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EVALUATION OF THE SWIMMING ABILITY OF WILD-CAUGHT *ONYCHOSTOMA BARBATULA* (CYPRINIDAE) AND APPLICATIONS TO FISHWAY DESIGN FOR RAPID STREAMS IN TAIWAN

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***ABSTRACT*. –** *Onychostoma barbatula,* a fish species commonly found in the upper- and mid-stream of mountain rivers in Taiwan, is migratory. Its swimming ability within specific habitats is likely to be very important to it as the ‘maximum critical swimming speed’ is considered a main survival factor. To obtain data that might be applied to the design of a fishway for *O. barbatula*, a laboratory study of *O. barbatula*’s maximum critical swimming speed was conducted in a circular tank with a high speed video camera system recording their swimming ability and pattern at four water temperatures (12, 16, 20 and 24°C) to reflect seasonal water temperatures. Specimens of *O. barbatula* (total body length (BL) ranging from 4.8 to 20.7 cm) were selected and their tail beat frequency (TBF in Hz), tail beat amplitude (TBA), and swimming pattern were measured and compared. Their swimming speed was significantly positively correlated with TBF. Their TBA, ranging from 0.14 to 0.18 BL, was only weakly correlated with swimming speed. When water temperature was increased, their maximum critical swimming speed increased progressively to 13.2 BL s^{-1} at 16°C but decreased beyond 16°C. In an anatomical study we found that the proportion of red muscle increased significantly between the ‘45 % of BL’ position and the caudal fin, with the caudal region possessing the greatest proportion of red muscle. *Onychostoma barbatula* primarily depends on caudal fin-generated forward thrust and this is no doubt related to the ‘fast swimming’ requirement imposed by its mountain stream habitat. We design a suitable fishway that will support the conservation of this species; it should have a minimal width of 9 cm. (for individual fish) and a maximal water-flow speed of about 126.7 cm s^{-1}.

***KEY WORDS.* –** *Onychostoma barbatula,* fishway, swimming speed, temperature, red muscle.

INTRODUCTION

Onychostoma barbatula (Cyprinidae) is widely distributed in Taiwan and mainland China (Tzeng et al., 2008). It inhabits in relatively cold, clear, and high altitude rivers as well as in fast flowing streams with rocky bottoms. It resides in the upper- and mid-stream and may move to warmer regions in winter. The high mountains of Taiwan Island provide short rivers and streams, mostly with a rapid flow rate, being particularly rapid in the upper-stream region (Tzeng, 1986; Shen et al., 1993; Wu et al., 2006). It is also a commercial freshwater fish in Taiwan. It feeds on filamentous algae attached to rock and also small invertebrates. During spring and autumn the fish migrate to the upper-stream for spawning (Tzeng, 1986, 2002). In Taiwan, there are around 8,000 weirs (3 to 25 m height) across the rivers that dam up their migration route (Chen & Fang, 1999). The proper design of fishway around these weirs, tailored to the stream type and particular fish species would most desirable. Thus, traditional fishways may be inappropriately designed. These existing fishways were often built using patterns suitable for larger fish species from North American or Japan (Tzeng, 1997; Wang, 1992). Consequently, the essential data on swimming ability from representative river fishes such as *O. barbatula* is urgently-needed so that improved fishway designs can be constructed.

In the marine environment, the scombroid fish including tuna have been reported to have excellent maximum critical swimming ability (over 10 BL s^{-1}; BL = total body length) and to carry out long distance migrations (Dewar & Graham, 1994; Syme & Shadwick, 2002). *O. barbatula* is a freshwater fish adapted to the specific rapid stream habitat in the mountains of Taiwan and should also have an excellent swimming capability. Among the dominant species of wild freshwater fishes, the fishes that can live in such rapid streams probably have fast-swimming capabilities and possess physiological mechanisms adapted to this unique environment (Plaut, 2001; Jain & Farrell, 2003; Ojanguren & Brana, 2003; Pedersen et al., 2008). However, there is little scientific literature reporting the swimming ability and endurance of this mountain river fish in Taiwan.

Swimming ability affects the most important activities in fishes such as searching for prey, avoidance of predators, even long-distance feeding or breeding migration (Videler, 1993; Reidy et al., 1995; Drucker, 1996; Johansen et al., 2007; Santos et al., 2007; Wu et al., 2007). Fish swimming performance can be classified into three parts on time gradation including burst, sustained and prolonged swimming (Beamish, 1978). Burst swimming is anaerobic swimming using white muscle for short periods (less than 15–20 s); fatigue occurs rapidly (Domenici & Blake, 1997). Long-term, sustained swimming by fish can be maintained for between 200-240 min and carried out by red muscle (Beamish, 1966; Brett, 1967; Stobutzki, 1998; Dudley et al., 2000). Sustained swimming is the most efficient swimming mode although with the lowest speed. Prolonged swimming also uses red muscle action but is maintained for just over 15–20 s until fish become fatigued (Beamish, 1978; Hammer 1995; Plaut, 2001). Maximum critical swimming speed (U_{crit}) is based on the range of prolonged swimming speed that would reflect actual behavior in its habitat. Maximum critical swimming speed can be accurately measured and fish fatigue observed in the experimental flow tank (Beamish, 1978; Fulton et al., 2001, 2005; Blake, 2004). The swimming ability of experimental fish may reveal their ability to cope with their real fast-flowing stream and river habitats.

Fishes are poikilothermal animals except for some larger scombroid species. Thus, a change of water temperature will affect their locomotive ability (Koch & Wieser, 1983; Priede, 1985; Beamish et al., 1989; Winger et al., 1999) and have major implications for their survival. Several swimming studies have investigated the action of red muscle and white muscle in fishes. Some species may have an intermediate layer of pink muscle. In addition, if the different life stages of fish live in different habitats, the trunk muscle and its muscle fiber composition are matched to the degree of swimming activity necessary (Dubowitz, 1985; Nanami, 2007).

Bainbridge (1958) and Webb (1971) demonstrated that trout modulated tail beat amplitude (TBA) at low speeds and modulated tail beat frequency (TBF) at high swimming speeds. However, Hunter & Zweifel (1971) found that at all swimming speeds fish modulated only the frequency. Wardle (1980) concluded that the swimming speed is the product of TBF and stride length. Among fish species, being adapted to different environments, the relationship between swimming speed and tail beat modulation is likely to vary and the measurement of swimming ability being required for each species.

Fish-swimming capability studies as applicable to fishway designs for mountain fishes, such as *O. barbatula* in Taiwan, are very limited. We therefore conducted a laboratory study to investigate the maximum critical swimming speed of *O. barbatula*. It was conducted in a circular tank with a high speed video camera system recording their swimming ability and pattern at four water temperatures (12, 16, 20 and 24°C) to reflect seasonal water temperature changes. We aimed to simulate particular ecological habitats in order to investigate various swimming patterns and to observe the physiological characteristics of the fish; we would then be able to consider how our data might relate to fish fitness or survival in the wild. Swimming ability in terms of swim pattern on its TBF and TBA was analysed. We also examined the maximum critical swimming speed (U_{crit}), by use of an experimental flow tunnel, with different water temperatures. Moreover, the histological composition of the fish trunk muscle was also relative to red and white muscle. Our results, such as TBA, were then used as essential parameters for the design of a fishway (e.g. determination of its breadth) that would allow migrating fish to swim through without stress. We have provided some recommendations for the design of suitable fishways.

MATERIALS AND METHODS

***Experimental fish, flow tank and photographic equipment.* –** From Aug.2003 to Aug.2004, specimens of *Onychostoma barbatula* were caught with fishhook and line from an upper-stream section of the River Keelung (25°2'N 121°46'E), Taiwan. The experimental fish, 4.8–20.7 cm BL, were then transported to an aquarium of 200 × 60 × 50 cm with a continuous filter system at a university laboratory. The water temperature was maintained at 20 ± 0.8°C (mean ± standard error) with a 12 h light and 12 h dark photoperiod. In order to avoid any influence from fishing shock each fish was cultured for more than three weeks before being used in the experiment. Fishes were fed three times each day with commercial fish food from shrimp and algae. Feeding was stopped 48 hours before the commencement of the experiment (Puckett & Dill, 1984; Beamish et al., 1989). The swimming test was carried out in a 938 × 314 × 154 cm experimental circular tank (Fig. 1-a). A propeller-driven flow-speed counter (SV-3, Shinozuka, Japan) capable of measuring flow rates of 0.0–2.0 ms^{-1} was used. A high speed video camera system with a 52 mm standard lens (Aspherical-1026412, Sigma, Japan), a CCD image sensor (CA-D1-0128S-STDN, Dalsa Inc., Canada), and a high speed photo processing system (Frame Grabber, Oculus-F/64, F64Pro, Coreco Inc., Canada) were used to capture and store the images.

***The fish locomotive TBF and TBA characteristics.* –** Each experimental fish was confined in a 33 × 27 × 28 cm working

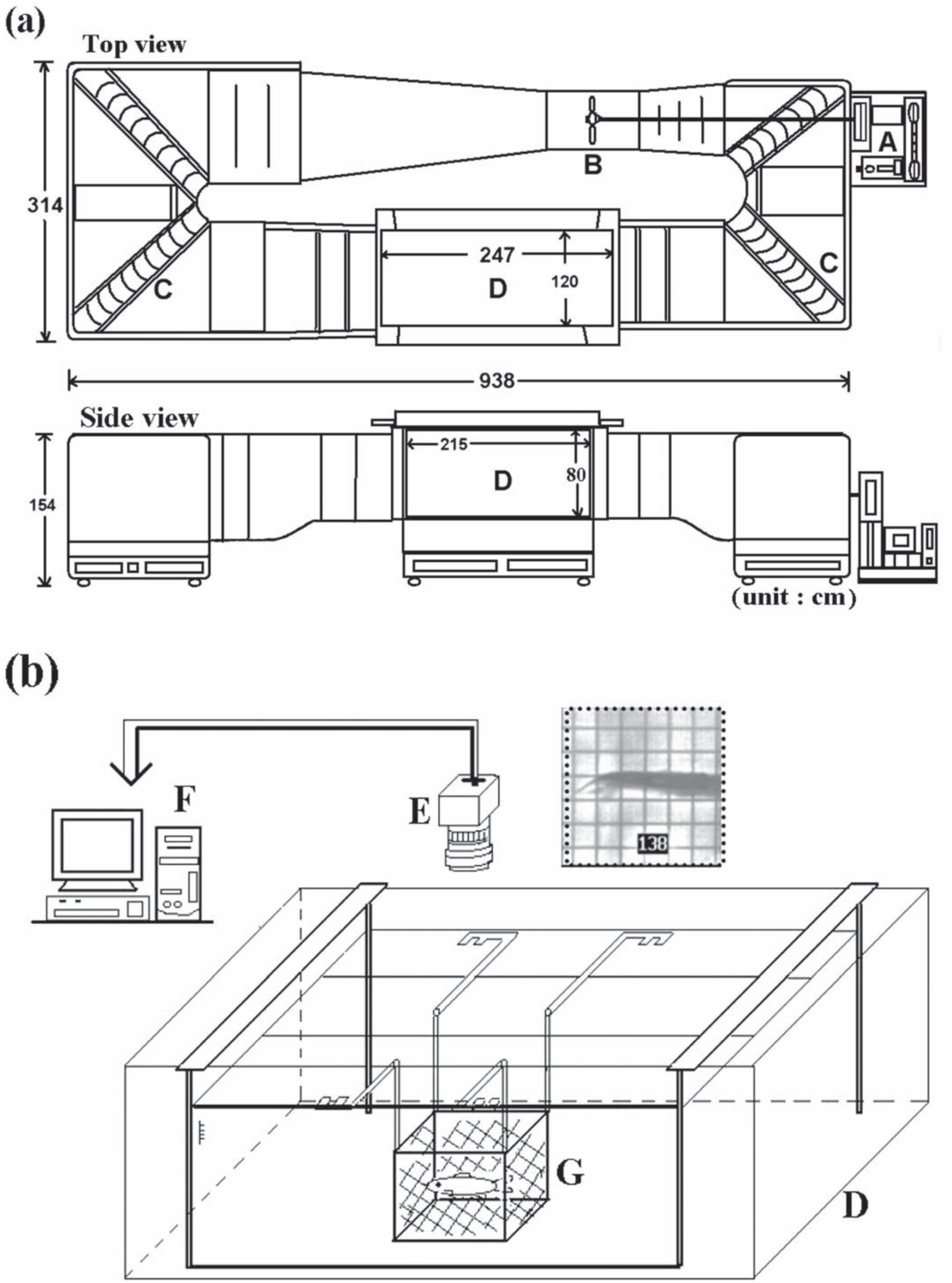

Fig. 1. (a) Experiment circular tank: A, Motor; B, Propeller; C, Flow stabilizer; D, Observation area; (b). Enlarged observation area: E, High-speed video camera; F, High-speed photo-processing system; G, Working section.

section with a 1.2 cm mesh size (Fig. 1-b, compartment G). Before the experiment, a plastic plate with a grid of 1.0 cm^2 was horizontally set at the center of the working section. A contrast photo was taken as a standard TBA measurement for calibration purposes. This plastic plate was then removed. Before each test, a movable flow speed counter (Propeller type, 15 kW-12 hp, SL Co., Taiwan) capable of measuring flow rates of 0.0–3.0 ms^{-1}, was used to measure the flow rate at the center of the working section. The experimental fish were placed in the working section with flow speed one total body length per second (1 BL s^{-1}) and allowed remain there for 30 minutes in order to adjust them to this stable and unhindered swimming environment (Stevens, 1979). Observations commenced with the water flow speed of 1 BL s^{-1} and continued as flow speed was gradually increased, by increments of 1 BL s^{-1} to 7 BL s^{-1}. One second video recordings of the swimming pattern were taken when the fish was directly in the center of the working section space. This process was repeated to measure different sizes of experimental fish (n = 6). Each experimental fish was used only for a single trial.

The same video recordings were used to measure the TBF. One ‘tail beat’ was defined as the movement of the caudal fin, beginning from extreme right (or left) side and oscillating to the extreme opposite side, then returning to the original side. The TBA was then measured by overlapping the video with the previously contrast photo; the maximum distance between the positions on the opposite sides reached by the caudal fin tip were measured. Therefore, the TBA was the ratio of caudal fin amplitude over total body length. A sequence of swimming pattern photos, with 0.04 s intervals, was extracted from the recorded video. A profile of the fish was then drawn from anterior tip (P = 0) to tail tip (P = 1) on a grid form that was separated into nine sections. The middle of the section line that crossed the profile represented the point of body axis. The changes with time in position of the corresponding points along the body axis were measured.

***Ratios of red muscle in trunk muscle.* –** In order to understand the histological characteristics of trunk muscle of *Onychostoma barbatula*, we selected 12 fish, averaging of 13 ± 1.1 cm BL. Each fish spine was cut at the rear of

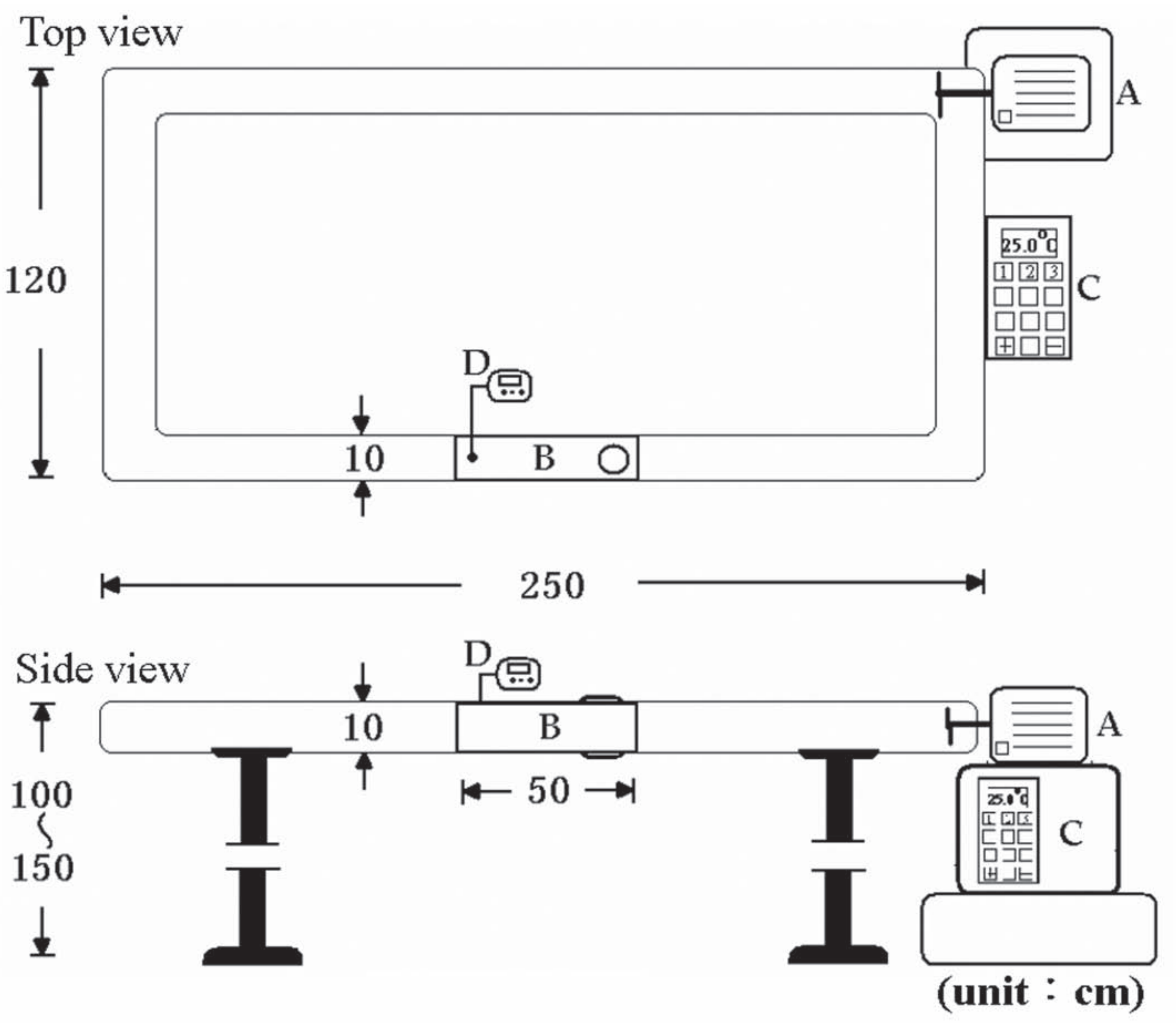

Fig. 2. Temperature-controlled flow tunnel: A, Motor; B, Experimental area; C, Temperature-controller; D, Flow velocity meter.

occipital bone to prevent jumping or body bending before freezing in a −20°C box. After freezing for 12 h, the fish body was sectioned at intervals of 10% of the total body length from snout to tail. The 7 trunk sections were composed respectively of 25, 35, 45, 55, 65, 75 and 85% of muscle. A digital camera was used to record this trunk muscle and the image files transferred to a computer. The "Mark and select area" function of an image processing system (Measurement Tools 1.23 Version, May Lab., Taiwan) was used (by detecting differences of contrast, saturation and hue) to determine and measure areas and proportions of trunk composed of red muscle. The epidermis, viscera and spines were deducted from the trunk cross sections.

Histology of red or white muscle fiber and their cross-sectional areas. – Another 10 fish specimen, averaging of 14 ± 1.3 cm BL, was cut for histological study. Caudal muscle was frozen with isopentane (Merck, Darmstadt, Germany) by liquid nitrogen in advance to fixation. The muscle samples were stored in a −75°C extra-low temperature freezer. The samples muscle tissue was stuck on the microtome base with investment balsam and successively sectioned by cryostate (BRIGHT OTF/AS-001, Huntingdon, UK) to 10 µm thickness under a −20~23°C environment. After sectioning the muscle samples were kept in room temperature for air-drying before histological staining with Harris hematoxyline and Eosin (H&E), Modified Gomori's Trichrome (MGT), Periodic Acid Schiff (PAS) and Adenosine Triphosphatase (ATPase, 4.0) then stored with Canada balsam. The stained samples were observed with optical microscope and recorded as digital images. The image processing system (above) was used to examine more than 50 cross-sections and determine the average area of red and white muscles.

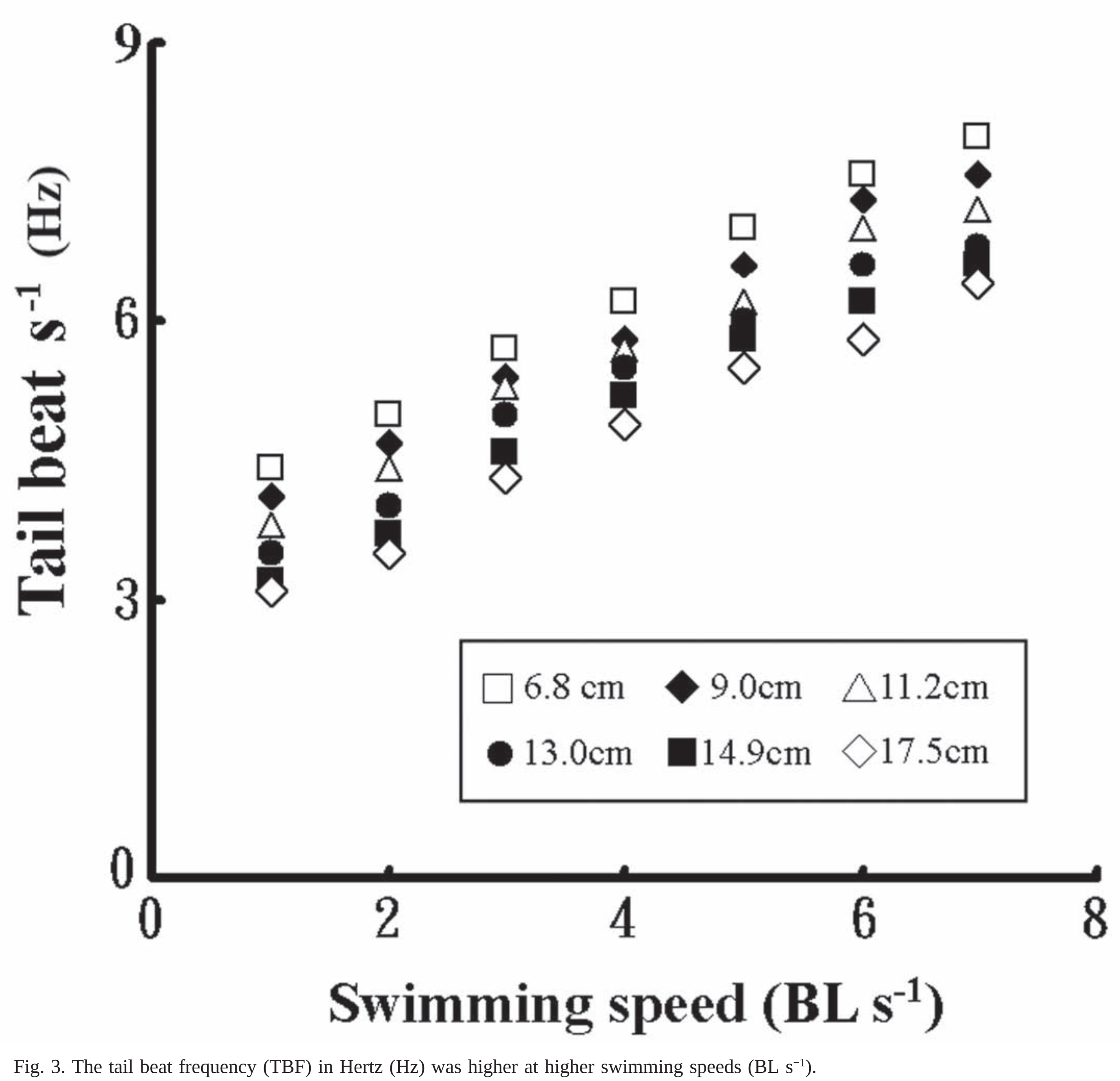

Fig. 3. The tail beat frequency (TBF) in Hertz (Hz) was higher at higher swimming speeds (BL s^{-1}).

Protocol used in measuring maximum critical swimming speed. **–** Experiments on maximum critical swimming speed took place in a temperature-controlled flow tunnel. This flow tunnel was 250 × 120 × 150 cm with an inside diameter of 10 cm (Fig. 2). A propeller-type of flow speed counter (15 kW-12 hp, SL Co., Taiwan) capable of measurements ranging from 0.0–3.0 ms^{-1} was used. The experimental fish were first kept in the tank for least 8 hours such that fish could adapt to the desired water temperature (Puckett & Dill, 1984). We then ensured that the experimental fish could swim stably and normally, uniformly maintaining their position in the imposed current. We increased the flow speed in increments of 10 cm s^{-1}, and intervals of thirty minutes until the experimental fish could no longer resist the flow and its caudal fin tip contacted with the rear area separation mesh (Puckett & Dill 1984, Reidy et al., 1995). The flow speed and period of maintained swimming were recorded. Individual maximum critical swimming speeds (U_{crit}) were then calculated (Brett, 1964) as $U_{crit} = U + (U_i \times (t / t_i))$, where U is our recorded penultimate maintained water flowing speed expressed in cm s^{-1}, U_i is the water flow speed increment expressed in cm s^{-1}, t is the time swum at the final water flow speed and t_i is the originally-set time interval for each particular water flow. This experiment was similar to the preceding one with four different water temperatures (12, 16, 20 and 24°C) that was designed to reflect seasonal temperature change.

RESULTS AND DISCUSSION

Fish swimming speed in relation to TBF and TBA. **–** Concern over the migration passage of *Onychostoma barbatula* focuses on the need for a fishway design that takes into account the swimming ability and pattern of this fish. TBF and TBA provide criteria for such a design. In addition, the engineering design and construction of such mountain river fishways also needs to be in harmony with the

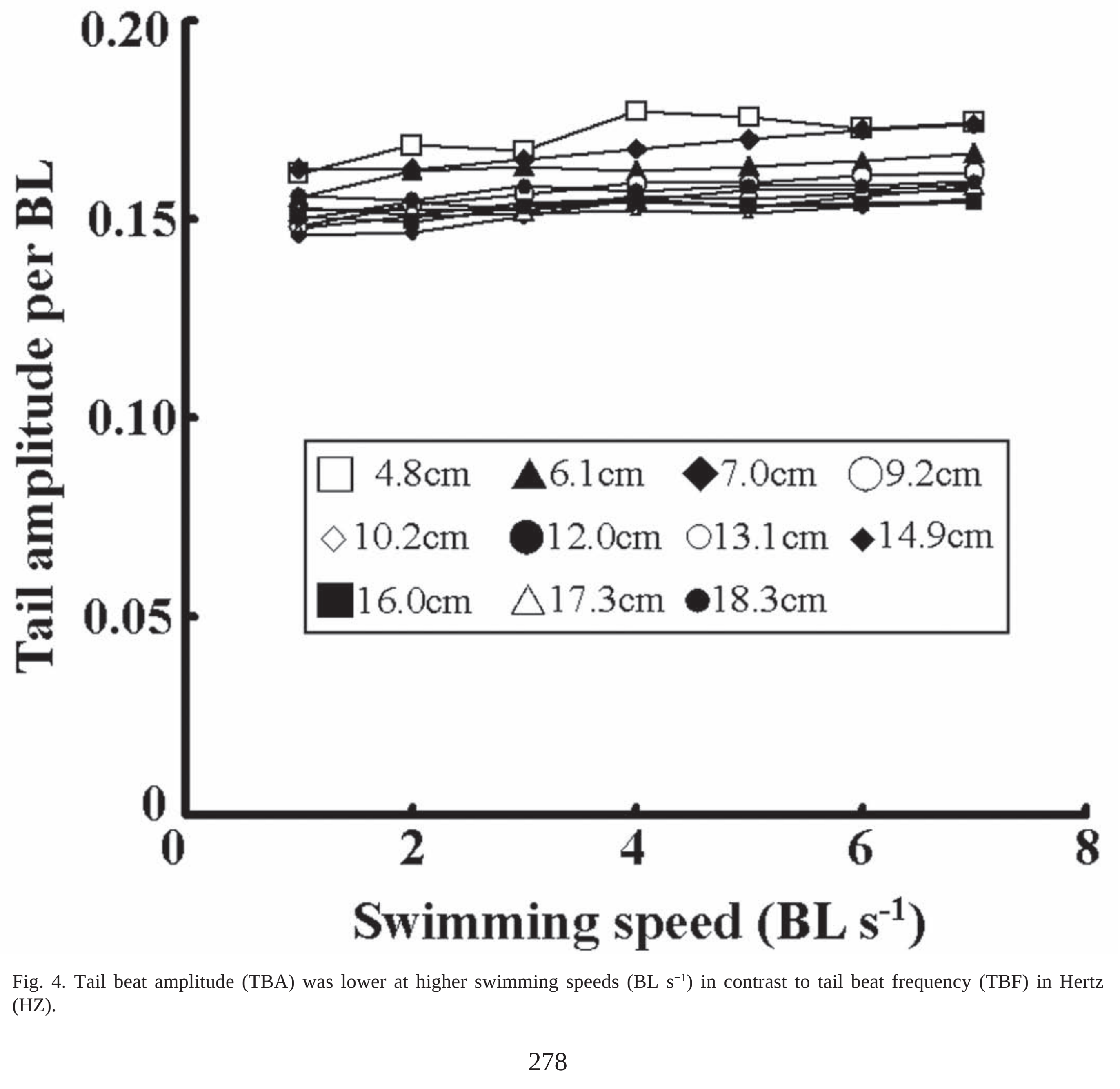

Fig. 4. Tail beat amplitude (TBA) was lower at higher swimming speeds (BL s^{-1}) in contrast to tail beat frequency (TBF) in Hertz (HZ).

ecological characteristics of the river. There was a positive linear relationships between TBF and the swimming speed of *O. barbatula* (Fig. 3). This is in agreement with results for rainbow trout obtained by Stevens (1979), Blake (1983) and Videler (1993). For rainbow trout, the relationship has the same slope, around 0.56 ± 0.03 (n = 6). By linear multiple regression analysis, TBF can be fitting by swimming speed (V) and total body length (BL) as follows:

$$TBF = 0.59V \times 0.14BL + 4.79, R^2 = 0.93$$

The TBAs for different body sizes of *O. barbatula* were independent of swimming speed (Fig. 4), as reported by Stevens (1979) and Puckett & Dill (1984). The average TBA was 0.16 ± 0.02 BL (one-way ANCOVA, $p < 0.001$) with a range from 0.14 to 0.18 BL. In Figs. 3 & 4, *O. barbatula* was primarily dependent upon the TBF, not the TBA, when increasing its swimming speed. We then suggested that the adjustment of TBF rather than TBA to increase swimming speed (Priede, 1985; Parrish & Kroen, 1988) may be a strategy for saving energy, as suggested by Puckett & Dill, 1984. The average TBA of *O. barbatula* was smaller than that of coho salmon which average 0.22 ± 0.01 BL (Puckett & Dill, 1984). The reason for this may be in the difference in the body forms of these two fish species. Our result reinforces the importance of studying the TBA of different species of fish to provide information for the designs of their respective fishways. In summary, the minimal width of fishway, calculated for the largest individuals of *O. barbatula*, 50 cm in length, to pass through, should be no narrower than 9 cm (= 50 cm × 0.18 BL).

The relationship between the swimming pattern and swimming speed. – A similar body curvature amplitude pattern was displayed at both swimming speeds, at 2 and 4 BL s^{-1} (Fig. 5). The swing amplitude of body axis reduced from snout (P = 0) to the 'quarter body length' (P = 0.25), at which position the fish had the minimal body swing (Fig. 5). The swing amplitude then increased from 'quarter body length' rearwards until the maximal swing was attained at the caudal fin tip (P = 1). This swimming pattern of swing amplitude along body axis has already been reported by

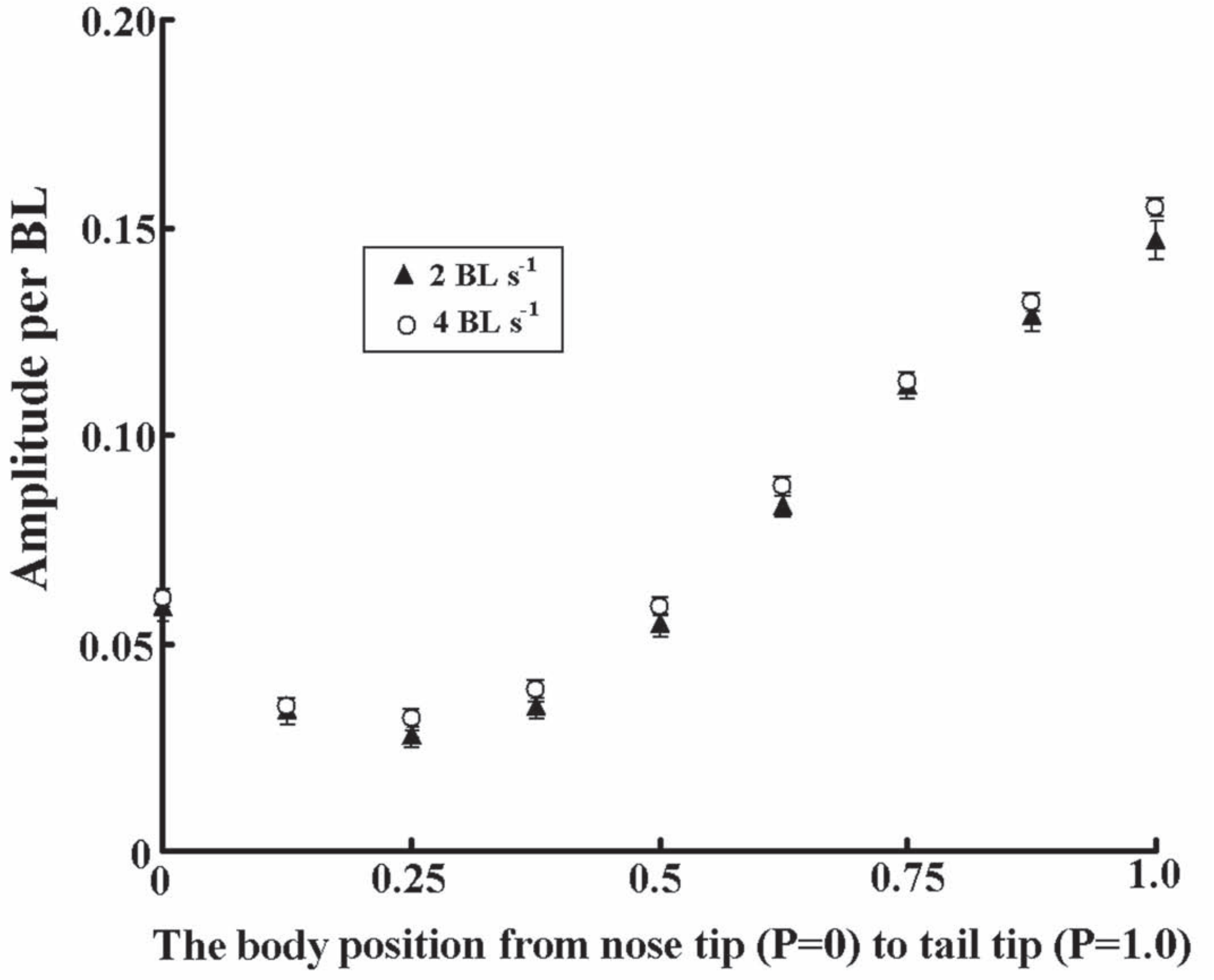

Fig. 5. The swing amplitude of each portion of fish body axis, where P on the X-axis is a ratio at fish body position of the distance from nose tip over total body length.

Hiraishi et al. (1984), Batty (1984) & Videler (1993) for rainbow trout, *Salmo gairdnerii iridens*. From the variations of each body axis in this experiment, we could conclude, as also indicated by Hiraishi et al. (1984) for rainbow trout, that at different swimming speeds, the axis of each moving part of *Onychostoma barbatula* did not change. Swimming speed would increase if swing frequency at each position of body axis was increased. This swimming pattern provides a scientific basis for the design of suitable of fishways for fish of different body shapes.

***Ratios and histology of red muscle in trunk muscle.* –** The proportion of red muscle to trunk muscle was 3.8 ± 0.3% from snout to 25% of BL (Fig. 6). The red muscle ratio exhibited no significant further increase from 35% BL to 45% of BL but increased significantly beyond 45% of BL to 4.8 ± 0.6%, and then to 6.0 ± 0.7%, 7.0 ± 0.9 % and 7.8 ± 0.5% at 55%, 65%, 75% and 85% of BL, respectively (Fig. 6). The trend of increasing proportion of red muscle from 25% to 45% of total body length was not so significant, this region in cross section possessing much of the viscera. At 85% of BL the cross-sectional area was almost as small as that of the caudal fin of fish yet the proportion of red muscle in this part was the greatest. The positive correlation between red muscle proportion and swimming ability of fishes (Greer-Walker & Pull, 1975; Batty, 1984) obviously suggests that forward thrust generation in *O. barbatula* primarily depends on its caudal fin**.**

With the H&E (Fig. 7), it was observed that large numbers of dark-stained nuclei occurred in the red muscle. Red muscle also differs from white in that the average cross

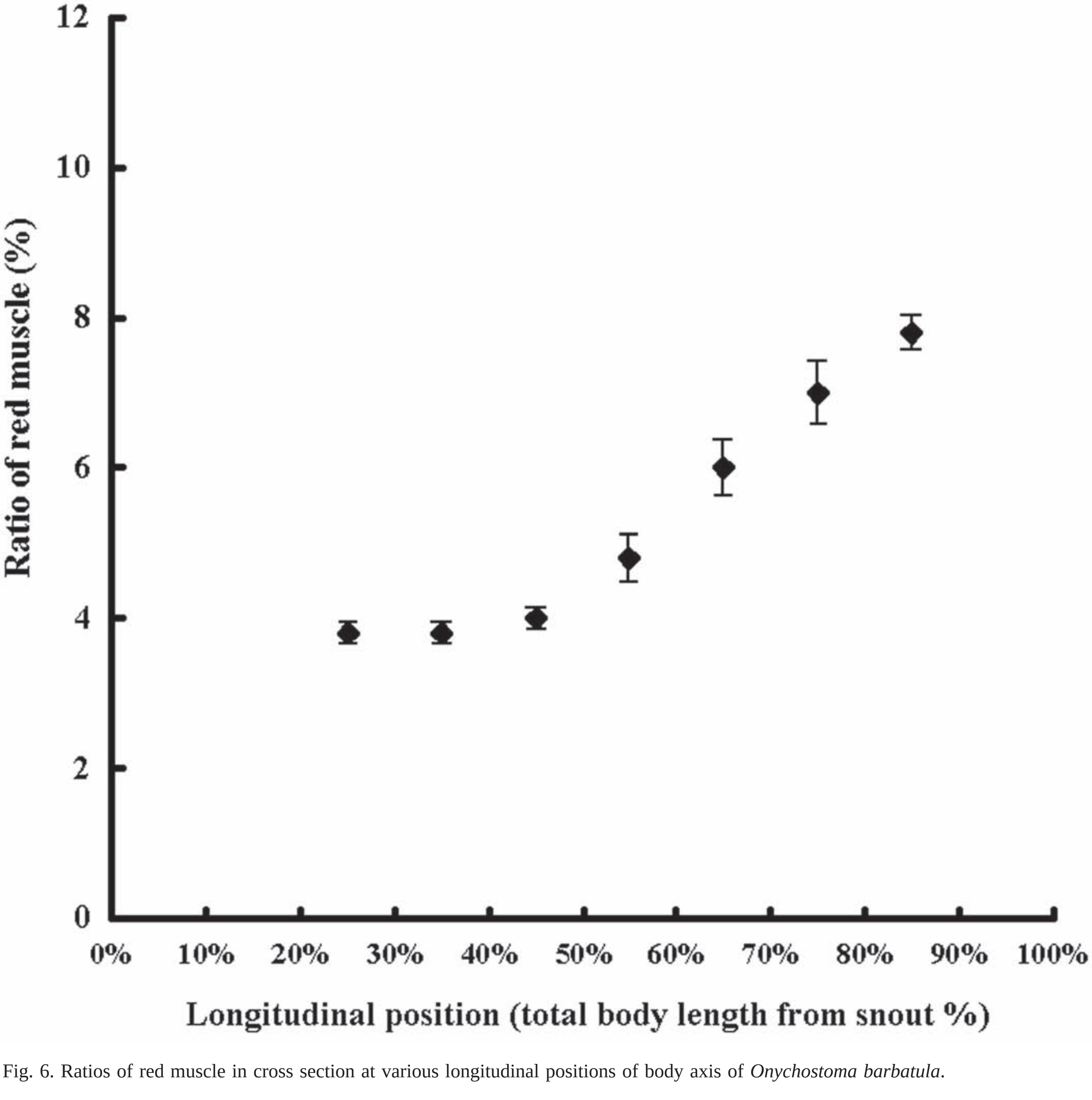

Fig. 6. Ratios of red muscle in cross section at various longitudinal positions of body axis of *Onychostoma barbatula*.

section area of red muscle fibers (370.51 ± 133.62 μm^2) is significantly smaller than that of white muscle (1273.96 ± 571.05 μm^2, n = 50, $p < 0.001$). It was shown (Fig. 7) through staining by MGT that the red muscle area (R) had a large inter-myofibrillar network. Staining by PAS and ATPase 4.0 showed that R contained more glycogen and therefore energy store, presumably for muscle contraction (Fig. 7). Our result suggests that the energy store in the red muscle fiber of fish is richer than in white muscle (see Greer-Walker & Pull, 1975) and could conduct long-term aerobic swimming, through repeated contraction of red muscle. In conclusion, the survival of *O. barbatula* among the upper- and mid-stream region, depends mainly upon its excellent swimming ability which is made possible through its possession of its specialised muscle structure.

***The relationship between maximum critical swimming speed and water temperature*. –** For the fish tested, the relationship between total body length and maximum critical swimming speed **(**water flow rate) is displayed in Fig. 8. The average water flow rate is 126.7 cm s^{-1} and ranges from 43.1 cm s^{-1} (4.8 cm BL) to 231.5 cm s^{-1} (19.7 cm BL). Also shown in Fig. 8 is the relationship between maximum critical swimming speed and water temperature. Water temperature generally had no significant effect on the maximum critical swimming speed of *O. barbatula* of different body lengths. When water temperature was increased from 12 to 16°C, the maximum critical swimming speed of *O. barbatula* increased. However, at temperatures over 16°C, the maximum critical swimming speed decreased gradually. This may be due to the limitations of circulatory or respiratory systems in supplying oxygen (Jain & Farrell, 2003). In addition, some studies also report an optimum temperature range for U_{crit}. For sockeye salmon, 15°C was the optimum temperature for U_{crit}, metabolic range (Brett, 1964) and cardiac performance (Brett & Glass, 1973). Wootton (1992) suggested that fish could actively find an optimal water temperature in its habitat and develop a better physiological condition (Brett & Glass, 1973; Wardle & He, 1988; Kaufmann & Wieser, 1992; Jobling, 1994). As suggested by Yanase et al. (2007), there might exist an optimal temperature for a fish to survive whilst swimming continuously. Within an optimal temperature range, it has been found that an increase of temperature enabled fish to reduce their muscle contraction time (Brett & Glass, 1973; Batty & Blaxter, 1992; Jobling, 1994; Yanase et al., 2007). This increasing muscle contraction could raise TBF and enhance swimming ability of fishes.

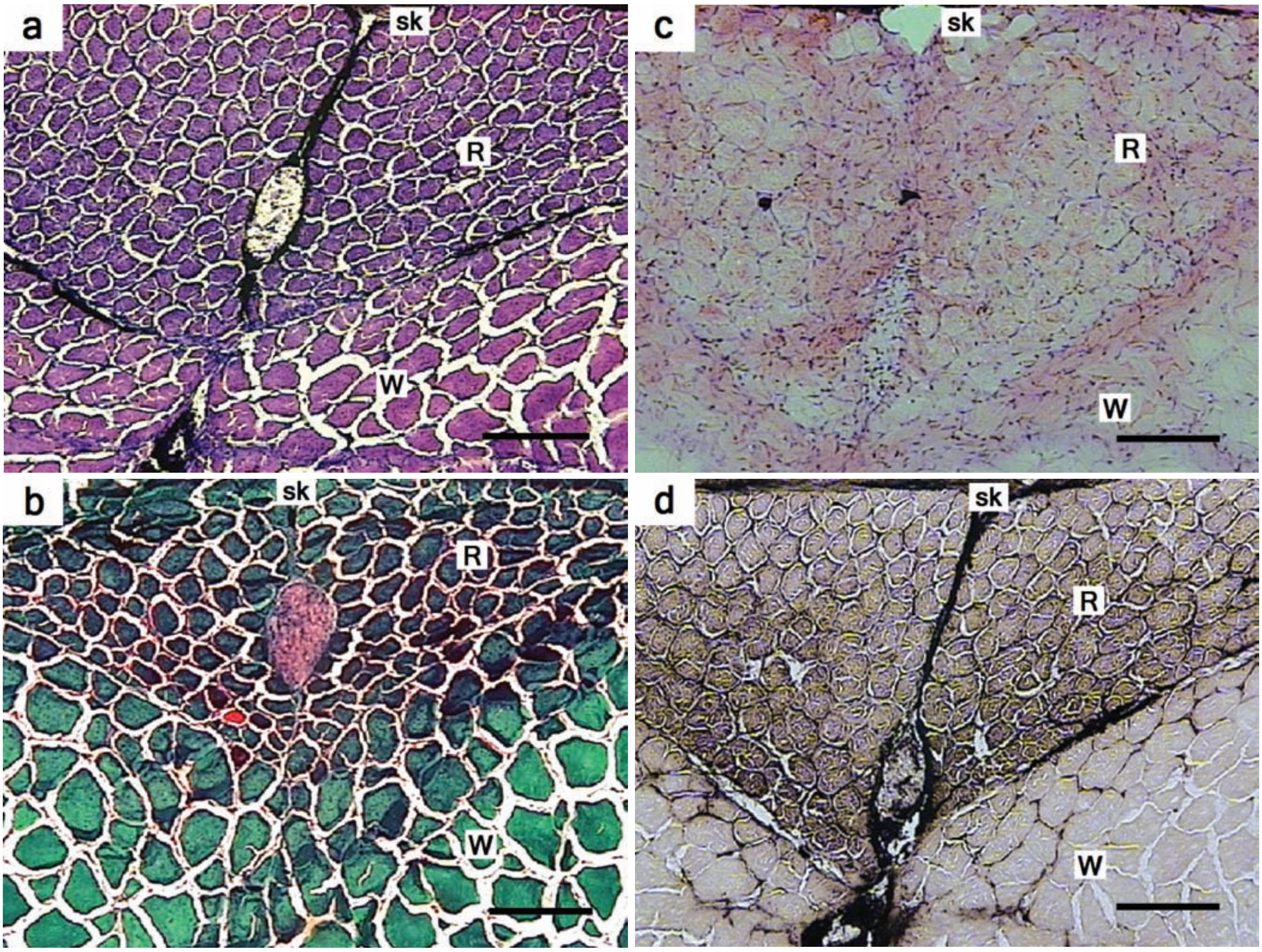

Fig. 7. Cross section of trunk muscle showing the distribution of muscle pattern in red (R) or white (W) muscles and skin (sk). a, stained with Harris hematoxyline and Eosin; b, modifi ed Gomori's trichrome; c, Periodic acid Schiff; d, adenosine triphosphatase. Scale bars = 100μm.

Biological guidelines for fishway design in Taiwan. **–** The fishway is the artificial structure or modification in rivers for fish passage. The fishway built in Taiwan were mainly based on guidelines from North American and Japan. However, these guidelines were often designed for larger fish species (e.g. salmon or trout), and therefore, they are not suitable for smaller fishes in rapid streams. Consequently, this study on swimming ability of *Onychostoma barbatula* is essential for fishway design for Taiwanese streams.

The components of fishway should include attraction features, entrances, fish collection, transportation channels and other considerations (Tzeng, 1997). These varieties of biological, hydrological and physical factors should be considered collectively for designing fishway. Therefore, biological information, including fish morphology and physiology related to swimming abilities and behavior, should be important and fundamental criteria for successful fishway designing. However, this kind of research has been neglected in Taiwan (Tzeng, 1997). The entrance flow is the key to attract fish to the fishway. For the fishway at weirs, the entrance flow must be adequate to compete with spillway or discharge flow so as to guide fish into the fishway. Fish swimming capabilities would affect design concepts and details of fishway (Santos et al., 2007), particularly on the fishway width or site condition, entrance attractive flow speed and passing through fishway requirements. In addition, understanding the fish swimming ability related to different water temperature is also important in setting the flow range of fishway with seasonal variations. Moreover, the migration timing or different fish size should also be important factors in designing fishways.

In conclusion, the *Onychostoma barbatula* is a great swimmer due to its swimming pattern and relatively large red to white muscle ratio. It swims efficiently in waters of 16°C, regardless of its body size, which is likely to be an adaptation for its life in rapid mountain rivers and streams. For conserving this species in rapid stream, this study provide a useful scientific basis for the design of appropriate fishways in regard to, their minimum breadth and most-suitable speed of water flow.

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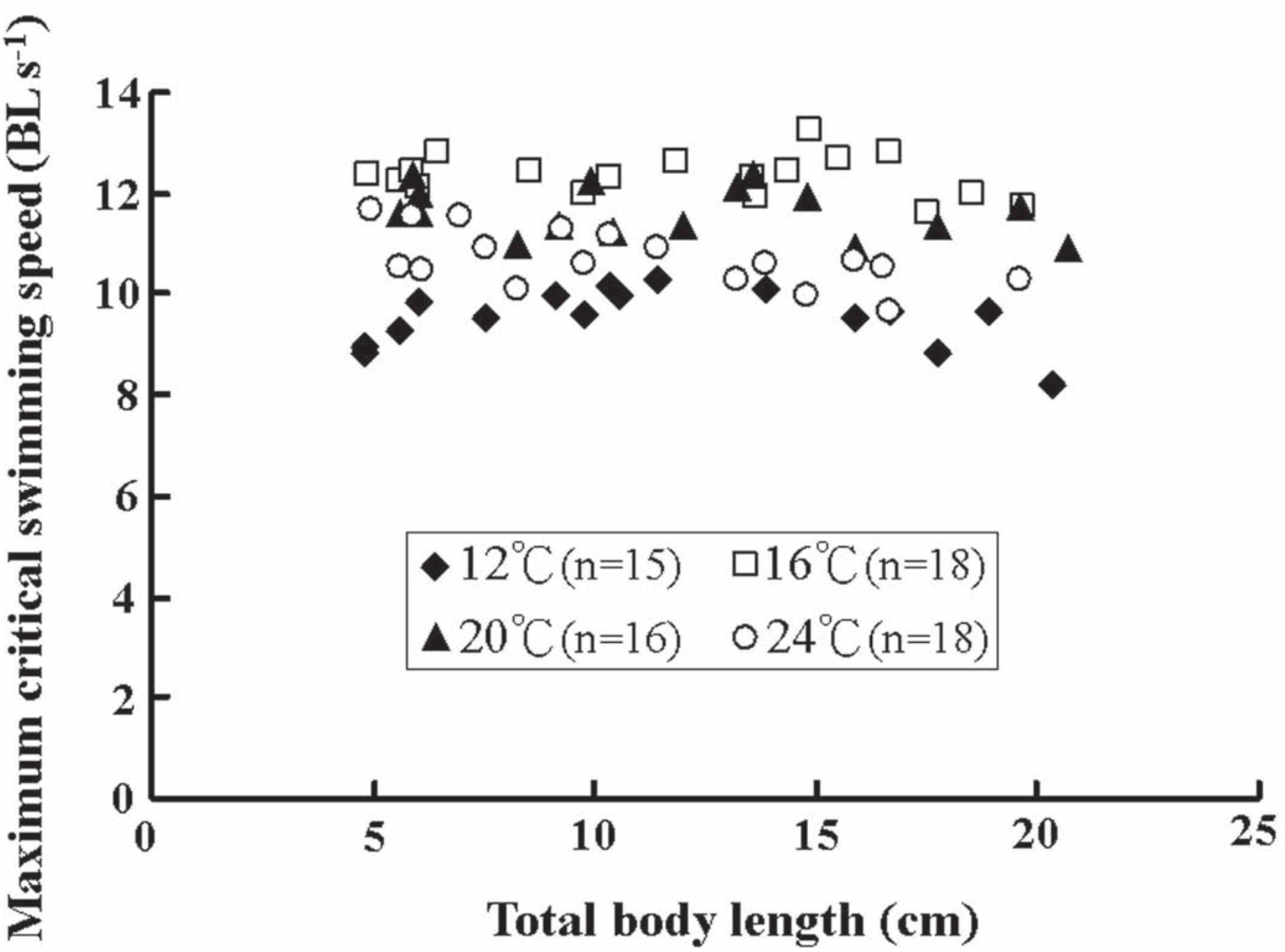

Fig. 8. The relationships between maximum critical swimming speed (BL s^{-1}) and total body length at various water temperatures.

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