Variations spatio-temporelles de la structure taxonomique et la compétition alimentaire des poissons du lac Tonlé Sap, Cambodge

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List of Publications

[1]. Kong H., Chevalier M., Laffaille P., Lek S., 2017. Spatio-temporal variation of fish taxonomic composition in a South-East Asian flood-pulse system. *PLOS One, 12(3): e0174582.*

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Résumé long

1. Contexte du système pulsé en milieu tropical

Les zones inondables sont définies comme des « zones périodiquement inondées par le débordement latéral des rivières ou des lacs et/ou par des précipitations directes ou des eaux souterraines » (Junk, 1997). Plusieurs études (par exemple Junk et al., 1989 ; Ward et al., 1999 ; Tockener & Stanford, 2002) ont observé que l'hétérogénéité spatiale et la dynamique hydrologique des rivières et des plaines inondables favorisent une biodiversité élevée et affectent les processus fonctionnels. Le système pulsé tropical influe sur la qualité de l'eau (Thomaz et al., 2007), la dynamique des nutriments (Melack & Forsberg, 2001) et les cycles de vie de nombreux organismes dans les habitats aquatiques des plaines inondables (par exemple Junk, 1985 ; Junk & Piedade 1997 ; Arrington et al., 2006 ; Neves dos Santos et al., 2008). Bien que le concept d'écosystème pulsé n'ait pas encore été validé dans les grandes rivières tempérées, Welcomme (1995) qui a mené une étude en Europe et Hesse et al. (1993) en Amérique du Nord, ont observé que le système fluvial tempéré et tropical avaient des processus similaires. Les connectivités des plaines inondables et l'hétérogénéité de l'habitat sont maintenues par des régimes hydrologiques naturels et des gradients environnementaux (Ward, 1998 ; Sparks et al., 1990).

En outre, il a été montré dans les rivières tropicales des plaines inondables que les impulsions périodiques d'inondation constituent la principale force structurante pour la communauté de poissons, la reproduction et influent fortement sur la distribution et l'abondance des poissons (Junk et al., 1989 ; Goulding, 1980). Des études dans le bassin de l'Amazone révèle qu'un grand nombre de poissons penettrent dans la plaine inondable de façon saisonnière pour se nourrir de fruits et de ressources terrestres (Goulding, 1980 ; Hamilton et Lewis, 1987 ; Goulding et al., 1988). Dans les fleuves des plaines inondables, les crues pulsées sont si prévisibles et durables que les plantes, les animaux et même les sociétés humaines se sont adaptés pour en tirer parti (Sparks, 1995). On pense que les crues pulsées sont le moteur de la grande biodiversité des plaines inondables en créant une

hétérogénéité des habitats (Junk & Piedade, 1993 ; Gopal & Junk, 2000). La plupart des grandes plaines inondables du monde sont grandement altérées par l'activité humaine. Par conséquent, les cours d'eau qui n'ont pas été impactés sont rares et risquent fort d'être modifiés dans un proche avenir (Gore & Sheilds, 1995 ; Sparks, 1995). Les plaines inondables tropicales sont les plus diversifiées de tous les écosystèmes (Gopal Junk, 2000), et seront donc les plus touchées par le développement, principalement parce que les plaines inondables tropicales sont situées dans les pays en développement dont le développement durable n'est pas toujours pris en compte (Roggeri, 1995).

Les écosystèmes d'eau douce soutiennent une riche biodiversité et fournissent de grands services écosystémiques aux besoins humains (Strayer & Dudgeon, 2010). Les plaines inondées comptent parmi les écosystèmes d'eau douce les plus diversifiés et les plus productifs de la planète (Kingsford 2000 ; Rosenberg et al., 2000). En dépit de leurs fonctions inestimables dans l'écosystème, on observe un déclin de la biodiversité aquatique des plaines inondables, principalement attribuable aux changements dans l'utilisation du sol et au climat (Verhoeven et al., 2006 ; Palmer et al., 2008). En outre, les écosystèmes des plaines inondables sont également menacés par l'altération des régimes d'écoulement induite par la construction de barrages (Dynesius & Nilsson 1994 ; Tockner et al., 2010) qui modifie la structure spatiale et temporelle de la communauté de poissons dans la plaine inondable.

2. Variation spatio-temporelle des communautés de poissons dans l'écosystème pulsé tropical

Les communautés biologiques varient beaucoup dans l'espace et le temps (Southwood, 1988). Les approches actuelles pour étudier l'écologie de communauté consistent à expliquer les modèles de distribution et d'abondance des espèces, en reliant les processus qui se produisent à différentes échelles spatiales et temporelles (Ricklefs &

Schluter 1993 ; Leibold et al., 2004). Dans les grandes plaines inondées, l'ajustement des communautés à chaque type de modèle de distribution peut varier en fonction de la fluctuation saisonnière du niveau d'eau (Winemiller, 1996 ; Arrington et al., 2005 ; Arrington & Winemiller, 2006). Les plaines inondées ont des fonctions écosystémiques uniques et importantes dans les paysages fluviaux où elles jouent souvent le rôle de « hot-spot » de la biodiversité en raison des variations complexes de l'habitat sur une vaste gamme d'échelles temporelles et spatiales (Swales et al., 1999 ; Tockner et al., 2010). La forte interconnexion entre les habitats pendant la période des hautes eaux offre une possibilité de mouvement aléatoire des poissons et peut favoriser des processus stochastiques sur la structure et la composition de la communauté. Pendant la saison sèche, les lacs et les canaux de la plaine inondée s'isolent et la densité des poissons augmente. La dynamique saisonnière des crues influe sur les processus écologiques et environnementaux en provoquant une connectivité latérale des plaines inondables aux habitats adjacents en influençant la qualité de l'eau et la dynamique des nutriments, ainsi que le cycle de vie de nombreux organismes (Tockner et al., 2000). Gopal & Junk (2000) et Lasne et al. (2007) ont révélé que la connectivité latérale est un élément clé pour de nombreux poissons et autres espèces aquatiques, car elle fournit des ressources et des habitats hétérogènes pour le frai, le développement des jeunes, la productivité et la biodiversité. Les modèles spatiaux et temporels de répartition et de diversité des poissons d'eau douce sont utiles pour comprendre les facteurs influençant la structure des communautés de poissons et la façon dont les communautés réagissent aux changements saisonniers des cycles hydrologiques (Belliard et al., 1997). Des études ont révélé que la structure temporelle de la communauté de poissons était liée à la dynamique des inondations (Smith & Petrere, 2008 ; Sousa & Freitas, 2008 ; González et al., 2009) et que les communautés de poissons dans les systèmes lentiques semblaient plus stables temporellement que ceux des systèmes lotiques (Merona, 1987). De plus, la dynamique synchrone des populations animales sur de grandes échelles spatiales apparaît comme un phénomène courant (Ratta et al., 1995 ; Cattadori et al., 2000 ; Post & Forchhammer, 2002 ; Cattanéo et al., 2003). L'identification des mécanismes à l'origine de la synchronisation

spatiale s'est avérée à la fois difficile mais centrale pour comprendre la régulation de la population.

3. Relations entre les poissons et le régime hydrologique

3.1. Distribution des poissons et régime de crue saisonnier

La distribution des poissons est étroitement liée au mode de migration d'un habitat à l'autre pour la reproduction, l'alimentation et la croissance en relation avec la fluctuation des changements saisonniers de l'environnement. Pereira (2003) a noté une large gamme d'adaptations chez les poissons, qu'elles soient morphologiques, écologiques, liées à la reproduction ou la physiologique. Le plus grand nombre d'espèces se trouve dans les régions tropicales surtout dans les bassins fluviaux d'Asie du Sud-Est, d'Afrique et d'Amérique du Sud (Malcolm, 1995).

Dans les régions tempérées, la température varie selon un schéma saisonnier, avec des variations de magnitude plus importantes à des altitudes élevées avec des précipitations plus imprévisibles, des écoulements d'eau de neige fondue et des crues saisonnières. L'ampleur des inondations dans la plupart des cours d'eau tempérés est très variable d'une année à l'autre et dans certains systèmes, par ex. Ogeechee River, au sud-est des États-Unis, les inondations peuvent ne pas se produire du tout pendant quelques années. Dans la plupart des cas, les inondations saisonnières dans la zone tempérée coïncident avec le réchauffement printanier, que certaines espèces de poissons sélectionnent pour la reproduction durant cette période (Benke et al., 2000).

Par contre, dans les régions tropicales, les crues des plaines sont presque toujours générées par les précipitations saisonnières importantes pendant la saison des pluies. Mais dans certains cas, les inondations locales coïncident avec les précipitations locales (e.g., haut d'Orinoco, haut de Parana, haut de Zambezi et rivière Fly), tandis que dans d'autres, telles que le Niger inférieur, le Congo et le fleuve Solomoes-Amazonie, les crues

saisonnières sont le plus fortement influencées par les précipitations dans les eaux en amont (Winemiller, 2004). En outre, en raison de la faible variation de la température dans les régions tropicales de faible altitude, l'hydrologie est le principal facteur de forçage environnemental de la dynamique écologique et la sélection naturelle. Le modèle saisonnier tropical a dominé la réflexion sur l'écologie du système fluvial des plaines inondables, mais la généralité de ce modèle et ses conséquences ont à peine été discutées.

Winemiller (2004) a identifié au moins trois types de rivières selon leur hydrologie : (1) tempérée à crue pulsée saisonnière, (2) tempéré à crue pulsée stochastique et (3) tropicale à crue pulsée saisonnière. La richesse globale en poissons est fortement liée à la taille du bassin (Oberdorff et al., 1995). Cependant, les poissons présentent une diversité taxonomique plus forte dans les cours d'eaux tropicaux par rapport aux cours d'eaux de tailles comparables de la région tempérée (Winemiller, 1991). Les poissons ont développé une adaptation physiologique, des stratégies d'histoire de vie et un comportement de frai et d'alimentation pour faire face à ces différents types de conditions d'écoulement fluctuantes des cours d'eau. Quoi qu'il en soit, le cycle hydrologique annuel influe sur les migrations et la distribution des espèces de poissons entre la plaine inondée et le lit principal des cours d'eau. L'abondance et la biomasse des espèces de poissons des plaines inondées varient selon les espèces et les captures de poissons qui en dépendent varient d'une année à l'autre en fonction de l'importance de la crue pulsée (Welcomme, 2003).

La variation saisonnière du niveau et du régime de l'eau affecte sévèrement la répartition des poissons des rivières, le comportement de migration des poissons ainsi que les prises annuelles. De nombreuses espèces de poissons se sont adaptées pour profiter des inondations saisonnières en se reproduisant au début de la saison des pluies, ce qui permet aux stades précoces de se nourrir et de croître dans les habitats inondés (Lowe-McConnell, 1987). Les baissent de niveaux d'eau réduisent la disponibilité de l'habitat aquatique et augmentent les densités de poissons et les interactions biotiques (Zaret & Rand, 1971). L'ichthyomasse et la capture de poissons dépendent de l'étendue du régime

d'inondation pendant la crue et de la quantité d'eau qui reste dans le système pendant la saison sèche. Le rapport entre la capture et l'inondation peut constituer la base d'un indice général pour l'évaluation des variations d'une année à l'autre dans une plaine inondable et de la différence entre les plaines inondables (Welcomme, 1976).

Le changement saisonnier du régime hydrique dans le système fluvial du Mékong entraîne deux schémas de migration chaque année (Kong et al., 2001). Le premier pic, de mai à juillet, coïncide avec la montée des eaux où de nombreuses espèces de poissons migrent vers les plaines inondées et ses affluents autour des grands lacs afin d'utiliser ces zones pour le frai et l'alimentation. Le deuxième pic de migration se produit entre la mi-octobre et le mois de février, lorsque le niveau d'eau du grand lac commence à se déverser dans la rivière Tonle Sap vers le bas Mékong. De nombreuses espèces migratrices saisonnières quittent la plaine inondable après avoir passé du temps pour la reproduction et la croissance dans le Mékong, les grands lacs et certaines zones du delta du Mékong (Warren et al., 1998 ; Baird, 2004). En outre, les poissons riverains migrent beaucoup en raison de la fluctuation annuelle importante du volume d'eau du système (Pantulu, 1986).

3.2. Relation entre le régime hydrologique annuel et le rendement de pêche

Les assemblages biotiques des systèmes de plaines inondables aquatiques ont un grand potentiel de remaniement aléatoire pendant la période d'inondation annuelle (Hoeighaus et al., 2003). Les poissons riverains sont très mobiles, se déplaçant sur de longues ou courtes distances le long de la rivière. Ils réagissent à l'inondation saisonnière et à l'augmentation du flux d'eau annuel avec des mouvements latéraux ou longitudinaux sur la plaine d'inondation et dans le lac. La plupart des poissons riverains se reproduisent au début de la saison de crue, la biomasse des poissons augmente rapidement pendant la saison des hautes eaux en raison de la croissance rapide des jeunes de l'année (Lowe-McConnell,

1987). Les mouvements saisonniers fortement prévisibles comprennent des phénomènes comme la migration à longue distance des poissons tropicaux en réponse à des crues saisonnières (Mathew, 1998). Les fluctuations saisonnières du niveau d'eau, ou crue pulsée, influent sur la dynamique des populations de poissons et sont positivement associées aux rendements de la pêche (Junk et al., 1989).

La hausse des niveaux d'eau déclenche les processus de production de poissons, car de nombreuses espèces de poissons fraient et migrent latéralement hors des chenaux vers les plaines inondables nouvellement inondées lorsque les niveaux d'eau augmentent (Gomes et al., 1997 ; Castello, 2008). Dans les plaines inondables, les taux de croissance et de recrutement des poissons augmentent généralement car les poissons peuvent mieux se protéger des prédateurs et ils ont à disposition des abondantes ressources alimentaires à base de plantes, notamment les algues, les détritus et les graines des arbres fruitiers (Goulding, 1980, Agostinho et al. 2004). Inversement, la baisse des niveaux d'eau déclenche des processus de mortalité en contraignant les poissons aux chenaux et aux lacs de la plaine inondable, où la densité accrue des poissons intensifie les taux de prédation alors que la qualité de l'eau est souvent médiocre (Welcomme, 1979 ; Matthews & Marsh, 2003). La variabilité interannuelle des impulsions d'inondation influe donc sur les rendements de la pêche. Des études antérieures ont montré que les années de fortes chaleurs peuvent augmenter la biomasse de poissons de l’année suivante en favorisant le recrutement et la croissance des poissons. Inversement, des années de basses eaux extrêmes peuvent réduire la biomasse en augmentant les mortalités naturelles (Lagler et al., 1971, Welcomme et Hagborg, 1977 ; Halls & Welcomme, 2004). Les indices de crues pulsée d'une année donnée ont été corrélés avec les rendements plurispécifiques annuels ou la biomasse dans les années suivantes : 92% au Niger, 82% dans le Shire, 57% au Kafue et 83% en Amazonie (Welcomme, 1979).

Dans le système du Mékong cambodgien, les facteurs environnementaux tels que le niveau d'eau, la durée de l'inondation, le moment de l'inondation, la régulation de

l'inondation et la qualité de la zone inondée sont les facteurs les plus critiques du stock et production (Baran & Cain, 2001). En outre, Zalinge (2003) a observé de 1995 à 2002 la pêcherie Dai dans la rivière Tonle Sap sur la configuration saisonnière du régime de crue du Mékong sur la hauteur de la plaine inondée des grands lacs. Cet auteur a indiqué que d'année en année les variations du maximum des niveaux d'inondation du Mékong sont liées à la forêt inondée du grand lac inondée qui affecte fortement le rendement annuel des poissons au Cambodge. En Amazonie, il a été observé que les eaux hautes et basses d'une année donnée affectaient les rendements des pêcheries deux et trois ans plus tard en modifiant la biomasse disponible, contribuant à 18% de la variabilité expliquée des rendements (Castello et al., 2015). Il a été observé que la fluctuation annuelle du régime hydrique dans le système fluvial du Mékong cambodgien affectait fortement la production annuelle de poisson en limitant ou en augmentant l'accés aux zones de frayères et d'alimentation des poissons (Zaling, 2002).

4. Les facteurs influançant sur la co-occurrence des espèces

Les écologistes ont essayé de comprendre des facteurs qui déterminent les changements saisonniers de la structure des communautés de poissons. Des auteurs (e.g., Hugueny et Paugy, 1995 ; Belliard et al., 1997 ; González et al., 2009 ; Sousa & Freitas, 2008 ; Smith & Petrere, 2008) ont observé que le changement saisonnier des cycles hydrologiques et la modification des caractéristiques de l'habitat étaient les principaux facteurs de structuration de la communauté de poissons. Mais peu d'études ont examiné les interactions biotiques des espèces. Récemment, les écologistes tentent d'accroître la connaissance des interactions biotiques interspécifiques (Wiens, 2011; Wisz et al., 2013), tandis que les études contemporaines et paléoécologiques des aires de répartition des espèces, des groupes fonctionnels et des patrons de richesse des espèces ont montré que

les interactions biotiques ont clairement laissé leur marque sur les distributions d'espèces (Wisz et al., 2013).

En outre, certains auteurs (e.g., Werner et al., 1983 ; Power et al., 1985) ont indiqué que les interactions peuvent conduire à des schémas de répartition à l'échelle fine. À plus grande échelle, la plupart des études suggèrent que la co-occurrence des poissons d'eau douce dépend principalement des conditions de l'habitat (Peres-Neto, 2004 ; Mouillot et al., 2007 ; Mouchet et al., 2013). Cependant, l'influence relative de l'habitat et des interactions biotiques est difficile à découpler à grande échelle spatiale. Par exemple, plusieurs études ont montré que les interactions biotiques peuvent être importantes, mais seulement dans certains contextes abiotiques (Hoeinghaus et al., 2007 ; Hein et al., 2014). En d'autres termes, les effets perçus des interactions biologique à de grandes échelles spatiales sont souvent des artefacts d'hétérogénéité d'habitat dans lesquels une espèce est favorisée par rapport à d'autres dans certaines conditions (Wenger et al., 2011). Quoi qu'il en soit, la plupart des recherches effectuées à ce jour suggèrent que les interactions biotiques sont sont moins importantes que les facteurs abiotiques pour expliquer la distribution de poissons d'eau douce à de grandes échelles spatiales (Peoples et Frimpong, 2015). A côté de cela, d'autres études ont observé que l'assemblage de communauté peut être fortement influencé par les interactions biotiques entre les espèces, en particulier par la compétition interspécifique (MacArthur & Levins, 1967 ; Schoener, 1974 ; Chase & Leibold, 2004). Néanmoins, le rôle de la compétition interspécifique dans la formation des communautés est une question complexe qui reste à étudier et à débattre. En abordant le rôle de la compétition interspécifique dans l'assemblage de communauté, beaucoup de travaux se sont concentrés sur la détection de la signature de la compétition dans les modèles de co-occurrence des espèces au sein des communautés (Gotelli & McCabe, 2002). Par conséquent, les changements saisonniers dans le cycle hydrologique et la ségrégation des espèces constituent le principal mécanisme de structuration des assemblages de poissons.

À cet égard, l'interaction des espèces et la co-occurrence dans la même niche écologique peuvent être partagées avec les mêmes ressources alimentaires au cours des années.

5. Variations saisonnières de la composition du régime alimentaire, de la largeur du spectre alimentaire et du chevauchement alimentaire dans le système d'inondation pulsée tropical

Les animaux modifient souvent leur régime alimentaire en fonction des changements dans la disponibilité des ressources (Buren et al., 2012), des conditions environnementales abiotiques (Stuart-Smith et al., 2004), du stade ontogénétique (Werner et Hall, 1988), de la concurrence (Kie & Bowyer, 1999) ... Des études sur l'écologie alimentaire des poissons ont été un outil important pour comprendre les modèles écologiques tels que la préférence d'habitat et les interactions poisson-habitat, souvent liés aux variations environnementales et à la disponibilité et l'accessibilité des ressources (Braga et al., 2012 ; Correa & Winemiller, 2014). Dans les rivières et les lacs tropicaux, l'inondation pulsée a été un élément moteur des assemblages de communautés de poissons et la dynamique des inondations dans les écosystèmes aquatiques tropicaux pourrait être un élément essentiel de la structure des communautés de poissons d'eau douce (Pool et al., 2017). Ces processus biologiques et écologiques ont influencé l'écologie alimentaire des poissons, entraînant des changements dans les aires d'alimentation et la disponibilité de la nourriture (Junk et al., 1989 ; Luz-Agostinho et al., 2008 ; Mortillaro et al., 2015). Ainsi, l'analyse du régime alimentaire peut révéler des informations importantes sur les ressources alimentaires disponibles pour les poissons, en particulier au cours des saisons (Persson, 1983 ; Lobon-Cervia & Rincon, 1994).

Parmi les poissons néotropicaux, la relation trophique est l'un des principaux défis pour comprendre les mécanismes écologiques et la coexistence d'espèces dans la communauté et la manière dont les ressources sont partagées (Esteves & Galetti, 1994).

Plusieurs études (e.g., Goulding, 1980 ; Prejs & Prejs, 1987 ; Olurin et al., 1991 ; Pouilly et al., 2003 ; Hahn et al., 2004 ; Mérona & Mérona, 2004 ; Pouilly & Rodríguez, 2004 ; Pouily et al., 2006) ont trouvé que la même ressource alimentaire peut être partagée par de nombreuses espèces de poissons et que chaque espèce peut exploiter successivement plusieurs sources de nourriture différentes au cours de l'année. Bien que la ségrégation trophique ait été identifiée comme le principal mécanisme de structuration des assemblages de poissons (Pianka, 1969 ; Ross, 1986), elle peut varier en fonction des conditions des sites et de la saisonnalité (Bouton et al., 1997). De plus, dans les écosystèmes néotropicaux d'eau douce, les changements cycliques se produisent en réponse à l'alternance des saisons sèches et humides. Le changement saisonnier affecte les ressources alimentaires de l'ichtyofaune et peut modifier le spectre trophique et le rythme d'alimentation du poisson, influençant les relations trophiques entre les espèces (Araújo-Lima et al., 1995 ; Winemiller & Jepsen, 1998 ; Hahn et al., 2004 ; Yamamoto, 2004). Cependant, le partage des ressources et d'autres facteurs qui permettent la coexistence des espèces sont peu compris par les écologistes (Esteves & Galetti, 1994 ; Gerking, 1994 ; Higgins & Strauss, 2008). Par conséquent, l'analyse alimentaire peut révéler des informations importantes sur la dynamique trophique et la répartition des ressources parmi les espèces de poissons (Ross, 1986), notamment en ce qui concerne les environnements subissant des changements soudains (Johnson & Arunachalam, 2012). De plus, Lowe-McConnell (1999) a également mentionné que l'ichtyofaune en général présentait des régimes plus spécialisés pendant la saison des hautes eaux, lorsque les aliments variaient et abondaient, et que les valeurs de chevauchement alimentaire étaient plus faibles chez les espèces durant cette période. Prejs & Prejs (1987) ont également signalé un fort chevauchement alimentaire pendant la saison sèche pour les communautés de poissons des rivières vénézuéliennes. Goulding (1980) et Goulding et al. (1988) ont trouvé des résultats similaires dans les rivières Machado et Negro en Amazonie. D'autre part, dans les cours d'eau panaméens, les chevauchements alimentaires entre espèces étaient relativement faibles pendant la saison sèche (Zaret & Rand, 1971), ce qu'ils attribuaient à une pénurie de ressources alimentaires. Inversement,

Peterson et al. (2017) ont observé que la diversité alimentaire diminuait lorsque les niveaux d'eau diminuaient et que la disponibilité des habitats et des ressources aquatiques diminuait, mais le chevauchement alimentaire interspécifique n'était pas plus faible. Enfin, Mérona & Mérona (2004) indiquaient qu'il n'y avait pas de différence entre les saisons en Rei Lake (Amazonas).

6. Objectifs spécifiques de la thèse

Le lac Tonlé Sap (TSL) est le plus grand lac naturel et système d'inondation pulsée de l'Asie du Sud-Est. Ce lac abrite près de 250 espèces de poissons, des animaux aquatiques menacés et en danger, et fournit environ 60% des captures de poissons continentaux au Cambodge. Les changements saisonniers dans les cycles hydrologiques influencent la structure des communautés de poissons, créent des habitats hétérogènes favorables pour le frai et la croissance, et finalement influencent la production halieutique annuelle du Cambodge. Cependant, très peu d'efforts se concentrent sur les changements saisonniers dans la communauté de poissons de TSL, les changements saisonniers dans les cycles hydrologiques et comment les communautés de poissons réagissent aux changements du cycle hydrologique annuel, en particulier comment les espèces changent leur régime alimentaire. La thèse est structurée en 4 chapitres afin de répondre à 4 objectifs de recherche. Le premier chapitre consiste à caractériser la variation temporelle de la composition spatiale des communautés de poissons de six sites du TSL et d’identifier les déterminants des variations temporelles de la contribution des sites et des espèces à la variation spatiale de la composition de la communauté. Le deuxième chapitre consiste à explorer la variabilité temporelle de la plupart des espèces de poissons et leur modèle de co-occurrence. Dans le troisième chapitre, nous examinons les plaines inondables des rivières tropicales en tant que système modèle afin d'étudier la réponse de la position trophique des poissons des changements de position trophique pour 4 poissons piscivores

communs à des variations régulières dans l'environnement. Enfin, le dernier chapitre vise à décrire les variations saisonnières du régime alimentaire et le chevauchement alimentaire de trois espèces poissons communs, abondants et commercialement importantes dans le TSL, mais aux cycles de vie différents.

7. Le lac Tonlé Sap

Le lac de Tonlé Sap (TSL), est un écosystème lac-rivière de forêt alluviale au régime d'écoulement alternatif. Le lac est un déversoir lors de l'inondation saisonnière du Mékong et sert de réservoir en période de basses eaux. La superficie du lac pendant la saison sèche (février à mai), est d'environ 2 700 km^2 pour une profondeur d'environ 1 mètre. Cette superficie est pratiquement multipliée par six quand arrive la saison des pluies, pour atteindre près de 16 000 km^2 et une profondeur de 9 mètres, noyant rizières et forêts. C'est le plus grand lac d'eau douce d'Asie du Sud-Est. C'est aussi l'une des zones de pêche d'eau douce les plus importantes et productives du monde avec près de 75% du volume annuel de pêche en eau douce du Cambodge, ce qui permet la survie de près de 2,5 millions de personnes. Les changements saisonniers du cycle hydrologique ont une influence sur la structuration des communautés de poissons à l'échelle temporelle et spatiale, mais aussi sur les comportements trophiques des principales espèces qui n'exploitent alors pas les mêmes habitats. Toutefois, le bassin versant du Mékong est en changement constant avec un développement important des infrastructures en lien avec l'eau : production d'hydro-électricité, besoins important en irrigation, maitrise des inondations, eau potable, … Les changements climatiques accélèrent les modifications du cycle hydrologique annuel. Il est alors supposé que ces modifications ont des effets forts sur les habitats et les proies disponibles et finalement sur la biodiversité, notamment de l'ichtyofaune et sur l'abondance des poissons disponibles pour les pêcheries.

8. Principaux résultats

Dans un premier temps, nous avons caractérisé les variations spatio-temporelles de la composition taxonomique des poissons et mis en lumière quels sont les déterminants de ces variations. À cette fin, nous avons estimé la diversité bêta comme la variance totale de la matrice site par communauté d'espèce et l'avons divisée en contribution locale à la diversité bêta (LCBD) et contribution des espèces à la diversité bêta (SCBD). Nous avons ensuite effectué plusieurs régressions linéaires pour déterminer si la richesse taxonomique, l'abondance des espèces et le niveau de l'eau expliquaient la variation temporelle de la contribution du site et de l'espèce à la diversité bêta. Nos résultats indiquent une forte variation temporelle de la diversité bêta due aux contributions différentielles des sites et des espèces à la variation spatiale de la composition taxonomique des poissons. Nous avons également constaté que la direction, la forme et l'effet relatif de la richesse spécifique, de l'abondance et du niveau de l'eau sur la variation temporelle des valeurs LCBD et SCBD varient grandement selon les sites. Ces résultats suggèrent ainsi une variation spatiale des processus conduisant à une variation temporelle de la composition de la communauté. Dans l'ensemble, nos résultats suggèrent que la composition taxonomique des poissons n'est pas distribuée de manière homogène dans l'espace et dans le temps et risque d'être affectée à l'avenir si la dynamique saisonnière d'écoulement du système est altérée par les activités humaines et/ou les changements climatiques.

Dans un second temps, nous avons cherché à étudier le modèle d'évolution temporel des principales espèces en terme d'occurrence et d'abondance à travers le cycle saisonnier hydrologique. Nous avons constaté que les profils d'occurrence et d'abondance variaient dans le temps en fonction des niveaux d'eau et du sens d'écoulement. Une forte variation temporelle de l'occurrence des espèces a été observée avec des espèces colonisant le lac alors que le niveau d'eau commence à monter telles que *Labiobarbus leptocheilus* et *Poropuntius deauratus*. Nous avons également observé que l'abondance de 17 espèces varient beaucoup alors que les 22 autres espèces étaient plus stables au cours de l'année

(principalement les espèces résidentielles de TSL). Les patrons de co-occurrence positive des espèces étaient généralement plus élevé que la co-occurrence négative des espèces quel que soit la saison. Les modèles de co-occurrence les plus positifs ont été observés pendant la période de baisse du niveau de l'eau alors que les poissons migrent des zones inondées, entrent en compétition pour les ressources et les habitats pendant la saison des basses eaux. L'étude de la répartition temporelle de la co-occurrence des espèces et de la façon dont la communauté réagit au changement saisonnier dans le cycle hydrologique fournissent des informations importantes pour la gestion et la conservation des pêcheries du TSL et le maintien de la biodiversité des poissons du bassin versant aval du Mékong.

Dans un troisième temps, les implications de la saisonnalité du cycle hydrologique sur la structure du réseau trophique ont été étudié. Cette relation a, jusqu'ici, été notoirement ignorée, en particulier dans le système de TSL. Pour notre étude, nous nous sommes concentré sur les changements saisonniers dans un attribut clé d'un réseau trophique, la position trophique verticale des consommateurs. Nous nous demandons si les poissons des plaines tropicales se comportent comme des omnivores saisonniers, en déplaçant leurs positions trophiques par rapport au pouls annuel, ou s'ils se nourrissent en omnivores statiques, à la même position trophique toute l'année, comme le suppose implicitement les travaux antérieurs. En utilisant des isotopes stables de l'azote (δ15N) pour 28 espèces, nous avons trouvé des preuves pour le TSL que les poissons se déplacent vers des positions trophiques inférieures pendant la saison des pluies et la remonté des niveaux d'eau. Les données disponibles sur l'alimentation provenant du lac et une revue de la littérature suggèrent qu'une exploitation accrue des plantes et/ou des invertébrés pourrait expliquer ces résultats. Cependant, la grande variation des changements de position trophique saisonnière observée entre les espèces (allant de -0,51 à +0,64 du niveau trophique de la saison sèche à la saison humide) indique que diverses réponses comportementales à la saisonnalité pourraient être essentielles pour réorienter le flux énergétique dans ces écosystèmes dynamiques. Sur la base de la littérature existante,

l'omnivorie saisonnière semble répandue dans d'autres taxons et écosystèmes, et mérite d'être étudiée davantage étant donné son influence potentielle sur la dynamique du réseau trophique dans des environnements fluctuants.

Dans un dernier temps, nous avons cherché à savoir si les changements saisonniers dans cycle hydrologique de TSL affectaient différemment le régime alimentaire et le chevauchement des niches trophiques de trois espèces de poissons communs, au cycle biologique différent (par ex. migration saisonnière) et commercialement importants (*Anabas testudineus*, *Boesemania microplepis* et *Notopterus notopterus*). Pour cela, les trois espèces ont été échantillonnées à quatre endroits répartis sur le lac, et leur contenu stomacal a été prélevé pour analyse. Les différences alimentaires ont été étudiées au cours des saisons en ce qui concerne la composition du régime alimentaire et la largeur de la niche trophique ainsi que la quantité du chevauchement alimentaire entre les espèces. Nous avons constaté que la proportion d'estomacs vides changeait de façon similaire d'une saison à l'autre pour les trois espèces, alors que les changements dans la composition du régime alimentaire étaient spécifiques à l'espèce. La largeur de la niche trophique variait d'une espèce à l'autre en toutes saisons, sauf pendant la saison des pluies, et tendait à être plus élevée pendant la saison sèche lorsque le chevauchement alimentaire était le plus faible. Nos résultats suggèrent une plasticité fort dans le comportement alimentaire des trois espèces, comme le démontrent les variations saisonnières à la fois de la largeur de la niche trophique et du chevauchement alimentaire. Ces variations peuvent s'expliquer par un certain nombre de facteurs et de processus, notamment les changements dans la disponibilité des ressources alimentaires ou les interactions compétitives entre les individus pour les ressources, dont l'influence relative peut varier selon l'ampleur et le moment de l'inondation. L'acquisition de connaissances sur l'évolution saisonnière de l'alimentation des poissons est pertinente pour la gestion et la conservation des pêches et nos résultats pourraient être utilisés pour guider le développement de l'aquaculture au Cambodge.

9. Conclusion générale

Le lac de Tonlé Sap (TSL) est la plus grande pêcherie continentale d'Asie du Sud-Est et soutient la survie de 2,5 millions de personnes autour du lac (Arias et al., 2013). Sa dynamique de crue combinée à l'inversion du flux du TSR en fait un système unique dans le monde qui soutient une biodiversité élevée en fournissant une grande diversité de nourriture et d'habitats pour de nombreux oiseaux et poissons. Cependant, la demande croissante d'eau à des fins agricoles et la construction de barrages hydroélectriques le long du Mékong (Arias et al., 2013) combinés aux effets du changement climatique menacent fortement ce système en modifiant et en réduisant l'intensité des inondations de 7% à 16% pendant la saison des pluies (Arias et al., 2012). De tels changements dans le régime hydrique auront probablement de fortes répercussions sur la composition des communautés de poissons en modifiant plusieurs événements phénologiques (Agostinho et al., 2004) tels que le moment de la migration ou du frai et en réduisant la quantité d'habitats submergés nécessaires pour la croissance et la reproduction. Ceci peut finalement conduire à une diminution de la productivité des poissons du TSL et de la biodiversité. Par exemple, en 2016, une centaine de tonnes de géniteurs de poissons sont morts dans la zone de conservation de Boeung Chhmar, qui est la principale zone de conservation de la TSL, en raison d'une sécheresse prolongée. Dans le système TSL, les fortes variations spatio-temporelles mises en évidence concernant le caractère unique des communautés de poissons sont probablement le résultat de variations spatiales des conditions environnementales et de la migration saisonnière d'espèces particulières dont l'occurrence dépendant de la connectivité latérale aux habitats des plaines inondables leur reproduction et leur survie.

Nous avons également constaté que le patron de la plupart d’occurrences et d'abondance d’espèces variaient dans le temps en fonction du changement saisonnier des cycles hydrologiques du système TSL. Les espèces migratrices et non migratrices étaient généralement séparées à toutes les saisons, particulièrement durant les périodes de basses eaux, en raison du changement de connectivité latérale dans le lac et de compétition pour

l'habitat et des ressources alimentaires en saison sèche. Les changements saisonniers du cycle hydrologique et de la connectivité latérale ont influé sur la présence et l'abondance des espèces et ont favorisé la ségrégation et l'agrégation des espèces dans le lac. Par conséquent, l'interaction entre les espèces et le changement de connectivité latérale dans le lac TSL fournit une rétroaction critique pour la gestion et la conservation des pêches, en particulier pour maintenir la biodiversité des poissons dans le bassin du Mékong et maintenir la nutrition et les revenus pour des millions de cambodgiens. Promouvoir la connectivité avec les habitats des plaines inondables est donc une étape importante vers le maintien de la biodiversité et de la productivité des poissons dont dépendent ces personnes pour leur subsistance.

La position trophique verticale et le concept connexe d'omnivorie de la chaîne alimentaire sont des attributs clés qui influencent la stabilité et les fonctions du réseau alimentaire (McCann et al., 2005 ; Post & Takimoto, 2007 ; Winemiller et al., 2014). Nos résultats pour les poissons des plaines inondées tropicales ont révélé que l'omnivorie de la chaîne alimentaire est dynamique en réponse à la variation saisonnière des cycles hydrologiques. Les changements saisonniers dans l'écologie trophique ne sont pas uniques aux poissons tropicaux ou aux plaines inondées. La connaissance de la façon dont les espèces et les écosystèmes répondent à la saisonnalité est cruciale pour anticiper les conséquences du changement climatique. Par exemple, des organismes capables d'une dynamique omnivore à des échelles de temps saisonniers pourraient être particulièrement importants pour le maintien du fonctionnement des écosystèmes face à l'évolution des conditions écologiques (Takimoto et al., 2002 ; McMeans et al., 2016). En outre, le maintien d'espèces couvrant une gamme de réponses trophiques, comme observé chez les poissons dans les plaines inondables tropicales, pourrait jouer un rôle important dans la protection des communautés locales contre les perturbations.

Dans le TSL, le changement saisonnier du régime alimentaire des poissons et la façon dont les poissons modifient leur comportement alimentaire au fil des saisons sont mal

élucidés. Par conséquent, comprendre comment le régime alimentaire de ces espèces change de façon saisonnière pourrait aider à acquérir des connaissances sur la façon dont la connectivité aux habitats des plaines inondables influence leur comportement alimentaire et la force de la compétition pour les ressources. Nos résultats suggèrent que la crue pulsée peut jouer un rôle dans la médiation des interactions compétitives entre les trois espèces étudiées en permettant aux espèces de modifier leur régime alimentaire à mesure que la disponibilité des ressources change avec le temps. Cela peut finalement promouvoir la biodiversité en offrant aux espèces des opportunités d'éviter la compétition et de vivre en harmonie avec d'autres espèces, présentant à l'origine des exigences alimentaires similaires. Cette harmonie est cependant menacée par l'accélération du développement des infrastructures hydrauliques (hydroélectricité, irrigation, contrôle des inondations et approvisionnement en eau) et du changement climatique, apportant des modifications considérables à la crue pulsée du lac Tonle Sap dans un avenir prévisible.

Mots clés : cycle hydrologique, régime d’écoulement alternatif, structure de communautés, variation spatio-temporelle, interaction entre espèces, compétition entre espèces, chevauchement de niche trophique, diversité bêta, LCBD, SCBD, omnivorie saisonnière.

Abstract

The Tonle Sap Lake (TSL), Cambodia, is a flood-pulse system. It is the largest natural lake in South- East Asia and constitutes one of the largest fisheries over the world, supporting the livelihood 2.5 million peoples. Seasonal change in annual hydrological cycle appears to have influence on fish community structure, both spatial and temporal variation, particularly on feeding behavior of TSL's fishes. Nonetheless, the Mekong River Basin is changing rapidly due to accelerating water infrastructure development (hydropower, irrigation, flood control, and water supply) and climate change, bringing considerable modifications to the annual flood-pulse of the TSL. Such modifications are expected to have strong impacts on fish biodiversity, abundance, reduced habitat and food availability within the lake. To invest how TSL's fish community structure responds to the seasonal change, how they shift their diet across hydrological cycles and feeding competing for food resource: First, we aim to characterize the spatio-temporal variations of fish taxonomic composition and to highlights the underlying determinants of these variations. For this purpose, we estimated beta diversity as the total variance of the site-by-species community matrix and partitioned it into Local Contribution to Beta Diversity (LCBD) and Species Contribution to Beta Diversity (SCBD). We then performed multiple linear regressions to determine whether species richness, species abundances and water level explained the temporal variation in the contribution of site and species to beta diversity. Our results indicate strong temporal variation of beta diversity due to differential contributions of sites and species to the spatial variation of fish taxonomic composition. We further found that the direction, the shape and the relative effect of species richness, abundances and water level on temporal variation in LCBD and SCBD values greatly varied among sites, thus suggesting spatial variation in the processes leading to temporal variation in community composition. Overall, our results suggest that fish taxonomic composition is not homogeneously distributed over space and time and is likely to be impacted in the future if the flood-pulse dynamic of the system is altered by human activities.

Second, we aim to investigate the temporal pattern of the most occurrence and abundance species and how their co-occurrence pattern across hydrological cycles. We found that occurrence and abundance patterns were temporally varied at all water level seasons. Strong temporal variation in species occurrence was occurred with visiting species such as *Labiobarbus leptocheilus* and *Poropuntius deauratus* while water level starts to fill into the TSL. We further observed that the abundance of 17 species was strongly varied while other 22 species (mainly TSL's residential species) were stable within the year. Positive species co-occurrence pattern was generally higher than negative species co-occurrence at all water level seasons. Highest positive co-occurrence patterns were found during the period of decrease and low water level seasons while fishes are migrating from flooded areas, competing for resource and habitats during low water season. Study on temporal distribution and species co-occurrence of fish and how community responds to the seasonal change in hydrological cycles provides critical information for fisheries management and conservation in the Tonle Sap Lake (TSL) as well as maintaining fish biodiversity in the Mekong system.

Third, the implications of seasonality on food web structure have been notoriously understudied in empirical ecology, particularly in TSL's system. The current study, we focus on seasonal changes in one key attribute of a food web, vertical trophic position of consumers. We ask whether tropical floodplain fishes behave as seasonal omnivores, by shifting their trophic positions in relation to the annual flood pulse, or whether they feed as static omnivores, at the same trophic position all year, as much empirical work implicitly assumes. Using stable nitrogen isotopes (δ15N) for 28 species, we find evidence within the Tonle Sap Lake, Cambodia, that fishes shift towards lower trophic positions during the wet season. Available diet data from the Tonle Sap and a literature review suggest that increased exploitation of plants and/or invertebrates could explain this finding. However, the large variation in seasonal trophic position shifts observed among species (ranging from -0.51 to 0.64 trophic levels from the dry to the wet season) argues that diverse behavioral

responses to seasonality could be central for re-routing energy flow in these dynamic ecosystems. Based existing literature, seasonal omnivory appears widespread in other taxa and ecosystems, and warrants further study given its potential influence on food web dynamics in fluctuating environments.

Last, we aimed to investigate whether seasonal changes in the water level of a flood-pulse system (the Tonle Sap Lake, Cambodia) differentially affect diet breadth and dietary overlap of three common and commercially important fish species (Anabas testudineus, Boesemania microplepis and Notopterus notopterus) presenting important differences in their life-cycle (e.g. seasonal migration). For this purpose, the three fish species were sampled at four locations spread over the lake and their stomach contents extracted for analyses. Dietary differences were investigated across seasons regarding the diet composition and diet breadth of each species as well as the amount of dietary overlap between species. We found that the proportion of empty stomachs changed similarly across seasons for the three species, thus suggesting that ecological differences between species are not sufficient to outweigh the effect of seasonal variations in resource abundance. In contrast, changes in diet composition were species-specific and can be explained by ecological and behavioral differences between species. Diet breadth differed between species in all seasons, except during the wet season, and tended to be higher during the dry season when dietary overlap was the lowest. These variations likely result from changes in the diversity and amount of resources and may lead to habitat use shifts with potential implications for competitive interactions. In particular, increasing connectivity to floodplain habitats may reduce the competitive pressure during the wet season, while resource scarcity during the dry season may constrain individuals to diversify their diet to avoid competition. Overall, our results suggest a considerable plasticity in the feeding behavior of the three species as demonstrated by seasonal variation in both diet breadth and dietary overlap. Such variations can be explained by a number of factors and processes, including changes in resource availability or competitive interactions between individuals for resources, whose

relative influence might vary depending on the magnitude and the timing of the flood-pulse driving the connectivity to floodplain habitats. Gaining knowledge on the seasonal evolution of fish's diet is relevant for fisheries management and conservation and our result could be used to guide aquaculture development in Cambodia.

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Keywords: Flood pulse system, hydrological cycle, fish community structure, spatio-temporal variation, species interaction, species competing, niche overlap, beta diversity, LCBD, SCBD, seasonal omnivory, feeding behavior, seasonal variation.

1. General Introduction

1.1. The context of flood pulse systems in the tropical system

Floodplains are defined as “areas that are periodically inundated by the lateral overflow of rivers or lakes and/or by direct precipitation or groundwater (Junk, 1997). Several studies (e.g. Junk et al., 1989; Ward et al., 1999; Tockener & Stanford, 2002) commonly observed that spatial heterogeneity and dynamic hydrology of rivers and floodplains support high biodiversity and affect functional processes. Evidences have been found in tropical flood pulses system causes lateral connectivity that influences and modifies ecosystem such as water quality (Thomaz et al., 2007), nutrient dynamics (Melack & Forsberg, 2001) and life cycles of many organisms within floodplain aquatic habitats (e.g. Junk 1985; Junk & Piedade, 1997; Arrington et al. 2006; Neves dos Santos et al. 2008). Althought, the flood-pulse concept has yet to be validated in large temperate rivers but Welcomme (1995) conducted a study in Europe and Hesse et al. (1993) in North America observed that temperate and tropical river system was a similar process. River floodplain connectivities and habitat heterogeneities are maintained by natural hydrologic regimes and environmental gradients (Ward, 1998; Sparks et al. 1990).

Furthermore, experience from tropical floodplain rivers observed that, periodic flood pulses is the main structuring force for the fish community, reproduction and also have a strong influence on the fish distribution and abundance pattern (Junk et al., 1989; Sousa & Freitas, 2008 and Goulding, 1980). Beside this, flood pulse systems are important in supporting recruitment for fish species (Sparks, 1995) while the experience from Amazon Basin revealed that great number of fishes starts to enter into floodplain seasonally to feed on fruit, seed and terrestrial resources (Goulding, 1980; Hamilton & Lewis,1987; Goulding et al., 1988). Floodplain Rivers, flood pulses are so predictable and long-lasting that plants, animals, and even human societies have adapted to take advantage of them (Sparks, 1995). Flood pulses are suggested to be the driving force for the high biodiversity of floodplains by creating heterogeneity of habitats (Junk & Piedade, 1993; Gopal & Junk, 2000). Most large

floodplain rivers of the world are greatly altered by human activity. Consequently, rivers that have not been altered are rare, and are more than likely to be altered in the near future (Gore and Sheilds, 1995 & Sparks, 1995). Tropical floodplains are the most diverse of all floodplain ecosystems (Gopal and Junk, 2000), and will, therefore be the most impacted by development, largely because tropical floodplains are located in developing countries that do not have the economy to establish environmental sustainability into the industry (Roggeri, 1995).

Freshwater ecosystems have been known to support a rich diversity of biological life and provide services to human activities (Strayer & Dudgeon, 2010). Floodplain wetlands are among the most diverse and productive freshwater ecosystems on the planet (Kingsford 2000; Rosenberg et al., 2000). Despite their invaluable ecosystem functions, a decline in wetland aquatic biodiversity has been observed that is mainly driven by changes in land use and climate (Verhoeven et al. 2006; Palmer et al., 2008). In addition to these, river floodplain ecosystems are also threatened by the alteration of flow regimes through the construction of dams (Dynesius & Nilsson 1994; Tockner et al., 2010) and leaded to change spatial and temporally of fish community structure within the floodplain.

1.2. Spatio-temporal fish community variations in tropical flood pulse systems

All biological communities vary greatly in space and time (e.g. Southwood, 1988). The current approaches to study community ecology are to explain the patterns of distribution and abundance of species, linking processes that occur at different spatial and temporal scales (Ricklefs & Schluter 1993; Leibold et al., 2004). In large floodplain rivers, the adjustment of communities to each kind of model can vary with seasonal water level fluctuation (Winemiller, 1996; Arrington et al., 2005; Arrington & Winemiller, 2006). Floodplains have unique and important ecosystem functions in riverine landscapes where

they frequently function as hot spots of biodiversity owing to complex patterns of habitat variation over a wide range of temporal and spatial scales (Swales et al., 1999; Tockner et al., 2010). High interconnection among habitats during high water season offers an opportunity to random reshuffling of fish and may promote stochastic processes on community structure and composition. During dry season, floodplain lakes and channels become isolated and fish densities increases. It is commonly found that the seasonal flood-pulse dynamics have influenced on ecological and environmental processes by causing lateral connectivity to adjacent floodplain habitats and by influencing water quality and nutrient dynamics and influencing the life cycle of many organisms (Tockner et al., 2000). Gopal & Junk (2000) and Lasne et al. (2007) revealed that lateral connectivity is a key element for many fish and other aquatic species because it provides resources and, heterogeneous habitats for spawning, rearing, favoring productivity and biodiversity. Studies of spatial and temporal patterns of distribution and diversity of freshwater fishes are useful to analyze factors influencing fish community structure and how communities respond to the seasonal change in hydrological cycles (Hugueny & Paugy 1995; Belliard et al., 1997). Serveral studies revealed that temporal pattern of fish community structure was related to the dynamic of the floods (Smith & Petrere, 2008; Sousa & Freitas, 2008; González et al., 2009) and fish communities in lentic systems seemed to be more stable temporally than those in the lotic ones (Merona, 1987). Furthermore, synchronous dynamics of animal populations over large spatial scales is emerging as a common phenomenon (Ranta et al. 1995; Cattadori et al., 2000; Post & Forchhammer 2002; Cattanéo et al., 2003). Identifying mechanisms that cause spatial synchronization has proved both difficult and central to understanding population regulation.

At spatial scale, lateral connectivity of flood pulse is the main force in structuring temporal fish community assemblages rather than that spatial scale (Sousa & Freitas, 2008), which contrasted fining with other studies which commonly found that floodplain fish community was observed that spatial separation of some species might be maintained,

depending on the precise environmental conditions, since the small haplochromines can tolerate low oxygen water unsuitable for the large perch (Fish, 1956; van Oijen et al., 1981; Chapman et al., 1995). In addition, several studies in Amazon regions and French Guiana investigated that lagoon fishes found within floating saprophyte habitats (Henderson & Hamilton 1995; Meschiatti et al., 2000), differences among habitats within a localized area (Cox Fernandes, 1997; Saint-Paul et al., 2000; Silvano et al., 2000; Petry et al., 2003), and differences between natural and flow-regulated rivers (Merigoux & Ponton, 1999).

1.3. The relationship between the annual hydrological regime and fish

1.3.1. Seasonal flood regime in temperate, tropical rivers and fish distribution

Fish distribution is strictly involved with the migration pattern from one habitat to another in term of breeding, rearing, feeding and growing as a result of the fluctuation of environment seasonal change. The vast array of adaptations that have evolved in fishes whether they are morphological, ecological, reproductive or physiological is simply amazing (Pereira, 2003). The largest numbers of species are found in tropical regions more than temperate regions, with freshwater species being most numerous in the river drainages of south-eastern Asia and South Africa (Malcolm, 1995).

In the temperate regions, temperature is variously in a predicable seasonal pattern, with the magnitude variation greater at higher latitude and elevations, regions having fairly unpredictable rainfall and lacking significant runoff from snowmelt display unpredictable, a seasonal flood pulses, for example temperate rivers along the north-western Gulf of Mexico coast of North America and some certain regions within Australia's Murry-Darling Basin. In Texas, the Brazos River shows unpredictable hydrology, both within and between years (Winemiller, 1996). Many temperate regions have cyclic pattern of precipitation and/or spring time melting of ice and snow that yield seasonal flood pulse. Seasonal flood in temperate

river also can be strongly influenced by evapotranspiration as a function of seasonal temperature regime (Benke et al., 2000). The magnitude of flooding in most temperate rivers is highly variable between year and in some systems, e.g. Ogeechee River, south eastern the United States, floods may not occur at all during some years. In most cases, seasonal flooding in the temperate zone coincides with springtime warming, which some fish species selects for reproduction in this period (Benke et al., 2000).

In contrast, in the tropical continental regions, the flood pulse of lowland rivers is almost universally driven by seasonal precipitation during the rainy season, but in some cases local flooding coincides with local precipitation (upper Orinoco, upper Parana, upper Zambezi and Fly Rivers), whereas in others seasonal flood pulse such as lower Niger, Congo and Solomoes-Amazon River is most strongly influenced by rainfall in distance head water (Winemiller, 2004). In addition, due to the temperature various relatively in little in tropical lowland regions, hydrology is the major factor that drives ecological dynamics and natural selection in respons to environmental variation. The tropical seasonal model has dominated thinking about the ecology of river floodplain river system but the global generality of this pattern and its consequence have scarcely discussed.

Winemiller (2004) identified at least there are three types of river according to their hydrology, temperate with seasonal flood pulse, stochastic flood pulse seasonal flood pulses and tropical with seasonal flood pulse. Global fish richness is strongly related to basin size (Oberdorff et al., 1995). However, fish shows higher taxonomic and ecological diversity in lowland continental rivers of tropic relative to comparable rivers of the temperate region (Winemiller, 1991). Fish have evolved physiological adaptation, life history strategies and spawning and feeding behaviour to cope with these different types of fluctuating flow condition in the river. Anyway, the annual hydrological cycle influences migrations, distribution of many fish species between floodplain and channel, deep pool habitats. The abundance, biomass of floodplain dependent species, and the fish catches that depend on them, fluctuate from year to year depending on the strength of flooding (Welcomme, 2003).

The seasonal change in water level and regime is critically affected on riverine fish distribution, fish migration behaviour as well as the annual catch. Many fish species adapted to take advantage of seasonal flooding by reproducing at the beginning of the wet season, which allows early life stages to feed and growth in inundated floodplain habitat (Lowe-McConnell, 1987). After floodwater recession reduces the availability of aquatic habitat and increases of fish densities and biotic interactions (Zaret & Rand, 1971). Ichthyomass and fish catch are depending on both extend of flooding regime during the high water and amount of water remaining in the system during the dry season. The relationship of catch to flood regime ratio may form the basic of a general index for the evaluation of both year to year variations within a floodplain, and difference between floodplain (Welcomme, 1976).

In the large tropical floodplain river inhabits, migratory fish species which carry out seasonal movements between spatially and temporally separated habitats. Such as in the Mekong River system, most important species in fisheries are greater or lesser extent, migratory or typically move between dry season refuse habitat and flood-season feeding and spawning habitat. Some species only move in short distance between river channels and adjacent flooded areas (Poulsen, 2001).

Seasonal change in water regim in the Cambodian Mekong River System causes two peak migration patterns in a year (Kong et al., 2001). The first peak, takes place from May to July coinciding with water level increasing or when the changes of the climate such as temperature, humidity and wind flow occurs. During that time many of fish species which utilize dry season “fasting” in refuse habitats such as deep pool in some upper part areas in Stung Treng and Kratie provinces that are well known as the critical habitat during the dry season migrates down into flooded-plains and tributaries around the Great lake system in order to using these areas for rearing, spawning and feeding. Second peak migration occurs from the middle of October to February when the water level in the Great Lake starts to release its water via the Tonle Sap River to the low Mekong and Bassac Rivers. Many seasonally migratory species move from the floodplain after spending time for rearing,

breeding and growing up to the Mekong River from as far away as the Great Lake and some areas in Vietnamese Mekong Delta (Warren et al., 1998; Baird, 2004). In addition, riverine fish are strongly migrating because of the considerable annual fluctuation of water volume of the system, all or almost fish in the Mekong River system must exhibit migration behaviour patterns, which major movement between spawning ground in inundate forests to the Great Lake and from the Great Lake to the Tonle Sap River and thence to the Mekong, and *vice versa* (Pantulu, 1986).

1.3.2. Relationship between the annual hydrological regime and fish yield

Biotic assemblages of aquatic floodplain systems have great potential randomly reshuffle during annual flood period (Hoeighaus et al., 2003). Riverine fish are very mobile, moving long or short distances up and down the river. They respond to the seasonal flood and the increasing of annual water level, which may arrive after the local rain have ceased, by making lateral or longitudinal movements out over floodplain and into its pool. Most riverine fish breed at the start of the flood season, the biomass of fishes increases rapidly during the high water season and a large proportion of it due to the rapid growth of the young of the year (Lowe-McConnell, 1987). Highly predictable seasonal movements include phenomena like long range migration of tropical fish in respons to seasonal flood (Mathew, 1998). Sasonal fluctuation of water level, known as flood pulses influence the dynamics of fish populations and positively associated with fishery yields (Junk et al., 1989).

Rising water levels trigger fish production processes, as many fish species spawn and migrate laterally out of river channels onto the newly flooded floodplains when water levels rise (Gomes et al., 1997; Castello, 2008). In the floodplains, fish growth and recruitment rates generally increase as fish find protection from predators and abundant plant-based food resources, including algae, detritus, and tree fruits and seeds (Goulding, 1980; Agostinho et al., 2004). Conversely, declining water levels trigger mortality processes by

constraining fish to river channels and floodplain lakes, where increased fish densities intensify predation rates and water quality is often poor (Welcomme, 1979; Matthews & Marsh, 2003). Interannual variability in flood pulses thus influences fishery yields. Previous studies have found that extreme high water years can increase biomass for harvesting in subsequent years by promoting fish recruitment and growth rates. Conversely, extreme low water years can reduce biomass for subsequent harvesting by increasing natural mortality rates (Lagler et al., 1971; Welcomme & Hagborg, 1977; Halls & Welcomme, 2004). Flood pulse indices in a given year have been correlated with annual multispecies yields or standing biomass in subsequent years: 92% in the Niger, 82% in the Shire, 57% in the Kafue and 83% in the Amazon (Welcomme, 1979).

In Cambodian Mekong River system, the environmental factors such as water level, duration of the flood and timing of the flood, regulation of flooding, quality of the flood zone, and dry seasonal refuses as the most critical factors which generally influenced on the annual fish stock and production in the Mekong River basin (Baran & Cain, 2001). In addition, Zalinge (2003) conducted the observation from 1995-2002 at Dai Fishery in the Tonle Sap river on the seasonal pattern of the Mekong flood regime on the height of the Great Lake flooded-plain. This autor indicated that from year to year the variations in maximum of Mekong flood levels are related to the Great Lake flooded-forest inundated strongly affects to the annual fish yield in Cambodia. Similar to Amazone region which was observed that high and low waters in any given year affected fishery yields two and three years later through changes in fish biomass available for harvesting, contributing 18% of the explained variability in yields (Castello et al., 2015). It was obserevd that the annual fluctuation in water regime in the Cambodian Mekong River system was strongly affected the annual fish production by limiting or increasing the spawning and feeding ground of fishes (Zaling, 2002).

1.4. Interactions or factors influence species pair co-occurrence

Ecologists have tried to understand factors that determine the seasonal change in fish community structure and how they respond to change. More works (e.g. Hugueny & Paugy, 1995; Belliard et al., 1997; González et al., 2009; Sousa & Freitas, 2008; Smith & Petrere, 2008) observed the seasonal change in hydrological cycles and change in habitat characteristics between dry and flood seasons are the main factors in structuring fish community but few studies have examined on how biotic interaction. Recently, ecologists try to increase acknowledge on interspecific biotic interactions can also be important (Wiens, 2011; Wisz et al., 2013) while evidence from the contemporary and palaeoecological studies of individual species ranges, functional groups, and species richness patterns have shown that biotic interactions have clearly left their mark on species distributions and realised assemblages of species across all spatial extents (Wisz et al., 2013)

Furthermore, somes authors (e.g. Werner et al., 1983; Power et al., 1985) indicated that interactions can drive fine scale distributional patterns. At larger scales, most studies suggested that freshwater fish co-occurrence is driven mostly by habitat conditions (Peres-Neto, 2004; Mouillot et al., 2007; Mouchet et al., 2013). However, the relative influence of habitat and biotic interactions are difficult to decouple at large spatial scales. For instance, several studies have found that biotic interactions can be important, but only in certain abiotic contexts (Hoeinghaus et al., 2007; Hein et al., 2014). In other words, perceived effects of interactions at large spatial scales are often artefacts of habitat heterogeneity in which one species is favoured over others in certain conditions (Wenger et al., 2011). Regardless, most research to date suggested that biotic interactions are less useful than abiotic factors for explaining freshwater fish distribution at large spatial scales (Peoples & Frimpong, 2015). Contrasted findings, where some other studies observed that community assembly may be shaped strongly by biotic interactions among species, and particularly by interspecific competition (Chase & Leibold, 2004; MacArthur & Levins, 1967; Schoener, 1974). Nevertheless, the role of interspecific competition in shaping communities is a

complex issue that remains under active investigation and debate. In addressing the role of interspecific competition in community assembly, much work has focused on detecting the signature of competition in species co- occurrence patterns within communities (Gotelli & McCabe, 2002). The central assumption of these analyses is that if competitive interactions scale up to shape community level species distribution patterns, nonrandom patterns of localized species co- occurrence should be observable within a community (Connor & Simberloff, 1979; Diamond, 1975). Therefore, seasonal change in hydrological cycle and species segregation is the main mechanism structuring fish assemblages. With this regards, species interaction and co-occurrence in the same ecological niche may be shared the same food resources within the years.

1.5. Seasonal variations in diet composition, diet breadth and dietary overlap in tropical flood pulse system

Animals often shift their diets in response to changes in resource availability (Buren et al., 2012), abiotic environmental conditions (Stuart-Smith et al., 2004), ontogenetic stage (Werner and Hall, 1988), competition (Kie & Bowyer, 1999). Studies on the feeding ecology of fishes have been an important tool to understand ecological patterns such as habitat preference and fish-habitat interactions, which are frequently related to environmental variations and with resource availability and accessibility (Braga et al., 2012; Correa and Winemiller, 2014). In tropical rivers and lakes, flood pulse has found as a driver force fish community assemblages and flood-pulse dynamic in tropical aquatic ecosystems may be an essential element supporting freshwater fish community structure (Pool et al., 2017). This biological and ecological process has influenced on feeding ecology of fishes, resulting in changes in foraging areas and food availability (Junk et al., 1989; Luz-Agostinho et al., 2008; Mortillaro et al., 2015). Thus, diet analysis can reveal important information on the food resources available to fish, particularly across seasons (Persson, 1983; Lobon-Cervia & Rincon, 1994).

Among Neotropical fishes, the tropic relationship is one of the major challenges to understand the ecological mechanisms and how numbers of species are able to coexist in the same community and the manner in which resources are shared (Esteves & Galetti, 1994). Several studies (e.g. Goulding, 1980; Prejs & Prejs, 1987; Olurin et al., 1991; Pouilly et al., 2003; Hahn et al., 2004; Mérona & Mérona, 2004; Pouilly & Rodríguez, 2004; Pouily et al., 2006) have found that the same food resource may be shared by numerous fish species and each species may successively exploit several different sources during the year. Although trophic segregation has been indicated as the main mechanism structuring fish assemblages (Pianka, 1969; Ross, 1986), this may vary according to sites conditions such as seasonality (Bouton et al., 1997). Furthermore, in Neotropical freshwater ecosystems undergo cyclic changes in response to alternating wet and dry seasons. The seasonal change affects the food resources for the fish fauna and may modify the trophic spectrum and the feeding rhythm of the fish, influencing the trophic relationships among species (Araújo-Lima et al., 1995; Winemiller & Jepsen, 1998; Hahn et al., 2004; Yamamoto, 2004). However, resource partitioning and other factors that allow the species to coexist are little understood by ecologist (Esteves & Galetti, 1994; Gerking, 1994; Higgins & Strauss, 2008). Therefore, dietary analysis may reveal important information about trophic dynamics and resource partitioning among fish species (Ross, 1986), especially with regard to environments that are subject to sudden changes, such as streams (Johnson & Arunachalam, 2012).

Furthermore, Lowe-McConnell (1999) has also mentioned that, fish fauna in general showed more specialized diets during the high water season when foods are varied, and lower food overlap values were recorded among species in this period. Also Prejs & Prejs (1987) reported high food overlap in the dry season for fish communities in Venezuelan rivers. Goulding (1980) and Goulding et al. (1988) observed in the Machado and Negro rivers in Amazonas (Brazil) was found similarly. On the other hand, in Panamanian streams observed that, diet overlaps between species were relatively low during the dry season

(Zaret & Rand, 1971), which they attributed to a shortage in food resources. Conversely, Peterson et al. (2017) observed that dietary diversity declined as water levels dropped and availability of aquatic habitats and resources declined, but interspecific dietary overlap was not lower whereas Mérona & Mérona (2004) pointed out that there was no difference in mean overlap for the Rei Lake (Amazonas) fish fauna between seasons.

1.6. Specific Objectives

Tonle Sap Lake (TSL) is the largest natural lake and flood pulse system in Souteasth Asia. This lake supports 242 fish species, other threatened and endangered aquatic animals, birds and provides about 60 percent of total inland capture fisheries in Cambodia. Seasonal change in hydrological cycles influence on fish community structure, create heterogeineous habitats for rearing, spawning and growing and as well as influence on annual fisheries production in Cambodia. However, very few efforts focus on seasonal change in TSL's fish community, influences by seasonal change in hydrological cycles and how fish community responds to the changes within the year, particularly how fish species shift their diet according to the seasonal changes of hydrological cycles.

The overall thesis is structured into 4 chapters in order to respond to 4 research objectives. First, is to characterise the temporal variation in the spatial composition of fish communities among six sites within the TSL during 141 weeks, and (2) to identify the determinants of the temporal variations in the contribution of site and species to spatial variation in community composition. According that we found in the first chapter that TSL is characterized by high fish species diversity and notably changed in habitat conditions across hydrological cycles, the second chapter is to explore the temporal pattern of the most occurred fish species and their co-occurrence pattern in the TSL floodplain lakes throughout four years' hydrological cycles. Third, we examine seasonally wet-dry tropical river floodplains as a model system in order to investigate the response of fish trophic position for 4 common carnivorous fishes to regular variation in the environment. Last, this study aimed

to describe the seasonal variations of the diet and feeding overlap of three different life cycles, common, abundant and commercially important fish species whithin the TSL (*Anabas testudineus*, *Boesemania microplepis* and *Notopterus notopterus*).

2. Materials and Methods

2.1. Study sites

The Tonle Sap Lake (TSL) is a reversal flow lake system and one of the Cambodia's most important natural resources, which is the largest natural flood pulse lake in Southeast Asia (Fig. 1). The TSL formed by the subsistence about 5,000 - 5,600 years ago. The Lake's biodiversity is in term of variety and abundance of species, as well as the extraordinarily complex and diverse interactions of the physical, biological and human system. The TSL receives around 50 percent of water discharge from the upper Mekong originating from the snow melt of the Tibetan Plateau and in addition, from the local rainfall surrounding the lake itself. The TSL system is a centre of Cambodian fishery production and it is globally significant, being nominated as a Biosphere Reserve in 1997 under the Man and Biosphere Program of UNESCO. A remarkable natural phenomenon that occurs on an annual basis makes the TSL and its system rich sources of freshwater fish in the world. TSL is connected with the Mekong in its southern part by a 120 km long river, the Tonle Sap River (TSR), which serves as an inlet and outlet for water fluxes. The lake expands to 4-6 times from the 2,700 km^2 (equals to 0.5 million hectares) to 9,000-16,000 km^2 (1.0 to 1.3 million hectares) and the water level increase from 1 or 2 meters in dry season up to 10-15 meters during the rainy season and covers about 5-8 percent of land area of Cambodia during the rainy season. The TSL's hydrological cycle was divided into four phases. The first phase (rising season) takes place from July to early September and is characterised by a strong water feed coming from the upper Mekong through the TSR and during which the water level strongly increases. The second phase (the wet season) lasts from the end of September to the end of October, and corresponds to a phase where about 1.3 million hectares of forest, shrublands, grasslands and agricultural lands are submerged. At this period the water level may attain up to 15 meters. The third phase (the receding season) occurs from the end of October to February, and is characterized by the reversal of the TSR flowing from the TSL to the China Sea in the south, resulting in a decrease of the water level of the lake. Finally, the

fourth phase (the dry season) lasts from April to May, and corresponds to the period where the water level is the lowest (i.e. 1 to 2 m).

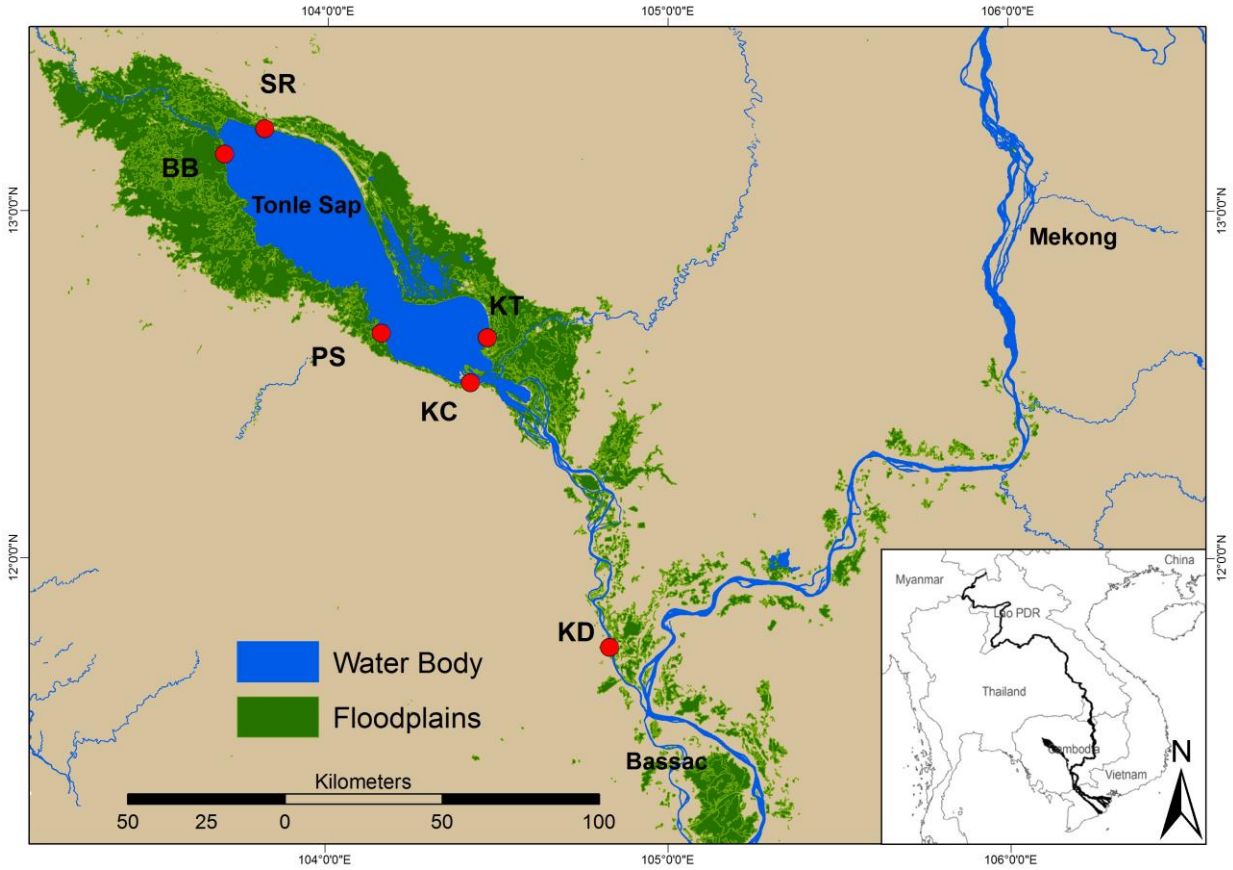

Fig. 1. Map of the study site around the Tonle Sap Lake (TSL) and in the Tonle Sap River (TSR). Red point indicates study sites around the TSL and on the Tonle Sap River.

2.2. Data collection

Daily catch monitoring data were derived from the Mekong River Commission (MRC), under the Assessment of Mekong Fisheries Component of the MRC Fisheries Program, and stable isotope and stomach content data was obtained from the Fisheries Administration and Maintaining productivity and incomes in the Tonle Sap fishery in the face of climate change (TLSCC)- Belmont forum project, funded by ANR.

First, the study on spatio-temporal variation of fish taxonomic composition in a South-East Asian flood-pulse system was relied on daily fish catches were monitored at five sites

located around the TSL and one site on the TSR (Fig 1). Two sites located in the northern part of the lake (Siem Reap [SR] and Battambang [BB]) while three sites namely Kampong Chhnang (KC), Kampong Thom (KT) and Pursat (PS) were located in its southern part. Another study catch monitoring site was located in the TSR (Kandal [KD]).

Second, the study on temporal distribution and species co- occurrence patterns of the most occurrence fish species in the Tonle Sap Lake Flood Pulse System was conducted only at five sites around the lake, namely KC, KT, SR, BB and PS. The reason of selecting five studied sites around the lake was due to the fact that we would like to better understand how the most occurred species responds to the seasonal change in hydrological cycles and how effect of heterogeneous habitat created by lateral connectivity act on species co-occurrence.

Third and fourth, data collection for the study on seasonal omnivory: the response of consumer trophic position to fluctuating environments and the study on seasonal variations in diet composition, diet breadth and dietary overlap between three commercially important fish species within a flood-pulse system was carried out under the collaboration between Inland Fisheries Research and Development Institute (IFReDI), Fisheries Administration and Maintaining productivity and incomes in the Tonle Sap fishery in the face of climate change (TLSCC)- Belmont forum project, funded by ANR. Stable isotope and stomach contents data were collected as part of a broader research effort involving surveys at multiple locations around the Tonle Sap (Siem Reap, Kampong Chhnang, Kampong Thom and Pursat Provinces; see Pool et al. 2017) during both seasons. This study was mainly focused on two data collection methods at four sites located around the lake. (i). tissue for stable isotopes were collected from 28 fish species sampled from November 2010 to April 2015 using multi-panel gill nets or by purchasing fish from local fishers or lakeside markets. Samples of aquatic invertebrate taxa used as baseline indicators of benthic and pelagic secondary production were sampled with dip nets and plankton nets. All samples were dried, homogenized and weighed into tin capsules before being analyzed for $\delta^{15}N$ *via* a Costech

ECS 4010 Elemental Analyzer coupled to a ThermoFinnigan MAT 253 isotope ratio mass spectrometer. (ii). The data collection for stomach content study was carried out at the same location where the collection of fish for stable isotope studies. Fish specimen for gut content study was conducted from June 2014 to March 2015 by local fishermen using gillnets with varying mesh sizes (2 to 6.5 cm), heights (1.5 to 2 m) and lengths (250 to 300 m), to capture individuals with varying sizes. Gillnets were deployed during the night and were let in the water for eight to ten hours. At least 20 specimens were collected and measured for each species and seasons in order to obtain a sufficient sample size for statistical inferences. To account for spatial variation in resource distribution in TLS and low local abundance in some cases, the specimens were collected at four locations: Kompong Thom (KT), Siem Reap (SR), Pursat (PS) and Kompong Chhnang (KC).

2.3. Data analysis

2.3.1. Spatio-temporal variation of fish taxonomic composition

To reduce the influence of rare and occasional species on the data analysis, daily catch monitoring data were aggregated into weekly data and therefore we have 141 weekly catch monitoring data for the completed two hydrological cycles.

2.3.1.1. Spatio-temporal variation of fish communities: contribution of sites and species

Weekly data were computed the total variance of the site-by-species community matrix as an estimate of beta diversity (BDTotal) and then partitioned this measure into Local Contribution to Beta Diversity (LCBD) and Species Contribution to Beta Diversity (SCBD), following Legendre & De Cáceres (2013). LCBD are comparative indicators of the ecological uniqueness of the sampling units and indicate how much each site contributes to beta diversity. Thus, a site with average and common species composition is expected to have a

value of zero whereas large values indicate sites with different communities. Such large values may either indicate a site with a high conservation value or, on the contrary, degraded or species poor sites with a need for restoration. On the other hand, SCBD indice indicates how much each species is contributing to beta diversity. Thus, a species present in all assemblages has a value of zero whereas species with large values are those that are present in only a few locations. LCBD and SCBD values were computed for each week from community composition matrices transformed using the Hellinger transformation (i.e. a measure of the dissimilarity in the species composition among locations). To test for differences in LCBD values computed for each week between the six sites, we used Kruskall-Wallis non-parametric analysis of variance followed by multiple comparisons Tukey post-tests to test for differences between each pair of sites. We further used a hierarchical cluster analysis to determine whether LCBD values calculated for each week and the different sites (i.e. the sampling units) could be grouped based on their similarity.

2.3.1.2. Determinants of temporal variation in LCBD and SCBD values

We used the Euclidian distance as a measure of similarity among the sampling units and sampling units were then aggregated using the Ward's method. Finally, compositional changes in fish com- munities were examined using non-metric multidimensional scaling which is a rank based method attempting to represent the pairwise dissimilarity between sampling units in a two dimensional space. Determinants of temporal variation in LCBD and SCBD values. We used multiple linear regressions to explain temporal variation in LCBD values at each site. Three variables were included as predictors in each model (one for each site): the site specific richness, the local abundance (i.e. the sum of abundances of all species) and the water level (measured at PS for sites located within the lake and measured at KD otherwise). These three variables were log(x+1) transformed prior to analysis to reduce the skewness of their distribution. A quadratic term was also included for each

predictor to allow for non-linear responses. From the complete model, we used a stepwise procedure based on the Akaike information criterion (AIC) to select the predictors that best explained temporal variation in LCBD values. The model retained was the one with the lowest AIC. From the selected models, we performed hierarchical partitioning to assess the relative contribution of each predictor.

Because SCBD is based on species and not sites, we have as many time series of SCBD indices as the total number of species sampled (i.e. 242). To avoid building and interpreting 242 linear models and because of the presence of a large number of zeroes for most species (i.e. rare species), we calculated for each week the number of species that contributed to total beta diversity above the mean of the entire pool of species. This was done by centering SCBD values for each week and keeping only the species with positive signs (Legendre & De Cáceres, 2013). We then used the same procedure as above and considered as predictors the water level, the overall species richness and the total abundances (i.e. measured over the six sites for each week) as well as their quadratic terms. We then used hierarchical partitioning to assess the relative contribution of each predictor. All annalyses were performed within the R environment software (RCore Team, 2013), using the packages vegan (Oksanen et al., 2015), hier.part (Walsh & MacNally, 2013) and the function beta.div described in (Legendre & De Cáceres, 2013).

2.3.2. Temporal distribution and species co-occurrence patterns of fish species in the Tonle Sap Lake Flood Pulse System

Only species occurring in at least 10% of the catch were used. Consequently, among the 242 fish species present in the database, 39 species were used here. Those species encompass five orders and 12 families (S1 Table) and correspond to more than 80% of total catch, totaling 10,320,691 individuals (BB=2,226,969; KC=3,056,632, KT=2,511,647;

PS=1,384,144 and KC=1,145,299). Daily catch data were aggregated into weekly data, thus resulting in 209 weekly catch data in total.

We used bubble plot on the weekly abundance data to investigate the temporal variation according to the change in hydrological cycles and the weekly abundance data were transformed to presence and absence data for investigating species occurrence. We used non-metric multidimensional scaling (NMDS) with dissimilarities between sampling units computed using Bray-Curtis distances (Bray & Curtis, 1957) to illustrate temporal changes in fish communities. We then performed Ward hierarchical clustering on the NMDS scores to identify groups of species based on abundance dissimilarities. Both analyses were performed using the package vegan (Oksanen et al., 2015) within the R environment software. We used a probabilistic approach to analyse species co-occurrence patterns. Basically, this approach compares species co-occurrence on observed sites to the distribution expected if the species were distributed independently from each other (Veech, 2013). It overall tests whether pairwise associations between species are random or significantly non-random, and whether significant associations are higher or lower than expected. Note that this approach only tests co-occurrence between two species and thus do not account for the fact that additional species may influence species occurrence. The simulated random data used for comparisons in this study were thirty-nine species with a 10 probability of occurrence during the period of five years were included in the analysis. This analysis was performed using the package “cooccur” (Griffith et al., 2016) and was run on the entire dataset (i.e. across the four hydrological cycles) as well as for each season (i.e. dry, wet, receding, and rising seasons). From the results, we generated heat maps to visualize species pairwise associations.

2.3.3. Seasonal omnivory: the response of consumer trophic position to fluctuating environments

Stable isotopes are expressed as delta values (δ) in permil (‰) relative to the international standard for nitrogen (atmospheric air). To identify the dietary drivers of observed seasonal shifts in $\delta^{15}N$-based trophic positions, stomach contents data were analyzed for 4 fish species (Table 1) that are considered piscivores with flexible diets that can include invertebrates and are reported as the proportion of fish, invertebrate and plant material by weight relative to total stomach contents weight (see Appendix 1 for more detail). Fish with completely empty stomachs were excluded (see Table S2 for sample size and body lengths).

We applied the following single source equation to calculate fish trophic positions

(Eqn 1) $TP_{consumer} = 2 + \delta^{15}N_{consumer} - \delta^{15}N_{baseline} / TDF$

where $\delta^{15}N_{baseline}$ is the mean $\delta^{15}N$ of all baseline samples (primary consumers) in each season (5.92 ‰ in the wet season, 6.15 ‰ in the dry season) and $\delta^{15}N_{consumer}$ is the $\delta^{15}N$ value for an individual fish. TDF (trophic discrimination factor) is scaled to account for lower discrimination in strictly carnivorous vs. more omnivorous fish. The seasonal shift in trophic position was calculated for each of the 28 species as the mean dry minus the mean wet trophic position. Positive values, therefore, supported our prediction of lower trophic positions in the wet season. Effect sizes with pooled standard deviations and 95% confidence intervals (Coe 2002) were calculated to explore variation around mean values for trophic position shifts. We then explored how the mean shift in seasonal trophic position related to mean body size across the 28 species using quadratic regression. Seasonal changes in each of the three stomach contents response variables (proportional weight of invertebrate, fish and plant material) were then explored using data for individual fish belonging to each of the 4 species, and analyzed using zero-inflated beta regression (due to the presence of zeros in the data) in R package zoib (Liu and Kong 2015). We included

season (wet and dry) and total body length as explanatory variables, and included both species and sampling location as random intercepts. To determine whether findings from the Tonle Sap are consistent with evidence from other tropical floodplains, we reviewed literature accounts to obtain fish trophic data recorded during different phases of the annual flood pulse. We focused this analysis on piscivores, especially those that sometimes include invertebrates in their diet. Each report for a single species or trophic guild constituted a single 'evidence item', with a total of 29 evidence items extracted from the 10 data sources that met our inclusion criteria.

2.3.4. Seasonal variations in diet composition, diet breadth and dietary overlap between three commercially important fish species within a flood-pulse system: the Tonle Sap Lake

Because the proportion of empty stomachs can provide information on resource availability and the ability of species to forage during periods of shortage (Arrington et al., 2002) we tested for seasonal variations in the proportion of empty stomachs using a chi-square test. For non-empty stomachs, we used an analysis of similarity (ANOSIM) to test for significant differences in the diet of species between the wet (from July to October) and the dry seasons (from December to May) followed by an analysis of similarity percentages (SIMPER) to assess the contribution of food items to the observed variations (Clarke, 1993). We focused on differences between the wet and the dry season because considering the four seasons would have implied to perform multiple tests (i.e. six for each species), necessitating p-values adjustments and thus a decrease in statistical power. Both analyses were based on a dissimilarity matrix built with Bray-Curtis distances to account for the large proportion of zeros in the community matrix. The ANOSIM statistic vary between zero and one and compares the mean of ranked dissimilarities between groups to the mean of ranked dissimilarities within groups. A value close to one suggests dissimilarity between groups, while a value close to zero suggests an even distribution of high and low ranks within and

between groups. The SIMPER analysis is based on the decomposition of the Bray -Curtis dissimilarity matrix and aim to assess the contribution of food items (or species) to the observed dissimilarities. For this analysis, we grouped food items into six broader categories (fish, insects, crustaceans, plants, mollusks and micro-fauna) following (Winemiller, 1990; Winemiller et al., 1995). The importance of each category within the diet was established as its average FOC divided by the sum of the average FOC of all categories and was calculated by species and seasons. To explore interspecific differences in diet composition across the four seasons, we used non-metric multidimensional scaling [NMDS, (Faith et al., 1987)]. This indirect gradient analysis approach uses rank order values to visualize and interpret differences between species, ultimately representing pairwise differences between samples in a low-dimensional space. The similarity between sampling units was calculated using Bray-Curtis distances. Beyond this graphical approach, we computed different statistics to evaluate and test how interspecific differences in diet varied across seasons. First, we used a multivariate homogeneity of group dispersions (Anderson, 2006) with 1000 permutations to (i) measure the diet breadth of each species in each season and (ii) test for interspecific differences in each season. In this analysis, diet breadth is estimated as the average distance of prey items to the group centroid within the multivariate space described by the NMDS with larger values indicative of a broader diet. The values by themselves have no ecological meaning but can be compared to determine to which extent diet breadth is changing between species and season. Second, we computed Pianka's symmetric index (Pianka, 1973) to measure niche overlap in diet composition between each pair of species in each season. Here, a value close to zero indicates no overlap whereas a value close to one indicates a strong overlap. To test the statistical significance of dietary overlap between each pair of species in each season, we conducted a bootstrap procedure by randomly sampling the rows of the community matrix. This procedure was repeated 1000 times and generated a distribution of Pianka's index for each pair of species under the null hypothesis that there is no variation in dietary overlap across seasons. For a given pair of species, we assessed the statistical significance of dietary overlap in each season by comparing the observed value to

the 95% confidence intervals of the corresponded distribution. All analyses were performed in R (R Core Team, 2014) using the package vegan (Oksanen et al., 2015).

3. Main Results

3.1. Spatio-temporal variation of fish taxonomic structure

Among the six studied sites and the 141-week samples, 12,455,409 individuals, belonging to 242 species, 123 genera and 49 families were captured (Annex 1). The number of species captured ranged from 2 to 53 while the number of individuals ranged from 9 to 352,594. Species richness and total abundances were both higher in KT relative to the other sites whereas there was a trend toward lower values in KD (Fig 2). In Table 1 we show the means and standard errors of the number of individuals captured within the six sampling sites for the 20 most abundant species.

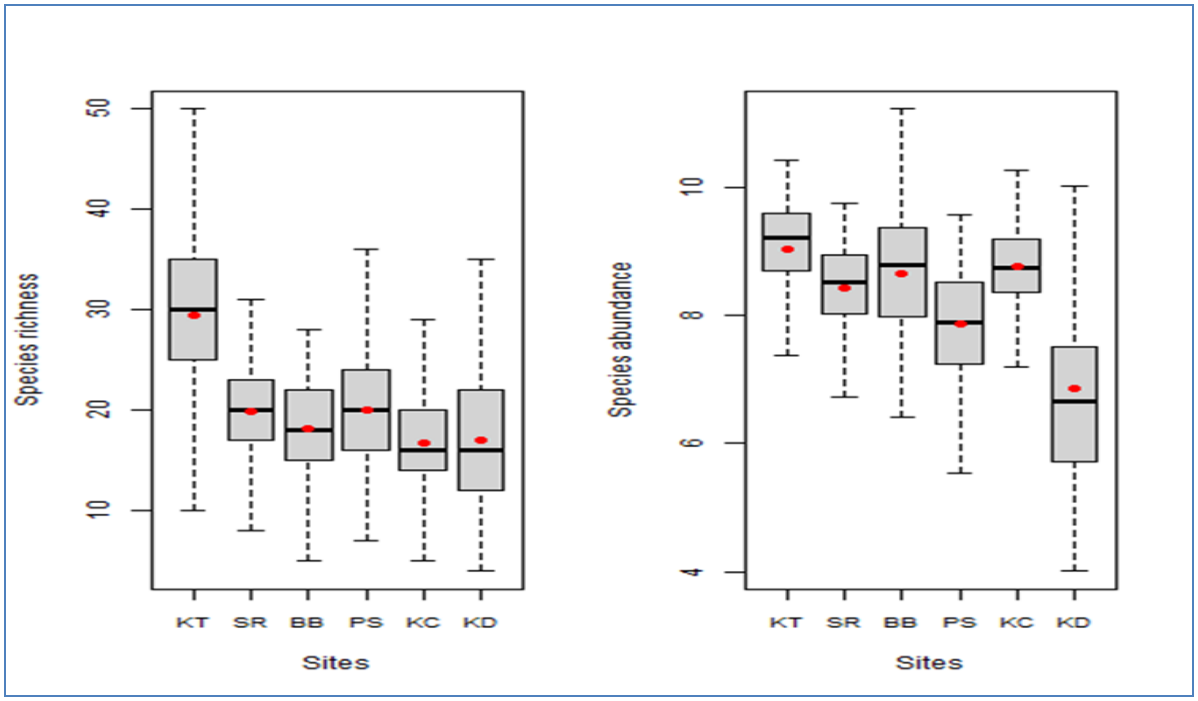

Fig. 2. Boxplots representing weekly species richness (a) and total abundances (b) at each site (for site code, see Fig.1). The horizontal black line represents the median whereas red points indicate the mean.

Table 1. Means and standard errors of the number of individuals captured for the 20 most abundant species found in our samples.

Species	BB	KC	KD	KT	PS	SR
Anabas testudineus	28±1.8	9.6±1.3	0.1±0	58±3.2	34.1±2	34.7±3.2
Cyclocheilichthys armatus	6±1.1	32.4±9.1	0.1±0	56.4±4.4	1.4±0.3	51.8±2.2
Henicorhynchus lobatus	95.6±10.7	171.6±15.5	497.5±77.7	285±15.2	56.3±3	58.2±3.2
Henicorhynchus siamensis	132.2±16.1	131.8±13.7	87.8±13.9	415.3±21.5	56.6±2.7	43.5±1.9
Labeo chrysophekadion	2±0.2	13.8±2.7	1.2±0.1	52.5±5	41.6±1.9	2±0.3
Labiobarbus lineatus	13.1±1.6	142.3±15.9	-	144.4±13.9	50.2±2.3	37.3±2.3
Labiobarbus siamensis	34.6±6.2	9.4±2	112.3±20.7	36.3±3	44.3±2.2	41.7±2.1
Mystus albolineatus	55±6.3	5.7±1	-	65.7±4.1	-	1.4±0.6
Mystus mysticetus	73.4±6.6	35.1±3.7	0.8±0.2	38.7±3.4	44.8±2.6	74.2±3.3
Mystus singaringan	31.3±2.5	52.7±6.2	0.3±0	53±3.9	14.2±1.4	34.7±2.2
Osteochilus vittatus	95.8±7.8	67.4±5.9	0.1±0	194.2±7.2	57.2±2.4	84.1±3
Pangasius macronema	2±1.7	2.6±0.5	59.1±3.6	12.2±1.8	2.4±0.3	0.4±0.2
Paralaubuca riveroi	-	-	171.9±33.6	-	-	-
Paralaubuca typus	26.4±4.4	102.8±8	139.8±30	19.9±2.3	16.3±1.3	28.6±2.3
Poropuntius deauratus	-	130.9±9.4	-	2.6±0.8	0.9±0.5	-
Puntioplites proctozysron	24.3±1.6	37.9±2.4	-	88.8±5.8	44.8±1.8	126.6±4.1
Rasbora tornieri	11.1±2.6	219±12.5	1±0.2	1.5±0.5	1.4±0.3	7.7±1.6
Trichopodus microlepis	334.4±17.1	9.8±1.1	-	15.6±3	43.7±2.6	57.6±3.8
Trichopodus trichopterus	364.4±18.1	25.5±2.1	-	114.2±7.5	74.2±4	56.8±2.5
Xenentodon cancila	-	175.5±8.7	3.3±0.9	0.5±0.2	0.6±0.2	-

3.1.1. Spatial and temporal variation of beta diversity

All sites and weeks confounded, LCBD values ranged between 0.08 and 0.31. Kruskall-Wallis revealed significant differences in LCBD values among sites (chi-squared=5487.62, df=5, P<0.001). Tukey post-tests revealed that LCBD values were higher in KD (median=0.244; sd=0.027) comparing to the other sites. The lowest values were

observed in KT (median=0.124; sd=0.021), SR (median=0.13; sd=0.021) and PS (median=0.13; sd=0.027) (Fig. 3). BB (median=0.181; sd=0.031) and KC (median=0.177; sd=0.04) displayed intermediate values (Fig. 3). The similarity trend of LCBD values allowed to group samples into four clusters (Fig. 4a). The two first clusters were mainly represented by BB and PS whereas the third one mainly represented KD, KT and SR while the fourth cluster was representative of KC (Fig. 4b).

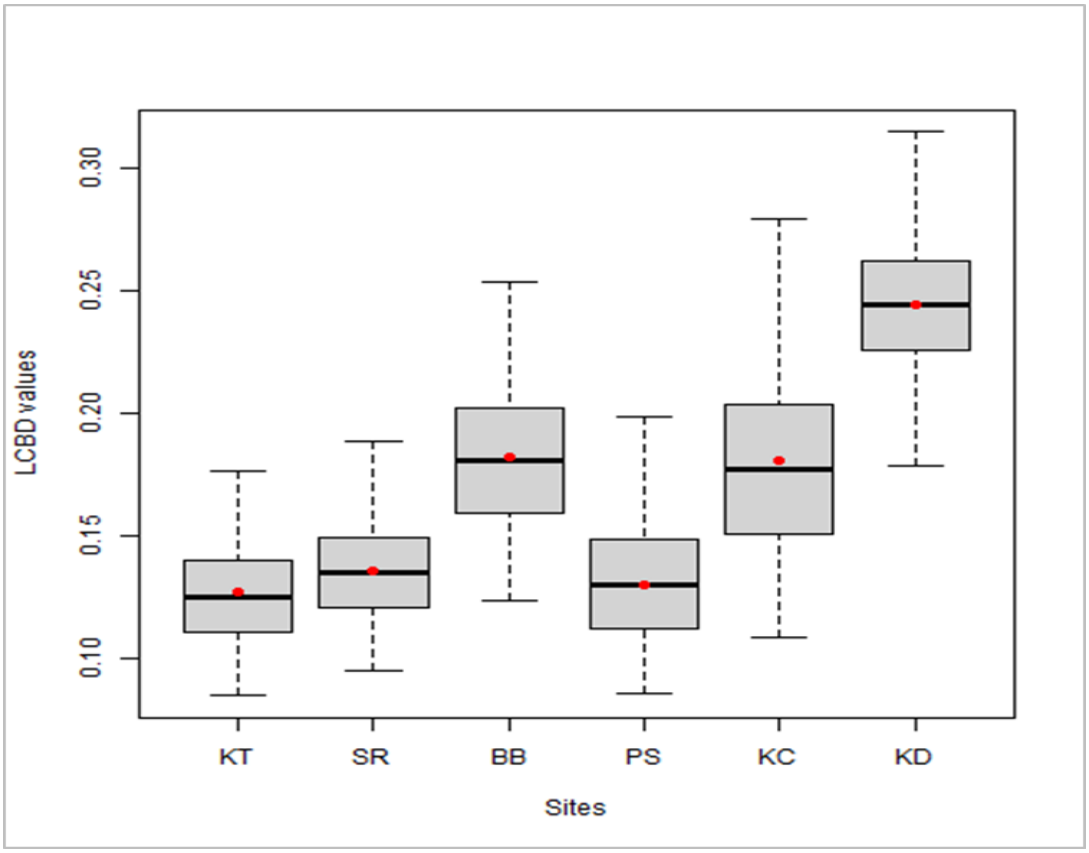

Fig. 3. Boxplots representing among site variation in LCBD values. The horizontal black line represents the median whereas red points indicate the mean. For site code, see Fig.1.

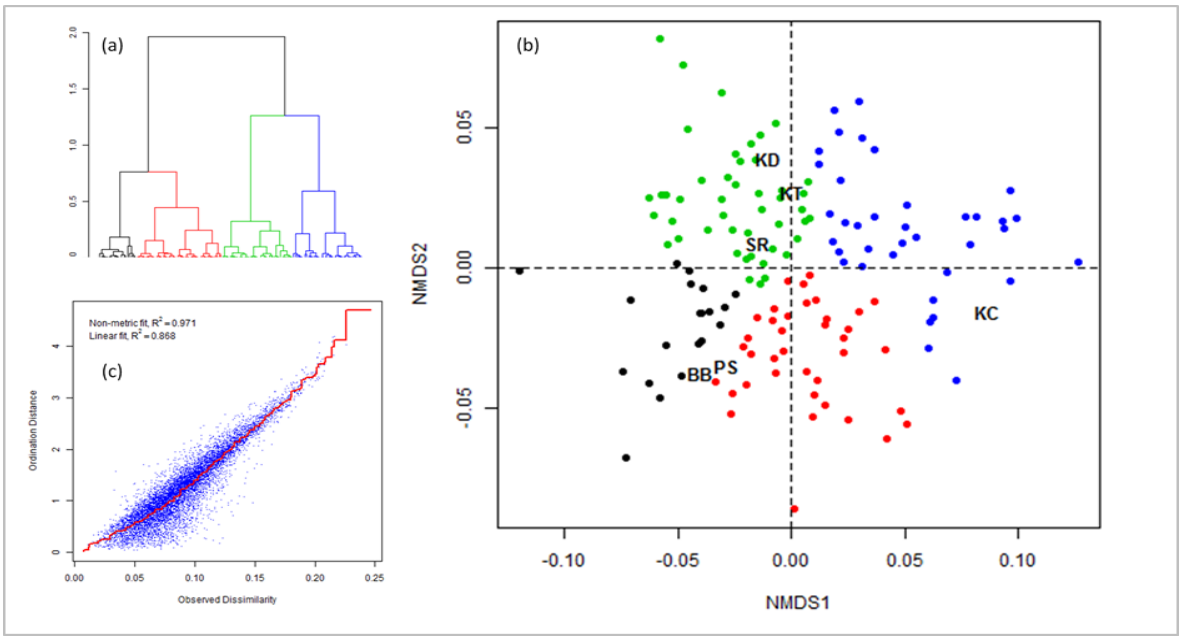

Fig. 4. Similarity amongLCBD values. (a) Hierarchical clustering of LCBD values according to their similarity (Euclidian distance) with the Ward's aggregation criteria. (b) Two-dimensional space defined by a non-metric multidimensional scaling (NMDS) approach representing the position of LCBD values and sites. In (a) and (b), the different colors represent the four groups identified by the cluster analysis. For site code, see Fig 1.

Among the 141 weeks considered, KT, PS and SR never displayed significant LCBD values, thus indicating that fish taxonomic structure in these sites do not explain temporal variation of fish community composition across the two hydrological cycles (Fig. 5). In contrast, BB, KC and KD had respectively 4.2%, 14.9% and 65.2% of their weeks that displayed significant LCBD values indicating strong temporal variation regarding the uniqueness of fish community structure within these three sites.

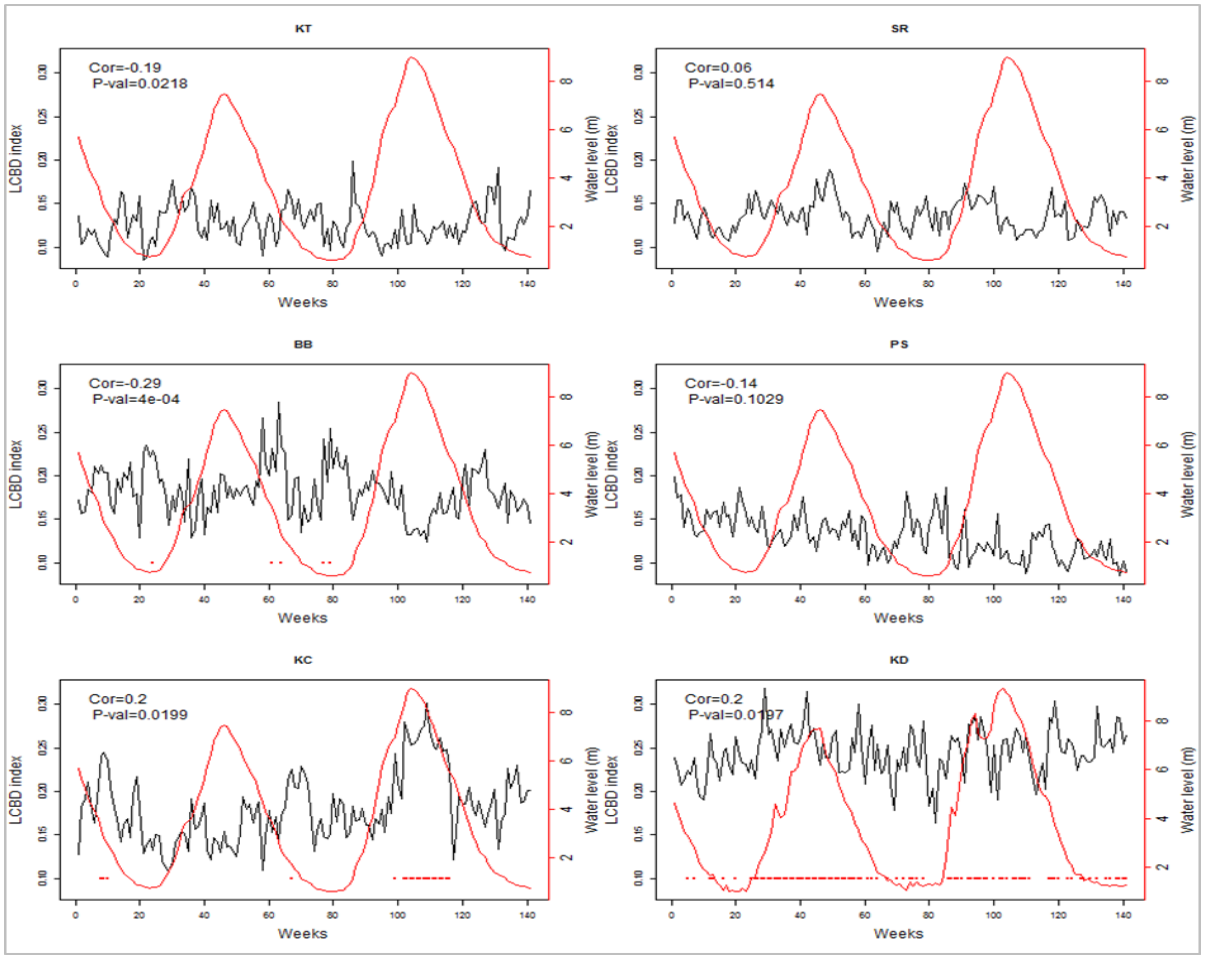

Fig. 5. Temporal evolution of LCBD values and water level (m) over the study period for the six sites considered. The red dots indicate weeks with significant LCBD values (corrected for multiple comparisons). For site code, see Fig.1.

More than 50% (i.e. 127) of the species contributed to beta diversity above the mean relative to the 242 species for at least one week (Fig. 6). Among them, 26 species contributed to beta diversity above the mean for more than 50% of the weeks (Supporting information, Annex 2), thus indicating a rather stable contribution of these species to spatial variation of community composition over time. Those species were mostly non-migratory (61%) with specific habitat requirements such as permanent lakes or reservoirs (Annex 2).

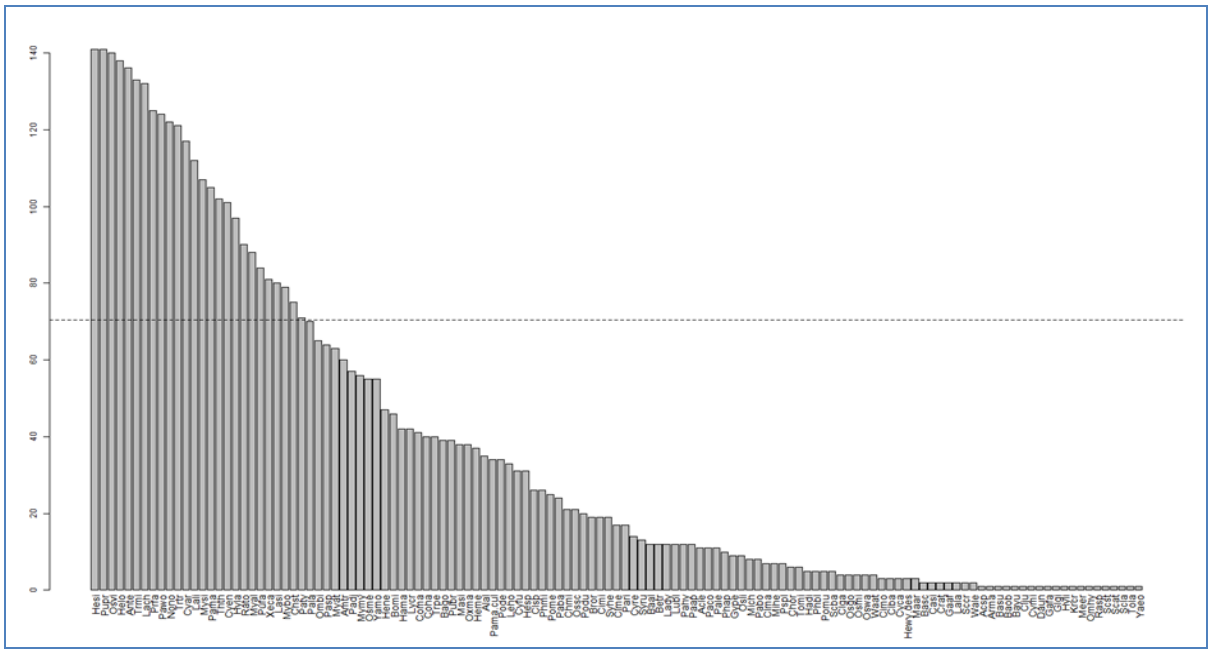

Fig. 6. Barplot representing the number of weeks where specific species contributed to beta diversity above the mean relative to the entire pool of species. The horizontal dashed line represents 50% of weeks. For species code, see Annex 1.

3.1.2. Determinants of variation in LCBD and SCBD values

Regarding to the temporal variation of LCBD values, we found that the influence of predictors greatly varied depending on the considered sites (Table 2). Species richness was positively related to LCBD values at BB and KC but the opposite was found at PS and KT. Furthermore, a non-linear influence of species richness (i.e. significant quadratic term) was detected at BB and KD. The influence of total abundances on LCBD values also varied depending on the site considered; a negative relationship was found at KT, SR and PS whereas a positive one was found at KD. Also, three sites (KT, PS and KD) had their LCBD values that were non-linearly influenced by total abundances. The water level was linearly related to LCBD values at BB and KD with positive and negative relationships, respectively. These two sites plus PS had their LCBD values that were non-linearly influenced by the water level. The hierarchical partitioning (Table 2) demonstrated that the species richness had the highest independent contribution in KT (61.6%), KD (36.4%) and KC (100%),

whereas total abundances presented the highest independent contribution in PS (67.4%) and SR (82.6%). Finally, the water level had the highest independent contribution only for BB (74.4%). Whatever the predictor considered, their contribution varied greatly depending on sites. For instance, the contribution of total abundances to the total variance varied from 12.8% in KT to 82.6% in SR. When considered in combination, the two biotic variables (species richness and total abundances) explained more than 65.3% of the total variance except in BB (25.5%).

Table 2. Results ontained from the stepwise procedure with coefficients associated to the model selected based on the Akaike Information criterion. (-) indicate that the predictor was not pertinent enough to explain temporal variation in the dependent variable. The models above the double line are related to temporal variation in LCBD values at each site whereas the model below the double line is related to the temporal evolution of the number of species which presented SCBD values above the mean relative to the other species. WL= water level; SR= local species richness; AB= local abundance. ^{2} denote quadratic terms. For site code, see Fig 1.

Sites	Intercept	WL	WL²	SR	SR²	AB	AB²	R²
KT	0.26	4.2×10E-02	-1.6×10E-02	-	-3.9×10E-03	-3.1×10E-02	2.0×10E-3	0.27
SR	0.19	-3.0×10E-02	1.1×10E-2	-	-	-	6.5×10E-04	0.16
BB	-0.06	5.4×10E-02	-2.4×10E-02	1.7×10E-01	-3.3×10E-02	-	-	0.15
PS	0.03	5.0×10E-03	-	-4.1×10E-03	-	4.8×10E-02	-3.7×10E-03	0.45
KD	0.29	-5.5×10E-02	2.6×10E-02	-	7.6×10E-03	-4.0×10E-02	2.3×10E-03	0.29
KC	0.22	-	-	3.9×10E-03	-	-	-	0.06
Nsp	-295.1	-	-	202.0	-22.7	-19.7	0.8	0.29

Regarding the temporal variation of the number of species that contributed to total beta diversity above the mean of the entire pool of species (SCBD values above the mean after centering), the water level was not included in the selected model (Table 3). The selected

model included a positive relationship with the species richness and a negative one with total abundances, thus reflecting the opposite effect of these two predictors on the number of species contributing to beta diversity. We further found a non-linear influence of both species richness and total abundances. The hierarchical partitioning revealed a very high contribution of the species richness with more than 80% of the variance explained (Table 3).

Table 3. Hierarchical partitioning indicating the relative contribution (in percentage; %LI) of each predictor to the variance explained by the models presented in Table 2. WL = water level; SR = local species richness; AB= local abundances. ² denote quadratic terms. For site code, see Fig.1.

	%LI					
Sites	WL	WL²	SR	SR²	AB	AB²
KT	11.3	14.3	-	61.6	6.4	6.4
SR	7.8	9.6	-	-	-	82.6
BB	31.5	42.9	11.9	13.7	-	-
PS	2.9	-	29.7	-	32.7	34.7
KD	14.7	20.0	-	36.4	16.4	12.5
KC	-	-	-	100.0	-	-
Nsp	-	-	41.8	39.7	9.6	8.7

3.2. Temporal distribution and species co-occurrence patterns of fish species in the Tonle Sap Lake flood pulse system

3.2.1. Temporal distribution of fishes according to hydrological cycles

Weekly species occurrence (Figure 7a) and abundance (Figure 7b) greatly varied across the four seasons. Generally, species occurrence was higher during the high and the receding water seasons, although opposite patterns exist for some species such as Labiobarbus leptocheilus (Lale) and Poropuntius deauratus (Pode). Strong seasonal variations were also visible regarding abundances with some species presenting particularly strong variations (e.g. Trichohodus trichopterus (Trtr), Mystus mysticetus (Mymy); Figure

7b). The results from the NMDS analysis revealed seasonal variations in community composition (Fig. 7c; axis two). Species assemblages seem to be quite different between the receding and the rising seasons. Species like Pode, Paralaubuca typus (Paty) or Puntioplites proctozysron (Pupr) were mostly associated with the receding water season, whereas species like Mystus bocourti (Mybo), Boesemania.microlepis (Bomi) and Pangasianodon hypophthalmus (Pahy) were mainly associated with the rising water season. The hierarchical clustering revealed that seasonal change in hydrological cycle is the main driver in seasonal variation of fish assemblages, thus fish community were classified into four assemblages (Fig 7d).

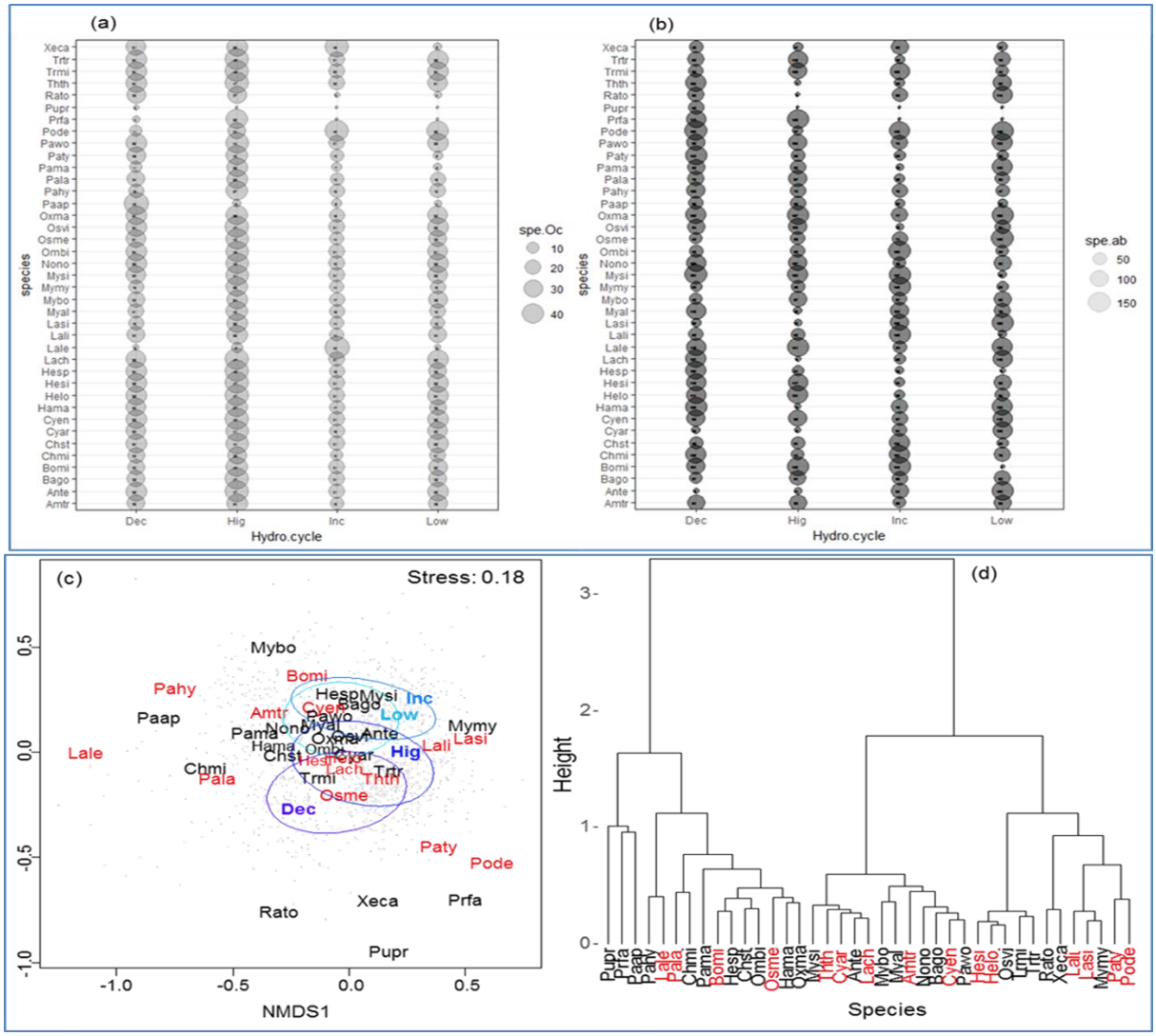

Fig. 7. Seasonal pattern of species distribution according to hydrological cycle of TSL. (a): Temporal change in species occurrence, (b): Temporal change in species abundance;

(c): species composition derived from nonmetric multidimensional scaling [stress: 0.18] and (d): Hierarchical clustering dendrogram of the NMDS scores using the Euclidian similarity matrix and Ward agglomeration method. Species abbreviation are in Annex 2: Table S2.

3.2.2. Co-occurrence of fish species

Result from the co-occurrence analysis performed on the whole dataset revealed 25.5% non-random pairwise associations among the 705 species pair considered (Table 4). Among those, 121 were positive, while 59 were negative (Fig. 8a). This analysis further revealed that two non-migratory species [i.e. *Puntioplites proctozysron* (Pupr) and *Anabas testudineus* (Ante)] and two migratory species [i.e. *Henicorhynchus siamensis* (Hesi) and *Henicorhynchus lobatus* (Helo)] show no particular association with any other species. By contrast, other species such as *Thynnichthys thynnoides* (Thth), *Parambassi wolffi* (Pawo) or Hemibagrus spilopterus (Hesp) were consistently positively associated with other species. No species only showed negative associations. Positive associations were found among migratory species which use the ecological nice and different feeding tropic [i.e. *Paralaubuca typus* (Paty), *Pangasius larnaudii* (Pala), *Osteochilus melanople* (Osme) and *Amblyrhynchichthys truncates* (Amtr)], between migratory and non-migratory species [e.g. *Pangasius.larnaudii* (Pala) and Parambassis apogonoides (Paap), *Paralaubuca typus* (Paty) and *Xenentodon cancila* (Xeca)] and among non-migratory species which use different feeding tropic [i.e. *Hampala macrolepidota* (Hama), *Rasbora tornieri* (Rato) and *Xenentodon cancila* (Xeca)].

Table 4. Summary of the co-occurrence analysis performed on the whole dataset and a subset of the dataset for each season.

Periods	Sites	Positive	Negative	Random co-occurrence	Percentage non-random
Dry	52	49	31	586	12.00
Rising	35	23	20	597	6.70
Wet	52	43	25	633	9.70
Receding	70	59	28	622	12.30
Whole	209	121	59	525	25.50

The same analysis performed for each season revealed that positive associations were overall more frequent than negative associations in all seasons (Fig. 8b). Random associations were maximized during the rising and the wet seasons, while they were minimized during the receding and the dry seasons (Table 4). Some species like *Mystus singaringan* (Mymy), *Labiobarbus siamensis* (Lasi) *or Labiobarbus lineatus* (Lali) were most involved into negative interactions (Fig 8b).

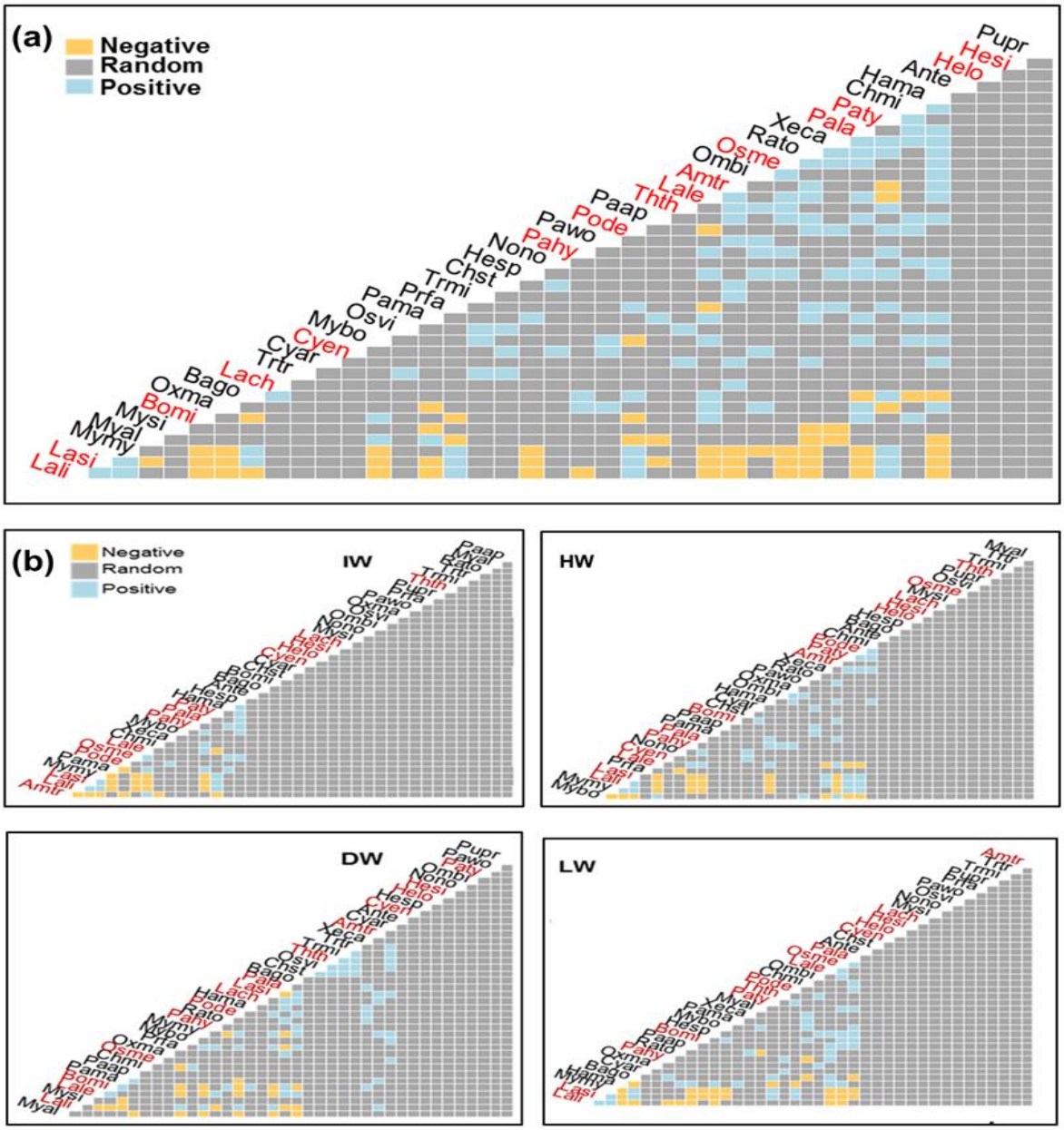

Fig. 8. Overall head map of pairwise species co-occurrence from the probabilistic model according to the four hydrological cycles. Species names are positioned to indicate the columns and rows that represent their pairwise relationships with other species. Abbreviation species in Annex 2. Red color indicates migration species and black color non-migratory species. IN= Increase water level season, HW= High water season level and DW= Decrease water level season, LW= Low water level season. Species abbreviation are Annex 2.

3.3. Seasona omnivory: the response of consumer tropic position to fluctuation environment

3.3.1. Tonle Sap fishes

Seasonal shifts in trophic position (mean dry – mean wet, for each of the 28 species) ranged from -0.51 to 0.64 and exhibited a hump-shaped relationship with mean body length based on quadratic regression (Fig. 9A), but was not statistically significant (P=0.08). Nonetheless, 8 species had seasonal trophic position shifts whose effect size ± 95% CI did not cross zero (Fig. 9A, Annex 3), and these 8 species followed the trend indicated by the quadratic regression. Specifically, mid-sized species (body size 108 to 220 mm) shifted towards lower wet-season trophic positions (positive values in Fig. 9A), whereas smaller and larger species exhibited the opposite trend (negative values in Fig. 9A). Baseline aquatic invertebrates (Table S3) and terrestrial invertebrates (e.g. spiders, beetles; data not shown) had lower $\delta^{15}N$ values than the 28 fish species from the Tonle Sap (Annex 3), confirming that greater consumption of invertebrates reduces trophic position in this system.

For the 4 species with stomach contents data, diets were dominated by fish and invertebrates with some plant material present (Annex 4). Zero-inflated beta regression revealed that the probability of invertebrates being eaten increased during the wet season and decreased with fish length. This is indicated by the parameter b0[2] (Annex 5), which shows a significant negative effect on the probability of zero (i.e. nothing is eaten), whereas length had a negative effect on the probability of invertebrate consumption (b[2] in Annex 5). Thus, smaller fish (i.e. *Anabas testudineus* and *Notopterus notopterus*) consumed significantly more invertebrates than larger, more piscivorous fish (i.e. *Channa* spp.), and the probability of invertebrates being eaten was significantly higher during the wet season (Fig. 9B). Season did not have a significant effect on the probably of plants or fish being eaten (Annex 5).

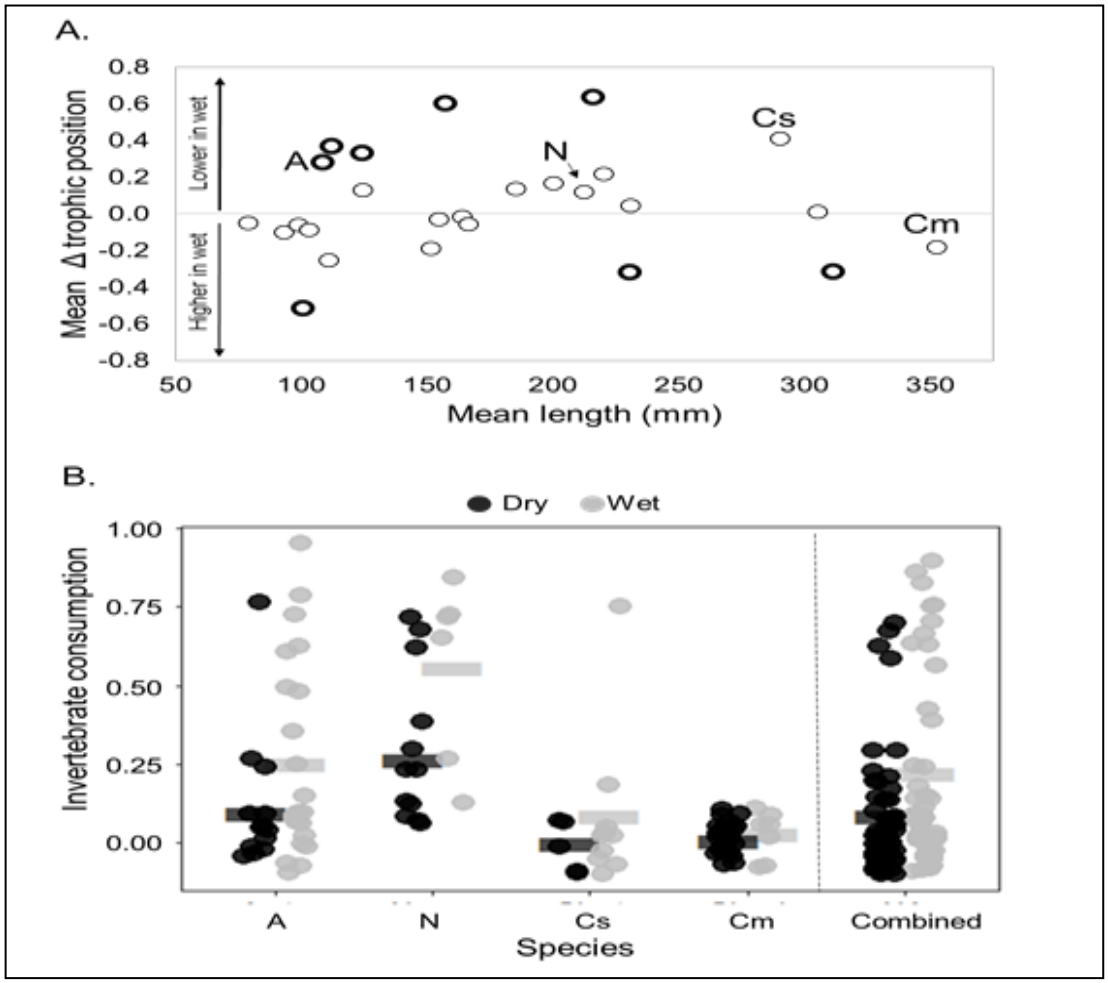

Fig. 9. A) Shift in the mean trophic position between seasons (i.e. mean dry – mean wet) for 28 Tonle Sap species spanning a range in body sizes (mean total length, mm). Species with large and significant seasonal shifts in trophic position (i.e. effect sizes whose 95% CI did not bound zero, Table S1) are indicated by symbols with thick black borders. Species with accompanying stomach contents data are abbreviated as follows: A= *Anabas testudineus*, N= *Notopterus notopterus*, Cs=*Channa striata*, Cm= *Channa micropeltes*. The grey line on represents zero shift in seasonal trophic position. B) Proportional consumption of invertebrates (by weight relative to total stomach contents) for specimens of four fish species (left) and combined data across species (right) during wet and dry seasons. Data points are jittered as per Weissberger et al. (2015) to reveal the presence of zeros. Mean invertebrate consumption by each species during each season is shown as a bar.

3.3.2. Result of literature review

Out of the 29 evidence items, seasonal diet information was provided for 28 cases and ^{15}N values were provided for 1 case (Table 5). Eleven evidence items supported the hypothesis of increased plant or invertebrate consumption during the wet-season flood pulse (Table 5). For the remaining 18 evidence items, 5 cases reported increased consumption of plants and invertebrates during the dry season or increased consumption of fish during the wet season (the opposite of our prediction), and 13 cases reported fish dominating the diet throughout the year. For classification purposes, we refer to species as 'omnivores' when their stomachs contained multiple prey types (invertebrates or plants and fish) and 'piscivores' when their stomachs contained >97% fish. Maximum body sizes of each species reported in the literature (actual body lengths of fish sampled in each study were not always provided for comparison) were smaller in omnivores (mean ± SD = 43 ± 71 and 21 ± 15 cm with and without *Wallago attu*, a large food-chain omnivore, respectively; Annex 3) than piscivores (55 ± 23 cm; Table 5). This pattern derived from the broader literature, whereby predators that predominantly reduced their trophic position in the wet season were smaller-bodied than those that fed on different types of fish all year, agrees with the pattern revealed by Tonle Sap isotopic data (Fig. 9A).

Table 5. Data extracted from a literature review performed to explore seasonal diet changes in tropical floodplain piscivorous food-chain omnivores. Reported maximum total body length (cm), dominant prey items and quantitative contribution to diet, when provided, are reported for each study, as is whether each study provided support for our hypothesis (i.e. lower trophic positions in the wet vs. dry season) or no support (no difference in trophic position or higher trophic positions in the wet season). References 5 and 8 classified fish prey by species and the functional group of the main fish prey consumed is provided in parentheses. Species with multiple prey types (fish plus invertebrates and/or plants) are noted as food chain-omnivores 'O' and species with >97% fish in their stomachs are listed as piscivores 'P'.

Species	Max. length	Dry season diet	Wet season diet	Lower TP in wet?	O or P	Ref.
Fish community	NA	Significantly higher δ^{15}N by 1.45‰	Lower δ^{15}N	Support	NA	1
Fish community	NA	5% aquatic inverts, 20% fish	18% aquatic inverts, 10% fish	Support	NA	2
Fish community	NA	Fish prey dominate	Plant and invertebrate prey dominate	Support	NA	3
Fish community	NA	29% invert., 25% detritus, 20%fish	30% invert., 17% detritus, 23% fish	No support	NA	4
Serrasalminae sp.	NA	Fish	Terrestrial plant matter and fish	Support	O	5
Hemigrammus marginatus	4.5	73% fish, 24% plant, 0.2% invert.	0% fish, 20% plant, 60% invert.	Support	O	6
Moenkhausia collettii	5	Invertebrates and fish	Invertebrates	Support	O	5
Hypselecara coryphaenoides	16	Fish	Invertebrates	Support	O	5
Serrasalmus marginatus	27	99% fish, 1% detritus	93% fish, 7% invert.	Support	P	6
Serrasalmus gouldingi	28	64% fish, 12% fruits/seeds,10% arthropods	45% fish, 40% fruits/seeds, 8% arthropods	Support	O	7
Hoplarchus psittacus	32	Fish	Aquatic invert. and fish	Support	O	5
Pimelodus maculatus	51	50% fish, 25% plants	32% fish, 57% plants	Support	O	6
Aphyocharax dentatus	7.2	33% invert., 16% fish	5% invert., 87% fish	No support	O	6
Pimelodella gracilis	18	21% plants, 15% fish, 14% invert.	2% plant, 67% fish, 26% invert.	No support	O	6
Pimelodus argenteus	25	39% plant, 18% invert., 10% fish	36% plant, 11% invert., 38% fish	No support	O	6
Acestrorhynchus lacustris	27	100% fish (herbivores)	100% fish (omnivores, herbivores)	No support	P	8
Acestrorhynchus lacustris	27	100% fish (herbivores)	100% fish (omnivores)	No support	P	8

Acestrorhynchus pantaneiro	35	100% fish	100% fish	No support	P	6
Plagioscion Ternetzi	39	100% fish	97% fish	No support	P	6
Hepsetus odoe	44	100% fish (omnivores)	100% fish (omnivores)	No support	P	9
Pygocentrus nattereri	50	100% fish	99% fish, 1% plant	No support	P	6
Hoplias malabaricus	65	100% fish (omnivores)	100% fish (piscivores)	No support	P	8
Hoplias malabaricus	65	100% fish (piscivores)	100% fish (omnivores)	No support	P	8
Cichla monoculus	70	93% fish, 7% plant	100% fish	No support	P	10
Hydrocynus forskahlii	78	100% fish (omnivores)	100% fish (piscivores, omnivores)	No support	P	9
Rhaphiodon vulpinus	80	100% fish	100% fish	No support	P	6
Salminus Brasiliensis	100	95% fish, 5% invert.	100% fish	No support	P	6
Wallago attu	240	10% fish, 30% prawn (during January)	30% fish, 0% prawn (during July)	No support	O	11

References: 1. Wantzen et al. 2002 (Pantanal wetland, Brazil); 2. Winemiller 1989 (Venezuelan Llanos); 3. Peterson 1997 (Venezuelan Llanos); 4. de Merona and Rankin-de-Merona 2004 (lago de Rei, Amazon); 5. Goulding 1988 (Rio Negro, Amazon); 6 Novakowski et al. 2008 (Pantanal wetland, Brazil); 7. Prudente et al. 2016 (Anapu River, Brazil); 8. Almeida et al. 1997 (Pantanal wetland, Brazil); 9. Winemiller and Kelso-Winemiller 1994 (Upper Zambezi, Zambia); 10. Oliveria et al. 2006 (Amazon River); 11. Islam et al. 2006 (Bangladesh).

3.4. Seasonal variations in diet composition, diet breadth and dietary overlap between three commercially important fish species within a flood-pulse system

The average size of captured individuals was 12.7 ± 2.1 cm for *A. testudineus*, 23.9 ± 13.9 cm for *B. microplepis* and 20.4 ± 2.4 cm for *N. notopterus.* The proportion of empty stomachs was 14.8% for *A. testudineus*, 12.3% for *B. microplepis* and 16.8% for *N. notopterus*. For all species, this proportion greatly varied across seasons and was maximal during the receding season and minimal during the dry season (Fig. 10). Seasonal variation in the proportion of empty stomachs was independent of species identity (χ^2=0.14, df=6: P=0.99). The diet of *A. testudineus* was mainly composed of fish (43%), insects (23%) and plants (17%) whereas *N. notopterus* mostly fed upon insects (49%), plants (28%) and fish (10%) (Fig.10). The diet of *B. microplepis* was mainly composed of fish (51%), crustaceans (21%), and plants (15%). The similarity analysis (ANOSIM) revealed a significant change in the diet composition of *A. testudineus* (p<0.01, r=0.16) and *N. notopterus* (p<0.01, r=0.13) between the wet and the dry season, whereas no significant difference was found for *B. microlepis* (p=0.42, r=0.004). The SIMPER analysis revealed that only a few food items significantly explained the seasonal differences found for *A. testudineus* and *N. notopterus*, with a particularly strong contribution of fish prey for the former and of insects for the latter (Table 6).

Table 6. Average percent contribution of food items to the dissimilarity of diet composition between the wet and the dry seasons for the three studied species. Only for A. testudineus and N. notopterus is there a significant contribution of food items to the seasonal dissimilarity of diet composition. Numbers within brackets are standard deviations.

Food items	*A. testudineus*	*B. microlepis*	*N. notopterus*
Fish	0.28 (0.25)	0.28 (0.22)	0.07 (0.11)
Plants	0.11 (0.13)	0.09 (0.09)	0.12 (0.11)
Insects	0.17 (0.19)	0.05 (0.1)	0.20 (0.15)
Micro-fauna	0.13 (0.14)	0.05 (0.06)	0.02 (0.05)
Crustaceans	0.04 (0.13)	0.17 (0.19)	0.07 (0.13)
Mollusks	0.01 (0.03)	0.01 (0.01)	0.02 (0.04)

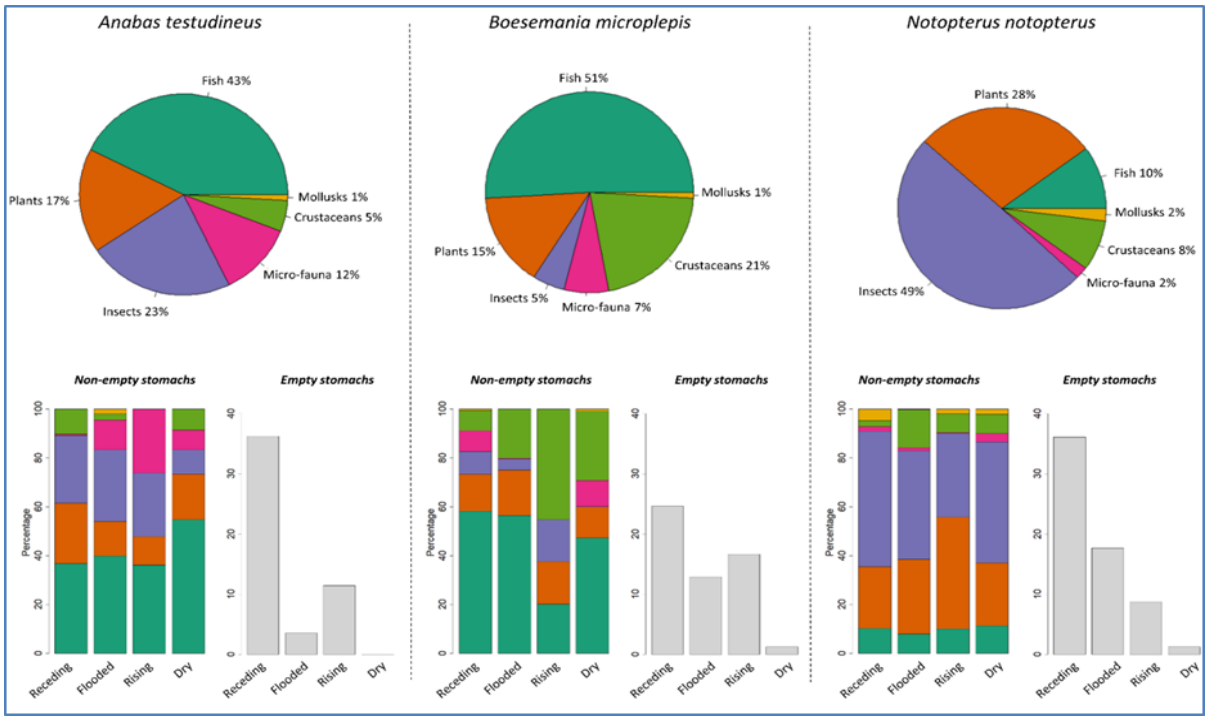

Fig. 10. Description of the diet of the three studied species and how they vary across seasons. For the sake of graphical clarity and because some items had a very low occurrence, items were grouped into six broader categories (mollusks, crustaceans, fish, plants, insects and micro-fauna). The pie charts represent the relative proportion of food items, all seasons confounded, and thus provide an overview of the main diet of the species. The barplots represent the seasonal variations in the proportion of food items within non-empty stomachs (colored barplots; on the left) and the seasonal variations in the proportion of empty stomachs (greyed barplots; on the right).

The NMDS highlighted strong seasonal variations in both diet breadth and dietary overlap between the three species (Fig. 11). Diet breadth significantly differed between the three species in all seasons (p<0.01), except the wet season (p=0.11; Table 7). It tended to be highest during the dry (from 0.48 to 0.54) and the receding seasons (from 0.45 to 0.53), and to be lowest during the two remaining phases (from 0.34 to 0.51) of the hydrologic cycle (Table 7). From a species perspective, diet breadth was quite stable across seasons for *N. notopterus* (from 0.46 to 0.51) but much more variable for the two other species, with variations from 0.38 to 0.54 for *A. testudineus* and from 0.34 to 0.53 for *B. microlepis* (Table 7).

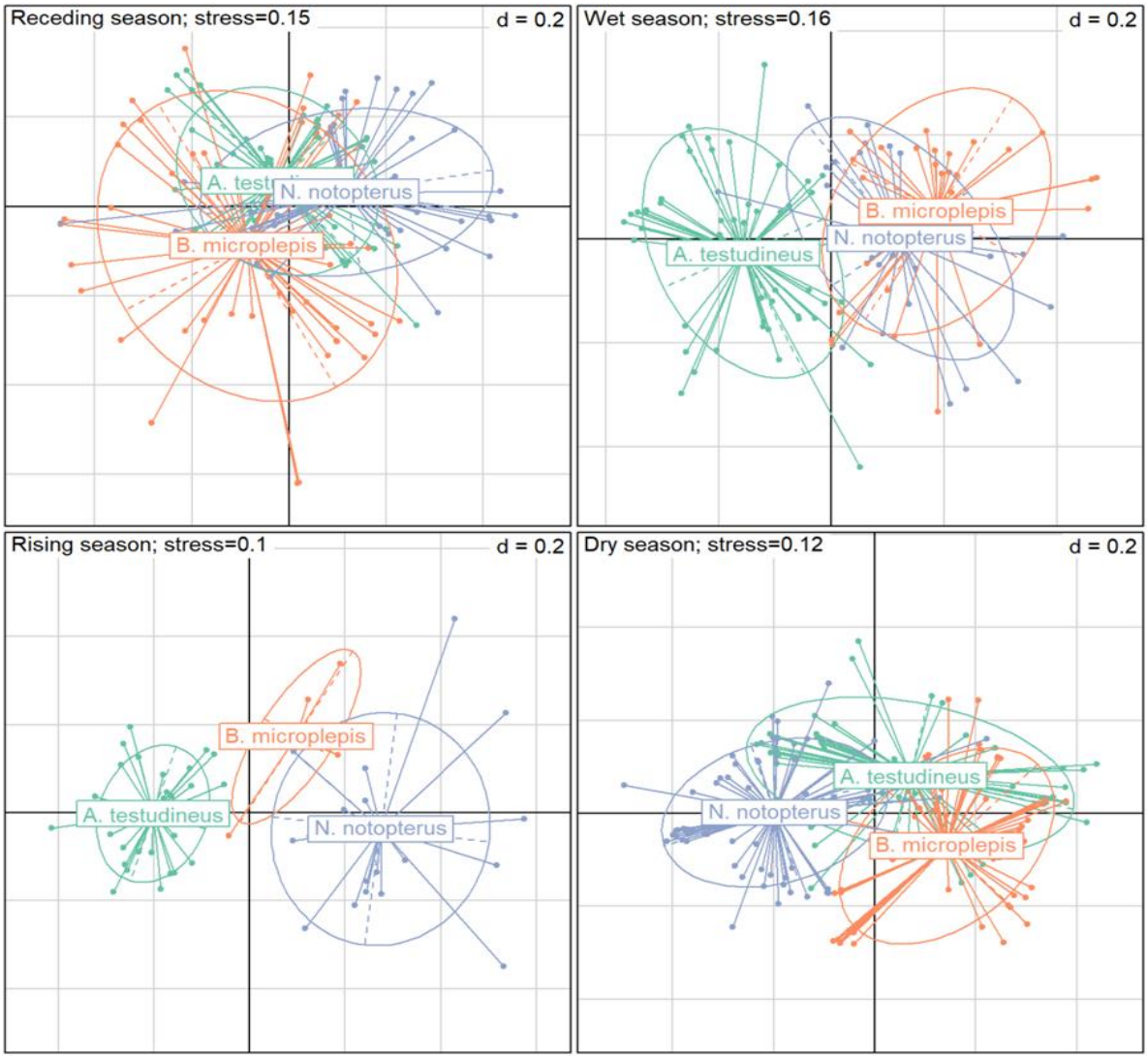

Fig. 11. NMDS biplots displaying the diet of the three species across the four seasons. The size of the ellipse represent species diet breadth whereas overlap between ellipses relates to dietary overlap between species.

Table 7. Diet breadth estimate for the three studies species across the four seasons. p-values were obtained using 1000 permutations on the community matrix. Values inferior to 0.05 point to a significant difference in the diet breadth of the three species.

Hydrological phase	*A. testudineus*	*B. microlepis*	*N. notopterus*	p-value
Receding season	0.45	0.53	0.47	0.002
Wet season	0.48	0.42	0.46	0.115
Rising season	0.38	0.34	0.51	0.004
Dry season	0.54	0.48	0.49	0.005

The bootstrap procedure performed on Pianka's index suggest that dietary overlap was different between the three species. This was revealed by differences in the null distributions, whose averages vary from 0.27 [95% CI=0.21-0.34] between *A. testudineus* and *B. microlepis* to 0.5 [95% CI=0.41-0.58] between *A. testudineus* and *N. notopterus*, while it was 0.3 [95% CI=0.23-0.37] between *B. microlepis* and *N. notopterus* (Fig. 12). Confidence intervals further suggest that the dietary overlap measured between *A. testudineus* and *N. notopterus* is significantly higher than the one measured between the two other pair of species (non-overlapping confidence intervals). We found evidence for seasonal variations in dietary overlap with minimum values observed during the rising season and maximum values observed during the receding season. In particular, dietary overlap between *A. testudineus* and *N. notopterus* was significantly higher during both the receding and the wet seasons, whereas it was significantly lower during the rising season (all $p<0.05$; Fig. 12). Likewise, dietary overlap between *B. microlepis* and *N. notopterus* was significantly higher during both the rising and the wet seasons (both $p<0.001$; Fig. 12). Dietary overlap between *A. testudineus* and *B. microlepis* was more stable across seasons, but was significantly higher than expected in the receding season ($p<0.01$; Fig. 12).

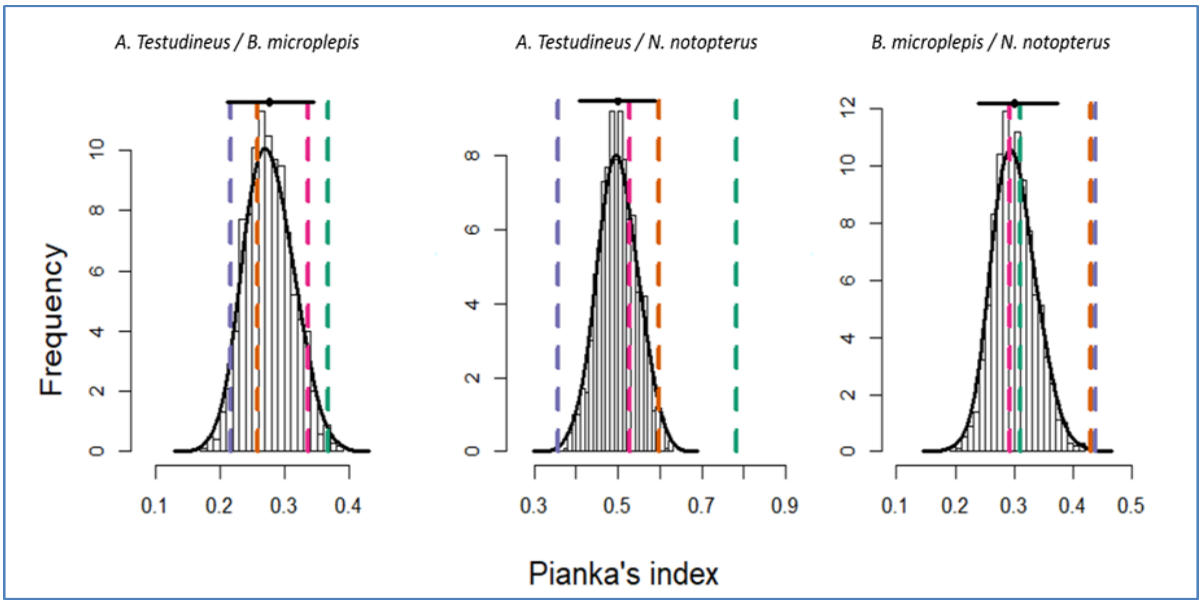

Fig. 12. Results from the bootstrap procedure conducted on Pianka's symmetric index, measuring the degree of niche overlap between the diets of two species. Histograms present the generated distribution of Pianka's index between two species under the null hypothesis

that there is no seasonal variation in dietary overlap. At the top of each histogram, the black horizontal bar represents the 95% confidence interval of the distribution while the black dot represents the average of the distribution. Colored vertical dashed lines point to the observed measure of niche overlap between two species in each season: receding season=green; wet season=orange; rising season=purple; dry season=pink. Any vertical line not overlapping the horizontal black line indicate a significant difference in the niche overlap for the corresponding season.

4. Discussion

4.1. Spatio-temporal variation of fish taxonomic structure in Tonle Sap Flood Pulse System, Tonle Sap Lake

4.1.1. Spatio-temporal variations of beta diversity

Our result revealeved that (i) some sites were more unique regarding fish community composition, (ii) some species highly contributed to spatial differentiation of fish communities and (iii) there is a strong temporal variation regarding the contribution of site to beta diversity. The determinants involved in these temporal variations and their contribution and the shape (i.e. linear or quadratic) of the relationship greatly varied among sites, thus reflecting spatial variation in the processes structuring fish communities.

Fish community compositions are expected to vary within floodplain systems (Lasne et al., 2007; Maire et al., 2013; Tondato et al., 2013). In accordance, we found large spatial variation in fish community composition reflected by differential contribution of sites to the dissimilarity between assemblages (i.e. to beta diversity). Similarly, Genner et al. (2004) found strong spatial variations in the community composition of rock-restricted cichlid fishes in Lake Malawi which was related to the geographic distances between locations and local habitat variables. In contrast, no spatial variation in fish community composition was found within the Dianshan Lake (China) which might be explained either by homogeneous environmental conditions (Hu et al., 2014) or by strong dispersal abilities of individuals homogenizing communities over large spatial scales (i.e. "mass effect"; Leibold et al., 2014). The large spatial variation in fish community composition found within the TSL may be explained by spatial variation in habitat availability and environmental conditions (environmental filtering) as well as by the migratory behavior of particular fish species. In accordance, a study conducted on 59 temperate lakes highlighted an influence of environmental variables in structuring fish com- munities both between and within lakes (Ives & Helmus, 2010).

We found temporal variation in the contribution of sites to the spatial variation in community composition, thus suggesting strong temporal variations in local species assemblage at large spatial scale. This result strengthens previous findings demonstrating spatio-temporal variations in community composition across seasons within the Dianshan Lake (Hu et al., 2014). More specifically, we found that three sites (BB, KC and KD) contributed strongly to the spatial variation in community composition. For BB and KC, the uniqueness of fish communities was occasional whereas the one at KD was rather stable over time with more than 60% of the weeks being unique in terms of community composition. Such stability can be explained by the fact that KD is the only site that is not located within the lake but within the river (TSR) which is a transitional zone for species migrating back and forth between the lake and the Mekong River. The uniqueness of species assemblages at BB mostly occurred during the dry season which can be explained by the presence of particular species moving back and forth from floodplain habitats to open water habitats within the lake and also by the influence of the Sangker River, located at the north of the lake. In contrast the uniqueness of species assemblages at KC and KD was evident during the wet season and can be explained by the fact that these sites are strongly influenced by the TSR.

Over the 242 species, 50% showed a significant contribution to spatial variation of fish communities. However, this contribution greatly varied over time. This was reflected by the fact that only 10% of the 242 species showed a significant contribution to spatial variation in com- munity composition for more than 50% of the weeks. Those species (e.g. *Mystus bocourti*, *Mystus albolineatus, Trichopodus microlepis, Anabas testudineus, Notopterus notopterus, Pristolepis fasciata, Channa striata*) were mostly non-migratory with specific habitat requirements. Such temporal stability suggests that these species probably depend upon the availability of critical habitats in both the wet and the dry seasons for growing or spawning. The low contribution of the remaining species to beta diversity can be explained by their widespread occurrence over the TSL, although seasonally.

4.1.2. Determinants of temporal variation in LCBD and SCBD

Local contributions to beta diversity (i.e. LCBD values) of the six sites displayed very different responses to species richness, total abundances and water level. Few studies have adressed the question of the determinants of temporal variations of LCBD values. Among them, a negative correlation between LCBD values and both species richness and total abundance has been reported in subtropical tree (Qiao et al., 2015), dung beetle (Da Silva et al., 2014), cattle tick com-munities (Biguezoton et al., 2016) and fish communities (Legendre & De Cáceres, 2013). Such a negative relationship indicates that as sites become less species-rich, they also tend to become more unique which could be explained by the occurrence of a disturbance such as pollution. In contrast, a positive relationship may arise because of the introduction of novel species (e.g. migratory species) within communities. Here we found contrasted patterns, revealing that different processes are shaping local fish communities.

We further found that both the shape and the relative effect of the three predictors greatly varied between sites. Indeed, we found a higher contribution of biotic variables (i.e. species richness and abundances) in explaining variation in site uniqueness over time relative to the water level (abiotic variable). This contrast with previous findings showing that abiotic vari- ables such as distance from the source, altitude and water discharge are key factors influencing species assemblages (Legendre & De Cáceres, 2013). Such discrepancy may stem from the fact that we focused on the temporal variation in site uniqueness whereas previous studies (Legendre & De Cáceres, 2013) were interested in its spatial variation. However, the higher contribution of biotic variables does not indicate that the water level has no influence on fish communities. Instead, one can imagine an indirect effect of the water level on fish communities where a change in this variable influences connectivity to floodplain habitats, in turn leading to local changes in species abundances and richness, and ultimately leading to spatial differentiation. The non-linear relationships highlighted here are also particularly interesting because they indicate that the local uniqueness of species

assemblages occur for intermediate values of water level, species richness and abundances. At both extreme of the gradient, communities are therefore more homogeneous which can be explained by the dominance of large scale processes (Leibold et al., 2004). For instance, water level reduction has been shown to influence community assemblage by influencing local individual abundances and by making it possible for species to colonize new local habitat patches (Layman et al., 2010) a process that can lead to community homogenization. Likewise, when the water level is very high, the presence of migratory species, dispersing over large distances, may homogenize fish communities. Such non-linear relationships have already been highlighted in birds where the community specialization index (a measure of the functional homogenization of communities) is maximal at intermediate values of fragmentation (Devictor et al., 2008).

Regarding temporal variation in the number of species that contribute to beta diversity above the mean of the entire pool of species (i.e. SCBD values) we found a high contribution of species richness whereas species abundances and water level only had a marginal effect. More specifically, we found a positive relationship with species richness indicating that as species richness is increasing, communities within the lake tend to become more dissimilar. This can be explained by the presence of particular species with strong ecological requirements and/or poor dispersal abilities, confined to particular area of the lake. However, the relationship highlighted was non-linear and actually peaked for intermediate values of species richness. Thus, at very high richness communities tend to be more similar, which can be explained the widespread occurrence of species with low ecological requirements and/or strong dispersal abilities homogenizing communities at large spatial scale.

4.2. Temporal distribution and species co-occurrence patterns of fish species

4.2.1. Temporal distribution according to hydrological cycles

Flood pulse is well known to influence on, both the distribution of organisms and abiotic conditions (Thomaz et al., 2007). By modifying connectivity patterns to floodplain habitats, flood pulse systems have important effects on community structure and composition, in turn influencing biotic interactions and local patterns of species occurrence, abundance and diversity (Arrington et al., 2005; Fernandes et al., 2009). In accordance, we found strong seasonal variations in species occurrences, abundances and biotic interactions. The stability of occurrence highlighted for most non-migratory species confirm that those species are TSL' resident which use TSL's habitat for all water seasons and lateral migration to nearby the lake, being particularly well adapted to oxygen depletion which occurs during the dry season. Those species likely undergo lateral migration to floodplain habitats during the onset of rainy season. On the contrary, we found strong seasonal variation regarding the occurrence of migratory species such as Labiobarbus leptocheilus (Lale). Overall these results are in accordance with some studies conducted in Amazon flood-pulse systems showing strong variations in abundance and occurrence depending on the water level and the migratory behavior of the different species (Castello, 2008; Röpke et al., 2016). We further found that abundances of migratory species where highest during the rising and the receding seasons, thus suggesting that those species migrate back and forth between the Mekong river and the TSL depending on habitat availability for rearing, spawning and feeding. This pattern is in line with those found in other tropical systems such as in the Yasuni River basin in the Ecuadorian Amazon, a tropical Lagoon and the Solimões River (Galacatos et al., 2004; Soyinka & Kassem, 2008; da Silva et al., 2013).

4.2.2. Pattern of pairwise species co-occurrence

Seasonal change in hydrological cycle has been shown to be the main driver causing variation in fish community structure and mediating species co-occurrence (Gabriela and Gonzalez, 2017). We found that positive associations were more frequent than negative associations in all seasons, particularly during the dry and the receding water seasons. We firstly suggest that as the area of the lake shrinks, species move from temporary floodplain habitats to permanent flooded areas and end-up using similar ecological niches, thus competing for similar resources [i.e. Paralaubuca typus (Paty), Pangasius.larnaudii (Pala), Osteochilus melanople (Osme) and Amblyrhynchichthys truncates (Amtr)]. Secondly, although there is positive species co-occurrence between different tropic guilds of some species in the TSL system, we assume that this pattern might be related to the species interaction between predator and prey [i.e. Hampala macrolepidota (Hama), Rasbora tornieri (Rato) and Xenentodon cancila (Xeca)]. In accordance, Bar-Massada (2015) and Echevarría & Rodríguez (2017) observed that niche overlap (i.e. species interaction) was smaller during hydrological phases where environmental heterogeneities are larger such that competition for space and other resources is weak. The pattern of co-occurrence highlighted here contrast to the ones found in Ecológica do Panga Reservoir in Minas Gerais (Brazil) where species co-occurrence appear to be mainly explained by competitive interactions between species instead of habitat affiliations (Camarota et al., 2016) and similarly to our case in the TSL. Likewise, co-occurrence pattern small fishes in Upper Parana´ River seemed to be independent of physical and chemical conditions, thus suggesting that biotic interactions mainly shapes community assembly (Ortega et al., 2015). The low percentage of non-random associations highlighted during the rising and the wet seasons can be explained by the fact that species move to floodplains habitats as the area of the lake expand, allowing them to forage on their preferred resources and to inhabit the optimal habitats for spawning and rearing. Thus, it seems that the diversification of habitats which is crucial for species have very specific ecological requirement, is the main driver explaining species co-

occurrence patterns. Our results therefore support the assumption that environmental filters have more influence than biotic interactions on the structure of fish assemblages (Peres-Neto, 2004; Mouchet et al., 2013). The fact that we found non-random associations between migratory and non-migratory species lends support to this hypothesis as these associations can be explained by seasonal changes in lateral connectivity caused by expansion-contraction cycles, allowing permanent resident species and transient species to use similar habitats. Contrasting results were however found in the literature. For instance, Peoples & Frimpong (2015) observed that habitat variables can explain the interaction observed between Chrosomus oreas and its host Nocomis leptocephalus whereas Márcia et al. (2006) observed that environmental variables are not the key factor explaining associations between different for fish species and that biotic interactions are more likely.

4.3. Seasonal omnivory: the response of consumer trophic position to fluctuating environments

The major finding of our study is that food-chain omnivory can be dynamic, with diets shifting to varying degrees in response to seasonal variation in environmental conditions and resource availability. In tropical floodplain ecosystems, fish trophic positions shift in response to seasonal patterns of hydrology. The vertical trophic position of most omnivorous fishes declined during the wet-season flood pulse. Many fish are capable of exploiting multiple food resources, but may track the most profitable food types when these are abundant during certain periods or within certain habitats (Winemiller, 1989; Correa & Winemiller, 2014). Larger piscivorous species, on the other hand, fed predominantly on fish throughout year and either increased or decreased their trophic position during the wet season. These large piscivores could also have tracked temporal and/or spatial variation in fish prey availability (e.g. Almeida et al., 1997). Interestingly, variation in trophic responses was large and not all species followed the same trend. Diverse feeding responses among coexisting species appears common in fish assemblages of tropical floodplains (Winemiller, 1989; Wantzen et

al., 2002; Correa & Winemiller, 2014) and may be important for the 'dynamic stability' (Leigh et al., 2010) and resiliency of these complex systems (Pettit et al., 2017). Our findings, combined with existing knowledge, suggest that seasonal omnivory could play a currently underappreciated role in sustaining energy and nutrient flow across changing conditions.

Based on combined stable isotope and stomach contents data, mid-sized omnivorous fishes from the Tonle Sap (i.e. *A. testudinus* and *N. notopterus*) reduced their trophic position and increased their consumption of invertebrates during the wet season. Five additional Tonle Sap species also showed large reductions (effect size that did not bound zero) in wet-season trophic positions, and 11 out of 16 literature reports for omnivores or entire fish assemblages showed increased consumption of plants or invertebrates during the wet season. Reduced wet-season trophic positions therefore appear common among omnivorous fishes of tropical floodplains. Species identified as strict piscivores, on the other hand, consumed fish almost exclusively throughout year. These piscivores likely possess morphological and behavioral traits that enable them to feed efficiently on fish while compromising foraging efficiency for other food resources (Almeida et al., 1997). Variable responses among piscivores to the flood pulse are consistent with previous studies that inferred piscivores track alternative fish prey depending on foraging tactics and habitat (Almeida et al., 1997; Winemiller & Kelso-Winemiller, 1994; Peterson, 1997). For example, sit-and-wait piscivores can exploit abundant juvenile fishes during the wet season by using vegetation as cover, whereas stalk-and-chase predators may be more efficient predators as water levels fall and prey encounter rates peak (Peterson, 1997). In South American floodplain, the tooth-snouted glass tetra, *Roeboides dayi* (Characidae), fed heavily on aquatic invertebrates when they were abundant during the wet season, and specialized on scales during the dry season when fishes were concentrated in shrinking pools (Winemiller, 1989; Peterson & Winemiller, 1997). While we focused on piscivores that also feed on invertebrates and sometimes even plant matter (i.e., piscivores that are food chain-omnivores), other functional groups are also alter their trophic positions seasonally. For

example, small omnivorous fishes, such as *Hemigrammus* spp. (total length <11 cm) and other tetras, can shift from feeding mostly on plant matter in the dry season to invertebrates during the flood pulse (Peterson, 1997; Goulding et al., 1988). This tracking of invertebrate abundance could explain higher trophic positions observed during the wet season for some Tonle Sap fishes. Based on these combined findings, it appears that fish perceive seasonal fluctuations in the abundance of alternative food resources differently, and most fishes are capable of responding by altering their diet and trophic position.

A positive relationship between trophic position and body size is not anticipated across entire tropical floodplain fish assemblages (Ou et al., 2017) because some herbivores and omnivores are large (e.g. the giant Mekong catfish, *Pangasianodon gigas*, is an omnivore, max. size = 300 cm; Rainboth, 1996) and some species with high trophic positions are small (e.g. African pike, *Hepsetus odoe,* as small as 10 cm were strongly piscivorous; Winemiller & Kelso-Winemiller, 1994). Body size was also not a significant predictor of the direction of seasonal trophic position shifts in the Tonle Sap, and not all fishes followed our prediction of reduced wet season trophic positions. Variation in seasonal diet shifts among floodplain fishes has been previously demonstrated by other studies using stable isotope (Wantzen et al., 2002) or dietary analysis (e.g. Winemiller, 1989; Novakowski et al., 2008; Mérona and Rankin-de-Mérona, 2004). The habitat heterogeneity of these systems and high variation among observed δ^{15}N values within and among species, further stresses the importance of considering dietary data along with δ^{15}N-based estimates of trophic position. However, the general trophic patterns in relation to hydrologic seasonality uncovered here, in spite of the complexity and dynamic nature of tropical floodplain ecosystems (Pettit et al., 2017), prompt us to consider further how seasonal omnivory could influence food web structure and stability.

The magnitude of seasonal trophic position changes reported here (plus or minus approximately half a trophic level) reflects changes in fish foraging behavior with consequences for food web structure, as well as individual fitness. For example, a shift from

eating 100% fish to eating 50% fish and 50% invertebrates (i.e. a reduction in trophic position of ~ 0.5) would likely change the number and strength of species interactions in the food web as well as the activity costs and growth of individual fish (Sherwood et al., 2002). Such temporally dynamic omnivory could also have consequences for stability. One theoretical study suggests that 'adaptive' omnivory, whereby consumers incorporate lower trophic level prey into their diet when preferred prey become rare, slightly increases stability relative to the case of fixed omnivory (Křivan & Diehl, 2005). Prey refugia, prey defense, stage-structured cannibalism, and adaptive foraging are all mechanisms that are thought to maintain omnivory at weak to intermediate interaction strengths in nature, and thus prevent strong and destabilizing omnivory (Kratina et al., 2012). Although not well considered theoretically, flexible food web properties, like omnivory, could be extremely important for stability in non-equillibrim or periodically forced systems (McCann & Rooney, 2009).

Temporally changing trophic positions also arise in other taxa and ecosystems, including stream macroinvertebrates (Hellmann et al., 2013), birds (Nakano & Murakami, 2001) and desert mammals (Soykan & Sabo, 2009). Consumer trophic positions can also remain static through time (Rybczynski et al., 2008). Temporal omnivory therefore appears variable in its direction and magnitude of change, a conclusion consistent with our findings from tropical floodplains. One could further consider how the location of a particular species would change depending on body size (e.g. throughout ontogeny) and how the capacity for seasonal omnivory differs among functional groups (e.g. omnivores vs. detritivores, Wantzen et al., 2002) and ecosystem types (e.g. between summer and winter in temperate or arctic systems), and how this variation influences food web structure and stability.

4.4. Seasonal variations in diet composition, diet breadth and dietary overlap between three commercially important fish species

In this study, we explored seasonal variations in the diet of three common, abundant and commercially important fish species presenting important differences within their life-

cycle but sharing similar habitats to gain knowledge about resource use and the potential for resource competition. Although we found large seasonal variations in the proportion of empty stomachs, we found no differences between species in this regard. In contrast, we found strong seasonal variations in the diet breadth and dietary overlap of the three species. Diet breadth was the largest during the dry and the receding seasons whereas dietary overlap between species was the lowest during the dry season. We also found evidence for seasonal variations in the diet of *A. testudineus* and *N. notopterus* with a differential contribution of food items, while no significant change was found for *B. microlepis*.

A similar seasonal variation in the proportion of empty stomachs suggests that ecological differences between species (e.g. reproductive behavior, foraging abilities) are probably not strong enough to outweigh the effect of seasonal variations in resource abundance. For the three species, the proportion of empty stomachs was the lowest during the dry season (i.e. when floodplain habitats are unachievable) but the highest during the receding season, which contrast to our expectation. One possible explanation would be that the high abundance and diversity of fish during the receding season, combined with the reversal of the river flow, that sweeps out resources from the system, would increase competition for resources, thereby decreasing the *per capita* consumption rate (Menge & Sutherland, 1987). In contrast, the low abundance and diversity of fish during the dry season might contribute to increase the species *per capita* consumption rate, although the amount of resources is lower relative to the receding season. Another, non-exclusive explanation would be that during the receding season, individuals rely on reserve energy stored during the wet season, while during the dry season, individuals have to maximize their energy intake to face an increase in metabolic demand caused by adverse conditions such as oxygen depletion (Arrington et al., 2002).

In contrast to the proportion of empty stomachs, we found differences in the seasonal variation of the stomach contents of the three species. Such variations likely result from temporary connections to floodplain habitats caused by expansion-contraction cycles of the

TSL's flooded area, providing access to new resources (Adama et al., 2014). For instance, the increase in the proportion of crustaceans and insects in the diet of *B. microlepis* between the dry and the rising seasons can be explained by the progressive connection to floodplain habitats making it possible for individuals to forage in previously unflooded areas where those items are rather abundant. Similar changes were observed within other tropical systems where seasonality was shown to influence fish diet through an increase in the frequency of particular food items such as terrestrial insects and amphipods during the rainy season (Tejerina-Garro et al., 1998). In line with our expectation, we found that fish prey contributed strongly to seasonal variations in the diet of *A. testudineus* with a substantial increase (i.e. around 10%) during the dry season. This suggest that the ability for this species to face adverse conditions (i.e. low levels of oxygen) makes it possible for individuals to exclude other competitors and to forage on the most profitable resource independently of the connection to floodplain habitats (Gurevitch & Padilla, 2004).

In line with our expectation and with previous findings (Hinojosa-Garro et al., 2013), we found that the diet breadth of the three species tended to be larger during the dry (and the receding) season. This result could be explained by an increase in both intra and interspecific competition, constraining individuals to adopt an opportunistic strategy and diversify their diet to reduce competition (Svanbäck & Persson, 2004). The diet breadth of the three species differed in all seasons, except the wet season. This lack of difference was due to an increase in the diet breadth of *A. testudineus* and *B. microlepis* combined with a decrease in the diet breadth of *N. notopterus* between the rising and the wet seasons, leading to a similar diet breadth between the three species (from 0.42 to 0.48). The increase observed for the first two species can be explained by an increase in the diversity and amount of resources combined with a release of the competitive pressure, making it possible for those species to diversify their diet. In contrast, the decrease observed for the last species can be explained by its ability to forage on a large array of resources during periods of shortage (habitat generalist) while during periods of resource abundance individuals can

focus on the most profitable resource. As expected, we found large seasonal variations in the diet breadth of *A. testudineus* and *B. microlepis* but low variations in the diet breadth of *N. notopterus*. The large variations observed for *A. testudineus* and *B. microlepis* are in accordance with their ecological status (invasive for the former and long-distant migrant for the latter), making it possible for these species to adapt their diet as the amount and the diversity of resources changes over time or space. In contrast, the large and stable diet breadth observed in *N. notopterus* could be attributed to its high mobility between diverse habitats that potentially contain different resources.

Regarding temporal changes in the availability, quantity and quality of food resources, species are expected to adjust their foraging behavior in order to maximize their energy intake and minimize dietary overlap (Corea & Winemiller, 2014). In this study, we found an overall high dietary overlap between species during the receding season (e.g. between *A. testudineus* and *N. notopterus)* and a lower dietary overlap during the rising season, particularly when *B. microlepis* was involved in the comparison, in accordance with our expectation. The pattern observed during the receding season can be explained by the progressive loss of resources, as the lake retracts, whereas the one observed during the rising season can be explained by the progressive connection to floodplain habitats providing opportunities for species to forage on different resources. Contrasted results have however been reported in the literature. For instance, some studies have found that dietary overlap tends to be the lowest during the dry season because fish tend to concentrate in small, well-oxygenated, areas (McConnell, 1964; Pusey & Bradshaw, 1996), whereas others (Zaret, 1972; Goulding, 1980b; Prejs & Prejs, 1987) found the opposite (i.e. high dietary overlap during the dry season). In flood-pulse systems, fish assemblages and diet composition have been shown to differ with respect to habitat heterogeneity, hydrological conditions and connectivity between adjacent systems (Taylor, 1997) while the intensity and the duration of the flood pulse have also been shown to strongly influence dietary overlap between species (Luz-Agostinho et al., 2008a). The absence of general pattern suggests

that seasonal changes in trophic dynamics are not fully explained by feeding strategies, that aim to reduce competition between species and individuals, but that feeding opportunism may be an important underlying factor (Prejs & Prejs, 1987). The discrepancies existing between previous studies and this one reflect the fact that different patterns can occur depending on the characteristics of the system, including its productivity, the nature of resources (e.g. autochtonous *vs.* allochtonous) and the characteristics of the species (e.g. generalist *vs.* specialist).

5. General conclusions and perspective

The TSL is the largest inland fisheries in South-east Asia and supports the livelihood of 2.5 million people around the lake (Arias et al., 2013). Its flood-pulse dynamic combined to the flow reversal of the TSR makes it a unique system worldwide supporting high biodiversity by providing a large diversity of food and habitats for many birds, reptiles and fishes. However, the growing demand for water for agricultural purposes and the construction of hydro-power dams along the Mekong river (Arias et al., 2013) combined to the effect of climate change is strongly threatening this system by altering and reducing flood intensity from 7% to 16% during the rainy season (Arias et al., 2012). Such changes in the water regime are likely to have strong impacts on fish community composition by modifying several phenological events (Agostinho et al., 2004) such as the timing of migration or spawning and also by reducing the amount of submerged habitats upon which fish depends for growing and spawning. This may ultimately lead to decrease in TSL fish productivity and biodiversity. For instance, in 2016, hundred tons of brood-stock fish died within the conservation zone of Boeung Chhmar, is the main conservation zone of the TSL (which is temporarily connected to the lake) due to a prolonged drought. In the TSL system, the strong spatio-temporal variations highlighted regarding the uniqueness of fish communities are likely to be the result of both spatial variations in environmental conditions and the seasonal migration of particular species which occurrence depends on the lateral connectivity to floodplain habitats critical for their reproduction and survival.

However, current dam construction and the construction planning of 42 additional dams in the upper parts of the Mekong in China, Laos and Thailand is posing considerable threats to the natural flood-pulse regime of the TSL. These changes are forecasted to reduce the annual flood magnitude and to modify the lateral connectivity to floodplain areas, ultimately altering the functioning of the ecosystem while reducing its productivity and affecting the livelihood of thousands of people (Arias et al., 2014). Our results highlight that species occurrence and abundance greatly varied according to seasonal changes in the

hydrology of the TSL's system. In addition, strong positive association were observed during the dry and the receding seasons, indicating that changes in habitat availability and species interaction (predator and prey) are probably the main driver of species co-occurrence in the system, both among small prolific species and between predators and preys. Understanding how fish communities respond and how species interaction to the seasonal change in TSL hydrological of the TSL's flood pulse systemprovides a critical framework for fisheries management and conservation, particularly for sustaining fish biodiversity and maintaining productivity upon which millions of people depend around the lake.

Furthermore, vertical trophic position and the related concept of food chain omnivory are key attributes that influence food web stability and functions (McCann et al., 2005; Winemiller et al., 2014; Post & Takimoto, 2007). Our findings for fishes inhabiting tropical floodplains revealed that food-chain omnivory is dynamic in response to seasonal change in hydrologicle cycles. Seasonal shifts in trophic ecology are not unique to tropical fishes or floodplains. Knowledge about how species and ecosystems respond to seasonality is crucial for anticipating the consequences of climate change. Organisms capable of dynamic omnivory on seasonal time scales, for example, could be particularly important for sustaining ecosystem functioning in the face of changing conditions (Takimoto et al., 2002; McMeans et al., 2016). Further, maintenance of species spanning a range of trophic responses, as observed among fishes in tropical floodplains, could play an important role in buffering local communities from perturbations.

In TSL, the seasonal change in dietary of fishes and how fishes shifting their feeding behavior across seasons are poorly understood. Therefore, understanding how diet of these species changes seasonally could help gain knowledge regarding how the connectivity to floodplain habitats influence their feeding behavior and the strength of competition for resources. Our results suggest that the flood-pulse may play a role in mediating the competitive interactions between the three species by making it possible for species to shift their diet as the availability of resources changes over time. This may ultimately promote

biodiversity by providing opportunities for species to avoid competition and live in harmony with other species, originally displaying similar dietary requirements. This harmony is however threatened by accelerating water infrastructure development (hydropower, irrigation, flood control, and water supply) and climate change, bringing considerable modifications to the flood pulse of the Tonle Sap Lake in the foreseeable future. The strong seasonal variations in diet composition highlighted here can be explained by a variety of mechanisms including changes in resource abundance and diversity, changes in the strength of competitive interactions between individuals and species as well as changes in ontogeny (Seegert et al., 2014). Teasing apart the relative influence of these factors is impossible with our data. The collection of additional data across seasons, for various organisms belonging to different trophic compartments (e.g. phytoplankton, zooplankton, invertebrates) and age classes (reflecting variable development stage) and in multiple locations spread over the lake (especially floodplain habitats) would help gain knowledge about (i) the nature of interactions between species and individuals and (ii) the extent to which they can shift their diet as the connectivity to floodplain habitats is changing. Such a study would not only improve our understanding of the mechanisms promoting biodiversity within flood-pulse systems but also help guide management strategies within the Tonle Sap.

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Publications

Temporal distribution and species co-occurrence patterns of fish species in the Tonle Sap Lake Flood Pulse System

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Abstract

Tonle Sap Lake (TSL) supports 60 percent of inland freshwater catch and provides heterogeneous habitats for threatened and endangered species of Cambodia. The main objective of this paper was to study on the temporal distribution of the most occurrence fish species, their co-occurrence pattern, and to test the influence of the seasonal change in hydrological cycles. We used daily catch monitoring data for the period of four years from 2012 to 2015, conducted by local fishermen at 5 sites around the TSL. Our finding revealed that, species occurrence and abundance was temporally varied. Strong temporal variation in species occurrence was occurred with visiting species such as *Labiobarbus leptocheilus*, and *Poropuntius deauratus* while water level starts to fill into the TSL. We further observed that the abundance of 17 species was strongly varied while other 22 species (mainly TSL's residential species) were stable within the year. Positive species co-occurrence pattern was generally higher than negative species co-occurrence at all hydrological season. Highest species positive co-occurrence patterns were found during the period of decrease and low water level seasons while fishes are migrating from flooded areas, competing for resource and habitats during low water season and the interaction between different tropic guilds of some species (predator and prey). Study on temporal distribution and species co-occurrence of fish and how community responds to the seasonal change in hydrological cycles provides critical information for fisheries management and conservation in the Tonle Sap Lake (TSL) as well as maintaining fish biodiversity in the Mekong system.

Key-words: species interaction, hydrological cycle, lateral connectivity, niche theory, competition, biotic interactions

Introduction

In community ecology, a major goal is to understand and identify what are the factors and processes that generate and shape communities (Chesson, 2000; Camarota et al., 2016) and especially what are the mechanisms that allow multiple species to coexist altogether (Sutherland et al., 2013). Although environmental factors have been shown to alter species distributions and community structures in a number of studies, biotic interactions have received less attention (Wiens, 2011; Wisz et al., 2013). Ecological niche theory has been extensively used to explain species assemblages within communities and postulates that species should differ in resource use to be able to coexist (Levine & HilleRisLambers, 2009). This is because, when species have similar ecological niches, the most competitive species is expected to exclude the ones having lower competitive abilities. However, species usually do not have the exact same ecological niche and likely differ with respect to several features such as habitat or feeding requirements. The consequence of this is that competitive interactions can still be at play within communities, even though theory predicts that such interactions should be low as the most interacting species should exclude each other through competition (MacArthur & Levins, 1967; Schoener, 1974). However, this is not because species are never found together that they necessarily compete between each other. For instance, non-overlapping habitat requirements between species can lead to differences in species geographical distributions such that species segregation can occur with little or no interactions between them (Ovaskainen et al., 2010). Patterns of species co-occurrence have been extensively used across the past decade to assess how interspecific interactions dictate community assemblage (Bar-Massada, 2015) whereas Kraft et al., 2007 argued that functional relationships between coexisting species could

reveal the relative influence of environmental constraints over competitive interactions. Furthermore, species pair co-occurrence pattern has becoming a main pursuit of ecologists, primarily because the coexistence of species is fundamentally important in evaluating various theories, principles and concepts. i.e including community assembly, equilibrium versus non-equilibrium organization of communities, resource partitioning and ecological character displacement, the local and regional species diversity relationship, and the meta-community concept (Veech, 2014). Overall, these studies highlighted that communities can be shaped by multiple factors whose contribution may vary depending on the system being studied. These factors include biotic interactions (Mérona & Mérona, 2004; Barili et al*.,* 2011), species-habitat interaction (Peres-Neto, 2004; Mouchet et al., 2013; Rodrigues et al., 2013; Peoples & Frimpong, 2015) and environmental filtering (Rondón Suárez et al., 2004; de Melo et al., 2009). Furthermore, it has been shown that competitive, facilitative or neutral interactions can play varying roles in shaping community composition . The co-occurrence of species that share resource requirements is governed by competitive (Diamond, 1975) and facilitative (Bruno et al., 2003). Understanding how biotic interactions vary over space and time is key to understand what are the processes shaping ecological communities.

Flood-pulse systems experience large seasonal variations in water level characterized by expansion-contraction cycles influencing lateral connectivity to floodplain habitats on which many organisms, such as fishes, rely for feeding and breeding (e.g., Jepsen et al*.,* 1997; Rodrigues et al*.,* 2013; Tanaka et al., 2015). By influencing fish community structure and population dynamics (Dudgeon, 2000) these variations have been shown to strongly influence among-species interactions in tropical floodplain (e.g. Luz-Agostinho et al., 2008; Sousa & Freitas, 2008;

Castello et al., 2015). For instance, the low availability of suitable habitats and food during the dry season usually entails high dietary overlap between species, potentially resulting in high competitive interactions (Winemiller & Pianka, 1990). Likewise, it has been hypothesized that during transient phases of the hydrological cycle (i.e. the phases where the water level either increase or decrease), communities may not have enough time to become saturated and may exhibit random patterns of species co-occurrence (Arrington et al., 2005). Overall, it turns that highly dynamic systems where community vary seasonally as a result of changes in habitat availability and food resources are well suited to study species co-occurrence patterns throughout hydrological seasons (Gabriela and Gonzalez, 2017).

The Tonle Sap Lake (TSL), located in Cambodia, is an important natural flood pulse system, is the largest natural lake in South-East Asia and was designed as a UNESCO Biosphere Reserve (Lamberts, 2006; Arias et al., 2014). The TSL hosts more than 240 fish species (Chan et al., 2017; Kong et al., 2017) and supports many endangered vertebrates (Campbell et al., 2006; Arias et al., 2013; Mak, 2015). This system is the most productive inland fisheries in the world providing livelihood supports, either directly or indirectly, for about two million people in the lower Mekong basin (Holtgrieve et al*.,* 2013; Yen et al*.,* 2009). The lateral connectivity between the main lake and its floodplain area mainly depends on water coming from the Mekong River, representing more than 50% of the water balance and its tributaries around the lake itself.

In this study, we aim to examine changes in co-occurrence pattern of the most abundant fish species within the TSL throughout four complete hydrological cycles

(i.e. four years). Given seasonal changes in the TSL's hydrological cycles and the lateral connectivity to floodplain habitats, we expect strong temporal variation in species occurrence and abundance within the TSL system. Those changes were in turn expected to entail strong temporal variations in species co-occurrence patterns among different tropic guild fish species (non and migratory species) and species interaction between predator and prey during dry season and during the filling of water from the Mekong up stream into the lake as migratory species are migrating to floodplain around the TSL.

Materials and Methods

Study site

The Tonle Sap Lake (TSL) is the largest natural flood pulse lake in Southeast Asia. TSL is connected with the Mekong in its southern part by a 120 km long river, the Tonle Sap River (TSR), which serves as an inlet and outlet for water fluxes (Figure 1). Every year, the lake undergoes a remarkable transformation. Its area is multiplied by four passing from 2,700 km^2 up to 9,000-16,000 km^2, while the water level increases from 1 or 2 meters in dry season (from April to May) up to 10-15 meters during the rainy season (from the end of September to the end of October (Kong et al. 2017). According to the seasonal change in water regime, The TSL is classified into four hydrological phases. First phase is the rising season, starts from July to early September, which strongly water feed about 70% from the upper Mekong and the rest from TSL's tributaries itself. The second phase is the flooding season starts at the end of September to early October which extends to surround the TSL about 1.25 million hectares of forest, agricultural land are submerged and may attain up to 15 meter depth. The third phase, is the receding season, occurs from the end of October to February and corresponds to the reversal of the river flow

from the TSL through the TSR, thus leading to a decrease of the water level of the lake. Last phase, the fourth phase, the dry season, lasts from April to May, and corresponds to a period where the water level is the lowest (one to two meters).

Data collection

Data were collected under technical and financial support from Mekong River Commission (MRC), in collaboration with Inland Fisheries Research and Development, Fisheries Administration. Fish data were collected at five sites located around the TSL (Fig. 1). Two sites were located in the northern part of the lake (Siem Reap [SR] and Battambang [BB]), while the three other sites were located in the southern part of the lake (Kampong Chhnang [KC], Kampong Thom [KT] and Pursat [PS]). Fish were sampled every day from January 2012 to December 2015 by 15 local fishermen (3 fishermen per site) using gillnets with varying mesh sizes (2 to 6.5 cm), heights (1.5 to 2 m) and lengths (250 to 300 m), to capture individuals and species with varying sizes. Fishes were identified to species level and counted. For unidentified individuals, specimens were brought back to the Inland Fisheries Research and Development Institute (IFReDI) and was performed by a professional taxonomist at. Individuals identified by fishermen were monthly cross-checked at fields by the IFReDI's team.

Data preparation and analysis

Only species occurring in at least 10% of the catch were used. Consequently, among the 242 fish species present in the database, 39 species were used here. Those species encompass five orders and 12 families (S1 Table) and correspond to more than 80% of total catch, totaling 10,320,691 individuals (BB=2,226,969, KC=3,056,632, KT=2,511,647, PS=1,384,144 and KC=1,145,299).Daily catch data were aggregated into weekly data, thus resulting in 209 weekly catch data in total.

We used bubble plot on the weekly abundance data to investigate the temporal variation according to the change in hydrological cycles and the weekly abundance data were transformed to presence and absence for investigating species occurrence. We used non-metric multidimensional scaling (NMDS) with dissimilarities between sampling units computed using Bray-Curtis distances (Bray & Curtis, 1957) to illustrate temporal changes in fish communities. We then performed Ward hierarchical clustering on the NMDS on the abundance dataset to identify groups of species based on abundance dissimilarities. Both analyses were performed using the package vegan (Oksanen et al., 2015) within the R environment software.

We used a probabilistic approach to analyse species co-occurrence patterns. Basically, this approach compares species co-occurrence on observed sites to the distribution expected if the species were distributed independently from each other (Veech, 2013). It overall tests whether pairwise associations between species are random or significantly non-random, and whether significant associations are higher or lower than expected. Note that this approach only test co-occurrence between two species and thus do not account for the fact that additional species may influence species occurrence. The simulated random data used for comparisons in this study were thirty-nine species, with a 10 probability of occurrence during the period of five years were included in the analysis. This analysis was performed using the package “cooccur” (Griffith et al., 2016) and was run on the entire dataset (i.e. across the four hydrological cycles) as well as for each season (i.e. dry, wet, receding, and rising seasons). From the results, we generated heat maps to visualize species pairwise associations.

Results

Weekly species occurrence (Fig. 2a) and abundance (Fig. 2b) greatly varied across the four seasons. Generally, species occurrence was higher during the high and the receding water seasons, although opposite patterns exist for some species such as *Labiobarbus leptocheilus* (Lale) and *Poropuntius deauratus* (Pode). Strong seasonal variations were also visible regarding abundances with some species presenting particularly strong variations (e.g. *Trichohodus trichopterus* (Trtr), *Mystus mysticetus* (Mymy); Fig. 2b).

The results from the NMDS analysis revealed seasonal variations in community composition (Fig. 2c; axis two). Species assemblages seem to be quite different between the receding and the rising seasons. Species like Pode, *Paralaubuca typus* (Paty) *or Puntioplites proctozysron* (Pupr) were mostly associated with the receding water season, whereas species like *Mystus bocourti* (Mybo), *Boesemania.microlepis* (Bomi) and *Pangasianodon hypophthalmus* (Pahy) were mainly associated with the rising water season. The hierarchical clustering revealed that seasonal change in hydrological cycle is the main driver in seasonal variation of fish assemblages, thus fish community were classified into four assemblages (Fig 2d).

Result from the co-occurrence analysis performed on the whole dataset revealed 25.5% non-random pairwise associations among the 705 species pair considered (Table 1). Among those, 121 were positive, while 59 were negative (Fig. 3a). This analysis further revealed that two non-migratory species [i.e. *Puntioplites proctozysron* (Pupr) and *Anabas testudineus* (Ante)] and two migratory species [i.e. *Henicorhynchus siamensis* (Hesi) and *Henicorhynchus lobatus* (Helo)] show no particular association with any other species. By contrast, other species such as *Thynnichthys thynnoides* (Thth), *Parambassi wolffi* (Pawo) or *Hemibagrus*

spilopterus (Hesp) were consistently positively associated with other species. No species only showed negative associations. Positive associations were found among migratory species which use the ecological nice and different feeding tropic [i.e. *Paralaubuca typus* (Paty), *Pangasius.larnaudii* (Pala), *Osteochilus melanople* (Osme) and *Amblyrhynchichthys truncates* (Amtr)], between migratory and non-migratory species [e.g. *Pangasius.larnaudii* (Pala) and *Parambassis apogonoides* (Paap), *Paralaubuca typus* (Paty) and *Xenentodon cancila* (Xeca)] and among non-migratory species which use different feeding tropic [i.e. *Hampala macrolepidota* (Hama), *Rasbora tornieri* (Rato) and *Xenentodon cancila* (Xeca)]. We further found that, positive biotic interaction between predators and preys [i.e. *Channa striata* and *Pangasius macronema* (Pama and *Mystus bocourti* (Mybo) and between *Channa microlepis* (Chmi) and *Paralaubuca typus* (Paty), *Pangasius larnaudii* (Pala) and *Xenendon cancila* (Xeca)]. The same analysis performed for each season revealed that positive associations were overall more frequent than negative associations in all seasons (Fig. 3b). Random associations were maximized during the rising and the wet seasons, while they were minimized during the receding and the dry seasons (Table 2). Some species like *Mystus singaringan* (Mymy), *Labiobarbus siamensis* (Lasi) or *Labiobarbus lineatus* (Lali) were most involved into negative interactions (Fig 3b).

Discussion

By modifying connectivity patterns to floodplain habitats, flood pulse systems have important effects on community structure and composition, in turn influencing biotic interactions and local patterns of species occurrence, abundance and diversity

(Arrington et al., 2005; Fernandes et al., 2009). In accordance, we found strong seasonal variations in species occurrences, abundances and biotic interactions. The stability of occurrence highlighted for most non-migratory species confirm that those species are TSL' resident which use TSL's habitat for all water seasons and lateral migration to nearby the lake, being particularly well adapted to oxygen depletion which occurs during the dry season. Those species likely undergo lateral migration to floodplain habitats during the onset of rainy season. On the contrary, we found strong seasonal variation regarding the occurrence of migratory species such as *Labiobarbus leptocheilus* (Lale). Overall these results are in accordance with some studies conducted in Amazon flood-pulse systems showing strong variations in abundance and occurrence depending on the water level and the migratory behavior of the different species (Castello, 2008; Röpke et al., 2016). We further found that abundances of migratory species where highest during the rising and the receding seasons, thus suggesting that those species migrate back and forth between the Mekong river and the TSL depending on habitat availability for rearing, spawning and feeding. This pattern is in line with those found in other tropical systems such as in the Yasuni River basin in the Ecuadorian Amazon, a tropical Lagoon and the Solimões River (Galacatos et al., 2004; Soyinka & Kassem, 2008; da Silva et al., 2013).

Seasonal change in hydrological cycle has been shown to be the main driver causing variation in fish community structure and mediating species co-occurrence (Gabriela and Gonzalez, 2017). We found that positive associations were more frequent than negative associations in all seasons, particularly during the dry and the receding water seasons. We firstly suggest that as the area of the lake shrinks, species move from temporary floodplain habitats to permanent flooded areas and

end-up using similar ecological niches, thus competing for similar resources [i.e. *Paralaubuca typus* (Paty), *Pangasius.larnaudii* (Pala), *Osteochilus melanople* (Osme) and *Amblyrhynchichthys truncates* (Amtr)]. Secondly, although there is positive species co-occurrence between different tropic guilds of some species in the TSL system, we assume that this pattern might be related to the species interaction between predators and preys [i.e. *Hampala macrolepidota* (Hama), *Rasbora tornieri* (Rato) and *Xenentodon cancila* (Xeca) and between *Channa microlepis* (Chmi) and *Paralaubuca typus* (Paty), *Pangasius larnaudii* (Pala) and *Xenendon cancila* (Xeca)]. In accordance, Bar-Massada (2015) and Echevarría & Rodríguez (2017) observed that niche overlap (i.e. species interaction) was smaller during hydrological phases where environmental heterogeneities are larger such that competition for space and other resources is weak. The pattern of co-occurrence highlighted here contrast to the ones found in Ecológica do Panga Reservoir in Minas Gerais (Brazil) where species co-occurrence appear to be mainly explained by competitive interactions between species instead of habitat affiliations (Camarota *et al.,* 2016) and similarly to our case in the TSL. Likewise, co-occurrence pattern small fishes in Upper Parana´ River seemed to be independent of physical and chemical conditions, thus suggesting that biotic interactions mainly shapes community assembly (Ortega et al., 2015). The low percentage of non-random associations highlighted during the rising and the wet seasons can be explained by the fact that species move to floodplains habitats as the area of the lake expand, allowing them to forage on their preferred resources and to inhabit the optimal habitats for spawning and rearing. Thus, it seems that the diversification of habitats which is crucial for species have very specific ecological requirement, is the main driver explaining species co-occurrence patterns. Our results therefore support the assumption that environmental filters

have more influence than biotic interactions on the structure of fish assemblages (Peres-Neto, 2004; Mouchet et al., 2013). The fact that we found non-random associations between migratory and non-migratory species lends support to this hypothesis as these associations can be explained by seasonal changes in lateral connectivity caused by expansion-contraction cycles, allowing permanent resident species and transient species to use similar habitats. Contrasting results were however found in the literature. For instance, Peoples & Frimpong (2015) observed that habitat variables can explain the interaction observed between *Chrosomus oreas* and its host *Nocomis leptocephalus* whereas Márcia et al. (2006) observed that environmental variables are not the key factor explaining associations between different for fish species and that biotic interactions are more likely.

Conclusion

TSL also plays an important role in sustaining fish diversity in the Mekong system by providing heterogeneous habitats for threatened and endangered Mekong species including fishes, birds, and probably the world's most endangered freshwater snakes (Campbell et al., 2006). However, current dam construction and the construction planning of 42 additional dams in the upper parts of the Mekong in China, Laos and Thailand is posing considerable threats to the natural flood-pulse regime of the TSL. These changes are forecasted to reduce the annual flood magnitude and to modify the lateral connectivity to floodplain areas, ultimately altering the functioning of the ecosystem while reducing its productivity and affecting the livelihood of thousands of people (Arias *et al.,* 2014). Our results highlight that species occurrence and abundance greatly varied according to seasonal changes in the hydrology of the TSL's system. In addition, strong positive association were

observed during the dry and the receding seasons, indicating that changes in habitat availability and species interaction (predator and prey) are probably the main driver of species co-occurrence in the system, both among small prolific species and between predators and preys. Understanding how fish communities respond and how species interaction to the seasonal change in TSL's flood pulse system provides a critical framework for fisheries management and conservation, particularly for sustaining fish biodiversity and maintaining productivity upon which millions of people depend around the lake.

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List of tables

Table 1. Summary of the co-occurrence analysis performed on the whole dataset and a subset of the dataset for each season.

Periods	Sites	Positive	Negative	Random co-occurrence	Percentage non-random
Dry	52	49	31	586	12.00
Rising	35	23	20	597	6.70
Wet	52	43	25	633	9.70
Receding	70	59	28	622	12.30
Whole	209	121	59	525	25.50

Table S1. List and characteristics of the 39 fish species included in this study. The characteristic abbreviations are as follow. For habitat: 1=demersal, 2=pelagic, 3=benthopelagic, 4=pelagic-neritic. For trophic guild: 1=algivore-detritivore, 2=invertivore-piscivore, 3=invertivore, 4=omnivore, 5=piscivore. Migratory status: NM=non-migratory species, M=migratory species.

Species	Species Abbreviation	Habitat	Trophic guild	Migration pattern
Amblyrhynchichthys truncates	Amtr	3	1	M
Anabas testudineus	Ante	1	2	NM
Barbonymus gonionotus	Bago	3	1	NM
Boesemania.microlepis	Bomi	3	2	M
Channa micropeltes	Chmi	3	5	NM
Channa striata	Chst	3	5	NM
Cyclocheilichthys armatus	Cyar	3	4	NM
Cyclocheilichthys enoplos	Cyen	3	4	M
Hampala macrolepidota	Hama	3	3	M
Henicorhynchus siamensis	Hesi	3	1	M
Hemibagrus spilopterus	Hesp	1	3	NM
Henicorhynchus lobatus	Helo	3	1	M
Labeo chrysophekadion	Lach	3	1	M
Labiobarbus lineatus	Lali	3	4	M
Labiobarbus leptocheilus	Lale	1	4	NM
Labiobarbus siamensis	Lasi	3	4	M
Mystus bocourti	Mybo	1	3	NM
Mystus albolineatus	Myal	1	2	NM
Mystus mysticetus	Mymy	1	3	NM
Mystus singaringan	Mysi	1	3	NM
Notopterus notopterus	Nono	1	2	NM
Osteochilus vittatus	Osvi	3	4	NM
Paralaubuca typus	Paty	3	3	M

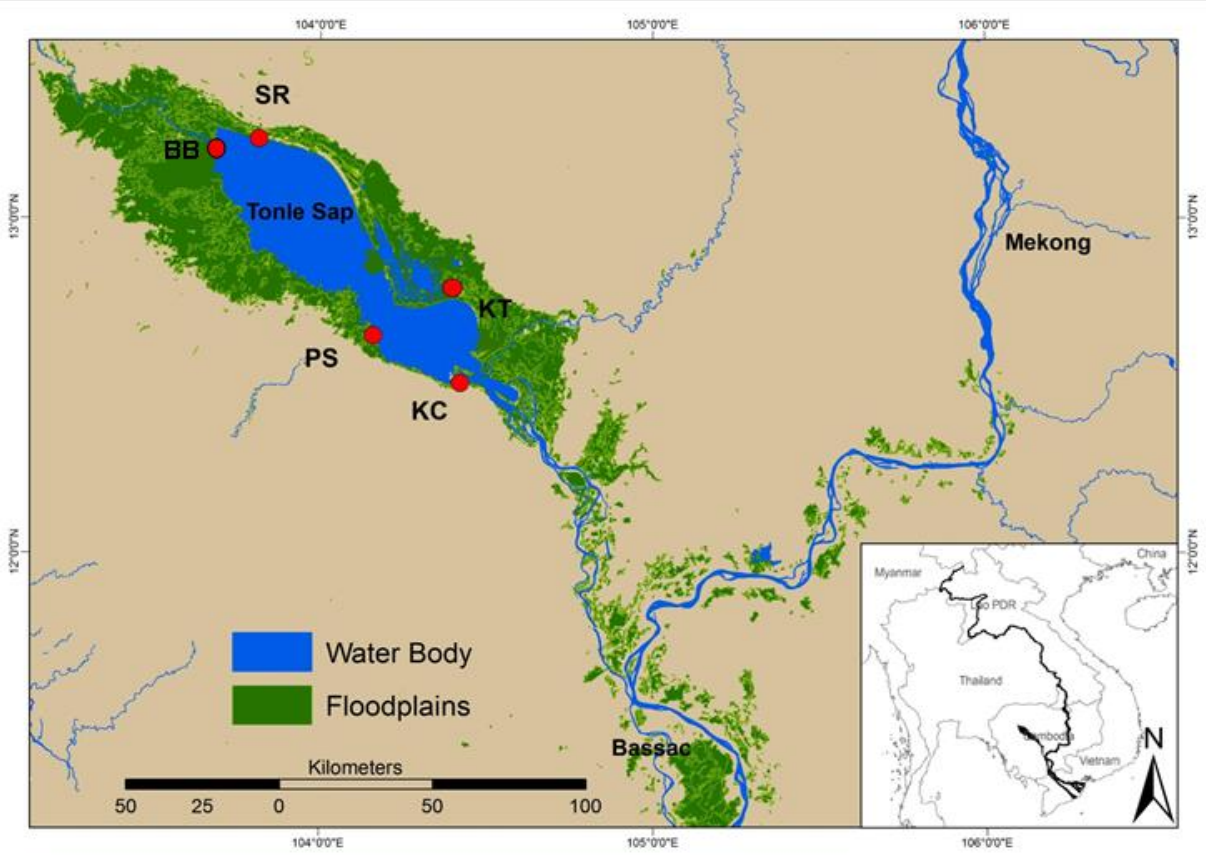
Parachela maculicauda	Pama	1	1	NM
Parambassi wolffi	Pawo	1	2	NM
Parambassis apogonoides	Paap	1	2	NM
Pristolepis fasciata	Prfa	1	3	NM
Puntioplites proctozysron	Pupr	3	4	NM
Ompok bimaculatus	Ombi	1	2	NM
Osteochilus.melanople	Osme	4	4	M
Oxyeleotris marmorata	Oxma	1	2	NM
Pangasianodon hypophthalmus	Pahy	3	4	M
Pangasius.larnaudii	Pala	3	4	M
Poropuntius deauratus	Pode	3	4	M
Rasbora tornieri	Rato	3	4	NM
Trichohodus trichopterus	Trtr	1	4	NM
Thynnichthys thynnoides	Thth	3	4	M
Trichopodus microlepis	Trmi	1	4	NM
Xenentodon cancila	Xeca	4	5	M

Figure legends

Figure 1. Location of the five sampling sites within the Tonle Sap Lake. SR = Siem Reap; BB = Battambang; KC = Kampong Chhnang; KT = Kampong Thom; PS = Pursat.

Figure 2. Bubble plot of Seasonal variations in (a) species occurrence, (b) species abundance, each bubble value represents the weekly catch according to hydrological cycles (c) NMDS biplot indicates species assemblages, and (d) Hierarchical clustering based on abundance dissimilarities. Species abbreviation are in table S1.

Figure 3. Overall head map of pairwise species co-occurrence from the probabilistic model according to the four hydrological cycles. Species names are positioned to indicate the columns and rows that represent their pairwise relationships with other species. Abbreviation species are in table S1. Species in red point to migratory species. Rising = season, HW= High water level season, DW= Decrease water level season and LW= Low water level season.


104°0'0"E
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Myanmar
Thailand
Vietnam
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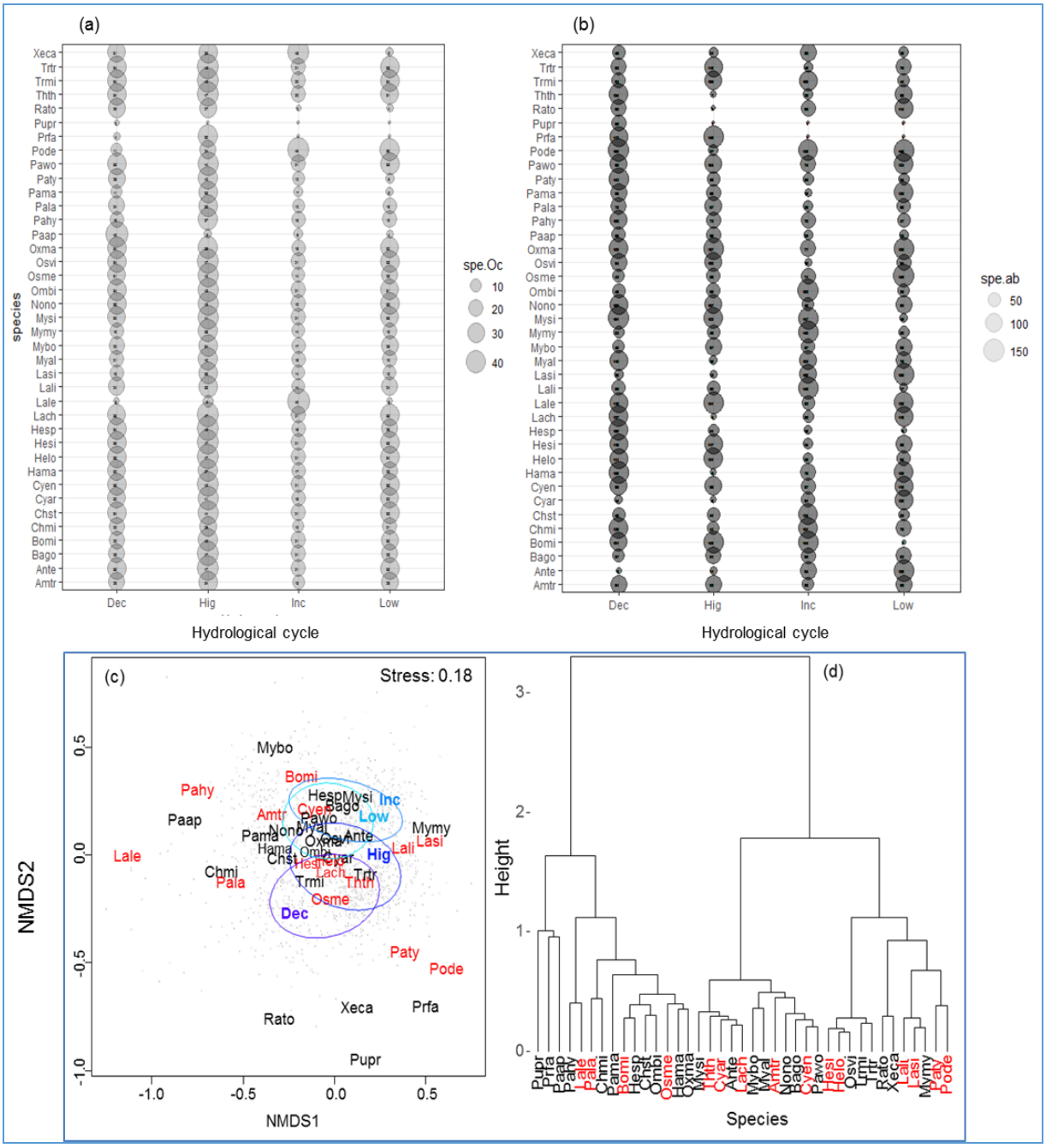
Figure 1.


(a)
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species
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NMDS1
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Figure 2.

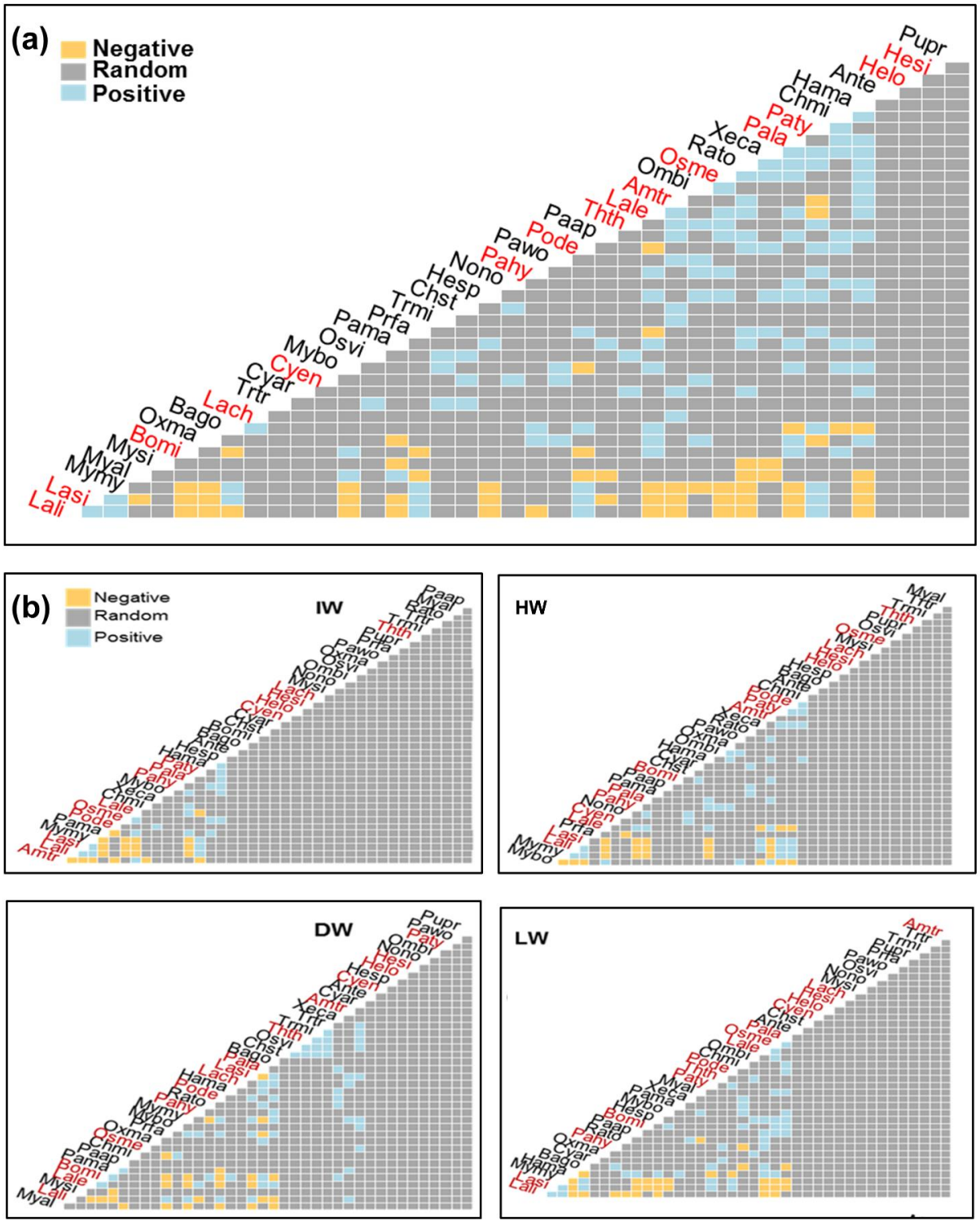

Figure 3.

Seasonal omnivory: the response of consumer trophic position to fluctuating environments

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[Ecology- In Revision]

Abstract

The implications of seasonality on food web structure have been notoriously understudied in empirical ecology. Here, we focus on seasonal changes in one key attribute of a food web, vertical trophic position of consumers. We ask whether tropical floodplain fishes behave as seasonal omnivores, by shifting their trophic positions in relation to the annual flood pulse, or whether they feed as static omnivores, at the same trophic position all year, as much empirical work implicitly assumes. Using ratios of nitrogen stable isotopes ($\delta^{15}N$) for 28 species, we find evidence within the Tonle Sap Lake, Cambodia, that fishes shift towards lower trophic positions during the wet season. Available fish dietary data from the Tonle Sap and a literature review suggest that increased exploitation of plants and/or invertebrates could explain this finding. However, the large variation in seasonal trophic position shifts observed among species (ranging from -0.51 to +0.64 trophic levels from the dry to the wet season) argues that diverse behavioral responses to seasonality could be central for re-routing energy flow in these dynamic ecosystems. Based on existing literature, seasonal omnivory appears widespread in other taxa and ecosystems, and warrants further study given its potential influence on food web dynamics in fluctuating environments.

Keyword: Food web, web dynamic, tropic level, stable isotope and tropic level

Introduction

Most ecosystems are characterized by seasonal variation in physical conditions (temperature, light, precipitation) that influences resource availability for organisms. The consequences of seasonal environmental variation for food web patterns and processes remain poorly understood, although this topic has garnered increasing interest among both aquatic and terrestrial ecologists (CaraDonna et al. 2017, Hampton et al. 2017, McMeans et al. 2015). Recent empirical and theoretical work argues that consumer trophic position and extent of food-chain omnivory (i.e., feeding on more than one trophic level) can vary across spatial gradients. For example, fish trophic position increases from small to large lakes in response to changes in resource availability (Post and Takimoto 2007, Tunney et al. 2012). Such adaptive foraging should promote food web stability based on theory (Kondoh 2003, McCann et al. 2005). While much of this work implicitly assumes that the extent of omnivory within any given system remains static through time, emerging evidence indicates that consumer trophic position often changes on an inter-annual (Ruiz-Cooley et al. 2017) and seasonal basis (Akin and Winemiller 2006, McMeans et al. 2015). Changes in omnivory through time could have equally important consequences as those recognized in space for food web structure and stability (Takimoto et al. 2002, Křivan and Diehl 2005, Kratina et al. 2012). Therefore, it remains important to explore if and how consumer trophic positions respond to temporal variation in nature, especially given that climate change is already altering existing seasonal signals in many of Earth's ecosystems (Wolkovich et al. 2014).

Here, we examine tropical river floodplains as a model system to investigate the response of fish trophic position to regular variation in the environment. Although seasonal diet data for fish are generally rare, they are more common for wet-dry periods in tropical systems than for summer-winter periods in temperate and arctic systems. We use ratios of stable isotopes of nitrogen ($\delta^{15}N$) to identify the magnitude and direction of trophic position shifts in 28 fish species sampled from the Tonle Sap in Cambodia (a huge fluvial system in

the Lower Mekong Basin) that span a range of body sizes. We then analyze dietary composition associated with trophic position shifts for 4 common carnivorous fishes that consume both invertebrates and fish using stomach contents data. We also evaluated dietary patterns for species from other tropical floodplain systems using data obtained from the literature. Use of combined $\delta^{15}N$ and dietary data provides a more comprehensive assessment of trophic ecology than use of either approach alone (Rybczynski et al. 2008). Recent work indicates that fishes in the Tonle Sap (Pool et al. 2017) and other tropical floodplains (e.g., Wantzen et al. 2002) become more generalized feeders with broader isotopic niches ($\delta^{15}N$ and $\delta^{13}C$) during the wet season. In some tropical rivers, seasonal floodplain inundation stimulates nutrient mineralization and aquatic primary and secondary invertebrate production (Junk et al. 1989); however, flooding can dilute dissolved inorganic nutrients and reduce aquatic primary production in tropical oligotrophic rivers (Cotner et al. 2006). Flood pulse recession, on the other hand, strands aquatic vegetation (Bayley 1988) and increases per-unit-area densities of fishes, which increases foraging efficiency of piscivores (Winemiller 1989, Wantzen et al. 2002). Given these seasonal dynamics, we test the hypothesis that during the wet season in floodplain systems, fishes capable of consuming both invertebrates and fish will broaden their diet to increasingly include invertebrates, resulting in shifts to lower trophic positions. Although based on tropical floodplains, our findings are broadly relevant for other ecosystems that undergo seasonal shifts in basal resources.

Methods

The Tonle Sap in Cambodia is the largest lake in the Mekong River Basin and Southeast Asia. This relatively shallow lake (maximum depth 15 m) experiences a single flood pulse annually (wet season: July to October, dry season November to June) (Kong et al. 2017). Stable isotope and stomach contents data were collected as part of a broader research effort involving surveys at multiple locations around the Tonle Sap (Siem Reap,

Kampong Chhnang, Kampong Thom and Pursat Provinces; see Pool et al. 2017) during both seasons. Tissue for stable isotopes were collected from 28 fish species (Table S1) sampled from November 2010 to April 2015 using multi-panel gill nets or by purchasing fish from local fishers or lakeside markets. Samples of aquatic invertebrate taxa used as baseline indicators of benthic and pelagic secondary production were sampled with dip nets and plankton nets (see Appendix 1 for details). All samples were dried, homogenized and weighed into tin capsules before being analyzed for $\delta^{15}N$ via a Costech ECS 4010 Elemental Analyzer coupled to a ThermoFinnigan MAT 253 isotope ratio mass spectrometer. Stable isotopes are expressed as delta values (δ) in permil (‰) relative to the international standard for nitrogen (atmospheric air). To identify the dietary drivers of observed seasonal shifts in $\delta^{15}N$-based trophic positions, stomach contents data were analyzed for 4 fish species (Table 1) that are considered piscivores with flexible diets that can include invertebrates. These data were collected from specimens sampled during July 2014-April 2015 (Kong et al. 2017) and are reported as the proportion of fish, invertebrate and plant material by weight relative to total stomach contents weight (see Appendix 1 for more detail). Fish with completely empty stomachs were excluded (see Table S2 for sample size and body lengths).

We applied the following single source equation to calculate fish trophic positions

(Eqn 1) $TP_{consumer} = 2 + \delta^{15}N_{consumer} - \delta^{15}N_{baseline} / TDF$

where $\delta^{15}N_{baseline}$ is the mean $\delta^{15}N$ of all baseline samples (primary consumers) in each season (5.92 ‰ in the wet season, 6.15 ‰ in the dry season; Table S3) and $\delta^{15}N_{consumer}$ is the $\delta^{15}N$ value for an individual fish. TDF (trophic discrimination factor) is scaled to account for lower discrimination in strictly carnivorous vs. more omnivorous fish (see Appendix 1 for details). The seasonal shift in trophic position was calculated for each of the 28 species as the mean dry minus the mean wet trophic positon. Positive values, therefore, supported our prediction of lower trophic positions in the wet season. Effect sizes with pooled standard deviations and 95% confidence intervals (Coe 2002) were calculated to explore variation

around mean values for trophic position shifts. We then explored how the mean shift in seasonal trophic position related to mean body size across the 28 species using quadratic regression. Seasonal changes in each of the three stomach contents response variables (proportional weight of invertebrate, fish and plant material) were then explored using data for individual fish belonging to each of the 4 species, and analyzed using zero-inflated beta regression (due to the presence of zeros in the data) in R package zoib (Liu and Kong 2015, see Appendix 1 for detail). We included season (wet, dry) and total body length as explanatory variables, and included both species and sampling location as random intercepts.

To determine whether findings from the Tonle Sap are consistent with evidence from other tropical floodplains, we reviewed literature accounts to obtain fish trophic data recorded during different phases of the annual flood pulse. We focused this analysis on piscivores, especially those that sometimes include invertebrates in their diet. Each report for a single species or trophic guild constituted a single 'evidence item', with a total of 29 evidence items extracted from the 10 data sources that met our inclusion criteria (see Appendix 1 for details).

Results

Tonle Sap fishes

Seasonal shifts in trophic position (mean dry – mean wet, for each of the 28 species) ranged from -0.51 to 0.64 and exhibited a hump-shaped relationship with mean body length based on quadratic regression (Fig. 1A), but was not statistically significant (P=0.08). Nonetheless, 8 species had seasonal trophic position shifts whose effect size ± 95% CI did not cross zero (Fig. 1A, Table S1), and these 8 species followed the trend indicated by the quadratic regression. Specifically, mid-sized species (body size 108 to 220 mm) shifted towards lower wet-season trophic positions (positive values in Fig. 1A), whereas smaller and larger species exhibited the opposite trend (negative values in Fig. 1A). Baseline aquatic

invertebrates (Table S3) and terrestrial invertebrates (e.g. spiders, beetles; data not shown) had lower $\delta^{15}N$ values than the 28 fish species from the Tonle Sap (Table S1), confirming that greater consumption of invertebrates reduces trophic position in this system.

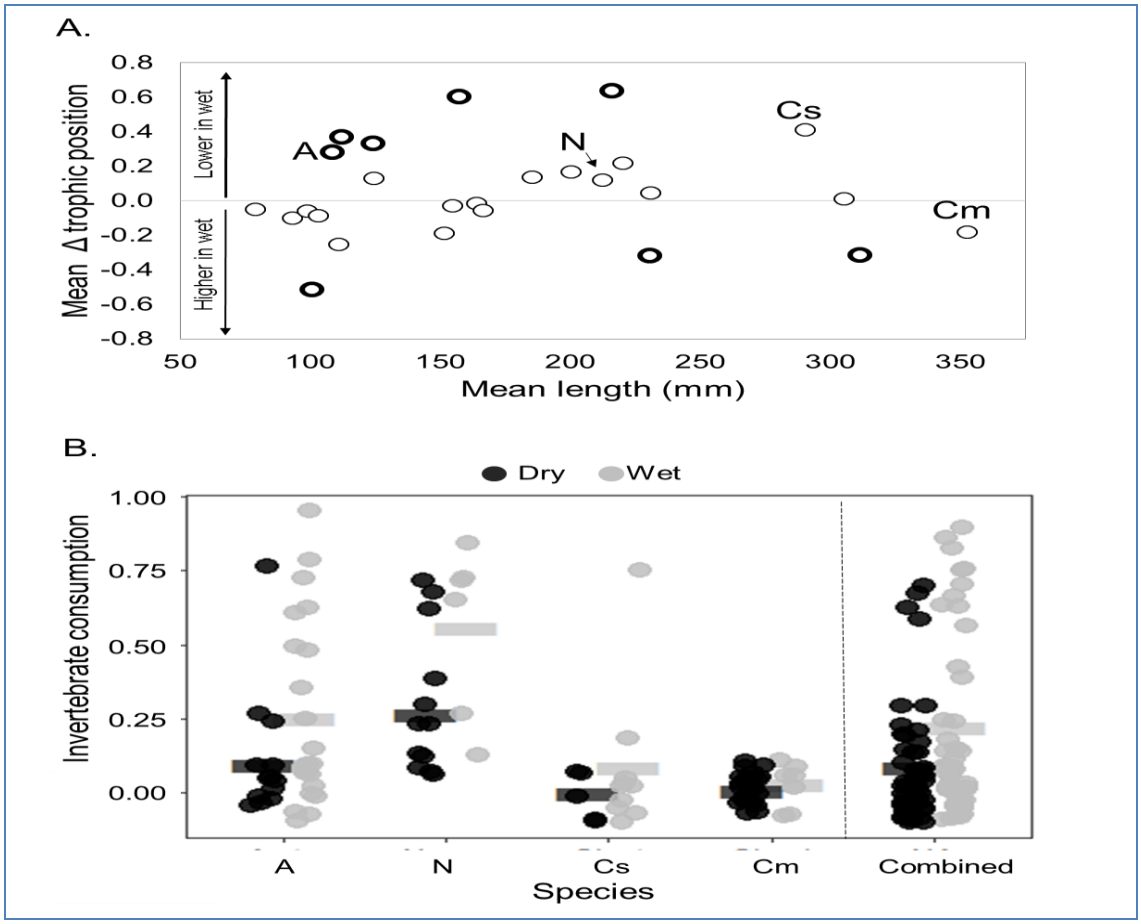

Fig. 1. A) Shift in the mean trophic position between seasons (i.e. mean dry – mean wet) for 28 Tonle Sap species spanning a range in body sizes (mean total length, mm). Species with large and significant seasonal shifts in trophic position (i.e. effect sizes whose 95% CI did not bound zero, Table S1) are indicated by symbols with thick black borders. Species with accompanying stomach contents data are abbreviated as follows: A= *Anabas testudineus*, N= *Notopterus notopterus*, Cs=*Channa striata*, Cm= *Channa micropeltes*. The grey line on represents zero shift in seasonal trophic position. B) Proportional consumption of invertebrates (by weight relative to total stomach contents) for specimens of four fish species (left) and combined data across species (right) during wet and dry seasons. Data points are jittered as per Weissberger et al. (2015) to reveal the presence of zeros. Mean invertebrate consumption by each species during each season is shown as a bar.

For the 4 species with stomach contents data, diets were dominated by fish and invertebrates with some plant material present (Table S2). Zero-inflated beta regression revealed that the probability of invertebrates being eaten increased during the wet season

and decreased with fish length. This is indicated by the parameter b0[2] (Table S4), which shows a significant negative effect on the probability of zero (i.e. nothing is eaten), whereas length had a negative effect on the probability of invertebrate consumption (b[2] in Table S4). Thus, smaller fish (i.e. *Anabas testudineus* and *Notopterus notopterus*) consumed significantly more invertebrates than larger, more piscivorous fish (i.e. *Channa* spp.), and the probability of invertebrates being eaten was significantly higher during the wet season (Fig. 1B). Season did not have a significant effect on the probably of plants or fish being eaten (Table S4).

Result of literature review

Out of the 29 evidence items, seasonal diet information was provided for 28 cases and $\delta^{15}N$ values were provided for 1 case (Table 1). Eleven evidence items supported the hypothesis of increased plant or invertebrate consumption during the wet-season flood pulse (Table 1). For the remaining 18 evidence items, 5 cases reported increased consumption of plants and invertebrates during the dry season or increased consumption of fish during the wet season (the opposite of our prediction), and 13 cases reported fish dominating the diet throughout the year. For classification purposes, we refer to species as 'omnivores' when their stomachs contained multiple prey types (invertebrates or plants and fish) and 'piscivores' when their stomachs contained >97% fish. Maximum body sizes of each species reported in the literature (actual body lengths of fish sampled in each study were not always provided for comparison) were smaller in omnivores (mean ± SD = 43 ± 71 and 21 ± 15 cm with and without *Wallago attu*, a large food-chain omnivore, respectively; Table 3) than piscivores (55 ± 23 cm; Table 1). This pattern derived from the broader literature, whereby predators that predominantly reduced their trophic position in the wet season were smaller-bodied than those that fed on different types of fish all year, agrees with the pattern revealed by Tonle Sap isotopic data (Fig. 1A).

Table 1. Data extracted from a literature review performed to explore seasonal diet changes in tropical floodplain piscivorous food-chain omnivores. Reported maximum total body length (cm), dominant prey items and quantitative contribution to diet, when provided, are reported for each study, as is whether each study provided support for our hypothesis (i.e. lower trophic positions in the wet vs. dry season) or no support (no difference in trophic position or higher trophic positions in the wet season). References 5 and 8 classified fish prey by species and the functional group of the main fish prey consumed is provided in parentheses. Species with multiple prey types (fish plus invertebrates and/or plants) are noted as food chain-omnivores 'O' and species with >97% fish in their stomachs are listed as piscivores 'P'.

Species	Max. length	Dry season diet	Wet season diet	Lower TP in wet?	O or P	Ref.
Fish community	NA	Significantly higher $\delta^{15}N$ by 1.45‰	Lower $\delta^{15}N$	Support	NA	1
Fish community	NA	5% aquatic inverts, 20% fish	18% aquatic inverts, 10% fish	Support	NA	2
Fish community	NA	Fish prey dominate	Plant and invertebrate prey dominate	Support	NA	3
Fish community	NA	29% invert., 25% detritus, 20%fish	30% invert., 17% detritus, 23% fish	No support	NA	4
Serrasalminae sp.	NA	Fish	Terrestrial plant matter and fish	Support	O	5
Hemigrammus marginatus	4.5	73% fish, 24% plant, 0.2% invert.	0% fish, 20% plant, 60% invert.	Support	O	6
Moenkhausia collettii	5	Invertebrates and fish	Invertebrates	Support	O	5
Hypselecara coryphaenoides	16	Fish	Invertebrates	Support	O	5
Serrasalmus marginatus	27	99% fish, 1% detritus	93% fish, 7% invert.	Support	P	6
Serrasalmus gouldingi	28	64% fish, 12% fruits/seeds,10% rthropods	45% fish, 40% fruits/seeds, 8% arthropods	Support	O	7
Hoplarchus psittacus	32	Fish	Aquatic invert. and fish	Support	O	5
Pimelodus maculatus	51	50% fish, 25% plants	32% fish, 57% plants	Support	O	6
Aphyocharax dentatus	7.2	33% invert., 16% fish	5% invert., 87% fish	No support	O	6
Pimelodella gracilis	18	21% plants, 15% fish, 14% invert.	2% plant, 67% fish, 26% invert.	No support	O	6
Pimelodus argenteus	25	39% plant, 18% invert., 10% fish	36% plant, 11% invert., 38% fish	No support	O	6
Acestrorhynchus lacustris	27	100% fish (herbivores)	100% fish (omnivores, herbivores)	No support	P	8
Acestrorhynchus lacustris	27	100% fish (herbivores)	100% fish (omnivores)	No support	P	8
Acestrorhynchus pantaneiro	35	100% fish	100% fish	No support	P	6

Plagioscion Ternetzi	39	100% fish	97% fish	No support	P	6
Hepsetus odoe	44	100% fish (omnivores)	100% fish (omnivores)	No support	P	9
Pygocentrus nattereri	50	100% fish	99% fish, 1% plant	No support	P	6
Hoplias malabaricus	65	100% fish (omnivores)	100% fish (piscivores)	No support	P	8
Hoplias malabaricus	65	100% fish (piscivores)	100% fish (omnivores)	No support	P	8
Cichla monoculus	70	93% fish, 7% plant	100% fish	No support	P	10
Hydrocynus forskahlii	78	100% fish (omnivores)	100% fish (piscivores, omnivores)	No support	P	9
Rhaphiodon vulpinus	80	100% fish	100% fish	No support	P	6
Salminus Brasiliensis	100	95% fish, 5% invert.	100% fish	No support	P	6
Wallago attu	240	10% fish, 30% prawn (during January)	30% fish, 0% prawn (during July)	No support	O	11

References: 1. Wantzen et al. 2002 (Pantanal wetland, Brazil); 2. Winemiller 1989 (Venezuelan Llanos); 3. Peterson 1997 (Venezuelan Llanos); 4. de Merona and Rankin-de-Merona 2004 (lago de Rei, Amazon); 5. Goulding 1988 (Rio Negro, Amazon); 6 Novakowski et al. 2008 (Pantanal wetland, Brazil); 7. Prudente et al. 2016 (Anapu River, Brazil); 8. Almeida et al. 1997 (Pantanal wetland, Brazil); 9. Winemiller and Kelso-Winemiller 1994 (Upper Zambezi, Zambia); 10. Oliveria et al. 2006 (Amazon River); 11. Islam et al. 2006 (Bangladesh)

Discussion

The major finding of our study is that food-chain omnivory can be dynamic, with diets shifting to varying degrees in response to seasonal variation in environmental conditions and resource availability. In tropical floodplain ecosystems, fish trophic positions shift in response to seasonal patterns of hydrology. The vertical trophic position of most omnivorous fishes declined during the wet-season flood pulse. Many fish are capable of exploiting multiple food resources, but may track the most profitable food types when these are abundant during certain periods or within certain habitats (Winemiller 1989, Correa and Winemiller 2014). Larger piscivorous species, on the other hand, fed predominantly on fish throughout year and either increased or decreased their trophic position during the wet season. These large piscivores could also have tracked temporal and/or spatial variation in fish prey availability (e.g. Almeida et al. 1997). Interestingly, variation in trophic responses was large and not all species followed the same trend. Diverse feeding responses among coexisting species appears common in fish assemblages of tropical floodplains (Winemiller 1989, Wantzen et al. 2002, Correa and Winemiller 2014) and may be important for the 'dynamic stability' (Leigh et al. 2010) and resiliency of these complex systems (Pettit et al. 2017). Our findings, combined with existing knowledge, suggest that seasonal omnivory could play a currently underappreciated role in sustaining energy and nutrient flow across changing conditions.

Based on combined stable isotope and stomach contents data, mid-sized omnivorous fishes from the Tonle Sap (i.e. *A. testudinus* and *N. notopterus*) reduced their trophic position and increased their consumption of invertebrates during the wet season. Five additional Tonle Sap species also showed large reductions (effect size that did not bound zero) in wet-season trophic positions, and 11 out of 16 literature reports for omnivores or entire fish assemblages showed increased consumption of plants or invertebrates during the wet season. Reduced wet-season trophic positions therefore appear common among omnivorous fishes of tropical floodplains. Species identified as strict piscivores, on the other hand, consumed fish almost exclusively throughout year. These piscivores likely possess

morphological and behavioral traits that enable them to feed efficiently on fish while compromising foraging efficiency for other food resources (Almeida et al. 1997). Variable responses among piscivores to the flood pulse are consistent with previous studies that inferred piscivores track alternative fish prey depending on foraging tactics and habitat (Almeida et al. 1997, Winemiller and Kelso-Winemiller 1994, Peterson 1997). For example, sit-and-wait piscivores can exploit abundant juvenile fishes during the wet season by using vegetation as cover, whereas stalk-and-chase predators may be more efficient predators as water levels fall and prey encounter rates peak (Peterson 1997). In South American floodplain, the tooth-snouted glass tetra, *Roeboides dayi* (Characidae), fed heavily on aquatic invertebrates when they were abundant during the wet season, and specialized on scales during the dry season when fishes were concentrated in shrinking pools (Winemiller 1989, Peterson & Winemiller 1997). While we focused on piscivores that also feed on invertebrates and sometimes even plant matter (i.e., piscivores that are food chain-omnivores), other functional groups are also alter their trophic positions seasonally. For example, small omnivorous fishes, such as *Hemigrammus* spp. (total length <11 cm) and other tetras, can shift from feeding mostly on plant matter in the dry season to invertebrates during the flood pulse (Peterson 1997, Goulding et al. 1988). This tracking of invertebrate abundance could explain higher trophic positions observed during the wet season for some Tonle Sap fishes (Fig. 1). Based on these combined findings, it appears that fish perceive seasonal fluctuations in the abundance of alternative food resources differently, and most fishes are capable of responding by altering their diet and trophic position.

A positive relationship between trophic position and body size is not anticipated across entire tropical floodplain fish assemblages (Ou et al. 2017) because some herbivores and omnivores are large (e.g. the giant Mekong catfish, *Pangasianodon gigas*, is an omnivore, max. size = 300 cm; Rainboth 1996) and some species with high trophic positions are small (e.g. African pike, *Hepsetus odoe,* as small as 10 cm were strongly piscivorous; Winemiller and Kelso-Winemiller 1994). Body size was also not a significant predictor of the direction of

seasonal trophic position shifts in the Tonle Sap (P=0.08), and not all fishes followed our prediction of reduced wet season trophic positions (Fig. 1A, Table 1). Variation in seasonal diet shifts among floodplain fishes has been previously demonstrated by other studies using stable isotope (Wantzen et al. 2002) or dietary analysis (e.g. Winemiller 1989, Novakowski et al. 2008, Mérona and Rankin-de-Mérona 2004). The habitat heterogeneity of these systems and high variation among observed $\delta^{15}N$ values within and among species, further stresses the importance of considering dietary data along with $\delta^{15}N$-based estimates of trophic position. However, the general trophic patterns in relation to hydrologic seasonality uncovered here, in spite of the complexity and dynamic nature of tropical floodplain ecosystems (Pettit et al. 2017), prompt us to consider further how seasonal omnivory could influence food web structure and stability.

The magnitude of seasonal trophic position changes reported here (plus or minus approximately half a trophic level) reflects changes in fish foraging behavior with consequences for food web structure, as well as individual fitness. For example, a shift from eating 100% fish to eating 50% fish and 50% invertebrates (i.e. a reduction in trophic position of ~ 0.5) would likely change the number and strength of species interactions in the food web as well as the activity costs and growth of individual fish (Sherwood et al. 2002). Such temporally dynamic omnivory could also have consequences for stability. One theoretical study suggests that 'adaptive' omnivory, whereby consumers incorporate lower trophic level prey into their diet when preferred prey become rare, slightly increases stability relative to the case of fixed omnivory (Křivan and Diehl 2005). Prey refugia, prey defense, stage-structured cannibalism, and adaptive foraging are all mechanisms that are thought to maintain omnivory at weak to intermediate interaction strengths in nature, and thus prevent strong and destabilizing omnivory (Kratina et al. 2012). Although not well considered theoretically, flexible food web properties, like omnivory, could be extremely important for stability in non-equillibrim or periodically forced systems (McCann and Rooney 2009).

Temporally changing trophic positions also arise in other taxa and ecosystems, including stream macroinvertebrates (Hellmann et al. 2013), birds (Nakano and Murakami 2001) and desert mammals (Soykan and Sabo 2009). Consumer trophic positions can also remain static through time (Rybczynski et al. 2008). Temporal omnivory therefore appears variable in its direction and magnitude of change, a conclusion consistent with our findings from tropical floodplains. One could further consider how the location of a particular species in Fig. 1A would change depending on body size (e.g. throughout ontogeny) and how the capacity for seasonal omnivory differs among functional groups (e.g. omnivores vs. detritivores, Wantzen et al. 2002) and ecosystem types (e.g. between summer and winter in temperate or arctic systems), and how this variation influences food web structure and stability.

Conclusions

Vertical trophic position and the related concept of food-chain omnivory are key attributes that influence food web stability and functions (McCann et al. 2005, Winemiller et al. 2014, Post and Takimoto 2007). Our findings for fishes inhabiting tropical floodplains revealed that food-chain omnivory is dynamic in response to seasonal hydrology. Seasonal shifts in trophic ecology are not unique to tropical fishes or floodplains. Knowledge about how species and ecosystems respond to seasonality is crucial for anticipating the consequences of climate change. Organisms capable of dynamic omnivory on seasonal time scales, for example, could be particularly important for sustaining ecosystem functioning in the face of changing conditions (Takimoto et al. 2002, McMeans et al. 2016). Further, maintenance of species spanning a range of trophic responses, as observed among fishes in tropical floodplains, could play an important role in buffering local communities from perturbations.

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Appendix 1. Detailed methods of sample collection and data analysis

Stomach contents data collection

Data collection was carried out under the collaborative work with the Inland Freshwater Research and Development Institute (IFReDI) of Cambodia, which is part of the Fisheries Administration (FiA). Two species (*Labeo chrysophekadion* and *Cyclocheilichthys enoplos*) were excluded due to low sample sizes (<5 individuals in a single season) and *Boesemania microlepis* was excluded because fish sampled in the dry season were significantly larger than wet season samples, precluding our ability to separate the effect of length from season on diet composition. Stomachs were removed and food items were identified as plant (identifiable material equalled seeds and roots), invertebrate (sum proportions of the individual taxa: Decapoda, Nematoda, Bivalvia, Coleoptera, Trichoptera, Odonata, Orthoptera, Gastropoda, Ephemeroptera, Hemiptera, Diptera, and unidentified aquatic insects), or fish. Wet weight was measured by gently blotting fluid from the surface of the food item with tissues paper and then weighing the item on an electronic balance to the nearest 0.01 mg.

Stable isotope analysis – baseline sampling and correction.

Snails and crabs (primary consumers of benthic primary production) and mussels and clams (primary consumers of water-column primary production) were sampled with dip nets. Zooplankton (primary consumers of water-column primary production) were sampled with plankton nets. Soft tissues of molluscs and crabs were removed for isotopic analysis, and zooplankton tissue was analyzed as bulk samples containing whole organisms.

Values of $\delta^{15}N$ varied less between benthic and pelagic baseline organisms and between seasons compared to $\delta^{13}C$ (not included here), which showed large differences between benthic and pelagic baselines in the wet season, but converged in the dry season (Table S3). Because the Tonle Sap Lake is a biogeochemically and spatially complex system, and we were interested in general patterns across the entire lake, we took the mean

$\delta^{15}N$ values across all baseline organisms (i.e. all benthic and pelagic for each season, Table S3) to capture the fact that: 1) fish are presumably mobile across sampled sites and regions given the known capacity of many to migrate horizontally or longitudinally, and 2) there is a high potential for fish to forage on both benthic and pelagic prey because this is a shallow lake (maximum lake depth is 1 and 15 m in the dry and wet season, respectively).

Stable isotope analysis – trophic discrimination factor

Individual trophic position was calculated from tissue $\delta^{15}N$ using a modified procedure based on Bastos et al. (2017). Specifically, given that TDF can increase with the contribution of plant material in the diet (Bastos et al. 2017), we modeled the trophic discrimination factor (TDF) as an exponential function of estimated relative piscivory. Here the assumptions are: 1) fish consuming plants will have a higher TDF than carnivorous fish, and 2) as individual $\delta^{15}N$ increases, the proportion of carnivory increases, eventually saturating at 100%. TEF_{carn} and TEF_{plant} (mean ± 1SD) were characterized from the recent meta-analysis by Bastos et al (2017). Uncertainty in those parameters were incorporated into the final TL calculation by running 1000 Monte Carlo simulation trials. Lastly, there are no direct measurement for the decay constant (*k*). We estimated this value to be approximately 1 based on general coherence between our estimates and those from Fishbase for species where data were available. Following the procedure of scaling TDF values, we confirmed that using a standard TDF of 3.4‰ (Post 2002) produced the same qualitative results.

Stable isotope analysis - consideration of turnover time

Estimated isotopic turnover time (half life) for each individual fish, based on their body mass (g), calculated using the equation for vertebrate ectotherm muscle provided by Vander Zanden et al. (2015) ranged from 34 to 140 days. We subtracted these half life estimates from the sampling date for each individual fish and used these isotope-adjusted dates to assign fish into the wet or dry season. In almost all cases, the sampling date and isotope adjusted date fell within the same season. Only fish sampled in July (the early wet season)

were re-assigned to the dry season, and fish sampled in November and December (the early dry season) were re-assigned to the wet season, because their isotopic signal was assumed to be more reflective of the season that preceded their date of capture.

Stomach content analysis using zoib

We modeled each of the 3 response variables using zero-inflated beta regression, in which likelihood is defined as a joint probability of two components: probability of observation's being zero and that, under beta distribution, the observation is not zero (Lui and Kong 2015). In the model, each of the probability components are modeled with linear combination of explanatory variables with logit link function. We used season (wet, dry) and body length as explanatory variables for both of the 2 components. The model is estimated using R package zoib and given the low sample sizes for each species in each season, all species are analyzed at once in the same model and species identity is added as a random intercept to control species specific responses.

Literature review

The literature review was carried out following the protocol of the Collaboration for Environmental Evidence (2013). The literature search was conducted in December 2016 and updated in November 2017 using the ISI web of science search engine and the search term combination "(food* OR diet*) AND tropical AND floodplain AND season*", which returned 85 studies. The inclusion criteria for each article in our systematic review was that each study: 1) be conducted in a large tropical floodplain river, 2) be conducted in a system with a single annual flood, characterized by sinusoidal hydrography, 3) provide diet information either for individual piscivore species or for the whole fish community that included piscivores, 4) included data for both the wet period and the dry period, and 5) be written in English. Of the 85 studies reviewed, only 3 met these criteria. An additional 4 articles that met our criteria were identified from the bibliographies of these studies, and 2 other articles, 1 book and 1 graduate thesis, were identified to produce a total of 11 data sources. Each report for a

single fish or fish community constituted a single ‘evidence item’ with a total of 29 evidence items extracted from the 11 data sources identified that met our inclusion criteria.

Table S1. Total body length (mm), seasonal shift (Δ) and effect size (±95% confidence intervals) of the Δ in trophic position (calculated as mean dry – mean wet trophic position) for 28 species from the Tonle Sap Lake. Species with bold values had effect sizes ± 95% CI that did not bound zero. Sample size (n) and total length in each season, and the putative functional group for each species based on previous diet data, is also provided ('Pisc. Omn.' are piscivorous omnivores that consume large amounts of both invertebrates and fish).

Species	Functional group	Mean length	Seasonal Δ trophic position	Effect size	± 95% CI	n dry	n wet	Mean $\delta^{15}N$ dry	Mean $\delta^{15}N$ wet	Mean dry length	Mean wet length
Trichopodus trichopterus	Omnivore	79	-0.05	-0.13	0.80	10	15	7.54	7.61	91	71
Rasbora aurotaenia	Omnivore	93	-0.10	-0.39	0.92	8	11	8.80	9.12	101	88
Pristolepis fasciata	Invertivore	99	-0.06	-0.19	0.62	16	27	9.30	9.52	96	100
Trichopodus microlepis	Omnivore	101	-0.51	-2.45	1.19	9	10	7.03	8.62	108	94
Paralaubuca typus	Invertivore	103	-0.08	-0.31	0.94	5	37	9.27	9.57	105	103
Anabas testudineus	Pisc. Omn.	108	0.28	0.99	0.93	11	9	9.12	8.19	114	101
Henicorhynchus siamensis	Detritivore	111	-0.25	-0.67	0.72	9	48	7.07	7.78	137	106
Thynnichthys thynnoides	Omnivore	112	0.37	1.53	0.79	9	39	8.19	6.90	120	110
Labiobarbus leptocheila	Omnivore	124	0.33	0.98	0.85	8	22	8.49	7.34	135	120
Parambassis wolffii	Piscivore	124	0.13	0.53	0.73	16	14	11.91	11.69	119	130
Barbonymus gonionotus	Omnivore	151	-0.19	-0.52	0.64	12	50	7.97	8.53	194	141
Mystus albolineatus	Pisc. Omn.	155	-0.03	-0.13	0.74	13	15	9.95	10.11	164	146
Osteochilus melanopleura	Omnivore	157	0.61	2.38	1.16	8	12	9.55	7.57	189	135
Puntioplites proctozysron	Omnivore	164	-0.01	-0.03	0.82	16	9	9.25	9.31	160	170
Ompok bimaculatus	Omnivore	166	-0.06	-0.19	0.98	12	6	9.73	9.97	164	171
Hemibagrus spilopterus	Invertivore	185	0.14	0.41	0.66	12	35	10.76	10.42	219	174
Macrognathus siamensis	Invertivore	200	0.17	0.45	0.91	12	8	8.56	7.99	204	194
Notopterus notopterus	Pisc. Omn.	212	0.12	0.34	0.82	14	10	9.98	9.64	206	220
Kryptopterus apogon	Piscivore	216	0.64	2.21	1.07	13	9	11.49	9.53	229	197
Clarias macrocephalus	Omnivore	220	0.22	0.81	1.04	15	5	8.92	8.18	233	182
Cyclocheilichthys enoplos	Omnivore	230	-0.32	-0.87	0.71	15	19	8.33	9.34	262	206
Labeo chrysophekadion	Detritivore	231	0.05	0.15	0.80	11	13	8.00	7.79	297	175

Channa striata	Piscivore	290	0.41	0.69	0.84	16	9	10.55	9.29	322	234
Pangasius larnaudii	Omnivore	305	0.01	0.04	0.86	7	20	10.84	10.94	343	292
Boesemania microlepis	Piscivore	311	-0.31	-1.02	0.88	13	10	11.56	12.78	321	298
Channa micropeltes	Piscivore	353	-0.18	-0.46	0.95	16	6	9.00	9.62	370	307

Table S2. Sample size (n) and total body length (mm) for fish sampled during each season for stomach content analysis from the Tonle Sap lake, Cambodia. Proportions of fish, invertebrates and plants in the stomach contents by weight. All values are mean ± SD.

Species	Season	Stomach content data				
		n	Length (mm)	Fish	Invert.	Plant
Anabas testudineus	Dry	13	122 ± 14	0.52 ± 0.22	0.10 ± 0.22	0.12 ± 0.17
Climbing Perch	Wet	22	118 ± 24	0.48 ± 0.33	0.25 ± 0.29	0.11 ± 0.16
Notopterus notopterus	Dry	12	197 ± 25	0.42 ± 0.26	0.27 ± 0.23	0.17 ± 0.07
Bronze Featherback	Wet	6	148 ± 107	0.20 ± 0.31	0.56 ± 0.35	0.10 ± 0.07
Channa striata	Dry	5	282 ± 55	0.57 ± 0.08	0.01 ± 0.00	0.08 ± 0.04
Striped Snakehead	Wet	10	256 ± 90	0.47 ± 0.13	0.09 ± 0.24	0.13 ± 0.04
Channa micropeltes	Dry	25	367 ± 45	0.68 ± 0.14	0.01 ± 0.04	0.11 ± 0.08
Giant Snakehead	Wet	7	395 ± 89	0.70 ± 0.10	0.03 ± 0.06	0.10 ± 0.05

Table S3. Baseline values of $\delta^{13}C$ and $\delta^{15}N$ sampled from the Tonle Sap Lake and used to calculate trophic positions for the present study. All values are mean ± SD.

Season	Baseline type	$\delta^{13}C$	$\delta^{15}N$	Mean baseline $\delta^{15}N$ used in TP calculations
Dry	Benthic	-29.23 ± 4.09	5.89 ± 1.87	6.15
	Pelagic	-29.10 ± 4.38	6.30 ± 1.96	
Wet	Benthic	-28.74 ± 3.32	5.67 ± 1.30	5.92
	Pelagic	-35.34 ± 4.78	6.16 ± 1.66	

Table S4. Results of zero inflated beta regression on the proportion of invertebrates, fish and plants in the stomachs of Tonle Sap Lake species. Season (wet, dry) and body length were included as explanatory variables and species and location as random variables.

Response variable	Parameter	Posterior mean	Posterior median	2.5% quantile	97.5% quantile
Proportion of invertebrate	bintercept	-3.95	-4.05	-5.73	-1.71
	bwet	-0.32	-0.33	-0.90	0.25
	bbodylength	-0.01	-0.01	-0.01	0.00
	b0intercept	0.63	0.55	-1.47	3.19
	b0wet	-1.14	-1.16	-2.03	-0.20
	b0bodylength	0.00	0.00	0.00	0.01
Proportion of fish	bintercept	-5.16	-5.15	-5.64	-4.68
	bwet	0.04	0.04	-0.08	0.15
	bbodylength	0.00	0.00	0.00	0.00
	b0intercept	-0.42	-0.46	-2.41	1.45
	b0wet	0.79	0.76	-0.47	2.28
	b0bodylength	-0.01	-0.01	-0.02	0.00

Proportion of plant	bintercept	-6.50	-6.50	-6.96	-6.06
	bwet	-0.25	-0.25	-0.51	0.01
	$b_{bodylength}$	0.00	0.00	0.00	0.00
	$b0_{intercept}$	-0.87	-0.87	-2.56	0.80
	$b0_{wet}$	-1.38	-1.35	-2.99	-0.01
	$b0_{bodylength}$	0.00	0.00	-0.01	0.00

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PLOS ONE

RESEARCH ARTICLE

Spatio-temporal variation of fish taxonomic composition in a South-East Asian flood-pulse system

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Abstract

The Tonle Sap Lake (TSL) is a flood-pulse system. It is the largest natural lake in South-East Asia and constitutes one of the largest fisheries over the world, supporting the livelihood of million peoples. Nonetheless, the Mekong River Basin is changing rapidly due to accelerating water infrastructure development (hydropower, irrigation, flood control, and water supply) and climate change, bringing considerable modifications to the annual flood-pulse of the TSL. Such modifications are expected to have strong impacts on fish biodiversity and abundance. This paper aims to characterize the spatio-temporal variations of fish taxonomic composition and to highlights the underlying determinants of these variations. For this purpose, we used data collected from a community catch monitoring program conducted at six sites during 141 weeks, covering two full hydrological cycles. For each week, we estimated beta diversity as the total variance of the site-by-species community matrix and partitioned it into Local Contribution to Beta Diversity (LCBD) and Species Contribution to Beta Diversity (SCBD). We then performed multiple linear regressions to determine whether species richness, species abundances and water level explained the temporal variation in the contribution of site and species to beta diversity. Our results indicate strong temporal variation of beta diversity due to differential contributions of sites and species to the spatial variation of fish taxonomic composition. We further found that the direction, the shape and the relative effect of species richness, abundances and water level on temporal variation in LCBD and SCBD values greatly varied among sites, thus suggesting spatial variation in the processes leading to temporal variation in community composition. Overall, our results suggest that fish taxonomic composition is not homogeneously distributed over space and time and is likely to be impacted in the future if the flood-pulse dynamic of the system is altered by human activities.

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Introduction

Tropical freshwater systems, especially floodplain lakes and rivers, support productive fisheries, providing food and incomes for millions of people worldwide, particularly in the poorest countries [1,2]. In 1990, it was estimated that over 120 million people were involved in fisheries related activities, including capture, processing and sale of fish with 95% of them located in developing countries [3]. In Malawi, fishing activities from Lake Chilwa support about US$18 million annually while Lake Naivasha support an export-oriented agriculture valued at US$ 613–640 million [4]. Likewise, annual fish production from the Tonle Sap Great Lake (TSL) was estimated at 180,000 to 250,000 tons, representing approximately 60% of the total fish production of Cambodia [5]. This fish resource provides food for 14 million people and represents approximately 16% of the Cambodia's gross domestic product [6,7].

The TSL is the largest natural lake in South-east Asia, the largest wetland in the Mekong region, the most productive inland fisheries in the world and is a hotspot for biodiversity (i.e. it was designated as a UNESCO Biosphere Reserve in 1997), providing essential habitats for many endangered fishes and birds [8,9]. The TSL is a typical seasonal flood-pulse system and is a key element for the annual Mekong's flood. From June until September, the lake fills and the water level increases from 1–2 meters up to 10–15 meters [10]. In September, the TSL reverses its flow direction toward the Tonle Sap River (TSR) until the end of February causing the water level to drop to its minimum level in April and May.

Seasonal flood-pulse dynamic influences many ecological and environmental processes by causing lateral connectivity to adjacent floodplain habitats and by influencing water quality and nutrient dynamics, thus influencing the life-cycle of many organisms [11]. Indeed, lateral connectivity is a key element for many fish and other aquatic species because it provides resources and spawning habitats favoring productivity and biodiversity, which may in turn affect ecosystem stability and resilience to perturbations [12]. Consequently, large spatio-temporal variations in community compositions are expected within flood-pulse systems. Understanding what are the factors involved in these variations may help adapt conservation strategies to promote biodiversity and maintain their value as a livelihood.

Studies focusing on the determinants of spatio-temporal variations of fish communities have mostly been conducted on temperate systems (e.g. [2,12–14]). The paucity of studies conducted on tropical systems represent a large gap regarding our understanding of their functionning because tropical systems differ in various ways from temperate ones. For instance, tropical lakes are usually subject to indiscriminate fisheries (e.g. all species and size classes are targeted) whereas fisheries in temperate lakes are strongly reglemented. Consequently, the patterns highlighted in temperate lakes may not hold in tropical ones. Studying community composition, how they vary spatially and temporally and what are the determinants of these variations is therefore an important step toward a better understanding of the functionning of tropical ecosystems [15]. This is of utmost importance if we are to better manage these ecosystems which sustain important biodiversity and fisheries.

Indeed, studying the variation in species composition among sites (i.e. spatial beta diversity) and seasons (i.e. temporal beta diversity) may help improve our understanding of the processes that generate and maintain biodiversity [16]. For instance, according to the niche theory, sites with similar environmental conditions should harbor similar species whereas the opposite is expected for sites with different environmental conditions [17]. Thus, if environmental conditions are similar within a given area low beta diversity is expected whereas the opposite is expected if environmental conditions are spatially hetrerogeneous. In this study, our aim was (1) to characterize the temporal variation in the spatial composition of fish communities among six sites within the TSL during 141 weeks, spanning two complete hydrological cycles

and (2) to identify the determinants of the temporal variations in the contribution of site and species to spatial variation in community composition. For this purpose, we used data collected at six locations from a community catch monitoring program conducted from 2012 to 2014. For each week, we quantified the spatial variation of fish community composition (beta diversity) and partitioned it into local contribution (LCBD) and species contribution (SCBD). We then used linear models to explore how temporal variations of LCBD and SCBD values varied depending on the water level, the species richness and the species abundance.

Material and methods

Study area

The TSL is located in the central part of Cambodia (Fig 1) and is the largest natural freshwater lake of South-east Asia. It covers an area of approximately 0.25 million hectares during the dry season and an area estimated between 1.0 to 1.3 million hectares during the peak flood in the wet season. The TSL is connected to the Mekong in its southern part by a 120 km long river,

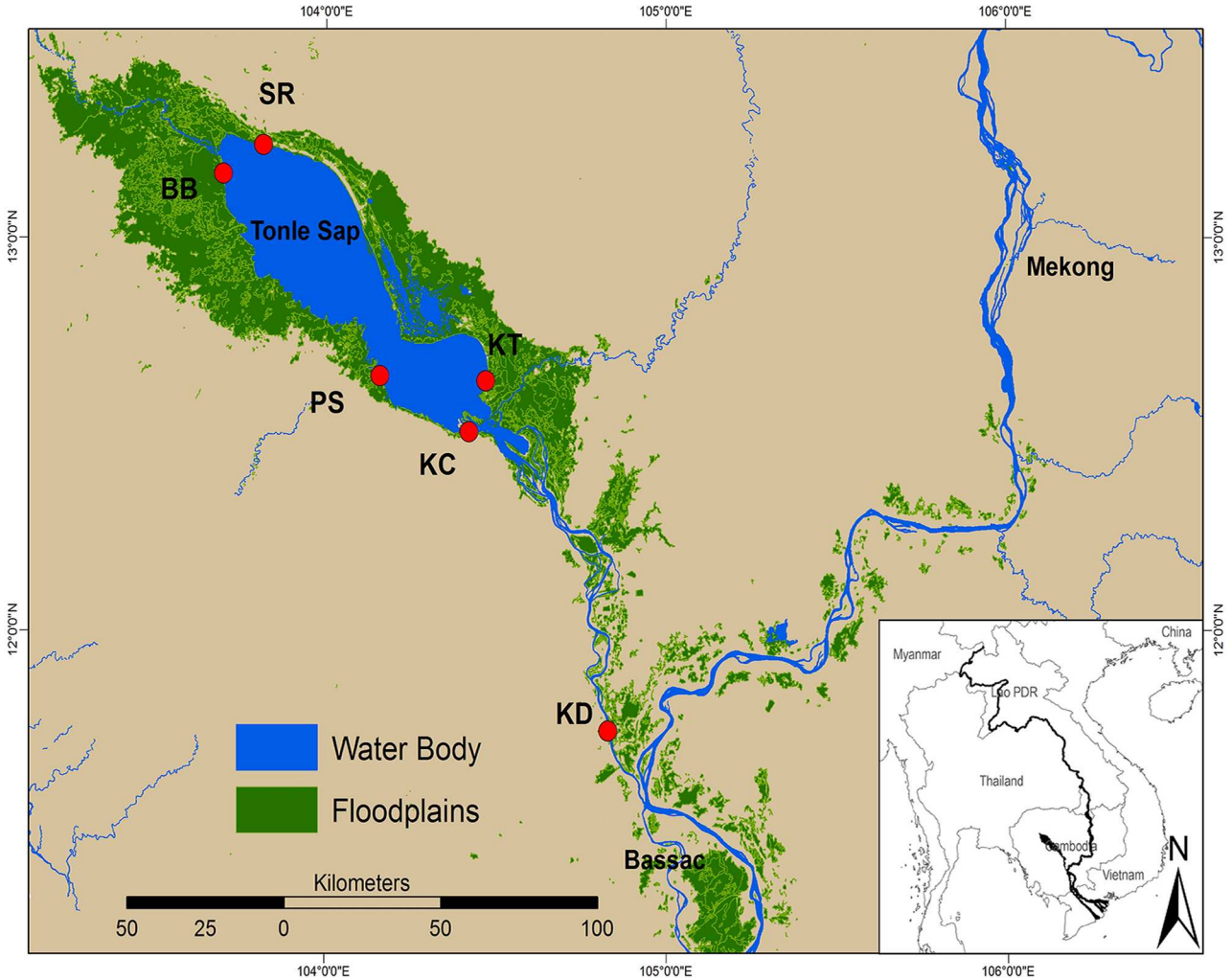

Fig 1. Localization of the six sampling sites. SR = Siem Reap; BB = Battambang BB; KC = Kampong Chhnang; KT = Kampong Thom; PS = Pursat; KD = Kandal. KD is located within the Tonle Sap River (TSR) whereas the five other sites are located within the Tonle Sap Lake (TSL).

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the Tonle Sap River (TSR), which serves as an inlet and outlet for water fluxes. The cycle of the water level of the TSL can be divided into four phases. The first phase, the rising season, lasts from July to early September and is characterized by a strong water feed coming from the upper Mekong through the TSR. During this phase, the water level of the lake increases by about 70%. The second phase, the flooding season, occurs from the end of September to early October, and corresponds to a phase where about 1.25 million hectares of forest and agricultural land are submerged. At this time, the water level may attain up to 15 meters. The third phase, the receding season, occurs from the end of October to February and corresponds to the reversal of the river flow from the TSL through the TSR, thus leading to a decrease of the water level of the lake. Finally, the fourth phase, the dry season, lasts from April to May, and corresponds to a period where the water level is the lowest (one to two meters).

Data collection

The fish data used in this study were derived from the Mekong River Commission (MRC), under the Assessment of Mekong Fisheries Component of the MRC Fisheries Program. The catch monitoring methods were derived from the MRC's regional monitoring program on fish abundance and diversity in the Lower Mekong Basin. Fish catches were monitored at five sites located around the TSL (Fig 1). Two sites (Siem Reap [SR] and Battambang [BB]) were located in the northern part of the lake while three sites (Kampong Chhnang [KC], Kampong Thom [KT] and Pursat [PS]) were located in its southern part. Fish catches were monitored at another one site located in the TSR (Kandal [KD]). Each site was monitored following a community catch monitoring program conducted on a daily basis from January 2012 to May 2014, thus covering two complete hydrological cycles. The catch monitoring methods were derived from the MRC's regional monitoring program on fish abundance and diversity in the Lower Mekong Basin [18]. The catches were performed by 18 local fishermen (3 fishermen per sites) using gillnets with 2 to 6.5 cm mesh sizes to capture as many species as possible. Fishes were identified to species level and counted. For unidentified individuals, the identification was performed later by a professional taxonomist in the laboratory. All fish records were collected monthly from fishermen and cross-checked by research officers to confirm the identifications following [19]. For further information on fish collection see [20]. Water level was measured in two locations; within the lake (PS) and within the river (KD).

The data were collected out in strict accordance with the Cambodian Fisheries Law on small-scale fishing. None of the studied species are classified as either endangered or protected according to the IUCN red list.

Data analysis

Daily data were aggregated into weekly data to reduce the influence of rare or occasional species on the analyses, thus resulting in 141 weekly catch data for each site.

Spatio-temporal variation of fish communities: contribution of sites and species. For each week, we computed the total variance of the site-by-species community matrix as an estimate of beta diversity (BD_{Total}) and then partitioned this measure into Local Contribution to Beta Diversity (LCBD) and Species Contribution to Beta Diversity (SCBD), following [16]. LCBD are comparative indicators of the ecological uniqueness of the sampling units and indicate how much each site contributes to beta diversity. Thus, a site with average and common species composition is expected to have a value of zero whereas large values indicate sites with different communities. Such large values may either indicate a site with a high conservation value or, on the contrary, degraded or species poor sites with a need for restoration. On the other hand, SCBD indices indicates how much each species is contributing to

beta diversity. Thus, a species present in all assemblages has a value of zero whereas species with large values are those that are present in only a few locations. LCBD and SCBD values were computed for each week from community composition matrices transformed using the Hellinger transformation (i.e. a measure of the dissimilarity in the species composition among locations).

To test for differences in LCBD values computed for each week between the six sites, we used Kruskall-Wallis non-parametric analysis of variance followed by multiple comparisons Tukey post-tests to test for differences between each pair of sites. We further used a hierarchical cluster analysis to determine whether LCBD values calculated for each week and the different sites (i.e. the sampling units) could be grouped based on their similarity. We used the Euclidian distance as a measure of similarity among the sampling units and sampling units were then aggregated using the Ward's method. Finally, compositional changes in fish communities were examined using non-metric multidimensional scaling which is a rank based method attempting to represent the pairwise dissimilarity between sampling units in a two dimensional space.

Determinants of temporal variation in LCBD and SCBD values. We used multiple linear regressions to explain temporal variation in LCBD values at each site. Three variables were included as predictors in each model (one for each site): the site specific richness, the local abundance (i.e. the sum of abundances of all species) and the water level (measured at PS for sites located within the lake and measured at KD otherwise). These three variables were log(x+1) transformed prior to analysis to reduce the skewness of their distribution. A quadratic term was also included for each predictor to allow for non-linear responses. From the complete model, we used a stepwise procedure based on the Akaike information criterion (AIC) to select the predictors that best explained temporal variation in LCBD values. The model retained was the one with the lowest AIC. From the selected models, we performed hierarchical partitioning to assess the relative contribution of each predictor.

Because SCBD is based on species and not sites, we have as many time series of SCBD indices as the total number of species sampled (i.e. 242). To avoid building and interpreting 242 linear models and because of the presence of a large number of zeroes for most species (i.e. rare species), we calculated for each week the number of species that contributed to total beta diversity above the mean of the entire pool of species. This was done by centering SCBD values for each week and keeping only the species with positive signs [16]. We then used the same procedure as above and considered as predictors the water level, the overall species richness and the total abundances (i.e. measured over the six sites for each week) as well as their quadratic terms. We then used hierarchical partitioning to assess the relative contribution of each predictor.

All annalyses were performed within the R environment software [21], using the packages vegan [22], hier.part [23] and the function beta.div described in [16].

Results

Among the six studied sites and the 141-week samples, 12,455,409 individuals, belonging to 242 species, 123 genera and 49 families were captured (S1 Table). The number of species captured ranged from 2 to 53 while the number of individuals ranged from 9 to 352,594. Species richness and total abundances were both higher in KT relative to the other sites whereas there was a trend toward lower values in KD (Fig 2). In Table 1 we show the means and standard errors of the number of individuals captured within the six sampling sites for the 20 most abundant species.

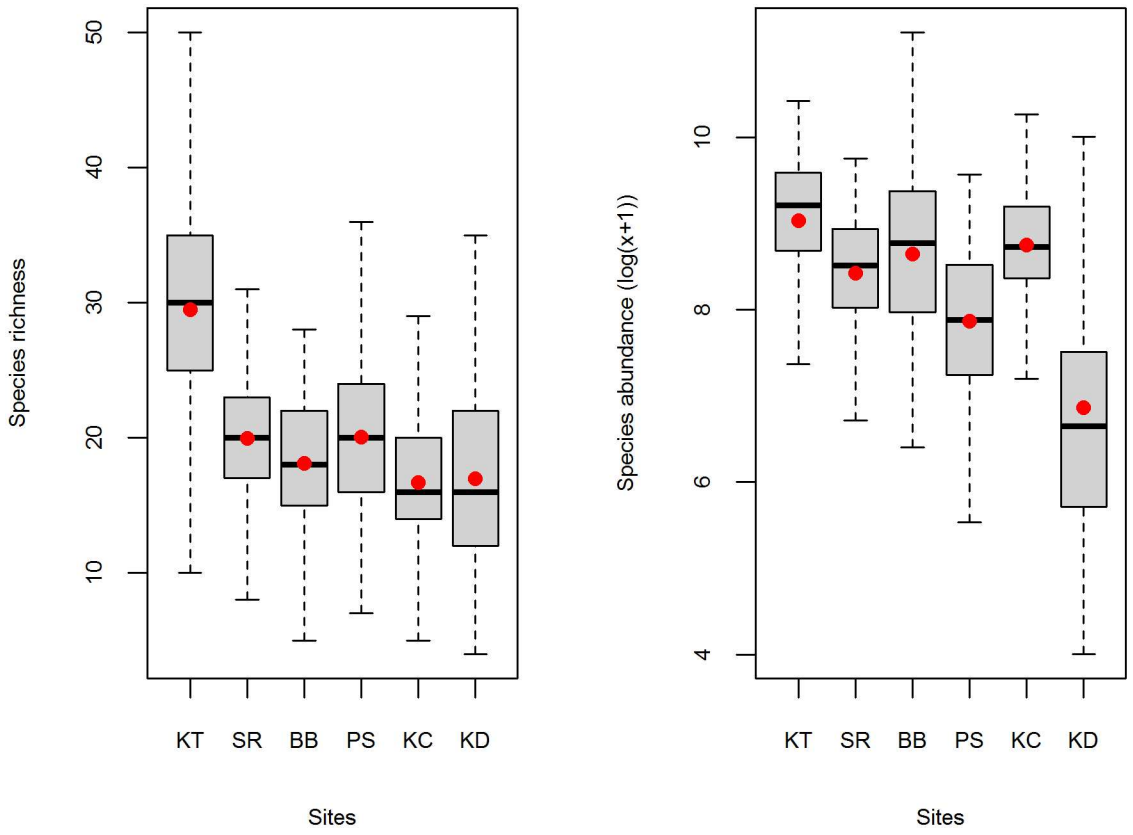

Fig 2. Among site variation in species richness (a) and total abundances (b). The horizontal black line represents the median whereas red points indicate the mean. For site code, see Fig 1.

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Spatio-temporal variation of beta diversity

All sites and weeks confounded, LCBD values ranged between 0.08 and 0.31. Kruskall-Wallis revealed significant differences in LCBD values among sites (chi-squared = 5487.62, df = 5, $P<0.001$). Tukey post-tests revealed that LCBD values were higher in KD (median = 0.244; sd = 0.027) compared to the other sites (Fig 3). The lowest values were observed in KT (median = 0.124; sd = 0.021), SR (median = 0.13; sd = 0.021) and PS (median = 0.13; sd = 0.027). BB (median = 0.181; sd = 0.031) and KC (median = 0.177; sd = 0.04) displayed intermediate values (Fig 3). Based on the similarity of LCBD values, samples were grouped into four clusters (Fig 4a). The two first clusters were mainly represented by BB and PS whereas the third one mainly represented KD, KT and SR while the fourth cluster was representative of KC (Fig 4b).

Among the 141 weeks considered, KT, PS and SR never displayed significant LCBD values, thus indicating that fish taxonomic composition within these sites do not explain spatial variation of fish community composition across the two hydrological cycles (Fig 5). In contrast, BB, KC and KD had respectively 4.2%, 14.9% and 65.2% of their weeks that displayed significant LCBD values indicating strong temporal variation regarding the uniqueness of fish community composition within these three sites.

More than 50% (i.e. 127) of the species contributed to beta diversity above the mean relative to the 242 species for at least one week (Fig 6). Among them, 26 species contributed to beta diversity above the mean for more than 50% of the weeks (S2 Table), thus indicating a rather

Table 1. Means and standard errors of the number of individuals captured for the 20 most abundant species found in our samples.

Species	BB	KC	KD	KT	PS	SR
Anabas testudineus	28±1.8	9.6±1.3	0.1±0	58±3.2	34.1±2	34.7±3.2
Cyclocheilichthys armatus	6±1.1	32.4±9.1	0.1±0	56.4±4.4	1.4±0.3	51.8±2.2
Henicorhynchus lobatus	95.6±10.7	171.6±15.5	497.5±77.7	285±15.2	56.3±3	58.2±3.2
Henicorhynchus siamensis	132.2±16.1	131.8±13.7	87.8±13.9	415.3±21.5	56.6±2.7	43.5±1.9
Labeo chrysophekadion	2±0.2	13.8±2.7	1.2±0.1	52.5±5	41.6±1.9	2±0.3
Labiobarbus lineatus	13.1±1.6	142.3±15.9	-	144.4±13.9	50.2±2.3	37.3±2.3
Labiobarbus siamensis	34.6±6.2	9.4±2	112.3±20.7	36.3±3	44.3±2.2	41.7±2.1
Mystus albolineatus	55±6.3	5.7±1	-	65.7±4.1	-	1.4±0.6
Mystus mysticetus	73.4±6.6	35.1±3.7	0.8±0.2	38.7±3.4	44.8±2.6	74.2±3.3
Mystus singaringan	31.3±2.5	52.7±6.2	0.3±0	53±3.9	14.2±1.4	34.7±2.2
Osteochilus vittatus	95.8±7.8	67.4±5.9	0.1±0	194.2±7.2	57.2±2.4	84.1±3
Pangasius macronema	2±1.7	2.6±0.5	59.1±3.6	12.2±1.8	2.4±0.3	0.4±0.2
Paralaubuca riveroi	-	-	171.9±33.6	-	-	-
Paralaubuca typus	26.4±4.4	102.8±8	139.8±30	19.9±2.3	16.3±1.3	28.6±2.3
Poropuntius deauratus	-	130.9±9.4	-	2.6±0.8	0.9±0.5	-
Puntioplites proctozysron	24.3±1.6	37.9±2.4	-	88.8±5.8	44.8±1.8	126.6±4.1
Rasbora tornieri	11.1±2.6	219±12.5	1±0.2	1.5±0.5	1.4±0.3	7.7±1.6
Trichopodus microlepis	334.4±17.1	9.8±1.1	-	15.6±3	43.7±2.6	57.6±3.8
Trichopodus trichopterus	364.4±18.1	25.5±2.1	-	114.2±7.5	74.2±4	56.8±2.5
Xenentodon cancila	-	175.5±8.7	3.3±0.9	0.5±0.2	0.6±0.2	-

means and standard errors are displayed for the six sampling sites.—indicate that the species has never been detected at this site. For site code see Fig 1. For a complete list of the species see S1 Table.

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stable contribution of these species to spatial variation of community composition over time. Those species were mostly non-migratory (61%) with specific habitat requirements such as permanent lakes or reservoirs (S2 Table).

Determinants of variation in LCBD and SCBD values

Regarding temporal variation of LCBD values, we found that the influence of predictors greatly varied depending on the sites considered (Table 2). Species richness was positively related to LCBD values at BB and KC but the opposite was found at PS. Furthermore, a non-linear influence of species richness (i.e. significant quadratic term) was detected at KT, BB and KD. The influence of total abundances on LCBD values also varied depending on the site considered; a negative relationship was found at KT and PS whereas a positive one was found at KD. Also, four sites (KT, SR, PS and KD) presented a non-linear relationship between LCBD values and total abundances. The water level was linearly related to LCBD values at all sites but KC with negative relationships at KD and SR and positive relationships at KT, SR and KD. A non-linear relationship was detected at KT, SR, BB and KD. When linear and quadratic terms were considered in conjunction, the hierarchical partitioning (Table 3) revealed that the species richness had the highest independent contribution in KT (61.6%), KD (36.4%) and KC (100%), whereas total abundances presented the highest independent contribution in PS (67.4%) and SR (82.6%). Finally, the water level had the highest independent contribution in BB (74.4%). Whatever the predictor considered, their contribution varied greatly depending on sites. For instance, the contribution of total abundances to the total variance varied from 12.8% in KT to 82.6% in SR. When considered in combination, the two biotic variables

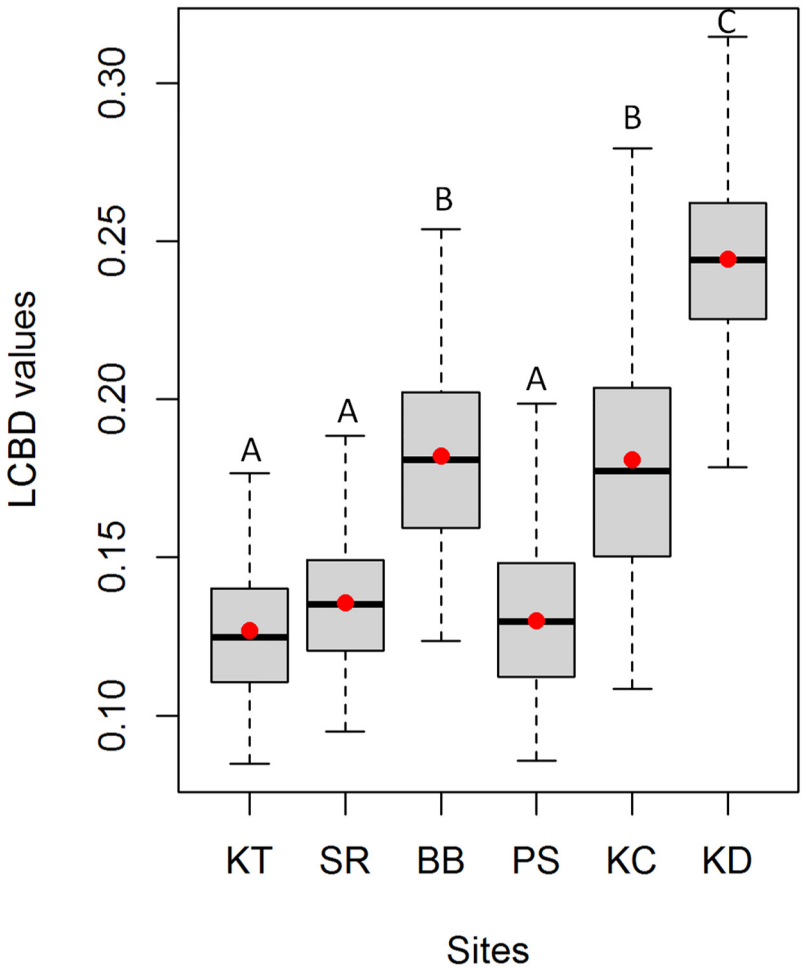

Fig 3. Among site variation in LCBD values. The horizontal black line represents the median whereas red points indicate the mean. The absence of common letter over of the boxplots indicate significant differences between sites in LCBD values (Tukey-post tests; $p < 0.05$). For site code, see Fig 1.

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(species richness and total abundances) explained more than 65% of the total variance except in BB (25.5%).

Regarding the temporal variation of the number of species that contributed to total beta diversity above the mean of the entire pool of species (SCBD values above the mean after centering), we found no influence of the water level (Table 2). The selected model included a positive relationship with the species richness and a negative one with total abundances, thus reflecting the opposite effect of these two predictors on the number of species contributing to beta diversity. We further found a non-linear influence of both species richness and total abundances. The hierarchical partitioning revealed a very high contribution of the species richness with more than 80% of the variance explained (Table 3).

Discussion

In this study, we aimed (1) to characterize the temporal variation in the spatial composition of fish communities (i.e. beta diversity) among six sites during 141 weeks, spanning two complete hydrological cycles and (2) to identify the determinants of the temporal variations in the contribution of site and species to spatial variation in community composition. We found that (1)

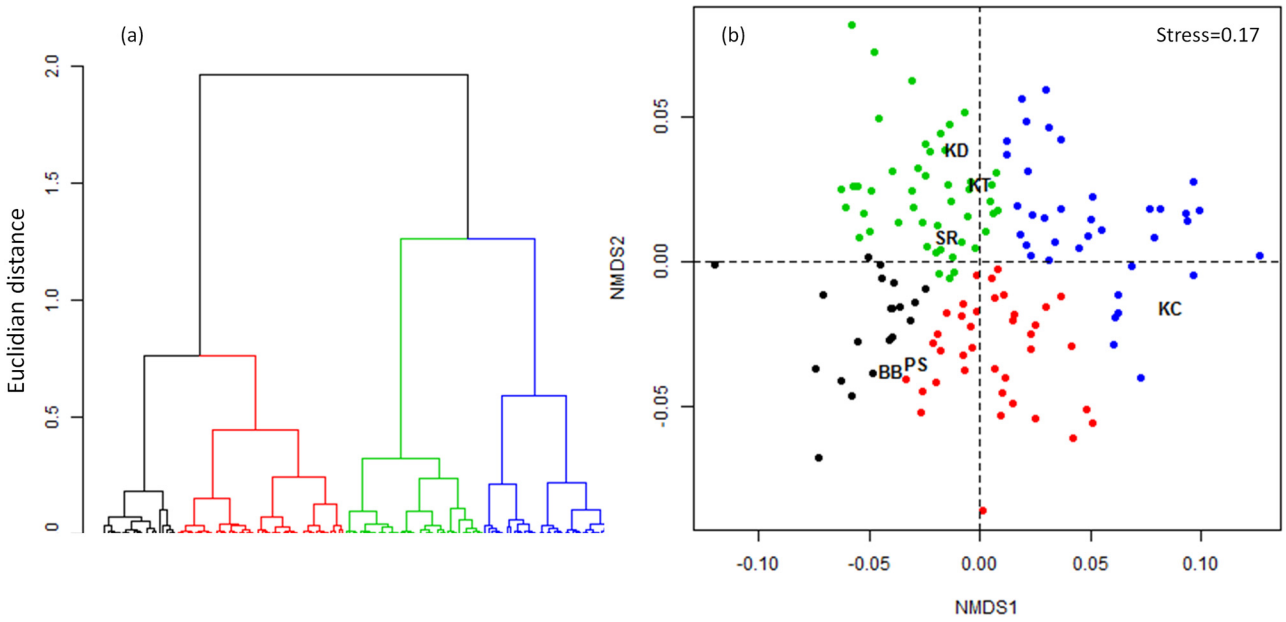

Fig 4. Similarity among LCBD values. (a) Hierarchical clustering of LCBD values according to their similarity (Euclidian distance) with the Ward's aggregation criteria. (b) Two-dimensional space defined by a non-metric multidimensional scaling (NMDS) approach representing the position of LCBD values and sites. In (a) and (b), the different colors represent the four groups identified by the cluster analysis. For site code, see Fig 1.

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some sites were more unique regarding fish community composition, (2) some species highly contributed to spatial differentiation of fish communities and (3) there is strong temporal variations regarding the contribution of site to beta diversity. The determinants involved in these temporal variations, their contribution and the shape (i.e. linear or quadratic) of the relationship greatly varied among sites, thus reflecting spatial variation in the processes structuring fish communities.

Spatio-temporal variations of beta diversity

Fish community compositions are expected to vary within floodplain systems [12,24,25]. In accordance, we found large spatial variation in fish community composition reflected by differential contribution of sites to the dissimilarity between assemblages (i.e. to beta diversity). Similarly, [26] found strong spatial variations in the community composition of rock-restricted cichlid fishes in Lake Malawi which was related to the geographic distances between locations and local habitat variables. In contrast, no spatial variation in fish community composition was found within the Dianshan Lake (China) which might be explained either by homogeneous environmental conditions [27] or by strong dispersal abilities of individuals homogenizing communities over large spatial scales (i.e. "mass effect"; [28]). The large spatial variation in fish community composition found within the TSL may be explained by spatial variation in habitat availability and environmental conditions (environmental filtering) as well as by the migratory behavior of particular fish species. In accordance, a study conducted on 59 temperate lakes highlighted an influence of environmental variables in structuring fish communities both between and within lakes [29].

We found temporal variation in the contribution of sites to the spatial variation in community composition, thus suggesting strong temporal variations in local species assemblages' at large spatial scale. This result strengthen previous findings demonstrating temporal variation

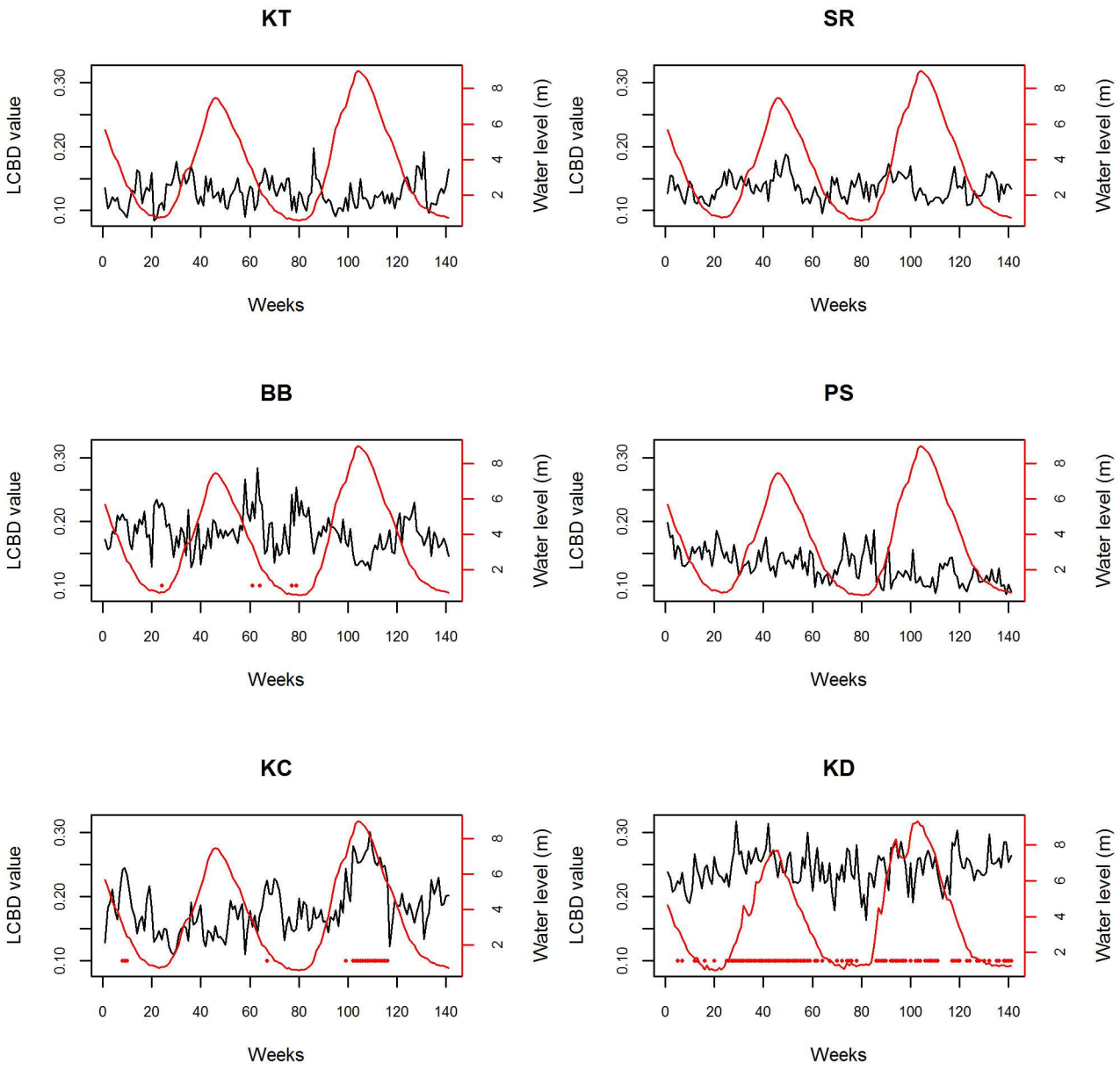

Fig 5. Temporal evolution of LCBD values and water level (m) over the study period for the six sites. The red dots indicate weeks with significant LCBD values (corrected for multiple comparisons). For site code, see Fig 1.

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in community composition across seasons within the Dianshan Lake [27]. More specifically, we found that three sites (BB, KC and KD) contributed strongly to the spatial variation in community composition. For BB and KC, the uniqueness of fish communities was occasional whereas the one at KD was rather stable over time with more than 60% of the weeks being unique in terms of community composition. Such stability can be explained by the fact that KD is the only site that is not located within the lake but within the river (TSR) which is a transitional zone for species migrating back and forth between the lake and the Mekong River. The uniqueness of species assemblages at BB mostly occurred during the dry season which can be explained by the presence of particular species moving back and forth from floodplain habitats to open water habitats within the lake and also by the influence of the Sangker River, located at

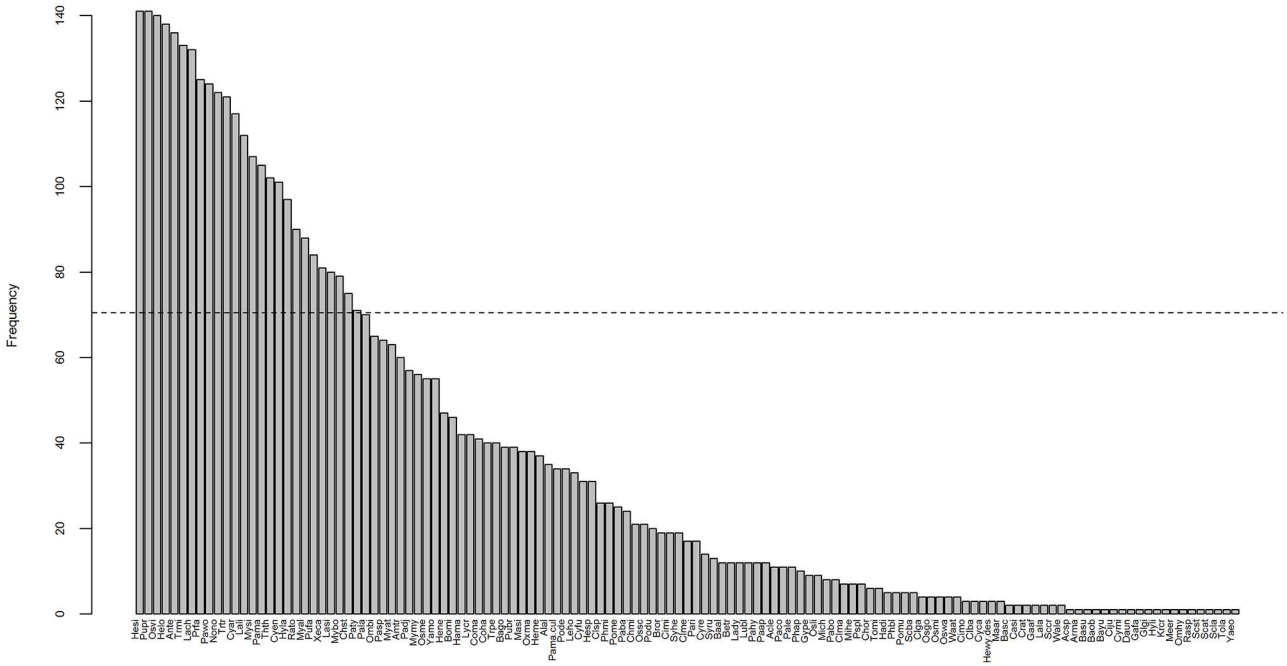

Fig 6. Number of weeks where species contributed to beta diversity above the mean relative to the entire pool of species. The horizontal dashed line represents 50% of weeks. For species code, see S1 Table.

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the north of the lake. In contrast the uniqueness of species assemblages at KC and KD was evident during the wet season and can be explained by the fact that these sites are strongly influenced by the TSR.

Over the 242 species, 50% showed a significant contribution to spatial variation of fish communities. However, this contribution greatly varied over time. This was reflected by the fact that only 10% of the 242 species showed a significant contribution to spatial variation in community composition for more than 50% of the weeks. Those species (e.g. *Mystus bocourti*, *Mystus albolineatus*, *Trichopodus microlepis*, *Anabas testudineus*, *Notopterus notopterus*, *Pristolepis fasciata*, *Channa striata*) were mostly non-migratory with specific habitat requirements. Such

Table 2. Results obtained from the stepwise selection procedure.

Sites	Intercept	WL	WL^2	SR	SR^2	AB	AB^2	R^2
KT	0.26	4.2×10E-02	-1.6×10E-02	-	-3.9×10E-03	-3.1×10E-02	2.0×10E-3	0.27
SR	0.19	-3.0×10E-02	1.1×10E-2	-	-	-	6.5×10E-04	0.16
BB	-0.06	5.4×10E-02	-2.4×10E-02	1.7×10E-01	-3.3×10E-02	-	-	0.15
PS	0.03	5.0×10E-03	-	-4.1×10E-03	-	4.8×10E-02	-3.7×10E-03	0.45
KD	0.29	-5.5×10E-02	2.6×10E-02	-	7.6×10E-03	-4.0×10E-02	2.3×10E-03	0.29
KC	0.22	-	-		3.9×10E-03	-	-	0.06
Nsp	-295.1	-	-	202.0	-22.7	-19.7	0.8	0.29

the coefficients displayed within the table are those that were extracted from the best model (through AIC). WL = water level; SR = local species richness; AB = local abundances. (-) indicate that the predictor was not pertinent enough to explain temporal variation in the dependent variables. The models above the double line are related to temporal variation in LCBD values at each site whereas the model below the double line is related to the temporal evolution of the number of species presenting SCBD values above the mean relative to the other species (Nsp). For site code, see Fig 1.

[2] denote quadratic terms.

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Table 3. Hierarchical partitioning indicating the relative contribution (in percentage; %LI) of each predictor to the variance explained by the models presented in Table 2.

	%LI					
Sites	**WL**	**WL^2**	**SR**	**SR^2**	**AB**	**AB^2**
KT	11.3	14.3	-	61.6	6.4	6.4
SR	7.8	9.6	-	-	-	82.6
BB	31.5	42.9	11.9	13.7	-	-
PS	2.9	-	29.7	-	32.7	34.7
KD	14.7	20.0	-	36.4	16.4	12.5
KC	-	-	-	100.0	-	-
Nsp	-	-	41.8	39.7	9.6	8.7

For site code see Fig 1. For predictor abbreviations, see Table 2.

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temporal stability suggests that these species probably depend upon the availability of critical habitats in both the wet and the dry seasons for growing or spawning. The low contribution of the remaining species to beta diversity can be explained by their widespread occurrence over the TSL, although seasonally.

Determinants of temporal variation in LCBD and SCBD

We found that the local contributions to beta diversity (i.e. LCBD values) of the six sites displayed very different responses to species richness, total abundances and water level. Few studies have adressed the question of the determinants of temporal variations of LCBD values. Among them, a negative correlation between LCBD values and both species richness and total abundance has been reported in subtropical tree [30], dung beetle [31], cattle tick communities [32] and fish [16] communities. Such a negative relationship indicates that as sites become less species-rich, they also tend to become more unique which could be explained by the occurrence of a disturbance such as pollution. In contrast, a positive relationship may arise because of the introduction of novel species (e.g. migratory species) within communities. Here we found contrasted patterns, revealing that different processes are shaping local fish communities.

We further found that both the shape and the relative effect of the three predictors greatly varied between sites. Indeed, we found a higher contribution of biotic variables (i.e. species richness and abundances) in explaining variation in site uniqueness over time relative to the water level (abiotic variable). This contrast with previous findings showing that abiotic variables such as distance from the source, altitude and water discharge are key factors influencing species assemblages [16]. Such discrepancy may stem from the fact that we focused on the temporal variation in site uniqueness whereas previous studies [16] were interested in its spatial variation. However, the higher contribution of biotic variables does not indicate that the water level has no influence on fish communities. Instead, one can imagine an indirect effect of the water level on fish communities where a change in this variable influences connectivity to floodplain habitats, in turn leading to local changes in species abundances and richness, and ultimately leading to spatial differentiation. The non-linear relationships highlighted here are also particularly interesting because they indicate that the local uniqueness of species assemblages occur for intermediate values of water level, species richness and abundances. At both extreme of the gradient, communities are therefore more homogeneous which can be explained by the dominance of large scale processes [28]. For instance, water level reduction has been shown to influence community assemblage by influencing local individual

abundances and by making it possible for species to colonize new local habitat patches [33], a process that can lead to community homogenization. Likewise, when the water level is very high, the presence of migratory species, dispersing over large distances, may homogenize fish communities. Such non-linear relationships have already been highlighted in birds where the community specialization index (a measure of the functional homogenization of communities) is maximal at intermediate values of fragmentation [34].

Regarding temporal variation in the number of species that contribute to beta diversity above the mean of the entire pool of species (i.e. SCBD values) we found a high contribution of species richness whereas species abundances and water level only had a marginal effect. More specifically, we found a positive relationship with species richness indicating that as species richness is increasing, communities within the lake tend to become more dissimilar. This can be explained by the presence of particular species with strong ecological requirements and/or poor dispersal abilities, confined to particular area of the lake. However, the relationship highlighted was non-linear and actually peaked for intermediate values of species richness. Thus, at very high richness communities tend to be more similar, which can be explained the widespread occurrence of species with low ecological requirements and/or strong dispersal abilities homogenizing communities at large spatial scale.

Conclusion

The TSL is the largest inland fisheries in South-east Asia and supports the livelihood of 2.5 million people around the lake [8]. Its flood-pulse dynamic combined to the flow reversal of the TSR make it a unique system worldwide supporting high biodiversity by providing a large diversity of food and habitats for many birds and fishes. However, the growing demand for water for agricultural purposes and the construction of hydro-power dams along the Mekong river [8] combined to the effect of climate change is strongly threatening this system by altering and reducing flood intensity from 7% to 16% during the rainy season [35]. Such changes in the water regime are likely to have strong impacts on fish community composition by modifying several phenological events [36] such as the timing of migration or spawning and also by reducing the amount of submerged habitats upon which fish depends for growing and spawning. This may ultimately lead to a decrease in fish productivity and biodiversity. For instance, in 2016, hundred tons of brood-stock fish died within the conservation zone of Boeung Chhmar (which is temporarily connected to the lake) due to a prolonged drought. The strong spatio-temporal variations highlighted regarding the uniqueness of fish communities are likely to be the result of both spatial variation in environmental conditions and the seasonal migration of particular species which occurrence depends on the connectivity to floodplain habitats critical for their reproduction and survival. Promoting the connectivity to floodplain habitats is therefore an important step toward the maintenance of fish biodiversity and productivity upon which millions of people depend for their livelihood.

Supporting information

S1 Table. List of the 242 fish species captured among the six sampling sites during 141 weeks (from January 2012 to May 2014) spanning two and half hydrological cycles.
(DOCX)

S2 Table. List and characteristics of the 26 fish species that contributed to total beta diversity above the mean of the entire pool of species (according to [19,37]). The first column indicates species habitat requirements: (a) low wetland, (b) shallow sluggish or flowing and standing-water with aquatic vegetation, (c) floodplain throughout the middle and lower

Mekong, (d) large and medium rivers and stream in the Mekong and Chao Phrya basins, (e) canals, ditches and reservoirs, (f) marine, freshwater, brackish and pelagic-neritic. The second column indicates species diet**:** (1) zooplankton, (2) crustaceans and mollusks, (3) insect, (4) algae and periphyton, (5) fish, (6) rotifers, (7) aquatic plants and fruits, (8) worm, (9) frogs (10) snakes. The third column indicates the species migratory strategy: Non migratory species (NM) and migratory species (M).
(DOCX)

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Funding acquisition: SL HK.

Methodology: MC SL.

Supervision: PL SL MC.

Visualization: MC HK.

Writing – original draft: HK.

Writing – review & editing: MC PL SL.

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RESEARCH ARTICLE

Seasonal variations in diet composition, diet breadth and dietary overlap between three commercially important fish species within a flood-pulse system: The Tonle Sap Lake (Cambodia)

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Data Availability Statement: The data underlying this study have been uploaded to GitHub and are accessible using the following link: https://github.com/Mathieu-Chevalier/Plos-One-data-stomach-content/blob/master/diet_data_3_species_TSL.txt.

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Abstract

Tropical lakes and their associated floodplain habitats are dynamic habitat mosaics strongly influenced by seasonal variations in hydrologic conditions. In flood-pulse systems, water level oscillations directly influence the connectivity to floodplain habitats for fish. Here, we aimed to investigate whether seasonal changes in the water level of a flood-pulse system (the Tonle Sap Lake, Cambodia) differentially affect diet breadth and dietary overlap of three common and commercially important fish species (*Anabas testudineus*, *Boesemania microplepis and Notopterus notopterus*) presenting important differences in their life-cycle (e.g. seasonal migration). For this purpose, the three fish species were sampled at four locations spread over the lake and their stomach contents extracted for analyses. Dietary differences were investigated across seasons regarding the diet composition and diet breadth of each species as well as the amount of dietary overlap between species. We found that the proportion of empty stomachs changed similarly across seasons for the three species, thus suggesting that ecological differences between species are not sufficient to outweigh the effect of seasonal variations in resource abundance. In contrast, changes in diet composition were species-specific and can be explained by ecological and behavioral differences between species. Diet breadth differed between species in all seasons, except during the wet season, and tended to be higher during the dry season when dietary overlap was the lowest. These variations likely result from changes in the diversity and amount of resources and may lead to habitat use shifts with potential implications for competitive interactions. In particular, increasing connectivity to floodplain habitats may reduce the competitive pressure during the wet season, while resource scarcity during the dry season may constrain individuals to diversify their diet to avoid competition. Overall, our results suggest a considerable plasticity in the feeding behavior of the three species as demonstrated by seasonal variation in both diet breadth and dietary overlap. Such variations can be explained by a

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number of factors and processes, including changes in resource availability or competitive interactions between individuals for resources, whose relative influence might vary depending on the magnitude and the timing of the flood-pulse driving the connectivity to floodplain habitats. Gaining knowledge on the seasonal evolution of fish's diet is relevant for fisheries management and conservation and our result could be used to guide aquaculture development in Cambodia.

Introduction

Seasonal change in hydrology is a prominent feature of freshwater ecosystems influencing populations, communities and ultimately ecosystem processes by modifying the connectivity to floodplain habitats [1]. Lateral connectivity influences many aspects of an organism's life cycle as well as local community composition by regulating access to resources and habitats for spawning, growing and rearing [2,3]. However, the connectivity to floodplain habitats is currently undergoing strong human pressures through dam constructions and river channelization [4], with consequences on organisms and ecosystem processes [5]. For instance, by altering natural river flow and by dampening seasonal fluctuations and thus connectivity to floodplain habitats [5], dams have a strong influence on population and community composition [6]. Such pressures are even more problematic in flood-pulse systems where seasonal changes in hydrology are of critical importance to maintain the productivity and the biodiversity of these systems [7]. Indeed, several studies [8,9] have shown that the flood-pulse is the main factor structuring fish communities and that flood-pulse modification could impact fish populations [10] as well as among-species interactions [11].

Studying stomach contents provides useful information regarding trophic relationships between species [12] but also ecosystem functioning by evaluating resource use efficiency [13] and could be used to assist the development of management and conservation strategies in a multi-species framework [14]. Several species have been shown to shift their diet across seasons as a result of variations in the connectivity to floodplain habitats [15,16]. For instance, in the Amazon basin, a great number of fishes enter the flooded forest during the high water season to feed on fruits, seeds and other terrestrial resources [17,18]. Thus, changes in diet composition can reflect changes in the availability and the quantity of food resources. However, given that the same resource can be shared by numerous species and that each species can successively exploit different resources during the same year [19,20], changes in diet composition could also be attributed to intra- and interspecific competition [21–23]. For instance, during the season of low resource abundance, diet breadth could increase to reduce intraspecific competition [24], while dietary overlap among species may decrease to reduce interspecific competition [25,26]. Furthermore, if all resources do not change uniformly, individuals are expected to forage according to the optimal foraging theory, by seasonally exploiting the most profitable resources, leading to seasonal diet shift [27]. Another layer of complexity arises from the fact that the above mentioned patterns can vary depending on species characteristics. For instance, a large diet breadth is a frequently cited characteristic of invasive species, allowing them to thrive in a wide range of environments and to potentially exploit different resources depending on the season [28]. Therefore, studying how the diet of species varies by season within a multi-species framework may help unravel the processes involved within a given ecosystem and provide knowledge about the nature of interactions that exist between individuals and species.

The Tonle Sap Lake (TSL) is the largest natural lake in Southeast Asia and was designated as a UNESCO Biosphere Reserve in 1997. The TSL has a flood-pulse functioning and provides

essential habitats for more than 242 fishes [29] and many endangered vertebrates [30–32]. The lateral connectivity between the main lake and its floodplain mainly depends on water coming from the Mekong River, representing more than 50% of the water balance. This connectivity is a key feature for many fishes and aquatic species, by providing access to habitats for rearing, spawning and growing [30,31], ultimately influencing community structure [29], system productivity [9] and population dynamics [33]. However, growing human pressures in the upper reaches of the Mekong River, through the establishment of large hydropower dams and reservoirs, large irrigation schemes, and rapid urban development, is putting water resources under stress and is strongly threatening the connectivity to floodplain habitats [4].

The aim of this study was to describe the seasonal variations of the diet of three common, abundant and commercially important fishes: *Anabas testudineus*, *Boesemania microplepis* and *Notopterus notopterus* [29]. We chose these species because they are widespread within the lake during the whole year and are known to occur in similar habitats [34], thus providing potential for interspecific competition. They nevertheless present important differences within their life-cycle, including contrasting seasonal migration patterns and tolerance to hypoxia [34–36]. To investigate seasonal variations in the diet composition and diet breadth of each species as well as the amount of dietary overlap between species, we analyzed the stomach contents of 623 specimens collected at four locations across four hydrological phases (dry, rising, wet and receding seasons) covering the dynamic of the TSL. Given seasonal changes in the water level and the lateral connectivity to floodplain habitats, our expectations were as follow. First, we hypothesized seasonal changes in the diet of the three species, regarding both the proportion of empty stomachs and the proportion of food items. In particular, we expected a higher proportion of empty stomachs during the dry season because of low resource abundance. We further hypothesized that the diet breadth of the three species would be larger during the dry season to reduce intraspecific competition for resources while it would be lower during the wet season because individuals would be able to forage on the most profitable resource due to an increase in both the availability and the diversity of food resources. Finally, we expected seasonal variations in dietary overlap and in particular a low dietary overlap during the dry season due to competitive exclusion for resources between species.

Materials and methods

Study species

Anabas testudineus is a demersal species, commonly found in sluggish, standing and stagnant waters with dense vegetation and mainly feed on shrimps and fish fry [37]. It belongs to the "*blackfish*" guild where fish move only locally from waterbodies to the surrounding floodplain during the wet season and return to the pools during the dry season. Those fishes are adapted to hypoxia and often present auxiliary respiratory organs that enable them to breathe atmospheric air or behaviors that give them access to the well-oxygenated surface films. They have a wide range of breeding behaviors that allows them to maintain eggs and newly hatched fry in relatively well-oxygenated localities.

Boesemania microplepis is a bentho-pelagic species, commonly found in flowing waters of large rivers and in the deep pools of the Mekong River even during the dry season [38]. It mainly feeds on crustaceans and small fishes [34]. This species is categorized as a "*whitefish*", comprising large, strongly migratory fishes that move large distances within the river channels between feeding and breeding habitats. Fish within this guild may pass their whole life history in the main channel or may move into the floodplains to feed. They are generally intolerant to hypoxia, preferring migration as a means to escape the adverse conditions during the dry season. Whitefish are generally one-shot spawners, scattering numerous eggs.

Notopterus notopterus is a species found in a wide range of habitats including fresh waters, standing and sluggish waters, floodplains, canals, and ponds. It mainly feeds on insects, fishes, crustaceans and roots [34]. This species belongs to the "*grayfish*" guild which is intermediate between the floodplain-resident and the long-distance migrant's guilds. Grayfish generally execute short migrations between the floodplain, where they reside during the wet season for breeding and feeding, to the main river channel, where they shelter in marginal vegetation or in the deeper pools of the channel over the dry season. These species are intolerant to hypoxia but present elaborate reproductive behaviors, which enable them to go into the floodplain for breeding during the dry season.

Given differences in the ecology and the behavior of the three species, specific patterns were expected. In particular, we hypothesized that *N. notopterus* would display low seasonal variations in its diet breadth because of its ability to migrate back and forth between different habitats, making it possible for individuals to forage on different resources and to maintain a broad diet during the whole year. *B. microplepis* tends to migrate to escape adverse conditions during the dry season and we therefore expected this species to present a low dietary overlap with respect to the two other species during this season. In contrast, we expected the diet of *A. testudineus* to change toward the most profitable resource (i.e. fish) during the dry season because of its ability to face adverse conditions and exclude other competitors.

Study area

Located in the central part of Cambodia, the TSL is the largest natural lake in Southeast Asia (Fig 1). During the dry season it covers an area of approximately 0.25 million hectares whereas during the peak flood in the wet season the area covered by the lake has been estimated between 1.0 to 1.3 million hectares. The TSL is connected to the Mekong River in its southern part by a 120 km long river, the Tonle Sap River (TSR) which serves as an inlet and outlet for water fluxes. The TSL's hydrological cycle can be divided into four phases [29]. The first phase (rising season) takes place from July to early September and is characterized by a strong water feed coming from the upper Mekong through the TSR and during which the water level strongly increases. The second phase (the wet season) lasts from the end of September to the end of October, and corresponds to a phase where about 1.25 million hectares of forest, shrublands, grasslands and agricultural lands are submerged. At this period the water level may attain up to 15 meters. The third phase (the receding season) occurs from the end of October to February, and is characterized by the reversal of the TSR flowing from the TSL to the China Sea in the south, resulting in a decrease of the water level of the lake. Finally, the fourth phase (the dry season) lasts from April to May, and corresponds to the period where the water level is the lowest (i.e. 1 to 2 m).

Data collection and dietary analysis

Data collection was carried out in collaboration with the Inland Fisheries Research and Development Institute (IFReDI) who issued the permission for collection and were collected in strict accordance with the Cambodian Fisheries Law on small-scale fishing. None of the studied species are classified as either endangered or protected according to the IUCN red list.

To match with the four natural phases of the TSL's hydrological cycle, fish were sampled every three months from the beginning of June 2014 to the end of May 2015 by local fishermen using gillnets with varying mesh sizes (2 to 6.5 cm), heights (1.5 to 2 m) and lengths (250 to 300 m), to capture individuals with varying sizes. Gillnets were deployed during the night and were let in the water for eight to 10 hours. The habitat where the nets were set varied depending on the water level. During the wet and the receding seasons, nets were set within floodplain

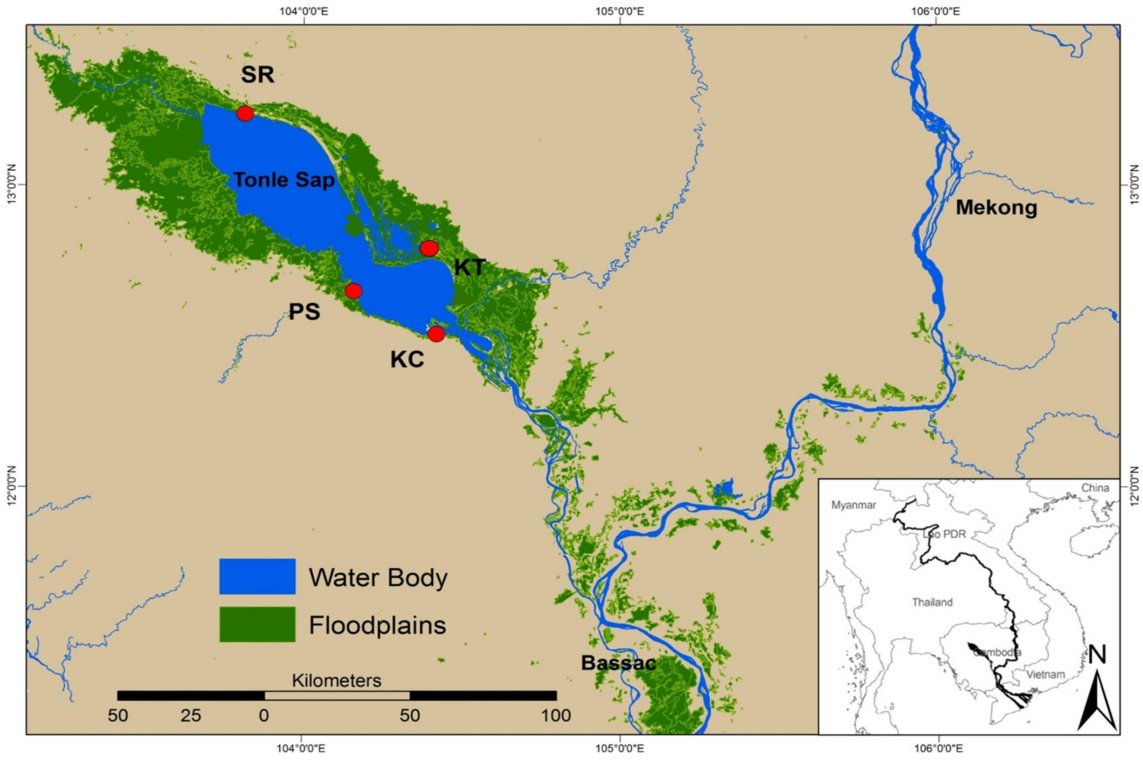

Fig 1. Map of the Tonle Sap Lake (TSL). Sampling locations are indicated by red dots. SR = Siem Reap, KT = Kampong Thom, PS = Pursat and KC = Kampong Chhnang.

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habitats (i.e. in the middle of shrubs, grasslands and trees) whereas during the dry and the rising seasons, nets were set in open water habitats as floodplain habitats are not accessible at this period of the year. To account for spatial variation in resource distribution within the TSL and low local abundance in some cases, the specimens were collected at four locations (Fig 1): Kompong Thom (KT), Siem Reap (SR), Pursat (PS) and Kompong Chhnang (KC). The three species were always found within the same nets, confirming that they share similar habitats and that they potentially compete for resources. The number of individuals associated to each species varied depending on the location and the season (Table 1). To avoid the breakdown of food items, specimens were immediately preserved in a cool container, and stomach contents were extracted at the laboratory and preserved in 97% ethanol. Thus, the death of fish specimens was induced by thermal shock, as recommended [39,40]. The proportion of empty stomachs was scored for each species and seasons. From the remaining stomachs, food items were identified to the lowest feasible taxonomic level following [41] and [42] using optical and

Table 1. Total number of individuals of the three species collected (i) at each location across the four seasons and (ii) during each season across the four locations.

Species	*Locations*				*Seasons*			
	KT	SR	KC	PS	Receding	Wet	Rising	Dry
Anabas testudineus	55	83	50	48	80	56	35	65
Boesemania microlepis	30	51	59	39	65	31	6	77
Notopterus notopterus	35	69	48	56	78	34	23	79

Abbreviations for locations: KT = Kompong Thom, SR = Siem Reap, PS = Pursat and KC = Kompong Chhnang.

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stereoscopic microscopes (Olympus: SZX7-Model SZX2-ILLK). For each food item, we calculated its frequency of occurrence (FOC) as the number of times a particular item occurred within a sample relative to the total number of items (empty stomach excluded). Among the four sampling campaigns, a total of 623 specimens were collected and analyzed for stomach contents (236 for *A*. *testudineus*, 179 for *B*. *microplepis* and 208 for *N*. *notopterus*). In total, 30 different prey types were found within the non-empty stomachs of the three species.

Statistical analysis

Because the proportion of empty stomachs can provide information on resource availability and the ability of species to forage during periods of shortage [12], we tested for seasonal variations in the proportion of empty stomachs using a chi-square test.

For non-empty stomachs, we used an analysis of similarity (ANOSIM) to test for significant differences in the diet of species between the wet (from July to October) and the dry seasons (from December to May) followed by an analysis of similarity percentages (SIMPER) to assess the contribution of food items to the observed variations [43]. We focused on differences between the wet and the dry season because considering the four seasons would have implied to perform multiple tests (i.e. six for each species), necessitating p-values adjustments and thus a decrease in statistical power. Both analyses were based on a dissimilarity matrix built with Bray-Curtis distances to account for the large proportion of zeros in the community matrix. The ANOSIM statistic vary between zero and one and compares the mean of ranked dissimilarities between groups to the mean of ranked dissimilarities within groups. A value close to one suggests dissimilarity between groups, while a value close to zero suggests an even distribution of high and low ranks within and between groups. The SIMPER analysis is based on the decomposition of the Bray-Curtis dissimilarity matrix and aim to assess the contribution of food items (or species) to the observed dissimilarities. For this analysis, we grouped food items into six broader categories (fish, insects, crustaceans, plants, mollusks and micro-fauna) following [22,44]. The importance of each category within the diet was established as its average FOC divided by the sum of the average FOC of all categories and was calculated by species and seasons.

To explore interspecific differences in diet composition across the four seasons, we used non-metric multidimensional scaling (NMDS [45]). This indirect gradient analysis approach uses rank order values to visualize and interpret differences between species, ultimately representing pairwise differences between samples in a low-dimensional space. The similarity between sampling units was calculated using Bray-Curtis distances. Beyond this graphical approach, we computed different statistics to evaluate and test how interspecific differences in diet varied across seasons. First, we used a multivariate homogeneity of group dispersions [46] with 1000 permutations to (i) measure the diet breadth of each species in each season and (ii) test for interspecific differences in each season. In this analysis, diet breadth is estimated as the average distance of prey items to the group centroid within the multivariate space described by the NMDS with larger values indicative of a broader diet. The values by themselves have no ecological meaning but can be compared to determine to which extent diet breadth is changing between species and season. Second, we computed Pianka's symmetric index [47] to measure niche overlap in diet composition between each pair of species in each season. Here, a value close to zero indicates no overlap whereas a value close to one indicates a strong overlap. To test the statistical significance of dietary overlap between each pair of species in each season, we conducted a bootstrap procedure by randomly sampling the rows of the community matrix. This procedure was repeated 1000 times and generated a distribution of Pianka's index for each pair of species under the null hypothesis that there is no variation in dietary overlap

across seasons. For a given pair of species, we assessed the statistical significance of dietary overlap in each season by comparing the observed value to the 95% confidence intervals of the corresponded distribution. All analyses were performed in R [48] using the package vegan [49].

Results

The average size of captured individuals was 12.7 ± 2.1 cm for *A. testudineus*, 23.9 ± 13.9 cm for *B. microplepis* and 20.4 ± 2.4 cm for *N. notopterus*. The proportion of empty stomachs was 14.8% for *A. testudineus*, 12.3% for *B. microplepis* and 16.8% for *N. notopterus*. For all species, this proportion greatly varied across seasons and was maximal during the receding season and minimal during the dry season (Fig 2). Seasonal variation in the proportion of empty stomachs was independent of species identity ($\chi^2 = 0.14$, df = 6: P = 0.99). The diet of *A. testudineus* was mainly composed of fish (43%), insects (23%) and plants (17%) whereas *N. notopterus* mostly fed upon insects (49%), plants (28%) and fish (10%) (Fig 2). The diet of *B. microplepis* was mainly composed of fish (51%), crustaceans (21%), and plants (15%). The similarity analysis (ANOSIM) revealed a significant change in the diet composition of *A. testudineus* ($p<0.01$, r = 0.16) and *N. notopterus* ($p<0.01$, r = 0.13) between the wet and the dry season, whereas no significant difference was found for *B. microlepis* ($p = 0.42$, r = 0.004). The SIMPER analysis revealed that only a few food items significantly explained the seasonal differences found for *A. testudineus* and *N. notopterus*, with a particularly strong contribution of fish prey for the former and of insects for the latter (Table 2).

The NMDS highlighted strong seasonal variations in both diet breadth and dietary overlap between the three species (Fig 3). Diet breadth significantly differed between the three species in all seasons ($p<0.01$), except the wet season ($p = 0.11$; Table 3). It tended to be highest during the dry (from 0.48 to 0.54) and the receding seasons (from 0.45 to 0.53), and to be lowest during the two remaining phases (from 0.34 to 0.51) of the hydrologic cycle (Table 3). From a species perspective, diet breadth was quite stable across seasons for *N. notopterus* (from 0.46 to 0.51) but much more variable for the two other species, with variations from 0.38 to 0.54 for *A. testudineus* and from 0.34 to 0.53 for *B. microlepis* (Table 3).

The bootstrap procedure performed on Pianka's index suggest that dietary overlap was different between the three species. This was revealed by differences in the null distributions, whose averages vary from 0.27 [95% CI = 0.21–0.34] between *A. testudineus* and *B. microlepis* to 0.5 [95% CI = 0.41–0.58] between *A. testudineus* and *N. notopterus*, while it was 0.3 [95% CI = 0.23–0.37] between *B. microlepis* and *N. notopterus* (Fig 4). Confidence intervals further suggest that the dietary overlap measured between *A. testudineus* and *N. notopterus* is significantly higher than the one measured between the two other pair of species (non-overlapping confidence intervals). We found evidence for seasonal variations in dietary overlap with minimum values observed during the rising season and maximum values observed during the receding season. In particular, dietary overlap between *A. testudineus* and *N. notopterus* was significantly higher during both the receding and the wet seasons, whereas it was significantly lower during the rising season (all $p<0.05$; Fig 4). Likewise, dietary overlap between *B. microlepis* and *N. notopterus* was significantly higher during both the rising and the wet seasons (both $p<0.001$; Fig 4). Dietary overlap between *A. testudineus* and *B. microlepis* was more stable across seasons, but was significantly higher than expected in the receding season ($p<0.01$; Fig 4).

Discussion

In this study, we explored seasonal variations in the diet of three common, abundant and commercially important fish species presenting important differences within their life-cycle but

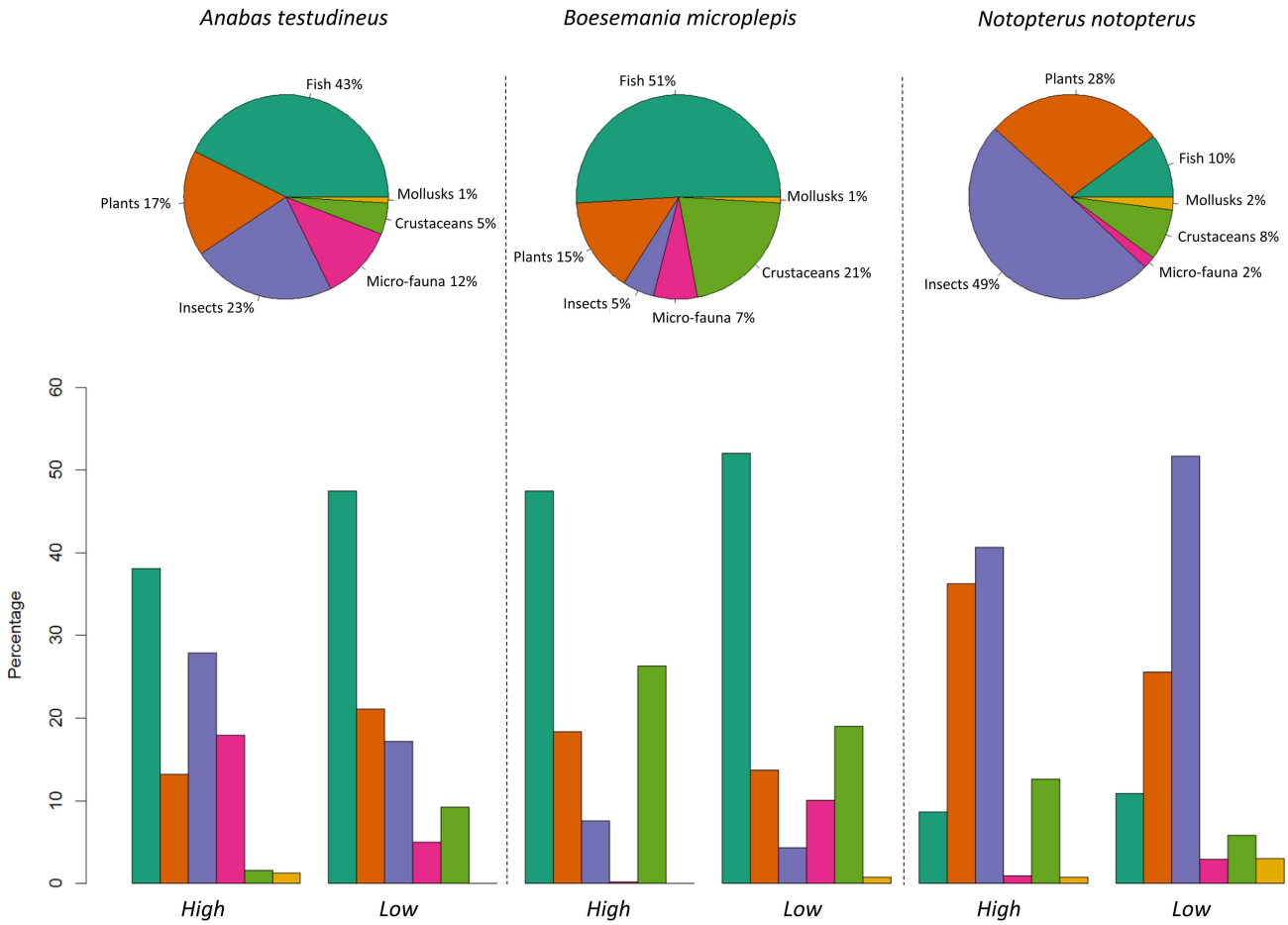

Fig 2. Description of the diet of the three studied species and how they vary across seasons. For the sake of graphical clarity and because some items had a very low occurrence, items were grouped into six broader categories (mollusks, crustaceans, fish, plants, insects and micro-fauna). The pie charts represent the relative proportion of food items, all seasons confounded, and thus provide an overview of the main diet of the species. The barplots represent the seasonal variations in the proportion of food items within non-empty stomachs (colored barplots; on the left) and the seasonal variations in the proportion of empty stomachs (greyed barplots; on the right).

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sharing similar habitats to gain knowledge about resource use and the potential for resource competition. Although we found large seasonal variations in the proportion of empty stomachs, we found no differences between species in this regard. In contrast, we found strong

Table 2. Average percent contribution of food items to the dissimilarity of diet composition between the wet and the dry seasons for the three studied species.

Food items	*A. TESTUDINEUS*	*B. MICROLEPIS*	*N. NOTOPTERUS*
Fish	0.28 (0.25)	0.28 (0.22)	0.07 (0.11)
Plants	0.11 (0.13)	0.09 (0.09)	0.12 (0.11)
Insects	0.17 (0.19)	0.05 (0.1)	0.20 (0.15)
Micro-fauna	0.13 (0.14)	0.05 (0.06)	0.02 (0.05)
Crustaceans	0.04 (0.13)	0.17 (0.19)	0.07 (0.13)
Mollusks	0.01 (0.03)	0.01 (0.01)	0.02 (0.04)

Only for *A. testudineus* and *N. notopterus* is there a significant contribution of food items to the seasonal dissimilarity of diet composition. Numbers within brackets are standard deviations.

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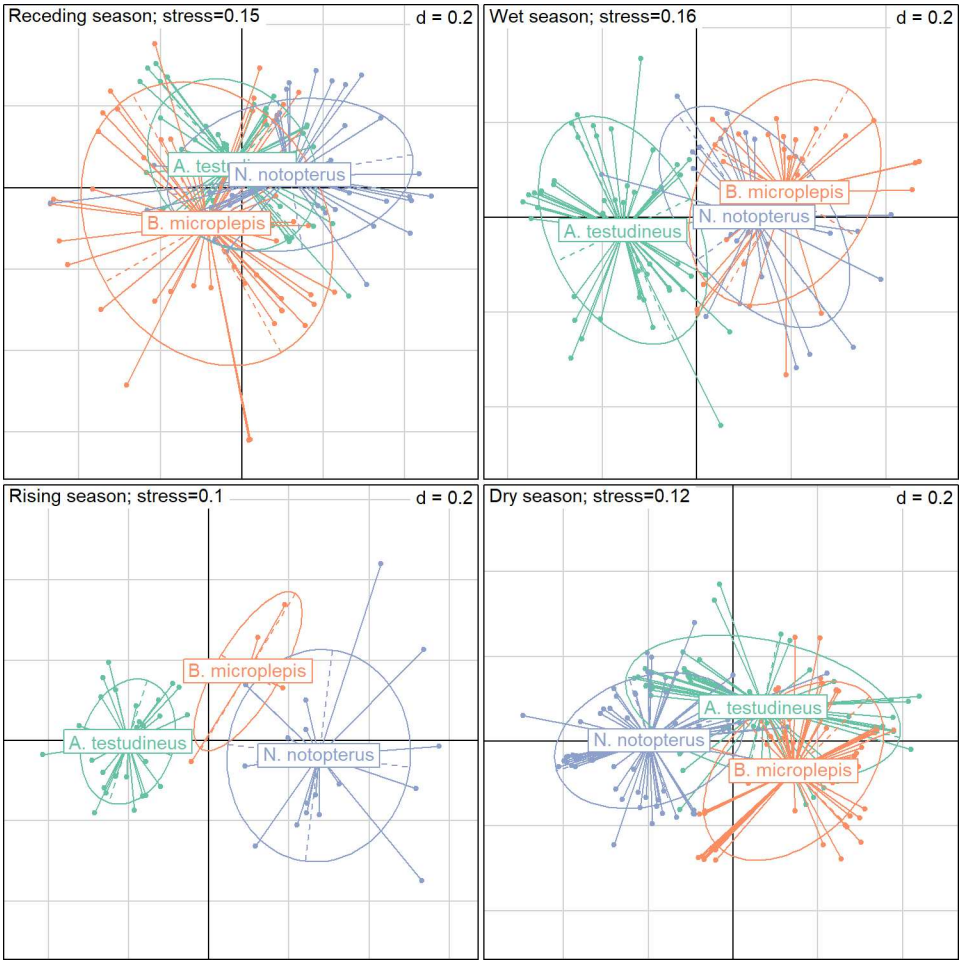

Fig 3. NMDS biplots displaying the diet of the three species across the four seasons. The size of the ellipse represent species diet breadth whereas overlap between ellipses relates to dietary overlap between species.

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seasonal variations in the diet breadth and dietary overlap of the three species. Diet breadth was the largest during the dry and the receding seasons whereas dietary overlap between species was the lowest during the dry season. We also found evidence for seasonal variations in the diet of *A. testudineus* and *N. notopterus* with a differential contribution of food items, while no significant change was found for *B. microlepis*.

A similar seasonal variation in the proportion of empty stomachs suggests that ecological differences between species (e.g. reproductive behavior, foraging abilities) are probably not strong enough to outweigh the effect of seasonal variations in resource abundance. For the

Table 3. Diet breadth estimate for the three studies species across the four seasons. *p*-values were obtained using 1000 permutations on the community matrix. Values inferior to 0.05 point to a significant difference in the diet breadth of the three species.

Hydrological phase	*A. TESTUDINEUS*	*B. MICROLEPIS*	*N. NOTOPTERUS*	P-VALUE
Receding season	0.45	0.53	0.47	0.002
Wet season	0.48	0.42	0.46	0.115
Rising season	0.38	0.34	0.51	0.004
Dry season	0.54	0.48	0.49	0.005

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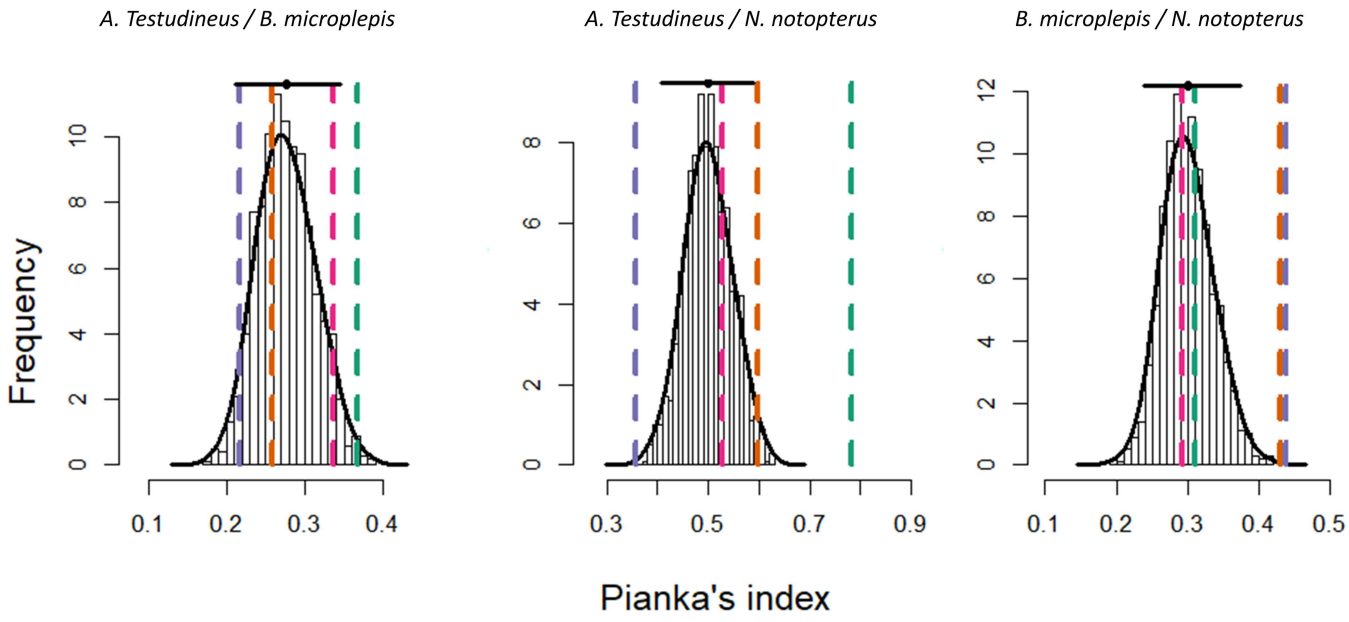

Fig 4. Results from the bootstrap procedure conducted on Pianka's symmetric index, measuring the degree of niche overlap between the diets of two species. Histograms present the generated distribution of Pianka's index between two species under the null hypothesis that there is no seasonal variation in dietary overlap. At the top of each histogram, the black horizontal bar represents the 95% confidence interval of the distribution while the black dot represents the average of the distribution. Colored vertical dashed lines point to the observed measure of niche overlap between two species in each season: receding season = green; wet season = orange; rising season = purple; dry season = pink. Any vertical line not overlapping the horizontal black line indicate a significant difference in the niche overlap for the corresponding season.

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three species, the proportion of empty stomachs was the lowest during the dry season (i.e. when floodplain habitats are unachievable) but the highest during the receding season, which contrast to our expectation. One possible explanation would be that the high abundance and diversity of fish during the receding season, combined with the reversal of the river flow, that sweeps out resources from the system, would increase competition for resources, thereby decreasing the *per capita* consumption rate [50]. In contrast, the low abundance and diversity of fish during the dry season might contribute to increase the species *per capita* consumption rate, although the amount of resources is lower relative to the receding season. Another, non-exclusive explanation would be that during the receding season, individuals rely on reserve energy stored during the wet season, while during the dry season, individuals have to maximize their energy intake to face an increase in metabolic demand caused by adverse conditions such as oxygen depletion [12].

In contrast to the proportion of empty stomachs, we found differences in the seasonal variation of the stomach contents of the three species. Such variations likely result from temporary connections to floodplain habitats caused by expansion-contraction cycles of the TSL's flooded area, providing access to new resources [51,52]. For instance, the increase in the proportion of crustaceans and insects in the diet of *B. microlepis* between the dry and the rising seasons can be explained by the progressive connection to floodplain habitats making it possible for individuals to forage in previously unflooded areas where those items are rather abundant. Similar changes were observed within other tropical systems where seasonality was shown to influence fish diet through an increase in the frequency of particular food items such as terrestrial insects and amphipods during the rainy season [53]. In line with our expectation, we found that fish prey contributed strongly to seasonal variations in the diet of *A. testudineus* with a substantial increase (i.e. around 10%) during the dry season. This suggest that the ability for this species to

face adverse conditions (i.e. low levels of oxygen) makes it possible for individuals to exclude other competitors and to forage on the most profitable resource independently of the connection to floodplain habitats [54].

In line with our expectation and with previous findings [55], we found that the diet breadth of the three species tended to be larger during the dry (and the receding) season. This result could be explained by an increase in both intra and interspecific competition, constraining individuals to adopt an opportunistic strategy and diversify their diet to reduce competition [24]. The diet breadth of the three species differed in all seasons, except the wet season. This lack of difference was due to an increase in the diet breadth of *A. testudineus* and *B. microlepis* combined with a decrease in the diet breadth of *N. notopterus* between the rising and the wet seasons, leading to a similar diet breadth between the three species (from 0.42 to 0.48). The increase observed for the first two species can be explained by an increase in the diversity and amount of resources combined with a release of the competitive pressure, making it possible for those species to diversify their diet. In contrast, the decrease observed for the last species can be explained by its ability to forage on a large array of resources during periods of shortage (habitat generalist) while during periods of resource abundance individuals can focus on the most profitable resource. As expected, we found large seasonal variations in the diet breadth of *A. testudineus* and *B. microlepis* but low variations in the diet breadth of *N. notopterus*. The large variations observed for *A. testudineus* and *B. microlepis* are in accordance with their ecological status (invasive for the former and long-distant migrant for the latter), making it possible for these species to adapt their diet as the amount and the diversity of resources changes over time or space. In contrast, the large and stable diet breadth observed in *N. notopterus* could be attributed to its high mobility between diverse habitats that potentially contain different resources.

Regarding temporal changes in the availability, quantity and quality of food resources, species are expected to adjust their foraging behavior in order to maximize their energy intake and minimize dietary overlap [52]. In this study, we found an overall high dietary overlap between species during the receding season (e.g. between *A. testudineus* and *N. notopterus)* and a lower dietary overlap during the rising season, particularly when *B. microlepis* was involved in the comparison, in accordance with our expectation. The pattern observed during the receding season can be explained by the progressive loss of resources, as the lake retracts, whereas the one observed during the rising season can be explained by the progressive connection to floodplain habitats providing opportunities for species to forage on different resources. Contrasted results have however been reported in the literature. For instance, some studies have found that dietary overlap tends to be the lowest during the dry season because fish tend to concentrate in small, well-oxygenated, areas [26,56], whereas others [17,21,25] found the opposite (i.e. high dietary overlap during the dry season). In flood-pulse systems, fish assemblages and diet composition have been shown to differ with respect to habitat heterogeneity, hydrological conditions and connectivity between adjacent systems [57] while the intensity and the duration of the flood pulse have also been shown to strongly influence dietary overlap between species [11]. The absence of general pattern suggests that seasonal changes in trophic dynamics are not fully explained by feeding strategies, that aim to reduce competition between species and individuals, but that feeding opportunism may be an important underlying factor [21]. The discrepancies existing between previous studies and this one reflect the fact that different patterns can occur depending on the characteristics of the system, including its productivity, the nature of resources (e.g. autochtonous *vs*. allochtonous) and the characteristics of the species (e.g. generalist *vs*. specialist).

Concluding remarks

This study is based on stomach contents analyses, for which a number of issues have been identified [58]. Indeed, stomach contents only reflect a "snapshot" of an individual's recent diet and can be highly variable among individuals [59]. Furthermore, stomach contents are usually biased toward recent dietary items and prey that does not readily digest, such as zooplankton, and can underestimate the amount of other preys, such as fish [60]. Differential digestion rates between species may also have an influence on the estimation of dietary overlap [58]. Likewise, since larger individuals tend to have larger stomachs, variations in diet composition mainly reflects variations in adult diets while among-species differences in diet breadth can be influenced by differences in species' sizes. Nonetheless, these issues should have a minimal influence on our results because (i) we have sampled individuals of various sizes in different locations, thus ensuring that we have a global overview of the diet of the different species and (ii) our analyses are based on the frequency of occurrence and thus are not influenced by the abundance of food items relative to other individuals or species. An alternative to stomach content analyses is to use stable isotopes of Carbon and Nitrogen to quantify the dietary composition of individuals [61]. However, limitations have also been raised regarding this approach [62] and it seems that the best way to proceed is actually to use both approaches as complementary insights can be gained relative to when they are used separately [60,61].

The strong seasonal variations highlighted here with respect to diet composition, diet breadth and dietary overlap can be explained by a variety of mechanisms including changes in resource abundance and diversity, changes in the strength of competitive interactions between individuals and species as well as changes in ontogeny [63]. Teasing apart the relative influence of these factors is impossible with our data. The collection of additional data across seasons, for various organisms belonging to different trophic compartments (e.g. phytoplankton, zooplankton, invertebrates) and age classes (reflecting variable development stage) and in multiple locations spread over the lake (especially floodplain habitats) would help gain knowledge about (i) the nature of interactions between species and individuals and (ii) the extent to which they can shift their diet as the connectivity to floodplain habitats is changing. Such a study would not only improve our understanding of the mechanisms promoting biodiversity within flood-pulse systems but might also help guide management strategies within the Tonle Sap.

Overall, our results suggest that the flood-pulse may play a role in mediating the competitive interactions between the three species by making it possible for species to shift their diet as the availability of resources changes over time. This may ultimately promote biodiversity by providing opportunities for species to avoid competition and live in harmony with other species displaying similar dietary requirements during some periods of the year. This harmony is however threatened by accelerating water infrastructure development (hydropower, irrigation, flood control, and water supply) and climate change, bringing considerable modifications to the flood pulse of the Tonle Sap Lake in the foreseeable future.

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Annexes

Annex 1: Table S1. List of 242 fish species found in TSL and TSR during the period of two and half water cycles from January 2012 to May 2014.

Scientific name	Species abbreviation	Genera name	Family name
Aaptosyax grypus	Aagr	Aaptosyax	Cyprinidae
Acanthopsis spp.	Acsp	Acanthopsoides	Cobitidae
Acanthopsoides delphax	Acde	Acanthopsoides	Cobitidae
Acanthopsoides gracilentus	Acgr	Acanthopsoides	Cobitidae
Achiroides leucorhynchos	Acle	Achiroides	Soleidae
Achiroides melanorhynchus	Acme	Achiroides	Soleidae
Albulichthys albuloides	Alal	Albulichthys	Cyprinidae
Ambastaia sidthimunki	Amsi	Ambastaia	Cobitidae
Amblyrhynchichthys truncatus	Amtr	Amblyrhynchichthys	Cyprinidae
Anabas testudineus	Ante	Anabas	Anabantidae
Anguilla marmorata	Anma	Anguilla	Anguillidae
Apocryptodon madurensis	Apma	Apocryptodon	Gobiidae
Arius maculatus	Arma	Arius	Ariidae
Arius venosus	Arve	Arius	Ariidae
Bagarius bagarius	Baba	Bagarius	Sisoridae
Bagarius suchus	Basu	Bagarius	Sisoridae
Bagarius yarrelli	Baya	Bagarius	Sisorinae
Bagrichthys majusculus	Bama	Bagrichthys	Bagridae
Bagrichthys obscurus	Baob	Bagrichthys	Bagridae
Balitoropsis zollingeri	Bazo	Balitoropsis	Balitoridae
Bangana sp.	Basp	Bangana	Cyprinidae
Bangana yunnanensis	Bayu	Bangana	Cyprinidae
Barbichthys laevis	Bala	Barbichthys	laevis
Barbodes binotatus	Babi	Barbodes	Cyprinidae
Barbodes rhombeus	Barh	Barbodes	Cyprinidae
Barbonymus altus	Baal	Barbonymus	Cyprinidae
Barbonymus gonionotus	Bago	Barbonymus	Cyprinidae
Barbonymus schwanenfeldii	Basc	Belodontichthys	Siluridae
Belodontichthys truncatus	Betr	Belodontichthys	Siluridae
Boesemania microlepis	Bomi	Boesemania	Sciaenidae
Brachirus harmandi	Brha	Brachirus	Soleidae
Brachirus orientalis	Bror	Brachirus	Soleidae
Butis amboinensis	Buam	Butis	Eleotridae
Carcharhinus dussumieri	Cadu	*Carcharhinus:*	Carcharhinidae
Catlocarpio siamensis	Casi	Catlocarpio	Cyprinidae
Channa gachua	Chga	Channa	Channidae
Channa lucius	Chlu	Channa	Channidae
Channa marulioides	Chma	Channa	Channidae
Channa marulius	Chma.us	Channa	Channidae
Channa micropeltes	Chmi	Channa	Channidae
Channa striata	Chst	Channa	Channidae
Chitala blanci	Chbl	Channa	Channidae

Chitala lopis	Chlo	Chitala	Notopteridae
Chitala ornata	Chor	Chitala	Notopteridae
Cirrhinus cirrhosus	Cici	Cirrhinus	Cyprinidae
Cirrhinus jullieni	Ciju	Cirrhinus	Cyprinidae
Cirrhinus microlepis	Cimi	Cirrhinus	Cyprinidae
Cirrhinus molitorella	Cimo	Cirrhinus	Cyprinidae
Clarias batrachus	Clba	Clarias	Clariidae
Clarias cataractus	Clca	Clarias	Clariidae
Clarias gariepinus	Clga	Clarias	Clariidae
Clarias macrocephalus	Clma	Clarias	Clariidae
Clarias meladerma	Clme	Clarias	Clariidae
Clarias sp.	Clsp	Clarias	Clariidae
Clupisoma longianalis	Cllo	Clupisoma	Ailiidae
Coilia lindmani	Coli	Coilia	Engraulidae
Coilia macrognathos	Coma	Coilia	Engraulidae
Corica soborna	Coso	Corica	Clupeidae
Cosmochilus harmandi	Coha	Cosmochilus	Cyprinidae
Crossocheilus atrilimes	Crat	Crossocheilus	Cyprinidae
Cyclocheilichthys apogon	Cyap	Cyclocheilichthys	Cyprinidae
Cyclocheilichthys armatus	Cyar	Cyclocheilichthys	Cyprinidae
Cyclocheilichthys enoplos	Cyen	Cyclocheilichthys	Cyprinidae
Cyclocheilichthys heteronema	Cyhe	Cyclocheilichthys	Cyprinidae
Cyclocheilichthys lagleri	Cyla	Cyclocheilichthys	Cyprinidae
Cyclocheilichthys repasson	Cyre	Cyclocheilichthys	Cyprinidae
Cyclocheilos furcatus	Cyfu	Cyclocheilichthys	Cyprinidae
Cynoglossus feldmanni	Cyfe	Cynoglossus	Cynoglossidae
Cynoglossus microlepis	Cymi	Cynoglossus	Cynoglossidae
Cyprinus carpio	Cyca	Cyprinus	Cyprinidae
Datnioides polata	Dapo	Datnioides	Labotidae
Datnioides undecimradiatus	Daun	Datnioides	Labotidae
Devario leptos	Dele	Devario	Cyprinidae
Discherodontus ashmeadi	Dias	Discherodontus	Cyprinidae
Discherodontus parvus	Dipa	Discherodontus	Cyprinidae
Esomus metallicus	Esme	Esomus	Cyprinidae
Folifer brevifilis	Fobr	Folifer	Cyprinidae
Gambusia affinis	Gaaf	Gambusia	Poeciliidae
Garra fasciacauda	Gafa	Garra	Cyprinidae
Glossogobius aureus	Glau	Glossogobius	Cobitidae
Glossogobius giuris	Glgi	Glossogobius	Cobitidae
Glyptothorax fuscus	Glfu	Glyptothorax	Sisoridae
Glyptothorax horai	Glho	Glyptothorax	Sisoridae
Glyptothorax laosensis	Glla	Glyptothorax	Sisoridae
Gymnothorax tile	Gyti	Gymnothorax	Muraenidae
Gyrinocheilus pennocki	Gype	Gyrinocheilus	Gyrinocheilidae
Hampala dispar	Hadi	Hampala	Cyprinidae
Hampala macrolepidota	Hama	Hampala	Cyprinidae
Helicophagus waandersii	Hewa	Helicophagus	Pangasiidae
Helostoma temminckii	Hete	Helostoma	Helostomatidae
Hemiarius stormii	Hest	Hemiarius	Ariidae

Hemibagrus filamentus	Hefi	Hemibagrus	Bagridae
Hemibagrus nemurus	Hene	*Hemibagrus*	Bagridae
Hemibagrus spilopterus	Hesp	Hemibagrus	Bagridae
Hemibagrus wyckii	Hewy	Hemibagrus	Bagridae
Hemibagrus wyckioides	Hewy.des	Hemibagrus	Bagridae
Hemimyzon pengi	Hepe	Hemimyzon	Balitoridae
Hemisilurus mekongensis	Heme	Hemisilurus	Siluridae
Henicorhynchus lobatus	Helo	Henicorhynchus	Cyprinidae
Henicorhynchus siamensis	Hesi	Henicorhynchus	Cyprinidae
Heteropneustes kemratensis	Heke	Heteropneustes	Heteropneustidae
Himantura undulata	Hiun	Himantura	Dasyatidae
Hypophthalmichthys molitrix	Hymo	Hypophthalmichthys	Cyprinidae
Hypophthalmichthys nobilis	Hyno	Hypophthalmichthys	Cyprinidae
Hyporhamphus limbatus	Hyli	Hyporhamphus	Hemiramphidae
Hypsibarbus lagleri	Hyla	Hypsibarbus	Cyprinidae
Hypsibarbus malcolmi	Hyma	Hypsibarbus	Cyprinidae
Hypsibarbus pierrei	Hypi	Hypsibarbus	Cyprinidae
Hypsibarbus suvattii	Hysu	Hypsibarbus	Cyprinidae
Hypsibarbus vernayi	Hyve	Hypsibarbus	Cyprinidae
Hypsibarbus wetmorei	Hywe	Hypsibarbus	Cyprinidae
Incisilabeo behri	Inbe	Incisilabeo	Cyprinidae
Kryptopterus cryptopterus	Krcr	Kryptopterus	Siluridae
Kryptopterus schilbeides	Krsc	Kryptopterus	Siluridae
Labeo chrysophekadion	Lach	Labeo	Cyprinidae
Labeo dyocheilus	Lady	Labeo	Cyprinidae
Labeo rohita	Laro	Labeo	Cyprinidae
Labiobarbus lineatus	Lali	Labiobarbus	Cyprinidae
Labiobarbus siamensis	Lasi	Labiobarbus	Cyprinidae
Labiobarbus sp. cf. lineatus	Lasp	Labiobarbus	Cyprinidae
Laides longibarbis	Lalo	Laides	Schilbeidae
Laubuka laubuca	Lala	Laubuka	Cyprinidae
Leptobarbus hoevenii	Leho	Leptobarbus	Cyprinidae
Lobocheilos melanotaenia	Lome	Lobocheilos	Cyprinidae
Lobocheilos rhabdoura	Lorh	Lobocheilos	Cyprinidae
Longiculter siahi	Losi	Longiculter	Cyprinidae
Luciosoma bleekeri	Lubl	Luciosoma	Cyprinidae
Lycothrissa crocodilus	Lycr	Lycothrissa	Engraulidae
Macrochirichthys macrochirus	Mama	Macrochirichthys	Cyprinidae
Macrognathus circumcinctus	Maci	Macrognathus	Mastacembelidae
Macrognathus siamensis	Masi	Macrognathus	Mastacembelidae
Mastacembelus armatus	Maar	Mastacembelus	Mastacembelidae
Megalops cyprinoides	Mecy	Megalops	Magalopida
Mekongina erythrospila	Meer	Mekongina	
Micronema cheveyi	Mich	Micronema	Siluridae
Micronema hexapterus	Mihe	Micronema	Siluridae
Misgurnus anguillicaudatus	Mian	Micronema	Siluridae
Monopterus albus	Moal	Monopterus	Synbranchidae

Mystacoleucus obtusirostris	Myob	Mystacoleucus	Cyprinidae
Mystus albolineatus	Myal	Mystus	Bagridae
Mystus atrifasciatus	Myat	Mystus	Bagridae
Mystus bocourti	Mybo	Mystus	Bagridae
Mystus mysticetus	Mymy	Mystus	Bagridae
Mystus singaringan	Mysi	Mystus	Bagridae
Mystus wolffii	Mywo	Mystus	Bagridae
Nemapteryx nenga	Nene	Nemapteryx	Ariidae
Neolissochilus blanci	Nebl	Neolissochilus	Cyprinidae
Netuma thalassina	Neth	netuma	Ariidae
Notopterus notopterus	Nono	Notopterus	Notopteridae
Ompok bimaculatus	Ombi	Ompok	Siluridae
Ompok hypophthalmus	Omhy	Ompok	Siluridae
Ophisternon bengalense	Opbe	Ophisternon	Synbranchidae
Osphronemus exodon	Osex	Osphronemus	Osphronemidae
Osphronemus goramy	Osgo	Osphronemus	Osphronemidae
Osteochilus lini	Osli	Osteochilus	Cyprinidae
Osteochilus melanopleurus	Osme	Osteochilus	Cyprinidae
Osteochilus microcephalus	Osmi	Osteochilus	Cyprinidae
Osteochilus schlegeli	Ossc	Osteochilus	Cyprinidae
Osteochilus vittatus	Osvi	Osteochilus	Cyprinidae
Osteochilus waandersii	Oswa	Osteochilus	Cyprinidae
Osteogeneiosus militaris	Osmi.ris	Osteogeneiosus	Ariidae
Oxyeleotris marmorata	Oxma	Oxyeleotris	Eleotridae
Pangasianodon gigas	Pagi	Pangasianodon	Pangasiidae
Pangasianodon hypophthalmus	Pahy	Pangasianodon	Pangasiidae
Pangasius bocourti	Pabo	Pangasius	Pangasiidae
Pangasius conchophilus	Paco	Pangasius	Pangasiidae
Pangasius djambal	Padj	Pangasius	Pangasiidae
Pangasius krempfi	Pakr	Pangasius	Pangasiidae
Pangasius kunyit	Paku	Pangasius	Pangasiidae
Pangasius larnaudii	Pala	Pangasius	Pangasiidae
Pangasius macronema	Pama	Pangasius	Pangasiidae
Pangasius nasutus	Pana	Pangasius	Pangasiidae
Pangasius polyuranodon	Papo	Pangasius	Pangasiidae
Pangasius spp.	Pasp	Pangasius	Pangasiidae
Pao cambodgiensis	Paca	Pao	Tetraodontidae
Pao leiurus	Pale	Pao	Tetraodontidae
Parachela maculicauda	Pama.cul	Parachela	Cyprinidae
Parachela siamensis	Pasi	Parachela	Cyprinidae
Paralaubuca barroni	Paba	Paralaubuca	Cyprinidae
Paralaubuca riveroi	Pari	Paralaubuca	Cyprinidae
Paralaubuca typus	Paty	Paralaubuca	Cyprinidae
Parambassis apogonoides	Paap	Parambassis	Ambassidae
Parambassis siamensis	Pasi.sis	Parambassis	Ambassidae
Parambassis wolffii	Pawo	Parambassis	Ambassidae
Periophthalmodon septemradiatus	Pese	Periophthalmodon	Gobiidae
Phalacronotus apogon	Phap	Phalacronotus	Siluridae

Phalacronotus bleekeri	Phbl	Phalacronotus	Siluridae
Phalacronotus micronemus	Phmi	Phalacronotus	Siluridae
Piaractus brachypomus	Pibr	Piaractus	Serrasalmidae
Polynemus dubius	Podu	Polynemus	Polynemidae
Polynemus melanochir	Pome	Polynemus	Polynemidae
Polynemus multifilis	Pomu	Polynemus	Polynemidae
Poropuntius deauratus	Pode	Poropuntius	Cyprinidae
Pristis microdon	Prmi	Pristis	Pristidae
Pristolepis fasciata	Prfa	Pristolepis	Pristolepididae
Probarbus jullieni	Prju	Pristolepis	Nandidae
Probarbus labeamajor	Prla	Probarbus	Cyprinidae
Pseudolais micronemus	Psmi	Pseudolais	Pangasiidae
Pseudolais pleurotaenia	Pspl	Pseudolais	Pangasiidae
Pseudomystus siamensis	Pssi	Pseudomystus	Bagridae
Puntioplites bulu	Pubu	Puntioplites	Cyprinidae
Puntioplites falcifer	Pufa	Puntioplites	Cyprinidae
Puntioplites proctozysron	Pupr	Puntioplites	Cyprinidae
Puntioplites waandersi	Puwa	Puntioplites	Cyprinidae
Puntius brevis	Pubr	Puntioplites	Cyprinidae
Raiamas guttatus	Ragu	Raiamas	Cyprinidae
Rasbora borapetensis	Rabo	Rasbora	Cyprinidae
Rasbora myersi	Ramy	Rasbora	Cyprinidae
Rasbora paviana	Rapa	Rasbora	Cyprinidae
Rasbora tornieri	Rato	Rasbora	Cyprinidae
Rasbora trilineata	Ratr	Rasbora	Cyprinidae
Rasbosoma spilocerca	Rasp	Rasbosoma	Cyprinidae
Rhinogobius taenigena	Rhta	Rhinogobius	Gobiidae
Scaphognathops bandanensis	Scba	Scaphognathops	Cyprinidae
Scaphognathops stejnegeri	Scst	Scaphognathops	Cyprinidae
Schistura aramis	Scar	Schistura	Namacheilidae
Schistura athos	Scat	Schistura	Namacheilidae
Schistura crabro	Sccr	Schistura	Namacheilidae
Schistura daubentoni	Scda	Schistura	Namacheilidae
Schistura latifasciata	Scla	Schistura	Namacheilidae
Scleropages formosus	Scfo	Scleropages	Osteoglossidae
Sikukia gudgeri	Sigu	Sikukia	Cyprinidae
Syncrossus beauforti	Sybe	Syncrossus	Cobitidae
Syncrossus helodes	Syhe	Syncrossus	Cobitidae
Systomus rubripinnis	Syru	Tenualosa	Clupeidae
Tenualosa thibaudeaui	Teth	Tenualosa	Clupeidae
Tenualosa toli	Teto	Tenualosa	Clupeidae
Thynnichthys thynnoides	Thth	Thynnichthys	Cyprinidae
Tor laterivittatus	Tola	Tor	Cyprinidae
Tor sinensis	Tosi	Tor	Cyprinidae
Tor tambroides	Tota	Tor	Cyprinidae
Toxotes chatareus	Toch	Toxotes	Toxotidae
Toxotes microlepis	Tomi	Toxotes	Toxotidae
Trichopodus microlepis	Trmi	Trichogaster	Osphronemidae
Trichopodus pectoralis	Trpe	Trichogaster	Osphronemidae

Trichopodus trichopterus	Trtr	Trichogaster	Osphronemidae
Wallago attu	aat	Wallago	Siluridae
Wallago leerii	Wale	Wallago	Siluridae
Xenentodon cancila	Xeca	Xenentodon	Belonidae
Yasuhikotakia eos	Yaeo	Yasuhikotakia	Botiidae
Yasuhikotakia lecontei	Yale	Yasuhikotakia	Botiidae
Yasuhikotakia modesta	Yamo	Yasuhikotakia	Botiidae

Annex 2: Table S2. List and characteristics of the 39 fish species included in this study. The characteristic abbreviations are as follow. For habitat: 1=demersal, 2=pelagic, 3=benthopelagic, 4=pelagic-neritic. For trophic guild: 1=algivore-detritivore, 2=invertivore-piscivore, 3=invertivore, 4=omnivore, 5=piscivore. Migratory status: NM=non-migratory species, M=migratory species.

Species	Species Abbreviation	Habitat	Trophic guild	Migration pattern
Amblyrhynchichthys truncates	Amtr	3	1	M
Anabas testudineus	Ante	1	2	NM
Barbonymus gonionotus	Bago	3	1	NM
Boesemania.microlepis	Bomi	3	2	M
Channa micropeltes	Chmi	3	5	NM
Channa striata	Chst	3	5	NM
Cyclocheilichthys armatus	Cyar	3	4	NM
Cyclocheilichthys enoplos	Cyen	3	4	M
Hampala macrolepidota	Hama	3	3	M
Henicorhynchus siamensis	Hesi	3	1	M
Hemibagrus spilopterus	Hesp	1	3	NM
Henicorhynchus lobatus	Helo	3	1	M
Labeo chrysophekadion	Lach	3	1	M
Labiobarbus lineatus	Lali	3	4	M
Labiobarbus leptocheilus	Lale	1	4	NM
Labiobarbus siamensis	Lasi	3	4	M
Mystus bocourti	Mybo	1	3	NM
Mystus albolineatus	Myal	1	2	NM
Mystus mysticetus	Mymy	1	3	NM
Mystus singaringan	Mysi	1	3	NM
Notopterus notopterus	Nono	1	2	NM
Osteochilus vittatus	Osvi	3	4	NM
Paralaubuca typus	Paty	3	3	M
Parachela maculicauda	Pama	1	1	NM
Parambassi wolffi	Pawo	1	2	NM
Parambassis apogonoides	Paap	1	2	NM
Pristolepis fasciata	Prfa	1	3	NM
Puntioplites proctozysron	Pupr	3	4	NM

Ompok bimaculatus	Ombi	1	2	NM
Osteochilus.melanople	Osme	4	4	M
Oxyeleotris marmorata	Oxma	1	2	NM
Pangasianodon hypophthalmus	Pahy	3	4	M
Pangasius.larnaudii	Pala	3	4	M
Poropuntius deauratus	Pode	3	4	M
Rasbora tornieri	Rato	3	4	NM
Trichohodus trichopterus	Trtr	1	4	NM
Thynnichthys thynnoides	Thth	3	4	M
Trichopodus microlepis	Trmi	1	4	NM
Xenentodon cancila	Xeca	4	5	M

Annex 3: Table S3. Total body length (mm), seasonal shift (Δ) and effect size (±95% confidence intervals) of the Δ in trophic position (calculated as mean dry – mean wet trophic position) for 28 species from the Tonle Sap Lake. Species with bold values had effect sizes ± 95% CI that did not bound zero. Sample size (n) and total length in each season, and the putative functional group for each species based on previous diet data, is also provided ('Pisc. Omn.' are piscivorous omnivores that consume large amounts of both invertebrates and fish).

Species	Functional group	Mean length	Seasonal Δ trophic position	Effect size	± 95% CI	n dry	n wet	Mean $\delta^{15}N$ dry	Mean $\delta^{15}N$ wet	Mean dry length	Mean wet length
Trichopodus trichopterus	Omnivore	79	-0.05	-0.13	0.80	10	15	7.54	7.61	91	71
Rasbora aurotaenia	Omnivore	93	-0.10	-0.39	0.92	8	11	8.80	9.12	101	88
Pristolepis fasciata	Invertivore	99	-0.06	-0.19	0.62	16	27	9.30	9.52	96	100
Trichopodus microlepis	Omnivore	101	-0.51	-2.45	1.19	9	10	7.03	8.62	108	94
Paralaubuca typus	Invertivore	103	-0.08	-0.31	0.94	5	37	9.27	9.57	105	103
Anabas testudineus	Pisc. Omn.	108	0.28	0.99	0.93	11	9	9.12	8.19	114	101
Henicorhynchus siamensis	Detritivore	111	-0.25	-0.67	0.72	9	48	7.07	7.78	137	106
Thynnichthys thynnoides	Omnivore	112	0.37	1.53	0.79	9	39	8.19	6.90	120	110
Labiobarbus leptocheila	Omnivore	124	0.33	0.98	0.85	8	22	8.49	7.34	135	120
Parambassis wolffii	Piscivore	124	0.13	0.53	0.73	16	14	11.91	11.69	119	130
Barbonymus gonionotus	Omnivore	151	-0.19	-0.52	0.64	12	50	7.97	8.53	194	141
Mystus albolineatus	Pisc. Omn.	155	-0.03	-0.13	0.74	13	15	9.95	10.11	164	146
Osteochilus melanopleura	Omnivore	157	0.61	2.38	1.16	8	12	9.55	7.57	189	135
Puntioplites proctozysron	Omnivore	164	-0.01	-0.03	0.82	16	9	9.25	9.31	160	170
Ompok bimaculatus	Omnivore	166	-0.06	-0.19	0.98	12	6	9.73	9.97	164	171
Hemibagrus spilopterus	Invertivore	185	0.14	0.41	0.66	12	35	10.76	10.42	219	174
Macrognathus siamensis	Invertivore	200	0.17	0.45	0.91	12	8	8.56	7.99	204	194
Notopterus notopterus	Pisc. Omn.	212	0.12	0.34	0.82	14	10	9.98	9.64	206	220
Kryptopterus apogon	Piscivore	216	0.64	2.21	1.07	13	9	11.49	9.53	229	197
Clarias macrocephalus	Omnivore	220	0.22	0.81	1.04	15	5	8.92	8.18	233	182
Cyclocheilichthys enoplos	Omnivore	230	-0.32	-0.87	0.71	15	19	8.33	9.34	262	206
Labeo chrysophekadion	Detritivore	231	0.05	0.15	0.80	11	13	8.00	7.79	297	175

Channa striata	Piscivore	290	0.41	0.69	0.84	16	9	10.55	9.29	322	234
Pangasius larnaudii	Omnivore	305	0.01	0.04	0.86	7	20	10.84	10.94	343	292
Boesemania microlepis	Piscivore	311	-0.31	-1.02	0.88	13	10	11.56	12.78	321	298
Channa micropeltes	Piscivore	353	-0.18	-0.46	0.95	16	6	9.00	9.62	370	307

Annex 4: Table S4. Sample size (n) and total body length (mm) for fish sampled during each season for stomach content analysis from the Tonle Sap lake, Cambodia. Proportions of fish, invertebrates and plants in the stomach contents by weight. All values are mean ± SD.

Species	Season	Stomach content data				
		n	Length (mm)	Fish	Invert.	Plant
Anabas testudineus	Dry	13	122 ± 14	0.52 ± 0.22	0.10 ± 0.22	0.12 ± 0.17
Climbing Perch	Wet	22	118 ± 24	0.48 ± 0.33	0.25 ± 0.29	0.11 ± 0.16
Notopterus notopterus	Dry	12	197 ± 25	0.42 ± 0.26	0.27 ± 0.23	0.17 ± 0.07
Bronze Featherback	Wet	6	148 ± 107	0.20 ± 0.31	0.56 ± 0.35	0.10 ± 0.07
Channa striata	Dry	5	282 ± 55	0.57 ± 0.08	0.01 ± 0.00	0.08 ± 0.04
Striped Snakehead	Wet	10	256 ± 90	0.47 ± 0.13	0.09 ± 0.24	0.13 ± 0.04
Channa micropeltes	Dry	25	367 ± 45	0.68 ± 0.14	0.01 ± 0.04	0.11 ± 0.08
Giant Snakehead	Wet	7	395 ± 89	0.70 ± 0.10	0.03 ± 0.06	0.10 ± 0.05

Annex 5: Table S5. Baseline values of $\delta^{13}C$ and $\delta^{15}N$ sampled from the Tonle Sap Lake and used to calculate trophic positions for the present study. All values are mean ± SD.

Season	Baseline type	$\delta^{13}C$	$\delta^{15}N$	Mean baseline $\delta^{15}N$ used in TP calculations
Dry	Benthic	-29.23 ± 4.09	5.89 ± 1.87	6.15
	Pelagic	-29.10 ± 4.38	6.30 ± 1.96	
Wet	Benthic	-28.74 ± 3.32	5.67 ± 1.30	5.92
	Pelagic	-35.34 ± 4.78	6.16 ± 1.66	

Annex 6: Table S6. Results of zero inflated beta regression on the proportion of invertebrates, fish and plants in the stomachs of Tonle Sap Lake species. Season (wet, dry) and body length were included as explanatory variables and species and location as random variables.

Response variable	Parameter	Posterior mean	Posterior median	2.5% quantile	97.5% quantile
Proportion of invertebrate	bintercept	-3.95	-4.05	-5.73	-1.71
	bwet	-0.32	-0.33	-0.90	0.25
	bbodylength	-0.01	-0.01	-0.01	0.00
	b0intercept	0.63	0.55	-1.47	3.19
	b0wet	-1.14	-1.16	-2.03	-0.20
	b0bodylength	0.00	0.00	0.00	0.01
Proportion of fish	bintercept	-5.16	-5.15	-5.64	-4.68
	bwet	0.04	0.04	-0.08	0.15
	bbodylength	0.00	0.00	0.00	0.00
	b0intercept	-0.42	-0.46	-2.41	1.45
	b0wet	0.79	0.76	-0.47	2.28
	b0bodylength	-0.01	-0.01	-0.02	0.00
Proportion of plant	bintercept	-6.50	-6.50	-6.96	-6.06
	bwet	-0.25	-0.25	-0.51	0.01
	$b_{bodylength}$	0.00	0.00	0.00	0.00
	$b0_{intercept}$	-0.87	-0.87	-2.56	0.80
	$b0_{wet}$	-1.38	-1.35	-2.99	-0.01
	$b0_{bodylength}$	0.00	0.00	-0.01	0.00