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Declines in the Mekong's Megadiverse Larval Fish Assemblages: Implications for Sustainable Development

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Abstract: Migratory fishes of the Mekong Basin are facing challenges from human-induced stressors. Quantifying the patterns of fish's early life stages provides important information on spawning seasons, spawning and nursery habitats, reproductive strategies, migration and dispersal patterns, and stock status. However, the ecology of the Mekong larval fishes, including patterns and drivers of larval fish dispersal, is not well understood. Here, we investigate the temporal variability of drifting larval and juvenile fish assemblages in the Cambodian Mekong River and identify their environmental drivers using long-term (10 year) daily fish larval/juvenile data collections. We found that, in the Mekong main channel, the larval and juvenile assemblages were dominated by longitudinal migrants from the families Cyprinidae and Pangasiidae. Peak abundance and richness were found to occur in July and August, respectively. We detected a significant decline in larval and juvenile abundance and richness over the study period. Cross-wavelet analysis revealed that water levels always lead larval abundance, but lag richness. In addition, cross-correlation analysis observed that peak abundance and richness occurred eight weeks and one week, respectively, before the peak water level. We also discovered that species abundance and richness had a strongly positive relationship with maximum water levels. Variation in fish larval and juvenile abundance and richness was also related to total phosphorus, nitrate, alkalinity, and conductivity. Maximum water levels and the key water quality parameters (e.g., phosphorus, nitrate, alkalinity, and conductivity) significantly influence larval and juvenile fish abundance and richness patterns. Therefore, safeguarding natural seasonal flows, especially maximum flows associated with the peak flood pulse, as well as maintaining good water quality, are key to the reproductive success of many migratory fishes and effective dispersal of offspring to the lower floodplain for nursing, rearing, and growth. Clean and unregulated rivers support productive and diverse fisheries.

Keywords: fish larval drift; temporal trend; time-series analysis; cross-wavelet power; phase relationship; cross-correlation function; time lag; Cambodia; Indochina

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1. Introduction

The dispersal of fish larvae downstream, also called 'larval drift', is a common event in rivers [1]. Fish spawn upstream with their eggs and larvae being carried downstream by the hydrologic discharge to rearing habitats in downstream floodplains. Such events are associated with the seasonal flood pulse (peak flow during the wet season), as evidenced in the Mekong River of Cambodia [2]. Indeed, quantifying the spatial and temporal dispersal patterns of fish larvae and juveniles provides important information on spawning seasons, spawning habitats, rearing grounds, reproductive strategies, and movement paths [1,3–5]. This information is essential for effective fishery management and conservation planning [1,3,5]. For example, many fishes within the Mekong River depend on natural seasonal variation in flow, existence, and access to suitable spawning habitats, and the connectivity between spawning, rearing, and feeding areas. The variability of larval fish abundance can also be used as a proxy to understand the reproductive success of spawning fish and the level of recruitment that replenishes fish stocks each year [1,6]. The variability often depends on multiple environmental factors, including water level (a proxy for discharge), water velocity, water temperature, pH, electrical conductivity, dissolved oxygen, rainfall, habitat availability and quality, food availability, and predation pressure [4,7]. These factors can accelerate or delay reproductive processes and generate favorable or unfavorable conditions for egg and larval development, growth, and survival [7–9]. Many freshwater fishes are reliant on environmental conditions to simulate spawning and determine their reproductive success [7–9]. For instance, seasonal hydrological variability may trigger fish migration and spawning, and often facilitates the successful dispersal of fish larvae downstream to rearing habitats. Higher seasonal flows have been shown to enhance habitat availability and connectivity, promote gene flow, and increase larval fish survival, which replenishes wild fish populations [1,3,6].

The Mekong River within Cambodia is characterized by a large variation in seasonal flows, a pronounced flood pulse, and a high diversity of fish species which support one of the world's most productive inland fisheries [10–12]. Many of the inland fishes are longitudinal migrants that migrate up the Cambodian Mekong River system from the lower floodplain during the dry season for refuge and spawning during the early wet season when the Mekong water levels rise [13–16]. Hundreds of species of larval fishes drift with the seasonal flood pulse to rearing habitats of the lower floodplains, such as the Tonle Sap river–floodplain lake, which supports the largest wetland–forest–grassland complex remaining in Southeast Asia, and the Mekong delta in Vietnam [13,15,17].

However, over the past two decades, the Mekong Basin has undergone rapid economic development and population growth, which has caused severe pressure on fishery resources. These pressures include indiscriminate fishing, dam development, agricultural intensification, habitat degradation, and climate change [18–20]. Indiscriminate fishing, for instance, has resulted in declining fish sizes in the catches where many of the large-sized fishes have been removed from the system [20,21], whereas hydropower dam construction has substantially negative impacts on migratory fish's life cycles, survival, and dispersal of eggs, larvae, and juveniles [5,20,22–24]. Therefore, information on the temporal variability and trends of larval fish abundance and richness as well as the environmental factors driving their temporal changes is needed to support environmental impact assessment, fishery management, and conservation initiatives. To date, no such study has been conducted on the long-term trends of larval fish abundance and richness in the Mekong River Basin. Here, we addressed this gap by (i) describing the overall assemblage composition of larval and juvenile fishes collected daily at the Mekong River in Phnom Penh from 2004 to 2013, (ii) investigating the temporal trends of larval and juvenile assemblage diversity (i.e., abundance and richness), and (iii) examining the effects of environmental drivers on the observed temporal trend of larval/juvenile fish abundance and richness collected over the study period.

2. Materials and Methods

2.1. Study Site

Plankton net sampling for larval and juvenile fishes was carried out in the Mekong River in Phnom Penh (N: 11°34′19″; E: 104°56′26″, Figure 1), located in Chong Chroy village, Chroy Changva district, Phnom Penh municipality. The sampling site was located on the right river bank, which is close to the confluence of the Tonle Sap-Mekong River in Phnom Penh. Water levels and physicochemical data were collected at the confluence (Figure 1).

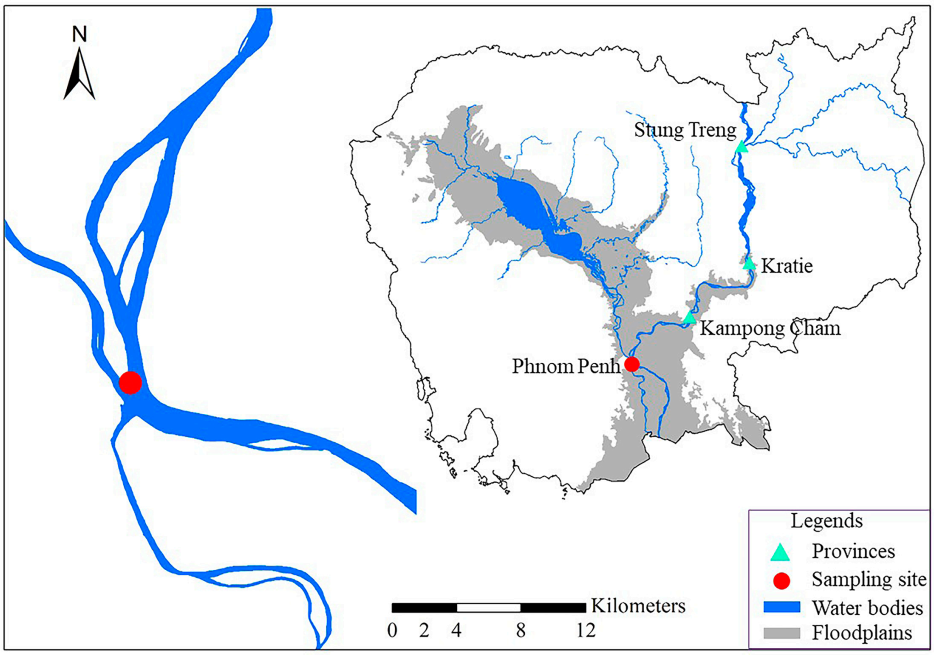

Figure 1. A map showing sampling sites of fish larvae and juveniles, water level, and physicochemical and climatic variables in the Mekong River in Phnom Penh between 1 June and 30 September from 2004 to 2013.

2.2. Data Collection

2.2.1. Larval and Juvenile Fish Data

Larval and juvenile fish data used in this study were obtained from the Inland Fisheries Research and Development Institute (IFReDI) of the Cambodian Fisheries Administration (FiA). Fish larvae and juveniles were sampled daily using a plankton net with 1 mm mesh size, 1 m diameter, and 5 m in length for 30 min four times per day (at 6:00–6:30, 12:00–12:30, 18:00–18:30, and 00:00–00:30 h) during a four-month period between 1 June and 30 September from 2004 to 2013. The plankton net was submerged 2 m (facing upstream against the water current) below the water surface. It was positioned on the right side of the river, approximately 30 m from the riverbank. The opening center of the net was equipped with a flow meter to measure velocity and filtered water volumes. Larvae and juveniles that were filtered by the plankton net were removed from the cod-end of the net and immediately preserved with 8% formaldehyde in the field. All samples were transported to the IFReDI's laboratory for identification and abundance estimates [25]. In the laboratory, samples were sorted and identified under a dissecting microscope to the lowest possible taxonomic level using fish larval and juvenile identification guides [26–28]. The species names were cross-checked and updated following [29].

2.2.2. Environmental Data

Water levels and physicochemical data were provided by the Mekong River Commission (MRC) Water Quality Monitoring Program (Figure 1). Water level data were recorded daily, while the physicochemical data were collected monthly between the 13th and 18th day of each month over the study period from 2004 to 2013 [30–33]. Water samples were collected at about 30–50 cm below the water surface [30–33] and were brought to the laboratory of the Ministry of Water Resources and Meteorology in Phnom Penh, Cambodia [34] for processing and analysis. Water quality parameters including dissolved oxygen (DO), total phosphorus (TP), ammonium (NH_4^+), total nitrite and nitrate (combined nitrate-NO_3^- and nitrite-NO_2, hereafter referred to as "NO_3^-"), total suspended solids (TSS), and alkalinity (ALK) were measured in the laboratory, while water temperature (WT), pH, and conductivity (CON) were measured in the field [34]. The water sampling, preservation, and chemical analytical procedures were based on methods described in the 20th edition of the Standard Methods for the Examination of Water and Wastewater or national standards complying with the requirements of method validation of ISO/IEC 17025-2005 [30–33]. Weekly and monthly maximum and minimum water levels were derived from daily water level data. Climatic data and monthly precipitation (PRE) were derived from the Centre for Environmental Data Analysis [35,36] and are available at http://data.ceda.ac.uk/badc/cru/data/cru_ts/cru_ts_4.01/data (accessed on 22 January 2020). Climatic data were extracted using the "ncdf4" [37] and "raster" packages [38] in R Statistical Programming Language.

2.3. Data Preparation

We used weekly data for the long-term trend analysis of fish larval and juvenile species abundance, richness, and relationship with water levels. Daily fish larval and juvenile species abundance samples (four samples/day) between 1 June and 30 September from 2004 to 2013 were first computed as daily mean species abundance and then were aggregated into weekly larval and juvenile abundance by species. Similarly, daily water level data were computed as the maximum water level for each week. We used maximum water levels because the quantity of larval drift downstream was shown to have a relationship with peak pulses [2]. It is noted that, to reduce the noise in the weekly data set, our analysis includes the first full week in June through the last full week of September from 2004 to 2013. Weeks with less than seven days were dropped from the analysis. We included a total of 165 weeks in our analysis.

For multiple linear regression (MLR), monthly fish larval and juvenile abundance and richness data were used to investigate the effects of environmental drivers on their variability. This is because the predictive variable data (i.e., physicochemical and climatic data) used in the model are available only at a monthly level. For this reason, data for all variables were then computed as monthly data, including monthly total abundance, total richness, and monthly maximum and minimum water levels.

2.4. Statistical Analyses

We used boxplots and bubble plots to describe and visualize the weekly abundance and richness of fish larvae and juveniles over the study period. Loess fitting was applied to understand seasonal changes in the weekly abundance and richness.

In addition, we employed the non-parametric Mann–Kendall (MK) test to explore the monotonic trends of species richness and abundance, to determine whether the trends were significantly positive (increase) or negative (decrease) based on the KM's coefficients, using the '*mk.test()*' function of the "trend" package [39]. Afterwards, the Seasonal and Trend decomposition based on Loess fitting (STL) was applied to decompose the time series of abundance and richness into the seasonal, trend, and remainder components [40]. The STL was computed using the '*stl()*' function of the "stats" package [41].

A Spearman's rank correlation test was carried out to explore the correlation between water levels and abundance and richness over the study period. A cross-wavelet transform (CWT) was performed to detect the phase relationship (i.e., whether in-phase or anti-phase) between the water levels and larval abundance and richness to identify whether the water levels lead or lag fish abundance and richness in the Mekong River. Specifically, in the CWT, x was the water level, and y was the larval richness or abundance. The CWT is commonly used to investigate the phase and coherency relationship between the two-time series [42]. In the CWT, the two-time series, $x(t)$ and $y(t)$, were defined as a cross-wavelet transform W_x and W_y, respectively. The CWT was calculated as $W_{xy}(\tau, s) = 1/sW_x(\tau, s)W_y{}^*(\tau, s)$, where τ is the time localization and s is the scale factor of frequency and wavelength, and * indicates the complex conjugate [43,44]. The level of a cross-correlation between the two-time series was expressed as a cross-wavelet power (CWP). The CWP was defined as the norm of $W_{xy}(\tau, s)$: $P_{xy}(\tau,s) = |W_{xy}(\tau, s)|$ [43]. The significance level of the CWT was expressed as a joint periodicity interval, or time between two successive repetitions. The phase difference between the two-time series was revealed by phase angle. The phase difference of x over y at the time and scale was defined as Angle(τ, s) = Arg(Wave.xy(τ, s)) [45]. The phase angle arrows pointing right (↗ and ↘) in an interval [$3\pi/2$, $\pi/2$] indicates the in-phase relationship, while arrows pointing left (↖ and ↙) in an interval [$\pi/2$, $3\pi/2$] illustrates the anti-phase (or out of phase) relationship. The phase angle illustrates arrows pointing right-up and left-down (↗ and ↙) when the first series leads the second, and the phase angle illustrates arrows pointing left-up and right-down (↖ and ↘) when the second series leads the first. The CWT was performed using the '*analyze.coherency()*' function of the "WaveletComp" package [43,45]. We then used the cross-correlation function (CCF) to define how periods of peak water levels and peak abundance and richness occurred.

We performed MLR to determine variables driving the temporal variability of larval and juvenile abundance and richness. In the model, the dependent variables were larval abundance and richness, while explanatory variables were physiochemical and climatic factors, e.g., AT, PRE, WT, pH, DO, TP, $NH_4{}^+$, $NO_3{}^-$, TSS, ALK, CON, Max WL, and Min WL (see Table 1 and Supplementary Materials Figure S1 for details about each variable). Before building the models, dependent and independent variables were log-transformed to remove the effects of the extreme values to meet the data normal distribution assumption. Then, a stepwise variable selection approach based on Akaike Information Criterion (AIC) was employed to retain the important variables using the '*stepAIC()*' function of the "MASS" package [46]. The influence of each variable on larval abundance and richness was evaluated based on the MLR standardized coefficients. '*varImp()*' function of the "caret" package [47] was applied to compute the relative contribution of each variable in explaining the temporal change of species abundance and richness. The model performance was assessed by using the coefficients of determination (adjusted R-square). All statistical analyses were performed using *R* program v.4.0.3 for Windows statistical software package (http://www.r-project.org) (accessed on 5 February 2020) [41].

Table 1. Summary of predictors used in the study.

Variable	Variable Type	Units	Minimum	Maximum	Mean	SD
PRE	Precipitation	mm	136.7	524.5	231.5	76.8
WT	Water temperature	°C	27.2	32.0	29.4	1.3
pH	Potential of hydrogen	-	6.18	7.77	6.94	0.36
DO	Dissolved oxygen	mg L^{-1}	4.53	8.35	6.98	0.64
TP	Total phosphorus	mg L^{-1}	0.005	0.57	0.17	0.11
NH_4	Ammonium	mg L^{-1}	0.003	0.22	0.06	0.05
NO_3	Total nitrite and nitrate	mg L^{-1}	0.02	0.55	0.24	0.10
TSS	Total suspended solids	mg L^{-1}	9.5	292.0	144.7	77.4
ALK	Alkalinity	mg L^{-1}	0.6	1.6	0.9	0.2
CON	Water conductivity	µS m^{-1}	7.7	20.5	12.9	3.1
Max WL	Max water level	m	2.5	10.7	7.2	2.3
Min WL	Min water level	m	1.8	9.3	5.4	2.5

3. Results

3.1. Fish Assemblage Composition and Structure

Over the 10-year period, 168 species belonging to 107 genera, 40 families, and 11 orders were recorded. Three main orders represented 86% of the total species counts, including Cypriniformes (49%, 83 species), Siluriformes (22, 37), and Perciformes (15, 25). Seven families accounted for 66% of the total species counts, including Cyprinidae (40%, 67 species), Pangasiidae (7, 12), Cobitidae (4, 7), Gobiidae (4, 7), Siluridae (4, 7), Bagridae (4, 6), and Botiidae (2, 4). In terms of relative abundance, samples were largely dominated by *Henicorhynchus* spp. (94.3%), followed by *Henicorhynchus siamensis* (1.6%), *Pangasius bocourti* (1.4%), *Pangasius* spp. (0.7%), *Pangasianodon hypophthalmus* (0.7%), *Clupeoides borneensis* (0.2%), *Labiobarbus leptocheilus* (0.1%), and *Barbonymus gonionotus* (0.1%). Ecologically, longitudinal migrants contributed 99% to the total abundance; whereas lateral migrants and floodplain residents each represented ~0.6%.

3.2. Relative Abundance of Fish Larvae and Juveniles by Family and Season

The relative abundance of fish larval and juvenile families greatly varied intra-(June–September) and inter-seasonally. Species belonging to Cyprinidae, Pangasiidae, Botiidae, and Cobitidae were among the most abundant, with Cyprinidae being by far the most dominant family in the density of fish larvae and juveniles carried by the Mekong flood downstream throughout the study period. Pangasiidae ranked second in terms of its abundance, followed by Clupeidae, Botiidae, and Cobitidae (Figure 2).

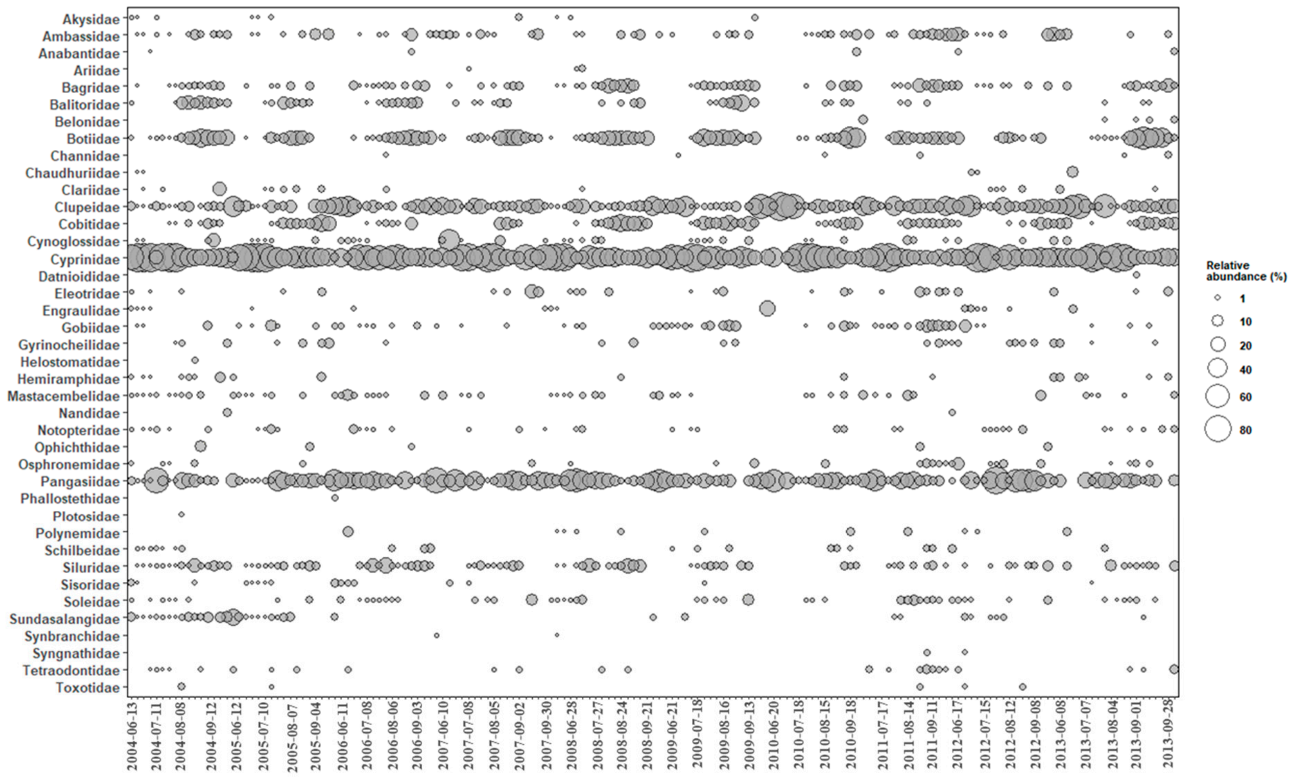

Figure 2. Intra- and inter-seasonal variation patterns of weekly fish larvae and juveniles by family over a 10-year period from 2004 to 2013 in the Mekong River in Phnom Penh. Circles represent relative abundance by family.

3.3. Intra-Seasonal Change of Fish Larval and Juvenile Abundance and Richness

Figure 3 shows intra-seasonal changes in weekly larval and juvenile abundance and richness over a 10-year period from 2004 to 2013. Overall, larval abundance tended to increase from June and peak in July (third week), then dramatically declined until September (Figure 3a). Furthermore, peak abundance occurred in late June and July (Figure 3a). For richness within the season, there was a gradual rise in richness beginning in June and peaking in August (third week), then a decline in richness was observed from late August to September (Figure 3b).

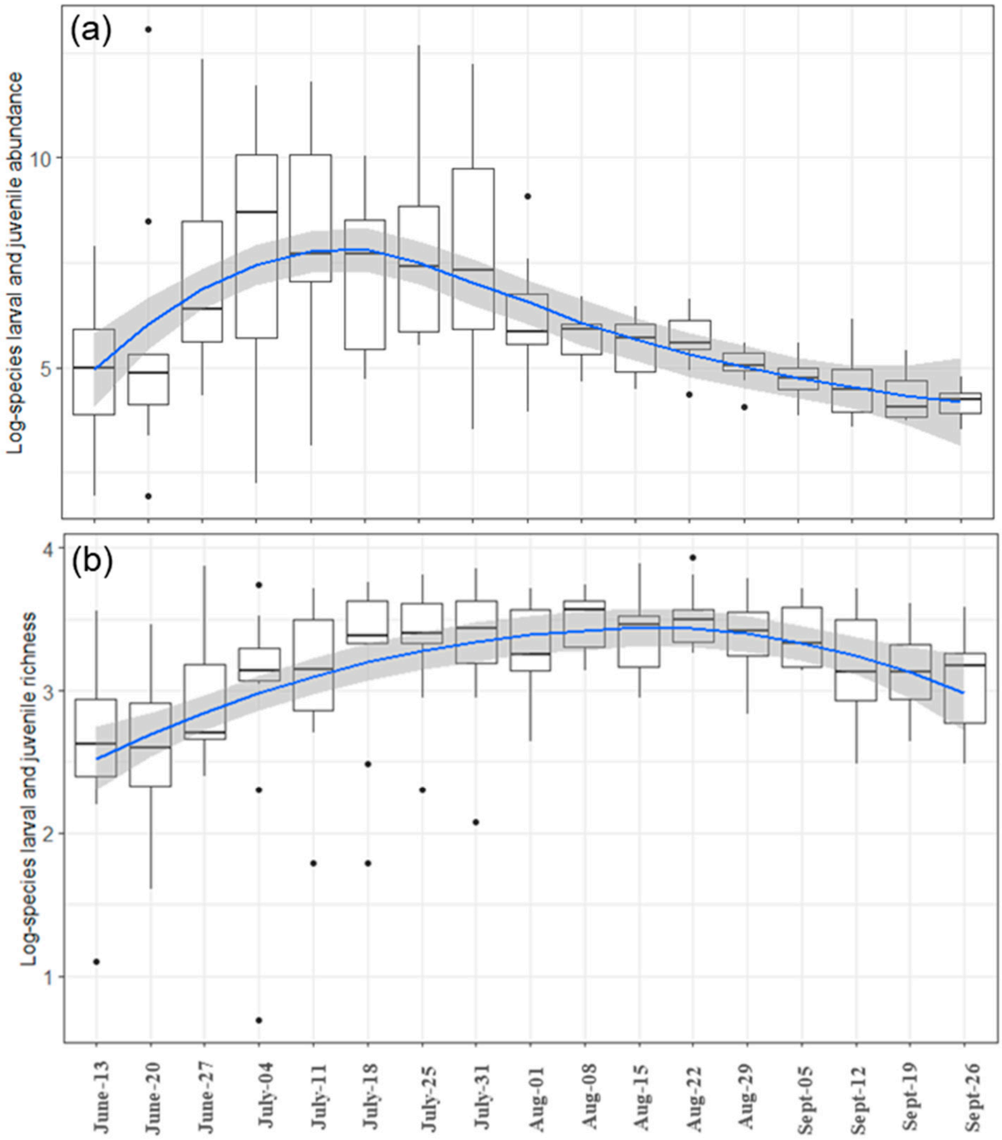

Figure 3. Intra-seasonal variability of log-transformed weekly species (**a**) abundance and (**b**) richness over a 10-year period between June and September from 2004 to 2013 in the Mekong River in Phnom Penh. The blue line is LOWESS smoother. Maximum abundance occurs in mid-July while richness occurs in mid-to-late August.

3.4. Long-Term Trends of Species Abundance and Richness

The analysis showed a significantly strong decreasing trend (MK, s = −2159, p = 0.0007) of fish larvae and juvenile abundance from 2004 to 2013 with no clear sign of recovery (Figure 4a). Overall, a significant declining trend was also found for species richness (MK, s = −1986, p = 0.001) from 2004 to 2013, with the lowest larval and juvenile species richness being observed in 2010 (Figure 4b). There was a slight recovery in the species richness after 2011; however, this trend declined again towards the end of the study period.

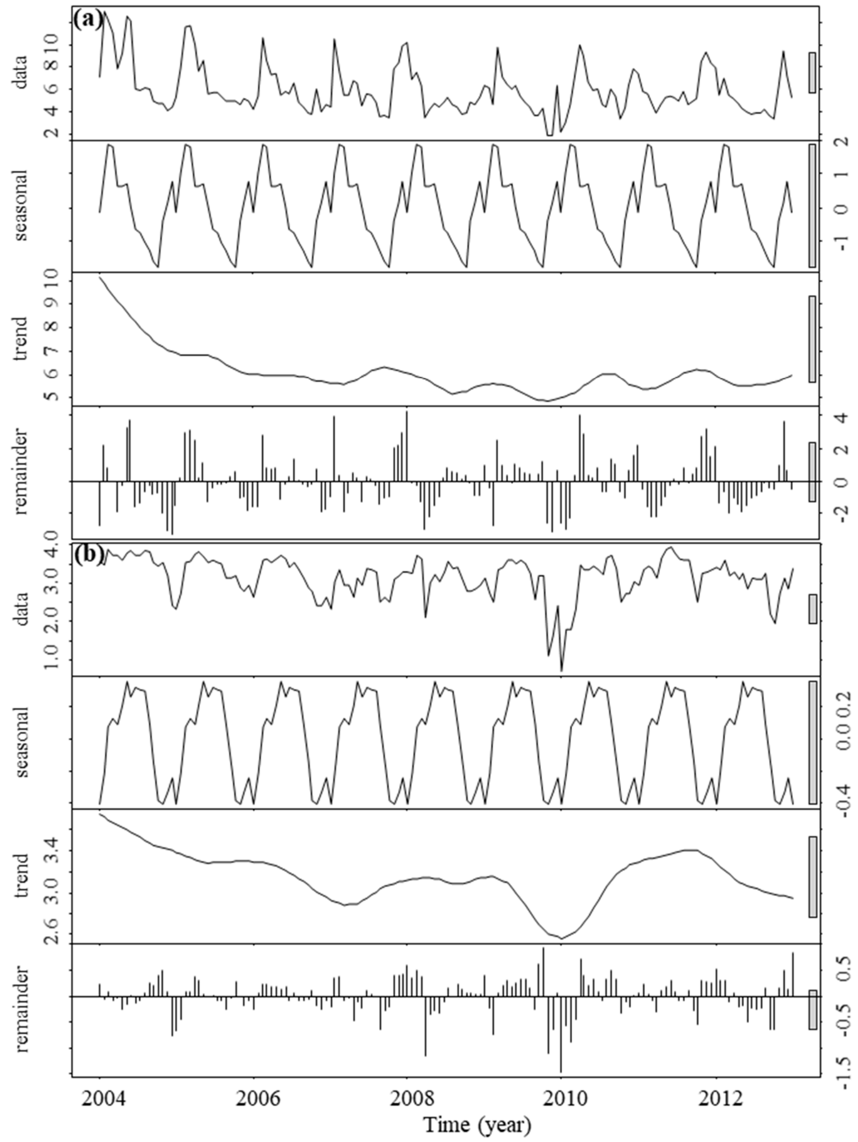

Figure 4. Decomposition plot of weekly larval and juvenile (**a**) abundance and (**b**) richness time series over a 10-year period between June and September from 2004 to 2013, in the Mekong River in Phnom Penh.

3.5. Phase Relationship between Water Levels and Fish Larval/Juvenile Abundance and Richness

Variability of fish larval and juvenile abundance and richness were significantly associated with water levels (Spearman's correlation test, $p < 0.01$). It was noted that clear peaks in abundance and richness were repeated interannually before peak water level throughout the study period (Figure 5a,b). The cross-wavelet analysis revealed a significant coherence of abundance and richness with water levels (Figure 5). The wavelet coherence analysis exhibited a significantly strong anti-phase relationship between water levels and abundance occurring at a high-frequency periodicity for about one week at week 5 (corresponding to the period between late June and early July), indicating that water levels lead fish abundance (Figure 5a, Supplementary Materials Figure S2). An in-phase relationship between water levels and richness was significantly detected, at a high-frequency periodicity at week 5 (corresponding to the period between late June and early July), indicating that peak water flow lags species richness (Figure 5b, Supplementary Materials Figure S2). Overall, we found that water levels always lead fish abundance but lag richness. More specifically, peak abundance and richness occurred eight weeks and one week, respectively, before the peak water level (Supplementary Materials Figure S3).

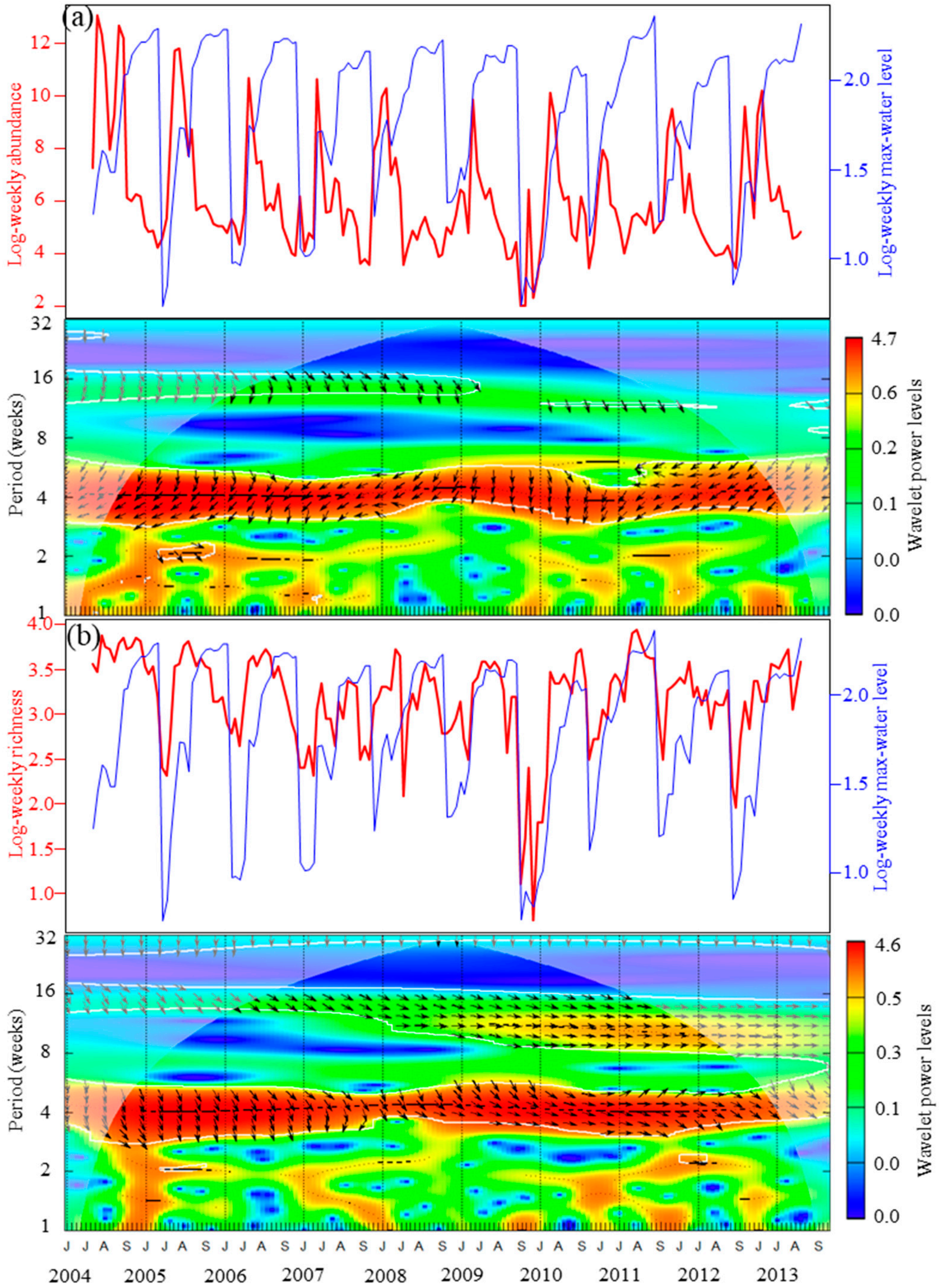

Figure 5. Time-series data of weekly fish larval/juvenile abundance and richness and maximum weekly water levels between 1 June and 30 September from 2004 to 2013. (**a**) Weekly abundance (*y*-axis) and maximum water levels (second *y*-axis) data series (upper panel) and cross-wavelet power spectrum of weekly abundance and water levels (lower panel), and (**b**) weekly richness (*y*-axis) and maximum water level (second *y*-axis) data series (upper panel) and cross-wavelet power spectrum of weekly richness and water levels (lower panel). The cone of influence with contour lines indicates the significance of joint periodicity. Areas in the upper corners outside the "cone of influence" in each plot indicate the exclusion of the areas from edge effects. The white contour line of the cross-wavelet power spectrum plot shows the significance between the two time series at 95% confidence interval. The red and blue colors indicate a strong and weak correlation, respectively. Arrows in each plot display phase differences (e.g., in-phase or anti-phase).

3.6. Environmental Determinants of Temporal Change of Fish Larval/Juvenile Abundance and Richness

The MLR model yielded adjusted R^2 = 0.70 and R^2 = 0.61 for larval and juvenile abundance and richness, respectively (Table 2). Specifically, the species abundance was positively related to the maximum water levels and the total phosphorus (TP) concentration and negatively correlated with the minimum water levels and the total nitrate (TN) (Table 2). Furthermore, we found that the minimum and maximum water levels were the two most influential drivers, explaining 56% of the total variance of species abundance (see Supplementary Materials Figure S4a). Moreover, species richness was positively associated with water conductivity and maximum water levels, but negatively correlated with alkalinity (Table 2). The maximum water levels were found to be the most significant driver explaining 38% of the total variance in species richness (see Supplementary Materials Figure S4b).

Table 2. The standardized regression coefficients of stepwise multiple linear regression between fish larval/juvenile abundance and richness and environmental variables. Bold indicates significant variables ($p < 0.05$). Signs of plus '+' and minus '−' show the positive and negative relationships between variables, respectively. The model performance of the MLR is indicated as the adjusted R^2. Significance levels are as follows: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Predictors	Species Abundance	Species Richness
Water temperature (WT)	+1.74	–
Precipitation (PRE)	–	−1.94
Total phosphorus (TP)	−**2.97** **	–
Total nitrate (NO_3)	**+2.45** *	–
Total suspended solids (TSS)	1.63	–
Alkalinity (ALK)	−1.59	−**3.02** **
Water conductivity (CON)	–	**+2.52** *
Max water level (Max-WL)	**+4.28** ***	**+4.81** ***
Min water level (Min-WL)	−**7.37** ***	–
Adjusted R^2	0.7	0.61

4. Discussion

4.1. Fish Larval and Juvenile Assemblage Composition

This is the first Mekong River study to investigate the temporal variability of fish larval assemblages and examine the relationship between this larval fish flux and environmental variables. Overall, the number of species, 168 in total, is similar to species counts from other unregulated, megadiverse tropical rivers, underscoring the richness and ecological complexity of the Lower Mekong Basin (LMB), and highlighting across-taxa adaption of life histories to the unique hydrology of the river. Both abundance and richness were positively correlated with maximum water levels, indicating the importance of the seasonal flood pulse for the reproductive success and the variability of fish larval/juvenile assemblage in the LMB. From June through September, representing the period of peak flow of the Mekong River at Phnom Penh, larval and juvenile drift samples were dominated by small-to-large-sized migratory fishes such as cyprinids, river catfishes, sheatfishes, and loaches. These species seasonally migrate between critical habitats to complete their life cycles, e.g., in lower floodplains for nursery and feeding during the wet season, and in the Mekong mainstream and its upstream tributaries for spawning and dry season refuge [15,16,48]. For example, *P. hypophthalmus* has been shown to migrate hundreds of kilometers out of the Tonle Sap River and up the Mekong River during the dry season [2,16]. During the period, many other longitudinally migratory species also migrate up the Mekong for upstream habitats, which are characterized by rapids, deep pools, and better water quality, for refuge and breeding [15,17]. During the early wet season, young and adults move downstream to feed in the lower floodplains such as the river-floodplain Tonle Sap Lake, Bassac River, and the Mekong delta [15–17,49]. We also observed relatively lower numbers and diversity of larvae and juveniles of laterally migratory fishes and floodplain residents at the sampling location. Most of these floodplain residents and lateral migratory fishes, such as *C. borneensis*, bragrid catfishes (e.g., *Hemibagrus spilopterus*, *Mystus* spp., etc.), and sheatfishes (e.g., *Ompok siluroides*, *Kryptopterus* spp., etc.), occur ubiquitously in the Mekong River system and also likely spawn during this period (June through September).

While the overall diversity of the larval/juvenile assemblage in the Mekong rivaled the diversity of rivers like the Amazon and Congo, the Mekong assemblage was dominated by two families of fish: Cyprinidae and Pangasiidae, underscoring the likely importance of flow and river connectivity for these two ecological and economically important groups of fishes. One genus of small cyrpinid, *Henicorhynchus* spp., comprised 94.3% of the total samples. Our findings are consistent with the results of previous Mekong-focused studies of diversity and abundance of larval fish drift, which also found that larvae and juveniles of *Henicorhynchus* spp. were the most dominant fish [17,50,51]. These results mirror broad patterns observed with adult *Henicorhynchus* spp. (i.e., *H. entmema* and *H. siamensis*), which are widely distributed in the Mekong River, Chao Phrya, and Mae Klong basins [27,52,53], and the most common species caught in the LMB [20,52,54–56]. These small *Henicorhynchus* spp. (i.e., *H. entmema* and *H. siamensis*) are long-distance migrants [16,57] that migrate out of the floodplains and the Tonle Sap Lake and up the Mekong River for spawning, feeding, and refuge habitats in the dry season [16]. Their dry season migration patterns are related to the flow of the Tonle Sap River [58] and lunar phases [16,55].

The second most dominant larval and juvenile species were members of Pangasiidae (riverine catfish), which were composed mainly of *Pangasius* spp. and *P. hypophthalmus*. Previous studies also indicated that riverine catfish larvae and juveniles were the second most dominant family after Cyprinidae [25,51] and the second most abundant in the LMB [17,23,25,50,51,59,60]. Consistently, adult riverine catfishes, such as *P. macronema*, *P. conchophilus*, and *P. larnaudii*, are commonly caught in the LMB [56,61]. *P. hypophthalmus*, albeit being classified as an endangered species, historically occurred across the Mekong and Chao Phrya [16,27,62]. The larval and juvenile abundance of *P. hypophthalmus* found in the Mekong River in Phnom Penh is the evidence that the Mekong River in Cambodia still hosts this endangered species and seems to be one of the key habitats for the species in the Mekong Basin.

Our study focused on larval drift near the riverbank of the Mekong River near Phnom Penh in the wet season. Previous studies have shown that higher diversity and additional species assemblages may be documented through the utilization of other types of sampling gear, during other months of the year, in more locations and habitats, using more replicates, or even by collecting opportunistically [17]. While not within the scope of this study, comparing larval and juvenile abundance and richness directly with adult fish stocks (either at species or community level), considering species-specific fecundity and life history, overlaying species distribution maps with larval fish data could yield further insights into patterns observed in this study.

4.2. Intra-Seasonal Variation

The highest abundance of larvae and juveniles were found to occur between late June and July, and the highest species richness occurred in August. The findings suggest that at least 168 Mekong fishes spawn during June, July, and August as previously documented in [21,63]. A recent study indicated that juvenile striped catfish that occurred in the Mekong River in Phnom Penh were about a month old [2]. This gives more evidence that many migratory species, contributing about 60% to the total annual catch in the Tonle Sap system [64], spawn mostly in June and July in the upstream Mekong River system, and for larval and juvenile striped catfish, their offspring reach lower floodplains one or two months later in the Tonle Sap Lake or the Mekong delta. Fish catch data confirm that juveniles of many of the same species occur in the floodplain and flooded forest of the Tone Sap Lake later in the wet season [65]. Therefore, maintaining the natural Mekong flood pulses in June is key to the reproductive success of many migratory fishes in Cambodia and likely in the entire lower Mekong River system. Similarly, flow modification, especially decreases in the wet season maximum water levels, would negatively impact spawning success and larval fish dispersal, with unknown but likely significant decrease in fish production and harvest.

4.3. Temporal Trends of Species Abundance and Richness

We found that the overall trends of both larval/juvenile abundance and richness were declining. The declining pattern may reflect the variation in the adult stock population, and this was also reflected in a decreasing fish yield, particularly in the Tonle Sap and Mekong-3S river system [20,56]. The decline in larval/juvenile abundance and richness observed in this study generates a negative feedback loop, which in return leads to the reduction in adult fish yield in the lower floodplains and thus the spawning fish stocks in the upstream river system. The decline in fish larvae/juveniles, as well as the adult fish catches, in fact, is a warning sign of a population decline in natural fish stocks and fishery sustainability.

The increase in efficiency of fishing gear, the intense fishing pressure, and human population growth are likely contributing to the decline in the brood stocks, leading to a significant drop in the larval/juvenile abundance and richness. The large- and medium-sized fishes in the Tonle Sap system have significantly declined [20], e.g., critically endangered (i.e., *P. gigas*, *Pangasius sanitwongsei*, *Catlocarpio siamensis*, *Probarbus jullieni*, and *Aaptosyax grypus*), endangered (i.e., *P. hypophthalmus*, *Probarbus labeamajor*, etc.), and vulnerable species (i.e., *Pangasius krempfi*, *Labeo pierrei*, *Cirrhininus microlepis*, etc.) [66]. Moreover, there was an overall decline in the larger, slower-growing, higher-trophic-level fishes in the Tonle Sap Lake system [20]. Our results are also consistent with the decline of these large- and medium-body-sized fishes, e.g., *Cyclocheilos enoplos*, *Henicorhynchus* spp., *Barbonymus gonionotus*, *P. hypophthalmus*, and *Phalacronotus* spp., in the TSL [67]. Furthermore, small mud carps of *H. lobatus* (currently revised as *H. entmema*), *H. siamensis*, and medium-body-size *Puntioplites proctozysron* were found to have significantly declined in the Mekong upstream and Sekong River [56]. Thus, the decline of these brooders is likely one of the causes that has led to the decline in fish larval and juvenile abundance and richness found in the Mekong River in Phnom Penh.

Moreover, illegal fish larval and juvenile collection for aquaculture and fish feed have probably accelerated the decline in fish recruitment. The wild larval and juvenile Pangasiids mixed with many other species, including Cyprinids, have been collected mainly for aquaculture since the 1980s [68]. Although the activity was banned in 1994 [68], illegal fish fry collection is still practiced, especially in Kandal and Kampong Cham provinces. Furthermore, indiscriminate fishing, such as exploitation of spawning stocks (stocks carrying eggs in the spawning season) and the use of mosquito netting with fences to harvest young fish in floodplains in the feeding/nursery habitats to feed aquaculture, is widely known to cause severe negative impacts on wild recruitment and thus populations.

The construction of hydropower dams is accelerating in the Mekong Basin [69–74]. Numerous studies have indicated the negative impacts of the dam on flow, water quality, sediment load, and nutrition, habitats and river connectivity, and fish productivity and biodiversity [23,56,69–75]. In addition, dams have the potential to interrupt essential corridors of larval drift and adult migration between downstream and upstream for fish completing their seasonal life cycles [73]. This causes a decline in fish larval densities and richness, which has a negative impact on fish reproduction, fish production, and diversity [22,23,76,77]. Several studies have shown that larval fish abundance and diversity are higher in unregulated rivers, and lower in regulated rivers [22,23,78]. As more dams are being built in the LMB, studies have shown a parallel decrease in fish abundance and diversity, and we would expect this pattern to hold true for larval fishes as well.

4.4. Phase Relationship between Water Levels and Fish Larval/Juvenile Richness and Abundance

We found an anti-phase relationship between water levels and larval/juvenile abundance (water levels lead species abundance), but an in-phase relationship between water levels and larval/juvenile richness (water levels lag species richness), indicating clear co-occurrence pattern and synchronization at the high-frequency periodicity from the late June to early July through 2004 to 2013. Our results are consistent with previous studies showing that higher water flows precede and trigger fish migration and spawning [58]. Furthermore, we also found that the peak abundance and richness occurred before the peak water levels at eight weeks and one week, respectively, suggesting that spawning activity occurs before peak flows which facilitate dispersal and maximize the habitat available to young fishes. Hydrological change might disrupt spawning success, and thus cause a reduction in the quantity of the larval/juvenile drift downstream [23,77–79]. The reduction in the recruitment of migratory fishes may also be reflected in the significant decline in the species evenness index, indicating changes in fish community structure with catches dominated by few small-sized species, and there was a significantly strong decline in the catches of large- and medium-sized species utilizing the Tonle Sap system [20].

4.5. Drivers Affecting Fish Larval/Juvenile Abundance and Richness

We observed that the larval and juvenile abundance and richness were positively correlated with the maximum water levels. The water level is the main trigger for many life stages of migratory fish in the Mekong, influencing spawning activities [14,15,49,80]. Our results indicated that the peak abundance of fish larvae and juveniles usually occurred between June and August, coinciding with increasing water levels. Peak flow pulses are crucial for carrying their eggs and larvae to favorable environments in the floodplain downstream. On the contrary, we observed that abundance was negatively associated with the minimum water level. In flood pulse systems, this life history trait results in higher survival rates, avoidance of predators, and potential starvation due to slow drift [1]. Our result showed that the larval and juvenile abundance was positively correlated with total nitrate concentration. The nitrate concentration is the primary nutrient that was used by algae, and later the algae were fed by zooplankton and fishes. Both zooplankton and phytoplankton were the primary food sources for fish larvae and juveniles over the drifting periods. Invertebrate species, e.g., shrimps, craps, and insects in the Mekong [81], were found in the drift with our fish larval samples, some of which can be predators or prey of fish larvae [51]. Water level increases during seasonal flooding transport sediment load and nutrients (e.g., nitrate concentration) downstream [70]. These sediments and nutrients provide food availability to feed fishes in floodplains. It was demonstrated that nitrate concentration was significantly correlated with the seasonal discharge [82]. In contrast, total phosphorus concentration is a primary cause that influences abundance decline. In addition, species richness was negatively associated with water alkalinity level. High alkalinity concentrations cause mortality of larvae and juveniles [83]. We also found that water conductivity was positively associated with species richness. High conductivity may indicate high minerals in the waters resulting from the runoff from the catchments surrounding the Mekong River during the Mekong's early flooding period. This finding was consistent with previous studies reporting that the abundance of some larval/juvenile fishes (e.g., *Pimelodus maculatus*, *Auchenipterus osteomystax*, and *Iheringichthys labrosus*) are positively related to river conductivity [4,7].

4.6. Livelihood and Management Implications

Massive larval drift, comprising billions of young fishes of at least 168 species, occurs along the Mekong River of Cambodia between June and August. The most common species found during this period are migratory, commercially important fishes that support some 60% of the Cambodian fish harvest, provide livelihoods and protein to millions, and contribute billions of dollars to the Cambodian economy [64]. *Henicorhynchus* spp., for example, is by far the most common drifting species, and is also one of the most commercially important taxa [27,57,84], contributing more than 40% to the commercial-scale Dai fishery's seasonal catch in the Tonle Sap River [58], and are used to produce a fish sauce, fish paste (*prahok*), smoked fish, and salted fish to be used by most rural Cambodians, particularly during the period when fish are scare or during rice-farming season [58,84]. The species is an important source of food and nutrition security.

Given that fish abundance and diversity are significantly influenced by the water levels, water management and flow modification caused by upstream hydropower operation has the potential to disrupt spawning, decrease recruitment, and harm fisheries and livelihoods throughout Cambodia and Vietnam. Water management by upstream users, as well as plans for future hydropower development, should consider a dam's impacts on river flows and its impacts on fishery recruitment and productivity. Decreases in water flows, or unseasonal alteration of natural flows, likely result in lower larval fish abundance and diversity, as well as other unintended negative consequences. These changes will cost downstream resource users in Cambodia and Vietnam tens of thousands of tons of lost harvest and hundreds of millions of dollars of economic loss. Leaders in Cambodia should advocate for environmental flows of sufficient quantity, timing, and quality of water to sustain the Mekong's flood pulse, associated larval fish drift, and dependent fisheries and livelihoods.

The spawning season for many commercially important migratory cyprinids and pangasiids, as well as over 100 species of other fish, takes place between May and September in the wet season and is concentrated mainly in late June and July. The current Cambodian Law on Fisheries prohibits fishing activities effective from 1 June to 30 August and from 1 July to 30 September for the inland fishery domains located in the north and south of Tonle Chaktomok, respectively [85]. This law should be effectively enforced during the closure period to allow migratory fishes to access their spawning habitats, a necessity for successful reproduction and subsequent dispersal and recruitment.

We also found a decline in both the abundance and richness of fish larvae and juveniles over the study period. This result is an important indicator of the natural fish stock reduction, requiring attention from fisheries' management. The protection of brood fishes should be effective for the Upper Cambodian Mekong River, especially for seasonal migration, spawning seasons, and grounds [16,63]. In addition, the maximum water levels have a strong positive association with larval/juvenile abundance and richness. Therefore, the combination of maintaining the Mekong natural flow pulses and fish migration corridors (connectivity between key critical habitats), as well as effective law enforcement for successful reproduction and rearing, is critical for effective management and conservation planning of the migratory fishes in the Mekong River system in Cambodia. At present, many dams are being planned and built in the LMB. These dams are altering the Mekong flows, which impact many fish species that have adapted to the seasonality and predictability of the natural flow for thousands of years. Quantifying the impacts of dams on the flow alterations in the Mekong upstream of Cambodia and how these flow alterations impact the reproductive success of the brood fishes would be very useful for sustainable water and fishery planning and management.

5. Conclusions

Understanding the temporal changes of fish larvae/juvenile assemblage composition, abundance and richness trends, and their determinants is of paramount significance for fishery management and conservation planning. Over the study periods (2004–2013), fish larval and juvenile assemblages consisted of 11 orders belonging to 40 families, 107 genera, and 168 species. Three orders that dominated the fish larval/juvenile assemblage were Cypriniformes, Siluriformes, and Perciformes. Similarly, six families that mainly represented larval/juvenile assemblage in the Mekong River in Phnom Penh included Cyprinidae, Pangasiidae, Cobitidae, Gobiidae, Siluridae, Bagridae, and Botiidae. The most dominant species included *Henicorhynchus* spp., *H. siamensis*, *P. bocourti*, *P. hypophthalmus*, *Pangasius* spp., *C. borneensis*, *L. leptocheilus*, and *B. gonionotus*. The assemblage was mainly represented by migratory fishes, particularly those belonging to Cyprinidae and Pangasiidae, the two most dominant families in the bulk of larval drift. Fish larval/juvenile abundance peaked in July, while richness peaked in August. These migratory larval/juvenile fishes are expected to replenish the fish stocks in the lower floodplains, such as the Tonle Sap Lake, seasonally. Changes in the fish larval/juvenile quantity are likely driven by the changes in the Mekong flow pulses in the early wet season, one of the key drivers that determine the reproductive success of many migratory fishes. Flow pulses and some key water quality parameters (i.e., nitrate, phosphorus, etc.) significantly influence the variability in the quantity of larvae/juveniles drifting downstream. Further, larval/juvenile abundance and richness exhibited a significant temporal downward trend. This indicates that there is less and less recruitment each year, and this is reflected in the declining catches of many migratory species in the downstream floodplains. Therefore, maintaining the natural flow pulses of the Mekong River, migration corridor, and river connectivity between the refuge, spawning and rearing habitats, and protecting and conserving these critical habitats, are important contributions to the successful reproduction and rearing of the migratory fishes and thus their stock health.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/su151813535/s1, Figure S1: Time series plot of predictors used in this study. For abbreviations in the plot, see Table 1; Figure S2: Average cross-wavelet power: richness and abundance vs. water series derived from Figure 5a (lower panel) and 5b (lower panel); Figure S3: Cross-correlation plots between weekly water levels in Phnom Penh (WL-PP) and weekly larval abundance (AB) and richness (SR). The blue solid vertical line shows lag zero. Values of the vertical line above and below horizonal dashed lines represent significantly positive and negative correlation coefficients. The red vertical dotted line represents the highest correlation coefficient between the two-time series, covering between June and September from 2004 to 2013; Figure S4: Relative contribution of predictive variables to (a) abundance and (b) richness. In the bar plots, red color represents strong contribution and blue weak. For abbreviations in the plot, see Table 1; Figure S5: Loess plot of relationship between weekly log-transformed maximum water levels and species larval and juvenile (a) abundance and (b) richness in the Mekong River in Phnom Penh.

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