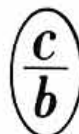


СЖЕКАН 15(3) 103-160 (1984)

✓  
THE SOVIET JOURNAL OF  
**ECOLOGY**  
ЭКОЛОГИЯ/ÉKOLOGIYA

TRANSLATED FROM RUSSIAN



CONSULTANTS BUREAU, NEW YORK

THE SOVIET JOURNAL OF ECOLOGY

Volume 15, Number 3

May-June 1984

501

# THE SOVIET JOURNAL OF ECOLOGY

A translation of *Ékologiya*

January, 1985

Volume 15, Number 3

May-June, 1984



## CONTENTS

Engl./Russ.

Age Structure and Dynamics of Small Isolated Populations of Ural Endemic Milk Vetches - P. L. Gorchakovskii and V. N. Zueva. . . . .	103	3
Critical Periods in the Seed Reproduction of the Norway Maple ( <i>Acer platanoides</i> L.) - Yu. Z. Kulagin and N. I. Mushinskaya. . . . .	111	12
Effect of Industrial Pollutants on the Ash Composition of Leaves from Woody Plants and Their Infestation by Arthropods - M. A. Makhovskaya, R. I. Zemkova, and S. A. Kruglikov . . . . .	115	17
Ground (Coleoptera, Carabidae) and Rove (Coleoptera, Staphylinidae) Beetles of Wheat and Corn Fields and Their Interaction with Surrounding Biotopes - J. Boháč and J. Pospíšil . . . . .	120	22
Soil Animals in the Biogenic Migration of Phosphorus in Forest-Steppe Ecosystems - A. D. Pokarzhevskii and S. A. Gordienko. . . . .	130	34
Thermoregulatory Responses to Cooling in Small Subarctic Mammals - V. G. Krivosheev, M. A. Vain-Rib, N. I. Dobrinskii, and A. A. Tsvetkova . . . . .	133	37
Some Characteristics of the Winter Diet of Moose - V. D. Kheruvimov. . . . .	137	42
Influence of Human Activity on the Natural Plague Focus in the Central Asian Desert - A. S. Burdelov and S. B. Pole. . . . .	142	48
Significance of Benthic Drift in the Biological Production of Rivers - V. V. Bogatov . . . . .	146	52
Distribution of Phyllophagous Insects in the Crown of Drooping Birch at the Northern Boundary of Tree Vegetation - I. A. Bogacheva . . . . .	153	60

The Russian press date (podpisano k pečati) of this issue was 8/7/1984.  
Publication therefore did not occur prior to this date, but must be assumed  
to have taken place reasonably soon thereafter.

SIGNIFICANCE OF BENTHIC DRIFT IN THE BIOLOGICAL PRODUCTION  
OF RIVERS

V. V. Bogatov

UDC 574.91:595(551.482)

New parameters are presented for comparing the drift of benthic invertebrates with the density of organisms on the bottom and the magnitude of the daily production of their population: The minimum drift distance and its intensity. The minimum drift distance is negatively correlated with the biomass of benthic animals and positively correlated with drift intensity. The drift of hydrobionts greatly exceeds their production. It is postulated that the benthic community of a stream can attain a more stable state as a result of drift.

Plankton is virtually absent in most rivers with a rapid current, and benthic invertebrates are the main source of food for many fish. Of importance in this case is the drift of benthic organisms, by which is understood the movement of invertebrate animals downstream in the river current.

Even the earliest studies of benthic drift showed that vast numbers of organisms are carried off in rivers. Therefore, many hydrobiologists in the 1950s and 1960s asked how benthic communities could sustain such a seemingly high level of depletion. Two hypotheses have been defined. The first, proposed by Müller (1954), consists of the so-called "colonization cycle," which involves the flight of adult insects upstream, oviposition, and the mass hatching of young in the upper reaches of the stream, followed by the drift of nonsexually mature larvae for the colonization of all accessible habitats and a new imago flight upstream for the completion of the cycle. Waters (1972), after analyzing numerous observations made by various authors, concluded that two elements of Muller's hypothesis (drift of benthic invertebrates and their movements upstream) are apparently unrelated to one another. To explain the mechanism of regulation of population density, Waters (1961) proposed a new hypothesis that assumes the compensation of drift by imago production regardless of the direction of imago flight. However, the existing parameters by which benthic drift has been estimated have not permitted a confirmation of Water's hypothesis.

The problem is that in the great majority of studies the drift of benthic invertebrates has been estimated by the quantity (biomass) of migrants removed across a unit of cross-sectional stream area or across the river profile per unit of time, or by the quantity (biomass) of animals per unit of volume of water or those trapped per unit of time. These parameters are highly dependent upon stream hydrodynamics, making their comparison and systemization quite difficult. Thus, Waters (1972), after analyzing 115 sources, was able to compare hydrobiont drift in different streams in only four studies. In this same review Waters proposed that the drift intensity in rivers with different runoffs be compared by the quantity (biomass) of organisms carried per day across the river profile divided by the discharge rate. Thus, as the author points out, an estimate is gained of the average density of migrants per unit discharge rate, equal to  $1 \text{ m}^3/\text{sec}$ . Actually, Waters' parameter denotes only the daily average quantity of organisms in  $86,400 \text{ m}^3$  water, since  $1 \text{ m}^3/\text{sec} \times 86,400 \text{ sec (24 h)} = 86,400 \text{ m}^3$ .

Unfortunately, the foregoing parameters permit no comparison of the drift of organisms taking into account their population density on the bottom. The ratios of the quantity of organisms in  $1 \text{ m}^3$  water (Radford and Hartland-Rowe, 1971) or in the water thickness above  $1 \text{ m}^2$  bottom area (Elliott, 1965) to the animal population density on  $1 \text{ m}^2$  bottom area proposed for these purposes do not take current velocity into account. This is a significant deficiency, since if the parameters are equal the drift will be greater in those regions of the river where the current velocity is higher. The inability to estimate benthic drift

---

Institute of Soil Biology, Far Eastern Scientific Center, Academy of Sciences of the USSR. Translated from *Ekologiya*, No. 3, pp. 52-58, May-June, 1984. Original article submitted July 15, 1983.

taking into account either the density of hydrobionts on the bottom or stream hydrodynamics has greatly complicated the study of the relation between the drift of benthic animals and their production.

Our research goals included study of the relative magnitude of invertebrate drift and production. In this case, attention was mainly directed at searching for quantitative estimates of the drift of organisms, considering not only the stream hydrology but also the dynamics of populations and the magnitude of their production.

The research material was provided by field observations of communities of benthic animals at two gates on the Ukhta R. (160 m distance between gates) and on the Pil'de R. (Lower Amur basin, 1977-1979). In addition, published data were used.

The streams studied are characterized by a gravel-pebble bottom on which amphipods and mayfly, caddisfly, stonefly, and midge larvae are dominant. The production of their populations was calculated using the specific productions presented by V. E. Zaika (1972). Measurements of the water discharge and current velocity were used to characterize the conditions in the hydrobiont habitats.

Earlier (Bogatov, 1979a) we showed that the drift of benthic animals  $N_d$ , expressed by the numbers (biomass) of animals carried during a specified time across an elementary area of a current cross-section of width  $l$  and height equal to the depth is determined by the migrational activity of the animals  $M$ , measured by the quantity (biomass) of organisms passing during the same time into the water thickness from a bottom area equal to  $l^2$ , and by the distance of their drift  $L$ :

$$N_d = LM/l, \quad (1)$$

Hence it follows that the population density  $N$ , expressed by the numbers (biomass) of individuals inhabiting a bottom area equal to  $l^2$ , is not directly related to the drift  $N_d$ . However, when  $N = M$ ,  $N$  will determine the maximum possible values of  $M$ . In this case  $L$  will take minimum values or, on the basis of Eq. (1),

$$L_{\min} = N_d l / M_{\max}, \quad (2)$$

and since  $M_{\max} = N$ , then

$$L_{\min} = N_d l / N. \quad (3)$$

It is apparent from Eq. (3) that the drift of organisms can be compared with an estimate of their population density on the bottom using the parameter  $L_{\min}$ , which denotes the distance by which benthic invertebrates can move in a stream if all animals in the population are involved in movement at an observed drift magnitude. It is important that the current hydrodynamics automatically be taken into account here.

When drift samples are taken in pools a large number of animals that normally inhabit riffles are noted among the drifting organisms. It is understood that in this case  $L_{\min}$  must be calculated from the population density observed in a riffle. And by contrast, when the migrants in a riffle include invertebrates whose habitat is confined to pools  $L_{\min}$  in this case should be calculated by the density the hydrobionts attained in the pools. In both cases the degree of contraction or expansion of the river bed in the riffle or pool must be accounted for. Thus, if the drift of animals in a pool is to be compared with their population density on  $1 \text{ m}^2$  area of riffle bottom, i.e.  $l = 1 \text{ m}$ , then the magnitude of  $N_d$  in the pool is calculated for an elementary current sectional area  $S$ , equal to

$$S = (l_1 \cdot l_2 / l_2) h M, \quad (4)$$

where  $l_1$  and  $l_2$  are the width of the pool and riffle, respectively, and  $h$  is the pool depth.

Our calculations of  $L_{\min}$  for, as an example, the *Gammarus lacustris* populations in Ukhta and Pil'de rivers showed that when  $l = 1 \text{ m}$  this parameter has a significant negative correlation (correlation coefficient  $r = -0.51$ ) with the amphipod biomass per  $1 \text{ m}^2$  bottom area (Fig. 1a). Insofar as the high crustacean biomass on the bottom was due primarily to adult individuals, it can be assumed that the obtained dependence is explained not by the extreme density of organisms but rather by the low intensity of migrations of adult *Gammarus*.



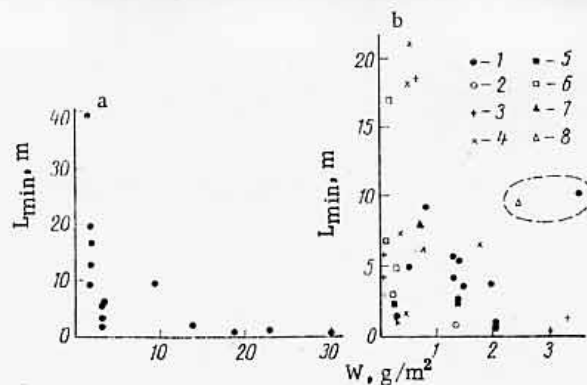


Fig. 1. Relation between minimum drift distance of hydrobionts ( $L_{\min}$ ) and their biomass on bottom ( $W$ ): a) *G. lacustris*; b) insect larvae: 1) *Cinygmula altaica*, 2) *Cinygmula* sp., 3) *Pseudocloeon fenestratum*, 4) *Ephemerella aurivillii*, 5) *Baetis* sp., 6) stonefly larvae, 7) *Baetis bioculatus*, 8) *Ameletus montanus*.

*rus*, since it is known that among hydrobionts of different age the individuals of earlier stages of development are most actively involved in drift (Bogatov, 1979b). The significant variability at a low animal biomass is explained by the relatively greater importance in this case of young amphipods, which possess a lesser resistance to changing environmental factors than do adult organisms.

A negative correlation between the  $L_{\min}$  of hydrobionts and their biomass on the bottom ( $r = -0.43$ ) was also noted for common larval insect forms (Fig. 1b). As in amphipods, significant variation in the intensity of larval drift was observed at a low biomass. We note that the high  $L_{\min}$  parameters in *Cinygmula altaica* and *Ameletus montanus*, indicated in Fig. 1b by the dashed circle, characterized animal populations in which many individuals were at the final stages of development, and mass imago emergence was imminent. Since it is known that the activity of insect larvae increases prior to imago emergence (Stoneburner and Smock, 1979), these data were ignored in calculating the correlation coefficient.

Our results made it possible to evaluate critically the generally accepted hypothesis explaining the drift of organisms by the competitive relationships between animals for substrate and food. Apparently, the assertion that competition induced by overpopulation is the major cause of drift cannot be considered convincing. It can be assumed that the attenuation of competitive relations between hydrobionts is best viewed as a result of the drift of organisms and not as its cause.

Calculations of  $L_{\min}$  for various invertebrate populations showed that the fluctuations in drift intensity under the action of environmental conditions sharply exceed the measured values. The  $L_{\min}$  magnitude is close to 10 m for insect larvae and 20 m for the more mobile amphipods. In this connection one can speak of a certain norm in the depletion of the animal biomass on the bottom within which the normal function of the community of benthic organisms is undisturbed. To express this norm of depletion we introduce the parameter of drift intensity  $C$ , which takes into account the fraction of the population production removed from the benthic community as a result of active drift:

$$C = (B_n/P_n) \cdot 100\%, \quad (5)$$

where  $P_n$  is the daily production of organisms on the bottom and  $B_n$  is the biomass of the organisms in the population carried across the river section in a day. Evidently, before examining the parameter of drift intensity  $C$  it is necessary to determine the boundaries of the population in the river and that part of the population with the production of which the biomass removed from the animal community as a result of drift will be compared.

It is important for the determination of population boundaries that there be no barrier preventing animal dispersal for species living under conditions of a rapid or slow current,

TABLE 1. Intensity of Hydrobiont Drift in Ukhta R.

Species	Date	Q <sub>d</sub> , m <sup>3</sup> /sec	Gate	S <sub>1</sub> , thousand m <sup>2</sup>	W <sub>b</sub> , g/m <sup>2</sup>	P <sub>n</sub>		C, ‰
						B <sub>n</sub> , g/day		
<i>Gam. lacustris</i>	19-20 VIII.77	0,12	U	10	2,44	122	97,5	80
	23-24 VIII.77	0,24	L	10	2,44	122	21,7	18
	24-25 VIII.77	0,38	U	10	2,44	122	90,5	74
	21-22 VIII.78	0,58	L	15	1,51	113	71,1	58
	15-16 VII.79	0,54	L	12,5	13,82	864	88,1	72
	9-10 X.79	0,45	L	12,5	22,79	912	21,9	18
	20-21 VIII.78	0,58	U	15	1,64	443	171	150
	21-22 VIII.78	1,12	U	15	1,64	443	118	104
	15-16 VII.79	0,54	L	12,5	0,50	113	237	209
	9-10 X.79	0,45	L	12,5	0,29	40	253	223
<i>Cin. altaica</i>	19-20 VIII.77	0,12	U	10	1,71	308	10,2	3
	23-24 VIII.77	0,24	L	10	1,71	308	3,6	1
	24-25 VIII.77	0,38	U	10	1,71	308	29,8	10
	21-22 VIII.78	0,58	L	15	1,64	443	4,9	2
	15-16 VII.79	0,54	L	12,5	0,50	113	17,5	6
	9-10 X.79	0,45	L	12,5	0,29	40	12,3	4
	20-21 VIII.78	0,58	U	15	1,64	443	25,8	6
	21-22 VIII.78	1,12	U	15	1,64	443	21,0	5
	15-16 VII.79	0,54	L	12,5	0,50	113	46,6	11
	9-10 X.79	0,45	L	12,5	0,29	40	53,2	12
<i>Am. montanus</i>	15-16 VII.79	0,54	L	12,5	2,45	551	94,2	17
	15-16 VII.79	0,54	L	12,5	0,06	13,5	1,4	10
<i>Ps. fenestratum</i>	18-19 IX.79	1,59	L	17,5	0,65	159	93,1	58
	9-10 X.79	0,45	L	12,5	0,05	6,9	1,7	25
	15-16 VII.79	0,54	L	12,5	0,45	101	2,9	3
<i>Eph. aurivillii</i>	18-19 IX.79	1,59	L	17,5	0,78	191	36,8	19
	9-10 X.79	0,45	L	12,5	0,35	48	20,8	43

Note. U denotes upper gate; L, lower gate; Q) water discharge; S<sub>1</sub>, stream area between source and observation gate; W<sub>b</sub>, benthos biomass on bottom.

pools or rifles. The true distance over which drifting organisms, move, for example during frequent summer floods, may be from several tens to several hundreds of meters per day (Bogatov, 1983). Insofar as the durations of the life cycle of amphipods and several common larval insect forms comprise about two years, it can be stated with assurance that certain hydrobionts during ontogenesis can, thanks to an active migration, transfer genetic information over quite large distances. Thus, in the semialpine streams we studied, which, as a rule, have a uniform character of substrate, the entire section of river inhabited by a given species can be considered as the population territory.

At each region of a river the drift of invertebrates across a current cross-section occurs from a specified area, the length of which corresponds to L. However, the organisms that are carried off are replaced by animals from a region upstream, which are in turn replaced by hydrobionts living even farther upstream, and so on. Because of this, the population density of the animals at a given point in the stream may long remain stable in spite of an intensive drift. It follows from the foregoing that the biomass of the organisms carried across the river profile must be considered the result of the distribution of the population production in the whole territory situated above the gate where the samples are

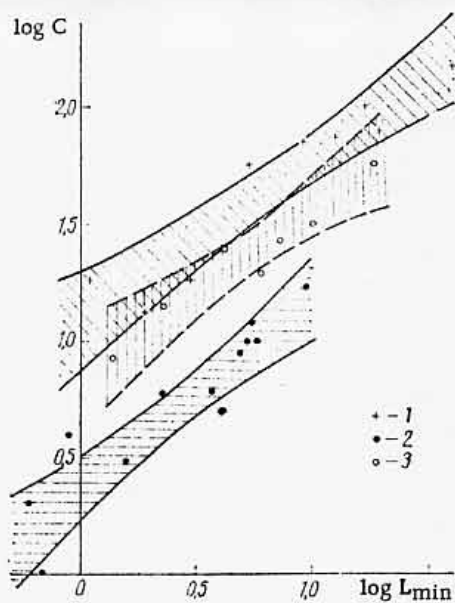


Fig. 2. Relation between parameter of drift intensity (C) and minimum drift distance ( $L_{\min}$ ) in *G. lacustris* (1) and mayfly larvae in summer (2) and autumn (3). Logarithmic scale.

collected and not only in the area from which the animals were directly removed, an assumption made, for example, by Waters and Hokenstrom (1980).

In calculating the intensity of the removal of benthic animals in Ukhta R. (Table 1) it was found that the biomass  $B_n$  of drifting *G. lacustris* at an  $L_{\min}$  of up to 15 m did not exceed the population's production, and the C parameter was within the range of 10–80%. The biomass of migrating amphipods exceeded their production in the river only during the flood of 1978. Clearly, the biomass of the *Gammarus* population would decline as a result of such drift. The  $B_n$  of mayfly larvae was considerably lower than the mayfly production even during floods, and C averaged 5–10%.

A calculation of C for hydrobionts (Fig. 2) made it possible to establish the high positive correlation of this parameter with the minimum drift distance in amphipods and mayfly larvae. On the basis of the obtained results, the relation between C and  $L_{\min}$  can be approximated by the following equations:

for *G. lacustris* drifting in the summer:

$$C = 12.24 \pm 2.23L_{\min}^{0.71 \pm 0.09}; \quad (6)$$

for mayfly larvae drifting in the summer:

$$C = 2.33 \pm 0.27L_{\min}^{0.82 \pm 0.12}; \quad (7)$$

for mayfly larvae drifting in the autumn:

$$C = 7.40 \pm 1.45L_{\min}^{0.71 \pm 0.12}. \quad (8)$$

Thus, it becomes possible for specific river regions to calculate C by way of  $L_{\min}$ , which is considerably easier to find than  $P_n$ . It is readily noted that there are statistically significant differences between Eqs. (6), (7), and (8) at the accepted level of significance, which are explained by the differing magnitude of the specific production, dependent both upon the temperature conditions of the stream and upon the systematic position of the hydrobionts.

In calculating C for *G. lacustris* in the Pil'de R. it was found that the fraction of the population's production removed as a result of drift from the region located above the observation site declined from 5.6% in the upper reaches of the river to 1.6% in the central region (Table 2). Thus, with distance from the river source an increasing portion of the population's production is distributed within the ecosystem of the given stream. Therefore, the relation between  $L_{\min}$  and C may have special features for each river segment. This conclusion is supported by the results calculated from the data of Pearson and Kramer (1972) on the distribution of the production of *Oligophlebodes sigma* and *Baetis bicaudatus* in the

TABLE 2. Intensity of Drift of *G. lacustris* in Pil'de R.

Station number	Date	Q, m <sup>3</sup> /sec	S <sub>1</sub> , thousands m <sup>2</sup>	P <sub>n</sub> ,	B <sub>n</sub>	C, %
				kg/day		
1	2-3 VII.78	7,6	259	84,5	4,75	5,6
2	7-8 VII.78	15,6	637	107,8	4,28	3,9
3	8-9 VII.78	15,6	724	113,2	3,50	3,1
4	15-16 VII.78	43,9	1799	197,5	3,11	1,6

TABLE 3. Production, Drift, and C Parameter in *O. sigma* and *B. bicaudatus* in Temple Fork R. (USA)

Station number	Production, g dry weight/m <sup>2</sup> per year		Drift, g dry weight across river profile per year		C, %	
	1968	1969	1968	1969	1968	1969
<i>O. sigma</i>						
1	1,28	1,29	30	134	4	17
2	3,85	3,47	2567	2318	11	11
3	4,30	3,31	5987	1335	9	3
<i>B. bicaudatus</i>						
1	1,96	1,95	1342	1990	112	167
2	1,18	1,07	2137	2621	26	35
3	2,13	1,76	1085	4381	4	18

Note. Production and drift cited from Pearson and Kramer (1972).

small mountain stream Temple Fork (Utah, USA). The observation stations were located at 0.2, 1.8, and 4.2 km from the source, while the average area of the river bottom was 620 m<sup>2</sup> between the source and the first station, 5856 m<sup>2</sup> between the first and second stations, and 9504 m<sup>2</sup> between the second and third stations. It was found that, with some exception, as the distance of the observation gate from the source was increased in Temple Fork, as in the Pil'de R., the fraction of production removed from the region located above the selected gate declined regularly, although the total hydrobiont drift in some cases increased (Table 3).

Evidently, estimation of the magnitude of the animal biomass removed from a community of organisms located in the region bounded by upper and lower gates requires knowledge of the magnitude of biomass at the input to the system, i.e. drift samples should also be taken at the upper gate. In this case C will be calculated as

$$C = \frac{B_n'' - B_n'}{P_n'} 100, \quad (9)$$

where P<sub>n</sub>' is the daily production of organisms in the population that are located in the region of river between the two gates, and B<sub>n</sub>' and B<sub>n</sub>'' are the biomasses of organisms carried in one day across the river profile at the upper and lower gate, respectively. In this case, the production will be removed from the animal community located in the region provided B<sub>n</sub>'' > B<sub>n</sub>'. However, situations are frequently encountered in practice where B<sub>n</sub>'' < B<sub>n</sub>', i.e. biomass can increase not only due to the production of hydrobionts but also due to their intensive drift from the upper regions of the river. In this case C will have negative values.

The obtained data make it possible to state certain postulates concerning the calculation of the food base of fish in streams, as well as the functional meaning of river benthos drift.

The calculation of the biocenotic production P<sub>b</sub> during some time period t<sub>1</sub>, t<sub>2</sub>, taking into account the relative significance of trophic levels, is presently very important for estimating the productivity of bodies of water (Alimov, 1979):



$$P_b = P_f + P_p - A_p, \quad (10)$$

where  $P_f$  and  $P_p$  are the prey and predator production, respectively, during the time  $t_1$ ,  $t_2$ , and  $A_p$  is the energy assimilated during the time  $t_1$ ,  $t_2$  by the predators included in the community.

Part of the biocenotic production in a river is constantly removed from the system as a result of active drift. The absolute magnitude of such removal may be high: Thus, the daily biomass of the removed benthos was 9-13 kg in the Pil'de R., and the total biadrift in the Ukhta R. ranged from 0.04 to 1.1 kg per day.

We assume that in alpine and semialpine streams the products of the vital activity of predators included in the biocenose are removed with the water masses due to vigorous water current. Then that part of the production of the benthic biocenose  $P_b''$  remaining in the region above the observation gate during the period  $t_1$ ,  $t_2$  can be calculated from the equality

$$P_b'' = (P_f + P_p) - (B_d + C_p), \quad (11)$$

where  $B_d$  is the biomass of organisms carried across the river profile during time  $t_1$ ,  $t_2$ , and  $C_p$  is the ratio of predators included in the community during the time  $t_1$ ,  $t_2$ .

The ratio of the biocenotic production to the energy expenditures by all animals in the community for metabolic processes ( $P_b/R_b$ ) is used as a parameter of the functional state of the system and is inversely related to its diversity (Alimov, 1982). At the same time the energy-metabolism expenditures for the biocenose  $R_b$  represent the sum of the expenditures for metabolism of all animals included in a specific community. In river biocenoses, due to the constant removal of a part of the community production as a result of drift, the  $P_b/R_b$  ratio will decline to  $P_b''/R_b$  at specific river regions. Consequently, it can be assumed that as a result of drift the benthic community of a stream is capable of passing to a more stable state, permitting the system to maintain a high diversity, since it is believed that the system is more stable at a low  $P_b/R_b$  ratio and higher diversity (Alimov, 1982). However, the foregoing hypothesis requires more careful empirical verification. Apparently, analogously to the action on an ecosystem of "moderate predation" (Paine, 1966), the diversity of a river biocenosis depends upon the effectiveness with which the monopoly of the dominant species declines during hydrobiont drift. It is also known that the removal of the "excess" biomass from an animal community is capable of stimulating the production of the remaining organisms (Watt, 1969).

It follows from the foregoing that benthic biocenoses may have a simplified structure in streams where for any reason hydrobiont drift does not occur. In fact, in a small stream (Reinike Island, Maritime Krai), the water of which filtered underground to prevent the removal of a part of the organismic biomass by means of a drift, we observed a community on a gravel-pebble substrate in June that consisted of only two species: *G. lacustris* and *Heptagenia* sp. Possibly, the low diversity and moderate density of the benthos in certain northern rivers in Sweden (Ulfstrand, 1968) and Chukota (Levanidov, 1976, 1977) may also be a result of the decline in the activity of benthic organisms during the maximum day length. It is important that the predator pressure in this case be negligible, which was, incidentally, noted by V. Ya. Levanidov (1976) in Chukota streams.

#### LITERATURE CITED

- Alimov, A. F., "Determination of biocenotic production," in: General Principles of the Study of Aquatic Ecosystems [in Russian], Nauka, Leningrad (1979), pp. 139-141.
- Alimov, A. F., "Structural-functional approach to the study of communities of aquatic animals," *Ekologiya*, No. 3, 45-51 (1982).
- Bogatov, V. V., "Methods for determining drift distance of benthic invertebrates (exemplified by *R. Bureya*)," *Ekologiya*, No. 4, 82-88 (1979a).
- Bogatov, V. V., "Active drift of benthic invertebrates in alpine and semialpine rivers of the Far East," in: Fourteenth Pacific Scientific Congress (Khabarovsk, August, 1979), Committee J. Abstracts of Reports [in Russian], Moscow (1979b), pp. 35-37.
- Bogatov, V. V., "Benthic invertebrates and their drift in some rivers of the Far East," Author's Abstract of Dissertation for Candidate of Biological Sciences, Zool. Inst. Akad. Nauk SSSR, Leningrad (1983).
- Elliott, J. M., "Invertebrate drift in a mountain stream in Norway," *Nor. Entomol. Tidsskr.*, 13, 97-99 (1965).

- Levanidov, V. Ya., "Biomass and structure of benthic biocenoses of small streams on the Chukotski Peninsula," in: Freshwater Fauna of the Chukotski Peninsula [in Russian], Vol. 36 (139), Biol.-Poch. Inst., Vladivostok (1976), pp. 104-122.
- Levanidov, V. Ya., "Benthos biomass of certain streams in the Chukotski Peninsula," *Gidrobiol. Zh.*, 13, No. 1, 56-62 (1977).
- Müller, K., "Investigations on the organic drift in North Swedish streams," Rep. Inst. Freshwater Res. Drottningholm, 35, 133-148 (1954).
- Paine, R. T., "Food web diversity and species diversity," *Am. Nat.*, 100, 65-75 (1966).
- Pearson, W. D., and Kramer, R. H., "Drift and production of two aquatic insects in a mountain stream," *Ecol. Mongr.*, 42, No. 3, 365 (1972).
- Radford, D. S., and Hartland-Rowe, R., "A preliminary investigation of bottom fauna and invertebrate drift in an unregulated and a regulated stream in Alberta," *J. Appl. Ecol.*, 8, 583-603 (1971).
- Stoneburner, D. L., and Smock, L. A., "Seasonal fluctuations of macroinvertebrate drift in a South Carolina Piedmont stream," *Hydrobiol.*, 63, No. 1, 49-56 (1979).
- Ulfstrand, S., "Benthic animal communities in Lapland streams," *Oikos Suppl.*, 10 (1968).
- Waters, T. F., "Standing crop and drift of stream bottom organisms," *Ecology*, 42, No. 3, 532-537 (1961).
- Waters, T. F., "The drift of stream insects," *Annu. Rev. Entomol.*, 17, 253-272 (1972).
- Waters, T. F., and Hokenstrom, J. C., "Annual production of the stream amphipod *Gammarus pseudolimnaeus* in Valley Creek, Minnesota," *Limnol. Oceanogr.*, 25, No. 4, 700-710 (1980).
- Watt, K. I. F., "Conceptual formulation and mathematical solution of practical problems in the dynamics of inputs and outputs of the population," in: *Studies on General Systems Theory* [in Russian], Progress, Moscow (1969), pp. 486-503.
- Zaika, V. E., *Specific Production of Aquatic Invertebrates* [in Russian], Naukova Dumka, Kiev (1972).

DISTRIBUTION OF PHYLLOPHAGOUS INSECTS IN THE CROWN OF  
DROOPING BIRCH AT THE NORTHERN BOUNDARY OF TREE VEGETATION

I. A. Bogacheva

UDC 591.543.43:595.70

The susceptibility of various parts of the crown of drooping birch to phyllophagous insects was studied in the Ob forest tundra. It was shown that insects prefer the south part of the crown and certain of its height levels (0-0.5 and 1-2 m). Such an insect distribution in the birch crown and, also, the daily vertical migration of weevils demonstrated by the method of stratified entomological sweeps are largely explained by the requirements for temperature conditions.

The stratification of the insect population declines in moving from the forest zone to polar deserts (Chernov and Matveeva, 1979). This is particularly evident in the fact that whereas the highest-level tree branches are the most thoroughly exploited in the taiga zone (Baranchikov, 1981), plants of the shrub stratum are most thoroughly exploited in forest tundra (Bogacheva, 1979a).

The upper stratum of vegetation in the Ob forest tundra is mainly represented by drooping birch (*Betula tortuosa* Ldb.). Although only a very small part of the birch production is used annually (Bogacheva, 1980), rather complex insect groupings are associated with this birch. This circumstance, as well as the comparatively large vertical extent of the upper stratum (up to 4-5 m), determined the selection of birch as an object for studying the spatial organization of consortia at the northern limit of the distribution of tree vegetation; data were collected for phyllophagous insects.

---

Institute of Plant and Animal Ecology, Ural Scientific Center, Academy of Sciences of the USSR. Translated from *Ekologiya*, No. 3, pp. 60-66, May-June, 1984. Original article submitted July 4, 1983.