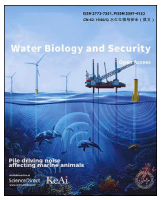
Water Biology and Security xxx (xxxx) xxx

Contents lists available at ScienceDirect

Water Biology and Security

journal homepage: www.keaipublishing.com/en/journals/water-biology-and-security



Research Article

Functional dynamics of the world's largest indiscriminate fishery over the last two decades

Ratha Chea[a,*], Thierry Oberdorff[b], Kong Heng[c], Solida Tan[d], Paul Baudron[e], Pascal Laffaille[b], Gaël Grenouillet[b,f]

[a] Laboratory of Freshwater Ecology (ECOFRESH), Department of Science, Faculty of Science Education, Battambang Teacher Education College (BTEC), Sangkat Ratanak, 021402, Battambang City, Cambodia
[b] Centre de Recherche sur la Biodiversité et l'Environnement (CRBE), Université de Toulouse, CNRS, IRD, Toulouse INP, 31062, Toulouse, France
[c] Inland Fisheries Research and Development Institute (IFReDI), Fishery Administration, Ministry of Agriculture, Forestry and Fisheries, 120101, Phnom Penh, Cambodia
[d] Faculty of Economics and Business Sciences, Università del Sannio, 82100, Benevento, Italy
[e] University of Montpellier, IRD, UMR G-Eau, 34196, Montpellier, France
[f] Institut Universitaire de France, 75231, Paris, France

ARTICLE INFO

Keywords:
Fishing pressure
Long-term trend
Fish community structure
Fish size
Functional guilds
Life history strategies
Tonle sap lake

ABSTRACT

Understanding how biological diversity responds to global environmental change is a central question in modern ecology. However, our ability to predict how the functional structure of fish communities responds to human disturbances remains limited. This study investigated the long-term trends in fish community diversity and functional structure in the Tonle Sap Lake system (Mekong Basin, Cambodia), which has the world's largest indiscriminate fishery. Using the longest available fish monitoring dataset from the *dai* (stationary trawl) fishery (2003–2022), we applied multivariate analysis on relative abundance data to examine temporal changes in both taxonomic (species richness, inverse Simpson index) and functional (fish maximum body length, functional guild, life history strategy) community structure. Our results reveal two key findings: (1) a clear and concerning decline in fish community diversity and change in community composition over the past two decades, and (2) novel evidence of long-term shifts in functional traits, particularly in fish functional guilds and life history strategies. Specifically, the fish community shifted from long-to short-distance migrant species, and from floodplain spawners to generalist guilds and estuarine/marine visitors. Additionally, large-bodied species with equilibrium and periodic strategies have been replaced by smaller-bodied, fast-growing, opportunistic species. These findings suggest a temporal shift from K-selected to r-selected communities. New management strategies, including reducing fishing pressure, are urgently needed to preserve the ecosystem function and ensure the long-term sustainability of Tonle Sap Lake's fishery.

1. Introduction

Understanding how ecological communities respond to environmental and anthropogenic pressures remains a central question in predicting changes within freshwater ecosystems. Functional ecology provides a valuable framework for assessing these dynamics, as it focuses on species' ecological traits and on how these traits shape ecosystem processes (Cadotte et al., 2011; Mouillot et al., 2013; Petchey and Gaston, 2006). By linking species' traits to environmental gradients and community responses, functional approaches often provide deeper insights into the mechanisms underlying biodiversity change and resilience (Lavorel and Garnier, 2002; McGill et al., 2006). These trait-based perspectives are particularly useful in investigating how ecosystem functioning is affected by compositional changes in communities subjected to environmental disturbance (Mouillot et al., 2013; Soininen et al., 2007).

Global biodiversity is facing unprecedented challenges due to the accelerating impacts of climate change, habitat degradation, pollution, and unsustainable exploitation of natural resources (Díaz et al., 2019; IPBES, 2019). These rapid changes undermine the stability and

* Corresponding author.
E-mail addresses: ratha.chea@btec.edu.kh (R. Chea), thierry.oberdorff@ird.fr (T. Oberdorff), kong_heng2002@yahoo.com (K. Heng), solidatan@gmail.com (S. Tan), paul.baudron@ird.fr (P. Baudron), pascal.laffaille@ensat.fr (P. Laffaille), gael.grenouillet@utoulouse.fr (G. Grenouillet).

Peer review under the responsibility of Editorial Office of Water Biology and Security.

https://doi.org/10.1016/j.watbs.2026.100552
Received 20 June 2025; Received in revised form 13 November 2025; Accepted 28 November 2025
Available online xxxx

Please cite this article as: Chea, R. et al., Functional dynamics of the world's largest indiscriminate fishery over the last two decades, Water Biology and Security, https://doi.org/10.1016/j.watbs.2026.100552

resilience of ecosystems, which are critical for sustaining the goods and services essential to human well-being (Cardinale et al., 2012). Addressing this crisis requires integrated collective efforts to mitigate the drivers of change while promoting conservation and sustainable management, ensuring that biodiversity can continue to support human well-being and global health in a changing world (IPBES, 2019; Rockström et al., 2009). In this context, freshwater ecosystems emerge as particularly vulnerable yet vital components of global biodiversity (Dudgeon, 2019; Oberdorff, 2022). Freshwater fish communities, in particular, are among the most important elements because of their ecological roles and sensitivity to environmental disruptions (Reid et al., 2019). As such, they provide a useful perspective for analysing the wider effects of biodiversity loss and for developing long-term management strategies. Moreover, investigating fish diversity, functional traits, and community dynamics provides holistic insights into how aquatic systems respond to pressures such as pollution, habitat fragmentation, climate change, and overexploitation (Olden et al., 2004; Poff et al., 2006). Consequently, fish communities usually serve as both indicators of ecosystem health and as drivers of ecological processes such as nutrient cycling and food web stability (Jackson et al., 2001). Therefore, comprehensive assessments of fish communities not only reveal the status of biodiversity but also inform sustainable fisheries management and conservation strategies that are essential for protecting ecosystem services and food security for millions of people, particularly in developing regions (Allan et al., 2005; Welcomme et al., 2010).

Despite growing interest in freshwater biodiversity over recent decades, significant knowledge gaps remain regarding the long-term temporal dynamics of taxonomic and functional diversity in fish communities, particularly in large floodplain ecosystems such as the Mekong River Basin, which supports over 66 million people (Ziv et al., 2012). While long-term monitoring of fish abundance and composition has provided valuable insights into the effects of anthropogenic pressures on community diversity and structure (Kang and Huang, 2022), relatively few studies have examined how functional diversity has changed over time, though several studies have documented the impacts of environmental pressures on the body size, trophic position, and migration status of the Mekong fishes (Chea et al., 2020, 2021; Chevalier et al., 2023; Montaña et al., 2020; Nuon et al., 2025; Ou et al., 2017; Zhang et al., 2021). However, comprehensive functional analyses that explicitly link fish community structure to environmental disturbances remain limited. This gap is critical, as functional traits are directly linked to ecosystem processes and stability. Changes in these traits may indicate ecosystem health degradation, even in cases where species diversity appears stable (Mouillot et al., 2013; Villéger et al., 2008). For instance, functional homogenization, where generalist species increasingly dominate the system, reduces the ability of the system to withstand or recover from further environmental disturbances (Clavel et al., 2011; Olden et al., 2006). However, empirical evidence of trait-based temporal dynamics is quite challenging to obtain, particularly in the Mekong region, where functional trait databases are limited (Sabo et al., 2017). Thus, addressing this knowledge gap through trait-based community studies is essential for understanding how long-term anthropogenic disturbances, such as habitat fragmentation by dams, overfishing, and climate change, have changed species composition and ecosystem function (Lamberts, 2008; Orr et al., 2012).

In this context, Tonle Sap Lake, known as one of the world's most productive inland fisheries and a hotspot of fish diversity, is now facing significant threats from overfishing, hydrological changes due to upstream dam development, deforestation, and water pollution (Arias et al., 2014; Kummu and Sarkkula, 2008). These multiple stressors have profoundly affected flood pulse dynamics, fish community composition, fishery yields, and overall ecosystem function (Halls and Burnhill, 2009; Ziv et al., 2012). Consequently, biodiversity loss and declining fishery productivity underline the urgent need for integrated management strategies that balance ecological conservation and socio-economic development (Bonheur and Lane, 2002; Kang and Huang, 2022). For instance, Ngor et al. (2018) revealed that over 78 % of fish species in Tonle Sape Lake are experiencing significant declines, with larger-bodied species being disproportionately affected. This trend, attributed to diverse anthropogenic pressures including overfishing (Ngor et al., 2018), suggests a shift toward smaller-bodied, more generalist species, raising concerns about the long-term sustainability of the ecosystem's function and having implications for sustainable fisheries management (Mouillot et al., 2014; Villéger et al., 2017).

Life history strategies, particularly r/K selection strategies (Pianka, 1970), provide a fundamental framework for examining how fish communities respond to environmental stressors. K-selected species are generally larger-bodied, longer-lived, and slower to mature, producing fewer offspring with greater parental investment. These traits are suitable for living in stable, predictable environments but make them more vulnerable to disturbance. In contrast, r-selected species are typically smaller-bodied, shorter-lived, and fast-reproducing, enabling rapid population growth in variable or degraded conditions (Pianka, 1970; Winemiller and Rose, 1992). Expanding on this framework, Winemiller and Rose (1992) proposed a triangular life history model specific to fishes, comprising opportunistic, periodic, and equilibrium strategies. Opportunistic species are small, fast-reproducing, and suited to highly disturbed habitats; equilibrium species are larger, with delayed maturity and stable recruitment in predictable environments; and periodic strategists exhibit high fecundity and seasonal reproduction, and are adapted to fluctuating systems like floodplains. As anthropogenic pressures such as overfishing, habitat fragmentation, and hydrological alteration intensify, communities shift away from K-selected and periodic strategists toward opportunistic species. This transition simplifies the life history strategies present, reducing ecological complexity and resilience (Mims and Olden, 2013; Winemiller, 2005).

In similar tropical freshwater systems in Amazonia and Africa, fishing pressure can substantially alter ecosystem dynamics by reducing populations of large-bodied and predatory species (Castello et al., 2013; Welcomme et al., 2006). This often results in shifts in community composition, trophic imbalances, and the loss of key ecological functions such as nutrient cycling, ecosystem resilience, and long-term fisheries sustainability (Arantes et al., 2019a, 2022; Winemiller et al., 2016). Indeed, both taxonomic and functional structure provides useful information on community dynamics. Taxonomic diversity provides a picture of which species occur in a given community (Magurran, 2013). Functional diversity, on the other hand, captures the range and distribution of a species' ecological characteristics, providing information about the roles that species play in ecosystems (Mouillot et al., 2013; Petchey and Gaston, 2006). Relying solely on taxonomic data may miss major ecological shifts, especially when species turnover involves taxa with similar functional roles. In contrast, functional metrics can identify changes in ecosystem functioning that species counts alone cannot, such as the loss of essential ecological traits (Villéger et al., 2008). Combining these two biodiversity components may provide better knowledge about ecosystem change and resilience, allowing for more effective conservation and ecosystem-based management strategies (Díaz et al., 2007; IPBES, 2019).

Our study investigated how the taxonomic and functional diversity of one of the world's largest indiscriminate fisheries, i.e., the Tonle Sap Lake fisheries, has changed during the last two decades. We focused specifically on the temporal change in the fish community's functional structure, i.e., functional guilds and life history strategies, beyond the documented declines in body size and trophic level already reported by Ngor et al. (2018). We hypothesized that increased anthropogenic stressors within Tonle Sap Lake over the last two decades, notably fishing pressure, not only reduced taxonomic diversity and altered community composition but also drove a shift in functional structure, from a K-selected to an r-selected fish community.

2. Materials and methods

2.1. Fish data

This study relied on the most extensive time-series dataset of fish catch records from the Mekong River Commission's standardized monitoring program, covering 2003 to 2022, based on data collected from the industrial-scale *dai* (stationary trawl) fishery operating along the Tonle Sap system in Cambodia. This seasonal fishery operates annually for six months, from October to March, at a fixed location on the river approximately 30 km north of Phnom Penh (Fig. 1) (Halls et al., 2013). The operation coincides with the reversal of water flow from Tonle Sap Lake back to the Mekong River at the end of the rainy season (MRC, 2005). Each year of operation is referred to as a fishing season. For instance, the 2003 fishing season began in October 2003 and ended in March 2004, while the 2004 season spanned from October 2004 to March 2005. This seasonal structure remained consistent throughout the study period from 2003 to 2022, although the duration of individual seasons could slightly vary among years. The *dai* fish catch data were obtained through the routine fisheries monitoring program supported technically and financially by the Mekong River Commission. *Dai* are a rather indiscriminate type of fishing gear; the gear's mesh size tapers from about 15 cm at the mouth to 1 cm at the codend. Sampling procedures and catch assessments for the *dai* fishery followed the general methodology and formula described in Stamatopoulos (2002). Fish data were collected both as total abundance (the number of individuals per species) and as catch per unit effort (CPUE) expressed in kilograms per unit effort (where a unit = one haul).

Monthly catch estimates were based on CPUE, which included CPUE for individual species and data on fishing effort, such as the number of daily hauls conducted by a *dai* unit in each stratum, the lunar period, and the *dai* type during each month of the fishing season. Although some reports noted increases in hauling duration during peak fish migration periods (Halls et al., 2013), the overall *dai* fishing effort (number of *dai* units, gear dimensions, fishing season, and fishery location) remained relatively stable throughout the study period. Further technical specifications of the *dai* gear are detailed in Loeung et al. (2003), while comprehensive descriptions of sample sizes, sampling protocols, data collection forms, species composition, fishing effort, catch estimation formulas, and the database system for data storage and management are available in Halls et al. (2013). The current *dai* fishery database includes records of 140 species collected over the 20-year monitoring period from 2003 to 2022. A detailed protocol for data collection and CPUE calculation, based on the methodology described in Halls et al. (2013), is provided in Supplementary Material S1 (Fig. S1, Table S1).

2.2. Functional trait data collection

Three functional traits (maximum body length, functional guild, and life history strategy) were chosen for their relevance in assessing community responses to environmental disturbances, particularly those driven by anthropogenic impacts. Maximum body length serves as a proxy for species trophic level and vulnerability to exploitation. Functional guild reflects feeding habitats and migratory behavior, both of which are sensitive to hydrological changes. Life history strategy captures reproductive trade-offs and indicates community resilience to disturbance. Together, these traits are essential for characterizing the functional response of fish communities to human-induced environmental change. Information on the three key functional traits was compiled from different sources. Maximum body length (maxL) for all species was obtained from FishBase (Froese and Pauly, 2025). Functional guild classifications were obtained from the Mekong River Commission, based on the framework established by Welcomme et al. (2006), which categorizes Mekong fish species into 10 functional groups based on their reproductive strategies and preferred habitat (Supplementary Material S2, Table S2) (MRC, 2021). Following the most recent classifications (MRC, 2021; Nuon et al., 2025), the 140 species included in our dataset were assigned to 9 functional guilds (Supplementary Material S2, Tables S2–S3): G1: rhithron residents (10 species), G2: long-distance white fishes (11 species), G3: short-distance white fishes

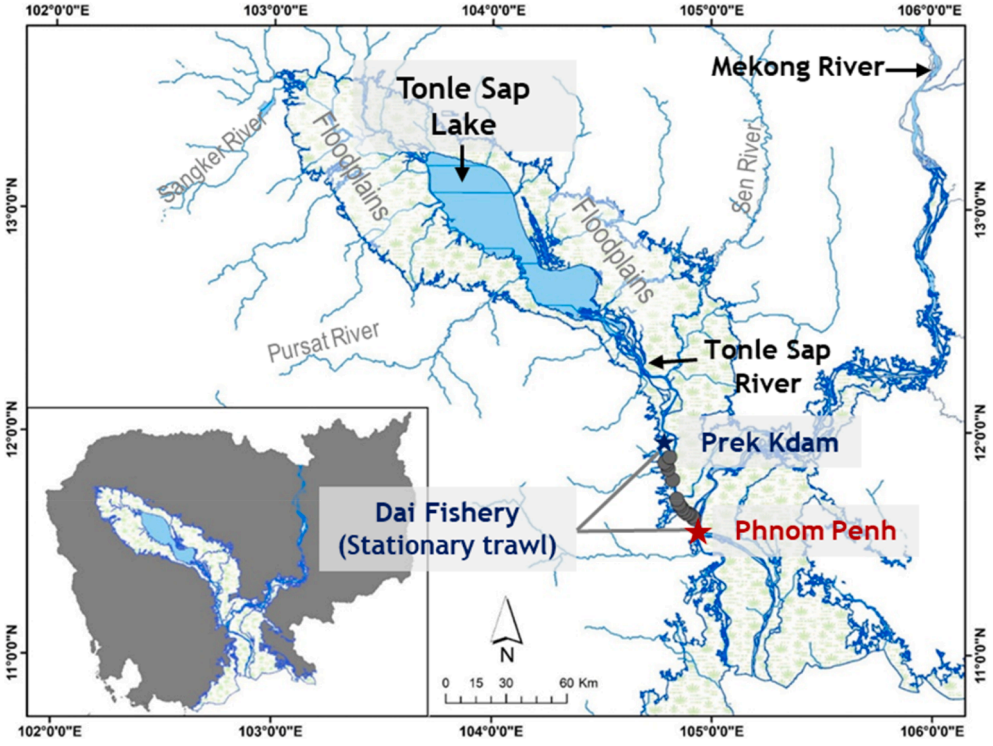


Fig. 1. Tonle Sap Lake and geographical location of *dai* (stationary trawl) fishery monitoring sites (grey circles). Dark grey areas show land (Cambodian provinces) and blue lines indicate floodplain boundaries.

(40 species), G4: floodplain spawners or grey fishes (24 species), G5: generalist fishes (15 species), G6: black fishes (14 species), G7: estuarine residents (18 species), G8: anadromous fishes (1 species), and G10: marine visitors (7 species). The single species in the anadromous functional guild (G8), *Pangasius krempfi*, was excluded from subsequent analyses due to its low representation, which could bias the functional group comparisons. Additionally, no species in our dataset belonged to the catadromous functional guild (G9).

Life history strategies were gathered from Chea et al. (2020), who described the temporal change in fish community structure within Tonle Sap Lake. These strategies follow the life history continuum proposed by Winemiller and Rose (1992), which classifies species into three categories: opportunistic, periodic, and equilibrium, based on their fecundity, juvenile survivorship, and reproductive age (Winemiller, 2005; Winemiller and Rose, 1992). Life history strategy data were available for 74 species (53 %); the remaining 66 species were excluded from the analyses involving this classification. These 74 species collectively accounted for more than 89 % of the total catch abundance over the 20-year period, thus allowing us to capture the dominant ecological trends within the fish community. Similar approaches have been employed in other tropical freshwater systems, where trait data completeness at the species level is often constrained (e.g., Mims and Olden, 2013; Arantes et al., 2019b). Therefore, the life-history strategy data presented here reflect the functional structure of the most ecologically and numerically important species in the Tonle Sap system. Among the 74 species retained, 16 exhibited an equilibrium strategy, 12 were classified as opportunistic, and 46 followed a periodic strategy. Detailed descriptions of functional guilds and life history strategies are provided in Supplementary Material S2 (Table S2).

2.3. Statistical analyses

To examine long-term trends in fish community diversity, the number of individuals per species was first converted to relative abundance. Community-level biodiversity indices, including species richness, the inverse Simpson's index ($\frac{1}{D} = \frac{1}{\sum_{i=1}^{R}\left(\frac{n_i(n_i-1)}{N(N-1)}\right)}$) (where D is the Simpson's index, R is the number of species, n_i is the number of individuals in species i, and N is the total number of species in the sample), and relative abundance, were then computed using the "base" and "vegan" packages in R (Oksanen et al., 2025; R Core Team, 2024). Long-term (inter-annual) trends in diversity metrics were assessed using linear models with year (2003–2022) as the explanatory variable, while intra-seasonal (monthly) variation was analyzed using Kruskal-Wallis tests with month (October–March) capturing temporal changes within a fishing season.

To assess temporal shifts in fish community composition (relative abundance) over the 20-year monitoring period, we applied a principal component analysis (PCA) to the relative abundance data. The table was structured with species in columns and years in rows. The relative abundance data were Hellinger-transformed prior to PCA to reduce the influence of dominant species and improve suitability for ordination. PCA summarizes multivariate community data into interpretable axes, in our case resulting in loadings of each species' relative abundance onto the principal components. This allowed us to identify key species driving among-year patterns in abundance and provided a consistent and informative framework for investigating long-term changes in the taxonomic composition and functional traits of the Tonle Sap fish community. The temporal trajectory of the fish community was captured in the first principal component (PC1), which was subsequently used as an explanatory variable representing temporal community change. PCA computations and visualizations were performed using the "ade4″, "vegan", and "factoextra" packages in R (Dray and Dufour, 2007; Kassambara and Mundt, 2020; Oksanen et al., 2025; R Core Team, 2024).

To investigate how functional traits responded to temporal shifts in community composition, statistical tests were conducted using species' relative abundance scores on PC1 as the explanatory variable. For qualitative traits (i.e., functional guilds and life history strategies), we applied non-parametric Kruskal-Wallis tests, while maximum body length (maxL) was analyzed using a linear model. Post-hoc pairwise comparisons were conducted using Dunn's test with the Holm–Bonferroni adjustment to control the family-wise error rate and to identify significant differences among trait groups (Dunn, 1964). Only trait groups with sufficient sample size were included in statistical tests; specifically, functional guild G8 was excluded from the tests because it contained only a single species. All analyses were performed in R version 4.4.1 (R Core Team, 2024).

3. Results

3.1. Trends in fish community diversity

The 20-year dataset (2003–2022) contained 140 fish species belonging to 39 families and 13 orders. Cypriniformes (44 %), Siluriformes (24 %), and Perciformes (18 %) represented 86 % of the total species, while Beloniformes, Clupeiformes, Synbranchiformes, and Pleuronectiformes accounted for most of the remaining 14 %. Cyprinidae was the most species-rich family (37 % of all species), followed by Bagridae, Pangasiidae, and Siluridae, which together accounted for 55 % of the total species (Supplementary Masterial S2, Fig. S2). Both species richness and the relative abundance of the fish community remained stable over the 20 years (Supplementary Material S2, Fig. S3). However, there was a significant negative trend for the inverse Simpson's diversity index over time ($R^2 = 0.08$, p-value $= 0.005$, Fig. 2a), indicating a gradual reduction in community diversity, likely reflecting increasing dominance by a few species and a loss of evenness in the fish community. Furthermore, the long-term data indicated that changes in fish community diversity were more pronounced within fishing seasons than among years. The reserve flow from Tonle Sap Lake to the Mekong River, which typically occurs from October to March, had a considerable impact on monthly averages of species richness, inverse Simpson's index, and relative abundance (Fig. 2b–d). As a result, both the diversity index and species richness peaked in November and progressively declined until March, when diversity reached its lowest level (Fig. 2b and c). In contrast, relative abundance peaked between December and January, then gradually declined in parallel with the decrease in diversity (Fig. 2d).

3.2. Temporal trends in fish community composition

Temporal changes in fish community composition were captured along the first axis of the PCA (PC1), with the first two axes explaining 29.7 % of the total variance (Fig. 3a). There was a clear temporal change along PC1, with earlier years associated with negative scores and recent years with positive scores (Fig. 3b). Over time, the fish community composition shifted from being dominated by large-to medium-sized catfish such as *Belodontichthys truncatus* (betr), *Wallago attu* (waat), *Pangasius larnaudii* (pala), *P. conchophilus* (paco), and *Pangasianodon hypophthalmus* (pahy), large carps like *Cyclocheilichthys enoplos* (cyen) and *Hypsibarbus malcolmi* (hyma), critically endangered species such as *Catlocarpio siamensis* (casi) and *Helicophagus waandersii* (hewa), and bagrids like *Hemibagrus nemurus* (hene) and *Mystus bocourti* (mybo), to being replaced by small-bodied species like *Henicorhynchus cryptopogon* (hecr), *H. siamensis* (hesi), *Paralaubuca barroni* (paba), *Xenentodon cancila* (xeca), *Rasbora borapetensis* (rabo), and *Yasuhikotakia modesta* (yamod). In addition, earlier years appeared to have more diverse communities, with a greater contribution of numerous migratory species compared to later years (Fig. 3a and b; Table S2; Supplementary Material S2). While inter-annual variability in community composition was high, the apparent homogenization over the last decade (2014–2022) reflects the dominance of a few species in fish communities (Fig. 3a and b).

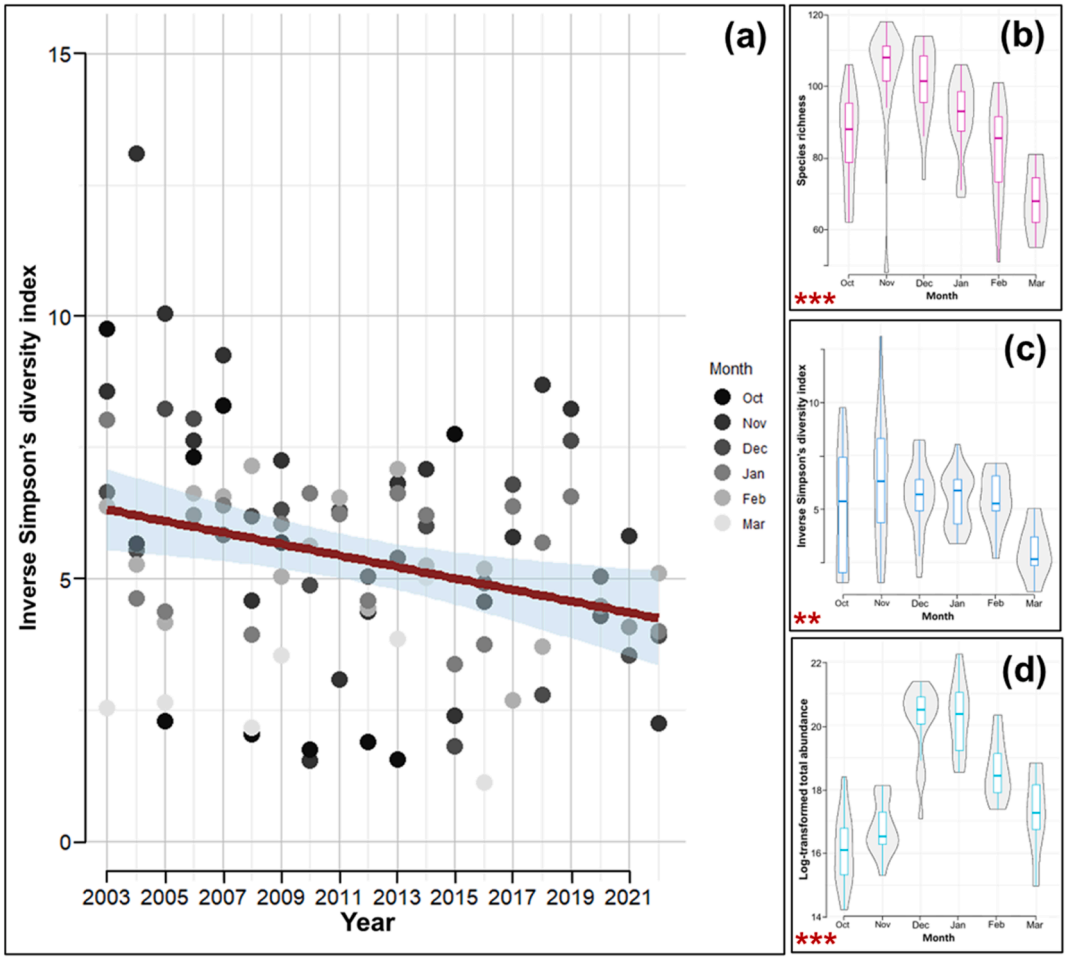


Fig. 2. Long-term trends in fish community diversity in the Tonle Sap system from 2003 to 2022. (**a**) Yearly change in the inverse Simpson's diversity index ($R^2 = 0.08$, $p = 0.005$). Seasonal variation within fishing seasons in (**b**) species richness, (**c**) inverse Simpson's diversity index, and (**d**) log-transformed total abundance. Violin plots depict the distribution of values for each month. The significance level from a Kruskal–Wallis test is indicated by asterisks ($*p < 0.05$, $**p < 0.01$, $***p < 0.001$).

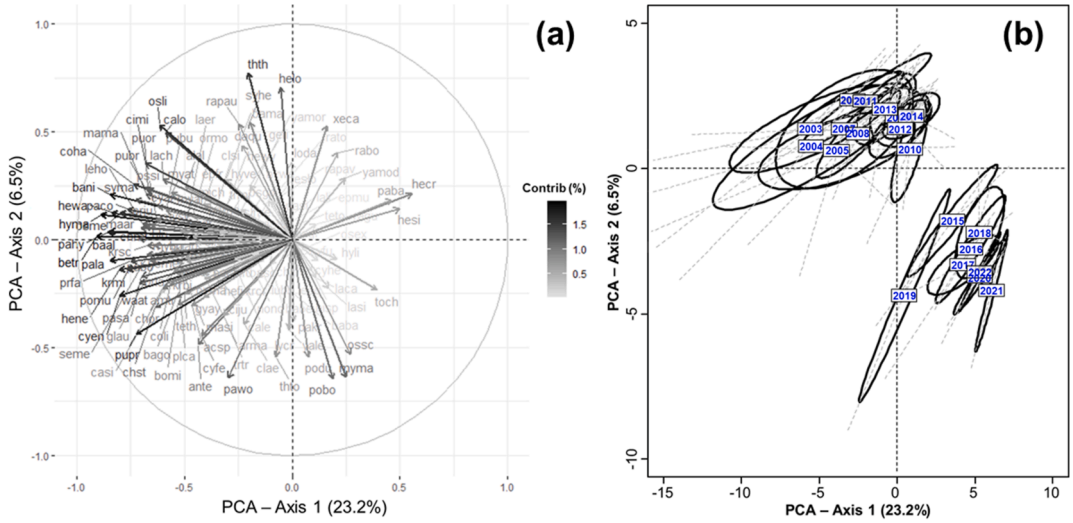


Fig. 3. Temporal change in fish community composition over 20 years (2003–2022) in the Tonle Sap system. (**a**) PCA correlation circle showing variation in species composition. A detailed description of fish codes is provided in Supplementary Material S2 (Table S2). (**b**) Temporal pattern of the fish community from 2003 to 2022. Ellipses indicate 68 % confidence intervals (approximately ±1 standard deviation) around the centroids for each year, with dotted lines showing the yearly centroids.

3.3. Temporal changes in functional traits

Long-term data showed a shift in functional traits of the Tonle Sap fish communities. Specifically, the temporal changes in fish communities were characterized by a decline in the maximum body size of the species within the community (R^2 = 0.09, p-value <0.001) (Fig. 4a). This means the community, once dominated by large-bodied species, has gradually transitioned to one dominated by smaller-sized species. In addition to the reduction in body size, temporal patterns revealed a shift in both functional guilds and life history strategies (Fig. 4b and c). The community was originally characterized by a diversity of migratory and specialist species, e.g., G2 (long-distance migrant), G3 (short-distance migrant), and G4 (grey fish or floodplain spawner), but these were gradually replaced by generalists (G5), rithron residents (G1), estuarine species (G7), and marine visitors (G10) (χ^2 = 22.07, p-value = 0.002; Fig. 4b). Consequently, life history strategies within the community significantly shifted from predominantly equilibrium and periodic strategists to a dominance of opportunistic strategists (χ^2 = 12.42, p-value = 0.001; Fig. 4c).

4. Discussion

The observed decline in the fish diversity index, despite stable species richness and relative abundance, provides strong evidence of long-lasting fishing pressure on the Tonle Sap system over the past two decades. Beyond changes in diversity and composition, the fish community has experienced significant shifts in functional traits, where large-bodied, commercially valuable species have declined, while smaller, opportunistic species have increased (Chea et al., 2020; Chevalier et al., 2023). These changes reduced community evenness and weakened ecosystem functioning and resilience, even though overall species richness has remained relatively stable (Chhuoy et al., 2023).

Seasonal variation in fish community diversity and abundance was also evident, reflecting the flood-pulse dynamics of the Tonle Sap system. Diversity and species richness increased following the onset of flow reversal in October and peaked in November, while relative abundance reached its maximum in December or January. This temporal lag likely reflects the delayed response of migratory fishes to hydrological changes, particularly among small-bodied cyprinids such as *Henicorhynchus* and *Paralaubuca* (Chea et al., 2020).

These findings are consistent with the role of flood dynamics in driving fish community structure and migration patterns in the Tonle Sap system (Arias et al., 2013; Chea et al., 2020). Despite increased fishing pressure, these seasonal trends suggest that hydrological cues continue to play a dominant role in shaping community dynamics. However, potential interactions between fishing intensity and flood timing may influence migration behavior, peak abundance periods, and species composition, highlighting the need for further research into these complex ecological interactions.

Over the past two decades, the Tonle Sap system has undergone significant environmental and anthropogenic changes. Total catch has remained stable (Supplementary Material S2, Fig. S4), even though the number of active *dai* units declined from 66 in 2014 to 44 in 2022 (Chevalier et al., 2023). This stable catch has been sustained alongside an extension of the fishing season to 7 or 8 months (October to April or May) in some years, such as the 2021–2022 fishing season, compared to the traditional 6-month season (October to March) (MRC, 2019). Concurrently, flood dynamics have become more variable in both timing and extent, largely due to upstream dam construction and shifting precipitation patterns (Supplementary Material S2, Fig. S5) (Chen et al., 2021; Kummu and Sarkkula, 2008; Ziv et al., 2012).

Climate change projections suggest further alterations in flood onset and duration, which may disrupt fish migratory cues and reduce habitat availability (Morovati et al., 2023). These changes will most probably lead to the decline of long-distance migratory species and floodplain spawners. Together, these interconnected anthropogenic changes will influence fish community structure and productivity, highlighting the urgent need for integrated monitoring and adaptive management strategies (MRC, 2019).

Moreover, our long-term data reveal that fishing pressure has probably driven a substantial shift in the functional composition of the Tonle Sap fish community. Historically dominated by large- and medium-sized species, the community is increasingly composed of smaller-bodied taxa. Ngor et al. (2018) documented a decline in average fish size and trophic level, exemplifying the process of "fishing down the food web". Our findings support this pattern and reveal a shift in functional guild composition, with long- and short-distance migratory species (G2 and G3) and floodplain spawners (G4) progressively replaced by generalists (G5) and estuarine (G7) and marine visitor species (G10) (Chevalier et al., 2023).

This last pattern confirms the process of "fishing down the food web", with high trophic level species strongly reduced in abundance and increasingly dominated by lower trophic level, fast-reproducing taxa. While some mid-trophic species persist, the overall trend is a clear shift

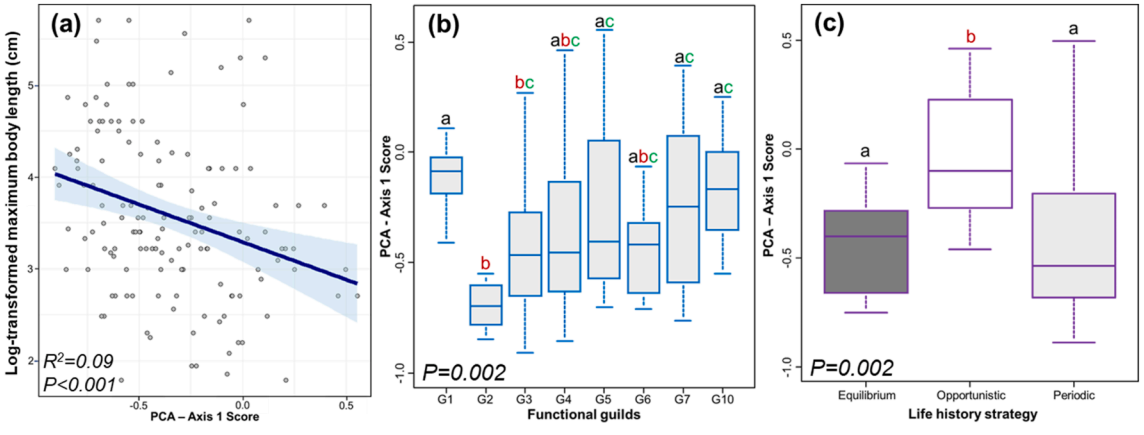


Fig. 4. Temporal change of fish community functional traits in the Tonle Sap system between 2003 and 2022. (**a**) Change in the maximum body length of fish species; (**b**) shifts in functional traits; and (**c**) changes in life history strategies. The solid blue line in panel (**a**) represents the trend in maximum body length fitted with a generalized linear model (R^2 = 0.09, p < 0.001). PCA Axis 1 (PC1) scores represent species scores from the first axis of the PCA, summarizing the main temporal change in fish community structure. Boxplots in panels (**b**) and (**c**) show the variation in PC1 scores, summarizing shifts in functional guilds and life history strategies, respectively. Boxes indicate the interquartile range with median PC1 scores, while shading in panel (**c**) denotes life history strategies: dark grey = equilibrium, light grey = periodic, and white = opportunistic. Groups with different letters are significantly different (Kruskal-Wallis, p < 0.05; Dunn's post-hoc test).

toward lower trophic levels, suggesting a loss of ecosystem complexity and resilience. Similar patterns have been observed in other freshwater systems worldwide. For example, in the Amazon Basin, overfishing has led to declines in large migratory catfish and a rise in smaller, fast-reproducing species, altering community structure and ecosystem function (Castello et al., 2013).

In the Mekong River, intense fishing pressure has similarly reduced populations of large-bodied species, favoring opportunistic fishes that can withstand disturbance and exploit altered habitats (Ziv et al., 2012). In African lakes such as Lake Victoria, intensive fishing and the introduction of non-native species have shifted communities toward smaller, resilient fishes, disrupting food webs and ecosystem services (Hecky et al., 2010; Ogutu-Ohwayo, 1990). In our case, the life history strategies of the fish community have shifted from predominantly K-selected species, characterized by equilibrium and periodic reproductive strategies, to r-selected opportunistic species.

Equilibrium strategists, such as *Channa* spp., *Notopterus notopterus* (nono), and *Anabas testudineus* (ante), are top predators that invest heavily in producing few, well-protected offspring, thereby playing critical roles in maintaining ecosystem stability (Ngor et al., 2018; Winemiller and Rose, 1992). Periodic strategists, including *Pangasianodon gigas* (pagi), *Boesemania microlepis* (bomi), and *Cyclocheilichthys enoplos* (cyen), reproduce seasonally with high fecundity and contribute substantially to ecosystem productivity and food security (Chevalier et al., 2023; Winemiller, 2005). However, these groups are increasingly being replaced by opportunistic species such as *Parambassis* spp., *Paralaubuca* spp., and *Rasbora* spp., which are small-bodied, fast-growing, highly productive, and well adapted to disturbed and fluctuating environments (Chevalier et al., 2023; Ngor et al., 2018).

This shift in functional traits and life history strategies has profound ecological implications, including reduced diversity, simplified trophic structures, and threats to the long-term sustainability of fisheries and the livelihoods of millions of people reliant on the Tonle Sap system (Chhuoy et al., 2023; Pauly et al., 1998). Despite these insights, significant knowledge gaps remain, especially regarding life history strategies, which are still unknown for nearly half the species in the system (Baran et al., 2007).

However, our 74 included species accounted for over 89 % of the total catch, effectively capturing the dynamics of the most abundant species. Focusing on dominant and well-characterized species provides fundamental insights into broad-scale functional patterns in highly diverse, data-limited tropical ecosystems. Such approaches have been widely applied in many tropical, neotropical, and Afrotropical regions, where high diversity and limited species trait data lead to a focus on key taxa to describe community ecological dynamics (Arantes et al., 2019b; Chea et al., 2020; Villéger et al., 2010; Walsh et al., 2022). For instance, Arantes et al. (2019b) used functional traits of dominant Amazonian fishes to detect shifts in community structure linked to hydrological alteration and fishing intensity. Similarly, Villéger et al. (2010) demonstrated how trait-based analyses of tropical lagoon fish assemblages could reveal community responses to habitat degradation by using a limited trait database.

Nonetheless, it is important to recognize the limitations and assumptions inherent to fishery-dependent data. For example, temporal changes in *dai* fishery design, the number of active units, and the length of the fishing season may have influenced the observed patterns. However, we strongly believe that the shifts in community composition, functional traits, and life-history strategies reflect ecological responses of the Tonle Sap fish community to long-term fishing pressures rather than being due to sampling effects, as analyses based on relative abundances and dominant species usually remain robust to these potential biases (Froese et al., 2012; Ngor et al., 2018).

Future scientific surveys would help validate these patterns and further strengthen our understanding of the ecological dynamics in this highly diverse freshwater ecosystem (Arantes et al., 2019b; Pauly et al., 1998; Villéger et al., 2010). Further research is essential to develop a comprehensive bio-ecological trait database for Tonle Sap Lake fishes, which will be critical for guiding effective conservation and management interventions in this globally significant freshwater ecosystem.

The long-term changes in fish community diversity, composition, and functional traits in the Tonle Sap systam clearly reflect the impact of the increase in anthropogenic disturbances, including overfishing. These pressures have not only altered species dominance but have also shifted the community toward smaller-bodied, opportunistic species, disrupting the ecological balance and reducing ecosystem resilience. These findings underscore the urgent need for targeted management strategies, informed by ecological data, to safeguard biodiversity, sustain fisheries, and support the livelihoods that depend on this critical freshwater system.

Nevertheless, while our findings reveal significant temporal shifts in fish community structure and functional composition, the drivers behind these changes remain speculative. Although increased fishing pressure is a logical explanation, given the growing human population and evidence from regional reports, it is still a hypothesis that should be confirmed in future studies integrating multi-factorial methodologies. Incorporating long-term data in climate change, hydrological alteration, habitat degradation, fragmentation, and socioeconomic analyses will greatly improve our knowledge of the mechanisms that underlie observed community changes in Tonle Sap Lake and the surrounding system.

5. Conclusions

Long-term time-series data from the Tonle Sap system provides new evidence of the profound impacts that anthropogenic disturbances, including indiscriminate fishing, have on the fish community's diversity, composition, and functional traits. Over the past two decades, these disturbances have emerged as dominant forces reshaping the community, not only in terms of species diversity and composition, but more critically in terms of the community's functional traits and life-history strategies.

Taxonomically, the fish community has undergone a transition from being dominated by long- and medium-distance migratory species to one increasingly composed of generalist, estuarine, and even marine visitor species. This shift reflects a broader ecological response to heavy anthropogenic disturbance, where specialist species are gradually being replaced by more disturbance-tolerant generalists.

Beyond the functional guilds, the temporal changes in fish community was marked by a shift from an equilibrium and periodic strategy community, which are typically large-bodied, slow-growing, and ecologically significant species, to a dominance of small, fast-growing r-selected species. These opportunists thrive in disturbed and variable environments, but their dominance indicates a simplification of trophic structures and reduced ecological stability. This long-term functional shift is unprecedented in the Mekong region and constitutes a critical warning signal for Tonle Sap basin management.

Our findings highlight the urgent need for integrated, science-based management strategies aimed at reducing fishing pressure and restoring the ecological integrity of the Tonle Sap ecosystem. Without timely action, the resilience of the lake's fisheries, and the livelihoods they support, will continue to erode under the combined pressures of overfishing and environmental change.

To address this challenge, management must prioritize a multi-scale approach (e.g., see Tickner et al. (2025) and Oberdorff (2022) for a review of potential technical solutions) that includes: (1) maintaining the natural dynamic of the fluvial system (e.g., connectivity, sediment transport, seasonal river flows), (2) improving wastewater treatment technologies and water reuse to reduce pollution from domestic and industrial point sources as well as maintaining sustainable water resources, (3) expanding the network of protected areas, and (4) reducing fishing pressure by lowering the number and duration of active *dai* units along the Tonle Sap River, alongside organizing spatially explicit

management measures targeting ecologically critical areas like upstream spawning grounds (e.g., Khone Falls, the Tonle Sap flooded forest).

Finally, complementing management efforts with high-resolution, long-term monitoring of fish diversity and hydrological parameters using hydrochemical time series and expanding bioecological research on the Tonle Sap–Mekong fish fauna are essential to refine management strategies and enable adaptive, evidence-based interventions that balance fishery yields with conservation, ensuring the long-term sustainability of the Tonle Sap Lake system.

CRediT authorship contribution statement

Ratha Chea: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Thierry Oberdorff:** Writing – review & editing, Methodology, Conceptualization. **Kong Heng:** Writing – review & editing, Data curation. **Solida Tan:** Writing – review & editing, Data curation. **Paul Baudron:** Writing – review & editing, Conceptualization. **Pascal Laffaille:** Writing – review & editing, Conceptualization. **Gaël Grenouillet:** Writing – review & editing, Visualization, Methodology, Conceptualization.

Funding

The study was financially supported by the JEAI-AGROECO Project "Preserving ecosystem function and productivity of the Tonle Sap system facing global change" and the mobility of researcher was supported by PHC Tonle Sap Project No. 51509WL.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

The authors are grateful to the Institut de Recherche pour le Développement (IRD), which financially supported the research project through the Laboratory of Freshwater Ecology (ECOFRESH), and thank the Inland Fishery Research and Development Institute (IFReDI) and the Mekong River Commission (MRC) for providing the fish data. Thanks to the PHC Tonle Sap Project No. 51509WL for researcher mobility support. CRBE was supported by "Investissement d'Avenir" grants (CEBA, ref. ANR-10-LABX-0025; TULIP, ref. ANR-10-LABX-41).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.watbs.2026.100552.

References

Allan, J.D., Abell, R., Hogan, Z.E.B., Revenga, C., Taylor, B.W., Welcomme, R.L., Winemiller, K., 2005. Overfishing of inland waters. Bioscience 55, 1041–1051.

Arantes, C.C., Fitzgerald, D.B., Hoeinghaus, D.J., Winemiller, K.O., 2019a. Impacts of hydroelectric dams on fishes and fisheries in tropical rivers through the lens of functional traits. Curr. Opin. Environ. Sustain. 37, 28–40.

Arantes, C.C., Laufer, J., Pinto, M.D. da S., Moran, E.F., Lopez, M.C., Dutka-Gianelli, J., Pinto, D.M., Chaudhari, S., Pokhrel, Y., Doria, C.R.C., 2022. Functional responses of fisheries to hydropower dams in the amazonian floodplain of the madeira river. J. Appl. Ecol. 59, 680–692.

Arantes, C.C., Winemiller, K.O., Asher, A., Castello, L., Hess, L.L., Petrere Jr, M., Freitas, C.E.C., 2019b. Floodplain land cover affects biomass distribution of fish functional diversity in the amazon river. Sci. Rep. 9, 16684.

Arias, M.E., Cochrane, T.A., Kummu, M., Lauri, H., Holtgrieve, G.W., Koponen, J., Piman, T., 2014. Impacts of hydropower and climate change on drivers of ecological productivity of southeast Asia's Most important wetland. Ecol. Model. 272, 252–263.

Arias, M.E., Cochrane, T.A., Norton, D., Killeen, T.J., Khon, P., 2013. The flood pulse as the underlying driver of vegetation in the largest wetland and fishery of the mekong basin. Ambio 42, 864–876. https://doi.org/10.1007/s13280-013-0424-4.

Baran, E., So, N., Arthur, R., Leng, S.V., Kura, Y., 2007. Bioecology of 296 Fish Species of the Tonle Sap Great Lake (Cambodia). Report for the Project "Influence of Built Structures on the Fisheries of the TonleSap. WorldFish, National Mekong Committee (CNMC) and Asian Development Bank (ADB). Phnom Penh, Cambodia, p. 166.

Bonheur, N., Lane, B.D., 2002. Natural resources management for human security in Cambodia's tonle sap biosphere reserve. Environ. Sci. Pol. 5, 33–41.

Cadotte, M.W., Carscadden, K., Mirotchnick, N., 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. J. Appl. Ecol. 48, 1079–1087.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., 2012. Biodiversity loss and its impact on humanity. Nature 486, 59–67.

Castello, L., McGrath, D.G., Hess, L.L., Coe, M.T., Lefebvre, P.A., Petry, P., Macedo, M.N., Renó, V.F., Arantes, C.C., 2013. The vulnerability of amazon freshwater ecosystems. Conserv. Lett. 6, 217–229.

Chea, R., Brosse, S., Lek, S., Grenouillet, G., 2021. Do morphological traits predict ecological guilds of the mekong fish fauna? Sustainability 13, 8401.

Chea, R., Pool, T.K., Chevalier, M., Ngor, P., So, N., Winemiller, K.O., Lek, S., Grenouillet, G., 2020. Impact of seasonal hydrological variation on tropical fish assemblages: abrupt shift following an extreme flood event. Ecosphere 11, e03303. https://doi.org/10.1002/ecs2.3303.

Chen, A., Liu, J., Kummu, M., Varis, O., Tang, Q., Mao, G., Wang, J., Chen, D., 2021. Multidecadal variability of the Tonle Sap Lake flood pulse regime. Hydrol. Process. 35, e14327. https://doi.org/10.1002/hyp.14327.

Chevalier, M., Ngor, P.B., Pin, K., Touch, B., Lek, S., Grenouillet, G., Hogan, Z., 2023. Long-term data show alarming decline of majority of fish species in a lower mekong basin fishery. Sci. Total Environ. 891, 164624.

Chhuoy, S., Hogan, Z.S., Chan, B., Chandra, S., Touch, B., Sor, R., Lek, S., Ngor, P.B., 2023. Declines in the Mekong's megadiverse larval fish assemblages: implications for sustainable development. Sustainability 15, 13535.

Clavel, J., Julliard, R., Devictor, V., 2011. Worldwide decline of specialist species: toward a global functional homogenization? Front. Ecol. Environ. 9, 222–228.

Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K., Robson, T.M., 2007. Incorporating plant functional diversity effects in ecosystem service assessments. Proc. Natl. Acad. Sci. 104, 20684–20689.

Díaz, S., Settele, J., Brondízio, E.S., Ngo, H.T., Agard, J., Arneth, A., Balvanera, P., Brauman, K.A., Butchart, S.H.M., Chan, K.M.A., et al., 2019. Pervasive human-driven decline of life on Earth points to the need for transformative change. Science 366. https://doi.org/10.1126/science.aax3100 eaax3100 (80-.).

Dray, S., Dufour, A.B., 2007. The ade4 package:implementing the duality diagram for ecologists. J. Stat. Software 22, 1–20.

Dudgeon, D., 2019. Multiple threats imperil freshwater biodiversity in the anthropocene. Curr. Biol. 29, R960–R967.

Dunn, O.J., 1964. Multiple comparisons using rank sums. Technometrics 6, 241–252. https://doi.org/10.1080/00401706.1964.10490181.

Froese, R., Pauly, D., 2025. Fishbase [WWW Document]. World Wide Web Electron. Publ. URL. https://www.fishbase.se/search.php.

Froese, R., Zeller, D., Kleisner, K., Pauly, D., 2012. What catch data can tell Us about the status of global fisheries. Mar. Biol. 159, 1283–1292.

Halls, A.S., Burnhill, T.J., 2009. Modelling the Cumulative Barrier and Passage Effects of Mainstream Hydropower Dams on Migratory Fish Populations in the Lower Mekong Basin (No. 25). Mekong River Commission.

Halls, A.S., Paxton, B.R., Hall, N., Ngor, Pengbun, Lieng, S., Ngor, Pengby, So, N., 2013. The Stationary Trawl (Dai) Fishery of the Tonle Sap-Great Lake System, Cambodia (No. 32), MRC Technical Paper, MRC Technical Paper. Mekong River Commission, Phnom Penh, Cambodia.

Hecky, R.E., Mugidde, R., Ramlal, P.S., Talbot, M.R., Kling, G.W., 2010. Multiple stressors cause rapid ecosystem change in Lake Victoria. Freshw. Biol. 55, 19–42.

IPBES, 2019. In: Brondízio, E.S., Settele, J., Díaz, S., Ngo, H.T. (Eds.), Global assessment report on biodiversity and ecosystem services. IPBES Secretariat, Bonn, Germany, pp. 1–1148. https://doi.org/10.5281/zenodo.3831673.

Jackson, D.A., Peres-Neto, P.R., Olden, J.D., 2001. What controls who is where in freshwater fish communities the roles of biotic, abiotic, and spatial factors. Can. J. Fish. Aquat. Sci. 58, 157–170.

Kang, B., Huang, X., 2022. Mekong fishes: biogeography, migration, resources, threats, and conservation. Rev. Fish. Sci. Aquac. 30, 170–194.

Kassambara, A., Mundt, F., 2020. Factoextra: Extract and visualize the results of multivariate data analyses. R Package Version 1 (0.7).

Kummu, M., Sarkkula, J., 2008. Impact of the mekong river flow alteration on the tonle sap flood pulse. Ambio 185–192.

Lamberts, D., 2008. Little impact, much damage: the consequences of mekong river flow alterations for the tonle sap ecosystem. Mekong Fisheries Network Conference Proceedings. Citeseer.

Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the holy grail. Funct. Ecol. 16, 545–556.

Loeung, D., Degen, P., Van Zalinge, N., Commission, M.R., 2003. Fishing Gears of the Cambodian Mekong.

Magurran, A.E., 2013. Measuring Biological Diversity. John Wiley & Sons.

McGill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. Trends Ecol. Evol. 21, 178–185.

Mims, M.C., Olden, J.D., 2013. Fish assemblages respond to altered flow regimes via ecological filtering of life history strategies. Freshw. Biol. 58, 50–62.

Montaña, C.G., Ou, C., Keppeler, F.W., Winemiller, K.O., 2020. Functional and trophic diversity of fishes in the Mekong-3S river system: comparison of morphological and isotopic patterns. Environ. Biol. Fish. 103, 185–200.

Morovati, K., Tian, F., Kummu, M., Shi, L., Tudaji, M., Nakhaei, P., Olivares, M.A., 2023. Contributions from climate variation and human activities to flow regime change of Tonle Sap Lake from 2001 to 2020. J. Hydrol. 616, 128800.

Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H., Bellwood, D.R., 2013. A functional approach reveals community responses to disturbances. Trends Ecol. Evol. 28, 167–177.

Mouillot, D., Villéger, S., Parravicini, V., Kulbicki, M., Arias-González, J.E., Bender, M., Chabanet, P., Floeter, S.R., Friedlander, A., Vigliola, L., 2014. Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. Proc. Natl. Acad. Sci. 111, 13757–13762.

MRC, 2021. Status and trends of fish abundance and diversity in the lower mekong basin during 2007–2018. MRC Tech. Pap. 66. https://doi.org/10.52107/mrc.qx5yo0.

MRC, 2019. State of the basin Report 2018. Mekong River Commission, pp. 1–274.

MRC, 2005. Overview of the Hydrology of the Mekong Basin. Mekong River Commission. Mekong River Commission, Vientiane.

Ngor, P.B., McCann, K.S., Grenouillet, G., So, N., McMeans, B.C., Fraser, E., Lek, S., 2018. Evidence of indiscriminate fishing effects in one of the world's largest inland fisheries. Sci. Rep. 8, 8947. https://doi.org/10.1038/s41598-018-27340-1.

Nuon, V., Chea, R., Hugueny, B., Grenouillet, G., 2025. Environmental pressures on mekong fish: insights from temporal functional diversity dynamics. J. Environ. Manag. 380, 125138. https://doi.org/10.1016/j.jenvman.2025.125138.

Oberdorff, T., 2022. Time for decisive actions to protect freshwater ecosystems from global changes. Knowl. Manag. Aquat. Ecosyst. 423 (19).

Ogutu-Ohwayo, R., 1990. The decline of the native fishes of lakes Victoria and Kyoga (East Africa) and the impact of introduced species, especially the Nile perch, Lates niloticus, and the Nile tilapia, Oreochromis niloticus. Environ. Biol. fishes 27, 81–96.

Oksanen, J., Simpson, G, Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., et al., 2025. Vegan: community ecology package. R package version 2.7–0.

Olden, J.D., Poff, N.L., Bestgen, K.R., 2006. Life-history strategies predict fish invasions and extirpations in the colorado river basin. Ecol. Monogr. 76, 25–40.

Olden, J.D., Poff, N.L., Douglas, M.R., Douglas, M.E., Fausch, K.D., 2004. Ecological and evolutionary consequences of biotic homogenization. Trends Ecol. Evol. 19, 18–24.

Orr, S., Pittock, J., Chapagain, A., Dumaresq, D., 2012. Dams on the Mekong river: lost fish protein and the implications for land and water resources. Glob. Environ. Change 22, 925–932.

Ou, C., Montaña, C.G., Winemiller, K.O., 2017. Body size–trophic position relationships among fishes of the lower Mekong basin. R. Soc. Open Sci. 4, 160645.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres Jr., F., 1998. Fishing down marine food webs. Science 279 (5352), 860–863.

Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. Ecol. Lett. 9, 741–758.

Pianka, E.R., 1970. On r-and K-selection. Am. Nat. 104, 592–597.

Poff, N.L., Olden, J.D., Vieira, N.K.M., Finn, D.S., Simmons, M.P., Kondratieff, B.C., 2006. Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. J. North Am. Benthol. Soc. 25, 730–755.

R Core Team, 2024. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Reid, A.J., Carlson, A.K., Creed, I.F., Eliason, E.J., Gell, P.A., Johnson, P.T.J., Kidd, K.A., MacCormack, T.J., Olden, J.D., Ormerod, S.J., et al., 2019. Emerging threats and persistent conservation challenges for freshwater biodiversity. Biol. Rev. Camb. Phil. Soc. 94, 849–873. https://doi.org/10.1111/brv.12480.

Rockström, J., Steffen, W., Noone, K., Persson, Å., Chapin, F.S., Lambin, E.F., Lenton, T. M., Scheffer, M., Folke, C., Schellnhuber, H.J., et al., 2009. A safe operating space for humanity. Nature 461, 472–475. https://doi.org/10.1038/461472a.

Sabo, J.L., Ruhi, A., Holtgrieve, G.W., Elliott, V., Arias, M.E., Ngor, P.B., Räsänen, T.A., Nam, S., 2017. Designing river flows to improve food security futures in the Lower Mekong Basin. Science 358 (6368), eaao1053.

Soininen, J., McDonald, R., Hillebrand, H., 2007. The distance decay of similarity in ecological communities. Ecography (Cop.) 30, 3–12.

Stamatopoulos, C., 2002. Sample-based fishery surveys: A technical handbook. FAO Fisheries Technical Paper No, 425. FAO, Rome, pp. 1–132. https://openknowledge.fao.org/handle/20.500.14283/y2790e.

Tickner, D., Schiller, L., Cooke, S.J., Ordóñez, E.B., Collier, U., Dalton, J., Harrison, I., Lifeng, L., Phang, S.C., Young, W.J., 2025. Addressing the policy and business drivers of global freshwater biodiversity loss. Environ. Rev. 33, 1–20.

Villéger, S., Brosse, S., Mouchet, M., Mouillot, D., Vanni, M.J., 2017. Functional ecology of fish: current approaches and future challenges. Aquat. Sci. 79, 783–801.

Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89, 2290–2301.

Villéger, S., Miranda, J.R., Hernández, D.F., Mouillot, D., 2010. Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. Ecol. Appl. 20, 1512–1522.

Walsh, G., Pease, A.A., Woodford, D.J., Stiassny, M.L.J., Gaugris, J.Y., South, J., 2022. Functional diversity of afrotropical fish communities across river gradients in the republic of Congo, west central Africa. Front. Environ. Sci. 10, 1–19. https://doi.org/10.3389/fenvs.2022.981960.

Welcomme, R.L., Cowx, I.G., Coates, D., Béné, C., Funge-Smith, S., Halls, A., Lorenzen, K., 2010. Inland capture fisheries. Philos. Trans. R. Soc. B Biol. Sci. 365, 2881–2896.

Welcomme, R.L., Winemiller, K.O., Cowx, I.G., 2006. Fish environmental guilds as a tool for assessment of ecological condition of rivers. River Res. Appl. 22, 377–396.

Winemiller, K.O., 2005. Life history strategies, population regulation, and implications for fisheries management. Can. J. Fish. Aquat. Sci. 62, 872–885.

Winemiller, K.O., McIntyre, P.B., Castello, L., Fluet-Chouinard, E., Giarrizzo, T., Nam, S., Baird, I.G., Darwall, W., Lujan, N.K., Harrison, I., 2016. Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. Science (80-.) 351, 128–129.

Winemiller, K.O., Rose, K.a., 1992. Patterns of life-history diversification in north American fishes: implications for population regulation. Can. J. Fish. Aquat. Sci. https://doi.org/10.1139/f92-242.

Zhang, C., Zhu, R., Sui, X., Li, X., Chen, Y., 2021. Understanding patterns of taxonomic diversity, functional diversity, and ecological drivers of fish fauna in the Mekong river. Glob. Ecol. Conserv. 28, e01711.

Ziv, G., Baran, E., Nam, S., Rodríguez-Iturbe, I., Levin, S.A., 2012. Trading-off fish biodiversity, food security, and hydropower in the Mekong river Basin. Proc. Natl. Acad. Sci. 109, 5609–5614.