

Identification of the Genetic Origin of the Largemouth Bass (*Micropterus salmoides*), an Invasive Fish Species, in South Korea

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Abstract : The largemouth bass (*Micropterus salmoides*), a carnivorous freshwater fish, is found ubiquitously worldwide and impacts the food-web structure of aquatic ecosystems. In this study, we collected largemouth bass specimens from seven study sites along the Seomjin River in southwestern Korea to identify their genetic origin and diversity. The collected fish were mostly small in size (< 100 mm). We performed cytochrome oxidase subunit I (COI) gene analysis. The deduced COI DNA sequences closely matched those of the *M. salmoides* largemouth bass from the USA. Twenty single nucleotide polymorphisms with alternative nucleotides were observed distinguishing the *M. salmoides* northern and Florida subspecies. In addition, phylogenetic analysis suggested that the origin of wild largemouth bass in southwestern Korea is the *M. salmoides* northern subspecies, and not the Florida subspecies, *M. floridanus*. Based on nucleotide variations among the northern subspecies, we analyzed eight haplotypes using all *M. salmoides* COI sequences in NCBI GenBank. Two types of COI haplotypes were found across the seven sites of southwestern Korea. One nucleotide variant was found only in the largemouth bass population of southwestern Korea. Network analysis indicated a major haplotype among the eight haplotypes. Our results provide fundamental information regarding the genetic origin and diversity of *M. salmoides* largemouth bass.

Keywords : Largemouth bass, *Micropterus salmoides floridanus*, Cytochrome oxidase subunit I (COI), Single nucleotide polymorphism (SNP), Haplotype

Introduction

The largemouth bass (*Micropterus salmoides*) is one of the most common carnivorous freshwater fish species in the world (Welcomme, 1992). It is an economically important fish species, widely distributed throughout the USA. Largemouth bass are popular as a sport fishing species, and they represent a keystone species in freshwater ecosystems due to their trophic position as an apex predator. Its impact on food-web structure and function has been widely investigated in aquatic ecosystems (Blanco *et al.*, 2003; Weyl *et al.*, 2010; Ellender *et al.*, 2011). Ellender *et al.* (2011) examined the rapid reinvasion of non-native largemouth and smallmouth bass into the Blindekloof stream in South Africa, demonstrating that predatory fish completely eliminate native species in occupied pools. High densities of *M. salmoides* exerted strong top-down control on food webs in shallow, saline Spanish Mediterranean lakes (Blanco *et*

al., 2003). Invasion of non-native largemouth and smallmouth bass completely eliminate native species in occupied pools in the Blindekloof stream in South Africa (Weyl *et al.*, 2010). In Korea, the largemouth bass was first introduced in 1973 from Louisiana, USA, by the Fisheries agency for the purpose of generating a food supply resource, and were released into the Paldang Lake (Lee *et al.*, 2008). Since then, it has become a widespread species in Korean rivers and lakes (Jang *et al.*, 2002; Lee *et al.*, 2008). At less than 80 mm in body length, they prey mainly on invertebrates, and as they grow, their diet shifts gradually to fish and crayfish (Olson, 1996; Post, 2003; Jang *et al.*, 2006; Yasuno *et al.*, 2012). When non-resident fishes are introduced into new habitats, there are no species with an ecological niche. As a result, ecological diffusion of introduced largemouth bass occurs readily in Korea, because of low inter-specific competition (Azuma, 1992). This has resulted in the reduction of native fish populations, which are a part of the prey

of the largemouth bass (Hong and Son, 2003). Thus, as an invasive alien species, they accelerate freshwater biodiversity loss and have enormous economic costs worldwide (Williamson, 1999; Mooney and Hobbs, 2000; Simberloff *et al.*, 2013).

The largemouth bass belongs to the family Centrarchidae, which includes two subspecies: the Northern subspecies, *Micropterus salmoides salmoides*, and the Florida subspecies, *Micropterus salmoides floridanus* (Li *et al.*, 2012). According to Aoki *et al.* (2006), two subspecies of North American largemouth bass are present in Japan. However, the existence of these species in Korea remains to be confirmed. There is little difference in morphological characteristics between the two largemouth bass subspecies (Clugston, 1964). Fish size differences exhibit clear morphological differences between the two bass species during developmental growth. The Florida subspecies grows more rapidly and reaches greater sizes than the Northern subspecies (Clugston, 1964). It is difficult to distinguish between the two species in juvenile individuals that are less than 100 mm in length (Clugston, 1964). Cytochrome oxidase subunit I (COI), a mitochondrial DNA gene, has been adopted as a molecular identification tool for species classification based on morphological characteristics (Hebert *et al.*, 2003; Ahmed *et al.*, 2019). COI DNA sequence comparisons have not only been used to identify fish larvae, but also to analyze intraspecific variation generating diversity among fish (Hou *et al.*, 2018; Ahmed *et al.*, 2019). This study aimed to identify the genetic origin and diversity of juvenile largemouth bass species collected from seven sites along the Seomjin River in southwestern Korea using COI DNA sequence analysis.

Materials and Methods

1. Study area and fish collection

Fish samples were collected at seven sites along the Seomjin River in southwestern regions of South Korea (Fig. 1): SJ1 (Boseong-gun in Jeollanam-do, 34°51'5" N, 127°9'37" E), SJ2 (Hwasun-gun in Jeollanam-do, 35°1'33" N, 127°6'49" E), SJ3 (Gokseong-gun in Jeollanam-do, 35°7'50" N, 127°17'26" E), SJ4 (Gurye-gun in Jeollanam-do, 35°17'53.6" N, 127°38'33" E), SJ5 (Sunchang-gun in Jeollabuk-do, 35°23'34" N, 127°12'32" E), SJ6 (Imsil-gun in Jeollabuk-do, 35°31'12" N, 127°7'5" E), and SJ7 (Imsil-gun in Jeollabuk-do, 35°36'40.8" N, 127°12'15.4" E). Sampling was performed in July 2018, and thirty individuals from each site were caught with cast nets (7 × 7 mm mesh size) and kick nets (5 × 5 mm mesh size) at the study sites. Basic morphological parameters (body length and biomass) of collected largemouth bass were measured and recorded.

2. DNA extraction and COI PCR amplification

Total DNA was extracted from muscle samples using a Genomic DNA extraction kit following the manufacturer's protocol (Bioneer Inc, Daejeon, Korea). Assessment of DNA quality was performed by electrophoresis on 1.0% agarose (w/v) gels, and total DNA concentrations were determined using a NanoDrop ND-2000 spectrophotometer (Implen, Munich, Germany). A partial fragment from the 5' end of the mitochondrial COI gene was amplified using fish-specific primers: FishForward1: TCAACCAACCACAAAGACATTG GCAC

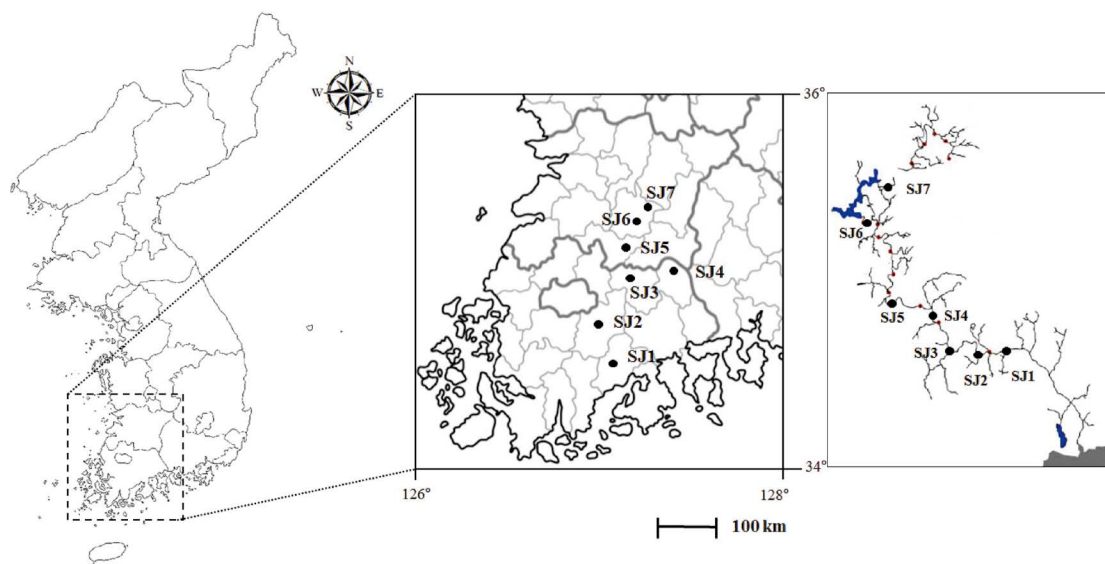


Fig. 1. Map of the study area in Korea, with collection sites (SJ1: 34°51'5" N, 127°9'37" E, SJ2: 35°1'33" N, 127°6'49" E, SJ3: 35°7'50" N, 127°17'26" E, SJ4: 35°17'53.6" N, 127°38'33" E, SJ5: 35°23'34" N, 127°12'32" E, SJ6: 35°31'12" N, 127°7'5" E, SJ7: 35°36'40.8" N, 127°12'15.4" E).

and FishReverse1: TAGACTTCTGGGTGGCCAAAG AATCA (Ward *et al.*, 2005). 30 µL polymerase chain reaction (PCR) mixtures contained 20 µL of sterilized ultrapure water, 3.0 µL of 10× PCR buffer, 1 µL of each primer (20 mmol/L), 1.5 µL dNTPs (2.5 mmol/L each), 0.5 µL Taq DNA polymerase (2.5 U/µL, TaKaRa Bio, China), and 3.0 µL of DNA template (30 ng/µL). The thermal cycling conditions for PCR amplification were as follows: 95°C for 7 min, 38 cycles at 95°C for 30 s, 52°C for 40 s and 72°C for 50 s, with a final extension at 72°C for 10 min. The PCR products were visualized after electro-

phoresis on 1.5% agarose gels. The PCR amplification products were purified from gel slices using a DNA Gel Extraction Kit (Solgent, Daejeon, Korea), and sequenced on an ABI3730xl DNA Analyzer platform.

3. Data analysis

The COI gene sequences were compared with homologous sequences belonging to the genus *Micropterus* in the NCBI GenBank database. Multiple sequence alignments were then conducted using CLUSTALW2 software (<http://www.ebi.ac.uk/>

Table 1. GenBank information and COI sequence homology of the *Micropterus salmoides* northern subspecies used in haplotype analysis

Species definition	GenBank Num.	Country	Homology (%)	Haplotypes
<i>Micropterus salmoides</i> Seomjin 1 in the study	Acc #**	Korea	100.00	GACTTA
<i>Micropterus salmoides</i> Seomjin 2 in the study	Acc #**	Korea	99.99	GACATA
<i>Micropterus salmoides</i>	DQ536425	USA	99.85	GACTTG
<i>Micropterus salmoides salmoides</i>	HQ391896	China	99.39	AATTCG
<i>Micropterus salmoides</i> voucher ihb201306756	KP112317	China	99.53	AATTCA
<i>Micropterus salmoides</i> voucher ihb201306759	KP112316	China	99.53	AATTCA
<i>Micropterus salmoides</i> voucher ihb201306760	KP112315	China	99.53	AATTCA
<i>Micropterus salmoides</i> voucher ihb201306761	KP112314	China	99.53	AATTCA
<i>Micropterus salmoides</i> voucher ihb201306762	KP112313	China	99.53	AATTCA
<i>Micropterus salmoides</i> voucher ihb201306763	KP112312	China	99.53	AATTCA
<i>Micropterus salmoides</i> voucher ihb201306765	KP112311	China	99.53	AATTCA
<i>Micropterus salmoides</i> voucher ihb201306764	KP112310	China	99.53	AATTCA
<i>Micropterus salmoides</i> isolate Msa_124	KF558299	USA	99.53	AATTCA
<i>Micropterus salmoides</i> voucher NAFF 4368	HQ557411	Canada	99.84	GATTTA
<i>Micropterus salmoides</i> isolate Msa_125	KF558301	USA	99.38	GACTTA
<i>Micropterus salmoides</i> voucher CCDB-28228-G05	MG423016	Canada	99.53	AATTCG
<i>Micropterus salmoides</i> voucher NXG2012197	KX145587	Canada	99.53	AATTCA
<i>Micropterus salmoides</i>	KX459325	USA	99.37	GATTCA
<i>Micropterus salmoides</i> voucher ROM:ICH:BCF-0215-1	EU524132	Canada	99.53	AATTCA
<i>Micropterus salmoides</i> voucher ROM:ICH:BCF-0171-3	EU524837	Canada	99.37	AATTCA
<i>Micropterus salmoides</i> strain Andong.L.0.1	MK560633	Korea	99.53	GTTTTA
<i>Micropterus salmoides</i> strain Andong.L.0.2	MK560634	Korea	99.53	GTTTTA
<i>Micropterus salmoides</i> strain Andong.L.2.7	MK560635	Korea	99.53	GTTTTA
<i>Micropterus salmoides</i> voucher MISA-IL-KA1R-2-2	HQ557266	Canada	99.21	AATTCA
<i>Micropterus salmoides</i> voucher NXG2012181	KX145274	Canada	99.53	AATTCA
<i>Micropterus salmoides</i> voucher NXG201286	KX145132	Canada	99.53	AATTCA
<i>Micropterus salmoides</i> voucher 14_schs_AM_Fish8	KT307155	Canada	99.53	AATTCA
<i>Micropterus salmoides</i> voucher MISA-NY-SACR-4-1	HQ557285	Canada	99.53	AATTCA
<i>Micropterus salmoides</i> isolate Msal15746	KJ843419	USA	99.53	GACTTA
<i>Micropterus salmoides</i> isolate Msal15615	KJ843418	USA	99.53	GACTTA
<i>Micropterus salmoides</i> isolate Msal15614	KJ843417	USA	99.53	GACTTA
<i>Micropterus salmoides</i> voucher NAFF 1406	JN027236	Canada	99.36	AATTCA
<i>Micropterus salmoides</i> voucher NXG201238	KX145023	Canada	99.53	AATTCA
<i>Micropterus salmoides</i> voucher MISA-NY-SACR-4-2	HQ557286	Canada	99.36	AATTCA
<i>Micropterus salmoides</i> isolate Msal7	KJ843416	USA	99.51	AATTCA

**Accession #s to be deposited in GenBank

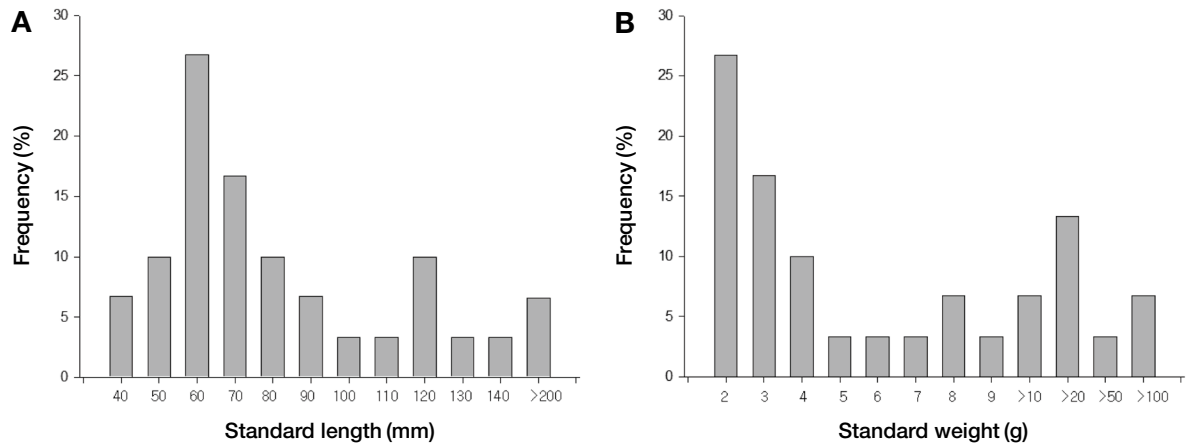


Fig. 2. The length and weight frequencies of the largemouth bass *M. salmoides* collected from seven sites on the Seomjin River in Korea.



Fig. 3. Multiple sequence alignment of the deduced COI in largemouth bass *Micropterus salmoides*. Twenty SNPs with alternative nucleotides between the Northern *M. salmoides* and the Florida *M. floridanus* subspecies are denoted by red asterisks. The blue rectangle marks specific SNP in largemouth bass from study sites in Korea. The arrows indicated six nucleotides for haplotype analysis in the *M. salmoides* largemouth bass northern subspecies. *M. salmoides* 1 (Korea): Acc #*, *M. salmoides* 2 (Korea): Acc #*, *M. salmoides* (USA): DQ536425, *M. salmoides* 1 (Canada): HQ557411, *M. salmoides* 2 (Canada): MG423016, *M. salmoides* 1 (China): HQ391896, *M. salmoides* 2 (China): KP112317, *M. floridanus* (China): HQ391897, *M. floridanus* (Philippines): KC684999, *M. floridanus* (USA): KJ843380. **Accession #s to be deposited in GenBank.

Tools/msa/clustalw2/) and then displayed using the GeneDoc Program (version 2.6.001). From phylogenetic analysis for DNA barcoding, seventeen different COI sequences were identified from GenBank in order to determine their similarity to

COI sequences of largemouth bass collected in Korea. Mega X software (version 10.04) was used to construct bootstrapped neighbor-joining trees with 1000 bootstrap replicates and to identify pairwise genetic distances. The relationships among

different haplotypes were analyzed using the NETWORK program (<http://www.fluxusengineering.com>).

Results and Discussion

1. COI gene characterization and homology analysis among *M. salmoides* largemouth bass

Largemouth bass have been widely distributed in reservoirs and rivers in Korea since their introduction in 1973, from Louisiana, USA, as a food supply resource (Lee *et al.*, 2008; Ellender *et al.*, 2011). However, no accurate information as to whether they belong to the Northern or Florida subspecies has been reported. In this study, most largemouth bass in the Seomjin River were 50 to 90 mm in body length and weighed less than 5 g (Supplementary Figs. 1 and 2). The body length and weight of the largest bass collected were 310 mm and 473 g, respectively, from the SJ 3 site (Fig. 1 and data not shown). To identify the origin of largemouth bass introduced in Korea, a 652 bp region of COI was amplified using genomic DNA of

the largemouth bass from Seomjin River (Fig. 3). The amplified COI sequences were found to be 99% homologous to those of *M. salmoides* (DQ536425) from the USA (Table 1), and 96%, 96%, and 97% homologous to those of *M. floridanus* from China (HQ391897), *M. floridanus* in the Philippines (KC684999), and *M. floridanus* in the USA (KJ843380), respectively. The deduced COI sequences closely matched those of the *M. salmoides* largemouth bass from USA. Twenty single nucleotide polymorphisms (SNPs) with alternative nucleotides were observed in the *M. salmoides* northern and Florida subspecies (red asterisk marked on Fig. 3). Li *et al.* (2012) also previously reported that there are 28 SNPs with alternative nucleotides in mitochondrial DNA in two subspecies of cultured and wild populations of largemouth bass.

2. Phylogenetic relationship among the genus *Micropterus* species using bass COI gene analysis

Phylogenetic analysis revealed that the largemouth bass in southwestern Korea clustered with *M. salmoides* (DQ536425)

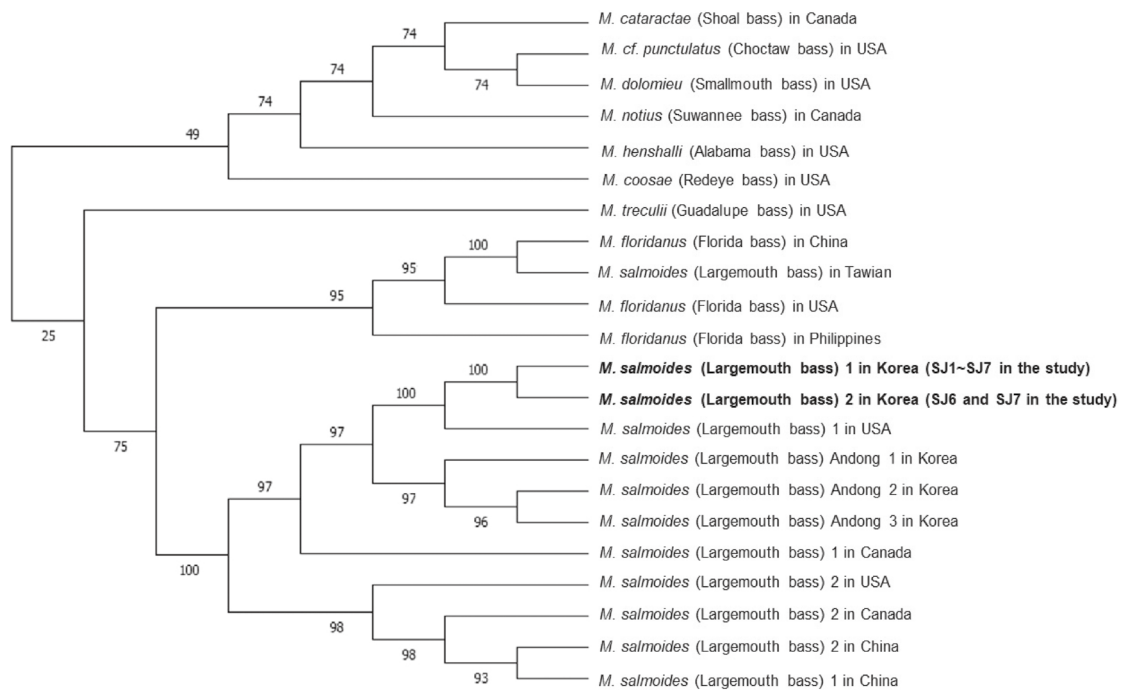


Fig. 4. Phylogenetic tree of the COI gene constructed by neighbor-joining analysis (bootstrap value = 1000). The numbers at the nodes are the percentage of bootstrap values. Amino acid sequences were aligned using Clustal X vers. 1.8. The following COI sequences were retrieved from GenBank; *Micropterus salmoides* 1 in Korea: Acc #**, *M. salmoides* 2 in Korea: Acc #**, *M. salmoides* 1 in USA: DQ536425, *M. salmoides* 2 in USA: KJ843437, *M. salmoides* Andong 1 in Korea: MK560633, *M. salmoides* Andong 2 in Korea: MK560634, *M. salmoides* Andong 3 in Korea: MK560635, *M. salmoides* 1 in Canada: HQ557411, *M. salmoides* 2 in Canada: MG423016, *M. salmoides* 1 in China: HQ391896, *M. salmoides* 2 in China: KP112317, *M. salmoides* in Taiwan: AP014537, *M. floridanus* in China: HQ391897, *M. floridanus* in Philippines: KC684999, *M. floridanus* in USA: KJ843380, *M. coosae* (red eye bass) in USA: KJ843437, *M. cataractae* (shoal bass) in Canada: JN027213, *M. henshalli* (Alabama bass) in USA: KJ843377, *M. cf. punctulatus* (choctaw bass) in USA: KJ843431, *M. dolomieu* (smallmouth bass) in USA: MF621711, *M. notius* (Suwannee bass) in Canada: JN027230, *M. treculii* (Guadalupe bass) in USA: MF977622. **Accession #s to be deposited in GenBank.

Table 2. Pairwise genetic distance among the genus *Micropterus* species from various countries based on the COI gene sequences

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1 <i>Ms</i> Seomjin1_Korea																						
2 <i>Ms</i> Seomjin2_Korea	0.001																					
3 <i>Mf</i> China	0.013	0.013																				
4 <i>Mf</i> Philippines	0.013	0.013	0.001																			
5 <i>Mf</i> USA	0.013	0.013	0.001	0.001																		
6 <i>Mc</i> Canada	0.059	0.059	0.059	0.059	0.059																	
7 <i>Mcfp</i> USA	0.032	0.032	0.032	0.032	0.032	0.052																
8 <i>Md</i> USA	0.059	0.059	0.045	0.045	0.045	0.059	0.038															
9 <i>Mh</i> USA	0.052	0.052	0.052	0.052	0.052	0.059	0.032	0.06														
10 <i>Mn</i> Canada	0.059	0.059	0.059	0.059	0.059	0.066	0.039	0.07	0.06													
11 <i>Mco</i> USA	0.007	0.007	0.013	0.013	0.013	0.059	0.031	0.06	0.05	0.059												
12 <i>Mt</i> USA	0.025	0.025	0.026	0.026	0.026	0.045	0.006	0.03	0.03	0.032	0.025											
13 <i>Ms</i> Tawian	0.013	0.013	0.001	0.001	0.001	0.059	0.032	0.05	0.05	0.059	0.013	0.026										
14 <i>Ms</i> 2 USA	0.002	0.002	0.026	0.026	0.026	0.073	0.045	0.07	0.07	0.073	0.012	0.039	0.03									
15 <i>Ms</i> 1 USA	0.001	0.001	0.013	0.013	0.013	0.059	0.032	0.06	0.05	0.059	0.007	0.025	0.01	0.013								
16 <i>Ms</i> 2 Canada	0.004	0.004	0.019	0.019	0.019	0.066	0.038	0.07	0.06	0.053	0.006	0.032	0.02	0.019	0.006							
17 <i>Ms</i> 1 Canada	0.006	0.006	0.013	0.013	0.013	0.059	0.032	0.06	0.05	0.059	0.007	0.025	0.01	0.013	0.004	0.006						
18 <i>Ms</i> 2 China	0.006	0.006	0.019	0.019	0.019	0.066	0.038	0.07	0.06	0.052	0.006	0.031	0.02	0.018	0.006	0.001	0.006					
19 <i>Ms</i> 1 China	0.006	0.006	0.019	0.019	0.019	0.066	0.038	0.07	0.06	0.052	0.006	0.031	0.02	0.018	0.006	0.001	0.006	0.001				
20 <i>Ms</i> Andong1_Korea	0.006	0.006	0.019	0.019	0.019	0.066	0.039	0.07	0.06	0.067	0.006	0.032	0.02	0.019	0.006	0.013	0.006	0.013	0.013			
21 <i>Ms</i> Andong2_Korea	0.006	0.006	0.019	0.019	0.019	0.066	0.039	0.07	0.06	0.067	0.006	0.032	0.02	0.019	0.006	0.013	0.006	0.013	0.013	0.001		
22 <i>Ms</i> Andong3_Korea	0.006	0.006	0.019	0.019	0.019	0.066	0.039	0.07	0.06	0.067	0.006	0.032	0.02	0.019	0.006	0.013	0.006	0.013	0.013	0.001	0.001	

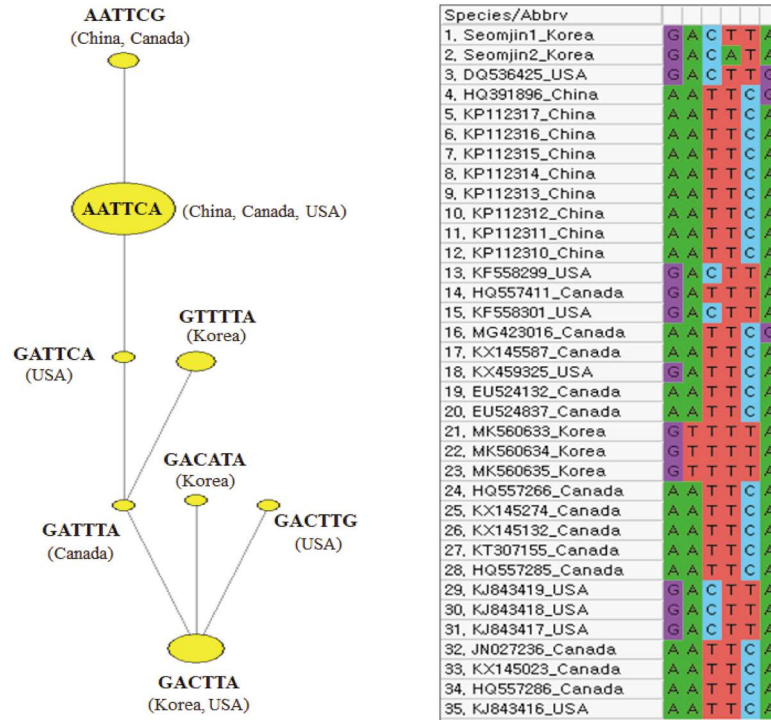


Fig. 5. Network analysis using haplotypes in the 35 *Micropterus salmoides* northern subspecies.

from the USA and Andong of Korea. Other *M. salmoides* in the USA exhibited one cluster with *M. salmoides* from China and Canada (Fig. 4) in neighbor joining trees. The northern subspecies of *M. salmoides* largemouth bass forms large clusters with most northern subspecies. In addition, *M. floridanus* (HQ391897) in China was clustered with *M. salmoides* (AP014537) from Taiwan, as well as with other *M. floridanus* from the USA and the Philippines. The shoal bass *M. cataractae* is evolutionarily related to the Suwannee bass *M. notius*, Alabama bass *M. henshalli*, and choctaw bass *M. cf. punctulatus* (Fig. 4 and Supplementary Fig. 2). Phylogenetic analysis suggested that the origin of wild largemouth bass in southwestern Korea is the *M. salmoides* northern subspecies, and not the Florida subspecies, *M. floridanus* (Fig. 4 and pairwise genetic distance = 0.001~0.006, see Table 2). The results also revealed that Taiwanese *M. salmoides*, registered as a northern subspecies in GenBank, is evolutionarily close to the largemouth Florida subspecies, and not to the northern subspecies (pairwise genetic distance = 0.001, see Table 2).

3. Genetic diversity in *M. salmoides* northern subspecies using haplotype and network analyses

To identify genetic diversity of the *M. salmoides* northern subspecies, we performed haplotype analysis with all *M. salmoides*

COI sequences in NCBI GenBank (Table 1). Eight haplotypes were characterized from COI sequence analysis of the *M. salmoides* largemouth bass based on nucleotide variations among the northern subspecies (arrow markers, Fig. 3). Two types of COI haplotypes were found across the seven sites of southwestern Korea. The type one haplotype was observed in all seven sites (SJ1~SJ7) of southwestern Korea. However, the type two haplotype was only observed in the Im-Sil area of sites 6 and 7. One nucleotide in the type two haplotype was unique in largemouth bass populations of southwestern Korea (blue rectangle, Fig. 3, and Table 1). These results suggested that the genetic diversity of largemouth bass was not high in the Seomjin River of southwestern Korea. Amplified fragment length polymorphism analysis also suggested that nine populations of largemouth bass display low genetic differentiation in Korea (heterozygosity 0.054~0.067, genetic diversity 0.069~0.085) (Lee *et al.*, 2008). The eight deduced haplotypes are shown in Fig. 5. Network analysis indicated that the major haplotype is that indicated as “AATTCA” from the *M. salmoides* northern subspecies in China, Canada, and USA. The haplotype “GACTTA” presented in *M. salmoides* largemouth bass in USA and Seomjin River sites of Korea in this study (Fig. 5). In addition, the haplotypes indicated as “GACATA” in this study and “GTTTGA” from GenBank were unique to *M. salmoides* largemouth bass of Korea. Such genetic analyses in largemouth

bass can be useful tools to identify origin and genetic distribution in bass populations.

Conclusions

Non-resident fishes such as largemouth bass (*M. salmoides*) have accelerated freshwater biodiversity loss due to reduction of native fish population as an invasive alien species. After their introduction to native ecosystems, there are no genetic identification of the largemouth bass, although their serious disturbance emerged in aquatic environments. In this study, we identified a genetic origin and diversity of the imported largemouth bass in southwestern Korea. Cytochrome oxidase subunit I (COI) gene analysis revealed that the largemouth bass from Seomjin River of Korea are genetically related to the *M. salmoides* largemouth bass from the USA. The size of collected largemouth bass were mostly small (< 100 mm). Two types of COI haplotypes and a major haplotype of the eight haplotypes were found across the seven sites of southwestern Korea. These results provide to genetic information of the *M. salmoides* largemouth bass in southwestern Korea for identifying the origin and diversity in natural ecosystem.

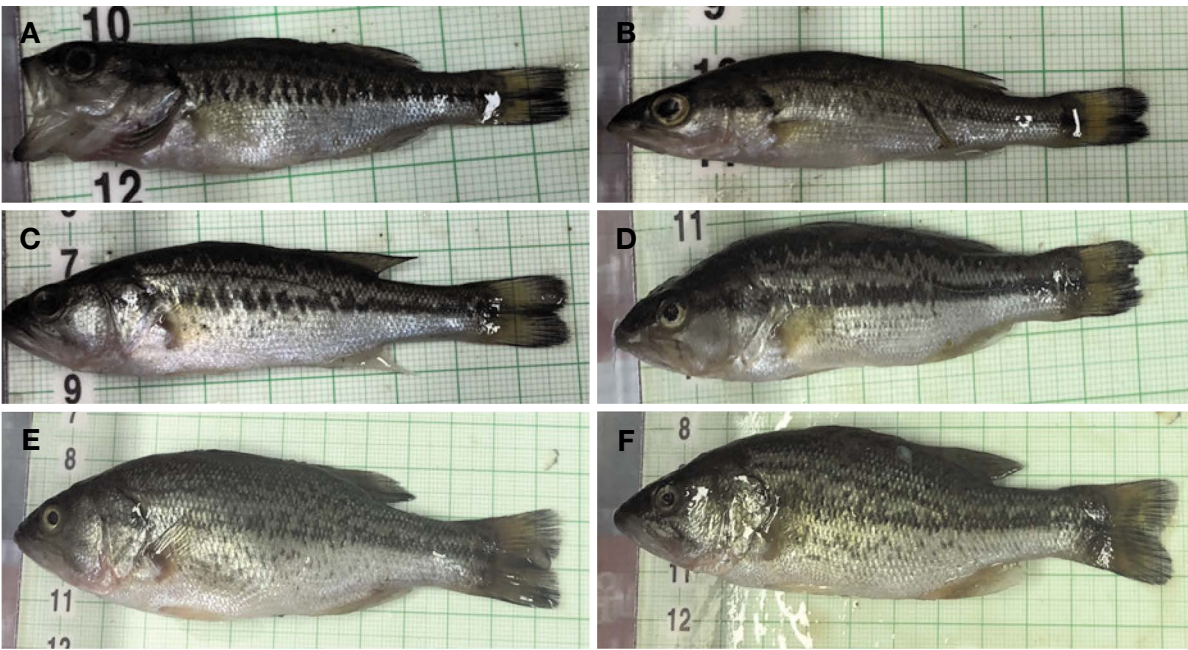
Acknowledgments

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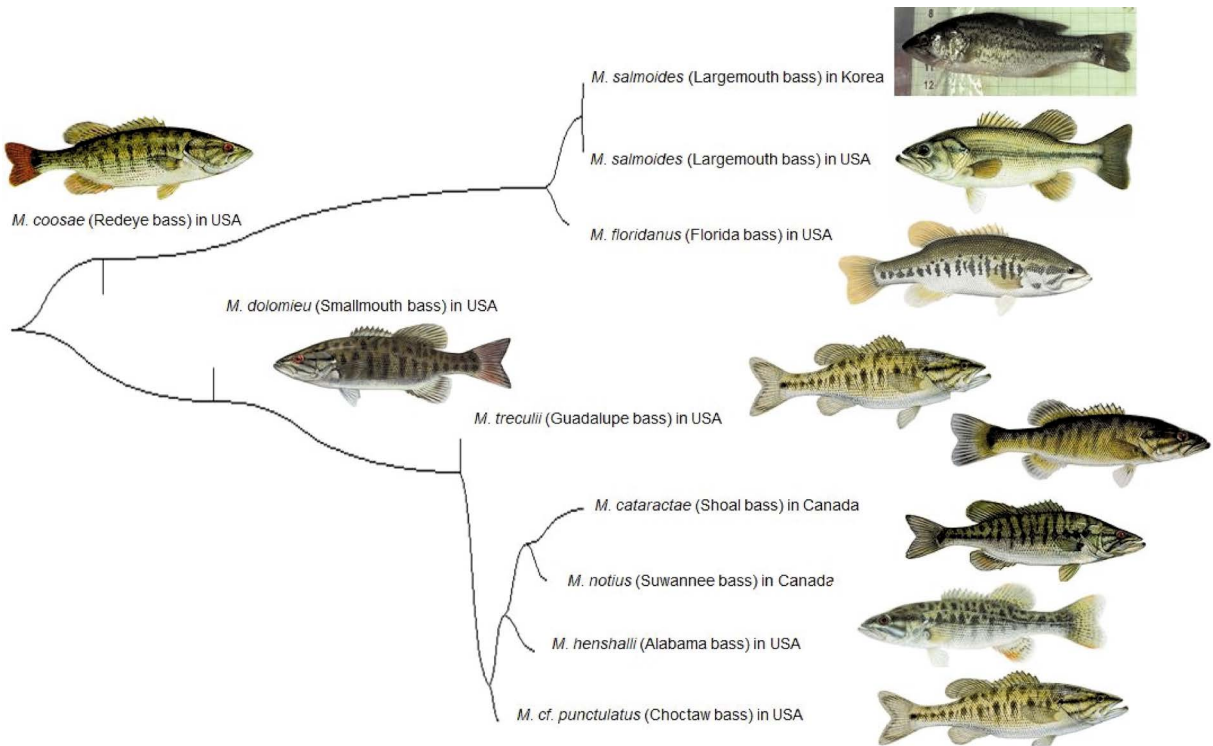
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Supplementary Fig. 1. Morphological identification of largemouth bass *M. salmoides*, following size distribution. (A) and (B) small bass (<60 mm), (C) and (D) small bass (60~100 mm), (E) and (F) intermediate bass (> 100 mm) collected from seven sites on the Seomjin River in Korea.



Supplementary Fig. 2. Phylogenetic relationship of the *Micropterus* fish using neighbor-joining analysis (COI gene).