БЪЛГАРСКА АКАДЕМИЯ НА НАУКИТЕ * BULGARIAN ACADEMY OF SCIENCES

Хидробиология . 37 * Hydrobiology . 37

*София, декември 1991 * Sofia, December 1991*

On adaptation of rheobionts to running waters

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The importance of water velocity as one of the main factors affecting the runnig waters biota has been repeatedly proven by many authors. According to Ж а д и н (1940) "Water velocity is the main factor for the distribution of the fauna in the river. It does not act as a separate factor, but jointly with other factors, such as the bottom, dissolved and suspended substances, dissolved gases and water chemistry." This is the basis of the main difference in the ecological situation in stagnant waters and running waters. It is not by chance that according to E i n s e l e (1960) a lake is in fact a river when a current exceeds 1 cm/s runs through it. This apparently rather vague characterization points to serious considerations of a chemical and biological nature.

Current velocity in streams and rivers creates specific environmental conditions, which differ substantially from those in stagnant waters. Above all, stream fauna always risks being washed away, without the possibility of returning to their original locations which would result in the total depopulation of running waters. During millions of years in the process of natural selection various stream organisms have worked out a number of complex morphological, physiological, ecological and biological adaptations in order to counteract this risk.

S t e i n m a n n (1907) in his "Tierwelt der Gebirgsbäche, eine faunistisch-biologische Studie" described a great variety of morphological adaptations of representatives of almost all classes of invertebrates. Later P o p o v i c i - B a z n o s e a n u (1928), N i e l s e n (1951), V e r r i e r (1953), voiced their rather strong criticism of these morphological adaptations, nevertheless their conclusions, that no morphological adaptations exist in the inhabitants of quick running streams, but only physiological adaptations against current speed stands no criticism. In my opinion (R u s s e v, 1961), at best these authors refute only the features noted by S t e i n m a n n (1907) as morphological adaptation, however the claim that such adaptation with stream species is simply wrong. Thus, contrary to V e r r i e r's claim (1953) that the larva of the mayfly *Habroleptoides modesta* (H a g e n) has no morphological adaptations, P l e s k o t (1953) in his study of the ecology of the same species describes and proves the existence of a number of morphological features counteracting the current. These are the flat dorsal, rounded upper part of the body, legs with strong muscles, lateral to the body, etc. which clearly come out with these rheophylic larvae when compared with their related species, inhabiting slower waters.

Б е ш о в с к и (1967, 1968) made a notable contribution in this field, in his extensive examination of larvae of dragon flies from stagnant waters and running waters, and also concerned the question of their morphological adaptations. Thus, according to Beshovsky, contrary to lymnophylic benthic dragon flies, rheophylis possess a number of morphological adaptations. These are a considerably depressed body and flat ventral surface, a reduced thorax ratio, an increased adhesion surface of the body to the substrate, the shape of the spikes on the body, the presence of digging spikes on the tibia, the reduction of the number of tarsal joints of the first pair of legs, used for digging, the elongated joint of the antenna (which the author attributed as a means for stabilization of the antennae against the current) as compared with the reduced number of up to 4 of the remaining antennae segments, as a result of the burying of the larvae in the bottom of streams.

A number of genera of mayfly larvae can be pointed out among other examples of morphological adaptation with rheobionts. The flat shield-shaped hairy head at the fore part, the almost perpendicular laterally situated legs of almost all Heptageniidae genera create sufficient contact with the stony surface, in order to avoid being carried away by the current. The Epeorus and Iron, found under stones in the middle of torrentical streams or by waterfalls, are of particular importance. Laterally to the flat abdomen are situated 7 pairs of gills arranged in a scale-like manner. Alongside with their respiratory function, the gills can ensure the necessary adhesion between the specimen and the rock, which, however weak, holds the rheobiont attached to the stone surface. A similar disposition, however less expressed, have the gills of Rhithrogena. Naturally, when the current is not dangerous to these larvae (i. e. at low or moderate current speed) they do not attach themselves to stones and can stay on the surface with no danger of being carried away. This explains some of the arguments used erroneously by P o p o v i c i - B a z n o s e a n u (1928) as a proof against the existence of morphological adaptation.

Nevertheless the most perfect apparatus for adhesion under the rocks belongs to the larvae of the family Blephariceridae (Diptera). Their body consists of 7 markedly separated segments with 6 well-developed suckers (one beneath the head, the others beneath the abdominal segments). Suckers attach themselves when a muscle contracts, lifting the chitin cone, thus creating a vacuum. The current cannot move the larvae, or carry them away. D o r r i e r and V a i l l a n t (1954) in their classical experiments have proven the possibility of *Liponeura cinerascens* L o e w. (Blephariceridae), as well as of representatives of Chironomidae, Simuliidae (Diptera), Baetis (Ephemeroptera) and Phryganea (Trichoptera) to resist a current speed of 2 m/s on the upper stony surphace. The larvae of Simuliidae (Diptera), besides a small sucker, have also a ring of radially situated rows of 60-80 chitin hooks and salivary glands, whose opening comes out of the lower jaw. These glands produce a secrete which hardens on contact with water, thus forming a thin silk-like thread. The larvae produce these threads along the rocks and attach their self through the numerous hooks arranged in the ring. Thus they not only stay on top of the rocks and resist the current, but can move from one position to another. H a r r o d (1965) demonstrated in laboratory tests that a minimal current speed of 19 cm/s is necessary to open the fans of the larvae. This comes to show that their preference for streams is not due so much to the need of more oxygen, but to the need of food. Some Trichoptera larvae, such as those of Rhyacophyla, attach themselves to web lines they secrete fixed at one end at rocks by means of sharp little claws, thus withstanding the current. Representatives of other genera of larvae of caddisflies gather various pebbles, leaves, detrite, snail shells etc. from bottom and stick them together with a secrete produced by their glands. The miniature cases they build not only protect them from predators but also do not allow the current to carry them away.

The current speed does not affect the small groups of fauna, in particular the microscopic Flagellata, Rhizopoda, Ciliata, Rotatoria, as well as the free living Nematoda, lower crustaceans, Hydracarina, etc., which is due to the thin water film, known as a boundary lamella or the border layer of Prand'l, situated at the bottom and practically immobile. For instance, Hydracarina which inhabit streams are 0,3-1,0 mm high, and therefore are protected by the boundary lamella, while those in stagnant waters are between 2 to 8 mm. Ambühl (1959) clearly demonstrated that the larvae of some mayflies may adapt to the changing situation in the boundary lamella and entirely settle in it, with the respective changes of the body form.

These small-sized as well as new-hatched other benthic organisms may enter the hyporheal interstitial under or at the very bottom of the river, in particular in the gravel-sand sediments of mountain streams and rivers. They penetrate such a depth where high waters or the "moving bottom" cannot affect them (Schwoerbel, 1971). According to this author the hyporheal interstitial protects the animals from both the current and the sudden changes of the temperature. He wrote: "Das hyporeische Interstitial ist für viele Fliesswassertiere ein Schutz vor der Strömung und ein Temperaturrefugium". Later Schwoerbel (1974) studied the question in detail. Naturally this biological adaptation of rheobionts is of great importance for after flooding the destroyed fauna is recovered to a certain extent for a comparatively short period, also from the penetration of fauna from the hyporheal interstitial.

Regardless of the various adaptations considered here, they by far do not exhaust all possible cases, and it has been established that running waters carry away tens and hundreds thousands of speciments, which have left their habitats. The quantity of fauna subject to biological drift grows at a higher velocity and effectively the entire fauna of the mountain stream is carried away. According to Müller (1970) from a stream in Sweden the biological drift was 884 000 specimens per 24 h in May (at a flow rate (Q) of 5 m/s) and 29 400 specimens in January (at a flow rate — 0,2 m/s). Müller considers the biological drift as a means of dissemination, for avoiding a high population in the upper stretch of stream, i. e. as a mechanism for avoidance of competition for food. The flight of *Caenis macrura* Steph. (Ephemeroptera) observed by Schoenemund (1930) against the current is considered by Müller together with the drift mechanism, as a "cycle of colonization".

The results on the biological drift of the Soviet Danube stretch (Оливари, 1961) are an indication of the existence of biological drift in larger rivers in their lower streches. I (Russev, 1972) consider this drift in lower reaches of large rivers something enforced, and not a phenomenon of adaptation. In the upper section of the lower reaches of the Danube for instance, the departure from a suitable habitat in gravel bottoms is in most cases fatal to the different species, as towards the lower reaches the gravel bottom is less in area and eventually disappears.

Roos (1957) has carried out interesting studies on migrations against and along the current of the imago of representatives of Trichoptera, Plecoptera, Ephemeroptera and Simuliidae, using nets, placed on stones in the middle of the Amman river (Sweden). His results show, that 70-80 percent of lotic types have large migrations against the current. These migrations are explained by the author with Müller's "cycle of colonization" (1954).

The mass flight of females of the mayfly *Palingenia longicauda* (Oliv.) against the current of the Danube which I observed, I described as a "compensatory flight prior to egg laying" (R u s s e v, 1959). This is a case of compensating microscopic eggs of females carried away by the stream surface about 2-3 km, as well the drift of metamorphism of nymphs during the swimming stage, up to the stream surface. Later the "compensation flight" was confirmed with all groups of insects with aquatic stages. Such general observations are provided (R u s s e v, 1973) with reports of 21 species of mayflies, involved in a compensatory flight, by K e l l e r (1975) and M ü l l e r (1982), who generally summarized scientific publications on the "colonization cycle" (or "cycle of distribution").

Further studies of Б о г а т о в (1984), Л е в а н и д о в а и Л е в а н и д о в (1965), Л е в а н и д о в и Л е в а н и д о в а (1979), M ü l l e r (1966, 1970), W a t e r s (1968, 1969, 1981, 1981a), W e n n i n g e r (1968), M ü l l e r-H a e c k e l (1966, 1973) as well as many others have explained the diurnal, seasonal and annual character and role of the drift from various aspects.

K o v a c h e v & U z u n o v (1987) have studied "drift intensity" (the quantity of organisms in 100 cubic meters/h), in a system of mountain streams (1520 m a. s. l.) under top-dressing of the water shed with urea. The statistical estimation shows that water quantity and temperature together are decisive for the size of the drift, while the fertilizer used is important for the quantity only.

Rheotropism of rheobionts (V e r r i e r, 1953) should also in my opinion be considered as one of the main adaptations for compensation for the drift.

Stream fauna, which cannot make the compensation flight, rheotropism or compensation swim, should in some way compensate for the constant carrying away by the current. In a survey of migrations of rheobionts (R u s s e v, 1972) I studied such a compensation and called it "animal and anthropogenic migration". Specimens of different species sometimes attach themselves to the legs of birds, the bodies of freshwater inhabiting mammals, on invertebrates (i. e. on the crab *Astacus leptodactylus* E s h h o l z.), glochidia (the larvae of shell fish), which attach themselves to the gills of fish, water mites etc. which attach themselves to flying insects and thus succeed in the animal distribution. Anthropogenic transformation occurs by means of attachement stream fauna to various vessels, as is the case with the shell *Dreissena polymorpha* P a l l a s, the amphipode *Corophium curvispinum* S a r s, with the Polychaeta *Hypania invalida* G r u d e and with many other instances. Of course it does not fall in the category of adaptations, but fulfils the same function.

Even the structure of eggs of water insect larvae, as well as the manner of egg laying has adaptations against being away by the current. A small number of species lay their eggs separately and apparently unprotected in streams. Thus with the Plecoptera order, the egg shell has little spurs, attachment surfaces, a sticky layer etc., with the function of a quicker attachment of the eggs to river vegetation or to some hard substrate. Female mayflies of the *Baetis* genus lay eggs and carefully glue them to the bottom side of stones by means of sticky secrete, which does not dissolve in the water. The "delayed time of hatching", discovered by I l l i e s (1959) is a specific form of protection against destruction of the population in the event of flooding and any other cause of moving by the current. By tracing the hatching of larvae of 8518 *Baetis* eggs taken from one site of hatching, a remarkably long period of hatching has been observed towards the last larva. The first larvae come out in several days; most of them, however, come out after over 200 days. This means that a unique mechanism of delayed hatching, which apparently does not depend so much on temperature, allows Baetis hatching of larvae practically throughout the year. The biological advantage of such an extended development is beyond doubt; a single stone in the upper reaches of a stream, where eggs of female *Baetis* have been hatched, may be an constant source of larvae throughout the entire year. If a flood in a particular section of the stream carries away the inhabitants or destroys them, several days are sufficient for a recolonization of the stones with newly hatched larvae of *Baetis*. As the latter are among the most freguent and numerous benthic larvae in streams, they constitute an important food source of the larger predator insects, and at the same time are a basic element of biocenoses. This is why this biological mechanism plays a major role in maintaining the balance in the biocenosis.

The adaptations considered so far and the relationships in the life of stream organisms are related only to the basic factor — the speed of the current. They show exceptional ecological harmony and the endless adaptive potential of stream biota in the course of millions of years to sudden changes or gradually changing ecological factors.

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Received on October 2, 1988

Адапатации реобионтов к жизни в текучих водах

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(Резюме)

Обобщены основные литературные данные по морфологической адаптации реобионтов в текучих водах, а также приведены и некоторые новые примеры. Дискутируются мнения некоторых ученых, что такая адаптация вообще не существует.

Рассмотрены биологические приспособления различных реобионтов для расселения в потоках и для компенсации биологического дрифта с помощью компенсационного полета, реотропизма, компенсационного плавания, анимального и антропогенного переноса, замедленного времени вылупления.

Эти приспособления рассматриваются как неограниченные возможности речной биоты приспосабливаться в течении миллионов лет к внезапно или постепенно изменяющимся экологическим факторам с целью охраны экологической гармонии в текущих водах.