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FRESHWATER ECOLOGY

Impact of seasonal hydrological variation on tropical fish assemblages: abrupt shift following an extreme flood event

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Abstract. Pulsing hydrology is a major factor affecting fish communities in tropical river-floodplain ecosystems. Species responses to flow alteration are however poorly understood and are thus difficult to predict. Here, we investigated temporal changes in fish community structure (taxonomic and functional) in the Tonle Sap Lake, a floodplain ecosystem in Cambodia that supports the world largest inland fisheries and a UNESCO biosphere reserve. Fish catches were monitored daily at five locations around the lake between 2012 and 2015, with 53 species obtained over the course of the field study. Nine fish traits were recorded and used to characterize the functional composition of fish communities. Temporal changes in functional community structure in response to hydrological variation were assessed using multiple co-inertia analysis (MCOA) and cross-correlation function (CCF) approaches. Analyses revealed an abrupt shift in functional structure following extreme flood events in 2013 that included a marked decrease in large-bodied fish at high trophic levels. Also observed were seasonal changes in the relative abundance of life-history strategies, feeding habits, and accessory respiratory adaptations. Black fish (species that are relatively sedentary with an equilibrium-type life-history strategy) dominated during low-water periods, whereas white fish (migratory species with opportunistic or periodic life-history strategies) were dominant during high-water periods. Dynamics of local assemblage structure were fairly synchronous spatially and were independent of the distance between locations. Species responses to the peak flood pulse were estimated to lag 1–2 months. Findings from this study indicate that management of fisheries resources in the Tonle Sap Lake should consider differential responses of species to hydrology as a function of life-history strategies and other functional traits as well as factors that may influence time lags in population and community changes to extreme flow events.

Key words: fish community; flood pulse system; functional traits; hydrological variation; spatial synchrony; Tonle Sap Lake.

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INTRODUCTION

Despite extensive research on plant and animal community structure and ecosystem functioning during the last few decades, our understanding of relationships between community taxonomic structure, species functional traits and ecological dynamics and processes remains limited (Winemiller et al. 2015). This understanding is essential for predicting population and community responses to multiple stressors impacting biodiversity and ecosystems globally (Olden et al. 2010). For most ecosystems, our knowledge of specific factors driving temporal and spatial variation in community structure of multiple fish species and large rivers is too limited to set up effective management strategies, and many have called for research that addresses this fundamental issue (Carmel et al. 2013, Sutherland et al. 2013).

Research on the drivers of community dynamics is especially critical for fisheries management, particularly within tropical regions where species abundance and diversity is high and fishing pressure often is intense. In Southeast Asia, the nutritional and economic demands placed on natural ecosystems are greatly challenging biodiversity conservation and environmental sustainability (Dudgeon 2011). Inland capture fisheries play a crucial role in regional food security, providing nearly 60% of the animal protein for human consumption, especially in developing countries such as Cambodia, Lao PDR, Vietnam (Hortle 2007, So et al. 2015). Accordingly, many Asian rivers are now facing increasing environmental degradation and pressures, that is, water pollution, eutrophication, habitat fragmentation, deforestation, which are adversely affecting biodiversity and ecosystem functions (Vörösmarty et al. 2010, Dugan et al. 2010, Ziv et al. 2012, Winemiller et al. 2016). Improved strategies for fisheries management and biodiversity conservation are needed to mitigate impacts and sustain ecosystem services. This will require understanding of how specific hydrological components influence spatial and temporal variation in fish community structure (Olden et al. 2010, Pool et al. 2010). Long-term monitoring of fish communities in rivers has provided an effective means to study compositional shifts; however, few such efforts have been made in rivers of Southeast Asia (Dudgeon 2003). The Mekong River and other large biodiverse rivers in Southeast Asia have extensive floodplains and wetlands that provide invaluable ecosystem services that support both biodiversity and human welfare. Tropical river-floodplain ecosystems have diverse fish communities that often support important commercial and subsistence fisheries. Fish production is enhanced by seasonal hydrological pulsing that connects and expands floodplain lakes (Junk et al. 1989, Junk and Wantzen 2004). In Cambodia, the Tonle Sap Lake (TSL) lies in a huge floodplain that is connected to the Mekong River via the Tonle Sap River. The lake volume changes dramatically between dry and wet seasons, from 2500 to 15,000 km^2, depending on the extent of flooding from the Mekong River (60%) and in the surrounding area (30%).

The river flood pulse concept (FPC), an influential conceptual framework describing flood pulse river dynamics, asserts that ecological dynamics and productivity of river-floodplain ecosystems are regulated by large seasonal changes in flows that affect lateral connections between aquatic and terrestrial landscapes (Junk et al. 1989, Junk and Wantzen 2004). This framework focuses on the lateral dimension of rivers and contrasts with the river continuum concept (RCC; Vannote et al. 1980) that asserts that local nutrient dynamics and productivity and nutrients are strongly dependent on the position within the longitudinal fluvial gradient and are influenced by upstream processes. The current consensus in river ecology emphasizes the hydrological regime as the principal driver of ecological dynamics (Simões et al. 2013, Humphries et al. 2014). Studies conducted on river-floodplain systems in the Americas, Europe, and Africa have documented variation in fish community taxonomic and functional structure in relation to hydrology and associated environmental conditions (Winemiller 1989, Merigoux and Ponton 1999, Merigoux et al. 2001, Tedesco et al. 2008, Pease et al. 2012). In the Pantanal wetlands of South America, the average trophic position of fishes declined during the transition from the dry season to the wet (flood) season (Wantzen et al. 2002). Merigoux and Ponton (1999) reported a positive correlation between the density of characiform fishes and flood level in river floodplains in French Guiana. Moreover, fish functional traits were strongly related to variation in aquatic habitats and flow regimes. Specifically, fish size at maturity, diameter of oocytes, parental care, and body height tended to decline with greater temporal variability in river hydrology (Merigoux and Ponton 1999, Merigoux et al. 2001). Functional traits thus help to mechanistically link temporal changes in river fish communities to environmental drivers. The present study investigates the extent to which the taxonomic and the functional structure of fish communities in the Tonle Sap Lake are explained by variation in hydrology and associated environmental conditions in this flood pulse system.

Whereas recent research on Tonle Sap Lake fishes has demonstrated changes in biomass or species richness related to the annual flood pulse (e.g., Ngor et al. 2018), here we focus on seasonal changes in both taxonomic and functional composition of fish communities. We examined the temporal dynamics of fish assemblages across multiple locations within the lake and their responses to the lake's hydrological regime. We hypothesized that both taxonomic and functional changes in fish community would be strongly driven by the annual flood pulse and that the spatial synchrony in fish assemblage composition would not be related to the geographical distance between sites owing to the strong synchronizing effect of hydrological changes impacting all location similarly (Liebhold et al. 2004).

MATERIALS AND METHODS

Study system: Tonle Sap Lake

The Tonle Sap Lake (TSL, Fig. 1) is the largest and most productive freshwater lake in Southeast Asia and well known for its extraordinary seasonal flood pulse, fish diversity, and productive fisheries. During the wet (monsoon) season (May–October), the lake receives water from tributary rivers surrounding the lake area and the Mekong River via the Tonle Sap River, which during this period reverses its flow as it receives flood waters from the Mekong River. Water levels rise on average from 1 to 9 m, causing a huge expansion of the lake (~500–600%) into surrounding floodplains. When the TSL discharges water to the Mekong River during the dry season, this additional water volume mitigates sea water intrusion in the Mekong Delta (MRC 2010). TSL drains 8065 km^2, ~11.3% of the total drainage area of the Mekong River Basin (MRB) and is characterized by annual rainfall ranges of 1300–1900 mm with an average temperature of 29°C (max: 33°C, min: 25°C). The hydrology of the lake is strongly dependent on the Mekong River flow regime with more than 60% of TSL's water flowing in from the Mekong, supplemented by river runoff from 12 sub-basins around the lake such as the substantial Stung Sen, Sangker, Pursat, Chinet river tributaries (Fig. 1). These sub-basins are nested within 5 provinces (Battambang [BB], Siem Reap [SR], Pursat [PS], Kampong Thom [KT], Kampong Chhnang [KC]; Fig. 1) around the lake, each containing floodplains that are mainly covered by shrubland, flooded forest, grass land, rice and lotus fields, which are the key habitats for many plant and animal species (Lamberts 2001, MRC 2010). The TSL supports more than 300 fish species and is an exceptionally productive ecosystem compared to other large lakes around the world (WorldFish 2007). The lake supports the world's largest inland fisheries, with harvests between 289,000 and 431,000 tons annually, representing more than 60% of Cambodian inland capture fisheries. Given these features, the TSL provides good model system to investigate community dynamics in a strongly pulsing environment.

Fish data

Fish data used in this study were collected during the "Fish abundance and diversity monitoring in the Tonle Sap Lake" project associated with the Mekong River Commission's (MRC) Fisheries programs (Ngor 2012). The monitoring program included five locations in five provinces surrounding the lake, that is, Kampong Chhnang, Pursat, Battambang, Siem Reap, and Kampong Thom (Fig. 1), from January 2012 to October 2015. At each location, three fishermen recorded their daily catches, species composition, individual abundance, as well as the type and dimension of fishing gear they used. The catch monitoring methods were adapted from the MRC's regional monitoring program on Fish abundance and diversity in the Lower Mekong Basin (FEVM 2007). Fishermen were trained to sample their typical daily catch, to identify the fish species, and to measure the length and weight of specimens. Each specimen was

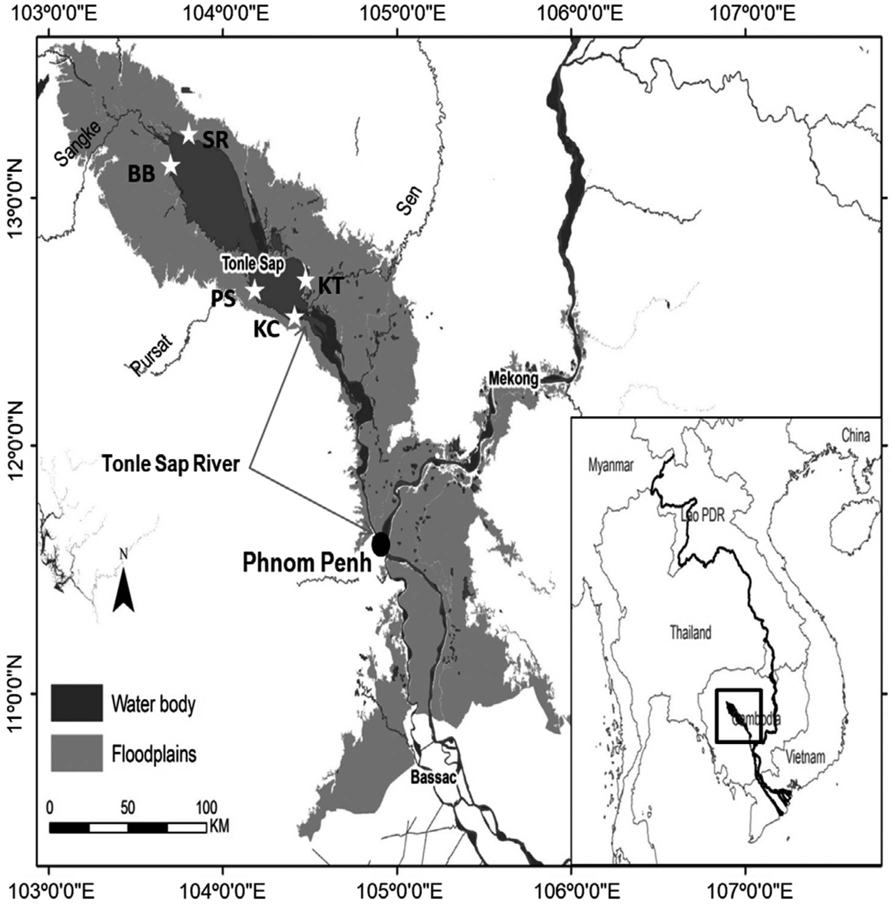

Fig. 1. Tonle Sap Lake and geographic locations of fish monitoring sites (star).

identified to the species level and validated with the use of fish photo flipcharts featuring more than 170 fish species found in the TSL. To ensure the quality of monitoring data, all records were independently reviewed by MRC scientists on a quarterly basis.

Only fish data collected using gillnets (98% of the fishing gears used) were selected for the study with mesh sizes ranging from 2 to 6.5 cm and an average dimension of 850 m in length by 1.5 m in depth. The catch was expressed in total number of individual specimens collected per species resulting in 209 species identified during the monitoring program. Only the species present >5% of the total observations, that is, 60 d over the whole sampling period (1172 d), were kept for analyses ($n = 53$ species). To minimize the range and reduce skewness of the distribution, fish abundances from the three fishermen were averaged at each site and $\ln(x + 1)$ − transformed.

Hydrological data

Daily water levels were collected for the same period (2012–2015) as fish data from the main hydrological station of MRC located in Kampong Loung (PS; Fig. 1). The water levels fluctuated seasonally with the lowest level in April–May and peak in September–October. Within the monitoring period, the flood in September 2013 was exceptional with the average return period (i.e., recurrence interval) of this hydrological event estimated to be 12 yr (MRC 2015).

Functional traits

Nine functional traits (maximum size, mean trophic level, habitat, life-history strategy, ecological guild, feeding habitat, spawning habitat, water column position, and accessory respiratory) were used to examine the association of community structure to functional traits. All traits were collected and updated from different sources (see Appendix S1: Table S1). Size, that is, the maximum total length of fish (cm) ever recorded for a species, trophic level, and habitat data were recorded from FishBase (Froese and Pauly 2019). The size and trophic level of fish ranged from 13 to 158 cm and from 2 to 4.5, respectively. Habitat associations were categorized into three types, that is, pelagic (PEL), benthopelagic (BEN), and demersal (DEM). The life-history strategies were based on the model developed by Winemiller and Rose (1992), which classify the life history of fish into three endpoint strategies, that is, equilibrium (EQU), periodic (PER), and opportunistic (OPP), based on the juvenile survivorship, fecundity, and the age of reproduction (Winemiller and Rose 1992, Winemiller 2005).

Each fish species was assigned to one of three migration guilds using data from the long-term bio-ecological study conducted by the Inland Fisheries Research and Development Institute (IFReDI) and the MRC (Poulsen et al. 2002, Baran et al. 2007, MRC 2018). White fishes perform annual long-distance migrations along the Mekong River mainstream or between the Tonle Sap Lake and Mekong River. Gray fishes migrate short distances, often between the Tonle Sap Lake, surrounding floodplains, tributaries, and/or Mekong River. Black fishes do not migrate and stay permanently in the same water body such as lakes, ponds, rivers, or paddy fields. Many black fishes possess accessory respiratory adaptations that allow them to tolerate water with low oxygen concentration.

Other traits such as spawning and feeding habitats were collected from MRC Mekong Fish Database (2003) Poulsen et al. (2004). Spawning habitats were categorized into two types, that is, floodplains (FLP) and river channels (RV), and two categories were used for feeding habits, that is, littoral (LIT) and offshore and littoral (OFF&-LIT). Last, the water column position and accessory respiratory traits were modified based on descriptions for tropical fishes from floodplain habitats in South America (Winemiller 1989). Species were classified as normally occupying a vertical position in the water column near the bottom-middle (B-M) or middle-surface (M-S), and as having (YES) or not having (NO) an accessory respiratory organ, such as a suprabranchial chamber (e.g., climbing perch, Anabantidae; snakehead, Channidae; or walking catfish, Clariidae).

Biological information for Tonle Sap fishes is scarce. Therefore, species trait values and classifications relied on previous studies conducted in the Mekong Basin, particularly the ecological and fish migration studies conducted by Poulsen et al. (2002, 2004). Some classifications were inferred by KOW based on information from other regions of the Lower Mekong Basin (Ou and Winemiller 2016, Ou et al. 2017, Bower and Winemiller 2019*a*, *b*) and floodplain systems in the Neotropics (e.g., Winemiller 1989).

Statistical analyses

Time series of fish data were analyzed using multiple co-inertia analysis (MCOA), which is a multi-table ordination method that can be used to assess ecological patterns in space and time based on the covariance optimization criterion between individual table ordinations and a reference ordination (Chessel and Hanafi 1996, Bady et al. 2004). Despite its ability to quantify spatiotemporal community patterns, MCOA is rarely used in ecological studies compared to other ordination methods, for example, principal component analysis (PCA), redundancy analysis (RDA), or canonical correspondence analysis (CCA). In our study, MCOA was the most appropriate ordination method because it allowed us to investigate changes in fish communities by simultaneously quantifying the temporal variations of fish assemblages of the individual tables (i.e., communities at each site) and by producing the reference ordination, which is the common structure shared by the individual tables. Thus, MCOA was performed on the 5 individual tables, that is, five monitoring sites (BB, SR, PS, KT, KC), and the reference structure can be viewed as the temporal pattern within the lake. Temporal changes in fish community composition were summarized by MCOA synthetic scores, which are the optimized covariance values from the individual tables. We used the coefficient RV, which measures the correlation between the temporal dynamics of the individual tables and of the temporal reference structure, to quantify the strength of the relationship between individual table and common structure (Robert and Escoufier 1976). This coefficient ranges from 0 to 1 with low values indicating a poor synchrony between the temporal patterns of individual tables (i.e., locations) and the reference structure. The reference structure refers to the temporal change of fish community composition for the Tonle Sap lake as whole. It is the common structure shared by the five individual fish tables (our five sampling sites) based on the covariance optimization criteria from the MCOA procedure.

Furthermore, to estimate spatial synchrony in temporal variations of community structure across the five sites, we used a multivariate normal distribution: $Y_{ij} \sim \mathrm{MVN}(\mu_j, \Sigma_{ij})$, where Y_{ij} are the coordinates at site j and time i along a given MCOA axis, μ_j are the site-specific means and Σ_{ij} is a variance–covariance matrix of the form:

$$\sum_{ij} = \begin{pmatrix} \sigma_1^2 & \cdots & \rho_{15}\sigma_1\sigma_5 \\ \vdots & \ddots & \vdots \\ \rho_{15}\sigma_1\sigma_5 & \cdots & \sigma_5^2 \end{pmatrix}$$

where diagonal elements represent the variance within each site and off-diagonal elements represent the covariance between sites. ρ is the temporal correlation coefficient between each site and represents the temporal synchrony in community structure (Santin-Janin et al. 2014). For two sites, ρ was calculated as

$$\rho_{jj'} = \frac{\sigma_j\sigma_{j'}}{\sqrt{\sigma_j^2\sigma_{j'}^2}},$$

where j stands for one site and j' for another site. To obtain the posterior distribution of ρ between each site combination, we adopted a Bayesian approach in combination with the Monte Carlo Markov Chain (Clark and Bjørnstad 2004). To ensure that the variance–covariance matrix (Σ) was positive definite, we used an inverse Wishart distribution, whereas diffuse priors (i.e., large uniform distributions) were used for the parameter μ_j. For each MCOA axis, we generated three chains with length 30,000 and discarded the first 20,000 as burn-in. For each chain, we chose initial values in different regions of parameter space. Convergence was visually assessed and confirmed using the Gelman and Rubin statistic (Gelman and Rubin 1992).

To examine the relationships between temporal changes in community structure and functional traits, the quantitative traits were regressed against MCOA coordinates using linear models, while the effect of qualitative traits was tested using non-parametric Kruskal–Wallis tests. All the relationships were tested for the first three axes of MCOA, and p-values were adjusted for multiple hypothesis testing using a Benjamini–Hochberg procedure (i.e., sequential modified Bonferroni correction). The tests of qualitative traits were performed only for the categories containing enough species. As a result, only PER and EQU were tested for life-history strategies, while OPP was excluded ($n = 2$). Finally, we assessed the changes in taxonomic structure by testing differences in the MCOA scores of the species from the five main fish families in the lake (i.e., Cyprinidae, Bagridae, Pangasidae, Siluridae, and Osphronemidae).

Linking community changes to hydrological regimes

To assess the link between temporal changes in the fish community and the hydrological regime of the lake, we used cross-correlation functions (CCF). CCF is used to quantify the relationship between two time series (x_t and y_t) as a function of time lag (h) between one to another, that is, the correlation between series x_{t+h} and y_t for $h = 0, \pm1, \pm2$ and so on (Venables and Ripley 2002). In our case, x_t and y_t were, respectively, the synthetic scores of MCOA and water level. The time lags (h, days), indicating the response of fish community to the hydrological changes, were estimated from the maximum value of CCF coefficients. Specifically, when the time lag h is negative ($-h$), it displayed the correlation between MCOA score at a time before t and water level at time t; in other words, MCOA score leads water level. On the other hand, MCOA score lags water level when the time lag h is positive (Shumway and Stoffer 2015).

All data analyses were conducted in R.3.6.1 using ade4 and R2jags packages (R Core Team 2019).

RESULTS

Temporal changes in fish community structure

The 53 fish species in the dataset represented 40 genera, 16 families, and 7 orders. Cypriniformes, Siluriformes, and Perciformes represented 90% of the total species, and the remaining orders (i.e., Clupeiformes, Beloniformes, Osteoglossiformes, Synbranchiformes) accounted for 10% (Appendix S1: Table S1). Cyprinidae was the most species-rich family (45% of species), followed by Bagridae (13%), Siluridae (8%), Pangasiidae (6%), and Osphronemidae (6%), with the remaining 11 families representing less than 20% of the species.

The temporal changes in fish community structure exhibited spatial synchrony across the five sites, with mean temporal correlation ρ ranging from 0.43 to 0.66 and no significant relationships between the strength of synchrony and the geographical distance between sites. Temporal changes in the TSL fish community were summarized by the reference pattern on the first three axes of MCOA, which explained 53.24% of the total variance from the fish abundance data sets (25.28% on F1 axis, 17.09% on F2 axis, and 10.87% on F3 axis; Fig. 2). The values of RV coefficients (a multivariate generalization of the correlation coefficient between two sets of variables) ranged from 0.52 (BB) to 0.75 (SR). On F1, the synthetic scores increased significantly over the study period from negative values to positive ones, revealing a marked shift in community composition after the wet season in 2013, while on F2 and F3, seasonal changes related to the flood pulse cycle were apparent (Fig. 2).

Six of the nine functional traits were strongly associated to the temporal changes in the fish community, with significant relationships detected on the first and third of MCOA axes. Indeed, F1 was characterized by a shift of size classes and trophic levels linked to the extreme flood event in 2013, with greater abundance of large-bodied fish with high trophic levels before the flood (Fig. 3). In addition, seasonal patterns in community structure apparent on F3 were associated with life-history strategy and movement guilds (Fig. 3, Appendix S1: Table S1 and Appendix S2: Table S1). Specifically, the community tended to be dominated by black fishes with an equilibrium-type life-history strategy during the dry season when water levels were low. When water level increased during the wet season, the community became dominated by gray and white fishes with periodic and opportunistic life-history strategies. Feeding habits and accessory respiratory traits were associated with seasonal hydrology as well, with higher abundance of species feeding in littoral areas and possessing accessory respiratory adaptations during the dry season, and more offshore feeding species that lack accessory respiratory adaptations during the wet season. Nevertheless, no significant relationships were observed on F2. Habitat, spawning habitat, and water column position were not related to temporal changes in community structure.

Linking the temporal changes in fish community to hydrological regime

The CCF revealed a significant relationship between the temporal changes in functional community structure and hydrological regime (Appendix S3: Fig. S1). The response of fish community summarized by the first two axes of MCOA lagged behind the hydrological regime, with time lags ranging between −38 and −58 d for F1, −50 and −60 d for F2, and +20 and +30 d for F3. Cross-correlations were lowest for F1 ($r^2 = 0.40$) and highest for F3 ($r^2 = 0.75$). These responses revealed that fish movements into and out of the lake occurred about one to two months before (F1 and F2) or after (F3) the peak of the annual flood pulse.

Discussion

Temporal changes in fish community structure

Fish communities in the Tonle Sap Lake underwent a major shift in size structure and distribution of species trophic positions in association with hydrological variation. During the low-water period, fish communities were dominated by medium-large fishes at relatively high trophic positions. In contrast, during the flood pulse, the relative abundance of large/medium-sized cyprinids and catfishes and several small cyprinids and gouramis (Osphronemidae), including species at relatively low trophic positions, increased rapidly. This shift was more abrupt following the extreme flood pulse in 2013 produced by an intense monsoon within the LMB (MRC 2015). This large, sustained flood pulse apparently led to a burst of recruitment by small fish species with opportunistic life-history strategies.

Hydrologically pulsing ecosystems in the tropics undergo significant changes in environmental

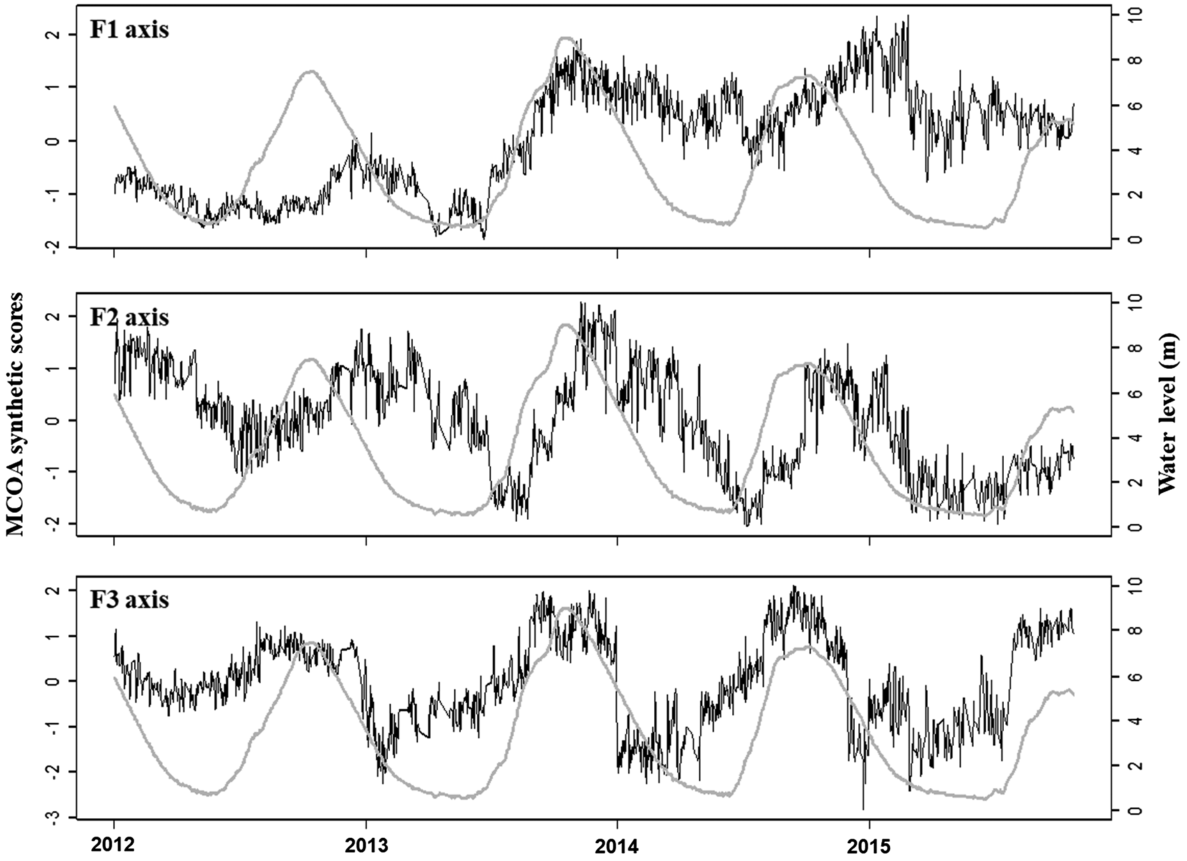

Fig. 2. Reference temporal changes of fish community structure in Tonle Sap Lake. Time series of MCOA synthetic scores on the first three axes from the reference fish abundance table. Gray line represents the daily water level fluctuation in the lake.

conditions between wet and dry seasons, and these seasonal changes have been hypothesized to be the primary driver of fish community dynamics (Junk et al. 1989, Junk and Wantzen 2004). Several studies conducted in Neotropical river floodplains have documented variation in fish community structure, with temporal variation often less pronounced than spatial variation (Merigoux and Ponton 1999, Tedesco et al. 2008, EspÍrito-Santo et al. 2009, Scarabotti et al. 2011, Pease et al. 2012, Arantes et al. 2018). In Amazonian floodplains, water level was shown to be the most influential factor shaping fish abundance and community structure (Castello et al. 2015); however, water level was strongly correlated with other environmental factors, for example, temperature, oxygen, pH, and dissolved nutrient concentrations. Most studies focusing on flood pulse systems have investigated temporal changes in diversity metrics, taxonomic composition, or trophic structure, with little attention to changes in the functional traits of communities (Brosse et al. 2007, Davidson et al. 2012, Chea et al. 2017, Kong et al. 2017, Piniewski et al. 2017). A study conducted in the Paraná River documented a reduction in biomass of large predators and a significant increase in abundance of small species during an extreme flood pulse (Agostinho and Zalewski 1995). Our study appears to be among the first to examine variation in functional structure of fish communities in relation to hydrology in a large pulsing system in Southeast Asia.

Black fishes with an equilibrium life-history strategy (*Trichogaster* spp.) dominated the TSL fish community during the low-water period,

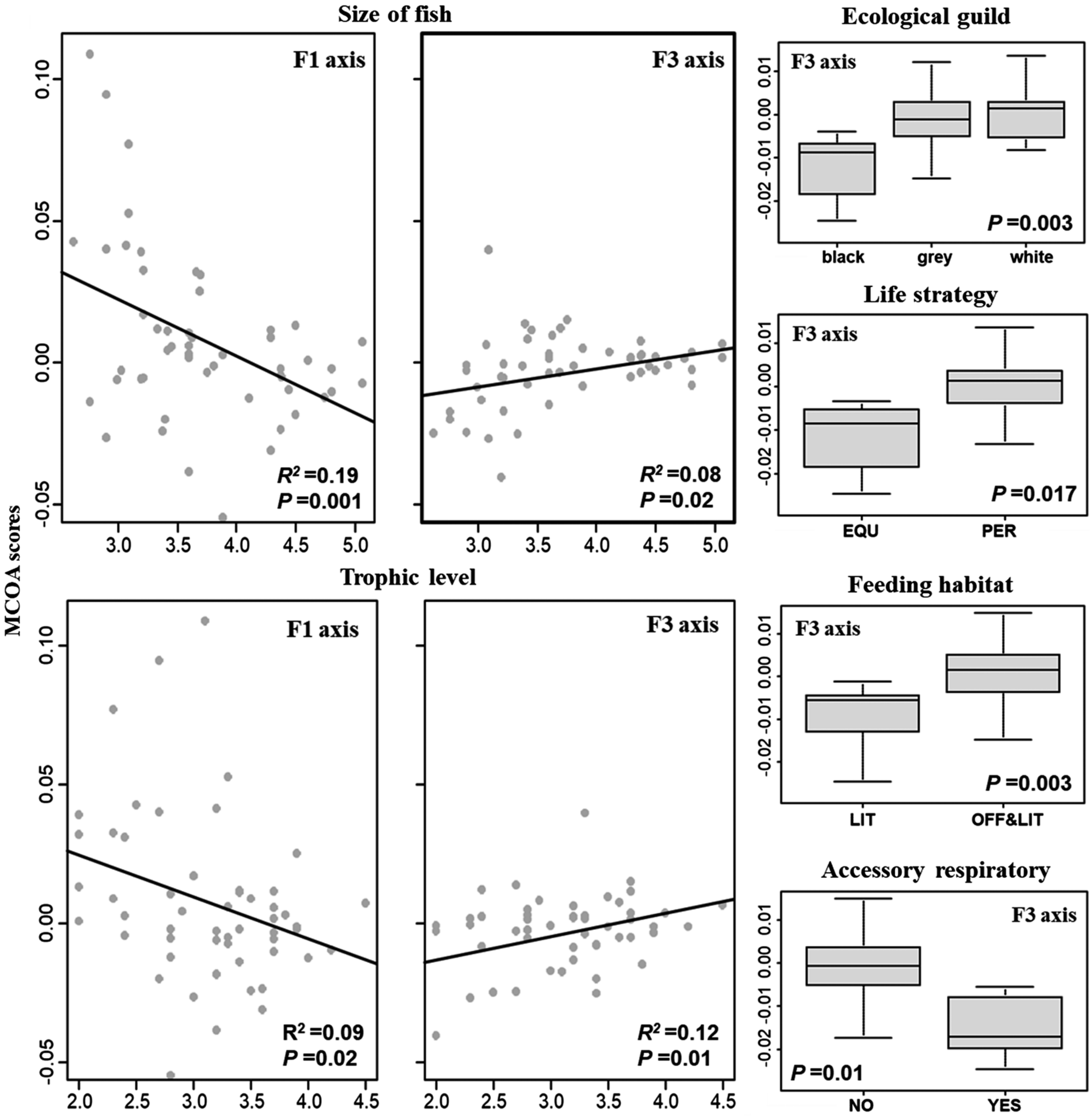

Fig. 3. Relationships between functional traits and fish community structure in the Tonle Sap Lake. Only significant ($P < 0.05$ after correcting for multiple testing) relationships are shown. F1 axis presented the rough shift in community structure (size classes and trophic levels) caused by flood disturbance, while the seasonal patterns in fish community were observed on F3. The size of fish is in log scale and the full names of acronyms are provided in Appendix S1: Table S1, while MCOA scores are shown in Appendix S2: Table S1.

and white fishes with an opportunistic strategy (*Paralaubuca* spp., *Henicorhynchus* spp.) had higher relative abundance near the peak of the flood pulse. Samples the ascending and descending limbs of the flood pulse were dominated by gray and white fishes with a periodic life-history strategy (*Mystus* spp., *Puntioplites proctozystron*). According to the life-history strategy framework proposed by Winemiller (1989, 2005) and Winemiller and Rose (1992), opportunistic strategists have short life spans, little or no parental investment, and multiple spawning events annually; thus, fish exhibiting opportunistic strategy are adapted to variable or harsh environments with unpredictable hydrology and capable of rapid population growth following flood disturbance as we observed in the TLS system (Winemiller and Rose 1992, Winemiller 2005). In contrast, equilibrium strategists have relatively low fecundity and high parental investment in individual offspring and often dominate in aquatic habitats with fairly stable perennial flows. Equilibrium strategists tended to be more abundant in the TLS during low-water periods, whereas opportunistic and periodic strategies tended to be less abundant. Periodic strategists in the TLS appear to be well adapted to seasonal hydrology and associated changes in environmental conditions in the riverscape. Periodic strategists, including large cyprinids and silurids, are characterized by delayed sexual maturation, high batch fecundity, contracted spawning periods, and episodic recruitment that occurs under suitable conditions. In the TLS, abundance of both opportunistic and periodic strategists was positively correlated with flow variability. Seasonal changes in the relative abundance of fish species with different life-history strategies observed in the TLS were consistent with previous observations documented in rivers of West Africa, North America, and the Amazon (Tedesco et al. 2008, Mims et al. 2010, McManamay and Frimpong 2015, Röpke et al. 2017).

In the TSL, we found that mud carp, gouramis and other small opportunistic species, were well adapted to exploit the heterogeneous and dynamic aquatic habitats in the surrounding floodplain, with their populations increasing rapidly during flow pulses. This observation is consistent with those from studies of fish assemblages in Neotropical floodplain rivers (Junk et al. 1989, Winemiller 1989, Merigoux and Ponton 1999, Agostinho et al. 2005, Tedesco et al. 2008). The increase of flood intensity during 2013 may have reduced natural and/or fishing mortality of small fishes because inundated riparian vegetation increases habitat structural complexity that provides refuge. The flood pulse also provides fishes with access to pools of food resources in expanding aquatic habitats of the floodplain. This mechanism was also highlighted in a recent study on trophic niche plasticity in the lake, which showed the expansion of fish isotopic niches during the wet season, reflecting assimilation of resources from a wider range of sources (Pool et al. 2017). In our study, the mean and range of fish trophic position values varied seasonally. A similar seasonal isotopic shift was observed for the fish community of the Pantanal wetland in Brazil, with an increase in mean trophic position during the transition to the dry season, and greater relative abundance of herbivorous fishes during the wet season (Wantzen et al. 2002). In TSL, we found similar patterns, particularly after the peak of the flood pulse, more predators (e.g., *Notopterus notopterus, Pangasius* spp., *Hemibagrus nemurus*) were less common in our samples during high-water periods. An additional factor that may affect patterns of fish abundance is physical disturbance associated with flooding. Rapidly rising flood waters can damage spawning grounds and harm fish eggs and larvae with a negative effect on recruitment. Stocks of species with equilibrium and periodic-type life-history strategies would be expected to recover slower than those of smaller, opportunistic species with rapid life cycles and higher reproductive effort (Agostinho and Zalewski 1995, Welcomme and Halls 2004).

The timing, magnitude, and duration of the annual flood pulse clearly influence almost every aspect of the TSL ecosystem (Welcomme and Halls 2004, Castello et al. 2015). Greater magnitude and duration of flood events are predicted to increase fish diversity and yields (Junk and Wantzen 2004). Depending on the geomorphology, geology and other aspects of the riverscape, effects from floods may last for several years after the events. For example, Castello et al. (2015) documented effects from a flood pulse on multispecies fishery yields in the lower Amazon floodplains that endured for three years. Carlson et al. (2016) reported a six-year effect of flood disturbance on fish diversity and community structure in the Missouri River Delta. The timing of shifts in the TSL fish community documented in the current study would be difficult to predict during any given year. Seasonal trends in fish size and tropic position were generally consistent throughout the study period (Fig. 2). Long-term monitoring of the fish catch and environmental conditions will be required to determine whether changes in response to extreme flood events persist or if there is a return to the previous state of the system and if so at which lag.

Fish migration patterns in Lower Mekong Basin have a strong influence in fish community structure of the TSL, with as many as one third of Mekong fishes (e.g., cyprinids and pangasiid catfishes) classified as white fish that undergo long-distance migrations between the lake and Mekong mainstream (Baran 2006, MRC 2007). Previous studies have documented how many TSL cyprinids (*Hypsibarbus* sp., *Puntioplites* sp., *Cyclocheilichthys* sp.) and catfishes (*Pangasius* sp., *Hemibagrus* sp.) begin their migrations at the end of the dry season and at the beginning of the wet season (Baran 2006, MRC 2007). Several months after the peak of the annual flood pulse and water begins to drain from TLS, cyprinids with more opportunistic-type life-history strategies (*Henicorhynchus* spp., *Labiobarbus* spp., *Paralaubuca* spp.) begin to dominate the fish catch. Black fishes (e.g., *Trichopodus* spp., *Clarias spp., Ananbas testudineus, Channa* spp.) are permanent residents of the lake and aquatic habitats in the floodplains, and some of these species have been reported to conduct lateral migrations between tributaries, floodplains, and the main body of the lake (Lamberts 2001, WorldFish 2007). Most of black fishes are carnivorous and can tolerate hypoxic conditions using accessory respiratory adaptations that allow them to obtain oxygen from air (Lamberts 2001, WorldFish 2007).

Generally, food resources are limited during the dry season, and many year-round resident fishes, that is, black and gray fish, feed primarily within the lake's littoral zone. During the annual flood pulse, nutrient inputs and aquatic ecosystem productivity increase (Kummu et al. 2006). In addition, fishes have greater access to allochthonous food resources within a greatly expanded littroal zone. Indeed, fish migrations in the Lower Mekong Basin and TSL appear to exploit spatial patterns and the pulsing nature of food resources. Consequently, temporal changes in fish community functional structure were expected to be stronger than changes in taxonomic structure per se.

As hypothesized, we found no significant relationship between temporal changes in the fish community structure and the geographical distance between sites. Previous studies on spatial synchrony (intra- and interspecific) in Africa and Europe also have failed to reveal significant relationships between the level of synchrony in community dynamics and distance between locations (Grenouillet et al. 2001, Tedesco et al. 2004). For instance, the sites located close to each other (i.e., BB and SR, Fig. 1), presented low synchrony values (ρ). Overall, the temporal dynamics of fish assemblage structures across the five locations were quite synchronous, suggesting that habitats and fishes throughout the lake respond in a similar manner and sequence to hydrological variation. Nevertheless, two locations, that is, BB and KT, showed slightly low value of RV compared to other locations, reflecting less synchrony with the reference structure. These low values of RV for sites BB and KT could be explained by the influence of large tributaries near these locations, that is, Sangker River and Sen River, respectively (Fig. 1). These two tributaries have densely vegetated floodplains that could provide shelter for fishes (Kummu et al. 2014). Although the high degree of synchrony in local fish assemblage dynamics suggests that TSL fisheries might be managed as a singular unit, we caution that a sufficient number of exceptional locations suggests that different management strategies may need to be devised for regions of the lake by taking into account unique landscape features.

Timing of changes in fish community structure in relation to hydrology

Major changes in fish community structure in relation to the peak of the annual flood pulse seemed to lag between one to two months (Appendix S3: Fig. S1). Several mechanisms could be responsible for time lags, including species reproductive biology and migratory behavior. Information is lacking for the reproductive physiology of fish native to the Lower Mekong Basin. In Brazilian river-floodplain systems, maturation of gonads in Characiform and Siluriform fishes was synchronized with the annual flood pulse (Chellappa et al. 2009, Röpke et al. 2019), but in floodplain systems in the Venezuelan Llanos and Central America, fishes from diverse taxa showed large interspecific variation in gonad maturation and reproduction in relation to pulsing hydrology (Winemiller 1989, 1993). In the Lower Mekong Basin, the first rainfall, which takes place about two months before the peak of the pulse, was shown to be the key factor triggering fish movement, particularly for cyprinids (e.g., *Cyclocheilichthys enoplus*), catfish (e.g., *Pangasius larnaudii, Wallago attu*), presumably in response to the changes in physicochemical characteristics of water receiving runoff from the early rains (Baran 2006, MRC 2007). Therefore, time lags in the fish community response to hydrology could be explained partly by fish migration triggered by the first rainfall and associated factors, for example, conductivity, turbidity, temperature. Another factor that may contribute to time lags is interspecific differences in the speed of migration between the Mekong River and TSL that affects timing of arrival in the TSL. Although the magnitude and duration of the annual flood pulse varies interannually, the timing of flooding within the lake does not vary much between years; nonetheless, it could be significant if the upstream development is intensified; and most white fish migrate long distances, responding to cues in the Mekong River that induce entrance into the Tonle Sap River and the lake (Baran 2006). Alternatively, the time lags can be driven by ecosystem dynamics and the availability and accessibility of food resource at locations throughout the landscape. The flood pulse influences water quality, nutrient dynamics, decomposition of detrital pools, aquatic ecosystem productivity, and fish access to allochthonous resources. Further research is needed to determine if time lags in fish assemblage changes in response to the hydrological regime may be explained by species response to environmental cues (hydrology, water physico-chemistry) affecting migratory behavior and reproductive physiology/behavior along with the spatiotemporal dynamics of resource availability and accessibility on the landscape.

Conclusions

The changes in the functional structure of TSL fish community in relation to the annual flood pulse were fairly consistent interannually, however, the extreme high magnitude flood of 2013 induced even greater change. The 2013 event reveals the potential for human alteration of the flow regime to affect fish ecology in this highly productive system. For example, development of hydropower in the Mekong mainstream likely would alter the timing, magnitude, and duration of inundation of the floodplains that surround the lake. Depending on life-history strategies, trophic ecology, migratory behavior and other characteristics, some species likely would be negatively impacted by such changes, while a few might increase in abundance. Small species with rapid life cycles and an opportunistic life-history strategy might be resilient to an altered flow regime, but large migratory species with slower life cycles (white fish with a periodic life-history strategy) and black fish (relatively sedentary species) that inhabit aquatic habitats in shallow littoral areas of the lake would likely decline in abundance. Clearly, fisheries management in a large, complex, and dynamic ecosystem such as the TSL will require multiple strategies applied in different locations and evaluated using an adaptive management approach (Cooperman et al. 2012).

Finally, we found that changes in the functional structure of the TSL fish community to the hydrological variations lagged between 1 and 2 months before or after the peak of the pulse. This finding should be investigated further to determine if yields could be optimized by adjusting the timing and places for fishing in a manner that minimizes disruption to spawning and recruitment while exploiting post-spawn fish after a period of rapid somatic growth. Improved knowledge of how functional traits affect fish population and community responses to hydrological regimes would greatly enhance our ability to forecast fisheries production under alternative scenarios of fisheries exploitation, land-use, and climate.

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