

Seasonal hydrology shifts production sources supporting fishes in rivers of the Lower Mekong Basin

Chouly Ou and Kirk O. Winemiller

Abstract: Seasonal hydrology is assumed to be an important reason why the Lower Mekong Basin supports highly productive and biodiverse inland fisheries. We used C and N stable isotope ratios of tissue samples to estimate primary production sources supporting fish biomass in the Mekong and three large tributaries in Cambodia. We used a Bayesian mixing model to estimate relative contributions of four alternative production sources — seston, benthic algae, riparian grasses, and riparian macrophytes. There was little seasonal variation in isotopic signatures of riparian plants, but benthic algae and seston showed large seasonal shifts in carbon ratios. Seston and benthic algae were the most important production sources supporting fish biomass overall during the dry season, and riparian vegetation was the most important source during the wet season. Sources contributed differentially to biomass of trophic and habitat guilds, especially during the dry season. A dam on the upper Sesan River has changed hydrology, channel geomorphology, and other factors and, compared with the other three rivers, its fish biomass appears to derive from algae to a greater extent.

Résumé : L'hydrologie saisonnière est présumée être une importante raison expliquant le fait que le bassin du cours inférieur du fleuve Mékong supporte des pêches continentales très productives et d'une grande biodiversité. Nous avons utilisé les rapports d'isotopes stables du C et du N d'échantillons de tissus pour estimer les sources de production primaire qui supportent la biomasse de poissons dans le Mékong et trois grands affluents au Cambodge. Nous avons utilisé un modèle de mélange bayésien pour estimer les contributions relatives de quatre sources de production différentes, soit le seston, les algues benthiques, les herbes riveraines et les macrophytes riverains. S'il y avait peu de variation saisonnière des signatures isotopiques des plantes riveraines, les rapports d'isotopes de carbone des algues benthiques et du seston présentaient d'importantes variations saisonnières. Le seston et les algues benthiques constituaient les sources de production primaire les plus importantes supportant la biomasse de poissons globalement durant la saison sèche, et la végétation riveraine était la source la plus importante durant la saison humide. Les sources contribuaient de différentes manières à la biomasse des guildes trophiques et d'habitat, particulièrement durant la saison sèche. Un barrage sur le cours supérieur de la rivière Sésan en a modifié l'hydrologie, la géomorphologie du chenal et d'autres facteurs et, comparativement à celle des trois autres rivières, sa biomasse de poissons semble être dérivée d'algues dans une plus grande mesure. [Traduit par la Rédaction]

Introduction

The natural flow regime is crucial for sustaining native aquatic biodiversity and maintenance of ecological processes in fluvial ecosystems (Bunn and Arthington 2002; Jardine et al. 2015). A 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, passive transport of production sources, and top-down control of basal resources (Power et al. 1996; Montoya et al. 2006; Roelke et al. 2006; Winemiller et al. 2006, 2014). 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, resource availability, and riparian community structure (Junk et al. 1989; Winemiller 2004; Roach 2013).

Humans have changed river flow regimes worldwide, especially through impoundment (Poff et al. 1997, 2007; Dudgeon 2000). River impoundments have caused major 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, with many native species responding with declines in reproduction, recruitment, and population abundance (Dudgeon 2010; Poff and Zimmerman 2010). Dams also trap sediments, which can alter sediment dynamics and geomorphology in downstream reaches and deltas (Kondolf et al. 2014). For example, research on the Paraná River (in Brazil) has revealed greater water clarity and ecological regime shifts in downstream reaches following dam construction (Hoeinghaus et al. 2007; Agostinho et al. 2008).

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

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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). The FPC proposes that lateral connectivity between the main channel and floodplain habitats is important in large river food webs. The FPC predicts that ecosystem dynamics are driven by seasonal floodplain inundation that introduces terrestrial material (e.g., invertebrates and macrophyte biomass) to the aquatic food web (Junk et al. 1989). The RPM stresses algal-grazer pathways as the main food chains maintaining fish diversity and production in large river food webs. 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 (Thorpe and DeLong 1994).

River food webs have been demonstrated to have both temporal and spatial variation in response to variation in abiotic factors and (or) species composition (Winemiller 1996; Jardine et al. 2015). None of the three models mentioned above integrate all the key dimensions and drivers of watershed characteristics (e.g., discharge, turbidity, sedimentation, light penetration) that affect temporal and spatial food web variation. A recent review of production sources for river food webs concluded that, in rivers with high rates of 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). Biochemical research on the Lower Mekong River in Cambodia, a sediment-laden river, indicated that during the dry season, fine particulate organic matter 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, we investigated primary production sources supporting fish biomass in the Lower Mekong River and three major tributary rivers in Cambodia. We estimated seasonal variation in contributions of primary production sources to fish assemblages in three rivers that have relatively low impact from dams and one river (Sesan) significantly impacted by upstream dams. We estimated basal production source contributions during the dry season when river discharge is low and water is relatively transparent. We repeated field surveys and estimates during the wet season when river discharge is high and variable and water is turbid. In accordance with Roach's (2013) model, we hypothesized that autochthonous primary production sources (algae) would support most fish biomass during the dry season, and allochthonous sources (C_3 plants) would be more important during the wet season. We further hypothesized that the river impacted by dams would reveal divergent patterns of seasonal assimilation of material originating from principal basal production sources.

Methods

The Mekong River

The annual flood pulse of the Mekong River supports one of the world's most productive and biodiverse inland fisheries (Welcomme 1979). Globally, the Mekong is the tenth longest river with the eighth greatest discharge and third richest in fish species richness (Welcomme 1985). Over 1000 fish species, belonging to 24 orders and 87 families, and more than 200 endemic freshwater species have been documented in the river (Mekong River Commission 2003). Estimates of fish biodiversity in the basin are conservative because there continually are new discoveries (Rainboth et al. 2012). The river contains several iconic aquatic species, including the giant Mekong catfish (*Pangasianodon gigas*), one of the largest freshwater fishes in the world, which can reach 300 kg, giant Mekong carp (*Catlocarpio siamensis*), giant stingray (*Himantura chaophraya*), and Irrawaddy freshwater dolphin (*Orcaella brevirostris*).

The Mekong River's natural flow regime and its fish diversity will be impacted by hydropower development in the region (Adamson et al. 2009; Dugan et al. 2010; Grumbine et al. 2012; Ziv et al. 2012). Three hydroelectric dams were completed in the Upper Mekong mainstem in China in 1995, 2003, and 2008 (Barlow et al. 2008). More than 100 dams have been proposed for the Lower Basin countries of Cambodia, Laos, Thailand, and Vietnam. Among the planned dams in the Lower Mekong Basin, two, which are located in Cambodia (Lower Sesan 2 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 effects on aquatic communities 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 mainstem of the Upper Mekong are predicted to trap at least 50% of the suspended sediment load delivered to the Lower Mekong (Lu and Siew 2005; Kummu and Varis 2007), and dams constructed within the lower basin will trap even more sediment, impacting the ecology of segments in downstream countries (Kummu et al. 2010; Xue et al. 2011).

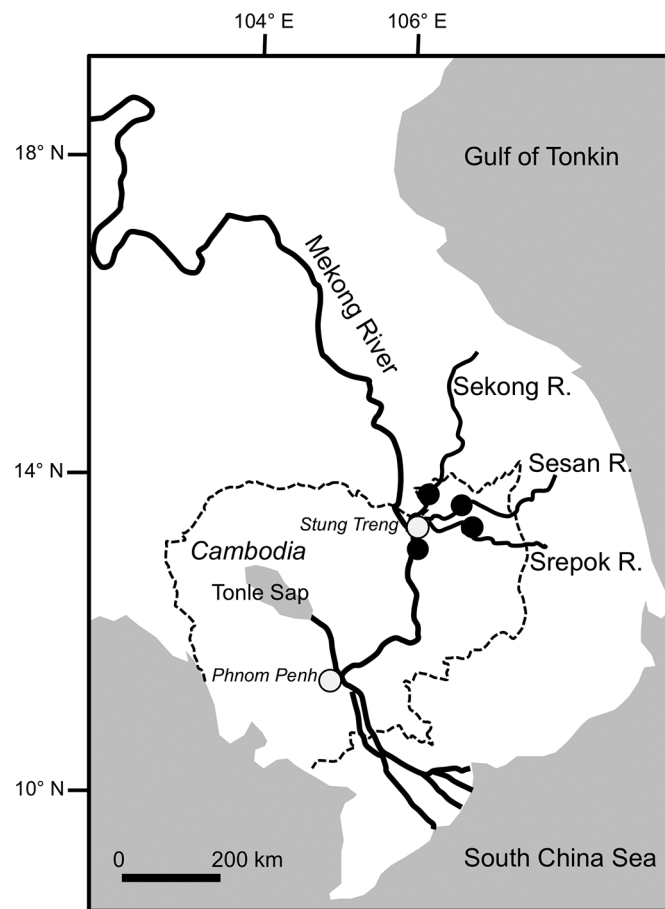
Study area

This study was conducted in four large floodplain rivers in the Lower Mekong 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. These rivers meet the Mekong River mainstem at Stung Treng, a provincial capital in Cambodia. We sampled a site on the Mekong River near Stung Treng (13.579383°N, 105.994366°E), the Sekong River at Siem Pang (14.11434°N, 106.39104°E), the Sesan River at Veurn Sai (13.94585°N, 106.79701°E), and the Srepok River at Lomphat (13.47508°N, 106.99683°E) (Fig. 1). Cambodia has a monsoon climate with a six-month dry season (November–April) and six months of rain (May–October).

Five hundred fish species have been recorded from the Mekong Basin in Cambodia (Rainboth 1996). About 40 km of the Mekong River, from the Stung Treng–Kratie provincial border to near the Cambodia–Laos border, and its riparian zone were designated as a RAMSAR Convention 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).

There currently are over a dozen hydroelectric dams in operation on the Sesan River. The largest, Yali Dam, is located upstream from our study site where there was a major waterfall in Vietnam, and blocks a formerly important fish migration route (Baran et al. 2011). A new dam, Lower Sesan 2, has been approved for construction at a downstream site in Cambodia. According to interviews with local residents, the Sesan's flow regime within our study reach is strongly regulated by upstream dams, and the lack of large migratory fishes already has affected livelihoods of local people living along the river. Compared with the Sekong and Srepok, the Sesan has lower flows and shallower water during the dry season (Baird and Meach 2005; Baran et al. 2011). The other two 3S rivers currently have dams (Sekong—4, Srepok—24), but these are smaller and located in headwaters >100 km upstream from our study sites; consequently, modifications of historic discharge patterns were not reported by local villagers. The Mekong Basin currently has 371 dams, and nearly 100 new hydroelectric dams are planned (Winemiller et al. 2016).

Fig. 1. Map showing the Lower Mekong River, Cambodia, and locations of study sites (solid black circles) on the Mekong, Sekong, Sesan, and Srepok rivers.



Sample collections and laboratory methods

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–August 2011). Interpretation of consumer assimilation of production sources depends, in part, on isotopic turnover rates in tissues. In fishes, tissue turnover is affected by several factors, including temperature, tissue type, body size, and growth rate (Vander Zanden et al. 2015). According to a literature review, isotopic half-life of fish muscle tissue averages about 25 days, with a range of 10–60 days (Boecklen et al. 2011). The nitrogen isotopic half-life in muscle tissue of an herbivorous Neotropical catfish was estimated at 18.2 days (McIntyre and Flecker 2006) and the carbon isotopic half-life in muscle of Chinese grass carp was 52.7 days (Xia et al. 2013). Because our samples were collected at least 3 months after the beginning of each designated hydrologic season, we assume that muscle tissue carbon and nitrogen ratios should largely reflect assimilation of in situ resources during the same season. Our assimilation estimates would be biased if isotopic turnover actually was much slower than previously reported, or if there were major changes in isotopic ratios of sources that occurred several days prior to collection of samples.

Attempts were made to collect the dominant (most obvious) basal production sources and fish species at each site. Whenever possible, 3–5 individuals of each taxon 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 samples (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 water was filtered through pre-combusted Whatman GF/F filters (pore size 0.7 μm) on which material was collected. 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 fishers. 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 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 (following the methods of Arrington and Winemiller 2002). Samples were analyzed for isotope ratios of carbon and nitrogen at the Analytical Chemistry Laboratory, Institute of Ecology, University of Georgia, USA. During mass spectrometry, two different standards were processed between every 12 tissue samples, and precision was $\pm 0.22\%$ for $\delta^{13}\text{C}$ and $\pm 0.20\%$ for $\delta^{15}\text{N}$.

Stable isotope analysis

We 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 (‰) standardized in relation to reference material (Pee Dee Belemnite for C, atmospheric nitrogen for N) and reported as $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$, where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$ (the ratio of heavy and light stable isotopes of carbon or nitrogen).

Using PAST statistical software (Hammer et al. 2001), two-tailed t tests were performed to test for seasonal differences in carbon and nitrogen stable isotope ratios of each major production source within each river. To account for multiple comparisons with $\alpha = 0.05$, the critical P was Bonferroni-corrected to 0.01. One-way ANOVA was performed to test for among-river differences in carbon and nitrogen stable isotope ratios of production sources during each season.

Mixing model

MixSIR (Moore and Semmens 2008) was used to estimate relative contributions of four alternative basal sources (seston, benthic algae, riparian C_3 macrophytes, and riparian C_4 grasses) to tissues of consumers. MixSIR uses a Bayesian framework that accounts for uncertainty associated with multiple sources and trophic fractionation (Woodland et al. 2012). We ran the model separately for each consumer species and for each season and site based on carbon and nitrogen isotope ratios of four major primary-production sources collected during the corresponding season and site. We did not correct consumer samples for lipids because carbon:nitrogen ratios were relatively low (mean = 3). For the model input, we used a trophic fractionation value of 2.5 for nitrogen (Vanderklift and Ponsard 2003) and 0.5 for carbon (McCutchan et al. 2003). The Bayesian model yields probability distributions of feasible solutions, and we recorded the median and 5% and 95% credible intervals for proportional contribution of each source to fish biomass.

Trophic guild and habitat guild classification

To determine whether functional groups assimilate production sources differentially, the mixing model was run again for each site and season with species grouped into guilds. Trophic guilds and habitat guilds were determined using information reported in FishBase (2012) and Rainboth (1996), as well as fish functional

Table 1. Richness and frequency (%) of species according to four trophic guilds in survey samples from four rivers during 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

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 non-trivial amounts of both animal and plant material, (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 were caught almost exclusively from the river channel and local fishers confirmed that they generally catch them in the channel and (2) *floodplain* if local fishers reported that adult size classes commonly are caught in both river and floodplain habitats or nearly exclusively in the latter.

Results

A total of 1087 individual fish and 109 primary production source samples was collected during the study. Mean sample size for fish species per site was 2.43 (range 1–12); mean sample size for production sources per site was 6.62 (range 5–8). Most of the fishes belong to the family Cyprinidae, followed by Siluridae, Bagridae, and Pangasiidae. During the dry season, 699 individual fishes and 44 basal source samples were obtained for analysis. Seventy-one species were obtained from the Mekong River near Stung Treng, 60 species from the Sekong, 31 species from the Sesan, and 56 species from the Srepok. During this season, we collected 27 (12%) detritivores, 80 (37%) insectivores, 57 (26%) omnivores, and 54 (25%) 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 reduced fishing success, and we collected 388 fish specimens and 65 basal production source samples during the wet season, mostly near the edge of the river channel. Among the 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 with 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 (13%) piscivores (Table 1).

Stable isotope signatures of basal production sources

Except for seston and benthic algae samples collected during the wet season, the four basal production sources (seston, benthic algae, C_3 macrophytes, C_4 grass) had little overlap in $\delta^{13}C$ values at each site during each season (Table 2, Fig. 2). In each of the four rivers, seston and benthic algae revealed large seasonal differences in $\delta^{13}C$ values (within-river seasonal shifts in mean $\delta^{13}C$ of seston ranged from 10.4‰ to 13.0‰; benthic algae ranged from 16.5‰ to 20.3‰), with both of these sources being significantly

heavier during the dry season (Table 2, Fig. 2; t test of seasonal mean difference yielded $P < 0.01$ in each case, $t_{[5-8]} = 5.31-19.24$). Carbon ratios of C_3 macrophytes and C_4 grass did not undergo significant seasonal shifts in any river. $\delta^{15}N$ values of sources overlapped broadly and were not significantly different within or among sites and seasons; however, C_4 grass tended to have lower values compared with other sources (Table 2, Fig. 2). Neither carbon nor nitrogen isotope ratios of any of the four sources differed significantly among the four rivers during either season (ANOVA, $P \geq 0.05$ in each case, $F_{[3,6-17]} = 0.05-3.32$).

Stable isotope signature of fishes

Overall, average carbon isotopic signatures of fishes were relatively ^{13}C depleted during the wet season compared with fishes collected during the dry season (Fig. 2). Most fishes had carbon isotopic signature values between those of benthic algae and seston (but closer to seston) during the dry season, and had carbon isotopic signature values closer to those of C_3 macrophytes during the wet season (Fig. 2). In each river and season, the distribution of fish $\delta^{15}N$ values ranged approximately 7‰, indicating nearly three trophic levels if one assumes an average trophic fractionation for $\delta^{15}N$ of about 2.5‰ (Vanderklift and Ponsard 2003).

Production source contributions

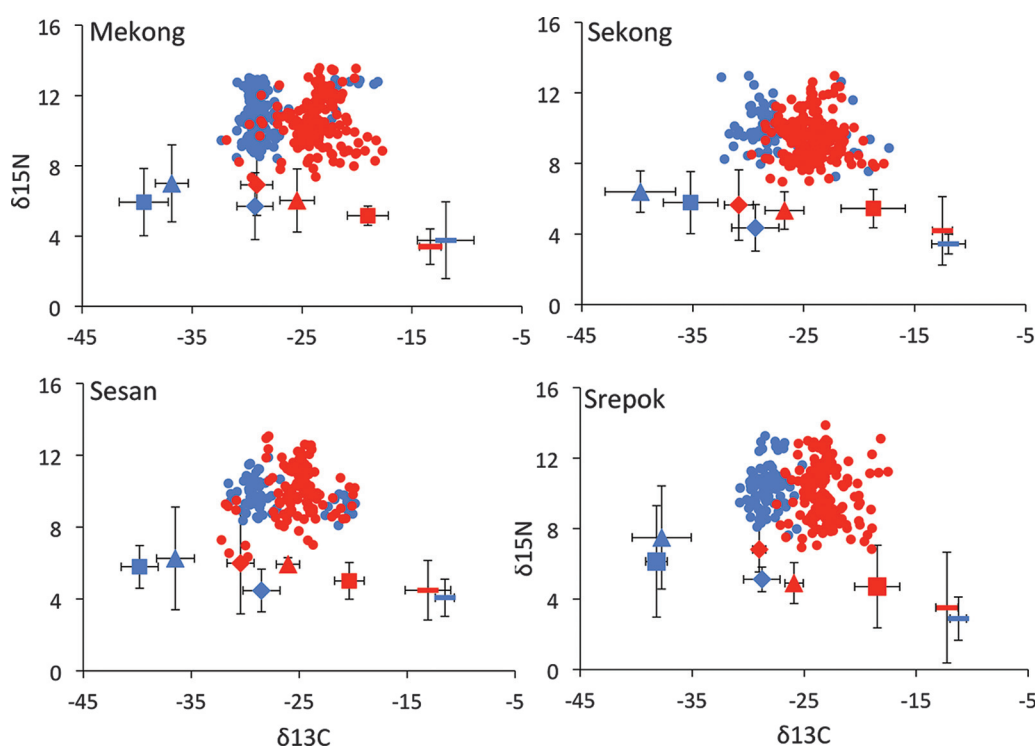
Isotopic differences between the four major primary production sources from each river during each season, especially for carbon (Table 2), facilitated discrimination of material assimilated by fishes. MixSIR estimated that seston and benthic algae were the principle sources contributing to fish biomass during the dry season (Fig. 3). Based on the 5th percentile of the probability distribution of feasible solutions, seston contributed over 10% to the biomass of more than three-fourths of the fishes across all four rivers (values were >10% for all fishes in the Sesan), and at the 95th percentile, seston contributed greater than 50% to biomass for over half of the fishes (Appendix A). During the dry season, benthic algae contributed >10% to biomass for about 40% of fishes (and nearly three-fourths of Sesan fishes) based on the 5th percentile estimate, and at the 95th percentile, the contribution of benthic algae was estimated at 31%–60% for more than half of the fishes. At the 5th percentile, the estimated contribution of riparian C_3 macrophytes to consumer biomass was <10% for about 60% of fishes (80% of Sesan fishes), and at the 95th percentile, C_3 macrophytes contributed 31%–70% to biomass of most fishes during the dry season. Riparian C_4 grass had 5th percentile estimates of <10% biomass contribution for more than 90% of fishes across all four rivers.

Model estimates for the wet season indicated that riparian C_3 macrophytes were the dominant basal production source supporting trophic pathways to fishes, and benthic algae were the least important for fishes in all four rivers (Fig. 4). At the 5th percentile, estimated contribution of benthic algae to fish biomass was <10% in all cases, and estimates for seston were <10% for over 90% of fishes (Appendix B). At the 5th percentile, riparian C_3 plants had estimated contributions to fish biomass >20% for most species in the four rivers, and at the 95th percentile, estimated contributions of C_3 plants for most fishes were >60%. During the wet season, riparian C_4 grasses contributed <10% to biomass of more than half of the fishes based on the 5th percentile estimate, and 21%–50% for most fishes based on the 95th percentile estimate.

Model estimates revealed some differences in proportional contributions of primary production sources to the four trophic guilds during the dry season, but few differences during the wet season (Appendices A and B). Benthic algae had the greatest proportional contribution to detritivore biomass during the dry season (e.g., *Gyrinocheilus pennocki*, *Mekongina erythrospila*, *Labeo chrysophekadion*), between 30% (5th percentile) and 60% (95th percentile). Estimated proportional contributions of seston and C_3 macrophytes to biomass of insectivorous fishes (e.g., *Cyclocheilichthys* and *Micronema* spp.) were large compared with estimates for benthic algae and C_4 grass. During

Table 2. Mean values (± 1 SD) of carbon and nitrogen stable isotope ratios for basal production sources from four rivers during dry and wet seasons.

Season	River	Sources							
		Seston		Benthic algae		C ₃ plants		C ₄ 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)

Fig. 2. Biplots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of primary producers and fishes from the four rivers during the dry and wet seasons. Blue symbols represents the wet season, red symbols represent the dry season, circles represent fish, squares represent benthic algae, triangles represent seston, diamonds represent C₃ macrophytes, and dashes (short horizontal lines) represent C₄ grasses.

the dry season, omnivores (e.g., several pangasiids) and piscivores (e.g., *Channa*, *Chitala*, *Wallago*) probably assimilated carbon originating from multiple sources, including 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 (Fig. 5).

Estimates of source contributions differed between fishes that are largely restricted to the river channel and fishes commonly found in floodplain habitats. C₃ plants apparently made greater contribution to biomass of fishes that inhabit floodplain habitats, with estimates ranging from 13% to 50%, compared with their estimated contributions to fishes inhabiting river channels that ranged from 1% to 44% (Appendices A and B). Although riparian C₄ grasses had low estimated contributions to fish biomass during the dry season, these plants may have contributed to biomass of certain species, especially air-breathing fishes, during the wet season and to some extent during the dry season (Appendices A and B). Fishes possessing aerial respiratory adaptations commonly inhabit floodplain pools; species in this group include clariid cat-

fishes (*Clarias batrachus*, *Clarias macrocephalus*, *Clarias melanoderma*), snakeheads (*Channa limbata*, *Channa lucius*, *Channa marulioides*, *Channa micropeltes*, *Channa striata*), and labyrinth fish (*Anabas testudineus*).

Discussion

Seasonal patterns

Carbon stable isotope signatures of benthic algae and seston in our study were much lower during the wet season compared with 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, water velocity outside the cell walls, and availability of dissolved inorganic carbon from various pools (Finlay et al. 1999; Finlay 2001, 2004). MacLeod and Barton (1998) found that enriched $\delta^{13}\text{C}$ corresponds to higher rates of photosynthesis. Carbon stable isotope ratios of algae have been shown to vary in association with climatic conditions and river discharge (Forsberg et al. 1988; Hamilton et al. 1992; Hamilton and Lewis 1992; Depetris and

Fig. 3. Frequency histograms (percentage of fishes in the sample) for the 5th (left column) and 95th (right column) percentile values for estimated percent contributions of alternative basal production sources to fish biomass in the Mekong, Sekong, Sesan, and Srepok rivers during the dry season.

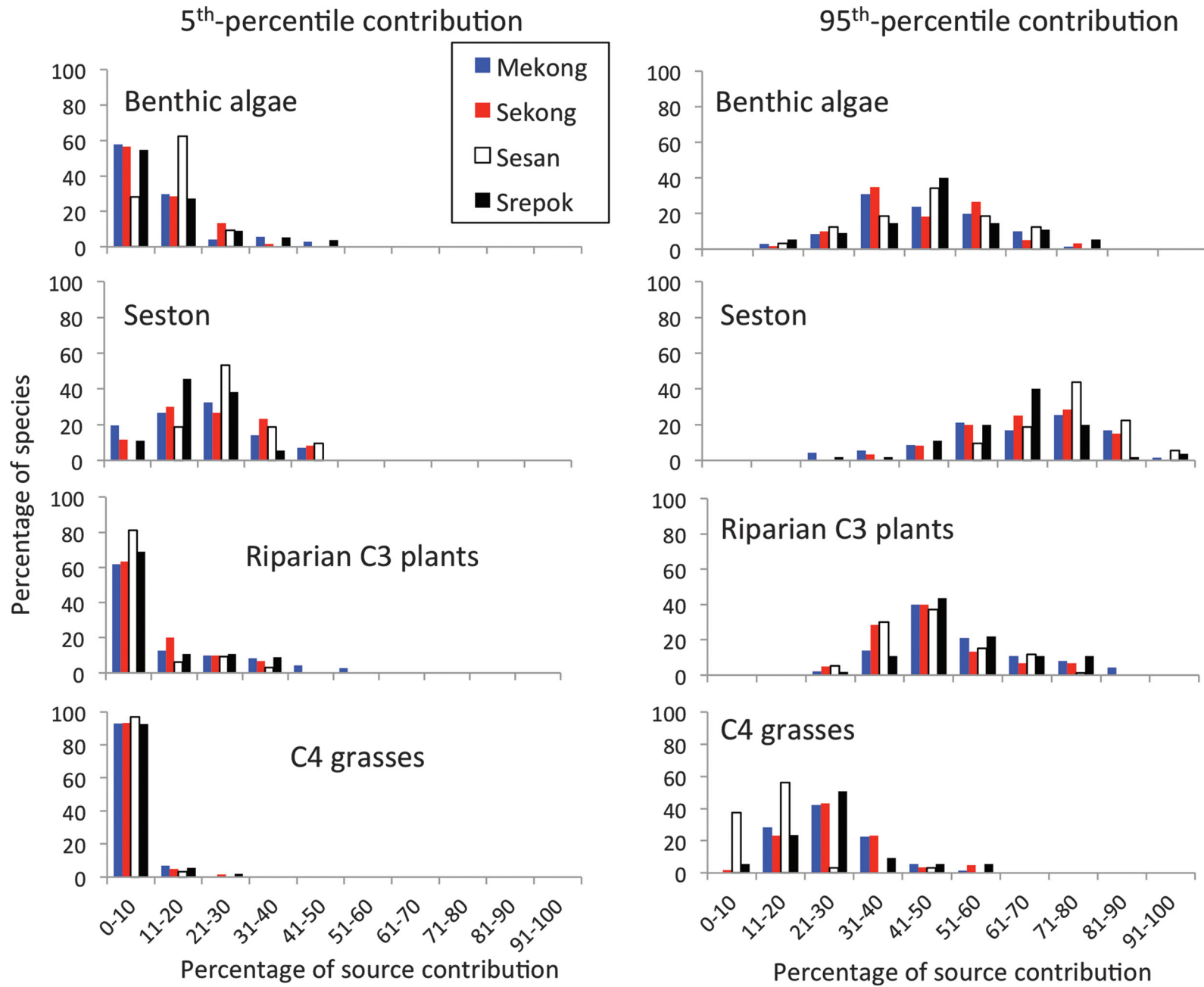


Fig. 4. Frequency histograms (percentage of fishes in the sample) for the 5th (left column) and 95th (right column) percentile values for estimated percent contributions of alternative basal production sources to fish biomass in the Mekong, Sekong, Sesan, and Srepok rivers during the wet season.

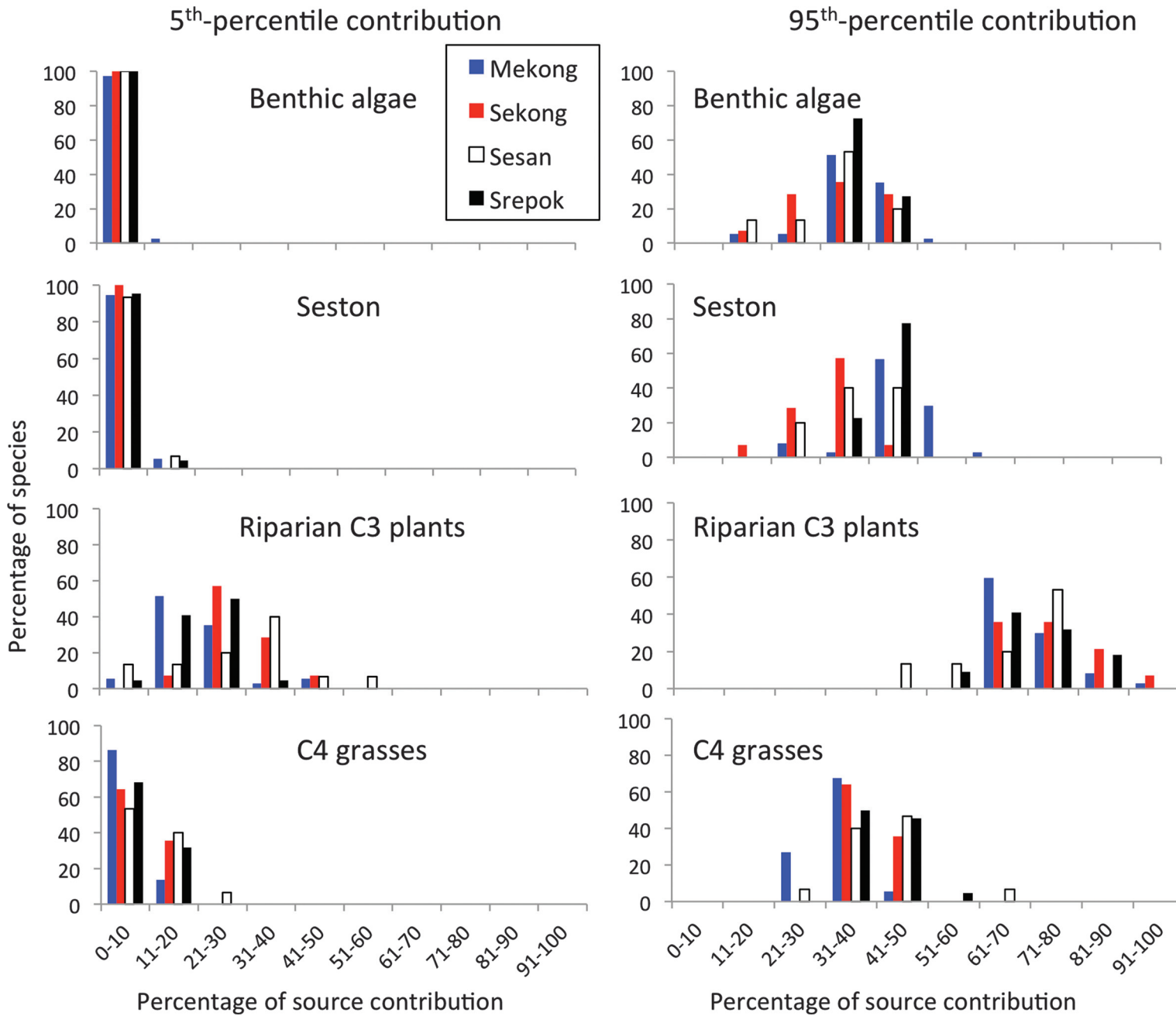
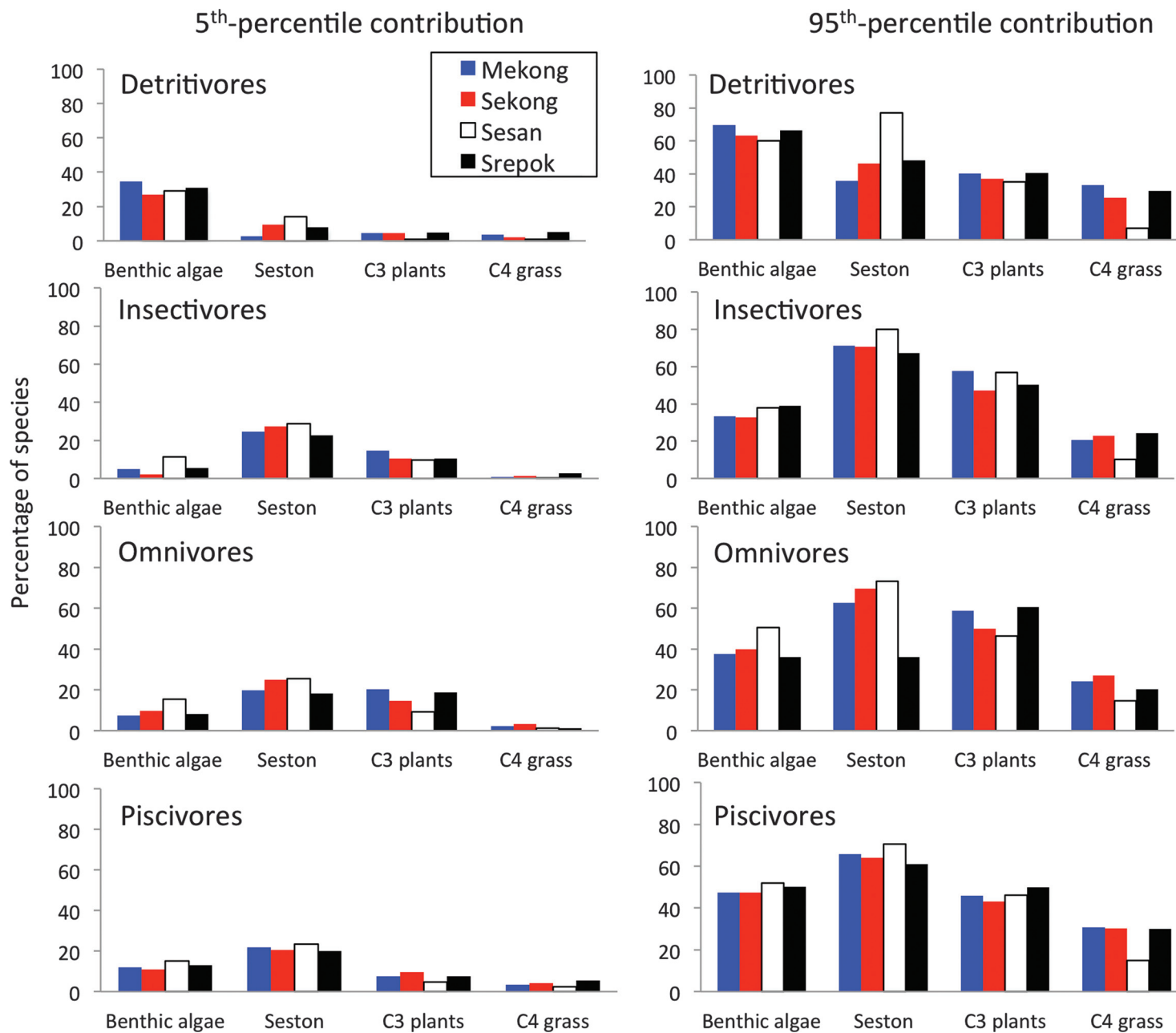


Fig. 5. Frequency histograms for the 5th (left column) and 95th (right column) percentile values for estimated percent contributions of alternative basal production sources according to fish trophic guilds during the dry season.



Kempe 1993; Hecky and Hesslein 1995). A meta-analysis of carbon stable isotope ratios of lotic periphyton indicated that water current velocity, canopy cover, and chlorophyll *a* density affect $\delta^{13}\text{C}$, with values also varying among taxonomic groups (Ishikawa et al. 2012). That study also reported large seasonal shifts of periphyton $\delta^{13}\text{C}$ in tropical lotic systems.

Our findings indicate that most fish species in each of the four Lower Mekong Basin rivers had assimilated variable mixtures of basal production sources collected from the study sites. However, 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. These differences in relative contributions of basal production sources to fish biomass probably reflect seasonal availability of alternative sources in these rivers. An investigation of seasonal variability in sources of particulate organic matter of the Lower Mekong River in Cambodia using elemental and lignin analysis (Ellis et al. 2012) found that fine particulate organic matter was dominated by autochthonous sources (derived from phytoplankton) during the dry season. During the wet season, a greater proportion of fine particulate organic matter was derived from vascular plants.

During periods of low flow in large rivers, ambient nutrient concentrations often are higher, water transparency increases, and productivity of algae increases (Kirk 1985; Montoya et al. 2006; Roach 2013). Several investigators have suggested that algae provide better nutrition and contain more digestible components compared with macrophyte tissues, much of which can be highly refractory (Sarkanen and Ludwig 1971; Renaud et al. 1999; Cotner and Biddanda 2002). Therefore, algae should enter grazer food chains 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 (e.g., Lewis 1988; Hamilton et al. 1992; Forsberg et al. 1993; Zeug and Winemiller 2008). A study in the Tonlé 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). Roach (2013) postulated that this pattern in rivers depends on soil characteristics and the degree to which flood pulses increase suspension of fine sediments that increase turbidity and reduce light penetration. Such conditions normally occur in rivers of the Lower Mekong Basin during the wet season.

In all four rivers, allochthonous production sources were estimated to be the most important sources supporting fish biomass during the wet season when flows were high and floodplains inundated. During the wet season, algal production probably declines due to scouring of substrates, suspension of fine sediments, increased turbidity, and reduced light penetration (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 seasonal availability of plant material, especially seeds and fruits, in seasonally flooded forests (Lowe-McConnell 1975; Goulding 1980; Correa et al. 2007; Correa and Winemiller 2014). 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,

several species of herbivorous fishes feed extensively on fruits, flowers, and seeds (Lowe-McConnell 1975; Goulding 1980; Correa et al. 2007; Horn et al. 2011). *Leptobarbus hoevenii*, *Mekongina erythrospila*, *Osphronemus goramy*, *Osphronemus 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).

The present study was conducted in rivers that experience extensive flooding during the wet season each year (duration ~6 months). Annual flood pulses of large tropical rivers provide fishes with access to both terrestrial and aquatic food resources in floodplains (Goulding 1980; Junk et al. 1989), and this seems to explain the high secondary productivity that supports major fisheries in these systems (Welcomme 1979; Goulding et al. 1988; Correa and Winemiller 2014). During annual flood pulses in the tropics, submerged riparian vegetation is consumed by herbivorous invertebrates and fishes that, in turn, are consumed by predatory fishes. During the flood pulse, fishes have greater access to terrestrial arthropods. Long flood duration also promotes decomposition of submerged terrestrial vegetation (Balcombe 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 C_3 plants and little from C_4 plants (Thorp et al. 1998; Zeug and Winemiller 2008; Roach et al. 2009). In our study, fishes from all four rivers appeared to assimilate little carbon from C_4 grasses compared with C_3 plants, and this was the case during both seasons. This is not surprising considering that these grasses generally have relatively low nutritional value compared with most C_3 macrophytes, and much less compared with algae. C_4 grass tissues contain compounds, such as hemicelluloses, cellulose and lignin, that are difficult for most animals to digest (Minson 1971). Nevertheless, C_4 grasses can be broken down by microbes and subsequently buried in sediments before entering the upper food web by way of organisms consuming 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 C_4 grasses by certain fishes, for example, *Schizodon fasciatus* from the Amazon River in Brazil and *Schizodon isognatus* from the Apure River in Venezuela. The present study indicates that C_4 grasses could be a 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 concluded air-breathing fishes from man-made ponds in the floodplain had assimilated variable amounts of carbon from C_4 grasses (Jackson et al. 2013).

Production sources supporting guilds

Estimates of basal production sources supporting fishes grouped according to trophic and habitat guilds revealed some general trends, especially during the dry season. Detritivores and algivores apparently had assimilated large fractions of material derived from benthic algae. Given that these fishes scrape or suck organic materials from substrates, they should have carbon stable isotope signatures that reflect values obtained for bulk samples of benthic microphytobenthos (referenced in this study as benthic algae, but perhaps also containing microorganisms and organic matter of allochthonous origin). Most fishes classified as insectivores apparently had assimilated material derived mostly from a single basal source, either seston or C_3 plants. Fishes classified

here as insectivores probably feed mostly on aquatic insect larvae, microcrustacea, and other aquatic invertebrates that consume some combination of algae and detritus derived from both autochthonous and allochthonous sources. MixSIR model estimates indicate that piscivores and omnivores likely had assimilated material from multiple basal sources, including benthic algae, seston, C_3 plants, and, to a much lesser extent, C_4 plants. These findings suggest that piscivores and omnivores assimilate material derived from diverse trophic pathways. Studies from other tropical river systems indicated that omnivory is widespread among fishes (Winemiller 1990; Polis et al. 1996), and many fishes of the Mekong have been classified as omnivores (Rainboth 1996).

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 that are largely restricted to the river channel, algae apparently made a greater contribution to fish biomass during the dry season, whereas C_3 macrophytes had relatively greater importance for fishes that typically inhabit floodplain habitats. Previous studies also found that fish inhabiting channel habitats are strongly supported by trophic pathways originating from algae (e.g., Forsberg et al. 1993; Lewis et al. 2001; Roach et al. 2009). Most channel-dwelling fishes in the Lower Mekong River show this pattern; however, a few species of loaches (e.g., *Acantopsis* and *Schistura* spp.) could have assimilated significant material originating from macrophytes. These loaches probably consume microcrustacea and other tiny aquatic invertebrates that consume detritus or 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, 2009b).

Previous research has estimated that most fishes inhabiting floodplain habitats are supported by trophic pathways originating from macrophytes as well as pathways that originate from algae (Rai and Hill 1984; Zeug and Winemiller 2008; Jackson et al. 2013). In our study, air-breathing fishes, such as *Channa* (Channidae) and *Clarias* (Clariidae) species, that often inhabit floodplain habitats, support this observation. These species apparently assimilate significant amounts of material derived from algae and macrophytes. A recent study in West Africa similarly concluded that air-breathing fishes from these families 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 thereby hindering 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 benthic algae was the principal production source supporting aquatic consumers of the Cooper Creek floodplain in central Australia. 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

Because the hydrology of the Sesan River is impacted by the Yali Dam in Vietnam, we anticipated that its fish assemblage and food web might differ from the other three rivers. Dams are barriers to longitudinal fish movement (Dugan et al. 2010), and the Mekong Basin contains many migratory species, some of which move hundreds of kilometres on a seasonal basis (Barlow et al. 2008; Baran and Myschowoda 2008). Fish species richness of our Sesan samples (32 dry, 19 wet) was much lower compared with the other rivers (55–71 dry, 31–45 wet). During the dry season, we obtained few

pangasiids (migratory fishes) in the Sesan compared with the other three rivers that are less impacted by dams. A review by Baran et al. (2011) found that the Sesan currently has far fewer migratory fishes compared with other Mekong tributaries, including the Sekong and Srepok rivers. Their study revealed that a number of migratory species, particularly those belonging to the Pangasiidae (e.g., *Pangasius conchophilus*), have declined in the Sesan (Baran et al. 2011). Similarly, Hoeinghaus et al. (2009) found that creation of 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). Proportions of species in various trophic guilds was very similar among the three relatively unimpacted rivers, but different for the Sesan (fewer detritivores and piscivores during both seasons, more insectivores during the dry season; Table 1).

By altering hydrology, dams also can affect food web ecology, including the seasonal availability of basal production sources and their contributions to fish biomass. Isotopic signatures of the four basal production sources in the Sesan were very similar to those in the other three rivers during each season. Estimates from the mixing model indicated that seston and benthic algae were the most important sources supporting food webs of all four rivers during the dry season, and estimates for the Sesan were highest. Local fishers from the village of Veurn Sai reported to us that reduced water discharge following construction of the Yali Dam had reduced substrate scouring and maintenance of deep pool habitat for fish. Reduced discharge also could have reduced sediment suspension, especially during the dry season, which might enhance algal production. A study conducted in rivers of the Paraná Basin in Brazil (Hoeinghaus et al. 2007) concluded that consumers inhabiting river reaches below impoundments are more dependent on algal production compared with reaches above the same impoundments. That study hypothesized that dams trap sediments, thereby increasing water transparency in tailwaters that allows greater light penetration and algae growth. Dams in the Lower Mekong Basin have been estimated to trap more than 50% of suspended sediment load (Kummu et al. 2010; Xue et al. 2011).

Our study also indicates that there is less contribution of C_3 macrophytes to fish biomass in the Sesan River compared with the other rivers. This might be due to a reduced annual flood pulse and more restricted access to 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 the Mekong have declined in recent years (Zalinge 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 with the other two tributary rivers.

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 they move from one landscape unit to another. They subsidize river food webs by enhancing the resource base for apex predators (Polis et al. 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.

A potential limitation of our study is that some Mekong fishes 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. 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 tissue, Buchheister and Latour 2010), our study design and interpretations should not be greatly influenced by recent arrival of migratory fishes that had assimilated sources from outside the location where they were caught. Our sampling was conducted in the middle of each season (3–4 months after the start of each season), which should have allowed 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 muscle tissue of migratory species within our data set reflected, to a large extent, assimilation of local food sources.

Our 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. Algae appear to be the most important production source supporting fish biomass during the dry season when water discharge is low and transparency is high, and riparian macrophytes are the most important production source supporting fishes during the wet season when discharge is high and water is turbid. Many studies of tropical river food webs have shown spatial rather than temporal variation, largely because they only collected samples from multiple rivers during a restricted period (e.g., Hoeinghaus et al. 2007, 2008, 2009; Roach et al. 2009; Jardine et al. 2012). Our findings stress the need 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.

Our 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. The findings emphasize the need for more evaluation of ecological impacts of hydropower development in the region (Dugan et al. 2010; Winemiller et al. 2016). The Yali Dam on the upper Sesan River has changed hydrology in the lower reaches, which, according to local fishers, has impacted river geomorphology and migratory fish stocks in the reach near Veurn Sai. The impact of dams on ecosystem functions, biodiversity, and human populations in the Lower Mekong Basin is potentially large and irreversible. Given that riparian vegetation appears to play a large role in supporting fish production in the Lower Mekong and 3S rivers, particularly during the wet season, there is an urgent need for further research of potential impacts from dams and deforestation in this region.

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Appendix A

Appendix Table A1 appears on the following pages.

Table A1. Contribution of production sources during the dry season.

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>Incisilabeo 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>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 vittatus</i>	O	C	31 (12–51)	42 (22–63)	14 (1–31)	15 (1–31)
	<i>Osteochilus melanopleurus</i>	O	C	11 (1–21)	35 (12–62)	53 (44–63)	4 (0–11)
	<i>Paralaubuca 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 stejnegeri</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 caudipunctata</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>Acantopsis</i> sp. 2	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</i> sp.	I	C	12 (1–24)	25 (1–48)	53 (33–74)	1 (0–21)
	Siluriformes						
	Sisoridae						
	<i>Bagarius suchus</i>	P	C	25 (11–43)	46 (22–71)	18 (1–42)	11 (2–21)
	Siluridae						
	<i>Belodontichthys truncatus</i>	P	C	34 (16–53)	35 (11–62)	20 (1–41)	9 (1–19)
	<i>Hemisilurus mekongensis</i>	O	C	27 (11–45)	47 (22–73)	15 (2–31)	12 (2–23)
<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 meladerma</i>	O	FP	28 (13–43)	28 (14–45)	14 (1–31)	30 (12–51)	
Ariidae							
<i>Hemiarus verrucosus</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 macronema</i>	O	C	10 (1–21)	36 (22–53)	52 (24–83)	4 (1–9)	

Table A1 (continued).

River	Consumers	TG	HG	Benthic algae	Seston	Riparian C ₃	C ₄ grasses
Sekong	Bagridae						
	<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>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						
	Mastacembelidae						
	<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)
	Pristolepidae						
	<i>Pristolepis fasciata</i>	O	FP	16 (1–33)	32 (15–52)	47 (42–54)	6 (1–12)
	Eleotridae						
	<i>Oxyeleotris marmorata</i>	I	FP	14 (1–31)	46 (32–61)	32 (21–42)	10 (1–21)
	Gobiidae						
	<i>Papuligobius 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 harmandi</i>	I	C	21 (2–41)	39 (11–72)	29 (1–61)	11 (1–22)
	Cynoglossidae						
	<i>Cynoglossus feldmanni</i>	I	C	15 (1–31)	52 (24–82)	25 (1–52)	11 (1–21)
	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 leptocheilus</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>Lobocheilus rhabdoura</i>	D	C	40 (23–61)	24 (3–45)	17 (2–33)	19 (3–36)	
<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>Oxygaster anomalura</i>	I	C	12 (1–23)	61 (42–83)	21 (2–41)	6 (0–11)	
<i>Parachela siamensis</i>	I	C	19 (2–39)	49 (32–67)	17 (2–32)	14 (3–25)	
<i>Paralabuca typus</i>	I	C	18 (2–35)	53 (33–74)	22 (6–41)	8 (1–17)	
<i>Poropuntius laeensis</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>Acantopsis</i> sp. 3	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)	

Table A1 (continued).

River	Consumers	TG	HG	Benthic algae	Seston	Riparian C ₃	C ₄ grasses
	Siluridae						
	<i>Belodontichthys truncatus</i>	P	C	16 (1–33)	52 (32–73)	23 (13–35)	11 (1–21)
	<i>Kryptopterus bicirrhis</i>	I	C	16 (2–32)	50 (30–71)	21 (2–43)	12 (2–24)
	<i>Kryptopterus geminus</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 paraschilbeides</i>	P	FP	25 (1–52)	32 (12–53)	34 (23–51)	10 (1–21)
	<i>Ompok bimaculatus</i>	P	C	32 (13–52)	36 (21–52)	15 (1–31)	22 (1–45)
	<i>Phalacrotonotus apogon</i>	P	C	34 (14–55)	44 (23–65)	16 (1–33)	7 (1–12)
	<i>Phalacrotonotus bleekeri</i>	P	FP	17 (2–33)	45 (21–72)	25 (15–38)	14 (1–31)
	<i>Wallago attu</i>	P	C	29 (14–45)	42 (14–71)	21 (14–32)	12 (2–23)
	<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>Pseudolais pleurotaenia</i>	O	C	20 (1–40)	52 (41–63)	25 (11–41)	5 (0–11)
	Bagridae						
	<i>Bagrichthys majusculus</i>	O	FP	11 (1–21)	46 (21–72)	36 (11–63)	11 (1–21)
	<i>Bagrichthys obscurus</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	P	C	23 (2–45)	48 (16–82)	16 (1–33)	14 (1–28)
	<i>Xenotodon cancala</i>						
	Synbranchiformes						
	Synbranchidae						
	<i>Ophisternon bengalense</i>	P	FP	25 (11–43)	32 (13–54)	15 (1–32)	32 (24–41)
	Mastacembelidae						
	<i>Macrornathus 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)
	Perciformes						
	Ambassidae						
	<i>Parambassis siamensis</i>	I	FP	16 (1–32)	57 (41–74)	23 (12–41)	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 gachua</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)
Sesan	Osteoglossiformes						
	Notopteridae						
	<i>Notopterus notopterus</i>	I	C	36 (16–57)	52 (35–68)	11 (1–22)	3 (0–5)
	Cypriniformes						
	Cyprinidae						
	<i>Barbonymus gonionotus</i>	O	C	35 (16–53)	45 (28–64)	16 (1–34)	6 (1–12)
	<i>Barbonymus schwanefeldii</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 leptocheilus</i>	D	C	41 (22–60)	38 (14–63)	17 (1–32)	5 (0–9)
	<i>Osteochilus schlegelii</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 paviana</i>	I	C	34 (12–57)	54 (34–75)	10 (1–21)	4 (0–7)
	<i>Rasbora</i> sp. 1	I	C	16 (1–33)	73 (52–96)	11 (1–23)	3 (0–6)
	<i>Rasbora</i> sp. 2	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>Acantopsis</i> sp. 1	I	C	16 (1–32)	64 (46–79)	16 (2–32)	6 (1–11)

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Table A1 (continued).

River	Consumers	TG	HG	Benthic algae	Seston	Riparian C ₃	C ₄ grasses
	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>Macragnathus siamensis</i>	I	FP	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)
	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>Trichopodus trichopterus</i>	I	FP	6 (1–12)	59 (46–73)	35 (27–44)	4 (0–10)
	Channidae						
	<i>Channa gachua</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>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>Labeo chrysophekadion</i>	D	C	48 (32–65)	28 (13–44)	16 (1–33)	12 (1–23)
	<i>Labiobarbus leptocheilus</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>Lobocheilus melanotaenia</i>	D	C	57 (43–72)	10 (1–21)	21 (1–42)	12 (1–22)
	<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 paviana</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>Acantopsis cf. gracilentus</i>	I	C	11 (1–21)	36 (23–51)	50 (43–57)	5 (0–11)
	Siluriformes						
	Sisoridae						
	<i>Bagarius bagarius</i>	I	C	17 (3–32)	44 (25–63)	22 (1–44)	12 (1–24)
	<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>Micronema moorei</i>	P	C	26 (11–44)	43 (23–64)	23 (1–45)	10 (1–20)
	<i>Ompok bimaculatus</i>	P	C	32 (14–52)	42 (25–61)	17 (3–44)	12 (2–24)
	<i>Phalacronotus apogon</i>	P	C	34 (15–57)	41 (13–72)	21 (1–41)	6 (0–11)
	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>Pseudolais pleurotaenia</i>	O	C	22 (3–42)	28 (14–42)	42 (32–52)	9 (1–18)

Table A1 (concluded).

River	Consumers	TG	HG	Benthic algae	Seston	Riparian C ₃	C ₄ grasses
	Bagridae						
	<i>Bagrichthys majusculus</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)
	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 gachua</i>	P	FP	26 (12–44)	34 (21–52)	15 (1–32)	26 (13–42)
	<i>Channa marulioides</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)

Note: Values are the medians and 5th–95th percentile ranges (in parentheses) of estimated percent contributions of production sources to fish biomass in the Mekong, Sekong, Sesan, and Srepok rivers during the dry season. TG, trophic guilds (D, detritivores; I, insectivores; O, omnivores; P, piscivores); HG, habitat guilds (C, channel; FP, floodplain).

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Appendix B

Table B1. Contribution of production sources during the wet season.

River	Consumers	TG	HG	Benthic algae	Seston	Riparian C ₃	C ₄ 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>Temualosa 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 gonionotus</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>Labeo chrysophekadion</i>	D	C	7 (0–15)	11 (1–22)	65 (48–82)	17 (1–33)
	<i>Labiobarbus siamensis</i>	D	C	18 (2–33)	20 (2–41)	47 (24–72)	15 (8–25)
	<i>Macrochirichthys macrochirus</i>	P	C	21 (1–41)	21 (1–42)	37 (13–62)	20 (6–35)
	<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						
	Sisoridae						
	<i>Bagarius bagarius</i>	P	C	18 (2–34)	26 (2–50)	41 (16–67)	16 (2–31)
	Siluridae						
	<i>Hemisilurus mekongensis</i>	P	C	19 (1–41)	24 (0–51)	42 (14–71)	16 (2–31)
	<i>Micronema cheveyi</i>	I	C	19 (4–35)	23 (4–43)	41 (21–62)	16 (5–27)
	<i>Phalacrotonotus apogon</i>	I	C	15 (2–31)	22 (3–42)	43 (22–64)	17 (3–32)
	<i>Phalacrotonotus bleekeri</i>	O	FP	19 (2–35)	19 (2–41)	46 (21–72)	18 (4–33)
	<i>Wallago attu</i>	P	C	10 (1–21)	14 (1–28)	66 (41–92)	10 (0–22)
	Clariidae						
	<i>Clarias batrachus</i>	O	FP	19 (2–35)	19 (6–34)	32 (4–61)	29 (14–45)
	Bagridae						
	<i>Bagrichthys majusculus</i>	O	FP	21 (2–41)	23 (4–45)	41 (22–63)	16 (2–31)
	<i>Bagrichthys obcurus</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 wyckiooides</i>	P	C	19 (2–35)	25 (4–26)	44 (23–65)	12 (1–23)
	<i>Mystus singaringan</i>	I	C	18 (1–38)	21 (2–42)	46 (21–72)	16 (2–31)
	Synbranchiformes						
	Mastacembelidae						
	<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)	
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)	
Pleuronectiformes							
Soleidae							
<i>Brachirus harmandi</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)

Table B1 (continued).

River	Consumers	TG	HG	Benthic algae	Seston	Riparian C ₃	C ₄ grasses
	Cypriniformes						
	Cyprinidae						
	<i>Barbonymus altus</i>	O	C	11 (1–23)	18 (6–31)	52 (34–72)	20 (7–34)
	<i>Barbonymus gonionotus</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>Henicorhynchus siamensis</i>	D	C	20 (1–41)	17 (2–33)	47 (24–73)	15 (0–31)
	<i>Hypsibarbus pierrri</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 paviana</i>	I	FP	22 (2–43)	17 (2–33)	47 (22–73)	16 (0–31)
	Siluriformes						
	Sisoridae						
	<i>Wallago attu</i>	P	C	11 (2–21)	13 (4–23)	52 (38–67)	24 (2–47)
	Siluridae						
	<i>Micronema cheveyi</i>	I	C	16 (1–32)	16 (0–33)	53 (22–84)	16 (1–32)
	<i>Phalacrotonotus apogon</i>	I	C	20 (1–41)	16 (1–32)	48 (23–74)	17 (3–32)
	Clariidae						
	<i>Clarias batrachus</i>	O	FP	10 (1–21)	10 (0–21)	57 (42–74)	26 (12–41)
	Pangasiidae						
	<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>Pseudolais pleurotaenia</i>	O	C	20 (1–42)	26 (5–48)	36 (11–61)	20 (0–41)
	Bagridae						
	<i>Bagrichthys majusculus</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 wyckioides</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						
	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 proctozysron</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)
	Clariidae						
	<i>Clarias batrachus</i>	O	FP	17 (1–33)	18 (2–35)	37 (14–62)	27 (11–43)
	Pangasiidae						
	<i>Pseudolais pleurotaenia</i>	O	FP	13 (1–31)	16 (2–37)	50 (32–72)	21 (3–34)
	Bagridae						
	<i>Bagrichthys majusculus</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>Macroglyphus siamensis</i>	I	FP	10 (1–21)	9 (0–20)	61 (51–73)	25 (12–43)
	<i>Mastacembelus armatus</i>	I	C	17 (2–34)	20 (1–41)	30 (8–54)	33 (24–42)

Table B1 (concluded).

River	Consumers	TG	HG	Benthic algae	Seston	Riparian C ₃	C ₄ grasses
	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 gonionotus</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>Cyclocheilichthys 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>Hemicorhynchus 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>Mystacoleucus atridorsalis</i>	I	FP	17 (1–33)	15 (0–31)	35 (14–57)	34 (23–46)
	<i>Puntioplites falcifer</i>	O	C	16 (1–32)	27 (12–43)	41 (12–71)	20 (0–41)
	<i>Rasbora paviana</i>	I	C	21 (1–42)	15 (1–32)	29 (6–53)	33 (15–52)
	Siluriformes						
	Siluridae						
	<i>Micronema cheveyi</i>	I	C	21 (2–41)	17 (0–33)	49 (24–75)	15 (0–31)
	<i>Phalacronotus apogon</i>	I	C	16 (2–31)	20 (1–41)	50 (21–82)	15 (0–31)
	<i>Wallago attu</i>	P	C	17 (1–33)	18 (2–34)	34 (16–54)	31 (11–53)
	Clariidae						
	<i>Clarias batrachus</i>	O	FP	18 (2–34)	21 (1–22)	36 (12–63)	28 (12–44)
	Pangasiidae						
	<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>Pangasuis pleurotaenia</i>	O	C	15 (1–32)	21 (1–42)	51 (23–82)	15 (0–32)
	<i>Pangasuis larnaudii</i>	O	C	21 (1–42)	15 (1–32)	46 (23–71)	20 (0–42)
	Bagridae						
	<i>Bagrichthys majusculus</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 wyckioides</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>Macrornathus siamensis</i>	I	FP	16 (2–33)	17 (1–34)	51 (22–81)	15 (0–32)
	<i>Mastacembelus armatus</i>	I	C	15 (1–32)	20 (0–41)	50 (21–82)	15 (0–31)
	Perciformes						
	Channidae						
	<i>Channa striata</i>	P	FP	17 (1–33)	18 (0–35)	34 (13–57)	32 (23–42)

Note: Values are the medians 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 wet season. TG, trophic guilds (D, detritivores; I, insectivores; O, omnivores; P, piscivores); HG, habitat guilds (C, channel; FP, floodplain).