Zoological Studies **47**(1): 25-36 (2008)

Zoological Studies

Relationship between the Formosan Landlocked Salmon *Oncorhynchus masou formosanus* Population and the Physical Substrate of Its Habitat after Partial Dam Removal from Kaoshan Stream, Taiwan

Lii-Chang Chung[1], Hsing-Juh Lin[1,*], Shao-Pin Yo[1], Chyng-Shyan Tzeng[2], Chao-Hsien Yeh[3], and Cheng-Hsiung Yang[2]

[1]*Department of Life Sciences, National Chung Hsing University, Taichung 402, Taiwan*
[2]*Institute of Bioinformatics and Structural Biology, and Department of Life Science, National Tsing Hua University, Hsinchu 300, Taiwan*
[3]*Department of Water Resources Engineering, Feng Chia University, Taichung 407, Taiwan*

(Accepted August 2, 2007)

Lii-Chang Chung, Hsing-Juh Lin, Shao-Pin Yo, Chyng-Shyan Tzeng, Chao-Hsien Yeh, and Cheng-Hsiung Yang (2008) Relationship between the Formosan landlocked salmon *Oncorhynchus masou formosanus* population and the physical substrate of its habitat after partial dam removal from Kaoshan Stream, Taiwan. *Zoological Studies* **47**(1): 25-36. In order to protect and restore the population of the Formosan landlocked salmon (*Oncorhynchus masou formosanus*, Jordan and Oshima) (Salmoidae), an endemic and endangered species of the central Taiwanese highlands, Shei-Pa National Park partially removed 4 dams from Kaoshan Stream during 1999-2001. The purpose of this study was to evaluate the relationship between the abundance of the Formosan landlocked salmon and the physical substrate of its habitat as a consequence of habitat modifications caused by partial removal of the dams from Kaoshan Stream. After removal of the dams, fish were able to freely travel up and down the stream, but the relative slope of the riverbank became steeper, and the velocity of the river increased leading to more-serious erosion than was found prior to dam removal. We applied a principal component analysis (PCA) method to determine the most significant factors affecting the fish population. The 1st principal component of the fish population explained 79% of the total salmon population variance. The 1st 2 principal components of substrate rock size explained 72% of the total substrate variance. By examining a contour plot, we found that when the percentage of boulders was higher, the salmon population accordingly increased. Moreover, poor breeding years that highly impact the salmon population appeared to be a result of flooding caused by typhoons during the breeding season from late Oct. to Dec. Following flooding, it appears that the river substrate had a higher percentage of boulders, which possibly benefited the salmon population. Consequently, partial dam removal may have improved the survival rate of the salmon population in response to floods. http://zoolstud.sinica.edu.tw/Journals/47.1/25.pdf

Key words: Boulders, Principal component analysis, Contour plot, Floods, Breeding season.

The Formosan landlocked salmon (*Oncorhynchus masou formosanus*, Jordan and Oshima) (Salmoidae) is an endangered and endemic glacial relict species, and is known as one of the southernmost natural salmon population in the world (Wang 1989, Lin et al. 1990, Kato 2003). Its distribution is limited to the basin of Chichiawan Stream located in Shei-Pa National Park (NP) in central Taiwan (Lin et al. 1987, Wang 1989, Tsao 1995). Due to declines in its abundance and its narrow range distribution, the World Conservation Union (IUCN) listed the species as critically endangered in 1996 (Kottelat 1996).

The Formosan landlocked salmon was once widely distributed in all 6 tributaries of the Tachia River including Chichiawan, Kaoshan, Yousheng, Nanhu, Sakaran, and Hohuan Streams (Fig. 1) before the development of agriculture in these

*To whom correspondence and reprint requests should be addressed. Tel: 886-4-22840416. Fax: 886-4-22874740. E-mail:hjlin@dragon.nchu.edu.tw

areas about 50 yr ago (Lin et al. 1990, Tsao et al. 1998). However, agricultural development and the establishment of dams to collect eroding silt and sand have limited the fish's population in Chichiawan Stream (Tsao 1995). As a result, the salmon's habitat has been drastically reduced, critically threatening its survival (Lin et al. 1990). In order to collect basic ecological information for the conservation and restoration of this species, Shei-Pa NP began conducting a population census of

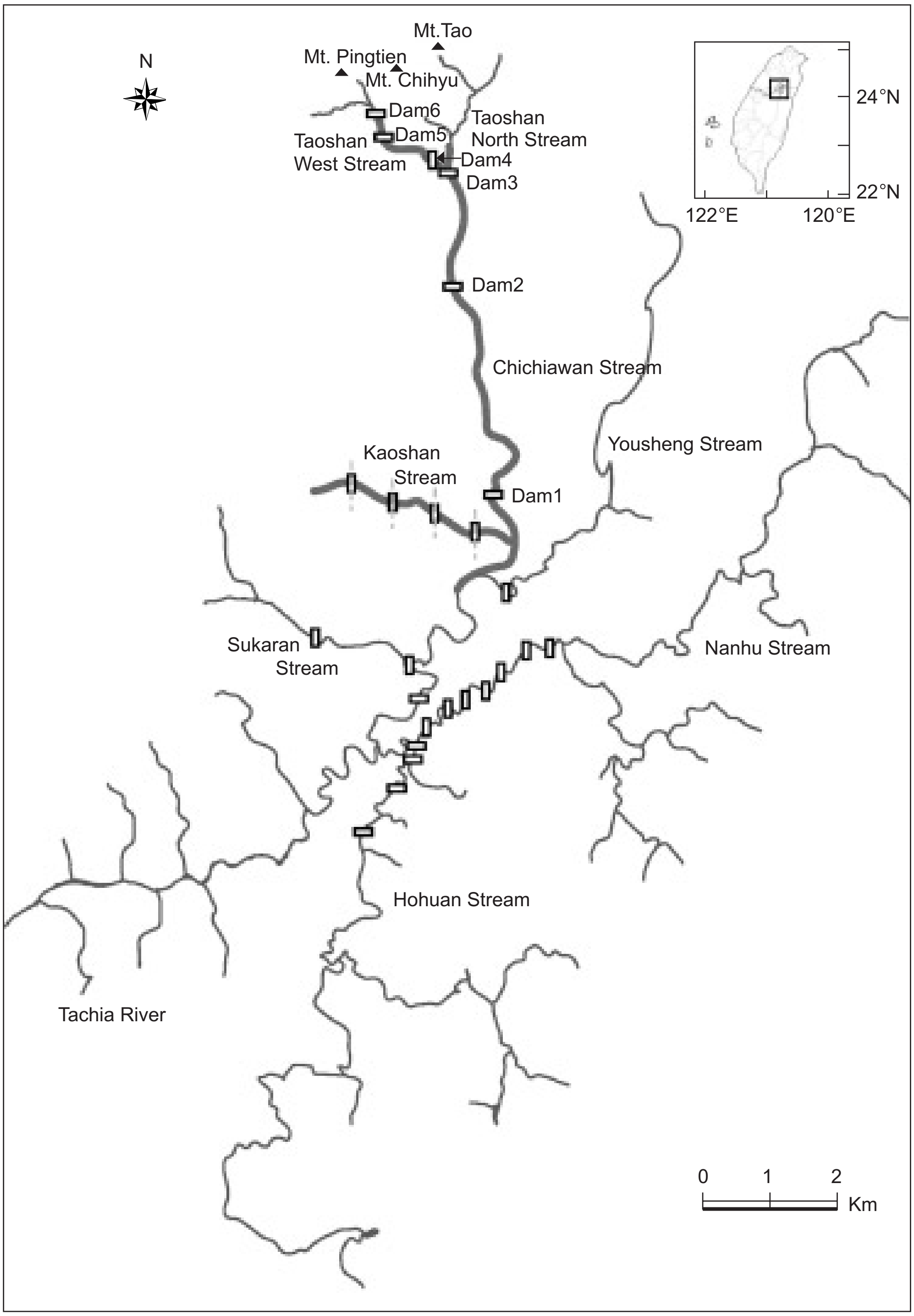

Fig. 1. Study site of the Formosan landlocked salmon (*Oncorhynchus masou formosanus*) in Taiwan. Inset, enlarged area within Taiwan. Four dams along Kaoshan Stream were partially removed between the summers of 1999 and 2001. (After Tsao et al. 1998)

the fish in 1994 to monitor its abundance, stage structures (salmon are divided into 3 stages according to total length: juvenile, subadult, and adult), and spatial distribution (Tzeng and Yang 2002).

Tzeng (2005) found that the abundance and distribution of the salmon population are greatly influenced by natural calamities such as stream flooding during the typhoon season. In addition, dams on the stream cause isolation of salmon populations, limiting their natural distribution by preventing them from moving back upstream after being flushed downstream during floods. From 1999 to 2001, Shei-Pa NP partially removed 4 dams from Kaoshan Stream in an attempt to reduce the effects of habitat modifications by human activities on salmon populations by unblocking the fish ladders (Yeh et al. 2002).

Many environmental factors may affect salmon habitat selection (Heggenes et al. 1991). Depth, current velocity, substrate, and cover are regarded as the most important physical habitat features determining habitat use by stream fishes (Shirvell and Dungey 1983, Greenberg and Stiles 1993). The substrate, which represents the cumulative effects of hydrological events (Davey and Lapointe 2007) in highly fluctuating mountain streams, plays an important role in salmon habitat selection (Bennett et al. 2003, Hedger et al. 2006). A substrate consisting of large cobbles and boulders provides shelter and overwintering sites for Atlantic salmon (*Salmo salar*) (Coulombe-Pontbriand and Lapointe 2004). In Taiwan, a study by Yeh (2005) indicated that the salmon population distribution is influenced by variations in seasonal silt deposition on the stream substrate which varies between dry and wet seasons. Furthermore, Lin et al. (2005) suggested that the proportion of boulders in the stream also affects salmon abundances. Therefore, the purpose of this study was to evaluate the relationship between the population dynamics of the Formosan landlocked salmon and the physical substrate of its habitat after partial removal of 4 dams from Kaoshan Stream.

MATERIALS AND METHODS

Study site

Kaoshan Stream (24°21'-24°31'N, 121°20'-121°35'E) is a tributary of Chichiawan Stream, on an upstream reach of the Tachia River (Fig. 1). The elevation is about 1700-1800 m, and rainfall is often concentrated between May and Sept. in the basin (Lin et al. 1990), at which time, flow discharges increase. Frequently, typhoons result in flooding of riparian areas in summer. The stream is about 3 km long with a mean gradient of 0.028-0.087. Its width ranges from 2.5 to 19 m, dissolved oxygen (DO) consistently exceeds 10 mg L^{-1}, pH values range 7.0-8.0, and turbidity ranges 0.02-0.50 NTU. The riparian vegetation is mostly dense virgin forest, free from agricultural development. Stream temperatures are commonly lower than 15°C. The area has an overall water quality index (WQI) of 93.84 ± 2.91 and is considered to be in the range of fine water quality (Kuan 2005).

Salmon survey method

The Formosan landlocked salmon is an iteroparous fish species (Healey et al. 2001). The fish begins to breed at the age of 2 yr and continues to reproduce each winter for the rest of its life (Kato 2003, Chung et al. 2007). We conducted a long-term monitoring program to survey the salmon population in Kaoshan Stream from winter 2001 to winter 2005. Total numbers of Formosan salmon were counted during the day by snorkeling twice per year, once in June or July (summer) and once in late Oct. (early winter) (Tzeng 2005). We conducted fish counts between 09:00 and 16:00 when underwater visibility is optimal (Heggens and Saltveit 1990). The stream was divided into sections: dams or abrupt changes in channel gradient formed the upper and lower boundaries of each section (Lin et al. 1990, Tzeng 2005). All snorkeling surveys began downstream of each section (~300 m long) and were completed in a single upstream pass. During each count, 2 trained snorkelers proceeded slowly side by side upstream in the middle of the channel and counted fish outward toward the streambank to avoid double counting (Lin et al. 1990, Tsao et al. 1998). Snorkelers recorded fish count data on their slates and paused periodically at the end of a section to relay information to a data recorder on the streambank (Tzeng 2005).

Because the salmon breeds only once a year, total lengths of different ages can easily be differentiated in the field (Tzeng 2005). We classified the Formosan salmon into 3 main life stages according to their total length: juveniles which are assumed to be 1-yr-old fish are 5-8 cm in summer (June) and 5-15 cm in winter (late Oct.); subadults which are assumed to be 2-yr-old fish are 8-15 cm in summer (June) and 15-25 cm in winter (late Oct.); and adults which are assumed to be ≥ 3-yr-old fish are > 25 cm in both seasons (Tzeng 2005, Chung et al. 2007). In order to maintain the accuracy of the size determination, estimating fish lengths was practiced prior to the count by estimating the lengths of objects of known size lying on the stream bottom (Tsao et al. 1998). In addition, the underwater slates the divers carried were marked with a ruler for size reference (Lin et al. 1990). On each occasion, the fish survey along Kaoshan Stream was completed within a week.

Physical substrate of the habitat

We established 20 m transect observation lines perpendicular to the thalweg line at each cross-section of Kaoshan Stream (Kaufmann et al. 1999). While the channel width and elevation were measured using an NTS-322 Electronic Total Station (South Surveying Instrument, NY, USA), the water depth, substrate composition, and surface flow velocity at 25%, 50%, and 75% of the wetted width along the transect line were manually estimated (Kaufmann et al. 1999). Due to limitations of the geomorphology and instrumentation, the velocity was estimated by drogue tracking (Rueda et al. 2003). According to Wentworth (1922) and Wang (1989), the substrate was categorized into 6 classes by particle size: smooth surface (< 0.2 cm in diameter), gravel (0.2-1.6 cm), pebbles (1.6-6.4 cm), rubble (6.4-25.6 cm), small boulders (25.6-51.2 cm), and boulders (> 51.2 cm). The discharge data of Chichiawan Stream were obtained from the *Hydrological Year Book of Taiwan* (2001-2005). Typhoon information was obtained from the Central Weather Bureau (available at http://rdc28.cwb.gov.tw/data.php).

Data analysis

Individual numbers of salmon were logarithmically transformed as log (x+1), and substrate percentages were standardized (with a mean of 0 and a standard deviation (SD) of 1) before the analyses. One-way analysis of variance (ANOVA) was used to examine differences in general habitat variables and salmon abundances among the 5 sections which were separated by the 4 residual dams. We applied a principal component analysis (PCA) (Hammer et al. 2001, Johnson and Wichern 2002) to determine what aspect of the substrate explained variations in salmon numbers. A contour plot was established by putting the salmon's

Table 1. General descriptions of the 5 sections of Kaoshan Stream. Habitat variables and abundances of the Formosan landlocked salmon (mean ± SD) are shown

Variable	Location					ANOVA	
	Dam no. 1 downstream	Dam no. 1 upstream	Dam no. 2 upstream	Dam no. 3 upstream	Dam no. 4 upstream	*F* value	*p* value
Elevation (m)	1714 - 1730	1732 - 1748	1750 - 1772	1773 - 1790	1792 - 1802		
Gradient (%)	0.11 ± 0.02	0.03 ± 0.004	0.08 ± 0.002	0.08 ± 0.01	0.06 ± 0.01	97.43	< 0.001***
Mean width (m)	5.38 ± 1.20	5.17 ± 0.86	5.89 ± 1.26	5.97 ± 1.28	4.97 ± 0.97	0.82	0.53
Mean depth (cm)	28.94 ± 8.06	31.19 ± 6.95	28.71 ± 6.35	32.92 ± 8.05	33.75 ± 8.00	0.59	0.67
Mean velocity (m/s)	1.27 ± 0.24	1.49 ± 0.47	1.30 ± 0.29	1.32 ± 0.41	1.26 ± 0.23	0.43	0.79
Substrate composition (%)							
Smooth (< 0.2 cm)	6.11 ± 7.39	4.10 ± 7.54	2.83 ± 3.66	3.05 ± 5.15	3.99 ± 6.45	0.35	0.84
Gravel (0.2 - 1.6 cm)	14.44 ± 14.41	10.36 ± 9.29	13.96 ± 11.47	9.46 ± 8.05	23.51 ± 19.07	1.46	0.23
Pebbles (1.6 - 6.4 cm)	23.88 ± 13.78	23.24 ± 17.27	25.45 ± 14.90	25.32 ± 13.40	9.23 ± 7.99	1.99	0.12
Rubble (6.4 - 25.6 cm)	24.94 ± 10.10	30.27 ± 19.63	28.34 ± 16.02	23.85 ± 8.46	18.82 ± 11.08	0.83	0.51
Small boulders (25.6 - 51.2 cm)	17.82 ± 13.03	17.75 ± 15.22	17.68 ± 15.56	17.97 ± 13.54	12.34 ± 8.34	0.27	0.90
Boulders (> 51.2 cm)	13.53 ± 14.33	11.83 ± 12.16	11.74 ± 13.25	20.73 ± 14.56	32.48 ± 20.34	2.73	0.04*
Salmon abundance							
Juveniles	19.43 ± 18.24	14.71 ± 17.04	29.25 ± 27.85	54.25 ± 66.77	65.20 ± 65.13a	1.62	0.20
Subadults	15.00 ± 6.73	10.29 ± 6.29	22.00 ± 23.20	25.75 ± 20.51	54.00 ± 33.11a	4.16	< 0.01**
Adults	8.57 ± 3.64	6.57 ± 4.72	8.50 ± 6.85	11.50 ± 6.72	26.20 ± 15.19a	5.82	0.001***

[a]After the summer of 2004, there was a natural gap of more than 1 m at dam no. 4 which salmon could not jump over. The mean value was estimated from data of winter 2001 to summer 2004.

1st PCA component on the z-axis and the substrate's 1st and 2nd PCA components on the x- and y-axes. We then evaluated relationships between the dynamics of the Formosan landlocked salmon and the physical substrate of its habitat after partial dam removal from Kaoshan Stream. We estimated the relative area of salmon abundances on the contour map. Finally, we used the PCA to construct a linear combination of the physical substrate to demonstrate whether changes in the substrate gradient had occurred following partial removal of the dams.

RESULTS

The gradient, percentage of boulders, and subadult and adult abundances significantly differed among the 5 sections of Kaoshan Stream (Table 1). The gradient was lower upstream of dam no. 1 (0.03 ± 0.004) than in the other sections. The gradients were all stable (with SDs of 0.004-0.02) following partial removal of the dams. The percentage of boulders and abundances of salmon were consistently higher upstream of dam no. 4 than in the other sections. However, juvenile abundances exhibited greater variations among the 5 sections.

The salmon population dramatically fluctuated overall as did the 3 different stages during summer and winter, ranging from 39 to 579 individuals with a mean number of 314 in Kaoshan Stream from 2001 to 2005 (Fig. 2). A peak in total numbers was found in summer 2004. The absence of flooding in the breeding and growth seasons between winter 2001 and summer 2002 was responsible for the high recruitment of juveniles at that time, when the population increased from 11 to 509 individuals in Kaoshan Stream (Figs. 2, 3). Typhoons Mindulle and Aere affected the Chichiawan Stream basin in summer 2004 causing flow discharges to exceed 50 and 200 m^3/s, respectively (Fig. 3). Figure 4A-H shows the percentages of different components of the physical substrate of habitats between prior dam locations during the winters of 2001 and 2005 in Kaoshan Stream. Moreover, boulders with diameters of > 25.6 cm, which offer good shelter for fish, decreased by 20%-40% in that period (Fig. 4E). During that time, the salmon population rapidly decreased from 579 to 100 individuals in Kaoshan Stream (Figs. 2, 3). Special attention should also be given to 2 other typhoons (Nock-Ten on 23-26 Oct. 2004 and Nanmadol on 3-4 Dec. 2004), as they brought abundant rainfall (> 20 m^3/s) in the winter breeding season of 2004 (Fig. 3). At that time, boulder cover exceeded 80% in all sections between dams on Kaoshan Stream (Fig. 4F). The salmon population of Kaoshan Stream simultaneously increased from 100 to 170 individuals instead of decreasing (Figs. 2, 3).

According to the PCA based on the 3 different salmon stage variables, the Eigenvalues and component loadings ($loading_{juvenile}$ = 0.59, $loading_{subadult}$ = 0.60, and $loading_{adult}$ = 0.54) indicated that each of the 3 stages of salmon was equally important to total salmon population variations in Kaoshan Stream (Table 2). The 1st component equation was: $PC1_{salmon}$ = 0.59(juveniles) + 0.59(subadults) + 0.54(adults) which explained 79.19% of the population variation. All 3 variables were significantly correlated (0.88, 0.94, and 0.85) with the $PC1_{salmon}$ (Table 2).

For the 6 variables of the physical substrate, results of the PCA indicated that the 1st 2 principal components sufficiently represented the variability of the substrate features. The 1st component was $PC1_{substrate}$ = -0.37(smooth) - 0.40(gravel) - 0.50(pebbles) - 0.07(rubble) + 0.53(small boulders) + 0.42(boulders), and it explained 45.39% of the substrate structural changes. The loading of the 1st component indicated that small boulders and boulders > 25.6 cm were the dominant factors. The variables of small boulders and boulders were significantly correlated (0.87 and 0.70) with $PC1_{substrate}$ (Table 3). However, the 2nd component was $PC2_{substrate}$ = -0.40(smooth) - 0.19(gravel) + 0.17(pebbles) + 0.74 (rubble) + 0.02(small boulders) - 0.48(boulders), and it explained 26.62% of the variation in substrate structural changes. The rubble variable (6.5-25.6 cm) with

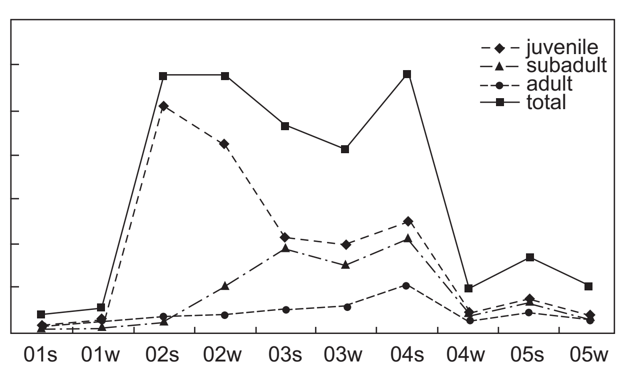

Fig. 2. Abundances of the 3 main life stages of the Formosan landlocked salmon (*Oncorhynchus masou formosanus*) population recorded in Kaoshan Stream from 2001 to 2005 (mean, 314; peak, 579 individuals in summer 2004). s, summer; w, winter.

its loading (0.74) and high correlation (0.94) was a key factor in $PC2_{substrate}$. The cumulative effect of both $PC1_{substrate}$ and $PC2_{substrate}$ explained 72% of variations in the physical substrate (Table 3). Gradient changes of the physical substrate following partial removal of the 4 dams are expressed in a PCA ordination biplot (Fig. 5). The x-axis represents values for the PC1, and the y-axis represents values for the PC2. It is evident that the physical substrates of the 5 sections in winter 2004 were aggregately located to the right of $PC1_{substrate}$.

The contour plot provides a convenient visual image of the spatial distribution of the Formosan landlocked salmon. The cross-axis shows the PC1 of the physical substrate (with dominant variables of small boulders and boulders); 0 shows the mean, and 1 and 2 show the standard deviations (SDs). The vertical axis shows the PC2 for the physical substrate (the dominant variable of which was rubble) (Fig. 6). Numbers 1, 2, and 3 in the legend represent the 1st component values ($PC1_{salmon}$ = 0.59(juveniles) + 0.59(subadults) + 0.54(adults)), which express the relative logarithmic value of salmon abundances. Moreover, the salmon abundance ($PC1_{salmon}$) shows the gradient distribution (Fig. 6). We estimated the area of the relative salmon abundances exceeding 3 ($PC1_{salmon}$ = 3 indicating the greatest abundance) distributed along the principal component map of the substrate. The contour enclosure occupied 94% of the area above the mean value (x-axis, $PC1_{substrate} \geq 0$) of the 1st substrate component, indicating that a high proportion of boulders would have a positive effect on the salmon population distribution.

Table 2. Eigenvalues and component loadings of the principal components based on coefficients of factors at different stages of the Formosan landlocked salmon. An asterisk (*) marks loadings that were considered to have substantially contributed to the principal components (PCs) (i.e., with correlation coefficients of ≥ 0.70). Only components with an Eigenvalue of > 1.0 were retained. Correlation coefficients are given in parentheses

Principal component	1	2	3
Eigenvalue	2.24	0.41	0.17
Percentage	79.19	14.65	6.16
Cumulative percentage	79.19	93.84	100
Loading			
log(juveniles)	0.59		
	(0.88*)	0.67	-0.45
log(subadults)	0.60		
	(0.94*)	0.01	0.80
log(adults)	0.54		
	(0.85*)	-0.74	-0.40

DISCUSSION

Since underwater observations are non-destructive and have a minimal impact on fish populations and environments (Roni and Fayram 2000), Thurow et al. (2006) suggested that they are a good technique for sampling sensitive species that are federally listed under the US *Endangered Species Act*. We had 3 reasons for conducting snorkeling and using the overall population investigation methods: 1) the Formosan landlocked salmon is endemic and critically endangered in Taiwan; 2) the water in Kaoshan Stream is very clear and therefore suitable for underwater observations; and 3) the existing salmon population distribution is contained within about a 3 km radius within this stream. This method was therefore appropriate and is considered feasible for enumerating the entire population (Tsao 1995, Chung et al. 2007).

Two structural changes occurred during our survey period. One occurred in the period between winter 2001 and summer 2002 and the other occurred between summer 2004 and winter 2005 (Fig. 2). We speculated that floods were responsible for the 2 structural changes we observed in the basin (Tzeng and Yang 2002, Tzeng 2005). In summer 2004, flooding caused by typhoons seriously impacted the salmon population which rapidly decreased from 579 to 100 individuals in Kaoshan Stream (Figs. 2, 3). Similarly, the total population in Chichiawan Stream decreased from 3228 to 1593 individuals during this period (Tzeng 2005). In the past 1/2 century (1949-2006) or so, only 2 typhoons have affected subtropical Taiwan in Dec. Unfortunately, typhoon Nanmadol (3-4 Dec. 2004) affected the Chichiawan Stream basin in winter 2004. At that time, the salmon population decreased from 1593 to 967 individuals, a decrease in the salmon population of 61% in Chichiawan Stream (Tzeng 2005). During the same period (winter 2004), there was < 20% boulder cover in Chichiawan Stream (Yeh 2005). On the contrary, the salmon population of Kaoshan Stream simultaneously increased from

100 to 170 individuals, an increase of 70%. Moreover, the boulder cover exceeded 80% in all sections between dams located in Kaoshan Stream. Therefore, salmon which had been washed downstream due to flooding were able to return upstream under the shelter of the boulders. This suggests that flooding might have affected fish populations in Kaoshan Stream less dramati-

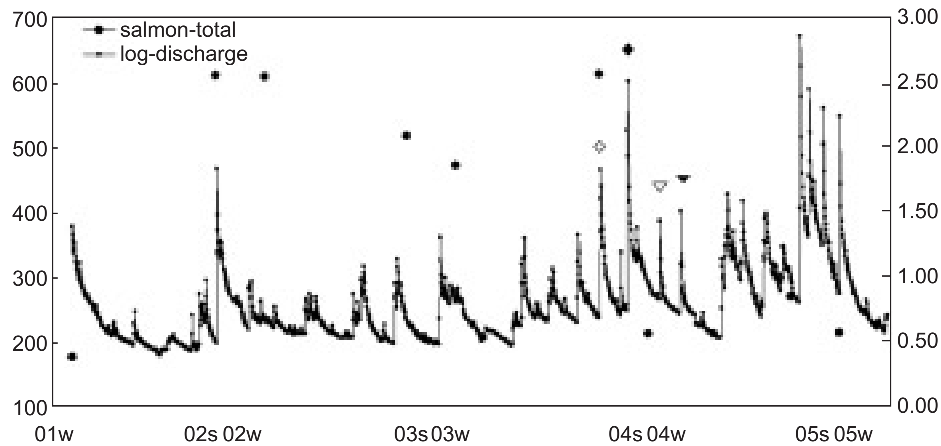

Fig. 3. Abundances of the Formosan landlocked salmon (*Oncorhynchus masou formosanus*) population recorded in Kaoshan Stream from 2001 to 2005 (left axis). Discharge values of Chichiawan Stream were logarithmically transformed (right axis). s, summer; w, winter; ◇, typhoon Mindulle (28 June 2004); ◆, typhoon Aere (23 Aug. 2004); ▽, typhoon Nock-Ten (23 Oct. 2004); ▼, typhoon Nanmadol (3 Dec. 2004).

Table 3. Eigenvalues and component loadings of the principle components (PCs) based on coefficients of factors of the substrate composition. An asterisk (*) indicates loadings that were considered to have substantially contributed to the PCs (i.e., with correlation coefficients of ≥ 0.70). Only components with an Eigenvalue of > 1.0 were retained (Correlation coefficients are given in parentheses)

Principal component	1	2	3	4	5	6
Eigenvalue	2.66	1.56	0.83	0.43	0.37	0.00
Percentage	45.39	26.62	14.23	7.41	6.33	0.02
Cumulative percentage	45.39	72.01	86.24	93.65	99.98	100
Loading						
Smooth	-0.37 (-0.60)	-0.40 (-0.50)	0.53	-0.44	0.45	-0.18
Gravel	-0.40 (-0.66)	-0.19 (-0.24)	-0.75	-0.24	-0.02	0.43
Pebbles	-0.50 (-0.83*)	0.17 (0.21)	0.37	0.36	-0.52	-0.44
Rubble	0.07 (0.11)	0.74 (0.94*)	0.01	-0.02	0.52	-0.42
Small boulders	0.53 (0.87*)	0.02 (0.03)	0.15	-0.57	-0.45	-0.41
Boulders	0.42 (0.70*)	-0.47 (-0.60)	0.00	0.53	0.24	-0.50

cally than those in Chichiawan Stream. The percentage cover of boulders might also have played an important role in ameliorating the flow velocity of the stream (Coulombe-Pontbriand and Lapointe 2004). We thus speculated that despite harsh flooding conditions, this population increase may

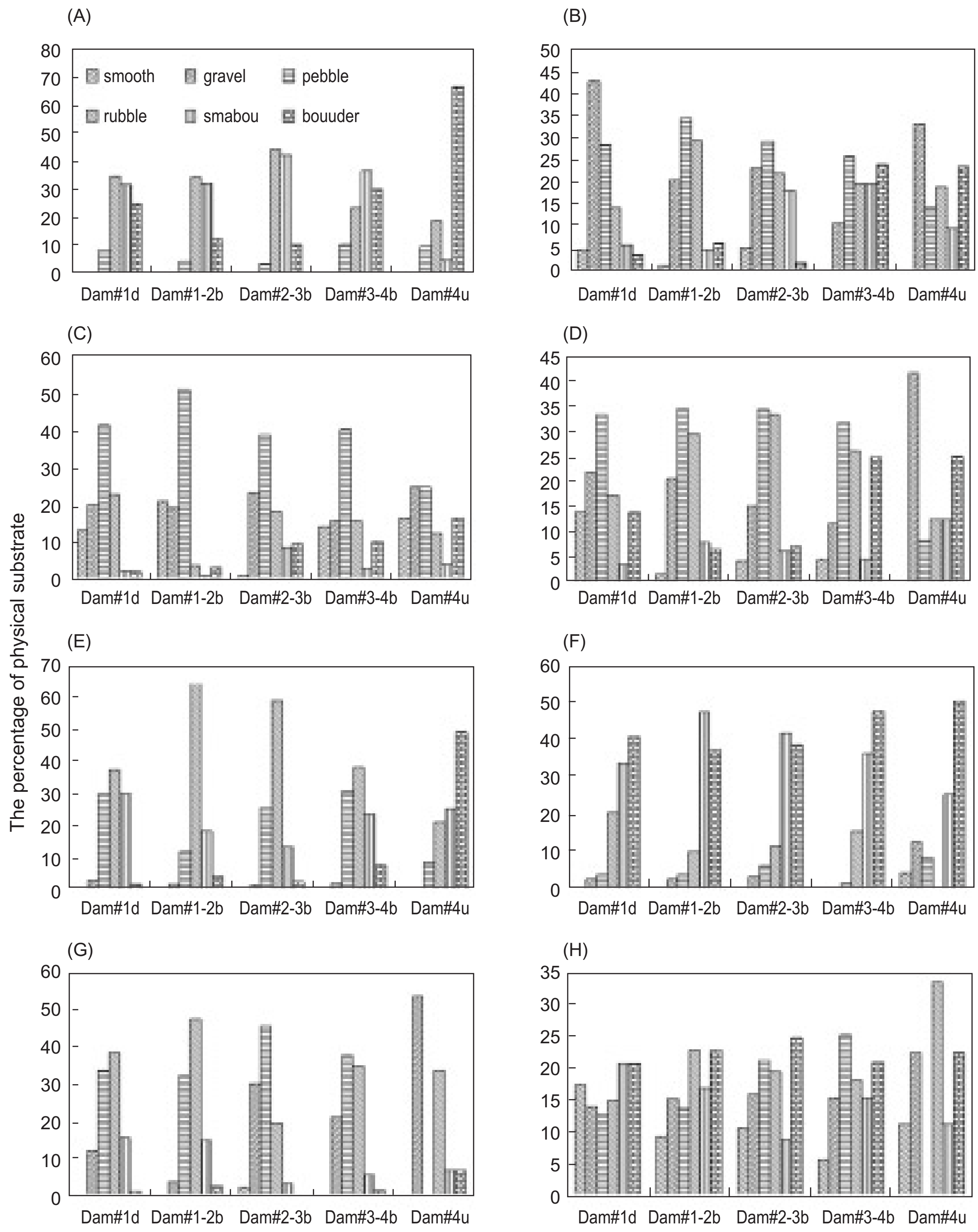

Fig. 4. Percentages of components of the physical substrate of salmon habitat between prior dam locations during the winters of 2001 and 2005 in Kaoshan Stream. s, summer; w, winter; Dam #1d, downstream of dam no. 1; Dam #1-2b, between dams no. 1 and no. 2; Dam #2-3b, between dams no. 2 and no. 3; Dam #3-4b, between dams no. 3 and no. 4; Dam #4u, upstream of dam no. 4; ▨, smooth; ▨, gravel; ▤, pebbles; ▨, rubble; ▥, small boulders; ▦, boulders. (A) 2001w, (B) 2002w, (C) 2003s, (D) 2003w, (E) 2004s, (F) 2004w, (G) 2005s, (H) 2005w.

have been the result of a high proportion of boulders observed between the remaining dams in winter 2004 (Bennett et al. 2003, Hedger et al. 2006).

In the absence of typhoons, the percentage composition of the physical substrate of the habitat did not adversely affect the salmon population during the study period of summer 2002 to summer 2004 (Fig. 3). However, flooding brought by typhoons might have washed salmon downstream, and in the absence of dams, salmon could return upstream. A high proportion of boulders benefits salmon by reducing the velocity of the stream and offering fish places of refuge. In fact, even in the case of a flood in the breeding season, a higher percentage of boulders helped the salmon population quickly bounce back (Nislow 1999, Harwood et al. 2002, Nykanen and Huusko 2003).

As a result of the removal of the dams, the velocity in the river increased, more-serious erosion occurred, and the river temperature decreased (Bartholow et al. 2005). Coincidently, the amount of aquatic insects, the primary food source for salmon, decreased. As a typical predator with a wait-and-sit foraging strategy (Valdimarsson and Metcalfe 1998), these fish spend most of their energy maintaining their position in a rapid current (Nislow et al. 1999). Interestingly, we found that salmon body sizes were relatively smaller in Kaoshan Stream than in Chichiawan Stream during the study period (Mann-Whitney test, $p < 0.001$, summer and winter 2005). Therefore, increasing the proportion of boulders in the riverbed might not only increase shelter spaces but also retard the flow velocity, allowing salmon to conserve their energy during floods (Lin et al. 1990, Coulombe-Pontbriand and Lapointe 2004).

Previously, Tzeng and Yang (2002) found that a good breeding season can lead to an increase in juvenile numbers. Our study provides further support for this hypothesis, since we also observed an increase in the number of juveniles following partial dam removal. When typhoons occur, floods wash salmon and sand and silt which have accu-

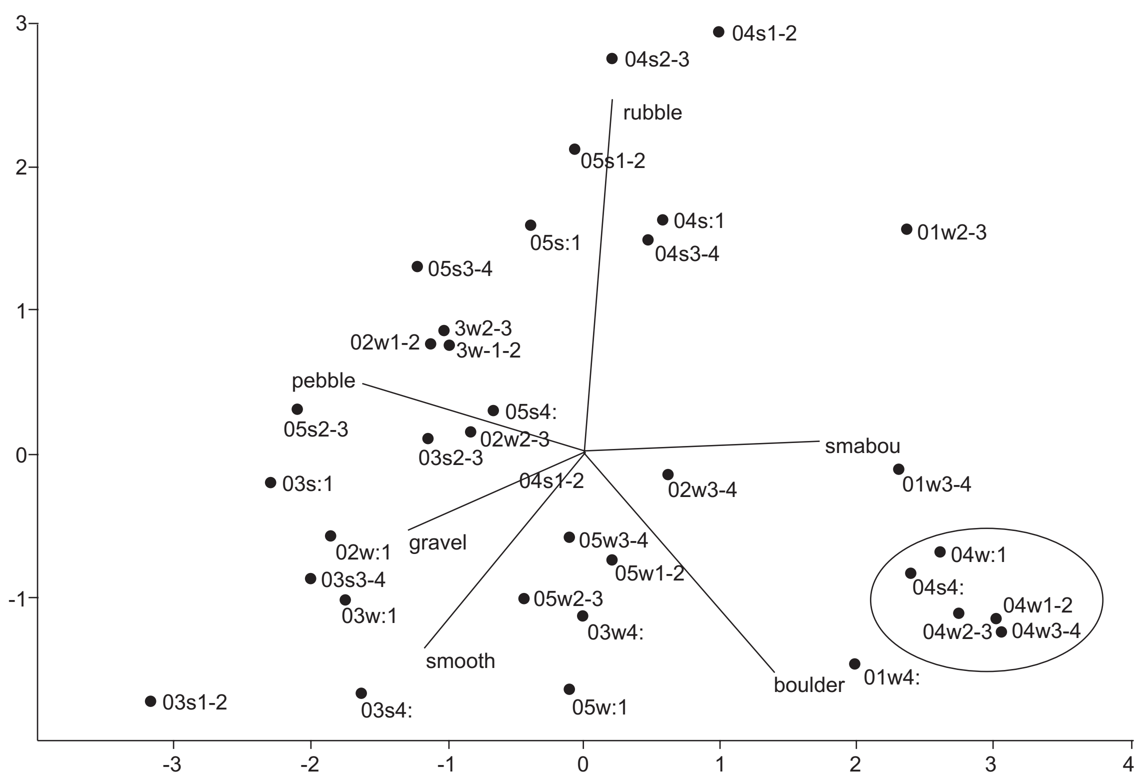

Fig. 5. Principal component analysis (PCA) ordination biplot of percentage variables of the physical substrate of the salmon habitat. 01, 2001; 02, 2002 03, 2003; 04, 2004; 05, 2005; s, summer; w, winter; :1, downstream of dam no. 1; 1-2, between dams no. 1 and no. 2; 2-3, between dams no. 2 and no. 3; 3-4, between dams no. 3 and no. 4; 4:, upstream of dam no. 4; the circle represents the percentages of the 2004 winter substrate. The x-axis ($PC1_{substrate}$) indicates that small boulders and boulders (> 25.6 cm) were the dominant factors. The y-axis ($PC2_{substrate}$) indicates that rubble was the dominant factor.

mulated upstream down the stream channel. In a dam-free environment, fish may be able to return upstream. During flooding, turbidity increases which impacts salmon egg development. When the stream velocity increases, so does dissolved oxygen (DO), while the water temperature decreases. This fact may reduce the effect of temperature as a limiting factor in summer (Yang 1997), thereby reducing competition pressure from coexistent species, such as the fish, *Varicorhinus barbatulus*, that cannot tolerate lower temperatures. However, the observed reduction in the number of aquatic insects, a primary food resource for salmon, may explain the smaller total length of salmon in Kaoshan Stream compared to that in Chichiawan Stream (Kuo 2005).

Habitat management plays an important role in wildlife conservation (Tsao et al. 1998). Throughout its life history, the Formosan landlocked salmon uses different microhabitats depending on its body size, foraging behavior, and breeding behavior (Lin et al. 1990, Tsao et al. 1998). We could likely gain further insights into salmon populations by applying the habitat-hydraulic model of Nykanen and Huusko (2003). We suggest that by integrating data types, we can more-successfully maintain an environment conducive to a sustainable salmon population. Although the Formosan landlocked salmon was once abundant in upstream tributaries of the Tachia River, the establishment of the check dam system limited their genetic diversity. With partial dam removal, the salmon habitat is now more diversified and therefore more favorable for the survival of different stages of salmon with different foraging and breeding demands (Hutchinson 1957, Paulsen and Fisher 2003).

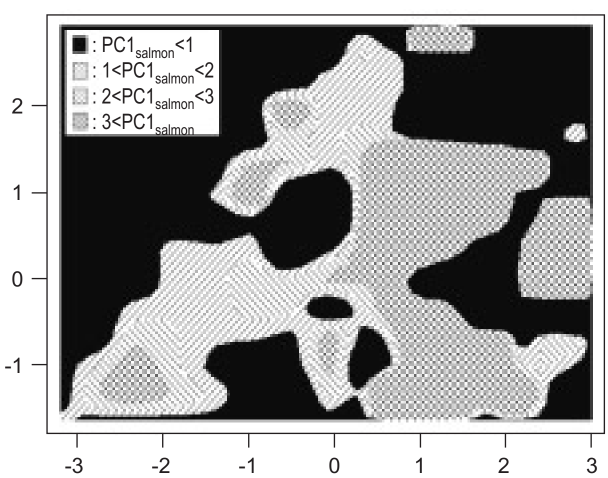

Fig. 6. Contour plot of salmon population abundances which were logarithmically transformed for the 1st principal component: $PC1_{salmon}$ (salmon total abundance); the x-axis is $PC1_{substrate}$ and the y-axis is $PC2_{substrate}$. , $PC1_{salmon} < 1$; , $1 \le PC1_{salmon} < 2$; , $2 \le PC1_{salmon} < 3$; , $3 \le PC1_{salmon}$.

Management implications

Maintaining boulders in stream may benefit salmon in different ways. Reductions in stream velocity and subsequent erosion benefit fish by creating suitable habitats like riffles and step-pools (Lai 1996). Also, an increase in shelter space can lead to a reduction in mortality by predation that is typically observed in clear, shallow-water stream habitats (Lin et al. 1990, Coulombe-Pontbriand and Lapointe 2004). Boulders also reduce energy expenditures by salmon when feeding (Harwood et al. 2002) and increase the probability of surviving early life stages (Nislow et al. 1999, Nykanen and Huusko 2003). Thus it appears that partial dam removal is an effective management approach for conserving the salmon population and maintaining genetic heterogeneity in Kaoshan Stream.

Acknowledgments: This study was supported by Shei-Pa National Park of Taiwan. We thank the volunteers who conducted the snorkeling censuses of the salmon population. We are grateful to Ms. Shu-Fen Yu for field assistance and advice. We also thank Ms. Jing-Fang Chung for her help with the figures.

REFERENCES

Anonymous. 1995-2005. Hydrological year book of Taiwan. Taipei, Taiwan: Water Resources Agency, Ministry of Economic Affairs. (in Chinese)

Bartholow JM, SG Campbell, M Flug. 2005. Predicting the thermal effects of dam removal on the Klamath River. Environ. Manage. **34:** 856-874.

Bennett DH, WP Connor, CA Eaton. 2003. Substrate composition and emergence success of fall Chinook salmon in the Snake River. NW Sci. **77:** 93-99.

Central Weather Bureau. Taipei, Taiwan: Central Weather Bureau, Ministry of Economic Affairs. Available at http://rdc28.cwb.gov.tw/data.php. Accessed 18 Oct. 2006.

Chung LC, HJ Lin, SP Yo, CS Tzeng, CH Yang. 2007. A stage-dependent population matrix model for the Formosan landlocked salmon (*Oncorhynchus masou formosanus*) in Taiwan. Raffles Bull. Zool. **Supplement 14:** 151-160.

Coulombe-Pontbriand M, M Lapointe. 2004. Landscape controls on boulder-rich, winter habitat availability and their effects on Atlantic salmon (*Salmo salar*) parr abundance in two fifth-order mountain streams. Can. J. Fish. Aquat.

Sci. **61:** 648-658.
Davey C, M Laponte. 2007. Sedimentary links and the spatial organization of the Atlantic salmon (*Salmo salar*) spawing habitat in a Canadian Shield river. Geomorphology **83:** 82-96.
Greenberg LA, RA Stiles. 1993. A descriptive and experimental study of microhabitat use by young-of-the-year benthic stream fishes. Ecol. Freshw. Fish **2:** 40-49.
Hammer Ø, DAT Harper, PD Ryan. 2001. PAST 1.37: palaeontological statistics software package for education and data analysis. Palaeontol. Electr. **4:** 1-9.
Harwood AJ, NB Metcalfe, SW Griffiths, JC Armstrong. 2002. Intra- and inter-specific competition for winter concealment habitat in juveniles salmonids. Can. J. Fish. Aquat. Sci. **59:** 1515-1523.
Healey M, P Kline, CF Tsai. 2001. Saving the endangered Formosa landlocked salmon. Fisheries **26:** 6-14.
Hedger RD, JJ Dodson, JF Bourque, NE Bergeron, PE Carbonneau. 2006. Improving models of juvenile Atlantic salmon habitat use through high resolution remote sensing. Ecol. Model. **197:** 505-511.
Heggenes J, TG Northcote, A Peter. 1991. Seasonal habitat selection and preferences by cutthroat trout (*Oncorhynchus clarki*) in a small, coastal stream. Can. J. Fish. Aquat. Sci. **48:** 1364-1370.
Heggenes J, SJ Saltveit. 1990. Seasonal and spatial microhabitat selection and segregation in young Atlantic salmon *Salmo salar* L., and brown trout *Salmo trutta* L., in a Norwegian river. J. Fish Biol. **36:** 707-720.
Hutchinson GE. 1957. Concluding remarks. Cold Spring Harbor Symp. Quant. Biol. **22:** 425-427.
Johnson RA, DW Wichern. 2002. Applied multivariate statistical analysis. 5th ed. Upper Saddle River, NJ: Prentice-Hall.
Kato F. 2003. Life histories of masu and amago salmon. *In* G Croot, L Margolis, eds. Pacific salmon life histories. Vancouver, Canada: UBC Press, pp. 449-452.
Kaufmann PR, P Levine, EG Robison, C Seeliger, DV Peck. 1999. Quantifying physical habitat in wadeable streams. Environmental Monitoring and Assessment Program. EPA/620/R-99/003. Washington, DC: Office of Research and Development, US Environmental Protection Agency, 149 pp.
Kottelat M. 1996. *Oncorhynchus formosanus*. *In* IUCN, Ver. 2.3. 2006 IUCN red list of threatened species. Available at http://www.iucnredlist.org. Accessed 25 December 2006.
Kuan WH. 2005. Long-term ecological monitoring and ecosystem modeling in the Wuling area － the study of water quality. Technical report. Taichung, Taiwan: Shei-Pa National Park Administration, 76 pp. (in Chinese)
Kuo MH. 2005. Studies on aquatic insect. Technical report. Taichung, Taiwan: Shei-Pa National Park Administration, 28 pp. (in Chinese)
Lai JS. 1996. The impacts of check-dams on the physical habitats of the Formosan landlocked salmon (*Oncorhynchus masou formosanus*). Master's thesis, National Taiwan Univ., Taipei, Taiwan. 112 pp. (in Chinese)
Lin HJ, PZ Wen, ML Laio, LC Chung, XX Zhang, CF Lee. 2005. Long-term ecological monitoring and ecosystem modeling in the Wuling area － the food source and model construction in stream ecosystem. Technical report. Taichung, Taiwan: Shei-Pa National Park Administration, 54 pp. (in Chinese)
Lin JY, EH Tsao, TC Lee, SL Yu. 2004. Stream physical parameters and habitat requirement: the case of the Formosan salmon. Ecol. Engin. **22:** 305-309.
Lin YS, SS Tsao, KH Chang. 1990. Population and distribution of the Formosan landlocked salmon (*Oncorhynchus mason formosanus*) in Chichiawan Stream. Bull. Inst. Zool. Acad. Sin. **29(Supplement 3):** 73-85.
Lin YS, PS Yang, SH Liang, SH Tsao, LC Juang. 1987. Ecological studies of Formosan landlocked salmon, *Oncorhynchus mason formosanus*. I. Preliminary study on the relationship between population distribution and environmental factors in Wuling Farm. Ecological Research no. 23. Taipei, Taiwan: Council of Agriculture, Executive Yuan, 66 pp. (in Chinese)
Nislow K, C Folt, D Parrish. 1999. Favorable foraging locations for young Atlantic salmon: application to habitat and population restoration. Ecol. Appl. **9:** 1085-1099.
Nykanen M, A Huusko. 2003. Size-related changes in habitat selection by larval graying (*Thymallus thymallus* L.). Ecol. Freshw. Fish **12:** 127-133.
Paulsen CM, TR Fisher. 2003. Detecting juvenile survival effects of habitat actions: power analysis applied to endangered Snake River spring-summer chinook (*Oncorhynchus tshawytscha*). Can. J. Fish. Aquat. Sci. **60:** 1122-1132.
Roni P, A Fayram. 2000. Estimating winter salmonid abundance in small western Washington streams: a comparison of three techniques. North Am. J. Fish. Manage. **20:** 683-692.
Rueda FJ, SG Schladow, SG Monismith, MT Stacey. 2003. Dynamic of large polymictic lake. I: field observation. J. Hydral. Eng. **129:** 82-91.
Shirvell CS, RG Dungey. 1983. Microhabitats chosen by brown trout for feeding and spawning in rivers. Trans. Am. Fish. Soc. **112:** 355-367.
Thurow RF, JT Peterson, JW Guzevich. 2006. Utility and validation of day and night snorkel counts for estimating bull trout abundance in first- to third-order streams. North Am. J. Fish. Manage. **26:** 217-232.
Tsao EHS. 1995. An ecological study of the habitat requirements of the Formosan landlocked salmon (*Oncorhynchus tshawytscha*). PhD dissertation. Colorado State Univ., Fort Collins, CO. 210 pp.
Tsao EHS, YS Lin, RJ Behnke, EP Bergersen. 1998. Microhabitat use by Formosan landlocked salmon, *Oncorhynchus masou formosanus*. Zool. Stud. **37:** 269-281.
Tzeng CS. 2005. Long-term ecological monitoring and ecosystem modeling in the Wuling area － studies on population ecology of the Formosan landlocked salmon. Technical report. Taichung, Taiwan: Shei-Pa National Park Administration, 38 pp. (in Chinese)
Tzeng CS, CH Yang. 2002. The effect of precipitations on the fluctuations in larva population size of Formosan landlocked masu salmon in the Chichiawan Stream basin. Natl. Park **12:** 111-124. (in Chinese)
Valdimarsson SK, NB Metcalfe. 1998. Shelter selection in juvenile Atlantic salmon, or Why do salmon seek shelter in winter? J. Fish Biol. **52:** 42-49.
Wang CMJ. 1989. Environmental quality and fish community ecology in an agricultural mountain stream system of Taiwan. PhD dissertation. Iowa State Univ., Ames, IA. 138 pp.
Wentworth CK. 1922. A scale of grade and class terms of

clastic sediments. J. Geol. **30:** 377-392.
Yang CH. 1997. The effect of the water temperature on Taiwan landlocked salmon (*Oncorhynchus masou formosanus*) in Chichiawan Stream basin. Master's thesis. National Tsing-Hua Univ., Hsinchu, Taiwan. 76 pp.
Yeh CH. 2005. Long-term ecological monitoring and ecosystem modeling in the Wuling area − the study of channel morphology and physical habitat in Chichiawan Stream. Technical report. Taichung, Taiwan: Shei-Pa National Park Administration, 67 pp. (in Chinese)
Yeh CH, PH Ling, CH Tuan. 2002. Implementation and current channel morphological condition of check dams' partial removal at Gau-Shan Creek. Natl. Park **12:** 191-203. (in Chinese)