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Morphological Adaptations of Benthic Invertebrates to Stream Flow – An Old Question Studied by Means of a New Technique (Laser Doppler Anemometry)

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Summary. The generally accepted concept that dorsoventral flatness and/or small size of benthic stream invertebrates staying on the surface of the bottom substratum allows a current-sheltered life in the boundary layer (Ambühl 1959) is checked by means of the new technique of Laser Doppler Anemometry (LDA). With LDA measurement of flow can be done nearly punctually without any mechanical disturbance. Mapping the current velocities around the body of *Ecdyonurus cf. venosus* (Insecta, Ephemeroptera) and *Ancylus fluviatilis* (Gastropoda) gives evidence that boundary layer separation occurs above the animals' bodies. Our results indicate that the velocities around the body of benthic stream invertebrates and probably the forces acting on them are much more complicate than is suggested by the currently accepted boundary layer concept.

Introduction

Since the formulation of the "Schub-Theorie" by Steinmann (1907) the dorsoventral flattening of the body of benthic stream invertebrates living on the surface of the substratum has been regarded as an adaptation to flow by reducing the shear of the current acting on the body (Thienemann 1926; Ruttner 1940; Wesenberg-Lund 1943). The habitus of animals, particulary dorsoventral flatness, was even an important criterium in establishing a general theorie of stream zonation, incorporating the topics "isocoenoses" and "life-form-types" in relation to flow conditions (Illies 1961a, b).

Until 1959 the "Schub-Theorie" was rarely criticized (Nielsen 1950). That year Ambühl (1959) noted in the course of laboratory studies that benthic invertebrates living outside the dead water are usually found in the boundary layer on the surface of the substratum (Fig. 1), a zone where velocities are reduced due to the friction forces. Dorsoventral flatness and/or small size could therefore be an adaptation to a "sheltered life in the boundary layer", thus avoiding forces of current to a greater extent than is assumed by the "Schub-Theorie". Though criticized by Decamps et al. (1972, 1975), this boundary layer concept is generally accepted (e.g. Illies 1961c; Hynes 1972; Moss 1980; Schwoerbel 1980; Streit 1980; Townsend 1980). It was recently tested in field studies in a modified form (Statzner 1981a, b), leading to new questions regarding adaptation to stream life and thereby to a study of flow conditions around the body of animals using Laser Doppler Anemometry (LDA), a technique described in detail by Durst et al. (1981). Since our first results

Fig. 1. Schematical representation of the nymph of *Ecdyonurus sp.* at high velocity (> 20 cm/s). Drawn according to photos (from Ambühl 1959). According to Ambühl's text the lines around the nymph are a schematical indication of stream-lines

are surprising and contradict the present ideas on this subject, they will be briefly communicated below.

Methods

Flow conditions were determined around dead animals glued onto 6 mm high segments cut from PVC-rods so that their position was as natural as possible. Velocities were measured with a DISA 55L Laser Doppler Anemometer Mark II. Two incident beams form the point of measurement in the flow. A particle passing through this measuring volume will scatter the light. The scattered light contains the doppler frequency, which is directly proportional to the velocity of the particle. Since zero velocity will not produce a doppler signal, the instrument is equipped with frequency translation facilities to overcome this problem. Using these frequency shift facilities a particle with zero or even negative velocity is detected. From the above it is obvious that the LDA-system will not work without the presence of an appropriate concentration of scattering particles. Therefore, it is often necessary to add particles (seed), and these must be of appropriate size. The typical size range is 0.1–10 μm.

The advantage of using LDA is: measurements of flow can be done nearly punctually without any mechanical disturbance. Also flow conditions near solids can be examined since the inertia of the scattering particles is negligible.

In the actual work the LDA-system had the following proporties: laser output power: 5 mW; focussing lens of beam separator: 12 cm; beam separation: 40 mm, i.e. measuring volume length: 0.72 mm, measuring volume width: 0.12 mm; frequency of local oscilator: 40.15 MHz; transducer set up: differential doppler mode, forward scatter; seed: commercial plastic paint. The laser system was mounted on a X-Y translator, and the flume on an Y-Z translator. Accuracy of positioning the measuring volume: better than 10 μm. Experiments were carried out in water.

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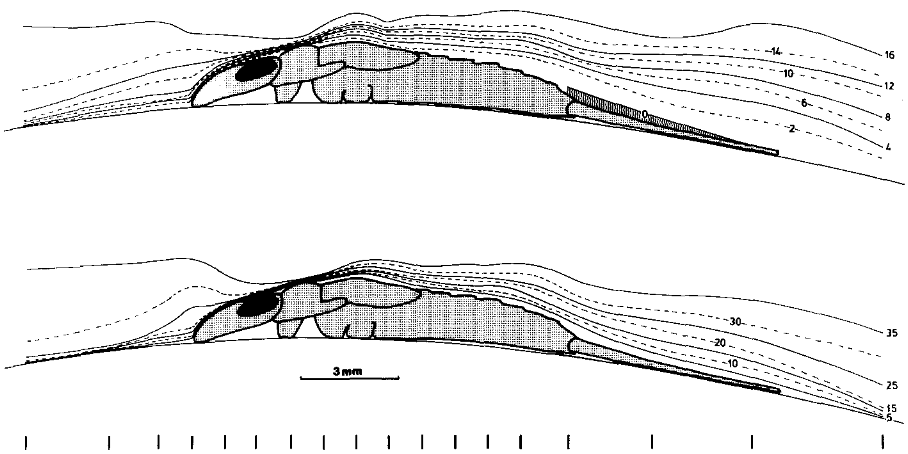

Fig. 2. Schematical (legs omitted!) drawing of the nymph of *Ecdyonurus cf. venosus* with the iso-vels around the median line of the animal's body in two hydrodynamic situations. Above/below: mean velocity in profile (cm/s): 18.1/38.6; mean velocity within the first 10 mm above the substratum (cm/s): 16.7/36.0; water depth above the highest point of the substratum (cm): 3.4/2.8. The iso-vels are constructed with the help of vertical profile measurements (at the points indicated by the vertical bars at the bottom of the graph) plotted from cubic spline calculations. Iso-vels are drawn for velocity steps of 2 cm/s (above) and 5 cm/s (below), below the zero line velocities fluctuate around zero

Results and Discussion

In the preliminary tests two species were studied: *Ecdyonurus cf. venosus* (Insecta, Ephemeroptera), of course, since it is the classical example of life in the boundary layer (Fig. 1), and *Ancylus fluviatilis* (Gastropoda), which according to different authors is supposed to be stream adapted in various ways such as its small size and life in the boundary layer (Streit 1980).

In both hydrodynamic situations in which *Ecdyonurus* was tested, the iso-vels (lines of equal mean velocity) show the same pattern (Fig. 2). A reduction of the velocity near the substrate occurs in front of the animal. From the tip of the head to the prothorax the iso-vels are compressed, i.e. the flow gradient increases vertically above the animal. In the region of the meso- and metathorax the flow gradient starts to decrease and above, as well as behind, the abdomen of the larva a boundary layer (or zone of dead water) occurs which is thicker than that in front of the animal.

Around *Ancylus* (Fig. 3) the flow conditions are somewhat similar to those around *Ecdyonurus*: reduction of bottom velocity in front, compression of the iso-vels, in this case up to the highest point of the shell, and then, due to the abrupt end of the animal, a distinct zone of dead water behind the body.

The friction forces acting on the animal reach a maximum in the zone of the steepest velocity gradient. Here high maximum velocities are found in the immediate vicinity of the surface of the animals body, e.g. 34.5 cm/s in a height of 20 µm above the first point at which doppler signals could be detected above the shell of *Ancylus* in the hydrodynamic situation shown at the bottom of Fig. 3. This velocity value reaches the level of mean velocities above the boundary layer found in front of the animal.

In three of the four cases tested here boundary layer separation is observed above the animal's body.

These results contradict those of Ambühl, since in our experiments flow goes not as smooth over the animal's body nor are the boundary layers as thick as reported by that author. The reasons for this contradiction should be briefly scrutinized.

Flumes used in such experiments have inherent hydraulic characteristics. The boundary layer characteristics are especially determined by the form, roughness and height of the substrate projections in relation to water depth and mean velocity in the

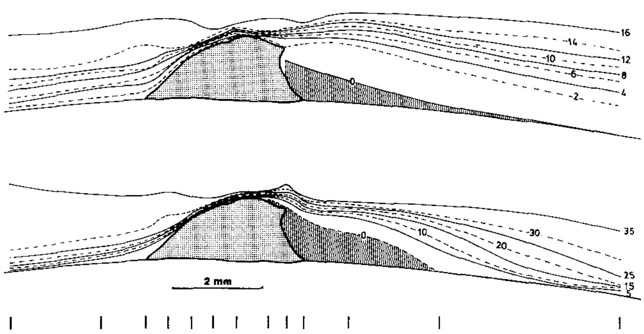

Fig. 3. *Ancylus fluviatilis*. Cf. Fig. 2 for further details

flume. Comparing the hydraulic character of Ambühl's flume with that of our it is quite evident, that at the same velocities boundary layers should have been smaller in Ambühl's flume, due to the relation of the height of the substrate projection (10–20 mm) to the water depth (5–35 mm) used by that author.

However, boundary layers were thicker in those experiments.

Therefore we presume that the differences between our findings and Ambühl's are caused by differences in the technique of velocity determination. Ambühl used particles of acetyl cellulose as tracer material. Direction and velocity of these particles were determined by photographs taken in flashing light (100 flashes/s). Ambühl himself described the particles as "relatively coarse", and from his photos one can estimate, that their diameter probably lay in the range of 0.5 mm or above, i.e. they were several orders of ten bigger than the tracer particles used in our experiments. Since we found that distinct vertical flow gradients near solids may occur within 0.1 mm, particularly in the zone where the iso-vels are compressed above the front side of the species tested here, we assume that large particles are unsuitable for detecting this phenomena and that the inertia of such large particles results in over-estimation of the boundary layer.

Our preliminary results give evidence, that the morphological adaptations of benthic invertebrates in relation to the "live in the boundary layer" are not as simple as has been assumed up to now. One can speculate, in the case of *Ecdyonurus*, that lifting forces acting on the animal, which are presumed to be most dangerous for stream invertebrates, are greatest just behind the zone of compression of the iso-vels, i.e. at the thorax, where the animal's legs are in contact with the bottom. As the velocity increases (above 50 cm/s) *Ecdyonurus* presses head and end of the abdomen more and more against the substratum, while the rest of the body is lifted, i.e. the animal arches its body (Butz 1979). Does this behaviour focus maximal lift forces on the thorax region, where the legs firmly hold onto the substrate?

And *Ancylus?* Is its body form of little importance because good marginal contact with the bottom and a broad foot assure its firm attachement?

Our present results as well as those obtained from studies on water pennies (Coleoptera, Psephenidae) (Smith and Dartnall 1980) indicate that the velocities around the body of benthic stream invertebrates and probably the forces acting on them are much more complicate than is suggested by the currently accepted boundary layer concept. We expect that flow around these animals is influenced by very inconspicious morphological structures, behavioural patterns, and a combination of both. Probably no "rule of thumb" as simple as the boundary layer concept exist at all and we will not be able to determine it through our future work. However, since our preliminary results doubt a concept, which is related to so many fields of stream ecology, we felt the necessity of this rapid communication.

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