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The Impact of Trophic Status and Climate Change on the Benthic Community in Lake Sevan, Armenia

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Abstract: *Artificial water level drop and eutrophication radically changed the ecosystem of Lake Sevan. During 1928-2018 the Values of Primary Production of the Lake (VPPL = phytoplankton production + phytobenthos production) and varied energy equivalent of biomass (B_Z) and gross production (P_Z) of zoobenthos varied by a factor of 10 or more. Strong positive dependencies of both B_Z and P_Z on VPPL were found. Similar dependencies were also revealed separately for Chironomidae, Oligochaeta and detritivores. Regression equations of dependencies were then used to estimate the development of zoobenthos under different trophic conditions: oligotrophic, mesotrophic and eutrophic. Significant climate change was observed over the past 80 years. From 1935–2012, the annual mean temperature in Armenia increased by 1.03°C. The climate change projections for Lake Sevan are an increase of mean annual water temperature of 0.5°C by 2030, 2°C by 2070 and 4°C by 2100 against the baseline of 9.1°C. Observations showed that in Lake Sevan an order of magnitude increase of VPPL results in an increase of the gross production of macrozoobenthos by factor of 7. Meanwhile, a 4°C temperature increase is estimated to increase the rate of zoobenthos production (P_Z/B_Z) only by a factor of 2. Therefore, the most effective measure required for the mitigation of climate change effects on the Lake Sevan ecosystem is keeping the trophic status of the lake as low as possible, and should include:*

- *runoff prevention of of organic materials from agricultural, industrial and domestic origins into Lake Sevan;*
- *prohibition of any activity that involves the use of organic phosphorus and organic nitrogen directly in the lake.*

Key words: *trophic status, zoobenthos, climate change, temperature increase.*

1. Introduction

Eutrophication and temperature increase radically change aquatic ecosystems. Climate change is among the most serious environmental challenges facing humanity and the ecosystems that provide the goods and services on which it relies (Harrod, 2016). Global mean surface temperatures have increased by 0.75°C over the past century, with the rate of change increasing from the 1970s (Trenberth *et al*., 2007). Warming has also been recorded in freshwater ecosystems worldwide (Bates *et al*., 2008), including mean water temperature increase 0.3ºC over the last 40 years in Lake Sevan (Poddubny, 2010a). Lakes are effective sentinels for climate change because they are sensitive to climate, respond rapidly to change, and integrate information about changes in the catchment. Fast turnover times from organismal to ecosystem scales in lakes are a prerequisite for detecting such rapid changes (Adrian *et al.*, 2009). Climate change is projected to cause significant alterations to aquatic food web structure, dynamics and biodiversity, and primary and secondary production (Wrona *et al.*, 2006). Among the effects of climate change are the increase of water temperatures with the consequent diminution of dissolved oxygen, and the reduction of available habitats for most stenothermal organisms.

An environmental forecast can be based on “one of two methodological approaches: first, by creating dynamic models in which systems are studied, and second, in statistical processing of time series of observations and extrapolation of these series to the future” (Mikhailovsky, 1983). Having the unique time series of 90 years of observations, the second approach will be the basis of our methodology.

Forecasting, and environmental forecasting in particular, is a risky and ungrateful process. A good example is the forecast of the development of ecosystems of lowland reservoirs built between 1930-1950 on the Volga, Kama (Russia) and Dnieper (Ukraine) rivers, made by leading hydrobiologists and ichthyologists of the USSR, who absolutely dido not took take into account the processes of self-dispersal of the northern species towards the south and vice versa. The errors of quantitative forecast were even more significant: the productivity of phytoplankton turned out to be much higher, and that of zooplankton and commercial fish – significantly less than predicted. In this case, errors in the forecast of fish productivity of reservoirs resulted in an overestimation of ten times of the actual zoobenthos biomass (Nikolayev, 1980).

Nevertheless, the need for environmental forecasts (of course, reliable!) is acute; the number of their potential consumers is growing. They are of particular importance in the light of the environmental impact assessment of projects (Rosenberg et al., 1994), in connection with the adoption of *The Law on Environmental Impact Assessment and Expertise*” (2014).

The impact of climate change on the different links of the aquatic food chain has been studied mainly in marine ecosystems. In the North Sea the main changes occurred in both phyto- and zooplankton and included a shift in phenology, the composition and abundance, an increase in phytoplankton biomass and associated decrease in zooplankton biomass (Reid, 2006). In the zoobenthos of the Barents Sea there was a positive correlation of the biomass of boreal species and a negative correlation of the biomass of arctic species with temperature fluctuations, in which there was a 3 to 7-year lag period of biomass response to temperature for several dominant species (Frolova *et al*., 2007). Climate change affects the distribution and productivity of fish species (Cheung *et al.,* 2010), has an impact on the sustainability of marine fisheries and aquaculture, and on the livelihoods of communities that depend on fisheries (Wrona *et al.*, 2006). Climate warming likely will cause a shift in the distribution limits for fish species with a change in growth performance and physiology, or even extinction of the species in the world (Mazumder *et al.*, 2015).

Meanwhile, there are very limited data on the impact of climate change on different aspects of functioning of aquatic food chains in freshwater ecosystems. The purpose of this work is to show on the example of Lake Sevan the impact of changes in trophic status and climate change on the benthos in a large freshwater high-altitude limnic waterbody. This is possible due to the unique and fairly intensive long-term historical data base for Lake Sevan (1928-2018). The spatial stability and relative longevity of macrobenthic organisms make them the most convenient objects in the study of long-term environmental changes (Viter, 2011), including for environmental forecasting.

Lake Sevan (40.47°N, 45.33°E) is located in the northern part of the Armenian Volcanic Highland, in Gegharkunik Province of Armenia. The basin of Lake Sevan makes up one sixth of the total territory of the country. Lake Sevan is the largest lake of the Caucasus Region and one of the largest freshwater mountain lakes in Eurasia. All other neighboring great lakes – the Caspian Sea, Lake Van, Lake Urmia and Lake Tuz are saline or hupersaline.

The importance of Lake Sevan in the economy of Armenia can scarcely be exaggerated: it is the main source of irrigation water and provides low cost energy and fish, recreation and tourism. Lake Sevan and the wetlands of the basin are significant breeding, resting, foraging and wintering areas for waterfowl.

To use the lake’s water effectively, Soviet managers devised a plan to preempt the evaporation process by reducing the lake’s surface area. The bed of the out-flowing Hrazdan River was excavated, and a tunnel for the outflow was constructed at a depth of 40 m below the lake surface. The tunnel was inaugurated in 1949; the plan involved taking of 1 km^3 water annually for energy and for irrigation. During

1949–1964 the lake level dropped at a rate 1 m year^{-1} (Lind and Taslakyan, 2005; Babayan *et al.*, 2005). Compared to 1931, the 2002 lake level was lowered almost 20 m, the surface area had decreased 13% and the volume 44% (Lyatti, 1932a; Jenderedjian *et al.*, 2005).

The water-level decreases, from this artificial outflow process, influenced an array of hydrological conditions in the lake and at the lakeshore; the lake has undergone such changes which naturally would take thousands of years. The most important of these were: the draining of wetlands, worsening water quality, invasive species succession and biodiversity loss. Lake Sevan experienced increasing eutrophication. This led to seasonal anoxia near the bottom, decreased water transparency, reduced areas of macrophytes, and increases of phytoplankton, zooplankton and zoobenthos production by an order of magnitude. Fish catches doubled due to introduced and invasive species. Meanwhile the number of endemic fish species declined to critical levels and all of them are listed in the Red Book of Armenia (Gabrielyan, 2010a, c, d). Lake Sevan caused deep violations of functional blocks and links in the ecosystem, an imbalance of production and destructive relationships, which led to species succession in all links of the food chain and to the intensification of bioproduction processes (Pavlov, 2010).

Recognizing the true values of wetlands, Armenia became a Contracting Party to the Convention on Wetlands on 6 November 1993 and designated three sites of international importance, including the Lake Sevan Ramsar site, which includes the lake and its basin.

The Lake Sevan management strategy was changed after the adoption of two laws about Lake Sevan. *The Law about Lake Sevan* (2001) “recognizes strategic significance” of the lake for the people of Armenia as an ecosystem with “economic, social, scientific, historical, cultural, aesthetical, recreational and spiritual value”. *The Law about Approval of Annual and Complex Measures on Conservation, Restoration, Reproduction, and Use of the Ecosystem of Lake Sevan* (2001) mandates the raising of the lake water level by 2029 to 1903.5 m above sea level “as a prerequisite for the restoration of the former quantitative and qualitative indicators of water and the prevention of eutrophication, as an elaborate presupposition of survival and water quality eutrophication”. In this case, one should have expected a steady increase in the thermal stability of the lake, an improvement in the oxygen regime of the bottom water layers, restriction of nutrient inputs from bottom sediments and a significant limitation of the catchment effect (Oganesyan *et al.*, 1977, 1985; Oganesyan and Parparov, 1986; Oganesyan, 1988; Danielyan *et al.*, 2011). However, it should be borne in mind that when developing the scientific basis of for the amount of lake level increase, the current projections of climate change were not taken into account.

In this paper, we analyze changes in the long-term (1928–2017) biomass and energetics, and energy budgets of major taxonomic groups of macrobenthic fauna in Lake Sevan. We quantify the relationships between primary production of the lake and the biomass and production of major zoobenthos taxa. Our objective is to understand the response of the zoobenthos community to changes in lake trophic levels, thereby providing baseline information that should assist managers when considering future water level and water intake manipulations. In particular, the results should assist with continued restoration and rehabilitation by taking into account projected global warming processes, as well as other major links of the lake's food chain: zooplankton and fishery.

2. Material and Methods

2.1. The study area

Lake Sevan is situated at an altitude 1900.38 m a. s. l., with a surface area 1238 km^2 and volume 38.1 km^3 (as of January 1, 2019). Prior to draining activities, the lake was situated at an altitude 1916.20 m a. s. l., the surface area was 1416 km^2 and volume 58.5 km^3 (as of January 1, 1931). A minimal water level of 1896.32 m a. s. l., surface area of 1236 km^2 and volume of 32.9 km^3 were observed in 2002.

The climate of Lake Sevan basin (4891 km^2) is influenced by its high-mountain location. On the shore the annual number of sunny hours varies from 2,328 to 2,779.

Mean temperature ranges from –5°C in January to 16°C in July, with average annual temperature 5°C. The duration of the frost-free period is about 150 days (Gyozalyan, 1979).

The average annual precipitation in the lake basin ranges from 380 mm on the southern shore to 940 mm on the slopes of mountains. Over the lake, from 340 to 720 mm of precipitation falls annually (Climatic Atlas of the Armenian SSR, 1975).

Lake Sevan consists of the deeper Minor Sevan and relatively shallow Major Sevan, which are separated from each other by capes, forming a wide (5.4 km) strait. The length of the lake is 72.5 km; the largest width of Major Sevan is 30 km, and the Minor Sevan – 14 km.

28 rivers and streams flow into Lake Sevan, and the River Hrazdan flows out of the lake.

Sevan is a dimictic lake with spring and summer circulation. During summer, Lake Sevan water is thermally stratified, with temperature-derived density differences separating the warm surface waters (the epilimnion), from the colder bottom waters (the hypolimnion).

The water of Lake Sevan has had high transparency, averaged over 12 m in the year, with a maximum up to 22 m. In 1978–2004, the water transparency averaged 2.5–4.5 m annually, with a maximum of 6–8 m. Starting in 2005 until 2014–2017 the water transparency increased to 6–12 m (Gyozalyan, 1981, 1984; Bobrov, 2010; Jenderedjian and Hakobyan, 2018).

Until the 1950's the lake was characterized by the year-round presence of dissolved oxygen in the water. In 1974–2007 in the bottom layers of water, areal anaerobic conditions for 2–4 months became common (Slobodchikov, 1955; Gyozalyan and Khorlashko, 1979; Gyozalyan, 1983, Poddubny, 2010b).

The water level increase led to an increase of transparency and improved oxygen conditions in the water near the bottom (Krylov *et al.*, 2016, 2018). However, during the water "bloom" in 2018 and 2019, water transparency dropped to 0.2–0.4 m in the zone of congestion of blue-green algae.

Bottom substrates are categorized as river sediments, stones, pure sands, silty sands, yellow (oxidized) and black (reduced) silt, and limestone bedrock. River sediments are present offshore of river mouths at depths of 3-7(13) m. Stones occur in limited areas at 2–3 m depths. Pure sands are common at depths up to 2–4 m and up to 25 m at the steep shores. Sands become siltier as depths increase. At 7–16 m the sediments become predominantly oxidized yellow silt. As the depths increase, the yellow color of the silt becomes darker, and at depths of 25–33 m the silt is black. During the circulation period (spring and summer), the black silts are covered with a yellow oxidized layer. Small areas of limestone bedrock are present at 26–43 m. The drop in water level has significantly reduced the areas of stones and sands from historic values (Lyatti, 1932b; Afanasyev, 1933; Jenderedjian *et al.,* 2007, 2012).

In the composition of phytoplankton three main groups of algae were found: diatoms (Bacillariophyta), green (Chlorophyta) and blue-green (Cyanophyta). Representatives of the yellow-green (Xanthophyceae), Peridinaceae, and Euglenophyta did not constitute a significant portion to the quantitative indicators but they are important as biodiversity indicators. Before the water level lowering the qualitative composition of phytoplankton of Lake Sevan was poor. In the cold season diatoms dominated, in the warm season – green algae. Blue-green algae in the lake played a subordinate role; representatives of the genus Anabaena were completely absent. As the water level decreased, qualitative changes in phytoplankton appeared – some species migrated to pelagial from the coves, others were found in the lake for the first time. Significant changes occurred from 1964, when the first mass "blooming" of the lake by blue-green algae was detected; the blue-green algae from genera Anabaena and Aphanizomenon appeared and began to dominate in the lake. Water "bloom" indicated a dramatic change towards eutrophication. By 1976, phytoplankton biomass increased 19 times compared with 1947 and became comparable with the biomass of eutrophic lakes. From the 1980s, there have been no continuous "blooms" of water in the lake, but local “blooms” have been observed every year in the shallow bays. Between 2004-2010 in the lake 164 taxa were registered: 83 (51%) diatoms, 54 (33%) - green and 16 (10%) - blue-green algae. The average phytoplankton and chlorophyll biomass values corresponded to the indices of mesotrophic lakes. However, in 2018 and 2019, an outbreak of a number of blue-green bacteria was observed, which led to intensive water “blooming” by blue-green algae, for the first time in 40 years. The reasons behind this were unprecedented high summer temperature – more than 3°C higher than the long-term average and an increase in the content of dissolved organic phosphorus (Vladimirova, 1947; Stroykina, 1953; Meshkova, 1962, 1975; Ghazaryan and Navasardyan, 1979; Legovich, 1979; Hovsepyan *et al.*, 2010; Hovsepyan, 2013; Environmental Monitoring and Information Center SNCO, report 2018).

48 zooplankton species were found in Lake Sevan: Rotifera 28, Copepoda 9 and Cladocera 11 species. During 1936–2018 the zooplankton average annual number ranged 12–138 thousand specimens m^{-3} and a biomass – of 0.4–2.0 g m^{-3} wet weight; rotifers and copepods were dominated in numbers, while daphnia and cladocerans dominated in terms of biomass. The main reason for the disappearance of a number of species and the appearance of new ones was the eutrophication of the lake. The subsequent water level increase from 2002 contributed to the introduction of plankton of a new species. Among them *Daphnia magna* was identified, which soon became the majority of zooplankton biomass. However, in 2018 *D. magna* completely dropped out of the zoobenthos composition, obviously, in connection with the water “blooming”, as well as with a significant increase in the number of whitefish. Changes in lake’s morphometry and fluctuations of trophic level did not have a noticeable effect on the vertical and horizontal distribution of zooplankton (Meshkova, 1947, 1953, 1962, 1975; Simonyan, 1976, 1991; Krylov *et al.*, 2010, 2013, 2018; Nikoghosyan and Hakobyan, 2012; Nikoghosyan, 2013).

The phytobenthos includes both microphytes and macrophytes. Microphytes include 25 species of green, 33 species of blue-green and about 200 forms of diatom algae. The development of fouling begins in early spring, when coastal stones are covering with cortical colonies of blue-green algae. Later, the first shoots of green algae appear. The maximum development of Enteromorpha and Cladophora is at the beginning of autumn. Diatoms observed in large quantities on the strings of green and on the colonies of blue-green algae. In these foulings are refuge and food for oligochaetae of the Naididae family, small larvae of mayflies, caddisflies and chironomids (Vladimirova, 1947; Jenderedjian and Poddubnaya, 1987).

Macrophytes consist of 6–7 species of cryptogam and 21 species of vascular plants. Of cryptogam plants *Chara globularis* and *Ch. intermedia* are widespread, of mosses – *Fontinalis antipyretica*. Of submerged flowering plants most common are pondweeds – *Potamogeton pectinatus* and *P. perfoliatus* and spiked water-milfoil (*Myriophyllum spicatum*). Semi-submerged vegetation occupies tranquil coastal zones in coves and bays, as well as temporarily or permanently separated from the lake wetlands: flowering rush (*Butomus umbellatus*), bulrushes *Scirpus compactus* and *S. tabernaemontani*, reed *Phragmites australis*, water knotweed (*Poligonum amphibium*), *Zannichellia major,* water crowfoot *Ranunculus divaricatus* and star duckweed (*Lemna trisulca*). Semi-submerged vegetation is important as a nesting site for wetland birds, amphibian breeding, feeding of juvenile fish. Prior to drawdown, macrophytes occupied depths up to 19 m with estimated maximum biomass 600,000 tones. During 1964–2018 maximal biomass fluctuated between 30,000–100,000 tones. The drastic changes in the biomass of macrophytes are explained by reducing of water transparency, leveling the coastline, and thereby increasing the depressing role of the surf (Arnoldi, 1929; Fridman, 1948; Ghambaryan, 1979, 1984; Barseghyan, 1990; Jenderedjian, 1996; Jenderedjian, *et al.*, 1999; Bobrov, 2010).

The zoobenthos consists of micro- (unicellular organisms), meio- (size below 3 mm), macro- (size 3-50 mm) and megabenthos (size above 50 mm) (Konstantinov, 1986).

From representatives of microbenthos only infusoria are studied; their number of species in fouling of Lake Sevan is close to 50 (Zharikov and Anokhina, 1984; Zharikov, 2010).

A total 100 species of meiobenthos animals were identified, including 48 representatives of the permanent components: hydra – 2, flatworms – 3, nematodes – 23, water bear – 1, ostracods – 9, water fleas – 5, cyclopids – 3, and harpacticides – 2. Among nematodes, there was a noticeable replacement of the oxyphilic species of family Chromadoridae on less demanding on water quality species of family Monchisteridae. In 1986-1993 the average annual number of meiobenthos varied within 93–195 thousand specimens m^{-2} with a biomass and gross production of 1.2–1.8 and 2.1–3.5 g m^{-2} wet weight, respectively (Fridman, 1948, 1950; Gagarin and Hakobyan, 1991, 1992; Hakobyan, 1996a. 1996b, 2010).

A total of 171 species of macrobenthic animals, mostly cosmopolitan Palearctic and Holarctic species, were described for Lake Sevan and small coastal water bodies. Of these 100 species (oligochaetae 26, leeches 8, limnid 11 and bivalve 7 molluscs, amphipods 2, larvae of dragonfly 1, mayflies 2, caddisflies 7, nonbiting midges 32, and bags 4) were found directly in the lake.

The only representative of megabenthos, the narrow-clawed crayfish (*Astacus leptodactylus*), was first found in Lake Sevan in the 1970s. Perfectly adapted to the conditions of the lake, crayfish acquired commercial importance in 1990s. The commercial pressure affects the state of the crayfish population by reducing the number of size-age groups. Crayfish is most common at depths of up to 20–22 m with the maximum reliable depth of capture 33 m. It prefers a silty, sandy bottom with thickets of macrophytes. The commercial pressure, poaching, use of nets and special not selective traps affects the state of the crayfish population by reducing the number of size-age groups. Currently commercial stocks of crayfish in Lake Sevan are under severe decline (Hovhannisyan and Ghukasyan, 1996; Hovhannisyan, 1998; Jenderedjian, 1998; Ghukasyan, *et al.*, 2006, 2010; Badalyan, 2012a, 2012b):

Ichthyofauna consists of 3 endemic – Ishkhan or Sevan trout (*Salmo ischchan*), Sevan scraper (*Varicorhinus capoeta sevangi*) and Sevan barbel (*Barbus goktschaikus*), 1 introduced – whitefish (*Coregonus lavaretus sevanicus*) and 5 invasive species – Prussian carp (*Carassius auratus gibelio*), South Caspian spirlin (*Alburnoides bipunctatus armeniensis*), topmouth gudgeon (*Pseudorasbora parva*), common carp (*Cyprinus carpio*), rainbow trout (*Parasalmo mykiss*). All native species are in serious decline and listed in the Red Data Book of Armenia (2010). Currently the most important commercial fish is the whitefish, which has been introduced in 1924–1927 to consume zooplankton resources underutilized by local fish species (Fortunatov, 1927). Until the end of 1950's, in the basis of fish catches were Ishkhan and Koghak. In 1970-1990's registered fish catches were on average 3 times higher than in 1920-1960's. It should be mentioned that according to expert estimations, poaching has always been higher than recorded catches (Gabrielyan, 2010b).

2.2. Material

Extensive historical data sets were used to evaluate the impacts of water level changes and associated changes on the zoobenthos (Table 1).

The energy values of biomass and gross production of major taxonomic and feeding groups of benthic animals were compared with the values of primary production of the lake VPPL = phytoplankton + phytobenthos productions (Tables 2 and 3).

Significant climate change has been observed over the past 80 years. From 1935–2012, the annual mean temperature in Armenia increased by 1.03°C andprecipitation decreased by 10%.

The climate change projections for Lake Sevan are (Table 4):

- increase of mean annual water temperature against the baseline 9.1°C in 2030 by 0,5°C, in 2070 by 2°C, and in 2100 by 4°C;
- decrease of annual inflow in 2030 by 7%, in 2070 by 14%, and in 2100 by 24%;

Table 1. Average annual biomass of different systematic groups of zoobenthos and zoobenthos energy biomass and annual gross production in Lake Sevan.

Year	Oligochaeta	Hirudinea	Gastropoda	Bivalvia	Amphipoda	Ephemeroptera	Odonata + Tricoptera	Chironomidae	Total macrobenthos	Summary biomass (B)	Summary gross production (P)	P/B
	g m^{-2} wet biomass									Joule m^{-2}		
1928	1.64	0.41	0.03	0.12	0.62	0.01	0.05	0.38	3.26	13,191	18,335	1.39
1938	2.05	0.51	0.12	0.31	0.56	0.01	0.03	0.46	4.05	15,826	22,631	1.43
1948	1.98	0.30	0.06	0.20	0.69	0.01	0.02	0.66	3.92	15,322	21,451	1.40
1955	4.13	0.33	0.13	0.25	0.67	0.01	0.02	1.16	6.60	26,911	36,868	1.37
1962	2.04	0.35	0.46	1.23	0.78	0.03	0.04	1.71	6.64	20,960	39,614	1.89
1966	2.63	0.50	0.45	1.09	0.60	0.06	0.03	3.10	8.46	27,027	65,676	2.43
1971	3.19	0.30	0.48	1.44	0.78	0.06	0.01	7.20	13.46	40,175	95,215	2.37
1976	7.04	0.28	0.35	0.85	0.45	0.04	0.00	21.90	30.91	92,576	240,698	2.60
1978	12.57	0.19	0.41	1.11	0.24	0.01	0.00	22.42	36.95	119,017	274,929	2.31
1979	12.05	0.21	0.36	1.11	0.19	0.01	0.00	18.80	32.73	107,332	235,057	2.19
1980	10.54	0.15	0.29	1.02	0.10	0.01	0.00	10.68	22.79	79,105	148,717	1.88
1981	9.77	0.09	0.26	0.82	0.10	0.01	0.00	6.20	17.25	63,723	102,594	1.61
1982	9.57	0.04	0.33	0.74	0.08	0.01	0.00	5.14	15.91	59,862	92,187	1.54
1983	10.53	0.03	0.31	0.72	0.04	0.00	0.00	5.50	17.13	64,982	94,224	1.45
1984	11.84	0.03	0.35	0.71	0.04	0.00	0.01	5.60	18.58	71,486	97,936	1.37
1985	10.57	0.03	0.29	0.48	0.07	0.00	0.01	7.66	19.11	70,380	112,608	1.60
1986	9.14	0.03	0.15	0.26	0.09	0.00	0.01	4.29	13.97	54,786	73,413	1.34
1987	8.38	0.02	0.08	0.18	0.04	0.00	0.00	2.53	11.23	46,317	54,191	1.17
1988	8.96	0.01	0.10	0.20	0.01	0.00	0.00	2.80	12.08	49,622	59,546	1.20
1989	7.43	0.01	0.05	0.10	0.03	0.00	0.00	2.21	9.83	40,817	48,572	1.19
1990	7.51	0.01	0.07	0.14	0.09	0.00	0.00	2.07	9.89	41,157	48,565	1.18
1991	7.54	0.01	0.08	0.13	0.06	0.00	0.00	3.03	10.85	43,588	60,587	1.39
2004	5.52	0.01	0.06	0.10	0.06	0.00	0.00	1.71	7.46	30,721	41,781	1.36
2008	6.91	0.01	0.04	0.01	0.23	0.00	0.00	3.05	10.25	41,099	61,649	1.50
2012	2.45	0.02	0.17	0.02	0.40	0.02	0.00	1.70	4.78	17,760	30,725	1.73
2015	1.77	0.03	0.01	1.13	0.23	0.01	0.00	2.77	5.94	17,768	39,090	2.20
2016	1.38	0.09	0.15	1.07	0.63	0.01	0.00	2.26	5.59	16,592	36,005	2.17
2017	0.77	0.14	0.22	0.44	0.73	0.02	0.01	1.08	3.40	10,745	22,457	2.09

References: 1928 (Arnoldi, 1929), 1938 (Fridman, 1950), 1955 (Markosyan, 1959), 1976 (Nikolayev, 1985), 1978 and 1980 (Ostrovsky, 1985), 1984–1991, 2004 (Jenderedjian, 2005; Jenderedjian et al., 2005), 2005–2017 (Hakobyan and Jenderedjian, 2010; Hakobyan 2016; Jenderedjian and Hakobyan, 2016, 2018), 1948, 1961, 1966, 1971, 1979, 1982–1983 (calculations based on archival materials of the Scientific Center of Zoology and Hydroecology).

Table 2. Perennial values of phytoplankton production of Lake Sevan (кJoule m^{-2} year^{-1})

Years	Production	Years	Production	Years	Production	Years	Production	Years	Production
1939	2400	1968	10700	1978	23870	1985	8220	1997	12800
1947	3500	1969	10400	1979	12790	1986	13260	2001	10400
1959	4610	1972	8900	1980	16640	1987	10660	2005	6100
1961	9700	1974	20100	1981	13350	1988	13310	2009	2900
1962	12500	1975	16300	1982	12480	1989	11390	2013	2800
1966	23300	1976	29590	1983	8680	1990	12570		
1967	12900	1977	31090	1984	12480	1991	14670		

References: Ghambaryan, 1968; Parparov, 1990; Simonyan, 1991; Jenderedjian, 2019.

- decrease of annual precipitation against the baseline 592 mm in 2030 by 3%, in 2070 by 6%, and in 2100 by 9%.

A projected lake water-temperature increases were used to estimate the expected changes in the functioning of macrozoobenthos in Lake Sevan.

Table 3. Development of macrophytes in Lake Sevan in different years

Year	Maximal biomass, tones	Energy equivalent, kJoule m^{-2} $year^{-1}$
1928	600,000	869
1948	200,000	296
1955	100,000	156
1961-1962	60,000	96
1966-1967	50,000	81
1974-1978	30,000	49
1980	17,000	28
1983	33,000	54
1984-1991	40,000-60,000	83 (66-99)
2004-2009	50,000-75,000	101 (81-121)
2010-2017	75,000-100,000	140 (120-160)

References: Arnoldi, 1929; Fridman, 1948, 1950; Ghambaryan, 1979, 1984; Barseghyan, 1990; Jenderedjian, 1996; Jenderedjian, et al. 1999; Bobrov, 2010.

Table 4. Climate change projections for Lake Sevan.

Year Mean annual	1961–1990	2030	2070	2100
Temperature, ºC	9.1	9.6	11.1	13.1
Precipitation, mm	592	573	557	540
Inflow, mln. m^3	787	734	673	595

Reference: Armenia's Third National Communication on Climate Change, 2015.

2.3 Methods

A single Petersen grab sample of 0.1 m^2 was obtained at each site visit during 1928–1971, and two Petersen grab samples of 0.025 m^2 per sample were obtained during 1976–2017. Samples were collected weekly, monthly or once in a year from 9 to 27 semi-transects at depths of 2, 4, 7, 10, 15, 20, 25, 30, 40, 50, and 60 m. Samples at 70 m were taken during 1928–1966 and at 80 m – during 1928–1948. The average biomass of bottom animals for each sampling depth and depth zones: littoral (0-8.5 m), sublittoral (8.5-27.5 m) and profundal (>27.5 m) was calculated separate for Major Sevan and Minor Sevan, the then for the whole Lake Sevan taking into account the distribution of areas between the corresponding isobaths (Kireev, 1933), adjusted for water level during the study period.

For calculation of productivity of zoobenthos, annual turnover ratios P/B of production (P) to biomass (B), from published studies for dominant species in Lake Sevan were used (Table 5).

To estimate annual energy budgets, the macrobenthic community of Lake Sevan was divided into four functional feeding groups: detritivores, herbivores, filter feeders (all together primary consumers or so called "peaceful"), and predators (secondary consumers).

Detritivores included Oligochaeta except the family Naididae, the gastropod *Valvata piscinalis*, and chironomid larvae (except *Procladius sp*., *Cryptochironomus sp*., and those species that inhabit periphyton and plants). Herbivores included all Gastropoda except *V. piscinalis*, the oligochaeta family Naididae (except *Chaetogaster spp.*), the amphipod *Gammarus pulex*, chironomid larvae that inhabit periphyton and plants, and mayfly (Ephemeroptera) larvae. All Bivalvia mollusks were considered to be filter feeders. Predators included the oligochaeta *Chaetogaster spp.*, leeches (Hirudinae), caddisflies (Trichoptera), and the chironomids *Procladius sp.* and *Cryptochironomus sp.* (Sushkina, 1949; Zhadin, 1952; Meshkova, 1957; Chekanovskaya, 1962; Mamayev, 1972; Lukin, 1976; Alimov *et al.*, 1977; Alimov, 1981; Manukyan, 1993; Silva *et al.* 2008). Because the amphipod *G. lacustris* inhabits a variety of substrata, it has mixed food sources (Markosyan, 1948). We assumed that the diet of *G. lacustris* consisted of 50% plants, 40%

detritus, and 10% living animals in littoral and of 90% detritus and 10% living animals in sublittoral and profundal, and its biomass was apportioned into the herbivore, detritivore, and predator categories accordingly (Jenderedjian et al., 2012: Jenderedjian and Hakobyan, 2017).

Table 5**.** Ratios (P/B) of annual production (P) to biomass (B) of dominant macrozoobenthos species.

Taxon	Year	Depth, m	P/B	Source
Oligochaeta				Jenderedjian,1989b, 1994a, 1994b
Limnodrilus hoffmeisteri	1984–1985	2–7	1.5–2.2	
Potamothrix alatus paravanicus	1984–1987	2–7	2.1–3.4	
		10–25	1.3–1.9	
		$30^{\text{Major Sevan}}$	0.9–1.1	
		$30^{\text{Minor Sevan}}$	0.2–0.4	
		40	0.4–0.5	
		50	0.2–0.3	
		60	0.1–0.2	
	1947–1948	40–80	0.4–0.6*	
Tubifex tubifex	1984–1985	2–7	1.6–2.2	
Hirudinea				
Glossiphonia complanata	1952–1954	6–10	1.4**	Meshkova, 1957
Helobdella stagnalis			2.4**	
	1974–1976		2.9	Nikolayev, 1980b, 1985
Herpobdella octoculata	1952–1954		3.3**	Meshkova, 1957
	1974–1976		6.0	Nikolayev, 1980b, 1985
Gastropoda				
Valvata piscinalis	1978	7–13	1.4	Ostrovsky, 1981
Bivalvia				Ghukasyan, 1990a, 1990b
Euglesa cingulata	1978	2–20	1.3**	
Euglesa nitida		2–15	2.5**	
Euglesa casertana		15–30	1.1**	
Amphipoda	1937–1939	7–13	2.0	Markosyan, 1948
Gammarus lacustris			1.4–1.5	Ostrovsky, 1983a
			4.7	Nikolayev, 1980a, 1985
	1974–1976	6–10	4.7	
	1980–1983	2–7	1.7–1.8	Manukyan, 1993
Ephemeroptera				Hakobyan and Ostrovsky, 1984
Caenis luctuosa	1979	2–4	4.2***	
Chironomidae				
Procladius culiciformes	1979–1980	10–20	6.5–7.5	Ostrovsky, 1984
	1947–1948	30–40	3.6**	Sharonov, 1951
Cladotanytarsus atridorsum		4–25	10.5**	
Paratanytarsus inopterus		1–14	9.5**	
Tanytarsus sevanicus		14–25	5.2**	
Cladopelma armeniaca		20–30	3.8**	
Glyptochironomus barbipes	1979–1980	2–5	5.0	Ostrovsky, 1983a
Chironomus plumosus	1974–1976	6–10	6	Nikolayev, 1981, 1985
	1979–1980	5–15	4.5–5.7	Ostrovsky, 1983b
		20–30	3.0–3.8	
Chironomus tentans	1947–1948	10–30	4.0**	Sharonov, 1951
Chironomus markosjani	1979–1980	10–25	1.4–2.7	Ostrovsky, 1986
	1947–1948	30–40	3.3**	Sharonov, 1951
Polypedilum scalaenum	1947–1948	1–10	8.8**	

*Recalculation accounting for oxygen content **Calculation by growth rate data ***Recalculation by seasonal P/B ratio

Three scenarios of trophic levels were considered: the annual VPPL 3, 10 and 30 mJoule m^{-2}, which overall correspond to Lake Sevan oligotrophic (1928-1959, 2010-2017), mesotrophic (1961-1972, 1979-2008) and eutrophic (1974-1979) periods, respectively. For those taxonomic groups that didn't revealed correlation with VPPL, the average weighted data for respective years were used.

The temperature factors $Q_{10} = 2.25$ for Oligochaeta and Amphipoda, $Q_{10} = 2.5$ for Hirudinea and insects larvae, and $Q_{10} = 3.2$ for molluscs were used to adjust production ratios (P/B) for water temperatures differing from the initial ones (Winberg, 1956, 1983; Sushchenya, 1972; Alimov, 1975, 1981; Kashirskaya *et al.*, 1980; Ivleva, 1981).

Biomass energy density values (joules per milligram wet weight) were established as follows: Oligochaeta 4.7, Hirudinea 4.2, Gastropoda 1.7, Bivalvia 1.3, Amphipoda 3.8, Ephemeroptera 3.8, Trichoptera 4.2, and Chironomidae 2.5 (Winberg, 1950; Birger *et al.*, 1967; Ostapenya, 1968; Sherstyuk, 1971; Kititsyna, 1978; Manukyan 1993).

An assumption has been made that the increase of annual water temperature on 2ºC degree will extend the duration of oxygen deficiency ($O_2 < 1$ m g^{-1}) period in the bottom layer of water on 1 month, regardless the trophic level of the lake (Rice, *et al.*, 2012). During the seasonal oxygen deficiency, the growth rate of benthic animals assumed to be zero (0). In practice, the latter was applied only to the dominant oligochaeta species *Potamothrix alatus paravanicus*, the only representative of macrozoobenthos, inhabiting in great numbers black silts in the profundal zone.

3. Results and Discussion

The perennial (1928-2017) changes of the macrozoobenthos biomass are given in the Figure 1.

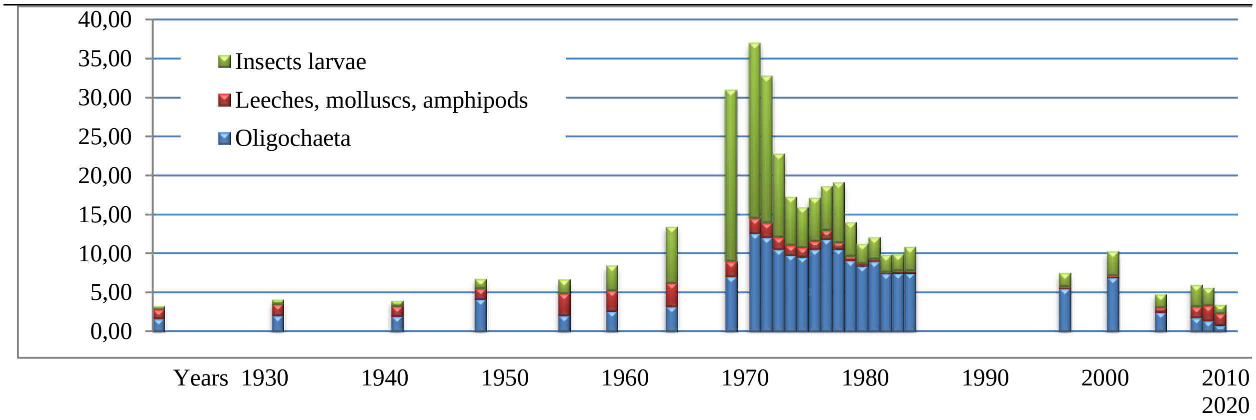

Figure 1. Perennial fluctuations of the macrozoobenthos biomass (g m^{-2} wet weight).
References: Arnoldi, 1929, Fridman, 1950, Markosyan, 1959, Nikolayev, 1985, Ostrovsky, 1985, Hakobyan and Jenderedjian, 2010; Hakobyan 2016; Hakobyan and Jenderedjian, 2016, 2018.

During the natural water level (1928-1932) and initial increase of water exploitation (1933-1948), the average annual biomass of zoobenthos community was 3-4 g m^{-2}, of which (mean ± standard deviation) oligochaetae 50±0.3%, insect larvae 14±2%, leeches, molluscs and amphipoda 35±2%; n=3.

The intensive use of ages-old water reserves (during 1949-1962 each year the outflow was more than 1 km^3 and the water level drop was about 1 m) for production of electricity and irrigation of fertile but dry Ararat Valley was followed by intensive water “bloom” in 1964 and until mid-1980’s. In 1955-1971 the zoobenthos biomass increased to 7-13 g m^{-2}, mainly due to increased biomass of insect larvae (oligochaetae 37±13%, insect larvae 34±12%, leeches, molluscs and amphipoda 29±8%; n=4).

The maximal biomasses of zoobenthos were recorded in 1976-1979 – 31-37 g m^{-2}, of which more than half were chironomid larvae (oligochaetae 31±6%, insect larvae 63±5%, leeches, molluscs and amphipoda 6±0.3%; n=3).

In subsequent years, the biomass of zoobenthos gradually decreased to 16-23 g m^{-2} in 1980-1985 (oligochaetae 57±5%, insect larvae 36±5%, leeches, molluscs and amphipoda 6±0.3%; n=6), 10-14 g m^{-2}

in 1986-1991 (oligochaetae 73±3%, insect larvae 25±3%, leeches, molluscs and amphipoda 6±0.3%; n=6), and 7-10 g m^{-2} in 2004-2008 (oligochaetae 71±3%, insect larvae 26±3%, leeches, molluscs and amphipoda 6±0.3%; n=2). During these years oligochaetae has made in average 2/3 of the zoobenthos biomass.

Lastly, in 2012-2017, the average biomass decreased to 3-6 g m^{-2}, the biomass has begun to resemble that of 1928-1948, and the taxonomic structure (oligochaetae 32±10%, insect larvae 39±5%, leeches, molluscs and amphipoda 29±11%; n=4) – that of 1955-1971.

A positive correlation revealed for the Lake Sevan zoobenthos biomass with VPPL fluctuations with the lag period of biomass response from 2 to 4 years; nevertheless, for oligochatea biomass the lag period was from 7 to 9 years, for chirinomids biomass – 2 years, for molluscs biomass – 5 years. For amphipods biomass the correlation with the VPPL was negative with the lag period from 3 to 4 years.

Changes in the taxonomic structure of zoobenthos by depth zones over time are given in Figure 2.

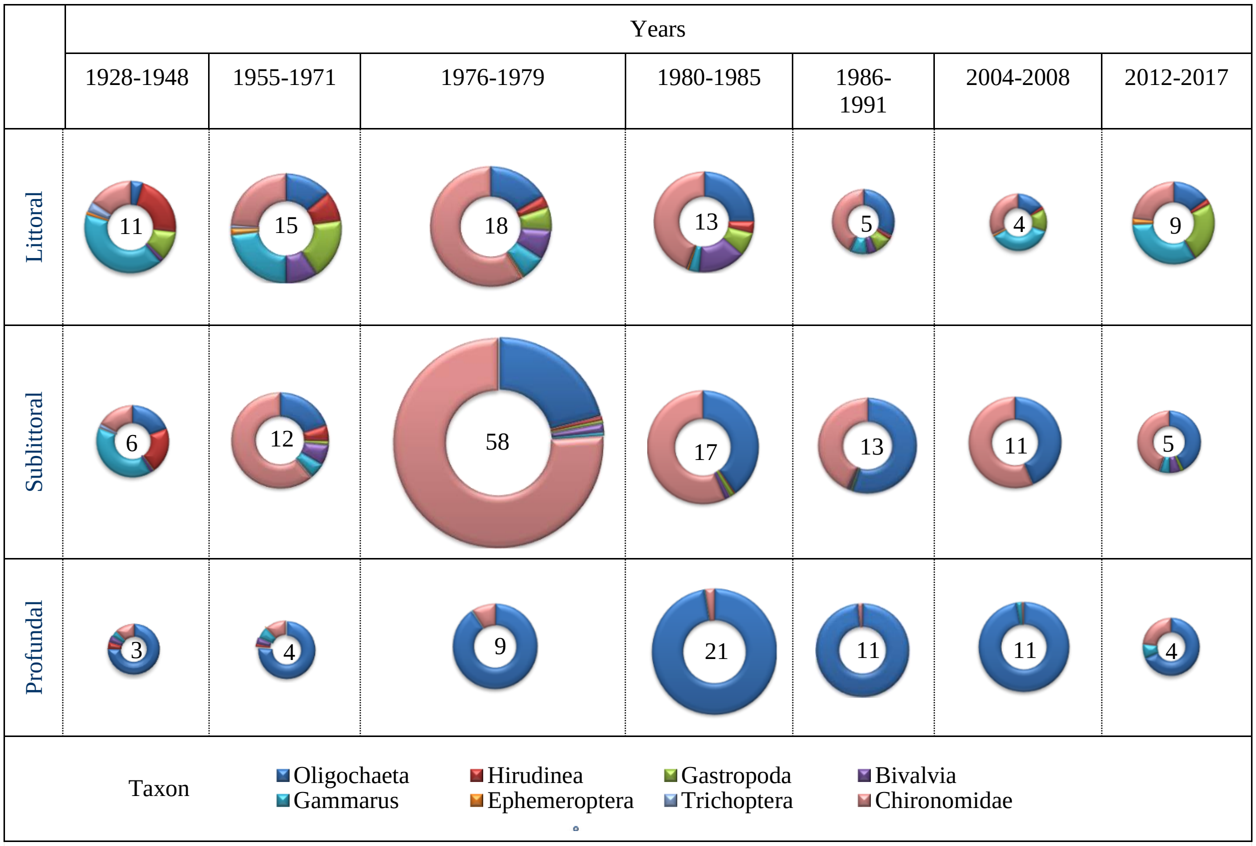

Figure 2. Biomass distribution of different taxonomic groups by depth zones of Lake Sevan in different years. The numbers in the circles mark the total wet biomass of zoobenthos (g m^{-2}).

In 1928-1948, the zoobenthos community was distinguished by high diversity in all depth zones. The highest biomass was in the littoral zone, the lowest in the profundal zone. The littoral was dominated by amphipods, while the subdominant groups were leeches, chironomids and gastropods. Amphipods were dominant in the sublittoral zone as well, while leeches, oligochaetae and chironomids subdominated. Oligochaetae dominated the profundal, and chironomids sub-dominated, with relatively high proportion of molluscs and amphipods, since the minimum oxygen saturation in the bottom water was more than half of the annual maximum (Lyatti, 1932b; Slobodchikov, 1955). The situation was similar in 1955-1971.

In 1976-1979, the maximum biomass of zoobentos shifted to the sublittoral zone mainly due to increase of the biomass of chironomid larvae. Due to worsening oxygen conditions in the bottom layer of water, with insufficient exception, only oligochaeta *P. alatus paravanicus* and small number of chironomid larvae *Procladius culiciformis* survived in the profundal zone.

In 1980-1985, the maximal biomass of zoobenthos shifted to the profundal zone.

The reverse processes were observed in 1986-1991 and 2004-2008. In these years, oligochaetae and larvae of chironomids together consisted 99% of the total biomass in sublittoral and profundal zones. With a few exceptions, leeches, molluscs and amphipods were observed only in the littoral zone.

In 2012-2017, in all depth zones, the structure of zoobenthos and biomass distribution over the depth zones became more or less similar to those in 1928-1948.

The foregoing indicates that the profundal zone zoobenthos biomass reacts slower to fluctuations of the VPPL slower and less pronounced than the sublittoral zone zoobenthos biomass. Indeed, the values of the zoobenthos biomass in sublittoral zone are the most consistent with the VPPL for the previous 2 years, while in the profundal – for the previous 7-9 years. In the littoral zone the zoobenthos biomass are the most consistent with the VPPL for the previous 1-2 years; however, the correlation here is less expressed, since the defining factor is the macrophyte component of VPPL, which is not only a source of food but also a refuge for benthic animals. The intensity of macrophytes development is the smaller, the greater is the value of primary production of plankton and its share in the total primary production energy flow decreases from 11±10% (n=5) in oligotrophic years a much lower proportion of 0.6±0.2% (n=6) in mesotrophic and 0.2±0.02% (n=3) in eutrophic years.

Perennial changes in the macrozoobenthos trophic structure are given in Figure 3.

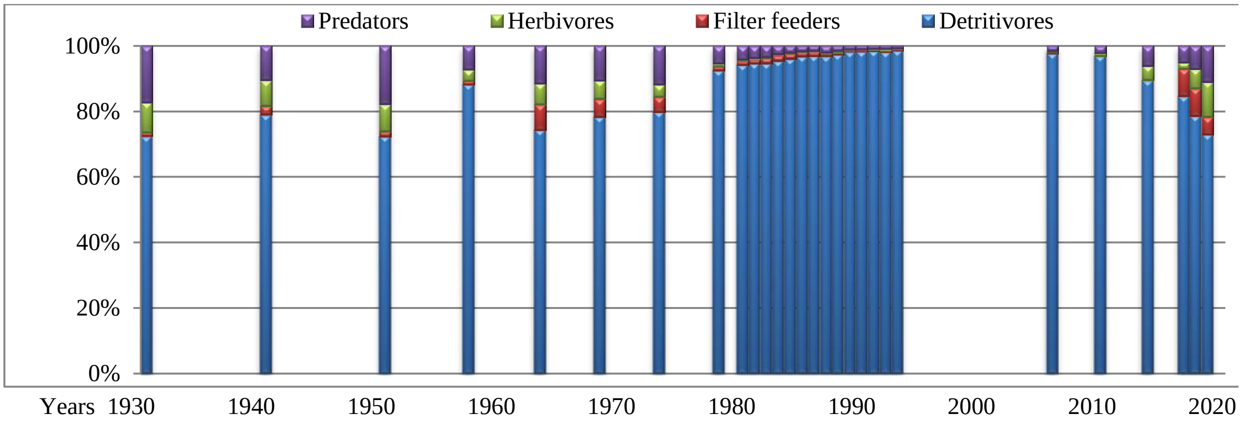

Figure 3. Perennial fluctuations in the macrozoobenthos trophic structure as per cent of the energy biomass.
References: Jenderedjian, *et al.*, 2012; Jenderedjian, 2019.

During 1928–1971, the proportions of biomass energy density (Joules m^{-2}) in the different feeding groups remained comparatively stable (predators 12±4%, detritivores 78±5%, herbivores 6±2%, and filter feeders 4±2%; n=7). Drastic changes occurred after 1971. In 1976–2008, the average proportion (n=17) of predators, herbivores, and filter feeders declined to 2±1%, 0.3±0.2% and 1.0±0.5%, respectively; in contrast, the proportion of detritivores increased to 97±2%. Reversive changes occurred in 2012-2017. In comparison with 1976-2008, the average proportion (n=4) of detritivores declined to 81±2%, predators, herbivores, and filter feeders increased to 7±3%, 6±4% and 6±4%, respectively. The trophic structure of zoobenthos has begun to resemble that of 1928-1971.

Thus, the changes that occurred in the quantitative and qualitative development of zoobenthos in 2004-2017 convincingly indicate a shift in the trophicity of Lake Sevan in the direction of oligotrophy: a significant reduction in the VPPL, improved oxygen conditions in the near-bottom water layers, and expansion of areas covered with macrophytes. This is also confirmed by an increase in the transparency of water from 2-6 m in 1978-2006 up to 5-15 m in 2010-2017, and the shift in the composition of zooplankton from smaller to larger species (Krylov *et al.*, 2018). Seems to be, the positive tendencies in the trophic status of Lake Sevan are mainly the consequence of an increase of 4 m of the lake level from 2002 to 2017.

The patterns described above confirm the earlier assumption that quantitative changes of zoobenthos biomass at a certain stage will be accompanied by qualitative changes in the zoobenthos structure (Jenderedjian, 2019).

Regretfully, in July 2018 and June 2019, week-long outbreaks of Lake Sevan water "blooming" took place, initiated by unprecedented high summer temperatures and increased concentrations of dissolved phosphates in the water. This coincided with increased water withdrawls from the lake and corresponding only 6 cm lake level increase during the past 8 years.

Based on emphircal equations (Table 6), under Lake Sevan conditions, with an increase of VPPL by an order of magnitude (from 3 to 30 mJoule m-^{2}) and the same temperature conditions, the biomass of oligochaetae will increase by 5 and gross production by 6 times, gastropods by 7 and 7 times, bivalve molluscs by 6 and 7 times, larvae of chironomids by 24 and 21 times, and biomass and production of amphipods will decrease by 4 and 4 times. The total biomass and production of zoobenthos will increase by 5 and 7 times, of which detritivores will increase 7 and 12 times.

Table 6. Parameters of dependence* equations ($Y = a \times X^b$, n – number of pairs, r^2 –correlation coefficient) of the biomass (B) and gross production (P) of different groups of benthic animals from the VPPL (PP_{-0}, $_{-1}$, ..., $_{-9}$ for the same and previous 1 ... 9 years), in Joule m^{-2}). The three right-hand columns show estimated values of the corresponding indicators with an annual primary production value of 3, 10, and 30 mJoule m^{-2}.

Taxonomic or trophic group*	Y	X	n	a	b	r^2	3,000,000	10,000,000	30,000,000
Oligochaeta	B_{Oli}	$PP_{-7:-9}$	22	0.301	0.712	0.68	12,342	29,096	63,636
	P_{Oli}	$PP_{-7:9}$	22	0.117	0.761	0.64	9,891	24,733	57,084
Molluscs	B_{Gas}	PP_{-5}	11	0.0002	0.838	0.60	56	154	385
	P_{Gas}	PP_{-5}	11	0.0003	0.848	0.60	91	253	642
Amphipoda	B_{Gam}	$PP_{-3:-4}$	12	3×10^7	–0.615	0.59	2,961	1,409	716
	P_{Gam}	$PP_{-3:-4}$	12	1×10^7	–0.545	0.55	4,205	2,178	1,195
Chironomidae	B_{Chi}	PP_{-2}	22	2×10^{-6}	1.383	0.81	1,815	9,595	43,842
	P_{Chi}	PP_{-2}	22	2×10^{-5}	1.332	0.80	8,483	42,173	182,203
Detritivores	B_{Det}	$PP_{-2:-4}$	22	0.055	0.839	0.74	14,169	38,874	97,684
	P_{Det}	$PP_{-2:-4}$	22	0.002	1.089	0.78	13,065	48,484	160,861
"Peaceful"	B_{Pea}	$PP_{-2:-4}$	22	0.127	0.787	0.75	15,031	38,816	92,317
	P_{Pea}	$PP_{-2:-4}$	22	0.009	0.990	0.77	18,119	59,531	176,729
Total macrozoobenthos	B_{Tot}	$PP_{-2:-4}$	22	0.321	0.737	0.75	18,041	43,796	98,431
	P_{Tot}	$PP_{-2:-4}$	22	0.075	0.870	0.72	24,084	68,45	177,966

*No dependence from the VPPL was revealed by leeches, mayflies and caddisflies, and predators, herbivores and filter feeders.
Reference: Jenderedjian, 2019.

From the above mentioned it may seem that the higher the trophicity of the lake, the more food is available for fish. This is not the case. Obviously, not all zoobenthos production is eaten by fish. Firstly, a significant part of it is eaten by zoobenthos predators themselves. Secondly, vast areas of the bottom of the lake (profundal, lower sublittoral) are permanently or temporarily inaccessible to fish due to unfavorable oxygen conditions. Thirdly, fish feed selectively, preferring certain groups of animals. In general, the animals that are most eaten by fish are those swimming in the near-bottom layer of water (amphipods, leeches), then that are located on or near the bottom surface (molluscs, insects larvae) and the least of all that are living in the bottom lake sediments (oligochaetae). However, the detailed analysis of the relationships between fish, benthos (and plankton) communities is an objective of another paper.

The long-term dynamics of actual (1928-2017) and forecasted (2030, 2070 and 2100) values of gross production (including consumption by second-order consumers, i. e., predatory zoobenthos) of macrobenthos animals are reflected in Figure 4.

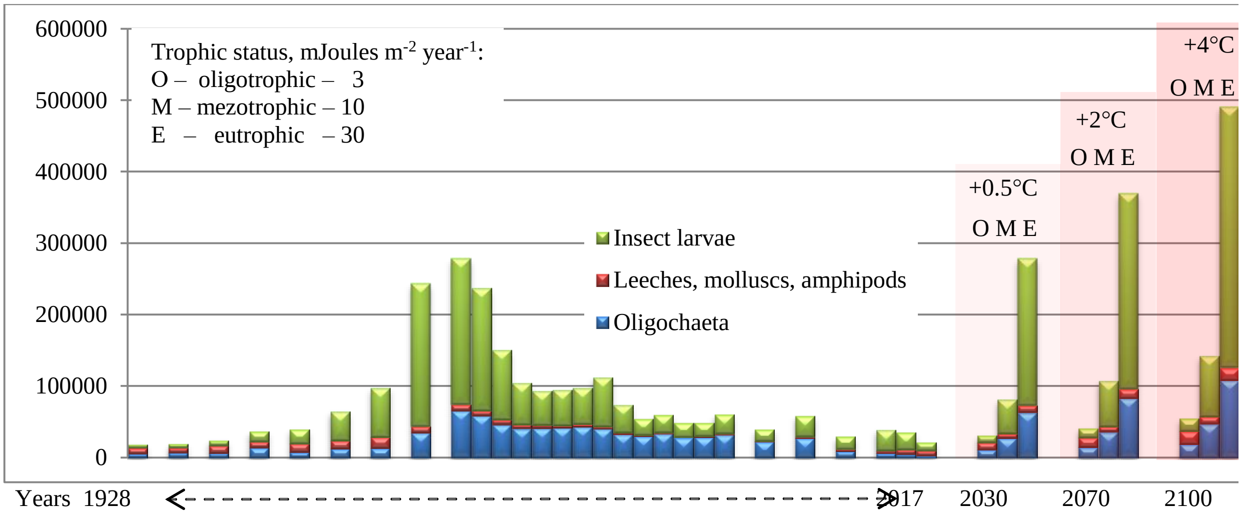

Figure 4. Perennial changes of the actual (1928-2017) and forecasted macrozoobenthos production (Joules m^{-2}) under projected water-temperature increase of 0.5ºC by 2030, 2ºC by 2070 and 4ºC by 2100.

In general, all other conditions being equal, an increase in temperature by 0.5ºC will lead to an increase in the zoobenthos production rate by 9%, by 2ºC – by 45%, and by 4ºC – by 90%. Meanwhile, the change of trophic status of the reservoir from oligotrophic to eutrophic leads to 740% increase in the gross production of zoobenthos. Although this forecast does not take into consideration the inevitable succession of cryophile species by more thermophile ones, however, it is evident that the most effective measure for mitigation and adaptation of possible negative consequences of climate change on the ecosystem of Lake Sevan will be the unconditional restriction of any type of invasion of organic matter of allochthonous origin into the lake.

4. Conclusions

- A positive correlation revealed for the Lake Sevan zoobenthos biomass with VPPL fluctuations with the lag period of biomass response 2-4 years; for oligochatea – 7-9 years, for chirinomids – 2 years, for molluscs – 5 years. For amphipods biomass the correlation with the VPPL was negative with a 3-4 year lag period.
- The lag period for the zoobenthos biomass response to the VPPL in littoral is from 1 to 2 years, in sublittoral – 2 years, and in the profundal – from 7 to 9 years.
- Quantitative changes of the zoobenthos biomass at a certain stage will be accompanied by qualitative changes in the zoobenthos trophic structure.
- An increase of the trophic level of Lake Sevan from oligotrophic to eutrophic will increase the gross production of zoobenthos by 740%.
- Temperature increases of 0.5, 2, and 4ºC will lead to estimated increases in zoobenthos production rate by 9%, 45%, and 90%, respectively.
- The most effective measure for mitigation and adaptation of possible negative consequences of climate change on the Lake Sevan ecosystem will be the complete restriction of any type of allochthonous organic matter of into the lake.

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