THÈSE

En vue de l'obtention du

DOCTORAT DE L'UNIVERSITÉ DE TOULOUSE

Délivré par :
Université Toulouse 3 Paul Sabatier (UT3 Paul Sabatier)

Cotutelle internationale avec :

Présentée et soutenue par :
Peng Bun NGOR

Le mardi 10 avril 2018

Titre :

Dynamique des peuplements de poissons dans le bassin inférieur du Mékong
Fish assemblages dynamic in the tropical flood-pulse system of the Lower Mekong River Basin

---

ED SEVAB : Écologie, biodiversité et évolution

Unité de recherche :
Évolution et Diversité Biologique

Directeur(s) de Thèse :

Sovan Lek (Professeur, Université Paul Sabatier, Toulouse)

Rapporteurs :
Anna Vila-Gispert (Adjunct Professeur, Université Girona, Espagne)
Stefan Schmutz (Professeur, Institute of Hydrobiology and Aquatic Ecosystem Management, Vienna, Austria)

Autre(s) membre(s) du jury :
Thierry OBERDORFF (Directeur de recherche, Institut de recherche pour le développement, Paris); Sébastien BROSSE (Professeur, Université Paul Sabatier, Toulouse); Gaël GRENOUILLET (Maître de conférences, Université Paul Sabatier, Toulouse); Nam SO (Chargé de recherch, Commission du Mékong, Vientiane); Christine AGRILLIER (Directeur de recherche, IRSTEA, Montpellier, France); Marta MUÑOZ (Professeur, Université Girona, Espagne)

PhD thesis

Fish assemblages dynamic in the tropical flood-pulse system of the Lower Mekong River Basin

Peng Bun NGOR

Jury composition

Anna Vila-Gispert	Adjunct Professor	Referee
Stefan Schmutz	Professor	Referee
Thierry OBERDORFF	Research director	Jury member
Sébastien BROSSE	Professor	Jury member
Gaël GRENOUILLET	Senior lecturer	Jury member
Nam SO	Researcher	Jury member
Christine AGRILLIER	Research Director	Jury member
Marta MUÑOZ	Professor	Jury member
Sovan LEK	Professor	PhD supervisor

Defended on 10 April 2018

University of Toulouse

This research was performed at:

Laboratoire Evolution & Diversité Biologique, UMR 5174, Université Paul Sabatier
– Toulouse III, 118 route de Narbonne, 31062 Toulouse cédex 4 – France.

Cite this document as:

Ngor P. B., 2018. Fish assemblages dynamic in the tropical flood-pulse system of the Lower Mekong River Basin. Thesis submitted in fulfilment of the requirements for the Degree of Doctor of Philosophy, University of Toulouse 3 Paul Sabatier, Toulouse, France.

Acknowledgements

First and foremost, my sincerest gratitude goes to Professor Sovan Lek, my supervisor, for his kindest support, valuable guidance and encouragement from the beginning to the completion of my PhD Program. This thesis would be impossible without his continuous assistance and constructive advice. I would like to profoundly thank Associate Professor Sithan Lek-Ang, my supervisor's wife, for her warm welcome and kindness to offer the homestay during my first arrival, and indeed both of whom offer both academic and personal supports during my entire stay in Toulouse. I am wholeheartedly thankful for their heartfelt support and care-taking.

I am also very grateful to His Excellency Eng Cheasan, Director General of the Fisheries Administration for his support to undertake my PhD Program. Sincere thanks are also given to Mr. Chheng Phen, acting director of the Inland Fisheries and Development Institute, Dr. So Nam, Chief of Environment Division of the Mekong River Commission for his cooperation and support in supplying the data for this study.

I am grateful to Dr. Thierry Oberdorff, Research Director at the French Research Institute for Development; Professor Gaël Grenouillet, Professor Sébastien Brosse and Dr. Loïc Tudesque at the Laboratoire Evolution et Diversité Biologique, Université de Toulouse; Professor Pierre Legendre, Département de Sciences Biologiques, Université de Montréal; Professor Kevin McCann, University of Guelph and Professor Bailey McMeans, University of Toronto Mississauga for their technical advice, comments and supports during data analyses and manuscript preparations. Last, but not least, my sincerest thanks go to Mr. Peter Degen who is always available for helping edit my writing and Mr. Kunthea Nuon for his technical support in GIS mapping.

I am indented to my PhD colleagues, Seng Ratha, Sor Ratha, Chea Ratha, Chan Bunyeth and Heng Kong for their academic, social and personal sharing, support and assistance especially during my stay in Toulouse. My sincere thanks are also given to Ms. Catherine Stasiulis, Ms. Romy Duchesne, Ms. Aurore Berthier and Ms. Dominique Pantalacci for their administrative support.

My deepest thanks go to my beloved parents and wife as well as my brothers and sisters for their unconditional company, endless love and support.

Finally, my special thanks are given to the Erasmus Plus Program, Belmont Forum (TLSCC project), CONCEA Program and Laboratoire Evolution & Diversité Biologique (EDB), Université de Toulouse for funding this study and support, Mekong River Commission (Fisheries Programme), the Inland Fisheries Research and Development Institute of the Fisheries Administration in Cambodia for giving the required datasets for the study.

PART I: SYNTHESIS

Table of Contents

PART II: PUBLICATIONS

Article 1. Large-scale patterns of fish diversity and assemblage structure in the longest-tropical river in Asia.

Ratha Chea, Sovan Lek, Peng Bun Ngor, Gaël Grenouillet 2016

Ecology of Freshwater Fish, 2016, 1–11

Article 2. Spatial and temporal variation in fish community structure and diversity in the largest tropical flood-pulse system of Southeast Asia.

Peng Bun Ngor, Gaël Grenouillet, Nam So, Sea Phem, Sovan Lek

Ecology of Freshwater Fish (accepted, in press)

Article 3. Evidence of indiscriminate fishing effects in one of the world's largest inland fisheries.

Peng Bun Ngor, Kevin McCann, Gaël Grenouillet, Nam So, Bailey McMeans, Evan Fraser, Sovan Lek

Scientific Reports 2018 (in revision)

Article 4. Flow alterations by dams shaped fish assemblage dynamics in the complex Mekong-3S river system.

Peng Bun Ngor, Pierre Legendre, Thierry Oberdorff, Sovan Lek

Ecological Indicators, 88 (2018), 103-114.

Article 5. Fish assemblage responses to flow seasonality and predictability in a tropical flood pulse system.

Peng Bun Ngor, Thierry Oberdorff, Phen Chheng, Christophe Baehr, Gaël Grenouillet, Sovan Lek

Ecoshpere (*in revision*)

PART I: SYNTHESIS

I. Introduction

Inland waters cover lakes, reservoirs, rivers, wetlands and coastal transitional waters (Welcome 2001, Welcomme et al. 2010), extending over an area of about 7.8 million km^2 (de Graaf et al. 2015). Inland waters cover only about 0.01% of the world's water and about 0.8% of the earth surface (Revenga and Kura 2003, Dudgeon et al. 2006), yet support humankind countless environmental goods and services, of which fish are among the most important resources, supplying food, nutrition, income, livelihoods and recreation to tens of millions of people on earth (Béné et al. 2015, de Graaf et al. 2015, Lynch et al. 2016). Some 13,000 inland fishes from 170 families strictly live in freshwaters (Lévêque et al. 2008), making up around 41% of all fish species and 20% of all vertebrate species (Helfman et al. 2009). Inland capture fisheries employ about 61 million people 50% of whom are women (Bartley et al. 2015). Globally, catches in inland waters yielded 11.9 million tonnes in 2014 (11.3% of the world total capture fish production) (FAO 2016), with an average annual growth between 2 and 3% since 1950 (Allan et al. 2005, Bartley et al. 2015). Albeit positive trends, fisheries data reported by FAO member states are of major concern in terms of its reliability (Watson and Pauly 2001, Bartley et al. 2015). World fisheries catches are shown declining when corrective measures are considered in its fish catch estimation (Watson and Pauly 2001, Pauly et al. 2002). Evidence suggests that inland wild fish are declining or overharvested particularly in the tropical Asia (Allan et al. 2005, Welcomme et al. 2010), the region exceptionally rich in flora and fauna, yet attract comparatively little ecological research and lesser conservation effort on biodiversity (Dudgeon 2000, Allen et al. 2012). A typical example of this is the Mekong River Basin and its fisheries, one among the world's most biodiverse rivers and has been designated to be part of the world's 35 biodiversity hotspots (Baird 2006, Mittermeier et al. 2011, Vaidyanathan 2011). Arguably, Tonle Sap, among the world's largest tropical floodplains, has been studied the least with regards to its hydrology-ecology interactions (Junk et al. 2006, Kummu et al. 2006, Arias et al. 2013, Sabo et al. 2017, Ngor et al. 2018a).

1.1 A brief about the Mekong system

1.1.1 The Mekong River

The Mekong River originating in Tibetan plateau and running for some 4,350 km through China, Myanmar, Lao PDR, Thailand and Viet Nam is the largest in Southeast Asia, the 12th longest on the planet, the 8th world's largest in terms of flows having a mean annual discharge of approximately 475 km^3 and the world's 21st largest in terms of area draining around 795,000 km^2 (van Zalinge et al. 2004, Gupta and Liew 2007). The Upper Mekong which is called *Lancang Jiang* contributes around 16% to the total annual mean flow while the Lower Mekong Basin (LMB) which begins at the Golden Triangle marking the borders of Thailand, Lao PDR, China and Burma, and consists of Cambodia, Lao PDR, Thailand and Viet Nam shares the remainder of the total flow (~84%). The Mekong's major tributaries systems develop in the LMB. Among these, the Sekong, Sesan, Srepok Rivers together known as the 3S system, contributing ~20% of flow and the Tonle Sap River and Lake (~9% of flow) are among the largest tributaries and constitute significant parts of the LMB (MRC 2005, 2010).

The Lower Mekong River (LMR) forms the Lao-Thai border for a river reach of approximately 900 km (van Zalinge et al. 2004). There is an inland delta at the geological fault line which forms the 21-meter high Khone Falls on the Lao-Cambodian border. At Kratie ~545 km from the sea, the river becomes a lowland river. At Phnom Penh, ~330 km from the sea, the Mekong River is joined by the Tonle Sap River, where it splits into the Mekong proper and the Bassac forming a large estuarine delta before discharging into the South China Sea.

The Mekong annual flood pulse takes place between June and October. It is influenced by the tropical monsoonal climate and flood runoff which converges and accumulates into a single seasonal flow. This results in a distinct seasonality in the annual hydrological cycle: flood (wet) season and low-flow (dry) season. During the flood season, the discharge is 30 times greater than in the dry season at Pakse and up to 53 times at Kratie (van Zalinge et al. 2004). The hydrological cycle (Fig. 1) is a main ecological driver structuring up- and downstream aquatic communities in the Mekong including fishes that seasonally migrate for spawning, feeding/rearing and refuge (Valbo-Jorgensen and Poulsen 2000, Poulsen et al. 2002, Baran 2006).

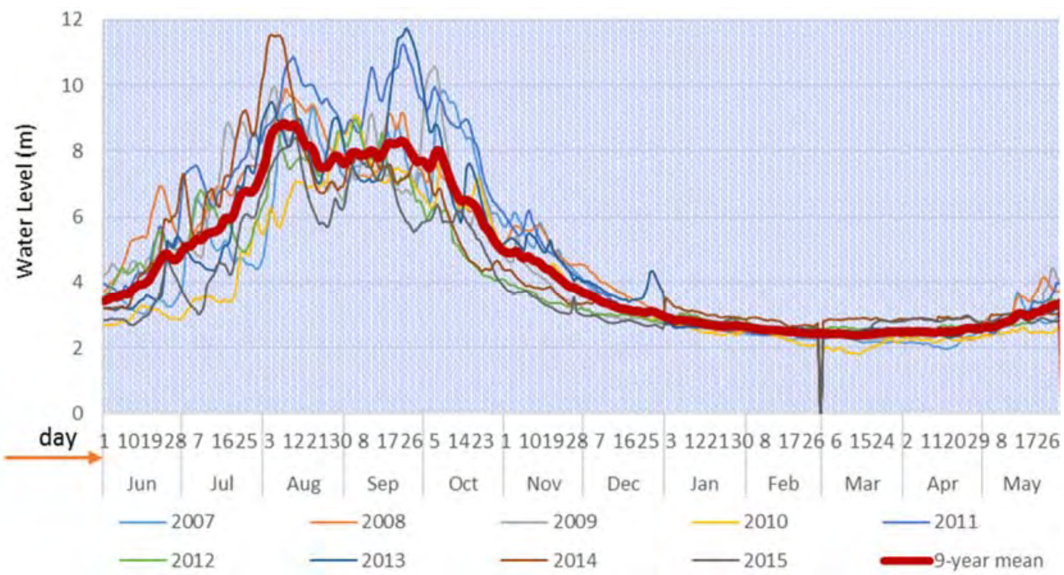


Fig. 1. Observed hydrological cycle patterns, based on daily water levels over nine-year period (2007-2015) on the Mekong mainstream in Stung Treng Province. Thick red line curve represents the nine-year mean daily water levels.

1.1.2 The 3S Rivers

The 3S Rivers drain northeastern Cambodia, southern Lao PDR, and Viet Nam's Central Highlands. Their sources originate in the Central Highlands of Viet Nam, from where the Sekong (SK)

River begins its flow toward southern Lao PDR and then northeastern Cambodia where it merges with the Sesan (SS) and Srepok (SP) Rivers. The Sesan and Srepok flow directly from Viet Nam to Cambodia, and the three rivers meet over an approximate distance of 40 km before forming the confluence with the Mekong mainstream at the provincial town of Stung Treng in Cambodia (MacQuarrie et al. 2013).

The 3S Basin covers a surface area of about 78,650 km^2 of which 33%, 29% and 38% is shared by Cambodia, Lao PDR and Viet Nam, respectively (Piman et al. 2013, Constable 2015). The basin's annual discharge contributes about 20% to the total annual flow of the Mekong mainstream (91,000 × 106 m^3 or an average of 2,886 m^3/s), making the 3S the largest tributary of the Mekong Basin (MRC 2005, Adamson et al. 2009), and the main hydrological contribution to the Mekong mainstream between Pakse, Lao PDR and Kratie, Cambodia. The 3S flow contribution indeed exceeds that from the upper Mekong in China (16%) (MRC 2005, Adamson et al. 2009) and plays a significant part in the seasonal reverse flow of the Tonle Sap River (MRC 2005). Therefore, flow regulations resulting from hydropower development in the 3S system could have significantly adverse effects, not only on flow regimes, ecosystems and overall biological integrity of the 3S system itself, but also on the Mekong-3S system, the downstream Tonle Sap system and the Mekong delta (Ziv et al. 2012, Arias et al. 2014b).

1.1.3 The Tonle Sap system

The Mekong River, roughly 4,300 km from its source (Halls et al., 2013a), meets with the Tonle Sap River on the right bank at the Chaktomuk junction in the capital city of Phnom Penh. The Tonle Sap Lake which is situated in the heart of Cambodia contains the largest continuous areas of natural wetland habitats remaining in the Mekong system (van Zalinge et al. 2004), and the largest wetlands in Southeast Asia. The lake was formed some 5 - 6000 years ago (Carbonnel 1963), is located at the apex of the Tonle Sap River around 130 km to the northwest of Chaktomuk junction. The Tonle Sap River and Tonle Sap Lake form the Tonle Sap River and Lake System (TSRL) which is of high biological productivity and considered as one of the world's largest tropical inland fisheries (Baran 2005, Baran et al. 2013b). It has become a world Biosphere Reserve approved by the United Nations Educational, Scientific and Cultural Organization (UNESCO) since 1997, given the wetlands of global significance for its biodiversity conservation value (Davidson 2006). The TSRL catchment covers an area of 85,790 km^2 or 11% of the Mekong Basin (MRC, 2003). The waters for the system originates mainly from the Mekong River (54%) while the lake tributaries contribute 34% and the rest is from precipitation (M. Kummu et al., 2014). During the wet season (June-October), Tonle Sap River flows from the Mekong River to the Tonle Sap Lake (inflow) when the Mekong waters rise faster than the lake, expanding its mean surface area from ~3,500 to ~14,500 km^2, inundating huge floodplain areas surrounding the TSRL, with maximum depths in the lake recorded at 6 to 9 meters in late September to early October and minimum depths of around 0.5 meter in late April (MRC, 2005).

The TSRL's fisheries productivity reaches its peak during this flooding period as both migratory fishes from the Mekong and resident fishes in the lake invade the floodplains for feeding/rearing and reproduction. Eggs, larvae and fry of fish that spawn upstream in the Mekong mainstream are also carried by the flow and dispersed into the TSRL's sourrounding floodplains through numerous channels, streams and man-made cannals for feeding/rearing, nurseries and growth. When the Mekong flood recedes (September/October) and the Tonle Sap River reverses its flow direction (outflow), large numbers of fish migrate back to the Tonle Sap Lake, then the Tonle Sap River and Mekong River for dry-season refuge. It is during this period of receeding water (October – March) when fishing activities are intensifying in the Tonle Sap Lake and River Systm as well as in the Mekong River. The fishery in Tonle Sap River is highly predictable, and usually peaks in December and January in a time window of 6/7-1 days before full moon during which the river is described as 'packed solid with fish' (Lieng et al. 1995 p. 257, Halls et al. 2013c). Such events can still be observed nowadays at the stationary trawl bagnet (*Dai*) fishery which has been operating in the Tonle Sap River for more than a century (Halls et al. 2013c).

1.2 The Mekong fisheries

Fish communities in the Mekong River Basin are extremely diverse and characterized by the presence of large distance migratory species (Rainboth 1996, Baran et al. 2001, Poulsen et al. 2002). Natural annual flood pulses inundate huge floodplain areas and drive enormous fish production upon which millions of people depend for their livelihoods (van Zalinge et al. 2004, Hortle 2007, So et al. 2015). The geographical space, habitat heterogeneity, river gradients and physicochemical as well as climatic factors, additionally, define broad-scale patterns of the spatial fish diversity and community composition of the river basin with species richness and level of endemism decreasing towards higher altitude (Kang et al. 2009, Chea et al. 2016).

1.2.1 Fish community structure

The Mekong Basin harbors an estimated 1,200 fish species (Rainboth 1996), with 877 species recorded, 18% of which is endemic to the system (Ziv et al. 2012, Baran et al. 2013b) while the Mekong Fish Database reports up to 911 species (MFD 2003). The LMB countries together possess one of the world's highest fish diversity per square kilometer; only French Guiana and Suriname in South America share similar or higher fish species diversity per unit area of land (Baran et al. 2013b). The largest fishery of the basin takes place in the extensive floodplain of the Tonle Sap (van Zalinge et al. 2004); the complex river-lake system which hosts an estimated 296 fish species, making it the third most fish species-rich lake after Lake Malawi (438 fish species) and Lake Tanganyika (316 fish species) (Baran et al. 2013b). Capture fisheries production in the LMB was estimated at approximately 2.3 million tonnes annually (MRC 2010, Hortle and Bamrungrach 2015), equivalent to around 2% of the world total fisheries production or approximately 19.3% of the world freshwater capture production which is 11.9 million tonnes (FAO 2016). Of the LMB's estimated fish biomass, white, black and grey fishes (see definitions in the next section) share ~34%, 50% and 16%, respectively; whereas of the total number of species, white, black and grey fishes represent 37%, 13% and 50%, respectively (Baran et al. 2013b).

Order	No. of species
Cypriniformes	382
Perciformes	206
Siluriformes	125
Clupeiformes	32
Beloniformes	27
Tetraodontiformes	20
Pleuronectiformes	18
Anguilliformes	14
Gasterosteiformes	13
Synbranchiformes	13
Rajiformes	12
Carcharhiniformes	8
Aulopiformes	7
Atheriniformes	7
Scorpaeniformes	7
Osteoglossiformes	5
Orectolobiformes	3
Cyprinodontiformes	2
Elopiformes	2
Batrachoidiformes	2
Lophiiformes	2
Characiformes	1
Gonorhychiformes	1
Osmeriformes	1
Gadiformes	1
Total	911

Source: MFD, 2003.

Mekong fishes have different sizes ranging from very small-sized gobies and minnows, which sexually mature at a length of less than 15 mm, to some of the largest inland fishes on the planet such as the Mekong giant catfish (*Pangasianodon gigas*, max. length ~3 m, max. published weight: 350 kg), the enormous stingray (*Himantura chaophrya*, max. length ~2.4 m ; max. published weight: 600 kg), and the Mekong giant carb (*Catlocarpio siamensis*, max. length 3 m, max. published weight 300 kg). Mekong fish size composition is given in Fig. 2.

Fishes in this basin are categorized into at least three broad ecological guilds in accordance with their ecological characteristics and migration patterns: white, black and grey fish (Poulsen and Albo-Jørgensen 2000, Welcome 2001, Poulsen et al. 2002). White fishes perform long-distance migrations between the Mekong mainstream and floodplains as well as major tributaries; the black fishes are floodplain residents, spending their life in lakes and swamps on floodplains adjacent to rivers and moving to flooded areas during the flood season; and grey fishes, ecologically intermediate between the white and black fishes, undertaking short-distance migrations in local tributaries and not spending their life in floodplain ponds during the dry season (van Zalinge et al. 2000, Welcome 2001, Valbo-Jørgensen et al. 2009, MRC 2010). Apart from these three main groups of fish, some freshwater fishes remain within the main river channels and many fishes are confined to tributaries and hill streams (Rainboth 1996). In the lower reaches of the river system in the Mekong delta, many euryhaline (salt-tolerant) coastal and estuarine fishes as well as some marine visitors are also present in reported catches (MRC 2010). In the Tonle Sap Basin, white fishes belong mostly to Cyprinidae and Pangasiidae while black fishes contain species from Channidae, Clariidae, Bagridae, Anabantidae and Osphronemidae and grey fishes refer to some species from Siluridae and Notopteridae (van Zalinge et al. 1998, Lim et al. 1999, Lamberts 2001, Welcome 2001, Campbell et al. 2006, Halls et al. 2013b, 2013c).

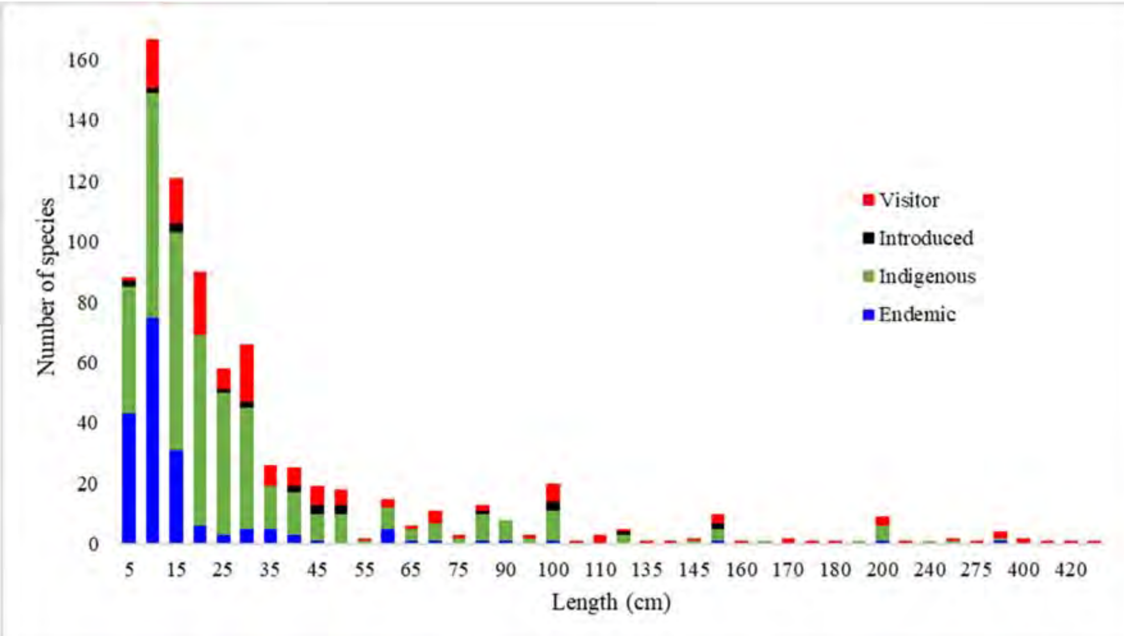


Fig. 2. Fish size composition of the Mekong Basin (data source: MFD 2003)

1.2.2 Fish migration system

Mekong fishes migrate longitudinally and laterally among critical habitats of the Mekong mainstream and its tributaries or between the floodplains and deeper areas of lakes or permanent water bodies. Migration usually takes place for all life stages of fish and is associated with dry-season refuging, flood-season feeding and rearing, and migrations for spawning as well as escaping from adverse environmental conditions (Welcome 2001, Poulsen et al. 2002). Generally, three different fish migration systems have been identified in the LMB (Valbo-Jorgensen and Poulsen 2000, Poulsen et al. 2002, 2004). The first migration system takes place in the lower part of the Mekong system between deep pools of the Mekong mainstream in Kratie-Stung Treng reach (dry-season refuge habitats) and the floodplain of Tonle Sap Lake, area South of Phnom Penh and the Mekong delta of Viet Nam together known as flood-season feeding and rearing habitats. The second occurs in the middle part of the LMB (between Khone Falls and Loei Province) and is characterized by the migration between the rapids and deep pools of the Mekong mainstream and the floodplain habitats which are connected with the Mekong's major tributaries. The third migration system occurs in the areas of upper part of the LMB in the downstream stretch of Loei River in Thailand to Luang Prabang in Lao PDR. This last migration reach is represented by rapids with deep pools and restricted floodplain habitats.

In the three migration systems, hydrology plays a central role in structuring up- and downstream fish community dynamics such as triggering fish to migrate among critical habitats during their life cycles (Poulsen et al. 2002, Baran 2006). General seasonal migration patterns of the Mekong fishes particularly those with white and grey ecological charateristics are reflected in seasonal hydrological patterns. For instance, fishes migrate for spawning in early wet season in May and June when the Mekong's water levels start rising. Afterwards, between July and November, both adult fish and larvae move to floodplains for feeding and growth. When water levels are falling particularly in December and January, these fishes migrate to permanent water bodies such as deep pools in the Mekong mainstream or lakes, and then remain sedentary in the permanent water bodies during the dry season (February – April). Fig. 3 gives a generalized life cycle of a Mekong fish species. Changes in hydrological patterns caused by anthropogenic activities such as infrastructure development are highly likely to distrupt the river biological system i.e. fish migration and reproduction success, which in effect alters fish community structure and reduce the overall fisheries productity in the Mekong system.

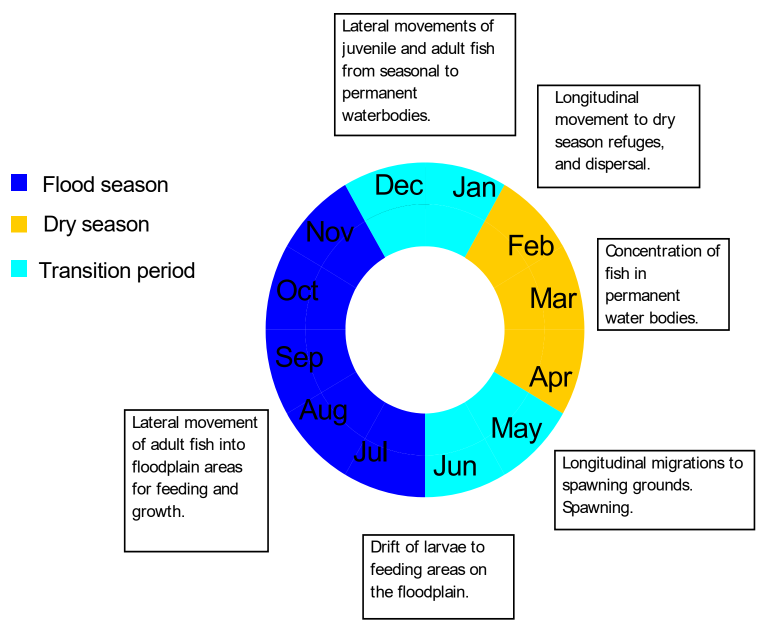


Fig. 3. A generalized life cycle of a Mekong fish species (Sverdrup-Jensen 2002)

1.2.3 Socio-economic importance of fisheries in the Lower Mekong Basin

In 2015, the total population of the LMB was estimated at 68.9 million (So et al. 2015). Some 80% of the LMB's dwellers is rural, and the economy highly depends on farming, fishing and aquaculture (Hortle 2009). About 66% of the LMB population was engaged in capture fisheries either part-time or seasonally (MRC 2010). At country level, ~80% of rural households in Cambodia, Lao

PDR and Thailand and 60-95% of households in Viet Nam delta were involved in capture fisheries (Hortle 2007). In large water bodies such as the Tonle Sap, commercial fishing appears to represent more than 40% of household (Ahmed et al. 1998).

Inland fish and other aquatic animals make up of more than half the animal protein consumed by people in the LMB which is more than three times the world average of 16% (Baran et al. 2013b), and which range from ~50% in Lao PDR and Thailand to ~60% in Viet Nam and ~80% in Cambodia (Hortle 2007). The average consumption of aquatic animals in the basin is 46 kg per capita per year, similar to the Southeast Asian rate of 51 kg/person/year but significantly higher than the world average of 24 kg/person/year (Baran et al. 2013b). Other inland aquatic animals such as frogs, insects, clams, shrimps, snails and snakes contribute ~6% to the total animal protein consumption (Hortle 2007).

A recent estimate indicates that, based on the first sale landing prices, the LMB capture fisheries is worth about US$11 billion annually in 2015 (So et al. 2015). The largest single fishery in the basin is the century-old *dai* or stationary trawl bagnet fishery on the Tonle Sap River. The fishery operates between October through March and targets mainly white and grey fishes that migrate out of the floodplains surrounding the Tonle Sap Lake to the main river channels for dry season refuge. Based on first-sale prices, the value of the fishery, on average, is estimated at around US$10 million seasonally (Ngor et al. 2015b). First sale fish prices recorded at the *dai* fishery indicate that there have been increasing fish prices observed particularly since the fishing season of 2006-2007 at the time when there was also global food crisis. Fish prices of small mud carps (*Henicorhynchus* spp.), recorded over 20-year period at the *dai* fishery are shown in Fig. 4. These are ecological keystone species which are the most abundant with their critical role in food security throughout the LMB and important prey species for many predatory fishes and Irrawaddy dolphins (Roberts and Baird 1995, Hurwood et al. 2008, Baird 2011, Fukushima et al. 2014, Ngor et al. 2015a).

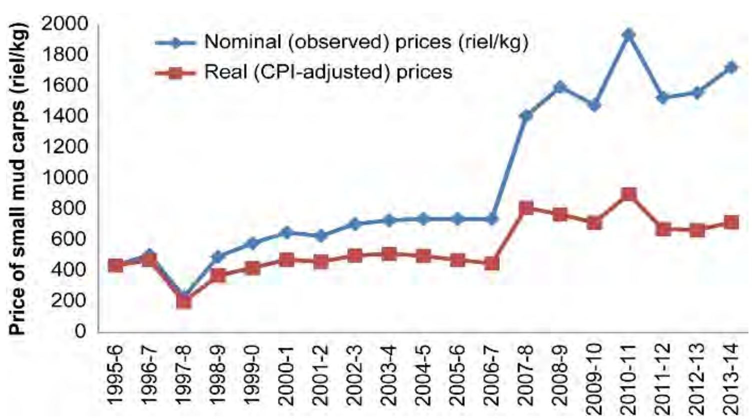


Fig. 4. First sale landing prices for small mud carps (*Henicorhynchus* spp.) 1995-2014 (Ngor et al. 2015b). Note: the average exchange rate is about Riel 4,000 to US$1.00.

1.3 Challenges of inland capture fisheries in the Lower Mekong Basin

Many freshwater faunal species particularly fishes have experienced severe declines in their ranges and abundances, and they are now far more endangered than their marine or terrestrial counterparts (Jenkins 2003, Strayer and Dudgeon 2010). In the Mekong Basin, several dangers are identified as threats to the sustainability of the Mekong fish and fisheries. These threats stem from sources both outside and inside the fishery sector including population growth, hydropower dams, water extraction and diversion for agriculture, widespread habitat fragmentation and loss, water quality degradation, mining, farming expansion and intensification, land-use change, urbanization, climate change, pollution, overharvesting and introduced species etc. Among these threats, water resources infrastructure development, habitat loss and open-access nature of fisheries (overharvesting) in the region are among the great dangers threatening the region's fishes and fisheries (van Zalinge et al. 2000, Welcome 2001, Halls and Kshatriya 2009, Valbo-Jørgensen et al. 2009, Welcomme et al. 2016, 2010, Ferguson et al. 2011, Ziv et al. 2012, Grumbine et al. 2012, Cochrane et al. 2014, Kummu et al. 2014, Winemiller et al. 2016, Sabo et al. 2017).

1.3.1 Water infrastructure development in the Mekong

During the last three decades or so, infrastructure development significantly poses by far the most significant threat to the Mekong River ecosystem, biodiversity and its fisheries (Arias et al. 2012, 2014b, Ziv et al. 2012, Piman et al. 2013, Cochrane et al. 2014, Winemiller et al. 2016, Sabo et al. 2017, Ngor et al. 2018b). For example, at least six large dams have been built in the upper Mekong River since mid-1990s (Fan et al. 2015, Winemiller et al. 2016) and in the LMB, two mainstream dams are under construction in Lao PDR and 10 others are planned. Among 144 tributaries dams, 42 are in operation, 27 under construction, 17 licensed and 58 planned by 2030 (Nielsen et al. 2015, Schmutz and Mielach 2015, Ngor et al. 2018b). These dams are known to disrupt river continuity, block migration routes of riverine fishes, dampen natural flood pulses, mute flow seasonality, fragment habitats, degrade water quality, and alter sediment and nutrient dynamics as well as other biogeochemical processes, which, in effect, alters the structure of aquatic faunal communities that adapt to natural seasonal flow dynamics as part of their life cycles (Collier et al. 1996, Agostinho et al. 2004, Graf 2006, Poff et al. 2007, Latrubesse et al. 2017, Sabo et al. 2017, Ngor et al. 2018b). Specifically, dams generate hydropower-related pulsed flows e.g. hydropeaking reacting to energy demands (from hourly to seasonally) which adversely affect riverine fishes and other aquatic organisms through, among other factors, stranding/extirpation, downstream displacement and spawning/rearing disruption (Young et al. 2011, Schmutz et al. 2015, Kennedy et al. 2016, Tonolla et al. 2017). In total, these pressures may lead to fish community compositional changes, fish recruitment failure and a continued diminishment of fisheries productivity in the system (Poulsen et al. 2002, ICEM 2010, Baird 2011, Grumbine et al.

2012, Ziv et al. 2012, Winemiller et al. 2016, Ngor et al. 2018b). Fig. 5 provides an overview of hydropower projects in the Mekong Basin.

For example, under the current functioning dams, the 3S's dry seasonal flow shows an increase of 28% and the wet seasonal flows a decrease of 4%, when measured at the 3S outlet (Piman et al. 2013). Similarly, hydropower dams upstream of the Mekong have caused the most distinct changes to the Mekong's flow, and their cascade impacts have been demonstrated from Chiang Sen in Thailand (the beginning of the LMB) as far as downstream in the Tonle Sap River in Cambodia which reduces flood pulses by 23% and 11% in rising and falling rates with observed changes taking place since 1991 (Arias et al. 2014a, Cochrane et al. 2014). These changes in natural flow dynamics and flood pulses have severe implications for fish community structure because, of an estimated 1200 fish species with 877 species recorded in the Mekong Basin (Rainboth 1996, Baran 2006, Baran et al. 2013b), about 87% are longitudinal and lateral migratory species (white and grey fishes) (MRC 2010, Baran et al. 2013b). Also, at least 89 migratory species including 14 endangered and critically endangered species characterize fish community from the 3S system (Baran et al. 2013a). In addition, of the 161 Mekong endemics, 17 species exist exclusively in the 3S Basin, and nowhere else on the planet (Baran et al. 2013a). More serious impacts are also expected for the fishes in the Tonle Sap Basin, hosting some 296 fish species (Baran 2005, Baran et al. 2013b). These fishes depend on natural seasonal-predictable flows and flood pulses as the main ecological trigger to disperse, reproduce and seek refuge (Valbo-Jorgensen and Poulsen 2000, Poulsen et al. 2002, 2004, Sverdrup-Jensen 2002, Baran 2006). Fig. 6 shows temporal change in daily water levels in the Mekong mainstream in Stung Treng Province over 95-year periods. Observably, there has been a general significant decrease in wet season flow (June-November), and an increase of dry season flow (December-May). Hydropower dams upstream in China have been attributed to cause the most 'distinct change' in the Mekong flow regimes as compared to other anthropogenic activities such as climate change (Cochrane et al. 2014, Winemiller et al. 2016, Sabo et al. 2017).

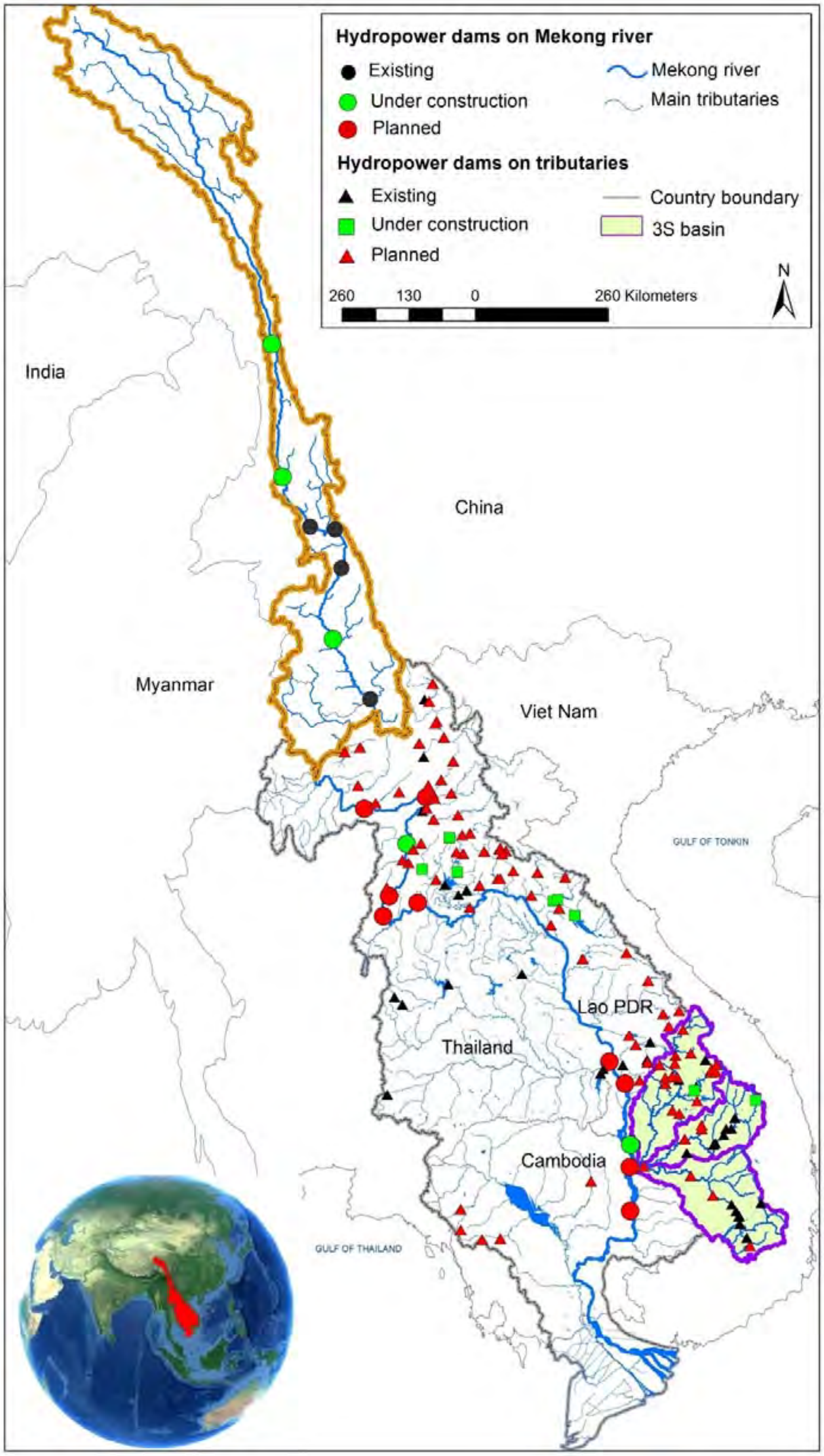


Fig. 5. Map showing hydropower dams in the Mekong Basin at different stages: existing, under-construction and planned. Data source: MRC hydropower project database 2015.

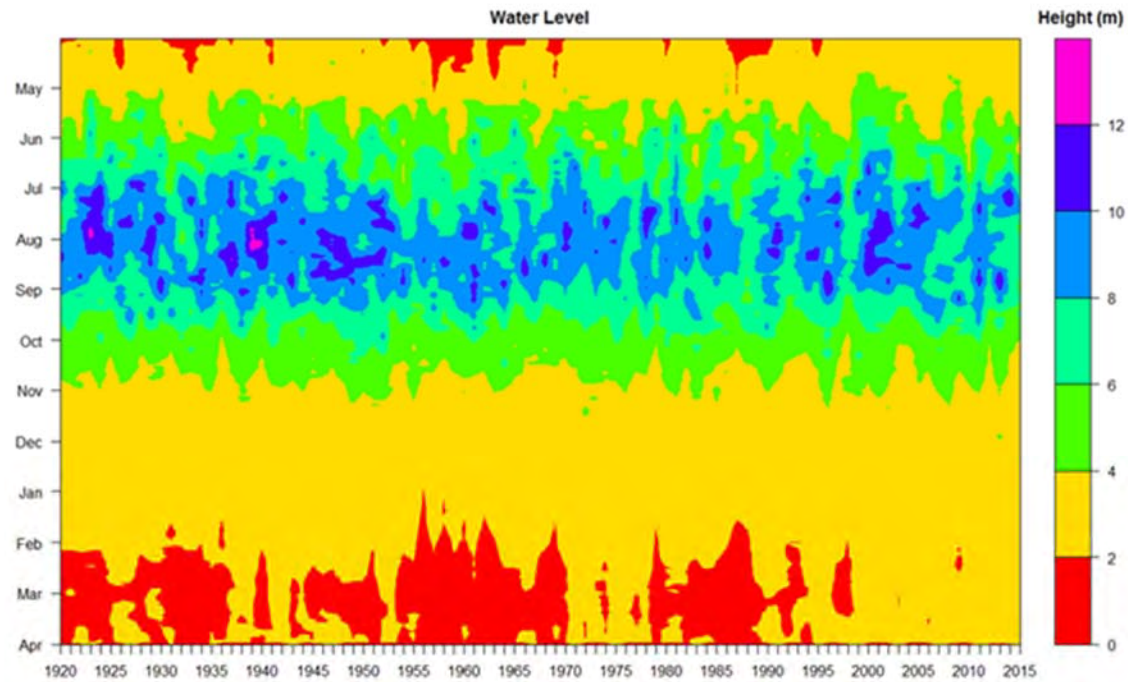


Fig. 6. Temporal raster plot of daily water levels (m) of the Mekong River, Stung Streng Province, 1920-2015.

Fig. 7 below, additionally, displays the maximum and minimum water levels in September and April respectively over 95-year periods in the Mekong mainstream in Stung Treng Province. A pronounced decrease in the maximum flow in September (wet season) and increase in minimum flow in April (dry season) are observed.

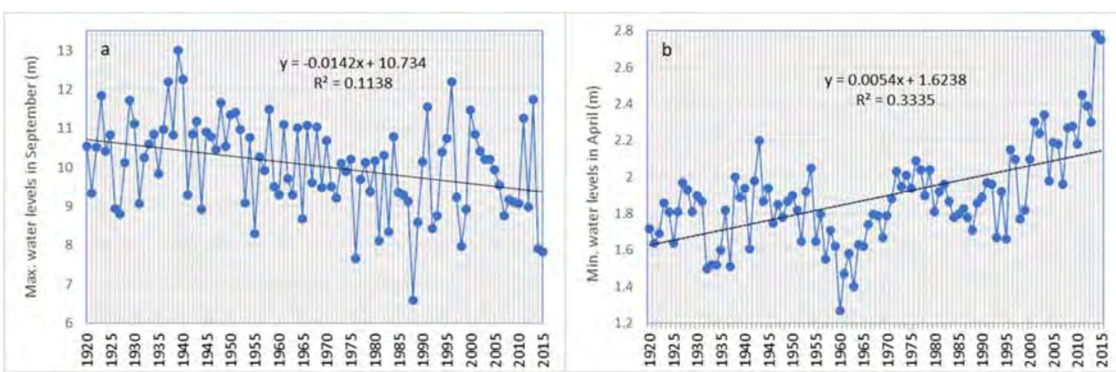


Fig. 7. (a) Maximum daily water levels in September and (b) minimum daily water levels in April between 1920 and 2015 with pronounced increase in the wet season and decrease in the dry season flows.

1.3.2 Habitat loss

Wetlands and river habitat degradation and losses in freshwater ecosystems are widespread worldwide. These habitats are critical for fish spawning, rearing, feeding, or for dry reason refuge. In the Mekong system, dry season refuge are usually situated in perminant water bodies or in the Mekong mainstream (with deep pools) such as in Kratie and Stung Treng Provinces in Cambodia and Champasack Province in southern Lao PDR. The critical habitats are also found either in the main river channel of the major tributaries or floodplains such as the 3S system, the Tonle Sap system and areas south of Phnom Penh and the Mekong delta. Natural flow dynamics ensure the lateral and longitudinal connectivity among these habitats. Many Mekong riverine fishes are known to migrate longitudinally up- and downstream and laterally between tributary rivers and floodplain areas to access the crtical habitats to complete their lifecycles. Therefore, dams physically block migrating fishes from accessing the critical habitats to complete their life cycle. Also, critical habitats such as deep pools that serve as dry season refuge in the main river channel are filled up with particles, sediments released by erosions triggered by hydropower related pulsed flows. As a result, fish is disabled to access these critical habitats which reduces feeding, rearing, spawinng and recruitment success, and thereby, diminishing the system's overall productivity.

Habitat loss is also linked to cumulative effects of flow regulation which is caused by water infrastructure development. Various models indicate that effects of hydropower dams distinctly reduce wet season water levels and increase dry season water levels (Piman et al. 2013, Arias et al. 2014a).The reduction in water levels in the flood season means that seasonally flooded habiats (spawning, rearing and feeding habitats) are less available for fish. In the Tonle Sap, seasonally flooded habitats and gallery forest are estimated to have been reduced by 13 to 22% and 75 to 83%, respectively, whereas the increase in water levels in dry season (i.e. 18 to 21% in the open area of Tonle Sap) is causing permanent submersion of existing vegetation and forests (Arias et al. 2012) triggering a permanent dieback situation of the plants in the submerged area. Thus, these type of changes in the Mekong's natural flow patterns ultimately lead to habitat fragmentation and destruction.

Moreover, other habitat losses are caused by the expansion of agriculture land, gathering of fuelwood, as well as enlargement of settlements in the LMB floodplains as a result of increasing population and government policies. Agriculture policies often focus more on the expansion and intensification of rice farming and industrial crop cultivation. The conversion of flooded forests into farmland and settlements have been accerlated during the last two decades (van Zalinge and Nao 1999, Hortle et al. 2004). These flooded forests are imortant for fishes as shelter, sources of food supply and breeding areas.

1.3.3 Open-access fisheries

Both increased fishing effort, efficiency of fishing gears and increased human population size have likely contributed to high fishing pressure and, thus, overexploitation of the fisheries resources. For example, the use of monofilament nylon gillnets in the LMB has accelerated the decline of some common and commercial species such as *Cirrhinus microlepis*, *Boesemania microlepis*, *Probarbus* spp. and *Tenualosa thibaudeaui, Pangasianodon hypophthalmus, Wallago leeri* (maxTL: 150cm) and Irrawaddy dolphins (van Zalinge and Nao 1999, Deap et al. 2003, Baird 2006). These highly efficient nets were considered as a 'wall-of-death' for many migrating fishes (Hortle et al. 2004 p. 33). The problems caused by these fishing techniques have likely been exacerbated by population growth in the countries sharing the LMB; statistics show that the population has increased about three folds between 1960 and 2015 with about 80-85% rural dwellers (World Bank Group 2015). Factors like free entry into fishing (open-access), affordability of fishing gears (Deap et al. 2003, Hortle et al. 2004), and the combination of rising population along with the lack of complementary and alternative livelihood options, has resulted in millions of people moving into the fishing sector. In addition, prevailing illegal fishing practices such as the use of dynamite, mosquito netting with fences and other destructive fishing methods have put high pressure on fish stocks in the region. Combined with many other streesors (i.e. hydrological alterations, pollution, invasive species and climate change), Mekong fishes and fisheries are facing severe challenges in sustaining its productivity that has for centuries supported millions of peoples' livelihoods in the region.

II. Objectives

As briefly described, rapid water infrastructure development in the Mekong region (particularly hydropower dams and irregation schemes) since 1991 have changed the perception of the pristine Mekong system, one of the world's most biodiverse river basins (Cochrane et al. 2014, Winemiller et al. 2016). The Mekong's natural flow patterns are considered a key environmental driver which plays a main role in structuring the communities of aquatic organsims both up and dowstream (Brownell et al. 2017). Although change in the Mekong flow patterns have been documented to a certain extent, its impacts on fishes and fisheries in some critical areas such as the Mekong-3S system and the Mekong largest wetland of the Tonle Sap are largely undocumented (Arias et al. 2012, Piman et al. 2013, Cochrane et al. 2014). Further, status and trends of fisheries in the LMB during this last decade have not been documented albeit the perception that the region's fisheries have been declining (MRC 2010). Aguably, among the tropical largest wetlands on the planet, the Mekong River and the Tonle Sap, which supports one of the world's biggest freshwater fisheries, have received little ecologcial research and conservation attention (Dudgeon 2000, Junk et al. 2006, Vaidyanathan 2011, Allen et al. 2012, Ngor et al. 2018a). Therefore, there is an urgent need to document and update the system's fish biodiversity, i.e.

to generate reliable information about fish species diversity, species' distribution, fish community composition and evolution through space and time. Combined with data on their ecological requirements the new insights from research can inform basin development planning as well as fisheries management and fish conservation actions.

In recognition of this important fact, the overall objective of the study is to investigate the dynamics of spatial and temporal fish community structure in the Lower Mekong system i.e. Lower Mekong River (LMR) and its major tributaries. To achieve the overall objective, the specific objectives are set out as follows:

(i) describe large-scale spatial fish diversity patterns and assemblage structure in LMR and its major tributaries.

(ii) examine spatial and temporal variation of fish assemblages in the complex Tonle Sap River and Lake system;

(iii) explore the signature of 'indiscriminate fishing' effects by examining the rates of temporal dynamics of the entire fish biomass composition of the Mekong's largest, commercial-scale stationary trawl bagnet *Dai* fishery operating in the Tonle Sap River.

(iv) investigate spatial and temporal fish community responses to flow changes in regulated and unregulated rivers of the Lower Mekong system.

This thesis is divided into two main Parts. Part I is the Synthesis and Part II comprises the corresponding publications. In this Synthesis, Article 1-5 contribute to the overall description on broad-scale spatial and temporal variation in fish diversity patterns and assemblage structure in the LMR and its major tributaries (objective i). While Article 1 describes spatial fish distribution patterns in the LMR (objective i), Article 2 specifically investigates spatial and temporal variation of fish assemblages in the complex Tonle Sap River and Lake system (objective ii). Article 3 exclusively examines the 'indiscriminate fishing' effects of the Tonle Sap fisheries, by analysing temporal changes in the biomass of 116 fish species that seasonally utilize the Tonle Sap River system (objective iii). Finally, Article 4 and 5 scrutinize the spatial and temporal fish community responses to flow changes in regulated and unregulated rivers of the Lower Mekong system.

III. Materials and methods

3.1 Study area

This study covers the Lower Mekong system: the LMR and its major tributaries. LMR extends from the Golden Triangle which marks the borders of Thailand, Lao PDR, China and Burma, and which consists of Cambodia, Lao PDR, Thailand and Viet Nam. Key largest tributaries of the LMB include the TSRL and the Sekong, Sesan and Srepok Rivers known as the 3S Rivers (Fig. 8).

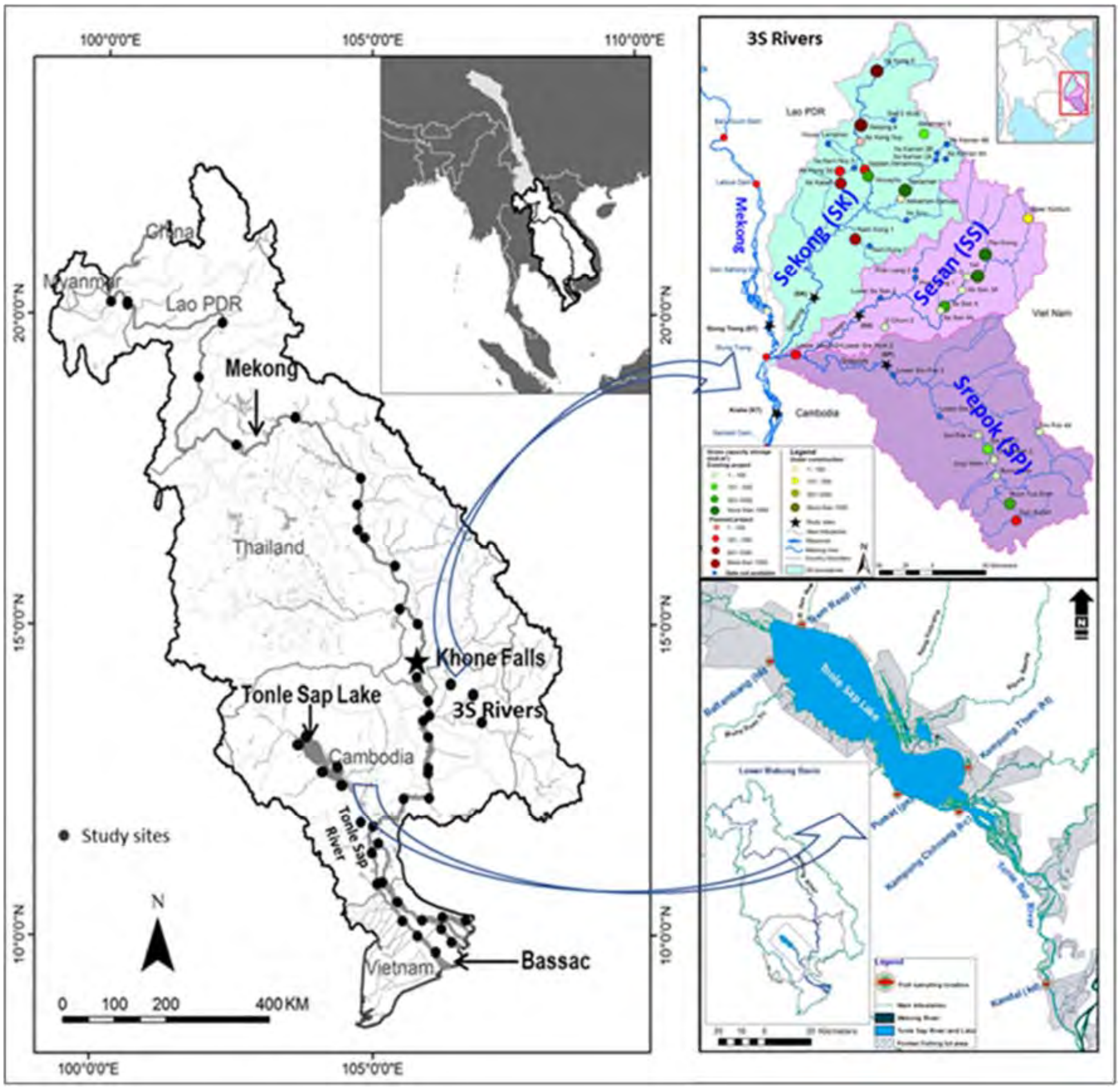


Fig. 8. Maps showing study sites in the Lower Mekong system.

3.2 Data collection

This study uses data from the long-term routine daily artisanal fish monitoring (2007-2014) in the LMB and a standardized catch assessment of the stationary trawl *Dai* fishery (2000-2015), the largest commercial fishery in the Mekong Basin. Data were made available by the Fisheries Program of the Mekong River Commission (MRC) that technically and financially supported the monitoring and catchment assessment programs.

For the daily artisanal fish monitoring, standard sampling procedures of the MRC (MRC 2007) were applied. Fishers were trained on sampling procedures, fish identification and the use of data recording forms. They were supervised by the fishery researchers from the fisheries line agencies and research institutes of the MRC member countries with technical support from the MRC fisheries monitoring specialist. Fish photo books containing more than 200 fish species were also made available for all fishers to assist them in fish identification. Fish captured were identified to the species level and counted. Unidentified species were kept in formalin and taken to laboratory in the central office in each of the respective countries for further identification by professional taxonomists. At the end of each sampling quarter, the fishery researchers collected all recorded forms and data from all fishers. The recorded data were cross-checked with fishers for its accuracy and completeness before being brought to the national central offices for transfer into the national fish monitoring databases. The databases were quarterly cleaned and synchronized into a regional database with the help of an MRC database expert and capture fisheries specialist prior to the analyses.

For the *Dai* fishery, time series data of the fishery's standardized catch assessment between 2000 and 2015 were used. The fishery operates seasonally from October through February/March in a specific location along the lower section of the Tonle Sap River, stretching about 4-30 km north of Phnom Penh. All *Dai* (64 units) are organized into 14 rows (row 2 to row 15) and operated individually or jointly of up to 7 units in a single row with the most upstream row 15 situated close to the Tonle Sap Lake. General concepts and formula for assessing catches and catch composition are outlined in Stamatopoulos (2002), and these concepts were used to frame the sampling protocols and assessing catches of the fishery. The sampling unit was based on *Dai* unit and a randomly stratified sampling method was used for the catch assessment. More specifically, *Dai* units were stratified based on: (i) administrative space divided into two strata (Phnom Penh Municipality and Kandal Province), (ii) time – the lunar period (low period and peak period) and (iii) *Dai* types (high yield and low yield *Dai* units). Random sampling on catches per haul or catches per unit of effort (CPUE; including CPUE for species in catch composition) and daily number of hauls of a *Dai* unit were conducted in each stratum, lunar period and *Dai* type within each month for monthly catch estimate. Likewise, fishing effort (number of active *Dai* units and active days) were recorded according to the stratification framework throughout each fishing month over the whole fishing season. Apart from sampling data on total catch for each species in each season, data were also obtained for the number, weight and length of some common and commercial individual fish specimens caught per day of each fishing season. These species (i.e. *Henicorhynchus lobatus, Labiobarbus lineatus, Pangasianodon hypophthalmus, Cyclocheilichthys enoplos, Cirrhinus microlepis, Osteochilus melanopleurus*) are among the most ecologically, socioculturally (food nutrition and security) and economically important species in the region (Rainboth 1996, Poulsen et al. 2004, Sabo et al. 2017). Therefore, they were used to examine the temporal changes in body weight and length for this study (Article 3).

In addition, this study uses a fish species list (about 900 species and their ecological attributes) that was obtained from the Mekong Fish Database (MFD 2003); the species list was updated by cross-checking with FishBase (Froese and Pauly, 2017), the Catalogue of Fishes Online Database and other literature sources i.e. (Rainboth 1996, Rainboth et al. 2012, Kottelat 2013). Moreover, other fish datasets i.e. maximum total length (maxTL), trophic level and habitats in the water column were consulted from FishBase.

Article 1 uses daily fish monitoring datasets from 38 sites along the Lower Mekong River collected from November 2000 to December 2001. Article 2 uses 4-year daily time-series datasets from artisanal fishers (stationary gillnets and cylinder traps) in six sites: first site located on the Tonle Sap River and the other five sites situated in each of the five provinces around the Tonle Sap Lake from 2012 to 2015, whereas Article 3 uses the 15-year standardized seasonal catch assessment data of 116 fish species from the commercial-scale *Dai* fishery in the Tonle Sap River from 2000 to 2015. Finally, Article 4 and 5 uses a 7-year daily stationary gillnet monitoring data (riverine habitat) from six sites in the complex Mekong-3S system and Tonle Sap River.

3.3 Statistical analysis

3.3.1 Seasonal partitioning

In the Tonle Sap system (Article 2), the unique tropical flood pulse with flow reversal system i.e. rising water levels with flow direction to the Tonle Sap Lake (inflow) and falling water levels with reverse flow direction to the Mekong River (outflow) plays a pivotal role in influencing the intra-annual variation in fish community structure. For this reason, three seasons are defined to reflect the importance of the TSRL flood pulse system, using the 10-year mean intra-annual variation of daily water levels measured at the Tonle Sap Lake (Kampong Loung in Pursat [PS]): inflow or high flow period (July-October), outflow (November-February) and low-flow (March-June). In the Cambodian Mekong and 3S systems, seasonality is defined by a general wet and dry season of the tropical zone for the investigation of the intra-annual variation of fish communities (Article 1, 4, 5). The seasonal partitioning was based on 9-year mean daily water levels of the Mekong River, when entering Cambodia (at Stung Treng [ST]), with wet season covering the period from June to November and dry season from December to May.

3.3.2 Data preparation

For Article 1, all fish catches are transformed into relative abundance to reduce the effect of varying fishing efforts between sites and averaged to annual mean relative abundance prior to analysis. For Article 2, 4, 5, daily abundance data on stationary gillnet (and cylinder traps for Article 2 only) are computed as mean daily samples and then aggregated into weekly species abundance data. Article 3 is based on seasonal catch assessment data from all 64 units of the stationary trawl bagnet (*Dai*) fishery operating in the Tonle Sap River.

3.3.3 Flow seasonality and predictability

To quantify the strength of seasonality, Colwell's seasonality index (Colwell 1974) on site daily water levels (Mekong, Sesan [3S], Tonle Sap) is computed using Colwells function of hydrostats package. The seasonality index M/P which is the Colwell's measure of contingency (M) standardized by Colwell's within-season predictability (P) (Colwell 1974, Tonkin et al. 2017) is used. In addition, modern wavelet analysis is applied to quantify the strength of predictability of site hydrology, using analyze.wavelet function, from WaveletComp package of the 'mother' Morlet wavelet (Roesch and Schmidbauer 2014).

3.3.4 Spatial and temporal description of fish community

All data analyses are performed in R (R Core Team 2017). Summary statistics, cluster analyses (using hclust with Ward hierarchical, and *K*-means clustering methods), boxplots, scatterplots, bubble plots, violin plots, jittering plots and histograms are applied to give a descriptive overview on the spatial and temporal dynamics of fish community structure, as well as weight and length of individual fishes by site and entire species pool in relevant study locations.

Unconstrained ordination techniques, e.g. Nonmetric Multidimensional Scaling (NMDS) and Principal Components Analysis (PCA) (Borcard et al. 2011, Kassambara 2017) are used to visualize fish assemblage samples in a two-ordination plane for the description and analyses of spatial and temporal variability of fish assemblage patterns in important areas of the LMB (Article 2, 4, 5). In addition, for time-series analyses, various time-series analytical tools are applied (Article 2-5). These tools include Whittaker–Robinson periodograms (Legendre and Legendre 2012, Dray et al. 2017), cross-correlation analyses (Shumway and Stoffer 2011), wavelet and cross-wavelet analyses (Roesch and Schmidbauer 2014).

For statistical tests, Permutational Multivariate Analysis of Variance (PERMANOVA) using adonis function of vegan package (with 999 permutations and bray method) is used to test the influence of different factors (e.g. cluster, season and year) on the fish community composition. Complementary, contrast methods are applied to test the pairwise differences between different levels in each of these factors, using pairwise.adonis function in R. In addition, non-parametric Wilcoxon rank-sum and Turkey's multiple comparison tests are performed to test the significant differences between variables i.e. survey sites or weeks/years over the study period. For correlation tests, non-parametric Spearman's correlation tests are used. Significance at the 0.05 level is applied for all tests. Further, to identify species indicator characterizing fish communities in a study site or a cluster, multipatt function from indicspecies package is applied (Cáceres and Legendre 2009, De Cáceres and Jansen 2011).

3.3.5 Species diversity

Richness is computed using specnumber function, whereas inverse Simpson index is computed using diversity function (method = ‘inv’) of vegan package. To compare species richness between sites, rarefaction technique (Article 2) is used to standardize sampling efforts and generate smooth curves for comparison. Rarefaction technique is performed using rarc function from rich package, and c2cv function is used to assess the significance of differences in species richness among sites (Rossi 2011).

Moreover, to investigate temporal dynamics of community composition, temporal beta diversity (Article 4) is computed using beta.div function of the adespatial package (Legendre and De Cáceres 2013, Dray et al. 2017). In estimating total beta diversity (BD_{total}), the total variance of Hellinger-transformed weekly assemblage abundance data is used (Legendre and De Cáceres, 2013). BD_{total} has a value between 0 and 1 for Hellinger-transformed data. BD_{total} can be compared among sites if the sampling units across the study sites are of the same size (Legendre and Salvat 2015), which is the case for the study (Article 4). If BD_{total} is equal to 1, all sampling units have a completely different species composition. BD_{total} is then partitioned into Local (temporal) Contributions to Beta Diversity (LCBD) and Species Contributions to Beta Diversity (SCBD). LCBD is a comparative indicator of the ecological uniqueness of the sampling units. LCBD values give a total sum of 1 for a given data matrix and can be tested for significance (at the 0.05 level in the present study [Article 4]). Species with SCBD indices well above the mean are regarded as important species contributing to beta diversity (Legendre and De Cáceres 2013).

3.3.6 Linear regression models

Linear regression is used to predict the rate of change in the total catch weight of 116 fish species recorded at the *Dai* fishery between 2000 and 2015 (Article 3). The temporal trend for each of the 116 species is expressed as a standardized regression coefficient to allow comparison among species. Linear regression models are also used to describe temporal changes of fish biomass in relation to maximum fish size and trophic positions as well as individual fish weights and length through time.

To identify the key species contributing to the temporal dynamics of species composition over the study period (Article 4), species with SCBD indices greater than the mean at each site are extracted from the community composition matrix. Redundancy Analysis (RDA) is then performed on the community composition data against time and its quadratic effect as explanatory variables. Using RDA, the relationship between the observations (sampling units), species and explanatory variables (the years) can be visualized. Further, to help identify the key species explaining the temporal shift in assemblage composition, indicator species characterizing fish assemblages at each site are computed using the multipatt function of the indicspecies package (Cáceres and Legendre 2009, De Cáceres and Jansen 2011) for comparison.

IV. Results

4.1 Summary of recorded catches in the Lower Mekong Basin

Of three MRC fisheries monitoring programs in the LMB during this last decade, namely the artisanal fish monitoring, the commercial *dai* fishery monitoring and *lee* trap monitoring, some 504 fish species and two groups of other aquatic animals (OAAs), which are freshwater prawns and clams, are recorded. These fish species belong to 252 genera, 78 families and 22 orders. Four main orders representing ~82% of the total species counts are: Cypriniformes (202), Siluriformes (101), Perciformes (94) and Clupeiformes (20) (Fig. 9).

Among the recorded 78 fish families, the top six families which account for 52% of total species counts are Cyprinidae (32%), Cobitidae (5%), Siluridae (4%), Bagridae (4%), Pangasiidae (4%), and Gobiidae (4%); each of the remaining 72 families comprise less than 4% of the species counts. Most of these top fish families also form the largest proportion of both total species abundance and biomass (Fig. 10 and 11).

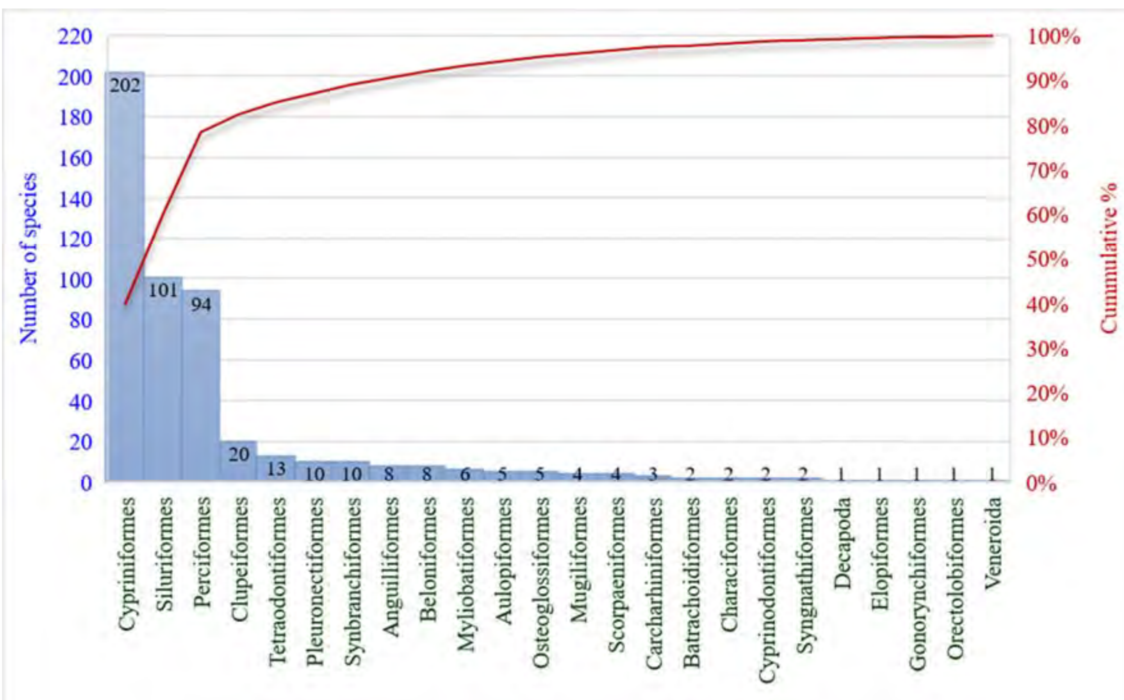


Fig. 9. Number of species by order: 22 fish orders and 2 orders of other aquatic animal (OAA)[1] i.e. Decapoda (freshwater prawns) and Veneroida (clams). Data source: MRC routine fish monitoring programs: commercial *Dai* fishery (2000-2014), *lee* trap fishery (2000-2014) and artisanal fisheries (2007-2014).

[1] They are NOT identified to species level but representing the common names of many species under each order.

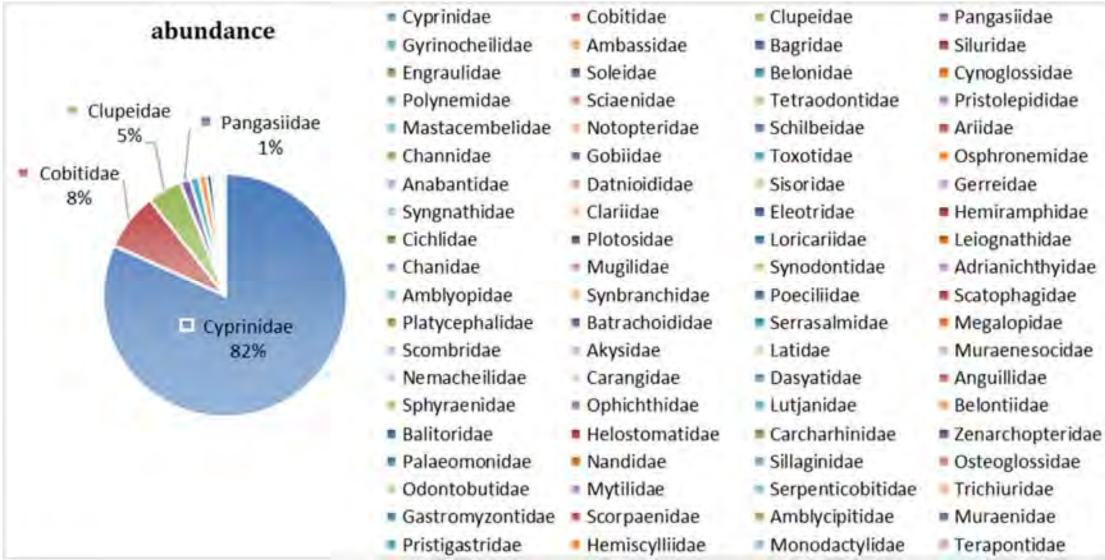


Fig. 10. Relative total abundance highlighting the four top fish families that contribute 96% to the total abundance and the list of other fish and two OAA families reported in the MRC fish monitoring programs. Data source: MRC routine fish monitoring programs: commercial *Dai* fishery (2000-2014), *lee* trap fishery (2000-2014) and artisanal fisheries (2007-2014).

Fig. 11. Relative total biomass highlighting the four top fish families that contribute 94% to the total fish biomass and the list of other fish and two OAA families reported in the MRC fish monitoring programs. Data source: MRC routine fish monitoring programs: commercial *Dai* fishery (2000-2014), *lee* trap fishery (2000-2014) and artisanal fisheries (2007-2014).

4.2 Overall fish assemblage structure and diversity

4.2.1 The Lower Mekong River

At reginal spatial scale, fish species richness is found to be linked to longitudinal river gradients with level of richness increasing towards lower altitude. From a one-year daily fish catch monitoring, the lowest richness occurs at the head of the LMR (17 species) and the level of richness increases gradually as the river reaches the mouth of the Mekong River in its delta (82 species) (Fig. 12a). This pattern is observed to exist consistently during both wet and dry seasons (Fig. 12b, c). On the contrary, the Inverse Simpson diversity index is found to be the highest (median: 10.5) in the middle part of the river system and lowest (median: 3.5) at the mouth of this river (Mekong delta) (Fig. 12a, b, c).

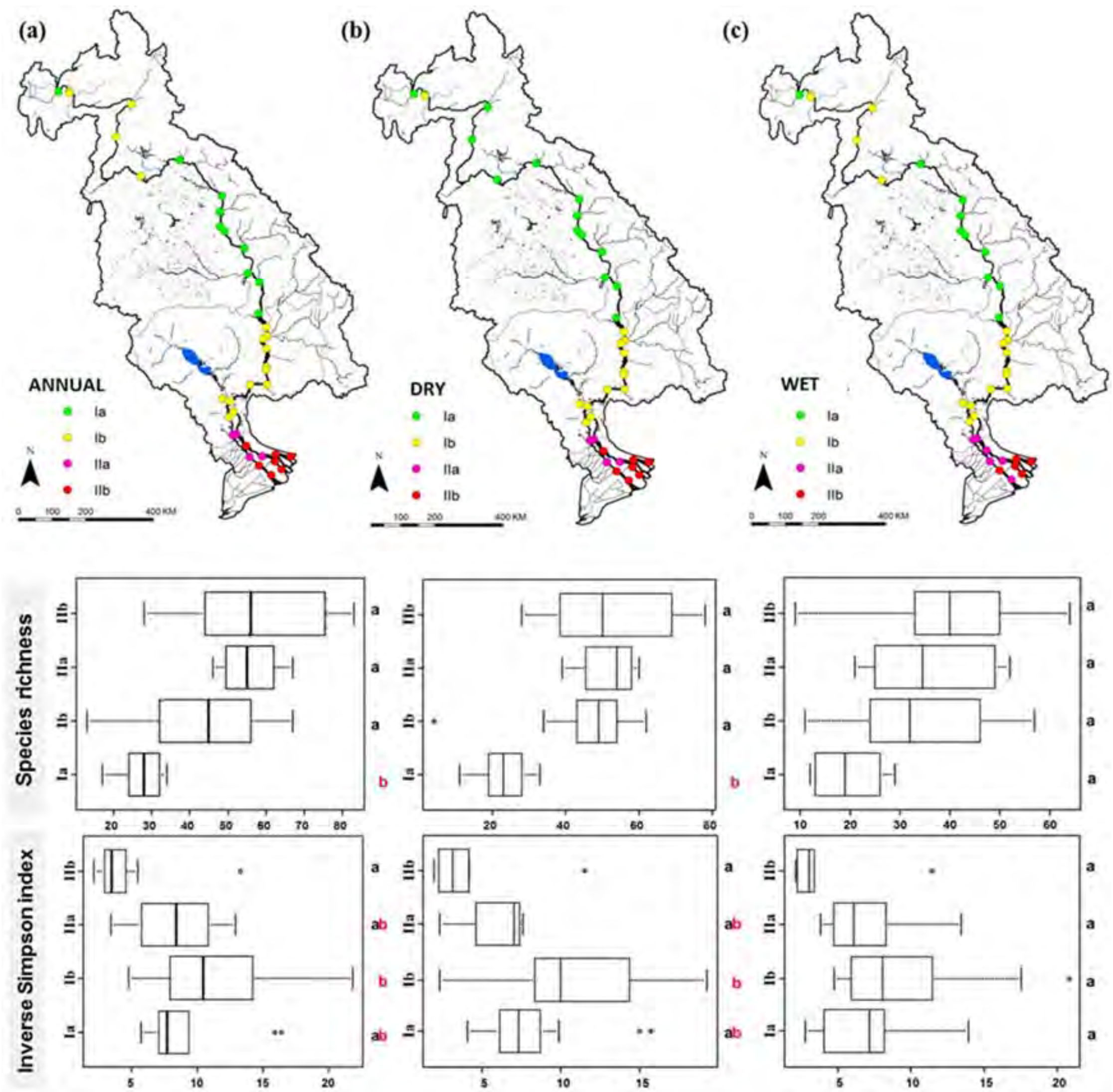


Fig. 12. Fish distribution and assemblage patterns in the Lower Mekong Basin. Annual (a), dry season (b) and wet season (c) clustering associated with species richness and inverse Simpson index of each

cluster (Ia, Ib, IIa, IIb). Mean values among clusters with a common letter are not significantly different at p-value=0.05 (Tukey's HSD tests).

Some 80 indicator fish species are identified from the four annual clusters as shown in Fig. 12a. Species indicators in each cluster are given in Annex 1. The highest number of indicator species is found in IIb (31 species), while the lowest is observed in Ia (11 species). The clusters in the Mekong delta (IIa and IIb) make up 66% of the total indicator species. The indicator species in Ia and Ib are mostly species from Cyprinidae, Pangasiidae, Siluridae and Bagridae families, namely *Cosmochilus harmandi, Bagnana behri, Helicophagus waandersii, Labeo chrysophekadion, Bagarius yarelli, Henicorhynchus* spp., *Micronema bleekeri and Hemibagrus nemurus*, which are known as potamodromous fish and indigenous to the LMB. Assemblage IIa contains 21 indicator species. Among them, many are known as freshwater and secondary freshwater fishes such as *Glossogobius giuris, Macrognathus siamensis, Acantopsis* sp., *Puntioplites proctozysron, Mastacembelus armatus and Mystus mysticetus*. Similarly, the main indicator species of IIb are mostly characterized by secondary freshwater fish and marine species, known as amphidromous and anadromous fishes, that is *Clupeichthys aesarnensis, Rasbora trilineata, Scomberomorus sinensis, Eleotris* spp., *Liza* spp., *Arius stormi, Toxotes* spp. and *Lates calcarifer*. Most of indicator species during the dry season are also identified as indicator species using annual assemblage compositions. Overall, dry season assemblages contain more indicator species (73 species) as compared to wet season assemblages (51 species), while many indicators species from annual IIa and IIb are absent in the wet season.

4.2.2 The complex Mekong-3S system

Over the 7-year period, 292 species have been recorded in the catch samples. Among those, 208 fish species are recorded in Kratie (KT), 196 in Stung Treng (ST), 177 in the Srepok River (SP), 133 in the Sesan River (SS) and 216 in the Sekong River (SK). These fishes belong to 14 orders, 48 families and 151 genera. Five main orders represent 90% of the total species count: Cypriniformes (146 species), Siluriformes (66), Perciformes (34), Pleuronectiformes (9) and Clupeiformes (6). The top five families accounting for 63% of total species counts are Cyprinidae (123 species), Bagridae (16), Cobitidae (16), Pangasiidae (15) and Siluridae (11).

In addition, boxplots on weekly abundance, richness and inverse Simpson diversity index (Fig. 13a-c) indicate that Kratie (KT) has lowest weekly abundance, whereas ST possesses the highest abundance. The abundance in SP is comparable to that of ST while the fish abundance in SS and SK displays intermediate status among the five sites. For richness, the Mekong sites has the highest richness (KT: median=23, sd=10.95; ST: median=27, sd=9.87) and inverse Simpson indices (KT: median=9.20, sd=5.30; ST: median=8.82, sd=5.10) relative to the 3S sites. Noticeably, SS shows both the lowest species richness (median=12, sd=5.14) and diversity index (median=5.45, sd=2.78) of all sites, whereas SP is comparable with KT in terms of species richness. Although SP had higher species richness (median=23, sd=7.52) than SK (median=19, sd=8.25), the diversity indices between the two sites are not significantly different (SP: median=6.89, sd=3.70; SK: median=7.49, sd=4.38).

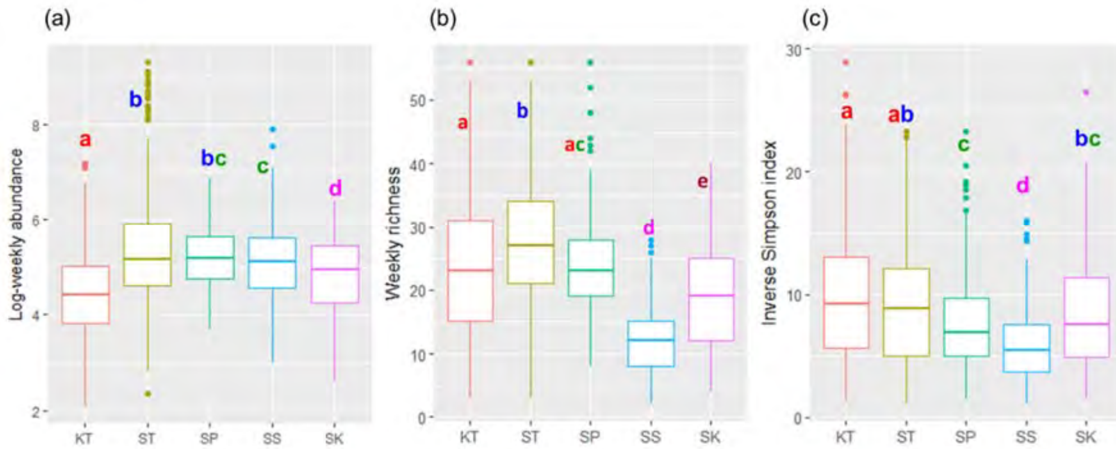


Fig. 13. Fish diversity in the Mekong-3S system. (a) Weekly species abundance (log-scale); (b) Weekly species richness; and (c) Weekly inverse Simpson diversity index. Mean values among sites with a common letter are not significantly different at the 0.05 level (Pairwise Wilcoxon Rank Sum Tests). For site names, KT=Kratie, SK=Sekong, SP=Srepok, SS=Sesan, and ST=Stung Treng.

4.2.3 The Tonle Sap system

In the Tonle Sap system, the largest wetlands and a major tributary of the Mekong Basin, 204 species from 114 genera, 38 families and 13 orders have been recorded over four-year monitoring period in six study sites on the Tonle Sap River and around the Tonle Sap Lake. The three main orders representing 87% of the total species count are Cypriniformes (100 species), Siluriformes (48) and Perciformes (29). Clupeiformes, Osteoglossiformes and Synbranchiformes, each containing five species; the rest contributes less than 6% to the total species counts. At family level, the top five families accounting for 60% of total species counts are Cyprinidae (80), Bagridae (12), Pangasiidae (11), Cobitidae (10) and Siluridae (10); each of the remaining 33 families comprise one to six species. At species level, ~62% of catches is dominated by 12 fish species namely *Henicorhynchus lobatus* (11%), *H. siamensis* (10%), *Trichopodus trichopterus* (7%), *Puntioplites proctozysron* (7%), *Osteochilus vittatus* (6%), *Trichopodus microlepis* (5%), *Labiobarbus lineatus* (4%), *Paralaubuca typus* (3%) and *Mystus mysticetus* (3%), *Notopterus notopterus* (3%) and *Rasbora tornieri* (3%). Ecologically, longitudinal migratory species (white fish) account for ~58% of total abundance, while floodplain resident black and lateral-migrant gray fishes contribute 19% and 21%, respectively. The rest (1%) is composed of estuarine species and marine visitors. Among the six survey sites, the highest species richness is observed in the middle section of the lake in Kampong Thom (KT) and Pursat (PS) while the lowest richness occurs in the northern part in Battambang (BB) (Fig. 14a). Similar richness is observed in Kandal (KD), Kampong Chhnang (KC) and Siem Reap (SR). Also, richness in PS is comparable with that of KD and SR. In addition, the lowest abundance is observed in KD, while the highest was reported in Kampong Thom (KT) (Fig. 15). Likewise, the highest diversity index occurs in the middle part of the lake in PS and KT while the lowest is observed in the river section in KD (Fig. 14b). Diversity index in KC is similar to that in BB.

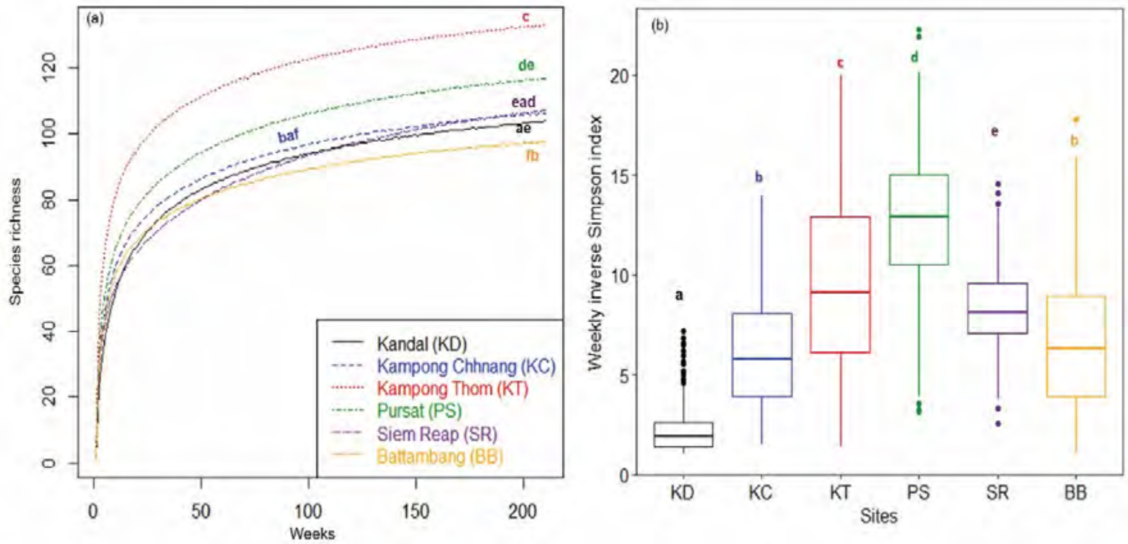


Fig. 14. Spatiotemporal comparison of site fish species richness and diversity in the Tonle Sap River and Lake: (a) site rarefaction curves on species richness; (b) site inverse Simpson index with south-north gradient along the Tonle Sap Rive and Lake. Sites with a common letter are not significantly different at p-value=0.05. For site names: KD=Kandal, KC=Kampong Chhnang, KT=Kampong Thom, PS=Pursat, SR=Siem Reap and BB=Battambang.

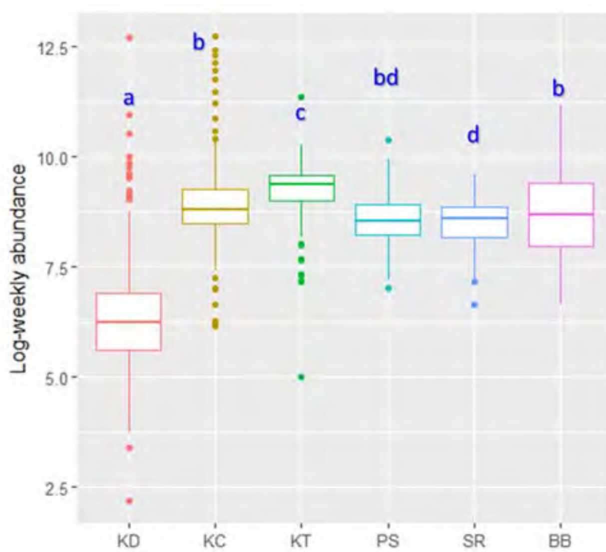


Fig. 15. Spatiotemporal comparison of site fish species abundance in the Tonle Sap River and Lake. Mean values among sites with a common letter are not significantly different at p-value=0.05 (Wilcoxon test). For site names, see Fig. 14.

4.3 Spatial variation in fish abundance distribution

4.3.1 The Lower Mekong River

The relative abundance of fish orders varies greatly along the longitudinal gradient of the LMR system, and this pattern is consistent between seasons for all fish orders except Clupiformes, Fig. 16, Wilcoxon test, p<0.05). Apart from the Mekong delta, that is particularly in Ia and Ib (see Fig. 12), Cypriniformes and Siluriformes dominated and occurred almost in every site, while their abundances declined dramatically in the delta. Additionally, Osteoglosiformes and Perciformes are found in some sites of Ib in Cambodia. In the delta (IIa and IIb), the fish composition is diverse and characterized by many species from different orders such as Clupeiformes, Perciformes, Pleuronectiformes, Synbranchiformes, Tetraodontiformes; among those, Perciformes and Clupeiformes are the most abundant (Fig. 16).

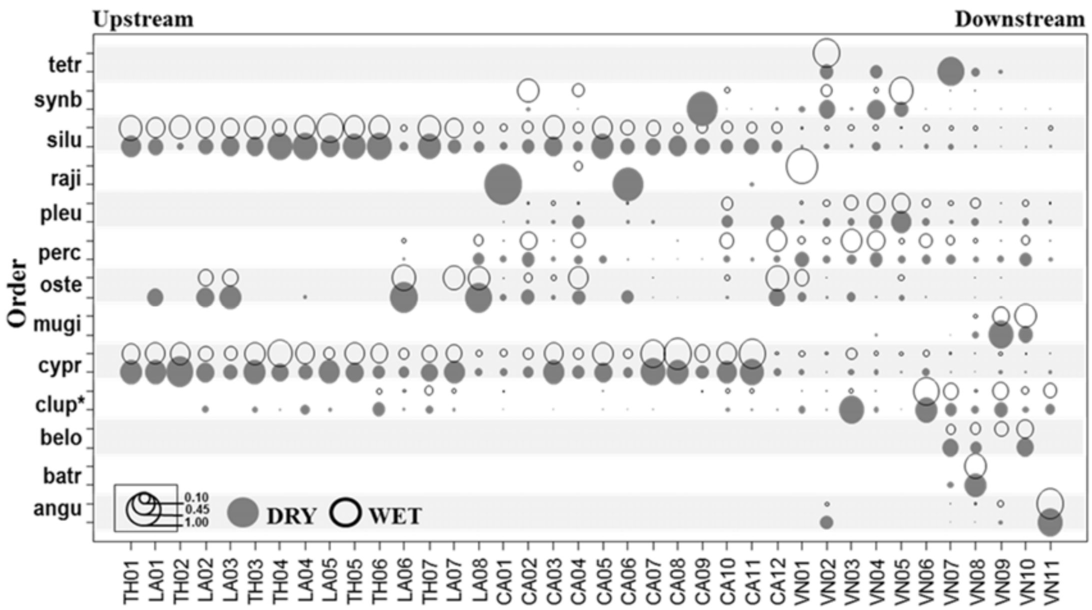


Fig. 16. Relative abundances of fish order along the Lower Mekong River. Open and closed circles denote the wet and dry seasons respectively. The acronyms in the vertical axis denote the species order: angu (Anguilliformes), batr (Batrachoidiformes), belo (Beloniformes), clup (Clupeiformes), cypr (Cypriniformes), mugi (Mugiliformes), oste (Osteoglossiformes), perc (Perciformes), pleu (Pleuronectiformes), raji (Rajiformes), silu (Siluriformes), synb (Synbranchiformes), tetr (Tetraodontiformes). The acronyms in the horizontal axis indicate the location of the sites: TH (Thailand), LA (Lao PDR), CA (Cambodia) and VN (Viet Nam). *denotes significant differences in fish relative abundance between seasons (Wilcoxon test, p-value=0.04).

4.3.2 The Mekong-3S system

K-means clustering (with five clusters) on a PCA plot (Fig. 17) shows that sites on the Mekong (cluster 4 and 5) overlap, indicating assemblage similarities between the two sites, while the 3S sites, particularly SK (cluster 1) and SS (cluster 2), are distant from the Mekong sites, suggesting distinct assemblages. SP (cluster 3) exhibits some similarities with the Mekong sites (ST). Assemblage dissimilarities are further observed among the 3S sites (axis 2).

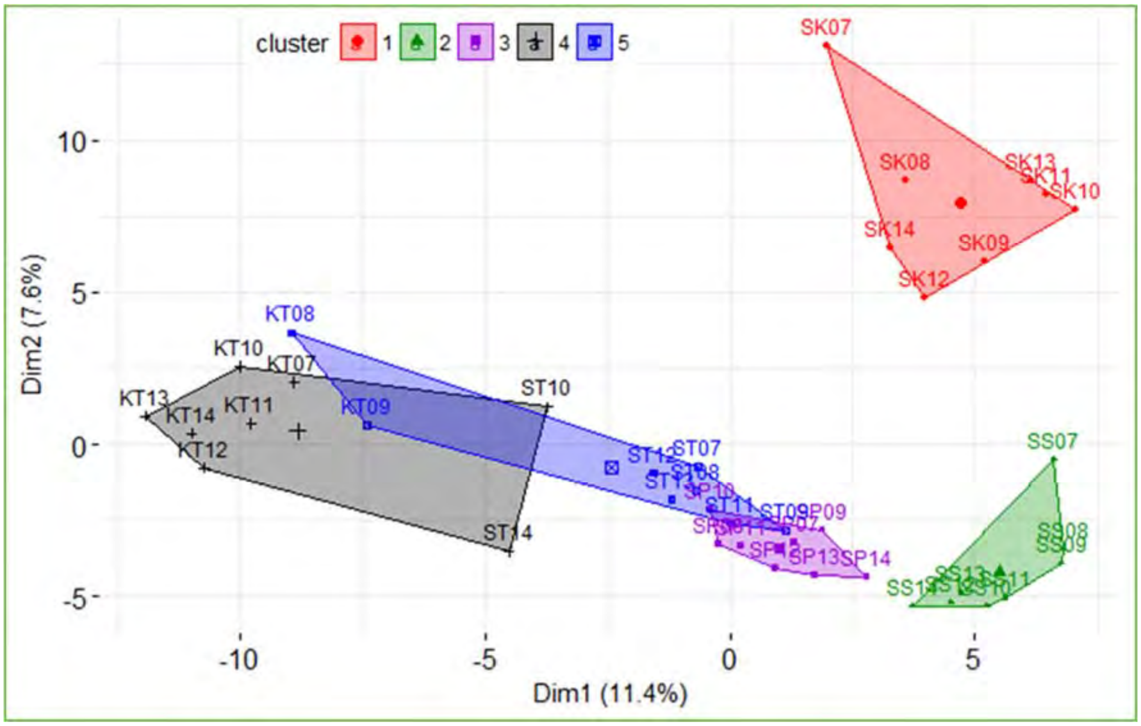


Fig. 17. Fish assemblage patterns in the Mekong-3S system, using *K*-means cluster on PCA plot (k=5) on Hellinger-transformed yearly assemblage data. Five convex hulls (with different colors) represent each assemblage cluster of the Mekong-3S system. A combination of two letters and two digits denotes the site name and year; for example, KT07 is Kratie in 2007. For site names, KT=Kratie, SK=Sekong, SP=Srepok, SS=Sesan, and ST=Stung Treng.

4.3.3 The Tonle Sap system

Based on fish community composition, KD in the most southern section of the system is significantly different from the other sites along the first axis of the NMDS, whereas the second axis mainly opposes BB in the northern part of the lake to the other sites (Fig. 18b). Hierarchical clustering with Ward agglomerative method allows classifying all weekly samples into three clusters (Fig. 18a) according to their species composition similarities. The first split of the dendrogram defines fish assemblages in riverine (cluster 1) and lacustrine environments (cluster 2 and cluster 3), while the second split separates the two main assemblages (clusters 2 and 3) in the middle and northern sections of the lake. The first cluster (159 samples) is mainly associated with samples from KD. The second, the largest cluster (613 samples), mainly groups samples from KC, KT, PS and SR, and the third cluster (456 samples) is related to samples from BB.

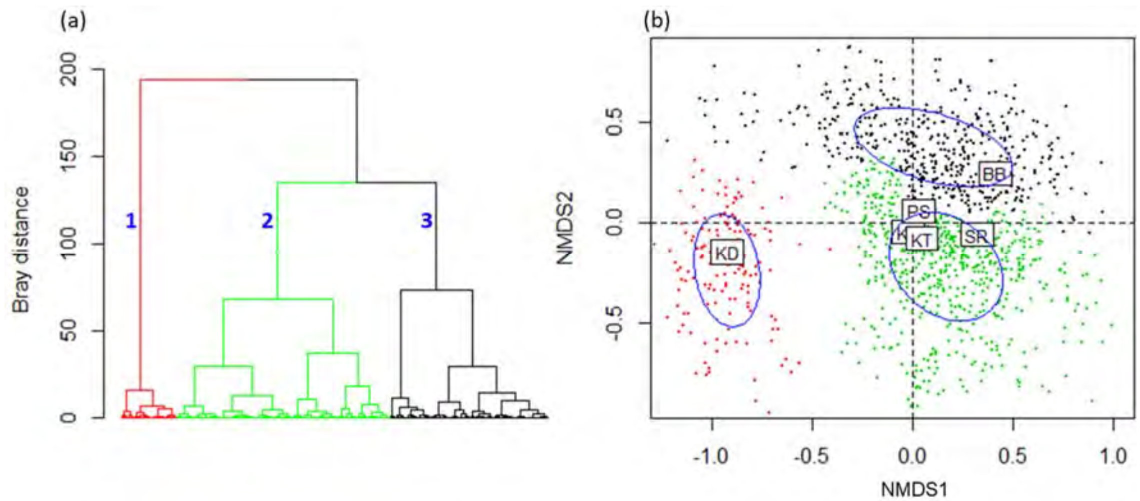


Fig. 18. NMDS biplot of the weekly fish abundance samples (with Bray-Curtis dissimilarity matrix), showing the Tonle Sap River and Lake (TSRL) fish community spatial variation. Dots on the biplots represent samples. (a) Ward hierarchical clustering dendrogram of the weekly samples showing 3 distinct clusters; (b) spatial distribution patterns of sites along the TSRL gradient grouped into three clusters. For site names: KD=Kandal, KC=Kampong Chhnang, KT=Kampong Thom, PS=Pursat, SR=Siem Reap and BB=Battambang.

Overall, 114 species have been reported in cluster 1, 182 in cluster 2 and 154 in cluster 3. The ten most abundant species for each assemblage cluster account for ~97% in cluster 1, ~58% in cluster 2 and ~65% in cluster 3 (Fig. 19a). Interestingly, two small-sized cyprinids: *Henicorhynchus lobatus* (Hlob) and *H. siamensis* (Hsia) make up of ~45% of the total abundance in cluster 1 while they account for only ~19% and ~16% in cluster 2 and cluster 3, respectively. Further, of the top ten species, only five species (~84%) dominate the catch in cluster 1, whereas in cluster 2 and 3, the ten dominant species share the catch proportionately between 3 and 10%. *Puntioplites proctozysron* (Ppro) is found among the top ten species for all clusters. Ecologically, catches in cluster 1 comprise ~96% of migratory white fish which decreases gradually to ~57% and ~52% in cluster 2 and cluster 3, respectively (Fig. 19b).

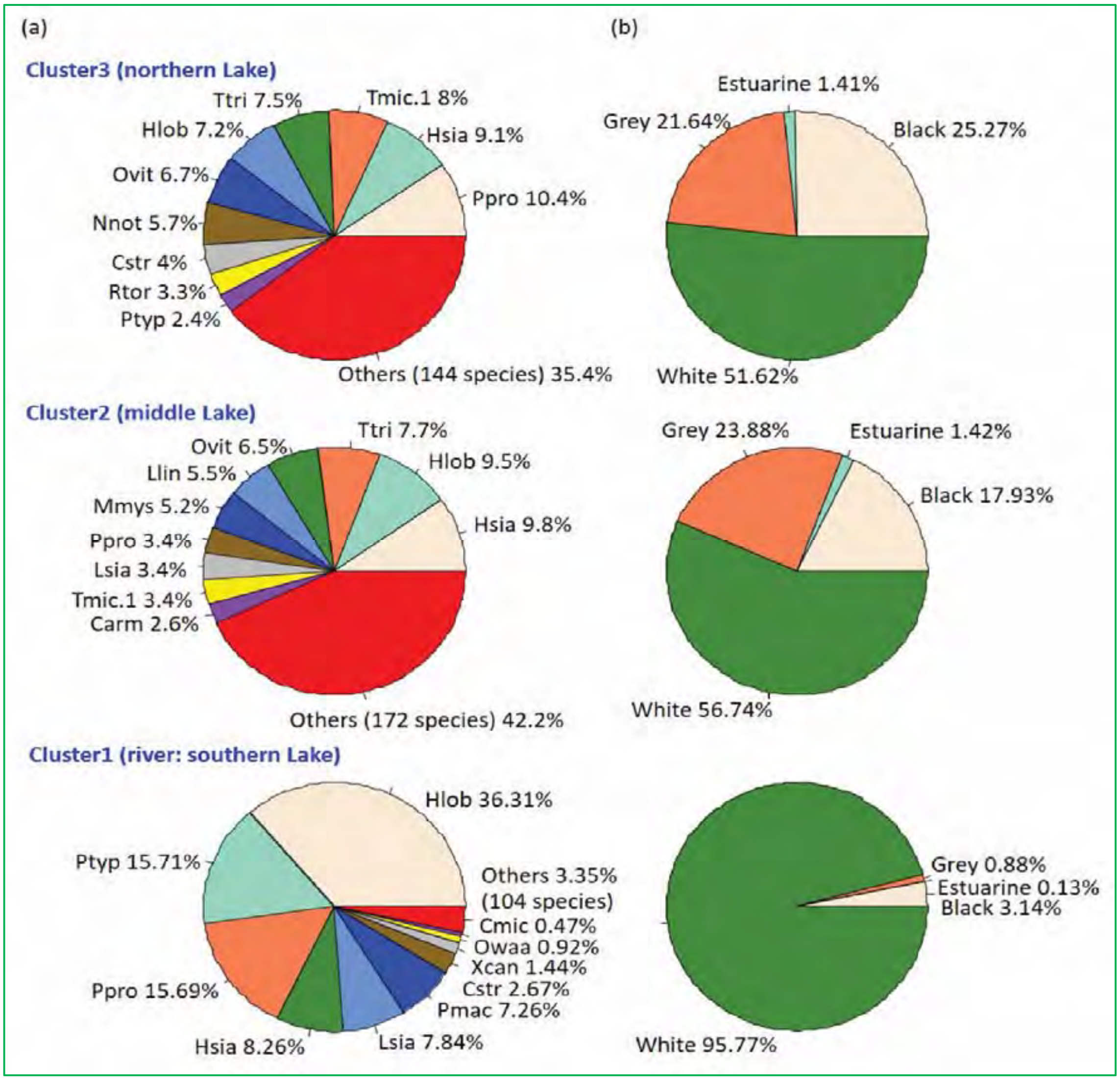


Fig. 19. Species relative abundance organized by cluster and fish migration guild. (a) Ten most abundant species by cluster. (b) Community composition by migration guilds. For cluster, see Fig. 17a, b. For species details and migration guilds, see S9, Article 2.

For the entire species pool of the TSRL, 96 indicator species are identified from the three assemblage clusters (for species details, see Article 2, S5). The largest number is observed in cluster 2 (45 species) while the least is detected in cluster 1 (20). Key indicator species with high indicator values characterizing cluster 1 belong to Pangasiidae (river catfishes), e.g. *Pangasius macronema, P. conchophilus* and *P. bocourti*; Cyprinidae (cyprinids) e.g. *Labiobarbus siamensis*, *Puntioplites falcifer, Paralaubuca typus* and *P. riveroi;* Siluridae (sheatfishes) e.g. *Phalacronotus bleekeri* and *Belodontichthys truncates* and Cobitidae (loaches) *Yasuhikotakia caudipunctata.* Interestingly, *Cyprinus carpio*, an exotic species is also identified for this cluster.

Key indicator species representing cluster 2 are those of Bagridae (Bagrid catfishes) such as *Mystus mysticetus* and *M. singaringan* (floodplain spawners)*;* Cyprinidae (white/gray fish) including *Labiobarbus lineatus, Osteochilus vittatus, Labeo chrysophekadion, Thynnichthys thynnoides* and *Henicorhynchus siamensis;* Anabantidae (climbing perches) i.e. *Anabas testudineus* (floodplain resident)*;* Pristolepididae (leaffish) i.e. *Pristolepis fasciata* (floodplain spawner)*;* Ambassidae (asiatic glassfish) i.e. *Parambassis wolffii* (floodplain spawner); Cobitidae i.e. *Yasuhikotakia modesta* (main channel spawner); Mastacembelidae (spiny eels) i.e. *Macrognathus siamensis* (floodplain resident)*;* Osphronemidae (gouramies) such as *Trichopodus trichopterus* (floodplain resident) etc.

Finally, main species which are indicative of cluster 3 include Notopteridae (featherbacks) i.e. *Notopterus notopterus;* Bagridae i.e. *Hemibagrus spilopterus;* Osphronemidae i.e. *Trichopodus microlepis* and *T. pectoralis;* Cyprinidae i.e. *Barbonymus gonionotus* and *Hampala macrolepidota*; Channidae (airbreathing snakeheads) i.e. *Channa striata*; Siluridae i.e. *Ompok bimaculatus,* Eleotridae (sleepers) i.e. *Oxyeleotris marmorata;* Clariidae (airbreathing catfishes) i.e. *Clarias microcephalus, C. meladerma* and *C. batrachus;* and Tetraodontidae (puffers) *Pao leiurus*.

4.4 Temporal dynamics of fish community

4.4.1 Temporal variation of fish community in the Tonle Sap River and Lake

4.4.1.1 Intra-annual (seasonal) variation in the TSRL fish community

Over the 4-year survey, it has been discerned that seasons related to the inflow (I), outflow (O) and low-flow (L) periods appear to significantly influence the variation in the TSRL fish community (Fig. 20a). PERMANOVA and contrast pairwise tests indicate significant differences among seasons with p-value=0.001 and between seasons with p-adjusted value=0.003 for all pairwise comparisons. Wilcoxon tests on NMDS site scores reveal significant differences between I and L on axis1 (p-value=0.044), and between O and I (p-value=0.004) as well as between I and L (p-value=0.008) on axis2. Generally, high abundance and richness occurs during the outflow period while lowest abundance and richness are observed during the inflow for all sites except for BB where richness is high during the inflow period.

Finally, significant changes in fish communities are also observed over the four-year period (Fig. 20b), with PERMANOVA test among years, p-value=0.001 and contrast pairwise tests between years, p-adjusted value=0.006 for all pairwise comparisons. Significant changes are mainly observed toward negative values along NMDS axis2. Wilcoxon tests show that 2012 is significantly differed from other years along axis1 (p-value<0.001), while along axis2, the differences between all pairs of years are significant at p-value<0.001. Overall, weekly abundances show some fluctuations with no clear trend over the four-year period for all sites; however, a decreasing trend is observed for weekly richness in the middle part of the lake (KC, PS, KT, SR).

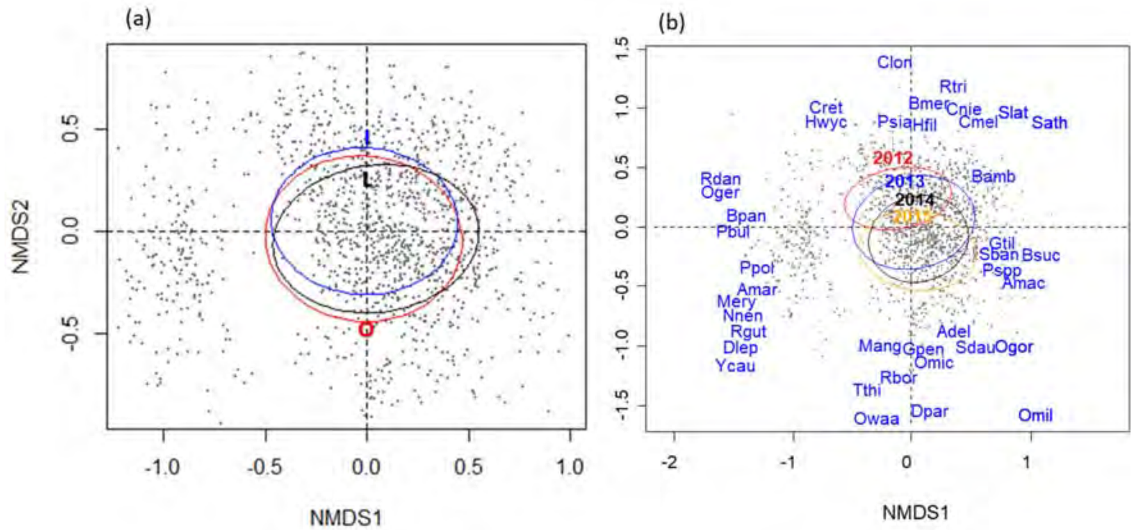


Fig. 20. NMDS biplots of the weekly fish abundance samples (with Bray-Curtis dissimilarity matrix), showing the Tonle Sap River and Lake fish community temporal variation. Dots on the biplots represent samples. (a) intra-annual (seasonal) variation: I, O, L respectively symbolizing Inflow (or high flow periods) (July-October), Outflow (November-February) and Low flow (March-June); (b) inter-annual variation among years (2012-2015). Names are abbreviations of fish species names. For fish species details, see S9, Article 2).

4.4.1.2 Inter-annual variation in the TSRL fish community

Further, significant links between either weekly abundance or richness and water levels in the lake (PS) are observed (Spearman correlation tests, p-value<0.05 for all sites except for BB). The cross-correlation analysis between the bivariate series for the two sites (Tonle Sap River, KD and Tonle Sap Lake, PS) point out that there is a positive relationship between the temporal variation in species abundance and richness, and hydrology (Fig. 21a-d). Overall, fish community responses appear to lag behind flow regime (i.e. water leads fish). The correlation lag for fish abundance versus water levels at maximum coefficient is estimated at -15 weeks in KD and -16 weeks in PS (Fig. 21a, b), whereas the correlation lag for species richness versus water levels is estimated at -8 weeks in KD and -10 weeks in PS. It is noteworthy that the time lag between water levels in the Tonle Sap River (KD) and those of the lake (PS) are estimated at about -2 weeks. Consequently, it is consistently seen that peak abundance and richness begin one to two weeks earlier in the lake than in the Tonle Sap River.

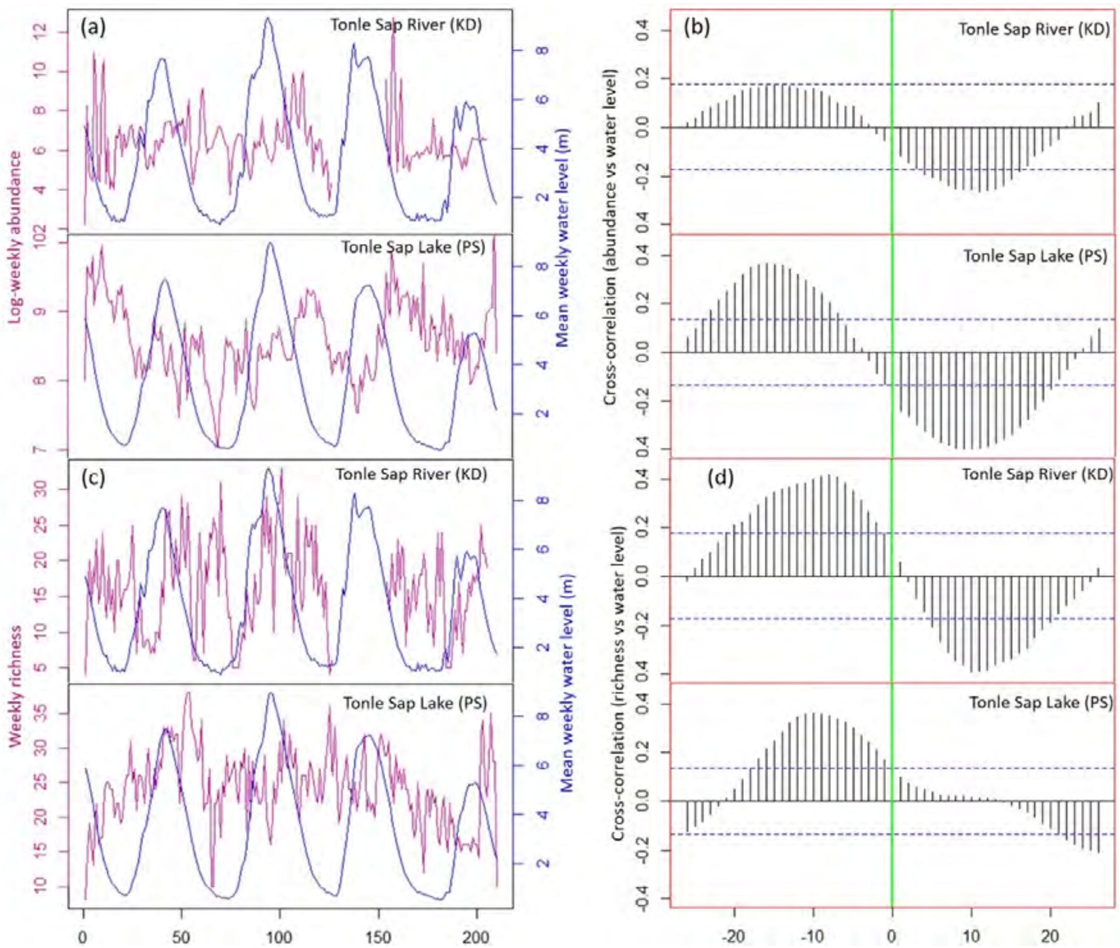


Fig. 21. Relationships between water levels and (a-b) species abundance and (c-d) richness in the TSRL. In cross-correlation plots, the dotted blue lines give the values beyond which the correlations are significantly different from zero. The X-axis (a) is the number of weeks for the period from 1 January 2012 to 31 December 2015.

4.4.1.3 Temporal changes in fish biomass and its relationships with max. length and trophic level

The distribution of the standardized regression coefficients for 116 species reported in the Mekong's largest commercial *Dai* fishery, which reflected the nature of the relationship between seasonal fish catch and time for each species over the last 15-year period, is skewed to the right, centered around -0.4, and spread between -0.78 and 0.66 (Fig. 22). Out of the 116-total species, 90 (78%) have negative standardized regression coefficients. These results indicate that the seasonal catches of these species harvested by the *Dai* fishery decline over the 15 years studied. On the contrary, there are also species (26 out of 116 or 22%) with positive standardized regression coefficients, indicating an increase in the catch of these species by the *Dai* fishery.

Interestingly, *Oreochromis mossambicus* is an exotic species that is among the largest positive coefficients observed. In addition, *Labiobarbus lineatus*, *Henicorhynchus lobatus* and *H. cryptopogon* (synonym of *Lobocheilos cryptopogon*) are all known to be highly prolific and form the largest proportion of the catch from the fishery. These species also have positive standardized coefficients. In fact, the increase in these species stabilizes the seasonal *Dai* catches as it is evidenced in the total catch of the fishery which was stationary over the study period (p-value=0.982, Fig. S8, Article 3).

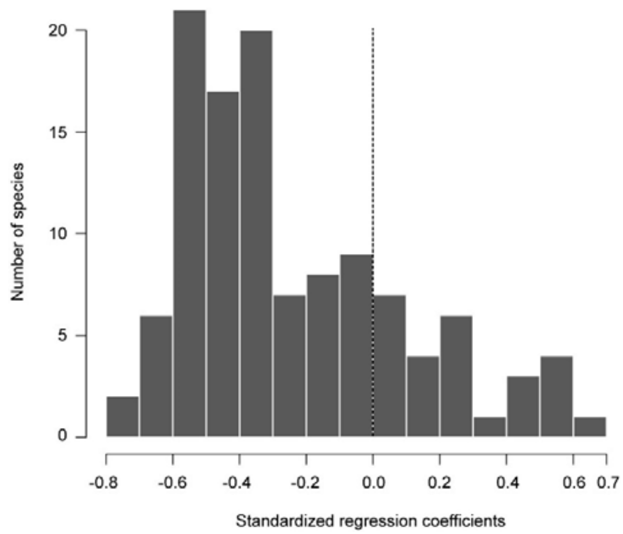


Fig. 22. Distribution of standardized regression coefficients of seasonal catches of 116 fish species recorded at the *Dai* fishery, Tonle Sap River from the fishing season of 2000/01 to 2014/15.

Species with declining catch in the *Dai* fishery are disproportionately represented by those with larger body sizes and higher trophic levels based on linear regressions (Fig. 23a, b), which demonstrates overall negative relationships between the log+1 transformed standardized regression coefficients and the corresponding log-transformed maxTL (slope=-0.08, p-value=0.08, r^2=0.03), and trophic level (slope=-0.15, p-value=0.024, r^2=0.04). In the regression model, five endangered and critically endangered species (solid points on Fig. 23a, b) are included. However, it is also likely that these species are very rare and, as such, their catches obtained in the catch assessment could be misleading. Therefore, when they are dropped from the analysis, the significant relationships are indicated with both maxTL (slope=-0.13, p-value=0.006, r^2=0.06) and trophic level (slope=-0.16, p-value=0.02, r^2=0.05).

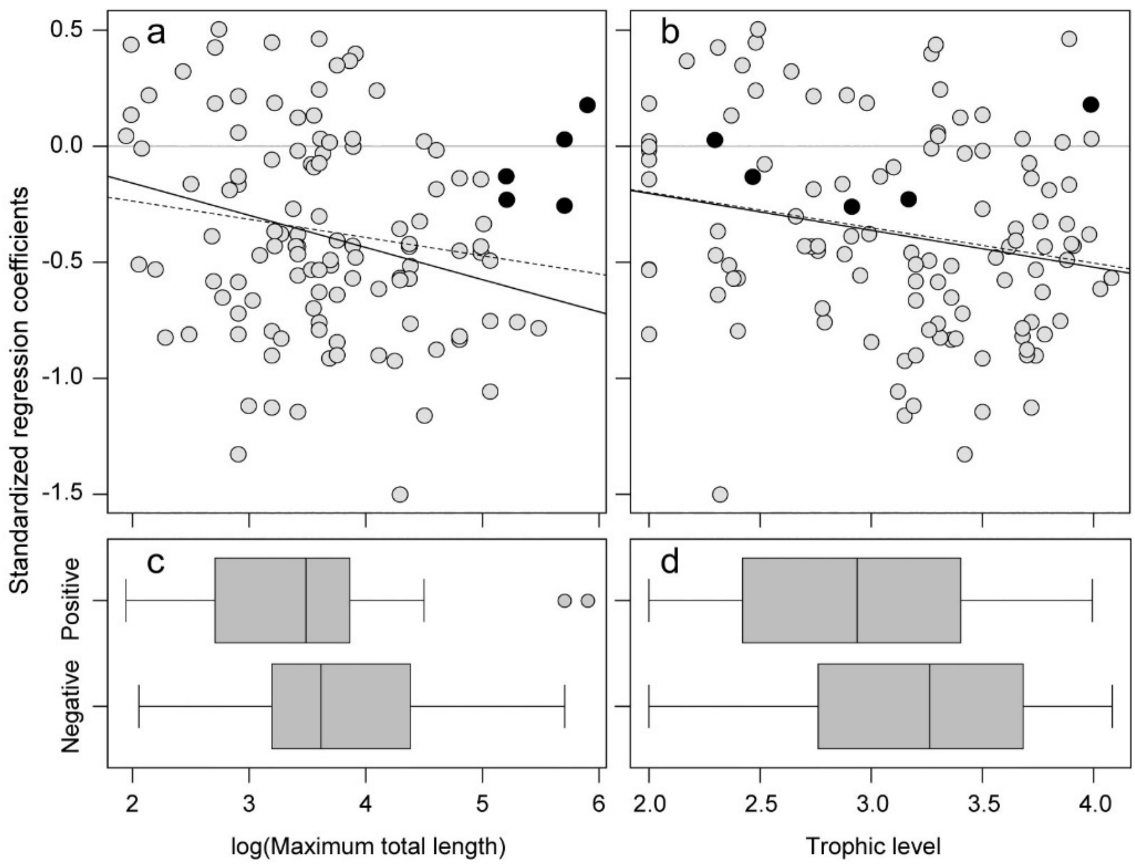


Fig. 23. Relationship between (log+1 transformed) standardized regression coefficients of species composition derived from seasonal catches of 116 fish species recorded at the *Dai* fishery in the Tonle Sap River from the fishing season of 2000/01 to 2014/15, and (a) their corresponding log-transformed maximum total lengths (maxTL in cm) and (b) trophic levels. Solid points represent endangered (en) and critically endangered (ce) species. Dashed lines show linear regression lines to predict the relationships when all species are considered, and solid lines are linear regression lines when en and ce are excluded from (a) and (b). Model summary (a) when all species are included: slope=-0.08, p-value=0.08, r^2=0.03; and when en and ce are excluded: slope=-0.13, p-value=0.006, r^2=0.06. Model summary (b) when all species are included: slope=-0.15, p-value=0.02, r^2=0.04; and when en and ce are excluded: slope=-0.16, p-value=0.02, r2=0.05. Boxplots show (c) distribution of maxTL and (d) trophic levels for the positive and negative standardized regression coefficient values of all 116 species. For Fig. 2c, Mann-Whitney rank sum test, p-value=0.02. For Fig. 2d, Mann-Whitney rank sum test, p-value=0.08.

When grouped by positive and negative standardized regression coefficient values (for all 116 species), maxTL is significantly greater for the species with negative standardized regression coefficients than the positive ones (Fig. 23c; Mann-Whitney rank sum test, p-value=0.02). Negative values of standardized coefficients are noted for species with maxTL corresponding to >45 cm (3rd quartile), whereas positive standardized regression coefficients are noted for species with maxTL <25 cm (2nd quartile). Species with both negative and positive coefficient values fall within maxTL of ~25 cm and ~45 cm. Trophic level does not significantly differ between negative and positive standardized regression coefficients (Fig. 23d; Mann-Whitney rank sum test, p-value=0.08). Nevertheless, species with negative standardized coefficients have higher trophic levels >3.3 (3rd quartile), and species with positive standardized regression coefficients have lower trophic levels (<2.75). Species with both negative and positive coefficient values fall within trophic levels of ~2.75 and ~3.3.

4.4.1.3 Temporal changes in the community weighted mean of maxTL and trophic level

Weighted mean maxTL and trophic level of seasonal total catch (Fig. 24a, b) oscillates with a mean range of ~25-55 cm and ~2.4-2.8, respectively, and significantly decline across the 15-year period (mean maxTL: slope=-1.26, p-value=0.007, r^2=0.44; mean trophic level: slope=-0.013, p-value =0.025, r^2=0.33). Although some small-bodied species including *Parachela siamensis* (maxTL: 18.3 cm; trophic level: 3.4), *Parambassis wolffii* (maxTL: 24.4 cm, trophic level: 3.72) and *Acantopsis* sp. cf. *dialuzona* (maxTL: 30.5, trophic level: 3.5) also exhibit significant declines in seasonal catches (standardized coefficients<-0.66), the combined findings indicate that smaller, lower trophic position species increase and compensate for declines in larger bodied, higher trophic position species in the Tonle Sap fishery over the study period.

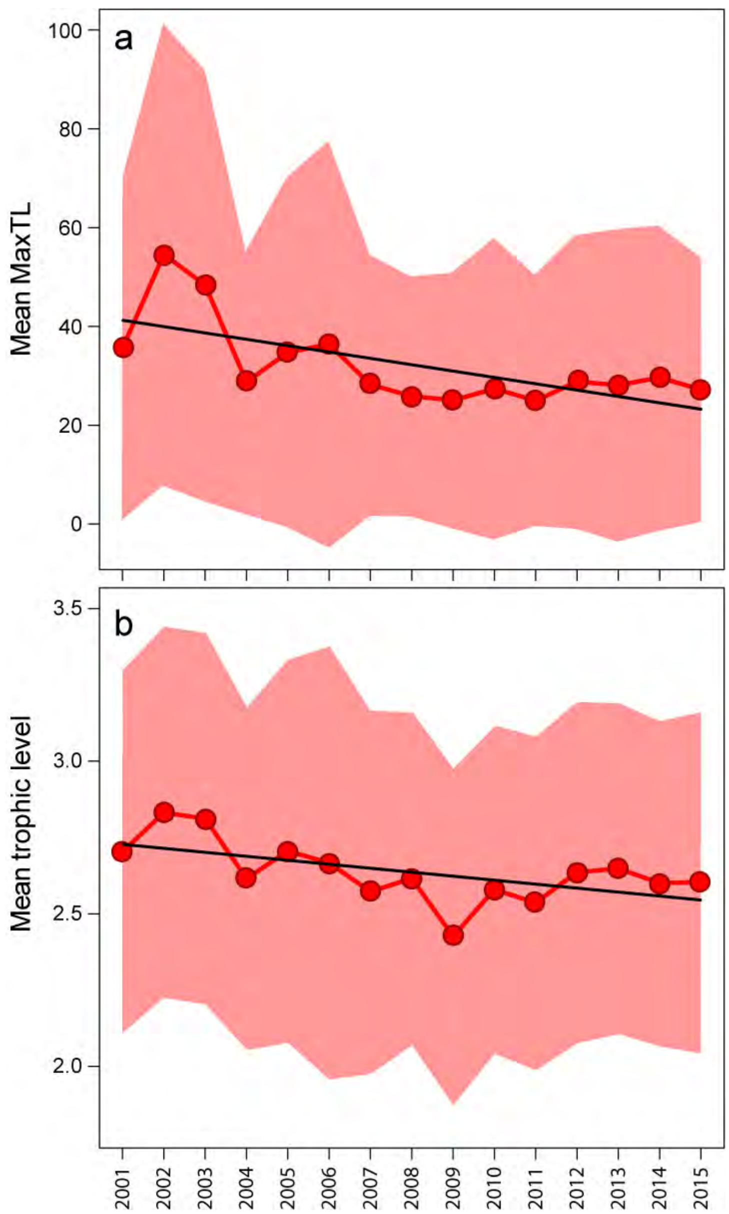


Fig. 24. Community weighted mean: (a) maximum total length (maxTL) and (b) trophic level in seasonal catches of the Dai fishery from the fishing season of 2000/01 to 2014/15. For Model summary (a), intercept=42.53, slope=-1.29, predictor p-value=0.007, r^2=0.44. For Model summary (b), intercept=2.74, slope=-0.013, predictor p-value=0.025, r^2=0.33. Pink shaded area denotes standard deviation around the mean values. 2001 represents the fishing season of 2000/2001 and the same for other years.

4.1.3.4 Temporal changes in the weight and length of individual fish

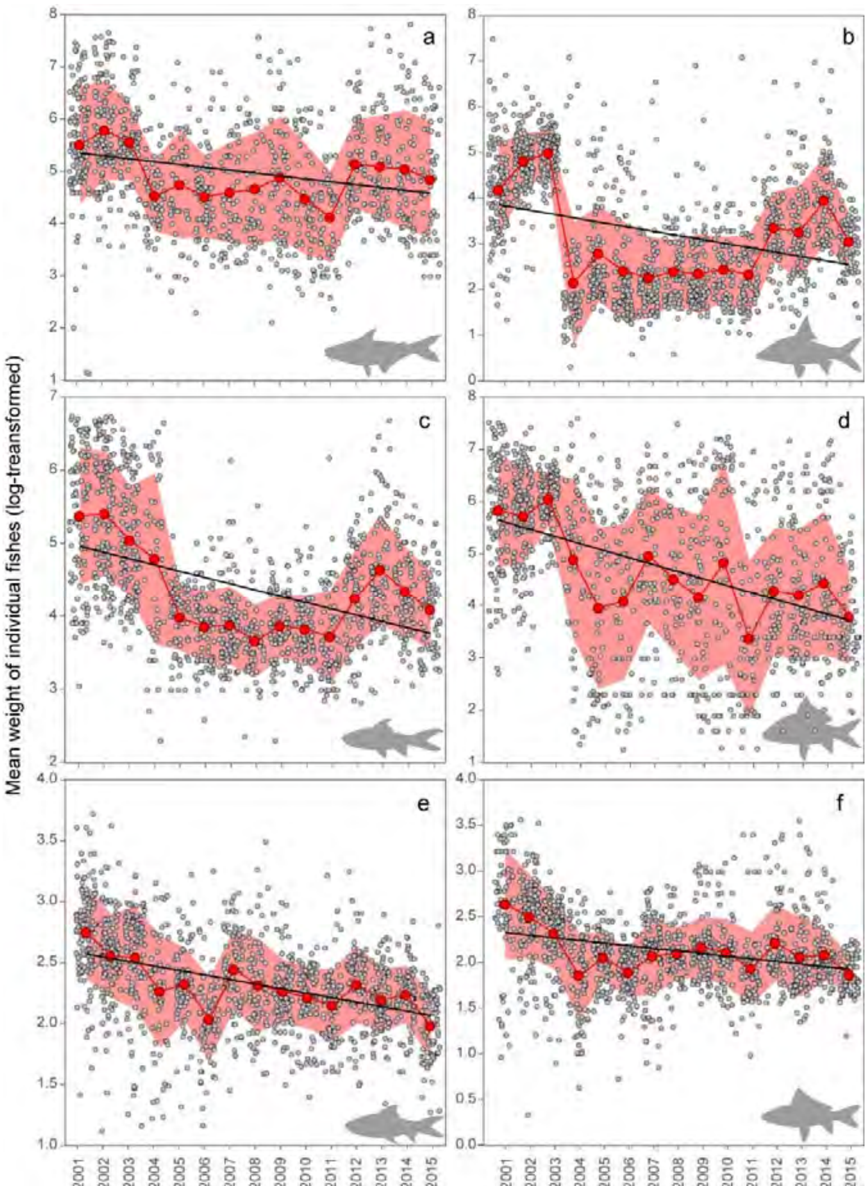


Fig. 25. Linear regressions demonstrate temporal change in log-transformed mean individual weight (g) by season of six common species, composing of large (a: *Pangasianodon hypophthalmus;* b: *Cyclocheilichthys enoplos)*, medium (c: *Cirrhinus microlepis;* d: *Osteochilus melanopleurus*) and small-sized species (e: *Henicorhynchus lobatus*; f: *Labiobarbus lineatus*) that possessed either negative (a-d) or positive (e, f) catch changes (expressed as standardized regression coefficients, Table S6) from the fishing season of 2000/01 to 2014/15. See Table S7 (Article 3) for parameter estimates. All slopes were significant (p-value<0.0001). Solid red dots indicate mean body weight and the pink shaded area denotes standard deviation for each survey season across the study period. 2001 represents the fishing season of 2000/2001 and the same for other years.

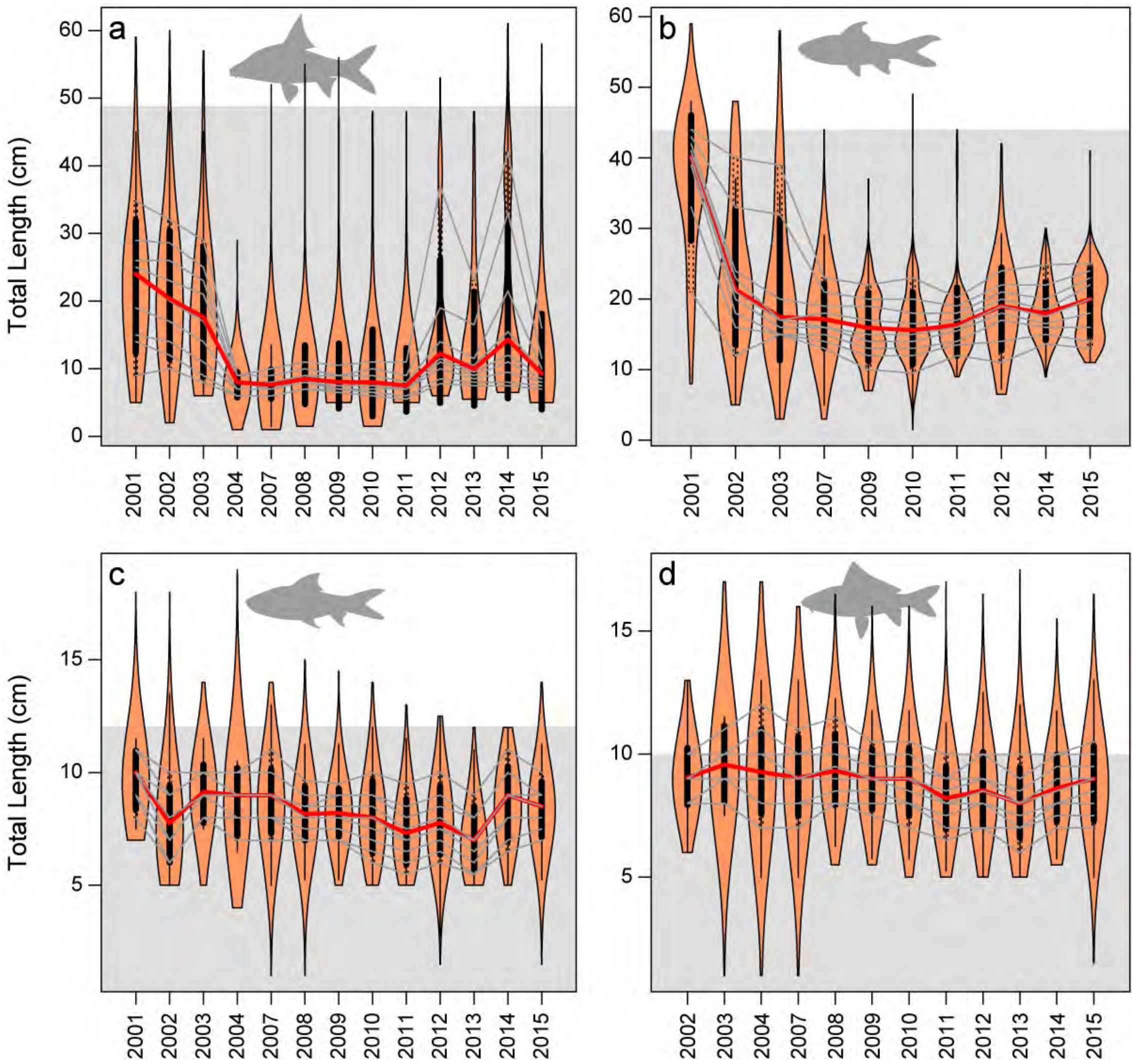


Fig. 26. Violin plots show temporal shift in length distribution of four species (a: *Cyclocheilichthys enoplos,* b: *Cirrhinus microlepis;* c: *Henicorhynchus lobatus;* d: *Labiobarbus lineatus*) from the fishing season of 2000/01 to 2014/15. Red solid line symbolizes median body size in each fishing season and grey thin lines indicate decile, dividing ten equal groups of a population. Area above the gray shaded area denotes estimated total length at maturity for each species. 2001 represents the fishing season of 2000/2001 and the same for other years.

The log-transformed mean fish body weight captured per day in the *Dai* fishery significantly decreases over the study period for all 6-species explored (p-value<0.0001; Fig. 25). These species span a range in body size (large, medium and small) and regression coefficients indicate that individual fish weight consistently declines through time for all 6 species regardless of body size (Fig. 25a-f).

Violin plots further elucidate the temporal changes of the total length for four common species (Fig. 26). For the large- and medium-sized species *Cyclocheilichthys enoplos* (maxTL: 90.3 cm) and

Cirrhinus microlepis (maxTL: 79.3 cm), both of which are mainly captured at juvenile sizes with an average total length<20 cm and 25 cm, respectively; body lengths have declined since the early 2000s when some comparatively large individuals (>30 cm) were present in the *Dai* fishery's catches (Fig. 26a, b). Noticeably, the medians for these large and medium-sized species are significantly lower than 49 and 44 cm (Fig. 26a, b), the estimated lengths at maturity for *C. enoplos* and *C. microlepis*, respectively. For the smaller species (maxTL<20 cm), *H. lobatus* and *L. lineatus*, which are common and highly productive, total length in the *Dai* catches have a median of ~9 cm, with some individuals possessing lengths greater than lengths at maturity which are ~12 cm for *H. lobatus* and ~10 cm for *L. lineatus* (Fig. 26c, d). Both species also exhibit gradual decrease in the median total length, but less pronounced than those of large-sized species.

4.4.2 Temporal dynamics of fish communities in the Lower Mekong system

4.4.2.1 Seasonality-predictability of site hydrology

Flows of the Mekong River in Kratie (KT) and Tonle Sap (TS) has more seasonal-predictable patterns than in Sesan River (SS) of the 3S where strong flow modifications are observed (Fig. 27a). As further evidenced in the wavelet plots (Fig. 27b), flows in TS and KT comparably exhibit very strong continuous seasonal-predicable patterns as indicated by the red color at ~52-week frequency (annual cycle). Such patterns are relatively weak in SS, with observed chaotic signals of strong wavelet power at multiple periods across the wavelet spectrum. Flow variation in KT and TS also demonstrates a secondary strong predicable power (red-yellow) at ~26-week frequency (semi-annual cycle), while no such patterns are captured in the wavelet power spectrum in SS (Fig. 27b). Such patterns are illustrated clearly in the average wavelet power across the full 7-year period, showing the strongest peaks at 52-week frequencies for all sites, with increasing average wavelet power (i.e. predictability strength) in the respective order of site SS, KT and TS (Fig. 27c). Colwell's seasonality index on hydrology consistently shows that flows in TS exhibit the strongest seasonality (M/P=0.93), whereas KT ranks second in its seasonal flow patterns (M/P=0.90) and SS shows the weakest flow seasonality (M/P=0.83).

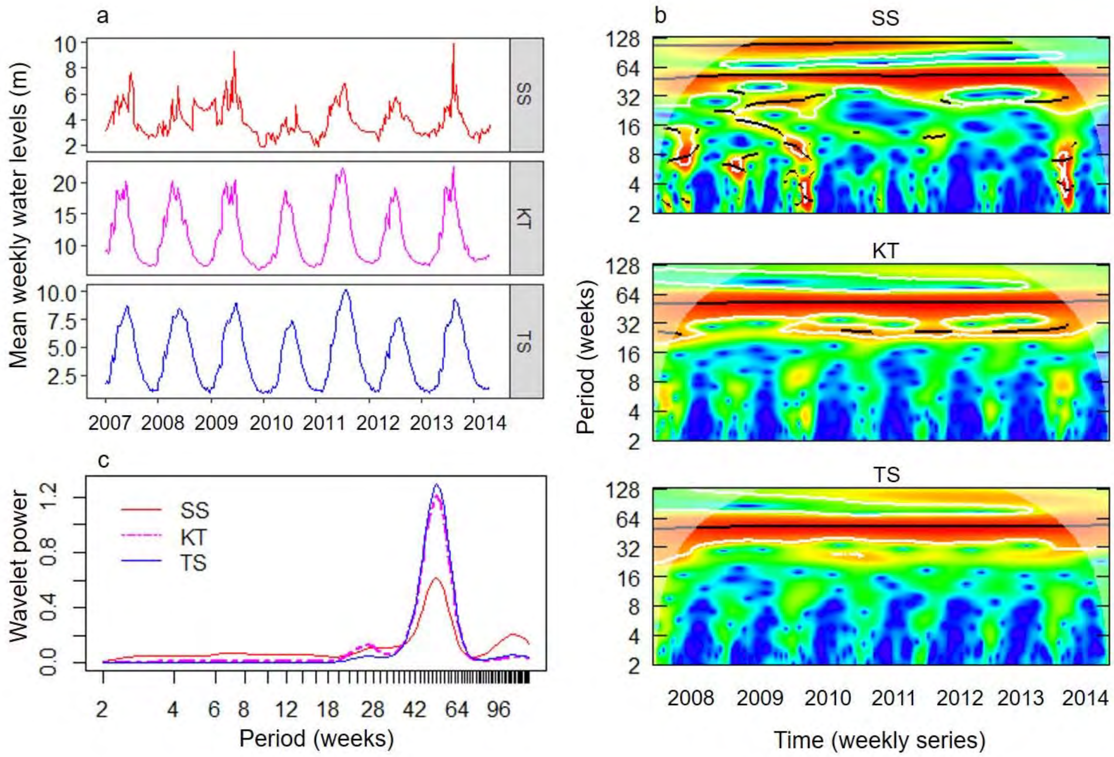


Fig. 27. Seasonality and predictability of 7-year weekly water levels of the three rivers: Sesan (SS), Mekong in Kratie (KT) and Tonle Sap (TS). (a) Site water level series. (b) Wavelet power spectrum of site water levels, with red representing stronger wavelet power and blue weak, (c) Site average wavelet power derived from (b). Note that Cowell's seasonality index (M/P) was 0.83 in SS, 0.90 in KT and 0.93 in TS.

4.4.2.2 Seasonal fish assemblage patterns

Seasonal fish abundances and richness show no significant differences between dry and wet seasons in SS. In KT, significantly higher richness is detected during the dry season, while no significant difference is observed for seasonal fish abundances. In TS, abundance is by far significantly higher during the dry season, while no significant difference is observed for seasonal richness (Article 5, S7a, b).

Clear differences in fish assemblages between dry and wet seasons are observed in SS and to a lesser extent in KT, while seasonal assemblages in TS appear less discriminated between the two seasons (Fig. 28). Temporal beta diversity shows a gradient of seasonal species turnover among sites with the highest values observed in SS and the lowest in TS (Fig. 29). KT displays intermediate values for both species turnover and nestedness in the three sites.

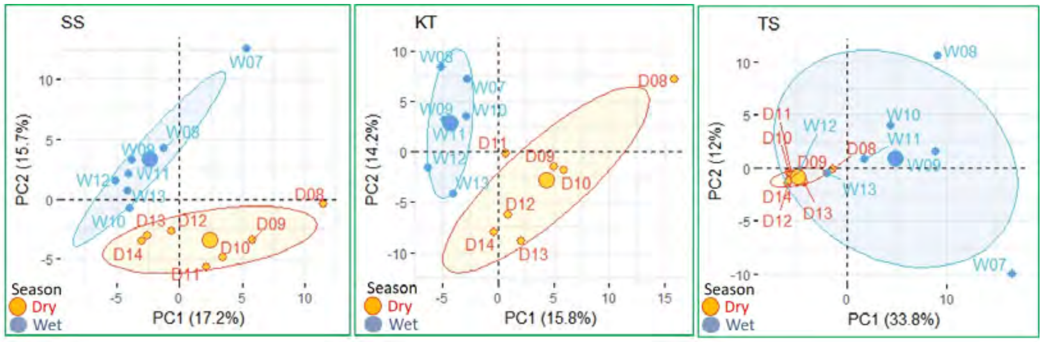


Fig. 28. Seasonal fish assemblage responses. PCA plots displaying seasonal fish assemblage patterns grouped by wet (W) and dry (D) seasons. The two digits after W and D indicate 'year', e.g. W07=wet season 2007 etc. For site names, see Fig. 27.

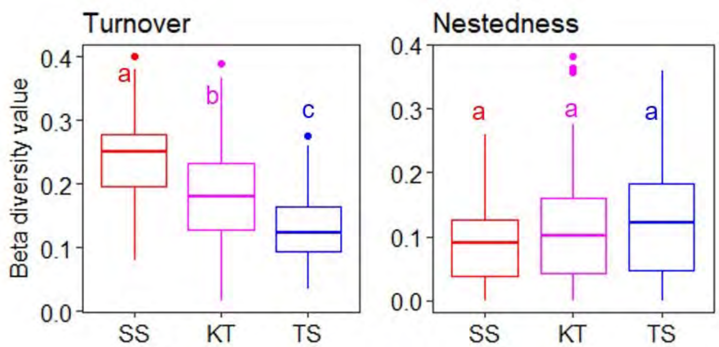


Fig. 29. Seasonal beta diversity partitioned into seasonal species turnover and nestedness using Sorensen dissimilarity index. Mean values among sites with a common letter are not significantly different at the 0.05 level (Pairwise Wilcoxon Rank Sum Tests). For site names, see Fig. 27.

4.4.2.3 Temporal dynamics of abundance and richness

Periodogram analyses on weekly abundance and richness (Fig. 30a, b) indicates that significant frequencies of semi-annual and annual cycles are exhibited in the Mekong mainstream sites, while no such patterns were displayed in the 3S sites. In KT, significant periods of weekly abundance (Fig. 30a) are found at 51-56 weeks, with harmonics at 104-109 and 154-160 weeks. The other significant periods (26 and 133-135 weeks) in this site show semi-annual cycles. A similar pattern is revealed for the site species richness (Fig.30b), where significant periods are detected at 48-57 weeks, with harmonics at 100-112 and 148-65 weeks. In ST, significant periods of species abundance occur at 52-48 weeks, with harmonics at 104-118 and 159-166 weeks; however, this pattern is less pronounced for the species richness. By contrast, there are no clear significant signals of semi-annual or annual cycles in the 3S sites. Additionally, far fewer significant periods with high frequencies are revealed in the 3S than the mainstream sites (KT and ST) for both abundance and richness.

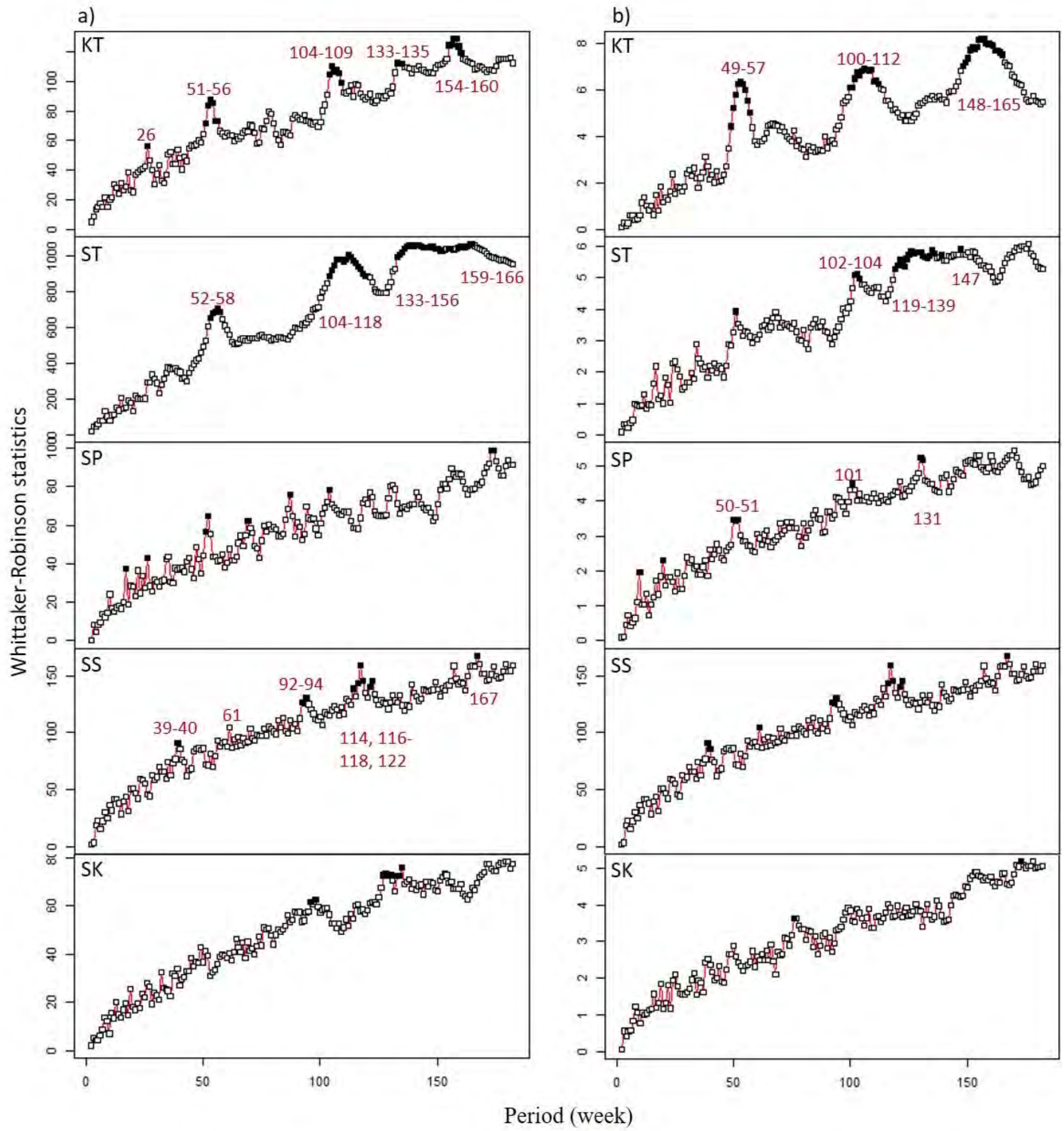


Fig. 30. Whittaker-Robinson periodograms computed for (a) weekly abundance and (b) richness, featuring periods between 2 and 182 weekly intervals from a 365-week data series from 01 June 2007 to 31 May 2014. The upper limit of the observation window of the periodograms is the number of observation intervals divided by 2 or a 182-week period. Black squares identify periods that are significant at the 0.05 level. For site names, KT=Kratie, SK=Sekong, SP=Srepok, SS=Sesan, and ST=Stung Treng.

4.4.2.3 Temporal dynamics of beta diversity

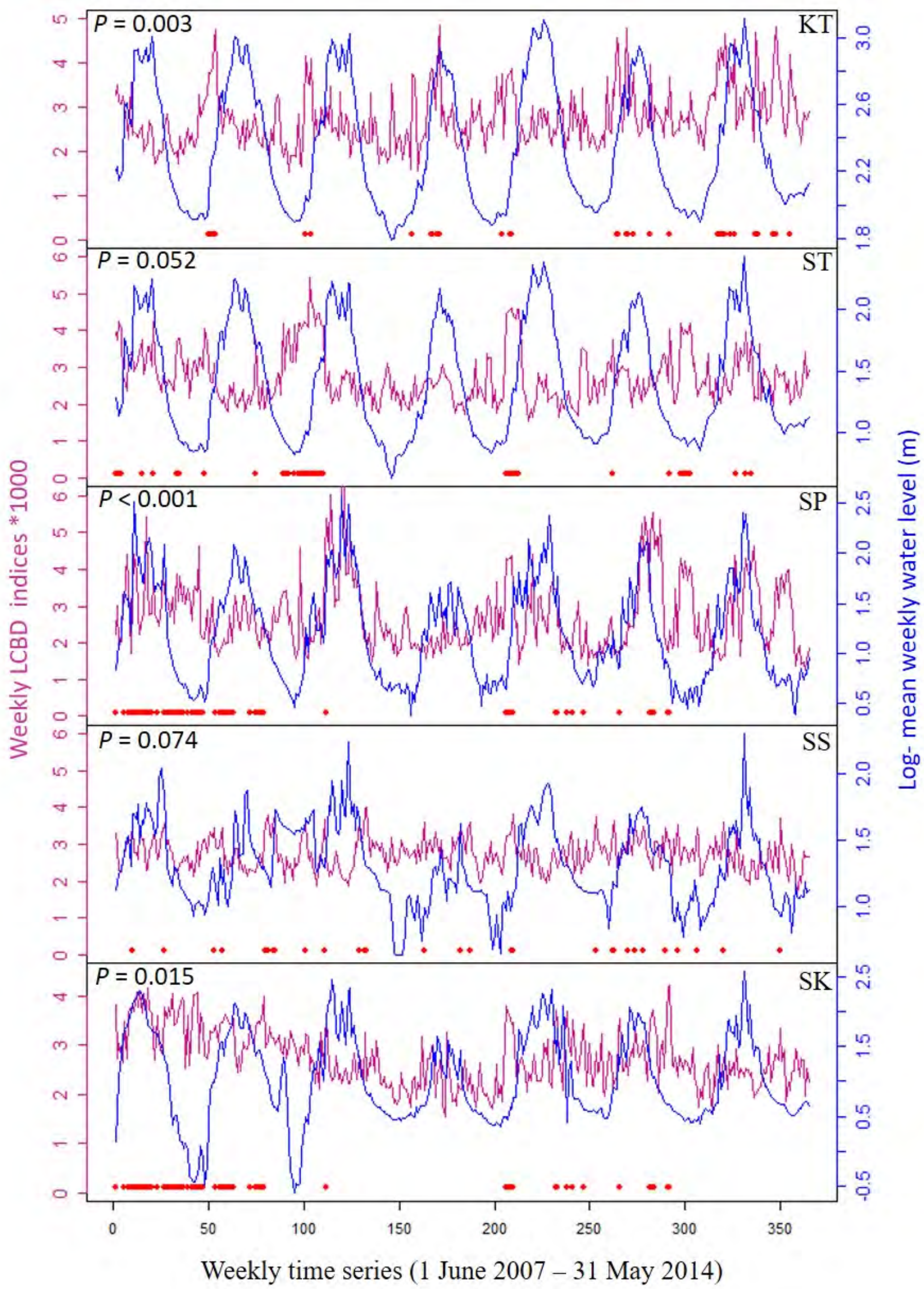


Fig. 31. Temporal changes in LCBD indices (red line) and mean log-transformed weekly water levels (blue line) over 7-year hydrological cycles on the five sites of the Mekong-3S River system. More predictable-seasonal flow patterns are shown in KT and ST, and unpredictable/regulated flows are displayed in SP, SK, and SS. The red dots indicate weeks with significant LCBD indices at the 0.05 level. P denotes the p-value of the pairwise correlation test using the Spearman method. For site names, see Fig. 30.

Total beta diversity (BD_{total}) indices estimated for the Mekong-3S sites are 0.50 in SP, 0.59 in ST, 0.66 in KT, 0.73 in SS and 0.74 in SK. Temporal Local Contributions to Beta Diversity (LCBD) weekly values range between 1.26E-03 and 6.36E-03; the LCBD values are small because they are made to sum to 1 across all weeks for each site. The site with the highest LCBD values is SS (median=2.71E-03, sd=4.33E-04), whereas the site with the lowest LCBD value is SP (median=2.53E-03, sd=9.69E-04). The other sites have intermediate values of weekly LCBD. Among the 365 weeks, 10% (35 weeks), 13% (48), 13% (46), 8% (29) and 18% (66) have statistically significant values of LCBD (assemblage composition being unique) in KT, ST, SP, SS and SK, respectively. This manifests strong temporal changes in the uniqueness of fish assemblage compositions over the study period for all sites. For the two Mekong sites (i.e. KT and ST), these significant temporal LCBDs (red dots on Fig. 31) are found to occur at the time when seasonal water levels start rising on the annual cycle basis, whereas no such patterns are exhibited in the 3S Rivers. Significant correlation between LCBDs and water levels are observed in KT ($P=0.003$), SP ($P<0.001$), and SK ($P=0.015$). While ST is on the margin ($P=0.052$), no significant correlation of the two variables is indicated in SS ($P=0.074$).

4.4.2.3 Temporal coherence of fish abundance/richness and flow

No clear peak in both weekly abundance and richness in relation to hydrological cycles is observed in SS (Fig. 32a, 33a). By contrast, a clear seasonal peak in abundance is repeated annually, i.e. before the peak water levels in KT (i.e. at the onset of wet season) and after the peak water levels in TS (i.e. during the falling water levels), whereas richness in both sites recur after the peak flows (i.e. during the dry season). Noticeably, fish abundance shows a significant declining trend in SS (p-value=0.03) and KT (p-value<0.0001), while richness exhibits significant decreasing trends for all sites (p-value<0.0001) (Article 3, S3).

Cross-wavelet analysis on variation of weekly abundance and richness with water levels shows that KT and TS are characterized by strong, coherent seasonality-predictability cross-wavelet power in the two data series at annual (~52 weeks) and semi-annual (26 weeks) frequencies (Fig. 32b, 33b). Such patterns are incoherent and mixed up in SS, as illustrated by disordered responses of the bivariate series with patchy red colors, fragmented ridges and arrows, pointing to different directions across the cross-wavelet power spectrum. These patterns are illustrated clearly in the average cross-wavelet power over the 7-year study period, showing the strongest peak at 52-week and secondary peak at 26-week frequencies for all sites, with SS having the weakest average cross-wavelet power relative to KT and TS (Fig. 34a, b). Noticeably, average cross-wavelet power for the abundance versus water series is muted in SS relative to KT and TS (7a).

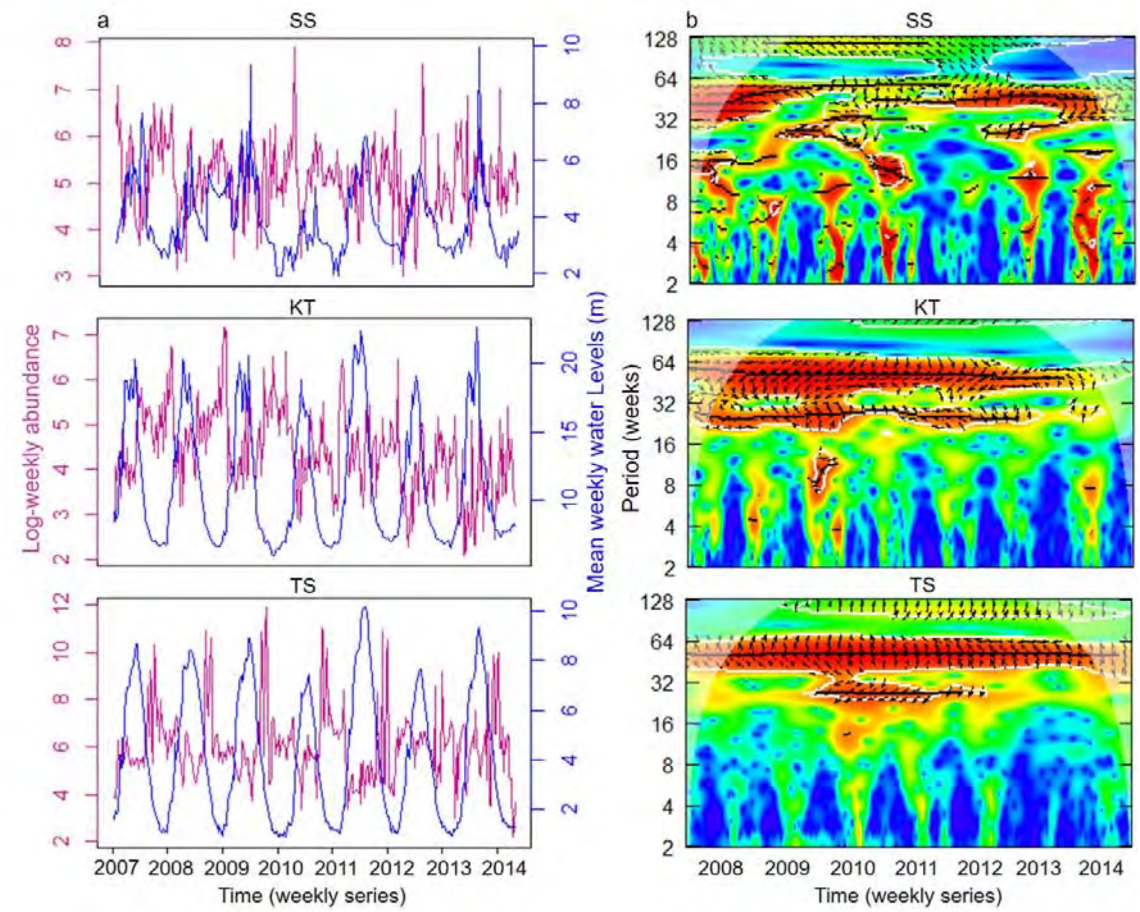


Fig. 32. Temporal variation of total weekly abundance (y) and mean weekly water levels (x as predictor). (a) Weekly abundance and mean water level data series, covering the period from 1 June 2007 to 31 May 2014. (b) Cross-wavelet power spectrum of weekly abundance and water levels. Red color represents stronger cross-wavelet power, and blue weak. Arrows in each plot depict phase-differences. Ridge lines illustrate cross-wavelet power coherence within a band of neighboring periods. Areas in the upper corners, outside the 'cone of influence' in each plot indicated the exclusion of areas from edge effects (with weak predictive ability). For site names, SS=Sesan, KT=Mekong River in Kratie, TS=Tonle Sap River.

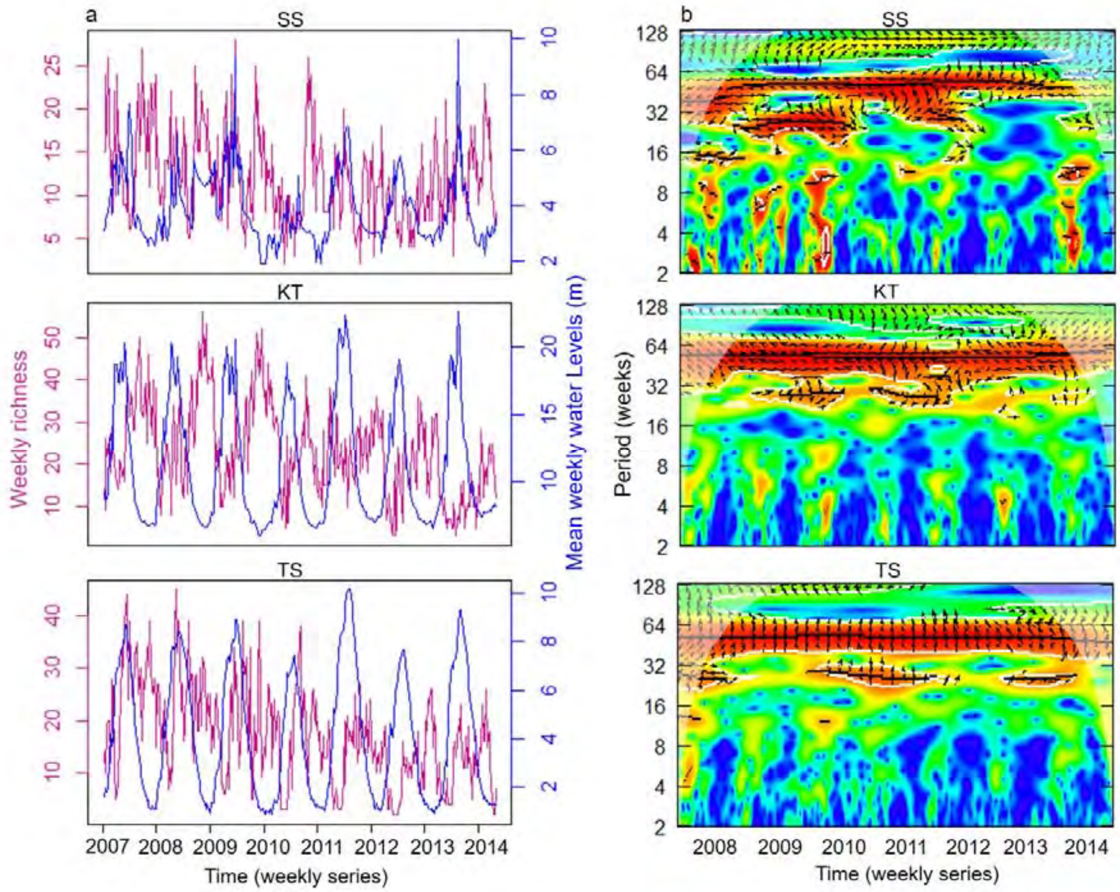


Fig. 33. Temporal variation of total weekly richness (y) and mean weekly water levels (x as predictor). (a) Weekly richness and mean water level data series, covering the period from 1 June 2007 to 31 May 2014. (b) Cross-wavelet power spectrum of weekly richness and water levels. Red color represents stronger cross-wavelet power, and blue weak. Arrows in each plot depict phase-differences. Ridge lines illustrate cross-wavelet power coherence within a band of neighboring periods. Areas in the upper corners, outside the 'cone of influence' in each plot indicated the exclusion of areas from edge effects (with weak predictive ability). For site names, see Fig. 32.

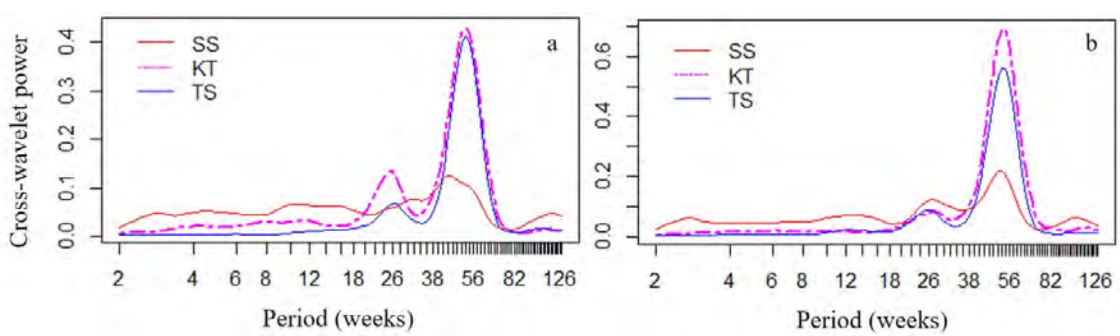


Fig. 34. Site average cross-wavelet power. (a) abundance versus water series derived from Fig. 32b and (b) richness versus water series derived from Fig. 33b. For site codes, see Fig. 32.

4.4.2.4 Temporal shifts in the species composition of the Mekong-3S system

RDA analysis on assemblage composition with (Species Contributions to Beta Diversity [SCBD] indices greater than mean) against time depicts a strong temporal shift in assemblage composition at all sites. In the Mekong mainstream (Fig. 35a), during the early years of the survey (2007-2010), temporal assemblage variability is mostly due to small-sized generalist and specialist species. After 2010, the composition tends to be disproportionally represented by specialists. Small-sized mud carps (maximum total length - maxTL<25 cm) i.e. *Henicorhynchus lobatus* (Hlobatu), *H. siamensis* (Hsiamen) and *Labiobarbus siamensis* (Lsiamen), the most common and abundant species in the LMB, are found to be characteristic and important species for both sites during the period 2007-2010. Afterwards, specialists disproportionally represent the assemblage in both sites. Some common specialists describing assemblages in the Mekong mainstream during 2011-2014 are short distance migrants and mainstream spawners such as *Hypsibarbus malcolmi* (Hmalcol), *Phalacronotus apogon* (Papogon.1), *Hypsibarbus lagleri* (Hlagler), *H. wetmorei* (Hwetmor); long distance migrants such as large-sized cyprinids (maxTL>60 cm) *Cosmochilus harmandi* (Charman), *Cirrhinus microlepis* (Cmicrol), *Cyclocheilichthys enoplos* (Cenoplo), *Labeo chrysophekadion* (Lchryso); and river catfishes, namely, *Helicophagus waandersii* (Hwaande) and *Pangasius conchophilus* (Pconcho) (only in ST). Important species contributing to overall site beta diversity are given in Annex 2.

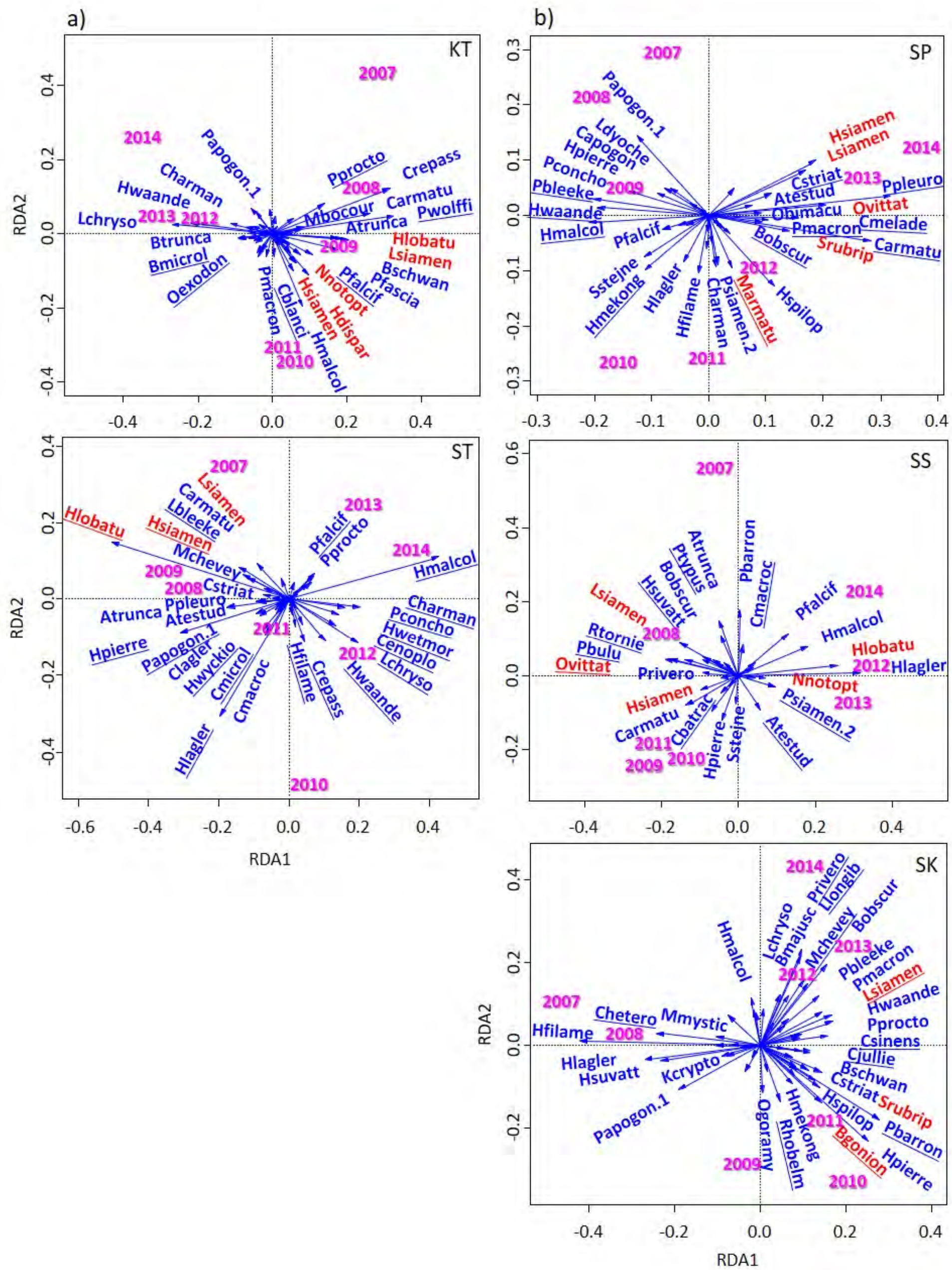


Fig. 35. RDA biplots of Hellinger-transformed assemblage data showing the important species (with SCBD indices greater than mean SCBD) contributing to the temporal shift in assemblage composition in each site. (a) Mekong River; (b) 3S Rivers. The biplots show species (arrows) and sampling units grouped by year. Names are abbreviations of fish species names. Species with very small contributions to the ordination are removed for clarity. Underlined species (blue) are indicator species identified by the multipatt function. Species in red have generalist habitat preferences. The assemblage ordination is explained by time (years) and its quadratic effect (not shown). Test of the multivariate RDA R-square: *P*<0.001. Full species names and ecological attributes are shown in Annex 3. For site names, see Fig. 30.

In contrast, temporal dynamics in assemblage composition shift from specialists (during the 2007-2010 period) to generalists (after 2010) in the 3S (Fig. 35b). The pattern is pronounced in SP and SK, where long-distance migratory species and main channel spawners with large-bodied sizes, such as *Phalacronotus apogon* (Papogon.1), *Hypsibarbus lagleri* (Hlagler), *Helicophagus waandersii* (Hwaande), *Hypsibarbus malcolmi* (Hmalcol), *Pangasius conchophilus* (Pconcho), *P. bleekeri* (Pbleeke), *Hypsibarbus pierrei* (Hpierre), etc., represent the assemblages between 2007 and 2010 and are then replaced by small-sized minnows and carps with generalist habitat preference, such as *Labiobarbus siamensis* (Lsiamen), *Systomus rubripinnis* (Srubrip), *Henicorhynchus siamensis* (Hsiamen) and *Osteochilus vittatus* (Ovittat), etc., between 2011 and 2014. This pattern is less clear in SS where the generalist *H. lobatus* significantly contributes to the temporal changes in assemblage composition during the 2011-2014 period. Moreover, assemblages in the SS during the entire period are largely represented by generalists and other small-sized minnows and carps, such as *Paralaubuca typus* (Ptypus), *P. riveroi* (Privero), *P. barroni* (Pbarron), *Rasbora tornieri* (Rtornie), *Cyclocheilichthys armatus* (Carmatu), etc. as found in SP and SK Further, assemblages in the 3S towards 2011-2014 are partly composed of black fishes (floodplain residents) such as climbing perch *Anabas testudineus* (Atestud), airbreathing catfish *Clarias batrachus* (Cbatrac) and snakehead *Channa striata* (Cstriat).

V. Discussion

5.1 Fish species richness and diversity

The LMB possesses extremely high fish diversity hosting one of the world's most prolific tropical freshwater capture fisheries (Rainboth 1996, Baran 2005, MRC 2010). Fishes of the basin are characterized by a diverse range of body size, habitat use and feeding ecology (Rainboth 1996, Rainboth et al. 2012, Ou et al. 2017). The complex seasonal flood pulses which create greater ecological niches for fishes and historical biogeography of the region etc. explain this high diversity (Rainboth 1996, Poulsen et al. 2002, Junk and Wantzen 2004).

The MRC routine fish monitoring programs during the last decade or so have recorded some 504 fish species belonging to 252 genera, 78 families and 22 orders in the LMB (Fig. 9-11). The richness reported from these monitoring accounts for 42% of the total estimated 1200 species or 57% of total 877 recorded fish species in the Mekong Basin (Rainboth 1996, Baran et al. 2013b). These species represent mainly the common fish species captured by common fishing gears used in the region e.g. *Dai* stationary bagnet, cylinder traps, gillnets, cast nets, hook and lines etc. details of which are described in (Deap et al. 2003). Cyprinidae are the largest family representing ~80% of both total abundance and biomass, while Pangasiidae, Siluridae, Cobitidae and Clupeidae each contributed between 1-8%. Other 73 families combined make up only less than 6% to both total abundance and biomass. The lesser number of reported richness is likely due to the area coverage in these monitoring programs which were limited to the Mekong mainstream and some of its major tributaries in the LMB. In fact, many freshwater fishes including euryhaline species are confined to tributaries, hill streams or estuarine/coastal areas of the Mekong delta (Rainboth 1996, MRC 2010, Rainboth et al. 2012).

In the Lower Mekong River, fish species richness distribution is found to link to the longitudinal river gradient with the level of richness increasing from headwaters towards the delta; however, highest species diversity occurs in the middle of the system in Cambodia (Fig. 12,16). The higher richness found in the delta is likely because the fish community in the area is composed of freshwater, brackish and marine species. Also, the increasing richness from up- to downstream gradients could be explained by "addition" concept where increasing richness is exhibited from the headwaters to lower part of the river (Matthews 1998). Moreover, the study results are, overall, in agreement with the river continuum concept where the species richness is found high at the lower river reach, while highest diversity index is exhibited in the middle range of the river system (Vannote et al. 1980, Statzner and Higler 1985). Further, high species diversity in the middle of the Lower Mekong River is likely attributed to the geographical location of the region, where many species cannot move up the Khone Falls, the geological fault line which forms the 21-meter high Khone Falls on the Cambodian-Lao border (Rainboth 1996, van Zalinge et al. 2004, Valbo-Jørgensen et al. 2009). The Mekong River section in Cambodia is characterized by low land and no barriers; allowing many Mekong fishes to migrate up- and downstream the Cambodian Mekong River system naturally. In addition, the essential connectivity between the Tonle Sap River and Lake system, and Mekong River creates favorable conditions for many Mekong fishes to complete their life cycle because the lake supports feeding and rearing grounds, while many deep pools below Khone Falls in the complex Mekong-3S River system are vital spawning habitats and dry season refuge (Poulsen et al. 2002, 2004, Baird 2011).

In the Mekong-3S system, more stable fish assemblages with higher richness and diversity indices occur in the Mekong mainstream in Kratie and Stung Treng, whereas lower richness and diversity indices are found in the 3S Rivers (Fig. 13). Noticeably, fish assemblages in Sesan River exhibit the lowest richness and diversity indices of all sites. Lower richness and diversity found in the 3S Rivers are generally attributed, by most researchers in the region, to flow regulations (hydropower-related pulsed flows) caused by the upstream functioning dams (Baran et al. 2013a). In other Mekong tributaries, lower species richness are also observed in regulated rivers (i.e. Gam and Mun Rivers) as compared to an unregulated ones (e.g. Sankgram River) (Phomikong et al. 2014). In fact, hydrological alterations have been previously identified to cause changes in fish assemblage structure (i.e. reduced species diversity, shift in compositional and life history structure) in other regions of the world e.g. central Amazonian and American rivers (Mims and Olden 2013, Röpke et al. 2017).

In the TSRL system, the study finds high species abundance, richness and diversity in the middle section of the lake (Fig. 14, 15). This is seemingly because this section is deeper and larger in terms of water depth and surface cover than the other sections within the system. The bathymetric map of the Tonle Sap Lake shows a general slope down towards the middle section from both southern section in Kampong Chhnang and northern section in Battambang (Campbell et al. 2006). In addition, the middle section has a higher degree of inundation throughout the year, which is contributed by at least three largest tributary rivers of the Tonle Sap sub-basin, namely the Sen River in Kampong Thom with a lower reach drainage within 230 km^2 of the lake, Chinit River in Kampong Thom with a total drainage area of 5,649 km and Pursat River in Pursat with catchment area of 5,965 km2 (CGIAR 2013, Nagumo et al. 2013, 2015). The large extent of inundation, combined with greater depths, tends to increase habitat connectivity and availability which creates more living space and stable environment. This gives fish species a colonizing advantage, which drives greater richness and diversity (Henriques-Silva et al. 2013). For example, Boeng Chhmar and its associated rivers and floodplains, covering an area of 28,000 ha in the middle section of the Tonle Sap Lake in Kampong Thom is described as a near-natural wetland, encompassing permanent open water surrounded by a creek system; the area has been designated a RAMSAR wetland of global significance since 1999 (The Ramsar Convention Secretariat 2014).

By contrast, relatively low richness and diversity are found in the southern (Kandal, Kampong Chhnang) and northern sites (Siem Reap, Battambang) where total species richness among these sites are similar. This is because sites in the southern part are representative of riverine habitat, mainly serving as a natural fish passageway for migratory species that seasonally migrate between the lake and the Mekong River to complete their life cycle (Poulsen et al. 2004, Halls et al. 2013c). This site is laterally connected with the surrounding floodplains only partly during the high-flow period and become disconnected for most parts of the year (Valbo-Jørgensen et al. 2009). Similarly, sites in the northern section have lesser connection with large and permanent wetted tributary rivers, and the main land use types of the location are rice farming, herbaceous floating vegetation and dense mats of water hyacinths as well as seasonal flooded grasslands (Hortle et al. 2008, MRC 2011 pp. 64–65). Such habitats favor mainly black (floodplain residents) and some gray (lateral migrants between floodplains and rivers) fishes capable of tolerating anoxia conditions (Welcome 2001, Aloo 2003).

5.2 Spatial variation in fish community structure

Overall, spatial abundance distribution patterns of the Mekong fishes are associated with their seasonal migration patterns and their population structure. Some Mekong fishes migrate upstream for reproduction, while others migrate downstream for feeding and rearing.

In the Lower Mekong River, clear broad-scale patterns of the assemblage structure are observed between the upper Lower Mekong River and its delta. Specifically, assemblages Ia and Ib (Fig. 12, 16) are characterized by cyprinids and catfishes (mostly potamodromous fishes) frequently occurring in a large-sized river, specifically in the Mekong mainstream i.e. *C. harmandi, L. chrysophekadion, H. waandersii, B. yarelli and Bangana behri* (Lucas et al. 2001). Below Khone Falls, the cyprinids in Ib are dominated by opportunist and small-sized species, such as *Henicorhynchus* spp., *Labiobarbus* spp., *Paralaubucca* spp., and *Thynnichthys thynnoides*. These species are known as fast growing with short lifespan and are reported to perform long-distance migration, commonly occurring between the Tonle Sap system and upstream Cambodian Mekong River system and beyond (Poulsen et al. 2002, 2004, Baird et al. 2003, Halls et al. 2013c).

In the Mekong delta, perch-like fishes (Perciformes) and clupeids (Clupeiformes) are common species in IIa and IIb; these groups of fish are tolerant to salinity and turbid water (Albert and Reis 2011). Nevertheless, many species in IIa, are characterized as stenohaline species such as *C. aesarnensis, Mastacembelus* spp., *Acanthopsis* spp., which are less tolerant to the brackish conditions of the delta. However, some of them need the marine environment to complete their life cycle including *Cynoglossus microlepis*, while others are said to reside permanently in the estuary, for example *G. giuris* (Valbo-Jørgensen et al. 2009, Froese and Pauly 2017). In IIb, marine species are dominant, among those are *Liza* spp., *Scomberomorus* sp., *Toxotes* spp., *Allenbatrachus grunniens, Boleophthalmus boddarti*; they are well suited to the marine environment with less light penetration (Moyle and Cech 1988). Of course, these species are known as amphidromous fishes and some of them are catadromous fishes, for example *Anguilla* sp., *Ellochelon vaigiensis, Mugil cephalus,* which inhabit fresh-brackish water and live permanently in the estuary like the small anchovies (*Coilia* sp. and *Tenualosa toti*) (Froese and Pauly 2017).

In the complex Mekong-3S system, fish assemblages in the Mekong sites are more species-rich and diverse as compared to the 3S (Fig. 13). This is expected as the Mekong River is deeper and larger in size, and species richness are generally found to have strong positive relationship with surface drainage area and flow (Guégan et al. 1998). Among the 3S, Srepok (SP) is the most species-rich and comparable to the Mekong River in Kratie. As discussed, high species richness in SP is perhaps because the river has the largest basin area (30,650 km^2) as compared to SK (28,820 km^2) and SS (18,890 km^2) (see Fig. 8) and is the deepest, with better flow conditions relative to Sekong (SK) and Sesan (SS) rivers (see S1, Article 4). In addition, some similarities of fish assemblage patterns found between SP and the Mekong sites (Fig. 17) are likely because SP had the highest number of migratory species (81) relative to SK (64) and SS (54) (Baran et al. 2013a). These migratory species e.g. Pangasiidae and Cyprinidae can migrate hundreds of kilometers between the mainstream, tributaries and floodplains during their life cycles (Poulsen et al. 2002, 2004, Sverdrup-Jensen 2002). Local fish migration behavior may additionally explain the pattern i.e. most cyprinids are known to migrate upriver along the edges of rivers; therefore, when fish leave the Mekong, enter the Sekong River (SK) and travel up along its southern bank, they will enter Sesan (SS) and will soon continue right into SP (Baran et al. 2013a) (see also Fig. 8). These factors combined with greater depths and better flow conditions in SP, tend to explain some similarities of the assemblage patterns between the two rivers.

In Tonle Sap River and Lake system fish fauna is distributed along a south-north gradient, classifying the entire community into three assemblage clusters (Fig. 18). Characteristic species in cluster 1 of the southern section are mainly restricted to migratory (riverine) white fishes such as river catfishes, cyprinids, loaches and sheatfishes. These white fishes are generally intolerant of anoxia, preferring migrations as a means to escape adverse environmental conditions in the dry season (Welcome 2001). Well-oxygenated water such as the lotic main river channel and deep pools are generally required for these species to shelter in the dry season (Halls et al. 2013a). In addition, the distribution of the white fish in this cluster is part of seasonal migrations to complete their life cycles, i.e. accessing the Tonle Sap floodplains for rearing and feeding, and returning to the Mekong mainstream for dry season refuge and spawning during early flooding cycle (Dudgeon 2000, Poulsen et al. 2002, 2004, Baran 2006, Kong et al. 2017).

Cluster 2 in the middle section of the lake is characterized by both restricted and widespread species including small bagrid catfishes (*Mystus* spp.), cyprinids, glassfishes, leaf fishes, climbing gouramies and spiny eels. Overall, this cluster is represented by high number of indicator species with different ecological attributes such as longitudinal migratory white fishes, floodplain residents (black fishes) and lateral migrants (gray fishes). This is likely due to overall environmental stability in this section, i.e. with deeper waters, larger surface cover and habitat connectivity through the permanent water bodies (i.e. Ramsar Wetlands of Boeng Chhmar) and presence of permeant wetted largest tributaries of the Tonle Sap Basin.

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

Consistently, the study finds very high relative abundance of white fish in cluster 1 (96%), and gradually along south-north gradient of the TSRL, the proportion of white fish decreases and is replaced by gray and black fishes towards cluster 2 and cluster 3 (Fig. 19). The results of this study also strengthen those of previous studies that specifically find high abundance of featherbacks and airbreathing catfishes in the northern section of the lake (Siem Reap, Battambang) (Lim et al. 1999), and snakeheads and gouramies in Battambang (Enomoto et al. 2011). In addition, the present results show that three species, namely, *Henicorhynchus lobatus* (Hlob), *H. siamensis* (Hsia), and *Puntioplites proctozysron* (Ppro) are ubiquitously abundant for all the three clusters. These species, particularly *Henicorhynchus lobatus* are among the ecological keystone species with its critical role in food security throughout the LMB and an important prey for predatory fishes and Irrawaddy dolphins (Baird 2011, Fukushima et al. 2014).

5.3 Temporal variation in fish community structure

In a tropical flood pulse system such as the Mekong, hydrologic variation is a key driver influencing the temporal dynamics of fish assemblage structure. This study finds both significant intra- and inter-annual variations of fish assemblages in the Tonle Sap specifically, and in the Lower Mekong system more generally.

5.3.1 Flow variation in the Lower Mekong system

While more natural flow conditions are observed in the Mekong River in Kratie (KT) and Tonle Sap River (TS), flows in the 3S Rivers e.g. Sesan (SS) appear to be highly altered by upstream dams, which weaken the flow seasonality and predictability strength of the system and generate strong aseasonality with unnatural sudden rising and falling water levels (Fig. 27). Such unnatural pulsed flows in SS can be related to hydropeaking which is commonly experienced with hydropower dams worldwide (Young et al. 2011, Kennedy et al. 2016) and known to alter hydraulic parameters such as water levels, velocity and bed shear stress (Meile et al. 2010, Young et al. 2011, Kennedy et al. 2016, Bejarano et al. 2017, Tonolla et al. 2017). Previous qualitative studies describe rapid rising and falling water levels in the downstream SS when the 720 MW Yali Falls dam was under construction in 1996 and became officially operational in 2000 (Ratanakiri Fisheries Office 2000, Baird et al. 2002, Claasen 2004, Hirsch and Wyatt 2004, Baird and Meach 2005, Rutkow et al. 2005). Flow alternations became even more severe when five more dams were commissioned between 2006 and 2011 (see Fig. 2, Article 4). As indicated in a recent study, the upstream SS's under-construction and operational dams in Viet Nam Highlands have caused an overall increase of 52% in dry season flow and a decrease of 22% in the wet season flow of this river near the Cambodia border (Piman et al. 2013). Therefore, strong aseasonal and unpredictable variabilities of flow evidenced in SS are highly likely explained by hydropower-related pulsed flows.

5.3.2 Intra-annual variation in fish community structure

In the TSRL system, the abundance and richness of fish communities is found significantly greater during the outflow period. (Fig. 20a and S3.7, Article 2). This is due to seasonally longitudinal migration of white fishes from the TSRL to the Mekong mainstream for dry-season refugia (Poulsen et al. 2002, 2004). Such seasonal migrations are reliably predictable as observed in the Mekong's largest *Dai* fishery operating in the Tonle Sap River for more than a century. The observed peaks often occur in a time-window of ~7-1 days particularly before the full moon of December and January (Halls et al. 2013c). Likewise during this outflow, gray and black fishes also undertake short-distance lateral movements from the nearby TSRL seasonal floodplains to the deeper area of the Tonle Sap Lake or the main river channel. Seasonal migrations during the outflow usually drive huge fishing activities in the TSRL and the LMB. By contrast, the least fish abundance in the TSRL is found during the inflow when white fishes longitudinally migrate for spawning in rapids, deep pools of the Mekong River, and mature fish, juveniles and larvae then migrate and drift down the river and invade the TSRL's surrounding floodplains for rearing and feeding (Valbo-Jørgensen et al. 2009). The lower abundance during the inflow is likely attributed to low fish density as fish is widely dispersed by the seasonal flooding to the floodplains and inundated forests surrounding the TSRL which makes capture difficult. The cross-correlation analysis points out that peak abundance and richness (Fig. 21b, d) are respectively related to the peak flow occurring about four months (-15 weeks in Kandal [KD] and -16 weeks in Pursat [PS]) and 2-2.5 months (-8 weeks in KD and -10 weeks in PS) earlier. Given that the peak flow occurs early October (MRC, 2005; S1), the peak abundance takes place in around January, whereas the peak richness happens early in between November and mid-December. The period for peak abundance and richness found from the cross-correlation analysis corresponds with the defined outflow (falling water level) period for this study (Article 2). Such seasonal patterns are also reported in other tropical river-floodplain fish communities such as the Amazonian Juruá River and forest streams (Silvano et al. 2000, Espírito-Santo et al. 2009), Venezuelan rivers (Hoeinghaus et al. 2003) and French Guiana (Boujard 1992) where greater abundance and richness with more species interactions are driven by the relative low flow.

In the Lower Mekong system, the study finds that fish assemblages in the highly regulated river (e.g. Sesan) is characterized by little seasonal variation in fish abundance, richness and distinct seasonal assemblage composition with high species turnover. Assemblages in highly seasonal-predictable rivers are represented by repeated seasonal-predictable peak abundance and richness at semi-annual and annual cycles, and more similar seasonal assemblage composition with low species turnover (Fig. 28, 29, 34). This is because, in aseasonal-unpredictable rivers, dams generate hydropower-related pulsed flows i.e. hydropeaking known to alter hydraulic parameters (Meile et al. 2010, Young et al. 2011, Kennedy et al. 2016, Bejarano et al. 2017, Tonolla et al. 2017) which fragment habitats and alter fish assemblage composition and diversity due to, among other factors, stranding, downstream displacement and creating false attraction flows that reduce spawning and rearing success of fish (Hunter 1992, McLaughlin et al. 2006, Habit et al. 2007, Poff et al. 2007, Clarke et al. 2008, Young et al. 2011, Schmutz et al. 2015, Kennedy et al. 2016). This results in strong temporal fish assemblage compositional changes with high species turnover. While partly in line with the recent Tonkin's et al. seasonality-predictability framework of highly seasonal-predictable environmental conditions promoting the greatest temporal changes in diversity (abundance and richness), the results of this study are overall not consistent with Tonkin's et al. framework hypothesizing that predictably seasonal environmental conditions promote the highest levels of temporal changes in assemblage composition with high species turnover due to the hypothetical distinct habitats and thus distinct fauna should appear between seasons (Tonkin et al. 2017). The study indicates that while the hypothesis works for stream invertebrates, with which Tonkin et al. used to validate their hypothesis, whether it applies to fish assemblages is far from evident. First, native fish assemblages are adapted to these predictable natural seasonal disturbances and are resistant to change and, second, the habitat does not change structurally during high flow periods, except for water volume and water velocity. Species not adapted to high water velocities will disperse to escape these periodic unfavorable conditions and latter recolonize the site during dry season periods. In the Mekong, the highly seasonal-predictable system, riverine fishes also are known to have overlapping seasonal migration patterns between critical habitats (dry-season refugia, spawning, feeding/rearing) (Valbo-Jorgensen and Poulsen 2000, Poulsen et al. 2002, 2004, Sverdrup-Jensen 2002, Baran 2006), and possibly have homing behavior and site fidelity (Dittman and Quinn 1996, Thorrold et al. 2001, O'Connor et al. 2005, Koehn et al. 2009, Duponchelle et al. 2016) which likely constitutes more similar seasonal assemblage composition with low species turnover.

5.3.3 Inter-annual variation in fish community structure

In the TSRL, inter-annual variation in the fish community structure are closely linked to hydrology. The annual peak flows in the Tonle Sap Lake are found highly contrasted during the four-year study period (Fig. 20b, 21), i.e. a peak flow of 9.9 m was recorded in 2011, while only 7.5 m was observed in 2012, 9.0 m in 2013, 7.3 m in 2014 and only 5.3 m in 2015. High flows e.g. in 2011 and 2013, may have facilitated fish spawning success, survival and growth as greater flood levels equated with the higher volumes of water in the TSRL and, hence, larger inundated areas of rearing/feeding habitats were available for fish. Prey species and juveniles could stay longer in rearing habitats which increases their survival rates. Higher flows also mean that more food become available and, thereby, competition for food among fish is reduced. In fact, the highest catch on record over 17-year monitoring period was observed in the fishing season of 2011/2012 at the Tonle Sap *Dai* fishery (Chheng et al. 2012).

Flows also constrain fish species with the longitudinal and lateral dispersal ability among habitats such as different river reaches and floodplains (Franssen et al. 2006, Bunn & Harthington 2002). The significant inter-annual changes (Fig. 20b) were also due to the presence of more species from high gradient river/streams and clear/fast flowing water in 2012 such as *Clupisoma longianalis* (Clorn), *Balitora meridionalis* (Bmer) and *Crossocheilus reticulatus* (Cret), *Hemibagrus wyckii* (Hwyc) and fewer slowly flowing/lowland rivers such as *Parachela siamensis* (Psia) and *Hemibagrus filamentus* (Hfil), while towards 2015, there were more species with the habitat preference of lowland rivers and peats such as *Osteogeneiosus militaris* (Omil), *Osteochilus microcephalus* (Omic), *Osphronemus goramy* (Ogor), *Tenualosa thibaudeaui* (Tthi) and fewer high gradient river fishes such as *Discherodontus parvus* (Dpar) and *Osteochilus waandersii* (Owaa).

In the Tonle Sap River (TS), long-term trends (2000-2015) in the seasonal catches of harvested species of the Mekong's largest commercial *Dai* fishery revealed that 78% of the 116-species are in decline (Fig. 22). The results are consistent with the prediction of an intensively exploited indiscriminate fishery. Consistent with indiscriminate fishing theory, a closer examination of the data indicates that the catch declines are disproportionally represented by the larger, slower growing, higher trophic level organisms of the Tonle Sap (Fig. 23). By contrast, the 22% of species caught by the *Dai* fishery that tend to show increases are disproportionally represented by small-bodied, faster growing lower trophic level organisms. In addition, significant declines of the mean fish size and trophic level are evidenced in the seasonal catches of the fishery over the study period (Fig. 24). Finally, the data consistently showed for common species spanning a range in adult body sizes that individual weights and lengths of all these species, even in many of the small-bodied species, have been significantly reduced over the last 15 years (Fig. 25, 26), a result that resonates with much research that has found that heavy fishing pressure is known to drive shifts in life history towards smaller sizes and earlier ages at maturation (Sharpe and Hendry 2009). The results also point out for select species that the number of immature fish captured has increased throughout the study period (Fig. 26). Moreover, a significant decreasing trend in species evenness is observed over the study period (Fig. S5, Article 3). Thus, although this fishery has been amazingly resilient to changes in total fish harvest levels, these results collectively are in agreement with predicted effects of indiscriminate fishing theory. Because this theory ultimately predicts declines in fish catches and diversity with sustained, heavy indiscriminate fishing pressure (Jacobsen et al. 2014, McCann et al. 2016, Andersen and Gislason 2017, Szuwalski et al. 2017), these findings may be seen as an 'early yet clear warning signal' of looming negative impacts of indiscriminate fishing in the Tonle Sap.

In the Lower Mekong system, the study finds that sites with altered flows (Sekong [SK], Sesan [SS], Srepok [SP] – 3S) caused by upstream operating dams exhibit lowest levels of temporal changes in diversity (abundance, richness and temporal beta diversity [LCBD indices]) as compared to the predictably seasonal ones (Mekong [KT, ST] and Tonle Sap [TS]) (Fig. 27, 30, 31). The results indicate that dams modulate flows and weaken the flows' seasonality and predictability strengths and thus mute seasonal variation of fish abundance, richness, temporal beta diversity (LCBD indices) in the 3S, whereas sites with more naturally predictable flow conditions (Mekong, Tonle Sap) promote reliable seasonal variation in fish abundance, richness and temporal beta diversity (LCBD) with regular-predictable peaks at semi-annual and annual frequencies. Such reliable recurrence and coherence patterns of hydrology and fish (Fig. 32-34, for Mekong [KT] and Tonle Sap [TS]) are indeed consistent with the existing knowledge about timing of fish migration, fishing and local fisheries management practices in the Lower Mekong system (Valbo-Jorgensen and Poulsen 2000, Bao et al. 2001, Poulsen et al. 2002, 2004, Baird et al. 2003, FiA 2006, Halls et al. 2013c). When the river seasonal-predictable flows are modified as evidenced in the 3S e.g. SS (Fig. 32-34), such reliably seasonal-predictable events of fish assemblages no longer exist.

Finally, the study finds that the temporal dynamics of assemblage composition are driven by specialist species in the Mekong mainstream (Fig. 35a) and by generalist species in the 3S (Fig. 35b). Key species contributing to the temporal changes in the Mekong sites during the last four years of the survey are disproportionately represented by specialists, including medium and large-sized cyprinids of the family Cyprinidae, river catfishes of Pangasiidae and sheatfishes of Siluridae. These fishes are often long-distance migrants and/or mainstream spawners and prefer mainstream rivers as their main habitats. The opposite is observed in the 3S Rivers, where small-sized species (minnows and carps) of cyprinids with generalist habitat preferences are among the key species contributing to the assemblage change. Further, some floodplain resident fishes, such as climbing perches, snakeheads and airbreathing catfishes, are also among the key species in the assemblage composition of the 3S Rivers towards the last few years of the survey. These fishes have airbreathing organs and can physically withstand adverse environmental conditions (MRCS 1992, Welcome 2001, Poulsen et al. 2002). This trend in assemblage composition of the Mekong-3S system is likely to resemble the environmental filtering by dams because many migratory (specialist) species that depend on seasonal flow dynamics to complete their life cycles are constrained or extirpated by flow disruption caused by dams (Liermann et al. 2012), which finally leads to increased faunal homogenization as observed in the middle Lancang-Mekong River (Li et al. 2013), many Chinese lakes connecting to the Yangtze River (Cheng et al. 2014), and rivers across the United States (Poff et al. 2007). These results also strengthen recent review and field studies that find fish assemblages in SS to be represented by small-sized and generalist species such as small mud carps (mTL<25 cm) of the family Cyprinidae, and fewer large-sized migratory species such as river catfishes of Pangasiidae (mTL>100 cm), relative to the Mekong mainstream sites (Baran et al. 2013a, Ou and Winemiller 2016, Ou et al. 2017).

VI. Conclusion and implications for fisheries management and conservation

6.1 Conclusion

Fishes and fisheries of the LMB are globally acknowledged for its extremely high diversity and productivity. 504 fish species belonging to 252 genera, 78 families and 22 orders were recorded in the MRC routine fish monitoring programs. Seasonal flood pulse dynamics play a key role in structuring the spatial and temporal dynamics of fish communities. Fish species richness of the LMR is found to increase along its longitudinal ecological gradient from the upper LMR towards its delta. In contrast, high species diversity occurs in the middle of the system in Cambodia. Species in the upper and middle of the LMR are more indicative of potamodromous cyprinids and river catfishes; while in the delta, fish communities are composed of both steno- and euryhaline species, represented mainly by perch-like fishes and clupeids. In the Tonle Sap system, both species richness and diversity are found highest in the middle of the lake. The spatial abundance distribution patterns display a river-lake gradient with three fish assemblages clustered according to their composition similarities and characterized by 96 indicator species. In the southern section, fish assemblages are characterized by longitudinal migratory fish (i.e. cyprinids, river catfishes, loaches, sheatfishes), while in the middle system, the assemblage is represented by species with combined ecological attributes (longitudinal and lateral migratory species, and floodplain residents). Towards the northern part, fish assemblages are composed by lateral migratory fishes (i.e. featherbacks, sheatfishes and puffers) and floodplain resident species (i.e. gouramies, airbreathing catfishes, sleepers, snakeheads). Besides, the analyses on trends in the seasonal catches of 116 species shows that while overall production is sustained over the last 15-year period, fish communities utilizing the Tonle Sap system resemble the signature of indiscriminate fishing effects, with strong evidence that many medium- to large-sized fishes are declining and being replaced by smaller-sized fishes that, in turn, are responding to fishing pressure with significant reductions in body size. In the 3S system, more stable fish communities are revealed in Srepok (SP) River than those in Sekong (SK) and Sesan (SS) Rivers. In the Lower Mekong system, upstream functioning dams are found to weaken flow seasonality-predictability strength of the 3S relative to the Mekong and Tonle Sap Rivers reflecting the system's different spatial and temporal responses of fish communities. Overall, there have been declining trends on local species richness and abundance with strong temporal variability in local beta diversity. Rivers with highly seasonal-predictable flows (Mekong, Tonle Sap) are indicated by seasonal assemblage variability and regular annual peaks of fish migration, while rivers with highly regulated flows (3S) are characterized by aseasonal assemblage changes. Moreover, rivers with predictably seasonal flows are characterized by broad similarities of seasonal fish assemblage composition with low species turnover, whereas disturbed rivers are represented by distinct seasonal assemblage composition with high species turnover. Temporal shifts in assemblage composition suggest ecological filtering by dams, which alters seasonal flow patterns and favors generalist species which are observed, especially, in the 3S system.

6.2 Implications for fisheries management and conservation

For centuries, fishes of the LMB have been supporting the livelihoods of communities and millions of people. Will the great resources sustain in supporting its environmental goods and services in the face of combined effects of increased fishing pressure, increasing hydropower dam development and other anthropogenic stressors such as land use change, invasive species and climate change? This study demonstrates that fish species richness, abundance and biomass are significantly decreasing over time. Overfishing is threatening Tonle Sap's fisheries. Flow alternations by dams particularly in the 3S severely affect fish community structure and gradually diminish the system's productivity. Several planned dams in the Lower Mekong system including those in the mainstream are being pushed forward to the construction phase. Possible collapse in resource productivity may be on the horizon, making it critical to the protection and conservation of fish biodiversity and ecosystems of the Mekong including those of the Tonle Sap and 3S Basins. In so doing,

- it is imperative to maintain the Mekong's robust and predictably seasonal flood pulse dynamics and habitat connectivity which ensures the dispersal ability of fishes in the region both longitudinally along the river mainstream and laterally between the river mainstream and floodplain habitats such as those of Tonle Sap and the 3S System.
- attention should be given to setting appropriate regulations based on known peak fish migrations at various time-scales of the year would allow migratory fish to pass through rivers and complete their life cycles. Also, strengthening the existing formal institutions and allocating sufficient resources to the fishery sector by the governments of countries sharing the LMB could contribute to better enforcement of the current fishery laws and regulations in each respective country in order to reduce prevailing illegal fishing practices particularly those occurring in critical fish habitats. For instance, the formal institutions such as fisheries sector administrations, fisheries communities or fisheries associations as well as the LMB transboundary fisheries management bodies which have been established in the form of community-based fisheries management and joint mechanisms for transboundary fisheries management by the LMB national governments and the Mekong Rover Commission should be strengthened and enabled to fulfill their mandates. Priority of the protection or conservation initiatives should be given to key critical fish habitats where fishes breed, feed and seek refuge, aiming at (1) letting fish spawn at least for the first time before capture, (2) let fish grow and (3) let the mega-spawners live to deal with overfishing (Froese 2004).
- decisive efforts should be made to minimise the dam impacts, (1) there should be a basin-scale integrated strategic plan (accounting for cumulative impacts on hydrology and ecosystem services) that finds the balance between exploiting hydropower potential and sustaining key resources, e.g. in dam site selection (Winemiller et al. 2016). (2) the best available technologies related to up- and downstream fish pass facilities (Schmutz and Mielach 2015) must be built for existing and planned dams to facilitate up- and downstream fish migrations. Flow designs or flow management measures that could mimic as far as possible the natural hydraulic variation should be applied as a mitigation measure because the variation is the main ecological driver for fish dispersal and reproduction success.
- finally, continued support for basin-wide fish monitoring programs is highly necessary to provide updated data for fisheries impact assessment studies and for updating the status of the LMB fishes

and fisheries. Fish monitoring methods may be revisited to suit specific research needs, yet a mechanism for sharing and integrating national datasets needs to be maintained and used to inform both fisheries management and other water development plans.

VII. Further research

The Lower Mekong system is one of the most biodiverse rivers in the world. However, it has received little ecology research on many aspects of its resources and ecology including fish, reptiles, invertebrate and primary producers (Dudgeon 2000, 2003, Junk et al. 2006, Kummu et al. 2006, Vaidyanathan 2011, Allen et al. 2012). While this study provides an important contribution to understanding fishes and fisheries of the LMB, much fish ecological research is urgently required for better planning, management and biodiversity conservation in response to rapid developments particularly hydropower dams in the river basin. To contribute to such urgent calls, some immediate fish ecology research is suggested as follows:

- Update the basin-scale study related to ecological drivers that determine the spatial uniqueness of the LMB fish taxonomic composition. The research would generate data and information useful for the local and basin-wide fisheries planning, management and conservation. This study can be achieved through the use of the available updates of MRC fish and environment monitoring data in the LMB, and the framework of analysis as developed by (Legendre and De Cáceres 2013).
- Apart from the taxonomic component of fish biodiversity, the assessment of functional diversity (i.e. the range of biological traits) to measure the range of functions performed by fish fauna in the system could be a good approach to understand the role of fish biodiversity in sustaining ecosystem services, as well as the effects of anthropogenic disturbances on fish biodiversity in the Mekong. Several recent literatures e.g. (S. Villéger , N. W. H. Mason 2008, Cilleros et al. 2016, Toussaint et al. 2016, Teichert et al. 2017, Vitule et al. 2017, Kuczynski et al. 2018) would provide the framework of analysis to start such studies. In addition, data, i.e. morphological traits and other ecological attributes for this study can be collected from various existing databases such as the Mekong Fish Database (MFD 2003), FishBase (Froese and Pauly 2017) and a recent online database (ffish.asia) providing high resolution photos of the Mekong fishes (Kano et al. 2013). A software package to measure e.g. fish morphological traits is now available in ImageJ (http://rsb.info.nih.gov/ij/index.html).
- Moreover, this study finds out that small-sized mud carps e.g. *Henicorhynchus* spp. and *Labiobarbus* spp. are among the ecologically keystone species of the LMB which serve as prey for many predators, and significantly contribute to food security of the people in the LMB. These species are among the most abundant species and highly resilient to fishing pressure. To

understand what determines the bio-ecological success of these species under high fishing pressure would help shed light on ideas or generate information which could contribute to better management and conservation of these important species in support of ecology and food security in the region.

- Last, but not least, Other Aquatic Animals (OAAs) such as mollusk and crustacean are highly abundant particularly in the Tonle Sap floodplain and lake and heavily exploited. These resources play vital roles in support of food web dynamics and ecology as well as sources of income and food security of the LMB dwellers. However, these important resources are generally forgotten in fisheries management legislation, many research agendas and water development discussions in the region. Research initiatives in support of appropriate planning, management and conservation actions for these resources ought to be promoted before the resources become extinct due to human actions.

References

Adamson, P. T., I. D. Rutherfurd, M. C. Peel, and I. A. Conlan. 2009. The Hydrology of the Mekong River. Pages 53–76*in* I. C. Campbell, editor.The Mekong Biophysical Environment of an International River Basin. 1st edition. Elsevier Inc., Amsterdam.

Agostinho, A. A., L. C. Gomes, S. Veríssimo, and E. K. Okada. 2004. Flood regime, dam regulation and fish in the Upper Paraná River: Effects on assemblage attributes, reproduction and recruitment. Reviews in Fish Biology and Fisheries 14:11–19.

Ahmed, M., N. Hap, V. Ly, and M. Tiongco. 1998. Socioeconomic Assessment of Freshwater Capture Fisheries of Cambodia: a report on a household survey. Project for the management of the freshwater capture fisheries of Cambodia, Mekong River Commission/Department of Fisheries/Danish International Development Agency, Phnom Penh.

Albert, S. J., and E. R. Reis. 2011. Introduction to neotropical freshwaters. Pages 3–16*in* S. J. Albert and E. R. Reis, editors.Historical biogeography of neotropical freshwater fishes. University of California Press, Berkeley Los Angeles.

Allan, J. D., R. Abell, Z. Hogan, C. Revenga, B. W. Taylor, R. L. Welcomme, and K. Winemiller. 2005. Overfishing of Inland Waters. BioScience 55:1041–1051.

Allen, D. J., K. G. Smith, and W. R. T. Darwall. 2012. The Status and Distribution of Freshwater Biodiversity in Indo-Burma. IUCN, Cambridge, UK and Gland, Switzerland.

Aloo, P. A. 2003. Biological diversity of the Yala Swamp lakes, with special emphasis on fish species composition, in relation to changes in the Lake Victoria Basin (Kenya): threats and conservation measures. Biodiversity & Conservation 12:905–920.

Andersen, K. H., and H. Gislason. 2017. Unplanned ecological engineering. Proceedings of the National Academy of Sciences 114:634–635.

Arias, M. E., T. A. Cochrane, M. Kummu, H. Lauri, G. W. Holtgrieve, J. Koponen, and T. Piman. 2014a. Impacts of hydropower and climate change on drivers of ecological productivity of Southeast Asia's most important wetland. Ecological Modelling 272:252–263.

Arias, M. E., T. A. Cochrane, D. Norton, T. J. Killeen, and P. Khon. 2013. The flood pulse as the underlying driver of vegetation in the largest wetland and fishery of the Mekong Basin. Ambio 42:864–876.

Arias, M. E., T. A. Cochrane, T. Piman, M. Kummu, B. S. Caruso, and T. J. Killeen. 2012. Quantifying changes in flooding and habitats in the Tonle Sap Lake (Cambodia) caused by water infrastructure development and climate change in the Mekong Basin. Journal of Environmental Management 112:53–66.

Arias, M. E., T. Piman, H. Lauri, T. A. Cochrane, and M. Kummu. 2014b. Dams on Mekong tributaries as significant contributors of hydrological alterations to the Tonle Sap Floodplain in Cambodia. Hydrology and Earth System Sciences 18:5303–5315.

Baird, I., M. Baird, M. C. Chum, S. Kim, M. Nuon, S. Phat, B. N. Phouy, S. Prom, S. Ros, H. Rushton, and P. Sia. 2002. A Community-Based Study of the Downstream Impacts of the Yali Falls Dam Along the Se San, Sre Pok and Sekong Rivers in Stung Treng Province, Northeast Cambodia. Se San District Agriculture, Fisheries and Forestry Office, Stung Treng, Cambodia.

Baird, I. G. 2006. Probarbus jullieni and Probarbus labeamajor: The management and conservation of two of the largest fish species in the Mekong River in southern Laos. Aquatic Conservation: Marine and Freshwater Ecosystems 16:517–532.

Baird, I. G. 2011. The Don Sahong Dam. Critical Asian Studies 43:211–235.

Baird, I. G., M. S. Flaherty, and B. Phylavanh. 2003. Rhythms of the river: lunar phases and migrations of small carps (Cyprinidae) in the Mekong River. Natural History Bulletin of the Siam Society

51:5–36.

Baird, I. G., and M. Meach. 2005. Sesan River Fisheries Monitoring in Ratanakiri Province, Northeast Cambodia: Before and After the Construction of the Yali Falls Dam in the Central Highlands of Viet Nam. 3S Rivers Protection Network and the Global Association for People and the Environment, Ban Lung, Ratanakiri, Cambodia.

Bao, T. Q., K. Bouakhamvongsa, S. Chan, K. Chhuon, T. Phommavong, A. F. Poulsen, P. Rukawoma, U. Suornratana, D. V. Tien, T. T. Tuan, N. T. Tung, J. Valbo-Jorgensen, S. Viravong, and N. Yoorong. 2001. Local knowledge in the study of river fish biology: experiences from the Mekong. Mekong River Commission, Phnom Penh.

Baran, E. 2005. Cambodia inland fisheries: facts, figures and context. WorldFish Center and Inland Fisheries Research and Development Institute, Phnom Penh, Cambodia.

Baran, E. 2006. Fish Migration Triggers and Cues in the Lower Mekong Basin and Other Freshwater Tropical Systems. Mekong River Commission, Vientiane.

Baran, E., S. Samadee, T. S. Jiau, and T. C. Tran. 2013a. Fish and fisheries in the Sesan, Sekong and Srepok River Basins (Mekong Watershed). ICEM – International Centre for Environmental Management, Hanoi.

Baran, E., N. So, P. Degen, X. Y. Chen, and P. Starr. 2013b. Update information on fish and fisheries in the Lower Mekong Basin. Catch and Culture 19:24–25.

Baran, E., N. P. van Zalinge, and P. B. Ngor. 2001. Floods, Floodplains and Fish Production in the Mekong Basin: Present and Past Trends. Pages 920–932*in* A. Ali, editor.Proceedings of the Second Asian Wetlands Symposium, 27-30 August 2001, Penang, Malaysia. Penerbit Universiti Sains Malaysia, Pulau Pinang, Malaysia.

Bartley, D. M., G. J. De Graaf, J. Valbo-Jørgensen, and G. Marmulla. 2015. Inland capture fisheries: Status and data issues. Fisheries Management and Ecology 22:71–77.

Bejarano, M. D., R. Jansson, and C. Nilsson. 2017. The effects of hydropeaking on riverine plants: a review. Biological Reviews:1–16.

Béné, C., M. Barange, R. Subasinghe, P. Pinstrup-Andersen, G. Merino, G.-I. Hemre, and M. Williams. 2015. Feeding 9 billion by 2050 – Putting fish back on the menu. Food Security 7:261–274.

Borcard, D., F. Gillet, and P. Legendre. 2011. Numerical Ecology with R. Page (R. Gentleman, K. Hornik, and G. G. Parmigiani, Eds.). Springer Science, New York.

Boujard, T. 1992. Space-time organization of riverine fish communities in French Guiana. Environmental Biology of Fishes 34:235–246.

Brownell, R. L., R. R. Reeves, P. O. Thomas, B. D. Smith, and G. E. Ryan. 2017. Dams threaten rare Mekong dolphins. Science 355:805.

Bunn, S. E., and A. H. Arthington. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management 30:492–507.

De Cáceres, M., and F. Jansen. 2011. indicspecies: Functions to assess the strength and significance of relationship of species site group associations. R package version 1.6.0. http://cran.r-project.org/web/packages/indicspecies.

Cáceres, M. De, and P. Legendre. 2009. Associations between species and groups of sites: indices and statistical inference. Ecology 90:3566–3574.

Campbell, I. C., C. Poole, W. Giesen, and J. Valbo-Jorgensen. 2006. Species diversity and ecology of Tonle Sap Great Lake, Cambodia. Aquatic Sciences 68:355–373.

Carbonnel, J. P. 1963. Vitesse d' accumulation des sediments recents du Grand Lac du Cambodge d'apres le carbone 14. Con·elations stratigraphiques et morphologiques. Comptes Rendus de l 'Academie des Sciences 257:25 14-2516.

CGIAR. 2013. Working paper on population growth and natural resource pressures in Pursat catchment. Australian Aid and CGIAR Challenge Program on Water and Food, Vientiane.

Chea, R., S. Lek, P. B. Ngor, and G. Grenouillet. 2016. Large-scale patterns of fish diversity and assemblage structure in the longest tropical river in Asia. Ecology of Freshwater Fish 2016:1–11.

Cheng, L., S. Blanchet, G. Loot, S. Villéger, T. Zhang, S. Lek, S. Lek-Ang, and Z. Li. 2014. Temporal changes in the taxonomic and functional diversity of fish communities in shallow Chinese lakes: The effects of river-lake connections and aquaculture. Aquatic Conservation: Marine and Freshwater Ecosystems 24:23–34.

Chheng, P., N. So, P. B. Ngor, and T. Nao. 2012. Record fish catch on Tonle Sap River. Catch and Culture 18:4–5.

Cilleros, K., L. Allard, G. Grenouillet, and S. Brosse. 2016. Taxonomic and functional diversity patterns reveal different processes shaping European and Amazonian stream fish assemblages. Journal of Biogeography 43:1832–1843.

Claasen, A. H. 2004. Abundance, distribution, and reproductive success of sandbar nesting birds below the Yali Falls hydropower dam on the Sesan River, northeastern Cambodia. WWF/Danida/WCS/BirdLife International, Phnom Penh.

Clarke, K. D., T. C. Pratt, R. G. Randall, A. Dave, and K. E. Smokorowski. 2008. Validation of the flow management pathway: effects of altered flow on fish habitat and fishes downstream from a hydropower dam. Canadian Technical Report of Fisheries and Aquatic Sciences 2784, Canada.

Cochrane, T. A., M. E. Arias, and T. Piman. 2014. Historical impact of water infrastructure on water levels of the Mekong River and the Tonle Sap system. Hydrology and Earth System Sciences 18:4529–4541.

Collier, M., R. H. Webb, and J. C. Schmidt. 1996. Dams and rivers: A Primer on the Downstream Effects of Dams. U.S. Geological Survey, Circular 1 1 2 6, Colorado.

Colwell, R. K. 1974. Predictability, constancy, and contingency of periodic phenomena. Ecology 55:1148–1153.

Constable, D. 2015. Atlas of the 3S Basins. International Union for Conservation of Nature and Natural Resources (IUCN), Bangkok.

Davidson, P. J. 2006. The biodiversity of the Tonle Sap Biosphere Reserve: 2005 status review. UNDP-GEF funded Tonle Sap Conservation Project, Phnom Penh, Cambodia.

Deap, L., P. Degen, and N. van Zalinge. 2003. Fishing gears of the Cambodian Mekong. Inland Fisheries Research and Development Institute of Cambodia & Mekong River Commission, Phnom Penh, Cambodia.

Dittman, A., and T. Quinn. 1996. Homing in Pacific salmon: mechanisms and ecological basis. The Journal of experimental biology 199:83–91.

Dray, S., G. Blanchet, D. Borcard, G. Guénard, T. Jombart, G. Larocque, P. Legendre, N. Madi, and H. H. Wagner. 2017. adespatial: Multivariate multiscale spatial analysis. R package version 0.0-8. http://cran.r-project.org/package=adespatial.

Dudgeon, D. 2000. The Ecology of Tropical Asian Rivers and Streams in Relation to Biodiversity Conservation. Annual Review of Ecology, Evolution, and Systematics 31:195–229.

Dudgeon, D. 2003. The contribution of scientific information to the conservation and management of freshwater biodiversity in tropical Asia. Hydrobiologia 500:295–314.

Dudgeon, D., A. H. Arthington, M. O. Gessner, Z.-I. Kawabata, D. J. Knowler, C. Lévêque, R. J. Naiman, A.-H. Prieur-Richard, D. Soto, M. L. J. Stiassny, and C. A. Sullivan. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews of the Cambridge Philosophical Society 81:163–82.

Duponchelle, F., M. Pouilly, C. Pécheyran, M. Hauser, J. F. Renno, J. Panfili, A. M. Darnaude, A. García-Vasquez, F. Carvajal-Vallejos, C. García-Dávila, C. Doria, S. Bérail, A. Donard, F. Sondag, R. V. Santos, J. Nuñez, D. Point, M. Labonne, and E. Baras. 2016. Trans-Amazonian natal homing in giant catfish. Journal of Applied Ecology 53:1511–1520.

Enomoto, K., S. Ishikawa, M. Hori, H. S., L. S. Srun, T. Nao, and H. Kurokura. 2011. Data mining and stock assessment of fisheries resources in Tonle Sap Lake, Cambodia. Fisheries Science 77:713–722.

Espírito-Santo, H. M. V., W. E. Magnusson, J. Zuanon, F. P. Mendoça, and V. L. Landeiro. 2009. Seasonal variation in the composition of fish assemblages in small Amazonian forest streams: Evidence for predictable changes. Freshwater Biology 54:536–548.

Fan, H., D. He, and H. Wang. 2015. Environmental consequences of damming the mainstream Lancang-Mekong River: A review. Earth-Science Reviews 146:77–91.

FAO. 2016. The State of World Fisheries and Aquaculture 2016. Contributing to food security and nutrition for all. Food and Agriculture Organization of the United Nations, Rome.

Ferguson, J. W., M. Healey, P. Dugan, and C. Barlow. 2011. Potential effects of dams on migratory fish in the Mekong River: Lessons from salmon in the fraser and Columbia Rivers. Environmental Management 47:141–159.

FiA. 2006. Law on Fisheries. Fisheries Administration, Ministry of Agriculture, Forestry and Fisheries, Phnom.

Franssen, N. R., K. B. Gido, C. S. Guy, J. A. Tripe, S. J. Shrank, T. R. Strakosh, K. N. Bertrand, C. M. Franssen, K. L. Pitts, and C. P. Paukert. 2006. Effects of floods on fish assemblages in an intermittent prairie stream. Freshwater Biology 51:2072–2086.

Froese, R. 2004. Keep it simple: Three indicators to deal with overfishing. Fish and Fisheries 5:86–91.

Froese, R., and D. Pauly. 2017. FishBase. www.fishbase.org.

Fukushima, M., T. Jutagate, C. Grudpan, P. Phomikong, and S. Nohara. 2014. Potential effects of hydroelectric dam development in the Mekong River basin on the migration of Siamese mud carp (Henicorhynchus siamensis and H. lobatus) elucidated by otolith microchemistry. PLoS ONE 9:1–13.

de Graaf, G., D. Bartley, J. Jorgensen, and G. Marmulla. 2015. The scale of inland fisheries, can we do better? Alternative approaches for assessment. Fisheries Management and Ecology 22:64–70.

Graf, W. L. 2006. Downstream hydrologic and geomorphic effects of large dams on American rivers. Geomorphology 79:336–360.

Grumbine, R. E., J. Dore, and X. Jianchu. 2012. Mekong hydropower: Drivers of change and governance challenges. Frontiers in Ecology and the Environment 10:91–98.

Guégan, J. F., S. Lek, and T. Oberdorff. 1998. Energy availability and habitat heterogeneity predict global riverine fish diversity. Nature 391:382–384.

Gupta, A., and S. C. Liew. 2007. The Mekong from satellite imagery: a quick look at a large river. Geomorphology 85:259–274.

Habit, E., M. C. Belk, and O. Parra. 2007. Response of the riverine fish community to the construction and operation of a diversion hydropower plant in central Chile. Aquatic Conservation: Marine and Freshwater Ecosystems 17:37–49.

Halls, A. S., I. Conlan, W. Wisesjindawat, K. Phouthavongs, S. Viravong, S. Chan, and V. A. Vu. 2013a. Atlas of deep pools in the Lower Mekong River and some of its tributaries. Mekong River Commission, Phnom Penh.

Halls, A. S., and M. Kshatriya. 2009. Modelling the cumulative barrier and passage effects of mainstream hydropower dams on migratory fish populations in the Lower Mekong Basin. Page

Technical Paper No. 25. Mekong River Commission, Vientiane.

Halls, A. S., B. Paxton, N. Hall, K. Hortle, N. So, T. Chea, P. Chheng, S. Putrea, S. Lieng, N. Peng Bun, N. Pengby, S. Chan, V. Vu, D. Nguyen Nguyen, V. Doan, V. Sinthavong, S. Douangkham, S. Vannaxay, S. Renu, U. Suntornatana, T. Tiwarat, and S. Boonsong. 2013b. Integrated Analysis of Data from MRC Fisheries Monitoring Programmes in the Lower Mekong Basin. Page MRC Technical Paper No. 33. Mekong River Commission, Phnom Penh.

Halls, A. S., B. R. Paxton, N. Hall, P. B. Ngor, S. Lieng, P. Ngor, and N. So. 2013c. The Stationary Trawl (Dai) Fishery of the Tonle Sap-Great Lake System, Cambodia. Mekong River Commission, Phnom Penh.

Helfman, G. S., B. B. Collette, D. E. Facey, and B. W. Bowen. 2009. The Diversity of Fishes: Biology, Evolution, and Ecology. Wiley-Blackwell, Malaysia.

Henriques-Silva, R., Z. Lindo, and P. R. Peres-Neto. 2013. A community of metacommunities : Exploring patterns in species distributions across large geographical areas. Ecology 94:627–639.

Hirsch, P., and A. Wyatt. 2004. Negotiating local livelihoods: scales of conflict in the Se San River Basin. Asia Pacific Viewpoint 45:51–68.

Hoeinghaus, D. J., C. . Layman, D. A. Arrington, and K. O. Winemiller. 2003. Spatiotemporal variation in fish assemblage structure in tropical floodplain creeks. Environmental Biology of Fishes 67:379–387.

Hortle, K. G. 2007. Consumption and the yield of fish and other aquatic animals from the Lower Mekong Basin. Page MRC Technical Paper No. 16. Mekong River Commission, Vientiane.

Hortle, K. G. 2009. Fisheries of the Mekong River Basin. Pages 1997–1249*in* I. C. Campbell, editor.The Mekong biophysical Environment of an International River Basin. First edit. Elsevier Inc., Amsterdam.

Hortle, K. G., and P. Bamrungrach. 2015. Fisheries Habitat and Yield in the Lower Mekong Basin. Page MRC Technical Paper No. 47. Mekong River Commission, Phnom Penh.

Hortle, K. G., S. Lieng, and J. Valbo-Jorgensen. 2004. An introduction to Cambodia's inland fisheries. Page Mekong Development Series No. 4. Mekong River Commission, Phnom Penh.

Hortle, K. G., R. Troeung, and S. Lieng. 2008. Yield and value of the wild fishery of rice fields in Battambang Province, near the Tonle Sap Lake, Cambodia. Page MRC Technical Paper No.18. Mekong River Commission, Vietiane.62 PP. Mekong River Commission, Vientiane.

Hunter, M. A. 1992. Hydropower flow fluctuations and salmonids: A review of the biological effects, mechanical causes, and options for mitigation. State of Washington Department of Fisheries, Washington.

Hurwood, D. A., E. A. S. Adamson, and P. B. Mather. 2008. Evidence for strong genetic strcuture in an economically important, highly vagile (Henicorhynchus lobatus) in the Mekong River. Ecology of Freshwater Fish 17:273–283.

ICEM. 2010. MRC Strategic Environmental Assessment (SEA) of hydropower on the Mekong mainstream. Mekong River Commission, Hanoi.

Jacobsen, N. S., H. Gislason, and K. H. Andersen. 2014. The consequences of balanced harvesting of fish communities. Proceedings. Biological sciences / The Royal Society 281:1–9.

Jenkins, M. 2003. Prospects for biodiversity. Science 302:1175–1177.

Junk, W. . J., and K. M. Wantzen. 2004. The flood pulse concept: new aspects, approaches and applications - an update. Pages 117–140*in* R. Welcomme and T. Petr, editors.Proceedings of the second international symposium on the management of large rivers for fisheries. FAO Regional Office for Asia and the Pacific, Bangkok.

Junk, W. J., M. Brown, I. C. Campbell, M. Finlayson, B. Gopal, L. Ramberg, and B. G. Warner. 2006.

The comparative biodiversity of seven globally important wetlands: A synthesis. Aquatic Sciences 68:400–414.

Kang, B., D. He, L. Perrett, H. Wang, W. Hu, W. Deng, and Y. Wu. 2009. Fish and fisheries in the Upper Mekong: Current assessment of the fish community, threats and conservation. Reviews in Fish Biology and Fisheries 19:465–480.

Kano, Y., M. S. B. Adnan, C. Grudpan, J. Grudpan, W. Magtoon, P. Musikasinthorn, Y. Natori, S. Ottomanski, B. Praxaysonbath, K. Phongsa, A. Rangsiruji, K. Shibukawa, Y. Shimatani, N. So, A. Suvarnaraksha, P. Thach, P. N. Thanh, D. D. Tran, K. Utsugi, and T. Yamashita. 2013. An online database on freshwater fish diversity and distribution in Mainland Southeast Asia. Ichthyological Research 60:293–295.

Kassambara, A. 2017. Pratical guide to cluster analysis in R: unsupervised machine learning. STHDA, Poland.

Kennedy, T. A., J. D. Muehlbauer, C. B. Yackulic, D. A. Lytle, S. W. Miller, K. L. Dibble, E. W. Kortenhoeven, A. N. Metcalfe, and C. V Baxter. 2016. Flow Management for Hydropower Extirpates Aquatic Insects, Undermining River Food Webs. BioScience 66:562–575.

Koehn, J. D., J. A. McKenzie, D. J. O'Mahony, S. J. Nicol, J. P. O'Connor, and W. G. O'Connor. 2009. Movements of Murray cod (Maccullochella peelii peelii) in a large Australian lowland river. Ecology of Freshwater Fish 18:594–602.

Kong, H., M. Chevalier, P. Laffaille, and S. Lek. 2017. Spatio-temporal variation of fish taxonomic composition in a South-East Asian flood-pulse system. PLoS ONE 12:1–16.

Kottelat, M. 2013. The Fishes of the inland waters of Southeast Asia: A catalogue and core bibliography of the fishes known to occur in freshwaters, mangroves and estuaries. The Raffles Bulletin of Zoology 27:1–663.

Kuczynski, L., J. Côte, A. Toussaint, S. Brosse, L. Buisson, and G. Grenouillet. 2018. Spatial mismatch in morphological, ecological, and phylogenetic diversity, in historical and contemporary European freshwater fish faunas. Ecography 41:1–10.

Kummu, M., J. Sarkkula, J. Koponen, and J. Nikula. 2006. Ecosystem Management of the Tonle Sap Lake: An Integrated Modelling Approach Ecosystem. Water Resources Development 22:497–519.

Kummu, M., S. Tes, S. Yin, P. Adamson, J. Józsa, J. Koponen, J. Richey, and J. Sarkkula. 2014. Water balance analysis for the Tonle Sap Lake-floodplain system. Hydrological Processes 28:1722–1733.

Lamberts, D. 2001. Tonle Sap fisheries: a case study on floodplain gillnet fisheries. Page RAP publication. Asia-Pacific Fisheries Commission, Food and Agriculture Organisation of the United Nations, Regional Office for Asia and the Pacific, Bangkok.

Latrubesse, E. M., E. Y. Arima, T. Dunne, E. Park, V. R. Baker, F. M. Horta, C. Wight, F. Wittmann, J. Zuanon, P. A. Baker, C. C. Ribas, R. B. Norgaard, and N. Filizola. 2017. Damming the rivers of the Amazon basin. Nature 546:363–369.

Legendre, P., and M. De Cáceres. 2013. Beta diversity as the variance of community data: Dissimilarity coefficients and partitioning. Ecology Letters 16:951–963.

Legendre, P., and L. Legendre. 2012. Numerical Ecology. Third Engl. Elsevier Science B.V., Great Britain.

Legendre, P., and B. Salvat. 2015. Thirty-year recovery of mollusc communities after nuclear experimentations on Fangataufa atoll (Tuamotu, French Polynesia). Proceedings of the Royal Society B: Biological Sciences 282:20150750.

Lévêque, C., T. Oberdorff, D. Paugy, M. K. J. Stiassny, and P. A. Tedesco. 2008. Global diversity of fish (Pisces) in freshwater. Hydrobiologia 595:545–567.

Li, J., S. Dong, M. Peng, Z. Yang, S. Liu, X. Li, and C. Zhao. 2013. Effects of damming on the biological integrity of fish assemblages in the middle Lancang-Mekong River basin. Ecological Indicators 34:94–102.

Lieng, S., C. Yim, and N. van Zalinge. 1995. Freshwater fisheries of Cambodia, I: The bagnet (Dai) fishery in the Tonle Sap River. Asian Fisheries Science 8:255–262.

Liermann, C. R., C. Nilsson, J. Robertson, and R. Y. Ng. 2012. Implications of Dam Obstruction for Global Freshwater Fish Diversity. BioScience 62:539–548.

Lim, P., S. Lek, S. T. Touch, S. O. Mao, and B. Chhouk. 1999. Diversity and spatial distribution of freshwater fish in Great Lake and Tonle Sap river (Cambodia, Southeast Asia). Aquatic Living Resources 12:379–386.

Lucas, M. C., E. Baras, T. J. Thom, A. Duncan, and O. Slavik. 2001. Migration and spatial behaviour. Pages 1–12Migration of freshwater fishes. lackwell Science Ltd, Osney Mead, Oxford OX2 0EL.

Lynch, A. J., S. J. Cooke, A. M. Deines, S. D. Bower, D. B. Bunnell, I. G. Cowx, V. M. Nguyen, J. Nohner, K. Phouthavong, B. Riley, M. W. Rogers, W. W. Taylor, W. Woelmer, S. Youn, and T. D. Beard. 2016. The social, economic, and environmental importance of inland fish and fisheries. Environmental Reviews 24:1–7.

MacQuarrie, P. R., R. Welling, L. Rammont, and G. Pangare. 2013. The 3S River Basin. IUCN, Switzerland.

Matthews, W. J. 1998. Patterns in freshwater fish ecology. Chapman & Hall, Massachusetts, USA.

McCann, K. S., G. Gellner, B. C. McMeans, T. Deenik, G. Holtgrieve, N. Rooney, L. Hannah, M. Cooperman, S. Nam, and H. Giacomini. 2016. Food webs and the sustainability of indiscriminate fisheries. Canadian Journal of Fisheries and Aquatic Sciences 73:1–10.

McLaughlin, R. L., L. Porto, D. L. Noakes, J. R. Baylis, L. M. Carl, H. R. Dodd, J. D. Goldstein, D. B. Hayes, and R. G. Randall. 2006. Effects of low-head barriers on stream fishes: taxonomic affiliations and morphological correlates of sensitive species. Canadian Journal of Fisheries and Aquatic Sciences 63:766–779.

Meile, T., J. L. Boillat, and A. J. Schleiss. 2010. Hydropeaking indicators for characterization of the Upper-Rhone River in Switzerland. Aquatic Sciences 73:171–182.

MFD. 2003. Mekong Fish Database: A taxonomic fish database for the Mekong Basin. Mekong River Commission, Phnom Penh.

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

Mittermeier, R. A., W. R. Turner, F. W. Larsen, T. M. Brooks, and C. Gascon. 2011. Global biodiversity conservation: The critical role of hotspots. Pages 3–22*in* F. . Zachos and J. . Habel, editors.Biodiversity hotspots: Distribution and protection of conservation priority areas. Springer-Verlag Berlin Heidelberg.

Moyle, P. B., and J. J. Cech. 1988. Fishes: an introduction to ichthyology. Prentice Hall, Upper Saddle River NJ 07458.

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

MRC. 2007. Monitoring Fish Abundance and Diversity in the Lower Mekong Basin: Methodological Guidelines. Mekong River Commission, Phnom Penh.

MRC. 2010. State of the Basin Report 2010. Mekong River Commission, Vientiane, Lao PDR.

MRC. 2011. Planning Atlas of the Lower Mekong River Basin. Mekong River Commission, Phnom Penh.

MRCS. 1992. Fisheries in the Lower Mekong Basin, Main Report and Annex. (Review of the fishery sector in the lower Mekong basin). Interim Committee for the Coordination of Investigations of the Lower Mekong Basin, Mekong River Commission Secretariat, Bangkok.

Nagumo, N., T. Sugai, and S. Kubo. 2013. Late Quaternary floodplain development along the Stung Sen River in the Lower Mekong Basin, Cambodia. Geomorphology 198:84–95.

Nagumo, N., T. Sugai, and S. Kubo. 2015. Fluvial Geomorphology and Characteristics of Modern Channel Bars in the Lower Stung Sen River, Cambodia. Geographical Review of Japan Series B 87:115–121.

Ngor, P. B., P. Chheng, and N. So. 2015a. Declines in catches of some large and medium-sized species in Tonle Sap River. Catch and Culture 21:4–7.

Ngor, P. B., G. Grenouillet, S. Phem, N. So, and S. Lek. 2018a. Spatial and temporal variation in fish community structure and diversity in the largest tropical flood-pulse system of Southeast Asia. Ecology of Freshwater Fish In press.

Ngor, P. B., P. Legendre, T. Oberdorff, and S. Lek. 2018b. Flow alterations by dams shaped fish assemblage dynamics in the complex Mekong-3S river system. Ecological Indicators 88:103–114.

Ngor, P. B., P. Starr, P. Chheng, and N. So. 2015b. Rising fish prices in Cambodia. Catch and Culture 21:50.

Nielsen, N. M., R. S. Brown, and Z. D. Deng. 2015. Review of Existing Knowledge on the Effectiveness and Economics of Fish-Friendly Turbines. Mekong River Commission, Phnom Penh.

O'Connor, J. P., D. J. O'Mahony, and J. M. O'Mahony. 2005. Movements of Macquaria ambigua, in the Murray River, south-eastern Australia. Journal of Fish Biology 66:392–403.

Ou, C., C. G. Montaña, and O. Winemiller. 2017. Body size – trophic position relationships among fishes of the lower Mekong basin. Royal Society Open Science 4:160645.

Ou, C., and K. O. Winemiller. 2016. Seasonal Hydrology Shifts Production Sources Supporting Fishes in Rivers of the Lower Mekong Basin. Canadian Journal of Fisheries and Aquatic Sciences 73:1–21.

Pauly, D., V. Christensen, S. Guénette, T. J. Pitcher, U. R. Sumaila, C. J. Walters, R. Watson, and D. Zeller. 2002. Towards sustainability in world fisheries. Nature 418:689–695.

Phomikong, P., M. Fukushima, B. Sricharoendham, S. Nohara, and T. Jutagate. 2014. Diversity and community structure of fishes in the regulated versus unregulated tributaries of the mekong river. River Research and Applications:14 pp.

Piman, T., T. A. Cochrane, M. E. Arias, A. Green, and N. D. Dat. 2013. Assessment of Flow Changes from Hydropower Development and Operations in Sekong, Sesan, and Srepok Rivers of the Mekong Basin. Journal of Water Resources Planning and Management 139:723–732.

Poff, N. L., J. D. Olden, D. M. Merritt, and D. M. Pepin. 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. Proceedings of the National Academy of Sciences of the United States of America 104:5732–5737.

Poulsen, A. F., and J. Albo-Jørgensen. 2000. Fish migrations and spawning habits in the Mekong Mainstream – a survey using local knowledge. Page AMFC Technical Report. Vientiane.

Poulsen, A. F., K. G. Hortle, J. Valbo-Jorgensen, S. Chan, C. K. Chhuon, S. Viravong, K. Bouakhamvongsa, U. Suntornratana, N. Yoorong, N. T.T., and B. Q. Tran. 2004. Distribution and Ecology of Some Important Riverine Fish Species of the Mekong River Basin. Mekong River Commission, Phnom Penh.

Poulsen, A. F., P. Ouch, S. Viravong, U. Suntornratana, and T. T. Nguyen. 2002. Fish Migrations of the Lower Mekong Basin: Implications for Development, Planning and Environmental Management. Mekong River Commission, Phnom Penh.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rainboth, W. J. 1996. Fishes of the Cambodian Mekong. Food and Agriculture Organisation of the United Nations, Rome.

Rainboth, W. J., C. Vidthayanon, and D. Y. Mai. 2012. Fishes of the Greater Mekong Ecosystem with Species List and Photoraphic Atlas. Museum of Zoology, University of Michigan, Ann Arbor.

Ratanakiri Fisheries Office. 2000. A Study of Downstream Impacts of the Yali Falls Dam in the Se San River Basin in Ratanakiri Province, Northeast Cambodia. The Fisheries Office, Ratanakiri Province in cooperation with the Non-Timber Forest Products (NTFP) Project, Ratanakiri Province, Cambodia.

Revenga, C., and Y. Kura. 2003. Status and trends of biodiversity of inland water ecosystems. Montreal.

Roberts, T. R., and I. G. Baird. 1995. Traditional fisheries and fish ecology on the Mekong River at Khone Waterfalls in Southern Laos. Natural History Bulletin of the Siam Society 43:219–26.

Roesch, A., and H. Schmidbauer. 2014. WaveletComp: Computational Wavelet Analysis. R package version 1.0. CRAN.R-project.org.

Röpke, C. P., S. Amadio, J. Zuanon, E. J. G. Ferreira, C. P. de Deus, T. H. S. Pires, and K. O. Winemiller. 2017. Simultaneous abrupt shifts in hydrology and fish assemblage structure in a floodplain lake in the central Amazon. Scientific Reports 7:1–10.

Rossi, J. P. 2011. Rich: An R package to analyse species richness. Diversity 3:112–120.

Rutkow, E., C. Crider, and T. Giannin. 2005. Down River. The consequences of Vietnam's Se San River dams on life in Cambodia and their meaning in International law. NGO Forum on Cambodia, Phnom Penh.

S. Villéger , N. W. H. Mason, D. M. 2008. New Multidimensional Functional Diversity Indices for a Multifaceted Framework in Functional Ecology. America 89:2290–2301.

Sabo, J. L., A. Ruhi, G. W. Holtgrieve, V. Elliott, M. E. Arias, P. B. Ngor, T. A. Räsänen, and S. Nam. 2017. Designing river flows to improve food security futures in the Lower Mekong Basin. Science 358:1–11.

Schmutz, S., T. H. Bakken, T. Friedrich, T. Greimel, A. Harby, M. Jungwirth, A. Melcher, G. Unfer, and B. Zeiringer. 2015. Response of fish communities to hydrological and morphological alterations in hydropeaking rivers of Austria. River Research and Applications 31:919–930.

Schmutz, S., and C. Mielach. 2015. Review of existing research on fish passage through large dams and its applicability to Mekong mainstream dams. Mekong River Commission, Phnom Penh.

Sharpe, D. M. T., and A. P. Hendry. 2009. Life history change in commercially exploited fish stocks: An analysis of trends across studies. Evolutionary Applications 2:260–275.

Shumway, R. H., and D. S. Stoffer. 2011. Time series analysis and its applications: with R examples. Third Edit. Springer Science+Business Media, New York.

Silvano, R. A. M., D. Benedito, and O. T. Oyakawa. 2000. Spatial and temporal patterns of diversity and distribution of the Upper Juruá River fish community (Brazilian Amazon). Environmental Biology of Fishes 57:25–35.

So, N., S. Phommakone, V. Ly, T. Samphawamana, H. S. Nguyen, M. Khumsri, P. B. Ngor, S. Kong, P. Degen, and P. Starr. 2015. Lower Mekong fisheries estimated to be worth around $ 17 billion a year. Catch and Culture 21:4–7.

Stamatopoulos, C. 2002. Sample-based fishery surveys: a technical handbook. Page FAO. Fisheries Technical Paper. Food and Agriculture Organisation of the United Nations, Rome.

Statzner, B., and B. Higler. 1985. Questions and comments on the River Continuum Concept. Canadian

Journal of Fisheries and Aquatic Sciences 42:1038–1044.

Strayer, D. L., and D. Dudgeon. 2010. Freshwater biodiversity conservation: recent progress and future challenges. Journal of the North American Benthological Society 29:344–358.

Sverdrup-Jensen, S. 2002. Fisheries in the Lower Mekong Basin: Status and Perspectives. Mekong River Commission, Phnom Penh.

Szuwalski, C. S., C. C. Matthew G. Burgess, and S. D. Gaines. 2017. High fishery catches through trophic cascades in China. PNAS 114:717–721.

Teichert, N., M. Lepage, A. Sagouis, A. Borja, G. Chust, M. T. Ferreira, S. Pasquaud, R. Schinegger, P. Segurado, and C. Argillier. 2017. Functional redundancy and sensitivity of fish assemblages in European rivers, lakes and estuarine ecosystems. Scientific Reports 7:1–11.

The Ramsar Convention Secretariat. 2014. Ramsar. http://www.ramsar.org/wetland/cambodia.

Thorrold, S. R., C. Latkoczy, P. K. Swart, and C. M. Jones. 2001. Natal Homing in a Marine Fish Metapopulation. Science 291:297–299.

Tonkin, J. D., M. T. Bogan, N. Bonada, B. Ríos-Touma, and D. A. Lytle. 2017. Seasonality and predictability shape temporal species diversity. Ecology 0:1–16.

Tonolla, D., A. Bruder, and S. Schweizer. 2017. Evaluation of mitigation measures to reduce hydropeaking impacts on river ecosystems – a case study from the Swiss Alps. Science of the Total Environment 574:594–604.

Toussaint, A., N. Charpin, S. Brosse, and S. Villéger. 2016. Global functional diversity of freshwater fish is concentrated in the Neotropics while functional vulnerability is widespread. Scientific Reports 6:1–9.

Vaidyanathan, G. 2011. Dam controversy: Remaking the Mekong. Nature 478:305–307.

Valbo-Jørgensen, J., D. Coates, and K. G. Hortle. 2009. Fish diversity in the Lower Mekong Basin. Pages 161 – 196*in* I. C. Campbell, editor.The Mekong Biophysical Environment of an International River Basin. 1st edition. Elsevier Inc., Amsterdam.

Valbo-Jorgensen, J., and A. F. Poulsen. 2000. Using local knowledge as a research tool in the study of river fish biology: Experiences from the Mekong. Environment, Development and Sustainability 2:253–276.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The River Continuum Concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130–137.

Vitule, J. R. S., A. A. Agostinho, V. M. Azevedo-Santos, V. S. Daga, W. R. T. Darwall, D. B. Fitzgerald, F. A. Frehse, D. J. Hoeinghaus, D. P. Lima-Junior, A. L. B. Magalhães, M. L. Orsi, A. A. Padial, F. M. Pelicice, M. J. Petrere, P. S. Pompeu, and K. O. Winemiller. 2017. We need better understanding about functional diversity and vulnerability of tropical freshwater fishes. Biodiversity Conservation 26:757–762.

Watson, R., and D. Pauly. 2001. Systematic distortions in world fisheries catch trends. Nature 414:534–536.

Welcome, R. L. 2001. Inland fisheries: ecology and management. 1st edition. Food and Agriculture Organization of the United Nations by Blackwell Science, Great Britain.

Welcomme, R. L., I. G. Baird, D. Dudgeon, A. and Halls, and D. Lamberts. 2016. Fisheries of the rivers of Southeast Asia. Pages 363–376*in* J. F. Craig, editor.Freshwater Fisheries Ecology. First edit. John Wiley & Sons, Ltd., UK.

Welcomme, R. L., I. G. Cowx, D. Coates, C. Béné, S. Funge-Smith, A. Halls, and K. Lorenzen. 2010. Inland capture fisheries. Philosophical transactions of the Royal Society of London. Series B, Biological sciences 365:2881–96.

Winemiller, K., P. McIntyre, L. Castello, E. Fluet-Chouinard, T. Giarrizzo, N. So, I. Baird, W. Darwall, N. Lujan, I. Harrison, M. Stiassny, R. Silvano, D. Fitzgerald, F. Pelicice, A. Agostinho, L. Gomes, J. Albert, E. Baran, M. Petrere, C. Zarfl, M. Mulligan, J. Sullivan, C. Arantes, L. Sousa, A. Koning, D. Hoeinghaus, M. Sabaj, J. Lundberg, J. Armbruster, M. Thieme, P. Petry, J. Zuanon, G. Vilara, J. Snoeks, C. Ou, W. Rainboth, C. Pavanelli, A. Akama, A. van Soesbergen, and L. Saenz. 2016. Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. Science 351:128–129.

World Bank Group. 2015. Population, total. Cambodia. http://data.worldbank.org/indicator/SP.POP.TOTL?locations=KH.

Young, P. S., J. J. Cech, and L. C. Thompson. 2011. Hydropower-related pulsed-flow impacts on stream fishes: A brief review, conceptual model, knowledge gaps, and research needs. Reviews in Fish Biology and Fisheries 21:713–731.

van Zalinge, N. P., T. Nao, and S. Nuov. 2000. Status of the Cambodian inland capture fisheries sector with special reference to the Tonle Sap Great Lake. Mekong River Commission/Department of Fisheries/Danida, Phnom Penh, Cambodia.

van Zalinge, N., L. Deap, P. B. Ngor, J. Sarkula, and J. Koponen. 2003. Mekong flood levels and Tonle Sap fish catches. Page 13pp. Second International Symposium on the Management of Large Rivers for Fisheries. Second International Symposium on the Management of Large Rivers for Fisheries, Phnom Penh.

van Zalinge, N., P. Degen, C. Pongsri, S. Nuov, J. G. Jensen, V. H. Nguyen, and X. Choulamany. 2004. The Mekong River System. Pages 335–357*in* R. Welcomme and T. Petr, editors.Proceedings of the second international symposium on the management of large rivers for fisheries. FAO Regional Office for Asia and the Pacific, Bangkok.

van Zalinge, N., and T. Nao. 1999. Summary of Project Findings: Present status of Cambodia's freshwater capture fisheries and management implications. Pages 1–20*in* N. P. van Zalinge, T. Nao, and L. Deap, editors.Present status of Cambodia's fisheries and management implications. Mekong River Commission and Department of Fisheries, Phnom Penh.

van Zalinge, N., T. Nao, and S. T. Touch. 1998. Where there is water, there is fish? Fisheries issues in the Lower Mekong Basin from a Cambodian perspective. Page 14Contribution to the Mekong Panel at the Seventh Common Property Conference of the International Association for the Study of Common Property, Vancouver, Canada, 10 - 14 June 1998. International Association for the Study of Common Property, Vancouver, Canada.

Ziv, G., E. Baran, N. So, I. Rodriguez-Iturbe, and S. A. Levin. 2012. Trading-off fish biodiversity, food security, and hydropower in the Mekong River Basin. Proceedings of the National Academy of Sciences 109:5609–5614.

Annexes

Annex 1. List of indicator species in each cluster in the Lower Mekong River. Given are the values of indicator species (IndVal) for each cluster with their associated significance levels (Sign. level) (***, p<0.01; ** p<0.01; *, p<0.05). Indicator species were identified using mean annual fish composition, as well as composition computed during dry and wet seasons separately.

Assemblage Ia : 11 species		**Annual**		**Dry**		**Wet**	
Scientific names	Code	IndVal	Sign. level	IndVal	Sign. level	IndVal	Sign. level
Cosmochilus harmandi	coha	0.922	***	-	-	0.905	***
Bangana behri	babe	0.885	***	0.752	**	0.845	**
Helicophagus waandersii	hewa	0.877	***	-	-	0.839	*
Labeo chrysophekadion	moch	0.86	***	0.826	***	0.899	***
Bagarius yarelli	baya	0.854	***	0.92	***	0.769	**
Mekongina erythrospila	meer	0.844	**	0.814	*	0.747	**
Labeo erythropterus	laer	0.788	**	0.783	*	-	-
Phalacronotus apogon	phap	0.787	**	0.818	***	-	
Pangasius conchophilus	paco	0.769	*	-	-	0.785	**
Tenualosa thibaudeaui	teth	0.767	*	0.79	*	-	-
Syncrossus helodes	syhe	0.748	*	-	-	0.673	*
Assemblage Ib: 17 species							
Henicorhynchus spp.	hecr	0.933	***	0.859	**	0.945	***
Thynnichthys thynnoides	thth	0.865	**	-	-	0.859	**
Wallago attu	waat	0.849	**	0.891	**	0.785	**
Belodontichthys dinema	bedi	0.843	**	0.961	***	0.804	**
Puntioplites falcifer	pufa	0.838	**	0.955	***	0.84	**
Micronema bleekeri	mibl	0.828	***	0.844	***	0.817	**
Labiobarbus lineata	lali	0.817	**	0.909	**	0.744	*
Osteochilus melanopleura	osme	0.813	**	0.927	***	0.75	**
Gyrinocheilus pennocki	gype	0.802	*	0.873	**	0.642	*
Cyclocheilichthys furcatus	cyfu	0.798	**	0.912	***	0.804	**
Pangasianodon hypophthalmus	pahy	0.78	*	0.863	**	0.708	*
Hemibagrus nemurus	hene	0.768	***	0.669	*	0.787	***
Paralaubuca typus	paty	0.768	*	-	-	0.784	*
Hemibagrus wyckioides	hewyd	0.736	*	0.775	*	-	-
Leptobarbus hoevenii	leho	0.728	*	-	-	-	-
Brachirus harmandi	brha	0.686	*	0.784	*	-	-
Bagrichthys macropterus	bama	0.64	*	0.679	*	-	-
Assemblage IIa: 21 species							
Macrognathus siamensis	masi	1	***	0.997	***	0.816	***
Acanthopsis sp.	acsp	0.995	***	0.861	**	0.816	**
Puntioplites proctozysron	pupr1	0.954	***	0.948	***	0.951	***
Mastacembelus armatus	maar	0.954	***	0.95	***	0.643	*
Cynoglossus microlepis	cymi	0.894	**	0.909	**	0.927	***
Hampala macrolepidota	hama	0.889	***	0.721	*	0.811	**

Plotosus canius	plca	0.877	**	0.713	*	0.869	**
Mystus singaringan	mysi	0.854	**	0.908	**	0.718	*
Mystus mysticetus	mymy	0.843	***	0.735	*	0.755	**
Osteochilus vittatus	osvi	0.822	**	-	-	0.794	**
Notopterus notopterus	nono	0.825	**	0.861	**	-	-
Cyclocheilichthys armatus	cyar	0.806	**	0.809	**	-	-
Glossogobius giuris	glgi	0.787	***	0.863	***	0.652	*
Brachirus orientalis	bror	0.787	**	0.855	**	0.728	**
Boesemania microlepis	bomi	0.775	*	-	-	-	-
Oxyeleotris marmorata	oxma	0.748	**	0.862	**	-	-
Bagrichthys obscurus	baob	0.707	**	0.707	**	-	-
Hypsibarbus vernayi	hyve	0.707	**	0.707	**	-	-
Pseudomystus siamensis	pssi	0.707	**	-	-	0.577	*
Puntioplites sp.	pupr2	0.707	**	0.707	**	-	-
Akisis sp.	aksp	0.693	*	0.686	*	-	-
Assemblage IIb: 31 species							
Clupeichthys aesarnensis	clae	0.954	***	0.946	***	0.987	***
Rasbora trilineata	ratr	0.927	***	0.926	**	0.977	***
Trichogaster trichopterus	trtr	0.821	**	-	-	0.766	**
Rasbora sp.	rasp	0.8	**	0.849	**	-	-
Scomberomorus sinensis	scsp	0.755	***	0.756	**	-	-
Toxotes chatareus	toch	0.755	**	0.756	***	0.775	***
Toxotes spp.	tosp	0.755	**	0.756	***	-	-
Arius stormi	arst	0.753	*	0.681	*	-	-
Liza spp.	lisp	0.751	**	0.752	**	0.629	*
Parambassis wolffi	pabwo	0.725	*	0.749	*	-	-
Anabas testudineus	ante	0.7	*	0.782	*	-	-
Hemisilurus mekongensis	heme	0.686	*	0.789	**	-	-
Polynemus dubius	podu	0.681	*	0.69	*	0.727	**
Lates calcarifer	laca	0.674	*	0.827	**	-	-
Eleutheronema tetradactylum	elte	0.656	*	0.655	*	-	-
Pangasius juvernile	paju	0.656	*	0.535	*	0.775	***
Scatophagus argus	scar	0.656	*	0.655	*	-	-
Zenarchopterus ectuntio	zesp	0.656	*	0.655	*	-	-
Ellochelon vaigiensis	liva	0.656	*	0.534	*	-	-
Coilia magrognathos	cosp2	0.636	*	-	-	0.624	*
Pseudapocryptes elongatus	psel	0.631	*	0.596	*	-	-
Acentrogobius sp.	acens	0.539	*	-	-	0.632	*
Allenbatrachus grunniens	algr	0.539	*	0.535	*	-	-
Arius spp.	arsp	0.539	*	0.535	*	-	-
Arius thallassinus	arth	0.539	*	0.535	*	-	-
Boleophthalmus boddarti	bobo	0.539	*	-	-	-	-
Butis butis	bubu	0.539	*	0.535	*	-	-

Hyporhamphus limbatus	hyli	0.539	*	-	-	-	-
Taenioides sp.	tasp	0.539	*	-	-	0.632	**
Trichogaster pectoralis	trpe	0.539	*	-	-	-	-
Xenentodon cancila	xeca	0.539	*	0.535	*	-	-

Annex 2. Important species contributing to overall beta diversity.

Species names and their ecological attributes are based on (Rainboth 1996, MFD 2003, Rainboth et al. 2012, Kottelat 2013, Froese and Pauly 2017). For site names, KT=Kraite, ST=Stung Treng, SP=Srepok, SK=Sekong.

- Habitat guild: (1) Rithron resident, (2) Main channel resident, (3) Main channel spawner, (4) Floodplain spawner, (5) Eurytopic (generalist), (6) Floodplain resident, (7) Estuarine resident, (8) Marine visitor, (9) Non-native.
- Migration guild: Black = non-migratory (floodplain resident), Grey = lateral migration between floodplain and mainstream, White = longitudinal migration (in river).
- Length category (Leng. Cate.): (G) Giant size (>=100 cm), (L) Large size 61-99 cm), (M) Medium size (26-60 cm), (S) Small size (<= 25 cm).

Species abbre-viations	Species name	Migra-tion guild	Habitat guild	Feeding guild	Max. total length (cm)	Length Cate-gory	Site names				
							KT	ST	SP	SS	SK
Aspp	*Acantopsis* sp.	Black	6	Carnivorous	-	-	0.005				
Atestud	*Anabas testudineus*	Black	6	Omnivorous	25.0	Small		0.009	0.036	0.100	0.014
Atrunca	*Amblyrhynchichthys truncatus*	White	3	Omni/Herbivorous	48.8	Medium	0.009	0.016		0.012	0.013
Baltus	*Barbonymus altus*	Grey	4	Omnivorous	25.0	Small					0.012
Bgonion	*Barbonymus gonionotus*	White	5	Omnivorous	40.5	Medium	0.007				0.022
Bmajusc	*Bagrichthys majusculus*	White	3	Omnivorous	-	-	0.006		0.013	0.008	0.011
Bmicrol	*Boesemania microlepis*	Grey	4	Omnivorous	122.0	Giant	0.023				
Bobscur	*Bagrichthys obscurus*	White	3	Omnivorous	30.4	Medium	0.018	0.006	0.026	0.023	0.024
Borient	*Brachirus orientalis*	White	8	Carnivorous	36.6	Medium	0.009				
Bschwan	*Barbonymus schwanenfeldii*	Grey	4	Omnivorous	42.7	Medium	0.017	0.006	0.021	0.021	0.012
Btrunca	*Belodontichthys truncatus*	White	3	Omnivorous	73.2	Large	0.020	0.006	0.008		
Byarrel	*Bagarius yarrelli*	White	1	Carnivorous	244.0	Giant					0.006
Capogon	*Cyclocheilichthys apogon*	Grey	4	Omnivorous	25.0	Small			0.010		
Carmatu	*Cyclocheilichthys armatus*	Grey	4	Omnivorous	23.0	Small	0.035	0.020	0.034	0.025	0.019
Cbatrac	*Clarias batrachus*	Black	6	Omnivorous	47.0	Medium			0.007	0.023	0.006
Cblanci	*Chitala blanci*	White	1	Carni/Omnivorous	146.4	Giant	0.016	0.005			0.005
Cenoplo	*Cyclocheilichthys enoplos*	White	2	Omnivorous	90.3	Large	0.014	0.012			
Cfurcat	*Cyclocheilos furcatus*	White	2	Carnivorous	-	-		0.007			
Cgachua	*Channa gachua*	Black	1	Carnivorous	24.4	Small			0.006		
Charman	*Cosmochilus harmandi*	White	2	Omnivorous	100.0	Giant	0.024	0.034	0.017		
Chetero	*Cyclocheilichthys heteronema*	Grey	4	Herbivorous	14.6	Small					0.016

Cjullie	*Cirrhinus jullieni*	White	3	Omnivorous	24.4	Small					0.009
Clagler	*Cyclocheilichthys lagleri*	Grey	4	Omnivorous	18.3	Small		0.007	0.011		0.008
Clopis	*Chitala lopis*	White	3	Piscivorous	183.0	Giant					0.010
Cmacroc	*Clarias macrocephalus*	Black	6	Carnivorous	120.0	Giant		0.010		0.017	0.005
Cmaruli	*Channa marulioides*	Black	6	Carnivorous	27.0	Medium	0.007				
Cmelade	*Clarias meladerma*	Black	6	Carnivorous	42.7	Medium			0.009		
Cmicrol	*Cirrhinus microlepis*	White	3	Omnivorous	79.3	Large		0.008			
Cmicrop	*Channa micropeltes*	Black	6	Carnivorous	158.6	Giant	0.005				
Cmolito	*Cirrhinus molitorella*	White	3	Herbivorous	55.0	Medium					0.010
Crepass	*Cyclocheilichthys repasson*	Grey	4	Omnivorous	32.2	Medium	0.021	0.041		0.008	
Csinens	*Clupisoma sinense*	White	3	Omnivorous	37.8	Medium			0.013		0.020
Cstriat	*Channa striata*	Black	6	Carnivorous	122.0	Giant	0.012	0.008	0.027	0.013	0.012
Dundeci	*Datnioides undecimradiatus*	White	3	Carnivorous	48.8	Medium	0.008				0.009
Gpennoc	*Gyrinocheilus pennocki*	White	3	Herbivorous	34.2	Medium	0.020				
Hdispar	*Hampala dispar*	White	5	Carnivorous	42.7	Medium	0.013		0.009	0.018	
Hfilame	*Hemibagrus filamentus*	White	3	Omni/carnivorous	50.0	Medium	0.007	0.007	0.012		0.028
Hlagler	*Hypsibarbus lagleri*	White	3	Omnivorous	48.8	Medium	0.007	0.052	0.021	0.034	0.028
Hlobatu	*Henicorhynchus lobatus*	White	5	Herbivorous	18.3	Small	0.050	0.202		0.090	0.022
Hmacrol	*Hampala macrolepidota*	White	5	Omnivorous	80.5	Large		0.006			
Hmalcol	*Hypsibarbus malcolmi*	White	3	Omnivorous	61.0	Large	0.026	0.030	0.068	0.032	0.010
Hmekong	*Hemisilurus mekongensis*	White	3	Omni/carnivorous	80.0	Large	0.007		0.028		0.012
Hpierre	*Hypsibarbus pierrei*	White	3	Omnivorous	36.6	Medium	0.007	0.036	0.010	0.032	0.033
Hsiamen	*Henicorhynchus siamensis*	White	5	Herbivorous	24.4	Small	0.015	0.023	0.017	0.034	0.016
Hspilop	*Hemibagrus spilopterus*	White	3	Carnivorous	37.7	Medium	0.021	0.025	0.021	0.012	0.030
Hstormi	*Hemiarius stormii*	White	7	Omnivorous	50.0	Medium	0.006				
Hsuvatt	*Hypsibarbus suvattii*	White	3	Omnivorous	42.7	Medium		0.006		0.016	0.014
Hwaande	*Helicophagus waandersii*	White	3	Molluscivorous	70.0	Large	0.027	0.017	0.066		0.007
Hwetmor	*Hypsibarbus wetmorei*	White	3	Omnivorous	25.0	Small	0.007	0.012		0.011	0.023
Hwyckii	*Hemibagrus wyckii*	White	3	Carnivorous	86.6	Large					0.006
Hwyckio	*Hemibagrus wyckioides*	White	3	Carnivorous	130.0	Giant	0.010	0.006	0.007		
Kcrypto	*Kryptopterus cryptopterus*	White	3	Carni/Omnivorous	16.8	Small					0.006
Lbleeke	*Luciosoma bleekeri*	White	3	Carni/Omnivorous	30.5	Medium		0.011			0.005
Lchryso	*Labeo chrysophekadion*	White	3	Herbi/Omnivorous	90.0	Large	0.033	0.027	0.014		0.006
Lcrocod	*Lycothrissa crocodilus*	White	7	Carnivorous	36.6	Medium	0.005			0.021	0.007
Ldyoche	*Labeo dyocheilus*	White	9	Herbivorous	90.0	Large			0.011		
Llongib	*Laides longibarbis*	White	3	Omnivorous	17.3	Small			0.007		0.014
Lsiamen	*Labiobarbus siamensis*	White	5	Omnivorous	22.0	Small	0.015	0.018	0.023	0.027	0.050
Malboli	*Mystus albolineatus*	Grey	4	Omnivorous	42.7	Medium					0.005
Marmatu	*Mastacembelus armatus*	White	5	Omnivorous	35.5	Medium			0.010		
Mbocour	*Mystus bocourti*	Grey	4	Carnivorous	29.3	Medium	0.009				0.011
Mchevey	*Micronema cheveyi*	White	3	Carnivorous	35.0	Medium		0.017	0.012		0.025
Merythr. 1	*Mekongina erythrospila*	White	1	Herbivorous	54.9	Medium	0.007	0.005			
Mmystic	*Mystus mysticetus*	Grey	4	Carnivorous	15.9	Small					0.005
Nnotopt	*Notopterus notopterus*	Grey	5	Omnivorous	73.2	Large	0.009	0.006	0.007	0.013	
Obimacu	*Ompok bimaculatus*	Grey	4	Carnivorous	51.8	Medium		0.006	0.010		
Oexodon	*Osphronemus exodon*	Black	1	Omnivorous	73.2	Large	0.023				

Ogoramy	*Osphronemus goramy*	Black	1	Omnivorous	85.4	Large	0.010		0.007		0.009
Omarmor	*Oxyeleotris marmorata*	White	5	Carnivorous	79.3	Large	0.009				
Omelano	*Osteochilus melanopleurus*	White	3	Herbivorous	73.2	Large	0.007				
Omicroc	*Osteochilus microcephalus*	White	5	Herbivorous	29.3	Medium					0.006
Oniloti	*Oreochromis niloticus*	White	9	Herbivorous	73.2	Large					0.008
Ovittat	*Osteochilus vittatus*	White	5	Herbi/omnivorous	39.0	Medium		0.013	0.025	0.030	
Papogon. 1	*Phalacronotus apogon*	White	3	Carnivorous	158.6	Giant	0.007	0.008	0.008		0.020
Pbarron	*Paralaubuca barroni*	Grey	4	Omnivorous	18.3	Small				0.021	0.051
Pbleeke	*Phalacronotus bleekeri*	White	3	Omni/carnivorous	73.2	Large	0.016	0.017	0.067	0.018	0.014
Pbulu	*Puntioplites bulu*	White	3	Herbi/Omnivorous	35.0	Medium				0.033	
Pconcho	*Pangasius conchophilus*	White	2	Omnivorous	146.4	Giant	0.005	0.020	0.028		
Pdubius	*Polynemus dubius*	White	7	Carnivorous	24.4	Small	0.006				
Pfalcif	*Puntioplites falcifer*	White	3	Omnivorous	38.3	Medium	0.058	0.049	0.030	0.036	0.031
Pfascia	*Pristolepis fasciata*	Black	4	Omnivorous	20.0	Small	0.029	0.006	0.013	0.011	
Pjullie	*Probarbus jullieni*	White	2	Omnivorous	183.0	Giant	0.009				
Plabeam	*Probarbus labeamajor*	White	2	Omnivorous	183.0	Giant	0.005				
Plabeam. 1	*Probarbus labeaminor*	White	2	Omnivorous	150.0	Giant		0.006			
Pmacron	*Pangasius macronema*	White	3	Omnivorous	36.6	Medium	0.014		0.027		0.020
Pmicron. 1	*Pseudolais micronemus*	White	3	Omnivorous	42.7	Medium		0.006			
Ppleuro	*Pseudolais pleurotaenia*	White	3	Omnivorous	42.7	Medium		0.006	0.025		
Pprocto	*Puntioplites proctozysron*	White	3	Omnivorous	30.0	Medium	0.023	0.007			0.015
Privero	*Paralaubuca riveroi*	Grey	4	Carnivorous	22.0	Small				0.017	0.023
Psiamen. 2	*Pseudomystus siamensis*	White	3	Omnivorous	18.3	Small	0.006		0.015	0.017	
Ptypus	*Paralaubuca typus*	White	2	Omnivorous	22.0	Small				0.009	0.009
Pwolffi	*Parambassis wolffii*	Grey	4	Carnivorous	24.4	Small	0.036				
Rhobelm	*Rasbora hobelmani*	Grey	4	Insectivorous	7.3	Small					0.010
Rtornie	*Rasbora tornieri*	Grey	4	Insectivorous	20.7	Small				0.018	
Srubrip	*Systomus rubripinnis*	White	5	Omnivorous	30.5	Medium			0.012	0.042	0.016
Sstejne	*Scaphognathops stejnegeri*	White	3	Omnivorous	30.5	Medium	0.018	0.010	0.033	0.052	0.021

PART II: PUBPLICATIONS

ARTICLE 1

Large-scale patterns of fish diversity and assemblage structure in the longest tropical river in Asia

Ratha Chea, Sovan Lek, **Peng Bun Ngor**, Gaël Grenouillet 2016

Ecology of Freshwater Fish, 2016, 1–11

Accepted: 8 July 2016

DOI: 10.1111/eff.12301

ORIGINAL ARTICLE

WILEY Ecology of FRESHWATER FISH

Large-scale patterns of fish diversity and assemblage structure in the longest tropical river in Asia

Ratha Chea[1,2] | Sovan Lek[1,2] | Pengbun Ngor[3] | Gaël Grenouillet[1,4]

[1]Université de Toulouse, Labo Evolution & Diversité Biologique, UMR5174 EDB CNRS-Université Paul Sabatier-ENFA, Toulouse, France

[2]Faculty of Agriculture and Food Processing, University of Battambang, Battambang City, Cambodia

[3]Fisheries Program, Mekong River Commission, Phnom Penh, Cambodia

[4]Institut Universitaire de France, Paris, France

Correspondence
R. Chea, Université de Toulouse, Labo Evolution & Diversité Biologique, UMR5174 EDB CNRS- Université Paul Sabatier-ENFA, Toulouse, France.
Email: chearatha@rocketmail.com

Abstract

Although the Mekong River is one of the world's 35 biodiversity hot spots, the large-scale patterns of fish diversity and assemblage structure remain poorly addressed. This study aimed to investigate the fish distribution patterns in the Lower Mekong River (LMR) and to identify their environmental determinants. Daily fish catch data (i.e. from December 2000 to November 2001) at 38 sites distributed along the LMR were related to 15 physicochemical and 19 climatic variables. As a result, four different clusters were defined according to the similarity in assemblage composition and 80 indicator species were identified. While fish species richness was highest in the Mekong delta and lowest in the upper part of the LMR, the diversity index was highest in the middle part of the LMR and lowest in the delta. We found that fish assemblages changed along the environmental gradients and that the main drivers affecting the fish assemblage structure were the seasonal variation of temperature, precipitation, dissolved oxygen, pH and total phosphorus. Specifically, upstream assemblages were characterised by cyprinids and *Pangasius* catfish, well suited to low temperature, high dissolved oxygen and high pH. Fish assemblages in the delta were dominated by perch-like fish and clupeids, more tolerant to high temperatures, and high levels of nutrients (nitrates and total phosphorus) and salinity. Overall, the patterns were consistent between seasons. Our study contributes to establishing the first holistic fish community study in the LMR.

KEYWORDS

distribution patterns, environmental gradient, fish assemblage, fishery, Lower Mekong River

1 | INTRODUCTION

Large tropical rivers represent ecosystems of historically immense value for humanity, both in terms of the high biodiversity they support and of the number of people whose livelihoods depend directly upon that biodiversity (Coates, 2001). Mekong River, the largest tropical river in Asia, is known as one of the world's 35 biodiversity hot spots (Mittermeier, Turner, Larsen, Brooks, & Gascon, 2011). It is a biologically diverse and highly productive ecosystem, ranked 3rd in terms of fish diversity (877 species, Ziv, Baran, So, Rodriguez-Iturbe, & Levin, 2012), just after the Amazon River Basin (3,000 species, Rainboth, 1996) and the Congo River Basin (991 species, Froese & Pauly, 2015); yet, on a per unit area basis and fish family diversity Mekong is indeed the richest. Annually, Mekong harvests 2.3 million tonnes of wild fish supporting the world's largest inland fishery and providing essential livelihoods, nutrition and food security for millions of people within the region (MRC 2015). The economic values of fisheries in Lower Mekong alone were estimated to be worth around 17 billion USD a year generating employments and constituting a safety net for more than 60 million people within the region, especially the poor households in rural communities (MRC 2015). More importantly, in combination with its socio-economic values, the Mekong River Basin accounts for high levels of endemism, for example among the known species, 219 are endemic to the basin (76% are cyprinids and 12% catfishes; Dudgeon, 2011). However, compared to other riverine ecosystems, that is temperate, neotropical and subtropical, still very little effort has been mobilised to study the ecological and biological compartments of this extremely productive system, for example fish, invertebrates and other primary producers (Coates, 2001; Dudgeon, 2003; Kottelat & Whitten, 1996). While previous studies have focused on the relationship between hydrology and fish production, the impact of dams as well as the migration patterns of certain common species, the spatial structure of the fish community as a whole has not been investigated (Baran, 2006; Dugan et al., 2010; Lucas, Baras, Thom, Duncan, & Slavik, 2001; Poulsen, Ouch, Sinthavong, Ubolratana, & Nguyen, 2002; Ziv et al., 2012) and the relative importance of environmental factors in structuring fish communities along the river remains to be studied. Accordingly, the large-scale distribution patterns of the fish community have neither been described nor documented, except some ecological and biological descriptions of single species (see Rainboth, 1996).

To date, the determination of factors structuring communities remains one of the major objectives in fish ecological studies and it is widely accepted that the structure of communities results from spatial variability of habitat, environmental variability and interactions among the organisms (Albert & Reis, 2011; Lujan et al., 2013; Olden et al., 2010; Zhao, Grenouillet, Pool, Tudesque, & Cucherousset, 2015). For instance, some authors revealed the prevailing roles of physicochemical factors in structuring fish communities (Pires, Pires, Collares-Pereira, & Magalhães, 2010; Tejerina-Garro, Fortin, & Rodríguez, 1998), while others reported the dominant effects of climatic factors (Buisson, Blanc, & Grenouillet, 2008; Guo et al., 2015). Considering large-scale patterns, the study of fish communities is always challenging, for example lack of environmental variables at the local scale, rarity of large data sets of fish composition, which are much more informative than simple presence–absence data, and limitation of modelling the nonlinear relationship between biotic and abiotic factors, especially for cross-border river basins (e.g. the Mekong; Amarasinghe & Welcomme, 2002; Oberdoff, Guegan, & Hugueny, 1995).

Furthermore, over the last 30 years, with the rapid growth of population, industrialisation, agriculture intensification and hydropower development in the basin, in both Upper and Lower Mekong Basins, it was reported that the basin is now facing increasing environmental degradation, that is water pollution, eutrophication, deforestation, which are adversely affecting the biodiversity within the whole region (Dudgeon, 2003, 2011; Vorosmarty et al., 2010). Therefore, biodiversity management and conservation efforts are needed to mitigate these impacts. Consequently, this requires an understanding of how environmental and anthropogenic factors shape the present biogeography of organisms (Olden et al., 2010; Pool, Olden, Whittier, & Paukert, 2010). In this context, the main objectives of the present work were: (i) to describe the fish diversity and assemblage structure in the Lower Mekong River (LMR) by examining the relative abundance of fish composition and the associated distribution patterns and (ii) to identify the physicochemical and climatic factors driving fish assemblage patterns. More specifically, our study contributes to establishing a baseline holistic fish community study in the LMR and to identifying the drivers controlling the fish assemblage patterns. These findings could have important implications for biodiversity management and conservation in the large river basins worldwide.

2 | MATERIALS AND METHODS

2.1 | Study area: The Lower Mekong River

The Mekong rises on the Tibetan plateau and runs for 4,350 km through six countries to the South China Sea, where it discharges annually on average 475,000 million m^3 (Lu & Siew, 2006). The Mekong River Basin covers an area of 795,000 km^2 and is functionally divided into two parts: the Upper Mekong Basin (UMB) and the Lower Mekong Basin (LMB; Lu & Siew, 2006). The upper part of the river, in China, is called the Lancang Jiang and is characterised by deep gorges and steep declines. At the Golden Triangle, where the borders of Laos, Myanmar and Thailand meet, the LMB starts, and the river (Lower Mekong River) runs for another 2,500 km to the sea (Fig. 1). The LMB consists of four riparian countries, that is Laos, Thailand, Cambodia and Vietnam and covers 77% of the total basin area with 60 million inhabitants. Geographically, the Lower Mekong River (LMR) forms a stretch of about 900 km, which marks the border between Laos and Thailand, and creates an inland delta at the Lao-Cambodian border known as Khone Falls (21 m high; Fig. 1; Roberts & Baird, 1995). Then, at Phnom Penh, the Mekong

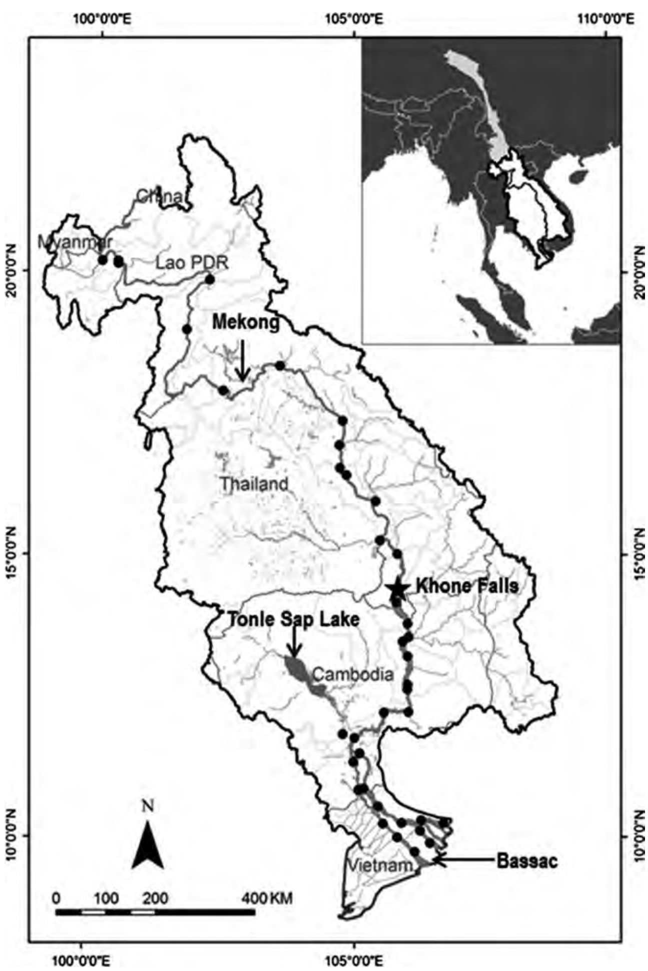


FIGURE 1 Lower Mekong Basin. Black dots represent the fish monitoring sites along the mainstream Lower Mekong River

TABLE 1 List of bioclimatic variables used in the study with the average and standard deviation

Variable	Unit	Variable type	Mean	SD
Bio1	(°C)	Annual Mean Temperature	26.76	0.90
Bio2	(°C)	Mean Diurnal Range (Mean of monthly (max temp − min temp))	9.15	1.71
Bio3	%	Isothermality (bio2/bio7); *100)	58.54	5.39
Bio4	(°C*100)	Temperature Seasonality (standard deviation *100)	1,569.82	736.45
Bio5	(°C)	Maximum Temperature of Warmest Month	34.23	0.98
Bio6	(°C)	Minimum Temperature of Coldest Month	18.39	3.57
Bio7	(°C)	Temperature Annual Range (bio5-bio6)	15.84	4.20
Bio8	(°C)	Mean Temperature of Wettest Quarter	27.20	0.31
Bio9	(°C)	Mean Temperature of Driest Quarter	24.83	2.19
Bio10	(°C)	Mean Temperature of Warmest Quarter	28.53	0.55
Bio11	(°C)	Mean Temperature of Coldest Quarter	24.50	2.03
Bio12	mm	Annual Precipitation	1,635.26	324.78
Bio13	mm	Precipitation of Wettest Month	329.85	90.95
Bio14	mm	Precipitation of Driest Month	4.18	3.27
Bio15	—	Precipitation Seasonality (Coefficient of Variation)	83.82	10.42
Bio16	mm	Precipitation of Wettest Quarter	869.21	251.89
Bio17	mm	Precipitation of Driest Quarter	25.31	12.84
Bio18	mm	Precipitation of Warmest Quarter	407.79	184.73
Bio19	mm	Precipitation of Coldest Quarter	63.51	46.40

Isothermality (bio3) is defined as the ratio of the diurnal range of temperature to the annual range.

connects with Tonle Sap Lake through Tonle Sap River. There, the river splits into two branches, that is Mekong proper and Bassac River, and forms a large estuarine delta before it empties in the sea. Under the influence of tropical Monsoon, the LMB's climate is basically divided into two seasons, that is dry (December–May) and wet (June–November) seasons, each lasting 6 months (Lu, Li, Kummu, Padawangi, & Wang, 2014). One of the important features of the Mekong's hydrological regime is the flow regulation by the Great Lake in Cambodia, that is the vast lake draining into the Mekong in the dry season and raising the water level in the delta for 5–6 months (Lu et al., 2014).

2.2 | Fish catch monitoring

The fish data used in this study were derived from the Mekong River Commission (MRC), under the Assessment of Mekong Fisheries Component of the MRC Fisheries Programme. The daily fish catches were monitored at 38 sites along the Lower Mekong mainstream from November 2000 to December 2001; the project was funded by the government of Denmark through DANIDA (Danish International Development Agency; Poulsen et al., 2002). Indeed, the fish survey was carried out along the main channel and consisted of eight sites located in Laos, seven in Thailand, 12 in Cambodia and 11 in Vietnam. Basically, at each location, fishermen recorded their daily catches in the logbooks, the maximum length of each species in every sample, the type of fishing gears used as well as the weather condition of the fishing day (e.g. high/low water level, rainy/sunny day). The catch monitoring methods were derived from the MRC's regional monitoring programme on Fish abundance and diversity in Lower Mekong Basin (FEVM 2007). Indeed, all fishermen were trained to use logbooks, sampling and subsampling techniques applied for the large catch during the peak seasons, identify the fish species, as well as measure length and weight of fish species. The taxonomic identification was performed to species level and to help with fish identification, the photograph flipcharts of more than 170 fish common species were provided to fishermen. Moreover, to ensure the quality of monitoring, all data were checked for errors and cleaned quarterly within the monitoring period by MRC's specialists. In total, about 14,368 observations have been recorded over the survey period and five main types of fishing gear were recorded, that is gillnets (47%), long lines and hooks (23%), traps (10%), bag nets (8%) and cast nets (7%; Sinthavong, 2006). The fishing efforts ranged from 1 to 24 hr depending on the seasons and type of the gear; nevertheless, the average efforts over the record period were between 6 to 7 hr/day. We used the whole data set for the statistical analyses.

2.3 | Climatic variables

Nineteen bioclimatic variables were derived from the WordClim database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), available at http://www.worldclim.org, describing the climate conditions for the period 1950–2000 with a spatial resolution of about 1 km^2 (Table 1).

2.4 | Physicochemical variables

Fifteen physicochemical variables were obtained from the MRC's water quality monitoring programme (Chea, Grenouillet, & Lek, 2016) and used to examine the link between physicochemical factors and fish assemblages (Table 2). The monitoring programme started in 1985 in Laos–Vietnam–Thailand and 1995 in Cambodia. At the basin scale, 117 sites were monitored monthly. The values of physicochemical variables of each fish site were attributed from the closest water quality monitoring sites (Table S1). In total, 22 of the whole number of monitoring sites were used for the analyses and the values of each parameter were expressed as annual median values (Table S1). The

TABLE 2 List of physicochemical variables used

Variables	Unit	Mean	*SD*
pH	—	7.38	0.33
Total suspended solids (TSS)	mg/L	124.47	84.70
Conductivity (EC)	μS/cm	202.19	105.07
Calcium (Ca^{+2})	mg/L	19.30	6.21
Magnesium (Mg^{+2})	mg/L	5.36	2.29
Sodium (Na^{+})	mg/L	12.56	17.22
Potassium (K^{+})	mg/L	1.85	1.01
Alkalinity (Alk)	mg/L	76.07	20.00
Chloride (Cl^{-})	mg/L	15.69	30.00
Sulphate (SO_4^{-2})	mg/L	14.22	5.99
Nitrate (NO_3^{-})	mg/L	0.23	0.07
Ammonium (NH_4^{+})	mg/L	0.05	0.02
Total phosphorus (TP)	mg/L	0.09	0.06
Dissolved oxygen (DO)	mg/L	7.09	0.69
Chemical oxygen demand (COD)	mg/L	2.59	1.13

average distance between fish and physicochemical sites was 27.36 (±27.08 *SD*) km.

2.5 | Statistical analysis

Here, we focused on patterns of community in terms of composition rather than abundance. Therefore, all fish catches were transformed into relative abundance to reduce the effect of varying fishing efforts between sites and averaged to annual mean relative abundance to summarise the data set. Next, we performed Ward hierarchical clustering based on the annual mean relative abundance to classify the fish sites into different groups according to their similarity in species composition (Murtagh & Legendre, 2014). Species richness and diversity index (i.e. inverse Simpson index) were computed to describe the clusters identified, and significant differences ($p < .05$) among clusters were tested using Tukey's HSD (Honest Significant Difference) tests.

Afterwards, the indicator species of each group of sites were determined using the "indicspecies" package to describe the differences in the clusters identified (De Cáceres, Legendre, & Moretti, 2010). For a given cluster, the indicator value of the species is the square root of the product of two quantities called A and B, that is predictive value and sensitivity. Quantity A is the probability of the target group of sites given that an individual species has been found and was defined as the mean abundance of the species in the target site group divided by the sum of the mean abundance value over all groups. Quantity B is the average relative abundance of individuals of the species at a site that belongs to the target site group and was determined as the relative frequency of occurrence of the species inside the target site group (De Cáceres et al., 2010). Hence, species with high indicator values were used as characteristic members of the cluster. The same procedure was performed simultaneously for dry and wet seasons of fish data sets.

To study the relationship between fish assemblages and environmental variables, ordination methods were performed on annual mean fish data. First, detrended correspondence analysis (DCA) was performed to select the appropriate ordination method for our study (i.e. redundancy analysis (RDA) versus canonical correspondence analysis (CCA; Legendre & Legendre, 2012). CCA was described as the most appropriate method as the calculated DCA ordination gradient was > 3 (i.e. 4.22 for our study), revealing that unimodal responses to environmental factors predominated (Ter Braak & Prentice, 1988). CCA is a constraint ordination method which reveals the relationships between community structure, sites and environmental variables (Legendre & Legendre, 2012). In the biplot of CCA, the importance of environmental variables is depicted by the length of the vectors, while the correlation between them is exhibited by the angle between the vectors. We used Monte Carlo permutation tests with 999 permutations to test whether the variables significantly ($p < .05$) explained the fish data (Legendre & Legendre, 2012).

Lastly, to examine the contribution of the two sets of environmental factors in explaining the variation in fish assemblages, variance partitioning was performed to see how the physicochemical and climatic variables contributed to explain fish assemblages (Borcard, Legendre, & Drapeau, 1992; Legendre & Legendre, 2012). Spatial vectors were also included in the variance partitioning to disentangle the influence of environmental and spatial factors on fish distribution. The geographic coordinates of the sites were modelled following the Asymmetric Eigenvectors Map (AEM) procedure proposed by Blanchet, Legendre, and Borcard (2008). Forward selection was performed on AEM vectors, and only significant environmental and AEM variables were kept for the analysis. The partitioning was performed through the "vegan" package and displayed in the form of a Venn diagram (Borcard et al., 1992). All statistical analyses were conducted in R 3.2.2 (R Core Team 2015).

3 | RESULTS

3.1 | Fish diversity and assemblage structure

A total of 182 species belonging to 110 genera, 42 families and 13 different orders were recorded by the fishermen at 38 monitoring sites. Three main orders accounted for 80% of the total number of species, that is Cypriniformes (54 species), Siluriformes (53 species) and Perciformes (39 species), while Anguilliformes, Batrachoidiformes, Beloniformes, Clupeiformes, Mugiliformes, Osteoglossiformes, Pleuronectiformes, Rajiformes, Synbranchiformes and Tetraodontiformes represented each of them < 5% of the total fish species richness.

The 38 monitoring sites were patterned into four different community assemblage clusters based on the similarity of their species composition (Fig. 2a). Two main community clusters were defined at the first split (clusters I and II), revealing the longitudinal characteristics of the Mekong system between the upper LMR and its delta. Subsequently, the main clusters were subdivided into four different groups considered as four different fish assemblages (Ia, Ib, IIa and

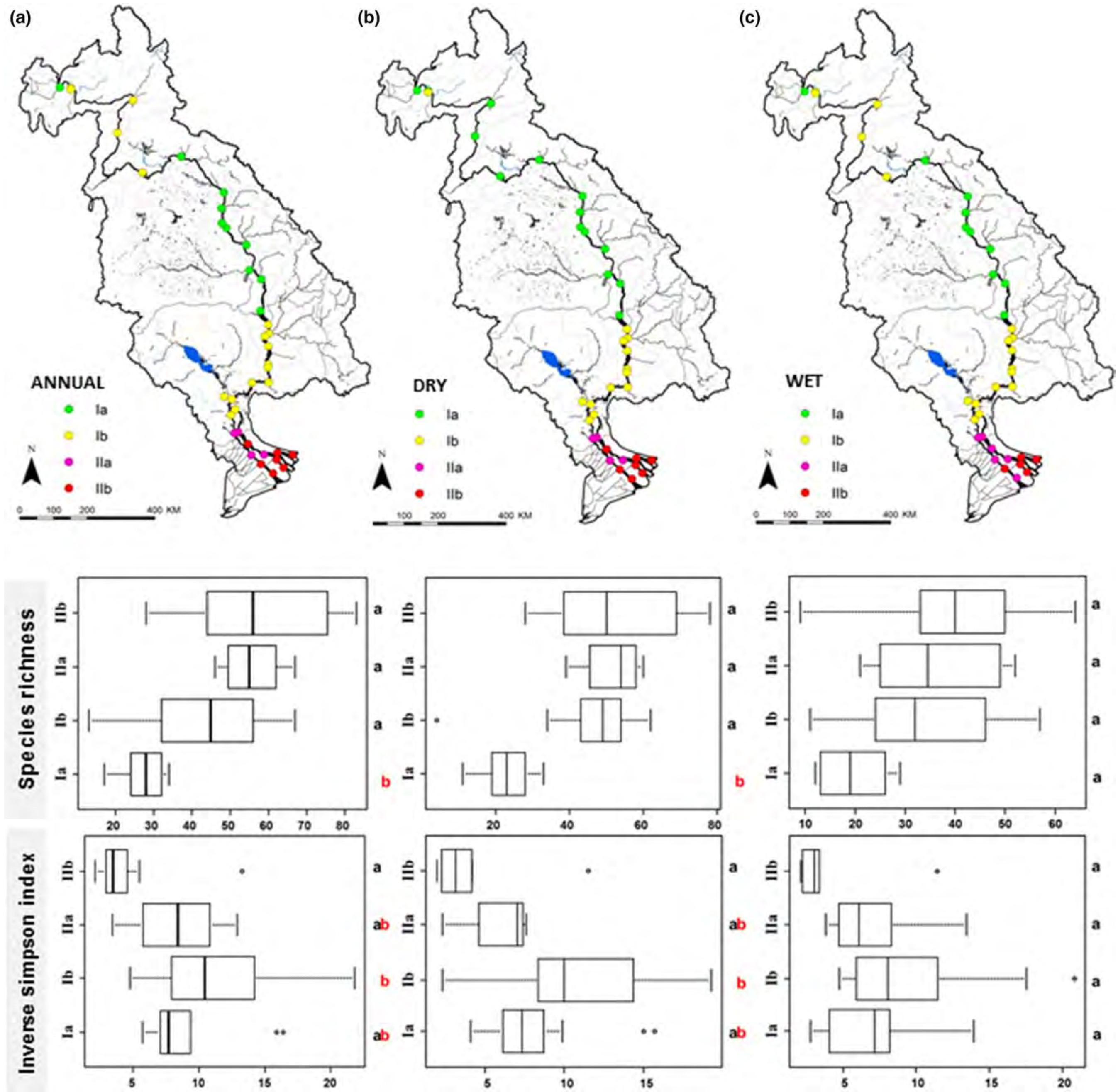


FIGURE 2 Fish distribution and assemblage patterns in Lower Mekong River. Annual (a), dry season (b) and wet season (c) clustering associated with species richness and Inverse Simpson index of each cluster (Ia, Ib, IIa, IIb). For each box plot, the dark line inside the box represents the median value, while the lines below and above indicate the 25 and 75 percentiles respectively. The whisker marks represent the minimum and maximum values. Mean values among clusters with a common letter are not significantly different at *p* = .05 (Tukey's HSD tests)

IIb) in the LMR (Fig. 2a). Indeed, cluster Ia was composed of 10 sites, stretching down in the upper part of the LMR, along the border between Laos and Thailand. Only one site of this cluster was found at the head of the LMB. Cluster Ib was composed of 17 sites, mainly located in Cambodia and four sites were found in upstream of the LMR, above Vientiane city. The smallest cluster IIa was made up of four sites, that is two sites located at the border of Cambodia and Mekong delta and other two sites in the middle part of the delta. Finally, the cluster IIb was characterised by seven sites in the lower part of the Mekong delta, known as the brackish zone; only one site of IIb was found in the middle part of the delta. Fish species richness of each assemblage ranged from 17 species at the head of the LMR to 82 at the mouth of the river (Fig. 2a). The highest species richness was found in IIb (median: 56 species), followed by IIa (55 species) and then Ib (45 species), and Ia contained the lowest species richness (28 species; Fig. 2a). Indeed, cluster Ia presented significantly lower species richness than the other three clusters, while no significant differences were observed between clusters Ib, IIa and IIb. Moreover, important variations in species richness were noticed between clusters Ib and IIb. In contrast, the diversity index was highest (median: 10.5) in Ib and lowest (median: 3.5) in IIb (Fig. 2a). Accordingly, the diversity in Ib was significantly different from IIb, while the others exhibited similar diversity indices (Fig. 2a).

The seasonal patterns were consistent between dry and wet season (Fig. 2b,c). During the dry season, fish assemblages were characterised by higher species richness than in wet season and the patterns of diversity were pronounced, especially between clusters Ib and IIb (Fig. 2b). By contrast, during the wet season, fish assemblage patterns were more similar to the annual patterns; and no significant differences in species richness and diversity were observed between the identified clusters (Fig. 2c).

Furthermore, the relative abundance of fish orders varied greatly along the longitudinal gradient of the LMR system, and this pattern was consistent between seasons for all except one fish order (i.e. Clupiformes, Fig. 3, Wilcoxon test, $p < .05$). Apart from the Mekong delta, that is particularly in Ia and Ib, Cypriniformes and Siluriformes dominated and occurred almost in every site, while their abundances decline dramatically in the delta. Additionally, Osteoglosiformes and Perciformes were found in some sites of Ib, that is the sites in Cambodia. In the delta (IIa and IIb), the fish composition was diverse and characterised by many species from different orders such as Clupeiformes, Perciformes, Pleuronectiformes, Synbranchiformes, Tetraodontiformes; among those, Perciformes and Clupeiformes were the most abundant (Fig. 3).

3.2 | Indicator species of clusters

A total of 80 indicator species were identified from the four annual clusters (Table S2). The highest number of indicator species was found in IIb (31 species), while the lowest was observed in Ia (11 species). The clusters in the delta (IIa and IIb) accounted for 66% of the total indicator species. The indicator species in Ia and Ib were mostly species from Cyprinidae, Pangasiidae, Siluridae and Bagridae families, that is *Cosmochilus harmandi*, *Bagnana behri*, *Helicophagus waandersii*, *Labeo chrysophekadion*, *Bagarius yarelli*, *Henicorhynchus* spp., *Micronema bleekeri and Hemibagrus nemurus*, which are known as potamodromous fish and indigenous to the LMB. Assemblage IIa contained 21 indicator species. Among them, many are known as freshwater and secondary freshwater fish such as *Glossogobius giuris*, *Macrognathus siamensis*, *Acanthopsis* sp., *Puntioplites proctozysron*, *Mastacembelus armatus and Mystus mysticetus*. Similarly, the main indicator species of IIb were mostly characterised by secondary freshwater fish and marine species, known as amphidromous and anadromous fish, that is *Clupeichthys aesarnensis*, *Rasbora trilineata*, *Scomberomorus sinensis*, *Eleotris* spp., *Liza* spp., *Arius stormi*, *Toxotes* spp., *Lates calcarifer*. Most of indicator species during the dry season were also identified as indicator species using annual assemblage compositions. Overall, dry season assemblages contained more indicator species (73 species) compared to wet season assemblages (51 species), while many indicators species from annual IIa and IIb were absent in the wet season (Table S2).

3.3 | Environmental determinants of the fish assemblages

The CCA model testing the association between annual fish assemblages and climatic variables was significant ($F = 1.55$, $p = .001$) and the first two axes explained 15.8% and 7.2% of the variation in fish composition respectively. Among the climatic variables tested, 18 had a significant ($p < .05$) effect on fish assemblage (Fig. 4a,b, Tables 1 and 3). Indeed, cluster Ia was mainly characterised by high values of bio15, bio16 and bio13 respectively the seasonal variation of precipitation,

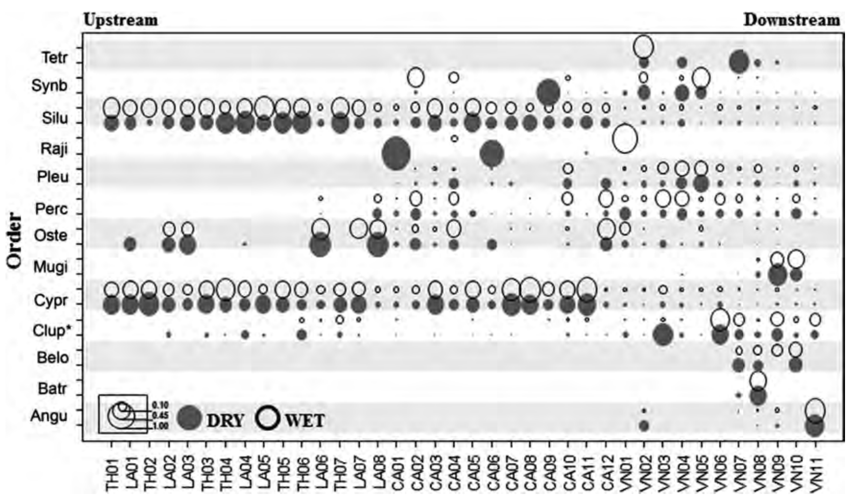


FIGURE 3 Relative abundances of fish order along the Lower Mekong River. Open and close circles denote the wet and dry season respectively. The acronyms in the vertical axis denote the species order: angu (Anguilliformes), batr (Batrachoidiformes), belo (Beloniformes), clup (Clupeiformes), cypr (Cypriniformes), mugi (Mugiliformes), oste (Osteoglossiformes), perc (Perciformes), pleu (Pleuronectiformes), raji (Rajiformes), silu (Siluriformes), synb (Synbranchiformes), tetr (Tetraodontiformes). The acronyms in the horizontal axis indicate the location of the sites: TH (Thailand), LA (Laos), CA (Cambodia) and VN (Vietnam). *denotes significant differences in fish relative abundance between seasons (Wilcoxon test, $V = 313$ and $p = .04$)

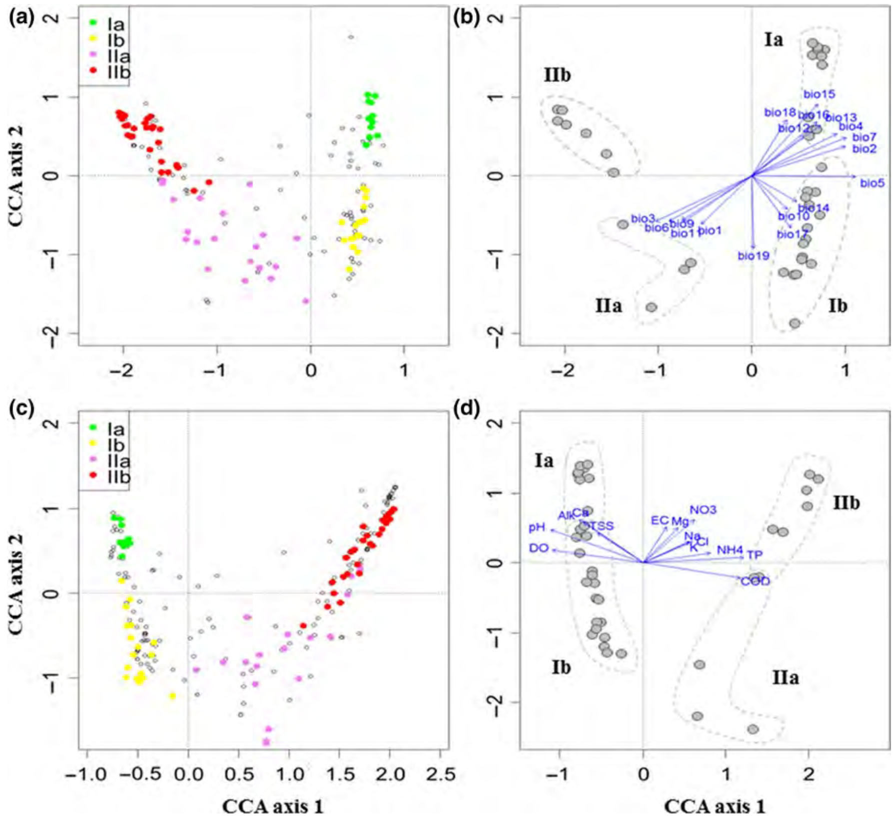


FIGURE 4 Canonical correspondence analysis (CCA) relating fish relative abundance to (a, b) climatic variables and (c, d) physicochemical variables. The different colour dots on the left plots represent the indicator species in each fish assemblage; while the grey dots on the right hand side indicate the fish monitoring sites. The blue arrows represent the vectors of environmental variables (i.e. climatic and physicochemical) and only significant variables ($p < .05$) are depicted. Details about the indicator species and environmental variables are given in Tables 1–3 and S2

the precipitation of the wettest month and wettest quarter. Similar climatic patterns were associated to Ib, except that high values of bio5 (maximal temperature of warmest month) and bio19 (precipitation of coldest quarter) were strongly associated with this cluster. In the Mekong delta, clusters IIa and IIb were characterised by high values of the isothermality (bio3), minimal temperature of the coldest month (bio6), the mean temperature of the driest quarter (bio9) and coldest quarter (bio11). Overall, in the upper part of the LMR, the clusters Ia and Ib were associated with high values of precipitation, while the delta clusters (IIa and IIb) were strongly characterised by high values of temperature.

In parallel, the CCA model testing the effect of physicochemical variables on annual fish assemblage composition was significant ($F = 1.77$, $p = .001$). The first two axes explained 22.5% of the variation in fish assemblage (15.5% and 7.0% respectively). Among the physicochemical variables tested, 14 had a significant effect on the fish assemblages ($p < .05$; Fig. 4c,d, Tables 2 and 3). Clusters Ia and Ib were strongly characterised by high values of DO, pH, Ca, alk and TSS; while the IIa and IIb were positively associated with high values of TP, COD and NH_4^+. In addition, cluster IIb was found to be associated with high levels of NO_3^- and Cl^- as well, especially for the sites close to the sea.

3.4 | Effects of environmental and spatial factors on the fish assemblages

Variance partitioning in fish assemblage composition indicated that both environmental (physicochemical and climatic) and spatial variables contributed significantly to explain patterns in fish assemblages (Fig. 5). The pure physicochemical factors explained 8.0% of variation in fish assemblages, while 10.9% and 4.0% were explained uniquely by climatic and spatial factors respectively. Physicochemical and climatic factors jointly explained 5.3% of the total variance, while the component shared by the three factors (physicochemical, climatic and spatial) explained 20.1% of the variation in fish assemblages. The adjusted R^2 from the model was 46.7%.

4 | DISCUSSION

4.1 | Fish diversity and assemblage structure

To our knowledge, this study is the first holistic fish community study to investigate the large-scale patterns of fish distribution and their environmental determinants in the lower Mekong river. In terms of fish diversity, the upstream part of the LMR exhibited the lowest species richness, while the highest richness was observed in the delta where fish species were composed of freshwater, brackish and marine species. Indeed, the longitudinal changes of species richness along the physical and chemical gradients, that is upstream–downstream, are well known in large-scale patterns of fish assemblages. Many discussions and explanations of the mechanisms responsible for such patterns have come up with the concept of “addition” leading to the increase in species richness from the headwaters to lower part of the river (see Matthews, 1998).

In contrast to species richness, cluster IIb exhibited the lowest diversity index, while the highest value was observed in Ib in Cambodia. Consequently, these patterns of diversity could reflect

TABLE 3 Canonical correlation coefficients of climatic and physicochemical variables with the first two canonical correspondence analysis axes (CCA1 and CCA2). The correlation of the explanatory variables to the final ordination (r^2) determines their importance in explaining fish assemblage composition, with their associated *p*-values computed from permutation tests. Variable codes are in Tables 1 and 2

Parameters	CCA1	CCA2	r^2	p
Climatic variables				
Bio1	−.664	−.748	.393	.001
Bio2	.937	.349	.676	.001
Bio3	−.870	−.493	.820	.001
Bio4	.861	.509	.658	.001
Bio5	1.000	−.010	.727	.001
Bio6	−.838	−.546	.656	.001
Bio7	.901	.434	.743	.001
Bio8	.272	−.962	.013	.756
Bio9	−.803	−.595	.518	.001
Bio10	.658	−.753	.191	.025
Bio11	−.783	−.622	.516	.001
Bio12	.736	.677	.336	.001
Bio13	.750	.662	.561	.001
Bio14	.830	−.557	.197	.020
Bio15	.613	.790	.788	.001
Bio16	.714	.700	.566	.001
Bio17	.538	−.843	.360	.002
Bio18	.463	.886	.382	.001
Bio19	.016	−1.000	.500	.001
Physicochemical variables				
pH	−.918	.397	.721	.001
TSS	−.789	.615	.236	.014
EC	.494	.869	.170	.043
Ca	−.780	.626	.476	.001
Mg	.637	.771	.213	.016
Na	.876	.482	.199	.023
K	.877	.480	.202	.021
Alk	−.768	.640	.415	.001
Cl	.890	.456	.217	.011
SO4	−.294	.956	.154	.066
NO3	.707	.708	.377	.001
NH4	.985	.174	.334	.005
TP	.998	.061	.736	.001
DO	−.987	.161	.600	.001
COD	.984	−.180	.703	.001

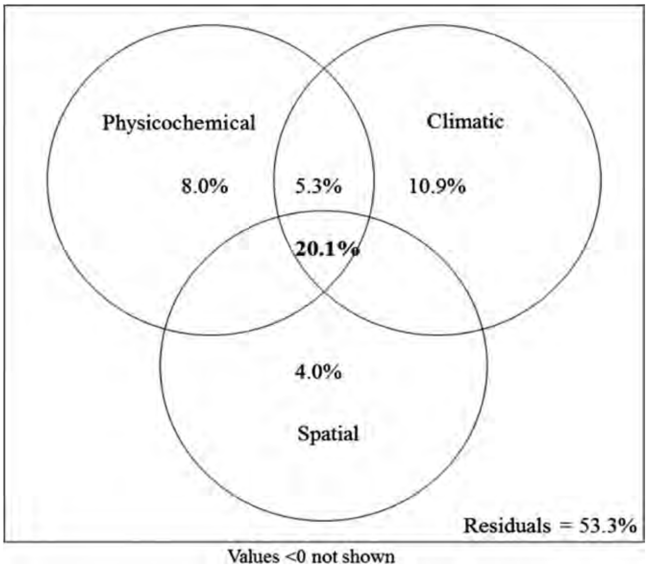


FIGURE 5 Venn diagram of variance partitioning results showing the relative effects of physicochemical, climatic and spatial factors alone and in combination with the variation of the fish assemblages. Numbers represent % variation explained by each factor. All pure factors were statistically significant (*p*-value < .05)

the river continuum concept (RCC) where the species richness is high at the lower part of the river and highest diversity is observed in the middle reach (Statzner & Higler, 1985; Vannote, Minshall, Cummins, Sedell, & Cushing, 1980). However, RCC is more applicable to small- to medium-sized rivers, that is probably not the case for the lower Mekong. Another reason for the high diversity in Cambodia could be the geographical conditions of the region, where many species cannot migrate up the Khone Falls (Valbo-Jorgensen, Coates, & Hortle, 2009). In Cambodia, the river is characterised by low land and no barriers; thus, many species could move easily up and down this part (Baran, So, & Leng, 2008). Besides, the vital connectivity between the Tonle Sap Lake and Mekong provides favourable conditions for many species to complete their life cycle as the lake provides feeding and nursing grounds, while many deep pools below Khone Falls and at large tributaries (3S river system) are essential for spawning and dry season refuge.

Dry season fish assemblages were characterised by significant changes in species richness and diversity along the LMR, similar to observed annual patterns. It can be due to the fact that fish may be concentrated in deep pools, microhabitats or main river course during the dry season, while fish would probably disperse more as the river expands with increased inundated floodplains and habitat diversity during wet season (Ferreira & Stohlgren, 1999; Junk, Barley, & Sparks, 1989; Silvano, do Amaral, & Oyakawa, 2000). Consequently, this concentration would lead fishermen to catch easily the fish with variety of species compared to wet season. Moreover, different patterns in community composition between seasons could be explained by the migratory fish movement in the basin (Baran, 2006). Therefore, the seasonal turnover may be attributed to the different catchability, habitat diversity and migration of fish within the basin. Similar conclusions have been previously reported from fish community studies in tropical Amazonian rivers (Albert & Reis, 2011; Matthews, 1998; Winemiller, 1996).

At the upper part of LMR, the different patterns in Ia and Ib between dry and wet seasons revealed the association of community structure with migration patterns (Fig. 2a,c). For instance, many wet season indicator species from Ia and Ib, that is *C. harmandi*, *Henicorhynchus* spp., *Pangasianodon hypophthalmus*, *H. nemurus*, are long-distance migrants, and their spawning ground was identified at uppermost parts of LMR (Baran, 2006; Poulsen et al., 2004). Similarly, to many Amazonian fish, some of the Mekong species were reported to migrate upwards for reproduction, while others migrate downwards for feeding and nursing (Poulsen et al., 2004). Accordingly, in the middle part of LMR, most of the migrants feed in Tonle Sap Lake and spawn below Khone Falls; while at upper part, the river serves both, that is spawning and feeding, for all migrants (Poulsen et al., 2004; Rainboth, 1996). Nevertheless, as a result of fish movement, no significant difference in diversity was observed during the wet season, revealing that diversity patterns were more homogenous compared to dry season and annual patterns.

Clear patterns of the assemblage structure were observed between the upper LMR and its delta. Specifically, assemblages Ia and Ib were characterised by cyprinids and catfish, species known to be potamodromous, which frequently occur in a large-sized river, specifically in the Mekong mainstream, that is *C. harmandi*, *L. chrysophekadion*, *H. waandersii*, *B. yarelli and Bangana behri* (Lucas et al., 2001). Below Khone Falls, the cyprinids in Ib were dominated by opportunist species, that is *Henicorhynchus* spp., *Thynnichthys thynnoides* and *Paralaubucca typus*; these species are known as fast growing with short lifespan and are reported to do the long-distance migration as well, commonly between Tonle Sap Lake and upstream Cambodian Mekong (Baran et al., 2008).

In the Mekong delta, the fish assemblages changed significantly, with sharp declines in fish abundances observed for cyprinids and catfish, known as stenohaline species with low tolerance to salinity (Valbo-Jorgensen et al., 2009). Obviously, the perch-like fish (Perciformes) and clupeids (Clupeiformes) were common species in IIa and IIb; these groups of fish are tolerant to salinity and turbid water (Albert & Reis, 2011). Nevertheless, in IIa, many species were known as stenohaline species, that is *C. aesarnensis*, *Mastacembelus* spp., *Acanthopsis* sp., which are less tolerant to the brackish conditions of the delta. However, some of them need the marine environment to complete their life cycle, for example *Cynoglossus microlepis*, while others were believed to reside permanently in the estuary, for example *G. giuris* (Froese & Pauly, 2015; Valbo-Jorgensen et al., 2009). In IIb, we found mostly marine species, that is *Liza* spp., *Scomberomorus* sp., *Toxotes* spp., *Allenbatrachus grunniens*, *Boleophthalmus boddarti*, which are well suited to the marine environment with less light penetration (Moyle & Cech, 1988). Of course, these species are known as amphidromous fish and some of them are catadromous fish, for example *Anguilla* sp., *Ellochelon vaigiensis*, *Mugil cephalus*, which inhabit fresh-brackish water and live permanently in the estuary like the small anchovies (*Coilia* sp. and *Tenualosa toti*; Froese & Pauly, 2015; Motomura, Iwatsuki, Kimura, & Yoshino, 2002).

So far, the difference in fish assemblage patterns could result from the different migration routes of fish within the basin, where it was estimated that about 40% of lower Mekong species are “white fish” that conduct long-distance migrations (Baran, 2006; Poulsen et al., 2004).

4.2 | Relative importance of environmental and spatial factors structuring the fish assemblages

Overall, our study showed that the seasonal variation of precipitation (bio15), the precipitation of the wettest month (bio16), the maximal temperature of warmest month (bio5), the precipitation of coldest quarter (bio19), as well as the isothermality (bio3), the minimal temperature of the coldest month (bio6) and the mean temperature of the driest quarter (bio9) were the key climatic factors driving the changes in fish assemblage structure. Obviously, the seasonal variations of temperature and precipitation have proved to be important factors affecting the distribution of organisms in ecosystems (Buisson et al., 2008; Cheung et al., 2009). Alternatively, TP, DO, COD and pH significantly influenced the spatial structure of the fish assemblages as well. Indeed, many studies have revealed the link between physicochemical factors, particularly nutrients and DO, and the patterns of fish assemblages along river systems (Fialho, Oliveira, Tejerina-Garro, & de Mérona, 2007; Trujillo-Jiménez, López-López, Díaz-Pardo, & Camargo, 2009).

According to the results of our study, the differences between upstream (Ia and Ib) and delta assemblages (IIa and IIb) were mainly explained by temperature as well as nutrients and the natural effects of seawater intrusion. Consequently, the upstream species were specialised for upstream conditions with high altitude, lower temperature, high rainfall, DO and pH, particularly in cluster Ia. By contrast, the delta species were suited to high levels of nutrients and could tolerate high temperature and salinity. These conclusions were also consistent with previous studies which reported that the upper Mekong fish were dominated by Cyprinidae, Balitoridae, Cobitidae and Sisoridae that all prefer cold, oxygen-rich water bodies (Valbo-Jorgensen et al., 2009), while Gobiidae, Polynemidae, Toxotidae, Eleotridae, Clupeidae and Engraulidae dominated in the delta, with species known to tolerate estuarine conditions, that is low oxygen, high nutrient, eutrophication and salinity.

So far, many studies on the environmental determinants of fish assemblage structure have reported the main contribution of physicochemical factors (Braaten & Guy, 1999; Pires et al., 2010; Trujillo-Jiménez et al., 2009), while others revealed a predominant role of climatic factors in structuring the spatial distribution of fish (Buisson et al., 2008; Guo et al., 2015; Reash & Pigg, 1990; Zhao et al., 2015). However, in our study, the combination of environmental and spatial factors provided a better explanation of the variation in fish assemblages. Thus, the physicochemical or climatic factors alone would not optimally explain the distribution patterns of fish assemblages (Lujan et al., 2013).

4.3 | Fish diversity management and conservation

Our results provide the current baseline information on fish assemblage structure in the LMR system. According to our results, fish conservation zones should be prioritised in the middle part of the LMR, that is mainly cluster Ib, where the highest diversity was exhibited. Moreover, conservation planning should also consider the upstream part of the LMR (Cluster Ia), between Khone Falls and Vientiane city, where high levels of endemism to the LMR system are recorded (Coates, 2001). Accordingly, it was reported that the construction of natural reserves would be an effective approach to protect fish biodiversity (Park, Chang, Lek, & Brosse, 2003). Besides, the conservation strategies should be prioritised to specialist groups of fish as they are endangered and vulnerable to environmental changes (Kang et al., 2009). Alternatively, conservation practices should be carried out in a networked region rather than in single reserve and different conservation strategies should be proposed according to the different objectives and eco-regions, for example upstream LMR and Mekong delta.

Furthermore, the maintaining of the connectivity between upstream–downstream habitats (including deep pools as dry refuge) and major tributaries (3S river systems, Tonle Sap River, the Great Lake and its floodplains) is essential for many short- and long-distance migrants such as *Pangasianodon gigas* and *Pangasius kremfi* to complete their life cycle. Therefore, we strongly support the concerns of biodiversity losses due to the construction of dams across the main channel (Hortle, 2007; Valbo-Jorgensen et al., 2009; Ziv et al., 2012). Meanwhile, water quality monitoring and improvement need to be addressed rigorously within the region (Chea et al., 2016; Dudgeon, 2011). For instance, our study exhibited the lowest fish diversity in the delta, likely to reflect water pollution effects on the fish community. Thus, the cyprinids and *Pangasius* catfish, which are the main sources of proteins (Hortle, 2007), would be strongly affected as they are unable to withstand significant changes in water condition. Nevertheless, our study revealed that the combination of both environmental and spatial factors contributes significantly in structuring the fish community along the LMR. Taking these factors into account appears therefore crucial if we are to initiate management strategies to ensure the conservation and sustainable use of fisheries resources in the Lower Mekong River.

ACKNOWLEDGEMENTS

We are grateful to the Erasmus Mundus TECHNO Program and the Belmont Forum (TLSCC project) for funding our study. Great thanks to the Mekong River Commission (MRC) for providing the fish and water quality data sets used in this study. We would like to thank to Dr. Peter Winterton for helping us to correct the English. Thanks to University of Battambang for the data request and our colleagues at the Laboratory of Evolution and Biological Diversity (EDB) for their support and discussion concerning data preparation and analysis. EDB laboratory was supported by "Investissement d'Avenir" grants (CEBA, ref. ANR-10-LABX-0025; TULIP, ref. ANR-10-LABX-41).

REFERENCES

Albert, S. J., & Reis, E. R. (2011). Introduction to neotropical freshwaters. In S. J. Albert, & E. R. Reis (Eds.), *Historical biogeography of neotropical freshwater fishes* (pp. 3–16). Berkeley, CA: University of California Press.

Amarasinghe, U. S., & Welcomme, R. L. (2002). An analysis of fish species richness in natural lakes. *Environmental Biology of Fishes*, *65*, 327–339.

Baran, E. (2006). *Fish migration triggers in the Lower Mekong Basin and other tropical freshwater systems*. MRC Technical Paper No. 14. Mekong River Commission, Vientiane. 56 pp. Retrieved from http://agris.fao.org/agris-search/search.do?recordID=QW2016000150

Baran, E., So, N., & Leng, S. V. (2008). *Integrating fish resources to agro-ecosystem analyses*. Fisheries Component. CGIAR Challenge Program on Water & Food, Phnom Penh, Cambodia. 65 pp. Retrieved from http://pubs.iclarm.net/resource_centre/WF_2581.pdf

Blanchet, F. G., Legendre, P., & Borcard, D. (2008). Modelling directional spatial processes in ecological data. *Ecological Modelling*, *215*, 325–336.

Borcard, D., Legendre, P., & Drapeau, P. (1992). Partialling out the spatial component of ecological variation. *Ecology*, *73*, 1045–1055.

Braaten, P. J., & Guy, C. S. (1999). Relations between physicochemical factors and abundance of fishes in tributary confluences of the Lower Channelized Missouri River. *Transactions of the American Fisheries Society*, *128*, 1213–1221.

Buisson, L., Blanc, L., & Grenouillet, G. (2008). Modelling stream fish species distribution in a river network: The relative effects of temperature versus physical factors. *Ecology of Freshwater Fish*, *17*, 244–257.

Chea, R., Grenouillet, G., & Lek, S. (2016). Evidence of water quality degradation in Lower Mekong Basin revealed by self-organizing map. *PLoS ONE*, *11*, e0145527.

Cheung, W. W. L., Lam, V. W. Y., Sarmiento, J. L., Kearney, K., Watson, R., & Pauly, D. (2009). Projecting global marine biodiversity impacts under climate change scenarios. *Fish and Fisheries*, *10*, 235–251.

Coates, D. (2001). *Biodiversity and fisheries management opportunities in the Mekong River Basin*. MRC Technical Paper. Mekong River Commission, Phnom Penh. 40 pp. Retrieved from https://www.cbd.int/doc/nbsap/fisheries/Coates.pdf.

De Cáceres, M., Legendre, P., & Moretti, M. (2010). Improving indicator species analysis by combining groups of sites. *Oikos*, *119*, 1674–1684.

Dudgeon, D. (2003). The contribution of scientific information to the conservation and management of freshwater biodiversity in tropical Asia. *Hydrobiologia*, *500*, 295–314.

Dudgeon, D. (2011). Asian river fishes in the anthropocene: Threats and conservation challenges in an era of rapid environmental change. *Journal of Fish Biology*, *79*, 1487–1524.

Dugan, P. J., Barlow, C., Agostinho, A. A., Baran, E., Cada, G. F., Chen, D., … Winemiller, K. O. (2010). Fish migration, dams, and loss of ecosystem services in the Mekong Basin. *Ambio*, *39*, 344–348.

Ferreira, L. V., & Stohlgren, T. J. (1999). Effects of river level fluctuation on plant species richness, diversity, and distribution in a floodplain forest in Central Amazonia. *Oecologia*, *120*, 582–587.

FEVM. (2007). *Monitoring fish abundance and diversity in the Lower Mekong Basin: Methodological guidelines*. Regional fish abundance and diversity monitoring programme. Phnom Penh, MRCS, 12 pp. Retrieved from http://www.mrcmekong.org/assets/Publications/technical/Tech-No33-Integreted-Analysis-of-Data.pdf

Fialho, A. P., Oliveira, L. G., Tejerina-Garro, F. L., & de Mérona, B. (2007). Fish-habitat relationship in a tropical river under anthropogenic influences. *Hydrobiologia*, *598*, 315–324.

Froese, R., & Pauly, D. (2015). *FishBase*. World wide web electron publication. Retrieved from http://www.fishbase.org, version (last accessed 25/11/2015).

Guo, C., Lek, S., Ye, S., Li, W., Liu, J., Chen, Y., & Li, Z. (2015). Predicting fish species richness and assemblages with climatic, geographic and morphometric factors: A broad-scale study in Chinese lakes. *Limnologica - Ecology and Management of Inland Waters*, *54*, 66–74.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, *25*, 1965–1978.

Hortle, K. G. (2007). *Consumption and the yield of fish and other aquatic animals from the Lower Mekong Basin*. MRC Technical Paper No. 16. Mekong River Commission, Vientiane. 87 pp. Retrieved from http://www.mrcmekong.org/assets/Publications/technical/tech-No16-consumption-n-yield-of-fish.pdf.

Junk, W. J., Barley, P. B., & Sparks, R. E. (1989).The flood pulse concept in river-floodplain systems. Proceedings of the International Large River Symposium. *Canadian Journal of Fisheries and Aquatic Sciences*, *106*, 110–127.

Kang, B., He, D., Perrett, L., Wang, H., Hu, W., Deng, W., & Wu, Y. (2009). Fish and fisheries in the Upper Mekong: Current assessment of the fish community, threats and conservation. *Reviews in Fish Biology and Fisheries*, *19*, 465–480.

Kottelat, M., & Whitten, J. A. (1996). *Freshwater biodiversity in Asia with special reference to fish*. World Bank Technical Paper 343. The World Bank, Washington, DC, USA. 59 pp.

Legendre, P., & Legendre, L. (2012). Canonical analysis. In P. Legendre, & L. Legendre (Ed.), *Numerical ecology* (3rd ed., pp. 575–633). Amsterdam: Elsevier.

Lu, X. X., Li, S., Kummu, M., Padawangi, R., & Wang, J. J. (2014). Observed changes in the water flow at Chiang Saen in the lower Mekong: Impacts of Chinese dams? *Quaternary International*, *336*, 145–157.

Lu, X. X., & Siew, R. Y. (2006). Water discharge and sediment flux changes over the past decades in the Lower Mekong River: Possible impacts of the Chinese dams. *Hydrology and Earth System Sciences Discussions*, *10*, 181–195.

Lucas, M. C., Baras, E., Thom, T. J., Duncan, A., & Slavik, O. (2001). Migration and spatial behaviour. In M.C. Lucas, & E. Baras (Ed.), *Migration of freshwater fishes* (pp. 1–12). Oxford: Blackwell Science Ltd.

Lujan, N. K., Roach, K. A., Jacobsen, D., Winemiller, K. O., Vargas, V. M., Ching, V. R., & Maestr, J. A. (2013). Aquatic community structure across an Andes-to-Amazon fluvial gradient. *Journal of Biogeography*, *40*, 1715–1728.

Matthews, W. J. (1998). *Patterns in freshwater fish ecology* (pp. 30–85). Dordrecht: Springer Science & Business Media.

Mittermeier, A. R., Turner, R. W., Larsen, W. F., Brooks, M. T., & Gascon, C. (2011). Global biodiversity conservation: The critical role of hotspots. In F. Zachos, & J. Habel (Eds.), *Biodiversity hotspots: Distribution and protection of conservation priority areas* (pp. 3–7). Heidelverg: Springer.

Motomura, H., Iwatsuki, Y., Kimura, S., & Yoshino, T. (2002). Revision of the Indo-West Pacific polynemid fish genus Eleutheronema (Teleostei: Perciformes). *Ichthyological Research*, *49*, 47–61.

Moyle, P. B., & Cech, J. J. (1988). *Fishes: An introduction to ichthyology* (pp. 193–211). Upper Saddle River, NJ: Prentice Hall.

MRC (2015). Fisheries research and development in the Mekong region. *Catch and Culture*, *21*, 1–56.

Murtagh, F., & Legendre, P. (2014). Ward's hierarchical agglomerative clustering method: Which algorithms implement Ward's criterion? *Journal of Classification*, *31*, 274–295.

Oberdoff, T., Guegan, J.-F., & Hugueny, B. (1995). Global scale patterns of fish species richness in rivers. *Ecography*, *18*, 345–352.

Olden, J. D., Kennard, M. J., Leprieur, F., Tedesco, P. A., Winemiller, K. O., & García-Berthou, E. (2010). Conservation biogeography of freshwater fishes: Recent progress and future challenges. *Diversity and Distributions*, *16*, 496–513.

Park, Y. S., Chang, J., Lek, S., & Brosse, S. (2003). Conservation strategies for endemic fish species threatened by the Three Gorges Dam. *Conservation Biology*, *17*, 1748–1758.

Pires, D. F., Pires, A. M., Collares-Pereira, M. J., & Magalhães, M. F. (2010). Variation in fish assemblages across dry-season pools in a Mediterranean stream: Effects of pool morphology, physicochemical factors and spatial context. *Ecology of Freshwater Fish*, *19*, 74–86.

Pool, T. K., Olden, J. D., Whittier, J. B., & Paukert, C. P. (2010). Environmental drivers of fish functional diversity and composition in the Lower Colorado River Basin. *Canadian Journal of Fisheries and Aquatic Sciences*, *67*, 1791–1807.

Poulsen, A. F., Hortle, K. G., Valbo-Jorgensen, J., Chan, S., Chhuon, C. K., Sinthavong, V., … Tran, B. Q. (2004). *Distribution and ecology of some important riverine fish species of the Mekong River Basin*. MRC Technical Paper No. 10. Mekong River Commission, Phnom Penh. 115 pp. Retrieved from http://www.mrcmekong.org/assets/Publications/technical/tech-No10-distribution-n-ecology-of-important.pdf.

Poulsen, A. F., Ouch, P., Sinthavong, V., Ubolratana, S., & Nguyen, T. T. (2002). *Fish migrations of the Lower Mekong River Basin: implications for development, planning and environmental management*. MRC Technical Paper No. 8. Mekong River Commission, Phnom Penh. 62 pp. Retrieved from http://www.mrcmekong.org/assets/Publications/technical/tech-No8-fish-migration-of-LMB.pdf.

R Core Team (2015). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rainboth, W. J. (1996). *Fishes of the Cambodian Mekong. FAO species identification field guide for fishery purposes*. FAO, Italy. 265 pp. Retrieved from http://library.enaca.org/inland/fishes-cambodian-mekong.pdf.

Reash, J. R., & Pigg, J. (1990). Physicochemical factors affecting the abundance and species richness of fishes in the Cimarron River. *Proceeding of the Oklahoma Academy of Science*, *70*, 23–28.

Roberts, T. R., & Baird, I. G. (1995). Traditional fisheries and fish ecology on the Mekong River at Khone Waterfall in Southern Laos. *Natural History Bulletin of the Siam Society*, *43*, 219–262.

Silvano, R. A. M., do Amaral, B. D., & Oyakawa, O. T. (2000). Spatial and temporal patterns of diversity and distribution of the Upper Jurua River fish community (Brazilian Amazon). *Environmental Biology of Fishes*, *57*, 25–35.

Sinthavong, V. (2006). Observations of the fisheries of the Mekong with notes on the life history strategies of four fish species (*Botia modesta*, *Henicorhynchus siamensis*, *Helicophagus waandersii* and *Probarbus jullieni*). Doctor of Philosophy: The University of Hull. 216 pp. Retrieved from http://lad.nafri.org.la/fulltext/2216-0.pdf.

Statzner, B., & Higler, B. (1985). Questions and comments on the river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, *42*, 1038–1044.

Tejerina-Garro, F. L., Fortin, R., & Rodríguez, M. A. (1998). Fish community structure in relation to environmental variation in floodplain lakes of the Araguaia River, Amazon Basin. *Environmental Biology of Fishes*, *51*, 399–419.

Ter Braak, C. J. F., & Prentice, I. C. (1988). A theory of gradient analysis. *Advances in Ecological Research*, *34*, 235–282.

Trujillo-Jiménez, P., López-López, E., Díaz-Pardo, E., & Camargo, J. A. (2009). Patterns in the distribution of fish assemblages in Río Amacuzac, Mexico: Influence of abiotic factors and biotic factors. *Reviews in Fish Biology and Fisheries*, *20*, 457–469.

Valbo-Jorgensen, J., Coates, D., & Hortle, K. G. (2009). Fish diversity in the Mekong River Basin. In C. I. Cambell (Ed.), *The Mekong biophysical environment of an international river basin* (pp. 162–185). Amsterdam: Elsevier Academic Press.

Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R., & Cushing, C. E. (1980). The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, *37*, 130–137.

Vorosmarty, C. J., McIntyre, P. B., Gessner, M. O., Dudgeon, D., Prusevich, A., Green, P., … Davies, P. M. (2010). Global threats to human water security and river biodiversity. *Nature*, *467*, 555–561.

Winemiller, K. O. (1996). Dynamic diversity in fish assemblages of tropical rivers. In M. L. Cody, & J. A. Smallwood (Eds.), *Long-term studies of vertebrate communities* (pp. 99–134). Orlando, FL: Academic Press.

Zhao, T., Grenouillet, G., Pool, T., Tudesque, L., & Cucherousset, J. (2015). Environmental determinants of fish community structure in gravel pit lakes. *Ecology of Freshwater Fish*, *25*, 412–421.

Ziv, G., Baran, E., So, N., Rodriguez-Iturbe, I., & Levin, S. A. (2012). Trading-off fish biodiversity, food security, and hydropower in the Mekong River Basin. *Proceedings of the National Academy of Science of the United States of America*, *109*, 5609–5614.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

ARTICLE 2

Spatial and temporal variations in fish community structure and diversity in the largest tropical flood-pulse system of Southeast Asia

Peng Bun Ngor, Gaël Grenouillet, Nam So, Sea Phem, Sovan Lek

Ecology of Freshwater Fish (accepted, in press)

Title: Spatial and temporal variation in fish community structure and diversity in the largest tropical flood-pulse system of Southeast Asia

Peng Bun Ngor[1,2¥], Gaël Grenouillet[2,3], Sea Phem[4], Nam So[1], Sovan Lek[2]

[1] Fisheries Administration, No. 186, Preah Norodom Blvd., Khan Chamcar Morn, P.O. Box 582, Phnom Penh, Cambodia.

[2] CNRS, Université Toulouse III Paul Sabatier, ENFA; UMR5174 EDB (Laboratoire Évolution & Diversité Biologique); 118 route de Narbonne, F-31062 Toulouse, France

[3] Institut Universitaire de France, Paris, France.

[4] Tonle Sap Authority, 364, Monivong Blvd., Khan Chamkar Mon, Phnom Penh, Cambodia.

[¥] Current address: CNRS, Université Toulouse III Paul Sabatier, ENFA; UMR5174 EDB (Laboratoire Évolution & Diversité Biologique); 118 route de Narbonne, F-31062 Toulouse, France.

Running head: Fish community structure and diversity in a tropical flood-pulse system

Corresponding author: pengbun.ngor@gmail.com

Abstract

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

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

1 | INTRODUCTION

The hydrology of the Mekong River is characterised by its extreme predictability, with regular wet and dry seasons throughout the basin (Adamson et al., 2009). The hydrology is controlled by the tropical monsoonal climate and flood runoff from the snowmelt in the Tibetan plateau as well as by its tributaries that converge and accumulate into a single large wet-seasonal peak flow (MRC, 2005; Adamson et al., 2009). The biological systems of the river basin have both developed in and adapted to these tropical flood-pulse environments, and the Mekong's predictable seasonal flood pulses are indeed a key ecological driver that supports one of the most biodiverse and productive inland fisheries in the world (Rainboth, 1996; Poulsen et al., 2002; MRC, 2003, 2010).

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

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

Despite being highly productive, the Mekong system, including the Tonle Sap, has received little ecological research on many aspects of its resources and ecology, including fish, reptiles, invertebrates and primary producers (Dudgeon, 2000, 2003; Sabo et al., 2017). Arguably, the TSRL, among the world's tropical floodplains, has been studied the least in terms of its hydrology-ecology interactions (Junk et al., 2006; Matti Kummu et al., 2006; Arias et al., 2013). The primary research conducted on fisheries has been very spotty and has mainly focused on biological assessments, e.g., Lamberts (2001), Enomoto et al. (2011) and Halls, Paxton, et al. (2013), or on broad-scale migration patterns, e.g., Poulsen et al., 2002, 2004. Few studies have been conducted on the fish community ecology in the TSRL, including Lim et al. (1999) who studied the spatial fish diversity and community patterns; additionally, the most recent study was on the determinants of species composition (i.e., beta diversity) (Kong et al., 2017).

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

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

2 | MATERIALS AND METHODS

2.1 | Study area

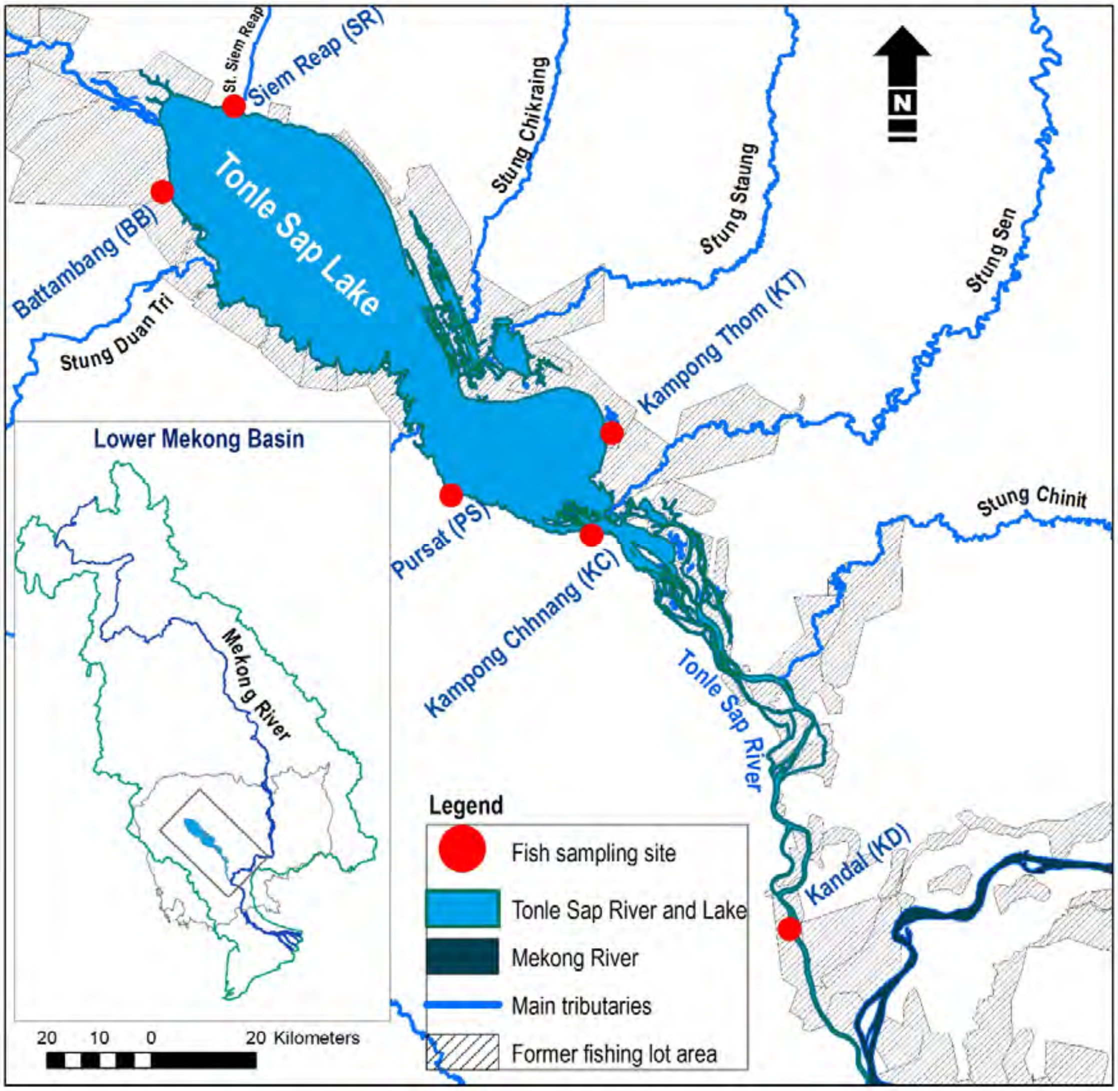


Fig. 1. Location of sampling sites along Tonle Sap Lake and River.

The Tonle Sap catchment covers an area of 85,790 km^2, or 11% of the Mekong Basin (MRC, 2003). The floodplain-lake is located at the apex of the Tonle Sap River approximately 130 km to the northwest of its junction with the Mekong River (Halls, Paxton, et al., 2013). Waters for the TSRL system originate mainly from the Mekong River (54%), while the lake tributaries contribute 34%, and the rest generates from precipitation (M. Kummu et al., 2014). During the wet season (i.e., June-October), the Tonle Sap Lake expands its mean surface area from ~3,500 to ~14,500 km^2, inundating huge floodplain areas surrounding the TSRL, with maximum depths in the lake recorded at 6 to 9 metres from late September to early October and minimum depths of approximately 0.5 metres in late April

(MRC, 2005). This study covers six sites situated along the geographical gradient of the TSRL from the southern section representing the Tonle Sap River in Kandal Province (KD) to Kampong Chhnang (KC), a transition zone connecting the Tonle Sap River with the lake, the middle portion of the lake in Kampong Thom (KT) to the east and Pursat (PS) to the west, and finally Siem Reap (SR) and Battambang (BB) located towards the northern end of the TSRL gradient (Fig. 1). The study sites include a river section with a lotic environment (i.e., KD), an ecotone between the river and the lake (i.e., KC), an open area of the lake with year-round wet large tributaries at two sites (i.e., KT and PS) and more swampy areas with dense floating vegetation, flooded plains and grass/shrub lands to the north, particularly in BB.

2.2 | Data collection

We used daily catch samples from the stationary gillnets fishery (length: 400 m ± 100 m, height: 0.7 - 4.5 m, mesh size: 2 - 6.5 cm, daily soak hours: 12 ± 2) and from the cylinder traps (1.6 m × 0.9 m, daily soak hours: 14 ± 2) fishery, the two most common fishing gears that are used daily in Cambodia (Deap, Degen, & van Zalinge, 2003; Hortle, Lieng, & Valbo-Jorgensen, 2004). The length variation in the stationary gillnets used was due to the available fishing grounds, which vary seasonally according to the hydrological cycles. When in operation, the cylinder trap was set facing the current along the bank of the stream/river or suspended off the bottom between poles in the flooded forests of Tonle Sap Lake. The soak hour refers to the time (hours) that the gear soaked in the water (MRC, 2007). These fishing gears allowed the capture of both migratory and floodplain resident species. Data collection was based on the Mekong River Commission's (MRC) standard sampling procedures for fish catch monitoring (MRC, 2007). Eighteen professional fishermen (three at each site), supervised by the fishery researchers from the Cambodia Inland Fisheries Research and Development Institute of the Fisheries Administration, the Tonle Sap Authority and the MRC monitoring specialists, participated in this daily fish sampling programme. A fish species list for the Mekong Basin (~900 species with ecological attributes) was obtained from the MRC Mekong Fish Database (MFD, 2003) and cross-checked with FishBase (Froese & Pauly, 2017) and other literature sources (Rainboth, Vidthayanon, & Mai, 2012; Kottelat, 2013). Based on their ecological attributes, fish species were grouped into (1) 'white fishes' for species that perform longitudinal migrations between the Mekong mainstream and floodplains as well as major tributaries, (2) 'black fishes' for floodplain residents that spend most of their life in lakes and swamps in floodplains adjacent to rivers (with no longitudinal migrations upstream) and move to flooded areas during the flood season, and (3) 'grey fishes', which are ecologically intermediate between the white and black fishes and undertake short-distance lateral migrations in local tributaries and do not spend their life in the floodplain ponds during the dry season (Welcome, 2001; Valbo-Jørgensen, Coates, & Hortle, 2009; MRC, 2010). In other words, grey fishes move to local river/stream channels during the dry season. The final group was 'estuarine fishes', which include estuarine residents and marine visitors. Sampled fish were identified to the species level and counted. Fish particularly those that were entangled in the gillnets were dead, and fishermen often consumed or sold them for other consumers. After field verification, field collected data were recorded into the national fish monitoring databases and were quarterly cleaned and synchronised by the responsible researchers with the help of the MRC database expert and fisheries monitoring specialists. Daily water levels at two sites: the Tonle Sap River in Kandal (latitude: 11.81329, longitude: 104.8041) and the Tonle Sap Lake in Pursat (latitude: 12.57662, longitude: 104.20779) were registered by the MRC.

2.3 | Statistical analysis

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

Species diversity

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

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

Spatiotemporal variation in fish assemblages

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

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

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

Temporal variation in fish abundance and richness in relation to hydrology

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

3 | RESULTS

3.1 | Fish community structure

Over the four-year monitoring period, 204 fish species were recorded in all catch samples. The species comprised 114 genera, 38 families and 13 orders. The three main orders represented 87% of the total species count and included Cypriniformes (100 species), Siluriformes (48) and Perciformes (29). Clupeiformes, Osteoglossiformes and Synbranchiformes each contained five species, and the rest contributed less than 6% to the total species counts. At the family level, the top five families that accounted for 60% of the total species counts included Cyprinidae (80), Bagridae (12), Pangasiidae (11), Cobitidae (10) and Siluridae (10), while each of the other 33 families comprised one to six species. At the species level, ~62% of catches were dominated by 12 fish species, namely, *Henicorhynchus lobatus* (11%), *H. siamensis* (10%), *Trichopodus trichopterus* (7%), *Puntioplites proctozysron* (7%), *Osteochilus vittatus* (6%), *Trichopodus microlepis* (5%), *Labiobarbus lineatus* (4%), *Paralaubuca typus* (3%), *Mystus mysticetus* (3%), *Notopterus notopterus* (3%) and *Rasbora tornieri* (3%). Ecologically, longitudinal migratory species (i.e., white fishes) accounted for ~58% of total abundance, while floodplain resident black and lateral-migrant grey fishes contributed 19% and 21%, respectively. The rest (1%) were composed of estuarine species and marine visitors.

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

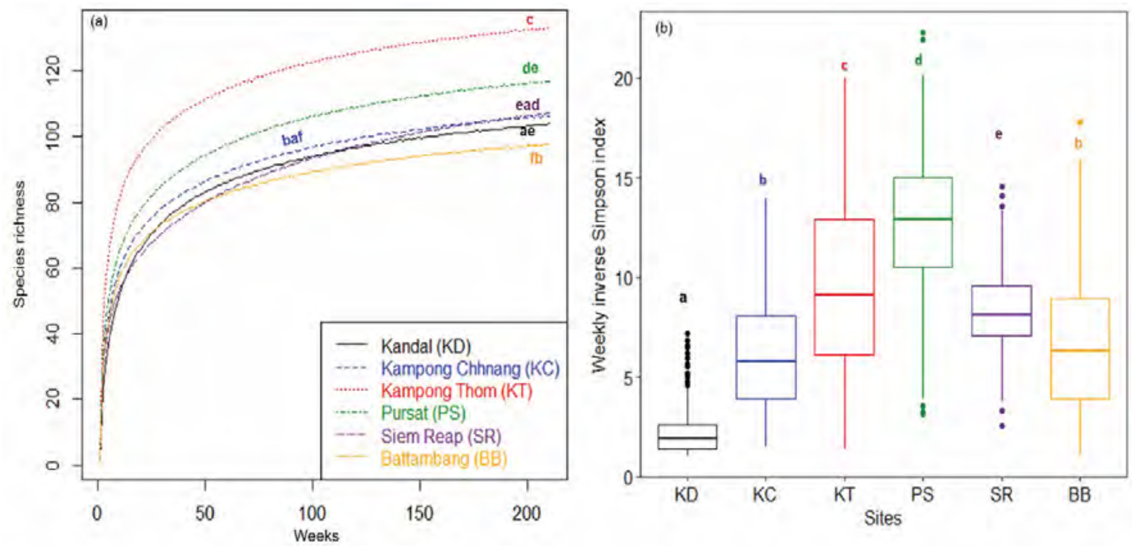


Fig. 2. Spatiotemporal comparison of site fish species richness and diversity in the TSRL: (a) site rarefaction curves on species richness; (b) site inverse Simpson diversity index with south-north gradient along the TSRL. Sites with a common letter are not significantly different at p = 0.05. Site codes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

3.2 | Spatiotemporal variation

Hierarchical clustering with the Ward agglomerative method enabled the classification of all weekly samples into three clusters (Fig. 3a) based on species composition similarities. The first split of the dendrogram defined fish assemblages in riverine (cluster 1) and lacustrine environments (cluster 2 and cluster 3), while the second split separated the two main assemblages (clusters 2 and 3) in the middle and northern sections of the lake. The first cluster (159 samples) was mainly associated with samples from KD. The second, i.e., the largest cluster (613 samples), mainly grouped samples from KC, KT, PS and SR, and the third cluster (456 samples) was related to samples from BB. Based on the system's fish community composition, KD (in the southernmost section of the system) was opposed to the other sites along the first axis of the NMDS; in contrast, the second axis mainly opposed BB (in the northern part of the lake) to the other sites (Fig. 3b).

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

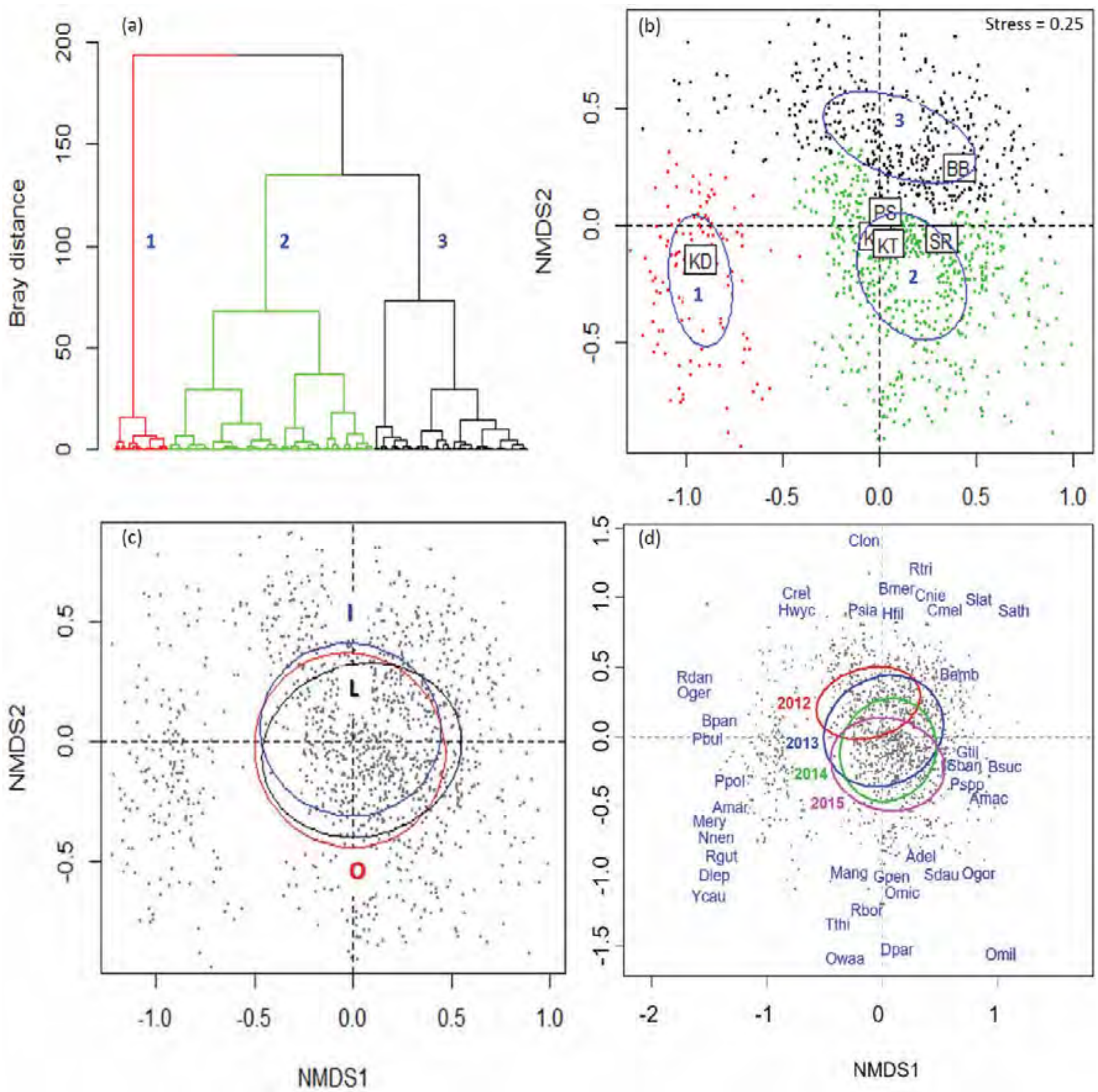


Fig. 3. NMDS biplot of the weekly fish abundance samples (with Bray-Curtis dissimilarity matrix), showing the TSRL community spatiotemporal variation. Dots on the biplots represent samples. (a) Ward hierarchical clustering dendrogram of the weekly samples showing 3 distinct clusters; (b) spatial distribution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

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

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

3.3 | Indicator species by cluster

Overall, 96 indicator species were identified from the three assemblage clusters (S5). The largest number was observed in cluster 2 (45 species), while the lowest number was detected in cluster 1 (20). Key indicator species with high indicator values that characterised cluster 1 in the southern river section belonged to Pangasiidae (river catfishes), such as *Pangasius macronema, P. conchophilus* and *P. bocourti*; Cyprinidae (cyprinids), such as *Labiobarbus siamensis*, *Puntioplites falcifer, Paralaubuca typus,* and *P. riveroi*; Siluridae (sheatfishes), such as *Phalacronotus bleekeri* and *Belodontichthys truncatus*; and Cobitidae (loaches), including *Yasuhikotakia caudipunctata.* Interestingly, *Cyprinus carpio*, an exotic species, was also identified in this cluster.

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

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

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

3.4 | Species relative abundance by cluster

Overall, 114 species were reported in cluster 1, 182 were reported in cluster 2 and 154 in cluster 3. The ten most abundant species for each assemblage cluster accounted for ~97% in cluster 1, ~58% in cluster 2 and ~65% in cluster 3 (Fig. 4a). Interestingly, two small-sized cyprinids, *Henicorhynchus lobatus* (Hlob) and *H. siamensis* (Hsia) comprised ~45% of the total abundance in cluster 1 but accounted for only ~19% and ~16% in cluster 2 and cluster 3, respectively. Further, of the top ten species, only five species (~84%) dominated the catch in cluster 1; in contrast, in clusters 2 and 3, the ten dominant species shared the catch more proportionately between 3 and 10%. *Puntioplites proctozysron* (Ppro) was found among the top ten species for all clusters. Ecologically, catches in cluster 1 were composed of ~96% of migratory white fishes, and this value decreased gradually to ~57% and ~52% in cluster 2 and cluster 3, respectively (Fig. 4b).

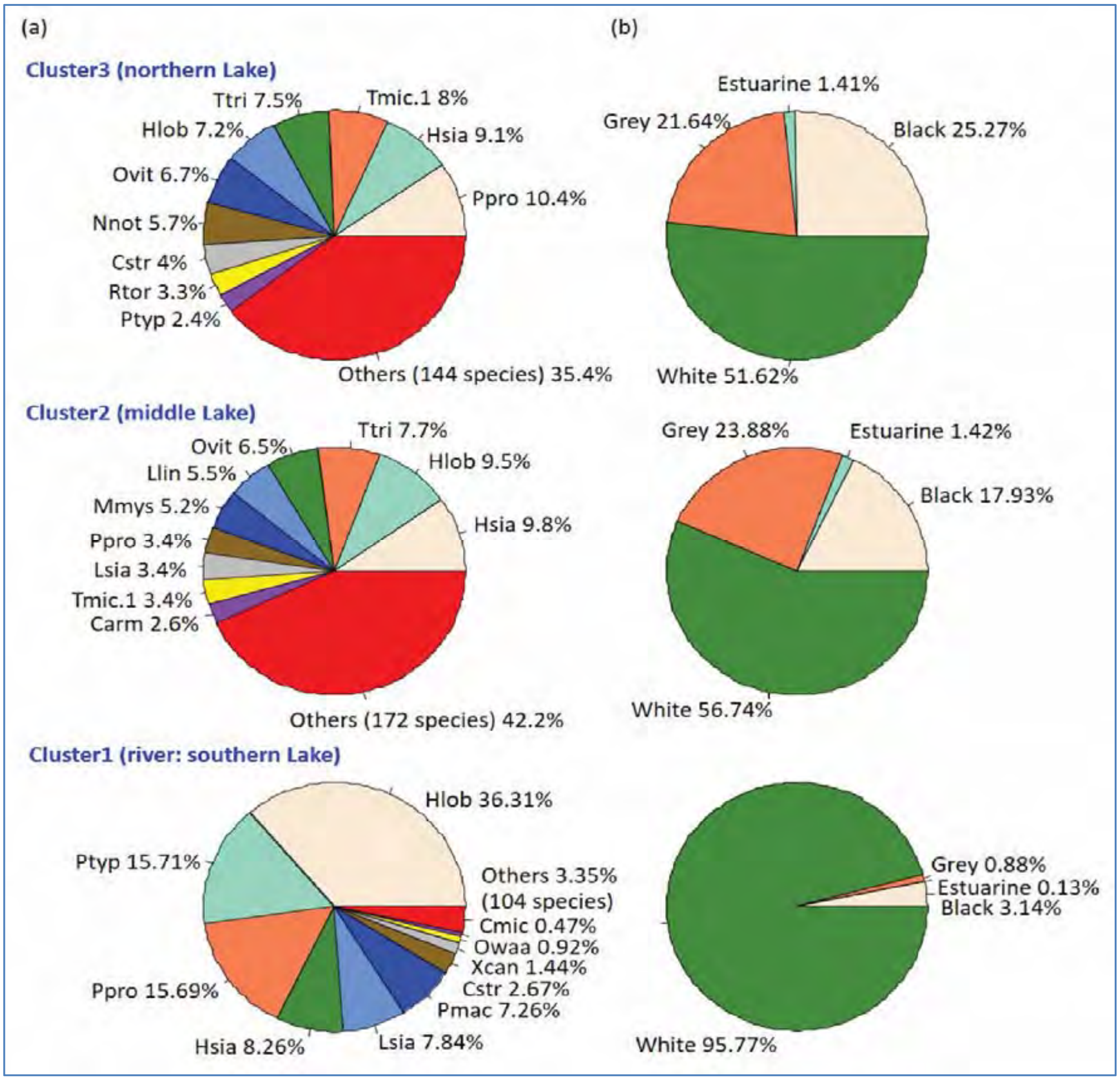


Fig. 4. Species relative abundance organised by cluster and fish migration guild. (a) Ten most abundant species by cluster. (b) Community composition by migration guilds. For clusters, see Fig. 3a, b. For species details and migration guilds, see S9.

Relationships between species abundance and richness and water levels

Significant links between either weekly abundance or richness and water levels were observed in the lake (PS) (Spearman correlation tests, $p < 0.05$ for all sites except BB). The cross-correlation analyses between the two time series for the two sites (Tonle Sap River, KD and Tonle Sap Lake, PS) where both fish and water level data series were available noted that there was a positive relationship between the temporal variation in species both abundance and richness and the hydrology (Fig. 5a-d). Overall, the fish community responses appeared to lag behind the flow regime (i.e., water led the fish).

The correlation lag for fish abundance versus water levels at the maximum coefficient was estimated at -15 weeks in KD and -16 weeks in PS (Fig. 5a, b); in contrast, the correlation lag for species richness versus water level was estimated at -8 weeks in KD and -10 weeks in PS. It is noteworthy that the time lag between the water levels in the Tonle Sap River (KD) and those of the lake (PS) was estimated at about -2 weeks (S6). Therefore, it was consistently observed that peak abundance and richness began one to two weeks earlier in the lake than in the Tonle Sap River. Additional investigations on the cross-correlation between weekly abundance and richness of sites around the lake using water levels from PS are provided in S7 and S8. For a full species list by genera, families and orders as well as key ecological attributes used in this study, see S9.

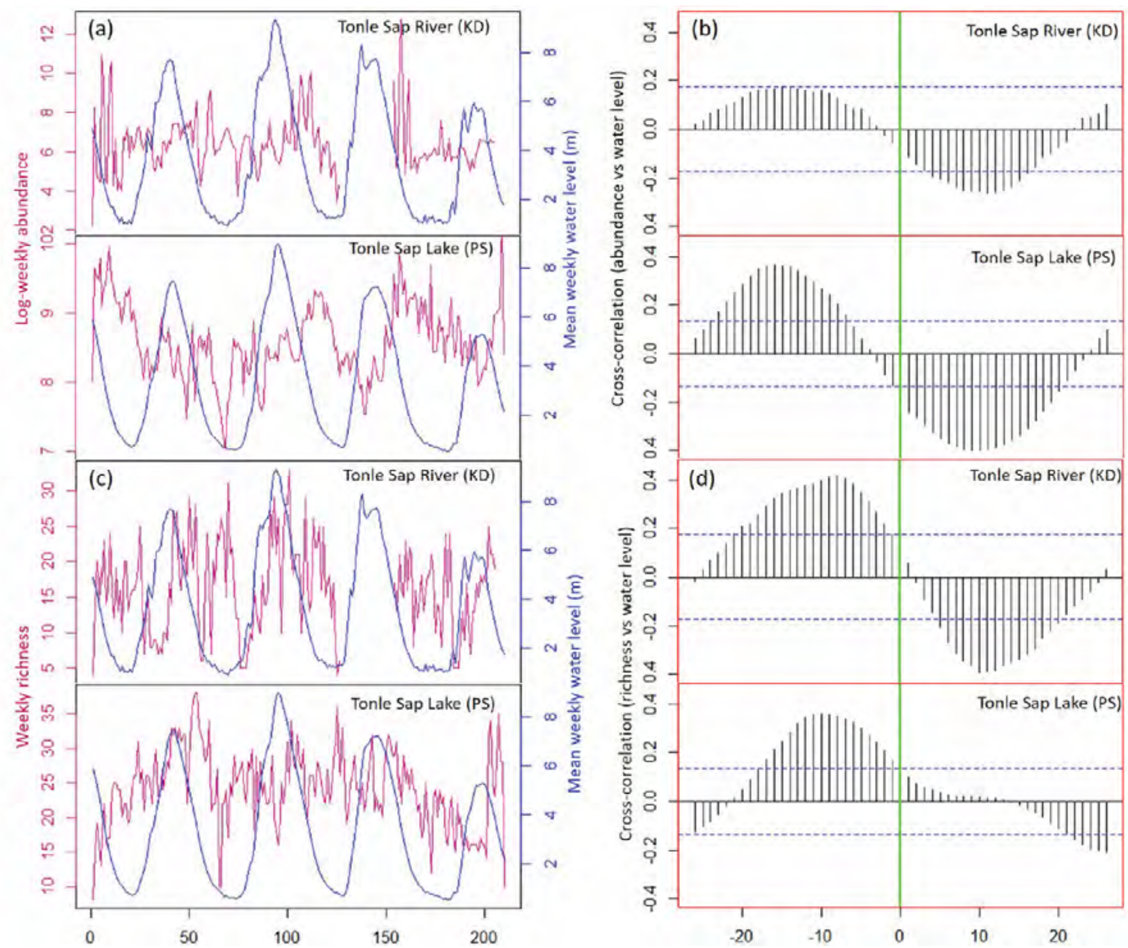


Fig. 5. Relationships between water level and (a-b) fish abundance and (c-d) species richness in the TSRL. In cross-correlation plots, the dotted blue lines provide the values beyond which the correlations are significantly different from zero. The x-axis is the number of weeks for the period from 1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

4 | DISCUSSION

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

4.1 | Richness and diversity

High species richness and diversity in the middle section of the lake (KT, PS) were likely because this section was deeper and larger in terms of water depth and surface cover than were other sections within the system. A bathymetric map of the Tonle Sap Lake reveals a general downward slope towards the middle section from both the southern section (KC) and the northern section in BB (Campbell et al., 2006). In addition, the middle section had a higher degree of inundation throughout the year, which was associated with at least three large tributary rivers of the Tonle Sap basin, namely, the Sen River of KT, with a lower reach drainage within 230 km^2 of the lake; the Chinit River of KT, with a total drainage area of 5,649 km; and the Pursat River of PS, with a catchment area of 5,965 km^2 (CGIAR, 2013; Nagumo, Sugai, & Kubo, 2013, 2015). The high degree of inundation, combined with greater depths, tended to increase habitat connectivity and availability, which created more living space and a more stable environment. This gives fish species a colonising advantage, which drives greater richness and diversity (Henriques-Silva, Lindo, & Peres-Neto, 2013). For example, Boeng Chhmar and its associated rivers and floodplains, which cover an area of 280 km^2 in the middle section of the lake in KT, were described as near-natural wetlands, encompassing permanent open water surrounded by a creek system; furthermore, the area was designated a RAMSAR wetland of global significance in 1999 (The Ramsar Convention Secretariat, 2014). In other tropical river-lake floodplain systems, water depth and surface cover are the two most significant variables that were found to explain higher species abundance and richness, e.g., in the Venezuelan Cinaruco River (Rodríguez & Lewis, 1997; Hoeinghaus et al., 2003) and the Brazilian Pantanal River (Fernandes, Machado, & Penha, 2010). Similarly, local features such as sites with permanent channel connection and water surface connectivity were also identified to positively influence local species richness in Artic lakes. Sites with these attributes were found to harbour both restricted and widespread species (Laske et al., 2016). Fish populations in these sites are likely to be sustained by immigration from adjacent habitats (Brown & Kodric-Brown, 1977).

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

4.2 | Spatial variation

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

Cluster 2 in the middle section of the lake was characterised by both restricted and widespread species, including small bagrid catfishes (*Mystus* spp.), cyprinids, glassfishes, leaf fishes, climbing gouramies and spiny eels. Overall, this cluster was represented by a high number of indicator species with different ecological attributes, such as longitudinal migratory white fishes, floodplain residents (i.e., black fishes) and lateral migrants (i.e., grey fishes). This result was likely due to the overall environmental stability in this section, i.e., deeper water, larger surface cover and habitat connectivity through the permanent water bodies (i.e., Ramsar Wetlands of Boeng Chhmar) and presence of permanent wet large tributaries of the Tonle Sap basin.

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

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

4.3 | Temporal variation

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

Seasonally, the abundance and richness of the TSRL fish communities were found to be significantly greater during the outflow period (S4.7). This was due to the seasonal longitudinal migrations of white fishes from the TSRL to the Mekong mainstream for dry-season refugia (Poulsen et al., 2002, 2004). Such seasonal migrations are usually predictable with the stationary trawl *Dai* fishery, which has operated in the Tonle Sap River for more than a century. The observed peaks often occur in a time-window of ~7-1 days, particularly before the full moon in December and January (Halls, Paxton, et al., 2013). Likewise, during this outflow, grey and black fishes also undertake short-distance lateral movements from the nearby TSRL seasonal floodplains to the deeper area of Tonle Sap Lake or the main river channel. Seasonal migrations during the outflow usually drive huge fishing activities in the TSRL, when the fisheries are opened for all as well as in many parts of the LMB. In contrast, we found the lowest fish abundance in the TSRL during the inflow when white fishes longitudinally migrate for spawning in the rapids and deep pools of the Mekong River, and mature fishes, juveniles and larvae then migrate and drift downstream and invade the surrounding TSRL floodplains for feeding and rearing (Valbo-Jørgensen, Coates, & Hortle, 2009). The lower abundance during the inflow was likely attributed to low fish densities, as fish were widely dispersed by seasonal floods to floodplains and inundated forests surrounding the TSRL, which makes them difficult to capture. Our cross-correlation analyses noted that the peak abundance and richness (Fig. 5a, c) were respectively related to the peak flow occurring about four months (-15 weeks in KD and -16 weeks in PS) and 2-2.5 months (-8 weeks in KD and -10 weeks in PS) earlier. While the peak flow occurs around early October (MRC, 2005; S2), the peak abundance occurs around January; in contrast, the peak richness occurs in between early November and mid-December. The period for the peak abundance and richness found from the cross-correlation analyses corresponded to the defined outflow (falling water levels) period for this study. Such seasonal patterns were also reported in other tropical river-floodplain fish communities, such as the Amazonian Juruá River and forest streams (Silvano, Benedito, & Oyakawa, 2000; Espírito-Santo et al., 2009), Venezuelan rivers (Hoeinghaus et al., 2003) and in French Guiana (Boujard, 1992), where greater abundance and richness with more species interactions were driven by the falling water levels (i.e., low flows).

The inter-annual variation in the TSRL fish communities found in this study could be explained by many reasons; however, the variation in annual flows (such as peak water levels) have been described as a main factor affecting the TSRL fish communities (Baran, van Zalinge, & Ngor, 2001; van Zalinge et al., 2003; Halls, Paxton, et al., 2013; Sabo et al., 2017). Our results highlighted that the changes in the TSRL fish community were significantly linked to hydrology. The annual peak flows in Tonle Sap Lake were highly contrasted during our study period, i.e., maximum water depths of 9.9 m were recorded in 2011, while only 7.5 m was observed in 2012, 9.0 m was observed in 2013, 7.3 m was observed in 2014 and only 5.3 m was observed in 2015. For example, the high flows in 2011 and 2013 may have facilitated fish spawning success, survival and growth, as greater flood levels equated with higher volumes of water in the TSRL, and thus, larger inundated areas of rearing/feeding habitats were available for fish. Prey species and juveniles could stay in rearing habitats longer, which increases their survival rates. Higher flows also mean that more food becomes available and, thereby, competition for food among fish is reduced. In fact, the highest catch on record over a 17-year monitoring period was observed in the fishing season of 2011/2012 at the Tonle Sap *Dai* fishery (Chheng et al., 2012). Our results also noted that fish communities in 2012 significantly differed from those in other years (S4.10, NMDS axis 1).

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

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

To conclude, understanding the dynamic nature of spatiotemporal variation and distribution patterns as well as indicator species in the TSRL fish communities is necessary to inform fisheries monitoring, management and conservation programmes. For instance, KD is a strategic location for fish diversity management and conservation initiatives, as "white fishes" must use this natural passageway to complete their seasonal life cycles between the Mekong River and the Tonle Sap floodplains. Similarly, the northern lake (BB) could serve as a location for the management and conservation of black fishes. For fisheries monitoring, the clusters and key indicator species identified in this study can be proposed for the long-term fish monitoring programmes to understand spatiotemporal changes and update the status and trends of the TSRL fisheries. The suggested timing of peak abundance and richness in relation to the peak flows of the TSRL could also be part of fish regulation and conservation initiatives. Finally, maintaining the naturally predictable seasonal rising and falling flood pulses as well as the longitudinal and lateral connectivity of the main habitats of the Mekong and its tributary systems, including the Tonle Sap River, are likely the key drivers to maintaining seasonal fish migrations and, hence, the TSRL's seasonal assemblage diversity and productivity. Given that hydropower dams are still being built in the Mekong, good design flows (Sabo et al., 2017) that would help reduce dam effects and boost fisheries production, e.g., in the Tonle Sap, should be prioritised and applied as one of the mitigation measures on existing and planned dams in the Mekong.

ACKNOWLEDGEMENTS

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

ADDITIONAL INFORMATION

Conflict of interests: The authors declare no conflict of interests.

Supplementary information: accompanies this paper.

REFERENCES

Adamson, P. T., Rutherfurd, I. D., Peel, M. C., & Conlan, I. A. 2009. The Hydrology of the Mekong River. In: I. C. Campbell, ed. The Mekong Biophysical Environment of an International River Basin (1st ed.). Elsevier Inc.: Amsterdam, pp. 53–76.

Aloo, P. A. 2003. Biological diversity of the Yala Swamp lakes, with special emphasis on fish species composition, in relation to changes in the Lake Victoria Basin (Kenya): threats and conservation measures. Biodiversity & Conservation, 12: 905–920.

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.

Baird, I. G. 2011. The Don Sahong Dam. Critical Asian Studies, 43: 211–235.

Baran, E. 2005. Cambodia inland fisheries: facts, figures and context. Phnom Penh, Cambodia: WorldFish Center and Inland Fisheries Research and Development Institute.

Baran, E. 2006. Fish Migration Triggers and Cues in the Lower Mekong Basin and Other Freshwater Tropical Systems. Vientiane: Mekong River Commission.

Baran, E., So, N., Degen, P., Chen, X. Y., & Starr, P. 2013. Updated information on fish and fisheries in the Mekong Basin. Catch and Culture, 19: 24–25.

Baran, E., Starr, P., & Kura, Y. 2007. Influence of built structures on Tonle Sap fisheries. Phnom Penh, Cambodia: Cambodia National Mekong Committee and the WorldFish Center.

Baran, E., van Zalinge, N. P., & Ngor, P. B. 2001. Floods, Floodplains and Fish Production in the Mekong Basin: Present and Past Trends. In: A. Ali, ed. Proceedings of the Second Asian Wetlands Symposium, 27-30 August 2001, Penang, Malaysia. Pulau Pinang, Malaysia: Penerbit Universiti Sains Malaysia.

Borcard, D., Gillet, F., & Legendre, P. 2011. Numerical Ecology with R. (R. Gentleman, K. Hornik, & G. G. Parmigiani, Eds.). New York: Springer Science.

Boujard, T. 1992. Space-time organization of riverine fish communities in French Guiana. Environmental Biology of Fishes, 34: 235–246.

Brown, J. H., & Kodric-Brown, A. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology, 58: 445–449.

Bunn, S. E., & Arthington, A. H. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management, 30: 492–507.

Cáceres, M. De, & Legendre, P. 2009. Associations between species and groups of sites: indices and statistical inference. Ecology, 90: 3566–3574.

Campbell, I. C., Poole, C., Giesen, W., & Valbo-Jorgensen, J. 2006. Species diversity and ecology of Tonle Sap Great Lake, Cambodia. Aquatic Sciences, 68: 355–373.

CGIAR. 2013. Working paper on population growth and natural resource pressures in Pursat catchment. Vientiane: Australian Aid and CGIAR Challenge Program on Water and Food.

Chheng, P., So, N., Ngor, P. B., & Nao, T. 2012. Record fish catch on Tonle Sap River. Catch and Culture, 18: 4–5.

Cochrane, T. A., Arias, M. E., & Piman, T. 2014. Historical impact of water infrastructure on water levels of the Mekong River and the Tonle Sap system. Hydrology and Earth System Sciences, 18: 4529–4541.

Davidson, P. J. 2006. The biodiversity of the Tonle Sap Biosphere Reserve: 2005 status review. Phnom Penh, Cambodia: UNDP-GEF funded Tonle Sap Conservation Project.

De Cáceres, M., & Jansen, F. 2011. indicspecies: Functions to assess the strength and significance of relationship of species site group associations. R package version 1.6.0. http://cran.r-project.org/web/packages/indicspecies.

Deap, L., Degen, P., & van Zalinge, N. 2003. Fishing gears of the Cambodian Mekong. Phnom Penh, Cambodia: Inland Fisheries Research and Development Institute of Cambodia & Mekong River Commission.

Dudgeon, D. 2000. The Ecology of Tropical Asian Rivers and Streams in Relation to Biodiversity Conservation. Annual Review of Ecology, Evolution, and Systematics, 31: 195–229.

Dudgeon, D. 2003. The contribution of scientific information to the conservation and management of freshwater biodiversity in tropical Asia. Hydrobiologia, 500: 295–314.

Dufrence, M., & Legendre, P. 1997. Species assemblage and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs, 67: 345–366.

Enomoto, K., Ishikawa, S., Hori, M., S., H., Srun, L. S., Nao, T., & Kurokura, H. 2011. Data mining and stock assessment of fisheries resources in Tonle Sap Lake, Cambodia. Fisheries Science, 77: 713–722.

Espírito-Santo, H. M. V., Magnusson, W. E., Zuanon, J., Mendoça, F. P., & Landeiro, V. L. 2009. Seasonal variation in the composition of fish assemblages in small Amazonian forest streams: Evidence for predictable changes. Freshwater Biology, 54: 536–548.

Fernandes, I. M., Machado, F. A., & Penha, J. 2010. Spatial pattern of a fish assemblage in a seasonal tropical wetland : effects of habitat , herbaceous plant biomass , water depth , and distance from species sources. Neotropical Ichthyology, 8: 289–298.

FiA. 2013. Annual report on fisheries sector 2013 and targets for 2014. Phnom Penh: Fisheries Administration, Ministry of Agriculture, Forestry and Fisheries.

Franssen, N. R., Gido, K. B., Guy, C. S., Tripe, J. A., Shrank, S. J., Strakosh, T. R., Bertrand, K. N., Franssen, C. M., Pitts, K. L., & Paukert, C. P. 2006. Effects of floods on fish assemblages in an intermittent prairie stream. Freshwater Biology, 51: 2072–2086.

Froese, R., & Pauly, D. 2017. FishBase. World Wide Web electronic publication. World Wide Web electronic publication.

Fukushima, M., Jutagate, T., Grudpan, C., Phomikong, P., & Nohara, S. 2014. Potential effects of hydroelectric dam development in the Mekong River basin on the migration of Siamese mud carp (Henicorhynchus siamensis and H. lobatus) elucidated by otolith microchemistry. PLoS ONE, 9: 1–13.

Halls, A. S., Conlan, I., Wisesjindawat, W., Phouthavongs, K., Viravong, S., Chan, S., & Vu, V. A. 2013. Atlas of deep pools in the Lower Mekong River and some of its tributaries. Phnom Penh: Mekong River Commission.

Halls, A. S., Paxton, B. R., Hall, N., Ngor, P. B., Lieng, S., Ngor, P., & So, N. 2013. The Stationary Trawl (Dai) Fishery of the Tonle Sap-Great Lake System, Cambodia. Phnom Penh: Mekong River Commission.

Henriques-Silva, R., Lindo, Z., & Peres-Neto, P. R. 2013. A community of metacommunities : Exploring patterns in species distributions across large geographical areas. Ecology, 94: 627–639.

Hoeinghaus, D. J., Layman, C. ., Arrington, D. A., & Winemiller, K. O. 2003. Spatiotemporal variation in fish assemblage structure in tropical floodplain creeks. Environmental Biology of Fishes, 67: 379–387.

Hortle, K. G., & Bamrungrach, P. 2015. Fisheries Habitat and Yield in the Lower Mekong Basin. MRC Technical Paper No. 47. Phnom Penh: Mekong River Commission.

Hortle, K. G., Lieng, S., & Valbo-Jorgensen, J. 2004. An introduction to Cambodia's inland fisheries.

Mekong Development Series No. 4. Phnom Penh: Mekong River Commission.

Hortle, K. G., Troeung, R., & Lieng, S. 2008. Yield and value of the wild fishery of rice fields in Battambang Province, near the Tonle Sap Lake, Cambodia. MRC Technical Paper No.18. Mekong River Commission, Vietiane.62 PP. Vientiane: Mekong River Commission.

Junk, W. J., Brown, M., Campbell, I. C., Finlayson, M., Gopal, B., Ramberg, L., & Warner, B. G. 2006. The comparative biodiversity of seven globally important wetlands: A synthesis. Aquatic Sciences, 68: 400–414.

Kong, H., Chevalier, M., Laffaille, P., & Lek, S. 2017. Spatio-temporal variation of fish taxonomic composition in a South-East Asian flood-pulse system. PLoS ONE, 12: 1–16.

Kottelat, M. 2013. The Fishes of the inland waters of Southeast Asia: A catalogue and core bibliography of the fishes known to occur in freshwaters, mangroves and estuaries. The Raffles Bulletin of Zoology, 27: 1–663.

Kummu, M., Sarkkula, J., Koponen, J., & Nikula, J. 2006. Ecosystem Management of the Tonle Sap Lake: An Integrated Modelling Approach Ecosystem. Water Resources Development, 22: 497–519.

Kummu, M., Tes, S., Yin, S., Adamson, P., Józsa, J., Koponen, J., Richey, J., & Sarkkula, J. 2014. Water balance analysis for the Tonle Sap Lake-floodplain system. Hydrological Processes, 28: 1722–1733.

Lamberts, D. 2001. Tonle Sap fisheries: a case study on floodplain gillnet fisheries. RAP publication. Bangkok: Asia-Pacific Fisheries Commission, Food and Agriculture Organisation of the United Nations, Regional Office for Asia and the Pacific.

Laske, S. M., Haynes, T. B., Rosenberger, A. E., Koch, J. C., Wipfli, M. S., Whitman, M., & Zimmerman, C. E. 2016. Surface water connectivity drives richness and composition of Arctic lake fish assemblages. Freshwater Biology, 2016: 1–15.

Lim, P., Lek, S., Touch, S. T., Mao, S. O., & Chhouk, B. 1999. Diversity and spatial distribution of freshwater fish in Great Lake and Tonle Sap river (Cambodia, Southeast Asia). Aquatic Living Resources, 12: 379–386.

Magurran, A. E. 2004. Measuring biological diversity. Malden, USA: Blackwell Science Ltd.

McCann, K. S., Gellner, G., McMeans, B. C., Deenik, T., Holtgrieve, G., Rooney, N., Hannah, L., Cooperman, M., Nam, S., & Giacomini, H. 2016. Food webs and the sustainability of indiscriminate fisheries. Canadian Journal of Fisheries and Aquatic Sciences, 73: 1–10.

MFD. 2003. Mekong Fish Database: A taxonomic fish database for the Mekong Basin. Phnom Penh: Mekong River Commission.

MRC. 2003. State of the Basin Report 2003. Phnom Penh: Mekong River Commission.

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

MRC. 2007. Monitoring Fish Abundance and Diversity in the Lower Mekong Basin: Methodological Guidelines. Phnom Penh: Mekong River Commission.

MRC. 2010. State of the Basin Report 2010. Vientiane, Lao PDR: Mekong River Commission.

MRC. 2011a. Assessment of Basin-wide Development Scenarios: Cumulative impact assessment of the riparian countries' water resources development plans, including mainstream dams and diversions (Vol. Basin Deve). Phnom Penh: Mekong River Commission.

MRC. 2011b. Planning Atlas of the Lower Mekong River Basin. Phnom Penh: Mekong River Commission.

MRCS. 1992. Fisheries in the Lower Mekong Basin, Main Report and Annex. (Review of the fishery sector in the lower Mekong basin). Bangkok: Interim Committee for the Coordination of

Investigations of the Lower Mekong Basin, Mekong River Commission Secretariat.

Murtagh, F., & Legendre, P. 2014. Ward's hierarchical agglomerative clustering method: Which algorithms implement Ward's criterion? Journal of Classification, 31: 274–295.

Nagumo, N., Sugai, T., & Kubo, S. 2013. Late Quaternary floodplain development along the Stung Sen River in the Lower Mekong Basin, Cambodia. Geomorphology, 198: 84–95.

Nagumo, N., Sugai, T., & Kubo, S. 2015. Fluvial Geomorphology and Characteristics of Modern Channel Bars in the Lower Stung Sen River, Cambodia. Geographical Review of Japan Series B, 87: 115–121.

Ngor, P. B., Legendre, P., Oberdorff, T., & Lek, S. 2018. Flow alterations by dams shaped fish assemblage dynamics in the complex Mekong-3S river system. Ecological Indicators, 88: 103–114.

Poulsen, A. F., Hortle, K. G., Valbo-Jorgensen, J., Chan, S., Chhuon, C. K., Viravong, S., Bouakhamvongsa, K., Suntornratana, U., Yoorong, N., T.T., N., & Tran, B. Q. 2004. Distribution and Ecology of Some Important Riverine Fish Species of the Mekong River Basin. Phnom Penh: Mekong River Commission.

Poulsen, A. F., Ouch, P., Viravong, S., Suntornratana, U., & Nguyen, T. T. 2002. Fish Migrations of the Lower Mekong Basin: Implications for Development, Planning and Environmental Management. Phnom Penh: Mekong River Commission.

R Core Team. 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing.

Rainboth, W. J. 1996. Fishes of the Cambodian Mekong. Rome: Food and Agriculture Organisation of the United Nations.

Rainboth, W. J., Vidthayanon, C., & Mai, D. Y. 2012. Fishes of the Greater Mekong Ecosystem with Species List and Photoraphic Atlas. Ann Arbor: Museum of Zoology, University of Michigan.

Rodríguez, M. A., & Lewis, W. M. 1997. Structure of fish assemblages along environmental gradients in floodplain lakes of the Orinoco River. Ecological Monographs, 67: 109–128.

Rossi, J. P. 2011. Rich: An R package to analyse species richness. Diversity, 3: 112–120.

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: 1–11.

Shumway, R. H., & Stoffer, D. S. 2011. Time series analysis and its applications: with R examples (Third Edit.). New York: Springer Science+Business Media.

Silvano, R. A. M., Benedito, D., & Oyakawa, O. T. 2000. Spatial and temporal patterns of diversity and distribution of the Upper Juruá River fish community (Brazilian Amazon). Environmental Biology of Fishes, 57: 25–35.

The Ramsar Convention Secretariat. 2014. Ramsar. Ramsar Sites Information Services.

Valbo-Jørgensen, J., Coates, D., & Hortle, K. G. 2009. Fish diversity in the Lower Mekong Basin. In: I. C. Campbell, ed. The Mekong Biophysical Environment of an International River Basin (1st ed.). Elsevier Inc.: Amsterdam, pp. 161 – 196.

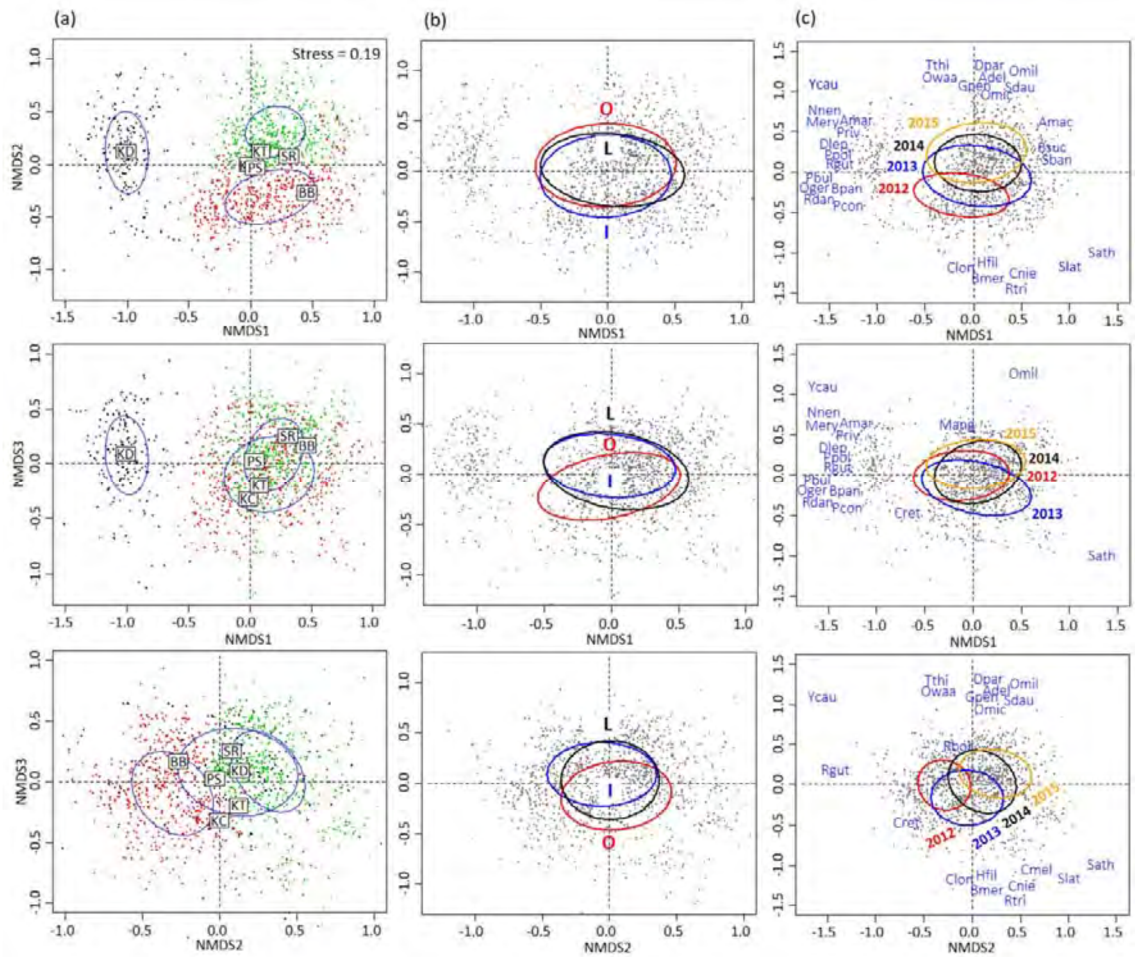
van Zalinge, N., Deap, L., Ngor, P. B., Sarkula, J., & Koponen, J. 2003. Mekong flood levels and Tonle Sap fish catches. In: Second International Symposium on the Management of Large Rivers for Fisheries. Phnom Penh: Second International Symposium on the Management of Large Rivers for Fisheries.

van Zalinge, N., Degen, P., Pongsri, C., Nuov, S., Jensen, J. G., Nguyen, V. H., & Choulamany, X. 2004. The Mekong River System. In: R. Welcomme & T. Petr, eds. Proceedings of the second international symposium on the management of large rivers for fisheries. Bangkok: FAO Regional Office for Asia and the Pacific.

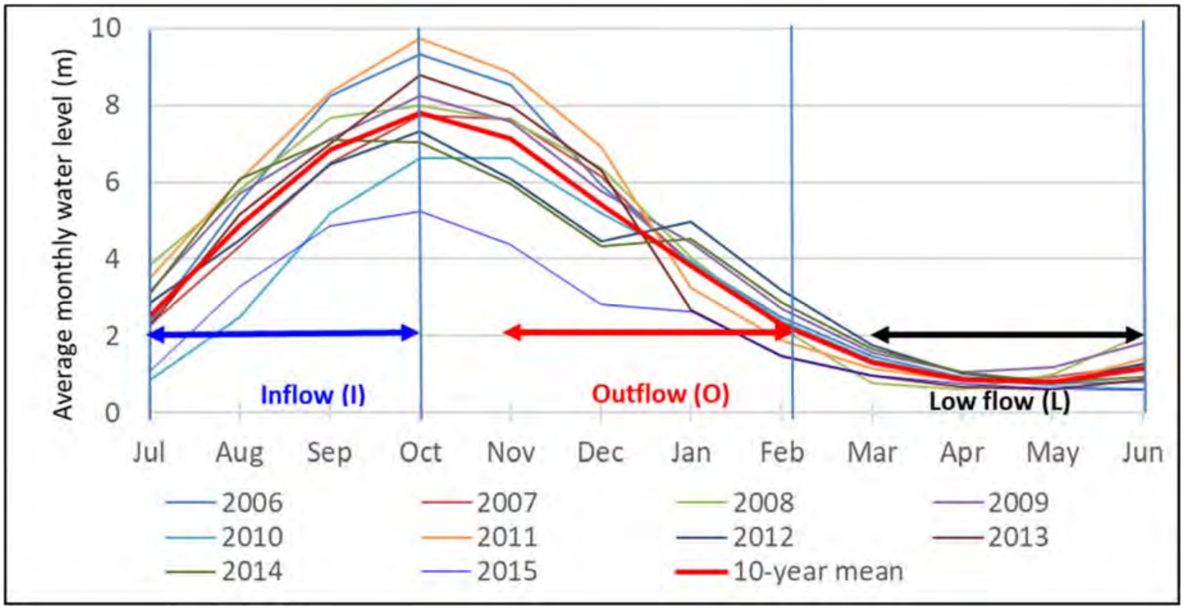
Welcome, R. L. 2001. Inland fisheries: ecology and management (1st ed.). Great Britain: Food and Agriculture Organization of the United Nations by Blackwell Science.

Supplementary Information (S)

Supplementary Information S1. Three-dimensional NMDS plots on the weekly abundance samples (Bray-Curtis dissimilarity matrix) showing the TSRL community spatiotemporal variation. (a) Spatial, (b) seasonal and (c) inter-annual variation. For (b), I, O, L, respectively symbolising the inflow, outflow and the low flow periods. For site codes, see Fig. 1. For season partitioning, see S2. For fish species details, see S9.

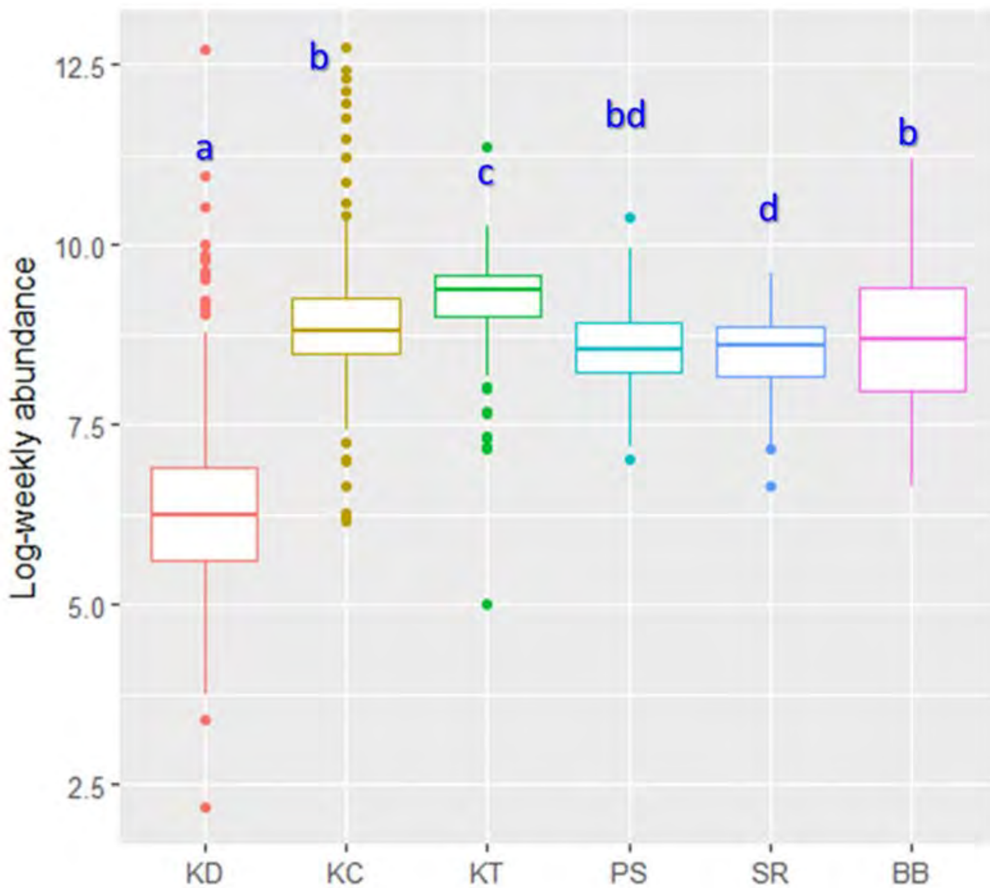


Supplementary Information S2. Intra-annual hydrological cycle of Tonle Sap Lake: partitioning seasons into: Inflow (I) or high flow period (July-October), Outflow (O) period (November-February) and Low-flow (L) period (March-June). Red line curve represents the 10-year mean of water levels in Tonle Sap Lake.



28

Supplementary Information S3. Spatiotemporal comparison of site fish species abundance in Tonle Sap Lake and River. Mean values among sites with a common letter are not significantly different at p-value = 0.05 (Wilcoxon test). For site names, see Fig. 1.



Supplementary Information S4. Results of Permutational Multivariate Analysis of Variance (PERMANOVA), contrast pairwise tests between different levels of factor (cluster, season and year) and boxplots comparing NMDS scores among these factor levels.

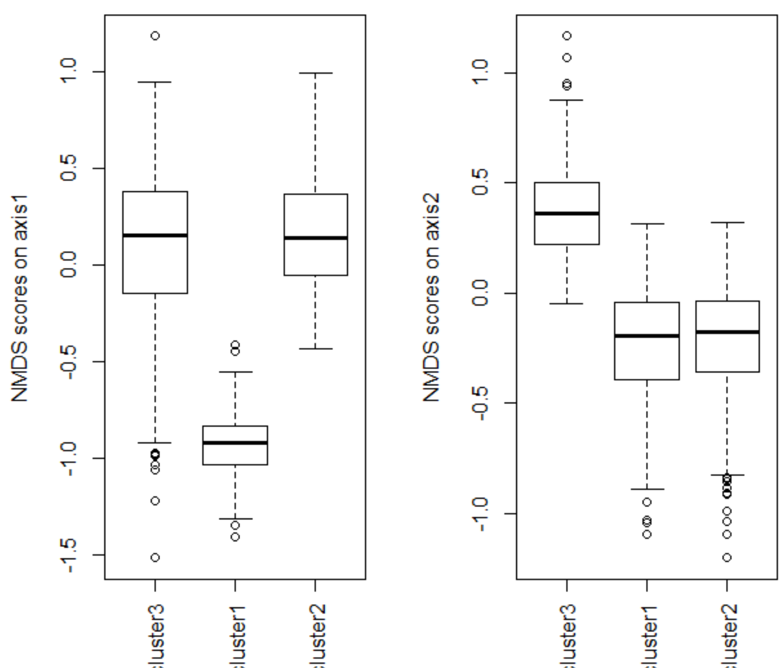
S4.1. PERMANOVA test among clusters

	Df	SumOfSqs	F	Pr(>F)	Sig. Level
cluster	2	70.85	117.41	0.001	***
Residual	1225	369.63			

S4.2. Contrast pair-wise tests between the different factor levels of cluster

No	pairs			F.Model	R2	p.value	p.adjusted	Sig. Level
1	cluster 1	vs	cluster 2	117.34	0.16	0.001	0.003	*
2	cluster 1	vs	cluster 3	71.16	0.06	0.001	0.003	*
3	cluster 2	vs	cluster 3	191.24	0.20	0.001	0.003	*

S4.3. NMDS scores comparing the three factor levels of cluster (Fig. 3b). Mean values among seasons with a common letter are not significantly different at p-value = 0.05 (Wilcoxon test).



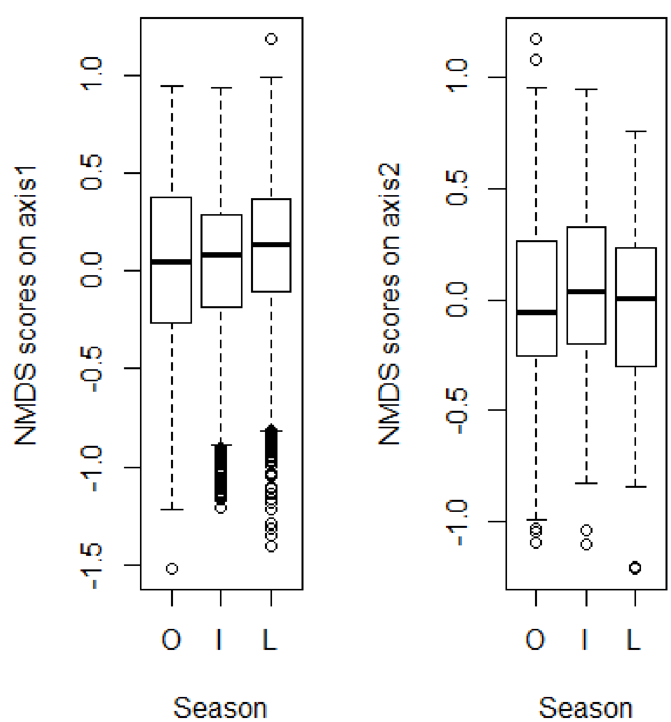
S4.4. PERMANOVA test among seasons

	Df	SumOfSqs	F	Pr(>F)	Sig. Level
season	2	8.39	11.889	0.001	***
Residual	1225	432.09			

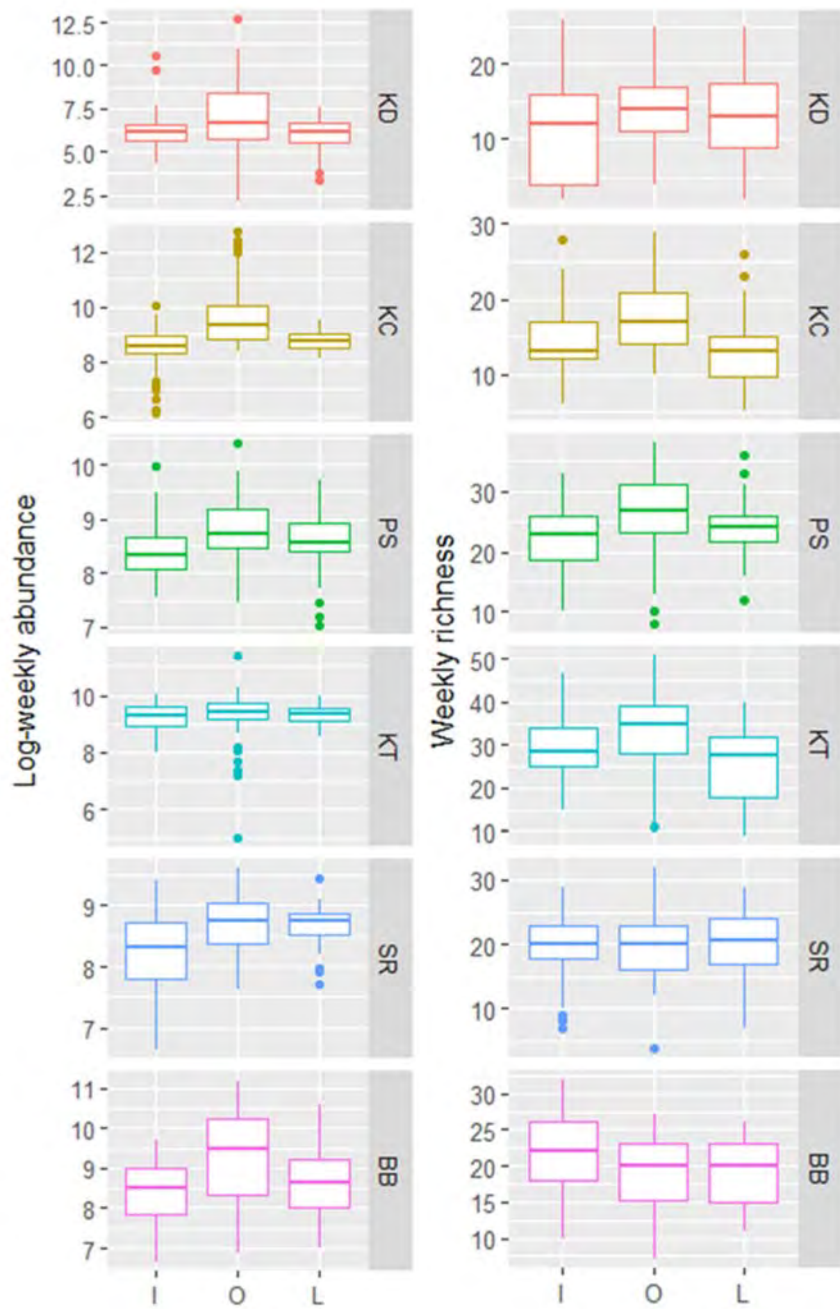
S4.5. Contrast pair-wise tests between different factor level of season (I = inflow/high-flow period, O = outflow period and L = low-flow period)

No	Pairs			F.Model	R2	p.value	p.adjusted	Sig. Level
1	O	vs	I	16.86	0.02	0.001	0.003	*
2	O	vs	L	12.27	0.02	0.001	0.003	*
3	I	vs	L	5.86	0.01	0.001	0.003	*

S4.6. NMDS scores comparing the three factor levels of season (Fig. 3c). O = Outflow period, I = Inflow period and L = Low-flow period. Mean values among seasons with a common letter are not significantly different at p-value = 0.05 (Wilcoxon test).



S4.7. Seasonal variations in weekly abundance and richness (I = inflow period, O = outflow period and L = low-flow period). Overall, Wilcoxon tests indicated statistical significant differences between all pairs of season at p-value < 0.05 for both abundance and richness. For site names, see Fig. 1.



32

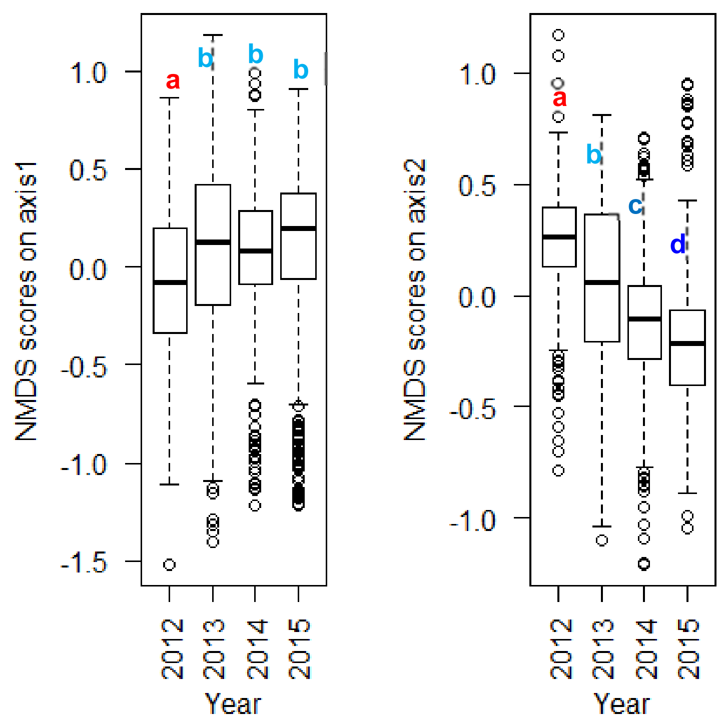
S4.8. PERMANOVA test among years

	Df	SumOfSqs	F	Pr(>F)	Sig. Level
year	3	20.51	19.924	0.001	***
Residual	1224	419.97			

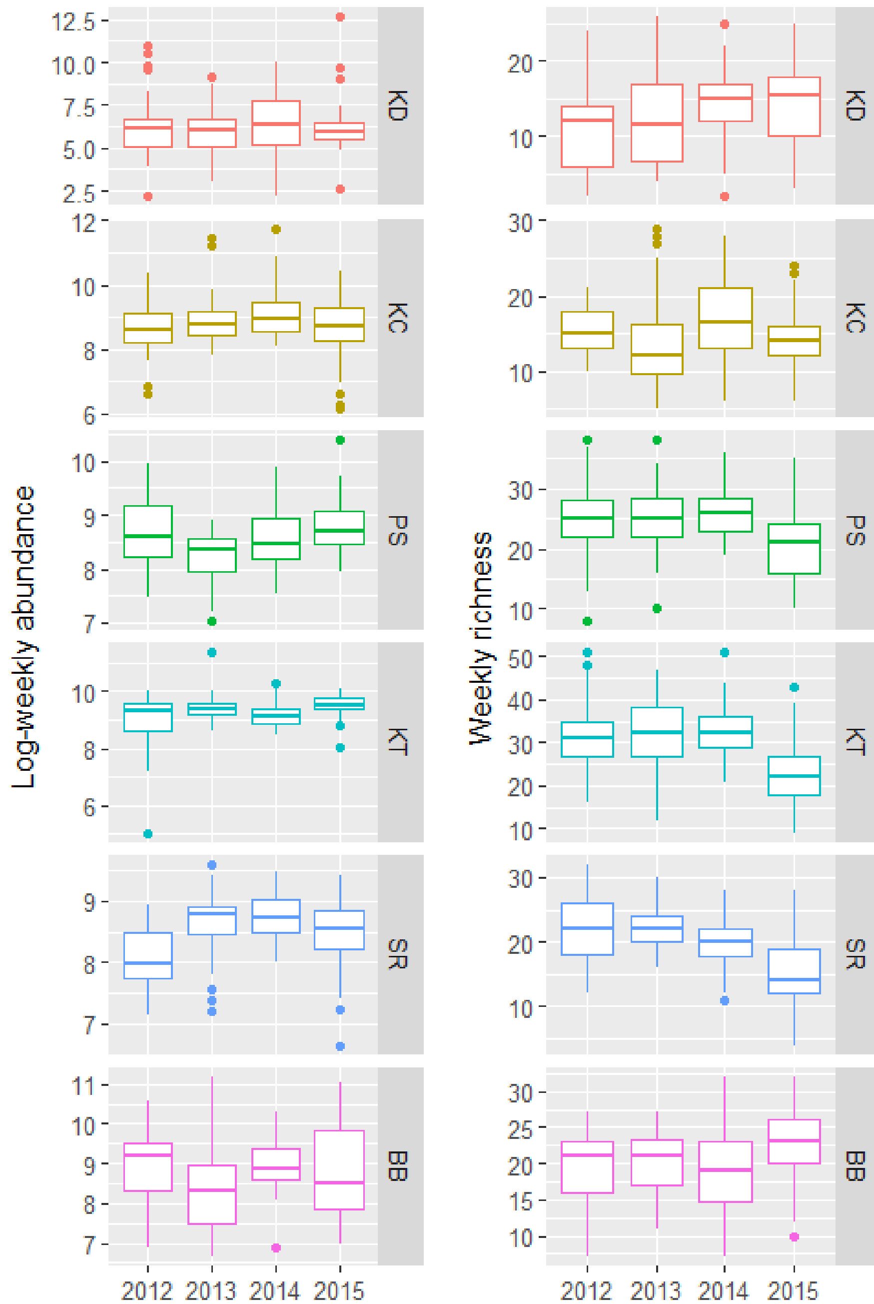
S4.9. Contrast pair-wise tests between different factor level of year

No	pairs			F.Model	R2	p.value	p.adjusted	Sig. Level
1	2012	vs	2013	15.52	0.02	0.001	0.006	*
2	2012	vs	2014	30.95	0.05	0.001	0.006	*
3	2012	vs	2015	34.44	0.05	0.001	0.006	*
4	2013	vs	2014	11.53	0.02	0.001	0.006	*
5	2013	vs	2015	16.86	0.03	0.001	0.006	*
6	2014	vs	2015	9.21	0.02	0.001	0.006	*

S4.10 NMDS scores comparing the four factor levels of year (2012-2015) (Fig. 3d). Mean values among seasons with a common letter are not significantly different at p-value = 0.05 (Wilcoxon test).



S4.11. Inter-annual variations in weekly abundance and richness. Overall, Wilcoxon tests indicated statistical significant differences at p-value < 0.05 between 2012-2014, 2013-2014 and 2014-2015 for abundance, and between 2012-2015, 2013-2015, 2014-2015 for richness. For site names, see Fig. 1.



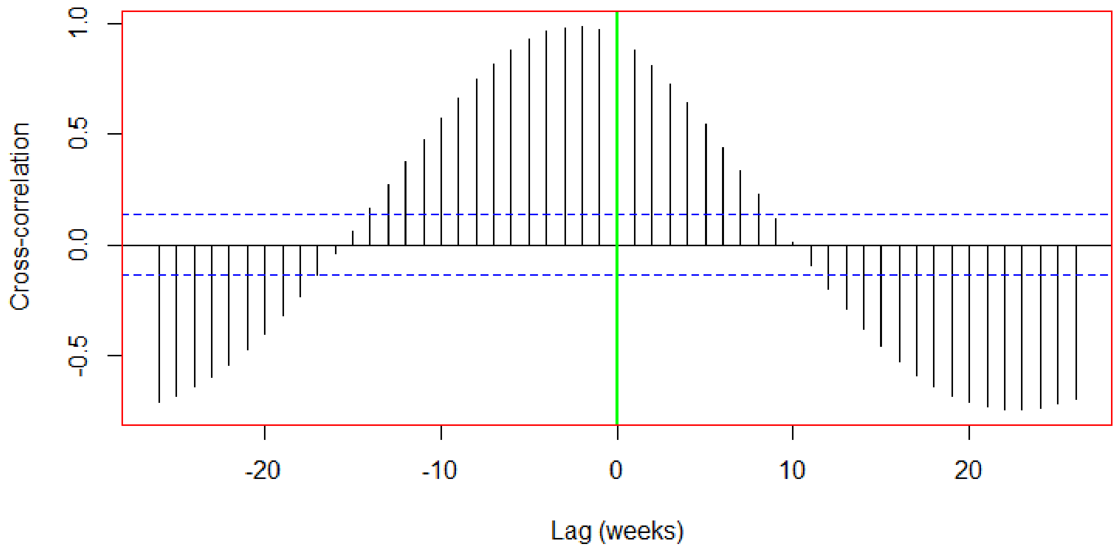
Supplementary Information S5. List of indicator species by cluster and season in Tonle Sap Lake and River. Given are the values of indicator species (IndVal) for each cluster and season with their associated significance levels (Sig. level) (***, p < 0.001; ** p < 0.01; *, p < 0.05). The indicator species for each of the three clusters were simultaneously computed from the TSRL fish community matrix; whereas, indicator species characterizing each season for a given cluster were concurrently computed from the community matrix for that cluster. For seasons, only indicator species that matched with those for the cluster were shown here.

abbre-viations	Species name	Cluster		Inflow (I)		Outflow (O)		Low-flow (L)	
		InVal	Sig. Level	InVal	Sig. Level	InVal	Sig. Level	InVal	Sig. Level
Fish assemblage cluster1 (20 species)									
Pmac	*Pangasius macronema*	0.92	***	-	-	-	-	-	-
Lsia	*Labiobarbus siamensis*	0.61	***	-	-	-	-	-	-
Pcon	*Pangasius conchophilus*	0.55	***	-	-	-	-	-	-
Pfal	*Puntioplites falcifer*	0.48	***	-	-	-	-	-	-
Ppol	*Pangasius polyuranodon*	0.46	***	-	-	-	-	-	-
Ptyp	*Paralaubuca typus*	0.46	**	-	-	0.73	***	-	-
Pble	*Phalacronotus bleekeri*	0.43	***	-	-	0.62	**	-	-
Priv	*Paralaubuca riveroi*	0.40	***	-	-	0.46	**	-	-
Btru	*Belodontichthys truncatus*	0.38	***	-	-	0.74	***	-	-
Bpan	*Brachirus panoides*	0.37	***	-	-	-	-	-	-
Pboc	*Pangasius bocourti*	0.36	***	-	-	-	-	0.53	**
Ycau	*Yasuhikotakia caudipunctata*	0.32	***	-	-	-	-	-	-
Mery	*Mastacembelus erythrotaenia*	0.28	***	-	-	-	-	0.35	**
Mche	*Micronema cheveyi*	0.26	**	-	-	0.57	***	-	-
Cgac	*Channa gachua*	0.25	***	-	-	-	-	-	-
Ccar	*Cyprinus carpio*	0.25	***	-	-	-	-	-	-
Psia.1	*Parambassis siamensis*	0.20	***	-	-	-	-	-	-
Nnen	*Nemapteryx nenga*	0.16	***	-	-	-	-	-	-
Hwaa	*Helicophagus waandersii*	0.12	*	-	-	-	-	-	-
Dpol	*Datnioides polota*	0.10	*	-	-	-	-	-	-
Fish assemblage cluster2 (45 species)									
Mmys	*Mystus mysticetus*	0.80	***	-	-	0.56	**	-	-
Llin	*Labiobarbus lineatus*	0.72	***	-	-	0.59	**	-	-
Ovit	*Osteochilus vittatus*	0.71	***	-	-	0.64	***	-	-
Ates	*Anabas testudineus*	0.68	***	-	-	-	-	-	-
Lchr	*Labeo chrysophekadion*	0.67	***	-	-	0.60	***	-	-
Tthy	*Thynnichthys thynnoides*	0.66	***	-	-	0.57	***	-	-
Pfas	*Pristolepis fasciata*	0.65	***	-	-	-	-	-	-
Hsia	*Henicorhynchus siamensis*	0.64	***	-	-	0.65	***	-	-
Ttri	*Trichopodus trichopterus*	0.63	***	-	-	0.67	***	-	-
Carm	*Cyclocheilichthys armatus*	0.61	***	-	-	0.56	***	-	-
Msin	*Mystus singaringan*	0.59	***	0.52	*	-	-	-	-
Pwol	*Parambassis wolffii*	0.57	***	-	-	-	-	-	-

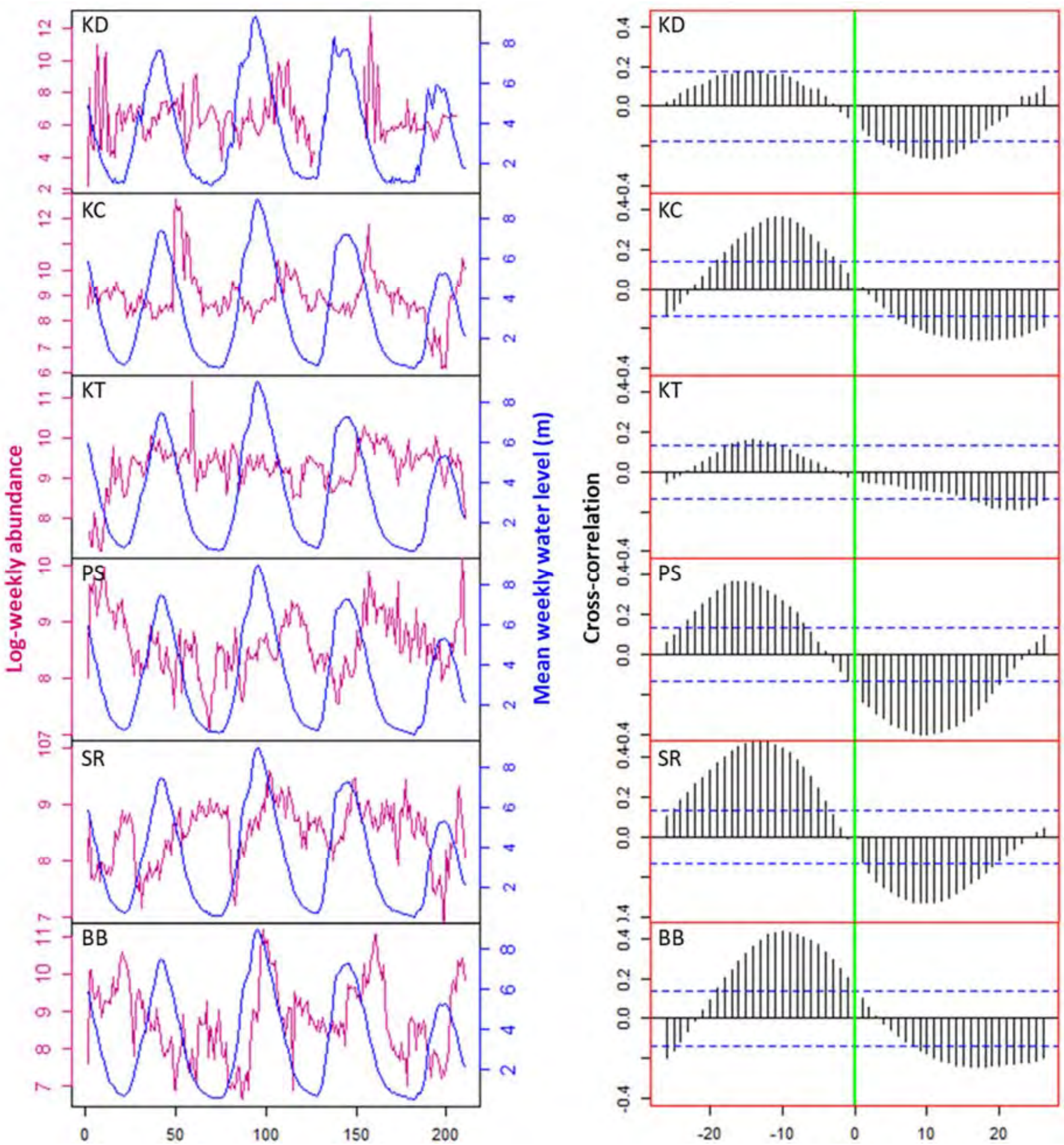
Ymod	*Yasuhikotakia modesta*	0.53	***	-	-	0.54	***	-	-
Msia	*Macrognathus siamensis*	0.51	***	-	-	-	-	-	-
Atru	*Amblyrhynchichthys truncatus*	0.48	***	-	-	-	-	-	-
Omel	*Osteochilus melanopleurus*	0.47	**	-	-	0.53	***	-	-
Crep	*Cyclocheilichthys repasson*	0.43	***	-	-	0.39	**	-	-
Cfur	*Cyclocheilos furcatus*	0.42	***	-	-	-	-	-	-
Mboc	*Mystus bocourti*	0.40	**	-	-	-	-	0.47	***
Lcro	*Lycothrissa crocodilus*	0.39	**	-	-	-	-	0.38	**
Malb.1	*Mystus albolineatus*	0.37	***	-	-	-	-	-	-
Papo.1	*Phalacronotus apogon*	0.37	**	-	-	-	-	-	-
Hdis	*Hampala dispar*	0.36	***	-	-	0.35	**	-	-
Char	*Cosmochilus harmandi*	0.35	*	-	-	0.47	***	-	-
Srub	*Systomus rubripinnis*	0.35	***	0.33	*	-	-	-	-
Aalb	*Albulichthys albuloides*	0.33	**	-	-	-	-	0.40	***
Lhoe	*Leptobarbus hoevenii*	0.33	*	-	-	-	-	-	-
Gpen	*Gyrinocheilus pennocki*	0.32	***	-	-	0.34	***	-	-
Osch	*Osteochilus schlegeli*	0.31	***	-	-	-	-	-	-
Ldyo	*Labeo dyocheilus*	0.28	***	-	-	0.37	***	-	-
Omic	*Osteochilus microcephalus*	0.27	***	-	-	0.26	*	-	-
Olin	*Osteochilus lini*	0.27	***	-	-	-	-	-	-
Corn	*Chitala ornata*	0.26	**	0.34	***	-	-	-	-
Hmal	*Hypsibarbus malcolmi*	0.25	***	-	-	-	-	-	-
Cmac.1	*Coilia macrognathos*	0.24	*	-	-	-	-	-	-
Hwyc.1	*Hemibagrus wyckioides*	0.23	**	0.23	*	-	-	-	-
Bsch	*Barbonymus schwanenfeldii*	0.22	**	-	-	0.23	*	-	-
Pmac.1	*Parachela maculicauda*	0.21	**	-	-	0.31	***	-	-
Gfas	*Garra fasciacauda*	0.21	**	0.27	**	-	-	-	-
Mmac	*Macrochirichthys macrochirus*	0.20	**	-	-	0.24	**	-	-
Clin	*Coilia lindmani*	0.17	*	-	-	-	-	-	-
Mcir	*Macrognathus circumcinctus*	0.17	**	-	-	0.23	**	-	-
Lmel	*Lobocheilos melanotaenia*	0.17	*	-	-	0.26	***	-	-
Cjul	*Cirrhinus jullieni*	0.15	*	-	-	-	-	-	-
Catr	*Crossocheilus atrilimes*	0.12	*	-	-	-	-	-	-
Fish assemblage cluster3 (31 species)									
Nnot	*Notopterus notopterus*	0.77	***	-	-	-	-	-	-
Hspi	*Hemibagrus spilopterus*	0.72	***	0.60	***	-	-	-	-
Tmic.1	*Trichopodus microlepis*	0.63	***	-	-	-	-	0.52	*
Bgon	*Barbonymus gonionotus*	0.60	***	0.57	**	-	-	-	-
Cstr	*Channa striata*	0.59	*	-	-	-	-	-	-
Obim	*Ompok bimaculatus*	0.57	***	-	-	-	-	0.55	*
Hmac	*Hampala macrolepidota*	0.57	***	-	-	-	-	-	-
Omar	*Oxyeleotris marmorata*	0.57	***	-	-	-	-	-	-
Tpec	*Trichopodus pectoralis*	0.57	***	-	-	-	-	0.45	*
Ceno	*Cyclocheilichthys enoplos*	0.56	***	-	-	-	-	0.58	*
Phyp	*Pangasianodon hypophthalmus*	0.55	***	-	-	-	-	-	-
Pmic	*Phalacronotus micronemus*	0.55	***	-	-	-	-	-	-
Hlag	*Hypsibarbus lagleri*	0.47	***	-	-	-	-	0.44	**
Bmic	*Boesemania microlepis*	0.47	***	-	-	-	-	-	-

Cmac	*Clarias macrocephalus*	0.42	***	0.44	**	-	-	-	-
Pdja	*Pangasius djambal*	0.41	***	-	-	-	-	-	-
Cmel	*Clarias meladerma*	0.40	***	-	-	-	-	-	-
Matr	*Mystus atrifasciatus*	0.31	**	-	-	-	-	0.43	***
Cbat	*Clarias batrachus*	0.30	***	-	-	0.34	**	-	-
Llep	*Labiobarbus leptocheilus*	0.28	**	-	-	-	-	-	-
Plei	*Pao leiurus*	0.27	***	-	-	-	-	0.30	**
Pbre	*Puntius brevis*	0.26	**	-	-	-	-	-	-
Plab	*Probarbus labeamajor*	0.26	**	-	-	-	-	-	-
Pspp	*Pangasius* sp.	0.25	**	-	-	-	-	0.30	*
Csp	*Clarias* sp.	0.25	***	-	-	-	-	0.26	*
Psia	*Parachela siamensis*	0.23	**	-	-	0.32	***	-	-
Mhex	*Micronema hexapterus*	0.21	**	-	-	0.27	**	-	-
Pjul	*Probarbus jullieni*	0.19	*	-	-	-	-	-	-
Aleu	*Achiroides leucorhynchos*	0.18	**	-	-	-	-	-	-
Pmul	*Polynemus multifilis*	0.18	**	-	-	-	-	0.27	**
Hver	*Hypsibarbus vernayi*	0.12	*	0.17	*	-	-	-	-

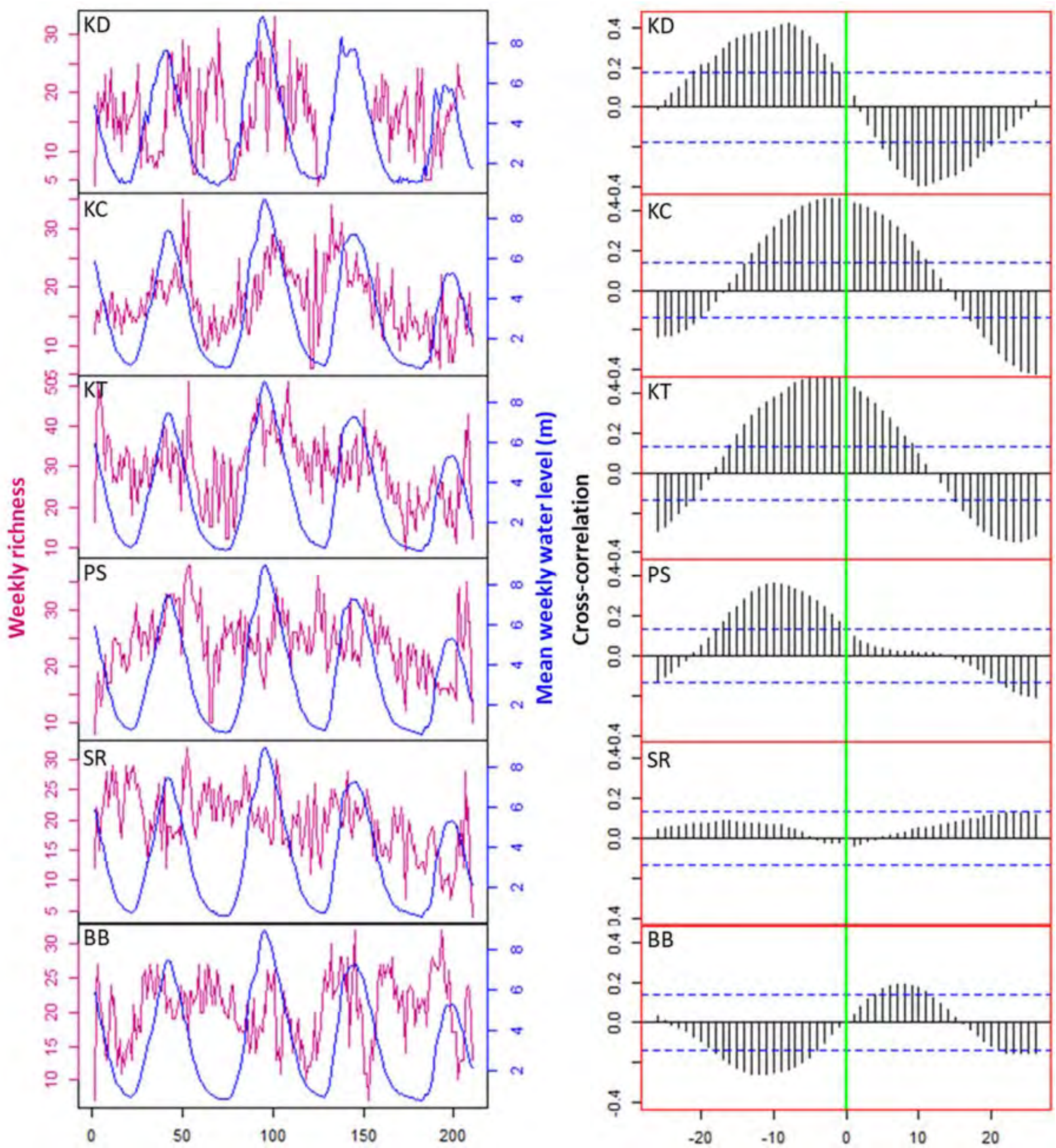
Supplementary Information S6. Cross-correlation between mean weekly water levels in Tonle Sap River in Kandal (KD) and Tonle Sap Lake in Pursat (PS). The correlation lag with the maximum coefficient was estimated at -2 weeks, implying that mean water levels in the Tonle Sap Lake lag around two weeks behind that of the Tonle Sap River. Maximum time lags for the cross-correlation plot were set at 52 weeks indicating an annual cycle.



Supplementary Information S7. Cross-correlation plots between fish community abundance and water levels in the TSRL. Mean weekly water levels in KD were used for cross-correlation plot in KD and mean weekly water levels in PS were used for cross-correlation plots in all sites around the lake. Correlation lags at the site maximum coefficient were estimated at -15 weeks (KD), -10 (KC), -14 (KT), -16 (PS), -13 (SR) and -10 (BB). Maximum time lags for the cross-correlation plots were set at 52 weeks indicating an annual cycle. For site names, see Fig. 1.



Supplementary Information S8. Cross-correlation plots between fish community richness and water levels in the TSRL. Mean weekly water levels in KD were used for cross-correlation plot in KD and mean weekly water levels in PS were used for cross-correlation plots in all sites around the lake. Correlation time lags at the site maximum coefficient were estimated at -8 weeks (KD), -2 (KC), -2 (KT), -10 (PS), 20 (SR) and 8 (BB). Maximum time lags for the cross-correlation plots were set at 52 weeks indicating an annual cycle. For site names, see Fig. 1.



40

Supplementary Information – S9: List of species names and their abbreviation by genera, families and orders. Species names and their ecological attributes are based on (Rainboth, 1996; MFD, 2003; Rainboth et al., 2012; Kottelat, 2013; Froese & Pauly, 2017).

- Habitat guild: (1) Rithron resident, (2) Main channel resident, (3) Main channel spawner, (4) Floodplain spawner, (5) Eurytopic (generalist), (6) Floodplain resident, (7) Estuarine resident, (8) Anadromous, (9) Catadromous, (10) Marine visitor, (9) Non-native.
  - Migration guild: Black = non-migratory (floodplain resident), Grey = short-distance lateral migration between floodplain and river channel, White = longitudinal migration (in river), Estuarine = Estuarine resident/marine visitor.

No	Abbr-eviaiton	Species name	genus	Family	order	Habitat guild	Migration guild
1	Bbag	*Bagarius bagarius*	Bagarius	Sisoridae	Siluriformes	1	White
2	Bmer	*Balitora meridionalis*	Balitora	Balitoridae	Cypriniformes	1	White
3	Bsuc	*Bagarius suchus*	Bagarius	Sisoridae	Siluriformes	1	White
4	Bzol	*Balitoropsis zollingeri*	Balitoropsis	Balitoridae	Cypriniformes	1	White
5	Cbla	*Chitala blanci*	Chitala	Notopteridae	Osteoglossiformes	1	White
6	Cgac	*Channa gachua*	Channa	Channidae	Perciformes	1	Black
7	Dash	*Discherodontus ashmeadi*	Discherodontus	Cyprinidae	Cypriniformes	1	White
8	Dlep	*Devario leptos*	Devario	Cyprinidae	Cypriniformes	1	White
9	Dpar	*Discherodontus parvus*	Discherodontus	Cyprinidae	Cypriniformes	1	White
10	Gfas	*Garra fasciacauda*	Garra	Cyprinidae	Cypriniformes	1	White
11	Gfus	*Glyptothorax fuscus*	Glyptothorax	Sisoridae	Siluriformes	1	White
12	Gksa	*Gobiidae ksan*	Gobiidae	Gobiidae	Perciformes	1	Black
13	Glao	*Glyptothorax laosensis*	Glyptothorax	Sisoridae	Siluriformes	1	White
14	Hpen	*Hemimyzon pengi*	Hemimyzon	Balitoridae	Cypriniformes	1	White
15	Lmel	*Lobocheilos melanotaenia*	Lobocheilos	Cyprinidae	Cypriniformes	1	White
16	Mobt	*Mystacoleucus obtusirostris*	Mystacoleucus	Cyprinidae	Cypriniformes	1	White
17	Nbla	*Neolissochilus blanci*	Neolissochilus	Cyprinidae	Cypriniformes	1	White
18	Oexo	*Osphronemus exodon*	Osphronemus	Osphronemidae	Perciformes	1	Black
19	Ofus	*Onychostoma fusiforme*	Onychostoma	Cyprinidae	Cypriniformes	1	White
20	Oger	*Onychostoma gerlachi*	Onychostoma	Cyprinidae	Cypriniformes	1	White
21	Ogor	*Osphronemus goramy*	Osphronemus	Osphronemidae	Perciformes	1	Black
22	Owaa	*Osteochilus waandersii*	Osteochilus	Cyprinidae	Cypriniformes	1	White
23	Pdea	*Poropuntius deauratus*	Poropuntius	Cyprinidae	Cypriniformes	1	White
24	Rgut	*Raiamas guttatus*	Raiamas	Cyprinidae	Cypriniformes	1	White
25	Sara	*Schistura aramis*	Schistura	Nemacheilidae	Cypriniformes	1	White
26	Sath	*Schistura athos*	Schistura	Nemacheilidae	Cypriniformes	1	White
27	Scra	*Schistura crabro*	Schistura	Nemacheilidae	Cypriniformes	1	White
28	Sdau	*Schistura daubentoni*	Schistura	Nemacheilidae	Cypriniformes	1	White
29	Sfor	*Scleropages formosus*	Scleropages	Osteoglossidae	Osteoglossiformes	1	Black
30	Slat	*Schistura latifasciata*	Schistura	Nemacheilidae	Cypriniformes	1	White
31	Tlat	*Tor laterivittatus*	Tor	Cyprinidae	Cypriniformes	1	White
32	Tsin	*Tor sinensis*	Tor	Cyprinidae	Cypriniformes	1	White
33	Ttam	*Tor tambroides*	Tor	Cyprinidae	Cypriniformes	1	White
34	Cmac.1	*Coilia macrognathos*	Coilia	Engraulidae	Clupeiformes	10	Estuarine
35	Cmic.2	*Cynoglossus microlepis*	Cynoglossus	Cynoglossidae	Pleuronectiformes	10	Estuarine
36	Gtil	*Gymnothorax tile*	Gymnothorax	Muraenidae	Anguilliformes	10	Estuarine
37	Mcyp	*Megalops cyprinoides*	Megalops	Megalopidae	Elopiformes	10	Estuarine
38	Ttol	*Tenualosa toli*	Tenualosa	Clupeidae	Clupeiformes	10	Estuarine
39	Ccar	*Cyprinus carpio*	Cyprinus	Cyprinidae	Cypriniformes	11	White
40	Ccir	*Cirrhinus cirrhosus*	Cirrhinus	Cyprinidae	Cypriniformes	11	White
41	Gaff	*Gambusia affinis*	Gambusia	Poeciliidae	Cyprinodontiformes	11	Black

42	Hmol	*Hypophthalmichthys molitrix*	Hypophthalmichthys	Cyprinidae	Cypriniformes	11	White
43	Ldyo	*Labeo dyocheilus*	Labeo	Cyprinidae	Cypriniformes	11	White
44	Lroh	*Labeo rohita*	Labeo	Cyprinidae	Cypriniformes	11	White
45	Mang	*Misgurnus anguillicaudatus*	Misgurnus	Cobitidae	Cypriniformes	11	White
46	Pbra	*Piaractus brachypomus*	Piaractus	Serrasalmidae	Characiformes	11	Black
47	Ppol	*Pangasius polyuranodon*	Pangasius	Pangasiidae	Siluriformes	11	White
48	Ceno	*Cyclocheilichthys enoplos*	Cyclocheilichthys	Cyprinidae	Cypriniformes	2	White
49	Cfur	*Cyclocheilos furcatus*	Cyclocheilos	Cyprinidae	Cypriniformes	2	White
50	Char	*Cosmochilus harmandi*	Cosmochilus	Cyprinidae	Cypriniformes	2	White
51	Csia	*Catlocarpio siamensis*	Catlocarpio	Cyprinidae	Cypriniformes	2	White
52	Pboc	*Pangasius bocourti*	Pangasius	Pangasiidae	Siluriformes	2	White
53	Pcon	*Pangasius conchophilus*	Pangasius	Pangasiidae	Siluriformes	2	White
54	Pdja	*Pangasius djambal*	Pangasius	Pangasiidae	Siluriformes	2	White
55	Phyp	*Pangasianodon hypophthalmus*	Pangasianodon	Pangasiidae	Siluriformes	2	White
56	Pjul	*Probarbus jullieni*	Probarbus	Cyprinidae	Cypriniformes	2	White
57	Plab	*Probarbus labeamajor*	Probarbus	Cyprinidae	Cypriniformes	2	White
58	Plar	*Pangasius larnaudii*	Pangasius	Pangasiidae	Siluriformes	2	White
59	Ptyp	*Paralaubuca typus*	Paralaubuca	Cyprinidae	Cypriniformes	2	White
60	Aalb	*Albulichthys albuloides*	Albulichthys	Cyprinidae	Cypriniformes	3	White
61	Adel	*Acanthopsoides delphax*	Acanthopsoides	Cobitidae	Cypriniformes	3	White
62	Agra	*Acanthopsoides gracilentus*	Acanthopsoides	Cobitidae	Cypriniformes	3	White
63	Agry	*Aaptosyax grypus*	Aaptosyax	Cyprinidae	Cypriniformes	3	White
64	Asid	*Ambastaia sidthimunki*	Ambastaia	Cobitidae	Cypriniformes	3	White
65	Atru	*Amblyrhynchichthys truncatus*	Amblyrhynchichthys	Cyprinidae	Cypriniformes	3	White
66	Bobs	*Bagrichthys obscurus*	Bagrichthys	Bagridae	Siluriformes	3	White
67	Bsp	*Bangana* sp.	Bangana	Cyprinidae	Cypriniformes	3	White
68	Btru	*Belodontichthys truncatus*	Belodontichthys	Siluridae	Siluriformes	3	White
69	Cjul	*Cirrhinus jullieni*	Cirrhinus	Cyprinidae	Cypriniformes	3	White
70	Clon	*Clupisoma longianalis*	Clupisoma	Schilbeidae	Siluriformes	3	White
71	Clop	*Chitala lopis*	Chitala	Notopteridae	Osteoglossiformes	3	White
72	Cmic.1	*Cirrhinus microlepis*	Cirrhinus	Cyprinidae	Cypriniformes	3	White
73	Cmol	*Cirrhinus molitorella*	Cirrhinus	Cyprinidae	Cypriniformes	3	White
74	Dund	*Datnioides undecimradiatus*	Datnioides	Datnioididae	Perciformes	3	White
75	Gpen	*Gyrinocheilus pennocki*	Gyrinocheilus	Gyrinocheilidae	Cypriniformes	3	White
76	Hfil	*Hemibagrus filamentus*	Hemibagrus	Bagridae	Siluriformes	3	White
77	Hlag	*Hypsibarbus lagleri*	Hypsibarbus	Cyprinidae	Cypriniformes	3	White
78	Hmal	*Hypsibarbus malcolmi*	Hypsibarbus	Cyprinidae	Cypriniformes	3	White
79	Hspi	*Hemibagrus spilopterus*	Hemibagrus	Bagridae	Siluriformes	3	White
80	Hsuv	*Hypsibarbus suvattii*	Hypsibarbus	Cyprinidae	Cypriniformes	3	White
81	Hver	*Hypsibarbus vernayi*	Hypsibarbus	Cyprinidae	Cypriniformes	3	White
82	Hwaa	*Helicophagus waandersii*	Helicophagus	Pangasiidae	Siluriformes	3	White
83	Hwet	*Hypsibarbus wetmorei*	Hypsibarbus	Cyprinidae	Cypriniformes	3	White
84	Hwyc	*Hemibagrus wyckii*	Hemibagrus	Bagridae	Siluriformes	3	White
85	Hwyc.1	*Hemibagrus wyckioides*	Hemibagrus	Bagridae	Siluriformes	3	White
86	Kcry	*Kryptopterus cryptopterus*	Kryptopterus	Siluridae	Siluriformes	3	White
87	Lble	*Luciosoma bleekeri*	Luciosoma	Cyprinidae	Cypriniformes	3	White
88	Lchr	*Labeo chrysophekadion*	Labeo	Cyprinidae	Cypriniformes	3	White
89	Mche	*Micronema cheveyi*	Micronema	Siluridae	Siluriformes	3	White
90	Mhex	*Micronema hexapterus*	Micronema	Siluridae	Siluriformes	3	White
91	Omel	*Osteochilus melanopleurus*	Osteochilus	Cyprinidae	Cypriniformes	3	White
92	Papo.1	*Phalacronotus apogon*	Phalacronotus	Siluridae	Siluriformes	3	White
93	Pble	*Phalacronotus bleekeri*	Phalacronotus	Siluridae	Siluriformes	3	White
94	Pbul	*Puntioplites bulu*	Puntioplites	Cyprinidae	Cypriniformes	3	White
95	Pfal	*Puntioplites falcifer*	Puntioplites	Cyprinidae	Cypriniformes	3	White
96	Pmac	*Pangasius macronema*	Pangasius	Pangasiidae	Siluriformes	3	White
97	Pmic	*Phalacronotus micronemus*	Phalacronotus	Siluridae	Siluriformes	3	White
98	Pple	*Pseudolais pleurotaenia*	Pseudolais	Pangasiidae	Siluriformes	3	White
99	Ppro	*Puntioplites proctozysron*	Puntioplites	Cyprinidae	Cypriniformes	3	White

100	Psia.2	*Pseudomystus siamensis*	Pseudomystus	Bagridae	Siluriformes	3	White
101	Pspp	*Pangasius sp.*	Pangasius	Pangasiidae	Siluriformes	3	White
102	Sban	*Scaphognathops bandanensis*	Scaphognathops	Cyprinidae	Cypriniformes	3	White
103	Sbea	*Syncrossus beauforti*	Syncrossus	Cobitidae	Cypriniformes	3	White
104	Shel	*Syncrossus helodes*	Syncrossus	Cobitidae	Cypriniformes	3	White
105	Tthi	*Tenualosa thibaudeaui*	Tenualosa	Clupeidae	Clupeiformes	3	White
106	Watt	*Wallago attu*	Wallago	Siluridae	Siluriformes	3	White
107	Ycau	*Yasuhikotakia caudipunctata*	Yasuhikotakia	Cobitidae	Cypriniformes	3	White
108	Ylec	*Yasuhikotakia lecontei*	Yasuhikotakia	Cobitidae	Cypriniformes	3	White
109	Ymod	*Yasuhikotakia modesta*	Yasuhikotakia	Cobitidae	Cypriniformes	3	White
110	Balt	*Barbonymus altus*	Barbonymus	Cyprinidae	Cypriniformes	4	Grey
111	Bmic	*Boesemania microlepis*	Boesemania	Sciaenidae	Perciformes	4	Grey
112	Brho	*Barbodes rhombeus*	Barbodes	Cyprinidae	Cypriniformes	4	Grey
113	Bsch	*Barbonymus schwanenfeldii*	Barbonymus	Cyprinidae	Cypriniformes	4	Grey
114	Carm	*Cyclocheilichthys armatus*	Cyclocheilichthys	Cyprinidae	Cypriniformes	4	Grey
115	Crep	*Cyclocheilichthys repasson*	Cyclocheilichthys	Cyprinidae	Cypriniformes	4	Grey
116	Lhoe	*Leptobarbus hoevenii*	Leptobarbus	Cyprinidae	Cypriniformes	4	Grey
117	Llau	*Laubuka laubuca*	Laubuka	Cyprinidae	Cypriniformes	4	Grey
118	Malb.1	*Mystus albolineatus*	Mystus	Bagridae	Siluriformes	4	Grey
119	Matr	*Mystus atrifasciatus*	Mystus	Bagridae	Siluriformes	4	Grey
120	Mboc	*Mystus bocourti*	Mystus	Bagridae	Siluriformes	4	Grey
121	Mmac	*Macrochirichthys macrochirus*	Macrochirichthys	Cyprinidae	Cypriniformes	4	Grey
122	Mmul	*Mystus multiradiatus*	Mystus	Bagridae	Siluriformes	4	Grey
123	Mmys	*Mystus mysticetus*	Mystus	Bagridae	Siluriformes	4	Grey
124	Msin	*Mystus singaringan*	Mystus	Bagridae	Siluriformes	4	Grey
125	Obim	*Ompok bimaculatus*	Ompok	Siluridae	Siluriformes	4	Grey
126	Ohyp	*Ompok hypophthalmus*	Ompok	Siluridae	Siluriformes	4	Grey
127	Osch	*Osteochilus schlegeli*	Osteochilus	Cyprinidae	Cypriniformes	4	Grey
128	Papo	*Parambassis apogonoides*	Parambassis	Ambassidae	Perciformes	4	Grey
129	Pcam	*Pao cambodgiensis*	Pao	Tetraodontidae	Tetraodontiformes	4	Grey
130	Pfas	*Pristolepis fasciata*	Pristolepis	Pristolepididae	Perciformes	4	Black
131	Pmac.1	*Parachela maculicauda*	Parachela	Cyprinidae	Cypriniformes	4	Grey
132	Priv	*Paralaubuca riveroi*	Paralaubuca	Cyprinidae	Cypriniformes	4	Grey
133	Psia	*Parachela siamensis*	Parachela	Cyprinidae	Cypriniformes	4	Grey
134	Pwol	*Parambassis wolffii*	Parambassis	Ambassidae	Perciformes	4	Grey
135	Rbor	*Rasbora borapetensis*	Rasbora	Cyprinidae	Cypriniformes	4	Grey
136	Rdan	*Rasbora daniconius*	Rasbora	Cyprinidae	Cypriniformes	4	Grey
137	Rspi	*Rasbosoma spilocerca*	Rasbosoma	Cyprinidae	Cypriniformes	4	Grey
138	Rtor	*Rasbora tornieri*	Rasbora	Cyprinidae	Cypriniformes	4	Grey
139	Rtri	*Rasbora trilineata*	Rasbora	Cyprinidae	Cypriniformes	4	Grey
140	Tthy	*Thynnichthys thynnoides*	Thynnichthys	Cyprinidae	Cypriniformes	4	Grey
141	Aleu	*Achiroides leucorhynchos*	Achiroides	Soleidae	Pleuronectiformes	5	White
142	Bgon	*Barbonymus gonionotus*	Barbonymus	Cyprinidae	Cypriniformes	5	White
143	Catr	*Crossocheilus atrilimes*	Crossocheilus	Cyprinidae	Cypriniformes	5	White
144	Corn	*Chitala ornata*	Chitala	Notopteridae	Osteoglossiformes	5	White
145	Cret	*Crossocheilus reticulatus*	Crossocheilus	Cyprinidae	Cypriniformes	5	White
146	Hdis	*Hampala dispar*	Hampala	Cyprinidae	Cypriniformes	5	White
147	Hlob	*Henicorhynchus lobatus*	Henicorhynchus	Cyprinidae	Cypriniformes	5	White
148	Hmac	*Hampala macrolepidota*	Hampala	Cyprinidae	Cypriniformes	5	White
149	Hsia	*Henicorhynchus siamensis*	Henicorhynchus	Cyprinidae	Cypriniformes	5	White
150	Llep	*Labiobarbus leptocheilus*	Labiobarbus	Cyprinidae	Cypriniformes	5	White
151	Llin	*Labiobarbus lineatus*	Labiobarbus	Cyprinidae	Cypriniformes	5	White
152	Lsia	*Labiobarbus siamensis*	Labiobarbus	Cyprinidae	Cypriniformes	5	White
153	Marm	*Mastacembelus armatus*	Mastacembelus	Mastacembelidae	Synbranchiformes	5	Estuarine
154	Mery	*Mastacembelus erythrotaenia*	Mastacembelus	Mastacembelidae	Synbranchiformes	5	White
155	Nnot	*Notopterus notopterus*	Notopterus	Notopteridae	Osteoglossiformes	5	Grey
156	Olin	*Osteochilus lini*	Osteochilus	Cyprinidae	Cypriniformes	5	White
157	Omar	*Oxyeleotris marmorata*	Oxyeleotris	Eleotridae	Perciformes	5	White
158	Omic	*Osteochilus microcephalus*	Osteochilus	Cyprinidae	Cypriniformes	5	White

159	Ovit	*Osteochilus vittatus*	Osteochilus	Cyprinidae	Cypriniformes	5	White
160	Psia.1	*Parambassis siamensis*	Parambassis	Ambassidae	Perciformes	5	Grey
161	Srub	*Systomus rubripinnis*	Systomus	Cyprinidae	Cypriniformes	5	White
162	Xcan	*Xenentodon cancila*	Xenentodon	Belonidae	Beloniformes	5	White
163	Asp	*Acanthocobitis* sp.	Acanthocobitis	Nemacheilidae	Cypriniformes	6	Black
164	Aspp	*Acanthopsis spp.*	Acanthopsis	Cobitidae	Cypriniformes	6	Black
165	Ates	*Anabas testudineus*	Anabas	Anabantidae	Perciformes	6	Black
166	Cbat	*Clarias batrachus*	Clarias	Clariidae	Siluriformes	6	Black
167	Cluc	*Channa lucius*	Channa	Channidae	Perciformes	6	Black
168	Cmac	*Clarias macrocephalus*	Clarias	Clariidae	Siluriformes	6	Black
169	Cmar	*Channa marulioides*	Channa	Channidae	Perciformes	6	Black
170	Cmel	*Clarias meladerma*	Clarias	Clariidae	Siluriformes	6	Black
171	Cmic	*Channa micropeltes*	Channa	Channidae	Perciformes	6	Black
172	Cnie	*Clarias nieuhofii*	Clarias	Clariidae	Siluriformes	6	Black
173	Csp	*Clarias* sp.	Clarias	Clariidae	Siluriformes	6	Black
174	Cstr	*Channa striata*	Channa	Channidae	Perciformes	6	Black
175	Emet	*Esomus metallicus*	Esomus	Cyprinidae	Cypriniformes	6	Black
176	Malb	*Monopterus albus*	Monopterus	Synbranchidae	Synbranchiformes	6	Black
177	Mcir	*Macrognathus circumcinctus*	Macrognathus	Mastacembelidae	Synbranchiformes	6	Black
178	Msia	*Macrognathus siamensis*	Macrognathus	Mastacembelidae	Synbranchiformes	6	Black
179	Pbre	*Puntius brevis*	Puntius	Cyprinidae	Cypriniformes	6	Black
180	Pcoc	*Pao cochinchinensis*	Pao	Tetraodontidae	Tetraodontiformes	6	Grey
181	Tmic.1	*Trichopodus microlepis*	Trichopodus	Osphronemidae	Perciformes	6	Black
182	Tpec	*Trichopodus pectoralis*	Trichopodus	Osphronemidae	Perciformes	6	Black
183	Ttri	*Trichopodus trichopterus*	Trichopodus	Osphronemidae	Perciformes	6	Black
184	Ajan	*Aulopareia janetae*	Aulopareia	Gobiidae	Perciformes	7	Estuarine
185	Amac	*Arius maculatus*	Arius	Ariidae	Siluriformes	7	Estuarine
186	Aven	*Arius venosus*	Arius	Ariidae	Siluriformes	7	Estuarine
187	Bamb	*Butis amboinensis*	Butis	Eleotridae	Perciformes	7	Estuarine
188	Bpan	*Brachirus panoides*	Brachirus	Soleidae	Pleuronectiformes	7	Estuarine
189	Clin	*Coilia lindmani*	Coilia	Engraulidae	Clupeiformes	7	Estuarine
190	Dpol	*Datnioides polota*	Datnioides	Datnioididae	Perciformes	7	White
191	Gaur	*Glossogobius aureus*	Glossogobius	Gobiidae	Perciformes	7	Estuarine
192	Ggiu	*Glossogobius giuris*	Glossogobius	Gobiidae	Perciformes	7	Estuarine
193	Hsto	*Hemiarius stormii*	Hemiarius	Ariidae	Siluriformes	7	White
194	Lcro	*Lycothrissa crocodilus*	Lycothrissa	Engraulidae	Clupeiformes	7	Estuarine
195	Nnen	*Nemapteryx nenga*	Nemapteryx	Ariidae	Siluriformes	7	White
196	Omil	*Osteogeneiosus militaris*	Osteogeneiosus	Ariidae	Siluriformes	7	Estuarine
197	Pdub	*Polynemus dubius*	Polynemus	Polynemidae	Perciformes	7	Estuarine
198	Plei	*Pao leiurus*	Pao	Tetraodontidae	Tetraodontiformes	7	Estuarine
199	Pmel	*Polynemus melanochir*	Polynemus	Polynemidae	Perciformes	7	Estuarine
200	Pmul	*Polynemus multifilis*	Polynemus	Polynemidae	Perciformes	7	Estuarine
201	Psep	*Periophthalmodon septemradiatus*	Periophthalmodon	Gobiidae	Perciformes	7	Black
202	Tmic	*Toxotes microlepis*	Toxotes	Toxotidae	Perciformes	7	Estuarine
203	Pkre	*Pangasius krempfi*	Pangasius	Pangasiidae	Siluriformes	8	White
204	Amar	*Anguilla marmorata*	Anguilla	Anguillidae	Anguilliformes	9	White

REFERENCES (for Supplementary Information)

Froese, R., & D. Pauly, 2017. FishBase. World Wide Web electronic publication. , www.fishbase.org.

Kottelat, M., 2013. The Fishes of the inland waters of Southeast Asia: A catalogue and core bibliography of the fishes known to occur in freshwaters, mangroves and estuaries. The Raffles Bulletin of Zoology 27: 1–663.

MFD, 2003. Mekong Fish Database: A taxonomic fish database for the Mekong Basin. Mekong River Commission, Phnom Penh.

Rainboth, W. J., 1996. FAO species identification field guide for fishery purposes. Fishes of the Cambodian Mekong. FAO, Rome.

Rainboth, W. J., C. Vidthayanon, & D. Y. Mai, 2012. Fishes of the Greater Mekong Ecosystem with Species List and Photoraphic Atlas. Museum of Zoology, University of Michigan, Ann Arbor.

ARTICLE 3

Evidence of indiscriminate fishing effects in one of the world's largest inland fisheries

Peng Bun Ngor, Kevin McCann, Gaël Grenouillet, Nam So, Bailey McMeans,

Evan Fraser, Sovan Lek

Scientific Reports (in revision)

Title: Evidence of indiscriminate fishing effects in one of the world's largest inland fisheries

Authors: Peng Bun Ngor[1,2¥], Kevin McCann[3], Gaël Grenouillet[2], Nam So[4], Bailey McMeans[5], Evan Fraser[3], Sovan Lek[2]

[1] Fisheries Administration, No. 186, Preah Norodom Blvd., Khan Chamcar Morn, Phnom Penh, Cambodia

[2] CNRS, Université Toulouse III Paul Sabatier, ENFA; UMR5174 EDB (Laboratoire Évolution & Diversité Biologique); 118 route de Narbonne, F-31062 Toulouse, France

[3] University of Guelph, Guelph Ontario, Canada

[4] Mekong River Commission

[5] University of Toronto Mississauga, Mississauga, Ontario, Canada

[¥] Current address: CNRS, Université Toulouse III Paul Sabatier, ENFA; UMR5174 EDB (Laboratoire Évolution & Diversité Biologique); 118 route de Narbonne, F-31062 Toulouse, France.

Corresponding author: pengbun.ngor@gmail.com

Abstract

While human impacts like fishing have altered marine food web composition and body size, the status of the world's important tropical inland fisheries remains largely unknown. Here, we look for signatures of human impacts on the indiscriminately fished Tonle Sap fish community that supports one of the world's largest freshwater fisheries. By analyzing a 15-year time-series (2000-2015) of fish catches for 116 species obtained from an industrial-scale '*Dai'* fishery, we find: (i) 78% of the species exhibited decreasing catches through time; (ii) downward trends in catches occurred primarily in medium to large-bodied species that tend to occupy high trophic levels; (iii) a relatively stable or increasing trend in catches of small-sized species, and; (iv) a decrease in the individual fish weights and lengths for several common species. Because total biomass of the catch has remained remarkably resilient over the last 15 years, the increase in catch of smaller species has compensated for declines in larger species. Our finding of sustained production but altered community composition is consistent with predictions from recent indiscriminate theory, and gives a warning signal to fisheries managers and conservationists that the species-rich Tonle Sap is being affected by heavy indiscriminate fishing pressure.

Keywords: freshwater fisheries, inland waters, declining catches, indiscriminate fisheries, Tonle Sap, Mekong Basin.

Introduction

Globally, inland waters extend over an area of about 7.8 million km^2 and are among the most biologically productive and diverse ecosystems on earth [1–3]. Inland capture fisheries are important sources of food security, livelihoods, and recreation for tens of millions of people worldwide [4,5]. Overall, inland fisheries employ approximately 61 million people [6] and represent 11.3% of the world total capture fish production [7]. These fisheries, however, are facing numerous challenges from human activities, namely, population growth, habitat degradation, hydrological changes, pollution, invasive species and climate change [1,8–11].

Worries over the fate of inland waters [12], along with the concern that higher trophic levels of marine food webs are being unsustainably exploited, have grown during the last decade. In particular, fisheries ecologists have recently argued that increased indiscriminate fishing pressure is reducing large-sized, slower-growing species with late maturity, and replacing them with smaller-sized, faster-growing species that mature earlier [13–16]. This leads to an overall reduction in the body size and, consequently, a reduction in the overall trophic level of the fish assemblage remaining in an ecosystem. Ultimately, these changes are expected to be reflected in catch composition [12,17–20]. Shifts through time in the slope of the catch-size spectra and decreases in the size of individual fish are also among the key structural and functional 'signatures' of indiscriminate fishing on the fish community [21]. Currently, however, much of the fisheries impact research has focused on marine systems and very little is known about freshwater fisheries in the sub-tropical and tropical environments such as the Mekong River Basin [22]. What limited evidence exists from inland tropical fisheries suggests declining catches, particularly in Asia and Africa where fish protein is of paramount importance in terms of food security. Hence, there are increasing calls in the literature that inland tropical fisheries should receive more research attention [1,4,5,8].

This paper contributes to the literature on inland tropical fisheries, demonstrating that larger higher trophic level fish are being depleted in one of the world's largest freshwater fisheries, while smaller, lower trophic levels organisms are increasing in a manner that sustains overall fish catches. Towards this, we study temporal dynamics of 116 fish species in the Tonle Sap over 15 years. The dataset was obtained from a standardized biological catch assessment of an industrial-scale '*Dai* fishery' that operates during the dry season in the Tonle Sap River. We explore how temporal trends of fish catch captured by this fishery relate to each species' maximum body size and trophic level. We also examine changes in the body weight and length of individual fish for select species over the assessment period.

Results

Summary of the fishery catch

Over the 15-year assessment period, 141 fish species belonging to 12 orders, 36 families and 93 genera were recorded. The four main orders, representing 90% of the total species counts were: Cypriniformes (59 species), Siluriformes (36), Perciformes (23) and Clupeiformes (7). The rest contained one to three species in each order. Five families forming 95% of the total catch were Cyprinidae (84%), Pangasiidae (4%), Cobitidae (4%), Siluridae (3%) and Cynoglossidae (1%). Three genera forming 66% of the total catch were Henicorhynchus (42%), Paralaubuca (12%), Labiobarbus (12%). Henicorhynchus contained three species namely *Henicorhynchus lobatus* (17%), *Henicorhynchus* sp. (15%) (synonym of *Lobocheilos cryptopogon* and *H. cryptopogon)* and *H. siamensis* (10%); whereas, Paralaubuca encompassed only one species *Paralaubuca barroni* (synonym of *P. typus*), and finally, Labiobarbus consisted of two species: *L. lineatus* (10%) and *L. siamensis* (2%). By size category, 75% of catch was from species with maximum total length (maxTL)<=30 cm, 9% with maxTL 31-60 cm, 9% with maxTL 61-90 cm and 6% with maxTL>90 cm. By trophic level, 70% of catch was from species with trophic level<=2.75, 27% with trophic level=2.76–3.75 and 3% with trophic level>3.75. Ecologically, 82% of catch was longitudinal (riverine) migratory species, 17% was lateral-migration species, and about 1% is from a combination of estuarine, marine and floodplain resident species. For relative catch weight of 116 species captured by the *Dai* fishery, see Supplemental Information Fig. S4. We also found an overall declining trend in species diversity (evenness index) (see Fig. S5), signifying that fish community was highly unevenly distributed particularly between 2008 and 2015.

Temporal change in fish catch and relationship with maximum length and trophic level

The distribution of the standardized regression coefficients for all 116 species, which reflected the nature of the relationship between seasonal fish catch and time for each species, was skewed to the right, centered around -0.4, and spread between -0.78 and 0.66 (Fig. 1). Out of the 116-total species, 90 (78%) had negative standardized regression coefficients. These results indicate that the seasonal catches of these species harvested by the *Dai* fishery declined over the 15 years studied. On the contrary, there were also species (26 out of 116 or 22%) with positive standardized regression coefficients, indicating an increase in the catch of these species by the *Dai* fishery. Interestingly, *Oreochromis mossambicus* is an exotic species that was among the largest positive coefficients observed. In addition, *Labiobarbus lineatus*, *Henicorhynchus lobatus* and *H. cryptopogon* (synonym of *Lobocheilos cryptopogon*) are all known to be highly prolific and form the largest proportion of the catch from the fishery. These species also had positive standardized coefficients (see Table S6 for standardized regression coefficients, maxTL and trophic level for each species). In fact, the increase in these species stabilized the seasonal

Dai catches as it was evidenced in the total catch of the fishery which was stationary over the study period (p-value=0.982, Fig. S8).

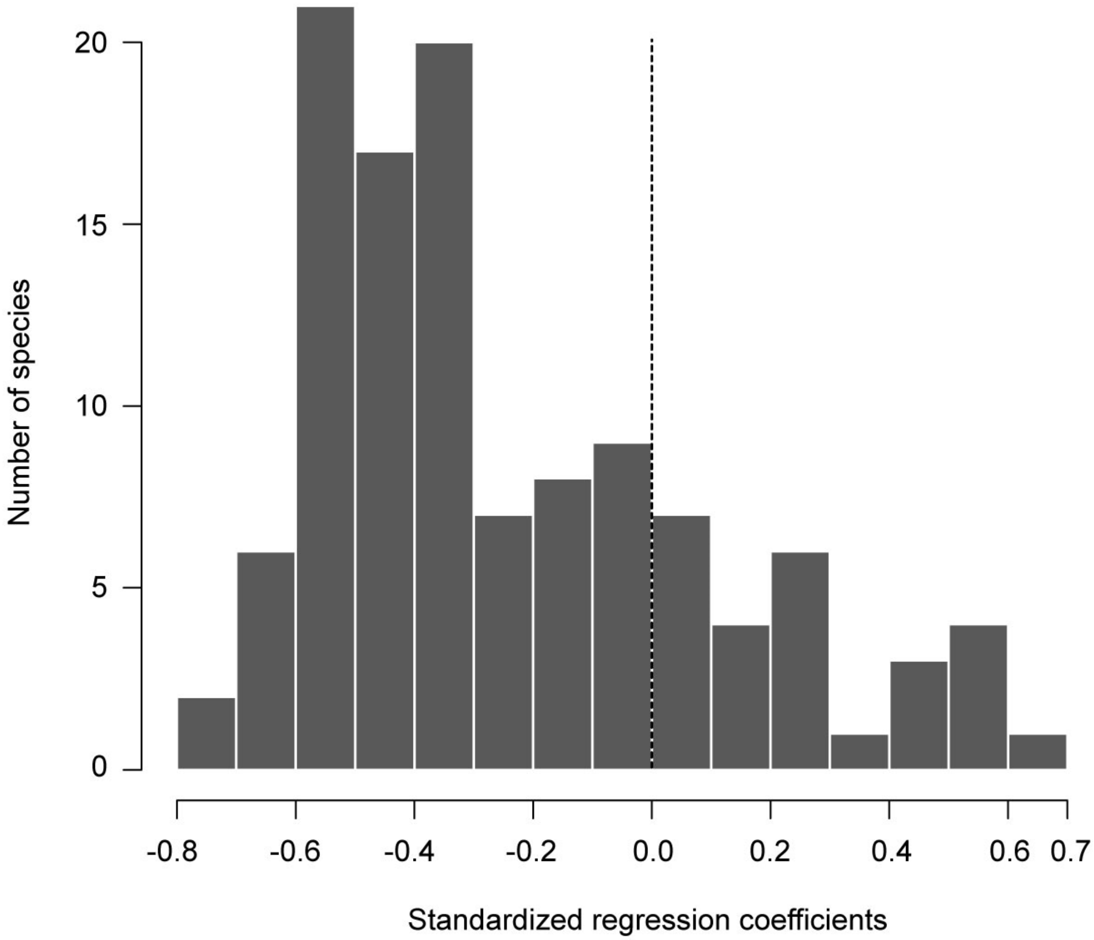


Fig. 1. Distribution of standardized regression coefficients of seasonal catches of 116 fish species recorded at the Dai fishery, Tonle Sap River from the fishing season of 2000/01 to 2014/15.

Species with declining catch in the *Dai* fishery were disproportionately represented by those with larger body sizes and higher trophic levels based on linear regressions (Fig. 2a, b), which demonstrated overall negative relationships between the log+1 transformed standardized regression coefficients and the corresponding log-transformed maxTL (slope=-0.08, p-value=0.08, r^2=0.03), and trophic level (slope=-0.15, p-value=0.024, r^2=0.04). In the regression model, five endangered and critically endangered species (solid points on Fig. 2a, b) were included. However, it was also likely that these species were very rare and, as such, their catches obtained in the catch assessment could be misleading. Therefore, when they were dropped from the analysis, the significant relationships were indicated with both maxTL (slope=-0.13, p-value=0.006, r^2=0.06) and trophic level (slope=-0.16, p-value=0.02, r^2=0.05).

When grouped by positive and negative standardized regression coefficient values (for all 116 species), maxTL was significantly greater for the species with negative standardized regression coefficients than the positive ones (Fig. 2c; Mann-Whitney rank sum test, p-value=0.02). Negative values of standardized coefficients were noted for species with maximum length corresponding to >45 cm (3rd quartile), whereas positive standardized regression coefficients were noted for species with maxTL <25 cm (2nd quartile). Species with both negative and positive coefficient values fell within maxTL of ~25 cm and ~45 cm. Trophic level did not significantly differ between negative and positive standardized regression coefficients (Fig. 2d; Mann-Whitney rank sum test, p-value=0.08). Nevertheless, species with negative standardized coefficients had higher trophic levels >3.3 (3rd quartile), and species with positive standardized regression coefficients had lower trophic levels (<2.75). Species with both negative and positive coefficient values fell within trophic levels of ~2.75 and ~3.3. Furthermore, weighted mean maxTL and trophic level of seasonal total catch (Fig. 3a, b) oscillated with a mean range of ~25-55 cm and ~2.4-2.8, respectively, and significantly declined across the 15-year period (mean maxTL: slope=-1.26, p-value=0.007, r^2=0.44; mean trophic level: slope=-0.013, p-value =0.025, r^2=0.33). Although some small-bodied species including *Parachela siamensis* (maxTL: 18.3 cm; trophic level: 3.4), *Parambassis wolffii* (maxTL: 24.4 cm, trophic level: 3.72) and *Acantopsis* sp. cf. *dialuzona* (maxTL: 30.5, trophic level: 3.5) also exhibited significant declines in seasonal catches (standardized coefficients<-0.66), our combined findings indicate that smaller, lower trophic position species increased and compensated for declines in larger bodied, higher trophic position species in the Tonle Sap fishery over the study period.

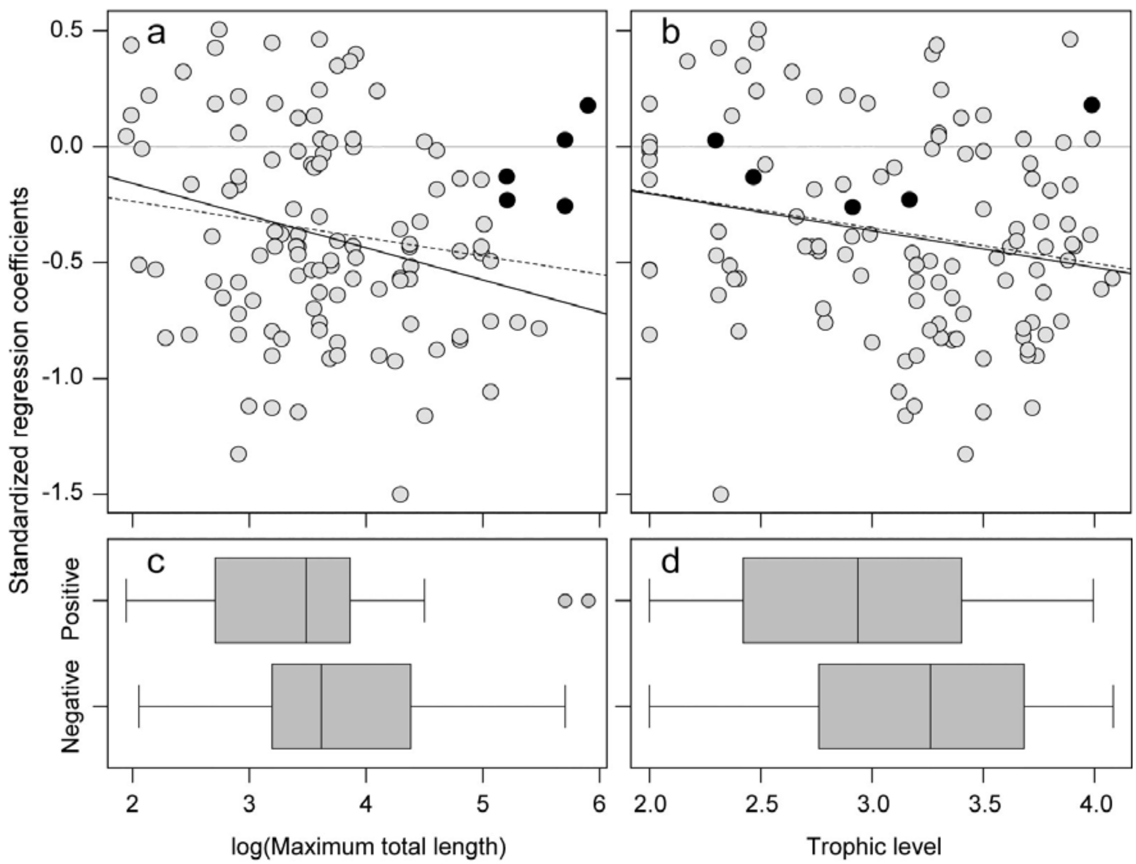


Fig. 2. Relationship between (log+1 transformed) standardized regression coefficients of species composition derived from seasonal catches of 116 fish species recorded at the *Dai* fishery in the Tonle Sap River from the fishing season of 2000/01 to 2014/15, and (a) their corresponding log-transformed maximum total lengths (maxTL in cm) and (b) trophic levels. Solid points represent endangered (en) and critically endangered (ce) species. Dashed lines show linear regression lines to predict the relationships when all species are considered, and solid lines are linear regression lines when en and ce are excluded from (a) and (b). Model summary (a) when all species are included: slope=-0.08, p-value=0.08, r^2=0.03; and when en and ce are excluded: slope=-0.13, p-value=0.006, r^2=0.06. Model summary (b) when all species are included: slope=-0.15, p-value=0.02, r^2=0.04; and when en and ce are excluded: slope=-0.16, p-value=0.02, r^2=0.05. Boxplots show (c) distribution of maxTL and (d) trophic level for the positive and negative standardized regression coefficient values of all 116 species. For Fig. 2c, Mann-Whitney rank sum test, p-value=0.02. For Fig. 2d, Mann-Whitney rank sum test, p-value=0.08.

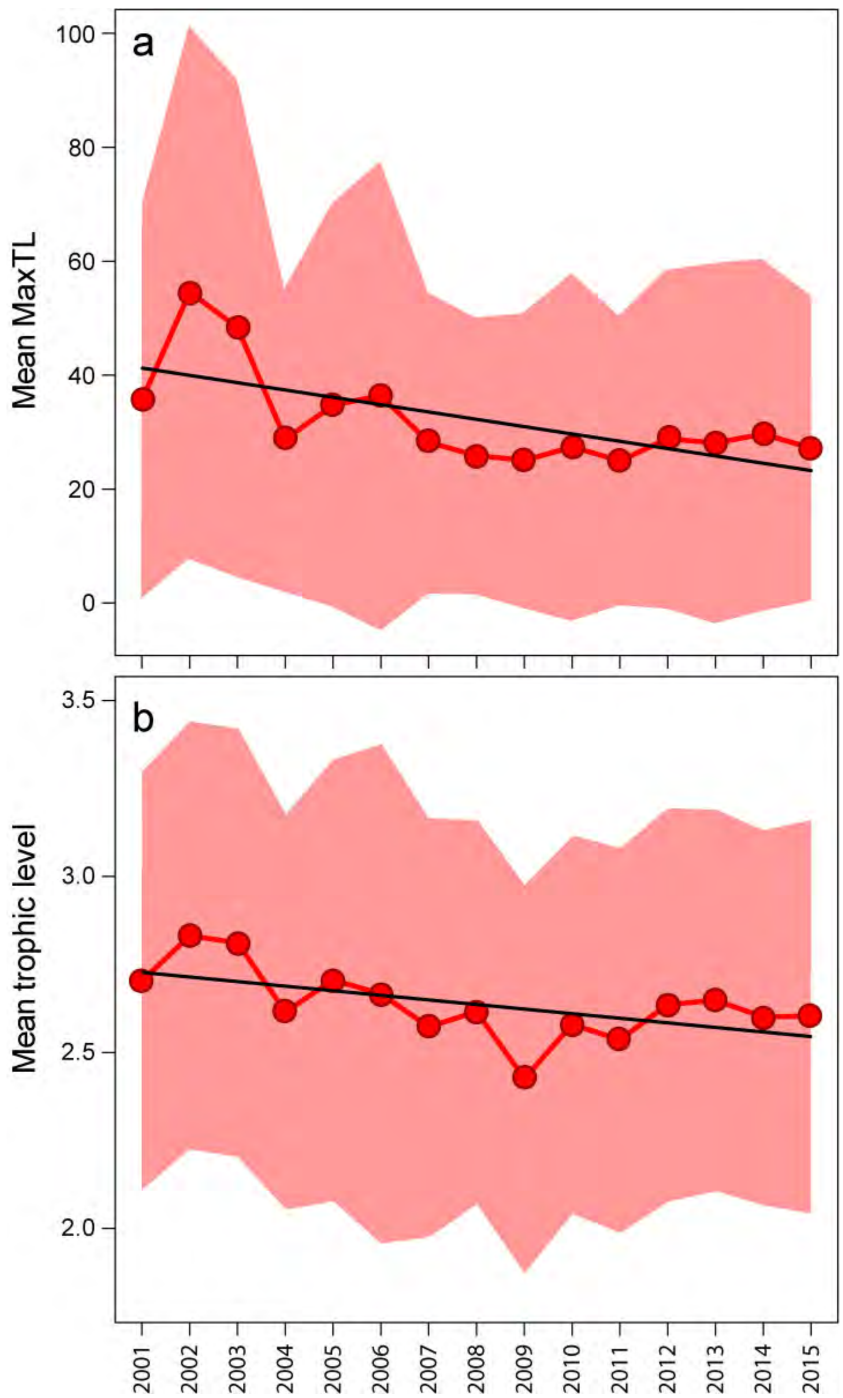


Fig. 3. Community weighted mean: (a) maximum total length (maxTL) and (b) trophic level in seasonal catches of the *Dai* fishery from the fishing season of 2000/01 to 2014/15. For Model summary (a), intercept=42.53, slope=-1.29, predictor p-value=0.007, r^2=0.44. For Model summary (b), intercept=2.74, slope=-0.013, predictor p-value=0.025, r^2=0.33. Pink shaded area denotes standard deviation around the mean values. 2001 represents the fishing season of 2000/2001 and the same for other years.

Temporal change in weight and length of individual fish

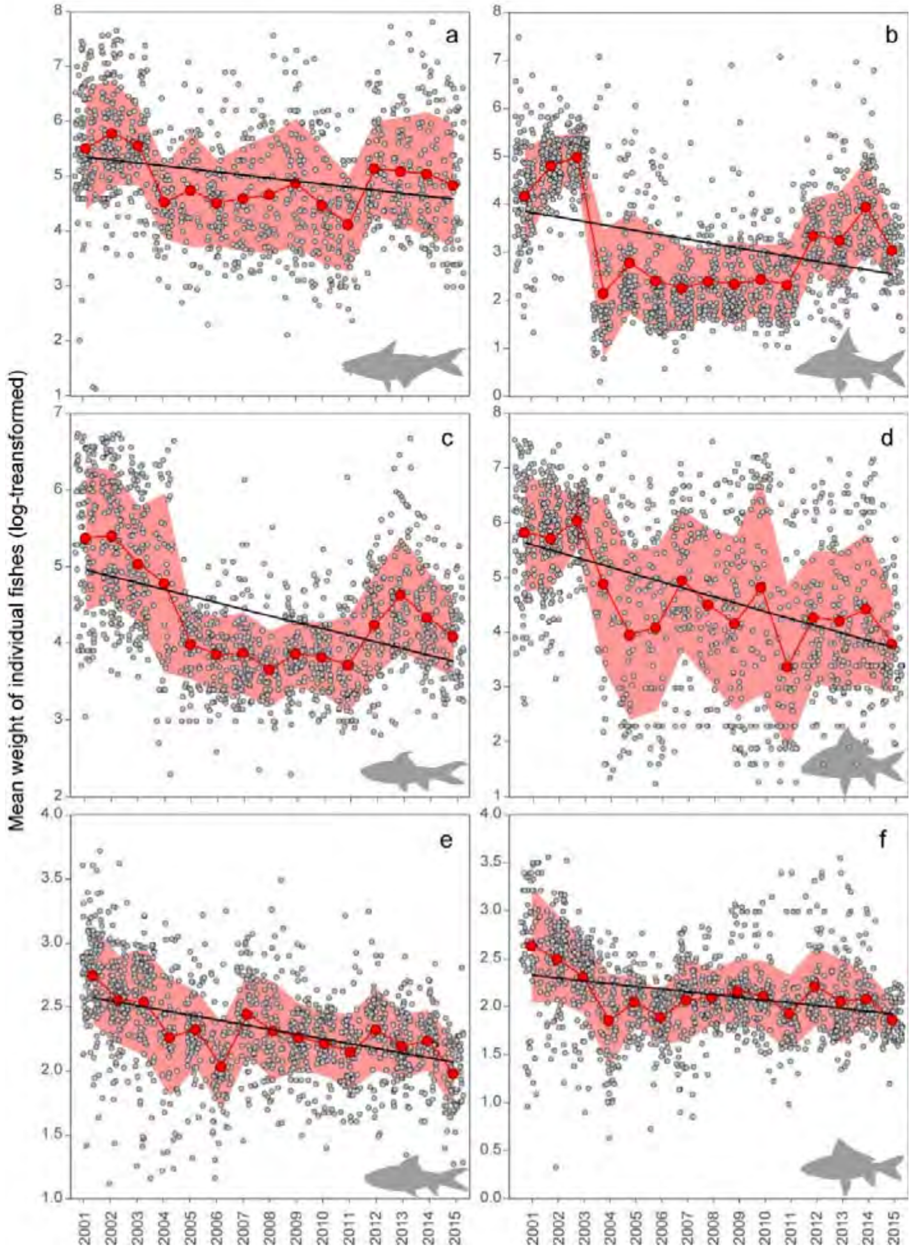


Fig. 4. Linear regressions demonstrate temporal change in log-transformed mean individual weight (g) by season of six common species, composing of large (a: *Pangasianodon hypophthalmus;* b: *Cyclocheilichthys enoplos)*, medium (c: *Cirrhinus microlepis;* d: *Osteochilus melanopleurus*) and small-sized species (e: *Henicorhynchus lobatus*; f: *Labiobarbus lineatus*) that possessed either negative (a-d) or positive (e, f) catch changes (expressed as standardized regression coefficients, Table S6) from the fishing season of 2000/01 to 2014/15. See Table S7 for parameter estimates. All slopes were significant (p-value<0.0001). Solid red dots indicate mean body weight and the pink shaded area denotes standard deviation for each survey season across the study period. 2001 represents the fishing season of 2000/2001 and the same for other years.

The log-transformed mean fish body weight captured per day in the *Dai* fishery significantly decreased over the study period for all 6-species explored (p-value<0.0001; Fig. 4; parameter estimates provided in Table S7). These species span a range in body size (large, medium and small) and regression coefficients indicated that individual fish weight consistently declined through time for all 6 species regardless of body size (Fig. 4a-f).

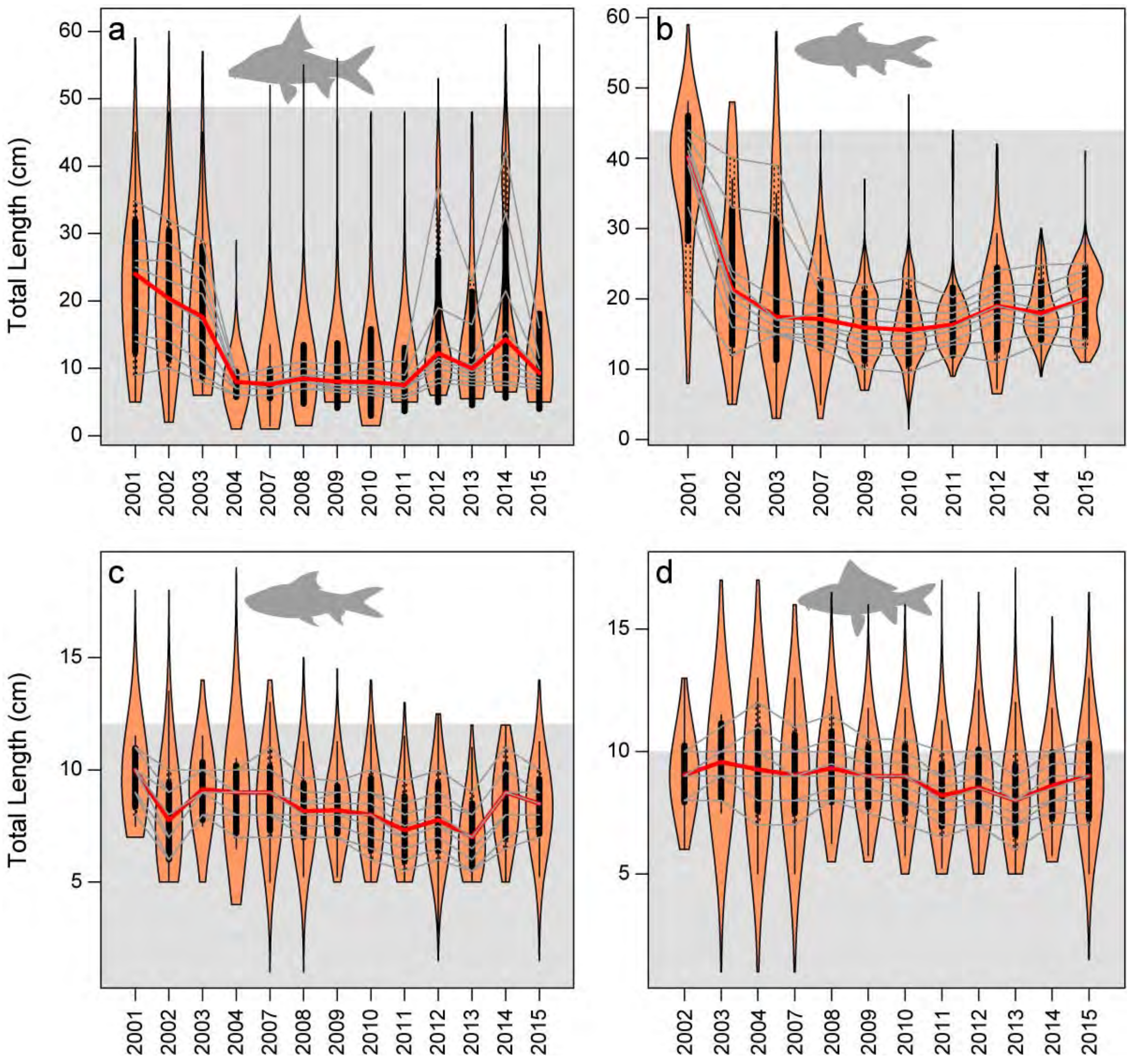


Fig. 5. Violin plots show temporal shift in length distribution of four species (a: *Cyclocheilichthys enoplos,* b: *Cirrhinus microlepis;* c: *Henicorhynchus lobatus;* d: *Labiobarbus lineatus*) from the fishing season of 2000/01 to 2014/15. Red solid line symbolizes median body size in each fishing season and grey thin lines indicate decile, dividing ten equal groups of a population. Area above the gray shaded area denotes estimated total length at maturity for each species. 2001 represents the fishing season of 2000/2001 and the same for other years.

Violin plots further elucidated the temporal changes of the total length for four common species (Fig. 5). For the large- and medium-sized species *Cyclocheilichthys enoplos* (maxTL: 90.3 cm) and

Cirrhinus microlepis (maxTL: 79.3 cm), both of which were mainly captured at juvenile sizes with the average total length<20 cm and 25 cm, respectively; body lengths have declined since the early 2000s when some comparatively large individuals (>30 cm) were present in the *Dai* fishery's catches (Fig. 5a, b). Noticeably, the medians for these large and medium-sized species were significantly lower than 49 and 44 cm (Fig. 5a, b), the estimated lengths at maturity for *C. enoplos* and *C. microlepis*, respectively. For the smaller species (maxTL<20 cm), *H. lobatus* and *L. lineatus,* which are common and highly productive, total length in the *Dai* catches had a median of ~9 cm, with some individuals possessing lengths greater than lengths at maturity which are ~12 cm for *H. lobatus* and ~10 cm for *L. lineatus* (Fig. 5c, d). Both species also exhibited gradual decrease in the median total length, but less pronounced than those of large-sized species.

Discussion

Trends in the seasonal catches of harvested species revealed that 78% of the 116-species are in decline. While we do not have fishery independent data to confirm the large *Dai* dataset, our results are consistent with the prediction of an intensively exploited indiscriminate fishery. Consistent with indiscriminate fishing theory, a closer examination of the data indicated that the catch declines are disproportionally represented by the larger, slower growing, higher trophic level organisms of the Tonle Sap. By contrast, the 22% of species caught by the *Dai* fishery that have tended to show increases are disproportionally represented by small-bodied, faster growing lower trophic level organisms. In addition, significant declines of the mean fish size and trophic level were evidenced in the seasonal catches of the fishery over the study period (Fig. 3a, b). Finally, the data consistently showed for common species spanning a range in adult body sizes that individual weights and lengths of all these species, even in many of the small-bodied species, have been significantly reduced over the last 15 years, a result that resonates with much research that has found that heavy fishing pressure is known to drive shifts in life history towards smaller sizes and earlier ages at maturation [23]. Our results also pointed out for select species that the number of immature fish captured has increased throughout the study period. Moreover, a significant decreasing trend in species evenness was observed over the study period (Fig. S5). Thus, although this fishery has been amazingly resilient to changes in total fish harvest levels, these results collectively are in agreement with predicted effects of indiscriminate fishing theory. Because this theory ultimately predicts declines in fish catches and diversity with sustained, heavy indiscriminate fishing pressure[13–15,24], our findings may be seen as an 'early warning signal' of looming negative impacts of indiscriminate fishing in the Tonle Sap.

Intriguingly, recent work has argued that such indiscriminately fished systems may generally occur in tropical systems where fish is the major source of animal protein [25]. Consistent with this conjecture, recent empirical fisheries data in the East China Sea[15], where fish is also a major source of protein, has argued that this fishery is relatively indiscriminate and has also showed a compensatory positive growth response by small fish to heavy fishing. Further, and consistent with our results, they argued that this compensatory response helped maintain fishery production[21]. This compensatory response is expected in indiscriminate fisheries as fishing effectively replaces slow growing larger, often higher trophic level fish, with faster growing smaller fish that tend to be from lower trophic levels [13–16]. This reduction of upper trophic level fish drives a cascading effect whereby released predation pressure allows lower trophic level species to flourish [15]. As shown in Fig. S8, CPUE (catch per *Dai* unit per day) in this large fishery fluctuated with no significant trend over the study period suggesting that the smaller fish growth rates are indeed compensating for reduction in upper trophic level catches. Given the reduction in mean body size and trophic level over time (Fig. 3a, b) as well as the average positive growth rates of small species (Fig. 1) our results suggest that small faster growing species are compensating for the heavy fishing pressure.

Our findings of declining catches of medium and large-sized species as well as falling mean body size of fish catches support general perceptions by fishers throughout the Lower Mekong Basin [26–28]. Our results, therefore, are consistent with existing knowledge that some giant- and large-sized fish populations in the Mekong region have declined since the 1900s. For example, the Mekong giant catfish (*Pangasianodon gigas*) (maxTL: 300 cm, max. weight: 350 kg), which was common and abundant in the 1900s, has almost disappeared from the Mekong River System [27,29]. Tonle Sap River is one of the last few places where a small number of individuals of this species are still occasionally captured [29]. In particular, the standardized regression coefficient for this species was almost zero (0.03), indicating little change in its contribution to the *Dai* catch since 2000. This perhaps reflects either effectiveness of conservation measures or that its population status is close to extinction. Likewise, the Mekong giant carp (*Catlocarpio siamensis)* (maxTL: 300 cm, max. weight: 300 kg) was seen regularly in the catch of 1938-39 and 1962-63 [30,31]. Nowadays, however, the Mekong giant carp has become critically endangered. Similarly, the Mekong shad (*Tenualosa thibaudeaui*) (maxTL: 60 cm) was still relatively abundant in the *Dai* catch in 1938-39 and 1962-63 and used to be one of the most important species. Nonetheless, it too has been experiencing drastic decline during the last two decades [32]. The list of large-bodied species in decline goes on. Jullien's golden carp *(Probarbus jullieni)* (maxTL: 183 cm, max. weight: 70 kg) was noticed as 'comparatively scarce' for at least 65 years in Thailand [33], and together with Thicklipped barb *(Probarbus labeamajor)* were later observed to be very abundant in 1970s in the Southern Laos and northern Cambodia (when the region was at war). Both have declined, particularly since 1990s when the region's border trade was re-opened up [22,34] and now these two species are considered to be endangered by the IUCN Red List. Similarly, other formerly-common and high value species, including *Cirrhinus microlepis* (maxTL: 79.3 cm), have been assessed as a vulnerable species in the IUCN Red List. Based on our analysis, these giant- and large-sized species have all declined during 2000-2015.

The decline in the giant and larger-bodied species is likely associated with their slower growth and late age at maturation. For instance, both *P. gigas* and C. *siamensis* do not reach maturity until ~7 years of age [35]. These larger species often require large geographical ranges to complete their lifecycle and undertake long migrations between critical habitats [32,36], making them more susceptible to capture before their first reproductive event. Given the increasing fishing pressure in the region, overfishing seems a likely cause of the decline observed in giant, large and medium sized fish in the Tonle Sap, which is consistent with previously observed declines in long-lived, late spawning freshwater fish stocks such as the Murray River cod in Australia and ~21 sturgeon stocks across Asia, Europe and America and Pirarucu (*Arapaima gigas*) in Amazon [37].

In contrast to large-bodied fish, the catch of some small-sized species such as *Labiobarbus* spp. (synonym of *Dangila* spp.) increased significantly over the study period. For instance, members of this genus accounted for ~5% of the *Dai* fishery catches between 1995 and 2000 [27] but increased to 19% in 2013/14[38]. Additionally, *Henicorhynchus* spp., which are ecologically important in the LMB [34,39], made up 25.4% of the total *Dai* catch weight in 1962-63 [31] but increased to 40% between 1995 and 2000 [27] and increased again to 43% in 2013/14 [38]. Comparable increasing trends are also manifested for other small-sized cyprinids that are likely more robust to fishing pressure and also reproduce quickly on the vast area of seasonal flooded land every year [13,15,26,32]once predatory pressures of higher trophic level fish [27,32,40] are reduced.

While our results from the Tonle Sap revealed that overall declining catches were associated with large-bodied species, some small-sized species were also declining. These species feed in higher trophic levels (3.4-3.7) than some giant- and large-sized species such as the Mekong giant catfish (2.3) and Mekong giant carp (2.92) which are detritus and algae feeders. It is also likely that threat status of freshwater fishes was not as clear-cut as that of the marine fishes as evidenced in a study of extinction risk of European freshwater fishes where small-bodied species were most at-risk due to their small geographical ranges[41]. Likewise, when comparing fish body-size distribution under different global extinction risk levels, threats were found to disproportionately occur to both large- and small-sized species[42]. It is likely that further research on individual life history traits may help shed light on reasons of the decline, which is warranted because overfishing is not be the only threat to the Tonle Sap's fishes.

Moreover, both increased efficiency of fishing gears and increased human population size have likely contributed to declining large-sized species in the Tonle Sap. In Cambodia, the use of monofilament nylon gillnets was to blame for the decline of *C. microlepis*, *B. microlepis*, *Probarbus* spp., *T. thibaudeaui, P. hypophthalmus, Wallago leeri* (maxTL: 150 cm) and Irrawaddy dolphins [22,40,43] and were considered as a 'wall-of-death' for many migrating fishes [28]. The problems caused by these fishing techniques have likely been exacerbated by population growth and the population of countries sharing the Lower Mekong Basin has increased about threefold between 1960 and 2015. Similarly, the Cambodia population has also grown almost threefold with ~85% rural dwellers [44]. Since entry into fishing is free, and fishing gears are very affordable, [28,43] a combination of forces including rising population along with the lack of other livelihood options, has resulted in millions of people moving into the fishing sector thereby increasing fishing effort and pressure on fish stocks.

Further, hydropower development in the region also poses an increasingly large additional threat to the Mekong fisheries. Numerous hydropower developments loom over the Mekong Basin threatening to alter flows, fragment habitats, block fish migration routes from completing lifecycle, degrade water quality and reduce the overall productivity of rivers resulting from nutrients and sediment losses. This is particularly troubling because the migratory species present in the Tonle Sap represent a third [45] of an estimated 1,200 fish species with 877 species recorded from the Mekong Basin [9,46]. In Cambodia, migratory species form 63% of catch by weight from Tonle Sap floodplains [27] and up to 82% from Tonle Sap River (Result Section).

The findings in this paper, for the first time, demonstrate evidence that the catches of the large- and medium-sized species in the Tonle Sap are declining while some small-sized, fast-growing species are increasing and contributing to the maintenance of the *Dai* fishery's overall catches in the past decades. This is akin to other notable indiscriminate fisheries such as that recently noted in the East China Sea where catches consisted of 1-year-old fish and the high exploitation level has been sustained for at least 10 fish generations[15]. This paper further demonstrates that even small-bodied species, so far capable of increasing their production on average, are showing significant reductions in body size with the consequence of an overall reduction in the percentage of mature individuals. This latter result is a warning signal to fisheries managers and conservationists that the species-rich Tonle Sap, so far able to maintain total harvest levels, may be close to its limit. The findings suggest that enhanced protection and conservation efforts are urgently needed to maintain food security in this region.

Fortunately, formal institutions for fisheries protection and conservation in Cambodia are now in place [47] with restrictions imposed on fishing seasons, gears and geographical areas (fish sanctuaries). Sufficient resource allocation to the sector are therefore necessary to enforce and monitor these fisheries regulations in order to protect and converse the fish biodiversity in the Tonle Sap, with the main aim to (1) let fish spawn at least for the first time before capture, (2) let fish grow and (3) let the mega-spawners live[48]. Tonle Sap River is specifically a natural passageway for many seasonal migratory fishes in the region. Setting appropriate regulations on the basis of known peak seasonal migrations during the inflow and outflow periods that allows some fishes (including endangered species) to pass through the river, would enable some juveniles and broodfishes to complete their life cycles, i.e. accessing the Tonle Sap floodplains and area south of Phnom Penh to feed, and the upstream of the Mekong mainstream and tributaries to seek dry-season refuge and breed [36,49]. Together with maintaining natural flow and hydraulic conditions for the longitudinal and lateral connectivity among these critical habitats that guarantee free migration routes for fishes are highly likely to be key drivers for the sustainability of the Tonle Sap fisheries. Further, the current formal fisheries management regime favors community-based fisheries co-management, where 516 community fisheries (CFis) including 228 in the Tonle Sap floodplains have been established countrywide[50]. Conservation priority should be given to the CFis situated in these key critical fish habitats. By effectively protecting and conserving these areas combined with appropriate hydraulic conditions, some juveniles and broodfishes may be maintained to sustain the seasonal reproduction, recruitment and growth. For future work, it is worth exploring a modelling approach which is able to suggest a management strategy that maximizes the present benefits from the Tonle Sap fishery while maintaining its long-term sustainability [51].

Methods

Dai fishery

This study used time series catch data of a standardized assessment on an industrial-scale '*Dai* fishery' between 2000-2015 (see also S1). The fishery seasonally operates between October and March in a specific location along the lower section of the Tonle Sap River, stretching about 4-30 km north of Phnom Penh. All *Dai* (64 units) are organized into 14 rows (referred to as row 2 to 15, with the most upstream row 15 situated closest to the Tonle Sap Lake; Fig. 6a) and operated singly or jointly of up to 7 units in a single row (Fig. 6b). A *Dai* unit can be uniquely identified through a combined alpha-numeric code of row number and the letter 'A' to 'H' of each individual *Dai* in that row. For example, *Dai* 2A indicates *Dai* A in row number 2. The transversal position of *Dai* rows within the river channel changes along up- and downstream axis (Table S2). In Row 2-4 and 7, *Dai* is positioned towards the right bank (facing upstream) while row 13 and 14 are anchored more to the left bank, and the other units are positioned around the center of the river. Such positions of *Dai* row remain relatively unchanged for more than a century, with the aim to maximize catches dependent on local river morphology and hydrology [52]. Every *Dai* row is never broad enough to block the river, because by law, they have to leave space for navigation [43,47].

*D*ai is a relatively indiscriminate fishing gear. The mesh sizes of the gear taper down from ~15 cm at the mouth to 1 cm at the codend. The *Dai* mouth is about ~25 m wide and its opening is determined by the water depth with the lower footrope (with chain) anchored at the river bottom and the upper rope on the water surface. The opening of the *Dai* mouth is maintained by the force of water current. The fishing gear is installed in the Tonle River to filter fish that migrate out of the Tonle Sap floodplains back to the Mekong River during the dry season each year. Overall, the fishing effort of the *Dai* fishery (number of *Dai* units, gear dimensions, season of fishing and geographical location of the fishery) remains relatively constant over the study period, although some increases in hauling time have been reported during the peak migration periods [52]. Technical details of the *Dai* gear are described in [43]. Assuming that (1) the migration of fish from nearby floodplains to the between-*Dai* rows and (2) removals of fish by other small-scale fishing gears operating between *Dai* rows could be ignored, the mean catch rate of the fishery has a general declining slope from row 15 down through row 2 (from closest to furthest away from the Tonle Sap Lake; Fig. 6a), indicating depletion response of fish population which is gradually removed from the system through cumulative *Dai* rows (fishing effort). Each *Dai* unit was predicted to remove 2.8% of migrating fish, and up to 83% of the fish arriving at row 15 were estimated to have captured by the 64 *Dai* units [52].

Fig. 6. *Dai* fishery in Tonle Sap River: location of *Dais* (a); an aerial photo of a *Dai* row with seven units in operation (b); catch per haul of a *Dai* in the peak period (c); seasonal fish supply from the *Dai* fishery for traditional fish paste (*prahok*) production for thousands of Cambodia farmers and rural dwellers (d). Map is created using ArcMap 10.2.2.

Data collection

Catch data from the *Dai* fishery were made available by the Fisheries Programme of the Mekong River Commission that technically and financially support the catch assessment programme. The catch of the fishery has been routinely assessed by the former Department of Fisheries (currently is the Fisheries Administration - FiA) and later by the Inland Fisheries Research and Development Institute (IFReDI) of the FiA in cooperation with its sub-national counterparts. General concepts and formula for assessing catches and catch composition are outlined in [53], and these concepts were used to frame the sampling protocols and assessing catches of the fishery. The sampling unit was based on *Dai* unit and a randomly stratified sampling method was used for this paper. More specifically, *Dai* units were stratified based on (Fig. S3): (i) administrative space divided into two strata: Kandal Province (row 15-7 containing 42 *Dai* units) and Phnom Penh Municipality (row 6-2, containing 22 units), (ii) time based on the lunar period: Peak Period occurring in a time-window between 7-1 days before full moon and Low Period, covering the rest of each month for the entire fishing season (iii) *Dai* types: High Catch *Dai* units (11 in Kandal and 6 in Phnom Penh) and Low Catch *Dai* units (31 in Kandal and 16 in Phnom Penh). Relative locations of all *Dai* units within the Tonle Sap River is given in (Table. S2). Sampling on catches per haul or CPUE; including CPUE for species in catch composition and the daily number of hauls of a *Dai* unit were conducted in each stratum, lunar period and *Dai* type within each month of the fishing season for monthly catch estimate. Likewise, fishing effort (number of active *Dai* units and active days) were recorded according to the stratification framework throughout each fishing month over the whole fishing season across the study period. Sampling takes place around 17 days/month with intensive sampling (every day) during Peak Period and every second or third day in the Low Period.

Catch Per Unit Effort or daily catch rate of the *Dai* unit (kg) is estimated as the product of sampled weight for haul, *i* and estimated number of hauls in a day [52]:

$$CPUE_{dd,mt,st,lu,dt,dai,i} = weight_{mt,st,lu,dt,dai,i} . haul_{dd,mt,st,lu,dt,dai} \qquad (1)$$

Where *dd*=day, *mt*=month, *st*=stratum, *lu*=lunar period, *dt*=*Dai* type, *dai*=individual *Dai* unit, weight=weight of haul, and haul=estimated number of hauls in a day. Mean daily CPUE is based on mean daily catch samples per haul multiplying by the total number of haul per day. The estimated monthly catch for a given stratum, lunar period and *Dai* type, is as follows:

$$Es.Mt.C_{mt,st,lu,dt} = \overline{CPUE}_{m,st,lu,dt} \times Es.FE_{mt,st,lu,dt} \qquad (2)$$

Where, *Es.Mt.C*=Estimated Monthly Catch, *Es.FE*=Estimated Fishing Effort. Estimated fishing effort is given by:

$$Es.FE_{mt,st,lu,dt} = AD_{m,st,lu,dt} \times AG_{mt,st,lu,dt} \qquad (3)$$

Where *AD* is number of active (fishing) days and *AG* is number of active (fishing) gears for a given stratum, lunar period and *Dai* type. Additionally, estimated monthly species composition is computed as follows:

$$Es.Mt.Species_{mt,st,lu,dt} = SPE_{m,st,lu,dt} \times Es.Mt.C_{mt,st,lu,dt} \quad (4)$$

Where *Es.Mt.Species* is Estimated Monthly Catch for a Species, SPE=a fraction of the total estimated catch corresponding to that species and is formulated from the proportion of that species found in the samples. The total catch estimated for a season is the aggregation of the monthly catch estimated for that season.

Apart from sampling data on total catch for each species in each season, data were also obtained for the number, weight and length of some common and commercial individual fish caught per day of each fishing season. These species are among the most ecological, sociocultural (food nutrition and security) and economic important species in the region [32,46,51]. Therefore, they were used to examine the temporal changes in body weight and length for this study (see Fig. 4, 5). Further description of the sample sizes, sampling protocols, data collection forms on catch, species composition and fishing effort, the formula for catch estimation as well as the database system to store and manage the collected data of the fishery are given in detail by [52].

The current *Dai* fishery database contains information on a total of 141 species. However, only 116 fish species were included in the analysis for this paper because data on the seasonal catches of the other species were sporadic throughout the time series. Furthermore, the species dropped from the analysis were quite marginal in terms of overall catch, and the total catch of the 25-fish species not included in this analysis only represented 0.38% of the total fishery's catch recorded between 2000-2015. Of 116 species, the analysis includes 5 endangered and critically endangered species namely *Probarbus jullieni, Probarbus labeamajor, Catlocarpio siamensis, Pangasianodon gigas* and *Pangasius sanitwongsei.*

In addition to the *Dai* fishery datasets, data was also obtained on maxTL and trophic level of fish species in the Tonle Sap from FishBase [54]. Fish species classification and their ecological attributes were based on the Mekong Fish Database [55], and are updated using FishBase [56], in cross-checking with the Catalogue of Fishes Online Database as well as other literature including [57,58].

Statistical analysis

All data analyses were performed in R Programme [59]. Linear regression was used to predict the rate of change in the total catch weight of 116 fish species recorded at the *Dai* fishery between 2000 and 2015. The temporal trend for each of the 116 species was expressed as a standardized regression coefficient to allow comparison among species. Standardized regression coefficients measure the change in the dependent variable resulting from a one-standard-deviation change in the independent variable [60]. In univariate linear regression, standardized regression coefficient equals the correlation coefficient (with its values varying between -1 and +1), the intercept equals zero, and the positive and negative signs of standardized coefficients or regression weights (slope) indicates the kind of correlation between the variables [61,62]. Linear regressions, and the generation of standardized regression coefficients, were performed using the 'lm' function of 'stats' package and 'lm.beta' function of 'QuantPsyc' package [59].

Histograms were used to visualize the distribution of standardized regression coefficient values of all species. Simple linear regressions were used to explore the global trend of the relationships between standardized regressions coefficients and species' maxTL and trophic levels (obtained through FishBase). For all regression analyses, normality was ensured by Shapiro tests (p-value>0.05). Log+1 transformation was applied to normalize the skewness of standardized regression coefficients prior to the linear regression analyses. In addition, weighted means of maxTL and trophic level in *Dai* catches by season were computed to examine trends of mean maxTL and tropical level across the 15-year study period. To explore temporal trends in the individual weights of the fish constituting the catch, the mean weight of all individuals captured per species per day was calculated and regressed against time. To deal with the data skewness, mean body weight was log-transformed before the analysis, and standard deviation for each species was also computed for each fishing season for the whole study period. This analysis was performed for six common species that spanned a range in standardized regression coefficient values (positive, zero, negative), body sizes and trophic levels, and included large- and medium-sized carps (*Cyclocheilichthys enoplos, Osteochilus melanopleurus,* and *Cirrhinus microlepis),* a large-sized river catfish (*Pangasianodon hypophthalmus),* as well as small-sized and highly productive mud carps (*Henicorhynchus lobatus* and *Labiobarbus lineatus)*. Being ecological, sociocultural and economic important species, the six species belong to the first two largest families (Cyprinidae and Pangasiidae) forming the largest proportion of the total catches (84% and 4% respectively) from the *Dai* fishery. In addition, *H. lobatus* is an ecological keystone species, the most abundant species with its critical role in food security throughout the Lower Mekong Basin (including the Tonle Sap) and an important prey species for many predatory fishes and Irrawaddy dolphins [63,64]. *Labiobarbus lineatus* shares similar ecological characteristics with *H. lobatus.* From the *Dai* fishery, *H. lobatus* and *L. lineatus* are among the most dominant species contributing ~17% and 10% to the *Dai's* total catch weight respectively. Finally, an attempt was also made to analyze the temporal changes in fish body length of the same six species (as we did with mean body weight). Given that, two of the six species (*P. hypophthalmus* and *O. melanopleurus)* contained relatively small sample sizes on length, only the other four species were included in the length frequency analysis. Nevertheless, the trends of the four species (Fig. 5a-d) still provide a good example of the status and trends of riverine fishes in the Tonle Sap and Lower Mekong Basin. Length frequency distributions of the four species were then examined across the study period using the 'violins' function from 'caroline' package in R [65].

References

1. Welcomme, R. L. *et al.* Inland capture fisheries. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **365,** 2881–96 (2010).

2. Tockner, K. & Stanford, J. a. Riverine flood plains: present state and future trends. *Environmental Conservation* **29,** 308–330 (2002).

3. de Graaf, G., Bartley, D., Jorgensen, J. & Marmulla, G. The scale of inland fisheries, can we do better? Alternative approaches for assessment. *Fisheries Management and Ecology* **22,** 64–70 (2015).

4. Lynch, A. J. *et al.* The social, economic, and environmental importance of inland fish and fisheries. *Environmental Reviews* **24,** 1–7 (2016).

5. Cook, S. J. *et al.* From ideas to action: Ten steps to responsible inland fisheries that support livelihoods, food security, and healthy aquatic ecosystems. in *Freshwater, Fish and the Future Proceedings of the Global Cross-Sectoral Conference* (eds. Taylor, W. W., Bartley, D. M., Goddard, C. I., Leonard, N. J. & Welcomme, R.) 343–351 (the Food and Agriculture Organisation of the United Nations and Michigan State University and American Fisheries Society, 2016).

6. Bartley, D. M., De Graaf, G. J., Valbo-Jørgensen, J. & Marmulla, G. Inland capture fisheries: Status and data issues. *Fisheries Management and Ecology* **22,** 71–77 (2015).

7. FAO. *The State of World Fisheries and Aquaculture 2016. Contributing to food security and nutrition for all*. (Food and Agriculture Organization of the United Nations, 2016).

8. Welcomme, R. L., Baird, I. G., Dudgeon, D., Halls, A. and & Lamberts, D. in *Freshwater Fisheries Ecology* (ed. Craig, J. F.) 363–376 (John Wiley & Sons, Ltd., 2016).

9. Ziv, G., Baran, E., So, N., Rodriguez-Iturbe, I. & Levin, S. A. Trading-off fish biodiversity, food security, and hydropower in the Mekong River Basin. *Proceedings of the National Academy of Sciences* **109,** 5609–5614 (2012).

10. Winemiller, K. *et al.* Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. *Science* **351,** 128–129 (2016).

11. Grumbine, R. E., Dore, J. & Jianchu, X. Mekong hydropower: Drivers of change and governance challenges. *Frontiers in Ecology and the Environment* **10,** 91–98 (2012).

12. Allan, J. D. *et al.* Overfishing of Inland Waters. *BioScience* **55,** 1041–1051 (2005).

13. McCann, K. S. *et al.* Food webs and the sustainability of indiscriminate fisheries 1. *Canadian Journal of Fisheries and Aquatic Sciences* **73,** 1–10 (2016).

14. Andersen, K. H. & Gislason, H. Unplanned ecological engineering. *Proceedings of the National Academy of Sciences* **114,** 634–635 (2017).

15. Szuwalski, C. S., Matthew G. Burgess, C. C. & Gaines, S. D. High fishery catches through trophic cascades in China. *PNAS* **114,** 717–721 (2017).

16. Costello, C. Fish harder; catch more? *Proceedings of the National Academy of Sciences* **114,** 1442–1444 (2017).

17. Pauly, D. *et al.* Towards sustainability in world fisheries. *Nature* **418,** 689–695 (2002).

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

19. Shin, Y. J., Rochet, M. J., Jennings, S., Field, J. G. & Gislason, H. Using size-based indicators to evaluate the ecosystem effects of fishing. *ICES Journal of Marine Science* **62,** 384–396 (2005).

20. Jennings, S. *et al.* Long-term trends in the trophic structure of the north sea fish community: Evidence from stable-isotope analysis, size-spectra and community metrics. *Marine Biology* **141,** 1085–1097 (2002).

21. Piet, G. J. & Jennings, S. Response of potential fish community indicators to fishing. *ICES Journal of Marine Science* **62,** 214–225 (2005).

22. Baird, I. G. Probarbus jullieni and Probarbus labeamajor: The management and conservation of two of the largest fish species in the Mekong River in southern Laos. *Aquatic Conservation: Marine and Freshwater Ecosystems* **16,** 517–532 (2006).

23. Sharpe, D. M. T. & Hendry, A. P. Life history change in commercially exploited fish stocks: An analysis of trends across studies. *Evolutionary Applications* **2,** 260–275 (2009).

24. Jacobsen, N. S., Gislason, H. & Andersen, K. H. The consequences of balanced harvesting of fish communities. *Proceedings. Biological sciences / The Royal Society* **281,** 1–9 (2014).

25. McIntyre, P. B., Liermann, C. A. R. & Revenga, C. Linking freshwater fishery management to global food security and biodiversity conservation. *PNAS* **113,** 12880–12885 (2016).

26. MRC. *State of the Basin Report 2010*. (Mekong River Commission, 2010).

27. van Zalinge, N., Nao, T. & Touch, S. T. Where there is water, there is fish? Fisheries issues in the Lower Mekong Basin from a Cambodian perspective. in *Contribution to the Mekong Panel at the Seventh Common Property Conference of the International Association for the Study of Common Property, Vancouver, Canada, 10 - 14 June 1998* 14 (International Association for the Study of Common Property, 1998).

28. Hortle, K. G., Lieng, S. & Valbo-Jorgensen, J. *An introduction to Cambodia's inland fisheries. Mekong Development Series No. 4* (Mekong River Commission, 2004).

29. Hogan, Z. S., Ngor, P. B. & van Zalinge, N. Status and conservation of two endangered fish species, the Mekong giant catfish Pangasianodon gigas and the giant carp Catlocarpio siamensis, in Cambodia's Tonle Sap River. *Natural History Bulletin of the Siam Society* **49,** 269–282 (2001).

30. Chevey, P. & Le Poulain, F. La pêche dans les eaux douces du Cambodge. *Océanogr. Indochine* **33,** 1–183 (1940).

31. Fily, M. & D'Auberton, F. *Cambodia. Report on fisheries technology in the Great Lake and the Tonle Sap, 1962-1963*. (National Museum of Natural History, 1965).

32. Poulsen, A. F. *et al. Distribution and Ecology of Some Important Riverine Fish Species of the Mekong River Basin*. *MRC Technical Paper No. 10* (Mekong River Commission, 2004).

33. Smith, H. M. *The Fresh-water fishes of Siam, or Thailand*. (United States National Museum Bulletin 188, 1945).

34. Roberts, T. R. & Baird, I. G. Traditional fisheries and fish ecology on the Mekong River at Khone Waterfalls in Southern Laos. *Natural History Bulletin of the Siam Society* **43,** 219–26 (1995).

35. Mattson, N. S., Buakhamvongsa, K., Sukumasavin, N., Nguyen, T. & Ouk, V. *Mekong giant fish species: on their management and biology*. (Mekong River Commission, 2002).

36. Poulsen, A. F., Ouch, P., Viravong, S., Suntornratana, U. & Nguyen, T. T. *Fish Migrations of the Lower Mekong Basin: Implications for Development, Planning and Environmental Management*. (Mekong River Commission, 2002).

37. IUCN. The IUCN Red List of Threatened Species. Version 2016-2. (2016).

38. Ngor, P. B., Chheng, P. & So, N. Declines in catches of some large and medium-sized species in Tonle Sap River. *Catch and Culture* **21,** 4–7 (2015).

39. Baird, I. G., Flaherty, M. S. & Phylavanh, B. Rhythms of the river: lunar phases and migrations of small carps (Cyprinidae) in the Mekong River. *Natural History Bulletin of the Siam Society* **51,** 5–36 (2003).

40. van Zalinge, N. & Nao, T. Summary of Project Findings: Present status of Cambodia's freshwater capture fisheries and management implications. in *Present status of Cambodia's fisheries and management implications* (eds. van Zalinge, N. P., Nao, T. & Deap, L.) 1–20 (Mekong River Commission and Department of Fisheries, 1999).

41. Reynolds, J. D., Webb, T. J. & Hawkins, L. A. Life history and ecological correlates of extinction risk in European freshwater fishes. *Canadian Journal of Fisheries and Aquatic Sciences* **62,** 854–862 (2005).

42. Olden, J. D., Hogan, Z. S. & Zanden, M. J. Vander. Small fish, big fish, red fish, blue fish: Size-biased extinction risk of the world's freshwater and marine fishes. *Global Ecology and Biogeography* **16,** 694–701 (2007).

43. Deap, L., Degen, P. & van Zalinge, N. *Fishing gears of the Cambodian Mekong*. (Inland Fisheries Research and Development Institute of Cambodia & Mekong River Commission, 2003).

44. World Bank Group. Population, total. Cambodia. *World Bank Group* (2015). Available at: http://data.worldbank.org/indicator/SP.POP.TOTL?locations=KH. (Accessed: 11th November 2016)

45. ICEM. *MRC Strategic Environmental Assessment (SEA) of hydropower on the Mekong mainstream*. (Mekong River Commission, 2010).

46. Rainboth, W. J. *Fishes of the Cambodian Mekong*. (Food and Agriculture Organisation of the United Nations, 1996).

47. FiA. *Law on Fisheries*. (Fisheries Administration, Ministry of Agriculture, Forestry and Fisheries, 2006).

48. Froese, R. Keep it simple: Three indicators to deal with overfishing. *Fish and Fisheries* **5,** 86–91 (2004).

49. van Zalinge, N. *et al.* The Mekong River System. in *Proceedings of the second international symposium on the management of large rivers for fisheries* (eds. Welcomme, R. & Petr, T.) 335–357 (FAO Regional Office for Asia and the Pacific, 2004).

50. Jentoft, S. & Chuenpagdee, R. *Interactive governance for small-scale fisheries: global reflections*. (Springer International Publishing Switzerland, 2015).

51. Sabo, J. L. *et al.* Designing river flows to improve food security futures in the Lower Mekong Basin. *Science* **358,** 1–11 (2017).

52. Halls, A. S. *et al. The Stationary Trawl (Dai) Fishery of the Tonle Sap-Great Lake System, Cambodia*. (Mekong River Commission, 2013).

53. Stamatopoulos, C. *Sample-based fishery surveys: a technical handbook. FAO. Fisheries Technical Paper* (Food and Agriculture Organisation of the United Nations, 2002).

54. Froese, R. & Pauly, D. FishBase. *World Wide Web electronic publication* (2017). Available at: www.fishbase.org. (Accessed: 1st February 2017)

55. MFD. *Mekong Fish Database: A taxonomic fish database for the Mekong Basin*. (Mekong River Commission, 2003).

56. Froese, R. & Pauly, D. FishBase. World Wide Web electronic publication. *World Wide Web electronic publication* (2017). Available at: www.fishbase.org. (Accessed: 1st February 2017)

57. Kottelat, M. The Fishes of the inland waters of Southeast Asia: A catalogue and core

bibliography of the fishes known to occur in freshwaters, mangroves and estuaries. *The Raffles Bulletin of Zoology* **27,** 1–663 (2013).

58. Rainboth, W. J., Vidthayanon, C. & Mai, D. Y. *Fishes of the Greater Mekong Ecosystem with Species List and Photorapic Atlas*. (Museum of Zoology, University of Michigan, 2012).

59. R Core Team. R: A Language and Environment for Statistical Computing. *R Foundation for Statistical Computing* **1,** 409 (2015).

60. Schroeder, L. D., Sjoquist, D. L. & Stephan, P. E. Understanding Regression Analysis: An introductory Guide. 95 (1986).

61. Stellefson, M. L., Hanik, B. W., Chaney, B. H. & Chaney, J. D. A Tutorial on Calculating and Interpreting Regression Coefficients in Health Behavior Research. *The Health Educator* **40,** (2008).

62. Vittinghoff, E., Glidden, D. V., Shiboski, S. C. & McCulloch, C. E. *Regression methods in biostatistics: linear, logistic, survival, and repeated measures models.* (Springer, 2012).

63. Fukushima, M., Jutagate, T., Grudpan, C., Phomikong, P. & Nohara, S. Potential effects of hydroelectric dam development in the Mekong River basin on the migration of Siamese mud carp (Henicorhynchus siamensis and H. lobatus) elucidated by otolith microchemistry. *PLoS ONE* **9,** (2014).

64. Baird, I. G. The Don Sahong Dam. *Critical Asian Studies* **43,** 211–235 (2011).

65. Schruth, D. A Collection of Database, Data Structure, Visualization, and Utility Functions for R. 38 (2013).

Acknowledgements

We are grateful to the Erasmus Plus, Belmont Forum (TLSCC project) and the European Erasmus+ credit mobility and capacity building CONSEA Programs for funding our study. This research was in part funded by Belmont Freshwater Grant and Canada First Research Excellence Fund to KSM. Cordial thanks to the Fisheries Programme of the Mekong River Commission, the Inland Fisheries Research and Development Institute and the Fisheries Administration, Cambodia for making available the *Dai* fishery datasets used in this study. We would like to thank Phen Cheng, Pengby Ngor, Loeung Deap, Phalla Tan, Yuthy Sar and numerous data collectors and supervisors contributing to the *Dai* fishery data collection and database management. Finally, great appreciation is extended to the Laboratory of Evolution and Biological Diversity (EDB lab) supported by 'Investissement d'Avenir' grants (CEBA, ref. ANR-10-LABX-0025; TULIP, ref. ANR-10-LABX-41).

Author contributions

SL supervised the project. PBN carried out fieldwork. PBN, SL and GG performed analysis. PBN wrote the draft manuscript. PBN, SL, KM, BM, EF, GG and NS commented, edited and revised the draft manuscript.

Additional information

Supplementary information: accompanies this paper.

Completing financial interests: The authors declare no competing financial interests.

Supplementary Information (S)

Supplementary information – S1

Tonle Sap River System

The TSRL is a flood pulse system, and is the largest wetland and an integral part of the history, culture, ecology and economics in Southeast Asia [1]. It is the only continuous area of natural wetland habitats remaining in the Mekong system [2]. UNESCO approved this area as a world Biosphere Reserve in 1997 [3]. During the dry season, the lake depth falls to 0.5 meter in late April with a surface area of about 2,000 km^2 [4]. During the wet season (June-October), the Tonle Sap River, whose normal flow is from the Tonle Sap Lake to the Mekong River, changes its direction when the Mekong waters rise faster than the Lake. The Lake expands its size four to six times (10,000 to 15,780 km^2) [5], inundating vast terrestrial floodplain areas surrounding TSRL. TSRL's biological productivity reaches its peak during this period as both migratory fishes from the Mekong and resident fishes in the Lake invade the floodplains for feeding, reproduction and nurseries. Eggs, larvae and fry of fish that spawn upstream in the Mekong mainstream are also carried by the flow and dispersed into the TSRL's sourrounding floodplains through numerious channels, streams and man-made cannals for feeding, nurseries and growth. When the Mekong flood recedes (September/October) and the Tonle Sap River reverses to its nornal flow, large numbers of fish migrate back to the Tonle Sap Lake, then the Tonle Sap River and Mekong River for dry-season refuges. It is during this period of receeding water (October – March) when *Dai* fishery operates to target these migratory fishes. The fishery usually peaks in December and January in a time window of 6-1 days before full moon during which the river is described as packed solid with fish.

Dai fishery

The *Dai* fishery or *Loh Dai*, was established around 140 years ago and resembles a stationary trawl net anchored within the river channel [1]. At present, it is the only industrial-scale inland fishery remaining in the Lower Mekong Basin (LMB). Catches from the fishery contribute an estimated 14% of the landings from the TSRL system (equivalent to 10% of total fish weight consumed in the LMB), and make up of ~7% to the total inland capture fisheries landings in Cambodia [1]. The *Dai* fishery seasonally operates in a specific location along the lower section of the Tonle Sap River, stretching about 4-30 km north of Phnom Penh. The river stretch covers two administrative zones: Phnom Penh Municipality and Kandal Province. All *Dai* units are organized into 14 rows and operated singly or jointly of up to 7 units in a single row (Fig. 1). *Dai* row 2-6 are situated in Phnom Penh municipality and row 7-15 are located in Kandal Province with the most upstream row 15 situated in Kandal Province close to the Tonle Sap Lake.

Between the 2000 and 2015 fishing seasons, the number of *Dai* seasonally operating in the Tonle Sap River varied between 60 and 64 units. Generally, a *Dai* unit is between 100 and 120 meters long and 25 meters wide. The net opening (mouth) is determined by the water depth of the river where it is positioned. The size and mesh sizes of the net taper down from the mouth (15 cm) to the cod-end (1 cm). Other details about gear dimensions are technically described by [6]. *Dai* fishery operation is regulated by a law on Cambodian fisheries [7]. *Dai* fishery is technically standardized in terms of both location and the gear use which are defined and controlled by the Cambodian law on fisheries. The so-called 'burden book', attached to the law, further describes management legislation to be complied by the *Dai* operators. The burden book explains operation rules such as rules on fishing season, *Dai* positions in the river, size restrictions of fishing gear, payment and harvest, detailed descriptions of which are explained by [1].

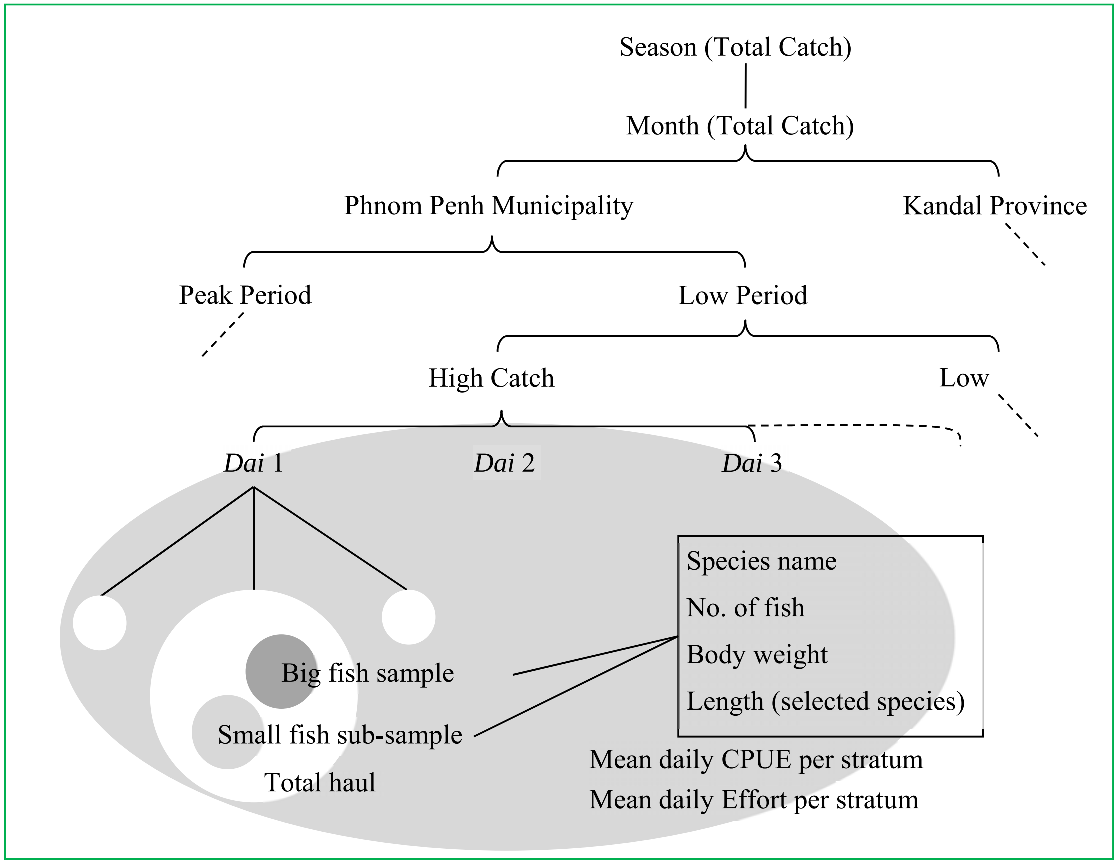
Supplementary information – S2

Table S2: Relative *Dai* locations in the Tonle Sap River. The table also indicates sampling stratification scheme which administratively stratifies into Kandal Province and Phnom Penh Municipality. Also, all *Dai* units are stratified into High Catch *Dai* (shaded cells) and Low Catch *Dai* (unshaded cells). The classification of High and Low Catch Dai units was based on the *Dai* catch census, conducted in 1996-1997. Source: adapted from [1,8,9].

Province	Row No.	Approximate cumulative distance between rows (km)	Coordinates		Relative transversal positions of *Dai* nets in the Tonle Sap River								Total number of *Dai* units forming each row
			North ends	East ends									
Kandal Province	Row 15	37.50	11º53.585’	104º48.580’		B	C	D	E	F			5
	Row 14	33.00	11º52.110’	104º47.266’	A	B	C						3
	Row 13	31.92	11º51.618’	104º47.675’	A								1
	Row 12	28.93	11º50.349’	104º48.111’		A	B	C	D	E		G	6
	Row 11	23.07	11º47.447’	104º49.383’		A’	A	B	C	D			5
	Row 10	13.17	11º42.257’	104º50.515’		A	B	C	D	E	F	G	7
	Row 9	10.77	11º40.963’	104º51.026’		B	C	D					3
	Row 8	4.87	11º40.477’	104º51.360’		B	C	D	E	F	G	H	7
	Row 7	4.28	11º39.685’	104º51.969’				C	D	E	F	G	5
Sub-Total	9 rows												42
Phnom Penh Municipality	Row 6	3.77	11º38.867’	104º52.581’			C	D	E	F	G		5
	Row 5	3.28	11º38.363’	104º53.328’		B	C	D	E	F			5
	Row 4	2.75	11º38.295’	104º53.809’					A	B	C	D	4
	Row 3	1.40	11º37.640’	104º54.705’					A	B	C	D	4
	Row 2	0.00	11º37.068’	104º55.116’					A	B	C	D	4
Sub-total	5 rows												22
Grand total	15 rows												64

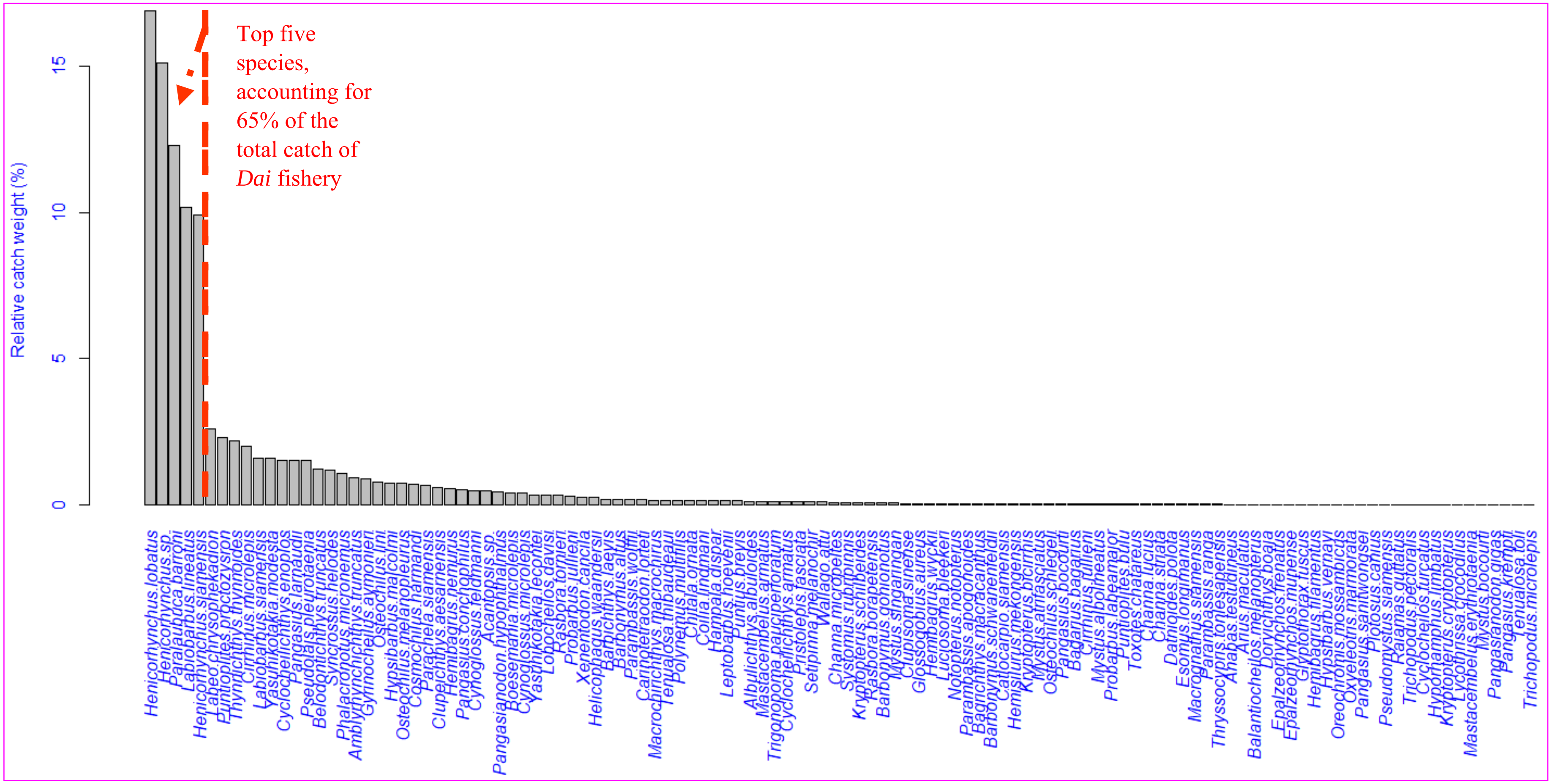
Supplementary information – S3

Fig. S3 Outline of the sampling stratification scheme for the *Dai* fishery catch assessment. The mean catch rate per haul (CPUE) is computed for a *Dai* unit on a day (large shaded area) within each stratum. The total catch is calculated by multiplying the stratum-specific estimate of the mean daily CPUE by the two stratum-specific raising factors: the number of active *Dais* and number of active days [1].



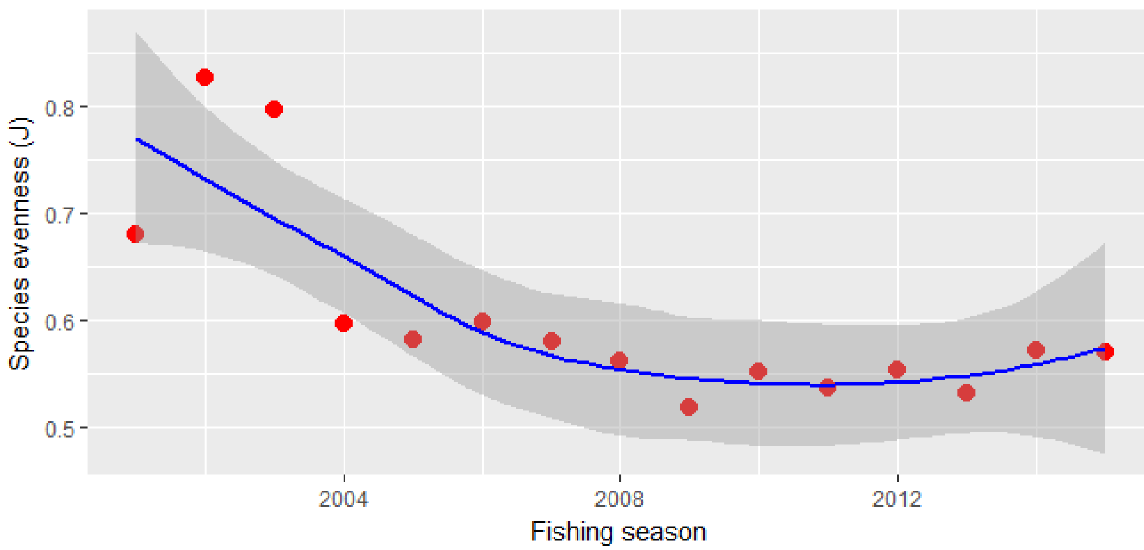
Supplementary information – S4

Fig. S4 Relative catch weight (%) of 116 fish species recorded at the *Dai* fishery between 2001 and 2015



Supplementary information – S5

Fig. S5 Temporal variations in species evenness recorded at the *Dai* fishery between 2000 and 2015. Species evenness (J) was computed based on **J=H/log(S)**, where H is Shannon diversity index and S is species richness. The value of species evenness varies between 0 and 1, with 0 signifying no evenness and one indicating a complete evenness. Red points are the species evenness values representing fish community for each fishing season. Blue solid line with shaded area around the smooth curve is loess fitting with 95% confidence interval. Overall declining trend of species richness is discerned over the study period between 2001 and 2015.



Supplementary information – S6:

Table S6: Species' standardized regression coefficients and ecological attributes

Species	Standardized regression coefficients	Status*	Guild**	maxTL	Trophic level
Acantopsis sp.	-0.68	ne	5	30.5	3.5
Albulichthys albuloides	-0.53	ne	5	36.6	2.79
Amblyrhynchichthys truncatus	-0.43	ne	5	48.8	2.4
Anabas testudineus	0.21	ne	1	25	2.98
Arius maculatus	-0.40	ne	5	80	3.36
Bagarius bagarius	-0.53	ne	5	200	3.72
Bagrichthys macracanthus	-0.43	ne	5	30.5	2.95
Balantiocheilos melanopterus	-0.57	ne	5	42.7	3
Barbichthys laevis	-0.26	ne	5	36.6	2.66
Barbonymus altus	-0.55	ne	3	24.4	2.4
Barbonymus gonionotus	-0.40	ne	5	40.5	2.36
Barbonymus schwanenfeldii	-0.47	ne	3	42.7	2.31
Belodontichthys truncatus	-0.43	ne	5	73.2	4.08
Boesemania microlepis	-0.13	ne	3	122	3.72
Carinotetraodon lorteti	0.15	ne	2	7.3	3.5

Catlocarpio siamensis	-0.23	ce	5	300	2.92
Channa lucius	-0.35	ne	1	48.8	3.91
Channa micropeltes	-0.53	ne	1	158.6	3.85
Channa striata	-0.57	ne	1	122	3.36
Chitala ornata	-0.56	ne	5	122	3.68
Cirrhinus jullieni	0.56	ne	5	24.4	2.48
Cirrhinus microlepis	-0.43	ne	5	79.3	2.38
Clupeichthys aesarnensis	0.25	ne	5	8.5	2.89
Clupisoma sinense	-0.03	ne	5	37.8	3.42
Coilia lindmani	-0.59	ne	2	24.4	3.74
Cosmochilus harmandi	-0.02	ne	5	100	2
Cyclocheilichthys armatus	-0.56	ne	3	26.45	3.38
Cyclocheilichthys enoplos	-0.69	ne	5	90.3	3.15
Cyclocheilos furcatus	-0.30	ne	5	73	3.65
Cynoglossus feldmanni	-0.02	ne	5	30.5	3.5
Cynoglossus microlepis	-0.60	ne	5	40	3.5
Datnioides polota	0.03	ne	2	37	3.68
Doryichthys boaja	0.49	ne	2	50	3.27
Epalzeorhynchos frenatus	0.53	ne	5	15	2.31
Epalzeorhynchos munense	0.38	ne	5	11.4	2.64
Esomus longimanus	-0.56	ne	1	9.8	3.31
Glossogobius aureus	-0.32	ne	2	30.5	3.98
Glyptothorax fuscus	-0.44	ne	5	14.8	3.2
Gyrinocheilus aymonieri	-0.07	ne	5	34.2	2.52
Hampala dispar	-0.59	ne	5	42.7	3.7
Helicophagus waandersii	-0.60	ne	5	70	3.15
Hemibagrus filamentus	-0.38	ne	5	50	3.56
Hemibagrus nemurus	-0.35	ne	5	79.3	3.62
Hemibagrus wyckii	-0.28	ne	5	86.6	3.76
Hemisilurus mekongensis	-0.53	ne	5	80	3.3
Henicorhynchus lobatus	0.24	ne	5	18.3	2.74
Henicorhynchus siamensis	-0.06	ne	5	24.4	2
Henicorhynchus sp.	0.20	ne	5	15	2
Hyporhamphus limbatus	-0.09	ne	2	35	3.1
Hypsibarbus malcolmi	-0.59	ne	5	61	3.2
Hypsibarbus vernayi	-0.31	ne	5	26.4	2.99
Kryptopterus bicirrhis	-0.15	ne	5	18.3	3.89
Kryptopterus cryptopterus	-0.17	ne	5	17	3.8
Kryptopterus schilbeides	-0.56	ne	5	12	3.78
Labeo chrysophekadion	0.02	ne	5	90	2
Labiobarbus lineatus	0.66	ne	5	15.5	2.49
Labiobarbus siamensis	-0.37	ne	5	22	2.3
Leptobarbus hoevenii	-0.36	ne	5	122	2.76
Lobocheilos davisi	-0.41	ne	5	9	2
Luciosoma bleekeri	-0.35	ne	5	30.5	3.78
Lycothrissa crocodilus	-0.07	ne	5	36.6	3.71
Macrochirichthys macrochirus	-0.58	ne	3	100	3.7
Macrognathus siamensis	-0.55	ne	1	36.6	3.26

Mastacembelus armatus	-0.50	ne	5	34.9	2.78
Mastacembelus erythrotaenia	-0.17	ne	5	100	2.74
Mystus albolineatus	-0.33	ne	3	42.7	3.65
Mystus atrifasciatus	-0.12	ne	3	18.3	3.04
Mystus bocourti	-0.24	ne	3	29.3	3.5
Mystus singaringan	-0.47	ne	3	36.6	3.77
Notopterus notopterus	-0.44	ne	3	73.2	3.6
Oreochromis mossambicus	0.45	ne	5	47.6	2.17
Osteochilus lini	-0.56	ne	5	18.3	2
Osteochilus melanopleurus	-0.78	ne	5	73.2	2.32
Osteochilus schlegeli	0.00	ne	3	49	2
Oxyeleotris marmorata	-0.34	ne	1	79.3	3.9
Pangasianodon gigas	0.03	ce	5	300	2.3
Pangasianodon hypophthalmus	-0.65	ne	5	158.6	3.12
Pangasius bocourti	-0.37	ne	5	146.4	3.18
Pangasius conchophilus	-0.35	ne	5	146.4	2.73
Pangasius krempfi	-0.13	ne	5	146.4	2
Pangasius larnaudii	-0.39	ne	5	158.6	3.26
Pangasius sanitwongsei	0.20	ce	5	366	3.99
Parachela siamensis	-0.73	ne	3	18.3	3.42
Paralaubuca barroni	0.06	ne	3	18.3	3.3
Parambassis apogonoides	-0.15	ne	3	12.2	2.87
Parambassis ranga	-0.01	ne	1	8	3.27
Parambassis wolffii	-0.68	ne	3	24.4	3.72
Phalacronotus micronemus	-0.46	ne	5	61	4.03
Plotosus canius	-0.28	ne	2	150	3.88
Polynemus multifilis	-0.41	ne	2	34.2	3.74
Pristolepis fasciata	-0.67	ne	3	20	3.19
Probarbus jullieni	-0.20	e	5	183	3.17
Probarbus labeamajor	-0.12	e	5	183	2.47
Pseudolais pleurotaenia	0.42	ne	5	42.7	2.42
Pseudomystus siamensis	-0.44	ne	5	18.3	3.3
Puntioplites bulu	0.14	ne	5	35	2.37
Puntioplites proctozysron	-0.35	ne	5	30	2.7
Puntius brevis	-0.32	ne	3	14.6	2.91
Raiamas guttatus	0.59	ne	5	36.6	3.89
Rasbora borapetensis	0.55	ne	3	7.3	3.29
Rasbora tornieri	-0.49	ne	3	20.7	3.2
Setipinna melanochir	-0.39	ne	2	40.3	3.88
Syncrossus helodes	0.28	ne	5	36.6	3.31
Systomus rubripinnis	-0.37	ne	5	30.5	2.88
Tenualosa thibaudeaui	-0.41	ne	5	36.6	2
Tenualosa toli	0.27	ne	5	60	2.48
Thryssocypris tonlesapensis	-0.40	ne	2	7.8	3.2
Thynnichthys thynnoides	-0.31	ne	3	25	2.31
Toxotes chatareus	0.03	ne	2	48.8	3.99
Trichopodus microlepis	-0.48	ne	1	16	3.36
Trichopodus pectoralis	-0.35	ne	1	25	2.76

Trigonopoma pauciperforatum	0.05	ne	3	7	3.3
Wallago attu	-0.54	ne	5	240	3.68
Xenentodon sp.	0.02	ne	5	40	3.86
Yasuhikotakia lecontei	-0.51	ne	5	18.3	3.41
Yasuhikotakia modesta	0.13	ne	5	30.5	3.4

*ne = not endangered, e = endangered, ce = critically endangered, ** 1 = black (resident) species, 2 = estuarine species, 3 = grey (lateral-migration) species, 5= white (longitudinal/riverine-migratory) species. maxTL= Maximum total length (cm).

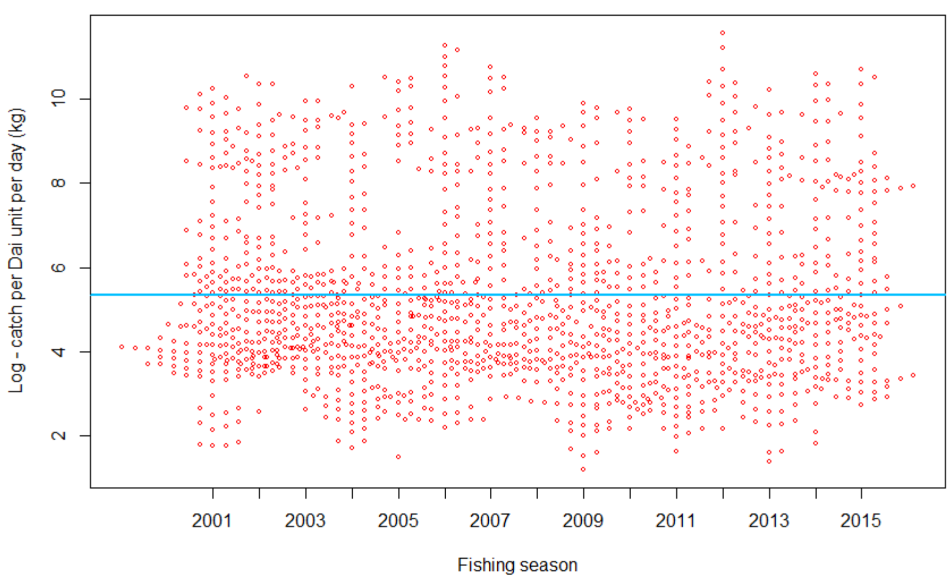
Supplementary information – S7

Table S7. Parameter estimates from Figure 4. All slopes were significant (p-value < 0.0001). Note that mean body weight is log-transformed.

Fig.4. label	Species name	Intercept	Slope (year)	R^2
a	*Osteochilus melanopleurus*	283.79	-0.139	0.17
b	*Cyclocheilichthys enoplos*	190.86	-0.094	0.10
c	*Pangasianodon hypophthalmus*	108.73	-0.0517	0.05
d	*Cirrhinus microlepis*	175.85	-0.085	0.17
e	*Henicorhynchus lobatus*	73.61	-0.036	0.17
f	*Labiobarbus lineatus*	59.47	-0.029	0.08

Supplementary information – S8

Fig. S8. Catch (kg) per *Dai* unit per day (log-scale) over the fishing season from 2000/2001 to 2014/2015. Year on the x-axis indicates fishing season. For example, 2001 represents the fishing season of 2000/2001 and the same for other years. The linear trend of the daily catch per *Dai* (against time) is relatively flatlined. Although the slope is negative, it was not significant (p-value = 0.982).



References (for Supplementary Information)

1. Halls, A. S. *et al. The Stationary Trawl (Dai) Fishery of the Tonle Sap-Great Lake System, Cambodia*. (Mekong River Commission, 2013).
2. van Zalinge, N. *et al.* The Mekong River System. in *Proceedings of the second international symposium on the management of large rivers for fisheries* (eds. Welcomme, R. & Petr, T.) 335–357 (FAO Regional Office for Asia and the Pacific, 2004).
3. Davidson, P. J. *The biodiversity of the Tonle Sap Biosphere Reserve: 2005 status review*. (UNDP-GEF funded Tonle Sap Conservation Project, 2006).
4. MRC. *Mekong: A River for the People*. (Mekong River Commission, 2007).
5. Rainboth, W. J., Vidthayanon, C. & Mai, D. Y. *Fishes of the Greater Mekong Ecosystem with Species List and Photoraphic Atlas*. (Museum of Zoology, University of Michigan, 2012).
6. Deap, L., Degen, P. & van Zalinge, N. *Fishing gears of the Cambodian Mekong*. (Inland Fisheries Research and Development Institute of Cambodia & Mekong River Commission, 2003).
7. FiA. *Law on Fisheries*. (Fisheries Administration, Ministry of Agriculture, Forestry and Fisheries, 2006).
8. Ngor, P. B. & van Zalinge, N. *Dai (Bagnet) fishery: 1994/95-2000/01: catch assessment methodology and results*. (Mekong River Commission/Department of Fisheries/Danida, 2001).
9. Ngor, P. B. Dai fisheries in the Tonle Sap River of Phnom Penh and Kandal province (including a Review of the Census Data of 1996-97). in *Management aspects of Cambodia's Freshwater Capture Fisheries and Management Implications, Eleven presentation given at the Annual Meeting of the Department of Fisheries of the Ministry of Agriculture, Forestry and Fisheries, 27-27 January 2000* (eds. van Zalinge, N. P., Nao, T. & Lieng, S.) 30–47 (Mekong River Commission and Department of Fisheries, 2000).

ARTICLE 4

Flow alterations by dams shaped fish assemblage dynamics in the complex Mekong-3S river system

Peng Bun Ngor, Pierre Legendre, Thierry Oberdorff, Sovan Lek

Ecological Indicators, 88 (2018), 103-114.

Ecological Indicators 88 (2018) 103–114

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Original Articles

Flow alterations by dams shaped fish assemblage dynamics in the complex Mekong-3S river system

Peng Bun Ngor[a,b,*], Pierre Legendre[c], Thierry Oberdorff[b], Sovan Lek[b]

[a] Fisheries Administration, No. 186, Preah Norodom Blvd., Khan Chamcar Morn, P.O. Box 582, Phnom Penh, Cambodia
[b] CNRS, IRD, Université Toulouse III Paul Sabatier, ENFA, UMR5174 EDB (Laboratoire Évolution & Diversité Biologique), 118 route de Narbonne, F-31062 Toulouse, France
[c] Département de Sciences Biologiques, Université de Montréal, C.P. 6128, Succursale Centre-ville, Montréal, Québec H3C 3J7, Canada

ARTICLE INFO

Keywords:
Dam effects
Fish abundance
Fish richness
Temporal beta diversity
Environmental filtering
Lower Mekong Basin

ABSTRACT

The Mekong, Sekong, Sesan, and Srepok (Mekong-3S) river system, a Ramsar wetlands of international importance and critical fish migration routes, is altered by dams that distort the seasonal flow dynamics, structuring dispersal and reproduction success of fishes. Here, we investigate the temporal responses of local fish beta diversity to hydrologic modification by the upstream functioning dams in five sites of the Mekong-3S system. The sampling design adopted (two sites on the Mekong River displaying relatively undisturbed flow and three sites in the 3S displaying a gradient in flow perturbation) allows us to focus on the effect of flow alteration on local fish assemblage compositions. By analysing 7-year daily fish monitoring data (06/2007–05/2014), we found that there have been overall declining trends in local species richness and abundance, with strong temporal variability in local beta diversity. Undisturbed sites are characterized by seasonal assemblage variability, while disturbed sites are characterized by aseasonal assemblage changes. Temporal shifts in assemblage composition suggest that dams alter seasonal flow patterns and favour generalist species. This study contributes to a better understanding of the temporal changes of tropical freshwater fish beta diversity in regulated and unregulated rivers. It is thus relevant for fisheries planning and conservation.

1. Introduction

The Mekong River Basin is one of the 35 biodiversity hotspots of the world (Mittermeier et al., 2011). Fish assemblages in this basin are extremely diverse and characterized by the presence of fish species undertaking large-scale seasonal migrations (Poulsen et al., 2002). The complex seasonal flood pulses and historical biogeography of the region partly explain this high diversity and seasonality (Poulsen et al., 2002; Rainboth, 1996). Rapid changes through time due to hydropower infrastructure development in the basin may change the abiotic and biotic components of the river ecosystem, including changes in river flow, habitat, food web, species distribution, and finally the river's overall biological integrity (Li et al., 2013; Macnaughton et al., 2015; Phomikong et al., 2014; Tonkin et al., 2017).

This study covers five sites. Three sites are in the lower reach of the three Mekong major tributaries: Sekong (SK), Sesan (SS) and Srepok (SP) rivers, called the 3S; and two sites are in the Mekong mainstream: up- and downstream of the 3S outlet (Fig. 1). All sites are part of the complex Mekong-3S system, located in north-eastern Cambodia in the Kratie (KT), Stung Treng (ST) and Ratanakiri provinces. The Mekong mainstream (KT and ST) is a critical habitat for many Mekong fishes, (Baran, 2006; Poulsen et al., 2004, 2002) and the Mekong River in ST has been designated a Ramsar wetlands of global significance since 1999 (Try and Chambers, 2006). The 3S rivers on the other hand, draining north-eastern Cambodia, southern Lao People's Democratic Republic (PDR), and Viet Nam's Central Highlands, join the Mekong River in ST. According to the Mekong River Commission (MRC), they contribute ~25% of the Mekong mean annual flow at KT and play a key role in the hydrology of the downstream Mekong, including the Tonle Sap River showing seasonal reverse flows (MRC, 2005). In addition, the 3S system is the main fish migration route from the lower Mekong system (Poulsen et al., 2004, 2002).

To address the energy needs and economic growth of the region, continued hydropower development has been underway in the Mekong River Basin. Six large hydropower dams have been constructed in the upper Mekong River in China since the mid-1990s (Fan et al., 2015; Winemiller et al., 2016). In the Lower Mekong Basin (LMB), according to MRC's Hydropower Project Database 2015, two mainstream dams

* Corresponding author at: CNRS, IRD, Université Toulouse III Paul Sabatier, ENFA, UMR5174 EDB (Laboratoire Évolution & Diversité Biologique), 118 route de Narbonne, F-31062 Toulouse, France.
E-mail address: pengbun.ngor@gmail.com (P.B. Ngor).

https://doi.org/10.1016/j.ecolind.2018.01.023
Received 20 July 2017; Received in revised form 10 January 2018; Accepted 12 January 2018

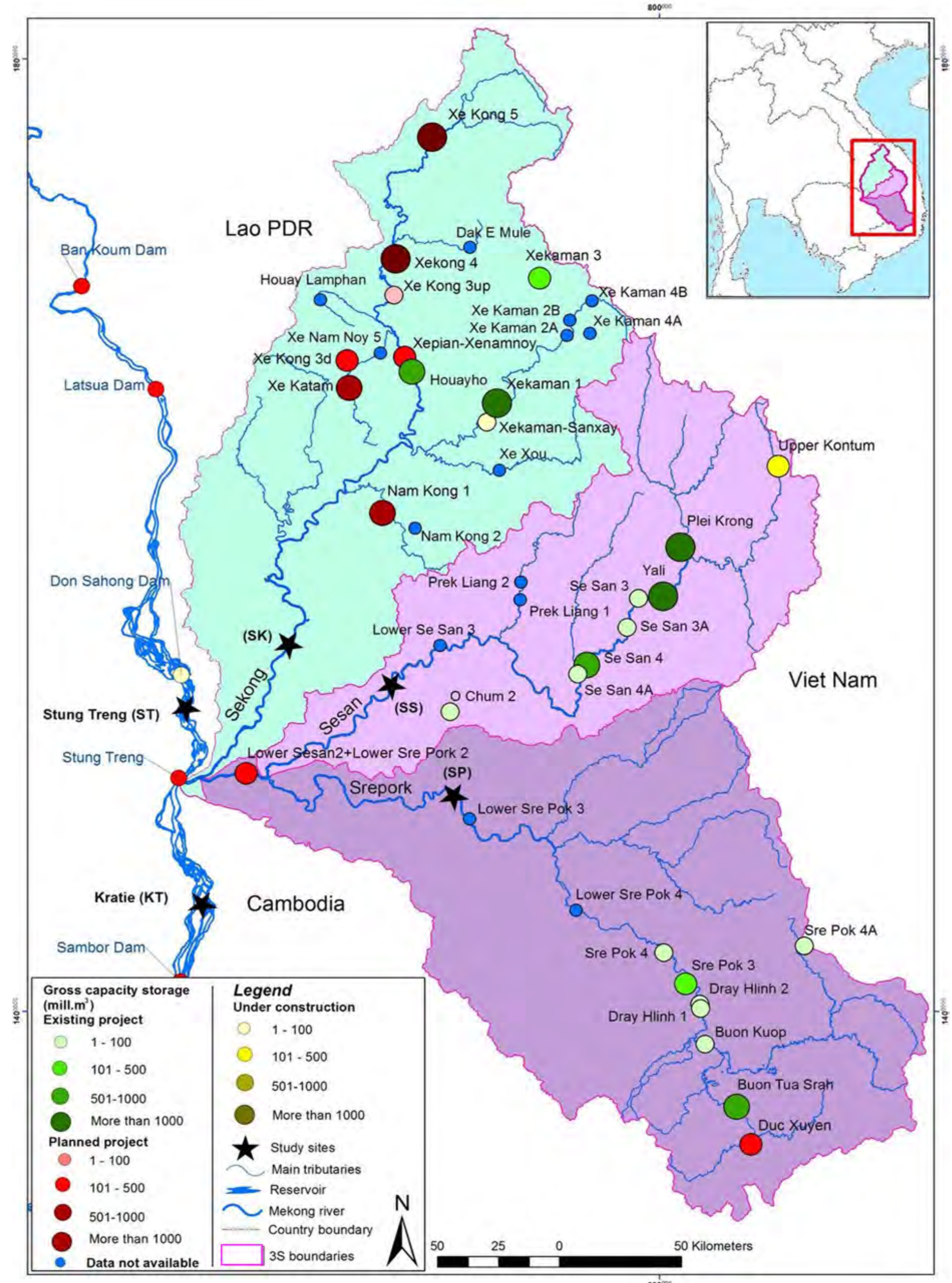


Fig. 1. Map showing the study sites and hydropower dam positions in the 3S sub-basin (Data source: MRC Hydropower Project Database 2015). Site names: KT = Kratie, SK = Sekong, SP = Srepok, SS = Sesan, and ST = Stung Treng.

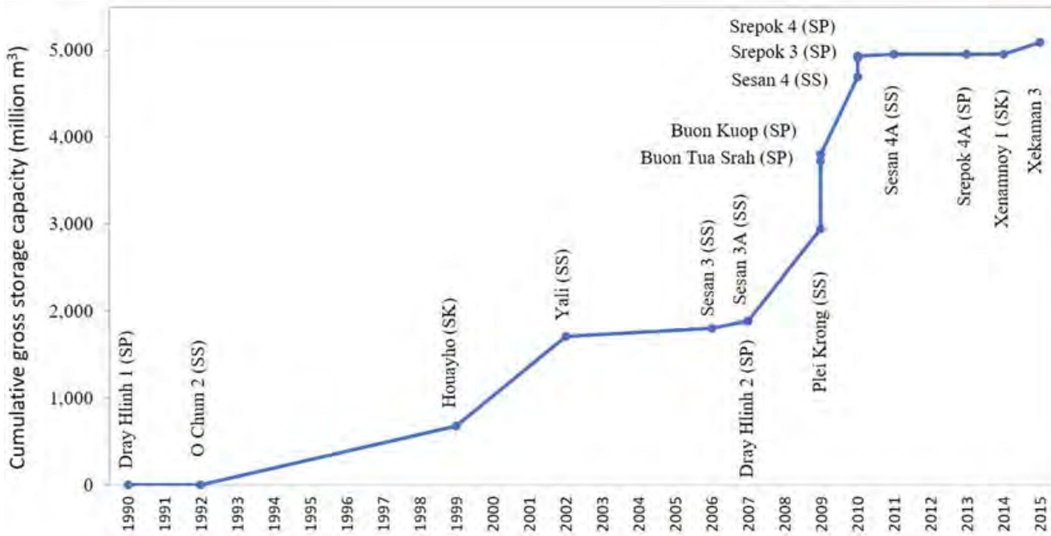


Fig. 2. Timeline and cumulative installed gross storage capacity of existing hydropower dams in the 3S sub-basin (Data source: MRC Hydropower Project Database, 2015).

are under construction in Lao PDR, and nine others are planned; in the LMB tributaries, 42 dams are in operation, 27 are under-construction, 17 are licensed and 58 are planned by 2030. In the 3S sub-basin alone, 17 dams have been functioning since the 1990s, with a total gross storage capacity of ~5100 million m^3 (Fig. 2).

Evidence suggests that these dams have significantly modified the natural flow dynamics of the Mekong River system, with undocumented effects on the river ecology and fisheries (Cochrane et al., 2014; Piman et al., 2013; Sabo et al., 2017; Winemiller et al., 2016; Ziv et al., 2012). In the 3S, the current functioning dams cause an increase of 28% in the dry seasonal flow and a decrease of 4% in the wet seasonal flow (Piman et al., 2013). Dams in the Upper Mekong in China reduce flood pulses, for example, by 23 and 11% in rising and falling rates, respectively, in the Tonle Sap River (Cochrane et al., 2014), a major tributary situated downstream of the Mekong-3S system. These changes in natural flood pulse dynamics are expected to have altered fish assemblage structure, because in the 3S system, at least 89 migratory species are found, including 17 endemic and 14 endangered or critically endangered species (Baran et al., 2013a), and in the Mekong Basin, among the 877 recorded species (Rainboth, 1996; Ziv et al., 2012) ~87% are migratory and mainstream spawners (Baran, 2006; Baran et al., 2013b). These fishes depend on natural seasonal flood pulses as the main ecological trigger to disperse, reproduce and seek refuges during their life cycles (Baran, 2006; Poulsen et al., 2004, 2002). Currently, however, far less is known about how downstream fish assemblages in the species-rich Mekong-3S system respond to such hydrologic flow modifications caused by the upstream functioning hydropower dams.

The five sites selected for this study, being located in the same ecoregion and thus displaying similar environmental conditions, allow comparing how fish assemblages respond to rivers displaying natural versus regulated flows caused by upstream functioning dams. Among the five sites, the mainstream sites (ST and KT) are the least altered by hydropower dams and characterized by more predictable-seasonal flow patterns (see Supplementary S1), as to date, there have been no functioning dams on the mainstream of LMB, which contributes 84% to the total annual flow of the Mekong Basin (MRC, 2010). By contrast, the 3S sites (SS, SP, and SK) are characterized by unpredictable flows (see S1) due to the storage effects of multiple dams acting upstream (Fig. 2). Among the three sites, SS and SK have flow patterns more severely altered as documented in (Baird et al., 2002; Baird and Meach, 2005; Baran et al., 2013a; Claasen, 2004; Hirsch and Wyatt, 2004; Rutkow et al., 2005) and shown in S1. Suffering different levels of flow disruption, the fish assemblages in these five sites are expected to display different inter-annual and seasonal responses (Röpke et al., 2017). According to Tonkin et al. (2017), fish assemblages in predictably seasonal flow conditions (i.e., ST and KT) should experience strong temporal (seasonal) turnover and should host high species diversity through more specialist species occupying available temporal niches. By contrast, fish assemblages in more unpredictable flow environments (3S) should show low temporal diversity and should harbour broad generalist species displaying little seasonal turnover.

Here, we examine the temporal dynamics of fish assemblage compositions among the five studied sites during the 7-year period between June 2007 and May 2014. Our central hypothesis is that assemblages in sites undergoing modifications in seasonal flow regime due to dams (3S) will display different temporal dynamics compared to assemblages in sites enjoying more natural flow regimes (Mekong). First, we expect that, by regulating flow regimes during the year, dams will decrease the seasonal responses of assemblages. Second, we expect that fish assemblages in sites undergoing flow regulation (3S) will experience a decrease in either species richness or diversity due to the escape of species from adverse environmental conditions, i.e., species strongly dependent on seasonal flow regimes to complete their life cycles. Third, and closely linked to our second expectation, we predict a switch in assemblage composition from more specialists in sites with predictable flow (Mekong) to more generalists in sites experiencing flow disruption (3S). To test these hypotheses, we use monitored daily fish and water level time-series data between 1 June 2007 and 31 May 2014, or 365 weeks, initiated by the MRC on our five sites for assessing the impact of water infrastructure development in the Mekong River Basin (MRC, 2007). While our work contributes to the overall science-based understanding of fish assemblage dynamics in the Mekong-3S system, its original focus is on fish temporal beta diversity and how flow alterations caused by upstream functioning dams shape the temporal dynamics of fish beta diversity (assemblage composition) in the Mekong-3S river system.

2. Materials and methods

2.1. Data collection

Stationary gillnets were used for data collection. MRC standard sampling procedures for fish catch monitoring were applied (MRC, 2007). Monitoring sites were selected to cover the Mekong-3S system and the main riverine habitats that display a gradient of flow perturbation from upstream hydropower dams. The sampling sites extend a few kilometres in length and are located on the backwaters and/or sandbars of the river reach in the village where the participating professional fishermen are based. These sampling sites stayed relatively unchanged over the study period. Daily, each fisherman (three for each site, and fifteen for the five study sites) used a set of stationary gillnets with a range of mesh sizes (length: 120 ± 50 m, height: 2–3.5 m, mesh size: 3–12 cm, soak hours/day: 12 ± 2). The fishermen were supervised by fishery researchers from the Inland Fisheries Research and Development Institute (IFReDI) of the Cambodia Fisheries Administration, with technical support from the MRC fisheries monitoring specialists. The main advantages of such sampling designs are lower cost, but provide a sustained and coherent long-term records of fish datasets for the time-series analysis. The fish species list (~900 species and including ecological attributes) comes from the MRC Mekong Fish Database (MFD) (MFD, 2003) and was cross-checked with FishBase (Froese and Pauly, 2017) and other literature sources (Kottelat, 2013; Rainboth et al., 2012). Captured fish were identified to the species level and counted. After field verification, field collected data were recorded into the national fish monitoring database, which was quarterly cleaned by research officers from the IFReDI with the help of the MRC database expert and fisheries monitoring specialists. Water levels at each sampling location were registered by MRC.

2.2. Data analyses

Daily fish samples were recorded as daily mean samples and then aggregated into weekly fish richness and abundance data by species over the period from 1 June 2007 to 31 May 2014. For the entire period of the study, we have 2557 mean daily samples, or a total for 365 weeks and 2 days. We thereafter dropped the 2 days and consistently used 365 weeks across all sites for the analysis. Likewise, daily water levels in each site were computed into mean weekly water levels for the same 365 weeks.

2.3. Overview of fish assemblage structure

To get an overview of the fish assemblage structure, *K*-means clustering (with five pre-determined clusters) on the Hellinger-transformed yearly fish assemblage data was computed to classify all observations in the Mekong-3S system. The Fviz_cluster function of the factoextra package was applied to visualize the assigned five *K*-means clusters, with observations represented by points, using Principal Components Analysis (PCA) (Kassambara, 2017). PCA is used because it provides the proportion of variance accounted for by the first two axes (Borcard et al., 2011). Boxplots of total weekly species richness and the inverse Simpson diversity index were also computed to describe the spatial and temporal dynamic patterns of the fish assemblage structure, both at each site and in the entire Mekong-3S system. The inverse Simpson index was used because it is a meaningful and robust diversity index that captures the variance of species abundance distribution while being less sensitive to species richness (Magurran, 2004). Non-parametric Pairwise Wilcoxon Rank Sum Tests were used for multiple comparison tests on species richness and diversity indices among the study sites.

2.4. Temporal dynamics of beta diversity

Beta diversity describes the variation in species composition among sites in a study area or among survey times for a survey across years (Legendre and De Cáceres, 2013; Legendre and Gauthier, 2014). In estimating total beta diversity (BD_{total}), the total variance of Hellinger-transformed weekly assemblage abundance data was used to reduce disproportionate effects of large abundance values (Legendre and De Cáceres, 2013). BD_{total} has a value between 0 and 1 for Hellinger-transformed data. BD_{total} can be compared among sites if the sampling units across the study sites are of the same size (Legendre and Salvat, 2015), which is the case for the present study. If BD_{total} is equal to 1, all sampling units have a completely different species composition. BD_{total} was then partitioned into Local (temporal) Contributions to Beta Diversity (LCBD) and Species Contributions to Beta Diversity (SCBD). LCBD is a comparative indicator of the ecological uniqueness of the sampling units. LCBD values give a total sum of 1 for a given data matrix and can be tested for significance (at the 0.05 level in the present study). BD_{total} and LCBD indices can be computed for repeated surveys, and thus form a time series (Legendre and Gauthier, 2014). SCBD indices, on the other hand, indicate the relative importance of each species affecting beta diversity patterns. Species biological traits, including feeding type, habitat preferences, body size and dispersal capacity, are likely to have an influence on SCBD (Heino and Grönroos, 2016). Species with SCBD indices well above the mean were regarded as important species contributing to beta diversity (Legendre and De Cáceres, 2013). All these indices were computed separately for each of the five study sites using the beta.div function of the adespatial package (Dray et al., 2017; Legendre and De Cáceres, 2013) with 9999 permutations in R (R Core Team, 2015).

To explain the temporal dynamics of LCBD in each site, weekly LCBD indices were modelled as a function of linear weekly abundance, weekly richness and mean weekly water levels. Standardised regression coefficients and *p*-values of each predictor were used to indicate the effect and significance level of each predictor on the LCBD. Standardised regression coefficients are used to make the regression coefficients more comparable to each other. All explanatory variables were log-transformed prior to the analysis to address the skewed distribution of the variables. To determine the relative contribution (in percentage) of each predictor to the total explained variance of each model, hierarchical partitioning of the significant variables from the LCBD models was computed using the hier.part function of the hier.part package in R.

Further, to examine how fish assemblages responded to seasonal hydrology changes, temporal LCBD indices were plotted against water levels across the 7-year hydrological cycles. Significant LCBD indices (being unique) were also visualised on the plot to investigate whether the temporal uniqueness of an assemblage composition (temporal significant LCBDs) occurred in relation to the site hydrological cycles or otherwise. Further, the non-parametric Spearman's correlation test was performed for each site to test the link between the two variables.

2.5. Temporal variation of assemblage structure

To identify significant seasonal assemblage variations, weekly periodic variability in species abundance and richness were examined using Whittaker–Robinson periodograms (Legendre and Legendre, 2012). The periodograms were computed using the WRperiodogram function of the adespatial package (Dray et al., 2017). This method was chosen because of its simplicity of interpretation; i.e., the period with maximum amplitude is taken as the best estimate for the true period of oscillation (Legendre and Legendre, 2012). Prior to analyses, the weekly data for each site were tested for stationarity. When stationarity was violated (i.e., KT, ST, SS, and SK, see S3), residuals from the linear regressions (against time) for individual sites were computed and used in the periodogram analyses. Periodogram graphs were plotted to visualize the seasonality of fish total abundance and richness at each site.

2.6. Temporal shift of species contributing to beta diversity

To identify the key species contributing to the temporal dynamics of species composition over the study period, species with SCBD indices greater than the mean at each site were extracted from the assemblage composition matrix. Given that our interest is in how assemblage composition shifts through time, Redundancy Analysis (RDA) was performed on the assemblage composition data against time and its quadratic effect as explanatory variables. The inclusion of a second-degree polynomial allows the assemblage time series to double back upon itself (Legendre and Salvat, 2015). The linear and quadratic effects of time on the assemblage data were both significant predictors of the assemblage variations among years (test of RDA R-square, $P < 0.001$). RDA is an extension of multiple regression analysis (Legendre and Salvat, 2015). Using RDA, the relationship between the observations (sampling units), species and explanatory variables (the years) can be visualized. Further, to help identify the key species explaining the temporal shift in assemblage composition, indicator species characterising fish assemblages at each site were computed using the multipatt function of the indicspecies package (Cáceres and Legendre, 2009; De Cáceres and Jansen, 2011) for comparison. Indicator species are species that are used as ecological indicators of community or habitat types, environmental conditions, or environmental changes (De Cáceres et al., 2010), whereas species with large SCBD values are those that are abundant and dominate the assemblage (Legendre and De Cáceres, 2013). Assemblage composition data were Hellinger-transformed prior to RDA computation.

3. Results

3.1. Overall assemblage structure

Over the study period, 292 species were recorded in the catch samples. Among those, 208 fish species were recorded in Kratie (KT), 196 in Stung Treng (ST), 177 in the Srepok River (SP), 133 in the Sesan River (SS) and 216 in the Sekong River (SK). These fishes belong to 14 orders, 48 families and 151 genera. Five main orders represent 90% of the total species count: Cypriniformes (146 species), Siluriformes (66), Perciformes (34), Pleuronectiformes (9) and Clupeiformes (6). The top five families accounting for 63% of total species counts were Cyprinidae (123 species), Bagridae (16), Cobitidae (16), Pangasiidae (15) and Siluridae (11). See S6 for a full species list by genera, families and orders.

K-means clustering (with five clusters) on a PCA plot (Fig. 3a) shows that sites on the Mekong (cluster 4 and 5) are overlapped, indicating assemblage similarities between the two sites, while the 3S sites, particularly SK (cluster 1) and SS (cluster 2), are distant from the Mekong sites, suggesting distinct assemblages. SP (cluster 3) exhibits some similarities with the Mekong sites (ST). Assemblage dissimilarities are further observed among the 3S sites (axis 2).

In addition, boxplots on weekly richness and inverse Simpson diversity index (Fig. 3b, c) indicate that the Mekong sites have the highest richness (KT: median = 23, sd = 10.95; ST: median = 27, sd = 9.87) and inverse Simpson indices (KT: median = 9.20, sd = 5.30; ST: median = 8.82, sd = 5.10) relative to the 3S sites. Noticeably, SS shows both the lowest species richness (median = 12, sd = 5.14) and diversity index (median = 5.45, sd = 2.78) of all sites, whereas SP is comparable with KT in terms of species richness. Although SP has higher species richness (median = 23, sd = 7.52) than SK (median = 19, sd = 8.25), the diversity indices between the two sites are not significantly different (SP: median = 6.89, sd = 3.70; SK: median = 7.49, sd = 4.38). Overall, the Mekong-3S system has experienced gradual diminishing trends of weekly fish abundance and richness, except for SK (S3), whereas trends of inverse Simpson diversity index are found to be declining, particularly in the Mekong sites (S2c).

3.2. Temporal dynamics of beta diversity

Total beta diversity (BD_{total}) indices estimated for the sites were 0.50 in SP, 0.59 in ST, 0.66 in KT, 0.73 in SS and 0.74 in SK. Temporal LCBD weekly values ranged between 1.26E − 03 and 6.36E − 03; the LCBD values are small because they are made to sum to 1 across all weeks for each site. The site with the highest LCBD values is SS (median = 2.71E − 03, sd = 4.33E − 04), whereas the site with the lowest LCBD value is SP (median = 2.53E − 03, sd = 9.69E − 04). The other sites have intermediate values of weekly LCBD. Among the 365 weeks, 10% (35 weeks), 13% (48), 13% (46), 8% (29) and 18% (66) have statistically significant values of LCBD (assemblage composition being unique) in KT, ST, SP, SS and SK, respectively. This manifested strong temporal changes in the uniqueness of fish assemblage compositions over the study period for all sites. For the two Mekong sites (i.e., KT and ST), these significant temporal LCBDs (red dots on Fig. 4) are found to occur at the time when seasonal water levels start rising on the annual cycle basis, whereas no such patterns are exhibited in the 3S rivers. Significant correlation between LCBDs and water levels are revealed in KT ($P = 0.003$), SP ($P < 0.001$), and SK ($P = 0.015$). While ST is on the margin ($P = 0.052$), no significant correlation of the two variables is indicated in SS ($P = 0.074$).

3.3. Temporal determinants of LCBD indices

Multiple linear regressions show that LCBD values are significantly related to the three predictors: total abundance, total richness and mean water level, depending on the study site (Table 1). Overall, the adjusted coefficient of determination (adjusted R^2) for each site model explains 50% in KT, 61% in ST, 31% in SP, 35% in SS and 62% in SK. Richness is the most contributed variable negatively explaining the temporal changes in LCBD for all sites. In contrast, positive relationships between LCBD and total abundance are exhibited in KT, ST and SP, while no such relationship is found in SS and SK. Water level is linearly linked to LCBD in all sites except for ST, with the significant negative linear relationships observed in KT and SS, and positive linear relationships in SP and SK.

Hierarchical partitioning (Table 1) highlights the high contribution of total richness and abundance in explaining LCBD variations (i.e., KT (85.55%), SS (94.99%), and SK (99.03%) for species richness, and KT (13.72%), ST (79.91%), and SP (53.16%) for abundance). Water level is found to independently contribute the highest proportion (33.30%) of the model total variance in SP.

3.4. Temporal variation of assemblage structure

Periodogram analyses on weekly abundance and richness (Fig. 5a, b) indicate that significant frequencies of semi-annual and annual cycles are exhibited in the Mekong mainstream sites, while no such patterns are displayed in the 3S sites. In KT, significant periods of weekly abundance (Fig. 5a) are found at 51–56 weeks, with harmonics at 104–109 and 154–160 weeks. The other significant periods (26 and 133–135 weeks) in this site show semi-annual cycles. A similar pattern was revealed for the site species richness (Fig. 5b), where significant periods are detected at 48–57 weeks, with harmonics at 100–112 and 148–65 weeks. In ST, significant periods of species abundance occur at 52–48 weeks, with harmonics at 104–118 and 159–166 weeks; however, this pattern is less pronounced for the species richness. By contrast, there are no clear significant signals of semi-annual or annual cycles in the 3S sites. Additionally, far fewer significant periods with high frequencies are revealed in the 3S than the mainstream sites (KT and ST) for both abundance and richness.

3.5. Species contributions to temporal beta diversity

A total of 96 species, i.e., 33% of the total species, bring important contributions to site beta diversity (above overall mean SCBD value), 13 of which are largely distributed across all sites (see S4, S5). Of the 96 species, 55 are identified in KT, 45 in ST, 44 in SP, 34 in SS and 56 in SK. Among these important species, the number of species that are also indicator species generated by the multipatt function in each site are as follows: 17 species in KT, 26 in ST, 14 in SP, 12 in SS and 17 in SK (see S4 and S5 for species details). Species with the highest SCBD indices are *Puntioplites falcifer* in KT, *Henicorhynchus lobatus* in ST, *Hypsibarbus malcolmi* in SP, *Anabas testudineus* in SS and *Paralaubuca barroni* in SK.

RDA analysis on assemblage composition (with SCBD indices greater than mean) against time depicts a strong temporal shift in assemblage composition at all sites. In the Mekong mainstream (Fig. 6a),

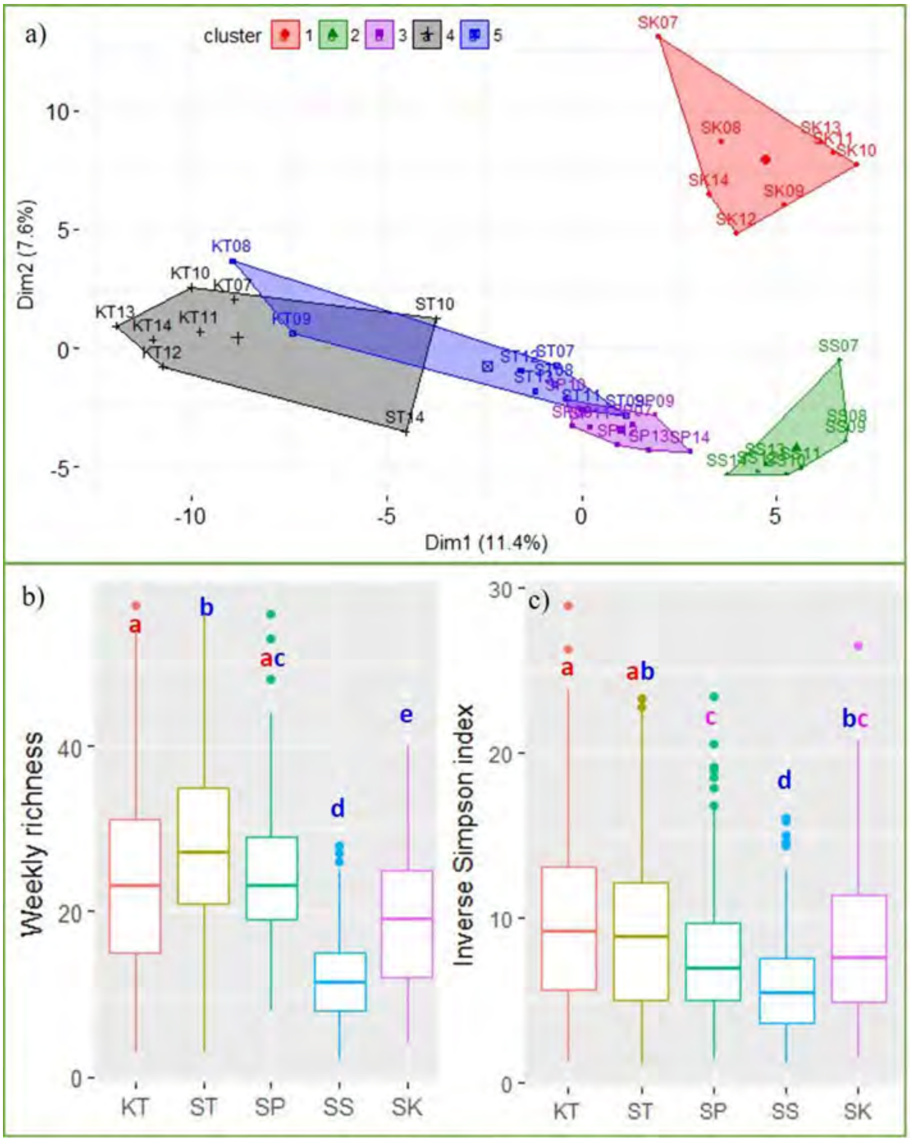


Fig. 3. Fish assemblage patterns in the Mekong-3S system. (a) *K*-means cluster on PCA plot (k = 5) on Hellinger-transformed yearly assemblage data. Five convex hulls (with different colours) represent each assemblage cluster of the Mekong-3S system. A combination of two letters and two digits denotes the site name and year; for example, KT07 is Kratie in 2007. (b) Boxplots of total weekly richness by site; (c) Boxplots of weekly inverse Simpson diversity index by site. Mean values among sites (Fig. 5b, c) with a common letter are not significantly different at the 0.05 level (Pairwise Wilcoxon Rank Sum Tests). For site names, see Fig. 1.

during the early years of the survey (2007–2010), temporal assemblage variability is mostly due to small-sized generalist and specialist species. After 2010, the composition tends to be disproportionally represented by specialists. Small-sized mud carps (maximum total length – mTL < 25 cm) i.e., *Henicorhynchus lobatus* (Hlobatu), *H. siamensis* (Hsiamen) and *Labiobarbus siamensis* (Lsiamen), the most common and abundant species in LMB, are found to be characteristic and important species for both sites during the period 2007–2010. Afterwards, specialists disproportionally represent the assemblage in both sites. Some common specialists describing assemblage in the Mekong mainstream during 2011–2014 are short distance migrants and mainstream spawners such as *Hypsibarbus malcolmi* (Hmalcol), *Phalacronotus apogon* (Papogon.1), *Hypsibarbus lagleri* (Hlagler), *H. wetmorei* (Hwetmor); long distance migrants such as large-sized cyprinids (mTL > 60 cm) *Cosmochilus harmandi* (Charman), *Cirrhinus microlepis* (Cmicrol), *Cyclocheilichthys enoplos* (Cenoplo), *Labeo chrysophekadion* (Lchryso); and river catfishes, namely, *Helicophagus waandersii* (Hwaande) and *Pangasius conchophilus* (Pconcho) (only in ST).

In contrast, temporal dynamics in assemblage composition shifted from specialists (during the 2007–2010 period) to generalists (after 2010) in the 3S (Fig. 6b). The pattern is pronounced in SP and SK, where long-distance migratory species and main channel spawners with large-bodied sizes, such as *Phalacronotus apogon* (Papogon.1), *Hypsibarbus lagleri* (Hlagler), *Helicophagus waandersii* (Hwaande), *Hypsibarbus malcolmi* (Hmalcol), *Pangasius conchophilus* (Pconcho), *P. bleekeri* (Pbleeke), *Hypsibarbus pierrei* (Hpierre), etc., represented the assemblages between 2007 and 2010 and were then replaced by small-sized minnows and carps with generalist habitat preference, such as *Labiobarbus siamensis* (Lsiamen), *Systomus rubripinnis* (Srubrip), *Henicorhynchus siamensis* (Hsiamen) and *Osteochilus vittatus* (Ovittat), etc., between 2011 and 2014. This pattern is less clear in SS; however, this site shows that the generalist *H. lobatus* significantly contributes to the temporal changes in assemblage composition during the 2011–2014 period. Moreover, assemblages in the SS during the entire period were largely represented by generalists as found in SP and SK and other small-sized minnows and carps, such as *Paralaubuca typus* (Ptypus), *P. riveroi* (Privero), *P. barroni* (Pbarron), *Rasbora tornieri* (Rtornie), *Cyclocheilichthys armatus* (Carmatu), etc. Further, assemblages in the 3S towards 2011–2014 are partly composed of black fishes (floodplain residents) such as climbing perches *Anabas testudineus* (Atestud), air-breathing catfishes *Clarias batrachus* (Cbatrac) and snakeheads *Channa striata* (Cstriat). Important species contributing to site beta diversity and their ecological attributes are given in S5.

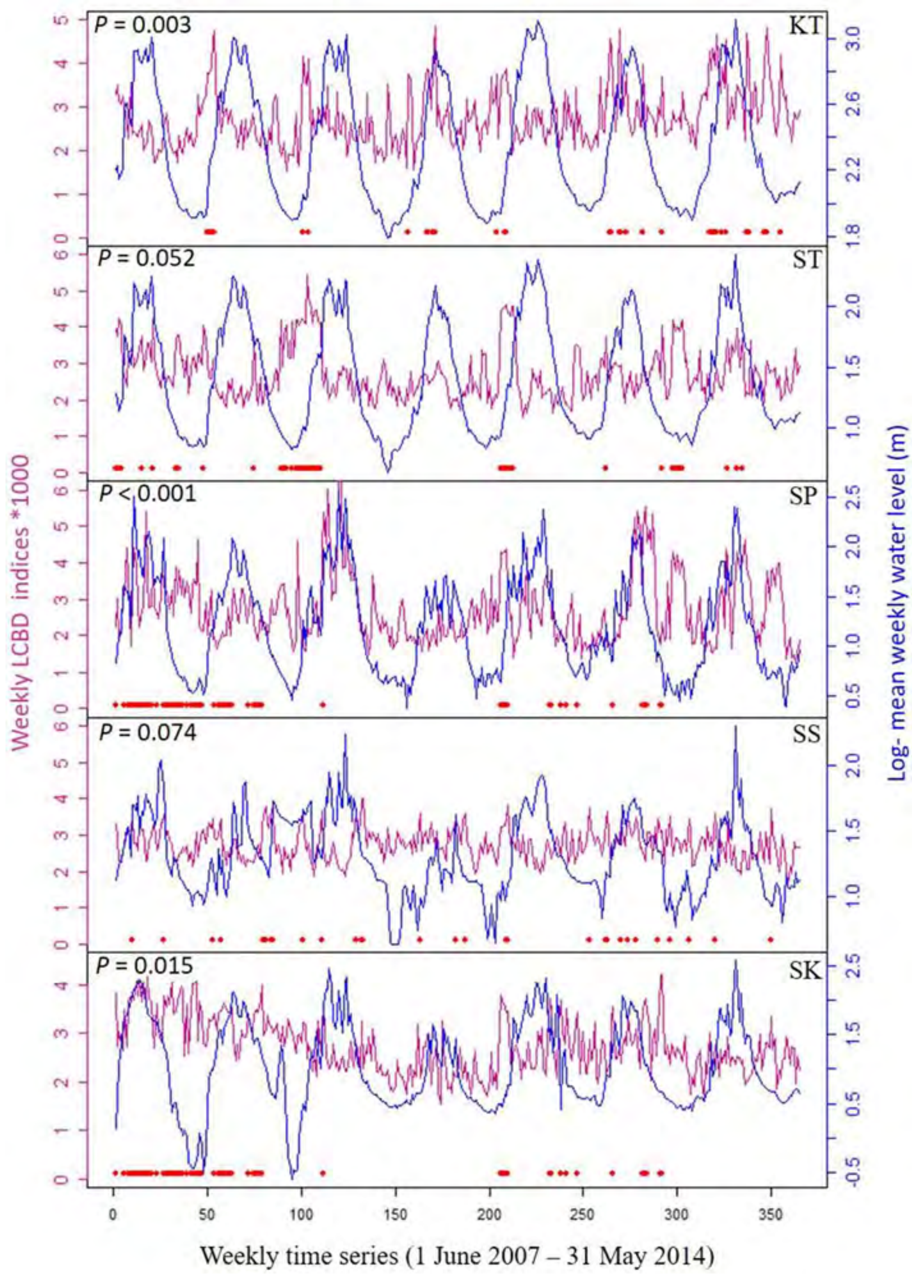


Fig. 4. Temporal changes in LCBD indices (red line) and mean log-transformed weekly water levels (blue line) over 7-year hydrological cycles on five sites of the Mekong-3S River system. More predictable-seasonal flow patterns are shown in KT and ST, and unpredictable/regulated flows are displayed in SP, SK, and SS. The red dots indicate weeks with significant LCBD indices at the 0.05 level. *P* denotes the *p*-value of the pairwise correlation test using the Spearman method. For site names, see Fig. 1.

4. Discussion

We find that fish assemblages in SP have some similar composition patterns to those of the Mekong sites. We also find strong temporal dynamics of fish assemblages in the complex Mekong-3S system, with total site beta diversity (BD_{total}) ranging between 0.50 and 0.74. Local species richness and abundance are the most important determinants explaining the temporal change in local beta diversity (LCBD). Our findings strengthen the results of previous studies highlighting the strong relationships of species richness and abundance with local LCBDs (Heino and Grönroos, 2016; Legendre and De Cáceres, 2013; Qiao et al., 2015). Water level is also an important ecological determinant that further explains these temporal changes (Table 1). In the Mekong-3S system, we observe that water levels in the Mekong sites show more seasonal-predictable patterns than those in the 3S sites where the seasonality of flow is disrupted by increasing dam operations in the upper reach of these rivers since 1990s (S1, Figs. 1, 2 and 4).

Some similarities of fish assemblage patterns in SP to those with the Mekong sites (Fig. 3a) are likely because SP has the highest number of migratory species (81) relative to SK (64) and SS (54) (Baran et al., 2013a). These migratory species e.g., Pangasiidae and Cyprinidae could migrate hundreds of kilometers between the mainstream, tributaries and floodplains during their life cycles (Poulsen et al., 2004, 2002; Sverdrup-Jensen, 2002). Local fish migration behaviour may additionally explain the pattern. Most cyprinids are known to migrate upriver along the edges of rivers; therefore, when fish leave the Mekong, enter the SK and travel up along its southern bank, they will enter SS and will soon continue right into SP (Baran et al., 2013a) (see also Fig. 1). Moreover, SP has greater depths and better flow conditions relative to SS and SK (see S1). These factors combined tend to explain some similarities of the assemblage patterns between the two rivers.

Overall, our results support the central hypothesis that fish assemblages in sites with unpredictable flows (3S) exhibit different temporal changes compared to fish assemblages in sites with predictable flow patterns (the Mekong) (Fig. 3a). As expected under our first hypothesis, assemblages in the Mekong (undisturbed sites) are characterized by a

Table 1
Standardised regression coefficients resulting from the multiple regression models of weekly LCBD values against the weekly total abundance (AB), weekly total richness (SR) and mean weekly water levels (WL) in each study site. All variables are log-transformed. R^2 = coefficient of determination. Asterisks indicate the significance levels associated with each predictor, with '*' at 0.05, '**' at 0.01, and '***' at 0.001. Plus '+' and minus '−' signs indicate the positive and negative relationships, and '**ns**' denotes 'not significant'. Values in brackets, resulting from hierarchical partitioning, indicate the relative independent contribution (in percentage) of each significant variable to the total explained variance. (−) denotes 'not available' for variables that are not significant at the 0.05 level.

Site	AB	SR	WL	Adjusted R^2
KT	$+5.355^{***}$ (13.72%)	-17.082^{***} (80.55%)	-5.727^{***} (5.73%)	0.50
ST	$+23.454^{***}$ (79.91%)	-13.213^{***} (20.09%)	-0.244^{ns} (−)	0.61
SP	$+10.152^{***}$ (53.16%)	-6.406^{***} (13.81%)	$+7.647^{***}$ (33.03%)	0.31
SS	$+1.358^{ns}$ (−)	-13.075^{***} (94.99%)	-3.057^{**} (5.01%)	0.35
SK	-0.926^{ns} (−)	-15.671^{***} (99.03%)	$+2.157^{*}$ (0.97%)	0.62

strong seasonal variability. This is depicted by the significant temporal LCBD signals showing the uniqueness of the fish assemblage compositions in KT and ST occurring in relation to the annual flow cycles, particularly when water levels start rising (Fig. 4). Many Mekong fishes are known to start their seasonal migration for spawning and feeding/rearing grounds when seasonal flooding in the Mekong begins in late May or June (Poulsen et al., 2004, 2002; Sverdrup-Jensen, 2002). Water levels are the most important ecological determinants in triggering these seasonal migrations (Baran, 2006). In contrast, the significant temporal LCBDs indicating the uniqueness of fish assemblages in the 3S sites (Fig. 4; SP, SS, and SK) are characterized by chaotic variations unrelated to the seasonal hydrological cycles. Flow perturbation caused by dams in the 3S system has decreased seasonal variation of flow, thus muting the seasonal structure of fish assemblages. The results from the periodogram analyses (Fig. 5) further indicate that in predictable systems (KT and ST), significant period signals with high frequencies of species abundance and richness are harmonic at semi-annual and annual cycles over the study period, which is not the case for the 3S sites. Our findings are consistent with the seasonality framework proposed by Tonkin et al. (2017), emphasizing that sites with

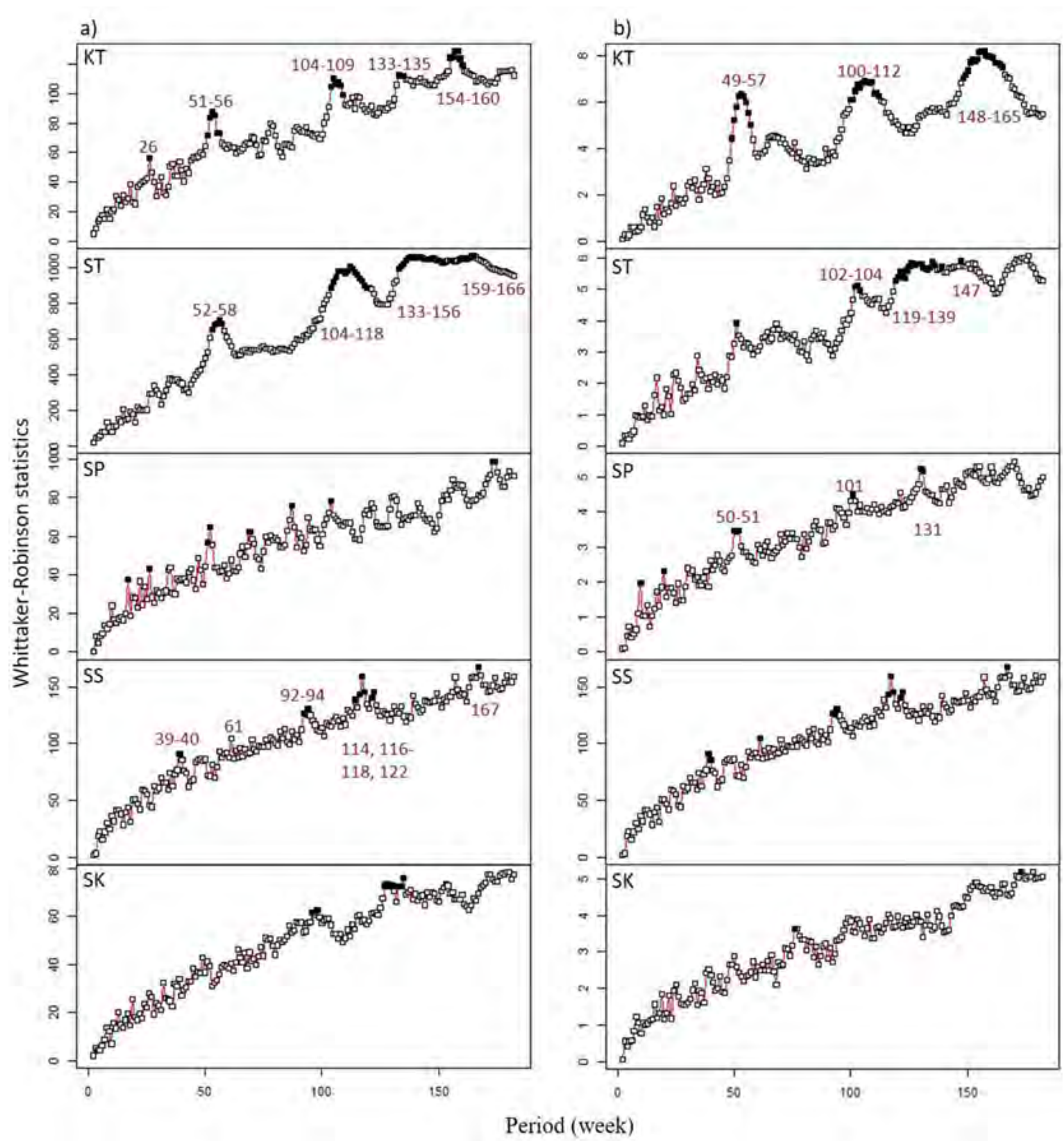


Fig. 5. Whittaker-Robinson periodograms computed for (a) weekly abundance and (b) richness, featuring periods between 2 and 182 weekly intervals from a 365-week data series from 01 June 2007 to 31 May 2014. The upper limit of the observation window of the periodograms is the number of observation intervals divided by 2 or a 182-week period. Black squares identify periods that are significant at the 0.05 level. For site names, see Fig. 1.

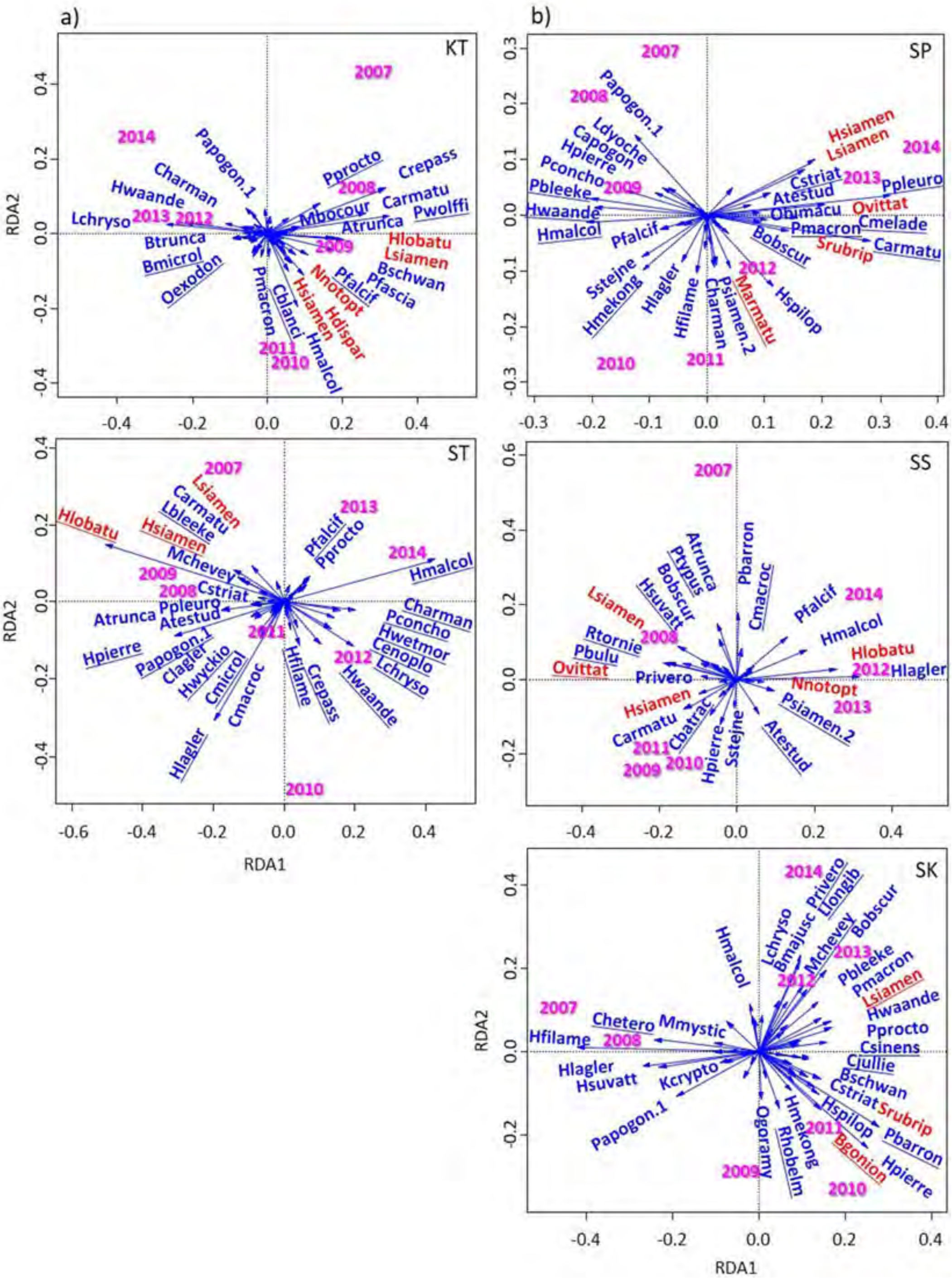


Fig. 6. RDA biplots of Hellinger-transformed assemblage data showing the important species (with SCBD indices greater than mean SCBD) contributing to the temporal shift in assemblage composition in each site. (a) Mekong River; (b) 3S Rivers. The biplots show species (arrows) and sampling units grouped by year. Names are abbreviations of fish species names. Species with very small contributions to the ordination are removed for clarity. Underlined species (blue) are indicator species identified by the multipatt function. Species in red have generalist habitat preferences. The assemblage ordination is explained by time (years) and its quadratic effect (not shown). Test of the multivariate RDA R-square: $P < 0.001$. Full species names and ecological attributes are shown in S5. For site names, see Fig. 1.

predictable environmental fluctuations are characterized by temporal (seasonal) assemblage change, whereas sites with unpredictable environmental conditions are represented by aseasonal assemblage variability, as exhibited in the 3S.

In addition, in line with our second expectation, we find that sites displaying flow disruptions (i.e., SP, SK, and SS) are generally poorer in species richness and lower in species diversity than sites with more stable seasonal flow patterns (i.e., KT and ST) (Fig. 3b, c). This pattern is most likely due to flow alterations caused by dams. In other Mekong tributaries, lower species richness has also been observed in regulated rivers (i.e., Gam and Mun Rivers) compared to an unregulated one (Sankgram River) (Phomikong et al., 2014), and hydrological alterations have also been previously identified to cause changes in fish assemblage structure (i.e., reduced species diversity, shift in compositional and life history structure) in central Amazonian and American rivers (Mims and Olden, 2013; Röpke et al., 2017). Further, a general decreasing trend in species abundance, richness and diversity index in the Mekong-3S system has been observed since 2010 (S2). This temporal variation is coincident with the threefold increase in hydropower dam reservoirs in the 3S sub-basin from 2007 to 2010 (Fig. 2) and the construction of a new mainstream dam (Xayaburi) in LMB, which has been underway since 2012 (International Rivers, 2014). In fact, hydropower dams severely alter flows of a river system, causing recruitment failure and diminishment of fisheries productivity at both local and regional spatiotemporal scales worldwide (Jellyman and Harding, 2012; Mims and Olden, 2013; Poff et al., 2007; Winemiller et al., 2016). However, the decreasing trends in species abundance, richness and diversity index are much stronger in sites of the 3S rivers and are attributed to the increasing river impoundment upstream (Fig. 2), which dampens flood pulses, mutes seasonal and inter-annual flow variation, disrupts flow connectivity among fish critical habitats, and alters food web dynamics that support fish diversity and biomass, as previously documented in (Arias et al., 2014; Baird et al., 2002; Baird and Meach, 2005; Claasen, 2004; Hirsch and Wyatt, 2004; Ou and Winemiller, 2016; Piman et al., 2013; Rutkow et al., 2005).

Relative to our third prediction, we find that the temporal dynamics of assemblage composition are driven by specialist species in the Mekong mainstream (Fig. 6a) and by generalist species in the 3S (Fig. 6b). The RDA biplots (Fig. 6a, b) illustrate that key species contributing to the temporal changes in the Mekong sites during the last four years of the survey are disproportionate towards specialists, including medium and large-sized cyprinids of the family Cyprinidae, river catfishes of Pangasiidae and sheatfishes of Siluridae. These fishes are often long-distance migrants and/or mainstream spawners and prefer mainstream rivers as their main habitats. The opposite is observed in the 3S rivers, where small-sized species minnows and carps of Cyprinidae with generalist habitat preferences are among the key species contributing to the assemblage change. Further, some floodplain resident fishes, such as climbing perches, snakeheads and airbreathing catfishes, are also among the key species in the assemblage composition of the 3S rivers towards the last few years of the survey. These fishes have airbreathing organs and can physically withstand adverse environmental conditions (MRCS, 1992; Poulsen et al., 2002; Welcome, 2001). This trend in assemblage composition of the Mekong-3S system is likely to resemble the environmental filtering by dams because many migratory (specialist) species that depend on seasonal flow dynamics to complete their life cycles are constrained or extirpated by flow disruption of dams (Liermann et al., 2012), which finally leads to increased faunal homogenization as observed in the middle Lancang-Mekong River (Li et al., 2013), many Chinese lakes connecting to the Yangtze River (Cheng et al., 2014), and rivers across the United States (Poff et al., 2007). Our results also strengthen recent review and field studies that find fish assemblages in SS to be represented by small-sized and generalist species such as small mud carps (mTL < 25 cm) of the family Cyprinidae, and fewer large-sized migratory species such as river catfishes of Pangasiidae (mTL > 100 cm), relative to the Mekong mainstream sites (Baran et al., 2013a; Ou et al., 2017; Ou and Winemiller, 2016).

Interestingly, *Henicorhynchus lobatus* is among the highest SCBD values found in ST, KT and SS. The species is known to be an ecological keystone species, playing a critical role in food security throughout LMB and being an important prey species for many predatory fishes and Irrawaddy dolphins (Baird, 2011; Fukushima et al., 2014). This species, together with its relative *H. siamensis,* are claimed by the villagers to have never been seen in the upper SS River in the last 10 years (Baran et al., 2013a). These species are therefore of high conservation value in KT and ST, and need restoration in the altered SS (Legendre and De Cáceres, 2013). Other generalist (*Labiobarbus siamensis*) and specialist species (*Puntioplites falcifer, Hypsibarbus malcolmi*) (migratory/mainstream spawners) share a similar status to *H. lobatus* and *H. siamensis* (among the highest SCBD values) and therefore deserve similar conservation attention. In addition, fish species that have high SCBD values and are the indicator species demonstrated in S4 represent dominantly abundant and ecologically important species in the Mekong-3S system. They therefore have high values for fisheries health monitoring and fish biodiversity conservation initiatives (De Cáceres et al., 2010; Legendre and De Cáceres, 2013).

5. Conclusion

The results of our study suggest that the hydrological conditions of rivers play a pivotal role in shaping the temporal dynamics of tropical freshwater fish assemblages. Flow patterns act as an environmental filtering process in influencing the spatial and temporal organisation of local and regional fish assemblage structures. It is evident that hydropower dams in the upper 3S rivers alter their natural flow seasonality and predictability. This has adversely impacted aquatic organisms adapted to the natural flow conditions for their life cycles. We find that there are overall declining trends in local fish species abundance and richness, with strong temporal variability in local beta diversity of the Mekong-3S system. The disturbed 3S rivers are represented by aseasonal assemblage changes, whereas the Mekong sites are characterised by seasonal assemblage variability. Temporal shifts in assemblage composition are driven by generalist species in the disturbed 3S rivers; whereas specialists are more representative of the Mekong River. The information presented here contributes to the understanding of fish assemblage responses to upstream flow modification and is thus important to better inform river fisheries monitoring, management and conservation initiatives. Our present work focused on temporal fish assemblage composition responses in relation to flow regulation. Therefore, our results would be beneficial for future work aiming to forecast future flow changes and how this affects fish diversity in the Mekong 3S-River System (Chau and Wu, 2010; Wang et al., 2017).

While further dam building is imminent in the Mekong River system, the combined effects of the present and future 3S dams are predicted to have catastrophic impacts on the fish productivity and diversity which secures food to > 60 million people of LMB (Hortle, 2007; Ziv et al., 2012). For this reason, we suggest that some mitigation measures must be undertaken to minimise such impacts. First, there should be a basin-scale integrative strategic plan (accounting for cumulative impacts on hydrology and ecosystem services) that finds the balance between exploiting hydropower potential and sustaining key resources, e.g., in dam site selection (Winemiller et al., 2016). Second, the best available technologies related to up- and downstream fish pass facilities (Schmutz and Mielach, 2015) must be built for existing and planned dams to facilitate up- and downstream fish migrations. Flow management measures that could mimic natural hydraulic variations, e.g., Sabo et al. (2017) should be privileged, as these variations are the main ecological trigger for fish dispersal and reproduction success in the Mekong. Indeed, rivers downstream of gradual release storage dams are found to have higher fish biomass and richness than those downstream of flow peaking storage dams (Guénard et al., 2016). Third, ecological effects of dams are not only restricted to ecosystem services and functioning but also to society, culture and livelihoods such as losses of property, employment, social connections and culture through human resettlements and the displacement of indigenous people. Best practice guidelines on a (participatory) Social Impact Assessment should be applied to assess such sociocultural costs at appropriate temporal and spatial scales (Tilt et al., 2008) for formulating acceptable compensation, resettlement and rehabilitation policies. Finally, institutions permitting and financing hydropower dam development should ensure that dam developers comply with these best practice guidelines during their project design, commission and decommission phases to meet both societal and environmental objectives; otherwise, key natural resources such as fisheries and rural communities that depend on those resources will continue to suffer from the impacts of dams.

Acknowledgements

We are grateful to the Erasmus Plus, Belmont Forum (TLSCC project) and the European Erasmus + credit mobility and capacity building CONSEA Programmes for funding our study. Cordial thanks to the MRC Fisheries Programme, Inland Fisheries Research and Development Institute and the Fisheries Administration, Cambodia for making available the datasets used in this study. We also thank Nam So, Phen Chheng, Solyda Putrea, Sokheng Chan and 15 fishers for supervising and implementing the field fish monitoring, Ratha Sor, Gaël Grenouillet and Fangliang He for their discussions on data analysis, and Kunthea Nuon for helping prepare the map for this study. Finally, we thank the Laboratory of Evolution and Biological Diversity (EDB lab) for their support. EDB lab 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 associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2018.01.023.

References

Arias, M.E., Piman, T., Lauri, H., Cochrane, T.A., Kummu, M., 2014. Dams on Mekong tributaries as significant contributors of hydrological alterations to the Tonle Sap Floodplain in Cambodia. Hydrol. Earth Syst. Sci. 18, 5303–5315. http://dx.doi.org/10.5194/hess-18-5303-2014.

Baird, I., Baird, M., Chum, M.C., Kim, S., Nuon, M., Phat, S., Phouy, B.N., Prom, S., Ros, S., Rushton, H., Sia, P., 2002. A Community-Based Study of the Downstream Impacts of the Yali Falls Dam Along the Se San, Sre Pok and Sekong Rivers in Stung Treng Province, Northeast Cambodia. Se San District Agriculture, Fisheries and Forestry Office, Stung Treng, Cambodia.

Baird, I.G., 2011. The Don Sahong Dam. Crit. Asian Stud. 43, 211–235. http://dx.doi.org/10.1080/14672715.2011.570567.

Baird, I.G., Meach, M., 2005. Sesan River Fisheries Monitoring in Ratanakiri Province, Northeast Cambodia: Before and After the Construction of the Yali Falls Dam in the Central Highlands of Viet Nam. 3S Rivers Protection Network and the Global Association for People and the Environment, Ban Lung, Ratanakiri, Cambodia.

Baran, E., 2006. Fish Migration Triggers and Cues in the Lower Mekong Basin and Other Freshwater Tropical Systems. Mekong River Commission, Vientiane.

Baran, E., Samadee, S., Jiau, T.S., Tran, T.C., 2013a. Fish and fisheries in the Sesan, Sekong and Srepok River Basins (Mekong Watershed). ICEM – International Centre for Environmental Management, Hanoi.

Baran, E., So, N., Degen, P., Chen, X.Y., Starr, P., 2013b. Updated information on fish and fisheries in the Mekong Basin. Catch Cult. 19, 24–25.

Borcard, D., Gillet, F., Legendre, P., 2011. Numerical Ecology with R. Springer Science, New York.

Cáceres, M. De, Legendre, P., 2009. Associations between species and groups of sites: indices and statistical inference. Ecology 90, 3566–3574. http://dx.doi.org/10.1890/08-1823.1.

Chau, K.W., Wu, C.L., 2010. A hybrid model coupled with singular spectrum analysis for daily rainfall prediction. J. Hydroinf. 12, 458–473. http://dx.doi.org/10.2166/hydro.2010.032.

Cheng, L., Blanchet, S., Loot, G., Villéger, S., Zhang, T., Lek, S., Lek-Ang, S., Li, Z., 2014. Temporal changes in the taxonomic and functional diversity of fish communities in shallow Chinese lakes: the effects of river-lake connections and aquaculture. Aquat. Conserv. Mar. Freshwater Ecosyst. 24, 23–34. http://dx.doi.org/10.1002/aqc.2418.

Claasen, A.H., 2004. Abundance, distribution, and reproductive success of sandbar nesting birds below the Yali Falls hydropower dam on the Sesan River, northeastern Cambodia. WWF/Danida/WCS/BirdLife International, Phnom Penh 10.13140/RG.2.2.26563.40488.

Cochrane, T.A., Arias, M.E., Piman, T., 2014. Historical impact of water infrastructure on water levels of the Mekong River and the Tonle Sap system. Hydrol. Earth Syst. Sci. 18, 4529–4541. http://dx.doi.org/10.5194/hess-18-4529-2014.

De Cáceres, M., Jansen, F., 2011. indicspecies: Functions to Assess the Strength and Significance of Relationship of Species Site Group Associations. R Package Version 1.6.0. http://cran.r-project.org/web/packages/indicspecies.

De Cáceres, M., Legendre, P., Moretti, M., 2010. Improving indicator species analysis by combining groups of sites. Oikos 119, 1674–1684.

Dray, S., Blanchet, G., Borcard, D., Guénard, G., Jombart, T., Larocque, G., Legendre, P., Madi, N., Wagner, H.H., 2017. Adespatial: Multivariate Multiscale Spatial Analysis. R Package Version 0.0-8. http://cran.r-project.org/package=adespatial.

Fan, H., He, D., Wang, H., 2015. Environmental consequences of damming the mainstream Lancang-Mekong River: a review. Earth-Sci. Rev. 146, 77–91. http://dx.doi.org/10.1016/j.earscirev.2015.03.007.

Froese, R., Pauly, D., 2017. FishBase. World Wide Web electronic publication [WWW Document]. World Wide Web Electronic Publication. URL www.fishbase.org (accessed 2.1.17).

Fukushima, M., Jutagate, T., Grudpan, C., Phomikong, P., Nohara, S., 2014. Potential effects of hydroelectric dam development in the Mekong River basin on the migration of Siamese mud carp (Henicorhynchus siamensis and *H. lobatus*) elucidated by otolith microchemistry. PLoS One 9. http://dx.doi.org/10.1371/journal.pone.0103722.

Guénard, G., Lanthier, G., Harvey-Lavoie, S., Macnaughton, C.J., Senay, C., Lapointe, M., Legendre, P., Boisclair, D., 2016. A spatially-explicit assessment of the fish population response to flow management in a heterogeneous landscape. Ecosphere 7, 1–13. http://dx.doi.org/10.1002/ecs2.1252.

Heino, J., Grönroos, M., 2016. Exploring species and site contributions to beta diversity in stream insect assemblages. Oecologia. http://dx.doi.org/10.1007/s00442-016-3754-7.

Hirsch, P., Wyatt, A., 2004. Negotiating local livelihoods: scales of conflict in the Se San River Basin. Asia Pac. Viewpoint 45, 51–68. http://dx.doi.org/10.1111/j.1467-8376.2004.00227.x.

Hortle, K.G., 2007. Consumption and the yield of fish and other aquatic animals from the Lower Mekong Basin, MRC Technical Paper No. 16. Mekong River Commission, Vientiane.

International Rivers, 2014. Xayaburi Dam: Timeline of Events. International Rivers. https://www.internationalrivers.org.

Jellyman, P., Harding, J., 2012. The role of dams in altering freshwater fish communities in New Zealand. N. Z. J. Mar. Freshwater Res. 46, 475–489. http://dx.doi.org/10.1080/00288330.2012.708664.

Kassambara, A., 2017. Practical Guide to Cluster Analysis in R: Unsupervised Machine Learning. STHDA, Poland.

Kottelat, M., 2013. The Fishes of the inland waters of Southeast Asia: a catalogue and core bibliography of the fishes known to occur in freshwaters, mangroves and estuaries. Raffles Bull. Zool. 27, 1–663.

Legendre, P., De Cáceres, M., 2013. Beta diversity as the variance of community data: Dissimilarity coefficients and partitioning. Ecol. Lett. 16, 951–963. http://dx.doi.org/10.1111/ele.12141.

Legendre, P., Gauthier, O., 2014. Statistical methods for temporal and space − time analysis of community composition data. Proc. R. Soc. 281, 20132728.

Legendre, P., Legendre, L., 2012. Numerical Ecology, Third Engl. ed. Elsevier Science B.V, Great Britain.

Legendre, P., Salvat, B., 2015. Thirty-year recovery of mollusc communities after nuclear experimentations on Fangataufa atoll (Tuamotu, French Polynesia). Proc. R. Soc. B: Biol. Sci. 282, 20150750. http://dx.doi.org/10.1098/rspb.2015.0750.

Li, J., Dong, S., Peng, M., Yang, Z., Liu, S., Li, X., Zhao, C., 2013. Effects of damming on the biological integrity of fish assemblages in the middle Lancang-Mekong River basin. Ecol. Indic. 34, 94–102. http://dx.doi.org/10.1016/j.ecolind.2013.04.016.

Liermann, C.R., Nilsson, C., Robertson, J., Ng, R.Y., 2012. Implications of dam obstruction for global freshwater fish diversity. Bioscience 62, 539–548.

Macnaughton, C.J., Mclaughlin, F., Bourque, G., Senay, C., Lanthier, G., Harvey-Lavoie, S., Legendre, P., Lapointe, M., Boisclair, D., 2015. The effects of regional hydrologic alteration on fish community structure in regulated rivers. River Res. Appl. http://dx.doi.org/10.1002/rra.2991.

Magurran, A.E., 2004. Measuring Biological Diversity. Blackwell Science Ltd, Malden, USA.

MFD, 2003. Mekong Fish Database: A Taxonomic Fish Database for the Mekong Basin. Mekong River Commission, Phnom Penh.

Mims, M.C., Olden, J.D., 2013. Fish assemblages respond to altered flow regimes via ecological filtering of life history strategies. Freshwater Biol. 58, 50–62. http://dx.doi.org/10.1111/fwb.12037.

Mittermeier, R.A., Turner, W.R., Larsen, F.W., Brooks, T.M., Gascon, C., 2011. Global biodiversity conservation: The critical role of hotspots. In: Zachos, F., Habel, J. (Eds.), Biodiversity Hotspots: Distribution and Protection of Conservation Priority Areas. Springer-Verlag, Berlin Heidelberg, pp. 3–22. http://dx.doi.org/10.1007/978-3-642-20992-5.

MRC, 2010. State of the Basin Report 2010. Mekong River Commission, Vientiane, Lao PDR.

MRC, 2007. Monitoring Fish Abundance and Diversity in the Lower Mekong Basin: Methodological Guidelines. Mekong River Commission, Phnom Penh.

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

MRCS, 1992. Fisheries in the Lower Mekong Basin, Main Report and Annex. (Review of the Fishery Sector in the Lower Mekong Basin). Interim Committee for the Coordination of Investigations of the Lower Mekong Basin, Mekong River Commission Secretariat, Bangkok.

Ou, C., Montaña, C.G., Winemiller, O., 2017. Body size – trophic position relationships among fishes of the lower Mekong basin. R. Soc. Open Sci. 4, 160645. http://dx.doi.org/10.1098/rsos.160645.

Ou, C., Winemiller, K.O., 2016. Seasonal hydrology shifts production sources supporting fishes in rivers of the lower Mekong Basin. Can. J. Fish. Aquat. Sci. 73, 1–21. http://dx.doi.org/10.1007/s13398-014-0173-7.2.

Phomikong, P., Fukushima, M., Sricharoendham, B., Nohara, S., Jutagate, T., 2014. Diversity and community structure of fishes in the regulated versus unregulated tributaries of the Mekong river. River Res. Appl. 14.

Piman, T., Cochrane, T.A., Arias, M.E., Green, A., Dat, N.D., 2013. Assessment of flow changes from hydropower development and operations in Sekong, Sesan, and Srepok Rivers of the Mekong Basin. J. Water Resour. Plann. Manage. 139, 723–732. http://dx.doi.org/10.1061/(ASCE)WR.1943-5452.

Poff, N.L., Olden, J.D., Merritt, D.M., Pepin, D.M., 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. Proc. Natl. Acad. Sci. U.S.A. 104, 5732–5737. http://dx.doi.org/10.1073/pnas.0609812104.

Poulsen, A.F., Hortle, K.G., Valbo-Jorgensen, J., Chan, S., Chhuon, C.K., Viravong, S., Bouakhamvongsa, K., Suntornratana, U., Yoorong, N., Nguyen, T.T., Tran, B.Q., 2004. Distribution and Ecology of Some Important Riverine Fish Species of the

Mekong River Basin. MRC Technical Paper No. 10. Mekong River Commission, Phnom Penh.
Poulsen, A.F., Ouch, P., Viravong, S., Suntornratana, U., Nguyen, T.T., 2002. Fish Migrations of the Lower Mekong Basin: Implications for Development, Planning and Environmental Management. Mekong River Commission, Phnom Penh.
Qiao, X., Li, Q., Jiang, Q., Lu, J., Franklin, S., Tang, Z., Wang, Q., Zhang, J., Lu, Z., Bao, D., Guo, Y., Liu, H., Xu, Y., Jiang, M., 2015. Beta diversity determinants in Badagongshan, a subtropical forest in central China. Sci. Rep. 5, 17043. http://dx.doi.org/10.1038/srep17043.
R Core Team, 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing.
Rainboth, W.J., 1996. Fishes of the Cambodian Mekong. Food and Agriculture Organisation of the United Nations, Rome.
Rainboth, W.J., Vidthayanon, C., Mai, D.Y., 2012. Fishes of the Greater Mekong Ecosystem with Species List and Photographic Atlas. Museum of Zoology, University of Michigan, Ann Arbor.
Röpke, C.P., Amadio, S., Zuanon, J., Ferreira, E.J.G., de Deus, C.P., Pires, T.H.S., Winemiller, K.O., 2017. Simultaneous abrupt shifts in hydrology and fish assemblage structure in a floodplain lake in the central Amazon. Sci. Rep. 7, 1–10. http://dx.doi.org/10.1038/srep40170.
Rutkow, E., Crider, C., Giannin, T., 2005. Down River. The Consequences of Vietnam's Se San River dams on Life in Cambodia and Their Meaning in International Law. NGO Forum on Cambodia, Phnom Penh.
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, 1–11. http://dx.doi.org/10.1126/science.aao1053.
Schmutz, S., Mielach, C., 2015. Review of existing research on fish passage through large dams and its applicability to Mekong mainstream dams. MRC Technical Paper No. 48. Mekong River Commission, Phnom Penh.
Sverdrup-Jensen, S., 2002. Fisheries in the Lower Mekong Basin: Status and Perspectives. MRC Technical Paper No. 6. Mekong River Commission, Phnom Penh.
Tilt, B., Braun, Y., He, D., 2008. Social impacts of large dam projects: A comparison of international case studies and implications for best practice. J. Environ. Manage. 1–9. http://dx.doi.org/10.1016/j.jenvman.2008.07.030.
Tonkin, J.D., Bogan, M.T., Bonada, N., Ríos-Touma, B., Lytle, D.A., 2017. Seasonality and predictability shape temporal species diversity. Ecology 1–16. http://dx.doi.org/10.1002/ecy.1761.
Try, T., Chambers, M., 2006. Situation Analysis: Stung Treng Province, Cambodia. Mekong Wetlands Biodiversity Conservation and Sustainable Use Programme, Vientiane.
Wang, W. chuan, Chau, K. wing, Xu, D. mei, Qiu, L., Liu, C. can, 2017. The annual maximum flood peak discharge forecasting using hermite projection pursuit regression with SSO and LS method. Water Resour. Manage. 31, 461–477. http://dx.doi.org/10.1007/s11269-016-1538-9.
Welcome, R.L., 2001. Inland Fisheries: Ecology and Management, 1st ed. Food and Agriculture Organization of the United Nations by Blackwell Science, Great Britain.
Winemiller, K., McIntyre, P., Castello, L., Fluet-Chouinard, E., Giarrizzo, T., So, N., Baird, I., Darwall, W., Lujan, N., Harrison, I., Stiassny, M., Silvano, R., Fitzgerald, D., Pelicice, F., Agostinho, A., Gomes, L., Albert, J., Baran, E., Petrere, M., Zarfl, C., Mulligan, M., Sullivan, J., Arantes, C., Sousa, L., Koning, A., Hoeinghaus, D., Sabaj, M., Lundberg, J., Armbruster, J., Thieme, M., Petry, P., Zuanon, J., Vilara, G., Snoeks, J., Ou, C., Rainboth, W., Pavanelli, C., Akama, A., van Soesbergen, A., Saenz, L., 2016. Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. Science 351, 128–129.
Ziv, G., Baran, E., So, N., Rodriguez-Iturbe, I., Levin, S.A., 2012. Trading-off fish biodiversity, food security, and hydropower in the Mekong River Basin. Proc. Natl. Acad. Sci. U.S.A. 109, 5609–5614.

ARTICLE 5

Fish assemblage responses to flow seasonality and predictability in a tropical flood pulse system

Peng Bun Ngor, Thierry Oberdorff, Phen Chheng, Christophe Baehr, Gaël Grenouillet, Sovan Lek

Ecoshpere (in revision)

Fish assemblage responses to flow seasonality and predictability in a tropical flood pulse system

Peng Bun Ngor[1,2,¥], Thierry Oberdorff[2], Chheng Phen[1], Christophe Baehr[3], Gaël Grenouillet[2,4], Sovan Lek[2]

[1.] Fisheries Administration, No. 186, Preah Norodom Blvd., Khan Chamcar Morn, P.O. Box 582, Phnom Penh, Cambodia.

[2.] CNRS, IRD, Université Toulouse III Paul Sabatier; UMR5174 EDB (Laboratoire Évolution & Diversité Biologique); 118 route de Narbonne, F-31062 Toulouse, France.

[3.] Météo-France CNRM/GMEI, 42 Avenue de Coriolis, 31057 Toulouse cedex, France.

[4.] Institut Universitaire de France, Paris, France.

[¥.] Current address: CNRS, IRD, Université Toulouse III Paul Sabatier; UMR5174 EDB (Laboratoire Évolution & Diversité Biologique); 118 route de Narbonne, F-31062 Toulouse, France.

Running head: Fish assemblage response to flow change

Corresponding author: Peng Bun Ngor (pengbun.ngor@gmail.com)

Abstract

Hydropower dams are looming in the Mekong Basin, affecting river flows that structure aquatic communities. Here, we quantitatively assessed flow seasonality and predictability in three sites located in three rivers displaying a gradient in flow alterations caused by upstream dams and investigated how fish assemblages responded seasonally and inter-annually to this gradient. By analyzing 7-year daily fish and water monitoring data, we found that dams disturbed the natural flow seasonality and predictability. While the river displaying the lower seasonality-predictability was characterized by a distinct seasonal variation in assemblage composition with high species turnover, rivers with stronger flow seasonality-predictability exhibited broadly similar seasonal patterns in fish assemblage composition with low species turnover and regular annual peaks of fish migration. These results challenge the expectation of higher species turnover in systems displaying higher flow seasonality and predictability and may be partly due to the strong adaptation of fish assemblages to these specific systems. By enhancing our understanding of biological systems in the highly seasonal-predictable and aseasonal-unpredictable environments of the lower Mekong system, these findings suggest that hydropower-related pulsed flows that can mimic as far as possible natural pulsed flows are critical to reduce downstream effects on aquatic organisms.

Keywords: hydropower dam, freshwater fishes, flow regulation, species turnover, Mekong River Basin.

INTRODUCTION

Construction of hydropower dams are continuously increasing mainly in developing countries and the emerging economies of Southeast Asia, South America and Africa (Zarfl et al. 2015). These dams are constructed or planned predominantly in the world's most bio-diverse river basins such as the Amazon, the Congo and the Mekong (Winemiller et al. 2016). The Mekong Basin was, for example, identified as one of the world's regions with high threats for water security to both humans and biodiversity (Mcintyre et al. 2010). In this basin, numerous large dams have been built since 1990s and several others are planned or under construction (Fan et al. 2015, Winemiller et al. 2016, Ngor et al. 2018) (see also Fig. 1, S1).

Among other things dams are known worldwide to disrupt river continuity, to block migration routes of riverine fishes, to dampen flood pulses and to mute flow seasonality. These disturbances alter in return the structure of aquatic assemblages that are seasonally adapted to natural seasonal flow dynamics (Collier et al. 1996, Agostinho et al. 2004, Graf 2006, Poff et al. 2007, Latrubesse et al. 2017, Sabo et al. 2017). Specifically, dams generate hydropower-related pulsed flows e.g. hydropeaking reacting to energy demands (from hourly to seasonally) which adversely affect riverine fishes and other aquatic organisms through stranding/ extirpation, downstream displacement and spawning/rearing disruption (Young et al. 2011, Schmutz et al. 2015, Kennedy et al. 2016, Tonolla et al. 2017).

Hydrology of the Mekong River is characterized by strong seasonality with regular wet and dry seasons highly predictable across years (MRC 2005, Adamson et al. 2009). Given that the structuring force of the Mekong fish assemblages is deeply embedded in the local seasonality and predictability of the Mekong's hydrological conditions, flow alterations caused by upstream dams (i.e. modifying timing, magnitude and frequencies of seasonal flow) should have implications for spatiotemporal dynamics of these assemblages (Valbo-Jorgensen and Poulsen 2000, Poulsen et al. 2002, Baran 2006, Adamson et al. 2009, Sabo et al. 2017).

The seasonality concept is widely applied to explain life history adaptations of organisms (Mcnamara and Houston 2008), changes in species trait distribution patterns (Fitzgerald et al. 2017), shifts in abundance and coexistence of species (Shimadzu et al. 2013), shifts in food web structure (McMeans et al. 2015) or changes in beta diversity patterns (Tonkin et al. 2017). In addition, to have a complete understanding of the temporal patterns of local assemblages, there is a need to consider the system predictability (Colwell 1974, Tonkin et al. 2017). By definition, "seasonality is the occurrence of certain obvious biotic and abiotic events or groups of events within a definite limited period or periods of the astronomic (solar, calendar) year" while predictability is " the regularity of recurrence of the within cycle (e.g. annual) distribution of events across multiple cycles" (Tonkin et al. 2017).

Here, we focused on a strongly tropical seasonal-predictable flood pulse system (MRC 2005, Adamson et al. 2009) (i.e. the lower Mekong system) and used Tonkin's et al. seasonality-predictability framework (Tonkin et al. 2017) to assess how hydrological alterations caused by upstream dams structured local fish assemblages. According to this framework, predictably seasonal environmental conditions should promote the highest levels of temporal changes in species abundance, richness and assemblage composition with high seasonal turnover due to hypothetical distinct habitats between seasons. On the other hand, aseasonal and unpredictable systems should generate the lowest temporal diversity, harboring assemblages that show little seasonal species turnover. In other words, species turnover would be maximized under highly predictable seasonal conditions, while nestedness (i.e. assemblages in one season being a subset of those in the other season) may dominate in unpredictable aseasonal environments (Tonkin et al. 2017). To test these hypotheses, we focused on three study sites experiencing different levels of flow alteration, and for which we expected a gradient in flow seasonality and predictability. Specifically, we first assessed how seasonality and predictability of flow patterns varied among the three sites. Second, we tested the hypotheses that seasonal variations in fish assemblage abundance, richness and composition were driven by flow seasonality and predictability using a unique 7-year daily fish and water level dataset monitored at the three sites. Seasonal patterns of fish trait were also examined to explain the seasonal variation in fish assemblage due to the expected gradient of flow alteration in the three sites.

METHODS

Study sites

This study covered three sites i.e. the Mekong mainstem at Kratie (KT), the Sesan River (SS) at Ratanakri joining the Sekong and the Mekong River in Stung Treng, and the Tonle Sap River (TS) at Kandal joining the Mekong River in the capital city of Phnom Penh (Fig. 1). At KT, the Mekong mean annual discharge is ~475 billion m^3 $year^{-1}$ varying from < 3000m^3 s^{-1} during low flows (March–April) to ~40000m^3 s^{-1} during high flows (August–September) (Adamson et al. 2009). SS covers ~24% of the total surface area (78,645 km^2) of the Sekong, Sesan, Srepok (3S), had mean daily water level of ~4.91 m (at Voeun Sai) for the period June 2007 – May 2014 and contributes ~20% to the Mekong total annual flows (MRC 2005, Adamson et al. 2009). TS sub-basin covers a catchment area of 85,790 km^2 (11% of the Mekong Basin (MRC 2003)) and receives 54% of its waters from the Mekong River, 34% from its lake tributaries and the rest from rainfalls (Kummu et al. 2014). Mean discharge at the Tonle Sap River was estimated at ~83.1 and ~81.9 billion m^3 during the inflow and outflow periods, respectively (Kummu et al. 2014). The selected study sites are all located in the most fish biodiverse ecoregions of the Lower Mekong Basin (LMB) (Poulsen et al. 2002, Chea et al. 2016). For example, TS and its floodplain lake is a World Biosphere Reserve under the United Nations Educational, Scientific and Cultural Organization (UNESCO) since 1997 (Davidson 2006), one of the world largest freshwater fisheries zone (Baran 2005).   Riverine fishes (87% of the total 1200 Mekong fishes) seasonally utilize these river systems as part of their life cycles (Rainboth 1996, Baran et al. 2013). Most species spawn and seasonally migrate down the river system in KT and Stung Treng to enter feeding and rearing habitats in the TS floodplains and areas southern Phnom Penh, or up the Sekong, Sesan (SS) and Srepok tributaries (3S) at the onset of the wet season, and later return in the Mekong mainstream (i.e. KT and

Stung Treng) to find refugia for sedentary periods at the onset of the dry season (Valbo-Jorgensen and Poulsen 2000, Poulsen et al. 2002, 2004, Sverdrup-Jensen 2002, Baran 2006).

While more natural flow conditions were observed in KT and TS, flows in SS appeared to be highly altered (compared to its pre-dam condition) by the functioning of upstream dams which weakens the flow seasonality and predictability strength of the system and generates strong aseasonality with unnatural sudden rising and falling water levels (see Supplementary Information S1, S2, Fig. 2). Such unnatural pulsed flows in SS can be related to hydropeaking which is commonly experienced with hydropower dams worldwide (Young et al. 2011, Kennedy et al. 2016) and known to alter hydraulic parameters such as water levels, velocity and bed shear stress (Meile et al. 2010, Young et al. 2011, Kennedy et al. 2016, Bejarano et al. 2017, Tonolla et al. 2017). Previous studies also qualitatively described rapid rising and falling water levels in the downstream SS when the 720 MW Yali Falls dam was under construction in 1996 and became officially operational since 2000 (Ratanakiri Fisheries Office 2000, Baird et al. 2002, Claasen 2004, Hirsch and Wyatt 2004, Baird and Meach 2005, Rutkow et al. 2005). Flow alternations became even more severe when five more dams were commissioned between 2006 and 2011 (Fig. 2b, S1). As indicated in a recent study, the upstream SS's under-construction and operational dams in Viet Nam Highlands caused an overall increase of 52% in dry season flow and a decrease of 22% in the wet season flow of this river near the Cambodia border (Piman et al. 2013). Therefore, strong aseasonal and unpredictable variabilities of flow evidenced in SS are highly likely explained by hydropower-related pulsed flows.

Data collection

Data collection was based on the standard sampling procedures of the Mekong River Commission (MRC) (MRC 2007). Fish catches were routinely monitored between June 2007 and May 2014 at the three studied sites. Our sampling sites stayed unchanged over the 7-year study period (i.e. the same habitats were prospected all along the period). Daily, a set of stationary gillnets (length: 120±50 m, height: 2–3.5 m, mesh size: 3-12 cm, soak hours/day: 12±2) was used to capture fish (three fishers for each site). The fishers were supervised by the fish monitoring officers from the Cambodia Inland Fisheries Research and Development Institute of the Fisheries Administration and the MRC. A list of about 900 Mekong fishes and their traits was derived from the Mekong Fish Database (MFD 2003). Captured fish were identified to the species level and counted; and their taxonomic classification as well as species traits were updated using FishBase (Froese and Pauly 2017) in cross-checking with (Rainboth 1996, Rainboth et al. 2012, Kottelat 2013). The collected fish data were recorded into the national fish monitoring database. Water levels at each location were registered by MRC. Key fish traits used in the analysis of seasonal patterns fall in five broad categories namely physical habitat guilds, migration guilds, maximum total lengths, trophic levels and positions in the water column. Details of each fish trait category are given in S10.

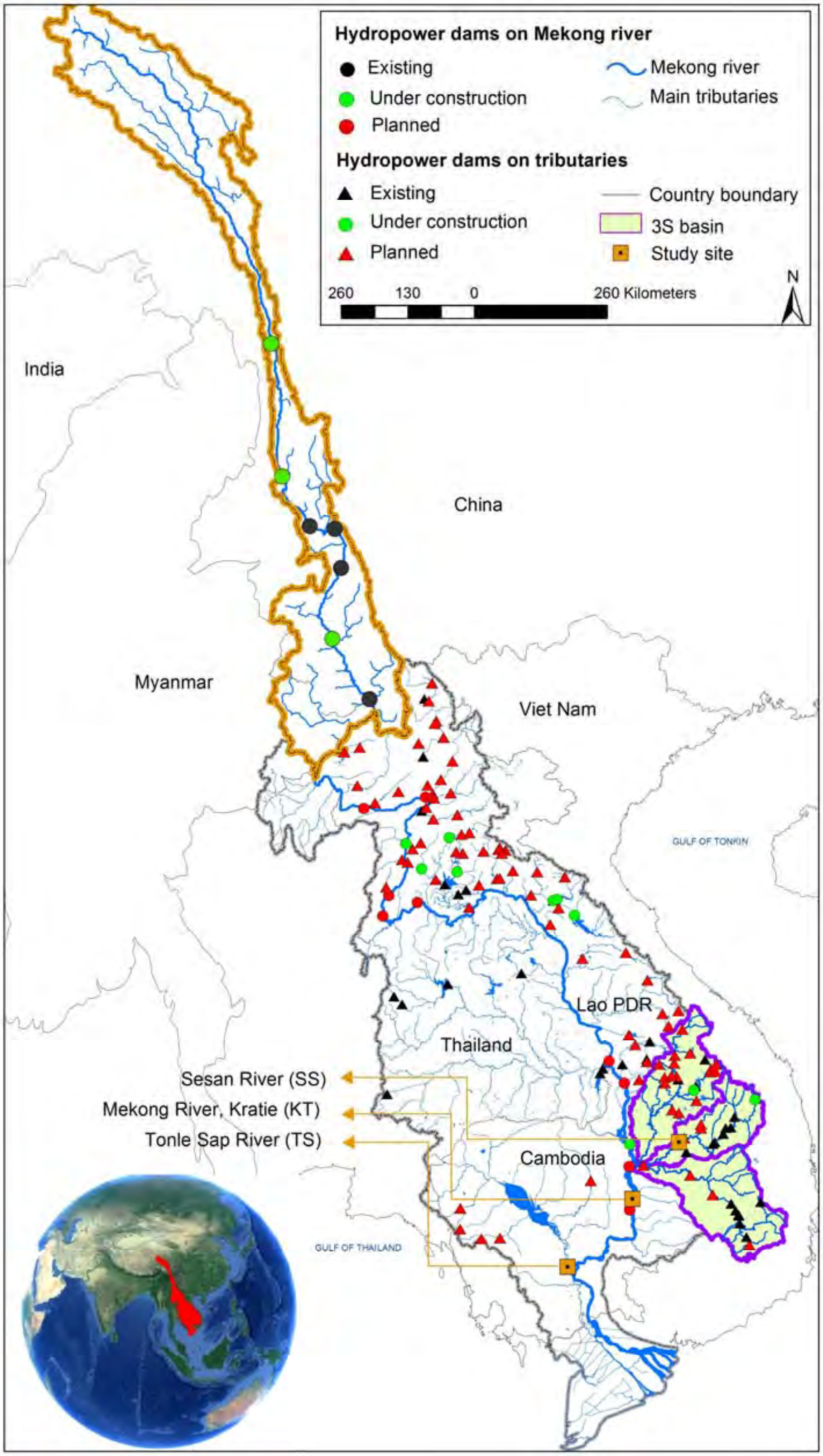


Figure 1. Map showing the study sites and hydropower dam positions in the Mekong Basin (Data source: MRC Hydropower Project Database 2015). Site codes: SS = Sesan River, KT = Mekong River in Kratie, TS = Tonle Sap River.

Statistical analyses

Daily species abundance collected by the three fishers in each site was computed as daily mean samples and then summed into weekly species abundance from 1 June 2007 to 31 May 2014 (i.e. 366 weeks). Similarly, site daily water levels were computed as mean weekly water levels for the same 366 weeks. All statistical analyses were performed in R (R Core Team 2015).

To quantify the strength of seasonality, Colwell's seasonality index (Colwell 1974) on site daily water levels was computed using Colwells function of hydrostats package (Bond 2016). The seasonality index M/P which is the Colwell's measure of contingency (M) standardized by Colwell's within-season predictability (P) (Colwell 1974, Tonkin et al. 2017) was used. Colwell's contingency (consistency of timing between years) quantifies the degree of repeatability of biological (e.g. fish migration) or physical (e.g. hydrology) periodic phenomena. The value of the seasonality index varies between 0 and 1, with 1 being the maximum seasonality value. In addition, wavelet analysis was applied to quantify the strength of predictability of site hydrology. The wavelet analysis is a harmonic analysis with a time-frequency representation of a signal. This harmonic analysis uses a special function called mother wavelets which allow time and scale localizations. Using the R-package WaveletComp, the Morlet mother-wavelet was selected (Roesch and Schmidbauer 2014) for the analysis. While being comparable to the Fourier analysis that detects the dominant frequencies over time series, wavelets offer the advantage of investigating multiple scales simultaneously (Torrence and Compo 1998, Tonkin et al. 2017). In the wavelet transform, a time-series is decomposed into time, frequencies and the power which can be examined in the three-dimensional space through the plot of the wavelet power spectrum (WPS). In WPS plot, "time" indicates the time series on the X-axis while the contribution of the "frequencies" is represented by "period" on the Y-axis. The "power" characterizes the magnitude of variance within the time series at a given wavelet. The WPS determines which features of the signal are determinant and contributive and which are less significant.

To compare seasonal fish assemblage responses among sites, we (i) defined the wet (June-November) and dry (December-May) seasons, based on 9-year mean daily water levels of the Mekong River, when entering Cambodia (at Stung Treng) (S3); (ii) computed weekly fish assemblage matrix in each site as mean seasonal assemblage matrix; (iii) applied Principal Components Analyses (PCA) on the Hellinger-transformed seasonal fish abundance and trait data matrices, using fviz_pca_ind function of factoextra package (Kassambara 2017) to visualize seasonal (dry and wet seasons) patterns of fish assemblages in each site. Hellinger transformation was applied because PCA is a linear ordination model that requires pre-transformation of the abundance data to meet the (multi)normal distribution assumption (Borcard et al. 2011). Finally, we computed the seasonal beta diversity, and partitioned it into turnover (i.e. species replacement in one season by different species in the other season) and nestedness (i.e. species in one season being a strict subset of the species at the other season) components, using beta.pair function with Sorensen dissimilarity index from betapart package (Baselga 2010, Baselga and Orme 2012). Also, species turnover and nestedness were computed separately for wet and dry seasons to examine how each season affects the observed turnover and nested pattern of beta diversity in each of the three study sites.

To identify significant interdependencies at multiple time-scales between fish assemblages and water levels over the study period, cross-wavelet analyses were performed on the weekly series of fish total abundance and richness (Y) and mean weekly water levels (second Y axis), using analyze.coherency function from WaveletComp package (Roesch and Schmidbauer 2014). Cross-correlation analysis (ccf function) on the abundance and richness (Y) and water series (second Y axis) in each site was used to derive the time lag with the maximum value of cross-correlation coefficients (Shumway and Stoffer 2011) that correlated the fish assemblage responses to site hydrological variations. Prior to cross-correlation analyses, fish abundance, richness and water data series were tested for stationarity (i.e. if there were significant linear temporal trends in the data). When stationarity was violated (as detected for abundance, richness and water data series in SS, abundance and richness data series in KT and richness data series in TS), residuals were computed to detrend the series (Legendre and Legendre 2012) and used in the cross-correlation analyses.

RESULTS

Seasonality-predictability of site hydrology

Colwell's seasonality index on hydrology consistently found that flows in TS exhibited the strongest seasonality (M/P = 0.93), whereas KT ranked second in its seasonal flow patterns (M/P = 0.90) and SS showed the weakest flow seasonality (M/P = 0.83). Flows in KT and TS had more seasonal-predictable patterns than in SS where strong flow variability was observed (Fig. 2a). As further evidenced in the wavelet plots (Fig. 2b), flows in TS and KT comparably exhibited very strong continuous seasonal-predicable patterns as indicated by a uniformly wide red band at ~52-week frequency (annual cycle). Such patterns were relatively weak in SS, with observed chaotic signals of strong wavelet power at multiple periods across the wavelet spectrum. Flow variations in KT and TS also demonstrated a secondary strong predicable power (red-yellow) at ~26-week frequency (semi-annual cycle), while no such patterns were captured in the wavelet power spectrum in SS (Fig. 2b). Such patterns were illustrated clearly in the average wavelet power across the full 7-year period, showing the strongest peaks at 52-week frequencies for all sites, with increasing average wavelet power (i.e. predictability strength) in the respective order of site SS, KT and TS (Fig. 2c).

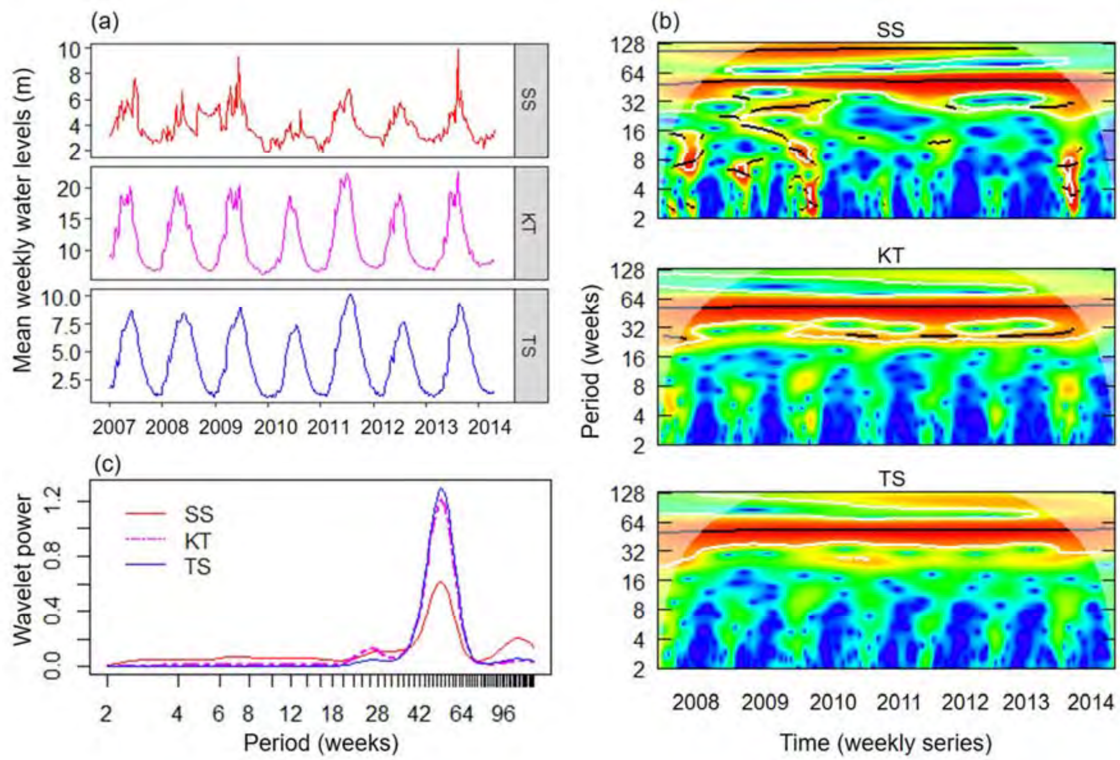


Figure 2. Seasonality and predictability of 7-year weekly water levels of the three rivers: SS, KT and TS. (a) Site water level series. (b) Wavelet power spectrum of site water levels, with red representing stronger wavelet power and blue weak, (c) Site average wavelet power derived from (b). Note that Cowell's seasonality index (M/P) was 0.83 in SS, 0.90 in KT and 0.93 in TS. For site codes, see Figure 1.

Fish assemblage patterns

Overall, 266 species were recorded from the three sites (133 in SS, 208 in KT and 143 in TS). Fish abundance (number of individuals) was higher in SS and TS than in KT (S4a). By contrast, KT was the most species-rich relative to SS and TS (S4b). Fish assemblages in SS and TS were disproportionately dominated by small body-sized generalist species, whereas assemblages in KT were more proportionally represented by species with different body-sized classes (small, medium, large and giant-sized species) (S5, S6). However, three small-sized generalists (from family: Cyprinidae, order: Cypriniformes) namely *Henicorhynchus lobatus*, *H. siamensis*, *Labiobarbus siamensis*, were dominantly ubiquitous in the three sites. While *H. lobatus* was the most abundant species in KT and TS, a small-sized floodplain resident climbing perch, *Anabas testudineus* (family: Anabantidae, order: Perciformes), ranked top in SS. See S5 for top 15 abundant species and S6 for mean weekly abundance of key species recorded in each of the three sites.

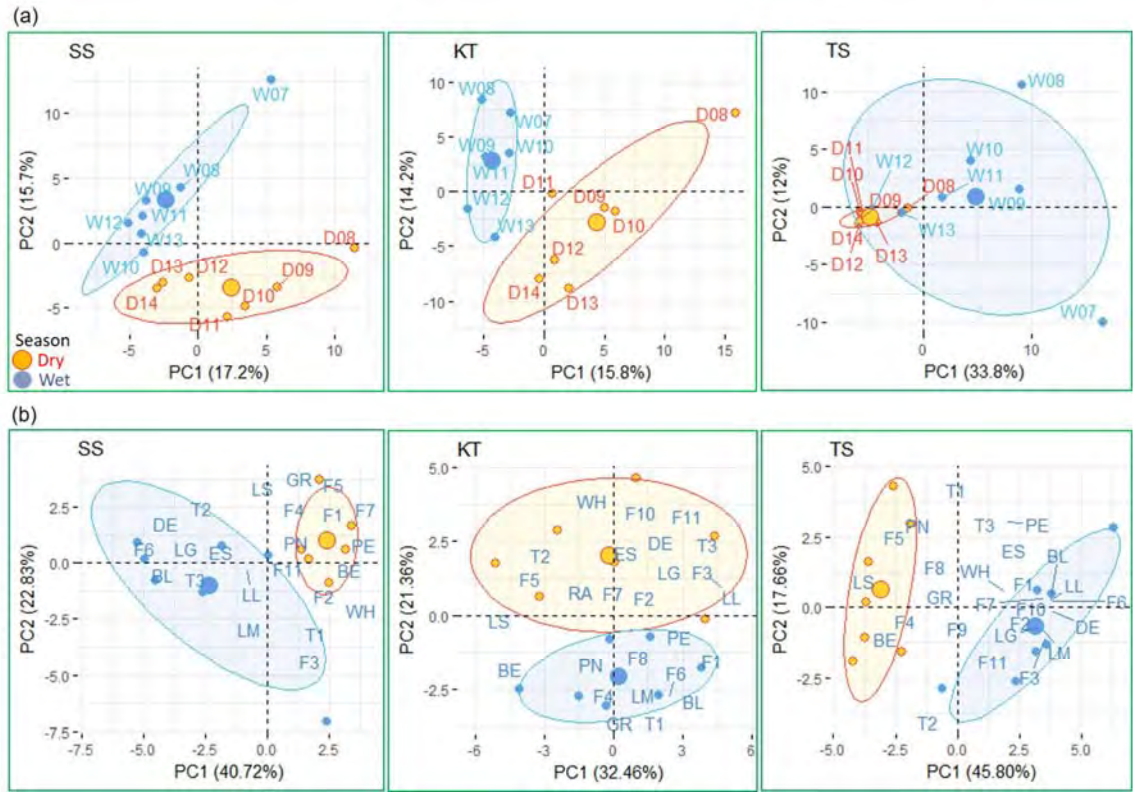


Figure 3. Seasonal fish assemblage and trait responses. PCA plots displaying (a) seasonal fish assemblage patterns and (b) seasonal fish trait patterns grouped by wet (W) and dry (D) seasons. For (a), the two digits after W and D indicate 'year', e.g. W07 = wet season 2007 etc. For (b), solid points indicate season as shown in (a) and the abbreviations denote fish traits including (1) physical habitat guilds i.e. F1 (Rithron resident), F2 (Main channel resident), F3 (Main channel spawner), F4 (Floodplain spawner), F5 (Eurytopic/generalist), F6 (Floodplain resident), F7 (Estuarine resident), F8 (Anadromous), F9 (Catadromous) F10 (Marine visitor), F11 (Non-native); (2) migration guilds i.e. WH (White fishes = longitudinal migratory species between Mekong River, lower floodplains and major tributaries, BL (Black fishes = non-longitudinal migratory or floodplain residents), GR (Grey fishes = lateral migration between floodplain and local rivers or streams); (3) maximum total lengths i.e. LG (Giant size, >=100 cm), LL (Large size, 61-99 cm), LM (Medium size, 26-60 cm), LS (Small size, <= 25 cm); (4) trophic levels i.e. T1 (trophic level <=2.75), T2 (trophic level, 2.76 – 3.75), T3 (trophic level, > 3.75) and (5) positions in the water column include BE (benthopelagic), DE (demersal), PE (pelagic), PN (pelagic-neritic), RA (Reef associated). For site codes, see Figure 1. For species trait details, see S10.

Seasonal fish abundances and richness showed no significant difference between dry and wet seasons (with p-values = 0.8 and 0.14, respectively) in SS (S7a, b). In KT, significantly higher richness was detected during the dry season (p-value = 0.04), while no significant difference was observed for seasonal fish abundances (p-value = 0.21). In TS, abundance was by far significantly higher during the dry season (p-value = 0.0006), while no significant difference was observed for seasonal richness (p-value = 0.52).

Clear differences in fish assemblages between dry and wet seasons were observed in SS and to a lesser extent in KT, while seasonal assemblages in TS appeared less discriminated between the two seasons (Fig. 3). Temporal beta diversity showed a gradient of seasonal species turnover among sites with the highest values observed in SS and the lowest in TS (Fig. 4). KT displayed intermediate values for both species turnover and nestedness in the three sites. In SS, high species turnover occurred during the dry season (p-value < 0.0001) and high nested pattern occurred during the wet season (p-value = 0.004). In KT, high species turnover occurred during the wet season (p-value < 0.0001) and no significant difference was revealed in seasonal nestedness. In TS, no significant difference between wet and dry seasons was observed for both species turnover and nestedness (Fig. 4b).

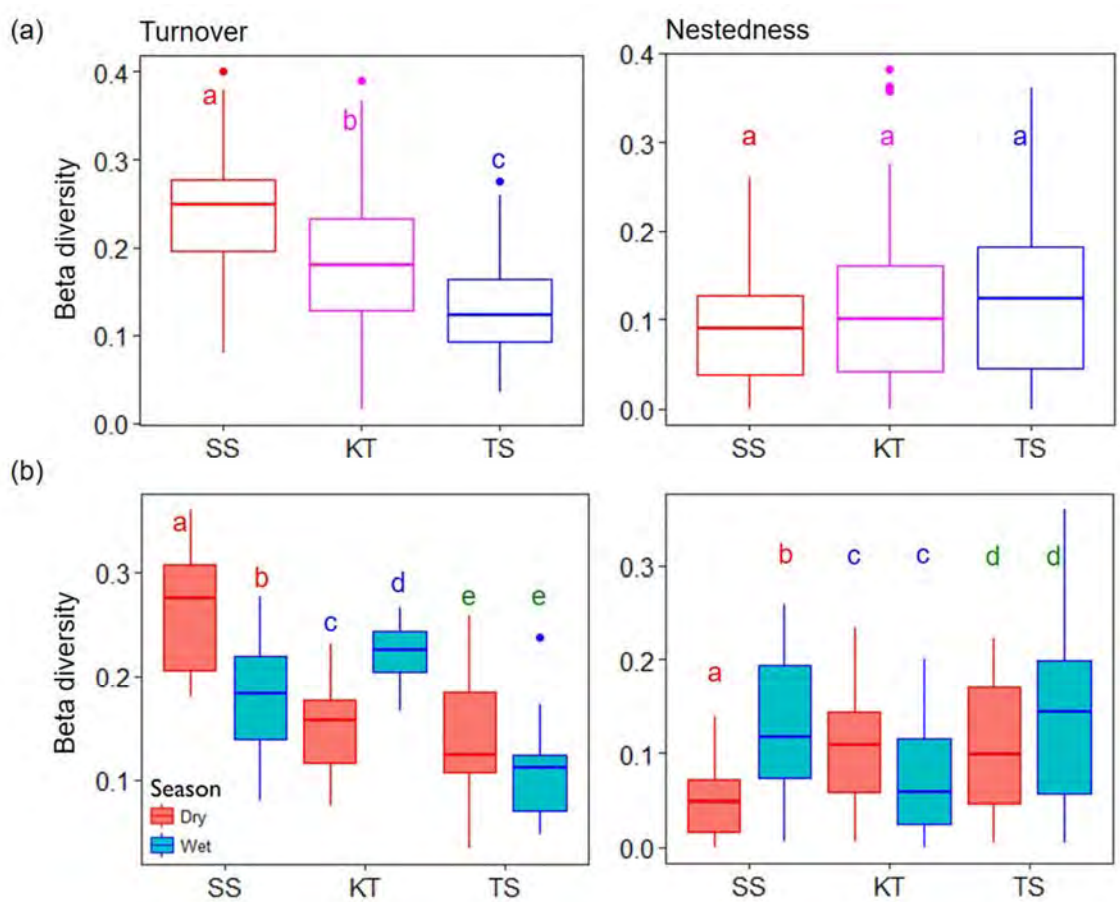


Figure 4. Seasonal beta diversity partitioned into seasonal species turnover and nestedness using Sorensen dissimilarity index. (a) Site seasonal species turnover and nested patterns. (b) Site species turnover and nestedness patterns by wet and dry seasons. Mean values among sites with a common letter are not significantly different at the 0.05 level (Pairwise Wilcoxon Rank Sum Tests). For site codes, see Figure 1.

Generally, there is a clear distinct pattern of fish traits between the wet and dry season for the three study sites regardless of different flow seasonality and predictability. Interestingly, longitudinal migratory species used SS and KT mainly during the dry season and TS during the wet season. Also, high trophic level floodplain resident species using demersal habitats appear to colonize tributary rivers (i.e. SS, TS) during the wet season (Fig. 3b).

Fish abundance and richness, and flow coherence

No clear peak in both weekly abundance and richness in relation to hydrological cycles was observed in SS (Fig. 5a, 6a). By contrast, a clear seasonal peak in abundance was repeated annually i.e. before the peak water levels in KT (i.e. at the onset of wet season) and after the peak water levels in TS (i.e. during the falling water levels), whereas richness in both sites was greater during the low flow. Noticeably, fish abundance showed a significant declining trend in SS (p-value = 0.03) and KT (p-value < 0.0001), while richness exhibited significant decreasing trends for all sites (p-value < 0.0001) over the study period (S8).

Cross-wavelet analysis on variation of weekly abundance and richness with water levels showed that KT and TS were characterized by strong, coherent seasonality-predictability cross-wavelet power in the two data-series at annual (~52 weeks) and semi-annual (26 weeks) frequencies (Fig. 5b, 6b). Such patterns were incoherent and mixed up in SS, as illustrated by disordered responses of the bivariate series with patchy red colors, fragmented ridges and arrows, pointing to different directions across the cross-wavelet power spectrum. These patterns were illustrated clearly in the site average cross-wavelet power over the 7-year study period, showing the strongest peak at 52-week and secondary peak at 26-week frequencies for all sites, with SS having the weakest average cross-wavelet power relative to KT and TS (Fig. 7a, b). Noticeably, average cross-wavelet power for the abundance versus water series was muted in SS relative to KT and TS (Fig. 7a).

Cross-correlation analyses (Fig. 8) revealed that abundance and richness in SS exhibited no seasonality, with almost no significant coefficients detected in the abundance series as compared to those of KT and TS. Correlation lags with maximum coefficients between abundance and water levels were estimated at -26 weeks in SS, 20 weeks in KT (before the peak flow in September) and -15 weeks in TS (after the peak flow in early October), whereas correlation lags with maximum coefficients between richness and water levels were estimated at -22 weeks in SS, -26 weeks in KT (after the peak flow or during the low flow period) and -10 weeks in TS (after the peak flow). It is noteworthy that the cross-correlation lag with the maximum coefficient between water levels in KT and TS was estimated at -4 weeks (S9). The list of fish species names, their abbreviations and traits by genera, families and orders is given in S10.

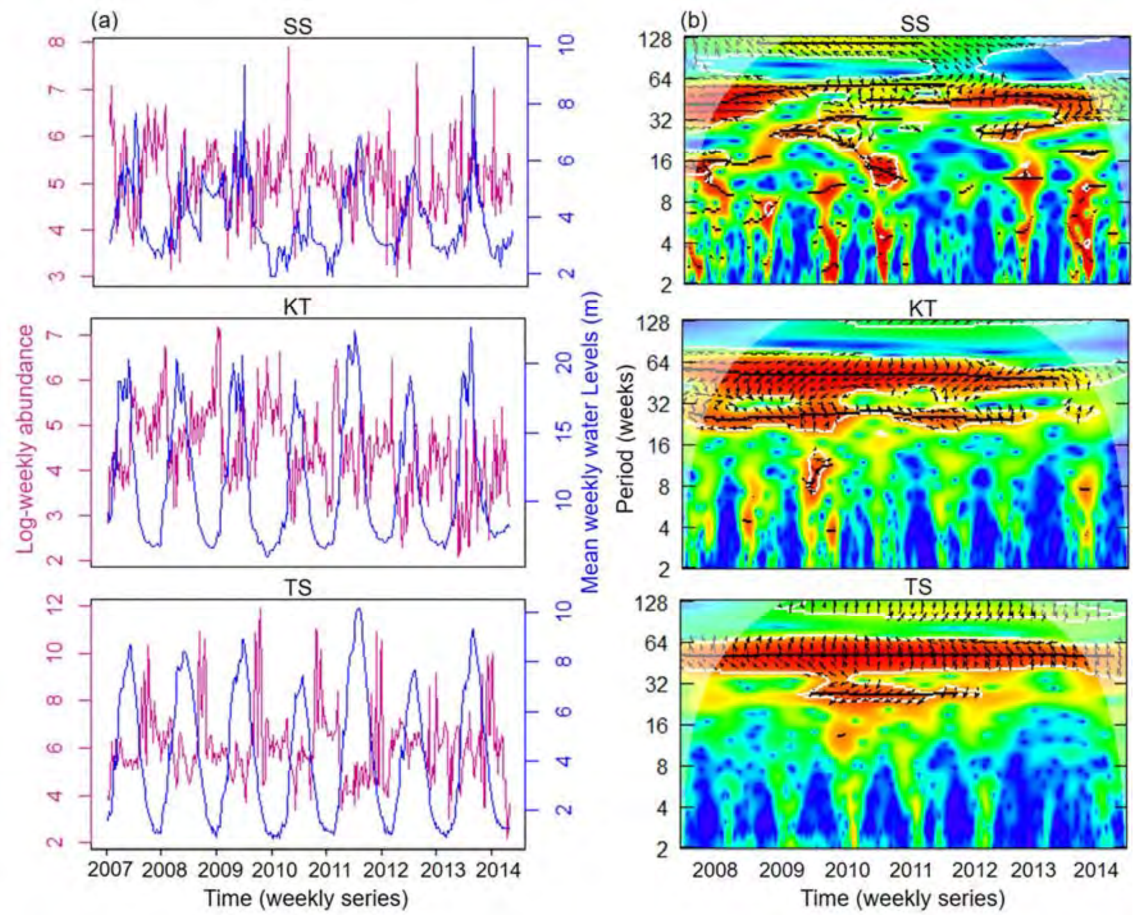


Figure 5. Temporal variations of total weekly abundance (Y) and mean weekly water levels (second Y axis). (a) Weekly abundance and mean water level data series, covering the period from 1 June 2007 to 31 May 2014. (b) Cross-wavelet power spectrum of weekly abundance and water levels. Red color represents stronger cross-wavelet power, and blue weak. Arrows in each plot depict phase-differences. Ridge lines illustrate cross-wavelet power coherence within a band of neighboring periods. Areas in the upper corners, outside the 'cone of influence' in each plot indicated the exclusion of areas from edge effects (with weak predictive ability). For site codes, see Figure 1.

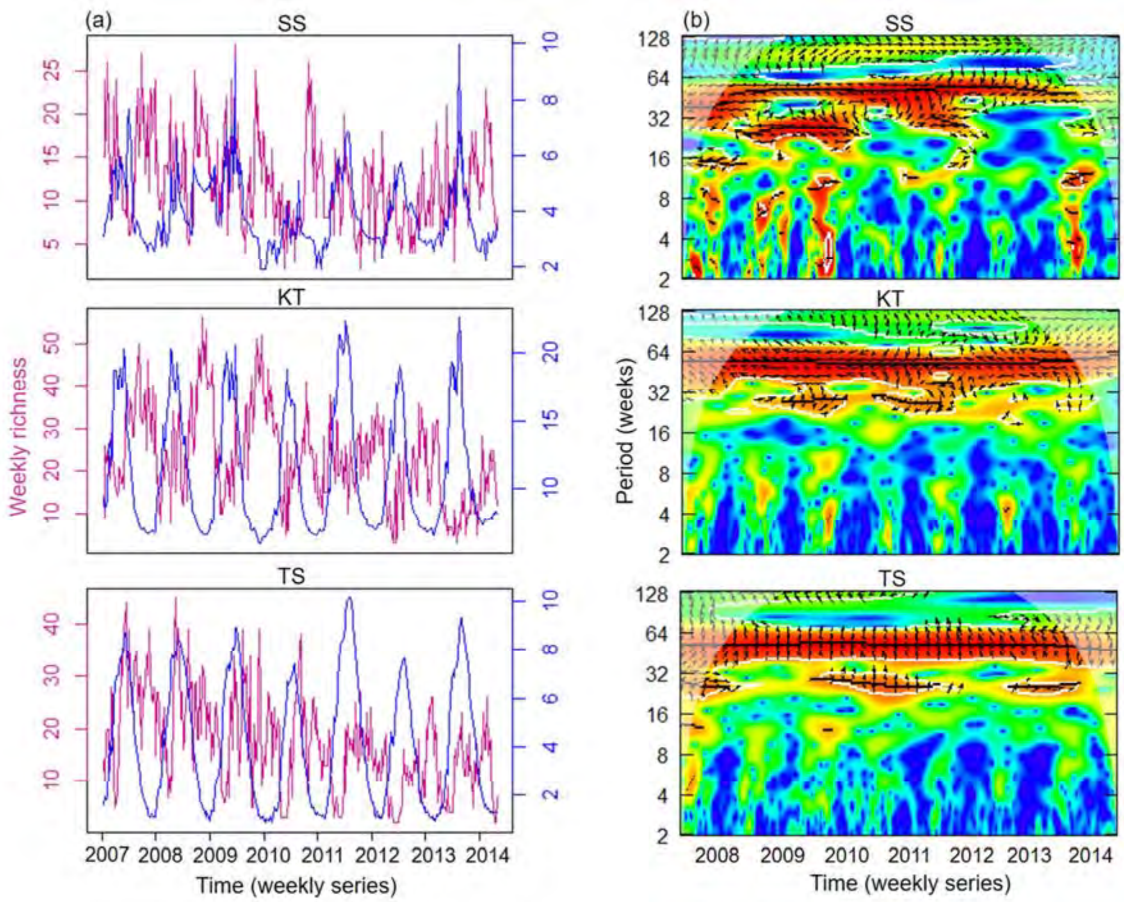


Figure 6. Temporal variations of total weekly richness (Y) and mean weekly water levels (second Y axis). (a) Weekly richness and mean water level data series, covering the period from 1 June 2007 to 31 May 2014. (b) Cross-wavelet power spectrum of weekly richness and water levels. Red color represents stronger cross-wavelet power, and blue weak. Arrows in each plot depict phase-differences. Ridge lines illustrate cross-wavelet power coherence within a band of neighboring periods. Areas in the upper corners, outside the 'cone of influence' in each plot indicated the exclusion of areas from edge effects (with weak predictive ability). For site codes, see Figure 1.

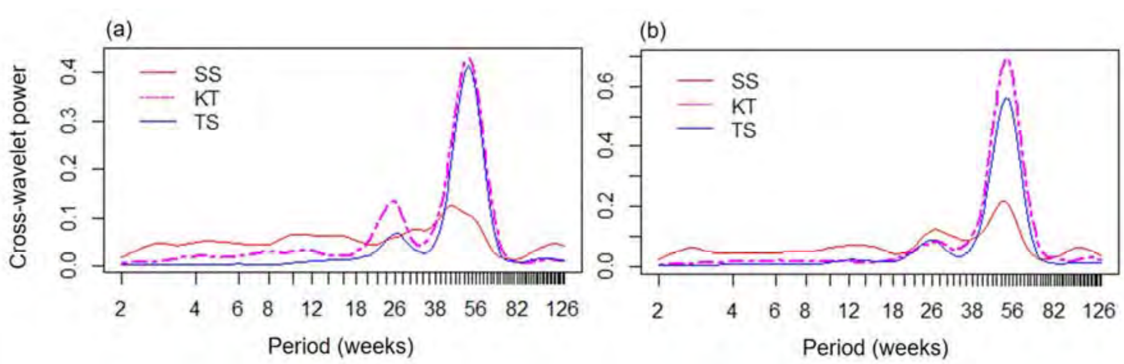


Figure 7. Site average cross-wavelet power. (a) abundance versus water series derived from Figure 5b; (b) richness versus water series derived from Figure 6b. For site codes, see Figure 1.

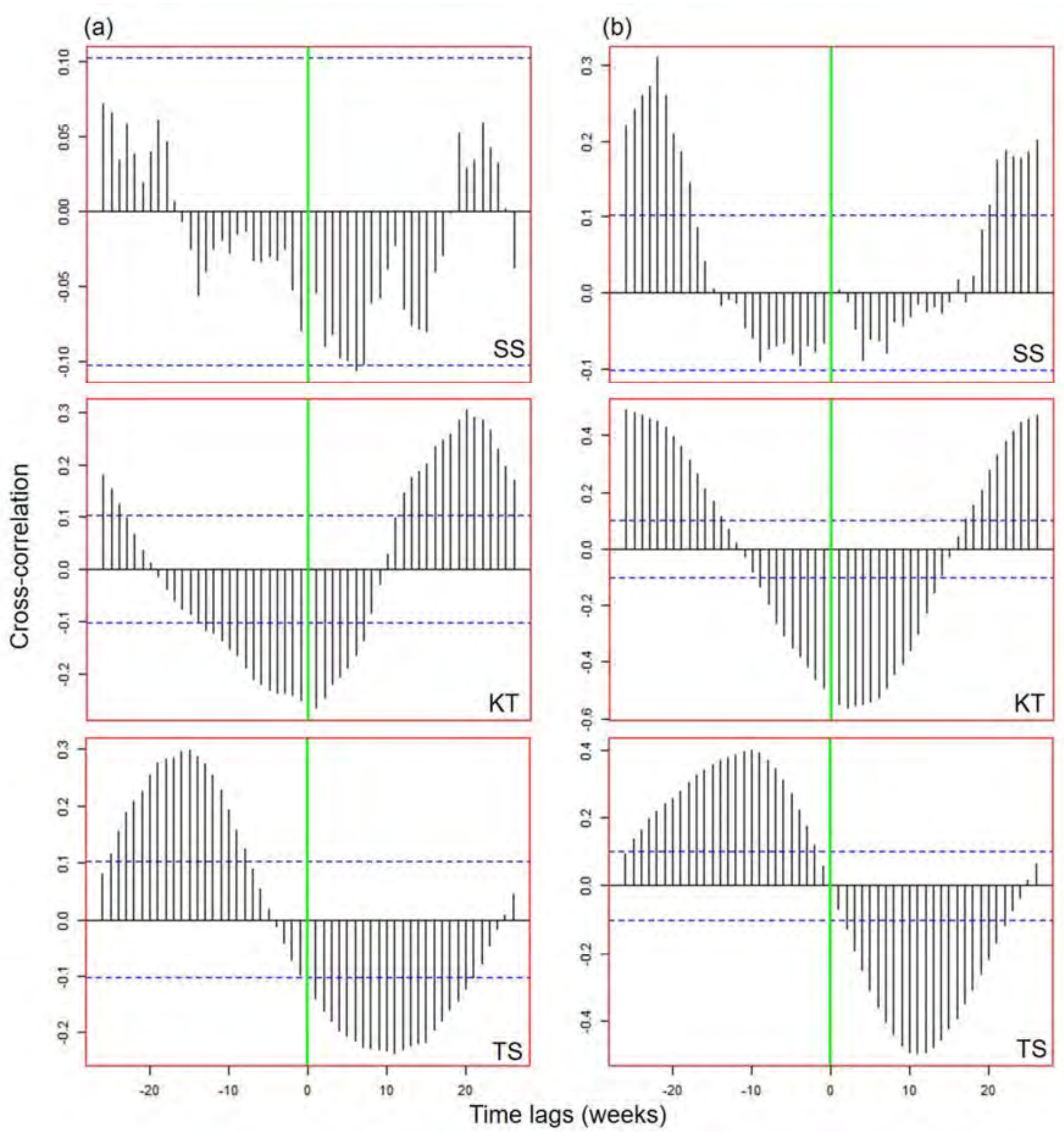


Figure 8. Cross-correlation plots between (a) weekly abundance (Y), (b) weekly richness (Y), and mean weekly water levels (second Y axis) in each site. In the cross-correlations, the dotted blue lines give the values beyond which the correlations are significantly different from zero. X-axis is the time lags, set at 52 weeks (i.e. annual cycle). Data series on fish and water levels used for the cross-correlation plots, covering the period from 1 June 2007 to 31 May 2014. For site codes, see Figure 1.

DISCUSSION

Overall our results support the hypothesis of a gradient in fish assemblage responses with flows seasonality-predictability, but surprisingly in a way contrary to the Tonkin's et al framework (Tonkin et al. 2017). Indeed, we found higher assemblages seasonal turnover and lower nestedness in the site experiencing seasonal flow disturbances (SS) than in the more pristine ones (KT, TS). At least one reason could explain these contrasted results. The main hypothesis evoked by Tonkin et al. to expect high seasonal turnover in assemblages is that distinct habitats and thus distinct fauna should appear between seasons. To validate their hypothesis, they used stream invertebrate assemblages. While this distinct habitat hypothesis could work for invertebrates (Tonkin et al. 2017), whether it applies to fish assemblages is far from evident. First, native fish assemblages are adapted to these predictable natural seasonal disturbances and are resistant to change and second the habitat does not change structurally during high flow periods, except for water volume and water velocity. Species not adapted to high water velocities will disperse to escape these periodic unfavorable conditions and latter recolonize the site during dry season periods. Following this reasoning we expect, as what we actually found, low turnover in sites displaying seasonal predictable flows and nested patterns in assemblage composition between high flow and low flow periods (high flow assemblages being a subset of low flow assemblages). This being said the high assemblage turnover found for our most disturbed site (SS) is more challenging to explain but could be related to hydropeaking.

Indeed, hydropeaking is known to fragment habitats altering fish assemblage composition and diversity due to, among other factors, stranding and downstream displacement, and reduced spawning and rearing success of fish (Hunter 1992, McLaughlin et al. 2006, Habit et al. 2007, Poff et al. 2007, Clarke et al. 2008, Young et al. 2011, Schmutz et al. 2015, Kennedy et al. 2016). First, fish stranding was reported in SS (Baird and Meach 2005). Also, riverine fishes sheltering in the river deep pools or potholes may be reluctant to leave during the low flow periods, and become stranded following rapid falls in flow (Young et al. 2011). Such stranding affects assemblage structure and population as fish can be extirpated through predation, temperature stress and/or oxygen depletion (Hunter 1992, Clarke et al. 2008, Young et al. 2011). As found in this study, significant high species turnover in SS occurred during the dry season periods (Fig. 4b). Second, fish in SS are likely displaced downstream by hydropeaking, and replaced by upstream fishes. Such downstream displacement happens particularly for juvenile and small-sized fishes, and species preferring littoral and backwater areas that either swim or passively drift with the current (Young et al. 2011). Experimental studies have shown that Cyprinidae could be displaced downstream because of their less aerobic red muscle (Bainbridge 1960, 1962). Finally, hydropeaking creates 'false attraction flows' giving false environmental cues for fish e.g. to migrate, spawn or for eggs to hatch afterwards facing stranding, eggs and nest sites dewatering, stress and insufficient food supply following sudden falls in flow and vice versa (Clarke et al. 2008, Young et al. 2011). Similar cases were reported in SS where nesting sites for snakeheads (Channidae) and giant gouramies (Osphronemidae) along the river edges were damaged or washed off and the river deep pools (fish dry-season refugia) were filled up by erosions, caused by hydropeaking (Baird and Meach 2005). The situation reduces spawning success, rearing survival and growth rate. While research on the impacts of hydropower-related pulsed flows on fish assemblages in the Mekong is still very limited, evidence from e.g. North America and Europe (Hunter 1992, McLaughlin et al. 2006, Habit et al. 2007, Poff et al. 2007, Clarke et al. 2008, Young et al. 2011, Schmutz et al. 2015) indicated that hydropower-related pulsed flows promote strong temporal assemblage compositional changes and high species turnover.

Further, inconsistent with Tonkin's et al framework, we found low species turnover in KT and TS. As discussed succinctly earlier this is likely because the river section between these sites is still free-flowing, and the riverine fishes that adapted to the system's naturally seasonal-predictable flow regimes have overlapping seasonal migration patterns and use the predictable-seasonal flow phenomena as gauges for the timing of their migrations to successfully access critical habitats i.e. dry-season refugia in KT (Mekong), spawning in KT, and rearing/feeding in TS (floodplains) (Valbo-Jorgensen and Poulsen 2000, Bao et al. 2001, Poulsen et al. 2002, 2004, Baran 2006, Valbo-Jørgensen et al. 2009). Moreover, in other river systems, riverine fishes are found to have homing behavior, and their movements from hundred to thousand kilometers between critical habitats are associated with spawning strategies e.g. Murray Darling golden perch (O'Connor et al. 2005), Murray cod (Koehn et al. 2009), Amazonian giant catfish (Duponchelle et al. 2016), salmonids and a marine fish (weakfish) (Dittman and Quinn 1996, Thorrold et al. 2001). The naturally adapted migration cycles of the riverine fishes in KT and TS of the lower Mekong system may resemble such natal homing and site fidelity; and as such, broadly similar seasonal assemblage composition with low species turnover are expected.

Besides, our results are partly in line with Tonkin's et al seasonality and predictability framework in that the disturbed site (SS) exhibited lowest levels of temporal changes in diversity (abundance and richness) as compared to the predictably seasonal ones (KT, TS). We found that dams modulated flows and weakened the flows' seasonality and predictability strengths and thus muted seasonal variations of fish abundance and richness in SS, whereas sites with more naturally predictable flow conditions (KT, TS) promote reliable seasonal variations in fish abundance and richness with regular-predictable peaks at semi-annual and annual frequencies (S7, Fig. 5, 6, 7, 8). As further evidenced in the seasonal trait patterns, longitudinal migratory species colonized the mainstream habitats (i.e. KT) during the dry season for refugia and spawning and dispersed to the lower floodplains via TS for rearing and feeding during the wet season (Fig. 3b). Such reliable recurrence patterns of hydrology and fish are indeed consistent with the existing knowledge about timing of fish migration, fishing and local fisheries management practices in the lower Mekong system (Valbo-Jorgensen and Poulsen 2000, Bao et al. 2001, Poulsen et al. 2002, 2004, Baird et al. 2003, FiA 2006, Halls et al. 2013). When the river seasonal-predictable flows are modified as evidenced in SS, such reliably seasonal-predictable events of fish assemblage no longer exist.

CONCLUSION

River flows structure riverine fishes that use seasonal-predictable hydrologic variations as gauges for the timing of their migrations to successfully access critical habitats in the lower Mekong system. We demonstrated that fish assemblages in highly regulated rivers were characterized by little seasonal variations in fish abundance, richness and distinct seasonal assemblage composition with high species turnover, whereas, assemblages in highly seasonal-predictable rivers were represented by repeated seasonal-predictable peak abundance and richness at semi-annual and annual cycles, and more similar seasonal assemblage composition with low species turnover. While partly in line with Tonkin's et al seasonality-predictability framework of highly seasonal-predictable environmental conditions promoting the greatest temporal changes in diversity (abundance and richness), our results are overall not consistent with Tonkin's et al framework hypothesizing that predictably seasonal environmental conditions promote the highest levels of temporal changes in assemblage composition with high species turnover. We explained that, in aseasonal-unpredictable rivers, dams generate hydropower-related pulsed flows i.e. hydropeaking which fragments habitats and alters fish assemblage composition and diversity due to stranding, downstream displacement and creating false attraction flows that reduced spawning and rearing success of fish. These resulted in strong temporal fish assemblage compositional changes with high species turnover. While in highly seasonal-predictable system, riverine fishes have overlapping seasonal migration patterns between critical habitats, and possibly have homing behavior and site fidelity which likely constitutes more similar seasonal assemblage composition with low species turnover. Our study also highlighted contrasted seasonal patterns in fish traits observed in the three rivers, with the Mekong mainstream being important refugia and spawning habitats for longitudinal migratory fishes during the dry season while the lower gradient river i.e. TS is their important rearing and feeding habitats during the wet season. This study contributes to the understanding of biological systems in the highly seasonal-predictable and aseasonal-unpredictable environments of the lower Mekong system. It also provides knowledge about the downstream ecological effects of and fish assemblage responses to hydropower-related pulsed flows. To date, dam site selection (Ziv et al. 2012, Winemiller et al. 2016) and advanced fish passage facilities (Schmutz and Mielach 2015) are among the important suggested measures to mitigate dam impacts. In addition, flow designs that could minimize the effects of hydropower-related pulsed flows on aquatic organisms i.e. mimic as far as possible natural seasonal hydrologic variations e.g. (Sabo et al. 2017) should be privileged for the appropriate applications of mitigation measures of the ever-growing dam construction in the Mekong.

ACKNOWLEDGEMENTS

We are grateful to the European Erasmus+ credit mobility and capacity building CONSEA Programs for funding our study. Cordial thanks to the Fisheries Programme of the Mekong River Commission, the Inland Fisheries Research and Development Institute and the Fisheries Administration, Cambodia for making available the fish monitoring datasets used in this study. We would like to thank Nam So, Solyda Putrea, Sokheng Chan and 9 fishers for supervising and implementing the field fish monitoring, Kunthea Nuon for helping prepare the map for this study. EDB lab was supported by 'Investissement d'Avenir' grants (CEBA, ref. ANR-10-LABX-0025; TULIP, ref. ANR-10-LABX-41).

Literature Cited

Adamson, P. T., I. D. Rutherfurd, M. C. Peel, and I. A. Conlan. 2009. The Hydrology of the Mekong River. Pages 53–76*in* I. C. Campbell, editor.The Mekong Biophysical Environment of an International River Basin. 1st edition. Elsevier Inc., Amsterdam.

Agostinho, A. A., L. C. Gomes, S. Veríssimo, and E. K. Okada. 2004. Flood regime, dam regulation and fish in the Upper Paraná River: Effects on assemblage attributes, reproduction and recruitment. Reviews in Fish Biology and Fisheries 14:11–19.

Bainbridge, R. 1960. Speed and stamina in three fish. Journal of Experimental Biology 37:129–153.

Bainbridge, R. 1962. Training , speed and stamina in trout. Journal of Experimental Biology 39:537–555.

Baird, I., M. Baird, M. C. Chum, S. Kim, M. Nuon, S. Phat, B. N. Phouy, S. Prom, S. Ros, H. Rushton, and P. Sia. 2002. A Community-Based Study of the Downstream Impacts of the Yali Falls Dam Along the Se San, Sre Pok and Sekong Rivers in Stung Treng Province, Northeast Cambodia. Se San District Agriculture, Fisheries and Forestry Office, Stung Treng, Cambodia.

Baird, I. G., M. S. Flaherty, and B. Phylavanh. 2003. Rhythms of the river: lunar phases and migrations of small carps (Cyprinidae) in the Mekong River. Natural History Bulletin of the Siam Society 51:5–36.

Baird, I. G., and M. Meach. 2005. Sesan River Fisheries Monitoring in Ratanakiri Province, Northeast Cambodia: Before and After the Construction of the Yali Falls Dam in the Central Highlands of Viet Nam. 3S Rivers Protection Network and the Global Association for People and the Environment, Ban Lung, Ratanakiri, Cambodia.

Bao, T. Q., K. Bouakhamvongsa, S. Chan, K. Chhuon, T. Phommavong, A. F. Poulsen, P. Rukawoma, U. Suornratana, D. V. Tien, T. T. Tuan, N. T. Tung, J. Valbo-Jorgensen, S. Viravong, and N. Yoorong. 2001. Local knowledge in the study of river fish biology: experiences from the Mekong. Mekong River Commission, Phnom Penh.

Baran, E. 2005. Cambodia inland fisheries: facts, figures and context. WorldFish Center and Inland Fisheries Research and Development Institute, Phnom Penh, Cambodia.

Baran, E. 2006. Fish Migration Triggers and Cues in the Lower Mekong Basin and Other Freshwater Tropical Systems. Mekong River Commission, Vientiane.

Baran, E., N. So, P. Degen, X. Y. Chen, and P. Starr. 2013. Updated information on fish and fisheries in the Mekong Basin. Catch and Culture 19:24–25.

Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography 19:134–143.

Baselga, A., and C. D. L. Orme. 2012. betapart : an R package for the study of beta diversity. Methods in Ecology and Evolution 3:808–812.

Bejarano, M. D., R. Jansson, and C. Nilsson. 2017. The effects of hydropeaking on riverine plants: a review. Biological Reviews:1–16.

Bond, N. 2016. Hydrologic Indices for Daily Time Series Data. CRAN.R-project.org.

Borcard, D., F. Gillet, and P. Legendre. 2011. Numerical Ecology with R. Page (R. Gentleman, K. Hornik, and G. G. Parmigiani, Eds.). Springer Science, New York.

Chea, R., S. Lek, P. B. Ngor, and G. Grenouillet. 2016. Large-scale patterns of fish diversity and assemblage structure in the longest tropical river in Asia. Ecology of Freshwater Fish 2016:1–11.

Claasen, A. H. 2004. Abundance, distribution, and reproductive success of sandbar nesting birds below the Yali Falls hydropower dam on the Sesan River, northeastern Cambodia. WWF/Danida/WCS/BirdLife International, Phnom Penh.

Clarke, K. D., T. C. Pratt, R. G. Randall, A. Dave, and K. E. Smokorowski. 2008. Validation of the flow management pathway: effects of altered flow on fish habitat and fishes downstream from a hydropower dam. Canadian Technical Report of Fisheries and Aquatic Sciences 2784, Canada.

Collier, M., R. H. Webb, and J. C. Schmidt. 1996. Dams and rivers: A Primer on the Downstream Effects of Dams. U.S. Geological Survey, Circular 1 1 2 6, Colorado.

Colwell, R. K. 1974. Predictability, constancy, and contingency of periodic phenomena. Ecology 55:1148–1153.

Davidson, P. J. 2006. The biodiversity of the Tonle Sap Biosphere Reserve: 2005 status review. UNDP-GEF funded Tonle Sap Conservation Project, Phnom Penh, Cambodia.

Dittman, A., and T. Quinn. 1996. Homing in Pacific salmon: mechanisms and ecological basis. The Journal of experimental biology 199:83–91.

Duponchelle, F., M. Pouilly, C. Pécheyran, M. Hauser, J. F. Renno, J. Panfili, A. M. Darnaude, A. García-Vasquez, F. Carvajal-Vallejos, C. García-Dávila, C. Doria, S. Bérail, A. Donard, F. Sondag, R. V. Santos, J. Nuñez, D. Point, M. Labonne, and E. Baras. 2016. Trans-Amazonian natal homing in giant catfish. Journal of Applied Ecology 53:1511–1520.

Fan, H., D. He, and H. Wang. 2015. Environmental consequences of damming the mainstream Lancang-Mekong River: A review. Earth-Science Reviews 146:77–91.

FiA. 2006. Law on Fisheries. Fisheries Administration, Ministry of Agriculture, Forestry and Fisheries, Phnom.

Fitzgerald, D. B., K. O. Winemiller, M. H. S. Pérez, and L. M. Sousa. 2017. Seasonal changes in the assembly mechanisms structuring tropical fish communities. Ecology 98:21–31.

Froese, R., and D. Pauly. 2017. FishBase. World Wide Web electronic publication. www.fishbase.org.

Graf, W. L. 2006. Downstream hydrologic and geomorphic effects of large dams on American rivers. Geomorphology 79:336–360.

Habit, E., M. C. Belk, and O. Parra. 2007. Response of the riverine fish community to the construction and operation of a diversion hydropower plant in central Chile. Aquatic Conservation: Marine and Freshwater Ecosystems 17:37–49.

Halls, A. S., B. R. Paxton, N. Hall, P. B. Ngor, S. Lieng, P. Ngor, and N. So. 2013. The Stationary Trawl (Dai) Fishery of the Tonle Sap-Great Lake System, Cambodia. Mekong River Commission, Phnom Penh.

Hirsch, P., and A. Wyatt. 2004. Negotiating local livelihoods: scales of conflict in the Se San River Basin. Asia Pacific Viewpoint 45:51–68.

Hunter, M. A. 1992. Hydropower flow fluctuations and salmonids: A review of the biological effects, mechanical causes, and options for mitigation. State of Washington Department of Fisheries, Washington.

Kassambara, A. 2017. Pratical guide to cluster analysis in R: unsupervised machine learning. STHDA, Poland.

Kennedy, T. A., J. D. Muehlbauer, C. B. Yackulic, D. A. Lytle, S. W. Miller, K. L. Dibble, E. W. Kortenhoeven, A. N. Metcalfe, and C. V Baxter. 2016. Flow Management for Hydropower Extirpates Aquatic Insects, Undermining River Food Webs. BioScience 66:562–575.

Koehn, J. D., J. A. McKenzie, D. J. O'Mahony, S. J. Nicol, J. P. O'Connor, and W. G. O'Connor. 2009. Movements of Murray cod (Maccullochella peelii peelii) in a large Australian lowland river. Ecology of Freshwater Fish 18:594–602.

Kottelat, M. 2013. The Fishes of the inland waters of Southeast Asia: A catalogue and core bibliography of the fishes known to occur in freshwaters, mangroves and estuaries. The Raffles Bulletin of Zoology 27:1–663.

Kummu, M., S. Tes, S. Yin, P. Adamson, J. Józsa, J. Koponen, J. Richey, and J. Sarkkula. 2014. Water balance analysis for the Tonle Sap Lake-floodplain system. Hydrological Processes 28:1722–1733.

Latrubesse, E. M., E. Y. Arima, T. Dunne, E. Park, V. R. Baker, F. M. Horta, C. Wight, F. Wittmann, J. Zuanon, P. A. Baker, C. C. Ribas, R. B. Norgaard, and N. Filizola. 2017. Damming the rivers of the Amazon basin. Nature 546:363–369.

Legendre, P., and L. Legendre. 2012. Numerical Ecology. Third Engl. Elsevier Science B.V., Great Britain.

Mcintyre, P. B., M. O. Gessner, D. Dudgeon, A. Prusevich, P. Green, S. Glidden, S. E. Bunn, C. J. Vo, C. A. Sullivan, C. R. Liermann, and P. M. Davies. 2010. Global threats to human water security and river biodiversity. Nature 467:555–561.

McLaughlin, R. L., L. Porto, D. L. Noakes, J. R. Baylis, L. M. Carl, H. R. Dodd, J. D. Goldstein, D. B. Hayes, and R. G. Randall. 2006. Effects of low-head barriers on stream fishes: taxonomic affiliations and morphological correlates of sensitive species. Canadian Journal of Fisheries and Aquatic Sciences 63:766–779.

McMeans, B. C., K. S. McCann, M. Humphries, N. Rooney, and A. T. Fisk. 2015. Food Web Structure in Temporally-Forced Food Web Structure in Ecosystems. Trends in Ecology & Evolution 30:662–672.

Mcnamara, J. M., and A. I. Houston. 2008. Optimal annual routines : behaviour in the context of physiology and ecology. Philosophical Transactions of the Royal Society B 363:301–319.

Meile, T., J. L. Boillat, and A. J. Schleiss. 2010. Hydropeaking indicators for characterization of the Upper-Rhone River in Switzerland. Aquatic Sciences 73:171–182.

MFD. 2003. Mekong Fish Database: A taxonomic fish database for the Mekong Basin. Mekong River Commission, Phnom Penh.

MRC. 2003. State of the Basin Report 2003. Mekong River Commission, Phnom Penh.

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

MRC. 2007. Monitoring Fish Abundance and Diversity in the Lower Mekong Basin: Methodological Guidelines. Mekong River Commission, Phnom Penh.

Ngor, P. B., P. Legendre, T. Oberdorff, and S. Lek. 2018. Flow alterations by dams shaped fish assemblage dynamics in the complex Mekong-3S river system. Ecological Indicators 88:103–114.

O'Connor, J. P., D. J. O'Mahony, and J. M. O'Mahony. 2005. Movements of Macquaria ambigua, in the Murray River, south-eastern Australia. Journal of Fish Biology 66:392–403.

Piman, T., T. A. Cochrane, M. E. Arias, A. Green, and N. D. Dat. 2013. Assessment of Flow Changes from Hydropower Development and Operations in Sekong, Sesan, and Srepok Rivers of the Mekong Basin. Journal of Water Resources Planning and Management 139:723–732.

Poff, N. L., J. D. Olden, D. M. Merritt, and D. M. Pepin. 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. Proceedings of the National Academy of Sciences of the United States of America 104:5732–5737.

Poulsen, A. F., K. G. Hortle, J. Valbo-Jorgensen, S. Chan, C. K. Chhuon, S. Viravong, K. Bouakhamvongsa, U. Suntornratana, N. Yoorong, N. T.T., and B. Q. Tran. 2004. Distribution and Ecology of Some Important Riverine Fish Species of the Mekong River Basin. Mekong River Commission, Phnom Penh.

Poulsen, A. F., P. Ouch, S. Viravong, U. Suntornratana, and T. T. Nguyen. 2002. Fish Migrations of the Lower Mekong Basin: Implications for Development, Planning and Environmental Management. Mekong River Commission, Phnom Penh.

R Core Team. 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rainboth, W. J. 1996. Fishes of the Cambodian Mekong. Food and Agriculture Organisation of the United Nations, Rome.

Rainboth, W. J., C. Vidthayanon, and D. Y. Mai. 2012. Fishes of the Greater Mekong Ecosystem with Species List and Photoraphic Atlas. Museum of Zoology, University of Michigan, Ann Arbor.

Ratanakiri Fisheries Office. 2000. A Study of Downstream Impacts of the Yali Falls Dam in the Se San River Basin in Ratanakiri Province, Northeast Cambodia. The Fisheries Office, Ratanakiri Province in cooperation with the Non-Timber Forest Products (NTFP) Project, Ratanakiri Province, Cambodia.

Roesch, A., and H. Schmidbauer. 2014. WaveletComp: Computational Wavelet Analysis. R package version 1.0. CRAN.R-project.org.

Rutkow, E., C. Crider, and T. Giannin. 2005. Down River. The consequences of Vietnam's Se San River dams on life in Cambodia and their meaning in International law. NGO Forum on Cambodia, Phnom Penh.

Sabo, J. L., A. Ruhi, G. W. Holtgrieve, V. Elliott, M. E. Arias, P. B. Ngor, T. A. Räsänen, and S. Nam. 2017. Designing river flows to improve food security futures in the Lower Mekong Basin. Science 358:1–11.

Schmutz, S., T. H. Bakken, T. Friedrich, T. Greimel, A. Harby, M. Jungwirth, A. Melcher, G. Unfer, and B. Zeiringer. 2015. Response of fish communities to hydrological and morphological alterations in hydropeaking rivers of Austria. River Research and Applications 31:919–930.

Schmutz, S., and C. Mielach. 2015. Review of existing research on fish passage through large dams and its applicability to Mekong mainstream dams. Mekong River Commission, Phnom Penh.

Shimadzu, H., M. Dornelas, P. A. Henderson, and A. E. Magurran. 2013. Diversity is maintained by seasonal variation in species abundance. BMC Biology 11:1–9.

Shumway, R. H., and D. S. Stoffer. 2011. Time series analysis and its applications: with R examples. Third Edit. Springer Science+Business Media, New York.

Sverdrup-Jensen, S. 2002. Fisheries in the Lower Mekong Basin: Status and Perspectives. Mekong River Commission, Phnom Penh.

Thorrold, S. R., C. Latkoczy, P. K. Swart, and C. M. Jones. 2001. Natal Homing in a Marine Fish Metapopulation. Science 291:297–299.

Tonkin, J. D., M. T. Bogan, N. Bonada, B. Ríos-Touma, and D. A. Lytle. 2017. Seasonality and predictability shape temporal species diversity. Ecology 0:1–16.

Tonolla, D., A. Bruder, and S. Schweizer. 2017. Evaluation of mitigation measures to reduce hydropeaking impacts on river ecosystems – a case study from the Swiss Alps. Science of the Total Environment 574:594–604.

Torrence, C., and G. P. Compo. 1998. A practical guide to wavelet analysis. Bulletin of the American Meteorological society 79:61–78.

Valbo-Jørgensen, J., D. Coates, and K. G. Hortle. 2009. Fish diversity in the Lower Mekong Basin. Pages 161 – 196*in* I. C. Campbell, editor.The Mekong Biophysical Environment of an International River Basin. 1st edition. Elsevier Inc., Amsterdam.

Valbo-Jorgensen, J., and A. F. Poulsen. 2000. Using local knowledge as a research tool in the study of river fish biology: Experiences from the Mekong. Environment, Development and Sustainability 2:253–276.

Winemiller, K., P. McIntyre, L. Castello, E. Fluet-Chouinard, T. Giarrizzo, N. So, I. Baird, W. Darwall, N. Lujan, I. Harrison, M. Stiassny, R. Silvano, D. Fitzgerald, F. Pelicice, A. Agostinho, L. Gomes, J. Albert, E. Baran, M. Petrere, C. Zarfl, M. Mulligan, J. Sullivan, C. Arantes, L. Sousa, A. Koning, D. Hoeinghaus, M. Sabaj, J. Lundberg, J. Armbruster, M. Thieme, P. Petry, J. Zuanon, G. Vilara, J. Snoeks, C. Ou, W. Rainboth, C. Pavanelli, A. Akama, A. van Soesbergen, and L. Saenz. 2016.

Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. Science 351:128–129.

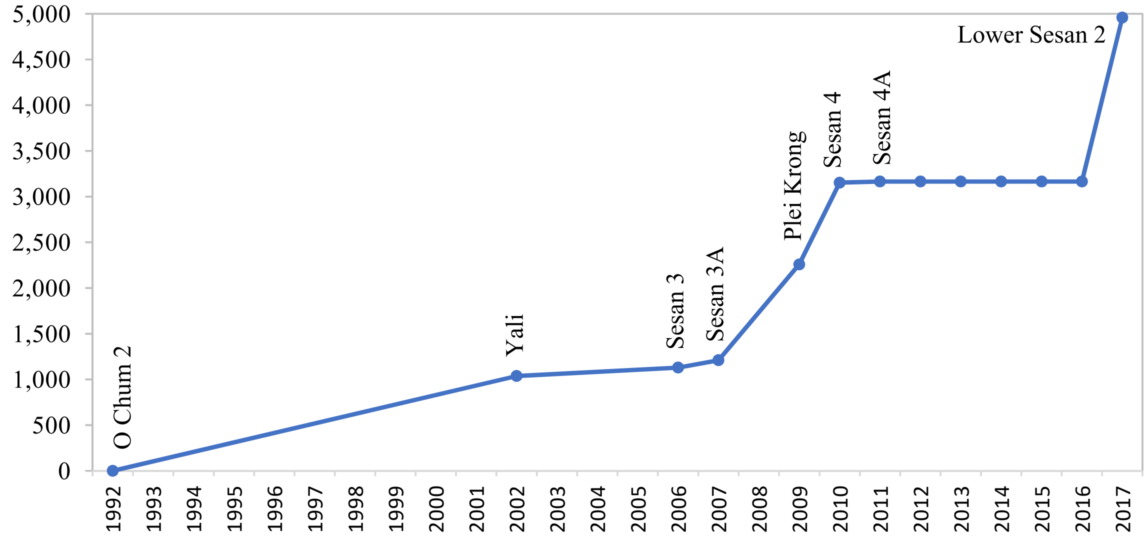
Young, P. S., J. J. Cech, and L. C. Thompson. 2011. Hydropower-related pulsed-flow impacts on stream fishes: A brief review, conceptual model, knowledge gaps, and research needs. Reviews in Fish Biology and Fisheries 21:713–731.

Zarfl, C., A. E. Lumsdon, and K. Tockner. 2015. A global boom in hydropower dam construction. Aquatic Sciences 77:161–170.

Ziv, G., E. Baran, N. So, I. Rodriguez-Iturbe, and S. A. Levin. 2012. Trading-off fish biodiversity, food security, and hydropower in the Mekong River Basin. Proceedings of the National Academy of Sciences 109:5609–5614.

Supplementary Information (S)

Supplementary Information (S1): Timeline and cumulative installed gross storage capacity of existing hydropower dams in the Sesan River Basin (Data source: MRC Hydropower Project Database, 2015). Note that Lower Sesan 2 dam has just recently been functioning since 2017.



Supplementary Information (S2): Seasonality and predictability strength of site hydrology for the period 1965-1969 (pre-dam) and 2007-2014 (this study).

Overall, daily water level data are collected routinely in the Lower Mekong Basin, and can be tracked back to around mid-1960s in some hydrological stations including our study sites i.e. the Mekong River in Kratie (KT) and Tonle Sap River (TS) at Prek Kdam. However, during the period, water level data are only partly available i.e. 1965-1969 and 1990s-present in Sesan River (SS). This is likely due to the remoteness of the site and because the region was at war especially between 1970 and 1990. Given that hydropower dams in SS began in the early 1990s (see S1), daily water level data for this river during the pre-dam are therefore only available between 1965 and 1969. For this reason, we assume that daily water levels consistently available from the three study sites for the period between January 1965 and December 1969 represent the baseline condition or what we refer to as the 'natural condition' for the three rivers.

Colwell's index and wavelet (see Method section in the manuscript for details) were used to quantify the strength of seasonality and predictability of site hydrology between the baseline condition (i.e. 1965-1969) and this study period (i.e. 2007-2014). Site average wavelet power (i.e. predictability strength) between the two periods was extracted from the wavelet plots for comparison.

Colwell's seasonality indices of site hydrology computed for the period 1965-1969 were: SS (0.86), KT (0.94) and TS (0.94), and for this study period 2007-2014 were: SS (0.83), KT (0.90) and TS (0.93). For the predictability strength of site hydrology for the two periods, see Figure S2.

Overall, there was little reduction in the seasonality index of site hydrology (i.e. 0.01-0.04) between the two periods: 1965-1969 and 2007-2014. Noticeably, there was a strong reduction in the predictability strength (~40%) of site hydrology at 52-week (annual) frequencies in SS (Figure S2). Also, the second strong predictability strength of site hydrology that occurred at 26-week (semi-annual) frequencies in 1965-1969 in SS had been muted for the period 2007-2014 due to hydrologic alterations. Predictability strength of site hydrology for KT and TS were still comparable between the two periods. It was highly likely that the change in the predictability strength in SS during the period 2007-2014 relative to its baseline condition (1965-1969) was due to upstream functioning dams of this river system (See also S1, Piman et al. 2013, Ngor et al. 2018).

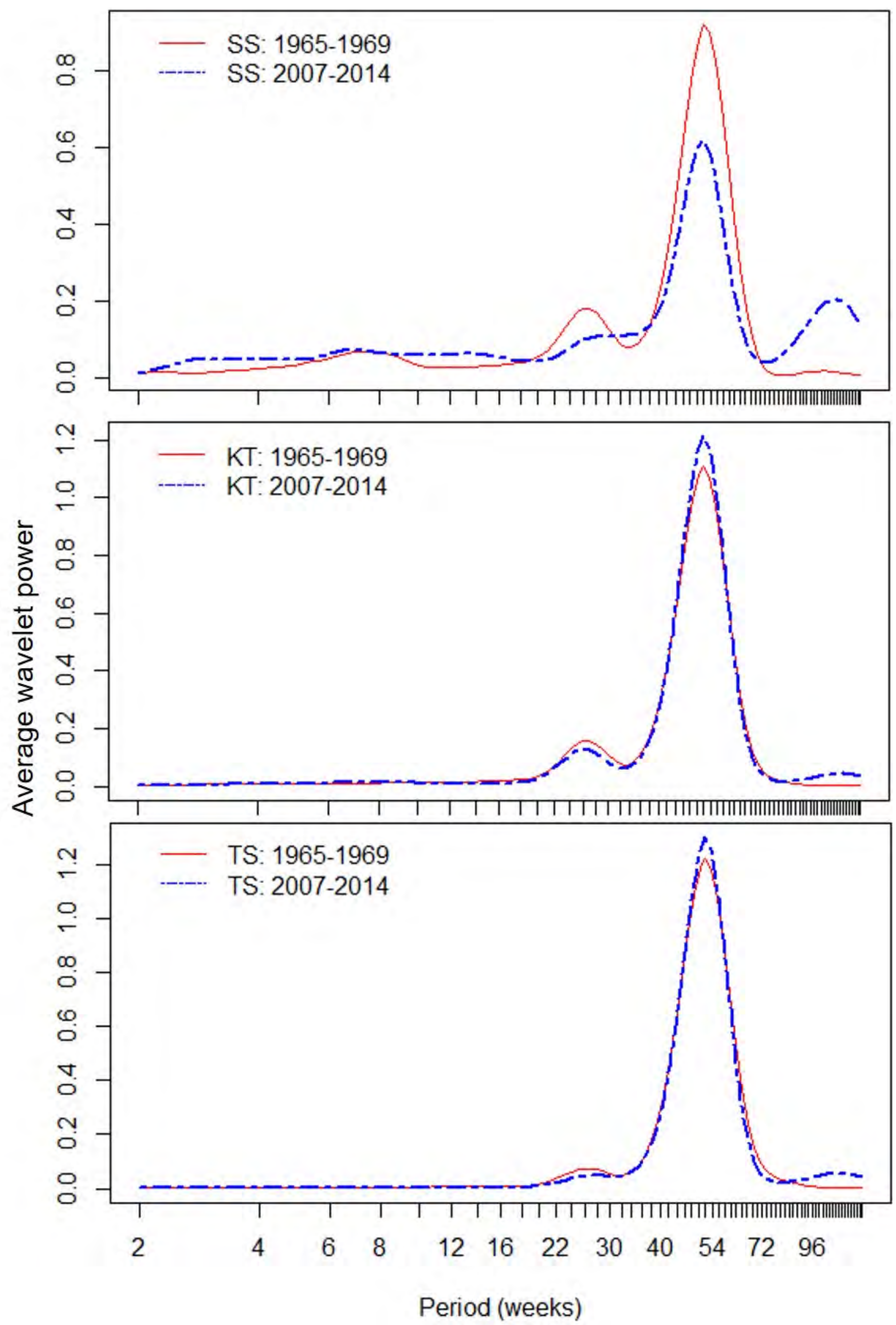
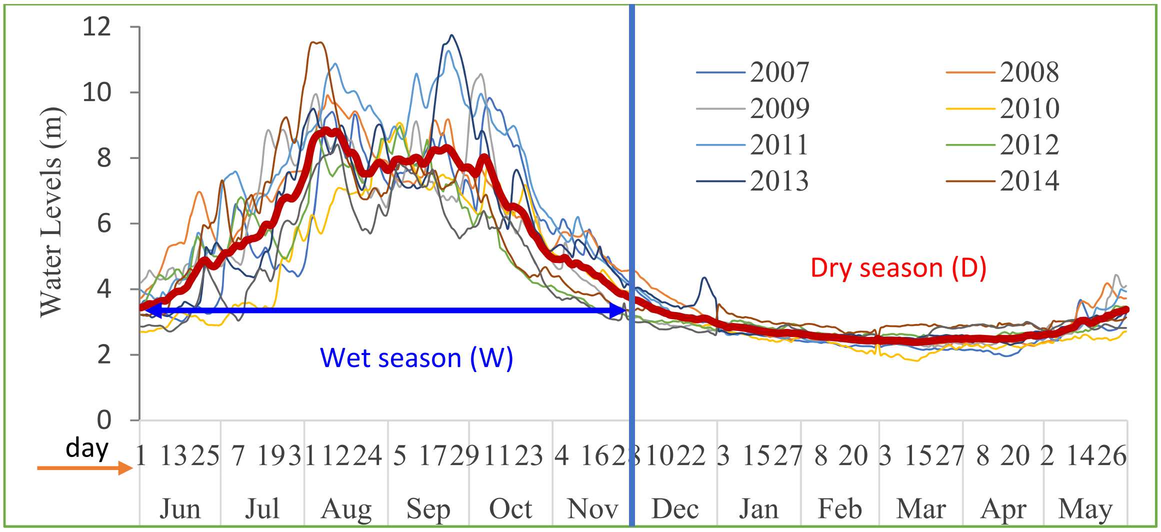
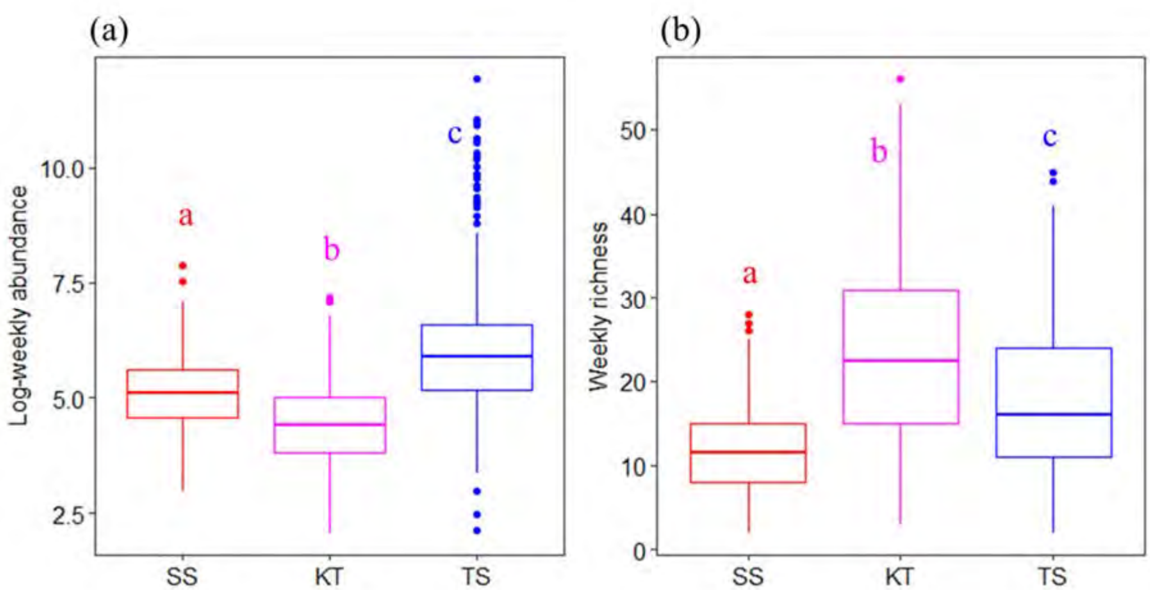


Figure S2: Average wavelet power on mean weekly water levels indicating changes in the predictability strength of site hydrology between the two periods: 1965-1969 and 2007-2014. For site codes, see Figure 1.

Supplementary Information (S3): Seasonality partitioning: Dry season (June-November) and Wet season (December-May). Data was based on mean 9-year daily water levels (red solid line) recorded at Stung Treng Hydrological Station, when the Mekong River enters Cambodia.



Supplementary Information (S4): Boxplots summarizing (a) site weekly abundance; (b) site weekly richness. Mean values among sites with a common letter are not significantly different at the 0.05 level (Pairwise Wilcoxon Rank Sum Tests). For site codes, see Figure 1.



Supplementary Information (S5): Pie charts summarizing top 15 most abundant species (number of individuals) in: (a) Sesan River (SS), (b) Mekong River in Kratie (KT) and (c) Tonle Sap River (TS). For the list of fish species names, their abbreviations and traits by genera, families and orders, see S10.

In SS, of 15 top abundant species (S5a), seven species were small-sized (max. body size <= 25cm) and the rest was medium-sized species (max. body size: 26-60 cm). A small-sized floodplain resident climbing perch, *Anabas testudineus* (Ates) ranked top (12%) in SS. Five dominant small-sized species were recorded in this site i.e., *Henicorhynchus lobatus* (Hlob), *H. siamensis* (Hsia), *Labiobarbus siamensis* (Lsia), *Systomus rubripinnis* (Srub), *Osteochilus vittatus* (Ovit).

In KT (S5b), of 15 top species, *H. lobatus, H. siamensis,* and *L. siamensis* were also among the top dominant species; however, the site assemblage composition was also shared by six medium sized species such as *Puntioplites falcifer* (Pfal), *P. proctozysron* (Ppro), *Hypsibarbus malcolmi* (Hmal), *Hemibagrus spilopterus* (Hspi); two large-sized species (max. body size: 61-99 cm) i.e., *Labeo chrysophekadion* (Lchr) and *Helicophagus waandersii* (Hwaa) and one giant-sized species (max. body size: >100 cm), the croakers *Boesemania microlepis* (Bmic).

In TS (S5c), assemblage composition was dominantly represented by small-sized minnows and carps, five of which i.e., *Henicorhynchus lobatus* (Hlob), *Paralaubuca riveroi* (Priv), *Labiobarbus siamensis* (Lsia), *Henicorhynchus siamensis* (Hsia), *Paralaubuca typus* (Ptyp), accounted for up to ~85% of the total abundance.

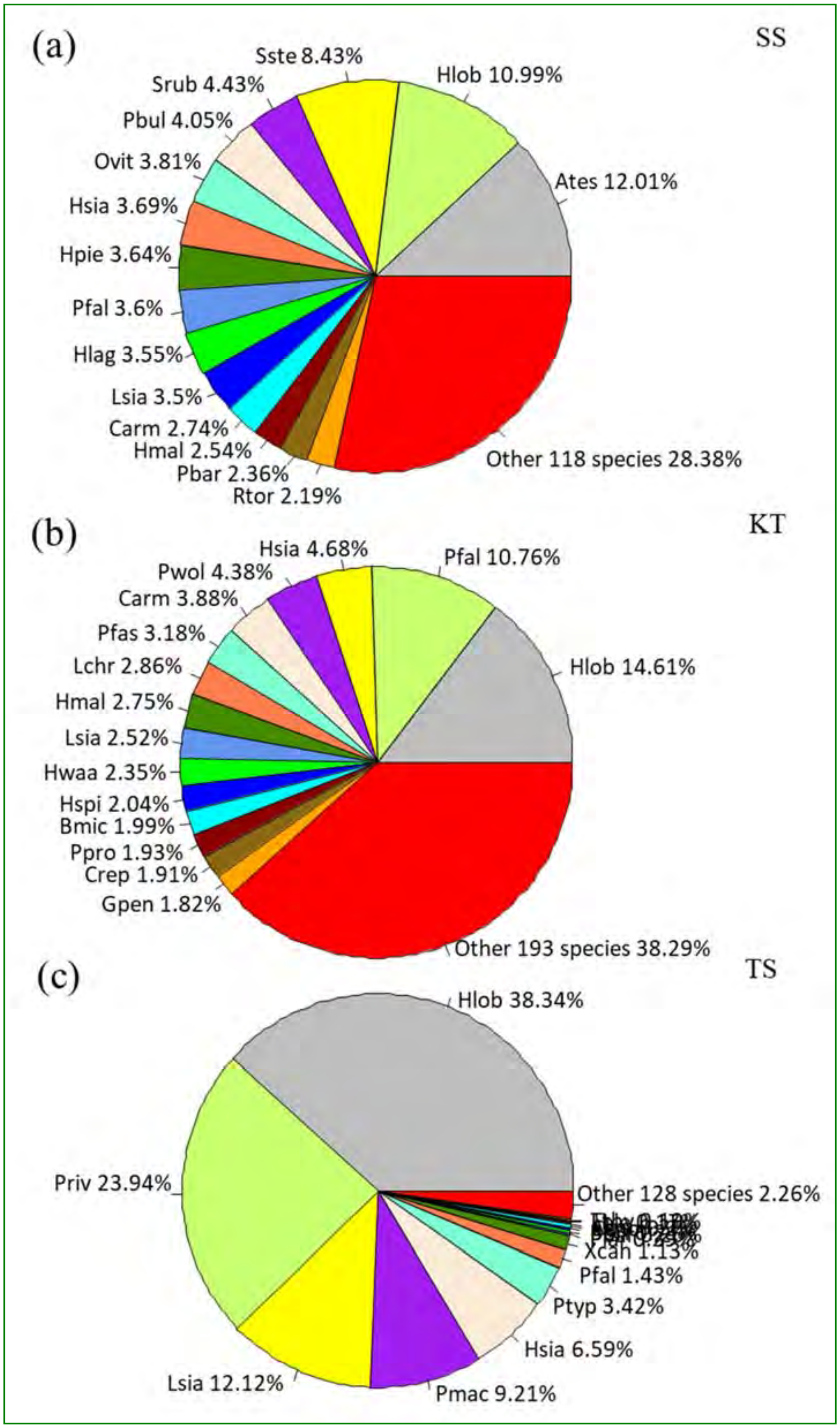


Figure S5. Top 15 most abundant species in each study site. For site codes, see Figure 1.

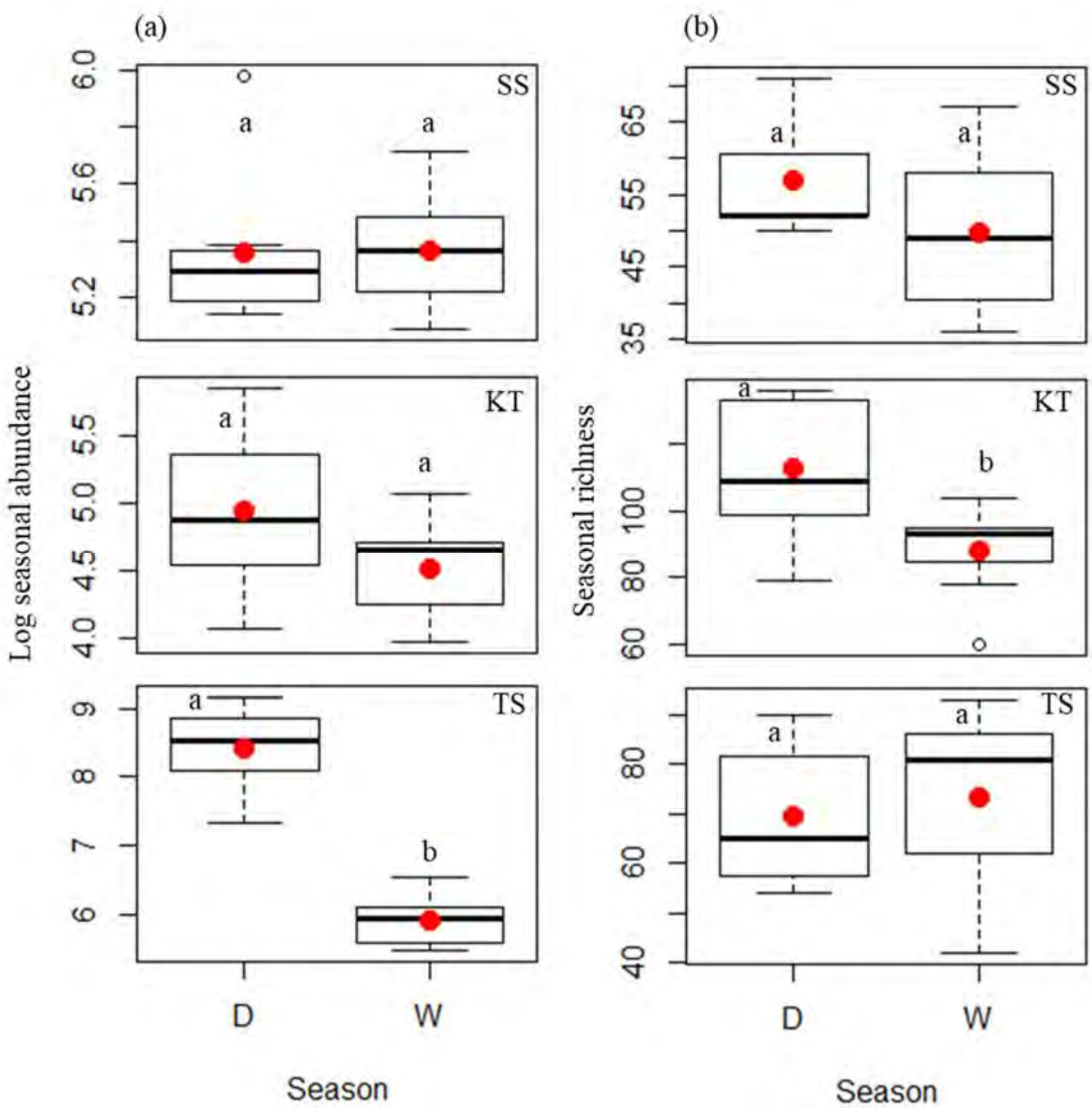
Supplementary Information – S6: Means and standard errors of weekly abundance (number of individuals) for 144 species (with mean value >=0.1). '–' denotes that species did not occur at this site. For the list of fish species names, their abbreviations and traits by genera, families and orders, see S10.

Code	Scientific name	SS	KT	TS
Hlob	*Henicorhynchus lobatus*	24.1±2.8	19.3±5.3	1054.8±349.3
Priv	*Paralaubuca riveroi*	3.6±0.6	0.7±0.3	658.6±235.5
Lsia	*Labiobarbus siamensis*	7.7±1	3.3±0.9	333.4±138.1
Pmac	*Pangasius macronema*	0.4±0.2	1.7±0.5	253.5±19.2
Hsia	*Henicorhynchus siamensis*	8.1±1	6.2±3.4	181.3±82.1
Ptyp	*Paralaubuca typus*	1.8±0.4	0.2±0.2	94±53.6
Pfal	*Puntioplites falcifer*	7.9±0.6	14.2±1.5	39.3±5.5
Xcan	*Xenentodon cancila*	0.1±0	0±0	31.2±12.3
Ates	*Anabas testudineus*	26.3±5.1	0.1±0	0.2±0.1
Sste	*Scaphognathops stejnegeri*	18.5±7.3	1.9±0.3	0±0
Pbar	*Paralaubuca barroni*	5.2±1.4	0.6±0.6	6.9±4.7
Carm	*Cyclocheilichthys armatus*	6±0.6	5.1±0.4	0.4±0.1
Srub	*Systomus rubripinnis*	9.7±1	0.3±0.1	0.3±0.1
Bori	*Brachirus orientalis*	-	0.7±0.1	5.7±0.6
Pbul	*Puntioplites bulu*	8.9±1.8	0.2±0.1	0.4±0.1
Pwol	*Parambassis wolffii*	-	5.8±0.5	0.4±0.1
Hlag	*Hypsibarbus lagleri*	7.8±3.2	0.5±0.1	0.9±0.1
Hmal	*Hypsibarbus malcolmi*	5.6±0.5	3.6±0.4	0±0
Rtor	*Rasbora tornieri*	4.8±0.9	0±0	4.2±1.7
Ovit	*Osteochilus vittatus*	8.3±0.8	0.3±0.1	0.3±0.1
Hpie	*Hypsibarbus pierrei*	8±1	0.6±0.2	0±0
Hspi	*Hemibagrus spilopterus*	1.9±0.2	2.7±0.3	3.9±0.6
Atru	*Amblyrhynchichthys truncatus*	1.9±0.3	0.9±0.1	5.6±1
Plar	*Pangasius larnaudii*	0±0	0.1±0	8±0.7
Ceno	*Cyclocheilichthys enoplos*	0.1±0	1.8±0.5	5.6±0.6
Lchr	*Labeo chrysophekadion*	0.1±0	3.8±0.3	3.3±0.3
Pfas	*Pristolepis fasciata*	2.2±0.4	4.2±0.4	0.4±0.1
Hdis	*Hampala dispar*	4.7±0.5	1.5±0.1	0.3±0.1
Cmic.2	*Cynoglossus microlepis*	-	0.2±0	3.9±0.6
Bmic	*Boesemania microlepis*	-	2.6±0.4	1.4±0.3
Pdub	*Polynemus dubius*	-	0.4±0.1	3.6±0.8
Tthy	*Thynnichthys thynnoides*	0±0	0.4±0.1	5.3±2.1
Bsch	*Barbonymus schwanenfeldii*	3.7±0.3	1.7±0.2	0.2±0.1
Lble	*Luciosoma bleekeri*	0.5±0.2	0.4±0.2	4.6±3
Pble	*Phalacronotus bleekeri*	1.9±0.2	1.6±0.2	1.7±0.5
Ccar	*Cyprinus carpio*	-	-	1.6±1
Hwaa	*Helicophagus waandersii*	0.3±0.1	3.1±0.5	1.1±0.4
Mmys	*Mystus mysticetus*	0±0	0.1±0	4.4±3.1
Ymod	*Yasuhikotakia modesta*	0.1±0	0±0	4.2±1
Crep	*Cyclocheilichthys repasson*	1.6±0.4	2.5±0.3	0±0
Mche	*Micronema cheveyi*	0.6±0.2	0.4±0.1	3.1±1.9
Lcro	*Lycothrissa crocodilus*	3.5±0.4	0.4±0	0.1±0

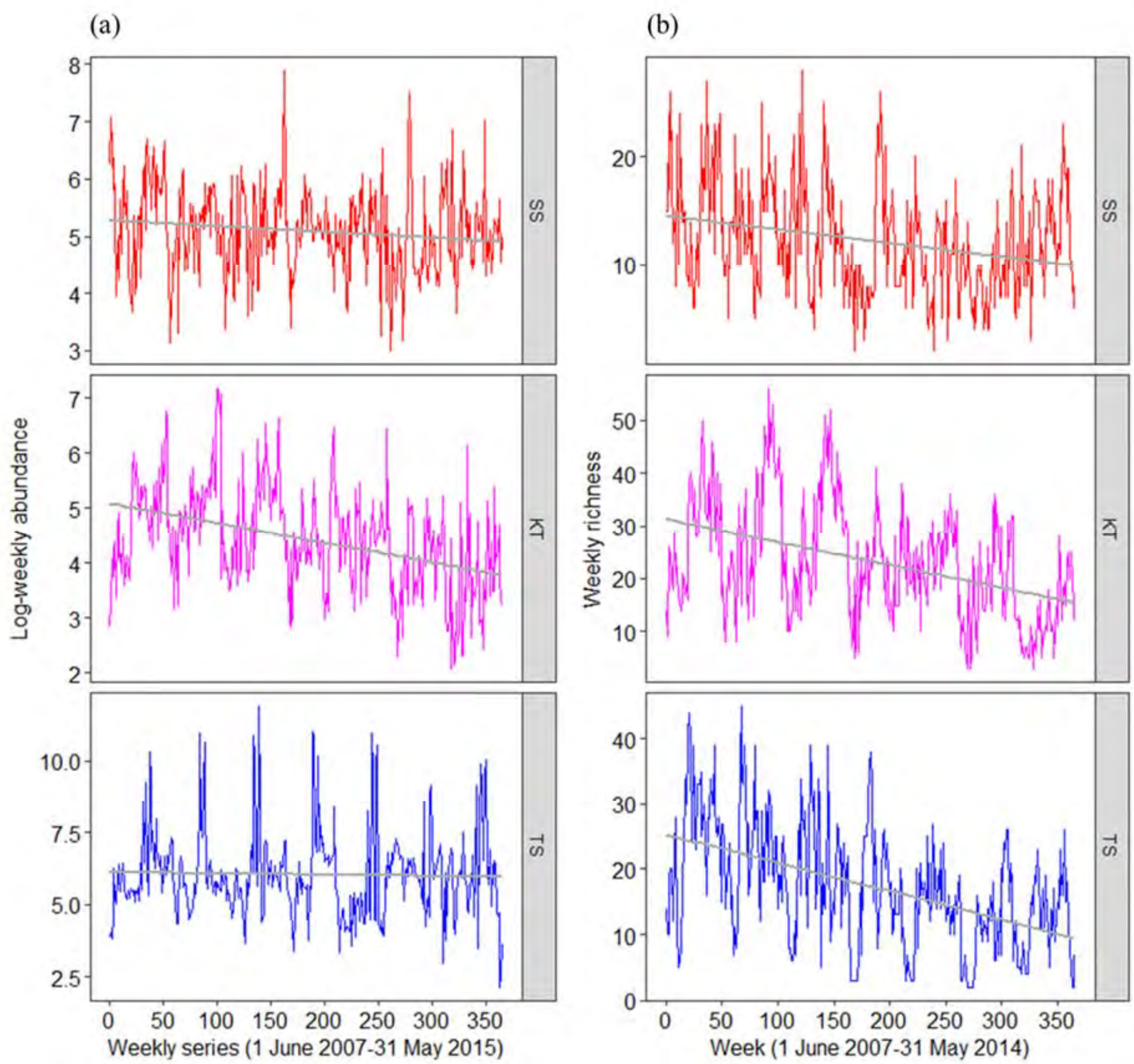
Nnot	*Notopterus notopterus*	2.2±0.9	1±0.1	0.7±0.1
Bobs	*Bagrichthys obscurus*	2.3±0.4	1.2±0.2	0.3±0.1
Psia.2	*Pseudomystus siamensis*	2.7±0.4	0.7±0.1	0.4±0.1
Cbat	*Clarias batrachus*	3.2±0.6	0.1±0	0±0
Char	*Cosmochilus harmandi*	0±0	2.3±0.2	1±0.1
Btru	*Belodontichthys truncatus*	0.1±0	1.5±0.2	1.4±0.2
Cstr	*Channa striata*	2±0.3	0.8±0.1	0.2±0
Hwet	*Hypsibarbus wetmorei*	1.4±0.3	0.6±0.1	-
Cmac	*Clarias macrocephalus*	2.6±0.5	0.1±0	0.1±0.1
Ppro	*Puntioplites proctozysron*	0.1±0	2.6±0.2	0.1±0.1
Gpen	*Gyrinocheilus pennocki*	0.2±0.1	2.4±0.3	0.1±0
Aspp	*Acantopsis* sp.	0.8±0.2	1.8±1.4	0±0
Dund	*Datnioides undecimradiatus*	-	0.8±0.1	-
Mboc	*Mystus bocourti*	0.1±0	0.8±0.2	1.5±0.3
Oexo	*Osphronemus exodon*	0±0	2.3±0.4	0±0
Msin	*Mystus singaringan*	0.1±0.1	0.1±0	2±0.4
Cbla	*Chitala blanci*	0±0	2.1±0.2	0±0
Kcry	*Kryptopterus cryptopterus*	0.9±0.5	0.5±0.3	-
Marm	*Mastacembelus armatus*	0.1±0	0.3±0	1.7±0.9
Pcon	*Pangasius conchophilus*	-	0.2±0	1.2±0.1
Csia	*Catlocarpio siamensis*	-	0±0	1.3±1.1
Pple	*Pseudolais pleurotaenia*	0.7±0.2	0.2±0.1	1±0.1
Clag	*Cyclocheilichthys lagleri*	1.5±0.3	0.3±0.1	0±0
Hsuv	*Hypsibarbus suvattii*	1.7±0.3	0.1±0.1	0±0
Capo	*Cyclocheilichthys apogon*	1.4±0.3	0.2±0.1	0±0
Bmaj	*Bagrichthys majusculus*	0.9±0.2	0.6±0.1	0±0
Hmac	*Hampala macrolepidota*	0.7±0.1	0.4±0.1	0.2±0
Lmel	*Lobocheilos melanotaenia*	0.3±0.1	0.3±0.1	0.7±0.4
Clin	*Coilia lindmani*	-	-	0.4±0.3
Omar	*Oxyeleotris marmorata*	0.2±0.2	0.7±0.1	0.3±0.1
Phyp	*Pangasianodon hypophthalmus*	-	0.1±0	0.7±0.1
Balt	*Barbonymus altus*	0.3±0.1	0.3±0.1	0.5±0.1
Shel	*Syncrossus helodes*	0.1±0	0±0	1±0.5
Msia	*Macrognathus siamensis*	0.5±0.1	-	0.2±0
Hwyc.1	*Hemibagrus wyckioides*	0±0	0.8±0.1	0.2±0
Omel	*Osteochilus melanopleurus*	0±0	0.4±0.1	0.6±0.1
Bgon	*Barbonymus gonionotus*	0.3±0.1	0.3±0.1	-
Cgac	*Channa gachua*	0.2±0.1	0±0	0.7±0.1
Hsto	*Hemiarius stormii*	-	0.4±0.1	0.2±0.1
Pboc	*Pangasius bocourti*	-	0±0	0.6±0.1
Pjul	*Probarbus jullieni*	0±0	0.9±0.2	0±0
Tmic.1	*Trichopodus microlepis*	0.9±0.4	0±0	0±0
Ogor	*Osphronemus goramy*	0.1±0	0.7±0.1	0±0
Ppol	*Pangasius polyuranodon*	0±0	0.2±0	0.6±0.1
Sban	*Scaphognathops bandanensis*	0.2±0.1	0.6±0.1	0±0
Clop	*Chitala lopis*	0.5±0.3	0±0	-
Cmic.1	*Cirrhinus microlepis*	0±0	0.2±0.1	0.5±0.1
Hfil	*Hemibagrus filamentus*	0±0	0.7±0.1	0±0
Obim	*Ompok bimaculatus*	0.4±0.1	0.2±0	0.1±0
Yeos	*Yasuhikotakia eos*	0±0	0±0	0.7±0.1
Cjul	*Cirrhinus jullieni*	0.5±0.1	0.1±0	0±0

Cmar	*Channa marulioides*	-	0.4±0.1	0±0
Lhoe	*Leptobarbus hoevenii*	-	0.2±0.1	0.2±0
Llon	*Laides longibarbis*	0.3±0.1	0.1±0	-
Plab	*Probarbus labeamajor*	-	0.4±0.1	0±0
Psia.1	*Parambassis siamensis*	-	0±0	0.4±0.2
Ttri	*Trichopodus trichopterus*	0.2±0.1	-	-
Aalb	*Albulichthys albuloides*	0.1±0.1	0.3±0.1	0.1±0
Cmol	*Cirrhinus molitorella*	0.3±0.1	0.1±0	0.1±0
Cmic	*Channa micropeltes*	-	0.3±0.1	0±0
Mmac	*Macrochirichthys macrochirus*	-	0.2±0	0.1±0
Raur	*Rasbora aurotaenia*	0.3±0.2	0±0	-
Corn	*Chitala ornata*	0±0	0.2±0.1	0.2±0.1
Papo.1	*Phalacronotus apogon*	0±0	0.4±0.1	0±0
Pmic.1	*Pseudolais micronemus*	0±0	0.4±0.2	0±0
Rgut	*Raiamas guttatus*	0.2±0.1	0.2±0	0±0
Amac	*Arius maculatus*	-	0.1±0	-
Chet	*Cyclocheilichthys heteronema*	-	-	0.1±0.1
Gfas	*Garra fasciacauda*	-	0.1±0.1	0.1±0
Gorn	*Gymnostomus ornatipinnis*	0.2±0.2	0±0	-
Hmek	*Hemisilurus mekongensis*	0±0	0.2±0	0.1±0
Ibeh	*Incisilabeo behri*	0.1±0	0.1±0	-
Ldyo	*Labeo dyocheilus*	0.1±0	0.2±0	0±0
Lgra	*Lobocheilos gracilis*	-	0.1±0	-
Lhis	*Laocypris hispida*	0.1±0.1	-	-
Lroh	*Labeo rohita*	-	0±0	0.2±0.1
Matr.1	*Mystus atrifasciatus*	-	0.1±0	-
Mery.1	*Mekongina erythrospila*	0±0	0.2±0.1	-
Mwol	*Mystus wolffii*	0.2±0.1	0±0	-
Omic	*Osteochilus microcephalus*	0.1±0.1	0.1±0	-
Papo	*Parambassis apogonoides*	-	0.1±0	-
Plab.1	*Probarbus labeaminor*	0±0	0.2±0	-
Pmel	*Polynemus melanochir*	-	0±0	0.2±0
Pnas	*Pangasius nasutus*	0.1±0.1	-	-
Tmic	*Toxotes microlepis*	-	0.1±0	0.1±0
Tpau	*Trigonopoma pauciperforatum*	0.1±0.1	-	-
Tsin	*Tor sinensis*	-	0.1±0	0.1±0
Byar	*Bagarius yarrelli*	0±0	0.2±0	0±0
Watt	*Wallago attu*	0±0	0.1±0	0.1±0
Bhar	*Brachirus harmandi*	0±0	0.1±0	-
Bsuc	*Bagarius suchus*	0±0	0.1±0	-
Cfur	*Cyclocheilos furcatus*	0±0	0.1±0	-
Csin	*Clupisoma sinense*	0.1±0.1	0±0	-
Hwyc	*Hemibagrus wyckii*	-	0.1±0	0±0
Mcyp	*Megalops cyprinoides*	-	0.1±0	0±0
Mobt	*Mystacoleucus obtusirostris*	-	0.1±0.1	0±0
Owaa	*Osteochilus waandersii*	0.1±0.1	0±0	-
Pcam	*Pao cambodgiensis*	-	0.1±0	0±0
Phar	*Paralaubuca harmandi*	0.1±0.1	0±0	-
Rhob	*Rasbora hobelmani*	0.1±0.1	0±0	-
Tthi	*Tenualosa thibaudeaui*	-	0.1±0	0±0
Malb.1	*Mystus albolineatus*	0±0	0.1±0	0±0

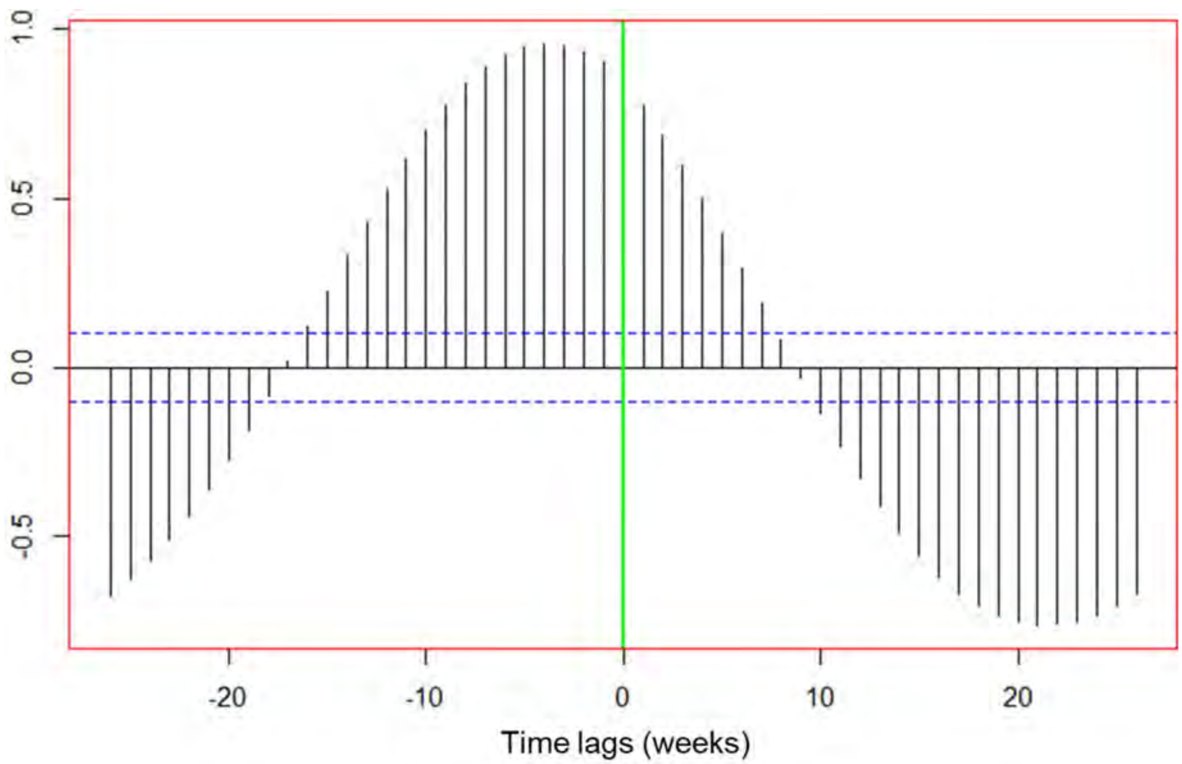
Supplementary Information – S7: (a) Seasonal abundance and (b) richness. Red solid points indicate the mean in each site. At x-axis, D = dry season and W = wet season. For seasonality partitioning, see S3. Mean values among sites with a common letter are not significantly different at the 0.05 level (Pairwise Wilcoxon Rank Sum Tests).



Supplementary Information (S8): Trends in (a) weekly abundance and (b) richness against time. For (a), significant declining trend is found in SS (p-value=0.03) and KT (p-value<0.0001) while no significant change is dectected in TS (p-value=0.68). For (b), significant decreasing trends are exhibited for all sites (p-value<0.0001). For site codes, see Figure 1.



Supplementary Information – S9: Cross-correlation plots of mean weekly water levels in KT (second Y axis) and mean weekly water levels (Y) in TS. In the cross-correlations, the dotted blue lines give the values beyond which the correlations are significantly different from zero. X-axis is the time lags, set at 52 weeks (i.e. annual cycle). Data series on water levels used for the cross-correlation plots, covering the period from 1 June 2007 to 31 May 2014. For site codes, see Figure 1. The cross-correlation lag with the maximum coefficient between water levels in KT and TS was estimated at -4 weeks.



Supplementary Information – S10: List of fish species names, their abbreviations and traits by genera, families and orders. Species names and traits are compiled based on (Rainboth 1996, MFD 2003, Rainboth et al. 2012, Kottelat 2013, Froese and Pauly 2017, Ngor et al. 2018a, 2018b).

- (1) Physcial habitat guilds include F1 (Rithron resident), F2 (Main channel resident), F3 (Main channel spawner), F4 (Floodplain spawner), F5 (Eurytopic/generalist), F6 (Floodplain resident), F7 (Estuarine resident), F8 (Anadromous), F9 (Catadromous) F10 (Marine visitor), F11 (Non-native);
- (2) Migration guilds include White fishes = longitudinal migratory species between Mekong River, lower floodplains and major tributaries, Black fishes = non-longitudinal migratory or floodplain residents, Grey fishes = lateral migration between floodplain and local rivers/streams; Estuarine fishes = estuarine residents and marine visitors.
- (3) Maximum total lengths include G (Giant >= 100 cm), L (Large, 61-99 cm), M (Medium, 26-60 cm), S (Small size <= 25 cm);
- (4) Trophic levels include troph1 (trophic level <= 2.75), troph2 (trophic level, 2.76-3.75), troph3 (trophic level > 3.75) and
- (5) Positions in the water column include benthopelagic, demersal, pelagic, pelagic-neritic, reef associated.

Code	Scientific name	Genus	Family	Order	Physical habitat guild	Migration guild	Position in water column	Max. Total length (maxTL, cm)		Trophic level (TP)	
								maxTL	Category	TP	Categetory
Chet	*Cyclocheilichthys heteronema*	Cyclocheilichthys	Cyprinidae	Cypriniformes	F4	Grey	benthopelagic	14.6	S	3.1	Troph2
Cjul	*Cirrhinus jullieni*	Cirrhinus	Cyprinidae	Cypriniformes	F3	White	benthopelagic	24.4	S	2.5	Troph1
Clac	*Corica laciniata*	Corica	Clupeidae	Clupeiformes	F3	White	pelagic	8.5	S	3.1	Troph2
Clag	*Cyclocheilichthys lagleri*	Cyclocheilichthys	Cyprinidae	Cypriniformes	F4	Grey	benthopelagic	18.3	S	3.4	Troph2
Clin	*Coilia lindmani*	Coilia	Engraulidae	Clupeiformes	F7	Estuarine	pelagic	24.4	S	3.7	Troph2
Clin.1	*Cynoglossus lingua*	Cynoglossus	Cynoglossidae	Pleuronectiformes	F10	White	demersal	45	M	3.5	Troph2
Clon	*Clupisoma longianalis*	Clupisoma	Schilbeidae	Siluriformes	F3	White	demersal	16.2	S	3.3	Troph2
Clop	*Chitala lopis*	Chitala	Notopteridae	Osteoglossiformes	F3	White	demersal	183	L	4.5	Troph3
Cluc	*Channa lucius*	Channa	Channidae	Perciformes	F6	Black	benthopelagic	48.8	M	3.9	Troph3
Cmac	*Clarias macrocephalus*	Clarias	Clariidae	Siluriformes	F6	Black	benthopelagic	120	L	3.7	Troph2
Cmar	*Channa marulioides*	Channa	Channidae	Perciformes	F6	Black	benthopelagic	27	M	NA	NA
Cmar.1	*Channa marulius*	Channa	Channidae	Perciformes	F6	Black	benthopelagic	183	L	4.5	Troph3
Cmel	*Channa melasoma*	Channa	Channidae	Perciformes	F6	Black	benthopelagic	36.6	M	4.2	Troph3

Cmel.1	*Clarias meladerma*	Clarias	Clariidae	Siluriformes	F6	Black	demersal	42.7	M	3.5	Troph2
Cmic	*Channa micropeltes*	Channa	Channidae	Perciformes	F6	Black	benthopelagic	158.6	L	3.8	Troph3
Cmic.1	*Cirrhinus microlepis*	Cirrhinus	Cyprinidae	Cypriniformes	F3	White	benthopelagic	79.3	L	2.4	Troph1
Cmic.2	*Cynoglossus microlepis*	Cynoglossus	Cynoglossidae	Pleuronectiformes	F10	White	demersal	39.7	M	3.5	Troph2
Cmol	*Cirrhinus molitorella*	Cirrhinus	Cyprinidae	Cypriniformes	F3	White	benthopelagic	55	M	2	Troph1
Corn	*Chitala ornata*	Chitala	Notopteridae	Osteoglossiformes	F5	White	pelagic	122	L	3.7	Troph2
Cpun	*Cynoglossus puncticeps*	Cynoglossus	Cynoglossidae	Pleuronectiformes	F10	White	demersal	42.7	M	3.3	Troph2
Crep	*Cyclocheilichthys repasson*	Cyclocheilichthys	Cyprinidae	Cypriniformes	F4	Grey	benthopelagic	28	M	2.62	Troph1
Cret	*Crossocheilus reticulatus*	Crossocheilus	Cyprinidae	Cypriniformes	F5	White	benthopelagic	20.7	S	2.3	Troph1
Csia	*Catlocarpio siamensis*	Catlocarpio	Cyprinidae	Cypriniformes	F2	White	benthopelagic	300	L	2.9	Troph2
Csin	*Clupisoma sinense*	Clupisoma	Schilbeidae	Siluriformes	F3	White	demersal	37.8	M	3.4	Troph2
Cstr	*Channa striata*	Channa	Channidae	Perciformes	F6	Black	benthopelagic	122	L	3.4	Troph2
Ctal	*Congresox talabon*	Congresox	Muraenesocidae	Anguilliformes	F10	Estuarine	demersal	80	L	4	Troph3
Dalb	*Danio albolineatus*	Danio	Cyprinidae	Cypriniformes	F4	Grey	benthopelagic	7.9	S	3	Troph2
Dash	*Discherodontus ashmeadi*	Discherodontus	Cyprinidae	Cypriniformes	F1	White	benthopelagic	16.6	S	3.3	Troph2
Dflu	*Dichotomyctere fluviatilis*	Dichotomyctere	Tetraodontidae	Tetraodontiformes	F7	Estuarine	demersal	17	S	3.4	Troph2
Dlao	*Dasyatis laosensis*	Dasyatis	Dasyatidae	Myliobatiformes	F3	White	demersal	255.8	L	3.5	Troph2
Dlep	*Devario leptos*	Devario	Cyprinidae	Cypriniformes	F1	White	benthopelagic	6.3	S	3	Troph2
Dpol	*Datnioides polata*	Datnioides	Datnioididae	Perciformes	F7	White	benthopelagic	34.5	M	3.68	Troph2
Dund	*Datnioides undecimradiatus*	Datnioides	Datnioididae	Perciformes	F3	White	benthopelagic	48.8	M	3.6	Troph2
Emet	*Esomus metallicus*	Esomus	Cyprinidae	Cypriniformes	F6	White	benthopelagic	9.1	S	3	Troph2
Emic	*Eugnathogobius microps*	Eugnathogobius	Gobiidae	Perciformes	F7	Estuarine	demersal	2.7	S	NA	NA
Gaff	*Gambusia affinis*	Gambusia	Poeciliidae	Cyprinodontiformes	F11	Black	benthopelagic	5.1	S	3.22	Troph2
Gaym	*Gyrinocheilus aymonieri*	Gyrinocheilus	Gyrinocheilidae	Cypriniformes	F3	White	demersal	34.2	M	2.5	Troph1
Gfas	*Garra fasciacauda*	Garra	Cyprinidae	Cypriniformes	F1	White	benthopelagic	13.4	S	2.4	Troph1
Gfus	*Glyptothorax fuscus*	Glyptothorax	Sisoridae	Siluriformes	F1	White	demersal	14.8	S	3.2	Troph2
Ggiu	*Glossogobius giuris*	Glossogobius	Gobiidae	Perciformes	F7	Estuarine	benthopelagic	61	L	3.7	Troph2
Gorn	*Gymnostomus ornatipinnis*	Gymnostomus	Cyprinidae	Cypriniformes	F5	White	benthopelagic	10.9	S	NA	NA
Gpen	*Gyrinocheilus pennocki*	Gyrinocheilus	Gyrinocheilidae	Cypriniformes	F3	White	demersal	34.2	M	2.5	Troph1
Hdis	*Hampala dispar*	Hampala	Cyprinidae	Cypriniformes	F5	White	benthopelagic	42.7	M	3.7	Troph2

Hfil	*Hemibagrus filamentus*	Hemibagrus	Bagridae	Siluriformes	F3	White	benthopelagic	50	M	3.6	Troph2
Himb	*Himantura imbricata*	Himantura	Dasyatidae	Myliobatiformes	F7	Estuarine	demersal	235.8	L	3.5	Troph2
Hkem	*Heteropneustes kemratensis*	Heteropneustes	Clariidae	Siluriformes	F6	White	demersal	32.9	M	3.4	Troph2
Hlag	*Hypsibarbus lagleri*	Hypsibarbus	Cyprinidae	Cypriniformes	F3	White	benthopelagic	48.8	M	2.8	Troph2
Hlim	*Hyporhamphus limbatus*	Hyporhamphus	Hemiramphidae	Beloniformes	F7	White	pelagic-neritic	35	M	3.1	Troph2
Hlob	*Henicorhynchus lobatus*	Henicorhynchus	Cyprinidae	Cypriniformes	F5	White	benthopelagic	18.3	S	2.8	Troph2
Hmac	*Hampala macrolepidota*	Hampala	Cyprinidae	Cypriniformes	F5	White	benthopelagic	85.4	L	4.2	Troph3
Hmal	*Hypsibarbus malcolmi*	Hypsibarbus	Cyprinidae	Cypriniformes	F3	White	benthopelagic	61	L	3.2	Troph2
Hmek	*Hemisilurus mekongensis*	Hemisilurus	Siluridae	Siluriformes	F3	White	demersal	80	L	3.3	Troph2
Hmol	*Hypophthalmichthys molitrix*	Hypophthalmichthys	Cyprinidae	Cypriniformes	F11	White	benthopelagic	105	L	2	Troph1
Hnob	*Hypophthalmichthys nobilis*	Hypophthalmichthys	Cyprinidae	Cypriniformes	F11	White	benthopelagic	167.9	L	2.83	Troph2
Hpap	*Hemimyzon papilio*	Hemimyzon	Balitoridae	Cypriniformes	F1	White	benthopelagic	7.2	S	2.9	Troph2
Hpie	*Hypsibarbus pierrei*	Hypsibarbus	Cyprinidae	Cypriniformes	F3	White	benthopelagic	36.6	M	3	Troph2
Hsia	*Henicorhynchus siamensis*	Henicorhynchus	Cyprinidae	Cypriniformes	F5	White	benthopelagic	24.4	S	2	Troph1
Hsig	*Himantura signifer*	Himantura	Dasyatidae	Myliobatiformes	F10	White	benthopelagic	235.8	L	3.5	Troph2
Hspi	*Hemibagrus spilopterus*	Hemibagrus	Bagridae	Siluriformes	F3	White	demersal	37.7	M	3.5	Troph2
Hsto	*Hemiarius stormii*	Hemiarius	Ariidae	Siluriformes	F7	White	demersal	50	M	4	Troph3
Hsuv	*Hypsibarbus suvattii*	Hypsibarbus	Cyprinidae	Cypriniformes	F3	White	benthopelagic	42.7	M	3	Troph2
Hund	*Himantura undulata*	Himantura	Dasyatidae	Myliobatiformes	F10	Estuarine	demersal	410	L	NA	NA
Hver	*Hypsibarbus vernayi*	Hypsibarbus	Cyprinidae	Cypriniformes	F3	White	benthopelagic	26.4	M	3	Troph2
Hwaa	*Helicophagus waandersii*	Helicophagus	Pangasiidae	Siluriformes	F3	White	demersal	70	L	3.2	Troph2
Hwet	*Hypsibarbus wetmorei*	Hypsibarbus	Cyprinidae	Cypriniformes	F3	White	benthopelagic	25	S	3	Troph2
Hwyc	*Hemibagrus wyckii*	Hemibagrus	Bagridae	Siluriformes	F3	White	demersal	86.6	L	3.8	Troph3
Hwyc.1	*Hemibagrus wyckioides*	Hemibagrus	Bagridae	Siluriformes	F3	White	demersal	130	L	3.7	Troph2
Ibeh	*Incisilabeo behri*	Incisilabeo	Cyprinidae	Cypriniformes	F3	White	benthopelagic	NA	NA	NA	NA
Kbic	*Kryptopterus bicirrhis*	Kryptopterus	Siluridae	Siluriformes	F3	White	benthopelagic	18.3	S	3.9	Troph3
Kcry	*Kryptopterus cryptopterus*	Kryptopterus	Siluridae	Siluriformes	F3	White	benthopelagic	16.8	S	NA	NA
Kdis	*Kryptopterus dissitus*	Kryptopterus	Siluridae	Siluriformes	F3	White	benthopelagic	21.5	S	4	Troph3
Ksch	*Kryptopterus schilbeides*	Kryptopterus	Siluridae	Siluriformes	F3	White	benthopelagic	12	S	3.8	Troph3
Lble	*Luciosoma bleekeri*	Luciosoma	Cyprinidae	Cypriniformes	F3	White	pelagic	30.5	M	3.8	Troph3

Lchr	*Labeo chrysophekadion*	Labeo	Cyprinidae	Cypriniformes	F3	White	benthopelagic	90	L	2	Troph1
Lcro	*Lycothrissa crocodilus*	Lycothrissa	Engraulidae	Clupeiformes	F7	White	pelagic	36.6	M	3.7	Troph2
Ldyo	*Labeo dyocheilus*	Labeo	Cyprinidae	Cypriniformes	F11	White	benthopelagic	90	L	2	Troph1
Lgra	*Lobocheilos gracilis*	Lobocheilos	Cyprinidae	Cypriniformes	F1	White	demersal	24	S	2	Troph1
Lhis	*Laocypris hispida*	Laocypris	Cyprinidae	Cypriniformes	F4	Grey	benthopelagic	6.1	S	NA	NA
Lhoe	*Leptobarbus hoevenii*	Leptobarbus	Cyprinidae	Cypriniformes	F4	Grey	pelagic	122	L	2.8	Troph2
Llau	*Laubuka laubuca*	Laubuka	Cyprinidae	Cypriniformes	F4	Grey	pelagic	7	S	3.2	Troph2
Llin	*Labiobarbus lineatus*	Labiobarbus	Cyprinidae	Cypriniformes	F5	White	benthopelagic	15.5	S	2.5	Troph1
Llon	*Laides longibarbis*	Laides	Schilbeidae	Siluriformes	F3	White	demersal	17.3	S	3.9	Troph3
Lmel	*Lobocheilos melanotaenia*	Lobocheilos	Cyprinidae	Cypriniformes	F1	White	demersal	24.4	S	2	Troph1
Lroh	*Labeo rohita*	Labeo	Cyprinidae	Cypriniformes	F11	White	benthopelagic	200	L	2.2	Troph1
Lset	*Luciosoma setigerum*	Luciosoma	Cyprinidae	Cypriniformes	F3	White	pelagic	31.7	M	4.2	Troph3
Lsia	*Labiobarbus siamensis*	Labiobarbus	Cyprinidae	Cypriniformes	F5	White	benthopelagic	22	S	2.3	Troph1
Lstr	*Luciocyprinus striolatus*	Luciocyprinus	Cyprinidae	Cypriniformes	F3	White	benthopelagic	244	L	2.5	Troph1
Malb	*Monopterus albus*	Monopterus	Synbranchidae	Synbranchiformes	F6	Black	demersal	122	L	2.9	Troph2
Malb.1	*Mystus albolineatus*	Mystus	Bagridae	Siluriformes	F4	Grey	demersal	42.7	M	3.7	Troph2
Mang	*Misgurnus anguillicaudatus*	Misgurnus	Cobitidae	Cypriniformes	F11	White	demersal	34.2	M	3.2	Troph2
Marg	*Monodactylus argenteus*	Monodactylus	Monodactylidae	Perciformes	F10	Estuarine	pelagic-neritic	31.1	M	2.95	Troph2
Marm	*Mastacembelus armatus*	Mastacembelus	Mastacembelidae	Synbranchiformes	F5	White	demersal	35.5	M	2.8	Troph2
Matr	*Mystacoleucus atridorsalis*	Mystacoleucus	Cyprinidae	Cypriniformes	F1	White	benthopelagic	9.8	S	2.9	Troph2
Matr.1	*Mystus atrifasciatus*	Mystus	Bagridae	Siluriformes	F4	Grey	demersal	18.3	S	3	Troph2
Mboc	*Mystus bocourti*	Mystus	Bagridae	Siluriformes	F4	Grey	demersal	29.3	M	3.5	Troph2
Mche	*Micronema cheveyi*	Micronema	Siluridae	Siluriformes	F3	White	benthopelagic	35	M	3.51	Troph2
Mchi	*Mystacoleucus chilopterus*	Mystacoleucus	Cyprinidae	Cypriniformes	F1	White	benthopelagic	11.1	S	2.9	Troph2
Mcir	*Macrognathus circumcinctus*	Macrognathus	Mastacembelidae	Synbranchiformes	F6	White	demersal	24.4	S	4	Troph3
Mcyp	*Megalops cyprinoides*	Megalops	Megalopidae	Elopiformes	F10	Estuarine	benthopelagic	150	L	3.5	Troph2
Mect	*Mystacoleucus ectypus*	Mystacoleucus	Cyprinidae	Cypriniformes	F1	White	benthopelagic	9.8	S	2.9	Troph2
Mery	*Mastacembelus erythrotaenia*	Mastacembelus	Mastacembelidae	Synbranchiformes	F5	White	demersal	100	L	2.7	Troph1
Mery.1	*Mekongina erythrospila*	Mekongina	Cyprinidae	Cypriniformes	F1	White	benthopelagic	54.9	M	2	Troph1
Mgul	*Mystus gulio*	Mystus	Bagridae	Siluriformes	F4	Grey	demersal	46	M	4	Troph3

Mmac	*Macrochirichthys macrochirus*	Macrochirichthys	Cyprinidae	Cypriniformes	F4	Grey	benthopelagic	100	L	3.7	Troph2
Mmul	*Mystus multiradiatus*	Mystus	Bagridae	Siluriformes	F4	Grey	demersal	15.6	S	3.1	Troph2
Mmys	*Mystus mysticetus*	Mystus	Bagridae	Siluriformes	F4	Grey	demersal	15.9	S	3.1	Troph2
Mobt	*Mystacoleucus obtusirostris*	Mystacoleucus	Cyprinidae	Cypriniformes	F1	White	NA	NA	NA	NA	NA
Mrhe	*Mystus rhegma*	Mystus	Bagridae	Siluriformes	F4	Grey	demersal	14.6	S	3.5	Troph2
Msem	*Macrognathus semiocellatus*	Macrognathus	Mastacembelidae	Synbranchiformes	F6	White	benthopelagic	23.4	S	3.3	Troph2
Msia	*Macrognathus siamensis*	Macrognathus	Mastacembelidae	Synbranchiformes	F6	White	benthopelagic	36.6	M	3.3	Troph2
Msin	*Mystus singaringan*	Mystus	Bagridae	Siluriformes	F4	Grey	demersal	36.6	M	3.8	Troph3
Mwol	*Mystus wolffii*	Mystus	Bagridae	Siluriformes	F4	Grey	demersal	20	S	3.3	Troph2
Nbil	*Netuma bilineata*	Netuma	Ariidae	Siluriformes	F7	Estuarine	demersal	71.73	L	3.83	Troph3
Nbla	*Neolissochilus blanci*	Neolissochilus	Cyprinidae	Cypriniformes	F1	White	benthopelagic	NA	NA	NA	NA
Nneb	*Nandus nebulosus*	Nandus	Nandidae	Perciformes	F7	White	benthopelagic	12	S	3.3	Troph2
Nnen	*Nemapteryx nenga*	Nemapteryx	Ariidae	Siluriformes	F7	White	demersal	30	M	NA	NA
Nnot	*Notopterus notopterus*	Notopterus	Notopteridae	Osteoglossiformes	F5	White	demersal	73.2	L	3.6	Troph2
Ntha	*Netuma thalassina*	Netuma	Ariidae	Siluriformes	F7	Estuarine	demersal	185	L	3.49	Troph2
Obim	*Ompok bimaculatus*	Ompok	Siluridae	Siluriformes	F4	Grey	demersal	51.8	M	3.89	Troph3
Oexo	*Osphronemus exodon*	Osphronemus	Osphronemidae	Perciformes	F1	Black	pelagic	73.2	L	2.7	Troph1
Ofus	*Onychostoma fusiforme*	Onychostoma	Cyprinidae	Cypriniformes	F1	White	benthopelagic	28.1	M	2.7	Troph1
Oger	*Onychostoma gerlachi*	Onychostoma	Cyprinidae	Cypriniformes	F1	White	benthopelagic	38.6	M	2.7	Troph1
Ogor	*Osphronemus goramy*	Osphronemus	Osphronemidae	Perciformes	F1	Black	benthopelagic	85.4	L	2.8	Troph2
Ohyp	*Ompok hypophthalmus*	Ompok	Siluridae	Siluriformes	F4	Grey	demersal	36.6	M	3.9	Troph3
Aalb	*Albulichthys albuloides*	Albulichthys	Cyprinidae	Cypriniformes	F3	White	benthopelagic	36.6	M	2.8	Troph2
Adel	*Acanthopsoides delphax*	Acanthopsoides	Cobitidae	Cypriniformes	F3	White	demersal	7.3	S	3.5	Troph2
Agra	*Acanthopsoides gracilentus*	Acanthopsoides	Cobitidae	Cypriniformes	F3	White	demersal	7.3	S	3.5	Troph2
Akop	*Ambassis kopsii*	Ambassis	Ambassidae	Perciformes	F7	Estuarine	demersal	10.2	S	3	Troph2
Aleu	*Achiroides leucorhynchos*	Achiroides	Soleidae	Pleuronectiformes	F7	White	demersal	9.8	S	3.5	Troph2
Amac	*Arius maculatus*	Arius	Ariidae	Siluriformes	F7	White	demersal	80	L	3.4	Troph2
Amad	*Apocryptodon madurensis*	Apocryptodon	Gobiidae	Perciformes	F7	Estuarine	demersal	9	S	2	Troph1
Amar	*Anguilla marmorata*	Anguilla	Anguillidae	Anguilliformes	F9	White	demersal	200	L	3.8	Troph3
Amel	*Achiroides melanorhynchus*	Achiroides	Soleidae	Pleuronectiformes	F7	White	demersal	17.1	S	3.5	Troph2

Asid	*Ambastaia sidthimunki*	Ambastaia	Cobitidae	Cypriniformes	F3	White	demersal	6.7	S	2.9	Troph2
Aspp	*Acantopsis sp.*	Acantopsis	Cobitidae	Cypriniformes	F3	White	demersal	NA	NA	3.5	Troph2
Ates	*Anabas testudineus*	Anabas	Anabantidae	Perciformes	F6	Black	demersal	25	S	3	Troph2
Atru	*Amblyrhynchichthys truncatus*	Amblyrhynchichthys	Cyprinidae	Cypriniformes	F3	White	benthopelagic	48.8	M	2.4	Troph1
Aven	*Arius venosus*	Arius	Ariidae	Siluriformes	F7	Estuarine	demersal	30	M	4	Troph3
Balt	*Barbonymus altus*	Barbonymus	Cyprinidae	Cypriniformes	F4	Grey	benthopelagic	25	S	2.4	Troph1
Bbag	*Bagarius bagarius*	Bagarius	Sisoridae	Siluriformes	F1	White	benthopelagic	200	L	3.7	Troph2
Bbin	*Barbodes binotatus*	Barbodes	Cyprinidae	Cypriniformes	F4	Grey	benthopelagic	24.4	S	2.7	Troph1
Bbut	*Butis butis*	Butis	Eleotridae	Perciformes	F7	Estuarine	demersal	15	S	4	Troph3
Bele	*Bangana elegans*	Bangana	Cyprinidae	Cypriniformes	F3	White	benthopelagic	4.3	S	2.8	Troph2
Bgon	*Barbonymus gonionotus*	Barbonymus	Cyprinidae	Cypriniformes	F5	White	benthopelagic	40.5	M	2.4	Troph1
Bhar	*Brachirus harmandi*	Brachirus	Soleidae	Pleuronectiformes	F5	White	demersal	12.2	S	3.5	Troph2
Bkoi	*Butis koilomatodon*	Butis	Eleotridae	Perciformes	F7	White	demersal	10.7	S	4	Troph3
Blae	*Barbichthys laevis*	Barbichthys	Cyprinidae	Cypriniformes	F3	White	benthopelagic	36.6	M	2.7	Troph1
Bmaj	*Bagrichthys majusculus*	Bagrichthys	Bagridae	Siluriformes	F3	White	demersal	NA	NA	NA	NA
Bmic	*Boesemania microlepis*	Boesemania	Sciaenidae	Perciformes	F4	Grey	benthopelagic	122	L	3.7	Troph2
Bobs	*Bagrichthys obscurus*	Bagrichthys	Bagridae	Siluriformes	F3	White	demersal	30.4	M	3.4	Troph2
Bori	*Brachirus orientalis*	Brachirus	Soleidae	Pleuronectiformes	F10	White	demersal	36.6	M	3.5	Troph2
Bpan	*Brachirus panoides*	Brachirus	Soleidae	Pleuronectiformes	F7	White	demersal	20	S	3.5	Troph2
Brho	*Barbodes rhombeus*	Barbodes	Cyprinidae	Cypriniformes	F4	Grey	benthopelagic	7.9	S	2.9	Troph2
Bsch	*Barbonymus schwanenfeldii*	Barbonymus	Cyprinidae	Cypriniformes	F4	Grey	benthopelagic	42.7	M	2.3	Troph1
Bsp.	*Bangana sp.*	Bangana	Cyprinidae	Cypriniformes	F3	White	NA	NA	NA	NA	NA
Bsuc	*Bagarius suchus*	Bagarius	Sisoridae	Siluriformes	F1	White	demersal	85.4	L	3.3	Troph2
Btru	*Belodontichthys truncatus*	Belodontichthys	Siluridae	Siluriformes	F3	White	demersal	73.2	L	4.1	Troph3
Byar	*Bagarius yarrelli*	Bagarius	Sisoridae	Siluriformes	F1	White	demersal	244	L	3.7	Troph2
Byun	*Bangana yunnanensis*	Bangana	Cyprinidae	Cypriniformes	F3	White	benthopelagic	30.9	M	2.2	Troph1
Caes	*Clupeichthys aesarnensis*	Clupeichthys	Clupeidae	Clupeiformes	F3	White	pelagic	8.5	S	2.9	Troph2
Capo	*Cyclocheilichthys apogon*	Cyclocheilichthys	Cyprinidae	Cypriniformes	F4	Grey	benthopelagic	25	S	2.9	Troph2
Carm	*Cyclocheilichthys armatus*	Cyclocheilichthys	Cyprinidae	Cypriniformes	F4	Grey	benthopelagic	26.5	M	3.38	Troph2
Catr	*Crossocheilus atrilimes*	Crossocheilus	Cyprinidae	Cypriniformes	F5	White	benthopelagic	8.9	S	2.5	Troph1

Cbat	*Clarias batrachus*	Clarias	Clariidae	Siluriformes	F6	Black	demersal	47	M	3.4	Troph2
Cbil	*Cynoglossus bilineatus*	Cynoglossus	Cynoglossidae	Pleuronectiformes	F10	White	demersal	44	M	3.5	Troph2
Cbla	*Chitala blanci*	Chitala	Notopteridae	Osteoglossiformes	F1	White	demersal	146.4	L	3.7	Troph2
Ccar	*Cyprinus carpio*	Cyprinus	Cyprinidae	Cypriniformes	F11	White	benthopelagic	120	L	3.4	Troph2
Ccat	*Clarias cataractus*	Clarias	Clariidae	Siluriformes	F6	White	demersal	NA	NA	NA	NA
Ccir	*Cirrhinus cirrhosus*	Cirrhinus	Cyprinidae	Cypriniformes	F11	White	benthopelagic	122	L	2.4	Troph1
Ceno	*Cyclocheilichthys enoplos*	Cyclocheilichthys	Cyprinidae	Cypriniformes	F2	White	benthopelagic	90.3	L	3.2	Troph2
Cfel	*Cynoglossus feldmanni*	Cynoglossus	Cynoglossidae	Pleuronectiformes	F10	White	demersal	30.5	M	3.5	Troph2
Cfur	*Cyclocheilos furcatus*	Cyclocheilos	Cyprinidae	Cypriniformes	F2	White	benthopelagic	NA	NA	NA	NA
Cgac	*Channa gachua*	Channa	Channidae	Perciformes	F1	Black	benthopelagic	24.4	S	3.8	Troph3
Cgar	*Clarias gariepinus*	Clarias	Clariidae	Siluriformes	F11	Black	benthopelagic	170	L	3.8	Troph3
Char	*Cosmochilus harmandi*	Cosmochilus	Cyprinidae	Cypriniformes	F2	White	benthopelagic	100	L	2	Troph1
Olin	*Osteochilus lini*	Osteochilus	Cyprinidae	Cypriniformes	F5	White	benthopelagic	18.3	S	2	Troph1
Omar	*Oxyeleotris marmorata*	Oxyeleotris	Eleotridae	Perciformes	F5	White	demersal	79.3	L	3.9	Troph3
Omel	*Osteochilus melanopleurus*	Osteochilus	Cyprinidae	Cypriniformes	F3	White	benthopelagic	73.2	L	2.3	Troph1
Omic	*Osteochilus microcephalus*	Osteochilus	Cyprinidae	Cypriniformes	F5	White	benthopelagic	29.3	M	2	Troph1
Osch	*Osteochilus schlegeli*	Osteochilus	Cyprinidae	Cypriniformes	F4	Grey	benthopelagic	46	M	2	Troph1
Ovit	*Osteochilus vittatus*	Osteochilus	Cyprinidae	Cypriniformes	F5	White	benthopelagic	39	M	2	Troph1
Owaa	*Osteochilus waandersii*	Osteochilus	Cyprinidae	Cypriniformes	F1	White	benthopelagic	25	S	2	Troph1
Pabe	*Pao abei*	Pao	Tetraodontidae	Tetraodontiformes	F3	Estuarine	demersal	12.6	S	3.3	Troph2
Papo	*Parambassis apogonoides*	Parambassis	Ambassidae	Perciformes	F4	Grey	demersal	12.2	S	2.9	Troph2
Papo.1	*Phalacronotus apogon*	Phalacronotus	Siluridae	Siluriformes	F3	White	benthopelagic	158.6	L	4.5	Troph3
Parg	*Plicofollis argyropleuron*	Plicofollis	Ariidae	Siluriformes	F7	White	demersal	50	M	2.75	Troph1
Pbai	*Pao baileyi*	Pao	Tetraodontidae	Tetraodontiformes	F1	Estuarine	demersal	14.6	S	3.3	Troph2
Pbar	*Paralaubuca barroni*	Paralaubuca	Cyprinidae	Cypriniformes	F4	Grey	benthopelagic	18.3	S	3.3	Troph2
Pble	*Phalacronotus bleekeri*	Phalacronotus	Siluridae	Siluriformes	F3	White	demersal	73.2	L	4.5	Troph3
Pboc	*Pangasius bocourti*	Pangasius	Pangasiidae	Siluriformes	F2	White	benthopelagic	146.4	L	3.2	Troph2
Pbra	*Piaractus brachypomus*	Piaractus	Serrasalmidae	Characiformes	F11	Black	pelagic	88	L	2.52	Troph1
Pbre	*Puntius brevis*	Puntius	Cyprinidae	Cypriniformes	F6	White	benthopelagic	14.6	S	2.9	Troph2
Pbul	*Puntioplites bulu*	Puntioplites	Cyprinidae	Cypriniformes	F3	White	benthopelagic	35	M	2.4	Troph1

Pcam	*Pao cambodgiensis*	Pao	Tetraodontidae	Tetraodontiformes	F4	Grey	demersal	18.7	S	3.3	Troph2
Pcan	*Plotosus canius*	Plotosus	Plotosidae	Siluriformes	F7	Estuarine	demersal	150	L	3.9	Troph3
Pcon	*Pangasius conchophilus*	Pangasius	Pangasiidae	Siluriformes	F2	White	benthopelagic	146.4	L	2.7	Troph1
Pdea	*Poropuntius deauratus*	Poropuntius	Cyprinidae	Cypriniformes	F1	White	benthopelagic	21.6	S	3.2	Troph2
Pdja	*Pangasius djambal*	Pangasius	Pangasiidae	Siluriformes	F2	White	benthopelagic	115.2	L	2.8	Troph2
Pdub	*Polynemus dubius*	Polynemus	Polynemidae	Perciformes	F7	White	demersal	24.4	S	3.7	Troph2
Pfal	*Puntioplites falcifer*	Puntioplites	Cyprinidae	Cypriniformes	F3	White	benthopelagic	38.3	M	2.6	Troph1
Pfas	*Pristolepis fasciata*	Pristolepis	Pristolepididae	Perciformes	F4	Grey	demersal	20	S	3.2	Troph2
Pgig	*Pangasianodon gigas*	Pangasianodon	Pangasiidae	Siluriformes	F2	White	benthopelagic	300	L	2.3	Troph1
Phar	*Paralaubuca harmandi*	Paralaubuca	Cyprinidae	Cypriniformes	F4	Grey	benthopelagic	26.7	M	3.3	Troph2
Phyp	*Pangasianodon hypophthalmus*	Pangasianodon	Pangasiidae	Siluriformes	F2	White	benthopelagic	158.6	L	3.1	Troph2
Pjul	*Probarbus jullieni*	Probarbus	Cyprinidae	Cypriniformes	F2	White	demersal	183	L	3.2	Troph2
Pkre	*Pangasius krempfi*	Pangasius	Pangasiidae	Siluriformes	F8	White	benthopelagic	146.4	L	2	Troph1
Pkun	*Pangasius kunyit*	Pangasius	Pangasiidae	Siluriformes	F7	White	benthopelagic	85.6	L	2.8	Troph2
Plab	*Probarbus labeamajor*	Probarbus	Cyprinidae	Cypriniformes	F2	White	benthopelagic	183	L	2.5	Troph1
Plab.1	*Probarbus labeaminor*	Probarbus	Cyprinidae	Cypriniformes	F2	White	benthopelagic	150	L	2.5	Troph1
Plar	*Pangasius larnaudii*	Pangasius	Pangasiidae	Siluriformes	F2	White	benthopelagic	158.6	L	3.3	Troph2
Plei	*Pao leiurus*	Pao	Tetraodontidae	Tetraodontiformes	F7	Estuarine	demersal	16.4	S	3	Troph2
Pmac	*Pangasius macronema*	Pangasius	Pangasiidae	Siluriformes	F3	White	benthopelagic	36.6	M	3.2	Troph2
Pmel	*Polynemus melanochir*	Polynemus	Polynemidae	Perciformes	F7	White	demersal	30.5	M	3.5	Troph2
Pmic	*Phalacronotus micronemus*	Phalacronotus	Siluridae	Siluriformes	F3	White	benthopelagic	61	L	4	Troph3
Pmic.1	*Pseudolais micronemus*	Pseudolais	Pangasiidae	Siluriformes	F3	White	benthopelagic	42.7	M	2.7	Troph1
Pnas	*Pangasius nasutus*	Pangasius	Pangasiidae	Siluriformes	F2	White	benthopelagic	90	L	2.8	Troph2
Ppar	*Puntigurus partipentazona*	Puntigurus	Cyprinidae	Cypriniformes	F4	Grey	benthopelagic	4.6	S	2.87	Troph2
Pple	*Pseudolais pleurotaenia*	Pseudolais	Pangasiidae	Siluriformes	F3	White	benthopelagic	42.7	M	2.4	Troph1
Ppol	*Pangasius polyuranodon*	Pangasius	Pangasiidae	Siluriformes	F5	White	benthopelagic	97.6	L	2.8	Troph2
Ppro	*Puntioplites proctozysron*	Puntioplites	Cyprinidae	Cypriniformes	F3	White	benthopelagic	30	M	2.7	Troph1
Priv	*Paralaubuca riveroi*	Paralaubuca	Cyprinidae	Cypriniformes	F4	Grey	benthopelagic	22	S	3.3	Troph2
Psia	*Parachela siamensis*	Parachela	Cyprinidae	Cypriniformes	F4	Grey	pelagic	18.3	S	3.4	Troph2
Psia.1	*Parambassis siamensis*	Parambassis	Ambassidae	Perciformes	F5	White	demersal	7.3	S	3.3	Troph2

Psia.2	*Pseudomystus siamensis*	Pseudomystus	Bagridae	Siluriformes	F3	White	demersal	18.3	S	3.3	Troph2
Psp.	*Pangasius sp.*	Pangasius	Pangasiidae	Siluriformes	F2	White	benthopelagic	NA	NA	NA	NA
Pste	*Pseudomystus stenomus*	Pseudomystus	Bagridae	Siluriformes	F3	White	demersal	12	S	3.2	Troph2
Ptyp	*Paralaubuca typus*	Paralaubuca	Cyprinidae	Cypriniformes	F4	Grey	benthopelagic	22	S	3.3	Troph2
Pwaa	*Puntioplites waandersi*	Puntioplites	Cyprinidae	Cypriniformes	F3	White	demersal	50	M	2.4	Troph1
Pwol	*Parambassis wolffii*	Parambassis	Ambassidae	Perciformes	F4	Grey	demersal	24.4	S	3.7	Troph2
Raur	*Rasbora aurotaenia*	Rasbora	Cyprinidae	Cypriniformes	F4	Grey	benthopelagic	18.3	S	2.6	Troph1
Rbor	*Rasbora borapetensis*	Rasbora	Cyprinidae	Cypriniformes	F4	Grey	benthopelagic	7.3	S	3.3	Troph2
Rdan	*Rasbora daniconius*	Rasbora	Cyprinidae	Cypriniformes	F4	Grey	benthopelagic	15	S	3.1	Troph2
Rgut	*Raiamas guttatus*	Raiamas	Cyprinidae	Cypriniformes	F1	White	benthopelagic	36.6	M	3.9	Troph3
Rhob	*Rasbora hobelmani*	Rasbora	Cyprinidae	Cypriniformes	F4	Grey	benthopelagic	7.3	S	3.2	Troph2
Rmye	*Rasbora myersi*	Rasbora	Cyprinidae	Cypriniformes	F4	Grey	benthopelagic	8.4	S	NA	NA
Rtor	*Rasbora tornieri*	Rasbora	Cyprinidae	Cypriniformes	F4	Grey	benthopelagic	20.7	S	3.2	Troph2
Rtri	*Rasbora trilineata*	Rasbora	Cyprinidae	Cypriniformes	F4	Grey	benthopelagic	13	S	3.3	Troph2
Sarg	*Scatophagus argus*	Scatophagus	Scatophagidae	Perciformes	F7	White	reef-associated	38	M	3	Troph2
Sban	*Scaphognathops bandanensis*	Scaphognathops	Cyprinidae	Cypriniformes	F3	White	benthopelagic	48.8	M	2.4	Troph1
Sbea	*Syncrossus beauforti*	Syncrossus	Cobitidae	Cypriniformes	F3	White	demersal	30.5	M	3.5	Troph2
Shel	*Syncrossus helodes*	Syncrossus	Cobitidae	Cypriniformes	F3	White	demersal	36.6	M	3.3	Troph2
Slan	*Schizothorax lantsangensis*	Schizothorax	Cyprinidae	Cypriniformes	F1	White	benthopelagic	37.9	M	2.3	Troph1
Srub	*Systomus rubripinnis*	Systomus	Cyprinidae	Cypriniformes	F5	White	benthopelagic	30.5	M	2.9	Troph2
Sste	*Scaphognathops stejnegeri*	Scaphognathops	Cyprinidae	Cypriniformes	F3	White	benthopelagic	30.5	M	2.6	Troph1
Tate	*Tor ater*	Tor	Cyprinidae	Cypriniformes	F1	White	pelagic	40.5	M	2.9	Troph2
Tcha	*Toxotes chatareus*	Toxotes	Toxotidae	Perciformes	F7	White	pelagic	48.8	M	4	Troph3
Tlat	*Tor laterivittatus*	Tor	Cyprinidae	Cypriniformes	F1	White	benthopelagic	73.2	L	2.9	Troph2
Tmic	*Toxotes microlepis*	Toxotes	Toxotidae	Perciformes	F7	White	pelagic	18.3	S	3.2	Troph2
Tmic.1	*Trichopodus microlepis*	Trichopodus	Osphronemidae	Perciformes	F6	Black	demersal	15.9	S	3.4	Troph2
Tpau	*Trigonopoma pauciperforatum*	Trigonopoma	Cyprinidae	Cypriniformes	F4	Grey	benthopelagic	7	S	3.3	Troph2
Tpec	*Trichopodus pectoralis*	Trichopodus	Osphronemidae	Perciformes	F6	Black	benthopelagic	25	S	2.8	Troph2
Tsin	*Tor sinensis*	Tor	Cyprinidae	Cypriniformes	F1	White	benthopelagic	56.7	M	3.3	Troph2
Ttam	*Tor tambroides*	Tor	Cyprinidae	Cypriniformes	F1	White	benthopelagic	122	L	2	Troph1

Tthi	*Tenualosa thibaudeaui*	Tenualosa	Clupeidae	Clupeiformes	F3	White	pelagic	36.6	M	2	Troph1
Tthy	*Thynnichthys thynnoides*	Thynnichthys	Cyprinidae	Cypriniformes	F4	Grey	benthopelagic	25	S	2.3	Troph1
Ttol	*Tenualosa toli*	Tenualosa	Clupeidae	Clupeiformes	F10	White	pelagic-neritic	60	M	2.48	Troph1
Ttri	*Trichopodus trichopterus*	Trichopodus	Osphronemidae	Perciformes	F6	Black	benthopelagic	18.3	S	2.7	Troph1
Watt	*Wallago attu*	Wallago	Siluridae	Siluriformes	F3	White	demersal	240	L	3.7	Troph2
Wlee	*Wallago leerii*	Wallago	Siluridae	Siluriformes	F11	White	demersal	150	L	4.5	Troph3
Xcan	*Xenentodon cancila*	Xenentodon	Belonidae	Beloniformes	F5	White	pelagic-neritic	40	M	3.9	Troph3
Ycau	*Yasuhikotakia caudipunctata*	Yasuhikotakia	Cobitidae	Cypriniformes	F3	White	demersal	11	S	3.4	Troph2
Yeos	*Yasuhikotakia eos*	Yasuhikotakia	Cobitidae	Cypriniformes	F3	White	demersal	11	S	3.5	Troph2
Ylec	*Yasuhikotakia lecontei*	Yasuhikotakia	Cobitidae	Cypriniformes	F3	White	demersal	18.3	S	3.4	Troph2
Ylon	*Yasuhikotakia longidorsalis*	Yasuhikotakia	Cobitidae	Cypriniformes	F3	White	demersal	9.8	S	3.4	Troph2
Ymod	*Yasuhikotakia modesta*	Yasuhikotakia	Cobitidae	Cypriniformes	F3	White	demersal	30.5	M	3.4	Troph2
Yspl	*Yasuhikotakia splendida*	Yasuhikotakia	Cobitidae	Cypriniformes	F3	White	demersal	12.2	S	3.5	Troph2

Literature Cited

Froese, R., and D. Pauly. 2017. FishBase. www.fishbase.org.

Kottelat, M. 2013. The Fishes of the inland waters of Southeast Asia: A catalogue and core bibliography of the fishes known to occur in freshwaters, mangroves and estuaries. The Raffles Bulletin of Zoology 27:1–663.

MFD. 2003. Mekong Fish Database: A taxonomic fish database for the Mekong Basin. Mekong River Commission, Phnom Penh.

Ngor, P. B., G. Grenouillet, S. Phem, N. So, and S. Lek. 2018a. Spatial and temporal variation in fish community structure and diversity in the largest tropical flood-pulse system of Southeast Asia. Ecology of Freshwater Fish In press.

Ngor, P. B., P. Legendre, T. Oberdorff, and S. Lek. 2018b. Flow alterations by dams shaped fish assemblage dynamics in the complex Mekong-3S river system. Ecological Indicators 88:103–114.

Piman, T., T. A. Cochrane, M. E. Arias, A. Green, and N. D. Dat. 2013. Assessment of Flow Changes from Hydropower Development and Operations in Sekong, Sesan, and Srepok Rivers of the Mekong Basin. Journal of Water Resources Planning and Management 139:723–732.

Rainboth, W. J. 1996. Fishes of the Cambodian Mekong. Food and Agriculture Organisation of the United Nations, Rome.

Rainboth, W. J., C. Vidthayanon, and D. Y. Mai. 2012. Fishes of the Greater Mekong Ecosystem with Species List and Photoraphic Atlas. Museum of Zoology, University of Michigan, Ann Arbor.

Université
de Toulouse

Université
Paul Sabatier
TOULOUSE III

DOCTORAT DE L'UNIVERSITE DE TOULOUSE
délivré par l'Université Toulouse III – Paul Sabatier

Spécialité :

RAPPORT DE SOUTENANCE

Nom du (ou de la) candidat(e) : Peng Bun Ngor
Date de soutenance : 10/04/2018
Président du jury : Thierry OBERDORFF

All Jury members were physically present at the thesis defence. During 40 minutes, M. Peng Bun Ngor has presented his results to the Jury. The presentation, very well illustrated, was done in English in a clear and detailed manner. The exposed results were challenging and important for advance in ecology in general and freshwater tropical ecology in particular. This excellent presentation was followed, during two hours, by a round of questions/answers with the Jury members. Throughout this discussion, M. Peng Bun Ngor has shown, in light of his relevant answers to both specific and more general questions, a researcher's great maturity. After deliberation, given the high scientific quality of the research exposed and the great importance of the results in an applied context, the Jury has unanimously decided to give to M. Peng Bun Ngor the title of Doctor of the Toulouse III University and has added its special congratulations to the candidate.

Le diplôme national de Docteur est délivré par l'Université Toulouse III – Paul Sabatier sans aucune mention.

Les Membres du Jury :

Nom	Signature	Nom	Signature
GRENOUILLET Gaël	[signature]	OBERDORFF Thierry	[signature]
MUÑOZ Maite	[signature]	BROSSE Sébastien	[signature]
So Nam	[signature]	LEK Sovan	[signature]
Anna Vila-Gispert	[signature]	Christine Argillier	[signature]

Fish assemblages dynamic in the tropical flood-pulse system of the Lower Mekong River Basin

The Mekong seasonal flow plays a pivotal role in structuring up- and downstream aquatic communities. The thesis investigates the dynamics of spatial and temporal fish community structure in the Lower Mekong system, i.e. the Lower Mekong River and its major tributaries. Using spatial and time-series datasets and univariate as well as multivariate statistical approaches, the thesis highlights:

- The importance of flow and other environmental factors in explaining spatial and temporal dynamics of fish diversity patterns and assemblage structure in the Lower Mekong system.
- The effects of indiscriminate fishing in one of the world's largest tropical inland fisheries, the Tonle Sap, with the finding of, despite overall stationary catch per unit effort (CPUE), strong alterations in assemblages composition, with decreasing trends in catches of large-sized species, and increasing trends in the catches of some small-sized species.
- Contrasted responses of fish assemblages to a gradient of disruption of flow seasonality and predictability due to dams in the Lower Mekong system.

The results obtained through this thesis contribute to the ecological understanding of fish assemblages and to the design of applications for long-term planning, monitoring, management and conservation of fisheries in the Mekong Basin and beyond. The thesis suggests that:

- Maintaining the Mekong robust and predictably seasonal flood pulse dynamics and habitat connectivity is imperative to ensure fish longitudinal and lateral dispersal ability among critical habitats for breeding, feeding and seeking refuge.
- Setting appropriate regulations based on known peak fish migrations at various spatiotemporal scales would allow migratory fish species to pass through rivers, access critical habitats and complete their life cycles. Also, enforcing and operationalizing the existing formal fisheries management mechanisms effectively at local, national and regional levels as well as allocating sufficient resources to the fishery sector to combat illegal fishing practices and implementing fisheries conservation measures in critical habitats would help deal with the problem of overharvesting.
- Hydropower-related pulsed flows that can mimic as far as possible the natural pulsed flows are critical to reduce downstream effects on aquatic organisms, and, thus, should be prioritized and applied as one of the measures to mitigate the impacts from existing and planned hydropower dams in the Mekong Basin.

Keywords: Fish assemblage richness and composition, assemblages turnover, environmental filtering, flow seasonality and predictability, fisheries effects, hydropower dams, Mekong Basin, Asia.

AUTEUR : Peng Bun NGOR

TITRE : Dynamique des peuplements de poissons dans le bassin inférieur du Mékong

DIRECTEUR DE THÈSE : Sovan LEK

LIEU ET DATE DE SOUTENANCE : Université Paul Sabatier, le 10 avril 2018

Le débit saisonnier du Mékong joue un rôle central dans la structuration amont/aval des communautés aquatiques. Cette étude examine les dynamiques de la structure spatiale et temporelle des communautés de poissons dans le bassin inférieur du Mékong, comprenant le Mékong aval et ses principaux affluents. L'application de méthodes statistiques univariées et multivariées, sur des bases de données spatiales et temporelles piscicoles et environnementales, met en évidence :

- Le rôle prépondérant des débits dans l'explication de la dynamique spatiale et temporelle des patrons de diversité et de structure des assemblages piscicoles dans la bassin aval du Mékong.
- Les effets de la pêche non sélective dans l'un des plus grands systèmes de production halieutique tropicale au monde, le lac le Tonlé Sap, avec la mise en évidence d'une production globalement durable marquée néanmoins par une composition altérée des communautés de poissons.
- Les réponses des assemblages de poissons face aux fluctuations saisonnières et à la stabilité des débits dans les rivières non régulées et régulées du bas Mékong.

Les résultats obtenus lors de cette thèse contribuent à la connaissance du fonctionnement des peuplements piscicoles et apportent une aide à la conception de plans de gestion et de conservation des ressources halieutiques et des autres ressources aquatiques dans le bassin du Mékong et au-delà. Cette étude suggère que :

- Le maintien de la dynamique saisonnière des débits et de la connectivité des habitats est impératif afin d'assurer la dispersion longitudinale et latérale des poissons vers des habitats vitaux pour leur reproduction, leur alimentation et leur protection.
- L'établissement d'une réglementation appropriée basée sur la connaissance des pics migratoires de poissons aux différentes échelles spatio-temporelles permettrait aux poissons migrateurs de franchir les rivières pour accéder à leurs habitats nécessaires à l'accomplissement de leur cycle de vie. Aussi, faire respecter et opérationnaliser de façon efficace les mécanismes officiels de gestion halieutique aux échelles locales, nationales et régionales, mais aussi allouer suffisamment de moyens pour le secteur de la pêche afin de lutter contre les pratiques de pêche illégale et pour la mise en œuvre de mesures de conservation contribuerait à résoudre les problèmes de surexploitation des ressources aquatiques.
- La mimique des variations naturelles des débits par les barrages hydroélectriques devrait être priorisées et appliquées comme une des mesures permettant d'atténuer leurs impacts sur les peuplements aquatiques du bassin du Mékong.

Mots-clés : Richesse et composition des peuplements de poissons, filtres environnementaux, saisonnalité et prédictibilité des débits, impact des pêcheries, barrages hydroélectriques, Bassin du Mékong, Asie.

DISCIPLINE ADMINISTRATIVE : ÉCOLOGIE

INTITULÉ ET ADDRESSE DE L'U.F.R OU DU LABORATOIRE :
Laboratoire Évolution et Diversité Biologique (EDB)
UMR5174 (CNRS/ENSFEA/IRD/UPS)
Université Paul Sabatier, Bâtiment 4R1
118 route de Narbonne, 31062 TOULOUSE CEDEX9 – FRANCE