

Original Articles

Flow alterations by dams shaped fish assemblage dynamics in the complex Mekong-3S river system

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ARTICLE INFO

Keywords:

Dam effects
Fish abundance
Fish richness
Temporal beta diversity
Environmental filtering
Lower Mekong Basin

ABSTRACT

The Mekong, Sekong, Sesan, and Srepok (Mekong-3S) river system, a Ramsar wetlands of international importance and critical fish migration routes, is altered by dams that distort the seasonal flow dynamics, structuring dispersal and reproduction success of fishes. Here, we investigate the temporal responses of local fish beta diversity to hydrologic modification by the upstream functioning dams in five sites of the Mekong-3S system. The sampling design adopted (two sites on the Mekong River displaying relatively undisturbed flow and three sites in the 3S displaying a gradient in flow perturbation) allows us to focus on the effect of flow alteration on local fish assemblage compositions. By analysing 7-year daily fish monitoring data (06/2007–05/2014), we found that there have been overall declining trends in local species richness and abundance, with strong temporal variability in local beta diversity. Undisturbed sites are characterized by seasonal assemblage variability, while disturbed sites are characterized by aseasonal assemblage changes. Temporal shifts in assemblage composition suggest that dams alter seasonal flow patterns and favour generalist species. This study contributes to a better understanding of the temporal changes of tropical freshwater fish beta diversity in regulated and unregulated rivers. It is thus relevant for fisheries planning and conservation.

1. Introduction

The Mekong River Basin is one of the 35 biodiversity hotspots of the world (Mittermeier et al., 2011). Fish assemblages in this basin are extremely diverse and characterized by the presence of fish species undertaking large-scale seasonal migrations (Poulsen et al., 2002). The complex seasonal flood pulses and historical biogeography of the region partly explain this high diversity and seasonality (Poulsen et al., 2002; Rainboth, 1996). Rapid changes through time due to hydropower infrastructure development in the basin may change the abiotic and biotic components of the river ecosystem, including changes in river flow, habitat, food web, species distribution, and finally the river's overall biological integrity (Li et al., 2013; Macnaughton et al., 2015; Phomikong et al., 2014; Tonkin et al., 2017).

This study covers five sites. Three sites are in the lower reach of the three Mekong major tributaries: Sekong (SK), Sesan (SS) and Srepok (SP) rivers, called the 3S; and two sites are in the Mekong mainstream: up- and downstream of the 3S outlet (Fig. 1). All sites are part of the complex Mekong-3S system, located in north-eastern Cambodia in the

Kratie (KT), Stung Treng (ST) and Ratanakiri provinces. The Mekong mainstream (KT and ST) is a critical habitat for many Mekong fishes, (Baran, 2006; Poulsen et al., 2004, 2002) and the Mekong River in ST has been designated a Ramsar wetlands of global significance since 1999 (Try and Chambers, 2006). The 3S rivers on the other hand, draining north-eastern Cambodia, southern Lao People's Democratic Republic (PDR), and Viet Nam's Central Highlands, join the Mekong River in ST. According to the Mekong River Commission (MRC), they contribute ~25% of the Mekong mean annual flow at KT and play a key role in the hydrology of the downstream Mekong, including the Tonle Sap River showing seasonal reverse flows (MRC, 2005). In addition, the 3S system is the main fish migration route from the lower Mekong system (Poulsen et al., 2004, 2002).

To address the energy needs and economic growth of the region, continued hydropower development has been underway in the Mekong River Basin. Six large hydropower dams have been constructed in the upper Mekong River in China since the mid-1990s (Fan et al., 2015; Winemiller et al., 2016). In the Lower Mekong Basin (LMB), according to MRC's Hydropower Project Database 2015, two mainstream dams

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<https://doi.org/10.1016/j.ecolind.2018.01.023>

Received 20 July 2017; Received in revised form 10 January 2018; Accepted 12 January 2018
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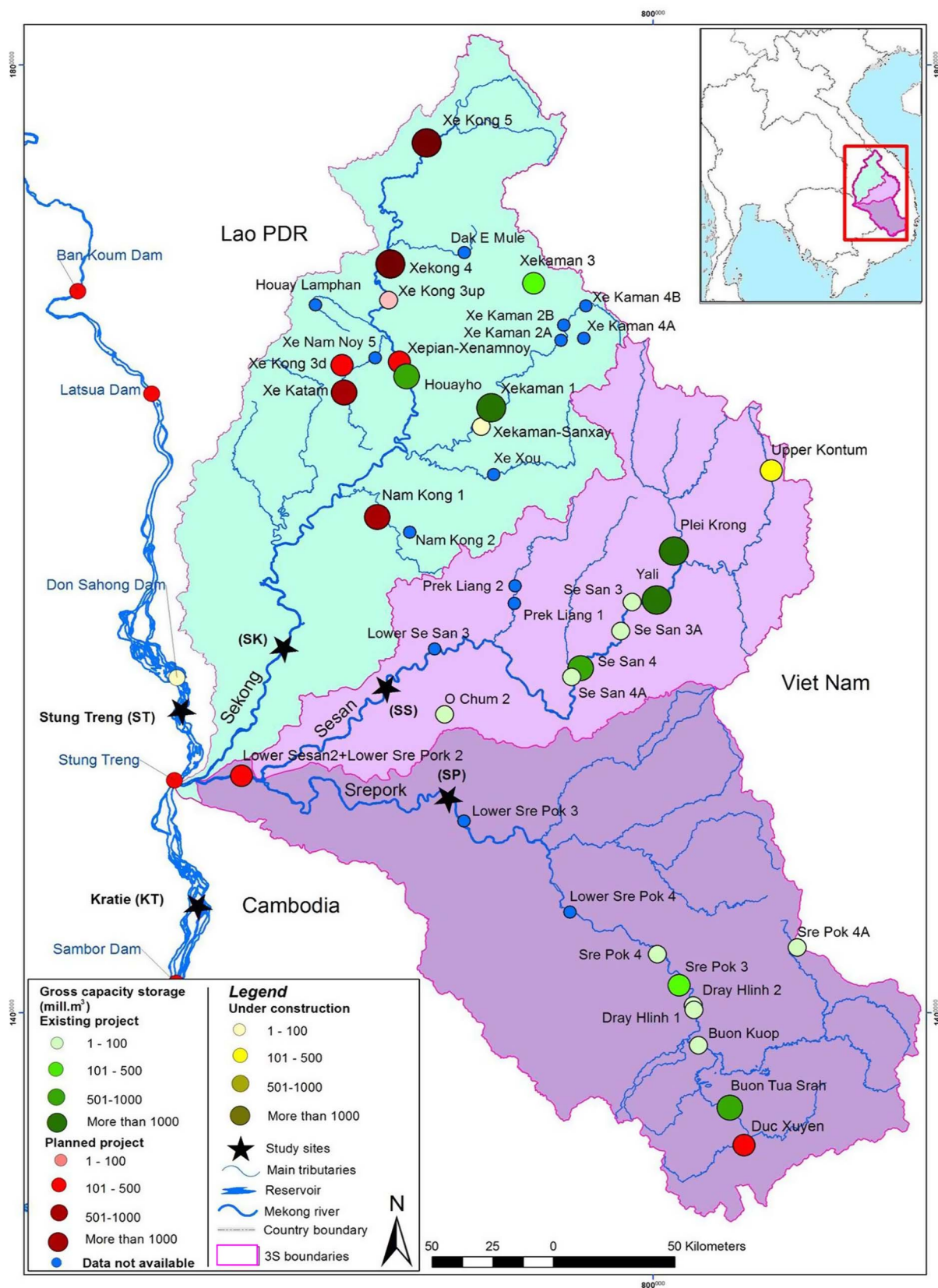


Fig. 1. Map showing the study sites and hydropower dam positions in the 3S sub-basin (Data source: MRC Hydropower Project Database 2015). Site names: KT = Kratie, SK = Sekong, SP = Srepok, SS = Sesan, and ST = Stung Treng.

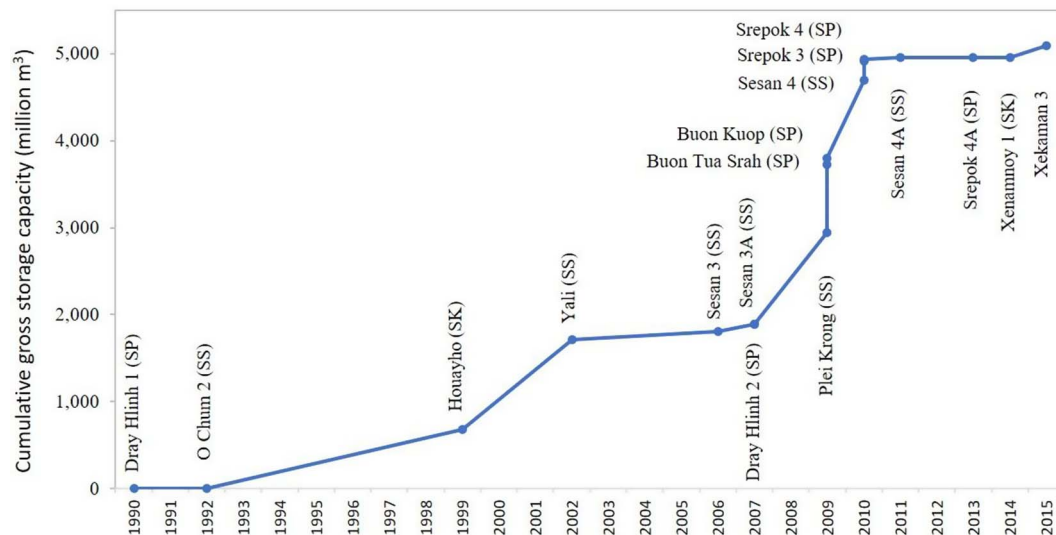


Fig. 2. Timeline and cumulative installed gross storage capacity of existing hydropower dams in the 3S sub-basin (Data source: MRC Hydropower Project Database, 2015).

are under construction in Lao PDR, and nine others are planned; in the LMB tributaries, 42 dams are in operation, 27 are under-construction, 17 are licensed and 58 are planned by 2030. In the 3S sub-basin alone, 17 dams have been functioning since the 1990s, with a total gross storage capacity of ~5100 million m³ (Fig. 2).

Evidence suggests that these dams have significantly modified the natural flow dynamics of the Mekong River system, with undocumented effects on the river ecology and fisheries (Cochrane et al., 2014; Piman et al., 2013; Sabo et al., 2017; Winemiller et al., 2016; Ziv et al., 2012). In the 3S, the current functioning dams cause an increase of 28% in the dry seasonal flow and a decrease of 4% in the wet seasonal flow (Piman et al., 2013). Dams in the Upper Mekong in China reduce flood pulses, for example, by 23 and 11% in rising and falling rates, respectively, in the Tonle Sap River (Cochrane et al., 2014), a major tributary situated downstream of the Mekong-3S system. These changes in natural flood pulse dynamics are expected to have altered fish assemblage structure, because in the 3S system, at least 89 migratory species are found, including 17 endemic and 14 endangered or critically endangered species (Baran et al., 2013a), and in the Mekong Basin, among the 877 recorded species (Rainboth, 1996; Ziv et al., 2012) ~87% are migratory and mainstream spawners (Baran, 2006; Baran et al., 2013b). These fishes depend on natural seasonal flood pulses as the main ecological trigger to disperse, reproduce and seek refuges during their life cycles (Baran, 2006; Poulsen et al., 2004, 2002). Currently, however, far less is known about how downstream fish assemblages in the species-rich Mekong-3S system respond to such hydrologic flow modifications caused by the upstream functioning hydropower dams.

The five sites selected for this study, being located in the same ecoregion and thus displaying similar environmental conditions, allow comparing how fish assemblages respond to rivers displaying natural versus regulated flows caused by upstream functioning dams. Among the five sites, the mainstream sites (ST and KT) are the least altered by hydropower dams and characterized by more predictable-seasonal flow patterns (see Supplementary S1), as to date, there have been no functioning dams on the mainstream of LMB, which contributes 84% to the total annual flow of the Mekong Basin (MRC, 2010). By contrast, the 3S sites (SS, SP, and SK) are characterized by unpredictable flows (see S1) due to the storage effects of multiple dams acting upstream (Fig. 2). Among the three sites, SS and SK have flow patterns more severely altered as documented in (Baird et al., 2002; Baird and Meach, 2005; Baran et al., 2013a; Claasen, 2004; Hirsch and Wyatt, 2004; Rutkow et al., 2005) and shown in S1. Suffering different levels of flow disruption, the fish assemblages in these five sites are expected to display different inter-annual and seasonal responses (Röpke et al., 2017).

According to Tonkin et al. (2017), fish assemblages in predictably seasonal flow conditions (i.e., ST and KT) should experience strong temporal (seasonal) turnover and should host high species diversity through more specialist species occupying available temporal niches. By contrast, fish assemblages in more unpredictable flow environments (3S) should show low temporal diversity and should harbour broad generalist species displaying little seasonal turnover.

Here, we examine the temporal dynamics of fish assemblage compositions among the five studied sites during the 7-year period between June 2007 and May 2014. Our central hypothesis is that assemblages in sites undergoing modifications in seasonal flow regime due to dams (3S) will display different temporal dynamics compared to assemblages in sites enjoying more natural flow regimes (Mekong). First, we expect that, by regulating flow regimes during the year, dams will decrease the seasonal responses of assemblages. Second, we expect that fish assemblages in sites undergoing flow regulation (3S) will experience a decrease in either species richness or diversity due to the escape of species from adverse environmental conditions, i.e., species strongly dependent on seasonal flow regimes to complete their life cycles. Third, and closely linked to our second expectation, we predict a switch in assemblage composition from more specialists in sites with predictable flow (Mekong) to more generalists in sites experiencing flow disruption (3S). To test these hypotheses, we use monitored daily fish and water level time-series data between 1 June 2007 and 31 May 2014, or 365 weeks, initiated by the MRC on our five sites for assessing the impact of water infrastructure development in the Mekong River Basin (MRC, 2007). While our work contributes to the overall science-based understanding of fish assemblage dynamics in the Mekong-3S system, its original focus is on fish temporal beta diversity and how flow alterations caused by upstream functioning dams shape the temporal dynamics of fish beta diversity (assemblage composition) in the Mekong-3S river system.

2. Materials and methods

2.1. Data collection

Stationary gillnets were used for data collection. MRC standard sampling procedures for fish catch monitoring were applied (MRC, 2007). Monitoring sites were selected to cover the Mekong-3S system and the main riverine habitats that display a gradient of flow perturbation from upstream hydropower dams. The sampling sites extend a few kilometres in length and are located on the backwaters and/or sandbars of the river reach in the village where the participating professional fishermen are based. These sampling sites stayed relatively

unchanged over the study period. Daily, each fisherman (three for each site, and fifteen for the five study sites) used a set of stationary gillnets with a range of mesh sizes (length: 120 ± 50 m, height: 2–3.5 m, mesh size: 3–12 cm, soak hours/day: 12 ± 2). The fishermen were supervised by fishery researchers from the Inland Fisheries Research and Development Institute (IFReDI) of the Cambodia Fisheries Administration, with technical support from the MRC fisheries monitoring specialists. The main advantages of such sampling designs are lower cost, but provide a sustained and coherent long-term records of fish datasets for the time-series analysis. The fish species list (~900 species and including ecological attributes) comes from the MRC Mekong Fish Database (MFD) (MFD, 2003) and was cross-checked with FishBase (Froese and Pauly, 2017) and other literature sources (Kottelat, 2013; Rainboth et al., 2012). Captured fish were identified to the species level and counted. After field verification, field collected data were recorded into the national fish monitoring database, which was quarterly cleaned by research officers from the IFReDI with the help of the MRC database expert and fisheries monitoring specialists. Water levels at each sampling location were registered by MRC.

2.2. Data analyses

Daily fish samples were recorded as daily mean samples and then aggregated into weekly fish richness and abundance data by species over the period from 1 June 2007 to 31 May 2014. For the entire period of the study, we have 2557 mean daily samples, or a total for 365 weeks and 2 days. We thereafter dropped the 2 days and consistently used 365 weeks across all sites for the analysis. Likewise, daily water levels in each site were computed into mean weekly water levels for the same 365 weeks.

2.3. Overview of fish assemblage structure

To get an overview of the fish assemblage structure, *K*-means clustering (with five pre-determined clusters) on the Hellinger-transformed yearly fish assemblage data was computed to classify all observations in the Mekong-3S system. The *Fviz_cluster* function of the *factoextra* package was applied to visualize the assigned five *K*-means clusters, with observations represented by points, using Principal Components Analysis (PCA) (Kassambara, 2017). PCA is used because it provides the proportion of variance accounted for by the first two axes (Borcard et al., 2011). Boxplots of total weekly species richness and the inverse Simpson diversity index were also computed to describe the spatial and temporal dynamic patterns of the fish assemblage structure, both at each site and in the entire Mekong-3S system. The inverse Simpson index was used because it is a meaningful and robust diversity index that captures the variance of species abundance distribution while being less sensitive to species richness (Magurran, 2004). Non-parametric Pairwise Wilcoxon Rank Sum Tests were used for multiple comparison tests on species richness and diversity indices among the study sites.

2.4. Temporal dynamics of beta diversity

Beta diversity describes the variation in species composition among sites in a study area or among survey times for a survey across years (Legendre and De Cáceres, 2013; Legendre and Gauthier, 2014). In estimating total beta diversity (BD_{total}), the total variance of Hellinger-transformed weekly assemblage abundance data was used to reduce disproportionate effects of large abundance values (Legendre and De Cáceres, 2013). BD_{total} has a value between 0 and 1 for Hellinger-transformed data. BD_{total} can be compared among sites if the sampling units across the study sites are of the same size (Legendre and Salvat, 2015), which is the case for the present study. If BD_{total} is equal to 1, all sampling units have a completely different species composition. BD_{total} was then partitioned into Local (temporal) Contributions to Beta

Diversity (LCBD) and Species Contributions to Beta Diversity (SCBD). LCBD is a comparative indicator of the ecological uniqueness of the sampling units. LCBD values give a total sum of 1 for a given data matrix and can be tested for significance (at the 0.05 level in the present study). BD_{total} and LCBD indices can be computed for repeated surveys, and thus form a time series (Legendre and Gauthier, 2014). SCBD indices, on the other hand, indicate the relative importance of each species affecting beta diversity patterns. Species biological traits, including feeding type, habitat preferences, body size and dispersal capacity, are likely to have an influence on SCBD (Heino and Grönroos, 2016). Species with SCBD indices well above the mean were regarded as important species contributing to beta diversity (Legendre and De Cáceres, 2013). All these indices were computed separately for each of the five study sites using the *beta.div* function of the *adespatial* package (Dray et al., 2017; Legendre and De Cáceres, 2013) with 9999 permutations in R (R Core Team, 2015).

To explain the temporal dynamics of LCBD in each site, weekly LCBD indices were modelled as a function of linear weekly abundance, weekly richness and mean weekly water levels. Standardised regression coefficients and *p*-values of each predictor were used to indicate the effect and significance level of each predictor on the LCBD. Standardised regression coefficients are used to make the regression coefficients more comparable to each other. All explanatory variables were log-transformed prior to the analysis to address the skewed distribution of the variables. To determine the relative contribution (in percentage) of each predictor to the total explained variance of each model, hierarchical partitioning of the significant variables from the LCBD models was computed using the *hier.part* function of the *hier.part* package in R.

Further, to examine how fish assemblages responded to seasonal hydrology changes, temporal LCBD indices were plotted against water levels across the 7-year hydrological cycles. Significant LCBD indices (being unique) were also visualised on the plot to investigate whether the temporal uniqueness of an assemblage composition (temporal significant LCBDs) occurred in relation to the site hydrological cycles or otherwise. Further, the non-parametric Spearman's correlation test was performed for each site to test the link between the two variables.

2.5. Temporal variation of assemblage structure

To identify significant seasonal assemblage variations, weekly periodic variability in species abundance and richness were examined using Whittaker–Robinson periodograms (Legendre and Legendre, 2012). The periodograms were computed using the *WRperiodogram* function of the *adespatial* package (Dray et al., 2017). This method was chosen because of its simplicity of interpretation; i.e., the period with maximum amplitude is taken as the best estimate for the true period of oscillation (Legendre and Legendre, 2012). Prior to analyses, the weekly data for each site were tested for stationarity. When stationarity was violated (i.e., KT, ST, SS, and SK, see S3), residuals from the linear regressions (against time) for individual sites were computed and used in the periodogram analyses. Periodogram graphs were plotted to visualize the seasonality of fish total abundance and richness at each site.

2.6. Temporal shift of species contributing to beta diversity

To identify the key species contributing to the temporal dynamics of species composition over the study period, species with SCBD indices greater than the mean at each site were extracted from the assemblage composition matrix. Given that our interest is in how assemblage composition shifts through time, Redundancy Analysis (RDA) was performed on the assemblage composition data against time and its quadratic effect as explanatory variables. The inclusion of a second-degree polynomial allows the assemblage time series to double back upon itself (Legendre and Salvat, 2015). The linear and quadratic effects of time on the assemblage data were both significant predictors of

the assemblage variations among years (test of RDA R-square, $P < 0.001$). RDA is an extension of multiple regression analysis (Legendre and Salvat, 2015). Using RDA, the relationship between the observations (sampling units), species and explanatory variables (the years) can be visualized. Further, to help identify the key species explaining the temporal shift in assemblage composition, indicator species characterising fish assemblages at each site were computed using the `multipatt` function of the `indicspecies` package (Cáceres and Legendre, 2009; De Cáceres and Jansen, 2011) for comparison. Indicator species are species that are used as ecological indicators of community or habitat types, environmental conditions, or environmental changes (De Cáceres et al., 2010), whereas species with large SCBD values are those that are abundant and dominate the assemblage (Legendre and De Cáceres, 2013). Assemblage composition data were Hellinger-transformed prior to RDA computation.

3. Results

3.1. Overall assemblage structure

Over the study period, 292 species were recorded in the catch samples. Among those, 208 fish species were recorded in Kratie (KT), 196 in Stung Treng (ST), 177 in the Srepok River (SP), 133 in the Sesan River (SS) and 216 in the Sekong River (SK). These fishes belong to 14 orders, 48 families and 151 genera. Five main orders represent 90% of the total species count: Cypriniformes (146 species), Siluriformes (66), Perciformes (34), Pleuronectiformes (9) and Clupeiformes (6). The top five families accounting for 63% of total species counts were Cyprinidae (123 species), Bagridae (16), Cobitidae (16), Pangasiidae (15) and Siluridae (11). See S6 for a full species list by genera, families and orders.

K-means clustering (with five clusters) on a PCA plot (Fig. 3a) shows that sites on the Mekong (cluster 4 and 5) are overlapped, indicating assemblage similarities between the two sites, while the 3S sites, particularly SK (cluster 1) and SS (cluster 2), are distant from the Mekong sites, suggesting distinct assemblages. SP (cluster 3) exhibits some similarities with the Mekong sites (ST). Assemblage dissimilarities are further observed among the 3S sites (axis 2).

In addition, boxplots on weekly richness and inverse Simpson diversity index (Fig. 3b, c) indicate that the Mekong sites have the highest richness (KT: median = 23, sd = 10.95; ST: median = 27, sd = 9.87) and inverse Simpson indices (KT: median = 9.20, sd = 5.30; ST: median = 8.82, sd = 5.10) relative to the 3S sites. Noticeably, SS shows both the lowest species richness (median = 12, sd = 5.14) and diversity index (median = 5.45, sd = 2.78) of all sites, whereas SP is comparable with KT in terms of species richness. Although SP has higher species richness (median = 23, sd = 7.52) than SK (median = 19, sd = 8.25), the diversity indices between the two sites are not significantly different (SP: median = 6.89, sd = 3.70; SK: median = 7.49, sd = 4.38). Overall, the Mekong-3S system has experienced gradual diminishing trends of weekly fish abundance and richness, except for SK (S3), whereas trends of inverse Simpson diversity index are found to be declining, particularly in the Mekong sites (S2c).

3.2. Temporal dynamics of beta diversity

Total beta diversity (BD_{total}) indices estimated for the sites were 0.50 in SP, 0.59 in ST, 0.66 in KT, 0.73 in SS and 0.74 in SK. Temporal LCBD weekly values ranged between $1.26E-03$ and $6.36E-03$; the LCBD values are small because they are made to sum to 1 across all weeks for each site. The site with the highest LCBD values is SS (median = $2.71E-03$, sd = $4.33E-04$), whereas the site with the lowest LCBD value is SP (median = $2.53E-03$, sd = $9.69E-04$). The other sites have intermediate values of weekly LCBD. Among the 365 weeks, 10% (35 weeks), 13% (48), 13% (46), 8% (29) and 18% (66) have statistically significant values of LCBD (assemblage

composition being unique) in KT, ST, SP, SS and SK, respectively. This manifested strong temporal changes in the uniqueness of fish assemblage compositions over the study period for all sites. For the two Mekong sites (i.e., KT and ST), these significant temporal LCBDs (red dots on Fig. 4) are found to occur at the time when seasonal water levels start rising on the annual cycle basis, whereas no such patterns are exhibited in the 3S rivers. Significant correlation between LCBDs and water levels are revealed in KT ($P = 0.003$), SP ($P < 0.001$), and SK ($P = 0.015$). While ST is on the margin ($P = 0.052$), no significant correlation of the two variables is indicated in SS ($P = 0.074$).

3.3. Temporal determinants of LCBD indices

Multiple linear regressions show that LCBD values are significantly related to the three predictors: total abundance, total richness and mean water level, depending on the study site (Table 1). Overall, the adjusted coefficient of determination (adjusted R^2) for each site model explains 50% in KT, 61% in ST, 31% in SP, 35% in SS and 62% in SK. Richness is the most contributed variable negatively explaining the temporal changes in LCBD for all sites. In contrast, positive relationships between LCBD and total abundance are exhibited in KT, ST and SP, while no such relationship is found in SS and SK. Water level is linearly linked to LCBD in all sites except for ST, with the significant negative linear relationships observed in KT and SS, and positive linear relationships in SP and SK.

Hierarchical partitioning (Table 1) highlights the high contribution of total richness and abundance in explaining LCBD variations (i.e., KT (85.55%), SS (94.99%), and SK (99.03%) for species richness, and KT (13.72%), ST (79.91%), and SP (53.16%) for abundance). Water level is found to independently contribute the highest proportion (33.30%) of the model total variance in SP.

3.4. Temporal variation of assemblage structure

Periodogram analyses on weekly abundance and richness (Fig. 5a, b) indicate that significant frequencies of semi-annual and annual cycles are exhibited in the Mekong mainstream sites, while no such patterns are displayed in the 3S sites. In KT, significant periods of weekly abundance (Fig. 5a) are found at 51–56 weeks, with harmonics at 104–109 and 154–160 weeks. The other significant periods (26 and 133–135 weeks) in this site show semi-annual cycles. A similar pattern was revealed for the site species richness (Fig. 5b), where significant periods are detected at 48–57 weeks, with harmonics at 100–112 and 148–65 weeks. In ST, significant periods of species abundance occur at 52–48 weeks, with harmonics at 104–118 and 159–166 weeks; however, this pattern is less pronounced for the species richness. By contrast, there are no clear significant signals of semi-annual or annual cycles in the 3S sites. Additionally, far fewer significant periods with high frequencies are revealed in the 3S than the mainstream sites (KT and ST) for both abundance and richness.

3.5. Species contributions to temporal beta diversity

A total of 96 species, i.e., 33% of the total species, bring important contributions to site beta diversity (above overall mean SCBD value), 13 of which are largely distributed across all sites (see S4, S5). Of the 96 species, 55 are identified in KT, 45 in ST, 44 in SP, 34 in SS and 56 in SK. Among these important species, the number of species that are also indicator species generated by the `multipatt` function in each site are as follows: 17 species in KT, 26 in ST, 14 in SP, 12 in SS and 17 in SK (see S4 and S5 for species details). Species with the highest SCBD indices are *Puntioplites falcifer* in KT, *Henicorhynchus lobatus* in ST, *Hypsibarbus malcolmi* in SP, *Anabas testudineus* in SS and *Paralabauc barroni* in SK.

RDA analysis on assemblage composition (with SCBD indices greater than mean) against time depicts a strong temporal shift in assemblage composition at all sites. In the Mekong mainstream (Fig. 6a),

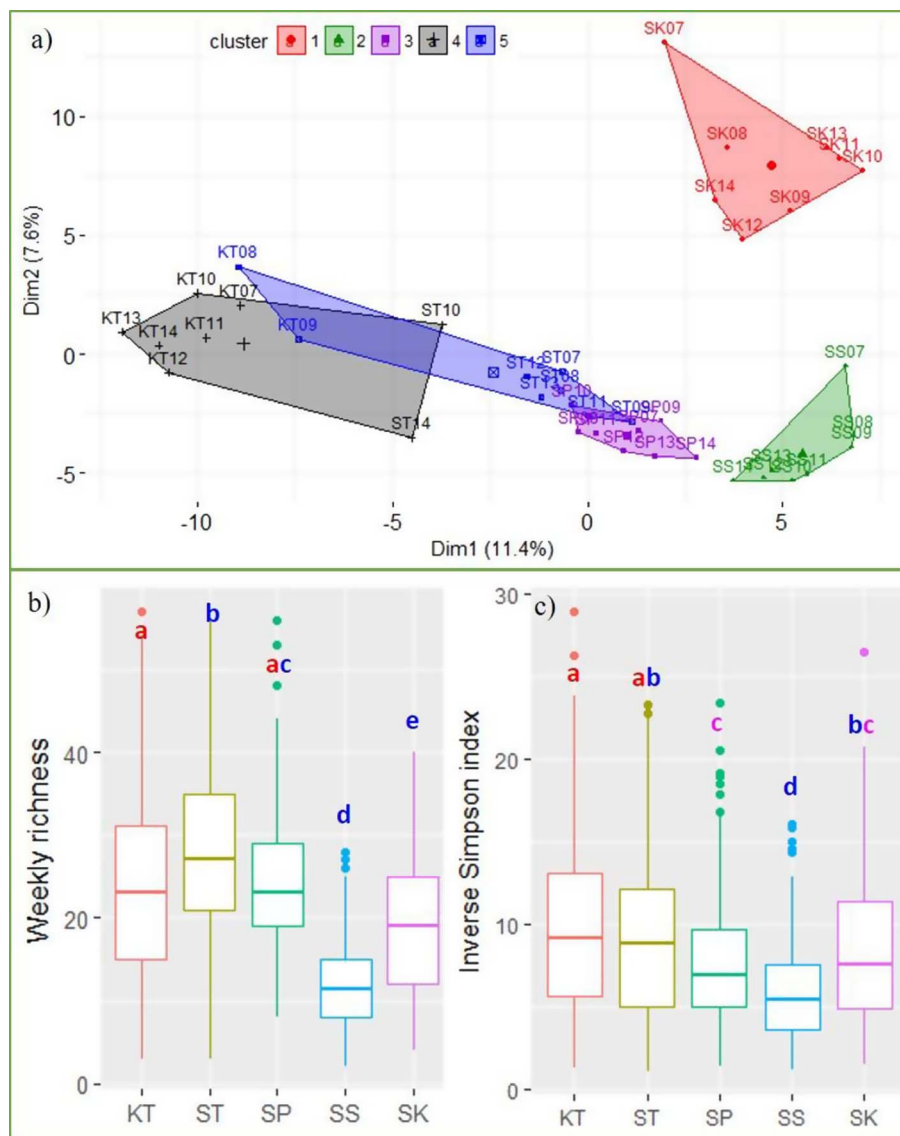


Fig. 3. Fish assemblage patterns in the Mekong-3S system. (a) K-means cluster on PCA plot ($k = 5$) on Hellinger-transformed yearly assemblage data. Five convex hulls (with different colours) represent each assemblage cluster of the Mekong-3S system. A combination of two letters and two digits denotes the site name and year; for example, KT07 is Kratie in 2007. (b) Boxplots of total weekly richness by site; (c) Boxplots of weekly inverse Simpson diversity index by site. Mean values among sites (Fig. 5b, c) with a common letter are not significantly different at the 0.05 level (Pairwise Wilcoxon Rank Sum Tests). For site names, see Fig. 1.

during the early years of the survey (2007–2010), temporal assemblage variability is mostly due to small-sized generalist and specialist species. After 2010, the composition tends to be disproportionately represented by specialists. Small-sized mud carps (maximum total length – $mTL < 25$ cm) i.e., *Henicorhynchus lobatus* (Hlobatu), *H. siamensis* (Hsiamen) and *Labiobarbus siamensis* (Lsiamen), the most common and abundant species in LMB, are found to be characteristic and important species for both sites during the period 2007–2010. Afterwards, specialists disproportionately represent the assemblage in both sites. Some common specialists describing assemblage in the Mekong mainstream during 2011–2014 are short distance migrants and mainstream spawners such as *Hypsibarbus malcolmi* (Hmalcol), *Phalacronotus apogon* (Papogon.1), *Hypsibarbus lagleri* (Hlagler), *H. wetmorei* (Hwetmor); long distance migrants such as large-sized cyprinids ($mTL > 60$ cm) *Cosmochilus harmandi* (Charman), *Cirrhinus microlepis* (Cmicrol), *Cyclocheilichthys enoplos* (Cenoplo), *Labeo chrysophekadion* (Lchryso); and river catfishes, namely, *Helicophagus waandersii* (Hwaande) and *Pangasius conchophilus* (Pconcho) (only in ST).

In contrast, temporal dynamics in assemblage composition shifted from specialists (during the 2007–2010 period) to generalists (after 2010) in the 3S (Fig. 6b). The pattern is pronounced in SP and SK, where long-distance migratory species and main channel spawners with large-bodied sizes, such as *Phalacronotus apogon* (Papogon.1),

Hypsibarbus lagleri (Hlagler), *Helicophagus waandersii* (Hwaande), *Hypsibarbus malcolmi* (Hmalcol), *Pangasius conchophilus* (Pconcho), *P. bleekeri* (Pbleeke), *Hypsibarbus pierrei* (Hpierre), etc., represented the assemblages between 2007 and 2010 and were then replaced by small-sized minnows and carps with generalist habitat preference, such as *Labiobarbus siamensis* (Lsiamen), *Systemus rubripinnis* (Srubrip), *Henicorhynchus siamensis* (Hsiamen) and *Osteochilus vittatus* (Ovittat), etc., between 2011 and 2014. This pattern is less clear in SS; however, this site shows that the generalist *H. lobatus* significantly contributes to the temporal changes in assemblage composition during the 2011–2014 period. Moreover, assemblages in the SS during the entire period were largely represented by generalists as found in SP and SK and other small-sized minnows and carps, such as *Paralaubuca typus* (Ptypus), *P. riveroi* (Privero), *P. barroni* (Pbarron), *Rasbora tornieri* (Rtornie), *Cyclocheilichthys armatus* (Carmatu), etc. Further, assemblages in the 3S towards 2011–2014 are partly composed of black fishes (floodplain residents) such as climbing perches *Anabas testudineus* (Atestud), air-breathing catfishes *Clarias batrachus* (Cbatrac) and snakeheads *Channa striata* (Cstriat). Important species contributing to site beta diversity and their ecological attributes are given in S5.

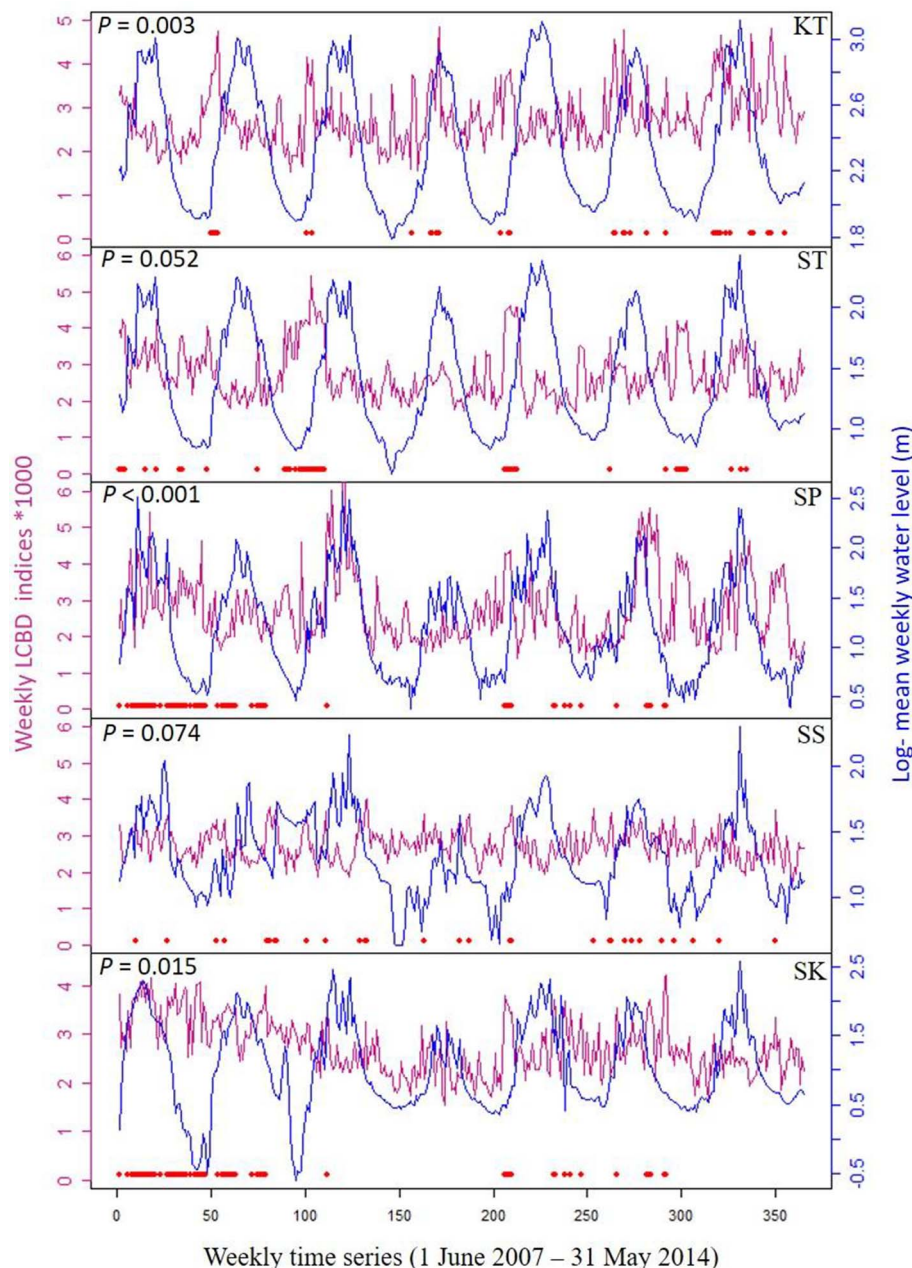


Fig. 4. Temporal changes in LCBD indices (red line) and mean log-transformed weekly water levels (blue line) over 7-year hydrological cycles on five sites of the Mekong-3S River system. More predictable-seasonal flow patterns are shown in KT and ST, and unpredictable/regulated flows are displayed in SP, SK, and SS. The red dots indicate weeks with significant LCBD indices at the 0.05 level. P denotes the p -value of the pairwise correlation test using the Spearman method. For site names, see Fig. 1.

4. Discussion

We find that fish assemblages in SP have some similar composition patterns to those of the Mekong sites. We also find strong temporal dynamics of fish assemblages in the complex Mekong-3S system, with total site beta diversity (BD_{total}) ranging between 0.50 and 0.74. Local species richness and abundance are the most important determinants explaining the temporal change in local beta diversity (LCBD). Our findings strengthen the results of previous studies highlighting the strong relationships of species richness and abundance with local LCBDs (Heino and Grönroos, 2016; Legendre and De Cáceres, 2013; Qiao et al., 2015). Water level is also an important ecological determinant that further explains these temporal changes (Table 1). In the Mekong-3S system, we observe that water levels in the Mekong sites show more seasonal-predictable patterns than those in the 3S sites where the seasonality of flow is disrupted by increasing dam operations in the upper reach of these rivers since 1990s (S1, Figs. 1, 2 and 4).

Some similarities of fish assemblage patterns in SP to those with the

Mekong sites (Fig. 3a) are likely because SP has the highest number of migratory species (81) relative to SK (64) and SS (54) (Baran et al., 2013a). These migratory species e.g., Pangasiidae and Cyprinidae could migrate hundreds of kilometers between the mainstream, tributaries and floodplains during their life cycles (Poulsen et al., 2004, 2002; Sverdrup-Jensen, 2002). Local fish migration behaviour may additionally explain the pattern. Most cyprinids are known to migrate upriver along the edges of rivers; therefore, when fish leave the Mekong, enter the SK and travel up along its southern bank, they will enter SS and will soon continue right into SP (Baran et al., 2013a) (see also Fig. 1). Moreover, SP has greater depths and better flow conditions relative to SS and SK (see S1). These factors combined tend to explain some similarities of the assemblage patterns between the two rivers.

Overall, our results support the central hypothesis that fish assemblages in sites with unpredictable flows (3S) exhibit different temporal changes compared to fish assemblages in sites with predictable flow patterns (the Mekong) (Fig. 3a). As expected under our first hypothesis, assemblages in the Mekong (undisturbed sites) are characterized by a

Table 1

Standardised regression coefficients resulting from the multiple regression models of weekly LCBD values against the weekly total abundance (AB), weekly total richness (SR) and mean weekly water levels (WL) in each study site. All variables are log-transformed. R^2 = coefficient of determination. Asterisks indicate the significance levels associated with each predictor, with ‘*’ at 0.05, ‘**’ at 0.01, and ‘***’ at 0.001. Plus ‘+’ and minus ‘-’ signs indicate the positive and negative relationships, and ‘ns’ denotes ‘not significant’. Values in brackets, resulting from hierarchical partitioning, indicate the relative independent contribution (in percentage) of each significant variable to the total explained variance. (–) denotes ‘not available’ for variables that are not significant at the 0.05 level.

Site	AB	SR	WL	Adjusted R^2
KT	+ 5.355*** (13.72%)	– 17.082*** (80.55%)	– 5.727*** (5.73%)	0.50
ST	+ 23.454*** (79.91%)	– 13.213*** (20.09%)	– 0.244 ^{ns} (–)	0.61
SP	+ 10.152*** (53.16%)	– 6.406*** (13.81%)	+ 7.647*** (33.03%)	0.31
SS	+ 1.358 ^{ns} (–)	– 13.075*** (94.99%)	– 3.057** (5.01%)	0.35
SK	– 0.926 ^{ns} (–)	– 15.671*** (99.03%)	+ 2.157 ⁺ (0.97%)	0.62

strong seasonal variability. This is depicted by the significant temporal LCBD signals showing the uniqueness of the fish assemblage compositions in KT and ST occurring in relation to the annual flow cycles, particularly when water levels start rising (Fig. 4). Many Mekong fishes are known to start their seasonal migration for spawning and feeding/rearing grounds when seasonal flooding in the Mekong begins in late May or June (Poulsen et al., 2004, 2002; Sverdrup-Jensen, 2002). Water levels are the most important ecological determinants in triggering these seasonal migrations (Baran, 2006). In contrast, the significant temporal LCBDs indicating the uniqueness of fish assemblages in the 3S sites (Fig. 4; SP, SS, and SK) are characterized by chaotic variations unrelated to the seasonal hydrological cycles. Flow perturbation caused by dams in the 3S system has decreased seasonal variation of flow, thus muting the seasonal structure of fish assemblages. The results from the periodogram analyses (Fig. 5) further indicate that in predictable systems (KT and ST), significant period signals with high frequencies of species abundance and richness are harmonic at semi-annual and annual cycles over the study period, which is not the case for the 3S sites. Our findings are consistent with the seasonality framework proposed by Tonkin et al. (2017), emphasizing that sites with

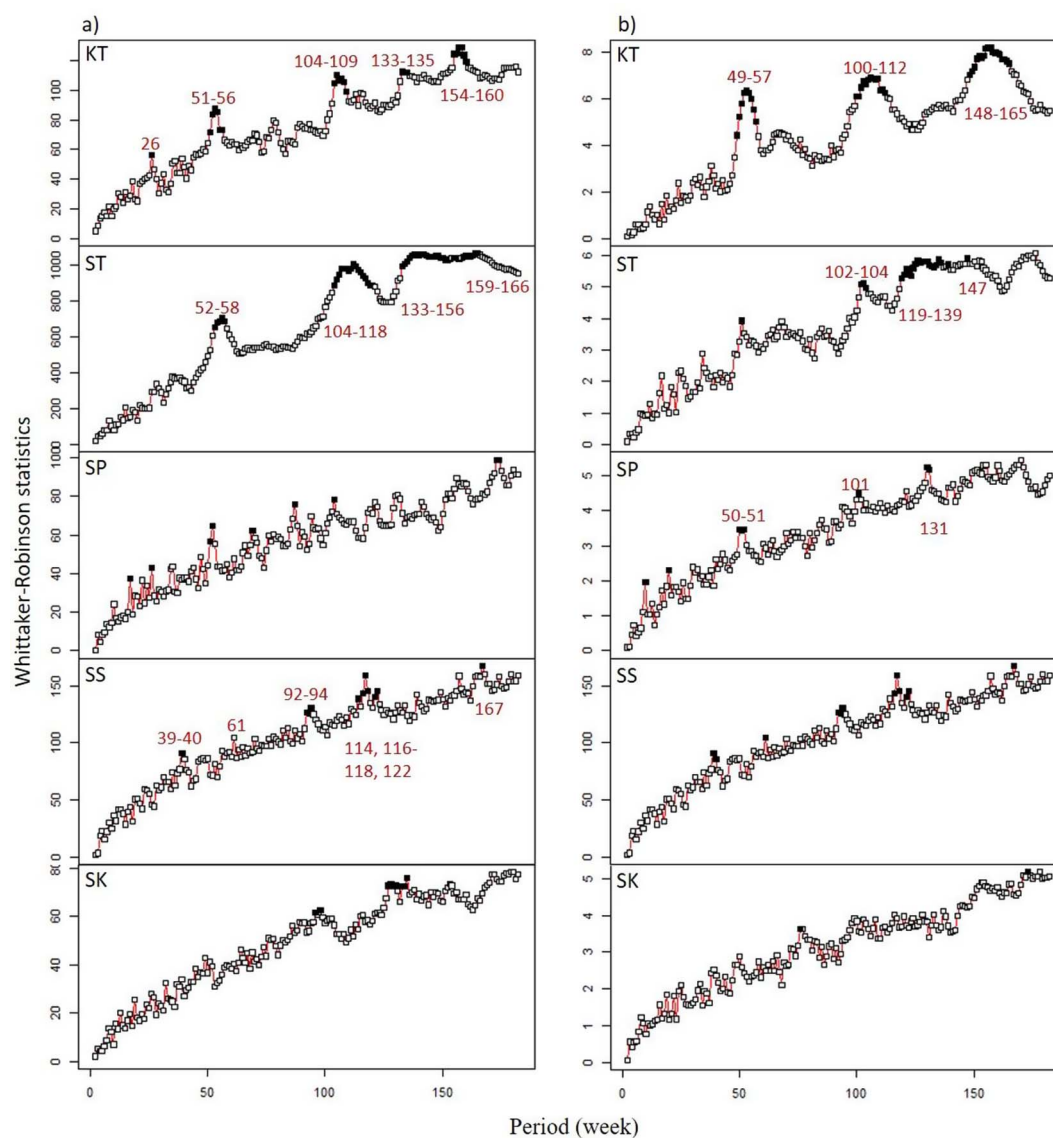


Fig. 5. Whittaker-Robinson periodograms computed for (a) weekly abundance and (b) richness, featuring periods between 2 and 182 weekly intervals from a 365-week data series from 01 June 2007 to 31 May 2014. The upper limit of the observation window of the periodograms is the number of observation intervals divided by 2 or a 182-week period. Black squares identify periods that are significant at the 0.05 level. For site names, see Fig. 1.

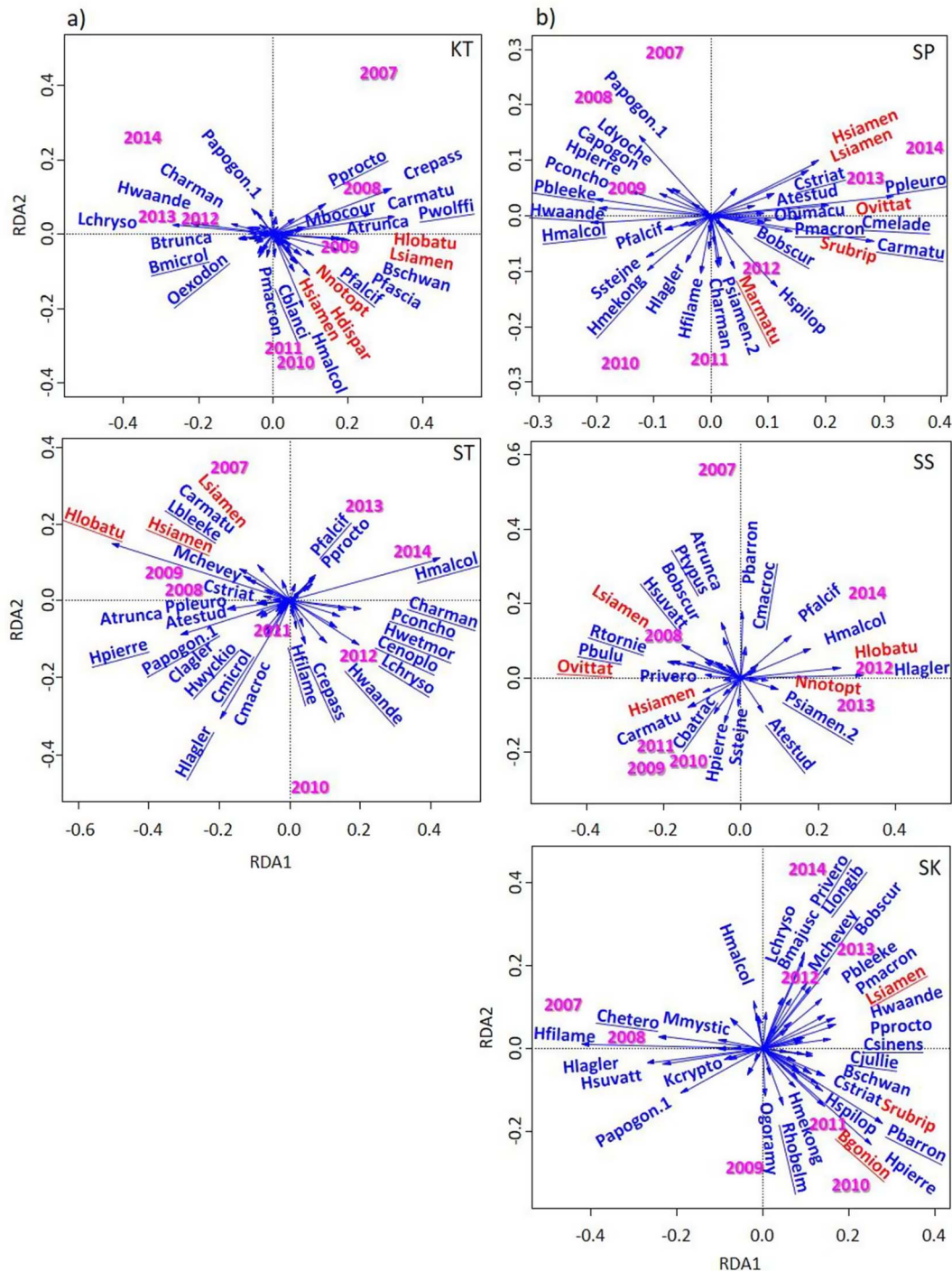


Fig. 6. RDA biplots of Hellinger-transformed assemblage data showing the important species (with SCBD indices greater than mean SCBD) contributing to the temporal shift in assemblage composition in each site. (a) Mekong River; (b) 3S Rivers. The biplots show species (arrows) and sampling units grouped by year. Names are abbreviations of fish species names. Species with very small contributions to the ordination are removed for clarity. Underlined species (blue) are indicator species identified by the multipatt function. Species in red have generalist habitat preferences. The assemblage ordination is explained by time (years) and its quadratic effect (not shown). Test of the multivariate RDA R-square: $P < 0.001$. Full species names and ecological attributes are shown in S5. For site names, see Fig. 1.

predictable environmental fluctuations are characterized by temporal (seasonal) assemblage change, whereas sites with unpredictable environmental conditions are represented by aseasonal assemblage variability, as exhibited in the 3S.

In addition, in line with our second expectation, we find that sites displaying flow disruptions (i.e., SP, SK, and SS) are generally poorer in species richness and lower in species diversity than sites with more stable seasonal flow patterns (i.e., KT and ST) (Fig. 3b, c). This pattern is most likely due to flow alterations caused by dams. In other Mekong

tributaries, lower species richness has also been observed in regulated rivers (i.e., Gam and Mun Rivers) compared to an unregulated one (Sankgram River) (Phomikong et al., 2014), and hydrological alterations have also been previously identified to cause changes in fish assemblage structure (i.e., reduced species diversity, shift in compositional and life history structure) in central Amazonian and American rivers (Mims and Olden, 2013; Röpke et al., 2017). Further, a general decreasing trend in species abundance, richness and diversity index in the Mekong-3S system has been observed since 2010 (S2). This

temporal variation is coincident with the threefold increase in hydropower dam reservoirs in the 3S sub-basin from 2007 to 2010 (Fig. 2) and the construction of a new mainstream dam (Xayaburi) in LMB, which has been underway since 2012 (International Rivers, 2014). In fact, hydropower dams severely alter flows of a river system, causing recruitment failure and diminishment of fisheries productivity at both local and regional spatiotemporal scales worldwide (Jellyman and Harding, 2012; Mims and Olden, 2013; Poff et al., 2007; Winemiller et al., 2016). However, the decreasing trends in species abundance, richness and diversity index are much stronger in sites of the 3S rivers and are attributed to the increasing river impoundment upstream (Fig. 2), which dampens flood pulses, mutes seasonal and inter-annual flow variation, disrupts flow connectivity among fish critical habitats, and alters food web dynamics that support fish diversity and biomass, as previously documented in (Arias et al., 2014; Baird et al., 2002; Baird and Meach, 2005; Claassen, 2004; Hirsch and Wyatt, 2004; Ou and Winemiller, 2016; Piman et al., 2013; Rutkow et al., 2005).

Relative to our third prediction, we find that the temporal dynamics of assemblage composition are driven by specialist species in the Mekong mainstream (Fig. 6a) and by generalist species in the 3S (Fig. 6b). The RDA biplots (Fig. 6a, b) illustrate that key species contributing to the temporal changes in the Mekong sites during the last four years of the survey are disproportionate towards specialists, including medium and large-sized cyprinids of the family Cyprinidae, river catfishes of Pangasiidae and sheatfishes of Siluridae. These fishes are often long-distance migrants and/or mainstream spawners and prefer mainstream rivers as their main habitats. The opposite is observed in the 3S rivers, where small-sized species minnows and carps of Cyprinidae with generalist habitat preferences are among the key species contributing to the assemblage change. Further, some floodplain resident fishes, such as climbing perches, snakeheads and airbreathing catfishes, are also among the key species in the assemblage composition of the 3S rivers towards the last few years of the survey. These fishes have airbreathing organs and can physically withstand adverse environmental conditions (MRCS, 1992; Poulsen et al., 2002; Welcome, 2001). This trend in assemblage composition of the Mekong-3S system is likely to resemble the environmental filtering by dams because many migratory (specialist) species that depend on seasonal flow dynamics to complete their life cycles are constrained or extirpated by flow disruption of dams (Liermann et al., 2012), which finally leads to increased faunal homogenization as observed in the middle Lancang-Mekong River (Li et al., 2013), many Chinese lakes connecting to the Yangtze River (Cheng et al., 2014), and rivers across the United States (Poff et al., 2007). Our results also strengthen recent review and field studies that find fish assemblages in SS to be represented by small-sized and generalist species such as small mud carps (mTL < 25 cm) of the family Cyprinidae, and fewer large-sized migratory species such as river catfishes of Pangasiidae (mTL > 100 cm), relative to the Mekong mainstream sites (Baran et al., 2013a; Ou et al., 2017; Ou and Winemiller, 2016).

Interestingly, *Henicorhynchus lobatus* is among the highest SCBD values found in ST, KT and SS. The species is known to be an ecological keystone species, playing a critical role in food security throughout LMB and being an important prey species for many predatory fishes and Irrawaddy dolphins (Baird, 2011; Fukushima et al., 2014). This species, together with its relative *H. siamensis*, are claimed by the villagers to have never been seen in the upper SS River in the last 10 years (Baran et al., 2013a). These species are therefore of high conservation value in KT and ST, and need restoration in the altered SS (Legendre and De Cáceres, 2013). Other generalist (*Labiobarbus siamensis*) and specialist species (*Puntioplites falcifer*, *Hypsibarbus malcolmi*) (migratory/mainstream spawners) share a similar status to *H. lobatus* and *H. siamensis* (among the highest SCBD values) and therefore deserve similar conservation attention. In addition, fish species that have high SCBD values and are the indicator species demonstrated in S4 represent dominantly abundant and ecologically important species in the Mekong-3S system.

They therefore have high values for fisheries health monitoring and fish biodiversity conservation initiatives (De Cáceres et al., 2010; Legendre and De Cáceres, 2013).

5. Conclusion

The results of our study suggest that the hydrological conditions of rivers play a pivotal role in shaping the temporal dynamics of tropical freshwater fish assemblages. Flow patterns act as an environmental filtering process in influencing the spatial and temporal organisation of local and regional fish assemblage structures. It is evident that hydropower dams in the upper 3S rivers alter their natural flow seasonality and predictability. This has adversely impacted aquatic organisms adapted to the natural flow conditions for their life cycles. We find that there are overall declining trends in local fish species abundance and richness, with strong temporal variability in local beta diversity of the Mekong-3S system. The disturbed 3S rivers are represented by aseasonal assemblage changes, whereas the Mekong sites are characterised by seasonal assemblage variability. Temporal shifts in assemblage composition are driven by generalist species in the disturbed 3S rivers; whereas specialists are more representative of the Mekong River. The information presented here contributes to the understanding of fish assemblage responses to upstream flow modification and is thus important to better inform river fisheries monitoring, management and conservation initiatives. Our present work focused on temporal fish assemblage composition responses in relation to flow regulation. Therefore, our results would be beneficial for future work aiming to forecast future flow changes and how this affects fish diversity in the Mekong 3S-River System (Chau and Wu, 2010; Wang et al., 2017).

While further dam building is imminent in the Mekong River system, the combined effects of the present and future 3S dams are predicted to have catastrophic impacts on the fish productivity and diversity which secures food to > 60 million people of LMB (Hortle, 2007; Ziv et al., 2012). For this reason, we suggest that some mitigation measures must be undertaken to minimise such impacts. First, there should be a basin-scale integrative strategic plan (accounting for cumulative impacts on hydrology and ecosystem services) that finds the balance between exploiting hydropower potential and sustaining key resources, e.g., in dam site selection (Winemiller et al., 2016). Second, the best available technologies related to up- and downstream fish pass facilities (Schmutz and Mielach, 2015) must be built for existing and planned dams to facilitate up- and downstream fish migrations. Flow management measures that could mimic natural hydraulic variations, e.g., Sabo et al. (2017) should be privileged, as these variations are the main ecological trigger for fish dispersal and reproduction success in the Mekong. Indeed, rivers downstream of gradual release storage dams are found to have higher fish biomass and richness than those downstream of flow peaking storage dams (Guénard et al., 2016). Third, ecological effects of dams are not only restricted to ecosystem services and functioning but also to society, culture and livelihoods such as losses of property, employment, social connections and culture through human resettlements and the displacement of indigenous people. Best practice guidelines on a (participatory) Social Impact Assessment should be applied to assess such sociocultural costs at appropriate temporal and spatial scales (Tilt et al., 2008) for formulating acceptable compensation, resettlement and rehabilitation policies. Finally, institutions permitting and financing hydropower dam development should ensure that dam developers comply with these best practice guidelines during their project design, commission and decommission phases to meet both societal and environmental objectives; otherwise, key natural resources such as fisheries and rural communities that depend on those resources will continue to suffer from the impacts of dams.

Acknowledgements

We are grateful to the Erasmus Plus, Belmont Forum (TLSCC project) and the European Erasmus + credit mobility and capacity building CONSEA Programmes for funding our study. Cordial thanks to the MRC Fisheries Programme, Inland Fisheries Research and Development Institute and the Fisheries Administration, Cambodia for making available the datasets used in this study. We also thank Nam So, Phen Chheng, Solyda Putrea, Sokheng Chan and 15 fishers for supervising and implementing the field fish monitoring, Ratha Sor, Gaël Grenouillet and Fangliang He for their discussions on data analysis, and Kunthea Nuon for helping prepare the map for this study. Finally, we thank the Laboratory of Evolution and Biological Diversity (EDB lab) for their support. EDB lab was supported by ‘Investissement d’Avenir’ grants (CEBA, ref. ANR-10-LABX-0025; TULIP, Ref. ANR-10-LABX-41).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2018.01.023>.

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