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RIVER AND STREAM ECOSYSTEMS

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THE ECOSYSTEM OF THE AMUR RIVER

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INTRODUCTION

The Amur river is the tenth river among the rivers of the world in terms of basin area – 1 885 000 km². It begins at the confluence of the Shilka and the Argun' rivers and enters the Amurskiy Liman of the Okhotskoye More (Sea of Okhotsk). The length of the Amur from the source of the Argun' (Khaylar) is 4440 km and from the confluence of the Shilka and the Argun' it is 2850 km.

In accordance with the structural pattern of its valley and bed, the Amur is traditionally divided into three parts: Verkhniy, Sredniy and Nizhniy. The Verkhniy Amur stretches from the source of the Argun' to Blagoveshchensk, the Sredniy Amur runs between Blagoveshchensk and Khabarovsk, and the Nizhniy Amur runs from Khabarovsk to its mouth (Fig. 19.1). The headwaters of the Amur show a foothill pattern; pebbles are dominant in the bed. Not far from Blagoveshchensk, the Amur divides into a number of branches and the flow velocity decreases. In addition, silt and sand are found along with the pebbles in the river bed. Below Blagoveshchensk, the Amur shows a flood-plain pattern; only in those places where the river cuts through the Khrebet Bureinskiy (Maly Khingan) does the current increase, the valley narrow, and the area of sandy and silty bottom decrease while the area of stony bottom increases. Below Khabarovsk, the Amur divides into branches forming a complex system of side channels. Near the village of Bogorodskoye, the river again encounters mountain ridges. Here, the flow velocity slows significantly and the river bed meanders.

The main left-hand tributaries of the Amur are the Zeya, Bureya and Amgun'; the right-hand tributaries are the Sungari (Sung-hua Chiang) and

Ussuri. The headwaters of the large tributaries and the majority of the smaller tributaries reveal a mountain pattern. In the flood-plain areas of the Nizhniy Amur and its tributaries, there are a few large, slowly flowing lakes connected with the river by permanent side-channels. On the left-hand side of the river there are the Ozero Bolon' (338 km²), Ozero Udyl' (330 km²), Ozero Orel' (314 km²), Ozero Chlya (140 km²), Padali (29 m²) and Mylka (8 km²); on the right-hand side are the Ozero Bol'shoeye Kizi (281 km²), Khummi (117 km²), Kadi (67 km²), Innokent'yevskoye (31 km²); Irkutskoye (14 km²) and Kaltakhyun (9 km²). In addition to these lakes there are a few smaller ones. In the Ussuri basin is located the largest of the lakes in the whole Amur basin, the Ozero Khanka (4190 km²); in the headwaters of the Amgun' is the rather large Ozero Chukchagirskoye (336 km²), and in the Gorin basin is the Ozero Evoron (194 km²). All the lakes are shallow, their depth being no more than 3 to 8 m as a rule.

HYDROLOGY

The main peculiarities of the hydrological pattern of the Amur, its tributaries and flood-plain lakes are determined by the monsoon climate, the major feature of which are rain floods. In summer, up to 80 to 90% of the total annual precipitation falls, often connected with typhoons. There may be as many as 10 to 15 floods in the small and mid-size rivers during the 140-day flood period (Stryapchy, 1979). Usually in the Nizhniy Amur in the warm part of the year, a continuous flood with three to five peaks is observed. The sharpest increases of flood waters are usually observed in July–September and, in the

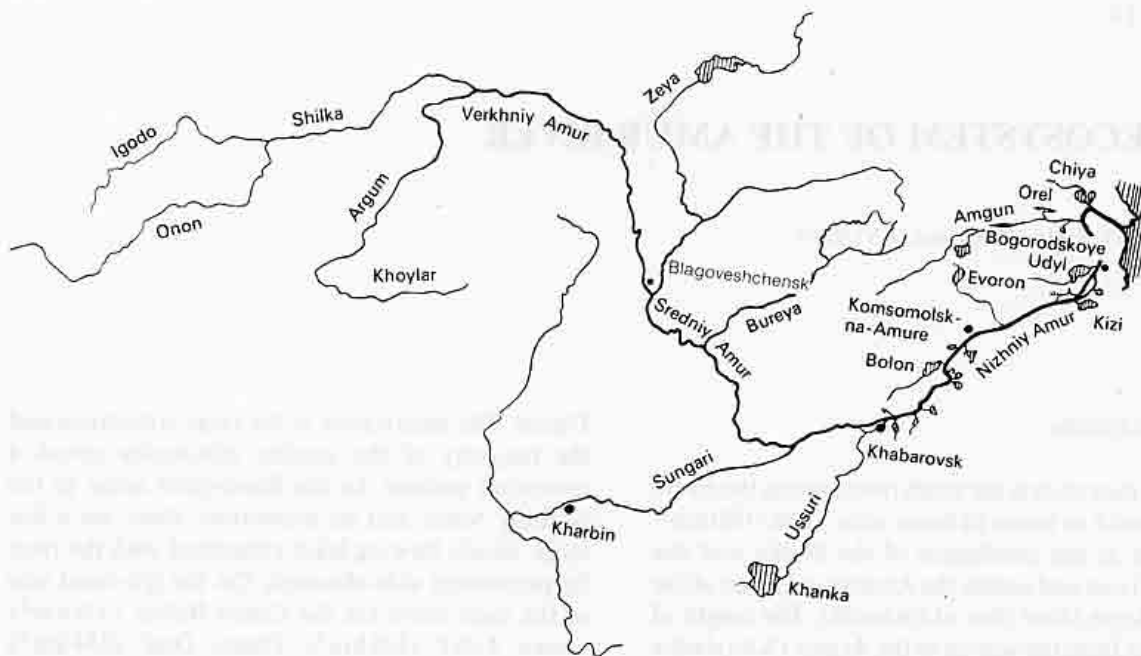


Fig. 19.1. Map of the Amur river basin.

upper parts of the Zeya and Bureya, they can reach 10 m and more. In winter, surface runoff to the rivers is very limited, and in many places it ceases completely because of freezing. The Amur flow varies greatly over time. For example, near Khabarovsk, water discharge in winter can fall to 150 to $200 \text{ m}^3 \text{ s}^{-1}$, while in the flood period it can reach $40\,000 \text{ m}^3 \text{ s}^{-1}$. The rainfall constitutes 75 to 80% of the annual flow, while the ground supply makes up only 5 to 8%; the remaining 15 to 20% of the total Amur flow depends on melting snow. Usually, during large floods, the flood-plain areas are submerged. Moreover, flood-plain lakes also receive Amur water; then, when the water level decreases, water flows back into the Amur, the lakes thus functioning as regulators of the flow.

Freezing-over in the Verkhniy Amur occurs from early November until early May; in the Nizhniy Amur from late November until late April. Snow cover is thin, which causes a deep freezing of the soil and formation of thick ice on rivers and lakes. Permafrost is found in most parts of the Amur basin.

WATER CHEMISTRY

The chemical composition of the Amur depends greatly on its water flow and the hydrological features in different seasons. On the whole, the river water is of calcium bicarbonate (HCO_3^-) type. Water mineralization is maximal in winter, and in the Nizhniy Amur it is within the range of 100 to 150 mg l^{-1} . During flood periods it falls to 33 to 75 mg l^{-1} and during the summer it is 60 to 80 mg l^{-1} .

Concentrations of the main biogenic elements phosphorus and nitrogen is maximal in late autumn, in winter and during the spring floods. During this period, HPO_4^{2-} ions range between 0.025 and 0.115 mg l^{-1} , NO_3^- from 0.75 to 2.4 mg l^{-1} , and NH_4^+ between 0.65 and 1.7 mg l^{-1} in the Nizhniy Amur. During summer, their content may decrease to 0.00 to 0.035, 0.00 to 1.2 and 0.2 to 1.0 mg l^{-1} , respectively.

Total organic matter, expressed as organic carbon, varies through the year between 4 and

26 mg l^{-1} , with maximal values found during the spring floods when organic matter enters the water basin with melted snow. During other times, the most typical organic-matter concentrations are between 10 and 18 mg l^{-1} , mostly found below large cities. On the whole, the total organic-matter flow in the Amur, for example in the vicinity of the village Bogorodskoye, ranges during the year from 10 to 30×10^3 kg d^{-1} .

The colour of the water in the Amur ranges from 8 to 220 units of the platinum-cobalt scale, and the pH from 6.4 to 9.0. The maximal values of colour intensity are found during floods and summer-autumn water-level maxima; those of pH occur in summer during periods of mass phytoplankton development.

During the warm period of the year, water temperatures in the upper parts of the rivers usually do not exceed 9 to 13°C, and in the Nyzhniy Amur, 20 to 25°C. The oxygen content of the Nyzhniy Amur ranges from 7 to 12 mg l^{-1} . Because of high turbulence, the vertical stratification of temperature and oxygen in the rivers is not pronounced. In winter, almost all of the lakes freeze to the bottom, and in some deep regions the concentration of oxygen falls to trace quantities, resulting in fish mortality.

Biochemical oxygen demand (BOD_5) of the Amur water is 0.5 to 2.5 mg O_2 l^{-1} , the highest values being found below waste-water outfalls of large cities. The maximal BOD_5 value in the Amur of 8.5 mg O_2 l^{-1} is found occasionally during the summer in the Amurskaya channel below the entrance of the Ussuri, which is characteristic of significant pollution from readily oxidized organic matter.

Water turbidity in the Amur is low. In different parts of the Nizhniy Amur, its mean annual values range from 70 to 100 g suspended matter m^{-3} . The highest content of suspended matter in the water is 300 to 400 $g m^{-3}$ and is found at the beginning of floods. During summer, the total suspended matter is minimal and, for example between Khabarovsk and Bogorodskoye, it is within the range of 30 to 60 $g m^{-3}$; below Bogorodskoye, where the flow velocity decreases, it is 17 to 30 $g m^{-3}$.

Water transparency in the Sredniy and Nizhniy Amur is dependent on turbidity values and ranges from 0.1 to 1.8 m during the season. The lowest transparency values (0.1–0.2 m) are found during periods when the water level is rising rapidly. Dur-

ing summer and in winter, transparency (as measured by the Secchi disc) is maximal and, for example between Khabarovsk and Bogorodskoye it is 0.5 to 1.4 m; below Bogorodskoye it is 1.0 to 1.8 m. Water transparency in large flood-plain lakes is also low and ranges from 0.07 to 1.4 m. However, in contrast to the Amur where the low values of water transparency typical of flood periods are determined mainly by mineral suspended matter, in the lakes the decreases of water transparency are most often related to algal development.

PLANT COMMUNITIES

Higher aquatic plants are not well developed in the Amur and its tributaries because of the great fluctuations in water level. Only in a very few sites in flood-plain lakes are there small patches of Cyperaceae and other plants.

Plankton is practically absent in mountain or foothill river reaches. Here the algal colonization of stones provides the primary production. In the flood-plain reaches of rivers with significant flow depth, low water transparency and frequent fluctuations of water level hamper the development of periphyton communities. The greater part of primary production is related to the photosynthetic activity of phytoplankton.

On the whole, during the warm part of the year, the concentration of chlorophyll *a* in the Amur plankton depends largely on the water flow, and in certain parts of the river the relationship is markedly inverse (Fig. 19.2). The largest amounts of planktonic algae are found below the entrance of the Sungari into the Amur. In the warm part of the year, up to 180 species of algae are there, about 90% of them being diatoms and green algae.

The degree of development of individual algal species or groups depends on both the hydrological pattern of the stream and the water temperature. Thus, during floods and summer-autumn temperature increases, diatoms of the genus *Aulacosira* prevail. The concentration of chlorophyll *a* during this period varies from 1.5 to 6.0 $mg m^{-3}$ and is distributed rather uniformly along the river profile. During summer, in addition to diatoms, blue-green algae of the genera *Anabaena*, *Aphanizomenon* and *Microcystis* are observed in great quantities in the plank-

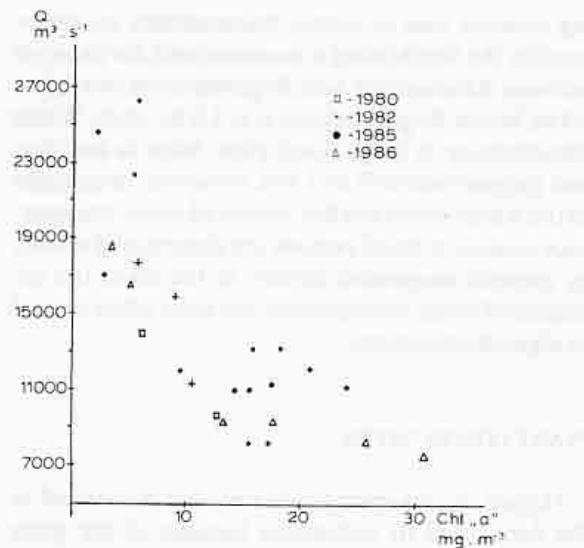


Fig. 19.2. Relationship between chlorophyll *a* content in the Amur plankton (chl "*a*") and water discharge in the Amur (Q) near Komsomol'sk-na-Amure.

ton. During low water, the concentration of chlorophyll *a* in different parts of the Nizhniy Amur changes from 8 to 20 mg m^{-3} and higher (Sirotsky, 1986). The lowest concentrations of chlorophyll *a* (up to 10 mg m^{-3}) are found above Khabarovsk and in the pre-mouth parts of the main tributaries of the Amur: in the Zeya up to 4.5 mg m^{-3} , in the Bureya up to 2 mg m^{-3} , in the Sungari up to 10 mg m^{-3} , in the Anya from 1.5 to 3.0 mg m^{-3} , and in the Argun' from 1.7 to 4.5 mg m^{-3} . In the Verkhniy Amur and in the mountain and foothill reaches of the rivers, the concentration of chlorophyll *a* in the water usually does not exceed 3 mg m^{-3} . The maximal concentrations of chlorophyll *a* ($> 20 \text{ mg m}^{-3}$) are most often found below Komsomol'sk-na-Amure, in the mouth of the Ussuri, as well as in the entrances of side channels into the Amur which connect it with the large flood-plain lakes which serve as the main source of phytoplankton.

In lakes, the concentration of chlorophyll *a* may vary between 8 and 260 mg m^{-3} . The degree of algal development increases as water level decreases. In anomalously low water, the lakes, such as Innokent'yevskoye, Padali and Mylka, lose their connection with the Amur. During this period, an abundant development of blue-green algae is found, which is often accompanied by mass mortality of fish. The

area of such lakes as Ozero Udyl' and Ozero Bol'shoye Kizi is significantly reduced, and they become a stream up to 200 m wide meandering along the lake bed. During this period, the concentration of chlorophyll *a* in the lake flow decreases significantly and is usually not more than 10 to 15 mg m^{-3} .

During summer or after floods, when the water from the lakes enters the Amur the concentration of chlorophyll *a* is distributed uniformly horizontally, and only in those places where rivers enter the lakes is the concentration usually low (Fig. 19.3a). During the flood period when the Amur water enters the lakes, in those places where the river and lake water meet—that is, in sites where temporarily there is no flow-zones of high productivity are formed in which a mass development of algae is observed (Fig. 19.3b). When the flood level decreases, the water from the lakes again enters the Amur and the horizontal distribution of the algae becomes uniform (Fig. 19.3c). During such periods in still

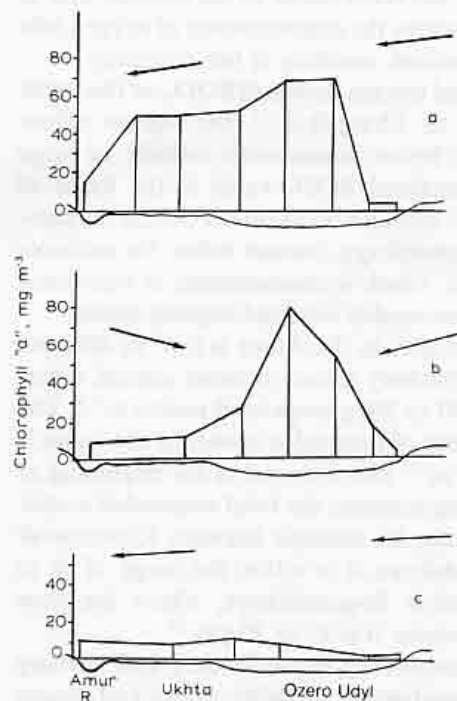


Fig. 19.3. Horizontal distribution of chlorophyll *a* in the Ozero Udyl', (a) at water level of 41 cm, before flood; (b) at 130 cm, during flood; (c) at 59 cm, after flood. Arrows show the direction of the stream.

weather in all flood-plain lakes, a close correlation is observed between the chlorophyll *a* content in plankton (C_{ch} , in mg m^{-3}) and water transparency (S , in m), which can be described by the equation:

$$S = 1.3 e^{-0.015C_{ch}}, \quad r = 0.95,$$

where e is the natural logarithmic base and 1.3 a constant value showing the possible transparency of water in the absence of algae. This correlation is indicative of the uniformity of phytoplankton and optical characteristics of the Amur lakes.

In the Amur, the concentration of chlorophyll *a* below Khabarovsk prior to freezing-over of the river decreases to 4 to 8 mg m^{-3} , and later, during the frozen period after a thick snow cover forms, it falls to 0.3 to 1.5 mg m^{-3} , less than 1.0 mg m^{-3} on the average. Simultaneously, on the lower surface of the ice and in its lower layers, an active development of cryoperiphyton initiates the development of a specific community of cryophilous micro-organisms (Yuriev and Lebedev, 1988). The algal component of cryoperiphyton in the Amur is represented by a population of a centric diatom *Aulacosira islandica* (O. Müller) Simonsen (= *Melosira islandica* O. Müll.). In the vicinity of large cities, a green alga, *Ankistrodesmus* sp., is also found. The colonies of *A. islandica* are distributed in the ice in the form of vertical bands, plates, or threads, consisting of bundles of algae up to 1 mm in diameter. The algae concentrate in the intercrystalline layers following the boundaries of the crystals and in microcracks. On the lower surface of the ice, they form "beards" trailing down into the water and washed by the current. The cells of *Ankistrodesmus* sp. are distributed haphazardly in the ice, mainly in the microcracks.

In the Amur, ice-cover algae usually appear in December when the ice is 60 to 70 cm thick. Coincident with thickening of the ice cover and a decrease of its growth rate, the biomass of algae in the lower layers of the ice and on its lower surface increases, reaching its maximum in mid-March. The highest value of the chlorophyll *a* content in cryoperiphyton communities is 240 mg m^{-2} . Within the long-term ice cover, the maximal biomass is near the base; for example, in the lowest 3 to 8 cm of ice 140 to 150 cm thick, 60 to 95% of the chlorophyll occurs, and its concentration here can reach 500 mg l^{-1} in melted ice. On the average, about 85% of the total chlorophyll *a* content of bulk ice is on the lower surface. In

late March to early April, algal biomass decreases rapidly because of ice thawing, accompanied by appearance of algae in the water under the ice. The rate of development of *A. islandica* on the lower surface of the ice is closely related to the thickness of the snow cover and the amount of light entering the water. Optimal light conditions for development of *A. islandica* occur in March on surfaces with snow cover of 1.5 to 5.5 g cm^{-2} (Fig. 19.4). This corresponds to a depth of snow cover of 2 to 12 cm, and light intensity under the ice of 1 to 18% of surface light intensity. In days of different nebulosity, the light intensity at noon on the lower surface of the ice varies from 200 to 9000 lux. In places free of snow, light inhibition of algae occurs. Here, with a surface light intensity of 20 to 50 thousand lux, the light intensity under the ice ranges from 7 to 25 thousand lux, and the chlorophyll *a* content is on average 5 mg m^{-2} . The minimum chlorophyll *a* concentration of 0.03 mg m^{-2} occurs in March under a snow cover of 40 cm, when the light intensity under the ice

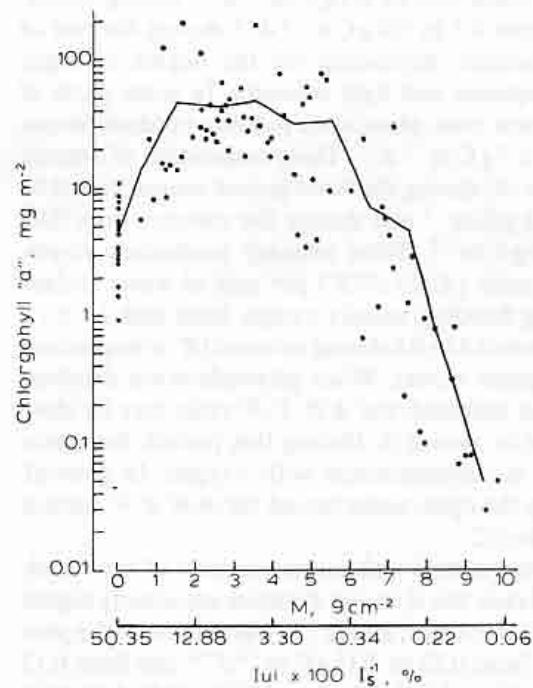


Fig. 19.4. Relationship between chlorophyll *a* concentration on the lower ice surface and snow mass cover or under-ice light intensity in the Amur River near the village of Bogorodskoye, March 1985–1988. Dots represent individual measurements; line is calculated.

is 30 lux, or 0.05% of the surface light intensity. We covered 30 m² of ice with a light-proof cover for over two months. The algae developed here under a light intensity of 0.01% of the surface light intensity. Data from this study indicated that the cryoperiphyton of the Amur is eurybiotic in relation to the light factor, and is able to function in a very wide range of light values, in contrast with ice flora from polar regions. The chlorophyll *a* concentration on the lower ice surface is on average about 30 mg m⁻² in March, which two to five times more than the pigment concentration in the water column.

PRIMARY PRODUCTION

In the Sredniy and Nizhniy Amur, more than 90% of planktonic algae suffer complete light inhibition because of the large mean depth of the river (> 10 m) and low water transparency. Related to this, relatively low values of primary production of plankton (*P*) are found; during the warm season, the values range from 0.06 to 0.3 g C m⁻² d⁻¹ during floods, and from 0.3 to 0.9 g C m⁻² d⁻¹ during the rest of the summer, depending on the degree of algae development and light intensity. In some parts of the Amur river, planktonic primary production can reach 1.7 g C m⁻² d⁻¹. Daily respiration of organic matter (*R*) during the flood period ranges from 0.04 to 0.21 g C m⁻³ and during the summer from 0.03 to 1.0 g C m⁻³. Total primary production/respiration ratio (*A/R'*) (*P/R'*) per unit of water surface during flooding usually ranges from 0.06 to 0.15, and from 0.2 to 0.6 during summer (*R'* = respiration per square metre). When phytoplankton development is maximal, the *A/R'* *P/R'* ratio may be close to one or exceed it. During this period, the Amur water is supersaturated with oxygen. In general, during the open-water period the *A/R'* *P/R'* ratio is close to 0.2.

In the central and outlet sections of the flood-plain lakes, the *A*, *P* and *R* values are usually higher than in the Amur, and in the warm parts of the year range from 0.12 to 2.31 g C m⁻² d⁻¹ and from 0.12 to 2.0 g C m⁻³ d⁻¹ respectively. The *P/R'* *A/R'* ratio during summer often is higher than one; however, on average during the vegetation seasons in different lakes, this ratio ranges from 0.8 to 1.0, which is four to five times higher than in the Amur.

In winter in the flood-plain section of the Amur, practically all primary production is from algae developing on the lower surface of the ice, because of the low density of algae in water and the low light intensity. In February–March primary production here ranges from 0.1 to 0.2 g C m⁻² d⁻¹, which is quite comparable to the mean value of *PA* during the typical warm part of the year. During the ice-cover period, the cryoperiphyton synthesizes about 9 g C m⁻², while the phytoplankton produces only 1.3 g C m⁻², or 13% of the total production during the same period. The value of under-ice ecosystem respiration varied between 0.3 and 1.4 g C m⁻² d⁻¹. The ratio of cryoperiphyton to total respiration was not more than 5%. The *P/R'* *A/R'* ratio increased from 0.01 in December to 0.22 in March, and during ice cover it averaged 0.08.

It is known that the value of *PA* per square metre of water is closely correlated with maximal photosynthetic rate (*P*_{max}) (*A*_{max}) and water transparency (*S*) and can be described by the equation:

$$P = P_{\max} S k_S, \quad A = A_{\max} S k_S,$$

where *k_S* is the coefficient of proportionality, considered to be equal to one on average (Boulon, 1983). The results of our studies during the warm part of the year showed that *P*_{max}*A*_{max} values under optimal light conditions depend on the chlorophyll *a* content of the plankton (*r* = 0.82), and are within the range of 0.1 to 0.4 g C m⁻³ d⁻¹, and 0.4 to 1.8 g C m⁻³ d⁻¹ during the summer. Maximal specific photosynthetic rate (*P*_m^b), which gives the amount of organic matter formed per mg of chlorophyll *a* per day in different hydrological reaches of the river, ranges from 13 to 120 and averages 55 ± 17 mg C (mg chlorophyll *a*)⁻¹ day⁻¹, which is characteristic of the plankton of most lakes and reservoirs of middle latitudes (Boulon, 1983). For lakes, *P*_{max}*A*_{max} values are usually within the range of 0.4 to 3.6 g C m⁻³ d⁻¹, reaching 6.6 to 7.5 g C m⁻³ d⁻¹ in some periods, which is four times as high as the highest values obtained for the Amur. Values for specific photosynthetic rate are within the limits of the analogous parameters obtained for the Amur, an average about 55 ± 24 mg C (mg chlorophyll *a*)⁻¹ day⁻¹. For cryoperiphyton, the *P*_m^b values are 5.2 to 9.4–6.5 mg C (mg chlorophyll *a*)⁻¹ d⁻¹ on average, which at 20°C would be 18.6 mg C (mg chlorophyll *a*)⁻¹ d⁻¹. Thus, the mean *P*_m^b values for cryoperiphyton are within the range of the lowest

values typical of summer phytoplankton. The annual primary production of the Nizhniy Amur is estimated at 40 to 50 g C m⁻² y⁻¹. The cryoperiphyton contribution to this value is 16 to 22%. Of the total annual primary production, 19 to 25% is synthesized under the ice, including phytoplankton production.

For the evaluation of the efficiency of photosynthetic activity of algae, it is important to calculate the value of utilization of total solar radiation (u) arriving at the surface of the water. The results show that in the Nizhniy Amur during the warm part of the year, u ranges from 0.01 to 0.44%. Moreover, values of u between 0.01 and 0.05% were observed mainly during floods, and values higher than 0.06% occurred during summer.

INVERTEBRATE COMMUNITIES

In mountain and foothill reaches of the Amur, zoobenthic organisms attain highest densities, among the most important being larvae of insects of the orders Diptera, Ephemeroptera, Plecoptera, and Trichoptera. Diptera are mainly represented by the larvae of Blepharoceridae, Chironomidae, and Simuliidae. In the middle part of the Bureya, where the river cuts through the Khrebet Turana, a unique population of fluorescent oligochaetes of the family Enchytraeidae occurs (Bogatov et al., 1980). Large colonies of the bivalves *Dahurinaia dahurica* and *Middendorffinaia mongolica* occur widely. In the foothill reaches of the Nizhniy Amur, amphipods (*Gammarus lacustris*) develop in large numbers, averaging about 10 to 20% of the numbers and biomass of the benthos.

In the flood-plain reaches of the rivers, invertebrate communities include both benthic and planktonic organisms. Among the planktonic invertebrates, Cladocera, Copepoda and Rotatoria are most widely distributed, reaching maximal development in the Nizhniy Amur. Maximal numbers and biomass of zooplankton are found after spring-summer floods, the values at the mouth being 1,000 to 3000 m⁻³ and 0.01 g m⁻³ respectively at the mouth, 1×10^4 to 3×10^4 m⁻³ and 0.1 g m⁻³ in the side channels, and 9×10^5 to 26×10^5 m⁻³ and 2 to 22 g m⁻³ in the backwaters. During this period, the zooplankton includes more than 20 crustacean species. In winter, the Amur zooplankton is very poor

and is represented by only two to three species; the number and biomass at the mouth of the Amur do not exceed 150 to 600 m⁻³ and 0.002 to 0.004 g m⁻³ respectively, and 750 to 1600 m⁻³ and 0.003 to 0.024 g m⁻³ in the side channels (Safonov, 1979).

The most important benthic organisms are the molluscs *Amuropaludina*, *Cristaria*, *Juga*, *Nodularia* and *Sinanodonta*, and immature stages of the Ephemeroptera, Plecoptera and Trichoptera. Significant development of Chironomidae, Odonata, Oligochaeta, and small bivalves of the family Pisidiidae occur in some parts of the river. The Nizhniy Amur basin is inhabited by a large number of rare mollusc species of the genera *Amuranodonta*, *Anemina*, *Buldowskia*, *Lanceolaria* and *Middendorffinaia*; these reach maximal species richness in the Ussuri basin (Zatravkin and Bogatov, 1987).

The quantitative composition of benthic organisms depends greatly on the substratum and hydrological regime of the river. The greatest population density of benthic invertebrates is observed on the silty bottom of the flood-plain reaches of the rivers during summer. Here, numbers, excluding molluscs, may range from 2000 to 30000 m⁻², and biomass from 1.5 to 40 wet weight g m⁻². Lowest numbers and biomass of benthic organisms during this period are found on dense sand, and are 50 to 100 m⁻² and 0.002 to 0.01 wet weight g m⁻², respectively. In foothill and mountain reaches of the rivers with gravel and pebble substrata, numbers of invertebrates may exceed 10000 to 20000 m⁻², with biomasses of 10 to 15 g wet weight m⁻².

Moderate fluctuations of the water level have no great effect on the development of zoobenthic communities. Following large floods along the entire river, repeated decreases in the number and biomass of benthic animals occur (Bogatov, 1978). The density of the organisms is restored rather quickly. However, during conditions of anomalously prolonged summer conditions lasting over 1 to 1.5 months, some mountain and foothill reaches without a dense riparian canopy develop extensive algal proliferation, which has an adverse impact on populations of Ephemeroptera, Plecoptera and Trichoptera, while populations of Chironomidae increase. In the upper reaches of the rivers where riparian canopies are partially or fully developed, no extensive development of algae occurs. Here, and especially in the open reaches of the rivers, the

trophic relations in the communities of benthic invertebrates become highly competitive because of a very limited amount of allochthonous organic matter reaching the stream. For example, in the Nizhniy Amur basin, the main detritivorous amphipods become predators and cannibals (Bogatov, 1991). Their numbers and biomass during this period increase noticeably, and at the end of summer, they may make up 90 to 95% of the total benthos.

Throughout the entire Amur basin, drift of benthic organisms occurs, and may be considered as their downstream movement with the flow of water. "Passive" or "random" drift is identified as resulting from living organisms accidentally leaving the bottom. "Behavioural" or "active" drift refers to those organisms actively leaving the bottom (Waters, 1972).

The motile invertebrates of the Amur basin which are dominant on the bottom make up the bulk of organisms rising actively into the water column. Their behavioural drift occurs, as a rule, at night or during twilight. Many attached organisms, or those having massive shells (Trichoptera, blepharocerids and molluscs) do not occur in the active drift. Evidently, oligochaetes, nematodes, ticks and fly larvae are casual constituents of the drift.

Individuals in the earlier stages of development occur most actively in the drift. More rarely, the size composition of migrants corresponds to that on the bottom. Different species usually reveal a different pattern of occurrence in the water column. Also, for those organisms prevalent in the drift in summer, an alternation of the intensity of migration is found, which usually shows only one major and one minor peak of activity. The total drift of organisms is expressed, for example, by the biomass of organisms passing through a portion 1 m wide of an imaginary cross section of the river extending from the surface to the river bed. This value, determined during the warmest part of the year under relatively stable hydrological conditions varies down the course of the river. In first order streams with a discharge of 0.2 to $3 \text{ m}^3 \text{ s}^{-1}$, drift ranges from 0.01 to 0.4 kg d^{-1} ; in streams of third and fourth order with discharge up to $40 \text{ m}^3 \text{ s}^{-1}$, drift ranges from 0.01 to 0.2 kg d^{-1} . In the deepest part of the Amur river near Khabarovsk, values up to 0.8 kg d^{-1} may be found (Levanidov and Levanidova, 1979).

Studies in the Amur basin (Bogatov, 1984) showed that the value of benthic drift (N_d) expressed

as the number or biomass of individuals carried per unit time past the hypothetical river section 1 m wide is determined by the migratory activity of animals (M) measured as the number or biomass of the organisms moved into the water column per day from a bottom area of l square metre and the distance of drift, L is:

$$N_d = (ML) \cdot l^{-1}$$

In turn, L depends on the time spent by invertebrates in the water column (T) and the flow velocity (V),

$$L = TV$$

In different species and size groups of organisms, the parameters M , L and T vary within wide limits. For example, the relative migratory activity M' (the M value related to the organism density on the bottom) of amphipods in the foothill reaches ranges from 3 to 110% of the total number, L varies from 15 to 500 m, T from 80 to 900 s. In different species of Ephemeroptera, M' usually ranges from 10 to 100% of the total number, L from 3 to 25 m, and T from 10 to 60 s. In the Nizhniy Amur, the mean drift distance of Plecoptera and Trichoptera larvae at a mean $T = 800$ s is about 0.5 km, and that of Ephemeroptera larvae is over 1 km (Bogatov, 1985).

During drift, the place of the displaced organisms is constantly being occupied by animals coming from higher reaches. Because of this, at a certain point of the stream, even when M' value is close to 100%, the settling density of invertebrates may remain stable for a long period. Thus, the biomass of organisms carried over a reach should be considered to be a result of the distribution of population production over the reach above the river section where the samples were taken. In this case, it becomes possible to calculate for a given site on the river the percentage of population production removed from the benthic community as a result of active drift (C), for example using the equation:

$$C = B_d/P_d$$

where P_d is the production of the organisms on the bottom over the whole area situated above the place where the drift samples were taken and B_d is the biomass of the organisms of the population carried over a river reach per day. Evaluation of C for populations of individual species carried out in small rivers of the Amur basin showed that, under

relatively stable hydrological conditions, the value of daily drift of biota is not higher than that of their daily production, and the value of C , on average, is 5 to 10% for benthic insect larvae and 10 to 80% for amphipods. As one moves away from the river source, the proportion of the production removed by drift from the site above the place of observations usually decreases, although the total drift of biota may increase (Bogatov, 1984).

During an increasing flood hydrograph, a close correlation was found between the values of M' and L for different animals on the one hand, and water discharge, Q , on the other. In particular, for an example of a population of *Gammarus lacustris* and *Cinygmula altaica* from the small Ukhta river (Nizhniy Amur basin), it was shown that, during the developing flood (up to a discharge of $0.38 \text{ m}^3 \text{ s}^{-1}$), the M' value for these populations naturally decreased while the value of L increased (Figs. 19.5, 19.6). Thus, the benthic organisms at the beginning of the flood were capable of sustaining a certain level of drift for some time, and a direct comparison of C in invertebrates during this period with Q did not show any consistent relationship (Table 19.1). With further increase in Q , values for L continued to increase and values for M' became stable; the drift of organisms increased spasmodically, and for

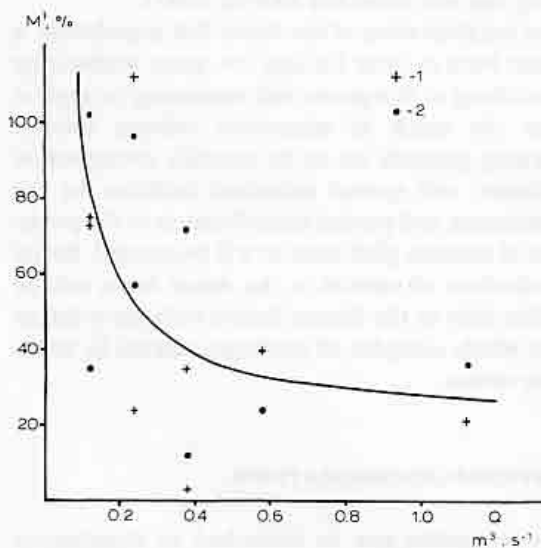


Fig. 19.5. Dependence of migratory activity (M') of *Gammarus lacustris* (1) and *Cinygmula altaica* (2) expressed in % of their number on the bottom on water discharge (Q) in the Ukhta river.

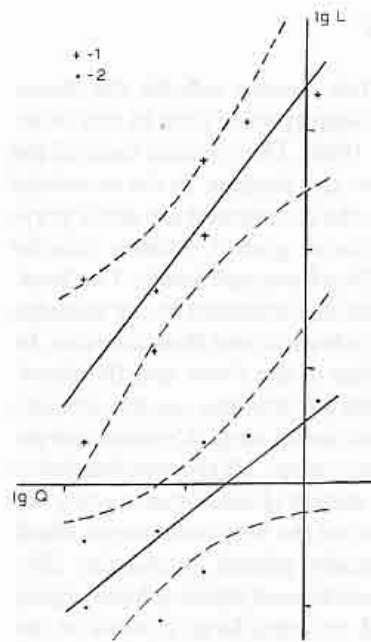


Fig. 19.6. Dependence of drift distance (L) of *Gammarus lacustris* (1) and *Cinygmula altaica* (2) on water discharge (Q) in the Ukhta river. Given on a logarithmic scale.

TABLE 19.1

Dynamics of the intensity of drift in the Ukhta river in the period of increasing flood

Water discharge ($\text{m}^3 \text{ s}^{-1}$)	0.12	0.24	0.38	0.58	1.12
Drift intensity (%)					
<i>Gammarus lacustris</i>	50	65	45	160	270
<i>Cinygmula altaica</i>	2	5	5	7	14

G. lacustris its level was higher than the population production. Evidently, the biomass of amphipods on the bottom must decrease as a result of drift.

On the whole, as a result of large floods, numbers and biomass of benthic macroinvertebrates decline, and a decrease in the dominance rank of individual species occurs, the river bed is scoured of excessive algal growth, and new supplies of allochthonous organic matter are delivered into the stream from the submerged part of the flood plain.

FISH COMMUNITIES

More than 120 fish species inhabit the Amur basin, which is significantly more than in any other Russian river (Berg, 1948). They inhabit most of the different water bodies and streams. In the mountain and foothill streams, the commonest are arctic grayling (*Thymallus arcticus grubei*), taimen (*Hucho taimen*), and lenok (*Brachymystax lenok*). The Sredniy and Nizhniy Amur are inhabited by the valuable sturgeons *Acipenser schrencki* and *Huso dauricus*. In the flood-plain reaches of the rivers and the flood-plain lakes, golden carp (*Carassius auratus gibelio*), Amur pike (*Esox reicherti*), carp (*Cyprinus carpio viridivoloceus*), silver carp, (*Hypophthalmichthys molitris*) and Amur catfish (*Parasilurus asotus*) occur. Here are also found the very rare species black Amur (*Mylopharyngodon piceus*), Aucha fish (*Siniperca chua-tsi*) and snakehead (*Ophicephalus argus*). In mid-summer and autumn, large schools of the far-eastern salmon leave the Sea of Okhotsk and the Tatarskiy Proliv and enter the Amur; these include *Oncorhynchus keta* typ., *O. keta* sub sp. *autumnalis* and *O. gorbuscha*. In autumn, the lamprey *Lampetra japonica* and in spring the smelt *Osmerus eperlanus dentex* leave the sea and enter the Amur.

For the majority of fish species, the Amur river, its tributaries, and flood-plain lakes represent a single ecological complex. In particular, many herbivorous commercial fish species of the Amur come to the flood-plain lakes for spawning and feeding in summer. Nevertheless, they winter only in the Amur because the lakes freeze. In winter, the main inhabitants of the smaller mountain and foothill tributaries migrate to the mouth of the Amur. The longest of the Amur first migrations are made by the migratory salmon. Large numbers of the huge autumn chum salmon (*Oncorhynchus keta*) go upstream in the Amur above Khabarovsk; the smaller-size chum salmon stay below Komsomol'sk-na-Amure. The main spawning areas for pink salmon (*Oncorhynchus gorbuscha*) are situated in the Amur estuary; large quantities of pink salmon enter the Amur tributary the Amgun' river. During upstream migrations, Amur salmon stop feeding. After reaching their spawning grounds and laying their eggs, they die. Downstream migration of the salmon fry occurs during darkness coincident with the active drift of river benthos (Levanidov, 1969). A large part

of the downstream migration of chum salmon fry leaves the Amur estuary and, skirting Sakhalin in the north, moves southward along its eastern coast to Japan. Some part of the young Amur humpback salmon (*Oncorhynchus gorbuscha*) population, after returning to the sea, migrate northward to the Sea of Okhotsk, while another part goes through the Proliv Nevel'skogo to feed in the Sea of Japan.

The state of stocks of both non-migratory and migratory species of Amur fish is closely connected to the hydrological regime of the Amur and the flood-plain lakes. Thus, in the years of low water in the Amur, there are no conditions for spawning of pike, and spawning of carp, catfish and golden carp is also limited. In the upper parts of the rivers in places where algal growth is high, a high mortality of fry is observed. In hard winters when the spawning rivers freeze, a great part of the eggs of the far-eastern salmon die. During the 1930s, the total annual catch averaged about 50 000 t, migratory salmon making up about 72% of this and non-migratory fish species about 28% (Nikolsky, 1953). However, during the last three decades, the Amur fish stocks have decreased greatly because of overexploitation and increasing environmental pollution. As a result of the complete deforestation in the upper parts of many spawning rivers, the spawning grounds of the Pacific salmon became shallower. In recent years, the total fish catch in the Amur usually has not exceeded 2000 to 5000 t.

For rehabilitation of the Amur fish population, a law has been in force the last few years prohibiting the catching of sturgeons and restricting to a great extent the catch of migratory salmon species. Spawning grounds are to be specially conserved in the future, and special industrial facilities for the maintenance and partial rehabilitation of the population of autumn pink salmon will be created. Better reproduction of salmon in the Amur basin will be possible only in the distant future with the solution of the whole complex of problems related to water conservation.

ECOSYSTEM GENERALIZATIONS

An ecosystem can be described as dynamic in space and time, an open natural complex formed by populations of organisms and their environment, and connected by stable flows of matter, energy and

information which provide its integrity, organization in structure and function, and regulation. Evidently, some spatially localized ecosystems may be considered as a subsystem or component of a higher-order ecosystem. From this point of view, the Amur river, together with its tributaries and flood-plain lakes, is a gigantic aquatic ecosystem. Its integrity and organization in structure and function are particularly visible in that the different sections of the lake-river system are used by many species of Amur fishes during spawning, feeding or hibernation. A specific role in the large-scale stable flows of substance and energy in the ecosystem, and use of the information flows for orientation in the environment, is displayed by the schools of Pacific salmon moving to their spawning grounds and by their young returning to sea.

Among other groups of river hydrobionts – algae, bacteria, invertebrates, etc. – stable interrelation under river-ecosystem conditions may be through the passive or active downstream drift of organisms, flight of the aquatic insect imagines to the upper and lower reaches of the rivers, migration of some species of invertebrates against the stream, drift of allochthonous and autochthonous organic substances downstream, and other relationships. In the upper mountain and foothill parts of the rivers, the basic interconnections occur between the associations of benthic organisms, while in the middle and lower flood-plain sections they occur largely between the benthic and planktonic communities, which occur in the river under fundamentally different spatial-temporal conditions. The habitat of the populations forming the benthic communities is related to certain parts of the river, and the development period of these populations is unlimited. Planktonic communities are formed of organisms entering the rivers mainly from the flood-plain basins. They live in the moving water mass, and hence the time for their development in the river is limited by the time the water takes to reach the mouth. Therefore, planktonic communities in the river are temporary, and these organisms cannot be strictly considered as belonging to any population. Nevertheless, in the Sredniy and Nizhniy Amur basins, such temporary communities play an important role because the main energy flows pass through them, in particular during summer low water. In winter, during frozen conditions, the role of planktonic communities is sharply reduced. On

the lower ice surface, another specific temporary community – cryoperiphyton – is formed, which provides a photosynthetic capability in the river during this period.

As the water mass moves from the source to the mouth, regular variations in environmental quality for the hydrobionts occur both due to abiotic factors and due to vital functions of the river organisms. These variations, in turn, are reflected in the structural-functional peculiarities of subsequent river communities. In the most schematic form, these variations have been generalized in the River Continuum Concept (Vannote et al., 1980), whose basic features are characteristic of the rivers of the Amur basin, too. As in other river basins of the world covered by forest, allochthonous organic substances in the form of leaf fall and other organic detritus have considerable importance in the biotic balance of hydrobionts in the upper reaches of the Amur basin rivers. Then, moving away from the river source, the greatest important in the energy flows of the community is from autochthonous organic material represented, mainly, by algae or mosses, and fine organic material carried by the stream. Accordingly, the trophic structure of benthic animal communities changes by decreasing the proportion of shredders and simultaneously increasing that of collectors and grazers. Closer to the flood-plain sections of the rivers, the planktonic communities become more and more important in the ecosystem.

In respect of the metabolism of the river community, the River Continuum Concept asserts that, in the upper and lower reaches, the $P/RP/R'$ ratio should be lower than one, while in the middle reaches of the river where the species diversity is largest, this ratio is equal to one or higher. Contrary to this situation, in the Amur, $P/RP/R'$ values close to one were most often found in the lower reaches during low water, but not in the middle part of the river. In the middle sections of the river at this time, anomalous development of algae accumulated on the stones and, consequently, higher $P/RP/R'$ values, could sometimes occur. However, as a result of this development of algae, the diversity of benthic communities decreases and, sometimes, a mass mortality of fish fry and larvae takes place. On the average, during the period of open water in all sections of the Amur river and its tributaries, including the middle sections, the $P/RP/R'$ ratio was much less than one,

which indicates a heterotrophic type of Amur ecosystem metabolism

It is known that, compared with the ecosystems of other large river basins in Russia such as the Volga, Ob', Yenisey and Lena, the Amur ecosystem is distinguished by high species abundance and quantitative development of the benthic animals and fishes (Berg, 1948; Levanidov, 1969), although the Amur basin is the only one of the great river basins in Russia which is located in a zone subject to the monsoon climate and, therefore, its ecosystem is continuously subject to large and catastrophic floods. It was found that, in the case of small floods, the Amur benthic communities have the ability to limit their drift and, therefore, to keep their structure. However, in the case of large floods, the magnitude of hydrobiont drift can greatly exceed that of production of their populations as a result of which the biomass of organisms on the bottom is markedly reduced. Thus, during the floods, what one may call "hyper-drift" ("negative drift": Bogatov, 1988) of organisms occurs at the ecosystem level in the river community—that is, the magnitude of drift of hydrobionts exceeds their production. It is noteworthy that the substance and energy accumulated in the biomass of drift organisms under conditions of high floods leave the ecosystem borders and do not participate in their subsequent circulation. Hence, the biomass of organisms drifted by floods may be considered as some indicator of "payment" of the river community for its existence under monsoon-climate conditions.

From the point of view of the entropy law, it is assumed that the degree of community order is maintained by respiration of the whole community—that is, because of the dispersion in space of heat energy which cannot be used (Odum, 1975). Using the community of aquatic animals as an example, Alimov (1989) showed that, with increase of their complexity, the ratio of community production (Pb) to total metabolic expenditures by all animal communities (Rb) decreases regularly. In this case, Pb/Rb ratio can be some indicator of the degree of community order (Yb). Then, for river ecosystems which irrevocably lose a considerable portion of community production during floods because of negative drift, the indicator Yb might be written as:

$$Yb = (Pb - Bb) / (Rb + Bb),$$

where Bb is the community biomass drifted by floods. This assumes that the high species abundance of Amur animals and, consequently, the relatively more complex structure of their communities, are maintained not only by respiration of the community but by the specific form of the production estrangement—that is, negative hydrobiont drift. This conclusion is indirectly confirmed by repeated observations of the intensive eutrophication of the Amur ecosystem for long, low-water periods, which lead to the simplification of community structure and to increase in the dominance of individual species. It is assumed that the physical disturbances in the river ecosystems caused by the floods are not stresses for the river community at the system level (Minshall et al., 1985; Minshall, 1988). However, if one estimates the role of floods from the point of view of maintaining some degree of stability of river ecosystems developed under monsoon-conditions, one can conclude that impacts caused by floods not only do not lead to stresses in the communities but also are necessary conditions for their existence.

Evidently, when some river ecosystems function under the continuous influence of extreme physical factors such as floods, droughts and river-bed freezing, a system of natural refugia can play a specific role in maintaining the communities, according to the Patch Dynamics Concept (Townsend, 1989). In the Amur basin, such refugia for some hydrobiont populations are, for example, cracks in the rocks during floods, and underflow or deep holes during droughts, while for many fishes living in the upper reaches of the rivers or flood-plain lakes, the main Amur river bed is a natural refuge during hibernation. It is important that in the ecosystem, if natural conditions return, the disturbed structure can be restored quite rapidly to the continuum. Therefore, the River Continuum Concept and Patch Dynamics Concept available today explain the features of river-ecosystem functioning from different points of view and can be considered as mutually supplementing—which allows one to examine the ecosystem conditions more fully and realistically, and creates the prerequisites for more accurate prediction of variation in these conditions including those due to anthropogenic impact.

The concept of the integrity of the ecological system of the great river basins permits one to determine a strategy directed to ecological optimization of water management.

As a basis for this strategy, one must assume that serious destruction of the river system is to be avoided and that maximum use is to be made of natural processes. Basic reconstruction of the river ecosystems should be expected to lead to the appearance of new, more acute ecological problems which may greatly decrease the efficiency of water management. In the Amur basin particular alarm is caused by plans under development for the creation of a reservoir cascade in the Amur and its large tributaries, and regulation of the great flood-plain lakes. Realization of these plans will destroy the ecosystem integrity, accelerate eutrophication processes, and, finally, lead to degradation of one of the most unique river basins in Russia.

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