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PRIMARY RESEARCH PAPER

Stable isotope analysis reveals relative influences of seasonal hydrologic variation and impoundment on assimilation of primary production sources by fish in the Upper Yesilırmak River, Turkey

Nehir Kaymak · Kirk O. Winemiller · Senol Akin · Zekeriya Altuner · Fatih Polat · Tarik Dal

Abstract This study analyzed variation in stable isotope ratios of aquatic and terrestrial primary producers and two common cyprinid fishes (*Capoeta banarescui* and *Squalius cephalus*) at seven sites in the upper Yeşilırmak River Basin, Turkey, to estimate relative contributions of basal production sources to fish biomass. We hypothesized that seasonal and spatial variation in fish assimilation of basal production sources would be affected by hydrological variation, with results for a reach downstream from a reservoir differing from those from upstream sites. Carbon and nitrogen isotopic ratios of primary producers and *S. cephalus* and δ^{15}N of *C. banarescui* revealed significant spatial variation. δ^{13}C of primary producers, δ^{15}N of *S. cephalus*, and both δ^{13}C and δ^{15}N of *C. banarescui* revealed significant seasonal variation. *C. banarescui* biomass in the river channel was mostly derived from terrestrial herbaceous plants, and its biomass in the reservoir derived mostly from aquatic plants. Estimated proportional contributions of herbaceous plants to both species were greatest at the downstream site during spring, and declined during summer in the case *C. banarescui*. Overall, the influence of the dam was small relative to effects from watershed characteristics and seasonal changes in temperature and hydrology.

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Introduction

Major sources of primary production, food resources, and abundance and feeding habits of aquatic organisms vary along fluvial gradients. Upstream processes in rivers influence downstream processes (river continuum concept, RCC), which results in structural changes in aquatic food webs from headwater streams to lower reaches. Dams disturb natural processes associated with longitudinal fluvial gradients and alter biotic communities and food web dynamics (Romanuk et al., 2006). Availability of primary production sources for aquatic consumers is influenced by hydrology (Roach et al., 2014), nutrient enrichment from agricultural and urban sources (Pingram et al., 2012), and dams that regulate flows in downstream reaches (Shannon et al., 2001; Hoeinghaus et al., 2007; Marty et al., 2008; Vörösmarty et al., 2010). Several studies concluded that flows released from reservoirs shifted diets of fishes and invertebrates in downstream reaches (Chester & Norris, 2006; Smokorowski et al., 2011), whereas other studies concluded no major effects (Chessmen et al., 2009; Rolls et al., 2012).

In their description of the RCC, Vannote et al. (1980) emphasized the importance of different primary production sources supporting consumers in different segments along the longitudinal fluvial continuum. Two alternative models for food web ecology of rivers are the riverine productivity model (RPM, Thorp & Delong, 1994) and the flood pulse concept (FPC, Junk et al., 1989). All three models have been supported by field studies. Herwig et al. (2004), Hadwen et al. (2010), and Chang et al. (2012) obtained results consistent with the RCC. Research on tropical and temperate floodplain rivers (Hoeinghaus et al., 2007; Zeug & Winemiller, 2008) revealed that flood pulses had a strong influence on the entrance of terrestrial primary production into aquatic food webs, a finding consistent with the FPC. Phytoplankton, benthic algae, and aquatic vascular plants were found to be the principal carbon sources assimilated by consumers in temperate, tropical, and dry-land floodplain rivers (Leigh et al., 2010; Hladyz et al., 2012; Jackson et al., 2013), but riparian vegetation also was important during periods of low as well as high flows, which is consistent with the RPM.

Most attempts to evaluate these models have investigated relatively large, lowland rivers over one or two seasons and limited ranges of discharge (Delong & Thorp, 2006; Herwig et al., 2007; Leigh et al., 2010), with only a few having examined highly regulated rivers (Ward & Stanford, 1983; Hoeinghaus et al., 2007). Here, we investigate food web dynamics of the upper Yesilirmak River in north-central Turkey, a system impacted by two reservoirs (Almus and Atakoy). Our study area was centered on the Almus Reservoir at elevations between 640 and 1,040 m. The climate is semi-arid and stream flows vary seasonally, with low flows between July and February and high flows between March and May. Using stable isotope ratios of two omnivorous fish species, *Capoeta banarescui* and *Squalius cephalus*, we tested predictions of alternative models for material and energy transfer in food webs and spatiotemporal variation of contributions from different primary production sources. We hypothesized that the dam affects assimilation of carbon sources by omnivorous fishes, and that this influence varies among locations within the drainage network. Specifically, fish biomass at relatively unimpacted upstream locations should derive mostly from riparian terrestrial plants as predicted by the River Continuum Concept. In river reaches with greater channel width and relatively less canopy cover, importance of benthic algae and phytoplankton should be greater (Vannote et al., 1980; Chang et al., 2012). Algae (phytoplankton) also should be important primary production source supporting fish biomass in the reservoir (Hoeinghaus et al., 2007). Downstream from the reservoir, drifting zooplankton from the reservoir represent a high-quality food resource for consumers and could thereby subsidize the food web (Doi et al., 2008; Mercado-Silva et al., 2009; Helmus et al., 2013; Power et al., 2013; Wellard Kelly et al., 2013). We hypothesized that during spring, when flows are higher, fish within the main channel assimilate more material derived from terrestrial production sources (Junk et al., 1989; Huryn et al., 2001; Herwig et al., 2004); during low-flow period in the summer, when flow conditions are more suitable for algal growth, aquatic benthic sources (e.g., benthic algae, filamentous algae) and phytoplankton should be more important because lower water velocity, greater light penetration, and higher temperatures promote algal growth in the river (Huryn et al., 2001; Finlay et al., 2002). To test these hypotheses, we analyzed and compared carbon and nitrogen stable isotope ratios of the principal primary production sources and two

omnivorous cyprinid fishes (*Capoeta banarescui* and *Squalius cephalus*) from locations above, within, and below Almus Reservoir on the Yeşilırmak River during three seasons.

Methods

Study area

The Yeşilırmak River, the second longest river in Turkey, originates within the Köse Mountains in northeastern Turkey and flows into the Black Sea. Northeastern Turkey has a semi-arid climate with large seasonal variation in temperatures. Water temperature ranges from −2 to 26°C annually. The river catchment is 36.114 km^2, and the river length is 519 km. Annual precipitation is 500 mm, and mean annual discharge of the Yeşilırmak is 5.80 km^3. Flows are low during winter and summer and high during spring in response to snowmelt and high rainfall (Jin et al., 2013). The river contains three main branches, the Tozanlı River in the upper catchment and the Kelkit and Çekerek rivers in the lower catchment. This study was conducted at locations within the relatively high-gradient upper Yesilirmak River. The natural flow of the upper Yesilirmak River is interrupted by two dams. Almus Reservoir (area 3,130 km^2; depth 78 m) (http://www.dsi.gov.tr) was constructed in 1966 for flood control, hydropower generation, and to supply water for irrigation. Atakoy Reservoir is small (in 1977; 0.5 km^2; depth 21.5 m) and supplies water for hydropower generation. Landscape of the upper catchment is dominated by meadows and pastures with small areas of agriculture (Akbulut, 2009). Water velocity is relatively high and turbidity is low. Fifty-three fish species have been recorded in the Yeşilırmak River (Demirsoy, 2006), including 50 native, one endemic, and three introduced species. Cyprinids are common and dominate commercial and recreational fisheries in the upper catchment of the Yeşilırmak Basin. Wels (*Silurus glanis*), crucian carp (*Carasssius carassius*), common carp (*Cyprinus carpio*), and rainbow trout (*Oncorhynchus mykiss*) have been stocked in the Almus Reservoir.

Aquatic food webs were investigated in three different river segments from January 2011 to September 2011: the littoral zone of the Almus Reservoir, five locations in river reaches located above the reservoir (812–1083 m elevation), and one location in a river reach downstream from the reservoir (Fig. 1). The reservoir shoreline has little vegetation cover and the region surrounding the reservoir is dominated by oak (*Quercus* spp.), poplar (*Populus* spp.), black pine (*Pinus nigra*), and Scots pine (*Pinus sylvestris*). Upstream sites 1 and 3 were in the main channel of the Yeşilırmak River, upstream site 2 was a tributary connected to the main channel. Current velocities are faster at upstream sites 1 and 2. Channel width of upstream site 3 is wider compared to the other upstream sites and downstream site. Tributaries 1 and 2 are small and flow directly into the reservoir. Oak, poplar, willow (*Salix* spp.), plane (*Platanus* spp.) and mahaleb cherry (*Prunus mahaleb*) trees, and herbaceous plants dominate riparian vegetation communities of the main channel and tributaries. The exceptions were site 2 bordered by pastures and site 3 bordered only by herbaceous plants. A single downstream station was sampled on the main river channel ∼ 25 km downstream from the dam (Fig. 1). Deciduous forest (willow, poplar, plane, alder (*Alnus* spp.)) and herbaceous plants dominated the riparian zone of this downstream site.

Fish and tissue sample collection

Two omnivorous fish species that were captured from each site (*Capoeta banarescui* and *Squalius cephalus*, except the latter species was not captured at tributary 1) were investigated to determine the extent that trophic ecology varies according to location within the river basin and relationship to the reservoir. Tissue samples were collected for analysis of isotopic ratios to estimate assimilation of alternative basal production sources. *Squalius cephalus* feeds on phytoplankton, zooplankton, meiofauna, insects, fish, macrophytes, and detritus (Caffrey et al., 2008; Akin et al., 2010 (unpublished report)). The diet of *Capoeta banarescui*, a recently described species endemic to Turkish rivers that drain into the southeastern Black Sea (Turan et al., 2006), consists of phytoplankton, benthic algae, aquatic plants, zooplankton, and invertebrates (Akin et al., 2010).

Tissue samples of fish and primary production sources were obtained at four sites (Upstream 3, Tributary 2, Reservoir, and Downstream) during winter (January 28–30, 2011), late spring (May

Fig. 1 Study locations and reservoir of the upper Yeşilırmak River Basin, Turkey (channel sites 1, 2, and 3, and tributaries 1 and 2 are located upstream from the reservoir, one site is located in littoral zone of the reservoir, and the downstream site is located below the dam)
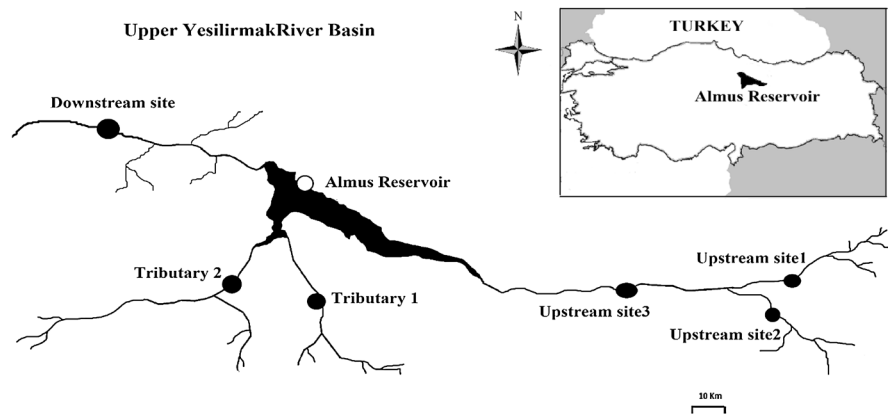
9–11, 2011), and late summer (September 9–11, 2011). The other 2 sites (Upstream 1 and 2) were sampled during spring and summer, and tributary 1 was sampled only during summer. Benthic macroinvertebrates were collected at the downstream site, and zooplankton were sampled from the reservoir and downstream site during summer in order to assess the potential contribution of zooplankton from the reservoir to fish biomass at the downstream site. At each site, we sampled four major groups of primary producers: trees (composite sample of live and recently fallen leaves from riparian trees), herbaceous plants (live leaves of dominant riparian herbaceous plants), seston, and benthic algae. Terrestrial vegetation (C_4 grass and *Rumex* sp.) was collected from the reservoir shore during summer, herbaceous plants were collected during spring, and submerged aquatic plants were collected during winter and spring. Filamentous algae (*Cladophora* sp.) samples were scraped from substrates, and were only found in amounts sufficient for collection during winter and spring at two sites: downstream site and tributary 2. Periphyton was scraped from dominant solid substrates, and then rinsed with distilled water to remove debris or microinvertebrates. Because these samples probably did not consist solely of benthic algae, we refer to this basal source as *phytomicrobenthos* (mostly benthic algae but possibly also containing fractions of detritus, fungi, bacteria, or protozoa) (Zeug & Winemiller, 2008). Water samples for seston were collected in 5-L opaque bottles and filtered through a 55-μm sieve to remove zooplankton and other large particles; remaining particles that settled onto the bottom were collected as seston samples that

were presumed dominated by phytoplankton. All samples were placed in plastic bags and stored on ice in the field and then in a freezer in the lab.

Zooplankton were collected from the reservoir and downstream site using horizontal and vertical tows of a standard plankton net (63 μm). Zooplankton samples were placed in an insulated box and transported to the laboratory for analysis. Benthic macroinvertebrates were collected using a Surber sampler with a 500-μm mesh net. Live invertebrates were transported to the laboratory and kept in containers with river water in a refrigerator for 24 h to allow them to empty their guts. Common aquatic macroinvertebrates were identified to order or family using keys provided by Bouchard (2004).

Fishes were collected with a bag seine at all sites. In the reservoir, fishes were collected at night (3 pm– 9am) using experimental gillnets with panels of 25-, 30-, 40-, 50-, 60-, 70-, and 80-mm mesh. In the river-channel sites, fishes were collected using an electroshocker during daytime. Captured fishes were stored on ice in the field. In the laboratory, fish individuals were identified to species, weighed, and measured for standard length.

Preparation of samples for isotopic analysis

In the laboratory, seston samples were filtered onto pre-combusted (450°C for 4 h) Whatman GF/F filters. Benthic and filamentous algae were rinsed with distilled water, and then any debris or invertebrates were removed during examination under a stereomicroscope. Benthic algae samples were suspended in distilled water and collected on GF/F filters. Leaves

were rinsed with distilled water to remove foreign particles. Boneless and skinless samples of fish muscle tissue were taken from the flank of each fish specimen, and then rinsed with distilled water.

Samples were dried at 60°C for 48 h; dried samples were ground to a fine powder, and then stored in glass vials. About 2 mg of each sample was obtained, weighed with a precision balance to 0.001 mg, and then sealed inside ultra-pure tin capsules. Samples were analyzed for carbon and nitrogen isotope ratios using mass spectrometry at the laboratory at the Analytical Chemistry Laboratory of the Institute of Ecology, University of Georgia, USA. The standard material for carbon was Pee Dee Belemnite limestone, and the nitrogen standard was atmospheric nitrogen gas. Ratios (R) of the heavy isotope to the light isotopes ($^{13}C/^{12}C$, $^{15}N/^{14}N$) were expressed in parts per thousand, relative to the standards in delta notation following the formula:

$$\delta X = \left[\left(R_{sample} / R_{standard} \right) - 1 \right] \times 10^3$$

Data analyses

The relative importance of production sources potentially assimilated by the two fish species was estimated based on $\delta^{13}C$ and $\delta^{15}N$ data using the SIAR mixing model in R (Parnell et al., 2010). This model produces a combination of feasible solutions for proportional contributions of alterative resources assimilated by consumer tissues. SIAR is based on a Bayesian approach that estimates probability distributions of resource contributions to consumer tissue by accounting for uncertainties associated with the input data (i.e., sources signatures and trophic enrichment factors (TEF)) (Parnell et al., 2010). Inputs are $\delta^{13}C$ and $\delta^{15}N$ for each potential resource and their associated standard errors, TEFs and their standard errors, and consumer isotopic signatures (França et al., 2011). We used a TEF value based on findings from a meta-analysis of trophic fractionation studies (Vanderklift & Ponsard, 2003). Trophic enrichment was 0.4 ± 1.3‰ for $\delta^{13}C$ (Post, 2002) and 2.54 ± 1.27 for $\delta^{15}N$. From the resulting assimilation estimates (proportional contributions), the mean and mode values and 1–99th‰ range (i.e., minimum and maximum) were calculated for the two omnivorous cyprinids.

We accounted for seasonal and spatial variation of production sources and consumers by comparing data from fish and basal sources collected at the same location on the same day. We performed an initial SIAR mixing analysis based on all six potential basal sources. Results indicated that C_4 plants and *Cladophora* sp. only contributed a maximum of 2–6%; and 2–21%, respectively, of the material assimilated by fish across all sites. Therefore, we eliminated these two sources and repeated the SIAR analysis with the remaining four sources as inputs in order to increase resolution for these important sources (Fry, 2006). We also estimated the potential contribution of zooplankton from the reservoir to fish biomass at the downstream site; isotopic values of zooplankton from the reservoir were input into the SIAR model along with macroinvertebrates from the downstream site and other alternative local production sources. Finally, the relationship between fish length and carbon isotopic signature was evaluated with regression analysis using R statistical software (version 3.0.2, R Project for Statistical Computing).

Results

Isotopic signatures: primary production sources

Ranges of mean $\delta^{13}C$ and $\delta^{15}N$ of trees in the upper Yesilirmak River were −30.93 to −25.48‰ and −4.54 to 7.13‰, respectively, and ranges of mean $\delta^{13}C$ and $\delta^{15}N$ of herbaceous plants were −31.94 to −25.89‰ and −0.21 to 7.89‰, respectively. Ranges of mean $\delta^{13}C$ and $\delta^{15}N$ of seston were −31.66 to −23.79‰ and −0.52 to 9.63‰, respectively. Seston from the downstream site had heavier $\delta^{13}C$ values relative to upstream sites and reservoirs, and seston from the reservoir had heavier $\delta^{15}N$ values. Isotope ratios of herbaceous plants, trees, and seston overlapped to varying degrees. $\delta^{13}C$ values of seston were more ^{13}C enriched than other primary producers (except phytomicrobenthos), and closest to values of trees and herbaceous plants from the shore of the reservoir and tributaries 1 and 2 (Figs. 2, 3). Seston from the reservoir and herbaceous plants from the downstream site had similar carbon and nitrogen isotope signatures. Trees and herbaceous plants had similar $\delta^{13}C$ values, but $\delta^{15}N$ values varied among sites. $\delta^{15}N$ values of trees were significantly higher at tributary 2 and those of herbaceous plants were significantly higher
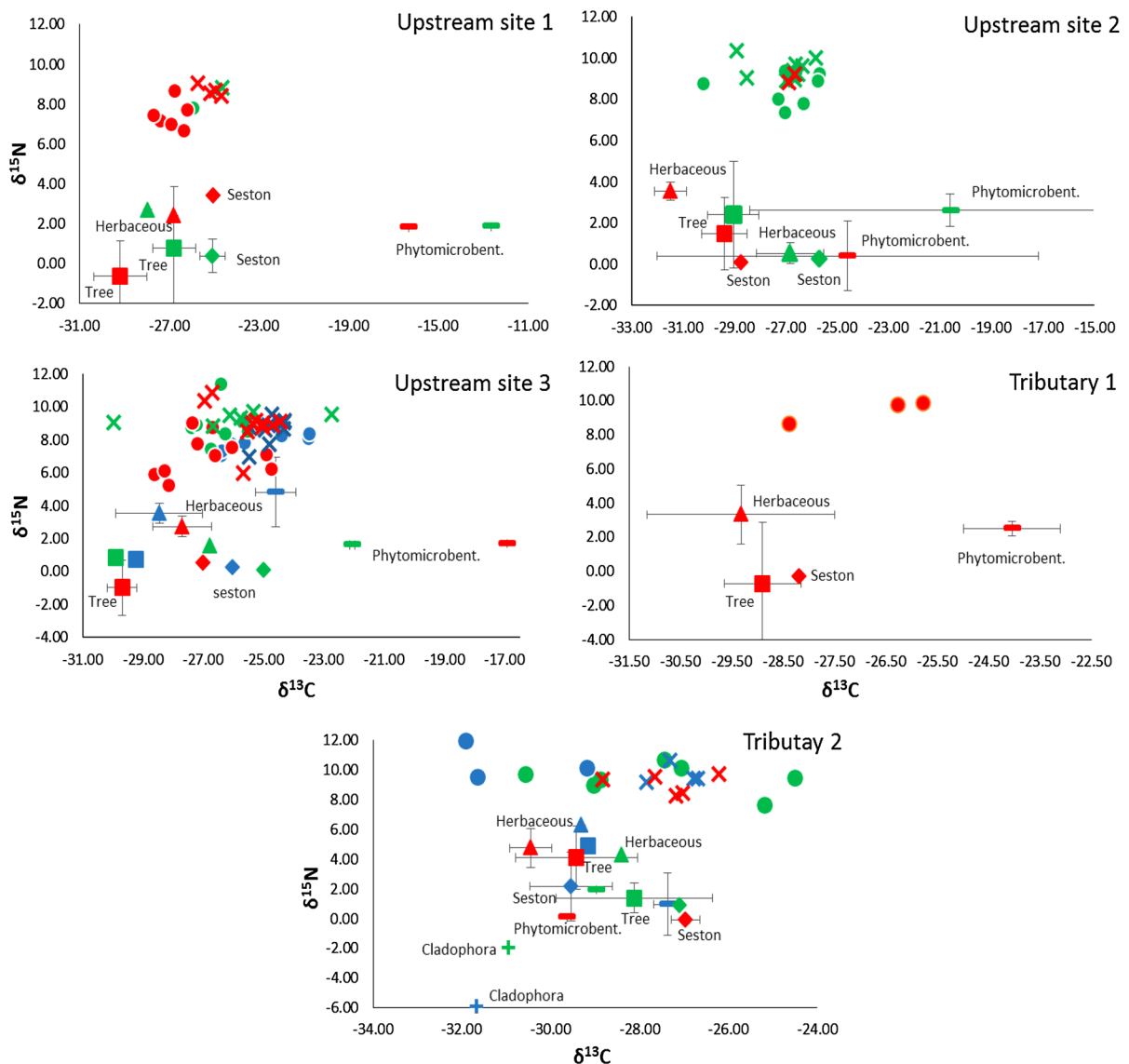
Fig. 2 Biplot of $\delta^{13}C$ and $\delta^{15}N$ values of tissues from fishes and primary production sources collected from upstream sites draining into the reservoir within the Upper Yeşilırmak River Basin, Turkey, during three seasons (*blue* = winter, *green* = spring, *red* = summer; x = *Squalius cephalus*, *filled circle* = *Capoeta banarescui*)

at the downstream site and tributary 2 (Figs. 2, 3). Ranges of mean $\delta^{13}C$ and $\delta^{15}N$ values of phytomicrobenthos were −29.83 to −12.63‰ and −0.79 to 5.38‰, respectively, and carbon ratios were lighter at tributary 2, and nitrogen ratios were heavier in the reservoir (Figs. 2, 3).

Mean $\delta^{13}C$ values of trees, seston, and phytomicrobenthos varied seasonally, whereas $\delta^{15}N$ values were relatively consistent among season. Trees and seston were more ^{13}C enriched during spring than

winter and summer, but phytomicrobenthos was relatively ^{13}C depleted during winter than spring and summer (Figs. 2, 3).

Isotopic signatures: omnivorous fishes

A total of 176 individuals of *Capoeta banarescui* and *Squalius cephalus* were captured across all survey sites and periods. $\delta^{13}C$ of *C. banarescui* muscle tissue ranged from −33.51 to −22.35‰ (mean =
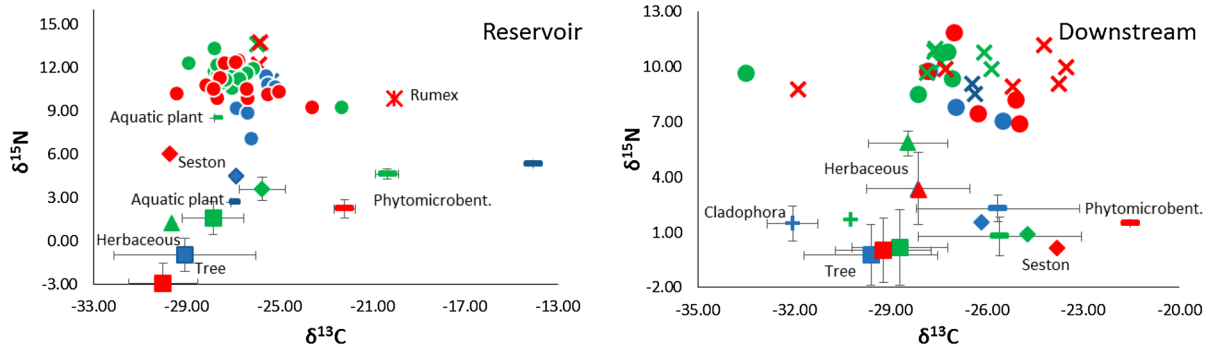
Fig. 3 Biplot of δ^{13}C and δ^{15}N values of tissues from fishes and primary production sources collected from the reservoir and one downstream site within the Upper Yeşilırmak River Basin, Turkey, during three seasons (*blue* = winter, *green* = spring, *red* = summer; x = *Squalius cephalus*, filled circle = *Capoeta banarescui*)

$-26.80‰ \pm 1.68$ SD), and δ^{15}N ranged from 5.28 to 13.32‰ (mean = 9.49‰ ± 1.80 SD) (Table 1; Figs. 2, 3). *Capoeta banarescui* had similar mean δ^{13}C values among sites, whereas δ^{15}N of this fish was higher in the reservoir and tributary two relative to other river sites (Table 1). The distribution of δ^{13}C values for *C. banarescui* (standard length ranging from 3.0 to 41.1 cm, with mean and standard deviation significantly greater for the reservoir sample (Table 1)) showed that they mostly depended on herbaceous plants in the river channel and aquatic plants in the reservoir (Figs. 2, 3).

Standard length and carbon signatures of *C. banarescui* pooled across all sites were not significantly correlated when data were pooled across both seasons ($r^2 = 0.03$, $P = 0.07$) or analyzed for winter and summer samples separately (winter—$r^2 = 0.02$, $P = 0.51$; summer—$r^2 = 0.06$, $P = 0.63$); however, the correlation was significant for spring ($r^2 = 0.10$, $P = 0.04$). For individual sites, carbon signatures pooled across seasons were significantly correlated with fish length only for tributary 2 ($r^2 = 0.81$, $P = 0.01$), reservoir ($r^2 = 0.13$, $P = 0.03$), and upstream site 3 ($r^2 = 0.22$, $P = 0.02$).

δ^{13}C values of *C. banarescui* from tributary 2 were higher during spring than winter, and higher at upstream site 3 during winter than summer (Table 1). At site 3, *C. banarescui* δ^{15}N was lower during summer than spring, and in the reservoir it was higher during spring than winter (Table 1). Fish length did not differ between seasons, except for site 3 where fish were longer during summer than winter (Table 1).

δ^{13}C of *S. cephalus* muscle tissue ranged from -31.90 to $-22.74‰$ (mean = $-26.13‰ \pm 1.47$

SD), and δ^{15}N ranged from 5.96 to 13.76‰ (mean = 9.43‰ ± 1.17 SD) (Table 1; Figs. 2, 3). *Squalius cephalus* was the most ^{13}C depleted at the tributary 2 and ^{13}C enriched at upstream site 1, 3 and in the reservoir. *S. cephalus* had highest δ^{15}N values in the reservoir, and similar δ^{15}N values among river and tributary sites (Table 1). On the other hand, δ^{13}C and δ^{15}N values of *S. cephalus* were distinct from values of *C. banarescui* in the reservoir and at upstream site 1 and tributary 2 (Table 1).

The correlation between *S. cephalus* standard length (range 4.40–43.7 cm) and δ^{13}C was not significant when data were pooled across all seasons and sites ($r^2 = 0.02$; $P = 0.21$) or pooled across sites for each season (winter—$r^2 = 0.02$, $P = 0.56$; summer—$r^2 = 0.06$, $P = 0.22$; spring—$r^2 = 0.01$, $P = 0.55$). When data were pooled across seasons for individual sites, δ^{13}C was significantly correlated with fish length only for tributary 2 ($r^2 = 0.61$, $P = 0.01$).

δ^{13}C and δ^{15}N values of *S. cephalus* were fairly consistent among sites and seasons, with only δ^{15}N differing between winter and spring at the downstream site (Table 1). Seasonal variation in the length of *S. cephalus* did not vary for each site (Table 1).

Spatial and seasonal variation of carbon sources supporting fish biomass

Isotopic values of the two species were vary within a given season and site in a part (Figs. 2, 3; Table 1). At the two most upstream sites on the river mainstream (upstream sites 1 and 2), herbaceous plants, trees, and seston were estimated by the SIAR model to be

Table 1 Mean $\delta^{13}C$ and $\delta^{15}N$ of muscle tissue from two omnivorous fishes and their mean standard length from samples collected during three seasons at seven sites within the Upper Yeşilırmak River Basin, Turkey (SD = standard deviation; N = the number of specimens), and mean $\delta^{13}C$ and $\delta^{15}N$ of zooplankton and benthic macroinvertebrates collected from the reservoir and downstream site during summer

Species/locations	Winter							Spring						
	$\delta^{13}C$	SD	$\delta^{15}N$	SD	SL	SD	N	$\delta^{13}C$	SD	$\delta^{15}N$	SD	SL	SD	N
Capoeta banarescui														
Upstream Site 1								−25.93	0.00	7.82	0.00	13.00	0.00	1
Upstream Site 2								−27.06	1.53	8.51	0.77	6.37	2.93	7
Upstream Site 3	−25.14	1.31	7.83	0.49	5.30	1.83	7	−26.48	0.71	8.94	1.20	9.77	3.20	7
Tributary 1														
Tributary 2	−30.92	1.51	10.57	1.28	4.10	0.79	3	−26.85	2.40	9.90	1.31	21.03	8.16	9
Reservoir	−26.12	0.70	9.81	1.52	21.30	5.93	7	−27.00	1.50	11.59	0.94	25.92	7.18	14
Downstream	−26.77	1.17	8.23	1.41	13.80	2.98	3	−29.00	3.04	9.60	0.95	11.00	2.58	4
Squalius cephalus														
Upstream Site 1								−24.61	0.00	8.83	0.00	9.50	0.00	1
Upstream Site 2								−26.97	0.92	9.42	0.46	8.41	2.82	11
Upstream Site 3	−24.85	0.45	8.67	0.72	13.37	10.57	11	−26.01	2.15	9.30	0.30	8.84	2.13	7
Tributary 1														
Tributary 2	−27.09	1.00	9.69	1.05	9.78	3.32	8							
Reservoir	−25.36	0.00	11.05	0.00	17.50	0.00	1	−25.94	0.00	13.58	0.00	26.80	0.00	1
Downstream	−26.42	0.06	8.80	0.39	17.00	0.99	2	−27.08	0.87	10.40	0.55	11.33	2.39	6
Zooplankton														
Reservoir														
Downstream														
Benthic macroinvertebrate														
Downstream														

Species/locations	Summer							Mean						
	$\delta^{13}C$	SD	$\delta^{15}N$	SD	SL	SD	N	$\delta^{13}C$	SD	$\delta^{15}N$	SD	SL	SD	N
Capoeta banarescui														
Upstream Site 1	−26.90	0.59	7.47	0.71	14.40	5.22	6	−26.76	0.65	7.52	0.66	14.2	4.79	7
Upstream Site 2								−27.06	1.53	8.51	0.77	6.37	2.93	7
Upstream Site 3	−26.87	1.34	7.08	1.22	13.30	4.91	10	−26.25	1.36	7.84	1.28	9.94	4.94	24
Tributary 1	−26.82	1.38	9.46	0.68	7.37	0.81	3	−26.82	1.38	9.46	0.68	7.37	0.81	3
Tributary 2								−27.87	2.83	10.07	1.28	16.8	10.35	12
Reservoir	−26.84	1.51	10.79	1.05	28.76	8.38	13	−26.76	1.38	10.92	1.27	26.06	7.74	34
Downstream	−26.25	1.23	8.85	2.01	13.54	2.68	5	−27.29	2.22	8.95	1.54	12.76	2.78	12
Squalius cephalus														
Upstream Site 1	−25.11	0.44	8.67	0.26	9.98	3.50	4	−25.01	0.44	8.7	0.24	9.88	3.04	5
Upstream Site 2	−26.77	0.17	9.02	0.26	7.30	0.42	2	−26.94	0.84	9.36	0.45	8.24	2.61	13
Upstream Site 3	−25.47	0.81	8.95	1.28	10.11	3.44	10	−25.36	1.24	8.93	0.91	11.08	7.08	28
Tributary 1														
Tributary 2	−27.38	0.96	9.07	0.66	8.74	5.91	5	−27.28	0.76	9.34	0.69	10.37	4.83	13
Reservoir	−25.86	0.04	12.98	1.11	23.50	2.83	2	−25.75	0.27	12.65	1.27	22.83	4.21	4
Downstream	−25.98	3.21	9.63	0.92	14.00	3.11	6	−26.51	2.13	9.84	0.89	13.29	3.18	14

Table 1 continued

Species/locations	Summer							Mean						
	δ^{13}C	SD	δ^{15}N	SD	SL	SD	N	δ^{13}C	SD	δ^{15}N	SD	SL	SD	N
Zooplankton														
Reservoir	−29.95	0.11	7.85	0.31										
Downstream	−29.10	0.00	3.69	0.00										
Benthic macroinvert														
Downstream	−28.83	0.48	3.66	0.64										

Table 2 Means and 1st–99th‰ ranges (in parentheses) of SIAR model-estimated proportions of source contributions to biomass of *Capoeta banarescui* and *Squalius cephalus* at seven sites

Species	Trees	Seston	Herbaceous plants	Phytomicrobenthos	Aquatic plants	*Rumex* sp.[a]
Capoeta banarescui						
Upstream site 1	0.30 (0.01–0.53)	0.19 (0.00–0.38)	0.48 (0.16–0.84)	0.03 (0.00–0.08)		
Upstream site 2	0.30 (0.01–0.54)	0.25 (0.00–0.47)	0.28 (0.00–0.50)	0.17 (0.00–0.35)		
Upstream site 3	0.04 (0.00–0.13)	0.06 (0.00–0.18)	0.75 (0.57–0.90)	0.15 (0.07–0.23)		
Tributary 1	0.25 (0.00–0.48)	0.26 (0.00–0.50)	0.28 (0.00–0.52)	0.21 (0.00–0.40)		
Tributary 2	0.27 (0.00–0.53)	0.15 (0.00–0.38)	0.43 (0.07–0.84)	0.15 (0.00–0.37)		
Reservoir	0.03 (0.00–0.07)	0.20 (0.00–0.41)	0.04 (0.00–0.12)	0.02 (0.00–0.06)	0.61 (0.39–0.79)	0.11 (0.02–0.19)
Downstream site	0.11 (0.00–0.35)	0.11 (0.00–0.30)	0.67 (0.31–0.96)	0.11 (0.00–0.30)		
Squalius cephalus						
Upstream site 1	0.25 (0.00–0.46)	0.29 (0.00–0.52)	0.34 (0.05–0.61)	0.12 (0.03–0.22)		
Upstream site 2	0.34 (0.09–0.58)	0.28 (0.02–0.49)	0.24 (0.01–0.43)	0.14 (0.03–0.26)		
Upstream site 3	0.05 (0.00–0.14)	0.10 (0.00–0.28)	0.61 (0.39–0.79)	0.24 (0.17–0.31)		
Tributary 1						
Tributary 2	0.27 (0.00–0.51)	0.22 (0.00–0.45)	0.29 (0.00–0.59)	0.23 (0.00–0.45)		
Reservoir	0.13 (0.00–0.28)	0.19 (0.00–0.35)	0.18 (0.00–0.33)	0.11 (0.00–0.24)	0.20 (0.00–0.37)	0.19 (0.02–0.33)
Downstream site	0.11 (0.00–0.32)	0.14 (0.00–0.36)	0.56 (0.23–0.89)	0.19 (0.00–0.38)		

The SIAR procedure is described by Parnel et al. (2010)

[a] *Rumex* sp. = samples of terrestrial vegetation

dominant production sources supporting both fish species (Figs. 2, 4; Table 2). At upstream site 3, herbaceous plants appeared to be the most important source supporting biomass of both species (Figs. 2, 4; Table 2). These two species appeared to assimilate more allochthonous (herbaceous plants and trees) and less autochthonous production sources (seston and phytomicrobenthos) at tributaries 1 and 2 (Figs. 2, 4; Table 2). In the reservoir, most of the assimilated biomass of *C. banarescui* was derived from aquatic plants and seston, whereas *S. cephalus* assimilated biomass from all basal production sources. Herbaceous plants appeared to

Table 3 SIAR model estimates of seasonal mean proportional contributions of production sources to biomass of *Capoeta banarescui* and *Squalius cephalus*

Species	Winter					Spring				
	Trees	Seston	Herbac.	Phytom.	Aquatic	Trees	Seston	Herbac.	Phytom.	Aquatic
Capoeta banarescui										
Upstream Site 1						0.26	0.25	0.26	0.23	
Upstream Site 2						0.44	0.20	0.25	0.11	
Upstream Site 3	0.12	0.16	0.35	0.36		0.35	0.21	0.29	0.15	
Tributary 1										
Tributary 2	0.27	0.24	0.30	0.19		0.22	0.22	0.35	0.21	
Reservoir	0.14	0.45		0.06	0.35	0.02	0.03	0.02	0.04	0.89
Downstream site	0.21	0.26	0.27	0.25		0.24	0.19	0.40	0.18	
Squatius cephalus										
Upstream Site 1						0.26	0.25	0.26	0.23	
Upstream Site 2						0.46	0.23	0.25	0.06	
Upstream Site 3	0.11	0.23	0.34	0.33		0.27	0.22	0.28	0.23	
Tributary 1										
Tributary 2	0.26	0.17	0.29	0.28						
Reservoir	0.25	0.26		0.23	0.26	0.20	0.20	0.20	0.20	0.20
Downstream site	0.22	0.27	0.26	0.25		0.24	0.20	0.48	0.08	

Species	Summer				
	Trees	Seston	Herbac.	Phytom.	*Rumex*
Capoeta banarescui					
Upstream Site 1	0.27	0.09	0.61	0.04	
Upstream Site 2					
Upstream Site 3	0.13	0.18	0.62	0.06	
Tributary 1	0.25	0.26	0.28	0.21	
Tributary 2					
Reservoir	0.02	0.64		0.03	0.31
Downstream site	0.28	0.20	0.34	0.17	
Squatius cephalus					
Upstream Site 1	0.28	0.25	0.36	0.11	
Upstream Site 2	0.25	0.25	0.24	0.25	
Upstream Site 3	0.20	0.25	0.35	0.19	
Tributary 1					
Tributary 2	0.29	0.33	0.22	0.16	
Reservoir	0.25	0.30		0.22	0.23
Downstream site	0.24	0.22	0.32	0.23	

The SIAR procedure is described by Parnel et al. (2010)

Herbac. herbaceous plants, *Phytom.* phytomicrobenthos, *Aquatic* aquatic plants

contribute greater to both fish biomass, whereas phytomicrobenthos particularly important for *S. cephalus* at downstream site (Figs. 3, 4; Table 2).

Results from the SIAR model indicated that trees accounted for a large fraction of two species biomass at upstream site 2 and site 3 for *C. banarescui*, and

herbaceous plants was also an important contributor to fish biomass, although *C. banarescui* from tributary 2 assimilated material from all food sources in spring. Herbaceous plant contributions to fish biomass were greater at the downstream site during the spring period of high fluvial discharge, and trees contributions for these species also were important at the downstream site (Figs. 2, 3; Table 3). In the reservoir, terrestrial and aquatic production sources accounted for significant fractions of *S. cephalus* biomass, but aquatic plants were the most important source supporting *C. banarescui* biomass during spring. At upstream sites (site 1 and 3) during low-flow conditions of summer, herbaceous plants were an important basal sources supporting *C. banarescui*, however both herbaceous plants and phytomicrobenthos were an important food source for this species at site 3 during winter (Figs. 2, 3; Table 3). *C. banarescui* seemed to assimilate material from all four sources during summer and winter at the downstream site and tributary 1 and 2 during summer and winter, respectively. During summer and winter, *S. cephalus* biomass at downstream and upstream sites likely was supported by all primary production sources (Figs. 2, 3; Table 3). In the reservoir, seston appeared to be the dominant basal sources supporting biomass of both species during summer and winter, but *Rumex* sp. also could have been an important source during summer, and aquatic plants appear to have been important during winter for biomass of *C. banarescui*. However *S. cephalus* assimilated material from multiple aquatic and terrestrial sources in the reservoir during winter and summer (Figs. 2, 3; Table 3).

Carbon isotopic signatures of zooplankton from the reservoir and downstream site were similar during summer (samples were not collected during other seasons), whereas the nitrogen signature of zooplankton from the reservoir was higher than that from zooplankton collected from the downstream site during summer. Isotopic signatures of zooplankton and benthic macroinvertebrates from the downstream site were similar (Table 1). Based on $\delta^{13}C$ and $\delta^{15}N$ signatures, benthic invertebrates and zooplankton seem to be important food resources for omnivorous fishes during summer at the downstream site. According to the SIAR results estimates, the two species probably assimilated more benthic macroinvertebrate biomass (mean contribution: 0.60) than zooplankton biomass (mean contribution: 0.40).

Discussion

Isotopic signatures of basal sources and omnivorous fishes

In the Yeşilırmak River, autochthonous sources (seston and phytomicrobenthos) tended to be more ^{13}C enriched than allochthonous sources (trees and herbaceous C_3 plants) and the former sources seemed to be the most important contributors to fish biomass within Almus Reservoir. Isotopic ratios of aquatic primary producers were generally more seasonally and spatially variable than terrestrial plants. $\delta^{15}N$ of all types of primary production sources varied considerably between locations. $\delta^{13}C$ of seston and phytomicrobenthos differed among locations; trees and herbaceous plants had relatively consistent $\delta^{13}C$ values across locations for a given season. $\delta^{13}C$ values of seston, phytomicrobenthos and trees varied among seasons, and were similar to values reported for these groups from other temperate rivers (Hladyz et al., 2012; Pingram et al., 2012; Growns et al., 2013). Mean $\delta^{13}C$ of phytomicrobenthos generally was lower at the downstream site and tributary 2, and higher in the reservoir relative to upstream sites. An explanation of this kind of longitudinal patterns is that local inorganic carbon sources, photosynthetic rate, and/or boundary layer effects influenced isotopic fractionation during carbon assimilation by algae at different sites (Finlay et al., 1999; Finlay, 2003). Composition of the phytomicrobenthos (algae, bacteria, fungi, and detritus) which can alter spatiotemporally, can also cause to change its isotope signatures (Hladyz et al., 2012).

The water released from the hypolimnion may contain dissolved inorganic carbon that is relatively depleted in ^{13}C and inorganic nitrogen enriched in ^{15}N (Growns et al., 2013), and this could have contributed to the spatial variation observed in $\delta^{13}C$ of phytomicrobenthos at the downstream site. Several studies have reported similar impoundment effects on benthic algae $\delta^{13}C$ signatures (Chen & Jia, 2009; Chessmen et al., 2009; Smokorowski et al., 2011). Unlike other studies that have demonstrated ^{15}N enrichment of benthic algae downstream from dams (Chessmen et al., 2009; Growns et al., 2013), our investigation found little difference in phytomicrobenthos $\delta^{15}N$ and fairly consistent $\delta^{15}N$ values for *Cladophora* and C_3 herbaceous plants across the study area. This finding for phytomicrobenthos is surprising given that the

composition of the riparian forests can influence $\delta^{15}N$ of inorganic nitrate in local stream water. Alder trees (*Alnus* spp.), which are abundant in Yesilirmak watersheds, can reduce $\delta^{15}N$ of inorganic nitrate in local stream water (Scott et al., 2009).

Our seston samples probably contained mixtures of phytoplankton and suspended fine particulate organic matter from autochthonous and allochthonous detritus. The isotopic composition of seston, therefore, may reflect a terrestrial to aquatic gradient (Kendall et al., 2001). Freshwater algae usually are more ^{13}C depleted and more ^{15}N enriched than allochthonous detritus (Chen & Jia, 2009). In the Yeşilırmak River, seston $\delta^{13}C$ was not appreciably lower at the downstream site when compared to values at other sites, which could indicate that allochthonous material dominates the seston in the river channel below the dam. The lowest $\delta^{13}C$ value for seston was recorded in the reservoir during summer, and this finding is consistent with a greater abundance of phytoplankton during the warm summer period.

Two omnivorous fish showed partially spatial and seasonal variation in their C or N isotopes values. Spatial differences in $\delta^{13}C$ of *S. cephalus* may be link to changes in food preference or the isotopic composition of its diet among sites. Two fish species from reservoir and *C. banarescui* from tributary 2 generally showed higher $\delta^{15}N$. Nutrient loading from urban centers and farms can elevate $\delta^{15}N$ values of aquatic primary consumers in streams of affect watersheds (Vander Zanden and Rasmussen, 1999; Vander Zanden et al., 2005; Bergfur et al., 2009). Although Almus Reservoir is naturally oligotrophic, the lake has a substantial human population within its watershed and also supports cage culture of fishes. The relatively high $\delta^{15}N$ of fish from tributary 2 most likely derived from high $\delta^{15}N$ of nitrogen in runoff from agriculture and domestic sewage.

Seasonal and spatial variation in $\delta^{13}C$ were not associated with standard length of either fish species, except for *C. banarescui* from tributary site 2 during spring, suggesting that these fishes do not undergo strong ontogenetic dietary shifts over the range of body sizes in our samples. At tributary site 2, isotopic signatures of small specimens (3.2–4.7 cm) captured during winter were depleted in ^{13}C (range δ^{13} −31.93 to −29.19‰; $\delta^{13}C$ mean −30.92‰) when compared to larger specimens (10.6–35 cm; range $\delta^{13}C$ −23.16

Fig. 4 Spatial variation among estimated contributions from ▶ primary production sources to biomass of *Capoeta banarescui* and *Squalius cephalus* in the Upper Yeşilırmak River Basin, Turkey (frequency and 1st–99th‰ ranges for SIAR-estimated proportional contributions)

to 30.57‰; $\delta^{13}C$ mean −26.85‰) captured during spring, and this implies that either fish changed their diet during spring, or larger fish had recently migrated into the area and reflected feeding histories at other sites. Conspecifics from the reservoir had $\delta^{13}C$ values (mean −27.0‰) similar to these large fish, suggesting that they had migrated upstream to spawn during spring. Specimens containing ripe eggs (S. Akin personal observation) during spring at site 2 provide further support that fish had migrated upstream to spawn. *Capoeta banarescui* consumes more chironomid larvae in this tributary compared to other sites in the basin where this resource is less abundant (Turan and Akin, unpublished data), and this is consistent with $\delta^{13}C$ values of chironomid larvae (−26.46‰).

Capoeta banarescui mean $\delta^{13}C$ changed seasonally at tributary 2, mean $\delta^{15}N$ changed seasonally in the reservoir, and means of both $\delta^{13}C$ and $\delta^{15}N$ changed seasonally at upstream site 3. *S. cephalus* mean $\delta^{15}N$ changed seasonally only at the downstream site, and there were no differences for mean $\delta^{13}C$. These results can be explained by two hypotheses. The first one is that isotopic composition of fish muscle tissue might have reflected seasonal variation in the isotopic composition of primary producers supporting the aquatic food web. The second one is that fish diets might have changed in response to seasonally abundant food resources. Interpretation on the basis of dietary temporal variation depends on isotopic turnover rates in tissues. Turnover rates are affected by multiple factors, including tissue type, body size, sexual maturity, and growth rate, with relatively fast turnover rates (<3 months) reported for fish muscle tissue (Buchheister & Latour, 2010; Jardine et al., 2011). For example, grass carp (*Ctenopharyngodon idella*) muscle was reported to turnover in about 53 days on average (Xia et al., 2013). According to Hladyz et al. (2012), isotopic composition of muscle probably does not reflect food resources when growth is limited, such as during winter, because energy is allocated to basal metabolism and gonad growth instead of somatic growth.
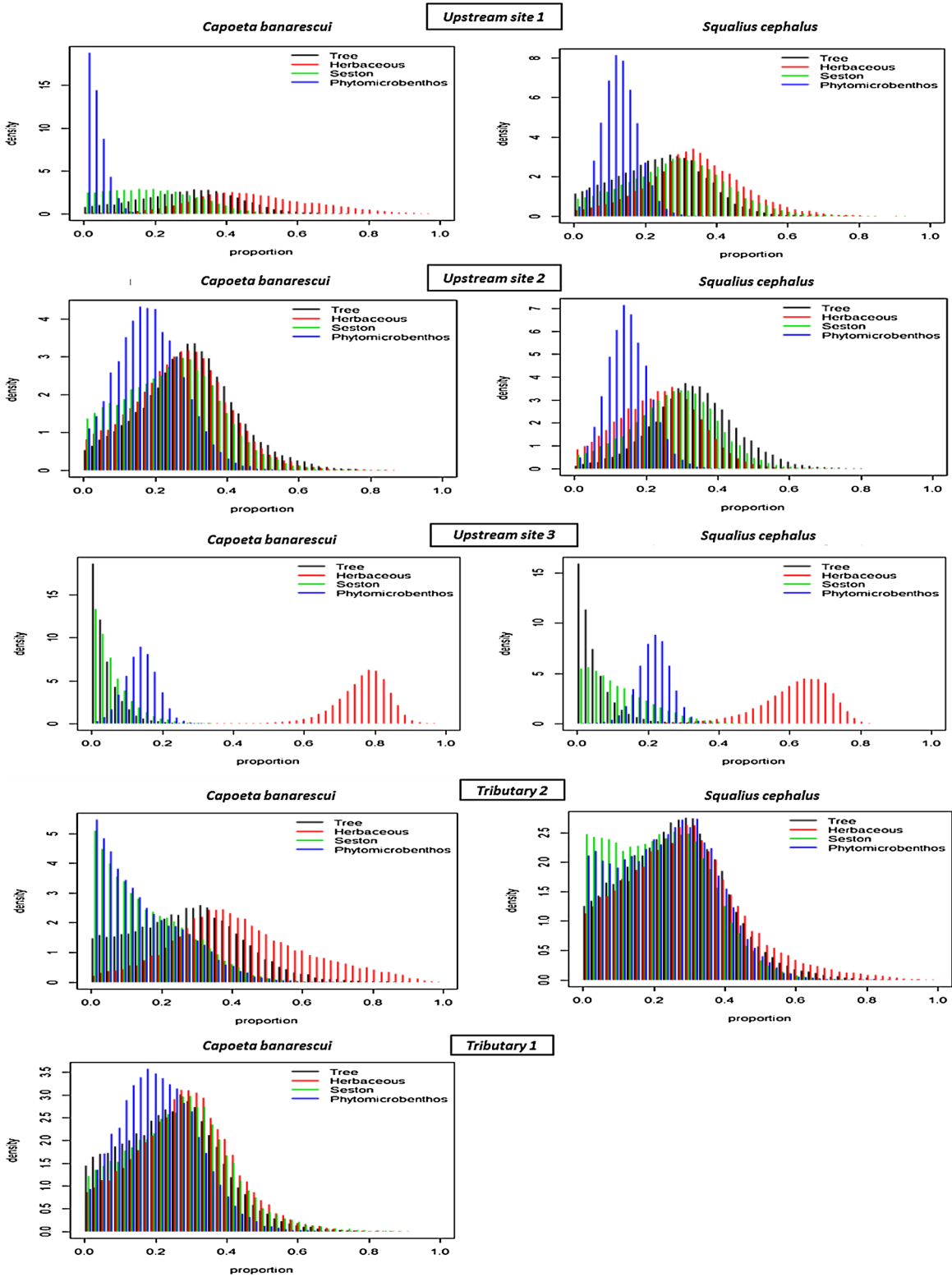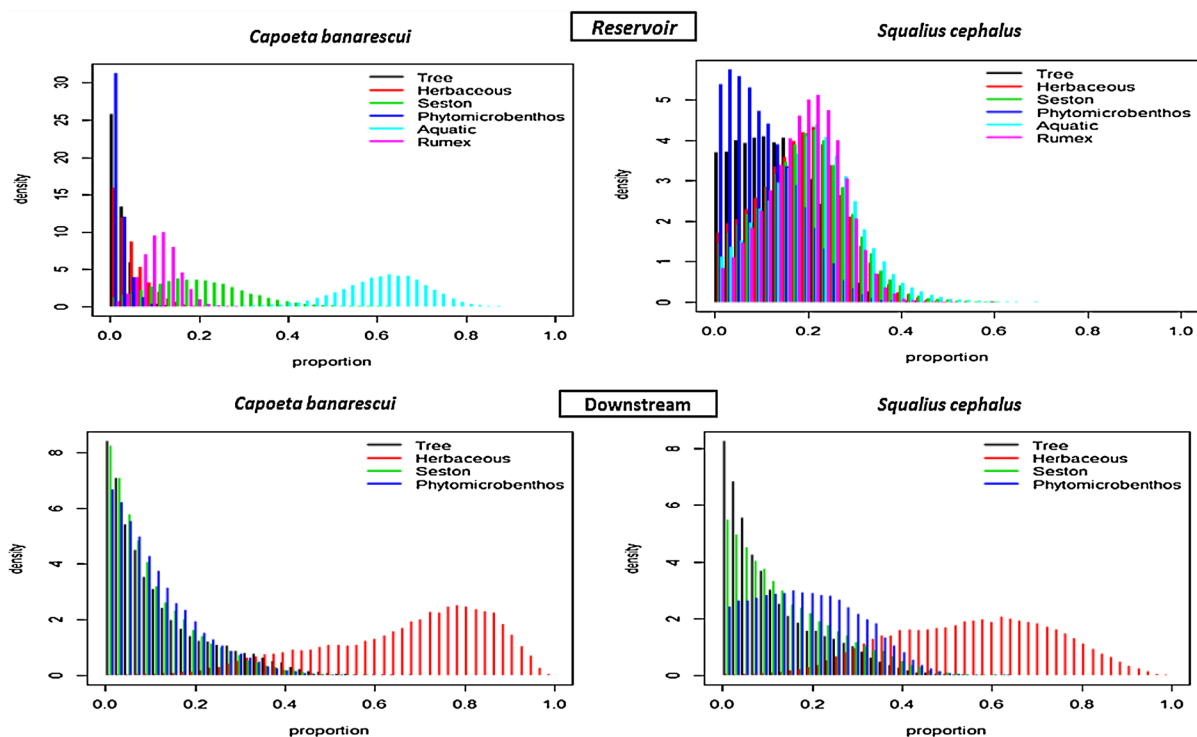
Fig. 4 continued

Carbon sources supporting fish biomass and river conceptual models

In order to estimate proportional contributions of alternative resources to consumer biomass, isotopic mixing models require sufficiently distinct values among the resources. Carbon and nitrogen isotope ratios of trees, herbaceous plants, and seston in the Yesilirmak River overlapped considerably, and this compromised our ability to discriminate production source contributions to fish biomass. Herbaceous plants, trees, and seston appeared to be important primary production sources supporting populations of both omnivorous fishes at the two most upstream sites on the river mainstream (sites 1 and 2), but herbaceous plants had an even greater contribution at upstream site 3. Hydrological dynamics influenced the relative importance of allochthonous production sources for fishes. Transported detritus, leaf litter, and herbaceous plants from headwaters probably accumulates at upstream site 3 where water velocity slows as it begins to enter the reservoir. Within Almus Reservoir, *C. banarescui* appeared to be supported mostly by autochthonous production (aquatic plants and seston to a lesser extent), whereas *S. cephalus* seemed to assimilate both allochthonous and autochthonous production sources. Other stable isotope investigations of lake and reservoir food webs have concluded that aquatic metazoan consumers relied on both terrestrial and benthic primary production (Solomon et al., 2011), phytoplankton (Hoeinghaus et al., 2007), benthic algae (Vander Zanden et al., 2011) and terrestrial detritus (Cole et al., 2006). Vannote et al. (1980) and Chang et al. (2012) reported that importance of benthic algae and phytoplankton should be greater with increasing channel size and decreasing canopy cover. The SIAR model estimated that riparian herbaceous plants were the most important source supporting biomass of two species at the downstream site and upstream site 3. In contrast, the contribution of seston contributions appeared to be greater at most of the upstream sites (1 and 2) when compared to upstream site 3 and downstream site.

At the downstream site, both omnivorous fishes appeared to assimilate material derived mostly from herbaceous plants. However, isotopic signatures of

zooplankton from the reservoir and downstream site suggest that zooplankton exported from the reservoir could have subsidized the downstream food web. Given the similarity of carbon isotopic signatures of zooplankton collected from the reservoir and downstream site, and considering that seston from downstream was heavier (−23.79‰) than zooplankton, it is possible that zooplankton drifting downstream from the reservoir may have directly or indirectly subsidized fishes at the downstream site. This interpretation is consistent with the findings from several studies that demonstrated how reservoirs subsidized downstream river food webs via export of plankton (Doi et al., 2008; Mercado-Silva et al., 2009; Helmus et al., 2013).

We hypothesized that during spring when flows are high and lateral connectivity is greater, terrestrial organic material assumes greater importance for aquatic food webs. Allochthonous production sources made major contributions to fish biomass at upstream survey sites. *Capoeta banrescui* and *S. cephalus* are both reported to feed on terrestrial insects, and they therefore should reflect terrestrial primary production sources during spring (Caffrey et al., 2008; Akin et al., 2010). The greater contribution of terrestrial matter to fish biomass at the site downstream from Almus Reservoir during spring could be related to higher turbidity during that period that reduced light penetration and autochthonous primary production (Roach et al., 2014). Wellard Kelly et al. (2013) found that benthic macroinvertebrates located just below the Glen Canyon Dam in the western United States depended on limnetic algae, whereas terrestrial detritus became more important with greater distance from the dam, especially during high flow periods. In contrast, some studies report that algal production was the dominant energy source in large river food webs during high-flow pulses (Huryn et al., 2001; Herwig et al., 2007; Hladyz et al., 2012). Despite the potential for more terrestrial plant and animal material to enter the littoral zone during spring, autochthonous production sources seemed to support most fish biomass, a finding that contrasts those from other studies (Herwig et al., 2004; Wang et al., 2011).

We hypothesized that during low-flow periods of summer, benthic algae and phytoplankton should become a more important production source supporting fishes in the Yeşilırmak River, because higher water transparency and temperature promote algal growth (Roach et al., 2014). Overall, our results did not support this hypothesis; however, findings for *S. cephalus* from tributary 2, upstream site 2, and the downstream site did not directly contradict this explanation. Terrestrial riparian vegetation was inferred to be the most important production source during summer at both downstream and upstream sites, a pattern observed by some other investigations (Reid et al., 2008; Hladyz et al., 2012). During spring, high flows and turbidity should reduce standing algae biomass and result in greater assimilation of material derived from riparian vegetation by fish and other aquatic consumers. The omnivorous fishes examined in our study assimilated material derived from mostly allochthonous sources throughout the year, a pattern consistent with findings from several other studies conducted in upper river catchments (Herwig et al., 2004; Hadwen et al., 2010; Chang et al., 2012). Fishes inhabiting the Almus Reservoir were the exception; there autochthonous production appears to be the most important energy source supporting *C. banarescui* and *S. cephalus*, trophic generalists able to inhabit at a wide range of lotic and lentic habitats. Isotopic ratios of both species differed along the longitudinal fluvial gradient, and patterns likely were influenced by the reservoir as well as inorganic nutrient loading from watersheds. Isotopic mixing model results indicated that, with the possible exception of the site located downstream from the dam, the influence of Almus Reservoir on sources of primary production assimilated by omnivorous fishes in this system was small relative to effects from watershed characteristics and seasonal changes in temperature and hydrology.

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