The Influence of Stream Barriers and The Hypothetical Origin of Highlands Fishes.

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Abstract

Instream barriers such as waterfalls and man-made dams may result in distinct fish assemblages on both sides of the barriers. To determine the influence of these barriers on fish assemblages, a study was conducted in Sungai Enam that have substantial barriers including an 18-m high waterfall with 6.1% slope. Fish were captured using a backpack electrofishing gear together with scoop nets. Thirteen fish species from six families were recorded along this stream, but only *Poropuntius smedleyi* (Cyprinidae) can be found along the stream and the reach above the waterfall. Studies on a second site, Sungai Kooi, that has a 65m high and 90° slope waterfall, revealed eight fish species from three families, but only *P. smedleyi* and *Devario regina* (Cyprinidae) occurred above the waterfall. The number of species in both streams increases from upstream to downstream. A chi-square test revealed that the total number of species among reaches in Sungai Enam differed significantly. Fish species found above the waterfall are known to have no special adaptations to climb or jump over the barriers. Therefore, to explain their existence above the substantial waterfalls especially in Sungai Kooi, we proposed three hypotheses: (1) the world was once flooded and there was no limitation to fish distribution, (2) fish species assemblages were separated by land uplifting, and (3) there are other stream branches enabling fish movement into respective streams. Further studies are required to confirm these hypotheses.

Introduction

Waterfalls are a natural barrier that are common in highlands' headwater streams. Depending on its size, a waterfall may affect stream communities[1,2], change the prey-predator dynamics[3], and longitudinal abundance of species[4] by preventing species exchange among reaches, and disrupt the movement of aquatic organisms[5]. A waterfall may also promote regional composition and endemism[5] as most fish are unable to jump high enough to transverse the barrier or move against the waterflow that such barriers create unless a fish ladder is provided[6].

As waterfalls may block fish movements, species that exist above a substantial waterfall probably have special behavioral and/or morphological adaptations, which include adaptable swimming patterns[7] and modification of pelvic fins[8]. In Malaysia, studies on fish movement across barriers are still lacking and to date, the fish species that are known to be able to move across barriers are solely based on the one and only list[8]. All the Malaysian fish species in this list were recorded at barriers less than 10m high.

Studies of fish assemblages along headwater streams with significant waterfalls raise questions about how such populations arose, since the waterfalls appear impossible for fish to pass. The present study attempts firstly to establish that such headwaters are populated by fish species and secondly the effect of the barriers on such fish assemblages. For this purpose, Sungai Enam, was selected as one of the field sites, since it has a large waterfall and various other natural and man-made barriers. Although the fish assemblages in this river have been studied for thirty years, no assessment has been made of the effect of the barriers along the stream.

The second field site was Sungai Kooi, a headwater stream in the same area. This stream has a 65m high waterfall, which forms a truly impassable barrier to fish. Therefore, the objectives of this study were to determine the existence of fish assemblages above significant barriers (e.g., waterfalls) and, also to determine the effects of barriers on fish assemblage along Sungai Enam and Sungai Kooi. We also suggest three most probable and logical hypotheses that may explain the existence of fish species above the significant waterfalls.

Materials And Methods

Study site and reaches selection.

Sungai Enam is a third order stream with a river mouth altitude ~ 230m above sea level, and is accessible by boat via Temengor Reservoir [or locally known as Tasik Banding (i.e., Banding Lake)], due to the construction of Temengor hydroelectric dam in 1970. Temengor Reservoir is located in Perak, Malaysia. Sungai Enam comprises a substantial waterfall (18m high), in addition to other waterfalls of variable sizes and heights. This study was carried out once a month from October 2014 to June 2015 using a stratified random sampling design. All pools within the selected reaches were stratified into three major zones (i.e., waterfalls, small dams, and small barriers) and nine reaches based on the existing barriers' location, which are W0 (above WA), W1 (below WA), W2 (above WB) and W3 (below WB), MB1 (below DA), MB2 (below DB), DU (upper downstream), DM (middle downstream) and DL (lower downstream) (Figs. 1 & 2). A random pool was then chosen from each reach during each sampling excursion.

The numbering of reaches started from the area located above the highest waterfall (W0) and ended at the river mouth (DL). In the downstream direction, WA is the first and the highest waterfall and WB is the second waterfall. DA and DB are the first and the second man-made dams, respectively. The slope of the waterfalls was estimated by using an Abney level formula[9].

A one-day intensive fish assemblage study was also carried out in Sungai Kooi (accessible via Temengor Reservoir) on February 4th, 2016 by applying a stratified sampling design. This site includes a 65m high waterfall (Fig. 3) and terrain which restricted extensive investigations and

for safety reasons, only one pool located immediately above the waterfall and two random pools located below the waterfall were selected.

Fish collection and identification

A Smith-Root LR-24 electrofisher backpack together with scoop nets, were used to capture fish at both sites. Captured fish were placed in a bucket filled with stream water to ensure the fish remained alive. All individuals were identified to species level using a standard taxonomic keys[10,11,12]. Most captured live fish were released back to their respective reach, although some specimens were kept as voucher specimens at the repository in our department. We confirmed that our study was performed in accordance with Universiti Sains Malaysia's animal ethics code of conduct. Research permission had been sought and granted from Perak's State Park, Perak's Economic Planning Unit (research permit reference: PTNPK/T/400/4/21.Bil(1) dlm.2016; Prk.Pk. 018/19 Jld. 9) and Perak's Department of Fisheries before to the study was conducted.

Data analysis

Fish assemblage data of the nine reaches were compiled, tabulated and Shannon-Weiner's diversity (*H'*), and Pielou's Evenness (*J'*) indices were calculated[13]. Cluster analysis using Jaccard's Similarity Coefficient (JSC) and unweighted pair group method (UPGMA)[14] was also conducted to determine similarity distance of fish occurrence among the reaches. Diversity and evenness indices and cluster analysis were calculated using Multivariate Statistical Package Software (MVSP) version 3.13d by Kovach Computing Services.

One-way ANOVA with permutation followed by Tukey post-hoc test were also conducted to determine the differences of number of species among the nine reaches based on nine months data. The number of species were log transformed and tested for normality prior to the tests. From this analysis, the effects of the waterfalls and the man-made dams on fish assemblage were determined. Total number of species recorded by each reach was also tested by using a Chi-square test with total number of species recorded for the entire Sungai Enam as expected value.

Results

Sungai Enam

Thirteen fish species comprising of six families were identified and recorded during this study period and the number of fish species showed increasing trend from upstream to downstream. *Poropuntius smedleyi*, was the only fish species found above the highest waterfall (WA; 18m high), whereas three species (*P. smedleyi*, *Neolissochilus soroides* and *Devario regina*) were found above the second waterfall (WB; eight meters high) (Table 1). *Monopterus javanensis* was only found at reaches with waterfalls. This result showed that fish do exist above waterfalls especially above WA in Sungai Enam. In MB1 and MB2, which are located below the man-made barriers (i.e., DA and DB, respectively) only eight and seven fish species were recorded, respectively. In comparison in the reaches with small barriers such as DU, DM, and DL, 10, 9 and 11 species, were noted, respectively. A chi-square test confirmed the significant differences of the number of species among the nine reaches studied.

Table 1: Checklist and distribution of fish species along Sungai Enam.

Family	Scientific Name	Local Name	English Name	WATERFALL				SMALL DAM		SMALL BARRIER		
				WA		WB		DA	DB	Upper	Middle	Lower
				A	B	A	B	B	B			
				W0	W1	W2	W3	MB1	MB2	DU	DM	DL
Channidae	*Channa striata*	Haruan	Snakehead	-	-	-	-	-	-	+	-	-
Clariidae	*Clarias leiacanthus*	Keli	Walking catfish	-	-	-	+	+	+	+	+	+
Cyprinidae	*Barbodes binotatus*	Tebal sisek	Spotted barb	-	-	-	-	+	-	+	+	+
	Devario regina	Danio	Queen danio	-	-	+	+	+	+	+	+	+
	Hampala macrolepidota	Sebarau	Hampala barb	-	-	-	-	+	+	+	+	+
	Neolissochilus soroides	Tengas	Brook carp	-	+	+	+	+	+	+	+	+
	Osteochilus vittatus	Terbol	Silver sharkminnow	-	-	-	-	+	+	+	+	+
	Poropuntius smedleyi	Tengas daun	Minnow/Carp	+	+	+	+	+	+	+	+	+
	Rasbora vulgaris	Seluang	Greater scissortail	-	-	-	-	-	-	+	+	+
	Tor tambroides	Kelah	River carp	-	-	-	+	+	+	+	+	+
Gobiidae	*Pseudogobiopsis oligactis*	Gobi	Gobby	-	-	-	-	-	-	-	-	+
Mastacembelidae	*Mastacembelus favus*	Tilan	Tiretrack eel	-	-	-	-	-	-	-	-	+
Synbranchidae	*Monopterus javanensis*	Belut	Longfin snake eel	-	+	+	+	-	-	-	-	-
		Total number of species	13	1	3	4	6	8	7	10	9	11

Note: '+' = present; '-' = absent; 'WA' = Waterfall A; 'WB' = Waterfall B; 'DA' = Dam A; 'DB' = Dam B; 'A' = Above; 'B' = Below;

'W0' = Waterfall 0; 'W1' = Waterfall 1; 'W2' = Waterfall 2; 'W3' = Waterfall 3; 'MB1' = Man-made Barrier 1; 'MB2' = Man-

made Barrier 2; 'DU' = Downstream (Upper); 'DM' = Downstream (Middle); 'DL' = Downstream (Lower).

Based on the Shannon-Wiener's diversity index (*H'*), reaches of small barriers had the greatest diversity index value (1.787), whereas reaches of waterfall scored the least (0.494). On the other hand, the fish community was more evenly distributed in reaches of small barriers (0.719) compared to reaches of small dam (0.597) and waterfall (0.276). This result suggests that waterfalls can potentially limit the distribution of fish species.

Jaccard's Similarity Coefficient (JSC) revealed a difference in the species profile within each area of the Sungai Enam. Fish species within DU and DM had the greatest similarity with 90%, followed by MB1 and MB2 (88%), whereas fish within W0 differed greatly to the other reaches with only 17% similarity (Fig. 4). This result indicates that fish in reaches with waterfalls are different than the fish from reaches with small dams and small barriers. This analysis suggests that natural barriers (i.e. waterfalls) influence fish assemblage in Sungai Enam.

Sungai Kooi

Eight fish species comprising three families were identified and recorded during the one-day intensive sampling excursion (Table 2). As in Sungai Enam, fish were found above the 65 m high waterfall in Sungai Kooi and the number of species showed an increasing trend from upstream to downstream. *P. smedleyi* and *D. regina* were the only fish species recorded at both above and below the 65m high waterfall. Other species were begun to be found below the waterfall at respective elevation. *Channa striata* was found at 403m above sea level (asl), followed by *C. leiacanthus* and *Neolissocheilus soroides* (334m asl), and *Barbodes binotatus, Crossocheilus oblongus, Hampala macrolepidota* and *Rasbora vulgaris* (296m asl).

Table 2
Checklist and distribution of fish species along Sungai Kooi.

Family	Scientific Name	Local Name	English Name	Above Waterfall			Below Waterfall		
				P1	P2	Total	P3	P4	Total
Channidae	*Channa gachua*	Haruan	Snakehead	+	-	+	-	-	-
Clariidae	*Clarias leiacanthus*	Keli	Walking catfish	-	-	-	+	-	+
	Barbodes binotatus	Tebal sisek	Spotted barb	-	-	-	-	+	+
	Crossocheilus oblongus	Selimang batu	Siamese algae eater	-	-	-	-	+	+
Cyprinidae	*Devario regina Hampala macrolepidota*	Danio Sebarau	Queen Danio Hampala barb	+	+	+	+	+	+
				-	-	-	-	+	+
	Neolissochilus soroides	Tengas	Brook carp	-	-	-	+	-	+
	Rasbora vulgaris	Seluang	Greater scissortail	-	-	-	-	+	+
	Total number of species			**2**	**1**	**2**	**3**	**5**	**7**
Note: '+' = present; '–' = absent; 'P'= Pool									

Discussions

Physical barriers such as dams and waterfalls may isolate stream branches, and potentially interrupt longitudinal gradients of fish distribution[15]. The influence of a single barrier on fish assemblages is well documented, but the influence of multiple barriers in small streams is not well characterized. Studies on the combination of natural barriers (e.g., waterfalls) and the man-made barriers (e.g., small dams), give an opportunity to better understanding how these interuptions in waterflow affect fish assemblages in headwater streams.

The increasing number of fish species from upstream to downstream in Sungai Enam and Sungai Kooi indicates that species profile is affected by the presence of physical barriers. This effect is more evident when barriers have a steep slope and larger height such as the W0 waterfall in Sungai Enam and the 65 m high waterfall in Sungai Kooi. A similar effect was also recorded by previous studies[16,17,18]. In Yakushima Island, Japan, a waterfall beyond 5 m in height had a significant negative effect on fish distribution[19].

Besides the barrier itself, the barrier's slope also plays a role in fish distribution. A steeper slope increases water velocity, discharge volume and momentum, thus, impeding the migratory passage of fish species due to physical resistance to movement they offer[20]. Water velocity controls the distribution of substrate and food as well as exerting a direct influence on the aquatic organism[21]. In terms of morphological or behavioural aspects, fish species, which lack capabilities or adaptations to transverse physical barriers in watercourses, will remain below the waterfall. Above the waterfall therefore, the abundance and biomass of fishes are significantly lower than in all other sites[8].

The existence of fish species below a barrier, may be due to the fish species being washed away[8] by strong water current from upstream that is known as stream drift[22]. Due to stream drift, fish assemblages in downstream is replenished by eggs and larvae[7] and the abundance of drifting fish of particular size, age, and taxa may increase as water velocity increases[23]. On the other hand, the existence of *P. smedleyi, D. regina* and *C. striata* above the waterfalls is still unresolved.

The ability to invade pools above a waterfall is of a tremendous importance to several fish species, allowing them to penetrate or repopulate habitats that otherwise could be impossible to access. For example, guppies (Balitoridae) had been recorded above waterfalls[19] and balitorids have special adaptations that enables them to resist strong water current[8]. These adaptations include the use of pectoral and pelvic fins which form a 'suction-cup' or the pre-valvular cavity[24] and enable fish to adhere to substrates amongst rapids and hence enable them to transverse waterfalls.

Even though most cyprinids do not have such organs that facilitate attachment to a substrate, it has been suggested that cyprinids have evolved from their descendants in terms of their evolution of body shape and mouth orientation enabling them to resist downstream displacement[25]. Such cyprinids are able to move against the water current due to their evolutionary convergence on a pelagic, large-eyed, upturned-mouth morphology and many have a fusiform body that helps to increase their swimming efficiency[25]. However, these adaptations are still not enough to completely explain how cyprinids transverse waterfalls.

In our investiagtion *P. smedleyi, D. regina* and *C. striata* were noted in watercourses upstream of waterfalls, and we propose three hypotheses which may explain this distribution: (1) the world was once flooded and all lands were submerged under water which gave fish freedom to extend their distribution. When the water subsided, fish got trapped in their respective habitat. This hypothesis also means that all freshwater species existed prior to the phenomena and may have been banished due to salt water intrusion, (2) some fish species which had an extensive distribution in freshwater, became isolated by the land uplifting phenomena that created the mountains and waterfalls, and (3) respective streams may have had another watercourse branch with a less gradient of slope which enabled fish passage to higher elevation, and thus bypass the stream branch which had a steeper slope or high waterfalls.

Although the first two hypotheses require extensive investigation of local geological evolution, a fossil-based comparative analysis has revealed that freshwater fish ancestor lineage goes back to marine species[26]. In addition, the uplifting of land in Asia, which occurred million years ago is thought to occur rapidly i.e over decades or over an extensive time period e.g over a million years[27]. The rate of land uplifting may have caused the destruction or alteration of the original stream. Mountains uplifting can either trigger the speciation process, or even reduce biodiversity[28]. However, the distribution of *P. smedleyi* throughout most states in Peninsular Malaysia and even in Thailand, Cambodia, Laos and Vietnam[29] highlights that if fish in each of these localities originated from the same ancestor species, then species evolution follows a certain embedded evolution template such as DNA rather than following natural selection that would probably had created different species.

Conclusions

Results from Sungai Enam and Sungai Kooi showed that there are fish above the waterfalls although these barriers may seem impossible for the fish to traverse, especially in Sungai Kooi. The man-made barriers in Sungai Enam had no influence on the number of fish species as the height of this barrier can still allow some fish species to move upstream. The number of fish species in Sungai Enam and Sungai Kooi increased in downstream direction with less species above the waterfall reaches compared to below the waterfall reaches indicating barriers can limit fish species from moving upstream. The three suggested hypotheses to explain the distribution of fish species below and above waterfalls require research.

Declarations

Acknowledgements

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Contributions:

Original idea by ZHH, ASRMS, SAMS. NFMF, ZHH, AAAA, ES, NAAS and MSM took part in data collection. Data analysis were conducted by NFMF, ZHH. The manuscript was written by ZHH NFMF DH.

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Ethics decclarations

Competing interests

The authors declare no competing interests.

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Figures

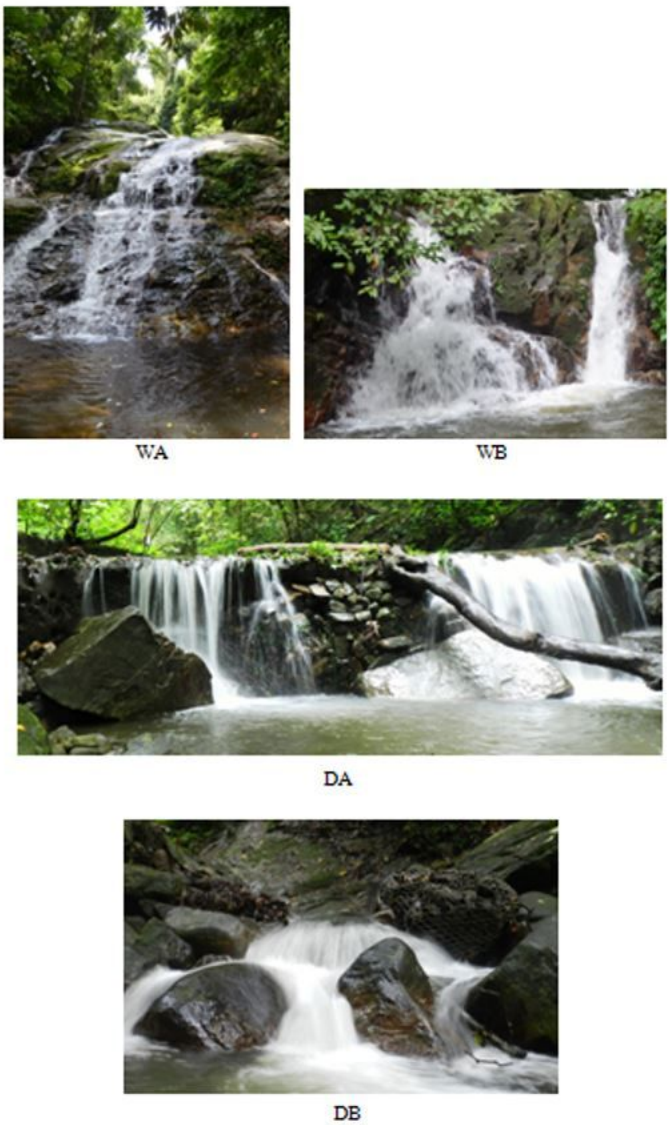

Figure 1

Physical barriers in Sungai Enam

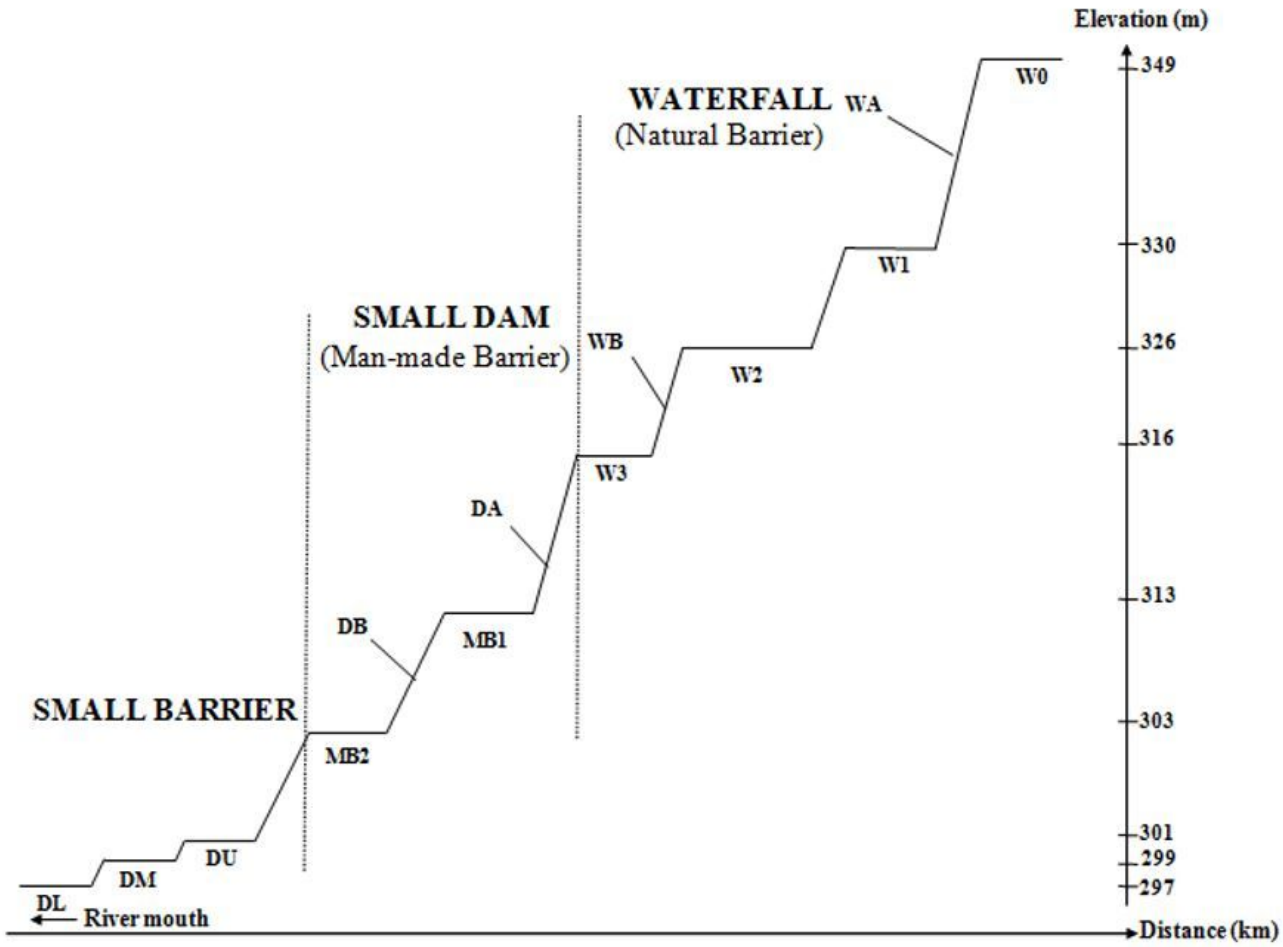

Figure 2

A diagram showing the location of the nine reaches and physical barriers in Sungai Enam (not to scale).

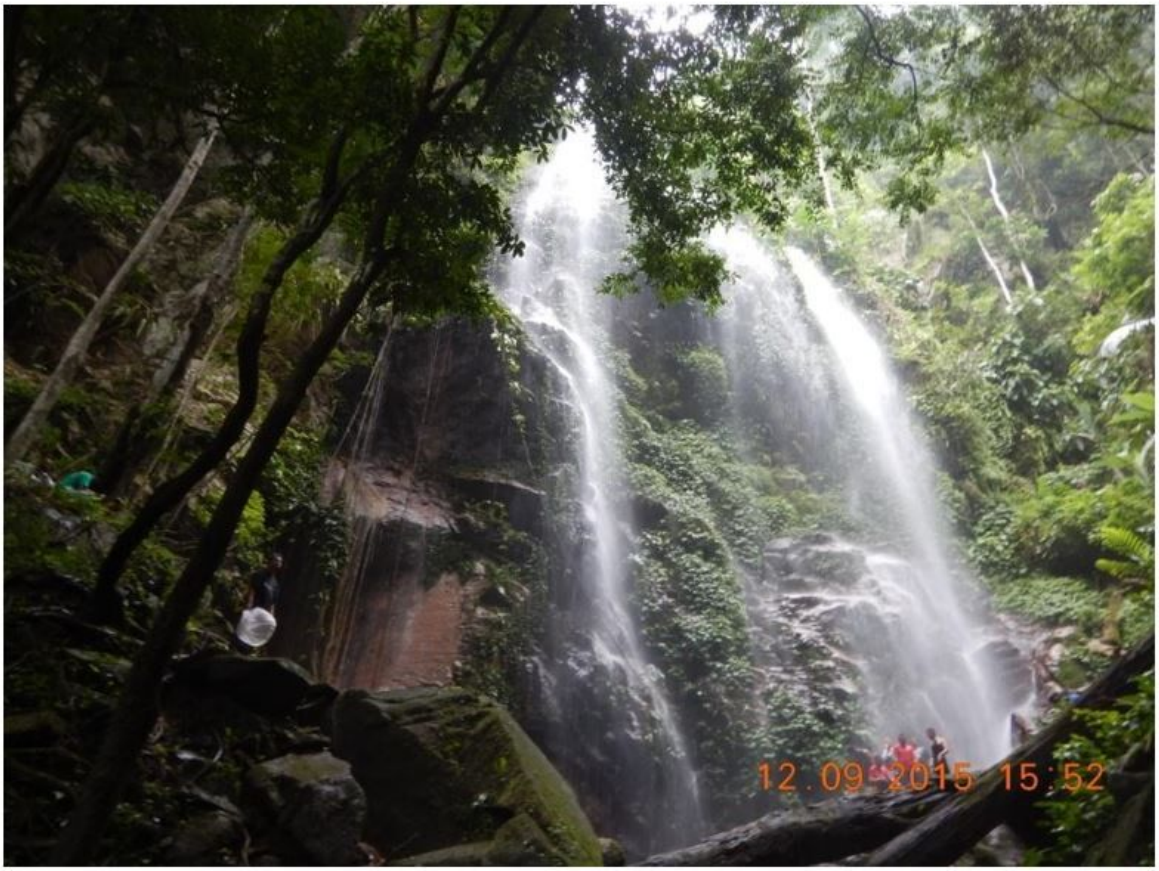

Figure 3

The 65 m high waterfall in Sungai Kooi

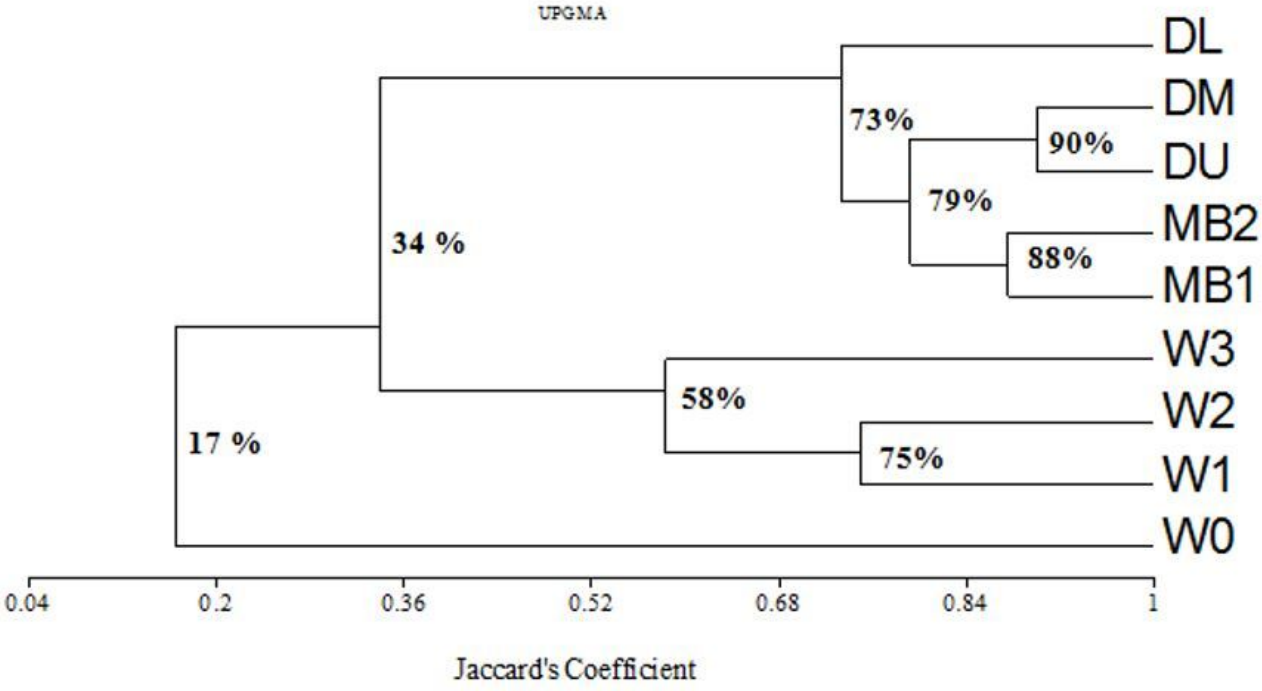

Figure 4

Dendrogram of Jaccard’s Similarity Coefficient (JSC) based on fish assemblages among the nine reaches along Sungai Enam.