

FLOODPLAIN RIVER FOOD WEBS IN THE LOWER MEKONG BASIN

A Dissertation

by

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ABSTRACT

The Mekong River is one of the world's most important rivers in terms of its size, economic importance, cultural significance, productivity, and biodiversity. The Mekong River's fisheries and biodiversity are threatened by major hydropower development and over-exploitation. Knowledge of river food web ecology is essential for management of the impacts created by anthropogenic activities on plant and animal populations and ecosystems. In the present study, I surveyed four tropical rivers in Cambodia within the Mekong River Basin. I examined the basal production sources supporting fish biomass in the four rivers during the dry and wet seasons and explored the relationship between trophic position and body size of fish at various taxonomic levels, among local species assemblages, and across trophic guilds. I used stable isotopes of carbon and nitrogen to estimate fish trophic levels and the principal primary production sources supporting fishes. My study provides evidence that food web dynamics in tropical rivers undergo significant seasonal shifts and emphasizes that river food webs are altered by dams and flow regulation. Seston and benthic algae were the most important production sources supporting fish biomass during the dry season, and riparian macrophytes appeared to be the most important production source supporting fishes during the wet season. In the river with strong flow regulation from an upstream impoundment, seston and benthic algae were even more important production sources supporting fishes during the dry season. My findings challenge the Eltonian theory of size-based trophic structure in food webs and also contradict the broadly accepted

prediction of the fishing-down-the-food-web concept. Eltonian and fishing-down-the-food-web concepts propose that trophic level is strongly correlated with body size, but I found no significant correlation between body size and trophic position for fish assemblages. Results suggest that body size distributions are not useful for prediction the trophic structure of communities with diverse detritivores, omnivores and insectivores, but that it is a good predictor of trophic position among piscivorous fishes.

To my grandmother Sun Lach.

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CHAPTER I

GENERAL INTRODUCTION

THE MEKONG RIVER BASIN

The Mekong River is one of the world's most important rivers in terms of its size, economic importance, cultural significance, productivity, and biodiversity (Campbell 2009). It is the tenth longest and eighth largest river in the world (Rainboth 1996). The Mekong River flows through six countries in Southeast Asia: China (Tibet), Myanmar, Laos, Thailand, Cambodia and Vietnam (the Mekong delta). The Mekong River Basin is divided into two main sections: the Upper Mekong, which spans from Jifu Mountains of Tibet Autonomous prefecture of China to the border of Burma and Laos, and the Lower Mekong, which covers the area from the Burma-Laos border to the Mekong Delta in Vietnam. The Mekong River plays a crucial role in the economy of many of these countries. China benefits from the river primarily through hydropower, and Thailand and Laos benefit from fisheries but recently have started to profit from hydropower development, whereas Cambodia and Vietnam mainly benefit from the river's fisheries (Ratner 2003, Campbell 2005).

The flow regime and annual flood pulse of the Mekong make it one of the world's most productive and biodiverse fisheries (Welcomme 1979, Campbell 2009). Fish production from the Mekong River is estimated at 2 million tons per year (Mekong River Commission 2003), which is more than 20% of the world's inland capture (Food

and Agriculture Organization 2004). Approximately 75 million people living in Southeast Asia, particularly those who live in the Lower Mekong Basin region, are dependent on the Mekong's fisheries. People from the Lower Mekong countries of Laos, Thailand, Cambodia and Vietnam have the highest consumption of protein from fish in the world. More than 70% of protein intake among Cambodians is reported to derive from wild-caught fish (Hortle 2007). The importance of fish in people's lives is demonstrated by a number of sayings in these countries: for example, the Thai proverb "in water there is fish; in rice fields there is rice," the Khmer proverb "where there is water, there is fish," and the Vietnamese proverb "nothing is better than rice eaten with fish, nothing is better than the love of a mother."

The Mekong River is the third richest in fish species diversity in the world after the Amazon River in South America and the Zaire River in Africa (Welcomme 1985). The river contains a high incidence of endemic species and more fish families than any other river in the world. Over one thousand fish species, belonging to 24 orders and 87 families, and more than two hundred endemic freshwater species have been documented in the river (Mekong River Commission 2003). Estimation of fish biodiversity of the basin has always been conservative because there continually are new discoveries. In many cases, a described taxonomic species turns out to be two or more species (Rainboth et al. 2012). In addition, the river contains several iconic aquatic species, including the giant Mekong giant catfish (*Pangasionodon gigas*), one of the largest freshwater fishes in the world, which can reach 300 kg, the giant Mekong carp (*Catlocarpio siamensis*), the seven-line barb (*Probarbus jullieni*), *Mekongina*

erythrospila, an endemic cyprinid in Cambodia, the giant stingray (*Himantura chaophraya*), and three freshwater dolphin species (*Orcaella brevirostris*, *Sotalia chinensis*, *Neophocaena phocaenoides*).

It is predicted that the Mekong River's natural flow regime and its great fisheries will be negatively affected by hydropower development in the region (Adamson et al. 2009, Dugan et al. 2010, Grumbine et al. 2012, Ziv et al. 2012). Three major dams were completed in the Upper Mekong mainstem in China in 1995, 2003 and 2008 (Barlow et al. 2008). There are more than 100 dams being proposed in the Lower Basin countries of Cambodia, Laos, Thailand and Vietnam. Among the planned dams in the Lower Mekong Basin, the two located in Cambodia (Lower Sesan II dam) and Laos (Xayaburi dam) have been recently approved for construction. Given that the majority of Mekong River fishes are migratory with movements and spawning cued by the annual flood pulse, these dams will have negative effect on aquatic community by fragmenting rivers in the longitudinal dimension, prohibiting colonization and community succession (Barlow et al. 2008, Baran and Myschowoda 2008, Dugan et al. 2010). In addition, the existing and planned dams on the mainstream of the Upper Mekong are predicted to trap at least 50% of the suspended sediment load annually in the Lower Mekong Basin region (Lu and Siew 2005, Kummu and Varis 2007), while the Lower Mekong's dams will trap even more sediment and impact the river's ecology in downstream countries (Kummu et al. 2010, Xue et al. 2010).

Fisheries in the region are also clearly impacted by over exploitation, although a reliable long term record of fish catch does not exist. Numerous reports and observation

have documented intense fishing pressure and its impact on the region (Hortle et al. 2004, Welcomme et al. 2010). Pressure on Lower Mekong fisheries has intensified in recent years due to rapid economic and population growth. In Cambodia, the population increased from about 1 million to 14 million during the three decades that followed the end of the Khmer Rouge regime in 1979. Fishing activity in this area involves about 150 gear types (Deap et al. 2003), and these do not include illegal methods introduced in the late 1970s, such as fine-mesh nylon fyke nets and electro fishing (Hortle 2009). Many fishers in the region, particularly in Cambodia, have reported a decline in the catch of large catfishes (e.g. pangasids) and catches increasingly dominated by small fishes over the past 30 years (Hortle et al. 2004). This pattern of change in catches has been attributed to the “fishing-down-food-web” model in which progressively smaller and less valuable species are exploited as larger and more valuable stocks are depleted (Pauly et al. 1998, Welcomme et al. 2010).

FOOD WEB ECOLOGY

Food webs are often described as structures that channel energy flow through ecological communities via consumer-resource interactions. Ecologists have suggested that food web approaches can provide key insights and solutions for environmental problems caused by anthropogenic impacts such as habitat fragmentation, species extinction, species invasion, pollution, and overexploitation of natural resources (Winemiller 2004).

One important component of food web structure is the set of primary production sources that support consumer populations (Winemiller 2004). A number of studies have indicated that floodplain river food webs are supported by autochthonous production sources such as algae (Forsberg et al. 1993, Thorp et al. 1998, Lewis et al. 2001, Roach et al. 2009). These studies have shown that autochthonous carbon sources (algae) are generally more productive than most macrophyte tissues, and thus can enter food webs more rapidly. However, there also is evidence indicating that tropical floodplains enhance fish production by providing access to high-quality food resources/allochthonous sources derived from terrestrial habitats, such as fruits and seeds (Lowe McConnell 1975, Junk et al 1989, Correa et al. 2007, Horn et al. 2011). In the tropics, rivers experience seasonal fluctuation in hydrology that influences the availability of food resources supporting aquatic consumers (Winemiller 2004, Dudgeon et al. 2010). Because most food web studies have been conducted within only one season (dry), there is a need for further investigation on seasonal shifts in production sources of tropical floodplain rivers where the seasonal hydrology regime shifts pronouncedly.

Another important component of food webs is vertical structure, the hierarchy of consumer trophic positions, which often is cited to be strongly correlated with body size (Elton 1927, Pauly et al. 1998, Cohen et al. 2003). Because an animal's body size influences consumer-resource interactions within the community (Pimm 1982, Cohen et al. 2009), it has been used in food web models to predict ecosystem stability, patterns of energy flow, and community response to disturbances such as fishing pressures (Pauly et al. 1998, Woodward et al 2005a). Body size determines the prey sizes that can be

captured and consumed; larger individuals frequently feed at higher trophic levels (Cohen et al 1993, 2003). A general assumption in food web models about the hierarchy of body size across trophic levels has been widely cited in marine and lake ecosystems (e.g. Pauly et al. 1998) but not in lotic or tropical freshwater ecosystems (e.g. Layman et al. 2005a). Given these mixed findings, there is a need to test this generalization about the relationship between body size and food web vertical structure.

Stable isotope techniques

Stable isotopes have been widely used in recent food web studies because of their ability to track the history of resource use by organisms (Fry 2006). The method provides robust means to study food web dynamics across spatial and temporal scales (Layman et al. 2005b). The traditional method of studying food webs is based on dietary data from gut contents analysis (GCA). GCA provides information on per capita consumption rates that determine both bottom-up (donor control) and top-down (predation control) dynamics in food webs. However, GCA has limitations, because it only provides a snapshot of the individual consumer's diet. Another limitation is that it requires large sampling effort in terms of specimens captured and examined, and the temporal and spatial scale of study. Due to these issues, stable isotope analysis has become popular in modern ecological research, especially in food web studies. Stable isotopes of carbon and nitrogen can be used to indicate dietary differences, carbon flow pathways, and consumer trophic positions on a continuum (Fry and Quinones 1994).

Objectives

For this study, I surveyed four rivers: the Mekong River, Sekong River, Sesan River, and Srepok River in northeastern Cambodia during the dry and rainy season periods. The flow regime of the Sesan River has been altered by the operation of a hydroelectric dam upstream. In Chapter II, I examine the basal production sources supporting fish biomass in the four rivers, and in Chapter III, I explore the relationship between trophic position and body size of fish at various taxonomic levels, among local species assemblages, and across trophic guilds.

Basal production sources supporting fish biomass during the dry and wet seasons

In the second chapter, I used stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) to estimate the primary production sources supporting fish biomass in the four rivers – three rivers unimpacted by dams and one dammed river (Sesan). I used the MixSIR model to estimate the probability distributions for the relative contributions of four alternative production sources – seston, benthic algae, riparian C_3 macrophytes, and riparian C_4 grasses. My results indicated that seston and benthic algae were the most important production sources supporting fish biomass during the dry season, and riparian macrophytes appeared to be the most important production source supporting fishes during the wet season. I also detected a potential effect of river impoundment on contributions of basal production sources to fish biomass. In the river with strong flow regulation from an upstream impoundment, seston and benthic algae were even more important production sources supporting fishes during the dry season.

The relationship between trophic position and body size

In the third chapter, I used trophic position estimated from ratios of nitrogen stable isotopes to examine the association between body length and trophic position of fish assemblages. I found no significant correlation between body size and trophic position based on the regional species assemblage. At the taxonomic level of order, I found significant relationships among species belonging to the orders Siluriformes and Perciformes but not Cypriniformes. Similarly, at the family level, I found significant correlations among the families Siluridae and Bagridae but not Cyprinidae. Additional regression analysis among species of different trophic groups indicated no body size-trophic level correlation for detritivores, omnivores and insectivores, but piscivores had a significant relationship. Further analysis of the relationship at the species level revealed ontogenetic diet shifts among all the examined piscivores but not for detritivores, omnivores, and insectivores. I concluded that, within species-rich tropical fish assemblages in which there is high incidence of detritivory and omnivory, trophic level and body size are uncorrelated.

CHAPTER II

SEASONAL HYDROLOGY DRIVES SHIFTS IN PRODUCTION SOURCES SUPPORTING FISHES IN THE LOWER MEKONG RIVER BASIN

INTRODUCTION

The natural flow regime is crucial for sustaining native aquatic biodiversity as well as supporting ecological processes and functions in fluvial ecosystems (Bunn and Arthington 2002, Poff and Zimmerman 2010). An extensive literature review of ecological responses to altered flow regimes revealed a strong relationship between changes in flow components (e.g. flow magnitude, frequency, duration, timing and rate of change) and changes in geomorphological and ecological dynamics (Poff and Zimmerman 2010). Flow regime alteration directly affects river ecology by changing physical disturbance dynamics, nutrient cycling, availability of basal resources, transport of production sources, and connectivity of corridors for movement and exchange of nutrients and aquatic organisms (Power et al. 1996, Winemiller 2004, Roelke et al. 2006, Winemiller et al. 2006, Richter et al. 2010). Changes in the timing of flow components alter the seasonal regime of flooding which, in turn, affects fish migration, availability and access of instream and off-channel habitats for aquatic organisms and riparian community structure (Junk et al. 1989, Winemiller 1990, 2004, Montoya et al. 2006).

Humans have changed river flow regimes worldwide, especially through impoundment (Poff et al. 1997, 2007, Dudgeon 2000, Richter et al. 2010). River

impoundments have created severe environmental and social impacts throughout the world. By negatively affecting biodiversity, dams have threatened food security, livelihoods and cultural values of people living along downstream reaches (Richter et al. 2010). Fishes are sensitive to flow regime alteration, including declines in species richness, and generally show negative responses in terms of reproduction, recruitment, and population abundance of native species (Dudgeon 2010). By trapping sediments and altering the downstream flow regime, dams also affect sediment dynamics. For example, research on the Paraná River (in Brazil) revealed much greater water clarity in a section below an impoundment that trapped sediments (Hoeinghaus et al. 2007).

Knowledge of river food web ecology is essential for management of anthropogenic impacts on fluvial ecosystems and their valuable services and resources (Winemiller 2004). Three widely-cited river food web models predict the sources of production that support aquatic organisms: the River Continuum Concept (RCC), the Flood-Pulse Concept (FPC) and the Riverine-Productivity Model (RPM). According to the RCC, fine particulate organic material originating from dead leaves and woody debris in upstream reaches are important inputs to large river food webs (Vannote et al. 1980). Vannote et al. (1980) argued that headwaters are tightly connected with the terrestrial ecosystem, which allows input of carbon sources to be transported downstream where direct interaction between aquatic and terrestrial systems is more limited. This model was developed based on observations of headwater streams, and only a few large river studies have provided evidence supporting this longitudinal view of fluvial food webs (Thorp et al. 1998).

The FPC proposes that lateral connectivity between the main channel and floodplain habitats is important in large river food webs. FPC predicts that ecosystem dynamics are driven by seasonal floodplain inundation that introduces terrestrial material (e.g. invertebrates and macrophyte biomass such as leaves, fruits, seeds) to the aquatic food web (Junk et al. 1989). This model proposes that the river channel serves primarily as corridor for aquatic organisms to move between important floodplain habitats, and that fishery yield is strongly associated with the magnitude and duration of seasonal flood pulses.

The RPM stresses algal-grazer pathways as the main food chains maintaining fish diversity and production in large river food webs. The RPM contrasts with the previous models by proposing that most carbon sources transported from upstream reaches and the floodplains are not assimilated by aquatic consumers because they tend to be of low nutritional value and relatively less labile than algae-derived material. The RPM hypothesizes that consumers obtain most of their carbon from autochthonous sources (e.g. benthic algae and phytoplankton) growing in the river channel, and a lesser amount of carbon is assimilated from sources in the riparian zone (Thorp and Delong 1994). However, the revised RPM (Thorp and Delong 2002) proposes that production sources that originate from the riparian zone support a great deal of microbial biomass that, via direct pathways, supports metazoan biomass in large rivers. The RPM stresses algal-grazer pathways as the main food chains maintaining fish diversity and production in large river food webs.

Food webs have been demonstrated to have both temporal and spatial variation in response to variation in abiotic factors and/or species composition (Winemiller 1990, 1996, Woodward and Hildrew 2002a). None of the three models stated above integrate all the key drivers/dimensions of watershed characteristics (e.g. turbidity, sedimentation, light penetration, seasonal hydrology, discharge) that reflect temporal and spatial food web variation. A recent review of production sources for river food webs concluded that, in rivers with rates of high erosion and sedimentation, aquatic consumers assimilate algae during low-water periods when water transparency is high, and during high-flow periods when water transparency is low, C_3 plants become a more important source supporting consumer biomass (Roach 2013). Likewise, research on the Lower Mekong River in Cambodia, a sediment-laden river, indicated that during the dry season, fine particulate organic matter (FPOM) suspended in the water column is mostly derived from algae, and, during the wet season, it is mostly derived from vascular plants (Ellis et al. 2012).

In this study, I examined primary production sources supporting fish biomass in four large rivers in the Lower Mekong River Basin. Specifically, I estimated seasonal variation in contributions of primary production sources to fish communities inhabiting three rivers that are essentially unimpacted by dams and one river significantly impacted by dams. I estimated these production source contributions during the dry season when river discharge is low and water is relatively transparent and stable. I repeated field research and estimates during the wet season when river discharge is high and variable and water is turbid. I hypothesized that in the rivers unimpacted by dams, autochthonous

carbon sources (algae) would be important sources supporting consumer taxa during the dry season, and allochthonous sources (C_3 plants) would be more important during the wet season. For the river impacted by dams, I hypothesized that the trapping of sediments upstream would increase water transparency and algal production below the impoundment, and this will cause algae to be a more important source for consumers compared to consumers in the relatively unaltered rivers.

MATERIALS AND METHODS

Study sites

This study was conducted in four large floodplain rivers in the Lower Mekong River Basin in Northeastern Cambodia: the Mekong, Sekong, Sesan and Srepok rivers. The Sekong, Srepok and Sesan rivers (known as the 3S rivers) are the Lower Mekong's major tributaries that drain northeastern Cambodia, southern Laos and the central highlands of Vietnam. They meet the Mekong River mainstream at Stung Treng, a provincial center of Cambodia. I sampled a site on the Mekong River near Stung Treng provincial center (13.579383N, 105.994366E), the Sekong River at Siem Pang (14.11434N, 106.39104E), the Sesan River at Veurn Sai (13.94585N, 106.79701E), and the Srepok River at Lomphat (13.47508 N, 106.99683 E) (Figure 1).

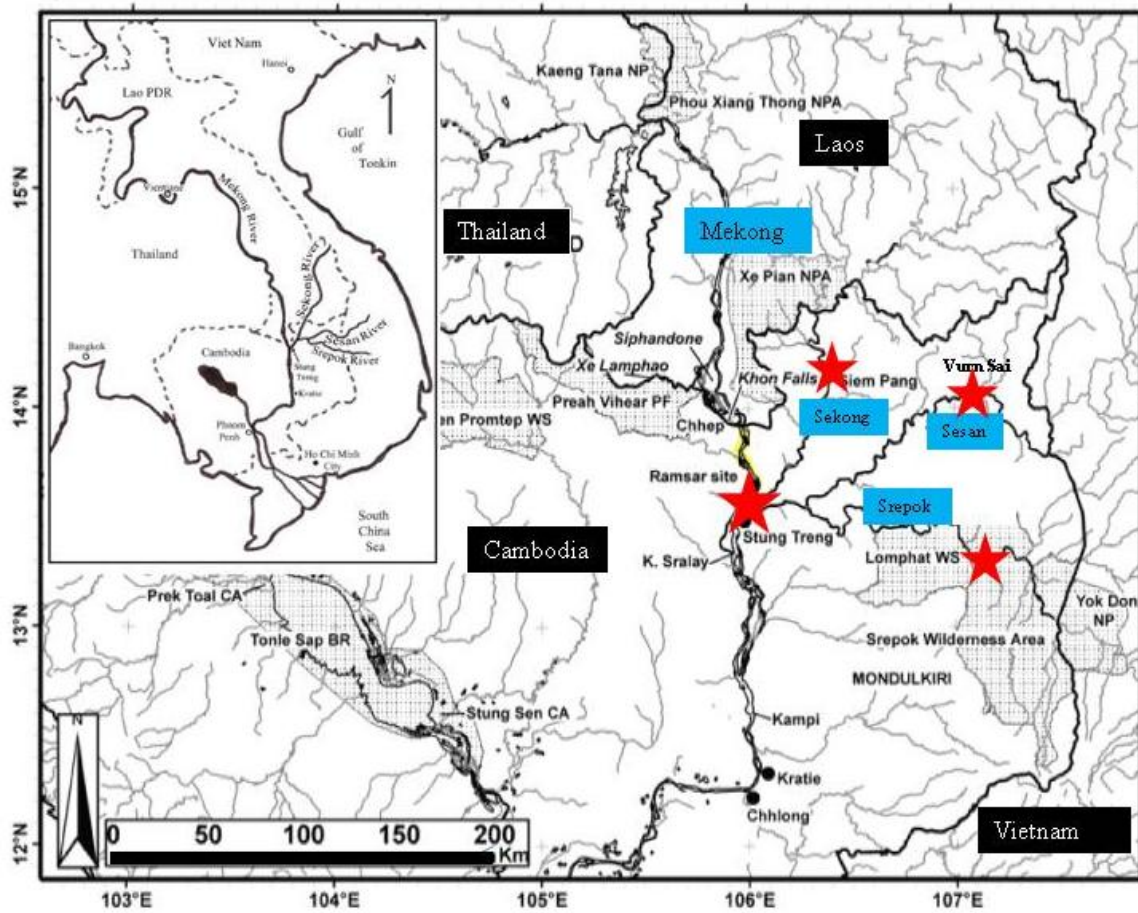


Figure 1. Map of the study sites. Red stars represent sampling locations on the Mekong, Sekong, Sesan and Srepok rivers.

The Mekong in Cambodia and the 3S rivers lie in a region that is critical for biodiversity conservation. Five hundred fish species have been recorded from the Cambodian Mekong (Rainboth 1996). About 40 km of the Mekong River, from the Stung Treng-Kratie province border and to near the Cambodia-Laos border, and its riparian zone were designated as a RAMSAR wetland of global significance because of its value for conservation of biodiversity in the Indo-Burma region. Watersheds of the 3S rivers have been recognized as critical areas for biodiversity conservation because they contain high species diversity and dozens of endemic and endangered species. Approximately 300 fish species, including at least 100 endemics and 14 endangered species, have been recorded from the 3S rivers (Baran et al. 2011). The 3S rivers contribute the largest single inflow (25%) to the Mekong's annual flow at Kratie province in Cambodia (Mekong River Commission 2008). Annual precipitation of the NE province of Cambodia is approximately 2 m with 80% generated from rainfall during the wet season (May to October). Peak rainfall in this region occurs during August and September.

The Mekong River and its tributaries (figures 2-5) in Northeastern Cambodia comprise a complex river system characterized by multiple sets of channels, abundant rapids, large and small pools, and mosaics of islands with diverse vegetation. The Mekong supports dense vegetation cover in three lateral zones: aquatic, riparian, and upland terrestrial. The Lower Mekong River, from the Laotian border to Kratie province (Cambodia), contains particularly diverse aquatic and riparian habitats. Some of the sections in this reach consist of a single broad channel (up to 1.5 km), whereas other

sections consist of many narrow channels with islands. Along the river channel, several habitat types are observed, such as small and periodically flooded vegetation, predominantly grass-covered islands, partially-submerged shrubs, mixed deciduous, semi-ever green forest, sandbars, and rocky shoals. Away from the river channel, vegetation is dominated by open deciduous dipterocarp forest. The stretch of the Sekong River from the border between Cambodia and Laos to its confluence with the Mekong River contains diverse habitats including rocky shoals, sand banks, and gallery forests dominated by deciduous dipterocarp species and broadleaf evergreen trees and riverine shrubs. The stretch of the Sesan River from the Cambodia-Vietnam border to its confluence with the Mekong River is characterized by sand and gravel bars supporting shrubs in the upper river section, and rocky and sandy bars with fewer shrubs in the lower section. Vegetation in the Sesan watershed is dominated by semi-evergreen and mixed deciduous and deciduous dipterocarp forests and shifting cultivation agriculture. The catchment of the Srepok River upstream of Lomphat is characterized by a mosaic of deciduous dipterocarp forest, small areas of semi-evergreen forest, and mixed deciduous forest. This river stretch contains numerous wetlands habitats, tributary streams, and oxbow lakes (BirdLife International, 2012).

There currently are six dams in operation on the Sesan River: Plei Krong, Yali, Sesan 3, Sesan 3A, Sesan 4A, Ochum 2. Yali Falls dam is situated upstream at the major waterfalls in Vietnam. Yali Falls serve an important pathway for fish migration in the Sesan River (Baran et al. 2011). In addition, a new dam named the Lower Sesan 2 has been approved recently for construction at a downstream site in Cambodia. In the Sesan

River, the flow regime is already regulated by dams in Vietnam, and ecological changes are primarily attributed to alteration of the natural flow regime. The livelihoods of local people living along the Sesan already have been adversely affected by the loss of large migratory fishes (Baran et al. 2011). The Sesan River now experiences reduced flow and shallower water during the dry season compared to the other two 3S tributaries (Baird et al. 2005, Baran et al. 2011).

Sample collection and laboratory methods

In all rivers, sampling sites were chosen in an attempt to collect representative samples of basal production sources and consumers from each river. I chose to sample major landing sites of each river where I obtained additional fishes from local fishers who come from diverse channel and off-channel habitats within the areas to sell their fishes. I sampled several (at least 3) localities of each site at different depth of water (shallow vs. deep). A series of habitat types include sand bank, woody debris, leaf litter, and rock shoals at each site were sampled using multiple sampling gear: seine nets, gill nets, cast nets, dip nets, and hook and line. This survey allowed me to collect diverse fishes from various habitat types. Seining effectively captures fishes that occupy shallow areas on sand bars and near river banks, especially small fishes. Gill nets with multiple mesh sizes effectively collect fishes of all sizes from open water as well as submerged woody areas. Cast nets catch fish in areas near the shoreline and also are effective in high velocity habitats with rocks. Dip nets are effective to catch fish from vegetation and leaf litter packs. Baited hooks catch predatory fishes from rocky habitats and deep pools.



Figure 2. Mekong River during the dry season (top) and wet season (bottom).



Figure 3. Sekong River during the dry season (top) and wet season (bottom).



Figure 4. Sesan River during the dry season (top) and wet season (bottom).



Figure 5. Srepok River during the dry season (top) and wet season (bottom).

In order to capture temporal variation of available basal production sources and aquatic consumers, samples of algae, riparian macrophytes, and fishes were collected from each site during both dry (January 2010, 2011) and wet seasons (July and August 2011). Each seasonal survey involved 3-4 weeks of effort. Attempts were made to collect the dominant (most obvious) basal production sources and common consumer taxa at all sites. It is assumed that the surveys captured the most common fishes and basal production sources at each site. Local fishermen confirmed the most common species for their areas. The surveys did not document the total biodiversity at the locations, and rare species or seasonal inhabitants undoubtedly were not captured. Whenever possible, 3-5 individuals of each species were obtained from each site.

Different parts (leaves, fruits, seeds) of common riparian plants were collected, cut into small pieces, placed in plastic bags and preserved in salt for later analysis in the laboratory. Benthic algae (phytomicrobenthos) were collected by gently scraping rocks and submerged tree branches. Seston samples (phytoplankton and other suspended organic matter) were collected from near the water surface with 1-L opaque bottles, and the water was filtered with precombusted Whatman GF/F filters (pore size 0.7 μm). Fishes were collected during the dry and wet seasons using a seine net, cast net, and dip net. Additional fish specimens were obtained from local fishermen. Fish muscle tissue samples were taken from the flank near the base of the dorsal fin. All samples were preserved in salt for later analysis in the laboratory.

In the laboratory, tissue samples were soaked in distilled water for 4-5 hours, rinsed, and dried in an oven at 60° C for 48 hours. After drying, samples were ground

into fine powder using an electronic ball-mill grinder. Subsamples were weighed to the nearest 0.02 mg and packaged into ultrapure tin capsules (follows methods of Arrington and Winemiller 2002). Samples were analyzed for isotope ratios of carbon and nitrogen at the Analytical Chemistry Laboratory, Institute of Ecology at the University of Georgia.

Stable isotope analysis

I used stable isotopes of carbon and nitrogen to estimate production sources (algae and macrophytes) assimilated by fish in the four rivers. Stable isotopes of carbon and nitrogen have been widely used in estimating the relative importance of basal source contributions to metazoan food webs. Isotope ratios were reported in parts per thousand (‰) relative to standards (PeeDee Belemnite for ^{13}C , and atmospheric nitrogen for ^{15}N) and reported as: $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] * 10^3$, where $R = ^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ (the ratio of heavy and light stable isotope of carbon or nitrogen). Trophic Position was calculated for each species using the formula (follow Vander Zanden and Rasmussen 1999, 2001): $\text{TP} = (\delta^{15}\text{N}_{\text{consumers}} - \delta^{15}\text{N}_{\text{basal source}})/2.5 + 1$, where $\delta^{15}\text{N}_{\text{consumers}}$ is the signature of $\delta^{15}\text{N}$ fishes and $\delta^{15}\text{N}_{\text{basal source}}$ is the mean value of $\delta^{15}\text{N}$ of primary production sources including algae and plants.

Mixing model

MixSIR (Moore and Semmens 2008) was used to estimate the relative contribution of four alternative basal sources (seston, benthic algae, riparian C_3

macrophytes, and riparian C₄ grasses) to tissues of consumers. MixSIR uses a Bayesian approach to estimate the probability distribution of the proportional contributions of each production source to consumers. The Bayesian approach incorporates sources of uncertainty by accounting for isotopic variation within source pools and trophic discrimination factors (e.g., trophic fractionation of stable isotope ratios). This approach allows input of variances (in the form of standard deviations) of source stable isotopic ratios. Different discrimination factors (differences in C or N between consumers and sources) can be entered for each consumer taxon. With these input options, this model enables more accurate depiction of the most likely proportional contributions of each source to consumers (Woodland et al 2012). However, MixSIR sometimes is unable to resolve source contribution when stable isotope signatures of sources are not sufficiently differentiated. This Bayesian approach provides outputs as a series of probability distributions, rather than a set of feasible solutions. It provides probability ranges of source contributions to consumer biomass, and these ranges provide the basis for inferences about trophic ecology. When the stable isotope ratios of sources are similar, the probability ranges of their contributions to a consumer's biomass will overlap broadly.

For this study, I ran the model separately for each consumer species and for each season and site based on carbon and nitrogen of primary production sources collected during the corresponding season and site. For the model input, I used the standard deviation of the trophic fractionation value of 2.5 for nitrogen (Vanderklift and Ponsard 2003) and 0.5 for carbon isotope fractionation (McCutchan et al. 2003). I did not correct

consumer samples for lipids because C:N ratios were relatively low (mean = 3). Minimum (5%), median (50%) and maximum (95 %) percent contribution of each source were recorded for each fish species in each river for both seasons.

Trophic guilds and habitat guilds classification

Fish trophic guilds and habitat guilds were determined using information reported in Fishbase and Rainboth (1996) as well as fish functional morphology. Fish trophic guilds were identified as: 1-*Piscivore* if the fish consumes primarily fishes and sometimes smaller amounts of crustaceans or other prey, 2- *Omnivore* if it consumes both zooplankton and phytoplankton, 3-*Detritivore* if it consumes detritus and/or algae, and 4- *Invertivore* if it consumes invertebrates (i.e. aquatic microcrustacea, macrocrustacea, aquatic insects, terrestrial arthropods) almost exclusively. Habitat guilds were characterized by habitats where fish spend most of their time. Two habitat guilds were identified: 1-*River channel* if adult size classes of the species are encountered almost exclusively within the river channel, and 2-*Floodplain* if adults commonly inhabit both river and floodplain habitats.

Statistical analysis

One way-ANOVA was used to compare the differences among carbon and nitrogen stable isotope signatures of production sources across the four rivers and each season. The test also was performed for comparison of estimated contributions of production sources in the four rivers and to compare estimated contributions of primary

production sources for the various fish trophic guilds. Finally, post-hoc Tukey HSD was used when significant value was detected in the former analyses. All analyses were performed using PAST (Hammer et al. 2001).

RESULTS

A total of 1,087 individual fishes and 109 primary production source samples were collected during the study. Most of the fishes belong to the family Cyprinidae, followed by Siluridae, Bagridae and Pangasidae. During the dry season, 699 individual fishes and 44 basal source samples were obtained for analysis. Seventy-one species were obtained from the mainstem of the Mekong River, 60 species from the Sekong, 31 species from the Sesan, and 56 species from the Srepok. During the dry season, I collected 27 (12%) detritivores, 80 (36%) insectivores, 57 (26%) omnivores, and 54 (24%) piscivores from the Mekong and 3S rivers (Table 1).

During the wet season, water in the river channels was high and swift and some fishes were dispersed in flooded riparian habitats. These conditions hindered fishing success, and I collected 388 fish specimens and 65 basal production source samples during the wet season. Among fishes, 46 species were collected from the Mekong, 31 species from the Sekong, 19 species from the Sesan, and 33 species from the Srepok. Compared to the dry season collection, the wet season survey yielded fewer fish specimens within each trophic guild. Nonetheless, all trophic guilds were represented

with 17 (13%) detritivores, 46 (36%) insectivores, 49 (38 %) omnivores, and 16 (12%) piscivores (Table 1).

Table 1. Richness and frequency (%) of species according to four trophic guilds (for the dry and wet seasons).

Season	River	Trophic Guilds							
		Detritivores		Insectivores		Omnivores		Piscivores	
		Richness	%	Richness	%	Richness	%	Richness	%
Dry	Mekong	9	12	24	34	23	32	15	21
	Sekong	8	13	23	38	11	18	18	30
	Sesan	1	3	18	56	7	22	6	19
	Srepok	9	16	15	27	16	29	15	27
Wet	Mekong	6	13	18	40	13	29	8	18
	Sekong	4	13	9	29	15	48	3	10
	Sesan	2	11	7	37	9	47	1	5
	Srepok	5	15	12	36	12	36	4	12

Stable isotope signature of basal production sources

The ranges of carbon stable isotopic values of the four basal production sources (seston, benthic algae, C₃ macrophytes, C₄ grass) were well differentiated ($P = 0.01$), with the exception for seston and benthic algae samples collected during the wet season. These isotopic differences enhance resolution in estimates of sources assimilated by consumers using the multiple-source mixing model (Fry and Sherr 1984). The ranges of the site means for $\delta^{15}\text{N}$ nitrogen isotopic values of basal sources were not significantly different ($P = 0.12$) among source groups from different rivers between seasons. Nitrogen isotopic $\delta^{15}\text{N}$ values of C₄ grass were relatively low compared to the other sources (Table 2).

Stable isotope signature of consumers

Overall, average carbon isotopic signatures of consumers were significantly ^{13}C depleted during the wet season compared to consumers collected during the dry season. Most fishes had carbon isotopic signature between the values of benthic algae and seston (but closer to seston) during the dry season, and had carbon isotopic signature values closer to those of C₃ macrophytes during the wet season (Figures 6-9).

Table 2. Mean values (\pm SD) of carbon and nitrogen isotope ratios for production sources (during two seasons at four rivers).

Season	River	Sources							
		Seston		Benthic Algae		C3 plants		C4 plants	
		$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Dry	Mekong	-25.45 (1.57)	6.03 (1.80)	-19.02 (1.87)	5.16 (0.55)	-29.12 (1.45)	6.91 (2.74)	-13.34 (0.98)	3.4 (1.01)
	Sekong	-26.74 (1.75)	5.33 (1.07)	-18.73 (2.89)	5.44 (1.09)	-30.85 (1.31)	5.64 (2.00)	-12.51 (0.91)	4.18 (1.94)
	Sesan	-26.04 (1.08)	5.93 (0.38)	-20.36 (1.37)	5.10 (1.02)	-30.43 (1.25)	6.00 (2.84)	-13.09 (2.12)	4.49 (1.66)
	Srepok	-25.91 (0.82)	4.91 (1.16)	-18.47 (2.01)	4.71 (2.35)	-29.02 (0.60)	6.82 (1.28)	-12.25 (1.41)	3.52 (3.14)
Wet	Mekong	-36.85 (1.49)	7.00 (2.19)	-39.40 (2.23)	5.93 (1.91)	-29.28 (1.64)	5.70 (1.9)	-11.93 (2.58)	3.76 (2.18)
	Sekong	-39.73 (3.18)	6.40 (1.17)	-35.20 (2.46)	5.78 (1.76)	-29.36 (2.13)	4.35 (1.32)	-11.95 (1.58)	3.43 (0.56)
	Sesan	-36.46 (1.76)	6.26 (2.86)	-39.78 (2.6)	5.79 (2.09)	-28.49 (1.72)	4.47 (1.19)	-13.51 (1.89)	4.07 (2.04)
	Srepok	-37.73 (2.64)	7.50 (2.93)	-38.19 (0.97)	6.14 (3.16)	-28.78 (1.62)	5.12 (0.7)	-11.23 (0.73)	2.90 (1.23)

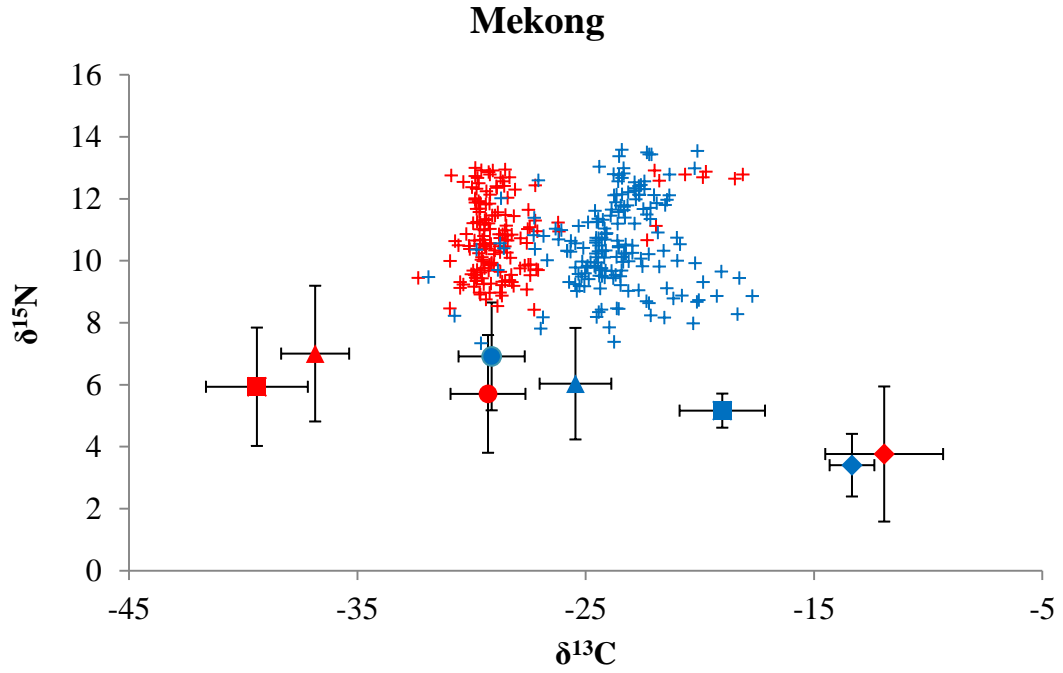


Figure 6. Biplot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of tissues from fishes and basal production sources collected from the Mekong River (during the dry and wet seasons). Red color represents wet season, blue represents dry season data, plus signs (+) represent fish, circle symbols (●) represent C_3 macrophytes, square symbols (■) represent benthic algae, triangle symbols (▲) represent seston, and diamond symbols (◆) represent C_4 grasses.

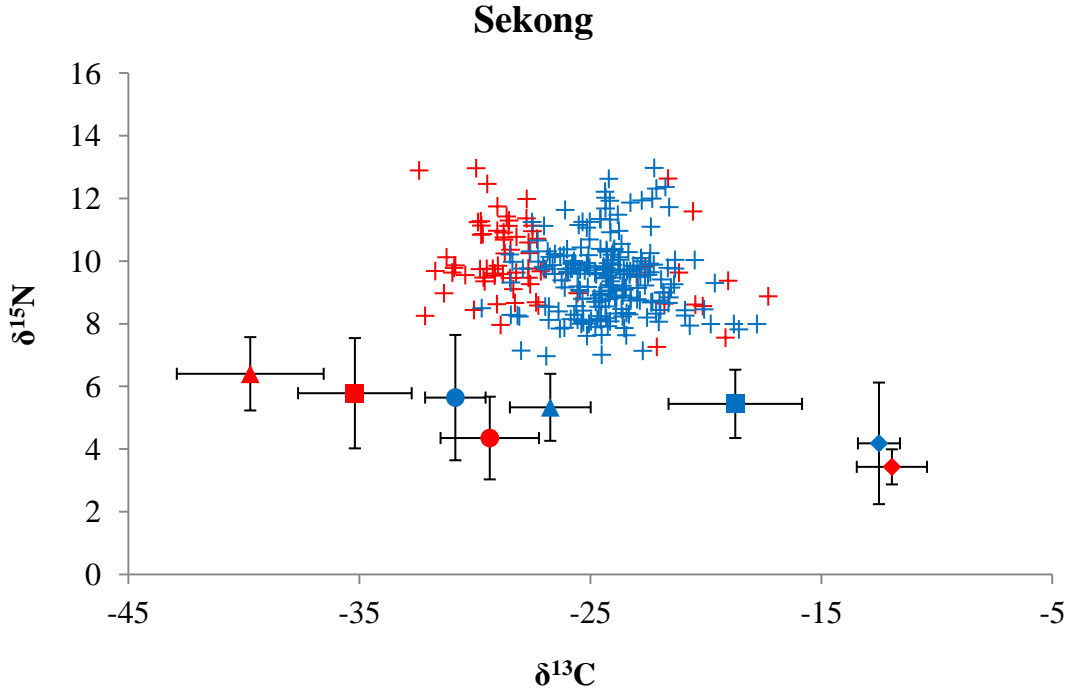


Figure 7. Biplot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of tissues from fishes and basal production sources collected from the Sekong River (during the dry and wet seasons). Red color represents wet season, blue represents dry season data, plus sign (+) represent fish, circle symbols (●) represent C_3 macrophytes, square symbols (■) represent benthic algae, triangle symbols (▲) represent seston, and diamond symbols (◆) represent C_4 grasses.

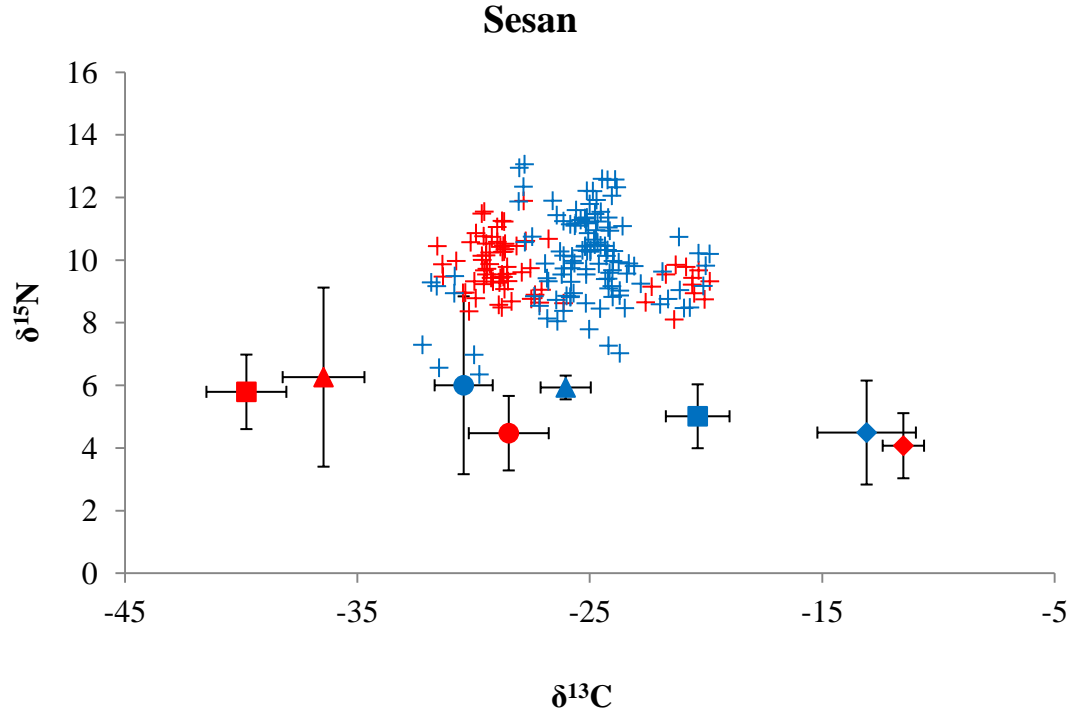


Figure 8. Biplot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of tissues from fishes and basal production sources collected from the Sesan River (during the dry and wet seasons). Red color represents wet season, blue represents dry season data, plus signs (+) represent fish, circle symbols (●) represent C_3 macrophytes, square symbols (■) represent benthic algae, triangle symbols (▲) represent seston, and diamond symbols (◆) represent C_4 grasses.

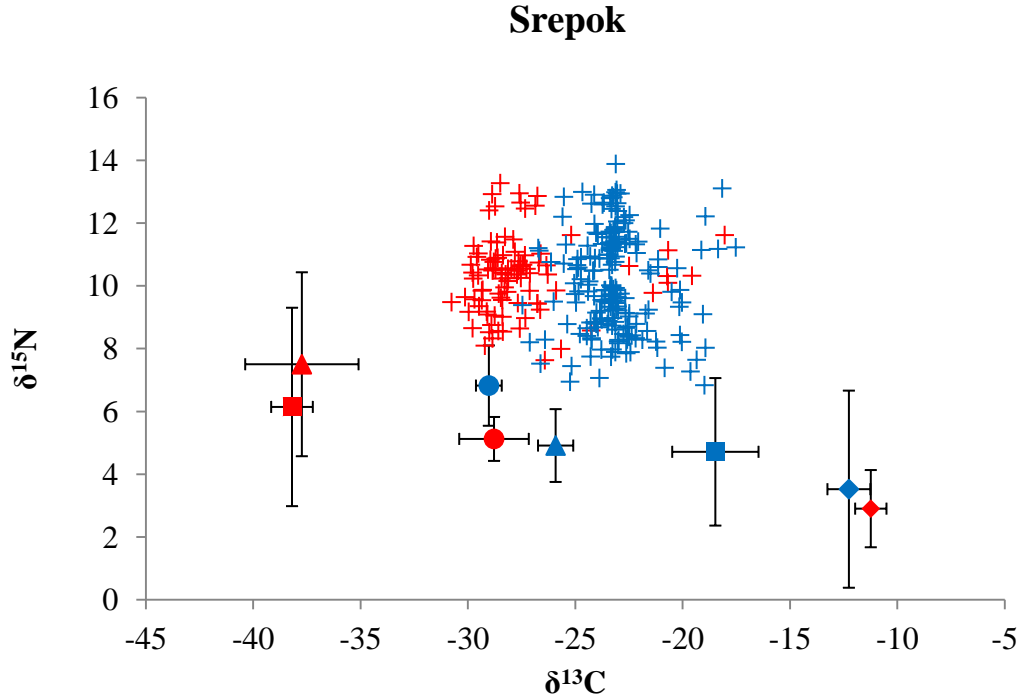


Figure 9. Biplot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of tissues from fishes and basal production sources collected from the Srepok River (during the dry and wet seasons). (Red color represents wet season, blue represents dry season data, plus signs (+) represent fish, circle symbols (●) represent C_3 macrophytes, square symbols (■) represent benthic algae, triangle symbols (▲) represent seston, and diamond symbols (◆) represent C_4 grasses).

Production source contribution

MixSIR results indicated that seston was the principle source contributing to fish biomass during the dry season (Figure 10). At the 5th percentile, seston had values > 10 for more than 75% of the fish for all four rivers (values were > 10 for all the fishes in the Sesan River), and at the 95th percentile values were > 50 for more than 50% of the fish in all the rivers. Benthic algae had 5th percentile values > 10 for about 40 % of the fish (approximately 70% of Sesan's fishes) and had 95th percentile values between 31 and 60 for more than 50% of fish. Riparian C₃ macrophytes had 5th percentile values < 10 for about 60% of the fishes (80% of Sesan fishes) and had 95th percentile values between 31 and 70 for the majority of fishes. Riparian C₄ grass had 5th percentile values < 10 for more than 90% of fishes in all four rivers.

MixSIR estimates for the wet season indicated that riparian C₃ macrophytes were the dominant basal production sources supporting trophic pathways to consumers, and benthic algae were the least important for all rivers (Figure 11). At the 5th percentile, benthic algae had values < 10 for all fishes, and seston had values < 10 for at least 90% of the fishes. Riparian C₃ plants had 5th percentile values > 20 for the majority of fishes from the four rivers and had 95th percentile value > 60 for most fishes. Riparian C₄ grasses had 5th percentile values < 10 for more than 50% of the fishes and had the 95th percentile values between 21 and 50 for the majority of fishes.

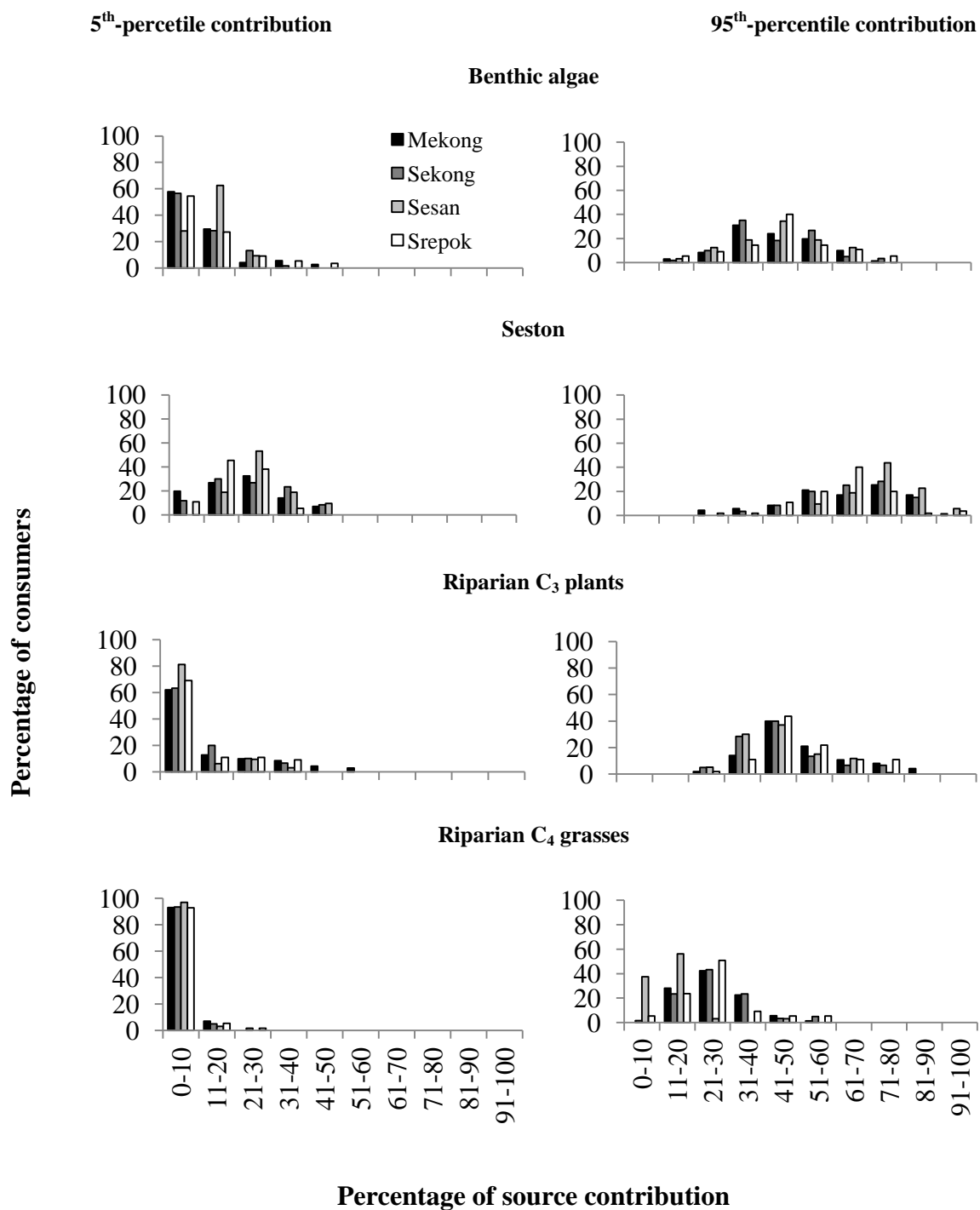


Figure 10. Frequency histograms of basal production sources contribution (5th and 95th-percentile) to fish biomass during the dry season.

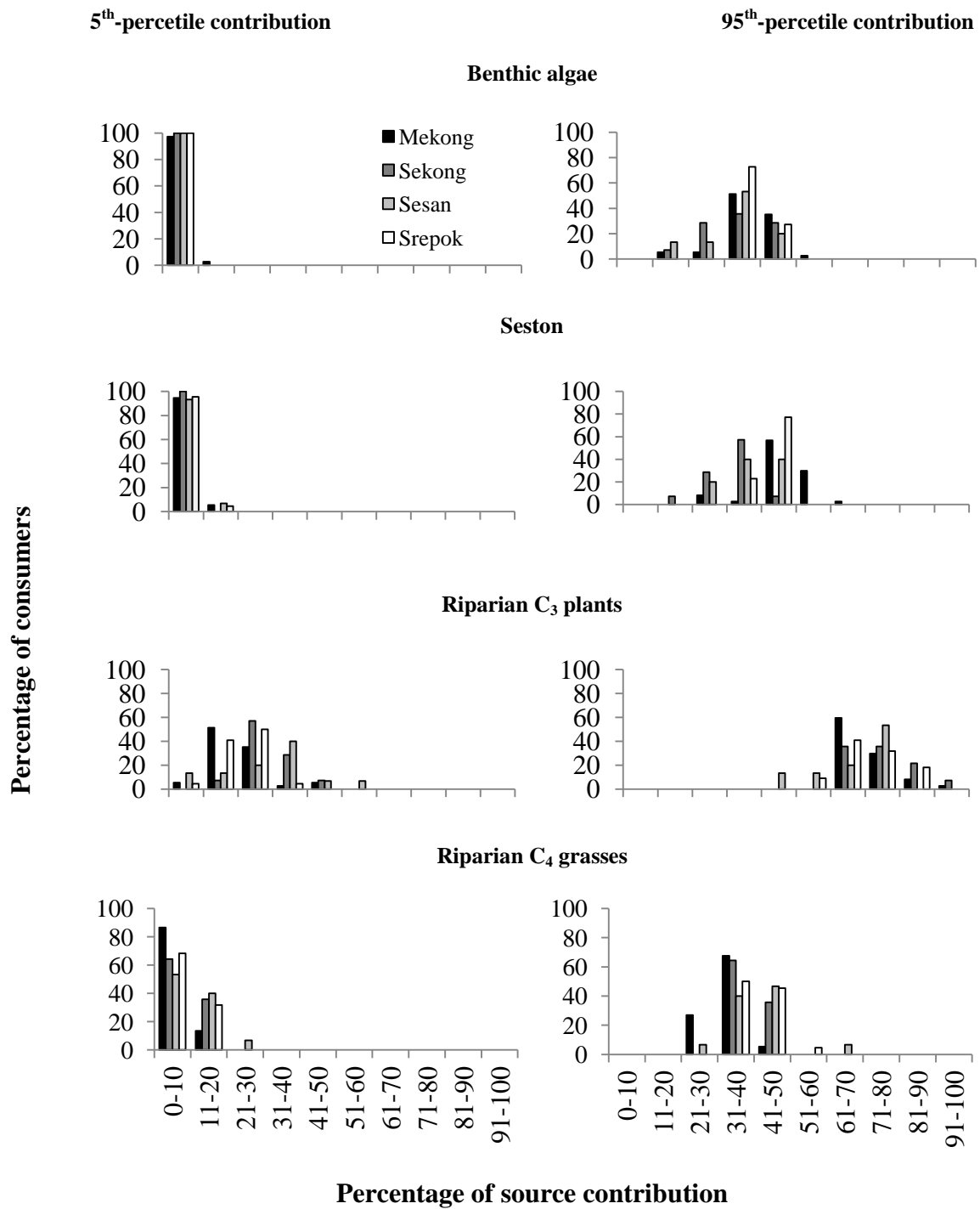


Figure 11. Frequency histograms of basal production sources contribution (5th and 95th-percentile) to fish biomass during the wet season.

For the dry season, MixSIR estimates revealed the differences in proportional contribution of primary production to each of the four trophic guilds (detritivores, insectivores, omnivores, and piscivores). At the 5th and 95th percentiles, benthic algae had the greatest contribution to detritivores (e.g. *Gyrinocheilus pennocki*, *Mekongina erythrospila*, *Morulus chrysophekadion*), between 30 and 60, respectively. Seston and C₃ macrophytes had higher estimated contributions than benthic algae and C₄ grasses to insectivores (e.g. loaches). During the dry season, omnivores (e.g. several pangasids) and piscivores (e.g. *Channa*, *Chitala*, *Wallago*) likely assimilate carbon originating from more than one source. These include seston, benthic algae, C₃ macrophytes and a minor fraction of C₄ grasses. All sources except C₄ grasses had estimated contributions to omnivores and piscivores > 10 at the 5th percentile and > 40 at the 95th percentile (Figure 12). MixSIR results also showed differences in estimated production source contributions between fishes that are largely restricted to the river channel and fishes commonly found floodplain habitats. C₃ plants seemed to have slightly higher contribution to fishes that inhabit floodplain habitats with contributions ranging from 13-50% (median = 31%), compared to its contribution to fishes inhabiting river channels that ranged from 1-44% (median = 22%).

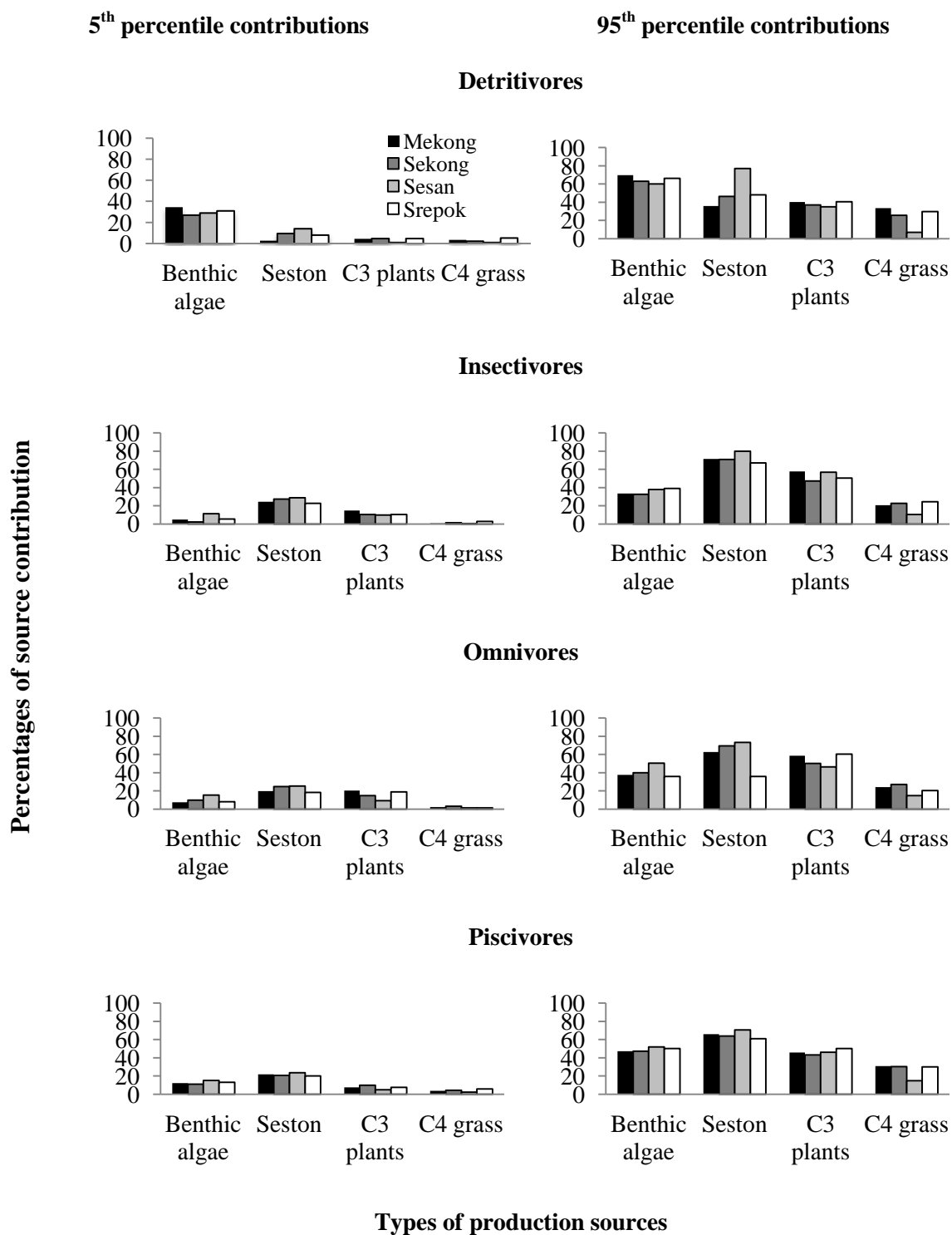


Figure 12. Frequency histograms of basal production sources contribution to fish

biomass among four trophic guilds during the dry season.

Although riparian C₄ grasses had the lowest estimated contributions to consumers during the dry season, these plants may have had a greater estimated contribution to certain groups of floodplain consumers during the wet season than did seston and benthic algae. C₄ grasses also appeared to be an important source supporting air-breathing fishes during both hydrological seasons. Fishes possessing aerial respiratory adaptations commonly inhabit floodplain pools; species in this group include clariid catfishes (*Clarias batrachus*, *C. macrocephalus*, *C. melanoderma*), snakeheads (*Channa limbata*, *C. lucius*, *C. marulioides*, *C. micropeltes*, *C. striata*), and labyrinth fish (*Pristolepis fasciata*) (Appendix 1).

DISCUSSION

Seasonal patterns

Carbon stable isotope signatures of benthic algae and seston were much lower during the wet (rainy) season compared to values obtained in the dry season. This variation can be influenced by differences in watershed geochemistry, variation among sources of inorganic carbon, differential diffusion rates of ¹³C and ¹²C during photosynthesis under varying environmental conditions, the effects of variance in water velocity outside the cell walls, and availability of dissolved inorganic carbon (DIC) from various pools (Finlay et al. 1999, Finlay 2001, 2004). Carbon stable isotope ratios of algae have been shown to vary in association with photosynthesis, discharge or climatic conditions (Forsberg et al 1988, Hamilton et al. 1992, Depetris and Kempe 1993, Hecky

and Hesslein 1995, MacLeod and Barton 1998). For example, MacLeod and Barton (1998) found that enriched $\delta^{13}\text{C}$ corresponds to higher rates of photosynthesis, whereas Depetris and Kempe (1993) reported algae with higher $\delta^{13}\text{C}$ during periods of lower rainfall and watershed runoff. Hecky and Hesslein (1995) reported that $\delta^{13}\text{C}$ of algae is higher in tropical lakes compared to temperate and arctic lakes.

My findings indicate that most fishes in each of the four Lower Mekong rivers had assimilated variable mixtures of basal production sources collected from the study sites. The most striking pattern was that, in all four rivers, there was a seasonal shift in the major basal production source supporting fish biomass. During the dry season, fish biomass appears to derive mostly from algae, and during the wet season C_3 macrophytes appear to be the most important source supporting fish biomass overall. Differences in the relative contributions of basal production sources to fish biomass probably reflect the seasonal availability of basal production sources in the four Lower Mekong rivers. Ellis et al. (2012) found that fine particulate organic matter (FPOM) in the Lower Mekong River in Cambodia was dominated by autochthonous sources (derived from phytoplankton) during the dry (low-water) season. During the wet season, they found a greater proportion of allochthonous FPOM derived from vascular plants (C_3 macrophytes) transported into the river from the watershed.

During periods of low flow in large rivers, ambient nutrient concentrations often are higher, water transparency increases, and productivity of algae increase (Kirk 1985, Roach 2013). Several investigators have suggested that algae provide better nutrition and contain more digestible components compared to macrophyte tissues, much of which

can be highly refractory (Sarkanen and Ludwig 1971, Legendre and Rassoulzadegan 1995, Renaud et al. 1999, Cotner and Biddanda 2002). Given that algae tend to be nutritious and relatively easy to digest, they can enter aquatic food webs efficiently (Thorp and Delong 1994, Delong and Thorp 2006). Several studies found that algae are an important production source supporting aquatic consumers during low-flow periods (Lewis 1988, Lewis et al. 2001, Hamilton et al. 1992, Forsberg et al. 1993, Roach 2009). A study in the Tonle Sap, the great lake of Cambodia that connects to the Mekong River, also concluded that algal production, rather than terrestrial organic material, was the major source supporting fish biomass during the annual low-water period (Campbell et al. 2009).

During the wet season when flows are high and the floodplain is inundated, allochthonous production sources were estimated to be the most important sources supporting fish biomass in the four study areas. During this season, algal production declines markedly due to sediment suspension, increased turbidity, limited light penetration, and scouring of substrate (Wissmar et al. 1981, Roach 2013). Although many C_3 plants in the tropics have relatively low nutritional value and also contain secondary chemical compounds that deter herbivory, they can become more nutritious following partial decomposition by bacteria and fungi that increases availability of nitrogen-rich material and causes leaching of defense compounds (Caraco et al. 1998, Davis et al. 2006). It also has been suggested that the high incidence of herbivory among fishes in the tropics may have evolved in response to the seasonal availability of plant material, especially seeds and fruits, in seasonally flooded forests (Lowe-McConnell

1969, Goulding 1980, Correa et al. 2007). Many fishes in the tropical rivers have physiological and morphological adaptations to feed on detritus or plant material (Goulding et al. 1988, Horn et al. 2011). It has been hypothesized that some plant species have coevolved with fish to release their seeds during floods so that fishes can consume and disperse them. In the Neotropics, there are several species of herbivorous fishes that extensively feed on fruits, flowers, and seeds (Lowe-McConnell 1975, Goulding 1980, Correa et al. 2007, Horn et al. 2011). *Mekongina erythrospila*, *Osphronemus goramy*, *O. exodon*, and several other Mekong fishes are reported to enter flooded forests to feed on fruits (Rainboth 1996). A few studies of temperate-zone rivers also have found that terrestrial carbon is an important source supporting aquatic consumers during high-flow pulses (Huryn et al. 2001, Zeug and Winemiller 2008), but it is likely that this material is not being consumed by fishes directly, because comparatively few temperate-zone fishes possess morphological traits indicative of granivory or frugivory (Correa et al. 2007, Horn et al. 2011, Correa and Winemiller 2013).

The present study was conducted in rivers that experience extensive flooding during the wet season each year (duration ~ 6 months), and this provides fishes with access to a variety of food resources in the floodplains. Annual flood pulses of large tropical rivers provide fishes with access to both terrestrial and aquatic food resources in floodplains (Lowe-McConnell 1969, Goulding 1980, Junk et al. 1989, Correa and Winemiller 2013), and this seems to explain the high secondary productivity that supports major fisheries in these systems (Welcomme 1979, Goulding et al. 1988,

Winemiller 2004, Correa and Winemiller 2013). During annual flood pulses in the tropics, submerged riparian vegetation is directly consumed by herbivorous invertebrates and fishes that, in turn, are consumed by predatory fishes. During the flood pulse, availability of terrestrial arthropods for fishes also increases. Long flood duration also promotes decomposition of submerged terrestrial vegetation (Balcome et al 2005, Rayner et al. 2010). Detritivorous fishes can then exploit the nutritious microbial biomass associated with decomposing submerged vegetation (Bowen et al. 1984, German et al. 2010, Lujan et al. 2011).

Studies also indicate that aquatic consumers mostly assimilate carbon derived from C₃ plants and little from C₄ plants (Thorp et al. 1998, Zeug and Winemiller 2008, Roach et al. 2009). In my study, consumers from all four rivers appear to assimilate little carbon from C₄ grasses compared to C₃ plants, and this was the case during both seasons. This is not surprising considering that these grasses generally have relatively low nutritional value compared to most C₃ macrophytes, and much less compared to algae. C₄ grass tissues contain compounds, such as hemicelluloses, cellulose and lignin, that are difficult for animals to digest (Minson 1971). Nevertheless, C₄ grasses can be broken down by microbes and subsequently buried in sediments before entering the upper food web by way of organisms that feed on detritus that has been processed through the microbial loop (Cole et al. 2011). Only a few studies (Forsberg et al. 1993, Jepsen and Winemiller 2007) have inferred significant assimilation of C₄ grasses by certain fishes, for example, *Schizodon fasciatus* from the Amazon River in Brazil and *S. isognatus* from the Apure River in Venezuela. My study indicates that C₄ grasses can be an important

production source in food chains leading to certain groups of fishes, such as air-breathing fishes (*Channa* and *Clarias*) that commonly inhabit floodplain pools and swamps. This is consistent with a recent study in the Oueme River in West Africa that found air-breathing fishes from man-made ponds in the floodplain had assimilated variable amounts of C₄ grasses (Jackson et al. 2013).

Production sources supporting trophic guilds

My findings also reveal variation in estimates of basal production sources supporting fishes of various functional groups. Differences in assimilation of material from alternative production sources by trophic guilds were only detected during the dry season. All detritivorous and algivorous fishes appear to have assimilated benthic algae. Given that these fishes scrape or suck organic materials from substrates, they should have carbon stable isotope δC^{13} signatures that reflect those of bulk samples of benthic microphytobenthos (referenced in this study as periphyton, but perhaps also containing microorganisms and organic matter of allochthonous origin). Most of the fishes classified as insectivores appear to have assimilated material derived from one basal source, either seston or C₃ plants. It is likely that insectivores consume aquatic invertebrates that feed on algae or allochthonous plant materials. MixSIR estimates indicate that piscivores and omnivores likely had assimilated material from multiple basal sources that include benthic algae, seston, C₃ plants and, to a much lesser extent, C₄ plants. These findings suggest that piscivores and omnivores assimilate biomass derived from diverse trophic pathways. Studies from other tropical river systems indicated that omnivorous foraging strategies are widespread among fishes (Winemiller

1990, Polis et al. 1996), and many fishes of the Mekong have been classified as omnivores (Rainboth 1996).

Production sources according to habitat types

Estimates of production sources assimilated by fishes in the two habitat guilds were different during the dry season but not during the wet season. For fishes restricted to the river channel, algae apparently made a greater contribution to fish biomass during the dry season, whereas C₃ macrophytes had relatively greater importance for fishes that inhabit floodplain habitats. Previous studies also found that fishes restricted to the river channel are mostly supported by trophic pathways originating from algae (Hamilton et al. 1992, Forsberg et al. 1993, Lewis et al. 2001, Roach 2009). Most of the channel-restricted fishes in the Lower Mekong River show this pattern, however a few species of loaches (e.g. *Acanthopsis* and *Schistura*) could have assimilated significant material originating from macrophytes. These loaches probably consume microcrustacea and other tiny aquatic invertebrates that consume detritus or the microorganisms that process macrophyte detritus despite its refractory nature (Caraco et al. 1998, Davis et al. 2006). Food web research on tropical streams in Hong Kong that employed analyses of gut contents and stable isotopes found that loaches (Balitoridae) consumed and assimilated bacteria (Lau et al. 2009a,b).

Previous research has estimated that most fishes inhabiting floodplain habitats are supported by trophic pathways originating from macrophytes as well as others that originate from algae (Rai and Hill 1984, Zeug and Winemiller 2008, Jackson et al.

2013). In this study, air breathing fishes, such as *Channa* and *Clarias* species, which often are found in floodplain habitats, support this observation. These species apparently assimilate significant amount of material derived from both algae and macrophytes. A recent study in West Africa similarly concluded that air-breathing fishes from floodplain habitats were supported by both macrophytes and microphytobenthos but not seston (Jackson et al. 2013). Shallow aquatic habitats in tropical river floodplains often are covered with dense mats of floating macrophytes that can reduce gas exchange at the surface and block light penetration in the water column and hinder algal production. Despite low water-column productivity, consumers in these habitats may assimilate material originating from epiphytic algae that may have low standing biomass but high turnover (Jackson et al. 2013). For example, Bunn et al. (2003) estimated that aquatic consumers of the Cooper Creek floodplain in central Australia were mostly supported by benthic algae/microphytobenthos. Likewise, Hamilton et al. (1992) found that algal production supports most of the biomass of fish assemblages in lagoons within the floodplains of the lower Orinoco River in Venezuela.

River impoundment impacts

Findings from this study reveal a potential effect of river impoundment on basal production sources and their contributions to fish biomass. Results from the mixing model indicated that seston and benthic algae are the most important in supporting food webs of the Sesan River (strongly impacted by Yali dam in Viet Nam) during the dry season, as was the case with the other three rivers, but also to a greater degree than

observed for the other rivers of the Lower Mekong. It is likely that lower average water velocities downstream from the impoundment create conditions conducive for algae production. A study conducted in rivers of the Paraná River Basin in Brazil (Hoeinghaus et al. 2007) also concluded that consumers inhabiting river reaches below impoundments are more dependent on algal production compared to reaches above the same impoundments. That study concluded that dams trap sediments and thereby increase water transparency in the dam tailwaters that allows greater light penetrance and algae growth. In particular, dams constructed in the Lower Mekong Basin are predicted to trap more than 50% of the suspended sediment load delivered downstream (Kummu et al. 2010, Xue et al. 2010).

My study also indicates that there is less contribution of C_3 macrophytes to fish biomass in the Sesan River compared to the other rivers during the dry season. This might be due to a reduced annual flood pulse and more restricted access to the floodplain habitats for migratory fishes. Most (85-90%) of the Mekong Basin's discharge occurs during the monsoon season. However, as a result of dam operations, water levels in some tributaries of Mekong Basin have declined in recent years (Zalinger et al. 2000, Lu and Siew 2005). This was especially apparent in the Sesan River during the dry season in 2010-2011, when discharge was very low compared to the other two tributary rivers (see Figures 3-5).

Dams also are strong barriers to longitudinal fish movement (Dugan et al. 2010). The Mekong River Basin contains many fishes that are considered highly migratory (perhaps more than 50% of the regional fish fauna), with some of species migrating

hundreds of kilometers on a seasonal basis (Barlow et al. 2008, Baran and Myschowoda 2008). During the dry season, I found very few pangasids (migratory fishes) in the Sesan River compared to the other three rivers that are not significantly impacted by dams. These migratory fishes may be unable to access the upper reaches of the Sesan due to the river's low discharge. A review by Baran et al. (2011) found that the Sesan River currently has far fewer migratory fishes compared to other Mekong tributaries, including the Sekong and Srepok Rivers. Their study revealed that a number of migratory species, particularly those belonging to the Pangasidae (e.g. *Pangasius conchophilus*), have declined in the Sesan River (Baran et al. 2011). Similarly, Hoeinghaus et al. (2009) found that impoundment the Itaipu Reservoir on the Paraná River in Brazil created a barrier to fish migration and altered the fish assemblage and fishery. Dams also have been demonstrated to have strong effects on fish community composition by favoring equilibrium strategists while adversely affecting populations of periodic and opportunistic strategists (Mims and Olden 2013).

Fish migration, isotopic ratios and tissue turnover

Migratory fishes are important components of river food webs because they assimilate and transport primary and secondary production as fishes move from one landscape unit to another. They subsidize river food webs by enhancing the resource base for apex predators (Polis et al. 1996, 1997, Winemiller and Jepsen 1998, Horn et al. 2011). Winemiller and Jepsen (1998) proposed that fish migrations in tropical rivers are

a response to spatial and temporal environmental variation, especially with regard to food resource availability, and physicochemical factors such as dissolved oxygen.

One potential limitation of my study is that many fishes of the Mekong are migratory and therefore could have previously consumed and assimilated food resources from locations distant from the study sites where they were captured (e.g. locations upstream or downstream or seasonal floodplain habitats). In addition, small migratory fishes that are prey for other fishes could have assimilated and transported material derived from sources at distant locations, and thereby imported it into food webs at the study locations (Polis et al. 1996, Winemiller and Jepsen 1998). Thus, it cannot be ruled out that some fishes might have migrated into the study areas with isotopic signatures derived from feeding at distant locations (Polis et al. 1996). A recent study of Australian tropical rivers demonstrated that a river having floodplain inundation of long duration revealed a weak relationship between isotopic signature of fishes and local sources (biofilm), whereas the river with a short flood period showed a stronger relationship between isotopic composition of fishes and in-situ resources (Jardine et al. 2012). Considering fish tissue turnover rate, (~ 1-3 months for muscle tissues, Buchheister and Latour 2010), my study design and interpretations should not be significantly influenced by recent arrival of migratory fishes that had assimilated sources from outside the location where they were caught. My sampling was conducted in the middle of each season (3-4 months after the start of each season), which should allow enough time for stable isotope ratios of fish muscle tissues to reflect consumption and assimilation of local food resources. In tropical rivers, major fish migrations generally occur near the

onset of the annual flood pulse, and again during the early phase of flood recession (Lowe-McConnell 1975, Goulding 1980). Therefore, it seems likely that any migratory species within my dataset should have reflected, to a large degree, the local food sources that were assimilated, at least with regards to muscle tissue.

CONCLUSION

In sum, my results support my hypotheses that algae were the most important production sources supporting fish biomass during the dry season, and riparian macrophytes were the most important production source supporting fishes during the wet season. My study revealed the importance of temporal variation of the flood pulse and availability of alternative primary production sources for fish stocks of the Lower Mekong River. Many tropical river food web studies reflect spatial rather than temporal variation because they only collected samples from multiple rivers during a restricted period such as dry season (e.g. Hoeinghaus et al. 2007, 2008, 2009, Roach et al. 2009, Jardine et al. 2012) instead of data collected from the same river during different seasons. My findings reinforce calls for more detailed studies of seasonal variation in food web structure and function in rivers, especially in tropical regions where seasonal flooding is often pronounced and prolonged.

My study not only adds to the body of evidence that food web dynamics in tropical rivers undergo significant seasonal shifts, but also emphasizes that river food webs are altered by dams and flow regulation. My findings emphasize the need for more

evaluation of ecological impacts of hydropower development in the region. Dams on upper reaches of the Sesan River have affected hydrology, production dynamics, food web structure, and large migratory fishes that are the important components of both the food web and fishery. The impact of dams on ecosystem functions, biodiversity, and human populations in this region is potentially large and irreversible. Results from my study also illustrate the need for consideration of impacts from deforestation in this region, because riparian vegetation clearly plays a significant role as a basal production source supporting fish biomass in these rivers, particularly during the wet season.

CHAPTER III

RELATIONSHIP BETWEEN BODY SIZE AND TROPHIC POSITION IN FISH ASSEMBLAGES OF TROPICAL RIVERS IN THE LOWER MEKONG BASIN

INTRODUCTION

Body size has been recognized as an important determinant of community structure because it influences ecological processes that affect consumer-resource interactions, life history traits, population dynamics, and metabolic rates (Elton 1927, Pimm 1982, Peters 1983, Yodzis and Innes 1992, Cohen et al. 1993, De Roos 2003, Brown 2004, Brose et al. 2006, Arim et al. 2007). Therefore, body size is a useful measurement to consider within ecological networks such as food webs (France et al. 1998, Jonsson et al. 2005, Woodward et al. 2005a, b, Cohen et al. 2009). Body size affects food web structure by determining consumption efficiency for food items of various sizes, and has been incorporated in food web models that seek to predict ecosystem stability, patterns of energy flow, and response to disturbances (Pauly et al. 1998, Brown et al. 2004, Woodward et al. 2005a, b). Food webs are frequently structured by body size so that predators are larger than their prey and larger individuals feed at higher trophic levels (Cohen et al. 1993, Reuman and Cohen 2004, Brose et al. 2006).

The relationship between body size and trophic levels of animals has long been a major focus of discussion among ecologists, and a hierarchy of increasing body size with

increasing trophic levels has been broadly accepted since Charles Elton's work in the early 1900s (Williams and Martinez 2000, Cohen et al. 1993, 2003, Warren 2005, Brose et al. 2006). Analyses of large datasets have tended to support Elton's idea by reporting positive relationships between body size and trophic position. Riede et al. (2011) found a trophic hierarchy pattern among organisms in marine and lake ecosystems. Romanuk et al.'s (2011) study also revealed a significant relationship between the trophic level and body size among 8361 species of fish recorded in the FishBase (www.Fishbase.org). Naisbit et al. (2012) analyzed 13 food web databases (containing 1077 species) and obtained similar results. An analysis of long-term data (40 years) on freshwater fish from Lake Biwa in Japan revealed a strong relationship between body size and $\delta^{15}\text{N}$ (an index of relative trophic position) for 60% of the years (Nakazawa et al. 2010). France et al. (1998) also documented a strong body size-trophic level correlation among aquatic organisms from a lake and seagrass meadow. A study by Jennings et al. (2001) found a strong correlation between body size (mass) and trophic position among 15 marine fish communities.

Although Elton's generalization has been widely accepted among ecologists, a few studies have provided evidence that either failed to support or only partially supported the body size-trophic level correlation. A food web study of a tropical floodplain river, reported no relationship between body size and trophic level among fishes (Layman et al. 2005a). A study from the North Sea found that the body size-trophic position relationship for fishes varies with scale of analysis; for example, there was no relationship at the species level, but there was a strong relationship at the

community level (Jennings et al. 2001). A study that examined the relationship at the species level found that trophic position of trout in Canada did not correlate with body size (Vander Zanden et al. 2000). Another study reported opposite results for native vs. invasive species, with body mass of native species revealing no relation with their trophic position compared to invasive species that showed a positive relationship (Swanson et al. 2003). Other investigations reported an absence of a body size-trophic level relationship among benthivores, omnivores or herbivores, but a strong relationship among carnivores (Jennings et al. 2002, Cocheret de la Morinière et al. 2003, Deudero et al. 2004, Riede et al. 2011). Likewise, a study of sharks reported variability in the body size-trophic position relationship, with carcharhinid sharks revealing a stronger correlation than zooplanktivorous sharks (Cortes 1999).

Recent studies have reported the role of phylogeny in the relationship between body size and trophic level. Several studies indicated that the body size is more strongly related to trophic position when species in the dataset are more closely related (Cattin et al. 2004, Romanuk et al. 2011, Naisbit et al. 2012). For example, Romanuk et al. (2011) found that the amount of variance explained by the relationship between the two variables increased from 20% to 37% when they performed the analysis on taxonomic orders compared to the same dataset with consumers defined at finer taxonomic levels. However, analyses of 249 sharks from the Caribbean indicated that closely related species of similar sizes often feed at different trophic levels (Rezende et al. 2009).

Given these mixed results for the relationships between trophic position and body size, there is a need for further investigation and refinement of the theory. Despite the

fact that there are many studies that reveal a strong relationship between body size and trophic level, most research on the topic has been conducted in temperate regions, either in marine or lake ecosystems, and only one was conducted in the tropics (e.g. Layman et al. 2005a). Most of these studies did not account for the influence of phylogeny.

Furthermore, there has not been any explicit analysis on the relationship within or across trophic guilds, even though there is evidence that guilds can influence this correlation.

This creates a major gap in our knowledge of ecological relationships within aquatic food webs in the tropics. Tropical rivers support tremendous biodiversity, often with high productivity that supports important fisheries. Therefore, a better understanding of the relationship between body size and trophic position in these ecosystems has immediate conservation applications (Purvis et al 2000, Olden et al. 2006, 2007).

The present study addresses the question of whether or not body size is a good predictor of trophic position in fish communities of tropical river systems, and assesses the influence of phylogeny and trophic guilds on this relationship. Specifically, I examined the relationship between trophic position and body size at the species, family, order, guild, and assemblage levels using data for fishes surveyed from four tropical rivers of the Lower Mekong River Basin. Trophic positions were estimated using stable isotope ratios of fish tissues, a method that allows consumers to be placed at positions along a vertical trophic continuum rather than categorized at discrete trophic levels.

MATERIALS AND METHODS

Study sites

Specimens analyzed for this investigation were collected during surveys of four rivers in northeastern Cambodia: the Mekong, Sekong, Sesan, and Srepok rivers. The latter three rivers are major tributaries of the Mekong and have been referred to as the 3S rivers. The stretch of the Mekong River and its riparian zone between Stung Treng and the Laos-Cambodia border was designated a RAMSAR wetland of global significance because of its biodiversity conservation value in the Indo-Burma region. Watersheds of the Sekong, Sesan and Srepok rivers also have been identified as critical areas for biodiversity conservation (Birdlife 2012). I sampled a site on the Mekong River near Stung Treng provincial center (13.579383N, 105.994366E), the Sekong River at Siem Pang (14.11434N, 106.39104E), the Sesan River at Veurn Sai (13.94585N, 106.79701E), and the Srepok River at Lomphat (13.47508N, 106.999683E).

Data collection and laboratory analysis

I collected fish tissues, benthic algae, seston, and common plants from one location of all four rivers during the dry season (January 2010 and January 2011) for stable isotope analysis. An attempt was made to collect tissue samples from the dominant (most obvious) basal production sources and common fishes at all sites. Whenever possible, 3-5 individuals of each species were obtained from each site. Different parts (leaves, fruits, seeds) of common riparian plants were collected, cut into

small pieces, placed in plastic bags and preserved in salt for later analysis in the laboratory. Phytomicrobenthos (benthic algae and associated biofilm) samples were collected by gently scraping rocks and submerged tree branches. Seston samples (phytoplankton and other suspended fine particulate matter) were collected from near the water surface with 1-L opaque bottles, and the water was filtered with precombusted Whatman GF/F filters (pore size 0.7 μm). Fishes were collected using multiple fishing gears, including seines, cast nets and dip nets. Additional fish specimens were obtained from local fishers who primarily fished with gill nets and baited hooks. Fish specimens were identified to species level and measured to the nearest 1.0 mm standard length (SL). Fish muscle tissue samples were taken from the flank near the base of the dorsal fin. Fish tissue samples were preserved in salt for subsequent analysis in the laboratory. Sample collection, preservation and laboratory preparation were done following Arrington and Winemiller (2002).

In the laboratory, tissue samples were soaked in distilled water for 4-5 h, rinsed, and dried in an oven at 60° C for 48 h. After drying, samples were ground into fine powder using an electronic ball-mill grinder. Subsamples were weighed to the nearest 0.02 mg and packaged into ultrapure tin capsules. Samples were analyzed for stable isotope ratios of nitrogen ($^{15}\text{N}/^{14}\text{N}$) at the Analytical Chemistry Laboratory of the Institute of Ecology at the University of Georgia. Samples were then dry combusted following micro-Dumas techniques with a Carlo Erba CHN elemental analyzer. Purified atmospheric gases of nitrogen (N_2) were introduced into a mass spectrometer, and isotopic composition was quantified relative to the standard (atmospheric nitrogen N_2).

Isotope ratios are reported in parts per thousand (‰) compared to standard values of atmospheric for nitrogen as $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$ where $R = {}^{15}\text{N}/{}^{14}\text{N}$.

Trophic position calculation

Stable isotopes of nitrogen have been widely used for estimating trophic position of metazoans in food web studies (Post 2002). For each fish species, trophic position (TP) was calculated using the formula (Vander Zanden and Rasmussen 1999, Post 2002): $TP = (\delta^{15}\text{N}_{\text{consumers}} - \delta^{15}\text{N}_{\text{basal source}})/2.5 + 1$, where $\delta^{15}\text{N}_{\text{consumers}}$ is the signature of $\delta^{15}\text{N}$ fishes and $\delta^{15}\text{N}_{\text{basal source}}$ is the mean $\delta^{15}\text{N}$ value of primary production sources including microphytobenthos, seston and macrophytes. The value 2.5 represents trophic fractionation of the isotopic ratio (the shift that occurs in material between its ingestion by a consumer and its assimilation into the consumer's tissue); here I use the mean trophic fractionation value derived from a meta-analysis of laboratory feeding studies involving diverse metazoan consumers (Vanderklift and Ponsard 2003). When calculating TP of fish specimens or species, the mean $\delta^{15}\text{N}$ of basal production sources was based on samples obtained from the same survey locality where the fish were collected.

Classification of species trophic groups

I classified fish into four trophic guilds according to information obtained from FishBase (2012) and Rainboth (1996) as well as interpretation of fish functional morphology. The four trophic guilds are: 1) *piscivore*: fish that consume mostly fish and,

in some cases, lesser proportions of decapod crustaceans; 2) *omnivore*: trophic generalists that consume variable proportions of phytoplankton, benthic algae, and aquatic invertebrates; 3) *detritivore*: fish that consume detritus and/or algae; and 4) *insectivores*: fish with diets strongly dominated by invertebrates.

Phylogenetic relationships

I created a phylogenetic distance matrix of fish species using taxonomic classification levels as proxies for relative degrees of evolutionary divergence. Phylogenetic distance was estimated by counting the number of nodes that separate each pair of species within the phylogenetic (taxonomic) tree following the method of Winemiller et al. (1995). I assigned a distance of 1 to species that belong to the same genus, 2 that belong to the same family, and 3 that belong to the same order. This method assumes that each taxonomic level has a uniform degree of evolutionary divergence for all branches (all branch lengths are equal), which obviously is false. Because a molecular time-calibrated phylogeny with branch lengths is not available for the entire fish assemblage, this proxy method provides a crude estimate of evolutionary relationships among species in the local assemblages. I assigned the taxonomic ranks using the recent taxonomy presented by Nelson (2006) and Rainboth et al. (2012).

Data analysis

First, I used the Mantel test to examine relationships between shared ancestry (i.e. phylogenetic dissimilarity estimated from taxonomic distance), body size, and

trophic position. Next, I performed a partial Mantel test (Smouse et al. 1986) to evaluate the influence of phylogeny on the relationship between body size and trophic position. The partial Mantel test also was used to assess the influence of phylogeny on the body size–trophic level relationship for each trophic guild separately.

I used linear regression to explore relationships between body size and trophic position. Body size (SL) was log-transformed before performing analyses. Linear regression analysis was conducted for a local fish assemblage, and for each taxonomic order and family that contained more than ten species. Regression analysis also was performed to investigate the relationship between body size and trophic level among the four trophic guilds. Mean, minimum, maximum, and variance of body size of each species were computed, and to avoid the effect of ontogenetic diet shifts within species, I used similar-sized individuals for computation of mean body size. In addition, analysis of ontogenetic niche shifts was performed on species for which I had large samples with large variance in body size. Finally, I used one-way ANOVA and post-hoc Tukey HSD to compare differences in variances and means of body size and trophic position among fish trophic groups. All analyses were performed using the software PAST (Hammer et al. 2001).

RESULTS

Taxonomic diversity within the species assemblage

Analyses of the relationship between fish body size and their trophic position were performed using 699 fish specimens belonging to 143 species, 73 genera, 26 families, and 7 orders collected from the four sites in the Lower Mekong River Basin. The most abundant order was Cypriniformes followed by Siluriformes and Perciformes. The most abundant family was Cyprinidae followed by Siluridae and Bagridae. Specimens ranged from 3 cm (*Schistura sp.*) to 60 cm (*Channa micropeltes*) standard length. Trophic guild classification yielded 23 detritivores (all belonging to Cypriniformes), 58 insectivores (31 Cypriniformes, 14 Siluriformes, 7 Perciformes, 3 Synbranchiformes, 2 Pleuronectiformes, 1 Osteoglossiformes), 36 omnivores (16 Cypriniformes, 15 Siluriformes, 4 Perciformes, 1 Synbranchiformes), and 26 piscivores (14 Siluriformes, 7 Perciformes, 3 Cypriniformes, 1 Osteoglossiformes).

Phylogenetic influence

The Mantel test did not indicate a significant association between phylogenetic similarity and similarity of trophic level ($P = 0.08$, $R = 0.04$) or phylogenetic similarity and body-size similarity ($P = 0.8$, $R = -0.02$). The partial Mantel test showed no significant association between the degree of phylogenetic similarity and the relationship between body size and trophic position ($P = 0.82$, $R = -0.02$). When the partial Mantel test was performed separately for each trophic guild, there were no significant patterns

of association between phylogenetic similarity and the relationship between body size and trophic level (detritivores, $P = 0.26$, $R = 0.01$; insectivores, $P = 0.97$, $R = -0.07$; omnivores, $P = 0.47$, $R = -0.0007$; piscivores, $P = 0.74$, $R = -0.05$).

Relationship between body size and trophic position

Based on the full species dataset, linear regression revealed no relationship between body size and trophic position ($F_{1,142} = 1.87$, $P = 0.17$, $R^2 = 0.013$). However, the correlation between body size and trophic position varied when each order was analyzed separately. The relationships between body size and trophic position was significant for Siluriformes ($F_{1,42} = 6.86$, $P = 0.01$, $R^2 = 0.14$) and Perciformes ($F_{1,20} = 6.40$, $P = 0.02$, $R^2 = 0.28$), but was not significant for Cypriniformes ($F_{1,69} = 3.58$, $P = 0.09$, $R^2 = 0.04$) (Figure 13). At the family level, linear regression revealed a significant association between mean standard length and mean trophic position for species belonging to the family Siluridae ($F_{1,12} = 19.20$, $P < 0.001$, $R^2 = 0.63$) and Bagridae ($F_{1,13} = 12.77$, $P = 0.003$, $R^2 = 0.51$) but not for species in the Cyprinidae ($F_{1,54} = 0.13$, $P = 0.71$, $R^2 = 0.002$) (Figure 14).

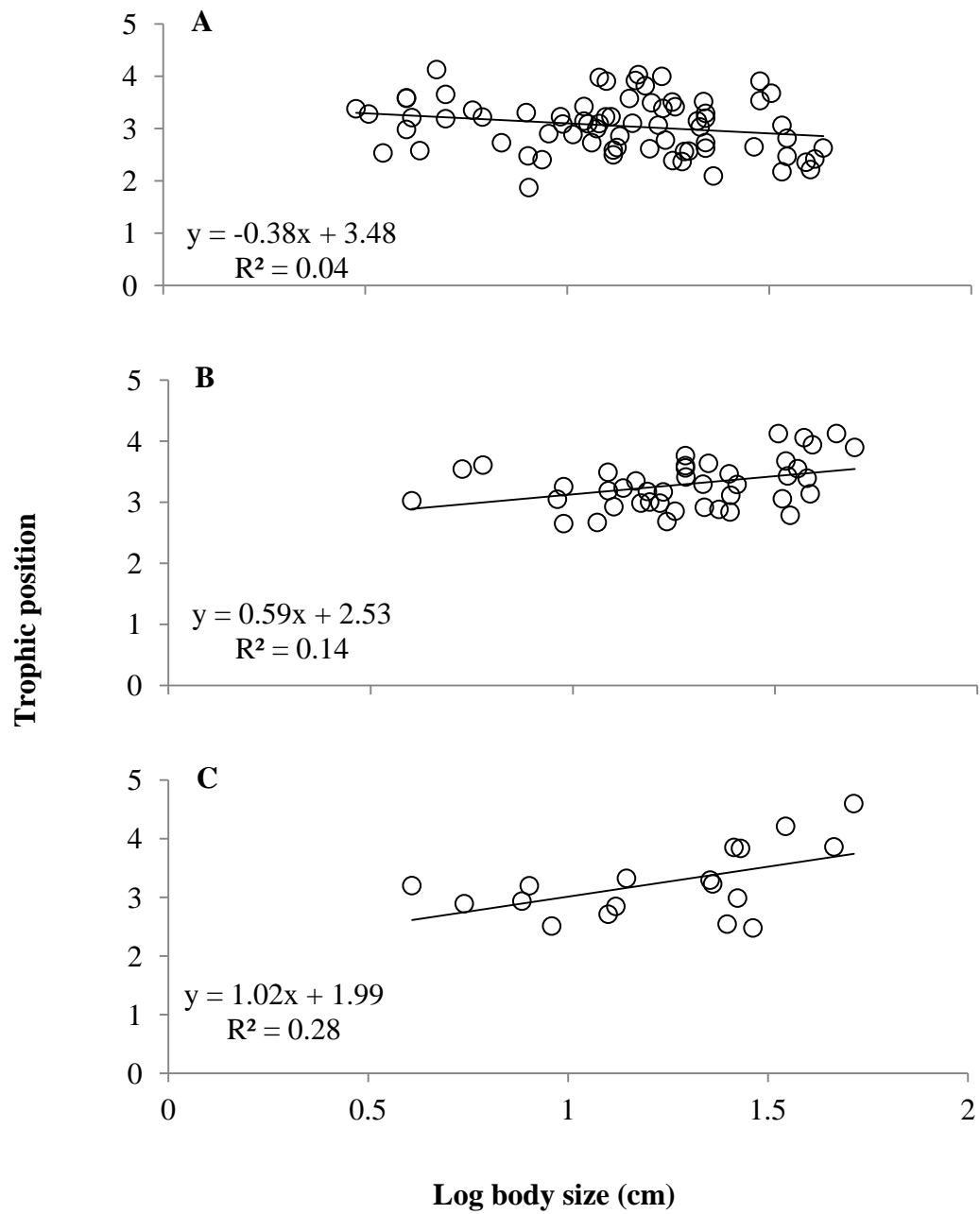


Figure 13. Relationship between trophic position and body size among orders (A. Cypriniformes, B. Siluriformes, and C. Perciformes).

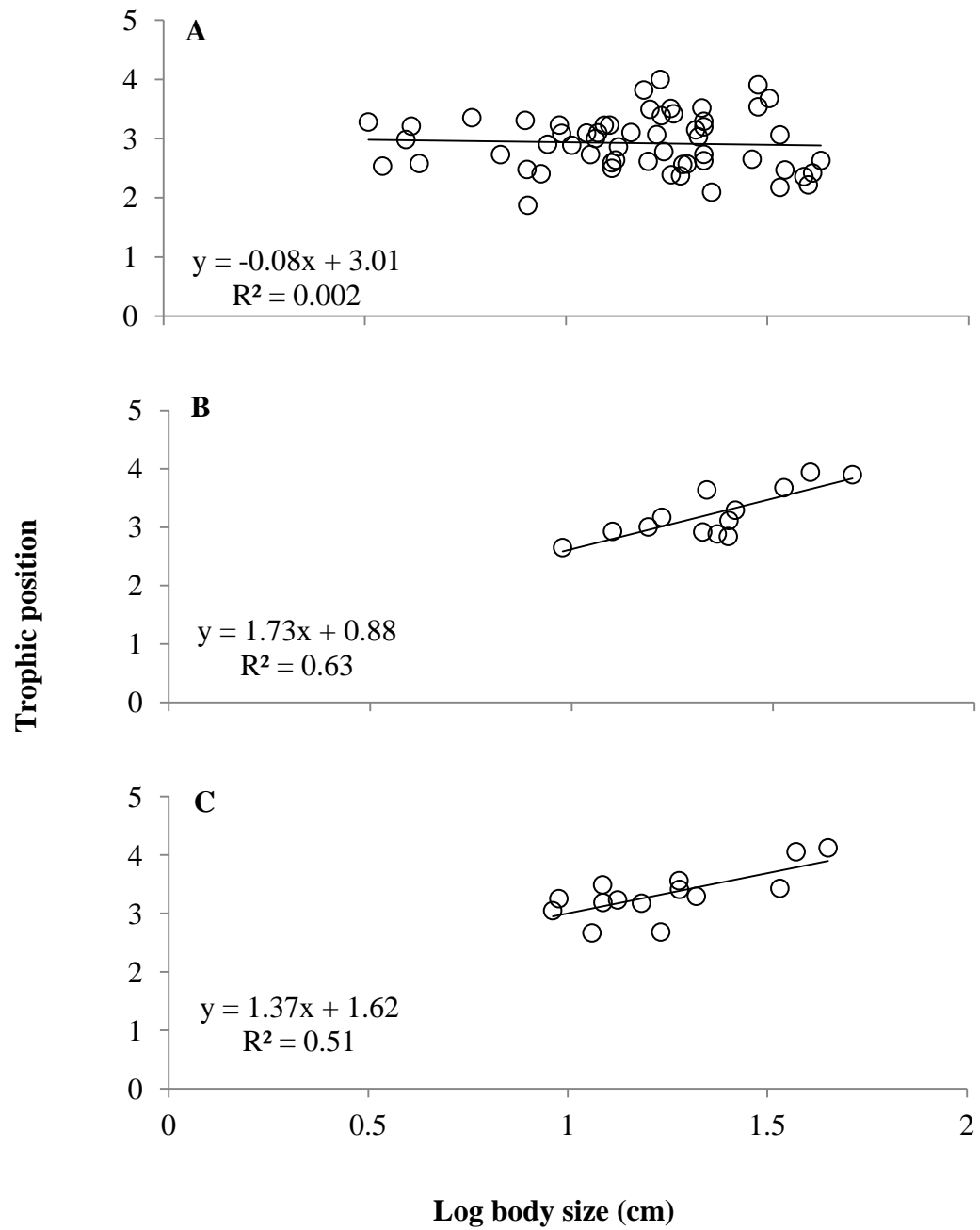


Figure 14. Relationship between trophic position and body size among families (A. Cyprinidae, B. Siluridae, and C. Bagridae).

The association between body size and trophic position indicated variation in the strength of the relationship among fish species of different trophic guilds (Figure 15). Fish body size and estimated trophic position were not correlated among detritivores ($F_{1,22} = 0.23$, $P = 0.63$, $R^2 = 0.01$), insectivores ($F_{1,57} = 2.55$, $P = 0.11$, $R^2 = 0.04$) and omnivores ($F_{1,35} = 1.42$, $P = 0.24$, $R^2 = 0.04$). In contrast, linear regression analysis showed a stronger and statistically significant relationship between trophic position and body size among piscivores ($F_{1,25} = 18.21$, $P < 0.001$, $R^2 = 0.43$). Among the 14 species with large samples encompassing broad ranges of body sizes, the correlation between body size and trophic level was significant for species: *Wallago attu*, *Hemibagrus wyckioides*, *Hemibagrus nemurus*, *Pangasius conchophilus*, *Channa limbata*, *Channa micropeltes*, and *Anabas testudineus*. Trophic level did not correlate with body size of *Hypsibarbus lagleri*, *Poropuntius normani*, *Labiobarbus leptocheila*, *Notopterus notopterus*, *Cyclocheilichthys mekongensis*, *Puntioplites falcifer*, *Hemibagrus nemurus*, *Pangasius conchophilus*, and *Mystus singaringan* (Figures 16-19).

ANOVA revealed that insectivores had the smallest body size ($\bar{X} = 12.2$ cm), piscivores had the largest body size ($\bar{X} = 29.2$ cm), and detritivores ($\bar{X} = 22.6$ cm) and omnivores, ($\bar{X} = 22.1$ cm) had intermediate body sizes (Figure 20). Comparison of mean trophic position among these trophic guilds indicated that detritivores had the lowest trophic level (2.6) followed by omnivores (2.8), insectivores (3.3), and piscivores (3.6) (Figure 21).

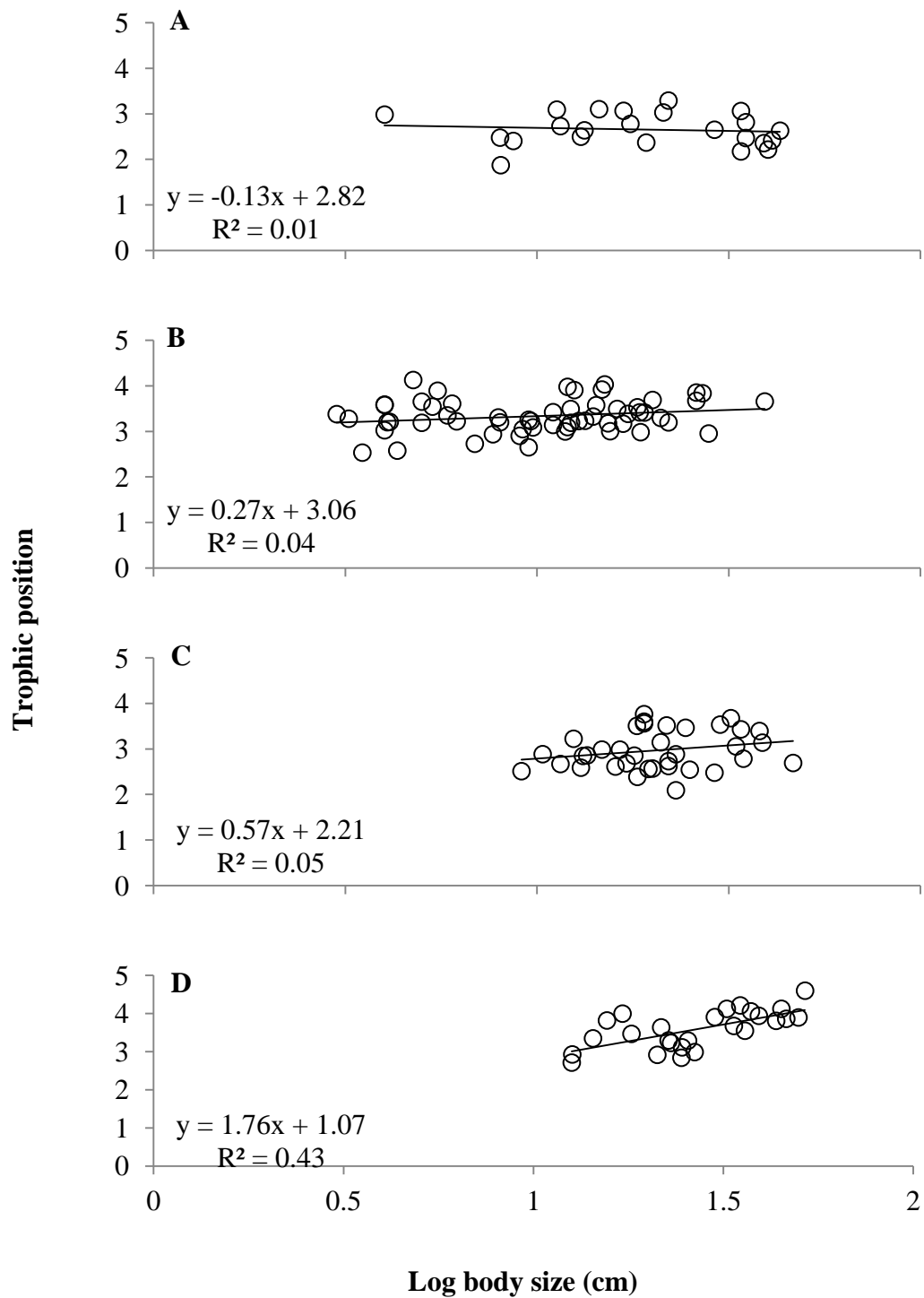


Figure 15. Relationship between trophic position and body size among fish trophic guilds (A. Detritivores, B. Insectivores, C. Omnivores, and D. Piscivores).

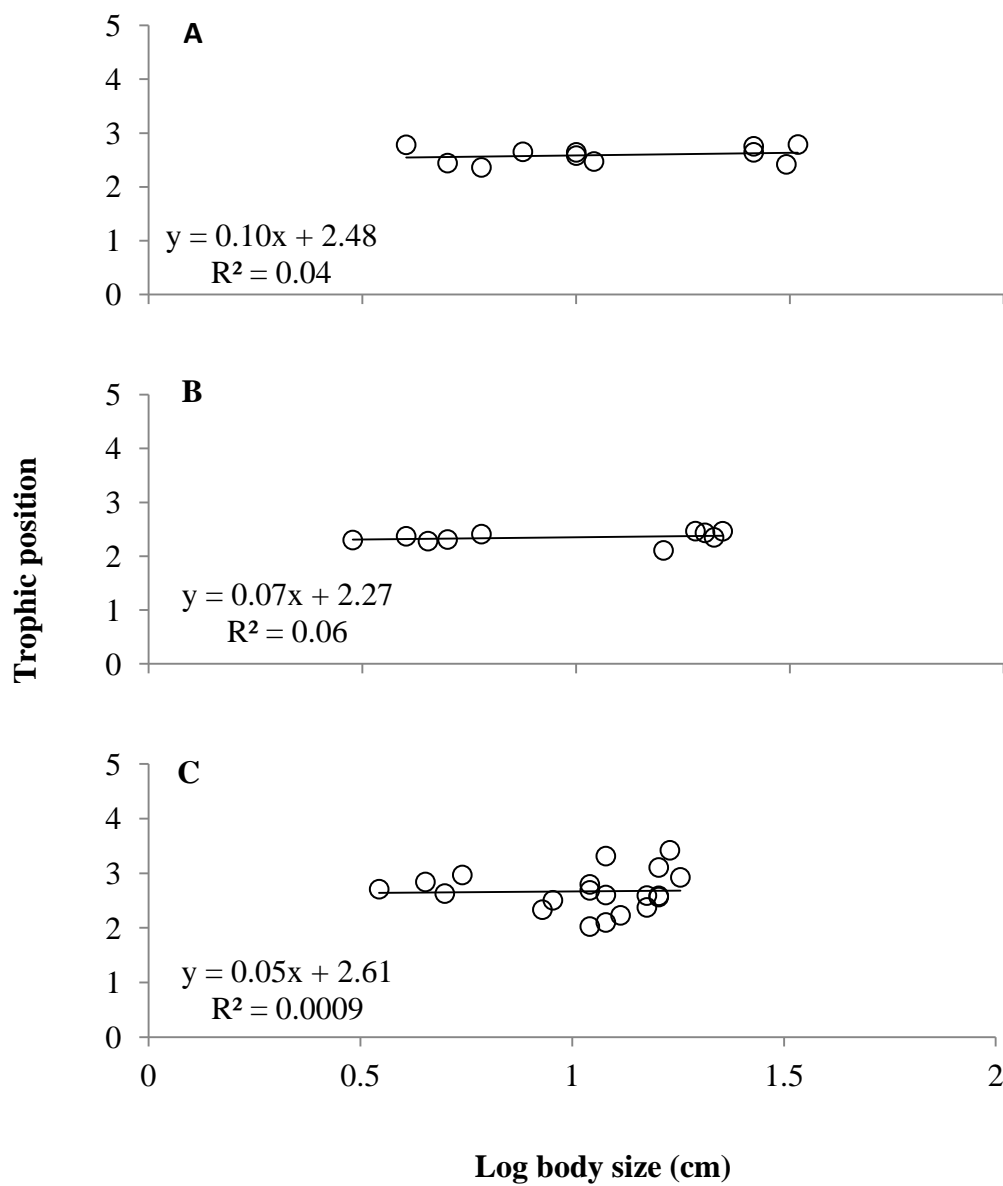


Figure 16. Relationship between trophic position and body size of three species of detritivores (A. *Hypsibarbus lagleri*, B. *Poropuntius normani*, C. *Labiobarbus leptocheila*).

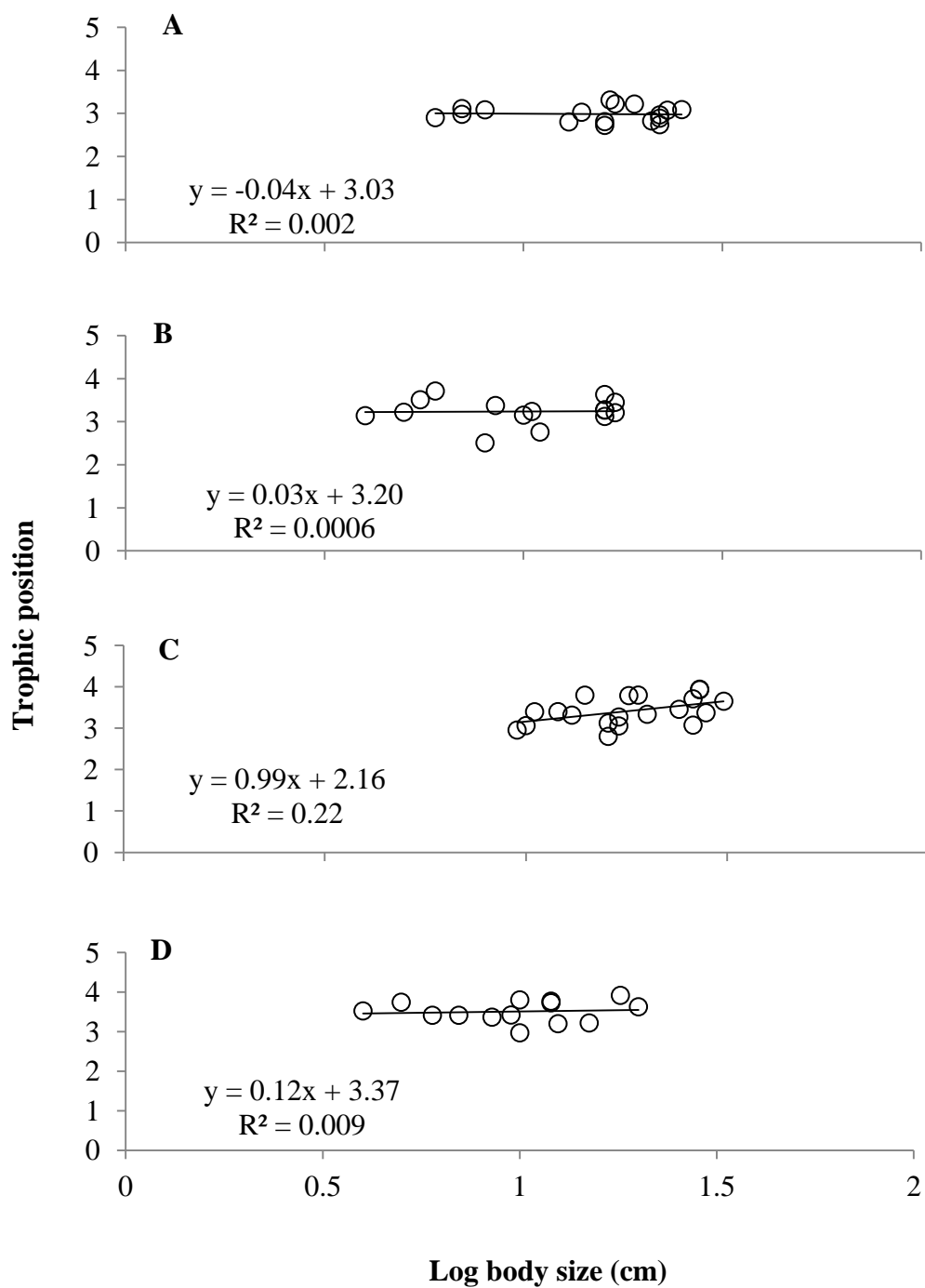


Figure 17. Relationship between trophic position and body size of four species insectivores (A. *Notopterus notopterus*, B. *Cyclocheilichthys mekongensis*, C. *Hemibagrus nemurus*, D. *Mystus singaringan*).

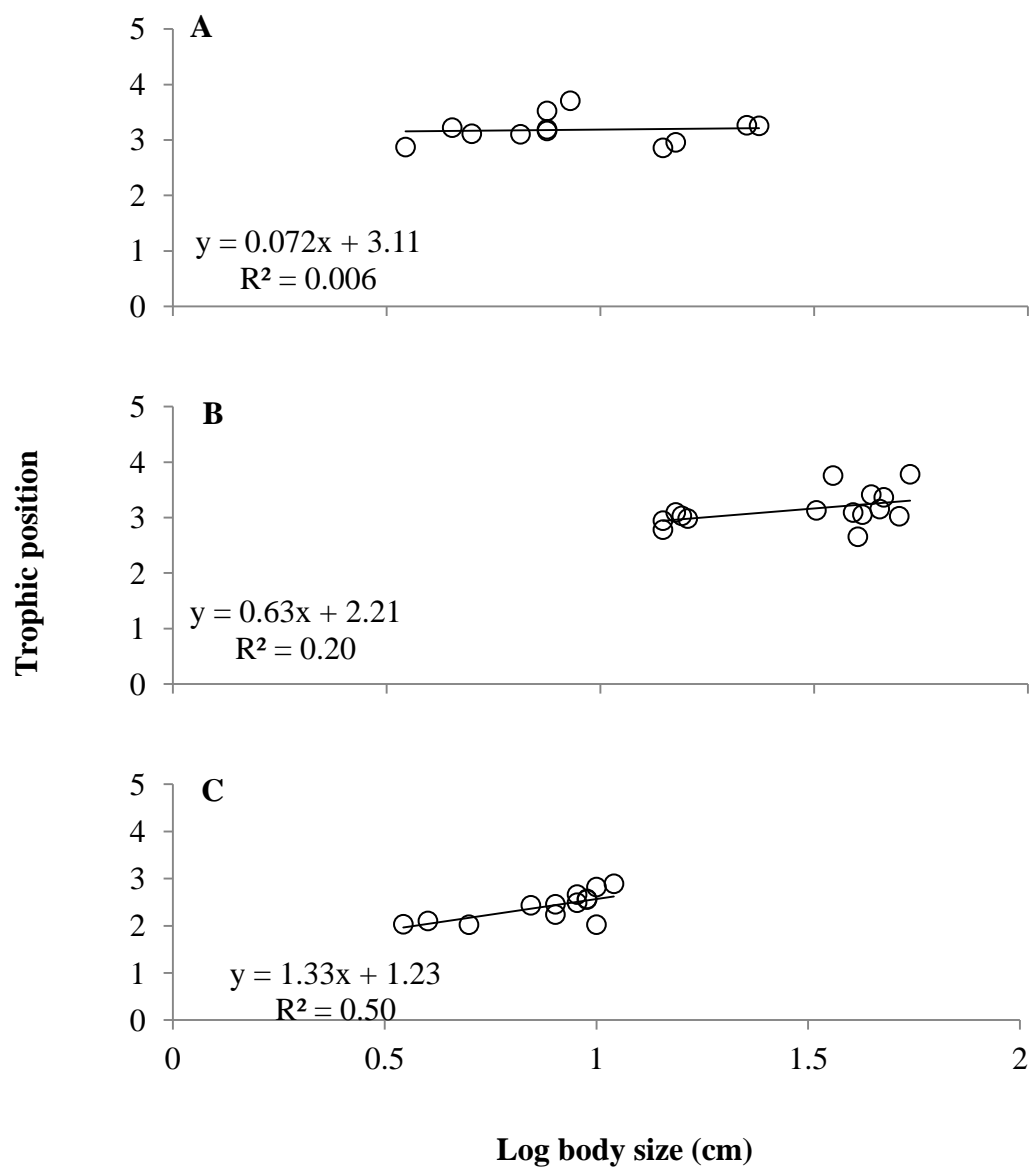


Figure 18. Relationship between trophic position and body size of three species of omnivores (A. *Puntioplites falcifer*, B. *Pangasius conchophilus*, C. *Anabas testudineus*).

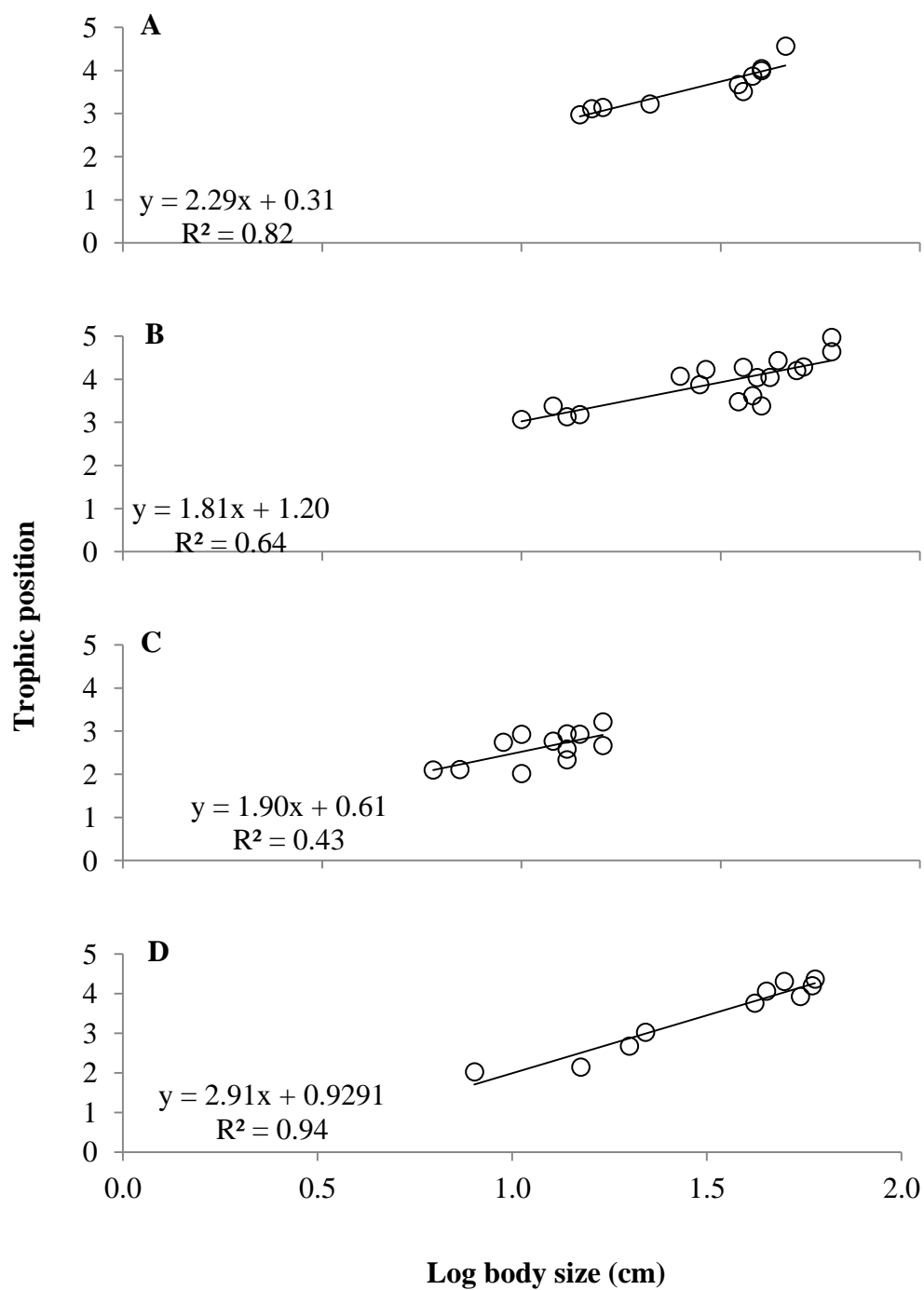


Figure 19. Relationship between trophic position and body size of four species of piscivores: A. *Wallago attu*, B. *Hemibargrus wyckiioides*, C. *Channa limbata*, D. *Channa micropeltes*.

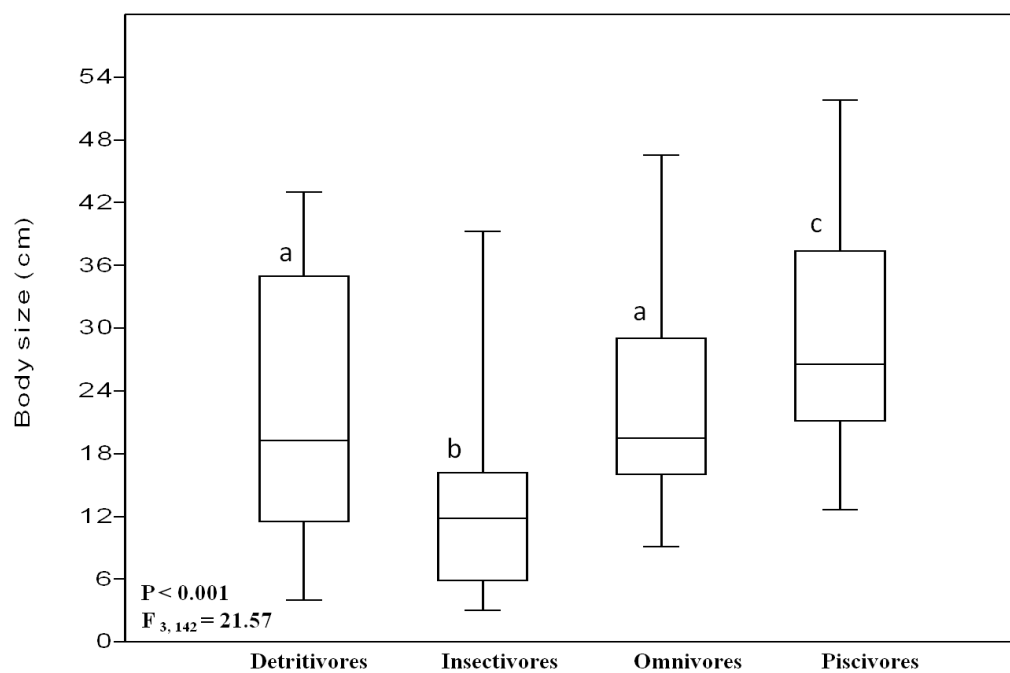


Figure 20. Body size of trophic groups of Lower Mekong River fishes (horizontal lines are mean values, boxes delimit + and – one standard deviation, and vertical bars delimit ranges).

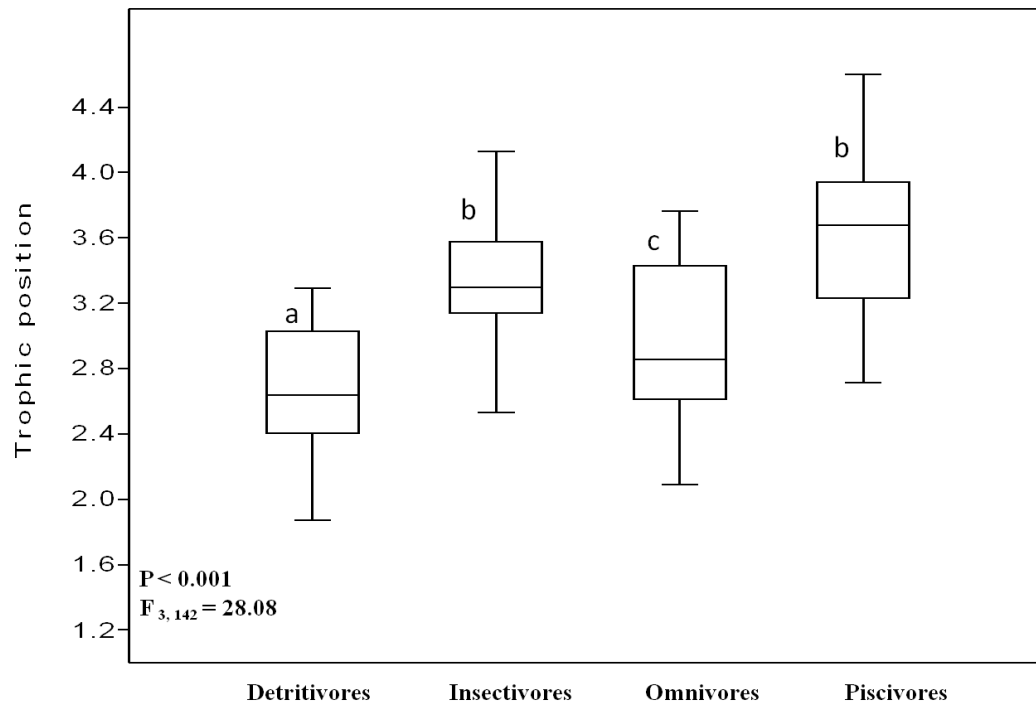


Figure 21. Trophic levels of trophic groups of the Lower Mekong River fishes (horizontal lines are mean values, boxes delimit + and – one standard deviation, and vertical bars delimit ranges).

DISCUSSION

Trophic structure of fish assemblages

My analysis of the species assemblages from the major rivers of the Lower Mekong Basin revealed no correlation between fish body size and trophic position. This finding challenges the Eltonian theory of size-based trophic structure in food webs, and also contradicts the broadly accepted prediction of the fishing-down-the-food-web model. Pauly et al. (1998) proposed that fish body size is positively correlated with trophic position, so that removal of the most valuable and largest fish from a system results in reduced overall food chain length. Owing to the fact that this model was largely based on marine commercial fisheries that are dominated by pelagic fishes, it might not be applicable for freshwater ecosystems that support subsistent fisheries, particularly systems like the Mekong with taxonomically and ecologically diverse fishes. Fishers in this region preferentially target high-value fishes that are normally large. However, these large species may occupy trophic positions that are either low (detritivores/herbivores) or high (piscivores/insectivores). In the Lower Mekong Basin, particularly within the 3S region of Cambodia, the average mesh size of fishing nets has declined in recent years (my personal observation and communication with fishers), and this appears to reflect recent reductions in standing stocks of large fishes (e.g. pangasid catfishes, large carps). Thus, intensive fishing pressure appears to have resulted in increased catches of small fishes, such as small cyprinids, that have rapid growth, early maturation, and high demographic resilience (Baran et al. 2011, Cooperman et al. 2012).

In diverse tropical river fish assemblages, overharvest of large piscivorous fishes can even increase average food chain length if large piscivores feed heavily on large detritivores and smaller mesopredators consume mostly invertivorous fishes (Layman et al. 2005b).

Compared to temperate regions, the tropics appear to have freshwater fish assemblages that contain particularly high diversity of primary consumers, including detritivores, herbivores and omnivores (Lowe-McConnell 1969, Goulding 1980, Winemiller 1991), and this certainly is the case in the Mekong (Rainboth 1996). In the Lower Mekong river system, cyprinids dominate local fish assemblages and this family is represented by diverse body sizes and many species that feed on algae or detritus (Rainboth 1996). For instance, *Garra fasciacuda* is a benthic algivore that attains a standard length of 10 cm, whereas another benthic algivore, *Morulus chrysophekadion*, can grow to 100 cm SL. *Rasbora hobelmani* can grow to 5 cm, and *Catlocarpio siamensis*, a critically endangered species, can reach 300 cm. The Lower Mekong also contains many large catfishes at low trophic positions, including the omnivorous Mekong giant catfish, *Pangasianodon gigas* that can grow to 300 cm (Rainboth 1996). The lack of correlation between body size and trophic level in the full assemblage dataset also is influenced by the presence of small species that occupy high trophic positions. For example, small loaches (e.g. *Schistura* and *Acanthopsis* spp.) are insectivores that have relatively high trophic positions.

To optimize their energy intake, large piscivores in the Lower Mekong River probably consume relatively large fishes that are detritivores and omnivores rather than

loaches and other small insectivores. When consumers exploit abundant prey at lower trophic levels, ecological efficiency is maximized via shorter food chains (Pimm and Lawton 1977, Lewis et al. 2001, Scharf et al. 2002). In the Lower Mekong, many large piscivorous fishes appear to be positioned relatively low in the food web indicating that they probably feed heavily on detritivores and omnivores at low trophic levels. Research on tropical floodplain river in Venezuela revealed that, during the descending phase of the annual flood pulse, large piscivores (*Cichla temensis*) consumed mostly large primary consumers (relatively large, benthivorous characiform fishes), which resulted in short food chains (Layman et al. 2005b). Relatively short food chains appear to be the rule in tropical river food webs (Winemiller 2004).

The role of phylogeny in assemblage trophic structure

The results from the Mantel and partial Mantel tests indicated that phylogeny did not influence the relationship between body size and trophic level of the Lower Mekong fish community. Orders and families did not have significantly different body size distributions. For example, Cypriniformes in this dataset ranged in size from 3 cm (e.g. *Schistura* sp.) to 40 cm SL (*Mekongina erythrospila*). Likewise, Siluriformes has very small (*Glyptothorax lampris*, 4 cm) and large species (*Hemibagrus wyckioides*, 45 cm). Similarly, at the family level (e.g. Cyprinidae, Siluridae, Bagridae), body size had broad and overlapping distributions. These patterns suggest evolutionary divergence within and among lineages that sometimes results in closely related species having different trophic levels that perhaps reflect adaptative divergence and niche partitioning (Cattin et

al. 2004). For example, two congeneric snakeheads with similar morphology, *Channa limbata* and *Channa micropeltes*, had different trophic levels (2 vs. 4, respectively).

Results for phylogenetic influence could have been biased by the use of taxonomy as a proxy for phylogenetic relationships. Even if the topology is reasonably accurate, the assumption that branch lengths are equal reduces resolution. Costa (2009) used taxonomy as a proxy to create a phylogenetic tree for marine predators, and he found no effect of phylogeny on the relationship between body size and trophic level. In contrast, a recent study by Naisbit et al. (2012), in which taxonomy was used to build a phylogeny, revealed that closely related species have similar trophic levels. Rezende et al. (2009) used molecular phylogenetic information for sharks, and they found that phylogeny influenced the body size–trophic level relationship. Without further analysis, it is not possible to determine if this is a general pattern.

The role of functional trophic guilds

Results from regression analysis for those orders (Perciformes and Siluriformes) and families (Siluridae and Bagridae) that had many piscivorous species indicated a relationship between body size and trophic position. The fact that piscivores, but not other guilds, show a significant relationship could be explained by optimal foraging theory and mouth gape limitation. According to the optimal foraging theory (MacArthur and Pianka 1966), predators should exploit the most profitable prey to maximize energy acquisition while minimizing their energy expenditure while searching or capturing prey (Werner and Hall 1976, Werner and Mittelbach 1981, Mittelbach and Osenberg 1993). It

has been suggested that to maximize their energy input, predators should consume the optimal prey size available to them, assuming all else being equal. A classic laboratory experiment demonstrated that bluegill sunfish (*Lepomis macrochirus*) fed selectively on the largest *Daphnia* when the *Daphnia* were abundant, but they fed on broad size spectrum of prey when zooplankton density was low (Werner and Mittelbach 1981). In several studies, piscivorous fishes that were larger fed at higher trophic levels (Cohen et al. 1993, 2003, France et al. 1998, Woodward and Hildrew 2002a, b, Deuder et al. 2004, Montaña and Winemiller 2013), which suggests that mouth gape influences prey selection by species that ingest their prey whole (Mittelbach and Persson 1998, Karpouzi and Stergiou 2003, Montaña et al. 2011). For example, a comparative study by Mittelbach and Persson (1998) indicated that diets of freshwater piscivores were strongly influenced by the sizes of prey items in relation to the size of the predator's mouth gape. An analysis of gut contents of piscivores from Venezuelan rivers indicated that the relative size of the predator's mouth gape, prey size, and prey abundance influenced size distributions of consumed prey (Montaña et al. 2011). There are some exceptional cases in which the relative size of piscivores and their prey are uncorrelated, for example species that feed on the scales, fins, or mucus of other fishes (Winemiller and Yan 1989, Winemiller 1989, Winemiller and Kelso-Winemiller 1993, Peterson and Winemiller 1997).

The Cyprinidae, a family that has many detritivores and algivores, had both small and large species at similar trophic positions. Absence of a body size–trophic level relation among detritivorous fishes has been reported in other studies (Jennings et al.

2001, 2002, Cocheret de la Morierie et al. 2003, Akin and Winemiller 2008, Riede et al. 2011). This can be explained by the fact that fishes of all sizes can efficiently consume tiny particles of detritus. In tropical rivers, detritivorous and algivorous fishes are diverse in terms of body size, morphology, and habitats they occupy (Winemiller 1991, Lujan et al. 2012). The guild of detritivorous/algivorous fishes in the Lower Mekong spans a broad range of body sizes. For example, there is a ten-fold difference in the body size of the detritivorous/algivorous cyprinids *Garra fasciacauda* and *Morulius chrysophekadion*.

Omnivores also revealed no correlation between body size and trophic level. Most omnivores consume a wide range of food resources, and broad diets could dampen a size-based trophic hierarchy if diverse food items are from multiple trophic levels (Pimm and Lawton 1977, Winemiller 1990, Polis et al. 1996). Another possible explanation is that omnivores of all sizes tend to feed low in the food web, which would reduce the body size-trophic level correlation (Polis et al. 1996, Arim et al. 2007, 2010).

Body size and trophic level also were uncorrelated among insectivores, and this could be explained by a lack of mouth gape limitation for this guild: both small and large fishes can efficiently ingest small aquatic invertebrates. The body size in this group ranged from 2 cm (e.g. *Schistura* spp.) to 90 cm SL (e.g. *Mastacembelus armatus*). Deudero et al. (2004) reported similar findings of a strong relationship between body size and trophic position for carnivorous fishes from shallow waters of the Mediterranean, but a weak relationship among invertebrate feeders. Akin and Winemiller (2008) found that small zooplanktivorous fishes had among the highest

trophic levels within an estuarine fish assemblage. When those species were removed from the regression analysis, the strength of the body–size trophic level relationships increased.

Ontogenetic diet shift

Ontogenetic niche shifts strongly influence food web dynamics, because various developmental stages are involved in different sets of trophic interactions (Werner and Gilliam 1984, Woodward and Hildrew 2002b). In the present study, the body size–trophic level relationship within species reflected ontogenetic diet shifts for piscivorous species but not for detritivores, omnivores and insectivores. Ontogenetic diet shifts have been documented for many piscivorous fishes (Winemiller 1989, Olson 1996, Post 2003). As they grow, piscivores generally shift from feeding on crustaceans and invertebrates to fish. For example, a comparative study of nine piscivorous fishes from a tropical stream in Venezuela showed that juveniles fed on aquatic microcrustacea and aquatic insects, and then gradually or abruptly switched to fish as subadults (Winemiller 1989). Some piscivores, such as largemouth bass and peacock cichlids, may become cannibals at larger size classes (Lowe-McConnell 1969, Olson 1996, Post 2003). My trophic level estimates for the snakehead (*Channa limbata*) agree with findings from dietary analysis performed by Ward-Campbell and Beamish (2005) in which juveniles fed on benthic invertebrates and then switched to a diet dominated by fish as adults.

Mekong fishes belonging to detritivore/algivore, omnivore, and insectivore guilds did not reveal ontogenetic shifts in trophic position. This contrasts with findings

from a study of an omnivorous characid (*Brycon guatemalensis*) in Central America in which fish shifted from feeding on invertebrates as juveniles to feeding on terrestrial vegetation, such as fruit and leaves, as adults (Drewe et al. 2004). The diet of gizzard shad (*Dorosoma cepedianum*), a North American clupeid, shifts from aquatic invertebrates to phytoplankton and detritus as fish grow from juvenile to subadult and adult (Mundahl 1988, Winemiller et al. 2007). Habitat and resource availability can influence ontogenetic diet shifts. Schaus et al. (2002) found that the gizzard shad diet shifted between detritus and zooplankton in response to changes in resource availability. Gizzard shad in the Brazos River, Texas, revealed high dietary overlap between juveniles and adults, and their isotopic differences were associated with residence in the main river channel versus oxbow lakes rather than diet composition (Zeug et al. 2009). Cocheret de la Moriniere et al. (2003) found little evidence of an ontogenetic shift in a diet among algivorous coral reef fishes. The lack of ontogenetic changes in trophic position among non-piscivorous Mekong fishes could be evidence of a lack of diet shifts in these species, but it also could be due to insufficient sampling of different size classes, time periods, and habitats.

CONCLUSION

In summary, my results suggest that body size is not a useful surrogate of trophic structure for a system with diverse detritivores, omnivores and insectivores, but that it is a predictor of trophic position among piscivorous fishes. Trophic guild strongly

influenced the relationship between body size and trophic level among Mekong fishes. Although there is an abundance of empirical and theoretical evidence demonstrating the role of body size in structuring food webs, to my knowledge, this study is the first explicit attempt to examine the influence of trophic guilds on the relationship.

In general, body size distributions of entire fish communities cannot be used to describe the trophic structure in the Mekong River Basin. Caution is warranted in the application of the body size–trophic level relationship to assess threats to freshwater biodiversity. I argue that the *fishing-down-the-food-web model* is not applicable to this tropical river system. Marine pelagic communities seem to conform to a size-based trophic hierarchy and the fishing-down model may apply for those systems. In the Lower Mekong region where many artisanal fishers preferentially target large fish with high market value, selective removal of large fishes is unlikely to reduce the mean trophic level of the catch, because these large fishes could be either detritivores/algitivores feeding at a low trophic level or predators feeding at high trophic levels. Overharvest of large fishes in the Mekong River system already has resulted in greater reliance on harvest of small fishes that have high demographic resilience, but that also represent a subset of trophic groups in the natural communities (e.g. detritivores, omnivores, zooplanktivores). This reduction in functional diversity likely will have consequences for ecosystem processes, including fishery productivity, that are difficult to predict at the present time.

CHAPTER IV

GENERAL CONCLUSIONS

One of the main challenges in ecology is to predict ecological responses to anthropogenic disturbances. Food web theory has been used by ecologists to predict impacts induced by anthropogenic activities on plant and animal populations and ecosystems. This dissertation explored river food web structures in the Lower Mekong River Basin, one of the largest yet least-studied river systems in the world. The Lower Mekong has enormous importance for human welfare and is a regional biodiversity hot spot. My dissertation produced several findings that have importance for conservation and management of fisheries in the Lower Mekong River region. Below, I will discuss the implications of my findings in the context of two major anthropogenic activities that are increasingly affecting this region – hydropower development and over-fishing.

Chapter II demonstrated seasonal changes in food web structure and sources of primary production entering the upper food web in the Mekong and its three major tributaries of Cambodia. These changes were associated with influences from the annual flood pulse created by monsoon rains that typify this region. Most large tropical rivers demonstrate seasonal hydrology that influences bio-physiochemical factors, which then determine changes in community structure and ecosystem dynamics. The onset of the seasonal flood pulse in the Mekong provides many fishes with environmental cues that trigger migration and/or reproduction. The flood pulse also influences the availability of habitats and alternative food resources for aquatic organisms. The present study revealed that, during the dry season, fishes assimilated material that was mostly derived from

algae, and during the wet season, fishes assimilated a great deal of material derived from macrophytes. Therefore, it is of utmost importance to maintain a flow regime that maintains a major seasonal flood pulse in the Mekong in order to sustain production sources that support fish production and biodiversity in the region.

Fish production and biodiversity of the Lower Mekong Basin are undeniably being threatened by dam construction and operation in the basin. The findings reported in chapter II highlight the negative effects of dams, which have a major influence on food web structure, including primary production sources and consumer community structure. Fishes in the river affected by dams (Sesan River) were shown to assimilate less macrophyte-derived material and more material derived from algae, and this was probably influenced by the trapping of fine sediments by the Yali dam located upstream. The finding also illustrates the impact of dams on the aquatic consumers, particularly migratory fishes. I encountered significantly fewer migratory fishes (e.g. pangasids) in the Sesan River. As suggested by many scientists, dams are barriers for migratory fishes, fragmenting rivers in the longitudinal dimension and inhibiting colonization and community succession (Poff et al. 1997). Because migratory fishes are very abundant in the Mekong River and breeding activity and migrations occur at the beginning of the wet season, dams in this region have irreversible and undeniable negative effects on fisheries (Bishop and Forb 1991, Barlow et al. 2008, Baran and Myschowoda 2008, Dugan et al. 2010). Hydroelectric development is expected to benefit national economies, but with collapses of fishery and declines of biodiversity, alternative renewable energy sources

that are less harmful to the environment, such as solar energy or biofuels, should be explored for future investment in this region.

In addition to dams, overexploitation of resources is a critical factor affecting fishery and biodiversity in the Mekong (Cooperman et al. 2012). The fishing-down-the-food-web concept has been widely accepted and used to assess the impact of over fishing. According to the fishing-down-the-food-web model (Pauly et al. 1998), the mean trophic level of the catch is strongly correlated with the body size distribution of species; therefore, selective removal of large fish reduces the mean trophic level. Chapter III explored the validity of the fishing-down-the-food-web model of fisheries management for the Lower Mekong Basin. Even though the Mekong River is experiencing overfishing that has resulted in the declines of stocks of large species, this does not translate into a decline in average community trophic level as predicted by the “fishing-down-the food-web” model. Findings reported in Chapter III indicated that body size generally does not correlate with trophic position for fish assemblages of the Lower Mekong. Therefore, the distribution of species body sizes cannot be used to assess the condition of fisheries in the Lower Mekong.

Despite the facts that mean trophic level has been used by the Convention on Biological Diversity to assess threats to global marine fisheries, its application to tropical inland fisheries seems inappropriate. Inland fisheries often are more complex than commercial marine fisheries. In tropical developing countries, inland fisheries involve multiple species, diverse functional groups, multiple gears, and diverse fishers and cultures. In the Lower Mekong region, many artisanal fishers preferentially target large

fish with high market value. These large fishes could be either detritivores feeding at a low trophic level or predators feeding at high trophic levels. Thus, the harvest of large fishes in the Mekong River system could result in either no change in the mean trophic level or even an increase in the mean trophic level if the fish catch were to become dominated by small piscivores that feed on small invertivorous fishes and small fishes that are zooplankton feeders.

Many fishery scientists have suggested that sustainable fisheries in developing countries are particularly difficult to achieve because of the lack of alternative sources of income among fishers and the lack of support and law enforcement from the government. Recently, Garcia et al. (2012) suggested “balanced harvesting” as a solution to unsustainable exploitation of common-pool resources like fisheries resources. Balanced harvesting refers to fishing activity that is evenly distributed across species, functional groups, and size categories. In theory, this practice would preserve the proportional species composition in the community, and thereby enhance sustainable exploitation of fish stocks while maintaining key ecosystem processes that depend on native biodiversity. However, this approach may not be a practical solution, particularly within developing countries where the governance of fisheries is weak. Maxwell et al. (2012) proposed that integrative management that balances not only fishing, but also impacts to other species in the ecosystem, is required in order to achieve sustainable fisheries. This view has been shared among previous scholars (e.g. Ostrom et al. 1998) who argued that institutional diversity is as important as biological diversity for sustainable uses of common pool resources.

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APPENDIX 1

Contribution of production sources during the dry season. Median and 5th-95th percentile ranges (in parentheses) of estimated contributions of production sources to fish biomass in the Mekong, Sekong, Sesan, and Srepok rivers during the dry season.

TG: Trophic guilds (D: Detritus, I: Insectivores, O: Omnivores, P: Piscivores), HG: Habitat guilds (C: Channel, FP: Floodplain).

River	Consumers	TG	HG	Benthic algae	Seston	Riparian C ₃	C ₄ grasses
Mekong	Osteoglossiformes						
	Notopteridae						
	<i>Chitala blanci</i>	P	C	26 (12-43)	36 (23-52)	26 (12-42)	15 (1-33)
	<i>Notopterus notopterus</i>	I	FP	15 (1-31)	46 (22-75)	35 (21-56)	5 (1-11)
	Cypriniformes						
	Cyprinidae						
	<i>Bangana behri</i>	D	C	42 (32-55)	21 (2-41)	27 (3-52)	10 (1-21)
	<i>Barbonymus altus</i>	O	C	25 (14-37)	52 (23-81)	20 (1-41)	5 (1-11)

<i>Cirrhinus microlepis</i>	O	C	31 (12-51)	33 (14-52)	25 (1-52)	10 (1-21)
<i>Cosmocheilus harmandi</i>	O	C	32 (13-52)	46 (21-72)	24(1-51)	5 (1-11)
<i>Cyclocheilichthys enoplus</i>	I	C	15 (1-31)	56 (33-81)	26 (1-53)	5 (1-11)
<i>Cyclocheilichthys lagleri</i>	I	C	15 (1-32)	51 (31-73)	28 (5-54)	6 (1-13)
<i>Cyclocheilichthys tapiensis</i>	I	C	15 (1-31)	59 (42-83)	25 (1-52)	5 (1-11)
<i>Hampala dispar</i>	P	C	22 (12-34)	45 (22-71)	19 (1-35)	15 (1-31)
<i>Henicorhynchus lobatus</i>	D	C	44 (29-60)	15 (1-30)	29 (10-48)	12 (2-21)
<i>Henicorhynchus siamensis</i>	D	C	58 (42-74)	16 (1-32)	16 (1-31)	13 (1-25)
<i>Hypsibarbus malcolmi</i>	D	C	43 (34-52)	16 (1-33)	26 (1-51)	17 (1-33)
<i>Hypsibarbus wetmorei</i>	D	C	47 (32-63)	21 (1-42)	16 (1-33)	15 (0-31)
<i>Labeo chrysophekadion</i>	D	C	48 (25-71)	13 (1-24)	21 (1-42)	18 (3-34)
<i>Labiobarbus siamensis</i>	D	C	52 (41-63)	27 (1-53)	15 (1-32)	8 (0-21)
<i>Macrochirichthys macrochirus</i>	P	C	31 (13-51)	42 (31-56)	20 (1-42)	10 (0-22)
<i>Mekongina erythrospila</i>	D	C	49 (27-70)	18 (1-36)	13 (1-27)	5 (1-12)
<i>Morulius chrysophekadion</i>	O	C	15 (1-31)	51 (32-72)	32 (12-53)	5 (0-11)

<i>Mystacoleucos marginatus</i>	I	C	14 (1-30)	61 (42-81)	21 (1-41)	4 (0-10)
<i>Opsarius pulchellus</i>	I	C	15 (1-32)	57 (32-85)	20 (1-42)	16 (1-32)
<i>Osteochilus hesseltii</i>	O	C	31 (12-51)	42 (22-63)	14 (1-31)	15(1-31)
<i>Osteochilus melanopleura</i>	O	C	11 (1-21)	35 (12-62)	53 (44-63)	4 (0-11)
<i>Paralauca typus</i>	I	C	16 (1-33)	62 (43-81)	20 (1-41)	4 (0-10)
<i>Probarbus jullieni</i>	O	C	32 (14-53)	44 (24-62)	15 (1-31)	11 (1-21)
<i>Puntioplites falcifer</i>	O	C	25 (13-41)	40 (21-73)	37 (1-74)	5 (1-11)
<i>Raiamus guttatus</i>	I	C	15 (1-31)	42 (12-74)	40 (1-82)	5 (1-11)
<i>Scaphognathops bandanensis</i>	O	C	16 (1-32)	37 (23-54)	39 (31-52)	9 (1-21)
<i>Scaphognathops stejneri</i>	O	C	10 (1-21)	41 (22-61)	45 (21-74)	5 (1-10)
<i>Tor sinensis</i>	O	C	15 (1-31)	31 (13-52)	46 (21-73)	8 (1-19)
Gyrinocheilidae						
<i>Gyrinocheilus pennocki</i>	D	C	54 (35-76)	12 (1-22)	13 (1-25)	20 (9-36)
Botiidae						
<i>Syncrossus helodes</i>	I	C	21 (4-41)	21 (1-41)	43 (23-64)	15 (1-32)

<i>Yasuhikotakia candipunctata</i>	I	C	10 (1-21)	21 (1-42)	67 (52-83)	4 (0-11)
<i>Yasuhikotakia modesta</i>	I	C	11 (1-22)	37 (22-51)	52 (41-64)	4 (0-11)
Cobitidae						
<i>Acanthopsis sp. 2</i>	I	C	10 (1-22)	35 (1-71)	47 (34-62)	11 (1-23)
Nemacheilidae						
<i>Nemacheilus longistriatus</i>	I	C	25 (1-43)	43 (14-87)	28 (9-50)	11 (1-19)
<i>Schistura sp.</i>	I	C	12 (1-24)	25 (1-48)	53 (33-74)	1 (0-21)
Siluriformes						
Siluridae						
<i>Belodontichthys truncatus</i>	P	C	34 (16-53)	35 (11-62)	20 (1-41)	9 (1-19)
<i>Kryptopterus limpok</i>	I	C	15 (0-31)	47 (25-71)	31 (1-60)	11 (1-23)
<i>Micronema cheveyi</i>	I	C	12 (1-22)	60 (42-81)	24 (1-52)	10 (1-21)
<i>Wallago attu</i>	P	C	25 (12-41)	37 (23-52)	24 (14-51)	15 (1-31)
<i>Wallago micropogon</i>	P	C	25 (11-42)	32 (14-53)	31 (12-51)	11 (1-23)
Clariidae						

<i>Clarias batrachus</i>	O	FP	35 (13-61)	26 (12-41)	15 (1-32)	25 (11-42)
<i>Clarias melanoderma</i>	O	FP	28 (13-43)	28 (14-45)	14 (1-31)	30 (12-51)
Ariidae						
<i>Hemiarus stormii</i>	P	C	34 (12-53)	36 (13-62)	23 (1-42)	10 (1-21)
Pangasiidae						
<i>Helicophagus waandersii</i>	I	C	15 (1-31)	51 (22-81)	29 (12-52)	9 (1-21)
<i>Pangasianodon hypophthalmus</i>	O	C	5 (1-11)	32 (12-53)	62 (52-72)	5 (0-11)
<i>Pangasius bocourti</i>	O	C	6 (1-11)	42 (31-54)	32 (19-46)	11 (1-22)
<i>Pangasius conchophilus</i>	O	C	16 (1-33)	54 (42-71)	24 (12-41)	7 (0-14)
<i>Pangasius larnaudii</i>	O	C	5 (1-12)	43 (12-75)	46 (32-61)	5 (1-11)
<i>Pangasius micronema</i>	O	C	10 (1-21)	36 (22-53)	52 (24-83)	4 (1-9)
Bagridae						
<i>Bagarius suchus</i>	P	C	25 (11-43)	46 (22-71)	18 (1-42)	11 (2-21)
<i>Hemibagrus spilopterus</i>	I	C	20 (1-42)	51 (31-82)	19 (1-43)	8 (1-16)
<i>Hemibagrus wyckioides</i>	P	C	26 (12-43)	42 (21-63)	27 (13-42)	5 (1-11)

<i>Hemisilurus mekongensis</i>	O	C	27 (11-45)	47 (22-73)	15 (2-31)	12 (2-23)
<i>Mystus singaringan</i>	I	C	9 (1-21)	48(20-75)	32 (1-64)	12 (1-24)
Beloniformes						
Belonidae						
<i>Xenentodon cancila</i>	P	C	19 (1-38)	41 (12-71)	30 (12-51)	10 (1-21)
Synbranchiformes						
<i>Mastacembelidae</i>						
<i>Mastacembelus armatus</i>	I	C	21 (1-42)	47 (13-84)	25 (1-52)	10(1-22)
Perciformes						
Datnioididae						
<i>Datnioides undecimradiatus</i>	P	C	33 (15-54)	31 (12-54)	21 (1-42)	15 (1-32)
Sciaenidae						
<i>Boesemania microlepis</i>	P	C	32 (14-52)	41 (22-61)	25 (1-51)	6 (1-12)
Nandidae (Pristolepidae)						
<i>Pristolepis fasciata</i>	O	FP	16 (1-33)	32 (15-52)	47 (42-54)	6 (1-12)

Eleotridae							
<i>Oxyeleotris exodon (marmorata)</i>	I	FP	14 (1-31)	46 (32-61)	32 (21-42)	10 (1-21)	
Gobiidae							
<i>Tridentiger ocellatus</i>	I	C	16 (1-31)	49 (25-74)	26 (2-52)	11 (2-21)	
Anabantidae							
<i>Anabas testudineus</i>	O	FP	15 (1-31)	27 (14-43)	45 (21-73)	15 (1-31)	
Osphronemidae							
<i>Osphronemus exodon</i>	O	C	24 (13-35)	25 (2-51)	45 (41-53)	5 (0-12)	
<i>Osphronemus goramy</i>	O	FP	6 (1-12)	28 (11-52)	56 (32-81)	12 (1-23)	
Channidae							
<i>Channa marulioides</i>	P	FP	32 (12-54)	43 (25-62)	6 (1-12)	21 (11-32)	
<i>Channa micropeltes</i>	P	C	15 (2-31)	53 (32-74)	16 (1-32)	21 (1-42)	
<i>Channa striata</i>	P	FP	25 (13-41)	43 (21-65)	11 (1-22)	24 (13-34)	
Pleuronectiformes							
Soleidae							

	<i>Brachirus orientalis</i>	I	C	21 (2-41)	39 (11-72)	29 (1-61)	11 (1-22)
	Cynoglossidae						
	<i>Cynoglossus puncticeps</i>	I	C	15 (1-31)	52 (24-82)	25 (1-52)	11 (1-21)
Sekong	Osteoglossiformes						
	Notopteridae						
	<i>Notopterus notopterus</i>	I	FP	12 (4-22)	43 (12-74)	31 (14-51)	15(1-31)
	Cypriniformes						
	Cyprinidae						
	<i>Barbonymus altus</i>	O	C	29 (14-45)	46 (33-61)	16 (1-32)	11 (1-22)
	<i>Cirrhinus jullieni</i>	O	C	29 (14-44)	46 (32-62)	15 (1-31)	11 (1-21)
	<i>Cyclocheilichthys mekongensis</i>	I	C	15 (2-31)	58 (43-74)	20 (2-38)	6(1-11)
	<i>Hampala macrolepidota</i>	P	C	22 (12-35)	47 (32-63)	21 (1-43)	11 (1-21)
	<i>Henicorhynchus lobatus</i>	D	C	38 (22-54)	25 (2-51)	17 (1-34)	20 (1-40)
	<i>Labeo chrysophekadion</i>	D	C	53 (31-74)	14 (1-31)	11 (1-25)	18 (1-36)
	<i>Labiobarbus leptocheila</i>	D	C	41 (23-62)	26 (4-49)	18 (3-34)	16 (1-33)

<i>Leptobarbus hoevenii</i>	D	C	42 (23-64)	24 (4-42)	22 (2-43)	11 (1-22)
<i>Lobocheilos delacouri</i>	D	C	40 (23-61)	24 (3-45)	17 (2-33)	19 (3-36)
<i>Morulios chrysophekadion</i>	D	C	45 (24-67)	32 (19-46)	16 (2-29)	7 (1-15)
<i>Osparius pulchellus</i>	I	C	16 (1-34)	55 (36-74)	20 (1-41)	10 (1-22)
<i>Osteochilus waandersii</i>	O	C	27 (13-42)	51 (32-71)	17 (1-33)	6 (1-12)
<i>Parachela siamensis</i>	I	C	19 (2-39)	49 (32-67)	17 (2-32)	14 (3-25)
<i>Paralaubuca typus</i>	I	C	18 (2-35)	53 (33-74)	22 (6-41)	8 (1-17)
<i>Poropuntius laoensis</i>	I	C	20 (1-41)	46 (23-70)	24 (4-45)	12 (1-23)
<i>Poropuntius normani</i>	D	C	33 (22-47)	36 (11-62)	22 (1-44)	11 (1-22)
<i>Puntioplites falcifer</i>	D	C	48 (37-58)	23 (4-42)	26 (1-52)	4 (0-10)
<i>Rasbora tornieri</i>	I	FP	15 (1-31)	42 (21-63)	33 (24-43)	11 (1-12)
<i>Rasbora trilineata</i>	I	FP	11 (1-21)	32 (12-53)	46 (32-61)	12 (1-23)
Botiidae						
<i>Yasuhikotakia modesta</i>	I	C	11 (1-21)	37 (16-58)	52 (32-73)	4 (0-11)
Cobitidae						

<i>Acanthopsis sp. 3</i>	I	C	11 (1-21)	36 (12-62)	47 (32-63)	7 (1-15)
Siluriformes						
Sisoridae						
<i>Bagarius bagarius</i>	I	C	16 (2-33)	56 (31-82)	16 (1-32)	11 (1-21)
<i>Bagarius suchus</i>	P	C	26 (11-43)	41 (12-71)	20 (1-39)	16 (2-31)
Siluridae						
<i>Belodontichthys truncatus</i>	P	C	16 (1-33)	52 (32-73)	23 (13-35)	11 (1-21)
<i>Kryptopterus bicirrhys</i>	I	C	16 (2-32)	50 (30-71)	21 (2-43)	12 (2-24)
<i>Kryptopterus kryptopterus</i>	P	C	31 (13-52)	42 (24-63)	15 (2-31)	12 (1-24)
<i>Kryptopterus limpok</i>	P	C	37 (12-64)	37 (21-55)	21 (2-41)	5 (0-11)
<i>Kryptopterus schilbeides</i>	P	FP	25 (1-52)	32 (12-53)	34 (23-51)	10 (1-21)
<i>Micronema apogon</i>	P	C	34 (14-55)	44 (23-65)	16 (1-33)	7 (1-12)
<i>Micronema bleekeri</i>	P	FP	17 (2-33)	45 (21-72)	25 (15-38)	14 (1-31)
<i>Ompok bimaculatus</i>	P	C	32 (13-52)	36 (21-52)	15 (1-31)	22 (1-45)
<i>Wallago attu</i>	P	C	29 (14-45)	42 (14-71)	21 (14-32)	12 (2-23)

<i>Wallago leeri</i>	P	C	25 (12-41)	41 (34-51)	26 (13-41)	11 (1-22)
<i>Wallago micropogon</i>	P	C	26 (13-42)	38 (15-64)	25 (12-41)	12 (2-23)
Clariidae						
<i>Clarias batrachus</i>	O	FP	32 (13-52)	33 (13-54)	15 (1-31)	22 (11-34)
<i>Clarias macrocephalus</i>	O	FP	25 (12-41)	41 (12-71)	5 (1-12)	32 (13-53)
Pangasiidae						
<i>Helicophagus waandersii</i>	I	C	15 (1-30)	58 (36-82)	18 (5-34)	10 (1-19)
<i>Pangasius bocourti</i>	O	C	21(2-43)	36 (12-63)	32 (22-45)	12 (2-23)
<i>Pangasius conchophilus</i>	O	C	15 (1-31)	41 (21-62)	36 (24-51)	11 (2-21)
<i>Pangasius larnaudii</i>	O	C	18 (2-35)	57 (41-74)	22 (13-34)	4 (0-10)
<i>Pangasius pleurotaenia</i>	O	C	20 (1-40)	52 (41-63)	25 (11-41)	5 (0-11)
Bagridae						
<i>Bagrichthys macracanthus</i>	O	FP	11 (1-21)	46 (21-72)	36 (11-63)	11 (1-21)
<i>Bagrichthys nitidus</i>	O	FP	16 (1-32)	36 (12-63)	37 (23-52)	11 (1-21)
<i>Hemibagrus nemurus</i>	I	C	18 (4-33)	49 (35-66)	18 (3-35)	12 (2-25)

<i>Hemibagrus wyckioides</i>	P	C	31 (12-51)	29 (15-45)	31 (14-52)	11 (1-21)
<i>Mystus albolineatus</i>	I	C	16(1-32)	49 (32-71)	17 (2-34)	18 (2-34)
<i>Mystus bocourti</i>	I	C	11 (1-21)	63 (36-89)	22 (2-42)	6 (0-12)
<i>Mystus multiradiatus</i>	I	C	12 (1-23)	54 (37-72)	21 (1-42)	16 (1-31)
<i>Mystus singaringan</i>	I	C	23 (2-45)	48 (15-84)	16 (1-32)	14 (1-29)
Beloniformes						
Belonidae						
<i>Xenotodon cancila</i>	P	C	23 (2-45)	48 (16-82)	16 (1-33)	14 (1-28)
Synbranchiformes						
Synbranchidae						
<i>Ophisternon bengalense</i>	P	FP	25 (11-43)	32 (13-54)	15 (1-32)	32 (24-41)
Mastacembelidae						
<i>Macrognathus semiocellatus</i>	I	FP	21 (2-41)	42 (24-63)	25 (12-43)	11 (1-22)
<i>Mastacembelus armatus</i>	I	C	17 (1-34)	42 (24-63)	19 (2-37)	22 (9-36)

Sesan	Perciformes						
	Ambassidae						
	<i>Parambassis siamensis</i>	I	FP	16 (1-32)	57 (41-74)	23 (12-41)	6 (0-11)
	Eleotridae						
	<i>Oxygaster anomalura</i>	I	C	12 (1-23)	61 (42-83)	21 (2-41)	6 (0-11)
	Anabantidae						
	<i>Anabas testudineus</i>	I	FP	23 (5-43)	43 (25-62)	29 (16-43)	6 (0-11)
	Channidae						
	<i>Channa limbata</i>	P	FP	11 (2-21)	38 (22-56)	34 (23-45)	19 (4-35)
	<i>Channa micropeltes</i>	P	C	37 (23-52)	32 (14-53)	23 (2-46)	11 (1-21)
	<i>Channa striata</i>	P	FP	33 (14-53)	32 (13-52)	12 (1-23)	26 (14-41)
	Osteoglossiformes						
Notopteridae							
	<i>Notopterus notopterus</i>	I	C	36 (16-57)	52 (35-68)	11 (1-22)	3 (0-5)
Cypriniformes							

Cyprinidae						
<i>Barbodes gonionotus</i>	O	C	35 (16-53)	45 (28-64)	16 (1-34)	6 (1-12)
<i>Barbonymus schwanenfeldii</i>	O	C	31 (12-51)	65 (41-92)	11 (1-21)	2 (0-5)
<i>Cyclocheilichthys apogon</i>	I	C	20 (1-42)	68 (54-83)	12 (1-22)	6 (1-12)
<i>Cyclocheilichthys mekongensis</i>	I	C	36 (11-62)	57 (43-72)	11 (1-22)	3 (0-5)
<i>Hampala dispar</i>	P	C	35 (11-62)	52 (33-72)	12 (1-22)	3 (1-6)
<i>Hampala macrolepidota</i>	P	C	27 (13-45)	44 (34-61)	17 (1-33)	11 (1-24)
<i>Labiobarbus leptocheila</i>	D	C	41 (22-60)	38 (14-63)	17 (1-32)	5 (0-9)
<i>Osteochilus schlegeli</i>	O	C	45 (26-64)	46 (22-71)	11 (1-22)	3 (0-6)
<i>Puntius orphoides</i>	O	C	32 (12-54)	52 (35-70)	14 (2-27)	5 (0-12)
<i>Raiamus guttatus</i>	I	C	37 (14-60)	47 (23-74)	11 (1-22)	5 (0-12)
<i>Rasbora hobelmani</i>	I	C	34 (12-57)	54 (34-75)	10 (1-21)	4 (0-7)
<i>Rasbora paviei</i>	I	C	16 (1-33)	73 (52-96)	11 (1-23)	3 (0-6)
<i>Rasbora sp.</i>	I	C	25 (1-51)	55 (41-72)	21 (1-42)	4 (0-8)
Botiidae						

<i>Syncrossus helodes</i>	I	C	13 (2-24)	46 (13-82)	41 (21-64)	3 (0-6)
<i>Yasuhikotakia modesta</i>	I	C	12 (1-23)	37 (14-60)	49 (30-69)	3 (0-6)
Cobitidae						
<i>Acanthopsis sp 1</i>	I	C	16 (1-32)	64 (46-79)	16 (2-32)	6 (1-11)
Siluriformes						
Clariidae						
<i>Clarias batrachus</i>	O	FP	39 (16-63)	45 (23-67)	12 (1-23)	5 (0-11)
Bagridae						
<i>Hemibagrus nemurus</i>	I	C	23 (1-46)	54 (44-65)	21 (1-42)	5 (0-11)
<i>Hemibagrus spilopterus</i>	I	C	27 (13-44)	48 (23-74)	22 (1-43)	6 (1-13)
<i>Hemibagrus wyckioides</i>	P	C	28 (14-43)	47 (23-74)	15 (1-32)	6 (1-12)
<i>Mystus singaringan</i>	I	C	22 (11-34)	51 (32-73)	25 (2-48)	4 (0-7)
<i>Pseudomystus siamensis</i>	I	C	29 (14-45)	52 (23-84)	16 (1-35)	5 (1-9)
Synbranchiformes						
Mastacembelidae						

<i>Macrognathus siamensis</i>	I	C	33 (13-55)	49 (26-74)	15 (1-32)	6 (1-11)
<i>Mastacembelus armatus</i>	I	C	32 (13-54)	53 (27-80)	12 (1-22)	4 (0-5)
Perciformes						
Ambassidae						
<i>Parambassis siamensis</i>	I	FP	34 (13-56)	43(14-72)	25 (11-43)	3 (0-5)
Nandidae (Pristolepidae)						
<i>Pristolepis fasciata</i>	O	FP	34 (14-52)	47 (34-62)	23 (11-35)	6 (1-11)
Anabantidae						
<i>Anabas testudineus</i>	O	FP	32 (11-52)	37 (17-63)	31 (16-45)	3 (0-6)
Osphronemidae						
<i>Trichogaster trichopterus</i>	I	FP	6 (1-12)	59 (46-73)	35 (27-44)	4 (0-10)
Channidae						
<i>Channa limbata</i>	P	FP	41 (23-62)	36 (14-58)	15 (1-31)	8 (1-17)
<i>Channa lucius</i>	P	FP	32 (13-56)	52 (32-73)	12 (1-24)	6 (0-12)
<i>Channa striata</i>	P	FP	32 (14-52)	52 (31-74)	12 (1-21)	6 (0-12)

Srepok	Osteoglossiformes						
	Notopteridae						
	<i>Chitala blanci</i>	P	C	26 (12-41)	47 (23-71)	22 (1-44)	5 (0-12)
	<i>Notopterus notopterus</i>	I	FP	16 (1-33)	37 (12-63)	38 (14-65)	12 (1-23)
	Cypriniformes						
	Cyprinidae						
	<i>Barbodes gonionotus</i>	O	C	16 (1-32)	49 (27-72)	28 (13-45)	11 (1-21)
	<i>Barbonymus altus</i>	O	C	15 (1-31)	35 (11-78)	42 (12-74)	10 (1-21)
	<i>Barbonymus gonionotus</i>	O	C	39 (24-56)	36 (24-51)	21 (2-41)	6 (1-11)
	<i>Cosmocheilus harmandi</i>	O	C	15 (1-31)	43 (14-72)	42 (22-63)	3 (0-6)
	<i>Cyclocheilichthys mekongensis</i>	I	C	21 (1-41)	44 (32-57)	21 (1-42)	14 (1-31)
	<i>Garra fasciacauda</i>	D	C	60 (45-76)	15 (1-32)	12 (1-25)	15 (1-31)
	<i>Hampala dispar</i>	P	C	26 (13-42)	38 (27-51)	24 (5-42)	12 (1-23)
	<i>Hampala macrolepidota</i>	P	C	28 (15-43)	42 (12-73)	22 (1-43)	11 (1-22)
	<i>Hypsibarbus lagleri</i>	D	C	47 (23-75)	25 (13-41)	16 (1-33)	12 (1-23)

<i>Hypsibarbus pierrei</i>	D	C	43 (23-66)	26 (1-52)	22 (1-44)	12 (1-22)
<i>Labiobarbus leptocheila</i>	D	C	43 (14-72)	29 (2-61)	25 (1-51)	5 (0-11)
<i>Labiobarbus siamensis</i>	D	C	45 (32-61)	31 (11-53)	14 (1-31)	10 (1-21)
<i>Lobocheilos melanotaenia</i>	D	C	57 (43-72)	10 (1-21)	21 (1-42)	12 (1-22)
<i>Morulios chrysophekadion</i>	D	C	48 (32-65)	28 (13-44)	16 (1-33)	12 (1-23)
<i>Mystacoleucos marginatus</i>	I	C	22 (1-44)	47 (22-75)	21 (1-42)	11 (1-21)
<i>Osteochilus cf. lini</i>	D	C	47 (31-65)	21 (1-42)	15 (1-31)	16 (1-33)
<i>Poropuntius normani</i>	D	C	43 (25-63)	26 (3-52)	26 (1-54)	4 (0-7)
<i>Probarbus labeaminor</i>	O	C	27 (13-42)	47 (31-65)	23 (1-45)	5 (0-11)
<i>Puntioplites bulu</i>	O	C	7 (1-14)	47 (24-73)	40 (25-57)	11 (1-22)
<i>Puntioplites falcifer</i>	O	C	25 (11-41)	49 (25-74)	22 (1-43)	2 (0-4)
<i>Rasbora paviei</i>	I	C	21 (1-41)	49 (17-85)	20 (1-41)	11 (1-21)
<i>Rasbora tornieri</i>	I	C	17 (1-34)	36 (13-62)	27 (2-52)	23 (3-42)
<i>Scaphognathops stejnegeri</i>	O	C	24 (14-35)	43 (16-72)	22 (1-44)	11 (1-22)
Cobitidae						

<i>Acanthopsis gracilentus</i>	I	C	11 (1-21)	36 (23-51)	50 (43-57)	5 (0-11)
Siluriformes						
Sisoridae						
<i>Glyptothorax fuscus</i>	I	C	17 (1-34)	51 (28-77)	22 (1-42)	11 (1-22)
<i>Glyptothorax lampris</i>	I	C	22 (2-42)	43 (24-63)	24 (2-46)	11 (1-22)
<i>Glyptothorax laoensis</i>	I	C	26 (4-48)	45 (27-65)	23 (2-44)	11 (1-21)
Siluridae						
<i>Kryptopterus moorei</i>	P	C	26 (11-44)	43 (23-64)	23 (1-45)	10 (1-20)
<i>Micronema apogon</i>	P	C	34 (15-57)	41 (13-72)	21 (1-41)	6 (0-11)
<i>Ompok bimaculatus</i>	P	C	32 (14-52)	42 (25-61)	17 (3-44)	12 (2-24)
Pangasiidae						
<i>Helicophagus waandersii</i>	O	C	6 (1-12)	39 (13-65)	38 (21-54)	18 (2-37)
<i>Pangasius larnaudii</i>	O	C	11 (1-21)	40 (25-56)	45 (23-72)	4 (0-9)
<i>Pangasius pleurotaenia</i>	O	C	22 (3-42)	28 (14-42)	42 (32-52)	9 (1-18)
Bagridae						

<i>Bagarius bagarius</i>	I	C	17 (3-32)	44 (25-63)	22 (1-44)	12 (1-24)
<i>Bagrichthys macracanthus</i>	O	C	27 (12-43)	51 (12-93)	18 (1-36)	5 (0-12)
<i>Bagrichthys obscurus</i>	O	C	10 (1-21)	42 (24-62)	43 (34-57)	4 (0-9)
<i>Hemibagrus filamentus</i>	I	C	22 (2-43)	45 (24-67)	30 (4-56)	6 (0-12)
<i>Hemibagrus nemurus</i>	I	C	15 (2-32)	47 (32-64)	21 (2-42)	16 (1-32)
<i>Hemibagrus wyckii</i>	P	C	32 (11-54)	41 (23-61)	21 (1-41)	11 (1-21)
<i>Hemibagrus wyckioides</i>	P	C	26 (11-45)	39 (17-65)	22 (2-44)	14 (2-23)
<i>Mystus singaringan</i>	I	C	26 (3-52)	47 (23-72)	22 (2-44)	6 (0-13)
<i>Pseudomystus siamensis</i>	I	C	15 (2-31)	44 (21-67)	22 (2-43)	8 (1-16)
Beloniformes						
Belonidae						
<i>Xenentodon cancila</i>	P	C	11 (1-22)	28 (13-45)	45 (35-54)	15 (2-33)
Synbranchiformes						
Mastacembelidae						
<i>Mastacembelus armatus</i>	I	C	22 (2-43)	37 (12-63)	16 (1-33)	25 (4-52)

Perciformes						
Datnioididae						
<i>Datnioides undecimradiatus</i>	P	C	24 (3-51)	41 (23-62)	22 (3-41)	11 (1-22)
Nandidae (Pristolepidae)						
<i>Pristolepis fasciata</i>	O	FP	24 (3-51)	28 (12-49)	34 (16-49)	15 (2-32)
Eleotridae						
<i>Oxyeleotris marmorata</i>	P	FP	32 (4-61)	33 (15-54)	30 (22-41)	5 (0-11)
Anabantidae						
<i>Anabas testudineus</i>	O	FP	9 (0-12)	37 (13-62)	44 (25-62)	13 (2-25)
Osphronemidae						
<i>Osphronemus exodon</i>	O	C	5 (0-12)	36 (12-61)	54 (33-79)	3 (0-7)
Channidae						
<i>Channa limbata</i>	P	FP	26 (12-44)	34 (21-52)	15 (1-32)	26 (13-42)
<i>Channa maruloides</i>	P	FP	34 (24-41)	29 (13-47)	14 (0-32)	22 (12-34)
<i>Channa micropeltes</i>	P	C	28 (15-44)	28 (13-45)	15 (0-33)	28 (15-46)

<i>Channa striata</i>	P	FP	27 (11-45)	33 (16-51)	19 (0-41)	21 (13-31)
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APPENDIX 2

Contribution of production sources during the wet season. Median and 5th-95th percentile ranges (in parentheses) of estimated contributions of production sources to fish biomass in the Mekong, Sekong, Sesan, and Srepok rivers during the dry season.

TG: Trophic guilds (D: Detritus, I: Insectivores, O: Omnivores, P: Piscivores), HG: Habitat guilds (C: Channel, FP: Floodplain).

River	Consumers	TG	HG	Benthic algae	Seston	Riparian C3	C4 grasses
Mekong	Osteoglossiformes						
	Notopteridae						
	<i>Chitala blanci</i>	P	C	21 (2-42)	31 (10-53)	36 (12-61)	15 (1-31)
	<i>Notopterus notopterus</i>	I	FP	21 (2-42)	22 (2-45)	37 (14-62)	19 (6-33)
	Clupeiformes						
	Clupeidae						
	<i>Tenualosa toli</i>	D	C	20 (1-41)	20 (0-41)	37 (13-62)	26 (12-41)
	Cypriniformes						

Cyprinidae

<i>Amblyrhynchichthys truncatus</i>	D	FP	21 (1-42)	30 (10-51)	39 (14-65)	10 (0-22)
<i>Barbonymus altus</i>	O	C	19 (1-41)	31 (10-52)	37 (13-62)	15 (0-31)
<i>Barbonymus goionotus</i>	O	C	22 (3-41)	22 (2-43)	43 (24-63)	14 (5-24)
<i>Barbonymus schwanenfeldii</i>	O	C	19 (2-36)	21 (2-42)	46 (24-72)	13 (0-23)
<i>Cyclocheilichthys enoplus</i>	I	C	17 (2-33)	25 (8-42)	46 (23-71)	13 (0-25)
<i>Cyclocheilichthys lagleri</i>	I	C	15 (1-31)	35 (11-62)	41 (12-72)	12 (0-25)
<i>Cyclocheilichthys mekongensis</i>	I	C	17 (1-34)	25 (2-48)	43 (14-75)	14 (2-26)
<i>Cyclocheilichthys tapiensis</i>	I	C	16 (1-32)	16 (1-33)	52 (31-74)	20 (0-41)
<i>Hampala dispar</i>	P	C	21 (2-41)	25 (1-52)	37 (14-63)	16 (2-32)
<i>Henicorhynchus lobatus</i>	D	C	17 (1-35)	22 (2-43)	41 (16-67)	19 (3-39)
<i>Hypsibarbus malcolmi</i>	D	C	16 (2-38)	25 (5-47)	39 (23-64)	20 (5-34)
<i>Labiobarbus siamensis</i>	D	C	18 (2-33)	20 (2-41)	47 (24-72)	15 (8-25)
<i>Morulius chrysophekadion</i>	D	C	7 (0-15)	11 (1-22)	65 (48-82)	17 (1-33)
<i>Paralaubuca conchophilus</i>	I	C	17 (2-34)	23 (3-45)	39 (17-62)	20 (7-34)

<i>Paralaubuca riveroi</i>	I	C	18 (2-34)	22 (2-42)	46 (23-72)	15 (0-31)
<i>Paralaubuca typus</i>	I	C	21 (1-41)	26 (3-51)	41 (21-62)	15 (0-31)
<i>Puntioplites falcifer</i>	O	C	18 (2-34)	22 (4-42)	47 (22-73)	11 (0-22)
<i>Raiamas guttatus</i>	I	C	18 (2-36)	30 (11-52)	37 (13-62)	16 (0-31)
<i>Scaphognathops bandanensis</i>	O	C	22 (2-42)	21 (1-42)	37 (14-62)	21 (12-33)
<i>Scaphognathops stejnegeri</i>	O	C	16 (1-32)	22 (2-43)	42 (13-71)	21 (12-33)
<i>Sikukia gudgeri</i>	O	C	20 (1-41)	25 (1-51)	46 (13-82)	10 (0-22)
Siluriformes						
Siluridae						
<i>Wallago attu</i>	P	C	10 (1-21)	14 (1-28)	66 (41-92)	10 (0-22)
Claridae						
<i>Clarias batrachus</i>	O	FP	19 (2-35)	19 (6-34)	32 (4-61)	29 (14-45)
Bagridae						
<i>Bagarius bagarius</i>	P	C	18 (2-34)	26 (2-50)	41 (16-67)	16 (2-31)
<i>Bagrichthys bleekeri</i>	O	FP	19 (2-35)	19 (2-41)	46 (21-72)	18 (4-33)

<i>Bagrichthys macracanthus</i>	O	FP	21 (2-41)	23 (4-45)	41 (22-63)	16 (2-31)
<i>Bagrichthys macropterus</i>	O	FP	18 (2-34)	25 (0-51)	41 (16-67)	17 (3-34)
<i>Bagrichthys obscurus</i>	O	FP	16 (1-31)	21 (2-41)	46 (21-72)	16 (2-31)
<i>Hemibagrus nemurus</i>	I	C	18 (2-34)	24 (4-45)	42 (21-63)	16 (2-31)
<i>Hemibagrus wyckioides</i>	P	C	19 (2-35)	25 (4-26)	44 (23-65)	12 (1-23)
<i>Hemisilurus mekongensis</i>	P	C	19 (1-41)	24 (0-51)	42 (14-71)	16 (2-31)
<i>Micronema apogon</i>	I	C	15 (2-31)	22 (3-42)	43 (22-64)	17 (3-32)
<i>Micronema cheveyi</i>	I	C	19 (4-35)	23 (4-43)	41 (21-62)	16 (5-27)
<i>Mystus singaringan</i>	I	C	18 (1-38)	21 (2-42)	46 (21-72)	16 (2-31)

Synbranchiformes

Mastacembelidae

<i>Macrochirichthys armatus</i>	I	FP	17 (1-34)	22 (1-43)	38 (14-63)	22 (6-36)
<i>Macrochirichthys macrochirus</i>	I	FP	21 (1-41)	21 (1-42)	37 (13-62)	20 (6-35)
<i>Mastacembelus armatus</i>	I	FP	18 (3-35)	23 (4-43)	47 (23-74)	13 (3-25)

Perciformes

Toxotidae							
	<i>Toxotes microlepis</i>	I	FP	21 (1-41)	33 (12-54)	36 (10-71)	15 (0-31)
Nandiae (Pristolepidae)							
	<i>Pristolepis fasciata</i>	O	FP	10 (1-21)	15 (0-31)	56 (32-81)	21 (12-31)
Osphronemidae							
	<i>Osphronemus exodon</i>	O	C	20 (0-42)	32 (13-54)	41 (12-71)	19 (2-36)
Channidae							
	<i>Channa micropeltes</i>	P	FP	6 (0-14)	11 (1-23)	44 (16-73)	38 (24-53)
	<i>Channa striata</i>	P	FP	10 (1-20)	14 (1-28)	42 (11-72)	33 (23-45)
Pleuroctiformes							
Soleidae							
	<i>Brachirus orientalis</i>	I	FP	31 (12-51)	25 (10-42)	32 (4-61)	15 (0-31)
Sekong	Osteoglossiformes						
Notopteridae							
	<i>Notopterus notopterus</i>	I	FP	11 (1-23)	16 (2-31)	51 (31-72)	26 (13-42)

Cypriniformes

Cyprinidae

<i>Barbonymus altus</i>	O	C	11 (1-23)	18 (6-31)	52 (34-72)	20 (7-34)
<i>Barbonymus goionotus</i>	O	C	13 (2-25)	14 (1-27)	52 (34-73)	22 (2-43)
<i>Barbonymus schwanenfeldii</i>	O	C	11 (1-22)	11 (1-23)	51 (35-68)	27 (12-44)
<i>Cyclocheilichthys lagleri</i>	I	C	21 (3-42)	16 (2-32)	43 (22-65)	20 (5-36)
<i>Cyclocheilichthys mekongensis</i>	I	C	15 (1-31)	24 (6-45)	36 (13-62)	27 (13-42)
<i>Cyclocheilichthys mekongensis</i>	I	C	17 (2-34)	16 (1-32)	50 (25-76)	16 (2-31)
<i>Henicorhynchus siamensis</i>	D	C	20 (1-41)	17 (2-33)	47 (24-73)	15 (0-31)
<i>Hypsibarbus pierri</i>	D	C	16 (1-32)	17 (1-33)	52 (23-82)	17 (2-33)
<i>Hypsibarbus wetmorei</i>	D	C	18 (2-33)	17 (1-34)	51 (32-73)	14 (5-23)
<i>Labiobarbus siamensis</i>	D	C	21 (2-41)	19 (2-38)	47 (21-74)	15 (0-31)
<i>Puntius orphoides</i>	O	C	11 (1-22)	11 (0-23)	52 (34-73)	26 (6-47)
<i>Puntoplites falcifer</i>	O	C	13 (2-25)	16 (2-31)	46 (21-72)	26 (11-43)
<i>Rasbora hoblma</i>	I	FP	22 (2-43)	17 (2-33)	47 (22-73)	16 (0-31)

Siluriformes

Siluridae

<i>Micronema apogon</i>	I	C	20 (1-41)	16 (1-32)	48 (23-74)	17 (3-32)
<i>Micronema cheveyi</i>	I	C	16 (1-32)	16 (0-33)	53 (22-84)	16 (1-32)
<i>Wallago attu</i>	P	C	11 (2-21)	13 (4-23)	52 (38-67)	24 (2-47)

Claridae

<i>Clarias batrachus</i>	O	FP	10 (1-21)	10 (0-21)	57 (42-74)	26 (12-41)
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Pangasidae

<i>Pangasius bocourti</i>	O	C	18 (2-34)	16 (1-32)	53 (24-83)	15 (0-32)
<i>Pangasius conchophilus</i>	O	C	8 (1-16)	10 (2-19)	64 (37-91)	18 (1-33)
<i>Pangasius larnaudii</i>	O	C	10 (1-21)	12 (3-22)	58 (42-74)	20 (4-36)
<i>Pangasius macronema</i>	O	C	17 (2-33)	16 (1-31)	52 (21-84)	17 (1-34)
<i>Pangasius pleurotaenia</i>	O	C	20 (1-42)	26 (5-48)	36 (11-61)	20 (0-41)
<i>Pangasius siamensis</i>	O	C	17 (2-32)	16 (2-31)	50 (26-74)	17 (2-33)

Bagridae

	<i>Bagrichthys macracanthus</i>	O	FP	22 (3-42)	17 (2-34)	41 (22-63)	21 (5-38)
	<i>Bagrichthys obscurus</i>	O	FP	8 (1-16)	16 (1-32)	57 (24-91)	21 (4-38)
	<i>Hemibagrus nemurus</i>	I	C	16 (0-32)	16 (1-32)	54 (25-83)	16 (1-32)
	<i>Hemibagrus wyckiodes</i>	P	C	16 (1-32)	17 (1-33)	51 (22-82)	17 (2-33)
	Synbranchiformes						
	Mastacembelidae						
	<i>Mastacembelus armatus</i>	I	FP	20 (1-41)	11 (0-21)	47 (33-62)	22 (12-33)
	Perciformes						
	Nandiae (Pristolepidae)						
	<i>Pristolepis fasciata</i>	O	FP	11 (1-22)	11 (0-22)	50 (36-64)	27 (12-45)
	Channidae						
	<i>Channa striata</i>	P	FP	15 (0-31)	6 (0-14)	52 (32-73)	28 (14-43)
Sesan	Osteoglossiformes						
	Notopteridae						
	<i>Notopterus notopterus</i>	I	FP	21 (2-43)	21 (1-44)	37 (13-61)	25 (12-41)

Cypriniformes

Cyprinidae

<i>Barbonymus altus</i>	O	C	16 (1-31)	18 (4-33)	49 (26-73)	18 (4-33)
<i>Barbonymus schwanenfeldii</i>	O	C	23 (3-43)	27 (10-44)	26 (7-46)	24 (7-41)
<i>Cyclocheilichthys lagleri</i>	I	C	7 (0-14)	10 (0-21)	64 (56-73)	20 (5-35)
<i>Cyclocheilichthys mekongensis</i>	I	C	15 (1-31)	17 (2-33)	48 (23-74)	18 (0-36)
<i>Hypsibarbus wetmorei</i>	D	C	15 (1-31)	24 (3-46)	51 (32-72)	11 (1-22)
<i>Labiobarbus siamensis</i>	D	C	11 (1-23)	15 (0-32)	51 (33-71)	26 (12-41)
<i>Puntius orphoides</i>	O	C	12 (1-23)	10 (1-25)	61 (43-78)	18 (2-36)
<i>Puntoplites falcifer</i>	O	C	11 (2-21)	22 (2-43)	47 (31-64)	20 (0-41)
<i>Puntoplites proctozsron</i>	O	C	16 (1-32)	20 (1-41)	31 (22-43)	36 (14-62)

Siluriformes

Siluridae

<i>Micronema cheveyi</i>	I	C	13 (1-32)	19 (0-37)	54 (33-76)	17 (0-33)
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Claridae

<i>Clarias batrachus</i>	O	FP	17 (1-33)	18 (2-35)	37 (14-62)	27 (11-43)
Pangasidae						
<i>Pangasius pleurotaenia</i>	O	FP	13 (1-31)	16 (2-37)	50 (32-72)	21 (3-34)
Bagridae						
<i>Bagrichthys macracanthus</i>	O	FP	17 (2-34)	16 (2-32)	43 (22-66)	25 (11-43)
<i>Bagrichthys obscurus</i>	O	FP	21 (0-41)	27 (12-43)	32 (13-52)	20 (6-35)
<i>Hemibagrus nemurus</i>	I	C	15 (1-32)	15 (0-31)	48 (31-66)	25 (11-42)
Synbranchiformes						
Mastacembelidae						
<i>Macrornathus siamensis</i>	I	FP	10 (1-21)	9 (0-20)	61 (51-73)	25 (12-43)
<i>Mastacembelus armatus</i>	I	FP	17 (2-34)	20 (1-41)	30 (8-54)	33 (24-42)
Perciformes						
Channidae						
<i>Channa striata</i>	P	FP	15 (2-35)	20 (2-46)	36 (14-62)	30 (19-41)
Srepok	Osteoglossiformes					

Notopteridae

<i>Chitala blanci</i>	P	C	20 (1-41)	17 (0-34)	37 (13-64)	26 (12-41)
<i>Notopterus notopterus</i>	I	FP	20 (1-41)	21 (2-41)	36 (12-62)	27 (11-44)

Cypriniformes

Cyprinidae

<i>Barbonymus altus</i>	O	C	17 (1-33)	20 (1-41)	48 (24-75)	17 (4-32)
<i>Barbonymus goionotus</i>	O	C	19 (2-36)	24 (3-45)	43 (24-63)	15 (0-32)
<i>Barbonymus schwanenfeldii</i>	O	C	17 (2-34)	21 (3-41)	47 (22-73)	15 (0-32)
<i>Cyclocheilichthy lagleri</i>	I	C	15 (1-31)	18 (1-35)	50 (31-72)	15 (0-32)
<i>Cyclocheilichthys mekongensis</i>	I	C	17 (2-34)	22 (3-42)	39 (12-67)	21 (7-35)
<i>Henicorhynchus siamensis</i>	D	C	18 (1-35)	22 (3-42)	39 (14-65)	21 (4-39)
<i>Hypsibarbus lagleri</i>	D	C	20 (1-41)	21 (1-42)	47 (23-72)	15 (0-32)
<i>Hypsibarbus malcolmi</i>	D	C	16 (1-34)	19 (0-41)	47 (31-63)	20 (1-40)
<i>Hypsibarbus wetmorei</i>	D	C	21 (2-41)	22 (2-43)	42 (11-71)	16 (1-33)
<i>Labiobarbus siamensis</i>	D	C	17 (1-35)	16 (2-32)	41 (22-63)	27 (14-43)

<i>Puntioplites falcifer</i>	O	C	16 (1-32)	27 (12-43)	41 (12-71)	20 (0-41)
<i>Rasbora hobelmani</i>	I	C	21 (1-42)	15 (1-32)	29 (6-53)	33 (15-52)
Siluriformes						
Siluridae						
<i>Micronema apogon</i>	I	C	16 (2-31)	20 (1-41)	50 (21-82)	15 (0-31)
<i>Micronema cheveyi</i>	I	C	21 (2-41)	17 (0-33)	49 (24-75)	15 (0-31)
<i>Wallago attu</i>	P	C	17 (1-33)	18 (2-34)	34 (16-54)	31 (11-53)
Claridae						
<i>Clarias batrachus</i>	O	FP	18 (2-34)	21 (1-22)	36 (12-63)	28 (12-44)
Pangasidae						
<i>Pangasius conchophilus</i>	O	C	21 (2-41)	22 (2-43)	37 (12-64)	19 (3-35)
<i>Pangasius macronema</i>	O	C	18 (1-35)	21 (1-42)	39 (15-63)	24 (3-42)
<i>Pangasius siamensis</i>	O	C	21 (1-41)	18 (2-35)	42 (21-63)	20 (4-36)
<i>Pangasius pleurotenia</i>	O	C	15 (1-32)	21 (1-42)	51 (23-82)	15 (0-32)
<i>Pangasius launidi</i>	O	C	21 (1-42)	15 (1-32)	46 (23-71)	20 (0-42)

Bagridae

<i>Bagrichthys macracanthus</i>	O	FP	16 (1-32)	21 (3-42)	51 (23-81)	15 (0-31)
<i>Bagrichthys obscurus</i>	O	FP	15 (0-32)	20 (0-41)	46 (21-72)	18 (3-35)
<i>Hemibagrus nemurus</i>	I	C	17 (1-33)	20 (0-42)	51 (23-81)	15 (0-32)
<i>Hemibagrus wyckiodes</i>	P	C	17 (1-34)	21 (2-41)	37 (13-62)	26 (11-42)
<i>Pseudomystus siamensis</i>	I	C	17 (1-34)	21 (1-42)	38 (15-63)	25 (11-42)

Synbranchiformes

Mastacembelidae

<i>Macrognathus armatus</i>	I	FP	17 (1-33)	20 (1-42)	38 (12-65)	26 (12-41)
<i>Macrognathus siamensis</i>	I	FP	16 (2-33)	17 (1-34)	51 (22-81)	15 (0-32)
<i>Mastacembelus armatus</i>	I	FP	15 (1-32)	20 (0-41)	50 (21-82)	15 (0-31)
<i>Mystacoleucus atridorsalis</i>	I	FP	17 (1-33)	15 (0-31)	35 (14-57)	34 (23-46)

Perciformes

Channidae

<i>Channa striata</i>	P	FP	17 (1-33)	18 (0-35)	34 (13-57)	32 (23-42)
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APPENDIX 3

Taxonomy and Trophic Position of fishes from the Lower Mekong River

Order	Family	Species name	Order rank	Family rank	Genus rank	TG	Mean SL	SD SL	Mean TP	SD TP
Osteoglossiformes	Notopteridae	Chitala blanci	1	1	1	P	43.50	3.12	3.81	0.21
Osteoglossiformes	Notopteridae	Notopterus notopterus	1	1	2	I	18.61	3.54	2.98	0.19
Cypriniformes	Cyprinidae	Paralauca typus	2	2	3	I	7.92	4.09	3.30	0.35
Cypriniformes	Cyprinidae	Macrochirichthys macrochirus	2	2	4	P	30.00	0.00	3.91	0.00
Cypriniformes	Cyprinidae	Parachanna siamensis	2	2	5	I	9.00	0.00	2.90	0.00
Cypriniformes	Cyprinidae	Opsarius pulchellus	2	2	6	I	4.13	2.02	3.21	0.48
Cypriniformes	Cyprinidae	Raiamus guttatus	2	2	7	I	16.17	4.25	3.49	0.13
Cypriniformes	Cyprinidae	Rasbora hobelmani	2	2	8	I	5.83	0.35	3.35	0.17
Cypriniformes	Cyprinidae	Rasbora paviei	2	2	8	I	4.32	0.61	2.58	0.36
Cypriniformes	Cyprinidae	Rasbora sp	2	2	8	I	3.23	0.53	3.28	0.36
Cypriniformes	Cyprinidae	Rasbora tornieri	2	2	8	I	6.88	1.44	2.73	0.25

Cypriniformes	Cyprinidae	Rasbora trilineata	2	2	8	I	3.50	0.50	2.53	0.06
Cypriniformes	Cyprinidae	Probarbus jullieni	2	2	9	O	21.75	0.96	3.52	0.26
Cypriniformes	Cyprinidae	Probarbus labeaminor	2	2	9	O	22.00	0.00	2.73	0.00
Cypriniformes	Cyprinidae	Tor sinensis	2	2	10	O	30.00	0.00	3.53	0.00
Cypriniformes	Cyprinidae	Cyclocheilichthys furcatus	2	2	12	I	18.50	0.00	3.42	0.00
Cypriniformes	Cyprinidae	Cyclocheilichthys lagleri	2	2	12	I	11.83	1.26	3.00	0.13
Cypriniformes	Cyprinidae	Cyclocheilichthys mekongensis	2	2	12	I	12.83	3.78	3.23	0.33
Cypriniformes	Cyprinidae	Cyclocheilichthys tapiensis	2	2	12	I	17.25	0.35	3.38	0.00
Cypriniformes	Cyprinidae	Mystacoleucos marginatus	2	2	13	I	9.63	2.29	3.23	0.35
Cypriniformes	Cyprinidae	Puntioplites bulu	2	2	14	O	13.00	0.00	2.59	0.00
Cypriniformes	Cyprinidae	Puntioplites falcifer	2	2	15	O	12.44	6.58	3.22	0.26
Cypriniformes	Cyprinidae	Barbonymus altus	2	2	16	O	13.50	1.78	2.86	0.25
Cypriniformes	Cyprinidae	Barbonymus gonionotus	2	2	17	O	22.00	0.00	2.62	0.00
Cypriniformes	Cyprinidae	Barbonymus schwanefeldii	2	2	17	O	10.33	0.58	2.88	0.20
Cypriniformes	Cyprinidae	Hypsibarbus lagleri	2	2	18	D	29.00	3.56	2.65	0.17

Cypriniformes	Cyprinidae	Hypsibarbus malcolmi	2	2	18	D	22.00	0.00	3.29	0.00
Cypriniformes	Cyprinidae	Hypsibarbus pierrei	2	2	18	D	34.00	0.00	3.06	0.00
Cypriniformes	Cyprinidae	Hypsibarbus sp.	2	2	18	D	8.03	0.55	1.87	0.03
Cypriniformes	Cyprinidae	Hypsibarbus wetmorei	2	2	18	D	35.00	0.00	2.47	0.00
Cypriniformes	Cyprinidae	Poropuntius laoensis	2	2	19	I	12.00	0.00	3.09	0.00
Cypriniformes	Cyprinidae	Poropuntius normani	2	2	19	D	19.25	2.50	2.37	0.17
Cypriniformes	Cyprinidae	Scaphognathops bandanensis	2	2	20	O	18.25	0.35	2.39	0.22
Cypriniformes	Cyprinidae	Scaphognathops stejnegeri	2	2	20	O	18.20	2.59	3.51	0.07
Cypriniformes	Cyprinidae	Puntius sp	2	2	21	D	11.25	1.06	3.09	0.40
Cypriniformes	Cyprinidae	Hampala dispar	2	2	22	P	17.14	3.06	4.00	0.29
Cypriniformes	Cyprinidae	Hampala macrolepidota	2	2	22	P	15.60	3.36	3.82	0.53
Cypriniformes	Cyprinidae	Puntius orphoides	2	2	23	D	13.00	1.00	2.50	0.37
Cypriniformes	Cyprinidae	Cirrhinus jullieni	2	2	24	D	8.00	0.00	2.48	0.00
Cypriniformes	Cyprinidae	Bangana behri	2	2	25	D	51.00	0.00	2.42	0.00
Cypriniformes	Cyprinidae	Henicorhynchus siamensis	2	2	26	D	4.00	0.00	2.98	0.09

Cypriniformes	Cyprinidae	Henicorhynchus lobatus	2	2	26	D	8.67	2.75	2.40	0.29
Cypriniformes	Cyprinidae	Labeo chrysophekadion	2	2	27	D	43.00	2.83	2.63	0.22
Cypriniformes	Cyprinidae	Labiobarbus leptocheila	2	2	28	D	13.28	2.90	2.64	0.40
Cypriniformes	Cyprinidae	Labiobarbus siamensis	2	2	28	D	17.50	0.71	2.78	0.69
Cypriniformes	Cyprinidae	Leptobarbus hoevenii	2	2	29	D	34.00	0.00	2.17	0.00
Cypriniformes	Cyprinidae	Lobocheilos delacouri	2	2	30	D	14.50	0.71	3.10	0.25
Cypriniformes	Cyprinidae	Lobocheilos melanotaenia	2	2	30	D	16.80	1.79	3.06	0.21
Cypriniformes	Cyprinidae	Labeo barbatulus	2	2	27	D	21.33	0.58	3.03	0.45
Cypriniformes	Cyprinidae	Osteochilus lini	2	2	31	O	19.50	0.00	2.56	0.00
Cypriniformes	Cyprinidae	Osteochilus hesseltii	2	2	31	O	20.00	0.00	2.57	0.00
Cypriniformes	Cyprinidae	Osteochilus melanopleura	2	2	31	O	21.00	0.00	3.15	0.00
Cypriniformes	Cyprinidae	Osteochilus schlegeli	2	2	31	O	23.00	0.00	2.09	0.00
Cypriniformes	Cyprinidae	Osteochilus waandersii	2	2	31	O	16.00	2.08	2.61	0.08
Cypriniformes	Cyprinidae	Garra fasciacauda	2	2	32	D	11.50	1.32	2.73	0.02

Cypriniformes	Cyprinidae	Mekongina erythrospila	2	2	33	D	39.00	0.00	2.36	0.32
Cypriniformes	Cyprinidae	Cirrhinus microlepis	2	2	34	D	40.00	0.00	2.21	0.00
Cypriniformes	Gyrinocheilidae	Gyrinocheilus pennocki	2	3	35	D	45.00	0.00	2.81	0.00
Cypriniformes	Botiidae	Syncrossus helodes	2	4	36	I	14.75	2.72	3.92	0.29
Cypriniformes	Botiidae	Yasuhikotakia candipunctata	2	4	37	I	11.00	0.00	3.42	0.00
Cypriniformes	Botiidae	Yasuhikotakia modesta	2	4	37	I	14.25	3.97	3.57	0.80
Cypriniformes	Cobitidae	Acanthopsis gracilentus	2	5	38	I	15.00	0.00	2.03	0.00
Cypriniformes	Cobitidae	Acanthopsis sp1	2	5	38	I	12.50	2.68	3.91	0.16
Cypriniformes	Cobitidae	Acanthopsis sp. 2	2	5	38	I	12.00	0.00	3.98	0.11
Cypriniformes	Cobitidae	Acanthopsis sp. 3	2	5	38	I	11.00	0.00	3.14	0.37
Cypriniformes	Cobitidae	Acanthopsis sp. 4	2	5	38	I	4.75	0.35	3.13	0.19
Cypriniformes	Cobitidae	Acanthopsis sp. 5	2	5	38	I	6.17	1.04	3.22	0.05
Cypriniformes	Nemacheilidae	Nemacheilus cf. longistriatus	2	6	39	I	5.00	0.00	3.65	0.00
Cypriniformes	Nemacheilidae	Schistura sp.1	2	6	40	I	3.00	0.00	3.38	0.00
Cypriniformes	Nemacheilidae	Schistura sp2	2	6	40	I	4.00	0.00	3.59	0.00

Cypriniformes	Nemacheilidae	Schistura sp.3	2	6	40	I	4.00	0.00	3.58	0.00
Cypriniformes	Nemacheilidae	Schistura sp. 4	2	6	40	I	5.00	0.00	2.19	0.00
Siluriformes	Sisoridae	Bagarius bagarius	3	7	41	P	14.33	2.08	3.35	0.35
Siluriformes	Sisoridae	Bagarius suchus	3	7	41	P	32.25	3.86	4.12	0.18
Siluriformes	Sisoridae	Glyptothorax fuscus	3	7	42	I	5.33	0.00	3.54	0.01
Siluriformes	Sisoridae	Glyptothorax lampris	3	7	42	I	4.00	0.00	3.02	0.00
Siluriformes	Sisoridae	Glyptothorax laoensis	3	7	42	I	6.00	0.00	3.61	0.00
Siluriformes	Siluridae	Belodontichthys truncatus	3	8	43	P	33.67	4.62	3.67	0.17
Siluriformes	Siluridae	Kryptopterus bicirrhis	3	8	44	I	9.50	0.00	2.65	0.20
Siluriformes	Siluridae	Kryptopterus cryptopterus	3	8	44	I	15.50	0.00	3.00	0.16
Siluriformes	Siluridae	Kryptopterus limpok	3	8	44	I	12.64	1.99	2.93	0.16
Siluriformes	Siluridae	Kryptopterus moorei	3	8	44	I	21.67	1.53	3.64	0.12
Siluriformes	Siluridae	Kryptopterus schilbeides	3	8	44	P	25.50	0.71	3.29	0.02
Siluriformes	Siluridae	Micronema apogon	3	8	45	P	24.60	2.19	3.11	0.16
Siluriformes	Siluridae	Micronema bleekeri	3	8	46	P	21.17	3.01	2.92	0.16

Siluriformes	Siluridae	Micronema cheveyi	3	8	46	I	16.75	1.77	3.17	0.41
Siluriformes	Siluridae	Ompok bimaculatus	3	8	47	O	23.00	0.00	2.88	0.32
Siluriformes	Siluridae	Wallago attu	3	8	48	P	39.17	3.92	3.94	0.36
Siluriformes	Siluridae	Wallago leerii	3	8	48	P	24.50	0.00	2.84	0.00
Siluriformes	Siluridae	Wallago micropogon	3	8	48	P	49.80	9.01	3.90	0.75
Siluriformes	Clariidae	Clarias batrachus	3	9	49	O	17.92	1.80	2.85	0.25
Siluriformes	Clariidae	Clarias macrocephalus	3	9	49	O	19.00	3.00	3.60	0.16
Siluriformes	Clariidae	Clarias melanoderma	3	9	49	O	19.00	0.00	3.76	0.00
Siluriformes	Ariidae	Hemibarbus stormii	3	10	50	P	36.00	0.00	3.55	0.00
Siluriformes	Pangasiidae	Helicophagus waandersii	3	11	51	O	24.38	4.96	3.46	0.20
Siluriformes	Pangasiidae	Pangasianodon hypophthalmus	3	11	52	O	33.00	0.00	3.06	0.00
Siluriformes	Pangasiidae	Pangasius bocourti	3	11	52	O	34.50	0.71	2.79	0.92
Siluriformes	Pangasiidae	Pangasius conchophilus	3	11	52	O	38.67	4.59	3.14	0.35
Siluriformes	Pangasiidae	Pangasius larnaudii	3	11	52	O	38.00	4.40	3.39	0.31
Siluriformes	Pangasiidae	Pangasius micronema	3	11	52	O	14.75	1.06	2.99	0.06

Siluriformes	Pangasiidae	Pangasius pleurotaenia	3	11	52	O	16.44	1.94	2.98	0.43
Siluriformes	Bagridae	Bagrichthys macracanthus	3	12	53	O	17.10	0.82	2.68	0.43
Siluriformes	Bagridae	Bagrichthys nitidus	3	12	53	O	11.50	0.00	2.67	0.12
Siluriformes	Bagridae	Bagrichthys obscurus	3	12	53	O	19.00	0.00	3.56	0.00
Siluriformes	Bagridae	Hemibagrus filamentus	3	12	54	I	21.00	0.00	3.29	0.00
Siluriformes	Bagridae	Hemibagrus nemurus	3	12	54	I	19.05	6.72	3.41	0.34
Siluriformes	Bagridae	Hemibagrus spilopterus	3	12	54	I	12.25	1.71	3.19	0.13
Siluriformes	Bagridae	Hemibagrus wyckii	3	12	54	P	37.33	2.08	4.06	0.18
Siluriformes	Bagridae	Hemibagrus wyckioides	3	12	54	P	44.91	8.96	4.12	0.49
Siluriformes	Bagridae	Hemisilurus mekongensis	3	12	54	O	34.00	0.00	3.43	0.00
Siluriformes	Bagridae	Mystus albolineatus	3	12	55	I	9.50	0.00	3.25	0.03
Siluriformes	Bagridae	Mystus bocourti	3	12	55	I	15.30	0.84	3.18	0.11
Siluriformes	Bagridae	Mystus multiradiatus	3	12	55	I	9.17	0.29	3.05	0.15
Siluriformes	Bagridae	Mystus singaringan	3	12	55	I	12.23	4.00	3.49	0.30
Siluriformes	Bagridae	Pseudomystus siamensis	3	12	56	I	13.33	1.53	3.23	0.24

Beloniformes	Belonidae	Xenentodon cancila	4	13	57	P	18.10	1.75	3.47	0.26
Synbranchiformes	Synbranchidae	Ophisternon bengalense	5	14	58	O	46.50	7.19	2.69	0.49
Synbranchiformes	Mastacembelidae	Macrognathus semiocellatus	5	15	59	I	20.00	0.00	2.69	0.00
Synbranchiformes	Mastacembelidae	Macrognathus siamensis	5	15	59	I	18.25	1.89	2.53	0.31
Synbranchiformes	Mastacembelidae	Mastacembelus armatus	5	15	60	I	39.22	9.07	3.66	0.28
Perciformes	Ambassidae	Parambassis siamensis	6	16	61	I	4.07	1.16	3.20	0.24
Perciformes	Datnioididae	Datnioides undecimradiatus	6	17	62	P	23.00	0.00	3.23	0.11
Perciformes	Sciaenidae	Boesemania microlepis	6	18	63	P	35.00	0.00	4.21	0.00
Perciformes	Nandidae	Pristolepis fasciata	6	19	64	O	13.17	2.62	2.85	0.74
Perciformes	Eleotridae	Oxyeleotris exodon (marmorata)	6	20	65	I	27.00	0.00	3.84	0.00
Perciformes	Eleotridae	Oxyeleotris marmorata	6	20	65	I	26.00	0.00	3.85	0.00
Perciformes	Eleotridae	Oxygaster anomalura	6	20	65	I	14.00	0.00	3.32	0.00
Perciformes	Gobiidae	Tridentiger ocellatus	6	21	66	I	5.50	0.50	3.59	0.39
Cypriniformes	Cyprinidae	Cosmocheilus harmandi	2	2	11	O	32.00	2.65	3.67	0.16

Cypriniformes	Cyprinidae	Cyclocheilichthys apogon	2	2	12	I	9.75	0.35	3.09	0.07
Cypriniformes	Cyprinidae	Cyclocheilichthys enoplus	2	2	12	I	22.00	0.00	3.20	0.00
Perciformes	Anabantidae	Anabas testudineus	6	22	67	O	9.10	1.17	2.51	0.26
Perciformes	Osphronemidae	Trichogaster trichopterus	6	23	68	I	8.00	0.00	2.20	0.00
Perciformes	Osphronemidae	Osphronemus exodon	6	23	69	O	29.00	1.41	2.48	0.11
Perciformes	Osphronemidae	Osphronemus goramy	6	23	69	O	25.00	0.00	2.54	0.00
Perciformes	Osphronemidae	Trichogaster trichopterus	6	23	70	I?	7.67	1.04	1.94	0.13
Perciformes	Channidae	Channa limbata	6	24	71	P	12.60	2.41	2.71	0.34
Perciformes	Channidae	Channa lucius	6	24	71	P	22.67	1.15	3.29	0.09
Perciformes	Channidae	Channa marulioides	6	24	71	P	46.25	9.71	3.86	0.32
Perciformes	Channidae	Channa micropeltes	6	24	71	P	51.83	7.41	4.60	0.23
Perciformes	Channidae	Channa striata	6	24	71	P	26.54	7.13	2.99	0.27
Pleuronectiformes	Soleidae	Brachirus orientalis	7	25	72	I	26.00	0.00	3.67	0.00
Pleuronectiformes	Cynoglossidae	Cynoglossus puncticeps	7	26	73	I	28.00	0.00	2.95	0.00