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

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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 Songkhram River showed the most diversity and abundance of migratory, white fish larvae. Conservation of integrity of the floodplain-river system of Songkhram 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; Hortle, 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 Songkram, 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). Songkram 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). Songkram 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 Songkram 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 up to 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
permuted 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 asarnensis 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              |           |       |   |   |   |     |
| *Notopterus notopterus*          | Nono      | WF    | √ | √ | √ | 20  |
| Family Clupeidae                 |           |       |   |   |   |     |
| *Clupeichthys aescarnensis*      | Clae      | GF    | √ | √ | √ | 930 |
| *Tenualosa thibaudeaui*          | Teth      | WF    | 0 | √ | 0 | 2   |
| Family Engraulidae               |           |       |   |   |   |     |
| *Setipinna melanochir*           | Seme      | WF    | √ | √ | 0 | 2   |
| Family Cyprinidae                |           |       |   |   |   |     |
| *Amblypharyngodon chalabhornae*  | Amch      | GF    | √ | √ | 0 | 2   |
| *Amblyrhynchichthys micracanthis*| Ammi      | WF    | 0 | √ | 0 | 5   |
| *Amblyrhynchichthys truncatus*   | Antr      | WF    | √ | √ | 0 | 4   |
| *Barbichthys laevis*             | Bala      | GF    | 0 | √ | 0 | 2   |
| *Barbonymus altus*               | Baal      | GF    | √ | √ | √ | 99  |
| *Barbonymus gonionotus*          | Bago      | WF    | √ | √ | 0 | 50  |
| *Barbonymus schwanefeldii*       | Base      | GF    | √ | √ | 0 | 40  |
| *Crossocheilus atrilimes*        | Crat      | GF    | √ | √ | 0 | 6   |
| *Crossocheilus oblongus*         | Crob      | GF    | 0 | √ | 0 | 3   |
| *Crossocheilus reticulatus*      | Cre       | GF    | √ | √ | 0 | 14  |
| *Cyclocheilichthys apogon*       | Cyap      | GF    | 0 | √ | 0 | 4   |
| *Cyclocheilichthys armatus*      | Cyar      | GF    | √ | 0 | 0 | 1   |
| *Cyclocheilichthys enoplos*      | Cyan      | WF    | √ | √ | 0 | 16  |
| *Epalzeorhynchos munense*        | Epmu      | GF    | 0 | √ | 0 | 1   |
| *Esomus metallicus*              | Esme      | GF    | √ | √ | √ | 83  |
| *Hampala dispar*                 | Hadi      | GF    | √ | √ | √ | 145 |
| *Hampala macrolepidota*          | Hama      | GF    | √ | √ | 0 | 3   |
| *Henicorhynchus lineatus*        | Heli      | WF    | √ | √ | 0 | 12  |
| *Henicorhynchus ornatipinnis*    | Heor      | WF    | √ | √ | 0 | 5   |
| *Henicorhynchus siamensis*       | Hesi      | WF    | √ | √ | 0 | 156 |
| *Labiobarbus leptocheilus*       | Lale      | WF    | √ | √ | 0 | 3   |
| *Labiobarbus siamensis*          | Lasi      | GF    | √ | √ | 0 | 1   |
| *Mystacoleucus atridorsalis*     | Myat      | WF    | √ | √ | √ | 35  |
| *Mystacoleucus ectypus*          | Myec      | WF    | √ | √ | √ | 502 |
| *Opsarius koratensis*            | Opki      | GF    | √ | √ | 0 | 40  |
| *Osteochilus vittatus*           | Osvi      | WF    | √ | √ | 0 | 16  |
| *Osteochilus linei*              | Osli      | GF    | √ | √ | 0 | 20  |
| *Osteochilus melanopleurs*       | Osme      | WF    | 0 | √ | √ | 2   |
| *Osteochilus microcephalus*      | Osni      | GF    | √ | √ | 0 | 32  |
| *Paralabuca riveroi*             | Pari      | WF    | √ | √ | 0 | 16  |
| *Parachela maculicauda*          | Pana      | GF    | √ | 0 | 0 | 17  |
| *Parachela oxygastroides*        | Paox      | GF    | 0 | √ | √ | 35  |
| *Parachela siamensis*            | Pasi      | GF    | √ | √ | 0 | 9   |
| *Puntioplites proctozystron*     | Pupr      | WF    | √ | √ | 0 | 29  |
| *Puntius aurotemnai*             | Puaa      | GF    | √ | √ | 0 | 9   |
| *Puntius binotatus*              | Pubi      | GF    | √ | √ | 0 | 2   |
| *Puntius brevis*                 | Pubr      | GF    | √ | √ | 0 | 18  |
| *Puntius orphoides*              | Puar      | GF    | 0 | √ | 0 | 3   |
| *Puntigrus partipentazona*       | Pupar     | GF    | √ | √ | 0 | 6   |
| *Raiamas guttatus*               | Ragu      | WF    | 0 | √ | 0 | 75  |
| *Rasbora aurotemnai*             | Raau      | BF    | 0 | √ | 0 | 1   |
| *Rasbora borapetus*              | Rabo      | GF    | √ | √ | 0 | 818 |
| *Rasbora daniconius*             | RaD       | GF    | √ | √ | 0 | 33  |
| *Rasbora dusonensis*             | Radu      | GF    | √ | √ | 0 | 351 |
| *Rasbora rubrodorsalis*          | Raru      | GF    | √ | √ | 0 | 17  |

(contd.......)
| Scientific name                               | Abb.  | Guild | M | S | G | No. |
|----------------------------------------------|-------|-------|---|---|---|-----|
| Rasbora trilineata                           | Ratr  | GF    | ✓ | ✓ | ✓ | 5   |
| Rasbosoma spilocerca                         | Rasп  | GF    | ✓ | ✓ | ✓ | 123 |
| Scaphognathops bandanensis                   | Schу  | WF    | ✓ | ✓ |   | 8   |
| Sikukia gudgeri                              | Sigu  | WF    | ✓ | ✓ |   | 3   |
| Thynnichthys thynnoides                      | Thyh  | WF    | ✓ | ✓ |   | 2   |
| **Family Cobitidae**                         |       |       |   |   |   |     |
| Acantopsis sp.                               | Acsp  | GF    | ✓ | ✓ | ✓ | 43  |
| Acantopsis choirohynchos                     | Acчh  | GF    | ✓ | ✓ |   | 5   |
| Acantopsis diadazona                         | Acдй  | WF    | ✓ | ✓ |   | 2   |
| Yasuhikotakia lecontei                       | Yale  | WF    | ✓ | ✓ |   | 8   |
| Yasuhikotakia modesta                        | Yamo  | WF    | ✓ | ✓ |   | 3   |
| Yasuhikotakia morleti                        | Ymor  | GF    | ✓ | ✓ |   | 2   |
| Lepidocephaliichthys hasselti                | Laha  | BF    | ✓ | ✓ |   | 2   |
| Pangio anguillaris                            | Paan  | WF    | ✓ | ✓ |   | 2   |
| **Family Bagridae**                          |       |       |   |   |   |     |
| Bagrichthys macropterus                      | Bama  | GF    | ✓ | ✓ |   | 2   |
| Mystus atrifasciatus                         | Myat  | BF    | ✓ | ✓ |   | 10  |
| **Family Siluridae**                         |       |       |   |   |   |     |
| Ompok siluroides                             | Omsі  | BF    | 0 | 0 | ✓ | 1   |
| **Family Pangasidiae**                       |       |       |   |   |   |     |
| Pangasius macroneuma                         | Pama  | WF    | ✓ | ✓ | | 2   |
| **Family Belonidae**                         |       |       |   |   |   |     |
| Xenentodon cancila                           | Xеca  | GF    | ✓ | ✓ | ✓ | 29  |
| **Family Hemirampphidae**                    |       |       |   |   |   |     |
| Dermogenys siamensis                         | Desі  | GF    | ✓ | ✓ | ✓ | 26  |
| **Family Mastacembelidae**                   |       |       |   |   |   |     |
| Macrogastus semicellatus                     | Mase  | WF    | ✓ | ✓ | | 17  |
| Macrogastus siamensis                        | Mасі  | BF    | ✓ | 0 | 0 | 2   |
| Mastacembelus favus                          | Mafia | BF    | ✓ | 0 | 0 | 1   |
| **Family Toxotidae**                         |       |       |   |   |   |     |
| Toxotes chatareus                            | Toсh  | GF    | ✓ | 0 | ✓ | 9   |
| **Family Nandidae**                          |       |       |   |   |   |     |
| Pristolepis fasciata                         | Prfa  | BF    | ✓ | ✓ | ✓ | 21  |
| Nandus nandus                                | Nана  | BF    | 0 | 0 | ✓ | 1   |
| **Family Cichlidae**                         |       |       |   |   |   |     |
| Oreochromis niloticus                        | Орні  | GF    | ✓ | ✓ | | 3   |
| **Family Eleotridae**                        |       |       |   |   |   |     |
| Oxyleotris marmorata                         | Оксм  | BF    | ✓ | ✓ | ✓ | 5   |
| **Family Gobiidae**                          |       |       |   |   |   |     |
| Gobiopterus chuno                            | Goch  | BF    | ✓ | ✓ | ✓ | 37  |
| Rhinogobius sp.                              | Rhсп  | BF    | ✓ | ✓ | 0 | 25  |
| **Family Anabantidae**                       |       |       |   |   |   |     |
| Anabas testudineus                           | Antе  | BF    | 0 | ✓ | ✓ | 4   |
| **Family Belontiidae**                       |       |       |   |   |   |     |
| Trichogaster trichopterus                    | Trтр  | BF    | 0 | ✓ | ✓ | 6   |
| Trichopsis pumila                            | Trpu  | BF    | ✓ | ✓ | ✓ | 39  |
| Trichopsis vittata                           | Trві  | BF    | ✓ | ✓ | | 19  |
| **Family Channidae**                         |       |       |   |   |   |     |
| Channa striata                               | Chst  | BF    | ✓ | ✓ | 0 | 44  |
| **Family Soleidae**                          |       |       |   |   |   |     |
| Brachirus harmandi                           | Brhra | GF    | ✓ | 0 | 0 | 1   |
| **Family Chaudhuriae**                       |       |       |   |   |   |     |
| Chaudhuria caudata                           | Chсa  | BF    | 0 | ✓ | 0 | 1   |
| **Family Balitoridae**                       |       |       |   |   |   |     |
| Homalogobioptoides smithi                    | Homs  | BF    | ✓ | ✓ | 0 | 1   |
| Nemacheilus pallidus                         | Nepа  | WF    | ✓ | ✓ | | 1   |

(cont'd.......)
Table 2. Ten top most abundant species collected from each river

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

See full scientific names in Table 1

Note: M = the Mun River, S = the Songkhram River and G = the Gam River
Table 3a. Average species richness (ASR ± SD) of larval fishes during the study

| River | Month | Aug.  | Oct.  | Dec.  | Feb.  | Apr.  | Jun.  | Average |
|-------|-------|-------|-------|-------|-------|-------|-------|---------|
| Mun   | Aug.  | 13 ± 5 | 19 ± 3 | 7 ± 7 | 14 ± 5 | 6 ± 2 | 6 ± 2 | 11 ± 6AB |
| Songkram | Aug.  | 21 ± 5 | 15 ± 1 | 10 ± 4 | 8 ± 2 | 5 ± 1 | 11 ± 2 | 12 ± 7AB |
| Gam   | Aug.  | 11 ± 6 | 8 ± 3 | 9 ± 2 | 6 ± 1 | 6 ± 2 | 9 ± 2 | 8 ± 3A  |
| Average | Aug.  | 15 ± 7 | 14 ± 8 | 9 ± 5 | 9 ± 4 | 5 ± 2 | 9 ± 3 | 10 ± 6 |

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

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

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

| River | Month | Aug-2009 | Oct-2009 | Dec-2009 | Feb-2010 | Apr-2010 | Jun-2010 | Average |
|-------|-------|----------|----------|----------|----------|----------|----------|---------|
| Mun   | Aug.  | 92 ± 62  | 79 ± 25  | 25 ± 26  | 45 ± 21  | 45 ± 7  | 89 ± 66  | 63 ± 44AB |
| Songkram | Aug.  | 149 ± 179| 117 ± 73 | 54 ± 14  | 58 ± 49  | 75 ± 31 | 97 ± 59  | 92 ± 86A |
| Gam   | Aug.  | 66 ± 57  | 36 ± 16  | 19 ± 6   | 36 ± 27  | 40 ± 38 | 43 ± 18  | 40 ± 31B |
| Average | Aug.  | 106 ± 118| 80 ± 56AB| 34 ± 23B | 47 ± 34B | 55 ± 31B| 78 ± 54AB| 67 ± 64  |

Same capital letter shows the values that are not significantly different at α = 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 | 0.062   | 60     | 0.062 | 0.062   |
Table 5. Probability of occurrence (%OP) (Mean±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   | Cluster II  | Cluster III  | Cluster IV  | Cluster V   |
|-----------------|-------------|-------------|--------------|-------------|-------------|
| Family Notopteridae |             |             |              |             |             |
| Nono            | 6.0 ± 0.8   | 7.5 ± 2.0   | 7.0 ± 0.9    | 6.4 ± 2.9   | 16.5 ± 3.7  |
| Family Clupeidae  |             |             |              |             |             |
| Clae            | 69.7 ± 4.9  | 68.2 ± 4.9  | 61.9 ± 6.6   | 61.4 ± 2.8  | 47.1 ± 6.0  |
| Teth            | 7.4 ± 5.3   | 3.1 ± 4.3   | < 1          | 44.5 ± 15.9 | 4.0 ± 5.0   |
| Family Engraulidae |             |             |              |             |             |
| Seme            | 8.0 ± 5.5   | 3.7 ± 4.7   | < 1          | 46.5 ± 15.8 | 5.7 ± 5.9   |
| Family Cyprinidae |             |             |              |             |             |
| Amch            | 39.4 ± 4.1  | 13.5 ± 9.7  | < 1          | 7.8 ± 7.9   | < 1         |
| Amni            | 26.4 ± 9.4  | 9.9 ± 7.4   | < 1          | 42.5 ± 12.6 | 3.5 ± 4.6   |
| Amtr            | 10.1 ± 6.2  | 5.9 ± 6.4   | < 1          | 54.1 ± 15.6 | 12.1 ± 9.5  |
| Bala            | 20.8 ± 5.4  | 7.6 ± 5.3   | < 1          | 8.6 ± 6.0   | < 1         |
| Baal            | 63.6 ± 12.6 | 28.8 ± 12.3 | 8.4 ± 3.0    | 29.7 ± 4.0  | 16.7 ± 6.2  |
| Bago            | 54.9 ± 5.8  | 40.7 ± 6.2  | 13.9 ± 5.7   | 45.4 ± 1.3  | 26.0 ± 9.7  |
| Basc            | 46.0 ± 16.7 | 14.8 ± 12.5 | 3.4 ± 3.9    | 2.3 ± 5.7   | < 1         |
| Crat            | 62.9 ± 6.7  | 22.2 ± 14.4 | 3.7 ± 1.7    | 29.4 ± 10.2 | 6.0 ± 1.4   |
| Crob            | 7.4 ± 5.3   | 3.1 ± 4.3   | < 1          | 44.5 ± 15.9 | 4.0 ± 5.0   |
| C0re            | 10.9 ± 3.8  | 6.6 ± 2.1   | 6.9 ± 3.2    | 4.0 ± 2.9   | 21.5 ± 6.4  |
| Cyp             | 10.3 ± 3.1  | 9.7 ± 2.2   | 28.6 ± 7.8   | 3.4 ± 1.3   | 18.5 ± 8.7  |
| Cyar            | 26.7 ± 9.5  | 8.3 ± 7.1   | 1.4 ± 1.6    | 1.6 ± 2.9   | < 1         |
| Cyen            | 18.8 ± 6.6  | 8.8 ± 5.5   | < 1          | 35.4 ± 6.3  | 10.3 ± 7.3  |
| Epnmu           | 0.7 ± 0.1   | 2.2 ± 1.5   | 2.8 ± 1.2    | 3.0 ± 2.4   | 13.3 ± 4.0  |
| Esme            | 32.7 ± 10.7 | 16.6 ± 8.4  | 7.8 ± 3.3    | 3.9 ± 4.0   | 5.6 ± 1.1   |
| Hadi            | 32.6 ± 1.8  | 51.7 ± 5.9  | 45.0 ± 7.7   | 20.2 ± 8.3  | 29.6 ± 3.3  |
| Hama            | 23.0 ± 8.4  | 8.7 ± 5.9   | 4.0 ± 2.1    | 2.1 ± 2.6   | 5.8 ± 1.6   |
| Heli            | 40.5 ± 10.1 | 15.5 ± 8.6  | 6.3 ± 2.9    | 27.1 ± 7.3  | 2.8 ± 3.4   |
| Heer            | 20.0 ± 3.9  | 9.8 ± 3.0   | 13.1 ± 3.4   | 19.2 ± 4.9  | 10.3 ± 2.9  |
| Hesi            | 49.5 ± 5.6  | 41.4 ± 11.5 | 14.9 ± 8.2   | 15.9 ± 8.2  | 6.4 ± 3.8   |
| Lale            | 2.9 ± 2.4   | 6.4 ± 4.0   | 16.5 ± 8.1   | 18.2 ± 4.4  | 20.9 ± 3.8  |
| Lasi            | 7.6 ± 5.3   | 3.8 ± 4.4   | < 1          | 45.5 ± 15.6 | 8.3 ± 5.2   |
| Myat            | 37.6 ± 3.2  | 23.5 ± 4.2  | 18.5 ± 3.3   | 47.1 ± 12.5 | 11.9 ± 4.0  |
| Myec            | 44.2 ± 7.4  | 50.5 ± 5.4  | 23.3 ± 8.3   | 58.3 ± 3.6  | 24.1 ± 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 |
| Osne  | 7.4 ± 5.4 | 3.5 ± 4.3 | <1 | 44.7 ± 15.9 | 5.5 ± 4.4 |
| Osni  | 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 |
| Paox  | 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 |
| Pube  | 1.8 ± 0.2 | 5.8 ± 2.8 | 9.8 ± 3.3 | 5.4 ± 3.5 | 24.2 ± 6.1 |
| Pueor | <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 |
| Aceri | 27.3 ± 5.4 | 17.1 ± 5.3 | 3.8 ± 2.4 | 14.0 ± 6.6 | 4.6 ± 2.9 |
| Yale  | 12.1 ± 3.6 | 4.6 ± 4.1 | <1 | 44.7 ± 15.7 | 3.5 ± 5.0 |
| Yamo  | 28.0 ± 7.5 | 10.3 ± 7.2 | <1 | 35.1 ± 10.4 | 2.6 ± 3.8 |
| Ymor  | 18.6 ± 2.2 | 9.2 ± 4.8 | <1 | 47.7 ± 14.7 | 5.8 ± 6.0 |
| Laha  | 3.1 ± 2.3 | 3.3 ± 1.9 | 3.7 ± 2.4 | 20.1 ± 6.0 | 15.3 ± 4.1 |
| Paan  | 22.7 ± 8.4 | 7.4 ± 6.3 | 1.5 ± 2.1 | <1 | <1 |
|       |         |         |         |         |         |
| 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.....)
%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 dusonensis, Clupeichthys aesarnensis, Rasbora borapetensis and Crossocheilus atrilimes. The other dominant larval species included six white fishes (e.g., Barbonymus gonionotus, Henicorhynchus siamensis and Mystacoleucus fasciata and Amblyrhynchichthys chulabhornae) and two black fishes (Pristolepis gudgeri 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 (e.g., 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 Amblyrhyhanchthys micracanthus. The larvae of other
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. dasoensis* 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., 2012). 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; Hortle, 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 *Heniochocinclus* 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 (Poulson 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 *Amblyrynchichthys truncates*, *Sikukia gudgeri*, *Parachela siamensis* and *Pangasius macrolena*, are known to be triggered by threshold or changes in discharge, water levels or current (Poulson 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., *Heniochocinclus* 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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