Fish assemblage responses to flow seasonality and predictability in a tropical flood pulse system

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Abstract. Hydropower dams are looming in the Mekong Basin, affecting river flows that structure aquatic communities. Here, we quantitatively assessed flow seasonality and predictability in three sites located in three rivers displaying a gradient in flow alterations caused by upstream dams and investigated how fish assemblages responded seasonally and inter-annually to this gradient. By analyzing 7-yr daily fish and water monitoring data, we found that dams disturbed the natural flow seasonality and predictability. While the river displaying the lower seasonality–predictability was characterized by a distinct seasonal variation in assemblage composition with high species turnover, rivers with stronger flow seasonality–predictability exhibited broadly similar seasonal patterns in fish assemblage composition with low species turnover and regular annual peaks of fish migration. These results challenge the expectation of higher species turnover in systems displaying higher flow seasonality and predictability and may be partly due to the strong adaptation of fish assemblages to these specific systems. By enhancing our understanding of biological systems in the highly seasonal–predictable and aseasonal–unpredictable environments of the lower Mekong system, these findings suggest that hydropower-related pulsed flows that can mimic as far as possible natural pulsed flows are critical to reduce downstream effects on aquatic organisms.

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Introduction

Construction of hydropower dams is continuously increasing mainly in developing countries and the emerging economies of Southeast Asia, South America, and Africa (Zarfl et al. 2015). These dams are constructed or planned predominantly in the world's most biodiverse river basins such as the Amazon, the Congo and the Mekong (Winemiller et al. 2016). The Mekong Basin was, for example, identified as one of the world's regions with high threats for water security to both humans and biodiversity (Mcintyre et al. 2010). In this basin, numerous large dams have been built since the 1990s and several others are planned or under construction (Fan et al. 2015, Winemiller et al. 2016, Ngor et al. 2018) (see also Fig. 1; Appendix S1: Fig. S1).
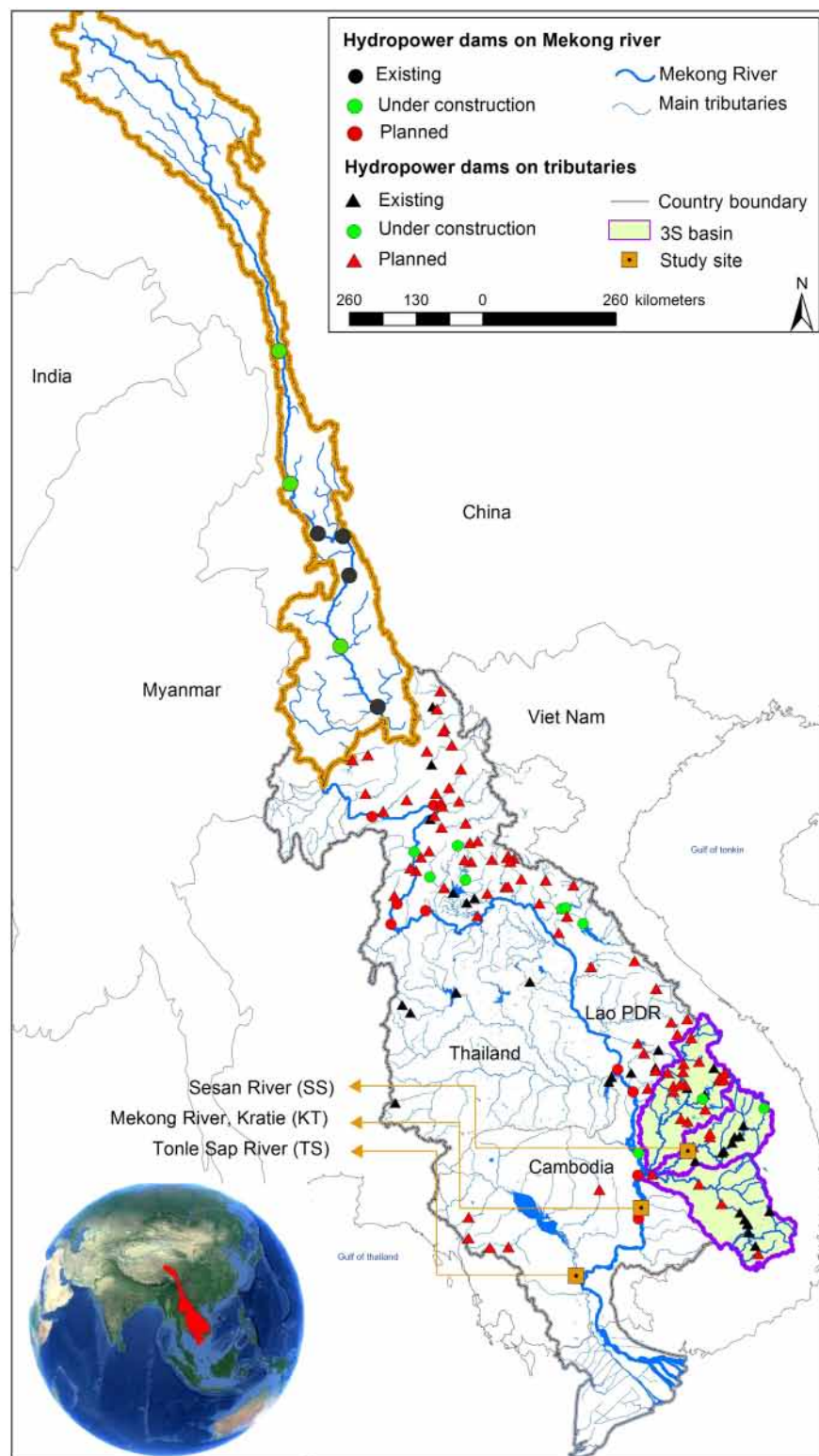
Fig. 1. Map showing the study sites and hydropower dam positions in the Mekong Basin (data source: MRC

(Fig. 1. *Continued*)
Hydropower Project Database 2015). Site codes: SS = Sesan River; KT = Mekong River in Kratie; and TS = Tonle Sap River.

Among other things, dams are known worldwide to disrupt river continuity, to block migration routes of riverine fishes, to dampen flood pulses, and to mute flow seasonality. These disturbances alter in return the structure of aquatic assemblages that are seasonally adapted to natural seasonal flow dynamics (Collier et al. 1996, Agostinho et al. 2004, Graf 2006, Poff et al. 2007, Latrubesse et al. 2017, Sabo et al. 2017). Specifically, dams generate hydropower-related pulsed flows, for example, hydropeaking reacting to energy demands (from hourly to seasonally) which adversely affect riverine fishes and other aquatic organisms through stranding or extirpation, downstream displacement, and spawning/rearing disruption (Young et al. 2011, Schmutz et al. 2015, Kennedy et al. 2016, Tonolla et al. 2017).

Hydrology of the Mekong River is characterized by strong seasonality with regular wet and dry seasons highly predictable across years (MRC 2005, Adamson et al. 2009). Given that the structuring force of the Mekong fish assemblages is deeply embedded in the local seasonality and predictability of the Mekong's hydrological conditions, flow alterations caused by upstream dams (i.e., modifying timing, magnitude, and frequencies of seasonal flow) should have implications for spatiotemporal dynamics of these assemblages (Valbo-Jorgensen and Poulsen 2000, Poulsen et al. 2002, Baran 2006, Adamson et al. 2009, Sabo et al. 2017).

The seasonality concept is widely applied to explain life history adaptations of organisms (Mcnamara and Houston 2008), changes in species trait distribution patterns (Fitzgerald et al. 2017), shifts in abundance and coexistence of species (Shimadzu et al. 2013), shifts in food web structure (McMeans et al. 2015), or changes in beta diversity patterns (Tonkin et al. 2017). In addition, to have a complete understanding of the temporal patterns of local assemblages, there is a need to consider the system predictability (Colwell 1974, Tonkin et al. 2017). By definition, "seasonality is the occurrence of certain obvious biotic and abiotic events or groups of events within a definite limited period or periods of the astronomic (solar, calendar) year," while predictability is "the regularity of recurrence of the within cycle (e.g. annual) distribution of events across multiple cycles" (Tonkin et al. 2017).

Here, we focused on a strongly tropical seasonal–predictable flood pulse system (MRC 2005, Adamson et al. 2009) (i.e., the lower Mekong system) and used Tonkin et al.'s seasonality–predictability framework (Tonkin et al. 2017) to assess how hydrological alterations caused by upstream dams structured local fish assemblages. According to this framework, we expect that (1) predictably seasonal environmental conditions should promote the highest levels of temporal changes in species abundance, richness, and assemblage composition and (2) seasonal turnover is stronger in these conditions due to distinct habitat conditions between seasons. On the other hand, aseasonal and unpredictable systems should generate the lowest temporal diversity, harboring assemblages that show little seasonal species turnover. In other words, species turnover would be maximized under highly predictable seasonal conditions, while nestedness (i.e., assemblages in one season being a subset of those in the other season) may dominate in unpredictable aseasonal environments (Tonkin et al. 2017). To test these hypotheses, we focused on three study sites experiencing different levels of flow alteration, and for which we expected a gradient in flow seasonality and predictability. Specifically, we first assessed how seasonality and predictability of flow patterns varied among the three sites. Second, we tested the hypotheses that seasonal variations in fish assemblage abundance, richness, and composition were driven by flow seasonality and predictability using a unique 7-yr daily fish and water level dataset monitored at the three sites. Seasonal patterns of fish traits (i.e., morphological and behavioral traits) were also examined to explain the seasonal variation in fish assemblage due to the expected gradient of flow alteration in the three sites.

METHODS

Study sites

This study covered three sites, that is, the Mekong mainstem at Kratie (KT), the Sesan River (SS) at Ratanakiri joining the Sekong and the Mekong River in Stung Treng, and the Tonle Sap River (TS) at Kandal joining the Mekong River in the capital city of Phnom Penh (Fig. 1). At KT, the Mekong mean annual discharge is ~475 billion m^3/yr varying from <3000 m^3/s during low flows (March–April) to ~40,000 m^3/s during high flows (August–September) (Adamson et al. 2009). Sesan covers ~24% of the total surface area (78,645 km^2) of the Sekong, Sesan, and Srepok (3S), had mean daily water level of ~4.91 m (at Voeun Sai) for the period June 2007–May 2014, and, together with Sekong and Srepok, contributes ~20% to the Mekong total annual flows (MRC 2005, Adamson et al. 2009). Tonle Sap sub-basin covers a catchment area of 85,790 km^2 (11% of the Mekong Basin [MRC 2003]) and receives 54% of its waters from the Mekong River, 34% from its lake tributaries, and the rest from rainfalls (Kummu et al. 2014). Mean discharge at the TS River was estimated at ~83.1 and ~81.9 billion m^3 during the inflow and outflow periods, respectively (Kummu et al. 2014). The selected study sites are all located in the most fish-biodiverse ecoregions of the Lower Mekong Basin (LMB; Poulsen et al. 2002, Chea et al. 2016). For example, TS and its floodplain lake is a World Biosphere Reserve under the United Nations Educational, Scientific and Cultural Organization (UNESCO) since 1997 (Davidson 2006), one of the world largest freshwater fisheries zones (Baran 2005). Riverine fishes (87% of the total 1200 Mekong fishes) seasonally utilize these river systems as part of their life cycles (Rainboth 1996, Baran et al. 2013). Most species spawn and seasonally migrate down the river system in KT and Stung Treng to enter feeding and rearing habitats in the TS floodplains and areas southern Phnom Penh, or up the Sekong, SS, and Srepok tributaries (3S) at the onset of the wet season, and later return in the Mekong mainstream (i.e., KT and Stung Treng) to find refugia for sedentary periods at the onset of the dry season (Valbo-Jorgensen and Poulsen 2000, Poulsen et al. 2002, 2004, Sverdrup-Jensen 2002, Baran 2006).

While more natural flow conditions are expected in KT and TS, flows in SS are anticipated to be highly altered (compared to its pre-dam condition) by the functioning of upstream dams which weakens the flow seasonality and predictability strength of the system (see Appendix S1: Figs. S1, S2). Marked flow alterations were already observed in previous studies that qualitatively described rapid rising and falling water levels in the downstream SS when the 720-MW Yali Falls Dam was under construction in 1996 and became officially operational since 2000 (Ratanakiri Fisheries Office 2000, Baird et al. 2002, Claasen 2004, Hirsch and Wyatt 2004, Baird and Meach 2005, Rutkow et al. 2005). Flow alternations are expected to be even more severe when five more dams were commissioned between 2006 and 2011 in the SS basin (Appendix S1: Fig. S1). As indicated in a recent study, the upstream SS's under-construction and operational dams in Viet Nam Highlands caused an overall increase of 52% in dry-season flow and a decrease of 22% in the wet-season flow of this river near the Cambodia border (Piman et al. 2013).

Data collection

Data collection was based on the standard sampling procedures of the Mekong River Commission (MRC) (MRC 2007). Fish catches were routinely monitored between June 2007 and May 2014 at the three studied sites. Our sampling sites stayed unchanged over the 7-yr study period (i.e., the same habitats were prospected all along the period). Daily, three sets of stationary gillnets (three fishers for each site) (length: 120 ± 50 m; height: 2–3.5 m; mesh size: 3–12 cm; soak h/d: 12 ± 2) were used to capture fish. The fishers were supervised by the fish monitoring officers from the Cambodia Inland Fisheries Research and Development Institute of the Fisheries Administration and the MRC. A list of about 900 Mekong fishes and their traits was derived from the Mekong Fish Database (MFD 2003). Captured fish were identified to the species level and counted, and their taxonomic classification as well as species traits was updated using FishBase (Froese and Pauly 2017) in cross-checking with Rainboth (1996), Rainboth et al. (2012), and Kottelat (2013). The collected fish data were recorded into the national fish monitoring database. Water

levels at each location were registered by MRC. Key fish traits used in the analysis of seasonal patterns fall in five broad categories, namely physical habitat guilds, migration guilds, maximum total lengths, trophic levels, and positions in the water column. Details of each fish trait category are given in Appendix S1: Table S2.

Statistical analyses

Daily species abundance collected by the three fishers in each site was computed as daily mean samples and then summed into weekly species abundance from 1 June 2007 to 31 May 2014 (i.e., 366 weeks). Similarly, site daily water levels were computed as mean weekly water levels for the same 366 weeks. All statistical analyses were performed in R (R Development Core Team 2017).

To quantify the strength of seasonality, Colwell's seasonality index (Colwell 1974) on site daily water levels was computed using Colwells function of hydrostats package (Bond 2016). The seasonality index M/P, which is the Colwell measure of contingency (M) standardized by Colwell's within-season predictability (P) (Colwell 1974, Tonkin et al. 2017), was used. Colwell's contingency (consistency of timing between years) quantifies the degree of repeatability of biological (e.g., fish migration) or physical (e.g., hydrology) periodic phenomena. The value of the seasonality index varies between 0 and 1, with 1 being the maximum seasonality value. In addition, wavelet analysis was applied to quantify the strength of predictability of site hydrology. The wavelet analysis is a harmonic analysis with a time–frequency representation of a signal. This harmonic analysis uses a special function called mother wavelet which allows time and scale localizations. Using the R package Wavelet-Comp, the Morlet mother wavelet was selected (Roesch and Schmidbauer 2014) for the analysis. While being comparable to the Fourier analysis that detects the dominant frequencies over time series, wavelets offer the advantage of investigating multiple scales simultaneously (Torrence and Compo 1998, Tonkin et al. 2017). In the wavelet transform, a time series is decomposed into time, frequencies, and the power which can be examined in the three-dimensional space through the plot of the wavelet power spectrum (WPS). In WPS plot, "time" indicates the time series on the

x-axis, while the contribution of the "frequencies" is represented by "period" on the y-axis. The "power" characterizes the magnitude of variance within the time series at a given wavelet. The WPS determines which features of the signal are determinant and contributive and which are less significant.

To compare seasonal fish assemblage responses among sites, we (1) defined the wet (June–November) and dry (December–May) seasons, based on 9-yr mean daily water levels of the Mekong River, when entering Cambodia (at Stung Treng) (Appendix S1: Fig. S3); (2) computed weekly fish assemblage matrix in each site as mean seasonal assemblage matrix; and (3) applied principal components analyses (PCAs) on the Hellinger-transformed seasonal fish abundance and trait data matrices, using fviz_pca_ind function of factoextra package (Kassambara 2017) to visualize seasonal (dry and wet seasons) patterns of fish assemblages in each site. Hellinger transformation was applied because PCA is a linear ordination model that requires pre-transformation of the abundance data to meet the (multi)normal distribution assumption (Borcard et al. 2011). Finally, we computed the seasonal beta diversity and partitioned it into turnover (i.e., species replacement in one season by different species in the other season) and nestedness (i.e., species in one season being a strict subset of the species at the other season) components, using beta.pair function with the Sorensen dissimilarity index from betapart package (Baselga 2010, Baselga and Orme 2012). Also, species turnover and nestedness were computed separately for wet and dry seasons to examine how each season affects the observed turnover and nested pattern of beta diversity in each of the three study sites.

To identify significant interdependencies at multiple timescales between fish assemblages and water levels over the study period, cross-wavelet analyses were performed on the weekly series of fish total abundance and richness (y) and mean weekly water levels (second y-axis), using analyze.coherency function from Wavelet-Comp package (Roesch and Schmidbauer 2014). Cross-correlation analysis (ccf function) on the abundance and richness (y) and water series (second y-axis) in each site was used to derive the time lag with the maximum value of

cross-correlation coefficients (Shumway and Stoffer 2011) that correlated the fish assemblage responses to site hydrological variations. Prior to cross-correlation analyses, fish abundance, richness, and water data series were tested for stationarity (i.e., if there were significant linear temporal trends in the data). When stationarity was violated (as detected for abundance, richness, and water data series in SS, abundance and richness data series in KT, and richness data series in TS), residuals were computed to detrend the series (Legendre and Legendre 2012) and used in the cross-correlation analyses.

RESULTS

Seasonality–predictability of site hydrology

Colwell's seasonality index on hydrology consistently found that flows in TS exhibited the strongest seasonality (M/P = 0.93), whereas KT ranked second in its seasonal flow patterns (M/P = 0.90) and SS showed the weakest flow seasonality (M/P = 0.83). Flows in KT and TS had more seasonal–predictable patterns than in SS where strong flow variability was observed

(Fig. 2a). As further evidenced in the wavelet plots (Fig. 2b), flows in TS and KT comparably exhibited very strong continuous seasonal–predictable patterns as indicated by a uniformly wide red band at ~52-week frequency (annual cycle). Such patterns were relatively weak in SS, with observed chaotic signals of strong wavelet power at multiple periods across the wavelet spectrum. Flow variations in KT and TS also demonstrated a secondary strong predictable power (red–yellow) at ~26-week frequency (semi-annual cycle), while no such patterns were captured in the WPS in SS (Fig. 2b). Such patterns were illustrated clearly in the average wavelet power across the full 7-yr period, showing the strongest peaks at 52-week frequencies for all sites, with increasing average wavelet power (i.e., predictability strength) in the respective order of site SS, KT, and TS (Fig. 2c).

Fish assemblage patterns

Overall, 266 species were recorded from the three sites (133 in SS, 208 in KT, and 143 in TS). Fish abundance (number of individuals) was higher in SS and TS than in KT (Appendix S1:
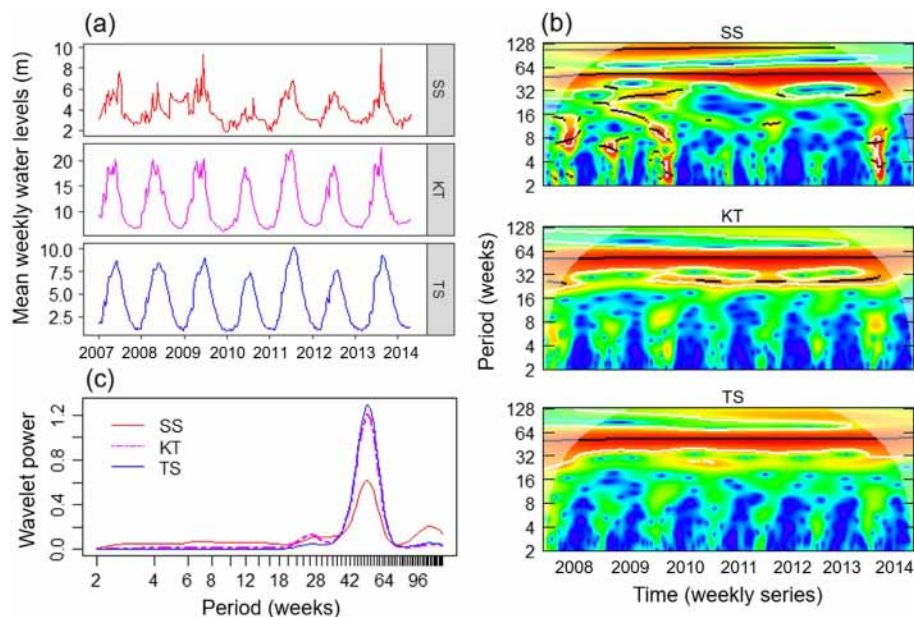

Fig. 2. Seasonality and predictability of 7-yr weekly water levels of the three rivers: Sesan (SS), Kratie (KT), and Tonle Sap (TS). (a) Site water level series. (b) Wavelet power spectrum of site water levels, with red representing stronger wavelet power and blue weak. (c) Site average wavelet power derived from (b). Note that Colwell's seasonality index (M/P) was 0.83 in SS, 0.90 in KT, and 0.93 in TS. For site codes, see Fig. 1.

Fig. S4a). By contrast, KT was the most species-rich relative to SS and TS (Appendix S1: Fig. S4b). Fish assemblages in SS and TS were disproportionately dominated by small body-sized generalist species, whereas assemblages in KT were more proportionally represented by species with different body-sized classes (small, medium, large, and giant-sized species) (Appendix S1: Fig. S5, Table S1). However, three small-sized generalists, namely *Henicorhynchus lobatus*, *Henicorhynchus siamensis*, and *Labiobarbus siamensis* (Cyprinidae, Cypriniformes), were dominantly ubiquitous in the three sites. While *H. lobatus* was the most abundant species in KT and TS, a small-sized floodplain-resident climbing perch, *Anabas testudineus* (Anabantidae, Perciformes), ranked top in SS. See Appendix S1: Fig. S5 for top 15 abundant species and Appendix S1: Table S1 for mean weekly abundance of key species recorded in each of the three sites.

Seasonal fish abundances and richness showed no significant difference between dry and wet seasons (with $P = 0.8$ and 0.14, respectively) in SS (Appendix S1: Fig. S6a, b). In KT, significantly higher richness was detected during the dry season ($P = 0.04$), while no significant difference was observed for seasonal fish abundances ($P = 0.21$). In TS, abundance was by far significantly higher during the dry season ($P = 0.0006$), while no significant difference was observed for seasonal richness ($P = 0.52$).

Clear differences in fish assemblages between dry and wet seasons were observed in SS and to a lesser extent in KT, while seasonal assemblages in TS appeared less discriminated between the two seasons (Fig. 3). Temporal beta diversity showed a gradient of seasonal species turnover among sites with the highest values observed in SS and the lowest in TS (Fig. 4). Kratie displayed intermediate values for both species turnover and nestedness in the three sites. In SS, high species turnover occurred during the dry season ($P < 0.0001$) and high nested pattern occurred during the wet season ($P = 0.004$). In KT, high species turnover occurred during the wet season ($P < 0.0001$) and no significant difference was revealed in seasonal nestedness. In TS, no significant difference between wet and dry seasons was observed for both species turnover and nestedness (Fig. 4b).

Generally, there is a clear distinct pattern of fish traits between the wet and dry seasons for the three study sites regardless of different flow seasonality and predictability. Interestingly, longitudinal migratory species used SS and KT mainly during the dry season and TS during the wet season. Also, high-trophic-level floodplain-resident species using demersal habitats appear to colonize tributary rivers (i.e., SS, TS) during the wet season (Fig. 3b).

Fish abundance and richness, and flow coherence

No clear peak in both weekly abundance and richness in relation to hydrological cycles was observed in SS (Figs. 5a, 6a). By contrast, a clear seasonal peak in abundance was repeated annually, that is, before the peak water levels in KT (i.e., at the onset of wet season) and after the peak water levels in TS (i.e., during the falling water levels), whereas richness in both sites was greater during the low flow. Noticeably, fish abundance showed a significant declining trend in SS ($P = 0.03$) and KT ($P < 0.0001$), while richness exhibited significant decreasing trends for all sites ($P < 0.0001$) over the study period (Appendix S1: Fig. S7).

Cross-wavelet analysis on variation of weekly abundance and richness with water levels showed that KT and TS were characterized by strong, coherent seasonality–predictability cross-wavelet power in the two data series at annual (~52 weeks) and semi-annual (26 weeks) frequencies (Figs. 5b, 6b). Such patterns were incoherent and mixed up in SS, as illustrated by disordered responses of the bivariate series with patchy red colors, fragmented ridges, and arrows, pointing to different directions across the cross- WPS. These patterns were illustrated clearly in the site average cross-wavelet power over the 7-yr study period, showing the strongest peak at 52-week and secondary peak at 26-week frequencies for all sites, with SS having the weakest average cross-wavelet power relative to KT and TS (Fig. 7a, b). Noticeably, average cross-wavelet power for the abundance vs. water series was muted in SS relative to KT and TS (Fig. 7a).

Cross-correlation analyses (Fig. 8) revealed that abundance and richness in SS exhibited no seasonality, with almost no significant coefficients detected in the abundance series as compared to those of KT and TS. Correlation lags
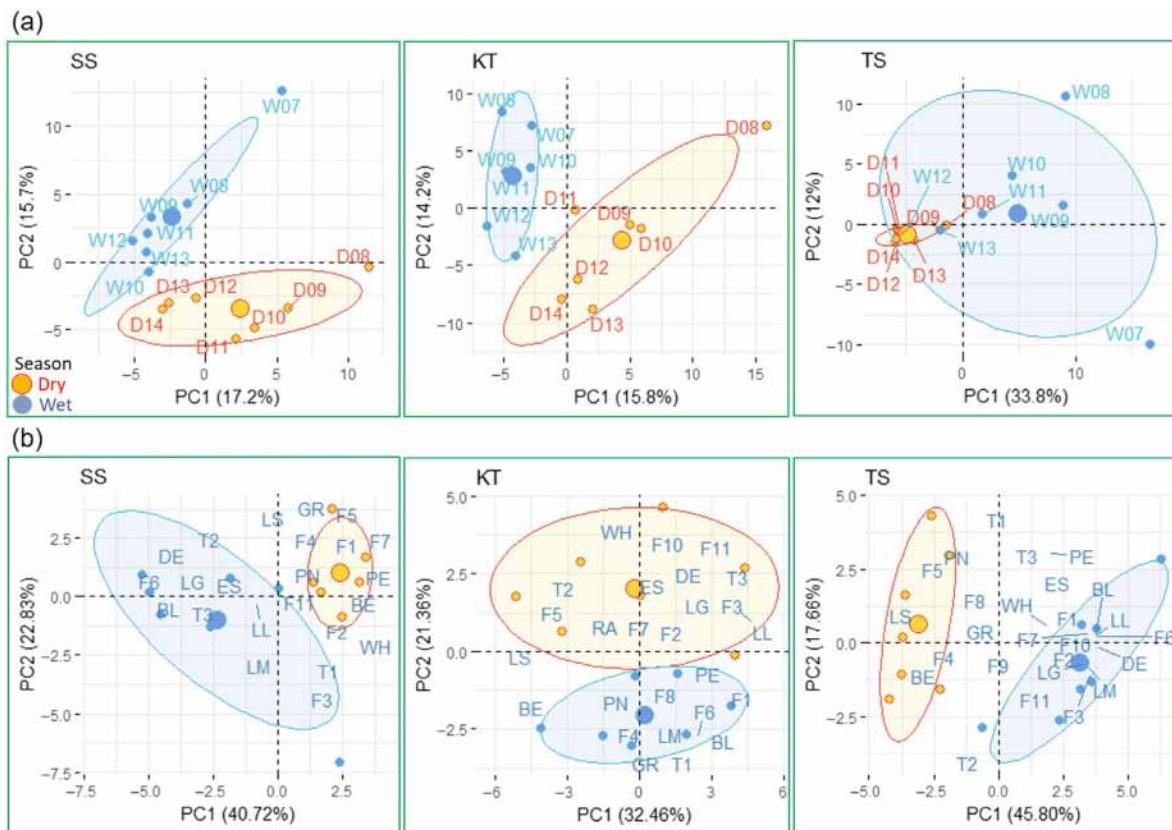
Fig. 3. Seasonal fish assemblage and trait responses. Principal components analyses plots displaying (a) seasonal fish assemblage patterns and (b) seasonal fish trait patterns grouped by wet (W) and dry (D) seasons. Smaller points indicate seasonal fish assemblages (a) and seasonal fish traits (b). Larger points symbolize the centroid of the ellipse that groups the seasonal fish assemblages (a) and seasonal fish traits (b) for the wet and dry seasons over the study period. For (a), the two digits after W and D indicate "year," for example, W07 = wet season 2007. For (b), the abbreviations denote fish traits including (1) physical habitat guilds, that is, F1 (rhithron resident), F2 (main channel resident), F3 (main channel spawner), F4 (floodplain spawner), F5 (eurytopic/generalist), F6 (floodplain resident), F7 (estuarine resident), F8 (anadromous), F9 (catadromous), F10 (marine visitor), and F11 (non-native); (2) migration guilds, that is, WH (white fishes = longitudinal migratory species between Mekong River, lower floodplains, and major tributaries), BL (black fishes = non-longitudinal migratory or floodplain residents), and GR (gray fishes = lateral migration between floodplain and local rivers or streams); (3) maximum total lengths, that is, LG (giant size ≥100 cm), LL (large size 61–99 cm), LM (medium size 26–60 cm), and LS (small size ≤25 cm); (4) trophic levels, that is, T1 (trophic level ≤2.75), T2 (trophic level 2.76–3.75), and T3 (trophic level >3.75); and (5) positions in the water column, that is, BE (benthopelagic), DE (demersal), PE (pelagic), PN (pelagic–neritic), and RA (reef-associated). For site codes, see Fig. 1. For species trait details, see Appendix S1: Table S2.

with maximum coefficients between abundance and water levels were estimated at −26 weeks in SS, 20 weeks in KT (before the peak flow in September), and −15 weeks in TS (after the peak flow in early October), whereas correlation lags with maximum coefficients between richness and water levels were estimated at −22 weeks in SS, −26 weeks in KT (after the peak flow or during the low-flow period), and −10 weeks in TS (after the peak flow). It is noteworthy that the cross-correlation lag with the maximum coefficient between water levels in KT and TS was estimated at −4 weeks (Appendix S1: Fig. S8). The list of fish species names, their abbreviations,
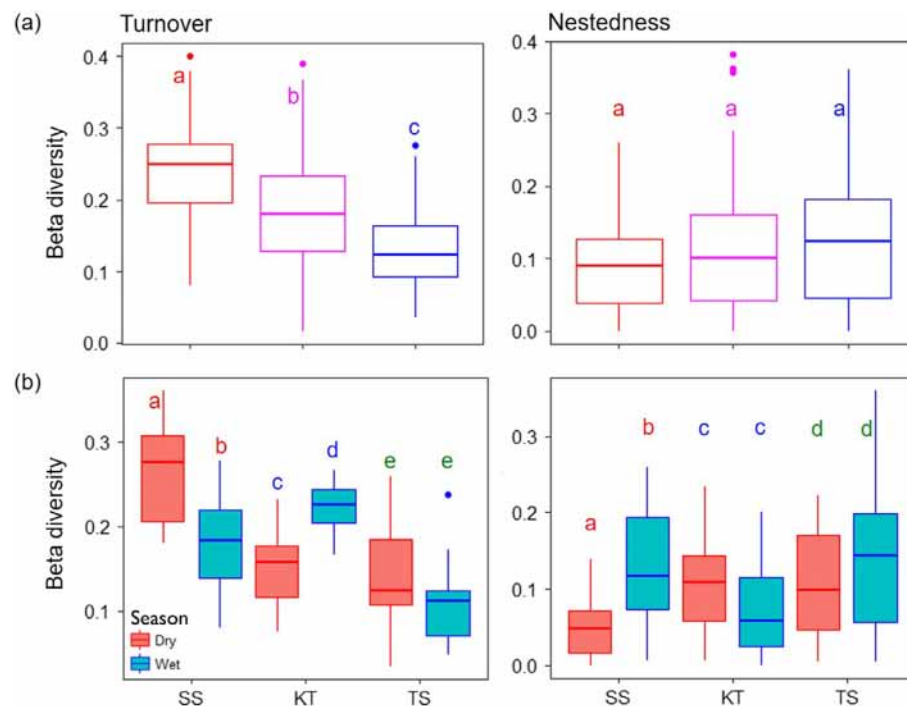
Fig. 4. Seasonal beta diversity partitioned into seasonal species turnover and nestedness using the Sorensen dissimilarity index. (a) Site seasonal species turnover and nested patterns. (b) Site species turnover and nestedness patterns by wet and dry seasons. Mean values among sites with a common letter are not significantly different at the 0.05 level (pairwise Wilcoxon rank-sum tests). For site codes, see Fig. 1.

and traits by genera, families, and orders is given in Appendix S1: Table S2.

DISCUSSION

Overall, our results support the hypothesis of a gradient in fish assemblage responses with flow seasonality–predictability, but surprisingly in a way contrary to Tonkin et al.'s (2017) framework. Indeed, we found higher assemblage seasonal turnover and lower nestedness in the site experiencing seasonal flow disturbances (SS) than in the more pristine ones (KT, TS). At least one reason could explain these contrasted results. The main hypothesis evoked by Tonkin et al. to expect high seasonal turnover in assemblages is that distinct habitats and thus distinct fauna should appear between seasons. To validate their hypothesis, they used stream invertebrate assemblages. While this distinct habitat hypothesis could work for invertebrates (Tonkin et al. 2017), whether it applies to fish assemblages is far from

evident. First, native fish assemblages are adapted to these predictable natural seasonal disturbances and are resistant to change, and second, the habitat does not change structurally during high-flow periods, except for water volume and water velocity. Species not adapted to high water velocities will disperse to escape these periodic unfavorable conditions and latter recolonize the site during the dry-season periods. Following this reasoning, we expect, as what we actually found, low turnover in sites displaying seasonal–predictable flows and nested patterns in assemblage composition between high-flow and low-flow periods (high-flow assemblages being a subset of low-flow assemblages). This being said, the high assemblage turnover found for our most disturbed site (SS) is more challenging to explain but could be related to hydropeaking.

Indeed, hydropeaking is widely known to alter hydraulic parameters such as water levels, velocity, and bed shear stress that fragments habitats
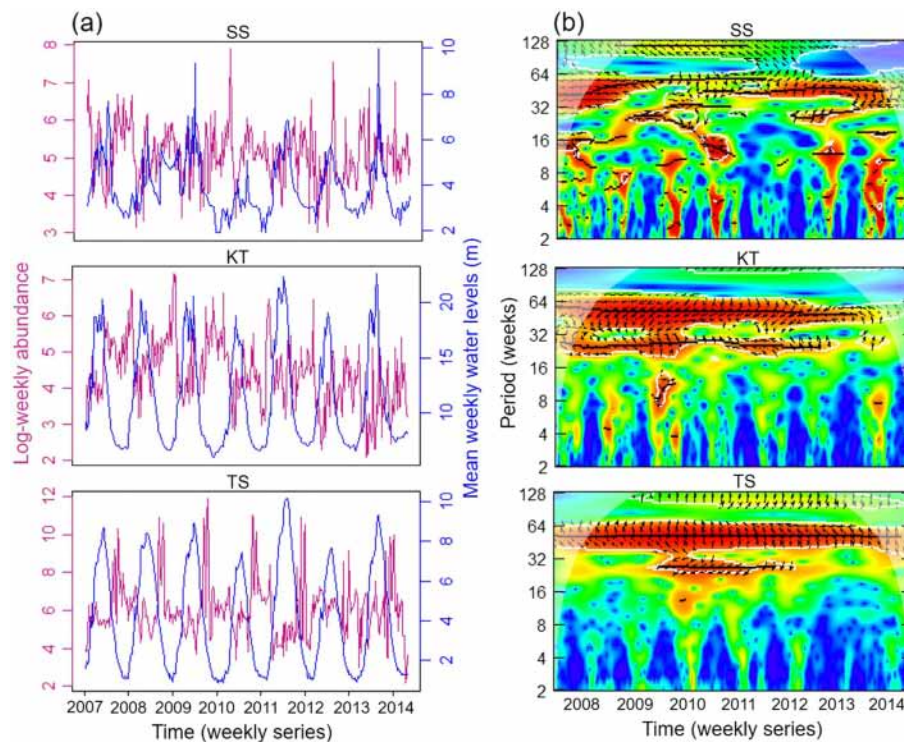
Fig. 5. Temporal variations of total weekly abundance (*y*) and mean weekly water levels (second *y*-axis). (a) Weekly abundance and mean water level data series, covering the period from 1 June 2007 to 31 May 2014. (b) Cross-wavelet power spectrum of weekly abundance and water levels. Red color represents stronger cross-wavelet power, and blue, weak. Arrows in each plot depict phase differences. Ridge lines illustrate cross-wavelet power coherence within a band of neighboring periods. Areas in the upper corners outside the "cone of influence" in each plot indicate the exclusion of areas from edge effects (with weak predictive ability). For site codes, see Fig. 1.

altering fish assemblage composition and diversity due to, among other factors, stranding and downstream displacement, and reduced spawning and rearing success of fish (Hunter 1992, McLaughlin et al. 2006, Habit et al. 2007, Poff et al. 2007, Clarke et al. 2008, Meile et al. 2010, Young et al. 2011, Schmutz et al. 2015, Kennedy et al. 2016, Bejarano et al. 2017, Tonolla et al. 2017). First, fish stranding was reported in SS (Baird and Meach 2005). Also, riverine fishes sheltering in the river deep pools or potholes may be reluctant to leave during the low-flow periods, and become stranded following rapid falls in flow (Young et al. 2011). Such stranding affects assemblage structure and population as fish can be extirpated through predation, temperature stress, and/or oxygen depletion (Hunter 1992, Clarke et al. 2008, Young et al. 2011). As

found in this study, significant high species turnover in SS occurred during the dry-season periods (Fig. 4b). Second, fish in SS are likely displaced downstream by hydropeaking and replaced by upstream fishes. Such downstream displacement happens particularly for juvenile and small-sized fishes, and species preferring littoral and backwater areas that either swim or passively drift with the current (Young et al. 2011). Experimental studies have shown that Cyprinidae could be displaced downstream because of their less aerobic red muscle (Bainbridge 1960, 1962). Finally, hydropeaking creates "false attraction flows" giving false environmental cues for fish, for example, to migrate, to spawn, or for eggs to hatch afterward facing stranding, egg and nest site dewatering, stress, and insufficient food supply following sudden
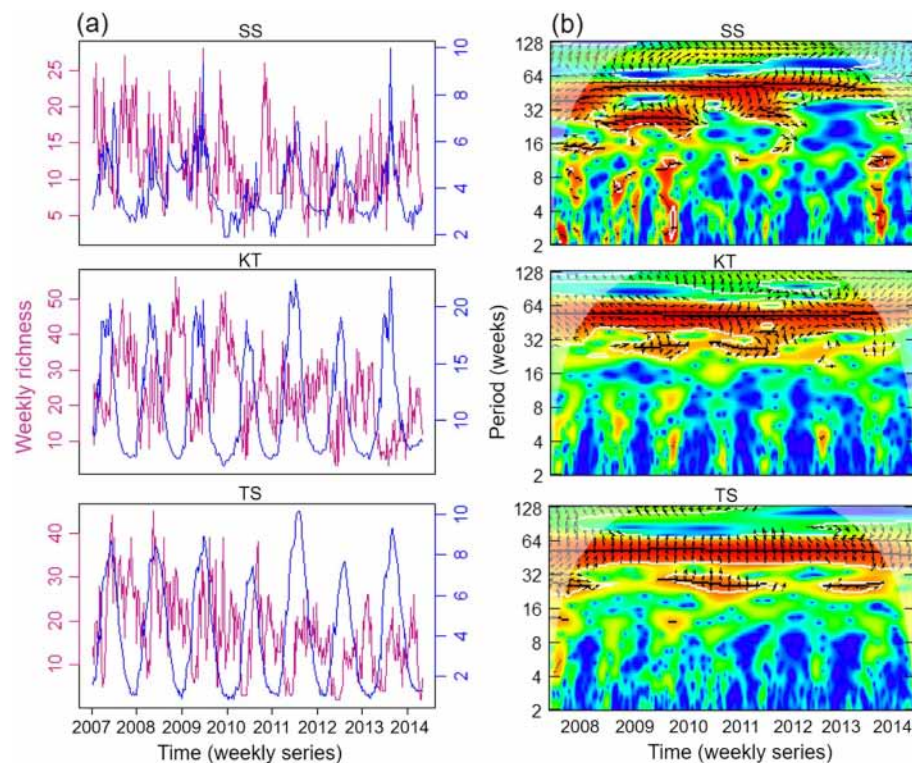
Fig. 6. Temporal variations of total weekly richness (*y*) and mean weekly water levels (second *y*-axis). (a) Weekly richness and mean water level data series, covering the period from 1 June 2007 to 31 May 2014. (b) Cross-wavelet power spectrum of weekly richness and water levels. Red color represents stronger cross-wavelet power, and blue, weak. Arrows in each plot depict phase differences. Ridge lines illustrate cross-wavelet power coherence within a band of neighboring periods. Areas in the upper corners outside the "cone of influence" in each plot indicate the exclusion of areas from edge effects (with weak predictive ability). For site codes, see Fig. 1.
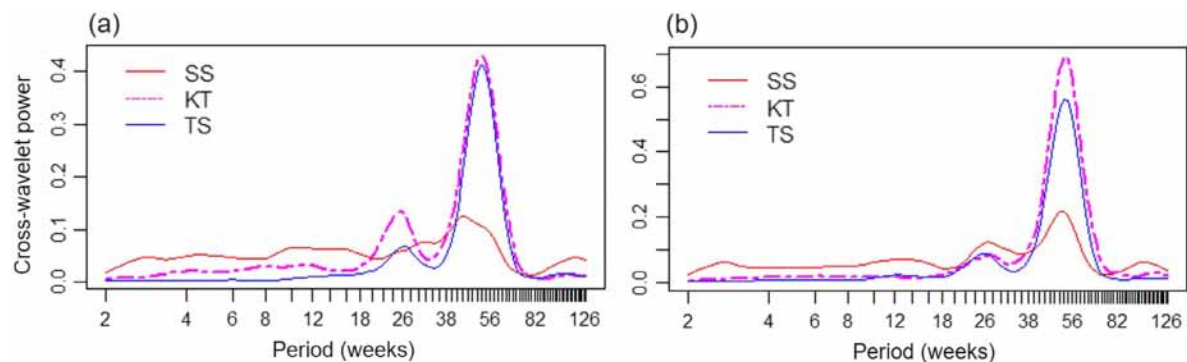

Fig. 7. Site average cross-wavelet power: (a) abundance vs. water series derived from Fig. 5b; and (b) richness vs. water series derived from Fig. 6b. For site codes, see Fig. 1.

falls in flow and vice versa (Clarke et al. 2008, Young et al. 2011). Similar cases were reported in SS where nesting sites for snakeheads (Channidae) and giant gouramies (Osphronemidae)

along the river edges were damaged or washed off and the river deep pools (fish dry-season refugia) were filled up by erosions, caused by hydropeaking (Baird and Meach 2005). The
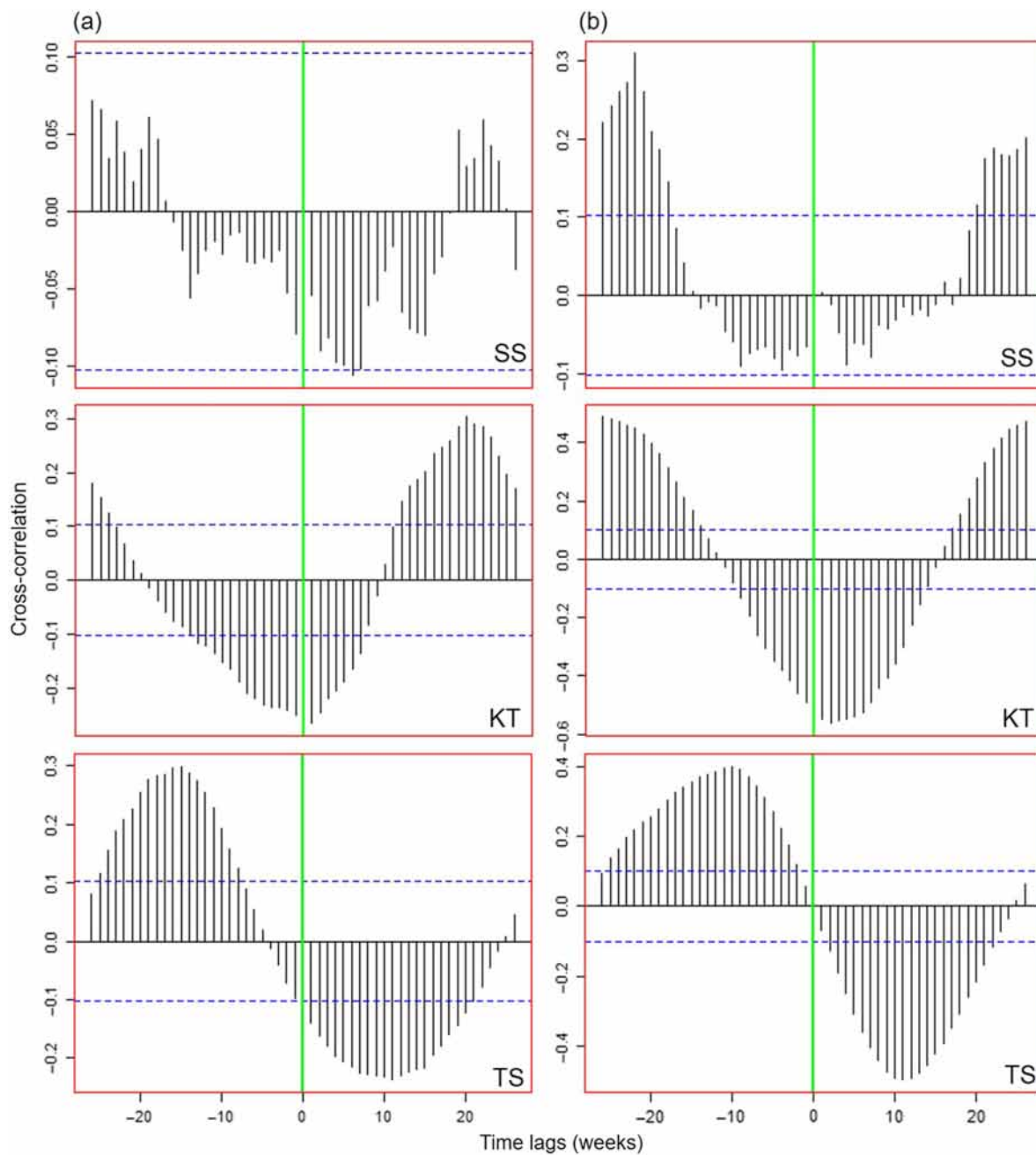
Fig. 8. Cross-correlation plots between (a) weekly abundance (y), (b) weekly richness (y), and mean weekly water levels (second y-axis) in each site. In the cross-correlations, the dotted blue lines give the values beyond which the correlations are significantly different from zero. x-axis is the time lags, set at 52 weeks (i.e., annual cycle). Data series on fish and water levels used for the cross-correlation plots, covering the period from 1 June 2007 to 31 May 2014. For site codes, see Fig. 1.

situation reduces spawning success, rearing survival, and growth rate. While research on the impacts of hydropower-related pulsed flows on fish assemblages in the Mekong is still very limited, evidence from, for example, North America and Europe (Hunter 1992, McLaughlin et al. 2006, Habit et al. 2007, Poff et al. 2007, Clarke et al. 2008, Young et al. 2011, Schmutz et al. 2015) indicated that hydropower-related pulsed flows promote strong temporal assemblage compositional changes and high species turnover.

Further, inconsistent with Tonkin et al.'s framework, we found low species turnover in KT and TS. As discussed succinctly earlier, this is likely because the river section between these sites is still free-flowing, and the riverine fishes that adapted to the system's naturally seasonal–predictable flow regimes have overlapping seasonal migration patterns and use the predictable-seasonal flow phenomena as gauges for the timing of their migrations to successfully access critical habitats, that is, dry-season refugia in KT (Mekong), spawning in KT, and rearing/feeding in TS (floodplains) (Valbo-Jorgensen and Poulsen 2000, Bao et al. 2001, Poulsen et al. 2002, 2004, Baran 2006, Valbo-Jørgensen et al. 2009). Moreover, in other river systems, riverine fishes are found to have homing behavior, and their movements from hundred to thousand kilometers between critical habitats are associated with spawning strategies, for example, Murray Darling golden perch (O'Connor et al. 2005), Murray cod (Koehn et al. 2009), Amazonian giant catfish (Duponchelle et al. 2016), salmonids, and a marine fish (weakfish) (Dittman and Quinn 1996, Thorrold et al. 2001). The naturally adapted migration cycles of the riverine fishes in KT and TS of the lower Mekong system may resemble such natal homing and site fidelity, and as such, broadly similar seasonal assemblage composition with low species turnover is expected.

Besides, our results are partly in line with Tonkin et al.'s seasonality and predictability framework in that the disturbed site (SS) exhibited lowest levels of temporal changes in diversity (abundance and richness) as compared to the predictably seasonal ones (KT, TS). We found that dams modulated flows and weakened the flows' seasonality and predictability strengths and thus muted seasonal variations of fish abundance and richness in SS, whereas sites with more naturally predictable flow conditions (KT, TS) promote reliable seasonal variations in fish abundance and richness with regular–predictable peaks at semi-annual and annual frequencies (Figs. 5–8; Appendix S1: Fig. S6). As further evidenced in the seasonal trait patterns, longitudinal migratory species colonized the mainstream habitats (i.e., KT) during the dry season for refugia and spawning and dispersed to the lower floodplains via TS for rearing and feeding during the wet season (Fig. 3b). Such reliable recurrence patterns of hydrology and fish are indeed consistent with the existing knowledge about timing of fish migration, fishing, and local fisheries management practices in the lower Mekong system (Valbo-Jorgensen and Poulsen 2000, Bao et al. 2001, Poulsen et al. 2002, 2004, Baird et al. 2003, FiA 2006, Halls et al. 2013). When the river seasonal–predictable flows are modified as evidenced in SS, such reliably seasonal–predictable events of fish assemblage no longer exist.

Conclusions

River flows structure riverine fishes that use seasonal–predictable hydrologic variations as gauges for the timing of their migrations to successfully access critical habitats in the lower Mekong system. We demonstrated that fish assemblages in highly regulated rivers were characterized by little seasonal variations in fish abundance, richness, and distinct seasonal assemblage composition with high species turnover, whereas assemblages in highly seasonal–predictable rivers were represented by repeated seasonal–predictable peak abundance and richness at semi-annual and annual cycles, and more similar seasonal assemblage composition with low species turnover. While partly in line with Tonkin et al.'s seasonality–predictability framework of highly seasonal–predictable environmental conditions promoting the greatest temporal changes in diversity (abundance and richness), our results are overall not consistent with Tonkin et al.'s framework hypothesizing that predictably seasonal environmental conditions promote the highest levels of temporal changes in assemblage composition with high species turnover. We explained that in aseasonal–unpredictable rivers, dams generate hydropower-related pulsed flows, that is, hydropeaking which fragments habitats and alters fish assemblage composition and

diversity due to stranding, downstream displacement, and creating false attraction flows that reduced spawning and rearing success of fish. These resulted in strong temporal fish assemblage compositional changes with high species turnover. While in highly seasonal–predictable system, riverine fishes have overlapping seasonal migration patterns between critical habitats, and possibly have homing behavior and site fidelity which likely constitutes more similar seasonal assemblage composition with low species turnover. Our study also highlighted contrasted seasonal patterns in fish traits observed in the three rivers, with the Mekong mainstream being important refugia and spawning habitats for longitudinal migratory fishes during the dry season while the lower gradient river, that is, TS, is their important rearing and feeding habitat during the wet season. This study contributes to the understanding of biological systems in the highly seasonal–predictable and aseasonal–unpredictable environments of the lower Mekong system. It also provides knowledge about the downstream ecological effects of and fish assemblage responses to hydropower-related pulsed flows. To date, dam site selection (Ziv et al. 2012, Winemiller et al. 2016) and advanced fish passage facilities (Schmutz and Mielach 2015) are among the important suggested measures to mitigate dam impacts. In addition, flow designs that could minimize the effects of hydropower-related pulsed flows on aquatic organisms, that is, mimic as far as possible natural seasonal hydrologic variations (Sabo et al. 2017), should be privileged for the appropriate applications of mitigation measures of the ever-growing dam construction in the Mekong.

Acknowledgments

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Supporting Information