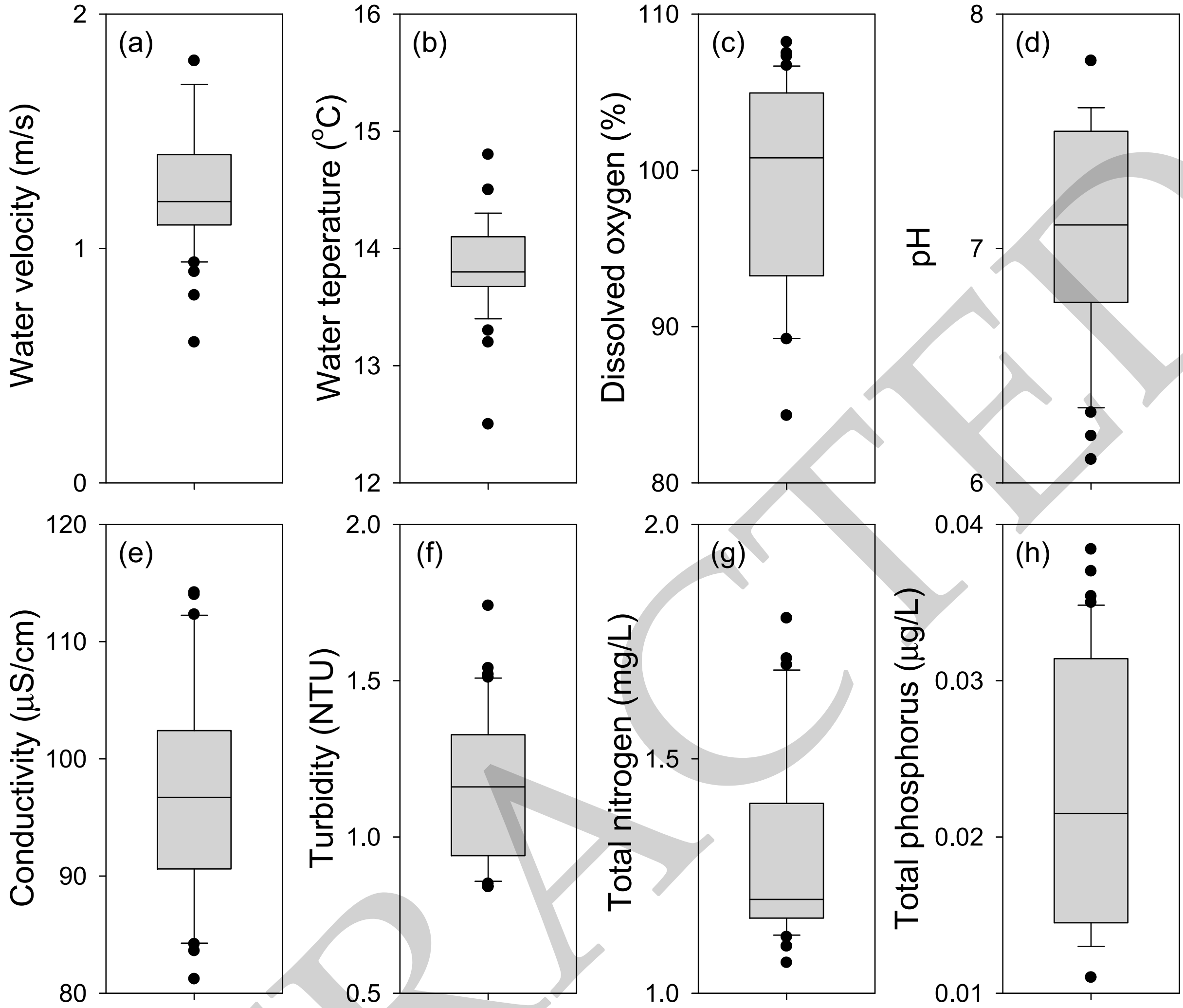

Figure 3. Range of 8 environmental variables, as measured in 52 sampling points, indicates the occurrence of *Pseudopungtungia nigra* during the study period (1997~2021). (**a**) Water velocity, (**b**) water temperature, (**c**) dissolved oxygen, (**d**) pH, (**e**) conductivity, (**f**) turbidity, (**g**) total nitrogen, and (**h**) total phosphorus. In the boxplots, the horizontal line in each box indicates the median, the lower and upper hinges represent the 1st and 3rd quartiles, the extremes of the whiskers indicate the most extreme data points within 1.5× the interquartile range, and the black circles represent outliers.

Table 2. One-way ANOVA comparing an annual difference (25 years) of 8 environmental variables in the distribution areas of *Pseudopungtungia nigra* during the study period (1997~2021). df, degrees of freedom; F, F-statistic.

Variables	df	F	*p*-Value
Water velocity (m/s)	23	0.437	0.652
Water temperature (°C)	23	0.352	0.707
Dissolved oxygen (%)	23	1.681	0.208
pH	23	1.420	0.263
Conductivity (µS/cm)	23	1.417	0.263
Turbidity (NTU)	23	1.962	0.163
Total nitrogen (mg/L)	23	0.921	0.318
Total phosphorus (µg/L)	23	2.212	0.134

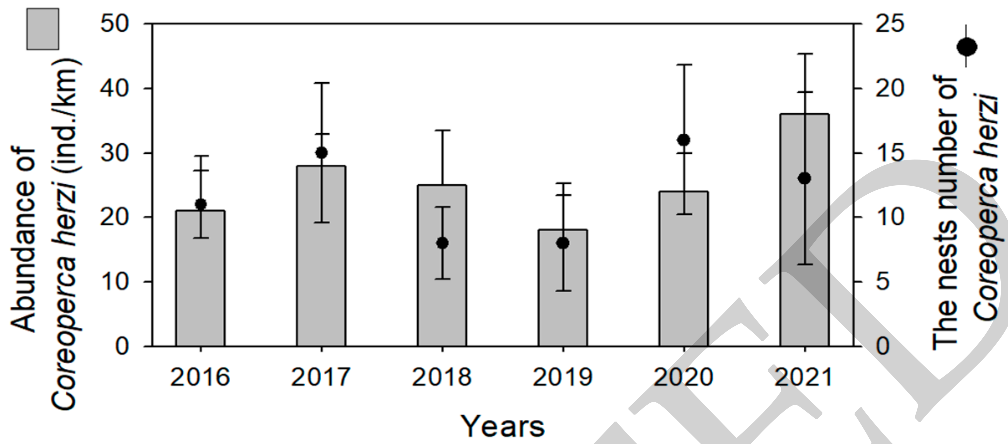

Figure 4. Abundance and number of nests of *Coreoperca herzi* identified during a six-year survey (2016~2021) in the upper reaches of Geum River. In the figure representing the nest number of *C. herzi*, the black dot represents the average value, and the black vertical line represents the average range.

The invading and spawning frequency (%) of *P. nigra* was the highest during 1–2 days after *C. herzi* nest formation (i.e., after the first spawning of *C. herzi* females), which was observed in all 60 nests of *C. herzi*, and a gradual reduction in invading and spawning frequency was observed after 3 days (Figure 5). The mean % invasion of *C. herzi* nests by *P. nigra* was 84%, and *P. nigra* ceased to invade the *C. herzi* nest from the seventh day. Of the 60 nests of *C. herzi*, 9 were abandoned from the nest protection by the *C. herzi* males. The *C. herzi* males abandoned the nests 2–3 days after nest formation, and the eggs of the *C. herzi* and *P. nigra* spawned in the abandoned nests failed to hatch. In the remaining 51 nests, the eggs of *P. nigra* began to hatch 8 days after the nest formation, and the maximum number of eggs hatched 10 days after the nest formation.

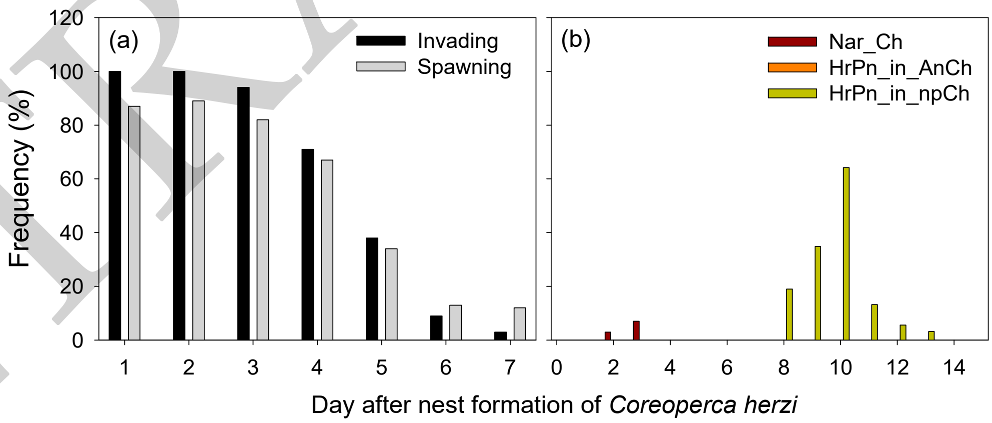

Figure 5. Invading, spawning, and hatching rates of *Pseudopungrungia nigra* from the day after the first spawning rate of *Coreoperca herzi* in the upper reaches of Geum River. (**a**) Invading and spawning frequency of *P. nigra*, (**b**) nest abandonment rate (%) of *Coreoperca herzi* (Nar_Ch), hatching rate of *P. nigra* in the nests abandoned by *Coreoperca herzi* (HrPn_in_anCh), and hatching rate of *P. nigra* in the nests protected by *Coreoperca herzi* (HrPn_in_npCh).

In the Uncheon Stream, *P. nigra* did not occur until 2017, but continuous distribution has been observed since 2018 (Figure 6). An average of four to seven *P. nigra* have been collected annually, but *C. herzi* was not detected during the survey period. In the Uncheon Stream, the nests of *P. nigra* were found in rocks and gravel. We found 7 to 13 nests of *P. nigra* in this region per year.

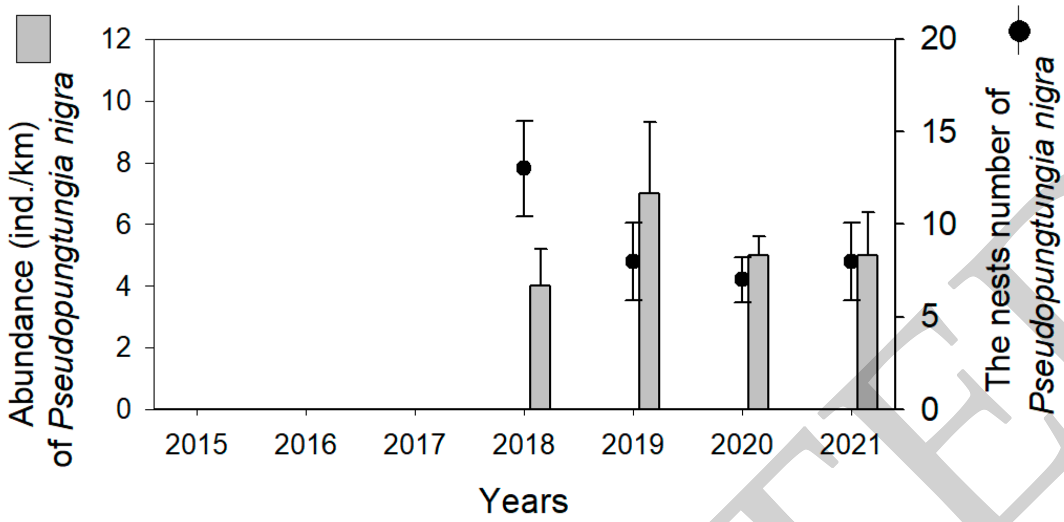

Figure 6. Abundance (individuals/km) and the number of nests of *Coreoperca herzi* and *Pseudopungtungia nigra* in Uncheon Stream.

4. Discussion

In this study, we found that the distribution of *P. nigra* remained largely the same in the Geum River basin for 25 years (1997–2021). Since 2011, *P. nigra* has occurred at five new distribution points, most of which are adjacent to or connected to existing distribution regions (see Figure 2). Thus, *P. nigra* can move from its current distribution region to newly observed regions. However, it is difficult to determine if the discovery of *P. nigra* at these points indicates a gradual spread of the distribution of *P. nigra* in the Geum River basin. Empirical studies reported that the distribution region of *P. nigra* is Mangyeong River and Uncheon Stream, including the upstream parts of the Geum River [10,11], supporting the distribution pattern of *P. nigra* in this study. *P. nigra* prefers upstream areas of rivers and streams where the riverbed is covered mainly by gravel, and the water flow is rapid [7,10]. These regions are characteristic of "fast velocity," "bottom diversity" (bottom coverage from boulder to gravel), and "high dissolved oxygen," which are conditions that favor the distribution of *P. nigra*. Despite the various anthropogenic disturbances, such as the construction of Yongdam Dam, river maintenance projects, fishing, and marsh snail collection, that occurred in this area, the continuous distribution of *P. nigra* indicates that the range of physical and chemical environmental variables did not influence the presence of *P. nigra* for 25 years. We confirmed that the year-wise differences between the eight environmental variables were insignificant in the distribution of *P. nigra* (see Table 2). The long-term maintenance of the habitat environment can be estimated as a result of the efforts to secure water sources and protect various endangered species in this area. In the Geum River's upper part, different endangered and endemic species, including *Hemibarbus mylodon* and *Coreoperca kawamebari*, are distributed; thus, the conservation value is very high. The Ministry of Environment, South Korea, had identified and protected *P. nigra* as a 'Specific Wild Fauna and Flora (1996)' and an 'Endangered Species (2005)'. However, as *P. nigra* is not found in other river basins, the current efforts to preserve and maintain *P. nigra* in the Geum River need to be continued.

Previous studies suggested that the reproduction of *P. nigra* occurs by brood parasitism in the nest of *C. herzi* [10]. In spring (May–June), *C. herzi* spawns on rocks or gravel under low water flow and forms a nest, and *P. nigra* invades the nest of *C. herzi* and spawns around the eggs of *C. herzi* [10,19]. Despite the threat of being predated by *C. herzi*, *P. nigra* infiltrates and spawns into the nest of *C. herzi* because the males of *C. herzi* tend to protect the nest [19]. The incubation period of *C. herzi* eggs is approximately 13–14 days after spawning, during which the *C. herzi* male protects the nest [19]. Although it is challenging for *P. nigra* to enter the nest protected by the *C. herzi* male, the eggs of a successful spawning are protected along with *C. herzi* eggs by *C. herzi* males, thereby increasing the chance of success in hatching. The aggressive *C. herzi* nest-invading efficiency of *P. nigra* is interpreted as a way to secure a sufficient period to protect its eggs. This is to match *C. herzi* eggs, which have an incubation period of 14 days, while *P. nigra* eggs have an incubation period of 9 to 10 days. Once the eggs of *C. herzi* hatch, the *C. herzi* males no longer protect their nests; therefore, if the eggs of *P. nigra* remain after 14 days, they could be consumed as food by other fish (e.g., *Nipponocypris temminckii* and *Odontobutis platycephala*). The invasion and spawning of *P. nigra* in *C. herzi* nests were observed in the upper reaches of Geum River. As *C. herzi* males rarely removed or consumed the eggs of *P. nigra*, these eggs that succeeded in invading and spawning into *C. herzi* nests at the start of the breeding season enjoy the benefit of "protection by *C. herzi* males." This advantage of the benefit can be much higher than the damage caused during the insertion into the nest of *C. herzi*. As the eggs of *P. nigra* spawned in the nest of *C. herzi* have little effect on the hatching rate of *C. herzi* eggs, *C. herzi* males do not react (e.g., remove or attack) to the eggs of *P. nigra* that have already been spawned in the nest.

This breeding strategy, called 'Brood parasitism', found in approximately 1% of birds in the biota worldwide (109 species, including cuckoos [20]), has not been reported or studied in other biological communities. Empirical studies on coevolutionary interactions between parasitic and host birds provide extensive information on singularity and sophistication [21–23]. The primary focus of this interaction is that host birds have evolved various defense mechanisms to resist brood parasitism, while parasites have responded with strategies such as enhancing the mimicry of eggs to prevent the host from resisting brood parasitism [24]. Parasitic behavior in non-bird biological communities is found in the cuckoo catfish *Synodontis multipunctatus* Boulenger 1898 (Siluriformes, Mochokidae) distributed in Lake Tancania, Africa. The reproduction of the cuckoo catfish depends on the Mouthbrooding cichlid fish that coexist in Lake Tanganyika [25]. The cichlid female collects the eggs that she spawns in her mouth and then collects sperm on the male's anal fin to fertilize the eggs in her mouth. The eggs hatch in the mother's buccal cavity and are stored for two to three weeks until the embryonic yolk sac is depleted. The cuckoo catfish is parasitic in the cichlid's mouth by inducing the female cichlid to pick up her eggs incorrectly [25,26]. The catfish's eggs hatch before the cichlid's eggs and then consume the cichlid's eggs as food. Meanwhile, most of the cichlid eggs are removed by the offspring of the parasitic catfish, and eventually, the female cichlid releases only the progeny of the parasitic cuckoo catfish. As this is the only brood parasitism strategy in empirical studies, breeding by parasitism in the fish group is rare.

We speculated that the case of *P. nigra* is a relatively stable breeding strategy compared to the brood parasitism of the cuckoo catfish. The breeding strategies adopted are the same regarding host fish dependency but differ significantly in terms of damage to the host and energy loss. The cuckoo catfish's offspring damages the cichlid's population growth by consuming the cichlid's eggs as food in the buccal cavity of the cichlid female [27]. In contrast, *P. nigra* relies only on the protection of the nest by the male *C. herzi* and has little effect on the eggs and offspring of *C. herzi*. Such differences can accelerate evolution in terms of host fish resistance. As reproduction and population growth are instinctive and basic demands for biota programmed in genes, strategic practices that resist or defend can occur quickly when disturbed. If the cichlid continues to be involved in brood parasitism of the cuckoo catfish, the cichlid's population growth will likely be reduced or endangered.

Conversely, if the cichlid's defense strategy to resist the brood parasitism of the cuckoo catfish is newly employed, a population reduction of cuckoo catfish is expected. Among the two biological communities, the biological interaction, which causes damage to the other and craves only its own interests, changes the previous relationship due to the resistance of the negatively affected organism. Naturally, in this case, the 'Evolutionary Arms Race' [28] is bound to accelerate, and such energy consumption ends when one side abandons or becomes extinct. In this respect, this host–parasite relationship is expected to last for a considerable period, given that in the case of *P. nigra*, it does not cause damage to the host fish (i.e., *C. herzi*). In addition, the potential distribution and brood parasitism of *P. nigra* in the study area are likely to be greatly influenced by biological factors such as feeding, competitors, diet, and feeding habits of adolescents and *C. herzi* adults. Nonetheless, such information has been insufficiently secured to date, and further investigations and experiments are needed to determine the distribution pattern and brood parasitism of *P. nigra* in the future. This study is the first international report on the interrelationship between *P. nigra* and *C. herzi*.

We assumed that *P. nigra* eggs not protected by *C. herzi* males would fail to hatch. In this study, the abandoned eggs of *C. herzi* and *P. nigra* were consumed by other fish (e.g., *Pungtungia herzi*, *N. temminckii,* and *O. platycephala*) or failed to hatch. Therefore, the possibility that not all *P. nigra* eggs that spawned in spaces other than the nest of *C. herzi* are consumed by other fish can be ruled out, mainly because *P. nigra* eggs were not observed in spaces other than *C. herzi* nests. Although more detailed investigations can demonstrate this possibility, it should be noted that *P. nigra* cannot reproduce independently in the Geum River basin without *C. herzi*. If there is a change in nest protection strategy by *C. herzi* males or a change in the response of *C. herzi* males to *P. nigra* eggs, it would be a challenge for *P. nigra* to increase its population in the Geum River basin. The long-term distribution (25 years) of *P. nigra* in the Geum River basin indicates that the habitat is also suitable for the population growth of *C. herzi*. In addition, these results can be associated with the absence of *P. nigra* distribution in other river basins. Therefore, future studies should compare the breeding behavior of *C. herzi* in the Geum River by collecting information on the breeding behavior of *C. herzi* in river basins other than the Geum River.

In Uncheon Stream, where *P. nigra* appeared in 2018, the results need to be interpreted differently because *C. herzi* is absent in this region. Owing to the high dependence of *P. nigra* on *C. herzi* in the upper reaches of the Geum River, the absence of *C. herzi* in Uncheon Stream questions the breeding strategy of *P. nigra*. Although it is yet to be established, this study assumed that *P. nigra*, which has newly begun to be distributed in the Uncheon Stream, is a hybrid. In this region, *P. herzi* was observed frequently along with *P. nigra*. Hence, it is possible that interbreeding occurred between these two species. In Uncheon Stream, the fact that the eggs of *P. nigra* were observed in rocks or gravel in addition to the nest of *C. herzi* indicates that *P. nigra* distributed in this area is less dependent on *C. herzi*. Before the annihilation of *P. nigra* in the Uncheon Stream, Kim et al. [29] suggested that cross-species of *P. nigra* and *P. herzi* were found in this region. These observations were made before the extinction of *P. nigra* in Uncheon Stream; however, the absence of *C. herzi* in this area cannot rule out the possibility of the emergence of *P. nigra* hybrid species. *Pseudopungtungia nigra* can reproduce even in the absence of *C. herzi* because *P. nigra* does not depend on the nest of *C. herzi* for breeding. To verify these hypotheses, it is necessary to analyze the likelihood of hybridization of *P. nigra* distributed in this region through genetic analysis. The *P. nigra* newly distributed in Uncheo Stream are estimated to be some of the individuals released in 2012.

5. Conclusions

The long-term distribution of *P. nigra* in the Geum River basin is attributed to brood parasitism permission of the host fish species (i.e., *C. herzi*) on *P. nigra* rather than physical and chemical environmental factors. However, owing to the high dependency of *P. nigra* on *C. herzi*, *P. nigra* is likely to become extinct in the event of a change in breeding behavior (e.g., increased vigilance against invading and spawning, and removal of *P. nigra* eggs by *C. herzi* males) or the absence of *C. herzi* (e.g., migration). Thus, there is a possibility that in the future, in South Korea, the insipid fish that is independent of the newly observed *P. nigra*, which is not dependent on *C. herzi,* in the Uncheon Stream basin will spread wider than *P. nigra* that is reliant on *C. herzi* in the Geum River. Therefore, it is necessary to additionally investigate the spawning characteristics of *P. nigra* distributed in the Uncheon Stream basin.

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