

Spatial and temporal variation in fish community structure and diversity in the largest tropical flood-pulse system of South-East Asia

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Funding information

Erasmus Plus; European Erasmus+ credit mobility and capacity building CONSEA Programme; Belmont Forum (TLSCC project)

Abstract

The Tonle Sap River and Lake (TSRL) is South-East Asia's largest tropical flood pulse with a flow-reversal system that supports one of the world's largest freshwater fisheries. However, among the world's tropical floodplains, the resources of the TSRL have received little ecological research. Here, we described the spatiotemporal TSRL fish diversity and community variation using daily records from 2012 to 2015 on fish abundance from six sites covering the TSRL system. We found that high fish diversity occurred in sites located in the middle of Tonle Sap Lake, and the lowest diversity was observed in the southern section. The spatial abundance distribution patterns displayed a river-lake gradient, with three fish assemblages that were clustered based on their composition similarities and were characterised by 96 indicator species. In the southern section, fish assemblages were characterised by longitudinal migratory fishes; in contrast, in the middle system, fish assemblages were represented by species with combined ecological attributes (i.e. longitudinal and lateral migratory species and floodplain residents). Towards the northern section, fish assemblages were composed of lateral migratory and floodplain resident species. Species richness and abundance peaked at approximately 2–2.5 and 4 months, respectively, after the peak flow in early October, during which Tonle Sap River resumes its normal flow direction (outflow). This suggests that seasonal flood pulses (i.e. rising and falling water levels) play a pivotal role in structuring spatiotemporal variation in the TSRL fish assemblages. Our study has implications for fisheries monitoring and conservation initiatives.

KEYWORDS

cross-correlation, distribution pattern, fish richness, Lower Mekong Basin, ordination, rarefaction, Tonle Sap

1 | INTRODUCTION

The hydrology of the Mekong River is characterised by its extreme predictability, with regular wet and dry seasons throughout the basin (Adamson, Rutherford, Peel, & Conlan, 2009). The hydrology is controlled by the tropical monsoonal climate and flood runoff from the snowmelt in the Tibetan plateau as well as by its tributaries that

converge and accumulate into a single large wet seasonal peak flow (Adamson et al., 2009; MRC, 2005). The biological systems of the river basin have both developed in and adapted to these tropical flood-pulse environments, and the Mekong's predictable seasonal flood pulses are indeed a key ecological driver that supports one of the most biodiverse and productive inland fisheries in the world (MRC, 2003, 2010; Poulsen, Ouch, Viravong, Suntornratana, & Nguyen, 2002; Rainboth, 1996).

This study focuses on the Tonle Sap River and Lake (TSRL), which is a key part of the Mekong's hydrological system (Adamson et al., 2009; MRC, 2005). The TSRL is a unique tropical flood pulse with a flow-reversal system that creates the only and largest continuous areas of natural wetlands in the Mekong Basin and South-East Asia (van Zalinge et al., 2004). It was designated a World Biosphere Reserve under the United Nations Educational, Scientific and Cultural Organization (UNESCO) in 1997 (Davidson, 2006). Two Ramsar wetlands of international importance were also designated in the TSRL: Boeng Chhmar in 1999 and Prek Toal in 2015 (The Ramsar Convention Secretariat, 2014).

The TSRL supports highly diverse communities of birds, reptiles, plants and mammals (Campbell, Poole, Giesen, & Valbo-Jorgensen, 2006) and is home to one of the world's largest inland fisheries (Baran, 2005; Baran, So, Degen, Chen, & Starr, 2013). The TSRL contributes ~70% to Cambodia's annual production of inland capture fisheries totalling 767,000 tonnes (FiA, 2013; Hortle & Bamrungrach, 2015). The TSRL hosts ~296 fish species, making it the third richest lake in terms of fish diversity after Lake Malawi and Lake Tanganyika (Baran, Starr, & Kura, 2007; Baran et al., 2013). Such high diversity makes it different from the lake and stream ecosystems in temperate and high-latitude regions, which are often less diverse and highly impacted by humans. Among other drivers such as accessible vegetation and high rates of nutrient cycling, the predictable and extensive seasonal flood-pulse cycles of the Mekong and TSRL system and its biogeography mainly explain the high fish stock diversity and productivity (Baran, van Zalinge, & Ngor, 2001; Rainboth, 1996; van Zalinge, Deap, Ngor, Sarkula, & Koponen, 2003).

Despite being highly productive, the Mekong system, including the Tonle Sap, has received little ecological research on many aspects of its resources and ecology, including fish, reptiles, invertebrates and primary producers (Dudgeon, 2000, 2003; Sabo et al., 2017). It may be argued that the TSRL, among the world's tropical floodplains, has been studied the least in terms of its hydrology-ecology interactions (Arias, Cochrane, Norton, Killeen, & Khon, 2013; Junk et al., 2006; Kummu, Sarkkula, Koponen, & Nikula, 2006). The primary research conducted on fisheries has been very spotty and has mainly focused on biological assessments, for example Lamberts (2001), Enomoto et al. (2011), Halls, Conlan, et al., 2013 and Halls, Paxton, et al. (2013), or on broadscale migration patterns, for example Poulsen et al., 2002, 2004. Few studies have been conducted on the fish community ecology in the TSRL, including Lim, Lek, Touch, Mao, and Chhouk (1999) who studied the spatial fish diversity and community patterns; additionally, the most recent study was on the determinants of species composition (i.e. beta diversity) (Kong, Chevalier, Laffaille, & Lek, 2017).

Therefore, to better monitor, manage and conserve the TSRL fisheries, there is an urgent need to update the information on the spatial and temporal fish diversity, community structure and distribution patterns, especially given the growing population, hydro-power dam development, climate change, decreasing flooded forest cover and indiscriminate fishing effects that have taken place in the Mekong Basin including the Tonle Sap system during recent decades.

For example, dams on the Mekong in China reduced the rising and falling flood-pulse rates by 23% and 11%, respectively, at the Tonle Sap (Cochrane, Arias, & Piman, 2014). This affects fish distribution patterns and their reproductive success, as natural flood pulses are a key environmental determinant in tropical freshwater systems and trigger fish migrations, colonisation of unoccupied niches and successful dispersal for spawning, rearing and refugia (Baran, 2006; Henriques-Silva, Lindo, & Peres-Neto, 2013; Ngor, Legendre, Oberdorff, & Lek, 2018; Sabo et al., 2017). The flooded forests around Tonle Sap Lake were forecasted to decline by 5,000 ha (1.1%) in an average year and up to 23,000 ha (5.3%) in a dry year due to ongoing water developments (i.e. hydropower, irrigation, water supply and flood protection) over the next 20 years (MRC, 2011a). The indiscriminate fisheries in the TSRL modify the structure of the fish community, leading to depleted species diversity, that seemingly put them at high risk of being severely affected by these environmental changes (McCann et al., 2016). Such indiscriminate fishing effects may be due to a variety of fishing gears, for example some 150 fishing gears have been documented in Cambodia (Deap, Degen, & van Zalinge, 2003). These fishing gears range from commercial and rather nonselective fishing gears, that is the century-old stationary trawl bagnet fishery and the barrage or fishing lot fishery (abolished since 2012) to artisanal fishing gears such as gillnets, traps, cast nets, hooks and lines, scooping devices, seine nets, covering devices, push nets, lift nets and bag nets. In general, these fishing gears target different fish species across sizes and trophic positions in the TSRL.

Hence, this study contributes to the call in the research literature for studies on fish community ecology and establishes baseline data and information about the spatiotemporal patterns in species diversity and community composition, which better inform fisheries management and conservation objectives in one of the world's largest tropical flood-pulse systems. The aims of this study were to (a) describe spatiotemporal patterns in the diversity and composition of fish assemblages in the complex TSRL system, (b) identify indicator species of different fish assemblages observed along the TSRL gradients and (c) explore the spatial and temporal variation in species abundance and richness in relation to hydrological regimes. For this investigation, we used daily time-series data from 2012 to 2015 on fish abundance from six sites and water levels from two sites; this selection represented the different geographical gradients along the TSRL system.

2 | MATERIALS AND METHODS

2.1 | Study area

The Tonle Sap catchment covers an area of 85,790 km² or 11% of the Mekong Basin (MRC, 2003). The floodplain lake is located at the apex of the Tonle Sap River approximately 130 km to the northwest of its junction with the Mekong River (Halls, Conlan, et al., 2013; Halls, Paxton, et al., 2013). Waters for the TSRL system originate mainly from the Mekong River (54%), while the lake tributaries contribute 34%, and the rest generates from precipitation (M. Kummu et al.,

2014). During the wet season (i.e. June–October), the Tonle Sap Lake expands its mean surface area from ~3,500 to ~14,500 km², inundating huge floodplain areas surrounding the TSRL, with maximum depths in the lake recorded at 6–9 m from late September to early October and minimum depths of approximately 0.5 m in late April (MRC, 2005). This study covers six sites situated along the geographical gradient of the TSRL from the southern section representing the Tonle Sap River in Kandal Province (KD) to Kampong Chhnang (KC), a transition zone connecting the Tonle Sap River with the lake, the middle portion of the lake in Kampong Thom (KT) to the east and Pursat (PS) to the west, and finally Siem Reap (SR) and Battambang (BB) located towards the northern end of the TSRL gradient (Figure 1). The study sites include a river section with a lotic environment (i.e. KD), an ecotone between the river and the lake (i.e. KC), an open area of the lake with year-round wet large tributaries at two sites (i.e. KT and PS) and more swampy areas with dense floating vegetation, flooded plains and grass/shrublands to the north, particularly in BB.

2.2 | Data collection

We used daily catch samples from the stationary gillnets fishery (length: 400 m ± 100 m, height: 0.7–4.5 m, mesh size: 2–6.5 cm, daily soak hours: 12 ± 2) and from the cylinder traps (1.6 m × 0.9 m, daily soak hours: 14 ± 2) fishery, the two most common fishing gears that are used daily in Cambodia (Deap et al., 2003; Hortle, Lieng,

& Valbo-Jorgensen, 2004). The length variation in the stationary gillnets used was due to the available fishing grounds, which vary seasonally according to the hydrological cycles. When in operation, the cylinder trap was set facing the current along the bank of the stream/river or suspended off the bottom between poles in the flooded forests of Tonle Sap Lake. The soak hour refers to the time (hours) that the gear soaked in the water (MRC, 2007). These fishing gears allowed the capture of both migratory and floodplain resident species. Data collection was based on the Mekong River Commission's (MRC) standard sampling procedures for fish catch monitoring (MRC, 2007). Eighteen professional fishermen (three at each site), supervised by the fishery researchers from the Cambodia Inland Fisheries Research and Development Institute of the Fisheries Administration, the Tonle Sap Authority and the MRC monitoring specialist, participated in this daily fish sampling programme. A fish species list for the Mekong Basin (~900 species with ecological attributes) was obtained from the MRC Mekong Fish Database (MFD, 2003) and cross-checked with FishBase (Froese & Pauly, 2017) and other literature sources (Kottelat, 2013; Rainboth, Vidthayanon, & Mai, 2012). Based on their ecological attributes, fish species were grouped into (a) "white fishes" for species that perform longitudinal migrations between the Mekong mainstream and floodplains as well as major tributaries, (b) "black fishes" for floodplain residents that spend most of their life in lakes and swamps in floodplains adjacent to rivers (with no longitudinal migrations upstream) and move to flooded areas during the flood season and (c) "grey fishes," that are

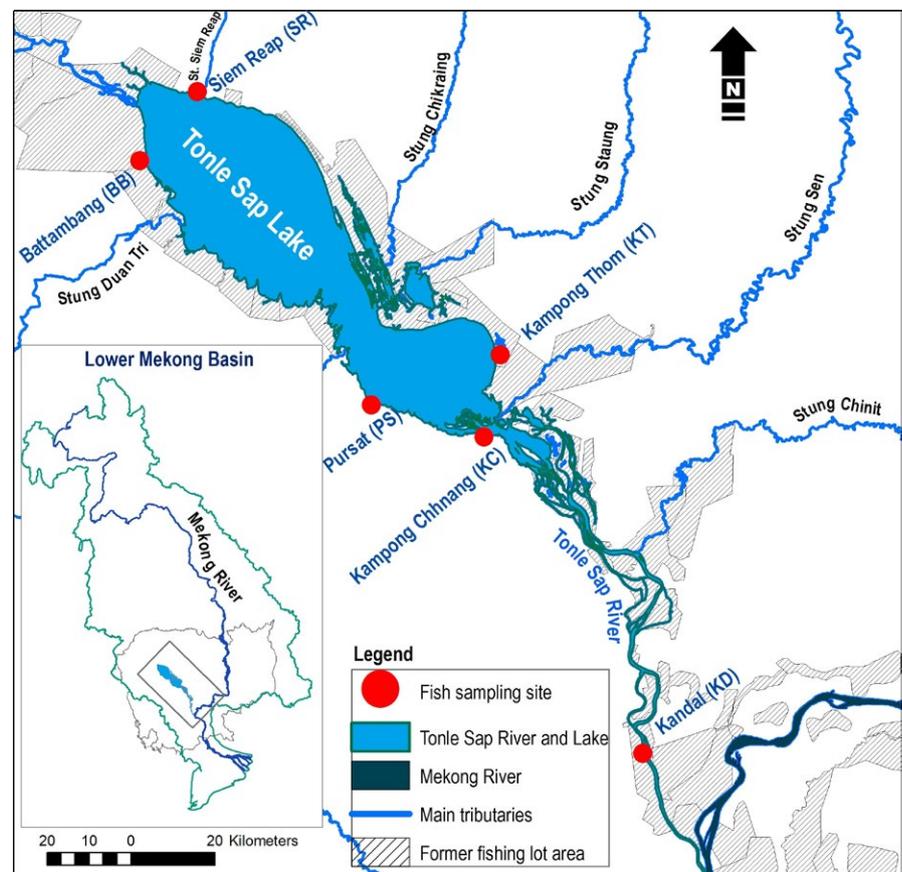


FIGURE 1 Location of sampling sites along Tonle Sap Lake and River

ecologically intermediate between the white and black fishes and undertake short-distance lateral migrations in local tributaries and do not spend their life in the floodplain ponds during the dry season (MRC, 2010; Valbo-Jørgensen, Coates, & Hortle, 2009; Welcomme, 2001). In other words, grey fishes move to local river/stream channels during the dry season. The final group was “estuarine fishes,” which include estuarine residents and marine visitors. Sampled fish were identified to the species level and counted. Fish particularly those that were entangled in the gillnets were dead, and fishermen often consumed or sold them for other consumers. After field verification, field collected data were recorded into the national fish monitoring databases and were quarterly cleaned and synchronised by the responsible researchers with the help of the MRC database expert and fisheries monitoring specialist. Daily water levels at two sites: the Tonle Sap River in Kandal (latitude: 11.81329, longitude: 104.8041) and the Tonle Sap Lake in Pursat (latitude: 12.57662, longitude: 104.20779) were registered by the MRC.

2.3 | Statistical analysis

Prior to analysis, daily fish samples were computed as daily mean samples from three fishermen and then aggregated into weekly fish richness and abundance data by species over the study period that lasted from 1 January 2012 to 31 December 2015 (i.e. 209 weeks) at each site. Likewise, daily water levels in both locations (the Tonle Sap River at KD and the lake at PS) were computed into weekly mean water levels for the same 209 weeks. All data analyses were performed in R (R Core Team, 2015).

2.3.1 | Species diversity

Rarefaction curves were constructed to describe variation in cumulative species richness among sites. The rarefaction technique is an important diagnostic tool that considers randomised richness against sampling intensity and is based on resampling with replacement so that the variance among randomisations remains meaningful for large numbers of sampling units or individuals (Rossi, 2011). To implement the rarefaction procedures, the “rarc” function (with 999 randomisations) from the “rich” package (Rossi, 2011) was used on the fish community matrix in each of the six study sites. Afterwards, the significance of differences in species richness among sites was tested by randomisation ($n_{\text{random}} = 999$) using the “c2cv” function from the “rich” package (Rossi, 2011).

Furthermore, weekly inverse Simpson indices were also computed to describe the weekly biological site diversity along the TSRL. The Simpson diversity index (D) was computed using the equation: $D = \sum(n/N)^2$, where n = the total number of organisms of a species, and N = the total number of organisms of all species. The inverse Simpson diversity index is $1/D$. The inverse Simpson index is a meaningful and robust diversity index that captures the variance in the distribution of species abundance (Magurran, 2004). At last, non-parametric pairwise Wilcoxon tests were performed to compare diversity indices among the sites.

2.3.2 | Spatiotemporal variation in fish assemblages

Nonmetric multidimensional scaling (NMDS), an unconstrained ordination method, was performed to describe the spatial, intra- and interannual variation in the TSRL fish community. NMDS with two and three dimensions was computed separately for the spatial, seasonal and interannual variation to examine the variability in the community data. As three-dimensional NMDS analysis revealed similar patterns, we therefore present results in two dimensions only (but see Supporting Information [Figure S1] for the three-dimensional analysis). First, NMDS was used to visualise the spatial abundance distribution patterns among sites along the TSRL gradients. Afterwards, Ward hierarchical clustering was computed to classify fish sites into different assemblages based on their similarities in species composition (Murtagh & Legendre, 2014). Next, we performed permutation tests (999 permutations) to identify indicator species of each assemblage cluster using the “multipatt” function from the “indicpecies” package to describe the spatial differences in each of those identified assemblage clusters (Dufrence & Legendre, 1997; De Cáceres & Legendre, 2009; De Cáceres & Jansen, 2011). Indicator species were also assessed for each season (defined below) to identify the species that characterised the seasonal fish assemblages in each identified cluster.

In addition, NMDS was performed to graphically display intra- (i.e. seasonal) and interannual changes in the species abundances of the entire system. For intraannual variation, three seasons were defined based on the 10-year mean intraannual variation in the daily water levels of the lake, that is inflow or high-flow period (July–October), outflow period (November–February) and low-flow period (March–June) (Supporting Information Figure S2). The partitioning of the three seasons reflects the importance of the TSRL flood-pulse system with the seasonal rising and falling flow regimes that influence the variation in the fish community structure (Baran, 2006; Poulsen et al., 2002).

NMDS was performed on the community abundance matrix using the “metaMDS” function of the “vegan” package with the Bray–Curtis dissimilarity index in R (Borcard, Gillet, & Legendre, 2011). We then performed permutational multivariate analysis of variance (PERMANOVA) using the “adonis” function of the “vegan” package (with 999 permutations and the Bray method) to test the influence of different factors (e.g. cluster, season and year) on the composition of the fish community. Afterwards, contrast methods were applied to test the pairwise differences between different levels in each of these factors using the “pairwise.adonis” function in R.

2.3.3 | Temporal variation in fish abundance and richness in relation to hydrology

Given that hydrology is a key driver that influences the temporal variation in the TSRL fish communities, the temporal changes between weekly species abundance and richness at each site in relation to water levels in Tonle Sap Lake were investigated.

Nonparametric Spearman's correlation tests were computed for each site to test the link between the two variables. Further, cross-correlation functions (CCF) were performed between both abundance and richness and water levels to describe the relationship between each of the two series. As water level data were available at the two sites in the Tonle Sap River (Kandal) and Tonle Sap Lake (Pursat), we used fish data from these two sites for the CCF analysis to assess fish community responses to changes in site hydrology. CCF determines which lags (h) of the time series, that is x_t , predicts the value of series y_t and the correlation between the series x_{t+h} and y_t for $h = 0$ is as follows: $\pm 1, \pm 2, \pm 3$, etc. (Shumway & Stoffer, 2011). Here, x_t (the predictor) and y_t were the site water levels and the site species abundance or richness respectively. The time lags (h in weeks) represented the responses of the fish community to the hydrological variation and were derived from the maximum value of the CCF coefficients. If the time lag h is negative (i.e. the left side of the plot), there is a correlation between the x -series at a time before t and the y -series at time t (or, to put it simply, x leads y). In contrast, if the time lag h is positive (i.e. the right side of the plot), it is said that x lags y (Shumway & Stoffer, 2011). Prior to CCF analyses, the time-series data were tested for stationarity at both sites for both fish and water levels, and no significant linear temporal trend was detected for all data series.

3 | RESULTS

3.1 | Fish community structure

Over the four-year monitoring period, 204 fish species were recorded in all catch samples. The species comprised 114 genera, 38 families

and 13 orders. The three main orders represented 87% of the total species count included Cypriniformes (100 species), Siluriformes (48) and Perciformes (29). Clupeiformes, Osteoglossiformes and Synbranchiformes each contained five species, and the rest contributed less than 6% to the total species counts. At the family level, the top five families that accounted for 60% of the total species counts included Cyprinidae (80), Bagridae (12), Pangasiidae (11), Cobitidae (10) and Siluridae (10), while each of the other 33 families comprised one to six species. At the species level, ~62% of catches were dominated by 12 fish species, namely, *Henicorhynchus lobatus* (11%), *H. siamensis* (10%), *Trichopodus trichopterus* (7%), *Puntioplites proctozysron* (7%), *Osteochilus vittatus* (6%), *Trichopodus microlepis* (5%), *Labiobarbus lineatus* (4%), *Paralaubuca typus* (3%), *Mystus mysticetus* (3%), *Notopterus notopterus* (3%) and *Rasbora tornieri* (3%). Ecologically, longitudinal migratory species (i.e. white fishes) accounted for ~58% of total abundance, while floodplain resident black and lateral-migrant grey fishes contributed 19% and 21% respectively. The rest (1%) were composed of estuarine species and marine visitors.

Among the six survey sites, the highest species richness was observed in the middle section of the lake in KT, while the lowest richness occurred in the northern part in BB (Figure 2a). Similar richness values were observed in KD, KC and SR. In addition, the richness in PS was comparable with that of KD and SR. In addition, the lowest abundance was observed in KD, while the highest abundance was reported in KT (Supporting Information Figure S3). Likewise, the highest diversity index occurred in the middle part of the lake in PS and KT, while the lowest diversity index was observed in the river section in KD (Figure 2b). The diversity index in KC was similar to that in BB.

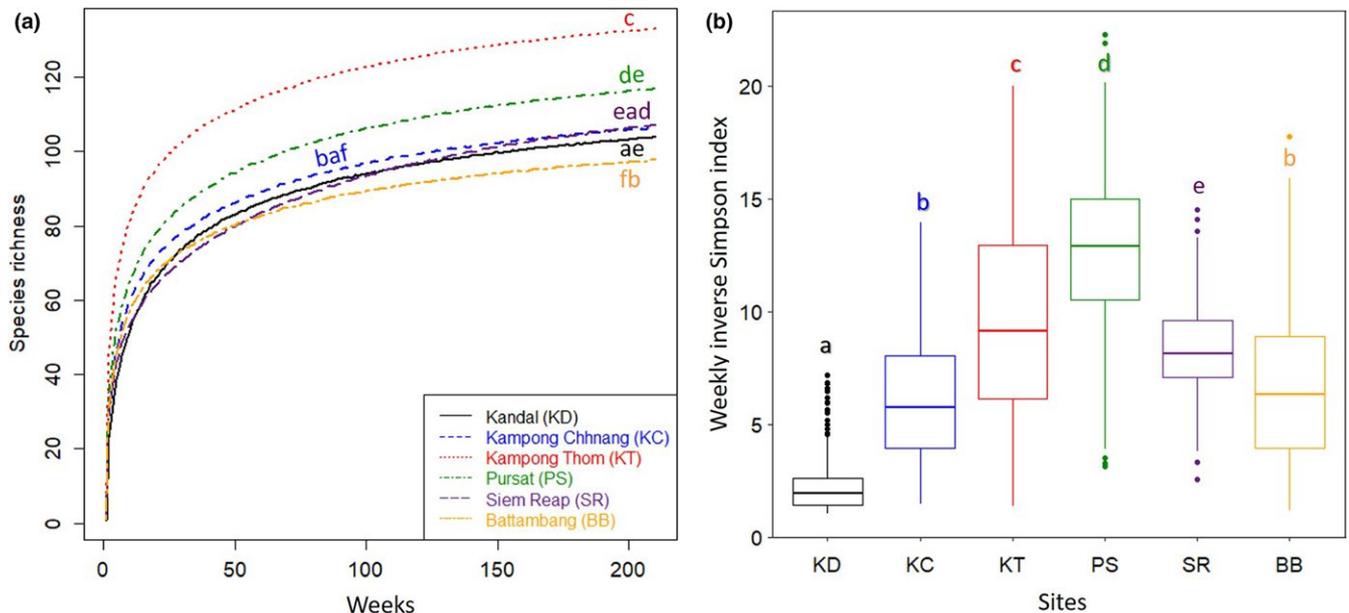


FIGURE 2 Spatiotemporal comparison of site fish species richness and diversity in the TSRL: (a) site rarefaction curves on species richness; (b) site inverse Simpson diversity index with south–north gradient along the TSRL. Sites with a common letter are not significantly different at $p = 0.05$ (Pairwise Wilcoxon Rank Sum Tests). Site codes are the same as those in Figure 1

3.2 | Spatiotemporal variation

Hierarchical clustering with the Ward agglomerative method enabled the classification of all weekly samples into three clusters (Figure 3a) based on species composition similarities. The first split of the dendrogram defined fish assemblages in riverine (cluster 1) and lacustrine environments (cluster 2 and cluster 3), while the second split separated the two main assemblages (clusters 2 and 3) in the middle and northern

sections of the lake. The first cluster (159 samples) was mainly associated with samples from KD. The second, that is the largest cluster (613 samples), mainly grouped samples from KC, KT, PS and SR, and the third cluster (456 samples) was related to samples from BB. Based on the system's fish community composition, KD (in the southernmost section of the system) was opposed to the other sites along the first axis of the NMDS; in contrast, the second axis mainly opposed BB (in the northern part of the lake) to the other sites (Figure 3b).

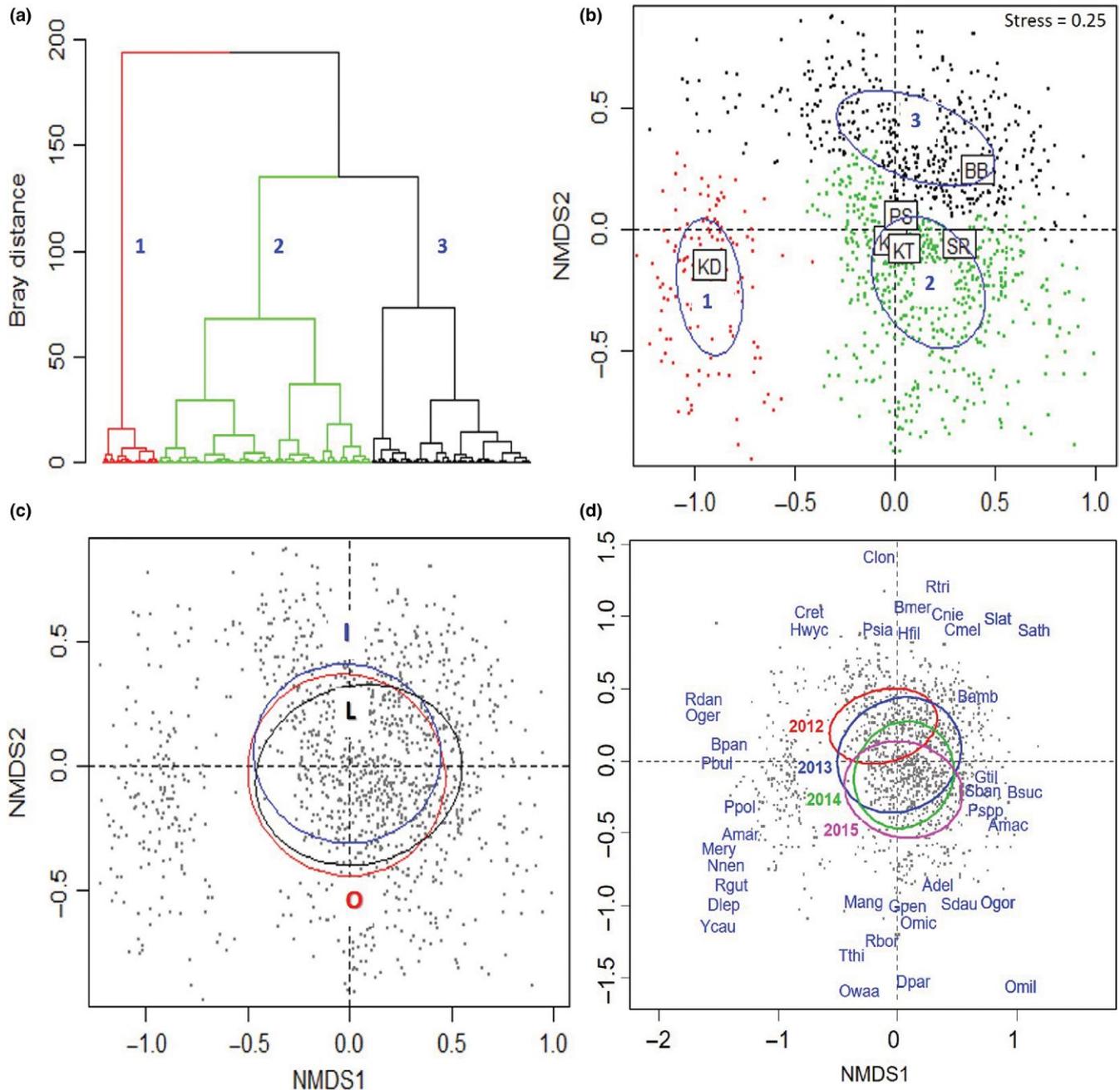


FIGURE 3 NMDS biplot of the weekly fish abundance samples (with Bray–Curtis dissimilarity matrix), showing the TSRL community spatiotemporal variation. Dots on the biplots represent samples. (a) Ward hierarchical clustering dendrogram of the weekly samples showing three distinct clusters; (b) spatial distribution patterns of sites along the TSRL gradient grouped into three clusters; (c) seasonal variation, categorised into three seasons: I, O, L, respectively, symbolising inflow (or high-flow periods) (July–October), outflow (November–February) and low flow (March–June); and (d) interannual variation among years (2012–2015). Names are abbreviations of fish species names. Site codes are the same as those in Figure 1. For fish species details, see Supporting Information Figure S9

PERMANOVA on the community composition among clusters indicated significant ($p = 0.001$) differences (Supporting Information Figure S4.1), and the contrast pairwise tests of the assemblages between clusters showed statistical significance at the p -adjusted value = 0.003 for all pairs (Supporting Information Figure S4.2). Wilcoxon tests on the NMDS site scores of the clusters revealed significant differences ($p < 0.001$) between cluster 1 and cluster 2 and between cluster 1 and cluster 3 on axis 1 as well as between cluster 1 and cluster 3 and between cluster 2 and cluster 3 on axis 2. For details on the use of NMDS scores to compare the three clusters, see Supporting Information Figure S4.3.

Seasons related to the inflow (I), outflow (O) and low-flow (L) periods appeared to significantly influence the variation in the TSRL fish communities (Figure 3c). PERMANOVA and contrast pairwise tests indicated significant differences among seasons, with $p = 0.001$ (Supporting Information Figure S4.4), and between seasons, with a p -adjusted value = 0.003, for all pairwise comparisons (Supporting Information Figure S4.5). Wilcoxon tests on the NMDS site scores revealed significant differences between I and L on axis 1 ($p = 0.044$) and between O and I ($p = 0.004$) as well as between I and L ($p = 0.008$) on axis 2. For details on using the NMDS scores to compare the three seasons, see Supporting Information Figure S4.6. In general, high abundance and richness occurred during the outflow period, and lowest abundance and richness were observed during the inflow for all sites except for BB, where richness was high during the inflow period (Supporting Information Figure S4.7). Seasonal patterns were also revealed in the axis 3 of the three-dimensional NMDS (Supporting Information Figure S1).

Significant changes in fish communities were also observed over the four-year period (Figure 3d) based on the PERMANOVA test among years, $p = 0.001$ (Supporting Information Figure S4.8), and contrast pairwise tests between years, p -adjusted value = 0.006 for all pairwise comparisons (Supporting Information Figure S4.9). Significant changes were mainly observed towards negative values along the NMDS axis 2. Wilcoxon tests showed that 2012 significantly differed from other years along axis 1 ($p < 0.001$); however, along axis 2, the differences between all pairs of years were significant at $p < 0.001$ (Supporting Information Figure S4.10). Overall, weekly abundance showed some fluctuations, with no clear trends over the four-year period for all sites; however, decreasing trends were observed for the weekly richness in the middle part of the lake (i.e. KC, PS, KT, SR) (Supporting Information Figure S4.11).

3.3 | Indicator species by cluster

Overall, 96 indicator species were identified from the three assemblage clusters (Supporting Information Figure S5). The largest number was observed in cluster 2 (45 species), while the lowest number was detected in cluster 1 (20). Key indicator species with high indicator values that characterised cluster 1 in the southern river section belonged to Pangasiidae (river catfishes), such as *Pangasius macronema*, *P. conchophilus* and *P. bocourti*; Cyprinidae (cyprinids), such as *Labiobarbus siamensis*, *Puntioplites falcifer*, *Paralabuca typos*

and *P. riveroi*; Siluridae (sheatfishes), such as *Phalacronotus bleekeri* and *Belodontichthys truncatus*; and Cobitidae (loaches), including *Yasuhikotakia caudipunctata*. Interestingly, *Cyprinus carpio*, an exotic species, was also identified in this cluster.

Key indicator species representing cluster 2 in the middle lake were those of Bagridae (Bagrid catfishes), such as *Mystus mysticetus* and *M. singaringan* (floodplain spawners); Cyprinidae (white/grey fishes), including *Labiobarbus lineatus*, *Osteochilus vittatus*, *Labeo chrysophekadion*, *Thynnichthys thynnoides* and *Henicorhynchus siamensis*; Anabantidae (climbing perches), that is *Anabas testudineus* (floodplain resident); Pristolepididae (leaf-fish), that is *Pristolepis fasciata* (floodplain spawner); Ambassidae (asiatic glassfish), that is *Parambassis wolffii* (floodplain spawner); Cobitidae, that is *Yasuhikotakia modesta* (main channel spawner); Mastacembelidae (spiny eels), that is *Macrogathus siamensis* (floodplain resident); and Osphronemidae (gouramies), such as *Trichopodus trichopterus* (floodplain resident).

The main species that were indicative of cluster 3 in the northern part of the lake included Notopteridae (featherbacks), that is *Notopterus notopterus*; Bagridae, that is *Hemibagrus spilopterus*; Osphronemidae, that is *Trichopodus microlepis* and *T. pectoralis*; Cyprinidae, that is *Barbonymus gonionotus* and *Hampala macrolepidota*; Channidae (airbreathing snakeheads), that is *Channa striata*; Siluridae, that is *Ompok bimaculatus* and Eleotridae (sleepers), that is *Oxyeleotris marmorata*; Clariidae (airbreathing catfishes), that is *Clarias microcephalus*, *C. meladerma* and *C. batrachus*; and Tetraodontidae (puffers), that is *Pao leiurus*.

Seasonally, key indicator species that matched with those belonging to cluster 1 included five species (25%) for the outflow and two species (10%) for the low-flow, while no species were identified for the inflow period. In cluster 2, 21 species (47%) were identified during the outflow, five species (11%) were identified during the inflow and three species (6%) were identified during the low-flow period. At last, for cluster 3, 10 species (32%) were identified for the low-flow, while four species (13%) were identified for the inflow and three species (10%) were identified for the outflow. For details of indicator species by cluster and season, see Supporting Information Figure S5.

3.4 | Species relative abundance by cluster

Overall, 114 species were reported in cluster 1, 182 were reported in cluster 2 and 154 in cluster 3. The ten most abundant species for each assemblage cluster accounted for ~97% in cluster 1, ~58% in cluster 2 and ~65% in cluster 3 (Figure 4a). Interestingly, two small-sized cyprinids, *Henicorhynchus lobatus* (Hlob) and *H. siamensis* (Hsia), comprised ~45% of the total abundance in cluster 1 but accounted for only ~19% and ~16% in cluster 2 and cluster 3 respectively. Further, of the top ten species, only five species (~84%) dominated the catch in cluster 1; in contrast, in clusters 2 and 3, the ten dominant species shared the catch more proportionately between 3 and 10%. *Puntioplites proctozysron* (Ppro) was found among the top ten species for all clusters. Ecologically, catches in cluster 1

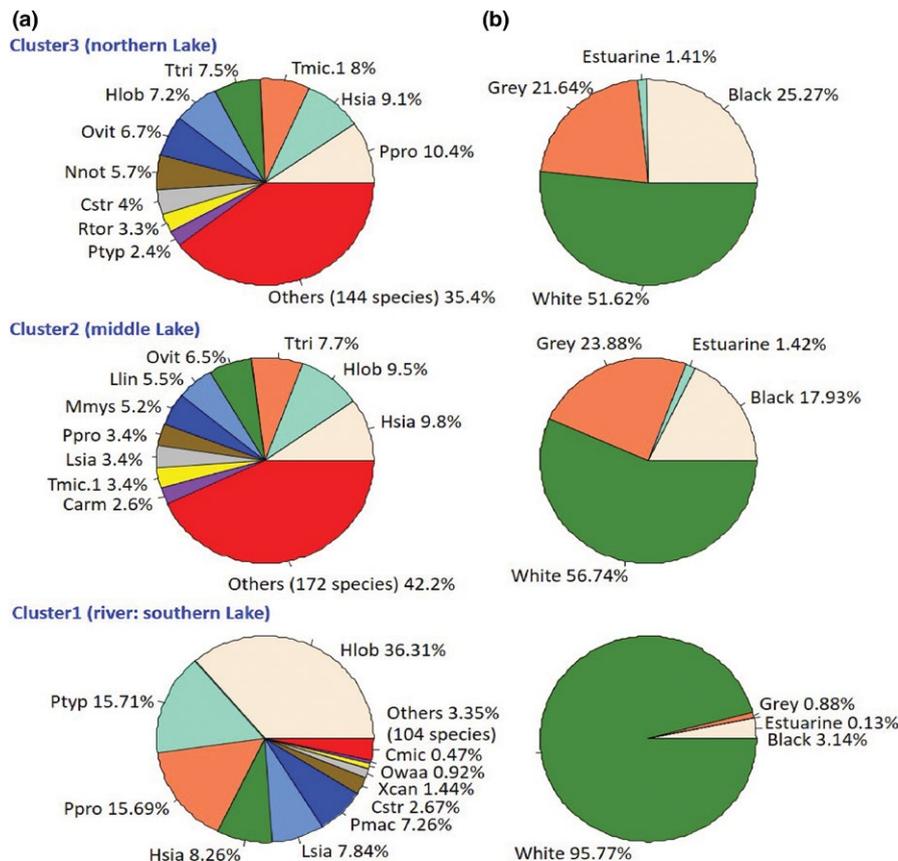


FIGURE 4 Species relative abundance organised by cluster and fish migration guild. (a) Ten most abundant species by clusters. (b) Community composition by migration guilds. For clusters, see Figure 3a,b. For species details and migration guilds, see Supporting Information Figure S9

were composed of ~96% of migratory white fishes, and this value decreased gradually to ~57% and ~52% in cluster 2 and cluster 3 respectively (Figure 4b).

3.4.1 | Relationships between species abundance and richness and water levels

Significant links between either weekly abundance or richness and water levels were observed in the lake (PS) (Spearman's correlation tests, $p < 0.05$ for all sites except BB). The cross-correlation analyses between the two time series for the two sites (Tonle Sap River, KD and Tonle Sap Lake, PS) where both fish and water level data series were available noted that there was a positive relationship between the temporal variation in both species abundance and richness and the hydrology (Figure 5a–d). Overall, the fish community responses appeared to lag behind the flow regime (i.e. water led the fish). The correlation lag for fish abundance versus water levels at the maximum coefficient was estimated at -15 weeks in KD and -16 weeks in PS (Figure 5a,b); in contrast, the correlation lag for species richness versus water level was estimated at -8 weeks in KD and -10 weeks in PS. It is noteworthy that the time lag between the water levels in the Tonle Sap River (KD) and those of the lake (PS) was estimated at about -2 weeks (Supporting Information Figure S6). Therefore, it was consistently observed that peak abundance and richness

began one to 2 weeks earlier in the lake than in the Tonle Sap River. Additional investigations on the cross-correlation between weekly abundance and richness of sites around the lake using water levels from PS are provided in Supporting Information Figure S7 and S8. For a full species list by genera, families and orders as well as key ecological attributes used in this study, see Supporting Information Figure S9.

4 | DISCUSSION

Overall, we found that the TSRL fish community structure varied through space and time. High species richness, abundance and diversity indices occurred in the middle system of the lake (i.e. KT, PS), while the lowest richness and diversity occurred in the river section (i.e. KD). The spatial distribution pattern in fish abundance displayed the river–lake gradient and differentiated the fish assemblages among the southern, the middle and the northern sections of the system. In the southern section, the fish assemblages were characterised mainly by longitudinal migratory white fishes, while in the middle system, the assemblages were represented by species with combined ecological attributes (i.e. white, black and grey fishes). Towards the northern part of the system, the fish assemblages were mainly composed of black and grey fishes. Seasonal flood pulses,

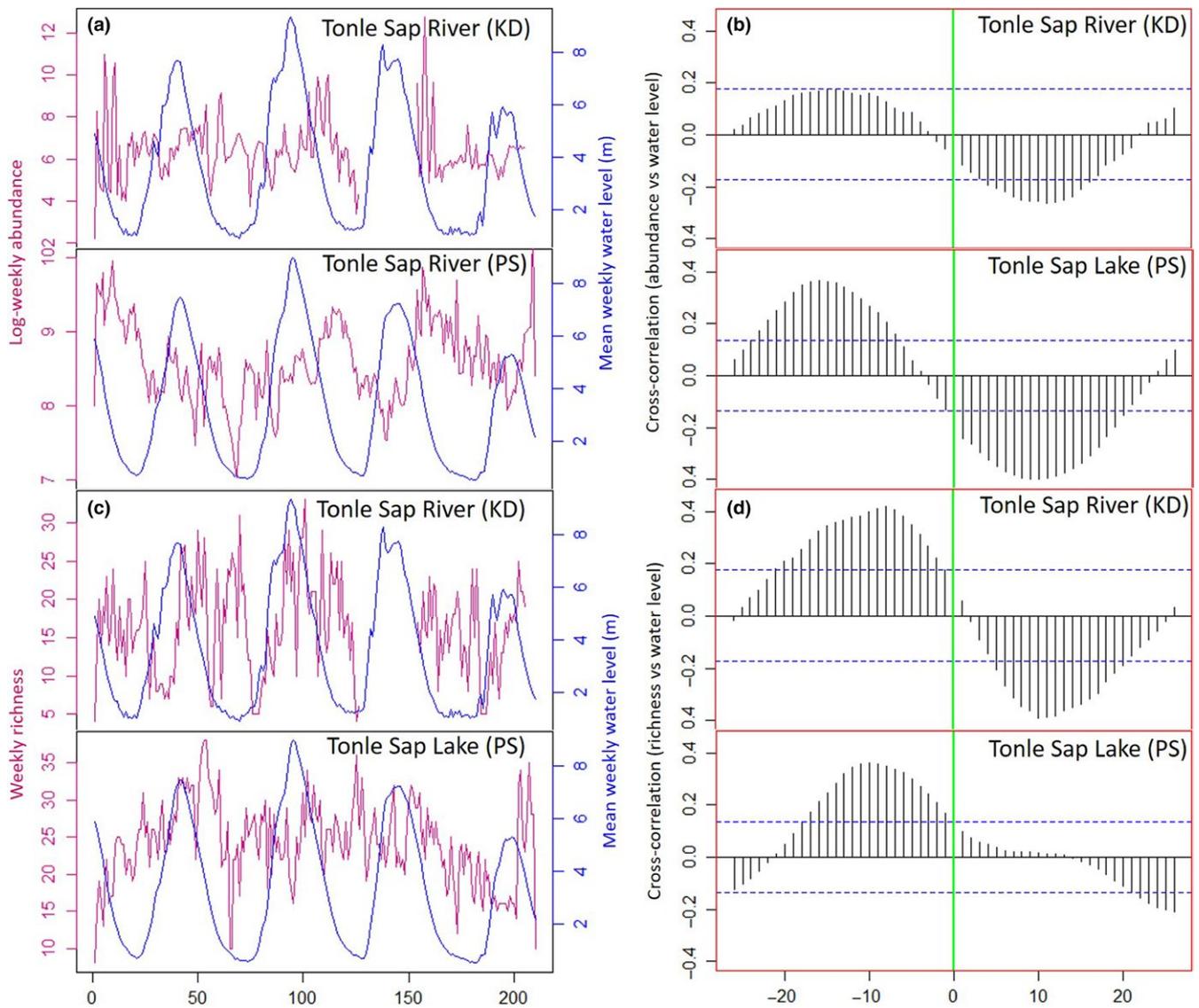


FIGURE 5 Relationships between water level and (a–b) fish abundance and (c–d) species richness in the TSRL. In cross-correlation plots, the dotted blue lines provide the values beyond which the correlations are significantly different from zero. The x-axis is the number of weeks for the period from 1 January 2012 to 31 December 2015

such as rising and falling water levels, played pivotal roles in influencing spatial and temporal variation in the TSRL fish community structure.

4.1 | Richness and diversity

High species richness and diversity in the middle section of the lake (KT, PS) were likely because this section was deeper and larger in terms of water depth and surface cover than were other sections within the system. A bathymetric map of the Tonle Sap Lake reveals a general downward slope towards the middle section from both the southern section (KC) and the northern section in BB (Campbell et al., 2006). In addition, the middle section had a higher degree of inundation throughout the year, which was associated with at least three large tributary rivers of the Tonle Sap basin, namely, the Sen River of KT, with a lower reach

drainage within 230 km² of the lake; the Chinit River of KT, with a total drainage area of 5,649 km²; and the Pursat River of PS, with a catchment area of 5,965 km² (CGIAR, 2013; Nagumo, Sugai, & Kubo, 2013, 2015). The high degree of inundation, combined with greater depths, tended to increase habitat connectivity and availability, which created more living space and a more stable environment. This gives fish species a colonising advantage, which drives greater richness and diversity (Henriques-Silva et al., 2013). For example, Boeng Chhmar and its associated rivers and floodplains, which cover an area of 280 km² in the middle section of the lake in KT, were described as near-natural wetlands, encompassing permanent open water surrounded by a creek system; furthermore, the area was designated a RAMSAR wetland of global significance in 1999 (The Ramsar Convention Secretariat, 2014). In other tropical river-lake floodplain systems, water depth and surface cover are the two most significant variables that were

found to also explain higher species abundance and richness, for example in the Venezuelan Cinaruco River (Hoeinghaus, Layman, Arrington, & Winemiller, 2003; Rodríguez & Lewis, 1997) and the Brazilian Pantanal River (Fernandes, Machado, & Penha, 2010). In a similar way, local features such as sites with permanent channel connection and water surface connectivity were also identified to positively influence local species richness in Arctic lakes. Sites with these attributes were found to harbour both restricted and widespread species (Laske et al., 2016). Fish populations in these sites are likely to be sustained by immigration from adjacent habitats (Brown & Kodric-Brown, 1977).

In contrast, relatively lower richness and diversity values were found in the southern (KD, KC) and northern sites (SR, BB), where total species richness among these sites were similar. This was because sites in the southern part were representative of riverine habitat, mainly serving as a natural fish passageway for migratory species that seasonally migrate between the lake and the Mekong River to complete their life cycle (Halls, Conlan, et al., 2013; Halls, Paxton, et al., 2013; Poulsen et al., 2002, 2004). This site is laterally connected to the surrounding floodplains only partly during the high-flow period and becomes disconnected during most parts of the year (Valbo-Jørgensen et al., 2009). In a similar way, sites in the northern section have fewer connections with large and permanent wet tributary rivers, and the main land-use types of the location are rice farming, herbaceous floating vegetation and dense mats of water hyacinths as well as seasonal flooded grasslands (Hortle, Troeung, & Lieng, 2008; MRC, 2011b, pp. 64–65). Such habitats strictly favour mainly black and some grey fishes that are capable of tolerating anoxic conditions (Aloo, 2003; Welcomme, 2001).

4.2 | Spatial variation

We found that fish fauna within the TSRL was distributed along the south–north gradient, classifying the entire community into three assemblage clusters. The characteristic species in cluster 1 of the southern section were mainly restricted to migratory (riverine) white fishes, such as river catfishes, cyprinids, loaches and sheatfishes. These white fishes are generally intolerant to anoxia, preferring migration as a means to escape adverse environmental conditions during the dry season (Welcomme, 2001). Well-oxygenated water, such as the lotic main river channel and deep pools, are generally required for these species to shelter during the dry season (Halls, Conlan, et al., 2013). In addition, the distribution of white fishes in this cluster was part of the seasonal migration conducted to complete their life cycles, that is accessing the Tonle Sap floodplains for rearing and feeding and returning to the Mekong mainstream for dry season refugia and spawning sites during the early flooding cycle (Baran, 2006; Dudgeon, 2000; Kong et al., 2017; Poulsen et al., 2002, 2004).

Cluster 2 in the middle section of the lake was characterised by both restricted and widespread species, including small bagrid catfishes (*Mystus* spp.), cyprinids, glassfishes, leaf fishes, climbing gouramies and spiny eels. Overall, this cluster was represented by a high

number of indicator species with different ecological attributes, such as longitudinal migratory white fishes, floodplain residents (i.e. black fishes) and lateral migrants (i.e. grey fishes). This result was likely due to the overall environmental stability in this section, that is deeper water, larger surface cover and habitat connectivity through the permanent water bodies (i.e. Ramsar Wetlands of Boeng Chhmar) and presence of permanent wet large tributaries of the Tonle Sap basin.

Indicator species for cluster 3 in the northern section were mainly restricted to black and grey fishes, such as gouramies, airbreathing catfishes, sleepers, snakeheads, featherbacks and sheatfishes as well as a few cyprinid white fishes with general habitat preferences, such as *Barbonymus gonionotus* and *Hampala macrolepidota*. The underlying reason for this result was that the cluster was associated with the lake's northern section, which encompasses mostly lentic habitats and poorly oxygenated waters compared to the open area of the lake (cluster 2), which has effective wind mixing conditions throughout the water column (van Zalinge et al., 2003). Black and some grey fishes are permanently found in such oxygen-poor habitats (Hortle et al., 2008; MRCS, 1992; van Zalinge et al., 2003). These fish groups are carnivores or detritivores, and some are able to migrate over land, including snakeheads, airbreathing catfishes, gouramies and bagrid catfishes, which have developed auxiliary organs for oxygen uptake from the atmospheric air (Lamberts, 2001; MRCS, 1992). In the Yala Swamp of Lake Victoria, African catfishes (i.e. black fishes) were also found to flourish in such poorly oxygenated habitats (Aloo, 2003).

Consistently, we found a very high relative abundance of white fishes in cluster 1 (96%); however, this proportion gradually decreased along the south–north gradient of the TSRL and was replaced by grey and black fishes towards cluster 2 and cluster 3 (Figure 4). The results of this study also supported previous studies that specifically found high abundances of featherbacks and airbreathing catfishes in the northern section of the lake (SR, BB) (Lim et al., 1999) as well as snakeheads and gouramies in BB (Enomoto et al., 2011). In addition, our results showed that three species were ubiquitously abundant for all the three clusters, namely, *Henicorhynchus lobatus* (Hlob) and *H. siamensis* (Hsia), and *Puntioplites proctozysron* (Ppro). These species, especially *Henicorhynchus lobatus*, are among ecological keystone species with critical roles in food security throughout the Lower Mekong Basin (LMB); additionally, these species are important prey for predatory species and Irrawaddy dolphins (Baird, 2011; Fukushima, Jutagate, Grudpan, Phomikong, & Nohara, 2014).

4.3 | Temporal variation

In a tropical flood-pulse system such as the Tonle Sap, hydrological variation is a key ecological driver that influences the temporal dynamics of fish assemblage structure. We found significant intra- (seasonal) and interannual variation in the TSRL fish communities.

Seasonally, the abundance and richness of the TSRL fish communities were found to be significantly greater during the out-flow period (Supporting Information Figure S4.7). This was due

to the seasonal longitudinal migrations of white fishes from the TSRL to the Mekong mainstream for dry season refugia (Poulsen et al., 2002, 2004). Such seasonal migrations are usually predictable with the stationary trawl *Dai* fishery, which has operated in the Tonle Sap River for more than a century. The observed peaks often occur in a time window of ~7–1 days, particularly before the full moon in December and January (Halls, Paxton, et al., 2013). Likewise, during this outflow, grey and black fishes also undertake short-distance lateral movements from the nearby TSRL seasonal floodplains to the deeper area of Tonle Sap Lake or the main river channel. Seasonal migrations during the outflow usually drive huge fishing activities in the TSRL, when the fisheries are opened for all as well as in many parts of the LMB. In contrast, we found the lowest fish abundance in the TSRL during the inflow when white fishes longitudinally migrate for spawning in the rapids and deep pools of the Mekong River, and mature fishes, juveniles and larvae then migrate and drift downstream and invade the surrounding TSRL floodplains for feeding and rearing (Valbo-Jørgensen et al., 2009). The lower abundance during the inflow was likely attributed to low fish densities, as fish were widely dispersed by seasonal floods to floodplains and inundated forests surrounding the TSRL, which makes them difficult to capture. Our cross-correlation analyses noted that the peak abundance and richness (Figure 5a,c) were, respectively, related to the peak flow occurring about 4 months (-15 weeks in KD and -16 weeks in PS) and 2–2.5 months (-8 weeks in KD and -10 weeks in PS) earlier. While the peak flow occurs around early October (MRC, 2005; Supporting Information Figure S2), the peak abundance occurs around January; in contrast, the peak richness occurs in between early November and mid-December. The period for the peak abundance and richness found from the cross-correlation analyses corresponded to the defined outflow (falling water levels) period for this study. Such seasonal patterns were also reported in other tropical river–floodplain fish communities, such as the Amazonian Juruá River and forest streams (Espírito-Santo, Magnusson, Zuanon, Mendonça, & Landeiro, 2009; Silvano, Benedito, & Oyakawa, 2000), Venezuelan rivers (Hoeinghaus et al., 2003) and in French Guiana (Boujard, 1992), where greater abundance and richness with more species interactions were driven by the falling water levels (i.e. low flows).

The interannual variation in the TSRL fish communities found in this study could be explained by many reasons; however, the variation in annual flows (such as peak water levels) has been described as a main factor affecting the TSRL fish communities (Baran et al., 2001; Halls, Conlan, et al., 2013; Halls, Paxton, et al., 2013; Sabo et al., 2017; van Zalinge et al., 2003). Our results highlighted that the changes in the TSRL fish community were significantly linked to hydrology. The annual peak flows in Tonle Sap Lake were highly contrasted during our study period, that is maximum water depths of 9.9 m were recorded in 2011, while only 7.5 m was observed in 2012, 9.0 m was observed in 2013, 7.3 m was observed in 2014 and only 5.3 m was observed in 2015. For example, the high flows in 2011 and 2013 may have facilitated fish spawning success, survival and

growth, as greater flood levels equated with higher volumes of water in the TSRL, and thus, larger inundated areas of rearing/feeding habitats were available for fish. Prey species and juveniles could stay in rearing habitats longer, which increases their survival rates. Higher flows also mean that more food becomes available and, thereby, competition for food among fish is reduced. In fact, the highest catch on record over a 17-year monitoring period was observed in the fishing season of 2011/2012 at the Tonle Sap *Dai* fishery (Chheng, So, Ngor, & Nao, 2012). Our results also noted that fish communities in 2012 significantly differed from those in other years (Supporting Information Figure S4.10, NMDS axis 1).

Flows also constrain fish species with longitudinal and lateral dispersal abilities among habitats, such as different river reaches and floodplains (Bunn & Arthington, 2002; Franssen et al., 2006). The significant interannual changes (Supporting Information Figure S4.10, NMDS axis 2) found in the study were also due to the presence of more species from the high-gradient river/streams and clear/fast flowing waters in 2012, such as *Clupisoma longianalis* (Clorn), *Balitora meridionalis* (Bmer), *Crossocheilus reticulatus* (Cret) and *Hemibagrus wyckii* (Hwyc), and fewer slowly flowing/lowland river species, such as *Parachela siamensis* (Psia) and *Hemibagrus filamentus* (Hfil); however, towards 2015, there were more species that preferred lowland rivers and peats habitat, such as *Osteogeneiosus militaris* (Omil), *Osteochilus microcephalus* (Omic), *Osphronemus goramy* (Ogor) and *Tenualosa thibaudeaui* (Tthi) and fewer high-gradient river fishes, such as *Discherodontus parvus* (Dpar) and *Osteochilus waandersii* (Owaa).

Human activities, such as ongoing water development projects in the Mekong River (Ngor et al., 2018; Sabo et al., 2017), intensive fishing and farming with the use of pesticides and chemical fertilisers as well as the clearance of flooded forests in the TSRL, could also influence the interannual changes in the TSRL fish communities, and this topic needs further investigation. In addition, during the time of the survey, a fisheries policy reform, leading to the abolition of all 35-century-old industrial-scale fishing lots (see Figure 1), took effect in 2012. This reform was argued to benefit artisanal (subsistence) fishers, although the impacts of this reform on the TSRL fish communities deserve further research.

To conclude, understanding the dynamic nature of spatiotemporal variation and distribution patterns as well as indicator species in the TSRL fish communities is necessary to inform fisheries monitoring, management and conservation programmes. For instance, KD is a strategic location for fish diversity management and conservation initiatives, as “white fishes” must use this natural passageway to complete their seasonal life cycles between the Mekong River and the Tonle Sap floodplains. In a similar way, the northern lake (BB) could serve as a location for the management and conservation of black fishes. For fisheries monitoring, the clusters and key indicator species identified in this study can be proposed for the long-term fish monitoring programmes to understand spatiotemporal changes and update the status and trends of the TSRL fisheries. The suggested timing of peak abundance and richness in relation to the peak flows of the TSRL could also be part of fish regulation and

conservation initiatives. At last, maintaining the naturally predictable seasonal rising and falling flood pulses as well as the longitudinal and lateral connectivity of the main habitats of the Mekong and its tributary systems, including the Tonle Sap River, are likely the key drivers to maintaining seasonal fish migrations and, hence, the TSRL's seasonal assemblage diversity and productivity. Given that hydropower dams are still being built in the Mekong, good design flows (Sabo et al., 2017) that would help reduce dam effects and boost fisheries production, for example in the Tonle Sap, should be prioritised and applied as one of the mitigation measures on existing and planned dams in the Mekong.

ACKNOWLEDGEMENTS

We are grateful to the Erasmus Plus, the Belmont Forum (TLSCC project) and the European Erasmus+ credit mobility and capacity building CONSEA Programmes for funding our study. Cordial thanks to the Fisheries Programme of the Mekong River Commission (MRC), the Inland Fisheries Research and Development Institute (IFReDI) of the Fisheries Administration and the Tonle Sap Authority of Cambodia for making available the fish monitoring data sets used in this study. We thank the two anonymous reviewers for their input and constructive advice to improve this manuscript. Sincere thanks are given to Peter Degen and Peter Starr for commenting on the earlier version of this manuscript. The EDB laboratory is supported by "Investissement d'Avenir" grants (CEBA, ref. ANR-10-LABX-0025; TULIP, ref. ANR-10-LABX-41).

CONFLICT OF INTERESTS

The authors declare no conflict of interests.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Ngor PB, Grenouillet G, Phem S, So N, Lek S. Spatial and temporal variation in fish community structure and diversity in the largest tropical flood-pulse system of South-East Asia. *Ecol Freshw Fish*. 2018;27:1087–1100. <https://doi.org/10.1111/eff.12417>