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## Relationship between Biomass and Drift of River Benthic Invertebrates

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**Abstract**—In order to estimate the relationship between biomass and drift of benthic invertebrates (*Gammarus lacustris* Sars., larvae of mayflies and chironomids), the specific drift rate and the ratio of drift rate to their biomass has been used. The negative correlation between the specific drift rate and the biomass density has been obtained. It indicates that competition between hydrobionts for space and food is not important for the drift. It has been suggested that the decrease in the specific rate of amphipods and the increase in their biomass in bottom sediments are associated with the patterns of feeding and sexual behavior of crustaceans, and the larvae of insects undergo a similar decrease in their specific rate due to the formation of aggregative behavior in them for the mass emergence of imagoes.

**Keywords:** river, benthos, amphipods, mayfly larvae, chironomid larvae, biomass, drift rate, specific drift rate, competition, behavior

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### INTRODUCTION

Drift of river benthos is the downstream movement of bottom invertebrates [33]. It may be “active” (“behavioral”), when hydrobionts get into the water column by themselves (this upward movement most often occurs at night), or “passive” (“random”), resulting from living organisms accidentally leaving the substrate. In certain cases, “catastrophic” drift takes place. The latter is caused by either extreme natural conditions (overflow and catastrophic flooding, etc.) or by anthropogenic factors (such as a volley of sewage). “Catastrophic” drift provokes structural changes in benthic communities or destroys them.

The first data on the active drift of hydrobionts [9, 21, 22, 28–30] showed that lots of living organisms may be carried by rivers. Thus, the question arises: what are the mechanisms enabling benthic communities in rivers to survive under such severe (one would think) exhaustion? Two hypotheses for the cause of “drift paradox” were suggested: Müller’s colonization cycle [21, 23] and Water’s compensatory production [29, 31]. The former is associated with amphibiotic insects and includes the upstream light of imagoes, the deposition of eggs and mass hatching in the upper reaches of the stream, the downstream drift of larvae colonizing all possible habitats, and the upstream movement of imagoes meant to close the cycle. According to the latter, the drifting of benthic invertebrates (including hydrobionts before flying) is compensated for by their production; i.e., drifting of spec-

imens is a function which indicates population productivity. The active drift was preliminarily explained as follows: during the warm period of the year, invertebrates may compete for resources (such as food and space) as they grow; therefore they drift and colonize new habitats. This explanation is also provided in the Russian literature covering this problem [7, 10, 11, 13, 14, etc.].

Subsequent investigations aimed at verifying the above hypotheses are contradictory. Their results are analyzed in the reviews [2, 27, 33, etc.]. In particular, when studying the effect of competitive behavior on the drift of invertebrates, attention was paid to the relation between the quantitative parameters of drift and the density of living organisms in bottom sediments. As a result, some researchers managed to find a positive correlation between benthos and drift [12, 19, 20, 25, etc.], while others did not [32, 34, etc.]. Ambiguous data were obtained during the direct estimation of competition between the larvae of insects. For example, Hildebrand [18] pointed out in his experiment that the drift of larval mayflies and trichopterans is influenced by their intraspecific competition for food; Bailey [15] found that the inter- and intraspecific competition for space influences the drift of larval mayflies. However, Statzner and Mogel [26] did not register any relation between inter- and intraspecific competition for space and food and the drift of *Baetis*. Similar results concerning the role

played by intraspecific competition between mayflies was obtained by Palmer [24].

The aim of this work is to study relationship between the population density of dominant species or groups of river benthic invertebrates and their drift rate, as well as estimate changes in the share of hydrobionts which underwent drifting, depending on their biomass in bottom sediments. In the latter case, it is suggested that, if competition between hydrobionts influences their drift, the share of drifting specimens should grow with an increase in the density of living organisms in bottom sediments.

## MATERIAL AND METHODS

The analysis is based on 18 daily observations of drift. The observations were performed during summer and autumn of 1976–1985 in the rivers flowing in the south of the Russian Far East. The rivers under study belong to the Amur River basin (Bureya River (in the upstream), Pil'da River (in the up- and midstream), and Ukhta River (in the downstream)) or the south of Primorskii krai (Komarovka and Kedrovaya Rivers (in the midstream)). The investigated stream flows are not affected by anthropogenic pollution. The Komarovka and Kedrovaya rivers flow through the territory of the Kedrovaya Pad' and Ussuri State Natural Biosphere Reserves. The river segments selected for observation were semimountain. They were characterized by cold water and a gravel–pebble bottom with float stones. In total, ~300 drift and 60 benthos samplings were taken. The following three groups of communities of benthic invertebrates were analyzed: amphipods (*Gammarus lacustris* Sars.); larvae of mayflies (*Cinygmula cava* (Ulmer), *Cinygmula* sp., *Baetis* (*Acentrella*) *fenestratus* (Kozlauskas), *B.* (*Baetis*) *bicaudatus* Dodds, *Baetis* sp., *Ephemerella aurivillii* Bengtsson); and larvae of chironomids (mostly from the fam. Orthocladiinae). The invertebrates migrating in water were collected by the drift nets. Each net had a mouth size of 25 × 25 cm and depth of ~1 m. When studying the daily dynamics of drift, the nets were set in the stream flow every 0.5–1 h at night or every 2–4 h during the day. The exposure time per drift sampling equaled 10 min. In order to maintain filtration characteristics of the drift net while sampling the invertebrates, the exposure time was divided into parts (for example, during the total 10-min exposure, the net was set two times for 5 min and, when the amount of suspended solid materials was increased, the net was set two times for 3 min and once for 4 min; then data from all samplings were integrated). The material was fixed either in a 70% solution of ethanol or in a 2–4% solution of formalin.

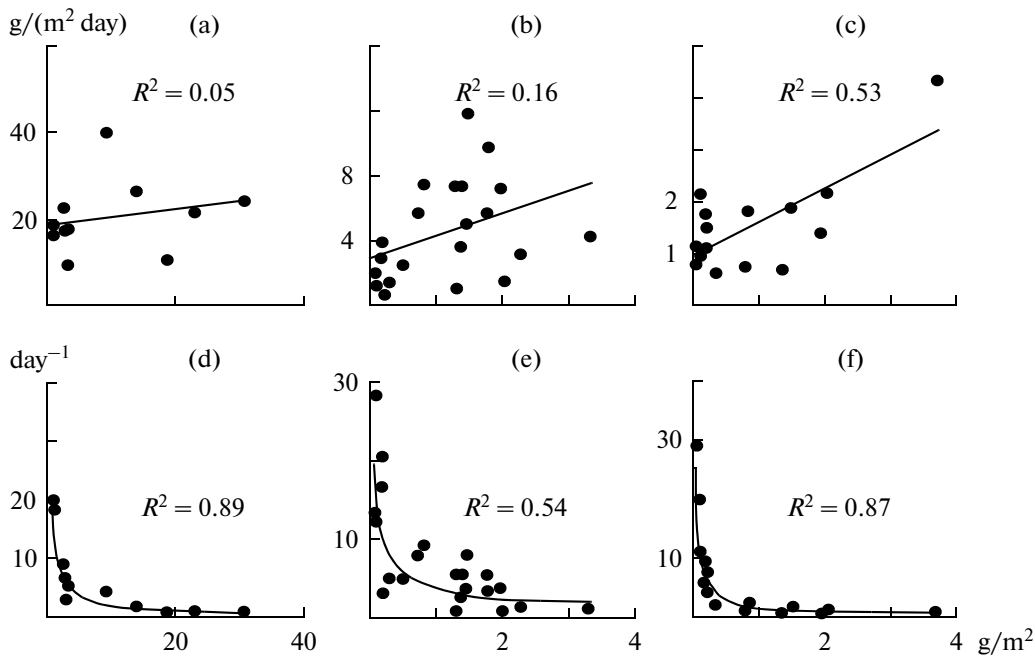
Benthos samplings were taken from the same sites as drift. For this purpose, a folding benthometer (25 × 25 m) was used [6]. From 3 to 4 zoobenthos samplings were taken in each sampling point. In order to eliminate the effect of disturbance on the process of drift, such pro-

cedures were carried out immediately after the drift samplings had been taken. The stream flow depth at the site, where drift and zoobenthos were sampled, is 0.25–0.4 m.

Based on the drift-net catches, the drift density ( $D_d$ ), i.e., number or biomass of migrants per unit volume of water, and the drift rate ( $D_R$ ), i.e., number or biomass of hydrobionts drifting through the certain current section over a particular period of time, were found. The drift density was calculated by dividing the catch (number or biomass of the living organisms) over the time of exposure ( $t_1, t_2$ ) by the volume of water ( $m^3$ ) filtrated through the net during the same period. The drift rate was calculated by multiplying the drift density by the water expenditure through the studied current section over a particular period of time. In each segment of the stream flow, the drift rate was assessed for a 24-h period. For this purpose, the drift materials obtained over certain time intervals were summed.

The drift rate ( $D_R$ ) in different river segments is most appropriately estimated through the number ( $D_{RN}$ , ind/( $m^2$  day)) or biomass ( $D_{RB}$ , mg/( $m^2$  day)) of living organisms, which were drifted daily not through the fixed current section (such as  $1 m^2$ ), but rather through that with a predetermined width of 1 m and height that equaled the segment depth ( $h$ , m) at the moment under study [3]. Therefore, changes in the hydrological regime of the stream flow influence the depth of the segment under study, i.e., current section.

Using this parameter makes it possible to compare the drift of hydrobionts at different river segments. In this case, regardless of the flow depth, expenditures, and current velocity,  $D_{RN}$  and  $D_{RB}$  will result from the multiplication of two parameters: the average length of drift in hydrobionts ( $L$ , m) and their daily migration activity ( $M$ ), which is measured by the number of ( $M_N$ , ind/( $m^3$  day)) or biomass ( $M_B$ , mg/( $m^3$  day)) of living organisms that move in 24 h upwards from the bottom sediments with an area of  $1 m^2 \times h$ . The most important thing about estimating benthos drift by the suggested method is that it allows one to calculate the specific drift rate ( $D_C$ ), which is the relation of the drift rate of hydrobionts to their number ( $N$ ) or biomass ( $B$ ) per  $1 m^2$  of bottom sediments. In this case,  $D_{CN} = D_{RN}/N$ , and  $D_{CB} = D_{RB}/B$ , where  $D_{CN}$  and  $D_{CB}$  is the specific drift of hydrobionts reflecting their abundance or biomass per  $1 m^2$  of bottom sediments. In work [3], this parameter was considered a hypothetical model of the minimum drift length, which occurs provided that all specimens in the population take part in migration. Since  $D_{RN}$  and  $D_{RB}$  are estimated daily,  $D_{CN}$  and  $D_{CB}$  will be expressed by  $day^{-1}$  [ind (g)/( $m^2$  day) : ind (g)/( $m^2$  day)]. Actually, the specific drift rate allows one to estimate the share of hydrobionts that took place in the daily drift as related to their number–biomass in bottom sediments: the higher the specific drift rate is, the more hydrobionts are drifting. This parameter is not popular among researchers.



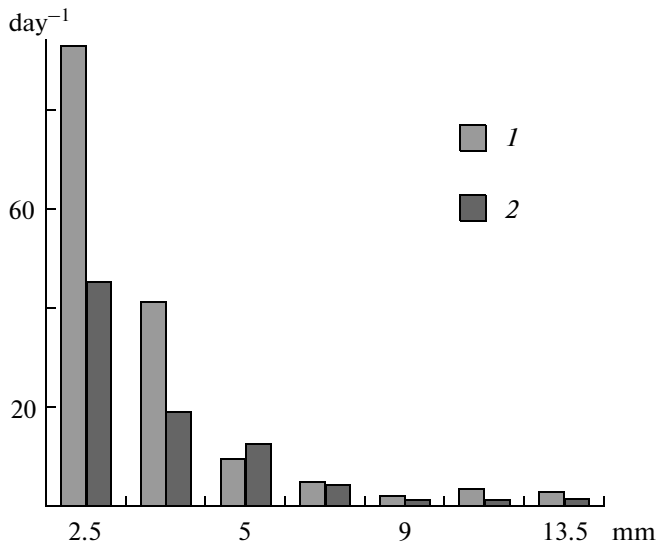
**Fig. 1.** Relationship between drift rate (a–c) and specific drift rate (d–f) in the rivers of the Lower Amur River basin and biomass of hydrobionts in bottom sediments ( $\text{g}/\text{m}^2$ ) in the warm seasons: (a, d) *Gammarus lacustris*, (b, e) larvae of mayflies, and (c, f) larvae of chironomids.

## RESULTS

Having estimated the drift rate of benthic invertebrates from different groups, a weak positive correlation was observed between the drift and the biomass density of hydrobionts in bottom sediments (Figs. 1a–1c). Therefore, during the warm period, i.e., as hydrobionts were actively growing, a direct comparison of the biomass and the drift rate indicated that there was a direct, though weak, relationship between these parameters. However, when the specific drift rate of the same hydrobionts was estimated, its significant negative correlation with the biomass was revealed (Figs. 1d–1f). In summer, the correlation coefficient in *Gammarus lacustris*, larvae of mayflies and chironomids equaled  $-0.5$ ,  $-0.4$ , and  $-0.5$ , respectively. As a result, the share of drifting organisms fell as the biomass of hydrobionts in bottom sediments increased. What is more, upon the low biomass of organisms, the specific drift rate of hydrobionts varied in a wide range, while the highest biomass favored the stably low share of drifting organisms. In particular, in amphipods, which are the most mobile representatives of zoobenthos, the widest range of the specific drift rate was observed at the biomass of up to  $5 \text{ g}/\text{m}^2$  ( $\sim 2$ – $20 \text{ days}^{-1}$ ). Consequently, the daily drift of crustaceans at a biomass of up to  $5 \text{ g}$  was 2–20 times higher than their biomass in bottom sediments. Upon the biomass of  $\sim 10 \text{ g}/\text{m}^2$ , the specific drift rate of gammarids did not exceed  $5 \text{ days}^{-1}$ . When the biomass was higher, it was  $< 2 \text{ days}^{-1}$ . The larvae of mayflies had their widest range of the specific drift rate at a biomass of up to

$2 \text{ g}/\text{m}^2$ . The same situation was found in the larvae of chironomids when their biomass reached  $0.5 \text{ g}/\text{m}^2$ . In both groups of hydrobionts, this parameter was  $\sim 30 \text{ days}^{-1}$ . The specific drift rate equaled  $< 2 \text{ days}^{-1}$  in the larvae of mayflies having a biomass of  $> 2 \text{ g}/\text{m}^2$ , as well as in the larva of chironomids with a biomass of  $> 1 \text{ g}/\text{m}^2$ . Upon the maximum biomass, the specific drift rate of all three groups of hydrobionts was  $< 1 \text{ day}^{-1}$ . This is evidence that all invertebrates under study had low migration activity when their biomass in bottom sediments was maximal; thereby the competition between hydrobionts had no influence on their drift.

The study of the specific drift rate in differently sized stages of amphipods and larvae of mayflies was also controversial. In particular, the highest specific drift rate of amphipods was observed in small specimens, which had higher specific growth rate. In particular, in September 1979,  $D_{CN}$  of juvenile amphipods from the Ukhta River having a body length of  $\sim 2.5 \text{ mm}$  equaled  $\sim 90 \text{ days}^{-1}$ . It was only  $\sim 2 \text{ days}^{-1}$  in larger ones ( $13.5 \text{ mm}$ ) (Fig. 2). In October (before ice formation), this parameter in the same groups of amphipods was significantly lower ( $\sim 45$  and  $1 \text{ days}^{-1}$ , respectively). What is more, the stably low specific drift in both cases were registered for mature specimens with a body length of  $> 7$ – $8 \text{ mm}$  [4]. The decrease in drifting activity of amphipods during the later autumn period may be caused by the drop in water temperature and, thus, the motion activity of hydrobionts [1, 8, 12, etc.]. The results indicated indirectly that there was a certain relation between the specific drift rate of hydrobionts



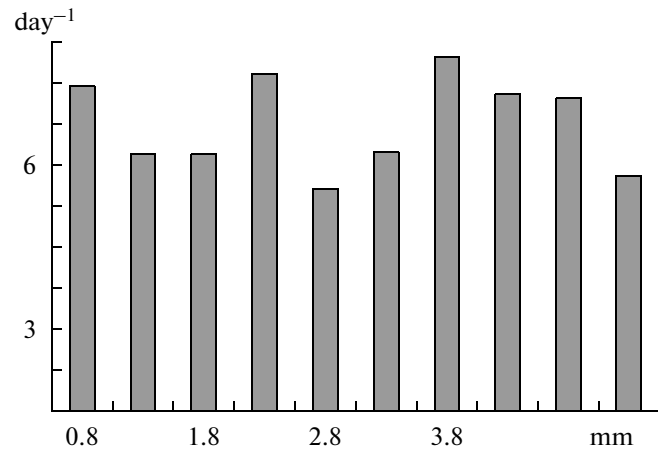
**Fig. 2.** Relationship between specific drift rate of size groups ( $\text{day}^{-1}$ ) and sizes (mm) of *Gammarus lacustris* in the Ukhta River (basin of the Lower Amur River) at the end of August (1) and October (2).

and their specific growth, because the specific growth of invertebrates slows down as they gain weight. However, some larvae of mayflies, such as *Baetis bicaudatus*, at the early stages of their development (in this case, up to 5 mm of the body length of individuals, provided that the maximum size of larvae is ~8–9 mm) demonstrated almost the same specific growth rate, which was about  $\sim 7 \text{ days}^{-1}$  (Fig. 3). Therefore, in the latter case, there is no reason for associating the migration of mayfly larvae with the specific production of differently sized individuals.

## DISCUSSION

Estimating the effect of competitive relations between different benthic organisms on their drift has been one of the most difficult and obscure methodological problems in fluvial hydrobiology until recently. Trying to solve this problem, the attention of researchers has been most often attracted to the mere presence or absence of a direct relationship between the population density of hydrobionts in bottom sediments and their drift. In addition to the above, most of these works were based on the standard parameters of density and drift rate, which was bound to influence the interpretation of their results. The problem got even more complicated, because the standard methods for estimating of drift (drift density of rate) were used when comparing the number of migrants in different river segments distinguished by their depth and current velocity [6].

As a rule, it was ignored that the competition did not always favor direct relationship between the mentioned parameters. For example, a direct relationship



**Fig. 3.** Ratio between specific drift rate of size groups ( $\text{day}^{-1}$ ) and sizes (mm) of the larval *Baetis bicaudatus* in the Pil'da River (basin of the Lower Amur River) in July.

between the density of hydrobionts in bottom sediments and their drift occurs if the share of migrating organisms remains stable either at different densities of hydrobionts or when the share of migrants decreases with the increase in their density, but still at a slower rate when compared to the increase in the density of organisms. The results proved these assumptions. In particular, a direct comparison of the biomass of hydrobionts and their drift showed a weak positive correlation of this relationship, which points to the more rapid biomass gain in the studied series of values when compared to similar rates of weight gain by migrants. An estimation of the specific drift rate of hydrobionts, which fell significantly with the increase in biomass, proves this conclusion (Figs. 1d–1f).

The results on the specific drift rate contradicted this hypothesis, which explains the drift of living organisms by their competition over substrate and food. Obviously, competition between the studied groups of invertebrates over space and food, if there is any, does not significantly influence the drift of hydrobionts. In the studied cases, when the biomass of all groups of invertebrates was maximum, their specific drift rate was  $< 1 \text{ days}^{-1}$ ; i.e., if all individuals are involved in drift, their drift length would be  $< 1 \text{ m}$ , which indicates that hydrobionts do not migrate at long distances when their biomass is maximum.

The decrease in the specific drift rate taking place as the biomass of amphipods and the larvae of insects (mayflies and chironomids) gets higher has a various functional importance. As far as amphipods are concerned, the results obtained by Williams and Moore [34] in the course of their laboratory experiments on *Gammarus pseudolimnaeus* Bousfield are interesting. The researchers placed 20, 50, 200, and 600 gammarids into the flow-through reservoirs and then observed changes in their drift. It turned out that the drift rate of amphipods underwent a significant

decrease when additional gammarids were added. Williams and Moore suggested the hypothesis that the decrease in the drift of *G. pseudolimnaeus* is associated with the feeding behavior of these crustaceans, which demonstrated collective feeding and often gathered in large numbers while consuming food (for example, 900 ind. per 0.1 m<sup>2</sup> of bottom sediments).

This feeding pattern is also known in other species of river amphipods [5]. Taking into consideration that the minimum specific drift rate is found only in mature *G. lacustris*, it may be accepted that a decrease in the drift of crustaceans taking place as their biomass in bottom sediments gets higher is associated not only with their feeding, but also with sexual behavior as well. In particular, after female amphipods lay eggs into the marsupium, they take care of juveniles together with males (the male grasps the female from behind and the pair remains in this position for several days). When the density of amphipods is high, it is probably easy for mating partners to meet. The high specific drift rate of immature individuals, which are mobile but are not good swimmers due to their small sizes, can be a consequence of their being often involved in drift by the water current.

As for the larvae of mayflies and chironomids, either a decrease in their specific drift rate and increase in the biomass in bottom sediments or stable specific drift rate at different stages of development may be associated with the formation of aggregative behavior for the mass (synchronous) emergence of imagoes. Since imagoes of the water insects under study live for only a few days or hours, they are not skilled fliers. The mouth parts of mayfly imagoes and the majority of chironomids are reduced. Usually, such insects mate during their mass flight and swarming. Therefore, a decrease in the specific drift rate of imagoes may be caused by the formation of aggregative behavior in invertebrates and the need for their maximum concentration in particular segments of the stream flow until their mass flight. This process is still not understood in detail. It appears that different species of rheophilic larvae can prepare themselves for mass flight according to different scenarios. For example, Hall et al. [17] emphasized that these are more mature and not juvenile nymphs of *Trycorythodes atratus* that are involved in drift. Obviously, the mass flight of imagoes having reduced mouth parts is related to not only ecological conditions in particular river segments, but also the aggregative behavior of adult larvae. At the same time, in order to find the mechanisms enabling aggregative behavior at the larval stage, further surveys are needed.

## CONCLUSIONS

It is proved that the drift rate of river benthic invertebrates should be estimated based on the number or biomass of living organisms that drift daily through the area of current section with a fixed width (1 m) and height that equals the depth of the river section at the moment

of studying. When estimating the specific drift rate of benthic invertebrates, which is the relation of the drift ratio to their biomass, a negative correlation was found between this parameter and the biomass of hydrobionts. Therefore, competition between the studied groups of benthic invertebrates over space and food, if there is any, cannot significantly influence their drift. It is assumed that the decrease in the specific drift rate of amphipods, which occurs as their biomass in bottom sediments gets higher, is associated with the patterns of feeding and sexual behavior of gammarids, and the same decrease in the specific drift rate of larval amphibiotic insects (mayflies and chironomids) is associated with the formation of their aggregative behavior for the mass emergence of imagoes.

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