
Observations on larval caddisfly, *Tinodes assimilis* (Trichoptera), galleries in a freshwater seep discharging to sea across a rocky foreshore

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ABSTRACT

Attention is drawn to the structure and pattern of dispersion of the larval galleries of the caddisfly *Tinodes assimilis* (Trichoptera) living in a freshwater seep discharging over a rocky foreshore near the Lion Rock, Isle of Cumbrae. An original method for measuring the sinuous galleries is explained. Gallery density, structure, dimensions, orientation and occupancy rate are investigated.

INTRODUCTION

Freshwater seeps flowing over open rocky-shore surfaces have received scant ecological attention. Boyce (2002) has stressed the inadequacy of our understanding of assemblages associated with stable cliff-seepage habitats in England. The fauna occupying this habitat has been termed the 'fauna hygropetrica' (see Popham 1952; Vaillant 1954); that is, animals occupying a microhabitat where a thin film of water flows permanently (or intermittently) over emergent structures. Insects form an important component of such ecosystems, especially in high latitudes. Jones (1969) investigated the emergence of Trichoptera from a small ground-fed stream flowing into the Menai Strait, North Wales; with *Tinodes assimilis* emerging from June to August. Regarding other rocky-shore dwelling dipterans, Neumann (1976) has reviewed the adaptations of chironomids to intertidal environments and Stuart (1941) has considered comparative aspects of the larval chironomid fauna of shore pools at Millport.

My attention was drawn to this topic by happening upon a conspicuous assemblage of larval caddisfly (*Tinodes assimilis* McLachlan) galleries, fixed to the bedrock bottom of a small freshwater seep overflowing the supralittoral zone of a solid sandstone rocky shore substratum locally. Caddisfly larvae are typical inhabitants of freshwater habitats. That said, although a long-established fact (McLachlan 1883), it is less widely appreciated that marine species also exist (Leader 1976). Case-building caddis larvae utilise a range of building materials to construct their portable houses and some non-case builders construct fixed galleries (Edington & Hildrew 2005: 83), each species

creating an abode of a particular form utilising a variety of building materials bound by silk secretions emanating from labial glands (Miall 1934; Otto & Svensson 1980; Hansell 1984; Michalek *et al.* 2005). Haage (1970) reported on the feeding habits of two Baltic caddis larvae living in the *Fucus vesiculosus* L. belt. No published data apparently exist on Trichoptera of Millport shores (Smith & Smith 1983), although the regional list published by King (1901) will have local relevance.

Dealing with the distribution of stream-bottom fauna, Allen (1959) stressed "particularly with small animals, it is rare to be able to observe and record the position of each individual in the undisturbed environment". Edgar & Meadows (1969) were able to make such observations on an artificial population of chironomid larvae (*Chironomus riparius* Meigen) building cases in an experimental freshwater tank. Following that work, Campbell & Meadows (1972) published observations on the under-stone dispersion pattern of larvae of a caddisfly in the field in the River Allander, Scotland. An opportunity to make similar field observations from a coastal locality was presented by the readily accessible natural Cumbrae freshwater-seep population described herein.

Destructive sampling was kept to a minimum in view of the small size of this population. Caddis identification was achieved using Edington & Hildrew's key (2005).

MATERIALS AND METHODS

Site description

The small, micro-topographically sheltered, freshwater seep studied (Fig. 1) exited over the shore composed of solid Old Red Sandstone on the east-facing coast of Great Cumbrae Island, between the concrete fixing stanchion for the WWII anti-submarine boom and the intrusive dyke at Lion Rock (O.S. Grid ref: NS179548; lat. 55° 45.135', long. 004° 54.196' as established using a Garmin *etrex* hand-held GPS). At the time of first sampling (July 2006), the seep (then only slow-flowing) at its narrowest was about 30 cm across and millimetres deep, broadening to double (and, under high-flow conditions, potentially triple) that as it traversed the black lichen (*Verrucaria maura* Wahlenb.) zone, its

bed coated with a shiny brown coating of unknown composition and its margins flanked by blackish-green bubbly looking excrescences of Cyanophyceae (cf. Little 1973). The caddis galleries were conspicuous as the only indication of macrofaunal colonisation of this outflow. After exiting from the terrestrial vegetation, the seepage flowed shallowly over a series of small (ca 5 mm water depth) shelves, creating pools (the slightly deeper and down-shore of which retained a mixture of flocculent silt and detritus and detached siltier tubes occupied densely by red-coloured, hypoxia tolerating larvae of the midge *Chironomus* sp.).



Fig. 1. The freshwater seep south of Lion Rock, Great Cumbrae Island (original photograph, © P. G. Moore).

Four progressively down-shore micro-sites were investigated: site 1, the uppermost, was a small flattish shelf (dip 5°) nearest the terrestrial vegetation; site 2, a narrow channel (15 cm) more steeply sloping (dip 10°) in the middle of the study area, and site 3 (subsections a and b) a similarly sloping (dip 10–20°), but broader (1 m), apron at the base of the area considered. Somewhat below site 3, *Enteromorpha* sp. was established in the seep's path. Adjacent shallow depressions to one side (south) of site 2, that were dry that July, showed evidence of previous colonisation (disintegrating residua of empty sandy galleries) indicative of an expanded distribution of *T. assimilis* during periods of greater water outflow. No stones or gravel impeded the smooth passage of the spillway, the bed of which formed a stepped two-dimensional habitat. The whole system resembles an inverted funnel in shape (Fig. 1).

Gallery construction

Intact galleries were examined visually using a Wild M7A stereo light microscope (under cold-light illumination) and a pooled sample (n = 5) disaggregated by immersion in dilute hydrogen peroxide solution (7 days) prior to gravimetric analysis (weighing to 3 decimal places) after grading

under water through an Endecott sieve series and subsequent drying at 60°C.

Gallery form, dimensions and orientation

Galleries meandered, varying in plan considerably but were never branched. The length of each gallery at the four sites was assessed by bending insulated copper wire to conform to the shape of the gallery as graphically recorded in free-hand scale drawings using a gridded quadrat, followed by straightening the wire against a millimetre scale. To test the validity of the above technique, pieces of copper wire of random lengths within the typical size range, and bent into a variety of shapes, were scattered onto a plane surface and then recorded graphically in the same way. Their drawn representations were then measured using the technique above before the actual sizes of the models were determined directly. These calibration data were then subjected to correlation analysis. The Pearson correlation coefficient resulting was 0.947 (n = 25, P<0.001). Since the method proved to be 95% accurate, the field data are considered to be accurate to one millimetre. Since one of the field data sets did not conform to a normal distribution, median lengths have been reported as well as means. Gallery widths were measured *in situ* using a vernier calliper.

The predominant orientation of galleries (all from samples taken within the seepage's prevailing flow regime) was also analysed from the scale drawings (Fig. 2). The angle of each gallery's prime anterior axis was recorded relative to the direction of flow and the distribution of those angles plotted as a rose diagram for each micro-site. Note was also taken of atypically long galleries radiating into a dried-up pool extension.

Gallery occupancy

A small sample (n = 10) of longer than average submerged galleries was taken (14 July 2006) to assess occupancy rate.

Dispersion pattern

The variance to mean ratio was calculated using count data from 30 haphazardly thrown 5 x 5 cm quadrats at each site. All data sets were tested for normality using the Kolmogorov-Smirnov test before parametric statistical analysis. The variance to mean ratios obtained were then entered in a χ^2 table at n-1 degrees of freedom (Elliott, 1983) to test for significance at P<0.05. An aggregated distribution has a variance to mean ratio > 1, a random distribution equal to 1 and a regular <1.

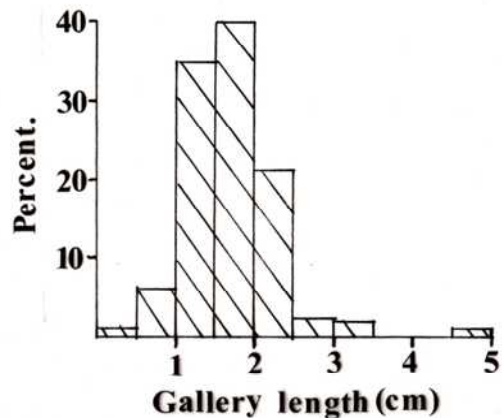


Fig. 2. Histogram of gallery lengths (cm) of *T. assimilis* from site 1 (n = 109).

RESULTS

The galleries were simple sub-cylindrical structures (stirrup-shaped in transverse section with the flat region attached to the substratum) exhibiting a wide variety of sinuous shapes. Depending on their disposition, typically, they measured between 1 and 2 cm in length (Table 1, Fig. 2). Width was more directly measurable and was 2.8 ± 0.1 (S.E.) mm (n = 10). The sample of selected larger galleries investigated showed that galleries could be many times the length of the major occupant (not unusually 3–5x; large larvae being typically *ca* 9mm long). Galleries were constructed predominantly (60%) from sand grains in the size range 250–500 μ m (median grain size; 356 μ m) (Table 2), plus the occasional tiny gastropod shell or vegetation fragment, cemented together with silken threads. A few of the galleries examined microscopically (30%) had fine, filamentous algal material associated with them but it is not clear whether that had colonised the gallery secondarily or been incorporated deliberately. Diatoms were also visible on the outside of the galleries. Galleries were variously orientated with respect to current direction, with some tendency to be angled somewhat obliquely to the flow but the effect was variable (Fig. 3). Some tendency was observed for gallery density to be greater along cracks in the rock

and at the foot of vertical fracture faces, presumably taking advantage of better fixation potential in two conjoined planes. Gallery density was significantly higher ($P < 0.01$) at site 2 where the water was more channelled and faster flowing. That site also had the the shortest galleries. Galleries were randomly distributed (Table 1). Sampling ten longer galleries revealed a 90% occupancy rate.

Table 2. Percentage composition (by weight) of the sand-grain fractions making up the galleries of *T. assimilis* (July 2006).

Grain size range (μ m)	%
>500	21
250-499	59
125-249	19
63-124	1

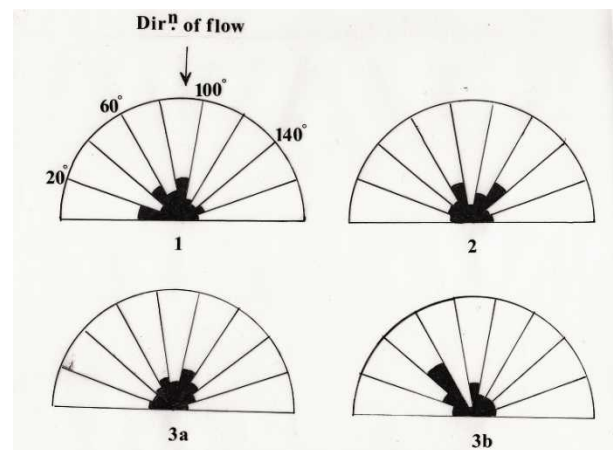


Fig. 3. Orientation of the mouth of *T. assimilis* galleries with respect to water-flow direction at the four micro-sites investigated.

Perhaps the constructors of exceptionally straggly galleries (<6 cm) in dried-up areas had continued building in an attempt to keep pace with water-level recession by extending the galleries towards the centre of small shrinking pools in a vain attempt to remain submerged. For how long such galleries remain intact after drying-out was not established but decomposition was noticeable several weeks after first encounter of some in an already dry state.

Table 1. Population densities (per 25 cm²) of larval caddisfly (*T. assimilis*) galleries together with data on the variance to mean ratio of population density estimates, on the significance of those ratios (assessed using χ^2), and on mean and / or median (latter where distribution non-normal) gallery lengths (cm) at the four progressively down-shore micro-sites studied, length data assessed from scale drawings made in situ, 13 July 2006 (Great Cumbrae Island).

Site no.	Mean density \pm S.E. (n)	Variance to mean ratio	Ratio signif.	Mean length \pm S.E. (n)	Median length (n)
1	4.83 \pm 0.47 (30)	1.34	P>0.05	1.8 \pm 0.1 (109)	1.7 (109)
2	11.43 \pm 0.57 (30)	0.85	P>0.05	Non normal	1.4 (113)
3a	7.30 \pm 0.37 (30)	0.57	P>0.05	1.6 \pm 0.04 (138)	1.6 (138)
3b	1.77 \pm 0.32 (30)	1.74	P>0.05	1.7 \pm 0.1 (35)	1.6 (35)

DISCUSSION

The psychomyiids *Tinodes assimilis* and *T. mackachlani* typically occupy vertical or near-vertical rock faces over which thin films of water are flowing; the so-called hygropetric habitat (Vaillant 1954). Popham (1952) reported that *T. assimilis* replaced the dipteran *Thaumalea testacea* at sites where the water flow was more rapid. According to Edgington & Hildrew (2005), in lowland areas *Tinodes mackachlani* may extend into more typical small stream habitats where it is frequently overlooked possibly as a result of the superficial resemblance of their galleries to the silt tubes of chironomids. Lacking supplementary cover of any kind locally, *T. assimilis* presumably relies for concealment at the Lion Rock seepage site on the fact that its galleries are made of the same sand-grain material as the country rock (not faecal material). Note, however, that Alderson's unpublished work (1969), reported by Edgington & Hildrew (2005: 90), described *T. assimilis* galleries elsewhere as consisting "largely of faecal pellets." Vaillant (1954), however, described *Tinodes* galleries as being made of sand and calcareous matter. Nevertheless these straggling galleries on Cumbrae, fixed along their whole length (see also Vaillant 1954), still looked conspicuous enough to the human eye (i.e. against the brown biofilm background cover); although the mouth of the gallery was not so obvious. Given the extent of their elevation up-shore, the freshness of the water and the extremely shallow water depth, it is hard to imagine that any marine organisms would predate upon these larvae. Shore margin-foraging birds, like rock pipits (*Anthus spinoletta* (L.)), might conceivably consume them. Stuart (1941: 500), though, found no evidence for bird predation on chironomid larvae in Millport shore pools (note also Leader 1976); indeed, he associated the population density of those larvae with an absence of avian predation.

The population densities recorded herein are in accord with those reported by Popham (1952) from Port Erin Bay, Isle of Man. The galleries of *T. assimilis*, constructed of densely-packed mineral particles locally, were quite robust; the silken bracing threads resisting tearing forces when galleries were being teased apart under the microscope to a notable extent. Hansell (1984) has commented on the compression / load bearing and elasticity aspects of caddis sand-grain houses versus palatability to larger predators (p. 138) (see also Otto & Svensson 1980).

It seems possible that, at least while hydrated, such relatively tough galleries might outlast their original architect. When occupied, they are capable of being exploited by several species simultaneously, the largest larva patently tolerating the presence of smaller chironomid larvae (unidentified) within the same gallery. This could be seen as adaptive, i.e. the smaller species benefiting from the greater strength of a larger gallery. Typically, caddis larvae go through

five instars prior to pupation (Hildrew pers. comm.). Otto & Svensson (1980) found that as the age of larval *Potamophylax cingulatus* (Steph.) increased, their cases became more and more resistant to pressure and less vulnerable to predation by trout. Gallery-sharing would obviate this problem for smaller cohabitants. Imms (1964: 579) commented that retreats are often common to several larvae. Otto & Svensson regarded case enlargement as being most pronounced among the organic gallery makers. Gallery enlargement by *T. assimilis* was most extreme in the dried-out depressions. Many species of caddis flies have flight-periods of several months, and this, together with the delayed hatching of some eggs, provides a safeguard for the population during adverse conditions, such as drought (Morrison 1990). Hickin (1967: 200) noted that *T. assimilis* can withstand a degree of drying of its surroundings. Mineral-grain selectivity for house construction by caddisfly larvae can alter depending upon particle availability (Statzner *et al.* 2005), and so could alter temporally in relation to varying water-outflow rates. Vaillant (1954) noted that *Tinodes* larvae can resist their galleries being washed away during heavy rainfall for some hours (but note above).

Populations of organisms can be spatially distributed according to three basic patterns: random, regular (under-dispersion) or contagious (over-dispersion or aggregated) (Elliott 1983). Of these, regular distributed patterns of dispersion are perhaps the least frequently encountered. Typically they occur in artificial conditions, e.g. tree plantings in an orchard, or where social factors govern behaviour that necessitate a territorial spacing-out of individuals of the same species, as among colonially nesting seabirds. Connell (1963), though, has also described territorial behaviour generating a regular dispersion pattern in the marine tubicolous amphipod crustacean *Erichthonius brasiliensis* (Dana) and Johnson (1959) described an even distribution in the tubicolous phoronid *Phoronopsis viridis* Hilton. Much more usual than regular dispersion patterns in the marine benthos are random or clumped distributions (Wilson 1976; Turra & Denadai 2006). Edgar & Meadows (1969), however, found that the tubes of *Chironomus riparius* were spaced-out in an experimental tank and that larvae deliberately re-sorted themselves to assume a regular distribution pattern if artificially placed into clumps. Campbell & Meadows (1972), by contrast, described aggregation in the caddisfly larva of *Potamophylax latipennis* (Curtis), an algal scraper, in its natural habitat (under stones of a particular size in a Scottish river). It was interesting that the site (no. 2) with the shortest galleries was also that with the highest density of galleries, suggestive of some degree of hostility and mutual avoidance of conspecifics, maybe involving defended foraging areas (cf. Johnson 1959; Connell 1963). The larvae of the freshwater caddisfly *Cheumatopsyche* sp. exhibited aggression and spacing under laboratory

conditions (Glass & Bovbjerg 1969). However, the randomness of the spatial distribution pattern here disclosed (Table 1) would count against that hypothesis in this instance.

The impact of crowding on gallery length (note Table 1) is consistent with *T. assimilis* feeding as a generalist epistratum scraper (requiring the larva to forage outside its gallery). Whether the preferred grains for gallery-construction represents outwash from the land or particles scraped-off the substratum, as during feeding, is uncertain. Galleries will be expensive to construct so occupants would, presumably, be loath to vacate them entirely and run the risk of not being able to regain their shelter. The extent of such emergence, however, could readily be up to one body length away from the gallery mouth, with home contact still being maintained using their hooked terminal appendages (Pryor 1951). Popham (1952) found the smallest larvae of *T. assimilis* in the dampest situations.

Considering the marginal importance of Cyanophyceae reported herein, it is interesting that Becker (1990) found that *T. rostocki* took very few Cyanobacteria (= Cyanophyceae) despite their abundance on stone surfaces. Cyanophyceae are generally unpalatable to marine grazers, both benthic and planktonic, due to their noxious allelochemical defences.

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REFERENCES

Alderson, R. (1969). *Studies on the larval biology of caddis flies of the family Psychomyiidae*. Unpublished Ph.D. Thesis, University of Wales.

Allen, K. R. (1959). The distribution of stream bottom faunas. *Proceedings of the New Zealand Ecological Society* 6, 5–8.

Boyce, D. C. (2002). A review of seepage invertebrates in England. *English Nature Research Report*, No. 452, English Nature, Peterborough.

Campbell, J. I. & Meadows, P. S. (1972). An analysis of aggregation formed by the caddisfly larva *Potamophylax latipennis* in its natural habitat. *Journal of Zoology (London)* 167, 133–147.

Connell, J. H. (1963). Territorial behavior and dispersion in some marine invertebrates. *Researches on Population Ecology, Kyoto University* 5, 87–101.

Edgar, W. D. & Meadows, P. S. (1969). Gallery construction, movement, spatial distribution and substrata selection in the larva of *Chironomus riparius* Meigen. *Journal of Experimental Biology* 50, 247–253.

Edington, J. M. & Hildrew, A. G. (2005). *A revised key to the caseless caddis larvae of the British Isles, with notes on their ecology*. Freshwater Biological Association, Scientific Publication, Ambleside, no. 53.

Elliott, J. M. (1983). *Some methods for the statistical analysis of samples of benthic invertebrates*. Freshwater Biological Association, Ambleside, Scientific Publication no. 25.

Glass, L. W. & Bovbjerg, R. V. (1969). Density and dispersion in laboratory populations of caddisfly larvae (*Cheumatopsyche*, Hydropsychidae). *Ecology* 50, 1082–1084.

Haage, P. (1970). On the feeding habits of two Baltic species of caddis larvae (Trichoptera). *Entomologica Scandinavica* 1, 282–290.

Hanna, H. H. (1961). Selection for case-building by larvae of caddis flies (Trichoptera). *Proceedings of the Royal Entomological Society (A)* 36, 37–47.

Hansell, M. H. (1984). *Animal architecture and building behaviour*. Longman, London.

Hickin, N. E. (1967). *Caddis larvae: larvae of the British Trichoptera*. Hutchinson and Co., London.

Imms, A. D. (1964). *A general textbook of entomology*. Ninth edition, revised. Methuen and Co. Ltd, London.

Johnson, R. G. (1959). Spatial distribution of *Phoronopsis viridis* Hilton. *Science*, 129, 1221.

Jones, N. V. (1969) The emergence of Trichoptera from a small ground-fed stream in N. Wales. *The Entomologist's monthly magazine* 105, 151–155.

King, J. F. X. (1901). Order Trichoptera, pages 302–305, in: Scott Elliot, G. F., Laurie, M. and Murdoch, J. B. (Eds), *Fauna, flora & geology of the Clyde area*. British Association for the Advancement of Science, Glasgow.

Leader, J. P. (1976). Marine caddis flies (Trichoptera: Philanisidae), pages 291–302, in: Cheng, L. (Ed.) *Marine insects*. North-Holland Publishing Company, Amsterdam.

Little, M. G. (1973). The zonation of marine supralittoral blue-green algae. *British Phycological Journal* 8, 47–50.

McLachlan, R. (1883). On a marine caddis-fly (*Philanisus*, Walker, = *Anomalostoma*, Brauer) from New Zealand. *Journal of the Linnean Society of London* 16, 417–421.

Miall, L. C. (1934). *The natural history of aquatic insects*. Macmillan and Co. Ltd, London.

Michalak, M., Tszydel, M., Bilska, J. & Krucińska, I. (2005). Products of caddis-fly larvae (Trichoptera) silk glands as a new natural textile fibre. *Fibres & Textiles* 13, 28–32.

Morrison, B. R. S. (1990). Recolonisation of four small streams in central Scotland following drought conditions in 1984. *Hydrobiologia* 208, 261–267.

- Neumann, D. (1976). Adaptations of chironomids to intertidal environments. *Annual Review of Entomology* 21, 387–414.
- Otto, C. & Svensson, B. S. (1980). The significance of gallery material selection for the survival of caddis larvae. *Journal of Animal Ecology* 49, 855–865.
- Popham, E. J. (1952). Some preliminary notes on the fauna hygropetrica of Lancashire and the Isle of Man. *Journal of the Society for British Entomology* 1952, 58–63.
- Pryor, M. G. M. (1951). On the abdominal appendages of larvae of Trichoptera, Neuroptera, and Lepidoptera, and the origins of jointed limbs. *Quarterly Journal of Microscopical Science* 92, 351–376.
- Scudder, G. G. E. (1976). Water-boatmen of saline waters (Hemiptera: Corixidae), pages 263-289, in: Cheng, L. (Ed.) *Marine insects*. North-Holland Publishing Company, Amsterdam.
- Smith, K. & Smith, V. (1983). *A bibliography of the entomology of the smaller British offshore islands*. E. W. Classey Ltd, London.
- Statzner, B., Mériçoux, S. & Leichtfried, M. (2005). Mineral grains in caddisfly pupal cases and streambed sediments: resource use and its limitation through conflicting resource requirements. *Limnology and Oceanography* 50, 713–721.
- Stuart, T. A. (1941). Chironomid larvae of the Millport shore pools. *Transactions of the Royal Society of Edinburgh* 60, 475–502.
- Turra, A. & Denadai, M.R. (2006). Microhabitat use by two rocky shore gastropods in an intertidal sandy substrate with rocky fragments. *Brazilian Journal of Biology* 66(1B), 351–355.
- Vaillant, F. (1954). *Tinodes algerica* McLachlan, the hygropetric larvae of the *Tinodes*. *Annals and Magazine of Natural History* 7, 58–62.
- Wilson, J. G. (1976). Dispersion of *Tellina tenuis* from Kames Bay, Millport, Scotland. *Marine Biology* 37, 371–376.