METABOLIC RATES OF EPHEMERID NYMPHS FROM SWIFTLY FLOWING AND FROM STILL WATERS

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I. INTRODUCTION.

It was shown in 1933 by Fox and Simmonds that certain species of mayfly nymphs (*Baetis rhodani*) and caddis larvae (*Hydropsyche* sp.) from a swift stream have a considerably higher oxygen consumption than nearly related and equal sized ephemerids (*Chloeon dipterum*) and trichopterids (*Limnophilus vittatus*[1]) from a pond, and that, within the confines of a single species of isopod Crustacea (*Asellus aquaticus*), individuals from a swift stream consume more oxygen than animals from sluggishly flowing water. The oxygen uptake was in each case measured under standard and similar conditions.

We have now obtained further evidence of the same phenomenon with other species of ephemerids and we have studied the comparative survival of nymphs in low concentrations of dissolved oxygen. The new results are reported below.

Two small species were studied, namely *Coenis* sp. and *Ephemerella ignita*. *Coenis* was found clinging to *Lemna* floating on the same pond at Alvechurch, Worcestershire, from which *Chloeon* had previously been taken. *Ephemerella* occurred on submerged roots in the same stream at Blakedown, Worcestershire, that harbours *Baetis*, but in less rapidly flowing water than the latter. The oxygen consumption of *Coenis* and *Ephemerella* was measured on the same day that the animals were caught.

Three large species were also studied and compared with one another. These were *Ephemera vulgata*, *E. danica* and *Ecdyonurus venosus*. Nymphs of the first-named species were found burrowing in mud at the edges of a small pond near Newdigate in Surrey. *Ephemera danica* was found burrowing in sand in a stream at Alvechurch and in another at Frankley in Worcestershire. *Ecdyonurus* was taken under stones in the rapid waters of the stream at Frankley.

Before being used for experiments, either on oxygen consumption or on survival, *Ephemera vulgata*, *E. danica* and *Ecdyonurus venosus* were kept for one night in the laboratory in still water taken from their own habitats. Previous to this treatment, *Ephemera vulgata* had arrived from Surrey by post, wrapped in damp moss.

[1] Fox and Simmonds (1933) called this larva *Molanna* sp., but subsequent identification of the imago has shown that it is really *Limnophilus vittatus*.

For experiments on survival (made in December), *Chloeon dipterum* was taken from a pond at Selly Park, Birmingham, and *Baetis rhodani* from the swift stream at Blakedown.

The alkali reserves of the waters were as follows: Alvechurch pond, 0·0028 N; Alvechurch stream, 0·0048 N; Blakedown stream, 0·0029 N; Cambridge tap water, 0·0044 N; Frankley stream, 0·0038 N; Newdigate pond, 0·0017 N; Selly Park pond, 0·0020 N.

II. OXYGEN CONSUMPTION.

Oxygen consumption was measured with a Barcroft manometer[1] at 10° C. Of the smaller species 100 individuals, and of the larger 5–15, were used for each experiment. The results are expressed as c.mm. oxygen at N.T.P. and dryness (Dixon, 1934) per gram dry weight per hour. The animals were either anaesthetised in 0·5 per cent. urethane, from which they completely recovered after the experiments,[2] or, in other experiments, they were not anaesthetised.

The results, which are shown in Tables I–III, confirm and extend the conclusions of Fox and Simmonds (1933); species from rapidly flowing water have a higher rate of metabolism than those from stagnant water, both being measured under identical conditions. With *Ephemera* and *Ecdyonurus* this has been demonstrated both with anaesthetised and unanaesthetised animals. With these animals a further interesting point appears from Tables II and III: *Ephemera vulgata*, found burrowing in mud in a stagnant pond, has a lower oxygen uptake than *E. danica*, found burrowing in sand in a stream.

Table IV summarises all the available data, namely those from Fox and Simmonds (1933) and those in the present paper.

Table I. *Oxygen consumption at* 10° C. *of small ephemerid nymphs in* 0·5 *per cent. urethane.*

Species	Habitat	Exp. no.	Mean dry weight of 100 animals mg.	Date	Oxygen consumption c.mm./gm./hour
Coenis sp.	Pond	1	89	June 22	230
		2	118	,, 22	288
		3	135	,, 27	321
		4	135	,, 28	321
					Mean 290
Ephemerella ignita	Stream	1	72	June 12	1116
		2	74	,, 12	929
		3	144	July 4	805
					Mean 950

[1] Throughout this investigation, and that of Fox and Simmonds (1933), the Barcroft apparatus was shaken at a uniform rate, namely thirty complete excursions per minute, the extent of each excursion being four centimetres.

[2] Dr O. Löwenstein, working in this laboratory, found that the nymphs of *Rithrogena semicolorata* from Frankley were rapidly killed by 0·5 per cent. urethane. This precluded a comparison of their oxygen consumption with that of *Ecdyonurus* and *Ephemera*. It is remarkable that animals so closely related as *Rithrogena* and *Ecdyonurus* should show such different sensitivities to a narcotic.

Table II. *Oxygen consumption at* 10° C. *of large ephemerid nymphs in* 0·5 *per cent. urethane.*

Species	Habitat	Exp. no.	Mean dry weight of one animal mg.	Date	Oxygen consumption c.mm./gm./hour
Ephemera vulgata	Burrowing in mud in pond	1	13	April 7	300
		2	13	,, 7	283
		3	13	,, 7	250
					Mean 278
Ephemera danica	Burrowing in sand in stream	1	12	April 3	442
		2	12	,, 3	401
		3	12	,, 3	410
		4	9	Oct. 17	358
		5	9	,, 17	350
		6	9	,, 17	274
		7	9	,, 19	369
		8	9	,, 19	355
		9	9	,, 19	389
		10	22	,, 30	486
		11	22	,, 30	315
		12	22	,, 30	293
					Mean 370
Ecdyonurus venosus	Under stones in swift stream	1*	6	March 7	590
		2*	6	,, 7	451
		3*	6	,, 18	627
		4*	6	,, 18	759
		5	7	April 11	690
		6	7	,, 11	505
					Mean 604

* These experiments were done in Frankley stream water, the remainder in Cambridge tap water.

III. SURVIVAL IN LOW OXYGEN CONCENTRATIONS.

When the amount of dissolved oxygen is progressively lowered, there comes a point at which the gill movements of *Ephemera* and *Ecdyonurus* nymphs cease. This is a precursor of death and is a convenient end-point for studying the lowest oxygen concentrations which the different animals can support.

Ephemera vulgata, *E. danica* and *Ecdyonurus* nymphs were put, ten at a time, into 100 c.c. stoppered bottles of Cambridge tap water containing amounts of dissolved oxygen only slightly greater than those at which gill movements cease. The bottles were put into a thermostat at 15° C. and were turned upside down once every 5 min. to stir their contents. Within 1–3 hours the animals, by their respiration, had reduced the oxygen concentration to the critical value. As soon as the gills ceased to beat, a sample of the water was removed and its oxygen analysed by the Winkler method, using the modification of Ellis (1934). Incidentally, it was found in all cases that the stoppage of gill movements by this means was reversible; the animals recovered fully in aerated water.

During the experiments carbon dioxide accumulated in the bottles, but only to a small extent. This is shown by the following controls, which were made on each

Table III. *Oxygen consumption at* 10° C. *of large ephemerid nymphs, unanaesthetised.*

Species	Habitat	Exp. no.	Mean dry weight of one animal mg.	Date	Oxygen consumption c.mm./gm./hour
Ephemera vulgata	Burrowing in mud in pond	1	13	April 7	826
		2	13	,, 7	695
		3	13	,, 7	698
					Mean 740
Ephemera danica	Burrowing in sand in stream	1	12	April 3	862
		2	12	,, 3	720
		3	12	,, 3	807
		4	9	Nov. 2	827
		5	9	,, 2	837
		6	9	,, 2	921
					Mean 829
Ecdyonurus venosus	Under stones in swift stream	1*	6	March 6	1005
		2*	6	,, 6	1269
		3*	6	,, 6	1460
		4*	6	,, 6	1242
		5*	6	,, 18	1270
		6*	6	,, 18	1406
		7	7	April 11	1549
		8	7	,, 11	1370
					Mean 1321

* These experiments were done in Frankley stream water, the remainder in Cambridge tap water.

occasion. Ten other individuals were put into a 100 c.c. bottle of fully aerated Cambridge tap water which was stoppered and kept at 15° C. When the gill movements had ceased in the water with low oxygen tension, the maximum *p*H decrease in the control bottles was from 7·9 to 7·4, and there was no alteration in the gill movements.

The concentrations of dissolved oxygen at which the gills ceased to beat were found to be as follows:

Ephemera vulgata: 0·22, 0·19, 0·25 c.c. per litre—mean 0·22.
E. danica: 0·45, 0·48, 0·37, 0·30, 0·16, 0·16 c.c. per litre—mean 0·32.
Ecdyonurus venosus: 0·70, 0·66, 0·75, 0·70 c.c. per litre—mean 0·73.

It is seen that both species of *Ephemera* can survive in water of a lower oxygen content than *Ecdyonurus*.

Experiments were also made to test the survival at low oxygen concentrations of the nymphs of *Chloeon dipterum* and *Baetis rhodani*. In this case the time factor in survival was studied. In each experiment five animals were put into 500 c.c. water of known low oxygen content in a stoppered bottle and the time was taken until death occurred. The relatively large volume of water ensured that the animals' respiration caused only an inappreciable change in oxygen or carbon dioxide content of the water during an experiment. The respective natural waters of the

Table IV. *Mean oxygen consumptions at* 10° C. *of anaesthetised fresh-water arthropods from different habitats.*

Series	Type of animal	Species	Mean dry weight of 10 animals mg.	Habitat	Anaesthetic	Mean oxygen consumption c.mm./gm./hour
1	Isopod crustacean	*Asellus aquaticus*	53	Slow stream	2 % urethane	505†
		Do.	47	Swift stream	Do.	863†
2	Trichopterid larvae	*Limnophilus vittatus**	46	Pond	0·25 % chloretone	511†
		Hydropsyche sp.	54	Swift stream	Do.	770†
3	Small ephemerid nymphs	*Chloeon dipterum*	3	Pond	0·5 % urethane	606‡
		Baetis rhodani	3	Swift stream	Do.	2571†
4	Small ephemerid nymphs	*Coenis* sp.	11	Pond	Do.	290
		Ephemerella ignita	10	Stream	Do.	950
5	Large ephemerid nymphs	*Ephemera vulgata*	130	In mud, in pond	Do.	278
		Ephemera danica	143	In sand, in stream	Do.	370
		Ecdyonurus venosus	65	Swift stream	Do.	604

* See footnote to p. 179.
† Calculated from Fox and Simmonds (1933).
‡ This is the mean of 600, given by Fox and Simmonds (1933), and 613 subsequently determined (June 1933) for animals from the pond at Selly Park.

Table V. *Survival of* Chloeon *and* Baetis *nymphs in water deficient in oxygen.*

Chloeon dipterum (from pond)			*Baetis rhodani* (from swift stream)		
Exp. no.*	Oxygen c.c./litre	Time of survival min.	Exp. no.*	Oxygen c.c./litre	Time of survival min.
1	1·1	129	1	3·5	33
2	0·9	131	2	3·5	33
3	0·9	100	3	3·0	30
4	0·8	122	4	2·9	16
5	0·8	90	5	2·4	6
			6	2·3	13
			7	2·2	11
			8	1·9	5
			9	1·8	4

* This does not give the order in which the experiments were done.

two species were used, and the temperature was 15° C. It is not possible in this case to use a cessation of gill movements as an end-point, for in *Chloeon* the gills beat intermittently, and the gills of *Baetis* do not beat. The moment of death, indicated by the animals turning on their back and no longer responding to stimulation by shaking the bottle, was taken as the end-point. The results, shown in Table V, extend the preliminary experiments of Fox and Simmonds (1933, Table IV). It is clear that the still-water form is much more resistant to oxygen-lack than the species from running water. This is correlated with the lower oxygen consumption of the former (*Chloeon dipterum* 606, *Baetis rhodani* 2571 c.mm./gm./hour, see Table IV).

IV. SUMMARY.

1. The oxygen consumptions of the small ephemerid nymphs *Ephemerella ignita* and *Coenis* sp. are (anaesthetised at 10° C.) 950 and 290 c.mm./gm./hour. Their habitats are respectively a stream and a pond.

2. The oxygen consumptions of the large ephemerid nymphs *Ecdyonurus venosus*, *Ephemera danica* and *E. vulgata* are (anaesthetised at 10° C.) 604, 370 and 278 c.mm./gm./hour. They live, respectively, under stones in a swift stream, burrowing in sand in a stream, and burrowing in mud in a pond.

3. *Ecdyonurus venosus* is less resistant to oxygen deficiency than *Ephemera danica* and *E. vulgata*; and *Baetis rhodani* (swift stream) is less resistant than *Chloeon dipterum* (pond).

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