

ANALYSIS OF THE TOP-DOWN AND BOTTOM-UP EFFECTS ON ZOOPLANKTON BIOMASS IN EUTROPHIC LAKE YENİÇAĞA

BURA UĞUR SORGUÇ¹, YASEMİN SAYGI^{1,2}

¹Department of Biology, Faculty of Science, Hacettepe University, Ankara, TÜRKİYE

²Biological Diversity Advanced Research Center (HUBIOM), Hacettepe University, Ankara, TÜRKİYE

ABSTRACT Several aquatic ecological studies have focused on the contrasting effects of top-down and bottom-up interactions on zooplankton communities. It is essential to comprehend the relative strength of these interactions to evaluate the trophic interactions of pelagic food webs, an area that is still extensively researched due to its complexity. Therefore, we examined the biomass of zooplankton over a one-year period in a freshwater lake that is subject to multiple stressors such as anthropogenic activities, eutrophication. Top-down effects, namely fish biomass, and bottom-up effects, including total phosphorus, total nitrogen, and chlorophyll a concentrations were considered. Structural equation modelling (SEM) was employed to evaluate the relative impact of top-down and bottom-up effects on zooplankton. The SEM analysis revealed that zooplankton is influenced by both top-down and bottom-up effects in Lake Yenicağa. The biomass of cladocerans was found to have a negative correlation with increasing chlorophyll a, while the Calanoida group was negatively affected by both fish biomass and chlorophyll a from top-down and bottom-up controls. The fish biomass had a positive effect on both Cyclopoida and Rotifera, but only Rotifera showed a negative interaction with chlorophyll a. Direct bottom-up effects of total phosphorus and total nitrogen on chlorophyll a were found, with total nitrogen having a stronger interaction than total phosphorus.

Keywords Lake Yenicağa, zooplankton, trophic interaction, structural equation modeling

1. INTRODUCTION

Trophic interactions are essential aspects of limnology and have been the focus of much scientific investigation within lakes. Trophic interactions occur when one organism feeds on another, involving the flow of energy within a community. The question of whether food webs are resource- (bottom-up) or predation- (top-down) controlled is one of the most fundamental research questions in ecology [1]. In the past, most scientists believed that the structure of the food web was primarily regulated by available resources, a concept known as bottom-up control [2]. This implies that phytoplankton is regulated by abiotic factors such as light and temperature, and the flow of nutrients, which in turn regulate zooplankton [3]. However, it is now evident that food webs can also be significantly regulated by top-down effects through consumers. For instance, zooplankton are regulated by fish, and phytoplankton are regulated by

zooplankton [4, 5]. In addition to biotic factors, nutrients such as total nitrogen and total phosphorus can also play a crucial role in freshwater ecosystems by affecting phytoplankton growth rates [6, 7]. Numerous scientific studies have focused on the contrasting impacts of fish feeding (top-down) and phytoplankton biomass (bottom-up) on zooplankton communities [4, 8, 9]. Recent studies have also acknowledged the significance of the conditions under which top-down and bottom-up effects prevail [10].

Zooplankton play a crucial role in transferring matter and energy from phytoplankton to fish. They act as primary consumers and regulate phytoplankton community structure in food webs. To make informed decisions about environmental management, such as biomanipulation, it is important to understand how this link between phytoplankton and zooplankton varies along trophic gradients [11, 12]. Identifying and comprehending the distinct effects exerted by both top-down and bottom-up forces on zooplankton can be challenging due to the diverse nature of zooplankton communities, which consist of various taxonomic and functional groups. Investigating the top-down and bottom-up effects on zooplankton is critical for food web studies [13].

Excessive nutrient inputs can cause eutrophication, which is a critical environmental problem that significantly degrades water quality. This phenomenon leads to changes in biodiversity that pose serious threats to aquatic ecosystems. The consequences include the decline of economically valuable fisheries, a shift in community composition from benthic periphyton and epiphytes to phytoplankton, and a limitation of zooplankton [14, 15, 16]. Shallow eutrophic lakes are characterized by high nutrient content, which can lead to serious ecological problems such as Cyanobacteria blooms. Although cyanobacteria are not normally a desired food source for zooplankton due to their low nutritional values, difficulty in digestion, and toxicity, several studies have shown that large zooplankton can remove small cyanobacteria in nutrient-enriched shallow lakes [17, 18, 19]. However, in such lakes, the fish community is frequently dominated by planktivorous species, which may prevent the development of large zooplankton that could control phytoplankton populations [20].

Several studies have investigated trophic interactions, specifically the top-down and bottom-up effects of organisms, in the food webs of shallow lakes in Turkey with varying nutrient levels and predation pressures [21-24]. The results of these studies revealed that food web dynamics can vary spatially and temporally across trophic gradients.

Lake Yeniçağa is a freshwater lake that has been significantly impacted by various human activities including the excessive expansion of residential areas and the drainage of agricultural areas. The main threats to the lake are the discharge of domestic, urban, and industrial waste, agricultural activities, and eutrophication. It is classified as a habitat of high biodiversity and a threatened natural habitat according to the criteria of Important Plant Areas in Turkey. The entire shoreline of the lake is surrounded by reeds (*Typha minima*, *Typha*

shuttleworthii), some of which are over 200 meters wide, providing resting and wintering areas for migratory bird populations. Furthermore, the catchment area connected to the lake has one of the largest peatlands in Turkey, with a depth of 2 meters. It is classified as a rich calcareous peatland under the Bern Convention [25, 26, 27].

This study aims to test the relative importance of top-down and bottom-up forces on zooplankton in a eutrophic shallow lake affected by massive cyanobacterial blooms using structural equation modeling. It was hypothesized that top-down interactions would have a greater impact on the Crustacea group compared to the Rotifera group because of their larger body size, particularly in the case of fish predation [28, 29]. Simultaneously, we proposed a second hypothesis that takes into account the trophic level of the lake. According to this hypothesis, phytoplankton would have a positive effect on the Cyclopoida and Rotifera groups, which typically thrive in eutrophic conditions. Conversely, the Cladocera and Calanoida groups, which exhibit higher biomass in oligotrophic waters, would be negatively impacted [29, 30]. This study is expected to be a valuable contribution to the existing literature on zooplankton food web interactions in shallow freshwater lakes with high levels of eutrophication.

2. MATERIALS AND METHODS

2.1. Study Area

The study was conducted in Lake Yeniçağa (40°47'N, 32°01'E), located in the interior of Western Black Sea, within the borders of Bolu city and north of Yeniçağa town. This shallow eutrophic lake covers approximately 1800 hectares, with mean and maximum water depths of 3.87 ± 0.87 and 6.0 m, respectively. Commercial fishing activities take place in the lake. The lake is inhabited by a total of four fish species feeding omnivorously, but the pelagic fish community is dominated by *Cyprinus carpio* and *Squalius cephalus*. The contribution of these species to total fish biomass is 96%. Since 2014, varying numbers of *Cyprinus carpio* larvae have been stocked in the lake each year, which can potentially control zooplankton through predation and indirectly affect phytoplankton [26, 31]. Over the past 30 years, urban and agricultural settlement in the basin has led to a significant increase in nutrient loading, resulting in accelerated eutrophication. This has caused water quality deterioration and increasingly severe cyanobacterial blooms. The phytoplankton flora of the limnetic zone of Lake Yeniçağa consists mainly of Chlorophyta, Bacillariophyta, Cyanobacteria, and Dinoflagellata. *Anabaena circinalis* and *Aphanizomenon flos-aquae* have been the most abundant species in the lake [25, 31, 32].

2.2. Sampling

The study was carried out in the limnetic zone of Lake Yeniçağa, which does not contain any vegetation. Monthly samples were collected from Lake Yeniçağa between December 2021 and November 2022, excluding January and February

due to a completely ice-covered lake surface. A total of three sampling stations were determined: the first site (1) was selected near the 100 m of the stream mouth (mean depth: 371 ± 53 cm), another site (2) was in the middle of the lake (mean depth: 455 ± 93 cm), a third (3) was located near the 100 m of the sewage outfall (mean depth: 335 ± 70 cm) (Figure 1).



FIGURE 1. Locations of sampling stations where field studies are carried out in Lake Yenicağa. Station 1: $40^{\circ}46'59.952''\text{N} - 32^{\circ}1'11.496''\text{E}$; Station 2: $40^{\circ}46'50.664''\text{N} - 32^{\circ}1'32.987''\text{E}$; Station 3: $40^{\circ}46'37.848''\text{N} - 32^{\circ}2'2.184''\text{E}$.

Water samples were collected from each site at the 0, 2, and deepest point of the water column (ca. 4m) using a 2 L Hydro-bios Ruttner water sampler. The samples were then combined in a bucket for analysis of physicochemical parameters. Turbidity was measured using an ORION AQ3010 turbidimeter. The transparency of the water was determined by monitoring Secchi depth (cm) with a white Hydro-bios Secchi disc (20 cm in diameter) in situ. Total nitrogen (TN) and total phosphorus (TP) concentrations in each sample were measured in the laboratory according to standard methods 4500 NO₂-B, 4500-Norg-B, 4500P-B, and 4500PE [33]. The concentration of chlorophyll a was determined using spectrophotometry at 665 nm after extracting the samples collected on GF/C filters with a hot methanol solution [34].

Zooplankton samples were taken monthly at three sampling stations. The samples were obtained by filtering 100 L of water samples and concentrated to 50 mL through a plankton net with a mesh size of 30 μm (HYDRO-BIOS, Althengolz, Germany). Surface sampling was made at a depth of 15-20 cm and vertical sampling was made by vertical tow from a few cm above sediment to surface. Concentrated zooplankton samples were gently preserved with a 4% (v/v) formaldehyde solution. Organisms from the Cladocera, Calanoida, Cyclopoida, and Rotifera groups were examined in a Sedgewick Rafter counting

cell with a volume of 1 ml and under a Leica DMR microscope (Wetzlar, Germany). The examination identified all samples, which were then counted and measured for total length under the microscope. At least 30 individual bodies of each species were measured under the microscope. The dry weight of species in the Cladocera, Calanoida, and Cyclopoida groups was calculated using the length-weight formulas provided by Dumont et al. [35] and Bottrell et al. [36]. To determine the biomass of the Rotifera group, we first calculated the biovolume of the samples using the formulas provided by Ejsmont-Karabin [37]. We then converted the data to dry weight values using the formulas given in Bottrell et al. [36].

Monthly fish sampling was conducted at three sampling stations with the assistance of Yeniçağa Fisheries Cooperative (Figure 1). Two nets were used at each sampling station. We performed fish sampling with multi-mesh gill nets (length 50 m; height 4 m) with mesh sizes knot to knot of 10, 32, 40, 60, 80, and 90 mm. The nets were set at dusk in areas where the water depth was less than 5 m and removed at dawn, with the duration of exposure recorded. Fish were counted, measured (total length), and weighed (fresh mass).

Catch Per Unit Effort (wCPUE) estimates of relative weight for all fish species were obtained using gillnetting and the following formula:

$$wCPUE = (CN \times (AS/AN))/t \quad (1)$$

where CN is the nominal catch (kg), AS is the area of the standard net (100 m²), AN is the area of the used net (m²) and t is the time of exposure (t). The results obtained from the formula were converted to kg/ha/h [38].

Carlson's trophic state indices (TSI) were calculated according to the provided equations [39].

$$TSI (\text{Chlorophyll } a) = 9.81 * \ln (\text{Chlorophyll } a) + 30 \quad (2)$$

$$TSI (\text{Total Phosphorus}) = 14.42 * \ln(\text{Total Phosphorus}) + 4.15 \quad (3)$$

$$TSI (\text{Secchi Depth}) = 60 - 14.41 * \ln(\text{Secchi Depth}) \quad (4)$$

2.3. Data Analysis

In this study, Structural Equation Modeling (SEM) was used to analyze the role of top-down and bottom-up controls in the food web, specifically their effects on the zooplankton community. SEM is a statistical analysis that estimates the relationships between variables. These variables can be either dependent or independent, factors, or measured variables. In comparison to other statistical tools such as factor analysis and multivariate regression, SEM has the ability to measure the errors of observed variables while simultaneously predicting causal relationships between both latent and manifest variables [40, 41]. Since 2000,

ecologists have been actively using SEM to study the complex interactions found in ecosystems [42]. SEM is distinguished from other data modeling methods by it is the ability to examine path relationships. It is increasingly popular among biologists as it helps to understand direct and indirect interactions within data [43]. Standardized path coefficients between two variables represent the relative strength of a relationship. In SEM, R² values indicate the proportion of variance explained by each variable. SEM assumes a predefined set of predictor variables that impact other variables, establishes the direction of these effects, and subsequently tests them using empirical data.

All data were $\log_{10}(x+1)$ transformed prior to analyses to ensure the assumptions of normality, homogeneity of variance, and linearity of the analysis. During the SEM analysis, Comparative Fit Index (CFI) and Standardised Root Mean Square Residual (srmr) values were calculated to test the validity of the path diagram, and R² and standardized estimates were determined [44]. In the literature, a CFI value greater than 0.95 and an srmr value less than 0.08 indicate a successful model [45, 46]. In our SEM, we obtained CFI values of 0.950 and srmr values of 0.058, confirming that the constructed model adequately explained the dataset. All path coefficients used in the analysis were standardized.

SEM was carried out using the R Statistical Software (v4.3.2) and the 'lavaan' and 'tidySEM' packages [47, 48].

3. RESULTS

In this study, Calanoid copepods were found to be the group that made the largest contribution to the zooplankton biomass in Lake Yeniçağa, while the group that contributed the least was the Cyclopoid copepods. Zooplankton biomass exhibited significant monthly changes, with the lowest values recorded as 8114 $\mu\text{g}/\text{m}^3$ during the summer period, and the highest values observed as 130779 $\mu\text{g}/\text{m}^3$ during the winter period. The biomass of Calanoid copepods ranged between 1125-91123 $\mu\text{g}/\text{m}^3$, with maximum values observed in the winter and minimum values in the spring. The biomass of the cladocerans ranged between 43-38794 $\mu\text{g}/\text{m}^3$, with the lowest biomass values observed in the summer, and the highest biomass values in the spring. Rotifera biomass also displayed significant monthly variation, with the lowest values recorded as 502 $\mu\text{g}/\text{m}^3$ during the winter and the highest values as 39416 $\mu\text{g}/\text{m}^3$ in the spring (Table 1).

TABLE 1. Mean, minimum, maximum, and standard deviation values of zooplankton biomass and fish wCPUE measured monthly in Lake Yeniçağa.

	Mean	Minimum	Maximum	SD
Cladocera Biomass ($\mu\text{g}/\text{m}^3$)	25073	43	38794	17228
Calanoida Biomass ($\mu\text{g}/\text{m}^3$)	25887	1125	91123	43559
Cyclopoida Biomass ($\mu\text{g}/\text{m}^3$)	5188	122	14178	6576
Rotifera Biomass ($\mu\text{g}/\text{m}^3$)	17542	502	39416	19896
Zooplankton Biomass ($\mu\text{g}/\text{m}^3$)	73690	8114	130779	51900
<i>Cyprinus carpio</i> (kg/ha/h)	43.43	16.91	57.61	22.98
<i>Squalius cephalus</i> (kg/ha/h)	13.54	5.32	19.03	7.25
<i>Tinca tinca</i> (kg/ha/h)	1.63	0.28	2.75	1.25
<i>Carassius gibelio</i> (kg/ha/h)	0.34	0.34	0.34	-
Total Fish (kg/ha/h)	58.71	22.51	79.39	31.45

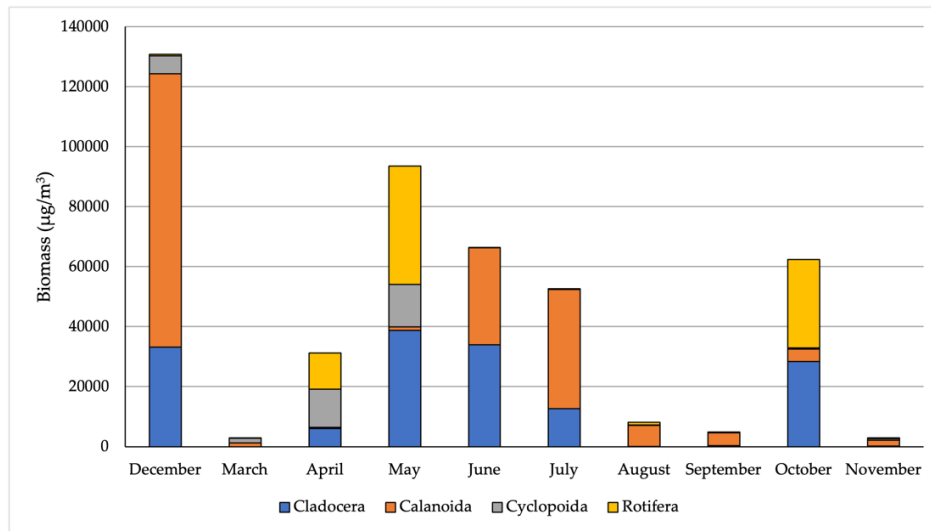


FIGURE 2. Monthly zooplankton biomass changes in Lake Yeniçağa.

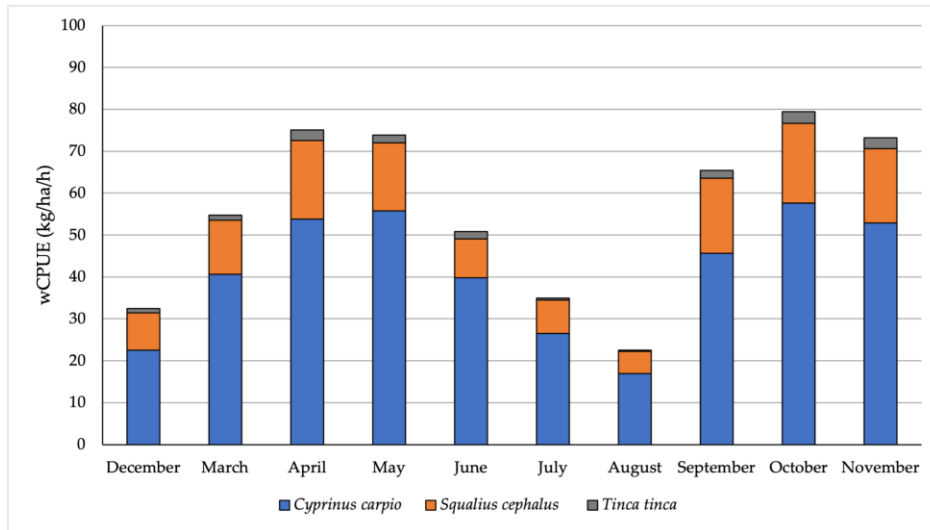


FIGURE 3. Monthly fish wCPUE changes in Lake Yeniçağa.

Nineteen taxa of zooplankton were identified in the lake, including 12 Rotifera, 4 Cladocera, and 3 Copepoda. The most significant contributors to the zooplankton community in terms of biomass were *Acanthodiptomus denticornis* (38%) from the Calanoida group, *Daphnia pulex* (31%), from the Cladocera group, and *Cyclops strenuus* (7%) from the Cyclopoida group. The biomass values of Rotifera were lower than those of other groups due to their small size, with *Asplanchna priodonta* (6%) making a significant contribution to rotifer biomass (Figure 2).

Among the fish species sampled in the lake, four fish species were identified: *Cyprinus carpio*, *Squalius cephalus*, *Tinca tinca*, and *Carassius gibelio*. *Cyprinus carpio* contributed the most to the fish biomass, while *Carassius gibelio* contributed the least. The total fish wCPUE values in Lake Yeniçağa were calculated between 22.51-79.39 kg/ha/h (Table 1). The wCPUE values of *Cyprinus carpio* varied between 16.91-57.61 kg/ha/h (Figure 3). The range of total lengths of the fishes was between 165-500 mm (mean 369 mm) for *C. carpio*, 150-330 mm (mean 241 mm) for *S. cephalus*, 182-316 mm (mean 212 mm) for *T. tinca*. During the studies, only one *C. gibelio* specimen was sampled, and the total length of the specimen was measured as 275 mm. Based on the literature data, we categorized the fish as omnivorous (bentho-planktivorous) depending on the measured body length [49, 50, 51].

During the study, chlorophyll a values in the lake ranged from 15.1 to 114.4 mg/m³, total nitrogen from 88 to 1987 µm/L, total phosphorus from 141 to 310 µm/L, Secchi depth from 60 to 300 cm, and turbidity from 1.17 to 41.53 ntu, as shown in Table 2. TN:TP ratios in Lake Yeniçağa were calculated to be between 0.60 and 9.24.

This study evaluated monthly chlorophyll a, total phosphorus, and Secchi depth values in Lake Yeniçağa using Carlson TSI Indices. Carlson TSI(TP) Index varied between 75.48 and 86.87 throughout the year with an annual average of 78.91. The Carlson TSI(CHLa) Index, was calculated between 57.23 and 77.10 throughout the year, with an annual average of 65.65. Carlson TSI(SD) Index ranged from 44.16 to 67.36 and the annual average of this value was determined to be 55.19 (Table 2).

TABLE 2. Mean, minimum, maximum, and standard deviation values of zooplankton biomass and fish wCPUE measured monthly in Lake Yeniçağa.

	Mean	Minimum	Maximum	SD
Chlorophyll a (mg/m ³)	42.06	15.10	114.44	28.70
Total Phosphorus (µg/L)	184	141	310	52.55
Total Nitrogen (µg/L)	986	88	1987	587.77
Secchi Depth (cm)	163.5	60	300	93.77
Carlson TSI (CHLa)	65.65	57.23	77.10	5.78
Carlson TSI (TP)	78.91	75.48	86.87	3.59
Carlson TSI (SD)	55.19	44.17	67.36	8.69
Turbidity (ntu)	8.19	1.17	41.53	2.59
TN:TP	5.36	0.60	9.24	3.18

The calculated Carlson TSI Index values based on the total phosphorus results indicated that the lake was at a hypertrophic level. The results obtained from chlorophyll a showed that the lake had a hypertrophic tendency but at a eutrophic level, while the Secchi depth values indicated that the lake was at a eutrophic level. Based on these results, the lake can be considered to be at the eutrophic level with a hypertrophic tendency.

Data on how much each variable can be explained by other variables in the SEM is presented in Table 3. The largest R² value was found to be 0.854 for chlorophyll a, while the smallest R² value was 0.426 for Cladocera. The results of the SEM, using fish, zooplankton, chlorophyll a, total nitrogen, and total phosphorus values in Lake Yeniçağa, are schematized in Figure 4. It was

observed that total nitrogen ($r = 0.62$, $p < 0.001$) and total phosphorus ($r = 0.57$, $p < 0.001$) values exhibited a positive interaction with chlorophyll a values. The standardized estimation values of the variables examined in the dataset are also presented in Table 4. It was understood that the effect of total nitrogen on chlorophyll a was higher than that of total phosphorus. The effect of chlorophyll a parameter on Rotifera ($r = -0.48$, $p < 0.001$), Cladocera ($r = -0.48$, $p < 0.001$), and Calanoida ($r = -0.71$, $p < 0.001$) was found to be negative. However, no significant relationship was found between chlorophyll a and Cyclopoida ($p = 0.15$). According to the statistically significant standardized estimation values, the zooplankton group most affected by chlorophyll a was the calanoids. The analysis results for fish-zooplankton interactions in the food web were statistically insignificant for the Cladocera group ($p = 0.30$). The effect of fish on the zooplankton community was found to have a negative effect on Calanoida ($r = -0.74$, $p = 0.002$) and a positive effect on Cyclopoida ($r = 0.82$, $p < 0.001$) and Rotifera ($r = 0.42$, $p < 0.001$). According to the standardized estimation values, the effect of fish on the Cyclopoida group was higher compared to other groups (Table 4).

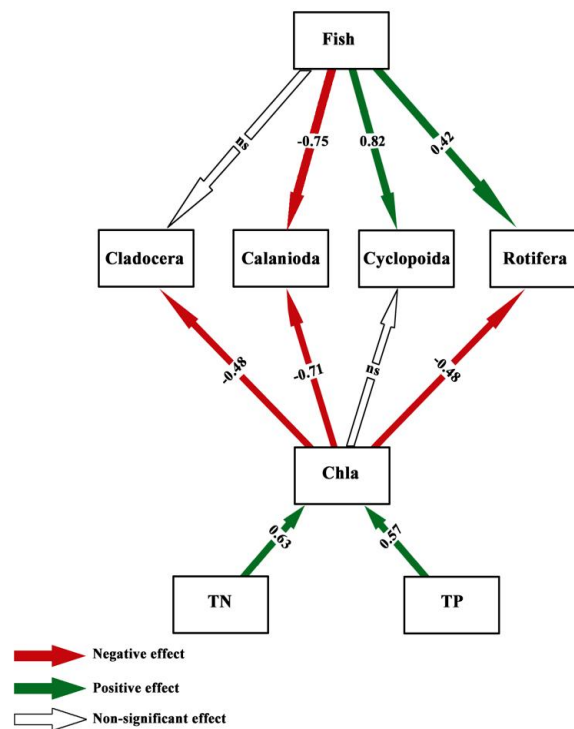


FIGURE 4. Path diagram obtained by using SEM of monthly determined fish, zooplankton, chlorophyll a, total nitrogen, and total phosphorus values in Lake Yeniçağa. Boxes represent observed variables. ($\chi^2 = 19.616$, $df = 9$, $p = 0.020$).

TABLE 3. R^2 values of variables used in SEM.

	Estimate
Chlorophyll a	0.854
Rotifera	0.633
Calanoida	0.481
Cyclopoida	0.546
Cladocera	0.426

TABLE 4. Standardized estimates, standard errors, z-values, and p-values in SEM (**: $p < 0.01$, ***: $p < 0.001$).

			Standardized Estimate	S.E.	z-value	p
Cladocera	<---	Fish	0.249	0.242	1.027	0.305
Cladocera	<---	Chlorophyll a	-0.482	0.130	-3.698	***
Calanoida	<---	Fish	-0.747	0.241	-3.096	**
Calanoida	<---	Chlorophyll a	-0.715	0.160	-4.458	***
Cyclopoida	<---	Fish	0.820	0.115	7.126	***
Cyclopoida	<---	Chlorophyll a	0.174	0.122	1.423	0.155
Rotifera	<---	Fish	0.421	0.120	3.509	***
Rotifera	<---	Chlorophyll a	-0.482	0.099	-4.875	***
Chlorophyll a	<---	Total Nitrogen	0.626	0.065	9.704	***
Chlorophyll a	<---	Total Phosporus	0.573	0.073	7.848	***

4. DISCUSSION

The main reason for eutrophication, one of the most important problems affecting freshwater ecosystems, is the excessive presence of nitrogen and phosphorus elements in the water column that are essential for phytoplankton growth [52]. Secchi depth, an indicator of water transparency and trophic level, is inversely proportional to the density of phytoplankton populations in the water as suspended matter scatters and weakens incoming light [53].

According to Carlson and Simpson [54], some interpretations can be made about ecosystem functioning based on the relationships between TSI indices calculated from chlorophyll a, total phosphorus, and Secchi depth values. In this study, to better understand the deviations in TSI values, the Trophic Index deviation graph, which is Carlson's two-dimensional approach has been used (Figure 5) [54, 55, 56]. Values below the horizontal axis indicate that chlorophyll a is not limited by phosphorus, while values above the horizontal axis indicate that it is limited by phosphorus. On the vertical axis, the values to the right of the line represent cases where the light transmittance is higher than the expected chlorophyll index. In this case, it shows that zooplankton use small-sized phytoplankton as food, and therefore large organisms such as filamentous cyanobacteria become dominant. Values to the left of the vertical axis indicate that water transparency is controlled by factors not dependent on phytoplankton [54]. According to the trophic index deviation graph given in Figure 5, almost all values for Lake Yeniçağa are gathered below the vertical axis and to the right of the horizontal axis. This suggests that phosphorus is not the limiting nutrient for chlorophyll a in the lake, and phytoplankton is dominated by larger-sized species, with zooplankton exerting grazing pressure on small-sized phytoplankton organisms.

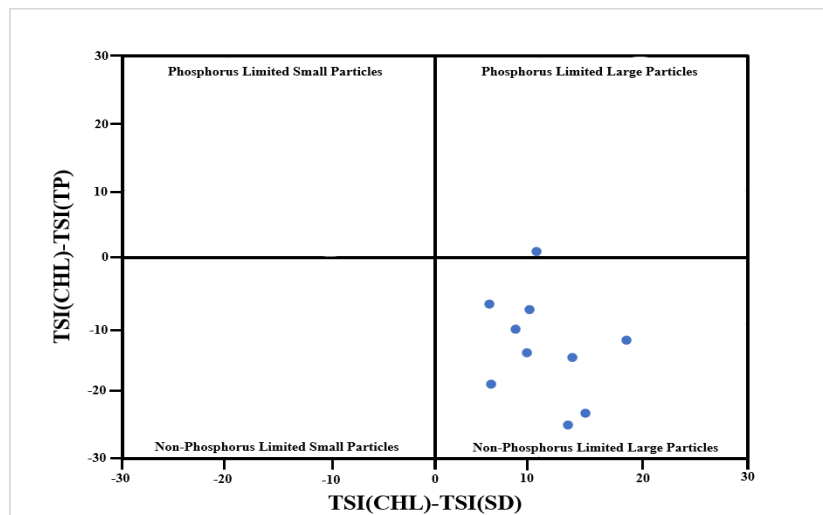


FIGURE 5. Deviations in the trophic state index.

TN:TP ratio provides information about the limiting element for photosynthetic organisms in an ecosystem. When the TN:TP ratio is lower than 10, nitrogen is considered the limiting nutrient, and when it is higher than 17, phosphorus is considered the limiting nutrient. Ratios between 10-17 indicate that both nitrogen and phosphorus are limiting nutrients [57]. The average TN:TP ratio (9.24 ± 3.18) in Lake Yeniçağa indicates that nitrogen is the limiting element for photosynthetic organisms. In lakes characterized by a low TN:TP ratio, the predominant phytoplankton are typically cyanobacteria, and these low ratios promote the growth of nitrogen-fixing cyanobacteria [58-60]. These results are consistent with our findings in the Carlson Trophic Index deviation graph. Additionally, the effect of total nitrogen and total phosphorus on chlorophyll a was evaluated using SEM. The analysis results showed that bottom-up controls had a positive effect on chlorophyll a. This finding is consistent with what is commonly observed in freshwater lakes and reservoirs [61]. The SEM analysis also revealed that the effect of total nitrogen on chlorophyll a is stronger than the effect of total phosphorus in Lake Yeniçağa.

The analyses conducted for Lake Yeniçağa revealed that zooplankton was influenced by both top-down and bottom-up controls, and different groups within the zooplankton community responded differently to these effects.

It is considered that the Cladocera group in Lake Yeniçağa is not controlled by top-down effects as no significant relationship was found between the biomass of fish and this group. It has been reported in the literature that omnivorous fish species exert feeding pressure on large-bodied Cladocera species [28, 62]. While there are studies that support this relationship, there are also some studies where no significance could be detected [63, 64]. Thus, our analysis results for cladocerans are partially contradictory to the literature. Fish species in Lake Yeniçağa, such as *Cyprinus carpio*, *Squalius cephalus*, and *Tinca tinca*, are not exclusively dependent on zooplankton, but are also omnivorous organisms that can feed on phytoplankton, insect larvae, and benthic macrovertebrates [65, 66]. Consequently, fish may have reduced the top-down pressure on cladocerans by shifting their food preference towards calanoids. On the other hand, the feeding habits of fish may also change depending on the turbidity level of the water they are in, and the effect of size-related predation may decrease due to turbidity [67]. Lake Yeniçağa can be classified as a lake with medium turbidity based on its turbidity values (mean: 8.19 ± 2.59). Studies have shown that the pigmentation rate of zooplankton affects the food selectivity of fish in turbid lakes. Therefore, transparent organisms with weak pigmentation can avoid predation pressure from fish in turbid environments [68, 69]. In the aquatic environment, cladocerans exhibit daily vertical or horizontal migration behaviours to escape predator pressure from fish. Experimental studies have shown that fish signals affect this migration behaviour [70, 71]. The SEM analysis results also indicated a negative bottom-up effect due to chlorophyll a on the cladocerans ($r = -0.48$). As the level of eutrophication increases in freshwater ecosystems, there is a decrease in the growth and fertility rates of cladocerans [72, 73]. Additionally, the increase in eutrophication in lake ecosystems triggers the overgrowth of

cyanobacteria, which provide poor nutrition for cladocerans and limit their energy for growth and reproduction, especially in the case of large-sized cladocerans [74,75,76]. Similarly, there are studies in which cladocerans are negatively affected by phytoplankton through bottom-up control. Elser et al. [77] stated that the grazing of *Daphnia* over phytoplankton in a lake at a high eutrophic level decreased considerably compared to a mesotrophic lake, and the increase in the trophic level turned the bottom-up effects on *Daphnia* into negative. This could explain why the Cladocera group in eutrophic Lake Yeniçağa was negatively affected by chlorophyll a.

The top-down effects on the Copepoda group in Lake Yeniçağa exhibited opposite patterns for the two different orders studied within this group. The biomass of calanoid copepods was negatively affected by the presence of fish ($r = -0.75$), while the biomass of cyclopoid copepods was positively affected ($r = 0.82$). According to Soto and Hurlbert [29], calanoid copepods are more sensitive to top-down effects than cyclopoid copepods. Calanoid copepods may enter into a food competition with cyclopoid copepods by consuming common food groups such as rotifers and protozoa with cyclopoid copepods, leading to a numerical decrease in the Cyclopoida group [29, 78]. The top-down control of calanoid copepods by fish in Lake Yeniçağa may indirectly affect the food competition between calanoid and cyclopoid copepods. This situation likely explains the positive association between fish CPUE and both Cyclopoida and Rotifera biomass. Matsuzaki et al. [63] found a positive relationship between Cyclopoida abundance and the CPUE of fish, while Li et al. [79] found a negative relationship between the increase in fish and calanoid biomass. The results obtained for copepods in Lake Yeniçağa are consistent with the literature.

The bottom-up effect, another effect seen in the Copepoda group, was clearly detected for the order Calanoida ($r = -0.71$), but no significant relationship was found for the order Cyclopoida ($p > 0.05$). It is known that calanoids are much more sensitive to eutrophication than cyclopoids and have lower biomass in eutrophic water systems [80-85]. In our study, SEM results revealed that both top-down ($r = -0.75$) and bottom-up ($r = -0.71$) controls acted together on the Calanoida group, and it was understood that these effects were close to each other. The only significant effect in cyclopoid copepods was a positive top-down interaction. It is thought that the reason for this positive effect is the food competition with the calanoids, which decreases as a result of the negative effect exerted by the fish. As an omnivorous species, *Acanthodiptomus denticornis*, the only Calanoida species identified in the study area, can feed on rotifers and ciliates [86]. At the same time, *Cyclops strenuus*, quantitatively the most dominant Cyclopoid Copepod species in the lake, has an omnivorous feeding characteristic and feeds on rotifers, other crustaceans, and phytoplankton [87]. For these reasons, it can be assumed that these two species entered into significant food competition.

Increasing the top-down effect of fish predation on Crustacea in the aquatic food web may reduce predation pressure and trigger an increase in both the abundance

and biomass of rotifers [88, 89, 90]. The results of SEM analysis in Lake Yeniçağa showed a positive top-down control on rotifers from fish ($r = 0.42$). An increase in fish biomass also indirectly increased Rotifera biomass, and there are studies consistent with our results [63, 91, 92]. Predation pressure from fish, which negatively controls the calanoids from the top-down, may have indirectly contributed to this increase. Since *Acanthodiptomus denticornis*, the only Calanoid species detected in Lake Yeniçağa, is a species that feeds on rotifers [86], the decrease in their abundance may have caused a decrease in the predation pressure on the Rotifera. On the other hand, studies in freshwater ecosystems reveal that rotifers are also controlled from the bottom-up, and this effect is higher than top-down control [30, 93]. In bottom-up controls, besides phytoplankton, there is also the effect of food sources such as bacteria, detritus, and Protista at a much higher rate. Due to the organism size of the filamentous algae, the lack of suitable nutrients for the rotifers reduces the filtration rate and creates negative effects on their nutrition and life cycles [75, 94-96]. In this respect, it can be thought that the negative interactions we detected between Rotifera and chlorophyll a are caused by dominant phytoplankton species (*Anabaena circinalis*, *Aulacoseira granulata*, *Aphanizomenon flos-aquae*) in the phytoplankton of Lake Yeniçağa [32]. According to the SEM analysis results in Lake Yeniçağa, the standardized path coefficient value was calculated as $r = -0.48$ in the bottom-up interaction of chlorophyll a. Rotifers can interact positively with phytoplankton with bottom-up control in the food web, but these effects are weaker than interactions with other food sources such as bacteria and Protista [30, 93, 97]. In the zooplankton community, organisms with small body sizes, such as rotifers, may consume food sources like bacteria and detritus in the absence of suitable phytoplankton nutrients [94, 98, 99]. This situation may also be applicable for the Rotifera group in Lake Yeniçağa. However, it is not possible to reach a definite judgment since we do not have data on supplementary food sources.

5. CONCLUSION

In this study, we examined top-down and bottom-up effects on zooplankton in Lake Yeniçağa, which shows a eutrophic level close to hypertrophic, using SEM. According to the results of the standardized path coefficients, the summary of bottom-up and top-down controls in the zooplankton community is as follows: a) The Cladocera group was controlled from the bottom up by phytoplankton, b) The Cyclopoida group was controlled from the top-down by omnivorous fish, c) Both top-down and bottom-up effects observed on the Calanoida and Rotifera groups were quite close to each other ($r = -0.75$ and -0.71 for Calanoida; $r = 0.42$ and -0.48 for Rotifera). For this reason, it was determined that both top-down and bottom-up controls acted together on these two groups.

We believe the data from this study can set an example for future research on the interactions between zooplankton, fish, and phytoplankton in Lake Yeniçağa, making it valuable for potential biomanipulation studies in the lake. To conduct the biomanipulation study, it is necessary to reduce the number of omnivorous

fish species that exert predation pressure on *Acanthodiptomus denticornis*, which is known to be an omnivorous species and can feed on phytoplankton in the lake [86]. Also, reducing fish biomass may indirectly affect the trophic level of the lake by decreasing internal loading [100]. We propose that a piscivorous species that can feed on these fish species should be introduced into the lake. However, it should be noted that any manipulation of the fish community in the lake will not be effective unless the untreated wastewater entering the lake is prevented.

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