A preliminary study of the predator-prey relationships of watermites (Acari: Hydrachidia) and blackfly larvae (Diptera: Simuliidae)

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Key words: Watermite, *Hygrobates fluviatilis; Lebertia porosa*; *Simulium* larvae; Predation

Introduction

The virtually worldwide occurrence of blackflies (Simuliidae) where flowing water exists, and their role as disease vectors of livestock and man, makes these haematophagous Diptera of considerable economic importance. Control of simuliid populations is usually achieved through the treatment of the larval stages with organophosphates. Biocontrol approaches have also focused on natural enemies of the immature stages. Recently, the microbial insecticide *Bacillus thuringiensis* var. *israelensis* has shown considerable potential in this respect, with minimal effects on non-target organisms (Lacy & Undeen, 1987; Becker & Margalit, 1993).

Adult simuliids oviposit either directly into the water, or onto some kind of substrate (stones, twigs, trailing vegetation, etc). The larvae hatch and drift some distance downstream before adhering to a suitable rock, or aquatic plant. Clean, fast-flowing, well-oxygenated water is preferred by larval simuliids, which filter fine organic particulate matter from the water through cephalic fans. The larvae go through 6-8 instars before pupating inside a tent-like cocoon. Upon emergence, the adult fly surfaces and crawls onto a dry substrate to allow the wings to expand and harden before flying off to mate, blood-feed, and oviposit (Crosskey 1990).

With the exception of birds, *e. g.* dippers, predators of immature simuliids generally inhabit the same aquatic habitat as their prey. Fish are usually credited with the greatest fraction of simuliid predation and Trichoptera, Odonata, Ephemeroptera and Plecoptera species as the most important invertebrate predators. Chironomids and other dipteran species have frequently been recorded as feeding on *Simulium* spp., and cannibalism also occurs (Davies 1981).

Perhaps the greatest, yet the most frequently overlooked of the simuliid predators, are watermites of the family Hydrachnidae (Hydrachnellae or Hydracarinae) which

due to their small size, are difficult to observe in the field. Also, because of their size and problems relating to their taxonomy, watermites have been neglected in studies of aquatic ecology.

In common with other mites, the life cycle of hydrachnid mites is made up of seven stages: egg, prelarva, larva, protonymph, deutonymph. tritonymph. and adult. Of these, only the larva, deutonymph and adult are active. Larvae are usually parasitic on insect hosts and are able to exploit hosts from different habitats: whether continually aquatic, associated with the water surface, or aerial insects with aquatic immature stages (Gledhill, 1985). It is, however, the impact of predation by the free-living adult which is the subject of this paper. The adult feeds by puncturing the soft-bodied simuliid larva and sucking the body fluids from its victim. The mite injects saliva which may contain a toxin to paralyze or subdue the host, thus allowing easier feeding. The effect of such feeding is invariably fatal to the *Simulium* larva (J.M. *pers. obs.*)

Virtually nothing is known about the role mite predators play in the regulation of aquatic invertebrate populations, with the exception of a series of papers by Ten Winkel (1987) and co-workers which have attempted to qualify mite consumption of chironomid larvae in lentic systems. Previous work on simuliid-mite host relationships has only considered the role of the blackfly as a dispersal agent for mite larvae (Gledhill *et al.*, 1982; Smith, 1988a; Gerson & Smiley, 1990). Because the possible role of watermites as simuliid predators has not previously been recognized this study has attempted to answer the following fundamental questions:

1. Which species of watermites predate simuliid larvae?
2. How many simuliid larvae does a mite consume?
3. Does the mite display preferences for certain prey stages?
4. Are watermites and *Simulium* larvae sympatric?

Methods

To answer the first question, initial observations of watermite predation of blackfly larvae were carried out in a glass aquarium, 45x30x6 cm, at room temperature. Large (approximately sixth instar) simuliid larvae were offered to watermites, and those observed feeding on simuliid larvae were removed with the simuliid for identification. The details of mite feeding behaviour were also observed. The species of watermites found in river sites were thus divided into predator and non-predator classes.

i) Fieldwork

Two sections of the River Ouse which were considered to be typical pool and riffle systems were chosen as the study sites (o.s. map no 152 grid ref. 335 695 and 340 679). The first section was 2.5 km in length and ran between two bridges (Hunter Street and London Road) in the town of Buckingham (Bucks. UK) and was visited on a weekly basis between 18.4.90 and 29.6.90. The second section was approximately 5km upstream of Buckingham, at the village of Radclive (Bucks.).

Ranunculus sp. was abundant for most of the summer and provided the habitat from which simuliids and watermites were sampled. Grazing of *Ranunculus* by ducks was insignificant at Radclive, which was taken as the main sampling site from mid-June onwards.

A single core sample was taken weekly at the Buckingham site, from a randomly chosen *Ranunculus* bed for the first 16 weeks of the study. This gave an estimate of the relative numbers of larval simuliids and watermite adults. The core sampler was 27cm in diameter, with an area of 572.5cm². Core samples were sieved and sorted in trays. Core samples were not replicated and cannot be regarded as more than indicators of the relative abundance of simuliids and predatory mites in these stretches of the river.

To answer the question 'Are watermites and *Simulium* larvae sympatric?', *Ranunculus* weedbeds from the water surface to a depth of approximately 3cm below the surface, were sampled using a 15cm quadrat at the Radclive site. One sample (225cm² area) was taken each day for 4 consecutive days between 23.7.90-26.7.90 inclusive, during which period the flow rate of the river did not significantly change. This sampling also gave an estimate of the relative abundance of other likely mite prey, (chironomid larvae and caddisfly nymphs) during this late July period. Data were averaged to give a mean density of each species over the 4 days.

ii) Laboratory studies

Simulium larvae were taken from the river by agitating a weedbed by hand: dislodged larvae were caught in a dip net placed immediately downstream of the weedbed. Larvae were sorted and kept alive in the lab in large beakers of river water on magnetic stirrers. Watermites were collected from the river in a similar manner. The two most abundant mite species showing predatory behaviour in the earlier observations were selected for experiments: *Hygrobates fluviatilis* (Ström) and *Lebertia (Pilolebertia) porosa* Thor.

Blackfly larvae require clean flowing water and an appropriate food supply to survive. Therefore, experiments were run using the following apparatus. This comprised a tray of 2mm thick glass 45cm x 30cm, slightly tilted and placed such that water overflowing from the tray poured over a lip 3cm high and into a recirculation tank from where it was pumped back to the top of the tray. Cells were constructed from large glass microscope slides and measured 7.5m long by 5cm wide by 5cm high. The front and back of the cells were covered in fine mesh (2μm) to permit the through-flow of water. Six cells were lined up across each tray, in one or more rows (6 or 12 cells in total) to give identical experimental chambers for confining mites and simuliids together.

Methylene blue dye was used to show uniformity of flow characteristics of each cell and to calculate the current speed of the apparatus which ran at a flow rate of 47 cm³ sec⁻¹. The water in the system was replaced each day with fresh river water to supply the simuliid larvae with food and to remove metabolic waste. Experiments were run at ambient temperatures.

iii) Experimental procedures

Mortality of *Simulium* larvae was avoided by replacing control and experimental larvae on a daily basis. Watermites were not so sensitive and remained *in situ* for the duration of each experiment. Death of simuliid larvae due to mite predation was determined by inspection of larvae under a dissecting microscope. The victims of mite attacks all bore a distinct puncture mark on the soft parts of the body, which when gently squeezed, allowed the escape of body contents. Mites were never observed feeding from dead *Simulium* larvae, thus, death by predation could be differentiated from death by other causes.

Two size classes of larvae were used in the experiments: small larvae were second and third instars with head capsule lengths of 0.37-0.54 mm. Large larvae were generally sixth instar with head capsule lengths of 0.75-0.86 mm and with obvious histoblasts. Head capsules were measured from the most anterior point between the cephalic fans to the posterior dorsal edge of the head capsule during a calibrated eyepiece graticule to an accuracy of 1.2×10^{-2} mm.

Experimental

Experiment 1: Rate of predation of large and small larvae by Hygrobates fluviatilis *and* Lebertia porosa.

In this experiment, 15 blackfly larvae of different size classes were placed in each cell together with 5 female watermites of one particular genus. Two lines of cells were set up in the tray. Small larvae were placed in the first row of cells: 2 cells contained *H. fluviatilis*, 2 cells contained *L. porosa,* and 2 cells were left as controls (simuliid larvae only). Large larvae were placed in the second line of cells together with mites of each species as for the small larvae. The position of each type of cell was randomized across the rows.

The experiment was run for 6 days and repeated for *H. fluviatilis* alone with a 5-day run. Thus, the *Lebertia* results are for 2 replicates, whereas the *Hygrobates* results are based on 4 replicates for 5 out of 6 days. Water temperatures during this period ranged between 19-23°C.

Experiment 2: Differential attack of small and large larvae by individual Hygrobates fluviatilis *females.*

H. fluviatilis females were confined individually in cells containing 5 small (second and third instar) and 5 large (sixth instar) larvae. Larvae were replaced each day as usual, and the daily mortality of each instar was recorded. A total of 9 experimental and 3 control cells were set up in two randomized rows of 6 cells. The experiment ran for 5 days. Water temperatures ranged from 21-23°C.

Results

Three species of watermite, out of seven species examined, clearly showed predatory

behaviour toward large simuliid larvae (Table 1). Both *Hygrobates fluviatilis* and *Lebertia porosa* were very common in the River Ouse and were thus selected for study. The observed responses of simuliid larvae to mite attack included convulsive bending and twisting of the body — presumably aimed at dislodging the mite. The larvae also produced strands of silk on occasions, which would entangle the mite and halt its attack. Such predator attacks on larvae may cause larvae to detach from their substrate and drift downstream to an alternative site. Such drift patterns are well known in Simuliidae (Muirhead-Thompson 1987), but there may well exist larval mortality risks associated with this behaviour.

Table 1. Species of adult watermites showing predatory or non-predatory behaviour towards simuliid larvae in a laboratory aquarium.

Predatory species	Non-predatory species
Lebertia (Pilolebertia) porosa Thor	*Torrenticola anomala* (Koch)
Hygrobates fluviatilis (Ström)	*Hydrodroma torrenticola* (Walter)
Hygrobates longipalpis (Herman)	*Aturus scaber* Kramer
	Midiopis orbicularis (Müller)

i) Fieldwork

Only two species of blackfly were routinely identified in field samples: *S. equinum* comprised 94.1% of the total field sample, and *S. ornatum* the remaining 5.9%. These species could easily be distinguished in the larval stage by head capsule markings. No distinction was made between these species of blackfly in the experiments.

Core sampling considered a cross-section of the weedbed, from surface to gravel bottom. The fact that the core samples were single (unreplicated) samples prevents any detailed analysis. *H. fluviatilis* was more common than *L. porosa.* The mean adult mite density ($\pm$SE) over the 16 weeks of the study was: 260.9 ± 42.3 m^{-2} for *H. fluviatils,* 102.6 ± 14.1 m^{-2} for *L. porosa,* and 35.9 ± 9.6 m^{-2} for other species. Watermites had significantly female biased secondary sex ratios: *H. fluviatilis* 38.9% male ($\chi^2=11.75$, d.f. $=1$, P<0.001, n=239), *L. porosa* 38.3% male ($\chi^2=5.15$, d.f. $=1$, P<0.05, n=94). Over 16 weeks the mean ($\pm$SE) simuliid larval density was 686.3 ± 135 m^{-2}. The spatial distribution of simuliids was more patchy than of mites. Simuliid densities from core samples ranged from 175 m^{-2} in mid-June at Buckingham, to 161 m^{-2} in late July at Radclive. A marked drop in the water level in late June permitted increased grazing of *Ranunculus* by ducks. This habitat destruction meant that from 7 June to 11 July no blackfly larvae were found in core samples. The mean simuliid density given above did not include this period. Watermite adults, however, were present for the entire season, presumably moving from the weed into the gravel riverbed.

Data from core sampling did not prove that mites and simuliids occurred together in the same micro-habitat and were therefore likely to interact. However, the results of the repeated, short-term sampling of *Ranunculus* quadrat (Table 2) showed that watermites occurred in abundance in this topmost fraction of the *Ranunculus* bed, in close proximity with the *Simulium* larvae. The mean density of blackfly larvae was more than an order of magnitude higher than any other species recorded, and far outnumbered the alternative mite prey items: chironomid larvae and caddisfly nymphs.

Table 2. Density of simuliid and chironomid larvae, caddisfly nymphs and predatory *H. fluviatilis* and *L. porosa* adults found in quadrat samples of *Ranunculus* on four successive days in July 1990 in the Great Ouse River at Radclive.

Species	Density of each invertebrate group m^{-2} at each sampling date				Mean ± SE
	23.7.90	24.7.90	25.7.90	26.7.90	
Blackfly larvae	5,956	11,156	11,956	11,022	10,022 ± 1,371
Watermite adults	755	800	889	711	789 ± 38
Caddisfly nymphs	356	2,533	489	400	945 ± 530
Chironomid larvae	178	222	222	311	233 ± 28

ii) Laboratory Studies

Only the deaths which could definitely be attributable to mite predation were recorded in the results of the laboratory work. With daily replacement of simuliid larvae, the frequency of unexplained deaths was consistently very low in all the laboratory work.

Experiment 1: Rate of predation of small and larve larvae

There were no significant differences in the number of sixth instar larvae eaten by each mite species ($\chi^2 = 0.93$, d.f. = 1, N.S.). This was an average of 0.48 larvae mite^{-1} day^{-1} for *H. fluviatilis* females and 0.58 larvae mite^{-1} for *L. porosa* females (Table 3). The mean number of second and third instar larvae predated was the same for both mite species at 1.40 larvae mite^{-1} day^{-1}. The rate of predation did not change appreciably during the period of the experiment for either mite species offered either larval size class.

Experiment 3: Differential attack of small and large larvae by H.fluviatilis

The logical progression of the first experiment was to see whether the differential rate of predation by watermites was expressed as a preference for one size class: when simultaneously offered large and small larvae, was one size exploited more

Table 3. Mean daily rates of predation of *Simulium* larvae by *H. fluviatilis* and *L. porosa* when confined separately with 5 mites and 15 larvae per cell over a six day period (Experiment 1 in text).

	Hygrobates fluviatilis		Lebertia porosa	
	2nd and 3rd instar	6th instar	2nd and 3rd instar	6th instar
Day 1	8.5	1.5	7.0	3.0
Day 2	8.5	2.8	8.5	4.0
Day 3	5.5	2.0	6.5	3.0
Day 4	7.25	3.0	5.5	3.5
Day 5	6.0	2.5	4.0	2.0
Day 6	5.5	3.0	6.5	2.0
Total number of larvae eaten	154	53	84	35
Number of replicate cells	4*	4*	2	2
Mean no. larvae eaten cell^{-1} day^{-1} (±SE)	7.0±0.46	2.41±0.15	7.0±0.62	2.92±0.23

*Four replicates for 5 out of 6 days of the experiment, 2 replicates thereafter.

than the other? The results in Table 4 were unambiguous. Overall, individual female *H. fluviatilis* preyed upon 17 times more second and third instar larvae than sixth instar ($\chi^2 = 143.1$, d.f. $= 1$, P<0.001). The rate of predation or size preferences did not change appreciably over the 5 days of the study. The reasons for such polarity in mite attacks are discussed later.

Discussion

The two most common mite species in the river both proved to be simuliid predators: *H. fluviatilis* and *L. porosa*, and were observed with simuliid larvae in the uppermost fraction of the *Ranunculus* bed. Usually, watermites are considered to be inhabitants of the riverbed. The fact that they were numerous in the same micro-habitat as simuliid larvae and were observed interacting with *Simulium* larvae suggests that mites may actively seek out simuliids as food.

When offered simultaneously, sixth instar *Simulium* larvae were almost completely neglected in favour of smaller, third instar larvae. There may be two reasons for this:

Table 4. Differential predation of *Simulium* larvae when five large and five small larvae were offered simultaneously to individual female *H. fluviatilis* (n=9) over a five day period (Experiment 2 in text).

	Number of larvae eaten each day	
	2nd and 3rd instar larvae	6th instar larvae
Day 1	17	0
Day 2	27	2
Day 3	27	0
Day 4	24	3
Day 5	27	
Total no. larvae eaten	122	7
Mean no. larvae eaten mite^{-1} day^{-1}	2.71	0.16

1. Larger larvae clearly represent a greater food resource. A single meal from a large larva may equate to several feeding bouts on smaller larvae.

2. Larger larvae may be better able to defend themselves against mite attacks (JM, pers. obs.). As such, the handling time and risk of injury to a watermite by attacking a large larva could outweigh the extra search time needed to find and feed from several smaller but more susceptible larvae.

There are, however, obvious criticisms of the laboratory experiments relevant to the findings we have presented:

i) *Simulium* larvae were the only food resource available to the watermites. In the natural habitat a larger choice of prey items are usually available in varying proportions for these predators.

ii) The relatively warm temperatures of the laboratory experiments (19-23°C) could have produced a higher level of mite activity than would be seen in a typical lowland river in mid-summer (14-20°C - TW, pers. obs.), and consequently may overestimate the rate of predation usually practised by watermites.

iii) Being contained in cells, *Simulium* larvae had no means of escape from mite attacks. The role of drift behaviour in lotic invertebrates in response to factors including predator attack, may be highly influenced in affecting prey selection by watermites, although this remains poorly understood. In addition, current speeds in the laboratory may not have accurately reflected the field situation.

High current speeds may limit the ability of watermites to hunt through weedbeds in search of prey.

However, if we consider the relative densities of simuliid and chironomid juveniles found in the quadrat samples taken in late July, blackflies outnumbered chironomids by 43 to 1. It seems unlikely that generalist predators such as watermites would avoid taking such abundant prey in favour of relatively rare alternative items.

By using data from laboratory and field together, the impact of mite predation on larval simuliid populations could be tentatively estimated (Table 5). These estimates are subject to the same criticisms as the laboratory results which may have

Table 5. Estimates of watermite predation in lotic systems using laboratory data on the rate of *Simulium* predation and field estimates of watermite densities.

	Population density estimated by core sample (Buckingham sample) (mean over season ±SE	Population density estimated by quadrat sample in July (Radclive sample) (mean ±SE
Simulium larval density (m^{-2})	686 ±135	10,022 ±1,371
Adult watermite density (m^{-2})		
H. fluviatilis	261 ±43	
L. porosa	103 ±14	
Total	363 ±52	789 ±38
Estimated predation from laboratory studies (larvae mite^{-1} day^{-1}	early instars: 1.4±0.09 late instars: 0.52±0.06	
Theoretical maximum *Simulium* mortality due to mite predation (larvae m^{-2} day^{-1})	early instars: 509 late instars: 189	early instars: 1105 late instars: 410

appeared unnaturally high, although estimates of mite population density compare well with published data (Ten Winkel, 1985, Wiles, 1990). In addition, adult feeding activity is most intense in late spring and early summer. By the late summer, reproduction has ceased and senescence causes a decline in the adult mite population. Most British simuliids are multivoltine, often having more than 3 or 4 generations annually (Crosskey, 1990). Consequently, mite predation is likely to have its largest effect on the early generations of these Diptera. By mid-season, mite nymphs (deuto-nymphs) would probably be more significant predators than their adult conspecifics.

Reported densities of simuliid larvae are highly variable depending on site, season, sampling method etc., but figures from southern English rivers peak at: 3×10^5 m^{-2} of substrate (Ladle et al. 1972), 1.6×10^5 m^{-2} on artificial samplers in Oxfordshire (TW, pers. obs.), 1.0×10^4 m^{-2} (this study, late July). With the lowest estimate of mite density as 363 m^{-2} and the shortest possible simuliid generation time, some 28 days at UK temperatures (Simmons & Edman, 1981; Ham & Bianco, 1984; Crosskey, 1990; TW, pers. obs.), then adult watermites could theoretically account for death of 1.4×10^4 early instars, or 5.4×10^3 late instars m^{-2} generation^{-1}. These figures represent a substantial impact on the peak simuliid populations.

Previous studies of watermite predation have focused on mosquito larvae as mite prey. The rates of predation observed in such studies were between 5 and 8 early instar mosquito larvae per mite per day (Laird, 1947, Smith, 1988b), which compared favourably with the values for small *Simulium* larvae herein. Ten Winkel (1985) studied the predation of chironomid larvae (mainly *Stictochironomous stictius*) by the adult watermite, *Hygrobates nigromaculatus*. He found that, in the absence of fish predation, this mite was primarily responsible for a decline in the chironomid larval population of 80% over the summer months in a Dutch lake. In the presence of cyprinid fish, Ten Winkel & Davids (1985), Ten Winkel & De Nobel (1987) later estimated annual chironomid predation by mites at 1×10^5 larvae m^{-2} yr^{-1}. This was somewhat less than their estimated predation by cyprinid fish: 1.33×10^5 larvae m^{-2} yr^{-1}. This level of mite predation with a mean *Hygrobates* population ($\pm$SE) of 650 ± 179 mites m^{-2} (Ten Winkel, 1985) suggests that an average mite preyed on approximately 150 chironomid larvae per year.

This study has only considered the role of predation by adult watermites on simuliid larvae. Observations in the laboratory indicated that adult mites will also attack *Simulium* pupae, despite the protection afforded by the pupal cocoon and cuticle (J.M., pers. obs.). The free-living deutonymph is also predatory and must feed before moulting into the inactive tritonymph stage. How many simuliid larvae are likely to be exploited by this younger deutonymph stage remains unknown. To our knowledge, mite-*Simulium* predator-prey relationships have not previously been recognized. We hope the results of this preliminary study stimulate a more thorough investigation of the predatory role watermites play in aquatic ecosystems.

Summary

The predatory nature of the adult stage of some aquatic mite species has not been appreciated. Two common species of UK watermite, *Hygrobates fluviatilis* and *Lebertia porosa* were shown to be predators of blackfly (Diptera: Simuliidae) larvae. The rate of adult mite predation of large (6th instar) and small (2nd + 3rd instar) *Simulium* larvae was determined in the laboratory as approximately 0.5 and 1.4 larvae mite^{-1} day^{-1} respectively. When offered small and large larvae simultaneously, *H. fluviatilis* showed a distinct preference to attack younger larvae. Watermites and *Simulium* larvae occurred together in the same micro-habitats and blackfly larvae were the most abundant food items available to mites searching

weedbeds. Tentative estimates of the possible impact of mite predators on larval blackfly populations were calculated as a maximum of *ca.* 1.4×10^4 *Simulium* larvae m^{-2} generation^{-1}.

References

Becker, N. & Margalit, J. (1993) Use of *Bacillus thuringiensis israelensis* against mosquitoes and blackflies. In: Entwistle, P., Cory, J.S., Bailey, M.J. & Higgs, S. (eds.): *Bacillus thuringiensis,* an environmental biopesticide. pp 147-170, Wiley, Chichester.

Crosskey, R.W. (1990) *The natural history of blackflies.* 711pp, Wiley, Chichester.

Davies, D.M. (1981) Predators upon blackflies. In: Laird, M. (ed.). *Blackflies: the future for biological methods in integrated control.* pp 139-158, Academic Press, London.

Gerson, U. & Smiley, R.L. (1990) *Acarine biocontrol agents.* 174pp, Chapman and Hall, London.

Gledhill, T. (1985) Water mites − predators and parasites. Freshwater Biological Association Annual Report, **53:** 45-59.

Gledhill, T., Cowley, J. & Gunn, R.J.M. (1982) Some aspects of the host-parasite relationships between adult blackflies (Diptera: Simuliidae) and larvae of the watermite *Sperchon setiger* (Acari: Hydrachellae) in a small chalk stream in southern England. *Freshwater Biology,* **12:** 345-357.

Ham, P.J. & Bianco, A.E. (1984) Maintenance of *Simulium Wilhelmia lineatum* Meigen and *Simulium erythrocephalum* de Geer through successive generations in the laboratory. *Canadian Journal of Zoology,* **62:** 870-877.

Lacey, L.A. & Undeen, A.H. (1987) The biological control potential of pathogens and parasites of black-flies. In: Kim, K.C. and Mettitt, R.W. (eds.) *Blackflies.* pp 327-340, Pennsylvania University Press.

Ladle, M., Bass, J.A.B. & Jenkins, W.R. (1972) Studies on production and food consumption by the larval Simuliidae (Diptera) of a chalk stream. *Hydrobiologia,* **39:** 429-448.

Laird, M. (1947) Some natural enemies of mosquitoes in the vicinity of Palmalmal, New Britain. *Transactions of the Royal Society New Zealand,* **76:** 453-476.

Muirhead-Thompson, R.C. (1987) *Pesticide impact on stream fauna with special reference to macroinvertebrates.* 275pp, Cambridge University Press.

Simmons, K.R. and Edman, J.D. (1981) Sustained colonization of the black fly *Simulium decorum* (Diptera: Simuliidae) in the laboratory. *Canadian Journal of Zoology,* **59:** 1-7.

Smith, B.P. (1988a) Host parasite interaction and impact of larval watermites on insects. *Annual Review of Entomology,* **33:.** 487-507.

Smith, B.P. (1988b) Potential of watermites as biological control agents. In: M.A. Hoy, G.L. Cunningham and L. Knutson (eds.) *Biological Control of pests by mites.* pp 79-83. University of California Special Publications No. 3304.

Ten Winkel, E.H. (1985) The influence of predation by the water mite *Hygrobates nigromaculatus* on a population of chironomid larvae. *Verh. Internat. Verein Limmnol.* **22:** 3230-3232.

Ten Winkel, E.H. (1987): *Chironomid larvae and their foodweb relations in the littoral zone on Lake Maarsseveen.* 145pp. PhD thesis, University of Amsterdam.

Ten Winkel, E.H. and Davids, C. (1985) Bioturbation by cyprinid fish affecting the food availability for predatory water mites. *Oecologia,* **67:** 218-219.

Ten Winkel, E.H. and De Nobel, J.G. (1987) Prey and nutritional characteristics of the watermites *Hygrobates nigromaculatus* Lebert and *Hygrobates trigonicus* Koenike. In: Ten Winkel, E.H., *Chironomid larvae and their foodweb relations in the littoral zone on Lake Maarsseveen.* PhD thesis, University of Amsterdam, 145pp.

Wiles, P.R. (1990) The Watermites (Acari: Hydrachinidia) of North Sulawesi. In: Knight, W.J. and Holloway, J.D. (eds.) *Insects and the rainforests of South-East Asia.* pp343.