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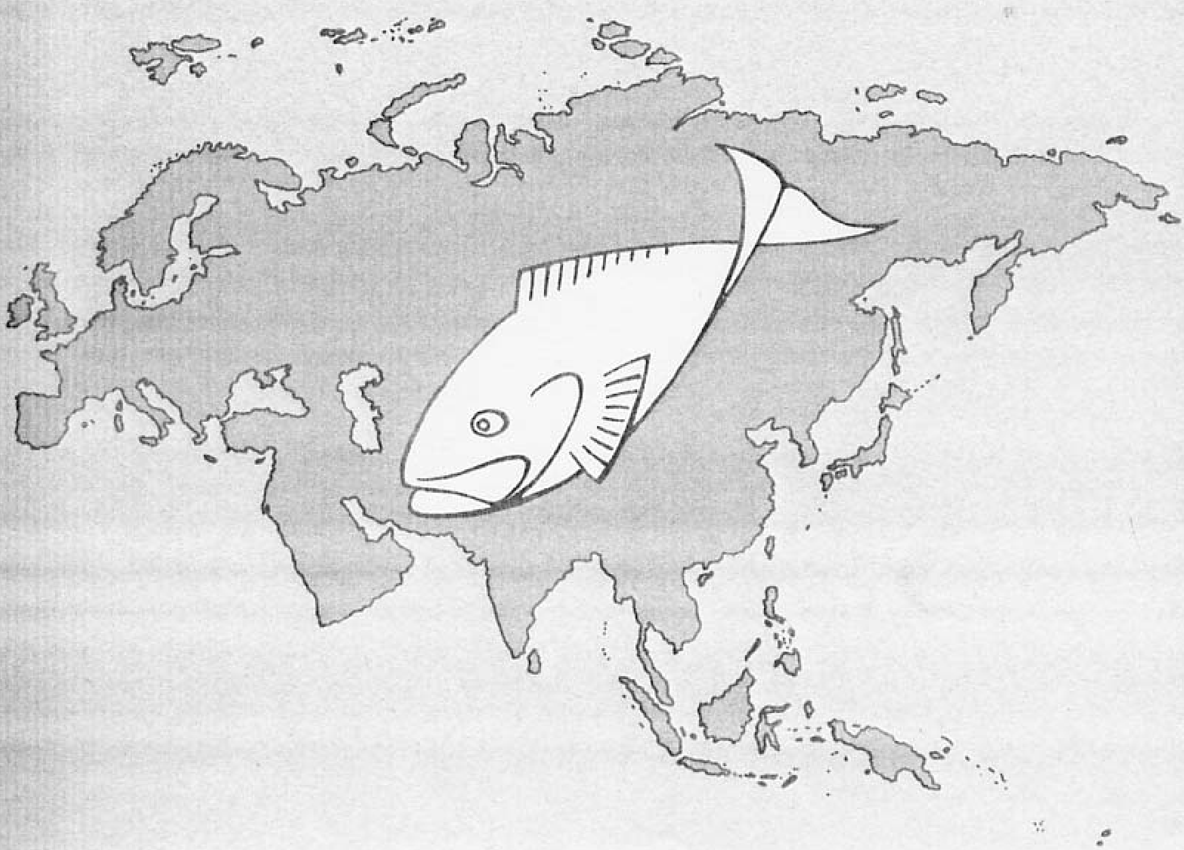

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CONTENTS

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Classification of Stream Benthos Drift

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Many problems in general ecology involving benthic invertebrates cannot be solved without knowing the characteristics of their drift, i.e., their downstream movement [19]. During early stages of research on benthos drift, Waters [18] suggested the following three types: catastrophic, behavioral or active, and constant or passive. This classification is now accepted by most investigators. It is assumed that catastrophic drift results from the action of extreme conditions (high water, drought, anchor ice, toxic pollution, and the like) on bottom fauna. It may considerably decrease the abundance and biomass of bottom communities [4, 17]. Behavioral drift is the result of active behavior, in which the organisms rise into the water of their own accord. Behavioral drift is assumed to maintain optimum population density [19]. Passive drift involves organisms that are randomly separated from the substrate and are present in the drift in small numbers during the entire 24-hour period; it is generally of little significance in functioning of benthic communities.

Investigation of the drift of benthic invertebrates in rivers of Amur Oblast and the Khabarovsk and Maritime krays during 1976-1980 found that this classification had major deficiencies.

First, as Waters notes [19], it is based on the factors that cause transport, which is a deficiency. It is not yet known with certainty why, for example, behavioral drift occurs. Our investigations have shown [6] that even competition for space and food is not its cause. It is obvious that a variety of factors govern the active ascent of organisms into midwater. Thus the existing classification does not cover all possible interactions between organisms and the environment and is consequently oversimplified. Based on Waters' principles, behavioral drift apparently is to be distinguished from passive drift only on a physiological basis, which is true of most elementary animal reactions to external stimuli [12].

Second, Waters' classification contains none of the analytical criteria that are needed for quantitative studies. For example, it gives no indication of how to differentiate behavioral and catastrophic drift from each other. In addition, catastrophic drift lumps together active and passive movement on the basis that the drift occurs under extreme conditions. There is thus a need for a new criterion specifying which environmental factors are extreme, and in addition the principle of classification is clearly violated, because the principles causing passive and behavioral drift are of different ecological significance. It is understandable that extreme environmental conditions could increase the rate of passive and behavioral drift, and consequently Waters' catastrophic drift is only a variety of these two types.

Observations of invertebrate drift indicate that these deficiencies can be avoided if we classify it in terms of its role in biological production in streams, i.e., decreases or increases in the biomass of certain groups in a given stream section over the course of a 24-hour period as a result of drift, rather than in terms of the factors that produce it. In such a procedure it is important to calculate the drift rate C, i.e., the percentage of the production of the population that is removed from the community as a result of drift [6]:

$$C = (B_d/P_n)\cdot 100\% \qquad (1)$$

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where P_n is the daily production of benthic organisms, and B_d is the biomass of organisms in the population removed through the cross sectional area of the river in a day. The latter quantity is here regarded as resulting from the distribution of population production over the entire territory above the cross section where the samples are collected, not just in the immediately adjoining area from which the individuals were carried [6]. To determine the amount of biomass removed from the community in the stream segment under study, bounded by the upper and lower cross sections, we need of course to know the biomass entering the system, i.e., we must take drift samples at the upper cross section as well. Then,

$$C = \frac{B'_{d'} - B'_d}{P'_n} \cdot 100\%, \tag{2}$$

where P'_n is the daily production of organisms in the population present in the stream segment between the two cross sections; and B'_d and $B'_{d'}$ are, respectively, the biomass of organisms carried through the upper and lower cross sections of the river in the course of a day.

Using this principle, we can distinguish three types of drift of zoobenthos.

1. Neutral or behavioral drift, as a result of which the biomass of organisms in the substrate is increased only by their production or is practically unchanged:

$$B_d \leqslant P_n - C_p, \tag{3}$$

where B_d is the biomass of organisms of the population carried through the stream cross section in the course of a day; P_n and C_p are, respectively, the daily production and the ration of predators in the stream segment above the observation cross section. In neutral drift, C will not exceed $100 - (C_p/P_n) \cdot 100\ \%$, and if we neglect the ration of predators, then $C \leq 100\%$.

Behavioral drift occurs in the segment bounded by the two cross sections if

$$B'_{d'} - B'_d \leqslant P'_n - C'_p \tag{4}$$

with

$$B''_d \geqslant B'_d\,. \tag{5}$$

where P_n is the daily production of organisms of the population that are present in the stream segment, and C'_p is the daily ration of predators in the stream segment.

Neutral drift is the most common type of migration and occurs most frequently in the absence of extreme conditions. For example, the value of C for insect larvae of the Ukhta River (lower Amur valley) in neutral drift ranges from 1% to 40% or even 60% in periods of high discharge. The figure is 13–80% for amphipods, but in the Pil'da River (Lake Udyl' basin) it ranges from 2% to 6% at various stations [6]. It appears that neutral drift maintains optimum population density and high diversity in the benthos.

2. Negative drift, in which the biomass of organisms in the bottom material decreases:

$$B_d > P_n - C_p. \tag{6}$$

Here C will always be greater than $100 - (C_p/P_n) \cdot 100\ \%$, or, neglecting the ration of predators, $C > 100\%$.

Negative drift occurs in a segment bounded by two cross sections when

$$B'_{d'} - B'_d > P'_n - C_p \tag{7}$$

with

$$B'_{d'} \gg B'_d. \tag{8}$$

Negative drift generally occurs in the presence of extreme conditions, but without breakdown of the community, i.e.,

$$B_{\min} < B(t_1) + P_n(t_1, t_2) - B_d(t_1, t_2) - C_p(t_1, t_2), \tag{9}$$

where $B_{\min}$ is the minimum biomass at which the community can maintain its integrity; $B(t_1)$ is the biomass in the bottom material at the time when extreme conditions begin; and (t_1, t_2) is the period over which the extreme conditions act.

Negative drift occurs when low concentrations of toxic chemicals occur [7] or in periods of high water. In catastrophic high water, negative drift may considerably decrease the benthos biomass in a relatively short time. For example, in the shallows of the Bomnak River (a tributary of the Zeya River) the abundance of invertebrates decreased by a factor of more than 20 and their biomass by a factor of 10 after 2 weeks of catastrophic high water in August 1975; about 2 months was required to restore the original levels [4]. In less extreme high water, negative drift can occur in individual populations. But the decrease in their biomass in the bottom material is small. For example, in a high water period in the Ukhta River in August 1978 only amphipods exhibited negative drift [6]. As a result, the drift intensities on the first and second days of high water were, respectively, 150% and 210%, whereas the decrease in biomass was only 0.6% of the original value.

3. Positive drift, which increases the faunal biomass in the bottom material. This drift can occur in segments when

$$B'_d > B'_{d'}. \tag{10}$$

In this type of drift C will always be negative.

Positive drift usually occurs when the abundance of organisms is being restored in biotopes that have been subjected to extreme conditions. But newly inundated soil is settled during high-water periods. In this situation, negative drift may occur in the river as a whole or in a segment of its main channel, whereas the drift will be positive in the newly settled bottom material. For example, according to Konstantinov [14] and Borutskiy et al. [8], who studied the settlement of soil inundated by rising water levels in the Amur River, the number of chironomid larvae in the inundated areas was close to the control value as early as the 8th day after inundation. But our investigations on the upper Zeya River indicated that the rate of settlement of newly inundated bottom material and the time required for subsequent stabilization of the community in which positive drift changed to neutral drift was considerably dependent on hydrologic conditions [5].

In the absence of extreme conditions, positive drift is exhibited by amphipods and insect larvae in the Ukhta River, where the channel enters open terrain after passing through a stand of taiga [6]. It appears that as a result of different illumination conditions during the night in the lower, open section of the river, the biomass of drifting organisms is with rare exceptions lower by a factor of 1.5 to 6 than in the upper section, with tree cover.

4. Catastrophic drift is caused when a disrupting event in a river ecosystem occurs. In this type of drift,

$$B_d(t_1, t_2) = B(t_1) + P_n(t_1, t_2) - C_p(t_1, t_2) \tag{11}$$

or

$$B_{\min} > B(t_1) + P_n(t_1, t_2) - B_d(t_1, t_2) - C_p(t_1, t_2). \tag{12}$$

Drift of this type occurs from pollution or natural catastrophes.

We observed catastrophic drift in the Bomnak River during a flood (August 1975), as a result of which the benthos biomass was obviously below B_{min}. This was probably the reason that a further decrease in the density of these organisms was observed after stabilization of river flow [4]. The amount of fine particle sediment in the substrate considerably decreased after the high flow event.

Chronic pollution causes the elimination of certain species from benthic communities, primarily intolerant insect and amphipod larvae [11, 13, 15, 20]. In the bottom material of highly polluted rivers the greatest abundance is attained by oligochaetes, which generally do not exhibit active drift.

5. Pre-imago drift, in which mass emergence of imagos occurs. This is a special type of drift in which only mature insect pupae and nymphs participate. In it, typically

$$B_k \gg P_n - C_p \tag{13}$$

or

$$B_k(t'_1, t'_2) \ll B(t'_1) + P_n(t'_1, t'_2) - B_{ex}(t'_1, t'_2) - C_p(t'_1, t'_2), \tag{14}$$

where B_k is the biomass of mature pupae and nymphs transported through a river cross section in a specific time period; B_{ex} is the biomass of exuviae cast off by mature pupae and nymphs in the river segment over the time period; and (t'_1, t'_2) is the duration of mass emergence. During mass emergence of imagos the biomass at the bottom of the stream may decrease to zero (Eq. 14). But in contrast to catastrophic drift, the bottom communities do not break down. We note that pre-imago drift is accompanied by an extremely high drift of exuvia of mature pupae and nymphs.

It was thought that the emergence of imagos of species inhabiting mountain and piedmont rivers extends over considerable time periods [9, 16]. But in the Amur basin, Baykova [1, 2] repeatedly observed mass emergence of the imagos of typical mountain-stream species, i.e., *Rhithrogena lepnevae* Br., *Cinygmula grandifolia* Tshern., *C. hirasana* Iman., *Ephemerella (Drunella) aculea* Allen., *Ephemera strigata* Eat., *E. formosana* Ulm., and *E. orientalis* McL. (syn. *amurensis* Navas). In the Amur River itself, mass emergence of imagos was exhibited by *Anagenesia paradoxa* Buld., *A. natans* Buld., *Polymitarcys virgo* Oliv., *Oligoneuriella mikulskii* Sowa, and others [1-3, 10].

CONCLUSIONS

The drift classification for stream invertebrates is inadequate for understanding benthos drift in terms of the population dynamics of benthic invertebrates. The deficiencies of the classification can be avoided if instead of considering causative factors, we distinguish drift types in terms of decrease or increase in the biomass of specific groups in a specific stream segment during the course of a day as a result of drift. Based on this approach we propose to distinguish five types of drift: neutral, negative, positive, catastrophic, and pre-imago. The use of analytic criteria in the new classification obviously makes it suitable for quantitative study of the functioning of benthic communities in streams.

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