LONG-TERM CHANGES IN THE LARGE LAKE ECOSYSTEMS UNDER POLLUTION: THE CASE OF THE NORTH-EAST EUROPEAN LAKES

ABSTRACT. A retrospective analysis of aquatic ecosystem long-term changes in the Russian large lakes: Ladoga, Onega, and Imandra, is given. The lakes in the past were oligotrophic and similar in their origin, water chemistry and fauna. The ecosystems transformed under the impact of pollution with toxic substances and nutrients. There are three stages of ecosystem quality: background parameters and degradation and recovery trends after the decrease of the toxic stress. On the stage of degradation, species abundance and community biodiversity were decreased. Eurybiontic species abundance and biomass were increased due to lack of competitive connections in toxic conditions and biogenic inflow. Small forms of organisms (r-strategists), providing more rapid biomass turnover in ecosystem, dominated in the formed plankton communities. On the stage of decrease of the toxic pollution, the lakes recolonization with northern species occurs, which is confirmed by replacement of dominating complexes, increasing index of plankton community biodiversity, and the rise of the mass of individual organisms of the communities. Accumulated nutrients in ecosystems are efficiently utilized at the upper trophic level. The ecosystem state after decrease of the toxic impact indicates formation of its mature and more stable modification, which differs from a natural one.

KEY WORDS: long-term pollution, aquatic ecosystem, reference condition, disturbance, recovery.

INTRODUCTION
Prolonged anthropogenic pollution of the environment, which dates back to the period of industrial revolution in the 18th century, dramatically manifested itself in negative environmental changes in the mid-19th century. Numerous investigations have given insight into the regularities of the anthropogenic environmental transformations and the responses of biologic systems to anthropogenic stress and revealed the severe hazard of environmental pollution by toxic substances.
In view of the cardinal importance of fresh water for the survival of the Earth’s population and its species diversity, the importance of the recovery of aquatic ecosystems and the preservation of their habitat is also evident.

It is worth mentioning that, as a rule, aquatic ecosystems experience a multi-contaminant stress. Hence, their degradation and recovery develop in a complicated, non-linear, and often unpredictable way. The ecological theory plays a key role in understanding the anthropogenic successions and the regularities of recovery. If the trajectories of successions of communities and ecosystems under the conditions of increasing and decreasing anthropogenic loads are known, it is possible to efficiently accelerate the processes of ecosystems recovery. The recovery of aquatic ecosystems due to decreasing anthropogenic inputs, including toxic pollutants, has been well documented in the scientific literature [Cairns, 2005; Harris, 2006; Palmer et al., 2007]. During the latest years, there has been a distinct tendency towards the decline of dangerous pollutants’ stream into environment, including water. Science has been compiling information on ecosystems recovery after the contaminating disturbance. However, only recently scientists have been attempting to predict all the scenarios of ecosystems recovery, including their successions after toxic disturbance [Cairns, 2005]. Many scientists raise a question: is it possible for ecosystems to recover after toxic disturbance, or they attain a new configuration?

Water ecosystems, as a rule, suffer multi-contaminating disturbance and that is why such processes as degradations and recoveries proceed completely, non-linearly, and often incalculably. The ecology theory plays a key role in understanding of anthropogenic successions and recovery mechanism. Knowing trajectory of successions of communities and ecosystems in conditions of increasing and decreasing pressure, one can coordinate actions aimed at acceleration of ecosystem recovery processes [Depledge, 1999; Palmer et al., 2007].

The representative example of long-term multi-contaminating pollution is the large Russian lakes: Lake Ladoga, Lake Onega and the subarctic lake of Imandra (Fig. 1). These three lakes, situated in the North-West of Russia, are characterized by one genesis of ecosystem formation during the postglacier period; for this reason they have common characteristics of water chemistry, as well as of fauna.

Objectives:

- to make a retrospective analysis of conditions of ecosystem elements and estimate their reference conditions on the base of a time-space analysis of dominant characteristics of the ecosystems;
- to reveal the main consistent patterns of successions of water ecosystems of northern lakes under anthropogenic load and their reduction: from background characteristics – through degradation – to recovery;
- to explain the trajectory of these changes according to the ecology theory and to estimate the ability of ecosystems to recover after toxic disturbance.

This paper is based on an analytical review of the relevant published results and also on more than 30-year investigations of the authors in this region [Krokhin, Semenovich, 1940; Moiseenko et al., 1996; Moiseenko, Yakovlev, 1990; Moiseenko, Kudrjavtzeva, 2002; Antopogenic Modification, 2002]. Although much information is available, there has been no continuous long-term monitoring of the lakes and, therefore, this paper is based on discontinuous information. In this review, attention is focused on the main parameters of water chemistry and key indicators of phytoplankton, zooplankton, benthos, and fish conditions that reflect ecosystem changes during different periods for Volkhov Bay of Ladoga Lake, Kondopoga Bay of Onega Lake and the Bol’shaya Imandra basin that suffered from the pollution of water with toxic agents and nutrients.
Fig. 1. Map of Imandra, Onega, and Ladoga lakes and locations of the main industries on their shores.
CHARACTERISTICS AND REFERENCE CONDITIONS OF THE LAKES

Lakes of Ladoga, Onega, and Imandra are situated in the North-Taiga ecoregion in the European part of Russia; Imandra lake is above the Polar cycle. Knowledge of reference conditions (ecological conditions found at undisturbed or minimally disturbed sites) is important when trying to manage anthropogenic stress [Falk et al., 2006]. The background conditions of the lake prior to industrialization provide a benchmark for water quality and ecosystem recovery.

Ladoga, which is the largest lake of Europe, is one of the 15 largest freshwater reservoirs in the world. The state of the environment in the Ladoga area affects the life standard of several million people living in 258 300 km² of the lake watershed area, which includes a great part of the Russian north-west and eastern Finland. Lake Ladoga covers an area of 17 700 km² (with its islands, 18 135 km²). The main feeder rivers are the Volkho, Svir, and Vuoksa, and the lake’s outlet is by way of the Neva River into the Gulf of Finland. Its maximum depth is 230 m.

Onega is the second largest lake in Europe after Lake Ladoga. The area of the lake is 9800 km², and the volume is 262 km³, with average and maximum depths of 30 and 120 m, respectively. Its watershed covers about 56 300 km² (including the lake itself), equaling to a quarter of the Lake Ladoga watershed area.

Imandra is situated within the Arctic Circle in the Kola Peninsula, Russia. The lake has an area of 813 km² (with its islands, 880 km²) with a catchment area of 12 300 km² and the volume of 11 km³. The lake has a complex shoreline and consists of three main basins connected by narrow passages, with maximum and average depths of 67 and 13 m, respectively.

The climatic factors of the North (high influence of atmospheric inputs, low temperatures, thin layer of soil, slow chemical weathering processes, and slow element cycling) form clear waters (the sum of ions is 20–55 mg/l). Prior to the 1930s, the lakes were typically oligotrophic with hydrocarbonate–calcium salt contents, low concentrations of suspended material and microelements; phosphor content (especially its bioavailable phosphates) was too low. High N/P ratio (43–45) limit productional processes by phosphor content. In general, nutrients and organic substances increase from arctic Imandra Lake to Ladoga, located in the Northern Taiga. Water inhabitants of the three lakes are typical oligotrophic cold-water species. Content and structure of phytoplankton from the investigated lakes is mainly similar to the content and structure of deep oligotrophic lakes [Lake Onega..., 1999; Lake Ladoga..., 2002; Anthropogenic modification..., 2002]. Dominant species in the three lakes are shown in Table 1, basic quantitative indexes, describing condition of natural ecosystems of these lakes during the pre-industrial period, are shown in Table 2. The table is compiled using data from: Voronikhin (1935); Poretskij et al. (1934); Krokhin and Semenovich (1940); Berg and Pravdin (1948); Sokolova (1956); Petrova (1987, 1971); Moiseenko and Yakovlev (1990), Petrovskaya (1966); Nikolayev (1972); Vandish (2002); Anthropogenic eutrophication... (1982); Sabylina (1999); Yakovlev (1998); Iliyashuk, B.P. (2002), Lake Onega... 1999; Lake Ladoga... 2002; Anthropogenic modification... 2002.

In the middle of the last century (1940s) diatoms, in particular Aulacoseira islandica, predominate in phytoplankton of Imandra, Ladoga, and Onega. Values of phytoplankton biomass were low, which is typical of oligotrophic northern lakes [Petrova, 1987]. Crustacea Cladocera and Copepoda typically dominated in zooplankton of Ladoga, Onega, and Imandra [Sokolova, 1956; Petrovska, 1966; Nikolayev, 1972; Vandish, 2002]. Midge larvae (Chironomidae), bivalves (Euglesa spp.) and crustacea (Monoporeia affinis, M. relicta, Pallasiola quadrispinosa) dominated in zoobenthos of the lakes. Oligochaeta...
Table 1. Dominating complexes of community structure of the Russian large lakes: Imandra, Onega, and Ladoga during the key periods of ecosystem modification

| Reference condition          | Intensive pollution and degradation          | Decreasing pollution and recovery            |
|-----------------------------|----------------------------------------------|---------------------------------------------|
| **Phytoplankton**           |                                              |                                             |
| Asterionella formosa, Dinobryon spp., Aulacoseira distans, A. italica, Tabellaria fenestrata | Aulacoseira islandica, Diatoma elongatum, Pandorina morum, Eudorina elegans, Microcystis | Asterionella formosa, Tabellaria fenestrata, Cryptomonas spp., Stephanodiscus spp. |
| **Zooplankton**             |                                              |                                             |
| Bosmina spp., Eudiaptomus gracilis, Conochilusspp., Killicotia longispina | Daphnia cristata, Synchaeta pectinata, Polyarthra sp., Bosmina obtusirostris | B. obtusirostris, Eudiaptomus gracilis, Kellikottia longispina, Asplanchna priodonta, Polyarthra spp. |
| **Zoobenthos**              |                                              |                                             |
| Trissocladius paratriticus, Tanytarsus spp., Monoporeia affinis, Pallasiola quadrispinosa, Procladius spp. | Chironomus spp. Procladius, Tubifex tubifex, | Monoporeia affinis, Tubifex tubifex, Chironomus spp., Tanytarsus spp., Procladius spp. |
| **Ichthyofauna**            |                                              |                                             |
| Salmo trutta, Coregonus lavaretus, C. albula, Salvelinus alpinus, Thymus thyallus | C. lavaretus, C. albula, Esox lucius, Perca fluviatilis, Phoxinus phoxinus | Coregonus lavaretus, C. albula, Esox lucius, Perca fluviatilis, Osmerus eperlanus |
Table 2. The main indicators* of water quality and community conditions of Russian large lakes during the key periods of ecosystem changes:
1 – reference condition, 2 – intensive pollution and degradation, 3 – decreasing pollution and recovery

| Variable                  | Periods | Lakes            |
|---------------------------|---------|-----------------|
|                           |         | Imandra | Onega | Ladoga |
| Ptot/PO₄, µg/l            | 1       | 6/1     | 8/1   | 10/3   |
|                           | 2       | 26/21   | 54/30 | 178/100|
|                           | 3       | 26/2    | 24/5  | 34/9   |
| Ntot/NO₃,µg/l             | 1       | 260/17  | 350/110| 450/130|
|                           | 2       | 436/102 | 750/120| 920/240|
|                           | 3       | 395/19  | 648/85| 890/230|
| Si, mg/l                  | 1       | 1121    |       |        |
|                           | 2       | 1.1     | 1.2   | 0.5    |
|                           | 3       | 0.42    | 0.1   | 0.2    |
| Chl “a” , mg/m³           | 1       | 0.3     | 0.7   | 0.7    |
|                           | 2       | 3.8     | 8.4   | 8.0    |
|                           | 3       | 3.6     | 6.8   | 7.9    |
| Toxic loads (ΣCi/MPCi)**  | 1       | 0.1     | 0.1   | 0.1    |
|                           | 2       | 3.2     | 0.7   | 0.8    |
|                           | 3       | 1.0     | 0.6   | 0.5    |

**Phytoplankton**

|                      |         | Imandra | Onega | Ladoga |
|----------------------|---------|---------|-------|--------|
| Biomass, g/m³        | 1       | 0.1     | 0.1   | 0.5    |
|                      | 2       | 3.6     | 2.4   | 5.5    |
|                      | 3       | 3.4     | 1.7   | 2.1    |
| Number, cell 10⁶/l   | 1       | 0.1     | 0.1   | 0.4    |
|                      | 2       | 3.8     | 3.6   | 12.3   |
|                      | 3       | 3.2     | 2.5   | 3.4    |
| H (Shannon’s index), bit/spec. | 1 | 3.2 | 3.7 | 3.4 |
|                      | 2       | 2.5     | 3.3   | 3.1    |
|                      | 3       | 3.1     | 3.8   | 3.6    |

**Zooplankton**

|                     |         | Imandra | Onega | Ladoga |
|---------------------|---------|---------|-------|--------|
| Biomass, g/m³       | 1       | 0.3     | 0.1   | 0.6    |
|                     | 2       | 1.7     | 2.9   | 2.8    |
|                     | 3       | 1.2     | 1.1   | 0.9    |
| Number, spec. 10⁹/m³| 1       | 15      | 3     | 13     |
|                     | 2       | 271     | 110   | 143    |
|                     | 3       | 107     | 80    | 34     |
were represented by the Lumbriculidae and Naididae families [Krokhin and Semenovich, 1940; Gerd, 1949; Sokolov, 1956; Alexandrov, 1968]. These lakes were typical whitefish lakes with the presence of trout and loach: *Coregonus albula* (L) is the main plankton feeder; *Coregonus lavaretus* (L) is the main benthophage. Among carnivorous fish lake salmon (*Salmo trutta trutta* (L)) dominates in Ladoga and Onega lakes; arctic char (*Salvelinus alpinus* (L)) dominates in Imandra lake [Galkin, 1966].

### ANTHROPOGENIC LOADS AND ECOSYSTEMS DISTURBANCE

Considerable industrial expansion in the 1930s resulted in the building of large industrial enterprises in the lake catchments. In the beginning of the last century, the first aluminum plant, pulp and paper factory and other plants were built on the shore of Ladoga Lake (Volkhov Bay). Plant pollution with phenols, lignosulfate, benzopyrene, and other toxic agents reached its maximum by the end of the 1960s. Phosphor load was associated with flux of toxic agents with industry wastewater (especially after using new raw materials by the aluminum plant: phosphorus-containing apatite-nepheline ores) and with wastewaters of the Volkhov town. According to scientists’ estimates phosphor flux into the lake increased a hundred times: in the 1970s–1980s, phosphor load was 6–7 thousand ton/year (Volkhov Bay’s part was 50–60% of the total value) [Lake Ladoga..., 2002]. It should be noted, that the area of this bay amounts only to 8% of the whole lake.
Lake Onega is polluted by wastewater of the largest in the country pulp-and-paper plant. The Kondopoga Bay receives large amounts of industrial wastewater and domestic sewage, which contains toxic pollutant and nutrients. Its area is less than 3% of the lake. The plant operated without waste-water treatment facility for 30 years. Wastewater treatment system was forced into application in the 1980s, however phosphor and nitrogen compounds were additionally applied as agents. Phosphor load to the Bay area increased to 0.56 g/m² per year and the nitrogen load reached 11.1 g/m² per year. However total phosphor load to the lake was 0.1 g/m² per year [Sabylina, 1999].

Lake Imandra has been subjected to more severe pollution than many Arctic lakes. Industrial development of copper- and nickel-rich, apatite-nephelinite, and iron deposits in the catchment area of Lake Imandra began in the 1930s. Anthropogenic pressure on the Imandra Lake began in the 1940s and reached its peak in the 1980s. Data are available for 1983–1992, when the effects of pollution were most evident. The lake was subjected to pollution by a number of contaminants including heavy metals, nutrients, sulphates, and chlorides. The main pollution occurred in the northern part of the lake (i.e., Bol’shaya Imandra) (38% of the all lake area).

Pollution of the lakes with toxic mixture of substances was dramatic. It is difficult to estimate exact dimensions of toxic flow into the ecosystems, but even available limited information is indicative of high toxic stress for water dwellers in the period of intense water pollution. In this period, industrial activity went with uncontrollable toxic wastewater and sewage bled-off into sections of the lakes. Thus, toxic pollution of the lakes went with the bulk input of nutrients (phosphor and nitrogen). Polluted bays (in Ladoga – Volkhov Bay; in Onega – Kondopoga Bay; in Imandra – White Bay) satisfy eutrophic condition by phosphor content (according to the R.A. Vollenweider classification, 1979) and adjacent large areas satisfy mesotrophic condition.

Water chemistry changes in all three lakes in the period of pollution were similar in type: water clarity has decreased; pH level, sulphates, chlorides, and biogenic elements content has increased; change in contaminants with toxic properties have also occurred. Thus, in the period of intense pollution habitat conditions for aquatic organisms in the analyzed bays became different from their native characteristics, and new property – water toxicity – has occurred and involved changes of structure of all ecosystem units (see Table 2).

During the summer period, phytoplankton biomass in polluted lake bays increased 20–30-fold because of large dimensions of nutrients input. Intensive cyanobacterial blooms were observed in Ladoga and Onega Lakes; in the arctic lake of Imandra they occurred to a lesser degree. Structural changes of phytoplankton community promoted intensive development of species, typical of eutrophic waters: blue-green, green, and cryptophyte algae dominated in that period (see Table 1).

In the period of intensive pollution of the lakes, zooplankton structure changed towards the dominance of eurybiontic species. Percentage of rotifers in the zooplankton structure in Imandra increased to 60%, which occurs because of rotifers’ high resistance to the impact of contaminants. At the same time, percentage of such specific northern water dwellers as Collotheca sp., Conochilus sp., Holopedium gibberum decreased. According to the data from [Vandish, 2002], total biomass of zooplankton community increased, whereas species diversity index decreased. Abundance of rotifers in Ladoga and Onega increased, whereas abundance of typical northern crustacean species decreased.

The total abundance and biomass of zoobenthos in the pollution zones of all lakes have steeply risen while their biodiversity
have decreased. Communities with high abundance and restricted biodiversity of Chironomus, Procladius, Nematoda, Tubifex tubifex, Limnodrilus hoffmeisteri developed in the contamination area. Species diversity index in the severely polluted zones was less than 1–2 bit/spec. Oligochaetes (up to 200 g/m²) and Chironomidae (up to 50g/m²) abundance dominated in benthos of Imandra Lake. At the same time, the ratio of pollution-sensitive Chironomidae larvae and bivalve mollusks decreased by more than 50%. One of two epibiotic crustaceans seen in Imandra Lake before (i.e., M. relicta) has probably petered out of the fauna. M. affinis appeared to be more resistant to heavy metals and biogenic elements polluting the lake [Moiseenko and Yakovlev, 1990].

Dramatic pollution of Ladoga and Onega lakes occurred in the period of flood-release outlet from the pulp-and-paper production and the total annihilation of bottom communities was observed [Polyakova, 1999; Slepukhina, 1992; Belkina et al., 2003]. Communities of some resistant species of chironomid-oligochaete complex were formed in conditions of moderate pollution. Rather large-size chironomids formed 10–50-fold higher biomasses in comparison with natural values thriving on organic substances and nutrients. Oligochaetes dominated in the zones with decreased toxicity and high accumulation of organic matter in the bottom silt.

Abundance of trout and loach in fish community significantly decreased because of their high water pollution sensitivity. These species completely disappeared in commercial catches of Imandra. Whitefish abundance decreased. Such diseases of whitefish as nephrocalcitosis (kidney stones), lipoid liver, cirrhosis, etc. were recorded also. Case frequency rate (% of those surveyed) was closely related to nickel concentration in water and its accumulation in kidneys [Moiseenko and Kudriavtseva, 2002]. Lake salmon abundance in Ladoga and Onega had decreased dramatically [Lake Onega..., 1999; Lake Ladoga..., 2002].

Productive areas of benthic communities developed and zoobenthos biomass increased, which attracted whitefish. By migrating to these food-rich areas, fish were exposed to the effects of toxic contaminants [Moiseenko and Yakovlev, 1990]. Disease occurrence of fish in these areas was dramatic, and the lethal outcome for the fish after staying was high. Criteria to determine fish conditions (by physiological indicators of intoxication) are important for assessing toxic effects and are used as integral parameter of ecosystem health [Adams and Ryon, 1994]. Using these criteria, fish diseases indicated the dramatic state of ecosystem health in Lake Imandra during the period of intensive pollution.

**TENDENCY TO RECOVERY**

In the 1990s, the anthropogenic load on the lakes decreased. Tendency to improvement of water quality and ecosystem recovery occurred in response to decreasing anthropogenic load to the Volkhov (Ladoga) and Kondopoga (Onega) Bays and reaches of Imandra.

Toxic matter concentration in water of the analyzed bays decreased: concentration of nickel as a major marker of pollution in Imandra decreased from 150 to 10 μg/l; concentration of lignosulphates and phenols, as markers of pulp-and-paper industry pollution, decreased in the Kondopoga Bay of Onega; concentrations of lignosulphates and phenols in Ladoga also decreased (see Table 2).

Concentration of common phosphorus forms in Ladoga and Onega decreased; whereas in Imandra, they remained at the same level; concentration of common nitrogen decreased in all three lakes only slightly. Concentrations of bioavailable phosphates and nitrates significantly decreased (6–20-fold), which indicates their more active utilization in the changed trophic ecosystem structure. Dynamics of silicon is of particular interest; its concentration did not improve and kept decreasing steadily, due to more
active absorption of it by developing diatoms.

Phytoplankton abundance decreased in the Volkhov Bay of Ladoga and the Kondopoga Bay of Onega; phytoplankton abundance in Imandra remained the same. Average biomass values in the lakes varied from 1.7 to 3.4 g/m³; chlorophyll “a” concentrations varied from 3.6 to 7.9 mg/m³. There was still a high abundance of species of the genera Cryptomonas, Stephanodiscus и Aulacoseira islandica. Relative abundance of cryptomonades, bluegreen, and green algae was still high in the phytoplankton structure.

In spite of the decrease of phosphor load in the bays of Ladoga and Onega in the period of recovery, maximal and average indexes of biomass and chlorophyll content remained very high in comparison with natural values. From the end of the 1990s to the beginning of the 2000s, the index of zooplankton community abundance had decreased and the biodiversity index had increased in the analyzed bays of Ladoga, Onega, and Imandra lakes (Table 2). Biomass had also decreased, but not so greatly, because of increasing abundance of larger Cladocerae (Bosmina obtusirostris) and Copepoda (Cyclops sp., Cyclops, Mesocyclops leuckarti) and depletion of ratio of small rotifers, typical pollution indicators. Valuable food Cladocerae (Holopedium gibberum, Daphnia sp., L. kindtii), which used to affect the lake before the peak of pollution, recovered. However, there was still only a trace amount of the most pollution-sensitive crustaceans (Leptodora kindtii, Polyphemus pediculus, Eudiaptomus graciloides, Heterocope appendiculata). Cladocera and Copepoda dominated in zooplankton in the Volkov Bay of Ladoga lake [Lake Onega..., 1999, Lake Ladoga..., 2002, Anthropogenic modification, 2002].

Zoobenthos was very slow to recovery. Its biomass in Imandra decreased, but it kept rising in Ladoga and Onega. Oligochaete-Chironomidae complex with the dominance of worms still dominated in benthos of the northern part of the Kondopoga Bay of Onega Lake, but epibiotic Amphipoda was not found there. During a 30-year period of operation of the wastewater treatment facilities that promoted dissipation of polluted waters, the conditions of benthos in the Kondopoga Bay improved; the number of species rose more than forty-fold and its biomass increased over twenty-fold, on average, compared to 1964 (the beginning of the observations.) In conditions of a significant decrease of toxic load and of good nutrients supply, epibiotic crustaceans M. Affinis dominated among invertebrates in profundal benthos of the arctic lake (the stretch of Bol’shaya Imandra). Their relative abundance grew almost twice – from 36% to 60% [Iliayashuk, 2002].

Abundance of valuable Salmonidae and Corigongidae did not grow in fish fauna, whereas pike and perch abundance increased. In response to the toxic load decrease, the incidence of fish diseases in Imandra Lake fell. According to the findings of 2003, fish’s physiological state improved [Moiseenko et al., 2006]. There are no such data about the other lakes. It should be noted, that during this period, there was an increase of illegal catch volume, which together with pollution and eutrophication could impact fish communities structure. It is complicated to define the determining factor of successions of fish communities, since it is impossible to take a proper account of real numbers of fish caught from the lake.

SIMILARITIES OF LAKE ECOSYSTEMS DEGRADATION AND RECOVERY

Often, modern changes of ecosystems under the impact of anthropogenic load do not have analogues in the past; that is why, in order to understand ecosystems recovery processes, it is necessary to apply theoretical principles of ecology to investigations of processes of community development and structure occurring with time [O’Nail, 1999; Falk et al., 2006; Palmer et al., 2007]. Ecosystems are self-regulating...
systems that have developed mechanisms for self-repair [Odum, 1985]. Following a decrease or removal of anthropogenic stress, natural processes bring the system back to the near equilibrium state [O’Nail, 1999]. The investigation of long-term pollution of the bays in the large lakes in the North of the European part of Russia has revealed common characteristics of ecosystems degradation and similarities of recovery processes after the anthropogenic stress decrease. All three lakes were characterized as oligotrophic with low concentrations of nutrients, suspended matter, and microelements. Dominant ichthyofauna consisted of psychrophilic stenoecic species typical of cold oligotrophic water in the North.

For more than half a century, industrial activity on the shores of the lakes had resulted in release of toxic elements and sewage into the ecosystems of the same zones of the lakes. According to [Odum, 1985], a limited influx of organic matter and nutrients into ecosystems represents an additional energy input, whereas a toxic contaminant is a stress factor, intensifying energy dissipation. The lakes’ ecosystems changed under the impact of two factors – energy input of nutrients influx and stress of toxic contamination. Applying Odum’s theory of the early succession stages of development and of unstable stressed ecosystems [1985] to the key indicators observed in the ecosystems of all three bays in the period of intensive pollution, it becomes clear that the lakes’ ecosystems have transformed from their stable natural state to a new phase that may be considered as a development stage. Let us now discuss attributes, characterizing water ecosystems of the three lakes in the period of their disturbance under the impact of multi-pollution.

Together with the growth of content of total phosphor, bioavailable forms (orthophosphate) grow too; the ecosystems are not able to utilize bioavailable forms at this stage of transformation and they become reserves of intensification of the production processes and biomass growth. Due to a high phosphor concentration, growth of biomass of primary producers (phytoplankton) occurs. The structure of the phytoplankton biomass changes towards the dominance of blue-green, green, and cryptophyte algae, as well as of pollution resistant algae. It is known, that mixotrophic nutrition is a feature of cryptophyte algae, and they provide rapid biomass turnover in ecosystems due to their small size.

The abundance of typical northern species, vulnerable to toxicants (see Tables 1 and 2), in zooplankton and benthos communities fell, that results in decrease of the total species diversity. The abundance of eurybiontic species in zooplankton and benthos communities grows owing to high concentrations of nutrients and lack of competitive connections with the typical dwellers of the northern water, vulnerable to toxic impact. Eurybiontic species dominance in all communities increases. Small size rotifers dominate in zooplankton communities. It is possible to retrace the process of formation of the high biomass of organisms of the chironomids-oligochaete complex in the benthos community in conditions of integrated pollution. Decrease of the nominal individual mass, typical for phyto- and zooplankton communities, indicates the dominance of small forms (r-strategists), providing more rapid biomass turnover in the ecosystem and utilization of energy subsidies, received additionally. Percentage of predatory species in zooplankton and fish decreases. The observed features indicate the critical state of the ecosystems of the three lakes in the zones of intensive pollution and correspond to the characteristics of their unstable stress state.

Let us consider, what kind of configuration ecosystems have after decrease of toxic pollution and to what extent they conform with a more stable (mature) modification in compliance with Odum’s ecology theory [1985].
At the background of high concentrations of total phosphor in the three lakes, the concentration of bioavailable phosphates decreases because of their rapid utilization in a new trophic structure of the ecosystems. In spite of decrease of phosphor flux into the ecosystems of Ladoga and Onega (in the polluted bays), the values of maximal and average biomass and the chlorophyll content during the period of pollution decrease are almost as high as during the period of intensive pollution.

A similar phenomenon occurred in the Great Lakes, i.e. the delayed response of phytoplankton to the decrease of phosphor load. For example, from 1968 to 1985, phosphor concentrations had been slowly decreasing in Ontario, and, by the 1985, they have decreased two-fold. However, the production of phytoplankton and chlorophyll "a" did not change before the beginning of the 1980s, and the tendency of the lake's oligotrophication appeared only in the subsequent years [Grey et al., 1994; Great Lake Ecosystem report, 2000]. The dominance of the blue-green algae was replaced by the dominance of the cryptophyte algae along with the decrease of the phosphor concentration and increase of the N/P ratio during the recovery period. This phenomenon also occurred in response to the decrease of phosphor load in a number of lakes in Sweden [Willen, 1987]. In Ladoga, cryptophytes algae have progressively developed during the recovery period. They have a high P/B ratio with a high rate of biomass turnover [Lake Ladoga..., 2002].

The species structure of the communities differed from the natural state: a number of species, typical for the natural conditions, did not recover or the recovery occurred only in isolated cases; dominance in the communities changed, e.g. species, which are solitary in nature, greatly increased in numbers; introducents appeared. At the same time, the biomass of zooplankton decreased, which can be explained by two factors: 1) an increase in the predominance of predatory forms in these zooplankton communities and 2) the increase in a number of fish due to reduced pressure on the population.

The species diversity of zooplankton communities grew, and the number of large forms (K-strategists) and prey organisms in its structure rose also; the nominal individual mass of the organisms increased respectively. Benthos communities were less active in recovery; their biodiversity was still low. However, large growth of prey species – relict crustacean M. affinis – in Imandra Lake indicates formation of a new structure. This species has an advantage in its development in conditions of the decrease of toxic load and favorable feeding. Water communities of Ladoga and Onega have also undergone considerable structural transformations under the impact of invasions of the Baikal amphipod Gmelinoides fasciatus (Stebbing) [Ladoga Lake..., 2002; Berezina and Panov, 2003]. Due to high numbers and rates of production, it rapidly gets involved in the ecosystems’ processes of transformation of matter and energy.

CONCLUSION
The information presented above indicates that recovery of an ecosystem depends not only on improvement of habitats, but also on complicated ecological mechanisms. One of these mechanisms is the maintenance of stability of a newly formed ecosystem and the complexity of a return to the early succession conditions. It is known that in any disturbed ecosystem, the processes of energy regulation and reorganization turn to the near equilibrium stable condition [Chapman, 1999; Power, 1999]. The important questions are: Which features characterize ecosystems trajectory and their new structure? To what extent they correspond with mature (climax) conditions?

The features of the ecosystem state after the decrease of toxic pressure, specifically, recolonization of the lakes with individual northern species, appearance of new introducents, increase of the role of the upper levels of the ecosystem trophic
structure, successful utilization of mineral forms of biogenic elements, and increase of the share of K-strategists – all these features of the ecosystem state after decrease of the toxic pressure, discussed in this paper, indicate formation of a mature and a more stable modification, which differs from the natural one. This trajectory of transformation from a natural state through disturbance to recovery corresponds to the mechanisms of ecosystem successions: from a natural state through development to a more stable mature (climax) modification according to Odum's theory [1985].

The analyzed example of the anthropogenic modifications of the northern water ecosystems (polluted bays of Imandra, Ladoga, and Onega lakes) showed that ecosystems, after their disturbance, do not revert to the natural state. The theoretical trajectory of the ecosystem modification is presented in Fig. 2. Therefore in this case, the term “recovery of ecosystems” can’t be identified with the notion of reversion to the natural state.

Since the scientific community is anxious about climate warming, in conclusion, we will note obvious phenomena that may take place in the northern ecosystems due to climate warming.

It is probable that increasing water temperature as a result of global warming will make a return to reference conditions impossible [Harris et al., 2006]. Temperature influences the following ecosystem functions: (1) rate of carbon fixation, (2) rate of nutrient increase/decrease, (3) rate of detritus processing and storage, (4) rate of suspended–solid trapping, and (5) nutrient trapping and storage [Cairns, 2005]. Accumulated nutrients will be more actively utilized in trophic chains, because in warmer conditions communities will move towards the predominant development of eurybiontic species. The influx of biogenic elements from the catchment areas is likely to increase with rising temperature and it will provide increasing productivity for pollution-resistant species. Climate warming is unlikely to favor fish species such as arctic char and trout, although other species such as whitefish, perch, minnow, and smelt may benefit from advantageous ecosystem changes. For example, higher bioproductivity of amphipods in warmer temperatures will

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Fig. 2. A theoretical trajectory of an ecosystem modification under toxic and nutrients impacts: the attributes of the disturbance unstable stage and of the new stable stage, after a decrease in toxic impacts
create more favorable conditions for feeding and growth of whitefish and will lead to an increase in their numbers. The lake is likely to change from mesotrophic to eutrophic in some areas, which is observed in present conditions of biogenic pollution.

Studies reviewed in this paper show the changing effects of man's impact on northern water ecosystems under varying conditions of anthropogenic pollution and impossible return to natural conditions after a period of heavy anthropogenic stress (toxins and nutrients), because aquatic ecosystems with new parameters attain stability.

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