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Ecomorphological Comparison and Habitat Preference of 2 Cyprinid Fishes, *Varicorhinus barbatulus* and *Candidia barbatus*, in Hapen Creek of Northern Taiwan

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Ling-Chuan Chuang, Yao-Sung Lin, and Shih-Hsiung Liang (2006) Ecomorphological comparison and habitat preference of 2 cyprinid fishes, *Varicorhinus barbatulus* and *Candidia barbatus*, in Hapen Creek of northern Taiwan. *Zoological Studies* **45**(1): 114-123. The morphological traits and habitat preferences of 2 common cyprinid fishes, *Varicorhinus barbatulus* and *Candidia barbatus*, were investigated in Hapen Creek, northern Taiwan from Aug. 1996 to Dec. 1998. Results showed that *C. barbatus*, which has a laterally compressed body and large pectoral fins, is a habitat specialist preferring pools with slow currents over riffles with fast currents, while *V. barbatulus*, which has a cylindrical body and small pectoral fins, is a habitat generalist with no special preference for either pools or riffles. The results of the stepwise multiple regression analyses suggested that fish density was significantly related to stream width, canopy cover, velocity shelter (IC3), and a combination of visual isolation and velocity shelter (IC4) for adult *V. barbatulus*, and to stream width, water depth, current velocity, and a combination of visual isolation and velocity shelter (IC4) for juvenile *V. barbatulus*. The densities of *C. barbatus* showed significant correlations with current velocity, stream width, and canopy cover for adults, and with current velocity, stream width, and a sand-gravel substrate for juveniles. Ecomorphological characters, such as body form and fin size, may be useful predictors of habitat preferences of freshwater fish and should be taken into account in stream management and ecological engineering.
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Key words: *Varicorhinus barbatulus*, *Candidia barbatus*, Morphology, Habitat, Taiwan.

Hydrological and geomorphological conditions of streams are highly variable and dynamic, and provide diverse habitats for fish and other aquatic life. Many studies have indicated that the morphological characters of fish are related to their habitat preferences for lentic or lotic waters (Wikramanayake 1990, Motta et al. 1995, Wood and Bain 1995, Bourke et al. 1997, Chan 2001, Langerhans et al. 2003).

Body shape and fin size are 2 important morphological characters of stream fish which affect static location and moving manipulation (Aleev 1969, Gatz 1979, Douglas and Matthews 1992). A cylindrical body that has a small ratio of surface area to body volume with stiff, short fins favors existence in swiftly flowing riffles, while those fish in slowly flowing pools are expected to have a deep, laterally compressed body with large fins that facilitate their turning ability and rapid angular acceleration (Gatz 1979, Webb 1984, Webb and Weihs 1986, Bisson et al. 1988). Therefore, morphological measurements may be a useful tool for predicting the habitat preferences of stream fish (Chan 2001).

Most fish in small, stable streams are presumably habitat specialists that have evolved various morphological and behavioral adaptations to exploit specific habitat types (Gorman and Karr

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1978, Wood and Bain 1995). Some studies indicated that many tropical stream fish specialize in habitat use and exhibit morphological segregation, with a close relationship between morphological and ecological characteristics (Wikramanayake 1990, Piet 1998). These ecomorphological specializations may serve to facilitate resource partitioning (Wikramanayake 1990).

Taiwan is a relatively small, mountainous island encompassing both tropical and subtropical regions. The Central Mountain Range (CMR), which runs along the island's main north-south axis, contains the majority of Taiwan's highest peaks reaching almost 4000 m. Streams originating in the CMR flow either west into the Taiwan Strait or east into the Pacific Ocean. Most streams are short and have fast currents. The temporally and spatially variable hydrological features are further underlain by frequent summer floods and irregular heavy rainfall. Several studies have been conducted to explore habitat utilization by freshwater fish in Taiwan (Huang 1998, Lee et al. 1998, Han et al. 2000, Yu and Lee 2002). Those studies focused on exploring the relationships between fish distribution and environmental factors, such as velocity, water flow, and water depth. However, until now, no specific examination has been made of the relationship between habitat use and mor-

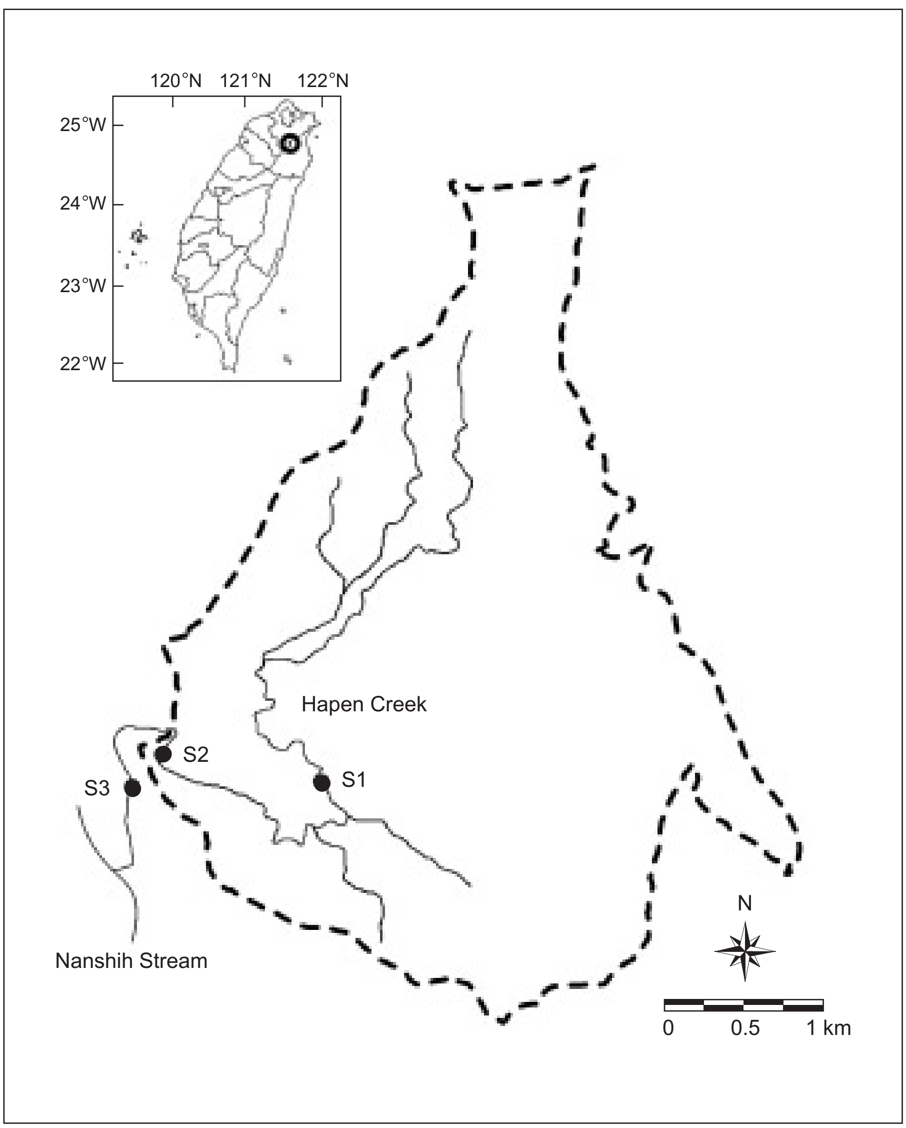

Fig. 1. Map showing sites (S1-S3) of fish sampling and data collection of hydrological and environmental variables in Hapen Creek of northern Taiwan. The dotted line denotes the boundary of the Fushan Experimental Forest.

phological traits.

Varicorhinus barbatulus and *Candidia barbatus* are 2 common cyprinid fishes that are sympatric in many mountain streams in Taiwan (Fang et al. 1993, Kuo 1996, Han et al. 1997, Wang and Shao 1997, Yeh et al. 2000). Thus, this study was designed to foster a basic understanding of which environmental factors possibly affect the coexistence of these 2 morphologically similar fish species in a hydrologically dynamic stream. The objectives of this study were to: (1) understand the habitat use by *V. barbatulus* and *C. barbatus* in Hapen Creek, a protected stream in northern Taiwan; and (2) examine the association of the morphology of each of these 2 fish species with stream hydrological characters to test the hypothesis that habitat use and morphological traits are related. This study is also a preliminary test of the use of ecomorphology as a tool to predict habitat partitioning. Additionally, the findings of this study will contribute to increasing the acceptance of and promoting applications of ecological engineering, specifically for structural design and construction, in the headwaters of streams of Taiwan.

MATERIALS AND METHODS

Study area and sampling sites

This study was conducted in Hapen Creek, a headwater tributary of the Nanshih River at elevations of 500-1200 m, where *V. barbatulus* and *C. barbatus* are abundant and sympatric. It is a natural, well-protected mountain creek in the Fushan Experimental Forest in northern Taiwan (Fig. 1).

The monthly mean air temperature ranged from 11.5 to 23.7°C over the same period of time. The riparian zone of Hapen Creek is covered primarily with natural broadleaf forest. The fish fauna include *V. barbatulus*, *C. barbatus*, *Crossostoma lacustre*, *Rhinogobius candidianus*, *Cobitis sinensis*, and *Acrossocheilus paradoxus*, of which *V. barbatulus* and *C. barbatus* are dominant cyprinids, while *A. paradoxus* is rare (Chang et al. 1998).

Gauging records of the Fushan meteorological station show that the mean annual precipitation in the Hapen Creek watershed was 4671 mm from 1996 to 1998. The annual mean rainfall record for the Fushan area approached 3660 mm in 1993-1997 (Hsia and Hwong 1999). Additionally, mean monthly rainfall data all exceeded 350 mm except for < 200 mm in Jan. Thus, there is no clear distinction between wet and dry seasons in this region (Hsia and Hwong 1999).

The mean annual discharge of Hapen Creek was 0.352 m^3/s, with the mean monthly discharge ranging between 0.012 and 0.063 m^3/s from 1993 to 2000. During summer, torrential rains brought by typhoons cause rapid increase in water flows and are the most-important factor affecting hydrological characteristics of the creek (Hsia and Hwong 1999).

The average gradient of the study area is 17.5 m/km (Chang et al. 1998). However, stream gradients vary along the sampled stream from flat to steep. Moreover, intermittent sections exist in the upstream area, while constant flow is maintained in the middle and lower parts. Thus, 3 sampled sections, S1, S2, and S3 (from upstream to downstream), were selected to reflect differences in flow patterns and channel slopes, and each section had 4 habitat units, i.e., 2 pools and 2 riffle areas. A riffle is a section of the stream where the water surface has visible standing or breaking anti-waves, whereas a pool is a section with a smooth water surface and no such breaking anti-waves (Gelwick 1990). The distances measured along the stream bed of S1, S2, and S3 to the confluence of the Hapen Creek with the main branch of the Nanshih River are 4.2, 1.6, and 0.7 km, respectively.

Fish sampling

Fish sampling was conducted at each study site every 2 months from Aug. 1996 to Dec. 1998. In total, 88 samples were collected from each of the riffles and pools. At each of the 2 habitat units, fish were sampled by electrofishing for a 15 min period from downstream to upstream. A battery-powered, backpack-mounted electrofisher (150-300 V, 1 A, pulsed DC) was used. Two field assistants collected stunned fish with dip nets. The fish we collected were identified to species level, their total lengths (TLs) were measured in the field, and then they were released alive at the site of capture.

Life stages and fish densities

The life stages (adult, juvenile, and fry) of *V. barbatulus* and *C. barbatus* were determined based on methods of (Yan 1993) and (Chang 1994), which use total length to classify the life stages of these 2 species. Individuals with a TL of ≥ 77 mm for *V. barbatulus* and ≥ 71 mm for *C. bar-*

batus were categorized as being mature and adults. Those between 31 and 77 mm for the former and between 31 and 71 mm for the latter were categorized as juveniles (Yan 1993, Chang 1994). Fry of < 31 mm in length were rarely collected; thus, they were excluded from the analyses. Fish density was calculated by dividing the number of fish collected by the habitat unit area (stream section length x mean stream width).

Morphological traits of fish

Twenty juveniles and 20 adults of *V. barbatulus* and *C. barbatus* were separately fixed in a 10% formalin solution in the field and brought back to the laboratory. They were then preserved in a 75% ethyl alcohol solution. For each fish, standard length (SL), maximum body depth (BD), and maximum body width (BW) were measured. Also, the distance from the anterior point of the snout to an imaginary vertical line at the point of the maximum body depth was measured as the Y-distance (Aleev 1969). Pectoral fin length (PL) was measured as the distance from the beginning of the pectoral base to the posterior end of the fin.

The morphological traits we examined included the relative body depth (RBD), compression index (CI), index of trunk shape (AleevY), and relative pectoral fin length (RPL). These traits are considered capable of appropriately reflecting the adaptation of fish to hydrological and habitat conditions (Aleev 1969, Gatz 1979, Watson and Balon 1984). The RBD value is BD divided by SL. A high RBD value indicates a fish's increased capacity to make vertical turns and is expected in fish from habitats with low water velocities (Nikolski 1933, Aleev 1969). The CI value is BW divided by BD. A low CI value indicates a comparatively laterally compressed body, and is expected in fish from habitats with low water velocities (Nikolski 1933). The AleevY value is the Y-distance divided by SL. A high AleevY value is assumed to improve the hydrodynamic ability of the fish and is expected in fish that spend a lot of time cruising (Aleev 1969). The RPL value is PL divided by SL. A high RPL value is indicative of an increased ability of fish to maneuver at low speeds (Gatz 1979).

Hydrological variables and habitat conditions

Hydrological variables and habitat conditions were measured at each of the riffles and pools by the methods described by Tsao (1995) immediately after the fish sampling. The parameters measured were stream width, water depth, current velocity, dominant substrate type, instream cover, and canopy cover.

In the field, 3 permanent transects perpendicular to the current flow were delineated along each habitat unit. Stream width was measured by the length of the transect above the water surface. Water depth, velocity, and substrata were measured at 1 m intervals along each transect. At each measurement point, depth was measured to the nearest cm with a metric stick (in cm), and the dominant substrate type was classified into 5 categories based on the diameter ranges: sand-gravel (< 16 mm), pebbles (16-64 mm), cobbles (64-256 mm), small boulders (256-512 mm), and large boulders (> 512 mm) (Tsao 1995). Current velocity was measured at 60% of depth from the water surface using a digital current meter (model 2100, Swoffer, Seattle, WA, USA) to reflect the mean velocity of the water column (Allan 1995). The mean width, depth, and velocity of each habitat unit were used to calculate the water flow. Four types of instream cover (IC) were recorded (IC1, open water; IC2, visual isolation; IC3, velocity shelter; and IC4, a combination of visual isolation and velocity shelter), each as a percentage of the surface area of the habitat unit. Visual isolation is caused by instream and offstream overhead items such as undercut banks, floating vegetation, and open log jams. Velocity shelter is derived from instream objects such as large rocks, bedrock ledges, and partially buried logs (Tsao 1995).

The canopy was measured with a spherical densitometer (model C, Forest Densitometer, Barthesville, OK, USA) set on the water surface along each transect. For each habitat unit, a canopy reading was generated by averaging 3 measurements. For each measurement, 4 densitometer readings, which were recorded in the middle point of the stream transect facing 4 directions (upstream, downstream, left and right), were averaged.

Data analyses

Unpaired *t*-tests were used to compare fish densities, stream width, water depth, standard deviation of water depth, current velocity, substrate type, instream cover, and canopy cover between riffles and pools, as well as morphological traits between the 2 fish species. Stepwise multiple regression analyses were used to determine which physical habitat characteristics were associated with fish densities, and adults and juveniles, respectively. Square root transformation was used to standardize variances and to improve the normality of the data (Sokal and Rohlf 1995).

RESULTS

General hydrological variables and habitat conditions

Hapen Creek is a small mountain stream with highly fluctuating hydrological variables and habitat conditions. During the study period, water flows varied between 0 and 4.85 m^3/s with an average of 0.75 m^3/s, and current velocities averaged 0.47 m/s with a range of between 0 and 1.32 m/s. In summer, some riffles lost their surface water, and the water flowed subterraneously beneath the gravel bottom. The mean water depth was 0.23 m with a range of 0.02 to 0.61 m, and the stream width averaged 6.1 m with a range of 1.7 to 10.5 m.

Along the stream, higher proportions of canopy cover and greater mean widths, velocities, and depths were recorded in the 2 downstream sampling sites than in the upstream one (Table 1). However, greater variations in canopy cover, velocity, and depth were found in the upstream section than in the downstream region. At the microhabitat scale, a higher proportion of canopy cover and a greater mean depth were found in pools than in riffles, while the flow velocity was faster in riffles than in pools.

Differences in habitat conditions between pools and riffles

Hydrological and environmental conditions of Hapen Creek showed obvious differences between

Table 1. Mean and coefficient of variation (CV) of canopy cover, depth, velocity, and width measurements of microhabitat and mesohabitat (combined) of 3 sampling sites during the study period (*n* is the sample size)

Sampling site	S1 (*n* = 28)			S2 (*n* = 30)			S3 (*n* = 30)		
Habitat types	pools	riffles	combined	pools	riffles	combined	pools	riffles	combined
Canopy cover (%)	88.3 (11.6)	39.9 (44.1)	64.2 (44.1)	79.6 (14.3)	75.3 (9.0)	77.5 (12.3)	87.4 (9.5)	75.4 (21.7)	81.4 (17.5)
Water depth (m)	0.22 (36.4)	0.11 (37.0)	0.17 (51.0)	0.29 (30.3)	0.20 (27.2)	0.24 (34.5)	0.41 (20.1)	0.25 (29.1)	0.33 (34.2)
Current velocity (m/s)	0.23 (87.1)	0.44 (60.8)	0.34 (76.4)	0.30 (79.0)	0.69 (31.4)	0.50 (60.7)	0.42 (50.9)	0.66 (40.0)	0.54 (49.3)
Stream width (m)	5.20 (21.6)	4.88 (34.2)	5.04 (28.2)	7.28 (31.3)	6.12 (18.5)	6.70 (28.0)	6.04 (19.0)	6.65 (21.7)	6.35 (21.0)

Table 2. Comparisons of hydrological and environmental variables (mean ± SD) between pools and riffles in Hapen Creek

Variable	Pools	Riffles	*t*- values
Stream width (m)	6.20 ± 1.81 (*n* = 88)	5.91 ± 1.59 (*n* = 88)	1.1
Water depth (m)	0.31 ± 0.11 (*n* = 88)	0.19 ± 0.08 (*n* = 88)	8.1***
Current velocity (m/s)	0.32 ± 0.23 (*n* = 88)	0.60 ± 0.27 (*n* = 88)	-7.4***
Substrate (%)			
Sand-gravel	9.2 ± 16.4	1.8 ± 5.3	4.0***
Pebbles	46.6 ± 22.6	32.3 ± 25.5	4.0***
Cobbles	17.7 ± 14.5	30.8 ± 27.4	-4.0***
Small boulders	8.0 ± 9.1	12.5 ± 12.4	-2.7**
Large boulders	18.5 ± 18.4	22.6 ± 25.1	-1.2
Instream cover (%)			
Open water	84.6 ± 19.2	75.6 ± 24.5	2.7**
Visual isolation	2.9 ± 5.5	1.4 ± 4.0	2.1*
Velocity shelter	5.3 ± 7.8	6.9 ± 9.3	-1.3
Combination of visual isolation and velocity shelter	7.3 ± 15.6	16.1 ± 21.3	-3.1**
Canopy cover (%)	85.1 ± 10.7	64.1 ± 21.8	8.1***

*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; indicating significant difference between pools and riffles.

pools and riffles (Table 2). The bottom substrates of the pools and riffles were predominantly composed of pebbles, cobbles, and large boulders, but the pools had a higher percentage composition of pebbles but lower compositions of cobbles, small boulders, and large boulders as compared to the riffles. Water depths in the pools were significantly deeper than those in the riffles, whereas current velocities in the riffles were significantly faster than those in the pools. There was no significant difference in stream width between pools and riffles for this mountain creek. The creek was mainly open water with little instream cover, but the canopy cover exceeded 80% over pools and 60% over riffles.

Morphological traits of the fish

Significant differences in CI, AleevY, and RPL values were found between *V. barbatulus* and *C. barbatus* (Table 3). CI and AleevY values of both juveniles and adults were significantly higher for *V. barbatulus* than for *C. barbatus*, indicating that *V. barbatulus* has a wider and more-cylindrically shaped body than *C. barbatus*. Juveniles of *V. barbatulus* had relatively shorter pectoral fins than those of *C. barbatus*, but no significant difference was found in adults between the 2 species, suggesting morphological variation in ontogeny of the 2 species.

Table 3. Comparisons of morphological traits (RBD, relative body depth; CI, compression index; AleevY, index of trunk shape; RPL, relative pectoral fin length) (mean ± SD) between *Varicorhinus barbatulus* and *Candidia barbatus* in Hapen Creek (n = 20)

Morphological trait	Juvenile		
	V. barbatulus	*C. barbatus*	*t*- value
RBD	0.24 ± 0.01	0.24 ± 0.01	0.05
CI	0.60 ± 0.04	0.51 ± 0.04	7.07***
AleevY	0.49 ± 0.01	0.45 ± 0.03	6.76***
RPL	0.19 ± 0.01	0.21 ± 0.01	-4.14***
Morphological trait	**Adult**		
	V. barbatulus	*C. barbatus*	*t*- value
RBD	0.26 ± 0.02	0.26 ± 0.02	-0.17
CI	0.59 ± 0.04	0.48 ± 0.08	5.86***
AleevY	0.50 ± 0.02	0.44 ± 0.04	6.92***
RPL	0.21 ± 0.01	0.20 ± 0.01	1.75

***$p < 0.001$; indicating a significant difference between the 2 species.

Fish densities

During the study period, 2089 individuals of *V. barbatulus* were collected: 797 fish from pools with a mean density of 9.0 (SD, 11.1) fish/100 m^2, and 1292 fish from riffles at 9.1 (SD, 8.4) fish/100 m^2. There were no significant differences in the densities of either juveniles or adults between pools and riffles (t = -1.7, p = 0.09; t = 1.0, p = 0.34, respectively) (Table 4), suggesting that *V. barbatulus* had no preference for either pools or riffles.

On the other hand, 2759 individuals of *C. barbatus* were collected: 1836 fish from pools with a mean density of 22.8 (SD, 31.7) fish/100 m^2, and 923 fish from riffles at 6.8 (SD, 9.2) fish/100 m^2. Significant differences were found in the densities of both juveniles and adults between pools and riffles (t = 3.9, p < 0.001; t = 4.5, p < 0.001, respectively) (Table 4), suggesting that *C. barbatus* showed a preference for pools over riffles.

Relationships of fish densities to hydrological and habitat variables

Results of the stepwise multiple regression analyses showed that fish densities of adult *V. barbatulus* (Afv) were significantly and negatively related to stream width (W) and velocity shelter (IC3), and positively related to canopy (P) and the combination of visual isolation and velocity shelter (IC4). The relationships are expressed by the following equation:

Table 4. Comparisons of fish densities between 2 habitat types, riffles and pools, for *Varicorhinus barbatulus* and *Candidia barbatus*

V. barbatulus (n = 88)

	Pools	Riffles	*t*- value
Juvenile	2.4 ± 3.8	3.5 ± 4.9	-1.7
Adult	6.6 ± 8.2	5.6 ± 5.4	1.0

C. barbatus (n = 88)

	Pools	Riffles	*t*- value
Juvenile	11.4 ± 20.0	2.9 ± 5.2	3.9***
Adult	11.4 ± 15.1	3.9 ± 4.8	4.5***

***$p < 0.001$; indicating a significant difference between pools and riffles.

Afv = 4.316 - 1.464W + 0.212P - 0.213IC3 + 0.104IC4;
R^2 = 0.331, *df* = 171.

The R^2 value suggests that 33.1% of the variance in fish densities could be explained by the 4 hydrological factors of stream width, canopy cover, velocity shelter, and the combination of visual isolation and velocity shelter, of which stream width accounted for 20.8%, and the other factors of canopy cover, velocity shelter, and the combination of visual isolation and velocity shelter accounted for 3.7%, 4.6%, and 4.0%, respectively (Table 5). Adults of *V. barbatulus* preferred small stream sections with more-extensive canopy cover, but were not affected by current velocity or conditions of the bottom substrate.

Juveniles of *V. barbatulus* (Jfv) were significantly and negatively correlated with stream width (W), water depth (D), and current velocity (V), and positively related to the combination of visual isolation and velocity shelter (IC4). The relationships are expressed by the following equation:

Jfv = 9.087 - 1.271W - 3.759D - 1.157V + 0.053IC4;
R^2 = 0.410, *df* = 171.

The R^2 value suggests that 41.0% of the variance in fish densities was explainable by the 4 hydrological factors of stream width, water depth, current velocity, and the combination of visual isolation and velocity shelter, of which the stream width accounted for 33.6% (Table 5). Juveniles of *V. barbatulus* preferred small stream sections with shallow water, but were not affected by canopy cover or conditions of the bottom substrate.

For adults of *C. barbatus*, the density (Afc) showed significant negative relationships with current velocity and stream width, but a positive one with canopy cover. The relationships are expressed by the following equation:

Afc = 8.902 - 3.767V - 1.878W + 0.321P;
R^2 = 0.444, *df* = 172.

The R^2 value suggests that 44.4% of the variance in the fish density was explainable by the 3 hydrological and environmental features, of which current velocity and stream width accounted for 36.7% of the variance (Table 5). Adults of *C. barbatus* preferred small stream sections and slow water flow in pools covered with canopy.

For juveniles of *C. barbatus*, the density (Jfc) showed significant negative relationships with current velocity and stream width, but a positive one with a sand-gravel substrate (SG). The relationships are expressed by the following equation:

Jfc = 11.297 - 3.695V - 2.353W + 0.222SG;
R^2 = 0.416, *df* = 172.

The R^2 value suggests that 41.6% of the variance in the fish density was explainable by the 3 hydrological and environmental features, of which current velocity and stream width accounted for 38.0% of the variance (Table 5). Juveniles of *C. barbatus* prefer small streams and slowly flowing water in pools with small bottom substrate of sand-gravel.

Table 5. Model summary of the stepwise multiple regressions of densities of *Varicorhinus barbatulus* and *Candidia barbatus* with habitat variables

V. barbatulus
Adult (total R^2 = 0.331, *n* = 176)

Variable	R^2	Regression coefficients	Standard errors	F
Width	0.208	-1.464	0.226	45.81***
Canopy	0.037	0.212	0.056	8.44**
Velocity shelter	0.046	-0.213	0.051	11.14***
Combination of visual isolation and velocity shelter	0.040	0.104	0.033	10.18**

Juvenile (total R^2 = 0.410, *n* = 176)

Variable	R^2	Regression coefficients	Standard errors	F
Width	0.336	-1.271	0.202	87.87***
Depth	0.045	-3.759	0.987	12.53***
Velocity	0.016	-1.157	0.437	4.53*
Combination of visual isolation and velocity shelter	0.014	0.053	0.027	3.98*

C. barbatus
Adult (total R^2 = 0.444, *n* = 176)

Variable	R^2	Regression coefficients	Standard errors	F
Velocity	0.250	-3.767	0.621	58.00***
Width	0.117	-1.878	0.275	32.03***
Canopy	0.077	0.321	0.066	23.85***

Juvenile (total R^2 = 0.416, *n* = 176)

Variable	R^2	Regression coefficients	Standard errors	F
Velocity	0.260	-3.695	0.822	61.10***
Width	0.120	-2.353	0.349	33.37***
Sand-gravel	0.037	0.222	0.067	10.85***

*$p \le 0.05$; **$p \le 0.01$; ***$p \le 0.001$; indicating a significant difference.

DISCUSSION

Densities of both adult and juvenile *V. barbatulus* decreased with an increase in stream width. Stream sections with greater amounts of overhead canopy and less instream cover were more-often selected by adult *V. barbatulus*. Because of the higher proportion of canopy cover present in pools than in riffles at all of the sampling sites, adults of *V. barbatulus* were mainly distributed in lentic waters of upstream areas. The habitat of juvenile *V. barbatulus* is characterized by shallow water depths and slow flow velocities, possibly in the near-shore region of pools in upstream sections.

The densities of both adult and juvenile *C. barbatus* correlated negatively with velocity. Stream width also showed a negative correlation with the density of *C. barbatus*, regardless of the life stage. Thus, *C. barbatus* prefers stream sections with lower current velocities and smaller stream widths. Additionally, although similar to *V. barbatulus* in habitat preference, *C. barbatus* may show a stronger preference for pool habitats of upstream sections, because current velocity explained a greater proportion of the numerical distribution of its variation. This interpretation is also supported by the significant preference of *C. barbatus* for pool habitats, while *V. barbatulus* displayed no preference for either pools or riffles.

Although results of this study showed that similarities in habitat preferences exist between these 2 species, minor differences related to their morphological traits are also present. *C. barbatus* has a laterally compressed body and larger pectoral fins, and was found to be more specialized in its habitat selection, preferring pools with slowly moving water. In contrast, with a cylindrical body and smaller pectoral fins, *V. barbatulus* had a weaker correlation with hydrological factors, and was found to be more of a habitat generalist than *C. barbatus*. The results confirmed the hypothesis that the morphological traits of *C. barbatus* and *V. barbatulus* are related to habitat preference (Motta et al. 1995, Wood and Bain 1995, Chan 2001, Langerhans et al. 2003), and the body shape and fin size are 2 important morphological traits of this aspect (Aleev 1969, Gatz 1979, Douglas and Matthews 1992). This also suggests that ecomorphological analyses can possibly be a valid tool to predict habitat preferences of other freshwater fishes of Taiwan.

These 2 cyprinid fishes are widely distributed in mid and upstream sections of the lotic waters in Taiwan. *V. barbatulus* is comparatively abundant in headwaters where gradients are steep, swift riffles are common, and monthly average water temperatures are below 17°C (Yang 1997, Chang et al. 1999). Alternatively, *C. barbatus* occurs mainly in mid-stream sections where mean water temperatures are about 21°C (Chang et al. 1999). For *V. barbatulus*, the cylindrical body shape with small pectoral fins may provide it with better swimming ability to disperse into creeks at high elevations. The weaker swimming ability of *C. barbatus*, due to its laterally compressed body and large pectoral fins, probably limits its distribution mainly to the mid-stream sections of rivers, where gradients are moderate and pools are common. A swimming performance study (critical swimming speed, CSS) indicated that the swimming ability of *V. barbatulus* (CSS, adults: 103.8 ± 13.8 cm/s, n = 20; juveniles: 67.3 ± 12.1 cm/s, n = 20) is better than that of *C. barbatus* (CSS, adults: 78.1 ± 6.6 cm/s, n = 20; juveniles: 50.9 ± 8.3 cm/s, n = 20) (authors' unpublished data), supporting arguments about the distribution of the 2 species.

Considerations for stream engineering

Both species are mainly distributed in smaller stream sections, such as small tributaries and headwaters. Greater dynamics in variations of current velocity and water depth were observed in the upstream site (S1) than in the downstream section (S3). This observation reflects that both species are able to tolerate, at least to a certain degree, variabilities in hydrological characteristics of their habitats.

The densities of these 2 species would be predicted to increase if streams are engineered into narrow channels dominated by slowly moving pool-type habitats. As the flow velocity decreases within the pooled habitat, the numerical abundance of *C. barbatus* would possibly increase more quickly than that *V. barbatulus* based on the results of this study. To further increase the density of both adult and juvenile *V. barbatulus* and adult *C. barbatus*, maintaining or planting riparian vegetation to retain or increase stream canopy cover should be beneficial.

With increasing numbers of headwaters, small tributaries, and mid-sections of streams being channelized and cemented over for various reasons, such as flood control, within the island of Taiwan, faster currents and fewer pool habitats will appear within these lotic waters (Tzeng 2003). If this trend of stream engineering continues, the population densities of both *C. barbatus* and *V.*

barbatulus should quickly diminish in these artificially straightened channels. If sedimentation also occurs, which is quite common within these artificially straightened channels, juvenile *C. barbatus* will be impacted the most among the various life stages of these 2 species.

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