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Microhabitat Use by Formosan Landlocked Salmon, *Oncorhynchus masou formosanus*

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Eric Hsienshao Tsao, Yao-Sung Lin, Robert J. Behnke and Eric P. Bergersen (1998) Microhabitat use by Formosan landlocked salmon, *Oncorhynchus masou formosanus*. *Zoological Studies* **37**(4): 269-281. Microhabitat requirements of the Formosan landlocked salmon (*Oncorhynchus masou formosanus*) were studied in four 85-m-long sections of the Chichiawan Stream. Underwater observations to locate the salmon, followed by measurements of physical habitat variables, were conducted along transects established at 5-m intervals. Available and occupied habitat units were compared to quantify water depth, current velocity, instream cover, and substrate type of suitable microhabitat. Data were pooled to represent salmon habitat use during 2 water temperature periods. Newly emerged fry extensively used habitats with nearly no current velocity and abundant instream cover. More than 50% of the salmon from 5 to 9 cm moved into deeper water having moderate current (0.1 to 0.86 m/sec) and less instream cover. Adult salmon used slower (less than 0.2 m/sec), shallower sites with abundant instream cover for resting, and fast velocity (0.6 to 1.1 m/sec), deeper sites with less instream cover for feeding. Spawning salmon preferred shallower waters (0.1 to 0.39 m), slower currents (0 to 0.3 m/sec), and small to moderate substrate sizes (< 25.6 cm). Microhabitat selection by Formosan landlocked salmon is related to fish size, water temperature, and life history activities.

Key words: Salmon, Microhabitat, Selection, Underwater observation.

It has long been realized that the amount of suitable habitat has an important effect in determining the abundance, growth, and other characteristics of salmonid populations in any water body (Shirvell and Dungey 1983). In general, habitat attributes can include physical features, water quality, and biological components (Marcus et al. 1990). Allee et al. (1949) defined microhabitat as the exact geographical locations and conditions where an animal spends all, or a portion, of its time. Since each organism has a definite optimal range of preferred habitat parameters, its population is often regulated by the availability of 1 or a few factors or requisites in short supply (Pianka 1988). In the past 4 decades, the severely restricted distribution and continuous decline in numbers of the Formosan landlocked salmon led to it being declared an endangered species in Taiwan in 1984 (Lin et al. 1987). Habitat alteration and degradation from major human impacts have been largely responsible for the greatly reduced range of this species (Lin et al. 1989, Wang 1989). Yet, little is known concerning the habitat requirements of the Formosan landlocked salmon. To ensure survival of the species, an understanding of microhabitat requirements is essential for natural resource managers seeking to restore degraded habitats or to identify new or former habitats suitable for reintroduction.

During ontogeny, salmonids typically exhibit different habitat requirements. Many studies have focused on habitat selection by different age groups and seasonal changes (Marcus et al. 1990, Heggenes et al. 1991b). But subtropical areas such as Taiwan do not have significant seasonal climatic changes. Nevertheless, water temperature

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and fish size may play the most significant roles in determining habitat selections. Water temperature will affect a fish's energy budget while a fish's size will often dictate how successful it competes for suitable habitat. In Chichiawan Stream, important habitat selection variables seem to be related to fish activity, bioenergetic profit taking when water temperature changes, and fish size which affects how it relates to or uses available habitat. Therefore, the objectives of this study were to investigate the following: 1) temporal changes in physical habitat availability within the stream; 2) salmon use of different habitats in relation to water temperature; 3) changes in habitat use with fish size; 4) changes in habitat use relative to different behavioral activities such as spawning, feeding, and resting; and 5) potential for developing a preference index for salmon habitat variables. Although many environmental factors may affect salmon habitat selection (Heggenes et al. 1991a), depth, current velocity, substrate, and cover are regarded as the most important physical habitat features determining the habitat use of stream fish (Shirvell and Dungey 1983, Greenberg and Stiles 1993). These 4 parameters were measured at the study sites in an attempt to define microhabitats for different size groups at different water temperatures. Microhabitat shifts through different activities and life stages are also identified and described.

MATERIALS AND METHODS

Study area

Study efforts were concentrated in Chichiawan Stream at Wuling Farm (Fig. 1). Chichiawan Stream drains from 3 mountains: Tao Shan (3324 m), Chihyu Shan (3301 m), and Pingtien Shan (3536 m) to its confluence with 5 other tributaries. The stream is about 15.3 km in length with a mean gradient of 0.13 (m/m) and a basin area of 76 km^2. Its width ranges from 7.1 to 12.3 m, dissolved oxygen is consistently greater than 7 mg/l, pH values range from 7.0 to 8.3, and hardness from 62 to 169 mg $CaCO_3$/l (Techi Reservoir Management Committee 1983, Lin et al. 1988). Historically recorded local air temperatures range from -8 to 29 °C (Wang 1989).

Since the 1960s, the west bank of the lower reach has been subjected to intensive agricultural development. Fifty percent of the landscape within Wuling Farm has been converted to agriculture. The eastern slope of the river valley is generally steep, and its vegetation is dominated by Taiwan two-needled pine (*Pinus taiwanensis*), oak (*Quercus variabilis*) associates (Liu and Su 1978), and Formosan alder (*Alnus formosana*). Herbaceous growth (such as *Miscanthus floridulus*), oval-leaved azaleas (*Rhododendron ovatum*), mountain asparagus (*Asparagus cochinchinesis*), and berry (*Rhubus aculeatiflorus*) form the understory of the riparian plant community (Tsao 1988). Chichiawan Stream is regarded as a moderately impacted agricultural stream (Wang 1989). Both the aquatic fauna (Huang 1987) and benthic algae present suggest that the downstream reach of the Chichiawan Stream is eutrophic.

Methods

Four study sites were selected along the Chichiawan stream (Fig. 1). Each site was 85 m long and further divided into 18 transects at 5-m intervals. Transects were located perpendicular to stream flow. Sampling points were established along stream cross-sectional transects starting from the west bank at 1-m intervals to the east bank. All established transects were permanently marked on the streambanks.

Stream physical habitat components and salmon microhabitat selections were monitored

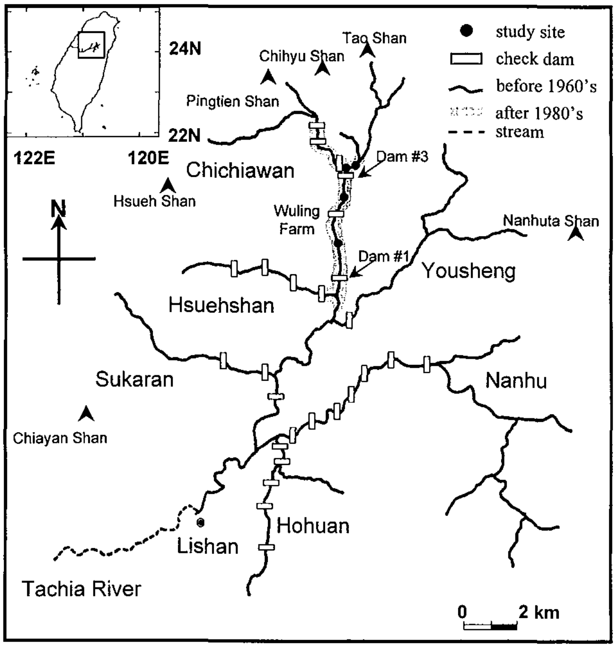

Fig. 1. Historical distribution of Formosan landlocked salmon and location of study sites along the Chichiawan Stream, 1 of 6 headwater tributaries of the Tachia River.

from May 1987 to April 1988 in concert with Tsao's M.S. study (1988). Within each study site, 3 transects were randomly selected and surveyed every other week. All transects were then evaluated seasonally (randomly within every 3-mo interval). Water temperature, depth, current velocity, and dominant substrate type were recorded along the transects at sampling points. Current velocity was measured at 60% of depth from surface using a Hydro-bio Kiel digital flow meter (Wang 1989). Dominant substrate type was ranked from 1 to 6 based on the diameter ranges (< 0.2 cm, 0.2 to 1.6 cm, 1.6 to 6.4 cm, 6.4 to 25.6 cm, 25.6 to 51.2 cm, and > 51.2 cm, respectively) of existing substrate (Platts et al. 1983).

Because the salmon population is endangered, no fish were captured. Underwater observations (Cunjak and Power 1986, Heggenes et al. 1990, Greenberg and Stiles 1993) were conducted to locate individual fish. Divers moved upstream zigzagging along the transects. The total length of each individual salmon was estimated by comparing nearby substrate. The substrate was then measured with a ruler to the nearest cm. The location of each salmon observed was recorded in a diver's notebook and microhabitat information was collected based on the closest sampling point where physical habitat variables were measured.

From Oct. to Dec. 1988, spawning habitat requirements were studied. Distribution of salmon redds was surveyed throughout a 4.2-km section between check dams #1 and #3. Observers walked upstream along the bank, and when salmon spawning activity was observed, the locations were recorded as distances from check dam #1. Redd site selection was delineated using an average 14-m-wide and 55-m-long grid system (1 m by 1 m, totaling 782 m^2) set within the stream 2.3 km above Dam #1 where the density of spawning pairs had been considered relatively high during the previous spawning season. Salmon spawning habitat was studied intensively within the grid system. Depth, surface current velocity, bottom current velocity, and substrate type were recorded at the corners of each grid intersection. Surface current velocity was measured at 5 cm below the surface; bottom current velocity was measured at 5 cm above the bottom. Within the study site, salmon spawning activities and pairs of spawners were also identified from the banks. After the redds were established, their location, depth, surface and bottom current velocities, and substrate types were recorded.

From 1989 to 1993, relationships between different salmon activities and microhabitat use were studied. Microhabitats were measured only after the activity of an individual fish was determined. For feeding, the criterion was movement of the fish away from and back to the occupied position that was associated with prey interception or chase activity as described by Shirvell and Dungey (1983). After an individual fish and its activity (resting or feeding) was identified (at least 3-5 min), its total length was then estimated. Microhabitat variables such as water depth, average current velocity, focal point depth, focal point velocity, and substrate types were measured at the location where the fish was observed. Instream covers such as large boulders, bedrock, or caves formed by different size rocks were also recorded. In 1993, current velocity was measured with a Swoffer Model 2100 current meter instead of the Hydro-bio digital flow meter. Instream cover was ranked from 1 to 4 (no cover, visual isolation, velocity shelter, and combination of velocity shelter and visual isolation, respectively) using the Index of Instream Cover (Bovee 1982).

Data were analyzed using the MANOVA test (SAS 1990). Measurements of each habitat variable were pooled from Dec. to April (cold water period) and from May to Nov. (warm water period). Physical habitats during the 2 periods were compared to assess spatial and temporal changes in habitat quantity and quality. Individual fish observed were divided into 4 size groups based on total length increments of < 5 cm, 5 to 9 cm, 10 to 17 cm (age 0$^+$), and > 17 cm (age I$^+$ and older), respectively. Microhabitats used by fish of different sizes during the 2 periods were then compared to find the most important criteria for habitat selection. Differences in microhabitats occupied by salmon during different activities were also compared.

The number of salmon redds observed within 200-m intervals along the 4.2-km section of the Chichiawan Stream was calculated to reveal spatial distribution. Habitat variables collected from the grid system were compared with those collected from salmon redds. Salmon redds identified within the grid were marked on a map to compare their spatial distribution against different habitat variables.

To provide reasonable criteria for existing vs. occupied microhabitats, existing and occupied habitat components were described first according to their relative frequency of occurrence. The relative frequency of occurrence was calculated as the number of observations with a single range of physical habitat variable values (for example, depth from 0.1 to 0.2 m) divided by total number of observations.

RESULTS

Within the study sites, significant differences in physical habitats occurred between the 2 water temperature periods (Table 1). Mean water depth and mean current velocity were higher during the high flow warm period (from May to Nov.). Standard deviations (SD) of mean depth were similar between the 2 periods, but a higher SD of mean current velocity was calculated for the warm period. This result suggests that greater fluctuations occurred in current velocities during the warm period. In addition, microhabitats with zero current velocity contributed less than 19% of total sampling points year round (Table 1). The substrate within the study sites was dominated by various sizes of boulders and tended to have a smaller average diameter during the warm period.

Salmon microhabitat use differed with fish size and temperature period ($N = 894$, $F = 2.56$, $p < 0.05$). Among the 4 habitat variables, current velocity ($F = 7.87$, $p < 0.01$), substrate type ($F = 5.56$, $p < 0.01$), and instream cover ($F = 21.04$, $p < 0.01$) were significantly different among salmon microhabitat use during their various life stages ($F = 12.47$, $p < 0.01$). Within each size group, individual fish occupied different microhabitats during different periods ($F = 7.36$, $p < 0.01$). This was especially noticeable between microhabitats at different current velocities ($F = 17.95$, $p < 0.01$). Only 36 newly emerged fry were observed during the cold period. With total lengths of < 5 cm, these fish were concentrated along stream margins with sufficient instream cover and nearly no current velocity (Table 2; Fig. 2). Size 2 fish with total lengths between 5 and 9 cm were only observed during the warm period. More than half of these fish moved into areas with deeper water, moderate current, or no instream cover (Table 2; Fig. 2). Eighty percent of them used microhabitats of 0.18 to 1.46 m depth with either slow or moderate current velocity (0.01 to 1.1 m/sec). Uses of microhabitats were similar among substrate sizes > 0.2 cm in diameter (types 2 to 6).

Fish from 10 to 17 cm (size 3) occupied similar microhabitats during both temperature periods. They tended to use areas with moderate current velocity (0.1 to 1.4 m/sec) and less instream cover year round (Table 2; Fig. 2). Most of these microhabitats were within riffles and runs. Size group 4 with total lengths > 17 cm (age I^+ and older) preferred significantly different habitats in the 2 temperature periods ($N = 467$, $F = 23.64$, $p < 0.01$). This was mainly due to different uses in current velocity ($F = 29.86$, $p < 0.01$) and instream cover associations ($F = 32.24$, $p < 0.01$). These fish used deep areas (depth > 1 m) year round, but some used sites with moderate depth as well. During the warm temperature period, most size 4 fish were either feeding or maintaining positions in microhabitats with moderate current velocity (0.3 to 1.2 m/sec) associated with less instream cover (Table

Table 1. Comparison of physical habitat components in four 85-m-long study sites between 2 temperature periods in Chichiawan Stream from 1987 to 1988 by MANOVA test

Wilks' Lambda		$F = 103.64$ ($p < 0.01$) **		
		Warm period (May-Nov.)	Cold period (Dec.-Apr.)	F value (p-value)
Depth (m)	Mean	0.45	0.42	10.10
	SD	0.34	0.36	(0.0015)**
Substrate type	Mean	4.39	4.51	10.71
	SD	1.21	1.19	0.0011**
Velocity (m/sec)	Mean	0.58	0.36	254.12
	SD	0.52	0.40	0.0001**
Percent of physical habitat with zero current velocity		17.11	18.52	

Note: substrate types were treated as classified values in MANOVA examination; total sampling points along transects: cold period $N = 1996$; warm period $N = 2509$; ** probability < 0.01.

2; Fig. 2). When the temperature dropped, they became less active, preferring either very slow current (< 0.2 m/sec) while resting or fast current (0.6 to 1.1 m/sec) while feeding, and they tended to use instream cover more often.

Salmon used different microhabitats for different activities. A comparison of size 4 salmon feeding and resting microhabitat selections using MANOVA test showed significant differences (N = 71, F = 13.13, $p < 0.01$) in focal point depth (N = 71, F = 20.17, $p < 0.01$), focal point velocity (N = 71, F = 31.62, $p < 0.01$), and instream cover (N = 71, F = 16.7, $p < 0.01$). Wide ranges of both mean current velocity and depth used by size 4 fish were observed. Feeding positions had higher focal velocity, slightly deeper water, and less instream cover than did resting positions. However, the physical attributes of the focal point and its water column were different (Fig. 3).

Within the grid area, the average depth was 0.39 m, the mean surface current velocity 0.21 m/sec, and the mean bottom current velocity 0.13 m/sec. The substrate was mainly formed by boulders with diameters > 25.6 cm. A total of 58 redds were recorded averaging 0.67 m (0.2-1.2 m) in length, 0.4 m (0.2-0.85 m) in width, and 0.27 m^2 (0.03-0.8 m^2) in surface area. Salmon redds had a patchy rather than random distribution within the grid system. The relative frequency of observation showed that areas with shallower water (0.1 to 0.39 m), slower current (0 to 0.3 m/sec), and small to moderate substrate types were selected by female salmon for spawning (Table 3). The redds had depths ranging from 0.1 to 0.63 m ($\overline{X}$ = 0.25 m), surface current velocity of < 0.58 m/sec ($\overline{X}$ = 0.09 m/sec), and bottom current velocity of < 0.44 m/sec ($\overline{X}$ = 0.06 m/sec). The difference between the available and occupied depths was significant (χ^2 = 54.86, $p < 0.01$), but analysis of both surface and bottom current velocity showed little difference between available and occupied spawning habitats (Table 3). However, the major determinant of redd

Table 2. Depth and current velocity of microhabitats used by different sizes of Formosan landlocked salmon during two temperature periods (1987 and 1988) in Chichiawan Stream

	Depth (m)					
Quantiles (%)	Cold period (Dec. to April)			Warm period (May to Nov.)		
	Size 1	Size 3	Size 4	Size 2	Size 3	Size 4
1	0.16	0.20	0.14	0.11	0.13	0.19
5	0.21	0.20	0.19	0.13	0.18	0.34
10	0.22	0.22	0.25	0.18	0.19	0.41
25	0.26	0.37	0.36	0.30	0.36	0.47
50	0.34	0.67	0.47	0.46	0.47	0.67
75	0.86	0.93	0.62	1.26	0.75	1.26
90	0.86	1.01	1.05	1.46	1.44	1.47
95	0.86	1.01	1.90	1.47	1.47	1.47
99	0.86	1.01	2.00	1.47	1.85	1.70
	Current velocity (m/sec)					
Quantiles (%)	Cold period (Dec. to April)			Warm period (May to Nov.)		
	Size 1	Size 3	Size 4	Size 2	Size 3	Size 4
1	0	0	0	0	0	0
5	0	0	0	0	0.02	0
10	0	0	0	0.01	0.10	0
25	0	0.12	0	0.10	0.37	0.10
50	0	0.45	0.19	0.41	0.75	0.27
75	0.02	0.73	0.56	0.86	1.09	0.97
90	0.02	0.90	1.00	1.11	1.37	1.15
95	0.08	1.04	1.11	1.44	1.44	1.31
99	0.08	1.04	1.11	1.68	1.51	1.51

Note: size 1: total length (TL) < 5 cm; size 2: TL = 5-9 cm; size 3: TL = 10-17 cm; size 4: TL ≥ 18 cm; the definition of quantiles is the same as in most standard statistics textbooks (for example, see chapter 3 *In* Healey 1993).

site selection was substrate type (Fig. 4). Gravel from 0.2 to 1.6 cm, pebbles from 1.6 to 6.4 cm, and cobbles from 6.4 to 25.6 cm in diameter dominated the substrate compositions of the redds. Females were observed to touch the substrate with their pelvic fins during the nest digging process. Small gravel and pebbles were swept from spawning habitats during nest construction. After eggs were deposited, the female moved upstream from the 1st redd and excavated additional substrate. The 1st redd was then covered by small bits of substrate transported from upstream by the current.

DISCUSSION

Many habitat studies have not addressed the basic biological assumption that some fish populations are limited by habitat parameters rather than by food, competition, predation, or fishing mortality (Bohlin 1977). However, the habitat limitation assumption seems to apply to the Formosan landlocked salmon. This unique salmon population exists only within 7 km of Chichiawan and Hsuehshan streams, both headwater streams of the Tachia River (Lin et al. 1987 1993). Two small fish, the shovelmouth minnow (*Varicorhinus barbatulus*) and Taiwan tasseled-mouth loach (*Crossostoma lacustre*), coexist with the Formosan landlocked salmon in the downstream sections of the Chichiawan and Hsuehshan streams, but the salmon is dominant in the fish community (Lin et al. 1989). Wang (1989) concluded that both shovelmouth minnow and Taiwan tasseled-mouth loach rely heavily on algal detritus and small insects as food and are ecologically distinctive in their microhabitat needs and seasonal diets. The Formosan landlocked salmon is insectivorous and appears better adapted to colder water than are the non-salmonid fishes. The limited areas of overlap (about 2 km of stream) and separated feeding niches from the minnow and loach populations suggest that interspecific competition has an insignificant effect on salmon habitat use.

Predation may also play major roles in determining habitat selection (Werner et al. 1983). The only potential salmon predator in its range is the Little Green Heron (*Butorides striatus amurensis*), an uncommon resident but common winter visitor along lake shores and mountain streams up to

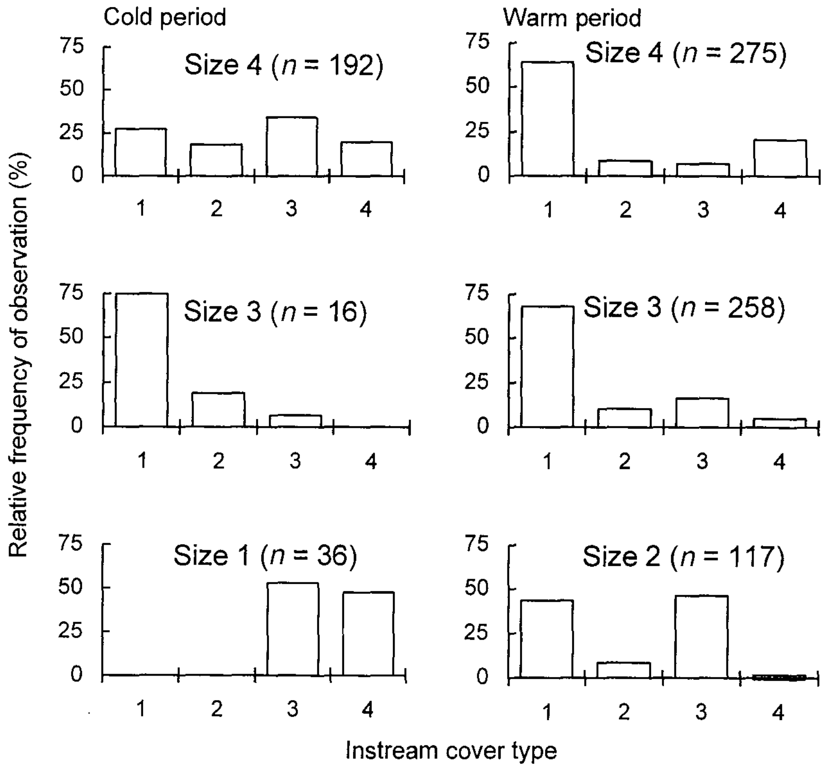

Fig. 2. Instream cover types of microhabitats used by different sizes of Formosan landlocked salmon (size 1: total length of < 5 cm; size 2: 6-9 cm; size 3: 10-17 cm; size 4: ≥ 18 cm) during two temperature periods (cold: Dec. to April; warm: May to Nov.) in Chichiawan Stream.

1500 m elevation in Taiwan (Chang 1980). This bird is solitary and is rarely observed within the historical range of the Formosan landlocked salmon. Therefore, the degree of predation pressure occurring in the study areas should be relatively low. Ueno (1938) reported that the Formosan landlocked salmon fed mainly on aquatic insects, especially trichopterins and plecopterins, but their stomach contents also included terrestrial insects and amphibians. The salmon were observed feeding on benthic and drifting macroinvertebrates, terrestrial insects, and the small frog, *Rana sauteri* (Tsao 1988). At least 6 orders, 31 families, and 61 species of aquatic insect larvae were recorded along the Chichiawan, Hsuehshan, and Yousheng streams during a preliminary study (Yang et al. 1986). Diverse aquatic macroinvertebrates combined with terrestrial species within the Wuling Farm watershed should provide abundant food resources for the salmon (Yang et al.

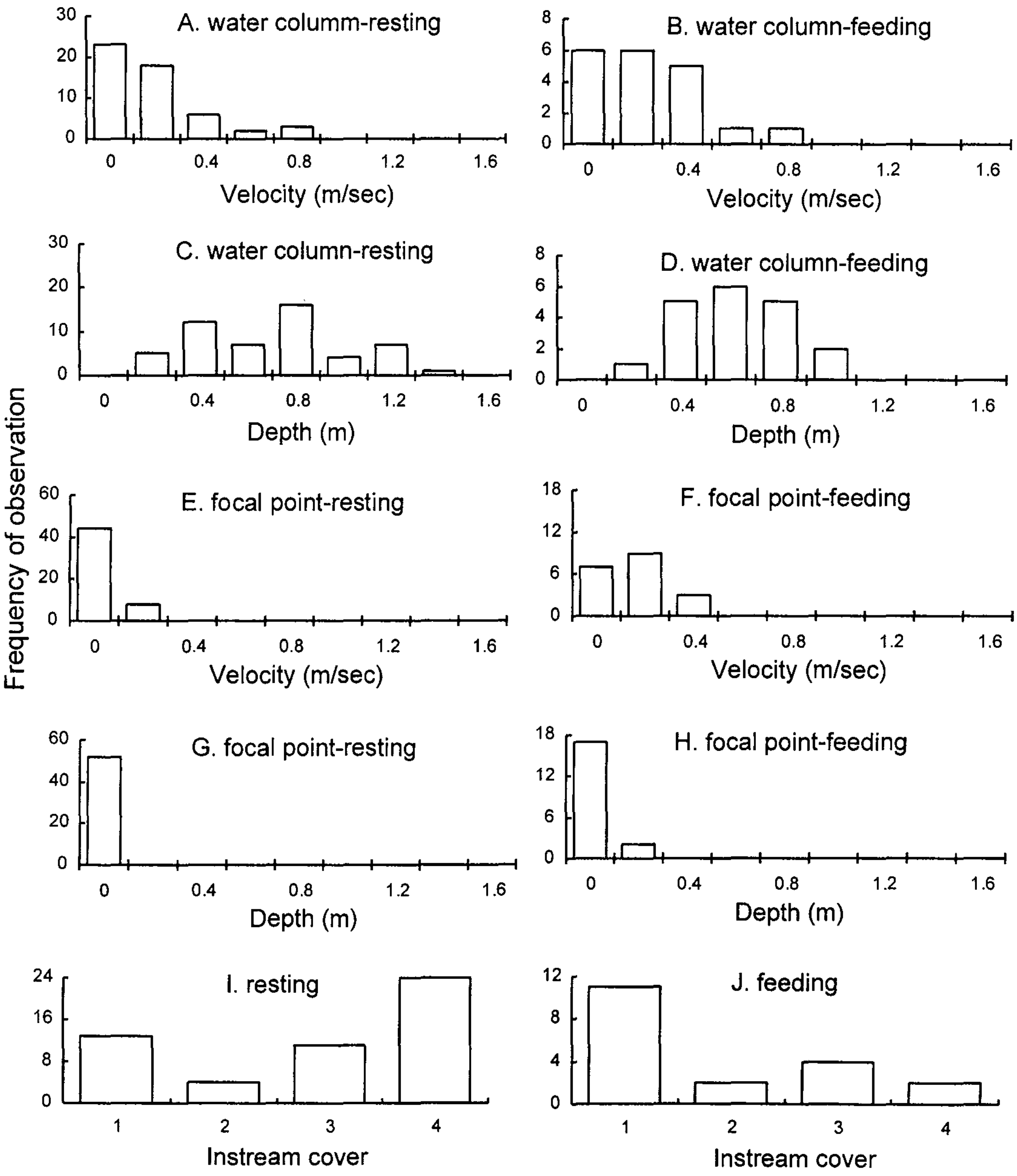

Fig. 3. Comparison of physical features of microhabitats used by size 4 (total length of ≥ 18 cm) Formosan landlocked salmon for feeding and resting: A to D: measurements of the water column where focal point existed; E to J: measurements of focal points occupied by the salmon.

1986, Huang 1987). This is indicated by growth reaching a total length of 16 cm within 10-mo after emergence (Tsao 1988). The relatively high growth rate indicates that food resources are not a significant limiting factor of the salmon population in Chichiawan Stream. All these results suggest that the salmon population is currently limited by habitat rather than by other factors.

Table 3. Comparisons of physical characteristics between available and occupied spawning microhabitat within the 1 m x 1 m grid system set in Chichiawan Stream from Oct. to Dec., 1988

Depth (m)	Available unit (n)	Spawning sites (n)	Chi-square (*p*-value)
0 – 0.09	75	0	54.86
0.1 – 0.19	106	26	(< 0.001)**
0.2 – 0.29	123	12	
0.3 – 0.39	103	10	
0.4 – 0.69	287	9	
0.7 – 1.00	88	0	
Surface current velocity (cm/sec)			
0 – 0.15	416	42	10.95
0.16 – 0.3	133	9	(0.012)*
0.31 – 0.6	164	7	
0.61 – 1.65	69	0	
Bottom current velocity (cm/sec)			
0 – 0.15	521	47	6.96
0.16 – 0.45	204	11	(0.073)
0.45 – 0.6	25	0	
> 0.6	32	0	
Substrate type (cm)			
1 (< 0.2)	1	0	60.79
2 (0.2 – 1.6)	47	10	(< 0.001)**
3 (1.6 – 6.4)	94	15	
4 (6.4 – 25.6)	233	33	
5 (25.6 – 51.2)	163	0	
6 (> 51.2)	244	0	

*probability < 0.05; **probability < 0.01.

One of the assumptions implied by the MANOVA test is that data points of each variable form a normal distribution. In this study, distributions of most microhabitat variables might not satisfactorily fit the assumption of normality. Although large numbers of samplings may compensate for the problem (Lindgren 1993), the several data sets in this study are relatively small. Therefore, the degree of violation in multivariate normality in this case is difficult to test and will require further study. Under this circumstance, application of MANOVA is still a useful tool but may provide a slightly weaker ability to diagnose differences among data sets. In recognition of the statistical limitations, caution was applied in our attempts to interpret and synthesize the data analyses in order to obtain some insights into salmon microhabitat use throughout their life stages.

The total depth, velocities, and substrate of existing microhabitats show that a wide range of physical configurations are provided by Chichiawan Stream, but they differ significantly during the 2 temperature periods. This is largely due to changes in discharge. Since summer and autumn floods are part of the typical precipitation pattern in Taiwan (ROC Water Resources Planning Commission 1977), higher flows may lead to increases in depth and current velocity. Strong currents usually result in downstream sediment transport, rearrangement of substrate components, and also changes in channel morphology through time. This

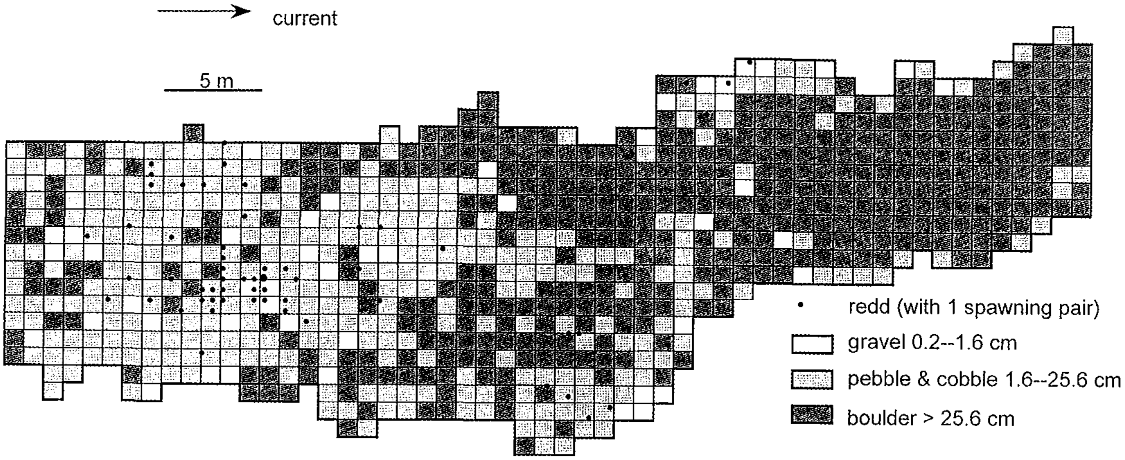

Fig. 4. Spatial distribution of Formosan landlocked salmon redds and dominant substrate types within the grid system (1 m × 1 m) set in Chichiawan Stream.

is a common phenomenon in most streams. The smaller sizes of substrate during the warm period could be due to the combination of both sediment transport from upstream sections and bank erosion caused by floods. Slightly higher mean water depth and mean current velocity were observed during the warm period when flows were higher. In addition, microhabitats with no current velocity are not very abundant year round. The measurement of physical habitats indicates that salmon are subjected to stronger and fluctuating currents with inadequate low velocity refuges during the warm period. This may require greater expenditure of energy for the fish to maintain their position in the stream. On the contrary, salmon expend less energy maintaining their position in the stable and slower current during the cold period.

The microhabitat an individual fish inhabits in a stream may reflect the consequences of behavioral need (Shirvell and Dungey 1983, Fausch 1984), compromised by morphological (Moyle and Baltz 1985, Bisson et al. 1988), bioenergetic (Rincon and Lobon-Cervia 1993), and ontogenetic constraints (Everest and Chapman 1972). In Hokkaido, Japan newly emerged masu (*Oncorhynchus masou*) fry school in shallow backwaters (0.05 to 0.1 m in depth) and slow currents (Kubo 1980). As the fry grow to 5-6 cm in fork length, they move to deeper areas with stronger currents (Krykhtin 1962). The sustained speed of small masu salmon (body weight < 6 g) ranges from 0.3 to 0.7 m/sec (Kobayashi and Ohkuma 1983). In late Oct., when water temperature begins to drop, juveniles tend to move from pool habitats to warmer downstream sections and use more instream cover (Inoue and Ishigaki 1968). Similar patterns of microhabitat selection were observed for the Formosan landlocked salmon. In our study, low velocity habitats and abundant instream cover were used extensively by newly emerged fry of 2.5 to 4 cm total length. Histograms of relative frequency of observation suggest that current velocity and instream cover play major roles in determining fry habitat use. This may relate to predator avoidance behavior and their limited swimming ability. Larger Formosan landlocked salmon from 5 to 9 cm (size 2) were only observed from May to August. More than half of these fish moved into deeper water (depth > 0.5 m), areas with moderate current (0.4 to 1.1 m/sec) or with no instream cover. This pattern suggests that the Formosan landlocked salmon starts to disperse from areas with nearly no current velocity and sufficient instream cover 3-mo after emergence, and that their microhabitat selection is size related.

Size-related microhabitat shifts are considered to be ontogenetic phenomena (Grossman and Freeman 1987). Studies have shown that there are age-related shifts by young-of-the-year rainbow trout into microhabitats with deeper and faster currents (Baltz and Moyle 1984, Moyle and Baltz 1985). Heggenes et al. (1990) reported that smaller Atlantic salmon parr are generally found in more shallow areas, with slower water velocities and smaller substrates. With increasing size, fish tend to move to deeper areas and also to regions with increasing water velocities and coarser substrate. Vondracek and Longanecker (1993) observed large rainbow trout in pools, intermediate-sized fish in runs, and small trout in riffles. Most 10- to 17-cm Formosan landlocked salmon inhabited riffles or runs with moderate current velocity (0.1 to 1.4 m/sec) and no instream cover. Habitat use between temperature periods was not significantly different, but when the water temperature dropped, these size 3 fish also tended to use more instream cover. On the other hand, most salmon 18 cm or larger were observed either in deep pools or shallow areas. During the warm temperature period, most of these fish used microhabitats with moderate current velocity and less cover. This shift in habitat use can be explained by their intensive feeding activities. When the temperature drops, they use either very slow current velocities for resting or fast current velocities for feeding and tend to use more instream cover. All Formosan landlocked salmon > 10 cm show a preference for deep water, but more salmon 18 cm or larger were recorded in deep pool areas. Larger fish are dominant over smaller fish, therefore, they are more likely to occupy a preferred microhabitat. Roper et al. (1994) indicated that salmon parr tend to be generalists in terms of microhabitat selection. Habitat use by age-0 steelhead was recorded as only slightly different from habitat availability (Roper et al. 1994). Results from our study suggest that the Formosan landlocked salmon young-of-the-year (total length of 10 to 17 cm) also tend to be microhabitat generalists. However, this result may be a function of intraspecific competition. When the demand for optimal habitat exceeds the supply, larger fish will occupy the most suitable habitats, and young-of-the-year fish have to use whatever other habitats remain.

Activity-specific microhabitat uses were also observed. Generally, salmon maintain focal positions in areas of low velocity and feed in adjacent areas where velocity is higher (Everest and

Chapman 1972, Smith and Li 1983). Activity-specific focal positions have also been observed in brown and rainbow trout (Jenkins 1969, Shirvell and Dungey 1983). Age I$^+$ and older Formosan landlocked salmon use slower, shallower sites with abundant instream cover for resting, and moderate velocity, deeper sites with less instream cover for feeding as their focal positions. Fishes were observed to wait at a focal point with a lower current velocity and then dart out into the current to catch food. In practice, it would be difficult to quantify available focal positions due to the uncertainty of the exact location of measurable physical variables within any water column. Measurement of physical variables can only be conducted to represent an individual water column instead of any specific focal point that may occur within it.

Bioenergetically, maximum net energy intake (Fausch and White 1981) and minimum energy cost (Fausch 1984, Facey and Grossman 1992) are both considered important to salmon holding their positions. According to the histograms of relative frequency of observations of physical variables of salmon microhabitats, optimum combinations of current velocity and instream cover may have affected the habitat use of Formosan landlocked salmon in Chichiawan Stream. Size 3 salmon spend most of their time in feeding positions, while size 4 fish use either feeding or resting positions. The use of interstitial spaces in the substrate as shelter by juvenile trout during the winter has been reported (Rimmer et al. 1983, Cunjak 1988, Heggenes and Saltveit 1990, Vondracek and Longanecker 1993). The Formosan landlocked salmon tends to seek out instream cover as overwintering shelter (Tsao 1988). The close association with overwintering shelter may allow the salmon to avoid swift currents and thus reduce energy loss in maintaining positions.

Formosan landlocked salmon spawning sites show a non-random distribution along Chichiawan Stream as well as within the grid system. This distribution indicates that most of the suitable spawning habitat may occur in the stream section between 1.3 to 2.7 km above check Dam #1. In Japan, sea-run masu salmon ascend long distances for spawning, but the landlocked masu salmon do not migrate far from the original (prespawning) habitat for spawning (Kimura 1989). Similarly, the Formosan landlocked salmon move only short distances from feeding or resting habitats to the spawning ground (Nakamura and Koshigi 1938, Teng 1959). In our study, observations of Formosan landlocked salmon spawning behavior show that the salmon have very specific spawning site requirements and redd construction patterns. However, these phenomena seem to be size related. Osanai and Otsuka (1967) reported that spawning anadromous masu salmon ascending the rivers of Hokkaido average about 50 cm in length. Their redds are built in areas with depths from 0.12 to 0.45 m and average current velocities of 0.46-0.56 m/sec. Redds are generally oval in shape, particularly in slow current. The average length is 1.24-2.1 m with width of 0.78-0.84 m. Substrate composition by weight was measured as 9% pebble and smaller gravel, 30% cobble, 30% small boulder, and 31% large boulder. The landlocked masu salmon (Yamame) on Hokkaido were usually less than 30 cm in total length. Their redds are found in gravel areas at the end of pools and along the sides of areas of rapid flow, where currents are smooth and moderate in speed (0.1 to 0.35 cm/sec), with substrate composed mainly of small (0.5 to 5 cm) pebbles (Kimura 1989). In Kamidani, River Yura of Japan, spawning of the fluvial form of masu salmon occurs only near the lower end of pools (including small sluggish areas), with constant current where the stream bed is mainly composed of 1- to 3-cm gravel (Maruyama 1981). A total of 58 Formosan landlocked salmon redds recorded within the grid system during our study were much smaller than those of the Japanese sea-run masu salmon. The average depth over redds (0.39 m) falls into the range of Japanese sea-run masu salmon redds but water velocities tend to be more similar to those of the landlocked Yamame. Spawning Formosan landlocked salmon prefer shallower waters, slower currents, and smaller to moderate substrate sizes within microhabitats available in the grid system. Gravel, pebble, and cobble dominate the substrate compositions of the salmon redds. These substrate sizes are similar to those preferred by steelhead and rainbow trout (*Oncorhynchus mykiss*), brown trout (*Salmo trutta*), cutthroat trout (*O. clarki*), and masu salmon (*O. masou*) (Osanai and Otsuka 1967, Orcutt et al. 1968, Kimura 1972, Shirvell and Dungey 1983, Crisp and Carling 1989, Thurow and King 1994). Reiser and Wesche (1977) suggested that temperature and substrate are among the most important physical components for salmonid redds. Shirvell and Dungey (1983) suggested that selection of current velocity for spawning may have evolved as a substitute for the proper substrate for salmonids.

Knowledge of the physical characteristics of suitable spawning habitat has fundamental and practical importance for the salmon recovery program. This study on Chichiawan Stream suggests that microhabitat use is related to fish size, water temperature, and activities throughout the life history of the Formosan landlocked salmon. While more information is still needed to define habitat use and habitat availability during resting and feeding activities, we have nevertheless identified important patterns of microhabitat use by this species. The success of management and conservation programs for the Formosan landlocked salmon can be improved by delineating these habitat uses when attempting to enhance existing habitat or identifying new sites for possible reintroduction.

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櫻花鉤吻鮭之微棲地使用

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在七家灣溪内選取四段長度85公尺的溪段，垂直流水方向間隔五公尺設一條穿越線，利用浮潛法記錄所觀察到櫻花鉤吻鮭 (*Oncorhynchus masou formosanus*) 個體的大小與行為，隨後並測量水體與鮭魚吻端位置的物理因子，包括水深、流速、底質石粒徑、溪流内遮蔽物有無等，據此比較不同水溫時期、不同魚體大小、不同行為下，櫻花鉤吻鮭所使用的微棲地物理因子之特徵。發現浮現初期的仔魚多集中水流速度緩慢與溪流内遮蔽物豐富的區域；目測體長超過5公分的幼魚則泰半移入水位較深、水流速較高（0.1至0.86 m/sec）的水域，且對溪流内遮蔽物的依賴程度不高。一齡以上的成魚喜好使用溪水較淺、水流速較緩（低於0.2 m/sec）且溪流内遮蔽物豐富的位置休息；溪水較深、水流速較高（0.6至1.1 m/sec）且溪流内遮蔽物缺乏的位置覓食。櫻花鉤吻鮭對生殖棲地的物理因子亦有極為嚴格的要求，傾向水位較淺（0.1至0.39 m）、水流速較緩（0至0.3 m/sec）、底質由中小型卵石、礫石所構成的環境。本研究結果顯示，櫻花鉤吻鮭對微棲地的使用會受溪水水溫、個體大小、及其當時行為之影響而有所差異。

關鍵詞：鮭魚，微棲地，選擇，水底觀察。

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