A Comparative Ecological Investigation of two Related Mayfly Nymphs

by

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(with 8 figs.)

The two closely related mayfly nymphs *Heptagenia sulphurea* (MÜLL.) and *Heptagenia fuscogrisea* (RETZ.) are often found in the same piece of water and look like each other. However they differ strictly in habitat and behaviour. The purpose of this paper is to describe some of these differences from observations in nature and in the laboratory under controlled conditions. Also described are some morphological differences regarded as important in the adaptation to the habitat.

The results are part of a current investigation on stream-dwelling animals.

METHODS

The two species are found in the stream Gudenå at Bredstenbro and Klostermølle. In places the bed of the stream is stony without vegetation and in places it is overgrown with plants, which also grow along the edge. Field observations were made at Mattrup å at Stidsmølle, where the water is shallow.

The animals were transported to the laboratory in dewar vessels. Here they were transferred to stream tanks with the same temperature as in the biotope. The temperatures were regulated by contact thermometers, which through hotwire relays activated solenoid valves. These valves regulated cooling water from a refrigerator (Hetofrieg).

The stream tanks were of the types shown in fig. 1. A propeller created a current around in the tank. The tank with the profiles

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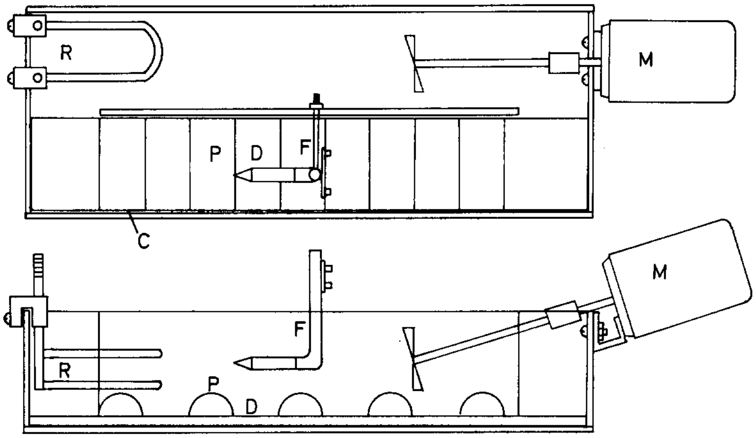

Fig. 1. Stream tank used in the studies on the behaviour. M: Motor with propeller. F: Flowmeasuring device. P: Current-exposed profile. D: Dead-water area. C: Crevice. R: Cooling coil.

shown on the figure was used in the experiments on the behaviour. The velocity over the most exposed parts was 30 cm/sec, while the current was strongly reduced between the profiles. Along the sides are crevices with some water movements. On the bottom are glued sand particles, which allow the animals to get a foothold.

THE HABITATS OF THE SPECIES

a) *In the biotope*

Both species are common in brooks and streams in Jutland. JENSEN (1956) mentions them as very common in the Skernå river system except in the smallest brooks.

They have different habitats. *H. sulphurea* is nearly always found on stones and gravel in the current. Only a few are found in the vegetation. On the stones they are usually placed on the upper surfaces, where they are pressed closely to the substrate facing towards the current.

H. fuscogrisea is never found on the stones or gravel, but exclusively in the vegetation. How pronounciated the difference in habitat is can be seen in fig. 2, which is the results from one single sample in Gudenå at Bredstenbro. Here the two species are living near each other: *H. sulphurea* on the stones and gravel. *H. fuscogrisea* in the vegetation in the current and along the bank. One remarkable thing to be noticed from this sample is, that *H. fuscogrisea* apparently

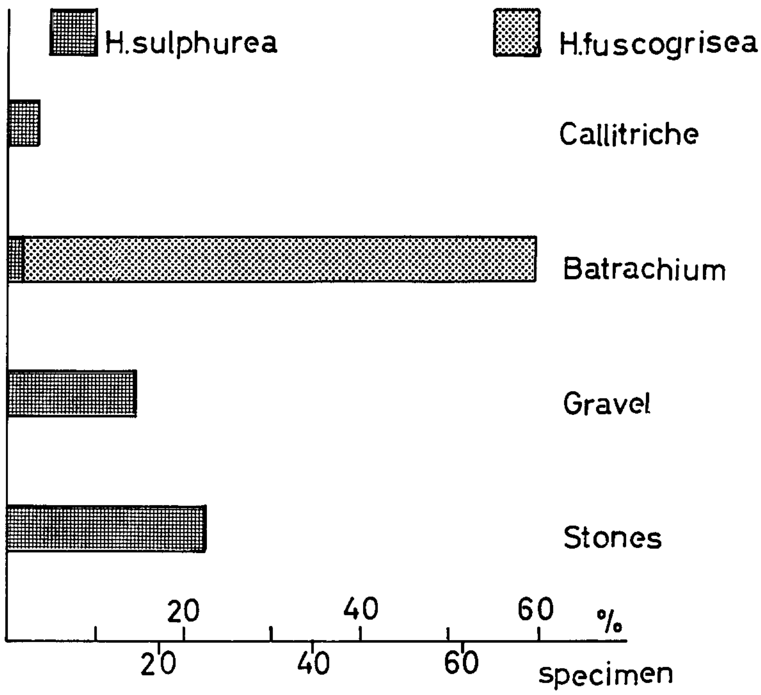

Fig. 2. The habitats of *H. sulphurea* and *H. fuscogrisea*. Gudenå at Bredstenbro January 12th 1965.

avoids the dense *Callitriche* and prefers the more open *Batrachium*.

MACAN (1961) reports the two species from lakes. NIELSEN (1950) says that *H. sulphurea* is found predominantly on lake shores, which, however, does not agree with the experience of the author and CARLO F. JENSEN (personal communication). *H. fuscogrisea* is often found in small pools near streams, especially in meanders.

b) Substrate preference experiments

In a stream tank were placed stones, various kinds of gravel and sand together with plants in separate polystyrene boxes, whose end-plates were removed after the introduction in the water. The current in the tank was 20 cm/sec.

With each of the two species an experiment was performed to show if they would prefer the same type of substrate in the stream tank as they did in nature. They were placed at random in the tank and their positions were registered two days later by isolating and removing each type of substrate.

The substrate offered to the animals is shown in fig. 3. All types were sterile except *Batrachium* and *Callitriche*.

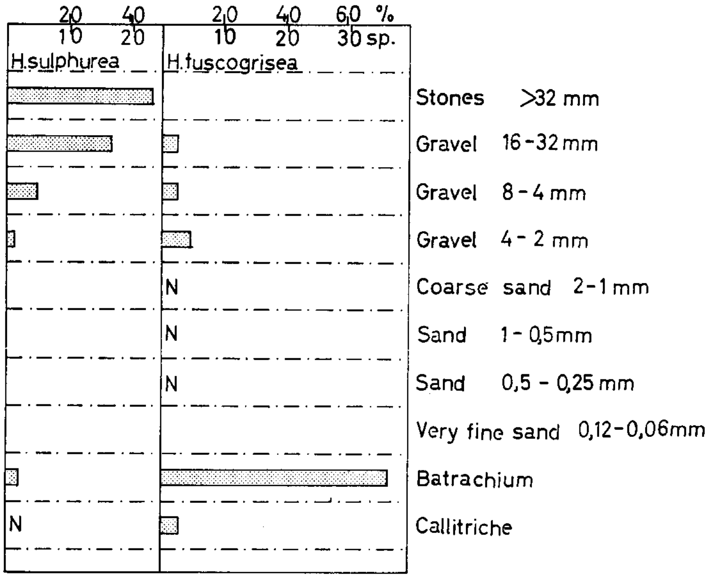

Fig. 3. Substrate preference experiments. "N" means type of substrate not offered to the species.

From the diagram it is seen that when *H. sulphurea* in a stream tank has the choice of substrates consisting of stones, various kinds of gravel and sand, and *Batrachium*, it prefers the stones and the coarsest gravel. Only a few were found in the *Batrachium*. This picture agrees well with the distribution in nature.

In the experiments referred to only big larvae were used. In another in which small and big larvae were used, it was observed that most of the big larvae were on the stones, while most of the small were on the gravel of the diameters between 32 and 16 mm.

In an experiment with *H. fuscogrisea* we also obtained results which were in agreement with the distribution in nature except that some specimens were found on the gravel in the stream tank. The reason for this may be that the current in the stream tank over the gravel is slower than in nature. But as a whole the experiments agree well with the distribution in nature. Most animals prefer *Batrachium*. In the experiment *Callitriche* was also introduced in order to check the observation that the species in nature avoids this kind of vegetation. The observation is confirmed by the experiment. Only a little part of the animals is in the *Callitriche*.

Behaviour in the current

a) Time elapsirg between release and a safe foothold in the substrate

In a stream there is a drift of animals which are carried downwards by the current. Usually there is a diurnal rhythm in this drift (Müller 1965), which reflects the activity of the animals (Madsen 1966). Streamdwelling animals must compensate this unidirectional force which tends to depopulate the stream. Direct compensatory forces are the active upstream movements by *Gammarus pulex* (Müller 1965) and by eggbearing females of various insects (Jensen 1956). Among indirect compensatory forces is the reaction by the animal when carried away by the current. An animal that regains a a foothold quickly after loosing it is adaptated to life in current.

In order to get an idea of this property by the two species, I have measured the time they were carried away by the current before they had a safe foothold in the substrate.

Experiments with the two species were carried out under exactly similar conditions.

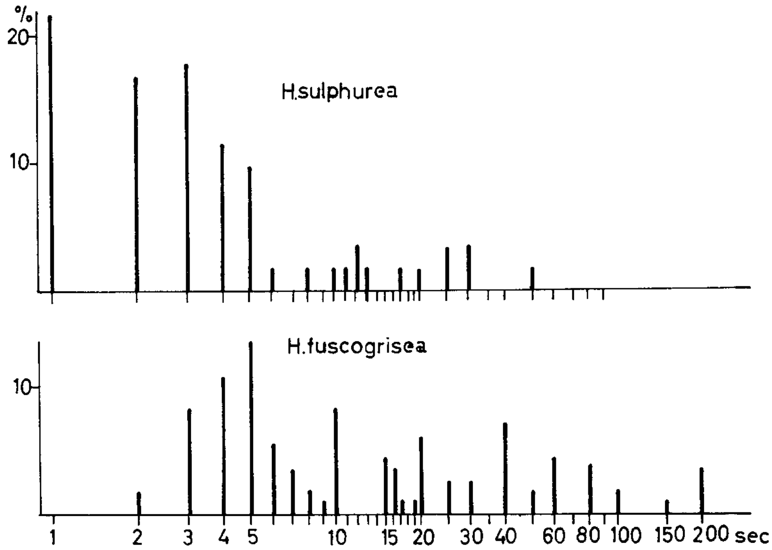

Fig. 4. Time elapsing between the release and a safe settling on the substrate. The vertical lines indicate the numbers having obtained a safe foothold in the times on the logarithmic time scale.

As seen in fig. 4 the results with the two are different. The vertical lines indicate the percentages of the specimen that have got a safe foothold in the substrate to the times indicated on the abscissa. Remark the logarithmic time scale.

H. sulphurea, the species from stones in the current, reacts faster than *H. fuscogrisea*, the species from vegetation. This is an adaptation to their different habitats.

b) Mode of reaction in the current

When *H. sulphurea* is swept away by the current it is rather passive, but as soon as it touches the substrate with its claws it has a safe foothold. *Brachyptera risi*, an other form from current exposed stones, has a similar reaction (MADSEN 1968). Only occasionally it swims. Where it lives the current is so turbulent that without swimming it will reach the substrate within a short time. When a specimen obtains a foothold on an exposed place, it stays there. It never goes immediately to the calm water. It is pressed tightly to the substrate. If the current ceases, most specimen react to this within a few minutes. They lift the body from the substrate, move around and occasionally leave it altogether and take a short swim. The cerci and abdomen sweep up and the gill blades are moving. As soon as the current starts again, they press the body close to the substrate and the movements of the gill blades cease. One specimen was seen running down to the calm water when the current started.

The mode of reaction to the current by *H. fuscogrisea* is different from the other species. When swept away by the current it swims continously against the current. If it touches a current exposed profile, it usually does not get a firm foothold and is often swept away again. If, however, it comes down in the calm water between the profiles, it remains there. If it gets a foothold on the current exposed substrate, it usually runs down to the calm water immediately. A specimen in the current exposed area does not press its body close to the substrate as did *H. sulphurea*.

c) Positions in the stream tank

In the stream tank described I have noticed the positions of the two species. The number on the current exposed areas, in the deadwater areas, and in the crevices along the sides are registered. Seven different experiments were made with *H. sulphurea* in January, March, June, and July with all sizes of larvae. With *H. fuscogrisea* four different experiments were made in January and March with all sizes except the small ones.

Observations on the positions of the animals are made some hours after the start of the experiment and repeated two to three times at intervals of some hours. The experimental material were 113 *H. sulphurea* and 75 *H. fuscogrisea.*

It is rather difficult to get an impression of the positions of *H. sulphurea* because it reacts quickly to the movements of the observer. This is also seen in nature, where it moves away from the upper surfaces of stones to more sheltered places when one comes near to it. Perhaps this may be the reason why NIELSEN (1950) characterises *H. sulphurea* as an inhabitant of the undersides of the stones. This behaviour may be an adaptation to its habitat, the upper surfaces of stones, where it is easily seen by the predators in the free water.

The observations in the stream tank are made with great care and any group, in which movements by any species were seen, was rejected. The best observations are made in dim red light.

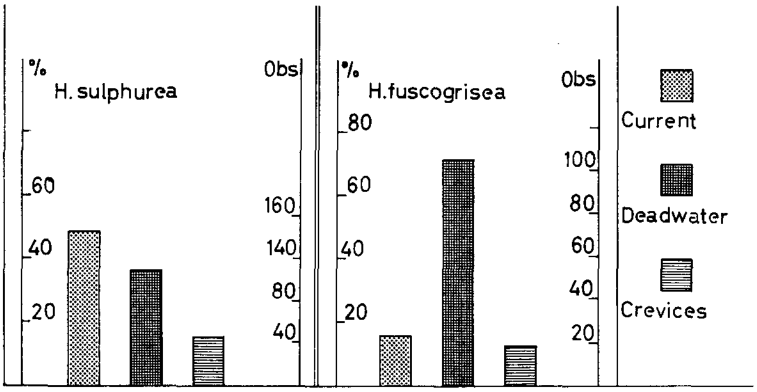

Fig. 5. Positions of the species in the stream tank containing places with current, deadwater areas, and crevices with some water movements.

The results are seen in fig. 5, where each column indicates the part of the animals in the current, in the deadwater, and in the crevices. Both the percentage distribution and the total numbers are shown.

Most *H. sulphurea* are observed on the current exposed areas, many are in the deadwater areas and a few are in the crevices along the sides. Most of the animals in the crevices were the small larvae although the crevices were wide enough to harbour the other sizes.

There was some flow through the crevices occupied by the small larvae. No larvae were observed in the crevices under the bottom-plate without any water movements.

H. fuscogricea has a distribution in the streamtank which differs from that of *H. sulphurea.* It occupies the areas with calm water between the profiles. Only a small proportion is in crevices or on the current exposed places. This is in agreement with its distribution in nature, where it is confined to areas with reduced current in the vegetation. Its partial avoidance of crevices may explain the small numbers found in the dense *Callitriche.*

d) Influence of temperature

It is evident from observation on the behaviour that the temperature is of importance for the time elapsing between the release of a specimen and its obtaining a safe foothold in the substrate. It is longer at lower than at higher temperature within an interval of temperatures occurring in the biotope.

The experiments referred to above are all performed at 14° C. Experiments referred to in this chapter are all made in winter when the temperatures in the stream, from which the experimental animals are taken, varied between 2 and 4° C. They were introduced immediately after the sampling in a stream tank at 4° C.

A few hours later experiments were made at 4° C. Then the temperature was changed to 14° C, and having been allowed for acclimatization 48 hours experiments were carried out.

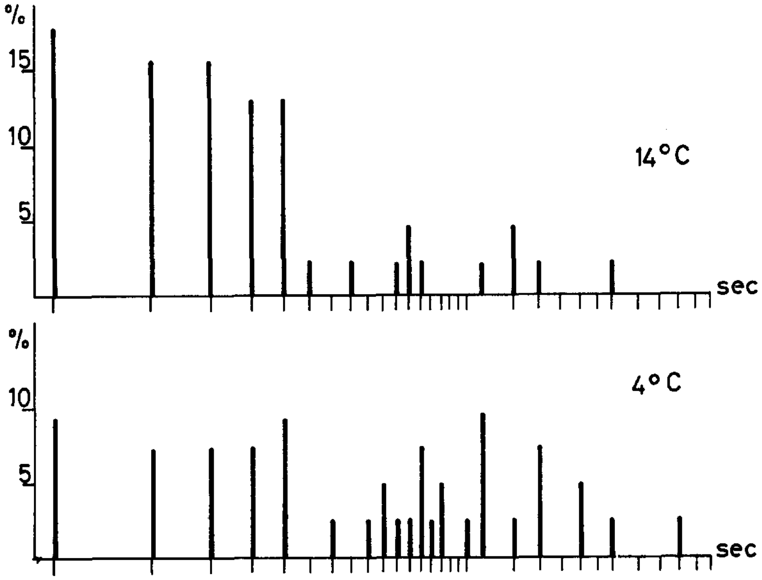

Fig. 6. Time elapsing between release and settling on the substrate at two different temperatures. The low temperature was near the temperature in the biotope, from which the experimental animals were taken. Time units as in fig. 4.

Results with *H. sulphurea* are shown in fig. 6. The time elapsing between release and a foothold by 14° C does not differ from those from summer (fig. 4), but there are differences between the experiments by 14° C and 4° C. The species reacts more slowly at the lower temperature. But once having obtained a foothold it usually remained there.

Similar results are obtained with *H. fuscogrisea*. Its swimming at the low temperature was very slow and after having obtained a foothold it often released again. Experiments at 14° C after only two hours acclimatization were similar to earlier observations at the same temperature.

THE MORPHOLOGICAL ADAPTATION

a) *The morphological adaptation to the current by H. sulphurea*

STEINMANN (1907) stresses the importance of morphological adaptations to the current, regarding the dorso-ventral flattening of the animals as one of the most characteristic features of the torrential animals. This was revised by DODDS & HISAW (1924) and NIELSEN (1950), who regarded the dorso-ventral flattening as an adaptation to life in the narrow crevices under the stones.

However, it is rather difficult to find crevices under the stones suitable for flat forms. Usually the stones in the current are well cemented in the sandy or gravelly substrate. Hence a cylindrical form might be a better adaptation to life under a stone in the stream than a dorso-ventral flattened form. In fact, many forms living under the stones are cylindrical, e.g. *Leuctra*.

The importance of the dorso-ventral flattening must be seen in the light of the boundary layer, which is a region near the substrate over which a liquid or gas flow. The velocity in this layer is reduced in comparison with velocities in layers at greater distances from the substrate. This layer was discovered by PRANDTL (1908) and is described in every textbook of hydrodynamics. Fifty years after its discovery it was applied in the studies of streamdwelling animals (AMBÜHL 1959).

When *H. sulphurea* is in the current, it presses its body close to the substrate. Not only over its substrate is a boundary layer, but over the animal itself is such a layer. Even in swift current the velocity near the animal is reduced.

The current goes over the head capsula of the animal because its edge is tightly pressed to the substrate. When the current leaves, the animal vortices are reduced because the abdomen is flattened and is pressed to the substrate. The long cerci may also be of importance in reducing the vortices.

Vortices might occur when the current leaves the hind edge of the femora, because this is not pressed to the substrate. When looking at the hind edge of the femora we see that it has a dense fringe of hairs. This fringe may reduce the effect of vortices behind and under the femora (Fig. 7).

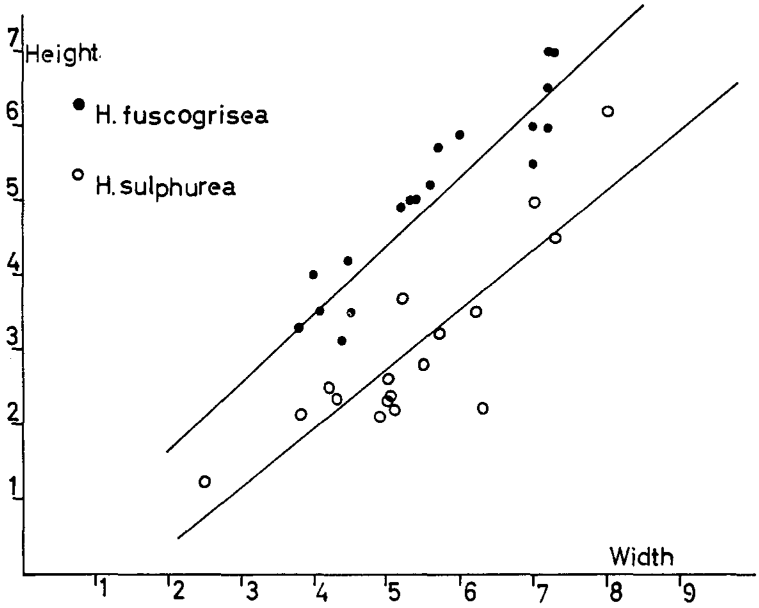

Fig. 7. Correlation between height and width of mesothorax by the two species.

b) A comparison of some morphological features by H. sulphurea and H. fuscogrisea

In the preceding parts differences between habitats and behaviour of the two species are described. Now we turn to look upon some morphological differences, which might be correlated with the differences in habitat and behaviour.

The first question which arises is whether *H. sulphurea* is more flattened than *H. fuscogrisea.* A first look gives the impression that *H. sulphurea* apparently is somewhat more flat than *H. fuscogrisea* and a measuring of height and width of the mesothorax shows that this really is the case. In fig. 7 the correlation is shown between the measurements from the two species. For each species is calculated the regression line.

As described before the stone living *H. sulphurea* has a dense fringe of hairs along the hind edge of the femur. *H. fuscogrisea* from the vegetation has not such a fringe. This supports that this fringe is an adaptation to torrential life.

H. sulphurea has only a thin fringe of hairs along the hind edge of the tibia, while this fringe is denser on *H. fuscogrisea.* This may be seen as an adaptation to the swimming this species performs when carried away by the current.

Also in the claws are differences. The inner edge of the claw of *H. sulphurea* is even on high magnification smooth, while it is toothed by *H. fuscogrisea* (fig. 8).

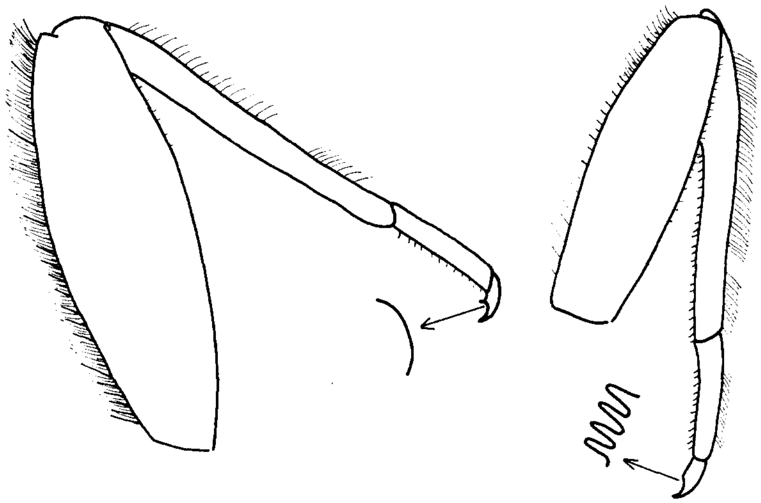

Fig. 8. Hind legs of *H. sulphurea* (left figure) and *H. fuscogrisea.*

The claws by *H. sulphurea* has in its proximal part a second point. It is interesting to note that such a point is also found by *Brachyptera risi*, which has a mode of life similar to *H. sulphurea.*

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ZUSAMMENFASSUNG

Heptagenia sulphurea wird auf Steinen, *H. fuscogrisea* in der Vegetation von Fließgewässern gefunden (Fig. 2).

In Experimenten wählte *H. sulphurea* Steine und groben Kies. *H. fuscogrisea* wählte *Batrachium* als Substrat, nur ein geringer Anteil der Larven fand sich auf *Callitriche* (Fig. 3).

Die Zeit, die zwischen Loslassen und erneutem Anhaften auf dem Substrat im strömenden Milieu verstreicht, war unterschiedlich bei den zwei Spezies. Die auf Steinen lebende Art reagierte schneller als die aus der Vegetation.

H. sulphurea verhielt sich, wenn sie von der Strömung ergriffen worden war, ziemlich passiv, doch trug die turbulente Strömung das Tier dem Substrat zu, so hatte es gewöhnlich sicheren Halt.

Im Strömungsaquarium bevorzugt *H. sulphurea* die strömungsexponierten Bereiche, aber viele waren auch im ruhigen Wasser (Fig. 5).

Wurde *H. fuscogrisea* von der Strömung ergriffen, so führte sie Schwimmbewegungen aus. Erreicht sie eine Haltmöglichkeit an strömungsexponiertem Platz, so wird sie oft weitergetragen. Die Tiere lassen sie meist in ruhigem Wasser nieder.

Im Strömungsaquarium bevorzugt *H. fuscogrisea* überwiegend die Regionen ruhigen Wassers (Fig. 5).

Die Zeit zwischen Loslassen und Festsetzen war deutlich durch die Temperatur beeinflußt (Fig. 6).

Der dichte Haarbesatz an der hinteren Kante der Femur von *H. sulphurea* wird als Anpassung an das Leben in der Strömung angesehen, weil er die Wirbelbildung herabsetzen kann. Der Haarbesatz entlang der Tibia bei *H. fuscogrisea* wird als Anpassung zum Schwimmen angesehen, zu dem diese Spezies befähigt ist, wenn sie von der Strömung ergriffen wird (Fig. 8).

Die Spezies von Steinen ist etwas mehr abgeflacht als die aus der Vegetation (Fig. 7).

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