Respiratory device or camouflage? – A case for the caddisfly

D. Dudley Williams, Annette F. Tavares and Eric Bryant

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Two hypotheses exist as to the function of the tubular cases constructed from silk and debris by caddisfly (Trichoptera) larvae. One proposes that they provide protection for the larvae by camouflaging them against their background or by providing resistance to the jaws of predators. The other proposes that the case acts as an aid to respiration as, by undulating its abdomen, the larva can create a flow of water through the case and over its gills. We measured, in respirometer chambers at 13°C, the uptake of dissolved oxygen by larvae of 22 species of caddisfly representing a variety of habitat types and phylogenetic lines. Oxygen uptake by larvae in their cases was compared with that of larvae without cases and the species fell into three basic groups: in Group A, representing seven families, the cases appeared to confer a respiratory advantage upon the larvae through reduced levels of oxygen uptake and moderation of respiration rates (i.e., by optimizing rather than maximizing oxygen consumption); in Group B, representing two families, the cases appeared to be a disadvantage to respiration (larvae in their cases consumed more oxygen than they did in the absence of their cases); and in Group C, representing the largest family, the Limnephilidae, for most of the species tested the cases appeared to confer no respiratory advantage (no differences between the amounts of oxygen consumed by larvae in their cases and alone). Given the many uses to which silk has been put in the Trichoptera, it seems reasonable to suppose that construction of a tubular case does not dictate a single function across all case-building species. Our data point to a respiratory function in some species but to a non-respiratory function (probably protection from predators) in others, particularly in the Limnephilidae.

D. D. Williams, A. F. Tavares and E. Bryant, Div. of Life Sciences, Scarborough Campus, Univ. of Toronto, 1265 Military Trail, Scarborough, Ontario, Canada M1C 1A4.

Introduction

The larvae of many species of caddisflies (Order: Trichoptera) have portable, tubular, open-ended cases that encircle their bodies, although members of the more primitive families have no case at all except for a shelter fixed to the substrate during the pupal stage. The cases are constructed from a variety of materials, ranging from plant material to sand grains, and are held together by strands of silk spun by the larva. Silk is present even in the most primitive families where it is used primarily for spinning food-capture nets, pupal cocoons and trail-lines (Ross 1964).

Although a rich variety of case types exists among species, the function of the case is not clear. One early

hypothesis was that the case provides protection for the larva by camouflaging it against the local microhabitat (Nielsen 1942). An alternative hypothesis was that the case acts as an aid to respiration as by undulating its body inside the case the larva can create a unidirectional flow of water over its abdominal gills (Milne 1938, Fig. 1). It has been suggested that the latter adaptation has been a major factor in allowing caddisflies to spread from their ancestral cool, running water habitats into standing waters (Wiggins 1977). However, if respiration is the primary reason for case construction, why, as Otto (1982) pointed out, do lotic species, surrounded as they are by water rich in oxygen, expend energy on building cases when other members of the lotic invertebrate community survive without them? If the case truly

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bestows a respiratory advantage upon the larva, it should be measurable. The purpose of this study then was to test the hypothesis that the caddisfly case aids larval respiration and that this adaptation may have allowed an expansion of habitat diversity in this group. This was done by the following means:

- 1) by measuring the oxygen uptake rates of a number of cased caddisfly species representing a variety of habitat types and phylogenetic lines, with measurements being done on both the larva in its case and the larva alone.

- 2) by measuring the lowest oxygen concentrations at which larvae (with and without their cases) could survive.

- 3) by measuring both of the above for a number of caseless caddisfly species for comparative purposes.

Materials and methods

Larvae of 22 species of caddisfly representing different phylogenetic lines were collected from a variety of habitats in southern Ontario. They were held, under natural photoperiod, in tanks of aerated water, supplied with food and natural substrate at 13°C for approximately two weeks prior to experimentation.

The rate of oxygen uptake at various dissolved oxygen concentrations was measured in small, sealed, cylindrical, plexiglas respirometer chambers (18 cm³ or 37 cm³ capacity, depending on the size of the species) filled with dechlorinated tapwater saturated with air at 13°C. Water in the chamber was kept in motion by means of a small magnetic stirrer to ensure uniformity of oxygen tension throughout the chamber. Single, large (fourth or fifth instar) larvae were placed in the chamber in a basket of 2mm mesh fibreglass screening which prevented them from contacting the stir-bar. The chamber was then fitted with a plexiglas lid in which the oxygen electrode (Beckman Oxygen Analyser) was seated, and sealed with petroleum jelly. The entire apparatus was housed in a controlled-temperature chamber at 13°C. Reduction in the oxygen level in the chamber was monitored continuously on a chart recorder set at 60 mm h⁻¹ until the oxygen tension reached a plateau (not shown in the figures) – indicating that the larva had ceased to respire. The larva was then removed, blotted dry, wet-weighed and examined for signs of life (the latter was repeated after the larva had been returned to oxygen-saturated water for 24 h). The rate of oxygen uptake by the larva was calculated at 1 mg l⁻¹ intervals from saturation down to the concentration at which respiration ceased and was expressed in terms of µgO₂ mg⁻¹ wet weight h⁻¹. The above procedure was repeated for each species three times: for the larva in its case, for the larva alone, and for the case alone – as it was found that the microorganisms living on the case surface often respired significant amounts of oxygen and this value had to be deducted from that of the larva in its case. Each of these procedures was replicated with six larva of each species.

Fig. 1. Diagram of the larva of *Phryganea cinerea* with part of the case removed to show the passage of water over its abdomen.

An overall mean oxygen uptake value was then calculated for each species by combining the data from these replicates across all levels of oxygen concentration (see Tab. 1). It is acknowledged that there was little control possible over relative activity levels of the various species while they were in the respirometer chamber and that this may have affected the levels of respiration to some extent. Generally, however, larvae in or out of their cases moved around little. In addition, cased and decased larvae were allowed to settle in oxygen saturated water, after having been removed from their holding tanks, prior to being placed in the respirometer chamber. As the residence time in the chamber spanned 24 h, any diel changes in respiration would have been detected though seasonal changes were not assessed.

Results

The species tested, together with the families to which they belong and the habitat types from which they were collected (habitat categories are based on Wiggins 1977), are listed in Fig. 2. All major habitat types are represented as are most trichopteran families; with six representatives of caseless caddisflies and 16 representatives of cased caddisflies. Plots of oxygen uptake curves for the various species are grouped, according to phylogeny, in Figs 3–8.

The two caseless philopotamid species, *Dolophilodes distinctus* (Walker) and *Chimarra aterrima* Hagen, had oxygen uptake rates that remained relatively constant within species with decreasing oxygen concentration (no differences between means; $p = 0.41$ and 0.59 , respectively, from ANOVA), but that were different between species ($p < 0.05$, from a t-test) (Fig. 3, Tab. 1). They were thus both acting as oxygen regulators with relatively high overall mean oxygen consumption rates (3.88 ± 0.46 and 2.06 ± 0.12 µg mg⁻¹ wet wt h⁻¹, respectively for *D. distinctus* and *C. aterrima*); both species typically inhabit cool streams (Ross 1944).

Hydropsyche sparna Ross and *Diplectrona modesta* Banks, although from different subfamilies within the Hydropsychidae had similar patterns of oxygen uptake, i.e., significantly higher rates at 7.0 mg l⁻¹ and above than at 5.0 mg l⁻¹ and below ($p < 0.05$ from ANOVA fol-

Fig. 3. Oxygen uptake curves of five caseless species of caddisflies belonging to the Hydropsychoidea. (Means $\pm$ 1 SE are shown).

Rhyacophila fuscata (Walker), found in a wide range of streams and rivers (Wiggins 1977), clearly acted as an oxygen conformer when faced with decreasing oxygen concentrations. Its oxygen consumption rate ranged from 0.86–0.35 $\mu\text{g mg}^{-1}$ wet wt h^{-1} (Fig. 4). *Glossosoma nigrum* Banks, a member of the Rhyacophiloidea and thus a relatively primitive cased-caddisfly, is found in cold rapid streams and had a very high rate of oxygen consumption without its case (range 6.0–3.1 $\mu\text{g mg}^{-1}$ wet wt h^{-1}) (Fig. 4). At high oxygen levels, it acted as an oxygen conformer but below 7.0 mg l^{-1} it became an oxygen regulator. In its case, the overall rate of oxygen consumption was significantly less ($p < 0.001$) and was more uniform, indicating that the larva in its case was acting as an oxygen regulator.

Ptilostomis ocellifera (Walker) (Phryganeidae) is a cased species found in a wide range of habitats including cool streams, lakes and temporary ponds (Wiggins 1977). The larva alone was an oxygen regulator at high oxygen concentrations but became a conformer at lower concentrations (Fig. 5). There was a similar pattern when the larva was in its case but the respiration rate was significantly less ($p < 0.001$) being approximately half that of the larva alone. *Banksiola* sp., another phryganeid, showed respiratory response patterns to decreasing oxygen concentration that were very similar to those of *P. ocellifera* (Fig. 5). *Banksiola* is commonly found in lakes, marshes and sluggish streams (Wiggins 1977). The third phryganeid, *Phryganea cinerea* Walker, also found in lakes and marshes, had a signifi-

Tab. 1. Mean oxygen uptake rates and lowest oxygen concentration attained by larval caddisflies with and without their cases.

Species	Family	Mean oxygen uptake rate ($\mu\text{g mg}^{-1}$ wet wt h^{-1})				Significant difference ($p < 0.05$)
		Larva alone ($\bar{x} \pm 1 \text{ SE}$)	n	Larva in case ($\bar{x} \pm 1 \text{ SE}$)	n	
<i>Dolophilodes distinctus</i>	Philopotamidae	3.88 ± 0.46	60	—	—	—
<i>Chimarra aterrima</i>	Philopotamidae	2.06 ± 0.12	40	—	—	—
<i>Parapsyche apicalis</i>	Hydropsychidae	0.44 ± 0.02	60	—	—	—
<i>Diplectrona modesta</i>	Hydropsychidae	3.70 ± 0.24	30	—	—	—
<i>Hydropsyche sparna</i>	Hydropsychidae	1.22 ± 0.07	55	—	—	—
<i>Rhyacophila fuscus</i>	Rhyacophilidae	0.64 ± 0.04	50	—	—	—
<i>Glossosoma nigrior</i>	Glossosomatidae	4.65 ± 0.28	60	0.67 ± 0.12	44	S
<i>Banksiola</i> sp.	Phryganeidae	0.62 ± 0.03	60	0.17 ± 0.02	32	S
<i>Phryganea cinerea</i>	Phryganeidae	0.17 ± 0.01	59	0.25 ± 0.02	60	S
<i>Ptilostomis ocellifera</i>	Phryganeidae	0.59 ± 0.03	60	0.27 ± 0.02	60	S
<i>Ironoquia punctatissima</i>	Limnephilidae	0.56 ± 0.03	60	0.49 ± 0.03	56	NS
<i>Limnephilus rhombicus</i>	Limnephilidae	0.16 ± 0.01	56	0.15 ± 0.01	58	NS
<i>Limnephilus indivisus</i>	Limnephilidae	0.50 ± 0.01	60	0.34 ± 0.01	59	S
<i>Nemotaulius hostilis</i>	Limnephilidae	0.70 ± 0.04	60	0.87 ± 0.15	44	NS
<i>Platycentropus amicus</i>	Limnephilidae	0.31 ± 0.01	58	0.30 ± 0.03	53	NS
<i>Pycnopsyche guttifer</i>	Limnephilidae	0.34 ± 0.01	60	0.27 ± 0.02	59	S
<i>7Pycnopsyche lepida</i> grp.	Limnephilidae	—	—	0.20 ± 0.02	58	—
<i>Lepidostoma vernale</i>	Lepidostomatidae	1.65 ± 0.09	60	0.51 ± 0.04	55	S
<i>Agarodes</i> sp.	Sericostomatidae	1.21 ± 0.08	60	0.20 ± 0.02	40	S
<i>Molanna</i> sp.	Molannidae	0.64 ± 0.03	60	0.29 ± 0.04	55	S
<i>Helicopsyche borealis</i>	Helicopsychidae	1.12 ± 0.12	44	2.73 ± 0.17	56	S
<i>Oecetis</i> sp.	Leptoceridae	2.21 ± 0.15	40	0.62 ± 0.06	46	S

cantly higher ($p < 0.05$) mean rate of oxygen uptake by cased larvae compared with larvae alone (Fig. 5). The graphs indicate that both the larvae alone and in their cases were acting as oxygen regulators above about 4.0 mg l^{-1} but switched to being conformers below that. The mean level of oxygen uptake of de-cased *P. cinerea* was significantly lower than that of de-cased larvae of the other two species of phryganeid ($p < 0.001$). Below an oxygen concentration of 8.0 mg l^{-1} , there was no statistical difference ($p > 0.1$) between the respiration rate of the limnephilid *Ironoquia punctatissima* (Walker) in its case and alone, and the larva responded as an oxygen conformer in both instances (Fig. 5). At oxygen concentrations of 9.0 and 10.0 mg l^{-1} , however, the larva in its case respired significantly less oxygen ($p < 0.05$). This species is typically found in temporary ponds and streams (Williams and Williams 1975).

Similar patterns of respiratory response to decreasing oxygen levels, to *I. punctatissima*, were seen in *Limnephilus indivisus* Walker and *L. rhombicus* L. (Fig. 6) although the mean oxygen consumption levels were significantly less ($p < 0.001$) in the latter. *Limnephilus rhombicus* is found frequently in slow-flowing, spring-fed streams in North America, but in ponds and canals in Europe (Flint 1960). *Limnephilus indivisus* is a temporary pond inhabitant.

Larvae of *Pycnopsyche guttifer* (Walker) (Limnephilidae), both in and out of their cases, were oxygen regulators above 5.0 mg l^{-1} but became oxygen conformers

below this concentration (Fig. 6). Only at lower concentrations was the rate of respiration by the larva in its case less than that of the larva alone. This species has a wide range of habitats, from small, cool streams to the slow-water areas of larger rivers and cool lakes (Williams and Williams 1980, 1981). Larvae of the *P. lepida* (Hagen) group are found in similar habitats to *P. guttifer* (Flint 1960, Williams and Williams 1980) and cased larvae had a similar respiration response curve, however the mean oxygen uptake rate was significantly higher ($p < 0.05$) in *P. guttifer* (Fig. 6; we did not measure the response curve for naked *P. lepida*).

In *Nemotaulius hostilis* (Hagen), a limnephilid caddisfly characteristic of small, weedy ponds and marshes often low in dissolved oxygen (Flint 1960, Wiggins 1977), there was no statistical difference ($p < 0.2$) between the overall mean respiration rates of the larvae in or out of their cases (Fig. 7). This was also true for the limnephilid *Platycentropus amicus* (Hagen) at most oxygen concentrations (Fig. 7); the genus is found in habitats ranging from cool streams to warm ponds (Wiggins 1977). The respiration curve for third instar larvae of *P. amicus* in their cases was similar to that of final instar larvae although the mean respiration rate was approximately twice as great in the earlier instar (Fig. 7) (means different at $p < 0.05$). Larvae of *Lepidostoma vernale* (Banks), found in springs and cold streams (Flint and Wiggins 1961), were oxygen conformers both in and out of their cases with the latter respiring at a rate approxi-

Effect of case*	Lowest oxygen concentration attained (mg l ⁻¹)				Significant difference (p<0.05)	Survival after 24 h. No. larvae used (No. surviving)		Effect of case
	Larva alone ($\bar{x} \pm 1$ SE)	n	Larva in case ($\bar{x} \pm$ SE)	n		Alone	In case	
-	0.04 $\pm$ 0.02	6	-	-	-	6 (0)	-	-
-	0.0	4	-	-	-	3 (2)	-	-
-	0.27 $\pm$ 0.02	6	-	-	-	6 (0)	-	-
-	0.21 $\pm$ 0.04	3	-	-	-	3 (2)	-	-
-	1.30 $\pm$ 0.36	6	-	-	-	6 (1)	-	-
-	0.23 $\pm$ 0.06	5	-	-	-	5 (0)	-	-
+ve	0.05 $\pm$ 0.03	6	0.13 $\pm$ 0.05	3	NS	8 (3)	8 (8)	+ve?
+ve	0.0	5	0.0	4	NS	6 (6)	-	0
-ve	0.0	5	0.06 $\pm$ 0.04	6	NS	some	some	0
+ve	0.10 $\pm$ 0.01	6	0.0	3	S	6 (6)	6 (6)	+ve
0	0.24 $\pm$ 0.01	6	0.10 $\pm$ 0.05	3	S	6 (4)	6 (3)	+ve
0	0.24 $\pm$ 0.01	6	0.03 $\pm$ 0.03	2	S	6 (5)	6 (5)	+ve
+ve	0.14 $\pm$ 0.03	6	0.02 $\pm$ 0.01	3	S	6 (4)	6 (6)	+ve
0	0.39 $\pm$ 0.07	6	0.0	5	S	6 (6)	-	+ve
0	0.0	6	0.0	6	NS	6 (6)	6 (5)	0
+ve	0.0	6	0.13 $\pm$ 0.08	4	NS	6 (0)	6 (1)	0?
?	-	-	0.10 $\pm$ 0.10	5	-	-	-	?
+ve	0.09 $\pm$ 0.03	6	0.0	1	NS	8 (5)	6 (2)	-ve?
+ve	0.0	6	0.0	4	NS	6 (6)	-	0
+ve	0.21 $\pm$ 0.03	6	0.0	5	S	7 (6)	some	+ve
-ve	0.05 $\pm$ 0.05	3	0.05 $\pm$ 0.05	4	NS	9 (5)	6 (6)	+ve?
+ve	0.05 $\pm$ 0.05	4	0.03 $\pm$ 0.02	3	NS	5 (5)	6 (5)	-ve?

* + ve = positive effect; - ve = negative effect

mately three times that of the larvae in their cases (Fig. 7).

Larvae of *Agarodes* sp. (Sericostomatidae), *Molanna* sp. (Molannidae) and *Oecetis* sp. (Leptoceridae) all occur in similar habitats (particularly the edges of lakes and rivers, Wiggins 1977) and had similar respiration curves (Fig. 8); all belong to the leptocerid branch of the Limnephiloidea. For these species, the larvae in their cases respired oxygen at rates that were significantly less ($p < 0.001$) than those seen in the de-cased larvae. The larvae alone appeared to be primarily oxygen conformers, while in their cases they were oxygen regulators. Mean oxygen consumption levels were highest in *Oecetis* sp. The fourth member of the leptocerid branch of the Limnephiloidea, *Helicopsyche borealis* (Hagen) (Helicopsychidae), showed a pattern very similar to *Agarodes* sp. for the larva alone, but the larva in its case consumed oxygen at a significantly higher level (approximately twice; $p < 0.001$) than the de-cased larva (Fig. 8). *H. borealis*, along with other members of the Helicopsychidae, builds a unique spiral-shaped case; it is typically found in running water and in the littoral zone of large lakes (Williams et al. 1983).

Mean oxygen uptake rates for each species are summarized in Tab. 1. In some instances, the amount of oxygen respired was significantly less ($p < 0.05$) when the larva was in its case. In a few species, the larva in its case respired oxygen at a higher rate than when alone. In yet a third group of species, there were no statistical

differences between the amounts of oxygen respired by the larvae alone and in their cases.

Tab. 1 also gives the lowest mean oxygen concentrations attained by the larvae in the respirometer chambers. In some species, the level attained by larvae in their cases was significantly lower ($p < 0.05$) than that attained by de-cased larvae, or they were the same but the percent survival was much higher in the former. In other species, the opposite trend was seen or the two levels were the same.

Discussion

Suggestion that the tubular cases of errant caddisfly larvae enhance respiratory efficiency was made at least as early as 1924 by Dodds and Hisaw. It is indisputable, based on tests with dyes, that water passes through the case, usually from anterior to posterior, and that undulations of the larval abdomen aid this. The three fleshy humps on the first abdominal segment appear to act as spacers to position the abdomen in the centre of the tube and the lateral hair fringe may increase flow efficiency (Ross 1967: Fig. 1). The rate of abdominal undulation increases in response to environmental changes such as a rise in temperature, a decrease in oxygen level and a decrease in current speed (Van Dam 1938, Fox and Sidney 1953, Feldmeth 1970) and, in the Limnephilo-

Fig. 4. Oxygen uptake curves of two species of Rhyacophilidae; one cased and the other caseless.

loidea, the extent of abdominal gill formation appears roughly correlated with the level of dissolved oxygen, the temperature and water velocity of the habitat in which each genus or family is found (Ross 1967, Wichard 1973). However, evidence for the case bestowing a respiratory advantage upon the larva is largely circumstantial. Only Jaag and Ambühl (1964) have demonstrated that, in one species of *Anabolia*, larvae in their cases were able to survive lower oxygen levels than the larvae alone. Wiggins (1977) proposed that there has been steady, increasing selective pressure for greater respiratory efficiency in those species that have invaded lentic waters. He pointed out that it can hardly be coincidence that of the seven families with representatives in standing waters, five build tubular cases – the Phryganeidae, Limnephilidae, Lepidostomatidae, Molannidae and Leptoceridae. Development of respiratory independence, he added, allowed these limnephiloids to exploit food unrelated to current.

However, more recently, it has been suggested that the ancestral caddisfly larva was an inhabitant of the shores of lentic or lotic-depositional waters (where it lived as a tube-dwelling detritivore in humus and detritus) rather than cool lotic-erosional habitats. From this ancestor sprang two evolutionary lines, one leading to the tube-case-making Integripalpia and the other to the retreat-making Annulipalpia (Weaver and Morse 1986).

In general, the sensitivity to oxygen and oxygen uptake rates of many freshwater organisms seem to reflect their habitat (Davis 1975). For example, for mayfly nymphs Fox et al. (1937) reported that species from swift water, such as those of *Baetis* had higher respiration rates and critical oxygen tensions than those, (e.g. *Cloeon*) from ponds. Similar findings have been reported for isopods and amphipods from habitats with different natural degrees of deoxygenation (Sprague 1963). This seems to be echoed to some extent in the caddisflies, as many caseless species from cool-lotic habitats such as *Hydropsyche sparna*, *Chimarra aterrima*, *Diplectrona modesta* and *Dolophilodes distinctus* had respiration rates that were high ($>1 \mu\text{g mg}^{-1} \text{ wet wt h}^{-1}$), while cased species from warm-lotic/lentic habitats e.g., *Platycentropus amicus*, *Pycnopsyche guttifer*, *Phryganea cinerea* and *Limnephilus rhombicus* had lower mean oxygen consumption rates ($<0.5 \mu\text{g mg}^{-1} \text{ wet wt h}^{-1}$). There are exceptions however, as *Parapsyche apicalis*, a caseless, cool-lotic species, had a low respiration rate whereas the cased, warm-lotic/lentic species *Oecetis* sp., *Agarodes* sp., and *Helicopsyche borealis* had high respiration rates when out of their cases. Nagell (1974) has cautioned that differences between oxygen consumption curves of two species does not necessarily imply a corresponding difference in their natural distributions. He admits, however, that the curve expresses essential physiological properties of the species and is especially useful when complemented and integrated with other facts, including ecological ones, about the species.

Species with similar, very wide habitat ranges, such as *Ptilostomis ocellifera* and *Platycentropus amicus* although they showed similar oxygen uptake responses, benefited differently from their cases, and species with similar, very narrow habitat types, such as *Phryganea cinerea* and *N. hostilis* differed in both amount of oxygen consumed and the role of their cases. Even congeneric species showed some differences, as was evident for the two species of *Pycnopsyche* and the two species of *Limnephilus*. Again, there were differences within a species, as small larvae of *P. amicus* respired oxygen at a higher rate than late instars, as has been shown in both the Plecoptera and Ephemeroptera (Nagell 1973) and in the Trichoptera (Otto 1974). The latter could be because, within the gills of limnephilids, the distances between tracheoles decrease in proportion to the decreasing radius of the tracheoles from one instar to the next (Wichard 1973).

It can be argued that removal of the larvae from their

Fig. 5. Oxygen uptake curves of four species of cased caddisflies belonging to the limnephilid branch of the Limnephiloidea.

Fig. 6. Oxygen uptake curves of two sets of congeneric species of cased caddisflies of the limnephilid branch of the Limnephiloidea.

Fig. 7. Oxygen uptake curves of three cased species belonging to the limnephilid branch of the Limnephiloidea.

Fig. 8. Oxygen uptake curves of four species of cased caddisflies belonging to the leptocerid branch of the Limnephiloidea.

cases stressed them and thus may have caused unnaturally high rates of respiration. From studies of locusts and cockroaches, it is clear that levels of octopamine (the insect equivalent of adrenaline, which mediates an excitation-induced hypertrehalosemic or hyperlipemic response) in the blood return to normal within 1 h despite continued stimulation (Goosey and Candy 1980, Bailey et al. 1983). Any elevated response in respiration should thus have been over in the first hour or so of the larva's residence in the respirometer chamber. This may account for the initially very high oxygen consumption rates of some species e.g., *Glossosoma nigrior* (Fig. 4). Despite this, the level of consumption by *G. nigrior* larvae deprived of their cases was the highest of all the case-building species – this may be a reflection of the primitive status of the Glossosomatidae within the case-building families. However, the level of oxygen consumption of *G. nigrior* in its case was significantly less (6–7 fold) than that of the larva alone. The latter was true also of *Lepidostoma vernale*, *Banksiola* sp., *Ptilostomis ocellifera*, *Limnephilus indivisus*, *Molanna* sp., *Oecetis* sp. and *Agarodes* sp. For this group of species (Group A; representing seven families), the cases appear to bestow a respiratory advantage upon the larvae because they reduce the level of oxygen uptake and also moderate the rate of uptake – as the curves for the larvae in their cases were generally flatter and the variance around the mean uptake values at each oxygen concentration was sometimes less (e.g., *Agarodes* sp., Fig. 8). Here, we interpret the case to be primarily designed to aid respiration by optimizing, rather than maximizing, the amount and rate of oxygen that the larva can extract from the water. This might be of particular advantage to species living in habitats where oxygen levels in the environment are seasonally variable. Many of the species in Group A are found in warm lotic, lentic or temporary habitats (Fig. 2). Support for an optimal level of oxygen consumption being more appropriate than a maximal one may be seen in the findings of Gamble (1969). In a laboratory study of two burrowing intertidal amphipods, he found that whereas *Corophium arenarium* had a definite preference for water of high oxygen content, *C. volutator* exhibited a slight preference for water of low oxygen tension; this mirrored the relative oxygen contents of their respective field distributions.

A second group of species is identifiable (Group B) and consists of *Phryganea cinerea* and *Helicopsyche borealis* (representing two families). In both species the oxygen consumption was significantly higher when the larvae were in their cases. This increase in oxygen consumption in cased individuals may be due to the physical constraints of a case designed, primarily, for some non-respiratory advantage. For example, the spiral case of *H. borealis* resists crushing well (Williams et al. 1983) but it is heavy and presumably requires greater oxygen consumption by the larva to move it around. In this sense the case must bestow a respiratory disadvantage on the larva.

Yet a third group (Group C; representing one family) consists of species in which the rate of oxygen consumption by the larvae alone was the same as that of the larvae in their cases; examples are *Ironoquia punctatissima*, *Limnephilus rhombicus*, *Pycnopsyche lepida*, *Platycentropus amicus* and *Nemotaulius hostilis*. For these limnephilids, the case appears to bestow no particular respiratory advantage. Most of these species, too, are to be found living in habitats subject to variation in oxygen supply (Fig. 2).

From Tab. 1 it is evident that supplementary to their role as reducers and moderators of oxygen consumption, presence of cases may benefit larval survival at low oxygen tensions e.g., *Ptilostomis ocellifera* and *Molanna* sp. In addition, in some of the limnephilids (*I. punctatissima*, *L. rhombicus* and *N. hostilis*) although the cases did not aid normal respiration, they did seem to aid larval survival at very low oxygen concentrations. However, the differences in oxygen concentration at which cased and de-cased larvae can survive were so small (yet they were statistically significant) that they may have little ecological significance.

Conclusions

It is clear, comparing patterns and rates of oxygen uptake between species, that there are both similarities and differences within habitat type and between phylogenetically related species. In terms of case function, for some species the case seems to act as an aid to respiration in that the rate of respiration is lower and less variable in the presence of the case and/or the case allows the larva to tolerate lower levels of oxygen before dying. For other species, the case appears to bestow no particular respiratory advantage and, in fact, Otto (1976, 1983) has observed that some lentic limnephilids abandon their cases at low oxygen concentrations. Riek (1970) has suggested that the limnephiloid families have arisen along more than one phylogenetic line from different non-case-building ancestors, and behaviour resulting in the construction of tube-cases is thought to have arisen independently at least twice, once in the Limnephiloidea and once in some of the Hydroptilidae (Rhyacophiloidea) (Wiggins 1977). Given the many uses to which silk has been put in the Trichoptera, it seems reasonable to suppose that construction of a tubular case does not dictate a single function across all case-building species. Nor does the mere possession of a tubular case automatically advantage a species' respiration as it may have to work in conjunction with appropriate physiological or morphological features peculiar to each species. The evidence reported in this study strongly points to a respiratory function in some species but to some other, non-respiratory function (perhaps camouflage or physical protection from predators; see Otto and Svensson 1980) in others. Thus in those groups of caddisflies conferred with a respiratory advantage,

the cases may well have enabled them to spread into lentic habitats, but this does not appear to be so for the Limnephilidae.

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References

- Bailey, B. A. and Downer, R. G. H. 1983. Haemolymph octopamine levels during and following flight in the American cockroach, *Periplaneta americana* L. - *Can. J. Zool.* 62: 19-22.
- Davis, J. C. 1975. Minimal dissolved oxygen requirements of aquatic life with emphasis on Canadian species: a review. - *J. Fish. Res. Bd Can.* 32: 2295-2332.
- Dodds, G. S. and Hisaw, F. L. 1924. Ecological studies of aquatic insects. II. Size of respiratory organs in relation to environmental conditions. - *Ecology* 5: 262-271.
- Feldmeth, C. R. 1970. The respiratory energetics of two species of caddisfly larvae in relation to water flow. - *Comp. Biochem. Physiol.* 32: 193-202.
- Flint, O. S. 1960. Taxonomy and biology of Nearctic limnephilid larvae (Trichoptera) with special reference to species in eastern United States. - *Ent. Am.* 40: 1-117.
- and Wiggins, G. B. 1961. Records and descriptions of North American species in the genus *Lepidostoma*, with a revision of the *Vernalis* group (Trichoptera: Lepidostomatidae). - *Can. Ent.* 93: 279-297.
- Fox, H. M. and Sidney, J. 1953. The influence of dissolved oxygen on the respiratory movements of caddis larvae. - *J. Exp. Biol.* 30: 235-237.
- , Wingfield, C. A. and Simmonds, B. G. 1937. The oxygen consumption of ephemeral nymphs from flowing and from still waters in relation to the concentration of oxygen in the water. - *J. Exp. Biol.* 14: 210-218.
- Gamble, J. C. 1969. Some effects of low environmental oxygen concentrations on the behaviour and survival of three tubicolous littoral crustaceans. - Ph. D. Thesis, Univ. of Wales.
- Goosey, M. W. and Candy, D. J. 1980. The D-octopamine content of the haemolymph of the locust, *Schistocerca americana gregaria* and its elevation during flight. - *Insect Biochem.* 10: 393-397.
- Jaag, O. and Ambühl, H. 1964. The effect of the current on the composition of biocoenoses in flowing water streams. - In Southgate, B. A. (ed.), *Advances in water pollution research*; Proc. Int. Conf., London, 1962, pp. 31-44.
- Milne, M. J. 1938. Case-building in Trichoptera as an inherited response to oxygen deficiency. - *Can. Ent.* 70: 177-180.
- Nagell, B. 1973. The oxygen consumption of mayfly (Ephemeroptera) and stonefly (Plecoptera) larvae at different oxygen concentrations. - *Hydrobiologia* 42: 461-489.
- 1974. The basic picture and the ecological implications of the oxygen consumption/oxygen concentration curve of some aquatic insect larvae. - *Ent. Tidskr.* 95: 182-187.
- Nielsen, A. 1942. Über die Entwicklung und Biologie der Trichoptera mit besonderer Berücksichtigung der Quelltrichopteren Himmerlands. - *Arch. Hydrobiol. Suppl.* 17: 266-631.
- Otto, C. 1974. Growth and energetics in a larval population of *Potamophylax cingulatus* Steph. (Trichoptera) in a South Swedish stream. - *J. Anim. Ecol.* 43: 339-361.
- 1976. Habitat relationships in the larvae of three Trichoptera species. - *Arch. Hydrobiol.* 77: 505-517.
- 1982. Habitat, size and distribution of Scandinavian limnephilid caddisflies. - *Oikos* 38: 355-360.
- 1983. Behavioural and physiological adaptations to a variable habitat in two species of case-making caddis larvae using different food. - *Oikos* 41: 188-194.
- and Svensson, B. S. 1980. The significance of case material selection for the survival of caddis larvae. - *J. Anim. Ecol.* 49: 855-865.
- Riek, E. F. 1970. Trichoptera. In: *The insects of Australia*. C. S. I. R. O. and Melbourne Univ. Press, Melbourne, pp. 741-764.
- Ross, H. H. 1944. The caddis flies, or Trichoptera, of Illinois. - *Bull. Illinois Nat. Hist. Survey.* 23.
- 1964. Evolution of caddisworm cases and nets. - *Am. Zool.* 4: 209-220.
- 1967. The evolution and past dispersal of the Trichoptera. - *Ann. Rev. Ent.* 12: 169-206.
- Schuster, G. A. and Etnier, D. A. 1978. A manual for the identification of the larvae of the caddisfly genera *Hydropsyche* Pictet and *Symphitopsyche* Ulmer in eastern and central North America (Trichoptera: Hydropsychidae). - U. S. Environ. Protection Agency Rep. EPA-600/4-78-060.
- Sprague, J. B. 1963. Resistance of four freshwater crustaceans to lethal high temperature and low oxygen. - *J. Fish. Res. Bd Can.* 24: 387-415.
- Van Dam, L. 1938. On the utilization of oxygen and regulation of breathing in some aquatic animals. - Volharding, Groningen.
- Weaver, J. S. and Morse, J. C. 1986. Evolution of feeding and case-making behaviour in Trichoptera. - *J. N. Am. Benthol. Soc.* 5: 150-158.
- Wichard, W. 1973. Morphogenesis of the respiratory epithelium in the tracheal gills of larval Limnephilini Kol. (Insecta, Trichoptera). - *Z. Zellforsch.* 144: 585-592.
- Wiggins, G. B. 1977. Larvae of the North American caddisfly genera (Trichoptera). - Univ. of Toronto Press.
- Williams, D. D. and Williams, N. E. 1975. A contribution to the biology of *Ironoquia punctatissima* (Trichoptera: Limnephilidae). - *Can. Entomol.* 107: 829-832.
- and Williams, N. E. 1981. Morphological and dietary variations in a riverine population of *Pycnopsyche guttifer* (Trichoptera: Limnephilidae). - *Aquat. Insects* 4: 21-27.
- and Williams, N. E. 1987. Trichoptera from cold freshwater springs in Canada: records and comments. - *Proc. ent. Soc. Ont.* (in press).
- , Read, A. T. and Moore, K. A. 1983. The biology and zoogeography of *Helicopsyche borealis* (Trichoptera: Helicopsychidae): a nearctic representative of a tropical genus. - *Can. J. Zool.* 61: 2288-2299.
- Williams, N. E. and Williams, D. D. 1980. Distribution and feeding records of the caddisflies of the Matamek River region, Quebec. - *Can. J. Zool.* 57: 2402-2412.