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Présentée et soutenue par :
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Titre :

Dynamique spatiale et temporelle des espèces et de communauté de poissons dans le système d'inondation pulsé de Tonle Sap
Spatial and temporal dynamics of fish species and community in Tonle Sap flood pulse system

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Title: Spatial and temporal dynamics of fish species and community in Tonle Sap flood pulse system

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Résumé

Le lac Tonle Sap (TSL) est l'un des plus grands lacs du monde et est connu comme un hot-spot de la biodiversité en Asie du Sud-Est. En raison de la grande diversité ainsi que de la productivité élevée de poissons, le lac contribue à un apport important en protéines pour la population cambodgienne. Cette étude vise principalement à étudier (1) la dynamique spatiale et temporelle de la composition des communautés de poissons, (2) les effets des facteurs environnementaux sur la distribution des espèces et (3) l'effet de l'abolition des lots de pêche sur la biomasse, les communautés de poissons et le structure des poissons. En utilisant des méthodes statistiques multivariées sur les données de poissons et de variables environnementales, je suis en mesure de mettre en évidence les principales conclusions suivantes:

- Les communautés de poissons du TSL étaient composées de deux assemblages de poissons: l'assemblage du nord, principalement caractérisé par des poissons noirs, et l'assemblage du sud, principalement lié aux poissons blancs, gris et estuariens. Les assemblages de poissons de la période 1994-1995 étaient représentés par l'abondance de tous les groupes fonctionnels, c'est-à-dire les poissons noirs, blancs et gris, et pour la période de 1996 à 1999, les assemblages étaient liés aux poissons blancs et gris.
- Les distributions des abondances espèces de poissons n'étaient pas homogènes dans le TSL. De plus, les aires de distributions des espèces étaient différentes et étaient régies par des combinaisons distinctes de caractéristiques de l'habitat et de facteurs climatiques.
- *H. lobatus* et *H. siamensis* peuvent coexister ensemble, mais la synchronisation et la migration de *H. lobatus* conduisent toujours à celles de *H. siamensis*. Ces résultats suggèrent que la population de *H. lobatus* est plus sensible aux variations d'impulsion de flux que celles de *H. siamensis*. Ceci indique que les variations des impulsions

d'écoulement sont les principaux déterminants responsables de la dynamique temporelle de chaque espèce.

- La réforme de la politique de la pêche menée par le gouvernement entre 2000 et 2012 pour remplacer les lots de pêches commerciales par une pêche plus raisonnable a bénéficié aux espèces de petite taille avec une migration à courte distance, un niveau trophique bas, et préfèrant l'habitat de surface dans la colonne d'eau. En revanche, elle a affecté négativement les espèces de grande taille avec une migration à longue distance, un niveau trophique élevé et benthopelagique.

Les résultats de cette étude fournissent des connaissances utiles qui pourraient être utilisées pour soutenir des actions de gestion et de conservation. Par exemple, en raison du déclin temporel des grandes espèces et de la biomasse totale du lac, nous recommandons une récolte équilibrée des espèces car cela pourrait réduire les effets de pêche sur les composantes de l'écosystème. Ainsi, le renforcement du droit de la pêche doit être fortement pris en considération pour éliminer les activités de pêche illégales dans le lac Tonle Sap afin de soutenir les ressources de pêche. De plus, il faudrait envisager des mesures de conservation axées sur les zones qui soutiennent constamment des niveaux élevés de biomasse de poissons. Les résultats suggèrent également de considérer les exigences environnementales de chaque espèce pour gérer efficacement les ressources halieutiques. En outre, la période de présence de certaines espèces clés devrait être prise en compte dans le cadre d'une règlementation ou d'une politique pour mieux gérer et conserver les espèces. La saisonnalité et la prévisibilité des inondations du Mékong devraient être maintenues pour soutenir la dynamique naturelle des espèces de poissons.

Mots-clés: pêche à grande échelle, réforme de la politique de pêche, composition des communautés de poissons, structure des communautés, impulsion d'inondation, distribution spatiale, préférence d’habitat, synchronisation des poissons

Abstract

Tonle Sap Lake (TSL) is one of the world's largest lakes and is a biodiversity hotspot in Southeast Asia. It supports high fish productivity which sustains protein supply for millions of people in the region. This study aims to investigate (1) spatial and temporal dynamics of fish community composition, (2) the effects of environmental factors on fish distribution and (3) effects of fishing lot abolishment on fish biomass, community and structure in TSL. By using multivariate statistical methods on fish and environmental data, the thesis highlights that:

- There were two fish assemblages in TSL: the northern assemblage, mostly characterised by black fishes, and the southern assemblage, mainly linked to white, grey and estuarine fishes. Fish assemblages from earlier years (1994 and 1995) were represented by the abundances of all functional groups, i.e. black, white and grey fishes, and from 1996 to 1999, the assemblages were linked only to white and grey fishes.
- Fish species distributions were not homogeneous within TSL. In addition, species distribution areas were different and were governed by distinct combinations of the local habitat characteristics and regional climatic factors.
- *H. lobatus* and *H. siamensis* can co-occur together, but synchronisation and migration of *H. lobatus* always lead those of *H. siamensis*. These results suggest that the population of *H. lobatus* is more responsive to flow pulse variations than those of *H. siamensis.*
- The fisheries policy reform introduced by the government in 2000 and 2012 to remove all the commercial fishing lots in favour of subsistence fisheries positively benefited small-sized species with short distance migration, low trophic level, and prefer the surface habitat in the water column. In contrast, it negatively affected the large-sized species with long-distance migration, high trophic level and preferred deeper water column.

The results of this study provide useful knowledge, which could be used to support management and conservation actions. For instance, due to the temporal decline of the large species and the total fish biomass of the lake, we recommend focusing on the balanced harvesting because it could reduce the effects of the fishing on the fish community. Thus, the fisheries law reinforcement must be highly taken into consideration to eliminate the widespread illegal fishing activities in the TSL to sustain fisheries sources for long-term use. Moreover, conservation actions should be focused on the areas that consistently support high fish biomass levels. The results also suggest considering the environmental requirements of each species to efficiently manage fish resources. Also, the timing of the occurrence of some keystone species should be taken into account as a part of a regulation or policy consideration to better manage and conserve the species. Seasonality and predictability of the Mekong floods should be maintained to sustain the natural dynamics of fish species.

Keywords: large-scale fisheries, fisheries policy reforms, fish community composition, community structure, flood pulse, spatial distribution, habitat preference, fish synchronisation

Contents

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Chapter I: General Introduction

1.1 Inland fisheries

The fish resource provides one of the primary sources of animal protein consumed worldwide and income, especially for people in developing countries (Allan et al., 2005). In developing countries, fish protein sources are mainly derived from the harvest of natural fish stocks, while those in developed countries are produced by recreational fisheries or aquaculture (Allan et al., 2005; Welcomme et al., 2010). Among the natural fish stock, poor people in developing countries are more dependent on inland fisheries resources than marine sources (McIntyre, Reidy Liermann, & Revenga, 2016). The main of the global inland fisheries sources are derived from developing countries (Bartley, Graaf, Valbo-Jorgensen, & Marmulla, 2015; De Graaf, Bartley, Jorgensen, & Marmulla, 2015). Worldwide, inland capture fisheries are from the lakes and wetland that cover an approximately total area of 7.8 million km^2 (De Graaf et al., 2015; Welcomme et al., 2010). Inland capture fisheries refer to the catch or harvest of natural stock of freshwater fish and other living organisms from freshwater bodies (Allan et al., 2005; Welcomme et al., 2010). Geographically, the area covered with surface waters are relatively from Southeast Asia, North America, East and Central West Africa, the northern part of Asia, Europe and South America. Inland capture fisheries represent only 6.3% of the global fish production and 95% of which are from developing countries, i.e. Asia and Africa (Bartley et al., 2015; De Graaf et al., 2015; Welcomme et al., 2010). Inland fisheries are not only important for protein sources and global food supply, but they also are of paramount importance for livelihoods of people in many parts of the developed and developing countries, and it provides employment to 61 million people (Allan et al., 2005; Bartley et al., 2015; Welcomme et al., 2010). In addition, approximately 1 billion people in the world, mostly in developing countries, depending on the protein sources derived from fish (Allan et al., 2005). Indeed, harvesting the natural fish stock has rapidly increased in developing countries, but decreased in developed countries while many commercial inland fisheries were replaced by recreational fisheries (Allan et al., 2005; Cooke & Cowx, 2004). Overall, from the report data, the global catch of inland fisheries is increased because of an increase in the exploitation in Asia and Africa and an increase in human population density (FAO, 2014; McIntyre et al., 2016). Meanwhile, the global inland capture fisheries trend has been stable from 2000 to 2004 containing approximately 8.6 million tonnes, however its products reached 10 million tonnes in 2008 and increased up to 11.63 million tonnes in 2012, that the highest contribution is from developing countries (Bartley et al., 2015; De Graaf et al., 2015; Welcomme, 2011). Nonetheless, these statistical data is not accurate (Allan et al., 2005; Bartley et al., 2015; De Graaf et al., 2015; Welcomme, 2011; Welcomme et al., 2010). However, with the correct estimation, the global catch of fisheries has been declining (Pauly et al., 2002; Watson, Watson, & Pauly, 2014). Evidence revealed the collapse or decline in inland fisheries resources due to intensive fishing and multiple uses (Allan et al., 2005; Bartley et al., 2015; Welcomme et al., 2010). Consequently, the excessive fishing of inland fisheries adversely influences human health, especially people in developing countries (Allan et al., 2005).

1.2 A general overview of the Mekong River

1.2.1 The Mekong River

The Mekong River is the largest river in South-East Asia. From its sources in the Tibetan Himalaya China, it flows through six countries, i.e. China, Myanmar, Lao PDR, Thailand, Cambodia and Viet Nam, and conversa distance of more than 4880 km (Figure 1.1; MRC 2005). The Mekong River covers a total drainage area of 795,000 km^2 (MRC, 2005). In term of mean water discharge, the Mekong River is ranked the eight world largest river, and it discharges approximately 475,000 million cubic meters of water into the South China Sea (Gupta, Hock, Xiaojing, & Ping, 2002; Matti Kummu & Sarkkula, 2008; Anders F Poulsen & Valbo-jørgensen, 2000). The Mekong River is classified into two parts: the Upper Mekong

River and the Lower Mekong Basin (MRC, 2005). The Lower Mekong Basin (LMB) includes portions of Thailand, Laos, Cambodia and Vietnam. The Mekong River is a typical floodplain river, dominated by the monsoon climate of Southeast Asia (A. Poulsen, Poeu, Viravong, Suntornratana, & Tung, 2002). It is a dynamic river system, alternating between a flood season from May to October and a dry season from November to April. The monsoon flood-pulse create the vast areas of seasonally inundated floodplains adjacent to the river channels every year. The hydrological cycle served as a determinant for seasonal migration of fish. Floodplains are extremely productive feeding habitats for most important fishes, whereas the river channels mainly serve as refuge habitats during the dry season (A. Poulsen et al., 2002).

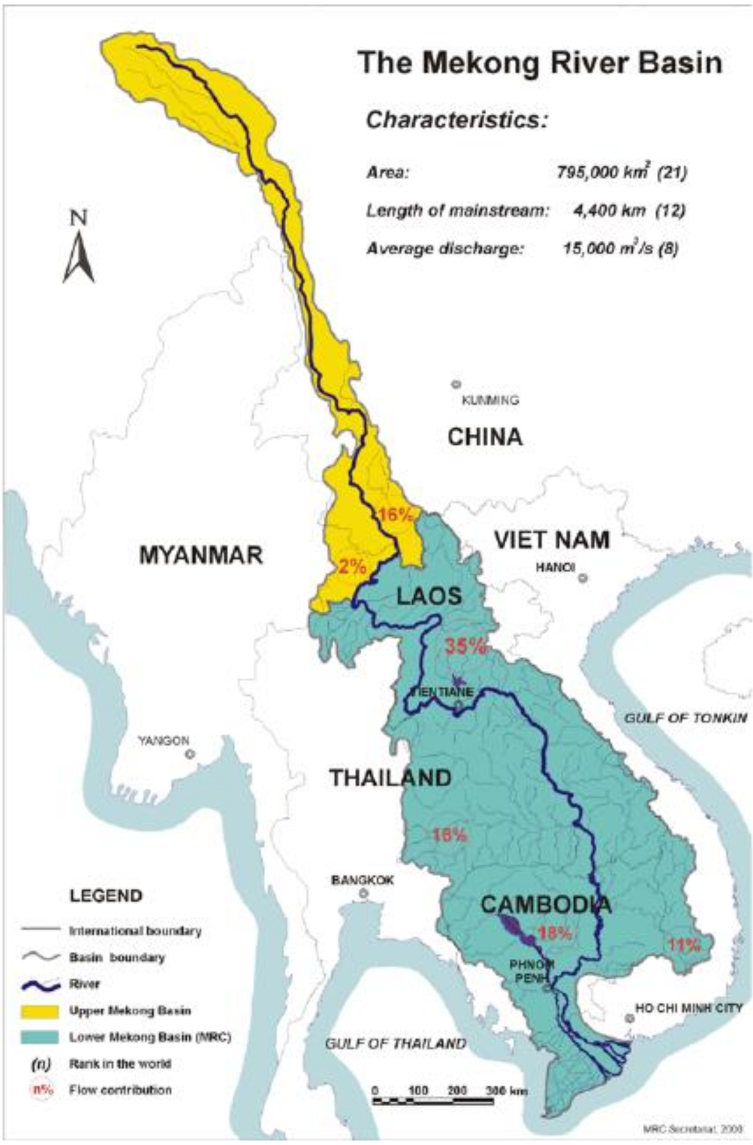

Figure 1.1 Geographical map of the Mekong River. (Sources: MRC 2010).

1.2.2 The Mekong fisheries

The Mekong River lies within the Indo-Burma biodiversity hotspot (Allen, Smith, & Darwall, 2012; Myers, Mittermeier, Mittermeier, Da Fonseca, & Kent, 2000) and is the second most diverse river system in the world, which host over 1200 fish species, after the Amazon River (Allan et al., 2005; Eric Baran, 2005; Brosse et al., 2013). However, only 50-100 species are common in the Mekong fishery. Moreover, many of which are still waiting for taxonomic identification and confirmation, thus the number of species is assumed to be higher than this. Apart from its important role as high diversity, the Mekong River is also one of the most intensive and productive inland fisheries in the world due to an extensive floodplain system nurtured by annual monsoons (Eric Baran, 2005; Eric Baran & Gallego, 2015) with annual yields of approximately 2.6 million tons, that have the largest contribution to the global inland capture fisheries (Hortle, 2007; Welcomme et al., 2010). It also has provided food sources and animal protein for 60 million people living in the region, that most of whom directly and indirectly rely on the fisheries resources of the Mekong River for their income and food security (MRC, 2010). In this regard, the average consumption of fish and other aquatic animals is estimated at 56 kilograms (kg) per capita per year in the lower Mekong Basin (Hortle, 2007). The system is highly productive due to an extensive floodplain system nurtured by annual monsoons (Eric Baran & Gallego, 2015).

1.3 A brief of Tonle Sap Lake

1.3.1 Tonle Sap Lake

Tonle Sap Lake is situated in the central of Cambodian consisting of the largest wetland area in Southeast Asia and covers about 5 to 8 per cent of the total land area (Matti Kummu & Sarkkula, 2008; MRC, 2003, 2005). Tonle Sap Lake and the Mekong River are connected to each other by Tonle Sap River (TSR) with 120 km long (M. Kummu et al., 2014). Tonle Sap Lake was characterized by a tropical monsoon climate (Arias, Cochrane, Norton, Killeen, & Khon, 2013). Hydrological flows of Tonle Sap Lake are influenced by flood waters of the Mekong River, and this creates a complex flood-pulse ecosystem (Arias et al., 2013; M. Kummu et al., 2014; MRC, 2005). The surface area of Tonle Sap Lake seasonally fluctuates from 2500 km^2 to 15000 km^2 driven by seasonal flood pulse from the Mekong River (M. Kummu et al., 2014).

1.3.2 Tonle Sap flood pulse system

Tonle Sap Lake is defined as a flood-pulse system due to its seasonal periodicity in hydrological flows. In the wet season (May-October), the water flows into Tonle Sap Lake through TSR due to increased water levels in the Mekong River, whereas in the dry season (November-April), a reverse flow occurs through TSR again due to the receding water levels in the Mekong River (MRC, 2005). The water levels highly vary between seasons; the water depth ranges from 0.5 metres in April (dry season) to 9 metres in September-October (rainy season). This variation leads to a varied surface area of Tonle Sap Lake throughout the year and thus creates more heterogeneous habitats compared to TSR (MRC, 2005). The flood pulse creates a substantial floodplain that is habitat for a variety of aquatic and terrestrial plant and animal species (Ian C. Campbell, Poole, Giesen, & Valbo-Jorgensen, 2006). A large number of floodplain areas were inundated and formed large breeding and spawning areas for the fishes (Eric Baran, Jantunen, & Kieok, 2007). Tonle Sap Lake also forms a natural reservoir that stores the floodwater for the Mekong system (Sarkkula et al., 2004). Tonle Sap Lake was characterized by a tropical monsoon climate (Arias et al., 2013). In these ecosystems, the pulsing is one of the major forces responsible for productivity and biotic interactions (Junk, Bayley, & Sparks, 1989). Here, the pulsing allow moving the littoral which enables the rapid recycling of organic matter and nutrient and then bring about the high productivities (Junk et al., 1989).

1.3.2 Tonle Sap Lake fisheries

Tonle Sap Lake is the largest natural inland lake in Southeast Asia (MRC, 2005) and hosts a diverse fish fauna, with 296 fish species (Eric Baran, So, Degen, Chen, & Starr, 2013). Tonle Sap Lake is therefore considered a biodiversity hotspot (Allen et al., 2012) and has had the status of a UNESCO world heritage biosphere reserve since 1997 (UNESCO, 2018). This lake is the world's fourth most productive inland fishery (Eric Baran, 2005) with annual estimated yields of 246,000 tons (Lieng & Zalinge, 2001).

Tonle Sap Lake plays a crucial role in providing fish products and protein to nearly two million people in the region (Ahmed, Hap, Ly, & Tiongco, 1998), and Tonle Sap Lake fisheries account for 60% of the total protein intake of the approximately 15 million Cambodian people (Ahmed et al., 1998; Lieng & Zalinge, 2001). The average consumption of fish and other aquatic animals is estimated at 71 kg per capita per year around Tonle Sap Lake in Cambodia (Ahmed et al., 1998). Income from inland capture fisheries and other aquaculture contribute about 10% of Cambodia Gross Domestic Product (GDP) (E Baran, Schwartz, & Kura, 2009).

1.4 Migration of fish in the Mekong River

Migration is the movement of an animal during one part of its life cycle (A.F. Poulsen, Ouch, Viravong, Suntornratana, & Nguyen, 2002). Migration of fish is an important ecological aspect of many tropical rivers. Different migration behaviours result from adaptions to hydrological and environmental conditions (Anders F Poulsen & Valbo-jørgensen, 2000). Migration of the Mekong fish are divided into three longitudinal migration (long distance migration), lateral migration (short distance migration) and non-migration (or floodplain resident) (A.F. Poulsen et al., 2002). The longitudinal migration refers to movement of the fish in the main river channels and their main tributaries, while the lateral migration refers to the migration of fish from the main river and tributaries to floodplain area during the flood season and back again during the dry season (Anders F Poulsen & Valbo-jørgensen, 2000). The migration of fish in the Mekong River serve the paramount importance for fisheries as the huge amount of fisheries resources are based on the exploitation of the migratory fishes (Anders F Poulsen & Valbo-jørgensen, 2000).

Cambodian river fish species are classified into three functional groups: blackfish, white and grey fish according to their habitat characteristics (A.F. Poulsen et al., 2002). Blackfish in the Mekong River includes climbing perch (*Anabas testudineus*), the clarias catfishes (e.g. *Clarias batrachus*) and the striped snakehead (*Channa striata*) (A.F. Poulsen et al., 2002). Black-fishes mostly live in lakes and swamps on the floodplains near river channels and migrate to flooded areas during the flooded season (A.F. Poulsen et al., 2002). They are adapted to a low oxygen environment, which enables them to stay in swamps and small floodplain lakes during the dry season. Blackfish are considered non-migratory species even though they migrate between permanent and seasonal water bodies (A.F. Poulsen et al., 2002). White-fishes mostly inhabit the turbid water river channels for some part of the year (A.F. Poulsen et al., 2002). Most white-fish species migrate into flooded areas during the monsoon seasons, and back to their river habitats at the end of the flood season (A.F. Poulsen et al., 2002). The Mekong white fish are cyprinids (e.g. *Cyclocheilichthys enoplos* and *Cirrhinus microlepis*), the river catfishes of the family Pangasiidae (A.F. Poulsen et al., 2002). During the dry season, larger white fish survive in deep pools of the main floodplain areas while blackfish spend their lives feeding and breeding in the floodplain water bodies (Deap, Degen, & Zalinge, 2003).

1.5 Descriptions and ecology of the main commercial fish species in Tonle Sap Lake

Striped snakehead *Channa striata* (Bloch, 1793)

The striped snakehead *Channa striata* were distributed in tropical Africa and southern Asia, i.e., Pakistan to Thailand and South China (Figure 1.2; Froese & Pauly, 2017). In Cambodia, *Channa striata* are the common fish species that were found in many places throughout the country, i.e., the Mekong Basin, Tonle Sap Lake and Tonle Sap River (Maurice Kottelat, 1985, 1998). In addition, they have been commonly introduced in rice field farming, and they are very important in Cambodian aquaculture (Chheng, Touch, Baran, & Leng, 2005). Biologically, the striped snakehead prefers the flood-plain lakes and smaller streams than in the Mekong mainstream (S. Chan et al., 2000). Moreover, they were mainly recorded in the still water and stagnant and muddy fresh water of plains habitats of the ponds, swamp, streams and lowland rivers with 1-2 metre in depth (Chheng et al., 2005). As the blackfish, the striped snakehead could adapt to the low oxygen environment during the season by burrowing themselves in the bottom mud of lakes, canals and swamps (Chheng et al., 2005). During the rainy season, they migrate upstream from the Mekong mainstream toward the flooded areas and move back to the permanent water bodies at the receding water, especially the early of the dry season (S. Chan et al., 2000). Ditches, ponds and flooded paddy fields have been known the important breeding ground of the striped snakehead. Meanwhile, in Cambodia, the breeding periods of this species were reported in May-June and November-December (Chheng et al., 2005). The striped snakehead has been known the parent care species in which the parents protect their babies by hiding below the surface water while the babies swim at the surface (Froese & Pauly, 2017). The main food contents for this species are bony fish, frogs, insects, earthworms, tadpoles and crustaceans (Rahman, 1989).

Figure 1.2 Photos of the striped snakehead *Channa striata* (Bloch, 1793). The photo were derived from Rainboth (1996). The maximum length of this species was 100 cm in standard length.

Giant snakehead *Channa micropeltes* (Cuvier, 1831)

Similar to the striped snakehead *Channa striata*, the distribution of the giant snakehead *Channa micropeltes* was found in both tropical Africa (Figure 1.3; Froese & Pauly, 2017). Like the strip snakehead, the giant snakehead *Channa micropeltes* is important for aquaculture, and they are also commonly introduced in the rice field farming (Chheng et al., 2005). The important habitats for *Channa micropeltes* were the standing or slowly flowing water of the deep and large streams and canals (Maurice Kottelat, 1998; Rainboth, 1996). They were also found in the swamp and the lowland river. In addition, small streams with dense vegetation habitats were important spawning ground for *Channa micropeltes*. They are Carnivorous top predator that forage primarily on fish and crustaceans (Froese & Pauly, 2017).

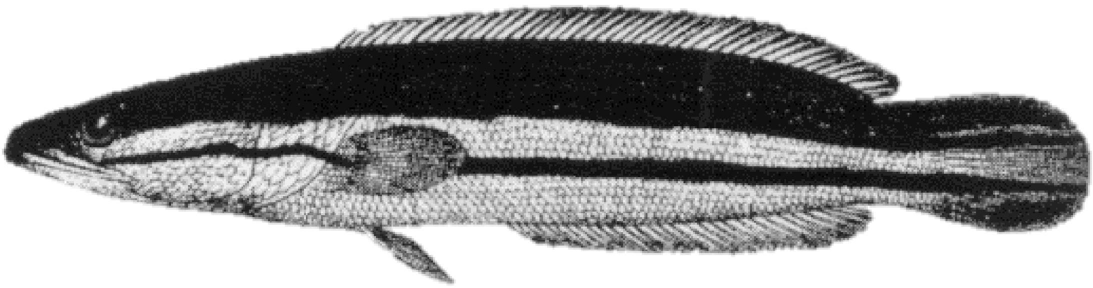

Figure 1.3 Photos of the giant snakehead *Channa micropeltes* (Cuvier, 1831). This photo was retrieved from Rainboth (1996). The maximum length of this species was 130cm in standard length.

Sutchi catfish *Pangasianodon hypophthalmus* (Sauvage, 1878)

The sutchi catfish *Pangasianodon hypophthalmus* were recorded from the Mekong Basin, including Tonle Sap Lake and Tonle Sap River (Figure 1.4; Maurice Kottelat, 1985; Lim, Lek, Touch, Mao, & Chhouk, 1999). They have been the longitudinal migratory fish that undertake the long-distance migration from rearing areas to spawn in unknown areas during May-July and move back to the mainstream to search for the rearing habitats when the river water level recedes between September-December (Hill & Hill, 1994). During the rainy season, from May to August, they move downstream from the Mekong Stung Treng to Kandal in Cambodia and continue migrating toward the Mekong Delta in Viet Nam (S. Chan et al., 2000). The purposes of this downstream migration were to spawn and feed and then migrate to the floodplain areas during the flooded season (S. Chan et al., 2000). The receding of the water, on the early of the dry season, appeared to be the main determinant that triggers this species to undertake the later migration from the flooded areas back into the Mekong at the end of the flood season (S. Chan et al., 2000). The young babies were commonly found in the lower Mekong while the large individuals were mainly observed in the in the Middle Mekong (Rainboth, 1996). They were reported to live in the deep and large rivers They have been the Omnivorous fish that feed on a variety of food types such as fish, crustaceans and vegetable debris (Rainboth, 1996).

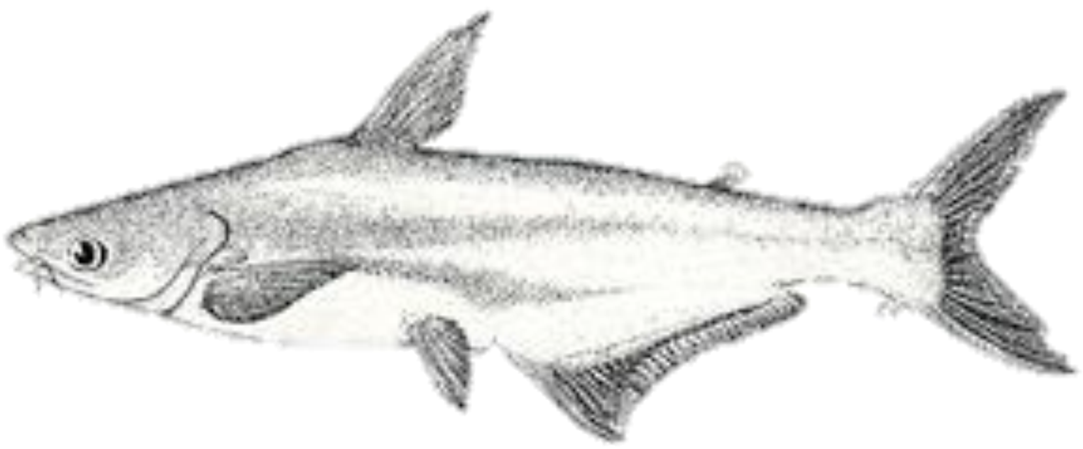

Figure 1.4 Photos of the sutchi catfish *Pangasianodon hypophthalmus* (Sauvage, 1878). The photo was derived from Rainboth (1996). The maximum length of this species

***Cyclocheilichthys enoplos* (Bleeker, 1850)**

Cyclocheilichthys enoplos has been known a longitudinal migratory species in the Mekong River that their distribution was found in the Mekong Basin, Stung Treng, the Tonle Sap River and the Tonle Sap Lake (Figure 1.5; Maurice Kottelat, 1985). The number of *Cyclocheilichthys enoplos* population start to be less and less below the Khone Fall to the Tonle Sap River and Tonle Sap Lake (Hill & Hill, 1994). During the flooded season, it was reported that *Cyclocheilichthys enoplos* migrate from the Mekong River toward the Tonle Sap

River and the Tonle Sap Lake (S. Chan et al., 2000). During the dry season, specifically when the water level recedes, the juveniles and adults move out of the lake flooded areas toward the river and migrate back toward the upstream in the Mekong. They were found at midwater to bottom levels of the mainstream and large tributaries of the Mekong River (Rainboth, 1996). The floodplain area or flooded riparian forests serve the important spawning grounds of *Cyclocheilichthys enoplos* (Froese & Pauly, 2017). The main food composition for young was zooplankton whereas the insect larvae, crustaceans and fish were the main foods for adults (Rainboth, 1996).

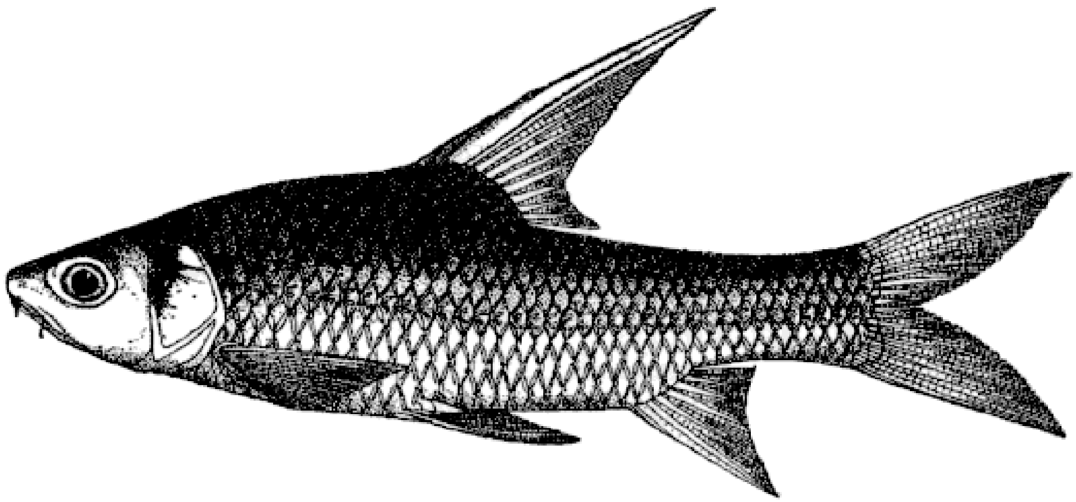

Figure 1.5 Photos of *Cyclocheilichthys enoplos* (Bleeker, 1850). The photo was derived from Rainboth (1996). The maximum length of this species was 74cm in standard length.

Trey Riel small mud carp *Henicorhynchus* spp

Trey Riel *Henicorhynchus* spp contains two main important species: *Henicorhynchus lobatus* and *H. siamensis*. Both species form the keystone species within the Mekong River (Figure 1.6; Froese & Pauly, 2017). The distribution of Trey Riel small mud carp was found in the Mekong River, Tonle Sap River and Tonle Sap Lake (M. Kottelat, 2001; Maurice Kottelat, 1985; Lim et al., 1999). They were found in the rapids and slow flowing water habitat in the mid-water to bottoms depths in large and small rivers (Froese & Pauly, 2017; Singhanouvong, Soulignavong, Vonghachak, Saadsy, & Warren, 1996). They undertook the longitudinal migration that moves into the floodplain area during the wet season for feeding and moves back to the rivers at receding water at the early October to December (Rainboth, 1996). The main food composition of Trey Riel small mud carp were plants, algae, periphyton and phytoplankton (Froese & Pauly, 2017).

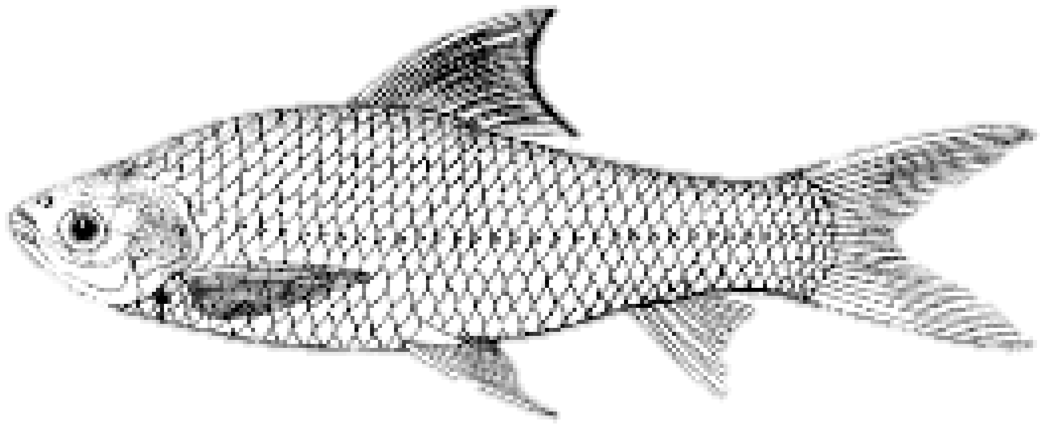

Figure 1.6 Photos of Trey Riel Siamese mud carp *Henicorhynchus siamensis* (Sauvage, 1881). This photo was extracted from Rainboth (1996). The maximum length of this species was 20 cm in standard length.

Java barb *Barbonymus gonionotus* (Bleeker, 1850)

Java barb *Barbonymus gonionotus* has been considered a migratory species that undertake the lateral migration moving from the Mekong River toward the small streams and tributaries and flooded area during the rainy reason and move back to the Mekong River during the dry season (Figure 1.7; S. Chan et al., 2000). They were found in at mid-water to bottom depths in rivers, streams, floodplains, and occasionally in reservoirs. Moreover, they live in the flooded forest during the flooded season (Rainboth, 1996). The first rain and rising water level were the important factors that trigger *Barbonymus gonionotus* to move from the Mekong River toward a tributary, canal or stream and then migrate to the flooded areas (S. Chan et al., 2000). The main food compositions for this species were planted matter leaves, weeds and invertebrates (Froese & Pauly, 2017).

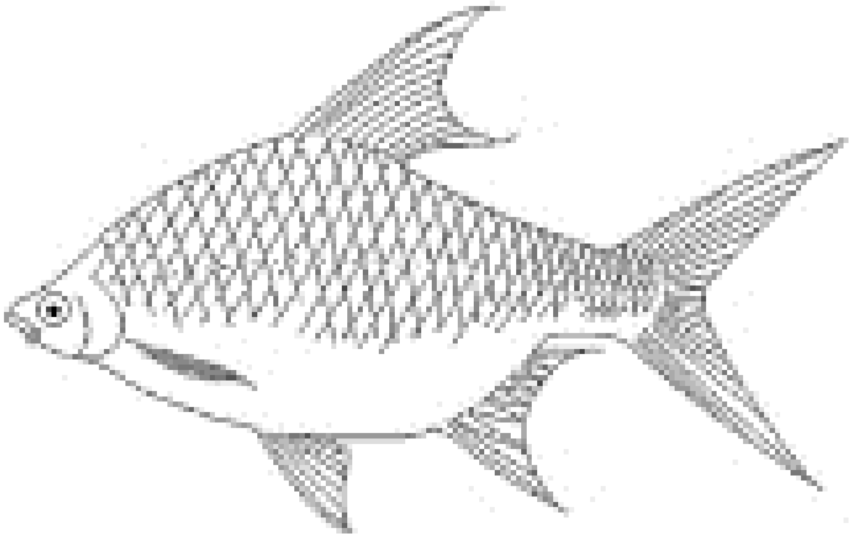

Figure 1.7 Photos of the Java barb Barbonymus gonionotus. The photo was derived from (Rainboth, 1996). The maximum length of this species

Moonlight gourami *Trichopodus microlepis* (Günther, 1861)

The moonlight gourami *Trichopodus microlepis* has been known as a common species in the floodplain of the lower Mekong (Figure 1.8; Froese & Pauly, 2017). They were found in the Mekong River in Cambodia and Viet Nam and Chao Phraya basins (M. Kottelat, 2001). They were mainly found in ponds and swamps, especially in the shallow sluggish or standing water habitats with a lot of aquatic vegetation (Froese & Pauly, 2017). Zooplankton, crustaceans and aquatic insects were the main food contents for the moonlight gourami (Chheng et al., 2005).

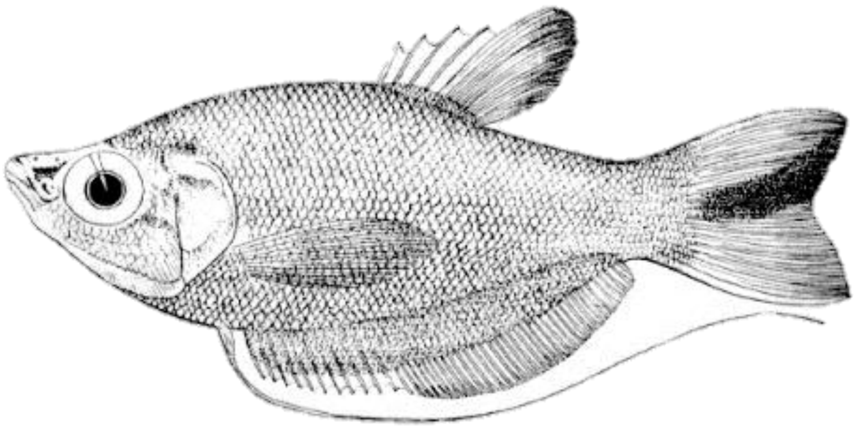

Figure 1.8 Photos of the moonlight gourami *Trichopodus microlepis* (Günther, 1861). The photo was derived Rainboth (1996). The maximum length of this species

1.6 Research problems, aims and objectives

Tonle Sap Lake (TSL) is the largest natural lake in Southeast Asia, and it is a diverse and productive lake (MRC, 2005). However, the knowledge of the fisheries and fish ecology in Tonle Sap Lake is poorly known. Given the fact that the fisheries of Tonle Sap Lake is being threatened by various factors such as intensive fishing through population growth, insufficient effectiveness of fisheries resources, and habitat disturbance (Allan et al., 2005), thus, there is a need to investigate the spatio-temporal dynamics of fish community, the effects of the removal of the commercial fishing lots of, the effects of environmental descriptors on distribution of fish species, and the role of the flood pulse on the spatio-temporal dynamics of fish species in Tonle Sap Lake.

On the other hand, regarding fish ecology, the distribution, and migration of fish species, many studies have been conducted in Tonle Sap Lake, e.g., fish species diversity and distribution (I.C. Campbell, Poole, Giesen, & Valbo-Jorgensen, 2006; Ian C. Campbell et al., 2006; B. Chan, Ngor, So, & Lek, 2017; Lim et al., 1999), fish beta diversity (Kong, Chevalier, Laffaille, & Lek, 2017), and the water quality-fish composition relationship (Chea, Grenouillet, & Lek, 2016), data mining and stock assessment of fisheries resources (Enomoto et al., 2011). However, knowledge of the parameters affecting the spatial distribution, spatio-temporal dynamics and migration of fish species in Tonle Sap Lake are poorly known. Therefore, determining the environmental factors on the distribution and migration of fish species is needed.

Besides the species distribution and ecological study, many studies have been highlighted and discussed about the effectiveness of the Cambodian fisheries policy reforms in Tonle Sap Lake in terms of property right, governance, management policy and legislation, and reviewed and expected the fisheries status based on the biological and ecological features of fish species, i.e. (Cooperman et al., 2012; Dina & Sato, 2014, 2015; Ratner, 2006; Ratner, Mam, & Halpern, 2014; Sok, 2014). However, providing the statistical evidence about the characteristics of fisheries and fish species impacted by this fisheries policy reforms is in the gap. Thus, providing evidence about the effects of the removal of the commercial fishing lots on fisheries and community and structure based on statistics data would be more informative.

The aims and specific objectives (or question) of the present study are:

1. Investigating the spatio-temporal changes in fish yields and fish communities in Tonle Sap Lake
   1.1. Illustrating the temporal trend of the main commercial fish and fish yields of Tonle Sap Lake.
   1.2. Investigating the relationship between the flood pulse and fish yields of Tonle Sap Lake
   1.3. Identifying the spatial and temporal patterns of fish community within Tonle Sap Lake.
2. Investigating the importance of the local habitat and regional climatic factors on the distribution of fish species in Tonle Sap Lake.
   2.1. Illustrating the spatial distribution of the main commercial fish species in Tonle Sap Lake.
   2.2. Determining the influence of the environmental factors on the spatial distribution of the main commercial fish species in Tonle Sap Lake.
3. Modelling the dynamics of fish species in the flood pulse system at spatial and time
   3.1. Is there any synchrony in occurrence between the two species, and is there a constant periodic occurrence of each species (e.g., re-occurring monthly or seasonally or annually)?

3.2. How is the period of synchronisation and movement patterns of each species varied across the Tonle Sap Ecosystem?

3.3. Is there any time-lagged relationship between the synchronisation of each species and water levels?

4. Assessing the effectiveness of the removal of the commercial fishing lots on fisheries, fish community composition and structure.

   4.1. Investigating the overall trends in fisheries in the two periods: before and after fishing lot abolishment.

   4.2. Analysing the variability or dynamics of fish community composition between two periods.

   4.3. Identifying the species that changed and linking the status of fish species (increasing, decreasing and non-change) with morphological and biological traits.

1.7 Hypotheses

The fisheries reforms allow removing all commercial fishing lots in favour of subsistence fisheries. Given that fishes could freely migrate and conduct substantial spatial distribution, we hypothesised that this fisheries policy reforms positively affect the long-distance migration of fish species. If the law enforcement is sufficient, it was expected that the removal of the commercial fishing lots that the fisheries policy reforms or the fishing lot abolishment might contribute to maintain fishery productivity and protect the biological diversity, and improve the sustainability of Tonle Sap Lake fisheries. In addition, the small fish species and floodplain residence fish species were expected to have benefitted from conservation area after the fisheries policy reforms (Cooperman et al., 2012). In contrast, while the area of the lake is open and free to access by all people, if the law enforcement is insufficient, the illegal fishing practices happen that lead the overfishing. Thus, the fisheries reforms would have negative effects on fisheries resources of TSL.

Moreover, it was hypothesised that the distribution of fish species within Tonle Sap Lake are heterogeneous. Fish species have a different response to the habitat characteristics and climatic feature. All species do not have the same perception of the heterogeneity of their habitat (Kolosa, 1989). Thus, we hypothesised that the responses of fish species to their environmental determinants are species-specific. The distribution of each species was not determined by the same environmental factors (Buisson, Blanc, & Grenouillet, 2008). Additionally, the distribution of fish species is regulated by the combined environmental descriptors. It was hypothesised that both local habitat and regional climate have the potential effects on the spatial distribution of fish species. This observation leads us to discuss the ecological significance of such a fish species distribution. This work could contribute to the modelling assessment of the factors and processes controlling freshwater ecology within Tonle Sap System.

Furthermore, while *Henicorhynchus lobatus* and *H. siamensis* have dissimilarities in ecological preferences and life history traits (Hurwood, Adamson, & Mather, 2006), we expected distinct periods of the occurrence, synchronisation and time-lagged relationship to be observed for each species in different parts of the Tonle Sap Ecosystem, following the variations in water levels. It was hypothesised that the flood pulse leads the synchronisation and movement pattern of the small mud carp species. Thus, the variation of flood pulse plays an important role in regulating the spatial and temporal dynamics of two small mud carp species in a large flood pulse system.

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Chapter II: Materials and Methods

2.1 Study area

This study covers the Tonle Sap System (TSE): Tonle Sap Lake and Tonle Sap River (Figure 2.1). Tonle Sap Lake is situated in the central of Cambodian consisting of the largest wetland area in Southeast Asia and covers about 5 to 8 percent of the total land area (Matti Kummu & Sarkkula, 2008; MRC, 2003, 2005). Tonle Sap Lake and the Mekong River are connected by Tonle Sap River (TSR) with 120 km long (M. Kummu et al., 2014). This study covers the spatial range approximately 300 x 300 km.

2.2 Data collection

This study uses three different datasets: catch assessment data of fishing lots, catch assessment data of mobile gear fishing, and catch monitoring survey data. The fish data were provided by the Fisheries Programme of the Mekong River Commission (MRC) in collaboration with the Cambodian Department of Fisheries (currently called the Fisheries Administration [FiA]) and financially supported by the DANIDA (Danish International Development Agency) (Ly and VanZalinge, 1998).

For catch assessment data of fishing lot, fish were collected from thirty-three fishing lots around TSL (Figure 2.1). Noticed that fishing lots are good fishing area demarcated by the government and give to the private sectors or fishers for commercial fisheries operation (Ly and VanZalinge, 1998). At each lot, the sampling was conducted during weekly sampling of thirty-three fishing lots around the lake from October to May each year from 1994-2000. The sampling method was designed and approved by the Department of Fisheries with technical support from MRC experts. At each lot, samplings were conducted by the provincial fisheries scientists and supervised by central fisheries scientists from the Cambodian Department of Fisheries. Herein, data collectors were trained in the basic concepts of sampling, identification and data record. With the heterogeneity and complexity of habitat in the fishing lot, many types of fishing gears were applied according to the specific habitat characteristic. For instance, the river barrages with U-shaped bag-nets were used for riverine fishing lots, and arrow-shaped bamboo fence traps for the lake floodplain fishing lots to maximise the catches. The catch assessment attempted to estimate the maximum catches within each fishing lot. Fish were identified to species and identification was based on the consultation with MRC experts following the keys in (Rainboth, 1996). Complete details on the fish sampling techniques and the catch assessment data are available in Ly & VanZalinge (1998). This data was used to study the spatio-temporal changes in the fish assemblage (chapter III) and the influence of the environmental factors on the distribution of fish species (chapter IV).

For catch assessment data of mobile fishing gear, the fish biomass data were monthly collected from TSL and TSR from 1994 to 2000. Here, the mobile fishing gear refers to the fishing that commonly used at the small-scale fishing at the family level (Deap, Degen, & VanZalinge, 2003). The sampling method was designed and approved by the Department of Fisheries with technical support from MRC's expert. The data were collected by local fishermen, and they were trained in the basic concepts of gears, specific terminology, technical drawing and reporting (Deap et al., 2003). Samplings were conducted on a daily basis from 1995 to June 2000 around TSL. In this study, we selected the fish data collected from the gill net with mesh size of <7 cm. Identification was based on the common names combined with a review of previous studies and consultation with MRC's experts; further, identification followed the keys in Rainboth (1996). This dataset was used to compare overall fisheries and fish community and structure before and after fishing lot abolishment (chapter VI).

For catch monitoring survey data, time series data were daily collected from January 2012 to December 2015 at three sampling sites in the TSE (as indicated in red circle dot), one of which is located in the northern TSL (hereafter abbreviated to "NL"), one in the southern TSL (abbreviated to "SL"), and the other one in the outlet river (abbreviated to "OR") of TSR

(Figure 2.1). The catch monitoring approach follows the MRC's regional monitoring method applied in the Lower Mekong Basin (MRC, 2008; P.B. Ngor, Theng, Phem, & So, 2014). The catch monitoring approach follows the MRC's regional monitoring method applied in the Lower Mekong Basin (MRC, 2008; P.B. Ngor et al., 2014). At each sampling site, nylon gillnets with 2 to 6.5 cm mesh sizes were used to capture as many fish species as possible (P.B. Ngor et al., 2014). Gillnets have been considered the most common and popular fishing gear used in the TSE and are suitable to be applied in different habitat types (MRC, 2008). The gillnets used had a length of 400 m ± 100 m (P.B. Ngor et al., 2014). The variation in the gillnet length is due to the habitat availability (e.g., inundated forest, open water of TSL, river, streams, and creeks), which varies according to the annual hydrological cycle. Fishes were identified to the species level following the identification guide by Rainboth (1996) and enumerated and recorded in a logbook. The logbooks were then collected from fishers on a quarterly basis and cross-checked by research specialists. Unidentified species were later identified by an expert taxonomist in the laboratory. This data was used for chapter V and VI.

Moreover, the morphological traits and trophic level position of 55 fish species were derived from the FishBase (Froese & Pauly., 2017). The information about biological traits of fish species (i.e. migration, the position of water column) was reviewed and derived from (Froese & Pauly, 2017; Peng Bun Ngor, Legendre, Oberdorff, & Lek, 2018; Poulsen et al., 2004). The migration and water column were orderly coded according to the characteristics. These attribute information were used for chapter VI.

Regarding the environmental parameters, the local habitat, climatic feature and water level were used. The surface area of land-cover types of each fishing lot was calculated from the Cambodian Land Use 1993 map that best fits the fish catch period (1994-2000)(used for chapter IV). Three land-cover types were considered: flooded forest (FF), open water (OW), and agricultural field (AF). Land cover was expressed as a percentage of coverage of each fishing lot. Additionally, nineteen bioclimatic variables were extracted from the 1-km^2-

resolution WorldClim layers for the period 1950-2000 (Hijmans et al. 2005). Despite the limited spatial range of this study (approximately 200 x 200 km), climate variables demonstrated substantial variations across the lake; thus, these variables are relevant for analysing the correlations between fish biomass and climate features (chapter V). Moreover, the water level data measured from site WS1 was analysed with the fish data collected from the NL and SL sites, whereas that from WS2 was analysed with the fish data collected from the OR site (in chapter VI).

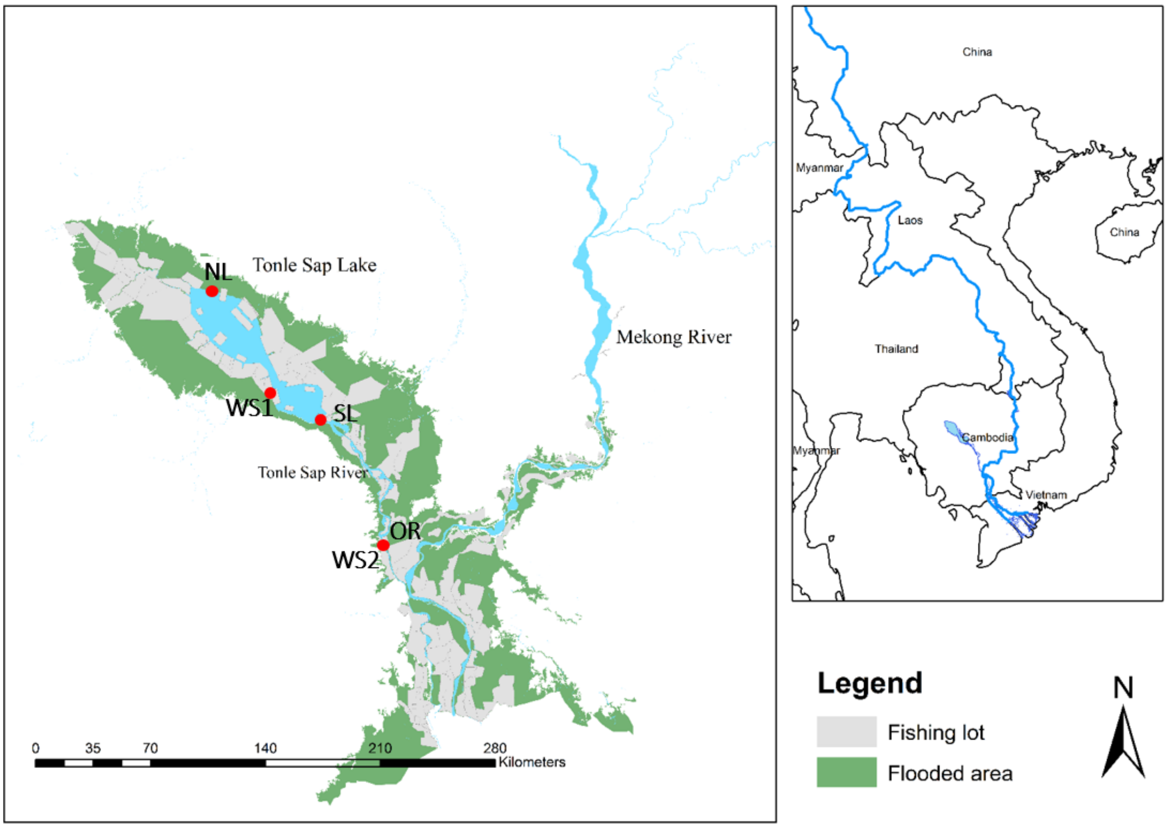

Figure 2.1 Map showing the fishing lots surrounding the floodplain of Tonle Sap Lake in Cambodia. “Wetland” refers to the flooded area during the wet season. The first letter in the code represents the province name: B (Battambang), S (Siem Reap), P (Pursat) and T (Kampong Thom) and is followed by the lot numbers in each province. Sampling sites (red dots) of the study area: NL, the northern TSL; SL: the southern TSL; OR, the outlet river of Tonle Sap River. WS1: water measurement station (red dot with a cross), WS2: the water measurement station situated at the same location as the “OR” fish sampling site.

2.3 Statistical analyses

2.3.1 Community clustering

Hierarchical clustering based on the Euclidian dissymmetry distance on the NMDS scores with Ward linkage method allowed to identify the fish assemblages (in chapter III only). Hierarchical cluster analysis in combination with multiscale bootstrapping generated probabilities was applied to investigate consistent spatial distribution patterns within the eight species (in article 3). For this study, the Bray–Curtis dissimilarity measures were compared for each grouping of the analysis (Bray & Curtis, 1957). For each measure of dissimilarity, the distance was calculated with Ward's linkage to compare the measures of dissimilarity for consistent grouping.

2.3.2 Comparative analysis

A Mann-Whitney test was used to test for significant differences between the two groups. Here, we used Mann-Whitney to test for significant difference in fish yields and species richness between the two assemblages (chapter III).

2.3.3 Predictive models

Linear models were used to detect temporal trends in yields of the most dominant fish species, the total fish yields of TSL over the past six years, and the relationship between fish yields and coefficient of variation in the water level (chapter III).

Moreover, generalised linear models (GLM) were used to investigate the relationships between the spatial distribution of each species and the local habitat and regional climatic factors (article 3). GLM is an extension of linear regression. Before building the GLM models, the explanatory variables of the local habitat and regional climatic variables were to normalised get the same scale of the variable. The response was the mean value of the annual biomass of each species. Step-wise approach with both backward and forward selection was applied to remove unimportant variables.

2.3.4 Multivariate analyses

Non-metric multidimensional scaling (NMDS) with Bray–Curtis similarities distance (Bray & Curtis, 1957) was performed to visualise sample of fish in a two-dimensional plot. For instance, NMDS was performed to illustrate the spatio-temporal change in the fish community (in chapter III) and a change in fish community composition between the BFA and AFA (in chapter VI), utilising the "vegan" package in *R* (Oksanen et al., 2015). The NMDS is a rank based method attempting to represent the pairwise dissimilarity between sampling units in a two-dimensional space. Stress ranges from 0 to 1 and any value less than 0.15 indicates a good fit (Clarke, 1993). In addition, three things the size of the convex hull, position (centroid) and structure were applied to test.

A principal component analysis (PCA) was performed to relate the status of fish species (i.e. decreasing, increasing, and non-change) to the morphological and biological traits (in chapter VI). The analysis allows us to say something about the changes that were related to some specific groups or functional traits and size class of fish species.

Analysis of similarity (ANOSIM, Clarke, 1993) was also used to test for significant difference in fish community composition between the two periods: before and after fishing lot abolishment. ANOSIM is a nonparametric multivariate procedure broadly analogous to analysis of variance (ANOVA) that has been widely used for testing whether or not groups of sites are statistically different with respect to their relative similarities in the community composition (Clarke, 1993). ANOSIM was conducted on Bray–Curtis dissimilarities matrix calculated among samples (Oksanen et al., 2015). The significance of the ANOSIM results was assessed according to the statistic-*R* value (correlation coefficients between groups) which provides a measure of effect size and a *P*-value (significant difference between groups) of the statistical significance which determined whether or not the result was likely due to a result of chance (Clarke, 1993). A statistic-*R* that ranges from -1 to +1, and that is based on the rank similarities of samples within versus among a priori groups. A large *R*-value (close to 1) is indicative of complete separation between groups, while a small value (close to 0) implies little or no separation, and *R*-values below zero suggest that dissimilarities are greater within groups than between groups (Clarke & Warwick, 2001). We conducted 999 random permutations to assess the statistical significance of *R* (in chapter VI).

Then, we further applied the similarity percentages (SIMPER, Clarke, 1993) procedure to assess which species was the most important contribution to the dissimilarity of the composition between the BFA and AFA. SIMPER identifies which fish species made the highest contribution to be different between the two groups in a Bray-Curtis dissimilarity matrix (Oksanen et al., 2015). The contribution of each species to Bray-Curtis measurement was calculated after root-root transformation, and then the species were ranked in two separated groups, percentage, and cumulative percentage (Clarke & Warwick, 2001). SIMPER produced average contribution from taxa to overall dissimilarity between two groups (i.e. a & b) (average), standard deviation of contribution (sd), ratio average to sd ratio (ratio), average abundances per group (av.a & av.b), and ordered cumulative contribution (cum) (Clarke & Warwick, 2001; Oksanen et al., 2015). We conducted 99 random permutations to assess the statistical significance of *R* (in chapter VI).

2.3.5 Time-series analyses

Cross-wavelet transform (CWT) was used to analyse occurrence correlation and recursivity (e.g., a recursive occurrence at an interval over a particular timescale) between the two time-series data of *H. lobatus* abundance (x) and *H. siamensis* abundance (y). The CWT analysis will also allow the determination of whether *H. lobatus* occurrence leads/or lags *H. siamensis* occurrence. Here, the 95% confidence interval was selected for the wavelet power as the significance criterion. Practically, the ability of the CWP to analyse coherency enabled us to highlight the co-occurrence and synchronisation periodicity of the two species. The CCFs were then employed to determine a period (e.g., how many weeks) when *H. lobatus* synchronisation and peak abundance leads/lags those of *H. siamensis*.

To investigate how periods of synchronisation and peak abundance vary across the studied sites, cross-correlation function (CCFs) were used to determine the time-lagged relationship of the abundance of each species between paired sites, e.g., *H. lobatus* abundance in NL (*x*) and SL (*y*). The results of this analysis were then used to identify the movement patterns of each species (e.g., a period it takes to migrate from NL to SL).

Finally, the CCFs were also employed to examine the time-lagged relationship between the water levels and the abundance of each species at each site. In this analysis, the water level data measured from site WS1 was analysed with the fish data collected from the NL and SL sites, whereas that from WS2 was analysed with the fish data collected from the OR site. By the end of this analysis, we were able to estimate the movement periods of both species, e.g., how many weeks the peak water level leads/lags the peak abundance of each species. Here, we selected the lag containing the highest correlation coefficients between the two time series as the time lag. The CCF allowed us to determine the link between the flow pulse and fish abundance and identify the time lag between the water level peak and fish synchronisation. The CCF, thus, enables the determination of the role of flood pulse in temporal dynamics of fish species in the TSE to be made.

All statistical analyses were performed using *R* program v.3.3.3 for Windows statistical software package (http://www.r-project.org)(R Core Team, 2017).

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Chapter III: Spatial and temporal changes in fish yields and fish communities in the largest tropical floodplain lake in Asia

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Abstract

Although Tonle Sap Lake (TSL) is the largest natural inland lake in Southeast Asia, little is known about the spatio-temporal patterns of its composition and yields. The present paper aimed to investigate the temporal change of yields of the most dominant fish species and to evaluate the spatio-temporal changes in the fish community and the indicator species of assemblages. Fish catch data were collected from thirty-three fishing lots around the lake during the open season from October to May each year between 1994 and 2000. The fish yields were dominated by few commercial fish species: *Channa micropeltes*, *Pangasianodon hypophthalmus*, *Channa striata*, *Cyclocheilichthys enoplos*, *Henicorhynchus* spp., *Barbonymus gonionotus*, *Micronema* spp. and *Trichopodus microlepis*. The standard linear regression coefficients of the fish yields versus year were negative for all these commercial species except *Trichopodus microlepis.* Moreover, the total fish yields of the lake were temporally declined (standard coefficient=-2.410, adjusted r^2=0.272). Nonmetric multidimensional scaling (NMDS) of the fish assemblage data showed a clear opposition between northern assemblage and southern assemblage along the first axis, and the temporal pattern of the samples from 1994-1999 was explained by the second axis. The fish species assemblage from earlier years (1994 and 1995) was characterised by the abundance of all functional groups of black-white-grey fish species, but more recent years (1996 to 1999) were linked to white and grey functional groups, which was explained by a decrease in many black fishes.

KEYWORDS: fishing lots, Tonle Sap Lake, indicative species, inland fisheries, fish yields

3.1 Introduction

The fish resource provides one of the primary sources of animal protein consumed worldwide, and income, especially for people in developing countries (Allan et al. 2005) (Welcomme et al. 2010). In developing countries, fish protein sources are mainly derived from the harvest of natural fish stocks, while those in developed countries are produced by recreational fisheries or aquaculture (Allan et al. 2005; Welcomme et al. 2010). Poor people in developing countries depend on inland fisheries sources more than marine sources (McIntyre et al. 2016). Harvesting natural fish stock has rapidly increased in developing countries, but decreased in developed countries (Allan et al. 2005). Overall, the global inland fish catch is reported to be increased because of an increase in the exploitation in Asia and Africa (FAO 2014) and an increase in human population density (McIntyre et al. 2016).

The Mekong River Basin lies within the Indo-Burma Biodiversity Hotspot and is the second most diverse river system in the world (Ziv et al. 2012). It is also one of the most intensive and productive inland fisheries in the world, and the Mekong River has the second highest level of river fish biodiversity after the Amazon River (Baran et al. 2013a). It provides food sources for millions of people in the region (Baran & Myschowoda 2008; Baran et al. 2013a). The Mekong capture fisheries made up two third of the inland fish production in the basin (Baran et al. 2007). The Mekong fisheries are not only important for capture fisheries, but also the economic value (Baran and Myschowoda, 2008).

Tonle Sap Lake (TSL) is a major natural reservoir in the Mekong River, and it is the largest natural inland lake in Southeast Asia (Chea et al. 2016b) and a biodiversity hotspot and a World Heritage Biosphere Reserve (Lamberts 2006). After the African Great Lakes, TSL has the second highest freshwater fish biodiversity in the world (Baran et al. 2013a), and it is one of the world's most productive fisheries and fish species-rich lakes (Arias et al. 2013). Furthermore, TSL plays a crucial role in providing fish products and protein to nearly two million people in the region (Holtgrieve et al. 2013), especially the communities living in the

Tonle Sap System that depend on natural resources of the lake (Lamberts 2006; Kimmu & Sarkkula 2008). Approximately half of Cambodian's population obtain benefits both directly and indirectly from TSL's fisheries resources (Keskinen et al. 2005). The lake is not only important for ecology, but also for the socio-economic and livelihood (Lamberts 2006).

In the Mekong River, intensive exploitation has not only been threatening large fishes, but also the overall catch and freshwater biodiversity in the region (Allan et al. 2005; Kano et al. 2013). Moreover, the overfishing in the Mekong River threaten the capture fisheries in TSL because of the connection between the Mekong River and TSL via the Tonle Sap River (TSR)(Allan et al. 2005). The overall catch has increased twice in the last decade (Baran et al. 2001), which has resulted from an increase in fishing activities, fishing effort and the use of modern and illegal fishing practice (Allan et al. 2005). Due to intensive fishing, the large migratory fishes (e.g., catfish and carp) have been reported to be declined, and the overall catch is dominated by small cyprinid fishes (i.e., *Henicorhynchus* spp.), which accounted for forty percent of the total captures (Allan et al. 2005).

The Tonle Sap fisheries are indiscriminate in that they exploit all types and size class of fish (McCann et al. 2015a). Indiscriminate fishing is common in developing countries where fish provide the main source of dietary protein. Despites the intense pressure of fishing, fisheries of the Mekong River and TSL are still productive. The short reproductive cycle of small fishes is believed to be the important factor influencing the fish production of the lake (Lamberts 2006). The life-history trait is the ecological driver that affects the population response to fishing pressure (Hsieh et al. 2006). Moreover, the health of the Mekong River and TSL system remain in good condition because the water regime and water quality are not much changed while the dam on the main Mekong River is not yet operated.

Ichthyological information for TSL still lacks as little research has been conducted. Surveys of the fish fauna in TSL are needed to better understand the fisheries, the fish community, and ecosystem function. By using annual fish catch data collected at thirty-three fishing lots from 1994 to 2000, the objectives of the present work were (i) to investigate the temporal change of yields of the most dominant species and (ii) to evaluate the spatio-temporal changes in the fish community and the indicator species of assemblages.

3.2 Materials and methods

3.2.1 Study area

Studies were carried out in TSL located in the central of Cambodia. TSL is connected to the Mekong River by the TSR (Arias et al. 2013), and the water flows in the TSR contain two directions, namely, inflow and outflow. From May to October, water flows into the lake through the TSR due to a large volume of water from tropical monsoon rainfall combined with snowmelt from the Tibetan Plateau (MRC 2005). In contrast, the water flows out from the lake into the Mekong River from November to April as the water level in the river decreases (Campbell et al. 2006b). Reverse flow resulted from the alteration of the water level between seasons (MRC 2005). Seasonal flooding benefits primary and secondary production and the surface area of the lake also varies between seasons as a result of alterations to the water regime (Holtgrieve et al., 2013).

3.2.2 Data collection

TSL freshwater fish catch data were collected by the Mekong River Commission in collaboration with the Cambodian Inland Fisheries Administration and financially supported by DANIDA (Danish International Development Agency) (Ly and VanZalinge, 1998). Data were collected from thirty-three fishing lots around the lake (Figure 3.1). The sampling method was designed and approved by Department of Fisheries with technical supports from MRC's experts. At each fishing lot, samplings were conducted on a weekly basis (four times per month) from October 1994 to May 2000 by the provincial fisheries researchers and supervised by central fisheries researchers from the Cambodian Department of Fisheries. Data collectors were trained in the basic concepts of sampling, identification and data record. The operation of the fishing lot was performed using river barrages with U-shaped bag-nets for riverine fishing lots and arrow-shaped bamboo fence traps for the lake floodplain fishing lots. Sampling and other works for species composition were followed as the method used in the stationary trawl (*Dai*) fisheries (see in Halls et al., 2013). In each sample, if the catch per unit effort (CPUE) per lift is less than 10kg, fish were separated and identified. Fish were identified to species, except for nine taxa that were identified to genus for certain genera covering several species. Identification was based on the consultation with MRC experts following the keys in (Rainboth, 1996). Full details on the fish sampling technique are available in Ly and VanZalinge (1998). A dataset of fish yields ($kg.ha^{-1}.y^{-1}$), which were measured as a function of the estimated catch per fishing lot per season (kg) divided by fishing lot area (ha) for a unit of time (year), was utilised for analyses. The water level was measured in the Tonle Sap River (Prek Kdam).

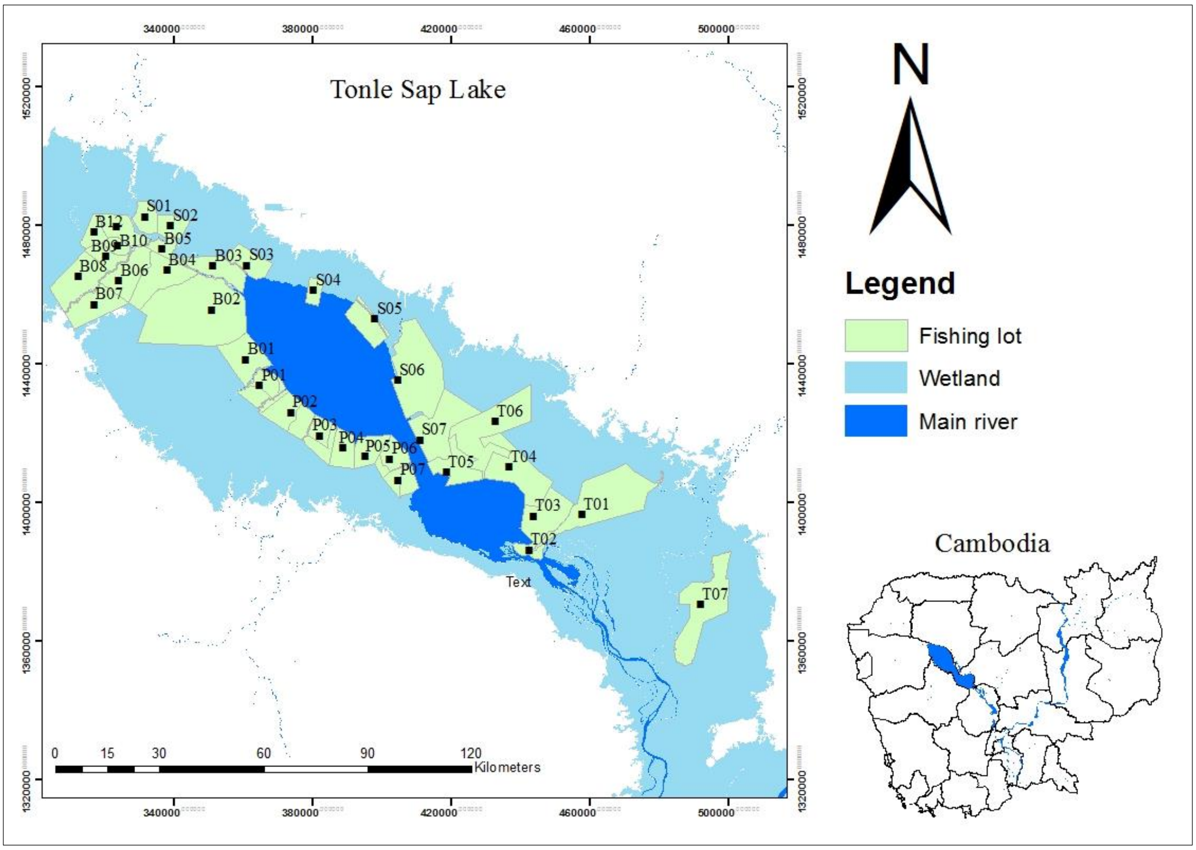

Figure 3.1 Map showing the fishing lots surrounding the floodplain of Tonle Sap Lake in Cambodia. "Wetland" refers to the flooded area during the wet season. The first letter in the

code represents the province name: B (Battambang), S (Siem Reap), P (Pursat) and T (Kampong Thom) and is followed by the lot numbers in each province.

3.2.3 Statistical analyses

A dot plot was used to create a rank-yields plot of fishes. Linear models were used to detect temporal trends in yields of the most dominant fish species, the total fish yields of the lake over the past six years, and the relationship between fish yields and coefficient of variation in the water level.

Non-metric multidimensional scaling (NMDS) ordination with the Bray-Curtis dissimilarity was used to reveal the spatio-temporal changes in the fish community by using the "metaMDS()" function from the vegan R-package (Oksanen et al., 2015). Hierarchical clustering based on the Euclidian dissymmetry distance on the NMDS scores with Ward linkage method allowed to identify the fish assemblages. Then, the cluster values were mapped using GIS to display the clustering results and the spatial distribution of fish yields around TSL. A Mann-Whitney test was used to test for significant differences in fish yields and species richness between assemblages. Indicative species of assemblages were also defined using a multi-level pattern analysis index (R-package indicspecies, De Cáceres and Legendre, 2009).

All statistical analyses were performed using the *R* program v.3.1.2 for Windows statistical software package (R Core Team 2014).

3.3 Results

3.3.1 Temporal trends of main commercial fishes, TSL's species richness, and fish yields

The yields–species rank plot of fishes caught by fishing lot revealed eight dominant species (Figure 3.2a) that accounted for 58% of the overall fish yields from TSL: *Channa* *micropeltes*, *Pangasianodon hypophthalmus*, *Channa striata*, *Cyclocheilichthys enoplos*, *Henicorhynchus* spp., *Barbonymus gonionotus*, *Micronema* spp. and *Trichopodus microlepis*. The standardised linear regression coefficients of fish yields versus year were negative (indicating a temporal decreasing trend in fish yields) for all species except *Trichopodus microlepis* (Table 3.1). Table 3.1 and Figure 3.2b showed the significant decreasing trends in 3 species: *Channa micropeltes*, *Henicorhynchus* spp., and *Micronema* spp. (negative standardised regression coefficient) and significantly increasing trend for *Trichopodus microlepis* (positive standardised regression coefficient). Moreover, the linear model showed that the total fish yields of TSL were decreased between years (standard coefficient = -2.410, adjusted r^2= 0.272, Figure 3.2c).

Table 3.1 Results of the linear regression showing temporal changes in the yields of eight dominant fishes from 1994 to 2000 with the standard linear regression coefficient, the coefficient of determination and the p-values.

Taxa	Standard coefficient	Adjusted r^2	*p*-value
Channa micropeltes	-6.074	0.877	0.003
Pangasianodon hypophthalmus	-1.838	0.322	0.139
Channa striata	-0.997	0.198	0.375
Cyclocheilichthys enoplos	-0.658	0.097	0.546
Henicorhynchus spp.	-6.874	0.902	0.002
Barbonymus gonionotus	-0.559	0.072	0.606
Micronema spp.	-4.578	0.799	0.010
Trichopodus microlepis	3.396	0.678	0.027

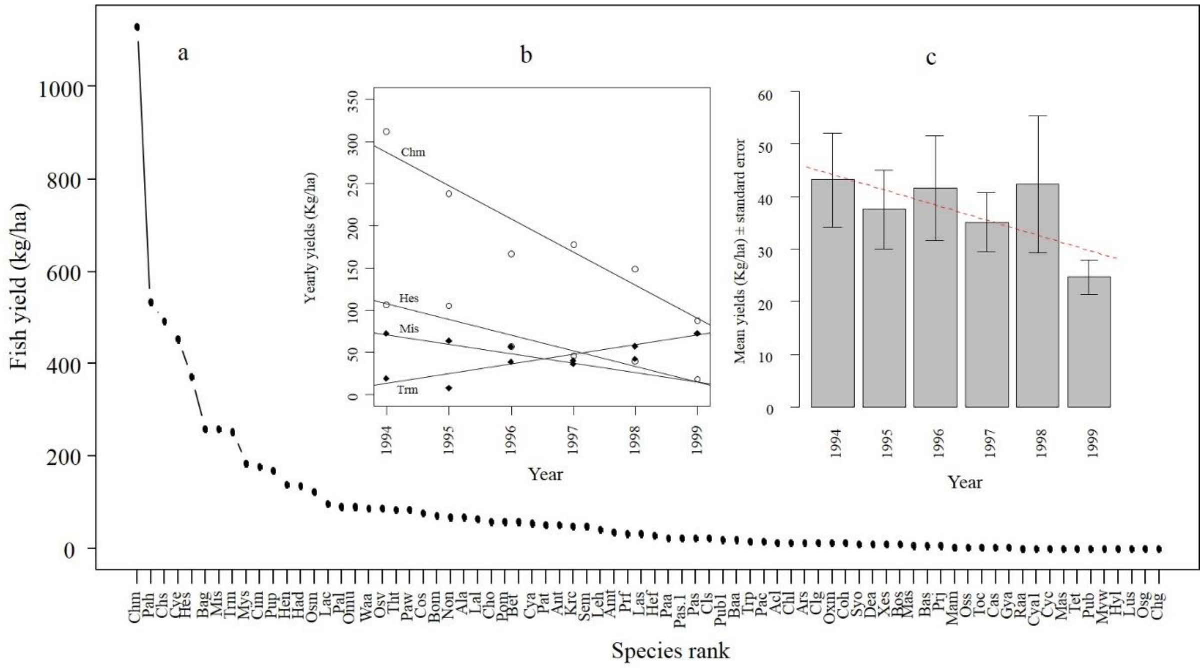

Figure 3.2 (a) Decreasing rank-yields plot of fish in Tonle Sap Lake caught by a fishing lot. (b) The significant temporal decrease/increase in the yields of four dominant species fitted by linear models. (c) Mean yields+- standard error showing the temporal change in total fish yields. Abbreviations are as follows: Chm: *Channa micropeltes*, Hes: *Henicorhynchus* spp., Mis: *Micronema* spp. and Trm: *Trichopodus microlepis*.

3.3.2 The fish yields-flood pulse relationship

Figure 3.3 showed that the fish yields of TSL are positively correlated with the water level variations, indicating that the water fluctuation is a key determinant regulating the fish yields of Tonle Sap Lake (adjusted r^2=0.194).

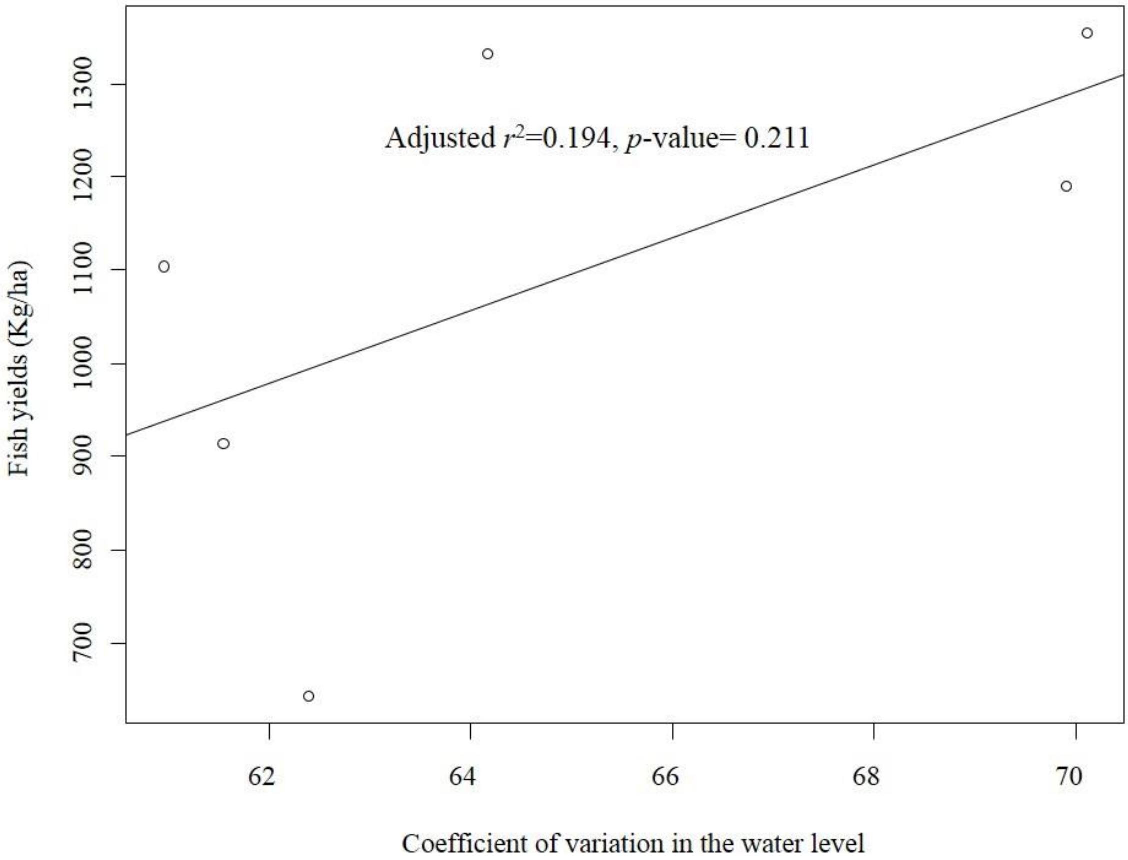

Figure 3.3 Plot showing the correlation between fish yields and the coefficient of variation in the water level.

3.3.3 Spatio-temporal variability in the fish community and its yields

The ichthyofauna was composed of 76 fish species distributed across 28 families and nine orders. The NMDS ordination of the fish yields data provided a stress value of 0.154, indicating a good ordination pattern. Hierarchical clustering of the NMDS scores revealed two assemblages: northern assemblage (AN), mostly located in the north of TSL, and southern assemblage (AS) primarily found in the sites of the south (Figure 3.4b). The NMDS ordination map revealed opposition between these two fish assemblages along the first axis of the ordination plane (Figure 3.4a). The black fishes were mostly associated with AN, except *Channa micropeltes*, *Channa lucius* and *Macrognathus siamensis* which were linked to AS.

White and grey fishes had wide range distribution covering both AN and AS and the estuarine fishes were only present in AS. Additionally, AN was primarily composed of the grey fish *Cyclocheilichthys apogon*, and AS was mostly consisting of the estuarine fish *Hyporhamphus limbatus*, the blackfish *Macrognathus siamensis*, the grey fish *Mystus wolffii* and four white fishes: *Devario aequipinnatus*, *Clupeichthys goniognathus*, *Botia* spp. and *Labiobarbus siamensis* (Figure 3.4a). Also, the multi-level pattern analysis index revealed 36 indicative species for both assemblages: 3 in AN and 33 in AS. The indicator species for AN were gourami, *Trichopodus microlepis*, the climbing perch, *Anabas testudineus*, and *Trichopodus pectoralis*, all of which were black fishes. AS comprised 33 indicative species that were dominated by 19 species of white fishes followed by grey, estuarine and black fishes with 7, 5 and 2 species, respectively (see details in Table 3.2). Moreover, the AS fish yields and species richness were significantly higher than those of AN (Mann-Whitney test, W=1032, $p<0.001$, Figure 3.4c and W=920, $p<0.001$, Figure 3.4d, respectively).

Figure 3.5a revealed a temporal change in the samples along the second axis from 1994-1999. Fish species from earlier years (1994 and 1995) were correlated with the negative values of axis 2 and determined by the abundance of all black-white-grey fish functional groups. However, the species from the more recent years (1996 to 1999) are in the positive part of axis 2 and linked to white and grey functional group species (Figure 3.5a). The distribution patterns of four fishing lots, namely S01, S02, S03, and P01, changed from AS to AN (Figure 3.5b, 3.5c, and 3.5d). These shifts occurred in the fishing lots located along the border between these two assemblages.

Table 3.2 The summary of the indicator species in each assemblage with the statistical and p-values.

Northern assemblage (AN): 3 species			
Species	Functional group	Statistic-value	*p*-value
Trichopodus microlepis	Black	0.924	0.005
Anabas testudineus	Black	0.891	0.005
Trichopodus pectoralis	Black	0.692	0.005
Southern assemblage (AS): 33 species			
	Functional group	Statistic-value	*p*-value
Parambassis wolffii	grey	0.927	0.005
Pangasianodon hypophthalmus	white	0.917	0.005
Chitala ornata	grey	0.906	0.005
Cirrhinus microlepis	white	0.901	0.005
Boesemania microlepis	grey	0.899	0.005
Wallago attu	white	0.897	0.005
Belodontichthys truncatus	white	0.892	0.005
Micronema spp.	grey	0.88	0.005
Labeo chrysophekadion	grey	0.864	0.005
Setipinna melanochir	estuarine	0.859	0.005
Polynemus multifilis	estuarine	0.825	0.005
Pangasius larnaudii	white	0.815	0.005
Albulichthys albuloides	white	0.786	0.005

Amblyrhynchichthys truncates	white	0.751	0.005
Coilia spp.	estuarine	0.722	0.005
Leptobarbus rubripinna	white	0.691	0.005
Probarbus jullieni	white	0.676	0.005
Arius spp.	white	0.668	0.005
Pangasius spp.	white	0.66	0.005
Hemibagrus filamentus	white	0.632	0.005
Cosmochilus harmandi	white	0.601	0.005
Parambassis apogonoides	grey	0.574	0.005
Achiroides leucorhynchos	white	0.495	0.005
Labiobarbus siamensis	white	0.473	0.005
Channa lucius	black	0.404	0.005
Catlocarpio siamensis	white	0.399	0.005
Mastacembelus spp.	black	0.393	0.005
Macrochirichthys macrochirus	white	0.386	0.005
Systomus rubripinnis	grey	0.385	0.01
Bagarius spp.	white	0.372	0.005
Botia spp.	white	0.372	0.005
Toxotes chatareus	estuarine	0.357	0.005
Tenualosa thibaudeaui	estuarine	0.326	0.005

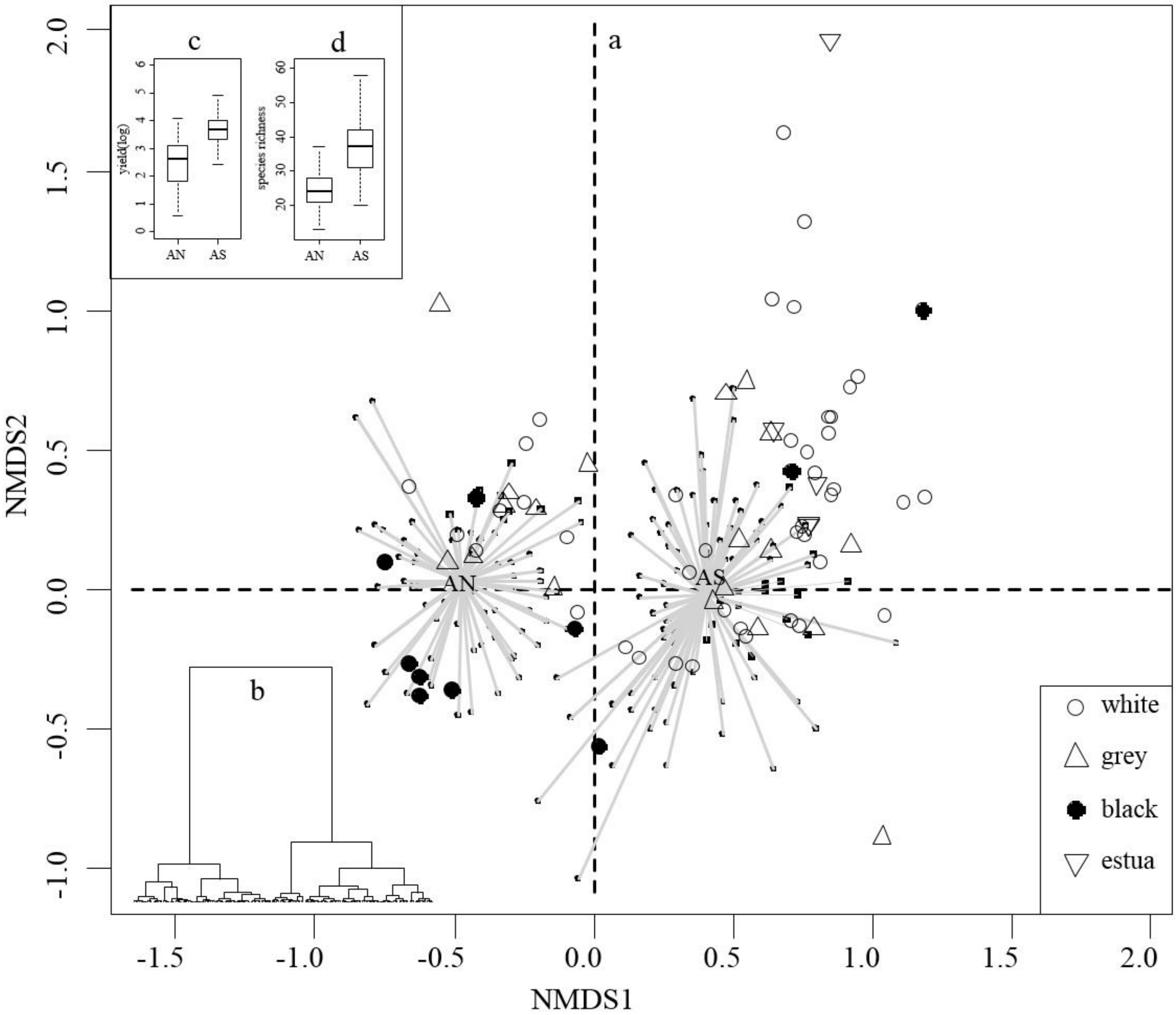

Figure 3.4 (a) Non-metric multidimensional scaling (NMDS) ordination of 172 samples in Tonle Sap Lake showing the spatial distribution of samples and species in two assemblages: AN and AS. (b) Hierarchical clustering dendrogram of the NMDS scores using the Euclidian similarity matrix and Ward agglomeration method. (c) Boxplot representing the median (----) and 25th and 75th percentiles of fish yields (kg/ha/year) at logarithm scale in both assemblages and (d) Boxplot representing the median (----) and 25th and 75th percentiles of species richness.

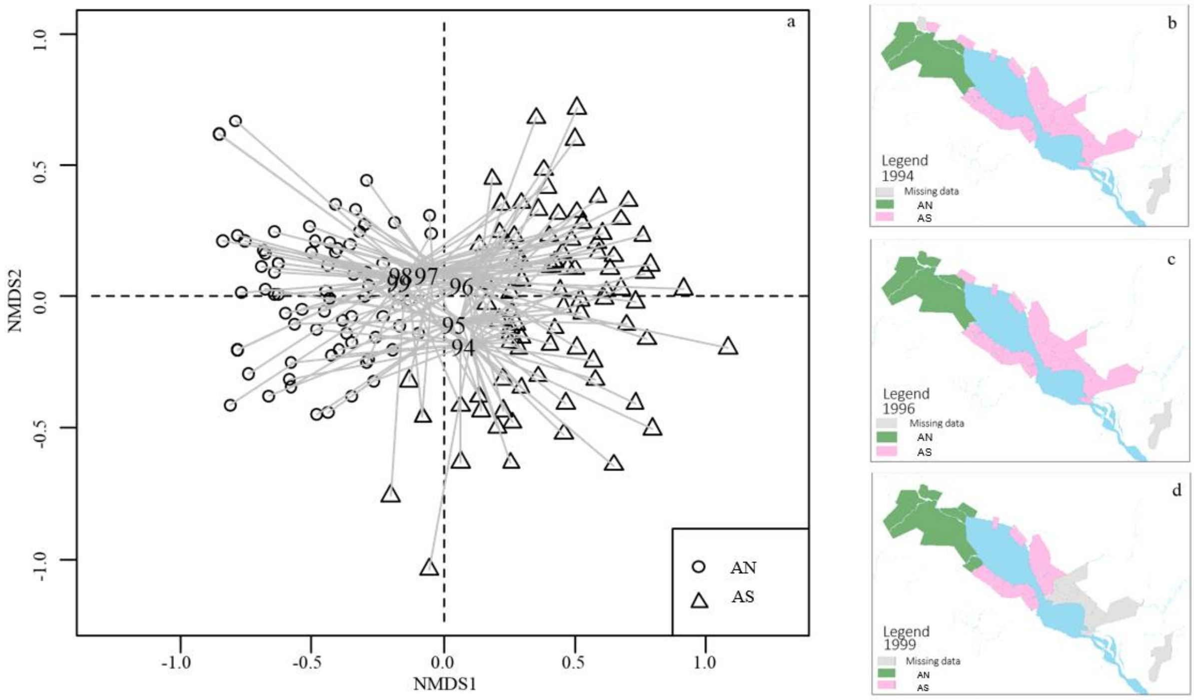

Figure 3.5 (a) The NMDS ordination map showing the temporal distribution pattern of samples from 1994 to 1999. (b) A map of Tonle Sap Lake showing the distribution of samples based on the assemblage identified by hierarchical clustering analysis in 1994, (c) in 1996 and (d) in1999. The green area represents AN, and the pink represents AS; grey indicates missing data.

3.4 Discussion

3.4.1 Temporal trends in fish yields of the main commercial fishes and total fish yields of the lake

The results suggested that the lake was dominated by few commercial fish species. Fish community composition follows the rule that a few species are highly abundant, many species are moderately abundant, and the remaining few species are rare (Welcomme 1999). Our results were consistent with the finding of the previous study which observed that few common species dominate TSL fisheries (Sverdrup-Jensen 2002). *Channa striata* were found to be the most common snakehead in Cambodia (Rainboth 1996) and distributed throughout TSL (Chheng et al. 2005). *Channa micropeltes* was found to be the second most dominant species in Cambodia (Chheng et al. 2005), and it is one of the ten most important fishes in TSL (Enomoto et al. 2011). *Henicorhynchus* spp. were the most important group regarding fisheries output for the Lower Mekong Basin (Poulsen et al. 2002b), and they accounted for fifty percent of the total annual catch of the *Dai* fisheries in the Tonle Sap River (Halls et al. 2013). Additionally, Lim et al. (1999) explained that TSL floodplain and the inundated forest were of significant importance for supporting large fish species because these species use this area for reproduction, feeding and spawning activities. Among the eight most important fishes, six species (except *Channa micropeltes* and *Channa striata*) were herbivorous, and this was the most dominant group in the lake.

The results contributed to provide evidence that the yields of some dominant fishes and the total fish yields have declined. Here, we discuss the fishing pressure as treatment effect on the decrease in the yields of the main commercial fishes. Fishing has a direct impact on the decline in fish population (Pauly et al. 2002; Hsieh et al. 2006). Overharvesting fish stock remains an intense pressure and result in the fisheries resources declined (Cooke & Cowx 2004; Anderson et al. 2008; McIntyre et al. 2016). Furthermore, besides the large commercial fishing (i.e., fishing lot operation and *Dai* fisheries), the mobile gear fishing at the family level is also presented in TSL (Bonheur and Lane, 2002). The large fish species are the primary target of catching by local fishers due to their high economic price in the market (Enomoto et al. 2011). At first, when the ecosystem is healthy, the fishermen prefer to harvest the large fishes. It is called "fishing down the food web" phenomenon (Pauly et al. 1998). Later, fishers attempt to catch all kind and size class of fish. The catch in the manner that all fish species and size class across the food webs were exploited is called the indiscriminate fishing (McCann et al. 2015a). Fishing has a direct influence on alteration of the fisheries production, fish composition and community, and ecosystem functioning (Anderson et al. 2008). Lambert (2006) said that, in TSL, due to the intensive pressure of fishing, the decline of the large fish species in the catch was found, and the catch was dominated by the small fishes with the short reproductive cycle. Fishing could alter the fish community and caused an increase in abundance or biomass of small fishes with rapid population growth (McCann et al. 2015a).

The yields of *Trichopodus microlepis* increased in the recent years while the yields of the carnivorous *Channa micropeltes* declined. In the ecosystem, *Channa micropeltes* is the top predator, and *Trichopodus microlepis* serve as prey. An increase in *Trichopodus microlepis* yields could be a result of a decrease in predatory fishes, especially *Channa micropeltes.* The loss of predators could alter the community structure so that small prey fish became dominant. This result is consistent with those of previous studies stating that TSL fisheries are now dominated by small fishes while the large fishes have declined (Enomoto et al. 2011). Moreover, catch of opportunistic species or small white fishes in the Mekong fishery was recorded (Cooperman et al. 2012). For instance, the catch of *Henicorhynchus* spp. represented fifty percent of the *Dai* fishery in the Tonle Sap River (Halls et al. 2013).

Among the eight most dominant species, *Pangasianodon hypophthalmus, Cyclocheilichthys enoplos*, *Henicorhynchus* spp., and *Barbonymus gonionotus* undertake the long migrations within Lower Mekong Basin (Rainboth 1996; Zalinge et al. 2003). Moreover, Halls et al. (2013) stated that these migratory species are challenged by the barrage system of river-spanning fences for *Dai* fishery in the Tonle Sap River. Moreover, Enomoto et al. (2011) illustrated that *Channa micropeltes* are caught to be raised in the aquaculture farm around TSL.

The results suggested that the total fish yields of the lake were temporally decreased. The sustainable fisheries have rarely been found (Jackson et al. 2001b). Additionally, (Allan et al. 2005) illustrated that the catch per fisherman, in the Tonle Sap System, had declined fifty percent. Moreover, overfishing in inland waters is occurring (Allan et al. 2005) and exploitation of fish stock appeard to have an adverse impact on the world's inland aquatic resource (McIntyre et al. 2007, 2016; Welcomme et al. 2010). In TSL, the overfishing was deemed to be the major determinant affecting the volume of total fish catch (Lamberts 2006).

3.4.2 Relationship between fish yields and flood pulse

The results suggested that the fish yields are positively correlated with the water level fluctuation. The result is consistent with a previous study stating that the fish catch is positively linked with the flood index in the Cross River floodplain ecosystem, Nigeria (Moses, 1987). The level and duration of flood influenced the breeding, growth, and survival of fish (Welcomme 1999). The seasonal flood pulse appeared to be the key factor affecting the fisheries resources in TSL (Lamberts 2006). Seasonal flooding benefits primary and secondary production (Holtgrieve et al., 2013). Moreover, the fish catch, in the floodplain system, was correlated with the flooding in the previous years (Allan et al. 2005).

3.4.3 Spatial and temporal change in fish communities and its yields

The north of the lake is covered by a wetland area comprising a large flooded forest, a shrub forest and vegetation cover such as water hyacinth (Enomoto et al., 2011). Black fishes are non-migratory, and they inhabit the lakes or swamps during the dry season and migrate to the flooded areas during the wet season (Campbell et al. 2006b). Although AN was mainly composed of grey fish *Cyclocheilichthys apogon*, the important indicator species of the assemblage were *Trichopodus microlepis*, the climbing perch, *Anabas testudineus*, and

Trichopodus pectoralis. These three fishes were black fishes that migrate between the lake and the floodplain (Halls et al., 2013) and they spend most of their lifespans in the flooded forest (Campbell et al. 2006b). As stated above, the northern part of the lake covers includes an area with a large flooded forest containing healthy habitats for these black species. *Trichopodus microlepis* prefer to inhabit the areas containing vegetation cover (Lamberts 2001). Furthermore, the results suggested that estuarine fishes were only present in AS, and the number of indicator species of AS was also higher than those in AN. This high species richness, a large number of indicator species, and large fish yields appeared to be impacted by the hydrological and geographical factors.

Lim et al. (1999) demonstrated that when the water level decreased, the migratory fishes move from the lake to the Mekong River, and they migrate back to the lake at the beginning of the rainy season. The migration of fish appeared to be the main factor that resulted in the high amount of fish captured in the inlet-outlet area of the lake (Enomoto et al., 2011). Therefore, it is logical that this area had a significant number of indicator species and high fish yields. White fishes undergo a long migration from the lake to the tributaries of the Mekong River (Zalinge et al., 2003). Most of the species that live in the Mekong River migrate to the lake during the rainy reason to reproduce; they spawn from May-August, likely move from the floodplain to the river in October, and migrate back in April or May (Lim et al., 1999). This migration occurs during the open fishing season, so migratory species were captured during the study period. The biological effects of streams appeared to be the factor that may influence the spatial change in the fish communities. The watershed for the southern part of the lake is larger than that of the north with a sureface area of 30098 km^2 and 20184 square kilometres, respectively (Nguyen et al., 2008). Furthermore, Vanni et al. (2006) illustrated that the watershed area and the tributaries are the primary sources of the lake's nutrients, which were observed to be the main factors influencing fish production.

3.5 Conclusion

Based on the catch data from the fishing lot from 1994-2000, our study showed that the lake was dominated by few commercial fish species: *Channa micropeltes*, *Pangasianodon hypophthalmus*, *Channa striata*, *Cyclocheilichthys enoplos*, *Henicorhynchus* spp., *Barbonymus gonionotus*, *Micronema* spp. and *Trichopodus microlepis*. All these dominant fishes were temporally declined, except *Trichopodus microlepis*. We noticed that the large fish species were temporally decreased and small fish species increased. Catching the larger fishes should be considered and balanced. Removal of the largest fish species that are the top predators could have a substantial top-down effect on food web dynamics. The lack of consideration of large fish harvesting could have an adverse impact on the fish community and lead unstable population change (Anderson et al., 2008). Additionally, total fish yields of the lake were temporally declined. Balanced harvesting is recommended because it could reduce the ecological effects of fishing on components of the ecosystem. Also, the water fluctuation is a key driver characterising the fish yields of the lake. The results showed the spatial and temporal changes in the fish communities and fish yields present in TSL. Here, the Tonle Sap fish communities are divided into two assemblages: AS and AN. The fish yields, species richness and indicator species of the AS were significantly higher than those of AN. Thus, the AS is the potential area for both yields and species richess where should be considered for the protected area. Indicator species indicated the diversity of other species, taxa or communities within an area. This information is of importance that could be used in making the decision for the particular area protection.

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Chapter IV: Influence of local habitat and regional climatic factors on the distribution of fish species in Tonle Sap Lake

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Abstract

The Tonle Sap Lake is the largest natural lake in Southeast Asia. Its high fish productivity makes it of paramount importance to sustain protein supply for the 15 million Cambodian people. Nevertheless, the ecology and spatial distribution of most fish species within the lake remain poorly known. Here we describe the spatial distribution of the eight most important commercial fish species in the lake and use Generalised Linear Models to correlate environmental descriptors to the biomass of the eight most abundant fish species. Fish species distributions differed between species and were governed by distinct combinations of habitat characteristics and climatic factors, suggesting that flooded forest areas and open waters play a crucial role, whereas agricultural lands do not sustain high fish biomasses. Consequently, some areas consistently host high fish biomasses across years and seasons and we therefore recommend to focus conservation actions to these area that sustain more than 40% of fish biomasses of the Tonle Sap Lake.

KEYWORDS: habitat use, floodplain, snakehead, gourami, migratory fishes, management, floodplain resident

4.1 Introduction

The Mekong River is the largest river in Southeast Asia and covers a drainage area of 795,000 km^2 (MRC, 2005). It lies within the Indo-Burma biodiversity hotspot (Allen, Smith, & Darwall, 2012) and is the second most diverse river system in the world after the Amazon River (Baran, 2005; Brosse et al., 2013). The Mekong River is also one of the most intensive and productive inland fisheries in the world (Baran, 2005) with annual yields of approximately 2.6 million tons (Hortle, 2007), providing food sources and animal protein for 60 million people living in the region (MRC, 2010). A substantial part of the Mekong fishery yields comes from the Tonle Sap Lake (TSL), the largest natural inland lake in Southeast Asia (MRC, 2005). This lake is the world's fourth most productive inland fishery (Baran, 2005) and its fisheries resources represent approximately 60% of Cambodia's total annual production of inland capture fisheries of 767,000 tonnes (Hortle & Bamrungrach, 2015). The TSL, therefore, plays a crucial role in providing fish products and protein to nearly two million people living in around TSL that rely on the fisheries resources as their primary food and economic resources (Ahmed, Hap, Ly, & Tiongco, 1998). Moreover, the TSL fisheries account for 60% of the total protein intake of approximately 15 million Cambodian people (Ahmed et al., 1998; Lieng & Zalinge, 2001). In addition to its crucial role as a protein resource, the TSL also hosts a diverse fish fauna, with 296 fish species (Baran, So, Degen, Chen, & Starr, 2013). The TSL is therefore considered as a biodiversity hotspot (Allen et al., 2012) and has had the status of a UNESCO world heritage biosphere reserve since 1997 (UNESCO, 2018).

Despite the ecological, biological, and economic importance of the TSL, knowledge on fish distribution patterns and determinants within the lake is limited. Previous studies investigated fish spatial distributions in the TSL (Campbell, Poole, Giesen, & Valbo-Jorgensen, 2006; Chan, Ngor, So, & Lek, 2017; Lim, Lek, Touch, Mao, & Chhouk, 1999) and considered stocks of the species (Enomoto et al., 2011; Yen, Sunada, Oishi, Ikejima, & Iwata, 2009). The relationship between environmental factors and the spatial distribution of the fish species has not been investigated to date in the TSL, although recognised as crucial for species management in lakes (Boulangeat, Gravel, & Thuiller, 2012; Olden & Jackson, 2001; Peoples & Frimpong, 2016).

In this study, we present information on the spatial distribution of the eight most abundant species over the entire TSL. Then, we related the distribution of each species to habitat and climate descriptors that are known as being influential on species distributions (Jackson, Peres-Neto, & Olden, 2001; Pont, Hugueny, & Oberdorff, 2005).

4.2 Materials and methods

4.2.1 Data collection

The TSL is located in the central part of Cambodia. It constitutes the largest wetland area in Southeast Asia (Matti Kummu & Sarkkula, 2008; MRC, 2003, 2005; Figure 4.1), and is connected to the Mekong River by the Tonle Sap River (TSR). The TSL area is characterised by a tropical monsoon climate (Arias, Cochrane, Norton, Killeen, & Khon, 2013), with a seasonal periodicity in hydrological flows, making the TSL a flood-pulse system. In the wet season (May-October), the water flows into TSL through TSR due to increased water levels in the Mekong River, whereas in the dry season (November-April), a reverse flow occurs through TSR again due to the receding water levels in the Mekong River (MRC, 2005). The surface area of TSL seasonally fluctuates from 2500 km^2 to 15000 km^2 driven by seasonal flood pulse from the Mekong River (M. Kummu et al., 2014; MRC, 2005). The water levels highly vary between seasons; the water depth ranges from 0.5 metres in April (dry season) to 9 metres in September-October (rainy season). This variation leads to a varied surface area of TSL throughout the year and thus creates heterogeneous habitats (MRC, 2005), that are inhabited by a variety of aquatic and terrestrial plant and animal species (Campbell et al., 2006).

The fish biomass data used in this study were provided by the Mekong River Commission (MRC) in collaboration with the Cambodian Department of Fisheries (currently called the Fisheries Administration [FiA]) and financially supported by DANIDA (Danish International Development Agency) (Ly and VanZalinge, 1998). The fish data were collected on thirty-three fishing areas delineated by the Royal Government of Cambodia for commercial fisheries, also called fishing lots (Figure 4.1). The sampling method was designed and approved by the Department of Fisheries with technical support from MRC experts. At each lot, samplings were conducted by the provincial fisheries scientists and supervised by central fisheries scientists from the Cambodian Department of Fisheries. Herein, data collectors were trained for sampling, identification and data record. With the heterogeneity and complexity of habitat in the fishing lot, many types of ~~the~~ fishing gears were applied according to the specific habitat characteristics. The data collections were conducted weekly from October to May (fishing period for the TSL fisheries) each year from 1994-2000. In each fishing lot, habitat characteristic is a complex combination of flooded forest, rice fields and open water. Therefore, multiple fishing techniques were used in each lot ensuring an equal fishing effort between lots (Ly and VanZalinge, 1998). For instance, the river barrages with U-shaped bag-nets were used for riverine fishing lots, and arrow-shaped bamboo fence traps for the lake floodplain fishing lots to maximise the catches (Ly and VanZalinge, 1998). These gears were used when the water recedes out of the inundated forest to capture fish migrating back to the lake (Ly and VanZalinge, 1998). Fish were identified to species and identification was validated by MRC experts following the keys in Rainboth (1996).

In this study, we considered the eight most important commercial fish species (*Channa micropeltes*, *Pangasianodon hypophthalmus*, *Channa striata*, *Cyclocheilichthys enoplos*, *Henicorhnychus* spp., *Barbonymus gonionotus*, *Micronema* spp., and *Trichopodus microlepis*) that account for 227 tons of fish per year on average that captured from the commercial fishing lots only [see supporting information material Table S1], and these fish species account for

58% of the total fish catches of the commercial fishing lot in the TSL (Chan et al., 2017). In addition, these species have been known as the most commercial important species of Cambodian inland fisheries (Chheng, Touch, Baran, & Leng, 2005) as well as the dominant species in the TSL (Ngor, Chheng, & So, 2015).

The biology of these species is well known, and each species has distinct habitat and ecological preferences. *C. striata* is a predator foraging on bony fish, frogs, insects, earthworms, tadpoles and crustaceans (Rahman, 1989). It inhabits flood-plain lakes and small streams. It is a common species in the still and stagnant areas of ponds, swamps, streams and lowland rivers with less than 2-metre depth (Chan et al., 2000; Chheng et al., 2005). During the rainy season, it migrates upstream from the Mekong mainstream toward the flooded areas and moves back to the permanent water bodies during the early dry season (Chan et al., 2000). *C. micropeltes* is a carnivorous top predator foraging primarily on fish and crustaceans (Froese & Pauly, 2017). It was observed in the standing or slowly flowing water of the deep and large streams and canals (Maurice Kottelat, 1998; Rainboth, 1996), but it also inhabits swamps and lowland rivers. *P. hypophthalmus* is a omnivorous fish feeding on a variety of food types such as fish, crustaceans and vegetable debris (Rainboth, 1996). It was observed in the deep and large rivers and undertake long-distance migration from rearing areas to spawn in unknown areas during May-July and move back to the mainstream to search for the rearing habitats when the river water level recedes between September-December (Hill & Hill, 1994). The adults of *C. enoplos* forage on the insect larvae, crustaceans and fish, whereas babies feed zooplankton (Rainboth, 1996). It was found at midwater to bottom levels of the mainstream and large tributaries of the Mekong River and flooded riparian forests (Froese & Pauly, 2017; Rainboth, 1996). It is a longitudinal migratory species in the Mekong River migrating from the Mekong River toward the Tonle Sap system during the flooded season and back toward the Mekong upstream when the water level recedes (Chan et al., 2000; Maurice Kottelat, 1985). *Henicorhynchus* spp. forage on plants, algae, periphyton and phytoplankton (Froese &

Pauly, 2017). It was found in the rapids and slow flowing water habitat in the mid-water to bottoms depths in large and small rivers (Froese & Pauly, 2017; Singhanouvong, Soulignavong, Vonghachak, Saadsy, & Warren, 1996a). It undertakes the longitudinal migration that moves into the floodplain area during the wet season for feeding and moves back to the rivers at receding water at the early October to December (Rainboth, 1996). *B. gonionotus* forages on plant leaves, weeds and invertebrates (Froese & Pauly, 2017). It is a migratory species that undertake the lateral migration moving from the Mekong River toward the small streams and tributaries and flooded area during the rainy reason and move back to the Mekong River during the dry season (Chan et al., 2000). It was found in mid-water to bottom depths in rivers, streams, floodplains, reservoirs and flooded forest flooded season (Rainboth, 1996). *T. microlepis* feeds on zooplankton, crustaceans and aquatic insects (Chheng et al., 2005). It is a common species in the floodplain of the Lower Mekong Basin and mainly found in ponds and swamps, especially in the shallow sluggish or standing water habitats with a lot of aquatic vegetation (Froese & Pauly, 2017).

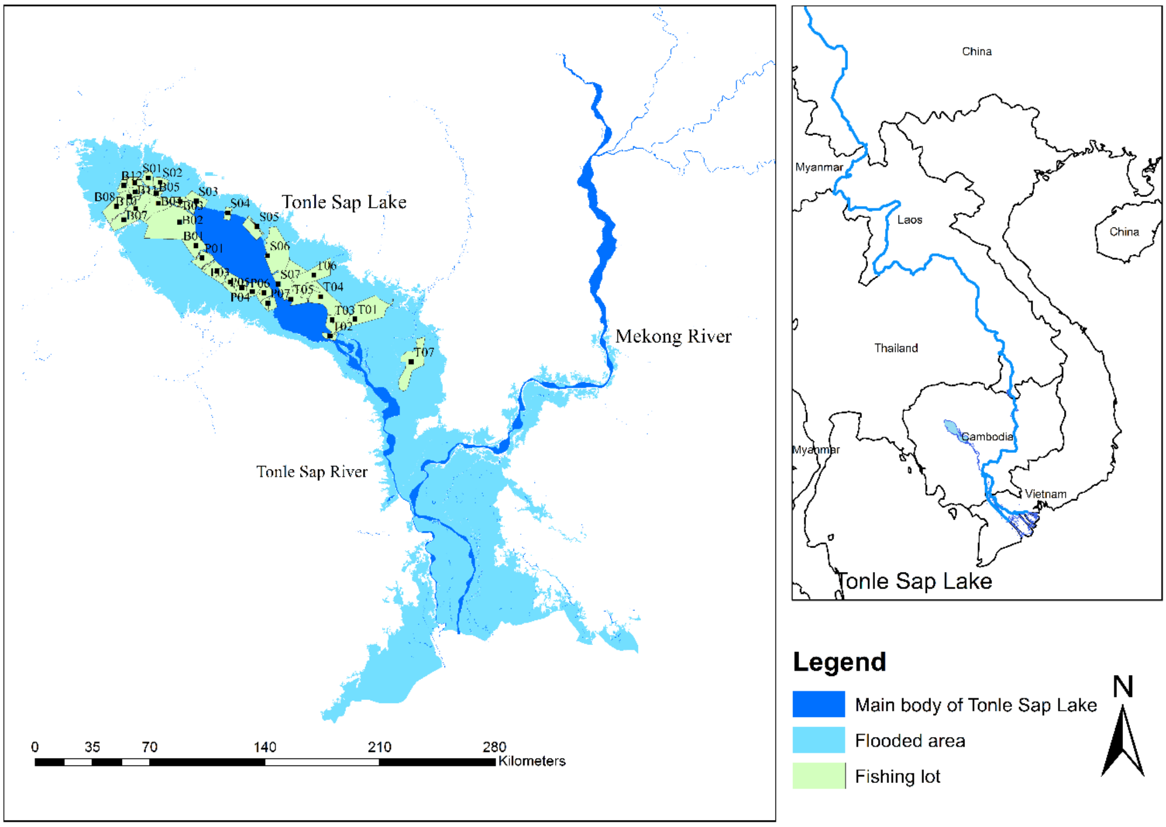

Figure 4.1 Map of the sampling sites in the Tonle Sap Lake floodplain. The minimal area of TSL during the dry season is in dark-blue and light blue represent maximal area of TSL during the flooded season. Fishing lots are in grey. The first letter of the code of the fishing lot represents the province name: B (Battambang), S (Siemreap), P (Pursat), and T (Kampong Thom). The two other characters represent the fishing lot number within each province.

4.2.2 Data preparation

The fishing lots from which the fish were collected were not uniform in size. Thus, annual fish biomass per hectare (kg/ha) was used to account for differences in sizes of fishing lots. ArcGIS version 10.2.03348 was used to determine the surface area of the three main land-cover types in each fishing lot, namely flooded forest (FF), open water (OW), and agricultural field (AF). Given that the fishing lots size are not uniform, each land cover type considered was expressed as a percentage cover (%). Land-cover data were extracted from the Cambodian Land Use 1993 map that best fits the fish catch period (1994-2000). Moreover, these data were strongly correlated to the data extracted from the land-use 2002 map for the flooded forest (Pearson correlation, r=0.979, p<0.001) and agricultural field (r=0.837, p<0.001), indicating that land use did not strongly change during the sampling period. Additionally, nineteen bioclimatic variables were extracted from the 1-km^2-resolution WorldClim layers for the period 1950-2000 (see supporting information material Table S2) (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). Despite the limited spatial range of this study (approximately 200 x 200 km), climate variables demonstrated substantial variations across the lake; thus, these variables are relevant for analysing the correlations between fish biomass and climate features (supporting information Table S2). The 19 bioclimatic variables were summarised using a principal component analysis (PCA), and the first three axes of the PCA accounted for 90.3% of the total variance in the climate data (64.60%, 15.15% and 10.79% respectively [see supporting information material S3]). The first axis (clim1) represents the temperature and precipitation range, with higher values corresponding to higher temperatures and precipitation. The second axis (clim2) represents the temperature range in the warm season, and the higher values correspond to the high temperatures in the warm season. The third axis (clim3) represents the precipitation range in the wet season, and the higher values correspond to the high precipitation in the wet season.

4.2.3 Statistical analyses

A PCA was performed to see the general tendency of association between the fish species and environmental descriptors using the “vegan” package (Oksanen et al., 2015). Then, the environmental variables: the local habitat (i.e. FF, OW, and AF) and the regional climatic factors (clim1, clim2, and clim3) were fitted onto the PCA biplot using the “envfit” function. This technique enabled us to identify the overall tendency of the relationship between the observed fish species and environmental descriptors.

Then, generalised linear models (GLM) were used to investigate the relationships between the spatial distribution of each species and the local habitat factors. GLM is an extension of linear regression. Before building the GLM models, the explanatory variables of the local habitat and regional climatic variables were standardised to get the same scale of the variable. The response was the mean value of the annual biomass of each species.

All statistical analyses were performed using R program v.3.1.2 for Windows statistical software package (http://www.r-project.org) (R Core Team 2014).

4.3 Results

4.3.1 Spatial distribution

Figure 4.2 shows a strong variability in fish biomass across fishing lots. Moreover, some lots consistently had similar fish biomass levels across time, whereas other lots showed quite unstable fish biomass levels. Interestingly, for most of the species, most high biomass fishing lots, despite a substantial temporal variability among the catches, consistently had high biomass levels for the considered species (Figure 4.2). From a spatial perspective, the snakehead *C. micropeltes* was most abundant in the central-northern part of the lake, although low abundances were found in the extreme northern area of the lake (Figure 4.3). *C. striata* and *T. microlepis* were more abundant in the northern part of the lake. In contrast, *C. enoplos*, *B. gonionotus, P. hypophthalmus,* and *Henicorhynchus* spp. biomass levels were highest in the southern part of the lake. *Micronema* spp. was also abundant in a few southern areas of the lake but also occupied a few areas in the northern part of the lake (Figure 4.3).

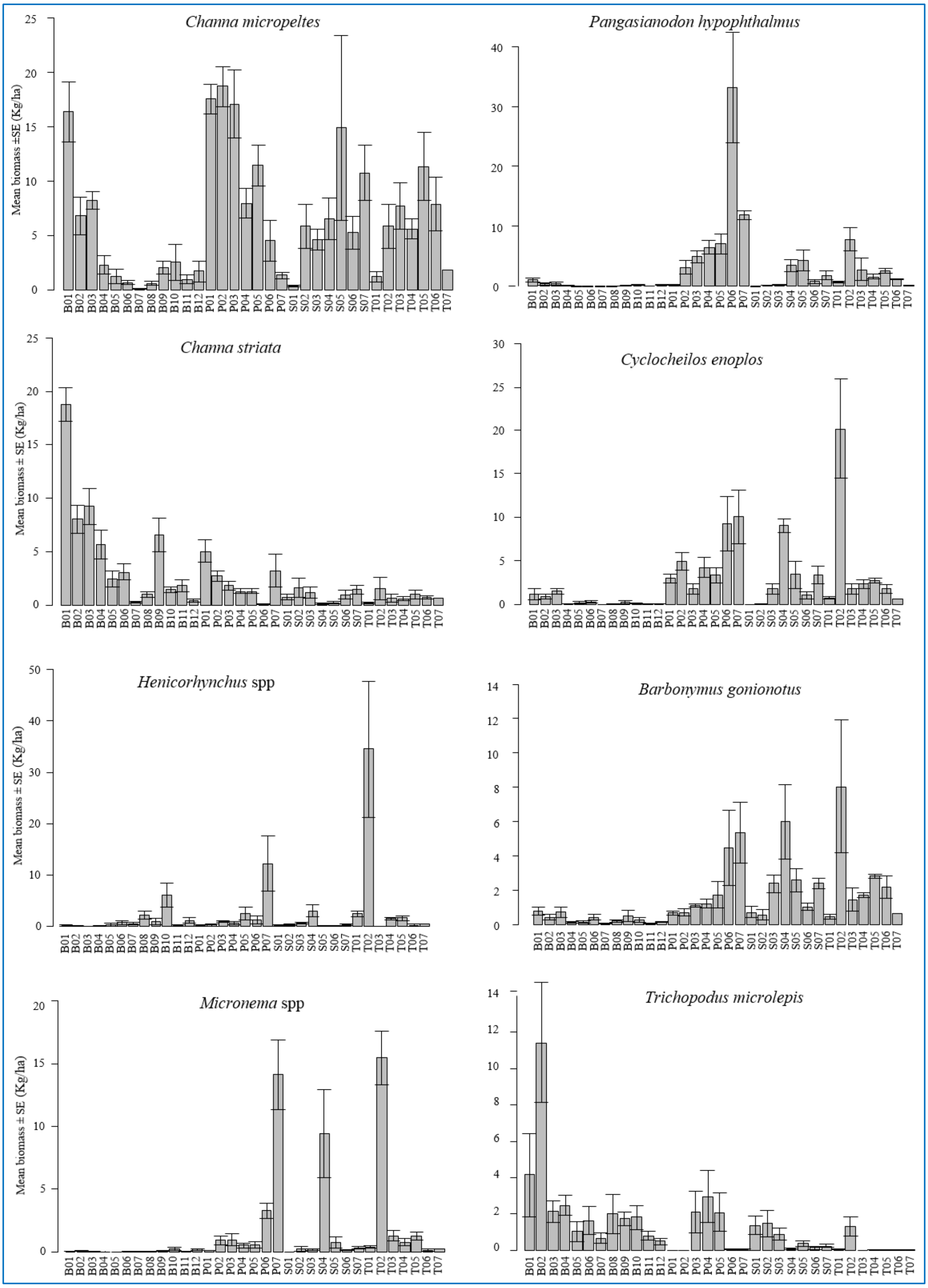

Figure 4.2 Mean ± SE bar plots showing the temporal variation in biomass (kg/ha) of the eight fish species within each fishing lot in the Tonle Sap Lake. The first letter of the code represents the province name: B (Battambang), S (Siemreap), P (Pursat), and T (Kampong Thom). The number corresponds to the name or number of a fishing lot in each province. The location of each fishing lot within the lake is shown in Figure 4.1.

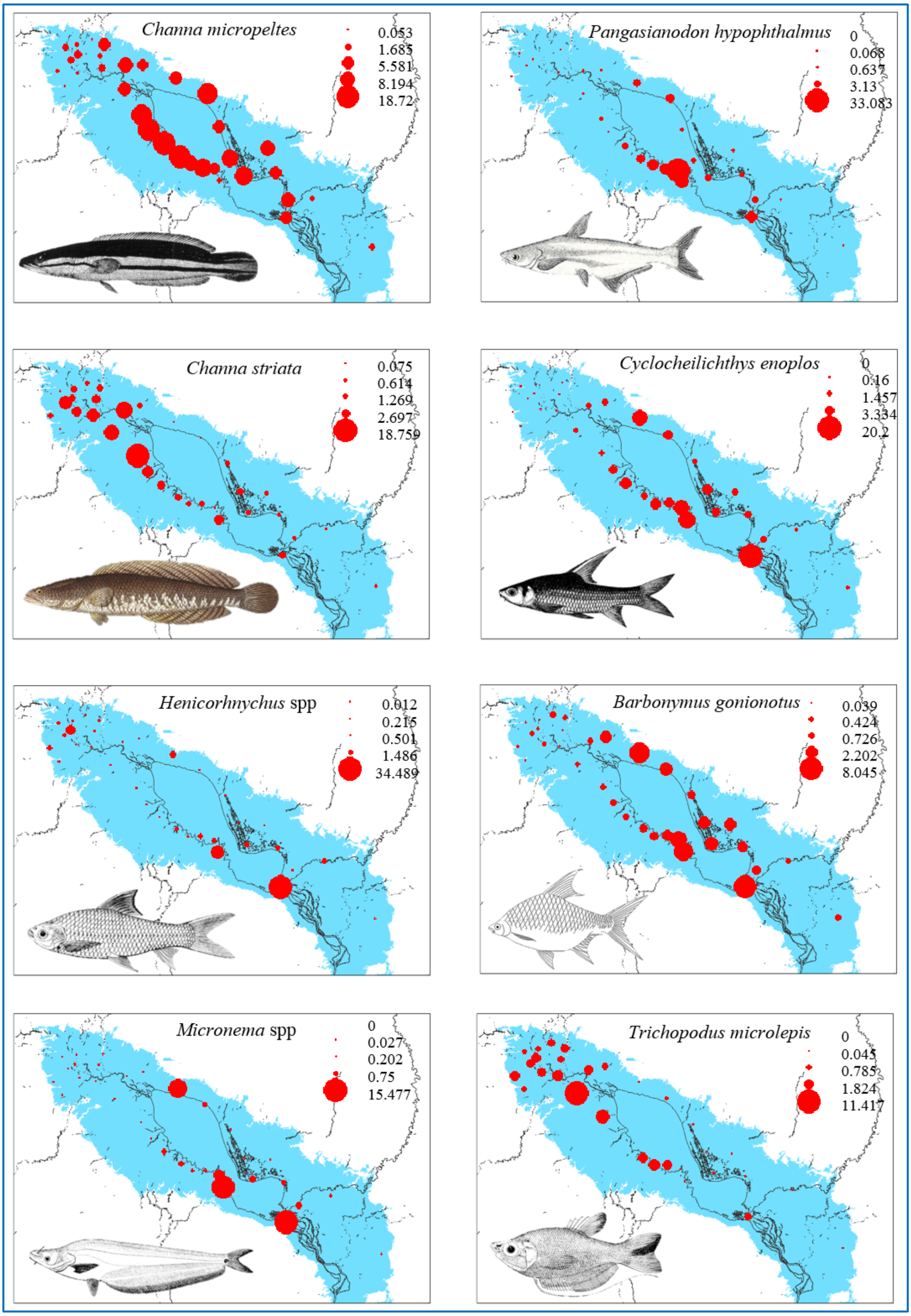

Figure 4.3 Bubble plots showing the spatial distribution of fish mean biomass of the eight fish species in the Tonle Sap Lake. The unit for the legends in the upper right of each plot are the mean annual fish biomass (kg/ha). The photos of fishes were redrawn from Rainboth (1996) and Froese & Pauly (2017).

4.3.2 Relationships between the local habitat and regional climatic factors with fish distribution

The PCA biplot illustrates the association between the fish species and environmental descriptors (Figure 4.4). The two first axes of the PCA accounted for 72.85% of the total variance (52.50% and 20.34%, respectively). There was a similarity in spatial distribution among floodplain resident fishes *C. micropeltes*, *C. striata*, and *T. microlepis* and five migratory species *P. hypophthalmus*, *C. enoplos*, *Henicorhynchus* spp., *B. gonionotus*, and *Micronema* spp.

In short, *C. striata* and *T. microlepis* were positively associated with the percentage cover of flooded forest (FF) and negatively correlated with temperature and precipitation range (clim1). Moreover, *C. enoplos*, *P. hypophthalmus*, *B. gonionotus*, *Micronema* spp., and *Henicorhynchus* spp. were positively correlated to the percentage cover of open water (OW) and temperature and precipitation range (clim1), but negatively associated to the percentage cover of flooded forest (FF). Moreover, *C. micropeltes* were negatively associated with the agricultural field (AF) and temperature range in the warm season (clim2) (Figure 4.4).

The GLM models that predicted species biomass from habitat type and climate data, although significant for all the species, showed an important variability in the model quality among the species, with determination coefficients (adjusted-R^2) ranging from 0.509 for *T. microlepis* to 0.836 for *C. enoplos* (Table 4.1). Then, the influence of each variable on fish species was assessed by the standardised coefficients of the variables in the GLMs.

The biomass of *C. enoplos* was negatively correlated the percentage cover of the flooded forest (FF), the percentage cover of open water (OW) and temperature and precipitation range (clim1). Moreover, the biomass of *P. hypophthalmus* was significantly associated a high value of the percentage cover of flooded forest (FF), the percentage cover of open water (OW), and temperature and precipitation range (clim1), but negatively associated with a temperature range in the warm season (clim2). The biomass of *C. striata* was positively correlated with the percentage cover of flooded forest (FF), the percentage cover of open water (OW), but negatively associated to the temperature and precipitation range (clim1), temperature range in the warm season (clim2), and the precipitation range in the wet season (clim3) (Table 4.1). In addition, the biomass of *Micronema* spp. was significantly correlated with a high value of the per cent cover of the flooded forest (FF) and the per cent cover of open water (OW), the precipitation range in the wet season (clim3). The biomass of *B. gonionotus* was positively associated with the percentage cover of open water (OW) and the precipitation range in the wet season (clim3). The biomass of *Henicorhynchus* spp. was negatively associated with the percentage cover of the agricultural field (AF), but positively correlated with temperature and precipitation range (clim1) and temperature range in the warm season (clim2). Also, the biomass of *C. micropeltes* was negatively associated with the temperature range in the warm season (clim2). Furthermore, the biomass of *T. microlepis* was significantly correlated with a low value of temperature range in the warm season (clim2) and the precipitation range in the wet season (clim3).

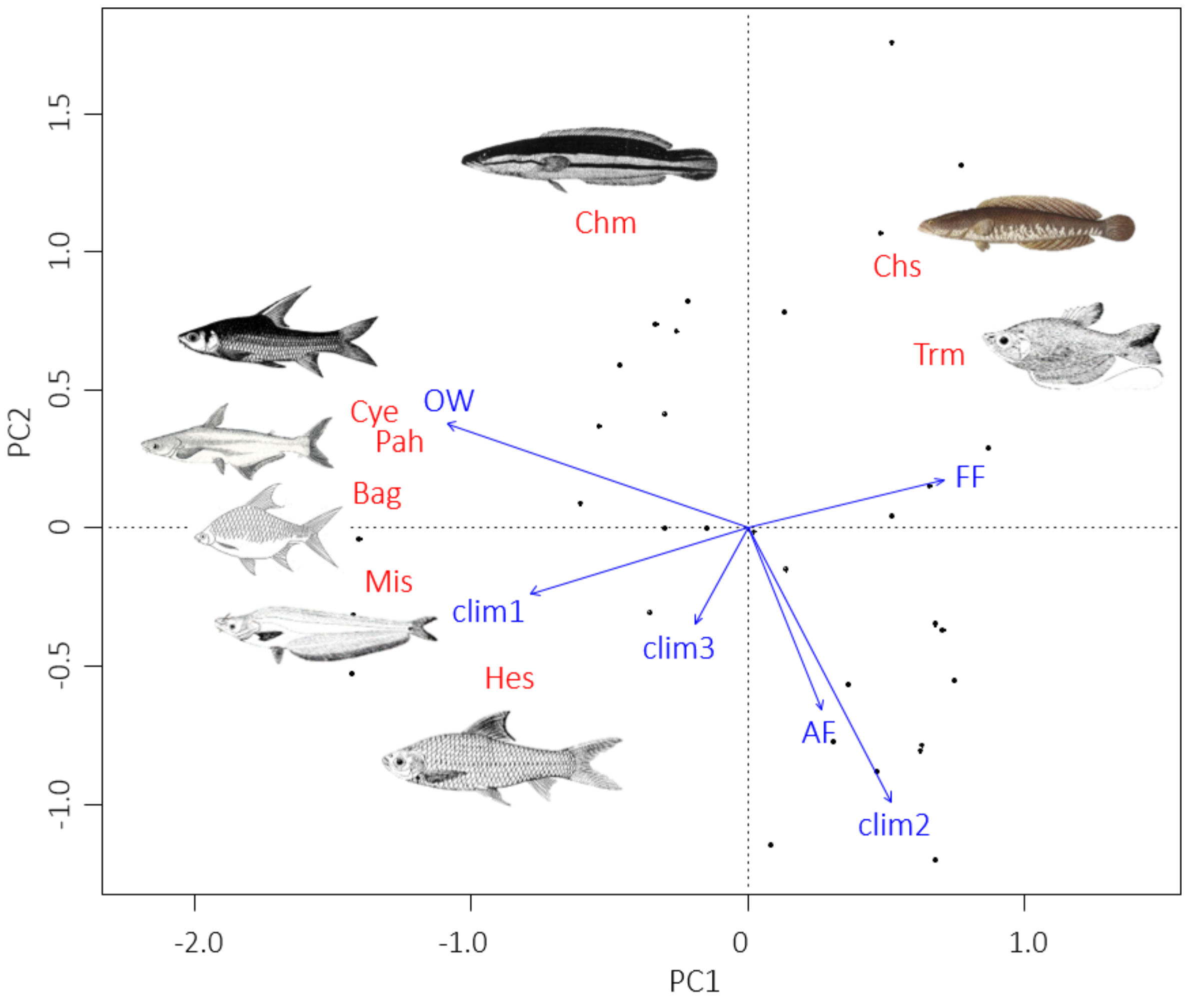

Figure 4.4 PCA biplot showing the association between fish species and environmental factors. Abbreviations are as follows: Chm: *Channa micropeltes*; Pah: *Pangasianodon hypophthalmus*; Chs: *Channa striata*; Cye: *Cyclocheilichthys enoplos*; Hes: *Henicorhnychus* spp.; Bag: *Barbonymus gonionotus*; Mis: *Micronema* spp.; Trm: *Trichopodus microlepis*; FF: the percentage cover of the flooded forest; OW: the percentage cover of the open water; AF: the percentage cover of the agricultural field; clim1: the temperature and precipitation range; clim2: the temperature range in the warm season; clim3:the precipitation range in the wet season; DSM: distance to the Mekong River.

Table 4.1 GLM standardized coefficients for the eight fish populations studied. Significant variables ($p < 0.05$) are in bold. Model performance for each species is indicated as the adjusted R^2. Chm = *Channa micropeltes*. Pah = *Pangasianodon hypophthalmus*. Chs = *Channa striata*. Cye = *Cyclocheilichthys enoplos*. Hes = *Henicorhnychus* spp. Bag = *Barbonymus gonionotus*. Mis = *Micronema* spp. Trm = *Trichopodus microlepis*. FF = the percentage cover of the flooded forest. OW = the percentage cover of the open water. AF = the percentage cover of the agricultural field. DSM = distance to the Mekong River. clim1 = the temperature and precipitation range. clim2 = the temperature range in the warm season. clim3 = the precipitation range in the wet season.

Variables	Chm	Pah	Chs	Cye	Hes	Bag	Mis	Trm
FF	0.702	4.117	1.883	2.711	-0.634	1.673	3.142	-0.859
OW	0.481	5.986	0.283	4.035	1.596	2.721	4.864	-1.519
AF	-0.748	1.383	1.013	-0.498	-2.191	-0.198	-0.641	-1.15
clim1	1.661	2.68	-2.578	2.583	4.252	1.203	0.97	-1.346
clim2	-6.669	-2.238	-3.143	-1.682	4.623	-0.333	1.507	-2.359
clim3	0.399	0.576	-3.463	1.771	-1.07	1.957	1.972	-2.708
Adj-R^2	0.685	0.833	0.627	0.836	0.709	0.741	0.760	0.509

4.4 Discussion

We have provided evidence that the eight fish species demonstrate heterogeneous distribution patterns within the lake. *Channa micropeltes* was distributed throughout the lake, whereas *Channa striata* and *Trichopodus microlepis* occurred more in the northern part of the lake. In contrast, *Pangasianodon hypophthalmus*, *Henicorhynchus* spp., *Cyclocheilichthys enoplos*, *Barbonymus gonionotus*, and *Micronema* spp. were distributed preferentially in the southern part of the lake. Moreover, floodplain resident species or non-migratory fish species are abundant in the floodplain area in the northern section of the lake (Poulsen, Ouch, Viravong, Suntornratana, & Nguyen, 2002), which is covered by flooded forest, shrub and aquatic vegetation (Enomoto et al., 2011). Those floodplain resident fishes spend most of their lifespans in the flooded forest, inhabiting the lake or swamps during the dry season and migrating to the flooded area during the wet season (Campbell et al., 2006). In contrast, the inlet-outlet area between the TSL and the Tonle Sap River (south of the lake) are colonised preferentially by migratory fish species, e.g., *C. enoplos, Henicorhynchus* spp., *B. gonionotus, Micronema* spp.

The observed fish distribution patterns were strongly related to local habitat characteristics. Each species is correlated to different habitat characteristic, supporting the hypothesis that the responses of fish species to their environmental determinants are species-specific (Kolosa, 1989). Local habitat is known as a major determinant of fish species spatial distribution in temperate rivers (e.g. Angermeier & Winston, 1998; Dunham, Cade, & Terrell, 2002) and lakes (e.g. Brosse, Grossman, & Lek, 2007; Brosse, Lek, & Dauba, 1999). This pattern also applies in tropical rivers such as the Mekong (Lammert & Allan, 1999; MRC, 2008). Within the TSL, we showed that the percentage cover of open water is positively correlated with the biomass of *P. hypophthalmus, C. enoplos, B. gonionotus, Micronema* spp. and *C. striata*, indicating that the open water is a significant habitat for these species. This result is consistent with previous studies demonstrating that the open water of the mainstream is important grounds for *C. enoplos*, *B. gonionotus*, *P. hypophthalmus* and *Micronema* spp. (M. Kottelat, 1998; M. Kottelat & Widjanarti, 2005; Rainboth, 1996; Singhanouvong, Soulignavong, Vonghachak, Saadsy, & Warren, 1996b; Talwar & Jhingran, 1991). These fish species are known to feed on zooplankton, insect larvae, and crustaceans in open water areas (Froese & Pauly, 2017). Also, *C. striata* may use the open water habitat for feeding, i.e. prey on small white fishes and shrimp. Moreover, the flooded forest was also positively correlated with the biomass of *C. striata*, *P. hypophthalmus*, *C. enoplos*, and *Micronema* spp. Despite its open water habits, *P. hypophthalmus*, *C. enoplos* and *Micronema* spp. also benefit from the habitat complexity provided by flooded forest areas that likely favours shelters against predation as well as providing appropriate spawning grounds for most species (Poulsen et al., 2004). Indeed, the flooded riparian forest is known as the principal spawning grounds for *C. striata*, *P. hypophthalmus*, *C. enoplos*, and *B. gonionotus* (Froese & Pauly, 2017; M. Kottelat & Widjanarti, 2005; Rainboth, 1996). The results are consistent with previous studies revealing that *C. striata* need flooded vegetation habitats for breeding and hatching (Menon, 1999; Rainboth, 1996). Moreover, the inundated forest might constitute an appropriate feeding ground that provides a large diversity of terrestrial prey (insects, frogs, small mammals) for this opportunistic predator. Furthermore, the per cent agricultural field (AF) was negatively correlated with *Henicorhynchus* spp., suggesting that the agricultural fields is not surrogate to the flooded forest areas as AF do not host high fish biomasses for most species.

Together with the physical environment, the distribution of fish was also related to climate factors. Although the link between climate and fish distribution is obvious in temperate rivers and streams (Buisson, Blanc, & Grenouillet, 2008; Heino, 2002), it has rarely been investigated in tropical environments, and the results of this study, together with those of Chea et al. (2016) on the Mekong mainstream, revealed that temperature and precipitation gradients associate with fish distributions in both the Mekong River and TSL. The temperature and precipitation were significantly associated with the distribution of the observed species. For instance, *C. striata* were significantly correlated with a low value of the temperature and precipitation range (clim1), while *P. hypophthalmus, C. enoplos, Henincorhynchus* spp. were correlated to a high value of the temperature and precipitation range (clim1). The floodplain resident appeared to be less caught during the high-temperature period. The floodplain resident fishes mostly live in the lakes and marshes or swamps on the floodplains near river channels and migrate to flooded areas during the flooded season (Poulsen et al., 2002). Indeed, floodplain resident fishes could adapt to the low oxygen environment, which enables them to survive in the swamps and small floodplain lakes during the dry season (Poulsen et al., 2002). Moreover, the floodplain fishes spend most of their lives feeding and breeding in the floodplain water bodies (Deap, Degen, & VanZalinge, 2003). In contrast, longitudinal migratory fish fishes appeared to be positively correlated with a temperature range, indicating that they are abundantly captured during the high-temperature period. In this case, during the dry season, the water level recedes, and longitudinal migratory fishes migrate from the TSL to the deep pool of the Mekong River (Poulsen et al., 2004). The precipitation appeared to be positively significant for longitudinal migratory/open water species (i.e. *Henicorhynchus* spp. and *B. gonionotus* and *Micronema* spp.), but negative to floodplain resident species, i.e. *C. micropeltes, C. striata* and *T. microlepis*. Indeed, tropical monsoon rainfall contributes to an increase in the water level or floods in the lake, which enables the dispersal of fishes, especially the longitudinal migratory fishes, in the floodplain area (MRC, 2005). In contrast, the floodplain resident *C. micropeltes, C. striata* and *T. microlepis* may not migrate and disperse greatly in the floodplain area during the high precipitation period or flood.

The spatial heterogeneity of fish biomass levels within the TSL provides important information for the management of the fish resources of the lake. First, some areas consistently have high fish biomass levels across years. For example, this is the case for lot T02, which is characterised by high biomasses of *C. enoplos, B. gonionotus, Henicorhynchus* spp., and *Micronema* spp. Herein, Lot T02 was characterised by two main habitat types, i.e. flooded forest (70%) and open water (30%), and there was no agricultural fields habitat. The large percentage cover of the flooded forest and open water are therefore of particular of importance to sustain the abundant biomass of *C. enoplos, B. gonionotus, Henicorhynchus* spp., and *Micronema* spp. in this location. Thus, specific attention should be given to the conservation of the environmental quality of this lot to maintain the productivity of the four considered species that account for more than 42% of the TSL catches. Second, among the eight considered species, different distribution patterns were observed, and some specific lots could be very important for one species but not for the others. For instance, lot P06 sustains more than 71% of *P. hypothalamus* biomass, whereas all the other lots sustain low biomass levels (less than 29%) of this species. This lot were composed of three habitat types: flooded forest (50%), open water (45%) and agricultural field (5%). The local habitat, which was mainly characterised by flooded forest and open water, is a key factor sustaining *P. hypothalamus* abundance in this lot. Third, among the eight species, only *C. micropeltes* was abundant in a substantial part of the lake, and the seven other species have much more restricted distributions. Overall, this information confirms that focusing conservation actions on a few, well-designed lots that have a high level of fish biomass for each species might be profitable for sustaining the fish biomass and productivity of the eight major TSL species.

Understanding the species-habitat relationships provides useful information to better understand the fish species environmental requirements and conserve local fish productivity, but this information might also be used to favour fish productivity in some areas of the lake that experience lower fish biomass levels. For instance, in this study, we showed that none of the fish species benefitted from agricultural landscapes, and therefore, these agricultural lands can be considered an equivalent to flooded forests to sustain fish populations. We, therefore, encourage not only conserving flooded forest areas that are known as crucial for tropical aquatic ecosystem functioning (Hughes, 2003; WWF, 2017) but also maintaining adequate habitats for most fish species benefit from flooded forest habitat.

Finally, the results, based on 1994-2000 fish catch data, might not reflect the current situation in the TSL, since human pressure has substantially changed over the past two decades (Baran & Gallego, 2015; NIS, 2013), with likely consequences on both aquatic habitats and land-use. It would, therefore, be useful to determine the extent to which the spatial distribution of current fish catches fit with the patterns we reveal and to analyse land-use changes experienced by the TSL during the past two decades. Similarly, global climate change likely affected fish distributions, and as demonstrated here, climate and precipitation are likely to affect species differentially. We, therefore, recommend an update of the fish and environment data on the TSL, while the results of the present paper could serve as a reference to quantify the changes in fish biomass levels and distributions in the lake. This need is of paramount importance to establish temporal trends on fish biomass in the TSL and therefore manage and sustain the fish resources of the lake that are crucial to a large part of the Cambodian people (Ahmed et al., 1998; Lieng & Zalinge, 2001).

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Supporting information

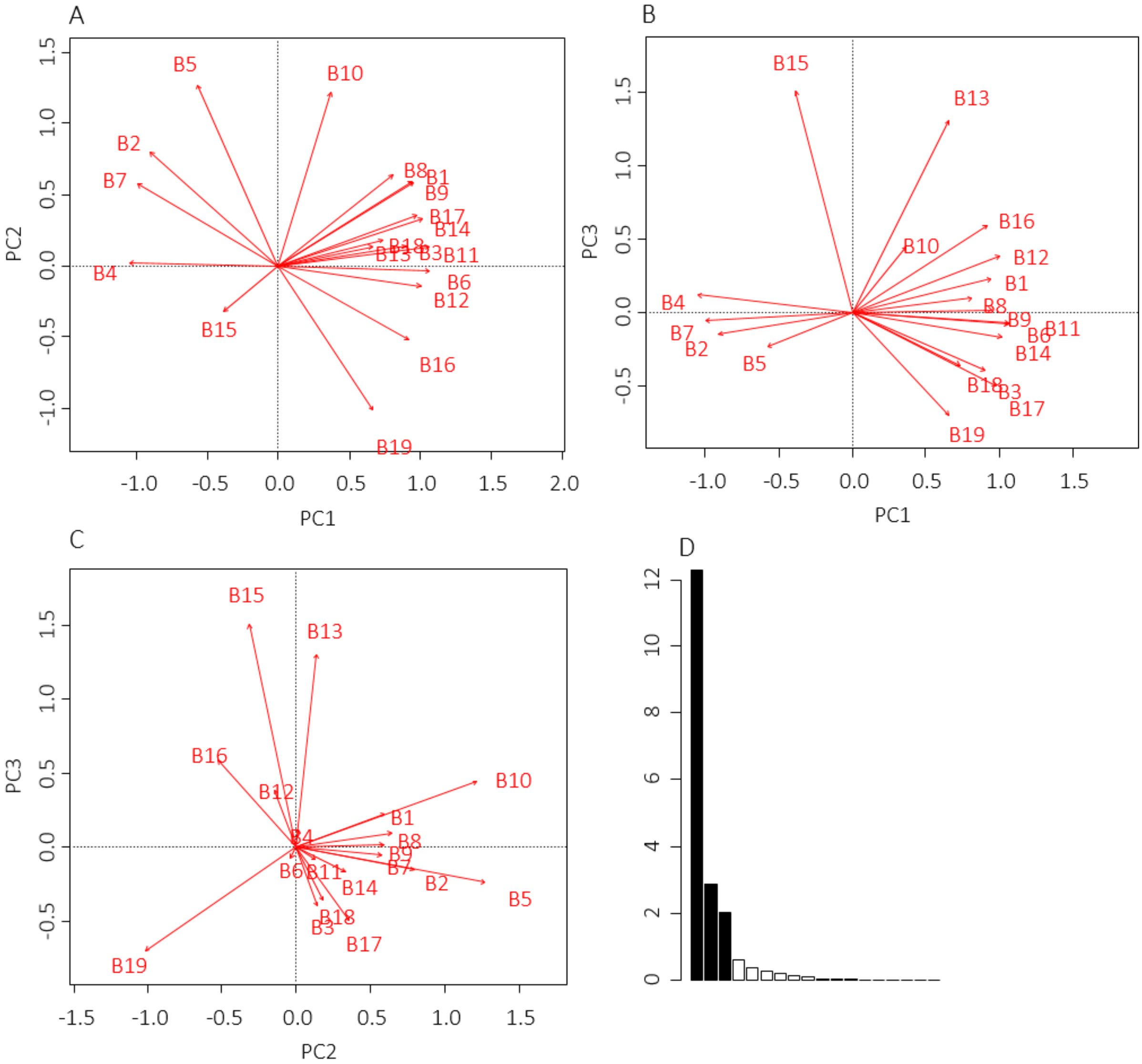
Table S1 Mean ± standard error of biomass (ton) of each species caught each year and the percentage of each species to the total catch.

Year	Chm	Pah	Chs	Cye	Hes	Bag	Mis	Trm
1994	114.16±20.90	27.80±10.92	41.05±11.51	19.39±4.44	17.81±6.33	14.34±3.40	10.63±4.62	12.77±9.13
1995	105.00±24.04	40.43±15.12	30.42±11.33	16.90±3.09	17.38±7.51	14.09±3.25	11.08±4.2	4.25±2.52
1996	64.49±18.74	15.54±5.10	31.13±11.8	26.75±5.32	11.37±4.78	12.10±2.39	7.44±2.59	39.54±27.98
1997	76.98±19.38	20.54±6.10	40.34±17.71	25.63±7.2	11.20±2.82	12.99±4.03	9.25±3.81	21.13±11.34
1998	59.08±14.01	18.36±5.34	51.57±25.73	24.18±6.78	11.38±3.24	16.31±4.01	10.24±3.85	50.55±41.01
1999	38.20±10.24	20.31±8.03	44.58±21.15	17.27±4.74	7.02±2.76	10.96±2.87	1.50±0.61	52.30±31.85
%	18.58	8.10	8.50	6. 90	5.06	4.03	3.70	4.10

Table S2 Summary of bioclimatic variables with their minimum and maximum values.

Variable	Unit	Variable type	Minimum	Maximum
B1	(°C)	annual mean temperature	27.3	27.7
B2	(°C)	mean diurnal range (mean of monthly (max temp - min temp))	8.8	9.6
B3	%	isothermality (B2/B7) (* 100)	56	58
B4	(°C*100)	temperature seasonality (standard deviation *100)	1424	1731
B5	(°C)	max temperature of the warmest month	34.7	35.5
B6	(°C)	min temperature of the coldest month	18.4	19.9
B7	(°C)	temperature annual range (B5-B6)	15	16.9
B8	(°C)	mean temperature of the wettest quarter	27.2	27.5
B9	(°C)	mean temperature of the driest quarter	25.3	25.9
B10	(°C)	mean temperature of the warmest quarter	29.2	29.4
B11	(°C)	mean temperature of coldest quarter	24.7	25.7
B12	mm	annual precipitation	1169	1481
B13	mm	precipitation of the wettest month	221	279
B14	mm	precipitation of the driest month	1	6
B15	mm	precipitation seasonality (coefficient of variation)	70	79
B16	mm	precipitation of the wettest quarter	549	696
B17	mm	precipitation of the driest quarter	22	41
B18	mm	precipitation of the warmest quarter	209	369
B19	mm	precipitation of the coldest quarter	73	117

S3 (A) Plane of the PCA showing the nineteen bioclime variables: (A) the first and second axes of PCA. (B) The first and third axes of the PCA. (C) The second and third axes of the PCA. (D) Eigenvalues of PCA. The description of each variable is shown in the supporting information Table S2.



Chapter V: Modelling dynamics of two small mud carp species in the Tonle Sap flood-pulse ecosystem using spatial and time-series data

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Abstract

The main challenges for ecological studies are the complexity and non-stationarity of data that are difficult to handle using traditional modelling methods. Thus, to address these problems, modern modelling techniques have been developed and introduced for applications. In time-series data, the cross-wavelet transform (CWT) and cross-correlation function (CCF) serve as promising tools to analyze the dynamics of fish populations through time and space. Here, we employed these two well-known time-series modelling approaches to model the spatial and temporal dynamics of small mud carp species (*Henicorhynchus lobatus* and *Henicorhynchus siamensis*) and examine the influence of flow pulses on their dynamics using spatial and time-series data collected from the Tonle Sap Lake and River System. The phase angle given by the CWT provided a useful tool for statistically detecting and reconstructing the phase relationship between the two time series of fish data. Moreover, the correlation coefficients at each lag between the water level and fish abundance identified by the CCF provided a mechanism to understand how the flow pulse influenced the dynamics of fish. The results showed that *H. lobatus* moved out of the floodplain and the lake earlier than *H. siamensis*. Herein, *H. lobatus* retreats slower than *H. siamensis* in the Tonle Sap Lake, but they retreated at similar speeds when they reach the Tonle Sap River. This suggests that the two species respond differently to the out-flow pulse only when they are inside the TSL, indicating the main role of flow pulses in determining the occurrence and movement of fish in the Tonle Sap Ecosystem. We also discussed the role and applications of these modelling approaches for linking the changes in environmental parameters and fish. The CWT and CCF, based on our results, are helpful modelling approaches for analyzing time-series data to understand the phase relationship and the periodicity of synchronisation (joint periodicity), i.e. the role of environmental factors in shaping fish occurrence and movement in a flood-pulse ecosystem.

KEYWORDS: co-occurrence; migration patterns; fish synchronisation; phase relationship; cross-wavelet transform; cross-correlation function

5.1. Introduction

Spatial and temporal dynamics of populations and communities have become an interesting research area for ecological studies (Mcgill et al., 2006; Vellend, 2010). This is because assessing the spatial and temporal dynamics of communities or a given species in an ecosystem can provide useful knowledge on how individuals of its population synchronise and migrate, e.g. before (leading), at the same time, or after (lagging) the synchronisation of its meta-community with which it interacts (Chevalier et al., 2018; Leibold et al., 2004; Wilson, 1992). Moreover, knowledge on the spatial and temporal dynamics of a target species can lead to a greater understanding of variations in its population size (e.g. where and when it fluctuates over time) and movements (e.g. up and downstream of a river), and the driving forces that govern such variations and movements (Begon et al., 1991; Juliano, 2007; Ruokolainen et al., 2009).

In aquatic environments, flood-pulse ecosystems refer to water bodies that are regulated by periodic inundation (i.e. flood pulses) that is coupled and decoupled from their interconnected water bodies/rivers. In these ecosystems, the pulsing is one of the major forces responsible for productivity and biotic interactions (Junk et al., 1989; Sverdrup-Jensen, 2002). For fishes, flow pulses play a pivotal role in their ecology because they create habitat diversities and improve food supply (DeGrandchamp et al., 2008; Valbo-Jorgensen, 2003), which are crucial for the survival and development of fishes. Fishes mainly use the main channels and floodplains of the system as a migration route, spawning ground or refuge during the dry season. This indicates that variation in flow pulses or water levels may have a strong influence on the spatial and temporal dynamics of fish communities occurring at different locations in the system being studied (Ngor et al., 2018b; Sabo et al., 2017; Stoffels et al., 2015).

The Tonle Sap Lake (TSL) is the largest freshwater lake in Southeast Asia and is the largest floodplain water body of the Mekong River basin (MRC, 2005). The TSL is connected to the Mekong River by the Tonle Sap River (TSR) (Figure 5.1). The TSL, the TSR, and their tributaries form a large natural ecosystem called the Tonle Sap Ecosystem (TSE) (Lamberts, 2006). The TSL hydrological flows are influenced by flood waters of the Mekong River, and this creates a complex flood-pulse ecosystem (Kummu et al., 2014; MRC, 2005). Due to this fact, combined with other suitable habitat conditions (e.g. feeding and breeding grounds, many surrounding tributaries, and heterogeneous land covers), the TSE supports high biodiversity, and thus provides substantial contributions of fisheries resources to the people in the region (Lieng and Zalinge, 2001). For example, 296 fish species have been reported from the TSE (Baran et al., 2013), of which 7 species (e.g. *Henicorhynchus* spp., *Labiobarbus* spp. and *Paralaubuca* spp.) are among the dominant species in the annual fish catch from the TSR (Halls et al., 2013; Ngor et al., 2015). However, knowledge on fish communities and dynamics are relatively limited in this flood-pulse ecosystem. To date, only few studies have been conducted in this system, e.g. fish species diversity and distribution (Campbell et al., 2006; Chan et al., 2017; Lim et al., 1999), fish beta diversity (Kong et al., 2017), fish community structure (Ngor et al., 2018a) and physiochemical-fish composition relationship (Chea et al., 2016). Moreover, no studies have attempted to investigate the spatial and temporal dynamics of key fisheries species and their relations to the water level variation over an extended period. For this reason, analyzing the spatial and temporal dynamics of keystone species, e.g. *Henicorhynchus* spp. (trey Riel) will provide essential knowledge and insights to better support fisheries monitoring and management.

Cross-wavelet transform (CWT, Grinsted et al., 2004) with phase angle and coherency parameters, is a local bivariate analysis that is commonly used for time-series data to analyze the relationships in time-frequency space, phase relationships and coherency between the two time series (Grinsted et al., 2004; Maraun and Kurths, 2004; Prokoph and Bilali, 2008). The main components of the CWT are to compare the frequency contents of the two time series and highlight the synchronicity of the series at a given period and across given ranges of time

(Roesch and Schmidbauer, 2014a). Moreover, the cross-correlation function (CCF) has been used to determine the correlation between the two time series as a function of the time lag or delay (Zhang and Wu, 2006). It produces global correlation coefficients between two time-series data at each lag. These two modelling techniques are useful tools to assess the influence of environmental variables (e.g. flow pulse) on the spatial and temporal dynamics of fish species.

By using the CWT and CCF, we studied the dynamics, i.e. by means of occurrence, synchronisation (i.e. the collective swimming of fish individuals in a large school), peak abundance, and behavioural movement patterns, of two small mud carp species [i.e. *H. lobatus* (Smith, 1945) and *H. siamensis* (Sauvage, 1881)] in the TSE. Additionally, we investigated the influence of water levels on their spatial and temporal dynamics. Our questions of interest are: 1) Is there any synchrony in occurrence between the two species, and is there a constant periodic occurrence of each species (e.g. re-occurring monthly or seasonally or annually)? 2) How is the period of synchronisation and movement patterns of each species varied across the TSE? 3) Is there any time-lagged relationship between the synchronisation of each species and water levels? Since it has been shown that *H. lobatus* and *H. siamensis* have dissimilarities in ecological preferences and life history traits (Hurwood et al., 2006), we expected distinct periods of the occurrence, synchronisation and time-lagged relationship to be observed for each species in different parts of the TSE, following the variation in water levels.

5.2. Materials and methods

5.2.1. Site descriptions

The study was carried out in the TSE, which is located in the northwest part of Cambodia (Figure 5.1). The TSE is a tropical flood-pulse system due to its seasonal and predictable periodicity in hydrological flows. In the wet season (May-October), the water flows into the TSL through the TSR due to increased water levels in the Mekong River, whereas in the dry season (November-April), a reverse flow occurs through the TSR again due to the receding water levels in the Mekong River (MRC, 2005). The water levels highly vary between seasons; the water depth ranges from 0.5 metres in April (dry season) to 9 metres in September-October (rainy season). In 2011, one of the wettest years, the maximum water level in the TSL was recorded at 9.9 metres (Ngor et al., 2018a). This variation leads to a varied surface area of the TSL throughout the year and thus creates more heterogeneous habitats compared to the TSR (MRC, 2005).

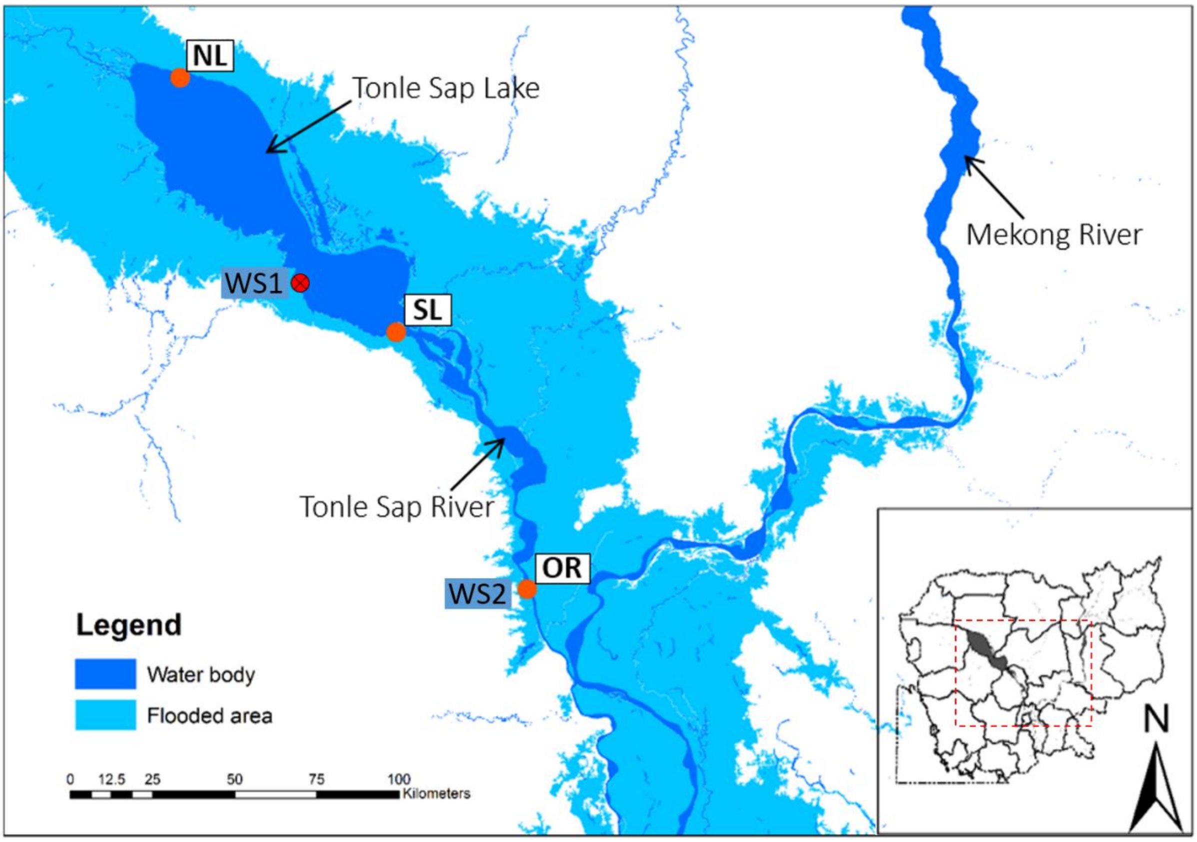

Figure 5.1 Sampling sites (red dots) of the study area: NL, the northern TSL; SL: the southern TSL; OR, the outlet river of the Tonle Sap River. WS1: water measurement station (red dot with a cross), WS2: the water measurement station situated at the same location as the "OR" fish sampling site.

5.2.2. Data collection and processing

The fish data used in this study were provided by the Mekong River Commission (MRC) Fisheries Programme. The fish catch monitoring approach follows the MRC's fish monitoring method applied in the Lower Mekong Basin (MRC, 2008; Ngor et al., 2014). In the present study, daily fish catch monitoring from January 2012 to December 2015 was selected from three sampling sites in the TSE (Figure 5.1) in the northern TSL (hereafter abbreviated to NL), in the southern TSL (SL), and the in the outlet river (OR) of the TSR (Figure 5.1).

At each sampling site, nylon gillnets with 2 to 6.5 cm mesh sizes were used to capture as many fish species as possible. Gillnets have been considered the most common and popular fishing gear used in the TSE and are suitable to be applied in different habitat types (MRC, 2008). The gillnets used had a length of 400 m ± 100 m. The variation in the gillnet length was due to the habitat availability (e.g. inundated forest, open water of the TSL, rivers, streams, and creeks), which varies according to the annual hydrological cycle. Fishes were identified to the species level following the identification guide by Rainboth (1996) in cross-checking with FishBase (Froese and Pauly, 2017) and Kottelat (2013) and enumerated and recorded in a logbook. The logbooks were then collected from fishers on a quarterly basis and cross-checked for its correctness and completeness of the recorded data by research specialists. Unidentified species were later identified by an expert taxonomist in the laboratory.

In this study, only two small mud carp species *H. lobatus* and *H. siamensis* were extracted from the fish monitoring database for analyses. *Henicorhynchus* spp. are indeed among the most ecologically and economically important species in the TSE (Fukushima et al., 2014; MRC, 2009; Ngor et al., 2015). They are significantly contributed to sustaining livelihoods and food security in the country and in the region, e.g. they make up the highest proportion (43%) by weight of *Dai* fishery catches in the TSR (Hall et al., 2007; Halls et al., 2013). Moreover, *Henicorhynchus* spp. are of major importance to produce fish paste (*Prahok*), smoked fish, salted fish and fish sauce, which can be kept for use particularly during rice-cultivation periods and when wild fish is scarce (Hall et al., 2007; Halls et al., 2013; MRC, 2009, 2002). The water level dataset used in this study was registered by the MRC. The daily water levels were measured and recorded from two sites in the TSL and TSR (Figure 5.1).

5.2.3. Modelling techniques and analyses

5.2.3.1. Modelling techniques

The CWT can locally detect, extract, and reconstruct the relationship between two nonstationary signals in frequency and time (Grinsted et al., 2004). The CWT of the two time series *x(t)* and *y(t)*, with cross-wavelet forms W_x and W_y, respectively, is calculated based on the formula $W_{xy}(\tau, s) = 1/s \cdot W_x(\tau, s) \cdot W_y{}^*(\tau, s)$, where τ is the time localization and s is the scale factor that determines the characteristic frequency or wavelength, and * denotes the complex conjugate (Prokoph and Bilali, 2008; Roesch and Schmidbauer, 2014a). Monte Carlo simulations are a general post hoc analysis performed to provide frequency-specific probability distributions.

The CWT provides an analogy of the cross-correlation with localization in time and scale. The correlation level between the two time series is measured using the cross-wavelet power (CWP), which is measured according to the norm of $W_{xy}(\tau, s)$: $P_{xy}(\tau, s) = |W_{xy}(\tau, s)|$. When the two time-series data have a high or a low CWP, it means that they have a high or low correlation, respectively. The contour line revealed by the CWT indicates the significance of the joint time interval (the interval of time containing a significant correlation between the two time series) (Roesch and Schmidbauer, 2014a).

The phase angle describes the phase difference between the two time-series data, of which the phase difference of *x* over *y* at the time and scale is based on the formula: Angle(τ, s) = Arg(Wave.xy(τ, s)) (Roesch and Schmidbauer, 2014a). The phase angle in an interval [3π/2, π/2], as shown by arrows pointing right (↗ and ↘), illustrates the in-phase relationship, whereas the phase angle in an interval [π/2, 3π/2], as shown by arrows pointing left (↖ and ↙), illustrates the anti-phase or the out of phase relationship. Specifically, when the arrows are pointing right-up and left-down (↗ and ↙), the first series leads the second, and when the arrows are pointing left-up and right-down (↖ and ↘), the second series leads the first. See Roesch and Schmidbauer (2014a) for details.

The CCF is a bivariate method applied to analyze the global correlation between the two time-series data. The CCF is a promising method that can be used to determine a level of similarity or correlation between the two time series as a function of the time lag or delay (Zhang and Wu, 2006). The CCF produces correlation coefficients (i.e. a positive and negative correlation) between the two time series at each lag. In the CCFs, the "input" time-series data represent the influential time series, and the "output" time-series data represent the affected time series (Welsh, 1999). The CCF of the two time series (*xt*) and (*yt*) is given by: $CCF(\tau) = \int x(t)y(t+\tau)\mathrm{dt}$, where the lag τ is the size of the time shift (Welsh, 1999).

In the CCF plot, the length of the vertical line indicates the value of the correlation coefficient between the two time series at each lag. The areas above and below the blue horizontal dashed-line represent a significant positive correlation and a significant negative correlation, respectively. In other words, the vertical line of the lag that is extended above the upper blue horizontal dashed-line represents a significant positive correlation, whereas the vertical line of the lag that is situated below the below blue horizontal dashed-line represents a significant negative correlation between the two time series.

5.2.3.2. Data analyses

The daily catch of the two species and water level data were summarised into a weekly basis based on mean, comprising a total of 210 weeks over the whole timescale of the study for the three sites. For each studied site, the CWT was used to analyze occurrence correlation and recursivity (e.g. a recursive occurrence at an interval over a particular timescale) between the two time-series data of *H. lobatus* abundance (*x*) and *H. siamensis* abundance (*y*) by utilising the function *analyze.coherency* in the "WaveletComp" package of *R* (Roesch and Schmidbauer, 2014b). Internally, the time series are standardised before they build the CWT. The CWT analysis also allows the determination of whether *H. lobatus* occurrence leads or lags *H. siamensis* occurrence. Here, the 95% confidence interval was selected for the wavelet power as the significance criterion. Practically, the ability of the CWT to analyze coherency enabled us to highlight the co-occurrence and synchronisation periodicity of the two species. The CCFs were then employed to determine a period (e.g. how many weeks) when *H. lobatus* synchronisation and peak abundance leads or lags those of *H. siamensis*, using the function *ccf* in the “stats” package of *R*.

To investigate how periods of synchronisation and peak abundance vary across the studied sites, the CCFs were used to determine the time-lagged relationship of the abundance of each species between paired sites, e.g. *H. lobatus* abundance in NL (*x*) and SL (*y*). The results of this analysis were then used to identify the movement patterns of each species (e.g. a period it takes to migrate from NL to SL). Swimming speed (km/day) of each species is therefore inferred from the time lags and distances between study sites.

Finally, the CCFs were also employed to examine the time-lagged relationship between the water levels and the abundance of each species at each site. In this analysis, the water level data measured from site WS1 was analyzed with the fish data collected from the NL and SL sites, whereas that from WS2 was analyzed with the fish data collected from the OR site. By the end of this analysis, we were able to estimate the movement periods of both species, e.g. how many weeks the peak water level leads or lags the peak abundance of each species. Here, we selected the lag containing the highest correlation coefficients between the two time series as the time lag. The CCF allowed us to determine the link between the flow pulse and fish abundance and identify the time lag between the water level peak and fish synchronisation. The CCF, thus, enables the determination of the role of flood pulse in spatial and temporal dynamics of fish species in the TSE to be made.

All statistical analyses were performed using *R* program v.3.3.3 for Windows statistical software package (http://www.r-project.org) (R Core Team, 2017).

5.3. Results

5.3.1. Occurrence correlations and periodicities

There was a correlation between the occurrence of *H. lobatus* and *H. siamensis*, and their periodic occurrence was also observed at each studied site (Figure 5.2). In NL, a significant positive correlation (meaning that *H. lobatus* led *H. siamensis*) occurred at a high-frequency periodicity of 46.9 to 52 weeks, as indicated by the in-phase relationship detected over the whole timescale of the study (Figure 5.2; Supplementary material S1). In SL, significant positive correlations were also observed at different periodicities (Figure 5.2). A rather weak, but significant, correlation that occurred at a high-frequency periodicity of 46.9 to 52 weeks was observed for the whole timescale of study, and strong correlations that occurred at low-frequency periodicities (3.9 to 4.4 weeks) were observed over a short timescale of study between late 2012 and early 2013, and between late 2014 and early 2015. In OR, significant positive and negative correlations were detected, as indicated by the in- and anti-phase relationships of the CWT analysis, respectively. The results also indicated a significant positive correlation that occurred at the high-frequency periodicities of 46.9 to 52 weeks. Stronger significant negative or positive correlations, which occurred at the lower-frequency periodicities (3.9 to 4.4 weeks), were observed over three short timescales (i.e. between December and February) of the study (Figure 5.2).

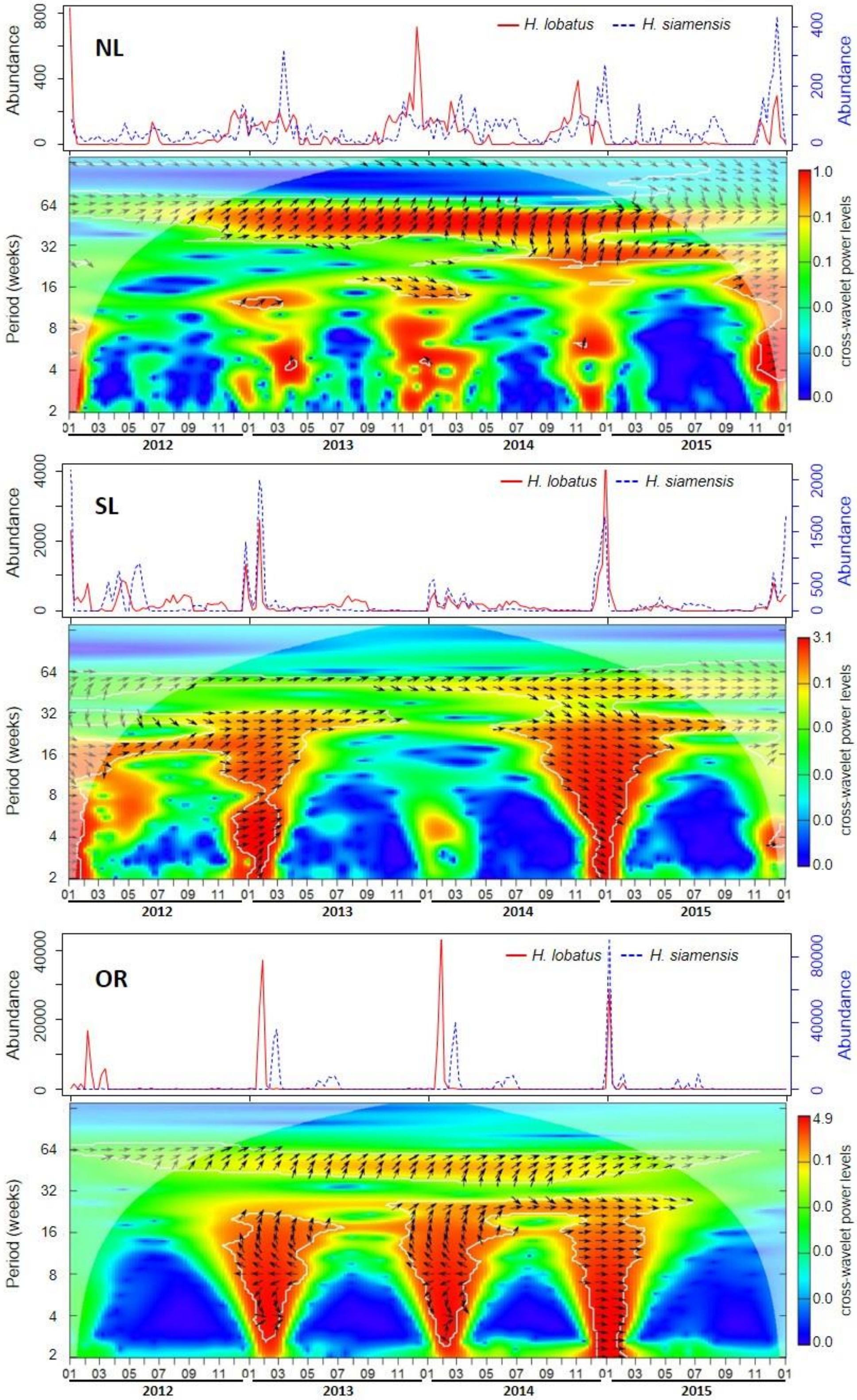

Figure 5.2 Time-series data of *H. lobatus* and *H. siamensis* abundance (upper panel) and the corresponding CWT results (lower panel) at each site. Abbreviations are as follows: NL: the northern TSL, SL: the southern TSL, OR: the outlet river. The white contour line of the CWT plots indicates the significance at 95% confident interval. A high correlation was represented by red and weak correlation by blue. A significant in-phase relationship (i.e. a positive

correlation) is shown with arrows pointing right, and a significant anti-phase relationship (i.e. a negative correlation) with arrows pointing left.

5.3.2. Synchronisation, peak abundance, and movement patterns

In NL, significant synchronisation and peak abundance of *H. lobatus* occurred within 6 weeks and 1 week, respectively, before those of *H. siamensis* (Figure 5.3). In SL and OR, the synchronisation of *H. lobatus* appeared to occur before that of *H. siamensis* but the peak abundance of both species occurred in the same week (Figure 5.3).

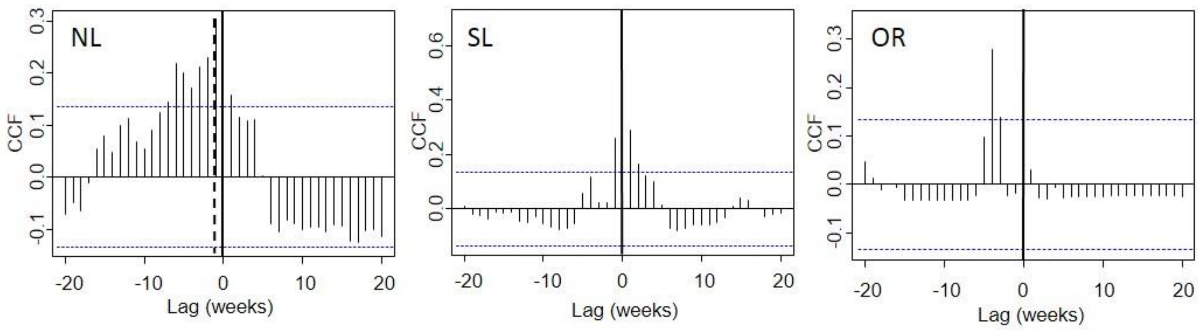

Figure 5.3 The CCF plots showing the time-lagged relationships between the two time series of the synchronisation and peak abundance of *H. lobatus* and *H. siamensis* at each site. Abbreviations are as follows: NL: the northern TSL, SL: the southern TSL and OR: the outlet river. In the CCF models, *H. lobatus* was a predictor (x), and *H. siamensis* was a dependent variable (y). The vertical bold-line indicates the time lag at time zero showing the peak abundance period of H. siamensis, the vertical dashed-line indicates peak abundance period of *H. lobatus*, and the two horizontal dashed-lines indicate significant correlation values (i.e. a positive for the upper one and a negative for the below one) at the 95% confident interval.

Based on the paired sites, the CCF bivariate plots (Figure 5.4) illustrated that after the peak abundance of *H. lobatus* observed in NL, it was detected again within 8 weeks in SL, and again within 1 week in OR. After the peak abundance of *H. siamensis* occurred in NL, it was detected again within 2 weeks in SL, and again within 1 week in OR.

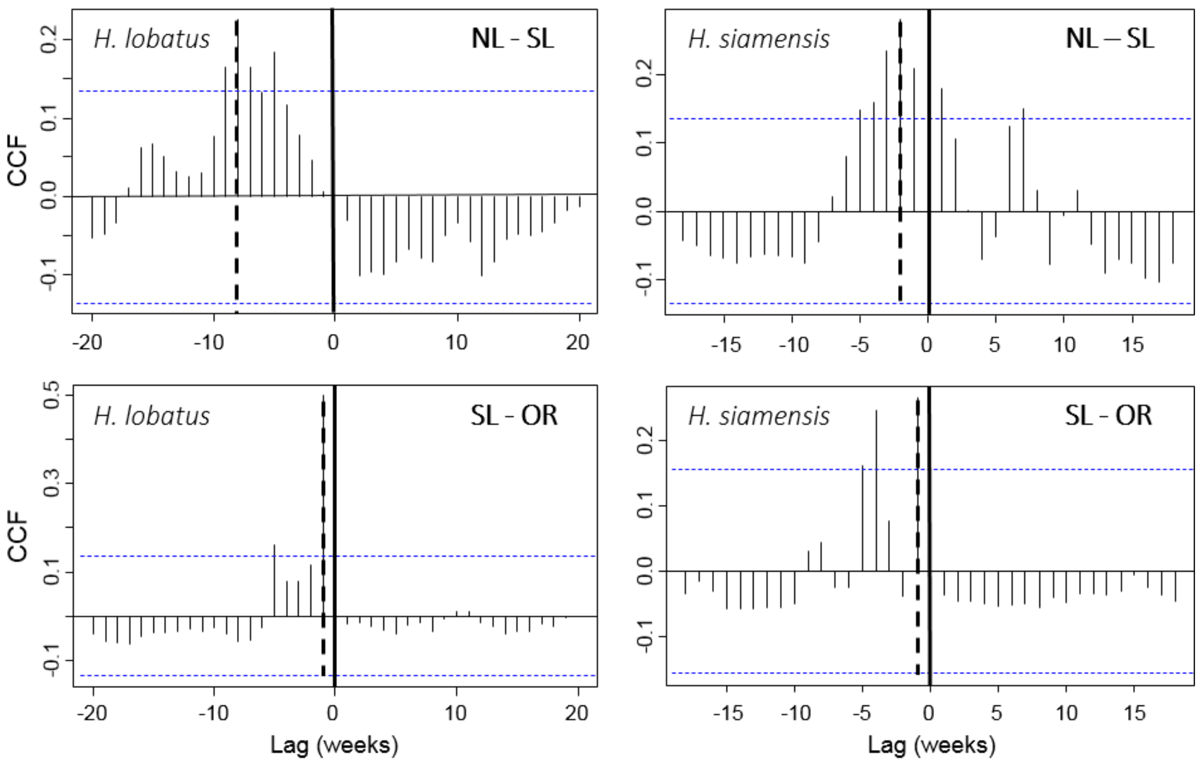

Figure 5.4 The CCF plots showing the time-lagged relationship of abundance of each species between paired sites, e.g. between the northern and southern TSL sites with NL as a predictor (x) and SL (y). Abbreviations are as follows. NL: the northern TSL, SL: the southern TSL and OR: the outlet river. The vertical bold-line indicates the lag at time zero (the peak value of y), the vertical dashed-line indicates the period with the highest correlation (the peak value of x), and the two horizontal dashed-lines indicate significant correlation values (i.e. a positive for the upper and a negative for the lower) at the 95% confident interval.

5.3.3. The time-lagged relationship with water levels

The results of the CCFs revealed that the highest water level always led the peak abundance of both species. The highest water level was 7 weeks ahead of the peak abundance of *H. lobatus* in NL, 14 weeks in SL, and 15 weeks in OR (Figure 5.5). On the other hand, the highest water level led the synchronisation and peak abundance of *H. siamensis* for 12 weeks in NL, 14 weeks in SL and 13 weeks in OR (Figure 5.6). Summaries of the in- and out-flow pulses, the peak water level, the peak abundance of the two fish species, and fish movement speed in the TSL are provided in Fig. 7.

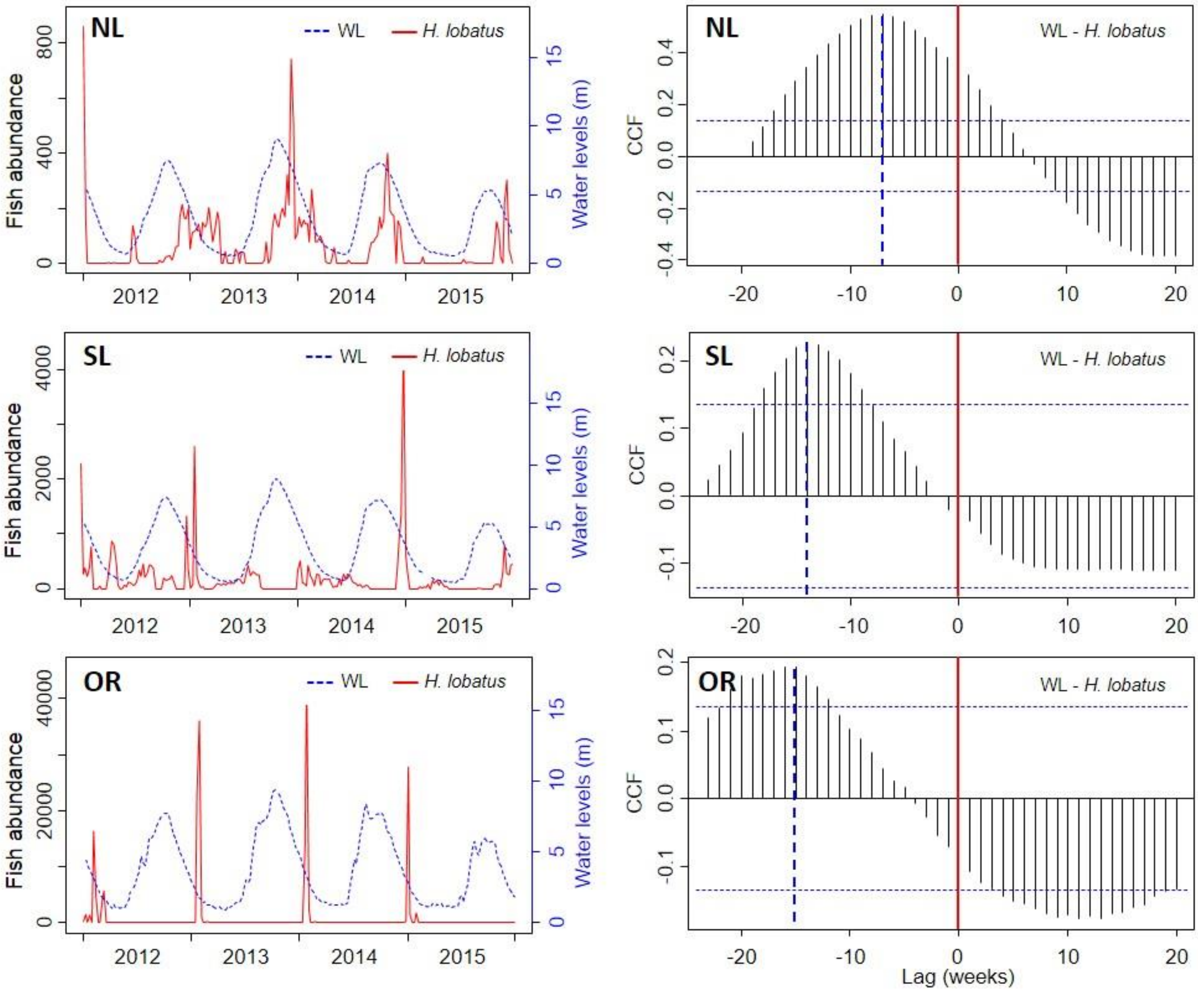

Figure 5.5 Time-series data of water levels (WL) and *H. lobatus* abundance (left panel), and the corresponding the time-lagged relationships obtained from CCF analysis (right panel) at each site. Abbreviations are as follows: NL: the northern TSL, SL: the southern TSL and OR: the outlet river. In the CCF models, WL was a predictor (x), and *H. lobatus* abundance was a dependent variable (y). On the CCF plots, the red vertical bold-line indicates the lag at time zero representing the peak period of fish abundance, the blue vertical dashed-line indicates the peak period of the water level, and the two blue horizontal dashed-lines indicate significant correlation values (i.e. a positive for the upper and a negative for the lower) at the 95% confident interval.

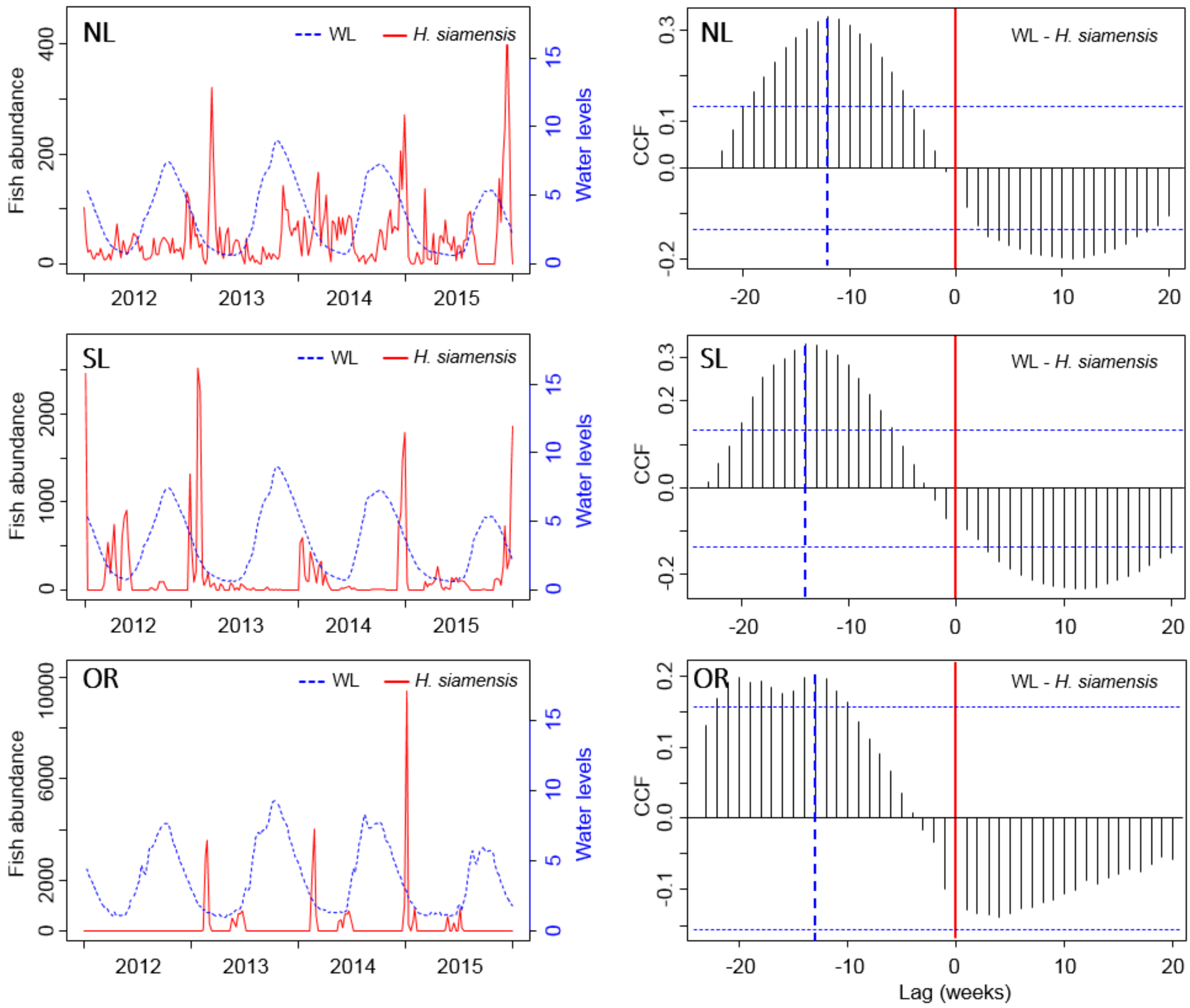

Figure 5.6 Time-series data of water levels (WL) and *H. siamensis* abundance (left panel), and the corresponding time-lagged relationships obtained from the CCF analysis (right panel) at each site. NL: the northern TSL, SL: the southern TSL and OR: the outlet river. In the CCF models, WL was a predictor (x), and *H. siamensis* abundance was a dependent variable (y). On the CCF plots, the red vertical bold-line indicates the lag at time zero representing the peak period of fish abundance, the blue vertical dashed-line indicates the peak period of the water level, and the two blue horizontal dashed-lines indicate significant correlation values (i.e. a positive for the upper one and a negative at the lower) at the 95% confident interval.

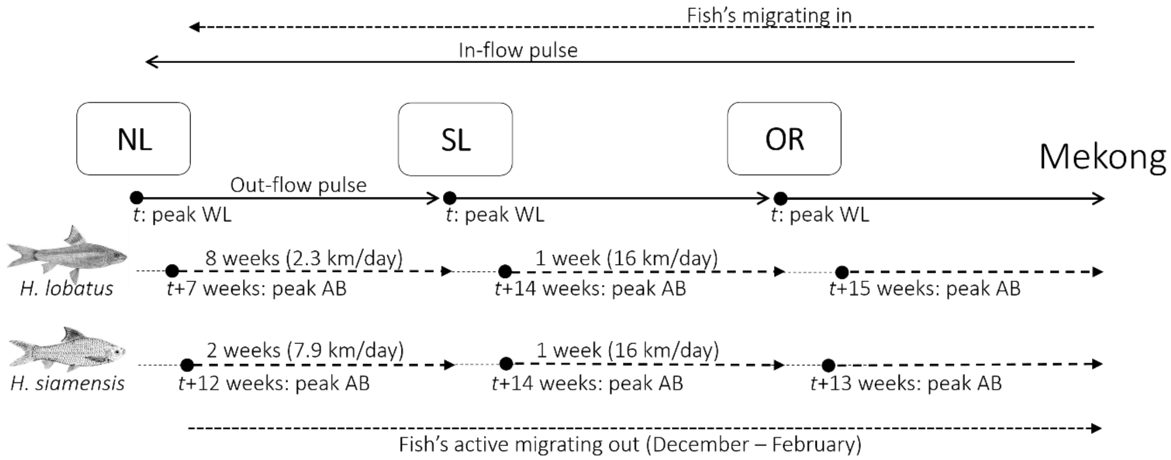

Figure 5.7 Summary of the synchronised movement pattern and speed of small mud carp species following flow pulses in the Tonle Sap Lake and Tonle Sap River. Abbreviations are as follows: t: time; WL: water levels; NL: the northern TSL; SL: the southern TSL; OR: the outlet river and AB: abundance. Photos of fish were retrieved from (Rainboth, 1996).

5.4. Discussion

5.4.1. Performance and applications of time-series analyses

The CWT and CCF play a significant role in our study. Explicitly, the CWT enabled us to highlight the co-occurrence and synchronisation of two species, whereas the CCF allowed us to determine the link between the flow pulse and fish abundance and identify the time lag between the peak of water level and fish synchronisation. The CCF thus allows us to identify the role of flood pulse in the dynamics of fish species in the TSE at both space and time. Our results could increase our understanding of how a flood-pulse system work. The CWT and CCF are helpful tools for time-series analysis to interpret how the flow pulse influences fish spatial and temporal dynamics. These two time-series modelling techniques provide complementary information for understanding the co-occurrence, synchronisation, and movement patterns of both fish species in a tropical flood-pulse ecosystem. The data used in this study were collected on a daily basis for four years (2012-2015), and such high-resolution data are rarely found in ecology. These high-resolution time-series data are valuable to build the CWT and CCF to model the spatial and temporal dynamics of fish species. Therefore, we believe that the results of this study can be used to improve flow pulse management and fishery resources conservation in the system.

5.4.2. The role of flow pulse in the spatial and temporal dynamics of fishes

We found a positive relationship of annual co-occurrence pattern between the two species at each site by the high-frequency periodicity of 46.9 to 52 weeks (corresponding to a period between October and December). However, the most distinctive pattern was found in only NL, as indicated by a very strong positive correlation (Figure 5.2; Supplementary material S1), suggesting that the most active and dynamic annual co-occurrence and synchronisation of the two species mainly happened in NL when their individuals are about to retreat to SL and then to OR, and finally to the Mekong River. For SL and OR, we found a strong and clear monthly co-occurrence pattern from December through February, as illustrated by the low-frequency periodicity of 3.9 to 4.4 weeks in the cross-wavelet analysis. This means that the monthly cycle of increasing (synchronisation and peak abundance) and decreasing trends in the abundance of each species occurs every month from December to February. Apart from falling water level, lunar phase appears to have a strong relationship with peak fish migration out of the TSL through the TSR as observed at the 100-year old *Dai* fishery (Ngor et al., 2018c). Therefore, related flow-pulse conditions play a key role in facilitating fish migrations, e.g. migration for dry season refuges, spawning and rearing/feeding. Changes in flow-pulse condition that caused by anthropogenic activities would disrupt spawning, rearing and feeding success of fish and thus their natural stocks.

Flow pulse is one of the main factors driving fish dynamics and their productions (Sverdrup-Jensen, 2002). Annual flow pulses, i.e. rising and falling water levels, play an important role in signalling fish migration and in opening up floodplain habitats for resources and fish reproduction (Poulsen et al., 2004, 2002; Sverdrup-Jensen, 2002; Welcomme, 1999). This pattern is also observed in our study, as inferred by the leading flow pulse over fish migrations into the TSL. The in-flow pulse from the Mekong River in the early wet season brings young individuals, newly hatched and countless larvae of *Henicorhynchus* spp. to the TSL and its surround floodplain area that are covered by flooded forest, shrub, and aquatic vegetation (Campbell et al., 2006; Poulsen et al., 2004; Sverdrup-Jensen, 2002). The area provides an array of food resources such as fruits, algae, aquatic vegetation and other macroinvertebrates (i.e. molluscs, insects, and crustaceans) (Sor et al., 2017). Additionally, the in-flow pulse also deposits a large volume of sediment flux into the TSL (Kummu et al., 2005), which contains paramount nutrient resources (e.g. phosphorus and nitrate contents) supporting the food webs in the Tonle Sap ecosystem as a whole (Sarkkula et al., 2004, 2003). The rich resources combined with large living space and stable environment in the TSE enhance the outburst of fish growth, including young individuals of *H. lobatus* and *H.*

siamensis particularly for the period from five to six months following the first in-flow pulse (Poulsen, 2003).

During the dry season, as expected, falling water lead to a more spontaneous response of small/short-bodied fishes. We found that the out-flow pulse triggers the retreat of each species to the Mekong River differently. Within the TSL, the out-flow pulse prompts the retreat of *H. lobatus* from NL to SL 7 weeks after the peak flow with the swimming speed of ~2.3 km/day, whereas *H.* siamensis retreated 12 weeks after the peak flow with swimming speed of ~7.9 km/day (Figure 5.4 & 7). In the small route from SL to the OR, individuals of the two species retreat with more or less the same speed (i.e. 1 week or ~16 km/day). This movement patterns could be explained by the heterogeneous and homogeneous habitats observed in the floodplain of the TSL and the river channel, respectively. Moreover, the speed of the out-flow pulse can also influence the retreat of each species to the Mekong River. As such, after the out-flow pulse begins, the species synchronise and migrate in a large school back to the TSL, then the TSR, and finally to the Mekong River for the dry season refuges and possibly for the spawning grounds upstream (DeGrandchamp et al., 2007; Ngor et al., 2018b). Our results further suggest that during the period of migrating out of the TSE, *H. lobatus*, but not *H. siamensis*, prefers moving to different habitats/floodplain areas within the TSL, where possible, retreating along with the gradually decreased water levels. Besides, the two species share similar movement patterns in the rivers that are characterised by a smaller passage and less variation in habitat characteristics. Therefore, all these flow pulse-related conditions play a key role in facilitating adult fish recruitment, which can guarantee an increased abundance of fish species observed at ~5 months after the in-flow pulse begins, as observed in our study and by Poulsen (2003).

5.4.3. Monitoring and management perspectives

Understanding the occurrence, synchronisation, and movement patterns of fish species and the influence of water level variation on their spatial and temporal dynamics provides useful knowledge to better understand fish species migration and behavioural ecology (Løkkeborg et al., 2002; Mcgill et al., 2006; Peoples and Frimpong, 2016; Pollock et al., 2014; Ruetz et al., 2005). This knowledge can be used to support more effective monitoring, management and conservation efforts at local and larger spatial and temporal scales. For instance, the timing of the retreat of the two species identified in this study delivers useful insights that can be used to support regulations and policy initiatives aiming for better management and conservation of the two species. Good initiatives will allow adult individuals to complete the next step of their life cycle, i.e. to freely pass through the TSR during their peak abundance. These individuals can consequently reach the refuge, spawning, rearing and feeding grounds in the upstream portions of the Mekong River, and its major tributaries and can thus sustain the annual production.

Furthermore, our findings can act as a fundamental baseline for investigations of other economically and ecologically important species. In the case that further studies investigating different keystone species find similar synchronisation and peak abundance periods and similar movement patterns and timing in their retreats, these results will together provide key knowledge to support better monitoring and management of fisheries resources in the TSE. Also, the spatial and temporal dynamics of fish are found to be fine-turned with the natural flow-pulse variation. Maintaining such conditions are therefore necessary for fish species to migrate to complete their life cycles. Human actions such as hydropower dams that alter natural flow-pulses of the Mekong, i.e. change in flow seasonality and predictability is highly likely to also alter fish assemblage structure and their composition, fish migration patterns and spawning decisions which consequently have severe implication on fish reproductive, rearing and feeding successes (Ngor et al., 2018b). Finally, our study demonstrated that the CWT and CCF are useful time-series modelling approaches for investigating the phase relationship, joint periodicity, and the time-lagged relationship between environmental parameters (e.g. water level) and fish species in the flood-pulse ecosystems.

5.5. Conclusions

Investigating the spatial and temporal dynamics of fish species enables ecologists and fisheries managers to better understand variation in their occurrence, synchronisation, peak abundance and movement patterns, and the key factors driving such variation. By using modern time-series modelling approaches, i.e. the CWT and CCFs, to analyze high-resolution time-series data, we found that for this study, the two small mud carp species can co-occur together, but the synchronisation and movements of *H. lobatus* always lead those of *H. siamensis*. The annual re-occurrence (a long periodicity) of each species was detected in NL between October and December, while their monthly re-occurrence (a short periodicity) was mainly observed in OR from December to February. Moreover, after water recession in the TSL, *H. lobatus* individuals began to retreat earlier than *H. siamensis* individuals. However, the former species retreats (~2.3 km/day) slower than the latter species (~7.9 km/day), but they retreated at similar speeds when they reached the outlet river (TSR) at ~16 km/day. These patterns were found to correspond to the variation in water levels across the TSE, suggesting that the flow pulse is one of the main factors responsible for the temporal dynamics of the small mud carp species in the TSE. Therefore, the seasonality and predictability of the Mekong River should be maintained to sustain the natural dynamics of fish species (e.g. the periods of recruitment, synchronisation, peak abundance and movements) that have long developed and adapted to such a flood-pulse system. The timing of migration and swimming speed of the two species identified in this study should be an important part of regulation or policy consideration to better manage and conserve the two species. The ability of the CWT to analyze coherency enabled us to highlight the co-occurrence and synchronisation periodicity of two species, whereas the CCF allowed us to determine the link between the flow pulse and fish abundance and identify the lag between the peak water peak and fish synchronisation. The CCF thus allows us to identify the role of flood-pulse in the dynamics of fish species in the TSE at spatial and temporal scales.

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Supplementary

Table S1: Mean of the cross-wavelet power showing synchronisation periods of two small mud carp species at three sampling sites. The period with high correlation and synchronisation are shown in bold. Abbreviations are as follows: mean-crs-pw: the mean of the cross-wavelet power between the two time series (i.e., *H. lobatus* and *H. siamensis*); NL: the northern TSL; SL: the southern TSL and OR: the outlet river.

period (week)	mean-crs-pw-NL	mean-crs-pw-SL	mean-crs-pw-OR
2.000	0.028	0.078	0.088
2.071	0.034	0.095	0.105
2.144	0.038	0.110	0.119
2.219	0.042	0.121	0.130
2.297	0.045	0.128	0.137
2.378	0.047	0.130	0.141
2.462	0.048	0.129	0.143
2.549	0.049	0.126	0.144
2.639	0.049	0.122	0.146
2.732	0.050	0.120	0.149
2.828	0.051	0.119	0.153
2.928	0.052	0.121	0.158
3.031	0.053	0.125	0.163
3.138	0.056	0.132	0.168
3.249	0.060	0.141	0.174
3.364	0.064	0.153	0.179
3.482	0.068	0.164	0.183
3.605	0.072	0.175	0.187
3.732	0.076	0.183	0.190
3.864	0.078	0.188	0.192
4.000	0.081	0.191	0.193
4.141	0.083	0.191	0.194
4.287	0.088	0.190	0.193
4.438	0.092	0.188	0.192
4.595	0.095	0.185	0.190
4.757	0.098	0.181	0.188
4.925	0.099	0.176	0.186
5.098	0.100	0.169	0.183
5.278	0.099	0.160	0.180
5.464	0.097	0.151	0.178
5.657	0.093	0.143	0.175
5.856	0.087	0.135	0.172
6.063	0.080	0.128	0.169
6.277	0.074	0.121	0.166
6.498	0.069	0.116	0.163

6.727	0.065	0.113	0.159
6.964	0.063	0.111	0.156
7.210	0.063	0.110	0.153
7.464	0.064	0.108	0.150
7.727	0.066	0.107	0.147
8.000	0.067	0.107	0.145
8.282	0.068	0.109	0.142
8.574	0.067	0.112	0.139
8.877	0.065	0.114	0.135
9.190	0.062	0.115	0.131
9.514	0.057	0.114	0.126
9.849	0.052	0.113	0.121
10.196	0.048	0.114	0.116
10.556	0.048	0.115	0.112
10.928	0.053	0.117	0.110
11.314	0.061	0.120	0.109
11.713	0.071	0.124	0.109
12.126	0.080	0.126	0.110
12.553	0.085	0.128	0.111
12.996	0.087	0.127	0.112
13.454	0.086	0.125	0.111
13.929	0.082	0.124	0.108
14.420	0.079	0.122	0.105
14.929	0.075	0.120	0.105
15.455	0.073	0.119	0.107
16.000	0.073	0.121	0.110
16.564	0.073	0.125	0.110
17.148	0.074	0.128	0.106
17.753	0.074	0.128	0.098
18.379	0.072	0.125	0.088
19.027	0.068	0.118	0.077
19.698	0.062	0.109	0.067
20.393	0.057	0.099	0.061
21.112	0.053	0.092	0.059
21.857	0.054	0.089	0.062
22.627	0.058	0.090	0.066
23.425	0.066	0.095	0.071
24.251	0.075	0.100	0.074
25.107	0.084	0.104	0.074
25.992	0.090	0.104	0.070
26.909	0.091	0.100	0.062
27.858	0.089	0.091	0.052
28.840	0.082	0.080	0.041
29.857	0.075	0.069	0.030
30.910	0.071	0.059	0.022

32.000	0.067	0.051	0.017
33.128	0.063	0.044	0.015
34.297	0.059	0.038	0.015
35.506	0.055	0.034	0.017
36.758	0.060	0.032	0.020
38.055	0.072	0.033	0.024
39.397	0.089	0.036	0.029
40.786	0.112	0.041	0.035
42.224	0.136	0.046	0.042
43.713	0.160	0.050	0.049
45.255	0.180	0.055	0.054
46.851	0.195	0.062	0.059
48.503	0.203	0.067	0.061
50.213	0.201	0.069	0.061
51.984	0.191	0.068	0.058
53.817	0.172	0.063	0.054
55.715	0.148	0.054	0.048
57.680	0.120	0.044	0.040
59.714	0.092	0.033	0.033
61.820	0.068	0.024	0.025
64.000	0.049	0.016	0.018
66.257	0.037	0.012	0.013
68.594	0.030	0.010	0.009
71.012	0.023	0.010	0.007
73.517	0.017	0.011	0.006
76.109	0.012	0.011	0.004
78.793	0.010	0.011	0.003
81.572	0.009	0.010	0.003
84.449	0.009	0.009	0.002
87.427	0.008	0.008	0.002
90.510	0.007	0.006	0.002
93.701	0.007	0.005	0.002
97.006	0.007	0.005	0.002
100.427	0.007	0.004	0.001
103.968	0.006	0.004	0.001
107.635	0.006	0.003	0.001
111.430	0.007	0.003	0.001
115.360	0.009	0.003	0.001
119.428	0.011	0.003	0.001
123.640	0.012	0.003	0.001
128.000	0.013	0.003	0.001
132.514	0.013	0.003	0.001
137.187	0.013	0.004	0.001

Chapter VI: Effectiveness of fisheries policy reforms to maintain fish diversity and abundance in Tonle Sap Lake

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Abstract

Tonle Sap Lake supports high fisheries products that are of paramount importance to supply protein for more than 15 million Cambodian people and export. Therefore, to sustain the fisheries resources, deal with conflicts raised between the local fishers and the owners of the commercial fishing lots, and ensure the equity of benefits from the resources derivation, the fisheries policy reforms was launched since 2005. It enabled the removal of all commercial fishing lots from Tonle Sap Lake in 2012. The fishing lot areas were apportioned to be conservation area and community fishing area that fisheries resources were managed by community fisheries. Meanwhile, both operation and removal of the commercial fishing lots have its own positive and negative effects on fish ecology and fisheries. Here, we investigated the effects of the fisheries policy reforms on the overall fisheries, fish community composition and structure in Tonle Sap Lake using time-series data of fish catch. We detected a stable trend in fish biomass in the before fishing lot abolishment period, whereas the temporally decreasing trend was observed in the after fishing lot abolishment period. Moreover, there was a significant change in fish community composition before and after fishing lot abolishment. Specifically, we found that although some species were not affected by the fisheries reform, others had an increasing or decreasing trend according to the species. Overall, the fisheries policy reforms positively benefited the small fish species with short distance migration, low trophic level, and inhabiting the surface of the water column. In contrast, the fisheries reforms negatively affected the large benthic fish species with long-distance migration and high trophic level. In conclusion, the decline in the fish biomass of the lake was affected by the fact that the local fishers attempt to exploit the common-pool fisheries resources of the lake as much as they can without thinking the adverse effects while the community fishing areas are freely accessible to fishing. This framework coined as "the tragedy of the commons", could generate a decline of fish resources in the Tonle Sap Lake and we suggest to improve fisheries rules and law enforcement to manage, conserve and ensure sustainability of the biodiversity and fisheries resources of the Tonle Sap Lake as well as Cambodia through improving the capacity for the local community, conserving the flooded forest and eliminating the illegal fishing practices.

KEYWORDS: fishing lot abolishment, the tragedy of the commons, indiscriminate fishing, fish community structure, size effect

6.1 Introduction

Tonle Sap Lake (TSL) is the largest natural inland lake in Southeast Asia (MRC 2005) and the world's fourth most productive inland fishery (Baran 2005). TSL fisheries resources represent approximately 60% of Cambodia's total annual production of inland capture fisheries of 767,000 tonnes (Hortle & Bamrungrach 2015). TSL, therefore, plays a crucial role in providing fish products and protein to nearly two million people in the region (Sabo et al. 2017). In addition to its crucial role as a protein source, TSL also hosts some 296 fish species (Baran et al. 2013). It is, therefore, considered a biodiversity hotspot (Allen et al. 2012) and has had the status of a world heritage biosphere reserve of the United Nations Educational, Scientific and Cultural Organization (UNESCO) since 1997 (UNESCO 2018).

The fishing areas delineated by the Royal Government of Cambodia for commercial fisheries are called fishing lots (Ly and VanZalinge, 1998). The operation system of the commercial fishing lots had been introduced since 1908 by French protectorate (MRC 2012). The procedures for the auction and management of the fishing lot are based on the sub-decree attached to the Cambodian fisheries law (Halls et al. 2013). Based on this law, the fishing lot operated from October to May. While generating national revenues from auctioning the productive fishing grounds, fisheries management through the application of fishing lot system was also a permanent source of conflicts between the commercial fishing lot owners and subsistence fishers on access rights to the fisheries resources (Bonheur & Lane 2002; Ratner 2006; Cooperman et al. 2012; Dina & Sato 2014).

For this reason, and to ensure the equity of benefits from the resources derivation, and sustain the fisheries resources, the Royal Government of Cambodia have introduced the fisheries policy reforms since 2001, and declared officially the removal of the commercial fishing lots from the Lower Mekong watershed in Cambodia on February 2012 (Ratner 2006; Cooperman et al. 2012; MRC 2012). Then, the area covered by the fishing lots (more than 1 million hectares) were apportioned to be conservation area (~24%) and community-use areas

(~76%) for the family level fishing purpose (Cooperman et al. 2012; MRC 2012). The purpose of the fisheries reforms was to support the community-based management in fisheries or other natural resources (Ratner 2006). Given that the large-scale fishing were beneficial to only small group people, i.e. the lot owners, the transition from the commercial fishing lots operation to community fisheries was aiming at sharing the properties (i.e. fisheries products and aquatic resources) to all, especially the local fishers for subsitence, because the propterties do not belong to a small group of people (Dina & Sato 2014).

There are positive and negative effects for both operation and removal of the commercial fishing lots on fish ecology and fisheries in Tonle Sap Lake. Within the commercial fishing lots system-based management, the barrage fishery limited the spatial distribution and migration of fish species. It was, moreover, believed that fish species had been intensively exploited in fishing lot system that represents 20% of the total Tonle Sap Lake area (Cooperman et al. 2012). Indeed, the barrage fishery systems of the fishing lots allow fishers to harvest fish population in the fishing lots boundary easily (Halls et al. 2013) resulting in an increase in fishing pressure on fisheries resources of the lake. However, the aquatic habitats, i.e. the inundated forest, grassland and shrubland and rice fields (Halls et al. 2013), were properly protected by the the commercial fishing lots owners to sustain the fisheries resources for their next harvest. In contrast, the removal of the commercial fishing lots allowed fish species to freely migrate and conduct a substantial spatial distribution which may facilitate for breeding and enhance the genetic pool. Nevertheless, the removal of the commercial fishing lots enabled the community fishing area to be freely accessible to all (Ratner 2006). Given that the fisheries law is poorly enforced, the illegal fishing practices prevail. Thus, fisheries resources had been intensively exploited by the local fishers (Ratner 2006). In addition, the aquatic habitats (i.e. flooded forest and shrubland) are degraded, e.g. through conversion of flooded forest into the agricultural fields (Cooperman et al. 2012).

To date, many studies have highlighted and discussed about the effectiveness of the Cambodian fisheries policy reforms in Tonle Sap Lake in terms of property right, governance, management policy and legislation, as well as reviewed and expected the fisheries status according to the biological and ecological features of fish species, i.e. (Ratner 2006; Cooperman et al. 2012; Dina & Sato 2014, 2015; Ratner et al. 2014; Sok 2014). However, providing the statistical evidence about the characteristics of fisheries and fish species that were impacted by this fisheries policy reforms are lacking.

Thus, the present study, we investigate the effects of the commercial fishing lot abolishment on a temporal change in fish catch and fish community structure in Tonle Sap Lake. Specifically, we first investigate the temporal trends in fish catches before and after the fishing lot abolishment. Second, we compare fish community composition before and after the fishing abolishment period. Then, we identified fish species changed between the two periods (e.g. whether they increased, decreased and were stable?). Finally, we associate the status of each fish species (i.e. increase, decrease and stable before and after the fishing abolishment) with their morphological and biological traits to examine whether changes were related to some specific functional traits of fish species.

6.2 Material and methods

6.2.1 Sites description

The study was carried out in Tonle Sap Lake located in the northwest part of Cambodia (Figure 6.1). TSL is the largest freshwater lake in Southeast Asia and is the largest floodplain of the Mekong basin. TSL is connected to the Mekong River by the Tonle Sap River (TSR). The lake area can be as large as 14,500 km^2, while the amount of water in the lake can be as much as 80 km^3, and the maximum water depth is 9 metres (MRC 2005). A large number of floodplain areas were inundated and formed large breeding, spawning, nursery and foraging areas for the fishes (Baran et al. 2007).

6.2.2 Data collection

This study used monthly fish catch weight data (kg) from stationary gillnets that were monitored before (1995-2000) and after (2012-2015) fishing lot abolishment around Tonle Sap Lake (Figure 6.1). The fish data used in this study were provided by the Fisheries Programme of the Mekong River Commission (MRC) in collaboration with the Cambodian Department of Fisheries (currently called the Fisheries Administration [FiA]) and financially supported by Danish International Development Agency (DANIDA) (Ly and VanZalinge, 1998). Our focus here was to compare fish community composition patterns between the two periods. We, thus, used only the datasets that contain the comparable method and fishing efforts between the two datasets, e.g. gillnet mesh size ranging from 2.5-7 cm for before lot abolishment data and gillnet mesh size ranging from 2 -6.5 cm for after lot abolishment data.

For the before fishing lot abolishment (BLA) period, the fish biomass data was monthly collected from TSL from 1995 to 2000. For after fishing lot abolishment (ALA) period, data collection were carried out on a daily basis in Tonle Sap Lake from January 2012 to December 2015, it later translated into monthly basis to be comparable between the two periods. The catch monitoring approach follows the MRC's regional monitoring method applied in the Lower Mekong Basin (MRC 2008; Ngor et al. 2014). The data were collected by the local fishers trained in sampling technique, fish identification and recording (Deap et al. 2003). Identification was based on the common names combined with a review of previous studies and consultation with MRC's experts; further, identification followed the keys in Rainboth (1996) and enumerated and recorded in a logbook. The logbooks were then collected from fishers on a quarterly basis and cross-checked by research specialists. Unidentified species were later identified by an expert taxonomist in the laboratory.

Fish morphological traits and trophic level data were derived from the FishBase (Froese & Pauly. 2017). The information about fish biological traits (i.e. migration and the position of water column) was reviewed and derived from (Poulsen et al. 2004; Froese & Pauly

2017; Ngor et al. 2018a). The summary of fish morphological and biological traits are given in Supporting Information S1.

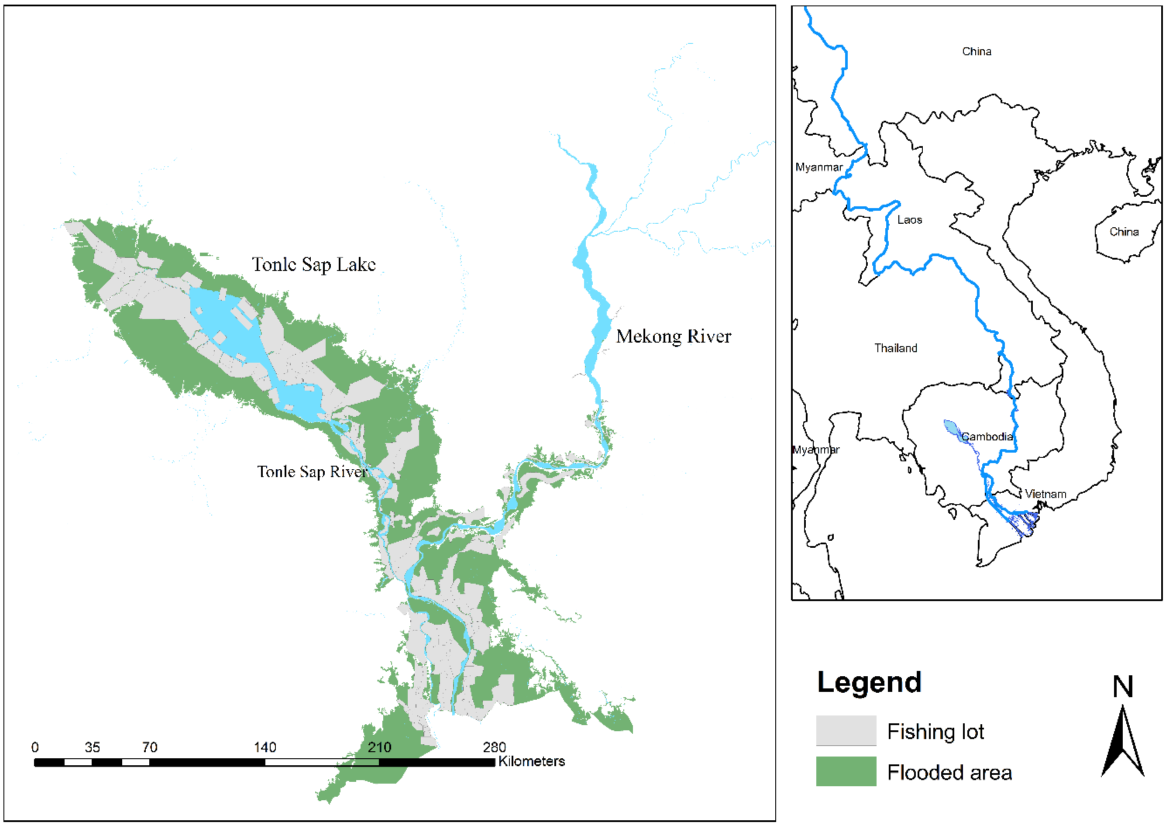

Figure 6.1 Map showing the fishing lots in Tonle Sap Lake, Tonle Sap River, Basac River, and Mekong River. The minimal area of TSL during the dry season is in blue and the green represent maximal area of TSL during the flooded season. Fishing lots are in grey.

6.2.3 Data preparation and statistical analyses

In this study, we focused on the most commercial 55 fish species because they were recorded in detail from the fishing gear catch assessment during before fishing lot abolishment. Further, the monthly fish catch weight data were transformed into monthly relative weight catches to reduce the effects of sampling efforts before comparison.

First, the temporal trend of fish biomass of the two periods was illustrated using the average monthly time-series data of fish biomass. Simple Moving Average (SMA) was performed to smooth the temporal trends in fish biomass.

Non-metric multidimensional scaling (NMDS) with Bray–Curtis similarities distance (Bray & Curtis 1957) was performed to illustrate a change in fish community composition between the BLA and ALA. The NMDS is a rank based method attempting to represent the pairwise dissimilarity between sampling units in a two-dimensional space.

Analysis of similarity (ANOSIM, Clarke, 1993) was also used to test for significant difference in fish community composition between the two periods: the BLA and ALA. ANOSIM is a nonparametric multivariate procedure broadly analogous to analysis of variance (ANOVA) that has been widely used for testing whether or not groups of sites are statistically different with respect to their relative similarities in the community composition (Clarke 1993). ANOSIM was conducted on Bray–Curtis dissimilarities matrix calculated among samples (Oksanen et al. 2015). The ANOSIM result was assessed according to a *P*-value (significant difference between groups) of the statistical significance which determined whether or not the result was likely due to a result of chance and the statistic-*R* value (correlation coefficients between groups) which provides a measure of effect size (Clarke 1993). A statistic-*R* value ranges from -1 to +1, and that is based on the rank similarities of samples within versus among a priori groups. A large *R*-value (close to 1) is indicative of complete separation between groups, while a small value (close to 0) implies little or no separation, and *R*-values below zero suggest that dissimilarities are greater within groups than between groups (Clarke & Warwick 2001). We conducted 999 random permutations to assess the statistical significance.

Then, we further applied the similarity percentages (SIMPER, Clarke, 1993) procedure to assess which species was the most significant contribution to the dissimilarity of the composition between the BLA and ALA. SIMPER identifies which fish species made the highest contribution to be different between the two groups in a Bray-Curtis dissimilarity matrix (Oksanen et al. 2015). The contribution of each species to Bray-Curtis measurement was calculated after square root transformation, and then the species were ranked in two separated groups, percentage, and cumulative percentage (Clarke & Warwick 2001). SIMPER analysis produced average contribution from taxa to overall dissimilarity between two groups (i.e. a & b) (average), standard deviation of contribution (sd), ratio average to sd ratio (ratio), average abundances per group (av.a & av.b), and ordered cumulative contribution (cum) (Clarke & Warwick 2001; Oksanen et al. 2015). We conducted 99 random permutations to assess the statistical significance.

Finally, a principal component analysis (PCA) was performed to relate the status of fish species (i.e. decreasing, increasing, and stable) to their morphological and biological traits. The analysis allows us to summarise information about the changes that were related to some specific groups or functional traits and size class of fish species.

We selected the 95% confidence interval as a significance criterion for ANOSIM and SIMPER. Also, NMDS, ANOSIM, SIMPER, and PCA were performed using the "vegan" package (Oksanen et al., 2015). The SMA was carried out using the "ggplot2" package (Wickham 2009). All statistical analyses were performed using *R* program v.3.3.3 for Windows statistical software package (http://www.r-project.org)(R Core Team 2017).

6.3 Results

We detected a stable trend in fish biomass collected from the before fishing lot abolishment period. In contrast, we observed a decreasing trend in fish biomass after the removal of the commercial fishing lots. Moreover, a lower seasonal variation in fish biomass was observed after the fishing lot abolishment (Figure 6.2)

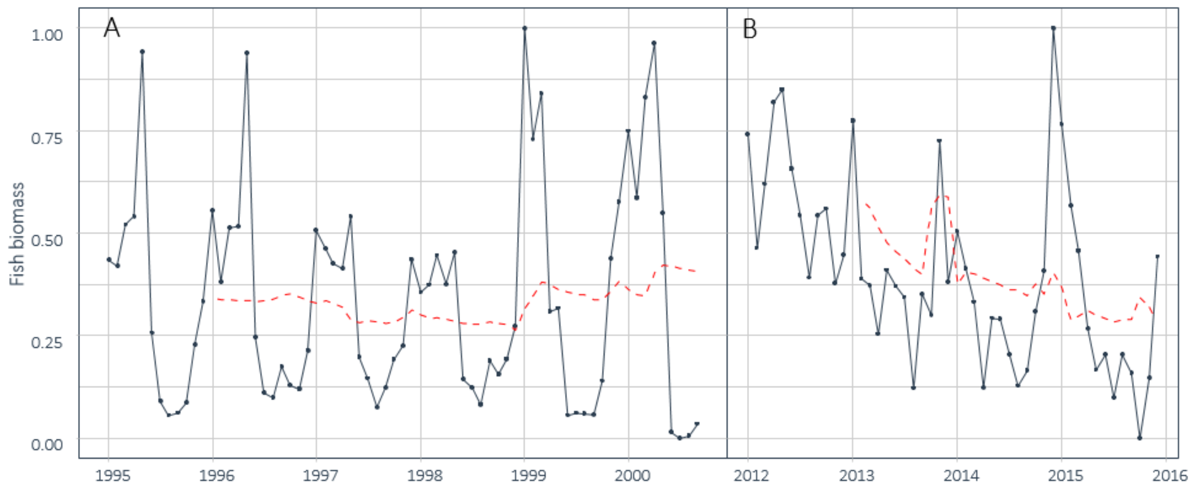

Figure 6.2 (A) A time-series of monthly fish biomass over a 6-yr period collected from the before fishing lot abolishment (1995-2000). (B) A time series of monthly fish biomass over a 4-yr period collected from the after fishing lot abolishment (2012-2015). A red line represents the mean fish biomass at the zero to one scale, whereas the black line represents the general trends of fish biomass performed by the simple moving average.

NMDS (stress=0.215) showed the difference in fish community composition between the two periods along the first axis. There was a significant change in fish community composition between the BLA and ALA as indicated by ANOSIM (global R_{ANOSIM}=0.377, *P*-value=0.001; Figure 6.3).

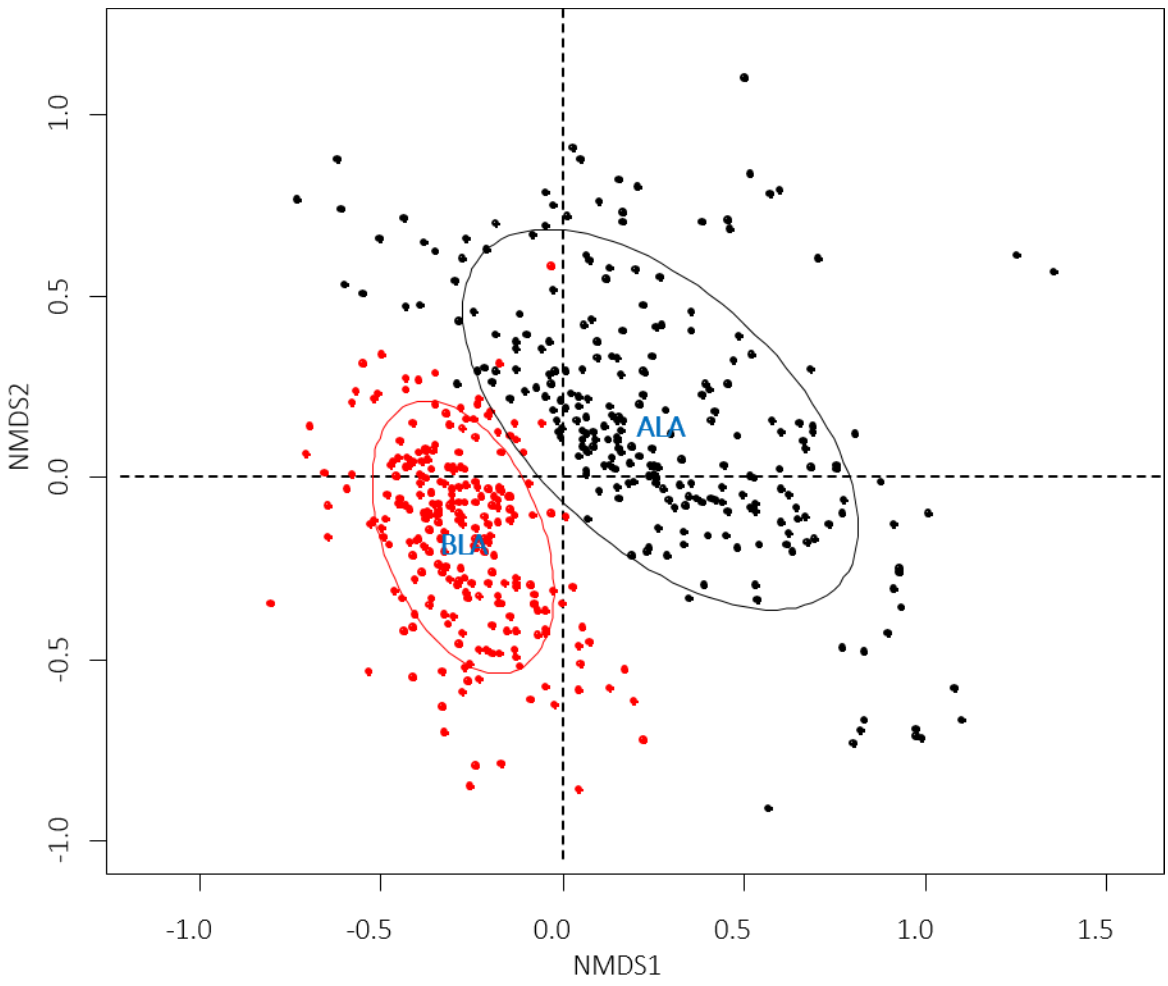

Figure 6.3 A two-dimensional NMDS plot showing the fish assemblages from the before after fishing lot abolishment. The red dots and black dots symbolise the samples of fish collected before and after fishing lot abolishment period, respectively. The ellipse represents the first standard deviation (1SD confident interval).

SIMPER analysis showed the species that contributed to the change between the BLA and ALA (Table 6.1). In short, some species had an increasing trend, whereas others species had a decreasing trend between the two periods, while other species are stable.

Table 6.1 SIMPER results showing the dynamics of fish species according to a pairwise comparison between before and after fishing lot abolishment. Abbreviations are as follows: av.before= average biomass for the before fishing lot abolishment period; av.after= average biomass for the after fishing lot abolishment period; comsum= ordered cumulative contribution; "-"=decreasing trend; "+"=increasing trend; "n"= non-change or stable. Fish species with significant change (*p*-value < 0.05) are in bold.

Species	code	av. before	av. after	cumsum	*p*-value	Change
Henicorhynchus spp.	Hespp	11.960	16.280	0.096	**0.010**	+
Cyclocheilichthys enoplos	Cyeno	13.397	2.791	0.181	**0.010**	-
Puntioplites proctozysron	Pupro	2.951	10.612	0.247	**0.010**	+
Mystus spp.	Myspp	3.575	8.897	0.301	**0.010**	+
Channa micropeltes	Chmic	7.044	0.696	0.351	**0.010**	-
Trichopodus microlepis	Trmic	5.163	4.168	0.398	**0.010**	-
Osteochilus vittatus	Osvit	4.503	7.930	0.445	**0.010**	+
Hypsibarbus spp.	Hyspp	6.358	4.640	0.483	**0.010**	-
Channa striata	Chstr	3.092	3.103	0.516	0.130	n
Labiobarbus leptocheilus	Lalep	3.991	0.939	0.547	**0.010**	-
Hemibagrus spilopterus	Hespi	4.172	1.743	0.578	**0.010**	-
Notopterus notopterus	Nonot	0.913	3.831	0.605	**0.010**	+
Xenentodon cancila	Xecan	0.358	3.284	0.631	**0.010**	+
Anabas testudineus	Antes	1.242	3.563	0.656	**0.010**	+
Cyclocheilichthys armatus	Cyarm	2.410	1.610	0.677	**0.010**	-
Labeo chrysophekadion	Lachr	1.653	2.760	0.696	**0.010**	+
Labiobarbus siamensis	Lasia	0.377	2.429	0.715	**0.010**	+
Clarias spp.	Clspp	0.516	2.233	0.733	**0.010**	+
Thynnichthys thynnoides	Ththy	1.894	1.543	0.749	**0.010**	-
Osteochilus melanopleurus	Osmel	2.291	0.974	0.765	**0.010**	-
Pangasianodon hypophthalmus	Pahyp	1.528	1.355	0.780	**0.010**	-
Paralaubuca typus	Patyp	0.842	1.579	0.795	**0.030**	+
Pristolepis fasciata	Prfas	0.780	2.136	0.809	**0.010**	+
Cirrhinus microlepis	Cimic	1.872	0.304	0.823	**0.010**	-

Parambassis wolffii	Pawol	1.523	1.503	0.837	0.320	n
Setipinna melanochir	Semel	1.837	0.000	0.850	**0.010**	-
Boesemania microlepis	Bomic	0.748	0.974	0.860	0.260	n
Hampala dispar	Hadis	1.359	0.188	0.870	**0.010**	-
Puntius brevis	Pubre	1.136	0.243	0.879	**0.010**	-
Coilia spp.	Cospp	0.922	0.383	0.888	**0.010**	-
Albulichthys albuloides	Alalb	0.671	0.504	0.896	**0.030**	-
Amblyrhynchichthys truncatus	Amtru	0.482	0.877	0.904	0.130	n
Oxyeleotris marmorata	Oxmar	0.043	1.077	0.912	**0.010**	+
Belodontichthys truncatus	Betru	0.966	0.145	0.919	**0.010**	-
Pangasius larnaudii	Palar	0.423	0.803	0.926	**0.030**	+
Wallago attu	Waatt	0.940	0.167	0.934	**0.010**	-
Parachela siamensis	Pasia	0.719	0.217	0.940	**0.010**	-
Pangasius spp.	Paspp	0.381	0.602	0.946	0.700	n
Polynemus multifilis	Pomul	0.802	0.032	0.952	**0.010**	-
Micronema spp.	Mispp	0.639	0.105	0.957	**0.010**	-
Ompok hypophthalmus	Omhyp	0.634	0.010	0.961	**0.010**	-
Systomus orphoides	Syorp	0.368	0.267	0.966	0.100	n
Chitala ornata	Chorn	0.516	0.121	0.970	**0.010**	-
Leptobarbus hoevenii	Lehoe	0.279	0.429	0.974	0.140	n
Trichopodus pectoralis	Trpec	0.062	0.530	0.978	**0.010**	+
Pao cambodgiensis	Pacam	0.517	0.009	0.982	**0.010**	-
Kryptopterus cryptopterus	Krcry	0.462	0.028	0.986	**0.010**	-
Cosmochilus harmandi	Cohar	0.130	0.381	0.989	**0.010**	+
Yasuhikotakia spp.	Yaspp	0.067	0.397	0.992	**0.010**	+
Probarbus jullieni	Prjul	0.273	0.085	0.995	0.130	n
Parambassis apogonoides	Paapo	0.100	0.249	0.997	0.590	n
Barbonymus altus	Baalt	0.048	0.132	0.998	0.060	n
Gyrinocheilus pennocki	Gypen	0.002	0.133	0.999	0.070	n
Achiroides leucorhynchos	Acleu	0.066	0.010	1.000	**0.010**	-
Channa lucius	Chluc	0.002	0.002	1.000	0.710	n

The two first axes of the PCA accounted for 64.81% of the total variance (37.89% and 26.92%, respectively; Figure 6.4). The water column depth opposite to trophic level of fish species in the first axis, and negative values correspond to the water column and positive value to the trophic level position. The migration distance and maximum total length of fish species were linked to the positive values of the second axis, and corresponding to the longer migration distance and larger fish species. The increasing changes were mainly found for the small fish species with short-distance migration, low trophic level, and surface water column position, e.g. *Henicorhynchus* spp. (Hespp), *Labiobarbus siamensis* (Lasia), *Clarias* spp. (Clspp) and *Anabas testudineus* (Antes) (Figure 6.4). However, an increasing change was found for the large fishes: *Xenentodon cancila* (Xecan), *Oxyeleotris marmorata* (Oxmar) and *Pangasius larnaudii* (Palar). Furthermore, the decreasing changes were observed mainly the large, long-distance migration, and higher trophic level fish species, e.g. *Cyclocheilichthys enoplos* (Cyeno), *Cirrhinus microlepis* (Cimic), *Channa micropeltes* (Chmic), *Wallago attu* (Waatt) and *Pangasianodon hypophthalmus* (Pahyp). However, there is still some mix while the decreasing change was observed for small fishes: *Trichopodus mirolepis* (Trmic), *Kryptopterus cryptopterus* (Krcry), *Hampala dispar* (Hadis), *Ompok hypophthalmus* (Omhyp), *Puntius brevis* (Pubre), *Labiobarbus leptocheilus* (Lalep), *Hypsibarbus* spp. (Hyspp), *Thynnichthys thynnoides* (Ththy), *Cyclocheilichthys armatus* (Cyarm), *Hemibagrus spilopterus* (Hespi) and *Parachela siamensis* (Pasia).

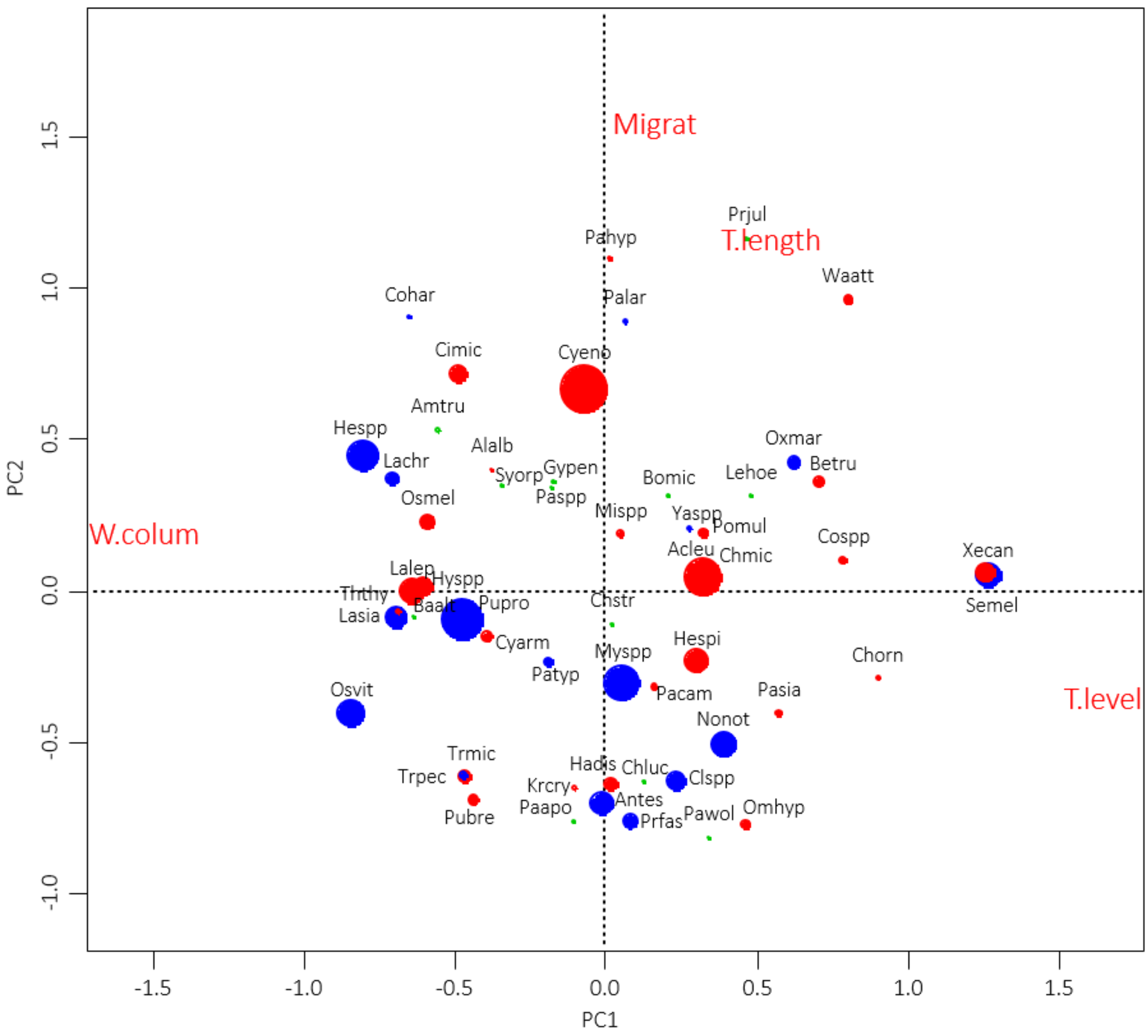

Figure 6.4 PCA biplot showing the association between the status of fish species (increase, decrease, and stable in catches before and after fishing lot abolishment) and their morphological and biological traits. The blue, red and green dots symbolise species with the increasing trends, decreasing trends, and stable, respectively. The size of the dot represents the level of change (proportion) of fish species between the two periods. Abbreviations include: T.Length= maximum total length; T.level= trophic level; W.colum= water column; Migrat= the distance of migration. The full names of fish species were given in Table 6.1.

6.4 Discussion

The Cambodian fisheries reforms allows the removals of the commercial fishing lots from the Tonle Sap Lake to be made. Thus, the area covered by the commercial fishing lots were converted into the conservation area and community fishery area (Cooperman et al. 2012; MRC 2012). The purpose of the commercial fishing lots removal is to share the properties (i.e. fisheries and aquatic resources) to the local fishers because the fisheries resources are not belong to a small group of people. Then, the management of the Tonle Sap fisheries resources was based on a number of community fisheries around the lake.

The results showed that the removal of the commercial fishing lots within Tonle Sap Lake enabled a decreasing trend of fish biomass. Inland fisheries are generally dynamic and rarely sustainable (Pauly et al. 2002; Welcomme et al. 2010). In this regards, overfishing is caused by an intensive fishing pressure formed the treatment effect on the decrease in fisheries resources of the Tonle Sap system (Ngor et al. 2018b) as well as in overall fisheries (Cooke & Cowx 2004; Anderson et al. 2008; McIntyre et al. 2016). While the community fishing areas are freely accessible, the fishers attempt to harvest the common-pool fisheries resources as much as they can without thinking the adverse effects, and this scenario is called “the tragedy of the commons”(Hardin 1968). The tragedy of the commons has become a central item to understand the local and global ecological problems (Vugt 2009). Within the public property, people are less responsible for the management and conservation of the resources. Thus, while law enforcement is inefficient, the illegal fishing practices and overexploitation exist (Ratner 2006). In this case, the fisheries resources of the lake were indiscriminately fished (Ngor et al. 2018b). Indiscriminate fishing refers to exploitation of fishes at all class and species and size class (McCann et al. 2015). Indiscriminate fishing resulted in changes in fish community and food web structure, i.e. the large species were decreased, and the community was dominated by the small fish species. Furthermore, illegal fishing practices are believed the main threatened factors on the fisheries resources through an increase in fishing effort.

Overharvesting fisheries resources due an increase in demand has been the threaten factor by human activity on the collapse or decline of the global fisheries (Jackson et al. 2001; Welcomme et al. 2010). Overharvesting fisheries resources across the assemblage tend to occur in tropical regions, where the poor are highly dependent on natural inland fisheries (Allan et al. 2005). Ideally, fishing has a direct impact on the decline in the fish population or the abundance of the target fish species (Pauly et al. 2002; Hsieh et al. 2006).

Moreover, the removal of the commercial fishing lots enabled also the high possibility of the inundated forest destruction because the local people moved in the area and cleared the inundated forest and converted the area into the agricultural field (Ratner 2006). In contrast, the flooded forest within the fishing lots area was protected properly by of the commercial fishing lots owners to sustain the fisheries resources for their next harvests. The policies on exploitation and habitat conservation within the commercial fishing lots were given in the log-book designed by the fisheries law, i.e. where the fisheries resources allowed to be harvested and where the flooded forest are suggested to keep conservation.

The results also illustrated that the removal of the commercial fishing lots enabled a change in fish community composition in the Tonle Sap Lake. Indeed, we observed that although some species are stable, some species hosted an increasing trend, and others had decrease trend. Also, principal component analysis provided statistical evidence and concise assessement of the change in fish community structure (Figure 6.4). The fisheries policy reforms negatively affected the large benthic fish species with long-distance migration, and high trophic level, e.g. *C. enoplos*, *C. microlepis*, *C. micropeltes*, *Wallago attu*, *P. hypophthalmus*, *B. truncatus* (Betru) and *C. ornata* (Chorn). In contrast, the success of the fisheries policy reforms was for the small fish with short distance migration, e.g. *Pristolepis fasciata*, *Clarias* spp., *Anabas testudineus*, *Mystus* spp and *Trichopodus pectoralis*.

In ecological aspects, removal of the commercial fishing lots gains the possibility for the longitudinal fish species to migrate freely in/across the Lower Mekong Basin, which enables fishes to occupy the substantial spatial distribution, breed and spawn in the upper stream of the Mekong River, exchange genetic components and enhance the genetic pool. Nevertheless, the long-distance migration of fish species gains high risk to be captured by many fishing gears along the migration routes toward the upstream of the Mekong River (Ngor et al. 2015). For instance, an estimated 7,000 boats of artisanal and subsistence fishers were catching fish in the Tonle Sap River in January 2005 (Halls et al. 2013). Furthermore, the stationary trawl (*Dai*) fishery in the Tonle Sap River gains high risk for the long-distance migratory species through the non-selective fishing by the barge-mounted drift net and their barrage system (Halls et al. 2013).

After the commercial fishing lots removal, the conservation area (non-fishing zone) were assigned to provide habitats for fish species to conserve the fishery resources (Cooperman et al. 2012). However, the conservation area appeared to benefit only some species, while other species were vulnerable to be harvested (Cooperman et al. 2012). Specifically, the small fish species and floodplain resident fish species i.e. *Clarias* spp., *Anabas testudineus*, *Pristolepis fasciata*, and *Mystus* spp., were expected to have benefitted from conservation area after the fisheries policy reforms (Cooperman et al. 2012). Moreover, Russ & Alcala (2015) revealed that the conservation area (non-harvest zone) benefit for sedentary fish species that utilise that habitat for a long period or permanently, while the migratory fish species were vulnerable to be harvested. Our results confirmed the hypothesis claimed by Cooperman et al. (2012) articulating that the conservation area in the Tonle Sap floodplains have benefited for the small, short lifespan and rapid growth fish species, while the long-distance migration fishes appeared to be problematic to fishing.

Decline in the large predatory fish not only affected the subset of the target species, but also the entire fish community of ecosystem (Friedlander & Demartini 2002; Frank et al. 2005) because decline in predatory fish could reduce the mortality rate of predation and gain a high probability of survival for prey or small fish species (Andersen & Gislason 2017).

Consequently, depletion of the large fish or top predators of the community has a potential top-down effects on the food web and influences an alteration of fish community and food web structure of the ecosystem in which the assemblage was replaced by small fish at the lower trophic levels (Pauly et al. 2002; Allan et al. 2005; Frank et al. 2005; Welcomme et al. 2010). Moreover, small fish species, i.e. opportunist, host short reproductive cycle which are less impacted by intensive fishing because smaller fish are more biologically productive (Lamberts 2006; Welcomme et al. 2010). There was also clear evidence that the dynamics of fish community and structure happened in the Tonle Sap River in which the catch of the large and medium fish was declined, and the catch of small fish species was increased (Ngor et al. 2015). In addition, indiscriminate fishing resulted in a decrease in the trophic level, total length and weight of fish in the dai fishery in the Tonle Sap River (Ngor et al. 2018b). For instance, we detected a temporal decline in total length and weight of the large and medium species, i.e. *Pangasianodon hypophthalmus*, *Cyclocheilichthys enoplos*, and *Cirrhinus microlepis*, whereas the catch of small *Henicorhynchus* spp. had been increasing (Ngor et al. 2015, 2018b).

In conclusion, we found that the fisheries policy reforms/commercial fishing lots abolishment in the Tonle Sap Lake enabled a decreasing trend in overall fish biomass of the lake. Such pattern could be explained by the fact that while the community fishing area is freely accessible to fishing, the local fishers attempt to harvest the common-pool resources of fisheries as much as they can without thinking the adverse effects; this scenario is called "the tragedy of the commons" (Hardin 1968). In this regards, within the public or open access resources, people are less responsible for the management and conservation of the resources and less consideration of regulation (Welcomme et al. 2010). Likewise, while the fishers still had some fishing gears in their hands, the large-scale operation was still happening in the Tonle Sap Lake as the law enforcement was insufficient (Cooperman et al. 2012). Moreover, the management capability of community fisheries is limited, in which the abilities to control and detect illegal fishing practices is low (Ratner 2006). In management perspective, designing the responsibility and accountability for the stakeholders for Tonle Sap Lake fisheries management, i.e. community, fishers, authorities, NGOs, and others institutions, was not precise (Ratner 2006; Cooperman et al. 2012). With the transition from commercial fishing lots to the community, the management was shifted from the private sector to under control of the local communities (for community fisheries and protected area) and the centralised authority (for open area). Ineffectiveness of the management generally lies with the centralised authorities because they cannot access the substantial area comprising complex habitat, multiple species and fishing gear (Welcomme et al. 2010).

Moreover, the results illustrated that the fisheries policy reforms enabled a change in fish community composition and structure in the Tonle Sap Lake. Specifically, we found that although some species were not affected by the fisheries reform, others had an increasing or decreasing trend according to the species. Overall, the fisheries policy reforms positively benefited the small fish species with short distance migration, low trophic level, and inhabiting the surface of the water column. In contrast, the fisheries reforms negatively affected the large benthic fish species with long-distance migration and high trophic level. Meanwhile, the dynamics of fish community composition and structure were influenced by the fact that the fish population had been indiscriminately fished (McCann et al. 2015; Ngor et al. 2018b). Furthermore, removing the top predators of the community enables an alteration of community structure and food web of the ecosystem (Frank et al. 2005). The failure of the Cambodian fisheries policy reforms were affected by the low effectiveness of fisheries resource management and insufficient law enforcement capacity that drive the overharvesting, and illegal fishing practices, and flooded forest habitat loss (Ratner 2006). If the law enforcement is sufficient, the fisheries policy reforms or the commercial fishing lot abolishment might significantly and positively contribute to maintain fishery productivity and protect the biological diversity, and improve the sustainability of the Tonle Sap Lake fisheries (Cooperman et al. 2012).

The overall fisheries trend and community structure of the Tonle Sap Lake provided by this study are of paramount importance for initiating the management policies and decision making. Moreover, the results from this study provided a baseline and lesson learn for fisheries resources management for other lakes. The failure of the removal of the commercial fishing lots that allows a decline in fish biomass from the Tonle Sap Lake provided a message for fisheries ecologists, policymakers and Royal Government of Cambodian for fisheries resources managment. Given that the removal of the commercial fishing lots negatively impacted on the large benthic fish species with the long-distance migration, thus we recommend focusing on the management and conversation of the species considered that form the top predators through the balanced harvesting or reducing the fishing effort or capacity to an acceptable level (Pauly et al. 2002). The balanced harvesting, by fishing individual of species according to their productivity status, could reduce the adverse ecological effects of fishing on the community and sustain fisheries resources (Garcia et al. 2012; Jacobsen et al. 2014). The protection and conservation of the large fish contributed to support the sustainability of fisheries and ecosystem (Birkeland & Dayton 2005). Moreover, law enforcement and regulation should be highly taken into consideration because it could avoid the overharvesting and could maintain and sustain the fisheries resources (Welcomme et al. 2010). We also suggest considering the conservation of the flooded forest to maintain fish productivity and ensure sustainability of the fisheries resources in the lake.

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Supporting Information

S1: Summary of morphological and biological traits for fish species. T.length: the maximum total length; T.level: the trophic level

species	T.Length	T.evel	water column	migration	Feeding
Henicorhynchus spp.	24.4	2	benthopelagic	longitudinal	algivore/detritivore
Cyclocheilichthys enoplos	90.3	3.2	benthopelagic	longitudinal	Omnivorous
Puntioplites proctozysron	30	2.7	benthopelagic	Lateral	Omnivorous
Mystus spp.	15.9	3.1	demersal	Lateral	invertivorous
Channa micropeltes	158.6	3.85	benthopelagic	floodplain resident	piscivorous
Trichopodus microlepis	25	2.8	benthopelagic	floodplain resident	Omnivorous
Osteochilus vittatus	39	2	benthopelagic	floodplain resident	Omnivorous
Hypsibarbus spp.	40.5	2.4	benthopelagic	Lateral	Omnivorous
Channa Striata	122	3.4	benthopelagic	floodplain resident	piscivorous
Labiobarbus leptocheilus	36.6	2.34	benthopelagic	Lateral	Omnivorous
Hemibagrus spilopterus	37.7	3.5	demersal	Lateral	invertivorous
Notopterus notopterus	73.2	3.6	demersal	floodplain resident	invertivore/piscivore
Xenentodon cancila	40	3.9	pelagic-neritic	longitudinal	Carnivorous
Anabas testudineus	25	3	demersal	floodplain resident	invertivore/piscivore
Cyclocheilichthys armatus	25	2.9	benthopelagic	Lateral	Omnivorous
Labeo chrysophekadion	90	2	benthopelagic	Lateral	algivore/detritivore
Labiobarbus siamensis	22	2.3	benthopelagic	Lateral	Omnivorous
Clarias spp.	47	3.4	demersal	floodplain resident	invertivore/piscivore
Thynnichthys thynnoides	25	2.3	benthopelagic	Lateral	Omnivorous
Osteochilus melanopleurus	73.2	2.3	benthopelagic	Lateral	Omnivorous
Pangasianodon hypophthalmus	158.6	3.1	benthopelagic	longitudinal	Omnivorous
Paralaubuca typus	22	3.3	benthopelagic	Lateral	invertivorous
Pristolepis fasciata	20	3.2	demersal	floodplain resident	invertivorous
Cirrhinus microlepis	79.3	2.4	benthopelagic	longitudinal	Omnivorous
Parambassis wolffii	24.4	3.7	demersal	floodplain resident	invertivore/piscivore
Setipinna melanochir	40.3	3.88	pelagic-neritic	longitudinal	Carnivorous
Boesemania microlepis	122	3.7	benthopelagic	Lateral	invertivore/piscivore
Hampala dispar	42.7	3.7	benthopelagic	floodplain resident	invertivorous
Puntius brevis	14.6	2.91	benthopelagic	floodplain resident	Omnivorous

Coilia spp.	31.7	3.7	pelagic	longitudinal	Carnivorous
Albulichthys albuloides	36.6	2.8	benthopelagic	longitudinal	Omnivorous
Amblyrhynchichthys truncatus	48.8	2.4	benthopelagic	longitudinal	Omni/Herbivorous
Oxyeleotris marmorata	79.3	3.9	demersal	longitudinal	Carnivorous
Belodontichthys truncatus	73.2	4.1	demersal	longitudinal	piscivorous
Pangasius larnaudii	130	3.3	benthopelagic	longitudinal	Omnivorous
Wallago attu	240	3.68	demersal	Lateral	piscivorous
Parachela siamensis	18.3	3.4	pelagic	Lateral	Canivorous/insectivorous
Pangasius spp.	36.6	3.2	benthopelagic	longitudinal	Omnivorous
Polynemus multifilis	30.5	3.5	demersal	longitudinal	Carnivorous
Micronema spp.	24	3.7	benthopelagic	longitudinal	Carnivorous
Ompok hypophthalmus	36.6	3.9	demersal	floodplain resident	invertivore/piscivore
Systomus orphoides	30.5	2.9	benthopelagic	longitudinal	Omnivorous
Chitala ornata	122	3.7	pelagic	floodplain resident	invertivore/piscivore
Leptobarbus hoevenii	122	2.8	pelagic	Lateral	Omnivorous
Trichopodus pectoralis	25	2.8	benthopelagic	floodplain resident	Omnivorous
Pao cambodgiensis	18.7	3.3	demersal	Lateral	Omnivorous
Kryptopterus cryptopterus	35	3.5	benthopelagic	floodplain resident	invertivore/piscivore
Cosmochilus harmandi	100	2	benthopelagic	longitudinal	Omnivorous
Yasuhikotakia spp.	30.5	3.4	demersal	longitudinal	invertivorous
Probarbus jullieni	183	3.17	demersal	longitudinal	Omnivorous
Parambassis apogonoides	12.2	2.87	demersal	floodplain resident	invertivore/piscivore
Barbonymus altus	24.4	2.4	benthopelagic	Lateral	Omnivorous
Gyrinocheilus pennocki	34.2	2.5	demersal	longitudinal	algivore/detritivore
Achiroides leucorhynchos	9.8	3.5	demersal	longitudinal	invertivorous
Channa lucius	48.8	3.9	benthopelagic	floodplain resident	Carnivorous

Chapter VII: Summary, conclusion and perspectives

7.1 Summary

Overall aims: Fish and fisheries resources have been the primary protein resources and consumed worldwide and income for people living in developing countries. In Cambodia, a large amount of resources are exploited from Tonle Sap Lake, which is the largest natural lake in Southeast Asia. Tonle Sap Lake is also a diverse and productive lake that host more than 296 fish species. Therefore, this lake plays an important role in supporting protein sources for nearly two million Cambodians and other people in the region and contribute approximately 60% to the total protein intake of Cambodian people. Moreover, fish species also served the significant role in the ecological and biological process of the system. Despite the ecological, biological, and economic importance of the Tonle Sap Lake, knowledge on fish distribution patterns, temporal changes, migration and the habitats of the fish were little known.

Here, this study intends to

(1) Investigate the spatial and temporal dynamics of fish community composition.

(2) The effects of the environmental factors on the spatial and temporal distribution of fish species.

(3) The effects of fishing lot abolishment on fish biomass, and community structure in the Tonle Sap Lake.

Locations: The study has been conducted in the Tonle Sap System (TSE): Tonle Sap Lake and Tonle Sap River, a tropical flood pulse system, Cambodia. Herein, the study the spatial range approximately 300 x 300 km. Tonle Sap Lake is situated in the central of Cambodian consisting of the largest wetland area in Southeast Asia. Also, the Tonle Sap River, with 120 km long, connects the Tonle Sap Lake to the Mekong River. Tonle Sap System is a complex flood-pulse system which its water level was characterized by the flood waters of the Mekong River regulated by tropical monsoon climate.

Data collection: In this study, we used three different data sets:

- The commercial fishing lot operation data (large-scale fishing): Data were collected from the 33 fishing lots around the Tonle Sap Lake from 1994-2000. This dataset was used in chapter III and chapter IV (please see details).
- The catch monitoring data (small-scale fishing): Data were collected from Tonle Sap Lake and TSR from 2012-2015. Statistical analyses applied in this study included.
- The small-scale fishing (mobile gear fishing) around Tonle Sap Lake: Data were collected from the mobile gear from 1995-2000.

Statistical analyses: In this study, we used many statistical and modelling approaches:

- Clustering analysis: Hierarchical Clustering.
- Multivariate analyses: Non-metric Multidimensional Scaling (NMDS), Principal Component Analysis (PCA), Analysis of Similarity (ANOSIM) and Similarity Percentage (SIMPER).
- Predictive models: Linear Model (LM) and Generalised Linear Model (GLM).
- Time-series analyses: cross-wavelet transform (CWT) and cross-correlation function (CCF).

Main results:

Spatial and temporal changes in fish yields and fish community

Overall, the results showed that fish communities of fishing lots (a large-scale fishery) in Tonle Sap Lake from 1994 to 2000 were dominated by a few main commercial fish species: *Channa micropeltes*, *Pangasianodon hypophthalmus*, *Channa striata*, *Cyclocheilichthys enoplos*, *Henicorhynchus* spp., *Barbonymus gonionotus*, *Micronema* spp. and *Trichopodus microlepis* that accounted for 58% of the overall fish catch of the lake. Their total catches are temporally declining, except *Trichopodus microlepis*. The total biomass was found to be positively correlated with the water level fluctuation, indicating its significant role in shaping fish biomass in lot fisheries. There were two fish assemblages: northern assemblage, that mostly characterised by black fishes, and southern assemblage, that was mainly linked to white, grey and estuarine fishes. The fish species assemblage from earlier years (1994 and 1995) was characterised by the abundance of all functional groups of black-white-grey fish species, but more recent years (1996 to 1999) were linked to white and grey functional groups, which was explained by a decrease in many blackfish species.

The effects of the local habitat and climate descriptors on fish distribution

Regarding the spatial distribution of the main commercial species, there was a strong variability in fish biomass across fishing lots. Some lots consistently had similar fish biomass levels across time, whereas other lots showed quite unstable fish biomass levels. Interestingly, for most of the species, most high biomass fishing lots, consistently had high biomass levels for the considered species, despite a substantial temporal variability among the catches. From a spatial perspective, fish species distributions were not homogeneous within Tonle Sap Lake differed among species. The snakehead *C. micropeltes* was most abundant in the central-northern part of the lake, although low abundances were found in the extreme northern area of the lake. *C. striata* and *T. microlepis* were more abundant in the northern part of the lake.

In contrast, *C. enoplos*, *B. gonionotus*, *P. hypophthalmus*, and *Henicorhynchus* spp. biomass levels were highest in the southern part of the lake. *Micronema* spp. was also abundant in a few southern areas of the lake but also occupied a few areas in the northern part of the lake. The heterogeneous distributions of fish species were governed by distinct combinations of habitat characteristics and climatic factors. The biomass of *C. micropeltes*, *C. striata* and *B. gonionotus* were negatively correlated with the percentage cover of the agricultural field. *P. hypophthalmus* were positively correlated with the percentage cover of flooded forest and open water. *C. enoplos* and *T. microlepis* were positively associated with the percentage cover of open water. In term of climate condition, the temperature was negative to longitudinal migratory fishes, but positive to floodplain resident fishes. Moreover, the longitudinal migratory fish were positively correlated with precipitation, but negatively associated to floodplain resident fishes.

Temporal dynamics of small mud carp species *Henicorhynchus lobatus* and *H. siamensis* in the flood pulse system

The results illustrated that *H. lobatus* and *H. siamensis* can co-occur together, but the synchronisation and movement of *H. lobatus* always lead those of *H. siamensis*. The annual re-occurrence (a long periodicity) of each species was detected in NL between October and December, while their monthly re-occurrence (a short periodicity) was mainly observed in OR from December to February. Moreover, after water recession in Tonle Sap Lake, *H. lobatus* individuals began to retreat earlier than *H. siamensis* individuals. However, *H. lobatus* species retreats (~2.3 km/day) slower than *H. siamensis* species (~7.9 km/day), but they retreated at similar speeds when they reached the outlet river (TSR) at ~16 km/day. These patterns were found to correspond to the variations in water levels across the TSE, suggesting that the flow pulse is one of the main factors responsible for the temporal dynamics of the small mud carp species in the TSE.

The effects of fishing lot abolishment on fisheries and fish community structure

We detected a stable trend in fish biomass in the before fishing lot abolishment period, whereas the temporally decreasing trend was observed in the after fishing lot abolishment period. Moreover, there was a significant change in fish community composition before and after fishing lot abolishment. Specifically, we found that although some species were not affected by the fisheries reform, others had an increasing or decreasing trend according to the species. Overall, the fisheries policy reforms positively benefited the small fish species with short distance migration, low trophic level, and inhabiting the surface of the water column. In contrast, the fisheries reforms negatively affected the large benthic fish species with long-distance migration and high trophic level. To sum up, the decline in the fish biomass of the lake was affected by the fact that the local fishers attempt to exploit the common-pool fisheries resources of the lake as much as they can without thinking the adverse effects while the community fishing areas are freely accessible to fishing. This framework coined as “the tragedy of the commons”, could generate a decline of fish resources in the Tonle Sap Lake.

7.2 Main conclusion and remarks

Spatial and temporal change in fish yields and fish assemblage

The results provided evidence that Tonle Sap Lake was dominated by few commercial fish species: *Channa micropeltes*, *Pangasianodon hypophthalmus*, *Channa striata*, *Cyclocheilichthys enoplos*, *Henicorhynchus* spp., *Barbonymus gonionotus*, *Micronema* spp. and *Trichopodus microlepis*. In short, we found that all these dominant fishes were temporally declined, except *Trichopodus microlepis*. Meanwhile, we noticed that the large fish species were temporally decreased and small fish species increased, thus creating the change in fish community structure and food web. Removal of the predatory fish could reduce the mortality rate of predation and gain a high probability of survival for prey or small fish species (Andersen & Gislason, 2017). The prey or small fish species, which is usually controlled by the predatory fish, appeared to have benefitted from the collapse of the large top predator fish species from the ecosystem (Andersen & Gislason, 2017). Thus, removal of the largest fish species that are the top predators could have a substantial top-down effect on food web dynamics. The collapse of the large predatory fish affects not only the subset of the target species but also the entire fish community of ecosystem. Also, fish yields of Tonle Sap Lake are positively correlated with the water level variations, indicating that the water fluctuation is a key determinant regulating the fish yields of Tonle Sap Lake. Also, Tonle Sap fish communities are divided into two assemblages: northern assemblage (mainly characterised by black floodplain residence fish species) and southern assemblage (mainly characterised by the white-migratory fish species). Specifically, the fish yields, species richness and indicator species of the southern assemblage were significantly higher than those of northern assemblage. Thus, the results suggest that southern assemblage is the potential area for both yields and species richness where should be considered for the protected area, especially this area form the crucial zone that connects the fish species between lake and river. This information is of importance that could be used in making the decision for the particular area protection.

The influence of the local habitat and climatic factor on the distribution of fish species

Overall, there was a strong variability in fish biomass across fishing lots. Some lots consistently hosted similar fish biomass levels across time, whereas other lots showed quite unstable fish biomass levels. Interestingly, for most of the species, most high biomass fishing lots, consistently had high biomass levels for the considered species, despite a substantial temporal variability among the catches. From a spatial perspective, fish species distributions were not homogeneous within Tonle Sap Lake and differed among species. The distribution of species was governed by distinct combinations of local habitat characteristics and regional climatic factors. Thus, the local habitats and regional climatic descriptors play a significant role in shaping the distribution of considered fish species in Tonle Sap Lake. Moreover, the results demonstrated that each species had distinct habitat preferences, supporting the hypothesis emphasised that the responses of fish species to their environmental determinants are species-specific (Kolosa, 1989). The distribution of each species was not determined by the same environmental factors (Buisson, Blanc, & Grenouillet, 2008). Thus, responses of considered fish species to their environmental determinants are species-specific.

The spatial heterogeneity of fish biomass levels within the Tonle Sap Lake provides important information for the management of the fish resources of the lake. First, some areas consistently have high fish biomass levels across years. For example, this is the case for lot T02, which is characterised by high biomasses of *C. enoplos*, *B. gonionotus*, *Henicorhynchus* spp., and *Micronema* spp. Herein, Lot T02 was characterised by two main habitat types, i.e. flooded forest (70%) and open water (30%), and there was no agricultural fields habitat. The large percentage cover of the flood forest and open water are very important to sustain the abundant biomass of *C. enoplos, B. gonionotus, Henicorhynchus* spp., and *Micronema* spp. in this location. Thus, specific attention should be given to the conservation of the environmental quality of this lot to maintain the productivity of the four considered species that account for more than 42% of the Tonle Sap Lake catches. Second, among the eight considered species, different distribution patterns were observed, and some specific lots could be very important for one species but not for the others. For instance, lot P06 sustains more than 71% of *P. hypothalamus* biomass, whereas all the other lots sustain low biomass levels (less than 29%) of this species. This lot were composed of three habitat types: flooded forest (50%), open water (45%) and agricultural field (5%). The local habitat, which mainly characterised by flooded forest and open water, is a key factor that makes *P. hypothalamus* abundantly present in this lot. Third, among the eight species, only *C. micropeltes* was abundant in a substantial part of the lake, and the seven other species have much more restricted distributions. Overall, this information confirms that focusing conservation actions on a few, well-designed lots that have a high level of fish biomass for each species might be profitable for sustaining the fish biomass and productivity of the eight major Tonle Sap Lake species.

Understanding the species-habitat relationships provides useful information to better understand the fish species environmental requirements and conserve local fish productivity, but this information might also be used to favour fish productivity in some areas of the lake that experience lower fish biomass levels. For instance, in this study, we showed that *C. micropeltes*, *C. striata* and *B. gonionotus* were adversely correlated with agricultural field and none of the fish species benefitted from agricultural landscapes, and therefore, these agricultural lands could be considered an equivalent to flooded forests to sustain fish populations. We, therefore, encourage not only conserving flooded forest areas that are known as crucial for tropical aquatic ecosystem functioning (Hughes, 2003; WWF, 2017) but also maintaining adequate habitats for most fish species.

Finally, the results, based on 1994-2000 fish catch data, might not reflect the current situation in the Tonle Sap Lake, since human pressure has substantially changed over the past two decades (Baran & Gallego, 2015; NIS, 2013), with likely consequences on both aquatic habitats and land-use. It would, therefore, be useful to determine the extent to which the spatial distribution of current fish catches fit with the patterns we reveal and to analyse land-use changes experienced by the Tonle Sap Lake during the past two decades. Similarly, global climate change likely affected fish distributions, and as demonstrated here, climate and precipitation are likely to affect species differentially. We, therefore, recommend an update of the fish and environment data on the Tonle Sap Lake, while the results of the present paper could serve as a reference to quantify the changes in fish biomass levels and distributions in the lake. This need is of paramount importance to establish temporal trends on fish biomass in the Tonle Sap Lake and therefore manage and sustain the fish resources of the lake that are crucial to a large part of the Cambodian people (Ahmed, Hap, Ly, & Tiongco, 1998; Lieng & Zalinge, 2001).

Temporal dynamic of two small mud carp species in the flood pulse system

Investigating the spatial and temporal dynamics of fish species enables ecologists and fisheries managers to better understand variation in their occurrence, synchronisation, peak abundance and movement patterns, and the key factors driving such variation. By using modern time-series modelling approaches, i.e. the CWT and CCFs, to analyse high-resolution time-series data, we found that for this study, the two small mud carp species can co-occur together, but the synchronisation and movements of *H. lobatus* always lead those of *H. siamensis*. The annual re-occurrence (a long periodicity) of each species was detected in NL between October and December, while their monthly re-occurrence (a short periodicity) was mainly observed in OR from December to February. Moreover, after water recession in the Tonle Sap Lake, *H. lobatus* individuals began to retreat earlier than *H. siamensis* individuals. However, the former species retreats (~2.3 km/day) slower than the latter species (~7.9 km/day), but they retreated at similar speeds when they reached the outlet river (TSR) at ~16 km/day. These patterns were found to correspond to the variation in water levels across the TSE, suggesting that the flow pulse is one of the main factors responsible for the temporal dynamics of the small mud carp species in the TSE. Therefore, the seasonality and predictability of the Mekong River should be maintained to sustain the natural dynamics of fish species (e.g. the periods of recruitment, synchronisation, peak abundance and movements) that have long developed and adapted to such a flood-pulse system. The timing of migration and swimming speed of the two species identified in this study should be an important part of regulation or policy consideration to better manage and conserve the two species. The ability of the CWT to analyze coherency enabled us to highlight the co-occurrence and synchronisation periodicity of two species, whereas the CCF allowed us to determine the link between the flow pulse and fish abundance and identify the lag between the peak water peak and fish synchronisation. The CCF thus allows us to identify the role of flood-pulse in the dynamics of fish species in the TSE at spatial and temporal scales.

Understanding the occurrence, synchronisation, and movement patterns of fish species and the influence of water level variation on their spatial and temporal dynamics provides useful knowledge to better understand fish species migration and behavioural ecology (Løkkeborg et al., 2002; Mcgill et al., 2006; Peoples and Frimpong, 2016; Pollock et al., 2014; Ruetz et al., 2005). This knowledge can be used to support more effective monitoring, management and conservation efforts at local and larger spatial and temporal scales. For instance, the timing of the retreat of the two species identified in this study delivers useful insights that can be used to support regulations and policy initiatives aiming for better management and conservation of the two species. Good initiatives will allow adult individuals to complete the next step of their life cycle, i.e. to freely pass through the TSR during their peak abundance. These individuals can consequently reach the refuge, spawning, rearing and feeding grounds in the upstream portions of the Mekong River, and its major tributaries and can thus sustain the annual production.

Furthermore, our findings can act as a fundamental baseline for investigations of other economically and ecologically important species. In the case that further studies investigating different keystone species find similar synchronisation and peak abundance periods and similar movement patterns and timing in their retreats, these results will together provide key knowledge to support better monitoring and management of fisheries resources in the TSE. Also, the spatial and temporal dynamics of fish are found to be fine-turned with the natural flow-pulse variation. Maintaining such conditions are therefore necessary for fish species to migrate to complete their life cycles. Human actions such as hydropower dams that alter natural flow-pulses of the Mekong, i.e. change in flow seasonality and predictability is highly likely to also alter fish assemblage structure and their composition, fish migration patterns and spawning decisions which consequently have severe implication on fish reproductive, rearing and feeding successes (Ngor et al., 2018b). Finally, our study demonstrated that the CWT and CCF are useful time-series modelling approaches for investigating the phase relationship, joint periodicity, and the time-lagged relationship between environmental parameters (e.g. water level) and fish species in the flood-pulse ecosystems.

The effects of the commercial fishing lots abolishment on fisheries, fish community composition and structure

We found that the fisheries policy reforms/commercial fishing lots abolishment in the Tonle Sap Lake enabled a decreasing trend in overall fish biomass of the lake. Such pattern could be explained by the fact that while the community fishing area is freely accessible to fishing, the local fishers attempt to harvest the common-pool resources of fisheries as much as they can without thinking the adverse effects; this scenario is called “the tragedy of the commons” (Hardin, 1968). In this regards, within the public or open access resources, people are less responsible for the management and conservation of the resources and less consideration of regulation (Welcomme et al., 2010). Likewise, while the fishers still had some fishing gears in their hands, the large-scale operation was still happening in the Tonle Sap Lake as the law enforcement was insufficient (Cooperman et al., 2012). Moreover, the management capability of community fisheries is limited, in which the abilities to control and detect illegal fishing practices is low (Ratner, 2006). In management perspective, designing the responsibility and accountability for the stakeholders for Tonle Sap Lake fisheries management, i.e. community, fishers, authorities, NGOs, and others institutions, was not precise (Cooperman et al., 2012; Ratner, 2006). With the transition from commercial fishing lots to the community, the management was shifted from the private sector to under control of the local communities (for community fisheries and protected area) and the centralised authority (for open area). Ineffectiveness of the management generally lies with the centralised authorities because they cannot access the substantial area comprising complex habitat, multiple species and fishing gear (Welcomme et al., 2010).

Moreover, the results illustrated that the fisheries policy reforms enabled a change in fish community composition and structure in the Tonle Sap Lake. Specifically, we found that although some species were not affected by the fisheries reform, others had an increasing or decreasing trend according to the species. Overall, the fisheries policy reforms positively benefited the small fish species with short distance migration, low trophic level, and inhabiting the surface of the water column. In contrast, the fisheries reforms negatively affected the large benthic fish species with long-distance migration and high trophic level. Meanwhile, the dynamics of fish community composition and structure were influenced by the fact that the fish population had been indiscriminately fished (McCann et al., 2015; Ngor, McCann, et al., 2018). Furthermore, removing the top predators of the community enables an alteration of community structure and food web of the ecosystem (Frank, Petrie, Choi, & Leggett, 2005). The failure of the Cambodian fisheries policy reforms were affected by the low effectiveness of fisheries resource management and insufficient law enforcement capacity that drive the overharvesting, and illegal fishing practices, and flooded forest habitat loss (Ratner, 2006). If the law enforcement is sufficient, the fisheries policy reforms or the commercial fishing lot abolishment might significantly and positively contribute to maintain fishery productivity and protect the biological diversity, and improve the sustainability of the Tonle Sap Lake fisheries (Cooperman et al., 2012).

The overall fisheries trend and community structure of the Tonle Sap Lake provided by this study are of paramount importance for initiating the management policies and decision making. Moreover, the results from this study provided a baseline and lesson learn for fisheries resources management for other lakes. The failure of the removal of the commercial fishing lots that allows a decline in fish biomass from the Tonle Sap Lake provided a message for fisheries ecologists, policymakers and Royal Government of Cambodian for fisheries resources management. Given that the removal of the commercial fishing lots negatively impacted on the large benthic fish species with the long-distance migration, thus we recommend focusing on the management and conversation of the species considered that form the top predators through the balanced harvesting or reducing the fishing effort or capacity to an acceptable level (Pauly et al., 2002). The balanced harvesting, by fishing individual of species according to their productivity status, could reduce the adverse ecological effects of fishing on the community and sustain fisheries resources (Garcia et al., 2012; Jacobsen, Gislason, & Andersen, 2014). The protection and conservation of the large fish contributed to support the sustainability of fisheries and ecosystem (Birkeland & Dayton, 2005). Moreover, law enforcement and regulation should be highly taken into consideration because it could avoid the overharvesting and could maintain and sustain the fisheries resources (Welcomme et al., 2010). We also suggest considering the conservation of the flooded forest to maintain fish productivity and ensure sustainability of the fisheries resources in the lake.

7.3 Perspectives

The information and insight of the fish ecology, distribution, migration and fisheries management and implication provided by this study are of paramount importance contributing to gain knowledge from Tonle Sap Lake. However, there are much more works needed to be studied and taken into consideration. In the future, I am interested to assess the overall fisheries, fish community composition and structure captured from the large-scale fishing (the operation of the commercial fishing lots) and small-scale fishing (mobile gear fishing at family level). This assessment can contribute to providing useful and fundamental evidence responding to the research questions: (1) Is the large-scale fisheries had more intensive pressure on the TLS fisheries than the small-scale fisheries? (2) Is there a difference in fish community composition and structure between these two fisheries types (large and small-scale fisheries)? (3) Is the fish captured from the different fisheries related to the morphological types? Does large scale fisheries capture large fishes and does the small-scale fisheries capture small fishes? Or both fisheries capture mixed small and large fishes? It was believed that the large-scale fishing is more pressure on Tonle Sap fisheries than small-scale fishing resulting in the removal of the commercial fishing lots from Tonle Sap Lake as well the Cambodian Mekong watershed. Then, if the results provide the evidence that the small-scale fishing had more pressure on Tonle Sap Lake fisheries than the large-scale fishing, we can provide more evidence to convince the failure of the government decision in the transition of the fishing lot-based management to community fisheries along with the results of chapter IV. In addition, this analysis could provide evidence about the characteristics of fish community composition and structure of these two kinds of fishing. Thus, the results would provide evidence about types of fishing in each, i.e. selective fishing or indiscriminate fishing or fishing down the food web?

Moreover, there is a need to understand the relationship between the fish market price and body length and size of fish species. This study would allow us to define how the fish market prices affected the catch of the large fish species by the fishers in Tonle Sap Lake while it was believed that the fish market prices have potential effects on the removal of the large fish (Tsikliras & Polymeros, 2014). Moreover, it is recommended to use the stage-based model to estimate the effects on stocks and revenues from the harvest (Reddy et al., 2014). It is also interesting to study the temporal trend in fish market prices and define their mediating effects on fish population and a change in fish community composition and structure in Tonle Sap Lake following the framework in (Reddy et al., 2014). If the data is available, it is more interesting to investigate the influence of the fish market prices on the fish consumption for food.

In addition to the effects on environmental factors on species distribution (chapter V), it is interesting to study the combined effects of the local habitat and biotic interaction on species distribution. For instance, it was suggested to highlight the biotic interaction and habitat drive positive co-occurrence between a paired-wise species (Peoples & Frimpong, 2016). Thus, we can use a two-species occupancy modelling approach to decouple the relative effects of biotic and abiotic interactions on co-occurrence of a paired-wise species. Using this approach, we the importance of negative biotic interactions (predation) and positive interactions (mutualism and facilitation) on co-occurrence of fish species. For instance, the biotic interaction and habitat descriptors shape the positive/negative co-occurrence between *Channa stratia* and *Trichopodus microlepis*, as well as those drive co-occurrence between *Channa micropeltes* and *Henicorhnychus* spp. Furthermore, many species in the system may be related to each other, thus it is also recommended to understand co-occurrence by modelling species simultaneously with a joint species distribution model (JSDM) (Pollock et al., 2014) and to understand more interaction between species using a multispecies occupancy model (Rota et al., 2016).

In order to give complementary information with temporal dynamic and migration of fish species in flood pulse system (chapter VI), it is needed to investigate the population dynamics of species in Tonle Sap Lake and its tributaries. For instance, how much the population of *Henicorhynchus* spp migrate to each tributary, i.e. Steueng Sangke River, Steueng Siem Steueng Reap River, Stueng Sen River, Steung Chinit River and Steung Pursat River.

Moreover, the linkage between gear selectivity and fish morphological traits. Then, we predict the fish species from different fishing gears (e.g. trap, gillnet, seine net, hook…) according to the morphological traits of fish species (body length, body depth, eye diameter and others). The details of morphological traits were given in (Toussaint, Charpin, Brosse, & Villéger, 2016). This analysis enabled us to define how the fish species in fishing gears related to morphological traits.

Finally, it is more interesting to deeply highlight functional diversity by linking the abundance data and morphological traits (see more morphological traits in Toussaint et al. 2016). With this perspective, we can investigate the spatial variations of the functional indices (functional richness, evenness, divergence and dispersal) in Tonle Sap Lake (i.e. the northern Tonle Sap Lake, southern Tonle Sap Lake or transitional zone, and TSR) and identify the environmental determinants shaping the changes in functional indices in Tonle Sap Lake, following the framework provided in (Brown et al., 2017). This analysis would give additional information in complement to the spatio-temporal change in beta-diversity provided by (Heng, Chevalier, Laffaille, & Lek, 2017). It is much more interesting to highlight the assembly rule, the comparison of the taxonomic richness and functional richness.

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