Dependence of the Respiration Rate of Aquatic Insects upon the Oxygen Concentration in Running and Still Water

by

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The relationships between respiration rate (RR) of rheophilous larvae of *Cinygmula grandifolia* Tshern. (Ephemeroptera), *Stenopsyche marmorata* Navás (Trichoptera) and *Skwala pusilla* (Klapálek) (Plecoptera) and oxygen concentration was examined in still and fast-flowing water. The flow did not influence these relationships for *C. grandifolia*, but did so for *S. marmorata* and *S. pusilla*. The sensitivity of the species to oxygen depletion in still water was negatively correlated with the development of tracheal gills. The reduction of sensitivity to oxygen deficit caused by the stream flow was about 17% of oxygen saturation (OS) for *S. pusilla* which has very small gills and about 20% for *S. marmorata* which have no tracheal gills.
     The distribution patterns of the species can be explained in terms of their RR – OS relationships to water flow. Larvae of *C. grandifolia* occupy biotopes with a relatively low water flow. The larvae of *S. marmorata* and *S. pusilla* are usually observed only in sections of river with rapid current. The distribution patterns of some other rheophilous insects attributed to different lines of adaptation for life in flowing water are discussed.

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INTRODUCTION

The occurence and distribution of aquatic insects in rivers may be controlled by many factors. Some of them such as food are well documented in the literature (e.g., Anderson and Sedell, 1979). Data concerning the influence of oxygen saturation (OS) in water on the species composition and the structure of animal communities in streams are much more scarce. This may by explained by the common opinion that this factor is not of importance for running waters. But the OS in running waters depends on the previous history of the water. Moreover, in the case of intense organic pollution, oxygen depletion becomes one of the most important factors determining the species composition and the structure of lotic communities (Uzunov and Kovachev, 1987).

     There is also another aspect of this problem. The sensitivity of many rheophilous species to low oxygen concentrations is closely associated with water flow (Philipson, 1954, Ambühl, 1959, 1961, 1962, Knight and Gaufin, 1964). According to this point of view the rheophilous species inhabiting biotopes with rapidly

flowing water are exposed to more comfortable conditions than species inhabiting biotopes with slow flowing water. Therefore, the patterns of species distribution under relatively favorable oxygen conditions may depend on the ability of species to take up oxygen from slow or fast flowing water.

The sensitivity of animals to oxygen depletion is well characterized by the relationship between their respiration rate (RR) and OS in water, which gives a physiological background to the oxygen preference of species.

There are many papers on the influence of oxygen depletion upon RR of aquatic insects in slow waters. Papers on the relationships between RR of rheophilous species and OS are more scarce (Mill, 1985). Some species are conformers and unable to maintain a constant level of RR in water when the OS is lower than 100% (Fox *et al.,* 1937, Kapoor and Griffiths, 1975, Golubkov and Kocharina, 1988, Golubkov and Tiunova, 1989). These animals are very sensitive to oxygen depletion and can be referred to as oxyphilous species. Others are able to regulate their RR over a more or less wide range of OS and can be considered as non-conformers (Golubkov and Tiunova, 1989).

One might expect that the distribution patterns of the conformers are constrained and non-conformers are not constrained by the OS in water. But there are some methodological problems in determining the range of preferable OS values for both conformer and non-conformer species, because, as mentioned above, these values may depend on the speed of water flow. Various methods of stirring water in respirometers have been used in the studies. However, in practically all treatments there was no smooth flow of water in the respiration bottles comparable with that in running waters.

This paper documents the results of experiments on the relationships between RR of rheophilous larvae of the mayfly *Cinygmula grandifolia* Tshernova, the caddisfly *Stenopsyche marmorata* Navás and the stonefly *Skwala pusilla* (Klapálek) and OS in still and swift water. The role of these relationships in determining the microdistribution of these and other rheophilous species in rivers is discussed.

MATERIAL AND METHODS

The studies were carried out in November, 1988 at the Hydrobiological Station of the Institute of Biology and Pedology (Far East Department of Academy of Science of the CIS) in the reserve "Kedrovaja Pad" situated along the west coast of Amur Bay. Larvae were obtained in the middle part of the Kedrovaja river where they were abundant.

Kedrovaja river is of the foothill type with swift-flowing water and a stony bottom. It has been described in previous papers (Golubkov and Tiunova, 1989, Kocharina, 1989). Measurements of the larval RR were carried out by the method of closed bottles in a respiration chamber of 115 ml at 6°C. The river water temperature ranged from 1 to 4°C during the experiments. The decrease in oxygen in the respirometer caused by animal respiration was measured. An oxygen Pb/Pt-electrode was hermetically mounted into the lid of the chamber and connected to a Micro-Ampère-meter, and OS was recorded every 10 minutes. The RR was calculated for periodes of 30-40 minutes, and each experiment lasted for 8-12 hours. During this period the oxygen content in the respirometer water fell from 50-95 to 3-10% of OS.

Experiments were conducted in two series. In the first the water in the respirometers was slightly stirred by rotation of a 0.5 cm long metal rod placed under the sensor membrane. It was moved by a

magnetic stirrer which was placed under the aquarium containing the respirometer. The rod was enclosed in a small chamber to protect the animals.

In the second series a cone of a netting with 0.4 mm meshes was placed in the respirometer, and its top was fixed around the electrode 3.5 cm above the bottom of respirometer. The base of the cone was attached closely to the bottom. A 2 cm long metal stirring rod was placed on the bottom, in the space isolated by the net, and was moved by the magnetic stirrer. This induced a circular current of 20-30 cm/s on the average. Animals were placed onto the outside of the cone net, and they used it to support themselves against the current.

Ten experiments were carried out. Four were with larvae of *C. grandifolia* (25-50 individuals in each): 2 experiments were carried out with the water flowing (series "with current") and 2 others with slight water movement in the respirometer (series "without current"). The wet weight of a single specimen of *C. grandifolia* was 11.8-12.7 mg. Larvae of *S. marmorata* were studied in four tests (8-20 individuals in each): 2 of them "with current" and 2 "without current". The range of larva weights in these esperiments was 60-85 mg. Two experiments were conducted with larvae of *S. pusilla:* 1 "with current" and 1 "without current". The average wet weights of 17 larvae used in each series were 66.4 and 73.9 mg respectively.

RESULTS

The results obtained for *C. grandifolia* are shown in Fig. 1a. It is seen that this species belongs to non-conformers, because the larvae are able to maintain a constant level of respiration within a fairly wide range of OS: from 40 to 100%. Fig. 1a also shows that the water flow did not diminish an inhibitory effect of low OC upon RR of larvae of this species. The range of OS, over which the respiration rate of animals was constant, remained practically invariable. This range of OS may be called the "oxygen adaptation zone" of the species.

Fig. 1b shows the results of RR measurements of *S. pusilla* larvae at various levels of OS. It can be seen that the RR of these animals was higher under conditions "with current" than under conditions "without current". The character of the relationships between the RR of *S. pusilla* larvae and OS is also different in the two series. In the one "without current", the RR declined progressively over the whole range of OS. In the series "with current" one can note the independence of RR of this species over a considerable range of OS.

The results obtained for *S. marmorata* larvae are shown in Fig. 1c. It can be seen that the RR in the series "with current" was much higher than in the series "without current".

DISCUSSION

It is known that the ability of aquatic insects to resist the effects of low OS is closely associated with their respiratory activity. There is always a boundary layer of water with a gradient of OS near the body surface (Mill, 1985), and larvae require a certain oxygen concentration at that surface to maintain the necessary rate of diffusion across it. The rate of diffusion depends on the OS of the main body of water and the thickness of the boundary layer, and the latter is connected with the rate of water flow.
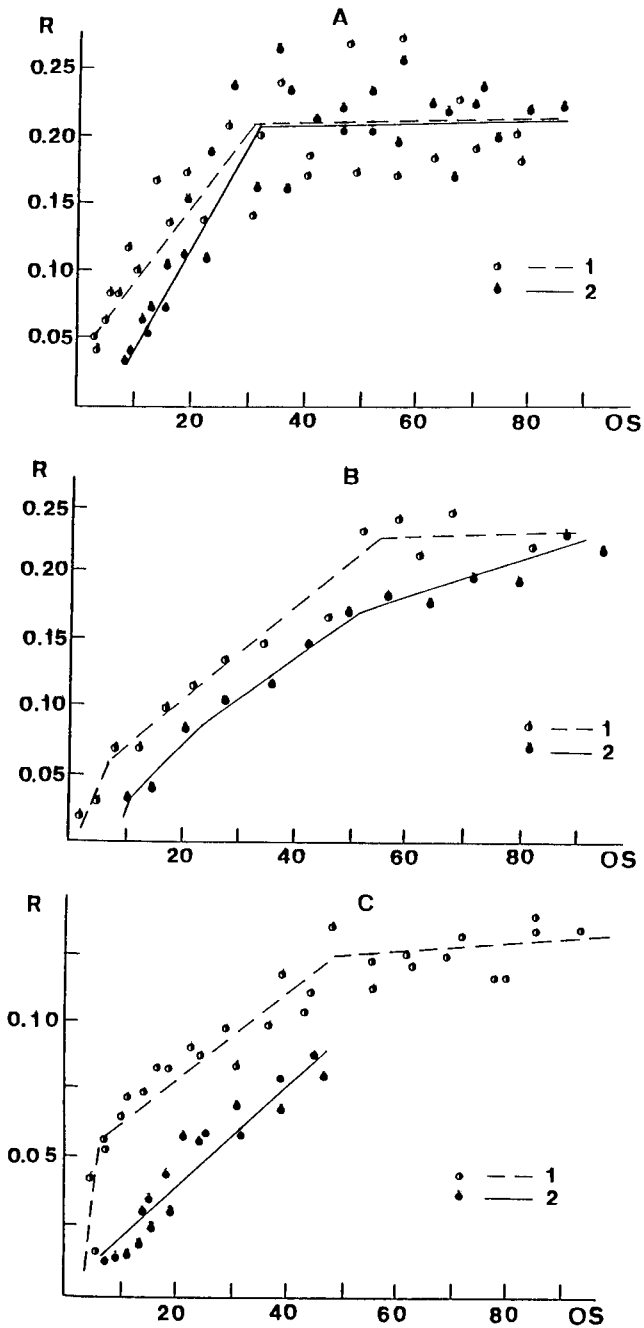
Fig. 1. The relationships between respiration rate (RR, ml O/g* h) of aquatic insects and oxygen concentration (OS, percent of saturation) in a respirometer in running (1) and still (2) water: A – *Cinygmula grandifolia*, B – *Skwala pusilla*, C – *Stenopsyche marmorata*.

Most aquatic insects are able to execute more or less effective respiratory movements to move water over the body surface. If these movements are not effective enough actual water movement is required to maintain the necessary level of RR of the animals producing a sufficient rate of diffusion through the respiratory surface. Thus, one may conclude that survival of aquatic insects at low OS under stagnant conditions is constrained by their ability to produce effective respiratory movements.

In our experiments all the species produced energetic respiratory movements at low OS in both series of experiments. But the effectiveness of the movements was different. The larvae of *S. grandifolia* were able to maintain the broad "oxygen adaption zone" in experiments both "with" and "without current" (Fig. 1a). This means that their respiratory movements were effective and they did not need fast flowing water to maintain the necessary rate of diffusion across the body surface.

In the experiments with *S. pusilla* larvae the situation was different. The RR of the animals in the series "with current" was markedly higher than in series "without current". This indicated that the respiratory movements of *S. pusilla* were unable to provide a sufficient rate of diffusion in still water.

With these observations in mind it is easy to explain the difference in the relationships between RR and OS of these larvae in still and running waters. According to the relationships in the series "with current" *S. pusilla* larvae would be considered "non-conformers", but they should be considered as "conformers" in the series "without current" (Fig. 1b). This contradiction is resolved if one assumes that the RR rate of animals in still water at the 100% OS was the maximum rate of respiration in the conditions of the respiration bottle. The increase in RR of animals when current was applied led to the respiration at 55-60% "with current" being equal to that at 100% when there was no current. Thus, in a current, a maximum rate was attained at 55-60% OS.

In *S. marmorata* the difference between RR of larvae in still and running waters was even more striking (Fig. 1c).

Therefore, in our experiments the larvae of *C. grandifolia* produced the most effective respiratory movements and the larvae of *S. mamorata* produced the least effective ones. It is difficult to arrive at the exact reasons for these differences, but the effectiveness of respiratory movements seems to be correlated with the development of tracheal gills. Larvae of *grandifolia* have well developed gills, larvae of *S. pusilla* have only a pair of small gills, and larvae of *S. marmorata* have no gills at all.

As was shown above, the water flow markedly influenced the sensitivity of larvae of *S. pusilla* and *S. marmorata* to oxygen depletion. A similar result was obtained previously on stonefly larvae of *Megarcys ochracea* (Klap.) (Golubkov and Tiunova, 1989). In a set of experiments carried out by the same method as used for this paper the RR of these animals was about 20% higher and the oxygen adaptation zone was about 12,5% of OS broader in the series "with current" than in the series "without current".

The same result was achieved indirectly by Philipson (1954), who studied the dependence of the frequency of respiratory movements of Trichoptera larvae upon the OS in a respirometer at various intensities of stirring of the water. He concluded that water flow greatly reduced sensitivity of rhephilous insects to oxygen depletion, as was indicated by decrease of the frequency of respiratory movements.

The effectiveness of respiratory movements of the species which we investigated was correlated with their microdistribution along the bed of Kedrovaja river. Larvae of *S. marmorata* and *S. pusilla* occupy sections with rapid current; in contrast, the larvae of *C. grandifolia* occupy sections with relatively weak water flow, and also sections with rapid current but under stones.

Thus, one may assume that the distribution of the larvae of *S. marmorata* and *S. pusilla* is constrained by their ability to take up oxygen from slow-flowing water. It should be also pointed out, that they are not very sensitive to oxygen depletion and their oxygen adaptation zone is rather broad in flowing water (Fig. 1b, c).

It seems very important to rank rheophilous species of aquatic insect by their relative ability to take up oxygen in slow and rapid waters. Generalizations of this kind are beyond the scope of this paper but some preliminary comments are possible.

As was shown in early work by Dodds and Hisaw (1924), the adaptation of mayfly nymphs to life in rivers with fast current was followed by flattening or rounding of the body. The species with flattened bodies mostly creep into narrow crevices under stones. Only a very few highly specialized genera (like *Iron*) can withstand fast-flowing water. As a rule they have more or less well developed tracheal gills and are able to produce effective respiratory movements.

Another direction of specialization among mayfly nymphs to swift-flowing waters was the development of a stream-lined form of body, which was followed by progressive reduction of gill lamellae (Dodds and Hisaw, 1924). The typical representatives of this development are species of *Baëtis,* some of which can withstand a very strong flow of water.

Our previous studies have shown that mayfly larvae of the first group (with flattened body) hiding themselves beneath the stones or occupying sections of the river with slow current have well developed gills and execute effective res-piratory movements. They are able to maintain a constant level of RR over a wide range of OS (about 50 - 100%) in still water (Golubkov and Tiunova, 1989). The experiments with *C. grandifolia* presented in this paper show that the rela-tionships between the RR of species of this group and OS does not depend upon water flow. These species are usually referred to as non-conformers.

Another category would be species of the second line of adaptation to life in running waters. The ability of the species with reduced gill lamellae to mantain a constant level of RR within a broad range of OS probably depends very much upon the water flow. In still water they have no oxygen adaptation zone and are therefore conformers, but in running waters at least some of them have this zone

and can find a range of OS where they can survive.

We think that these speculations are valid also to some extent for stonefly larvae. In our experiments with *M. ochracea* the lower limit of oxygen adaptation of these animals was about 40% of OS in the series "with current" and about 50% in the series "without current" (Golubkov and Tuinova, 1989). So the sensitivity of this species does not depend very much upon the water flow. But in experiments with *S. pusilla* presented here current was very important to maintain the constant level of RR within a broad range of OS.

Thus, it is logical to assume that distribution patterns of the first group of species, which avoid water flow, are less dependant on the OS in slow-flowing water than are those in the second one, which expose themselves to current. But distribution patterns of the second group are constrained by their ability to consume oxygen from the water. For example, if one assumes that OS in a particular river will decrease for some reason from 100 to 70%, most of the first group species will be unaffected, but the second group will be stressed. The most probable response of this group will be their disappearance from sections of river with relatively slow current but the continuation of their existence, or perhaps an increase in their numbers, in sections with fast current.

Among caddisfly larvae the situation is greatly complicated by their ability to manipulate the substratum, and this has led to a great variety in their reactions to oxygen depletion (Williams *et al.*, 1987).

It would, though, be wrong to think that all rheophilous species of mayflies belonging to these two groups may survive well in slow or in fast water under slight decreases of OS. For example, the mayfly *Ameletus cedrensis* Sinitshenkova shows quite different adaptations. Larvae of *Ameletus* swim well and have some morphological features that favour swimming (Dodds and Hisaw, 1924). One of them is the reduction of gill lamellae. In Kedrovaja river these larvae never occur in sites with fast current but only near the bank in places with slow or no flow where they occupy the upper surface of stones. They are typical conformers (Golubkov and Tiunova, 1989). Therefore, adaptations for fast swimming, but not for living in fast-flowing waters, have led to conformism of this species. The larvae of *A. cedrensis* would be very sensitive to oxygen depletion for they have no ability to displace to faster flowing water; they have no adaptations to withstand the current. It is also difficult to imagine, that they would be able to move faster to ventilate their respiratory surfaces, and this may account for the sensitivity of this species to oxygen depletion.

CONCLUSIONS

The problems of maintaining a necessary level of RR in flowing and still water seem to constrain the distribution patterns of aquatic insects in running water. Some species avoid a current hiding beneath the stones or occupying places with slow current. Our experiments with *C. grandifolia* have shown that larvae of this

group of species are able as a rule to execute effective respiratory movements and to maintain a constant level of RR over a fairly wide range of OS in both running and still water.

Another group of species exposing themselves to current are not as a rule able to maintain a constant level of RR in still water by executing effective respiratory movements. They are usually classed as conformers, but as has been shown in experiments with *S. pusilla,* at least some of them have a constant level of RR in fast flowing water. Therefore, a decrease in OS in water should reduce their distribution in sections of river with relatively slow-flowing water, but would not do so in fast flowing water.

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