

Article

Cambodian Freshwater Fish Assemblage Structure and Distribution Patterns: Using a Large-Scale Monitoring Network to Understand the Dynamics and Management Implications of Species Clusters in a Global Biodiversity Hotspot

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Abstract: Mekong River Basin is one of the world's fish biodiversity hotspots. Fisheries of the Cambodian Mekong are characterized by high diversity and productivity. However, few studies have focused on broad scale patterns and fish assemblage structure of this important system at a national level. Here, we describe spatial and seasonal variation in fish assemblages by analyzing one year of daily fish catch data sampled at 32 sites covering Cambodia's main inland water bodies. We recorded 125 fish species. Four clusters were distinguished based on assemblage composition similarity, and 95 indicator species were identified to characterize each of the identified assemblage clusters. High diversity fish assemblages were associated with the upper Mekong system and Mekong/Bassac/Tonle Sap Rivers in Kandal Province and southern Tonle Sap Lake while lower diversity assemblages were observed in the Mekong River in Kratie and the northern area of the Tonle Sap Lake. We find significant variation in the assemblage composition between wet and dry seasons, indicating strong seasonal species turnover within clusters. Length–weight relationship analysis indicated a negative allometric growth among a majority of indicator species, reflecting suboptimal conditions for growth. Our study establishes contemporary structure and diversity patterns in the Lower Mekong River system of Cambodia, which can be used to map fish biodiversity hotspots and assess key indicative fish stocks' statuses for conservation and management.

Keywords: species distribution; fish richness; indicator species; length–weight relationship; tropical flood pulse fisheries; inland water; Lower Mekong Basin

1. Introduction

Tropical freshwater systems such as the Amazon, Congo, and Mekong are home to about one-third of Earth's freshwater fish species [1]. The Mekong River, the world's 12th longest river [2,3] and one of the 35 global hotspots [4], supports a high diversity of aquatic fauna such as fish, molluscs, crustaceans, reptiles, insects, amphibians, and birds [5–9]. The Mekong hosts an estimated 1200 fish species [7]. Eighteen percent of the total richness is endemic to the system [10]. Despite being highly diverse, fish communities in the Lower Mekong Basin (LMB) are dominated by species belonging to five main families including Cyprinidae, Cobitidae, Pangasiidae, Siluridae, and Clupeidae, and cyprinids represent ~80% in both biomass and abundance [11]. In Cambodia, at least 411 fish species have been recorded from inland waters [12], and actual fish richness is likely higher [7]. Cambodia possesses the highest fish diversity index among the LMB countries [13] and is an important fish diversity hotspot for the Mekong Basin.

Biodiversity patterns and fisheries in the Mekong vary spatiotemporally throughout its basin—an area that includes the Mekong mainstem, its tributaries, streams, and floodplains, all of which are interconnected and influenced by strong seasonal flood pulses [3,14–18]. The Tonle Sap River and Lake (TSRL) of the lower Mekong system is a unique, flow reversal flood-pulse system, and is a key element for the annual Mekong's flood that creates the largest natural wetland in Southeast Asia [19]. This unique seasonal flood pulse system creates heterogenous habitat complexity and resource availability, supporting one of the largest inland fisheries on the planet.

Many Mekong fish conduct large-scale seasonal migrations [7]. Based on their ecological characteristics, fish in the basin are categorized into: (i) “white fish” i.e., species performing longitudinal migrations between the Mekong mainstream, floodplains and tributaries; (ii) “black fish” i.e., floodplain residents spending most of their life in lakes and swamps in floodplains adjacent to rivers, and move to inundated areas during the high flooding period; (iii) “grey fish” i.e., species undertaking short-distance lateral migrations in local tributaries and do not spend their life in the floodplain ponds during the dry season; and (iv) “estuarine fish” including estuarine residents and marine visitors [18,20–22]. Longitudinal migrants comprised 63% of fish catch from the Tonle Sap Lake (TSL) [14]. Longitudinal migrant's life cycles involve the seasonal migration between critical habitats i.e., for breeding and dry season refuge in the Cambodia upper Mekong system, and for rearing and feeding in the lower Mekong floodplains such as the TSRL and the habitats southern Phnom Penh [15,23,24].

The entire region supports highly productive fisheries, particularly in the floodplain lakes and rivers. These fisheries provide food and income for tens of millions of people, most of whom are impoverished [25,26]. Annual fish yield estimates for the LMB, comprising Cambodia, Laos, Thailand, and Vietnam, are in the range of 1.3 to 2.7 million tonnes [27], representing 19.3% of the world freshwater capture fishery production or ~2% of the world total fish production [28]. In Cambodia, the national total inland fish yield was estimated at ~767,000 tonnes per annum with the TSL and its tributaries contributing more than 70% [27]. This fish resource provides essential livelihoods, food and nutrition for more than 15 million people, representing between 12 to 18% of the gross domestic product in Cambodia over the last two decades [10,19,29,30]. The fish and fisheries of the LMB are now threatened by overharvest, habitat degradation and fragmentation, and unsustainable development. Given current development pressure, and the livelihood and socio-cultural significance of inland fish resources to the people and countries of the LMB, there has been an increase in scientific research on fish community ecology with fisheries management and conservation implications. Most of these fish community ecology studies are still spotty and have focused on the TSRL system e.g., spatial and temporal variation of fish diversity and assemblage structure [18,31–33], species diversity and ecology [8] and determinants of beta diversity [34]. Few studies have extended their geographical scope to cover other major inland waters of Cambodia, i.e., the Mekong–Sekong, Sesan, and Sprepok (3S) Rivers system [17,35,36] and the mainstream of the Lower Mekong River [13] which are increasingly impacted by the development of dams, alteration of floodplain habitats and other disturbances. Moreover, current routine fish monitoring programs implemented in Cambodia inland waters have

focused on indicative trends in the fish abundance and diversity at specific sites [11,37]. While such monitoring is important to understand the temporal, long-term change, it limits our understanding of the country-wide spatial and seasonal distribution patterns of freshwater fish diversity and assemblage structure in this species-rich and highly productive system.

Further, the conditions of fish stocks within different fish assemblages distributed in the main inland water bodies in Cambodia are poorly known. The very few existing investigations into basic fish stock indicators—such as changes in species length or weight distributions [38] and length–weight relationships—have so far been focused only on the TSL [39]. Indeed, these fish condition indicators are useful to help assess stock status and the likely environmental conditions e.g., habitat quality [40–42], hydrology [16], human pressure [38], food availability, and water quality in which they inhabit [40,43,44].

In this study, we (i) describe spatial and seasonal patterns in the diversity and fish assemblage structure of Cambodia's major inland waters, (ii) identify indicator species of different fish assemblages observed spatially and seasonally in the system and (iii) examine length–weight relationship of key indicator species identified in those distinct fish assemblages in order to provide update information about the growth conditions of the indicative fish stocks in the inland waters of Cambodia. To achieve the study objectives, we used one-year daily fish catch monitoring data collected in 2017 from 32 sites covering key freshwater systems in Cambodia i.e., lower Mekong River, Bassac River, TSRL, upper Mekong River and the 3S Rivers. The results of our study contribute to quantitative, science-based knowledge on spatial and seasonal fish assemblage dynamics. Our results can be used to inform the management of Cambodia's fish biodiversity hotspots and to provide guidance on the population status of key indicative fish stocks representing ecologically distinct fish assemblages from different habitats. The information ultimately may help guide management and conservation interventions, particularly in the time of local, regional, and global change.

2. Materials and Methods

2.1. Study Site

Flowing ~5000 km from its source in Tibet to Vietnam, the Mekong River creates an inland delta at the Lao-Cambodia border known as Khone Falls [2] then flows through Cambodia ~510 km, with an average river width of ~1.5 km [45]. At Stung Treng in the upper part of Cambodia, the Mekong is connected by the combined flow of three major tributaries, the 3S Rivers flowing from southern Laos and the Central Highlands of Vietnam [46]. Near Phnom Penh, at the head of its delta, the Mekong River forms a complex river-lake ecosystem of the TSRL and the smaller Bassac River [2,47]. The Mekong proper and Bassac River form a large estuarine delta before emptying into the South China Sea [2]. During the wet season (June–November), the Mekong's waters rise significantly, causing a reversal of flow of the Tonle Sap River (TSR) and flooding the TSL and the surrounding plains [48]. In the dry season (December–May), one of the unique features of the Mekong's hydrological regime is flow regulation by the TSL, that is the vast lake outflow into the Mekong and increasing the water level in the delta for about 5–6 months [48]. Indeed, the seasonal flood pulse and the connectivity between the Mekong and its major tributaries (i.e., the 3S Rivers and TSRL as well as the lower floodplain areas south of Phnom Penh and the Mekong Delta) are critically important to sustain the inland fisheries in Cambodia and the LMB [16,17,23,24,38].

This study examines daily fish catches from thirty-two sites geographically covering the main freshwater habitats of inland fish and their migration corridors (connectivity) in Cambodia including the Mekong River and its major tributaries (the 3S Rivers) from the northeast representing the upper Cambodian Mekong (Mekong-3S) system in Stung Treng (ST) and Rattanakiri (RK) Provinces to the Mekong River in Kratie (KR) Province. Along the lower Cambodian Mekong system, the study sites extend from the Mekong River, TSR (that connects Mekong River and TSL) and Bassac Rivers in Kandal (KD) Province (southern Phnom Penh) to the provinces around the TSL namely Kampong Chhnang (KC) in southern TSL, Kampong Thom (KT) and Pursat (PS) in the middle of the TSL and Siem Reap

(SR) and Battambang (BB) situated towards the northern end of the TSL (Figure 1). Study sites in the upper Mekong system represent the dry season refuge and spawning grounds for many migratory (white) fish while the study sites in the Mekong's lower floodplains represent rearing grounds for the white fish and can be both spawning and rearing grounds for floodplain residents (black fish), some grey fish and species with general habitat preferences (generalists). The study sites in the upper Mekong system are characterized by lotic environment with rapids and deep pools (where white fish seek refuge for sedentary periods at the onset of the dry season, and spawn at onset of the wet season) while the sites in the lower floodplains are distinguished by river-floodplain lakes, oxbows, vegetations, flooded forests, swampy areas, and agricultural fields. See Supplementary Material Table S1 for geographic positions of the study sites. Each study site (where fish were sampled) could extend a few kilometers in the village where each participating fisher was based over the study period.

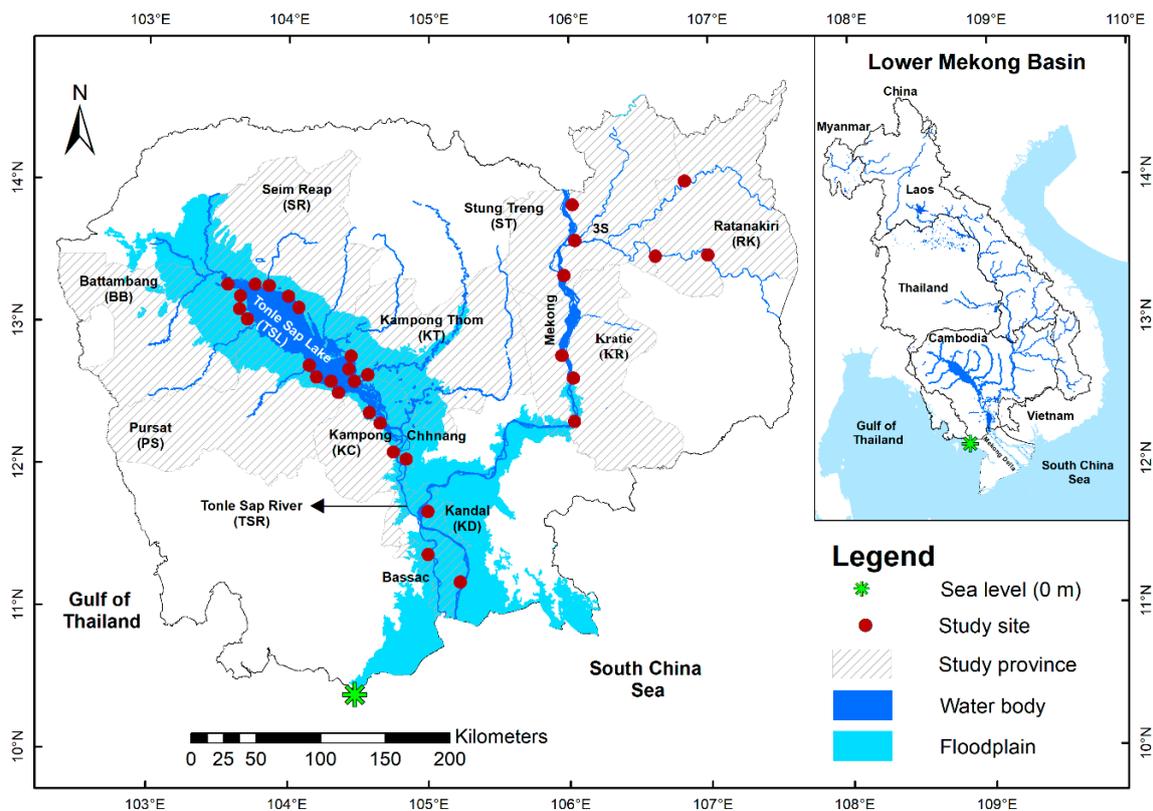


Figure 1. Fish monitoring sites covering the main inland water bodies in Cambodia.

2.2. Data Collection

Daily fish abundance data from January to December 2017 were extracted from the fish monitoring database of the Inland Fisheries Research and Development Institute (IFReDI) of the Fisheries Administration of Cambodia. The field data collection was implemented by IFReDI. Thirty-two professional fishers from 32 sites, geographically spreading across the main inland water bodies in Cambodia, were involved in the field data collection (Figure 1). Daily, fish samples were taken by the 32 fishers from the 32 study sites for the whole year 2017. The fish monitoring protocols used for the field data collection were based on methods described by [49] and approved by the IFReDI. The participating fishers were selected based on their willingness to participate, ability to read and write Khmer, basic knowledge of numeracy and fishing most days during the year including peak migration periods. A photograph of a sample (with photo number) each week was also taken for the species composition, and for length measurement where fish of the same species were laid on a size standard board for photographing. These were important for checking the accuracy of the

recorded data. The daily catches (i.e., number of individuals and weight), and length and weight data by species and gear type were recorded on to data sheets prepared and provided by the IFRaDI's fisheries research officers. Overall, several fishing gears namely stationary gillnets, cylinder traps, small bagnets, castnets, hook long lines and drifting gillnets were used to capture fish. However, among these, stationary gillnets and traps were the common fishing gears used by most inland fishers in Cambodia. The two fishing gears, each equally contributed 42% to the total yearly abundance in 2017. This study used the total daily fish abundance (as the Catch Per Unit Effort—CPUE) recorded by all participating fishers. The daily fishing time (soak hours) was about 12 ± 2 h for stationary gillnets and 14 ± 2 h traps [18,35]. We assumed that fishers maximizing their daily catches, capturing as many fish as possible for each day over the study period because fisheries in this region are indiscriminate, and are of paramount importance for food security (daily protein) and daily livelihoods [38,50].

All fishers were trained by the fisheries research officers from the IFRaDI on the basic concepts of fish taxonomic identification, data recording, photography, sampling and subsampling techniques applied for the large catches. They were also supplied with cameras, standard measuring boards and calibrated electric scales accurate to 1 mm and 1 g to measure the total length and weight of fish species, respectively. Fish were identified to the species level using the keys in [7] and the species names were updated using [12] for this study. Lastly, to ensure the quality of monitoring, IFRaDI's research officers visited all fishers to collect the recorded fish catch and length–weight data sheets, checked for errors and cleaned the data on a quarterly basis before entering the data into the Fish Monitoring Database. Fishers were also tested by the research officers in the subsequent field trips to ensure the accuracy and completeness of data recording for the study.

2.3. Data Analyses

All daily fish catch data were computed as daily mean samples by province to reduce the noise in the data sets (3 fishers for each province, with exception of 5 provinces containing up to 4 participating fishers) and then transformed into the weekly relative abundance to reduce the effect of varying fishing efforts among the study sites. Totally, we had 468 weekly samples (or 52 weekly samples for each province) for the nine study provinces. Afterwards, we performed Ward hierarchical clustering using Bray–Curtis method based on the weekly relative abundance to classify all fish samples from all study sites into different fish assemblage clusters according to their similarities in the species composition [51]. The hierarchical clustering was performed on fish community matrices for the spatial (annual), wet (June–November) and dry (December–May) seasons. The seasonal classification (wet versus dry seasons) was based on 9 years of (2007–2015) mean daily water levels of the Mekong River, when entering Cambodia at Stung Treng Province [17]. Likewise, species richness and diversity (i.e., inverse Simpson diversity index) were computed for the annual and seasonal assemblages to describe the variation of the spatial and seasonal fish diversity for the identified assemblage clusters. The Simpson diversity index (D) was computed using the equation: $D = \sum (n/N)^2$, where n is the total number of organisms of a species, and N is the total number of organisms of all species. The inverse Simpson diversity index is $1/D$. In addition, species rank-abundance plots [52] and species evenness index ($J = H/\log(S)$, where H is Shannon diversity index and S is species richness) were computed to further define and discriminate the ecological fish assemblages. Significant differences ($p < 0.05$) of species richness, evenness and diversity indices among clusters and between wet and dry seasons were tested using pairwise Wilcoxon rank sum and Kruskal–Wallis tests.

Nonmetric Multidimensional Scaling (NMDS) was performed to describe the spatial and seasonal variation in fish assemblages. NMDS was performed on the community relative abundance matrices using “metaMDS” function of “vegan” package with Bray–Curtis dissimilarity index [53] in R-program. We then computed indicator species which are “species that are used as ecological indicators of community or habitat types, environmental conditions, or environmental changes” [54]. Indicator species were assessed based on the significant indicator value of each individual species using the framework developed by [55–57]. According to these authors, the indicator value (IndVal) of a species

for a given cluster is defined as the product of two quantities, called A and B. For species abundance data (as it is the case for this study), quantity A was defined as the mean abundance of the species in the target site group divided by the sum of the mean abundance values over all groups. Quantity B was defined as the relative frequency of occurrence of the species inside the target site group. Indicator values were then tested by 999 permutations, allowing to identify characteristic members of the cluster. Indicator species were computed using “multipatt” function from “indicpecies” package [56]. Finally, Permutational multivariate analysis of variance (PERMANOVA) using “adonis” function of “vegan” package (with 999 permutations and the Bray method) were also computed to test the influence of different factors (i.e., cluster and season) on the composition of the fish assemblages. Afterwards, contrast methods were applied to test the pairwise differences between different levels in each of these factors using the “pairwise.adonis” function in R-program.

To examine fish condition, simple linear regression models were applied to study the length–weight relationship (LWR) of key indicator species identified for each fish assemblage cluster. Only indicator species with the sample sizes greater or equal to 30 were included in the analyses. The relationship between length and weight was expressed by an exponential equation $W = a \times SL^b$ [58,59] where W is the total weight (g), SL is the standard length (cm), and a is the intercept of regression line and b is the slope (regression coefficient). In this study, we used total lengths (TL, cm) and weight (g) of indicator species identified for all fish assemblage clusters covering the main freshwater bodies in Cambodia. These parameters were estimated by the least squares regression method, and then can be linearized as $\log(W) = \log(a) + b \times \log(TL)$. Fish growth conditions can be inferred from the value of slope b of the linear model i.e., isometric growth ($b = 3$), positive allometric growth ($b > 3$) and negative allometric growth ($b < 3$) [59]. An ideal fish maintaining the same shape as it grows has slope $b = 3$ (isometric growth). However, in the real world, most fish change their shape as they grow, and b is usually different from 3. When b is less than 3, the fish is slimmer with increasing length (negative allometric growth). When b is greater than 3, fish become heavier (positive allometric growth), reflecting optimum condition for growth [60]. Adjusted r^2 was used to assess the performance of the regression model.

3. Results

3.1. Fish Community Composition

Over the one-year daily fish abundance monitoring at 32 monitoring sites, 125 fish species were recorded (Supplementary Material Table S4 for the list of species names by orders and families). These fish belonged to 15 different orders, 33 families and 89 genera. Of these, three main orders represented 86% of the total species count, including Cypriniformes (56 species), Siluriformes (32), and Perciformes (19) while Osteoglossiformes, Anguilliformes, Synbranchiformes, Pleuronectiformes, Clupeiformes, Tetraodontiformes, Beloniformes, Syngnathiformes, Myliobatiformes, and Mugiliformes each represented <5% of the total fish species counts. At the family level, the top three families that accounted for 58% of the total species counts included Cyprinidae (52), Bagridae (10), Pangasiidae (10), while each of the other 30 families comprised one to seven species. At the species level, ~50% of catches were dominated by 10 fish species, namely, *Gymnostomus lobatus* (9%), *Puntioplites proctozysron* (9%), *Trichopodus trichopterus* (6%), *Osteochilus vittatus* (5%), *Anabas testudineus* (5%), *Cyclocheilichthys enoplos* (4%), *Mystus mysticetus* (3%), *Labeo chrysophekadion* (3%), *Hypsibarbus malcomi* (3%) and *Hemibagrus spilopterus* (3%). Ecologically, white fish (longitudinal migrants) represented ~60% of the total abundance (number of individuals); whereas, black (floodplain residents) and grey fish (lateral migrants), each accounted for ~19%. Estuarine species contributed only ~2% to the total abundance.

3.2. Spatial and Seasonal Variation of Cambodian Inland Fish Assemblages

Hierarchical cluster analysis with Ward agglomerative method divided weekly samples into four different assemblage clusters based on species composition similarity (Figure 2(a1)). The first split of the dendrogram (Figure 2(a1)) defined two main fish assemblages i.e., Cambodia’s lower

Mekong floodplain covering sites in KD and TSL, and the upper Mekong-3S system including sites in KR, ST and RK. In the subsequent splits, the two main assemblage clusters from the first split of the dendrogram were subdivided into four distinct fish assemblage clusters i.e., cluster 1 and 2 for Cambodia’s lower Mekong floodplain, and cluster 3 and 4 for Cambodia’s upper Mekong-3S system. Cluster 1 contained 114 samples mainly associated with the most northern sites in the TSL in BB and SR while cluster 2 was composed of 194 samples, associated with sites in the south and middle of the TSL (KC, KT, PS), in the TSR and sites in the Mekong and Bassac Rivers up- and down-stream of Phnom Penh municipality in KD (Figure 2(a2)). Cluster 3 consisted of 64 samples mainly connected with sites in KR and some fish samples from KD. Finally, cluster 4 were made up of 105 samples from sites in ST and RK of Cambodia Mekong-3S system (Figure 2(a2)).

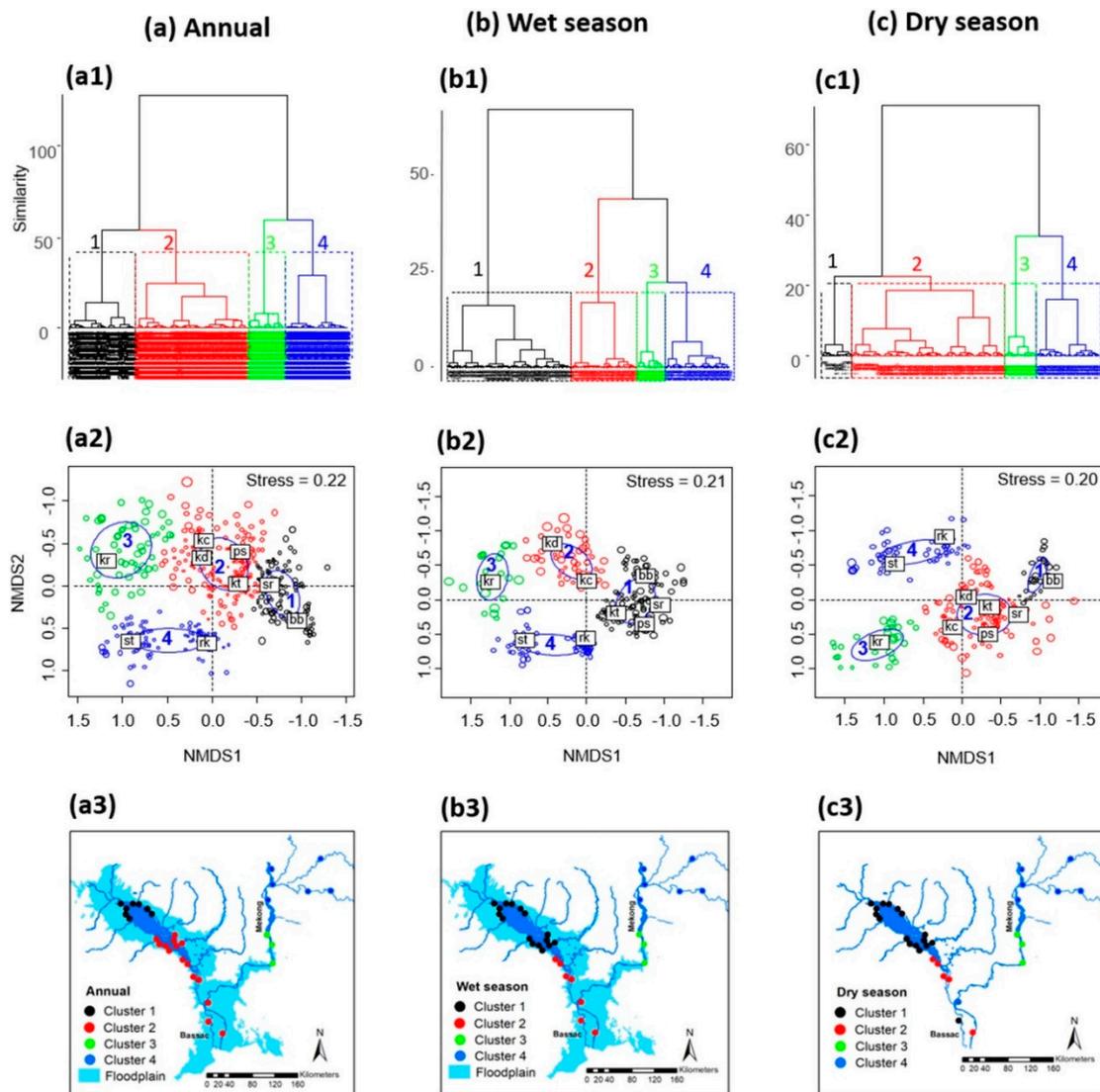


Figure 2. Freshwater fish distribution patterns in Cambodia: (a) Annual, (b) wet season and (c) dry season. (a1,b1,c1) are the Ward hierarchical clustering dendrograms of the weekly relative abundance showing four distinct clusters for the annual, wet season and dry season, respectively. (a2,b2,c2) are NMDS biplots of the relative weekly fish abundance samples (with Bray–Curtis dissimilarity matrix) showing distribution patterns of freshwater fish assemblages in Cambodia for the annual, wet season and dry season, respectively. (a3,b3,c3) are fish assemblage clusters visualized on the map for the annual, wet season and dry season, respectively. The letters on the MNDS biplots indicate the abbreviations of the study province name. For the province names, see Figure 1.

Fish assemblages for wet and dry seasons revealed similar patterns i.e., four distinct clusters (Figure 2(b1–b3,c1–c3)). However, fish samples belonging to each identified cluster were greatly varied particularly for cluster 1 (26 samples for dry season and 103 samples for wet season) and cluster 2 (136 samples for dry season and 53 samples for wet season) (Figure 2(b2,c2)).

PERMANOVA on annual fish assemblages indicated that all assemblages from the four clusters were significantly different ($p = 0.001$) (Supplementary Material Table S2.1), and the contrast pairwise tests of the assemblages between clusters also showed statistical significance at the $p = 0.001$ for all pairs (Supplementary Material Table S2.2). Wilcoxon rank sum tests on the NMDS site scores of the clusters revealed significant differences ($p = 0.001$) for all pairs on axis 1 and axis 2 (Supplementary Material Figure S2.3).

PERMANOVA on seasonal fish assemblages indicated that assemblages from wet and dry seasons within each cluster and between clusters were significantly different at ($p = 0.001$) (Supplementary Material Table S2.4), and the contrast pairwise tests of the assemblages between wet and dry seasons showed statistical significance at the $p = 0.001$ for all pairs (Supplementary Material Table S2.5). Moreover, Wilcoxon rank sum tests on the NMDS site scores of the wet and dry seasons revealed significant differences ($p = 0.001$) for all pairs on axis 1 and axis 2 (Supplementary Material Figure S2.6). For the details on the use of NMDS scores to compare wet and dry seasons, see Supplementary Material Tables S2.6 and S2.7.

3.3. Species Richness, Evenness and Diversity

Among the annual assemblage clusters identified, the highest richness (median = 25, sd = 5.02) and inverse Simpson diversity index (median = 10.9, sd = 3.10) were observed in assemblage cluster 4 (ST and RK) while the lowest richness (median = 11, sd = 3.75) and inverse Simpson diversity index (median = 1.5, sd = 1.15) occurred in assemblage cluster 3 (KR). Annual assemblage cluster 2 (KD and TSR) ranked second, with richness (median = 19, sd = 3.99) and diversity index (median = 5.5, sd = 2.95). Annual assemblage cluster 1 (SR and BB) ranked third, with richness (median = 16, sd = 4.28) and diversity index (median = 3.6, sd = 2.64) (Figure 3(a1,a2)).

When analyzing seasonal patterns (Figure 3(b1,b2)), significant higher species richness and inverse Simpson diversity index were found in the wet season for cluster 1 and 4 while the opposite pattern was observed for cluster 2. No significant difference in seasonal species richness was revealed for cluster 3, although significantly higher diversity index for this cluster was detected in the dry season.

Similarly, species rank-abundance plot with the shallowest slope, represented by the highest species evenness index (i.e., species abundance were more evenly distributed in the samples) were discerned in cluster 4 while the steepest slope, represented the lowest evenness index (i.e., species abundance were unevenly distributed in the samples) was revealed in cluster 3. Cluster 2 and 1 ranked second and third, respectively in terms of the values of species evenness index. Such similar patterns were also observed for the wet and dry seasons (Figure 4).

Overall, from the annual weekly samples, we found significant differences in species evenness index among identified assemblage clusters (Pairwise Wilcoxon rank sum test, $p < 0.001$). We also detected significant differences of species evenness index between the wet and dry seasons in all assemblage clusters (Kruskal–Wallis test, $p = 0.001$), except for cluster 3.

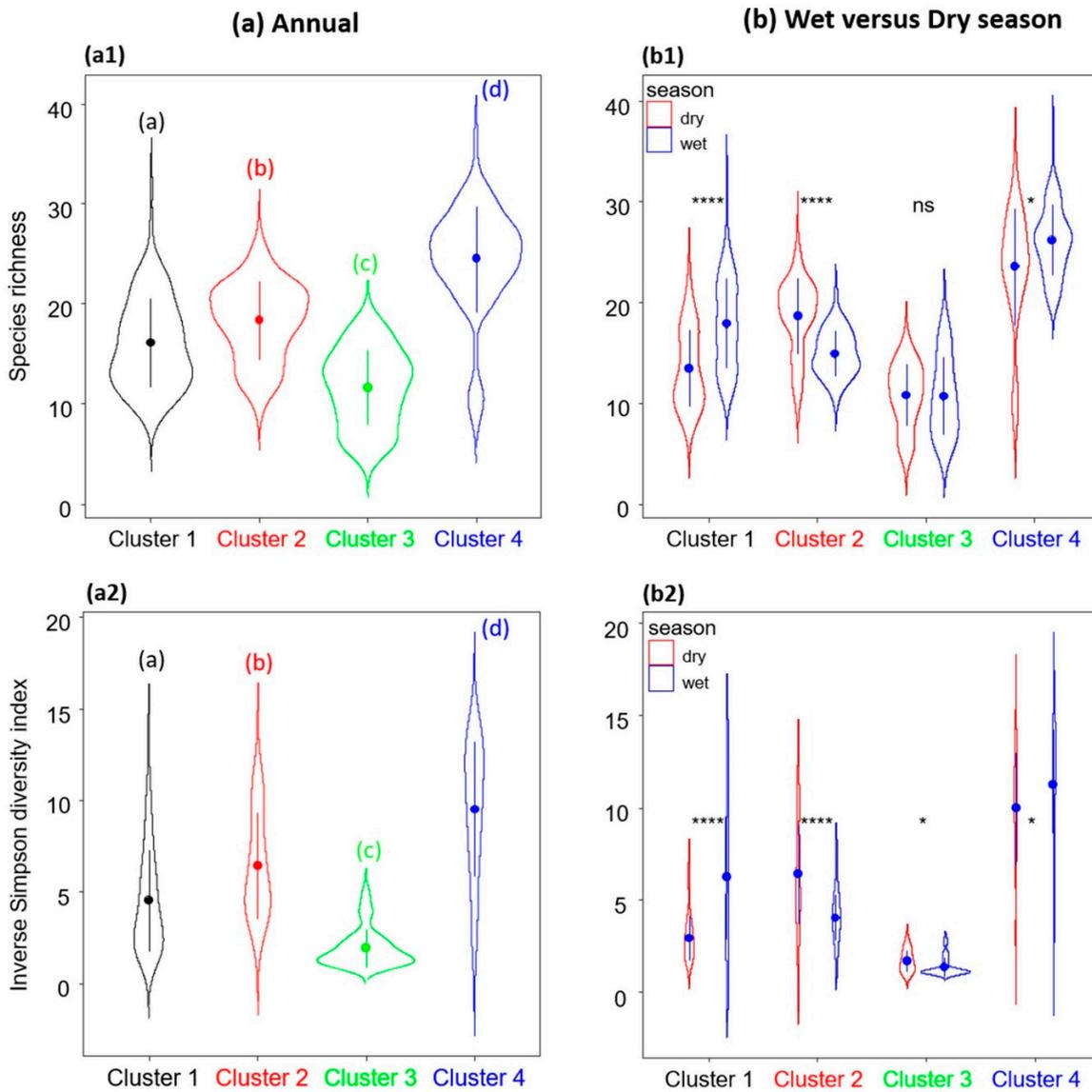


Figure 3. Violin plots showing fish species diversity based on weekly samples by cluster: (a) annual, (b) wet versus dry season. (a1,b1) show species richness, (a2,b2) inverse Simpson diversity indices. Clusters with a common letter are not significantly different at $p = 0.05$ (Pairwise Wilcoxon rank sum tests); sign (****) and (*) indicates significant differences at $p < 0.001$ and $p \leq 0.05$, respectively between wet and dry seasons, and “ns” denotes “non-significance” (Kruskal–Wallis test). Points indicate the median of the data and (violin) boxes indicate the interquartile range.

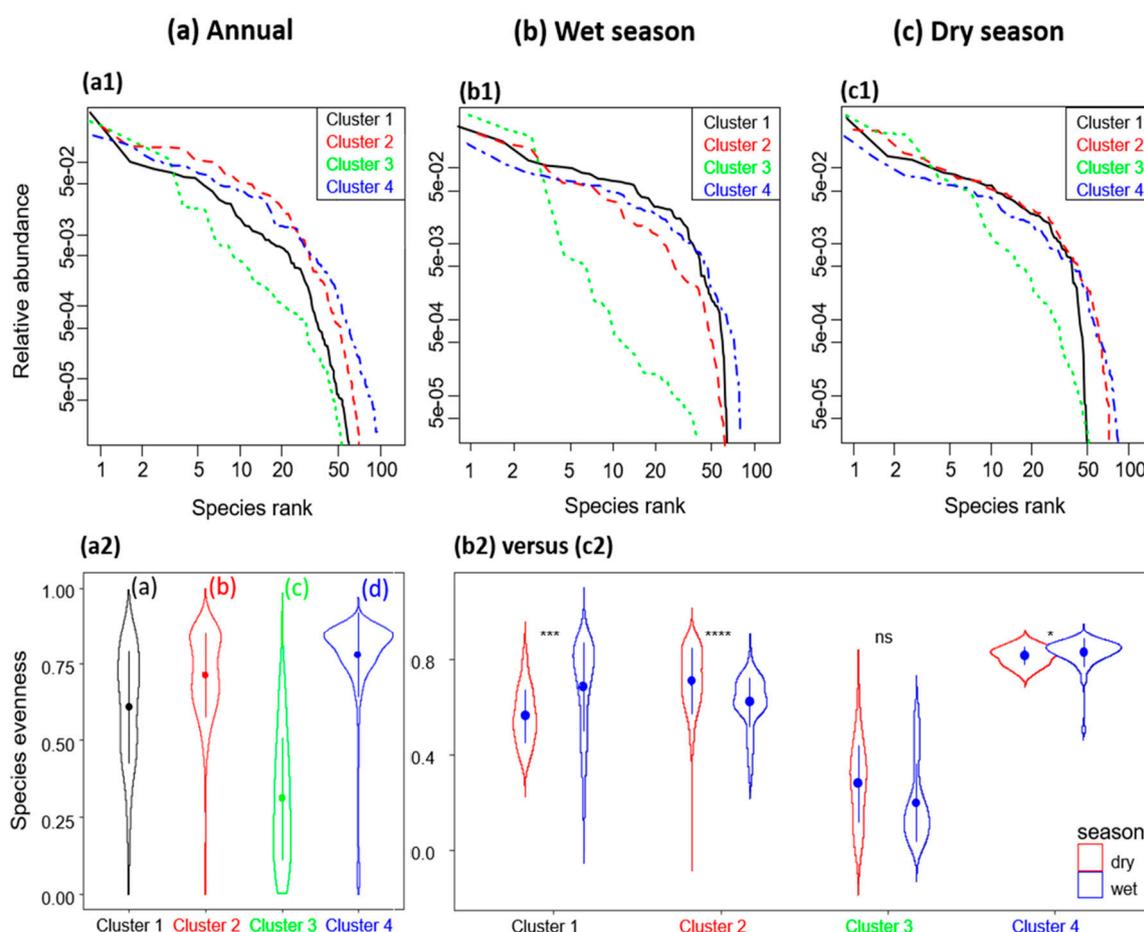


Figure 4. Rank-abundance plot by cluster: (a) annual, (b) wet season and (c) dry season. (a1,b1,c1) are relative abundance curves (log-scale), (a2,b2,c2) show species evenness indices. Clusters with a common letter are not significantly different at $p = 0.05$ (Pairwise Wilcoxon rank sum tests); sign (****) and (*) indicates significant differences at $p < 0.001$ and $p \leq 0.05$, (***) indicates significant difference at $p = 0.001$, respectively between wet and dry seasons, and “ns” denotes “non-significance” (Kruskal–Wallis test).

3.4. Indicator Species by Cluster

A total of 95 significant indicator species were identified from the four annual assemblage clusters (Supplementary Material Table S3). Almost 50% of the indicator species were observed in cluster 4 (46 species), while the lowest number was observed in cluster 3 (11 species). Indicator species representing cluster 1 in the northern TSL mainly contained, in terms of species counts, almost 40% of black fish, ~28% of grey fish, ~27% of white fish and the rest were estuarine species. Black fish characterizing this cluster included Osphronemidae (gouramies), i.e., *Trichopodus trichopterus*, *T. microlepis*, *T. pectoralis*; Anabantidae (climbing perches) i.e., *Anabas testudineus*; Cyprinidae (cyprinids) i.e., *Puntius brevis*; Mastacembelidae (spiny eels) i.e., *Macrognathus siamensis*; whereas, grey fish consisted of Bagridae (bagrid catfishes), i.e., *Mystus multiradiatus*, *M. mysticetus*; Ambassidae (asiatic glassfishes) i.e., *Parambassis wolffii*, *P. siamensis*; cyrinids i.e., *Rasbora aurotaenia* and *Parachela siamensis*. Few white fish found in this cluster were cyprinids i.e., *Labiobarbus leptocheilus*, *Albulichthys albuloides* and Siluridae (sheatfishes) i.e., *Kryptopterus geminus*. Estuarine species included Polynemidae (threadfins) i.e., *Polynemus aquilonari*. Key indicator species represented this cluster for both wet and dry seasons included only black and grey fish namely *Trichopodus* spp., *P. wolffii* and *P. brevis* and *P. siamensis*; and an estuarine species namely *P. aquilonari*.

Cluster 2 was associated with the Mekong/Bassac/TSR in Kandal (KD) Province and the middle portion of the TSL. Indicator species for this cluster were constituted mainly by white (~55%) and grey

fish (~30%) of the total species count while the rest was black (~5%) and estuarine fish (~10%). White fish included mainly Cyprinidae (cyprinids) e.g., *Labeo chrysophekadion*, *Gymnostomus lobatus*, *Puntioplites proctozyron*, *Osteochilus vittatus*, *Cyclocheilos enoplos*, *Barbonymus gonionotus*, *Amblyrhynchichthys micracanthus* and *Cosmochilus harmandi* while grey fish were mainly made up of cyprinids i.e., *Thynnichthys thynnoides*, *Leptobarbus rubripinna*; Sciaenidae (croakers) i.e., *Boesemania microlepis*; Bagridae (bagrid catfishes) i.e., *Mystus bocourti*, *M. albolineatus*; and Tetraodontidae (puffers) i.e., *Pao turgidus*. Black fish included Channidae (snakeheads) i.e., *Channa lucius*. Estuarine species included Gobiidae (gobies) i.e., *Glossogobius aureus* and Toxotidae (archerfishes) i.e., *Toxotes chatareus*. Key indicator species identified for this cluster for both wet and dry seasons were grey fish i.e., *L. rubripinna* and *B. microlepis*.

Indicator species describing cluster 3 related to sites in KR and KD were composed mostly of white fish (~73%) while, for black, grey and estuarine fish, each accounted for only (~9%). White fish included Pangasiidae (river catfishes) i.e., *Pangasianodon hypophthalmus*; Siluridae (sheatfishes) i.e., *Phalacronotus microneme*, *Belodontichthys truncatus* and *Wallago attu*; cyprinids i.e., *Labiobarbus siamensis*, *Gymnostomus siamensis*, *Thryssocypris tonlesapensis* and *Oxygaster pointoni*. Interestingly, two exotic species i.e., *Oreochromis niloticus* (Nile tilapia, black fish) and *Hypophthalmichthys molitrix* (silver carp, white fish) were also indicative for this cluster (with samples from KD). Estuarine species included Polynemidae (threadfins) i.e., *Polynemus melanochir*. No species indicators were identified for both wet and dry seasons for this cluster.

Indicator species identified for cluster 4 were mainly white fish (~74%); while black, grey and estuarine fish represented ~11%, ~9%, ~6% of the species count, respectively. White fish constituted to this cluster were Cyprinidae (cyprinids) e.g., *Hypsibarbus malcomi*, *Scaphognathops bandanensis*, *Systemus rubripinnis*, *Hampala macrolepidota*, *Osteochilus schlegelii*, *Cirrhinus microlepis*, *Osteochilus lini*, *Hypsibarbus wetmorei*, *Puntioplites bulu*, *Probarbus jullieni*, *Mystacoleucus marginatus*, *Labeo pierrei*, *Aptosyax grypus* etc.; Bagridae (bagrid catfishes) i.e., *Hemibagrus wyckioides*, *H. spilopterus*, *Bagrichthys obscurus* and *Hemibagrus wyckii*; Sisorinae (Sisorid catfishes) i.e., *Bagarius bagarius*; Pangasiidae (river catfishes) e.g., *Helicophagus leptorhynchus*, *Pangasius conchophilus*, *P. macronema* and *P. larnaudii* and Cobitidae (loaches) i.e., *Yasuhikotakia modesta*; Siluridae (sheatfishes) i.e., *Phalacronotus bleekeri* and Notopteridae (featherbacks) i.e., *Chitala ornata* and *C. blanci*. Grey fish included cyprinids i.e., *Cyclocheilichthys armatus* and *Barbonymus altus*; featherbacks i.e., *Notopterus notopterus*; (Mastacembelidae) spiny eels i.e., *Mastacembelus armatus*; sheatfishes i.e., *Ompok siluroides*; while black fish comprised Channidae (snakeheads) i.e., *Channa striata*; Pristolepididae (leaf-fishes) i.e., *Pristolepis fasciata*; Eleotridae (sleepers) i.e., *Oxyeleotris marmorata*; Osphronemidae (gouramies) i.e., *Osphronemus exodon*. Estuarine species identified for this cluster were Plotosidae (eel-tail catfish) e.g., *Plotosus canius*; Mastacembelidae (spiny eels) i.e., *Mastacembelus armatus*, Coiliinae (enchovies) i.e., *Setipinna melanochir*. ~30% of indicator species identified for the annual assemblages were also the indicator species for assemblages of wet and dry seasons, the highest number of seasonal indicator species of all four clusters.

3.5. Length–Weight Relationship of Indicator Species

As indicated above, 95 key indicator species were identified for all four clusters. However, only 45 species (all species with sample sizes > 30) were included here for the LWR analysis. Of the 45 indicator species, the analysis included 11 species in cluster 1, 13 species in cluster 2, 4 species in cluster 3 and 17 species in cluster 4 (Figure 5a). The total sample size used for LWR analysis was 23,408 individuals, belonging to 4 orders and 11 families. Among those, Cyprinidae comprised 20 species, Siluridae (13 species), Osphronemidae (3 species), Notopteridae (2 species), Ambassidae (2 species) while each of the other remaining 6 families contained only one species (Table 1).

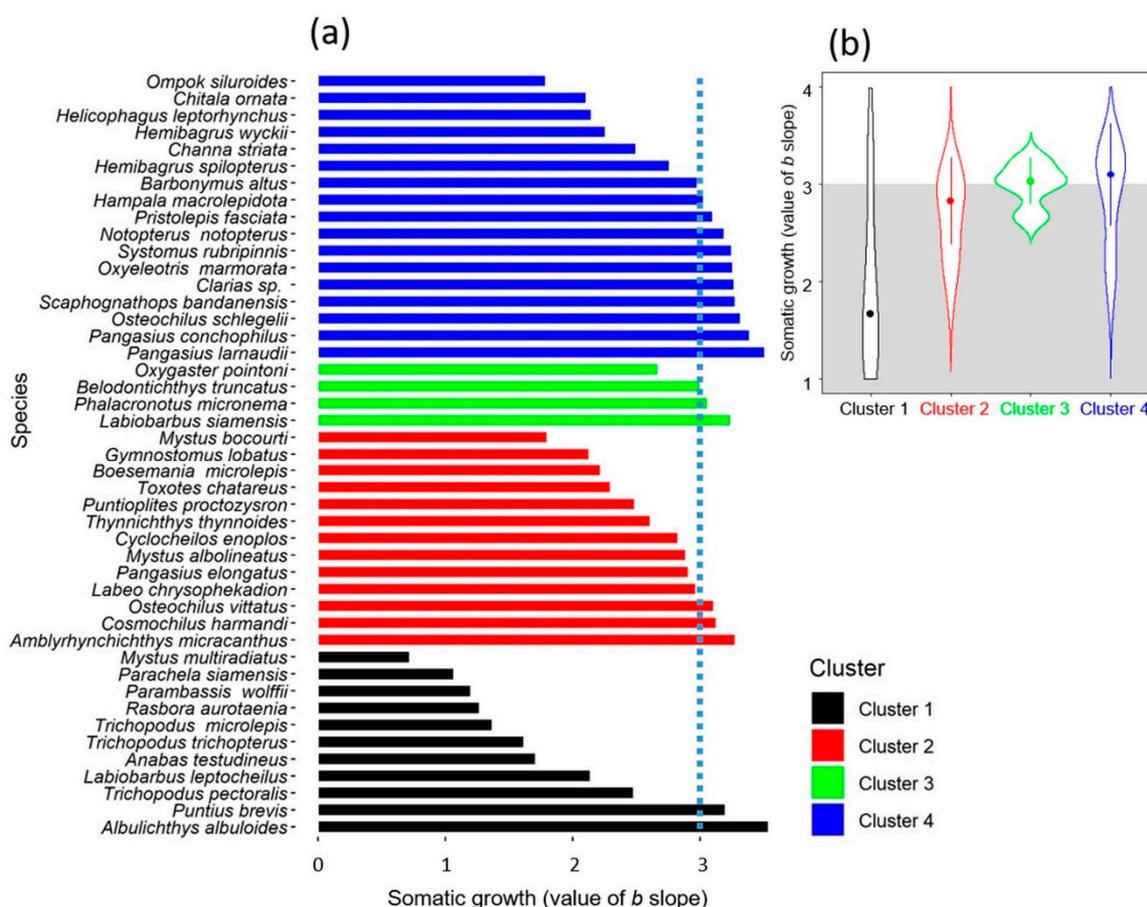


Figure 5. Fish growth conditions, determined by regression coefficient values (slope b) of the length–weight linear models for 45 indicator species characterizing freshwater fish assemblages in Cambodia inland water bodies: (a) regression coefficient values (slope b) by indicator species: isometric growth ($b = 3$), positive allometric growth ($b > 3$) or negative allometric growth ($b < 3$). (b) violin plots summarizing regression coefficients of the length–weight linear relationship by fish assemblage cluster. Area above the grey shaded area denotes regression coefficient values $b > 3$, positive allometric growth.

The results of the length–weight regression models of the 45 fish indicated highly significant LWR ($p < 0.001$) for all species (Table 1). The coefficients of determination (adjusted r^2) ranged between 0.21 for *Rasbora aurotaenia* and 0.99 for *Cosmochilus harmandi*. Specifically, adjusted r^2 values were from 0.90–0.99 for 11 species (24.44%), 0.80–0.89 for 11 species (23.44%), 0.70–0.79 for 5 species (11.11%), and ≤ 0.69 for 18 species (40%). Moreover, the slope b values ranged from 0.72 for *Mystus multiradiatus* to 3.54 for *Albulichthys albuloides*. The median value of slope b was 2.83 (sd = 0.73).

Overall, the results showed that 27 species (60.00%) had negative allometries ($b < 3$), 3 species (6.67%) isometries ($b = 3$), and 15 species (33.33%) positive allometries ($b > 3$). Besides, violin plots on slope b values by cluster indicated that the Mekong-3S system and middle section of the Mekong River had the slope b value of around 3 (cluster 4: median = 3.1; sd = 0.52, cluster 3: median = 3.03; sd = 0.23). In other words, more than 50% of the study indicator species from those areas had either isometric or positive allometric growth while the lower Mekong system experienced lower slope b values (cluster 1: median = 1.62; sd = 0.90, cluster 2: median = 2.83; sd = 0.44) (see also Figure 5b).

Table 1. Length–weight relationships of 45 indicator species by annual fish assemblage cluster. Parameter estimates of the linear models: a = intercept, b = slope [negative allometric growth ($b < 3$), isometric growth ($b = 3$), and positive allometric growth ($b > 3$)]. N = number of observations. All slopes were significant at $p < 0.001$. Summary of slope b values by fish assemblage cluster is given in Figure 5b.

| Cluster | Species | N | Total Length (cm) | | | | Weight (g) | | | | a | b | Adjusted R ² |
|---------------------------------|--|------|-------------------|-------|-------|------|------------|---------|--------|----------|----------|------|-------------------------|
| | | | Min | Max | Mean | SE | Min | Max | Mean | SE | | | |
| Cluster 1 | <i>Albulichthys albuloides</i> | 58 | 8.40 | 20.00 | 13.84 | 0.33 | 3.40 | 80.00 | 26.38 | 2.27 | 0.002070 | 3.54 | 0.93 |
| | <i>Anabas testudineus</i> | 826 | 3.00 | 25.20 | 11.66 | 0.08 | 0.90 | 200.00 | 33.36 | 0.74 | 0.418952 | 1.71 | 0.32 |
| | <i>Labiobarbus leptocheilus</i> | 1058 | 3.30 | 19.50 | 12.11 | 0.07 | 3.50 | 77.50 | 19.77 | 0.39 | 0.083743 | 2.14 | 0.66 |
| | <i>Mystus multiradiatus</i> | 486 | 2.70 | 17.20 | 10.59 | 0.13 | 2.60 | 33.50 | 12.55 | 0.27 | 2.117000 | 0.72 | 0.27 |
| | <i>Parachela siamensis</i> | 992 | 3.00 | 15.00 | 9.96 | 0.05 | 2.20 | 35.60 | 9.93 | 0.13 | 0.786628 | 1.07 | 0.26 |
| | <i>Parambassis wolffii</i> | 1362 | 2.60 | 25.00 | 8.79 | 0.06 | 1.80 | 165.20 | 12.61 | 0.29 | 0.786628 | 1.20 | 0.30 |
| | <i>Puntius brevis</i> | 296 | 5.70 | 11.20 | 7.47 | 0.08 | 2.40 | 68.00 | 9.31 | 0.74 | 0.010889 | 3.20 | 0.61 |
| | <i>Rasbora aurotaenia</i> | 171 | 6.50 | 13.90 | 10.25 | 0.10 | 2.80 | 23.60 | 10.07 | 0.28 | 0.491644 | 1.27 | 0.21 |
| | <i>Trichopodus microlepis</i> | 683 | 2.30 | 14.00 | 10.25 | 0.08 | 2.00 | 68.00 | 15.10 | 0.38 | 0.548812 | 1.37 | 0.45 |
| | <i>Trichopodus pectoralis</i> | 239 | 2.90 | 24.20 | 12.54 | 0.31 | 2.10 | 208.10 | 42.97 | 2.87 | 0.055023 | 2.48 | 0.85 |
| <i>Trichopodus trichopterus</i> | 2720 | 2.00 | 14.20 | 8.71 | 0.05 | 0.10 | 81.00 | 15.93 | 0.30 | 0.367879 | 1.62 | 0.53 | |
| Cluster 2 | <i>Amblyrhynchichthys micracanthus</i> | 244 | 8.00 | 23.10 | 11.65 | 0.14 | 4.70 | 134.50 | 18.36 | 1.21 | 0.004844 | 3.28 | 0.87 |
| | <i>Boesemania microlepis</i> | 320 | 2.60 | 85.00 | 22.53 | 1.05 | 4.50 | 4000.00 | 452.96 | 52.12 | 0.110803 | 2.22 | 0.69 |
| | <i>Cosmochilus harmandi</i> | 52 | 10.00 | 70.00 | 24.61 | 2.11 | 8.80 | 4500.00 | 436.16 | 128.30 | 0.007227 | 3.13 | 0.99 |
| | <i>Cyclocheilos enoplos</i> | 916 | 4.20 | 65.00 | 15.86 | 0.22 | 3.30 | 2500.00 | 67.04 | 5.96 | 0.013982 | 2.83 | 0.88 |
| | <i>Gymnostomus lobatus</i> | 3673 | 1.00 | 18.90 | 11.31 | 0.03 | 1.40 | 86.70 | 17.43 | 0.18 | 0.088922 | 2.13 | 0.51 |
| | <i>Labeo chrysophekadion</i> | 898 | 1.00 | 68.10 | 14.09 | 0.24 | 2.60 | 4570.00 | 80.47 | 11.61 | 0.010998 | 2.97 | 0.90 |
| | <i>Mystus albolineatus</i> | 111 | 7.00 | 18.50 | 10.52 | 0.15 | 3.60 | 41.00 | 9.48 | 0.51 | 0.009658 | 2.89 | 0.81 |
| | <i>Mystus bocourti</i> | 494 | 7.20 | 26.50 | 12.25 | 0.11 | 4.70 | 113.50 | 18.92 | 0.77 | 0.168638 | 1.80 | 0.27 |
| | <i>Osteochilus vittatus</i> | 511 | 6.50 | 19.80 | 12.97 | 0.13 | 4.10 | 126.10 | 29.00 | 0.95 | 0.008148 | 3.11 | 0.89 |
| | <i>Pangasius elongatus</i> | 32 | 13.10 | 40.10 | 16.95 | 0.95 | 21.30 | 573.00 | 56.22 | 17.91 | 0.010462 | 2.91 | 0.97 |
| | <i>Puntioplites proctozysron</i> | 2997 | 3.20 | 33.40 | 12.79 | 0.07 | 2.20 | 600.00 | 38.00 | 0.85 | 0.047359 | 2.49 | 0.67 |
| | <i>Thynnichthys thynnoides</i> | 369 | 7.30 | 15.60 | 10.51 | 0.06 | 4.30 | 43.80 | 12.73 | 0.25 | 0.025991 | 2.61 | 0.68 |
| | <i>Toxotes chatareus</i> | 89 | 7.50 | 13.50 | 10.05 | 0.13 | 7.60 | 33.00 | 18.12 | 0.62 | 0.085435 | 2.30 | 0.69 |
| Cluster 3 | <i>Belodontichthys truncatus</i> | 43 | 14.70 | 35.50 | 23.93 | 0.96 | 18.80 | 224.50 | 94.43 | 10.04 | 0.005462 | 3.00 | 0.90 |
| | <i>Labiobarbus siamensis</i> | 700 | 7.40 | 24.80 | 11.12 | 0.08 | 2.80 | 153.80 | 15.42 | 0.53 | 0.005407 | 3.24 | 0.93 |
| | <i>Oxygaster pointoni</i> | 176 | 8.40 | 16.00 | 11.24 | 0.07 | 6.10 | 35.30 | 12.50 | 0.28 | 0.018873 | 2.67 | 0.80 |
| | <i>Phalacronotus micronema</i> | 179 | 9.00 | 51.50 | 23.77 | 0.77 | 2.80 | 560.00 | 109.98 | 8.95 | 0.004087 | 3.06 | 0.90 |

Table 1. Cont.

| Cluster | Species | N | Total Length (cm) | | | | Weight (g) | | | | a | b | Adjusted R ² |
|-----------------------------|-----------------------------------|-------|-------------------|-------|-------|-------|------------|---------|--------|----------|----------|------|-------------------------|
| | | | Min | Max | Mean | SE | Min | Max | Mean | SE | | | |
| Cluster 4 | <i>Barbonymus altus</i> | 100 | 7.90 | 22.80 | 14.69 | 0.31 | 6.60 | 231.40 | 60.73 | 4.53 | 0.016408 | 2.98 | 0.72 |
| | <i>Chitala ornata</i> | 37 | 10.00 | 72.00 | 34.34 | 2.88 | 21.40 | 2700.00 | 519.44 | 112.24 | 0.184520 | 2.11 | 0.84 |
| | <i>Channa striata</i> | 296 | 9.00 | 46.00 | 20.02 | 0.48 | 6.40 | 1100.00 | 106.97 | 7.74 | 0.039557 | 2.50 | 0.77 |
| | <i>Clarias</i> sp. | 35 | 12.50 | 31.60 | 20.87 | 0.69 | 16.90 | 263.50 | 79.21 | 9.25 | 0.003247 | 3.27 | 0.93 |
| | <i>Hampala macrolepidota</i> | 86 | 8.00 | 42.10 | 17.85 | 1.01 | 4.60 | 930.00 | 131.68 | 20.17 | 0.010673 | 3.03 | 0.94 |
| | <i>Helicophagus leptorhynchus</i> | 46 | 20.00 | 52.40 | 32.57 | 0.97 | 60.00 | 877.00 | 240.52 | 24.27 | 0.115325 | 2.15 | 0.59 |
| | <i>Hemibagrus spilopterus</i> | 445 | 7.80 | 43.00 | 19.92 | 0.31 | 5.10 | 900.00 | 102.48 | 5.76 | 0.016573 | 2.76 | 0.77 |
| | <i>Hemibagrus wyckii</i> | 107 | 16.00 | 75.50 | 33.77 | 1.13 | 25.00 | 3820.00 | 573.45 | 72.62 | 0.127454 | 2.26 | 0.52 |
| | <i>Notopterus notopterus</i> | 188 | 8.60 | 27.50 | 18.01 | 0.31 | 9.40 | 350.00 | 68.10 | 5.04 | 0.004844 | 3.19 | 0.79 |
| | <i>Ompok siluroides</i> | 177 | 3.10 | 35.00 | 13.92 | 0.37 | 3.10 | 260.00 | 26.50 | 2.72 | 0.165299 | 1.79 | 0.64 |
| | <i>Osteochilus schlegelii</i> | 150 | 7.50 | 21.00 | 11.94 | 0.15 | 4.10 | 186.20 | 20.98 | 1.39 | 0.004942 | 3.32 | 0.91 |
| | <i>Oxyeleotris marmorata</i> | 112 | 10.50 | 44.00 | 20.27 | 0.58 | 14.30 | 1800.00 | 162.36 | 23.77 | 0.005976 | 3.26 | 0.94 |
| | <i>Pangasius conchophilus</i> | 44 | 22.00 | 68.00 | 36.95 | 1.47 | 40.00 | 2135.00 | 490.30 | 74.37 | 0.001747 | 3.39 | 0.88 |
| | <i>Pangasius larnaudii</i> | 56 | 12.40 | 56.20 | 34.97 | 1.36 | 19.20 | 2608.00 | 735.28 | 102.20 | 0.001782 | 3.51 | 0.84 |
| | <i>Pristolepis fasciata</i> | 676 | 4.00 | 19.00 | 9.92 | 0.10 | 1.90 | 172.50 | 25.47 | 1.00 | 0.016083 | 3.10 | 0.88 |
| | <i>Scaphognathops bandanensis</i> | 97 | 9.30 | 29.00 | 17.34 | 0.48 | 7.30 | 320.00 | 82.92 | 7.11 | 0.804615 | 3.28 | 0.89 |
| <i>Systemus rubripinnis</i> | 61 | 10.00 | 16.20 | 13.49 | 0.20 | 14.80 | 75.10 | 35.89 | 2.10 | 0.007083 | 3.25 | 0.79 | |

4. Discussion

Our study describes the spatial and seasonal variation of fish diversity and assemblage structure as well as fish growth conditions in the species-rich and highly productive region of the lower Mekong system in Cambodia. Our study focused on commercial or subsistence fish catch and showed that despite high basin-wide diversity, catches were dominated by a small subset of orders, families, and species—which varied in importance based on season, habitat, and geography. Based on species composition similarity, we found two broad distinct fish assemblages characterizing the freshwater fish community in Cambodia: one assemblage connected with the lower floodplains and the second assemblage associated with the upper Mekong system. These assemblages further subdivided into four assemblage clusters: the lower floodplain assemblages were related to assemblages in BB and SR (northern TSL, cluster 1) and assemblages in KT, PS, KC (southern/middle TSL), the Mekong and Bassac Rivers in KD (cluster 2); whereas, the upper Mekong fish assemblages were linked to KR and partly KD (cluster 3) and in ST and RK (Mekong-3S, cluster 4). In addition, fish assemblage composition among clusters displayed a geographical gradient from assemblages of mainly migratory white fish in the upper Mekong (cluster 3, 4) to assemblages of mainly white and grey fish in KD and southern TSL (cluster 2), and finally assemblages characterized mainly by black and some grey fish towards the northern TSL (cluster 1). Upper Mekong assemblage composition particularly in the Mekong-3S (ST/RK) were found to be more evenly distributed and diverse and have better growth conditions than those in the lower Mekong system especially in the northern TSL.

4.1. Spatial and Seasonal Variation of Fish Assemblages

The observed spatial distribution patterns of freshwater fish assemblages likely corresponded with heterogeneous habitat characteristics, environmental conditions of the freshwater bodies in Cambodia, and the unique hydrology and connectivity of the overall system. In the lower floodplain in the northern TSL (cluster 1), we found that fish assemblages were represented mostly by black and grey fish, species with restricted range of migration within the lakes and swamps in the floodplains (or local tributaries). These species included climbing perches, gouramies, spiny eels, asiatic glassfishes, sheatfishes and few small-sized cyprinids e.g., *Rasbora* spp. They are among the species that could tolerate harsh environmental conditions such as poorly oxygenated or higher temperature waters especially during the dry season [18,41,61]. Among these indicator species, gouramies, glassfishes and small-sized cyprinids (i.e., *Parachela siamensis* and *Puntius brevis*) also characterized the annual, wet and dry season assemblages for the cluster. Indeed, fish assemblages in this cluster are associated with the lentic environment and the habitats that are distinguished by swampy areas with flooded forests, rice paddies, dense floating vegetations and grass/shrublands [18,31]. Such habitat types favor black and some grey fish. For instance, to adapt to such environment conditions, some black fish (e.g., gouramies and climbing perches) have developed their auxiliary organs to uptake oxygen from the atmospheric air and may move over land or hibernate in holes or vegetation roots during the dry season [62–64]. Our findings in fact update and support the results of the previous studies which demonstrated that these black and grey fish were distributed more in the northern TSL [18,31,41,65]. In the swamp of Lake Victoria, black fish e.g., African catfishes were also found to thrive in such lentic and poorly oxygenated habitats [66] and North American catfishes were found to withstand low oxygenated or high water temperature environment [67].

Fish assemblage composition changed from black and grey fish in the northern TSL to assemblages mainly composed of white and grey fish in the southern TSL, TSR, and Bassac River (cluster 2). This fish assemblage cluster characterized mainly by small, medium, and large-sized cyprinids, croakers, small-sized bagrid catfishes and puffers. The habitats connected with this assemblage cluster include main rivers (Mekong and Bassac in KD), tributaries (TSR), flooded plains, rice paddies and shrublands surrounding those main rivers and tributaries, and the southern TSL. Basically, these white and grey fish migrate to the main river channels or open area of the TSL with better oxygenated water and water quality, especially during the dry season. Among this group, cyprinids likely perform (large-scale)

longitudinal migrations seasonally; whereas, the others migrate laterally between seasonal flooded plains and rivers or local tributaries [7,18,20,63,68–70]. Importantly, the area also plays a pivotal connectivity role (i.e., a junction joined by upper Mekong, lower Mekong, Bassac and TSR) as a seasonal migration corridor for the white fish to access critical habitats in the lower floodplain e.g., the TSL for rearing and feeding during the flooding period, and in the upper Mekong River system of Cambodia or beyond for dry season refuge and spawning. An example of such a predictable seasonality of fish passing through the Mekong River in this area is the fish larvae drift in the wet season between June and September each year [71] and century-old stationary bag net (dai) fishery operating seasonally in the TSR in the dry season between October and February/March [16,38,72,73]. Further, the ecotone i.e., the bottleneck of the TSR, connecting the Mekong River to the TSL was also identified as the International Union for Conservation of Nature's (IUCN) key biodiversity area in the LMB given its importance for persistence of globally significant biodiversity [74], especially for white and grey fish.

In the upper Cambodian Mekong (cluster 3 and 4), fish assemblage composition was dominated by white fish such as cyprinids, river catfishes, (large-sized) bagrid catfishes, sheatfishes and loaches etc. A majority of these fish are seasonally long-distance migrants, that generally require highly oxygenated water and are intolerant to poor water quality. Of the two clusters, cluster 4 appeared to have the largest number of indicator species for the annual, wet and dry season assemblages. By contrast, no indicator species were identified for both wet and dry seasons in cluster 3. This may indicate that areas or river sections associated with assemblage cluster 3 also serve as a seasonal passageway mainly for white fish i.e., connecting them between the upstream (Mekong-3S) and downstream (lower floodplain e.g., TSL) habitats while cluster 1 and 4 serve as critical habitats for rearing/feeding, reproduction and refugia at different life stages during their life cycles. Noticeably, indicator species characterizing fish assemblage cluster 4 also comprised several IUCN Red List species with statuses of being vulnerable (*Osphronemus exodon*, *Cirrhinus microlepis*), near threatened (*Bagarius bagarius*, *Chitala blanci*, *Cirrhinus molitorella*), endangered (*Probarbus jullieni*) or critically endangered (*Aptosyax grypus*). Indeed, assemblage cluster 4 still hosts some of the rarest, flagship and/or endemic freshwater fish species in the Mekong Basin and the world [63,75,76] and this area has been identified by [24,68,71,77,78], and by the results of this study—as a biodiversity hotspot.

Moreover, white fish were indicative for the two upstream fish assemblage clusters (KR and ST/RK) likely because the area is lotic with diverse habitat types including the Mekong Basin's largest tributaries, the 3S system. Also, the upper Cambodian Mekong is characterized by wide main channels, rapids and deep pools [79,80]. These habitat complexities serve as spawning grounds and dry season refugia of riverine fish including river catfish, large and medium sized cyprinids, large-sized bagrid catfishes, sheatfishes, featherbacks, and several of the world's rarest inland fish [68,76,81,82]. In fact, the upstream river section (KR/ST) is also the home range of the critically endangered Irrawaddy dolphin [83] and has been designated as Ramsar wetlands of international importance [77] and one of the IUCN's key biodiversity areas in the LMB [74]. Further, areas in KR and ST/RK are less populated than those in the lower floodplains such as in KD and the provinces around the TSL [84]. The upstream areas are also less likely affected by urbanization and agricultural activities (e.g., crops and rice farming), compared to areas in the lower floodplains e.g., KD and the provinces around the TSL where rice farming and agricultural crops tend to dominate the land cover types [85,86]. Overall, these may partly explain the better overall environmental quality e.g., in terms of habitats and water quality for the upstream assemblage clusters that were represented mainly by white fish including several of the world's rarest freshwater fish species.

Also, it is noteworthy that two exotic species i.e., tilapia and silver carp were identified as indicator species for the assemblage cluster associated with KR/KD. While the reproductive status of silver carp in the natural environment is not known, tilapia is well-established in the Mekong system [87]. Seasonal catches of tilapia were reported to have increased in the Mekong's lower floodplains i.e., Vietnam Mekong delta and Tonle Sap ecosystem over the last two decades [38,87]. However, the status of invasion from these species on the Cambodia inland waters remains unclear given

that they have value as food fish for the locals. With increasing hydropower dam reservoirs in the region, these introduced species may thrive as it has been the case for the golden apple snails [88,89]. Future study would benefit from the assessment of these introduced species on natural environment and wild fish populations.

4.2. Species Diversity

We found the highest diversity (i.e., richness, diversity, and evenness indices) in cluster 4 (ST/RK) for the annual, wet and dry season assemblages while lowest diversity was found in cluster 3 (KR). This is probably related to the geographical position and environmental and habitat quality in each cluster (explained above). In addition, we found significant variation of species diversity between wet and dry seasons for all clusters except for cluster 3. Specifically, significantly higher diversity was shown in the wet season in cluster 1 and 4 while the opposite was observed, particularly in cluster 2 where significantly higher species diversity was discerned in the dry season. Such seasonal variation was likely due to fish seasonal migrations between critical habitats during their life cycles. In the wet season, many white fish are known to disperse for spawning in the Mekong mainstream and rapids in areas associated with cluster 4, and migrate to tributaries and lower floodplains e.g., TSL for rearing and feeding [68,90,91]. Fish larvae also drift from the upstream Mekong with water currents to the lower floodplains for rearing [71,92]. Significant increase in the species diversity (e.g., richness and abundance) was observed in the Cambodia upstream Mekong in the early wet season [17,35]. Such migration patterns also occur within the lower floodplain when water levels increase as fish move to the surrounding flooded plains and forests (cluster 1) for foraging and reproduction [18,21]. In both the Mekong mainstream and floodplains, many fish tend to get captured during the (early) wet season dispersal period for reproduction, rearing and feeding, which likely drives the higher diversity. The increase in species diversity in cluster 1 during the wet season could also be explained by the “addition” concept where white and grey fish invade lower floodplains as environmental conditions (temperature, dissolved oxygen, also access to food and habitat) improve, primarily for rearing and feeding [93]. Our results indeed strengthened a recent study which highlighted the increase in fish abundance and diversity in the TSL during flooding periods [33]. Such a pattern was also observed in flooded plains southeastern Cambodia [94] and in Congo River [95].

By contrast, in the dry season, when water recedes, fish withdraw from adjacent flooded forests to the deeper or open area of the water bodies such as the TSL. White and grey fish may further migrate to the tributaries rivers such as the TSR and up the Mekong River for dry season refuge e.g., the Mekong-3S system [15,96]. When these fish leave the lower floodplain, huge fisheries occur e.g., in the TSR and other mainstems in KD and KR, and these likely drive higher species richness in the dry season for cluster 2 and 3 as many species are harvested when they migrate back from the floodplains to main river channels for dry season refuge.

4.3. Fish Growth Conditions

Overall, we found that ~60% of the indicator species in the four identified fish assemblage clusters had negative allometric growth, with a majority of indicative fish stocks representing the lower floodplain assemblages in cluster 1 and 2. This is likely due to overfishing or indiscriminate fishing in the TSRL, where a variety of fishing gears are used to exploit fish across seasons, habitats, species and sizes [50,97,98]. Indeed, our results further confirm the past and recent studies stressing the overfishing effects of the TSRL fisheries, with decreasing fish mean body sizes, and catches being dominated by small-bodied species [38,50,99–101]. By contrast, the upstream Mekong fish assemblages were relatively healthier in terms of growth conditions likely because of better overall environmental stability (discussed above). Areas associated with these clusters (cluster 3 and 4) host some of the world’s critically endangered species e.g., Mekong giant catfish, giant salmon carp, and Irrawaddy dolphins.

Other human activities likely contributing to the negative allometric growth condition of fish, particularly in the lower floodplain, could be due to flow alterations, resulting from water infrastructure

development upstream of the Mekong and climate change [1,102–104], flooded forest fires/clearance and deforestation [86,105,106], agriculture expansion and intensification [41] and other development activities taking place in the floodplain e.g., irrigation dams etc. [107]. For instance, the reduction in seasonal flow to the lower floodplain caused by dams and climate change could reduce inundated area, which means that less rearing/feeding habitats and fewer food sources are available for fish, adversely affecting their growth. In addition, reduction in seasonal discharge combined with intensive agricultural activities at the lower floodplain could increase the prevalence of hypoxia as a consequence of increased accumulations of nutrients and organic materials. Such hypoxia conditions reduce fish growth, length and body condition, and increase in the age at maturation which, in turn, affects fish recruitment and spawning biomass of the fish populations [108].

While fish growth conditions from the length–weight analysis provide basic information about the growth patterns of the fish stocks, few caveats to the conclusions are warranted. First, the positive allometric growth found in the upstream of the Cambodia Mekong system may also be affected by the species' different reproductive stages being sampled (e.g., gonad development) and thus the weight of the study species because many white fish are known to spawn in the early wet season and the data used in this study did not allow for sex disaggregation prior to the length–weight analysis. Second, the analysis could also be constrained by the sampling efforts and season (e.g., wet versus dry seasons) where fish samples used for this study were combined from several types of fishing gears (with stationary gillnets and traps being the most common gears) and across fishing seasons with different feeding and growth conditions. Third, different phases of fish growth (e.g., by age class) may also influence the slope b values in the LWR. These constraints are widely discussed e.g., [60,109,110]. Therefore, future length–weight investigations may be beneficial and could address these limitations.

4.4. Management Implications

Inland fish assemblage composition is broadly similar across the country because of large-scale seasonal migration between critical habitats. This becomes a challenge for fisheries managers who are trying to prioritize fish species that utilize specific habitats for fisheries management and conservation interventions. Our results indeed provide the most current baseline information about spatial and seasonal distribution patterns in the fish diversity and assemblage structure as well as the statuses of key indicative fish stocks in the inland waters of Cambodia. We have successfully demonstrated to ecologically discriminate the Cambodia inland fish assemblages into four distinct clusters based on the assemblage composition similarities. Indicator species characterizing each assemblage cluster were also prioritized and grouped according to their migration patterns and statuses in the IUCN Red List. Lower floodplain fish assemblages (cluster 1, 2) were characterized mainly by black and grey fish; whereas, the upper Mekong fish assemblages (cluster 3, 4) were represented mostly by white fish. While areas associated with fish assemblage cluster 1 (northern TSL) serve mainly as feeding/rearing grounds, cluster 4 (Mekong-3S system) acts as both the dry season refuge and spawning ground for many Mekong migratory fish, and cluster 2 (KD) and 3 (KR) play a critical connectivity role as a seasonal fish migration corridor among these important habitats for many (white and grey) fish to complete their life cycles. Therefore, fish diversity monitoring, management and conservation planning should be guided by these research results, considering (i) the key critical habitats of ecologically distinct fish assemblages, (ii) prioritized key indicator species representing each different fish assemblage and the habitats they inhabit, and (iii) the connectivity necessary for seasonal fish migration among these critical habitats. Similarly, given limited resources, combating illegal fishing practices should be prioritized according to the critical habitats where inland fish breed, seek refuge, and feed. Also, since the current fisheries management in Cambodia is in favor of the establishment of viable and operational community fisheries (CFis) as indicated in the strategic planning framework for fisheries 2015–2024 [111], the priority of support should be given to the CFis situated in these fish critical habitats. This study also illustrated the importance of high spatial resolution fish data in understanding the

spatial variation in fish diversity, distribution and assemblage structure as compared to the temporal, time-series fish data for assessing the fisheries trends at some specific sites such as the dai fishery [38].

Moreover, we found that fish from lower floodplain assemblages were experiencing negative allometric growth (indicative of poor environmental conditions or overfishing), compared to the upper Mekong fish assemblages where more than 50% of the study indicative fish stocks had either isometric or positive allometric growth (suggesting healthier stocks). This information is essential for inland fish biodiversity mapping, which may warrant protection for areas/habitats with healthier fish population (Cambodia upper Mekong system) or restoration for areas/habitats (i.e., lower floodplains including the TSL) with degraded fish assemblages. Further, the study elucidated that fisheries in the lower floodplains such as the TSRL depend upon upstream healthy fish stocks i.e., white and grey fish that likely originate elsewhere outside the Tonle Sap sub-basin e.g., the (Cambodia upper) Mekong River, but they replenish the lower floodplain fish stocks through injecting new recruits every year through their seasonal reproduction and migrations. Likewise, healthy inland fish in the (upper) Mekong also depend on good habitat quality in the lower floodplains and the connectivity (free flowing river) in cluster 2 and 3 to access the critical habitats in the upstream Mekong and lower floodplain for spawning and dry season refuge as well as for rearing and feeding during their life cycles. Therefore, anthropogenic activities e.g., infrastructure development in the Mekong River, its tributaries and lower floodplains that alter seasonal flow pulses, obstruct the free flowing river, and disconnect these (critical) habitats are highly likely to cause long-term, detrimental effects on many wild, native inland fish populations in Cambodia and possibly the Lower Mekong Basin.

Supplementary Materials: The following are available online at <http://www.mdpi.com/2073-4441/12/9/2506/s1>. Table S1: Geographical positions of the study sites, S2: Results of Permutational Multivariate Analysis of Variance (PERMANOVA), contrast pairwise tests between different levels of factor (cluster and season), Table S2.1: PERMANOVA test on the dissimilarity in the assemblage composition among the four clusters identified for the inland waters in Cambodia, Table S2.2: Contrast pair-wise tests between pair of clusters for all assemblage clusters identified for inland waters of Cambodia, Figure S2.3: Boxplots showing Nonmetric Multidimensional Scaling (NMDS) site scores comparing the four factor levels of fish assemblage cluster, Table S2.4: PERMANOVA test on the dissimilarity in assemblage compositions between wet and dry seasons, Table S2.5: Contrast pair-wise tests between different factor level of season (Wet and Dry season), Figure S2.6: Boxplots showing Nonmetric Multidimensional Scaling (NMDS) site scores comparing the two factor levels of wet versus dry seasons, Table S2.7: Contrast pair-wise tests between the different factor levels of cluster (dry season), Table S2.8: Contrast pair-wise tests between the different factor levels of cluster (wet season), Table S3: List of indicator species by cluster and season characterizing freshwater fish assemblages in Cambodia, Table S4: List of fish species names by orders and families.

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