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Biotic interactions, energy pathways and trigger factors of ecosystem dynamics in shallow saline lakes

Key words: saline lakes, primary production, secondary production, zoo-plankton, zoobenthos, energy pathways, regime shift

Summary

Environmental variables, food-web dynamics and energy pathways were investigated in ecosystems of six shallow lakes of the Crimea with salinity ranging from 24 to 340 ‰. There were considerable inter- and intra-annual fluctuations in the abiotic characteristics of the lakes. All the lakes had a very high concentration of total phosphorus in the water (up to 5.6 gP m⁻³) due to a great influence of the watershed on the lakes. A high level of primary production (up to 14.9 gC m⁻² d⁻¹) was found in the most of the lakes. The lowest primary production was found in the most saline lake with a dense population of the filtrator, *Artemia urmiana*. Grazing benthic energy pathways were dominant at salinities between 24 and 58 ‰. Greater levels of salinity led to a gradual reduction of benthic and increase of planktonic energy pathways. A fast shift from turbid to clear-water regime was observed in one of the lakes, caused by annual variations in weather conditions.

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1. Introduction

Hypersaline lakes and lagoons are widespread in arid and semi-arid climatic zones (Williams 1998). Due to energy flow and carbon cycling, these aquatic systems play an important role in global biochemical processes and are known for high rates of organic matter and calcium carbonate burial. Nevertheless, there are only a few studies of food web structure and functioning of these ecosystems (Vareschi 1987, Alcorlo *et al.* 2001). One of the reasons for the shortage of such information is a great seasonal and interannual variability of environment in saline lakes (Strachlow *et al.* 2005). Pronounced changes in water and salinity levels may act as catastrophic disturbance events causing regime shifts in the lake ecosystems (Williams 2002, Strachlow *et al.* 2005). The most traditional and successful direction of research dealing with biota of salt lakes is investigations of the influence of salinity upon the species composition and abundance of planktonic and benthic communities (*e.g.* Timms 1981, Pinder *et al.* 2005). They have shown that diversity of planktonic and benthic communities decrease with increasing salinity. That may influence the ecosystem function (Golubkov *et al.* 2007). Primary (natural) and secondary (anthropogenic) salinization may be considered as a major threat to the lake ecosystem integrity and amount of water resources in semi-arid and arid regions of the world (Williams 2002, Strachlow *et al.* 2005).

The conceptual model, which has been successfully applied recently to examine impacts of salinization and eutrophication on salt lakes and wetland by Australian scientists (Davis *et al.* 2003, Strachlow *et al.* 2005, Timms 2005, Sim *et al.* 2006a, 2006b, Segal *et al.* 2006), can be considered as an alternative to the above presented influence of salinization on lake ecosystem. They suggested that a moderate salinity results in the dominance of a small number of salt-tolerant species of macrophytes and with the increasing salinity the system shifts to a benthic microbial community composed mostly of cyanobacteria and halophilic bacteria. This model was successfully applied to describe alternative states in Australian wetlands.

The present study was designed to provide more information about the changes in food web structure and energy pathways in hypersaline lakes and to designate the factors responsible for dynamics of their ecosystems. We suggested that an increase in salinity is followed by a decrease of biodiversity causing a shortening of food webs and that salinity fluctuations may cause shifts in ecosystem water regime along the salinity gradient.

2. Materials and methods

Energy fluxes and food web dynamics were investigated in the ecosystems of six saline lakes: Kojashskoe, Tobechnikskoe, Kirkojashskoe, Shimakhanskoe, Marfovskoe and Bakalskoe in spring, late summer and winter of 2004 and 2005. The lakes are situated in the eastern and western parts of the Crimea. Their general morphometric characteristics are given in Table 1. Narrow spits separate three lagoon-derived lakes (Kojashskoe, Tobechnikskoe and Bakalskoe) from the Black Sea. Three other lakes have a continental origin and are situated in land depressions several kilometers away from the sea coast. All the lakes are shallow with a maximum depth equal or smaller than 1.55 m (Tab. 1). They have no inflows or outlets and are surrounded by steppe grassland. The water inflows into the lakes are the result of atmospheric precipitation, filtration from subsoil waters and from the sea (in the case of lagoon-derived lakes). There are a large village and a cattle-breeding farm on the shore of Marfovskoe Lake.

Temperature, salinity, Secchi depth (*Sec*) and concentration of total phosphorus in the water were determined at 2–3 sampling stations in each lake. Water samples were hydrolysed with H_2SO_4 and the molybdate “blue” method (Golterman 1969) was used to evaluate the total phosphorus concentration. Suspended particulate matter (*PM*) content in the water was determined after a filtration through Sinpore filters (0.85 μm) using gravimetric technique. Before the weighting, the filters were washed in distilled water. Each filter was neatly put upward on the Petri dish with distilled water, and salt from the filter passed to the distilled water. After that the filters

were dried and weighed. The concentration of particulate matter was calculated from the difference between the weight of filters before and after the filtration. Particulate organic matter (*POM*) content was determined after a filtration through the Whatman GF/F filters (0.7 μm) with a subsequent dichromate acid oxidation (Golterman 1969). Chlorophyll *a* concentrations were estimated by filtering 100 ml of water samples through 0.85 μm Sinpor filters, followed by a 90 % acetone extraction and spectrophotometric determination at two wavelengths (Strickland and Parsons 1968). Salinity of the water was determined by means of ATAGO S/MILL salinity refractometer.

Table 1. Limnological features of six hypersaline lakes in the Crimea in 2004–2005

Lake Origin	Coordinates	Area km ²	Maximum depth m
Kojashskoe Lagoon derived	45°02'50" N, 36°11'10" E	7.00	0.50
Tobechikskoe Lagoon derived	45°10'35" N, 36°22'10" E	20.00	1.45
Bakalskoe Lagoon derived	45°44'45" N, 33°10'30" E	8.00	0.70
Kirkojashskoe Continental	45°04'40" N, 36°13'00" E	1.25	1.55
Shimakhanskoe Continental	45°06'00" N, 36°15'20" E	2.64	1.25
Marfovskoe Continental	45°12'00" N, 36°06'50" E	2.65	0.35

Rates of plankton primary production at the water surface (A_{opt}) and the decomposition of organic matter were measured by means of oxygen method of light and dark bottles (Golterman 1975): bottles (100 ml volume) were filled with water from the sampling stations and placed at a depth of 5–10 cm for 2–6 hours in the littoral area of the lakes in the middle of the day (from 11.00 a.m.). The measurements were conducted in three replicates. The daily rate of gross primary production (A , J m^{-2}) was calculated according to Håkanson and Boulion (2002): $A = A_{opt} \cdot \text{Sec}$. To calculate A for the diurnal interval,

A was multiplied by T/t , where T is duration of daylight interval and t is the exposition time of the bottles. The Winkler method was used to determine oxygen content in the control bottles at the beginning of the experiment and in the light and dark bottles at the end of the experiment. The values of primary production were recalculated to energy units using a factor $k = 9.94 \text{ J mgO}_2^{-1}$ (Håkanson and Boulion 2002).

For algae biomass estimates, *Cladophora* spp. was collected at 6 stations in Tobeichiskoe Lake during the intensive filamentous algae blooms in August 2005 by means of a plastic tube with 25 cm diameter. Samples were then dried and weighed. Rates of *Cladophora* primary production were determined by the oxygen method in 100 ml dark and light bottles. After the measurements, filamentous algae mass was dried and weighed. The primary production of *Cladophora* algae (A , kJ m^{-2}) was calculated as $A = B C_{wcl}$, where C_{wcl} ($\text{kJ (gDWm}^{-2})^{-1}$) is a specific rate of their primary production and B (gDWm^{-2}) is their biomass.

To collect crustacean zooplankton, 60 l of water were filtered through a 110 μm plankton net. Rotifer samples were collected directly in 500 ml bottles. Zoobenthos was sampled using a Petersen grab (1/40 m^2) or a core sampler (1/250 m^2) and sieved in the field using a 0.25 mm mesh. Each sampling had 3 replicates at each station. Samples of zooplankton and zoobenthos were preserved in 4% formalin before species identification and counts. Weight W of zooplankton was calculated by means of equations W (DW, mg) = $0.00103 L^{2.66}$ for *Artemia* spp. (Khmeleva 1968), W (WW, mg) = $0.036 L^{2.74}$ for *Arctodiaptomus salinus* (Daday) (Salazkin *et al.* 1984), W (WW, mg) = $0.074 L^{3.05}$ for *Moina mongolica* Daday (Balushkina and Winberg 1979), W (WW, mg) = $0.12 L^{3.00}$ for Rotifera (Ruttner-Kolisko 1977), where L is length (mm) of animals. According to Khmeleva (1968), dry weight of *Artemia* averages approximately 11% of wet weight.

To calculate the metabolic losses of energy in the process of respiration (D , $\text{kJ m}^{-2} \text{ d}^{-1}$) of the zooplankton and zoobenthos the following equations describing relationships between the respiration rate R_{20}

($\text{mlO}_2 \text{ h}^{-1}$) and wet body weight of animals W (g) at the temperature of 20°C were used:

- Artemia* spp.: $R_{20} = 0.082 W^{0.702}$ (Suschenya 1972),
Arctodiaptomus salinus: $R_{20} = 0.200 W^{0.759}$ (Suschenya 1972),
Moina mongolica: $R_{20} = 0.143 W^{0.803}$ (Suschenya 1972),
 Rotifera: $R_{20} = 0.106 W^{0.796}$ (Galkovskaya 1980),
 Polychaeta: $R_{20} = 0.130 W^{0.810}$ (Kamliuk 1974),
 Amphipoda: $R_{20} = 0.142 W^{0.790}$ (Suschenya 1972),
 Chironomidae: $R_{20} = 0.088 W^{0.750}$ (Balushkina 1987),
 Others: $R_{20} = 0.143 W^{0.750}$ (Hemmingsen 1960).

The mean body weight of different groups of animals found in the samples was used for calculating R_{20} . Van't Goff's coefficient ($Q_{10} = 2.25$) was used to adjust R_{20} to the actual water temperature (Winberg 1983): $R = R_{20} 2.25^{(T-20)/10}$. The respiratory losses of energy by animal communities (zooplankton or zoobenthos) was calculated as $D = 24RkN$, where N is the animal numbers, and k is the oxycalorific coefficient equal to $3.4 \text{ kcal mlO}_2^{-1}$ or $14.2 \text{ J mlO}_2^{-1}$ (Winberg and Duncan 1971).

Daily production (P , $\text{kJ m}^{-2} \text{ d}^{-1}$) of zooplankton and Polychaeta was calculated by means of production efficiency coefficient K_2 : $P = DK_2 / (1 - K_2)$ (Winberg and Duncan 1971). The value of K_2 was accepted as 0.4 for Rotifera and Polychaeta, 0.3 for Cladocera (Salazkin *et al.* 1984) and 0.6 for *Artemia* spp. (Khmeleva 1968).

Daily production of chironomids was calculated according to the equation of Balushkina and Petrova (1989):

$$P = 0.08W^{1.07}NK,$$

where W is the mean body weight of chironomid larvae (WW, g), N is their abundance (ind. m^{-2}) and K is the calorific value of biomass unit (kJ gWW^{-1}).

Daily production of other benthic animals was calculated as $P = C_w B K$, where C_w is the specific daily rate of production ($\text{kJ m}^{-2} \text{ d}^{-1} (\text{gWW m}^{-2})^{-1}$), B is their biomass (gWW m^{-2}) and K as above is the calorific value of biomass unit (kJ gWW^{-1}). Specific rate of production was calculated as:

$$\text{Amphipoda: } C_w = -0.044 + 0.239W^{-0.36} \text{ (Panov 1988),}$$

Coleoptera: $C_w = 0.0049 e^{0.092T}$ (Golubkov 2000), where T is water temperature.

For Oligochaeta and Hirudinea C_w was accepted as 0.03 (Finogenova and Lobasheva 1987), for Gastropoda – 0.01 and for Bivalvia – 0.025. Rates of food consumption (C , kJ m^{-2}) were calculated as $C=(P+R)/U$, where U is efficiency coefficient of food assimilation (accepted as 0.8 for predators and 0.6 non-predators). Calorific value of a biomass unit was assumed to be 11 kJ gWW^{-1} for Arthropoda, 4.7 kJ gWW^{-1} for Bivalvia with shell and 7.7 kJ gWW^{-1} for Gastropoda with shell (Golubkov 2000).

NAO (North Atlantic Oscillation) index, also number of windy days (with wind speed greater than 5 m sec^{-1}) and air temperature in the eastern Crimea were used to evaluate the role of the weather conditions in ecosystem regime shift in Tobeichiskoe Lake. Average NAO index values for spring and summer months of 2004 and 2005 were calculated from <http://www.cpc.noaa.gov/products/precip/CWlink/pna/norm.nao.monthly.b5001.current.ascii.Tab>. Data on wind speed and air temperature were received from <http://www.gismeteo.ru>.

3. Results

3.1. Lake abiotic characteristics and primary production

All the lakes had very high concentrations of total phosphorus P_{tot} in the water (Tab. 2). The highest concentrations of P_{tot} were observed in Marfovskoe Lake due to a run off from the large village and cattle-breeding farm. Only 5 cm Secchi depth was measured in this lake in summer 2005. The other lakes also had very high average concentrations of P_{tot} in the water. On the other hand, a decrease in P_{tot} was observed in Bakalskoe Lake in 2005, as compared to 2004, probably as a result of the partial rupture of its spit and the input of marine water into the lake. The concentration of suspended particulate matter PM in the most saline Kojashskoe Lake reached almost 1 kg m^{-3} in April and August 2005, and as a result the Secchi depth

Table 2. Concentrations of chlorophyll *a* (*Chl a*), total phosphorus (P_{tot}), suspended particulate matter (*PM*), suspended organic particulate matter (*POM*) and suspended mineral particulate matter (*MM*), and Secchi depth (*Sec*) in the water of saline lakes. SE is indicated in parentheses.

Chl <i>a</i> mg m ⁻³	Period	Kojashskoe		Tobechikskoe		Bakalskoe		Kirkojashskoe		Shimakhanskoe		Marfovskoe	
		Lake	Lake	Lake	Lake	Lake	Lake	Lake	Lake	Lake	Lake	Lake	Lake
	Aug 2004	0.21 (0.01)	4.59 (0.21)	2.21 (0.17)	5.68 (1.18)	7.78 (0.48)	16 (2)						
	Apr 2005	8.04 (3.20)	2.00 (0.17)	0.80 (0.11)	9.72 (0.37)	39.50 (0.62)	259 (12)						
	Aug 2005	3.79 (0.21)	0.71 (0.14)	2.64 (0.31)	254.99 (84.18)	7.00 (2.09)	301 (25)						
	Dec 2005	49.54 (3.98)	2.87 (0.05)	-	43.72 (3.37)	36.66 (0.91)	703 (29)						
P_{tot} mg m ⁻³	Aug 2004	303 (33)	240 (30)	175 (15)	238 (14)	685 (10)	1090 (123)						
	Apr 2005	705 (108)	190 (10)	130 (50)	460 (49)	825 (3)	2200 (235)						
	Aug 2005	293 (41)	80 (0)	25 (0)	510 (77)	510 (42)	5625 (576)						
	Dec 2005	290 (28)	33 (5)	-	200 (35)	190 (14)	3100 (212)						

PM g m ⁻³	Aug 2004	34 (1)	59 (19)	88 (3.5)	25 (1)	33 (1)	1117 (103)
	Apr 2005	891 (1)	39 (2)	19 (1)	173 (7)	195 (7)	1327 (16)
	Augt 2005	796 (114)	31 (2)	13 (1)	307 (14)	138 (52)	7327 (413)
	Dec 2005	79 (7)	5 (1)	-	30 (1)	14 (1)	135 (4)
POM g m ⁻³	Aug 2004	1.72 (0.44)	5.35 (0.40)	12.64 (0.19)	24.93 (1.18)	6.23 (0.20)	115 (8)
	Apr 2005	19.72 (3.20)	4.10 (0.56)	1.71 (0.04)	36.23 (2.27)	33.01 (3.58)	115 (2)
	Aug 2005	7.48 (1.49)	1.51 (0.00)	0.69 (0.07)	24.35 (1.71)	7.84 (0.86)	332 (11)
	Dec 2005	9.80 (1.41)	1.35 (0.32)	-	8.10 (0.42)	4.35 (0.03)	82(7)
Sec m	Aug 2004	0.48 (0.02)	0.48 (0.02)	0.40 (0.01)	0.60 (0.03)	0.39 (0.01)	-
	Apr 2005	0.10 (0.01)	0.58 (0.02)	0.07 (0.04)	0.33 (0.02)	0.28 (0.02)	0.14 (0.01)
	Aug 2005	0.22 (0.06)	1.10 (0.04)	0.58 (0.02)	0.23 (0.02)	0.55 (0.01)	0.05 (0.01)
	Dec 2005	0.20 (0.03)	0.88 (0.05)	-	0.50 (0.03)	0.60 (0.03)	0.13 (0.02)

Table 3. Rates of primary production (*A*) and decomposition (*M*) of organic matter by plankton in the saline lakes. SE is indicated in parentheses.

Lake	Primary production kJ m ⁻² day ⁻¹				Decomposition kJ m ⁻² day ⁻¹				<i>A/M</i>			
	August 2004	April 2005	August 2005	Dec. 2005	August 2004	April 2005	August 2005	Dec. 2005	August 2004	April 2005	August 2005	Dec. 2005
Kirkojashskoe	102(6)	112(1)	624(1)	48(5)	86(5)	268(0.01)	1470(256)	36(3)	1.2	0.42	0.45	1.34
Shimakhanskoe	192(17)	208(15)	251(9)	44(2)	158(43)	607(118)	291(4)	40(5)	1.36	0.36	0.86	1.13
Marfovskoe	-	194(20)	-	74(24)	-	405(87)	-	116(43)	-	0.5	-	0.65
Kojashskoe	5(1)	9(1)	8(1)	11(1)	7(2)	34(5)	13(1)	12(1)	0.61	0.27	0.65	0.91
Tobechikskoe	133(6)	35(5)	28(1)	61(8)	69(8)	66(6)	31(3)	62(16)	1.95	0.53	0.94	1.04
Bakalskoe	74(5)	10(1)	28(1)	-	81(18)	6(1)	14(1)	-	2.08	1.60	2.00	-

was only about 0.2 m at that time (Tab. 2). Particulate organic matter *POM* was low (1–3% of *PM*). Therefore, most of the *PM* was mineral.

There were considerable inter- and intra-annual fluctuations in the water salinity of the lakes (Tab. 2). An especially high salinity level was observed in the hot and droughty summer of 2005. There was no correlation between the concentrations of P_{tot} and water salinity, but plankton primary production was positively related to total phosphorus ($R^2 = 0.85$, $n = 21$). The highest values of primary production were recorded in the continental lakes (Tab. 3). Lagoon-derived lakes had lower plankton primary production and decomposition of organic matter. Most of the lakes had high levels of primary production in the winter time (Tab. 3).

The lowest value of primary production was recorded in the most saline Kojashskoe Lake in August 2004. At the same time, a very high abundance (7230 ind. m^{-3}) and biomass (17.87 gWW m^{-3}) of the grazer *Artemia urmiana* Günther were observed in this lake. The highest rate of primary production was documented in Kojashskoe Lake in the winter time, when the biomass of zooplankton was very low (Tab. 4). There was some increase in the ratio between the rates of primary production and decomposition of organic matter (*A/M*) in all the lakes during the annual cycle of 2005 (Tab. 3).

3.2. Ecosystem regime shift

In Tobeichiskoe Lake the highest rate of phytoplankton primary production was observed in August 2004. In 2005 it was much lower (Tab. 3), but very high biomass (392 ± 21 gDW m^{-2}) and primary production (1965 kJ $m^{-2} d^{-1}$) of benthic *Cladophora vadorum* Kutz. and *Cl. albida* Kutz. were recorded in the lake at that time. There was also a considerable decrease in the concentration of chlorophyll *a*, suspended *PM* and suspended *POM* and an increase of Secchi depth in August 2005, as compared with August 2004 (Tab. 2).

Changes in the activities of primary producers in Tobeichiskoe Lake were related to the differences in the weather conditions. Average NAO index was positive (0.35) in 2004 and negative in 2005 (–0.60).

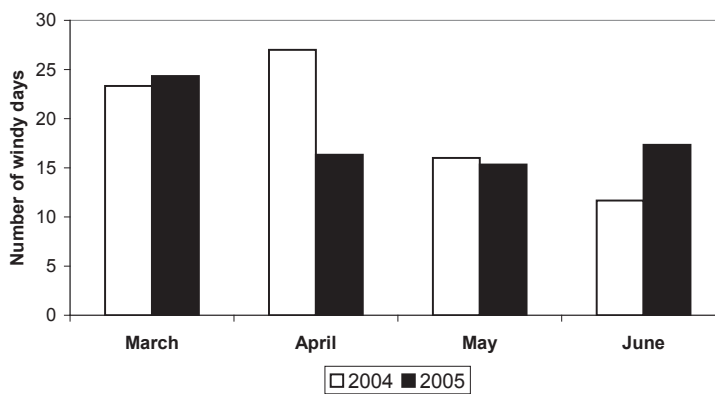
Table 4. Salinity (S), abundance and biomass of zoobenthos (N_b, B_b) and zooplankton (N_{zp}, B_{zp}) in the saline lakes.

Lake	Period	S ‰	N_b ind. 10^3 m^{-2}	B_b $g\ m^{-2}$	N_{zp} ind. 10^3 m^{-2}	B_{zp} $g\ m^{-2}$	B_b/B_{zp}
Bakalskoe	Aug 2004	29	13	27.36	11.5	0.43	63.63
Bakalskoe	Apr 2005	25	4	45.87	0.6	0.02	2293.60
Bakalskoe	Aug 2005	38	16	173.68	0.16	0.0002	868400.00
Kirkojashskoe	Aug 2004	24	12	35.16	400.5	8.75	4.02
Kirkojashskoe	Apr 2005	30	43	75.39	491.1	19.23	3.92
Kirkojashskoe	Aug 2005	35	46	89.99	1389.8	22.62	3.98
Kirkojashskoe	Dec 2005	38	30	103.65	121.7	1.22	84.96
Shimakhanskoe	Aug 2004	30	12	42.88	1076.9	8.16	5.25
Shimakhanskoe	Apr 2005	37	9	55.23	448.2	16.28	3.39
Shimakhanskoe	Aug 2005	55	9	3.34	1314.9	35.75	0.09
Shimakhanskoe	Dec 2005	61	0.2	0.08	49.74	0.092	0.87
Tobechikskoe	Aug 2004	57	6	32.50	165.2	7.55	4.30
Tobechikskoe	Apr 2005	58	1	7.33	9.4	0.38	19.29
Tobechikskoe	Aug 2005	100	15	16.94	8.4	0.53	31.96
Tobechikskoe	Dec 2005	86	0.04	0.21	0.22	0.092	2.28
Marfovskoe	Apr 2005	97	0.3	0.53	0.1	1.15	0.46
Marfovskoe	Aug 2005	260	0	0	0.0	0.00	-
Marfovskoe	Dec 2005	131	0	0	0	0	-
Kojashskoe	Aug 2004	275	0	0	3.3	7.07	0
Kojashskoe	Apr 2005	184	0	0	12.0	7.19	0
Kojashskoe	Aug 2005	340	0	0	1.6	1.82	0
Kojashskoe	Dec 2005	235	0	0	0.04	0.0002	0

There were much more windy days in April 2004, as compared with April 2005, during the period of intensive algal growth (Fig. 1A). Another interannual difference was a higher air temperature in 2005, as compared with 2004 (Fig. 1B). As a result, the salinity in Tobichikskoe Lake increased from 58‰ in August 2004 to 100‰ in August 2005. This led to the elimination of omnivores (*Gammarus aequicauda*) and an establishment of *Artemia* population, because

predation of *G. aequicauda* was probably the main factor impeding the development of the large planktonic grazer *A. parthenogenetica* in the lake. The increase of *Artemia* population resulted in an increase of grazing pressure upon phytoplankton and clearance of water in the lake. Strong negative relationships between the biomass of *Artemia* spp. and phytoplankton primary production were recorded both in Tobichikskoe and Kojashskoe lakes (Fig. 2).

A)



B)

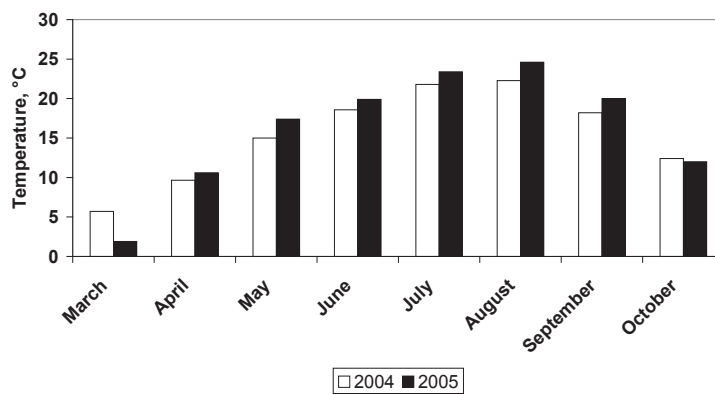


Fig. 1. Number of windy days (with wind speed greater than 5 m/s) in a period of intensive growth of benthic filamentous algae (A) and average air temperature (B) in the eastern Crimea in 2004 and 2005.

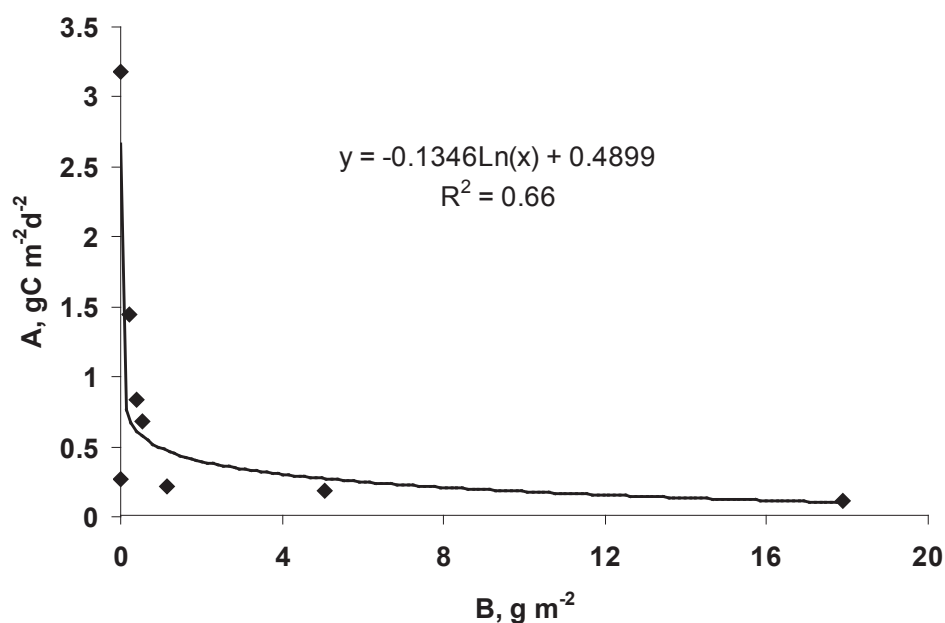


Fig. 2. Relationship between primary production of plankton (A) and biomass of *Artemia* spp. (B) in Tobeichiskoe and Kojashskoe lakes.

3.3. Animal communities

The brine shrimps *Artemia* spp. inhabited the lakes with a salinity level of >60‰. *A. urmiana* was the only zooplankton species in the most saline Kojashskoe Lake. *A. parthenogenetica* (Barigozzi) was found in the highly saline Marfovskoe Lake in August 2004 and April 2005 and in Tobeichiskoe Lake after its salinity increased to 86 – 100 ‰. The other lakes had no populations of brine shrimp during the whole study period, though its cysts were found in zooplankton samples from all the lakes. Three species of mezozooplankton, the rotifer *Brachionus plicatilis* Müller and the crustaceans *Moina mongolica* and *Arctodiaptomus salinus*, contributed greatly to zooplankton biomass in the three less saline lakes and also in Tobeichiskoe Lake, when its salinity was lower than 60‰. In addition, *Daphnia ulomskyi* Behning was found in small amounts in Kirkojashskoe Lake and the copepod *Acartia tonsa* Dana in Bakalskoe Lake. The latter (marine)

species probably penetrated the lake from the Black Sea after a partial destruction of its spit in 2004–2005. The biomass of zooplankton in this group of lakes was low in the wintertime in December 2005 (Tab. 4). There was a dense population of planktonic *A. urmiana* in the most saline Kojashskoe Lake. The ration of zooplankton in August 2004 was higher than phytoplankton primary production (Tab. 5). On the other hand, there was almost no adult individuals of zooplankton in the lake in wintertime (Tab. 4), because most of the *Artemia* population switched to sexual reproduction and produced winter eggs. Active stages of *Artemia* spp. did not occur in the lakes under salinity less than 80‰, but resting eggs were found in all the lakes.

Larvae of *Baeotendipes tauricus* Tshernovskij (Chironomidae, Diptera) were widely distributed and dominant in most lakes with salinity up to 100‰. The most diverse fauna of bottom animals was found in Bakalskoe Lake. In addition to *G. aequicauda* and *B. tauricus*, which dominated in August 2004, the typical marine species *Hediste diversicola* (Müller), *Polydora ciliata* (Johnston) (Polychaeta), Corophiidae gen. sp. (Amphipoda) and *Idotea baltica* (Isopoda) were also common. These species were dominant in the bottom community in August 2005 when zoobenthic biomass reached very high values (Tab. 4). In contrast to zooplankton, there was no macrobenthos in the most saline Kojashskoe Lake and in Marfovskoe Lake at salinity greater than 97‰ (Tab. 4).

The highest zoobenthic biomass levels (Tab. 4), and a domination of benthic over planktonic grazing energy pathways (Tab. 5) were observed for the salinity range of 25 – 60‰. The production of benthic non-predators in Kirkojashskoe Lake at the salinity of 38 ‰ reached $33 \text{ kJ m}^{-2} \text{ d}^{-1}$ and their ration – $144 \text{ kJ m}^{-2} \text{ d}^{-1}$. A further increase in salinity led to a reduction of benthic animal communities and an increase of importance of planktonic energy pathways. In the most saline Kojashskoe Lake, where no macrozoobenthos was found, production of planktonic animals reached $4.9 \text{ kJ m}^{-2} \text{ d}^{-1}$ and their ration $12.03 \text{ kJ m}^{-2} \text{ d}^{-1}$ (Tab. 5).

There were no zooplanktonic predators in the lakes. Predatory fishes present in Bakalskoe Lake (jellyfish *Rhizostoma* sp. and

Table 5. Salinity (S), primary production (A), production and ration of: zooplankton (P_z and C_z), non-predatory (P_{bpr} and C_{bpr}) and predatory (P_{bpr} and C_{bpr}) macrozoobenthos in the ecosystems of the saline lakes

Lake	Period	S ‰	A $\text{J m}^{-2} \text{d}^{-1}$	P_z $\text{J m}^{-2} \text{d}^{-1}$	C_z $\text{J m}^{-2} \text{d}^{-1}$	P_z/A %	P_{bpr} $\text{J m}^{-2} \text{d}^{-1}$	C_{bpr} $\text{J m}^{-2} \text{d}^{-1}$	P_{bpr}/A %	P_{bpr} $\text{J m}^{-2} \text{d}^{-1}$	C_{bpr} $\text{J m}^{-2} \text{d}^{-1}$	P_{bpr}/P_{bpr} %
Bakalskoe	Aug 2004	29	74404	293	1714	0.4	10074	43848	13.6	961	1547	9.5
Bakalskoe	Apr 2005	25	9614	42	84	0.4	3344	15633	34.9	878	2341	26.3
Bakalskoe	Aug 2005	38	28006	0.1	0.4	0.0003	12665	61028	45.3	418	2147	3.3
Kirkojashskoe	Aug 2004	24	101992	4264	21820	4.2	13752	55343	13.5	209	752	1.5
Kirkojashskoe	Apr 2005	30	111606	7942	44141	7.1	14003	62491	12.5	0	0	0
Kirkojashskoe	Aug 2005	35	623656	10492	51581	1.7	33147	144085	5.3	293	1463	0.9
Kirkojashskoe	Dec 2005	38	47652	138	677	0.3	8109	31308	17.04	4	59	0.05
Shimakhanskoe	Aug 2004	30	66880	4556	19897	6.8	13501	51790	20.2	42	125	0
Shimakhanskoe	Apr 2005	37	208164	6813	37841	3.3	12916	44977	6.2	0	0	0
Shimakhanskoe	Aug 2005	55	251218	15382	79587	6.1	1463	3093	0.58	1045	1839	71.4

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Shimakhanskoe	Dec 2005	61	43890	13	59	0.03	5	28	0.01	0	0	0	0
Tobechikskoe	Aug 2004	57	132924	3762	20775	2.8	11161	41716	8.4	1003	3511	9.0	
Tobechikskoe	Apr 2005	58	35112	460	1296	1.3	1797	6312	5.1	0	0	0	
Tobechikskoe	Aug 2005	100	28424	502	1212	1.8	5183	26000	18.24	0	0	0	
Tobechikskoe	Dec 2005	86	60610	13	29	0.02	7	38	0.01	0	0	0	
Marfovskoe	Apr 2005	97	194370	6	17	0.003	167	669	0.08	0	0	0	
Marfovskoe	Aug 2005	260	27170	0	0	0	0	0	0	0	0	0	
Marfovskoe	Dec 2005	131	73986	0	0	0	0	0	0	0	0	0	
Kojashskoe	Aug 2004	275	4598	3135	7482	68.2	0	0	0	0	0	0	
Kojashskoe	Apr 2005	184	9196	4932	12038	53.6	0	0	0	0	0	0	
Kojashskoe	Aug 2005	340	7942	836	2048	10.5	0	0	0	0	0	0	
Kojashskoe	Dec 2005	235	11286	0.3	1	0.002	0	0	0	0	0	0	

Mnemiopsis leidyi Agassiz), penetrated there from the Black Sea in 2004. Due to their large size (5–20 cm), they were not collected in our zooplankton samples and were not included in energy flux calculations. The predatory beetle *Hygrotus enneagrammus* (Ahrens) typical for saline environments, was found in the moderately saline Kirkojashskoe and Shimakhanskoe lakes. Omnivores *Gammarus aequicauda* Martynov (Amphipoda) occurred in Tobechikskoe and Bakalskoe lakes in August 2004. This species was not found in Tobechikskoe Lake in August 2005, when the salinity increased up to 100‰. Thus, benthic predators occurred in the lakes at salinity no more than 57‰ (Table 5).

3.4. Effectiveness of the energy transfer in the lake ecosystems

The highest effectiveness of energy transfer from the primary producers (trophic level I) to the consumers of the first order was recorded in the most saline Kojashskoe Lake (Tab. 6).

Table 6. Average rate of primary production (A), production of non-predatory zooplankton (P_z), non-predatory (P_{bnpr}) and predatory (P_{bpr}) zoobenthos and effectiveness of transformation of energy to the second ($II = (P_z + P_{bnpr})/A$) and third ($III = P_{bpr}/P_{bnpr}$) trophic levels in the ecosystems of the saline lakes with different average salinity (S)

Lake	S ‰	A $J\ m^{-2}day^{-1}$	P_z $J\ m^{-2}day^{-1}$	P_{bnpr} $J\ m^{-2}day^{-1}$	II %	P_{bpr} $J\ m^{-2}day^{-1}$	III %
Bakalskoe	28	37327	125	8694	23.6	752	8.5
Kirkojashskoe	33	221247	5727	17263	10.4	125	0.2
Shimakhanskoe	47	142538	6688	6981	9.6	293	0.9
Tobechikskoe	79	64288	1170	4556	8.9	251	4.4
Marfovskoe	186	98253	2	42	0.1	0	0.0
Kojashskoe	312	8276	2215	0	27.0	0	0.0

The trophic structure there was very simple: the only macroinvertebrate consumer was *A. urmiana*. The ratios of its production and ration to primary production of plankton were on average about 27

and 65%, respectively. The lowest food web transfer effectiveness was recorded in Marfovskoe Lake, which was affected by severe eutrophication and drought in summer time. The extremely high concentration of organic matter led to anoxic conditions at night-time and to the elimination of planktonic and benthic animals from the lake. In all the lakes, transfer efficiency of energy from trophic level II to trophic level III (i.e. ratio between the production values of predatory vs. non-predatory zoobenthos) was much lower than transfer efficiency from trophic level I to trophic level II (Tab. 6). On average, they constituted 2.3 and 13.3%, respectively.

Ecosystems of Kirkojashskoe and Shimakhanskoe lakes had a very low efficiency of the energy transfer to trophic level III. Ecosystems of Marfovskoe and Kojashskoe lakes had no consumers II (trophic level III) at all (Tab. 6). The best-developed trophic level III was recorded in the community of Bakalskoe Lake with the lowest level of water salinity (Tab. 6). In fact, the food chain in this lake had four trophic levels, since the fishes were also present. The energy transfer efficiency to the trophic level III was twice as lower in Tobechnikskoe Lake than in Bakalskoe Lake. Hypereutrophic Kirkojashskoe and Shimakhanskoe lakes had a very low transfer efficiency to the trophic level III. The highly eutrophic and saline Marfovskoe Lake and extremely saline Kojashskoe Lake had no secondary consumers (macroinvertebrate predators) at all (Tab. 6).

4. Discussion

4.1. Primary production

All the lakes studied had a high level of primary production even in the wintertime. This resulted from lower water freezing points at high salinities and the absence of ice cover even at low air temperature, which is a characteristic feature of saline lakes in the temperate climate.

Apart from P_{tot} concentration, which corresponded to eutrophic or, in some cases, to hypereutrophic conditions, according to the

classification of Håkanson and Boulion (2001), concentration of *Chl a* and the level of primary production *A* were not very high and often corresponded to the levels in mesotrophic inland waters. This means that certain factors inhibited algae growth in these potentially very productive systems. Such a factor might be an increase of saline water turbidity due to its higher density and lower rate of sedimentation and higher level of resuspension of *PM*, as compared to fresh water, because the sinking velocity decrease and vertical settling flux of *PM* increase if the difference between the fluid density and density of the particles becomes less (Bloesch 2003). A high concentration of suspended *PM* reduces light penetration into the lake water and may constrain the primary production of phytoplankton (Hamilton and Mitchell 1996). Thus, the concentration of *PM* reached almost 1 kg m^{-3} in April and August 2005 in the most saline Kojashskoe Lake and the Secchi depth was only about 0.2 m at that time. Concentration of *POM* was low (1–3 % of *PM*), hence, most of the *PM* was mineral. A low water transparency induced by a resuspension of mineral particles, may be one of the reasons for rather a low *Chl a* or *A* values in highly saline lakes, despite the high P_{tot} concentrations.

There were strong negative relationships between the levels of biomass of filtrators (*Artemia* spp.) and of phytoplankton primary production in the lakes. Thus, a high pressure of herbivore zooplankton may be another factor responsible for relatively low levels of *Chl a* in the lakes. The ration of zooplankton (which consisted only of *A. urmiana*) in the most saline Kojashskoe Lake was higher than phytoplankton primary production in summer 2004 and spring 2005. On the other hand, the biomass of zooplankton in this lake was very low in winter, because most of the *Artemia* population switched to sexual reproduction and produced winter eggs. As a result, concentration of *Chl a* was much higher in winter than in spring and summer. Therefore, the organic matter produced during winter was stored as lake detritus and could be used by brine shrimp in spring and summer. The content of *POM* was the highest in winter and especially high in spring after the period of low biomass of *A. urmiana*. It should also be mentioned that Kojashskoe Lake is the only place in Europe

where this species of *Artemia* was recorded (Abatzopoulos *et al.* 2009). Additionally nitrogen content can also be critical to algal growth in saline lakes (*e.g.* Thornton 1986).

4.2. Ecosystem regime shifts and climatic fluctuations

The concept of two ecosystem states, a clear-water community (dominated by macrophytes) and a turbid-water community (dominated by phytoplankton), has been developed for shallow freshwater lakes undergoing eutrophication (*e.g.* Scheffer 1990, 1998). According to this concept at some intermediate nutrient concentrations both states are possible. Depending on an external forcing ecosystem shift from one state to another is possible without changes in nutrient loading. Davis *et al.* (2003) suggested that moderate salinity results in the dominance of a small number of salt-tolerant macrophyte species (*e.g.* *Ruppia*) and with increasing salinity the system shifts to benthic microbial community composed mostly of cyanobacteria and halophilic bacteria. Our investigation has shown that ecological regime of Crimean shallow saline lakes is also vulnerable to climatic fluctuation. A sharp ecosystem shift from turbid to clear water state was observed in Tobeckhiskoe Lake in 2005. A considerable decrease of phytoplankton primary production, *PM*, *POM* and *Ch a* concentrations and increase of Secchi depth and biomass of benthic filamentous macroalgae were observed in this lake in August 2005, as compared with August 2004.

The changes in the community of primary producers in Tobeckhiskoe Lake were in accordance with differences in the weather conditions. Average *NAO* index calculated for spring and summer months was positive (0.35) in 2004 and negative in 2005 (−0.60). The positive *NAO* index corresponds to cyclonic windy and rainy conditions, whereas the negative one to anticyclonic conditions and relatively sunny weather in the temperate zone of Europe. Indeed, there were much more windy days in the eastern Crimea in April 2004 than in 2005 (*NAO* indices were 1.15 and −0.30, respectively) during the period of intensive algal growth. The windy conditions should

result in intensive resuspension of bottom sediments, decrease of water transparency and light limitation for *Cladophora* growth at the bottom of the lake. As is known, a resuspension of bottom sediments by wind in shallow lakes prevents the recolonisation by macrophytes (Blindow *et al.* 2002), because the high turbidity restricts the growth of submerged vegetation by light limitation.

Another difference in weather conditions was a warmer vegetation season in 2005 than 2004. As a result, salinity in Lake Tobeichskoe increased almost twice in summer 2005 as compared to summer 2004. This led to the elimination of omnivores *G. aequicauda* and establishment of *Artemia* population in the lake because predation of *G. aequicauda* was, probably, the main factor impeding the development of large planktonic grazer *A. parthenogenetica* in the lake. A vulnerability of *Artemia* to vertebrate and invertebrate predators was earlier pointed out by many authors (*e.g.* Wurtsbaugh 1991, Williams 1998). The establishment of *Artemia* population in Tobeichskoe Lake resulted in an increase of grazing pressure upon phytoplankton and clearance of water in the lake, which could have facilitated the stabilization of clear water state. Strong negative relationships between the biomass of *Artemia* spp. and phytoplankton primary production were found in both Tobeichskoe and Kojashskoe lakes. The increase of water transparency in Tobeichskoe Lake facilitated the growth of bottom filamentous algae of *Cladophora* spp., which further impeded resuspension in the lake and contributed to the considerable decrease of *PM*, *POM*, and the increase of Secchi depth in August 2005 (as compared with 2004). The ability of submerged vegetation to enhance water clarity by reducing resuspension of bottom material, suppressing algal growth, competing for nutrients and releasing allelopathic substances has been shown for freshwater lakes (*e.g.* Takamura *et al.* 2003, James *et al.* 2004, Gross *et al.* 2007).

The regime shift in Tobeichskoe Lake was induced by a primary salinization as resulted from the changes in weather conditions. Such regime shifts may also be induced by a secondary (anthropogenic) salinization. For instance, that was the case in the Crimean Saki Lake with turbid water at salinity of 65‰ (in 1987). In 1989-1990 the water

salinity increased to 90–120‰, after a small freshwater inflow brook had been dammed to increase production and quality of therapeutic mud (Ivanova *et al.* 1994). In 1990 the biomass of *Artemia* increased 5-fold and the primary production of phytoplankton decreased 25-fold causing a shift from turbid to clear water stage. Dense mats of *Cladophora* sp. were established at the bottom accounting for 96% of the primary production.

In the case of lagoon-derived lakes, there may occur one more impact of weather conditions on ecosystem water regime: thus, in 2004 windy conditions resulted in a partial destruction of the spit of Bakalskoe Lake. In the previous years, when the spit was intact and water salinity was higher, dense mats of *Cladophora* covered the bottom of the lake (Shadrin *et al.* 2004), and its ecosystem had a clear-water regime. However, after the spit was partly destroyed, Bakalskoe Lake became turbid with a high level of phytoplankton production and no benthic *Cladophora* mats could be found. A similar ecosystem shift that resulted from a change in weather conditions, was observed in a hypersaline coastal Araruama Lagoon in Brazil (Moreira-Tureq 2006). Thus, fluctuations in weather conditions are a principal factor responsible for a great variability of ecosystem regimes in hypersaline lakes and lagoons.

In the scheme of evolution of Australian saline lakes as a result of their salinization and eutrophication proposed by Sim *et al.* (2006b), the initial lake ecosystem state is a macrophyte-dominated clear-water stage with the upper salinity threshold 30–40‰. A further salinization leads to a clear-water regime characterized by a benthic microbial community, if there is no eutrophication of the system. In the saline Crimean lakes we observed a more complicated ecosystem dynamics resulting from changes in weather conditions and hydrological regime. An increase of salinity in lagoon-derived lakes led to regime shifts from turbid to clear water stage, where macroalgae (*Cladophora* spp.) play the role of macrophytes. Similarly to the macrophytes, they prevent resuspension of bottom sediments and incorporate and store nutrients from the water column. It is important, that in contrast to macrophyte-dominated stage with the upper limit of salinity up to

30–40‰ (Sim *et al.* 2006a), the macroalgae-dominated stage occurs at more saline conditions, about 100‰. The trigger factor for such a shift must be the change in the community structure: the disappearance of predators and a development of population of large grazers (*Artemia*), which increase a top-down effect of zooplankton.

A further increase of salinity (higher than 100‰) in lagoon-derived lakes leads to a collapse of benthic energy pathways and a development of planktonic energy pathways due to dense populations of *Artemia* species. This stage was observed in the highly saline Kojashskoe Lake. In spite of a high concentration of nutrients in the water column, the biomass of phytoplankton for the most part of the year corresponded more to the clear water stage, due to a high clearance rate of zooplankton and high turbidity of the water, which was mostly related to inorganic suspended matter. Therefore, at a very high salinity in shallow lakes one may observe a “pseudo turbid” stage. In this case a high turbidity is a result of a high water density and low sedimentation rate of *PM*, but not of a high phytoplankton production level. In some specific conditions, a dominance of benthic microbial communities is also possible. In the Crimea such communities were observed in saline very shallow waters (up to 15 cm), where wave action was limited. In more deep waters microbial mats are easily detached from the bottom sediments.

4.3. Dynamics of food-webs along the salinity gradient

As in the other saline lakes (*e.g.* Timms 1981), there was rather a steep decrease in zoobenthic biomass in the Crimean lakes as salinity increased. The upper limit of salinity for macrozoobenthos was about 100‰. One of the reasons for deterioration of benthic animal communities in these lakes is a low oxygen saturation of water at high salinity (Golubkov *et al.* 2007). Another possible reason may be a positive buoyancy of animals under high salinity levels. Water with salt concentration of 100 – 110‰ has the density close to body density of animals, for example, of the benthic amphipod *Gammarus pulex* (Moore *et al.* 1997). Therefore, a higher salinity leads to positive

buoyancy for benthic species and their incapacity to colonize bottom environments. Body density of planktonic species, as a rule, is lower than that of the benthic ones. For instance, neutral buoyancy for *Artemia franciscana* is observed at salinity 43–48‰. Salinities of 100 ‰ and higher considerably decrease the downward swimming of this species and constrain the animals at the top of the water column (Davenport and Healy 2006).

Well developed trophic level III (macroinvertebrate predators) was observed only in the ecosystem of Bakalskoe Lake with the lowest level of salinity and moderate level of primary production among the investigated lakes. Hypereutrophic Kirkojashskoe and Shimakhanskoe lakes had very low energy transfer efficiencies to the level of secondary consumers, probably, due to a high level of eutrophication. The highly eutrophic and saline Marfovskoe Lake and the extremely saline Kojashskoe Lake had no secondary consumers at all. Therefore, both salinization and eutrophication of saline lakes may negatively affect higher trophic levels and shorten community food chains.

A similar effect was described for multitrophic aquatic ecosystems affected by acidification stress. It has been shown, that as acidity increases, species more frequently disappear from the higher than lower trophic levels (Petchey *et al.* 2004). Several mechanisms – longer generation times, lack of resting stages and dependence of species of higher trophic levels on the presence of species at lower trophic level – were suggested to explain this regularity. Thus, a shortening of food chain may be considered as a general community response to different environmental stressors: salinization, eutrophication and acidification.

5. Conclusions

The investigation of Crimean salt lakes has shown several ecosystem states along a salinity gradient: a turbid phytoplankton-dominated state at relatively low salinities (<60‰), a clear-water macroalgae-dominated state at intermediate salinities (up to 100‰), and a “pseudo turbid” state of highly saline lakes (probably >150‰).

In the latter case a high turbidity is the result of a high water density and low sedimentation rate of particulate matter, but not of a high level of phytoplankton production (as in lakes with lower salinity).

In general, the importance of energy pathways through planktonic food-webs increases with salinity due to positive buoyancy for benthic species and their incapacity to colonize bottom environments in highly saline lakes. Therefore, high water density may be an important factor affecting food web structure and ecosystem regime in hypersaline lakes.

Ecosystems of hypersaline lakes have low resilience to external factors. Fluctuations in weather conditions are the principal factor responsible for the great variability of energy pathways and ecosystem regime shifts in hypersaline lakes and lagoons. Both salinization and eutrophication of saline lakes negatively affect higher trophic levels and result in shortening of food chains.

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