Relationship between the drift of macroinvertebrates and the activity of brown trout in a small stream

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Brown trout *Salmo trutta* were most active in a small stream at night, dusk and dawn when drift rate was highest, but correlations between hourly drift rates and the trout's activity varied substantially between individuals, between different dates for a single individual, and between different periods of the daily cycle. On some occasions, the trout were responsive to the total drift rate, either at night or during the day, and on others to the largest drifting organisms only (terrestrial organisms, adults of Ephemeroptera, Diptera and Trichoptera). The study supports the idea that trout adapt their activity pattern to the abundance of drifting prey, either as generalists towards any organism, or as specialists towards the largest ones.

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Key words: foraging; drift; macroinvertebrate; stream; salmonids; *Salmo trutta*; telemetry.

INTRODUCTION

Bottom dwellers and benthic foragers rely on food resources whose availability varies more between different sites than between different times of the day (Ware, 1972; Baras, 1993). By contrast, most salmonids are sit-and-wait predators that forage essentially on drifting prey (Elliott, 1967, 1970, 1973; Tusa, 1968; Neveu & Thibault, 1977; Cada *et al.*, 1987; Angradi & Griffith, 1990), whose abundance and diversity varies considerably between seasons, from day to day, and during the course of the day (Cada *et al.*, 1987; Brittain & Eikeland, 1988). Malmqvist (1988), Flecker (1992) and Douglas *et al.* (1992) postulated further that benthic macroinvertebrates drifted under low light intensity as a consequence of the predation pressure by visual predators, like salmonids. From spring to early autumn, salmonids usually occupy a small-sized home range (e.g. Ovidio, 1999, for brown trout *Salmo trutta* L. in the Aisne stream), and they may adapt to the variable availability of food resources through time budgeting. Most studies in natural environments where gut fullness of salmonids was analysed with respect to the intensity of drift, concluded that the two variables were correlated (Elliott, 1970; Allan, 1978, 1981; Bachman, 1984; Wilzbach *et al.*, 1986; Angradi & Griffith, 1990; Forrester *et al.*, 1994), and that feeding occurred at the time of the highest drift density (Elliott, 1970, 1973).

However, the time scale for these analyses generally exceeded by far the periodicity of drift and trout activity, and this lack of accuracy might be of

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importance for the understanding of fine-scale time budgeting, considering that trout can behave as generalists or as specialists (Bryan & Larkin, 1972; Bridcut & Giller, 1995). To date, a single, pioneer study has investigated the relationships between the drift of invertebrate prey and the foraging activity of salmonids in natural environments (cutthroat trout *Oncorhynchus clarki pleuriticus* Richardson; Young *et al.*, 1997). However, it provided little insight into interindividual differences, and did not permit an analysis of individual behaviour with respect to fine-scale temporal variations in the abundance of drift in the activity centre of trout.

This study examined the diel behaviour of radio-tagged brown trout in a small stream of the Belgian Ardenne, and examined whether changes in activity level matched variations in drift abundance and composition.

MATERIAL AND METHODS

The Aisne stream is a small (40 km long; sub-basin: 184 km^2; mean annual discharge: 2·4 m^3 s^{-1}) tributary of the River Ourthe (River Meuse Basin) which flows into the River Ourthe at Bomal-sur-Ourthe. Its slope is 2·78‰, and water temperature averages 9·4° C (0–19° C) in the study area (0·5–2·0 km upstream of the confluence with R. Ourthe; width: ≤14 m). The fish assemblage is typical of the trout–grayling zones (Huet, 1949), and contains brown trout, grayling *Thymallus thymallus* (L.), sculpin *Cottus gobio* (L.), stone loach *Barbatula barbatula* (L.) and minnow *Phoxinus phoxinus* (L.).

Three wild trout (A, B and C, 399, 325 and 420 mm L_F, and 611, 398 and 995 g, respectively) were captured by electrofishing in spring 1996. Radio transmitters (40 MHz, coiled antenna, ATS Inc., <2·0% of fish body weight) were implanted surgically into the intraperitoneal cavity of anaesthetized trout, according to the methodology evaluated by Birtles (1995). Tagged trout were released at their exact place of capture, immediately after they recovered their equilibrium and showed spontaneous swimming (*c*. 5 min after surgery).

The activity of trout was measured during seven 24-h cycles (one trout examined per cycle; Table I) from early June to early August 1996. Every 10 min, fish were located to an accuracy of *c*. 0·5 m by reference to labelled marks lining the banks of the river and triangulation using conventional methods. However, conventional tracking cannot discriminate between very small-scale changes in position and activity, especially for sit-and-wait predators. Therefore, motion-sensitive transmitters were used, tuned to transmit at 40 ± 1 and 80 ± 1 pulses min^{-1}, depending on the orientation of the fish. Each fast movement or change of direction by the fish caused the signal to shift from one pulse rate to the other. Each time the fish was positioned in the stream, transmitter pulse rates were recorded over 1 min, and activity indices were deduced from the frequency of changes between pulse rates (ΔR min^{-1}, Baras, 1995; Baras *et al.*, 1998). Activity indices were expressed as a proportion of the maximum activity level, which is 53 ΔR min^{-1} for a transmitter shifting in between 40 and 80 pulses min^{-1}. This methodology was preferred to the analysis of transmitter signal strength (Clapp *et al.*, 1990) since the signal strength of an immobile radio transmitter is not strictly constant (Baras, 1996), due to the passage of other fish and obstacles to signal propagation (e.g. leaves, branches) in the stream.

Hourly samples were collected in a standard drift net (900 cm^2 opening; 500 μm mesh; Megeco Ltd, France) that was positioned at the downstream limit of the pool–riffle sequence occupied by the trout (10–15 m downstream of the trout's location). As in the study by Young *et al.* (1997), the bottom of the net was close to the substratum, and the top extended always above the water surface. Immediately after collection, drift samples were identified to taxonomic genera, and individuals of each genus were counted. This procedure was deemed to have little effect on trout behaviour since no trout moved consecutively to drift collection. Young *et al.* (1997) suggested that drift biomass

TABLE I. Characteristics of the seven 24-h cycles when the activity of radio-tagged trout (A, B or C) was compared to drift rate. Water temperature is the mean over the 24-h cycle. Dark: 22.30–04.30 h; light: 05.30–21.30 h. DAA: longitudinal extent of daily activity area. Activity is the mean number of changes of pulse rates per minute (ΔR min^{-1}) of the activity transmitter (1-min samples at 10-min intervals), expressed as a proportion of the maximum rhythm (53 ΔR min^{-1}, see Methods)

Cycle	Date in 1996	Water T° (°C)	Drift (items h⁻¹; mean ± s.d.)				#	Trout		Activity (%; mean ± s.d.)			
			24-h	Dark (night)	Light (day)	Twilight (dawn and dusk)		Fork length (mm)	DAA (m)	24-h	Dark (night)	Light (day)	Twilight (dawn and dusk)
1	3 June	13·7	107 ± 52	147 ± 66	91 ± 34	121 ± 54	B	30·5	9	26 ± 49	43 ± 40	21 ± 36	49 ± 49
2	11 June	16·0	129 ± 86	235 ± 70	75 ± 21	176 ± 119	A	39·9	66	70 ± 28	51 ± 43	77 ± 23	81 ± 17
3	19 June	12·9	68 ± 26	89 ± 18	57 ± 25	79 ± 8	B	30·5	3	19 ± 25	43 ± 25	8 ± 19	22 ± 28
4	2 July	12·3	84 ± 42	114 ± 46	76 ± 34	104 ± 61	C	42·0	41	17 ± 26	17 ± 23	17 ± 28	30 ± 43
5	10 July	12·8	56 ± 12	38 ± 15	21 ± 5	25 ± 6	B	30·5	5	45 ± 43	77 ± 25	34 ± 40	79 ± 23
6	24 July	14·8	67 ± 68	140 ± 88	38 ± 18	106 ± 136	A	39·9	80	9 ± 8	9 ± 2	9 ± 8	9 ± 0
7	7 August	16·3	74 ± 93	180 ± 117	26 ± 15	183 ± 132	A	39·9	16	15 ± 8	13 ± 8	17 ± 8	9 ± 9

provided a better measure of nutritional value than the abundance of items, and used the former factor in their analyses. However, trout may be more sensitive or responsive to the number of drifting organisms rather than to their weight.

For this reason, the hourly activity levels of trout were compared (Spearman rank correlations) with variations in the numbers rather than biomass of drift. Because the composition of the drift was too diversified for these analyses to be conducted at the genus level, drift items were grouped in eight categories: larvae of Ephemeroptera (LE), larvae of Trichoptera (LT), larvae of Diptera (LD), adults of these three orders (AE, AT and AD, respectively), terrestrial insects (Ter) and Crustaceans (*Gammarus* sp., G). Distinct analyses were conducted for night-time (<0·1 lx) and daytime (excluding dawn and dusk), considering that brown trout is a visual predator (Ware, 1972), and that the discrimination between different components of the drift requires minimum light intensity. Contrary to the study by Young *et al.* (1997), data from 24-h cycles on individual trout were treated separately in order to test for differences between individual trout, and to determine whether a single trout behaved consistently over several 24-h cycles.

RESULTS

Patterns of diel movement varied substantially between individual trout and days of study. Trout B never moved over more than 9 m, whereas trout A occupied daily activity areas ranging from 16 to 80 m (Table I). Trout generally were more active during hours of darkness than during daylight, but the difference was not significant (mean ± S.D.: $19\cdot3 \pm 13\cdot1$ *v.* $13\cdot6 \pm 12\cdot9$ ΔR min^{-1}, paired *t*-test, $t=1\cdot11$, $P=0\cdot3078$, d.f.=6), essentially due to huge variations of activity between successive hours. A common feature of all 24-h cycles was that an individual trout could be active during the day, at night or twilight, with no clear-cut diel pattern. Mean daily activity levels were independent of the size of the daily activity area ($P=0\cdot8003$), and both variables were independent of the mean drift rate over the 24-h cycle ($P=0\cdot8863$, and $P=0\cdot8844$, respectively), and of water temperature ($P=0\cdot3493$ and $P=0\cdot6107$, respectively).

Drift rate was higher at night than during the day (mean ± S.D.: 135 ± 64 *v.* 56 ± 27 items h^{-1}; unpaired *t*-test, $t=6\cdot09$, $P<0\cdot0001$, d.f.=166), but it fluctuated considerably between 24-h cycles (Table I). During cycle 2 in early June 1996, the hourly drift rate averaged 129 ± 87 items h^{-1} and peaked at 300 items h^{-1} in between 00.00 and 01.00 hours [Fig. 1(a)], whereas it averaged 26 ± 12 items h^{-1} and never exceeded 70 items h^{-1} during cycle 5 in early July. Larvae of Ephemeroptera were the most abundant items both at night (45·0%) and during the day (35·4%). Larvae and adults of Trichoptera, terrestrial insects and aquatic crustaceans drifted more frequently at night too. Adults of Ephemeroptera, larvae and adults of Diptera showed no clear-cut day–night periodicity, essentially due to the occurrence of episodes of high drift in the mid-morning or mid-afternoon, which alternated with periods of low drift.

Correlations between the hourly activity levels of trout and hourly drift rates varied substantially between 24-h cycles depending on individual fish, time of the year, water temperature and drift abundance (Table II). On one occasion only (cycle 7), no single correlation was found between the abundance of drifting organisms and the activity of trout. During cycles 2, 3, 4 and 6, the activity of trout was correlated significantly with the total drift rate over the entire 24-h
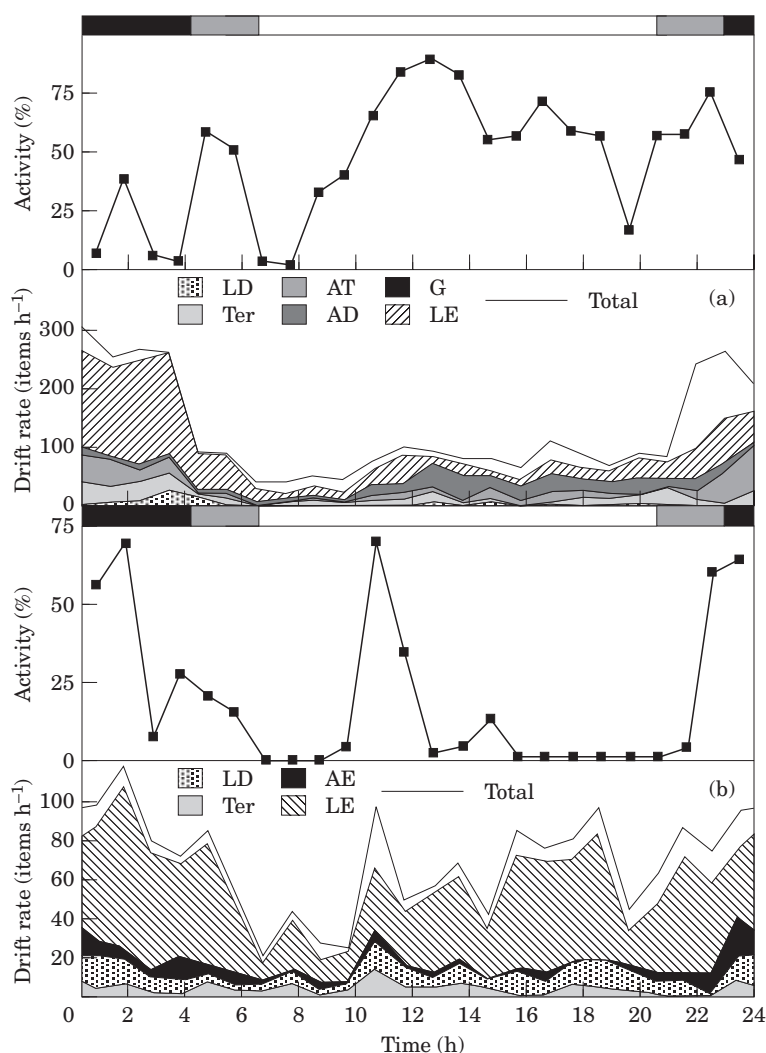
FIG. 1. Hourly variations of drift rate and activity of radio-tagged brown trout in the Aisne stream in summer 1996. Activity is the mean the number of changes of pulse rates of the motion-sensitive transmitter over six 1-min samples per hour (ΔR min^{-1}). (a) Cycle 2, trout A; (b) cycle 3, trout B (see Table I). Correlations between drift and activity of trout are given in Table II. LE: larvae of Ephemeroptera; LT: larvae of Trichoptera; LD larvae of Diptera; AE, AT and AD are adult insects of these three orders; G: crustaceans of the genus *Gammarus*; Ter: adult terrestrial insects.

cycle, but more significant correlations were obtained with the largest items of the drift [adults of Diptera (2), Ephemeroptera (3, 4), and Trichoptera (4, 6), terrestrial insects (4) or larvae of Ephemeroptera and Trichoptera (6)]. During cycle 1, the trout's activity was in phase with the total drift rate during daytime only, and in phase with drifting adults of Ephemeroptera at night. During cycle 5, trout B was apparently responsive to drifting adults of Trichoptera during night-time only.

TABLE II. Relationship (Spearman rank correlations) between the hourly activity index (change of pulse rates of activity transmitters over 1 min intervals every 10 min) of three brown trout (A, B, C) in the Aisne stream in summer 1996, and drift rate over the entire 24 h cycle (d.f.=23), during the day (excluding dawn and dusk; d.f.=15) or at night (d.f.=5). Characteristics of cycles 1–7 as in Table I. G: crustaceans of the genus *Gammarus*; Ter: adult terrestrial insects; LE: larvae of Ephemeroptera; LT: larvae of Trichoptera; LD larvae of Diptera; AE, AT and AD are adult insects of these three orders. TD is total drift rate. — stands for no significant correlation ($P>0.05$). * ≤ 0.05; ** ≤ 0.01; *** ≤ 0.001

Cycle	Trout	24 h	Night	Day
1	B	—	AE ($r=0.839$)*	TD ($r=0.706$)**
2	A	TD ($r=0.421$)*	AD ($r=0.750$)*	—
3	B	AE ($r=0.556$)**	LD ($r=0.877$)**	—
		TD ($r=0.420$)*	AE ($r=0.798$)*	
4	C	Ter ($r=0.586$)**	Ter ($r=0.818$)*	Ter ($r=0.507$)*
		TD ($r=0.539$)**	AE ($r=0.807$)*	
			AT ($r=0.761$)*	
			TD ($r=0.751$)*	
5	B	AT ($r=0.408$)*	AT ($r=0.768$)*	—
6	A	LE ($r=0.526$)**	—	LE ($r=0.816$)***
		TD ($r=0.448$)**		TD ($r=0.689$)**
				AT ($r=0.547$)*
				LT ($r=0.512$)*
7	A	—	—	—

DISCUSSION

This preliminary study supports the idea that trout generally adapt their activity pattern to the abundance of drifting prey, and substantiates the conclusions of authors who reported a correspondence between the composition of drift and the diet of salmonids (Cada *et al.*, 1987; Hubert & Rhodes, 1989; Angradi & Griffith, 1990; Forrester *et al.*, 1994; Young *et al.*, 1997). The correlation between the activity of all brown trout and the drift rate over the seven 24-h cycles investigated here, was similar to that reported by Young *et al.* (1997) for cutthroat trout ($R=+0.35$ *v.* $R=+0.43$, respectively). However, much better correlations were obtained when examining the behaviour of individual trout (Table II), indicating that some trout were indeed time budgeting whereas others were not, or to a lesser extent. This supports the idea that trout may exhibit a wide range of behavioural tactics, and that speculations about the adaptive nature of their behavioural responses require the analysis of individual behaviour. Inter- and intra-individual differences in diel movement and activity may originate from variations of foraging efficiency or tactics in different habitat types (Ringler, 1983; Nielsen, 1992; Young *et al.*, 1997). However both trout that were investigated over different 24-h cycles during this study used the same pool–riffle sequence consistently throughout. Decreasing drift rates throughout the summer (Table I) might have caused brown trout to turn to benthic foraging (Bachman, 1984) or to piscivory, and

thus to exhibit activity patterns independent of drift rate (Young *et al.*, 1997), but this remains to be determined experimentally.

Salmonids can detect prey at low light intensities (0·03–0·1 lx; Tanaka, 1970; Robinson & Tasch, 1979; Henderson & Northcote, 1985). Hence there was no doubt that brown trout in the present study were able to detect and capture drifting prey during the day, at dawn or dusk, when light intensity was ≥ 1 lx. Terrestrial insects, and adults of aquatic insects such as Ephemeroptera, Diptera and Trichoptera are much bigger items than larvae. Furthermore, these large prey are found more frequently at the surface of the water, where they represent more visible targets to salmonids than prey drifting within the water column (Angradi & Griffith, 1990; Young *et al.*, 1997). This might account for why the activity of brown trout was correlated more frequently with the abundance of these organisms in the present study, and why these taxa are generally overabundant in the diet of salmonids during spring and summer (Wilzbach *et al.*, 1986). This may also suggest that some trout behave as generalists towards any organism, or as specialists towards the largest ones.

In the present study, trout were always more active at dusk and dawn and during the night, than during the day. The high nocturnal activity levels observed here contrast, to some extent, with the observations that salmonids are essentially active at dusk and dawn during the summer (Ware, 1972; Elliott, 1973; Allan, 1981; Heggenes *et al.*, 1993). Based on the correlations between hourly drift rates and fish activity, it can be put forward reasonably that brown trout were more active at night because the drift rate was higher during this period. Whether light intensity was sufficient to enable brown trout to detect, select and capture prey visually at night is uncertain. Trout may rely on senses other than vision to detect prey at low light intensity (e.g. vibrations, noise). Most probably these senses have less resolution than vision for discriminating between different prey, and cause brown trout to react to any prey, contrary to what happens during hours of light, when trout can select prey visually depending on their nature or position in the water column.

Correlations between drift rate and the activity of brown trout were generally higher at night than during the day, and this may be accounted for by several complementary hypotheses. Territoriality and agonistic interactions in salmonids are inhibited generally under low light levels (Héland, 1991). Hence the activity of trout during the night might be related more closely to foraging than during daytime, when additional social and anti-predator behaviour may mask partly the correlation between food availability and fish activity (i.e. high activity at periods of low drift). This possible confusion originates directly from the limited capacity of telemetry techniques to discriminate between different behaviours. Possibly correlations at night were better because drift rates were higher during night-time than during daytime, and exceeded some form of threshold above which trout were responsive to drift. The observation that the diurnal activity of brown trout was correlated ($P<0\cdot10$) to drift rates >70 items h^{-1}, whereas no significant correlation was observed for lower rates, supports this hypothesis, but experimental confirmation is required. By analogy with studies of the trout's diet, which showed the correspondence between the feeding times of trout and drift composition (Elliott, 1970, 1973), it is likely that brown trout fed predominantly during periods of high drift (i.e. at night, or occasionally

during the day). This suggests further that the trout had presumably reached satiation before mid-day, and showed least appetite and response to prey drifting later in the day (i.e. low activity under relatively high drift). Because all factors concur with a least correlation between activity and drift during hours of light, their respective importance cannot be determined.

Before telemetry emerged as a major tool in fish behavioural ecology, the limiting factor when analysing the relationships between drift and fish activity was the frequency of gastric sampling. Nowadays, it is possible to determine the activity or position of fish with a resolution of a few seconds when using data-collecting computers connected to automatic listening (Baras *et al.*, 1998) or positioning stations (Lagardère *et al.*, 1996), and this exceeds by far the frequency of drift sampling with standard procedures. Coupling fine scale telemetry to fine scale drift sampling through suction pumps (Armitage, 1978; Dumont *et al.*, 1996) might represent a substantial progress in the understanding of the trout's adaptive behaviour.

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