THE OXYGEN CONSUMPTION OF EPHEMERID NYMPHS FROM FLOWING AND FROM STILL WATERS IN RELATION TO THE CONCENTRATION OF OXYGEN IN THE WATER

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(With One Text-figure)

Fox & Simmonds (1933) and Fox *et al.* (1935) have shown that certain may-fly nymphs, a caddis larva and an isopod from swift streams have a higher oxygen consumption than nearly related forms from still waters or slow-flowing streams. Their results were summarized in Table IV[1] of Fox *et al.* (1935). It has since been shown by Washbourn (1936) that the oxygen consumption of trout fry reared in swiftly flowing water is greater than that of fry reared in slow water.

Wolsky & Holmes (1933) found the oxygen consumptions of four individuals of the crayfish *Astacus leptodactylus* Eschscholtz, from Lake Balaton, to be 90, 103, 104 and 105 mg. of oxygen per kg. of animal per hour at 19–21° C., the animals weighing 16, 22, 36 and 64 g. respectively. The mean of these values for oxygen consumption is 101. Without studying the problem we are now considering, Wolsky (1934) later found that the oxygen consumptions of seven individuals of *A. torrentium* (Schrank), living in a swift stream in Hungary, were 160, 188, 157, 157, 170, 102 and 137 mg. oxygen per kg. of animal per hour at 19–21° C., the animals weighing 8, 8, 15, 17, 17, 21 and 32 g. respectively. The mean of these values for oxygen consumption is 153. The oxygen consumption of *A. torrentium* is thus 50 per cent greater than that of *A. leptodactylus*, and the relation between oxygen consumption and weight suggests that habitat, not size, was responsible for this difference.

The species of ephemerid nymphs which we have studied were the following. *Cloëon dipterum* L. from the pond at Selly Park, Birmingham; *Ephemera vulgata* L. from a pond at Beam Brook, Newdigate, Surrey;[2] *Leptophlebia vespertina* L. and *L. marginata* L. from Lake Windermere; *Baëtis scambus* Eaton and *Baëtis* sp. from swift streams at Alvechurch, Worcestershire, and at California, near Birmingham. *B. scambus* were taken from the Alvechurch stream in May shortly before emergence. The mean dry weight of ten individuals was 30 mg. *Baëtis* sp. were small nymphs

[1] There are two misprints in the table: the weight of ten animals, both of *Cloëon* and *Baëtis*, should be 30 mg., not 3 mg.

[2] We have to thank Mr R. S. A. Beauchamp and Mr L. Haig for sending the *Leptophlebia* and the *Ephemera* to Birmingham, and Mr N. D. Riley for identifying *B. scambus* and *L. vespertina*.

from both streams, selected for uniformity of size, the mean dry weight of ten individuals being 13 mg. They may be young stages of *B. scambus*. *Baëtis* sp. was

Table I. *The oxygen consumption of* Baëtis *sp.*

Exp. no.	Date	Mean dry weight of 10 animals mg.	Oxygen concentration c.c./l.		Oxygen consumption c.mm./g./hr.	
			In exp.	Mean	In exp.	Mean
1	June 24	10	14·2		3190	
2	,,	10	14·2		3200	
3	,,	8	14·2		3540	
4	,,	9	14·2		3510	
5	,,	10	14·3		3050	
6	June 26	9	15·0		4200	
7	,,	8	15·1	14·6	3490	4000
8	,,	9	15·1		4390	
9	,,	9	15·1		4060	
10	July 31	11	14·3		5190	
11	,,	11	14·5		4720	
12	,,	12	14·3		4400	
13	,,	13	14·5		4240	
14	June 16	12	11·9		3800	
15	,,	12	11·9		4480	
16	,,	12	12·0		3590	
17	,,	13	12·0		3790	
18	,,	11	11·9		3550	
19	July 1	10	12·4		4380	
20	,,	10	12·5	12·3	4250	4100
21	,,	10	12·4		3810	
22	July 29	11	12·8		4270	
23	,,	11	12·7		4170	
24	,,	10	12·7		4240	
25	,,	10	12·7		4850	
26	Oct. 29	14	8·0		2740	
27	Oct. 30	15	7·9		2620	
28	,,	15	7·9		2650	
29	,,	15	7·7		2360	
30	Nov. 1	15	7·9		2850	
31	Nov. 9	21	7·9		2610	
32	Nov. 13	22	7·9		2260	
33	,,	15	7·9	7·7	2680	2700
34	May 16	16	7·3		2280	
35	,,	14	7·3		3610	
36	,,	12	7·4		3520	
37	May 19	15	7·4		2570	
38	,,	16	7·4		2560	
39	,,	15	7·4		2510	
40	Nov. 7	23	5·5		1770	
41	,,	20	5·3	5·3	1660	1670
42	,,	22	5·1		1580	
43	Nov. 5	15	4·0	4·0	1330	1350
44	,,	19	4·0		1370	
		Mean 13				

found in the rapid water in the middle of the streams; our specimens of *B. scambus* were taken in less swift water near the banks of the stream.

The alkali reserves of the waters in which the animals lived were as follows:

Windermere, 0·0003 *N*; Newdigate, 0·0017 *N*; Selly Park, 0·0020 *N*; California, 0·0027 *N*; Alvechurch, 0·0048 *N*.

All experiments were done at 10° C., on the day following that on which the animals arrived in the laboratory. The animals were not anaesthetized. For each set of experiments an appropriate quantity of sodium bicarbonate was added to Birmingham tap water (which has an alkali reserve of 0·0003 *N*) to bring it to the normality of the natural water in which the particular species lives. The water was then either saturated with air at 10° C., or nitrogen or oxygen was passed through it until it had approximately the required oxygen content. This was done by passing the gas through a measured volume of water at a known rate for a previously determined time, the rate of flow of the gas being measured with Beckett's (1917) glass

Table II. *The oxygen consumption of* Baëtis scambus

Exp. no.	Date	Mean dry weight of 10 animals mg.	Oxygen concentration c.c./l.		Oxygen consumption c.mm./g./hr.	
			In exp.	Mean	In exp.	Mean
1	May 9	28	12·1		1620	
2	,,	26	12·5		1660	
3	,,	31	13·3	12·8	2230	1870
4	,,	30	12·8		1550	
5	,,	28	13·1		2310	
6	May 10	30	7·4		2230	
7	,,	32	7·3		2150	
8	,,	28	7·4		1790	
9	May 12	31	7·3		1670	
10	,,	28	7·4	7·4	1750	1870
11	,,	31	7·4		1390	
12	,,	31	7·4		1470	
13	May 19	30	7·4		2200	
14	,,	31	7·4		2160	
15	May 27	28	4·9		1520	
16	,,	31	4·9		1800	
17	,,	33	4·9	4·9	1570	1700
18	,,	30	4·9		1840	
19	,,	33	5·0		1780	
		Mean 30				

meter. For each experiment the prepared water was siphoned into a small wide-mouthed bottle provided with a stopper, and a sample of the water was taken for analysis of its oxygen content. A number of animals was put in the bottle, which was then stoppered and placed in a thermostat. Every 5 min. the bottle was turned upside-down sharply to stir the water inside it. Each experiment lasted 1–2 hours, the bottle being of such a size that the oxygen content of the water was reduced by about 10–15 per cent in that time. At the end of the experiment a further water sample was taken from the bottle and analysed for oxygen, after which the total amount of water in the bottle was measured. The animals were then dried at 110° and weighed.

In the earlier experiments, oxygen was analysed by Nicloux's (1930) modification of the Winkler method. The procedure can be simplified without loss of accuracy by having a simple analysis tube in place of Nicloux's λ-tube. In later experiments a much more convenient variety of the Winkler method due to van Dam (1935) was used, which requires only 1·5 c.c. water for analysis. We improved van Dam's syringe-pipette by replacing the metal collar with a pair of lock-nuts, the thread of the screw being continued higher up the axis of the screw to accommodate the lock-nuts. The dead space of the syringe-pipette was first filled with 40 per cent

Table III. *The oxygen consumption of* Leptophlebia vespertina

Exp. no.	Date	Mean dry weight of 10 animals mg.	Oxygen concentration c.c./l.		Oxygen consumption c.mm./g./hr.	
			In exp.	Mean	In exp.	Mean
1	Feb. 15	29	7·6	7·5	2220	2130
2	,,	28	7·5		2310	
3	,,	28	7·6		2180	
4	,,	27	7·5		2240	
5	,,	26	7·5		2040	
6	,,	28	7·5		1760	
7	Feb. 13	34	4·9	4·9	1940	1810
8	,,	32	4·9		1690	
9	Feb. 22	29	4·0	4·0	2190	1970
10	,,	42	3·9		1860	
11	,,	28	4·0		2080	
12	,,	42	4·0		1830	
13	,,	43	4·0		1870	
14	Feb. 13	32	2·5	2·5	1340	1780
15	,,	26	2·6		2220	
16	Feb. 29	32	2·1	2·0	1770	1490
17	,,	36	2·1		1940	
18	,,	36	2·0		1420	
19	,,	40	2·0		1320	
20	Mar. 15	48	2·0		830	
21	,,	45	2·0		1880	
22	,,	49	2·0		1460	
23	,,	44	2·0		1280	
24	Mar. 6	54	1·5	1·7	990	770
25	,,	49	1·5		530	
26	,,	56	1·8		1420	
27	,,	54	1·8		580	
28	,,	56	1·9		470	
29	,,	54	1·9		620	
		Mean 38				

manganous chloride solution, then, after having been rinsed, the nozzle of the syringe was plunged into the experimental water and the syringe filled with this water. The alkaline iodide solution (strength: 33 g. NaOH + 10 g. KI in 100 c.c.) was then taken in and the syringe shaken. The oxygen content of the reagents in the quantities used is negligible. Three minutes were allowed for oxygen absorption, and then *o*-phosphoric acid was drawn into the syringe to dissolve the precipitate. The iodine liberated was titrated with standard sodium thiosulphate, using a 0·1 c.c. Reyberg (1925) burette. This method is accurate to 1 per cent.

Table IV. *The oxygen consumption of* Leptophlebia marginata

Exp. no.	Date	Mean dry weight of 10 animals mg.	Oxygen concentration c.c./l.		Oxygen consumption c.mm./g./hr.	
			In exp.	Mean	In exp.	Mean
1	Mar. 15	190	7·7	7·7	2320	1390
2	,,	190	7·8		1830	
3	,,	210	7·8		1000	
4	Mar. 23	200	7·7		1640	
5	,,	230	7·7		1310	
6	,,	190	7·7		1870	
7	Apr. 22	260	7·6		1060	
8	,,	280	7·6		1080	
9	,,	370	7·6		930	
10	,,	340	7·6		1130	
11	,,	360	7·6		670	
12	,,	320	7·6		880	
13	Apr. 29	300	7·7		1780	
14	,,	260	7·7		1780	
15	,,	260	7·7		1780	
16	,,	230	7·7		1290	
		Mean 260				

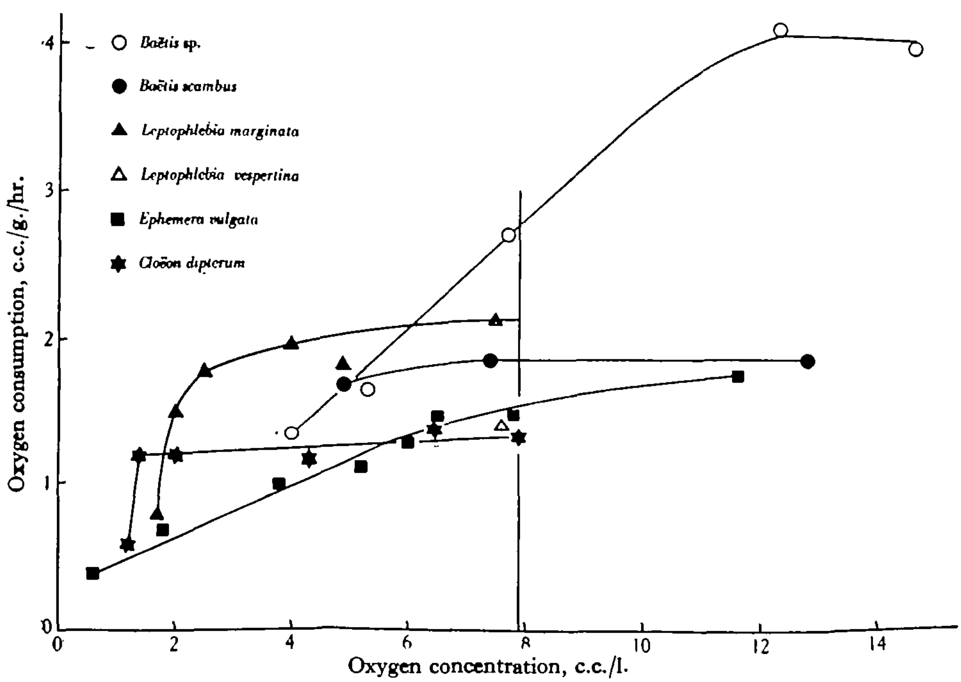

Fig. 1. Oxygen consumptions at 10° C. of ephemerid nymphs at various oxygen concentrations, from the data of Tables I–VI. The vertical line at the oxygen concentration of 7·9 c.c. per litre marks the oxygen content of water in equilibrium with the atmosphere.

The experimental data are given in Tables I–VI[1] and Fig. 1. The curves show that, in air-saturated water, most oxygen is consumed by the small nymphs of *Baëtis* sp. The larger *B. scambus*, of which *Baëtis* sp. may be young forms, use much less oxygen. The pond species *Cloëon dipterum* and *Ephemera vulgata* use less oxygen

Table V. *The oxygen consumption of* Ephemera vulgata

Exp. no.	Date	Mean dry weight of 10 animals mg.	Oxygen concentration c.c./l.		Oxygen consumption c.mm./g./hr.	
			In exp.	Mean	In exp.	Mean
1	Apr. 23	260	11·6		2250	
2	,,	270	11·5		1520	
3	,,	270	11·5	11·6	1570	1770
4	,,	200	11·6		1730	
5	,,	190	11·7		1760	
6	Dec. 12	170	7·9		1470	
7	,,	180	7·8	7·8	1450	1470
8	,,	150	7·8		1480	
9	,,	150	7·9		1490	
10	Feb. 14	190	6·5		1960	
11	,,	180	6·5		1890	
12	,,	180	6·5		1820	
13	Feb. 20	170	6·3	6·5	1210	1470
14	,,	190	6·4		1020	
15	Apr. 10	200	6·5		1390	
16	,,	200	6·5		1190	
17	,,	230	6·5		1170	
18	Dec. 17	160	6·0		1340	
19	,,	170	6·0	6·0	1090	1270
20	,,	150	6·1		1390	
21	Mar. 28	170	5·0		1260	
22	,,	180	4·9		1250	
23	Mar. 29	190	5·5	5·2	1150	1110
24	,,	170	5·3		1050	
25	,,	190	5·3		840	
26	Mar. 27	160	4·0		1080	
27	,,	170	4·0	3·8	1060	1010
28	,,	200	3·5		900	
29	Mar. 13	190	2·2		990	
30	,,	200	2·2		810	
31	,,	190	1·7		740	
32	Mar. 20	180	1·6	1·8	710	700
33	,,	200	1·6		670	
34	,,	190	1·6		500	
35	,,	180	1·6		470	
36	Apr. 18	220	0·5		450	
37	,,	240	0·6	0·6	360	370
38	,,	240	0·6		300	
		Mean 190				

than either of the *Baëtis*, as does also *Leptophlebia marginata* from Lake Windermere. *L. vespertina*, however, which is also from Lake Windermere, consumes more oxygen than *Baëtis scambus*.

[1] From a comparison of Table V with Table III of Fox *et al.* (1935) it is seen that the Winkler method used in the present investigation gives higher values for oxygen consumption than the Barcroft manometer used in the earlier investigations.

Table VI. *The oxygen consumption of* Cloëon dipterum

Exp. no.	Date	Mean dry weight of 10 animals mg.	Oxygen concentration c.c./l.		Oxygen consumption c.mm./g./hr.	
			In exp.	Mean	In exp.	Mean
1	Nov. 16	28	7·9		980	
2	,,	29	7·9		1470	
3	,,	31	7·9	7·9	1480	1310
4	,,	25	7·9		1110	
5	,,	27	7·9		1290	
6	,,	28	7·9		1410	
7	May 24	24	5·9		1210	
8	,,	23	5·9		1230	
9	June 5	16	6·2		1560	
10	,,	16	6·2		1630	
11	,,	18	6·1		1370	
12	,,	19	6·1		1320	
13	Dec. 2	31	7·0	6·4	1390	1400
14	,,	27	6·9		1370	
15	Dec. 3	35	6·5		1550	
16	,,	39	6·4		1570	
17	,,	30	6·4		1520	
18	,,	38	6·5		1350	
19	,,	36	6·4		1270	
20	,,	35	6·5		1260	
21	June 7	19	4·1		1010	
22	,,	23	4·1		1010	
23	,,	23	4·1		1050	
24	June 13	20	4·5		1390	
25	,,	20	4·5		1370	
26	,,	20	4·5	4·3	1350	1170
27	June 25	19	3·9		1290	
28	,,	19	3·9		940	
29	Nov. 20	40	4·6		1250	
30	,,	39	4·7		1280	
31	,,	39	4·6		930	
32	,,	32	4·7		1150	
33	June 14	19	2·1		1500	
34	,,	18	2·1		1380	
35	July 3	22	1·8		1470	
36	,,	19	1·8		970	
37	July 5	21	1·9		1390	
38	,,	18	2·1		1060	
39	,,	19	2·1	2·0	950	1180
40	Nov. 21	35	1·9		990	
41	,,	40	1·9		1100	
42	Nov. 25	36	2·1		1020	
43	,,	38	2·2		1230	
44	,,	34	2·1		1210	
45	,,	34	2·1		1110	
46	Nov. 28	37	1·3		1330	
47	,,	35	1·3	1·4	1000	1190
48	,,	30	1·5		1430	
49	,,	32	1·4		1000	
50	June 18	19	1·3		610	
51	,,	17	1·4		490	
52	,,	20	1·4		370	
53	July 16	17	1·3		490	
54	,,	16	1·3	1·2	490	590
55	Nov. 26	38	1·1		770	
56	,,	38	1·1		710	
57	Nov. 28	36	0·9		600	
58	,,	36	1·0		750	
		Mean 26				

Fig. 1 shows that in comparing species in the same genus, the larger form has the lesser oxygen consumption. In air-saturated water, *Leptophlebia marginata* (mean dry weight of ten animals, 260 mg.) uses two-thirds of the oxygen used by *L. vespertina* (38 mg.), and *Baëtis scambus* (30 mg.) uses two-thirds of the oxygen used by *Baëtis* sp. (13 mg.).

It is seen from Fig. 1 that the oxygen consumption of *Baëtis* sp. falls as soon as the oxygen content of the water diminishes, and continues to fall as a linear function of the oxygen concentration. The oxygen consumption of *Baëtis* is not recorded at oxygen concentrations lower than 4 c.c. per litre because the animals die below this concentration (cf. Fox *et al.* 1935, Table V). When the oxygen concentration of the water is raised above that in equilibrium with the atmosphere, the oxygen consumption of *Baëtis* sp. continues to rise, but eventually becomes constant, after it has attained 1½ times its normal value. The larger form, *Baëtis scambus*, however, forms a striking contrast to the small *Baëtis* sp.: between 5 and 12 c.c. oxygen per litre its oxygen intake is almost constant.

In the case of *Ephemera vulgata* the oxygen consumption is seen from Fig. 1 to diminish, as a linear function of oxygen concentration, soon after the oxygen content of the water falls below atmospheric equilibrium, although the line slopes less steeply than that of *Baëtis* sp.[1] Above 7·9 c.c. per litre the oxygen intake of *Ephemera vulgata* rises very little.

Cloëon dipterum forms an extreme contrast to *Baëtis* sp. and *Ephemera vulgata.* From air-saturated water down to an oxygen content of 1·4 c.c. per litre, the oxygen intake of *Cloëon dipterum* is virtually constant. Beneath 1·4 c.c. per litre it falls off steeply.

The oxygen consumption of *Leptophlebia vespertina* somewhat resembles that of *Cloëon dipterum.* It decreases slowly as the oxygen content of the water falls, until 2·5 c.c. per litre is reached, below which there is a sudden drop.

We can now arrange the species studied in the following order, commencing with that which is most dependent on the oxygen content of the environment and ending with one whose oxygen consumption is independent of the oxygen concentration in the water: (1) *Baëtis* sp., (2) *Ephemera vulgata*, (3) *Leptophlebia vespertina* and *Baëtis scambus*, (4) *Cloëon dipterum.* The most dependent species, *Baëtis* sp., lives in streams where the oxygen supply must always be abundant; but so does *B. scambus.* The most independent form, *Cloëon dipterum*, was taken from a pond where the oxygen content falls low at night (unpublished data). If the behaviour of *Cloëon dipterum* is adaptive, however, that of *Ephemera vulgata* is apparently not so, for the latter species was found buried in mud in a pond, yet its oxygen intake drops as soon as oxygen decreases in the water.

[1] A. H. Morgan & J. F. Wilder (*Physiol. Zoöl.* **9**, 1936, 153) measured the oxygen consumption of the nymphs of *Hexagenia recurvata*, a near relation of *Ephemera vulgata*, which lives in similar habitats, confining the nymphs in a closed vessel from which water samples were taken at intervals. They state that "In their rate of oxygen consumption nymphs of *Hexagenia recurvata* are independent of the oxygen tension from 9·75 to 2·34 c.c." But this is not borne out by their Table II, giving oxygen consumption in milligrams (to four significant figures) per gram body weight. At 12·3°, for example, in three successive 5-hour intervals, the oxygen consumed by recently collected nymphs was 5·5, 3·9 and 2·8 mg., the initial oxygen content of the water not, however, being stated.

SUMMARY

The data are best summarized by reference to Fig. 1.

An extreme contrast is presented by *Cloëon dipterum* and *Baëtis* sp. in the relation between oxygen consumption and oxygen concentration in the water. When the oxygen in the water diminishes, the oxygen consumption of *Cloëon dipterum* does not decrease until the oxygen has fallen below one-fifth air saturation, whereas the oxygen consumption of *Baëtis* sp. falls immediately the oxygen in the water decreases. Above air saturation, the oxygen consumption of *Baëtis* sp. rises until it reaches 1½ times its value in nature.

The oxygen consumption of *Baëtis scambus* is almost independent of oxygen in the water, both above and below air saturation.

The oxygen consumption of *Ephemera vulgata* falls soon after the oxygen in the water begins to diminish. Above air saturation it rises slightly.

Leptophlebia vespertina somewhat resembles *Cloëon dipterum*: its oxygen consumption falls slowly until one-third air saturation is reached, below which there is a sudden drop.

There is a relation between oxygen consumption and size of animal. The oxygen consumption of the larger species *Leptophlebia marginata* is lower than that of the smaller species *L. vespertina*, and the oxygen consumption of the larger *Baëtis scambus* is lower than that of the smaller *Baëtis* sp.

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