

## Spatial and temporal variation in food web structure of an impounded river in Anatolia

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**Abstract.** Dams interrupt the longitudinal connectivity of rivers by impeding the movement of water, sediments and organisms, which, in turn, could affect aquatic biodiversity and food web ecology. Using stable isotope analysis, we examined spatiotemporal variation in food web structure at four sites in the upper Yeşilırmak River, Anatolia Peninsula, Turkey, in relation to environmental parameters and a dam. It was apparent that the dam created discontinuity in the longitudinal fluvial gradient of fish species richness, with more species observed at upstream sites. Fish assemblages from different sites and seasons occupied distinct areas of isotopic space. Isotopic niche space, trophic diversity, variation in  $\delta^{13}\text{C}$  of basal resources and assemblage redundancy were all higher for the fish assemblage at the site downstream from the dam compared with the site above the dam, a possible indication of greater interspecific dietary variation. Food chain length (the range in  $\delta^{15}\text{N}$ ) was lower at the downstream site, possibly resulting from a greater tendency towards omnivory. The findings strongly suggest that the dam affects not only environmental conditions and fish diversity, but also trophic ecology. The results of the present study emphasise the need for research to assess potential effects of new dams in Anatolia on aquatic communities and ecosystem dynamics in rivers.

**Additional keywords:** Bayesian mixing model, Cyprinidae, fish assemblage, hydroelectric dam, isospace, stable isotope, trophic ecology.

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### Introduction

The sustainability of biodiversity and ecosystem functioning depends on knowledge of the structure and functions of species assemblages, and this understanding is challenged by natural variation in both time and space. In rivers, assemblage trophic structure varies spatially in association with longitudinal and lateral gradients of geomorphology, environmental conditions and disturbance regimes (Winemiller 1990; Hoinghaus *et al.* 2007; East *et al.* 2017). Trophic interactions in river communities also respond to temporal variation in abiotic environmental variables, such as temperature (Glazier 2012; Hette-Tronquart *et al.* 2016) and hydrology (Roach *et al.* 2009).

River hydrology strongly affects the amount and quality of alternative sources of primary production available to aquatic organisms (Vannote *et al.* 1980; Power *et al.* 2013; Roach *et al.* 2014). Greater environmental heterogeneity in larger aquatic ecosystems appears to be associated with greater trophic diversity and less omnivory (Post *et al.* 2000).

Human actions also affect trophic structure and functions of river communities. For example, Chester and Norris (2006) and Smokorowski *et al.* (2011) reported that aquatic macroinvertebrates and fish underwent significant dietary shifts following dam construction. Helmus *et al.* (2013) found that fish inhabiting tail waters of a dam in central Mexico were feeding heavily

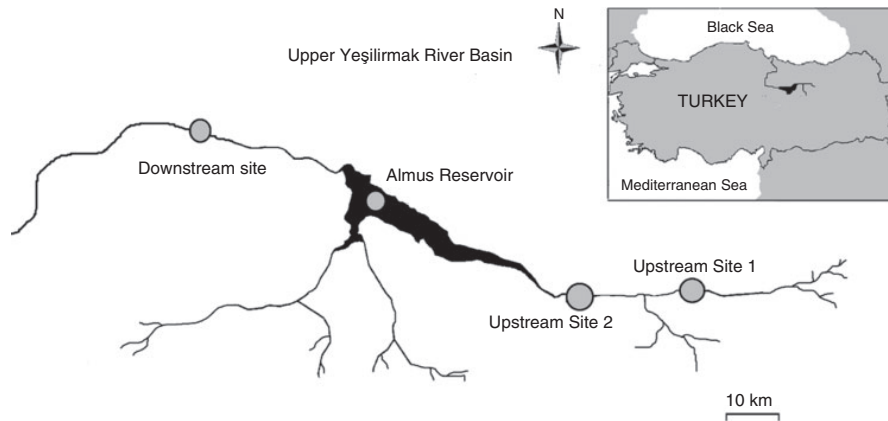


Fig. 1. Location of the study sites in the main channel of the upper Yeşilirmak River, Turkey.

on reservoir-derived zooplankton, a food web spatial subsidy that resulted in high fish densities. When the dam gates were closed, water flow and the zooplankton subsidy ceased, and fish were concentrated in pools and switched to feeding on benthic macroinvertebrates. In addition to creating barriers to longitudinal habitat connectivity, river impoundments alter the magnitude, timing and duration of flow pulses, as well as sediment dynamics, all of which cause shifts in resource availability, assemblage structure and food web dynamics (Hoeinghaus *et al.* 2008; Wang *et al.* 2016).

Understanding how dams alter community trophic structure is critical for fisheries management. Herein we report findings of a study of spatial and temporal variation in fish assemblage trophic ecology in a major river in northern Anatolia. The Yeşilirmak River is the second longest river in Turkey and is affected by threats common to rivers in semi-arid regions, including changes in flow regime by dams and catchment land use. The natural flow of the river has been altered by operation of five power plants, and a previous study (Akin *et al.* 2011) found that variations in trophic position and niche breadth of perch (*Perca fluviatilis*) were associated with impoundment in the lower Yeşilirmak River. Kaymak *et al.* (2015) analysed how the Almus Dam affected assimilation of carbon sources by two omnivorous cyprinids (*Capoeta banarescui* and *Squalius cephalus*) in the upper Yeşilirmak Basin. In that study, analysis of carbon and nitrogen isotope ratios revealed spatial and seasonal variation for both fish as well as production sources supporting their biomass. Isotope mixing model results indicated that herbaceous plants, trees and seston were the most important production sources supporting both fish species at upstream sites on the river mainstream, with herbaceous plants making an even greater contribution at sites directly above and below the reservoir. The effect of the dam on the trophic ecology of these omnivorous fish appeared to be small relative to effects from watershed characteristics and seasonal changes in temperature and hydrology. The present study extends previous research on the upper Yeşilirmak River to examine relationships of environmental variables at locations above and below the Almus Dam with the food web structure of local fish assemblages. Using stable isotope-based community metrics, we investigated how

assemblage trophic structure differs among locations (two upstream sites, one reservoir site and one site below the reservoir) across seasons.

Fluvial gradients in river networks affect aquatic food webs through changes in ecosystem productivity, availability of resources and consumer assemblage structure (Hoeinghaus *et al.* 2007; Winemiller *et al.* 2011). We hypothesised that by altering and fragmenting instream habitat, the Almus Dam disrupts natural trends in fish assemblage structure and trophic ecology along the longitudinal fluvial gradient. For example, community trophic structure along the longitudinal fluvial gradient may not conform to the river continuum model (Vannote *et al.* 1980). Kaymak *et al.* (2015) found little direct effect of the Almus Reservoir on the trophic ecology of two omnivorous cyprinids; however, the entire fish assemblage may reveal different patterns. For example, the greater ecosystem size and abundant (and perhaps heterogeneous) resources of the reservoir should affect trophic ecology at the assemblage level. We also predicted that assemblage trophic structure should change seasonally in response to variations in hydrology and temperature.

## Materials and methods

### Study area

The Yeşilirmak River, the second longest river in a semi-arid climate of Turkey, originates within the Köse Mountains in north-eastern Turkey and flows into the Black Sea. The Yeşilirmak catchment covers an area of 36 114 km<sup>2</sup>, and is ~519 km long. Annual precipitation is 500 mm, and water temperature ranges from -2 to 26°C (Jin *et al.* 2013). Mean annual discharge of the Yeşilirmak River is 5.80 m<sup>3</sup> s<sup>-1</sup>. Precipitation and discharge tend to be low during summer and high during spring when precipitation and snowmelt are high (Jin *et al.* 2013). The river has three main branches: the Tozanlı in the upper catchment and the Kelkit and Çekerek in the lower catchment. The present study was conducted in the Tozanlı River (Fig. 1), where the catchment is dominated by meadows and pastures with minor agricultural components. Relative to the lower reaches of the Yeşilirmak, the upper Yeşilirmak River

has relatively high water velocity and low turbidity. Two dams (Almus and Atakoy reservoirs) were constructed on the upper Yeşilirmak. The Almus Reservoir (area 3.130 km<sup>2</sup>, mean depth 30 m; Kaymak 2015) was constructed in 1966 for flood control, hydropower generation and to supply water for irrigation. The Almus Reservoir is also used for cage culture of rainbow trout (*Oncorhynchus mykiss*). The Atakoy Reservoir is further upstream, smaller (area 0.50 km<sup>2</sup>) and was constructed in 1977 to supply water for hydropower generation. Eighteen fish species have been recorded within the upper catchment of the Yeşilirmak River Basin (Kaymak 2015). In terms of both number of species and population abundance, Cyprinidae is the most dominant family in the upper catchment. In addition to rainbow trout, wels catfish (*Silurus glanis*), crucian carp (*Carassius carassius*) and common carp (*Cyprinus carpio*) have been stocked in the Almus Reservoir. A cyprinid endemic to the Yeşilirmak Basin, namely *Capoeta banarencui*, was recently described (Turan *et al.* 2006). Unfortunately, we have no pre-impoundment data for fish assemblage composition. During the present study, a small number of the native cyprinid *Capoeta sieboldii* were found only at one upstream site (Site 2 of the present study) and in the reservoir during spring, but, according to local fishermen and own observations (N. Kaymak, pers. obs.), this species has not been captured or observed subsequently.

Components of the aquatic food webs were sampled at four sites (Fig. 1) during three seasons (winter, spring and summer; except upstream Site 1, which was surveyed only during spring and summer) from January 2011 to September 2011. Site 1 (885 m above sea level) and Site 2 (812 m above sea level) were located in the upstream area of the river. Site 1 was located ~20 km above the Almus Reservoir, had substrate dominated by rock and cobble, and was bordered by natural forest with highly canopy cover. Because Site 1 was added to the study design late, it was not surveyed during winter. Site 2 was located ~5 km above the reservoir, had mostly cobble substrate, and lacked forest canopy cover. Oak (*Quercus* spp.), poplar (*Populus* spp.), willow (*Salix* spp.), plane (*Platanus* spp.) and mahaleb cherry (*Prunus mahaleb*) trees dominated the riparian zone along this reach. Site 3 was located within the littoral zone of the Almus Reservoir (792 m above sea level) near an area used for trout cage culture. The riparian zone had little vegetation cover and the surrounding forest was dominated by oak, poplar, black pine (*Pinus nigra*), and Scots pine (*Pinus sylvestris*). We collected Samples were collected from a downstream section of the reservoir close to the dam. Site 4 was a segment of the river channel (640 m above sea level) ~25 km downstream from the Almus Reservoir. We selected this location based largely on accessibility under a range of weather conditions. Substrate at this site was dominated by rocks and cobbles covered by dense growth of filamentous algae (*Cladophora* sp.). The riparian zone of this site was dominated by deciduous forest (willow, poplar, plane and alder (*Alnus* spp.)) and herbaceous plants. The regional catchment is dominated by agriculture, especially vegetable farms.

#### Environmental parameters

Abiotic environmental parameters were measured at each site during each season. For analysis of water quality parameters (NO<sub>3</sub><sup>-</sup>, NO<sub>2</sub><sup>-</sup>, NH<sub>4</sub><sup>+</sup> and PO<sub>4</sub><sup>3-</sup>), a 1-L sample of surface water was

collected at three different locations within each study site. Samples were immediately placed on ice. In the laboratory, each sample was filtered through precombusted Whatman GF/F filters (Merck, Darmstadt, Germany). The filtrate was then used to measure soluble phosphorus (PO<sub>4</sub><sup>3-</sup>), NO<sub>3</sub><sup>-</sup>, NO<sub>2</sub><sup>-</sup> and NH<sub>4</sub><sup>+</sup> using calometric kits and the WTW model Photo Flex Turb (Xylem Analytics Germany Sales GmbH & Co. KG, Weilheim, Germany). The turbidity and pH of unfiltered water samples were also measured using the Photo Flex Turb. Water temperature, conductivity and dissolved oxygen (DO) were measured *in situ* using portable meters (Model 85; Yellow Spring Instrument, Xylem Analytics, UK) at each site and in each season. Water velocity was measured using velocity meters (Model FP 201; Global Water, Gold River, CA, USA). To measure chlorophyll (Chl)-*a*, 1 L of water was collected at each site and placed in polyethylene bottles. After the water samples had been filtered through a Whatman GF/F filter, the filters were placed in 90% acetone for 24 h at 4°C in the dark (Wetzel and Likens 1991). Chl-*a* concentrations were measured using a spectrophotometer (at 665, 664 and 750 nm). Channel width was measured at all channel sites.

#### Food web components

Common primary production sources and consumers were sampled at each site during winter (28–30 January 2011), late spring (9–11 May 2011) and late summer (9–11 September 2011). At a given location, tissue samples of basal production sources and consumer taxa were collected on the same day. Three major groups of primary producers common to all four sites were sampled: riparian plants (composite sample of live and recently fallen leaves from riparian trees, as well as live leaves from dominant riparian herbaceous plants, all of which were plants that use the C<sub>3</sub> photosynthesis pathway), seston and biofilm (mostly benthic algae). Filamentous algae (*Cladophora* sp.) were scraped from substrates, but sufficient amounts for analysis were only obtained during winter and spring at the channel site downstream from the reservoir. Other benthic algae samples were obtained by scraping the thin layer of biofilm from dominant solid substrates and then rinsing the material with distilled water to remove any associated detritus or micro-invertebrates. Because these samples probably did not consist solely of benthic algae, we refer to this basal source as ‘biofilm’ (mostly benthic algae but possibly also containing small fractions of detritus, fungi, bacteria, or protozoa; Zeug and Winemiller 2008). Submerged aquatic vascular plants were sampled only in the reservoir during spring when they were abundant. Water samples were collected in 5-L opaque bottles and filtered through a 63-µm sieve to remove zooplankton; remaining particles that settled onto the bottom were collected as seston samples. All samples were placed in plastic bags and stored on ice in the field and then in a freezer in the laboratory.

Zebra mussels (*Dreissena* sp.) were collected from rocks in the littoral zone of the reservoir during winter. Freshwater crabs (*Potamon* sp.) were captured in the upstream channel site. Zooplankton were collected using a standard plankton net (63 µm) with horizontal and vertical (depth from 0 to 10 m) tows in lentic (from offshore) and lotic (only at downstream) habitat against the current for 20 min. Zooplankton samples

were transported to the laboratory for analysis. Benthic invertebrates dwelling in coarse woody debris, leaf packs, tufts of filamentous algae growing on the substratum or within loose sediments to a depth of 10 cm were collected using a Surber sampler or kick net with 500- $\mu$ m mesh. Common macroinvertebrates were transported live to the laboratory and then housed in containers with river water within a refrigerator for 24 h to allow them to empty their guts before they were killed for the collection of tissue samples. Common aquatic invertebrates were identified to Order or Family levels using keys provided by Bouchard (2004).

Fish were collected from the river channel and reservoir using an electroshocker during the daytime. In the reservoir, fish also were collected during evening and at night (1500–2100 hours) using experimental gill nets with panels of 25-, 30-, 40-, 50-, 60-, 70- and 80-mm mesh. Fish specimens were killed in an ice bath and stored on ice for transport to the laboratory, where they were identified to species level, weighed and measured for standard length (SL).

#### Sample preparation for stable isotope analysis

In the laboratory, leaves, biofilm and filamentous algae were rinsed with distilled water, and then any debris or invertebrates were removed during examination under a stereomicroscope. Biofilm and seston samples were filtered onto precombusted (450°C, 4 h) Whatman GF/F filters. For zebra mussels, each tissue sample consisted of the muscular feet from 10–15 specimens, whereas for freshwater crabs a sample of soft tissue was separated from the carapace of an individual specimen. Zooplankton samples were filtered through precombusted (450°C, 4 h) GF/F filters. All invertebrate samples were rinsed with distilled water. Boneless and skinless samples of muscle tissue were extracted from the flanks of fish specimens below the dorsal fin and then rinsed with distilled water. For larger consumers (fish, benthic macroinvertebrates), each sample consisted of a single individual; however, for smaller consumers, a sample was a composite of ~10 individuals to generate minimal weights (2 mg) for stable isotope analyses. Samples were dried at 60°C for 48 h. Dried samples were ground into a fine powder and stored in glass vials. Approximately 3 mg of each sample was subsequently weighed to 0.001 mg and sealed inside ultrapure tin capsules (Elemental Microanalysis Ltd, Okehampton, UK). Samples were analysed for carbon and nitrogen isotope ratios using mass spectrometry at the Analytical Chemistry Laboratory of the Institute of Ecology, University of Georgia (Athens, GA, USA). Ratios (R) of the heavy to light isotopes (i.e.  $^{13}\text{C}/^{12}\text{C}$ ,  $^{15}\text{N}/^{14}\text{N}$ ) are expressed in parts per thousand, relative to the standards in delta notation according to the following formula:

$$\delta X = ((R_{\text{sample}} \div R_{\text{standard}}) - 1) \times 1000$$

in which the standards are Pee Dee Belemnite limestone and atmospheric molecular nitrogen for C and N respectively.

#### Data analyses

In all, 328 consumers, representing 15 fish and 18 invertebrate taxa, and 155 basal source samples were analysed for stable isotope ratios. Trophic positions (TP) of consumers were

estimated based on fractionation of  $\delta^{15}\text{N}$  between consumers and primary production sources. The TP of each consumer was calculated using the formula given by Cabana and Rasmussen (1996):

$$TP = ((\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{reference}}) \div 3.4) + 1$$

where  $\delta^{15}\text{N}_{\text{reference}}$  was the mean  $\delta^{15}\text{N}$  value of all primary production sources (riparian plants, seston, biofilm etc.). A different reference nitrogen value was used for each site because the mean nitrogen value of basal carbon sources exhibited spatial variation and some carbon sources were not present at all sites (e.g. aquatic plants were only found in the reservoir, *Cladophora* sp. were only obtained from the downstream site). Local fish assemblages were dominated by omnivorous species. The trophic fractionation factor ( $\Delta\delta^{15}\text{N}$ ) for omnivorous fish ranges from 3.2 to 4.6‰, and we used the reported mean value of 3.4 (Vander Zanden and Rasmussen 1999, 2001; Post 2002).

The spatial and seasonal variations in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of basal production sources and common fish taxa (those obtained from all sites during all seasons) were compared using two-way analysis of variance (ANOVA). In addition, the spatial and seasonal effects on TP of conspecific fish (intraspecific variation) were compared using two-way ANOVA with Type II sum of squares. Pairwise differences were tested using Tukey's post hoc test. All analyses were conducted using SAS (ver. 9.1, SAS Institute, Cary, NC, USA).

The relative importance of potential primary production sources assimilated by aquatic consumers (fish and benthic macroinvertebrates) was estimated based on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of tissues from common primary producers and consumers using the Bayesian stable isotope mixing model SIAR (Stable Isotope Analysis in R, Parnell et al. 2010) in R (ver. 3.0.2, R Foundation for Statistical Computing, Vienna, Austria). Prior to analyses, we plotted consumer (fish and macroinvertebrates) and basal source data (riparian plants, seston, biofilm from all sites, *Cladophora* sp. from the downstream site and aquatic plants from the reservoir) with their standard deviations. Isotope ratios of carbon tend to be conserved across trophic levels, and we used a  $\delta^{13}\text{C}$  trophic fractionation of  $0.4 \pm 1.3\text{‰}$  per trophic level (Post 2002). We used the reported mean value of 3.4 (Vander Zanden and Rasmussen 1999, 2001; Post 2002) for the  $\delta^{15}\text{N}$  trophic enrichment of fish. Because data points for some invertebrate and fish taxa were unreplicated at the habitat scale, we used the SIAR function 'siarsolomcmcv4', which does not include a residual error term (Parnell et al. 2010).

Six community-wide metrics based on stable isotope data (Layman et al. 2007a) were used to describe variation in trophic structure of fish assemblages at each site during each season. Analyses were based on fish assemblages, because fish species were captured fairly consistently among sites and seasons. These metrics reflect assemblage trophic niche space as the area occupied within a  $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$  biplot: range in  $\delta^{13}\text{C}$  (CR), range in  $\delta^{15}\text{N}$  (NR), mean distance to the centroid (CD), and total area (TA). CR is a measure of basal  $\delta^{13}\text{C}$  variation, NR provides information on the food chain length, CD indexes trophic diversity within the assemblage and TA represents the total trophic niche space occupied by the assemblage. The extent of trophic redundancy within the assemblage was measured by



**Table 1. Environmental parameters measured at four sites during winter, spring and summer, and mean values from January 2011 to September 2011 in the main channel of the upper Yeşilirmak River**  
NTU, nephelometric turbidity units; DO, dissolved oxygen; Chl-*a*, chlorophyll-*a*

|                 | NH <sub>4</sub> <sup>+</sup><br>(mg L <sup>-1</sup> ) | NO <sub>2</sub> <sup>-</sup><br>(mg L <sup>-1</sup> ) | NO <sub>3</sub> <sup>-</sup><br>(mg L <sup>-1</sup> ) | PO <sub>4</sub> <sup>3-</sup><br>(mg L <sup>-1</sup> ) | Turbidity<br>(NTU) | Temperature<br>(°C) | DO<br>(mg L <sup>-1</sup> ) | Conductivity<br>(µS cm <sup>-1</sup> ) | pH   | Chl- <i>a</i><br>(µg L <sup>-1</sup> ) | Velocity<br>(cm s <sup>-1</sup> ) | Channel width<br>(m) |
|-----------------|---|---|---|--|--------------------|---------------------|-----------------------------|--|------|--|-----------------------------------|----------------------|
| Upstream Site 1 |   |   |   |  |                    |                     |                             |  |      |  |                                   |                      |
| Spring          | 0.00  | 0.03  | 1.90  | 5.45   | 30.85              | 19.05               | 9.38                        | 337.85                                 | 8.40 | 0.00                                   | 136.60                            | 16.50                |
| Summer          | 0.00  | 0.02  | 0.40  | 5.80   | 6.69               | 18.90               | 7.99                        | 394.25                                 | 8.10 | 0.30                                   | 115.00                            | 14.00                |
| Mean            | 0.00  | 0.03  | 1.15  | 5.63   | 18.77              | 19.05               | 8.69                        | 337.85                                 | 8.25 | 0.15                                   | 125.80                            | 15.25                |
| Upstream Site 2 |   |   |   |  |                    |                     |                             |  |      |  |                                   |                      |
| Winter          | 0.50  | 0.00  | 1.77  | 4.47   | 2.85               | 3.80                | 12.74                       | 224.53                                 | 8.25 | 0.00                                   | 86.00                             | 32.00                |
| Spring          | 0.28  | 0.03  | 0.70  | 5.07   | 23.00              | 18.57               | 8.90                        | 330.23                                 | 8.32 | 0.00                                   | 124.00                            | 35.60                |
| Summer          | 0.00  | 0.02  | 4.00  | 3.10   | 3.53               | 20.00               | 9.24                        | 173.20                                 | 8.13 | 0.80                                   | 93.00                             | 33.70                |
| Mean            | 0.26  | 0.02  | 2.16  | 4.21   | 9.79               | 14.12               | 10.29                       | 242.65                                 | 8.23 | 0.27                                   | 101.00                            | 33.76                |
| Almus Reservoir |   |   |   |  |                    |                     |                             |  |      |  |                                   |                      |
| Winter          | 0.53  | 0.00  | 0.15  | 3.73   | 1.10               | 6.78                | 11.15                       | 217.35                                 | 8.05 | 1.10                                   |                                   |                      |
| Spring          | 0.01  | 0.03  | 1.35  | 3.08   | 2.42               | 15.30               | 10.03                       | 254.45                                 | 8.14 | 1.20                                   |                                   |                      |
| Summer          | 0.00  | 0.02  | 1.68  | 4.43   | 4.15               | 16.30               | 6.29                        | 259.08                                 | 7.86 | 5.50                                   |                                   |                      |
| Mean            | 0.18  | 0.01  | 1.06  | 3.74   | 2.55               | 12.79               | 9.16                        | 243.63                                 | 8.02 | 2.60                                   |                                   |                      |
| Downstream site |   |   |   |  |                    |                     |                             |  |      |  |                                   |                      |
| Winter          | 0.47  | 0.00  | 2.70  | 3.27   | 6.82               | 6.70                | 12.73                       | 304.30                                 | 7.61 | 0.40                                   | 100.30                            | 26.00                |
| Spring          | 0.11  | 0.04  | 0.57  | 6.90   | 63.93              | 11.47               | 11.50                       | 266.03                                 | 7.50 | 0.60                                   | 198.60                            | 28.50                |
| Summer          | 0.00  | 0.02  | 0.40  | 3.53   | 2.01               | 11.67               | 10.87                       | 399.37                                 | 7.68 | 0.00                                   | 130.00                            | 10.00                |
| Mean            | 0.19  | 0.02  | 1.22  | 4.57   | 24.25              | 9.95                | 11.70                       | 323.23                                 | 7.60 | 0.07                                   | 142.96                            | 21.50                |

two additional metrics, namely mean nearest neighbour distance (MNND) and standard deviation of the nearest neighbour distance (SDNND). Theoretically, smaller MNND and SDNND indicate greater trophic redundancy (groups have more similar trophic niches; Abrantes *et al.* 2014). TA is highly sensitive to sample size, with a positive relationship (Jackson *et al.* 2011); therefore, Bayesian standard ellipse area (SEA<sub>b</sub>) and sample size-corrected standard ellipse area (SEA<sub>c</sub>) were used to quantify the trophic niche space of fish assemblages. The Bayesian assemblage metrics and standard ellipse areas were calculated using Stable Isotope Bayesian Ellipse (SIBER) in R (Jackson *et al.* 2011).

Where appropriate, data are presented as the mean ± s.d.

## Results

### Environmental variation

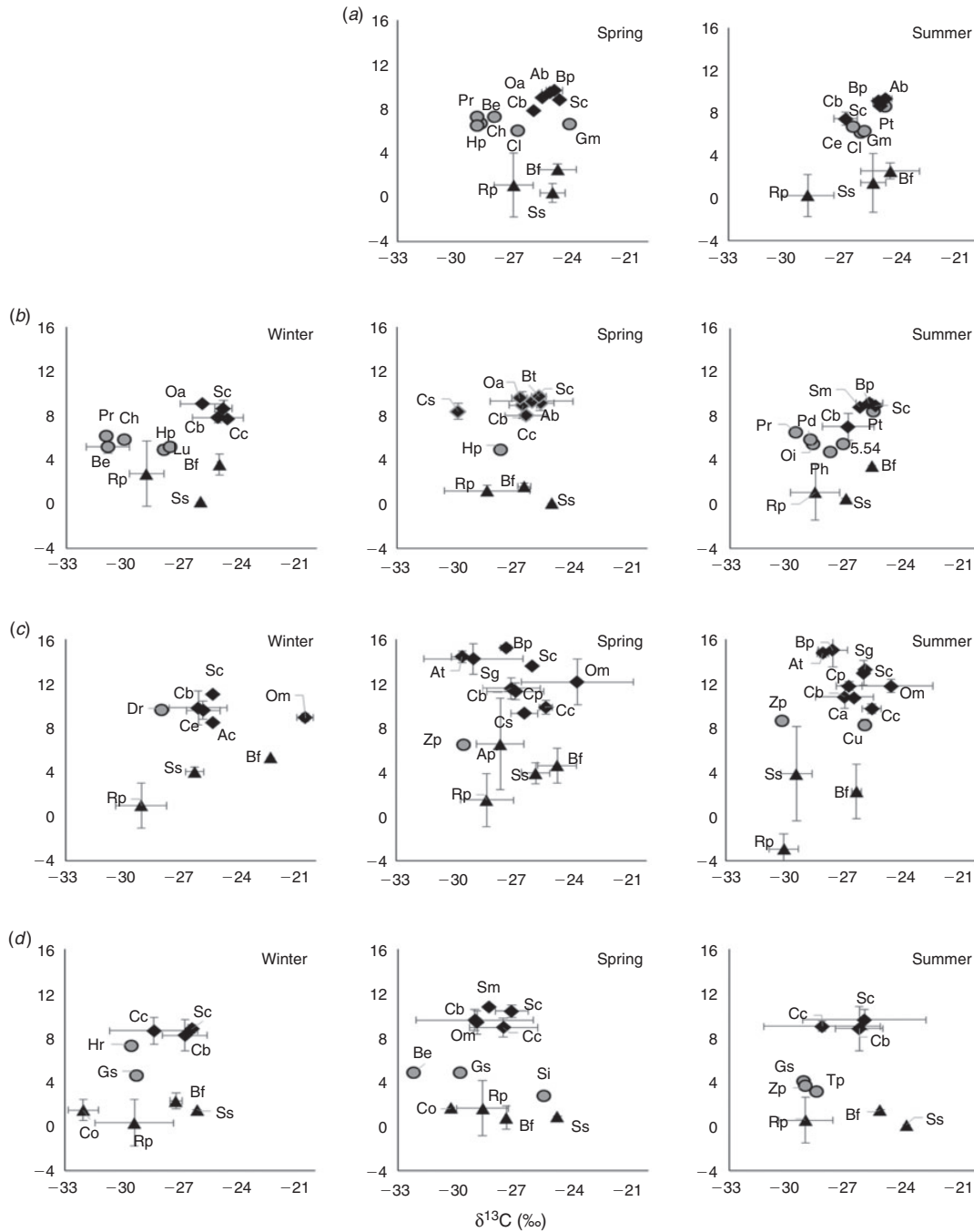
Mean values for water velocity and DO were higher, and mean values for water temperature and pH were lower at the downstream channel site compared with the upstream channel sites (Table 1). Nutrient concentrations (especially NO<sub>3</sub><sup>-</sup> and PO<sub>4</sub><sup>3-</sup>) were generally high across all study sites, with highest PO<sub>4</sub><sup>3-</sup> concentrations at upstream Site 1 and highest NO<sub>3</sub><sup>-</sup> concentrations at upstream Site 2. Turbidity and conductivity were highest at the downstream site and upstream Site 1. Mean Chl-*a* concentrations in the water column were higher in the reservoir than the channel sites, and water column Chl-*a* concentration at upstream Site 2 was higher than that at the downstream site (Table 1).

### Spatial and temporal variation in food web structure

Even though seston (-26.37 ± 1.73‰; *n* = 25) and biofilm (-25.56 ± 1.39‰; *n* = 19) appeared to be more <sup>13</sup>C enriched relative to riparian plants (-28.77 ± 1.48‰; *n* = 92), riparian

plants had considerable variation in δ<sup>13</sup>C and δ<sup>15</sup>N values, and the isotope values of these three sources overlapped at nearly all sites during each season (Fig. 2). There was no significant interaction between season and site for any primary production sources except δ<sup>13</sup>C of seston (Appendix 1). However, only in summer were the δ<sup>13</sup>C values of seston significantly lower in the reservoir than other sites (Appendices 1, 2). During winter, δ<sup>13</sup>C values of riparian plants were significantly lower than in other seasons, and riparian plants had higher δ<sup>15</sup>N at upstream Site 2 than at all other sites (Appendices 1, 2). Biofilm was significantly enriched in <sup>15</sup>N in the reservoir relative to downstream site (Appendices 1, 2).

In all, 15 common fish and 18 invertebrate taxa were collected from the four study sites (Fig. 2; Appendix 2), with fish species richness highest in the reservoir (11 taxa) and upstream Site 2 (9), and lowest at the downstream site (5) and upstream Site 1 (5). Only a single individual of two species (*O. mykiss* and *Seminemacheilus* sp.) was collected at the downstream site in spring. More invertebrate taxa were collected at upstream Site 2 (10 taxa), and the fewest were obtained at the downstream site (5) and from the reservoir (3; Fig. 2; Appendix 2). Average δ<sup>13</sup>C of fish assemblages decreased from upstream Site 1 to the downstream site (from -25.41 to -27.36‰ respectively). Highest average δ<sup>15</sup>N for fish assemblages was found in the reservoir, especially during summer. *C. banarensis*, *S. cephalus* and *Chondrostoma colchicum* were collected at all four study sites in all seasons (Fig. 2; Appendix 2), with these three species exhibiting high variations in δ<sup>13</sup>C at the downstream site (from -24.98 to -33.51‰ (s.d. 2.22), from -23.52 to -31.90‰ (s.d. ±2.13) and from -24.48 to -32.35‰ (s.d. ±2.19) respectively), and each of these species exhibiting high isotope variation during each season (Appendix 2). There was no significant interaction between season and site for δ<sup>13</sup>C



**Fig. 2.** Biplot of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of tissues from consumer taxa and primary production sources collected from (a) upstream site 1, (b) upstream site 2, (c) reservoir and (d) downstream site in the upper Yeşilirmak River reaches located above, within and below the Almus Reservoir during winter, spring and summer (closed circle, primary production sources; open diamond, macro invertebrates; closed triangle, fishes). Codes designate taxa (see Appendix 2).

and  $\delta^{15}\text{N}$  for *C. colchicum*, *C. banarescui* and *S. cephalus*, except for  $\delta^{13}\text{C}$  of *C. banarescui* (Appendix 1). *C. banarescui* in the reservoir had the lowest  $\delta^{13}\text{C}$  and highest  $\delta^{15}\text{N}$  values during

spring (Fig. 2; Appendices 1, 2). *O. mykiss* was more  $^{13}\text{C}$  enriched in the reservoir during winter compared with conspecifics at the downstream site. *Barbus plebejus* in the reservoir

**Table 2.** Mean trophic positions of conspecifics captured from four river segments in the main channel of the upper Yeşilirmak River

| Fish species                   | Family        | Upstream Site 1 | Upstream Site 2 | Reservoir | Downstream |
|--------------------------------|---------------|-----------------|-----------------|-----------|------------|
| <i>Atherina boyeri</i>         | Atherinidae   |                 |                 | 4.63      |            |
| <i>Seminemacheilus</i> sp.     | Nemacheilidae |                 | 3.09            |           | 3.89       |
| <i>Oxynoemacheilus angorae</i> | Nemacheilidae | 3.18            | 3.22            |           |            |
| <i>Alburnoides bipunctatus</i> | Cyprinidae    | 3.32            | 3.18            |           |            |
| <i>Alburnus chalcoides</i>     | Cyprinidae    |                 |                 | 2.85      |            |
| <i>Barbus tauricus</i>         | Cyprinidae    |                 | 3.35            |           |            |
| <i>Barbus plebejus</i>         | Cyprinidae    | 3.28            | 3.20            | 4.79      |            |
| <i>Cyprinus carpio</i>         | Cyprinidae    |                 |                 | 3.73      |            |
| <i>Squalius cephalus</i>       | Cyprinidae    | 3.10            | 3.11            | 4.08      | 3.61       |
| <i>Capoeta banarescui</i>      | Cyprinidae    | 2.75            | 2.79            | 3.57      | 3.34       |
| <i>Carassius carassius</i>     | Cyprinidae    |                 |                 | 3.51      |            |
| <i>Chondrostoma colchicum</i>  | Cyprinidae    |                 | 2.81            | 3.22      | 3.33       |
| <i>Capoeta sieboldii</i>       | Cyprinidae    |                 | 2.95            | 3.09      |            |
| <i>Oncorhynchus mykiss</i>     | Salmonidae    |                 |                 | 3.40      | 3.48       |
| <i>Silurus glanis</i>          | Siluridae     |                 |                 | 4.48      |            |

had higher  $\delta^{15}\text{N}$  and lower  $\delta^{13}\text{C}$  values relative to conspecifics from other sites throughout the year (Fig. 2; Appendix 2).

SIAR mixing model results indicated that food webs were supported by both autochthonous (biofilm and seston) and allochthonous (riparian plants) sources, but the proportional contributions of these sources differed along the longitudinal fluvial gradient. Riparian plants contributed most to consumer biomass at upstream Site 1, whereas biofilm and riparian plants supported a large fraction of fish and invertebrate biomass respectively at upstream Site 2 (Appendix 3). In the reservoir, the various primary production sources contributed fairly equally to the biomass of most fish, the exception being that aquatic plants and biofilm were major contributors to the biomass of *C. banarescui*, *C. colchicum*, *C. carpio* and *O. mykiss* (Appendix 3). At the downstream site, most consumer taxa assimilated biomass from all basal production sources (Appendix 3). There was little seasonal variation in the proportional contribution of production sources to consumer biomass in the reservoir and downstream site. At upstream Site 1, riparian plants appeared to be more important for fish biomass during spring, whereas seston supported a substantial proportion of the biomass of many taxa during summer, and the proportional contribution of biofilm to fish biomass increased during winter and decreased during spring and summer at upstream Site 2 (Fig. 2; Appendix 4). Mean TPs of fish ranged from 2.75 (*C. banarescui*) to 3.32 (*Alburnoides bipunctatus*) at upstream Site 1, from 2.79 (*C. banarescui*) to 3.35 (*Barbus tauricus*) at upstream Site 2, from 2.85 (*Alburnus chalcoides*) to 4.48 (*B. plebejus*) in the reservoir and from 3.33 (*C. colchicum*) to 3.89 (*Seminemacheilus* sp.) at the downstream site (Table 2). There was no significant interaction between site and season when the TPs of conspecific fish were compared, with the exception of *C. banarescui* (Appendix 1). The mean TP of *C. banarescui* was lower at the upstream sites than at the downstream site and reservoir (Appendix 1; Table 2). The mean TP of *S. cephalus* was also lower at the upstream sites than at the downstream site and reservoir, and was lowest during winter. The mean TP of *C. colchicum* was lower at upstream Site 2 than at the downstream site and reservoir, and did not differ significantly among seasons. The mean TP of

*B. plebejus* was higher in the reservoir than at the upstream sites (Appendix 1; Table 2).

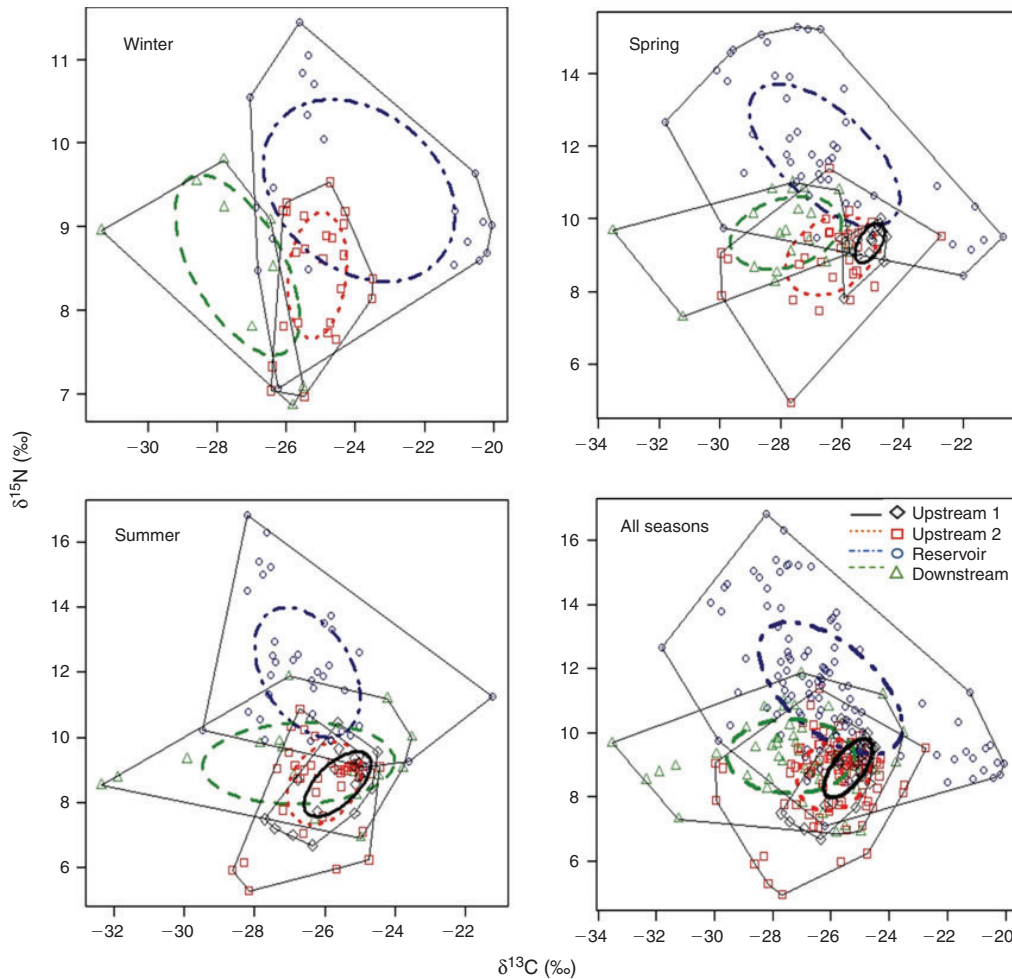
#### Spatial and seasonal variation in community-wide metrics

Fish assemblage isotopic spaces in biplots differed among sites (Fig. 3). The isotopic spaces of fish assemblages at upstream Sites 1 and 2 overlapped broadly, and upstream sites had less overlap with the reservoir and downstream site (Fig. 3).  $\text{SEA}_b$  and community-wide metrics (NR, CR, CD, TA) were greatest for the reservoir compared with the other three sites (Fig. 3, 4; Table 3). Although CR and CD were lower at upstream sites relative to the downstream site, NR was higher at upstream Site 2 than at Site 1 and the downstream site (Table 3). The SDNND was nearly the same across all sites, whereas the MNND was greater at the downstream site than at the other three sites (Table 3).

All community-wide metrics and  $\text{SEA}_b$  increased progressively from upstream Site 2 to the reservoir, but decreased at the downstream site during winter (Fig. 3, 4; Table 3). During spring,  $\text{SEA}_b$ , CR and CD appeared to increase from Site 1 to the reservoir, but decreased at the downstream site; NR also increased gradually from Site 1 to Site 2 and declined from the reservoir to the downstream site (Fig. 3, 4; Table 3).  $\text{SEA}_b$ , CR, CD tended to increase gradually from upstream Site 1 to the downstream site during summer (Fig. 3, 4; Table 3). During summer, NR increased from Site 1 to the reservoir, and then decreased at the downstream site. During all three seasons, largest values for MNND and SDNND were associated with the downstream site (Table 3).

#### Discussion

By modifying habitat and fish species distributions and local assemblages, the Almus Dam has affected the structure of Yeşilirmak River food webs in reaches both downstream and upstream. As we hypothesised, the dam has disrupted the normal longitudinal fluvial gradient of fish species richness and trophic structure. Fish species richness and isotopic spaces occupied by local assemblages were greatest in the reservoir. Lowest fish



**Fig. 3.** Isotopic spaces (based on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) occupied by fish communities at the four study sites (upstream Sites 1 and 2, Almus Reservoir and the downstream site) during winter, spring, summer and all seasons combined. Solid lines bound the convex hull area of the fish assemblage for each site and season. Ellipses enclose the sample size-corrected, standard ellipse areas (SEAs, containing ~40% of the data) representing the isotopic spaces of fish communities at each site during each season.

diversity and largest isotopic spaces were observed for fish assemblages at the downstream site, with upstream sites being intermediate.

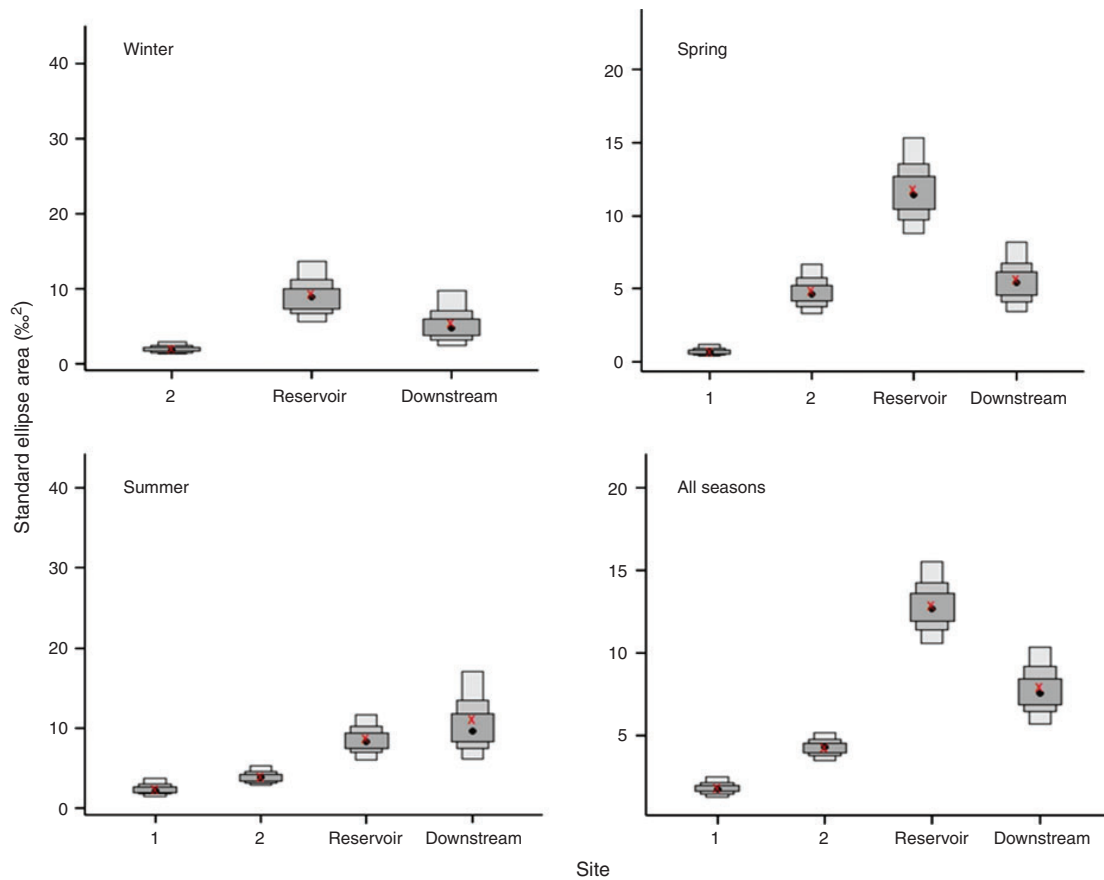
*Spatial variation in food web structure*

Proportional contributions of riparian plants, biofilm and seston shifted from upstream Site 1 to the downstream site; nonetheless, these three sources were always estimated to be significant contributors to fish biomass. Variation in  $\delta^{13}\text{C}$  was higher in riparian plants than biofilm and seston, and these two sources overlapped considerably with the upper range of riparian plants, which compromised source discrimination by the mixing model. Overlap between algal and terrestrial  $\delta^{13}\text{C}$  has been reported for habitats with fast-flowing water (Finlay and Kendall 2007). Our seston samples were a proxy for pelagic phytoplankton, and were more  $^{13}\text{C}$  depleted and more  $^{15}\text{N}$  enriched than allochthonous detritus (DeLong and Thorp 2006).

Our seston samples probably contained various amounts of particulate organic matter derived from phytoplankton, periphyton and riparian vegetation, and therefore may have isotope signatures that reflect a mixture of sources. Seston  $\delta^{13}\text{C}$  tended to be higher at upstream channel sites, and this may reflect greater fractions of material of allochthonous origin. Consequently, relationships between consumers and carbon sources were often not well resolved by the mixing model. Further reducing resolution of the isotopic mixing model estimates is widespread omnivory, which tends to increase food web connectivity (Blanchette *et al.* 2014).

Low fish diversity at the downstream site is counter to the longitudinal trend of species richness that is generally observed for fish (Dodd *et al.* 2003; Lessard and Hayes 2003; Poulet 2007). We hypothesised that the Almus Dam would affect this spatial trend via effects on habitat feature, dynamics and connectivity. At the site below the reservoir, only three fish





**Fig. 4.** Bayesian estimates of standard ellipse area (SEA<sub>b</sub>) modes (black dots) and size-corrected standard ellipse area (SEA<sub>c</sub>) mode (red crosses) overlaying grey-shaded density plots representing 50, 75 and 95% credible intervals for winter, spring, summer and all seasons combined at the four sites. 1, upstream Site 1; 2, upstream Site 2.

species (*S. cephalus*, *C. banarescui*, *C. colchicum*) were captured during every season. These omnivorous cyprinids consume a variety of aquatic invertebrates, as well as terrestrial and aquatic vegetation (Akin *et al.* 2016; S. Akin, C. Sahin, B. Verep, D. Turan, A. M. Gozler, A. Bozkurt, K. Çelik, E. Cetin, A. Aracı and I. Sargin, unpubl. data), and their broad diets were reflected by wide ranges in  $\delta^{13}\text{C}$  values. Although fish diversity was lowest at the downstream site, the local assemblage occupied the largest isotopic niche space (SEA<sub>b</sub>) and trophic diversity (CD, CR). In contrast, ranges of  $\delta^{15}\text{N}$  (NR) of fish at the downstream site were significantly lower than those of fish in the reservoir and upstream Site 2. Five fish species at Site 2 (*A. bipunctatus*, *B. plebejus*, *B. tauricus* and two nemacheilid taxa) consume mostly benthic invertebrates, including insect larvae, and little algae (Akin *et al.* 2010), and therefore occupy higher trophic levels than the omnivorous fish that dominated the downstream site.

Collapse of isotopic niche space may reflect an overall simplification of food web structure, which could make top predators more susceptible to population fluctuations (Layman *et al.* 2007b). High trophic diversity (CD) of the downstream assemblage could be associated with dominance by trophic

generalists and demographic resilience. Trophic generalists may be less susceptible to negative effects because of their ability to shift among alternative food resources (Layman *et al.* 2007b). Many river-dwelling fish are trophic generalists that can feed opportunistically when habitat fragmentation reduces the availability of certain food resources and increases the availability of others (Mazumder *et al.* 2016). Even when trophic generalists persist in highly fragmented ecosystems, their ecological roles may be significantly altered (Layman *et al.* 2007b). Alternatively, fish assemblages with a large isotopic space could be comprised of diverse trophic specialists (Bearhop *et al.* 2004); however, this does not appear to be the case in our downstream site of the Yeşilirmak River. Dams alter natural hydrological regimes, including the intensity, duration and timing of flow pulses, and consequently affect the quantity and quality of food resources available to fish (Agostinho *et al.* 2004). Some aquatic organisms increase omnivory in response to environmental changes caused by dams (Hette-Tronquart *et al.* 2013, 2016). Consistent with this idea, the prevalence of omnivory at the downstream site may represent a response to less-predictable food resource availability resulting from the modified flow regime (Blanchette *et al.* 2014).

**Table 3.** Layman's community-wide metrics (NR, range in  $\delta^{15}\text{N}$ ; CR, range in  $\delta^{13}\text{C}$ ; CD, mean distance to the centroid; MNND, mean nearest neighbour distance; SDNND, standard deviation of the nearest neighbour distance; TA, total area) and standard Bayesian ellipse area ( $\text{SEA}_b$ ) and size-corrected standard ellipse areas ( $\text{SEA}_c$ ) of fish at each study site and in each season

Mean values are based on all seasons

|                 | Number of samples | NR   | CR    | CD   | MNND | SDNND | $\text{SEA}_b$ | $\text{SEA}_c$ | TA    |
|-----------------|-------------------|------|-------|------|------|-------|----------------|----------------|-------|
| Upstream Site 1 |                   |      |       |      |      |       |                |                |       |
| Winter          |                   |      |       |      |      |       |                |                |       |
| Spring          | 14                | 2.18 | 1.48  | 0.57 | 0.32 | 0.32  | 0.68           | 0.74           | 1.98  |
| Summer          | 20                | 3.76 | 3.22  | 1.20 | 0.44 | 0.32  | 2.30           | 2.42           | 6.40  |
| Mean            | 34                | 3.76 | 3.22  | 1.01 | 0.28 | 0.25  | 1.76           | 1.82           | 6.55  |
| Upstream Site 2 |                   |      |       |      |      |       |                |                |       |
| Winter          | 24                | 2.56 | 2.94  | 1.02 | 0.29 | 0.18  | 1.94           | 2.03           | 4.99  |
| Spring          | 33                | 6.45 | 7.23  | 1.44 | 0.54 | 0.58  | 4.76           | 4.91           | 24.32 |
| Summer          | 40                | 5.59 | 4.20  | 1.35 | 0.35 | 0.28  | 3.89           | 3.99           | 14.28 |
| Mean            | 97                | 6.45 | 7.23  | 1.37 | 0.24 | 0.23  | 4.26           | 4.30           | 28.34 |
| Almus Reservoir |                   |      |       |      |      |       |                |                |       |
| Winter          | 21                | 4.37 | 6.98  | 2.78 | 0.55 | 0.34  | 8.89           | 9.36           | 18.25 |
| Spring          | 49                | 4.83 | 11.10 | 2.58 | 0.50 | 0.43  | 11.56          | 11.80          | 43.05 |
| Summer          | 38                | 7.74 | 8.24  | 2.06 | 0.52 | 0.53  | 8.48           | 8.72           | 34.66 |
| Mean            | 108               | 9.76 | 11.75 | 2.65 | 0.38 | 0.34  | 12.78          | 12.90          | 62.00 |
| Downstream site |                   |      |       |      |      |       |                |                |       |
| Winter          | 9                 | 2.94 | 5.82  | 1.70 | 0.84 | 0.76  | 4.82           | 5.51           | 7.69  |
| Spring          | 21                | 3.70 | 7.77  | 1.59 | 0.71 | 0.81  | 5.39           | 5.68           | 16.90 |
| Summer          | 16                | 4.96 | 8.83  | 2.49 | 0.93 | 0.56  | 10.48          | 11.23          | 24.15 |
| Mean            | 46                | 5.01 | 9.99  | 2.00 | 0.53 | 0.38  | 7.78           | 7.95           | 34.16 |

The fish assemblage at upstream Site 1 (located furthest upstream) had the smallest isotopic niche space ( $\text{SEA}_b$ ). This site also had a smaller NR, CR and CD, all of which are indicative of lower trophic diversity. This was also supported by low MNND and SDNND (high trophic redundancy) at this site, suggesting fish at Site 1 exploit similar resources within the same habitats. These findings may reflect the low availability of aquatic primary production due to substrate scouring during flow pulses, as well as shading from dense riparian canopy cover. In contrast, upstream Site 2 had the lowest turbidity and water velocity, as well as highest nutrient concentrations ( $\text{NO}_3^-$ ,  $\text{NH}_4^+$ ), conditions that should promote algal production (Roach *et al.* 2014). Although upstream Sites 1 and 2 had assemblage isotopic niche spaces that overlapped broadly, Site 2 had greater species diversity, isotopic niche space and isotopic community metrics (except for MNND and SDNND, which were similar).

The reservoir had highest fish diversity and broadest ranges for  $\delta^{13}\text{C}$  (from  $-20.05$  to  $-31.80\%$ ) and  $\delta^{15}\text{N}$  (from  $7.07$  to  $16.83\%$ ). The isotopic space occupied by the reservoir fish assemblage diverged from those of the three channel sites, and the reservoir assemblage also had highest values for  $\text{SEA}_b$  and most other community metrics, which may reflect exploitation of more diverse resources (food or habitat) (Layman *et al.* 2007b). Food chain length (NR) was positively correlated with ecosystem size in an impounded Neotropical river (Hoeinghaus *et al.* 2008). This trend in the Yeşilirmak River may be influenced by greater functional diversity from the establishment of exotic predatory fish within the reservoir (e.g. *O. mykiss*, *S. glanis*, *Atherina boyeri*). Estimated TPs of certain fish species from the reservoir were higher than those of conspecifics from channel sites. High TP estimates for reservoir fish could have

been affected by high  $\delta^{15}\text{N}$  values of dissolved inorganic nitrogen derived from agricultural run-off (Bergfur *et al.* 2009; Winemiller *et al.* 2011). Nutrient loading derived from row crops and cage aquaculture may account for higher  $\delta^{15}\text{N}$  of biofilm and seston in the reservoir. Blooms of cyanobacteria are promoted by nitrogen and phosphorus loading, and can cause  $^{15}\text{N}$  enrichment (Roach 2013) and  $^{13}\text{C}$  depletion (Weissenberger *et al.* 2012) at higher trophic levels. Therefore, in the Almus Reservoir, the higher  $\delta^{15}\text{N}$  values of zooplankton and fish could have resulted from assimilation of material originating from  $^{15}\text{N}$ -enriched cyanobacteria. High TP estimates for fish at the downstream site also could have been influenced by consumption of  $^{15}\text{N}$ -enriched zooplankton exported from the reservoir.

#### Seasonal variation in food web structure

Seasonal differences in food web structure were observed at all four sites.  $\text{SEA}_b$  and all community-wide metrics were highest during summer and lowest during winter at upstream Site 1 and the downstream site. During summer, habitat at Site 1 consists of series of riffles and small pools, with higher nutrient concentrations and lower turbidity and current velocity compared with winter and spring. Thus, it is reasonable to assume that periphyton and phytoplankton production (higher Chl-*a*) would be higher in this habitat during summer. Variation in habitat heterogeneity in response to seasonal hydrology could also contribute to seasonal shifts in trophic niche space at upstream Site 1. As noted above, fish from the downstream site had isotopic signatures consistent with the consumption of zooplankton from the reservoir during summer. Phytoplankton and zooplankton from reservoirs are often exported to downstream food webs (Doi *et al.* 2008), but this subsidy decreases with distance

from the reservoir (Mercado-Silva *et al.* 2009). Given the similarity of the isotopic signature of zooplankton in the reservoir and downstream site during summer (mean  $\delta^{13}\text{C}$   $-29.95$  and  $-29.1\%$  respectively), and considering that seston at the downstream site was relatively  $^{13}\text{C}$  enriched ( $-23.79\%$ ) compared with zooplankton, it seems likely that zooplankton drifting downstream from the reservoir subsidised, either directly or indirectly, the biomass of the three fish species. In this regard, the findings of the present study are similar to those of previous studies (Acharyya *et al.* 2012; Fisher 2013).

In contrast with fish from the downstream site, those from upstream Site 2 and the reservoir tended to have greater  $\text{SEA}_b$  and values for other community-wide metrics (except NR in the reservoir) during spring than other seasons. High intraspecific variation in isotope signatures of reservoir fish during spring probably reflects dietary differences rather than spatial variation in basal sources of the reservoir (e.g. *O. mykiss*, *S. glanis*; Appendix 2). In the Yeşilirmak River, spring flow pulses probably reduce the availability of benthic algae, aquatic invertebrates or both. When preferred resources become scarce under conditions of high turbidity and low aquatic primary production, consumers may exploit suboptimal resources (Layman *et al.* 2007b) and partition their trophic niches in response to competition (Bolnick 2001). The reservoir fish assemblage also revealed the greatest seasonal shift in NR, indicating changes in the average length of food chains supporting fish. Food chain length was greater in the reservoir during summer, perhaps as a function of greater solar irradiance and temperatures resulting in higher aquatic primary production.

The expansion of the assemblage isotope space at upstream Site 2 during spring appears to have been influenced largely by an increase in the abundance of a single species with low  $\delta^{13}\text{C}$ . *C. sieboldii* was rare or absent at most sites during most periods of the present study, but a few individuals were caught at Site 2 and in the reservoir during spring. The  $\delta^{13}\text{C}$  of this species averaged  $-29.84\%$ , compared with a range of  $-25.64$  to  $-26.64\%$  for other fish at upstream Site 2. The Almus Dam not only changed hydrology and instream habitat, but also fragmented the home range of *C. sieboldii* and other fish species. Impoundments are barriers to fish movement, and fragmented populations are at greater risk of extirpation (Pavlova *et al.* 2017), whether or not free-flowing reaches are located upstream or downstream from the dam (Winston *et al.* 1991). Other factors frequently contribute to declines of native fish in impounded rivers. For example, Quist *et al.* (2004) reported a decline in native cyprinids in the Missouri River, US, after reservoirs altered the flow regime, substrate composition and turbidity while increasing habitat suitability for exotic piscivores.

## Conclusion

River impoundment and its associated environmental changes have changed the food web structure at locations throughout the Upper Yeşilirmak River. Fish diversity in our samples did not increase incrementally from upstream to downstream locations as expected, but decreased sharply at the site below the reservoir and was greatest at the upstream channel site nearest the reservoir. In general, Almus Dam created conditions that favour fish

that are trophic generalists. The reach downstream from the reservoir revealed greatest variation in  $\delta^{13}\text{C}$  of basal resources, as well as the isotopic space occupied by the fish assemblage. A few omnivorous cyprinids are now dominant in tail waters of the dam. Our findings reveal that local food web structure varies in relation to seasonal and spatial variation in environmental conditions, both of which are affected by natural gradients as well as the impoundment. The findings have important implications for development plans in this region. Although 23 hydroelectric dams are present and 3 hydroelectric power plants are under construction in the Yeşilirmak River (Anonymous 2015), it remains uncertain at present how many more dams will be constructed in the future. The effects of these dams on biota and ecosystem processes are largely unknown. Further research, including studies of fish population structure and community and ecosystem ecology, is needed for the mitigation of effects while supporting sustainable socioeconomic development in the region.

## Conflicts of interest

The authors declare that they have no conflicts of interest.

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**Appendix 1. ANOVA results for season and site effects on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of primary production sources and fish taxa, and the trophic position (TP) of fish in the upper Yeşilirmak River**  
 Significant *P*-values are in bold. up1, upstream Site 1; up2, upstream Site 2; down, downstream site; HSD, honestly significant difference; *C. banarescui*, *Capoeta banarescui*; *S. cephalus*, *Squidilus cephalus*; *C. colchicum*, *Chondrostoma colchicum*

| Sources               | Main test |       |                 |                 |      |        |                        |                 |    |                 | Pair-wise Tukey's HSD test |                 |                            |
|-----------------------|-----------|-------|-----------------|-----------------|------|--------|------------------------|-----------------|----|-----------------|----------------------------|-----------------|----------------------------|
|                       | Season    |       |                 | Sampling area   |      |        | Sampling area × season |                 |    |                 |                            |                 |                            |
|                       | d.f.      | SS    | <i>F</i> -value | <i>P</i> -value | d.f. | SS     | <i>F</i> -value        | <i>P</i> -value | SS | <i>F</i> -value |                            | <i>P</i> -value |                            |
| $\delta^{13}\text{C}$ |           |       |                 |                 |      |        |                        |                 |    |                 |                            |                 |                            |
| Riparian              | 2         | 41.5  | 4438            | <b>0.0148</b>   | 3    | 10.40  | 0.741                  | 0.5305          | 5  | 15.50           | 0.665                      | 0.6513          | Winter < spring and summer |
| Season                | 2         | 59.14 | 57913           | < <b>0.0001</b> | 3    | 27.34  | 17850                  | <b>0.0003</b>   | 5  | 17.80           | 6974                       | <b>0.0015</b>   | Spring = winter > summer   |
| Biofilm               | 2         | 1422  | 0.332           | 0.7274          | 3    | 3815   | 0.594                  | 0.6366          | 5  | 23541           | 2200                       | 0.1542          |                            |
| $\delta^{15}\text{N}$ |           |       |                 |                 |      |        |                        |                 |    |                 |                            |                 |                            |
| Riparian              | 2         | 31.70 | 2804            | 0.0665          | 3    | 80.70  | 4756                   | <b>0.0041</b>   | 5  | 43.10           | 1526                       | 0.1908          | Up2 > reservoir, down, up1 |
| Season                | 2         | 35.01 | 1885            | 0.1861          | 3    | 91.31  | 3278                   | 0.0504          | 5  | 6.46            | 0.139                      | 0.9804          | Reservoir > down           |
| Biofilm               | 2         | 3770  | 1429            | 0.2946          | 3    | 16283  | 4116                   | <b>0.0486</b>   | 5  | 8323            | 1262                       | 0.3658          |                            |
| Fish                  |           |       |                 |                 |      |        |                        |                 |    |                 |                            |                 |                            |
| $\delta^{13}\text{C}$ |           |       |                 |                 |      |        |                        |                 |    |                 |                            |                 |                            |
| <i>C. banarescui</i>  | 2         | 17.66 | 4578            | <b>0.0138</b>   | 3    | 7.98   | 1379                   | 0.2572          | 5  | 18.79           | 1949                       | 0.0981          | Spring < winter and summer |
| <i>S. cephalus</i>    | 2         | 11.22 | 2454            | 0.0988          | 3    | 10.71  | 1562                   | 0.2135          | 4  | 2.73            | 0.299                      | 0.8769          |                            |
| <i>C. colchicum</i>   | 2         | 0.89  | 0.149           | 0.8619          | 2    | 49.49  | 8333                   | <b>0.0015</b>   | 3  | 6.05            | 0.679                      | 0.5726          | Reservoir > down           |
| $\delta^{15}\text{N}$ |           |       |                 |                 |      |        |                        |                 |    |                 |                            |                 |                            |
| <i>C. banarescui</i>  | 2         | 38.11 | 17599           | <b>0.0002</b>   | 3    | 144.39 | 44455                  | < <b>0.0001</b> | 5  | 17.95           | 3316                       | <b>0.0098</b>   | Reservoir > down > up1-2   |
| <i>S. cephalus</i>    | 2         | 2.77  | 0.763           | 0.473           | 3    | 54.27  | 9948                   | <b>0.0028</b>   | 4  | 2.80            | 0.385                      | 0.818           | Reservoir > down and up1-2 |
| <i>C. colchicum</i>   | 2         | 1232  | 0.624           | 0.5431          | 2    | 12051  | 6109                   | <b>0.0064</b>   | 3  | 1083            | 0.366                      | 0.778           | Reservoir > down and up1-2 |
| TP of fish            |           |       |                 |                 |      |        |                        |                 |    |                 |                            |                 |                            |
| <i>C. banarescui</i>  | 2         | 30.23 | 2.61            | 0.081           | 3    | 21.52  | 27.24                  | <b>0.001</b>    | 5  | 17.41           | 6.36                       | <b>0.001</b>    | Reservoir > down > up1-2   |
| <i>C. colchicum</i>   | 2         | 3801  | 1.59            | 0.223           | 2    | 20.56  | 13.70                  | <b>0.001</b>    | 3  | 21.36           | 2.02                       | 0.134           | Up2 < reservoir, down      |
| <i>S. cephalus</i>    | 2         | 35.62 | 14.99           | <b>0.001</b>    | 3    | 17.65  | 24.49                  | <b>0.001</b>    | 4  | 18.45           | 2.20                       | 0.08            | Reservoir > down > up1-2   |

**Appendix 2. Mean ( $\pm$ s.d.)  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of primary production sources, invertebrate and fish collected at each site and season in the main channel of the upper Yeşilirmak River**  
*n*, number of samples analysed followed in parentheses by the number of individuals or the range in the number of individuals included in each sample

| Code                           | Winter                    |                           | Spring                    |                           | Summer                    |                           | Mean                      |                           |
|--------------------------------|---------------------------|---------------------------|---------------------------|---------------------------|---------------------------|---------------------------|---------------------------|---------------------------|
|                                | $\delta^{13}\text{C}$ (‰) | $\delta^{15}\text{N}$ (‰) | $\delta^{13}\text{C}$ (‰) | $\delta^{15}\text{N}$ (‰) | $\delta^{13}\text{C}$ (‰) | $\delta^{15}\text{N}$ (‰) | $\delta^{13}\text{C}$ (‰) | $\delta^{15}\text{N}$ (‰) |
| <b>Upstream Site 1</b>         |                           |                           |                           |                           |                           |                           |                           |                           |
| Primary production sources     |                           |                           |                           |                           |                           |                           |                           |                           |
| Riparian plants                |                           |                           |                           |                           |                           |                           |                           |                           |
| Rp                             |                           |                           |                           |                           |                           |                           |                           |                           |
| Seston                         |                           |                           |                           |                           |                           |                           |                           |                           |
| Ss                             |                           |                           |                           |                           |                           |                           |                           |                           |
| Biofilm                        |                           |                           |                           |                           |                           |                           |                           |                           |
| Bf                             |                           |                           |                           |                           |                           |                           |                           |                           |
| Invertebrates                  |                           |                           |                           |                           |                           |                           |                           |                           |
| Calopterygidae                 |                           |                           |                           |                           |                           |                           |                           |                           |
| Cl                             |                           |                           |                           |                           |                           |                           |                           |                           |
| Gomphidae                      |                           |                           |                           |                           |                           |                           |                           |                           |
| Gm                             |                           |                           |                           |                           |                           |                           |                           |                           |
| Potamon sp.                    |                           |                           |                           |                           |                           |                           |                           |                           |
| Pt                             |                           |                           |                           |                           |                           |                           |                           |                           |
| Baetidae                       |                           |                           |                           |                           |                           |                           |                           |                           |
| Be                             |                           |                           |                           |                           |                           |                           |                           |                           |
| Perlodidae                     |                           |                           |                           |                           |                           |                           |                           |                           |
| Pr                             |                           |                           |                           |                           |                           |                           |                           |                           |
| Chloroperlidae                 |                           |                           |                           |                           |                           |                           |                           |                           |
| Ch                             |                           |                           |                           |                           |                           |                           |                           |                           |
| Heptageniidae                  |                           |                           |                           |                           |                           |                           |                           |                           |
| Hp                             |                           |                           |                           |                           |                           |                           |                           |                           |
| Coenagrionidae                 |                           |                           |                           |                           |                           |                           |                           |                           |
| Ce                             |                           |                           |                           |                           |                           |                           |                           |                           |
| Fish                           |                           |                           |                           |                           |                           |                           |                           |                           |
| <i>Alburnoides bipunctatus</i> |                           |                           |                           |                           |                           |                           |                           |                           |
| Ab                             |                           |                           |                           |                           |                           |                           |                           |                           |
| <i>Barbus plebejus</i>         |                           |                           |                           |                           |                           |                           |                           |                           |
| Bp                             |                           |                           |                           |                           |                           |                           |                           |                           |
| <i>Capoeta banareseui</i>      |                           |                           |                           |                           |                           |                           |                           |                           |
| Cb                             |                           |                           |                           |                           |                           |                           |                           |                           |
| <i>Oxynoemacheilus angorae</i> |                           |                           |                           |                           |                           |                           |                           |                           |
| Oa                             |                           |                           |                           |                           |                           |                           |                           |                           |
| <i>Squalius cephalus</i>       |                           |                           |                           |                           |                           |                           |                           |                           |
| Sc                             |                           |                           |                           |                           |                           |                           |                           |                           |
| <b>Upstream site 2</b>         |                           |                           |                           |                           |                           |                           |                           |                           |
| Primary production sources     |                           |                           |                           |                           |                           |                           |                           |                           |
| Riparian plants                |                           |                           |                           |                           |                           |                           |                           |                           |
| Rp                             |                           |                           |                           |                           |                           |                           |                           |                           |
| Seston                         |                           |                           |                           |                           |                           |                           |                           |                           |
| Ss                             |                           |                           |                           |                           |                           |                           |                           |                           |
| Biofilm                        |                           |                           |                           |                           |                           |                           |                           |                           |
| Bf                             |                           |                           |                           |                           |                           |                           |                           |                           |
| Invertebrates                  |                           |                           |                           |                           |                           |                           |                           |                           |
| Baetidae                       |                           |                           |                           |                           |                           |                           |                           |                           |
| Be                             |                           |                           |                           |                           |                           |                           |                           |                           |
| Chloroperlidae                 |                           |                           |                           |                           |                           |                           |                           |                           |
| Ch                             |                           |                           |                           |                           |                           |                           |                           |                           |
| Perlodidae                     |                           |                           |                           |                           |                           |                           |                           |                           |
| Pr                             |                           |                           |                           |                           |                           |                           |                           |                           |
| Heptageniidae                  |                           |                           |                           |                           |                           |                           |                           |                           |
| Hp                             |                           |                           |                           |                           |                           |                           |                           |                           |
| Oligoneuridae                  |                           |                           |                           |                           |                           |                           |                           |                           |
| Oi                             |                           |                           |                           |                           |                           |                           |                           |                           |
| Potamanthidae                  |                           |                           |                           |                           |                           |                           |                           |                           |
| Ph                             |                           |                           |                           |                           |                           |                           |                           |                           |
| Perlidae                       |                           |                           |                           |                           |                           |                           |                           |                           |
| Pd                             |                           |                           |                           |                           |                           |                           |                           |                           |
| Gomphidae                      |                           |                           |                           |                           |                           |                           |                           |                           |
| Gm                             |                           |                           |                           |                           |                           |                           |                           |                           |
| Potamon sp.                    |                           |                           |                           |                           |                           |                           |                           |                           |
| Pt                             |                           |                           |                           |                           |                           |                           |                           |                           |
| Leuctridae                     |                           |                           |                           |                           |                           |                           |                           |                           |
| Lu                             |                           |                           |                           |                           |                           |                           |                           |                           |
| Fish                           |                           |                           |                           |                           |                           |                           |                           |                           |
| <i>Alburnoides bipunctatus</i> |                           |                           |                           |                           |                           |                           |                           |                           |
| Ab                             |                           |                           |                           |                           |                           |                           |                           |                           |
| <i>Barbus plebejus</i>         |                           |                           |                           |                           |                           |                           |                           |                           |
| Bp                             |                           |                           |                           |                           |                           |                           |                           |                           |
| <i>Capoeta banareseui</i>      |                           |                           |                           |                           |                           |                           |                           |                           |
| Cb                             |                           |                           |                           |                           |                           |                           |                           |                           |
| <i>Oxynoemacheilus angorae</i> |                           |                           |                           |                           |                           |                           |                           |                           |
| Oa                             |                           |                           |                           |                           |                           |                           |                           |                           |
| <i>Squalius cephalus</i>       |                           |                           |                           |                           |                           |                           |                           |                           |
| Sc                             |                           |                           |                           |                           |                           |                           |                           |                           |
| <i>Capoeta sieboldii</i>       |                           |                           |                           |                           |                           |                           |                           |                           |
| Cs                             |                           |                           |                           |                           |                           |                           |                           |                           |

(Continued)

Appendix 2. (Continued)

| Code                            | Winter                    |                           | Spring                    |                           | Summer                    |                           | Mean                      |                           |
|---------------------------------|---------------------------|---------------------------|---------------------------|---------------------------|---------------------------|---------------------------|---------------------------|---------------------------|
|                                 | $\delta^{13}\text{C}$ (‰) | $\delta^{15}\text{N}$ (‰) | $\delta^{13}\text{C}$ (‰) | $\delta^{15}\text{N}$ (‰) | $\delta^{13}\text{C}$ (‰) | $\delta^{15}\text{N}$ (‰) | $\delta^{13}\text{C}$ (‰) | $\delta^{15}\text{N}$ (‰) |
| <i>Chondrostoma colchiticum</i> | -24.65 ± 0.12             | 7.75 ± 0.15               | -26.32 ± 1.11             | 8.01 ± 0.42               | -26.28 ± 0.43             | 8.85 ± 0.42               | -25.65 ± 1.21             | 7.91 ± 0.34               |
| <i>Barbus tauricus</i>          |                           |                           | -25.64 ± 0.40             | 9.73 ± 0.38               |                           |                           | -25.64 ± 0.40             | 9.73 ± 0.38               |
| <i>Seminemacheilus</i> sp.      |                           |                           |                           |                           |                           |                           | -26.28 ± 0.48             | 8.85 ± 0.42               |
| Almus Reservoir                 |                           |                           |                           |                           |                           |                           |                           |                           |
| Primary production sources      |                           |                           |                           |                           |                           |                           |                           |                           |
| Riparian plants                 |                           |                           |                           |                           |                           |                           |                           |                           |
| Rp                              | -29.07 ± 1.33             | 0.99 ± 2.05               | -28.29 ± 1.38             | 1.49 ± 2.40               | -30.01 ± 0.77             | -2.93 ± 1.33              | -28.91 ± 1.64             | 0.30 ± 3.35               |
| Ss                              | -26.31 ± 0.48             | 4.04 ± 0.41               | -25.74 ± 0.74             | 3.91 ± 0.97               | -29.35 ± 0.80             | 3.86 ± 4.26               | -27.06 ± 1.63             | 3.92 ± 3.05               |
| Bf                              | -22.36                    | 5.31                      | -24.62 ± 1.02             | 4.60 ± 1.59               | -26.23 ± 0.26             | 2.27 ± 2.44               | -24.82 ± 1.64             | 3.81 ± 1.96               |
| Ap                              |                           |                           | -27.58 ± 1.24             | 6.55 ± 4.16               |                           |                           | -27.58 ± 1.23             | 6.55 ± 4.16               |
| Invertebrates                   |                           |                           |                           |                           |                           |                           |                           |                           |
| <i>Dreissena</i> sp.            | -28.06                    | 9.68                      |                           |                           |                           |                           | -28.06                    | 9.68                      |
| Culicidae                       |                           |                           |                           |                           | -25.80                    | 8.26                      | -25.80                    | 8.26                      |
| Zooplankton                     |                           |                           | -29.50 ± 2.12             | 6.50 ± 3.54               | -30.13 ± 0.25             | 8.68 ± 0.93               | -30.84 ± 2.48             | 9.51 ± 4.06               |
| Fish                            |                           |                           |                           |                           |                           |                           |                           |                           |
| <i>Alburnus chalcoides</i>      |                           |                           |                           |                           |                           |                           |                           |                           |
| Ac                              | -25.37                    | 8.49                      |                           |                           |                           |                           | -25.37                    | 8.49                      |
| <i>Capoeta banareseui</i>       |                           |                           |                           |                           |                           |                           |                           |                           |
| Cb                              | -26.12 ± 1.51             | 9.81 ± 1.52               | -27.00 ± 1.50             | 11.59 ± 0.94              | -26.84 ± 1.51             | 10.79 ± 1.05              | -26.76 ± 1.38             | 10.92 ± 1.27              |
| <i>Chondrostoma colchiticum</i> |                           |                           |                           |                           |                           |                           |                           |                           |
| Cc                              | -25.87 ± 0.87             | 9.58 ± 0.82               | -25.22 ± 0.34             | 9.85 ± 0.63               | -25.44 ± 0.48             | 9.74 ± 0.44               | -25.49 ± 0.60             | 9.73 ± 0.61               |
| <i>Oncorhynchus mykiss</i>      |                           |                           |                           |                           |                           |                           |                           |                           |
| Om                              | -20.56 ± 0.41             | 8.94 ± 0.36               | -23.57 ± 2.90             | 12.16 ± 2.09              | -24.43 ± 2.18             | 11.80 ± 0.59              | -22.59 ± 2.62             | 10.33 ± 1.79              |
| <i>Squalius cephalus</i>        |                           |                           |                           |                           |                           |                           |                           |                           |
| Sc                              | -25.36                    | 11.05                     | -25.94                    | 13.58                     | -25.86 ± 0.04             | 12.98 ± 1.11              | -25.75 ± 0.27             | 12.65 ± 1.22              |
| <i>Atherina boyeri</i>          |                           |                           |                           |                           |                           |                           |                           |                           |
| At                              |                           |                           | -29.56 ± 0.55             | 14.43 ± 0.50              | -27.98 ± 0.30             | 14.76 ± 0.37              | -29.11 ± 0.90             | 14.52 ± 0.46              |
| <i>Barbus plebejus</i>          |                           |                           |                           |                           |                           |                           |                           |                           |
| Bp                              | -27.29 ± 0.25             | 15.24 ± 0.03              | -27.29 ± 0.25             | 15.24 ± 0.03              | -27.46 ± 0.76             | 15.04 ± 1.53              | -26.33 ± 0.70             | 15.09 ± 1.39              |
| Cs                              |                           |                           | -26.33 ± 0.70             | 9.31 ± 0.26               |                           |                           |                           | 9.31 ± 0.26               |
| <i>Capoeta sieboldii</i>        |                           |                           |                           |                           |                           |                           |                           |                           |
| Cp                              | -26.79 ± 1.49             | 11.30 ± 0.73              | -26.79 ± 1.49             | 11.30 ± 0.73              | -26.61 ± 0.67             | 11.80 ± 0.38              | -27.03 ± 0.92             | 11.48 ± 0.48              |
| <i>Cyprinus carpio</i>          |                           |                           |                           |                           |                           |                           |                           |                           |
| Sg                              |                           |                           | -28.98 ± 2.59             | 14.24 ± 1.38              | -25.79                    | 13.30                     | -28.19 ± 2.65             | 14.01 ± 1.22              |
| <i>Carassius carassius</i>      |                           |                           |                           |                           |                           |                           |                           |                           |
| Ca                              |                           |                           |                           |                           | -26.35                    | 10.72                     | -26.35                    | 10.72                     |
| Downstream site                 |                           |                           |                           |                           |                           |                           |                           |                           |
| Primary production sources      |                           |                           |                           |                           |                           |                           |                           |                           |
| Riparian plants                 |                           |                           |                           |                           |                           |                           |                           |                           |
| Rp                              | -29.39 ± 2.04             | 0.32 ± 2.10               | -28.60 ± 1.33             | 1.61 ± 8.49               | -29.04 ± 1.40             | 0.55 ± 2.06               | -29.03 ± 2.23             | 0.84 ± 2.17               |
| Ss                              | -26.15                    | 1.51                      | -24.71                    | 0.89                      | -23.79                    | 0.14                      | -24.88 ± 0.16             | 0.84 ± 1.62               |
| Bf                              | -27.23 ± 0.32             | 2.30 ± 0.72               | -27.36 ± 0.06             | 0.77 ± 1.04               | -25.16                    | 1.49                      | -26.87 ± 0.64             | 1.52 ± 1.84               |
| <i>Cladophora</i> sp.           |                           |                           |                           |                           |                           |                           |                           |                           |
| Co                              | -32.05 ± 0.78             | 1.48 ± 0.94               | -30.23                    | 1.69                      |                           |                           | -31.44 ± 0.40             | 1.55 ± 2.23               |
| Invertebrates                   |                           |                           |                           |                           |                           |                           |                           |                           |
| Hirudinea                       |                           |                           |                           |                           |                           |                           |                           |                           |
| Hr                              | -29.59                    | 7.36                      |                           |                           |                           |                           | -29.59                    | 7.36                      |
| <i>Gammarus</i> sp.             |                           |                           |                           |                           |                           |                           |                           |                           |
| Gs                              | -29.29                    | 4.67                      | -29.79                    | 4.86                      | -29.16                    | 4.11                      | -29.42 ± 0.33             | 4.55 ± 0.38               |
| Baetidae                        |                           |                           | -32.20                    | 4.88                      |                           |                           | -32.20                    | 4.88                      |
| Zooplankton                     |                           |                           |                           |                           |                           |                           |                           |                           |
| Zp                              |                           |                           |                           |                           | -29.10                    | 3.69                      | -29.10                    | 3.69                      |
| Tipulidae                       |                           |                           |                           |                           | -28.49                    | 3.20                      | -28.49                    | 3.20                      |
| Simuliidae                      |                           |                           |                           |                           |                           |                           |                           |                           |
| Si                              |                           |                           | -25.43                    | 2.81                      |                           |                           | -25.43                    | 2.81                      |
| Fish                            |                           |                           |                           |                           |                           |                           |                           |                           |
| <i>Capoeta banareseui</i>       |                           |                           |                           |                           |                           |                           |                           |                           |
| Cb                              | -26.77 ± 1.17             | 8.23 ± 1.41               | -29.00 ± 3.04             | 9.60 ± 0.95               | -26.25 ± 1.23             | 8.85 ± 2.00               | -27.29 ± 2.55             | 8.95 ± 1.54               |
| <i>Chondrostoma colchiticum</i> |                           |                           |                           |                           |                           |                           |                           |                           |
| Cc                              | -28.38 ± 2.28             | 8.64 ± 1.22               | -27.52 ± 1.77             | 8.93 ± 0.86               | -28.17 ± 3.03             | 9.04 ± 0.46               | -27.92 ± 2.19             | 8.90 ± 0.82               |
| <i>Squalius cephalus</i>        |                           |                           |                           |                           |                           |                           |                           |                           |
| Sc                              | -26.42 ± 0.06             | 8.80 ± 0.39               | -27.08 ± 0.87             | 10.40 ± 0.55              | -25.98 ± 3.21             | 9.63 ± 0.92               | -26.51 ± 2.05             | 9.84 ± 0.89               |
| <i>Oncorhynchus mykiss</i>      |                           |                           |                           |                           |                           |                           |                           |                           |
| Om                              |                           |                           | -28.89 ± 0.02             | 9.40 ± 1.05               |                           |                           | -28.89 ± 0.02             | 9.40 ± 1.05               |
| <i>Seminemacheilus</i> sp.      |                           |                           |                           |                           |                           |                           |                           |                           |
| Sm                              |                           |                           | -28.28                    | 10.80                     |                           |                           | -28.28                    | 10.80                     |

Appendix 3. SIAR (Stable Isotope Analysis in R) model estimates (1st–99th percentiles) of percentage contributions of primary production sources to fish and macroinvertebrate biomass at four study sites in the upper Yeşilirmak River across all sample seasons

Production sources with values  $\geq 45\%$  for the 99th percentile are shown in bold

|                                | Upstream Site 1   |                  |            |                   | Upstream Site 2   |                   |           |                   | Almus Reservoir |                   |         |         | Downstream site   |           |           |            |
|--------------------------------|-------------------|------------------|------------|-------------------|-------------------|-------------------|-----------|-------------------|-----------------|-------------------|---------|---------|-------------------|-----------|-----------|------------|
|                                | Riparian          | Seston           | Biofilm    | Riparian          | Riparian          | Seston            | Biofilm   | Riparian          | Riparian        | Seston            | Biofilm | Aquatic | Riparian          | Seston    | Biofilm   | Cladophora |
| <b>Fish</b>                    |                   |                  |            |                   |                   |                   |           |                   |                 |                   |         |         |                   |           |           |            |
| <i>Alburnoides bipunctatus</i> | 42 (17–69)        | 18 (0–34)        | 39 (9–67)  | 21 (0–43)         | 31 (0–59)         | <b>48 (0–83)</b>  | 18 (0–38) | 28 (0–53)         | 31 (1–56)       | 23 (5–40)         |         |         |                   |           |           |            |
| <i>Alburnus chalcoides</i>     |                   |                  |            |                   |                   |                   | 31 (0–61) | 22 (0–47)         | 11 (0–32)       | 36 (0–69)         |         |         |                   |           |           |            |
| <i>Atherina boyeri</i>         |                   |                  |            |                   |                   |                   | 26 (0–46) | 24 (0–44)         | 14 (0–31)       | 36 (1–65)         |         |         |                   |           |           |            |
| <i>Barbus plebejus</i>         | 42 (17–67)        | 19 (0–35)        | 38 (11–66) | 19 (0–34)         | 21 (0–44)         | <b>60 (29–86)</b> |           |                   |                 |                   |         |         |                   |           |           |            |
| <i>Barbus tauricus</i>         |                   |                  |            | 22 (0–43)         | 32 (10–58)        | <b>46 (0–81)</b>  |           |                   |                 |                   |         |         |                   |           |           |            |
| <i>Capoeta banarescui</i>      | <b>47 (24–71)</b> | 25 (0–50)        | 28 (0–53)  | 26 (0–45)         | 6 (0–17)          | <b>68 (9–91)</b>  | 3 (0–9)   | 18 (0–35)         | 13 (0–26)       | <b>66 (53–79)</b> |         |         | 23 (0–46)         | 26 (0–46) | 29 (0–55) | 23 (0–42)  |
| <i>Capoeta sieboldii</i>       |                   |                  |            | 38 (11–74)        | 29 (0–60)         | 33 (0–65)         |           |                   |                 |                   |         |         |                   |           |           |            |
| <i>Carassius carassius</i>     |                   |                  |            |                   |                   |                   |           |                   |                 |                   |         |         |                   |           |           |            |
| <i>Chondrostoma colchicum</i>  |                   |                  |            | 23 (0–48)         | 25 (0–54)         | <b>52 (23–91)</b> | 4 (0–10)  | 19 (0–37)         | 40 (23–57)      | 37 (22–53)        |         |         | 23 (0–46)         | 20 (0–39) | 28 (0–53) | 29 (6–50)  |
| <i>Cyprinus carpio</i>         |                   |                  |            |                   |                   |                   | 7 (0–19)  | 19 (0–42)         | 12 (0–27)       | <b>62 (37–84)</b> |         |         |                   |           |           |            |
| <i>Oncorhynchus mykiss</i>     |                   |                  |            | 3 (0–9)           | 12 (0–34)         | 36 (1–63)         | 3 (0–9)   | 12 (0–34)         | 36 (1–63)       | <b>49 (23–72)</b> |         |         | 26 (0–50)         | 20 (0–42) | 24 (0–46) | 30 (0–54)  |
| <i>Oxyonemacheilus angorae</i> | 35 (0–74)         | 42 (0–83)        | 23 (0–51)  | 31 (0–51)         | 27 (0–49)         | 42 (0–72)         | 23 (0–47) | 25 (0–50)         | 21 (0–44)       | 30 (0–58)         |         |         | <b>72 (52–92)</b> | 8 (0–22)  | 10 (0–27) | 9 (0–25)   |
| <i>Seminemacheilus</i> sp.     |                   |                  |            | 32 (0–56)         | 29 (0–54)         | 39 (0–70)         | 15 (0–35) | 24 (0–35)         | 31 (0–56)       | 30 (0–54)         |         |         | 20 (0–42)         | 33 (6–57) | 32 (0–61) | 15 (0–33)  |
| <i>Silurus glanis</i>          | <b>48 (20–75)</b> | 22 (0–41)        | 30 (2–62)  | 7 (0–16)          | 6 (0–17)          | <b>87 (31–99)</b> |           |                   |                 |                   |         |         |                   |           |           |            |
| <i>Squalius cephalus</i>       |                   |                  |            |                   |                   |                   |           |                   |                 |                   |         |         |                   |           |           |            |
| <b>Invertebrates</b>           |                   |                  |            |                   |                   |                   |           |                   |                 |                   |         |         |                   |           |           |            |
| Baetidae                       | <b>58 (27–93)</b> | 19 (0–48)        | 22 (0–54)  | 31 (0–60)         | 34 (0–61)         | 35 (0–62)         |           |                   |                 |                   |         |         |                   |           |           |            |
| Chloroperlidae                 | <b>52 (17–90)</b> | 23 (0–54)        | 24 (0–24)  | <b>65 (35–96)</b> | 19 (0–48)         | 16 (0–44)         |           |                   |                 |                   |         |         |                   |           |           |            |
| Culicidae                      |                   |                  |            | 4 (0–10)          | <b>45 (23–60)</b> | 19 (0–37)         | 4 (0–10)  | <b>45 (23–60)</b> | 19 (0–37)       | 32 (22–48)        |         |         |                   |           |           |            |
| <i>Dressenia</i> sp.           |                   |                  |            | 7 (0–19)          | <b>63 (37–84)</b> | 12 (0–27)         | 7 (0–19)  | <b>63 (37–84)</b> | 12 (0–27)       | 18 (0–35)         |         |         |                   |           |           |            |
| Gomphidae                      | 27 (0–55)         | 34 (0–64)        | 39 (0–73)  | 35 (2–64)         | 31 (0–58)         | 34 (0–62)         |           |                   |                 |                   |         |         |                   |           |           |            |
| Calopterygidae                 | 34 (0–62)         | 31 (0–60)        | 35 (0–66)  |                   |                   |                   |           |                   |                 |                   |         |         |                   |           |           |            |
| Coenagrionidae                 | 37 (1–67)         | 31 (0–62)        | 32 (0–65)  |                   |                   |                   |           |                   |                 |                   |         |         |                   |           |           |            |
| <i>Gammarus</i> sp.            |                   |                  |            |                   |                   |                   |           |                   |                 |                   |         |         |                   |           |           |            |
| Hirudinea                      |                   |                  |            |                   |                   |                   |           |                   |                 |                   |         |         |                   |           |           |            |
| Hepageniidae                   | <b>59 (29–94)</b> | 19 (0–47)        | 22 (0–53)  | 38 (0–68)         | 33 (0–61)         | 29 (0–55)         |           |                   |                 |                   |         |         |                   |           |           |            |
| Leuctridae                     |                   |                  |            | 36 (0–65)         | 32 (0–60)         | 32 (0–60)         |           |                   |                 |                   |         |         |                   |           |           |            |
| Oligoneuridae                  |                   |                  |            | <b>48 (13–84)</b> | 26 (0–55)         | 25 (0–54)         |           |                   |                 |                   |         |         |                   |           |           |            |
| Perlidae                       | <b>51 (18–87)</b> | 24 (0–52)        | 25 (0–55)  | <b>51 (18–87)</b> | 24 (0–52)         | 25 (0–55)         |           |                   |                 |                   |         |         |                   |           |           |            |
| Potamanthidae                  |                   |                  |            | 39 (3–69)         | 33 (0–62)         | 28 (0–55)         |           |                   |                 |                   |         |         |                   |           |           |            |
| Perlodidae                     | <b>63 (34–95)</b> | 18 (0–46)        | 19 (0–48)  | <b>63 (34–94)</b> | 18 (0–44)         | 20 (0–49)         |           |                   |                 |                   |         |         |                   |           |           |            |
| Simuliidae                     |                   |                  |            |                   |                   |                   |           |                   |                 |                   |         |         |                   |           |           |            |
| Tipulidae                      |                   |                  |            |                   |                   |                   |           |                   |                 |                   |         |         |                   |           |           |            |
| <i>Potamon</i> sp. (Crab)      | 29 (0–68)         | <b>45 (0–83)</b> | 27 (0–57)  | 42 (0–74)         | 15 (0–38)         | 43 (0–83)         |           |                   |                 |                   |         |         |                   |           |           |            |
| Zooplankton                    |                   |                  |            | 20 (0–43)         | 23 (0–48)         | 14 (0–77)         | 20 (0–43) | 23 (0–48)         | 14 (0–77)       | 42 (11–78)        |         |         | 28 (0–51)         | 19 (0–39) | 22 (0–44) | 32 (3–57)  |

Appendix 4. SIAR (Stable Isotope Analysis in R) model estimates (1st–99th percentiles) of percentage contributions of primary production sources to fish and macroinvertebrate biomass during three seasons at four sites in the upper Yeşilirmak River

Production sources with values  $\geq 45\%$  for the 99th percentile are shown in bold

| Station and consumer           | Winter     |           |                    |         | Spring     |                   |           |                  | Summer  |            |                   |                   |                   |
|--------------------------------|------------|-----------|--------------------|---------|------------|-------------------|-----------|------------------|---------|------------|-------------------|-------------------|-------------------|
|                                | Riparian   | Seston    | Biofilm            | Aquatic | Cladophora | Riparian          | Seston    | Biofilm          | Aquatic | Cladophora | Riparian          | Seston            | Biofilm           |
| Upstream Site 1                |            |           |                    |         |            |                   |           |                  |         |            |                   |                   |                   |
| <i>Alburnoides bipunctatus</i> |            |           |                    |         |            | 30 (6–53)         | 33 (2–58) | 37 (8–65)        |         |            | 18 (0–42)         | 42 (3–76)         | 40 (4–70)         |
| <i>Barbus plebejus</i>         |            |           |                    |         |            | 29 (1–53)         | 34 (0–63) | 37 (3–67)        |         |            | 12 (0–28)         | <b>53 (22–88)</b> | 35 (5–60)         |
| <i>Capoeta banarensis</i>      |            |           |                    |         |            | <b>50 (21–84)</b> | 20 (0–45) | 30 (0–61)        |         |            | 32 (0–54)         | <b>49 (15–91)</b> | 19 (0–42)         |
| <i>Oxyaenacheilus angorae</i>  |            |           |                    |         |            | <b>58 (32–87)</b> | 16 (0–40) | 26 (0–52)        |         |            |                   |                   |                   |
| <i>Squalius cephalus</i>       |            |           |                    |         |            | <b>54 (28–87)</b> | 17 (0–41) | 29 (0–57)        |         |            | 15 (0–37)         | <b>47 (10–85)</b> | 38 (4–65)         |
| Calopterygidae                 |            |           |                    |         |            | 42 (3–74)         | 25 (0–52) | 33 (0–69)        |         |            | 28 (0–53)         | 39 (2–72)         | 33 (0–61)         |
| Gomphidae                      |            |           |                    |         |            | 31 (0–59)         | 27 (0–55) | 42 (2–79)        |         |            | 37 (0–51)         | 40 (2–73)         | 33 (0–62)         |
| <i>Potamon</i> sp.             |            |           |                    |         |            |                   |           |                  |         |            | 20 (0–61)         | 44 (0–91)         | 36 (0–81)         |
| Baetidae                       |            |           |                    |         |            | <b>65 (3–78)</b>  | 13 (0–35) | 22 (0–66)        |         |            |                   |                   |                   |
| Perlodidae                     |            |           |                    |         |            | <b>70 (38–99)</b> | 11 (0–32) | 19 (0–54)        |         |            |                   |                   |                   |
| Chloroperlidae                 |            |           |                    |         |            | <b>62 (28–95)</b> | 15 (0–39) | 23 (0–60)        |         |            |                   |                   |                   |
| Heptageniidae                  |            |           |                    |         |            | <b>67 (2–77)</b>  | 12 (0–34) | 21 (0–66)        |         |            |                   |                   |                   |
| Coenagrionidae                 |            |           |                    |         |            |                   |           |                  |         |            | 29 (0–55)         | 40 (2–75)         | 31 (0–60)         |
| Upstream Site 2                |            |           |                    |         |            |                   |           |                  |         |            |                   |                   |                   |
| <i>Alburnoides bipunctatus</i> |            |           |                    |         |            | 21 (0–50)         | 34 (0–65) | <b>45 (4–83)</b> |         |            |                   |                   |                   |
| <i>Barbus plebejus</i>         |            |           |                    |         |            |                   |           |                  |         |            | 35 (22–50)        | 18 (0–40)         | <b>47 (29–64)</b> |
| <i>Capoeta banarensis</i>      | 12 (0–28)  | 6 (0–17)  | <b>82 (61–98)</b>  |         |            | 21 (0–43)         | 36 (2–65) | 43 (10–76)       |         |            | <b>51 (26–75)</b> | 11 (0–34)         | 38 (10–64)        |
| <i>Oxyaenacheilus angorae</i>  | 34 (11–56) | 24 (0–48) | 42 (10–76)         |         |            | 27 (0–53)         | 35 (0–66) | 38 (2–69)        |         |            |                   |                   |                   |
| <i>Squalius cephalus</i>       | 9 (0–19)   | 7 (0–24)  | <b>84 (64–100)</b> |         |            | 30 (0–59)         | 31 (0–62) | 39 (1–75)        |         |            | 29 (0–47)         | 21 (0–47)         | <b>50 (29–72)</b> |
| <i>Capoeta sieboldii</i>       |            |           |                    |         |            | 36 (0–70)         | 32 (0–63) | 32 (0–63)        |         |            |                   |                   |                   |
| <i>Chondrostoma colchicum</i>  | 24 (0–52)  | 29 (0–60) | <b>47 (8–86)</b>   |         |            | 28 (0–56)         | 34 (0–64) | 38 (1–71)        |         |            |                   |                   |                   |
| <i>Barbus tauricus</i>         |            |           |                    |         |            | 20 (0–48)         | 35 (0–66) | <b>45 (6–82)</b> |         |            |                   |                   |                   |
| <i>Seminemachetius</i> sp.     |            |           |                    |         |            |                   |           |                  |         |            | 38 (12–62)        | 29 (0–57)         | 33 (4–58)         |
| Baetidae                       | 31 (0–60)  | 40 (5–68) | 30 (0–53)          |         |            |                   |           |                  |         |            |                   |                   |                   |
| Chloroperlidae                 | 38 (2–65)  | 35 (0–63) | 27 (0–55)          |         |            |                   |           |                  |         |            |                   |                   |                   |
| Perlodidae                     | 40 (2–75)  | 31 (0–60) | 29 (0–55)          |         |            |                   |           |                  |         |            |                   |                   |                   |
| Heptageniidae                  | 37 (0–70)  | 35 (0–64) | 28 (0–54)          |         |            | 35 (0–63)         | 31 (0–60) | 34 (0–64)        |         |            | <b>70 (47–95)</b> | 16 (0–40)         | 14 (0–34)         |



