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Effect of the Human Utilization of Northern Snakehead (*Channa argus* Cantor, 1842) on the Settlement of Exotic Fish and Cladoceran Community Structure

Jong-Yun Choi * and Seong-Ki Kim

National Institute of Ecology, Seo-Cheon Gun 325-813, Chungcheongnam Province 1210, Korea; skkim@nie.re.kr
* Correspondence: jyc311@naver.com; Tel.: +82-41-950-5473

Abstract: Empirical studies suggest that changes in the density of top predators, such as carnivorous fish, in freshwater food webs, strongly affect not only fish communities but also various primary and secondary consumers. Based on these findings, we explored how differences in the utilization of carnivorous fish (i.e., Northern Snakehead, *Channa argus*) by humans affected the fish and cladoceran community structure as well as the settlement of exotic fish species (i.e., *Lepomis macrochirus* and *Micropterus salmoides*) in 30 wetlands located in the upper and lower reaches of the Nakdong River. Our results show that in the mid–lower reaches of the Nakdong River, the density of *C. argus* was low, while high densities of *L. macrochirus* and *M. salmoides* were observed. Exotic fish species are frequently consumed by *C. argus*, leading to a low density of *L. macrochirus* and *M. salmoides* in the upper reaches, which supported a high density of *C. argus*. However, in the mid–lower reaches, the density of *L. macrochirus* was high because of the frequent collection of *C. argus* by fishing activities. The dominance of *L. macrochirus* significantly changed the structure of cladoceran communities. *L. macrochirus* mainly feeds on pelagic species, increasing the density of epiphytic species in the mid–lower reaches. The continued utilization of *C. argus* by humans induced a stable settlement of exotic fish species and strongly affected the community structures of primary consumers in the 30 wetlands. The frequency of *C. argus* collection has to be reduced to secure biodiversity in the mid–lower reaches of the Nakdong River, which will reduce the proportion of exotic fish species and increase the conservation of native fish.

Keywords: human disturbance; freshwater food web; habitat heterogeneity; piscivorous fish; epiphytic cladoceran; biodiversity

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1. Introduction

Local food webs are determined by interactions between prey and predators [1,2]. Predators can drastically reduce the abundance of prey, sometimes contributing to their local extinction [3], and the prey develop defensive mechanisms based on morphological changes or behavioral responses to avoid predators [4,5]. A relatively fast evolution of predators or prey (e.g., efficient foraging strategies of predators or efficient defense mechanisms of prey) can break the balance of the local food web. Diverse interactions occur between predator and prey after a long "evolutionary arms race" [6], leading to the construction of a stable food web. Frequent encounters between predators and prey in a habitat increase the number of interactions, which can lead to the depletion or reduction of their densities [7,8]. In particular, the number of encounters between species or populations in freshwater ecosystems, such as streams, wetlands, and ponds, is relatively high because the spatial range is narrower than in other ecosystems (terrestrial and oceanographic ecosystems) [9]. Therefore, variations in population due to the introduction and settlement of animals in this region may break stable interrelationships [10], which strongly influences the spatiotemporal distribution of animals. Thus, interactions, such as predation, are

important factors in empirical studies on the biological distribution and species diversity in freshwater ecosystems [11,12].

The recent influx of exotic species due to climate change and the active exchange between various countries have greatly contributed to the change in freshwater food webs [13]. The stable settlement of biological groups belonging to the lower stage of the freshwater food web (primary or secondary consumers) is difficult or time-consuming because they must be considered both predators and food sources. In contrast, top predators in the upper stages of the food web tend to settle relatively quickly in a new area because of the absence of predators [14]. In particular, the foraging activities of fish communities, as the top predators in the freshwater food web, are strong and continuous and, thus, their introduction and changes in their community structures negatively affect prey groups such as zooplankton and invertebrates [15,16]. Bunnell et al. [17] suggested that interannual changes in the fish community at Huron Lake, USA, led to low densities of cladoceran and cyclopoid copepods and a low abundance of calanoid copepods. Furthermore, Choi et al. [18] reported that strong foraging activities of fish in freshwater wetlands increase the utilization of aquatic macrophytes by *Diaphanosoma brachyrum*. Areas densely covered with various types of aquatic macrophytes (e.g., free floating, floating leaved, and submerged macrophytes) provide prey groups, such as zooplankton and invertebrates, a complex habitat structure, and a refuge to avoid fish predation [19,20].

Changes in the fish community affect both inter- and intra-community interactions. Because exotic fish species that successfully settled in a certain area either consume native fish species or are stronger in food competition, they have a strong impact on the species composition and dominance of fish populations [21,22]. The results of an empirical study showed that the cichlid community in Lake Victoria has abruptly been reduced by an exotic Nile tilapia (*Oreochromis niloticus*), which was introduced by humans [23]. In addition, ten species of native fish in 14 waterways of the lowland backwaters of the Po River in northeastern Italy have locally gone extinct due to eight exotic fish species that settled in 1991 [24]. Ecosystem disturbance due to the introduction of exotic fish species can also be frequently observed in South Korea. In the 1970s, South Korea released exotic fish species, including *Lepomis macrochirus* and *Micropterus salmoides*, to rivers, wetlands, and reservoirs to promote species diversity in fish communities. These two species of exotic fish have continued to spread and are frequently observed in the whole country [25]. The predatory role of *L. macrochirus* and *M. salmoides* causes a low biodiversity of native prey communities [26,27]. In particular, the freshwater ecosystems of South Korea are supported by a relatively low water flow, a high abundance of aquatic macrophytes, and the continued spread of *L. macrochirus*, which prefers such habitats and causes various disturbances [28]. The reduction of biodiversity or a simplified food web structure are caused by the introduction of exotic fish species such as *L. macrochirus*.

The successful settlement of *L. macrochirus* in South Korea's wetlands is partly due to appropriate habitat environments (e.g., high coverage with aquatic macrophytes), but the main factor affecting the settlement is the absence of predators. The results of previous studies suggested that it is difficult for *L. macrochirus* to become dominant because it is frequently consumed by piscivorous fish, such as northern pike, *Esox lucius* [29,30], but the intermittent distribution of carnivorous fish (i.e., *Channa argus*) in South Korea insignificantly contributes to the settlement of *L. macrochirus* [31]. Although *C. argus* is almost the only predator of *L. macrochirus* in South Korea, its distribution is extremely limited. This "predator absence" largely contributes to the stable settlement of exotic fish species [32,33] and is an important factor changing the balance among existing interactions based on the trophic cascade of prey groups within the freshwater food web.

Therefore, we focused on the different utilization of *C. argus* by humans in different South Korean regions in this study. In the wetlands in the mid–lower reaches of the Nakdong River, the utilization of *C. argus* by humans is common, whereas it is barely collected in the upper reaches. We assume that this difference in the use of *C. argus* by humans affects the abundance of this species in wetlands and reservoirs and leads to

changes in the cladoceran community used as food for fish as well as the introduction and stable settlement of exotic fish species (*L. macrochirus*). The influence of *C. argus* on the introduction and settlement of exotic fish species plays an important role in forming a stable food web and securing biodiversity in the freshwater ecosystem, but there is a lack of studies related to this topic. The aims of this study were to elucidate (1) changes in the structure of the fish community based on environmental variations, (2) the effect of the spatial distribution and food preference of *C. argus*, and (3) the response of the structure of the cladoceran community to exotic fish species (*L. macrochirus*). We predict that fishing of *C. argus* by humans accelerates the stable settlement of exotic species and leads to changes in the cluster structure of crustaceans. To test this hypothesis, we evaluated the (1) effect of the presence of *C. argus* on the distribution of exotic fish species, (2) the microhabitat utilization and food consumption of *C. argus*, and (3) effects of changes of dominant cladoceran species on the distribution of exotic fish.

2. Materials and Methods

2.1. Study Area

The freshwater ecosystem in South Korea is dominated by five large river catchments (Nakdong, Han, Geum, Yeongsan, and Seomjin rivers). The catchment patterns directly or indirectly affect small streams and various lentic ecosystems, such as wetlands and reservoirs. The catchment area of the Nakdong River Basin is the largest (drainage area, 23,384.21 km^2; Figure 1), and most of the surrounding areas are covered by soil with a poor drainage capacity, which is conducive for the formation of wetlands. In the past, the river basin contained numerous wetlands, but they have mostly disappeared due to anthropogenic activities, such as the construction of farmland, expansion of residential areas, embankments, and road construction [34]. Currently, 146 wetlands or reservoirs can be found in the area and most of them are densely covered with aquatic macrophytes, such as *Phragmites australis*, *Paspalum distichum*, *Salvinia natans*, and *Trapa japonica*, from spring (May) to autumn (November) [35].

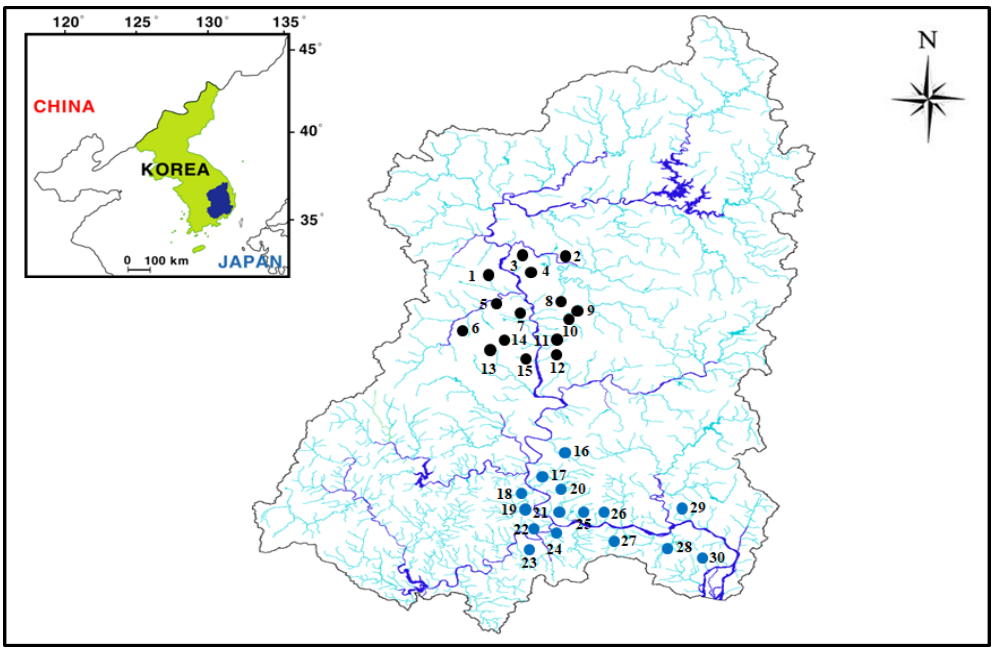


Figure 1. Map showing the 30 wetlands located in southeastern South Korea. The wetlands are shown as solid circles (●). The small map in the upper left corner indicates the Korean Peninsula. Sites 1 through 15 are in the upper reaches of the Nakdong River (black circles) and sites 16 through 30 are in the mid–lower reaches (blue circles).

A large city (Daegu Metropolitan City) in the mid-reaches divides the Nakdong River Basin into upstream and downstream areas. In Changnyeong-gun, Uiryeong-gun, Miryang-si, and Gimhae-si, which belong to the mid–lower reaches of the Nakdong River, unique cultures of *C. argus* can be observed. Local residents collect *C. argus* from wetlands and reservoirs in the mid–lower reaches of the Nakdong River and use it as food or restorative (traditional medicine). In contrast, in most parts of South Korea, including the upper reaches of the Nakdong River, *C. argus* is rarely used by humans. Although the effect of *C. argus* on humans has yet to be verified, people living in the mid–lower reaches of the Nakdong River have long recognized that *C. argus* is effective as restorative. Currently, *C. argus* is frequently collected by humans in this area. We selected 30 wetlands in the upper and mid–lower reaches of the Nakdong River in this study to determine the effects of human-induced fish collection (*C. argus*) on various biological groups, including fish (Figure 1). Among the wetlands, 15 are located in the upper reaches of the Nakdong River and the remaining 15 are distributed in the mid–lower reaches. Table 1 summarizes the main morphometric and limnological characteristics of the wetlands. These wetlands contain areas covered with aquatic macrophytes as well as open areas (at a similar rate). Very shallow wetlands with water surfaces that are almost completely covered with aquatic macrophytes were excluded from this study. The wetlands have similar sizes (mean ± standard deviation: 155,845 ± 8516 m^2) and their main water sources are streams or drainageways. The water depth is very shallow (below 5 m) and the average residence time is short (annual average of 0.5 year or less). We selected three sampling points in each wetland and investigated the fish community and environmental variables at each sampling point.

Table 1. Morphometric and limnological characteristics of the 30 wetlands. Fluctuation refers to the annual water level fluctuation (values >1 m are regulated).

No.	Main Water Source	Altitude (m)	Area (m^2)	Fluctuation (m)	Mean Depth (m)	Maximum Depth (m)	Mean Residence Time (Year)
1	Stream	11.6	26,400	2.8	3.1	3.8	0.22
2	Drainageway	6.6	7800	<1	2.8	3.1	0.32
3	Stream	16.4	13,700	2.5	2.7	2.9	0.31
4	Stream	18.2	20,400	<1	4.1	4.6	0.16
5	Rainfall/ground	27.4	17,600	<1	2.4	2.7	0.36
6	Rainfall/ground	23.2	6700	<1	0.8	1.1	0.21
7	Drainageway	14.5	31,600	<1	1.6	2.0	0.12
8	Stream	12.8	13,600	1.7	3.4	3.6	0.21
9	Stream	16.5	15,900	1.1	2.8	3.2	0.15
10	Rainfall/ground	9.2	22,600	<1	1.2	1.8	0.43
11	Drainageway	11.8	25,600	<1	0.7	1.6	0.41
12	Stream	20.7	4000	3.4	2.3	3.1	0.31
13	Stream	17.6	27,600	2.8	1.1	1.6	0.22
14	Rainfall/ground	26.7	250,000	<1	0.8	1.4	0.42
15	Stream	24.3	137,957	1.7	1.8	2.2	0.18
16	Stream	30.5	109,000	2.5	1.6	2.1	0.11
17	Drainageway	23.4	51,000	1.2	1.3	1.6	0.44
18	Stream	18.2	24,680	1.8	1.7	2.0	0.26
19	Rainfall/ground	26.1	84,140	<1	1.2	1.8	0.41
20	Stream	20.7	51,700	<1	2.3	3.0	0.48
21	Stream	24.7	67,100	2.4	2.4	2.8	0.20
22	Stream	16.2	75,000	<1	0.8	1.4	0.41
23	Rainfall/ground	21.8	69,400	2.8	0.7	1.2	0.28
24	Drainageway	14.7	102,000	1.4	1.3	1.6	0.34
25	Stream	20.8	84,180	2.5	1.2	1.7	0.27
26	Rainfall/ground	12.8	98,483	<1	1.8	2.4	0.31
27	Stream	17.2	68,200	<1	2.0	2.8	0.27
28	Drainageway	20.7	49,000	1.8	1.7	2.4	0.34
29	Stream	24.1	64,570	1.2	1.4	2.3	0.29
30	Stream	24.7	117,957	1.4	2.3	2.7	0.37

2.2. Monitoring Strategy

We monitored the study sites in spring (May 2013) and autumn (October 2013) to compare the environmental parameters and distribution of aquatic animals (fish and cladocerans) between the upper and mid–lower reaches of the Nakdong River. Environmental variables (i.e., water temperature; dissolved oxygen, DO; pH; conductivity; turbidity; total nitrate, TN; and total phosphorus, TP) were measured using water samples collected from each of the study sites. A YSI DO meter (Model 58; Yellow Springs Instruments, Yellow Springs, OH, USA) was used to measure the water temperature and DO. The conductivity and pH were recorded using a conductivity meter (Model 152; Fisher Scientific, Hampton, NH, USA) and an Orion 250A pH meter (Orion Research Inc., Boston, MA, USA), respectively. The 10 L water samples were transported to the laboratory immediately after sampling to measure the turbidity as well as TN and TP concentrations. The turbidity was measured using a turbidimeter (Model 100B; HF Scientific Inc., Ft. Myers, FL, USA). The remaining water samples were filtered through 0.45 µm mixed cellulose ester membrane filters to measure TN and TP concentrations (A045A047A; Advantech Co. Ltd., Taipei, Taiwan). We determined the TN and TP concentrations spectrophotometrically using the method described by Wetzel and Likens [36].

Fish, including *C. argus*, were collected at three sampling points of each study site using cast (7 × 7 mm) and scoop (5 × 5 mm) nets along a 50 m transects. At each sampling location, both the cast and scoop nets were used for 30 and 20 min, respectively. Fish samples were identified at the species level according to Kim and Park [37] and the classification system of Nelson et al. [38]. Fish species that were difficult to identify in the field were fixed using a methanol–formaldehyde solution (3:1) and subsequently identified in the laboratory. To explain the different densities of *C. argus* from the wetlands in the upper and mid–lower reaches of the Nakdong River, we investigated the fishing activities of *C. argus* by humans for three years (2013 to 2015) in three wetlands (sites 19, 26, and 30) in the mid–lower reaches of the Nakdong River.

In this study, we additionally investigated the total 30 wetlands after prior fish collection to identify the spatial distribution of the target fish species (*C. argus*, *L. macrochirus*, and *M. salmoides*). The littoral zone of each wetland was shallow and the central area was deep, leading to separate microhabitats. Macrophytes were only abundant in the littoral zone. We established three sampling zones: vegetated bed (VB), edge of vegetated bed (EVB), and open water (OW) zones. We firstly defined the range of the EVB to clearly present the range of the VB and OW. The EVB was a space located between the VB and OW and is approximately 1–1.5 m wide. Three sample replicates were obtained for the monitoring of each sampling zone. We then investigated the spatial distribution of *C. argus*, *L. macrochirus*, and *M. salmoides* in each sampling zone. We collected fish using cast (7 × 7 mm) and scoop (5 × 5 mm) nets along 300 m transects in each zone. At each sampling location, both the cast and scoop nets were used for 30 and 20 min, respectively. Among the fish collected in each sampling zone, we counted only the target fish species, that is, *C. argus*, *L. macrochirus*, and *M. salmoides*, and excluded other fish species from the investigation. Furthermore, to identify the food consumption tendency of *L. macrochirus*, we immediately fixed the gut of *L. macrochirus* collected from three wetlands (sites 19, 26, and 30) in the mid–lower reaches of the Nakdong River using a methanol–formaldehyde solution (3:1). We identified and counted all cladoceran species in the gut contents of *L. macrochirus*. The abundance of each species of cladoceran in the gut of *L. macrochirus* was calculated as the abundance per weight of the gut.

We also investigated the cladocerans in the VBs of the six wetlands (sites 3, 7, 12, 19, 26, and 30) to identify differences in the structure of the cladoceran community between the upper and mid–lower reaches of the Nakdong River. To determine the cladoceran abundance in each wetland, water samples were collected using a 10 L water sampler (length: 20 cm; width: 30 cm; height: 70 cm) and filtered through a plankton net (32 µm mesh size). The filtrates were fixed in formalin (final concentration: 4% formaldehyde) [39]. The cladocerans were counted and the species were identified using a Zeiss Axioskop

40 microscope (Zeiss, Göttingen, Germany) at 200× magnification and the classification key prepared by Mizuno and Takahashi [40]. The rotifers were distinguished to be either epiphytic or pelagic species in accordance with Sakuma et al. [41] and Gyllström et al. [42].

2.3. Stable Isotope Analysis

To identify the interactions between fish communities, including *C. argus*, we conducted stable isotope analysis of the dominant fish species of six wetlands (three sites, that is, sites 3, 7, and 12, in the upper reaches of the Nakdong River and three sites, that is, sites 19, 26, and 30, in the mid–lower reaches). Six fish species were collected from the three wetlands in the upper reaches of the Nakdong River, with a relatively high fish species diversity. In contrast, only three fish species (*C. argus*, *L. macrochirus*, and *M. salmoides*) from the three wetlands in the mid–lower reaches of the Nakdong River, with a relatively lower biodiversity, were utilized for the stable isotope analysis. We divided the samples into small (<10 cm) and large (>10 cm) categories according to the body size of each *L. macrochirus* and *M. salmoides* to further analyze the consumption patterns of C. argus with respect to exotic fish species. Sufficient tissue material was collected from each fish species to meet the minimum dry weight required for stable isotope analysis (1.0 mg per sample).

The carbon and nitrogen measurements of the fish species were separately conducted. For the accurate interpretation of trophodynamics using carbon stable isotope data, tissue lipids must be extracted. The carbon isotope signature depends on the protein content of the tissue; the presence of lipids can affect the reliability of the isotope analysis. The lipid content varies depending on the tissue type and is ^{13}C-depleted relative to proteins. Therefore, tissue samples containing lipids may produce an unstable carbon isotope signature. In contrast, lipid extraction affects the δ^{15}N value. Therefore, we divided the samples into groups comprising carbon- and nitrogen-signature samples. Lipids were removed only from carbon-signature samples. The two samples were compared using δ^{13}C and δ^{15}N analyses [43]. The carbon-signature samples were placed in a solution of methanol–chloroform–triple-distilled water (2:1:0.8 *v*/*v*/*v*) for 24 h.

All fish samples were freeze-dried and ground with a mortar and pestle. All powdered samples were frozen (−70 °C) prior to the analyses. Carbon and nitrogen isotope ratios were determined using continuous-flow isotope mass spectrometry (CF-IRMS, ISOPRIME 100; Micromass Isoprime, GV Instruments Ltd., Manchester, UK). Prior to the analysis, the samples were placed in a sealed CF-IRMS overnight with a He flow (99.999%) of a few mL/min. The instrument linearity (dependence of δ^{13}C and δ^{15}N on the signal amplitudes at the collectors) was tested daily and confirmed to be <0.03‰/nA in the range of 1–10 nA. We loaded 100 ± 10 µg silver-encapsulated cellulose samples (no carbon was added to the samples inside the capsules), producing a signal of ~4–6 nA at the collectors, in a 99-position zero-blank CF-IRMS, which were converted to a mixture of carbon monoxide, carbon dioxide, water, and hydrogen gases over glassy carbon chips in a quartz tube at 1080 °C, within a stream of carrier He (99.999%) with a flow rate of 110 mL/min. The data were expressed as the relative per mil (‰) difference between the sample and the conventional standard (Pee Dee Belemnite carbonate for carbon and atmospheric N_2 for nitrogen) according to the following equation:

$$\delta X\ (‰) = [(R_{sample}/R_{standard}) - 1] \times 1000, \quad (1)$$

where X is ^{13}C or ^{15}N and R is the ^{13}C:^{12}C or ^{15}N:^{14}N ratio, respectively. A secondary standard with a known correlation with international standards was used as reference. The standard deviations of δ^{13}C and δ^{15}N of 20 replicate analyses of the peptone standard (δ^{13}C = −15.8‰ and δ^{15}N = 7.0‰, Merck) were ±0.1‰ and ±0.2‰, respectively.

2.4. Data Analysis

We used one-way ANOVA to examine (i) the differences in environmental variables and fish communities depending on the area (i.e., between the upper and mid–lower reaches of the Nakdong River) and season (i.e., spring and autumn), and (ii) the differences

in fish (*C. argus*, *L. macrochirus*, and *M. salmoides*) in three microhabitats (i.e., VB, EVB, and OW). Tukey's test was used for additional post-hoc comparison to determine which differences were statistically significant. The statistical analyses were conducted using SPSS for Windows (IBM Corp. V. 20.0. Armonk, NY). Differences and relationships were considered significant at $p < 0.05$. We tested homoscedasticity and homogeneity of the data.

We used non-metric multidimensional scaling (NMDS) to examine fish distribution patterns according to environmental variations in the 30 wetlands. The NMDS ordination plots were generated based on Euclidean distance, and goodness of fit was assessed in terms of loss of stress. Each variation was log-transformed after being assessed for normality with the Shapiro–Wilk test. The stress value for the two-dimensional solution was 0.132, which was lower than the generally accepted maximum stress value of <0.2. The significance of the fitted vectors was assessed using 3000 permutations, with $p < 0.05$ considered significant. NMDS ordination was conducted with the R package "vegan" (version 2.5-3).

3. Results

3.1. Environmental Variables and Fish Distribution

Although we obtained very high or low values for some study sites, the environmental variables of the two areas (the wetland groups of the upper and mid-lower reaches of the Nakdong River) did not statistically differ (one-way ANOVA, $p < 0.05$; Table 2). However, we observed a clear seasonality of the environmental variables. The conductivity, turbidity, and macrophyte biomass were higher in autumn than in spring (conductivity, f = 1.795, $p < 0.05$; turbidity, f = 2.048, $p < 0.05$; macrophyte biomass, f = 1.847, $p < 0.05$). The environmental variables obtained in this study were similar to the limnological characteristics of wetlands or shallow reservoirs in temperate areas, such as South Korea.

Table 2. Seasonal changes of environmental variables in the 30 investigated wetlands in the upper and mid–lower reaches of the Nakdong River. WT, water temperature; DO, dissolved oxygen; Cond., conductivity; TN, total nitrogen; TP, total phosphorus; MB, macrophyte biomass. Each value represents the mean and standard deviation.

Area	Season	WT (°C)	DO (%)	pH	Cond. (μS/cm)	Turbidity (NTU)	TN (mg/L)	TP (μg/L)	MB (g)
Upper	Spring	20.3 ± 1.2	68.3 ± 21.5	8.1 ± 0.2	335 ± 22.5	12.6 ± 3.5	1.3 ± 0.6	11.4 ± 4.5	14.3 ± 8.5
	Autumn	19.8 ± 0.7	31.3 ± 13.4	7.6 ± 0.6	274 ± 30.8	24.4 ± 8.4	1.8 ± 0.7	16.3 ± 3.8	32.2 ± 13.5
Mid-lower	Spring	19.5 ± 1.1	53.8 ± 17.4	7.8 ± 0.3	389 ± 28.4	16.3 ± 5.1	1.1 ± 0.5	14.3 ± 2.4	18.2 ± 6.1
	Autumn	19.8 ± 1.3	44.7 ± 10.8	7.3 ± 0.4	315 ± 21.8	28.3 ± 9.1	1.6 ± 0.7	18.8 ± 4.1	46.2 ± 15.4

The species number of fish of each wetland group in the upper and mid–lower reaches of the Nakdong River differed (Figure 2). The spring species number of fish was higher in wetlands in the upper reaches than in the mid–lower reaches (f = 1.847, $p < 0.05$; 8–15 species upstream; 2–6 species downstream). Notable differences were also observed in autumn (f = 1.916, $p < 0.05$; 8–14 species upstream; 2–6 species downstream). However, the fish abundance in the upper and mid–lower reaches of the Nakdong River slightly differed. The clear difference in the number of fish species between the two regions was closely related to the distribution of *L. macrochirus* and *M. salmoides*. Among the fish communities collected from wetlands in the mid–lower reaches of the Nakdong River, the relative abundance of *L. macrochirus* and *M. salmoides* was >90%, but the species diversity of other fish was relatively lower. In contrast, wetlands in the upper reaches of the Nakdong River exhibited a low density of *L. macrochirus* and *M. salmoides*, but the species number of other fish was relatively higher. *Carassius* was dominant in wetlands in the upper reaches of the Nakdong River (average: 13.3 individuals), followed by *C. argus* (average: 9.4 individuals). The density of *C. argus* collected from each wetland differed from that of *L. macrochirus* and *M. salmoides*. The density of *C. argus* was high in wetlands in the upper reaches of the Nakdong River (average 9.4 individuals per wetland). However, *C. argus* was not observed in wetlands in the mid–lower reaches of the Nakdong River or only one or two

individuals were obtained (Figure 2c,d). This difference in the density of *C. argus* between the two regions was closely related to the fishing activities of humans. The results of NMDS indicated that the measured environmental variables did not influence the density of fish species. The annual fishing frequency of *C. argus* in three wetlands (19, 26, and 30) in the mid–lower reaches of the Nakdong River was high (Figure 3). Fishing activities start in March and last until August and are mainly concentrated in May and June.

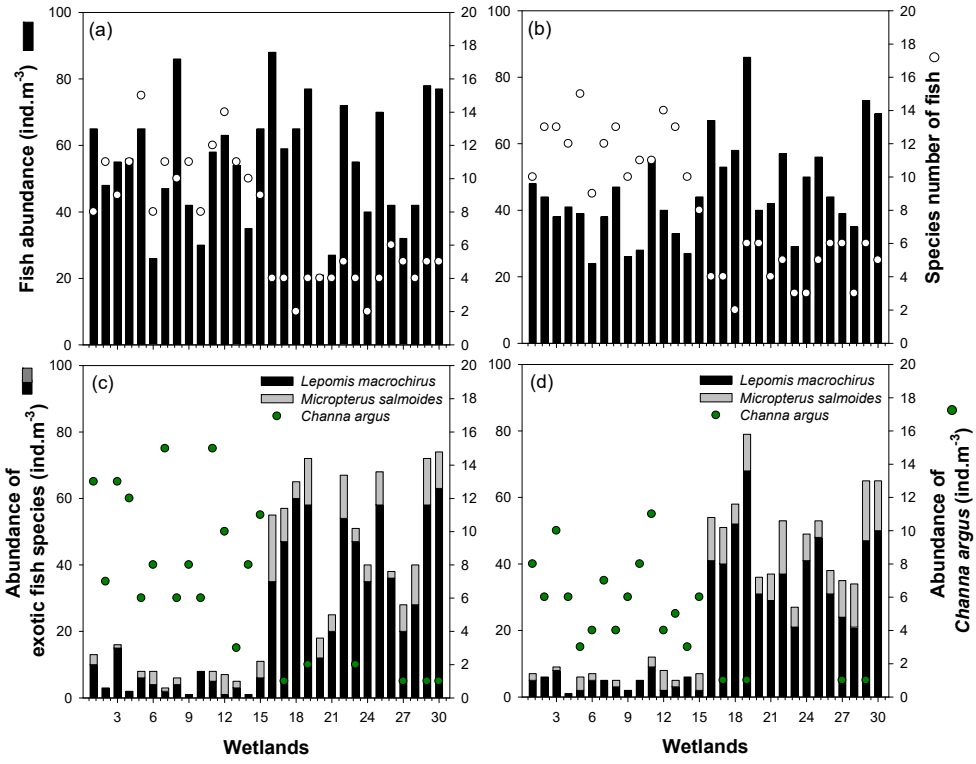


Figure 2. Fish abundance in the 30 investigated wetlands in the upper and mid–lower reaches of the Nakdong River. Abundance and species number of fish in spring (**a**) and autumn (**b**). Abundance of *Channa argus*, *Lepomis macrochirus*, and *Microterus salmoides* in spring (**c**) and autumn (**d**).

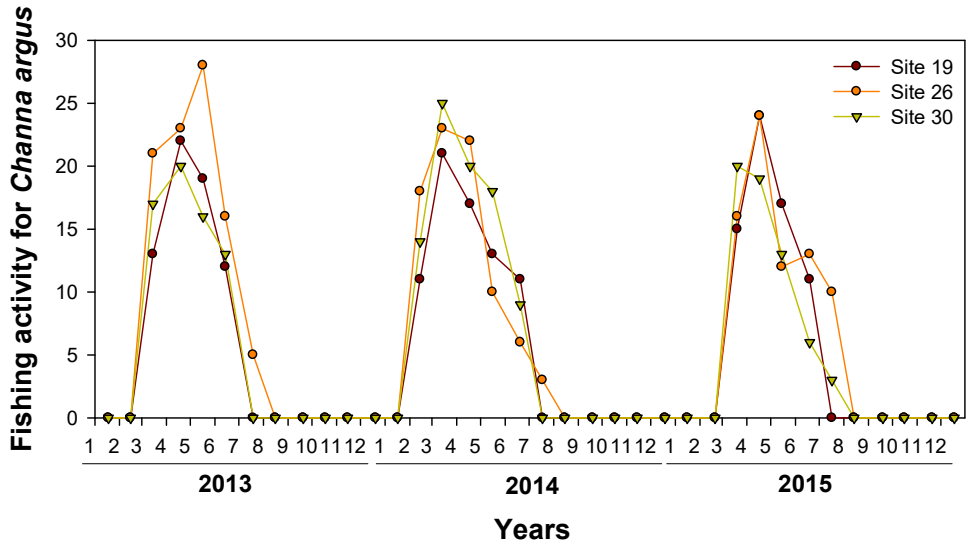


Figure 3. Interannual fishing frequency of *Channa argus* in three wetlands (site 19, 26, and 30) in the mid–lower reaches of the Nakdong River.

3.2. Microabitat Utilization and Food Preference of Channa Argus

The densities of *C. argus* clearly differed in the three different microhabitats (i.e., VB, EVB, and OW) in the upper reaches of the Nakdong River (Figure 4 and Table 3; one-way ANOVA; $p < 0.05$). However, in wetlands in the mid–lower reaches of the Nakdong River, the density of *C. argus* was low, and differences between the microhabitats were insignificant. In wetlands in the upper reaches of the Nakdong River, *C. argus* was abundant in VBs (average: 8.8 individuals), and its density was very high compared with that in the OW (not-collected) and EVB (average: 1.6 individuals). The spatial distribution of *C. argus* was similar in spring and autumn.

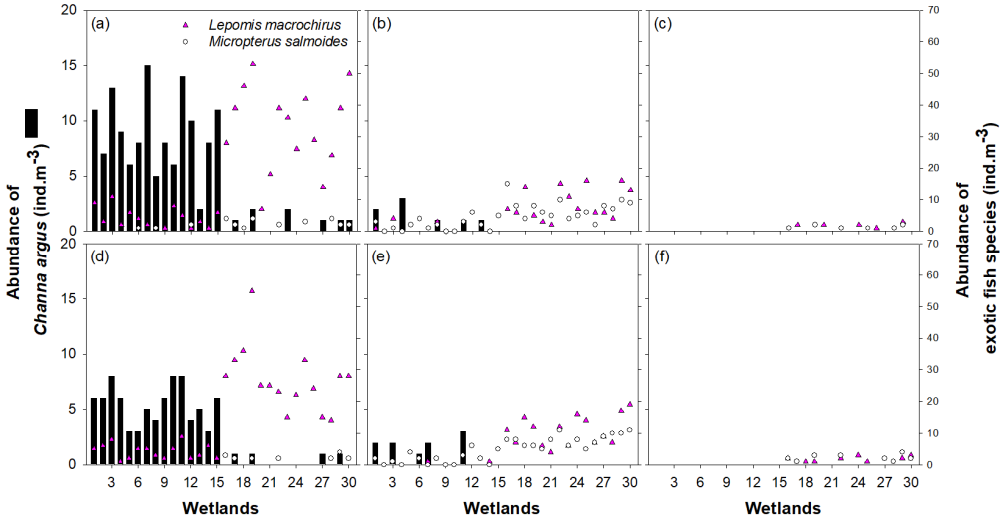


Figure 4. Abundance of *Channa argus* and exotic fish species (*Lepomis macrochirus* and *Micropterus salmoides*) in the three different microhabitats (vegetated beds, edge of vegetated beds, and open water zones) of the 30 investigated wetlands. Vegetated beds in spring (**a**) and autumn (**d**), edge of vegetated beds in spring (**b**) and autumn (**e**), and open water zones in spring (**c**) and autumn (**f**).

Table 3. Results of one-way ANOVA comparing fish density between the three different microhabitats (i.e., vegetated beds, VB; edge of vegetated beds, EVB, and open water zones, OW) in the upper and mid-lower reaches of the Nakdong River.

Region	Season	Fish	df	F	*p*
Upper part	Spring	*Channa argus*	2	3.217	<0.05
		Lepomis macrochirus	2	1.841	<0.05
		Micropterus salmoides	2	1.354	0.216
	Autumn	*Channa argus*	2	3.015	<0.05
		Lepomis macrochirus	2	1.038	0.441
		Micropterus salmoides	2	1.127	0.342
Mid-lower part	Spring	*Channa argus*	2	0.815	0.568
		Lepomis macrochirus	2	2.816	<0.05
		Micropterus salmoides	2	2.054	<0.05
	Autumn	*Channa argus*	2	0.982	0.510
		Lepomis macrochirus	2	2.268	<0.05
		Micropterus salmoides	2	1.815	<0.05

In the wetlands in the upper reaches of the Nakdong River with a high density of *C. argus*, the densities of *L. macrochirus* and *M. salmoides* in different microhabitats did not significantly differ. However, the densities in the three microhabitats in wetlands in the mid–lower reaches of the Nakdong River significantly differed. In contrast to the EVB and OW, a high density of *L. macrochirus* in the mid–lower reaches of the Nakdong River was observed in VBs (Figure 4; one-way ANOVA; $p < 0.05$). However, the density of *M.*

salmoides was higher in the EVB than in the VB or OW (Figure 4 and Table 3; one-way ANOVA; $p < 0.05$). A different density of the target fish species in the three microhabitats was found in both spring and autumn.

Although the $\delta^{13}C$ and $\delta^{15}N$ values of fish communities in the different wetlands differed, the interrelationships (prey–predator or competition) between fish colonies only slightly varied (Figure 5). In general, the stable carbon and nitrogen isotope values of predators were ~1‰–2‰ and 2‰–3‰ heavier, respectively, than those of prey. Based on the different stable isotope values of prey and predators, *C. argus* consumed fish species such as *L. macrochirus* and *M. salmoides*. The consumption of *L. macrochirus* and *M. salmoides* by *C. argus* slightly differed. *C. argus* consumed small and large groups *of L. macrochirus*, whereas it preferred small-sized individuals of *M. salmoides*. The consumption of *L. macrochirus* and *M. salmoides* by *C. argus* was higher in wetlands in the mid–lower reaches of the Nakdong River.

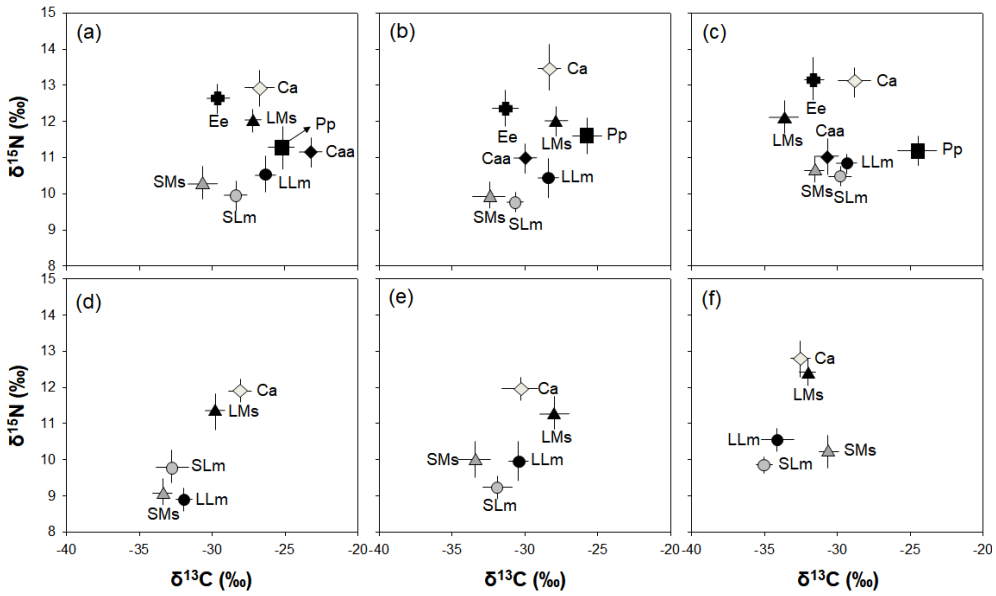


Figure 5. Carbon and nitrogen isotope plots of samples (n = 5) in each of the six wetlands in the upper (**a**–**c**) and mid–lower reaches (**d**–**f**) of the Nakdong River. (**a**) site 3, (**b**) site 7, (**c**) site 12, (**d**) site 19, (**e**) site 26, and (**f**) site 30. Ca, *Channa argus*; Caa, *Carassius auratus*; Ee, *Erythroculter erythropterus*; Pp, *Pseudorasbora parva*; SLm, small *Lepomis macrochirus*; LLm, large *Lepomis macrochirus*; SMs, *Micropterus salmoides*; LMs, large *Micropterus salmoides*.

3.3. Utilization of the Cladoceran Community by Lepomis Macrochirus

Lepomis macrochirus selectively consumed a few cladoceran species (Table 4). We frequently observed pelagic cladoceran species, such as *Daphnia obtusa*, *Diaphanosoma brachyurum*, *Moina macrocopa*, and *Simocephalus vetulus*, in the gut of *L. macrochirus* collected from the three wetlands (19, 26, and 30 wetlands) in the mid–lower reaches of the Nakdong River. In contrast, the concentration of epiphytic species, such as *Alona guttata*, *Chydorus sphaericus*, and *Pleuroxus aduncus*, in the gut of *L. macrochirus* was low.

Although the concentration of epiphytic species in the gut of *L. macrochirus* was lower, they were abundant in the field (Figure 6). The density of epiphytic species, such as *A. guttata*, *C. sphaericus*, and *P. aduncus*, in the three wetlands in the mid–lower reaches of the Nakdong River was high. In contrast, in the wetlands in the upper reaches of the Nakdong River, in which the density of *L. macrochirus* was relatively lower, the densities of epiphytic and pelagic cladoceran species were similar.

Table 4. Diet composition (ind. gut weight^{-1}) of *Lepomis macrochirus* in spring and autumn in the three wetlands (19, 26, and 30) in the mid–lower reaches of the Nakdong River. The species marked with an asterisk (*) were considered to be epiphytic cladoceran species in accordance with Sakuma et al. (2000) and Gyllström et al. (2005). The indicated number (19, 26, and 30) is the wetland number.

Diet Composition (Cladocerans)	19		26		30	
	Spring	Autumn	Spring	Autumn	Spring	Autumn
Acroperus harpae (Baird, 1834) *	-	0.7 ± 0.2	-	-	-	-
Alona guttata (Sars, 1862) *	2.7 ± 0.4	-			1.2 ± 0.5	-
A. rectangula (Sars, 1862) *	-	-	0.8 ± 0.1	0.3 ± 0.0	-	-
Bosmina longirostris (Müller, 1785)	-	-	10 ± 3.4	5.4 ± 2.1	13 ± 4.8	15 ± 7.8
Camptocercus rectirostris (Schoedler, 1862) *	1.6 ± 0.2	1.2 ± 0.4	-	-	-	-
Chydorus sphaericus (Müller, 1785) *	-	2.8 ± 1.1	-	-	1.3 ± 2.7	-
Daphnia obtusa (Kurz, 1874)	21 ± 11.4	8.1 ± 2.4	13 ± 6.7	9.1 ± 4.1	24 ± 13.5	20 ± 7.1
Diaphanosoma brachyurum (Lievin, 1848)	-	-	34 ± 21.8	41 ± 28.1	13 ± 5.1	16 ± 12.7
Graptoleveris testudinaria *	-	2.1 ± 0.8	-	-	0.4 ± 0.1	-
Ilyocryptus spinifer (Herrick, 1882) *	-	-	-	0.2 ± 0.0	-	-
Moina macrocopa (Straus, 1820)	15 ± 9.4	23 ± 18.4	20 ± 11.7	28 ± 17.4	17 ± 11.7	22 ± 14.7
Pleuroxus aduncus (Jurine, 1820) *	-	1.5 ± 0.7	0.5 ± 0.1	-	2.1 ± 0.8	-
P. laevis (Sars, 1861) *	-	-	0.7 ± 0.3	-	-	-
Simocephalus expinosus (Koch, 1841)	10 ± 6.4	7 ± 3.7	-	-	10 ± 7.4	13 ± 8.4
S. vetulus (Müller, 1776)	24 ± 13.4	16 ± 10.4	28 ± 20.7	30 ± 17.7	25 ± 18.2	29 ± 23.7
Scapholeberis kingi (Sars, 1903)	2 ± 0.4	6 ± 2.7	-	-	-	-

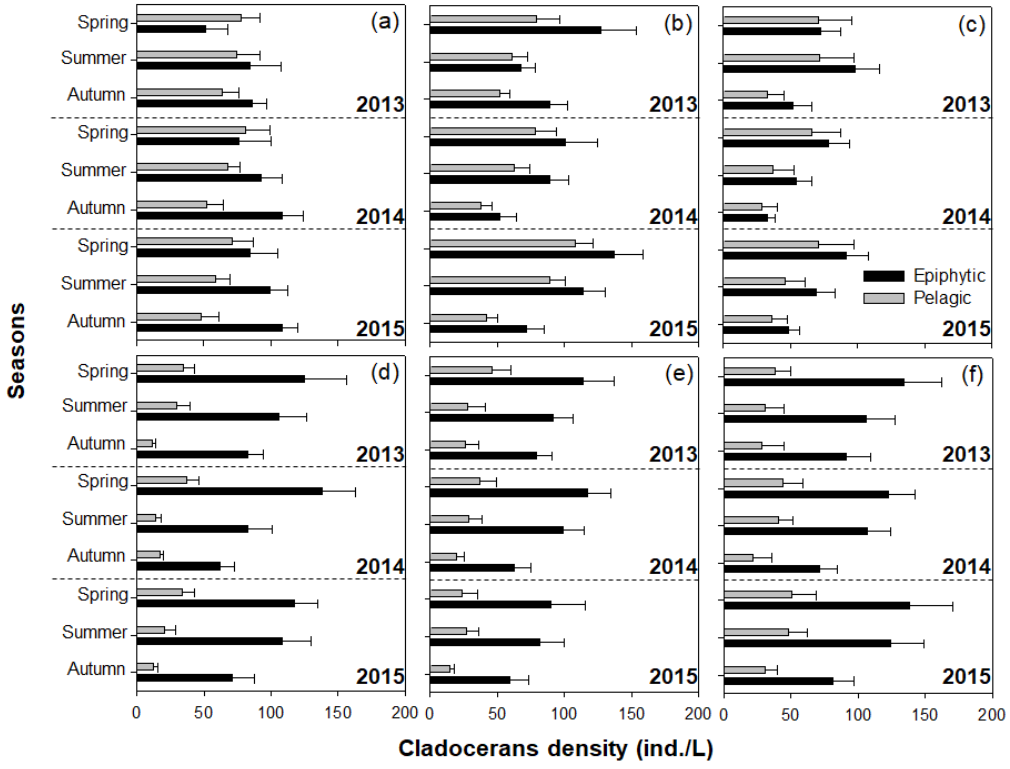


Figure 6. Seasonal distribution (2013–2015) of cladocerans in the wetlands in the upper (**a**–**c**) and mid–lower reaches (**d**–**f**) of the Nakdong River. (**a**) site 3, (**b**) site 7, (**c**) site 12, (**d**) site 19, (**e**) site 26, and (**f**) site 30.

4. Discussion

4.1. Effects of Environmental Characteristics on the Settlement of Exotic Fish in Freshwater Wetlands

Freshwater wetlands in South Korea are generally small, and the water commonly deepens toward the center. Choi et al. [35] reported that the littoral areas of freshwater wetlands in South Korea have an average water depth of 1 to 2 m, whereas the water depth of

the central parts is 3 to 4 m. In the 1970s, natural wetlands in South Korea were considered to be useless areas and were reclaimed for agricultural and residential construction [44]. Most of the remaining wetlands and reservoirs were artificially constructed. Rainfall in South Korea is concentrated in summer [45] and relatively low in the other seasons, making it relatively difficult to secure water resources. Therefore, wetlands or reservoirs were artificially created around farmland or residential areas. These wetlands were constructed to secure a relatively large amount of water in a small area; therefore, the water becomes deeper in the central part. Currently, these wetlands are used as habitats for various aquatic organisms rather than for the supply of water because the farmland area has been reduced, and dams or weirs have been constructed in streams and rivers to secure water resources.

Based on the environmental characteristics of these wetlands, various microhabitats formed. Littoral areas have shallow depths and are covered with various aquatic macrophyte species, which can cause habitat structures that clearly differ from those in the central parts of wetlands. The results of empirical studies showed that areas with a dense cover of aquatic macrophytes can be used as habitats for various animals, such as young fish and zooplankton [46,47], because their structures are physically complex [48,49]. Young fish use aquatic macrophytes as refuge to avoid carnivorous fish; therefore, their density is higher in the littoral area compared with the central part of the wetlands [50]. Similarly, based on the dense cover of aquatic macrophytes, we assume that *L. macrochirus* is abundant in littoral areas, avoiding predation by *M. salmoides*. In areas densely covered with aquatic macrophytes, *M. salmoides* are mainly distributed in the central part of wetlands because the food in littoral areas is limited due to the high coverage with aquatic macrophytes. Therefore, the spatial distribution of *L. macrochirus* and *M. salmoides* differs.

Based on these findings, we assume that aquatic macrophytes are abundant in wetlands located in South Korea and largely contribute to the stable settlement of *L. macrochirus*. This can be explained as follows: (1) The littoral area of wetlands is rich in food, such as zooplankton and invertebrates. The foraging activities of most native fish species are significantly restricted in areas with abundant aquatic macrophytes [16]; therefore, the prey is protected in littoral areas; (2) The food activity of *L. macrochirus* is unrestricted in areas with abundant aquatic macrophytes. Most of the wetlands in South Korea were constructed close to agricultural or residential areas. Aquatic macrophytes excessively grow in these areas because nutrients, such as phosphorus and nitrogen, are continuously supplied, and the consumption of prey by *L. macrochirus* is very efficient; and (3) In areas densely covered with aquatic macrophytes, *L. macrochirus* can achieve a stable population growth without frequent interference by predators or competitors. Competitors or predators do not threaten *L. macrochirus* because native *M. salmoides* avoids areas with abundant aquatic macrophytes. In addition, we observed a high density of *L. macrochirus* in the wetlands in the mid–lower reaches of the Nakdong River, which is due to the low density of *C. argus*, that is, carnivorous fish.

4.2. Effect of the Fishing Activity by Humans on the Settlement of Exotic Fish

The density of *C. argus* significantly differed in each wetland group in the upper and mid–lower reaches of the Nakdong River. During the study period, an average of nine *C. argus* individuals was observed in wetlands in the upper reaches of the Nakdong River, whereas the number of individuals was relatively lower in the mid–lower reaches (average of 0.5 individuals). The annual collection of *C. argus* by humans was high in the mid–lower reaches of the Nakdong River, which caused the low density of *C. argus* in this area. It is also possible that the high density of *L. macrochirus* and *M. salmoides* contributed to the low density of *C. argus* through food exploitation as a competitor of young *C. argus*. However, this possibility may be valid only after the density of *L. macrochirus* and *M. salmoides* increased due to the continuous decrease of *C. argus* by humans. Continued fishing activities can break the balance of wetland food webs because the *C. argus* density was reduced and its stable population growth hindered. Because *C. argus* is a top predator in the freshwater food web, the variability in its population affects the distribution or

species diversity in the primary or secondary consumer communities belonging to the lower levels of the food web. The results of previous studies showed that human activities, such as fishing and leisure activities, continuously and extensively affect freshwater food webs [51,52]. In particular, fish are highly utilized by humans for ornamental purposes or as staple food source. In contrast, the abundance of *C. argus* in wetlands in the upper reaches of the Nakdong River was high. In this area, *C. argus* is rarely collected by humans, which has a positive effect on stable population growth.

We suggest that the different densities of *C. argus* in the two regions significantly contributed to the stable settlement of exotic fish species such as *L. macrochirus*. The abundance of *L. macrochirus* in wetlands in the mid–lower reaches of the Nakdong River was high, which was due to the low density of *C. argus*. Choi and Kim [28] also suggested that the settlement in wetlands in the mid–lower reaches of the Nakdong River with abundant aquatic macrophytes is efficient because the environmental conditions (e.g., diverse food items, refuge presence to avoid predators) are conducive to a stable distribution and population growth of *L. macrochirus*. Although wetlands in the upper reaches of the Nakdong River have environmental characteristics similar to those in the mid–lower reaches, the density of *L. macrochirus* in this area was relatively low. The results of our stable isotope analysis show that *L. macrochirus* was frequently consumed by *C. argus*, which means that the high density of *C. argus* in wetlands in the upper reaches of the Nakdong River significantly contributed to the lower density of *L. macrochirus*. The results of empirical studies also suggested that artificial density changes in top predators, such as *C. argus*, negatively affect fish community structures [53]. Rowe [54] reported that the introduction of six fish species (*Scardinius erythrophthalmus*, *Tinca*, *Perca fluviatilis*, *Ameiurus nebulosus*, *Carassius auratus*, and *Cyprinus carpio*) significantly reduced the species diversity of fish. Similarly, we observed a low species diversity of fish communities and a low density of native fish in wetlands in the mid–lower reaches of the Nakdong River, which was due to the high density of *L. macrochirus*. Approximately 2 to 6 species of native fish were found in the mid–lower reaches of the Nakdong River, whereas 8 to 16 species were observed in the upper reaches. Therefore, we believe that the absence of top predators due to the continued collection of *C. argus* by humans in the mid–lower reaches of the Nakdong River significantly contributed to the stable settlement of *L. macrochirus*, resulting in the reduction of the density or species diversity of native fish.

4.3. Effect of the Cladoceran Community on the Settlement of Exotic Fish

The results of empirical studies showed that *L. macrochirus* consumes more zooplankton or invertebrates than fish, in contrast to the feeding tendency of *M. salmoides* [55,56]. Choi and Kim [28] also suggested that *M. salmoides* consumes young fish, including *L. macrochirus*, whereas *L. macrochirus* prefers zooplankton and invertebrates. In particular, *L. macrochirus* favorizes the cladoceran community [57], which is important for energy acquisition for spawning and population growth. Although the foraging activities of most fish are significantly restricted in areas densely covered with aquatic macrophytes, such as wetlands in Korea [58], the feeding activity of *L. macrochirus* is efficient in the presence of a moderate cover of aquatic macrophytes [59]. The predation of *L. macrochirus* continues to deplete the food sources for native fish species with similar ecological positions in freshwater food webs, which is a major factor leading to a fish density reduction and a low species diversity.

Based on our results, we assume that the density differences of *L. macrochirus* in the wetland groups in the upper and mid–lower reaches of the Nakdong River changed the structure of the cladoceran community. The wetlands in the mid–lower reaches of the Nakdong River with a high density of *L. macrochirus* were dominated by epiphytic species, such as *Chydorus sphaericus*, *Alona guttata*, and *Pleuroxus aduncus*, whereas the density of pelagic species, such as *Daphnia obtusa*, *Diaphanosoma brachyurum*, and *Simocephalus vetulus*, was relatively lower. Successful feeding of most fish depends on the effective prey search of the predator, and conspicuous prey is frequently consumed [60]. Pelagic species move more

frequently compared with epiphytic species, which is beneficial for prey search [61,62]. Based on this behavioral pattern of pelagic cladoceran species, phytoplankton floating in water is filtered out [63]. Furthermore, the pelagic species are more vulnerable to the prey search of fish because they immediately leave their residence when a predator appears. The prioritized search for pelagic cladoceran species by fish can lead to the high consumption of pelagic species by *L. macrochirus*. In contrast, epiphytic species crawl over the surface of leaves or stems of aquatic macrophytes, making the consumption by predators relatively difficult because there is little movement [64]. Because the gut of epiphytic species is twisted, the gut passage time is relatively slow and it takes a long time to reach starvation [65]. Therefore, frequent movement for feeding is unnecessary. However, pelagic species move fast and have a straight gut and relatively fast digestion and, thus, continuously consume [66]. Based on the different movements of the two types of cladocerans, *L. macrochirus* consumes more pelagic than epiphytic species; consequently, the density of epiphytic species was high in wetlands with abundant *L. macrochirus*.

Although the results of empirical studies suggested that aquatic macrophytes are utilized as refuge by various animals to avoid predatory fish, including crustaceans [67–69], the results of this study show that vegetated areas with a high density of *L. macrochirus* do not provide efficient habitats for cladocerans. We observed a low density of pelagic cladocerans in wetlands in the mid–lower reaches of the Nakdong River in which *L. macrochirus* is dominant. However, pelagic species were abundant in wetlands in the upstream of the Nakdong River with a low density of *L. macrochirus*. In contrast, epiphytic cladoceran species were abundant in both regions, regardless of the *L. macrochirus* density. Therefore, we assume that the role of aquatic macrophytes as a refuge for pelagic species in Korean wetlands strongly depends on the distribution of *L. macrochirus*. Epiphytic cladocerans were dominant in wetlands in the mid–lower reaches of the Nakdong River and did not contribute to population growth because they are not suitable as food sources for native fish.

4.4. Human Culture and Freshwater Ecosystems

The collection of *C. argus* by humans was concentrated in the mid–lower area of the Nakdong River. Because the utilization of freshwater fish as a food source for humans is a major route of heavy metal exposure to humans, the use of freshwater fish is decreasing globally. In South Korea, the use of freshwater fish gradually decreases due to water pollution or the reduced use as food [70]. However, the annual collection rate of *C. argus* by fishing activities in the mid–lower reaches of the Nakdong River is high and, thus, has a strong influence on the community structures of fish, including *C. argus*. Although positive effects of *C. argus* on humans have not been scientifically proven, long-term use of *C. argus* by humans in this area is expected. South Koreans tend to trust superstitions and culture more than scientific evidence. The residents in the mid-lower area of the Nakdong River strongly believe in the effect of *C. argus* as medicine.

Although this study mainly discusses the negative aspects of human culture, such as *C. argus* collection, humans can also positively affect biological communities. Vyas et al. [71] suggested that the presence of various historic sites is important for biodiversity conservation. It has been suggested that human activities are significantly reduced at historic sites because historic culture is of spiritual importance to humans. Historic sites include a wide range of natural areas, such as forests and oceans, but also historical man-made buildings or monuments. In addition, in areas such as the Demilitarized Zone (DMZ) in Korea, the distribution of biological species that are highly sensitive to artificial disturbances is high because of the relatively low human impact [72]. However, such cases only represent a small fraction, and most human activities and cultures are major factors causing a reduction in biodiversity. Human activities generally modify and alter the natural state of areas, which in turn damages the habitats of various organisms. Based on this study, the frequent collection of *C. argus* by fishing activities induced the stable settlement

of exotic fish species, such as *L. macrochirus*, which led to changes in the structures of cladoceran communities.

Based on these results, we propose that artificial disturbances, such as *C. argus* collection, should be gradually reduced to secure biodiversity, including fish in the mid-lower reaches of the Nakdong River. The continuous wide-ranging effects of most human activities contribute to the reduction of species diversity and the change in the distribution of various organisms. However, it is difficult to completely eliminate human activity in a region because it represents a culture that stems from mental perception. Therefore, it is necessary to establish a management plan that clearly identifies the types of human activities that constantly negatively affect the ecosystem as well as measures to gradually reduce them. This is similar to the change of the perception of humans with respect to *C. argus* in the mid–lower reaches of the Nakdong River, which can have a positive effect on the density of *C. argus* and the structure of the fish community. In the future, the frequency of human exploitation in this region must be reduced, which will have a negative impact on already settled exotic fish species. This will also contribute to the restoration of the density of native fish and the enhancement of species diversity.

5. Conclusions

This study shows that human fishing activities of *C. argus* not only contributed to the stable settlement of exotic fish species, but also resulted in changes in cladoceran community structure. Wetlands in the mid-lower reaches of the Nakdong River had a low density of *C. argus* due to fishing activities, which consequently led to the stable settlement and high population growth of the exotic fish *Lepomis macrochirus*, being prey to *C. argus*. In contrast, wetlands located in the upper reaches of the Nakdong River supported a high density of *C. argus*, had a low density of exotic species, and a high species diversity of fish. These differences in fish communities also influenced the cladoceran community structure. The successful settlement of *L. macrochirus* increased the dominance of epiphytic species in the wetlands due to the concentrated predation of pelagic species. Because a change in the density of top predators, such as *C. argus*, altered the lower-level fish community in the freshwater food web and influenced the stable settlement of exotic fish species, artificial disturbances, such as fishing activities, need to be minimized to secure biodiversity and maintain ecosystem health.

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