



Larval fish assemblage patterns in three tributaries of Mekong River in Thailand

PISIT PHOMIKONG¹, SURIYA UDDUANG², MICHIO FUKUSHIMA³, BOONSONG SRICHAREONDHAM⁴, DEEKA RATTANACHAMNONG⁴ AND TUANTONG JUTAGATE¹

¹Faculty of Agriculture, Ubon Ratchathani University, Warin Chamrab, Ubon Ratchathani - 34190, Thailand

²Faculty of Agriculture and Technology, Rajamangala University of Technology Isan, Surin Campus, Muang Surin - 32000, Thailand

³National Institute for Environmental Studies, Onogawa 16-2, Tsukuba, Ibaraki 305-8506, Japan

⁴Department of Fisheries, Chatuchak, Bangkok - 10900, Thailand

e-mail: tuantong.j@ubu.ac.th

ABSTRACT

The assemblage patterns of larval fishes from three neighboring tributaries viz., Songkram, Gam and Mun of the Mekong River in Thailand were investigated between August 2009 and June 2010. These rivers interact with their floodplains, which are important spawning and nursery grounds for the Mekong fishes. There is no dam along the Songkram River; meanwhile the Gam River has several irrigation dams with a fish ladder at each dam site and the Mun River has a hydropower dam with a fish ladder and sluice gates that are opened during the wet season each year. A total of 97 fish species were collected from the study sites. Assemblage of Gam River was dominated by larvae of resident, black fish species. Assemblage of Mun River during sluice gate opening scheme was similar to that of Songkram River during wet season. Assemblage during flood period of Songkram River showed the most diversity and abundance of migratory, white fish larvae. Conservation of integrity of the floodplain-river system of Songkram River is among the crucial strategies for sustaining fish diversity and fisheries in the Lower Mekong River Basin.

Keywords: Damming, Fish larvae, Mekong, Tributaries

Introduction

Only a small fraction of the world's river systems remains unaffected by humans (Vorosmarty *et al.*, 2010). Human activities, such as urbanisation, industrialisation and engineering schemes like reservoirs and irrigation, strongly influence riverine fish diversity. Many studies have been carried out to understand the impacts of these activities to the integrity of riverine fish diversity, in particular by that of river damming. Damming the river has a profound effect on migratory fishes by disrupting their migratory routes and cause decline of fish diversity due to habitat fragmentation as well as an increase of faunal similarity or biotic homogenisation (Li *et al.*, 2013; Kano *et al.*, 2016).

Damming the river not only impacts adult fishes but also their larvae. The effects of hydrological and habitat changes could result in differences in larval communities in upstream and downstream of dam (Agostinho *et al.*, 2004; Cheshire *et al.*, 2012). This phenomenon has become more serious in the river basins that contain high fish biodiversity such as the Amazon, Congo and Mekong (Winemiller *et al.*, 2016). In the Lower Mekong Basin (LMB), over 780 fish species, belonging to 91 families, have been

described (Valbo-Jorgensen *et al.*, 2009). LMB has received international attention due to intense dam development in the region. There are 6 large dams on the upper Mekong and at least 11 dams are scheduled to be installed on the middle and lower reaches, including 41 dams in the tributaries, which will be completed before 2030 (Dugan *et al.*, 2010; Winemiller *et al.*, 2016).

Less attention has been paid to the effects of damming the Mekong's tributaries as compared to dams on the mainstream (*e.g.* Baran and Myschowoda, 2009; Dugan *et al.*, 2010; Ferguson *et al.*, 2011; Li *et al.*, 2013). It is not an exaggeration to say that the integrity of LMB fish diversity is from the tributaries, which are also acknowledged to be the main driving force behind fish production in the basin (Baran and Myschowoda, 2009; Valbo-Jorgensen *et al.*, 2009). These tributaries are characterised as lowland rivers with extensive large floodplains (Poulsen *et al.*, 2002). These floodplains function as habitat for larvae and age 0+ fishes, by providing sanctuary from unfavourable harsh conditions of the river, shelter from predators and abundant food sources (Baran, 2006; Hurtle, 2009; Valbo-Jorgensen *et al.*, 2009).

Although larval and juvenile fish are more sensitive to habitat changes than adults, they have been paid less attention in the LMB. Success of their survival is directly dependent upon connectivity of the main channel and its backwaters as well as period of flooding (Hortle, 2009; Valbo-Jorgensen *et al.*, 2009). The consequential changes of habitats and hydrological regimes as well as barrier across the channel by a dam will cause inevitable effects to the abundance, diversity and assemblages of larval fish in LMB. So far, investigations on impacts of damming the Mekong tributaries, as well as the trade-off of floodplain services to fish species have been described on adults (*e.g.* Jutagate *et al.*, 2007; Ziv *et al.*, 2012; Li *et al.*, 2013). No studies have so far been made on the impacts to the larvae, though recruitment is a critical issue for sustaining the river integrity and fishery of the basin. This study, therefore, aims to investigate the differences in species richness, abundance and assemblage structures of fish larvae between the dammed and undammed tributaries of the Mekong. These rivers share similar environments, but differ in levels of hydrological regulation by damming and are the ideal locations for impact study (Ferguson *et al.*, 2011).

Materials and methods

Study area

Larval fish were sampled from three Mekong tributaries in Thailand, namely the Songkhram, Gam and Mun rivers (Fig. 1). They drain from the Khorat Plateau (155,000 km²) in north-eastern Thailand and are situated in the middle Mekong migration system *i.e.*, between Vientiane to the upstream of Khone Falls, which is characterised by large tributaries and local wetlands. Fishes and their larvae tend to migrate between these two habitats and the Mekong mainstream (Poulsen *et al.*, 2002). Songkhram River is the second largest tributary (13,000 km²) in Thailand. Its mean discharge (~300 m³ s⁻¹) constitutes about 2% of that of the Mekong River (Hortle and Suntornratana, 2008). Songkhram River originates at an altitude of 300 m above mean sea level and flows about 430 km eastwards to the Mekong mainstream. It is the only Mekong tributary in Thailand that has no dams along the course of its mainstream.

Gam River is the third largest (3,440 km²) Mekong tributary in Thailand. It is about 100 km long and 20–40 m wide and has a series of five low-head irrigation dams along the river; also the uppermost section is connected to the large swamp named Nong Harn (Ko-anantakul *et al.*, 1993). The lowermost dam was completed in 2009 and is located about 2 km from the Mekong confluence. To mitigate the impact of this dam series on fish migration, a fish ladder is attached to each dam (Pongsri *et al.*, 2008). Mun River is the largest tributary in Thailand (117,000 km²) and the longest (641 km) in north-eastern Thailand. A run-of-the-

river hydropower dam called the Pak Mun Dam, which is 17 m high and 300 m long at the dam site, is located 6 km upstream from the confluence with the Mekong mainstream. The main mitigation for fish migration between the Mekong mainstream and Mun River, is the opening of all sluice gates annually during the wet season, which occurred from July to October during the study period (Jutagate *et al.*, 2005; Phomikong *et al.*, 2015).

Sampling protocol

Larval fish were sampled every two months in the three rivers between August 2009 and June 2010, generating a data set from a total of 18 surveys, which covered the annual hydrological cycle in the LMB (MRC, 2005). In each river, the survey was conducted at four to five sites, located in lower reaches at roughly 20 to 30 km intervals (Fig. 1). The lowermost site of Songkhram River was about 5 km from the Mekong confluence whereas the first sampling site of the Mun River was about 2 km upstream of the dam. The five sampling sites in the Gam River were located 2 km above each of the five irrigation dams. Larvae were collected using fine seine nets, for approximately 30 min per site and operated during daytime as suggested by Hortle (2004), from 06:00 hrs until noon.

The seine nets used in the study were designed specifically for larvae. The net consisted of two wing ends, each measuring 20 m long and 4 m high, with 1 mm stretched mesh. It was towed along a transect from midstream to the flooded river bank, covering an area of 100 m². The abundance of captured larvae was expressed as number per 100 m². All samples were preserved in 95% ethanol *in situ* for later detailed examination to (a) identify upto species level wherever possible, in the laboratory following Termvidchakorn and Hortle (2013) and (b) migratory guild levels, *i.e.* black, white and grey fishes. Black fishes are resident and typically found in floodplain habitats, white fishes are long-distance migrants between rivers and floodplains and grey fishes are intermediate in their migration habit and move locally between a floodplain and a dry-season refuge (Hortle, 2009; Valbo-Jorgensen *et al.*, 2009).

Data analyses

Differences in cumulative species richness across sampling sites, month and river were tested by Friedman's test, the non-parametric repeated measured ANOVA. Species richness and (log (x+1)) abundance for the sampling sites were compared with two-way ANOVA with rivers and months as factors. The Bonferroni post-hoc test was applied when the Friedman's test and ANOVA revealed significant differences.

The multivariate assemblage data of each survey at species and migratory guild levels were analysed by

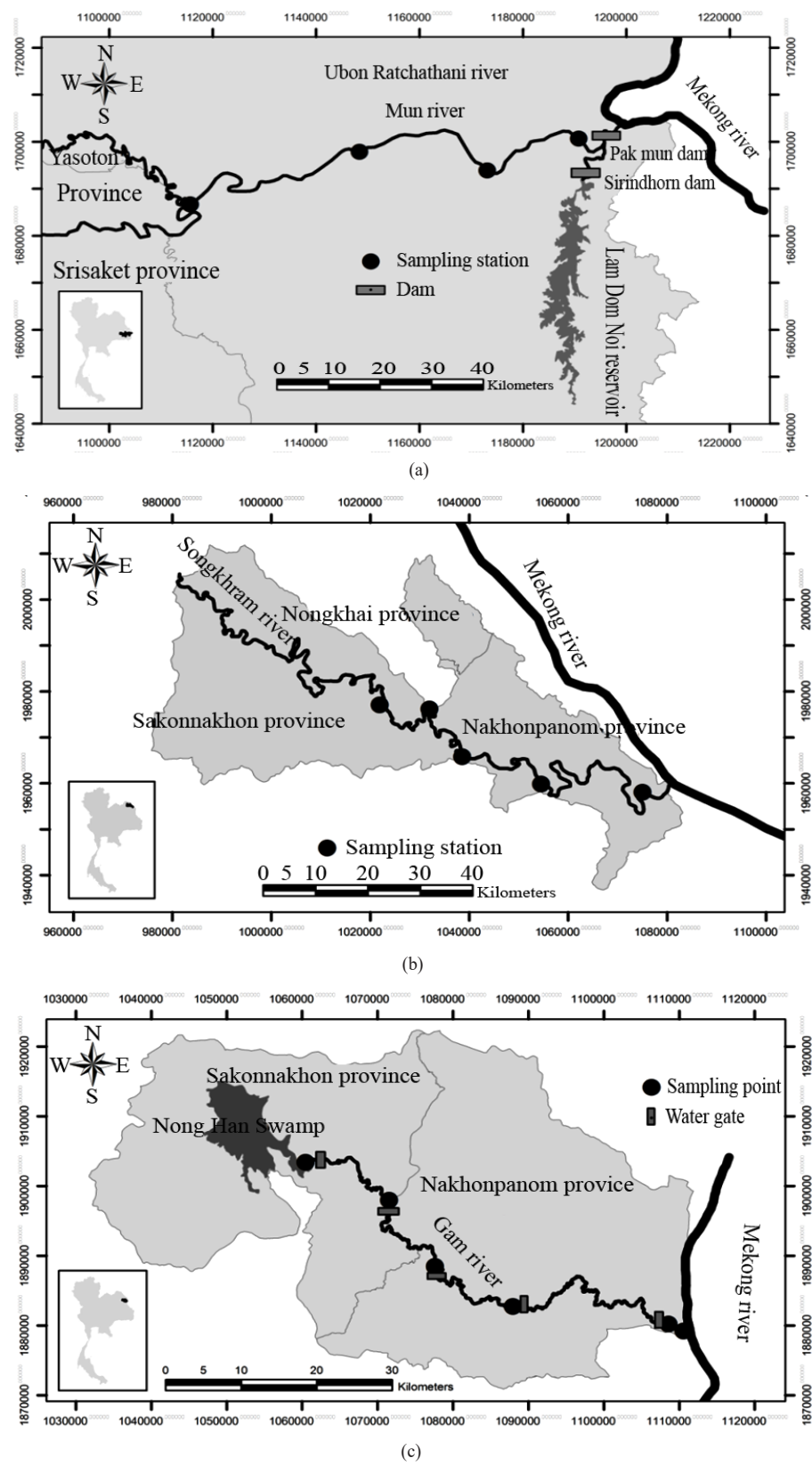


Fig. 1. Map of fish sampling sites in the three Mekong tributaries: Mun, Songkhram and Gam rivers

permutational multivariate ANOVA (PERMANOVA, Anderson, 2001) to assess the spatio-temporal differences of larval fish assemblages during the study, given that the variables failed normality and homogeneity of variance tests. The variables were the abundance of individual species and the abundance in each guild. The unrestricted PERMANOVA was tested based on 999 permutations to detect differences at $\alpha = 0.05$ (Anderson, 2001). Larval assemblage data were fourth root transformed, to prevent highly abundant species from unduly influencing the similarity measure (Cheshire *et al.*, 2012).

The self-organising map (SOM, Kohonen 2001), which is a kind of artificial neural network, was used to visualise and cluster the spatio-temporal assemblage patterns of fish larvae. The typical structure of an SOM consists of two layers: input and output layers, which are connected with the weight vectors. The input layer receives input values from the data matrix, *i.e.*, the abundance of each larval fish from 97 species of 18 survey samples in this study. The output layer consists of output neurons, which are displayed as a hexagonal lattice for better visualisation. The number of output map units for the output layer (*i.e.*, map size) was determined as $5\sqrt{n}$, where n = number of samples. During the analysis, the SOM algorithm calculates the connection intensities between input and output layers using an unsupervised competitive learning procedure (Lek and Guegan, 1999). The samples with similar species composition were grouped to the same or to nearby neurons (Kohonen, 2001), while the connection intensity of the SOM represents approximately the occurrence probability (%OP) of each species in patterned samples (Lek and Guegan, 1999; Kohonen, 2001).

The hierarchical cluster analysis (Ward distance) was employed to detect the cluster boundaries on the SOM map by calculating the Euclidean distance between the weight vectors of each SOM unit (Lek and Guegan, 1999). The SOM was analysed using MATLAB and the software package “somtoolbox” developed by the Laboratory of Computer and Information Science (CIS), Helsinki University of Technology. The analysis of similarity (ANOSIM) was applied to test for significant differences among clusters by using the probability of occurrence. Analysis of PERMANOVA and ANOSIM was done using package “vegan” (Oksanen, 2013), in Program R (R Development Core Team, 2014).

Results

A total of 5,202 fish larvae were collected throughout the study. The larvae belonged to 97 species from 28 families (Table 1). Larvae of cyprinid fishes were most diverse; meanwhile number of species within the remaining families ranged between 1 and 8. The two larval species *Clupeichthys*

aesarnensis and *Rasbora borapetensis* were far more abundant than any others. More than 250 individuals of these two species were captured in all three rivers and ranked as first and second most abundant species respectively in the Mun and Gam Rivers. However, in the Songkhram River, *Sundasalanx mekongensis* and *Mystacoleucus ectypus* were more abundant. More than 450 individuals of each species were caught and were ranked first and second in abundance (Table 2).

Species richness and abundance for each river and in each sampling event increased in the wet season and decreased in the dry season, *i.e.*, from February to April. Both parameters were almost always highest in the Songkhram River. Cumulative species richness (CSR) showed marked differences among rivers (Friedman $\chi^2 = 7.91$, $p = 0.02$) and sampling months (Friedman $\chi^2 = 12.38$, $p = 0.03$). Songkhram River had the highest CSR in August 2009 and the lowest CSR was observed in the Gam River in April (Fig. 2).

The results from two-way ANOVA indicated significant differences ($p < 0.05$) among rivers and months for both average species richness per site (ASR, Table 3a) and average abundance (AAB, Table 3b) per site. However, a significant difference due to the interaction between river and month was observed only for ASR ($F = 2.769$, $p < 0.01$; Table 3a). High and low fluctuations in ASR were observed in the Mun and Gam rivers, respectively, meanwhile ASR in the Songkhram River was more related to hydrological cycle, *i.e.*, continuously decreasing from flood (August to October) to dry season and increasing at the onset of the rainy season, *i.e.*, transition-I period, in June. Changes in AAB were of a similar pattern for all three rivers, *i.e.*, peaking in August, dropping until December before starting to increase; however the rivers differed in degree of abundance.

Variations in abundance of the fish larvae in each migratory guild of each tributary are summarised in Fig. 3. In the Songkhram River, the proportion of white fish larvae (abundance) were high almost all year round, even during dry season, implying the temporal variation in the migration patterns of the adult white fishes. The larvae of grey fishes dominated in both Gam and Mun rivers all year round. However, the larvae of white fishes in the Mun contributed substantially in the flood season and then abruptly decreased to minimal in the dry season, when the abundance of black fish larvae became higher. Larvae of black fish contributed in the 2 sampling events in the Gam River, *i.e.*, at the transition-II period, between flood and dry seasons (December 2009) and the onset of rainy season (June 2010).

The larval assemblages significantly varied both in terms of guild and species assemblages by river, month of sampling as well as their combinations (Table 4). The similarities and characteristics of the assemblage patterns,

Table 1. List of species, abbreviation (Abb.), migratory guilds, their presence (✓) and absence (0) and total numbers (No.) of larval fishes, collected from the 3 tributaries of the Mekong River

Scientific name	Abb.	Guild	M	S	G	No.
Family Notopteridae						
<i>Notopterus notopterus</i>	Nono	WF	✓	✓	✓	20
Family Clupeidae						
<i>Clupeichthys aesarnensis</i>	Clae	GF	✓	✓	✓	930
<i>Tenuulosa thibaudeaui</i>	Teth	WF	0	✓	0	2
Family Engraulidae						
<i>Setipinna melanochir</i>	Seme	WF	✓	✓	0	2
Family Cyprinidae						
<i>Amblypharyngodon chulabhornae</i>	Amch	GF	0	✓	0	2
<i>Amblyrhynchichthys micracanthus</i>	Ammi	WF	0	✓	0	5
<i>Amblyrhynchichthys truncatus</i>	Amtr	WF	✓	✓	0	4
<i>Barbichthys laevis</i>	Bala	GF	0	✓	0	2
<i>Barbonymus altus</i>	Baal	GF	✓	✓	✓	99
<i>Barbonymus gonionotus</i>	Bago	WF	✓	✓	0	50
<i>Barbonymus schwanefeldii</i>	Basc	GF	✓	✓	✓	40
<i>Crossocheilus atrilimes</i>	Crat	GF	✓	✓	0	6
<i>Crossocheilus oblongus</i>	Crob	GF	0	✓	0	3
<i>Crossocheilus reticulatus</i>	Crre	GF	✓	✓	0	14
<i>Cyclocheilichthys apogon</i>	Cyap	GF	0	✓	✓	4
<i>Cyclocheilichthys armatus</i>	Cyar	GF	✓	0	0	1
<i>Cyclocheilichthys enoplos</i>	Cyen	WF	✓	✓	0	16
<i>Epalzeorhynchus munense</i>	Epmu	GF	✓	0	0	1
<i>Esomus metallicus</i>	Esme	GF	✓	✓	✓	83
<i>Hampala dispar</i>	Hadi	GF	✓	✓	✓	145
<i>Hampala macrolepidota</i>	Hama	GF	✓	✓	0	3
<i>Henicorhynchus lineatus</i>	Heli	WF	✓	✓	✓	12
<i>Henicorhynchus ornatipinnis</i>	Heor	WF	✓	✓	✓	5
<i>Henicorhynchus siamensis</i>	Hesi	WF	✓	✓	✓	156
<i>Labiobarbus leptocheilus</i>	Lale	WF	✓	✓	✓	3
<i>Labiobarbus siamensis</i>	Lasi	GF	✓	✓	0	1
<i>Mystacoleucus atridorsalis</i>	Myat	WF	✓	✓	✓	35
<i>Mystacoleucus ectypus</i>	Myec	WF	✓	✓	✓	502
<i>Opsarius koratensis</i>	Opko	GF	✓	✓	✓	40
<i>Osteochilus vittatus</i>	Osvi	WF	✓	✓	✓	16
<i>Osteochilus lini</i>	Osli	GF	✓	✓	✓	20
<i>Osteochilus melanopleurs</i>	Osme	WF	0	✓	✓	2
<i>Osteochilus microcephalus</i>	Osmi	GF	✓	✓	0	32
<i>Paralaubuca riveroi</i>	Pari	WF	✓	✓	0	16
<i>Parachela maculicauda</i>	Pama	GF	✓	0	0	17
<i>Parachela oxygastroides</i>	Paos	GF	0	✓	✓	35
<i>Parachela siamensis</i>	Pasi	GF	✓	✓	0	9
<i>Puntioplites proctozystron</i>	Pupr	WF	✓	✓	0	29
<i>Puntius aurotaeniatus</i>	Puau	GF	✓	✓	✓	9
<i>Puntius binotatus</i>	Pubi	GF	✓	✓	0	2
<i>Puntius brevis</i>	Pubr	GF	✓	✓	✓	18
<i>Puntius orphoides</i>	Puor	GF	0	0	✓	3
<i>Puntigrus partipentazona</i>	Pupar	GF	✓	✓	0	6
<i>Raiamas guttatus</i>	Ragu	WF	0	✓	0	75
<i>Rasbora aurotaenia</i>	Raau	BF	0	0	✓	1
<i>Rasbora borapetensis</i>	Rabo	GF	✓	✓	✓	818
<i>Rasbora daniconius</i>	Rada	GF	✓	✓	✓	33
<i>Rasbora dusonensis</i>	Radu	GF	✓	✓	✓	351
<i>Rasbora rubrodorsalis</i>	Raru	GF	✓	✓	✓	17

(contd.....)

Scientific name	Abb.	Guild	M	S	G	No.
<i>Rasbora trilineata</i>	Ratr	GF	0	✓	0	5
<i>Rasbosa spilocerca</i>	Rasp	GF	✓	✓	✓	123
<i>Scaphognathops bandanensis</i>	Scba	WF	0	✓	0	8
<i>Sikukia gudgeri</i>	Sigu	WF	0	✓	0	3
<i>Thynnichthys thynnoides</i>	Tyth	WF	0	✓	0	2
Family Cobitidae						
<i>Acantopopsis</i> sp.	Acsp	GF	✓	✓	✓	43
<i>Acantopopsis choirorhynchus</i>	Acch	GF	0	✓	0	5
<i>Acantopopsis dialuzona</i>	Acdi	WF	0	✓	0	2
<i>Yasuhikotakia lecontei</i>	Yale	WF	0	✓	0	8
<i>Yasuhikotakia modesta</i>	Yamo	WF	✓	✓	0	3
<i>Yasuhikotakia morleti</i>	Yamor	GF	✓	✓	0	2
<i>Lepidocephalichthys hasselti</i>	Laha	BF	0	✓	0	2
<i>Pangio anguillaris</i>	Paan	WF	0	✓	0	2
Family Bagridae						
<i>Bagrichthys macropterus</i>	Bama	GF	0	✓	0	2
<i>Mystus atrifasciatus</i>	Myatr	BF	✓	✓	0	10
Family Siluridae						
<i>Ompok siluroides</i>	Omsi	BF	0	0	✓	1
Family Pangasiidae						
<i>Pangasius macronema</i>	pama	WF	0	✓	0	2
Family Belonidae						
<i>Xenentodon cancila</i>	Xeca	GF	✓	✓	✓	29
Family Hemiramphidae						
<i>Dermogenys siamensis</i>	Desi	GF	✓	✓	✓	26
Family Mastacembelidae						
<i>Macrogathus semiocellatus</i>	Mase	WF	✓	✓	0	17
<i>Macrogathus siamensis</i>	Masi	BF	✓	0	0	2
<i>Mastacembelus favus</i>	Mafa	BF	✓	0	0	1
Family Toxotidae						
<i>Toxotes chatareus</i>	Toch	GF	✓	0	✓	9
Family Nandidae						
<i>Pristolepis fasciata</i>	Prfa	BF	✓	✓	✓	21
<i>Nandus nandus</i>	Nana	BF	0	0	✓	1
Family Cichlidae						
<i>Oreochromis niloticus</i>	Orni	GF	0	✓	0	3
Family Eleotridae						
<i>Oxyeleotris marmorata</i>	Oxma	BF	✓	✓	✓	5
Family Gobiidae						
<i>Gobiopsis chuno</i>	Goch	BF	✓	✓	✓	37
<i>Rhinogobius</i> sp.	Rhsp	BF	✓	✓	0	25
Family Anabantidae						
<i>Anabas testudineus</i>	Ante	BF	0	✓	✓	4
Family Belontiidae						
<i>Trichogaster trichopterus</i>	Trtr	BF	0	✓	✓	6
<i>Trichopsis pumila</i>	Trpu	BF	✓	✓	✓	39
<i>Trichopsis vittata</i>	Trvi	BF	✓	✓	✓	19
Family Channidae						
<i>Channa striata</i>	Chst	BF	✓	✓	0	44
Family Soleidae						
<i>Brachirus harmandi</i>	Brha	GF	✓	0	0	1
Family Chaudhuriidae						
<i>Chaudhuria caudata</i>	Chca	BF	0	✓	0	1
Family Balitoridae						
<i>Homalopteroides smithi</i>	Hosm	BF	✓	✓	0	1
<i>Nemacheilus pallidus</i>	Nepa	WF	0	✓	0	1

(contd.....)

Scientific name	Abb.	Guild	M	S	G	No.
<i>Nemacheilus platiceps</i>	Nepl	WF	0	✓	0	3
Family Adrianichthyidae						
<i>Oryzias minutillus</i>	Ormi	BF	✓	✓	✓	3
Family Sundasalangidae						
<i>Sundasalanx mekongensis</i>	Sume	WF	✓	✓	✓	751
Family Tetraodontidae						
<i>Tetraodon cambodgiensis</i>	Teca	GF	✓	✓	✓	4
<i>Tetraodon cochinchinensis</i>	Teco	GF	✓	0	0	1
<i>Tetraodon suvatti</i>	Tesu	GF	0	✓	✓	1
<i>Tetraodon turgidus</i>	Tetu	GF	✓	0	0	10
Family Akysidae						
<i>Akysis varius</i>	Akva	GF	0	✓	0	1
Family Osphronemidae						
<i>Betta smaragdina</i>	Besm	BF	0	0	✓	2
Family Ambassidae						
<i>Parambassis siamensis</i>	Pasia	GF	✓	✓	✓	216

Note: M = the Mun River, S = the Songkhram River and G = the Gam River

Table 2. Ten top most abundant species collected from each river

Mun River		Songkhram River		Gam River	
Species	No.	Species	No.	Species	No.
<i>C. aesarnensis</i>	325	<i>S. mekongensis</i>	700	<i>C. aesarnensis</i>	299
<i>R. borapetensis</i>	261	<i>M. ectypus</i>	459	<i>R. borapetensis</i>	268
<i>R. dusionensis</i>	172	<i>C. aesarnensis</i>	306	<i>P. siamensis</i>	121
<i>B. altus</i>	66	<i>R. borapetensis</i>	288	<i>R. spilocerca</i>	105
<i>S. mekongensis</i>	51	<i>R. dusionensis</i>	168	<i>T. pumila</i>	33
<i>P. siamensis</i>	44	<i>H. siamensis</i>	140	<i>H. dispar</i>	26
<i>P. riveroi</i>	38	<i>H. dispar</i>	96	<i>P. oxygastroides</i>	18
<i>M. ectypus</i>	34	<i>R. guttatus</i>	75	<i>R. dusionensis</i>	10
<i>O. microcephalus</i>	30	<i>E. metallicus</i>	67	<i>M. atridorsalis</i>	10
<i>P. proctoysron</i>	28	<i>P. siamensis</i>	52	<i>M. ectypus</i>	9

See full scientific names in Table 1

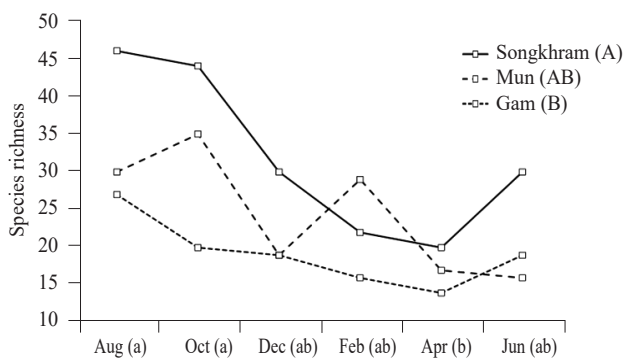


Fig. 2. Fluctuations in species richness of larval fishes among the rivers and months. Same letter indicates that the values are not significantly different at $\alpha = 0.05$. Capital and small letters are for rivers and months, respectively

of the three tributaries, were graphically elucidated by mean of SOM (Fig. 4), using 20 nodes of output layer, which was divided into five main clusters, *i.e.*, numbered I to V. Each

cluster was significantly different from the others (ANOSIM test, $p = 0.014$). The samples from the Gam River formed a single cluster (*i.e.*, cluster III). The larval assemblage of the Mun River during the flooded period (October) was similar to the assemblages of the Songkhram River in August and December (*i.e.*, cluster I), meanwhile the assemblages of the remaining months of sampling in the Mun River were grouped together (cluster V). Samples from the Songkhram River in the dry to the onset of wet seasons (February to June) showed resemblance in larval assemblages (cluster II), whereas the sample in the flood period (cluster IV) showed a unique pattern of larval assemblage.

The characteristic of each fish larval assemblage pattern was explained by the probability of occurrence (%OP, Table 5) of each guild as well as the dominant species in each cluster, which was arbitrarily set at the average %OP of 40%. All clusters, except cluster IV, showed mixing of the three guilds among the 30 highest

Table 3a. Average species richness (ASR $\pm$ SD) of larval fishes during the study

River	Month						Average
	Aug.	Oct.	Dec.	Feb.	Apr.	Jun.	
Mun	13 $\pm$ 5bcde	19 $\pm$ 3ab	7 $\pm$ 7ef	14 $\pm$ 5bcd	6 $\pm$ 2ef	6 $\pm$ 2ef	11 $\pm$ 6AB
Songkram	21 $\pm$ 5a	15 $\pm$ 11abc	10 $\pm$ 4cdef	8 $\pm$ 2cdef	5 $\pm$ 1f	11 $\pm$ 2cdef	12 $\pm$ 7A
Gam	11 $\pm$ 6cdef	8 $\pm$ 3def	9 $\pm$ 2cdef	6 $\pm$ 1ef	6 $\pm$ 2f	9 $\pm$ 2cdef	8 $\pm$ 3B
Average	15 $\pm$ 7A	14 $\pm$ 8A	9 $\pm$ 5B	9 $\pm$ 4B	5 $\pm$ 2B	9 $\pm$ 3B	10 $\pm$ 6

Same capital letter shows the values that are not significantly different at $\alpha = 0.05$, for rivers (last column) and months (last row)

Same small letter shows the values that are not significantly different at $\alpha = 0.05$, for the sample surveys (river x month)

Table 3b. Average abundance (ABB $\pm$ SD, not log-transformed) of larval fishes during the study

River	Month						Average
	Aug.	Oct.	Dec.	Feb.	Apr.	Jun.	
Mun	92 $\pm$ 62	79 $\pm$ 25	25 $\pm$ 26	45 $\pm$ 21	45 $\pm$ 7	89 $\pm$ 66	63 $\pm$ 44AB
Songkram	149 $\pm$ 179	117 $\pm$ 73	54 $\pm$ 14	58 $\pm$ 49	75 $\pm$ 31	97 $\pm$ 59	92 $\pm$ 86A
Gam	66 $\pm$ 57	36 $\pm$ 16	19 $\pm$ 6	36 $\pm$ 27	40 $\pm$ 38	43 $\pm$ 18	40 $\pm$ 31B
Average	106 $\pm$ 118A	80 $\pm$ 56AB	34 $\pm$ 23B	47 $\pm$ 34B	55 $\pm$ 31B	78 $\pm$ 54AB	67 $\pm$ 64

Same capital letter shows the values that are not significantly different at $\alpha = 0.05$, for rivers (last column) and months (last row)

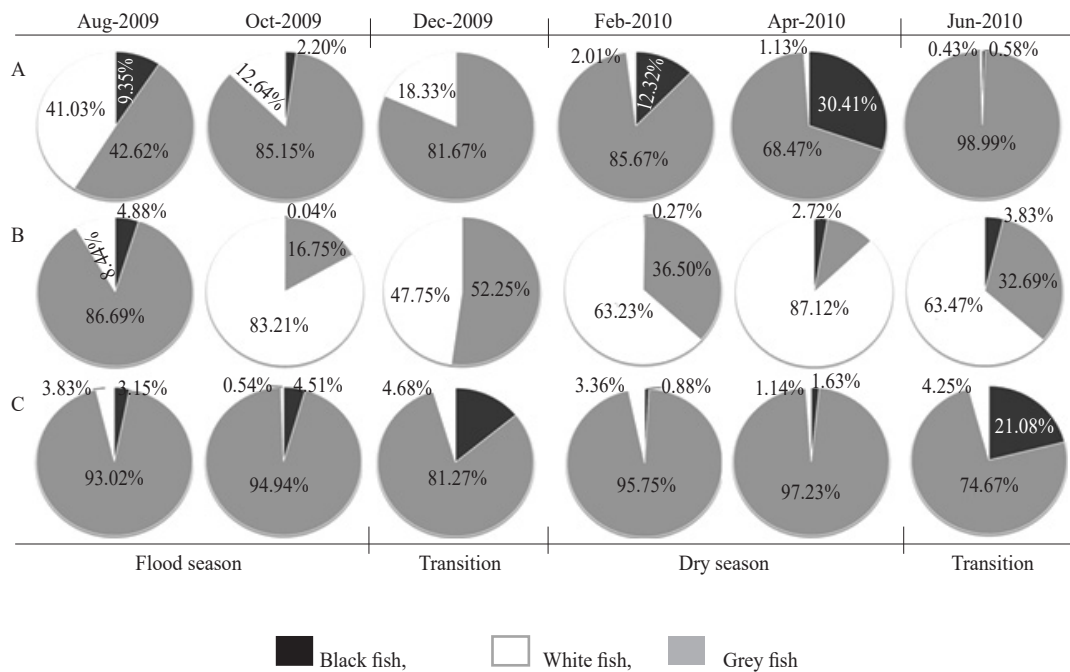


Fig. 3. Proportion in abundance of the fish larvae in each guild during the study period

Table 4. Two-way multivariate PERMANOVA for differences among rivers and months for species-and guild-assemblage composition

Source of variation	Species assemblage			Guild assemblage		
	df	MS	p value	df	MS	p value
River	2	2.186	0.001	2	0.702	0.001
Month	5	0.576	0.001	5	0.177	0.003
River x Month	10	0.367	0.001	10	0.157	0.001
Residual	60	0.213		60	0.062	

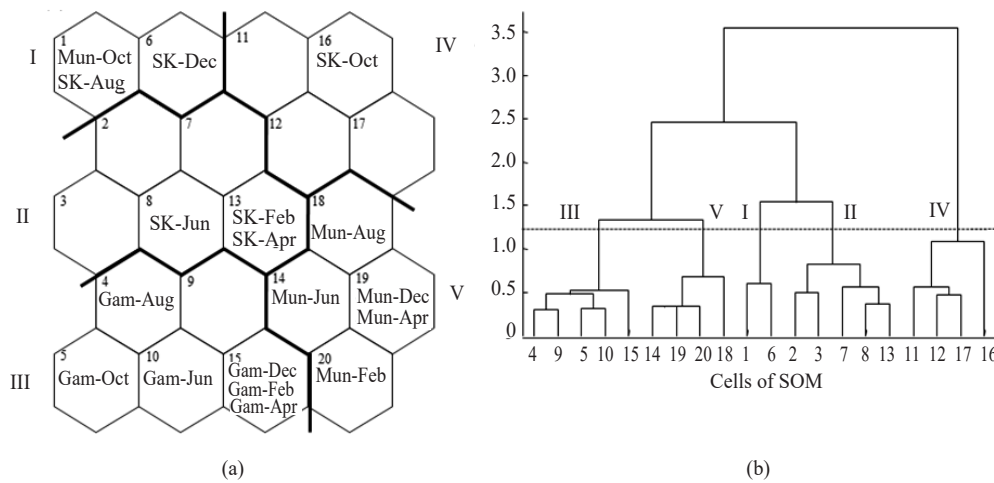


Fig. 4. (a) Distribution of survey samples in the self-organising map (SOM) cells. (b) The similarity of neighboring cells have been grouped in clusters (bold line) using hierarchical clustering using the Ward linkage method

Table 5. Probability of occurrence (%OP) (Mean $\pm$ SD) of individual fish larval species in each cluster. Values were obtained from the weight of virtual vectors of the trained SOM

Abb.	Cluster				
	I	II	III	IV	V
Family Notopteridae					
Nono	6.0 $\pm$ 0.8	7.5 $\pm$ 2.0	7.0 $\pm$ 0.9	6.4 $\pm$ 2.9	16.5 $\pm$ 3.7
Family Clupeidae					
Clae	69.7 $\pm$ 4.9	68.2 $\pm$ 4.9	61.9 $\pm$ 6.6	61.4 $\pm$ 2.8	47.1 $\pm$ 6.0
Teth	7.4 $\pm$ 5.3	3.1 $\pm$ 4.3	< 1	44.5 $\pm$ 15.9	4.0 $\pm$ 5.0
Family Engraulidae					
Seme	8.0 $\pm$ 5.5	3.7 $\pm$ 4.7	< 1	46.5 $\pm$ 15.8	5.7 $\pm$ 5.9
Family Cyprinidae					
Amch	39.4 $\pm$ 4.1	13.5 $\pm$ 9.7	< 1	7.8 $\pm$ 7.9	< 1
Ammi	26.4 $\pm$ 9.4	9.9 $\pm$ 7.4	< 1	42.5 $\pm$ 12.6	3.5 $\pm$ 4.6
Amtr	10.1 $\pm$ 6.2	5.9 $\pm$ 6.4	< 1	54.1 $\pm$ 15.6	12.1 $\pm$ 9.5
Bala	20.8 $\pm$ 5.4	7.6 $\pm$ 5.3	< 1	8.6 $\pm$ 6.0	< 1
Baal	63.6 $\pm$ 12.6	28.8 $\pm$ 12.3	8.4 $\pm$ 3.0	29.7 $\pm$ 4.0	16.7 $\pm$ 6.2
Bago	54.9 $\pm$ 5.8	40.7 $\pm$ 6.2	13.9 $\pm$ 5.7	45.4 $\pm$ 1.3	26.0 $\pm$ 9.7
Basc	46.0 $\pm$ 16.7	14.8 $\pm$ 12.5	3.4 $\pm$ 3.9	2.3 $\pm$ 5.7	< 1
Crat	62.9 $\pm$ 6.7	22.2 $\pm$ 14.4	3.7 $\pm$ 1.7	29.4 $\pm$ 10.2	6.0 $\pm$ 1.4
Crob	7.4 $\pm$ 5.3	3.1 $\pm$ 4.3	< 1	44.5 $\pm$ 15.9	4.0 $\pm$ 5.0
Crre	10.9 $\pm$ 3.8	6.6 $\pm$ 2.1	6.9 $\pm$ 3.2	4.0 $\pm$ 2.9	21.5 $\pm$ 6.4
Cyap	10.3 $\pm$ 3.1	9.7 $\pm$ 2.2	28.6 $\pm$ 7.8	3.4 $\pm$ 1.3	18.5 $\pm$ 8.7
Cyar	26.7 $\pm$ 9.5	8.3 $\pm$ 7.1	1.4 $\pm$ 1.6	1.6 $\pm$ 2.9	< 1
Cyen	18.8 $\pm$ 6.6	8.8 $\pm$ 5.5	< 1	35.4 $\pm$ 6.3	10.3 $\pm$ 7.3
Epmu	0.7 $\pm$ 0.1	2.2 $\pm$ 1.5	2.8 $\pm$ 1.2	3.0 $\pm$ 2.4	13.3 $\pm$ 4.0
Esme	32.7 $\pm$ 10.7	16.6 $\pm$ 8.4	7.8 $\pm$ 3.3	3.9 $\pm$ 4.0	5.6 $\pm$ 1.1
Hadi	32.6 $\pm$ 1.8	51.7 $\pm$ 5.9	45.0 $\pm$ 7.7	20.2 $\pm$ 8.3	29.6 $\pm$ 3.3
Hama	23.0 $\pm$ 8.4	8.7 $\pm$ 5.9	4.0 $\pm$ 2.1	2.1 $\pm$ 2.6	5.8 $\pm$ 1.6
Heli	40.5 $\pm$ 10.1	15.5 $\pm$ 8.6	6.3 $\pm$ 2.9	27.1 $\pm$ 7.3	2.8 $\pm$ 3.4
Heor	20.0 $\pm$ 3.9	9.8 $\pm$ 3.0	13.1 $\pm$ 3.4	19.2 $\pm$ 4.9	10.3 $\pm$ 2.9
Hesi	49.5 $\pm$ 5.6	41.4 $\pm$ 11.5	14.9 $\pm$ 8.2	15.9 $\pm$ 8.2	6.4 $\pm$ 3.8
Lale	2.9 $\pm$ 2.4	6.4 $\pm$ 4.0	16.5 $\pm$ 8.1	18.2 $\pm$ 4.4	20.9 $\pm$ 3.8
Lasi	7.6 $\pm$ 5.3	3.8 $\pm$ 4.4	< 1	45.5 $\pm$ 15.6	8.3 $\pm$ 5.2
Myat	37.6 $\pm$ 3.2	23.5 $\pm$ 4.2	18.5 $\pm$ 3.3	47.1 $\pm$ 12.5	11.9 $\pm$ 4.0
Myec	44.2 $\pm$ 7.4	50.5 $\pm$ 5.4	23.3 $\pm$ 8.3	58.3 $\pm$ 3.6	24.1 $\pm$ 11.3

(Contd.....)

Abb.	Cluster				
	I	II	III	IV	V
Opko	13.9 ± 0.5	17.3 ± 2.6	9.9 ± 2.6	18.3 ± 1.6	9.1 ± 4.2
Osvi	40.7 ± 12.7	16.7 ± 10.1	7.6 ± 2.7	4.9 ± 4.5	7.3 ± 1.8
Osli	50.2 ± 14.8	26.1 ± 12.0	13.5 ± 3.5	7.2 ± 6.1	11.2 ± 2.2
Osme	7.4 ± 5.4	3.5 ± 4.3	< 1	44.7 ± 15.9	5.5 ± 4.4
Osmi	3.6 ± 1.6	5.5 ± 2.2	6.1 ± 2.9	11.5 ± 2.2	20.4 ± 5.3
Pari	23.5 ± 6.1	12.0 ± 3.2	4.5 ± 1.4	12.0 ± 2.6	8.8 ± 5.0
Pama	7.4 ± 5.3	3.1 ± 4.3	< 1	44.5 ± 15.9	4.0 ± 5.0
Paos	24.3 ± 7.3	17.0 ± 6.7	22.9 ± 7.4	3.3 ± 3.5	2.6 ± 2.6
Pasi	7.5 ± 5.3	3.4 ± 4.2	< 1	44.7 ± 15.8	6.4 ± 4.2
Pupr	4.0 ± 1.8	3.4 ± 3.2	< 1	5.3 ± 4.6	5.5 ± 2.1
Puau	17.6 ± 5.0	14.0 ± 2.0	22.9 ± 8.3	6.6 ± 2.7	25.8 ± 9.4
Pubi	28.4 ± 8.3	13.8 ± 4.9	4.0 ± 1.8	6.9 ± 3.3	3.5 ± 2.6
Pubr	1.8 ± 0.2	5.8 ± 2.8	9.8 ± 3.3	5.4 ± 3.5	24.2 ± 6.1
Puor	< 1	2.5 ± 1.9	9.4 ± 7.1	< 1	1.7 ± 0.5
Pupa	34.1 ± 7.7	15.0 ± 8.3	5.2 ± 1.7	17.1 ± 4.0	8.8 ± 5.4
Ragu	8.0 ± 4.2	17.9 ± 5.4	6.7 ± 4.4	23.0 ± 2.2	10.8 ± 5.5
Raau	< 1	2.5 ± 1.9	9.4 ± 7.1	< 1	1.7 ± 0.5
Rabo	65.2 ± 8.9	51.7 ± 5.8	63.3 ± 4.7	31.4 ± 7.4	56.2 ± 6.6
Rada	26.4 ± 2.3	18.2 ± 2.9	12.9 ± 2.4	26.6 ± 2.3	24.7 ± 2.7
Radu	78.4 ± 6.9	40.9 ± 12.0	19.9 ± 3.0	56.8 ± 5.8	37.6 ± 5.1
Raru	35.4 ± 0.5	15.2 ± 6.6	14.5 ± 5.4	11.0 ± 6.9	12.1 ± 4.9
Ratr	35.2 ± 3.3	12.5 ± 8.3	< 1	27.0 ± 8.8	< 1
Rasp	6.5 ± 2.7	16.9 ± 4.6	31.4 ± 5.2	22.0 ± 4.0	19.1 ± 1.0
Scba	25.2 ± 8.5	9.4 ± 6.8	< 1	35.0 ± 10.3	2.8 ± 3.8
Sigu	11.0 ± 6.3	12.5 ± 3.6	2.0 ± 3.7	46.9 ± 14.9	5.5 ± 5.4
Tyth	7.4 ± 5.3	3.1 ± 4.3	< 1	44.5 ± 15.9	4.0 ± 5.0
Family Cobitidae					
Acsp	59.9 ± 1.9	40.4 ± 7.7	15.7 ± 6.5	58.6 ± 4.5	21.9 ± 12.6
Acch	27.3 ± 5.4	17.1 ± 5.3	3.8 ± 2.4	14.0 ± 6.6	4.6 ± 2.9
Acdi	12.1 ± 3.6	4.6 ± 4.1	< 1	44.7 ± 15.7	3.5 ± 5.0
Yale	28.0 ± 7.5	10.3 ± 7.2	< 1	35.1 ± 10.4	2.6 ± 3.8
Yamo	18.6 ± 2.2	9.2 ± 4.8	< 1	47.7 ± 14.7	5.8 ± 6.0
Yamor	3.1 ± 2.3	3.3 ± 1.9	3.7 ± 2.4	20.1 ± 6.0	15.3 ± 4.1
Laha	22.7 ± 8.4	7.4 ± 6.3	1.5 ± 2.1	< 1	< 1
Paan	9.6 ± 2.6	25.2 ± 5.6	10.1 ± 6.4	6.3 ± 3.6	3.9 ± 1.9
Family Bagridae					
Bama	7.4 ± 5.3	3.1 ± 4.3	< 1	44.5 ± 15.9	4.0 ± 5.0
Myatr	3.4 ± 1.4	3.1 ± 3.0	< 1	13.9 ± 3.6	8.5 ± 5.0
Family Siluridae					
Omsi	2.3 ± 0.1	10.9 ± 4.5	15.2 ± 4.8	2.4 ± 1.3	5.3 ± 1.5
Family Pangasiidae					
Pamac	1.1 ± 0.2	3.4 ± 2.0	6.1 ± 3.2	3.4 ± 3.0	21.4 ± 6.5
Family Belonidae					
Xeca	44.0 ± 2.2	37.7 ± 5.4	31.8 ± 5.0	23.9 ± 6.2	17.2 ± 3.5
Family Hemiramphidae					
Desi	4.8 ± 1.3	6.1 ± 1.4	9.2 ± 2.6	3.5 ± 2.2	18.7 ± 5.9
Family Mastacembelidae					
Mase	8.2 ± 0.3	5.3 ± 2.8	< 1	17.1 ± 3.3	9.0 ± 5.5
Masi	2.7 ± 0.9	2.8 ± 2.7	< 1	9.6 ± 3.6	8.1 ± 4.6
Mafa	29.4 ± 8.6	11.2 ± 5.6	1.8 ± 0.8	11.2 ± 2.3	7.3 ± 4.6
Family Toxotidae					
Toch	1.7 ± 0.6	5.8 ± 3.4	7.2 ± 2.0	7.3 ± 3.8	18.4 ± 2.7
Family Nandidae					
Prfa	52.5 ± 14.2	38.0 ± 14.2	22.1 ± 9.8	8.2 ± 7.6	3.9 ± 3.6
Nana	< 1	4.9 ± 2.8	23.0 ± 5.5	2.0 ± 1.1	8.8 ± 3.3

(Contd.....)

Abb.	Cluster				
	I	II	III	IV	V
Family Cichlidae					
Orni	22.7 ± 8.4	7.4 ± 6.3	1.5 ± 2.1	< 1	< 1
Family Eleotridae					
Oxma	4.8 ± 1.9	13.1 ± 3.6	11.5 ± 2.7	10.0 ± 3.0	13.0 ± 1.8
Family Gobiidae					
Goch	6.7 ± 1.6	16.5 ± 2.5	20.7 ± 1.8	11.5 ± 3.8	20.0 ± 2.1
Rhsp	2.6 ± 1.1	4.6 ± 3.3	3.1 ± 1.7	10.9 ± 4.8	16.7 ± 4.7
Family Anabantidae					
Ante	11.2 ± 2.1	10.1 ± 0.8	5.4 ± 1.8	6.1 ± 2.2	4.8 ± 2.4
Family Belontiidae					
Trtr	22.7 ± 8.4	7.6 ± 6.2	2.5 ± 1.7	< 1	< 1
Trpu	20.9 ± 6.0	23.9 ± 7.1	53.4 ± 8.6	7.3 ± 2.9	26.9 ± 9.1
Trvi	10.8 ± 3.7	5.3 ± 2.3	4.3 ± 1.7	2.7 ± 1.3	10.2 ± 2.7
Family Channidae					
Chst	14.2 ± 1.3	25.8 ± 2.2	11.3 ± 4.9	13.5 ± 4.2	15.9 ± 4.1
Family Soleidae					
Brha	2.7 ± 0.9	2.8 ± 2.7	< 1	9.6 ± 3.6	8.1 ± 4.6
Family Chaudhuriidae					
Chca	2.7 ± 1.7	8.4 ± 4.5	3.6 ± 2.4	7.5 ± 2.9	6.9 ± 3.2
Family Balitoridae					
Hosm	3.1 ± 1.5	9.8 ± 4.6	7.3 ± 3.0	8.0 ± 3.4	16.1 ± 1.7
Nepa	20.8 ± 5.4	7.6 ± 5.3	< 1	8.6 ± 6.0	< 1
Nepl	22.1 ± 1.3	12.8 ± 4.4	1.3 ± 2.6	46.4 ± 14.8	3.5 ± 5.3
Family Adrianichthyidae					
Ormi	27.1 ± 8.0	18.3 ± 4.8	11.6 ± 2.5	5.6 ± 3.7	10.6 ± 2.7
Family Sundasalangidae					
Sume	42.3 ± 9.7	36.3 ± 8.5	9.0 ± 7.3	70.1 ± 10.5	19.3 ± 12.6
Family Tetraodontidae					
Teca	41.9 ± 13.0	25.4 ± 8.4	25.4 ± 9.8	9.2 ± 4.3	7.9 ± 3.1
Teco	< 1	1.4 ± 0.6	3.7 ± 2.3	< 1	9.2 ± 4.8
Tesu	23.1 ± 5.4	18.5 ± 3.3	15.3 ± 5.0	11.0 ± 6.0	5.7 ± 1.7
Tetu	2.7 ± 0.9	2.8 ± 2.7	< 1	9.6 ± 3.6	8.1 ± 4.6
Family Akysidae					
Akva	20.8 ± 5.4	7.6 ± 5.3	< 1	8.6 ± 6.0	< 1
Family Osphronemidae					
Besm	2.3 ± 0.1	10.9 ± 4.5	15.2 ± 4.8	2.4 ± 1.3	5.3 ± 1.5
Family Ambassidae					
Pasia	56.1 ± 4.9	48.5 ± 4.9	60.4 ± 8.3	56.9 ± 6.1	37.7 ± 4.2

See full scientific names in Table 1

%OP species, though dominated by grey fish larvae. Non-significant differences in %OP among guilds were found in clusters I and II. Nineteen (19) larval species in cluster I had an average %OP of more than 40% (Fig. 5a).

There were mostly grey fish (11 species) such as *Rasbora dasonensis*, *Clupeichthys aesarnensis*, *Rasbora borapetensis* and *Crossocheilus atrilimes*. The other dominant larval species included six white fishes (e.g., *Barbonymus gonionotus*, *Henicorhynchus siamensis* and *Mystacoleucus ectypus*) and two black fishes (*Pristolepis fasciata* and *Amblypharyngodon chulabhornae*). Cluster II (Fig. 5b) was dominated by six grey fishes (e.g., *C. aesarnensis*, *Hampala dispar*, *R. borapetensis*) and three white fishes (*M. ectypus*, *H. siamensis* and *B. gonionotus*).

The average %OP of white fishes was significantly lower than the two remaining guilds in cluster III (Fig. 5c). Only five larval species were dominant in this cluster. Four of these were grey fishes (i.e., *R. borapetensis*, *C. aesarnensis*, *Parambassis siamensis* and *H. dispar*) and a black fish, *Trichopsis pumila*. It is worth noting that there were nine black fishes among the 30 highest %OP species in this cluster, which was more than in the other clusters. Cluster IV had a unique characteristic, with no black fishes included among the 30 highest %OP species (Fig. 5d). The 15 dominant white fishes also included species with relatively low %OP (<1%) in other clusters, for example *Sikukia gudgeri*, *Setipinna melanochir*, *Pangasius macronema* and *Amblyrhynchichthys micracanthus*. The larvae of other

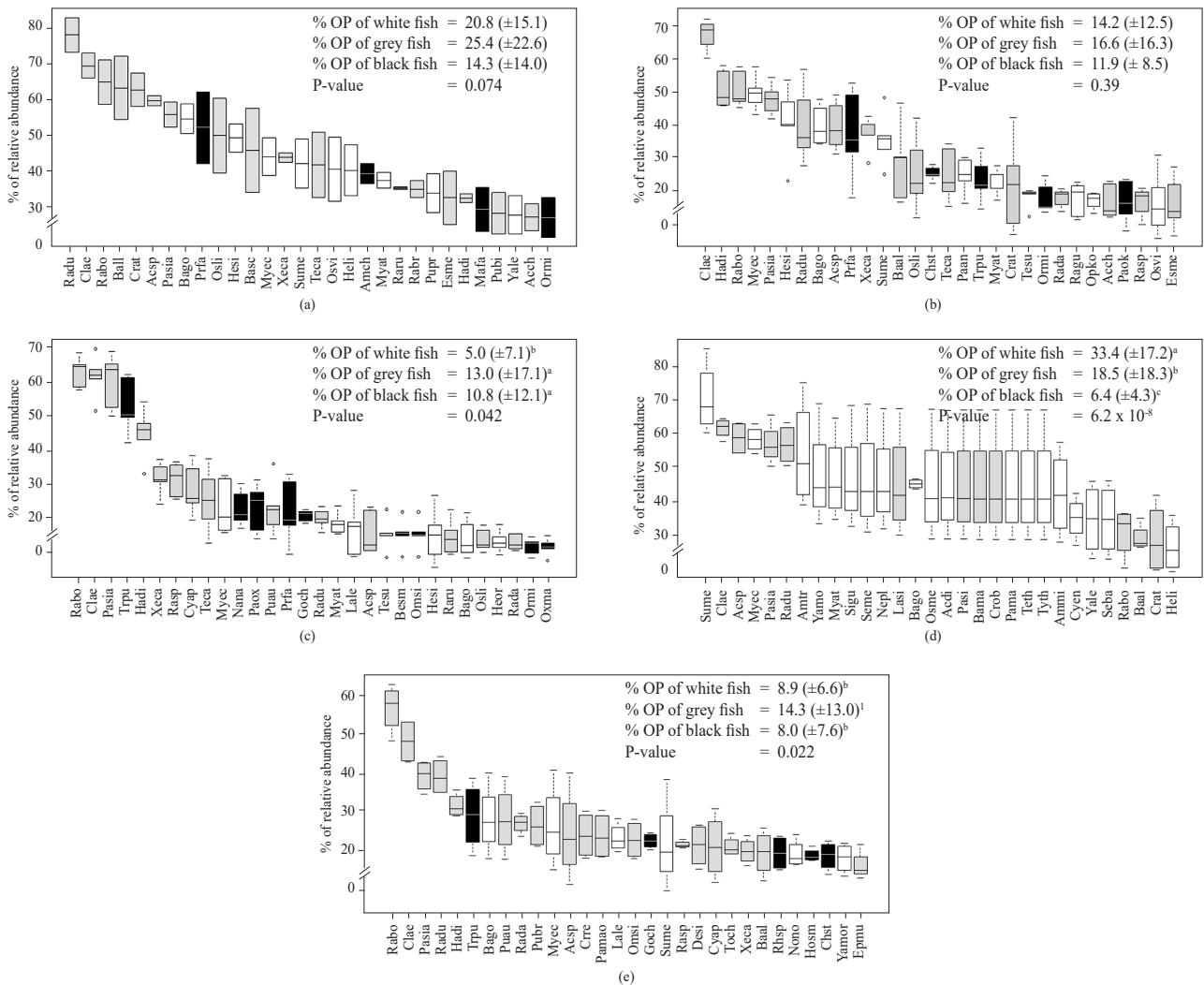


Fig. 5. Box plots showing occurrence probability (%OP) of the first 30 highest %OP species (see full scientific names in Table I) in each of five clusters

Larval assemblage patterns in the (a) Mun River (October) and the Songkhram River (August and December); (b) Songkhram River (February, April and June); (c) Gam River (all sampling months); (d) Mun River (February, April, June and December); (e) Songkhram River (October)

Note (1) Values were obtained from the connection intensity of the SOM; (2) Colour of the box represents the migratory guild, i.e. black, white or grey.

important white fishes associated in this cluster included *Cyclocheilichthys enoplos* (35.4%OP), *Scaphognathops bandanensis* (35.0 %OP) and *Henicorhynchus lobatus* (27.1%OP), which were also less than 1%OP in other clusters. The %OP for grey fish larvae was significantly higher than the other two guilds in cluster V (Fig. 5e) but only two species (i.e., *R. borapetensis* and *C. aesarnensis*) were dominant.

Discussion

Most of the dam projects always overlook the effect on biodiversity and fisheries (Winemiller *et al.*, 2016). This study revealed how the diversity, abundance and assemblage patterns of the fish larvae in the three Mekong tributaries in Thailand differ with different set of impacting effects that

results from damming. Information could be further used for trade-off analysis for sustaining the diversity and ecosystem services by fisheries in LMB (Kano *et al.*, 2016; Winemiller *et al.*, 2016).

In LMB, the confluence of each tributary serves as a corridor connecting floodplain for a number of adult fish species and their larvae (Baran *et al.*, 2001; Valbo-Jorgensen *et al.*, 2009). The general pattern of occurrence of the fish larvae is related to the pattern of flooding of the tributary, which is a fairly predictable monotonic flood pulse each year, starting from June or July and lasting until September or October (Hortle 2009; Valbo-Jorgensen *et al.*, 2009). At the onset of flood, the floodplain residents and the migrating adults spawn in the floodplain, which takes place while the water level still increases, ensuring that eggs and

larvae are carried by the water into nursery areas (Campbell, 2009). Later, the fish larvae and juveniles of the non-flood spawners drift along the reverse flow from the Mekong mainstream into these floodplains (Suntornratana *et al.*, 2002; Thach *et al.*, 2006).

The high number of cumulative species richness of these three tributaries and in particular during the flood season in the Songkhram River (46 species), implies the important function of these three tributaries as the habitat for larvae of Mekong River fish. Most of the dominant species were the larvae of small-sized grey fishes, such as *C. aesarnensis*, *R. borapetensis*, *R. dusoensis* and *P. siamensis*, which are species known to be well adapted to lentic conditions and spawn throughout the year with plural generation alternations per year (Jutagate *et al.*, 2003; Okutsu *et al.*, 2011; Suvarnaraksha *et al.*, 2011). The schooling of small-sized adult white fishes of cyprinid groups, mostly *Mystacoleucus* spp. and *Rasbora* spp. and also *Sundasalanx mekongensis* are commonly known for their *en masse* migrations during the flood season to the Mekong tributaries, in particular the Songkhram River (Suntornratana *et al.*, 2002).

The comparison of abundance and diversity of fish larvae from the three rivers studied, revealed impact of the interruption of connectivity between the Mekong mainstream to her tributaries. Both of the dammed rivers (Gam and Mun) had lower diversity and abundance of fish larvae than the undammed Songkhram River. The lower number of larval species found in the Gam River could be attributed to the direct blockage of routes of larval drifting and adult migrations (Baran and Myschowoda, 2009; Suzuki *et al.*, 2011) or to the consequence of inadequate food and habitat for larvae and juveniles in the floodplain, which is also caused by river damming (Baran and Myschowoda, 2009; Cheshire *et al.*, 2012; Gogola *et al.*, 2013). Both diversity and abundance of fish larvae were significantly related to season, *i.e.* higher in the wet/flood season and lower in the dry season. This also indicated the relationship between fish larvae and the river hydrology, in which excessive flows at the wrong time of the year, due to the regulation by dam, could wash the drifting larvae past the target floodplains resulting in the loss of most individuals (Campbell, 2009; Hurtle, 2009).

Assemblage patterns were clearly separated according to the degree of regulation and season. The regulated Gam River formed a unique larval fish assemblage pattern. This assemblage was dominated by larvae of the adults that are commonly found in reservoirs (Jutagate *et al.*, 2012; 2016), which implies a lentic environment between each dam in the series. The lowest contribution to %OP of the white fish larvae, compared to any other cluster, would indicate that only few adults of white fishes, such as *Mystacoleucus* spp. and *Henicorhynchus* spp. could ascend

the fish ladders constructed at these dam sites (Pongsri *et al.*, 2008). Except for the assemblage pattern in October, a year-round, uniform pattern of larval assemblage was observed in the Mun River. This should be attributed to the regulation and blockage of the Pak Mun Dam as it also impacts adults (Jutagate *et al.*, 2005; 2007), for which the species composition was relatively similar to reservoir fish community (Jutagate *et al.*, 2016), as was the Gam River. However, due to the contribution of white fish larvae, whose adults benefit from opening all sluice gates during the wet season (Jutagate *et al.*, 2005; 2007), the assemblage of the larvae in October was similar to that of the Songkhram River during the flood season. Kano *et al.* (2016) also demonstrated that the removal of the Pak Mun Dam in Mun River would result in the huge recovery of species richness, in particular for the white fishes.

High %OP of white fish larvae during the flood season in the Songkhram and Mun River and during the late flood season in the Songkhram River indicated that they complied with the flood recruitment model (King *et al.*, 2003), that flooding cued the adults to spawn and the larvae benefited from the floodplain to survive and grow. The larvae of white fishes and many grey fishes were far more abundant in terms of their %OP in the other assemblage patterns. The adults of these fishes are known to migrate into the Songkhram River during the onset of the rainy season for spawning (Poulsen *et al.*, 2002; Suntornratana *et al.*, 2002) and so their larvae could be present soon afterwards, including drift of larvae from the Mekong to the floodplain of the tributaries (Thach *et al.*, 2006; Valbo-Jorgensen *et al.*, 2009). Upstream migration of the adults of most of larvae in this assemblage, such as *Amblyrhynchichthys truncates*, *Sikukia gudgeri*, *Parachela siamensis* and *Pangasius macronema*, are known to be triggered by threshold or changes in discharge, water levels or current (Poulsen *et al.*, 2002; Baran, 2006).

Assemblage pattern during the transition from dry to wet season in the Songkhram River was a mix of all migratory guilds but %OP of all individual species was lower than 20%. Most common were small grey fishes with protracted spawning periods. These small grey fishes as well as the medium sized cyprinids such as *Hampala* spp., *Henicorhynchus* spp., *Barbonymus* spp., are known to start migration from the Mekong into the tributaries during February and March, then mature and spawn as early as the water level starts rising in May (Warren *et al.*, 1998; Suntornratana *et al.*, 2002; Baran, 2006; Boonthai *et al.*, 2016).

The present study clearly showed that concern should be focused also on the larvae in the tributaries. Heterogeneity in fish larvae among the three studied rivers, in terms of presence, abundance and assemblage, were related to life

history and regulation by dams. Conserving the integrity of the floodplain-river system of the Songkhram River is among the most crucial options for sustaining fish diversity and fisheries in the middle migratory system of the LMB, in particular for the white fishes.

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