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Morphophysiological Rearrangements in Fish in Response to Pollution (in the Light of S.S. Shvarts' Theory)

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Abstract—The results of a study on morphophysiological variation in fish inhabiting a subarctic lake exposed to chronic industrial pollution are described using an example of cisco, *Coregonus lavaretus.* It is shown that indices of the heart, liver, kidneys, gills, and fatness in these fish are increased significantly and have retained increased values for the past 20 years. The observed changes are analyzed on the basis of biochemical data. The results of studies on the dynamics of hematological parameters in fish are used for characterizing the development of toxicosis. Adaptive rearrangements associated with an increase in the metabolic rate and the activation of protective systems in the fish are explained in the context of S.S. Schvarts' concept. The idea is proposed that the additional "energy cost" of detoxification may be responsible for morphophysiological variation in fish under conditions of water pollution.

Key words: morphophysiological indicators, toxic load, protective functions, "energy cost"

According to the concept proposed by S.S. Shvarts (1958, 1980), any change in the living conditions of animals is directly or indirectly associated with changes of energy balance in animals, and this inevitably leads to the corresponding morphophysiological shifts (an increase in the relative size of the heart and kidneys, hemoglobin concentration in blood, etc.). If these changes involve living under extreme conditions (a severe climate, low atmospheric pressure, permanent exertion, etc.), animals expend much energy. This correlation is so apparent that it is regarded as a law. The ability of animals to increase the rate of energy metabolism in order to survive under stress, which has been acquired in the course of evolution, is the most important preadaptation to environmental changes (Shvarts, 1980; Yablokov and Yusufov, 1981; Begon *et al.*, 1989; Grant, 1991).

The method of morphophysiological indicators as an approach to the assessment of adaptive response attracted special attention in the 1960s owing to the advancement of Shvarts' ideas concerning the ecological regularities of microevolution (Shvarts, 1958; 1980; Shvarts *et al.*, 1964). Specialists in fish ecology addressed the problem of variation in the indices of fish organs under different conditions (Dobrinskaya, 1964a, 1964b; Bozhko, 1969; Brusynina, 1971; Smirnov *et al.*, 1972). Our research on the effects of pollution on fish actively developed in the 1970s, when Shvarts' ideas were very popular. We proceeded from the following assumptions: (1) anthropogenic water pollution creates "extreme" living conditions for aquatic organisms; (2) toxic agents exert additional pressure on the organism, and this can lead to changes in metabolic rate; and (3) to survive under new conditions of toxic water pollution, organisms expend additional amounts of energy on detoxification and this should affect their morphophysiological indices.

Note that aquatic organisms, compared to terrestrial, depend on environmental factors to a greater extent because of the important role played by the processes of ecological metabolism in aquatic ecosystems and the greater rate of pollutant spread in water (Patin, 1979). In the preface to the book by Smirnov *et al.* (1972), Shvarts stated that fish are ideal objects for studying the laws governing the variation of organisms.

In 1978 and 1979, I performed studies on fish of subarctic Lake Imandra, which had been polluted with discharge from enterprises of the copper–nickel and apatite–nepheline industries (since the 1940s) and, later, with heated water discharge from a nuclear power plant and municipal sewage. The purpose of this work was to analyze variation in the indices of internal organs (the ratios of organ weight to body weight) and hematological parameters in cisco (*Coregonus lavaretus*) inhabiting zones differing in the pattern and intensity of pollution. It was shown that chronic exposure to toxic agents in natural water bodies leads to an increase in the relative weight of fish organs (Moiseenko, 1984, 1992). These results provided the basis for formulating the concept concerning regularities of the toxicological process and "energy cost" that the organism must pay for detoxification and survival under conditions of chronic water pollution (Moiseenko, 1992, 1997).

Taking into account the necessity of verifying this hypothesis with regard to all factors that could affect the significance of results and the validity of the conclusions, comprehensive studies on morphophysiological indices of *C. lavaretus* population were performed in the same regions after almost 20 years, in 1996 and 1997. Water pollution during this period was significantly lower because of recession and cutbacks in production at mining and smelting works.

The purpose of these studies was to reveal the type and stability of adaptive morphophysiological changes, to analyze the response of fish to the toxic load and its decrease, and to explain the mechanisms of survival under anthropogenically transformed conditions in the light of Shvarts' concept.

To date, some other studies on *C. lavaretus* from Lake Imandra have been accomplished. Their results are necessary for discussing and understanding the causes and mechanisms of morphophysiological variation in fish. In particular, specialists revealed trends in the development of toxicosis in fish by analyzing hematological indices (Moiseenko, 1998), characterized fish pathologies on the basis of histological data (Moiseenko and Lukin,1999), and analyzed corresponding changes at the biochemical level (Kirilyuk and Smirnov, 1993; Smirnov and Kirilyuk, 1994).

MATERIALS AND METHODS

This work was based on materials concerning morphophysiological indices of *C. lavaretus*. The genus *Coregonus* (whitefish) is dominant in the ichthyofauna of many water bodies located in northern regions of the world. Species of the genus are polymorphic and can produce numerous forms and races in different water bodies. This is evidence for their recent evolutionary origin and high flexibility (Reshetnikov, 1980). At the same time, they are narrowly adapted to living in conditions of a cold climate, being oxyphilic and cold-loving. Thus, whitefish are stenobiontic, which makes them highly sensitive to water quality and responsive to changes of the ecological situation in a water body. On the one hand, these species are vulnerable to anthropogenic impact; on the other, they are capable of rapid transformation and adaptation to environmental changes.

Benthophagous species are more suitable as the objects of studies aimed at assessing the effects of pollution on fish: they do not make long-distance migrations, and abundant material for analyzing changes in the physiological parameters depending on the levels of pollution can be obtained within the range of a local population. Several zones were distinguished in Lake Imandra with respect to the degree of water pollution: (I) pollution with high doses (20–500); (II) medium, or chronic doses (3–20); and (III) low doses (1–10) of toxic agents ($\Sigma C_i/MAC_i$); (IV) the zone affected by heated water discharge from a nuclear power plant (Δt 3–8°C); and (V) conventional control area where pollution approached the level of MACs.

Fish in these zones were caught using a standard set of sink nets 25 m long and 1.5 m high. In 1978 and 1979, these were nets with 36- to 40-mm mesh; in 1996 and 1997, nets made of nylon monofilament with mesh sizes of 10, 12.5, 16.5, 22, 25, 30, 38, and 46 mm (Lundgren Fiskeredskapsfabrik AB, Sweden) were used, and, hence, a greater number of size groups was included in the analysis. Hematological parameters of live fish were analyzed according to Krylov (1974). Clinical and anatomical examination was performed to reveal symptoms of poisoning and pathological changes in the fish organism. After fish were processed according to the conventional biological scheme (Pravdin, 1966), their organs (gills, liver, kidneys, and heart) were weighed on an electronic balance to an accuracy of 0.05 g.

Organ indices were determined as the weight ratios of organ to carcass to exclude the effects of variable factors, such as the degree of stomach fullness and others. Fatness was estimated according to Clarke, i.e., as the ratio of carcass weight to length. This index of fish has recently found wide use in ecotoxicological studies as the index of the organism state (Adams and Ryon, 1994). Data were processed statistically on a Digital PC using the STATISTICA applications software package (StatSoft Inc.).

RESULTS AND DISCUSSION

Natural Variation of Morphophysiological Indices

In studying the effects of pollution on the morphophysiological indices of fish, it is necessary to be careful about the identity of the groups under comparison and to exclude the effect of natural variation in these indices, which can depend on both endogenous (age, sex, gonad maturity) and exogenous factors (seasonal dynamics of environmental conditions, food supply, etc.). Hence, the study began with a detailed analysis of the effects of these factors on organ indices in fish of the control group (from relatively pure zones of the lake). No significant differences were revealed between the indices of fish belonging to close age groups (Table 1). There was no more than a tendency toward an age-related decrease in the heart index and an increase in the liver and kidney indices. The liver index of mature females (stages 4–5 of gonad maturity) differed from that of mature males; in immature fish, no sexual dimorphism was revealed (Table 2). These results agree well with published data (Dobrinskaya, 1964a; Bozhko, 1969; Smirnov *et al.*,1972).

The seasonal dynamics of environmental conditions proved to be reflected in morphophysiological indices: in winter, the indices of internal organs were the highest (see Table 2), which is accounted for by both more severe living conditions during the long polar winter (the so-called winter stress syndrome; Lemly, 1996) and the depletion of fat resources. The lowest indices

Table 1. Age-related variation of organ indices in *Coregonus lavaretus* from Lake Imandra, ‰

Age	Heart	Liver	Kidneys	Gills
2+	$\frac{2.27 \pm 0.5}{9}$	$\frac{8.03 \pm 0.6}{6}$	$\frac{7.02 \pm 0.8}{8}$	–
3+	$\frac{2.04 \pm 0.2}{45}$	$\frac{9.6 \pm 0.43}{39}$	$\frac{7.3 \pm 0.2}{58}$	$\frac{16.9 \pm 0.5}{20}$
4+	$\frac{1.85 \pm 0.1}{104}$	$\frac{9.83 \pm 0.3}{109}$	$\frac{7.3 \pm 0.2}{120}$	$\frac{17.4 \pm 0.3}{46}$
5+	$\frac{1.66 \pm 0.1}{107}$	$\frac{10.4 \pm 0.4}{104}$	$\frac{8.0 \pm 0.2}{95}$	$\frac{16.5 \pm 0.3}{29}$
6+	$\frac{1.61 \pm 0.1}{30}$	$\frac{10.6 \pm 1.1}{21}$	$\frac{7.8 \pm 0.5}{18}$	$\frac{16.8 \pm 0.7}{7}$
7+	$\frac{1.65 \pm 0.1}{14}$	$\frac{11.3 \pm 0.5}{4}$	$\frac{6.5 \pm 0.9}{3}$	–

Note: Here and in Tables 2 and 3, figures above and under the line show the average values and the numbers of fish studied, respectively.

were observed in summer and autumn, i.e., during the period most favorable for fattening.

Specific Features of the Toxicological Process in Fish from Polluted Zones

To understand the variability of morphophysiological indices, let us briefly consider characteristics of the toxicological process in the fish organism using hematological indices, which are informative in this respect (Moiseenko, 1998).

In the zone of heavy pollution (I), the toxicological process develops rapidly: mass erythrocyte destruction is observed, indicating that fish soon will die; at an almost normal hemoglobin concentration (80–110 g/l), the erythrocyte sedimentation rate (ESR) increases sharply from 2 (in the norm) to 11 mm/h. In the zones of chronic pollution (II and III), changes in the hematological indices provide evidence that toxicosis develops more slowly, i.e., takes a chronic course. The fish stock in these zones is very diverse with respect to hemoglobin concentration and includes individuals with both high and very low indices, from 160 g/l (pachyemia) to 20 g/l (anemia). This variability is accounted for by both the duration of exposure to the effect of toxic agents and individual fish tolerance to these agents. In the zone affected by heated waters (IV), hematological indices vary broadly (hemoglobin concentration, from 60 to 180 g/l), which is attributable to the effects of increased water temperatures and adaptation to them.

On the basis of hematological studies, four stages of the toxicological process were distinguished: contact, mobilization, destabilization, and degradation (Moiseenko, 1998). Figure 1 shows changes in the hemoglobin concentration, ESR, and blood count (erythrocyte, immature red cells, and white cells) at these stages. At the first two stages, young and reserve cells are released in circulation, which leads to pachyemia; in blood smears, polychromasy, anisocytosis, and abnormally dividing cells are observed; the leukocyte count increases, and the differential blood count is characterized by an increase in

Table 2. Seasonal and sex-related variation of organ indices in *Coregonus lavaretus* from Lake Imandra, ‰

Season	Sex and stage of gonad maturity	Heart	Liver	Kidneys	Gills
Winter	Females, I–II	$\frac{1.9 \pm 0.1}{20}$	$\frac{14.3 \pm 0.6}{11}$	$\frac{11.0 \pm 0.6}{14}$	$\frac{18.5 \pm 0.6}{16}$
	Males, I–II	$\frac{1.9 \pm 0.1}{18}$	$\frac{12.5 \pm 0.5}{13}$	$\frac{11.1 \pm 0.6}{15}$	$\frac{17.8 \pm 0.5}{17}$
Spring	Females, I–II	$\frac{1.96 \pm 0.1}{127}$	$\frac{12.4 \pm 0.3}{166}$	$\frac{7.9 \pm 0.2}{204}$	$\frac{18.7 \pm 0.4}{44}$
	Males, I–II	$\frac{2.3 \pm 0.2}{81}$	$\frac{11.9 \pm 0.3}{127}$	$\frac{7, 7 \pm 0.2}{171}$	$\frac{19.8 \pm 0.6}{23}$
Autumn	Females, II–III	$\frac{1.72 \pm 0.1}{126}$	$\frac{10.3 \pm 0.2}{248}$	$\frac{7.2 \pm 0.1}{254}$	$\frac{16.9 \pm 0.3}{60}$
	Males, II–III	$\frac{1.78 \pm 0.1}{84}$	$\frac{9.6 \pm 0.3}{167}$	$\frac{7.3 \pm 0.2}{173}$	$\frac{17.7 \pm 0.6}{28}$
	Females, IV–V	$\frac{1.56 \pm 0.1}{100}$	$\frac{16.7 \pm 0.5}{42}$	$\frac{6.9 \pm 0.3}{71}$	$\frac{17.8 \pm 0.7}{16}$
	Males, IV–V	$\frac{1.82 \pm 0.1}{42}$	$\frac{9.0 \pm 0.3}{44}$	$\frac{7.0 \pm 0.4}{51}$	$\frac{17.1 \pm 0.8}{12}$

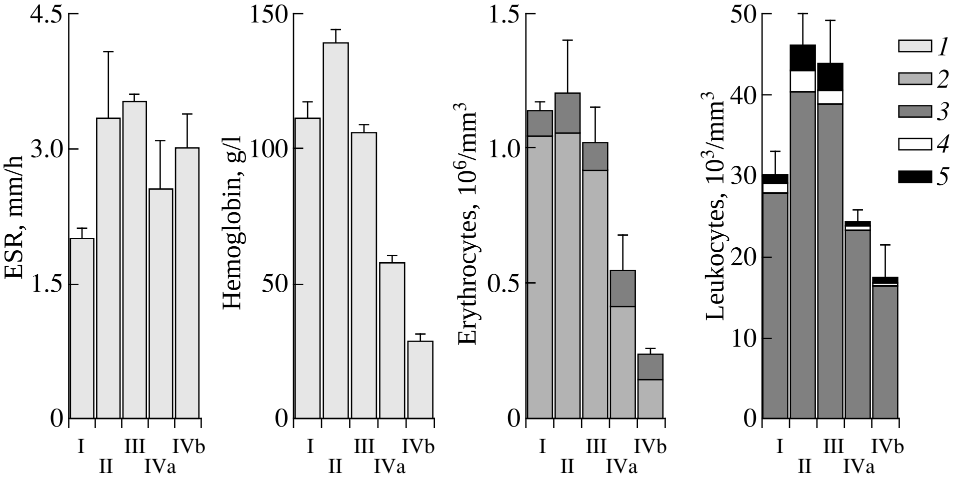

Fig. 1. Variation in hematological indices of fish at different stages of toxicosis: (I) contact, (II) mobilization, (III) destabilization, (IVa, IVb) degradation; (*1*) mature erythrocytes, (*2*) immature erythrocytes (polychromatophilic, basophilic, and normoblasts), (*3*) lymphocytes, (*4*) monocytes, (*5*) neutrophils.

the proportions of young lymphocytes, neutrophils, and monocytes. In some experimental toxicological studies, an increase in the hemoglobin content as the initial response to poisoning was observed (Krylov, 1974; Ivanova, 1976; Zhiteneva *et al.*,1989).

At the destabilization stage, the process of cell destruction is counterbalanced by the recruitment of reserve cells. This stage may be conventionally regarded as the threshold of irreversible changes. Methodologically, this threshold for whitefish is diagnosed when the hemoglobin concentration decreases to 80 g/l and young, disintegrating, and pathological cells appear in blood smears. When the protective systems are exhausted, the fish organism enters the stage of degradation characterized by gradual cell destruction and developing anemia, which leads to premature death.

Shvarts (1980) regarded pachyemia as a mechanism of adaptation to extreme conditions. Our data show that the hemopoietic system of fish at the initial stages of exposure to toxic agents demonstrates a protective response by releasing young and reserve cells into the circulating blood.

Effects of Pollution on the Indices of Internal Organs

The effects of pollution on the morphophysiological indices was assessed by analyzing the groups of immature fish of similar age composition (4+, 5+, and 6+) that were caught in each zone during the summer–autumn period favorable for fattening. This allowed us to reduce natural variation in the indices. Food supply to all these groups was sufficient: eutrophication in zones of toxic water pollution leads to the formation of fairly rich feeding grounds with abundant chironomids and oligochaetes belonging to several species tolerant to pollution (Moiseenko and Yakovlev, 1990; Moiseenko and Lukin, 1999).

The heart. Under optimal ecological conditions, the heart index of whitefish is the lowest. Under the toxic load, the heart weight increases, so that the index can increase by 60% (Table 3). Exposure to the effects of toxic agents apparently activates the protective systems of the fish organism and accelerates the metabolic rate, which, in turn, leads to the increased functional load on the heart and the corresponding adaptive rearrangements of this organ. According to numerous experimental data (Hughes and Abeney, 1977; Smart, 1978; Malyarevskaya, 1979; Luk'yanenko, 1983; Karpovich and Luk'yanenko, 1988; *Aquatic Toxicology…*, 1988; Flerov, 1989), exposure to toxic agents leads to an increase in the respiration rate, heart rate (tachycardia), and oxygen consumption, thus creating an additional load on the heart that may be responsible for an increase in the heart weight. Thus, the heart index in fish is related to the metabolic rate. Shvarts (1980, p. 41) emphasized that the intensification of metabolism leads to an increase in the heart size, and this trend is characteristic of fish exposed to the effect of toxic agents.

The liver plays a crucial role in detoxifying harmful substances, and its relative weight increases under toxic conditions. The highest liver indices were characteristic of fish from the zone of chronic pollution, in which the relative liver weight was sometimes five to seven times higher than in the control (Table 3). These fish were also characterized by the lowest hemoglobin content, which provided evidence for a correlation between changes in the liver index and the hemoglobin content. For instance, the maximum liver index in *C. lavaretus*, 62‰ (normal value is 9–10‰) was observed at a hemoglobin concentration of 23 g/l. Thus, the increase of the organ weight associated with detoxification processes in the organism continues at the stage of degradation. It may be assumed that the survival of these fish at such a

Table 3. Morphophysiological indices of fish under conditions of water pollution with (**I**) high, (**II**) chronic, and (**III**) low doses of toxic substances and (**IV**) heated water discharge from a nuclear power plant and (**V**) in a conventionally clean control area

Zone	Period, years	Excess over MAC for toxic agents, $\Delta(C_i/MAC_i)$	Hemoglobin		Organ indices, ‰								Fatness	
			g/l	*t*	heart	*t*	liver	*t*	kidneys	*t*	gills	*t*	according to Clarke	*t*
I	1978–1979	40–500	$\frac{88.3 \pm 3.1}{40}$	5.8***	$\frac{1.68 \pm 0.05}{41}$	4.4***	$\frac{9.9 \pm 0.3}{49}$	5.8***	$\frac{8.95 \pm 0.5}{9}$	3.8***	$\frac{22.9 \pm 0.5}{48}$	3.4***	$\frac{1.19 \pm 0.02}{53}$	5.5***
	1996–1997	20–80	$\frac{91.7 \pm 1.9}{38}$	6.3***	$\frac{1.65 \pm 0.04}{53}$	3.8***	$\frac{9.8 \pm 0.4}{46}$	4.4***	$\frac{7.8 \pm 0.4}{83}$	2.2*	–		$\frac{1.18 \pm 0.1}{87}$	5.9***
II	1978–1979	8–20	$\frac{73.6 \pm 4.9}{40}$	6.8***	$\frac{1.59 \pm 0.04}{164}$	2.8**	$\frac{21.3 \pm 1.6}{49}$	7.9***	$\frac{8.2 \pm 0.4}{20}$	3.1***	$\frac{21.6 \pm 0.6}{37}$	0.9	$\frac{1.25 \pm 0.02}{57}$	7.0***
	1996–1997	5–15	$\frac{79.3 \pm 2.6}{33}$	9.1***	$\frac{1.61 \pm 0.07}{32}$	2.2*	$\frac{13.2 \pm 0.8}{25}$	5.9***	$\frac{7.8 \pm 0.3}{41}$	2.8**	–		$\frac{1.27 \pm 0.02}{52}$	9.5***
III	1978–1979	3–10	$\frac{110 \pm 5.8}{9}$	0.1	$\frac{1.7 \pm 0.06}{9}$	3.5**	$\frac{10.1 \pm 0.8}{9}$	2.9**	$\frac{8.1 \pm 0.7}{9}$	1.8	$\frac{23.0 \pm 0.9}{9}$	2.0	$\frac{1.1 \pm 0.5}{9}$	1.3
	1996–1997	2–5	$\frac{94.0 + 1.7}{80}$	5.8***	$\frac{1.77 \pm 0.05}{65}$	5.1***	$\frac{10.6 \pm 0.3}{72}$	8.6***	$\frac{8.1 \pm 0.2}{75}$	4.6***	–		$\frac{1.14 \pm 0.01}{100}$	3.9***
IV	1978–1979	Δt 3–8°	$\frac{116 \pm 3.4}{50}$	1.3	$\frac{1.53 \pm 0.04}{65}$	1.8	$\frac{9.4 \pm 0.3}{66}$	4.6***	$\frac{7.9 \pm 0.2}{31}$	4.2***	$\frac{21.0 \pm 0.3}{80}$	1.8	$\frac{1.16 \pm 0.05}{50}$	4.4***
	1996–1997	Δt 3–5°	$\frac{104 \pm 3.4}{20}$	1.5	$\frac{1.8 \pm 0.12}{26}$	2.9**	$\frac{8.5 \pm 0.3}{31}$	2.1*	–		–		$\frac{1.04 \pm 0.01}{49}$	1.5
V	1978–1997	<1	$\frac{111 \pm 2.2}{43}$		$\frac{1.41 \pm 0.04}{44}$		$\frac{7.6 \pm 0.3}{50}$		$\frac{6.7 \pm 0.2}{67}$		$\frac{20.1 \pm 0.3}{70}$		$\frac{1.05 \pm 0.02}{75}$	

Note: Asterisks indicate significant differences between groups of fish from polluted and control zones: * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.

low hemoglobin content might be accounted for by a high efficiency of protective response manifested in the ability to increase the relative liver weight by a factor of 6.

At high doses of toxic agents, destructive factors apparently prevail over protective mechanisms; hence, an increase in the liver index under these conditions, although statistically significant, proved to be less pronounced than upon chronic exposure. In whitefish from Lake Imandra, lipoid degeneration of the liver with signs of cell necrosis and excessive connective tissue growth was observed (Moiseenko and Lukin, 1999). Both pathologically altered and normal tissues were found in the liver of these fish, which may be accounted for by the relationship of destructive and regeneration processes. Their ratio eventually determines fish viability.

The thermal factor did not cause such profound rearrangements in the liver, although the significant increase of its weight in fish from the corresponding zone (IV) may indicate the intensification of the metabolism under heat stress.

Note that at present, when the pollution level decreased, the liver index (although still high) decreased, on average, twofold as compared with that in 1978 and 1979. The role of the liver as a detoxification system has been established in the course of evolution, and, hence, this organ (in particular, its weight) is most sensitive to the toxic load. Adams and Ryon (1994) characterized the increase of the liver index in response to the toxic load as an informative criterion and demonstrated its significance for indicating fish population health upon pollution of natural water bodies.

Biochemical studies provided data on the activation of cytochromes, monooxidases, and other enzymes responsible for detoxification in the liver of fish from polluted water bodies (Sidorov and Yurovitskii, 1991; Smirnov and Kirilyuk, 1994). Experiments on the effects of toxic agents on fish confirmed the increase of biochemical activity in the liver (Vysotskaya *et al.*, 1994; Nemova *et al.*,1994). To survive upon chronic exposure to toxic agents, fish activate their detoxification systems, which leads to the increase of the liver weight. Adams and Ryon (1994) showed that fish exposure to chronic pollution (1) improves the ability of the liver to produce enzymes for detoxification, (2) increases the rate of glycogen and lipid accumulation, and (3) activates the processes of proteins and lipid metabolism leading to the release of physiologically free energy. Thus, the level of detoxification metabolism in the liver is associated with its relative size, and the latter can obviously be affected by pathological processes in the organ. The regeneration capacity of the liver as a protective function is well-known. Owing to this capacity, the values of the liver index in fish upon long-term exposure to low doses of toxic agents are significantly higher than upon exposure to high doses.

Kidneys. The basic function of the kidneys is to excrete metabolic products, but their anterior portions are involved in hemopoiesis. Shvarts in the work “The Method of Morphophysiological Indicators in Animal Ecology” (1958) emphasized that the relative kidney weight is a sensitive indicator of the metabolic rate in both homoiothermal and poikilothermal animals; however, published data on kidney indices in fish are absent.

The analysis of the variation in relative kidney weight in fish from the zones of pollution showed that this parameter is highly responsive to ecological changes in the water body, including the toxic load. A statistically significant increase in the kidney weight was observed in all these zones (Table 3), confirming the increasing role of this organ in excreting metabolic products and toxic compounds.

It was shown (Yurovitskii and Sidorov, 1993) that the most significant changes in the kidneys upon fish poisoning occur at a biochemical level. In Lake Imandra, heavy metals cause pathological changes in fish kidneys, and diseases such as nephrocalcitosis and fibroelastosis are common among local fish (Moiseenko and Lukin, 1999). Therefore, the increase of the organ weight in zones of high and medium toxicity may be an integrated result of both pathological changes and an increase in the metabolic rate. Although the level of water pollution and fish morbidity have decreased to date, the indices of the liver and other organs remain as high as they were 20 years ago. The kidney indices were also sufficiently high in fish from the zone polluted with low doses of toxic agents (although kidney pathology was not observed) and the zone affected by heated waters. The increase in the role of this organ in excreting metabolic products upon an increase in the metabolic rate may be regarded as a mechanism of fish adaptation to any extreme conditions.

Gills play an important physiological role as a respiratory organ. However, published data on their relative weight are scarce (Bozhko, 1969). Gill indices in cisco from the zones of pollution were higher than in control fish (Table 3). Possibly, the protective response of gills to the presence of toxic agents in water is manifested in the growth and thickening of their epithelium, which leads to an increase in their relative weight. On the other hand, numerous experiments proved that exposure to toxic agents or other stress factors leads to an increased respiration rate, gill hyperventilation, and high oxygen consumption (Veselov, 1969; Malyarevskaya, 1979; Luk’yanenko, 1983; Karpovich and Luk’yanenko, 1988; *Aquatic Toxicology* …, 1988). The physiological role of gills increases under conditions of accelerated metabolism and high oxygen consumption, and this creates an additional load on the organ; hence, their relative weight increases.

Changes in Fat Accumulation Indices

Fat accumulation is closely associated with all the physiological processes in the fish organism and, hence, can serve as an indicator of its adaptive changes.

Published experimental data provide evidence that fish exposure to toxic influences often leads to exhaustion, weight loss, and a decrease in fatness (Metelev *et al.*, 1971; Luk'yanenko, 1983).

In studies on natural water bodies, an inverse situation was observed: in chronically polluted waters, fatness and the amount of visceral fat in *C. lavaretus* and *C. albula* in autumn proved to be higher than in fish from control water areas (Moiseenko, 1992, 1997). The results of this study also indicate that fatness in fish from the zones of chronic toxic pollution is significantly higher than in the control zone (Table 3). Biochemical data confirmed that the level of reserve lipids in the muscle tissue of fish from these zones is higher than in fish from clean waters (Kirilyuk and Sidorov, 1994).

Nikol'skii (1974) and Shvarts (1980) regarded fat accumulation as a mechanism providing for the formation of an "energy depot" in populations exposed to the effects of unfavorable environmental factors. At the biochemical level, it was shown that juvenile fish in the critical periods of life (e.g., during wintering or seaward migrations of anadromous and semianadromous fish) are characterized by an increase in the contents of lipids in red muscles, the gills, and the intestine and in the contents of phospholipids and highly saturated fatty acids of the linolenic series (Shatunovskii, 1993). Kirilov (1983) provided evidence that in the course of adaptation to new conditions in the reservoir, whitefish accumulate considerable resources of energy substrates, which is manifested in increased fatness, including the amount of visceral fat. Yurovitskii and Sidorov (1993) revealed an increase in the contents of phospholipids in all organs of *C. albula* from a lake polluted with herbicides.

It is probable that chronic environmental pollution activates mechanisms regulating growth and fat accumulation in fish, as the organism must have sufficient energy reserve to survive under extreme conditions.

The pattern of changes in the lipid status of fish upon an acute short-term exposure to toxic agents sharply differs from that upon chronic exposure. In the former case, obvious cell pathology associated with an increase in the lysolecithin concentration is manifested; in the latter, the fish organism recovers owing to lipid synthesis (Yurovitskii and Sidorov, 1993).

Thus, biochemical mechanisms account for differences in the processes of fat accumulation in fish upon acute and chronic poisoning and for the increase in indices of fatness and the amount of visceral fat. From the ecological standpoint, the ability of individuals to shift the direction of metabolism from the expenditure of plastic substances for growth to the accumulation of fat is a mechanism of response to stress that provides for survival and acquires adaptive significance under conditions of pollution.

Justification of the Concept of "Energy Expense" for Detoxification

Pollution is a factor that is rapidly (on the evolutionary scale) changing environmental conditions, often making them extreme for the existence of living organisms. The environment acquires a new quality, namely, toxicity. In the past, environmental conditions provided for the formation of characteristics and their combinations allowing the species to survive within a certain range of fluctuations in abiotic factors (Shvarts, 1980). It is assumed that organisms are not adapted to the present or the future but are living consequences of their own past (Begon *et al.*,1989). Organisms respond to environmental changes, including toxic pollution, depending on the mechanisms of survival under stress that have been formed in the course of evolution. Mechanisms of self-regulation in animals belong to general properties that have been formed in the course of evolutionary development; their role consists in maintaining balance with changing environmental conditions, rather than general stability, and providing for species survival (Nikol'skii, 1974). Organisms are historically preadapted to fluctuations in the abiotic parameters; i.e., they have certain potential adaptations that manifest themselves upon changes in environmental parameters (Yablokov and Yusufov, 1981).

The results of studies on the morphophysiological indices of *C. lavaretus* from Lake Imandra indicate that the weight of organs increases under extreme conditions created by the presence of toxic agents. It may be assumed that a high reactivity of functionally important organs is associated with the intensification of metabolic processes aimed at detoxifying toxic substances and excreting the resulting products. An increase in the relative organ weight and pachyemia upon exposure to chronic pollution are the consequences of the increase in the metabolic rate, which is confirmed by the results of biochemical research (Sidorov and Yurovitskii,1991; Yurovitskii and Sidorov, 1993; Nemova *et al.*,1994; Adams and Ryon, 1994). Interactions of fish with the changing environment are regulated through metabolic changes (Nikol'skii, 1974). It is logical to conclude that the general biological mechanisms of response to stress are the first to operate under extreme conditions of water pollution. When changes go beyond the framework of the species adaptation potential, pathologies and dysfunctions develop in the organism and eventually lead to its death. As activation of protective functions and pathological changes in the organism are interrelated, the corresponding processes are difficult to distinguish from one another.

The generalized scheme of the development of toxicosis in fish is shown in Fig. 2. Theoretically, protective mechanisms reach a peak of activity at the compensation threshold, thus retarding or preventing the development of pathologies. The critical threshold is characterized by the exhaustion of protective systems, and pathological changes in the organism begin to pre-

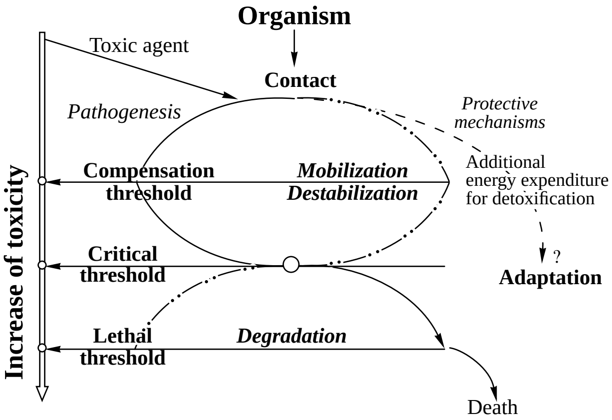

Fig. 2. Scheme of the development of toxicosis in the fish organism.

vail over the repair processes, which ultimately leads to the lethal outcome. At the same time, morbidity in a fish stock is nonuniform, and this fact may be attributed to differences not only in the duration and strength of toxic effects, but also in the individual tolerance of specimens to the corresponding toxic agents.

There is a controversial problem of adaptive changes that allow a population to exist and maintain its size under conditions of chronic pollution, regardless of the toxic load. In our case, Lake Imandra has been polluted for more than half a century, but the fish population maintains its size and continues to reproduce (Moiseenko, 1997). In fish exposed to chronic and weak pollution, the indices of internal organs are significantly higher than in the control fish, and their increased values have been maintained from generation to generation for 20 years.

The general biological law of individual response to stress and Shvarts' concept that any additional energy expenditures lead to an increase in the weight of the internal organs provide a basis for the conclusion that the activation of protective functions, which manifests itself in the increased organ indices, indicates that the organism pays an additional "energy cost" for detoxification and survival under technogenically transformed environmental conditions.

Thus, rearrangements leading to the increase of the metabolic rate in conformity with the evolutionarily established mechanisms for improving viability and their preadaptation to unfavorable conditions acquire special adaptive significance under present-day conditions of water pollution. An increase in the weight of the internal organs allows an individual to maintain the energy balance under a high metabolic load, and the rearrangement of the metabolism in the direction of fat accumulation provides for the formation of a necessary "energy depot." Individuals capable of additional energy expenditures for detoxifying small doses of toxins entering their organisms have an advantage with respect to survival in the polluted environment.

As for the method of morphophysiological indicators proper, Shvarts (1980) noted that a simplified approach, when the weight of a certain organ is used "as a thermometer" for estimating metabolic rate in energy units, is inadmissible. He emphasized that it is necessary to "use the weights of organs as indicators of a probable change in the level of metabolism, which offers an opportunity to reveal the factors responsible for changes in energy expenditures for the vital activities of organisms depending on the combination of environmental factors or population structure."

CONCLUSION

Shvarts' concept of variation in the morphophysiological indices under extreme conditions, which obviously include environmental pollution, is of great significance for studies on current ecological problems. The results of research on the indices of the internal organs in fish inhabiting a polluted natural water body provided evidence for the necessity of obtaining additional biochemical, histological, and toxicological data to explain the causes and mechanisms of morphophysiological rearrangements and their significance for organisms from the ecological standpoint.

Activation of protective functions upon poisoning leads to an increase in indices of the internal organs against the background of their pathological changes. The ability of individuals to sustain additional energy expenditures for detoxification and to change their metabolism in order to forming an energy "depot" at the expense of structural growth has a special adaptive value under present-day conditions of environmental pollution.

In recent years, the problem of anthropogenic microevolutionary transformations in populations has become very important. Biological investigations provided many examples demonstrating that the organic world responds to environmental pollution by active microevolutionary processes (Kolchinskii, 1990; Severtsov, 1990). For instance, organ indices in fish at the peak of pollution in 1978 and 1979 exceeded the norm; by 1996–1997, water quality had improved and morbidity among fish had decreased significantly; however, organ indices retained their high values. If individuals capable of maintaining a high metabolic rate and increasing the weight of functionally important organs have an advantage with respect to survival under conditions of chronic poisoning, the population frequencies of alleles determining these traits may increase. However, the question concerning the stability of the corresponding changes is difficult to answer without special genetic analysis.

Hopefully, the theoretical aspects of morphophysiological variation in organisms inhabiting polluted natural water bodies and the corresponding experimental evidence will be of interest to researchers investigating the processes of evolutionary adaptation to anthropogenic factors in wild animals. Evolutionary phenomena are difficult to understand without taking into account the ecological aspect, i.e., the concept of interactions between organisms and their physical, chemical, and biological environment (Dobzhansky, 1954).

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