

Review

Large Russian Lakes Ladoga, Onega, and Imandra under Strong Pollution and in the Period of Revitalization: A Review

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Abstract: In this paper, retrospective analyses of long-term changes in the aquatic ecosystem of Ladoga, Onega, and Imandra lakes, situated within North-West Russia, are presented. At the beginning of the last century, the lakes were oligotrophic, freshwater and similar in origin in terms of the chemical composition of waters and aquatic fauna. Three stages were identified in this study: reference condition, intensive pollution and degradation, and decreasing pollution and revitalization. Similar changes in polluted bays were detected, for which a significant decrease in their oligotrophic nature, the dominance of eurybiont species, their biodiversity under toxic substances and nutrients, were noted. The lakes have been recolonized by northern species following pollution reduction over the past 20 years. There have been replacements in dominant complexes, an increase in the biodiversity of communities, with the emergence of more southern forms of introduced species. The path of ecosystem transformation during and after the anthropogenic stress compares with the regularities of ecosystem successions: from the natural state through the developmental stage to a more stable mature modification, with significantly different natural characteristics. A peculiarity of the newly formed ecosystems is the change in structure and the higher productivity of biological communities, explained by the stability of the newly formed biogeochemical nutrient cycles, as well as climate warming.

Keywords: large lakes; long-term pollution; aquatic ecosystem; reference condition; disturbance; recovery

1. Introduction

Large lakes are water resources and drivers of human development. Considering the great importance of fresh water in providing populations of the regions with drinking water and fish products, it is of particular relevance to study not only the effects of pollution but also the possibility of recovering aquatic ecosystems after their acute pollution.

Numerous studies have provided insight into the regularities of anthropogenic environmental transformations of lakes within polluted sites and the responses of biological systems to anthropogenic stress, and have revealed the severe hazard of toxic substances that result from environmental pollution [1–5]. Recently, there has been a tendency to reduce the flow of hazardous pollutants into the environment, including lakes. The scientific community has begun to accumulate data on the recovery of aquatic ecosystems of lakes, including the Laurentian Great Lakes and large European lakes, after pollution stress [6–12].

An example of long-term multi-contaminating pollution (Cu, Ni, P, phenols, oil and lignosulfonates) is the large lakes of Russia, including Ladoga, Onega, and the subarctic lake Imandra (Figure 1). These

lakes are located in the North-West of Russia. For more than 80 years, the lakes have been a source of freshwater for human consumption and industrial use, a place for recreation and tourism, and a resource supporting fisheries. Large amounts of pollutants were input into the lakes between 1930 and 1990, and the catchment area was also polluted with airborne contaminants. Since 1990, as a result of the economic crisis in Russia, anthropogenic pressure on the lakes has decreased. The recent recovery of the economy has occurred simultaneously with technological modernization and tighter controls of pollutant emissions into the lake and atmosphere.

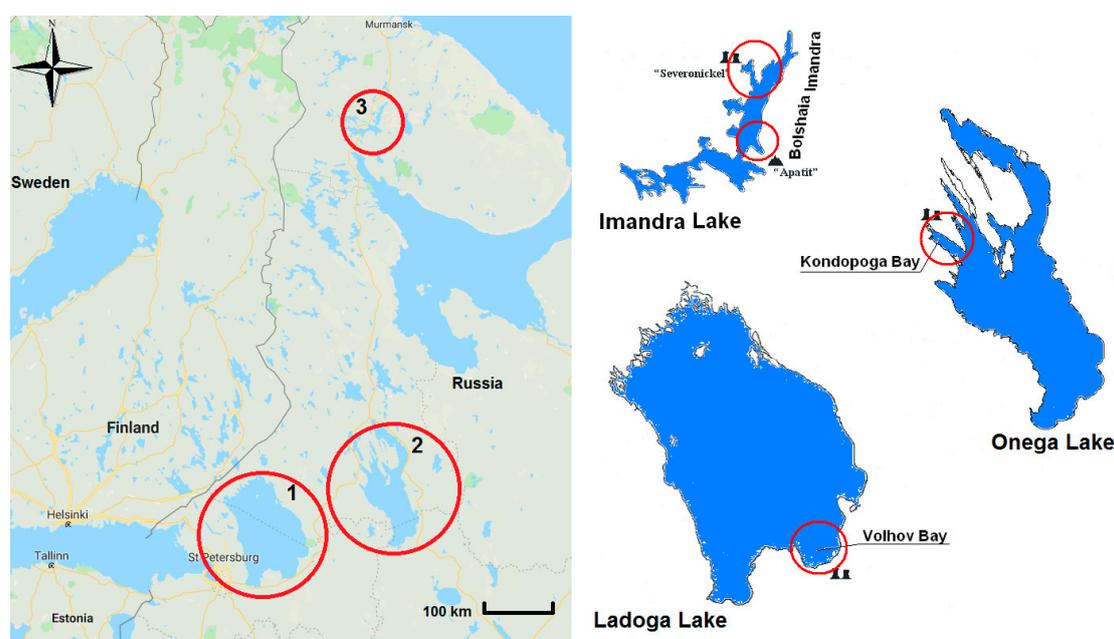


Figure 1. Map of Imandra, Onega, and Ladoga lakes and the location of the main industries on their shores.

Understanding the impact of anthropogenic contamination on aquatic ecosystems and their subsequent recovery as a result of decreasing anthropogenic stress is important for successful environmental management.

The objectives of this study are as follows:

1. To characterize the main parameters of the large lakes and estimate their reference conditions on the basis of a time-space analysis of dominant characteristics;
2. To identify the main patterns of changes in the aquatic ecosystems of the lakes under the conditions of anthropogenic loads and their reduction, from background characteristics through degradation to recovery;
3. To explain the course of these changes from the perspective of ecological theory and to assess the possibility of ecosystems returning to their natural state after toxic stress.

This paper is based on an analytical review of published studies characterizing the natural state of the lakes before industrial activity [13–18]; changes in the main indicators of the polluted bays, which occurred in the mid 1960–1970s of the last century up to the 2000s [19–21]; and the state of the ecosystems in the same bays after stopping the pollution [22–25]. In this review, attention is focused on the main parameters of water chemistry and indicators of phytoplankton, zooplankton, benthos, and fish condition, which reflect ecosystem changes during different periods for Volkhov Bay of Lake Ladoga, Kondopoga Bay of Lake Onega, and Bol'shaya Imandra. These bays are characterized by the pollution of water with toxic agents and nutrients.

Although much information is available, there has been no continuous long-term monitoring of the lakes, so this paper is based on discontinuous information. Detailed descriptions of the study

methods have been given in the literature cited above [26,27]. The data are based on a large number of various samples distributed over lakes. Sampling was carried out in both coastal and pelagic zones and in deeper parts of the lake.

2. Main Features of the Natural Condition of the Lakes

The generalized characteristics of the three lakes are presented in Table 1. A number of common features are characterized for both the water chemistry and fauna, according to the unified genesis formation of the lake ecosystem in the postglacial period. Low mineralization of water, due to the natural features of the geological structure of the catchment area, is a common characteristic of lakes. The lakes are dimictic, and the maximum temperature of the surface water layer is 20 °C. The maximum transparency of water reaches 7 m across the Secchi Disk (SD).

Table 1. The generalized characteristics of the three lakes.

Parameters	Lake Ladoga		Lake Onega		Lake Imandra	
	Whole Lake	Volkhov Bay	Whole Lake	Kondopoga Bay	Whole Lake	Bolshaya Imandra
Area, km ²	18,300	1464 (8%)	9800	224 (2.7%)	813	244 (30%)
Depth, m, max./average	230/47	20/7	120/30	82/21	67/13	67/17
Volume km ³	838	-	262	-	11	-
Water residence time, years	11	3	15	5	6	4
SD, m	2.9 ± 0.9	0.7 ± 0.2	4 ± 1.2	2.5 ± 1.1	5 ± 1.2	2.5 ± 0.8
	0.5–6.6	0.5–1.2	0.5–6	0.5–3.2	1.2–7.1	1.2–3.5
Σ ions, mg/L	63.7 ± 7.5	95 ± 12.0	36.6 ± 4.5	36.5 ± 2.3	81.3 ± 27	82 ± 9
	55–173	86–173	27–56	30–45	13–176	67–112

Ladoga is the largest of the investigated lakes. It is the largest lake in Europe and one of the 15 largest freshwater reservoirs in the world. At least 40 rivers and large streams flow into the Ladoga, the largest of which is Svir River, which brings water from Lake Onega, and one river flows out—the Neva River. In the southern half of the lake, there are three large bays: The Svir, Volkhov, and Shlisselburg bays. Being located in the northern part of the basin, maximum depth of Lake Ladoga reaches 230 m. In deep areas, most of the lake's water mass is concentrated. Due to the large size of the basin and the accumulation of a large volume of water in it, water exchange in the lake is slowed down, despite the significant flow coming from the vast catchment. The water of Lake Ladoga is low in salt (the average sum of ions is 63.7 mg/L), and is comparable to the Laurentian Great Lakes in a natural state and to the water of Lake Baikal. According to the ratio of the main water ions of Lake Ladoga, they are generally classified as hydrocarbonate-calcium, which is typical for surface waters of the entire north-western region, containing low concentrations of phosphorus. This peculiarity of Lake Ladoga's water is due to the composition of the catchment area where the flow entering the lake is formed, which consists of poorly soluble crystalline rocks. Water replacement in the lake occurs once every 11 years [22].

Lake Onega is the second largest lake in Europe after Lake Ladoga. Due to its more northern location, the lake is characterized by lower concentrations of salts and nutrients. The duration of the residence time is about 15 years [28]. The content of mineral salts is slightly lower than in Lake Ladoga, whilst the ionic composition is similar.

Lake Imandra lies beyond the Arctic Circle, on the watershed divide between the Kola Peninsula and the mainland of the Scandinavian Shield. About 20 tributaries flow into the lake and one river—the Niva—flows out of Imandra to run into the White Sea. The lake has a complex shoreline and consists of three main basins (Bolshaya, Yokostrovskaya, and Babinskaya) connected by narrow passages, with maximum and average depths of 67, 32, and 13 m, respectively. The natural conditions of the formation

of aquatic ecosystems of the Arctic basin, namely, the high contribution of atmospheric precipitation, thin soil and vegetation cover, low temperatures, and, accordingly, slowed-down biogeochemical circulation processes of nutrients, have formed a freshwater and oligotrophic reservoir.

The dominant complexes in the three lakes are shown in Figure 2 (reference condition). Diatoms dominate in the phytoplankton of lakes, in particular, *Aulacoseira islandica*. In the seasonal dynamics of biomass, one spring or summer peak of development can be observed. The values of phytoplankton abundance and biomass are low, which is typical of northern oligotrophic lakes [29,30]. A feature of these lakes is the formation of primary production by the diatoms of the flora and the weak development of macrophytes. Macrophytes do not play a significant role in cold-water lakes such as the lakes of the North-West of Russia, and they are absent in Lake Imandra. Onega and Ladoga lakes have small local accumulations in closed bays and shallow water [22,31].

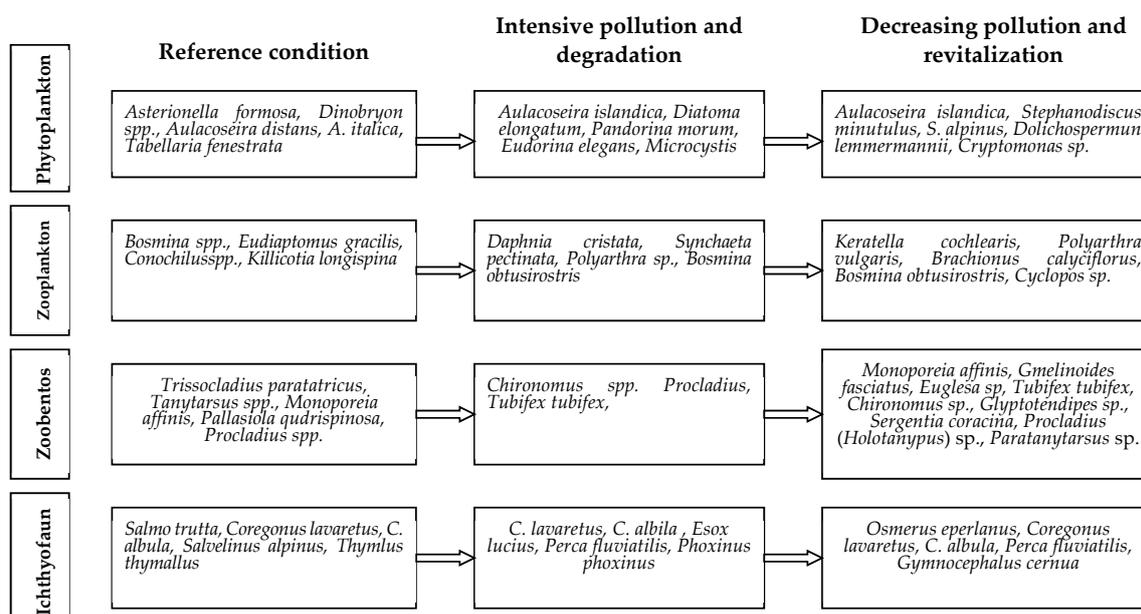


Figure 2. Dominating complexes of the community structure of the large Russian lakes Imandra, Onega, and Ladoga during the key periods of ecosystem modification.

The predominance of Cladocera and Copepoda is a characteristic feature of zooplankton of the lakes [32]. In zoobenthos, midge larvae (Chironomidae), bivalves (*Euglesa* spp.), and crustacea (*Monoporeia affinis* and *Pallasiola quadrispinosa*) dominate. Oligochaeta are represented by the Lumbriculidae and Naididae families [13,33,34].

The basis of commercial catches in the lake is valuable whitefish (various forms of whitefish, vendace, and ripus) and large staple fish (pike-perch, bream, etc.). The vendaces *Coregonus albula* (L) are the main planktophages, whilst whitefish (*Coregonus lavaretus* (L)) are the main benthophages. The lake salmon *Salmon trutta* (L), pike, and perch are among the predatory fish in the lakes [20,22,35]. The more northern Lake Imandra is different. In this lake, there are no bream, but there are vendace, whitefish, trout, and char [20].

A comparative analysis of the three lakes shows that despite the great similarity of the lakes in terms of the hydrochemical regime, flora, and fauna, a regular increase in trophic status is observed from north to south, from the cooler Lake Imandra to Lake Ladoga [19–22].

3. Anthropogenic Loads in the Bay

Considerable industrial expansion in the 1930s resulted in the building of large industrial enterprises in the lake catchments. Contaminated bays are marked in Figure 1: on Ladoga, Volkhov;

on Onega, Kondopoga; and on Imandra, Bolshaya Imandra were exposed to strong anthropogenic loads. Pollution in the area and their characteristics are presented in Table 2.

The first aluminum plant in Russia, a pulp and paper mill, and other industries were built on the shore of Lake Ladoga, in Volkhov Bay, at the beginning of the last century. Contamination by sewage waters of these industries containing phenols, lignosulfate, benzoperen, and other toxic substances reached a maximum in the late 1960s. Toxic substances entering the lake were accompanied by a nutrient load, with both the production of effluents (especially after the aluminum plant switched to new raw materials—phosphorus-containing apatite-nepheline ores) and the sewage waters of the Volkhov town. Based on scientists' estimates, the flow of phosphorus into the lake increased hundreds of times, and the load of phosphorus in this area of the lake in the 1970s–80s amounted to 6000–7000 tons/year (the share of Volkhov Bay accounted for 50–60% of the total value) [19,35]. It should be emphasized that the area of the polluted bay was 8% of the lake area, but the pollution of this bay with a mixture of toxic substances and nutrients was significant.

Certain bays, the Kondopoga bays, are experiencing the highest anthropogenic impact, as a result of which their ecosystems have moved into the mesotrophic category and acquired the features of a eutrophic system, according to hydrobiological indicators. Wastewater from the industrial complex of Petrozavodsk is characterized by a high phosphorus load in the ecosystem of Petrozavodsk Bay. Lake Onega is polluted to the largest extent due to the country pulp-and-paper plant. Kondopoga Bay receives a large amount of industrial wastewater, which contains toxic pollutants and nutrients. The plant was operated without a wastewater treatment facility for 30 years. The wastewater treatment system was introduced in the 1980s, but phosphorus and nitrogen compounds were additionally used as reagents. The phosphoric load in the bay increased even more and became 0.56 g/m²/year, with a nitrogen load of 11.1 g/m²/year. At the same time, the total phosphorus load in the lake was 0.1 g/m² year [36]. The total area of pollution is now less than 3% of the entire lake.

Industrial field development on the shores of Lake Imandra began in the 1930s–1940s. The mining and metallurgical, mineral processing, and chemical industries are concentrated on the shores of the northern part of the lake—Bolshaya Imandra. These were developed in order to provide powerful Cu-Ni-metallurgical smelting facilities in the Kola North in 1934. Among the Arctic regions, the Imandra catchment area is characterized by the highest concentrations of industry and population, with more than 300,000 people living in its catchment area.

Water pollution, which began in the 1930s–1940s, peaked by the 1970s–1980s. For many years, the lake was polluted with various types of wastewater, among which the greatest danger was represented by toxic effluents of copper-nickel and apatite-nepheline production. The Bolshaya Imandra (northern part) was contaminated, which accounted for almost 30% of the lake's area.

Table 2. The main indicators * of water quality and community conditions ($X \pm$ standard error (SE)/min-max) of Russian large lakes during the key periods of ecosystem modification: 1—Reference condition. 2—Intensive pollution and degradation. 3—Decreasing pollution and revitalization.

Lakes Area	Bolshaya Imandra			Kondopoga Bay of Onega Lake			Volkhov Bay of Ladoga Lake		
Periods	1	2	3	1	2	3	1	2	3
pH	7.1 ± 0.2 6.4–7.2	7.3 ± 0.3 6.3–8.2	7.4 ± 0.2 6.9–7.7	7.0 ± 0.2 6.3–7.2	7.6 ± 0.3 6.5–8.4	7.4 ± 0.3 6.5–7.8	7.3 ± 0.2 6.5–7.5	7.5 ± 0.3 6.6–9.3	7.4 ± 0.2 6.7–9.0
P _{tot} , µg/L	6 ± 1 2–10	70 ± 30 2–176	26 ± 7 13–68	8 ± 1 3–11	54 ± 15 6–98	23 ± 9 8–36	10 ± 1 1–25	178 ± 50 180–260	30 ± 5 10–137
PO ₄ , µg/L	1 ± 0.1 0–8	21 ± 5 2–154	6 ± 2 0–12	1 ± 0.1 0.1–9	30 ± 12 5–69	4 ± 1 0–15	3 ± 0.2 0.3–7	100 ± 11 5–9	8 ± 1 0.4–5
N _{tot} , µg/L	10 ± 3 10–100	436 ± 98 164–1925	203 ± 35 106–402	350 ± 50 150–420	750 ± 75 450–900	620 ± 55 400–820	450 ± 27 120–610	920 ± 97 540–1620	805 ± 56 730–1230
NO ₃ , µg/L	1 ± 0.2 0–35	102 ± 31 1–1271	7 ± 1 1–158	110 ± 9 10–220	120 ± 9 44–150	77 ± 21 35–140	130 ± 12 50–150	240 ± 17 120–450	220 ± 25 96–361
Si, µg/L	0.6 ± 0.2 0.3–0.7	1.1 ± 1.1 0.1–5.2	0.6 ± 0.3 0.1–1.5	2.0 ± 0.2 0.2–2.5	1.2 ± 0.2 0.1–3.8	0.3 ± 0.1 0.1–1.5	1.0 ± 0.1 0.6–1.2	0.5 ± 0.1 0.3–0.9	0.2 0.1–0.5
Chl “a”, µg/m ³	0.3 ± 0.1 0.2–0.5	3.8 ± 0.7 2–7	3.4 ± 0.5 1.5–6	0.7 ± 0.1 0.2–0.9	8.4 ± 0.7 0.5–11	8.6 ± 0.5 1.5–18	0.7 ± 0.1 0.3–9	8.0 ± 0.5 2–39	9.6 ± 1 0.6–10.3
Toxic loads (ΣCi/MPCi) **	0.1 ± 0.1 0.02–0.4	27.0 ± 7 12–35	2.1 ± 1 1.2–17	0.1 ± 0.1 0.01–0.03	0.7 ± 0.3 0.4–1.3	0.9 ± 0.2 0.4–2.3	0.1 ± 0.1 0.02–0.6	0.8 ± 0.2 0.2–2.5	0.8 ± 0.2 0.2–2.7
Phytoplankton									
Biomass, g/m ³	0.1 ± 0.1 0.01–0.5	3.6 ± 0.5 0.4–20.5	3.8 ± 0.3 0.5–9.2	0.1 ± 0.1 0.05–0.5	2.4 ± 0.9 0.5–5.9	2.2 ± 0.5 0.5–3.6	0.5 ± 0.1 0.1–0.9	5.5 ± 1.2 0.2–7.8	2.5 ± 0.7 0.2–6.7
Number, cell 10 ⁶ /L	0.1 ± 0.1 0.01–0.3	3.8 ± 0.3 0.9–7.8	4.4 ± 0.3 0.7–8.2	0.1 ± 0.1 0.02–0.5	3.6 ± 1.4 0.5–8.3	3.4 ± 1.2 0.4–8.5	0.4 ± 0.2 0.04–0.9	12.3 ± 3.8 1–17	3.7 ± 2.2 1–9
H (Shannon’s index)	3.2 ± 0.2 3.0–3.5	2.5 ± 0.2 2.0–3.5	2.8 ± 0.2 2.0–3.6	3.7 ± 0.5 3.1–3.9	3.3 ± 0.6 2.9–3.8	4.6 ± 0.3 3.0–4.8	3.4 ± 0.2 3.1–3.9	3.1 ± 0.7 2.5–3.8	5.4 ± 0.4 2.8–5.6
Zooplankton									
Biomass, g/m ³	0.3 ± 0.1 0.2–1.0	1.7 ± 1.1 1–3.5	0.8 ± 1 0.5–2.5	0.3 ± 0.1 0.1–0.6	2.9 ± 0.7 0.8–4.1	1.4 ± 0.5 0.9–3.2	0.6 ± 0.2 0.3–0.7	2.8 ± 0.4 0.6–3.1	1.9 ± 0.3 0.6–2.5
Number, spec, 10 ³ /m ³	15.0 ± 10 10–100	271.0 ± 139 78–320	445.0 ± 99 98–510	10.0 ± 1.2 5–20	110.0 ± 37 15–130	91.0 ± 25 20–110	13.0 ± 7.2 10–120	143.0 ± 45 48–240	58.0 ± 27 22–121
H (Shannon’s index)	2.8 ± 0.2 2.5–3.0	1.9 ± 1 1–2.5	2.0 ± 0.4 1.5–3	2.3 ± 0.4 2–3	1.7 ± 0.5 1–3.5	3.7 ± 0.4 2–4	-	-	4.1 ± 0.5 2.8–4.3
Macrozoobenthos									
Biomass, g/m ²	0.6 ± 0.1 0.3–0.8	49.0 ± 9 5–60	23.8 ± 7 7–50	0.6 ± 0.2 0.4–1	3.2 ± 1.1 1–58	15.2 ± 3.6 5–60	1.6 ± 0.3 0.2–13	4.8 ± 2.4 0.2–19	12.9 ± 7.1 1–28
Number, spec, 10 ³ /m ²	0.5 ± 0.1 0.4–0.7	6.2 ± 2 1–12	4.8 ± 3 1–9	0.2 ± 0.1 0.1–0.4	2.4 ± 1.5 0.5–41	8.5 ± 2.3 1–50	0.8 ± 0.2 0.2–5	1.1 ± 0.9 0.4–6.5	3.7 ± 1.5 0.6–10.1
H (Shannon’s index)	3.5 ± 0.2 2.1–3.8	1.6 ± 0.3 1.0–2.2	1.2 ± 0.2 1.0–2.1	2.6 ± 0.5 2.2–3.1	2.0 ± 0.7 1.1–2.9	2.2 ± 0.3 1.7–3.0	-	-	2.4 ± 0.5 1.5–3.2

* Numerical values indicators which are taken from below quoted literature [13–39] are resulted. ** Toxic loads: ΣCi/MPCi - sum concentration of pollutant (Ni, Cu, Pb, phenol and lignosulfonate) normalized to Guide Line concentration for Russian aquatic life.

4. Through Disturbance to Recovery

4.1. Pollution-Caused Changes

Contamination of the bays of the lakes with a mixture of toxic substances and nutrients was dramatic during 1970–1980. It is difficult to estimate the exact volumes of the maximum flow of toxic substances into the lakes (such information is limited). However, according to the available information, we can make a judgement about the high toxic stress exerted on the aquatic inhabitants during the period of intensive water pollution and disturbance of the natural biogeochemical cycles. Industrial activity during this period was accompanied by the formation of sewage waters, which were released into the same areas of the lakes as toxic water, without proper cleaning. This led to the simultaneous contamination of the lakes by heavy metals, organic ecotoxicants, and nutrients (phosphorus and nitrogen). The main changes in the species composition of communities are presented in Figure 2, and the numerical values can be seen in Table 2. A review of the data on changes in water communities in polluted bays is of the greatest interest for understanding anthropogenic successions in cold-water lakes.

The water chemistry changes in all three lake's bays are the same for this period: the transparency decreased, and the pH, sulfates, chlorides, and nutrients increased. The biogeochemical cycle of nutrients changed dramatically. In relation to natural indicators, both the total concentration and the content of bioavailable nutrient forms increased, which contributed to the development of phytoplankton communities. The polluted bays (Volkhov Bay of Lake Ladoga Lake, Kondopoga Bay of Lake Onega, and Bolshaya Imandra) began to correspond to the eutrophic status, according to phosphorus and chlorophyll "a" contents (in line with the classification of RA. Vollenweider [37]), and the adjacent water areas that were large enough began to correspond to the mesotrophic status. The indicator chlorophyll "a" increased by more than 10 times (Table 2). Si absorption occurs due to the intensive development of diatoms.

The habitat conditions for aquatic organisms became different from the natural characteristics in the period of intensive pollution in the bays; a new property appeared—water toxicity—which resulted in changes in the structure of all parts of the ecosystem [20,34,35]. The phytoplankton biomass in the polluted bays of the three lakes in the summer period increased by 20–30 times as a result of the huge amounts of nutrient inputs (Table 2). Intensive cyanobacterial blooms were observed in Lake Ladoga and Lake Onega and also in the arctic lake of Lake Imandra. There were structural changes in the phytoplankton community towards the intensive development of species typical of eutrophic water bodies. Cyanobacteria, as well as green and cryptophytic algae, dominated during this period.

In the polluted bays of Lake Ladoga and Lake Onega, there was an increase in the number of rotifers and a decrease in crustacean species typical of the north. In terms of the structure of zooplankton of Lake Imandra, the rotifer content increased to 60% of the total biomass, which was associated with their greater resistance to pollutants (Figure 2), while the content of typical inhabitants of the waters of the North *Collotheca* sp., *Conochilus* sp., and *Holopedium gibberum* decreased. According to O.I. Vandysh [20], the total biomass of the zooplankton community increased, while the species diversity index decreased (Table 2).

The total abundance and biomass of zoobenthos in the polluted areas in all the lakes increased dramatically against the background of reducing their biodiversity. Here, a community of high numbers with a limited species composition has formed Chironomus, Procladius, Nematoda, *Tubifex tubifex*, and *Limnodrilus hoffmeisteri*. The index of species diversity in areas of high pollution was less than 1–2 (Table 2). According to the data of T.N. Polyakova and T.D. Slepukhina [33,34,38] on the polluted bays of Lake Ladoga and Lake Onega, in the period of catastrophic discharges of pulp and paper production wastewaters, complete destruction of bottom biocenoses was observed in the bottom deposits with moderate pollution-formed communities, represented by several stable species of the chironomid–oligochaete complex. Relatively large chironomids (Chironomus and Procladius) formed biomass 10–50 times higher in comparison with natural indicators, as a result of the accumulation

of a large amount of organic and nutrient substances at the bottom. In areas where the toxicity was decreasing, there was a high accumulation of organic sludge in the bottom sediments, and oligochaetes (Tubificidae) prevailed [19,21,22].

In Lake Imandra, oligochaetes (up to 200 g/m²) and chironomids (up to 50 mg/m²) prevailed in the contaminated areas. At the same time, the proportion of both chironomid larvae that are sensitive to pollution and bivalve mollusks (*Euglesa* spp.) in the total number of benthic invertebrates decreased by more than two times. Of the two previously noted in Imandra relic crustaceans, *Monoporeia relicta* likely disappeared from the fauna. The species *M. affinis* turned out to be significantly more resistant to pollution of the lake with heavy metals and nutrients [39].

In the fish community, the abundance of loaches and lake trout decreased significantly due to the high sensitivity of these species to water pollution. In the commercial catches, they practically disappeared. At the same time, a significant ranking in the catches was attributed to species such as smelt, which was previously found in single-unit quantities. Additionally, the whitefish abundance decreased.

The fish population has also changed. In Lake Ladoga and Lake Onega, the abundance of lake salmon has drastically decreased. According to Arshanits [40], pathologies and dysfunctions of the body (especially those of the liver and kidney) under the influence of toxic substances were identified in the fish of Volkhov Bay of Lake Ladoga.

In Lake Bolshaya Imandra, diseases of whitefish were also recorded, such as nephrocalcosis (kidney stones), lipid degeneration of the liver, cirrhosis, etc. The frequency of the case rate (% of those surveyed) was closely related to the nickel concentration in water and its accumulation in the kidney [41]. Along with the general pathologies, the fish appeared to have specific diseases characteristic of each of the areas. In the area of influence of copper–nickel effluent, nephrocalcosis was recorded, and in the area of effluent of apatite-nepheline production, myopathy and nephrocalcosis were recorded. Criteria used to determine the fish condition (by physiological indicators of intoxication) are important for estimating toxic effects and are used as integral parameters of ecosystem health [42]. With the use of these criteria, fish diseases indicated the dramatic ecosystem health in Bolshaya Imandra and Ladoga Bay during this period of intensive pollution. Productive areas of benthic communities developed, which attracted whitefish due to the high biomass of zoobenthos. By migrating to these food-rich areas, fish were exposed to the effects of toxic contaminants [39].

4.2. Tendency to Recovery

In the 1990s, the anthropogenic load in the lakes decreased due to the economic crisis and the suspension of industrial production. In response to a decrease in the anthropogenic load in the Volkhov (Lake Ladoga) and Kondopoga (Lake Onega) bays, as well as the Bolshaya Imandra, in the 1990s, tendencies toward the improvement of water quality and recovery of the ecosystem were defined.

The concentrations of toxic substances in the water of the studied bays decreased: in Lake Imandra, the concentration of nickel as the main marker of pollution decreased from 150 to 10 µg/L, and the concentration of lingosulfate and phenols in the Kondapoga and Volkhov bays decreased.

The content of common forms of phosphorus in Lake Ladoga and Lake Onega decreased, and in Imandra, it remained at the same level; the total nitrogen concentrations only slightly dropped in all three lakes (Table 2). Concentrations of bioavailable phosphates and nitrates significantly decreased (6–20 times), which indicated their more active utilization in altered biogeochemical cycles. The dynamics of silicon is interesting since its concentrations have not recovered, but have been systematically decreasing year by year, which is associated with its more active absorption of diatoms blooming in the modern period (Table 2).

The abundance of phytoplankton dropped in the Volkhov and Kondopoga bays, whilst in Lake Imandra; it remained at the same level. The average values of biomass in the lakes varied from 1.7 to 3.4 g/m³ (Table 2), and the concentrations of chlorophyll “a” ranged from 3.6 to 7.9 mg/m³. The relative abundance of cryptomonads, green algae, and cyanobacteria remains high in the phytoplankton

biomass structure. Macrophytes were not characteristic in the studied bays, as well as in deep-water cold lakes as a whole. Their development was not observed during the period of pollution.

Despite the decrease in the phosphorus load in the bays of the Ladoga and Onega lakes, as well as the Bolshaya Imandra, the maximum and average values of the phytoplankton biomass and chlorophyll content remained very high during the recovery period compared with the reference condition.

A decrease in the number of zooplankton communities and an increase in species diversity in the bays of Ladoga, Onega, and Imandra lakes were noted in the late 1990s–early 2000s (Table 2). The biomass also declined, but not to such a great extent. This was due to the increase in the number of larger Cladocerae (*Bosmina obtusirostris*) and copepods (*Cyclops* sp., *Mesocyclops leuckarti*), and a decrease in the proportion of small rotifers, typical indicators of pollution. Cladocerae *Holopedium gibberum*, *Daphnia* sp., and *L. kindtii* that were previously common in the lake, but disappeared during the period of maximum water pollution, which were valuable in terms of fodder, recovered. However, the crustaceans *Leptodora kindtii*, *Polyphemus pediculus*, *Eudiaptomus graciloides*, and *Hetercope appendiculata* that are the most sensitive to pollution are still found in small abundances. A characteristic feature of the zooplankton of Volkhov Bay is the predominance of Cladocera over Copepoda [22,35].

Zoobenthos shows great inertia to recovery. Whilst, in the Bolshaya Imandra, its biomass decreased, in the bays of Lake Ladoga and Lake Onega, it continued to increase until the 2000s. Changes in the structure and increase in the quantitative indicators of zoobenthos of Lake Ladoga, especially in the deepest areas, indicate an increase in the trophic status of bottom biotopes. Benthos communities in open areas of the lake are characterized by stability. Production indicators of zoobenthos development are low in the northern deep-water areas of Lake Ladoga and much higher in the south, particularly in Volkhov Bay. The macrobenthos of Volkhov Bay differs from the benthic communities of other parts of the coastal area of the lake by a high level of quantitative development. Two large rivers flow into the southern bay: The Volkhov and the Syas, determining the natural features and significant anthropogenic load in this part of the lake. The abundance of benthos varies from 500 to 10,000 spec./m², and the biomass varies from 0.98 to 28.00 g/m² [22].

In the benthos of the northern part of Kondopoga Bay of Lake Onega, the oligochaete–chironomid complex still prevails, with a predominance of worms and no relict amphipods. Over 30 years of operation of wastewater treatment plants, the level of quantitative development of benthos increased, on average, by more than 40 times in Kondopoga Bay, and the biomass increased almost 20 times compared with the initial observation period (1964).

Research in 1998–2016 [24] showed that large-scale transformation of the deep-water benthic communities occurred in various areas of Lake Onega. In the northwestern bays (Kondopoga) and deep-water areas, the abundance and biomass of benthic communities decreased, and their production has reduced by 2–4 times in the last 25 years. However, in 1998–2005 in the Kondopoga bay, the total number was 1780–9360 spec./m² and the total biomass was 2.18–13.96 g/m²; in 2011–2016, these figures dropped to 680–2720 spec./m² and 0.32–7.68 g/m², respectively. Relict amphipods are absent in the northern part. Significant areas of technogenic deposits in this zone still do not contain macrobenthos organisms. The reason for the decrease in the benthos indicators may be the inhibitory effect of iron, whose accumulation in the sludge is associated with an increase in the supply of this element in the composition of humus substances with river waters due to climatic changes in the catchment area [24].

In the modern period (after 2010), in Lake Imandra, against the background of a decrease in the content of toxic heavy metals, a high concentration of nutrients remains, which has led to the formation of mesotrophic phytoplankton communities [43]. Under the current conditions, the amount of abnormally high quantitative indicators of phytoplankton (bloom), which appear during the season, has increased. In the eutrophied areas, the mass development of cyanoprokaryotes (*Dolichospermum lemmermannii*) has regularly begun. The biomass and abundance of phytoplankton are rising, and the number of organisms in the zooplankton community is increasing, indicating a boost in the proportion of small forms of zooplankton [44]. The biomass of benthos in some areas reaches very high values—up to 52 g/m². Under the conditions of a significant reduction of the toxic load on the Bolshaya Imandra

reach and with a good supply of nutrients in the profundal benthos of the Arctic lake, crustaceans represented by relict *M. affinis* became dominant among the invertebrate groups, and their relative abundance increased by almost two times—from 36% to 60% [20].

Fish diseases almost never occur and their symptoms are mild, which indicates an improvement in the “health” of the ecosystem. Despite the reduction in toxic load, the decline in the proportion of salmon and whitefish is progressing with the simultaneous increase in the abundance of smelt, pike, and perch [25].

5. Discussion: Is it Possible to Recover the Lakes?

The example of long-term pollution of large lakes' bays in North-West Russia has revealed common features of the degradation of ecosystems, as well as similarities and differences in recovery processes after the reduction of anthropogenic stress. The theory of alternative states in restorative ecology has been developed, which shows that newly acquired properties of ecosystems achieve stability and ecosystems after anthropogenic perturbations cannot be identical to those that are natural [45–47]. Specific examples relate to the response of ecosystems to phosphorus reduction. It was shown that a decrease in phosphorus intake does not lead to the restoration of natural conditions, since the internal load is preserved and the ecosystem structure changes during the period of pollution [48–50].

In our studies, two exposure factors were considered—phosphorus loading and toxic stress. Odum [51] considers a small influx of organic matter and nutrients into the ecosystem as additional energy subsidies, while toxic pollution is a stress factor that increases energy dissipation. In the past, all three lakes were characterized as oligotrophic and freshwater, with low concentrations of salts, nutrients, suspended matter, and trace elements. The aquatic communities were mainly represented by cold-water stenobiontic species, as is characteristic of fresh waters of the North. For more than half a century, industrial activity in their catchments led to the flow of toxic and domestic wastewater into the ecosystem, which was released into the bays of the lakes. The lake ecosystems were modified by two active factors—energy subsidies in the form of nutrient influx and stressful conditions of toxic pollution (Figure 3).

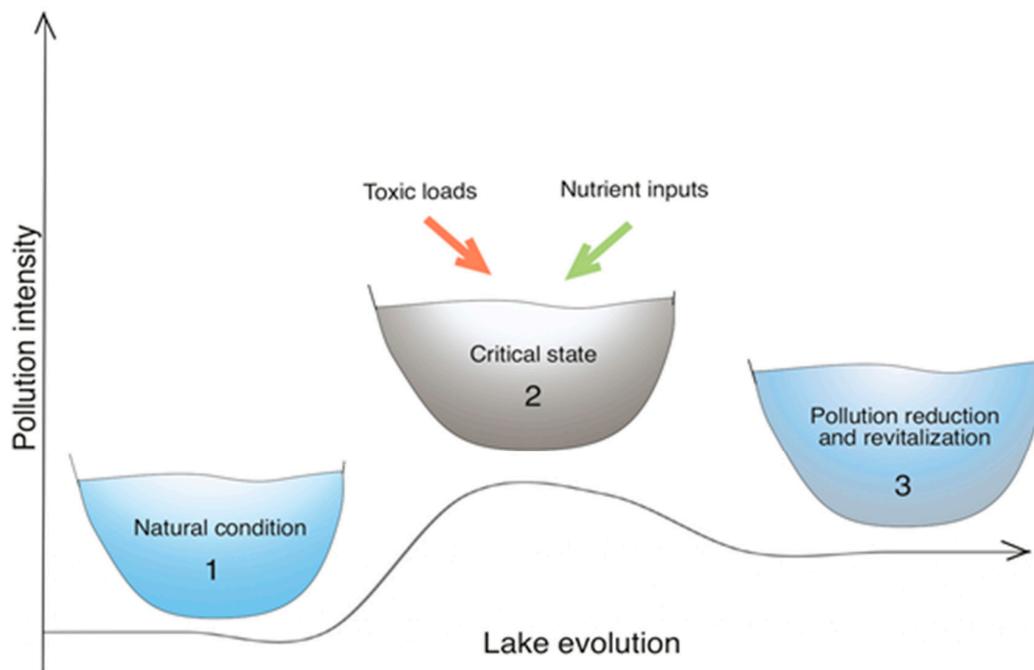


Figure 3. Features of the ecosystem state in different periods: (1) natural condition: biogeochemical cycles during periods of seasonal fluctuations are stable, the matter and energy intake is balanced by the respiration and production costs, and dominant species are constant due to the cold fresh waters; (2) critical state: production and destruction processes are imbalanced, the content of bioavailable forms of nutrients and toxic elements increases, and there is an increasing dominance of eurybiontic species in contrast to the decline in biodiversity in each community; (3) revitalization: bioavailable nutrient forms are utilized in newly formed biogeochemical cycles, the productivity of communities and their biodiversity increase due to eurybiontic species and introducers, and the species dominance and community structure are different from those of the natural state.

Comparing the key indicators of ecosystems (Figure 3) in all bays during the period of intensive pollution with signs of an unstable stress ecosystem (or at early successive stages of development), according to Odum, shows the lake ecosystems are transformed from a stable natural state into a new stage and that biogeochemical cycles are destroyed according to the observed signs that correspond to the developing stage (unstable) [51].

Let us highlight the main attributes characterizing the aquatic ecosystems of all three lakes' bays during their disturbance under the influence of multiple pollution based on the analysis of literature data [19,20,31]. Along with the increase in total phosphorus, the role of bioavailable forms (the ecosystem is not able to use it at this stage of transformation) increases and they become a reserve for the intensification of production processes and the growth of biomass.

Due to high concentrations of phosphates and nitrates, there is an increase in the biomass of primary producers—phytoplankton. The structure of phytoplankton biomass changes towards the prevalence of green and cryptophytic algae and cyanobacteria that are resistant to pollution. It is known that cryptophytic algae are capable of mixotrophic feeding and, being small-sized, provide a quick biomass cycle in the ecosystem.

In the communities of zooplankton and benthos, the abundance of typical northern species that are vulnerable to toxicants decreases, which leads to a decrease in the total species diversity. The abundance of eurybiontic species in zooplankton and benthic communities increases due to high concentrations of nutrients and the lack of competition with typical inhabitants of northern waters vulnerable to toxic effects. In zooplankton, the species dominance of eurybiontic species, small rotifers,

increases. In the benthic communities under the conditions of complex pollution, the formation of a high biomass of the chironomid–oligochaeta complex is traced.

The indicator of a nominal individual mass of organisms, as a characteristic of phyto- and zooplankton communities, decreases. This indicates the predominance of small forms, ensuring a faster cycle of biomass in the ecosystem and the utilization of additional energy subsidies (nutrients) in biogeochemical cycles. The share of predatory species in zooplankton and fish decreases.

The above attributes indicate the critical state of the ecosystems of the three lakes in areas of intense pollution and correspond to signs of their unstable stress state.

Since the 1990s, toxic and nutrient inputs have drastically decreased in the contaminated bays, which should theoretically indicate recovery trends. In the same period (the last two decades), according to a second assessment report on climate [52], along with a decrease in influx, a temperature increase in the North-Western regions of Russia has been proved (an average increase of 0.53 °C every decade). Introduced species have appeared that were not previously found in these lakes.

Against the background of persistently high concentrations of total phosphorus in the lakes, the concentration of bioavailable phosphates in water declines, which indicates their rapid utilization in the biogeochemical cycles of the ecosystem. In the Ladoga and Onega lakes (in the polluted bays), despite the decrease in the flow of phosphorus into the ecosystem, the maximum and average values of biomass and chlorophyll "a" concentration in the period of pollution reduction are as high as during the period of intensive pollution [21,22]. A similar phenomenon was noted in the Great Lakes, i.e., a delay of phytoplankton response to a decrease in phosphorus load. For example, in Ontario, from 1968 to 1985, there was a gradual decrease in phosphorus concentrations, the amount of which was halved by 1985. However, the production of phytoplankton and chlorophyll "a" concentration did not change until the early 1980s, and only in subsequent years was the oligotrophication trend of the lake defined [53,54]. With a decrease in the phosphorus concentration and an increase in the nitrates/phosphates (N/P) ratio during the recovery period, the dominance of cyanobacteria was replaced by cryptophytes. This phenomenon was observed in a number of lakes in Sweden and North America in response to a decrease in the phosphorus load [55,56]. In Lake Ladoga, during the recovery period, cryptophytes developed dramatically [22]. They have a high production/biomass (P/B) ratio and high biomass cycle [57].

We observed a gradual decrease in the Si content during the recovery period, along with a decrease in bioavailable forms of phosphorus. The source of Si is the chemical weathering of rocks and in water systems, and it is absorbed by diatoms. A decrease in the concentration of phosphorus during both intense pollution and the recovery period indicates the predominance of absorption processes by developing diatoms over its intake due to the chemical weathering of rocks. Biosilicification drives a decline of dissolved Si, both in freshwater and marine ecosystems, as confirmed in scientific publications [58,59].

The species diversity of zooplankton communities has increased and the number of the largest forms in planktonic communities, and therefore, the conditional individual mass of organisms has increased accordingly [60,61].

Benthic communities are more resistant to recovery and their biodiversity is still low compare with plankton. The formation of a new structure is evidenced by, e.g., the mass development of a predatory species, such as *Monoporeia affinis* in Lake Imandra. This species has a developmental advantage under the conditions of a reduced toxic load and favorable feeding conditions.

The benthic communities of the littoral zone of Ladoga and Onega have recently undergone significant structural changes under the influence of the so-called "biological contamination"—an invasion of the Baikal amphipod *Gmelinoides fasciatus* (Stebbing) [22,35,62]. Due to high quantitative indicators and production rates, it is quickly included in the ecosystem processes of the transformation of matter and energy. The perch nutrition includes the new species and thereby becomes included in food chains [23]. The penetration of *G. fasciatus* into Lake Ladoga and Lake Onega led to an increase in the productivity of benthic communities and the more efficient utilization of energy entering the

littoral area. The studied feeding habits [22] of *G. fasciatus* make it possible to conclude that this species has occupied a free ecological niche using trophic resources that were not consumed before.

Until the mid-2000s, among the amphipods in the littoral of Lake Ladoga, the aforementioned colonizer *G. fasciatus* dominated, which entered Lake Ladoga in the late 1980s. In 2006, a new species was first found in the lake at the confluence of Volkhov River—a representative of the Ponto–Caspian complex *Pontogammarus robustoides* G. O. Sars. However, in 2009, it was revealed that *P. robustoides* had already become the dominant amphipod species in Volkhov Bay. In different parts of the littoral zone, its abundance varies from 700 to 1300 spc./m², and its biomass ranges from 3 to 14.5 g/m² [22]. *Pontogammarus*, as well as Gmelinoids, exhibit pronounced euryphagia and are able to consume a wide range of plant and animal food [63]. In 2009, another alien species, the amphipod *Chelicorophium curvispinum* (G. O. Sars), was first discovered in Volkhov Bay of Lake Ladoga. The abundance of *C. curvispinum* varied from 56 to 1480 spc./m², its biomass ranged from 0.13 to 1.6 g/m². These species were represented all age stages, including females with eggs. This fact indicates that *C. curvispinum* has also been acclimated in Lake Ladoga. The discovery of new alien invasive amphipod colonizers, *P. robustoides* and *C. curvispinum*, in Lake Ladoga, makes it very necessary to conduct further detailed studies of the spread of new species in Lake Ladoga because of the new threats of ecosystem rearrangements in the littoral area of the largest European lake.

The analysis of the literature [22,24,25,28,43,44,60,61] indicates that during the period of a reducing anthropogenic load, a new species structure of communities is formed that is different from the natural one: (i) nutrients are involved in biogeochemical cycles, as evidenced by their low concentrations of bioavailable forms in relation to high total contents; (ii) a number of species characteristic of the natural state are not recovered or are found in single-unit abundance; (iii) dominance changes in communities, e.g., species that are single in their natural state, develop in high abundance; and (iv) new introduced species are emerging that are actively exploring new ecological niches.

These facts show that ecosystem recovery not only depends on the improvement of habitat status but is also controlled by complex ecological mechanisms. One of these mechanisms is employed to maintain the involvement of nutrients in the biogeochemical cycle in a newly formed ecosystem, which makes it difficult for the ecosystem to return to early successional conditions. The second mechanism is the role of the internal load, which is highlighted in other work [48–50]. Our studies on Lake Imandra showed the development of an oxygen deficiency and the appearance of a redox cycle in the bottom horizons, involving a large group of toxic metals. It was proved that iron and manganese are involved in the bottom cycle as well as a large group of toxic metals [64]. Perhaps this phenomenon can cause the inertia of benthic communities to recover while reducing toxic metal pollution.

Another feature of the impact of polluted bays which are not isolated from the lake should be noted. On the one hand, there will be the resettlement of adapted species from pollution zones, and on the other hand, the migration of new recruits to pollution zones. Therefore, to one degree or another, these pollution zones can affect other parts of the lake.

The signs of the state of the ecosystem after the decrease in the toxic pressure indicate a tendency to form mature, more stable modification, resulting in a system different from the natural one. This path of transformation from a natural state through disturbance to recovery, to some extent, is consistent with the laws of ecosystem succession [51]: from the natural state through the developmental stage to a more stable climax modification.

It is difficult to answer the question of how large the climate contribution is to this transformation. In the community structure, an increase in the number of more thermophilic species and the productivity of ecosystems that could have been affected by climate warming is noted. Additionally, introduced species appear.

The following question arises: is it possible to return to the natural state after toxic disturbance or does the lake ecosystem acquire a new structural and functional organization?

The theory of restorative successions after anthropogenic perturbations is covered in a number of fundamental studies [11,13,47]. The restoration of ecosystems occurs according to laws that are

inherent in nature, i.e., within the natural succession of ecosystems, for example, the settlement of newly formed lakes and their natural aging. Undoubtedly, it is important to restore the conditions that characterized the lakes in their natural state, but according to most researchers, this should not be a guide for the formation of future ecosystems. Corporate evolutionary development must be factored into ecosystem restoration. According to [47], it is important to maintain ecosystems and restore their stable functions that serve the benefit of man, i.e., high water quality, biodiversity, and productivity.

The considered example of anthropogenic modifications of the northern aquatic ecosystems (polluted bays of Imandra, Ladoga, and Onega lakes) demonstrated that ecosystems, after their disturbance, do not pre-establish in a natural condition, which has also been noted by several authors [6,7,9,11,46,65]. Therefore, in this case, the term “ecosystem recovery” cannot be identified with the concept of returning to a pre-industrial state.

6. Conclusions

Aquatic ecosystems of lakes suffer from multi-contaminant stress. Therefore, both degradation and recovery proceed in a complex, non-linear, and often unpredictable way. Ecology theory plays a key role in the understanding of anthropogenic successions and patterns of recovery. If we know the trajectory of changes in biogeochemical cycles, as well as the succession of communities and ecosystems under the conditions of increasing and decreasing anthropogenic loads, we can more accurately direct practical actions to accelerate ecosystem recovery processes. The past state should not be a target function for ecosystem recovery. It is necessary to maintain ecosystems and their stable biogeochemical functions that are beneficial to humans, i.e., high water quality, biodiversity, and productivity.

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