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Habitat use by the Formosan landlocked salmon *Oncorhynchus masou formosanus*

Chorng-Bin Hsu[1], Chyng-Shyan Tzeng[2], Chao-Hsien Yeh[3], Wen-Hui Kuan[4], Mei-Hwa Kuo[5], Hsing-Juh Lin[1, 6,*]

[1]Department of Life Sciences, National Chung Hsing University, Taichung 402, Taiwan
[2]Institute of Bioinformatics and Structural Biology, National Tsing Hua University, Hsinchu 300, Taiwan
[3]Department of Water Resources Engineering and Conservation, Feng Chia University, Taichung 407, Taiwan
[4]Department of Safety, Health and Environmental Engineering, Ming Chi University of Technology, Taipei 243, Taiwan
[5]Department of Entomology, National Chung Hsing University, Taichung 402, Taiwan
[6]Biodiversity Research Center, Academia Sinica, Taipei 115, Taiwan

ABSTRACT: The critically endangered Formosan landlocked salmon *Oncorhynchus masou formosanus* is one of the southernmost natural salmon populations in the world, which only occurs in Chichiawan Stream and its tributaries in the Wuling basin of subtropical Taiwan. We examined habitat uses by different size classes of the Formosan salmon and the sympatric shovelmouth minnow *Varicorhinus barbatulus*, and identified the relative importance of environmental variables, biotic components and seasonal effects in explaining the variance in the relative occurrences of fish at the catchment scale. After removing seasonal effects, 74.9 % of the variation in the relative occurrence of fish was explained by the measured environmental variables and biotic components. Habitat uses by the Formosan salmon and shovelmouth minnow were distinct. The shovelmouth minnow occurred more frequently at sites with a high concentration of NH_3-N and high proportions of gravel and riffles, while the Formosan salmon utilized sites at high elevations. Habitat uses by Formosan salmon of different size classes varied slightly. Juvenile and subadult salmon inhabited sites with lower temperatures and current velocities, but adult salmon occurred more frequently with large-grain-sized substratum. Our study showed that variations in the relative occurrence of fish in the Wuling basin were best explained by physicochemical parameters (38.8 %), followed by substratum composition (11.4 %). The variations exclusively explained by mesohabitat composition, seasonal effects, and biotic components were not significant. This conclusion has important consequences for local managers and conservationists.

KEY WORDS: Physicochemical parameter · Substratum · Habitat composition · Biotic component · Chichiawan Stream · Taiwan

INTRODUCTION

Habitats are areas that offer the resources and conditions which support occupancy by a species (Morrison et al. 2006). Wildlife management and conservation plans are often based upon patterns of habitat use by focal species. Habitat attributes in streams are comprised of physical features, water quality, and biotic components (Marcus et al. 1990). Hydrology, current velocity, water depth, and substratum are often the most important variables affecting habitat use by stream fishes (Sheppard & Johnson 1985, Heggenes 1990, 1996, Lamouroux et al. 1999, Yu & Lee 2002, Balcombe & Arthington 2009). However, biotic attributes of habitats, such as aquatic insects and periphyton, which serve as food resources, and their relative importances are generally less often addressed.

Previous studies have shown that habitat use by fishes varies with their age and size class and also with season. Heggenes (1996) indicated that habitat use

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*Corresponding author. Email: hjlin@dragon.nchu.edu.tw depended on fish species and size. Habitats being occupied by different size classes may reflect ontogenetic habitat shifts (Nowak et al. 2004), showing microhabitat segregation of fishes of different sizes (Greenberg et al. 1996, Mäki-Petäys et al. 1997). Many stream fishes also shift habitat use by season (Baltz et al. 1991, Harvey & Stewart 1991, Heggenes et al. 1991, Bonneau & Scarnecchia 1998, Nagayama & Nakamura 2007). Other factors, such as predation and competition, are of great importance in habitat use by stream fishes (Grossman et al. 1987, 1998, Schlosser 1987, Greenberg 1994).

Integration of catchment-scale considerations into management and conservation planning has recently gained momentum (Smith et al. 2003). Most of the above-mentioned studies on habitat use by stream fishes focused on attributes at the scale of the microhabitat (i.e. the position of the fish) or mesohabitat (i.e. riffles and pools). For stream management, knowledge of habitat requirements at the micro- or mesohabitat scale is valuable in mitigating the effects of habitat alterations caused by stream regulation and restoring stream habitats for fish conservation. However, habitat preferences of fish are highly variable and vary in time and space (Heggenes & Saltveit 1990). Fish may choose microhabitats with optimum combinations of 2 or more variables rather than positions with preferred levels of a single variable. In addition, habitat variables usually cannot be properly separated in field studies (Heggenes 1990). Bult et al. (1998) argued that habitat selection studies should focus on identifying scales most appropriate to management questions. Streams are recognized as patchy habitats (Hynes 1970). Stream monitoring and management are usually carried out at the catchment scale, which contains various types of microhabitats and wide ranges of variables. Studies at the catchment scale provide information not only on fish distributions, thus revealing habitat preferences, but also interactive effects of environmental variables on habitat use, which can greatly improve our ability to manage and conserve these fishes.

Chichiawan Stream, which is an upper tributary of the Tachia River, is the last refuge of the endemic Formosan landlocked salmon *Oncorhynchus masou formosanus*, one of the southernmost natural salmon populations in the world (Oshima 1955). The Formosan salmon moves upstream and downstream for only short distances (Makiguchi et al. 2009). It was formerly distributed in all upper tributaries of the Tachia River and served as one of the main food sources for local residents (Kano 1940). Overexploitation and habitat degradation due to agricultural development and establishment of check dams led to severe decreases in the abundance and distributional area of the Formosan salmon after the 1960s (Tsao 1995). The Formosan salmon was listed as an endangered species by the Taiwanese government in 1984 when the population declined to about 200 individuals (Lin et al. 1987). The Word Conservation Union (IUCN) further listed this fish as a critically endangered species (Kottelat 1996). At present, the salmon population is distributed only in reaches of Chichiawan Stream and its tributaries of the Wuling basin located in the Shei-Pa National Park, central Taiwan.

Due to its critically endangered status, the abundance of the Formosan salmon has been extensively monitored since 1984 (Tzeng 2005). Results of the monitoring implied that habitat is of great importance in determining the abundance of this species. Natural calamities, such as typhoons and floods, are thought to be the most important factors influencing population dynamics (Tzeng 2005). Substratum composition (e.g. substrate size, Tsao et al. 1998, Chung et al. 2008) and hydrological conditions (e.g. current velocity and water depth, Tsao et al. 1998) were also emphasized as important factors in habitat use by the Formosan salmon. A variety of ecological engineering methods were used to protect the Formosan salmon, including the construction of a hatchery center and sheltered channels, stream bank treatment, and demolition of check dams (Lin et al. 2004, Chung et al. 2008). However, there is little empirical evidence indicating relationships between the occurrence of the Formosan salmon and environmental variables. Moreover, the shovelmouth minnow *Varicorhinus barbatulus* is the second most abundant fish species in these streams (Tzeng 2005). Although their diets differ, the shovelmouth minnow was observed to compete with juvenile salmon for space (Tsao et al. 1996). The relative importance of physicochemical parameters, compositions of the mesohabitat and substrata, biotic components, and seasonal effects on the occurrence of the Formosan salmon in the Wuling basin have never been examined.

This work is an integrated study that focused on examining habitat uses by the Formosan salmon and the sympatric shovelmouth minnow at the catchment scale. The aims of this study were to (1) examine habitat uses by the 2 most abundant fish species in relation to size classes in Chichiawan Stream, and (2) identify the relative importance of the influences of environmental variables, including physicochemical parameters and compositions of the mesohabitat and substrata, and biotic components on the relative occurrences of the 2 fish species.

MATERIALS AND METHODS

Study area and sampling sites. The study was conducted in the Wuling basin, comprising 3 third-order streams (Chichiawan, Yousheng, and Kaoshan) and

2 second-order streams (Taoshan West and Taoshan North; Fig. 1). The stream beds were primarily created by deposition of weathered sandstone and slate. The mean water temperature is 12°C, ranging from 18°C in summer to 10°C in winter. The mean annual precipitation is 1642 mm; the mean monthly rainfall is generally <100 mm in the dry season (September to March), and frequently exceeds 220 mm in the wet season (April to August; 1971 to 2000 data from Wuling station, Climatological data annual reports, Taiwan Central Weather Bureau). The mean discharge was 1.84 to 2.30 $m^3 s^{-1}$ in the dry season and 2.58 to 2.96 $m^3 s^{-1}$ in the wet season (Chung et al. 2008).

Chichiawan Stream originates from Mt. Tao (3324 m), Mt. Chihyu (3301 m), and Mt. Pingtein (3536 m). It is 15.3 km long and 7.1 to 12.3 m wide with a mean gradient of 130 m km^{-1} and a catchment area of 76 km^2 (Lin et al. 1990). The stream bed consists of a high proportion of pebbles (42%) in winter, but is dominated by cobbles (26%) and boulders (21%) in summer (Yeh 2006). Taoshan West and Taoshan North Streams are the upper reaches of Chichiawan Stream and are bordered by riparian forest. The lower reach of Chichiawan Stream was developed for agriculture, including an area of 104 ha of vegetables, apples, peaches, and pears. It is considered to be moderately influenced by agriculture (Yu & Lin 2009).

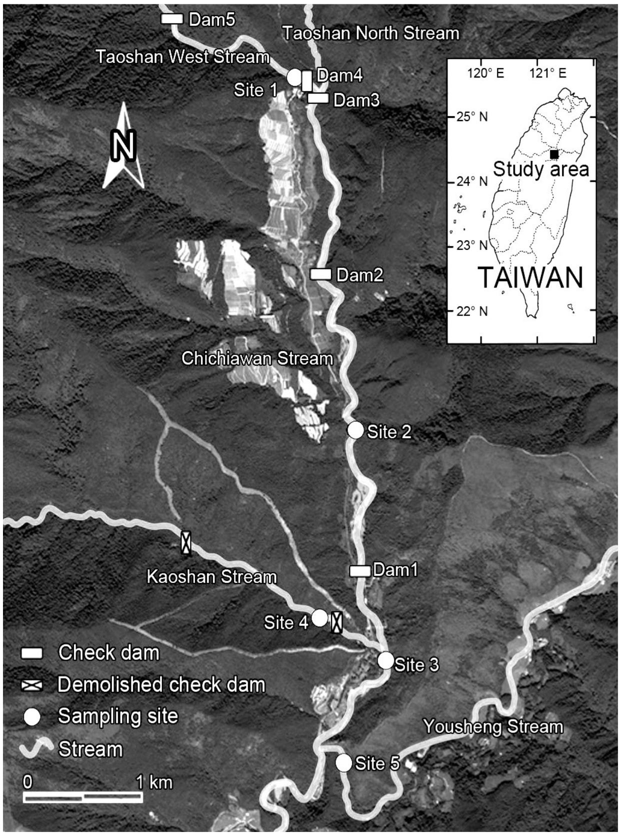

Fig. 1. Study area and locations of the 5 sampling sites in the Wuling basin

Kaoshan Stream is 10.6 km long with a mean gradient of 140 m km^{-1} and a catchment area of 40 km^2. The streambed is dominated by pebbles (39%) and cobbles (27%) in winter, but consists of a high proportion of boulders (44%) in summer (Yeh 2006). This catchment is covered by natural forests, and no agriculture is present, so the stream is assumed to be in a pristine state for comparison (Yu & Lin 2009). Yousheng Stream is 11.4 km long with a mean gradient of 68 m km^{-1} and a catchment area of 31 km^2. The substrate is dominated by gravel (39%) and pebbles (39%; Yeh 2006). The entire stream with an area of 295 ha has been intensively developed for farming vegetables since the 1970s. The stream has been channelized, and the natural riparian vegetation has been almost completely removed. It is regarded as highly influenced by agriculture (Yu & Lin 2009). Canopy cover was higher in Kaoshan Stream (90%) and the upper reaches of Chichiawan Stream (86%) and lower in the lower reaches of Chichiawan Stream (57%) and Yousheng Stream (50%).

Five long-term monitoring sites were selected in the Wuling basin (Fig. 1). Site 1, the upstream site, was located in Taoshan West Stream at an elevation of 1900 m. Sites 2 and 3 were located on Chichiawan Stream. Site 2 was in the midstream reach of Chichiawan Stream, between check dams 1 and 2, where agricultural land use is dominated by the farming of fruits and vegetables. Check dam 2 was demolished by a flood caused by a typhoon in 2004. Site 3 was downstream of the confluence with Kaoshan Stream. The elevation was 1790 m at Site 2 and 1742 m at Site 3. Site 4 was located in Kaoshan Stream at an elevation of 1776 m. Check dams along the entire stream were demolished in 2001. Site 5 was located in the downstream section of Yousheng Stream before its confluence with Chichiawan Stream. The elevation at this site was 1770 m.

Environmental variables, including physicochemical parameters and compositions of the mesohabitat and substrata, biotic components, including densities of aquatic insects and periphyton biomass, and fish abundances, were determined seasonally in January (winter), April (spring), July (summer), and October (autumn) at each site for over 3 yr from winter 2005 to winter 2008.

Physicochemical parameters. We measured 13 physicochemical parameters at each site. On each sampling occasion, water temperature, pH, conductivity, turbidity, and dissolved oxygen (DO) were measured *in situ* with portable meters (YSI 6560 multiparameter monitoring sensors) between 07:00 and 10:00 h. Water depth and current velocity at 60% of the depth from the surface were determined with a velocimeter (Son Tek Flow Tracker Handheld ADV). Water samples for other parameters were immediately placed on ice in a cooler and brought back to the laboratory for analyses of nitrite (NO_2^-), nitrate (NO_3^-), ammonium (NH_4^+), total phosphorus (TP), total organic carbon (TOC), biological oxygen demand (BOD), and SiO_2 following standard methods of the American Public Health Association (Clesceri et al. 1998).

Mesohabitat and substratum composition. Four types of habitat were classified according to the values of the Froude number (*Fr*). *Fr* is a dimensionless velocity–depth ratio, which is calculated by the following formula:

$$Fr = \frac{Vm}{\sqrt{gY}} \tag{1}$$

where *Vm* is the mean velocity at a sample point (m s^{-1}), *Y* is the water depth (m), and *g* is the acceleration due to gravity (9.81 m s^{-2}).

In hydraulic terms, *Fr* classifies flow as either subcritical ($Fr < 1$) or supercritical ($Fr > 1$) (Davis & Barmuta 1989). In this study, we defined the flow condition of 4 types of habitats: pools ($Fr < 0.095$), runs ($0.095 < Fr < 0.255$), riffles ($0.255 < Fr < 1$), and rapids ($Fr > 1$). The proportions of the 4 habitat types at each site on each sampling occasion were estimated.

The substratum was classified into 6 types according to the grain size: smooth surface (<0.2 cm), gravel (0.2–1.6 cm), pebbles (1.6–6.4 cm), cobbles (6.4–25.6 cm), small boulders (25.6–51.2 cm), and large boulders (>51.2 cm). Proportions of the 6 substratum types at each site on each sampling occasion were estimated.

Periphyton. Epilithic algal samples were collected from randomly selected rocks (n = 9) at each site on each sampling occasion. On each rock, a frame made of steel was used to define a sampling area of an algal patch of 12.5 cm^2, and 4 algal patches were scraped off a surface area of 50 cm^2 with a toothbrush. The scraped algae were then washed off the toothbrush and rocks with 50–100 ml of filtered stream water. In the laboratory, the algal samples were centrifuged for 10 min to concentrate them to 5 ml. A 3 ml subsample was extracted for chlorophyll (chl) *a* in 90% acetone for 24 h at 4°C in the dark and determined spectrophotometrically (Lobban et al. 1988). The other 2 ml subsample was fixed in Lugol's solution for taxon identification using a light microscope with differential interference contrast (Zeiss Axioplan 2).

Aquatic insects. Benthic aquatic insects were sampled using a Surber sampler (with an area of 30.48 × 30.48 cm and a mesh size of 250 µm). Six random samples in runs and riffles were taken at each site on each sampling occasion. Samples were preserved in 70% ethanol in the field and transported to the laboratory. All aquatic insects were identified to genus or species using available keys (Kang 1993, Merritt & Cummins 1996, Kawai & Tanida 2005) except for the Chironomidae, members of which were classified into Tanypodinae and non-Tanypodinae only. The mean density of aquatic insects was calculated for each site.

Fish. The Formosan landlocked salmon *Oncorhynchus masou formosanus* and the shovelmouth minnow *Varicorhinus barbatulus* are the 2 most abundant fish species in the Wuling basin. Other sympatric fishes, such as the tasseled-mouth loach *Formosania lacustre* and candidius goby *Rhinogobius candidianus*, only occurred in very low abundances (Tzeng 2005) and were not included in the analyses. Due to the critically endangered status of the Formosan salmon, underwater observation is the only way to estimate its occurrence in the streams. This is a non-destructive method and has minimal impact on the fish population and environment. This technique has long been used to estimate both relative and total abundances (Slaney & Martin 1987) and to study fish habitat use, especially regarding riverine juvenile salmonid populations (O'Neal 2007).

Fish populations were counted by snorkeling during the daytime between 10:00 and 17:00 h. Counting began at the downstream end at each site (~300 m long) and was completed in a single upstream pass. Two trained snorkelers slowly swam upstream in parallel with the main channel and counted fish outwards and towards the bank nearest to them to avoid double-counting. Fish length estimation was practiced prior to the actual counting on objects of known length lying on the stream bottom with the help of a ruler for size estimation.

The Formosan salmon reaches sexual maturity and begins breeding in its second (subadult) to third year (adult; Chung et al. 2007). Its longevity is about 3 yr. Generations of the fish overlap. The 3 main life stages can be classified according to the fish total length (Chung et al. 2007): 5–15 cm for juvenile salmon, 15–25 cm for subadult salmon, and >25 cm for adult salmon. There has been little study of the biology of the shovelmouth minnow. Classification of size classes was based on the total length of the Formosan salmon. The total abundance of each size class for both fishes was recorded at each site. Relative occurrences were calculated by dividing the abundances of various size classes for both fishes by the total number of individuals recorded at each site.

Data analysis. Differences in physicochemical parameters, compositions of the mesohabitat and substrata, density of aquatic insects, and periphyton biomass in terms of chl *a* concentrations among sampling sites and among seasons were examined using Kruskal-Wallis non-parametric tests with *a posteriori* Student-Newman-Keuls (SNK) comparisons (Zar 1996).

Habitat uses by different size classes of both fishes were analyzed using multivariate techniques. Relative occurrences of various size classes for both fishes were used as response variables. A prior detrended correspondence analysis (DCA) was first conducted to assess the gradient length of the first DCA axis, which was 3.243 (in SD units) in the range between 3 and 4. The result suggested that both types of ordination methods, linear and unimodal models, were appropriate for the analysis (ter Braak & Šmilauer 2002). In this study, we used a linear model (e.g. redundancy analysis, RDA) to analyze these data. In the RDA models, environmental variables, biotic components, and seasonal effects were used as explanatory variables. Seasonal effects were coded as dummy variables. Due to the large number of explanatory variables, we ran the analysis using the automatic forward-selection mode, and only variables explaining a significant proportion of the remaining variation were included (based on a Monte Carlo test with 4999 permutations at $p < 0.1$). Since most of the environmental variables and relative occurrences of fish showed seasonal variability, a partial RDA was performed to remove the seasonal effects.

Borcard et al. (1992) developed a new method for partitioning variations among components in ecological datasets using canonical ordination techniques. Their studies highlighted the importance of the potential overlap in various components. In this study, we emphasized the proportion of variations in the relative occurrence of fish that could be exclusively explained by each category of variables. We performed a series of partial RDAs to quantify the relative contribution of each category of the environmental variables, including physicochemical parameters and compositions of the mesohabitat and substrata, biotic components, and seasonal effects to the total variation explained (TVE) of the relative occurrence of fish. In the partial RDA, variables not of direct interest were included as covariables, and the effects of these variables on the variance in the relative occurrence of fish were partitioned out (Legendre & Legendre 1998). The statistical significance of the proportion of variations in the relative occurrence of fish explained by each category of variables was examined with a Monte Carlo permutation test (ter Braak & Šmilauer 2002).

Kruskal-Wallis tests and SNK comparisons were conducted using the software package SAS 9.1 (SAS Institute 2003). All multivariate analyses were performed using CANOCO for Windows v. 4.52 (ter Braak & Šmilauer 2002). For the multivariate analysis, the relative occurrence of fish was transformed using the formula $\log(100x + 1)$ provided by the CANOCO software (ter Braak & Šmilauer 2002). The density of aquatic insects was $\log(x + 1)$ transformed. The concentration of periphyton chl *a* was also log transformed. Among physicochemical parameters, pH, TOC, temperature, and current velocity were not transformed. DO, BOD, conductivity, and concentrations of SiO_2, TP, NH_3-N, and NO_x-N (NO_2-N + NO_3-N) were log transformed, and turbidity was square root transformed to improve the multivariate normality. Compositions of the substrata and mesohabitat were arcsine square root transformed (Zar 1996).

RESULTS

Physicochemical parameters

The 5 sampling sites showed similar physicochemical characteristics, except for conductivity and concentration of NO_x-N ($p < 0.001$, Kruskal-Wallis tests, Table 1). Mean values of conductivity and concentrations of NO_x-N were highest at Site 5, followed by Site 2 (Table 1). Both variables were correlated with fertilizers derived from agricultural activities, suggesting that the water quality was affected by the intensive agricultural activities in streams of the Wuling basin.

Most of the physicochemical parameters varied seasonally (Table 2). DO and concentrations of NH_3-N, TP, and TOC showed higher values in spring ($p < 0.01$, Kruskal-Wallis and SNK tests). BOD was higher in winter and lower in spring and summer ($p < 0.001$). Turbidity was higher in summer than in spring ($p < 0.01$).

Compositions of the mesohabitat and substrata

Riffles were the most typical mesohabitat across all sampling sites, comprising about 55 to 71% of the reach area (Table 1). Mesohabitat compositions did not significantly differ among sites ($p > 0.05$, Kruskal-Wallis test). Substratum compositions were dominated by pebbles (21 to 41%) and cobbles (21 to 36%; Table 1). Significantly higher proportions of gravel and pebbles and lower proportions of large boulders were observed at Site 5 ($p < 0.05$, Kruskal-Wallis and SNK tests).

There were significant seasonal differences in compositions of the mesohabitat and substrata (Table 2). Proportions of runs were significantly higher in winter, but those of riffles were significantly higher in summer ($p < 0.001$, Kruskal-Wallis and SNK tests). Proportions of small and large boulders were significantly lower in winter ($p < 0.05$, Kruskal-Wallis and SNK tests).

Table 1. Mean (± SE) of physicochemical parameters and mesohabitat and substratum compositions at 5 sampling sites (Kruskal-Wallis test followed by Student-Newman-Keuls multiple comparisons). Different superscripts for sites indicate a significant difference (n = 12, except for total phosphorus and NH_3-N, n = 11). NTU: nephelometric turbidity units. *p < 0.05, **p < 0.01, ***p < 0.001, all other values are not significant

Environmental variable	Site 1	Site 2	Site 3	Site 4	Site 5	Kruskal-Wallis test
Physicochemical parameter						
Dissolved oxygen (mg l^{-1})	10.2 ± 0.3	9.5 ± 0.4	9.8 ± 0.4	9.8 ± 0.4	9.3 ± 0.4	3.53
Turbidity (NTU)	0.47 ± 0.11	0.82 ± 0.23	1.09 ± 0.27	1.99 ± 0.80	1.94 ± 0.60	5.53
pH	7.69 ± 0.13	7.66 ± 0.11	7.59 ± 0.11	7.60 ± 0.12	8.00 ± 0.16	6.93
Conductivity (µs cm^{-1})	186.1 ± 15.4^{b}	240.2 ± 18.8^{ab}	201.0 ± 13.9^{b}	188.0 ± 11.9^{b}	283.6 ± 17.4^{a}	18.61***
Biochemical oxygen demand (mg l^{-1})	1.15 ± 0.83	1.07 ± 0.66	1.27 ± 0.75	1.17 ± 0.78	1.12 ± 0.62	1.34
SiO_2 (mg l^{-1})	2.81 ± 0.56	3.09 ± 0.59	3.33 ± 0.59	3.61 ± 0.60	3.08 ± 0.53	1.16
Total phosphorus (ppm)	0.032 ± 0.017	0.015 ± 0.006	0.008 ± 0.003	0.013 ± 0.005	0.027 ± 0.010	1.69
NH_3-N (mg l^{-1})	0.022 ± 0.013	0.023 ± 0.015	0.026 ± 0.014	0.033 ± 0.024	0.046 ± 0.020	4.84
Total organic carbon (mg l^{-1})	0.652 ± 0.092	0.670 ± 0.096	0.701 ± 0.093	0.686 ± 0.093	0.946 ± 0.114	4.56
NO_x-N (mg l^{-1})	0.123 ± 0.019^{d}	1.223 ± 0.100^{b}	0.326 ± 0.056^{c}	0.163 ± 0.024^{d}	1.838 ± 0.193^{a}	47.53***
Temperature (°C)	11.8 ± 1.0	13.0 ± 0.8	12.5 ± 0.9	11.8 ± 0.7	14.8 ± 0.7	8.64
Current velocity (m s^{-1})	0.39 ± 0.06	0.37 ± 0.06	0.48 ± 0.07	0.50 ± 0.05	0.40 ± 0.06	4.78
Mesohabitat composition (%)						
Pools	14.4 ± 7.9	6.1 ± 5.2	3.2 ± 2.7	9.1 ± 3.6	13.0 ± 6.5	7.13
Runs	15.5 ± 4.5	15.3 ± 7.4	19.5 ± 7.3	18.9 ± 6.6	14.9 ± 6.5	2.71
Riffles	60.0 ± 8.2	70.7 ± 9.0	66.7 ± 7.1	54.9 ± 8.2	69.1 ± 10.5	3.50
Rapids	9.8 ± 3.1	7.5 ± 3.8	10.1 ± 5.3	8.8 ± 5.9	3.2 ± 1.6	3.68
Substratum composition (%)						
Smooth surface	4.4 ± 1.6	4.2 ± 1.5	3.7 ± 1.4	4.0 ± 1.1	5.7 ± 1.8	0.79
Gravel	19.2 ± 4.2^{ab}	10.7 ± 2.0^{b}	24.4 ± 3.9^{ab}	12.2 ± 2.2^{ab}	27.0 ± 4.4^{a}	11.40*
Pebbles	39.9 ± 5.9^{a}	29.4 ± 5.3^{ab}	28.3 ± 6.1^{ab}	21.2 ± 2.9^{b}	40.8 ± 3.0^{a}	13.79**
Cobbles	20.5 ± 4.2	35.6 ± 3.3	21.4 ± 4.0	33.1 ± 4.9	20.6 ± 4.3	10.14*
Small boulders	12.7 ± 3.7	13.8 ± 3.2	13.9 ± 2.4	15.4 ± 3.3	4.7 ± 2.7	9.31
Large boulders	2.9 ± 1.4^{ab}	5.7 ± 2.4^{ab}	7.9 ± 1.7^{a}	13.9 ± 5.3^{a}	1.2 ± 0.8^{b}	12.62*

Table 2. Mean (± SE) of physicochemical parameters and mesohabitat and substratum compositions in 4 seasons (Kruskal-Wallis test followed by Student-Newman-Keuls multiple comparisons). Different superscripts for seasons indicate a significant difference (n = 15, except for total phosphorus and NH_3-N, n = 10 in winter). NTU: nephelometric turbidity units. *p < 0.05, **p < 0.01; ***p < 0.001, all other values are not significant

Environmental variable	Spring	Summer	Autumn	Winter	Kruskal-Wallis test
Physicochemical parameter					
Dissolved oxygen (mg l^{-1})	10.7 ± 0.3^{a}	9.4 ± 0.2^{b}	9.1 ± 0.4^{b}	9.7 ± 0.3^{b}	13.60**
Turbidity (NTU)	0.61 ± 0.26^{b}	1.82 ± 0.34^{a}	1.81 ± 0.72^{ab}	0.81 ± 0.19^{ab}	11.48**
pH	7.90 ± 0.10	7.67 ± 0.09	7.42 ± 0.15	7.85 ± 0.09	7.01
Conductivity (µs cm^{-1})	225.2 ± 16.4	191.7 ± 12.0	228.1 ± 18.9	234.1 ± 17.9	3.62
Biochemical oxygen demand (mg l^{-1})	0.33 ± 0.08^{b}	0.23 ± 0.08^{b}	0.66 ± 0.12^{a}	3.41 ± 1.08^{a}	20.37***
SiO_2 (mg l^{-1})	2.31 ± 0.37	3.80 ± 0.61	3.22 ± 0.43	3.38 ± 0.52	5.26
Total phosphorus (ppm)	0.026 ± 0.011^{a}	0.037 ± 0.009^{a}	0.003 ± 0.001^{b}	0.006 ± 0.003^{b}	18.57***
NH_3-N (mg l^{-1})	0.088 ± 0.022^{a}	0.010 ± 0.006^{b}	0.011 ± 0.004^{b}	0.002 ± 0.000^{b}	15.66**.
Total organic carbon (mg l^{-1})	0.922 ± 0.084^{a}	0.544 ± 0.081^{b}	0.576 ± 0.056^{b}	0.882 ± 0.091^{a}	12.37**
NO_x-N (mg l^{-1})	0.733 ± 0.217	0.835 ± 0.213	0.645 ± 0.166	0.725 ± 0.209	0.92
Temperature (°C)	11.3 ± 0.5^{c}	16.1 ± 0.5^{a}	13.4 ± 0.5^{b}	10.3 ± 0.5^{c}	34.85***
Current velocity (m s^{-1})	0.33 ± 0.05	0.49 ± 0.04	0.43 ± 0.05	0.47 ± 0.06	5.24
Mesohabitat composition (%)					
Pools	20.5 ± 8.5	1.5 ± 0.7	3.2 ± 1.8	11.5 ± 3.0	6.36
Runs	8.9 ± 2.5^{b}	6.1 ± 1.9^{b}	11.1 ± 3.9^{b}	41.2 ± 7.2^{a}	18.69***
Riffles	60.7 ± 8.1^{b}	86.3 ± 4.5^{a}	66.5 ± 6.3^{b}	43.8 ± 7.4^{b}	17.12***.
Rapids	6.9 ± 2.7	3.8 ± 2.0	17.5 ± 6.0	3.3 ± 1.4	5.40
Substratum composition (%)					
Smooth surface	5.0 ± 1.6	5.9 ± 1.6	3.3 ± 1.0	3.4 ± 1.0	1.59
Gravel	16.5 ± 3.7	25.3 ± 4.2	13.1 ± 2.8	19.9 ± 2.3	6.42
Pebbles	30.4 ± 5.6	27.3 ± 4.2	29.2 ± 2.5	40.8 ± 5.3	3.45
Cobbles	22.3 ± 4.2	23.1 ± 3.7	31.7 ± 2.6	27.9 ± 5.1	3.67
Small boulders	13.9 ± 3.3^{ab}	12.5 ± 3.7^{ab}	16.0 ± 2.5^{a}	6.0 ± 1.6^{b}	8.47*
Large boulders	11.6 ± 4.3^{a}	5.8 ± 2.1^{ab}	6.6 ± 1.8^{a}	1.3 ± 0.8^{b}	8.72*

Fish

The Formosan salmon was distributed at all sites in Taoshan West, Chichiawan, and Kaoshan Streams, but not at Site 5 in Yousheng Stream (Fig. 2). This species reproduces in winter (November, Chung et al. 2007), and the relative occurrence of small-sized individuals (i.e. juveniles) was thus observed to increase in summer and decrease during autumn and winter, while those of large (adults) and medium-sized (subadults) salmon remained constant from spring to autumn and decreased in winter (Fig. 2). The shovelmouth minnow was dominant at Site 3 in Chichiawan Stream and Site 5 in Yousheng Stream, contributing more than half to the fish populations. Small numbers were found at Site 2. The relative occurrence of the shovelmouth minnow was constant from winter to summer, but was lower in autumn. The dominant size class of the shovelmouth minnow was small-sized fish (juveniles; Fig. 2).

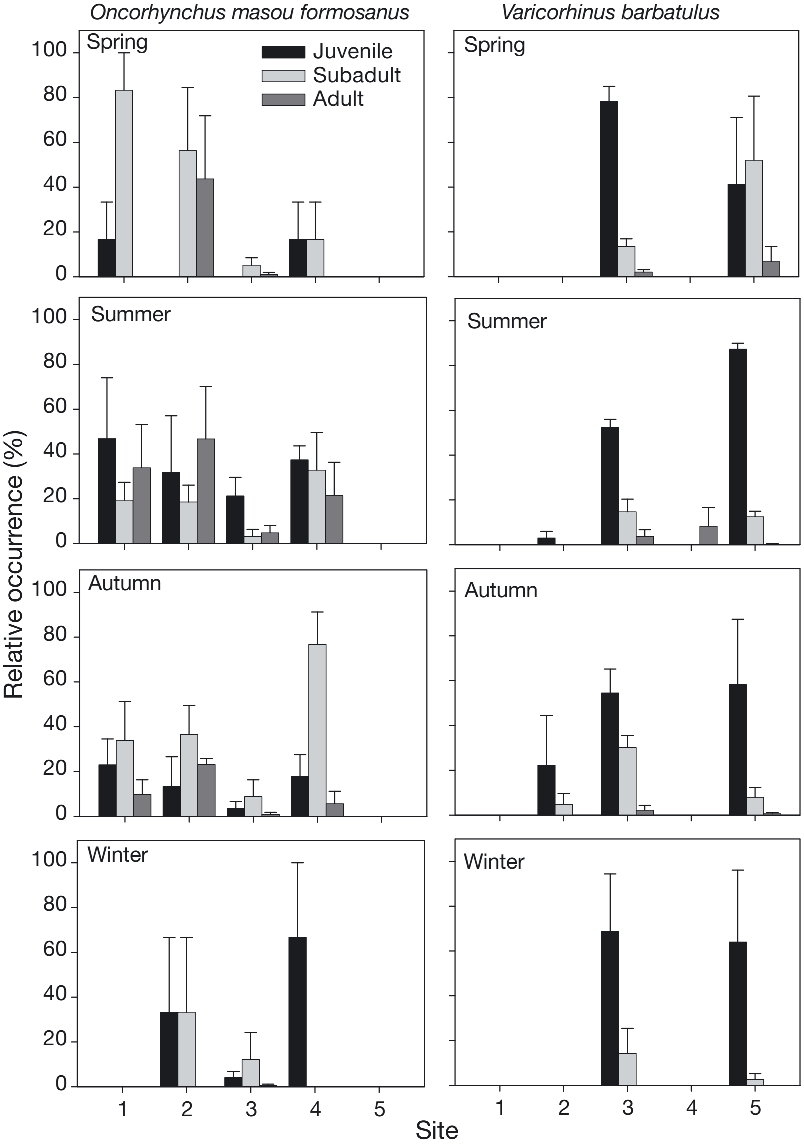

Fig. 2. *Oncorhynchus masou formosanus* and *Varicorhinus barbatulus.* Relative occurrence (mean ± SE) of the Formosan landlocked salmon and shovelmouth minnow at 5 sampling sites for each season (n = 3)

Periphyton and aquatic insects

Diatoms were the most dominant taxa of the epilithic algae in streams of the Wuling basin, followed by cyanobacteria and green algae. Most diatoms belonged to pennate genera, of which *Achnanthidium atomus, A. minutissimus,* and *Platessa hustedtii* were the most abundant species. The cyanobacteria, including *Oscillatoria* spp., *Chroococcus* spp., and *Lyngbya* sp., and the green alga *Cladophora* sp. occurred more frequently in winter. Concentrations of periphyton chl *a* showed seasonal variations ($p < 0.05$, Kruskal-Wallis test), with higher values during spring and winter than in autumn (Fig. 3a). An extremely high value of chl *a* concentration of 335 µg m^{-2} was recorded in 2005, which caused a high mean value at Site 5 in summer. Among-site differences in chl *a* concentrations were marginally significant ($p = 0.083$, Kruskal-Wallis test, Fig. 3a).

Aquatic insects living in Chichiawan Stream were dominated by grazers and filter-feeders. Dominant grazers belonged to the Baetidae, Heptageniidae, Glossosomatidae, and Uenoidae. Dominant filter-feeders were *Simulium* spp. (Simuliidae) and Chironomidae. Densities of aquatic insects significantly differed among seasons ($p < 0.001$, Kruskal-Wallis test), but not among sites ($p = 0.316$, Kruskal-Wallis test). Except for Site 1, the highest density occurred in winter, the density decreased in spring and summer, and the lowest density was found in autumn (Fig. 3b).

Fish habitat uses

Relative occurrences of various size classes for both fishes were significantly related to the measured variables ($F = 2.50$, $p < 0.001$, Monte Carlo permutation test with 4999 permuta-

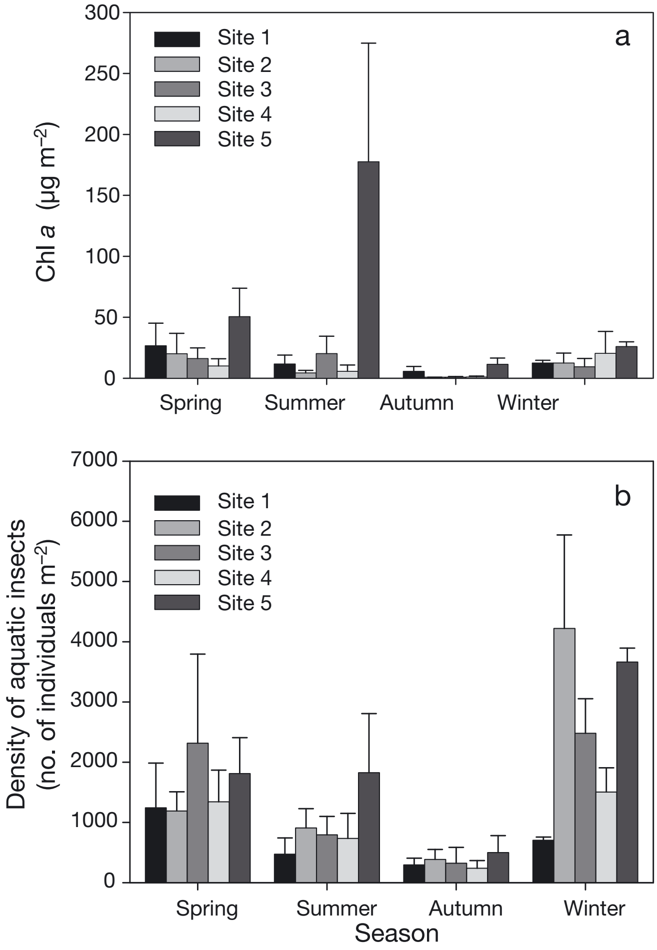

Fig. 3. Mean values (± SE) of (a) concentration of periphyton chl *a* and (b) density of aquatic insects at 5 sampling sites for each season. Sample sizes for each season were 3, 3, 2, and 2 for chl *a*, and 3, 3, 3, and 2 for aquatic insects at each site

tions), which altogether explained 76.9% of the variance (Table 3a). Results of the forward selection of variables significantly explained the variance in fish occurrence (Table 4). Physicochemical parameters, including elevation, temperature, turbidity, velocity, and concentrations of NH_3-N and SiO_2, accounted for 39% of the variance in the relative occurrence of fish, substratum composition accounted for 9%, and seasonal effects accounted for 4% (Table 4a).

The ordination plot shows relationships of the relative occurrences of different size classes for both fishes with environmental variables, biotic components, and seasonal effects, which reflect habitat use by the 2 species (Fig. 4). The relative occurrence of the Formosan salmon increased with increasing elevation and proportions of cobbles and large boulders, while that of the shovelmouth minnow increased with higher temperature and concentration of NH_3-N (Fig. 4). The relative occurrence of juvenile salmon showed a clear seasonal pattern, with a higher value in summer. The relative occurrence of adult salmon was positively correlated with the proportions of cobbles and large boulders and the density of aquatic insects, while that of juvenile salmon was negatively correlated with temperature and the concentration of NH_3-N. Different size classes of the minnow appeared to utilize similar habitats (Fig. 4).

Because there were clear seasonal variations in the relative occurrence of the fish, environmental variables, and biotic components, we used a partial RDA to relate the measured variables and the relative occurrence of fish after removing seasonal effects. The total variance was 0.919, and the overall canonical eigenvalue was 0.688, suggesting that 74.9% of the variance in the relative occurrence of fish could be explained by all of the environmental variables and biotic components ($F = 2.50$, $p < 0.001$, Monte Carlo permutation test with 4999 permutations, Table 3b). Eight variables, including elevation, temperature, turbidity, DO, concentrations of NH_3-N and SiO_2, and proportions of gravel and riffles, were selected using forward selection, which, combined, explained about 51.5% of the variance in the relative occurrence of the fish (Table 4b). The relative occurrence of the shovelmouth minnow was higher at sites with a high concentration of NH_3-N and high proportions of gravel and riffles. In contrast, the Formosan salmon used sites at high elevations (Fig. 5). Habitat uses by different size classes of the

Table 3. Summary of the redundancy analysis (RDA) of fish relative occurrence data from 5 sampling sites as constrained by environmental variables and biotic components with (a) seasonal effects included and (b) seasonal effects excluded

	RDA axis				Total variance
	1	2	3	4	
(a) Seasonal effects included					
Eigenvalue	0.452	0.140	0.088	0.039	1.000
Species–environment correlation	0.928	0.867	0.859	0.730	
Cumulative % variance					
of species data	45.2	59.2	68.1	72.0	
of species–environment relation	58.8	77.0	88.5	93.6	
Sum of all eigenvalues					1.000
Sum of all canonical eigenvalues					0.769
(b) Seasonal effects excluded					
Eigenvalue	0.440	0.111	0.069	0.034	1.000
Species–environment correlation	0.925	0.843	0.812	0.766	
Cumulative % variance					
of species data	47.8	59.9	67.4	71.1	
of species–environment relation	63.9	80.0	90.0	94.9	
Sum of all eigenvalues					0.919
Sum of all canonical eigenvalues					0.688

Formosan salmon varied slightly. Juvenile and subadult salmon inhabited sites with lower temperatures, NH_3-N concentrations, and riffle proportions, but adult salmon occurred more frequently at sites with lower turbidity, SiO_2 concentrations, and gravel proportions (Fig. 5).

Relative importance of environmental variables, biotic components, and seasonal effects

Variations in the relative occurrences of Formosan salmon and shovelmouth minnow in the Wuling basin were best explained by physicochemical parameters, followed by the substratum composition. These 2 categories of variables exclusively accounted for 38.8 and 11.4 % of the total variation, respectively (Table 5). Variations exclusively explained by mesohabitat composition, seasonal effects, and biotic components were not significant (<5 %, $p > 0.05$, Monte Carlo permutation test with 4999 permutations; Table 5).

Table 4. Ranking of variables that significantly (Monte Carlo permutation tests in the redundancy analysis [RDA], $p < 0.1$) influenced fish distributions. Variables that best explain the variance in the relative occurrence of fish are ranked first, while the remaining variables are ranked on the basis of the additional fit based on the model selection with (a) seasonal effects included and (b) seasonal effects excluded

Selected variable	*F*	p	Explained Variance	Explained %	Correlation Axis 1	Correlation Axis 2
(a) Seasonal effects included						
Elevation	11.49	<0.001	0.19	19.0	0.60	−0.06
NH_3-N	4.56	0.003	0.07	7.0	−0.34	−0.10
Temperature	3.64	0.009	0.06	6.0	−0.19	−0.28
Cobbles	3.87	0.004	0.05	5.0	0.30	−0.23
Summer	3.11	0.017	0.04	4.0	0.09	0.08
Large boulders	2.59	0.033	0.04	4.0	0.12	−0.10
SiO_2	2.33	0.047	0.03	3.0	−0.08	0.34
Aquatic insects	1.92	0.092	0.03	3.0	0.05	−0.14
Turbidity	2.15	0.062	0.02	2.0	−0.04	0.09
Velocity	2.00	0.078	0.02	2.0	−0.02	0.05
Total	4.44	<0.001	0.53	53.0		
(b) Seasonal effects excluded						
Elevation	11.51	<0.001	0.19	20.7	0.59	−0.12
Temperature	5.47	0.001	0.08	8.7	−0.45	−0.34
Gravel	5.16	0.002	0.07	7.6	−0.43	0.20
NH_3-N	2.61	0.033	0.03	3.3	−0.33	0.02
SiO_2	2.38	0.040	0.03	3.3	−0.07	0.24
Turbidity	2.13	0.064	0.03	3.3	−0.09	0.21
Riffles	2.40	0.040	0.02	2.2	−0.14	0.03
Dissolved oxygen (DO)	1.91	0.097	0.02	2.2	−0.08	−0.14
Total	4.88	<0.001	0.47	51.5		

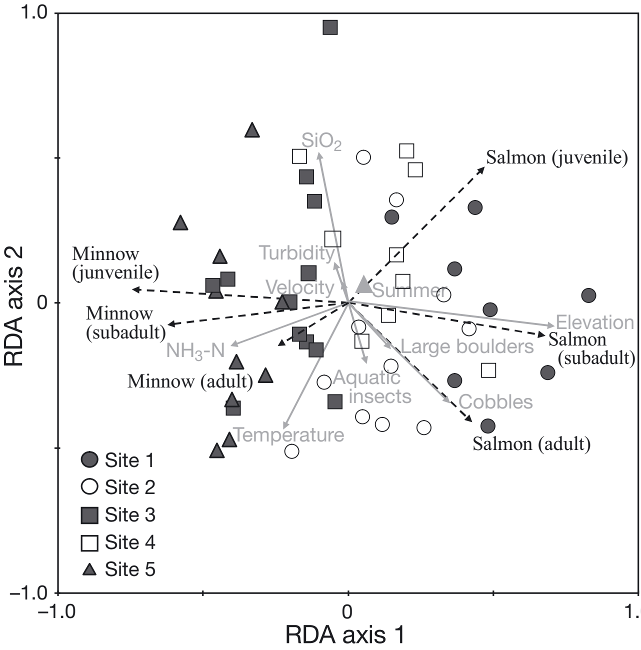

Fig. 4. First 2 axes of redundancy analysis (RDA) ordination plots describing the relationships of selected variables (grey solid arrows) with the relative occurrences of samples and fish of different size classes (black dashed arrows). The selected seasonal effect (Summer) was treated as a nominal variable and is given as a centroid (▲)

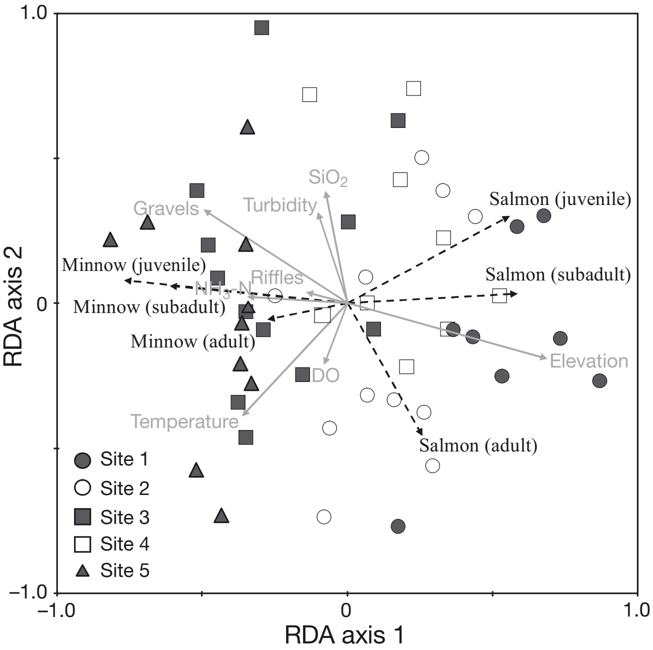

Fig. 5. First 2 axes of the partial redundancy analysis (RDA) ordination plots describing the relationships of selected variables (grey solid arrows) with samples and the relative occurrences of fish of different size classes (black dashed arrows) after seasonal effects were removed

Table 5. Summary of the partial redundancy analysis (RDA) used to examine the variance exclusively explained by each category of variables. The total variance, sum of all canonical eigenvalues, and significance levels of the *F*-test for all RDA axes are shown

Analysis	Category of variable	Total variance	Sum of all canonical eigenvalues	*F*	p
1	All	1.000	0.769	2.498	< 0.001
2	Physicochemical parameters	0.619	0.388	2.718	< 0.001
3	Substratum composition	0.345	0.114	1.724	0.037
4	Mesohabitat composition	0.276	0.045	1.023	0.422
5	Seasonal effects	0.269	0.038	1.151	0.309
6	Biotic components	0.269	0.038	1.721	0.098

DISCUSSION

Habitat uses by the 2 sympatric fish species were distinct in the Wuling basin. The Formosan salmon used sites at high elevation with large-grain-sized substratum and low concentrations of nutrients and pollutants, while the shovelmouth minnow occurred more frequently in fine-grain-sized substratum with a higher tolerance to pollution. Adaptation of the Formosan salmon to low temperatures appeared to be one of the major factors, although there was no significant difference in seasonal variations of temperatures among sites. Salmon populations used habitats at lower temperatures and were distributed in reaches at higher elevations than shovelmouth minnow populations. A study on a related salmon species (*Oncorhynchus masou*) at the reach scale in Japan also revealed that high water temperatures limited the population size (Inoue et al. 1997). Stream reaches with a maximum summer temperature of <17°C can be considered the threshold for Formosan salmon distribution (Tzeng 2005). Food sources of the 2 fish species also differed. The Formosan salmon is insectivorous (Tsao 1988), but the shovelmouth minnow relies heavily on algae (Wang 1989). Interspecific competition between the 2 fish species may also be important for habitat differentiation. The large-sized shovelmouth minnow may compete with salmon fry for space by forcing them to use marginal or less favorable habitats (Tsao et al. 1996).

Habitat uses differed slightly among different size classes or life stages of the Formosan salmon. Different sized salmon inhabited different microhabitats, which varied in depth, current velocity, cover, and substratum composition (Tsao et al. 1998). However, the ranges of these variables among different size classes of the salmon largely overlapped. For example, juvenile, subadult, and adult salmon were usually observed at depth ranges of 0.11–1.47, 0.13–1.85, and 0.19–1.70 m, respectively, during the warm season (Tsao et al. 1998). These results imply that all life stages of the salmon can coexist within the same reaches, but they occupy different microhabitats. Our results further demonstrated that adult salmon occurred more frequently with large-grain-sized substratum, but juveniles and subadults inhabited sites with lower temperatures and current velocities (Fig. 5). Ontogenetic microhabitat shifts of the Formosan salmon might be induced by tolerance to fast velocities and high temperatures or may be due to intraspecific competition (Grossman & Freeman 1987, Tsao et al. 1998). Juvenile masu salmon of different sizes were found to use different reaches in a regulated river in winter (Nagayama & Nakamura 2007). Similar phenomena have also been observed for other salmon species (Baltz et al. 1991, Heggenes et al. 1991).

This is the first study to evaluate the relative importance of habitat attributes to populations of the Formosan salmon. It is clear that physicochemical parameters were more important than compositions of the substrata and mesohabitat, which suggests that variables changed by human activities are crucial in shaping the distribution of the salmon. Apart from temperature, other physicochemical characteristics were also important in explaining variations in the relative occurrences of the 2 fish species in the Wuling basin. Anthropogenic pollutants, such as NH_3-N, and turbidity, both derived mainly from agricultural activities in the catchment of Yousheng Stream, showed adverse effects on the salmon population (Site 5 in Figs. 4 & 5). Yu & Lin (2009) also found adverse effects of agricultural activities on epilithic algal abundances and structure in this area. Compositions of the substrata and mesohabitat are usually correlated and vary spatially and temporally with current velocity and discharge in lotic systems. Increased discharges may increase the velocity and proportions of riffles and rapids and decrease the composition of small substrata. Tsao et al. (1998) concluded that each type of substratum and mesohabitat is important because each supports various activities of the salmon at different life stages. Based on a geographical information system (GIS) model, Tsao et al. (1996) suggested that at least 25 % of the reach area were runs used as spawning habitats and 25 % of the reach area were pools used as refuges during floods, and these habitats were crucial to support a self-sustaining salmon population. Large boulders and downstream pools are essential because they can be used by the Formosan salmon as shelter during floods (Chung et al. 2008).

Seasonal effects on habitat use by the Formosan salmon were not significant. Except for juveniles in summer, seasonal variations in the relative occurrences of the 2 fish species were not evident (Fig. 2). Seasonal changes in environmental variables were primarily attributable to heavy precipitation in summer. Induced floods are considered to be among the main factors influencing the salmon population (Chung et al. 2008). However, our results implied that the Formosan salmon used the same stream reaches in different seasons, although Tsao et al. (1998) reported seasonal changes in microhabitat selection by the salmon. Using nano-tagging, the results of a study by Makiguchi et al. (2009) also showed that floods did not affect the habitat use or position of adult salmon in Chichiawan Stream. Therefore, the effects of fluctuations in water level and current velocity on habitat use by the Formosan salmon appeared to be relatively small (e.g. Flodmark et al. 2006).

Biotic components were less important than environmental variables in influencing the distribution of the Formosan salmon and sympatric shovelmouth minnow, which suggests that the 2 fish species do not experience bottom-up control by food sources. Both fish species are known to use aquatic insects as their main food sources, and the shovelmouth minnow also consumes periphyton, filamentous algae, and aquatic plants (Wang 1989). The insignificance of biotic components in explaining variations in fish occurrence implies that they are not a limiting factor for the 2 fish populations. Total numbers of individual salmon often represented only 30 % of the carrying capacity estimated based on a long-term monitoring program in Chichiawan Stream (Chung et al. 2007). Trophic models of Chichiawan Stream also showed that the abundance of aquatic insects available for the Formosan landlocked salmon was much higher than the amount consumed by the salmon (H. Lin unpubl. data). Meanwhile, fishing for both fish species in the Wuling basin is prohibited by the Taiwanese government. Another biotic component affecting habitat uses by the salmon is bird predation (Werner et al. 1983). The only potential predator of salmon in Chichiawan Stream is the striated heron *Butorides striatus amurensis*, the abundance of which is low in the Wuling basin. Predation pressure on the Formosan landlocked salmon is thus considered to be low.

In conclusion, variations in the relative occurrences of the Formosan salmon and shovelmouth minnow in the Wuling basin were best explained by physicochemical parameters, followed by compositions of the substrata and mesohabitat. Anthropogenic factors, such as hydrological changes, recreational pressures, and agricultural activities, combined with natural disturbances, such as floods caused by typhoons, have caused spatial and temporal changes in stream attributes in the Wuling basin. To conserve the Formosan landlocked salmon, human activities should be managed in order to reduce changes in physicochemical parameters as a first priority, and must be effective at the catchment scale.

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