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Effects of Aquatic Macrophytes on Spatial Distribution and Feeding Habits of Exotic Fish Species *Lepomis macrochirus* and *Micropterus salmoides* in Shallow Reservoirs in South Korea

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Abstract: Aquatic macrophytes determine the physical complexity of aquatic environments and may influence the distribution and feeding habits of fish species. We explored the influence of different microhabitats, including vegetated beds (VB), edges of vegetated beds (EVB), and open water zones (OW), on two exotic fish species (*Lepomis macrochirus* and *Micropterus salmoides*) in shallow reservoirs. *Lepomis macrochirus* was more abundant in VB than in other zones and *M. salmoides* was mainly distributed in EVB. In VB, *L. macrochirus* mainly consumed branchiopods and isopods, while *M. salmoides* in EVB relied on relatively larger food items, such as dipterans, odonatans, and young fish. The consumption of young fish by *M. salmoides*, including *L. macrochirus*, showed little difference between winter and summer. Based on these findings, we suggest that young *L. macrochirus* (~20 cm) utilize VB as a refuge to avoid predation by *M. salmoides*. Meanwhile, *M. salmoides* mainly occupied in areas surrounding VB, preying on animals at these edges. As such, the presence of aquatic macrophytes appears to plays a key role in the survival and population growth of *L. macrochirus*. Proper management of aquatic macrophytes can help reduce populations of exotic fish and support native fish species.

Keywords: habitat heterogeneity; piscivorous fish; prey size-selectivity; prey-predator interaction; freshwater refugia

1. Introduction

Habitat complexity directly affects food webs by altering predator–prey interactions due to changes in the physical environment [1–5]. Habitats with high structural heterogeneity provide refugia from predators and substrates suitable for spawning and foraging, supporting a greater diversity of animals [6,7]. Habitat heterogeneity in freshwater ecosystems is primarily determined by the physical structure and composition of macrophytes [8,9], with submerged macrophytes increasing physical complexity, providing suitable habitat for various animals [10,11]. Macrophytes' architecture has a significant bearing on food sources due to detritus tapping [12] and the growth of periphytic microalgae [13], supporting the formation of distinct animal communities [14–16], including both epiphytic and planktonic types, and diverse species composition. Habitat complexity controls energy transfer through food webs by direct and indirect influences on top-down and bottom-up pathways [5,17] and may affect the strength of links between littoral and pelagic habitats, especially in small aquatic systems [6].

Freshwater macrophytes are effective in restricting the foraging activity of predators such as piscivorous fish [18,19], which are key determinants of ecosystem function [20]. Aquatic macrophytes are actively utilized as refugia for the survival and population growth of prey species such as

zooplankton, invertebrates, and young fish. Young fish in particular use macrophytic refugia to avoid predation [21,22]. Increasing complexity provides increased opportunities for refuge, decreasing predator capture efficiency [23]. Furthermore, macrophytes support a high density of potential prey sources such as invertebrates, increasing their appeal as habitats for young fish [24–27]. In contrast, predatory fish are highly active in spaces where aquatic macrophytes are scarce or absent, and indiscriminate predation leads to a decrease in food sources and food scarcity, influencing predator population growth. This can result in decreased biodiversity. Larger fish are mainly observed in lakes or streams with fewer aquatic macrophytes [28], and the survival rate of young fish is lower in these areas compared to wetlands with a diverse array of macrophytes. As such, macrophytes can be regarded as essential habitat space for aquatic prey species (e.g., zooplankton, invertebrates, and young fish).

There are spatial limits to the area covered by macrophytes that can support prey individuals, and drift of prey animals can lead to insufficient space. Under these circumstances, prey animals may be detected by predators at the edge of vegetated beds. The growth and development of aquatic macrophytes is often seasonal, such that the spatial structure of a habitat may change over time. The development of various plant species creates habitats with complex structures. This habitat, in turn, supports diverse animals and provides an appropriate environment for successful survival and propagation [29,30]. However, when aquatic macrophytes provide relatively low cover and simple habitat structures, they are less able to support diverse aquatic animals. In simple habitat structures in cooler environments, predators generally have reduced food consumption [31], slow digestion rates [32], reduced swimming abilities [33], and limited mobility and activity [34]. Nonetheless, some fish species remain active in the winter, and their continued food consumption increases prey mortality and influences prey populations during the subsequent season.

Since their introduction in South Korea in the 1970s, the bluegill sunfish, *Lepomis macrochirus*, and the largemouth bass, *Micropterus salmoides*, have quickly spread through streams, reservoirs, and wetlands. As exotic species and top predators, they likely disturb ecosystems by preying on native fish, in the same way as *Cichla kelberi* in a reservoir located in the upper Paraná River in Brazil [35,36]. Pumpkinseed and largemouth bass are ecologically diverse and influenced by habitat complexity and, as such, are good models for testing the importance of habitat complexity and species interactions on ecosystem properties [37]. We aimed to elucidate the relative influence of aquatic macrophytes on the spatial distribution and feeding habits of *L. macrochirus* and *M. salmoides*. While the distribution and feeding habits of these species appear to be determined by local habitat structure and complexity, the importance of the relationship between seasonal succession and spatial distribution of fish and aquatic macrophytes has only recently been recognized. The pattern of macrophyte utilization by exotic fish species is still unclear, and their distribution is often underestimated. In shallow water ecosystems where macrophytes frequently dominate, these species are important in determining biodiversity [38]. We predicted that spatial distributions of the exotic fish species would differ according to macrophyte microhabitats and have a clear influence on the population growth of prey species. To test this objective, we surveyed 42 lentic ecosystems in South Korea, including physicochemical parameters of water, macrophytes, and fish assemblages. Based on the results, we explored the interactions between macrophytes and the fish community. To inform the removal and management of exotic fishes, as well as provide important data for identifying food webs within a freshwater ecosystem in order to infer its condition.

2. Materials and Methods

2.1. Study Area

South Korean freshwater ecosystems are temperate, with four distinct seasons, leading to a dynamic succession of biological communities. We selected reservoir sites located in southeastern South Korea near the mid- to lower parts of the Nakdong River. Historically, there have been numerous riverine

reservoirs in the river basin, but much of this area has disappeared due to anthropogenic activities [39]. Agriculture is the dominant land use in the basin, and non-point source pollution continuously influences the reservoir ecosystems [40].

Currently, a total of 146 reservoirs are present in the Nakdong River basin [26]. All selected sites were dominated by *L. macrochirus* and *M. salmoides*, with low abundance or absence of other fish species. We explored the reservoirs for simultaneous presence of vegetated and open water zones. Forty-two reservoirs with both vegetated zones and open water zones were selected (Figure 1). Table S1 summarizes some of the main morphometries and limnological features of the reservoirs. Very shallow reservoirs with water surface area almost completely covered by macrophytes were excluded from this study.
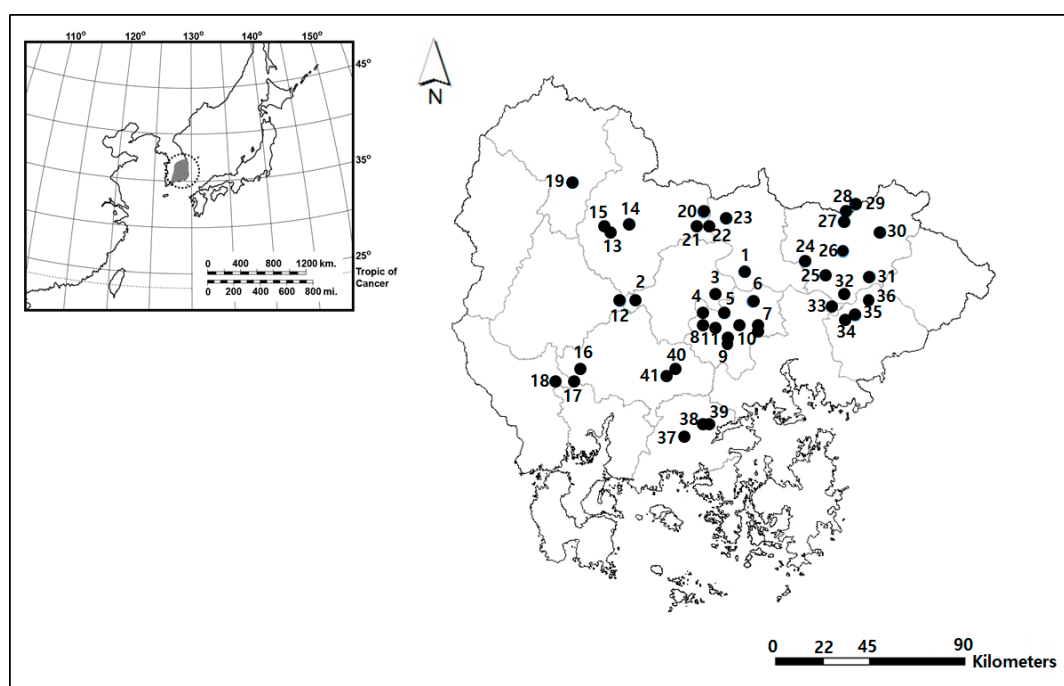
Figure 1. Map showing the 42 study sites located in southeastern South Korea. The study sites are shown as solid circles (●). The small map in the upper left corner indicates the Korean Peninsula.

Selected reservoirs were of a similar size (mean ± SD: 155,845 ± 8516 m^2), and most were utilized as agricultural water supply. The littoral zone of each reservoir was shallow with a deeper central area, resulting in clear separation of microhabitats with macrophytes being abundant only in the littoral zone. On this basis, we established three sampling zones including vegetated bed (VB), edge of vegetated bed (EVB), and open water (OW) zones. At the each of sampling zone, three replicates were established for monitoring. We then investigated environmental parameters and fish distribution in replicates of each zone.

2.2. Monitoring Strategy

We monitored the study sites in winter (December 2012) and summer (August 2013) to compare environmental parameters and fish distribution between seasons. Water depth, water temperature, dissolved oxygen concentration, conductivity, and pH were measured in the three zones at each reservoir. The EK-500 echo sounder was used to measure maximum water depth. We used a dissolved oxygen (DO) meter (model 58; YSI Inc., Yellow Springs, OH, USA) to determine water temperature and dissolved oxygen, and 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) at 0.5 m depth. Water from 0.5 m depth to the surface was sampled using a 2 L

column sampler. To determine chlorophyll *a* concentration, water samples were filtered through 0.45 μm mixed cellulose ester membrane filters (A045A047A; Advantech Co. Ltd., Taipei, Taiwan). The filtered membranes were carried out in cold 90% acetone, in darkness, at 20 °C for 4 h. To improve extraction, the cells were disintegrated for 2 min in an ultrasonic bath. To remove cell debris and filter particles, the pigment extract was centrifuged at 5000 rpm for 5–10 min. The extinction was estimated at 600 and 750 nm with spectrophotometer (Japan Fantec Research Institute, Shizuoka, Japan) and using 1 cm glass cuvette [41]. The concentration of chlorophyll a was estimated by the formula: Chlorophyll $a = 11.403 \cdot (A_{600}\text{-}A_{750}) \cdot V_a \cdot V_b^{-1}$, derived on the basis of a factor. Designations at the formulas are: V_a-extract volume (mL) and V_b-sample volume (mL). Ten liters of water was filtered through a 68 μm mesh plankton net at each sampling zone to collect invertebrates, which were preserved in 5% formaldehyde. The collected invertebrates were classified as branchiopods, isopods, dipterans, and odonatans and counted using a stereozoom microscope at 200× magnification (Axioskop 40; Zeiss, Oberkochen, Germany).

Both *L. macrochirus* and *M. salmoides* were collected in the three zones of each reservoir. We collected fish using a gill net (6 × 6 mm), cast net (7 × 7 mm), and scoop net (5 × 5 mm) along 300 m transects in each zone. At each sampling location, the gill net was set for 3 h after placement while the cast net and scoop net were used for 30 min and 2 min, respectively. Collected fish were identified, counted, and measured for which length. The total number of fish captured at each sampling date was used to evaluate spatial changes in their abundance during the survey. Fish specimens were immediately fixed in a methanol-formaldehyde solution and kept for gut content analysis. We identified and counted all prey organisms, including branchiopods, isopods, dipterans, odonatans, and young fish in the gut contents of *L. macrochirus* and *M. salmoides*. The abundances of different prey items were calculated based on the number of each item in the gut relative to the total number of items. After fish collection, we measured width of per every 50 m of total 300 m transects in vegetated bed of each reservoir. The six widths of vegetated bed were averaged and utilized as the representative vegetated bed width of each reservoir.

2.3. Data Analysis

We used a two-way ANOVA to analyze statistical differences in the densities of *L. macrochirus* and *M. salmoides*, the effects of different habitat zones, and season. We also used a one-way ANOVA to analyze differences in environmental parameters and Invertebrate groups between each zone. The relationships between fish abundance and environmental parameters were tested using stepwise multiple regression in each of season. We confirmed the absence of error (Type I, Type II, etc.) and that the results were consistent regardless of the order that parameters were added.

We also utilized regression analysis to observe the relationship between *L. macrochirus* abundance and the area of VB in each reservoir. We tested linear, exponential, inverse, power, and logistic functions to determine the equation generating the best curve fit. Among the regression results, the curve-fitting equation that returned the highest determination coefficient was selected to explain the observed relationships. All statistical analyses were conducted using SPSS for Windows ver. 20 (IBM Corp. Released 2011. IBM SPSS Statistics for Windows, Version 20.0. Armonk, NY: IBM Corp.). Differences and relationships were considered significant at $p < 0.05$.

3. Results

3.1. Environmental Parameters and Invertebrate Distribution

Vegetated bed width, depth, water temperature, dissolved oxygen, pH, conductivity, and chlorophyll *a* did not differ among reservoirs or seasons, but did differ among the three habitat type zones (Table 1). The greatest difference was observed in DO concentration among zones, where DO concentration was higher in OW than in VB or EVB. Particularly, the DO in winter was statistically different among zones (one-way ANOVA, F = 2.81, P < 0.05). In VB and EVB, DO moderately increased

during winter, but did not do so in OW. Depth was greatest in OW with little difference between the seasons. The width of vegetated beds was greater in summer, likely due to their seasonal growth and development. Other environmental factors differed few between zones.
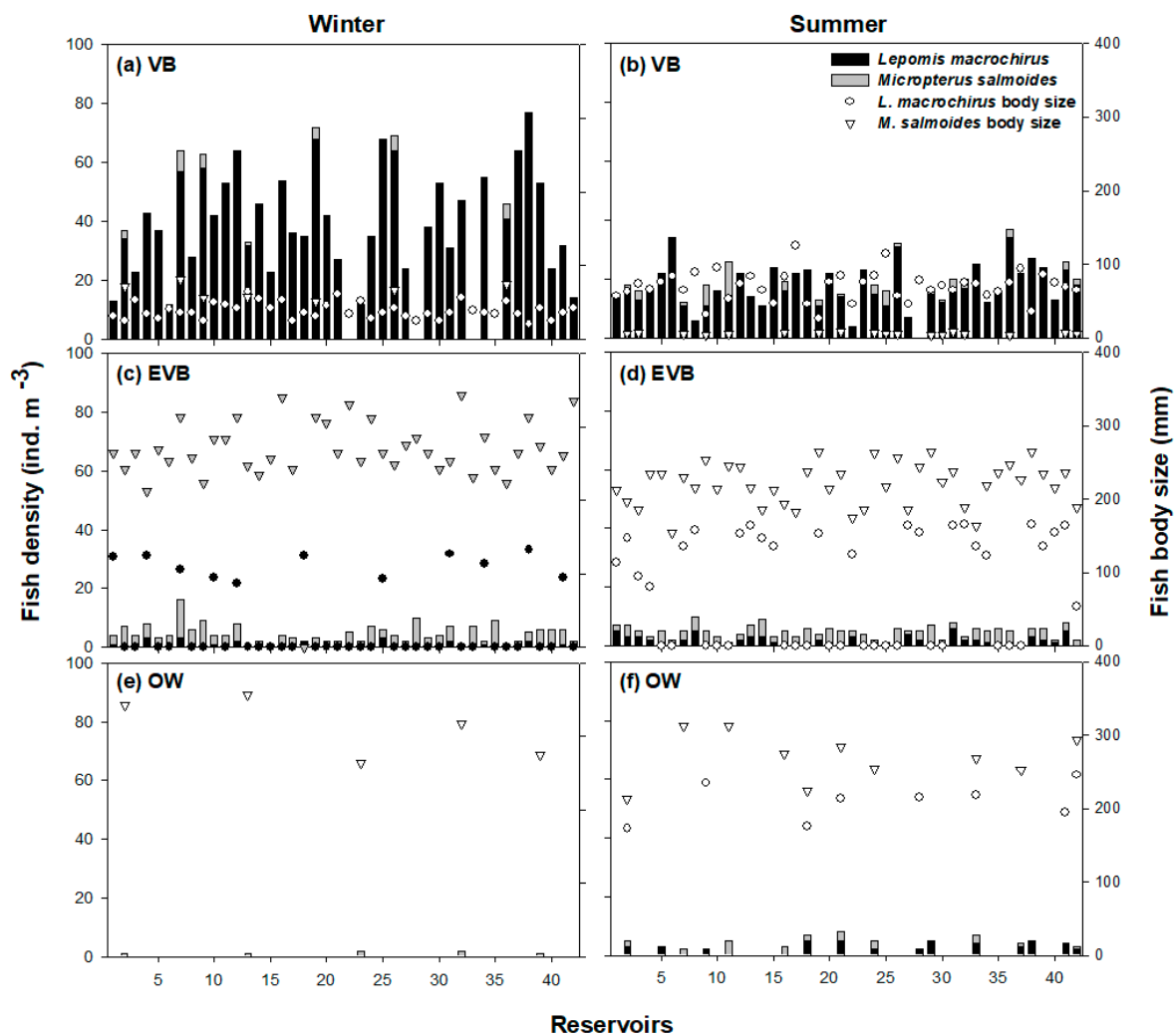
Table 1. Environmental parameters and invertebrate groups in three zones of 42 reservoirs. VB: vegetated beds; EVB: edge of vegetated beds; OW: open water zones. VW, Vegetated bed width; WT, Water temperature; DO, Dissolved oxygen; Con., Conductivity; Chlorophyll a, Chl. A.

Factors	Winter			Summer		
	VB	EVB	OW	VB	EVB	OW
VW (cm)	50.9 ± 26.9	-	-	147.6 ± 72.9	-	-
Depth (m)	0.6 ± 0.4	1.8 ± 2.7	3.7 ± 4.8	0.9 ± 0.6	2.2 ± 1.9	3.9 ± 5.7
WT (°C)	2.7 ± 1.7	2.4 ± 1.6	2.4 ± 2.1	28.4 ± 18.4	27.4 ± 15.6	27.2 ± 18.7
DO (%)	71.6 ± 23.7	86.2 ± 21.2	91.7 ± 26.8	17.4 ± 11.4	45.2 ± 20.7	98.6 ± 22.7
pH	8.4 ± 1.4	7.2 ± 0.9	7.1 ± 1.3	6.7 ± 2.7	7.5 ± 2.8	7.6 ± 1.7
Cond. (µS/cm)	227.8 ± 137	234.1 ± 128	232.7 ± 134	342.8 ± 247	357.7 ± 285	312.4 ± 257
Chl. *a* (µg/L)	5.7 ± 6.3	6.4 ± 3.7	5.6 ± 4.5	34.7 ± 31.7	36.4 ± 27.1	46.7 ± 26.7
Branchiopods (ind/L)	0.7 ± 6.4	-	-	92.3 ± 28.3	32.1 ± 17.1	17.8 ± 12.4
Isopods (ind/L)	6.8 ± 3.7	2.4 ± 6.9	-	34.7 ± 13.1	24.7 ± 10.4	16.3 ± 7.4
Dipterans (ind/L)	-	-	-	12.4 ± 6.8	6.7 ± 3.6	3.3 ± 2.7
Odonatans (ind/L)	2.4 ± 1.4	-	-	17.4 ± 7.2	10.4 ± 5.4	2.5 ± 2.7

Invertebrate groups (branchiopods, isopods, dipterans, and odonatans) were more abundant in VB and EVB than OW (Table 1). Branchiopod density was significantly higher in VB than in EVB or OW in both seasons (one-way ANOVA, F = 2.81, $p < 0.05$).

3.2. Distribution of Species among Different Zones

Less than 5% of the fish collected were other species (than *L. macrochirus* and *M. salmoides*), and were thus negligible. The abundance and body size of *L. macrochirus* and *M. salmoides* differed among the three zones (Figure 2). *Lepomis macrochirus* was more abundant in VB than in other zones in both the summer and winter, although it became more abundant overall in winter (winter: 37 ± 20.4 ind./m^3; summer, 17 ± 7.2 ind./m^3). We observed clear size differences in *L. macrochirus* between different zones. The smallest body sizes of *L. macrochirus* were found in VB. Interestingly, the body size of *L. macrochirus* was less than 20 cm in winter. However, individuals in EVB and OW had body sizes >20 cm, though fewer individuals were present. Meanwhile, few *M. salmoides* were found in VB, and they were mainly distributed in EVB. Their body sizes followed a pattern similar to *L. macrochirus*, whereby VB areas supported smaller individuals and the largest individuals were present in OW, followed by EVB. In EVB, *M. salmoides* individuals were relatively larger in winter than in summer, while in OW, their body size was similar across seasons. Finally, in OW, *M. salmoides* density was lower in winter than in summer.

Figure 2. Density and body size of *Lepomis macrochirus* and *Micropterus salmoides* in three zones of 42 reservoirs. VB: vegetated beds; EVB: edge of vegetated beds; OW: open water zones. VB (**a**), EVB (**c**), and OW (**e**) in winter, and VB (**b**), EVB (**d**), and OW (**f**) in summer.

The results of the two-way ANOVA indicated that habitat and season affected both fish species (Table 2). Distribution of *L. macrochirus* was significantly influenced by both habitat and season, while *M. salmoides* was influenced only by microhabitat. Stepwise multiple regression examining the influence of habitat on the abundance of *L. macrochirus* in winter (Table 3) showed strong positive relationships with the biomass of aquatic macrophytes (t = 10.541, $p = 0.000$) and dissolved oxygen. These observations could explain the presence of *L. macrochirus* predominantly in VB. However, the fishes were not related with environmental parameters in summer. The regression analysis between the abundance of *L. macrochirus* and VB area in winter indicated a positive relationship ($r^2 = 0.67$, $p < 0.05$, Figure 3). In contrast, VB did not show any statistically significant correlation with abundance of *L. macrochirus* in summer and *M. salmoides* did not show any significant relationship with VB area in any season. *M. salmoides* density was only negatively related to pH (Table 3).

Table 2. Two-way ANOVA results for the effects of habitat (vegetated beds, edge of vegetated bed, and open water zones) and season (winter and summer) on density of *Lepomis macrochirus* and *Micropterus salmoides*.

Fish	Component of Variance	df	Residual df	F	P
	Habitat	2	246	233.32	0.00
Lepomis macrochirus	Season	1	246	3.56	0.03
	Habitat x Season	3	246	194.2	0.00
	Habitat	2	246	87.43	0.02
Micropterus salmoides	Season	1	246	0.77	0.91
	Habitat x Season	3	246	8.24	0.63

Table 3. Summary of stepwise multiple regression analysis to predict density of fish (response variable) with respect to environment parameters (explanatory variables) in winter. Data were transformed prior to analyses using either the arcsine-square root or log (all other variables) transformation.

Response Variable	Explanatory Variables	B_j	t	*p*-Value
Lepomis macrochirus	Macrophyte biomass (g)	0.018	10.541	0.000
	Dissolved oxygen (%)	−0.141	−2.342	0.037
Micropterus salmoides	pH	−0.197	−2.778	0.032
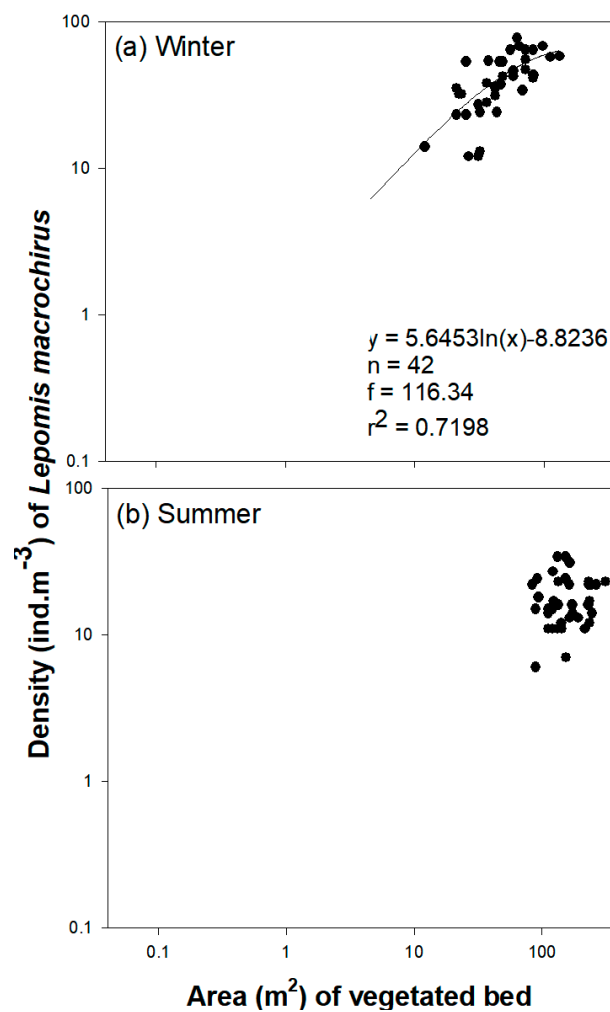
Figure 3. Relationship between *Lepomis macrochirus* density and vegetated bed width across 42 reservoirs in South Korea during winter (**a**) and summer (**b**).

3.3. Prey Consumption Patterns

In summer, both species actively consumed prey in mainly VB and EVB (Table 4). The *L. macrochirus* diet differed between VB and EVB: branchiopods and isopods were utilized in VB, but only dipterans and odonatans were used in EVB. In contrast, *L. macrochirus* in OW consumed only isopods. In *M. salmoides*, greater prey consumption took place in EVB than in VB or OW, but there was no overall preference for specific prey items. In VB, *M. salmoides* preferentially selected food items with relatively small body size such as branchiopods, isopods, and dipterans. Meanwhile, its gut contents in OW included both odonatans and young fish. Young *L. macrochirus* were utilized as a food source for *M. salmoides* in OW and EVB, but not in VB. In VB, *M. salmoides* were of a similar size to *L. macrochirus* (in VB). The fishes were little consumed on prey items in winter, but interestingly, the consumption of young fish by *M. salmoides* showed little difference between winter and summer.

Table 4. Diet composition (ind. gut weight^{-1}) of *Lepomis macrochirus* and *Micropterus salmoides* in winter and summer in three zones at 42 reservoirs. VB: vegetated beds; EVB: edge of vegetated beds; OW: open water zones. YOY fish: young of the year fish.

Fish Species	Diet Composition	Winter			Summer		
		VB	EVB	OW	VB	EVB	OW
Lepomis macrochirus	Branchiopods	-	-	-	72.8 ± 64.6	35.4 ± 47.3	-
	Isopods	8.4 ± 12.4	-	-	112.1 ± 82	51.4 ± 32.1	13.4 ± 22.4
	Dipterans	-	-	-	26.5 ± 32.1	66.7 ± 60.4	-
	Odonatans	-	-	-	13.5 ± 22.7	33.1 ± 32.4	-
	Young fishes	-	-	-	-	-	-
Micropterus salmoides	Branchiopods	-	-	-	14.7 ± 5.7	2.0 ± 0.6	-
	Isopods	-	-	-	26.4 ± 66.4	12.4 ± 7.7	-
	Dipterans	-	-	-	32.4 ± 75.1	53.4 ± 35.7	-
	Odonatans	-	-	-	12.5 ± 44.1	44.5 ± 22.8	11.4 ± 16.7
	Young fishes	-	6.4 ± 3.6	4.6 ± 4.1	-	6.7 ± 3.7	9.4 ± 13.5

4. Discussion

4.1. Microhabitat Characteristics Influence Fish Distribution

The abundance of *L. macrochirus* and *M. salmoides* clearly differed among the three microhabitats. VB supported a high abundance of fish, especially small *L. macrochirus*. In contrast, *M. salmoides* of 40–60 cm body size were mainly distributed in EVB. Since aquatic macrophytes provide appropriate habitat for animals such as invertebrates and young fish and refugia from larger fish predators [16,18,42,43], most animals utilizing macrophyte habitats have smaller body size and concentrate themselves in VB when predators are present in high abundance [42].

Micropterus salmoides is known as a strong predator, which creates disturbance in ecosystems as they indiscriminately prey on eggs of other fish species, young fish, and invertebrates [44]. We observed that *M. salmoides* consumed various prey and, in particular, utilized young fish as a food source. In spite of this, *M. salmoides* did not linger in VB zones. Savino and Stein [45] suggested that it actively forages in areas of moderate or sub-moderate aquatic macrophyte cover. Since most of South Korea's reservoirs have been constructed to secure agricultural water, the bulk of the surrounding land is agricultural or residential, resulting in a high influx of total nitrate and phosphorus, which induces excessive growth of aquatic macrophytes. For this reason, most of the reservoirs' littoral areas show high coverage of emergent macrophytes such as *Phragmites communis* and/or *Paspalum distichum*, which is unsuitable habitat for fish such as *M. salmoides*. Accordingly, we found that *M. salmoides* abundance was relatively lower in reservoirs with high coverage of aquatic macrophytes. *M. salmoides* did not frequent VB habitat, and instead consumed prey items in EVB areas. We often found young individuals (<20 cm) of *L. macrochirus* in the gut content of *M. salmoides* collected from EVB, suggesting that *M. salmoides* could consume *L. macrochirus* individuals of the size found in VB. In contrast, *L. macrochirus* has a rhomboid body form advantageous in swimming among the stems and leaves of aquatic macrophytes. In addition, *L. macrochirus* predation is influenced less by the abundance of aquatic macrophytes due to

its mode of feeding (they suck in food with water). Previous studies have suggested that *L. macrochirus* can feed effectively in the complex habitat space created by aquatic macrophytes [46]. For *M. salmoides*, however, the abundance of aquatic macrophytes is a significant limiting factor in its foraging activities. Moreover, the structural complexity of VB supports a high density of prey items such as invertebrates, which utilize it as a refuge from predation [25,47]. Therefore, aquatic macrophytes can be interpreted as important in maintaining the coexistence of *L. macrochirus* and *M. salmoides*, enabling them to partition their space. As the littoral zones of South Korean reservoirs are suitable for development of aquatic macrophytes, they can support population growth of *L. macrochirus* and *M. salmoides.*

Most of the environmental variables examined did not show significant differences among the three microhabitats, reflecting very little physicochemical variation. This indicates that the distribution patterns of *L. macrochirus* and *M. salmoides* were primarily influenced by habitat structure and prey-predator interactions. As the exception, clear differences in DO during summer were the result of restricted oxygen exchange with the atmosphere under high summertime macrophyte coverage in VB areas [48]. We did not deal with the environmental variables of the bottom layer because it is rich in organic matter, which does not reflect the physicochemical characteristics of water. The bottom layer reflects higher conductivity and lower dissolved oxygen concentrations than the surface or middle layer. In addition, *L. macrochirus* and *M. salmoides* do not distribute well at the bottom layer. They avoid dark bottom layer because their foraging activity use sight. Although the bottom layer may exhibit different characteristics from other layers, it is not important to understand the distribution of *L. macrochirus* and *M. salmoides*.

Among invertebrate groups, branchiopods and isopods were more abundant in VB than EVB or OW. Some studies have suggested that submerged parts of macrophytes are utilized as both substrate for epibiotic species as well as refugia from predation [3,26]. The various plant species create complex spatial structures, decreasing the foraging efficiency of visual predators such as fish. Therefore, the presence of VB can support the survival and population growth of various prey such as invertebrates. As an exception, *L. macrochirus* did feed in VB, and was sometimes present at high densities in this zone. It is possible that VB areas with a high abundance of *L. macrochirus* were not suitable refugia for invertebrates [23]. However, we found that *L. macrochirus* consumed various invertebrate species, including branchiopods such as *Daphnia* and *Simocephalus* spp. and isopods such as *Cyclops* and *Mesocyclops* spp. These pelagic species are preferred by consumers because they are easily pursued and captured by fish predators [49]. However, species such as *Alona* and *Chydorus* spp., which attach to the stems and leaves of macrophytes, are not as easily consumed by fish [50]. When easy-to-exploit resources such as planktonic species are exhausted, epiphytic species can be used as alternative food sources for secondary consumers [51]. Thus, research on epiphytic species is needed to understand biodiversity and food webs in freshwater ecosystems.

4.2. Role of Winter Macrophytes for Lepomis macrochirus

The feeding habits of *L. macrochirus* and *M. salmoides* differed between winter and summer, with more varied prey captured in summer. Interestingly, consumption of young fish by *M. salmoides* was similar in winter and summer, with an average capture rate of an average of 6.7 fish during the summer within EVB and an average of 6.4 fish in winter, indicating no significant influence of water temperature. Fish predation was generally higher during warm periods and lower in winter. In general, all foraging related capacities, as well as other vital rates in ectotherms including fish, are strongly dependent on water temperature, in turn imposing strong constraints on energy acquisition, physiological adaptations, and behavior [52]. Access to resources becomes so limiting that starvation is initiated. Larger individuals can survive for longer than smaller individuals because of their higher ratio of energy reserves to metabolic rate. Likewise, invertebrates such as *Daphnia* show depressed feeding activity in winter, with consequent slow growth rates [53]. Life cycles, lifespan, offspring number, and tolerance are also determined by temperature [54]. When food consumption decreases, individuals minimize their energy expenditure by reducing movement. In EVB, however, *M. salmoides*

foraging posed a consistent threat to *L. macrochirus* regardless of season, leading to *L. macrochirus* moving into VB zones. However, although aquatic macrophytes can provide physical refuge for *L. macrochirus*, seasonal growth patterns of aquatic macrophytes lead to changes in habitat complexity and structure. Therefore, *L. macrochirus* utilizes growing and developing aquatic macrophytes during spring and fall, while winter withering leads to a reduction in its habitat space. However, winter does not cause a total eradication of aquatic macrophytes. While free-floating hydrophytes such as *Spirodela polyrhiza* L. and *Salvinia natans* L. and submerged hydrophytes such as *Ceratophyllum demersum* L., *Potamogeton crispus* L., and *Vallisneria natans* (Lour.) H. Hara mostly wither and die back to the benthos during winter, the leaves and stems of emergent hydrophytes such as *Phragmites communis* Trin., *Zizania latifolia* (Griseb.) Turcz., and *Paspalum distichum* var. *indutum* Shinners maintain a similar morphology during summer and winter. The emergent hydrophytes that maintain their shape during winter function as highly important refugia for *L. macrochirus* to avoid predation by *M. salmoides*. However, these winter habitats provide a very small area of refuge compared to their summer area. Furthermore, emergent hydrophytes typically develop at a depth of 1–2 m. Therefore, the habitable area of each reservoir differs, presenting varying refuge effectiveness for *L. macrochirus*. Predictably, *L. macrochirus* density increased as VB area increased. Since only *L. macrochirus* able to secure the remaining VB as a refuge during winter can survive predation by *M. salmoides*, a seasonal decrease in the *L. macrochirus* population is likely to take place. These factors likely contribute to the persistent coexistence of *M. salmoides* predators and *L. macrochirus* prey within a limited habitat space.

L. macrochirus that do secure refuge in VB during winter become important primary individuals for population growth the following year. In addition, reservoirs with a wide VB area during winter support a greater density of *L. macrochirus* individuals to reproduce the following summer. In contrast, reservoirs with a smaller VB area during winter will require more time for the population size to reach pre-summer levels, even if a wide VB area is secured in the following year. In cases where a large area of VB is available during the summer but is absent in the winter, or when only a very small area can be utilized, a considerable number of *L. macrochirus* are likely to be captured by *M. salmoides*, contributing to population growth of the latter species. Consequently, the area of VB during winter is an important factor in determining the next generation of *L. macrochirus*, and likely influences its continued survival and growth.

4.3. Absence of Predation on L. macrochirus and M. salmoides

The absence of predators also likely contributes to the spread of *L. macrochirus* and *M. salmoides*. *Channa argus* (Perciformes: Channidae) is at the top of the food chain in South Korea's freshwater ecosystems, and while it does consume fish such as *L. macrochirus* and *M. salmoides* [55], its population is in decline and does not provide a strong top-down influence. *Channa argus* is native to South Korea and is regularly captured for use in traditional medicine. Its fishery is most intensive during May and June, within the range of 80 to 100 fishing activity every year. This fishing season takes place when their preferred VB habitat has lower cover and coincides with spawning [56], making this fishery a significant factor in its decline. *Channa argus* is fished intensively in southern provinces (especially Gyeongsangnam-do and Gyeongsangbuk-do), with decreasing annual catches; moreover, *C. argus* was observed at only three sites in this study. Its absence as an apex predator increases the population size and dominance of *L. macrochirus* and *M. salmoides* and decreases the overall health of the ecosystem [57]. As a result, *L. macrochirus* and *M. salmoides* are now the most frequently observed species in most South Korean freshwater ecosystems.

4.4. Strategy for Managing Exotic Fish Species

Our study sites supported a high abundance of *L. macrochirus* and *M. salmoides*, and the density of other species was considerably lower. In spite of the fact that *L. macrochirus* constituted more than 70% of the fish biomass at some sites, which was higher than that of *M. salmoides*, policies and planning for its management by the government and civic groups have not been as extensive. This may be

because these groups place comparatively low importance on shallow wetlands and reservoirs with minimal current and abundant macrophytes, such as those preferred by *L. macrochirus*. These areas have historically been perceived as low in value, and have been developed for farmland, embankment construction, and health control, leading to degradation or extinction of many wetlands. There is increasing awareness of their importance to biodiversity and landscape value, and conservation efforts have been implemented, but these ecosystems are often subject to disturbance for use as water resources.

Meanwhile, *M. salmoide*s dominate in deeper water bodies with lower macrophyte cover (i.e., OW). Construction and refortification for securing water, drought and flood prevention, and power generation are carried out at such areas, and their ecosystem services are better recognized. As such, management by removal of exotic fish species such as *M. salmoides* is carried out consistently. Furthermore, research and media coverage of issues such as predator-prey interactions, influence on the ecosystem, and environmental risk tend to focus on *M. salmoides*. As a result, *L. macrochirus* is widely distributed across South Korea [58], representing a persistent threat to native fish species and their habitats. Nine wetlands in South Korea, including the Upo wetland, belong to the Ramsar Convention on Wetlands and receive protection and management. However, reports indicate a significantly higher relative richness of exotic fish species such as *L. macrochirus* within these wetlands [59]. Therefore, while the removal and management of *M. salmoides* in areas such as dam reservoirs and deep lakes is taking place, there is an urgent need for management of *L. macrochirus* in shallow wetlands or reservoirs to guard against the decrease and extinction of native fish species.

Our findings indicate that the abundance of aquatic macrophytes in each reservoir influences the density of *L. macrochirus*. As agricultural and/or residential areas surround most wetlands, runoff of nutrients such as nitrate and phosphorus can increase the growth of aquatic macrophytes. Controlling these factors by reducing or purifying runoff could help reduce macrophyte cover and remove *L. macrochirus*. Management of *M. salmoides* by means other than physical removal is more difficult due to their high density, active foraging, and high fertility rates. Nutrient loading control can reduce the abundance of aquatic macrophytes, and consequently reduce the acceleration of the interaction (i.e., foraging of young *L. macrochirus* to *M. salmoides*) between *L. macrochirus* and *M. salmoides*. It can be increased the populations and density of native fish species and contribute to securing biodiversity.

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