Turk. J. Fish.& Aquat. Sci. 19(2), 99-107
http://doi.org/10.4194/1303-2712-v19_2_02

RESEARCH PAPER

Turkish Journal of
FISHERIES and
AQUATIC SCIENCES

Trophic Pathways from Pelagic and Littoral Sources Supports Food Web in an Eutrophic Natural Lake (Lake Zinav, Turkey)

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Article History
Received 25 January 2017
Accepted 12 March 2018
First Online 15 March 2018

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Keywords
Stable isotope analysis
Gut content
Invasive fish
Habitat coupling
Cyprinids

Abstract

Stable isotope analysis was used to determine which basal sources supporting native and invasive cyprinid fishes are important in a dimictic-eutrophic lake (Lake Zinav, Turkey). We sampled potential primary producers (littoral, pelagic sources and detritus), fish and macroinvertebrates from littoral and pelagic zones of the lake during spring and summer in 2013. The relative importance of basal sources assimilated by invasive (*Carassius*spp.) and native fishes (*Squalius cephalus*, *Capoeta banarescui*,*Cyprinu scarpio*) was estimated using SIAR mixing model. Consumers such as collector-gatherer (1) (-35.33‰) and *S. cephalus, Carassius*spp., and *C. carpio* had more ^{13}C depleted (-32.12, -31.09, -31.54‰, respectively), while *C. banarescui*, collector-gatherer (2), and etc. had more ^{13}C enriched values (-25.03, -26.55‰, respectively). SIAR and gut contents indicate that main energy sources were highly variable among fishes, three main sources contributed to invasive fish, but littoral sources for *C. banarescui*, pelagic sources for *S. cephalus,* and detritus and pelagic sources for *C. carpio*were important. Consumer's biomass were also partially linked to detritus. Our study suggested that all species promoted coupling of pelagic and littoral pathways, and competition for resources among invasive and native fishes was likely to cause resources sharing, and to shift to suboptimal resources.

Introduction

Eutrophication leading to higher algal biomass and turbidity and decreased dissolved oxygen concentrations which in turn result in decrease in abundance and diversity of organisms and loss of ecosystem functions is considered as one of the important factors to change trophic status of the ecosystem that affects primary production sources supporting consumers (Anderson, Glibert& Burkholder, 2002). Lake metazoan often assimilate energy derived from both autochthonous sources like macrophyta, benthic and pelagic algae and allochthonous sources like terrestrial vegetation. The relative availability of these resources is controlled by terrestrial inputs, and their effects on light and low nutrient levels limit production of pelagic algae in the low-productivity lakes (Solomon *et al*., 2011). Allochthonous and autochthonous organic matters are been rich in anoxic water and sediments compared to the overlying oxic water, and anoxic metabolism may account for a substantial part (20–60%) of the carbon metabolism and the heterotrophic microbial production (Grey, 2016), followed by consumption of these microbes by protozoans (flagellates, ciliates, etc.) or zooplankton in the receiving aquatic system (Jones, Grey, Sleep &Arvola, 1999; Cole *et al*., 2011), thus transferred to higher trophic levels within freshwater environments. A variety of processes at multiple trophic levels create linkages among terrestrial, pelagic, and benthic energy pathways in lake food webs (Schindler &Scheuerell 2002; Vadeboncoeur *et al*. 2003). For instance, benthic consumers may utilize pelagic production that settles on the bottom, pelagic consumers may utilize dissolved or particulate terrestrial detritus, and fishes may consume benthic, pelagic, or terrestrial prey (Solomon *et al*., 2011).

The relative contribution of autochthonous and allochthonous basal sources supporting consumers differ among lake systems. Grey, Jones and Sleep, (2000) concluded that the relative importance of allochthonous sources of organic carbon decreases with increasing lake trophy. When phytoplankton production is limited in oligotrophic lake, zooplankton assimilate planktonic heterotrophs and detritus via the microbial pathway (Van Duinen*et al*., 2006). Vadeboncoeur *et al*. (2003) assumed that primary and secondary consumer production strongly depends on littoral-benthic algae in oligotrophic lake. However Mao, Gu, Zeng, Zhou and Sun (2012) reported from food web of eutrophic lake studies that phytoplankton were the major primary production sources supporting consumers, and strongly linked to benthic secondary production in eutrophic lakes (Hershey *et al*., 2006). For dystrophic lakes, Lau, Sundh, Vrede, Pickova and Goedkoop (2014) indicated that consumers predominantly rely on energy from autochthonous primary production sources.

Lake Zinav is dimictic and the biggest landslide lake, and has regional and national importance because of its natural structure, biological diversity, and unique landscape in Tokat Province, Turkey. The lake has been determined as eutrophic lake. Degradation of the lake water quality due to increasingly being enriched with organic matter seemed to cause eutrophication and algal blooms. Temperature stratification started to develop in spring and reached its peak during summer. Mixing period for the lake was between January and April. The dissolved oxygen concentration had a minimum value at a depth of 5 m (0.08 mg/l) in summer indicating anoxic conditions (Buhan*et al*., 2013). Due to anoxic condition, fishes inhabits only macrophyte dominated littoral zone of inlet and outlet of the lake. Taxa belongs to Cyprinidae such as, *Carassius* spp. are the most widely distributed invasive fishes in Turkey from Asia and Europe, and have been introduced intentionally or not, through various human activities in Lake Zinav. This invasive fish is benthopelagic and omnivores, and mostly consume Gastropods, Dipterans, Cladocerans, Copepods, and Ostracods(Balik, Karasahin, Ozkok, Cubuk&Uysal, 2003) as in other cyprinids (*C. carpio, S. cephalus, C. banarescui*) in the Lake Zinav. *C. carpio* was very abundant in Lake Zinav. After the introduction of *Carassius* spp., abundance of *C. carpio* declined drastically in the lake (Fisherman observation). *Carassius* spp. tends to be a keystone species, and have strong effect on the species composition and trophic linkages, for example, predator–prey links and resource competition. Therefore, they might be expected to resources overlap with other cyprinids.

Understandings of the trophic ecology of invasive species are very important to mitigate the impacts of invasion, and robust risk assessment. Natural abundance of stable isotopes might provide as tracer of trophic structure, and important information about food source and organic matter processing (Peterson & Fry, 1987). The objectives of this study were to determine (1) the relative importance of primary production sources supporting the food web of Lake Zinav, (2) the trophic interaction between invasive and native fishes in Lake Zinav.

Materials and Methods

Study Site

Lake Zinav, located between 37^{o} 13’-37^{o} 21’N and 40^{o} 32’-40^{o} 23’ E in the Central Black Sea

Region situated in the northwest district of Reşadiye county of Tokat Province in Turkey (Figure 1). Lake Zinav is the biggest natural lake in the Kelkit river basin. It has a total surface area of 61 km^2, with a maximum depth of 20 m. Northeastern Turkey has a semi-arid climate with large seasonal variation in temperatures(Kundell, 2009). Water temperature reaches the lowest value of 0.77 ºC in March and the highest of 24.91ºC in August (Buhan*et al*., 2013). The Lake Zinav is a dimictic lake, which is circulated in spring

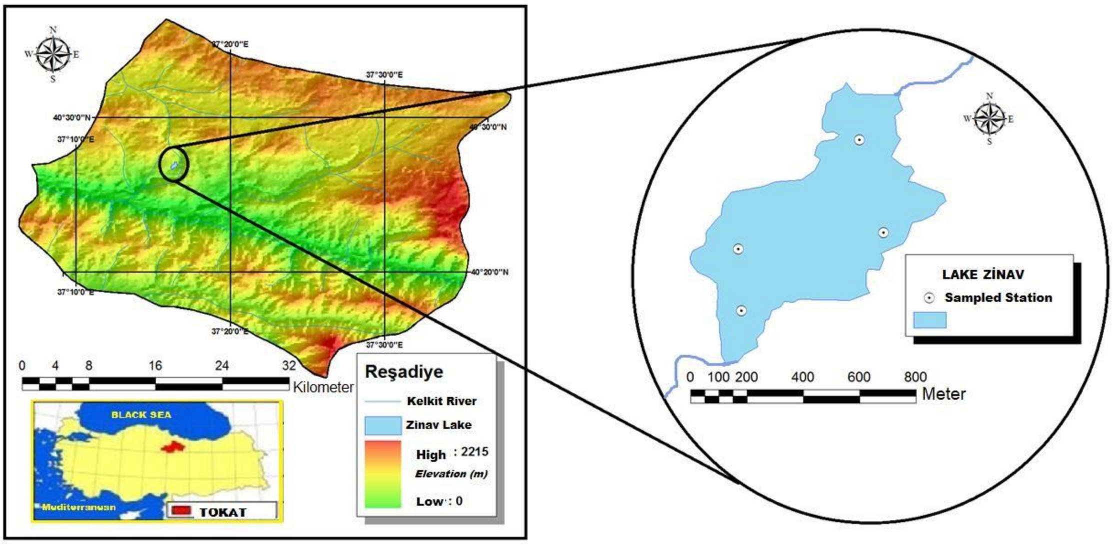


Figure 1. Location of study sites in the Lake Zinav, Turkey.

and fall, and thermally stratified in summer. The lake has been determined as a eutrophic characteristic and undergone eutrophication (Buhanet al., 2013). The lake and its basin are under the threats of household sewage, manure and agricultural discharge, and forest destruction. The other main factors affecting ecology of the lake are construction of hydroelectric power house and channelizing of the stream flowing into the lake. Basin of eutrophic Lake Zinav can be divided into two main areas: a sheltered, macrophytedominated littoral zone from inflow (northeast coast) and outflow (southwest coast) of the lake, and unvegetated littoral zone that occupies the northwest and southeast coast of the lake (Figure 1).

Food Web Components

Primary production sources and consumers (fishes, pelagic and benthic macroinvertebrates) for stable isotope analyses were collected from Lake Zinav during spring and summer in 2013. Several basal source groups derived from terrestrial and aquatic organic matters were collected from littoral and pelagic zone of the lake. Detritus originating from dead or recently fallen leaves from terrestrial vegetation was collected from the substrate. Green leaves of the dominant submersed and floating leaved macrophyte were collected by hand, and macrophytes and associated epiphytonwere sampled from plant clippings and stems below water line. Hence two sources were combined based on similarities of theirs $\delta^{13}C$ values, and referred to as “littoral sources” (epiphyton and macrophyte-derived energy source). Water samples were collected in 5-

L opaque bottles and filtered through a 60-µm sieve to remove zooplankton; remaining particles that settled onto the bottom were collected as seston samples (< 60µm) that were dominated by phytoplankton. Seston was sampled at surface and a depth of approximately 10m in both seasons but seston samples taken at surface during spring and 10 meter during summer were not read properly in mass spectrometry. After that we referred to seston as “pelagic sources”. Microscopic observations showed that dominant species of seston were various cysts, diatoms protozoa (ciliate), and less cyanobacteria during spring, and during summer cyanobacteria (*Anabaena* sp., *Aphanizomenon*sp.) were more abundant taxa of seston, followed by dinoflagellates (*Ceratium* sp. and *Peridinium* sp.), *Euglena* spp.,*Scenedesmus* spp., *Peridinium* sp. and diatoms. In the laboratory, seston, epiphyton samples were filtered onto pre-combusted (450ºC for 4 h) Whatman GF/F glass fiber filters and then immediately frozen.

Zooplankton were collected from offshore area of the lake using standard plankton net (60 µm). Zooplankton samples were placed in an insulated box and transported to the laboratory for identification and analysis. The zooplankton community in Lake Zinav was dominated by *Difflugia*spp. (Arcellinida, Amoebozoa) was the dominant taxa and *Keratella* and *Filinia* spp. (Rotifera), cladocera were also found in the lake surface area in spring. However, rotifers with *Keratella* spp. and *Asplanchna* spp. and copepods with cyclopoida, calanoida and nauplii the most abundant in summer.

Chironomidae (Diptera larvae)were collected with an Ekman grab on the lake bottom (sublittoral zone of unvegetated southeast coast, ~5m), and *Chironomus* (Blood-red Chironomidae) made up the overwhelming majority of Chironomidae samples. Baetidae (*Baetis* spp.) and Nematoda were sampled only littoral zone of unvegetated southeast coast of the lake. Other benthic invertebrates inhabiting in macrophyte-dominated littoral zone were collected by sweeping both macrophye and benthos with a pond net. They 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 euthanasia to obtain tissue samples. Common aquatic invertebrates were identified to order or genus using keys provided by Bouchard (2004).

Fishes were collected during dawn (5am - 8am) in macrophyte -dominated littoral zone of the lake using experimental gillnets with panels of 25, 30, 40, 50, 60, 70 and 80-mm mesh. We captured only 2 individuals of *C. carpio* during all study periods. Fish specimens were euthanized in an ice bath and stored on ice for transport to the laboratory where they were identified to species, weighed, and measured for standard length. To understand what these fishes consume, we analyzed some individual’s gut contents using a stereomicroscope or light microscope.

Fish Gut Content Analyses

We did not remove gut contents from macroinvertebrate samples. 30 individuals of fish species (*Carassius* spp.: 8, *S. cephalus*: 13, *C. banarescui*: 7, *C. carpio*: 2) were dissected for gut content analyses, which were quantified volumetrically using the method by Akin (2001). Data were reported as the proportional volumetric consumption of food items in stomachs of fishes. Stomachs were later opened and the contents were collected into petri dishes for enumeration and identification. All prey items were removed from the anterior half of the gut and examined under a dissecting microscope, or compound microscope. Each prey item was identified to the lowest possible taxonomic level.

Stable Isotope Analysis

In the laboratory, white muscle tissue was removed posterior to the dorsal fin of a total of 16 fish specimens for stable isotope analysis. For larger consumers (fish, benthic macroinvertebrates), each sample consisted of a single individual, but for smaller consumers (benthic invertebrates), samples were a composite of several individuals (an average of 10 individuals from each invertebrate sample) to generate minimal weights (3 mg) for stable isotope analyses. All primary production and consumer samples were dried to constant weight at 60 ºC for 48 hours in an oven. Dried samples were ground into a fine powder and stored in glass vials. Each sample subsequently was weighed to 0.001 mg and sealed inside ultra-pure tin capsules (Elemental Microanalysis Limited ®). Samples were analyzed for carbon and nitrogen isotope ratios using mass spectrometry at the Analytical Chemistry Laboratory of the Institute of Ecology, University of Georgia, USA. Analytical precision for both carbon and nitrogen stable isotope was 0.10‰. Ratios (R) of the heavy isotope to the light isotopes ($^{13}C/^{12}C$, $^{15}N/^{14}N$) were expressed in parts per thousand, relative to the standards in delta notation following the formula:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$$

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

Data Analyses

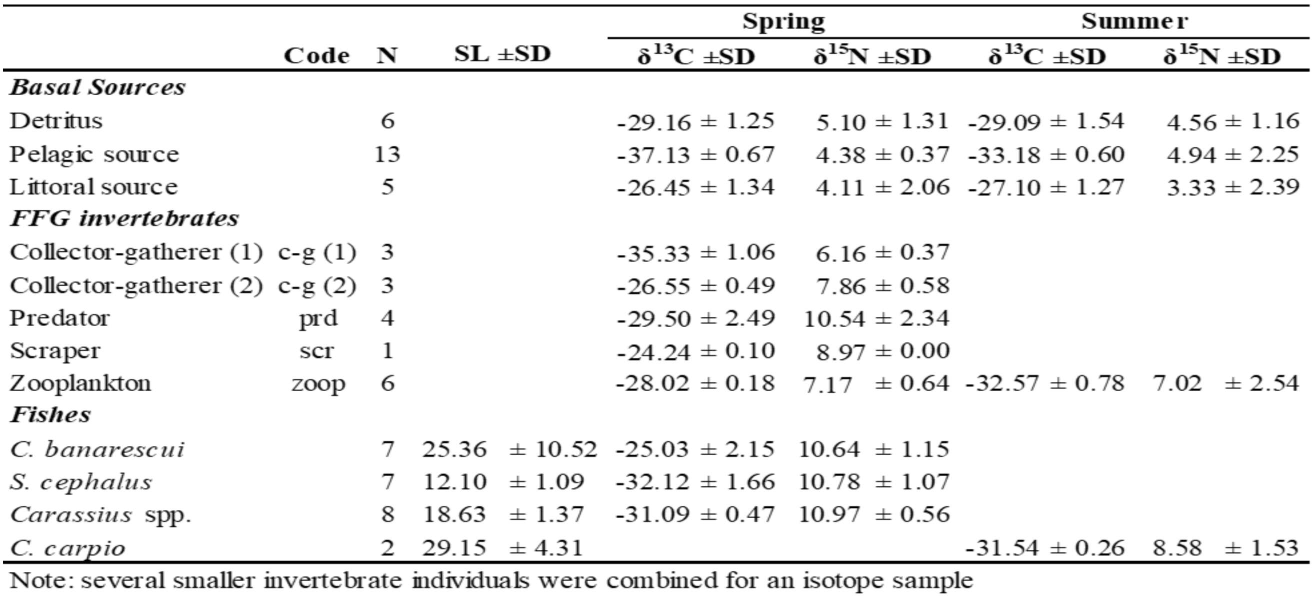
Benthic invertebrate taxa were classified into 3 functional feeding groups (FFG) according to their feeding mode (Mandaville, 2002): collectors-gatherer (c-g), scraper (scr) (*Gyraulus* sp., Gastropoda) and predators (prd) (Hirudinea, Odonata larvae) (Table 1). Food was obtained from bottom detritus for collector, live benthic invertebrates for predator, and periphyton, or attached algae for scraper. Collectors-gatherers were divided in two subgroups based on $\delta^{13}C$ values: c-g (1) with ^{13}C-depleted (*Chironomus* sp. (Chironomidae), *Baetis* sp. (Baetidae) larvae, Nematoda) and c-g (2) with ^{13}C-enriched (*Gammarus* sp. (Amphipoda), *Physella* sp. (Gastropoda), *Lumbricina* sp. (Annelida)) (Table 1).

The relative contribution of primary production sources assimilated by aquatic consumers was estimated based on $\delta^{13}C$ and $\delta^{15}N$ values of tissues from common primary producers and consumers using a Bayesian stable isotope mixing model, SIAR (Parnel, Inger, Bearhop& Jackson, 2010) in R statistical software (version 3.0.2, R Project for Statistical Computing). This model produces a combination of feasible solutions for proportional contributions of alterative primary production sources assimilated by consumer tissues. SIAR is based on a Bayesian approach that estimates probability distributions of source contributions to consumer tissue by accounting for uncertainties associated with the input data (i.e., sources signatures and trophic enrichment factors (TEF)) (Parnell *et al.*, 2010). In the first place the food sources (primary producers) assimilating from fish and invertebrates (consumers) were estimated using SIAR. Inputs are $\delta^{13}C$ and $\delta^{15}N$ for each 3 potential primary production sources and their associated standard errors, a trophic enrichment value (TEFs) and their standard errors, and consumer isotopic signatures (Franca *et al.,* 2011). We used a TEF value a TEFs of 0.4±1.3‰ for $\delta^{13}C$ and 3.4 ±1‰ for $\delta^{15}N$ (Post 2002) for all end members. Because we only had single data points (unreplicated data) for scraper group (*Gyraulus* sp.) in this study, we used the special SIAR function “siarsolomcmcv4” that does not include a residual error term instead of “siarmcmcdirichletv4” command in SIAR mixing model (Inger, Jackson, Parnell &Bearhop, 2010).

Results

Stable Isotope Composition of Primary Production Sources

Table 1. Summary of $\delta^{13}C$ and $\delta^{1}N$ values measured for basal sources and macroinvertebrates, and standard length (SL), $\delta^{13}C$ and $\delta^{15}N$ values measured for fishes sampled during spring (May 2013) and summer (July 2013) seasons from the Lake Zinav (N: the number of individuals analyzed for stable isotope analyses; SD: standard deviation



				Spring		Summer	
	Code	N	SL ±SD	$\delta^{13}C$ ±SD	$\delta^{15}N$ ±SD	$\delta^{13}C$ ±SD	$\delta^{15}N$ ±SD
Basal Sources							
Detritus		6		-29.16 ± 1.25	5.10 ± 1.31	-29.09 ± 1.54	4.56 ± 1.16
Pelagic source		13		-37.13 ± 0.67	4.38 ± 0.37	-33.18 ± 0.60	4.94 ± 2.25
Littoral source		5		-26.45 ± 1.34	4.11 ± 2.06	-27.10 ± 1.27	3.33 ± 2.39
FFG invertebrates							
Collector-gatherer (1)	c-g (1)	3		-35.33 ± 1.06	6.16 ± 0.37		
Collector-gatherer (2)	c-g (2)	3		-26.55 ± 0.49	7.86 ± 0.58		
Predator	prd	4		-29.50 ± 2.49	10.54 ± 2.34		
Scraper	scr	1		-24.24 ± 0.10	8.97 ± 0.00		
Zooplankton	zoop	6		-28.02 ± 0.18	7.17 ± 0.64	-32.57 ± 0.78	7.02 ± 2.54
Fishes							
C. banarescui		7	25.36 ± 10.52	-25.03 ± 2.15	10.64 ± 1.15		
S. cephalus		7	12.10 ± 1.09	-32.12 ± 1.66	10.78 ± 1.07		
Carassius spp.		8	18.63 ± 1.37	-31.09 ± 0.47	10.97 ± 0.56		
C. carpio		2	29.15 ± 4.31			-31.54 ± 0.26	8.58 ± 1.53

Note: several smaller invertebrate individuals were combined for an isotope sample

Littoral source was always enriched in ^{13}C relative to other primary production sources (spring: -26.45‰, summer: -27.10‰). Mean $\delta^{13}C$ values for detritus ranged from −29.16‰ (spring) to −29.09‰ (summer) (Table 1, Figure 2). Pelagic source was the most ^{13}C-depleted potential basal sources, ranging from -37.13‰ (spring) to -33.18‰ (summer). $\delta^{13}C$ value of potential primary production sources did not appear to differ seasonally except pelagic source which had relatively higher $\delta^{13}C$ values in summer compare to spring (Table 1, Figure 2). Although all primary production sources had similar average signatures of $\delta^{15}N$ during spring (from 4.11‰ to 5.10‰), the mean $\delta^{15}N$ values of detritus and pelagic source (4.56‰ and 4.94‰) were higher than those of littoral source (3.33‰) during summer (Table 1).

Stable Isotope Composition of Consumers

A total of 11 taxa of benthic invertebrates of which 6 were collector-gatherer, 4 were predator, and 1 was scraper during spring was analyzed (Table 1). The mean $\delta^{13}C$ values of c-g (1) ranged from -36.29‰ for *Chironomus* spp. to -34.18‰ for *Baetis* sp., whereas c-g (2) had $\delta^{13}C$ values from -26.85‰ for *Gammarus* sp. to -26.06‰ for *Physella* sp., and $\delta^{15}N$ values of c-g (1) (5.78 – 6.52‰) were lower than those of c-g (2). Members of c-g (1) had lower $\delta^{13}C$ values relative to members of c-g (2) (7.20 - 8.31‰). The $\delta^{13}C$ values of the predator samples varied from -32.46‰ in Libellulidae nymph (Odonata) to -27.37‰ in Hirudinea. The highest $\delta^{15}N$ value of leeches (Hirudinea) placed this taxa at the top of the food web. There were seasonal differences in $\delta^{13}C$ of zooplankton but not in $\delta^{15}N$. $\delta^{13}C$ value of zooplankton were relatively higher in spring (-28.02‰) than in summer (-32.57‰) (Table 1, Figure 2).

Cyprinid was the only fishes taxa captured from the Lake Zinav. Among cyprinid fish *Capoetabanarescui, Squaliuscephalus* and *Carassiusspp.* were collected only during spring, but *Cyprinuscarpio* was collected only during summer in the lake. The $\delta^{13}C$ values were

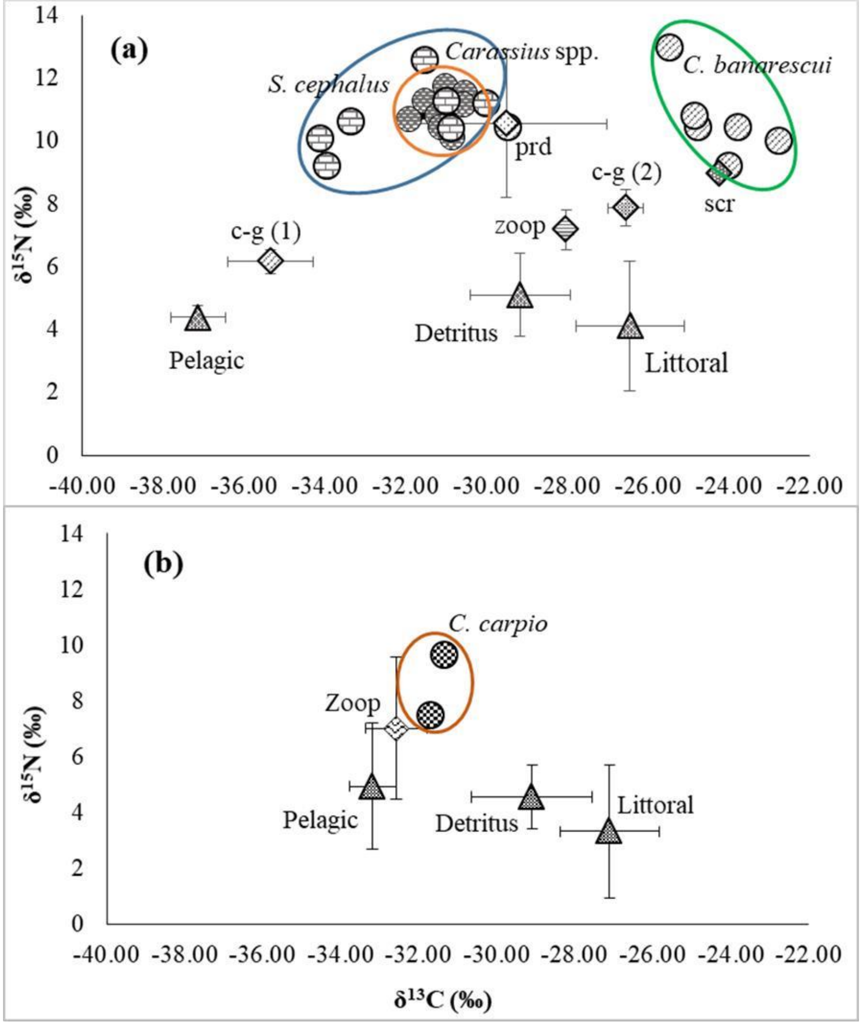


Figure 2. Stable isotope signatures ($\delta^{13}C$ and $\delta^{1}N$) for primary production sources (triangle symbols (▲)), invertebrates and zooplankton (diamond symbols (♦)) and fish (circle symbols (●)) in the Lake Zinav during (a) spring 2013, and (b) summer seasons 2013. Code designate different taxa (see Table 1 for key). The circles represented isotopic space of each fish taxa during spring and summer.

different among fish species, whereas $\delta^{15}N$ values were not, ranging from 10.64‰ to 11.05‰ (Table 1, Figure 2). While *S. cephalus* and *Carassius* spp. had similar $\delta^{13}C$ values (-32.12‰ and -31.12‰), *C. banarescui* tend to be more^{13}C-enriched (-25.03‰), and had higher variation in $\delta^{13}C$ (-22.78 to -29.49‰ ± 2.15 SD) relative to other fishes. *C. carpio* captured during summer had relatively light carbon (-31.54‰) and nitrogen (8.58‰) ratios (Table 1). An isotope bi-plot of fishes clearly shows that fishes varied in carbon isotopic composition, *S. cephalus* and *Carassius* spp. from spring, and *C. carpio* from summer have most depleted in ^{13}C relative to *C. banarescui*(Table 1, Figure 2).

Overview of Fish Diets

A total of 16 different prey types were found in all fishes guts, the major prey items consumed by 4 fish taxa (as percentage of total volume extracted) detritus (35%), pelagic crustaceans (cladocera, calanoida, cyclopoida, harpacticoida) (20%), filamentous algae (such as *Cladophora, Spirogyra, Ulothrix* sp.), (18%), chironomid larvae (13%), chironomid adults (5%), insects parts (4%), diatoms (2%). Other prey items had percentage volumes less than 1%. Filamentous algae (63% of diet by volume) and chironomid larvae (22%), diatoms (5%), pelagic crustaceans (5%), other insect parts (3%), and simuulidae larvae (2%) were consumed by *C. banarescui.* which ingested the highest number of different prey items. Calanoida (28%), cyclopoida (22%), chironomid adults (20%) and larvae (18%), cladocera (10%), and aquatic plants (2%) comprised the diet of *S. cephalus*. A substantial proportion of *Carassius* spp. diet was accounted for by detritus (58%), with a smaller proportion of filamentous algae (11%), pelagic crustacean (15%), chironomid larvae (9%), and diatom (7%). Detritus (84%), some insects part (11%) and chironomid larvae (5%) were consumed by *C. carpio*.

Primary Production Sources Supporting Aquatic Consumers

During spring, SIAR mixing model results indicated that littoral sources (61%) accounted for a large fraction of *C. banarescui*, with detritus also being an important contributor (34%) (Figures 2, Figure 3). *S. cephalus* assimilated organic matter derived from mostly pelagic sources and detritus, accounting for 57% and 30%, respectively. Detritus, pelagic and littoral sources were contributed equally to biomass of invasivefish,*Carassius* spp. Pelagic source (64%) was the principal sources supporting c-g (1). Littoral source (47%) and detritus (37%) apparently supported significant proportions of c-g (2) (Figures 2, Figure 3). Predator invertebrates and zooplankton seemed to assimilate material from littoral source and detritus, whereas littoral source (69%) was the main sources supporting biomass of scraper in spring (Figures 2, Figure 3). During summer, pelagic source contributed up to 46% - 44% of carbon assimilated by *C. carpio* and zooplankton biomass, detritus (28%-30%) and littoral source (26% -27%) were secondarily important (Figures 2, Figure 3).

Discussion

Stable isotopes and diet-based results demonstrate that littoral trophic pathways account for more than half of total invertebrate's biomass, whereas fishes use different trophic pathways (littoral, pelagic or detrital). However fishes that are generally thought as pelagic consumed partially zoobenthos (chironomidae larvae or adults), indicating cross-chain omnivory and trophic coupling between benthic and pelagic pathways (Vander Zanden&Vadeboncoeur,2002). Wagner, Volkmann and Dettinger-Klemm (2012) reported that chironomid pupae ascending from the sediment to the water surface represented a trophic linkage between the benthic and the pelagic food web via predation by pelagic fish.

Pelagic source $\delta^{13}C$ varied seasonally in the Lake Zinav, and this variation could be linked to variation in the relative contribution of different sources to seston, degree of isotopic fractionation during carbon fixation, phytoplankton species composition, temperature, degree of lipid production (McCusker, Ostrom, Ostrom, Jeremiason& Baker, 1999), composition of dissolved inorganic carbon (DIC) (CO_2 or HCO_3) and pH (Zeng, Kong, Zhang, Tan &Wul, 2008; Caroni, Free, Visconti &Manca, 2012) as well as fractions of terrestrial detritus within pools of suspended fine particulate organic matter (Kendall, Silva & Kelly, 2001). Rautio and Vincent (2007) reported that artic water bodies with high pH (>8) had higher HCO_3^- concentration in DIC than subarctic water with low pH (< 7). Since HCO_3^- is enriched in ^{13}C by ~10‰ relative to CO_2, the primary producers were isotopically heavier in the arctic than in the subarctic. In this study, pelagic source were sampled at surface during summer and a depth of approximately 10m which were highly negative (-37.13‰) in spring. Previous study from Lake Zinav showed that surface water had high pH (8.36) and low turbidity (5.05 NTU) in summer and low pH (6.95) at depth of ~10m and high turbidity (8.40 NTU) in spring (Buhan*et al.*, 2013), consisted of mostly blooms of cyanobacteria in summer, whereas diatom and protozoa dominated in spring. Recent studies have found that cyanobacteria showed a strong preference for HCO_3^- which has been associated with the very low CO_2-affinity of RubisCO type IB (Hoins *et al.*, 2016). We, therefore, suggested that the seasonal differences in $\delta^{13}C$ values of pelagic source were explained by pH, composition of algae and contribution of terrestrially derived organic matter based on higher turbidity. Pelagic source (seston) from Lake Zinav were more ^{13}C depleted compared with previously measured values from rivers and dam lakes of Central Black Sea region where this current study was performed (Akin *et*

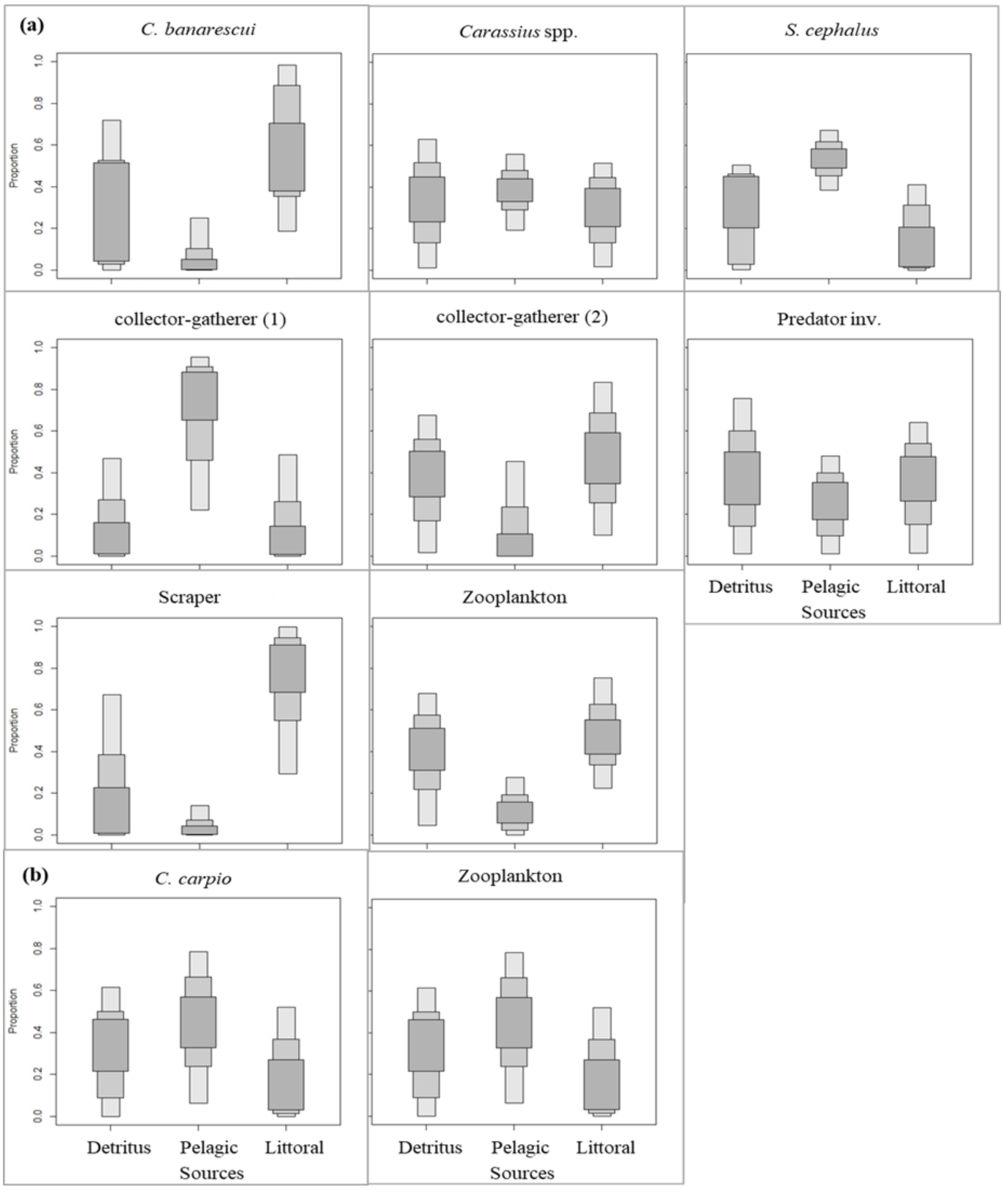


Figure 3. Box plots derived from the stable isotope analysis in SIAR mixing model, showing the contribution of three basal sources to the diets of all consumers (fishes and invertebrates) during spring (a), and summer (b). The proportions show credibility intervals plotted at 95, 75 and 25% credibility intervals.

al., 2010; Kaymak*et al.*, 2015), and those from other eutrophic lakes (Zhou *et al.*, 2011; Mao *et al.,* 2012; Gao, Zhong, Ning, Liu &Jeppesen, 2017). This might be suggested that carbon derived from microbial loop by bacterioplankton in water column of Lake Zinav, such as nitrification (Kelley & Coffin, 1998), sulfur (Doi *et al.*, 2006) and methane oxidation (Jones & Grey, 2011).

Seasonal variation was observed in δ^{13}C values of zooplankton which was 5% lower in summer than in spring. Examining the carbon isotopic ratio of zooplankton and mixing model indicated that zooplankton assimilated organic matter from pelagic source (mostly cyanobacteria) and detritus in summer, whereas littoral source and detritus made up a substantial part of food of the zooplankton in spring. Buhan*et al.*, (2013) found that phytoplankton biomass (chlorophyll-a) were lower in spring (19µg/l) than in summer (53µg/l), this was associated with much ^{13}Cenriched value which was reflected in zooplankton in Lake Zinav. Few studies using stable isotope analysis showed that relative enrichment in δ^{13}C in zooplankton during spring was associated with increased contribution of macrophytes and associated periphyton to biomass of zooplankton (Jones & Waldron 2003; De Kluijver *et al.*, 2015). Macrophytes and associated periphyton have usually higher δ^{13}C values compared with phytoplankton (Fry, 2006). Zooplankton are known to feed primarily on phytoplankton, but sometimes can obtain organic matter from allochthonous sources (Cole *et al.*, 2011) and/or dissolved organic carbon derived from macrophytes and the attached periphyton during detritus formation (Findlay *et al.*, 1986). Some authors reported that bacteria or fungi attached to flocculated particulate organic matter and grazed by directly heterotrophic flagellates and Amoebozoa (Kankaala, Taipale, Li & Jones, 2010; Jassey, Shimano, Dupuy, Toussaint & Gilbert, 2012) which were the dominant taxa of zooplankton in the Lake Zinav. Hence, macrophytes and associated periphyton could support zooplankton biomass via microbial pathway (De Kluijver *et al*., 2015). In contrast, when chlorophyll-a concentration was higher during summer, $\delta^{13}C$ values of zooplankton and pelagic source were very similar, suggesting that zooplankton assimilated more on pelagic source and less on the carbon subsidy from littoral source derived from macrophyte–periphyton. Copepods consisted of main component of zooplankton in summer in the lake are selective feeders and generally consume larger particles of high quality, such as phytoplankton.

Some collector taxa (c-g (1)) from unvegetated area such as *Chironomus* sp., *Baetis* sp., and nematoda exhibited a strongly depleted $\delta^{13}C$ values from littoral to sublittoral with depth. These taxa classified as detritivores, and have been considered to utilize phytoplankton and phytodetritus, settling down through the water column to the sediment surface (Jones & Grey 2011). Based on the isotopic values and mixing model in this study, pelagic source accounted for the observed ^{13}C depletion seen in these taxa. Therefore, the process of benthic-pelagic coupling has been considered important in lake food webs. On the other hand, other collector taxa (c-g (2)) (Oligochaeta, *Physella* sp., *Gammarus* sp.), which inhabits the macrophyte dominated littoral zone, were generally ^{13}C enriched than taxa form c-g (1), indicating a stronger reliance on detritus from riparian plants and macrophyta and associated periphyton from littoral zone. Similar results also have been reported in other studies that these taxa assimilated the energy derived from autochthonous aquatic vascular plants and epiphytes (Cremona *et al*., 2010; Boll *et al*., 2012).

In this study, fishes inhabited only macrophyte dominated littoral zone with depth of area not exceeding 2 m because of a prevailing anoxic condition in deeper parts of lake. Our stable isotope bi-plot demonstrated that native fishes (*S. cephalus* and *C. carpio*) showed similar trophic niche with invasive fish (*Carassius*spp.), while native *C. banarescui* displayed different trophic niche. There are no resources overlapping among native fishes, but some resources overlap was observed between native *S. cephalus* and invasive *Carassius* spp. in spring. Stable isotope and gut content analysis indicated that native *S. cephalus* consumed mostly zooplankton, indicating that most of its diet was pelagic origin, filamentous algae from littoral source for *C. banarescui*, and detritus which may be originated from allochthonous or autochthonous sources, filamentous algae, invertebrates were a common food item for *Carassius* spp. in spring. These results indicated that invasive fish was opportunistic feeders, meaning they ate just about anything that can fit in their mouth. During summer, *C. carpio* consumed detritus more than that of *Carassius* spp., indicating that two fish species were likely to exploit the detritus that originates from sedimentation of planktonic algae based on the stable isotope values. The high portion of such low-energy foods in diets of these fish taxa may be indicative for a competition induced niche shift to sub-optimal food sources (Didenko&Kruzhylina, 2015). Specialization in habitat resources and food partitioning is one of the primary mechanism to reduce interspecific competition, and facilitate the co-occurrence of related species (Guo *et al*., 2014). Increased competition for resources among invasive and native fishes could cause to shift to suboptimal resources in order to meet energy requirements. Other studies also suggests that native and invasive fishes can shift their trophic niche as a result of inter-specific competition, either by incorporating coexisting invaders in their diet and/or by shifting their diet to novel resources (Jackson *et al*. 2012; Jackson & Britton, 2014). All cyprinid fishes consumed similar diet items but different proportion, and assimilated energy from different trophic pathways (littoral or pelagic), but to some extent, detritus from terrestrial and/or aquatic sources via microbial pathways supported all consumers in Lake Zinav. Even species that are generally thought as pelagic or littoral were partially supported by zoobenthos or zooplankton, respectively, indicating trophic coupling between littoral and pelagic pathways. Coupling of pelagic and littoral habitats can occur directly via movement of fish between habitats and indirectly via horizontal migrations of zooplankton from the pelagic to the littoral zone where they seek refuge from fish predation (Vesterinen, 2013).

The larger variance found in $\delta^{13}C$ between individuals of *C. banarescu*caught in the Lake Zinav, suggesting a greater complexity in primary production sources or variation in habitat use in order to minimize resource overlap among fishes, and avoid inter-intraspecific competition. Populations consuming a wider range of diet and those that forage in a range of geographical areas could display wider isotopic variation (Bearhop, Adams, Waldrons, Fuller & Macleod, 2004). Although we did not encounter in samples collected from the lake, simuliidae larvae were found in the guts of this species. Buhan*et al*. (2013) reported that simuliidae larvae and filamentous algae from the tributary had enriched and depleted $\delta^{13}C$ value (-25.64 and -30.13‰, respectively), thus some individuals of *C. banarescui*move between the lake and tributary for feeding, and might have reflected carbon signatures of diets from the tributary.

As a conclusion, this study demonstrated that littoral zone with macrophyte dominated influenced the functioning of food web structure. Pelagic source and phytodetritus is likely to utilize by zooplankton, *C. carpio* in summer and *S. cephalus*, *Carassius* spp., and collector gatherer invertebrates such as chironomid larvae and nematods in spring. During spring, detritus, macrophytes and associated periphyton made an important contribution for consumers, especially *C. banarescui*, and most benthic invertebrates and zooplankton. Littoral sources production not only supports littoral communities, but also subsidizes the diet of pelagic consumers (Vander Zanden, Vadeboncoeur& Chandra, 2011), and fishes would promote coupling of the littoral and pelagic food webs. Although all native and invasive cyprinid fishes predominated only in littoral zone of the lake, the proportion of diets differed among species, suggesting high degree of resource sharing between cyprinids to avoid competition. But, the further studies are needed to understanding of how seasonal and spatial variation in hydrology affect stable isotope values of producers and consumers and its effect on function and structure of lake food web, also expose qualitative and quantitative of bacterial biomass and estimate the relative contribution of Lake food web.

Acknowledgements

We would like to thank Dr. Mehm*et al*i Kocer for identification of zooplankton taxa. We also should thank Assoc. Prof. Dr. Hakan Mete Dogan for producing Figure 1. This study was supported by TUBITAK (The Scientific and Technological Research Council of Turkey) (Project Number: 110Y117), Turkey. This study also was presented at the International Symposium on Fisheries and Aquatic Sciences (FABA), November 03-05, 2016, Antalya, Turkey as an oral presentation.

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