Fish Diversity, Habitat Preference and Assemblage Patterns During the Dry Season in the Upper Petchaburi River, Thailand

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ABSTRACT

Fish diversity and assemblage patterns in relation to habitat characteristics were investigated in the Petchaburi River, Thailand, during the dry season and early rainy season (January to June 2019). Sampling was carried out in four stations on the river, from the upper portion downstream to the Kaeng Krachan Reservoir. A total of 5,416 individual fish were sampled from 31 species. Mean abundance was 44.6±40.1 fish per 100 m^2, mean species richness was 10.8±4.0, mean Shannon diversity H' index was 1.75±0.44, and mean evenness J' index was 0.32±0.05. These indices increased from upstream to downstream. They also tended to increase from the onset to middle of the dry season, then decreased at the onset of the rainy season. Co-inertia analysis indicated habitat preference in some species; for example, *Tor tambroides* was positively correlated with macrophytes, shade, bedrock, and boulders, whereas *Aperioptus delphax* preferred high velocity flows in dense vegetation, with sand and cobble substrates. The assemblage patterns were analyzed both for Q-mode (station×month) and R-mode (species) clustering, and habitat specificity of some species was clearly observed. Results of this study are timely useful for resource management and conservation, regarding that the Kaeng Krachan National Park has just been announced as UNESCO Natural World Heritage site in July 2021.

Keywords: Co-inertia analysis, Fish assemblages, Habitat characteristics, Q- and R- modes, River

INTRODUCTION

The fish species present at a particular location of a river in a particular season (i.e., assemblage pattern) is related to their life histories and habitat preferences, which could be considered from macro scale to micro scale (Onoda *et al*., 2009; Barriga *et al*., 2013; Melcher *et al*., 2018). Differences in physical habitat along the river influence the species diversity of fishes as well as their distribution and abundance. Habitat preference also reflects the differences in ecological requirements of fishes, in particular for feeding and reproduction (Röpke *et al*., 2017; Keller *et al*., 2019). In general, the preferences are based on both biotic factors, such as food availability, predation risk and competition, and abiotic ones, such as depth, water velocity and substrate (Vlach *et al*., 2005). Field experiments that apply a habitat modeling approach will provide the most reliable data and information on conditions affecting fish preferences (Melcher *et al*., 2018). Habitat modeling also allows understanding of both quality and quantity of the habitats of individual species, or group of species, within a river reach (Beamish *et al*., 2006; Suvarnaraksha *et al*., 2012; Melcher *et al*., 2018).

As elsewhere in the tropics, the hydrological regimes of rivers in Thailand fluctuate greatly in response to season. The dry season is normally

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from January to April, and the onset of rainy season occurs in May or June. A high abundance and diversity of fish species can be expected during the wet season due to the large water volume. The available habitats accordingly are expanded, and can harbor both resident and migratory fishes (Galacatos *et al*., 2004). Moreover, primary production is also increased because organic nutrients in sediments are mineralized and inorganic nutrients are leached into flood waters (Winemiller and Jepsen, 1998). During the dry season, on the other hand, fishes are normally confined to a restricted area with contracting aquatic environments (Lowe-McConnell, 1987). Keller *et al*. (2019) mentioned that factors including competition and predation can strongly influence fish assemblage patterns at the end of the dry season, when water levels are at their lowest.

Because of the importance of fishes for both livelihood (human food resource) and services (e.g., nutrient recycling) in the river system, the present study aims to examine relationships between habitat characteristics and the distribution and assemblages of fishes during the dry season in the upper portion of the Petchaburi River, in the western region of Thailand. The Petchaburi is an important river in Thailand and it can be divided roughly into three sections: the upstream zone, the Kaeng Krachan Reservoir, and the downstream zone. The latter connects to the Gulf of Thailand at Bang-tabun Bay (Srisomwong *et al*., 2019) (Figure 1). It is also noteworthy that a large portion of the river basin is located within Kaeng Krachan National Park, which was recently granted status as a UNESCO Natural World Heritage site (UNESCO, 2021). Although there is much evidence showing extensive fish diversity and high abundance in the Petchaburi River (Kunlapapuk *et al*., 2015), characteristics of fish habitat have not been well documented. The present study, accordingly, was undertaken with the hypothesis that different habitats harbor different levels of abundance and diversity of fishes, as well as different fish assemblages.

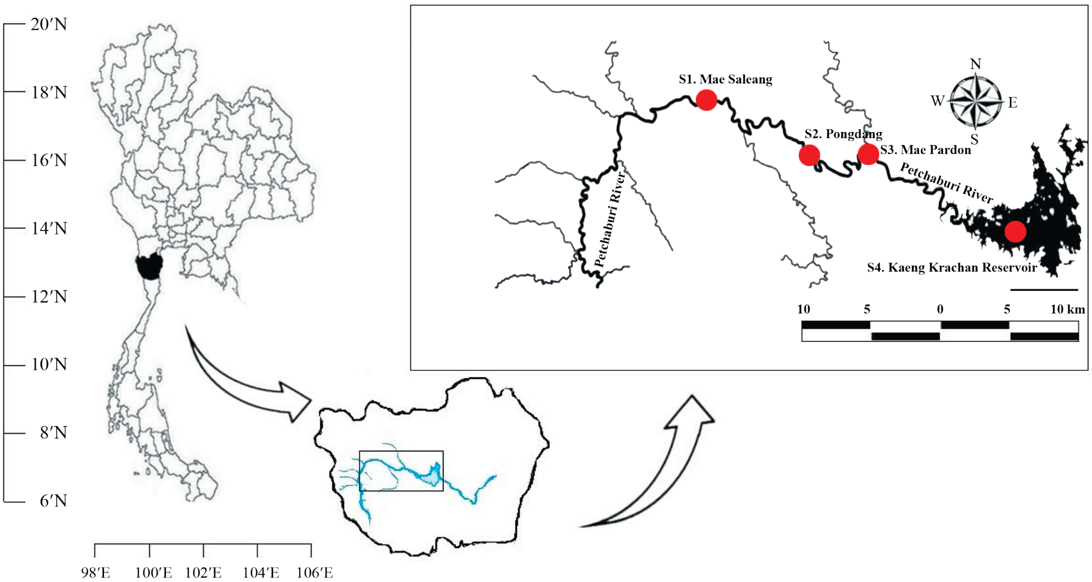

Figure 1. Location and sampling stations (dots) of Petchaburi River, Petchaburi Province, Thailand.

MATERIALS AND METHODS

Study area

The Phetchaburi River is located in western Thailand, with headwaters in the Tenasserim Hills and running 227 km eastward to the Gulf of Thailand. The river and its tributaries are relatively high in fish species diversity; 240 fish species have been recorded here, comparable to 389 species found in the Chao Praya River, the largest river of Central Thailand (Vidthayanon, 2017). The river originates from a high mountain range (700 m above mean sea level) with slopes greater than 35 % in the upstream areas, which are within the boundary of a tropical rain forest reserve, Kaeng Krachan National Park (Wijitkosum and Sriburi, 2019). The river has generally good water quality, with DO levels >4 $mg \cdot L^{-1}$ throughout the system, and average runoff of 2.64 million $m^3 \cdot d^{-1}$ (Regional Irrigation Office 14: Kaeng Krachan Dam office, *personal communication*).

Data collection

Four stations in the upstream area were selected as sampling sites (Figure 1 and Table 1). The lowest altitude site was in the Kaeng Krachan Reservoir, while the other stations were upstream, within pool areas of the river. Field sampling was conducted monthly between January and June 2020, when the sampling sites were accessible due to the relatively low water level and current velocity. Permission to conduct the sampling was officially granted by the Director-General of the Department of National Parks, Wildlife and Plant Conservation. For fish sampling, gill nets with various mesh sizes (20, 30, 40, 55, 70, and 90 mm stretched mesh) were used for 12 h (6 p.m. to 6 a.m.), with three replications. The collected specimens were first identified to species according to Vidthayanon *et al*. (1997) and the Mekong River Commission (2008), and then counted and weighed (0.1 g). Catch data (i.e., number and weight) were converted to units of "100 m^2 night" (European Committee for Standardization, 2005).

Table 1. Location and description of the four sampling stations used in this study.

Sampling station	Geographical co-ordinates	Description
S1: Mae Saleang (154 m asl)	12.979917ºN; 99.371876ºE	The station is about 40 km upstream from Kaeng Krachan Reservoir, and is characterized by steep slope and strong current, with several rapids. The river bed is rock and boulder. Average depth is about 2 m.
S2: Pongdang (121 m asl)	12.943908ºN; 99.448413ºE	The station is 17 km downstream from S1, and contains rapids and pools. Riparian vegetation is ubiquitous and dense. Average depth is about 1.5 m.
S3: Mae Pardon (110 m asl)	12.948875ºN; 99.486411ºE	This area is connected to a tributary of the Petchaburi River, 9.5 km downstream from S2 and 13.5 km upstream from Kaeng Krachan Reservoir. The river banks are covered with rocks and river bottom is largely muddy and sandy. Average depth is about 1 m.
S4: Kaeng Krachan Reservoir (99 m asl)	12.898681ºN; 99.571302ºE	This site is an open-water area of the reservoir, about 3 km from the inlet of the Phetchaburi River. Water is still and average depth is about 14 m.

Note: the number in parentheses after each sampling station name is the altitude (m above mean sea level)

Parameters used for describing habitat characteristics (Pusey *et al*., 2004) included (i) depth (Portable Depth Sounder Hondex-PS-7); (ii) water velocity at 20 % of total depth (Global water FP111 Flow Probe: Extendable Handle); (iii) percent cover of each micro-habitat type: riparian vegetation, macrophytes, and shade (note that contributions of these variables were not required to add up to 100 %); and (iv) percent cover by substrate types (detritus, mud, silt, sand, gravel, cobble, boulder and bedrock) which were visually estimated and summed to 100 %.

Data analysis

Abundance (fish per 100 m^2), species richness, and diversity indices (Shannon–Wiener H' index and evenness J' index) of each sample were calculated. H' and J' were calculated with the equations

$$H' = -\sum_{i=1}^{S} p_i \ln(p_i)$$

$$J' = H'/H'_{max}$$

Where p_i is the proportion of individuals belonging to the i^{th} species; S is species richness (number of different species present), and H'_{max} is the maximum possible value of H′ (i.e., if every species was equally likely) and $H'_{max} = \ln S$ (Hill, 1973).

Because all indices noted are non-normally distributed (p>0.05), statistical differences among sampling times and stations were tested by the Kruskal-Wallis test; the Dunn's post-hoc test was applied if significant difference was found at $\alpha = 0.05$. Co-inertia analysis, which is essentially a two-table ordination method of canonical correspondence analysis (Dolédec and Chessel, 1994), was applied to model the association between fish species and habitat characteristics. Significance of the resulting co-structure between the environmental and fish datasets was examined by a Monte-Carlo permutation test, which repeated 1,000 co-inertia analyses of both datasets after random permutations. The permutation MANOVA (PERMANOVA; Anderson, 2001) was applied to test whether the factors month and station affected the difference in fish species composition (designated as dependent variable). Hierarchical agglomerative clustering analysis with the Bray–Curtis similarity index was applied to the log-transformed abundance data to characterize patterns both for Q mode (sample clustering), and R mode (species clustering). Differences among clusters were statistically tested with analysis of similarities (ANOSIM). All statistical analysis was done by R (R Development Core Team, 2020), with the package vegan (Oksanen *et al*., 2020) and ade 4 (Thioulouse *et al*., 2018).

RESULTS

Thirty-one species belonging to 10 families were collected during 24 sampling events (4 stations ×6 months). The most diverse family was Cyprinidae (19 species), followed by Bagridae (4 species); the remaining eight families contained one species each. Of 5,416 individuals collected, *Mystacoleucus marginatus* was the most abundant species (49.9 %), followed by *Puntioplites proctozysron* (10.99 %) and *Cyclocheilicthys repasson* (6.30 %). The remaining species each represented less than 5 % of the combined sample. In terms of occurrence frequency, *M. marginatus* was found in every sample, and eight species had an occurrence frequency over 50 %. The total weight of fish samples was 192,188.69 g, with *Hypsibarbus vernayi* the most dominant species by weight (23.35 %). Relative abundance of each collected fish species (in terms of number and weight in the combined sample) and percent occurrence (among sampling events) are presented in Table 2.

The common fish species (>50 % occurrence) were generally more abundant in lower altitude sampling stations (Figure 2). The two species *Mystacoleucus marginatus* and *Cyclocheilicthys repasson* were common in all sampling stations. Means for abundance, species richness, H' index and J' index in each month and each station are presented in Tables 3 and 4, respectively. The average abundance during the study was 44.6±40.1 individuals. Highest abundance (152 individuals) was found at station 3 in February, and the lowest

(9 individuals) was from station 1 in January. The average species richness was 10.8±4.0. The highest and lowest species richness were both found in station 3, in February (20) and May (5), respectively. The H' index ranged from 0.92 (station 3 in May) to 2.63 (station 1 in February), with an average of 1.75±0.43. The average J' index was 0.317±0.053 and varied between 0.225 (station 3) and 0.423 (station 1); both maximum and minimum values were from January. Significant temporal differences (Table 3) were found for species richness ($p = 0.017$) but not the H' index ($p = 0.371$). Meanwhile, abundance ($p = 0.010$) and J' index ($p = 0.017$) showed significant spatial differences (Table 4).

Table 2. Percentage of abundance and occurrence of fish species across all sampling stations in the Petchaburi River, Thailand.

Family	Scientific Name	Abbreviation	%Number	%Weight	%Occurrence
Notopteridae	*Notopterus notopterus*	Nono	0.11	0.24	16.7
Cyprinidae	*Barbonymus gonionotus*	Bago	1.28	10.78	37.5
Cyprinidae	*Cirrhinus molitorella*	Cimo	1.16	7.30	62.5
Cyprinidae	*Cyclocheilicthys apogon*	Cyap	4.67	3.03	66.7
Cyprinidae	*Cyclocheilicthys repasson*	Cyre	6.30	5.70	95.8
Cyprinidae	*Hampala macrolepidota*	Hama	1.41	2.24	62.5
Cyprinidae	*Henicorhynchus lobatus*	Helo	0.02	0.01	4.2
Cyprinidae	*Hypsibarbus vernayi*	Hyve	3.10	25.35	62.5
Cyprinidae	*Labiobarbus siamensis*	Lasi	0.24	0.79	20.8
Cyprinidae	*Lobocheilus rhabdoura*	Lorh	0.14	0.84	20.8
Cyprinidae	*Mystacoleucus marginatus*	Myma	49.87	17.72	100.0
Cyprinidae	*Opsarius koratensis*	Opko	0.62	0.07	16.7
Cyprinidae	*Osteochilus microcephalus*	Osmi	2.47	5.51	66.7
Cyprinidae	*Osteochilus vittatus*	Osvi	3.78	3.58	54.2
Cyprinidae	*Paralaubuca* sp.	Pasp	0.14	0.03	4.2
Cyprinidae	*Puntioplites proctozysron*	Pupr	10.99	6.65	62.5
Cyprinidae	*Puntius brevis*	Pubr	2.18	0.39	33.3
Cyprinidae	*Raiamas guttatus*	Ragu	0.04	0.18	8.3
Cyprinidae	*Rasbora paviana*	Rapa	0.81	0.18	25.0
Cyprinidae	*Tor tambroides*	Tota	0.16	1.00	12.5
Cobitidae	*Aperioptus delphax*	Apde	0.60	0.57	16.7
Bagridae	*Hemibagrus filamentus*	Hefi	0.06	0.33	8.3
Bagridae	*Hemibagrus spilopterus*	Hesp	0.13	0.65	20.8
Bagridae	*Hemibagrus wyckioides*	Hewy	0.05	0.04	8.3
Bagridae	*Pseudomystus siamensis*	Pssi	0.30	0.33	25.0
Belonidae	*Xenentodon cancila*	Xeca	0.53	0.38	25.0
Mastacembelidae	*Mastacembelus armatus*	Maar	0.29	0.94	33.3
Ambassidae	*Parambassis siamensis*	Pasi	3.41	0.15	29.2
Eleotridae	*Oxyeleotris marmorata*	Oxma	0.41	1.81	25.0
Pristolepididae	*Pristolepis fasciatus*	Prfa	4.17	1.93	25.0
Cichlidae	*Oreochromis niloticus*	Orni	0.54	1.29	25.0

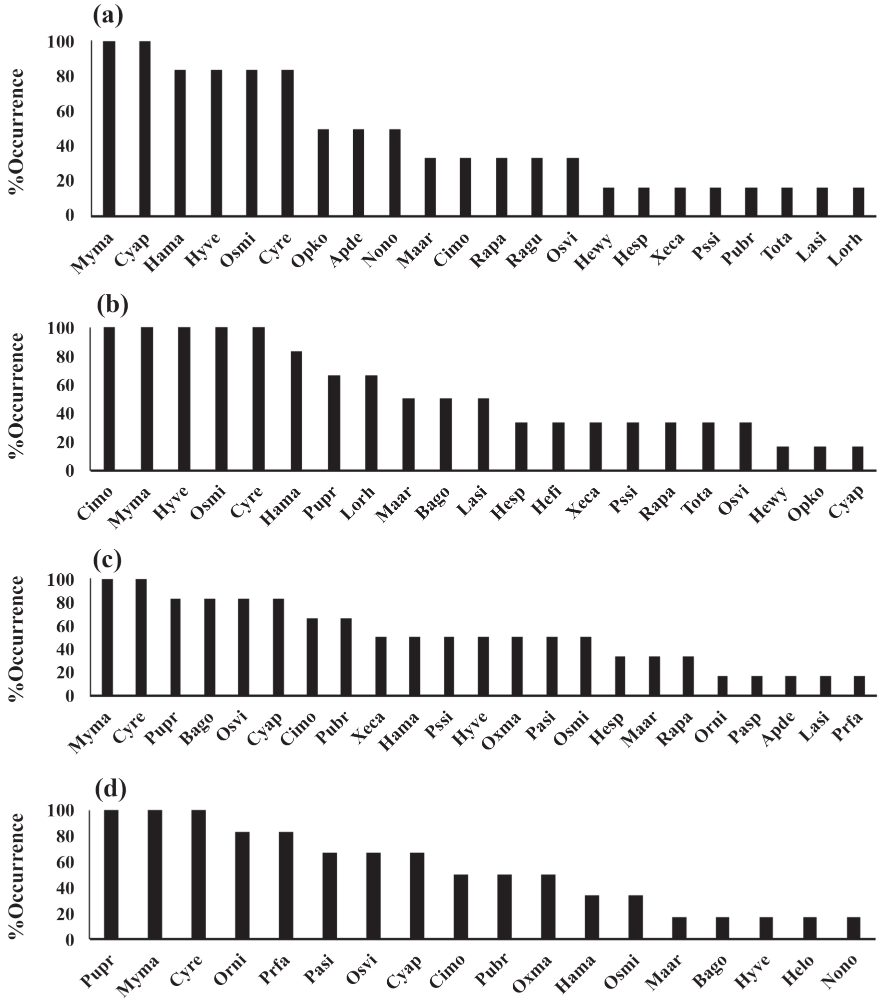

Figure 2. Percent occurrence of fishes from each sampling station during the study period: (a) S1: Mae Saleang; (b) S2: Pongdang; (c) S3: Mae Pardon; (d) S4: Kaeng Krachan Reservoir; species abbreviations as detailed in Table 2.

Table 3. Means (±SD) of abundance (fish per 100 m^2), species richness and diversity indices of fish averaged across four sampling stations between January and June 2020.

Parameter	p-value	Jan	Feb	Mar	Apr	May	Jun
Abundance	0.671	45.5±31.5^{a}	61.5±67.3^{a}	76.6±59.0^{a}	34.7±15.9^{a}	22.7±1.5^{a}	26.2±8.2^{a}
Species Richness	0.017	12.5±4.6^{ab}	15.5±3.1^{a}	13.0±2.9^{ab}	7.7±1.2^{ab}	7.5±2.0^{b}	8.2±0.9^{ab}
H’ index	0.047	1.95±0.37^{ab}	2.25±0.33^{a}	1.78±0.44^{ab}	1.46±0.18^{b}	1.56±0.44^{ab}	1.53±0.42^{ab}
J’ index	0.558	0.33±0.06^{a}	0.31±0.05^{a}	0.28±0.04^{a}	0.33±0.05^{a}	0.35±0.06^{a}	0.31±0.07^{a}

Note: Means in a row with different superscript letters are significantly different ($p<0.05$).

Table 4. Means (±SD) of abundance (fish per 100 m^2), species richness and diversity indices of fish averaged across six sampling events in four sampling stations.

Parameter	p-value	Station 1	Station 2	Station 3	Station 4
Abundance	0.010	21.5 ± 10.2^{a}	25.3 ± 5.4^{ab}	77.5 ± 57.8^{b}	54.0 ± 37.7^{ab}
Species Richness	0.775	9.8 ± 3.4^{a}	11.5 ± 3.6^{a}	12.0 ± 5.9^{a}	9.6 ± 2.9^{a}
H' index	0.371	1.96 ± 0.48^{a}	1.93 ± 0.41^{a}	1.51 ± 0.45^{a}	1.61 ± 0.30^{a}
J' index	0.017	0.36 ± 0.05^{a}	0.32 ± 0.04^{ab}	0.26 ± 0.03^{b}	0.33 ± 0.05^{ab}

Note: Means in a row with different superscript letters are significantly different ($p<0.05$)

PERMANOVA revealed that species composition was significantly affected by station ($p<0.001$) but not by month ($p = 0.504$). The results of the co-inertia analysis between the sampled fishes and environments showed clear preferences of fish species for individual habitat characteristics (Figure 3). The first two axes explained 93.54 % of the total variability in the fish and habitat data. Eight fish species, including *Hypsibarbus vernayi* (Hyve), *Lobocheilus rhabdoura* (Lorh) and *Tor tambroides* (Tota) were positively correlated to macrophytes, shade, bedrock, and boulders, as well as high altitude. High water velocity occurred together with dense vegetation within stations 1 and 3, where the substrate was sand and cobble; these features were preferred by 10 species, such as *Pseudomystus siamensis* (Pssi), *Rasbora paviana* (Rapa), *Aperioptus delphax* (Apde) and *Mastacembelus armatus* (Maar). Deep areas with gravel and silt bottoms were favored by five fish species, including *P. proctozysron* (Pupr) and the exotic *Oreochromis niloticus* (Orni).

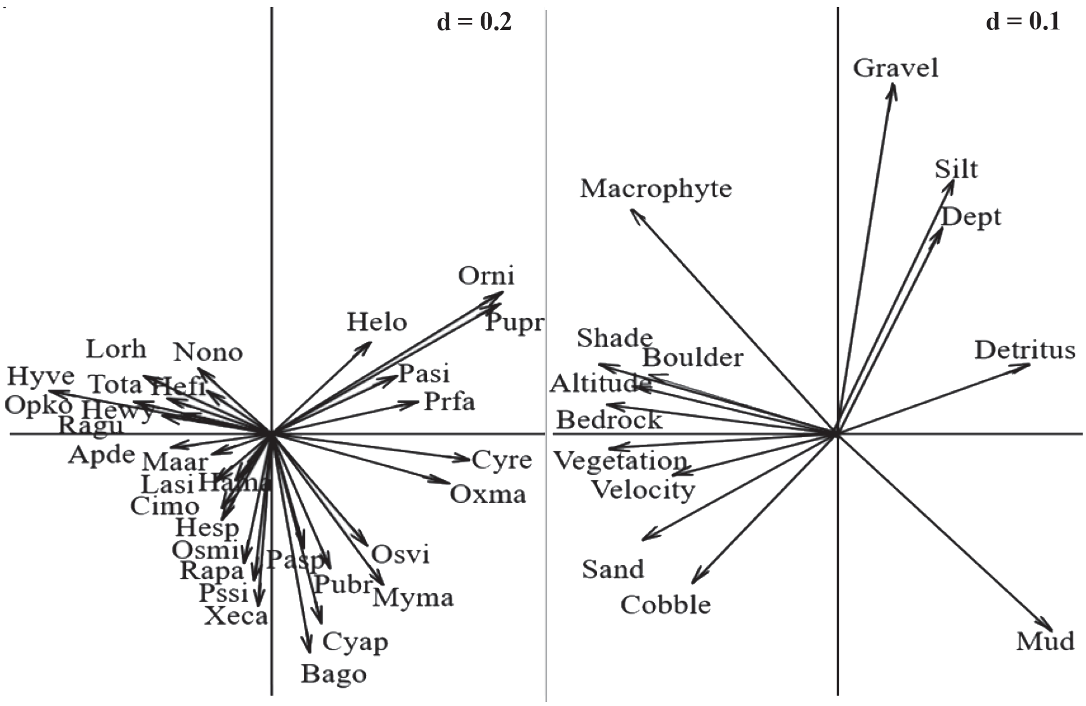

Figure 3. Co-inertia analysis between fish species (left) and environmental features (right) indicating habitat preferences of fishes; species abbreviations as detailed in Table 2.

Hierarchical clustering divided the samples (Q mode) and species (R mode) into four and five groups, respectively (Figure 4). ANOSIM indicated significant difference among the groups for both Q and R modes (p<0.001). Groups Q3 and Q4 each represented a single sampling event, and both were from station 4, in February and June, respectively. These two clusters comprised fewer species than the other clusters and differed from each other by the dominance of *P. proctozysron* (Pupr) in Q4. Group Q1 was composed mainly of sampling events at station 1 and characterized by species compositions with various non-dominant species. Meanwhile, group Q2 was dominated by *M. marginatus* (Myma) and further divided into three sub-groups. Sub-group Q2a consisted of only one sampling event (station 3 in February), when only a few species were collected. Sub-group Q2b was a mixture of sampling events at stations 2 and 3, while sampling events at station 4 were exclusively clustered into sub-group Q3. The R-mode classification showed two groups containing a single species: *Paralaubuca* sp. (Pasp) in R4 and *Henicorhynchus lobatus* (Helo) in R5. Group R1 consisted of generalist fish species, such as *P. proctozysron* (Pupr) and *M. marginatus* (Myma), which can occupy both flowing and stagnant water. Meanwhile, fishes in group R2 were species inhabiting stagnant water, such as *Oxyeleotris marmorata* (Oxma) and *Oreochromis niloticus* (Orni). Group R3 contained many species and was characterized by fishes that tend to favor flowing water (as commonly found in stations 1 and 2), including *Tor tambroides* (Tota), *Labiobarbus siamensis* (Lasi) and *Lobocheilus rhabdoura* (Lorh).

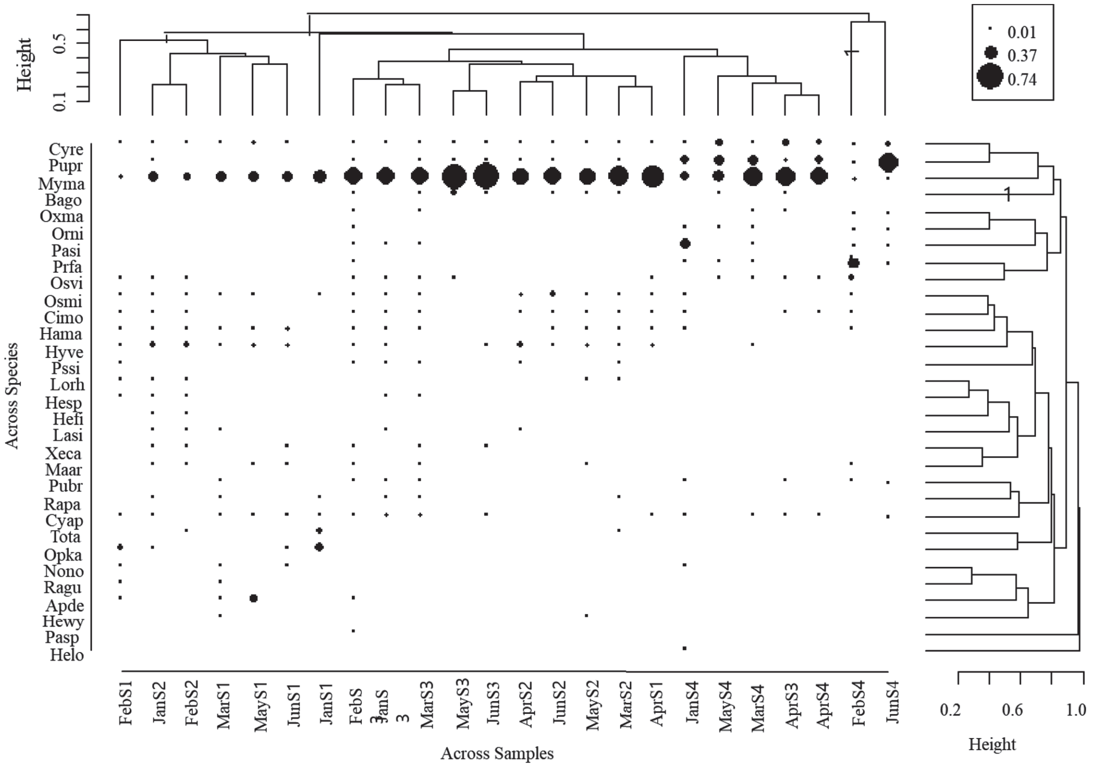

Figure 4. Dendrogram showing hierarchical relationships across samples (Q mode) and across species (R mode) of the study.

DISCUSSION

Connections between tropical rivers and lakes, or between rivers and reservoirs, are known to serve as spawning and nursery grounds for numerous fish species during the rainy and flood seasons (Suvarnaraksha *et al*., 2011; Jutagate *et al*., 2016). However, the importance of this interface in the dry season in less understood, particularly the role of the riverine zone as a refuge. The present study, therefore, highlights the diversity, habitat preference and assemblages of fishes in such a setting, namely the upper Petchaburi River and Kaeng Krachan Reservoir.

The ranges of species richness (10-12) and H′ index (1.5-2.0) found in stations 1 to 3, where altitude is 110-150 m above mean sea level, are similar to the Ping-Wang River of Thailand (species richness 10-20; H′ index 1.5-2.3; altitude above 100 m asl) (Suvarnaraksha *et al*., 2012). Dominance by species from Family Cyprinidae is not surprising, because it is the largest family of freshwater fishes in Southeast Asia. This family consistently contributes over 40 % of species richness (Vidthayanon *et al*., 1997; Beamish *et al*., 2006). The two most common species found in this study, *Mystacoleucus marginatus* and *Cyclocheilicthys repasson*, are known as bentho- and meso-pelagic stream and river residents, behaviorally adapted to lentic environments (Froese and Pauly, 2020). Abundance and diversity indices in stations 1 to 3 were high during the middle of the dry season (February and March), but became low in April and May, implying that the fish moved out from the refuge that those stations provide when the water level rose at the onset of the rainy season. This pattern is similar to the migratory patterns of fishes in the Lower Mekong Basin, where fish inhabit deep pools during the dry season and move elsewhere at the onset of rainy season (Baird *et al*., 2005). High abundance and species richness in station 3 conforms to the stream gradient model, as both parameters tended to increase down-gradient, together with depth and habitat heterogeneity (Capone and Kushlan, 1991).

Fish assemblages occurred non-randomly in each representative habitat. Empirically based habitat suitability models can provide links to environmental factors. The co-inertia results (Figure 4) identify the environmental conditions and features that are preferred by fishes in the study area during the dry season. Habitat characteristics of the study area are classified as transitory, with sampling stations ranging from foothills to lowlands (Suvarnaraksha *et al*., 2012). The flow regime in this zone is among the major factors of the physical habitat, and serve to determine biotic composition (Melcher *et al*., 2018). The strong flow through the foothills with bedrock and boulder substrates commonly favors relatively fusiform fishes that prefer to forage in the fast-flowing water adjacent to boulders (Ng, 2004; Suvarnaraksha *et al*., 2012). *Lobocheilus rhabdoura* and *Tor tambroides* found in this study have such habitat preferences. Numerous species were found in areas with dense vegetation, sand and cobble bottoms, and relatively strong water flow, which is typical habitat found in the zone of transition to the lowland (Welcomme *et al*., 2006; Keller *et al*., 2019). The limnophilic species (e.g., *Oreochromis niloticus*) and facultative riverine species (e.g., *Puntioplites proctozysron*) were highly correlated with water depth, since they were dominant in the reservoir area, and hence also correlated with the detritus, gravel and silt substrates found in that station (Capone and Kushlan, 1991; Espa *et al*., 2019).

Fishes can be grouped into guilds according to their habitat preference, and their presence and abundance is highly related to habitat characteristics and hydrological cycles (Keller *et al*., 2019). The traditional fish guild classification for river ecosystems uses environmental guilds, as described by Welcomme *et al*. (2006). According to this system, fishes in group R1, commonly found in all Q modes to varying degrees, can be considered to represent the eurytopic guild, and eupotamonic benthic sub-guild. Fishes in this guild are able to adapt their behaviors to altered hydrological conditions and are commonly found in both lentic and lotic environments (Röpke *et al*., 2017). This is the key reason why species in this R mode were found in every sampling event. Group R2 are eurytopic fishes in the eupotamonic riparian sub-guild, which tend to live in littoral areas and are more lentic than the eupotamonic benthic guild (Welcomme *et al*., 2006; Jutagate *et al*., 2011). This explains why fishes in this guild are abundant in mode Q2c. Group R3 is composed of small cyprinids that mostly occupy flowing sections of the river, or the rhithronic zone (Suvarnaraksha *et al*., 2012) and classified as the pool and riffle guild. The fishes in this guild are often micro-habitat specific and rely on a delicate balance of their preferred habitat characteristics (Beamish *et al*., 2006; Tongnunui *et al*., 2009). They accordingly are rarely found in downstream river reaches or lentic environments, as was observed in this study. Welcomme *et al*. (2006) stated that changes in hydrological regime, either flow or water level, would create disturbance to the habitat preferred by this guild and potentially lead to species extirpation.

CONCLUSION

Understanding the habitat preferences of any fish species or assemblage is important for habitat rehabilitation and species conservation. Over 5,000 individuals from 31 species that were sampled in this study reflect the importance of the upper portion of the Petchaburi River as a dry-season refuge. The essential role of physical habitat characteristics in shaping the diversity and assemblage patterns of fishes are also revealed. Results show that some fish species, such as *Tor tambroides*, have to inhabit flowing water, while others, such as *Mystacoleucus marginatus*, are behaviorally adapted to live in both lotic and lentic water conditions. The habitat-preference information obtained from the present study is essential for further resource management and conservation. For example, it can be applied to enhance in-river and riverbank habitats in the Kaeng Krachan National Park, which is now a UNESCO Natural World Heritage site. Further studies should apply an empirically based habitat suitability approach to describe the biological processes that affect population dynamics of species assemblages.

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