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Dominance of autochthonous trophic base in northeast Asian stream food webs pre- and post-monsoon

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ABSTRACT

Spatial and temporal variability in the trophic base of food webs is an inevitable ecological attribute in aquatic ecosystems with the role of aquatic and terrestrial sources varying from system to system. Despite high algal biomass, an apparent increase in terrestrial detritus during the East Asian summer monsoon would be expected to alter the dominant food web base from the pre- to post-monsoon period. The δ^{13}C and δ^{15}N values of common aquatic invertebrates and fish were compared with those of their potential sources of organic matter across the upstream channel and lacustrine habitats during the pre- and post-monsoon periods in the Se-oak Stream system of Korea. The purpose was to identify the variability in trophic structure (niche and diversity) at the community level and to quantify the contribution of terrestrial and aquatic carbon sources to the food web base. The δ^{13}C and δ^{15}N values of the major potential organic matter sources differentiated allochthonous leaf litter and riparian vegetation from autochthonous biofilm and seston, but with no significant spatial and temporal changes. The δ^{13}C values of consumers fell within a narrower range than that of organic matter sources, consistent with the instream biofilm and seston values. However, the consumer δ^{15}N values spanned a broad range, increasing from invertebrates to fish. The resultant niche overlaps of consumers in the isotopic niche space between seasons and locations, their narrower horizontal niche breadths compared to organic matter sources, and the isotope mixing-model estimates indicated that aquatic production was the primary source of organic matter supporting the aquatic food webs. Overall, the results revealed a consistent dominance of autochthonous trophic bases in both lotic and lentic food webs before and after the summer monsoon. Our findings, which highlight the trophic importance of aquatic algal production facilitated by anthropogenic nutrients in this shallow, low-turbidity, and well-illuminated stream food web, may provide insight into ecosystem processes that counteract potential terrestrial-aquatic links to influence food web dynamics based on natural nutrient sources in deep, highly turbid, or shaded stream counterparts.

1. Introduction

Assessing the trophic base of food webs may be a fundamental challenge in understanding ecosystem dynamics, function, and stability because basal resources can serve as a major descriptor of the organisation of populations, communities, and thus the web architecture (Price, 1992). Spatial and temporal variability in food web pathways is an inevitable ecological attribute of aquatic ecosystems (Kitching, 1987; Warren, 1989; Winemiller, 1996). In lotic ecosystems, longitudinal changes in abiotic factors (including surficial geology, land use, hydrologic regime, and regional climate) constrain the structural and dynamic organisation of local habitat features, which in turn drive biological organisation (Meyer et al., 1988; Poff et al., 2006; Poole, 2010). Likewise, seasonal variation in habitat characteristics, resource availability, and community patterns in association with succession and life history strategies can facilitate food web dynamics in streams (Huryn et al., 2001; Winemiller, 1996; Yang et al., 2008). While our understanding of trophic pathways of organic matter supporting aquatic food webs has been advancing, system-to-system differences in trophic bases reveal the necessity for further regionally specific case studies related to climate variability, geomorphology, hydrology, and land use in geographic regions (Hall et al., 2000; Wang et al., 2014; Zeug and

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Winemiller, 2008).

The Korean Peninsula experiences the East Asian monsoon with heavy rainfall (nearly 70 % of the annual precipitation) in midsummer (late June to July) and a long dry season that precedes the monsoon rains (Kang et al., 2010; Yoo et al., 2021). River water levels are precipitously elevated during the episodic floods that can occur during the short monsoon period. The Geum River is one of the largest rivers in Korea, with a drainage basin of 9,810 km^2 and a length of 396 km (Kang et al., 2010). As with other major rivers in Korea, a multipurpose dam (Daecheong Reservoir) was constructed in the middle reach of the river to mitigate seasonal water instability (Yoo et al., 2021). Since damming of the river (surface area of 72.8 km^2) in 1980, the upstream channel of the river has been divided into a lotic ecosystem, which is connected to forested and agricultural watersheds, and a deep (mean water depth of 21 m) and stagnant lentic system, which induces a dramatic increase in the standing crop of phytoplankton (Mamun et al., 2020; Park et al., 2016; Shin et al., 1999, 2003). A large quantity of terrestrial organic matter is transported from the catchment area to the upstream area and the reservoir through tributaries, generating a seasonal pulse due to the extreme monsoonal flow (Park and Ock, 2017; Jin et al., 2020). In contrast, instream production of phytoplankton and algal biofilms constitutes the greatest source of organic matter during the dry season (Kim et al., 2000; Kang et al., 2019). The seasonal patterns in sources and fluxes of organic matter are known. However, knowledge of dominant carbon sources that support the stream and lacustrine food webs is necessary to further understand effects of the summer monsoon on the spatial and temporal variability in their trophic structures. This void is largely due to a lack of comprehensive food web research across different local abiotic and biotic features, as well as methodological limitations encompassing multi-trophic organisms.

The utility of stable isotope (SI) measurements of organisms and potential sources of organic matter to evaluate prey-predator interactions and food web structures has been established in aquatic ecosystems (Layman et al., 2012). Carbon isotope ratio ($\delta^{13}C$) values allow for the identification of original sources of carbon actually assimilated by fauna because source $\delta^{13}C$ values are conserved with little change through trophic transfers (DeNiro and Epstein, 1978; Peterson and Fry, 1987). In contrast, nitrogen isotope ratio ($\delta^{15}N$) values provide a proxy for consumer trophic positions because of a stepwise enrichment along trophic transfers (DeNiro and Epstein, 1981; Minagawa and Wada, 1984; Post, 2002). Accordingly, stable isotope-based metrics have been developed to characterise trophic structures (niche and diversity) at the individual, population, and community levels (Cucherousset and Villéger, 2015; Layman et al., 2007). A number of isotope mixing models have also been applied to identify the proportional contribution of food resources to consumer diets (Layman et al., 2012).

Since terrestrial and aquatic primary producers are isotopically distinct, SI analysis has been successfully used to differentiate trophic pathways of allochthonous and autochthonous carbon for aquatic consumers, exemplifying conceptual models of energy flow processes in river systems. Based on the data compiled from temperate and Arctic rivers, an increasing trend in the $\delta^{13}C$ values of consumers from headwater streams to main channels can reveal the transition in the relative importance of terrestrial and algal carbon sources to downstream consumers (Finlay, 2001), corroborating the river continuum concept (Vannote et al. 1980). Several lines of evidence are compatible with the riverine productivity model (Thorp and Delong, 1994). Close relationships between consumer and algae $\delta^{13}C$ values have been highlighted by the dominant contribution of algal diets in an arid zone floodplain river of Australia (Bunn et al., 2003) and a glacial stream of the Swiss Alps (Zah et al., 2001), and by the flume experiment (Kühmayer et al., 2020). In contrast, isotope mixing-model estimates demonstrated that terrestrial plants are the primary carbon sources supporting consumers in the main channels of the Brazos River, Texas (Zeug and Winemiller, 2008) and the middle Yangtze River (Wang et al., 2014), emphasising the flood pulse concept (Junk et al., 1989). Furthermore, an increase in $\delta^{13}C$ values for consumers from summer to autumn reflected the seasonally increasing availability of biofilm over terrestrial carbon in a grassland river of New Zealand (Huryn et al., 2001) and an Australian tropical river (Beesley et al., 2020), supporting the resource pulse concept (Yang et al., 2008).

We examined the $\delta^{13}C$ and $\delta^{15}N$ values of invertebrates and fish across the upstream channel and lacustrine habitats of the Daecheong Reservoir during the pre- and post-monsoon periods in summer, comparing with the corresponding SI values of terrestrial leaf litter, riparian vegetation, and instream biofilm and phytoplankton. We aimed to quantify the contribution of terrestrial and aquatic carbon sources to the food web base according to stream position subjected to different hydrologic regimes and to improve our knowledge of the potential impacts of the summer monsoon on food web variabilities in lotic and lentic ecosystems. Based on different levels of physical connectivity between the stream and its catchment, we expected that the contribution of allochthonous sources (leaf litter and riparian vegetation) to the basal carbon pools of food webs would decrease towards downstream reaches; conversely, the contribution of autochthonous sources (algal biofilm and phytoplankton) would increase. Assuming a dramatic flow pulse and increased headwater stream-catchment connectivity during the summer monsoon, we also hypothesised that the dominance of instream versus terrestrial sources in the trophic base of food webs would alternate between the pre- and post-monsoon periods. We tested spatial and temporal shifts in stream food web structures by SI analyses of organic matter sources assimilated by consumers, trophic niches at the community level, and the proportional contribution of each source to consumer nutrition.

2. Materials and methods

2.1. Study sites

The study was conducted in the So-oak Stream system, which constitutes a 29-km-long tributary and joins the Daecheong Reservoir through the confluence of the Sohwa and Kumgu Streams in the upper reach of the Geum River in the middle part of Korea (Fig. 1). Its watershed area (537 km^2) contains narrow intermontane plains of forested canopy and agricultural land in the upper reach, and broader flat plains of agricultural land and urban areas in the middle reach. The bedrock of this area is primarily schist. The stream system is confined by banks and has a limited connection with the watershed area. The substratum of the stream channel consists of boulders and pebbles covered by thick biofilms (Shin et al., 2003). The riparian littoral zone is well developed along the channels, which is covered by highly dense vegetation and intermittently inundated by heavy rainfall. Annual mean discharge at the middle reach of the stream (Site M1) is 1.8 m^3/s (GRFCO, 2019). Mean daily discharge as a representative base flow ranges from 0.4 to 4.7 m^3/s between January and May. Extremely high flows occur during the summer monsoon (late June to July) because of increasing discharge by heavy rains, ranging from 0.2 to 27.8 m^3/s (Fig. S1). Nutritional conditions of the stream water are influenced largely by high loading of nutrients from paddy fields during the monsoon in the upper reach and an influx of treated wastewater (1.9×10^4 m^3/d) in the middle reach, varying from eutrophic (0.6–21.3 $\mu g\ L^{-1}$ in chlorophyll *a* concentration) in the lotic zone to hypertrophic (13.1–1692.2 $\mu g\ L^{-1}$) in the lentic reservoir (Shin et al., 2003).

We selected three locations in the upper (U1, U2) and middle (M1, M2) reaches along the main channel and the reservoir (R1, R2); there were two sampling sites for each location (Fig. 1). The uppermost sites U1 and U2 (88 m above sea level, m a.s.L.) are approximately 21 km and 17 km above reservoir R1, respectively (Table 1). These upper-reach sites are located approximately 200 m from mountain forests and are positioned between agricultural land areas. The 20–50 m wide riparian zone on both sides of the water flow is almost covered by dense plant

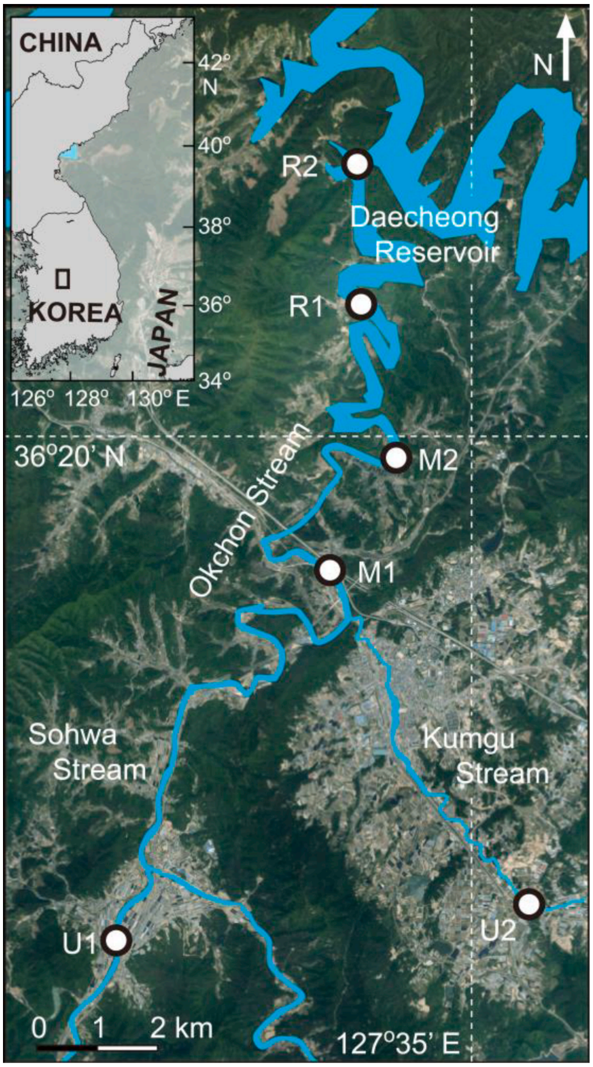

Fig. 1. Map showing the location of Daecheong Reservoir and its tributaries (small panel), and the sampling sites of So-oak Stream. U1 and U2, the upper reach of the stream; M1 and M2, the middle reach of the stream; R1 and R2, the lacustrine reservoir.

populations of *Persicaria thunbergii*, *Carex forficula*, and *Salix gracilistyla*. Bedload transport is lacking, even during the summer monsoon season. Sites M1 and M2 (80.5 m a.s.l.) of the middle reach are located approximately 13 km and 8 km upstream from reservoir R1, respectively. At these sites, the stream channel flows through a steep valley, and the nutritional status of the water is greatly influenced by urban wastewater and agricultural land discharge (Shin et al., 1999, 2003; Park et al., 2016). The riparian vegetation consists of dense grasses and weeds, especially *Persicaria thunbergii*, *Amaranthus lividus*, and *Carex forficula*. Sites R1 and R2 (≤80 m a.s.l.) are located in the persistently stagnant lentic reservoir. These sites were chosen to provide a comparison with lotic food webs.

2.2. Topographic and hydrologic features

Considering that stable isotope values in consumer tissues reflect time-integrated assimilation for feeding history over days to months, sampling was conducted on 17–18 May (deemed spring hereafter) and 27–28 August (deemed summer hereafter) 2019 to obtain trophic information of consumers during the pre-monsoon and monsoon periods, respectively. The stream stage recorded at site M1 indicated that while the spring sampling timeframe corresponded to the low base-flow period, the summer sampling timeframe reflected a prolonged period of high discharge following frequent monsoonal rains (Fig. S1). It was presumed that such a seasonal variation in water flows would modulate terrestrial inputs to the stream, creating pulses of terrestrial and riparian detritus during the summer monsoon.

Table 1
Topographic and hydrologic features of the study sites in the So-oak Stream and the Daecheong Reservoir.

	Upper reach	Middle reach	Reservoir
Altitude (m above sea level)	88	76–81	74–76
Distance from the forest (m)	200	0–230	0
Mean stream/reservoir stage (m)	0.2	0.2–0.4	5–14
Bankfull width (m)	19–68	78–126	200
Riparian width/Bankfull width (%)	45–62	0–72	—
Riparian vegetation coverage (%)	100	100	—
Mean daily discharge (m^3 s^{-1})	0.2–0.4	0.5–0.6	—
Water			
Water temperature (°C)	15.7–25.2	17.5–28.4	23.1–30.2
Turbidity (NTU)	2.7–6.3	5.8–12.7	18.7–112.3
Chlorophyll *a* (μg l^{-1})	1.14–4.91	4.38–11.24	9.28–46.61
Suspended particulate matter (mg l^{-1})	4.24–10.43	6.08–14.65	18.21–28.67
Particulate organic carbon (mg l^{-1})	0.24–0.56	0.46–0.84	0.57–1.86
Particulate nitrogen (mg l^{-1})	0.05–0.13	0.13–0.19	0.11–0.46
C:N (molar ratio)	5.0–6.1	4.1–6.4	4.7–6.0
Biofilms			
Chlorophyll *a* (mg m^{-2})	23.7–87.3	47.5–86.6	—
Ash-free dry matter (g m^{-2})	8.4–28.5	16.7–51.4	—
Particulate organic carbon (mg m^{-2})	11.5–41.6	27.5–46.3	—
Particulate nitrogen (mg m^{-2})	1.7–6.0	4.7–8.3	—
C:N (molar ratio)	6.2–8.1	5.9–7.7	

The altitude of each site was estimated using a 1:50000 topographic map. The distance from the forest, bankfull width, and riparian width were averaged from five to eight measurements in the field. Riparian vegetation cover was observed by eye at three randomly selected transects. The height of the water surface at the stream reaches was estimated by five to ten measurements depending on the active channel width using a Philadelphia rod, allowing for measurements of the cross-section of the inner berm where water flows. Data for the mean daily reservoir stage were obtained from the GRFCO (2019). The speed at which the water flowed was measured using a flow meter (Electronic Flow Meter, General Oceanics Inc., Miami, FL, USA). Then, the stream discharge rate at each site was calculated by multiplying the cross-sectional area by the water speed. Water temperature and turbidity were measured using a YSI ProDSS Water Quality Meter (Yellow Springs, OH, USA).

2.3. Sample collection

Organic matter sources were categorised into six types and collected from the stream channel, the nearest riparian zone, and the forested canopy. From the instream autochthonous sources, the biofilm contained a mixture of small autotrophic and heterotrophic components, and non-living detritus. In the channel of each stream site, five small rocks (diameter, 10–15 cm) with visible mats of biofilm were randomly collected. Biofilm was collected by gently scraping the rock surface using a toothbrush, washing with distilled water, and storing the liquid in acid-washed polypropylene bottles. The rock surface area exposed to ambient water was estimated for subsequent quantification measurements. For measurements of seston components (including phytoplankton and suspended particulate organic matter), water samples were collected below the water surface at each site using a 20-L Van Dorn water sampler and immediately pre-filtered through a 180 μm

Nitex nylon mesh screen to remove zooplankton and any large particles. All pre-filtered water samples were filtered again in the adjacent wet laboratory under gentle vacuum (150–200 mmHg). For $\delta^{13}C$ and $\delta^{15}N$ determinations, approximately 10 L of water was filtered through Whatman GF/F filters (ϕ 25 mm; pore size, 0.7 μm). For quantification of seston and chlorophyll *a* contents, 1 L of water per analysis was filtered through precombusted (450 °C, 2 h) Whatman GF/F filters (ϕ 47 mm; pore size, 0.7 μm). For particulate organic carbon (POC) and particulate nitrogen (PN) determinations, 0.5 L of water was filtered through Whatman GF/F filters (ϕ 25 mm; pore size, 0.7 μm). The filters were then folded, wrapped in aluminium foil, and stored on ice. Aquatic macrophytes (*Potamogeton malaianus* and *Potamogeton oxyphyllus*) were collected by cutting the leaves, and filamentous algae were collected when available using a stainless steel knife. For the allochthonous sources, dominant riparian vegetation samples (20 cm × 20 cm) were acquired at each site of the stream reaches by cutting the plants with a pair of scissors. Terrestrial leaf litter was randomly collected by hand from the nearest forested canopy of the upper reach.

For consumers, zooplankton were sampled at each site using a plankton cast net (frame diameter, 20 cm; mesh size, 100 μm). Invertebrates were sampled (as many genera as possible) at each site of the stream reaches by repetitive kick sampling (dip net; mesh size, 250 μm) and by hand from the bedrock surface, under stones, and in stone crevices. Fish were sampled using a hand-thrown cast net (1.2 m radius; mesh size, 4 mm) and a kick net handled with bamboo bars (110 cm × 140 cm; mesh size, 4 mm) at the stream sites, and a fyke net (3.5 m long; codend mesh size, 15 mm) at the reservoir sites. All collected samples were transported to the laboratory on ice.

2.4. Environmental variable analyses

After extraction with 90 % acetone for 24 h in the dark at − 20 °C, chlorophyll *a* concentrations in water and biofilms were analysed using a fluorometer (Turner Designs, Sunnyvale, CA, USA) following the procedure of Holm-Hansen et al. (1965). The preweighed filters containing seston were oven dried at 60 °C for 72 h and reweighed after cooling to room temperature in a vacuum desiccator. The concentration of seston was determined by the mass difference of the filters before and after filtration. The ash-free dry mass of the biofilms was determined by the mass difference before and after combustion at 450 °C for 4 h. The samples for POC and PN measurements were processed by fuming with HCl overnight to remove carbonates and drying at 60 °C for 72 h in a drying oven. The filters containing seston and biofilm samples were wrapped in tin plates and cups, respectively. The POC and PN concentrations were determined using an elemental analyser (Vario Micro Cube, Elementar, Hanau, Germany).

2.5. Sample processing and analysis for stable isotopes

Immediately after transportation to the laboratory, floral and faunal specimens were identified to the lowest taxonomic level possible. The samples were first rinsed with Milli-Q water. Only the flesh tissue of invertebrate consumers was prepared by dissection after extracting their viscera. The fish were dissected, and only white muscle tissues were collected. All prepared samples were lyophilised and pulverised to a fine powder with a mortar and pestle. The resulting dry powder was divided into subsamples for $\delta^{13}C$ and $\delta^{15}N$ determinations. For $\delta^{13}C$ determination of zooplankton and fish, defatting was conducted in a mixed (2:1) solution of methanol and chloroform (Bligh and Dyer, 1959) to eliminate lipids that may be more ^{13}C-depleted than other biochemical compounds (proteins and carbohydrates) (Gannes et al., 1997). All the samples for $\delta^{13}C$ analysis were treated with 1 N HCl to remove inorganic carbonates and were dried again. Zooplankton samples were pooled for each site and sampling date to provide sufficient material for isotope measurements. For the other invertebrate and fish consumers, a minimum of duplicates, each of which included one individual, were analysed to reduce pseudo-replication. All samples were analysed twice before (for $\delta^{15}N$) and after (for $\delta^{13}C$) acidification, the former to avoid the effect of acid treatment on $\delta^{15}N$ values (Bunn et al., 1995).

Prior to SI determination, the powdered and homogenized samples (ca. 1.5 mg dry weight) were wrapped in tin cups and introduced into an elemental analyser (Vario Micro Cube, Elementar) to oxidize at a high temperature (1030 °C). For filters containing seston, the samples were wrapped in tin plates. The $\delta^{13}C$ and $\delta^{15}N$ values were determined using a continuous flow isotope ratio mass spectrometer (IsoPrime, GV Instruments, Manchester, UK) coupled with an elemental analyser. Three capsules of the International Atomic Energy Agency standards CH-6 (sucrose) and N1 (ammonium sulphate) were analysed at the beginning of each series of measurements to calibrate the instrument and internal laboratory urea standard. Every 5–10 samples, two capsules of urea were analysed to obtain precision by correcting for potential machine drift. The isotopic composition data are expressed as conventional δ notations relative to the standard gases of Pee Dee Belemnite for carbon and atmospheric N_2 for nitrogen, and reported as parts per thousand (‰). The analytical precision, based on 20 replicates of urea, was < 0.1 ‰ for $\delta^{13}C$ and < 0.2 ‰ for $\delta^{15}N$.

2.6. Data analysis and isotopic niche metrics

To examine the spatial and temporal variability in SI values of organic matter sources, a permutational analysis of variance (PERMANOVA based on Bray–Curtis similarity) was performed on two factors: location, fixed with three levels of upper reaches, middle reaches, and reservoir; and season, fixed with two levels of pre- and post-monsoon (Anderson et al., 2008). Then, a PERMANOVA was performed using a one-factor design (fixed with six levels: seston, biofilms, aquatic macrophytes, filamentous algae, riparian vegetation, and forest leaf litter) to test significant differences among primary sources of organic matter. Finally, when significant differences were detected, differences in $\delta^{13}C$ and $\delta^{15}N$ values were tested separately by one-way univariate PERMANOVA. Subsequent pairwise comparisons between all groups were also performed, categorising organic matter sources on a $\delta^{13}C$-$\delta^{15}N$ biplot. The significance level was set at $P < 0.05$, and P-values were calculated using 9999 permutations of residuals with unrestricted permutation of raw data.

To detect spatial and temporal variability in SI signatures of invertebrates and fish (excluding amphibians due to a lack of replicate samples) at entire community levels and to test if such variabilities could be attributed to the summer monsoon event, a PERMANOVA design was employed based on two factors: location and season. When significant differences were detected, a two-way univariate PERMANOVA was performed separately on $\delta^{13}C$ and $\delta^{15}N$ values, followed by pairwise comparisons for significant factors. To reduce bias due to unbalanced sample sizes (N) among species, we used the mean SI values per species.

We then examined the associations between consumers and source SI values within the $\delta^{13}C$-$\delta^{15}N$ biplot space and evaluated trophic diversity using community-wide isotopic niche metrics (Layman et al., 2007). First, we assessed the niche overlap of individual communities (fish and invertebrates) between seasons in the isotopic space using standard ellipse areas corrected for small sample sizes (SEAc) (Jackson et al., 2011). This approach is less susceptible to sample size and extreme values than other methods, allowing comparisons of the percentage overlap of the surfaces of smaller ellipses. Second, we compared three community-wide isotopic metrics between seasons: $\delta^{15}N$ range (NR, as a vertical niche descriptor and a proxy of trophic lengths), $\delta^{13}C$ range (CR, as a horizontal niche descriptor and a proxy of the breadth of dietary sources) based on the SI values of fish and invertebrate communities, and SEAc at the whole community level (fish and invertebrates combined). Comparisons of these measures of trophic diversity were made using Student's t-tests. Third, we identified the community-wide isotopic overlap between locations by calculating isotopic nestedness (INes) on a two-dimensional standardised (0–1-scaled to avoid bias due to differences in the ranges of SI values) space of $\delta^{13}C$ and $\delta^{15}N$ (Cucherousset and Villéger, 2015). Based on the convex hull area, which represents the volume of the standardised space encompassing all specimens (Layman et al., 2007), we estimated the INes by measuring the ratio between the niche volume overlapped and the minimal volume filled by a community. The INes index ranges from 0 (no overlap between the tested groups) to 1 (complete overlap). Unless otherwise stated in the text, all other tests were performed using the R 4.1.1 software (R Core Team, 2021).

2.7. *Mixing model calculation and trophic position estimation*

To estimate changes in source contribution to the trophic base of stream and reservoir food webs, we employed the Bayesian SI mixing model package ‘MixSIAR’ (v. 3.1.9; Stock and Semmens, 2016). Plots of $\delta^{13}C$ and $\delta^{15}N$ values of organic matter sources and PERMANOVA tests indicated that both SI values were distinct between the source materials collected at different localities. Accordingly, we pooled potential basal resources into five groups: Seston-biofilm, aquatic macrophytes, filamentous algae, riparian vegetation, and forest leaf litter. Seston and biofilms had overlapping isotope ranges and thus were combined to improve model performance and test our hypothesis. The pooled SI values of the individual sources were input as the mean and standard deviation. Given the longitudinal continuity of the stream channel surveyed and narrow ranges in $\delta^{13}C$ of the consumers, we ran the mixing model using the SI values of consumer species with ‘community’ (invertebrates and fish, individually) as a random factor and ‘location’ and ‘season’ as fixed factors. For the mixing model calculations, we used trophic enrichment factor (TEF) values of 0.75 ± 0·11 ‰ and 2.75 ± 0·10 ‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively, reported as the overall means of estimates from an extensive review of the literature (Caut et al., 2009). For a more comprehensive understanding of carbon flow from primary producers, we adjusted the consumer SI values using TEF to consider the multiple trophic steps prior to data input. The model was fitted via Markov Chain Monte Carlo, and model convergence was examined via Gelman–Rubin and Geweke diagnostics. Median source proportions of the community trophic base and 95 % credibility intervals (CIs) were estimated by the posterior density distribution for each case.

The trophic positions (TPs) of the species were estimated based on the fractionation of $\delta^{15}N$ values between prey and predators (Post, 2002; Vander Zanden and Rasmussen, 1999). The trophic position of each consumer was calculated using the following equation:

$$TP = \left[\left(\delta^{15}N_{consumer} - \delta^{15}N_{reference}\right)/2.75\right] + 2$$

where $\delta^{15}N_{consumer}$ is the mean $\delta^{15}N$ value of the consumer species; $\delta^{15}N_{reference}$ is the mean $\delta^{15}N$ value of the primary consumers (grazer-scrapers *Neocaridina deniculata* and *Serratella rufa*; collector-gatherers *Phoenanthus coreanus*, *Chironomus* sp., and *Cloeon dipterum*; and filter-ers zooplankton) that possessed the lowest $\delta^{15}N$ values within the local community on each sampling occasion; 2.75 ‰ is the mean TEF value per trophic level as described earlier; and 2 indicates the TP of the baseline (i.e., primary consumers). TP values below 2 for zooplankton were assigned to a TP value of 2. $\delta^{15}N_{reference}$ values were calculated separately for each location and season to compare consumer TP estimates between locations and seasons (Zeug and Winemiller, 2008).

3. Results

3.1. *Environmental characteristics*

The altitude distribution across the longitudinal axis of the channel reach to the reservoir indicated a fairly gentle gradient of the study stream system (Table 1). The mean bankfull width varied from 19 to 126 m at the channel reaches to 200 m in the reservoir. The inner berm where water flows was shallow (≤0.4 m) and thus wadeable at both reaches. In contrast, the reservoir sites were deeper (5–14 m) than the channel reaches, and thus required a surveying vessel for access. Despite the geomorphic characteristics of bank confinement, the stream channel has riparian wetlands that account for a large part (45–62 % and 0–72 % at the upper and middle reaches, respectively) of the bankfull area and are fully covered by vegetation. The mean daily discharge at both reaches was nearly identical between seasons because of our sampling date, with easy access for surveying during the post-monsoon period. Water turbidity was consistently higher at the stream reaches than at the reservoir, reflecting longitudinal distributions of chlorophyll *a* and seston concentrations. The POC and PN concentrations were generally lower at the channel reaches than at the reservoir. As measured indirectly through chlorophyll *a*, ash-free dry mass, POC, and PN contents, biofilm biomass was consistently high at both reaches. The C:N molar ratios varied from 4.1 to 6.4 for seston and from 5.9 to 8.1 for biofilms.

3.2. $\delta^{13}C$ *and* $\delta^{15}N$ *values of primary organic matter sources*

The $\delta^{13}C$ and $\delta^{15}N$ values of six categories of organic matter sources ranged from − 30.1 ± 0.3 ‰ (riparian herbage *Erigeron annuus* at the upper reach in May) to − 18.4 ± 0.1 ‰ (filamentous algae at the upper reach in August) and from 6.6 ± 0.1 ‰ (seston at the upper reach in May) to 21.1 ± 1.6 ‰ (leaf litter of upland forest *Ginkgo biloba* at the middle reach in May) (Fig. 2; Table S1). The two-way PERMANOVA test revealed that there was a significant difference in SI values of the source groups of organic matter among locations (Pseudo-$F_{2,109} = 3.67$, $P = 0.019$) but not between seasons (Pseudo-$F_{1,109} = 0.41$, $P = 0.660$), with no interaction effect of location × season (Pseudo-$F_{2,109} = 0.36$, $P = 0.803$) (Table S2). Such a spatial difference in isotope values of the sources was attributed to our sampling regime nested in the “location” factor for producers (e.g., leaf litter of forest canopy at the upper reach, biofilm and riparian vegetation at the channel reaches) that have significantly different isotope signatures (Pseudo-$F_{5,109} = 63.01$, $P = 0.001$; Table S3).

The univariate PERMANOVA tests for the individual isotope values indicated that both $\delta^{13}C$ and $\delta^{15}N$ values were significantly different among the sources of organic matter (Pseudo-$F_{5,109} = 211.25$ and 21.42, $P = 0.001$ for both; Table S4). Pairwise comparisons characterised the $\delta^{13}C$ and $\delta^{15}N$ values of instream, riparian, and forest sources of organic matter. The mean $\delta^{13}C$ value (−19.4 ± 0.9 ‰, $N = 6$) of filamentous algae was the highest in all source types ($P < 0.001$ for all). The mean $\delta^{13}C$ value (−22.2 ± 1.1 ‰, $N = 13$) of seston was equivalent ($P = 0.070$) to that of biofilms (−21.2 ± 1.5 ‰, $N = 16$) but was much higher

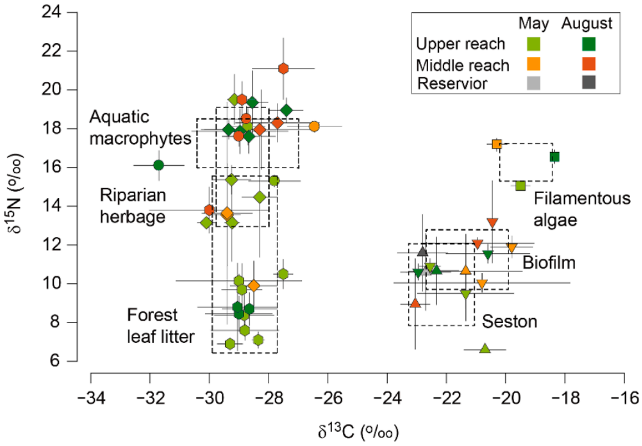

Fig. 2. Bi-plots of $\delta^{13}C$ and $\delta^{15}N$ values measured for potential sources of organic matter in the So-oak Stream system. Different sources are indicated by different symbols. Values are mean $\delta^{13}C$ and $\delta^{15}N$ values (‰ ± 1 SD, standard deviation). Dashed-line boxes represent ± 1 SD of mean $\delta^{13}C$ and $\delta^{15}N$ values of respective sources.

(P = 0.001) than those of instream aquatic macrophytes, riparian vegetation, and forest leaf litter (−28.7 ± 1.8 ‰, $N = 12$; −28.9 ± 0.9 ‰, $N = 40$; and − 28.8 ± 1.1 ‰, $N = 28$, respectively) (Fig. 2). The mean δ^{15}N values of organic matter sources distinguished seston-biofilm-leaf litter (9.9 ± 2.2 ‰, $N = 13$; 11.2 ± 1.6 ‰, $N = 16$; 11.0 ± 4.7 ‰, $N = 28$) from aquatic macrophytes-filamentous algae-riparian vegetation (17.3 ± 1.3 ‰, $N = 12$; 16.3 ± 1.0 ‰, $N = 6$; 16.0 ± 3.1 ‰, $N = 40$) ($P <$ 0.003).

3.3. δ^{13}C and δ^{15}N values of consumers

A total of 25, 23, and 21 consumer taxa (invertebrates and fish) at the upper reach, lower reach, and reservoir, respectively, were collected for stable isotope analyses (Tables S5 and S6). The mean δ^{13}C values of aquatic consumers varied between − 25.2 ± 0.7 ‰ (*Hydropsyche* sp. in August at the upper reach) to − 18.7 ± 0.4 ‰ (*S. rufa* in May at the middle reach), falling within narrower ranges of 3.6–6.0 ‰ at the three locations than the δ^{13}C range (13.4 ‰) for the six sources of organic matter (Table S1) and consistent with the ranges observed with instream seston, biofilm, and filamentous algae (Fig. 3). The mean δ^{15}N values ranged from 8.5 ± 0.2 ‰ (zooplankton in May at the upper reach) to 22.4 ± 0.7 ‰ (*Rhynchocypris oxycephalus* in August at the reservoir), spanning a broad range of 13.9 ‰ and increasing from invertebrates to fish.

The two-way PERMANOVA test revealed a significant difference in SI values for fish between seasons (Pseudo-$F_{1,39} = 3.83$, $P = 0.032$) but not among locations (Pseudo-$F_{2,39} = 9.78$, $P = 0.144$), with no interaction effect of location × season (Pseudo-$F_{2,39} = 1.76$, $P = 0.165$) (Table 2). Subsequent two-way univariate PERMANOVA tests for individual SI values of δ^{13}C and δ^{15}N revealed that such a seasonal variation in fish SI values was attributed to their δ^{15}N values (Pseudo-$F_{1,39} = 5.89$, $P = 0.016$) with no interaction effect (Pseudo-$F_{2,39} = 1.34$, $P = 0.259$). The two-way PERMANOVA test for the SI values of invertebrates showed no significant difference for either factor location (Pseudo-$F_{2,39}$ = 0.96, $P = 0.432$) or season (Pseudo-$F_{1,39} = 2.43$, $P = 0.102$), with no interaction effect of both factors (Pseudo-$F_{2,39} = 0.45$, $P = 0.617$).

3.4. Community-wide isotopic niche metrics

The trophic diversity metric of the invertebrate community measured by the standard ellipse area (SEAc) overlapped in the pre- and post-monsoon seasons considerably (47 % niche overlap) and highly (92 % niche overlap) in the upper and middle reaches, respectively (Fig. 4a, b). No overlap testing was conducted at the reservoir because we failed to sample invertebrates (except for zooplankton). The fish community SEAc overlapped highly (93 % and 60 %, respectively) between seasons at the middle reach and reservoir (Fig. 4b, c), but not at the upper reach (Fig. 4a). Such an absence of overlap in the fish community at the upper reach reflected seasonal changes in the vertical niche axis (δ^{15}N range).

When we combined invertebrates and fish, three community-wide SI

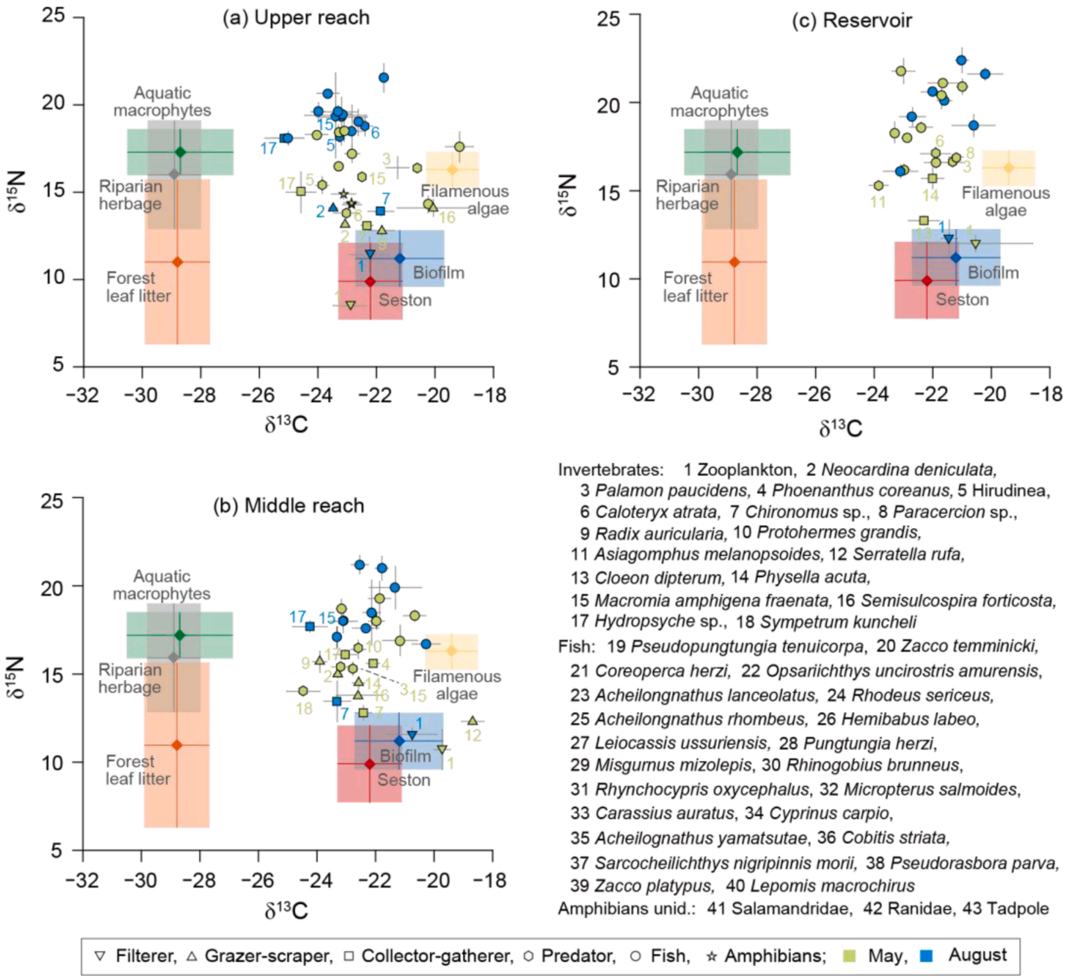

Fig. 3. Bi-plots of δ^{13}C and δ^{15}N values measured for consumers (invertebrates and fish) and potential sources of organic matter in May (light green) and August (sky blue) in the So-oak Stream system: (a) upper reach, (b) middle reach, and (c) reservoir. Species codes are shown in the bottom right-hand corner. Values are mean δ^{13}C and δ^{15}N values (‰ ± 1 SD). Feeding guilds of the invertebrate species were classified according to previous reports (see Supplementary data, Table S8). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Results of two-way PERMANOVA tests highlighting spatial and temporal variability in isotope ratios of consumers (fish and invertebrates) based on the Bray-Curtis similarities. Bolds represent a significance at $P < 0.05$.

	Fish				Invertebrates			
Source	df	MS	Pseudo-*F*	*P*	df	MS	Pseudo-*F*	*P*
Location	2	18.23	1.87	0.144	2	18.58	0.96	0.432
Season	1	37.45	3.83	0.032	1	46.99	2.43	0.102
Location × Season	2	17.24	1.76	0.165	1	8.66	0.45	0.617
Residuals	39	9.78			39	19.34		
Total	44				43			
Univariate for fish								
			$\delta^{13}C$				$\delta^{15}N$	
Source	df	MS	Pseudo-*F*	*P*	df	MS	Pseudo-*F*	*P*
Location	2	15.77	2.40	0.123	2	33.35	1.72	0.191
Season	1	0.44	0.06	0.806	1	114.04	5.89	0.016
Location × Season	2	15.48	2.35	0.110	2	26.00	1.34	0.259
Residuals	39	6.58			39	19.36		
Total	44				44			

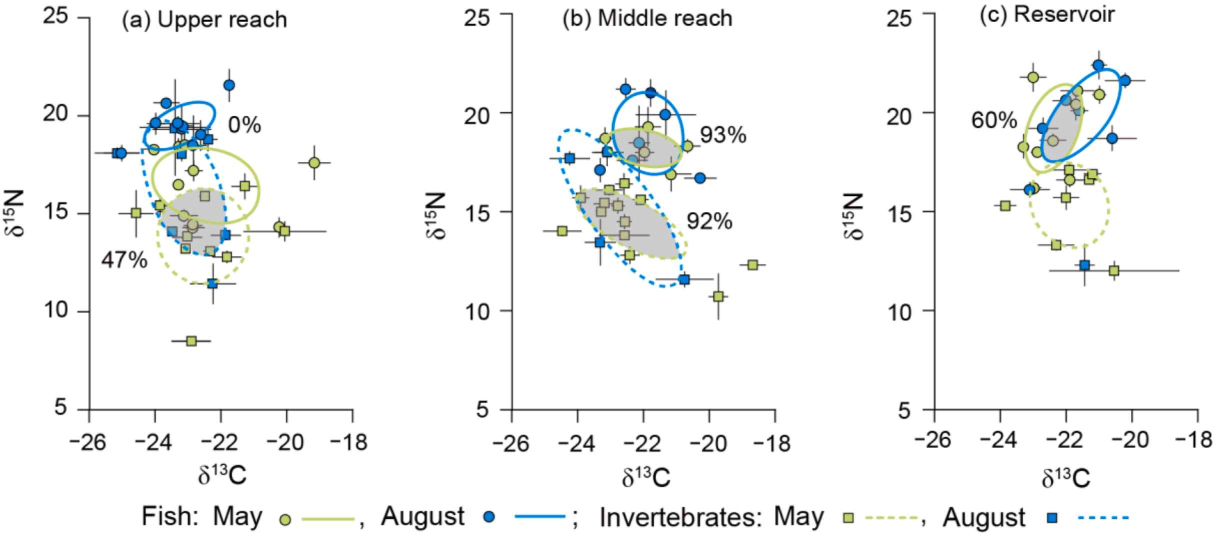

Fig. 4. Standard ellipse area (SEAc) illustrating the isotopic niches of invertebrate (light green) and fish (sky blue) communities collected in May (solid circle) and August (dashed circle) in the So-oak Stream system: (a) upper reach, (b) middle reach, and (c) reservoir. The overlap between communities in May vs August is expressed as grey areas and percentage values. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

niche metrics (NR, CR, and SEAc) did not show seasonal changes (Table 3). The mean $\delta^{15}N$ and $\delta^{13}C$ ranges (NR and CR) between the invertebrate and fish communities at the three sampling locations were consistent between seasons (Student's *t*-test, $P = 0.369$ and 0.702 for NR and CR, respectively). The whole community SEAc measure showed no seasonal changes in the size of community SI niches ($P = 0.527$).

Table 3
Results for the community-wide metrics based on the $\delta^{13}C$ and $\delta^{15}N$ values of fish and invertebrate communities at the respective sites, providing information on trophic diversity ($\delta^{15}N$ range, NR; $\delta^{13}C$ range, CR; standard ellipse areas corrected for small sample sizes, SEAc). NR and CR indicate the ranges between mean $\delta^{13}C$ and $\delta^{15}N$ values of fish and invertebrate communities. Mean $\delta^{13}C$ and $\delta^{15}N$ values of invertebrate community at the reservoir in August were based on zooplankton values. Student *t*-test of the results for three community-wide metrics between seasons.

	Upper reach		Middle reach		Reservoir		*t*-test
	May	August	May	August	May	August	*P*
NR	2.63	3.29	3.77	3.68	3.83	(7.51)	0.369
CR	0.08	0.17	0.40	0.88	0.45	(0.20)	0.702
SEAc	10.88	8.78	10.28	12.06	8.46	11.34	0.527

Furthermore, community-wide SI niches overlapped closely between locations (Fig. 5). The INEs values were calculated as 0.84 between the upper and middle reaches, 0.86 between the upper reach and reservoir, and 0.79 between the middle reach and reservoir, highlighting little spatial shift.

3.5. *Carbon sources supporting aquatic food webs and trophic position of consumers*

Posterior densities of proportional contribution estimates of source materials indicated that the seston-biofilm combination was the dominant carbon source supporting lotic and lentic food webs in both pre- and post-monsoon seasons (Fig. 6). The median contributions of seston-biofilm-derived carbon to production of the invertebrate community ranged from 58.0 % (30.2–75.5 %, 95 % CI) at the upper reach in May to 88.1 % (70.4–97.5 %, 95 % CI) at the reservoir in August, indicating that they were predominant contributors in the main channel and reservoir in both seasons (Table S7). The contributions of aquatic macrophytes, filamentous algae, riparian vegetation, and terrestrial leaf litter to the basal nutrition of invertebrate communities were relatively small (median < 10 %), but were consistent at most locations in both seasons, with

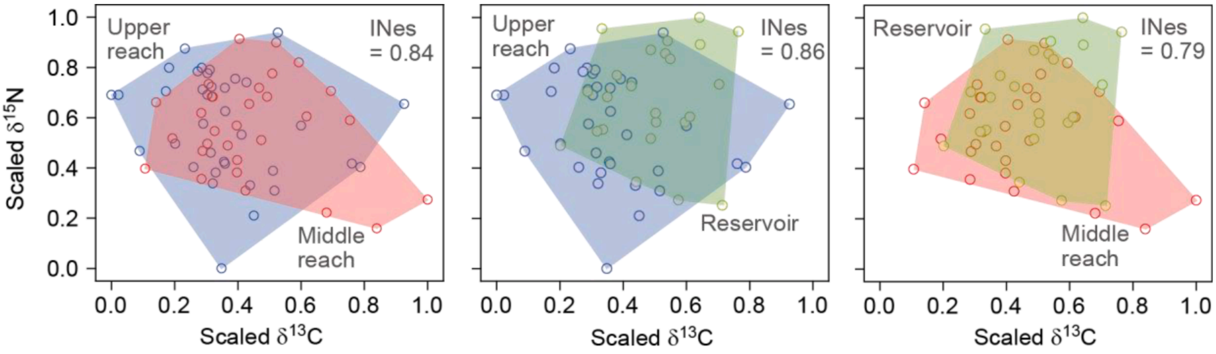

Fig. 5. Isotope overlap metrics scatterplot and associated convex hull for the δ^{13}C and δ^{15}N values of consumers at the whole community levels (fish and invertebrates combined) at the upper and middle reaches and the reservoir. Based on a convex hull area, isotopic niches between whole communities of two locations were compared by their overlap (position and area) in the isotopic space by calculating isotopic nestedness (INes).

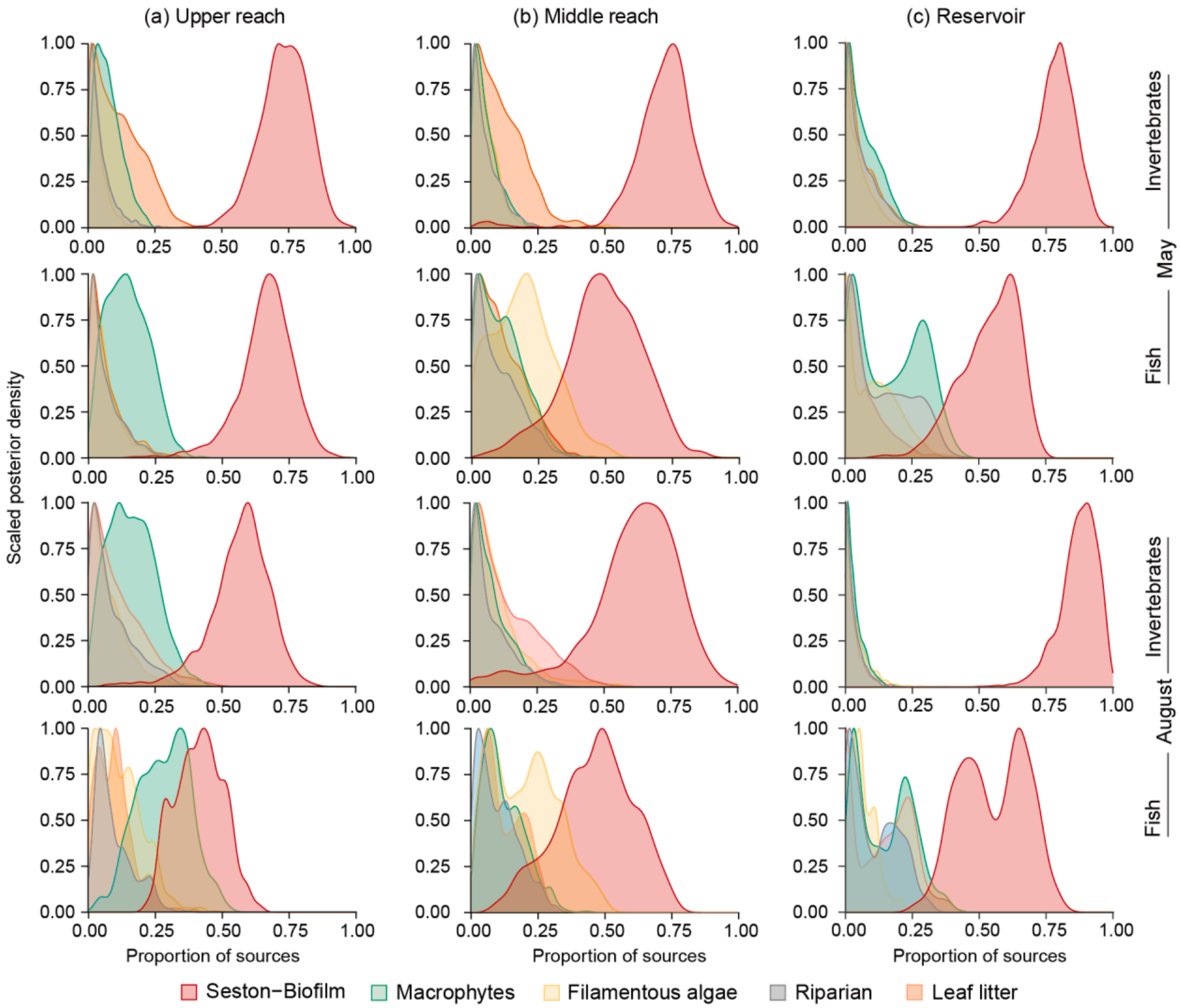

Fig. 6. Scaled posterior densities of proportional contribution estimates of potential primary organic matter sources fueling invertebrate and fish communities in May (upper) and August (lower) in the So-oak Stream system: (a) upper reach, (b) middle reach, and (c) reservoir.

the exception of macrophytes (median 15.9 %, 2.4–34.1 %) at the upper reach in August. Likewise, the model estimates revealed a dominant reliance of fish production on seston-biofilm sources with median proportions of 41.8 % (26.4–58.7 %) at the upper reach in August to 67.2 % (42.1–83.8 %) at the upper reach in May. Aquatic macrophytes subsidised the fish communities considerably, with median contributions between 10.1 % (1.6–29.6 %) at the middle reach and 28.5 % (10.1–47.4 %) at the upper reach in August. The remaining carbon sources (i.e., filamentous algae, riparian vegetation, and terrestrial leaf litter) made substantial yet small contributions (median 4.1–19.6 %) compared to the two former sources, with no clear variation in their proportional contributions to the basal carbon sources of fish communities in the main channel and the reservoir between seasons.

The TPs of invertebrates were nearly identical between locations and seasons (Kruskal–Wallis test, $\chi^2 = 1.628$, df = 4, $P = 0.804$), with a TP range of 2.0–4.4 (Fig. 7; Table S8). Fish generally occupied higher TPs than the invertebrate community, with a TP range for fish of 3.1–5.7. Despite a slight increase in their δ^{15}N values in August (Table 2; Fig. 4), the estimated TPs for fish did not change between locations and seasons (Kruskal–Wallis test, $\chi^2 = 2.709$, df = 5, $P = 0.745$), reflecting the baseline δ^{15}N values of primary consumers at each location in different months (Table S6).

4. Discussion

The major river corridors, including the upper Geum River, in the Korean Peninsula have a dramatic increase in fluxes of terrestrial and riparian plant debris (woody debris and leaf litter) with rainfall during the monsoon season every summer (KEI, 2013; Yu et al., 2002). It has been assumed that the trophic base of these stream food webs shifts from autochthonous to allochthonous sources, as potential terrestrial sources of organic matter increase during the summer monsoons. Contrary to this expectation, our isotopic evidence suggests a consistent dominance of autochthonous trophic bases in both lotic and lentic food webs before and after the summer monsoons in the So-oak Stream system. Close niche overlaps of consumers in isotopic niche spaces between seasons and locations, as well as their narrower horizontal niche breadths compared to organic matter sources, indicated the prevalence of a particular trophic base in the stream food webs. Our isotope mixing-model estimates revealed that instream production (i.e., biofilm and seston) was the primary source of organic matter supporting the aquatic food webs, with no conspicuous longitudinal and seasonal trends in the trophic base. Despite a slight increase in their δ^{15}N values in the post-monsoon season, the TP ranges of the fish communities at each location were nearly identical between seasons. Additionally, it should be noted that the δ^{15}N values from producers to consumers in the So-oak Stream system were significantly elevated compared to those of other “pristine” river systems worldwide (Bunn et al., 2003; Huryn et al., 2001; Wang et al., 2014; Zah et al., 2001; Zeug and Winemiller, 2008).

Potential sources of organic matter, which were our focus, were readily distinguishable from each other by their δ^{13}C and δ^{15}N values. Instream autochthonous sources (i.e., seston, biofilm, and filamentous algae) had much lower negative δ^{13}C values compared to those of terrestrial sources (i.e., leaf litter and riparian coverage), as is generally observed in river systems worldwide (Wang et al., 2014; Zah et al., 2001; Zeug and Winemiller, 2008). The δ^{13}C values of aquatic macrophytes and filamentous algae were arrayed within close δ^{13}C ranges to terrestrial sources and instream seston-biofilm, respectively. In contrast, the former aquatic sources were separable by higher δ^{15}N values than the latter sources. Unexpectedly, overlapping SI signatures between instream seston and biofilm impeded the separate estimation of their roles in consumer nutrition. Sestonic organic matter is composed of a mixture of various aquatic and terrestrial materials (Huryn et al., 2001). In the present study, the C:N molar ratios of sestonic organic matter were consistent between locations and seasons (4.1–6.4), which were very close to those of biofilm (5.9–8.1) but much less than those of terrestrial and riparian plant sources (20.3–45.2 and 18.1–32.8, respectively; data not shown). Higher C:N ratios in terrestrial compared to aquatic materials have long been recognised in freshwater ecosystems (Reid et al., 2008; Wetzel, 2001; Zah et al., 2001). Given the high standing stock of phytoplankton and sparse abundance of filamentous algae and aquatic macrophytes, the observed isotopic and elemental composition of seston indicates a dominant contribution of instream autochthonous sources (e.g., biofilm and phytoplankton) to the particulate organic matter pool in the So-oak Stream system. Based on their similar isotope ranges, we combined the SI signatures of seston and biofilm into overall means of -21.6 ± 1.4 ‰ and 10.6 ± 1.9 ‰ for δ^{13}C and δ^{15}N values, respectively, as an instream source differentiated from filamentous algae and aquatic macrophytes.

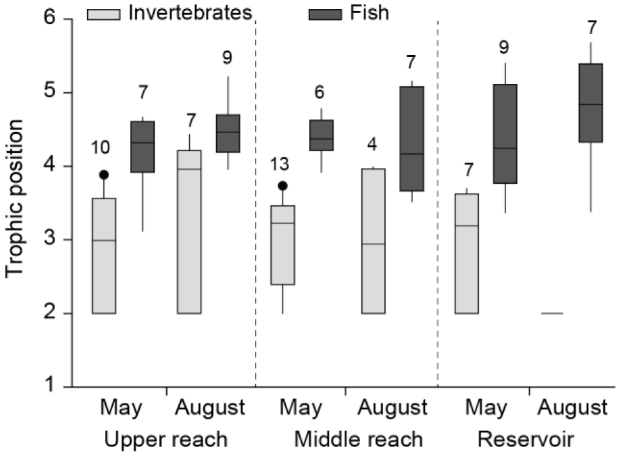

Fig. 7. Differences in trophic positions of invertebrate and fish communities between locations and seasons analyzed by a Kruskal–Wallis rank sum test. The box-whisker plot displays medians and distribution of estimated TPs. The whiskers represent the lowest and highest estimated values. Arabic numerals indicate the number of samples.

There was no evidence indicating a significant seasonal change in the δ^{13}C values of the potential sources of organic matter. In contrast to our expectation based on the highly increased terrestrial inputs during the summer monsoon, as mentioned earlier, the seasonal coincidence in δ^{13}C values of seston, although observed immediately after high-flow periods, suggests a low availability of terrestrial sources in the sestonic organic matter pool. This may indicate that fast-flowing water during monsoons sweeps terrestrial and riparian debris downstream with no sedimentation on the boulder and pebble substratum of the stream channel (KEI, 2013; Yu et al., 2002). In contrast, the observed δ^{13}C values for instream producers suggest that CO_2 limitations due to changes in current velocity (Finlay et al., 1999), water temperature (MacLeod and Barton, 1998), and rates of primary production (Hicks, 1997) are unlikely to influence temporal variations in their δ^{13}C values in our system. Rather, favourable conditions for aquatic primary production in association with shallow water, low turbidity, and a lack of shading may facilitate the availability of instream sources (Huryn et al., 2001). As a result, the δ^{13}C values of consumers and thus community-wide SI niches would confirm to the relative availability of different sources of organic matter at the respective stream reaches.

Our isotopic niche metrics revealed a consistent trophic structure at the community level of consumers with respect to time and space. The SEAc values for invertebrate and fish communities at respective locations as well as whole communities in combination indicted a high degree of overlap between pre- and post-monsoon periods. Furthermore, as indicated by the high INes values between locations, community-wide SI niches did not show a spatial shift. These results suggest great compositional uniformity in trophic diversity over time and space (Layman et al., 2007). Indeed, there were no significant changes in the horizontal trophic niche or estimated trophic position of fish across the locations between seasons. The small and uniform CR values (i.e., narrow δ^{13}C ranges between invertebrate and fish communities) at the community level at each location between seasons indicate a homogeneous pattern of resource exploitation by consumers with no niche expansion, elimination, and contraction before and after the monsoon (Burdon et al., 2020). The consumer NR values (δ^{15}N ranges, 2.63–3.87), which reflect invertebrate-fish interactions (Post, 2002), were also nearly identical temporally and spatially, further supporting this explanation. Such a similarity in the SI niche metrics emphasises the absence of directional reshaping of food-web properties across the stream channel as well as between pre- and post-monsoon periods (Burdon et al., 2020).

As evidenced by the isotope mixing-model estimations, the community SI niche metrics reflected the consistent dominance of aquatic autochthonous production to the nutrient-sustaining invertebrate and, in turn, fish communities. This result may be supported by the high availability of instream biofilms and seston (Delong and Thorp, 2005) and their high nutritional value relative to leaf litter (Guo et al., 2016). Despite the low nutritive value (based on relatively high C:N ratios), terrestrial detritus, when available, can serve as an important basal resource for primary consumers and higher-level animals in stream food webs (Hall et al., 2000; Zeug and Winemiller, 2008). Therefore, the relative contributions of autochthonous and allochthonous sources can shift with season and location because of changes in their availability in combination with hydrologic conditions (Beesley et al., 2020; Huryn et al., 2001: Reid et al., 2008). In contrast, we found little evidence of variation in the proportional contributions of terrestrial materials (leaf litter and riparian vegetation) to the basal carbon sources of whole communities in the stream channel and reservoir in both seasons, highlighting a minor role of terrestrial inputs as a trophic subsidy after the monsoonal rainfall. The lack of change in trophic structure in response to flooding was exemplified by the Mississippi and Ohio Rivers (Delong et al., 2001) and a glacial stream in the Swiss Alps (Zah et al., 2001).

In this context, our findings are broadly comparable with the riverine productivity model (Thorp and Delong, 1994), as defined for trophic theories in lotic food webs (see Introduction). Potential inputs of terrestrial materials could be predicted by the river continuum concept (Vannote et al. 1980), the flood pulse concept (Junk et al., 1989), and the resource pulse concept (Yang et al., 2008), but are much less important, even at the upstream headwater reach near the forest canopy. A recent study of the middle Yangtze River (China) indicated that terrestrial organic matter is the primary nutritional support for consumers at lotic and even lentic sites, reflecting the limited algal production due to high turbidity, high flow, and great depth (Wang et al., 2014). In contrast, our results clearly suggest a low degree of trophic connectivity between the stream-channel food web and watershed production. This is likely due to the lack of deposition and retention of terrestrial detritus. As speculated by Zeug and Winemiller (2008), monsoonal floods in the So-oak Stream may transport terrestrial material downstream with insufficient time for its decomposition and/or access and processing by invertebrates. The stream water body is confined between riparian zones within stream banks that are established to protect agricultural and (sub)urban lands from the overflow of the river. Riparian zones span a considerably wide area between the stream banks (Table 1) but encounter only sporadic flooding due to erratic rainfall. These geomorphic and hydrologic features may impede the direct connectivity between aquatic consumers and terrestrial invertebrates. In comparison with the Yangtze River, which experiences the summer monsoon at similar latitude, our upstream sites of the Geum River are characterised by low turbidity, shallow depth, and high algal production. Flushing huge amounts of anthropogenic nutrients from agricultural and urban areas may facilitate algal blooms (e.g., attached algae and floating cyanobacteria) in the lotic channel and the lentic reservoir (Park et al., 2016; Shin et al., 2003).

Despite the similar TP ranges of both invertebrate and fish communities between the lotic and lentic food webs, the food-chain lengths were slightly higher in the reservoir (5.2–5.7) than in the stream channel (4.6–5.2) and slightly higher in August (5.2–5.7) than in May (4.6–5.2). While increasing resource accessibility (availability of basal resources and prey) decreases food-chain length in response to changes in environmental conditions (Tunney et al., 2012), a reduction in the horizontal trophic niche increases it (Burdon et al., 2020). However, these dynamics are unlikely to occur in the So-oak Stream food web. The observed longer food-chain lengths would be associated with prey utilisation patterns based on the occurrence of larger fish in the deeper water of the reservoir and in August due to seasonal ontogeny (Choi et al., 2020; Kim et al., 2011), as indicated by the expansion of their vertical niche axis (Fig. 4).

One of the most probable explanations for the observed higher δ^{15}N values at all trophic levels (from producers through invertebrates to fish) compared to those in pristine river systems is that anthropogenic nitrogen can be incorporated into the So-oak Stream food web (Lee et al., 2018; Mayer et al., 2002). Much higher δ^{15}N values of anthropogenic nitrate relative to natural sources are transferred to the δ^{15}N values of aquatic flora and subsequently to those of the fauna that consume these vegetation sources (Pastor et al., 2014; Smucker et al., 2018). Indeed, our δ^{15}N values for primary sources of organic matter (6.6–21.1 ‰) were much higher than those of leaf litter (−3.1 ± 2.4 ‰) and seston (−1.3 ± 1.1 ‰) collected from high-altitude forest streams adjacent to the study reaches (unpublished data). These highly elevated δ^{15}N values are likely explained by those (8.2–13.4 ‰) of dissolved NO_3, as observed in the neighbouring upstream Yeongsan River water, which reflect greater contributions of anthropogenic sources such as sewage (11.2 ‰) and manure (15.0 ‰) compared to natural sources such as soil (4.1 ‰) and precipitation (−7.2 ‰) from the watershed (Nam et al., 2019). In addition, our fish data (14.3–22.4 ‰) are the highest δ^{15}N values compared to previously reported levels (Bunn et al., 2003; Huryn et al., 2001; Wang et al., 2014; Zah et al., 2001; Zeug and Winemiller, 2008). Given that most fish occupy more than tertiary trophic levels in stream food webs and may have similar trophic fractionation values of δ^{15}N (Lee et al., 2018; Zeug and Winemiller, 2008), our fish δ^{15}N values provide clear evidence for the prevalence of anthropogenic nitrogen in the So-oak Stream food web.

5. Conclusions

Our SI measurements of common consumers and potential organic matter sources allowed us to analyse both the spatial and temporal patterns of the stream food web structure. Despite the apparent increase in terrestrial detritus during the East Asian summer monsoon period, no isotopic evidence indicated longitudinal and seasonal trends in the trophic base of the aquatic food web in the So-oak Stream ecosystem. Isotopic niche indices and mixing-model estimates revealed that aquatic production was the primary source of organic matter, supporting both lotic and lentic food webs before and after the summer monsoon. Such trophic consistency likely led to nearly identical TP ranges for consumers between seasons. This could be explained by algal production facilitated by anthropogenic dissolved nutrients, as evidenced by the elevated δ^{15}N values at the ecosystem level and the transport of terrestrial and riparian detritus downstream by fast-flowing water during monsoons. Further research efforts are needed to compare the potential terrestrial-aquatic link to food web dynamics based on natural nutrient sources in deep, highly turbid, or shaded streams and to improve our understanding of the variability in the food web base in association with the availability of basal resources in morphologically and hydrologically contrasting river systems in the East Asian monsoon climate zone.

CRediT authorship contribution statement

Hee Yoon Kang: Conceptualization, Investigation, Methodology. **Jae-Ki Shin:** Conceptualization, Methodology. **Hyun Je Park:** Investigation, Resources. **Byeong-Gweon Lee:** Methodology, Resources. **Chang-Keun Kang:** Conceptualization, Investigation, Resources.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.109268.

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