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MICRODISTRIBUTION AND COLONIZATION OF *SIMULIUM VITTATUM* (DIPTERA: SIMULIIDAE) LARVAE ON NATURAL AND ARTIFICIAL SUBSTRATES

by

Sherry Alison Beckett

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submitted to the
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ABSTRACT

Black fly larvae are relatively sessile suspension-feeders that rely on the current of lotic waters to carry suspended food particles to specialized feeding structures (labral fans), and require a substrate for attachment. Simulium vittatum Zetterstedt (Diptera: Simuliidae) most commonly occurs on hard substrate (stones). Periphyton on the substrate may deter larval colonization or establishment.

I conducted a field study of natural substrates (cobbles) in two streams to examine microhabitat selection by larvae through correlations of black fly density with measured abiotic quantities. Flow variables (Froude number) best explained larval densities whereas combined substrate surface qualities (evenness, amount of periphyton) were of secondary importance. Positive correlations were found between simuliid densities and those of other taxa, especially chironomids (Diptera), suggesting co-occurrence.

Laboratory experiments examined larval black fly responses to specific substrate characteristics (evenness, texture, periphyton). At low density (2-4 larvae/cm^2), larvae avoided smooth, even substrates. At high density (10+ larvae/cm^2), there was no apparent selection, except in the presence of periphyton. Then, texture was important: more larvae remained on smooth, even and uneven tiles after 24 h than on rough, even and uneven tiles, presumably due to lower periphyton levels on smooth tiles relative to rough tiles. However, behavioural aggregation responses predominated over substrate responses in that larvae formed bands transverse to the direction of water flow, on all tile types, at all densities.

A field colonization experiment demonstrated that black flies colonize new habitat (ceramic tiles) quickly (within 24 h). Numbers subsequently decline with time due to habitat degradation as periphyton

and other materials accrue. Biotic interactions played a complex role. Other taxa on young tiles apparently exerted a negative influence on simuliids. Although periphyton levels were equivalent among treatments, biotic patterns suggested that grazer/collector-gatherers might facilitate simuliid colonization on older substrates, perhaps by consuming and thereby reducing accrued periphyton. Amount of material on hard substrates appears to be most important in controlling black fly microdistribution within areas of suitable flow, although surface textural features and biotic interactions may modify responses.

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GENERAL INTRODUCTION

Simulium vittatum Zetterstedt is one of five multivoltine simuliid species complexes in North America, comprised of two sibling species (morphologically identical, but differing at the chromosomal level; Adler and Kim 1984). Simulium vittatum is widely distributed throughout the world (Crosskey 1981). Simuliids are restricted to faster-flowing areas in lotic systems (Cummins 1987). Most species of black fly larvae are suspension-feeders (Cummins 1987), consuming mainly particulate organic matter (0.5 μm - 150 μm; Kurtak 1978, Ross and Craig 1980, Wotton 1985), but they may browse periphyton occasionally (Chance 1970). Kurtak (1978) estimated filtering efficiency to be 1-10% of particles available within the size fraction consumed by larvae. Hart and Latta (1986) found efficiency to be less than 1%.

The ecological significance of black flies lies in their interactions in the food web of both the aquatic and terrestrial systems. In the water, larvae process ultra-fine and fine particulate organic matter, recycling the particles back into the energy flow of the system. They also act as prey for some taxa, including hydropsychid caddisflies (Peterson and Davies 1960), Dugesia flatworms (Hansen et al. 1991), and some fishes (Davies 1991), especially during their presence in the drift. Larvae are hosts for pathogens such as mermithid nematodes, and most mortality in the life cycle occurs during the egg stage and first larval instar (Cummins 1987).

In terrestrial systems, winged adults can serve as vectors of serious disease. In Africa and parts of Central America, for example, black flies are carriers of the filarial nematode Onchocerca volvulus that causes river blindness in humans. Thus, they form an important link in the life cycle of this organism and other parasites. Flies also provide an important food source for other invertebrates and vertebrates. Adults also seek vertebrate hosts (humans, cattle,

poultry) for bloodmeals, and economically, their abundance creates problems in the associated industries, as well as in the development of certain areas such as northern Canada.

Black flies (Diptera: Simuliidae) are holometabolous insects; development proceeds through egg, larva, pupa and adult stages. Eggs, encased in a gelatinous matrix, are deposited at dusk singly, in strings or in clusters directly into the water at streamside or onto vegetation or other available substrate. Larvae hatch within a few days (during summer), and attach to substrate in suitable areas of flow. Feeding continues for 2-4 weeks (during summer), but overwintering larvae may live for as much as six months (Colbo and Wotton 1981). The number of larval instars in the Simuliidae varies from 6-9, depending on the species (Colbo and Wotton 1981). Simulium vittatum typically has 5-7 larval instars (Ross and Merritt 1978, Colbo and Okaeme 1988, Colbo 1989), but can vary from 5-11, depending especially upon temperature (Ross and Merritt 1978, Porter and Colbo 1981, Colbo 1989). The pharate pupa (final larval instar) feeds and spins a silk cocoon for the pupa that will firmly attach to the substrate. Pupae are cone-shaped, and face the posterior end (small end) into the current. Respiration occurs through spiracular gills. The pupal stage lasts 3-4 days (summer). Adult terrestrial flies float to the water surface in an air bubble to emerge. Adults feed on plant nectar prior to mating in swarms. Simulium vittatum exhibits facultative autogeny (i.e., provided that larvae have obtained high quality food in sufficient quantities, a blood meal is not required for maturation of the eggs, and females oviposit following nectar feeding). If larval conditions were poor, female adults seek a host (following nectar feeding), digest a bloodmeal (3-6 days), and await development of the eggs (3-7 days), prior to oviposition. Black flies are capable of multiple broods, and each successive brood requires a blood meal (Colbo and Wotton 1981).

A fundamental concept in ecological studies is to understand the distribution of biota. Ecologists attempt to identify patterns of distribution and determine the mechanisms accounting for these patterns (Hart 1983). In lotic systems, abiotic and biotic factors may both contribute to such patterns in varying degrees, as well as to the abundances of the organisms involved (Power et al. 1988).

Simulium vittatum Zetterstedt inhabits primarily stony substrates (Colbo and Moorhouse 1979, Adler and Kim 1984) in riffles, but given suitable flow, may also adhere to trailing grasses (Adler and Kim 1984). Typically, larvae are patchily distributed (Hart 1986), and even within areas of apparently suitable flow, may be present on some cobbles, but absent from adjacent ones. On single stones, areas may be densely packed with larvae while other portions of the same stone remain vacant (Colbo 1987). Hart (1986) suggested that hydrodynamically-suitable feeding sites may be in short supply, thus creating patchy distributions, and forcing larvae to aggregate in the suitable areas.

Black fly immatures tend to aggregate (Wiley and Kohler 1984). Among the various formations exhibited are straight rows or bands (Colbo 1987, Eymann 1990, S.A. Beckett pers. obs.), reticulate patterns ("zigzag" curved rows; Eymann 1991, J.J.H. Ciborowski, Univ. of Windsor, pers. comm.), clusters (Colbo 1979, Eymann 1985, Ciborowski and Craig 1989, S.A. Beckett pers. obs.), and randomness (Eymann 1985, Ciborowski and Craig 1989, S.A. Beckett pers. obs.).

Eymann (1990) suggested that while there is overlap among species in these orientations, not all orientations are displayed by all species, indicating that some level of specificity occurs at the species level. Within aggregations, larvae are commonly observed with relatively equal spacing between neighbours (Colbo 1979, Colbo and Moorhouse 1979, Eymann 1985, Hart 1986, 1987a, Ciborowski and Craig

1989, Eymann 1990, J.J.H. Ciborowski, Univ. of Windsor, pers. comm., S.A. Beckett pers. obs.). These non-random distributions suggest that larvae may select particular microhabitats over others, and particular orientations within these areas.

Intraspecific interactions may be involved in the regularity of separation (distance) between individual larvae. Hart (1986, 1987a) suggested that larvae may be defending a resource (food, space) through territorial behaviour. He found aggressive behaviour was directed principally to the upstream larva that could interfere with the interception of particles for the downstream larva. Wiley and Kohler (1981) found that most intraspecific interactions between simuliid larvae resulted in displacement of at least one member of the pair. Eymann and Friend (1988) noted aggressive interactions resulting in displacement as well. Ciborowski and Craig (1989), however, have suggested that larvae within aggregations may derive additional benefits during feeding provided that larvae are oriented parallel to adjacent individuals.

Indirect evidence suggests that interspecific interactions may also affect larval distributions. Similarities in the mode of feeding (suspension-feeding) and microhabitat preferences may result in the co-occurrence of hydropsychids and black flies. However, these similarities also suggest that the two taxa may interact aggressively to each procure resources from the other. Chutter (1968) found a negative correlation between the presence of hydropsychids and simuliids. Hydropsyche appears to exclude Simulium with time given an absence of environmental disturbance (Cooper and Hemphill 1983, Hemphill 1991). Hemphill (1988) has observed interference interactions between the two genera. Peterson and Davies (1960) noted that hydropsychids were the major predator of black fly larvae in an Ontario stream. Hershey and

Hiltner (1983) found that black fly abundance in experimental cages decreased in the presence of caddisfly larvae.

Many abiotic variables have been argued to affect the distribution of black fly larvae at various spatial scales. These include current velocity (Wu 1931, Phillipson 1956, Phillipson 1957, Chutter 1968, Wotton 1985, Ciborowski and Craig 1989), depth (Carlsson 1962, Lewis and Bennett 1975, Fredeen and Spurr 1978), micro-hydrodynamics (Hocking and Pickering 1954, Maitland and Penney 1967, Décamps et al. 1975, Craig and Chance 1982, Chance and Craig 1986, Craig and Galloway 1987, Lacoursière 1989, Eymann 1990), physical and chemical variables (Corkum and Currie 1987, Ciborowski and Adler 1990), temperature (Colbo and Porter 1981), food (Colbo and Porter 1981, Eymann 1985, Ciborowski and Craig 1989), and substrate (Fredeen and Spurr 1978, Colbo and Moorhouse 1979, Gersabeck and Merritt 1979, Adler and Kim 1984, Das et al. 1988).

Observations in the field imply that black fly larvae avoid substrates with surface coverings of periphyton or silt. Rühm and Pegel (1986b) and Gersabeck and Merritt (1979) noted that larvae colonized clean artificial substrates, but vacated those overgrown with periphyton. Hershey and Hiltner (1988) found that simuliids shifted positions on single cobbles from top surfaces to sides and bottoms where less periphyton occurred. Hemphill (1991) and Hemphill and Cooper (1983) found that scoured substrates in the field remained colonized while controls were abandoned with increasing periphyton growth. Wu (1931) observed the same effect for silt accumulations. To date, these variables have not been assessed experimentally in the laboratory.

Since the larval growth period largely determines future reproduction of the adult, selection of the optimal habitat should be important in the larval stage to ensure maximum reproduction. Since intake of food during the larval stage affects later reproductive output

(the type of reproductive strategy (autogeny or anautogeny), number of batches of eggs, number of eggs per batch, size of eggs), of the adults (Anderson 1987), larvae should optimize their feeding efficiency and food intake to produce the maximum number of eggs. The amount and quality of food acquired by the larva directly affects the size of larvae, which partially determines the number of eggs as a female adult. Larger females produce more eggs (Anderson 1987). Size could also potentially affect the competitive ability of larvae to acquire food (Gersabeck and Merritt 1979, Wiley and Kohler 1981). Therefore, black fly larvae should expend some effort assessing environmental conditions to select the optimal feeding locality. Given the costs to future reproduction and the necessary trade-offs between current velocity and substrate, larvae should select optimal positions in the water column, and on the substrate, to gain the greatest net benefit from their selection of microhabitat. Therefore, microhabitat selection should affect the spatial distribution of larvae.

Simuliids can disperse to vacant habitats or arrive in colonized areas, thereby changing abundances, by looping, drifting on silken threads (life-lines), drifting freely, or by the oviposition behaviour of the adult females. Black fly larvae can disperse for short distances, such as over single stones or among adjacent stones, by looping (Colbo and Moorhouse 1979, Eymann and Friend 1988, Reidelbach and Kiel 1990). This behaviour involves bending the body toward the substrate, producing silk, engaging the anterior proleg, and pulling the posterior end of the body to the new silk patch. Larvae may disperse for greater distances by releasing from the substrate, trailing on a single strand of silk (life-line; Colbo and Moorhouse 1979, Wotton 1986), or by entering the current to drift freely to another habitat (Colbo and Moorhouse 1979, Gersabeck and Merritt 1979, Reidelbach and Kiel 1990). Adler et al. (1983a) noted that larval black flies entered the drift primarily at night.

This study was initiated to examine microhabitat selection of Simulium vittatum Zetterstedt larvae at the micro-scale of investigation (single cobbles). Among abiotic variables potentially affecting these distributions, substrate has received minor consideration. I manipulated substrate characteristics with greater detail to determine their role (importance relative to flow parameters) in the selection of microhabitat. The pattern of colonization and potential mechanisms underlying this pattern were also addressed.

Chapter I describes a survey of natural substrates conducted in two third-order southwestern Ontario streams whereby correlations between a series of potentially influential abiotic variables and black fly densities were used to identify S. vittatum larval microhabitat. Chapter II presents the results of laboratory manipulations of substrates varying in texture, evenness, and periphyton growth. Chapter III describes the development of the community using artificial substrates in the field. The aim of this study was to determine the pattern of larval black fly colonization and attempt to discern the mechanisms accounting for the observed pattern.

I. A SURVEY OF THE LARVAL MICROHABITAT OF S. VITTATUM (DIPTERA: SIMULIIDAE) IN TWO SMALL SOUTHWESTERN ONTARIO STREAMS

INTRODUCTION

One of the major goals in studies of ecology is to explain the distributions of organisms, which are typically non-random. One mechanism by which animals become distributed among habitats (or microhabitats) is habitat selection. Indirect evidence of habitat selection can be obtained through detecting correlations between a variety of factors in the environment and the density of the organism. More conclusive evidence can be obtained through experimental manipulations involving removal or addition of organisms.

This chapter describes the results of a survey of Simulium vittatum Zetterstedt larval microhabitat in two southwestern Ontario streams. Microhabitat preference was identified by associating simuliid density with a variety of abiotic variables measured during the studies. To address a potential biotic influence to S. vittatum distribution, correlations between the most abundant taxa collected and the presence of black fly larvae were investigated.

Habitat is the area in which an animal lives. It is characterized by abiotic and biotic variables. Partridge (1978) describes a habitat as a conglomerate of physical and biotic factors which together make up the place in which an animal lives. Examples of habitats are ponds, marshes, or streams. On a finer scale, the specific locality within the habitat where an animal lives could be termed a microhabitat. There may be many microhabitats within a single habitat.

Habitat selection is the choice of a place to live (Partridge 1978). Habitat selection involves three assumptions. First, it involves the ability of the organism to distinguish among particular biotic and abiotic environmental factors and to respond to them. Second, the quality of patches, as perceived by the organism, differs in the habitat, implying that some areas are more advantageous than others.

Third, there is a heritable component, and populations adapt to the choices available.

The preferred microhabitat of black fly immatures (larvae and pupae) is hard stony substrates or vegetation (grasses) in the riffles of streams and rivers. This apparent preference may be species-dependent (Boobar and Granett 1978, Fredeen and Spurr 1978, Colbo and Moorhouse 1979, Gersabeck and Merritt 1979, Adler and Kim 1984, Das et al. 1988, Pruess 1989). These filter-feeding insects live only in lotic habitats because they rely on the current to carry suspended food particles into their specialized cephalic fans. Simulium vittatum occurs primarily on hard inorganic (cobble) substrates, but may also attach to vegetation (grasses).

On a smaller scale, within larval black fly microhabitat (individual cobbles in riffles), it is commonly observed that larvae are patchily distributed over the substrate (Hart 1986). Larvae may occur on one cobble, but not the adjacent one. Similarly, larvae may occur clumped over a small portion of a single cobble, leaving the remainder of the cobble vacant. Within patches of larvae, individuals may be randomly distributed or they may form dense aggregations. These aggregations may involve larvae that are arranged into groups (Wolfe and Peterson 1958, Maitland and Penney 1967, Elliott 1971, Colbo 1979, Eymann 1985, Ciborowski and Craig 1989), randomly assorted (Eymann 1985, Ciborowski and Craig 1989), or in bands. Band orientation may be parallel to the current (S.A. Beckett pers. obs.) or more frequently, perpendicular to the current (Brenner and Cupp 1980, Colbo 1987, Eymann 1990, S.A. Beckett pers. obs.). Further, within patches, simuliids tend to be uniformly spaced (Hocking and Pickering 1954, Colbo 1979, Colbo and Moorhouse 1979, Eymann 1985, Hart 1986, Colbo 1987, Hart 1987a, Eymann and Friend 1988, Ciborowski and Craig 1989, Eymann 1991, S.A.

Beckett pers. obs.). These dense black fly patches also tend to have relatively few other taxa associated with them.

The distribution of black fly microhabitats is non-random within stream reaches, being restricted to riffles or other areas where suitable substrate projects into areas of suitable flow (e.g., trailing grass blades in non-riffle areas). In addition, the distribution of black fly larvae within microhabitats is also non-random. These distributional patterns suggest that black flies may actively seek some microhabitats over others. Alternatively, differential desertion of microhabitats or mortality could produce the same pattern. Each process would support a hypothesis of microhabitat selection. The first would suggest selection of the preferred microhabitat while the second would involve departure from, or avoidance of, a less preferred habitat.

Both biotic and abiotic factors can potentially affect the distribution of larvae. Indirect evidence suggests biotic (intra- and inter-specific) interactions may influence simuliid microdistribution. Regular separation distances between adjacent larvae in groups is frequently observed (Hocking and Pickering 1954, Colbo 1979, Colbo and Moorhouse 1979, Eymann 1985, Hart 1986, Colbo 1987, Hart 1987a, Eymann and Friend 1988, Ciborowski and Craig 1989, Eymann 1991, S.A. Beckett pers. obs.) and suggestive of territorial behaviour, and defense of a resource (Hart 1986, 1987a). The lack of other organisms occurring in close proximity to these larval aggregations is suggestive of interspecific interactions that may possibly result in the exclusion of other taxa. Hemphill (1988) has observed interference between S. vittatum larvae and Hydropsyche oslari. If black fly larvae can exclude other taxa from their preferred microhabitat, then they may be competitive dominants. However, the role of competition may be minor if the succession of biota (insects, algae) results in the separation of

black fly taxa from other insects. This pattern may be due to such successional changes in the natural progression of river fauna.

Many abiotic variables have been argued to affect the distribution of black fly larvae at various spatial scales (Ross and Merritt 1987). The most important abiotic variable affecting black flies is current velocity (Wu 1931, Phillipson 1956, 1957, Chutter 1968, Wotton 1985, Ciborowski and Craig 1989). Substrate may also affect larval distributions. Larval species may have a predisposition for one substrate type over another (Colbo and Moorhouse 1979, Gersabeck and Merritt 1979, Adler and Kim 1984, Das et al. 1988, Pruess 1989).

For black fly larvae, the current is important to larval feeding because 1) it brings food particles to the larva; 2) it determines the rate of particle delivery, and 3) it determines the orientation of the larva and its ability to remove the particles from the water. Since faster current delivers more food, it should thus be more desirable for a larva to select microhabitats with faster rather than slower-flowing water. However, the interaction between the substrate, organism, and current velocity also influences the optimality of the larva's choice of microhabitat. Shear stress and drag forces increase with the current velocity (Vogel 1981, Eymann 1991). Therefore, larvae would be expected to balance the benefit of greater rates of food delivery from higher current velocities with the costs of increasing shear stress and drag (Hart et al. 1991). As a result, areas of maximum velocity in the stream may not be the optimal microhabitat for larvae.

A second feature of the microhabitat which would be expected to influence microhabitat selection by black fly larvae is substrate. Most larval species require a hard, stable substrate such as stone to which the posterior end of the larva is attached by a pad of silk. Anchoring of the larva is crucial to the ability of the larva to filter feed. The

characteristics of the substrate may influence the ability of the larva to become securely attached to the surface, since the silk pad may adhere better to some types of surfaces than others. Studies by Fredeen and Spurr (1978), Colbo and Moorhouse (1979), Gersabeck and Merritt (1979), Adler and Kim (1984), and Das et al. (1988) suggest substrate preference may occur among larvae of black flies. However, these studies did not examine the effects of specific substrate attributes. Aspects such as texture (the size and type of surface projection and irregularity), evenness (the presence or absence of coarse surface projections), accumulation of periphyton, or of silt, could affect larval attachment.

These abiotic factors, and others (depth, temperature, physico-chemical parameters; Ross and Merritt 1987), and potentially biotic factors also, ultimately influence larval feeding. Food intake during the larval stage affects larval size and therefore, the reproductive output of the female adult (number of batches of eggs, number of eggs per batch), the fitness of the progeny (egg size), as well as reproductive strategy (autogeny vs. anautogeny; Anderson 1987). In addition, larval size may also affect competitive ability (Gersabeck and Merritt 1979). Therefore, one may expect larvae to select optimal microhabitats, which maximize food intake.

The aim of my study was to examine larval microhabitat selection in two southwestern Ontario streams. I studied the field distribution of black fly larvae at the microhabitat scale (on individual rocks), with particular emphasis on the influence of substrate variables on larval microdistribution. Cobbles were selected from a range of conditions within the microhabitat of stream riffles to correlate the distribution of larvae with a variety of biotic and abiotic variables.

My specific objectives in this field study were:

1. To determine which abiotic variables influence microhabitat selection of S. vittatum larvae;
2. To determine which, if any, taxa co-occur with black fly larvae;
3. To examine the potential effects of larval size with respect to larval microdistribution; and
4. To determine the generality of these abiotic and biotic factors to larval black fly microhabitat selection.

To fulfill Objective 1, the microhabitat of simuliid larvae was identified by correlating the abiotic variables with black fly densities, while in Objective 2, I attempted to identify co-occurring taxa by correlating black fly density with densities of the most abundant (>1%) biota. The third objective was to evaluate correlations between the distribution of small and large larvae (using measurements of larvae collected in Hobbs-Mackenzie Creek) and the microhabitat factors. The fourth objective compared the results from the two rivers, potentially yielding patterns of a generalized response to these variables by black fly larvae.

MATERIALS AND METHODS

Experimental Design

Surveys were conducted in two third order southwestern Ontario streams. One survey was conducted in Wigle Creek, 2 August 1989. The second survey was conducted in Hobbs-Mackenzie Creek (HMC), 12-13 July 1990. By selecting two streams with different characteristics (see below, description of 'study sites'), the generality of larval responses to the abiotic factors could be assessed. Practical considerations (streams located reasonably close to the Univ. of Windsor, accessibility to streams, presence of moderate S. vittatum population densities) also contributed to the choice of these particular streams for study.

In each stream, individual cobbles (14.6 - 223.3 cm^2) were collected. All biota were enumerated from each cobble. Various abiotic variables were measured for each single cobble. Cobbles were subjectively evaluated for specific substrate attributes. These independent variables (abiotic factors, substrate characteristics) were used to determine the preferred microhabitat of S. vittatum larvae inferred from larval density in the field. Additionally, the other macroinvertebrate taxa found on cobbles were tabulated to determine the presence of potentially co-occurring taxa. Potential habitat segregation due to size of black fly larvae (as measured by head width) was investigated by separately relating the abiotic variables to the mean larval size per cobble face.

Study Sites

Studies were conducted in Wigle Creek, Kingsville, Ontario, and in Hobbs-Mackenzie Creek, Arkona, Ontario (Fig. 1.1). Wigle Creek is a third order (sensu Strahler 1957) southwestern Ontario stream that flows through farmland. This is a highly productive stream, sparsely shaded by shrubs and a few trees. The study site was located within the Kingsville Golf and Curling Club, immediately downstream of a small

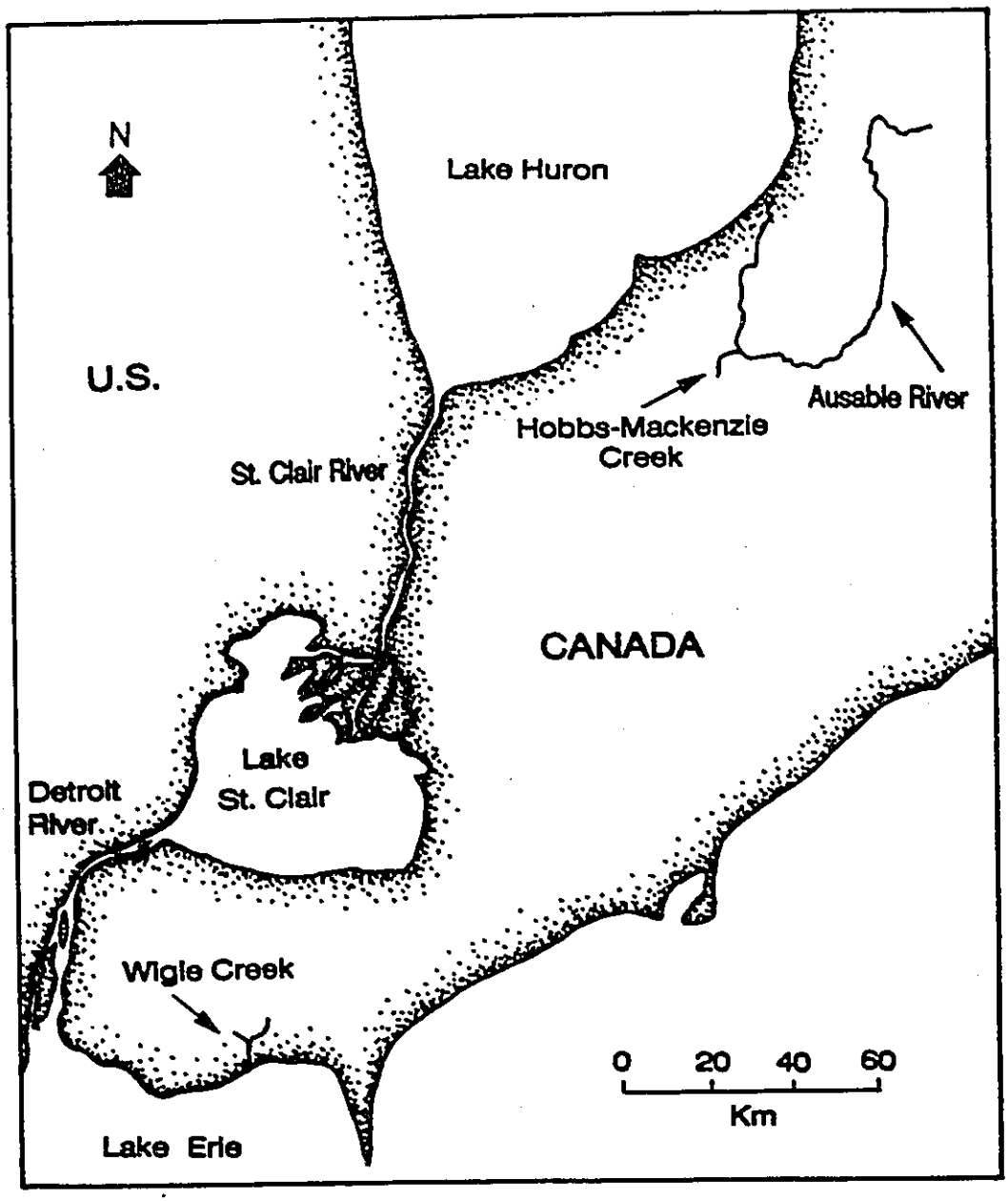


Figure 1.1 Map showing locations of study streams, Wigle Creek, near Kingsville, Ontario and Hobbs-Mackenzie Creek, near Arkona, Ontario, both within the eastern deciduous forest biome of North America.

(approximately 1.3 m wide) dam (42°02'24" N, 82°45'57" W). There are both pools and riffles at the study site. Although the substrate is predominantly cobbles and boulder, there are a few gravel and sand patches, particularly in the pool areas. Water levels were relatively constant during the month of July, and there were no major rainstorms or periods of prolonged light showers for approximately 2-3 weeks prior to the study. Chironomids and simuliids are the dominant taxa present at the site. Simulium vittatum appears in early spring (mid-to late-April), but in late July Simulium decorum Walker begins to appear also, and becomes the more common species present by mid-August (S.A. Beckett pers. obs.).

Hobbs-Mackenzie Creek, also third order, is a tributary of the Ausable River (fifth order), which flows into Lake Huron near Pinery Provincial Park. The study portion of Hobbs-Mackenzie Creek is in a forested river valley located within an agricultural area. It is highly shaded by the forest canopy, which also provides large amounts of leaf fall in the autumn. The study site was located within the Rock Glen Conservation Area (43°05'10" N, 81°48'47" W). There are pools and terraced riffles throughout the stream. The substrate is diverse with primarily small and large cobble, and boulder. There are also patches of gravel, sand and silt. Water levels rose (5-8 cm) during the last week of June, but subsided shortly thereafter. Water levels were relatively constant during the two weeks prior to the study. Benthic taxa are diverse, and small fishes are often present in pool areas. Simulium vittatum is the most abundant simuliid species present in the tributary, although Simulium tuberosum Lundström also occurs in the stream. The species appear to be temporally separated. Simulium vittatum appears in early spring (late April-early May), but numbers decline by late May, at which time the relative proportion of S. tuberosum increases (S.A. Beckett pers. obs.). Prosimulium

mixtum/fuscum complex occurs in the stream during winter (J.J.H. Ciborowski, Univ. of Windsor, pers. comm.).

Sampling Protocol

Sample Collection

Cobbles potentially supporting Simulium vittatum larvae were collected from Wigle Creek, 2 August 1989 and 12-13 July 1990 from Hobbs-Mackenzie Creek. Individual cobbles (Wigle Creek, n=33; Hobbs-Mackenzie Creek, n=70) were selected according to two surface features (evenness and periphyton cover), in areas that varied in depth and current velocity. Cobbles were categorized by visual inspection with respect to periphyton cover and evenness. To ensure that each combination of evenness and periphyton cover was adequately represented, I attempted to obtain a minimum of five cobbles from each combination of the two substrate variables (evenness, periphyton cover), in Wigle Creek. This sample size was not always possible to obtain within specific combinations because "uneven" cobbles were relatively rare.

For Hobbs-Mackenzie Creek, cobbles were selected according to the same criteria as for Wigle Creek. Cobbles were again obtained from areas varying by depth and current velocity. For this river, I attempted to obtain a minimum of 10 cobbles for each cobble surface combination exposed to low and moderate current velocities (current velocity visually assessed, and subsequently measured; substrate attributes (evenness, periphyton cover) visually assessed). No substrate combination had less than nine sample cobbles.

Animals and periphyton were collected separately from the top and bottom faces of the cobbles by placing nylon netting over the top surface. A dip net (mouth 20 cm x 15 cm, mesh 250 μm) was placed directly behind individual cobbles to capture any other animals drifting from the top surface of the cobble. The cobble was placed into an

enamelled tray and the animals and adhering materials were brushed from the uncovered bottom surface, (preserved in Kahle's solution), to comprise the bottom face sample. For the upper face sample, the netting was removed from the top face and preserved in Kahle's solution together with the dip net contents and the animals and material from the top face. In addition, in Wigle Creek, a paint brush and knife were used to remove aufwuchs from the vertical face of a dam (50 cm^2, n=2; 19.5 cm^2, n=2).

Measurements of Abiotic Variables

Depth and current velocity were measured at the location of each cobble sampled. Single measurements of stream discharge (3 in Wigle Cr., taken on the top of the dam), suspended solids (3 in each stream), dissolved oxygen (modified Winkler titration), conductivity (YSI meter, model 33), and temperature were also made. To measure suspended solids, 250 mL of stream water was filtered at the study site onto a preweighed membrane filter (0.45 μm pore size). The filter was wrapped in aluminum foil and placed on ice. In the laboratory, the filter was dried in an oven (GCA model 18EG) for 24 h at 60°C, and then re-weighed.

In both streams, a single measurement of depth was taken from the upper face of each cobble to the water surface. For analytical purposes, this depth was also used to represent the depth for the bottom face sample. In both streams, current velocity (Wigle Creek, Ott C-2 meter, one 50 s reading; Hobbs-Mackenzie Creek, velocity head tube (Ciborowski 1991) was measured at the top face of the cobble, 2 cm above the cobble surface. The velocity head tube is limited in its ability to distinguish between current velocities under 20 cm/s. However, most cobbles were obtained in areas with velocities of 20 cm/s or more. For dam face samples collected from Wigle Creek, it was not possible to measure current velocity at the exact location that the sample was collected. Therefore, current velocity was estimated by a measurement

taken at the nearest point possible to the location of sample removal (Ott C-2 meter). Because the instruments used to measure current velocity did not allow microscale measurements of this variable, I used the mean velocity of water above each cobble as a surrogate measurement for both the top and the bottom surface. This is justifiable provided that there is a good correlation between the variable of interest and the surrogate variable.

Laboratory Sample Processing

Sample Sorting and Taxomomic Identification

Samples were washed through a 90-μm sieve to remove preservative. A 90-μm sieve was selected because the amounts of organic and inorganic sample material passing through this sieve size were negligible. Organisms were sorted under a dissecting microscope (Wild Leitz M5A 12x, 25x, 50x), enumerated, and tabulated. Insects were identified to the lowest practical taxonomic level according to the keys of Merritt and Cummins (1984). Hirudinea were identified using the keys of Pennak (1978). Black flies were identified to species using the key of Currie (1986). Samples were preserved in 70% ethanol. Chironomidae were mounted in CMC-9AF® mounting medium on microscope slides, as whole specimens for younger instars, or separately as head and body for larger individuals. Specimens were identified to genus using the keys of Oliver and Roussel (1983), and Wiederholm (1983) under a compound microscope (Kyowa Medilux-12 400x, 600x, 1000x).

Measurement of Larval Size

The size of black flies collected during my study at Hobbs-Mackenzie Creek was estimated by measuring the width of the head capsule between the centres of the eyespots. Only specimens that were undamaged were measured and used for analysis of size data. Specimens that were visibly distorted by preservation when viewed under the microscope (e.g. swollen head capsule or body) were excluded.

My justification for measurement of head capsule width was based on the literature pertaining solely to larval black flies, and the inconsistencies with respect to the feature selected as described here. Body length is often variable within black flies, depending largely upon rearing conditions (Merritt et al. 1982). Thus, it is rarely used as a measure to estimate larval size because of the ensuing complications in comparisons with other work. A more effective estimate of body size is to measure a sclerotized or less variable structure (e.g., head width). Ideally, proportionality is maintained among such structures and body size, such that the ratio of head width (or any feature measured) to body size remains relatively constant (Daly 1985). Although head width is often the measurement of choice (because of its sclerotization) within insect taxa, Jedlicka (1978) and McCreadie and Colbo (1990) note that, at least for some species of black fly larvae, relative size of this structure may vary depending on the temperature during development.

No single structure has been consistently measured for black fly larvae. Among the measured structures reported in the literature are postgenal length (Fredeen 1976, Colbo and Okaeme 1988, Baba and Takaoka 1989, Colbo 1989, Mohsen et al. 1989, Baba and Takaoka 1990, 1991), head length (Baba and Takaoka 1989), maximum head width (Mohsen et al. 1989, McCreadie and Colbo 1990) maximum width of cephalic apotome (Colbo and Okaeme 1988, Baba and Takaoka 1989, Colbo 1989, McCreadie and Colbo 1990), distance between corner teeth of hypostoma (Baba and Takaoka 1989, Colbo 1988, 1989), distance between first pair of hypostomal setae (Colbo 1988, 1989), length of apical antennal segment (Colbo, 1988, 1989, Mohsen et al. 1989), and relative body size (length; Mohsen et al. 1989, Baba and Takaoka 1991).

Substrate Surface Area

The surface area of each face of all cobbles was estimated by covering the surface with aluminum foil. The aluminum foil was

photocopied, and then the image was measured using a planimeter. The top face was all surface area exposed to the water column. Thus, placement of the netting over the cobble, and holding snugly, delineated top from bottom faces. The area in contact with the stream bed was thus considered the bottom surface. Rühm and Pegel (1986a) documented that only large larvae were located on the underside of stream stones during winter. I have also observed this phenomenon during the summer season, and particularly during early spring and early autumn (S.A. Beckett, Z.E. Kovats pers. obs.). For some cobbles, a small interstitial area was present between the curved edges of the cobble, and the bottom surface in actual contact with the sediments. This interstitial area, exposed to the water, was considered as part of the top surface of the cobble. I attempted to ensure that the netting was placed over this area. However, in practicality, it is probable that for some cobbles the netting was not constricting enough to capture within the netting organisms in this interstitial edge. Therefore, some organisms included in the "bottom" sample may have been organisms from this interstitial area which technically would have been part of the netting top sample. Therefore, in a conservative manner, it is presumed that some bottom face samples may have overestimated black fly densities.

Detrital Material

For both streams, the dry mass of the detrital material (organic and inorganic) was obtained by drying each sample for 24 h at 60°C (GCA model 18EG oven) to provide a measure of total detrital biomass (dry mass) per cobble face. For Hobbs-Mackenzie Creek, this material was then ignited in a muffle furnace (Fisher Isotemp model 184A) for 3 h at 550°C to obtain ash-free dry mass (AFDM) as a measure of the organic material present per face.

Data Analysis

Forward stepwise multiple linear regressions (Sokal and Rohlf 1981) were used to analyze the relationship between abiotic variables and black fly densities. For each river, one regression was used to analyze the effects of the abiotic variables on black fly densities.

Dry mass, ash-free dry mass, silt, as well as all taxa, were converted to densities (quantity/cm^2) prior to analysis. All data (excluding the two-state substrate variables) were Ln(x+1) transformed. Dixon's test (Dixon and Massey 1957) for outliers was performed on all data, and outliers were removed prior to statistical analysis.

To examine biotic associations, Spearman's rank correlation coefficient (Sokal and Rohlf 1981) matrices were generated for all pairwise combinations of taxa that occurred in abundances of at least 1% of the total number of organisms collected (within each stream).

To detect any differences in microhabitat choice due to differences in S. vittatum larval size, a forward stepwise multiple linear regression analysis was used. The dependent variable was black fly size (head width); the independent variables were the same abiotic factors used in the regressions for assessing their effects on black fly densities.

Abiotic Variables

The dependent variable in these regression analyses was black fly larval density. The abiotic factors were the independent variables. Included in the regression used to examine the effects of the abiotic variables were those factors measured in the field (current velocity, depth), several factors based on calculations from measurements in the field (Froude number; a measure of turbulence, given by the formula $Fr= v^2/gd$ where v= current velocity, g= acceleration due to gravity, d=

water depth), the square of Froude number, the square of current velocity, and the interaction term (product) produced between depth and current velocity; one component of Reynolds number also used to describe the turbulence of the flow and given by the formula Re= vd/ν, where v= current velocity, d= water depth, and ν = kinematic viscosity), the detrital material (dry mass for both rivers; ash-free dry mass and silt for Hobbs-Mackenzie Creek), and substrate size (surface area). The substrate attributes, also incorporated in the same regression analysis, were included as two-state variables whereby the distinction between alternative states of the variable was represented by different numbers. These variables were cobble face (bottom=0, top=1), aspect (horizontal cobble=0, vertical wall=1), evenness (even=0, uneven=1), and periphytic cover (absent=0, present=1).

Biotic Variables

The biotic components (dominant taxa) included in the Spearman rank correlation matrices for each river were based on the densities of each taxon collected. Only those taxa comprising at least 1% of the total number of insects collected were included in the analysis. All biota were converted to densities and Ln(x+1) transformed prior to statistical analysis.

Larval Size

Samples for the larval size component of the study were those collected from Hobbs-Mackenzie Creek. Mean larval size (mean head width of larvae per cobble face) was used as the dependent variable in a forward stepwise multiple linear regression. Each cobble face was represented by a single mean size per cobble face, calculated according to the number of larvae per head width, per cobble face, and divided by the total number of larvae in the respective sample. The independent variables were the abiotic factors. These analyses were performed on

Ln(x+1) transformed data because the data were not normally distributed, but skewed to the right.

RESULTS

Physico-Chemical Variables

Table 1.1 lists the physico-chemical parameters measured during the studies. Although both streams are third order, Wigle Creek had greater discharge than Hobbs-Mackenzie Creek. Oxygen in both streams exceeded 100% saturation. Suspended solid concentrations were much higher in Wigle Creek than Hobbs-Mackenzie Creek. Hobbs-Mackenzie Creek is highly shaded, whereas Wigle Creek is much more open. More photosynthetic activity from planktonic algae probably occurs in Wigle Creek (especially in the pond upstream of the dam) than in Hobbs-Mackenzie Creek, which could contribute to the difference in suspended solids levels, which are an estimate of the available food for the black fly larvae.

Wigle Creek, 1989

A total of 4,557 animals was collected from 70 samples during the study. For a complete listing of all taxa collected per sample, and their abundances, refer to Appendix I.1. Four samples were collected from the face of a dam, and 66 samples represented the top and bottom faces of 33 cobbles. Thirty-one taxa were collected (Fig. 1.2). Although the taxonomic richness was relatively high, there were few organisms in the majority of taxa represented. The three most abundant genera were dipteran larvae. The most abundant taxon was S. vittatum whereas the other two were chironomid genera (Polypedilum spp. and Orthocladius spp.).

Among the 31 taxa collected, only eight genera individually comprised more than 1% of the total number of animals collected (Table 1.2). These eight taxa represented the dominant (most abundant) taxa and accounted for 77% of all animals collected. Of these, seven genera were dipteran larvae, representing two families, (Simuliidae and

Table 1.1 Selected physico-chemical variables measured at the study sites, Wigle Creek, 2 August 1989, and Hobbs-Mackenzie Creek (HMC), 12-13 July 1990.

FACTOR	MEASUREMENT	
	WIGLE	HMC
Air Temperature (°C)	29 ± 0.5	26 ± 0.5
Water Temperature (°C)	21 ± 0.5	21 ± 0.5
Conductivity ($\mu S/cm^2$)	590	590
Dissolved Oxygen (mg/L)	11	11
Suspended Solids (mg/L)	35.9 ± 0.2	0.35 ± 0.003
Discharge (m^3/s)	0.09 + 0.02	0.05

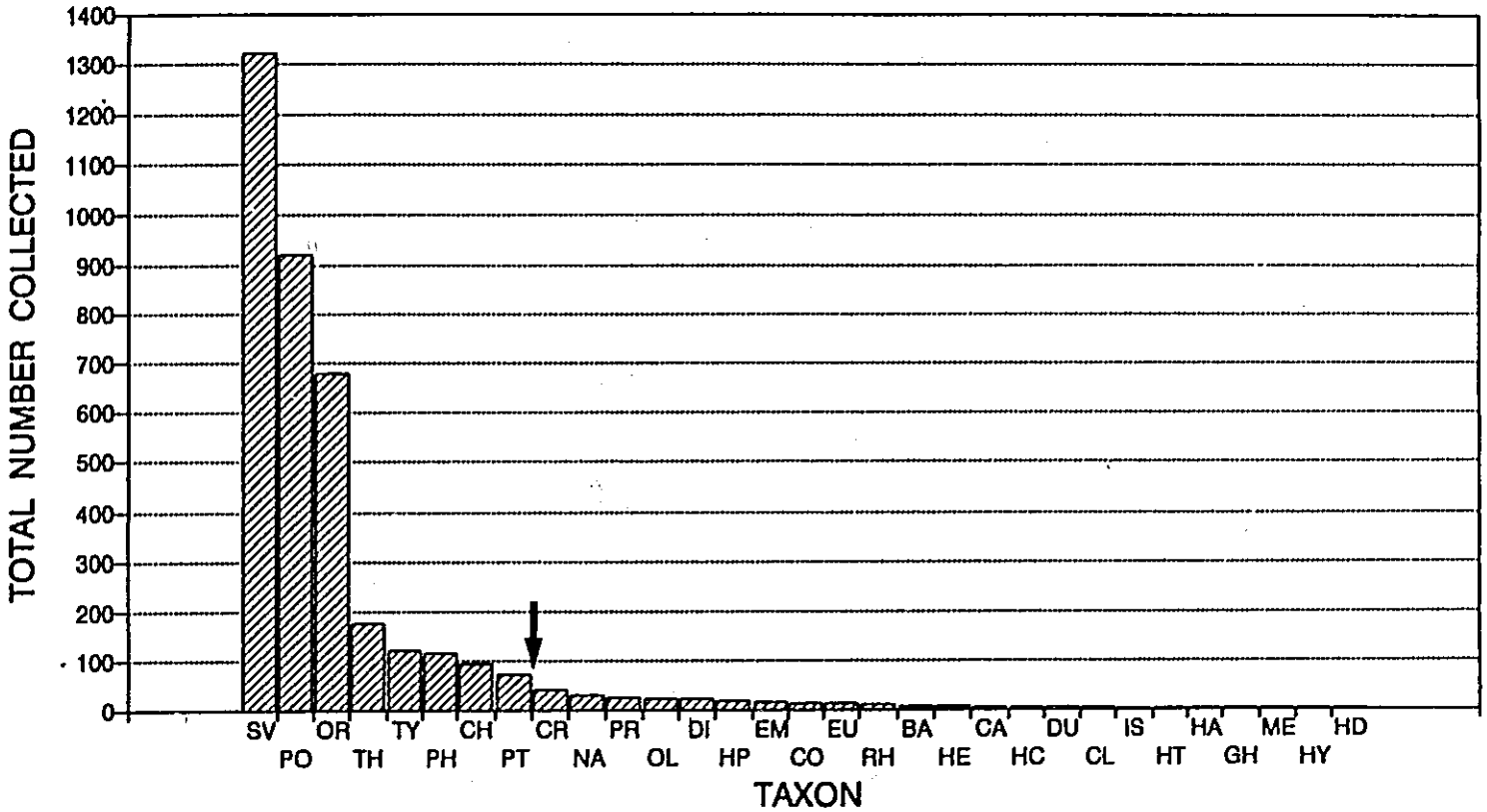


Figure 1.2 Taxonomic composition and abundances of all taxa collected from Wigle Creek, 2 August, 1989 (n=70). Immature chironomids, (instars too small to identify to generic level), were pooled as a single group, and included in the total number of organisms collected, but were excluded as a taxonomic group for taxonomic composition and analyses. Chironomid pupae, were treated similarly. Taxa are abbreviated as: SV: S. vittatum, PO: Polypedilum, OR: Orthocladius, TH: Thienemanniella, TY: Thienemannimyia, PH: Physa, CH: Chironomus, PT: Paratanytarsus, CR: Cricotopus, NA: Nanocladius, PR: Paratendipes, OL: Oligochaeta, DI: Dicrotendipes, HP: Hydropsyche, EM: Empididae, CO: Corynoneura, EU: Eukiefferiella, RH: Rheotanytarsus, BA: Baetis, HE: Hexatoma, CA: Caenis, HC: Hesperocorixa, DU: Dugesia, CL: Calopteryx, IS: Isotomurus, HT: Hydroptila, HA: Hydracarina, GH: Glossophonia heteroclides, ME: Mesovelia, HY: Hydrophilidae, HD: Hydra. Arrow indicates limit of 8 most abundant taxa (each >1% of total animals collected).

Table 1.2 The dominant taxa collected during the study in Wigle Creek, 2 August 1989 (n=70). The taxa listed represent at least 1% each of the total number of animals collected during the study. Note that immature chironomids, in parentheses, were not considered as a taxonomic group, but were included in the total number of animals collected.

TAXON	NO. INDIVIDUALS	PERCENT OF TOTAL ANIMALS
S. vittatum	1321	29.0
Polypedilum spp.	921	20.2
(Immature Chironomidae)	(760)	(16.7)
Orthocladius spp.	679	14.9
Thienemanniella spp.	177	3.9
Thienemannimyia spp.	123	2.7
Physa spp.	118	2.6
Chironomus spp.	93	2.0
Paratanytarsus spp.	72	1.6

Chironomidae), while the remaining taxon was Physa, a pulmonate snail (2.6%).

Simulium vittatum was the most abundant taxon collected (1,321 individuals), accounting for 29% of all of the animals (Fig. 1.2, Table 1.2). Two chironomid genera, Polypedilum spp. (921 individuals) and Orthocladius spp. (679 individuals) occurred frequently in samples, and accounted for 20% and 15% of the total number of animals collected, respectively (Fig. 1.2, Table 1.2). A large proportion of the chironomid larvae (760 individuals or 16.7%) were too immature to be identifiable. Therefore, although they were included in the total number of animals collected, they were not considered for discussion as a taxonomic group or in statistical analyses. Other chironomids included in this assemblage were Thienemanniella spp., Thienemannimyia spp., Chironomus spp., and Paratanytarsus spp. Paratanytarsus spp. was the only potential filter-feeding insect other than S. vittatum included in the list, and Thienemannimyia spp. was the only predator among these taxa. The other six chironomid genera in this group were orthoclads, as were the majority of chironomid taxa collected in the study.

Abiotic Variables

Table 1.3 lists the abiotic variables included in the regression analysis. For a complete listing of all abiotic raw data, refer to Appendix I.2.

The samples from the vertical face of a dam (n=4) clearly dominated the analysis. These areas were populated with much higher densities of S. vittatum than the cobbles. This unique habitat probably is more preferred due to the shallow, fast water and its critical flow characteristic. Since these samples tended to dominate the regression analysis, they were excluded from further analyses. Having removed

Table 1.3 List of independent abiotic variables (measured or calculated from measurements) included in a forward stepwise multiple linear regression, and the alternative states (for binary variables) or range (for continuous variables) for Wigle Creek, 2 August 1989 (n=64).

VARIABLE	ALTERNATIVE (BINARY) OR RANGE (CONTINUOUS)
SUBSTRATE BINARY VARIABLES	
Evenness	Even (0) or Uneven (1)
Periphyton Cover	Absent (0) or Present (1)
Aspect	Horizontal (0) or Vertical (1)
Face	Bottom (0) or Top (1)
CONTINUOUS VARIABLES	
Substrate Size (Surface Area) (cm^2)	19.3 - 222.7
Dry Mass (of adhering material) (mg/cm^2)	0.001 - 11.661
Current Velocity (cm/s)	0 - 53.8
(Current Velocity)^2 (cm^2/s^2)	0 - 2539
Depth (cm)	1 - 28
Depth x Current Velocity (cm^2/s)	0 - 454
Froude Number	0 - 0.37
(Froude Number)^2	0 - 0.136

these samples, only cobble samples remained, and the factor of aspect was therefore removed.

Of the remaining 11 abiotic variables included in the regression analysis (Table 1.3), five significantly influenced the distribution of black fly larvae (Table 1.4). Froude number, a measure of turbulence, was highly significant (Table 1.4, $p<0.001$), accounting for 19% of the variation in larval densities. The square of Froude number was also significant (Table 1.4, $p<0.01$), accounting for an additional 11% of the overall variation. Combined, these results indicate that greatest abundances of black fly larvae occurred at an intermediate Froude number. The empirically determined maximum value of Froude number is approximately 0.25, based on a quadratic equation from the regression analysis of the form $y = a + bx - cx^2$. Solving for the derivative of this equation with slope of zero, the greatest abundance of black flies occurred where the Froude number was approximately 0.25. Abundance declined at both higher and lower Froude numbers.

Three variables relating to features of the substrate accounted for a significant proportion of variation in black fly density. These were periphyton cover, dry mass, and evenness (Table 1.4, $p<0.01$, $p<0.01$, and $p<0.05$, respectively). Periphyton cover and substrate evenness had positive relationships with the occurrence of black flies. More larvae occurred on even than uneven surfaces. The variable of periphyton cover was a visual estimate of the amount of detrital material on the substrate at the time of sample collection. This initial assessment was subjective for categorizing substrates quickly in the field, and is thus less reliable than an actual measurement. A more accurate measure of the detrital material present on each cobble face was obtained in the laboratory using the measurement of dry mass. Dry mass was negatively associated with black fly numbers and accounted for

Table 1.4 Summary of the regression coefficients and coefficients of determination (R^2) for the abiotic factors significantly influencing the distribution of *S. vittatum* larvae in Wigle Creek, 2 August 1989 from a forward stepwise multiple linear regression (n=64). Standard error is abbreviated by S.E.

FACTOR	REGRESSION COEFFICIENT	S.E.	R^2
Intercept	0.038		
Froude Number	2.722***	0.535	0.19
(Froude Number)^2	-5.513**	1.711	0.11
Periphyton Cover	0.102**	0.034	0.05
Dry Mass	-0.164**	0.057	0.06
Evenness	0.101*	0.044	0.05
Total			0.46

*** p<0.001 ** p<0.01 * p<0.05

6% of the overall variation. In all, these abiotic variables accounted for 46% of the variation in black fly densities.

Interestingly and unexpectedly, black fly densities were not related to cobble face. Densities were relatively equal between top and bottom faces of cobbles. This may have been partially a result of sampling error incurred during capture of larvae from the interstitial area of cobble edges. Nevertheless, I have observed larvae on the underside of cobbles during early and late, spring (1990, Little River, Windsor, Ontario and Hobbs-Mackenzie Cr.) and autumn seasons (1989, Little River; 1990, Little River and Hobbs-Mackenzie Cr.; S.A. Beckett and Z.E. Kovats, pers. obs.). Thus, while bottom densities may have been potentially elevated slightly by larvae in the interstitial area, it is unlikely that all larvae tabulated for bottom faces were a result of this complication.

Co-occurring Taxa

Although many taxa were collected in the study, only three chironomid genera were found to be strongly associated with stones inhabited by simuliid larvae. These three taxa, Thienemanniella spp., Polypedilum spp., and Orthocladius spp. were significantly positively correlated with black fly abundance (Table 1.5, Spearman's rank correlation, $p<0.05$ experiment-wise probability). Many of the other abundant taxa (Table 1.2) were also highly correlated with each other (Table 1.5, $p<0.05$ experiment-wise probability).

Hobbs-Mackenzie Creek, 1990

In all, 140 samples from top and bottom faces of cobbles were collected in the stream. The total number of animals collected in the study was 7,069. For a complete listing of all of the taxa collected per sample, and their abundances, see Appendix I.3. Thirty-one taxa were collected (Fig. 1.3) of which nine each comprised at least 1% of

Table 1.5 Matrix of correlation coefficients generated from a Spearman's rank correlation analysis among the most abundant taxa (>1%) from Wigle Creek, 2 August 1989 (n=64). Bold type indicates a significant correlation with experiment-wise error of $p<0.05$. Taxa are abbreviated as: S. vitt: S. vittatum, Thien: Thienemanniella spp., Poly: Polypedilum spp., Ortho: Orthocladius spp., Chiron: Chironomus spp., Th'myia: Thienemannimyia spp., Para: Paratanytarsus spp.

	S. vitt	Physa	Thien	Poly	Ortho	Chiron	Th'myia	Para
S. vitt	1	0.054	0.658	**0.565**	**0.488**	0.230	0.080	0.261
Physa		1	0.194	-0.003	-0.080	0.304	0.329	**0.568**
Thien			1	**0.706**	**0.655**	**0.423**	0.321	**0.360**
Poly				1	**0.598**	0.218	0.333	0.267
Ortho					1	**0.367**	0.316	0.231
Chiron						1	**0.569**	**0.564**
Th'myia							1	**0.440**
Para								1

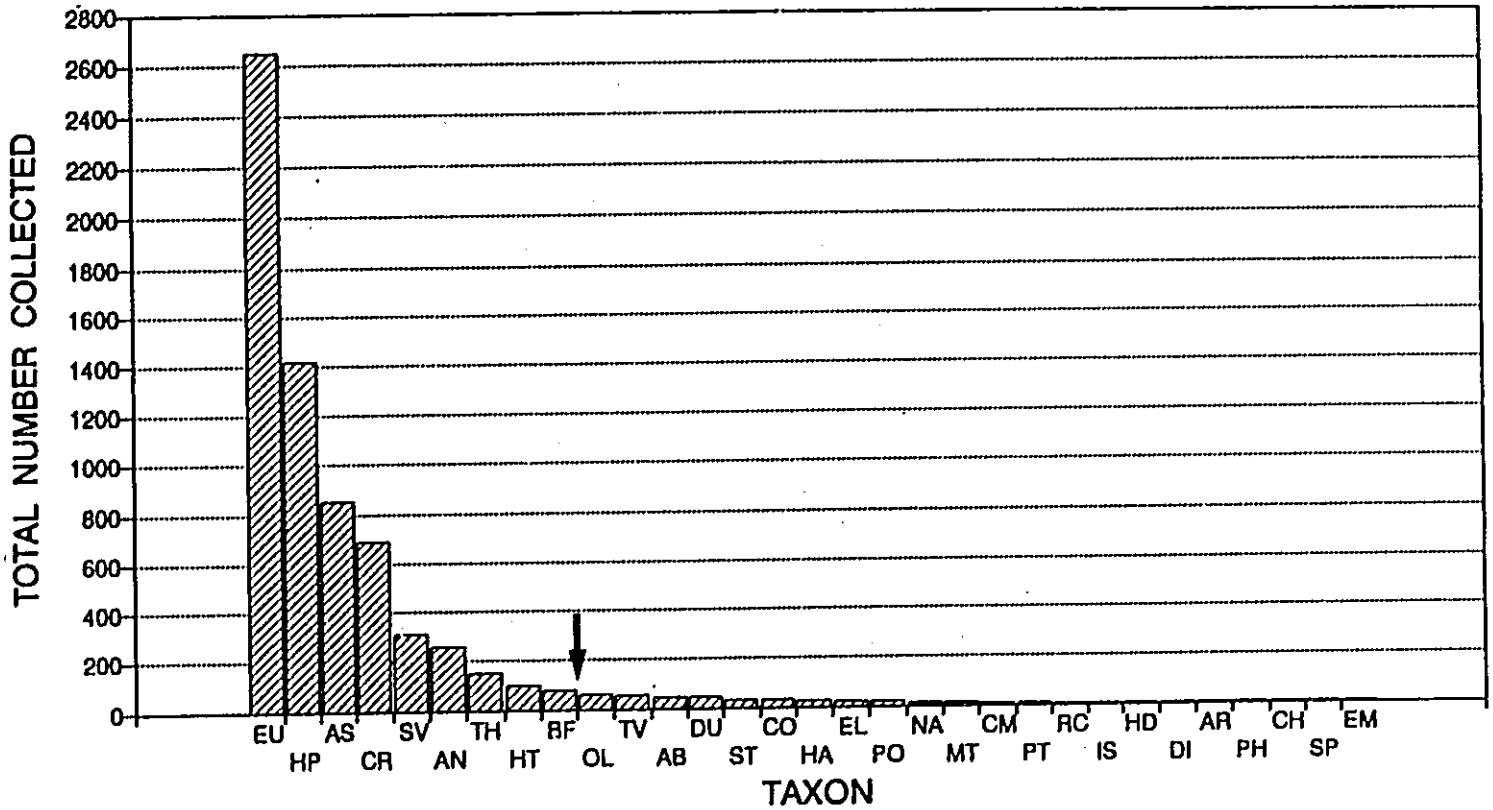


Figure 1.3 Taxonomic composition and abundances of all taxa collected from Hobbs-Mackenzie Creek, 12-13 July, 1990 (n=140). Immature chironomids, (instars too small to identify to generic level), were pooled as a single group, and included in the total number of organisms collected, but were excluded as a taxonomic group for taxonomic composition and analyses. Taxa are abbreviated as: EU: Eukiefferiella, HP: Hydropsyche, AS: Asellus, CR: Cricotopus, SV: S. vittatum, AN: Antocha, TH: Thienemanniella, HT: Hydroptila, BF: Baetis flavistriga, OL: Oligochaeta, TV: Tvetenia, AB: Ablabesmyia, DU: Dugesia, ST: Stenonema, CO: Corynoneura, HA: Hydracarina, EL: Elmidae, PO: Polypedilum, NA: Nanocladius, MT: Metriocnemus, CM: Chimarra, PT: Paratanytarsus, RC: Rheocricotopus, IS: Isotomurus, HD: Hydra, DI: Dicrotendipes, AR: Atrichopogon, PH: Physa, CH: Chironomus, SP: Sphaerium, EM: Empididae. Arrow indicates limit of 9 most abundant taxa (each >1% of total animals collected).

the total number of organisms collected (Table 1.6), and, comprised 92% of all animals collected.

As in Wigle Creek, few taxa were highly abundant in this stream. Eukiefferiella spp., a chironomid larva, was the most abundant organism (2,626 individuals or 37%) collected during the study in Hobbs-Mackenzie Creek (Fig. 1.3, Table 1.6). Hydropsyche spp., a filter-feeding caddisfly larva, occurred frequently in samples also (1,417 individuals or 20.1%, Fig. 1.3, Table 1.6). Asellus, a crustacean detritivore, was the third most abundant taxon (850 individuals, or 9.7%, Fig. 1.3, Table 1.6), and Cricotopus spp., also a chironomid larva, was fourth (687 individuals, Fig. 1.3, Table 1.6) accounting for 9.7% of all animals collected. Black fly larvae were the fifth most abundant taxon, and accounted for only 4.4% of the organisms collected. Other taxa that occurred with abundances of 1% or more included the tipulid larva Antocha spp. with 3.6% (Table 1.6), the chironomid Thienemanniella spp. with 2.1% (Table 1.6), an herbivorous caddisfly Hydroptila spp. with 1.4% (Table 1.6), and a mayfly Baetis flavistriga McDunnough with 1.1% (Table 1.6). In total, these nine taxa represented the dominant (>1% abundances) organisms from the 31 taxa collected from the 33 cobbles. Similarly to Wigle Creek, some unidentifiable early instar chironomid larvae (194 individuals or 2.7%) were collected. They were included in the total number of animals collected, but were not considered for discussion as a taxonomic group or in statistical analyses.

Abiotic Variables

Of seven features of the substrate surface, three were included as binary variables (evenness, periphyton cover and face), and four were continuous variables of measured quantities (surface area, dry mass, ash-free dry mass, and silt). Six other abiotic variables were included in the regression analysis (Table 1.7). For a complete listing of the raw data for the abiotic variables, see Appendix I.4.

Table 1.6 The dominant taxa collected during the study in Hobbs-Mackenzie Creek, 12-13 July 1990 (n=140). The taxa listed represent at least 1% each of the total number of animals collected during the study. Note that immature chironomids, in parentheses, were not considered as a taxonomic group, but were included in the total number of animals collected.

TAXON	NO. INDIVIDUALS	PERCENT OF TOTAL ANIMALS
Eukiefferiella spp.	2626	37.4
Hydropsyche spp.	1417	20.1
Asellus spp.	850	12.0
Cricotopus spp.	687	9.7
S. vittatum	308	4.4
Antocha spp.	256	3.6
(Immature Chironomidae)	(194)	(2.7)
Thienemanniella spp.	151	2.1
Hydroptila spp.	98	1.4
Baetis flavistriga	78	1.1

Table 1.7 List of independent abiotic variables (measured or calculated from measurements) included in a forward stepwise multiple linear regression, and the alternative (for binary variables) or range (for continuous variables) for Hobbs-Mackenzie Creek, 12-13 July 1990 (n=140).

VARIABLE	ALTERNATIVE (BINARY) OR RANGE (CONTINUOUS)
SUBSTRATE BINARY VARIABLES	
Evenness	Even (0) or Uneven (1)
Periphyton Cover	Absent (0) or Present (1)
Face	Bottom (0) or Top (1)
CONTINUOUS VARIABLES	
Substrate Size (Surface Area) (cm^2)	14.6 - 223.3
Dry Mass (of adhering material) (mg/cm^2)	0.026 - 31.406
Ash-Free Dry Mass (mg/cm^2)	0.002 - 3.790
Silt (mg/cm^2)	0 - 27.687
Current Velocity (cm/s)	10 - 51
(Current Velocity)^2 (cm^2/s^2)	99 - 2659
Depth (cm)	0.5 - 13
Depth x Current Velocity (cm^2/s)	6 - 411
Froude Number	0.034 - 2.71
(Froude Number)^2	0.001 - 7.350

Of the 13 variables potentially important to S. vittatum distribution, only Froude number, a measure of turbulence, (Table 1.8, $p<0.001$), and the size of the substrate (Table 1.8, $p<0.001$) were significantly related to black fly density. There was a positive relationship between black fly larval density and Froude number. More black flies occurred in areas with higher Froude (shallow water, fast current velocity) than low Froude (deeper, slower water). Substrate size was negatively associated with black fly density. More S. vittatum larvae occurred on smaller cobbles. These two factors accounted for only a small portion (27%) of the total variation.

Co-occurring Taxa

Densities of five of the eight most abundant (>1% of total numbers) taxa (Table 1.6), were significantly correlated with S. vittatum abundance (Table 1.9, Spearman's rank correlation, $p<0.05$ experiment-wise probability). The detritivore, Asellus, and two chironomids, Cricotopus spp. and Thienemanniella spp., were not. All associations between organisms were positive.

Larval Size

Head width of a total of 255 undamaged black fly larvae was measured from the Hobbs-Mackenzie Creek study. A broad range of larval sizes was collected during the study (Fig. 1.4).

To determine whether larval size influenced the microhabitat selected, mean larval size per cobble face, the dependent variable, was regressed against the independent abiotic variables (Table 1.7). None of the abiotic variables (Table 1.7) included in the regression was significant ($n=61$, $p>0.05$).

Table 1.8 Summary of the regression coefficients and coefficients of determination (R^2) for the abiotic factors significantly influencing the distribution of S. vittatum larvae collected from cobbles in Hobbs-Mackenzie Creek, 12-13 July 1990 from a forward stepwise multiple linear regression. Standard error is abbreviated by S.E.

FACTOR	REGRESSION COEFFICIENT	S.E.	R^2
Intercept	0.158		
Froude Number	0.169***	0.026	0.20
Surface Area	-0.039***	0.011	0.07
Total			0.27

*** $p<0.001$

Table 1.9 Matrix of correlation coefficients generated from a multiple Spearman rank correlation analysis among the dominant taxa (>1%) from Hobbs-Mackenzie Creek, 12-13 July 1990 (n=140). Bold type indicates significant correlations with experiment-wise error of $p<0.05$. Taxa are abbreviated as: S. vitt: S. vittatum, H'psych: Hydropsyche, B. flav: B. flavistriga, H'tila: Hydroptila, Euk: Eukiefferiella, Thien: Thienemanniella, Crico: Cricotopus.

	S. vitt	Asellus	H'psych	Antocha	B. flav	H'tila	Euk	Thien	Crico
S. vitt	1	0.123	**0.410**	**0.382**	**0.530**	**0.449**	**0.364**	**0.318**	**0.247**
Asellus		1	**0.249**	**0.598**	**0.447**	**0.672**	**0.188**	**0.394**	**0.475**
H'psych			1	**0.465**	**0.407**	**0.521**	**0.291**	**0.428**	**0.356**
Antocha				1	**0.608**	**0.741**	**0.546**	**0.542**	**0.699**
B. flav					1	**0.706**	**0.487**	**0.463**	**0.507**
H'tila						1	**0.622**	**0.640**	**0.689**
Euk							1	**0.432**	**0.536**
Thien								1	**0.394**
Crico									1

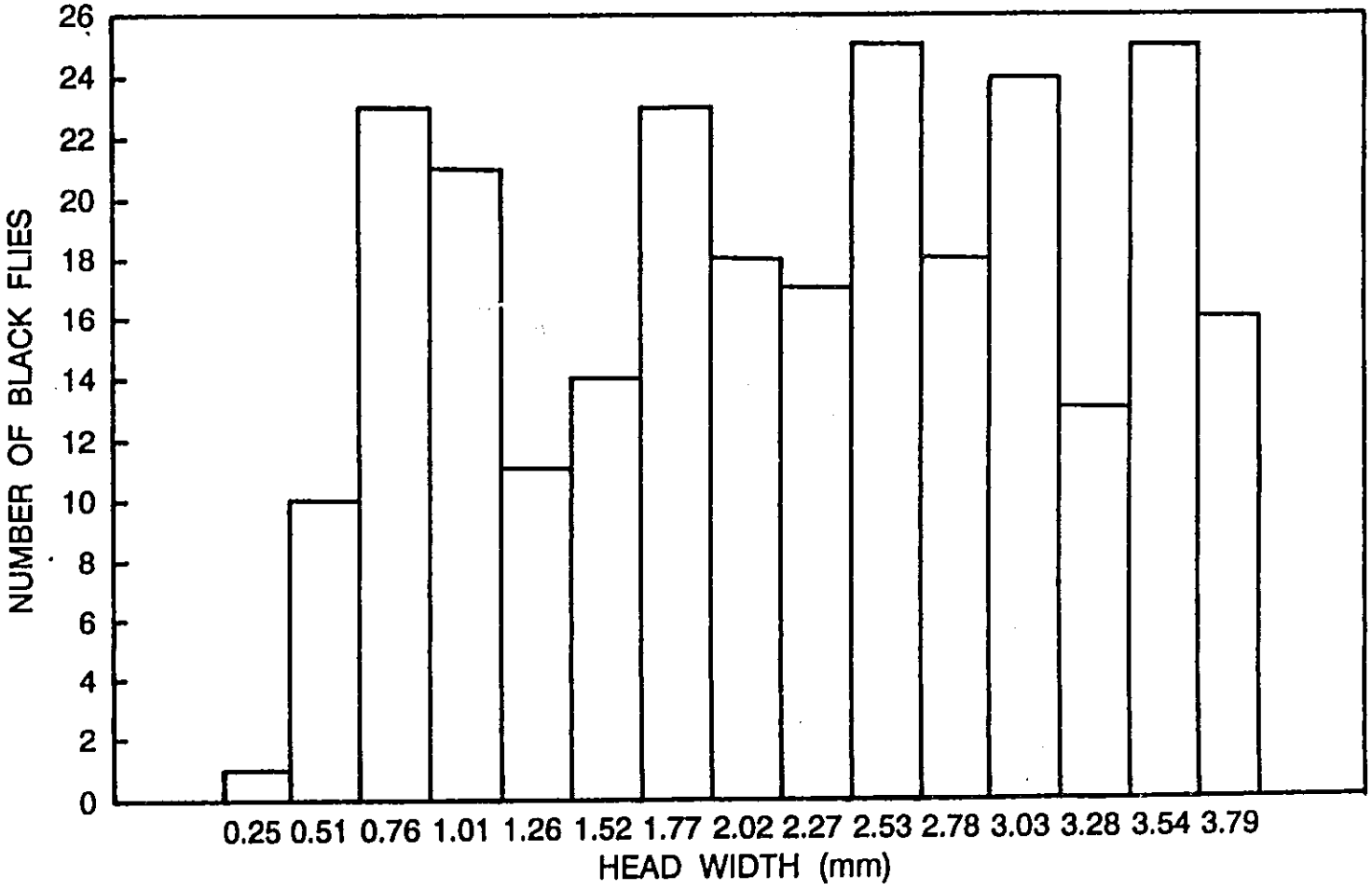


Figure 1.4 Distribution of the sizes of S. vittatum larvae collected 12-13 July, 1990 from Hobbs-Mackenzie Creek, as measured by head width (measured as the distance between the centres of the eyespots; n=255 larvae).

DISCUSSION

Taxonomic Richness and Composition

Thirty-one taxa were collected during each study. However, considerably more animals were collected from Hobbs-Mackenzie Creek (7,069) than from Wigle Creek (4,557). Both streams had few taxa (3-4) comprising the majority of animals collected.

Taxonomic composition in both streams was dominated by collector-gatherer and grazing taxa. Filter-feeders were represented by S. vittatum, Paratanytarsus spp., Rheotanytarsus spp., and Hydropsyche spp. Hydropsychids also graze algae, mainly diatoms, from the substrate (Wiggins 1977). Predatory taxa included Hydra spp., Dugesia spp., Glossophonia heteroclides, Ablabesmyia spp., Thienemannimyia spp., Hesperocorixa spp., and Calopteryx spp. However, few individuals represented these taxa. Although not specifically observed during this study (but seen on occasion during the summer seasons in this and previous years), small forage fishes were also present in Hobbs-Mackenzie Creek. Although they tended to occur in pool areas, they may have encountered and consumed small numbers of black flies. In Wigle Creek, carp were observed above the dam. Occasionally, fish were swept over the dam, but these generally tended to swim downstream. I observed no fish at the study site in this stream. Although some fish species (e.g., trout) may periodically consume substantial numbers of simuliid larvae, generally, fish do not appear to be major predators of black fly larvae (Davies 1991). It is therefore possible, but unlikely, that fish in my study streams had a significant impact on black fly populations.

Dunnigan (1991) collected 34 taxa during a study conducted in Hobbs-Mackenzie Creek that examined the occurrence of benthic macroinvertebrates and the presence of periphyton biomass. His samples were collected using a modified Hess sampler delineating 80 cm^2 from

areas of cobbles and boulder-dominated substrates. The taxonomic richness in my studies is comparable to his findings. However, the Chironomidae were identified to generic level in my studies, which substantially increased the apparent diversity. The overall taxonomic composition in the stream is probably much higher than reported from my study, which was limited to cobbles within riffles. Additionally, my study was limited in temporal scope, conducted as a "snapshot" study within the summer season rather than a long-term survey over several seasons or several years. As in my study, Dunnigan (1991) found that the majority of taxa were represented by only a few individuals, and relatively few taxa had abundances of 1% or more of the total collected.

Larval Black Fly Habitat and Microhabitat Selection from Previous Studies

Some studies have examined the features of larval black fly habitat on a broad scale (Wu 1931, Zahar 1951, Hocking and Pickering 1954, Maitland and Penney 1967). Most of this work was done in the field, although some studies included limited supplementary laboratory investigations of a particular aspect (e.g., Wu 1931; oxygen) or field manipulations of a particular variable (Maitland and Penney 1967; Simulium density was estimated using bricks). All of these studies provided detailed descriptive accounts of field observations, and life history. Black fly habitats were described in varying detail, including such conditions as flow (e.g., current velocity), substrates colonized by larvae, physical and chemical characteristics of the stream, and descriptions of the simuliid species present in the river.

These studies have contributed useful background information on the ecology of the Simuliidae. Unfortunately, much of the information is qualitative or descriptive, lacking experimental manipulation. Nevertheless, these studies have provided invaluable knowledge of black flies and deserve merit. Note that these studies were done on a much broader scale than my study.

More recently, Colbo and Moorhouse (1979) conducted a distributional survey of black flies in Australia. Although this survey was termed a microdistributional study, there is no explanation of how collections were done (except "by hand") from the sites along rivers, nor mention of specific attributes or measurements at each specific substrate. Similarly, Adler and Kim (1984) examined microhabitat preference of S. vittatum larvae. However, their measurements of physical and chemical characteristics were taken within the site rather than at individual sampling points within the sites. They addressed microhabitat preference of S. vittatum sibling species by correlating the proportional composition of the siblings with the substrates sampled (grass or stones). Their study reached beyond that of Colbo and Moorhouse (1979) by attempting to associate the presence of other taxa with the presence of a particular S. vittatum sibling.

My study was designed to examine the distribution of S. vittatum larvae at the microhabitat level (individual cobbles within riffles). With the exception of Morin (1991; single cobbles, but abiotic measurements were collected within the site, not at single cobble locations), this local-scale approach of natural substrates differs from previous studies that examined microhabitat of larval black flies. My study examined single cobbles differing by specific surface characteristics (evenness and periphyton cover). I also investigated the top and bottom faces of each cobble separately. A series of abiotic measurements and flow parameters were obtained for each individual cobble. My study also quantified the material (organic and inorganic) on each substrate, as well as the biota present on each cobble. It also examined the entire community on the cobbles, rather than the simuliid population only.

Larval Microhabitat Choice Derived From Abiotic Factors

The significant abiotic variables in my study were related to the two basic categories of substrate and water flow. The samples collected from the dam face at the Wigle Creek study site had higher densities of larvae than individual stones. Hocking and Pickering (1954) also found that larvae colonized vertical surfaces before other substrates, as in my study. This is probably related to the type of flow (critical flow) over the surface. Fast flowing, shallow water is conducive to high larval densities (Craig and Galloway 1987). Wotton (1992) found densities of Simulium noelleri on vertical wooden plates on a dam face to be 63-88/cm^2, although observations of the same species at a similar dam were typically one million/m^2. Also, microdistributional patterns may be strongly related to oviposition behaviours of the adult females (Zahar 1951, Colbo and Moorhouse 1979).

To investigate what variables influenced the distribution of larvae among cobbles, the samples from the dam face were omitted from subsequent analyses. The stepwise multiple linear regressions for both streams indicated that both flow and substrate influenced microhabitat selection, but flow variables were more important to the preference of a particular microhabitat. Froude number explained the most variation in the distribution of black flies. Larval response to this variable suggested an intermediate Froude number (between 0 and 1) was optimal rather than favouring a maximum (>1) or minimum (0) value.

Flow Variables

Froude number describes the "roughness" of the water flow, or its mixing capacity, and can be related to the type of flow present. It is based on a combination of water depth (d), gravitational force (g= 9.81 m/s^2), and current velocity (v). Generally, black flies are hypothesized to occur in greater densities in areas where critical flow occurs (i.e., areas where Froude number = 1.0; Craig and Galloway 1987).

In areas where Froude number exceeds 1.0, supercritical flow occurs and air bubbles are entrained in the water (Newbury 1984). These bubbles may lodge on head fans, thereby interfering with feeding. In regimes with Froude number of < 1.0, subcritical flow occurs and black flies are again hypothesized to occur in fewer numbers. This may be due to slower rates of food delivery in reduced currents.

In both studies, Froude number was a significant influence to black fly densities (Wigle Creek, positive Froude number and its square, negative; Hobbs-Mackenzie Creek, positive Froude number). Combined, these results suggest that larvae select areas of intermediate Froude number, avoiding areas at both the upper and lower extremes. There is conflicting evidence in the literature concerning the effect of Froude number. Osborne et al. (1985) found larvae inhabited areas of low turbulence. In a study of 34 riffles, Morin and Peters (1988) suggested that simuliid larvae occurred with greater frequency in shallow water because these areas acted as shelters from turbulence found in deeper areas. At a finer scale, Maitland and Penney (1967) found that turbulence was maximum at the back surface of boulders where black fly pupae occurred in greatest numbers. The larvae preferred the top surface of boulders at the leading edge. Here, turbulence occurred, but was much less than the back of the boulder. Kurtak (1978), studying feeding of individual larvae in experimental troughs, suggested that, at least for one black fly species, more turbulent flow seemed to enhance feeding efficiency as evidenced by an accelerated rate of particle ingestion. However, Décamps (1975) observed that larvae generally occurred on boulders in zones of torrential flow in which many microcurrents circulated, creating an area of relatively high turbulence. Brenner and Cupp (1980) found that densities of three black fly species (S. vittatum, S. decorum, S. pictipes) were greatest in areas with high turbulence. These areas were the baffles in laboratory rearing troughs where many microcurrents probably occurred. Although

turbulence was implicated as one factor accounting for the observed distributions, none of the studies assessed the degree of turbulence by measurement (of Froude number).

Although current velocity was not a statistically significant factor in my study, independently of Froude number, its important influence on larval distribution has been well-studied (Wu 1931, Phillipson 1956, 1957, Wotton 1978, Colbo and Moorhouse 1979, Ciborowski and Craig 1989) as have the micro-hydrodynamic effects associated with flow (Décamps 1975, Craig and Chance 1982, Chance and Craig 1986, Craig and Galloway 1987, Lacoursière 1989). The majority of samples collected during my studies were probably from areas well within the natural range of current velocities for S. vittatum. Therefore, the lack of collections from areas at the extremes of this limit could have allowed this variable to exert a limited effect. Furthermore, the sample size of individual black flies was relatively low at the time of the study, especially in Hobbs-Mackenzie Creek, which could also mask effects: both suitable and unsuitable areas may have lacked black flies.

Substrate Variables

Substrate variables also had statistically significant effects on larval microdistribution, although they were secondary to the effect of Froude number. In Wigle Creek, significant effects were noted from periphyton cover (5%, Table 1.4, $p<0.01$), amount of dry mass (6%, Table 1.4, $p<0.01$), and substrate evenness (5%, Table 1.4, $p<0.05$). These substrate characteristics accounted for 16% of the variation in simuliid density in Wigle Creek.

Periphyton cover was a visual estimate used to assess the debris present on a cobble quickly in the field. However, the actual amount present on each cobble was measured in the laboratory, and therefore, dry mass is a more reliable reflection of the material present. Dry

mass was negatively associated with larval density, suggesting that more larvae occurred on cobbles that had lower accumulations of inorganic and organic material. Evenness was positively associated with larval density, suggesting that more larvae occurred on cobbles with uneven surfaces than on cobbles with even surfaces.

In Hobbs-Mackenzie Creek, substrate size (surface area) showed a highly significant effect (Table 1.8, $p<0.001$) on simuliid distribution, and explained 7% of the variation. Substrate surface area was negatively associated with larval density suggesting that larvae selected smaller cobbles over larger ones. No other abiotic variables measured in either study had any significant effects on black fly densities on cobbles.

Several researchers have commented that black flies tend not to be found in areas covered with silt (Wu 1931, Zahar 1951, Rühm and Pegel 1986b, S.A. Beckett pers. obs.) or periphyton build-up (Carlsson 1962, Gersabeck and Merritt 1979, Hershey and Hiltner 1988, Pruess 1989, S.A. Beckett pers. obs.), based on field observations. This avoidance is postulated to occur because of reduced ability of larvae to attach the silk pad to these surface coatings (Barr 1982), rendering such areas unsuitable. My experimental studies investigating the effect of periphyton on larval simuliid substrate choice (Chapter II) strongly reinforce this explanation.

Larvae were more abundant on uneven than even substrates. This may have been due to the interaction between periphytic colonization and settling of silt onto the cobbles, or it may have been a result of hydrodynamic conditions. Periphyton appears to accumulate more quickly on uneven surfaces due to the crevices that can provide a refuge for algal propagules, or crevices may trap debris (DeNicola and McIntire 1990a, 1990b, Dudley and D'Antonio 1991). Thus, one would expect fewer

simuliids on uneven substrates because of greater amounts of organic and inorganic materials on the surface. However, a more complex surface of depressions and projections may provide depositional areas (depressions), and scoured areas (projections) which could be differentially colonized by biota, including simuliids. Algae, diatoms and detritus could potentially settle, developing a more diverse surface for food and shelter. Depressions could attract scavengers and detritivores, while convexly curved areas could attract suspension-feeders taking advantage of hydrodynamic conditions. Although my study indicated more larvae were present on uneven substrates, the scale of my study did not permit a more detailed investigation regarding the positions of larvae on these substrates. Perhaps larvae seek the projections on uneven surfaces, while other macroinvertebrates inhabit the crevices, and scour the surface, depleting settled material for food and shelter. Walsh et al. (1981) found more larvae on plastic spheres than on polystyrene spheres and attributed the difference in numbers between the two substrates to be due to a preference for roughness. However, their substrates differed not only in texture, but also in evenness. Thus, it is difficult to determine to which variable the larvae were responding in the study of Walsh et al.

Although substrate particle size has been shown to affect habitat selection and community structure (Allan 1975, Mackay and Kalff 1969, Cummins and Lauff 1969), it is not clear why substrate size would be an important variable influencing black fly colonization. One possibility is that larger substrates are more stable (Maitland and Penney 1967, McAuliffe 1984a). This greater stability might allow larvae to feed continuously rather than producing new silk pads, repairing old ones, or risking injury as a result of dislodgement from overturning stones. Décamps et al. (1975) noted that small populations of black fly larvae established on stable stones with diameters larger than approximately 10

cm. The majority of cobbles from my study were at least of comparable size to Décamps, and therefore, could be considered as large, stable stones by Décamps standards, but as small substrates in my study. Also, stone stability probably affects the successional stage of algae, and subsequently, the succession of colonizing macroinvertebrate species. Additionally, stability of the substrate, as a function of size, could also affect the quantity of material growing on, or settling onto, the substrate surface (e.g., smaller stones may be overturned more frequently than large stones, thereby reducing periphyton and biota). The stability of stones will depend upon the size and flow variation characteristic of individual streams (Newbury 1984).

Dunnigan (1991) found significantly higher abundances of Simulium on cobble than on boulder substrates in Hobbs-Mackenzie Creek. He suggested that the curved surfaces of the cobbles provided a more hydrodynamically suitable surface than the boulders. Substrates protruding out of the stream bottoms are typically more likely to provide areas of critical flow than are flat surfaces (Newbury 1984).

I examined microhabitat selection for the S. vittatum complex as morphospecies rather than as cytospecies. Adler and Kim (1984) and Ciborowski and Adler (1990) provided evidence that habitat differences may occur at the cytospecies level. Therefore, variation not explained by the abiotic factors probably represents in part the differences in habitat occurring at the level of cytospecies, an aspect not considered in my study.

Biotic Associations between S. vittatum and other taxa

My study involved correlating a series of abiotic variables and densities of co-occurring genera with the density of black fly larvae to gain insight into their microhabitat preferences and biotic associations. I found that in Wigle Creek most biotic associations on

these cobbles were among chironomid genera. A greater variety of taxa had significant associations in Hobbs-Mackenzie Creek. In both rivers, significant correlations occurred among grazers or detritivores, the exception being between suspension-feeding simuliids and hydropsychids. The many significant correlations suggested that most taxa on the surfaces sampled have similar habitat requirements or preferences.

Alternatively, interactions could also contribute to significant biotic associations. For example, grazing of the periphytic community may promote the occurrence of a more diverse community, due to successional changes in both the algae and the consuming biota, but may also allow colonization of black flies through a reduction of periphyton and detritus. Although larval black fly aggregations are typically described as monotypic, or implied to be, it may be that smaller organisms (e.g., chironomids) are present, but undetected by visual inspection (naked eye). Studies investigating only the black fly population, rather than the entire assemblage, could thus overlook other small organisms actually present.

Although Baetis flavistriga was the most highly correlated taxon with Simulium vittatum (in Hobbs-Mackenzie Creek), there is no evidence in the literature to suggest that this taxon should exert an important influence on the microdistribution of black fly larvae. However, similarities in feeding (filtering of the seston), territorial behaviour, and the requirement for space suggest that (competitive) interactions could occur between hydropsychid and simuliid larvae, thereby affecting larval black fly microdistributional patterns. Hemphill (1988, 1991) and Hemphill and Cooper (1983) have noted aggressive interactions occur between black fly larvae and hydropsychid larvae.

Hydropsychid caddisfly larvae are typically a dominant component of the fauna in Hobbs-Mackenzie Creek (Dunnigan 1991, S.A. Beckett and J.J.H. Ciborowski, Univ. of Windsor, pers. obs.). Hydropsyche spp. was one of the most abundant taxa collected during my study in Hobbs-Mackenzie Creek, and these larvae were much more common than S. vittatum. The statistically significant, positive association between the densities of Hydropsyche spp. and Simulium vittatum may have reflected similar microhabitat preferences, since each feeds primarily by filtering the seston. Other suspension-feeders were virtually absent; only five Paratanytarsus spp. individuals were collected among all samples. In Wigle Creek, the reverse distribution was found: hydropsychids were rare (although high densities were observed earlier in the season; S.A. Beckett pers. obs.), but simuliids were the most abundant taxon present. Again, a single suspension-feeder dominated this feeding group, and other filterers were rare in terms of diversity as well as abundances.

Hydropsychid and simuliid abundances are probably a reflection of life history characteristics. It is less likely that S. vittatum competitively excluded Hydropsyche from cobbles in Wigle Creek. My observations of aggressive interactions between these two taxa suggest that black fly larvae are inferior competitors to the caddisfly larvae, and that caddisflies tend to dislodge black flies frequently. Other studies by Hemphill and Cooper (1983) and Hemphill (1988, 1991) have also found interactions to favour caddisfly larvae when they co-occur.

Although disturbance has been demonstrated to play an important role for black fly distributions by opening space for colonization prior to hydropsychid invasion and subsequent dominance of the patch (Hemphill and Cooper 1983, Hemphill 1991), recent disturbance was lacking in my study streams. This alternative could explain the observed pattern of hydropsychid dominance in Hobbs-Mackenzie Creek, but not Wigle Creek.

There, predation by hydropsychid larvae may have partially contributed to low simuliid densities. Peterson and Davies (1960) concluded that hydropsychids had a major impact on black fly densities in a central Ontario stream (Algonquin Provincial Park). Englund (1992) noted that Hydropsyche siltalai reduced Simulium truncatum density in the field through predation, while the presence of their hydropsychid nets caused increased rates of black fly immigration and emigration, and Rühm and Pieper (1989) found evidence that hydropsychid species consumed simuliids more often than a variety of other potential predators tested (some of which included dragonflies, beetles, caddisflies, stoneflies, mayflies, leeches, and fish). Although such interactions potentially occur in both of my study streams, it is more probable that temporal segregation, due to life history characteristics, and seasonal patterns of abundance (not only between these taxa, but possibly the community as a whole) were operating in each of my streams, at the times the studies were conducted.

The absence of a variety of suspension-feeding taxa could be due to competitive displacement by superior competitors, predation, differences in microhabitat preferenda, or community succession. Each of these possibilities could be addressed with experimental manipulations, but the mechanism(s) accounting for these observations in my streams were beyond the scope of these studies.

It is often assumed that immature simuliids (larvae and pupae) occurring in high densities monopolize the space they are occupying (i.e., to the exclusion of other taxa; Hart 1986). My results suggest that this conclusion may be misguided, due possibly to casual observation, rather than scientific manipulation. Many other taxa may be present, although they may be in low abundance relative to black flies. In both of the streams I sampled, on single stones, black flies occurring at a range of densities co-existed with up to 30 additional

taxa, eight of which were more common than the majority of taxa. Densities of black flies collected from the dam face at Wigle Creek were slightly higher than those from cobbles exposed to similar current velocity (density range, dam: 0.2-1.9/cm^2; cobbles: 0.3-1.4/cm^2), and other animals, mostly chironomids, were collected in the same sample, but in lower densities (density range for all non-simuliids combined, dam (6 taxa): 0.2-1.1/cm^2; cobbles (3 taxa): 0.6-1.2/cm^2).

The co-occurrence of these taxa with S. vittatum larvae may be related to the density of S. vittatum. My study did not involve extremely high densities of simuliids. Perhaps co-existence of taxa occurs at low and moderate densities, but not at high densities (i.e., these taxa can co-occur because the level of interspecific interference is not sufficient to limit feeding, growth, and survival). Lastly, co-occurrence due to facilitation is another possibility that could lead to small numbers of other taxa closely associated with black flies. Further experimental work would be necessary to examine these possibilities.

At the local scale employed in my studies (single cobble faces), I did not address the specific positions of any taxon, or relative positions of animals of different taxa co-occurring on cobbles. Specifically, were these co-occurring taxa within black fly aggregations, or did they occupy positions peripheral to them?

From my cobble study at Hobbs-Mackenzie Creek, it is not possible to address the spatial relationship of non-black fly taxa to black flies on cobble faces, since black fly densities were very low, and thus, aggregations were absent. Similarly, in Wigle Creek, I did not specifically examine larval positions relative to the positions of the other taxa present, although densities were high enough to permit this during the summer season.

Based on personal observations in the field, however, I speculate that the presence of other taxa in minor proportions is not a density-dependent occurrence, but occurs regardless of black fly density. During S. vittatum larval collections in the summer of 1990 (during the population peak), cobbles and boulders were covered by extremely high densities of black fly larvae. Two cement culverts at the dam at Wigle Creek were also densely populated by black fly larvae. I removed black fly masses from these culverts, and found a variety a taxa within the bucket at the laboratory upon transfer to the maintenance tank. Similarly, I collected larvae at the same time from only densely colonized cobbles, and brushed larvae by hand from only regions of the stones where larvae occurred in very dense aggregations. Since there were more larvae available than I could possibly maintain or use in the laboratory, I did not collect larvae peripheral to aggregations. I collected larvae during this peak abundance over a five day period, with three separate collections. Handling and examining the cobbles in the field (by unaided eye), there appeared to be no other animals present on the cobbles. However, having returned to the laboratory with several of the cobbles, I observed the presence of small hydropsychid larvae, flatworms, mayflies, and especially, chironomids. These were noticeable, upon transfer of larvae to the maintenance tank, in both the bucket that contained a few cobbles, as well as the bucket that contained no cobbles. Again, these non-simuliid taxa comprised minor proportions of the total number of animals collected.

These observations support the notion that at least some non-black fly taxa occur within black fly aggregations, but the generality of this occurrence among species or among rivers remains questionable. I would speculate that, given the widespread distribution of some of the taxa collected with black flies (e.g., Chironomidae), and the general tendency of black flies to aggregate, this phenomenon is not restricted to Wigle Creek, but probably occurs in other streams as well.

In summary, I suspect that past distributional surveys have misrepresented the presence of other taxa because of the scale of the studies (broad rather than local), the qualitative nature of the studies, or the methodology employed in collecting samples in the field. Additionally, most studies have limited their scope to the simuliids only, foregoing the additional effort required for an investigation of other taxa. Chironomids in particular are small larvae that can easily be overlooked, particularly if cobbles have even minimal algal growth or debris present on the surface, or are covered by closely packed simuliids. Nevertheless, collection at an even smaller scale (i.e., within versus peripheral to aggregations) must be conducted to properly address this issue.

S. vittatum Larval Size

The S. vittatum larvae collected during the Hobbs-Mackenzie Creek survey were measured for comparisons in microhabitat selection between larvae of varying sizes. The broad range of larval sizes collected during my study could have been due to differences in growth rates, in exposure to temperatures, or to multiple cohorts. Since this study was conducted in the summer season (July) when warm temperatures prevailed, the size structure of the population was probably a result of the three factors mentioned above. Fast turnover in generations, multiple broods of eggs, with variation in temperature, could produce multiple cohorts and varying growth rates with rapid turnover.

Since the potential exists for larvae of different size to respond differently to the same variables (Colbo and Moorhouse 1979, Gersabeck and Merritt 1979, Wotton 1985, Pruess 1989), larval size was regressed against the abiotic variables. None of the abiotic variables considered in my study was statistically significant (n=61, number of measured specimens=255, $p>0.05$). This suggests that larval responses to the

variables examined are generalized behaviours of S. vittatum larvae, independent of size.

Although my study detected no differences in microhabitat selection between small and large larvae, I surveyed only a small (low population density) larval population. A study collecting greater abundances of larvae may have produced clearer and stronger results. Rühm and Pegel (1986a) found that small larvae segregated from large larvae on single stones. However, there was a seasonal component: large larvae tended to be on the underside of stones during winter, while small larvae tended to occur atop stones during summer. Colbo and Moorhouse (1979) noted that larger instars of Simulium ornatipes were more abundant toward the centre of an Australian stream where the current velocity was greater, whereas small larvae were more prevalent toward the stream periphery where the current was slower, suggesting that different-sized larvae may prefer different current characteristics. Wotton (1982) described differences in the ranges of current velocity inhabited by early and late instar larvae, as well as feeding efficiencies. His findings suggested that smaller instars were more tolerant of lower velocities than larger larvae. His subsequent study (1985) showed that early instars were capable of using finer particles than later instars, but that late instar larvae ingested more particles than early instars, suggesting that intra-specific competition between larvae of varying size was reduced through partitioning of the size fraction filtered by larvae. Although not conclusive evidence for differential habitat selection based upon body size, it demonstrates the potential for segregation to occur. These studies provide some evidence that larvae in different instars may select different microhabitats. This aspect could be further pursued with experimental manipulations using larvae of different instars.

Although my study did not detect important differences in the field distribution of larvae with respect to variation in size and abiotic factors, I consistently observed that only small early instar larvae perched on Cladophora filaments, never larger, older instars, both in the field and in the laboratory maintenance tank. Perhaps this (Cladophora) niche is not suitable to larger larvae. Conversely, Cladophora could be a secondary substrate utilized by small larvae due to inferior competitive ability and loss of prime habitat to larger stronger individuals. Since large larvae should have a competitive advantage relative to small larvae, one might expect differences in microhabitat selection, whereby the large larvae colonized the best microhabitats, and the smaller individuals colonized primarily the areas of lesser quality.

I also observed differences between small and large larvae in the positions assumed on the cobble substrates provided in the maintenance tank, and in the field. Larvae tended to form two types of associations. The first was mixed groups of larvae incorporating a variety of sizes in the group. The second formation was one in which the smaller larvae formed parallel bands in front of the larger larvae. These orientations, however, were merely observational, and were not subjected to quantification or statistical analysis. Colbo and Moorhouse (1979) also observed the latter formation in the field. Wiley and Kohler (1981) noted that displacement of small larvae by larger individuals was common, and often resulted in small larvae assuming positions at the downstream edges of aggregations. Wotton (1985) found the reverse pattern: small Simulium noelleri larvae were positioned inside aggregations.

Again, differences due to size possibly occur at an even finer scale than my study could detect. For example, distributional differences due to size may occur at the level of larval choice in

positions on a substrate, or within a group. Microcurrents around individual larvae on the substrate, and interactions between larvae, may influence the choice in position on the substrate. Hart (1986, 1987a) has shown that black fly larvae will aggressively interact for preferred feeding positions. Eymann's (1985) work describing larval behaviour, and that of Eymann and Friend (1988) supports this also.

The influence of size could be manifested in other behavioural differences such as activity patterns. For example, Wotton (1985) found differential patterns of movement between large and small larvae. Large larvae were more inclined to travel upstream regardless of the velocity of the current, whereas small larvae tended to travel only in reduced current velocities. Any one of these possibilities could be the mechanism producing size assortment. Clearly, there is a need for experimental studies to evaluate these (and potentially other) possibilities.

Generality

My study has shown that the microhabitat of larval black flies as determined by responses to abiotic factors, can be generalized at least to temperate lotic systems, in spite of differing characteristics of the streams. While the specific factors influencing microhabitat distribution may differ among streams, the characteristics of flow appear to be the dominant factor, with substrate characteristics secondary to flow. Differences among streams (e.g. temperature, degree of shading, nutrient input levels) probably result in different specific microhabitat factors affecting larval densities. This generality is also evident from the numerous published studies supporting the important influence of hydrodynamics and other various potential influences such as food, water chemistry, substrate, and temperature (Ross and Merritt 1987).

Conclusions

My study examined single cobbles, each having its specific surface characteristics as well as its set of abiotic factors. I investigated not only the black fly larvae present on each of the two cobble faces, but also the other biota comprising the community on each cobble. My study indicated that while both substrate characteristics and flow parameters were related to the microdistribution of S. vittatum larvae, flow parameters were apparently more influential. Froude number explained more variation in black fly density than any other variable, for both streams. Important substrate variables included evenness, amount of accumulated material on the surface (periphyton or inorganic), and substrate size.

Black flies apparently co-exist with a variety of other taxa consisting of primarily herbivores and detritivores. Hydropsyche, which can select either filter-feeding or grazing strategies, was the only co-occurring filter-feeder of relatively high abundance, but only in one of the streams (Wigle Creek) studied.

I could detect no differences in microhabitat with respect to mean size of simuliids, at least at this scale of investigation. Given the importance of flow conditions to larval feeding, one might expect larvae to select similar microhabitats, regardless of size.

Future Research

Further investigations are needed to evaluate the importance of accumulated debris to microhabitat sites by black fly larvae. My studies suggest that accumulations of silt and/or periphyton may deter black fly colonization, but do not conclusively demonstrate which variable, if either, is more detrimental. Examination of algal species and diatoms would also provide useful information regarding the effect of periphyton. Perhaps some types of organic surface coverings are more

frequently avoided than others (e.g., Cladophora may be a refuge for early instars, whereas slippery diatoms may be undesirable for all larval sizes).

It may be productive to examine hydrodynamic variables such as current velocity at the micro-scale using natural substrates in the field, but such investigations would be difficult and require specialized equipment. However, field measurements of this type might be more realistic than simulated, controlled laboratory conditions and elucidate more clearly the choice of larval positions (aggregations) in the field.

Long-term studies examining the distribution of larvae among seasons and years is lacking. Such studies would promote a better understanding of the natural temporal variation in densities, life history (e.g., emergence of cohorts), community succession, and the role of disturbance (response of black fly populations to varied degrees of disturbance).

It seems that more research needs to proceed at an even finer scale of investigation, specifically at the level of individuals. Where do aggregations occur with respect to micro-flow patterns? How do these aggregations form? What is the turnover rate of individuals (i.e., immigration of new colonists, emigration of present aggregation members)? In conjunction with the factors associated with the formation of aggregations, further work is required with respect to the presence of other co-occurring taxa. My study suggests that herbivores and detritivores tend to occur with simuliids, but numbers of other suspension-feeders are limited. Is this pattern due to interactions, habitat preference, or temporal succession? If interactions are the cause, is it one of commensalism (a potential reduction of periphyton and/or inorganic debris, allowing black flies to maintain their

positions), competition (whereby black flies exclude other suspension-feeders), or competition (in which black flies are continually removed by other superior suspension-feeders throughout time)? Answers to some of these questions would help to assess whether monocultures of black flies undergo a successional pattern to multi-taxon assemblages through time, and would certainly provide useful information regarding the role, and importance, of interspecific interactions to black fly distributional patterns. Not only the types of other taxa associated with black flies, but also the density and proximity of organisms to simuliids would increase understanding of distributional patterns among seasons, and among streams. One might also wish to consider body size of these associated taxa, since it was generally small-sized taxa, or early instars, that occurred with black fly larvae in my studies.

Finally, the aspect of simuliid larval size warrants further examination. My observations of larvae on Cladophora, and within aggregations (in the maintenance tank), suggested that small larvae could segregate from larger larvae at least occasionally to use this resource. Is this a differential response to microhabitat features (e.g., flow patterns) or biotic interactions (e.g., large larvae competitively exclude small larvae)? This aspect could be further addressed by examining the effect on fitness parameters such as growth rate, larval size, and adult fecundity.

II. THE ROLE OF SUBSTRATE SURFACE TEXTURE, EVENNESS, PERIPHYTON, AND LARVAL DENSITY IN SUBSTRATE SELECTION BY *SIMULIUM VITTATUM* (DIPTERA: SIMULIIDAE)

INTRODUCTION

This series of experiments was designed to gain further insight into the preferred microhabitat of S. vittatum larvae. My previous surveys suggested two factors (evenness, periphyton) influenced microdistribution. In this chapter, my experiments addressed substrate choice by larvae, as well as any potential effect of density to this choice. Since larvae occur at variable densities in the field, and substrates vary naturally by texture, evenness, and degree of periphytic coating in the field, these experiments may allow more accurate predictions regarding the microdistribution of larvae in the field.

In this study, standardized artificial substrates (tiles) were used to minimize the effect of black fly sensitivity to hydrodynamic parameters (current velocity, direction and type of flow, turbulence). Tile surfaces were modified to examine the influence of three attributes of hard inorganic substrate (e.g., cobble): substrate surface texture, evenness, and periphytic growth.

Substrate is an important component of microhabitat for benthic macroinvertebrates (Hynes, 1970). It provides shelter, food, refuge from predators, and protection from disturbance (scouring). It also provides the materials for building shelters (burrows, tubes, cases), may alter flow patterns, change the direction of current, and affect turbulence (Minshall, 1984). Substrates may be organic (leaves, twigs) or inorganic (cobbles, silt), composed of a variety of particle types and sizes, and their surfaces may be modified by features such as texture, evenness, hardness or colour, any of which could potentially affect choice of microhabitat by the organism.

For black fly larvae, substrate provides sites for attachment, a necessary prerequisite to larval feeding, subsequent growth, and later pupal attachment. Black fly larvae are suspension-feeders that collect

fine particulate organic matter (0.5 μm - 150 μm) from the seston using specialized labral (cephalic) fans. Since different substrates affect flow patterns (Vogel 1981), and black fly larvae are sensitive to micro-hydrodynamics (Hocking and Pickering 1954, Maitland and Penney 1967, Décamps et al. 1975, Craig and Chance 1982, Osborne et al. 1985, Chance and Craig 1986, Craig and Galloway 1987, Lacoursière 1989, Eymann 1990), substrate type may affect larval attachment and/or larval feeding. Thus, substrate selection may play an important role in larval black fly microhabitat selection, contributing to the unusual microdistributional patterns observed in nature. Such distributions include the formation of bands of larvae perpendicular or parallel to the direction of water flow, dense patches of larvae, randomness, and frequently, uniform spacing between individuals.

Many materials of various shapes have been used as artificial substrates in attempts to collect black fly larvae more easily or to monitor population densities. These include plastic tapes (Williams and Obeng 1962, Pegel and Rühm 1976, Fredeen and Spurr 1978, Ross and Merritt 1978, Gersabeck and Merritt 1979, Rühm and Pegel 1986a, 1986b, Pruess 1989), wooden boards or floats (Grenier 1949, Carlsson 1962, Carlsson 1967), cones of plastic, metal or concrete (Johnson and Pengelly 1966, Benfield et al. 1974), ceramic tiles (Zahar 1951, Lewis and Bennett 1974, Gersabeck and Merritt 1979), polystyrene foam spheres (Wolfe and Peterson 1958, Walsh et al. 1981,), fabric (Tarshis 1968), bricks (Ali et al. 1974, Downes and Lake 1991), nets and tins (Wanson and Henrard 1945, Elliott 1971), and plant material attached to ropes (Yakuba 1959, Disney 1972). Most frequently, artificial substrates have been deployed in rivers to determine densities of black fly larvae (Wolfe and Peterson 1958, Lewis and Bennett 1974, Fredeen and Spurr 1978, Ross and Merritt 1978) in attempts to design more effective sampling regimes for control strategies or evaluate existing programs of insecticide application to rivers. However, artificial substrates have

been used as well to determine species composition (Lewis and Bennett 1974), or optimal periods (duration) of colonization (Gersabeck and Merritt 1979, Pruess 1989).

In my study, modified ceramic tiles were used to examine substrate selection by Simulium vittatum larvae in the laboratory (Chapter II), and the dynamics of black fly colonization and the ensuing development of the community under natural field conditions (Chapter III). Gersabeck and Merritt (1979) used white ceramic tiles and clear plastic tapes to assess physical factors affecting black fly colonization and substrate type. A limited number of studies have compared the performance of artificial substrates to natural substrates (Williams and Obeng 1962, Benfield et al. 1974, Lewis and Bennett 1974, Boobar and Granett 1978, Walsh et al. 1981). Lewis and Bennett (1974) proposed use of a standardized artificial substrate for more reliable comparison of larval densities among field surveys, and advocated that ceramic tiles might be the most practical and advantageous substrate. Their collections on tiles and natural substrates showed similar densities and species composition (but see Morin 1987).

Substrate texture is characterized by size and type of surface projections and irregularities. Tiles with a smooth face have finer, smaller surface features than those with a rough face. Evenness refers to the presence or absence of coarse surface projections. An even surface is uniformly flat or level while an uneven surface is irregular, with crests and valleys. Smooth, even tiles have the least surface complexity; rough, uneven tiles have the most surface complexity. Substrate roughness has profound effects on the pattern of water flow above it (Vogel 1981). I anticipated that an even face would support more tranquil water flow over its surface, perhaps contributing to more efficient black fly feeding relative to an uneven substrate face. Vortices in water flow caused by substrate surface irregularities might

interfere with smooth passage of water through the labral fans during feeding. Similarly, different types of substrate projections and their sizes were expected to affect adhesion of silk to the substrate. Rough substrates were expected to anchor silk better than smooth surfaces. Additionally, substrate textural features could also alter flow patterns over the substrate surface. More roughly-textured surfaces may contribute to less tranquil flow than smoothly-textured surfaces.

Anecdotal descriptions of field distributions of black fly larvae suggest that there is a negative association between black flies and periphytic growth (algae, diatoms, fungi, and their secretions attached to the substrate surface). This pattern has been attributed to the potential interference of periphytic growth with larval silk attachment (Zahar 1951, Carlsson 1962, Gersabeck and Merritt 1979, Pruess 1989). This aspect, however, has not yet been examined experimentally, and therefore, its effects remain largely speculative. Additionally, the presence of periphyton on the substrate surface could disrupt flow patterns at the microscale.

While it is generally accepted that the distribution of black fly larvae is influenced highly by current velocity and flow (Wu 1931, Phillipson 1956, 1957, Wolfe and Peterson 1958, Craig and Chance 1982, Chance and Craig 1986, Wotton 1985, Ciborowski and Craig 1989, Ciborowski and Adler 1990), the role of substrate is not yet clear. Adler and Kim (1984) provided some evidence for potential substrate selection by black fly larvae. They found a tendency for the IIIL-1 sibling species of Simulium vittatum to occur more often on cobbles while the sibling IS-7 more frequently inhabited vegetation (grasses), and Fredeen and Spurr (1978) found greatest larval densities of Simulium on smooth substrate surfaces.

Although flow (Froude number) was the most important factor explaining black fly larval densities in both surveys (Chapter I), I chose to manipulate specific substrate features in this series of laboratory experiments under conditions of suitable flow (Froude number 0.90, current velocity 19-20 cm/s, water depth 0.4-0.5 cm). My distributional surveys of natural substrates (cobbles) in Hobbs-Mackenzie Creek, and Wigle Creek, both small southwestern Ontario streams (Chapter I), indicated that the microhabitat component of substrate was secondary to the importance of flow. The surveys also suggested that two attributes of substrate in particular (evenness and periphyton cover) played a role in black fly microdistribution. Given the limitations of my experimental system, quantification of micro-hydrodynamic aspects were not feasible for study. However, the effects of flow could be controlled suitably to allow the effects of substrate to be addressed in greater detail than past studies. Accordingly, I conducted laboratory experiments to assess the relative importance of three substrate surface features (substrate evenness, texture, periphyton).

My objectives in these experiments were:

1. To determine the relative importance of substrate selection as it relates to microhabitat selection by black fly larvae;
2. To assess specific substrate surface features of texture, evenness, and periphyton cover in choice of substrate by larval black flies; and
3. To examine the effect of larval density on substrate choice (given a finite set of alternative surfaces), under controlled laboratory conditions.

MATERIALS AND METHODS

Experimental Design

I conducted four laboratory experiments that manipulated three aspects of substrate surface features (evenness, texture, and periphyton) and two levels of S. vittatum density (low, high). Evenness and texture were incorporated into the substrate (tile) surfaces, while periphyton was allowed to develop on the surface for the final experiment. The order of these experiments is outlined in Table 2.1.

In all experiments, it was anticipated that attachment of larvae to the substrate may vary with texture, and differences in flow patterns as affected by evenness may affect larval choice of substrate. Therefore, larvae may select one substrate type over the other three in any of the experiments.

The original design for this experimental series was intended to determine the most and least preferred substrate type for low and high larval densities of black flies. Each subsequent experiment was thus dependent upon the outcome of the preceding experiment. A completely balanced design of the experiment would entail one experiment each using tiles without periphyton at low and high larval density, and tiles with periphyton at low and high larval density. For practical reasons (seasonal abundance of larvae), the experiments involving low larval density in the absence of periphyton were conducted first, followed by the high larval density treatment without periphyton. During this time period, other tiles were colonized by periphyton to be used in experiments involving larvae at low and high densities. Seasonal abundance of larvae dictated the high larval density experiment be conducted prior to the low larval density experiment. However, sudden pupation of larvae and subsequent emergence of the population precluded the final experiment (low larval density, tiles with periphyton) from

Table 2.1 Summary of the series of laboratory experiments conducted, indicating conditions of tiles and density of larvae.

Experiment	Date	Larval Density	Periphyton
1	9-10 May	Low (2-4/cm^2)	Absent
2	19-20 July	Low (2-4/cm^2)	Absent
3	1-2 August	High (10+/cm^2)	Absent
4	3-4 August	High (10+/cm^2)	Present (Low, High)

occurring. The experimental series was, therefore, conducted as described below.

Experiments 1 and 2 involved tiles devoid of periphyton, and low black fly density. Field data (Chapter I) suggested that evenness was a factor influencing larval black fly distribution. Thus, one might anticipate that uneven tiles would be preferred. At low larval density, more intense substrate selection was expected to occur for the more suitable substrates than at high larval density, due to the absence of crowding and potential competition, and the presence of unlimited space. Under conditions of low larval density, most larvae should occupy the best habitat (substrate) available. This prediction follows traditional ecological habitat selection models (Fretwell and Lucas 1969, Rosenzweig 1981, 1991). Duplication of the experiment allowed testing of the experimental system to ensure reasonable repeatability of results.

At high larval density and in the absence of periphyton, it was anticipated that substrate selection for the more suitable substrate (uneven) would be less pronounced relative to the low density treatments because patches (tiles) of differing quality would be exploited according to their rank (benefit) in descending order, such that the best areas would be filled first with individuals, and each patch successively in order. Limited space and competition for the most suitable area would result in patches with varying qualities to be inhabited. As each successive patch becomes occupied, the benefit of occupying the best patch should equal the benefit of a larva entering the next best patch, and similarly, for all subsequent larvae selecting a patch (tile). This prediction follows the ideal free distribution models of habitat selection (Fretwell and Lucas 1969, Rosenzweig 1981, 1991). Differences in larval response due to density could be examined by comparing the three experiments.

In Experiment 4, periphyton was present on all tiles, rough tiles having greater quantities than smooth tiles. Larvae were expected to select surfaces with less periphyton (smooth) since periphyton has been suggested to negatively affect larval attachment.

Collection Site

For practical reasons (availability of larvae, proximity of streams to the Univ. of Windsor, accessibility to stream), black fly larvae were collected in 1990 from Wigle Creek (Fig. 2.1), a third order (sensu Strahler 1957) southwestern Ontario stream that flows through farmland. This is a highly productive stream, partially shaded by shrubs and trees. The collection site was located within the Kingsville Golf and Curling Club, immediately downstream of a 0.1 ha pond controlled by a small dam (42°02'24" N, 82°45'57" W). There are both pools and riffles downstream of the dam. The stream is approximately 5 m wide at the site, and water depth is variable. Within pools, depths occurred in the range of 15-75 cm, while in the riffle areas (where black fly larvae occurred), depths occurred in the range 1-28 cm. Although cobble and boulder dominate the site, there are a few gravel and sand patches, particularly in the pool areas. Chironomids and simuliids are the dominant taxa present at the site (Chapter I). Simulium vittatum appears in early spring (mid to late April), but in late July Simulium decorum begins to appear also, and becomes the more common species present by mid-August.

Field Collection of Black Fly Larvae

Larvae were removed from the stream between 1100 h and 1500 h EDT. To collect larvae, cobbles were removed from the stream and held inside a pail containing stream water. The cobble surface was brushed gently by hand to dislodge larvae. Dense patches of black flies on boulder surfaces were sampled by placing a small net (mouth 300 cm^2, mesh 250 μm) immediately downstream of the patch and brushing them gently by hand

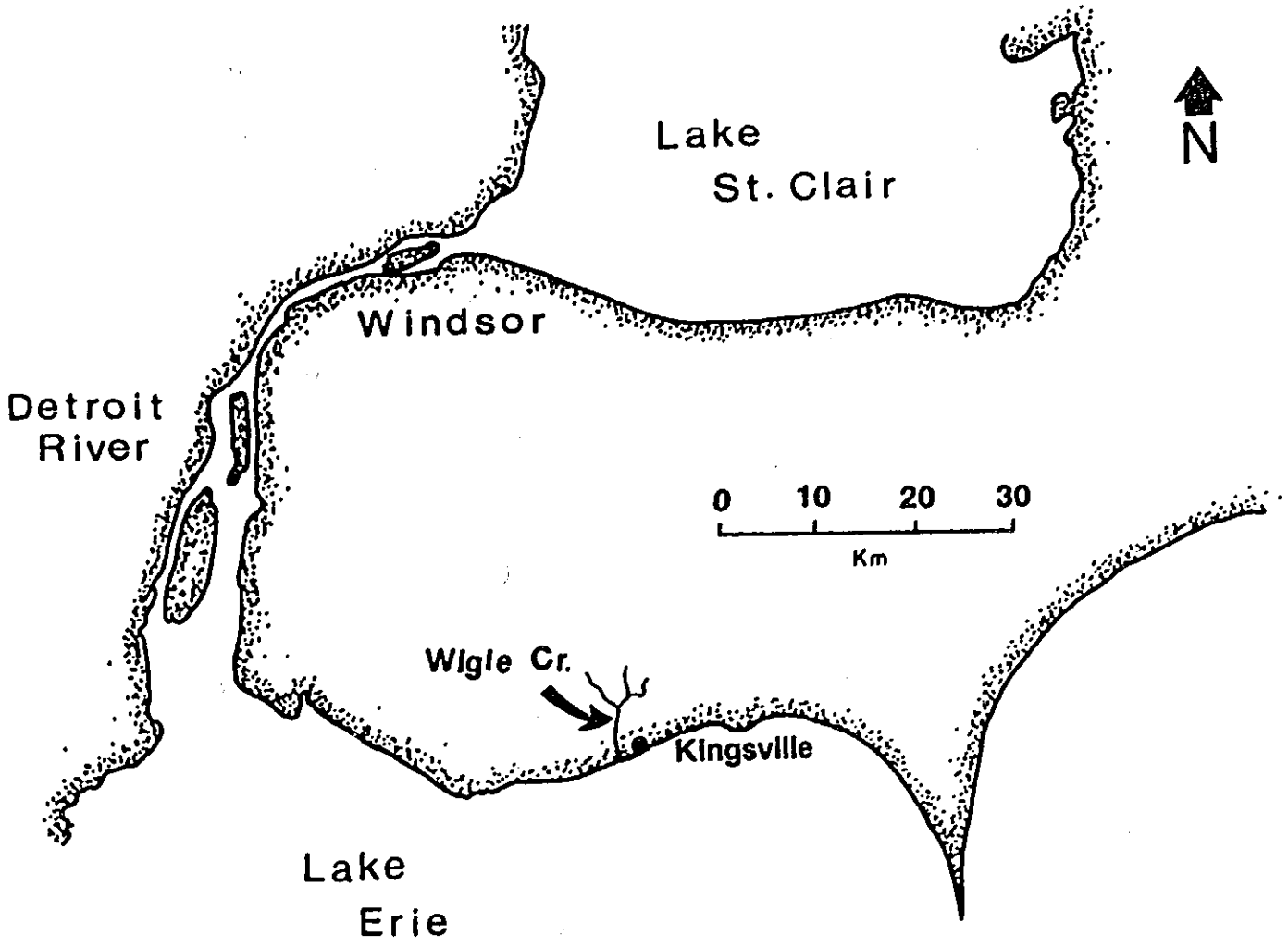


Figure 2.1 Location of Wigle Creek, the source of black fly larvae for the series of laboratory experiments.

from the surface into the net. A few cobbles were placed on the bottom of the pail to provide substrate. Water was aerated with a battery-powered air compressor during collection and transport (approx. 1 h) to the laboratory. Most larvae adhered to the sides of the plastic pail during transport. Black flies were transferred as quickly as possible to the laboratory maintenance tank (Fig. 2.2, Fig. 2.3) for holding prior to use in experiments. To add larvae to the maintenance tank, most of the water was siphoned from the tank, and the stream water containing the larvae was poured gently into the chamber. Larvae were used within 1 wk of collection. No larva was used more than once.

Laboratory Maintenance of Larvae

Larvae were maintained in a large, plastic, air-powered recirculating tank (Fig. 2.3) modelled after a design of Gee and Bartnik (1969). This holding tank (37 L) was connected to a filter (Aquachiller® Filtracan model 365) and cooling unit (Aquachiller® model 365) that regulated temperature (12-15°C spring; 20-23°C summer) and pumped water through the system. Aerated RO-pure® (dechlorinated) water was added every second day to the tank to compensate for evaporation. Within the tank, 4 1-L glass jars were used as supports for a plexiglass platform (24.5 cm x 18 cm; Fig. 2.2). Natural cobbles and Cladophora were arranged on the platform of the maintenance chamber to simulate natural stream bottom. Perforated plastic tubing (Nalgene® 0.75 cm internal diam.), connected to a filter and wall air-source generated the current in the system and aerated the water (Fig. 2.3). Upper surfaces of cobbles were approximately 3 cm below the water surface and current velocity ranged from 27-30 cm/s. A 16:8 h L:D photoperiod was followed throughout. On alternate days, larvae in the maintenance tank were fed alfalfa powder (2-3 g) prewetted with a few drops of 70% ethanol in 50 mL water. This mixture was poured at the upstream end of the tank over the bubbler to distribute the food throughout the tank.

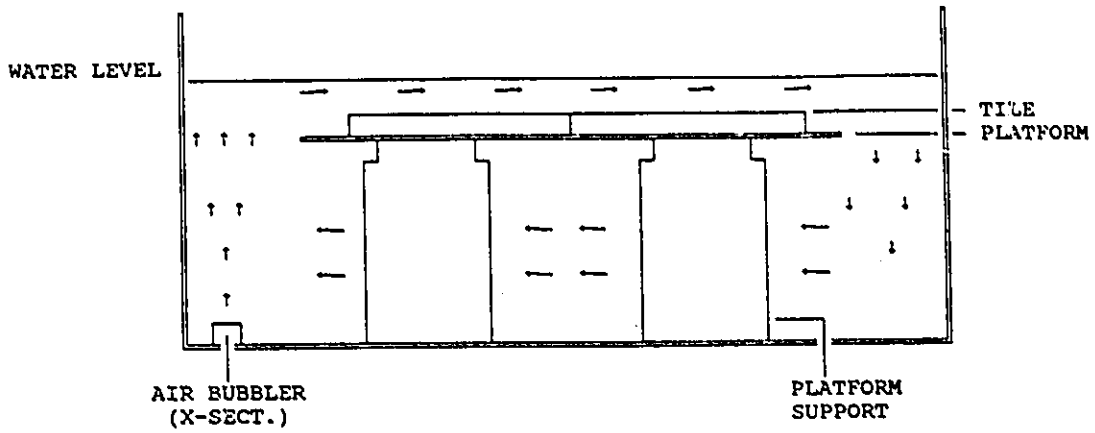


Figure 2.2 Schematic diagram depicting the side view of an experimental chamber, and of the laboratory maintenance tank. Convection is powered by air bubbles rising to the surface, displacing water vertically in the process. Tiles were placed on a platform in experimental tanks, while cobbles were placed on the platform in the maintenance tank. Direction of water flow is indicated by the arrows.

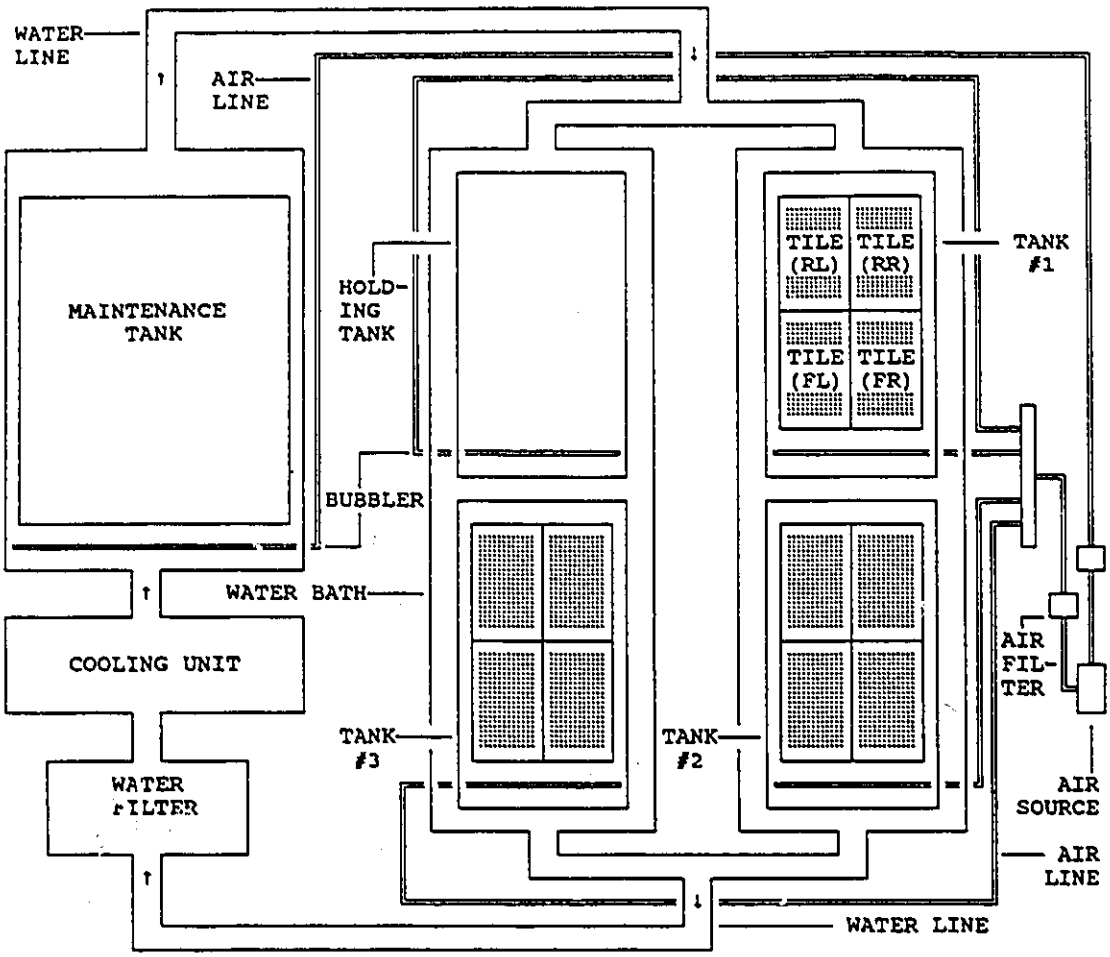


Figure 2.3 Schematic diagram depicting the top view of the experimental apparatus. One of each type of tile was placed on the platform in each of the three experimental chambers. Direction of water flow is indicated by the arrows. Tile positions within replicate tanks are abbreviated by FR: front right, FL: front left, RL: rear left, RR: rear right.

Preparation of Tiles

Tiles With No Periphytic Growth

Hobbs-Mackenzie Creek, the major study stream for distributional (Chapter I) and colonization (Chapter III) studies has predominantly dolomite bedrock. White sand and diatomaceous earth were chosen as surface materials to modify the experimental tiles to simulate the natural bedrock. The most common surface type in Hobbs-Mackenzie Creek is "smooth, even". The upper surface of unglazed ceramic tiles (4.5 cm x 9.5 cm) was modified to control evenness, by applying a thin layer of extra-coarse, exterior, white stucco (Glidden® Extra-coarse, Exterior, White, Stippletone). This stucco contains gravel and sand. To create uneven tile surfaces, stucco was spread onto the tile surface, and allowed to dry for 3 days. Tiles were placed in a drying oven (GCA model 18EG) for 12 h at 60°C and then air-dried at room temperature for another seven days. For tiles with even surfaces, no stucco was applied. To further modify tiles to incorporate texture differences, washed, coarse, white marble sand (250 μm - 500 μm) was applied to "rough" tiles, and washed white diatomaceous earth (particle size <90 μm) was applied to "smooth" tiles. For each tile type, two parts material (sand or diatomaceous earth) was mixed with one part epoxy resin (Glidden® industrial-strength epoxy chemical resistant finish). The mixture was spread thinly over the tile, and allowed to air-dry for 7 d at room temperature. After this procedure, tiles were dried at 60°C for 48 h to harden the surface, air-dried at room temperature for a further 7 d to allow potentially toxic residues to evaporate, and soaked in tap water for two weeks until there was no dectectable odour of epoxy residues.

A collection of 450 live larvae placed within an experimental chamber with a random assortment of one of each tile type for 3 days did not exhibit any mortality. Therefore, it was concluded that any potentially toxic residual effects from preparation of the tile surfaces

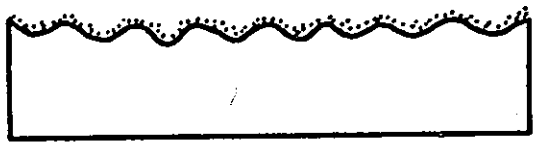
was negligible. These surfaces constituted the final substrate surface for tiles lacking periphyton. Substrate surface choices, as represented by tile types are summarized as: smooth, even (SE): diatomaceous earth only; smooth, uneven (SU): layer of coarse stucco covered by diatomaceous earth; rough, even (RE): coarse white sand only; rough, uneven (RU): layer of coarse stucco covered by coarse white sand (Fig. 2.4).

Tiles With Periphytic Growth

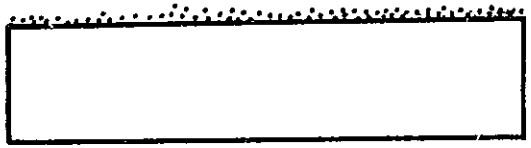
Tiles were prepared as above. Surfaces were further modified by placing tiles in two recirculating streams (each with 40 L dechlorinated tap water) for algal colonization. The streams are described in detail by Ciborowski and Craig (1989). Each artificial stream was stocked with one-half (6 L) of an algal slurry (12 L stream water, and the periphyton scraped from all surfaces of six Wigle Creek cobbles). Stream water collected from the site was added to fill the artificial streams. During the algal colonization period, water evaporating from the artificial streams was replaced by one-half stream water and one-half RO-pure® water. Streams were placed in a greenhouse and exposed to 24 h light (daylight during the day, fluorescent growth lights at night) for 3 weeks. Streams were then moved outside (roof of Biology Building, University of Windsor) for exposure to natural light conditions.

A total of 12 tiles (3 experimental tanks, each containing one of each type of the four tile types) was required for the experiment involving tiles colonized by periphyton (Experiment 4). In each of the two recirculating streams, 12 tiles were placed on the stream bottom. Each stream had three tiles of each surface type randomly arranged.

Tiles were visually inspected periodically during the algal colonization phase of tile preparation in recirculating streams. After seven weeks (June-July), tiles were considered to have adequate levels

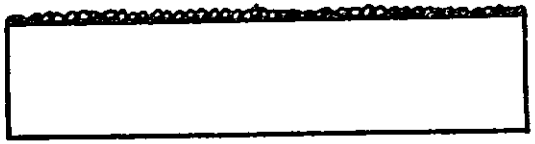


Smooth Uneven (SU)



Smooth Even (SE)

Rough Uneven (RU)



Rough Even (RE)

Figure 2.4 The diagram illustrates the concepts of surface texture (different particle types and sizes) and surface evenness (uniformity of surface levelness). Tiles were modified to reflect alternative states of texture (smooth, rough) and evenness (even, uneven).

of periphyton present for the experiment. This judgement was based on the following observations: there were distinct tufts of algae present on tiles; on most tiles, these tufts had spread over the majority of the tile surface and to a lesser extent onto the tile sides; a slimy coating had also developed over all surfaces, (including the walls of the artificial stream). For "rough" tiles, the algal mat was approximately 0.5 cm thick. "Smooth" tiles had many fewer tufts, but a slimy and slippery coating was present on all tile surfaces. It was apparent that the periphyton present on the tiles was attractive to insects. In particular, Hydropsychidae caddisfly larvae had colonized the streams, and some of the tiles. They had set up distinct territories on some of the tiles. These territories were very obvious as a result of the grazing activities of the resident caddisfly larvae. Therefore, the tiles had reached levels that were appealing to taxa dependent upon periphyton for food or shelter. Since this also indicated a danger in depletion of the algal resource accumulated onto the tiles, the tiles were removed for the experiment. Tiles (three of each of the four tile types) were selected randomly from the two streams. However, during this process, tiles that had been colonized by caddis larvae were not retained. There were more tiles available which had not yet been invaded by caddis larvae than were invaded.

Measurement of Periphyton Biomass on Tiles

Upon completion of the experiment involving tiles with periphyton (Experiment 4), the biomass present on each tile that was actually used in the experiment (12 tiles; three tiles of each of the four tile types) was determined.

Loose periphyton was brushed from the tile with a toothbrush. The remaining periphyton was allowed to air-dry overnight and was removed with a toothbrush the next day. (This was found to be more efficient than scraping wet tiles). Periphyton from each tile was collected onto

preweighed filter paper, and dried for 24 h at 60°C, to determine the dry mass, then ignited in a muffle furnace (Fisher Isotemp model 184A) for 3 h at 550°C for determination of ash-free dry mass (AFDM).

Experimental Apparatus

One of each of the four tile types was placed on a plexiglass platform in each of three experimental tanks (30 x 20 x 15 cm aquaria, Fig. 2.2). (A fourth chamber was used as a temporary storage tank (Fig. 2.3) for larvae 24 h prior to the start of an experiment. It was identical to the experimental tanks, except that neither a platform nor tiles were provided as substrate). Arrangement of tiles (on platforms) with different surfaces varied among replicates and among experiments. Positions of the tiles on the platforms are given in Table 2.2. An air bubbler (Hagen Air Curtain®, 10 cm long) was placed at one end of each tank to provide aeration and current. A 4-way air control valve fed each tank filtered air from a single wall unit.

Current velocity was calibrated for each tank using a small (1 cm^2) styrofoam block and a stop watch. The time required for the styrofoam piece to travel across and to the far edge of the tiles was measured, and current velocity was calculated as distance travelled over time. All tanks had velocities in the range of 19-20 cm/s.

To maintain a constant temperature during experiments, experimental chambers were placed inside a larger aquarium that served as a water bath (Fig. 2.3). Water was circulated through the maintenance tank and the water bath during experiments. However, water within the experimental tanks did not mix with the circulating water.

Experiments were conducted over a 24 h period under fluorescent lighting. Experiments commenced during light hours, but included eight hours of darkness, to simulate the natural light regime. Dechlorinated

Table 2.2 Positions of tiles on platforms in experimental chambers for each experiment. Position of replicate chambers corresponds to positions indicated in Fig. 2.3. Tile postions are as indicated in Fig. 2.3 and are abbreviated by FL: front left, FR: front right, RL: rear left, RR: rear right. Tile types are abbreviated as SE: smooth even, RE: rough even, SU: smooth uneven, RU: rough uneven.

	Replicate 1				Replicate 2				Replicate 3			
	Tile Position											
	FL	FR	RL	RR	FL	FR	RL	RR	FL	FR	RL	RR
Experiment 1	RU	SE	RE	SU	RU	SU	SE	RE	SE	RE	RU	SU
Experiment 2	RU	SU	SE	RE	RE	SE	SU	RU	SE	RU	SU	RE
Experiment 3	SE	RE	RU	SU	RU	SE	RE	SU	RU	SU	SE	RE
Experiment 4	SE	RE	RU	SU	SE	RU	RE	SU	RU	SU	SE	RE

tap water was aerated for 24 h in experimental tanks. Water depth was from 0.4-0.5 cm above tile surfaces. Starting times of replicate tanks were staggered by approximately 1 h for all experiments.

Pilot Studies

Trials Using Natural Cobbles

Initially, even and uneven-surfaced natural cobbles were arranged on the platform in the maintenance tank such that approximately equal surface area of each type was available and was distributed in equal proportions among upstream, central, and downstream positions. Black flies were exposed to a water velocity of 27-30 cm/s and water depth of 3-5 cm above cobble surfaces. Larvae were fed once during the course of the experiment. For six preliminary trials, black fly larvae were pipetted onto cobbles at low density (2 larvae/cm^2). The number of larvae per surface type was recorded at 15 min intervals for 5.5 h, under light conditions. An 8 h period of darkness was followed by a final series of observations at 24, 25, and 26 h.

Trials Using Artificial Substrates (Tiles)

To evaluate utility of tiles, a preliminary experiment was conducted in two replicate tanks with smooth, even and smooth, uneven tiles (4.5 cm x 19.5 cm), at low larval density (2 larvae/cm^2). Experimental protocol was identical to that below. At the conclusion of this experiment (24 h), there were more larvae than expected on uneven surfaces, and fewer larvae than expected on even surfaces, in both replicates. However, in neither case was there a significant difference, although there was a trend in the first replicate by 24 h (chi-square, df=1, $0.05<p<0.10$). Since there was a consistent tendency for more larvae to occur on the uneven substrate, and fewer to occur on the even substrate, it was decided that variation among tiles due to hydrodynamic factors was reduced to an extent that differences due to

substrate could be detected. Thus, tiles were accepted as suitable substitutes for natural substrates.

Experimental Protocol

Larvae were handled as little as possible prior to use to reduce potential stress on the animals. A subsample of specimens was identified to species after completion of experiments (Table 2.3, Table 2.4). Larvae were examined under a dissecting microscope (Wild M8A) with 25x or 50x magnification, for species verification, using the taxonomic key of Currie (1986).

Experimental densities of larvae used were based on observations of larvae in the holding tank as well as work by Eymann (1985). He found that S. vittatum larvae occurred at mean densities of 4.7 larvae/cm^2 under laboratory conditions. I placed a 1 x 1 cm grid on the side panel of the maintenance tank (25 cm^2 total) at two locations that supported typical larval density, and recorded the number of larvae per square. This procedure was repeated on several days. Mean ($\pm$ 1 S.E.) larval density was 5.3 $\pm$ 0.5 larvae/cm^2. Thus, 2 larvae/cm^2 was chosen for low density manipulations (range of 2-4 larvae/cm^2) and 10 or more larvae/cm^2 for high density.

To determine whether light was distributed evenly over all experimental tanks, light levels were measured within each experimental tank, at each end of the tank (Gossen light meter model 1.71-292 with 20x filter magnifier). There were no significant differences in light levels among tanks or within tanks (Appendix II.1; nested ANOVA, $p>0.05$, $n=3$).

Twenty-four h prior to the start of an experiment, the water bath and experimental chambers were filled with dechlorinated water to the appropriate levels, and aerated until the start of the experiment.

Table 2.3 Species composition of black flies collected from Wigle Creek, and used in laboratory experiments (Experiment 1, low larval density, bare tiles, 19-20 July 1990). Tile types are denoted by SE (smooth even), RE (rough even), SU (smooth uneven), and RU (rough uneven), and black fly species are abbreviated as S.V. (*Simulium vittatum*) and S.D. (*Simulium decorum*).

		LARVAE		PUPAE	
TREATMENT	REPLICATE	S.V.	S.D.	S.V.	S.D.
SE	1	60	0	1	0
	2	52	0	0	0
	3	77	0	0	0
RE	1	134	0	6	0
	2	95	1	6	0
	3	97	0	0	0
SU	1	124	1	13	0
	2	123	0	8	0
	3	123	1	0	0
RU	1	71	1	6	0
	2	79	0	0	0
	3	167	4	0	0
TOTAL		1202	8	40	0

S. vittatum: 99.36%
S. decorum: 0.64%

Table 2.4 Species composition of black flies collected from Wigle Creek, and used in laboratory experiments (Experiment 4, high larval density, periphyton covered tiles, 3-4 August 1990). Tile types are denoted by SE (smooth even), RE (rough even), SU (smooth uneven), and RU (rough uneven), and black fly species are abbreviated as S.V. (*Simulium vittatum*) and S.D.(*Simulium decorum*). Missing data are abbreviated by NA = not available.

		LARVAE		PUPAE	
TREATMENT	REPLICATE	S.V.	S.D.	S.V.	S.D.
SE	1	367	23	48	0
	2	535	13	42	2
	3	379	9	18	0
RE	1	192	27	36	1
	2	407	50	44	4
	3	585	52	8	0
SU	1	775	42	39	0
	2	NA	NA	NA	NA
	3	NA	NA	NA	NA
RU	1	519	52	52	1
	2	NA	NA	NA	NA
	3	371	17	28	0
TOTAL		4130	285	315	8

S. vittatum: 93.82%
S. decorum: 6.18%

Black fly larvae were removed by pipette from the maintenance tank and placed in the temporary storage tank. (This facilitated transfer of larvae to experimental units). Food was added as in the maintenance tank (3 mg/L).

Approximately 1 h prior to the start of the experiment, water levels were adjusted (to compensate for evaporation), and current velocities were checked. Black flies were counted and pipetted sequentially from the temporary storage tank onto the four tiles in the first experimental tank. Care was taken to transfer, as closely as possible, equal numbers of larvae onto each of the four tiles. The air bubbler (temporarily removed during transfer), was replaced and the animals were fed as usual (3 mg/L, within natural field conditions).

Numbers of larvae on each tile were counted to provide a time zero reading, and the tiles were photographed. While the photographs were taken, the air bubbler was temporarily removed (maximum 15 s) to allow for maximum resolution and clarity of the photographs. Tiles were photographed and numbers of larvae per tile were counted at 20 min. intervals for 4 h. A final count and photograph was taken 24 h after the start of the experiment. After the 24 h reading, each tile was transferred to a fingerbowl of water. Larvae were removed from tiles and preserved in 70% ethanol. Photographs provided a permanent record of numbers per tile, as well as of changes in positions of larvae over time.

Larvae in low density treatments were counted and recorded during the experiment. For high density treatments, the negatives of the photographs were projected onto paper, images of larvae were traced, and individuals were counted from these drawings.

Statistical Analysis

The 24 h time point data were analyzed for differences in the number of larvae among differing surface types using a repeated measures cross-classified analysis of variance on Ln transformed data (SAS statistical package). This test was used to analyze the relationship among the means of the different tile types at initial time (t=0) with the means at the final time (t=24 h). The analysis accounts for a time effect by comparing the proportion of larvae based upon initial number of larvae on each of the tiles with the proportion on each tile type at 24 h. It was expected that 24 h would be adequate for substrate selection to occur. Intermediate time points were used for descriptive purposes to monitor larval movement and activity during the experiment.

Differences in periphyton (as measured by AFDM) and total detritus (as measured by dry mass) levels among tile types were tested using a two-way analysis of variance (Sokal and Rohlf 1981) on Ln(x+1) transformed data.

RESULTS

Pilot Studies

Trials Using Natural Cobbles

For all pilot experiments, black fly larvae were subsequently identified as Simulium decorum. Larvae were quick to assume positions near neighbouring individuals (aggregate). Within the first 4 h, larvae began forming rows perpendicular to the flow. There was little change throughout the remaining time of the experiment. However, there were notable differences among cobbles in number of larvae present, and these differences appeared to be related to flow patterns over the cobbles. Also, it was clear that many larvae deserted cobbles for more favourable areas in the tank, generally those with more turbulence and faster flow (e.g., near or on the bubbler). These responses were typical of behaviours observed in the natural habitat.

Trials Using Artificial Substrates (Tiles)

In two replicates, there were more larvae than expected on uneven surfaces, and fewer than expected on even surfaces (Fig. 2.5, Appendix II.2A, II.2B). Note that in Figure 2.5, for replicate 1, the expected number of larvae per tile was generated from the total number of larvae occupying the tiles at each time interval, assuming a ratio of 1:1 based on initial conditions, (no preference by larvae for either tile type presented in the trial). For replicate 2, tiles began with unequal numbers of larvae. Therefore, the expected number of larvae per tile was based on the initial percentage of larvae (68.75% on uneven, 32.25% on even) rather than a 1:1 ratio. Although there was no significant difference between the numbers of black flies on the two tile types (chi-square, $n=2$, $p>0.05$), there was a trend for more larvae to occur on uneven than even surfaces. Although both replicates were to start with equal numbers of larvae on each tile type, larvae looped off of the smooth, even tile (upon touching the surface) and onto the smooth, uneven tile, or appeared to be less successful in attaching the silk pad

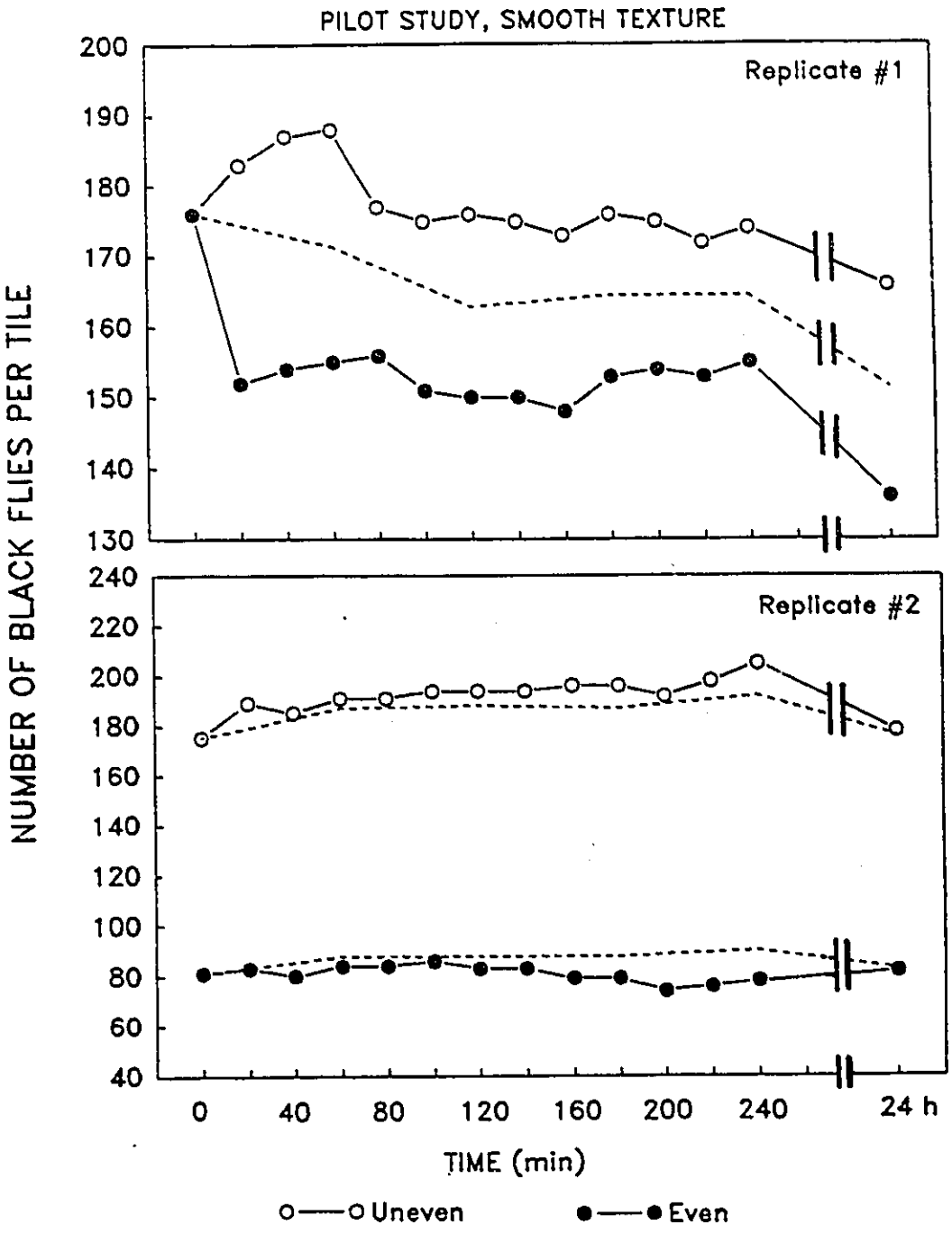


Figure 2.5 Numbers of S. vittatum positioned on tiles with the same texture (smooth), but different evenness, during pilot experiments. The dashed line indicates the expected number of larvae per tile assuming no preference by larvae for either tile type. Note that the y-axis scales differ between replicate tanks.

as the current velocity was increased to the full level for the experiment. This accounted for the difference in starting numbers per tile in the second replicate.

Experiments

Species Composition

The majority of larvae (99% in Experiment 1, 94% in Experiment 4) were Simulium vittatum (Table 2.3, Table 2.4). Most larvae were late instars, and only a small percentage of larvae metamorphosed into pupae during the course of experiments. In total, 5,998 larvae were examined under 25x magnification for species identification. Of the 4 experiments, all larvae from experiments 1 and 4 were selected for species identification and determination of the proportion of each species involved in the experiment. Ideally, the series of experiments would have been conducted with only the single species, S. vittatum. These two experiments were chosen for species composition analysis because Experiment 1 had the least number of S. decorum (based on a May month of collection) and Experiment 4 had the greatest number of S. decorum (based on an August month of collection). This combination of experiments was considered to be a reasonable means of conservatively estimating the number of S. vittatum used in the experimental series.

Experiment 1: Low Larval Density; Tiles Devoid of Periphyton

Neither evenness nor texture exhibited significant effects on the number of black fly larvae remaining on substrates after 24 h, but a significant interaction did occur between the two factors (Appendix II.5, Table 2.5; repeated measures cross-classified ANOVA, n=3, $p<0.027$). There were more larvae on rough even substrates initially and at 24 h than were present on smooth even substrates, but there were more larvae on smooth uneven substrates than on rough even substrates, at both times (Fig. 2.6A).

Table 2.5 Summary of the repeated measures cross-classified ANOVA for Experiment 1 (low larval density, periphyton absent, 9-10 May 1990).

FACTOR	DF	SS	MS	F	p
Replicate	2	0.197	0.098		
Evenness	1	0.362	0.362	4.5	0.08
Texture	1	0.097	0.097	1.2	0.31
Evenness x Texture	1	0.682	0.682	8.5	0.03
Replicate x Evenness x Texture (Error 1)	6	0.481	0.080		
Time	1	0.375	0.375	19.3	0.002
Evenness x Time	1	0.050	0.050	2.9	0.15
Texture x Time	1	0.016	0.016	0.8	0.40
Evenness x Texture x Time	1	0.042	0.042	2.2	0.18
Error 2	8	0.155	0.019		

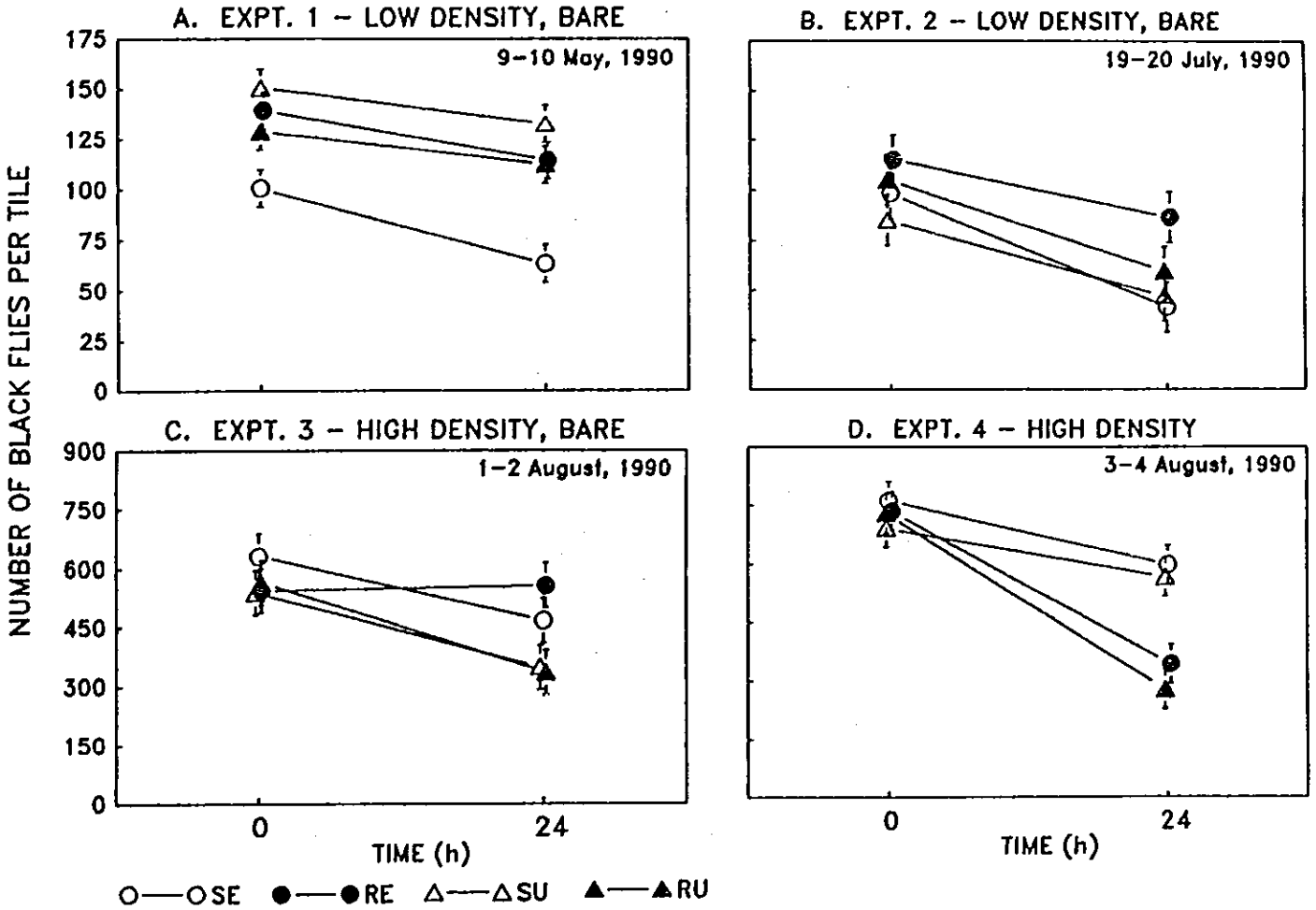


Figure 2.6 Least squares mean number of larvae per tile type at t=0 and t=24 h for each of the four experiments: A) Experiment 1, B) Experiment 2, C) Experiment 3, D) Experiment 4. Density refers to larval density (low, 2-4 larvae/cm^2; high, 10+ larvae/cm^2). Bare refers to absence of periphyton on tiles.

There was some consistency among replicates, with smooth tiles tending to have fewer larvae than rough tiles, in two of three replicates (Fig. 2.7 repl. 1 and 2), and particularly in the third replicate (Fig. 2.7, repl. 3). Smooth, even tiles had fewer larvae or nearly so than other tile types by the end of the experiment (Fig. 2.7, Fig. 2.8). The significant interaction between evenness and texture suggests that simuliids may have been avoiding the smooth, even substrate, which had the lowest proportion of larvae throughout the experiment (Fig. 2.8). Interspersion of the two rough treatments with the smooth, and of the even with the uneven treatments suggests that larvae did not show a consistent preference for either single attribute (texture, evenness) of tile surfaces.

Experiment 2: Low Larval Density; Tiles Devoid of Periphyton

Raw data are given in Appendix II.6. Texture was a significant influence to substrate selection by larvae (Table 2.6, $p<0.025$), but evenness was not (Table 2.6, $p>0.05$). Rough tiles initially, whether even or uneven, had more larvae than smooth tiles, whether even or uneven. At 24 h, rough substrates continued to have higher numbers of larvae than smooth substrates, rough even tiles having more larvae than any other tile type, smooth even the least (Fig. 2.6B).

Among replicates, replicate 3 appeared to be more different from replicates 1 and 2 than they were from each other. The decline in attached black flies between 4 h and 24 h in this experiment (Fig. 2.9) was less pronounced than in the first experiment (Fig. 2.7) under the same conditions. The difference between tile types in the number of larvae on tiles was due to texture (Table 2.6; repeated measures cross-classified ANOVA, $n=3$, $p<0.025$). Although no preference was exhibited by black flies for any one surface type, given the limited choices, larval behaviour indicated an avoidance of smooth, even tiles, which had the fewest number of larvae throughout the 24 h period for two

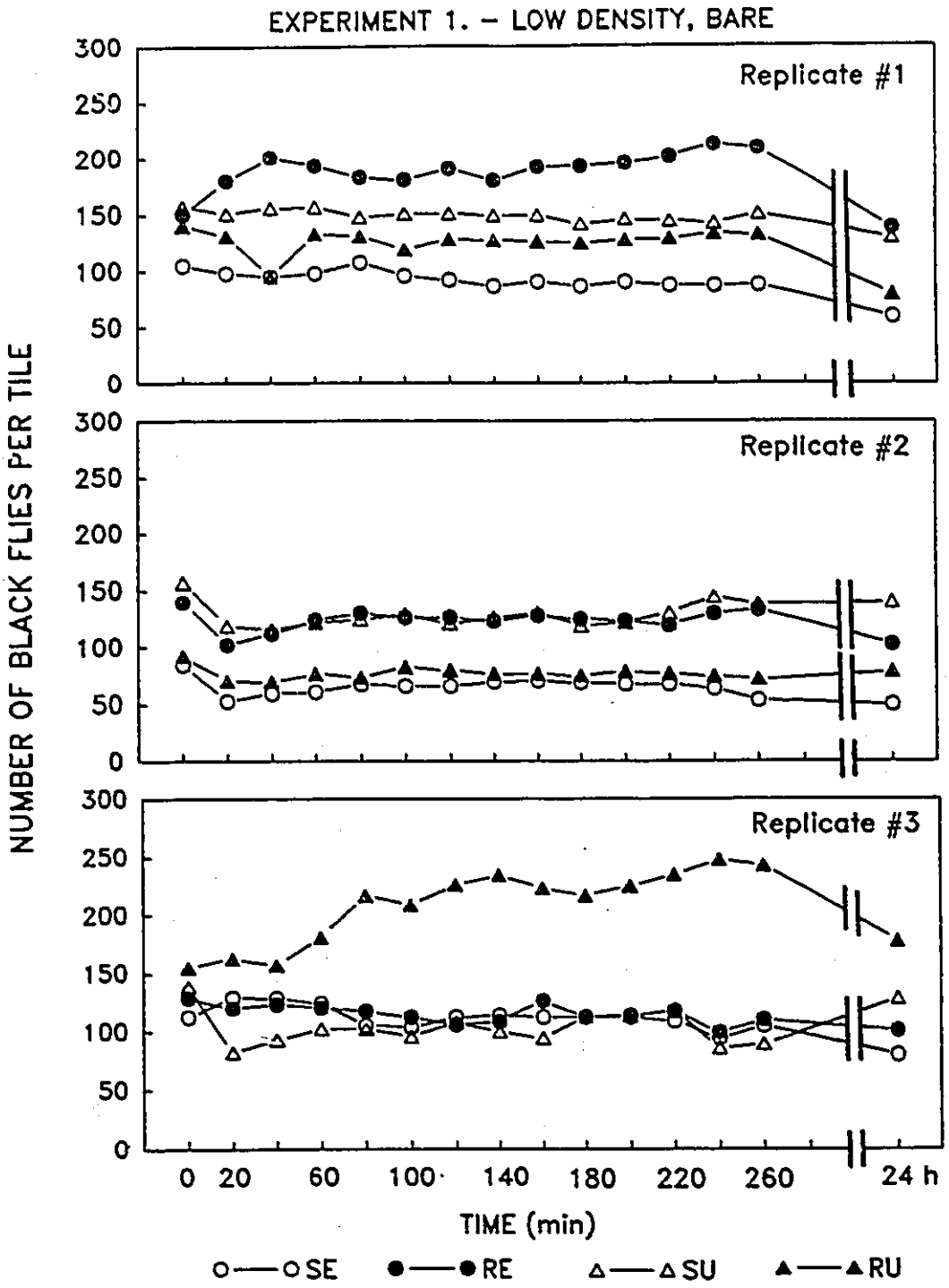


Figure 2.7 Numbers of S. vittatum larvae occurring on tiles with different surface features over a 24 h period for each of the three replicates. The experiment (9-10 May, 1990) involves low larval density and tiles free of periphyton.

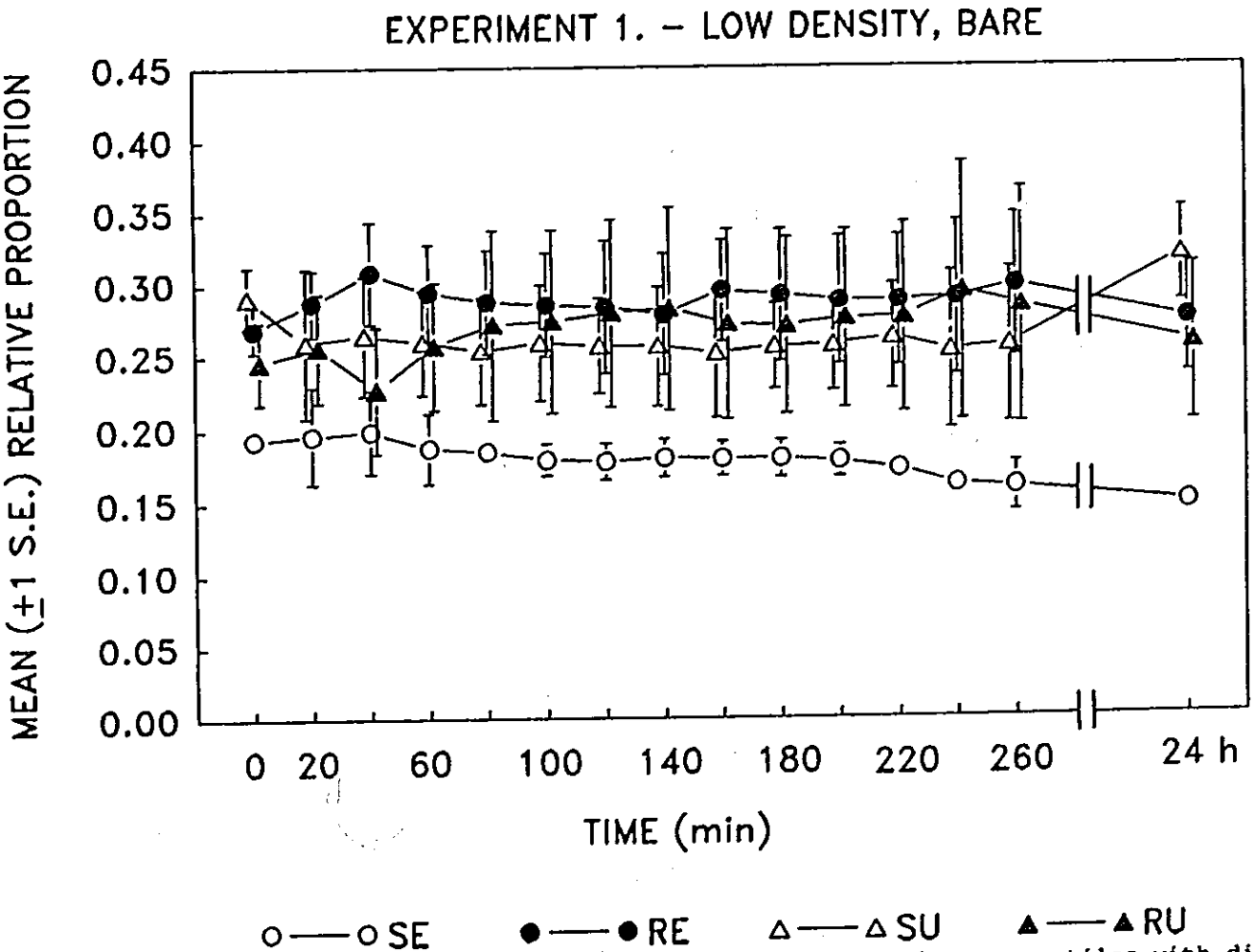


Figure 2.8 Mean (±1 S.E.) relative proportions of *S. vittatum* larvae on tiles with different surface features over a 24 h period. The experiment (9-10 May, 1990) involves low larval density and tiles free of periphyton.

Table 2.6 Summary of the repeated measures cross-classified ANOVA for Experiment 2 (low larval density, periphyton absent, 19-20 July 1990).

FACTOR	DF	SS	MS	F	p
Replicate	2	1.816	0.908		
Evenness	1	0.158	0.158	2.05	0.20
Texture	1	0.680	0.680	8.83	0.03
Evenness x Texture	1	0.140	0.140	1.82	0.23
Replicate x Evenness x Texture (Error 1)	6	0.464	0.077		
Time	1	2.89	2.89	13.89	0.006
Evenness x Time	1	0.018	0.018	0.09	0.78
Texture x Time	1	0.123	0.123	0.59	0.46
Evenness x Texture x Time	1	0.183	0.183	0.88	0.38
Error 2	8	1.662	0.208		

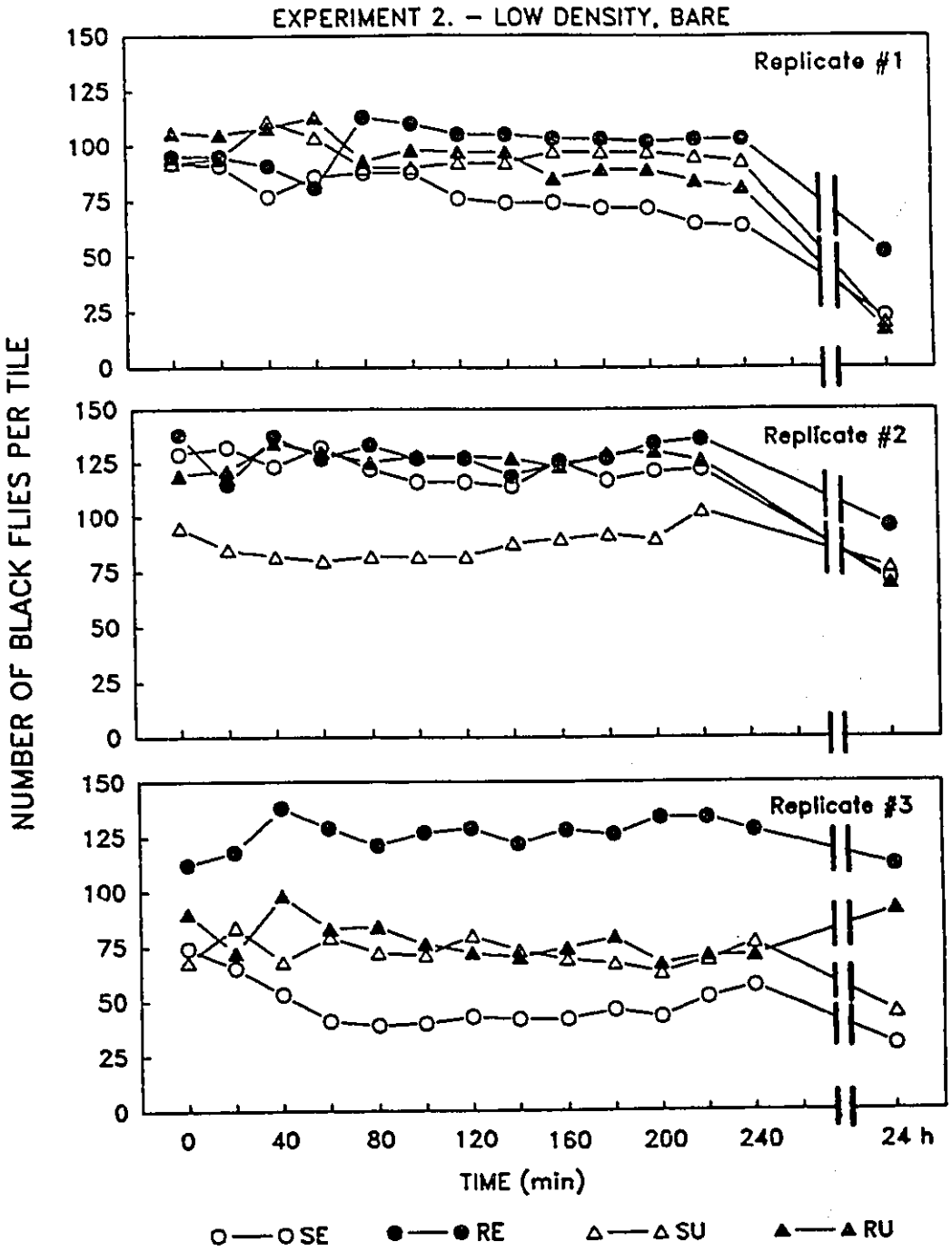


Figure 2.9 Numbers of S. vittatum larvae occurring on tiles with different surface features over a 24 h period for each of the three replicates. The experiment (19-20 July, 1990) involves low larval density and tiles free of periphyton.

replicates (Fig. 2.9 repl. 1 and 2) or was so by 24 h (Fig. 2.9 repl. 3). This result was partially due to the behaviour of larvae as they were pipetted onto the tile at the beginning of the experiment. Larvae began to loop from smooth, even tiles almost immediately to the other three tile types. This pronounced response did not occur with any of the other surface types. To partially compensate for this effect, larvae were always added to the smooth, even tiles last (thereby biasing the result in a conservative manner). This response is consistent with the behaviour observed in the pilot experiment involving smooth tile substrates. As in the first experiment, mean relative proportions of simuliids on the 4 substrates in the second experiment suggested that black flies deserted smooth, even tiles (Fig. 2.10).

Although the two experiments are suggestive of an avoidance behaviour of black fly larvae toward smooth, even tiles, there is no consistency between experiments regarding selection of one surface type in favour of another.

Experiment 3: High Larval Density; Tiles Devoid of Periphyton

Neither factor nor the interaction between them had a significant effect on the number of black flies on different tile surfaces (Appendix II.7, Table 2.7; repeated measures cross-classified ANOVA, $n=3$, $p>0.05$). Rough tiles began with approximately equal numbers of black flies, but diverged by 24 h: rough, even had the most larvae of all tile types, while rough, uneven had the least. More larvae were present on smooth, even tiles initially than on the other three tile types, on which relatively equal numbers occurred. At 24 h, separation of even from uneven tiles occurred, even tiles having greater black flies, but this difference was not statistically significant. There was no larval choice for either a particular texture or a particular evenness in this experiment (Fig. 2.6C).

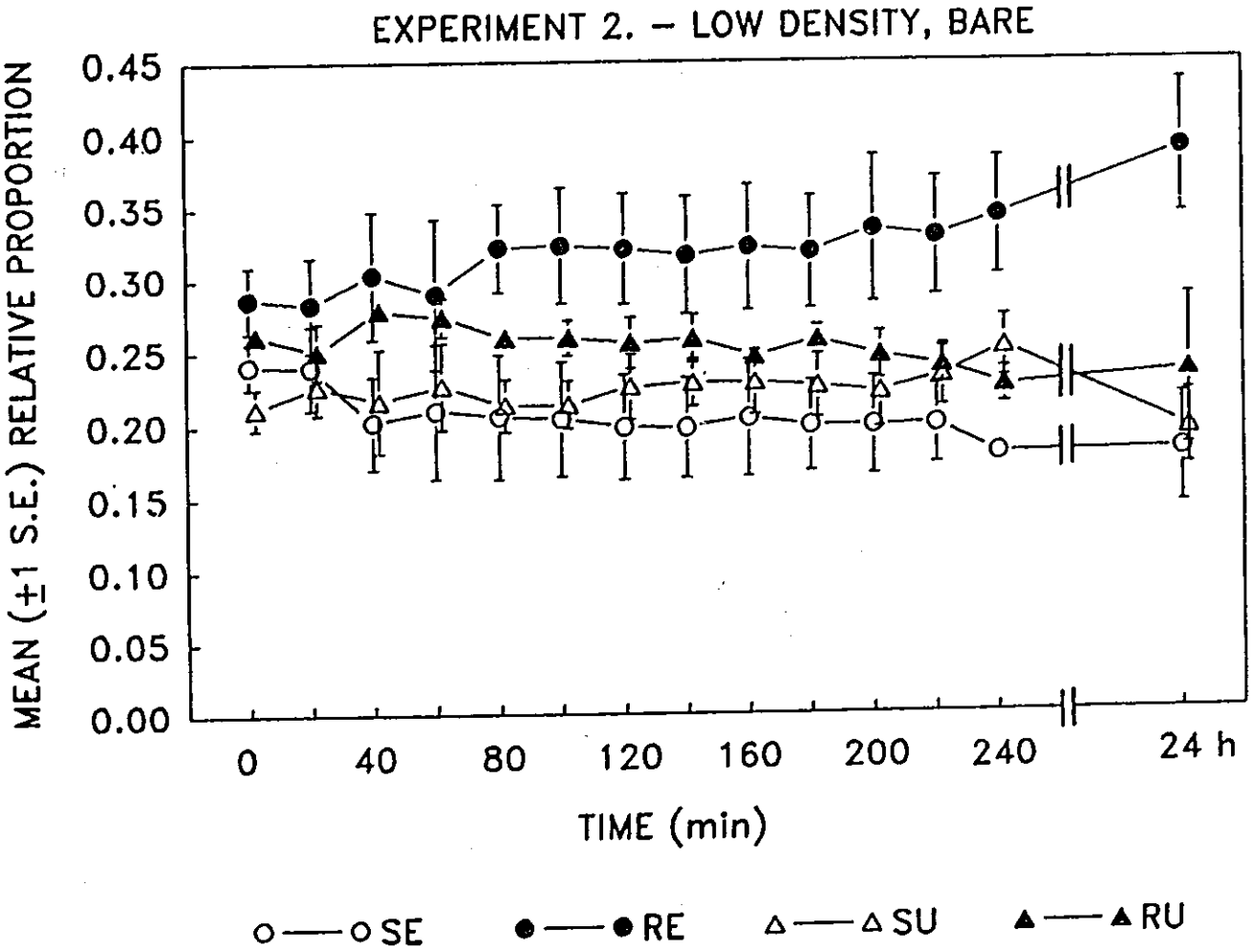


Figure 2.10 Mean (±1 S.E.) relative proportions of S. vittatum larvae on tiles with different surface features over a 24 h period. The experiment (19-20 July, 1990) involves low larval density and tiles free of periphyton.

Table 2.7 Summary of the repeated measures cross-classified ANOVA for Experiment 3 (high larval density, periphyton absent, 1-2 August 1990).

FACTOR	DF	SS	MS	F	p
Replicate	2	0.471	0.471		
Evenness	1	0.256	0.256	1.73	0.24
Texture	1	0.00008	0.00008	0.0005	0.98
Evenness x Texture	1	0.0003	0.0003	0.002	0.97
Replicate x Evenness x Texture (Error 1)	6	0.888	0.148		
Time	1	0.625	0.625	11.16	0.01
Evenness x Time	1	0.198	0.198	3.54	0.10
Texture x Time	1	0.015	0.015	0.27	0.62
Evenness x Texture x Time	1	0.043	0.043	0.77	0.41
Error 2	8	0.450	0.056		

Results from individual tanks were inconsistent with respect to selection of substrate type (Fig. 2.11). In the first replicate (Fig. 2.11 repl. 1), there were slightly more black flies on rough tiles than smooth, but the second replicate (Fig. 2.11 repl. 2) was opposite to this. However, all substrate types converged by 24 h to relatively equal numbers of black flies distributed among all tiles. In the third (Fig. 2.11 repl. 3), the proportion of larvae on even tiles diverged from uneven tiles, there being more larvae on even than uneven tiles, a pattern inconsistent with the other replicates. Simuliids did not favour any one of the substrates over the others. The proportion of black flies on all tile types converged to having relatively equal numbers of larvae on each tile type by 24 h regardless of initial number (Fig. 2.12). There was little indication of (substrate) selection among tiles by larvae (Fig. 2.12, Table 2.7).

Experiment 4: High Larval Density; Tiles with Periphyton

Raw data are given in Appendix II.8. Conducted 3-4 August 1990, Experiment 4 was a high larval density treatment with periphyton-coated tiles. Smooth tiles, independent of evenness, had more larvae at 24 h than rough tiles. Initially, smooth even tiles had slightly more larvae than rough even tiles, but while numbers declined only slightly over 24 h on smooth tiles, they declined to a much greater extent on rough even tiles. Similarly, for uneven tiles, fewer larvae were initially present on smooth uneven tiles than on rough uneven tiles, but at the end of the experiment, more larvae remained on the smooth uneven tiles than on the rough uneven tiles (Fig. 2.6D).

Regardless of initial numbers per tile, rough tiles had consistently lower numbers of larvae than smooth tiles by the end of the experiment for all replicates (Fig. 2.13). Larval proportions among tile types showed the same pattern (Fig. 2.14). Differences among substrates were due to texture (Table 2.8; repeated measures

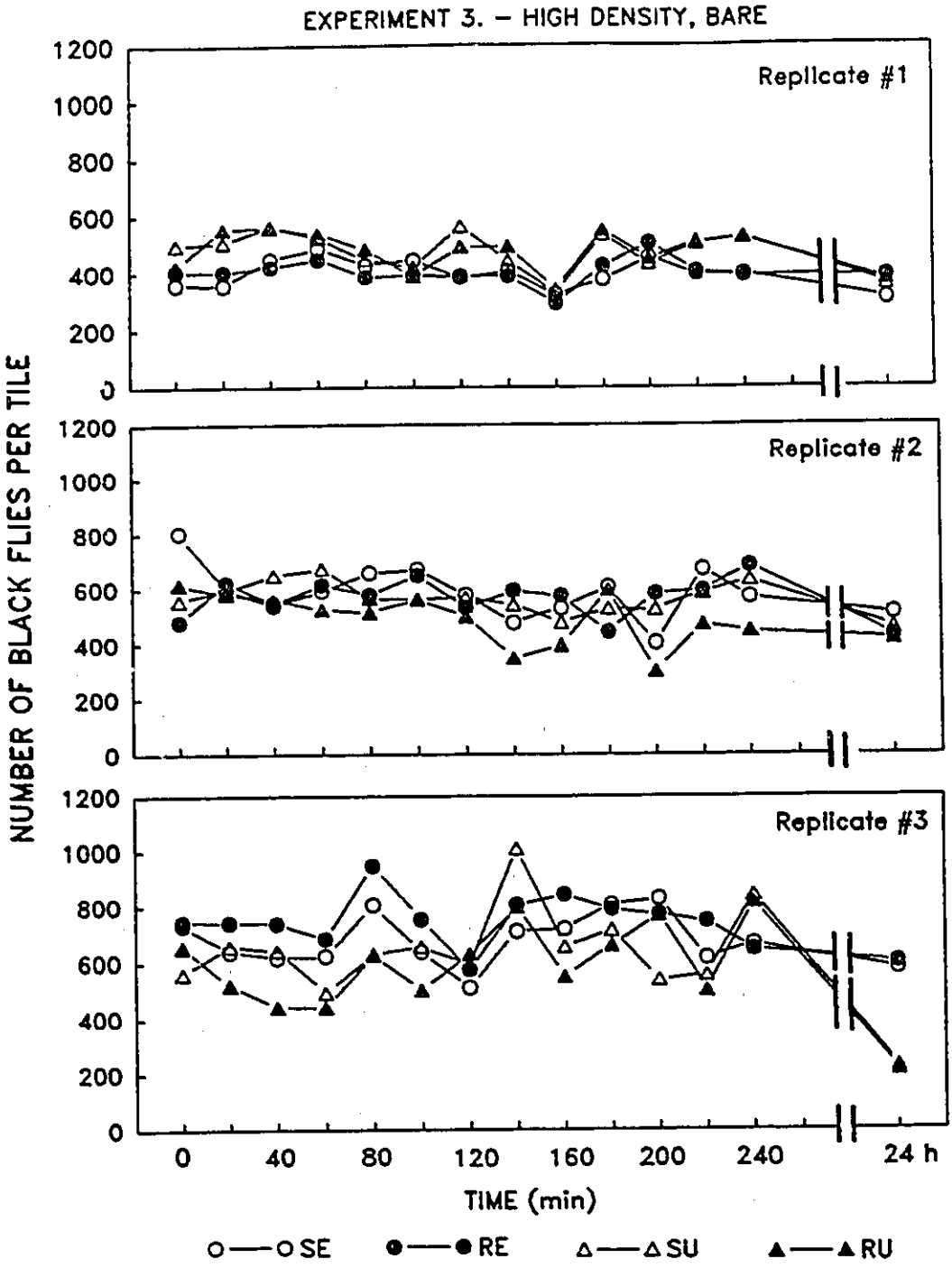


Figure 2.11 Numbers of S. vittatum larvae occurring on tiles with different surface features over a 24 h period for each of the three replicates. The experiment (1-2 August, 1990) involves high larval density and tiles free of periphyton.

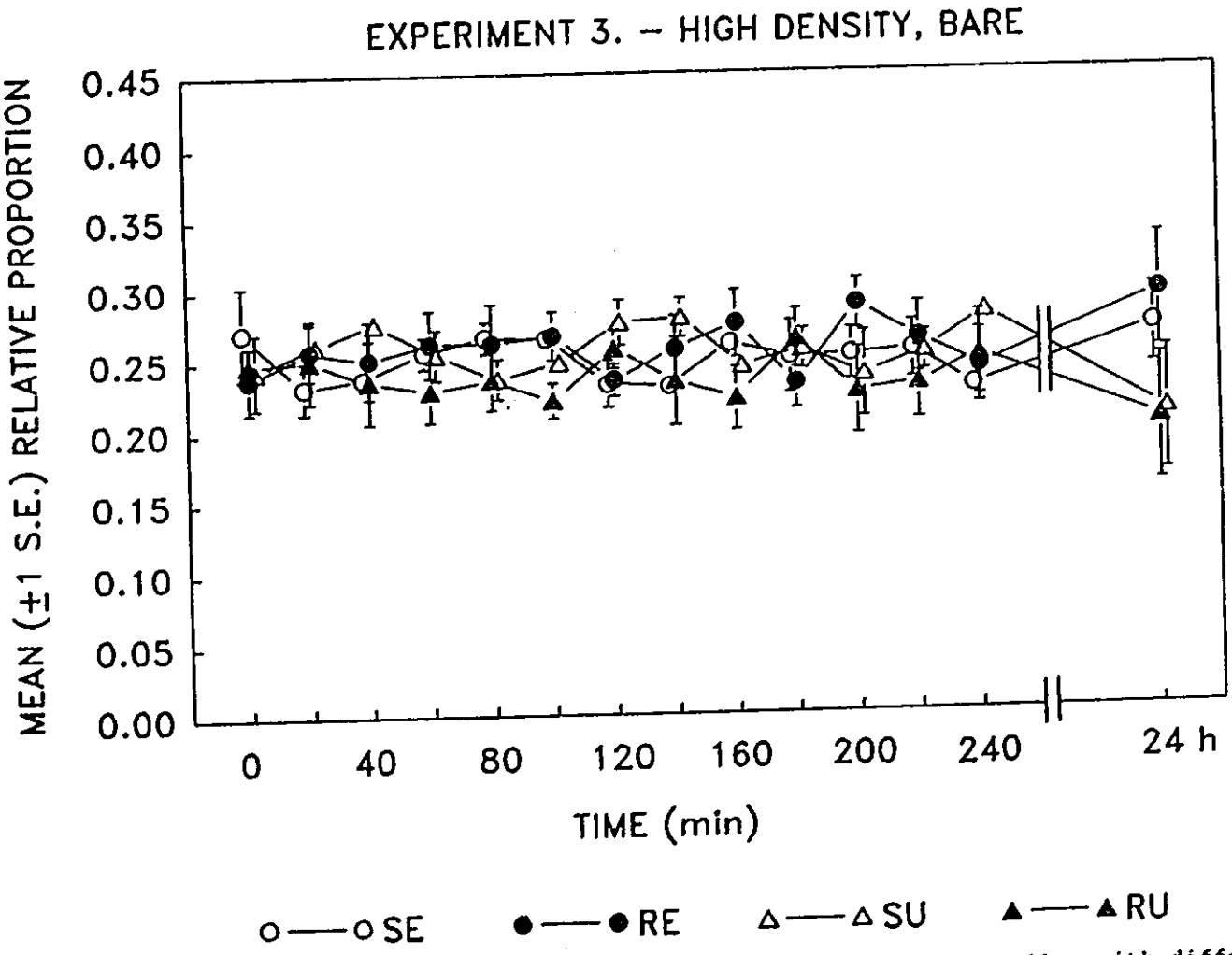


Figure 2.12 Mean (±1 S.E.) relative proportions of S. vittatum larvae on tiles with different surface features over a 24 h period. The experiment (1-2 August, 1990) involves high larval density and tiles free of periphyton.

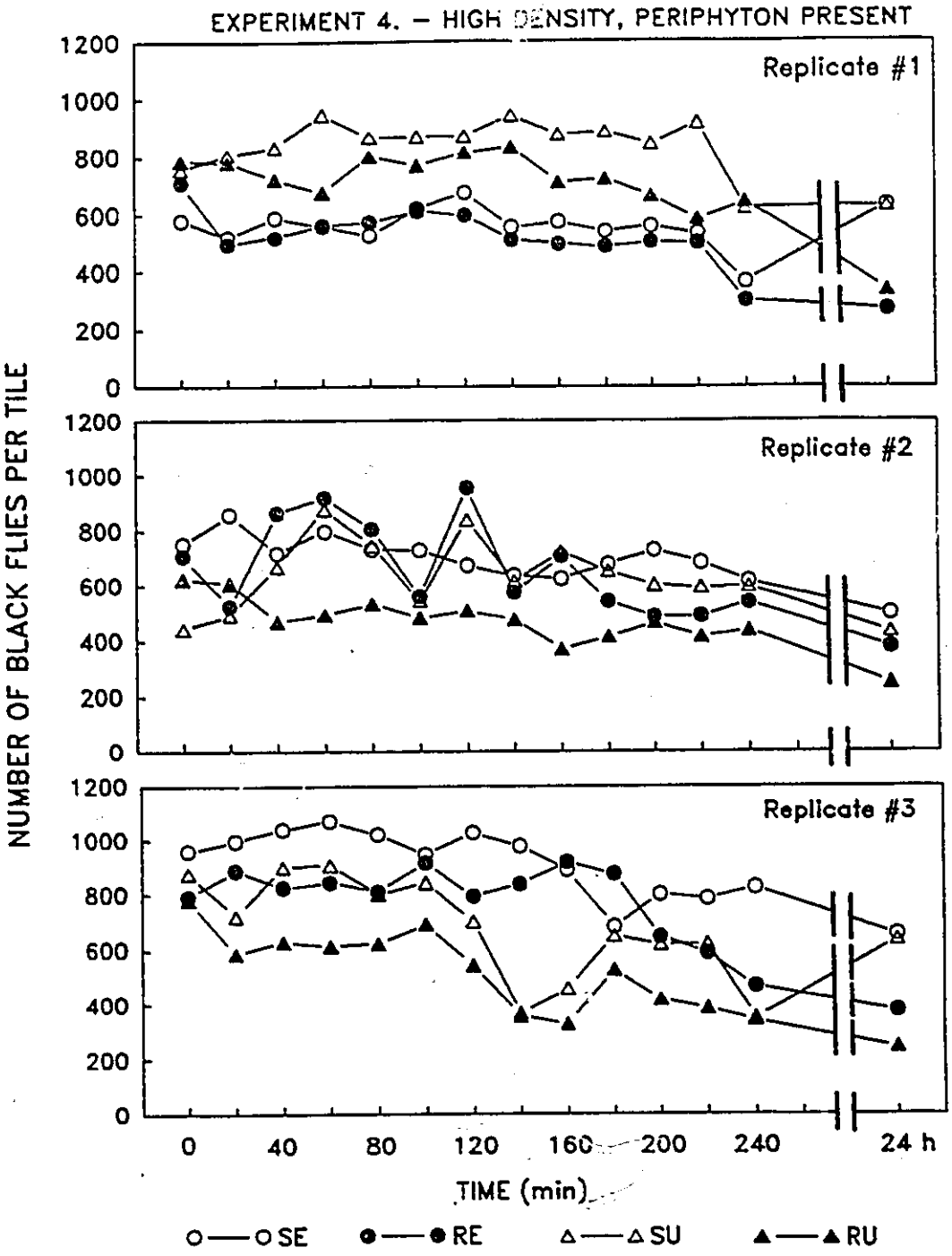


Figure 2.13 Numbers of S. vittatum larvae occurring on tiles with different surface features over a 24 h period for each of the three replicates. The experiment (3-4 August, 1990) involves high larval density and tiles with periphyton.

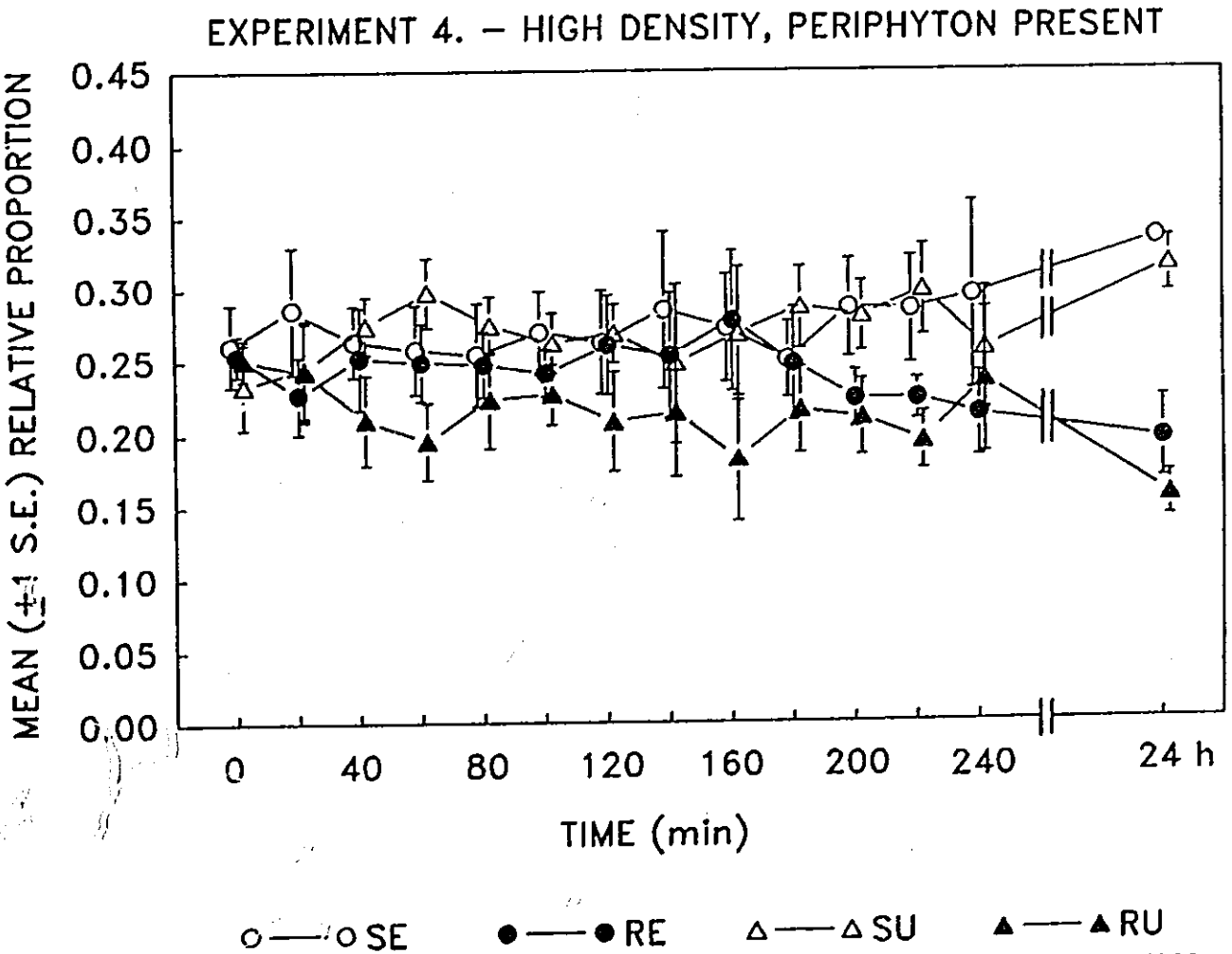


Figure 2.14 Mean (±1 S.E.) relative proportions of S. vittatum larvae on tiles with different surface features over a 24 h period. The experiment (3-4 August, 1990) involves high larval density and tiles with periphyton.

Table 2.8 Summary of the repeated measures cross-classified ANOVA for Experiment 4 (high larval density, periphyton present, 3-4 August 1990).

FACTOR	DF	SS	MS	F	p
Replicate	2	0.231	0.116		
Evenness	1	0.060	0.060	1.13	0.33
Texture	1	0.533	0.533	10.06	0.02
Evenness x Texture	1	0.0008	0.0008	0.04	0.91
Replicate x Evenness x Texture (Error 1)	6	0.320	0.053		
Time	1	1.721	1.721	90.50	0.0001
Evenness x Time	1	0.007	0.007	0.37	0.55
Texture x Time	1	0.668	0.668	35.16	0.0003
Evenness x Texture x Time	1	0.024	0.024	1.26	0.30
Error 2	8	0.152	0.019		

cross-classified ANOVA, n=3, $p<0.020$), with significantly fewer larvae on rough than smooth tiles.

Comparison of mean detrital biomass (as measured by dry mass) per tile type (Fig. 2.15, raw data in Appendix II.3) indicated significantly more detritus on rough than smooth tiles (two-way ANOVA, n=3, $p<0.001$). Neither evenness nor the interaction between the two variables were significant (two-way ANOVA, n=3 $p>0.05$). This pattern was also evident for periphytic biomass (as measured by ash-free dry mass; Fig. 2.16, raw data in Appendix II.4). Rough tiles had significantly more biomass than smooth tiles (two-way ANOVA, n=3, $P<0.001$), but neither evenness nor the interaction showed a significant effect (two-way ANOVA, n=3, $p>0.05$).

General Trends - All Experiments

Initial numbers of black flies on tiles affected the final outcome of the experiment in low density treatments. When initial numbers of black fly larvae on a given tile type were either especially low or especially high, relative to the other tile types, those tiles tended to remain particularly low or high, respectively, at 24 h also.

For all experiments, there was a significant time effect (Expt. 1, Table 2.5, $p<0.02$; Expt. 2, Table 2.6, $p<0.006$; Expt. 3, Table 2.7, $p<0.01$; Expt. 4, Table 2.8, $p<0.0001$). With the single exception of rough uneven tiles in Experiment 4 that showed a slight increase in numbers of larvae by 24 h, black flies on all other substrates in all experiments declined from initial numbers over 24 h. Note that time effects in all analyses refer to the time component within individual experiments (i.e., changes in abundance of larvae on the four substrate types over 24 h) rather than the progression of the experiments through time (i.e., the order in which experiments were conducted from May through August).

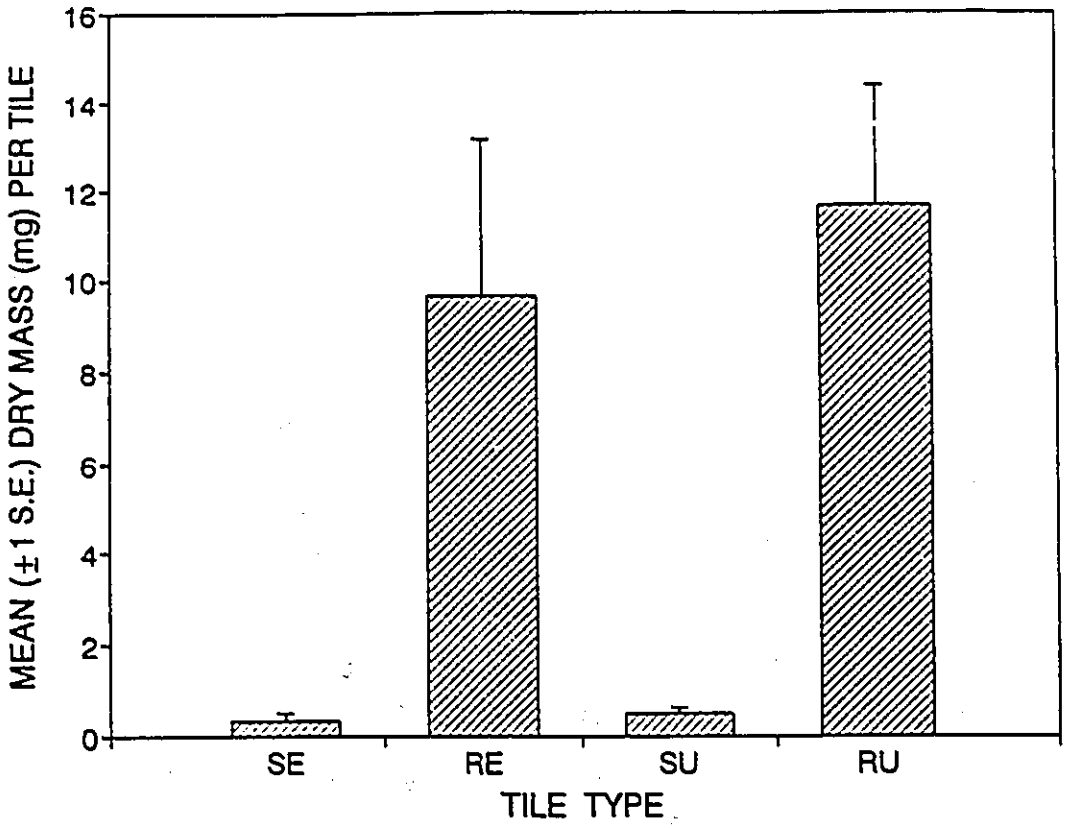


Figure 2.15 Mean (±1 S.E.) of total detrital biomass, (as measured by dry mass), accumulated on tiles of different surface types from Experiment 4 (3-4 August, 1990) involving high larval density and tiles with periphyton.

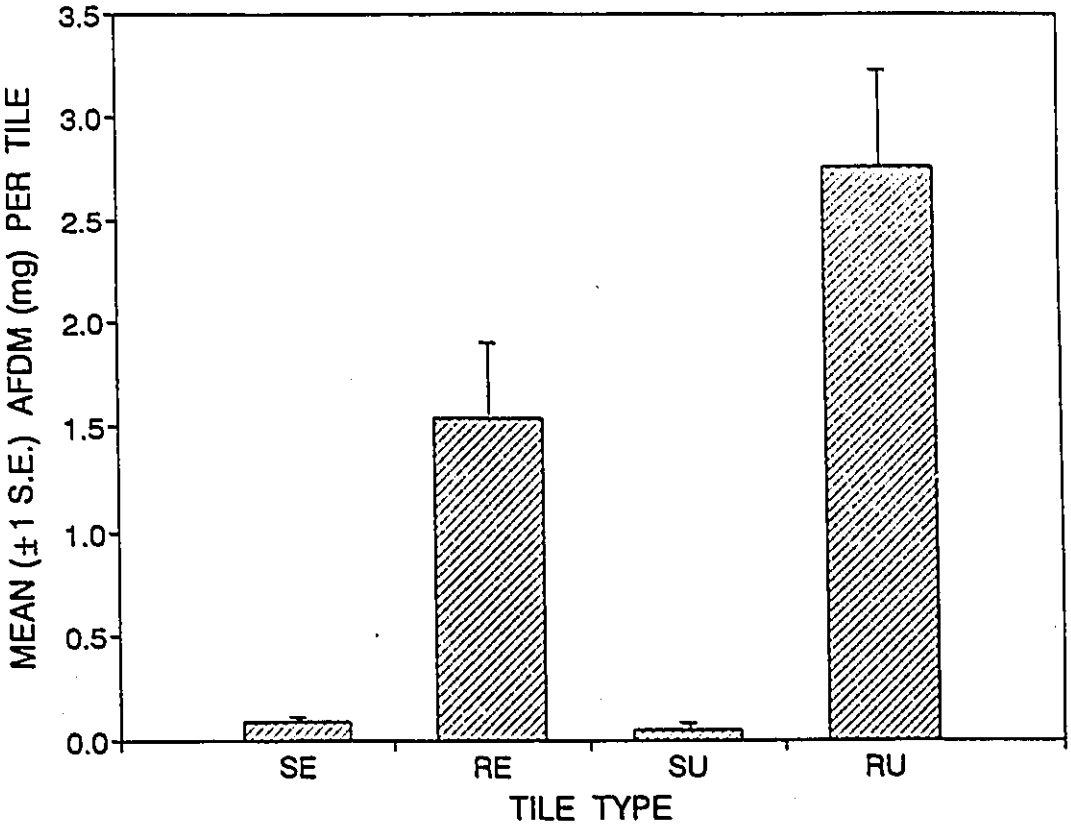


Figure 2.16 Mean (±1 S.E.) of periphytic biomass, (as measured by ash-free dry mass), accumulated on tiles of different surface types from Experiment 4 (3-4 August, 1990) involving high larval density and tiles with periphyton.

Behavioural Observations

Generally, black flies were less active in low density than high density treatments. At low density, there was less movement among tiles (Fig. 2.8, Fig. 2.10, Fig. 2.12, Fig. 2.14) and within single tiles (Fig. 2.7, Fig. 2.9, Fig. 2.11, Fig. 2.13) than at high density. This is indicated by the fluctuations in larval proportions remaining per tile through time for low (Fig. 2.8, Fig. 2.10) and high (Fig. 2.12, Fig. 2.14) density treatments.

In all experimental treatments, black flies formed rows (bands) perpendicular to the flow in the tank. Regardless of tile type or larval density, black flies began to aggregate within 4 h of the start of the experiment, on all tile types. However, in high density treatments, these aggregations were much more distinct by 4 h (Fig. 2.17, Fig. 2.18, Fig. 2.19). Photographs of one replicate of each experiment were selected as representatives for replicates of each experiment. (Photographs are not available for Experiment 2).

There appeared to be little consistency in substrate preference (in the absence of periphyton on tile surfaces) exhibited by black flies (given the four substrate choices), in either low density treatments (Fig. 2.8, Fig. 2.10), or high density treatments (Fig. 2.12). However, the larvae may have been exercising behavioural avoidance of the smooth, even substrate at low density (Experiments 1 and 2). This substrate had fewest larvae in most cases of replicates for both experiments of low density (Fig. 2.7, Fig. 2.9), and showed greater decline in numbers remaining on the tile at 24 h in Experiment 1 (Fig. 2.7). In Experiment 1, there was a significant interaction effect (Table 2.5) while in Experiment 2, there was a significant texture effect (Table 2.6). This probably reflects an avoidance of the smooth, even surface in particular, rather than a preference for a particular surface. Additionally, the proportion of simuliids was lowest on smooth, even

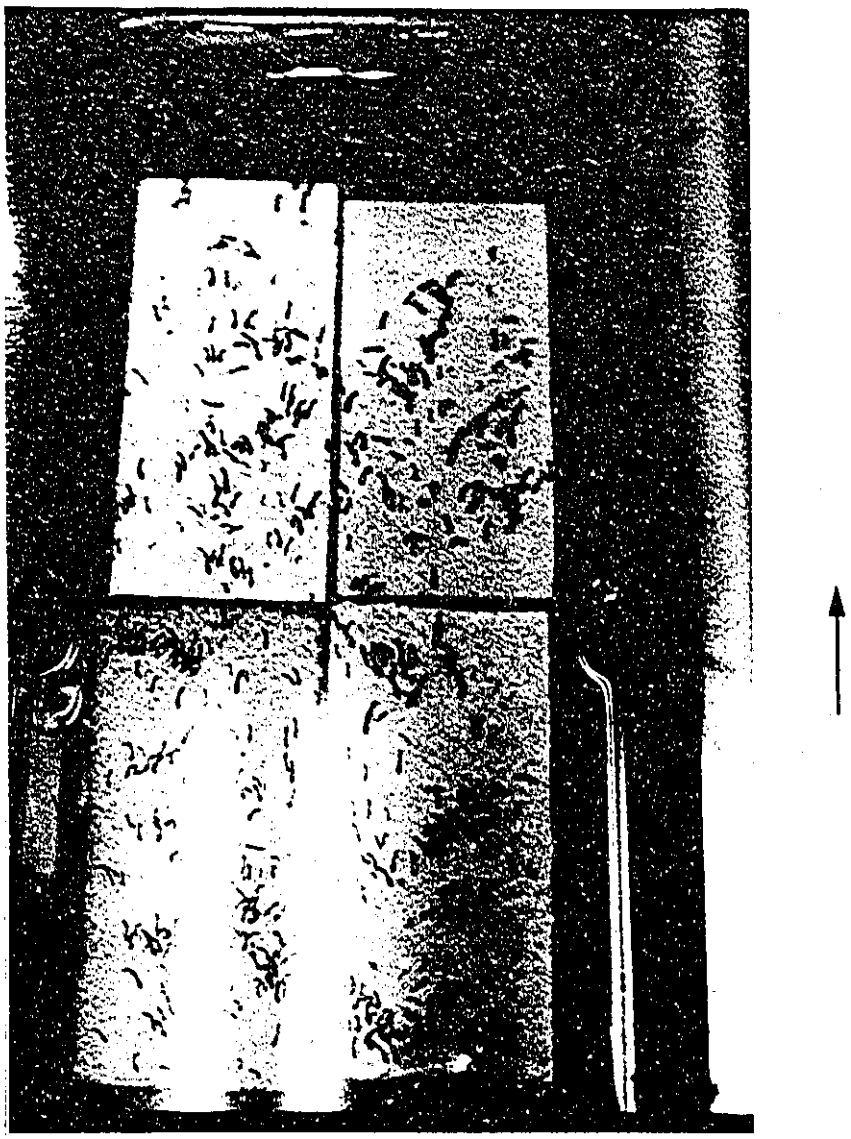


Figure 2.17 Positions of S. vittatum larvae on tiles differing by surface texture and evenness during a low larval density, bare tile treatment (Experiment 1, Replicate 1, 9-10 May, 1990). Arrow indicates direction of flow. Progression of larval bands by aggregating behaviour is evident from: A) t=0 h

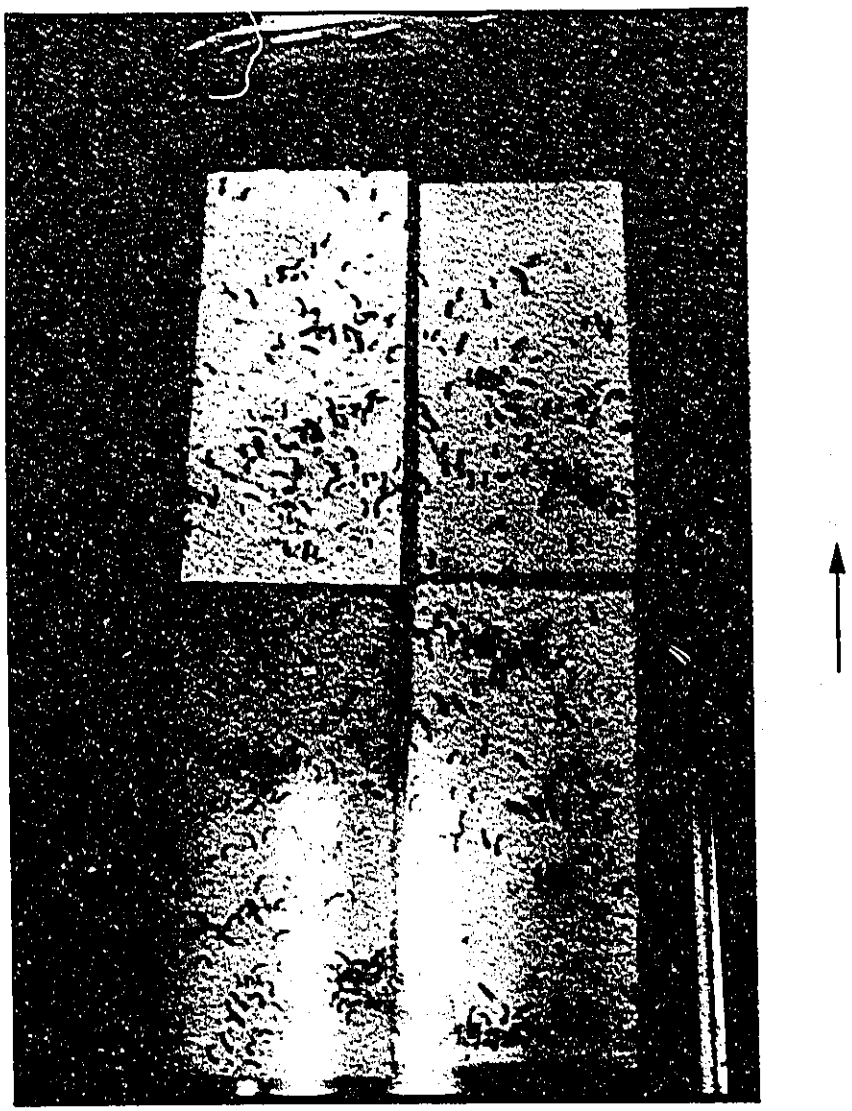


Figure 2.17 Experiment 1, Replicate 1, Continued. B) t=4 h

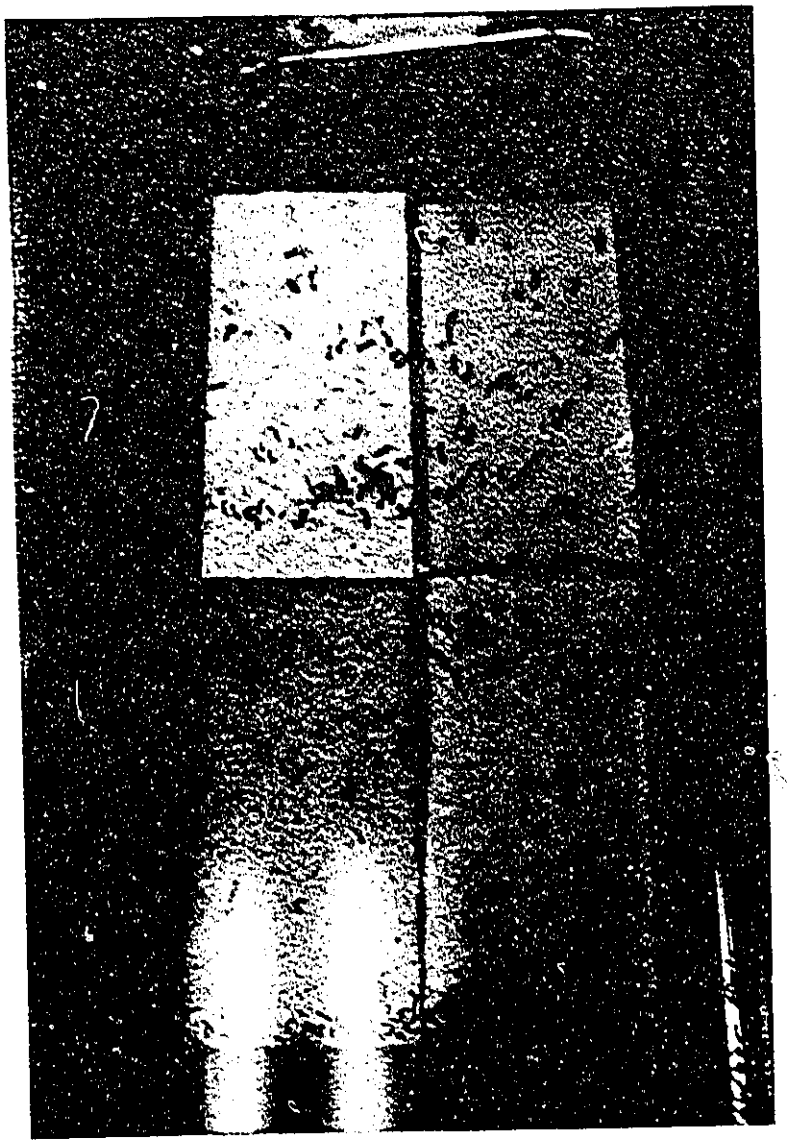


Figure 2.17 Experiment 1, Replicate 1, Continued. C) t=24 h.

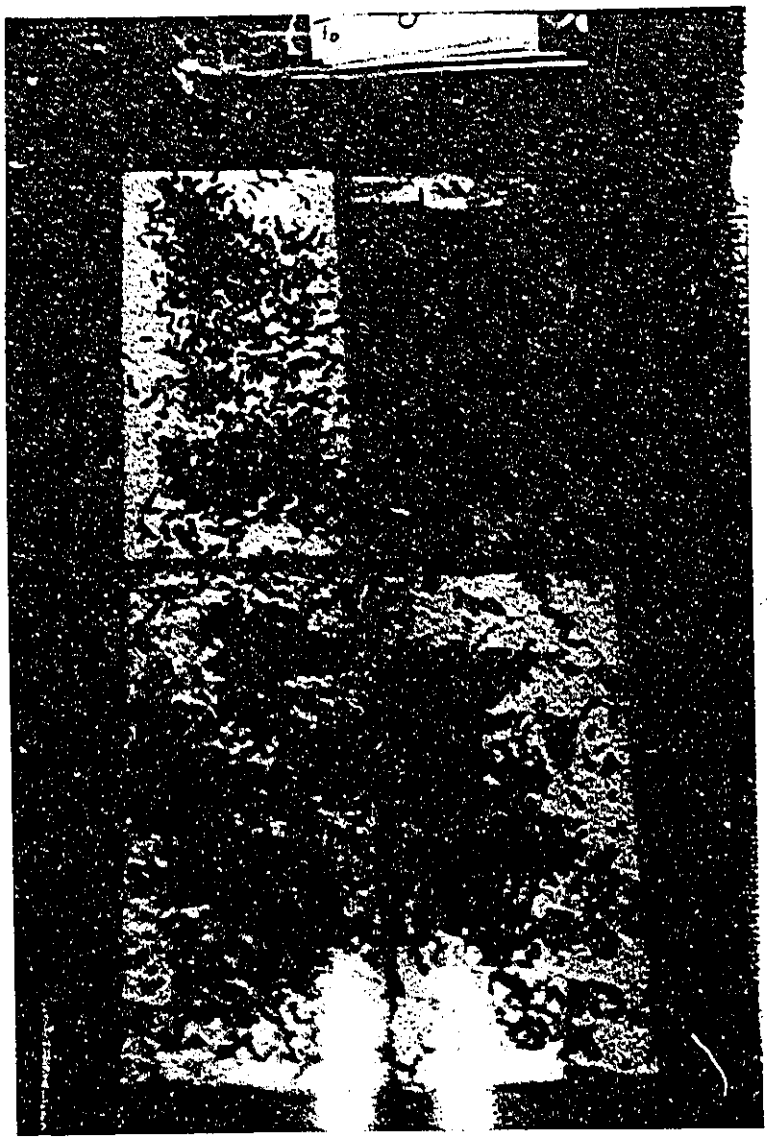


Figure 2.18 Positions of S. vittatum larvae on tiles differing by surface texture and evenness during a high larval density, bare tile treatment (Experiment 3, Replicate 2, 1-2 August, 1990). Arrow indicates direction of flow. Progression of larval bands by aggregating behaviour is evident from: A) t=0 h

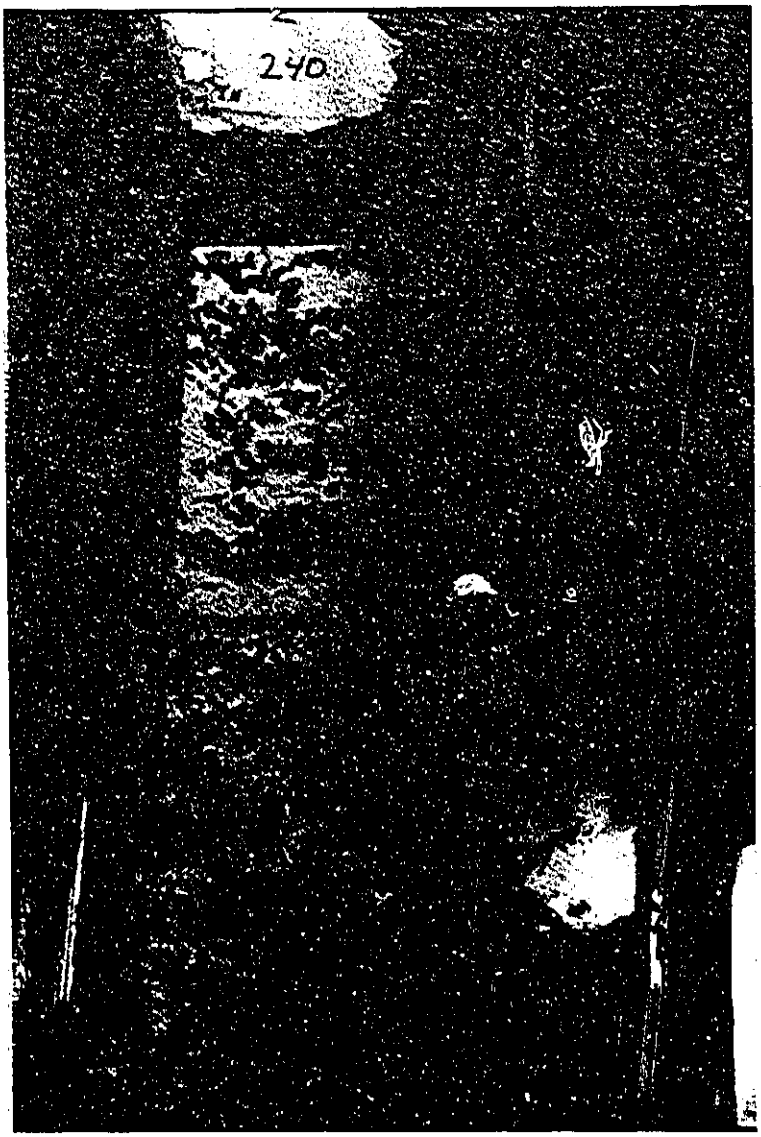


Figure 2.18 Experiment 3, Replicate 2, Continued. B) t=4 h

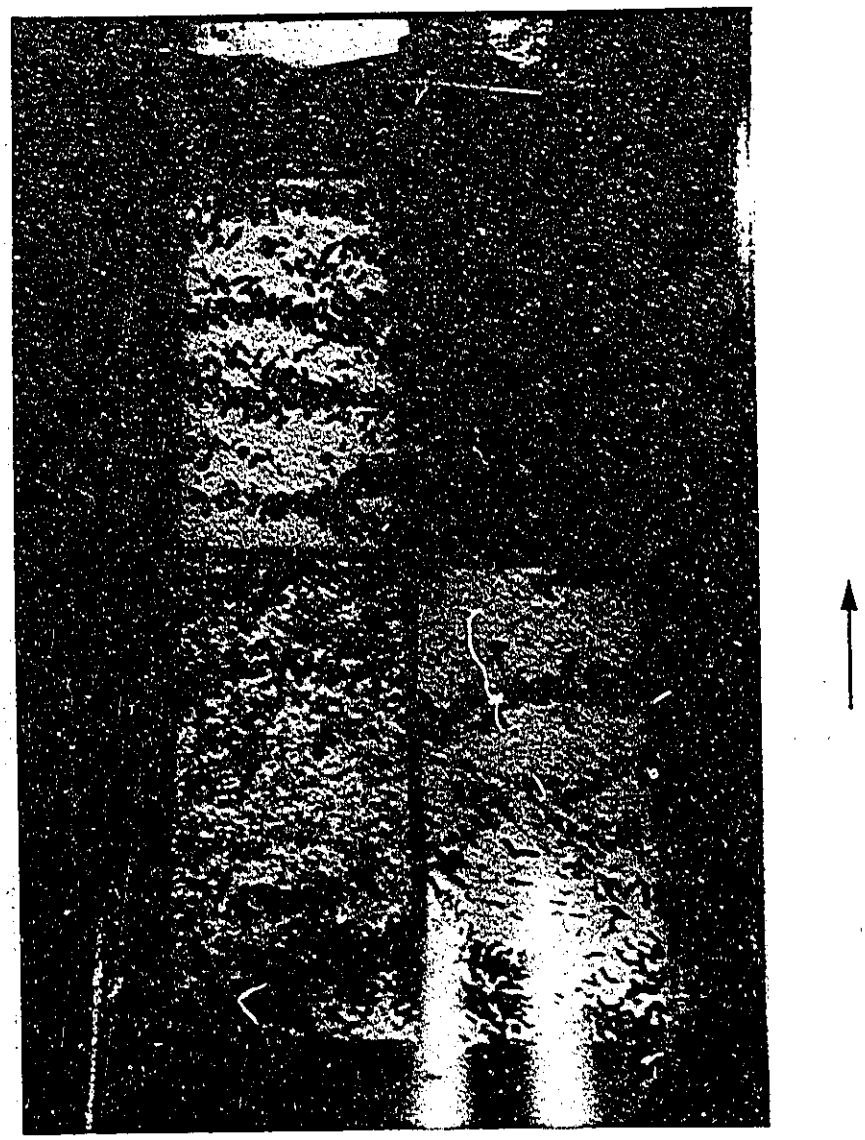


Figure 2.18 Experiment 3, Replicate 2, Continued. C) t=24 h.

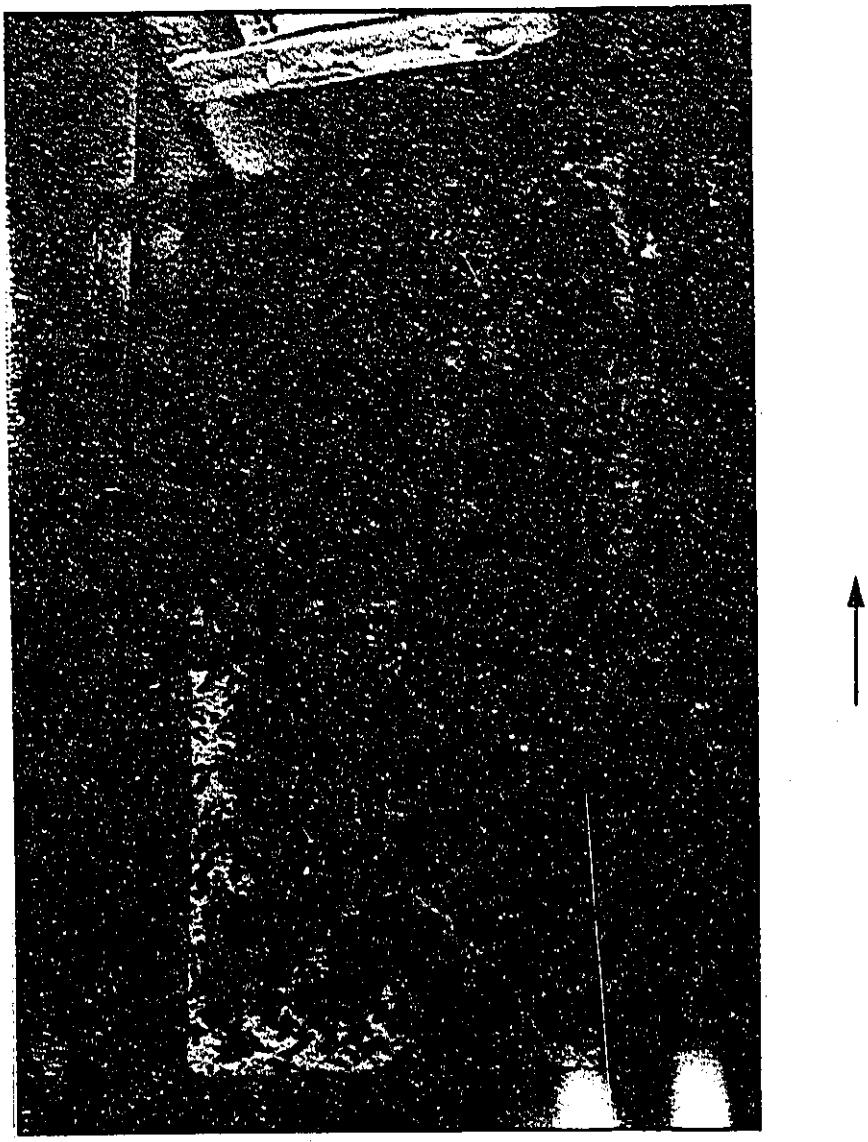


Figure 2.19 Positions of S. vittatum larvae on tiles differing by surface texture and evenness during a high larval density, periphyton-covered tile treatment (Experiment 4, Replicate 3, 3-4 August, 1990). Arrow indicates direction of flow. Progression of larval bands by aggregating behaviour is evident from: A) t=0 h

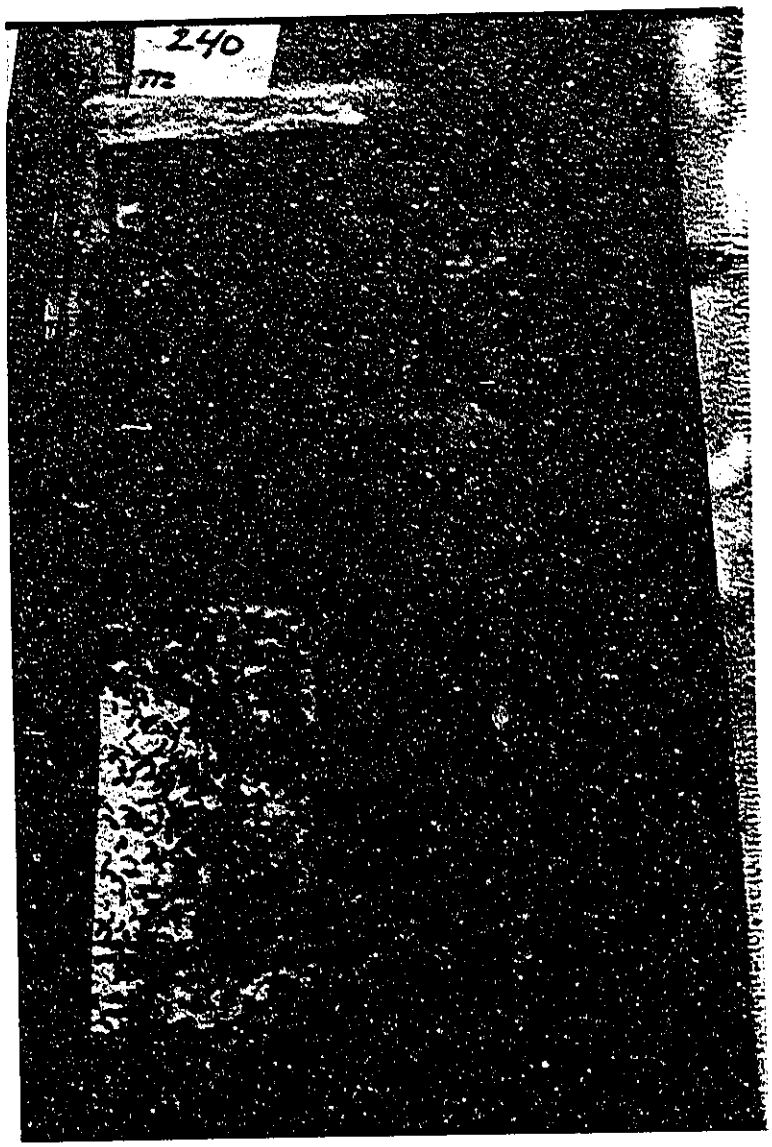


Figure 2.19 Experiment 4, Replicate 3, Continued. B) t=4 h

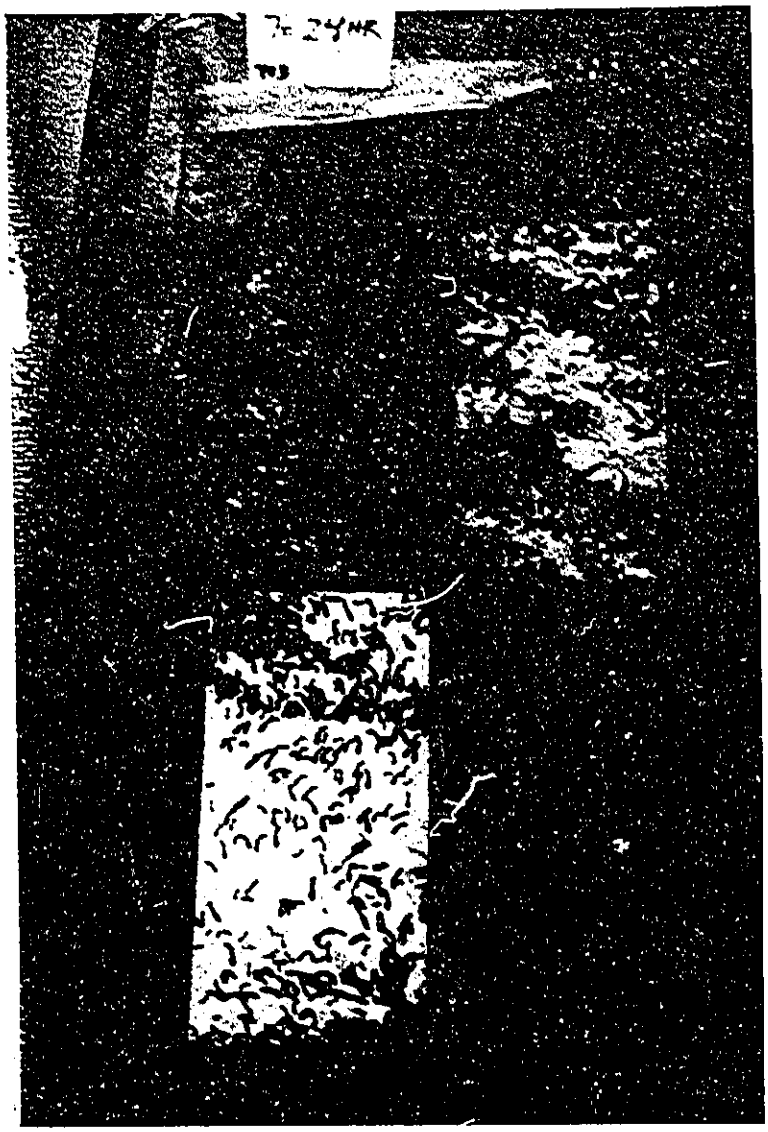


Figure 2.19 Experiment 4, Replicate 3, Continued. C) t=24 h.

tiles at low density (Fig. 2.8, Fig. 2.10). There was no substrate preference in high density, bare tile treatments (Table 2.7), but the substrate selection for tile texture, evident at low density, was reversed at high density on tiles that had a periphytic coating (Table 2.8). In the presence of periphyton, texture exhibited a significant effect on substrate selection. More S. vittatum larvae occurred on smooth than rough tiles (Fig. 2.14), corresponding to both lower levels of detrital biomass (Fig. 2.15) and periphytic biomass (Fig. 2.16).

DISCUSSION

Pilot Experiments: Selection of Laboratory Manipulations

Laboratory experiments can be used to clarify an ecological process, reveal the mechanism underlying an ecological phenomenon, permit one to observe behaviours more closely, uncover additional hypotheses about the natural environment, or test a specific hypothesis with maximum control of variables. Increased repeatability and replication under controlled laboratory conditions allows the result to be more easily interpreted due to a reduction in the environmental variation. However, the drawback of laboratory experiments is their reduced realism. Although one attempts to simulate the natural habitat, its simplification detracts from the realism and general applicability of the research. A carefully constructed laboratory experiment must therefore attempt to find the most advantageous balance between the positive and negative aspects of laboratory studies. In this work, laboratory experiments allowed investigation of one aspect of S. vittatum's behaviour involved in microhabitat selection, specifically that of substrate selection. Under controlled conditions, simulating the natural habitat, this process could be examined at a local scale.

My distributional field surveys (Chapter I) suggested that evenness and periphyton growth were characteristics of the substrate surface that influenced black fly microhabitat selection. Specifically, Simulium vittatum larvae were more abundant on uneven cobbles with minimal periphyton. However, the variation in flow patterns, water velocity, water depth, accumulated debris on the substrate, its (substrate) size and shape, and the co-existence of other insects on cobbles with black flies in the stream created great difficulty in determining the role of substrate in microhabitat selection. Consequently, laboratory experiments were deemed the most suitable method for investigating the role of specific aspects of substrate. This series of experiments was designed to identify the role of

substrate in microhabitat selection and the effect of three specific characteristics of the substrate. The greatest advantage of laboratory studies in this research was the ability to control for much of the variation associated with the interaction of flow across the substrate surface, without compromising realism too harshly. To maintain maximum realism, pilot experiments were initiated using cobbles.

Pilot Experiments: Utility of Natural Substrates

The pilot experimental series indicated that a standardized artificial substrate would be more suitable than natural cobbles for several reasons. Regardless of care taken to procure cobbles of similar size, colour, evenness, and shape, there was variability among cobbles in each respect. This created problems regarding flow across cobbles. Some cobbles induced faster local flow, more evenly distributed across the cobble surface, and some cobbles extended closer to the water surface than others. This created patchiness in black fly distribution not only among cobbles, but on individual cobbles also. Some areas were apparently suitable on cobbles, while other areas were not, due to the shape and position of the cobble in the current. Since black flies are sensitive to hydrodynamic conditions, this would be a crucial aspect to control and standardize for such effects. Slight differences in the degree of colour (darkness or lightness of cobbles) among the cobbles also created problems for observing and counting the larvae quickly and accurately. There was considerable variation in the degree of evenness among individual cobbles with uneven surfaces. In these experiments, it seemed that variation in hydrodynamic parameters could have masked any potential substrate preferences due to a lack of control on these variables.

To minimize these problems, an artificial substrate was sought. A standardized hydrodynamic arena would allow results from substrate

differences to be demonstrated more clearly. Any potential selection of substrate by larvae would be more visible.

Pilot Experiments: Utility of Tiles

Tiles were selected as the substrate because they could be standardized for colour, evenness, texture, surface area, hardness, and flow patterns. They could also be easily positioned in the tanks and larvae were very visible on them. It was also desirable to use the same substrates for a colonization experiment in the field (Chapter III), and thus, it was important to select a substrate that would be relatively inconspicuous and stable, easily transported, easily manipulated, and inexpensive.

Aside from their practicality, tiles have previously been used with success. Lamberti and Resh (1985) assessed the effectiveness of clay tiles in capturing the benthic faunal composition of natural substrates. They found that tile communities (bacterial and algal populations, as well as macroinvertebrates), including densities of species, were comparable to the natural substrates. Moreover, tiles required much fewer replicates to precisely represent the natural benthic density. In an examination of factors affecting the growth of periphyton on the top surfaces of tiles positioned alternately at two different heights in laboratory streams, DeNicola and McIntire (1990a, 1990b) found that recessed tiles acquired more periphyton than upper tiles. This type of experimental arrangement mimicked the uneven surface of cobbles, and the interstitial areas between them. Their results indicated that recessed areas accumulated more periphyton and algal assemblages followed a course typical of the field environment in the absence of grazing taxa. The interactions occurring between algal assemblages and stream macroinvertebrates consuming these resources have also been successfully demonstrated with the use of tiles in field experiments manipulating grazer density and periphyton resources

(Lamberti and Resh 1983, McAuliffe 1984b, Feminella et al. 1989, Dudley and D'Antonio 1991). A standardized substrate such as tiles has been suggested to reduce variability and possibly sampling effort (Lewis and Bennett 1974, Gersabeck and Merritt 1979, Rosenberg and Resh 1982, Lamberti and Resh 1985).

Lewis and Bennett (1974) evaluated comparability of colonization by black fly larvae on tiles and natural stony substrates. Similar simuliid taxonomic composition and densities occurred on both types of substrates, as did other macroinvertebrates. Tiles have been used successfully to collect black flies in the field (Zahar 1951, Lewis and Bennett 1974, Gersabeck and Merritt 1979), to monitor population densities (Lewis and Bennett 1974), to investigate colonization (Gersabeck and Merritt 1979), and in the laboratory for studies of reactions to current velocity and food levels (Eymann 1985, Ciborowski and Craig 1989), intraspecific interactions (Eymann 1985, Ciborowski unpubl.), and predation (Ciborowski and Craig 1991).

One criticism of tile usage, particularly for black fly research, is the frequently uneven distribution of larvae on the tile. That is, space is often available, but not colonized. Whether this is a reflection of hydrodynamics (Colbo 1979), or innate black fly behaviours (aggregating tendency), controversy exists over their use. However, Eymann (1990) has shown that S. vittatum may have specific patterns of distribution, one of which is contagious and unlikely to cover the entire suitable area available. Given that such distributions occur naturally, tiles are an accurate representation of the naturally patchy field distribution. Even the use of tiles will involve some degree of heterogeneity in flow across the substrate surface. For this reason, the use of tiles has been criticized in the past (Colbo 1987, Morin 1985, 1987). Although problems dealing with flow patterns still exist with tiles, such difficulties are much reduced, compared to natural

substrates. Since the characteristics of the substrate (size, roughness, shape), as well as the presence of the black fly itself induce change in flow, removing all of the variation from the effect of this variable is not possible or realistic. For example, surface roughness, and the shape of the substrate will cause differences in the flow between the central area and the edges of the tile.

Tiles were employed as a compromise in these experiments. Before using any substrate, natural or artificial, it must be clearly understood what the important questions are and whether the substrate selected will allow reasonable control over the variables.

In the pilot experiments, larval behaviour on cobbles and tiles was similar to the natural habitat. However, with the replacement of cobbles for tiles, other potentially influential variables could be controlled.

Effects of Substrate Surface Features

Texture and Evenness

Gersabeck and Merritt (1979), Boobar and Granett (1978), Colbo and Moorhouse (1979), and Das et al. (1988) have each provided evidence that black flies exhibit preferences for specific substrates. The preference for a flexible substrate such as vegetation contrasting with a solid and stable substrate such as stones appears to be species-dependent. A clear demonstration of this is the stony substrates preferred by the sibling species IIIL-1 and the grass vegetation preferred by the IS-7 sibling of the S. vittatum complex (Adler and Kim 1984).

In my pilot experiments using tiles, more larvae than expected (based on initial numbers) remained on the uneven surface while more than expected deserted the even tile. This difference was not statistically significant, but did suggest that black flies could

discriminate between the two alternate states of evenness. This outcome confirmed that tiles were suitable for the experiments: larvae could discriminate between the surfaces, and this difference was at a detectable level. As well, variation due to flow had been considerably reduced with the use of tiles.

Pilot experiments involved only smooth tiles. Although the trial suggested evenness was slightly influential, its effect was not significant. In the experimental series, texture was a factor in substrate selection by larvae of S. vittatum in low density treatments. There was a significant interaction between texture and evenness in Experiment 1 (Table 2.5), suggesting an avoidance of smooth, even tiles, while in Experiment 2, texture had a significant effect (Table 2.6). At high larval density without periphyton (Experiment 3), there was no evidence of either a preference for any single tile type, nor an avoidance of any single tile type (Table 2.7).

Clifford et al. (1989) quantitatively measured the roughness of sand cast tiles, wherein rough tiles were ten times rougher than the smooth tiles. They found that texture influenced colonization of some invertebrates, but not others. However, there was no indication that black flies were collected during the study. Greater diversity and abundances occurred on rougher tiles. Clifford et al. (1989) speculated that, for some taxa, rough substrates may allow animals to gain a more secure grip to the surface, or more food may be available on rougher surfaces because of accumulated particles in the grooves and crevices. Hart (1978) suggested that greater surface complexity of the particles allowed the development of a more diverse food base, which consequently attracted a greater diversity of macroinvertebrates. Erman and Erman (1984) also found more immature mayflies and stoneflies on natural substrates with increasing roughness.

Décamps et al. (1975) examined black fly larval densities on natural stones from streams in the Pyrennes. Larger, more stable stones with smooth surfaces had greatest densities.

Black flies sampled by polystyrene balls and plastic balls by Walsh et al. (1981) were more numerous on rough (polystyrene) than smooth (plastic) spheres. However, these spheres involved not only different materials (which may in themselves affect ability to attach), but also differences in surficial features (evenness). In this respect, these results are similar to the low density treatments in my experiments in which there was avoidance of the smooth, even surface, comparable to the plastic spheres used by Walsh and associates. Although they conclude that the rough surface is more efficient for maximizing collections, according to my definitions of texture and evenness, it is not possible to discern to which factor larvae were responding in their study.

Insect morphology may also influence substrate selection. Larvae of mayflies, caddisflies, stoneflies, and aquatic beetles are generally dorsoventrally flattened, have legs and may or may not have long antennae or cerci for sensing vibrations. In contrast, blackfly larvae lack legs, cerci, and long antennae, and the body shape is highly streamlined. As Casey and Clifford (1989) suggested, many insect taxa may prefer rough substrates as they may reduce the chance of being swept downstream. Black fly larvae adhere to the substrate in an upright, standing or leaning position. Their body shape and lack of appendages reduces the drag, which would otherwise be much greater, but also limits their ability to hold onto the substrate by gripping onto surface features. Although black flies also adhere to the surface, their body plan may lead to other preferred substrate types. One might speculate that, given suitable flow regime, black fly substrate selection is

largely dependent upon ability to attach a silk pad to the substrate surface.

At the microtexture scale involved in my experiments, overlap of particles (due to size and shape), and the type of particle, create minute surface irregularities, such as tiny protrusions and depressions. These tiny surface features may be important to black flies initiating attachment to the surface. Perhaps these tiny projections serve to snag the silk line, allowing the larva to crawl to the surface to form the silk pad. These surface features may also play a facilitative role in silk pad attachment, thereby rendering smooth, even substraten less attractive than other substrates due to their lack of surface irregularities. Although larvae are capable of attaching to such surfaces (smooth, even substrates had larvae present throughout all experiments), it may be more difficult, and therefore, less preferred. Given alternate choices, larvae may select substrates other than smooth even when others are available.

Another potential explanation to account for avoidance of smooth even surfaces concerns flow patterns and their effects on black fly feeding ability. Some studies have suggested some species of black flies prefer torrential flow (Décamps et al. 1975), while others suggest that less turbulent flow, but fast current in general (Phillipson 1956, 1957) is preferred. However, since microhydrological measurements are not available for the tiles used in my experiments, reliable conclusions regarding this aspect cannot be reached. One may speculate, that in addition to influencing initial larval attachment, tile surfaces also affected larval substrate selection or avoidance by altering flow patterns.

In summary, it would seem that in the absence of periphyton, neither texture nor evenness exhibited a strong enough influence to

cause larvae to select one substrate over another, with the exception of an avoidance of smooth even surfaces at low density.

Modifying Effects of Periphytic and Detrital Accumulation

Experiment 4 involved an additional modification to tile surfaces, periphytic growth. When substrates had periphyton present, texture was clearly a discriminating factor for larvae. Smooth tiles had significantly more larvae than rough tiles (Table 2.8). In all likelihood, larvae selected tiles based on the level of periphyton (as measured by ash-free dry mass). The interaction between periphyton and texture was consistent and significant, in that rough tiles, whether even or uneven, retained much more periphyton than smooth tiles (even or uneven). The choice of simuliids (smooth) reflected the differences in periphyton levels among the four tile types offered. Fewer larvae occurred on rough tiles, which had significantly higher levels of periphyton than smooth tiles. The occurrence of periphyton apparently reversed the preferences previously displayed by larvae at low densities.

Various authors have noted a negative relationship between periphytic growth (sometimes referred to as slime) and black fly presence in the field (Zahar 1951, Carlsson 1962, Gersabeck and Merritt 1979, Pruess 1989, S.A. Beckett pers. obs.). Pruess (1989) attributed a decrease in colonizing larvae on plastic tapes to periphytic accumulation, although periphyton levels were not manipulated, and intraspecific competition could not be excluded. In an Alaskan river, Hershey and Hiltner (1988) found that more larvae of two black fly species occurred on stones with low periphyton levels, or shifted positions to the sides and bottoms of periphyton-covered stones.

Further evidence of the detrimental effect of periphyton build-up on simuliid attachment comes from experiments manipulating the effects

of disturbance. Hemphill and Cooper (1983) varied the frequency of disturbance in a California stream by scrubbing boulders at various time intervals to simulate scouring. Blackflies responded to the manipulation by exhibiting higher abundances in treatment areas than unmanipulated controls. In a further investigation, Hemphill (1991) suggested that disturbance and interspecific competition (between Hydropsyche oslari caddis larvae and Simulium virgatum) controlled the distribution of black fly larvae. The issue of competition could not be fully resolved due to the design of the experiment, but the effect of reduced periphyton levels by scouring suggests that disturbance acts as a natural mechanism to remove the periphytic barrier, rendering these areas accessible to black fly colonists. Downes and Lake (1991) also conducted a field experiment using natural and artificial substrates (bricks) to examine the effect of scouring on black fly colonization. Their study revealed that, although both species responded to disturbance events, only one was dependent upon disturbance. Larvae attached to areas with reduced algal growth and reduced numbers of other taxa.

Significant differences occurred in total biomass (dry mass) and periphyton (measured as AFDM) between smooth tiles and rough tiles in my experiments. However, significant differences in accumulation of either material were not detected with differences in evenness.

Other workers also have found greater levels of periphyton accumulation on tiles with more pronounced surface features. DeNicola and McIntire (1990a, 1990b) demonstrated that algal cells colonized depressed areas between tile substrates more readily due to easier deposition of cells resulting from lowered shear stress, and flow in many directions. Dudley and D'Antonio (1991) examined texture in relation to algal colonization and found successful establishment of propagules was partially determined by disturbance and texture. Rough

surfaces provided some protection of established algae to remain in crevices after a disturbance event, as were newly-arrived propagules protected. Macroalgae had higher densities on rough tiles for these reasons. This would explain the mechanism by which more epilithic biomass accumulated on the rough tiles in my experiment than on the smooth tiles.

Total accumulation of debris (dry mass) may also have affected larval choice of substrate. In my study, larvae preferred to settle on smooth tiles, which in addition to having the lowest AFDM, also accumulated the lowest dry mass. My results agree with other published accounts (Rühm and Pegel 1986b). Wu (1931) found that few larvae occurred on cobbles that became covered with a film of sediment. During a dry summer, Zahar (1951) noticed that larvae deserted areas in which sediment deposition occurred on stones.

Regardless of the type of material (silt or periphyton), surface deposits appear to interfere with some aspect of larval function. This function is most likely attachment to the substrate, due to the inability of larvae to become anchored to substrates colonized by algae, diatoms, or bacteria, or covered by inorganic material. These surface coverings tend to create a slimy and slippery covering to which silk probably adheres poorly. In experiments manipulating periphyton levels, my results strongly suggest that black flies avoid periphyton, a result which has only been described anecdotally previously. This phenomenon probably occurs regardless of density since it affects black fly larvae at the individual level.

In my study, larvae did not show a more pronounced response for one factor over the other (periphyton, total detritus). However, periphyton was the manipulated variable. This material was organic, living or dead. Any silt occurring on tiles was considered to be a

natural accumulation from suspended particles in the stream water collected initially and added to the artificial streams. Another source of silt and minerals occurred during the algal scrapings of the cobbles in the field which were used to "seed" the laboratory streams for algal colonization of tiles. Additional inorganic material could have entered the laboratory streams during algal colonization of the tiles by the wind or from precipitation of calcium carbonate during algal photosynthesis. Dry mass included not only silt and other inorganic materials, but also the organic periphyton.

Detrital accumulation (measured by dry mass), was, in order of decreasing quantity, greatest on rough uneven, rough even, smooth uneven, and smooth even tiles. Larvae were, in order of increasing abundance, greatest on smooth even, smooth uneven, rough even, and rough uneven tiles. This pattern of larval abundance on tiles matched total dry mass accumulated on tiles with exact correspondence (rather than periphyton), even though the differences in accumulation of dry mass were not significantly different between smooth even and uneven, and rough even and uneven. My results suggest that both periphyton and total dry mass are negative cues to larval settlement. Since larvae responded similarly to total detrital accumulation and periphytic accumulation, it is not possible to conclude that one factor exerts more influence than the other.

Effects of Density

There were some differences due to density effects. In low density treatments, larvae exhibited an apparent avoidance of smooth, even substrates (as evidenced by a significant interaction in Experiment 1, Table 2.5, $p<0.03$). Fewer larvae also tended to occupy this tile type in Experiment 2 (Fig. 2.9). However, only texture was significant (Table 2.6, $p<0.03$). At high larval density, and in the absence of periphyton, there was no evidence of either substrate selection or

substrate avoidance by 24 h (Table 2.7, $p>0.05$), consistent with the ideal free distribution models (Fretwell and Lucas 1969, Rosenzweig 1981, 1991). With periphyton, however, larvae selected tiles according to texture (Table 2.8, $p<0.02$), favouring smooth tiles apparently in response to levels of organic and/or inorganic matter.

At high density, larvae were more active than at low density. As a result, row formations were much more distinct at high than low densities by 4 h. Larvae formed bands perpendicular to the direction of flow on both bare and periphyton-coated tiles. Rows extended directly across tiles of different texture or evenness.

This type of formation is unusual for stream macroinvertebrates, but is common among black fly larvae. It has also been reported for atyid shrimp in a Costa Rican stream (Covich 1988), and brachycentrid caddisflies (Wetmore et al. 1990), both filter-feeding taxa. This pattern (rows) has been observed for black fly larvae in the field as well as in laboratory flumes (Brenner and Cupp 1980, Colbo 1987, Eymann 1990, S.A. Beckett pers. obs.). In all cases, black flies aggregated to form dense bands of individuals perpendicular to the direction of flow.

Within the bands that formed in my experiments, individuals were separated from neighbours with regular spacing. Such uniform spacing is common and well-documented (Hocking and Pickering 1954, Colbo 1979, Colbo and Moorhouse 1979, Eymann 1985, Hart 1986, Colbo 1987, Hart 1987a, Eymann and Friend 1988, Ciborowski and Craig 1989, Eymann 1991, S.A. Beckett pers. obs.).

There may also be a minimum time interval required for initial assessment of environmental conditions (in this experiment, current velocity, substrate, and density) by larvae, prior to movements to aggregate. Evidently, this time requirement is less than 4 h. In

laboratory experiments examining the formation of larval aggregations by S. vittatum, Ciborowski and Craig (1989) found clustering of individuals with uniform spacing, as well as randomness, but no row formations developed. These patterns emerged within 3 h. They found that the rapidity of larval relocation movements were dependent on the strength of the current. Travel was slower in higher current velocities. Eymann (1985) found a 3-day requirement for stable distributions to form.

Although tiles reduced variation in flow patterns, they could not create complete uniformity among all areas of all tiles. These row formations suggest that the larvae detected specific more suitable locations on all tiles over other areas on the tiles. There was relatively equal response among tile types regarding row formation. Some rows continued across to the adjacent tile, even in trials with periphyton-covered tiles. Because rows continued to form across all tile types, regardless of the surface type, I speculate that such patterns formed in response to hydrodynamic parameters. Greater turbulence occurred at the tank end with the air bubbler, and the velocity of the water was slightly greater here than toward the opposite end of the tank. There appeared to be some degree of uniformity in terms of the spacing between rows. This may reflect the wavelength of water moving from the bubbler, over the tiles, and back down toward the bubbler. The formation of these rows is a complicated issue which cannot be resolved from my experimental set-up.

Craig and Chance (1982) discovered vortices were formed during larval feeding and suggested the downstream travel of these vortices could facilitate feeding of downstream larvae, but Hart (1986) demonstrated that upstream individuals could interfere with the feeding of downstream larvae by intercepting particles. These arguments suggest that consecutive bands should be spaced at distances that allow the vortices to dissipate before reaching the next band of larvae. Nowell

and Jumars (1984) suggest that approximately 20 cylinder diameters (here, simuliid body diameters) would be required for complete dissipation of upstream effects on flow. Distances between transverse rows of larvae were not directly measured in my study. However, some rows were at least 20 larval body diameters apart (>2 cm), but others were closer together than 2 cm.

The Reynolds number (Re= vd/ ; where v= current velocity, d= water depth, = kinematic viscosity), similar to Froude number, is also useful for describing the turbulence of flow. When Re is high (>2000), flow is generally considered to be "rough"; when low, flow is considered to be "smooth". In general, streams have turbulent flow (Re>>2000). Re was approximately 1000 in my experimental tanks. At this level, flow was transitional. This means that flow was turbulent at some points in time, but laminar at others (J.A. McCorquodale, Univ. of Windsor, pers. comm.). The variation in the distance between transverse bands in my experimental aquaria may have partially reflected this variability in flow conditions. My experimental system did not permit control of fine-scale features of flow. Direct observation of flow patterns (the crests of waves travelling along the substrate surface) suggested that the appearance of larval bands occurred where the crests of successive waves occurred. Probably, these larval bands were formed in response to hydrodynamic conditions, at a scale not quantified in my experiments. However, the potential role of intraspecific interactions in the formation of these bands can not be excluded.

The spaces that I observed between adjacent individuals were much smaller than the spaces between consecutive bands. This would suggest that the spacing between individuals was controlled by larvae, perhaps in defense of a territory for control of food resources or space (Hart 1986, 1987a), or in a protocooperative relationship due to facilitative effects of flow between closely-packed individuals (Craig and Chance

1982, Chance and Craig 1986). Ciborowski and Craig (1989) concluded that optimal interlarval positions within patches of larvae are dependent on hydrodynamic conditions (flow). They suggested a greater benefit could be obtained in positions adjacent to other individuals, such as occurs during banding, under conditions of food limitation and lower than optimal current velocity. Ciborowski (unpubl.) has postulated facilitation of feeding occurs between pairs of larvae oriented in the same direction (both right or both left) due to accelerated flow between neighbours. In this preliminary stage, the model proposes that rows may be unstable, but further testing and possible refinement of the model is necessary. Banding formations were not investigated in my experiments, but the most likely explanation for their appearance is hydrodynamic variability within the tanks, to which the larvae are particularly sensitive.

Conclusions

My experiments showed that two of the three substrate attributes (texture, evenness) played a minor role in larval selection of substrate. Neither texture nor evenness influenced larval choice of the substrate, except in the case of the smooth even surface, which was avoided. The additional variable of periphyton was important to substrate selection. Simuliids avoided these substrates, which they presumably perceived to have deteriorated. More roughly-textured surfaces favoured the accumulation of periphyton and silt. Under these conditions, texture becomes a variable of importance in substrate selection, and rough surfaces are avoided.

There was more activity at high density, but this did not affect the selection of substrate, except perhaps to override an avoidance of smooth tiles. However, it did result in the aggregations typical of simuliids becoming more distinct in less time than for low density.

Most importantly, the tendency to aggregate was shown to override any selection of substrate.

At this microscale of substrate selection, black fly larvae choose substrates with low periphyton levels, but the behaviour to aggregate, such as banding, is seemingly in response to hydrodynamic conditions on all surface types.

Based on this investigation, one might speculate that greatest densities of black fly larvae would occur on substrates free of periphyton or any other type of surface covering, in areas with suitable flow conditions (shallow, faster water). Such substrates could include recently-scoured stones, surfaces in riffles where deposition is low relative to other areas, or recently-overturned stones. The more recently the surface has undergone removal of surficial material, the more likely it may be colonized by larvae. Natural disturbance events could thus play an important role regarding larval black fly colonization (Hemphill and Cooper 1983, McAuliffe 1983, Hemphill 1991, Downes and Lake 1991), and overall distribution within the stream. Given that surfaces with less debris are most attractive, smaller substrates (small cobbles) may be colonized more often than larger substrates (large cobbles) because they may be overturned, and thus scoured, more frequently. This expectation is consistent with my results of field distributions of larvae in HMC (Chapter I). One might also predict that, in the presence of both even and uneven substrate surfaces, uneven surfaces would be colonized first, in preference to even surfaces.

Future Research

Future directions must examine the aspects of periphyton and siltation more closely. To which factor the larvae are primarily responding needs further attention, and at what scale is this occurring.

Also, factors including algal species composition, and the amount of biomass present, may contribute to larval settlement. Black fly larvae may respond to filamentous algae differently than to diatoms and bacteria. Attachment to macroalgae may be similar to attachment to flexible grass leaves, but diatoms may create a surface too slippery for any attachment. Alternatively, larvae may find such areas suitable during the development of the algal community, but find them detrimental at a later stage of algal succession.

It is unlikely that such a sensitive response is species-specific among black flies, but differential effects among instars (age, size) or sibling species, may be involved, particularly when the potential effects of intraspecific competition, and aggregation, are considered. I observed early instar larvae on strands of filamentous algae (in the laboratory maintenance tank, as well as in the field), but not larger instars. These habitats may be suitable for limited periods of time for particular larval stages. Conversely, they may be tolerable, but less favourable habitats, serving as refuges for the ousted smaller larvae during competitive bouts with larger larvae or other taxa that are superior competitors (e.g., Hydropsyche, Hemphill 1988, 1991).

Finally, the effects due to other community members must be examined in relation to black fly responses to periphyton or detritus. It is unlikely that the mechanism involved is as simple as a presence/absence periphytic/detrital effect. Other taxa that depend on periphyton or detritus for resources of shelter, refuge, and particularly food, may alter the patch, thereby affecting the suitability of the area for black flies. Such changes could be due to successional events of algal species, insect taxa or microbes, decomposition of decaying material, or changes in abundances of each.

III. COLONIZATION OF ARTIFICIAL SUBSTRATES BY *SIMULIUM VITTATUM* LARVAE IN A SOUTHWESTERN ONTARIO STREAM: BIOTIC AND ABIOTIC EFFECTS

INTRODUCTION

This chapter describes a short-term (28-day) field experiment examining the colonization process of black fly larvae. Artificial substrates (tiles) were placed randomly and sequentially in Hobbs-Mackenzie Creek during June 1990, and underwent repeated manipulations according to three treatments. These treatments were designed to address the temporal pattern of colonization (Treatment 1, no taxa removed), and the roles of potential biotic interactions (Treatment 2, black flies removed; Treatment 3, all taxa removed) and microhabitat quality (Treatment 3) to this pattern.

Colonization is a dynamic process of immigration and emigration of individuals to and from an area, and may be studied at many spatial and temporal scales. Colonization may be broadly defined as the process leading to the establishment of individuals, populations, or species in areas in which they were previously absent (Sheldon 1984). Microhabitat selection could be considered one potential outcome of the colonization process.

The behaviour of adult ovipositing females may also determine which habitats are colonized by simuliid larvae. Müller (1974) postulated that upstream flight of gravid female aquatic insects allowed eggs to be deposited in upstream habitats, and larvae that may later drift downstream, which results in colonization of new areas. In this manner, females may compensate for the downstream drift of insects that occurs during the larval stages of growth. Adler et al. (1983b) showed that a high proportion of Simulium vittatum Zetterstedt females flew upstream prior to oviposition. Thus, adult dispersal activity can result in colonization of new habitats by larvae, or changes in abundances of presently colonized patches.

Studies of colonization have been conducted on a wide range of spatial and temporal scales, but most frequently, studies have been done on short-term scales (less than 1 yr, within single streams; Sheldon 1984). Some studies have employed artificial substrates such as baskets filled with natural substrates of varying particle size (Sheldon 1977, Ciborowski and Clifford 1984, Clements et al. 1989), introduction of polyethylene tapes (Pruess 1989) or bricks (Robinson et al. 1990), or Hester-Dendy (multi-plate) samplers (Hill and Matter 1992). Colonization has also been studied through manipulation of study plots within streams (Doeg and Lake 1989, Brooks and Boulton 1991, Malmqvist et al. 1991).

Both biotic and abiotic factors may influence colonization of a habitat. Biotic interactions may restrict the number of co-occurring individuals. Although black flies commonly occur in dense aggregations (Wiley and Kohler 1984), their uniform spacing within aggregations (Hocking and Pickering 1954, Colbo 1979, Colbo and Moorhouse 1979, Eymann 1985, Hart 1986, Colbo 1987, Hart 1987a. Eymann and Friend 1988, Ciborowski and Craig 1989, Eymann 1991, S.A. Beckett pers. obs.) suggests that intraspecific interactions may be involved to maintain the even spacing between individual larvae. Hart (1986, 1987a) and Eymann and Friend (1988) have examined intraspecific interactions and found that larvae aggressively interact. Hart (1986, 1987a) suggested that such interactions may occur in response to defense of a resource (food or space). Wiley and Kohler (1981) reported that interactions between larvae of two black fly species resulted in displacement of one of the larvae in the majority of interactions. Although aggressive encounters occur, Ciborowski and Craig (1989) proposed that larvae may receive facilitative effects from neighbouring individuals when oriented in parallel positions. Interspecific interactions, indicative of interference, have been documented between black fly larvae and hydropsychids (Hemphill and Cooper 1983, Hemphill 1988). I have

observed that these interactions favour the caddisfly larvae, the black flies typically being displaced from the substrate (S.A. Beckett pers. obs.). Conversely, interactions between Asellus and simuliids were indicative of superior competitive ability by black fly larvae (S.A. Beckett pers. obs.).

The most widely cited abiotic factor affecting black fly colonization is flow characteristics (Phillipson 1956, 1957, Chance and Craig 1982, Craig and Chance 1986, Craig and Galloway 1987, Ciborowski and Craig 1989, Lacoursière 1989). In addition, observations of simuliid distributions in the field suggest that substrates with silt (Wu 1931) or periphyton (Zahar 1951, Gersabeck and Merritt 1979, Pruess 1989) may be avoided by larvae. My distributional surveys (Chapter I) and laboratory manipulations of periphyton (Chapter II) concur. Recently disturbed (scoured) stones tend to have more larvae than undisturbed stones (Hemphill and Cooper 1983, Hershey and Hiltner 1988, Hemphill 1991, Downes and Lake 1991).

I chose to examine colonization using tiles because they standardize the effects of substrate texture, evenness, and surface area. A standardized substrate also aided to control varying flow patterns inherent over natural substrates of variable size and shape. Initial substrate quality (absence of periphytic growth) would also be identical for all substrates. Furthermore, tiles were amenable to a field experiment because they were inexpensive, easily transported, relatively inconspicuous, and easily handled and manipulated. Black fly larvae were reasonably visible on these substrates.

In this study, on 14 dates, six tiles in each of three treatments were placed randomly in the stream in areas with suitable flow conditions (visually estimated) for colonization by Simulium vittatum larvae. All tiles were removed on the final day of the experiment.

This design (sequential introduction/simultaneous recovery of tiles) allowed phenological changes in abundances of taxa to be separated from changes in habitat quality, a potentially confounding variable. Ciborowski and Clifford (1984) showed that a design of simultaneous removal of substrates compared with one of sequential removal (over a number of days) could show considerable differences in colonization patterns, the first method approximating equilibrium models, the latter approximating a linear increase in numbers. The latter method (sequential removal) cannot distinguish between changes in abundances of taxa over time due to cohort effects or other successional events (e.g., changes in the substrate quality due to algal colonization). A simultaneous removal design ensures that the samples retrieved are of the same sampling population, and have been exposed to the same environmental variation, at least shortly before retrieval of samples (Ciborowski and Clifford 1984).

Objectives

Temporal Pattern

The first objective in my experiment was to determine the temporal pattern of colonization by black flies, other taxa, and periphyton. This objective was examined using Treatment 1 (no taxa removed from tiles). Since no organisms were removed from these tiles, succession of the community, including taxonomic richness, the number of individuals per taxon (black flies and non-black fly taxa) and the development of periphyton on tiles, could be observed over time.

Theoretically, the number of individuals arriving to the habitat with rate r will be followed by a period of relatively constant numbers of individuals (N), with time. This stabilization in numbers would be expected as a result of a balance between the (constant) number of individuals immigrating and the (constant) proportion of individuals

emigrating, assuming an absence of biotic interactions and constant environmental conditions (Fig. 3.1; H_0).

I predicted rapid initial colonization by black flies, followed by a relatively constant period in numbers, and a subsequent decline in numbers, with time (Fig. 3.1; H_1). Since black flies tend to be opportunistic colonists (Downes and Lake 1991), I predicted that the initial phase of colonization by black fly larvae would be rapid (Fig. 3.1; A). As the rate of immigration decreased, numbers were expected to become relatively constant (Fig. 3.1; B). The effect of biotic interactions was expected to reduce this plateau from that of the theoretical curve (Fig. 3.1, shaded area). Subsequent to this balance of arrivals and departures, habitat quality was expected to decline, due to periphytic growth and settling of silt, resulting in increased emigration. Thus, a corresponding decrease in the number of larvae present on the substrate was expected to coincide with deterioration of the substrate (Fig. 3.1; C).

Substrate Quality

The second objective examined potential changes in the quality of the substrate for black flies with time. Treatment 3 described this aspect. Since all taxa, including black flies, were removed from these tiles repeatedly through time, only the effect due to substrate quality (tile age) remained. For this objective, the colonization time for taxa was 24 h (all tiles were manipulated 27 June and removed 28 June). However, staggered placement of tiles resulted in tiles of different age. Substrate change as a consequence of age was evaluated by comparing periphyton (AFDM) and total detritus (dry mass) among all treatments.

Since tiles were introduced to the stream in the most suitable black fly habitats available (visually estimated at the time of

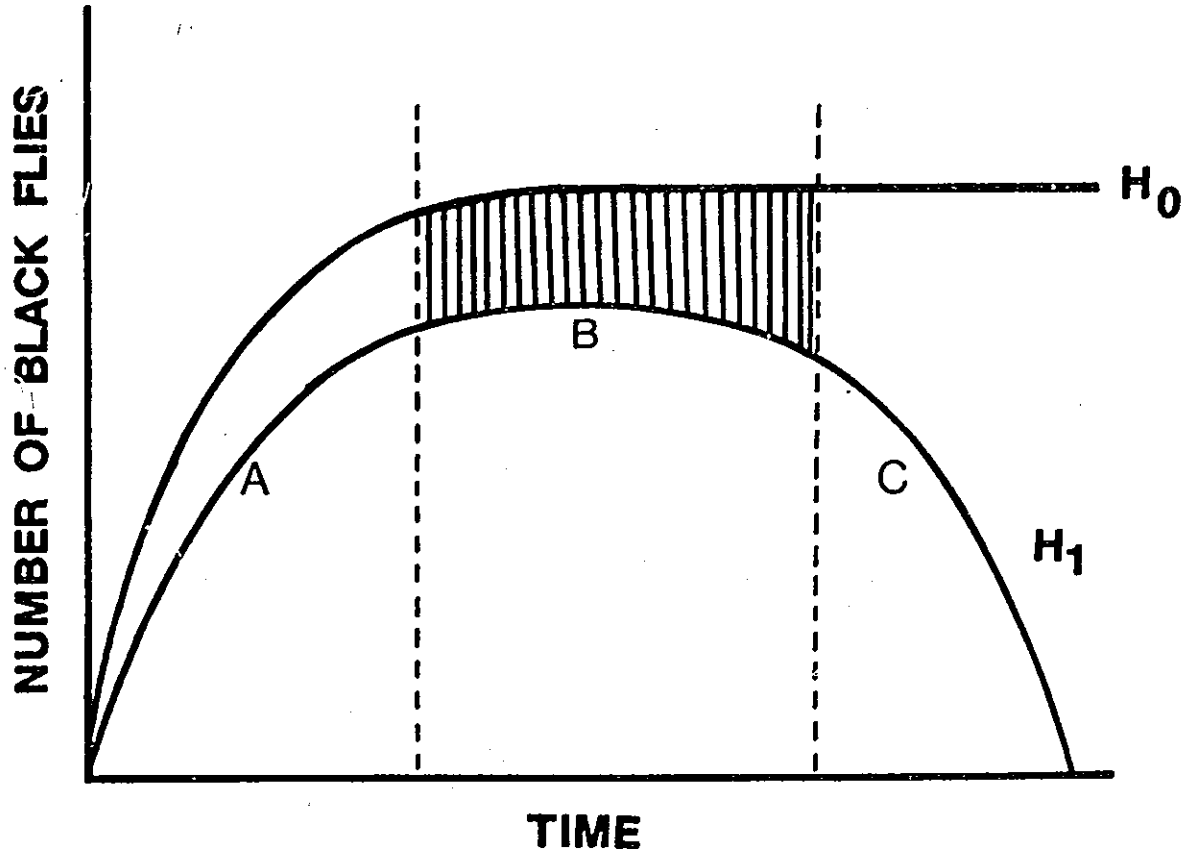


Figure 3.1 The predicted pattern of black fly colonization in the absence (H_0) and presence (H_1) of biotic interactions. 'A' denotes the expected rapid increase of black flies, 'B' stable phase, and 'C' decline. The shaded area denotes the reduction in numbers, relative to H_0, due to biotic interactions.

placement and subsequently current velocity and depth were measured), and tiles were free of organic (periphyton) and inorganic (silt) material, initial substrate quality was assumed to be high. If substrate quality remained constant, then black fly densities should remain constant following initial colonization as a result of equal numbers of larvae immigrating and emigrating (Fig. 3.2; H_0).

I hypothesized that substrate quality would not remain constant with time (tile age), but would decline due to periphytic growth and/or accumulation of silt on tiles. A corresponding reduction in the number of black flies present on tiles was expected to occur as the substrate quality deteriorated for black flies (Fig. 3.2; H_1).

Biotic Interactions

The third objective examined the potential role of interspecific interactions to larval black fly colonization. For this comparison, treatments 2 and 3 were used. Black fly larvae (only) were repeatedly removed from tiles of Treatment 2, whereas in Treatment 3 tiles, all taxa were repeatedly removed. For testing of the objective, a 24 h period of colonization occurred for all taxa, but tiles differed with respect to age because of serial placement through time.

Assuming interspecific interactions do not affect black fly colonization, then numbers of black flies on Treatment 2 tiles and Treatment 3 tiles should not differ significantly (Fig. 3.3; A).

If biotic interactions affected black fly colonization, I expected there to be a negative effect. Since black flies were removed from Treatment 2 tiles, these tiles could be used to examine the potential effects of established non-black fly taxa to invading black fly colonists. Since established individuals (of all taxa) were absent on Treatment 3 tiles, black fly numbers were expected to be higher on these

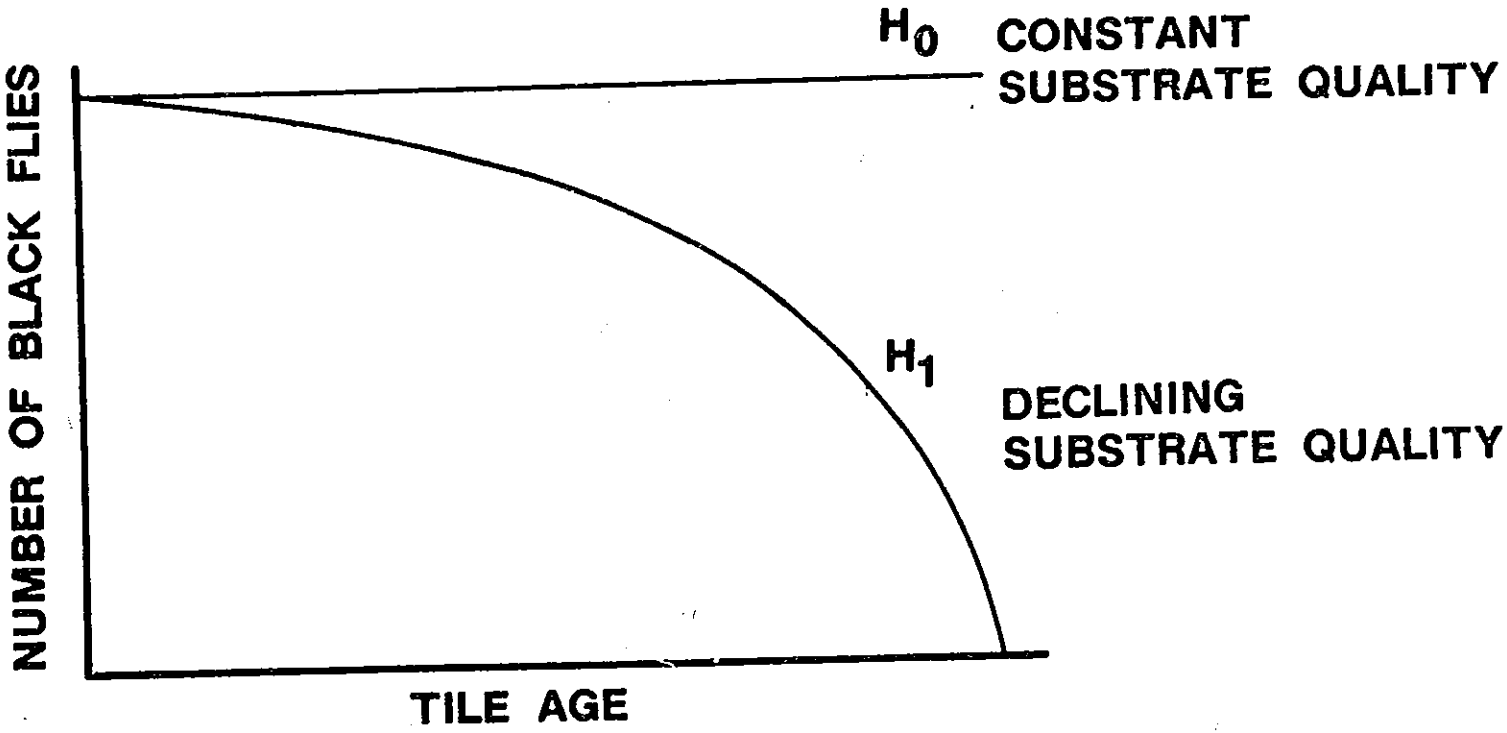


Figure 3.2 The predicted pattern in the number of black flies given constant substrate quality (H_0) and declining substrate quality (H_1). Fewer black flies were expected on tiles of increasing age, due to periphyton accumulation.

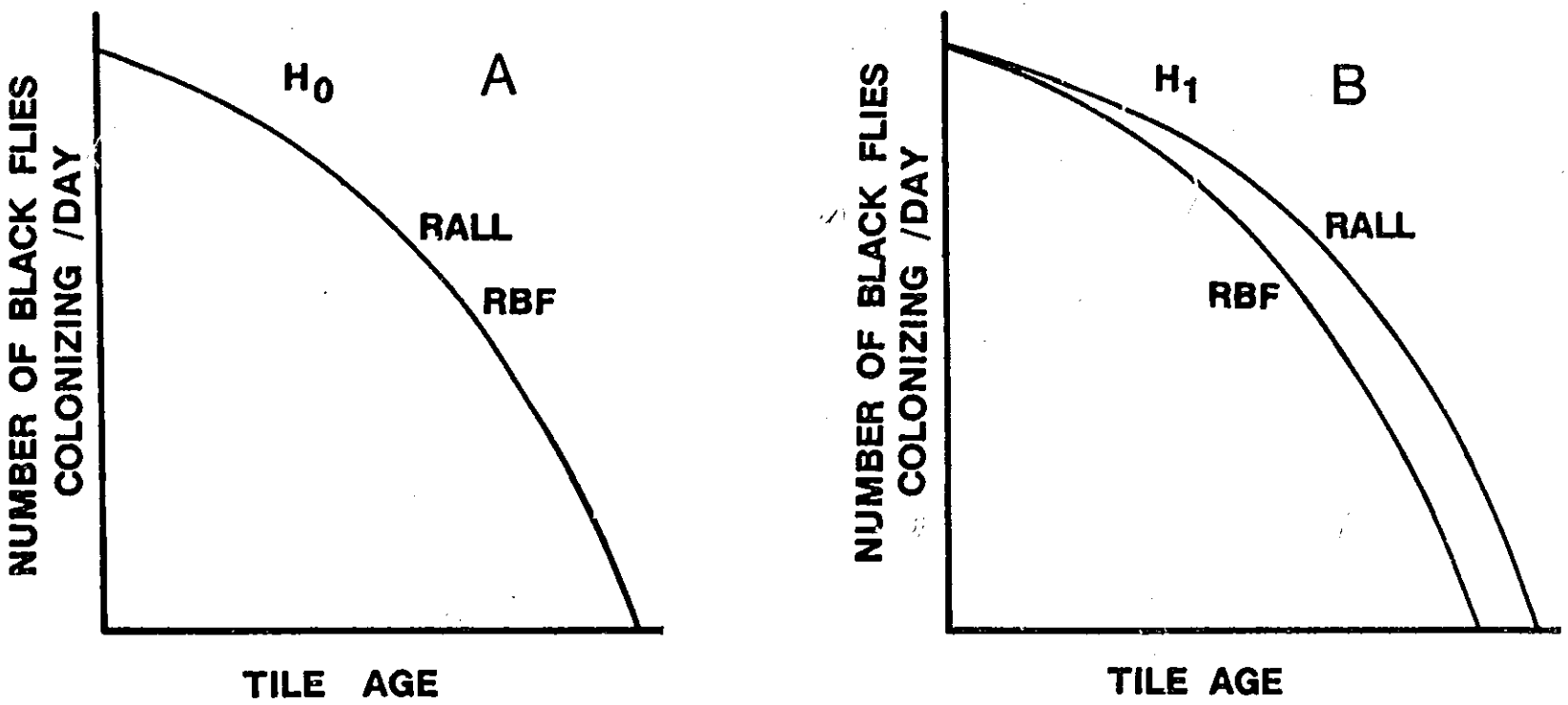


Figure 3.3 In the absence of any interaction effect, equal numbers of black flies immigrating over 24 h to tiles of different age between RBF (Treatment 2; removal of black flies) and RALL (Treatment 3; removal of all taxa) treatments, were predicted. More larvae were expected on RALL than RBF tiles if biotic interactions interfered with black fly colonization. Curves in A and B are all expected to decline if habitat quality is decreasing as a function of tile age (due to periphyton and detritus accumulations).

tiles than on Treatment 2 tiles because of the lack of potential competitors and potential aggressive interactions. These tiles should therefore be more easily invaded if biotic interactions interfere with black fly colonization (Fig. 3.3; B).

MATERIALS AND METHODS

Study Site

This field experiment was conducted in Hobbs-Mackenzie Creek, near Arkona, Ontario (Chapter I, Figure 1.1). This experiment was conducted in Hobbs-Mackenzie Creek (rather than Wigle Creek) for several reasons. First, it was considered to be more representative of small temperate streams than Wigle Creek because of the presence of a dam at the Wigle Creek study site. Second, the long stream reach of Hobbs-Mackenzie Creek had abundant terraced riffles throughout, whereas Wigle Creek had limited site availability. Third, familiarity with the stream and access to data from previous studies conducted in this stream allowed comparisons of my results to those of previous studies regarding temporal variation of stream fauna (taxonomic composition and abundance). Stream familiarity reduced the risk of loss of the artificial substrates by a sudden increase in stream discharge by avoiding the months most with such typical sudden spates. Familiarity with the stream also permitted assessment of the time (month) at which larvae were most likely to be abundant (June).

A 1 km reach of stream was used, commencing just after the pool at the bottom of a waterfall (upstream), and ending just upstream of a depositional area before a walking bridge (downstream), approximately 100 m from the confluence of the Ausable River and Hobbs-Mackenzie Creek. This 1 km reach was partitioned into upstream, central, and downstream portions of the study stream. Markers (orange vinyl flagging tape) were wrapped around streamside trees, at the boundaries of these sections. Each section was approximately the same length, the central section being slightly longer than upstream and downstream sections. Refer to Chapter I for further details concerning the study stream.

Experimental Design

This study was conducted 1 - 28 June 1990. June was selected as the study month because the black fly population was expected to be at moderate densities, and to avoid spring spates and high water levels (typically greatest in May; J.J.H. Ciborowski, Univ. of Windsor, pers. comm.; S.A. Beckett pers. obs.).

Table 3.1 outlines the dates for the placement of tiles, manipulations of tiles, and tile removal (completion of study). The table also outlines the schedule of manipulations and measurements taken per sampling date. In total, 14 days were used for placement of tiles and for manipulations, whereas a fifteenth day was required for removal of all tiles from the stream.

During the first two weeks of the study, tiles were placed in the stream, and manipulations were conducted at 3-day intervals. During the third week of the study, tile placement and manipulations occurred on alternate days. During the fourth and final week of the study, new tile placement and/or manipulations were conducted daily. These intervals were chosen because it was expected that greater changes in the number of black flies, the number of taxa, the total number of organisms, and substrate quality (increased deposition of silt, increased growth of algae) would occur toward the end of the study than near the beginning of the study.

A total of 252 tiles (9.5 x 9.5 cm) were divided equally among three treatments. Each date of tile placement included six tiles per treatment (18 tiles per day). Of these, two replicates per treatment were placed in each of upstream, downstream, and in the central region of the study portion of the stream.

Table 3.1 Experimental design of field colonization study, showing dates of tile placement, manipulations, visual counts, and water chemistry measurements. Tiles manipulated (column 4) are identified by the number of days they remained in the stream. Note that all tiles were removed on 28 June 1990. (WCO = water chemistry only; NWC = no water chemistry)

Calendar Date	Tile Placement	No. of Days In Stream	Tiles Manipulated	Photographs, Visual Counts, Water Chemistry
1	x	27		WCO
2				x
3				x
4	x	24	27	x
5				x
6				x
7	x	21	27, 24	x
8				
9				x
10	x	18	27, 24, 21	x
11				
12				
13	x	15	27, 24, 21, 18	x
14				
15				

Table 3.1 (Continued).

Calendar Date	Tile Placement	No. of Days In Stream	Tiles Manipulated	Photographs, Visual Counts, Water Chemistry
16	x	12	27, 24, 21, 18, 15	x
17				
18	x	10	27, 24, 21, 18, 15, 12	x
19				
20				
21	x	8	27, 24, 21, 18, 15, 12, 10	NWC
22	x	6	27, 24, 21, 18, 12, 10, 8	x
23	x	5	6	x
24	x	4	27, 24, 21, 18, 15, 12, 10, 8	x
25	x	3	6, 5, 4	x
26	x	2	6, 5, 4, 3	x
27	x	1	27, 24, 21, 18, 15, 12, 10, 8, 6, 5, 4, 3, 2	x
28	removal		27, 24, 21, 18, 15, 12, 10, 8, 6, 5, 4, 3, 2, 1	x

Treatment 1 was the no removal (NR) treatment. These tiles had no taxa removed during manipulation. This treatment served to elucidate the temporal pattern of colonization by all taxa and periphyton development. Treatment 2 was a black fly removal (RBF) treatment. During manipulation, all visible black flies were removed from the top surfaces of tiles and collected. Treatment 3 consisted of the removal of all taxa (RALL) from the top surfaces of tiles. The latter two treatments served to examine potential interactions between black flies and other taxa colonizing the tiles.

In addition to tiles for manipulation, six large cobbles were randomly selected (two per stream reach) to monitor natural densities over time. These cobbles also served to compare natural fluctuations in the stream water level over time.

Preparation of Tiles

Upper surfaces of ceramic tiles (9.5 x 9.5 cm) were modified similarly to the smooth, even surface used in the laboratory experiments (Chapter II). Procedures identical to those described for the preparation of tiles used in the laboratory were used in the preparation of these tiles. The detailed methodology concerning tile surface preparation is described in Chapter II. Although laboratory studies suggested that the smooth, even surface was the least preferred surface, under conditions of low density, the tiles for this field experiment were modified to reflect the smooth, even surface because it mimicked best the natural bedrock in the stream.

Tiles were coded with a single dot, 5 mm diameter, of water-resistant paint (NR: red, RBF: yellow, RALL: pink) on the downstream right corner of the top surface to enable quick identification of the appropriate manipulation in the field, and to avoid unnecessary disturbance of colonized tiles. On the bottom surface of the tile, the

tile was again identified with the tile number (1-252), treatment, and number of days the tile was to be in the stream.

Sampling Protocol

In the field, photographs of tiles were taken first, followed by visual counts, and then manipulations. Detailed methodology is outlined below. Tiles were handled from the downstream-most tile to the upstream-most tile to minimize disturbance of tiles from human movements. Of particular note is that on **each date following the day of initial placement of tiles**, photographs, visuals counts, and manipulations were made for **all** tiles in the stream. Exceptions occurring during the final week of study are listed in Table 3.1.

Monitor Cobbles

Six large stream cobbles were randomly selected within the study reach of the stream. These cobbles were used to monitor colonization of natural substrates, to monitor background densities of taxa, to monitor natural fluctuations in the stream water level, and to provide a means of comparing the response of biota to these substrates with their response to the tiles, throughout the duration of the study.

I selected the monitor cobbles on 30 May 1990, and placed stakes (numbered one through six) at each cobble. Assuming that periphyton could develop during the course of the study, and water levels could decline, I selected cobbles in areas that I subjectively judged would remain suitable over the duration of the study. These cobbles were checked again for suitability (current velocity within tolerable range for black flies; water depth over cobble surfaces at least 5 cm to allow for the possibility of declining water levels over time; minimal algal growth present) on 1 June 1990 at the commencement of the study.

On days of tile placement and manipulation, the monitor cobbles were photographed, and visual counts of organisms of an area equal to the viewer box (see below) bottom were taken (not the entire surface area of the cobble). Care was taken to view and count the same area of the cobble consistently. Unlike the tiles, organisms present on these substrates were not collected or otherwise disturbed.

Mean current velocity (one 50-s reading, Ott C-2 meter at 0.6x depth from the stream bottom to the surface of the water) and depth of the cobble (from the top surface of the cobble to the water surface) were measured concurrently as an indication of natural fluctuations in the stream. Because the photographs are necessary for discussion of the monitor cobbles, and the progressive visual counts throughout the experiment, the monitor cobbles will not be discussed in this thesis, except as general observations.

Tile Placement

Tiles were usually placed in the stream by 1200 h. Occasionally, tiles were not placed until 1500 h. On each date of tile placement, two tiles per treatment were placed randomly in the most suitable microhabitats available (estimated visually by shallow depth and moderate current velocity) in upstream, central, and downstream portions of the stream. Tiles were placed such that the coloured dot was always in the downstream corner. Tile locations were marked by placing a wooden stake near each tile. The stake was marked by flagging tape, and the treatment and tile number were again marked on the stake.

Depth and current velocity were measured for each tile. Depth was measured from the top surface of the tile to the surface of the water. Current velocity (one 50-s reading, Ott C-2 meter) was measured on the top surface of the tile.

Photographs

Prior to manipulation, tiles were photographed to provide a permanent record of the positions colonists occupied. A camera (35 mm SLR camera with 135 mm lens) was mounted inside a viewer box constructed of transparent polystyrene (31 x 18 x 13 cm). Inside the box, a wooden frame was inserted. The camera fit snugly into the frame with the lens directed toward the bottom of the box. A small hole was drilled into the plexiglass front of the box to allow the cable release to be in a position that would easily allow the camera to be activated. By looking through the camera, the tiles could be brought into focus most of the time by holding the box directly over the tile to be photographed and adjusting the depth of the box in the water. High-speed film (Ilford HP-400) was used at 1000 ASA to compensate for conditions of low light (due to natural shading, overcast, cloudy, or drizzling weather conditions). Photograph results will not be discussed in this thesis.

Visual Counts

After photographs were taken, and prior to manipulation, all organisms on tiles were counted and recorded. A clear view of the tile surface was obtained by holding the bottom surface of the viewer box (with mounted camera) just under the water's surface. It was not necessary to look through the camera to accomplish this.

Tile Manipulation

All tiles were handled similarly during manipulation, which differed only with respect to the organisms removed, according to the treatment. Preliminary trials of capturing organisms on tiles indicated that lifting the tiles partially into a small dip-net was necessary for best results. Organisms tended to drift toward the net, but tended to be swept to the outward edges of the net unless the tile was placed partially within the net. To circumvent this problem, it was necessary to carefully raise tiles slightly, placing them such that one-half of

the tile was inside the mouth of the net (mouth 20 cm x 25 cm, mesh 250 μm), located directly behind the tile. At all times, tiles remained submerged.

Treatment 1 tiles (NR) were tapped lightly with forceps (10 sec, approximating the time for manipulations of tiles in other treatments), then replaced to their previous positions in the stream. Any dislodged organisms were collected in the dip net and preserved in Kahle's solution. Treatment 2 tiles (RBF) had black flies removed. These were easily dislodged by touching the larva, or its silk pad, with forceps. The same procedure (touching organisms) was used to dislodge all organisms from tiles of Treatment 3 (RALL). Only organisms on the upper surface of the tile were counted and removed. Organisms on the sides of tiles were assumed to be potential colonists to the upper surface and were not disturbed.

During the course of the study, some tiles overturned. Provided that they were still submerged, the tile was turned over to its original position, and retained for the remainder of the study. On these occasions, any organisms which may have colonized either surface of the tile were disregarded (manipulation was completed, but animals were not enumerated or collected), and the tile was not photographed. If, at any time, the tile was no longer submerged, the tile was removed from the study. Occasionally, a few tiles were washed from their original positions to a position slightly downstream. Provided that such tiles were submerged, they were returned to their original position and retained in the study. At the conclusion of the study, 228 (90%) of the original 252 tiles were recovered.

Measurements of Water Chemistry

On most dates of tile manipulation, measurements of suspended solids, dissolved oxygen (modified Winkler titration), water

temperature, air temperature, pH (pH indicator paper), and conductivity (YSI meter, model 33) were made. These measurements were taken between 1200 h to 1500 h, in the central study section. Measurements were not taken at the identical site within the central study section to avoid potential "spot" effects (sampling an atypical site regularly as representative of the stream). To measure suspended solids, 250 mL of stream water was filtered at the study site onto a preweighed membrane filter (0.45 μm pore size), wrapped in aluminum foil, and placed in a freezer in the laboratory. The filter was later dried in an oven (GCA model 18EG) for 24 h at 60°C, and then re-weighed.

Simultaneous Removal of Tiles

All tiles were removed 28 June 1990. All tiles were photographed, visual counts recorded, and manipulations completed according to the regular procedures throughout the experiment.

Upon completion of manipulations, current velocity (one 50-s reading, Ott C-2 meter) and water depth were measured. Tiles not selected for chlorophyll *a* sampling were removed from the stream and preserved in Kahle's solution for later analysis. Before placing tiles in the sample bag, tile sides and bottoms were brushed clean of debris and animals using a 4 x 2 cm nylon brush. Tiles (n=129), representing the full range of colonization periods employed, were randomly selected for chlorophyll *a* analysis from each of the three treatments.

From selected tiles (n=129), two 4-cm^2 scrapings, delineated by a flexible plastic template, were removed for chlorophyll *a* analysis. The two samples were combined and filtered using a hand-held vacuum pump onto a single Whatman® GF/C glass-fibre membrane filter. The sample was lightly sprinkled with magnesium carbonate for preservation, and wrapped in aluminum foil. Samples were placed in a sealed plastic bag and placed on ice as completed. Samples were stored frozen in the

laboratory for later analysis. The tiles were placed in Kahle's solution for preservation and later analysis after removing organisms and debris from the bottom and sides of the tiles with a nylon brush.

Laboratory Sample Processing

Sample Sorting and Taxonomic Identification

Samples were sorted and identified with methods identical to those described in Chapter I. The manipulation samples (collected in bags throughout the study) and the tile samples (the organisms on the actual tiles upon removal) were sorted and tabulated separately.

Some samples became dehydrated during storage. These samples were rehydrated by washing the sample with tap water through a 90-μm sieve (to remove preservative), and soaking the sample for 24-48 h (depending on the size of the sample) in a dilute detergent solution (2-4 mL dishwashing detergent in 50 mL tap water). The sample was then rinsed through a 90-μm sieve (to remove the detergent) and heated (medium setting) for approximately 8 h on a hotplate. Occasionally, a longer time period was necessary (12 h; particularly samples with large hydropsychids). For most samples, this method was sufficient to rehydrate most taxa, including black fly larvae. This method worked particularly well for chironomids. Rehydration of chironomid head capsules was necessary for identification to the generic level. Chironomidae were mounted on microscope slides in CMC-9AF® mounting media and identified using the keys of Oliver and Roussel (1983) and Weiderholm (1983).

Measurement of Larval Size

Measurement of black fly larval size was done according to the methods described in Chapter I. Specimens that were distorted by preservative, rehydration, or crushed by tiles were excluded. The data for this aspect of the study will not be discussed in this thesis.

Measurement of Periphyton and Total Detritus

Measurements of total detritus (dry mass) and periphyton (ash-free dry mass; (AFDM)) on tile surfaces were obtained according to the methods described in Chapter I.

Chlorophyll a Analysis

Chlorophyll a concentrations were determined according to the methods of Lorenzen (1967) as modified by Golterman et al. (1978). Due to difficulties encountered during chlorophyll a analyses, accurate results could not be obtained for this parameter. Thus, data from these analyses will not be discussed.

Data Analysis

Organisms collected from manipulations on 28 June 1990, and from the actual tiles removed on 28 June 1990 were combined to form a single sample (hereafter referred to as actual counts) for each tile number. These samples were intended to be combined as they represented portions of the same sample, the manipulation samples representing the taxa removed from the tile to complete the treatment. The data discussed in this chapter represent the visual counts and actual counts from the last day of the study.

All data (biotic and abiotic) were Ln(x+1) transformed. Outliers were removed according to Dixon's test (Dixon and Massey 1957) following adjustment for abiotic factors (see below). Grazing taxa and collector-gatherers were identified according to descriptions by Merritt and Cummins (1984). Dry mass and ash-free dry mass are reported on a whole tile (top surface) basis.

Comparison of Visual Counts and Actual Counts of Taxa

To determine the correspondence between visual counts (from the viewer box) and the actual counts (combined samples of manipulations and

the actual tiles), simple linear regressions (Sokal and Rohlf 1981) were performed on data (numbers per tile) from 28 June 1990 (day of tile removal). Separate analyses were performed for total number of organisms, black flies, and grazer/collectors, for each of the three treatments. Actual counts for total organisms, black flies, and grazer/collectors (Appendix III.1A, III.1B, III.2A, III.2B) were the dependent variable, while the corresponding visual counts (Appendix III.3) were the independent variables. Because correlations were poor, the data discussed in this chapter, and further analyses, represent actual count data rather than visual count data.

Adjustment of Actual Counts for Significant Abiotic Effects

Forward stepwise multiple linear regressions (Sokal and Rohlf 1981) were used to assess potential abiotic effects on black fly larval densities (dependent variable). Analyses were performed on Ln(x+1) transformed data. Independent variables used in the analyses included current velocity and water depth recorded at the time of tile removal (Appendix III.5), (current velocity)^2, Froude number, (Froude number)^2, and the product of current velocity and depth. Separate regressions were performed for each of the 14 time periods (tile placement to removal) represented in the data. Using the regression equations for significant factors (Appendix III.6), adjusted numbers of black flies, grazer/collectors, and total animals were calculated for each time period, using the mean value of the variable significantly affecting numbers of animals. Following adjustment of numbers, outliers were removed according to Dixon's test.

Effects due to Biotic Interactions

Data were plotted to allow direct visual comparisons of black flies and grazer/collectors among treatments 2 and 3. An analysis of covariance (ANCOVA; Sokal and Rohlf 1981) was used on linear portions of

the data (days 15-27) to assess differences between numbers of black flies present on tiles of treatments 2 and 3.

Periphyton and Detrital Accumulation

After removal of outliers by Dixon's test, an analysis of covariance (ANCOVA) was used to assess differences among treatments for dry mass and ash-free dry mass per tile on Ln(x+1) transformed data.

RESULTS

Water Chemistry

Dissolved oxygen concentrations generally exceeded 100% saturation, pH was circumneutral, and conductivity was within typical ranges for this stream (500-700 $\mu S/cm^2$; Table 3.2). Temperature was variable (14-21°C), but within normal spring temperatures for the area. One major rainfall occurred on the evening of 3 June 1990, and water levels increased 15-20 cm, and turbidity also increased considerably, but levels receded within 2-4 days. Rainfall on 22 and 23 June raised water levels again by approximately 5 cm. Lower temperatures during the last week of the study reflected periods of rain and generally overcast conditions. Suspended solid concentrations were low, but consistent with past measurements (0.2 mg/L; Dunnigan 1991), in part reflecting the shaded (canopy cover) conditions of the stream.

Visual Counts Versus Actual Counts

Results of simple linear regressions used to assess correspondence of visual (Appendix III.3) and actual counts (Appendix III.1A, III.1B, III.2A, III.2B) are presented in Table 3.3. Among all treatments and for all taxonomic groups, coefficients of determination were relatively low between actual counts and visual counts. The correspondence between actual counts and visual counts was greatest for black fly larvae (Fig. 3.4) in treatments 1 and 2 (Treatment 1, R^2=0.44; Treatment 2, R^2=0.66), but low for Treatment 3, R^2=0.09). Correspondence for grazer/collector taxa was less than that for black flies (Treatment 1, R^2=0.19; Treatment 3 (R^2=0.22), except for Treatment 2 (R^2=0.44). Similarly, visual and actual counts showed weak correspondence for the total number of individuals per tile (Treatment 1, R^2=0.21; Treatment 2, R^2=0.25; Treatment 3, R^2=0.24). Although visual counts tended to underestimate black fly abundance, correspondence of counts from the two methods was acceptable for this animal, and the method of viewer box counts shows potential for future black fly studies, pending some modification. In

Table 3.2 Water chemistry parameters measured during the colonization experiment conducted 1 - 28 June 1990 in Hobbs-Mackenzie Creek. Dash (--) indicates missing data.

CALENDAR DATE	CONDUCTIVITY ($\mu S/cm^2$)	DISSOLVED OXYGEN (mg/L)	WATER TEMP. (°C)	AIR TEMP. (°C)	pH	SUSPENDED SOLIDS (mg/L)
June 1	550	9	14	25	7.0	0.334
June 2	600	9	19	25	7.3	0.343
June 3	510	9	16	16	7.2	0.336
June 4	510	9	11	17	6.5	0.431
June 5	540	10	14	17	7.0	0.363
June 6	525	10	17	--	7.0	0.359
June 7	600	9	17	20	7.0	0.352
June 9	690	8	21	25	7.0	0.376
June 10	550	7	14	--	7.0	0.371
June 11	530	9	18	20	7.0	0.381
June 13	580	9	21	28	7.0	0.338
June 16	650	15	20	25	7.0	0.344
June 18	600	10	22	27	7.0	0.335
June 20	510	8	16	--	7.0	0.338
June 22	550	10	18.5	--	7.0	0.342
June 23	590	9	16	17	7.2	0.346
June 24	680	6	15	12.5	7.0	0.337
June 25	620	6	19	19	7.2	0.340
June 26	500	9	20	19	7.0	0.336
June 27	600	11	17	15	7.0	0.336
June 28	550	10	19	15	7.0	0.340

Table 3.3 Simple linear regressions assessing the correspondence between actual counts (dependent variable) and visual counts (independent variable). Separate analyses were performed for black flies, grazer/collectors, and total individuals collected per tile, for each of the 3 treatments, prior to removal of outliers. Treatment 1 = no removal; Treatment 2 = black fly removal; Treatment 3 = removal of all taxa. Standard error is abbreviated by S.E.

Group	Treatment	Sample Size	Y-Intercept (1 S.E.)	Slope (1 S.E.)	R^2
Black Flies	1	75	3.288 0.899	0.487 0.064	0.44
Grazer/collectors	1	75	13.181 3.374	2.717 0.662	0.19
Total Individuals	1	75	43.534 8.729	2.164 0.488	0.21
Black Flies	2	76	1.458 0.386	0.781 0.065	0.66
Grazer/collectors	2	76	13.163 2.375	4.161 0.546	0.44
Total Individuals	2	76	45.733 7.273	3.905 0.792	0.25
Black Flies	3	76	3.489 0.831	0.551 0.204	0.09
Grazer/collectors	3	76	13.665 2.339	2.253 0.505	0.22
Total Individuals	3	76	37.892 7.252	4.280 0.881	0.24

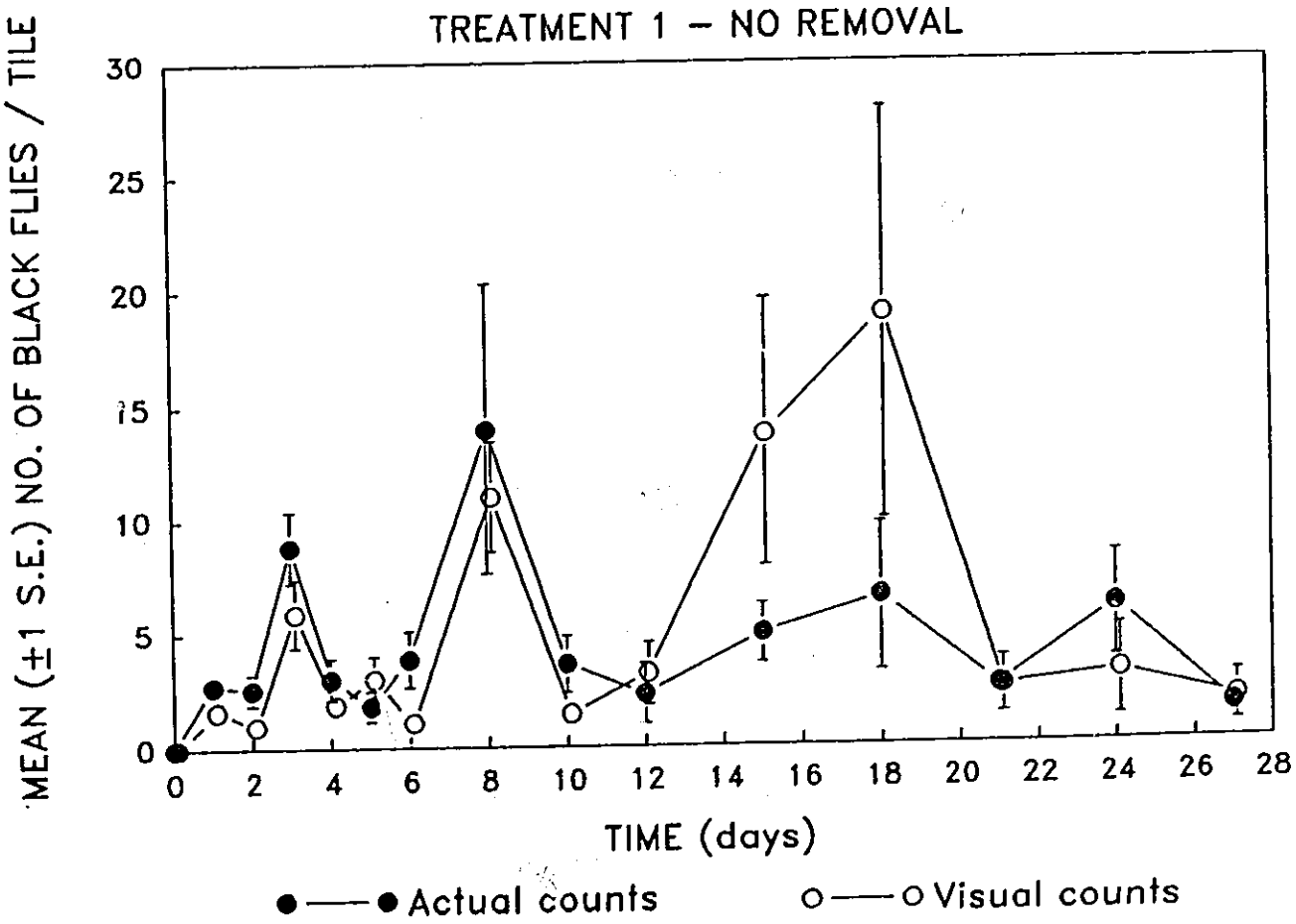


Figure 3.4 Comparison of visual counts and actual counts for black flies (n=75 tiles).

general, underestimation was greater for grazer/collectors and total individuals than for black flies. The major cause of underestimation was the presence of very small chironomids, which dominated the numbers of grazer/collectors, but were not always visible on tile surfaces, especially on those tiles with well-developed periphytic growth.

Taxonomic Richness

A total of 35 taxa were collected from Treatment 1 tiles, but many occurred in very low abundances (Appendix III.1A, III.1B, III.2A, III.2B, III.7). Eight dominant taxa (see "Taxonomic Composition" below) appeared on tiles within 24 h, and taxonomic richness remained relatively constant throughout the duration of the study (Fig. 3.5). These eight abundant taxa together accounted for more than half of the total taxonomic richness on tiles for the first five days, after which their proportion of the overall taxonomic richness decreased to approximately 50%.

Newly recorded taxa (cumulative number) showed a steady increase through time, and the total number had not stabilized by 28 days. However, relatively few new taxa were recorded on the older tiles (one new taxon per 3-day period after 18 days; Appendix III.7), and these taxa contributed few individuals to total abundances.

Taxonomic Composition

A total of 3,571 individuals representing 35 taxa was collected from Treatment 1 tiles (Appendix III.1A, III.1B, III.2A, III.2B). Chironomidae were the most abundant group collected, accounting for 44.9% of all individuals.

Eight taxa, each comprising at least 1% of the total number of individuals collected, were designated as dominant taxa (Table 3.4). Five of the dominant taxa were grazer/collector animals (the chironomid

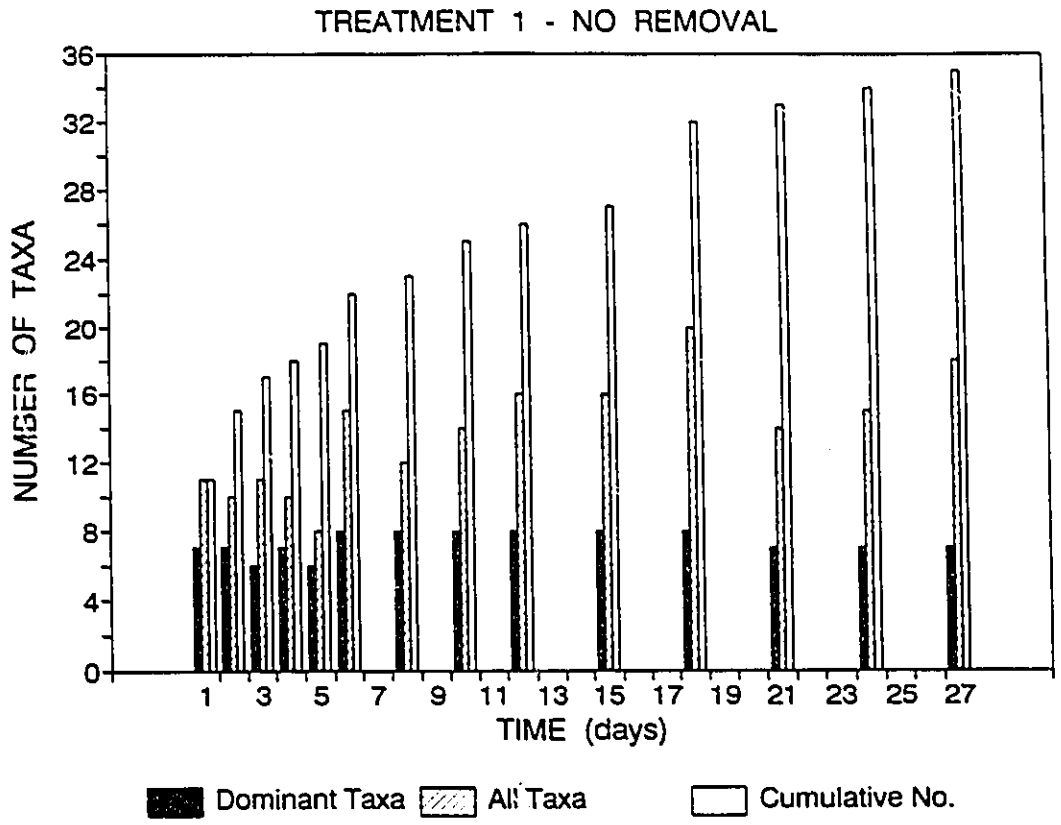


Figure 3.5 Taxonomic richness for NR treatment (Treatment 1) tiles, showing accumulation of the dominant taxa present, all taxa present, and cumulative total of taxa recorded with time (n=75 tiles).

Table 3.4 Dominant taxa collected during the colonization experiment in Hobbs-Mackenzie Creek, 1 - 28 June 1990. The taxa listed represent at least 1% each of the total number of animals collected in Treatment 1. Note that immature chironomids, in parentheses, were not considered as a taxonomic group, but were included in the total number of animals collected (n=200 tiles).

TAXON	NO. INDIVIDUALS	PERCENT OF TOTAL ANIMALS
Eukiefferiella spp.	1034	29.0
Hydropsyche spp.	883	24.7
S. vittatum	530	14.8
Asellus	308	8.6
Thienemanniella spp.	245	6.9
Baetis flavistriga	139	3.9
Cricotopus spp.	97	2.7
(Immature Chironomidae)	(91)	(2.6)
Tvetenia spp.	37	1.0

genera Eukiefferiella, Thienemanniella, Cricotopus, and Tvetenia, and the mayfly Baetis flavistriga McDunnough). Other grazing taxa, whose individual abundances were too low to qualify as 'dominant', included the tipulid larva Antocha, the snail Physa, the caddisfly Hydroptila, and many chironomid genera (Appendix III.1A, III.1B, III.2A, III.2B).

The isopod, Asellus, a detritivore, was frequently observed. Its importance on the upper tile surface, however, was probably overestimated because Asellus on the underside of tiles tended to drift into the net during tile manipulation.

Two suspension-feeders were abundant also; S. vittatum (14.8% of total animals) and the hydropsychid caddisfly Hydropsyche spp. (24.7%). Simulium vittatum was the third most abundant taxon in this study. Suspension-feeders (S. vittatum, Hydropsyche spp., Rheocricotopus spp.) comprised 39.7% of the total number of animals collected on Treatment 1 tiles.

Although immature chironomids comprised 2.6% of all individuals collected, they were excluded from analyses as a taxonomic group because these early instars could not be identified to the generic level.

Objective 1: Temporal Pattern

The theoretical pattern for black flies, given constant environmental conditions and absence of biotic interactions, predicted eventual equilibrium subsequent to the initial colonization phase (Fig. 3.1; H_0). My expectations also included a reduction in numbers with time following this period of relatively constant numbers (Fig. 3.1; H_1).

The pattern of colonization (number of animals) for all taxa was obtained from Treatment 1 (no removal of any taxon; Appendix III.1A,

III.1B, III.2A, III.2B). In general, variation among tiles on specific days was high (Fig. 3.6). Heavy rainfall on the evening of 3 June reduced black fly numbers, but recovery was rapid (two days). Other taxa did not show any noticeable effect.

Simuliids

Black flies colonized rapidly. Numbers on tiles aged 24 h to 12 d fluctuated somewhat, but were relatively constant with respect to tile age; numbers on tiles 15 days old or older tended to decline (Fig. 3.6). Stepwise polynomial regression of black fly density against time indicated that the pattern of abundance was better explained by a quadratic function than by a linear function (Table 3.5, $p<0.001$). Thus, black fly densities in Treatment 1 became significantly reduced on the oldest tiles. This result supported the pattern predicted for black flies in Objective 1: rapid colonization (because simuliids tend to be opportunists; Downes and Lake 1991), constancy (due to a balance between immigration and emigration; Sheldon 1984), and decline (due to periphyton growth, detritus accrual, and/or biotic interactions assessed by larvae as a reduction in tile quality) in black fly densities, through time.

Grazer/collectors and Total Animals

Because grazer and collector-gatherer taxa comprised the majority of animals, and could potentially affect the number of black flies present by reducing the organic material accumulating on the substrate (see below, 'substrate quality'), these taxa were also considered as a group.

Grazing taxa and collector-gatherers comprised the largest proportion of individuals (46.3%) on tiles. Grazer/collectors gradually reached a relatively constant density by day 10, and appeared to increase in abundance near the end of the study (Fig. 3.6). There was

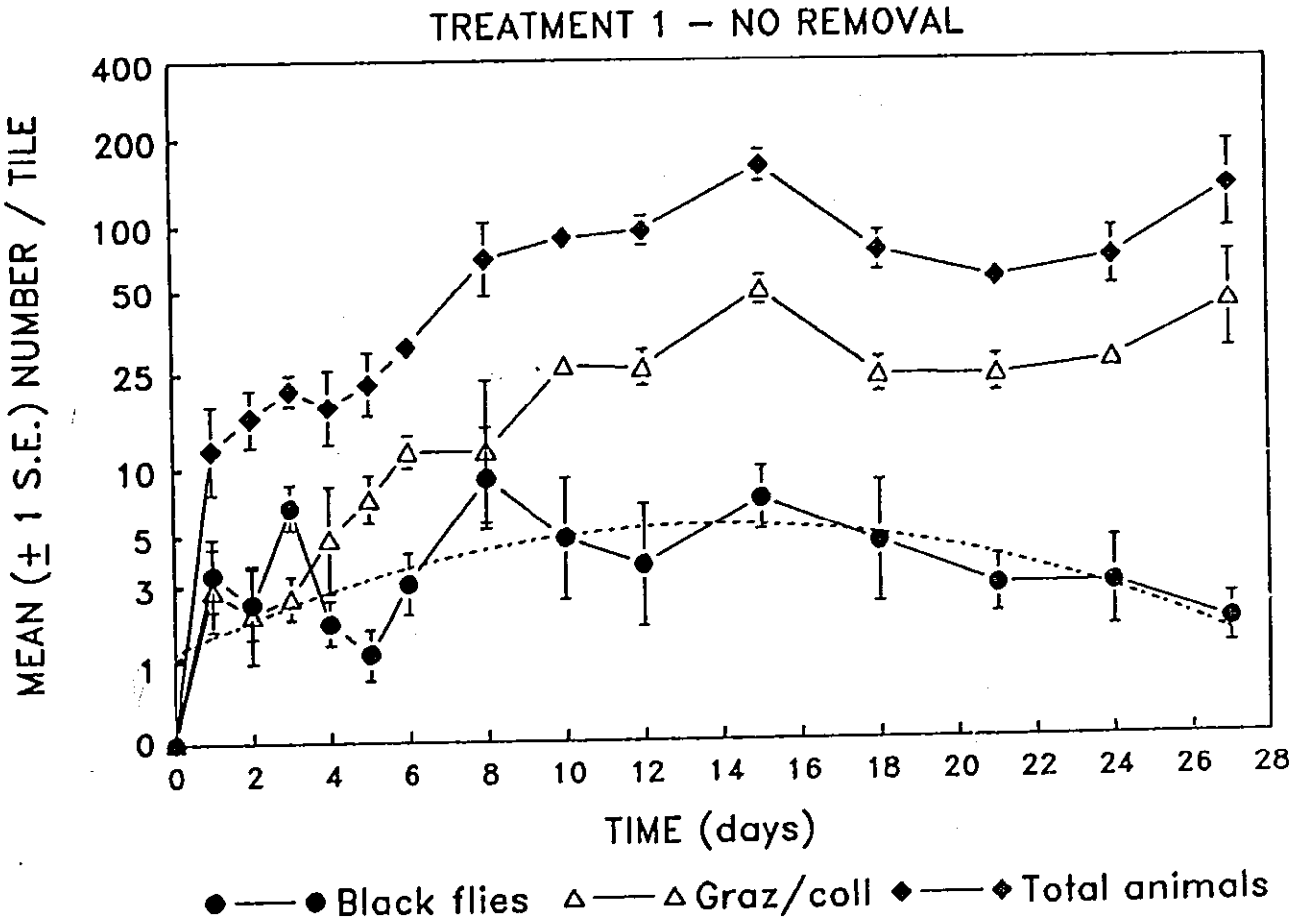


Figure 3.6 Temporal patterns of black flies (n=74 tiles), grazer/collectors (n=74 tiles), and all individuals (n=74 tiles) with time. Grazer/collectors and total animals increased throughout the experiment. Black flies colonized rapidly, numbers on tiles became relatively constant, and subsequently declined. Equation of the curve is $Ln(y+1) = 0.815 + 0.166x - 0.006x^2$, as determined by forward stepwise multiple linear regression (Table 3.5). (Graz/coll = grazer/collectors).

Table 3.5 Summary of the regression coefficients and coefficients of determination (R^2) from a forward stepwise multiple linear regression for black flies from Treatment 1 (no removal) assessing the effect of time (n=75 tiles).

FACTOR	REGRESSION COEFFICIENT	S.E.	R^2
Intercept	0.815		
Time (Days)	0.166***	0.043	0.02
$(Time)^2$	0.006***	0.002	0.14
Total			0.16

*** $p<0.001$

no indication of decline in grazer/collector abundance on tiles that had been in place for the longest period of time, although the rate of immigration had decreased substantially.

The temporal pattern in total number of animals on tiles appeared to reflect that of grazers and collector-gatherers (Fig. 3.6). The initial increase was comprised primarily of grazer/collector taxa and detritivores, since black fly numbers were generally low, and predatory taxa were few (8 taxa) and relatively rare (1.8% of total numbers).

Organic Material

Amounts of periphyton (AFDM; Fig. 3.7) and total detritus (dry mass; Fig. 3.8) increased exponentially as a function of time on Treatment 1 tiles (Appendix III.5). Replicated least squares regression yielded a linear relationship with respect to tile age when periphyton and total detritus were Ln(x+1) transformed (AFDM, Table 3.6, R^2=0.68, $p<0.001$; dry mass, Table 3.7, R^2=0.65, $p<0.001$)

Objective 2: Substrate Quality

Objective 2 addressed change in substrate quality over time, and its potential effect on black fly colonization. Since Treatment 3 tiles had all taxa repeatedly removed, this effect could be assessed using this treatment, without the interference of potential biotic interactions. If accumulating debris has no negative effect, then black fly numbers colonizing per day should be equivalent on tiles of all ages (Fig. 3.2; H_0). If periphyton or detritus inhibit colonization, then fewer black flies should occur on older tiles. I predicted that a decline in black fly numbers (colonizing over 24 h) would occur on tiles of increasing age due to the development of periphyton and/or accumulation of detritus (Fig. 3.2; H_1).

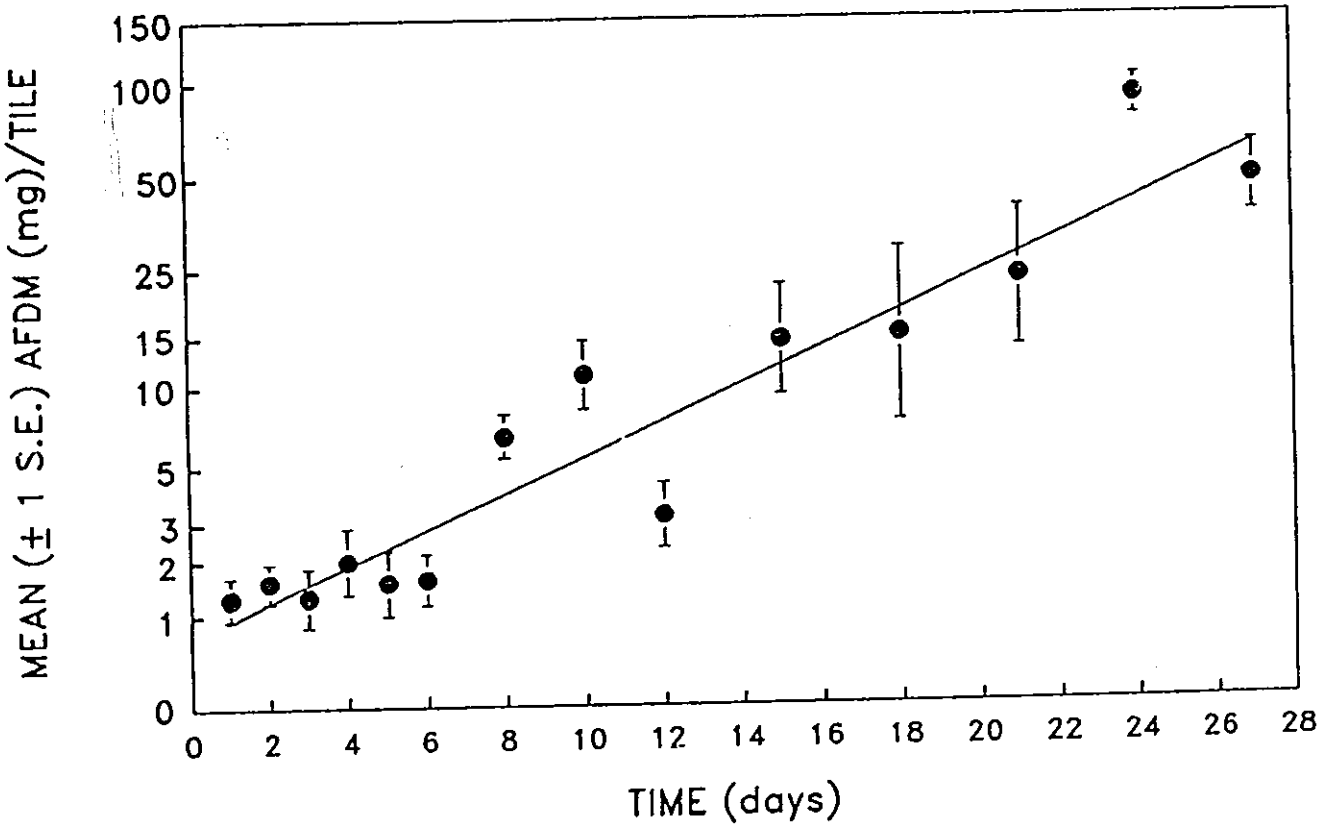


Figure 3.7 Temporal pattern of periphyton (measured as AFDM mg/tile) accumulation (n=68 tiles). Growth was exponential. The curve represents least squares regression: ($Ln(y+1) = 0.131x + 0.528$; $R^2=0.68$). Note log scale on y-axis.

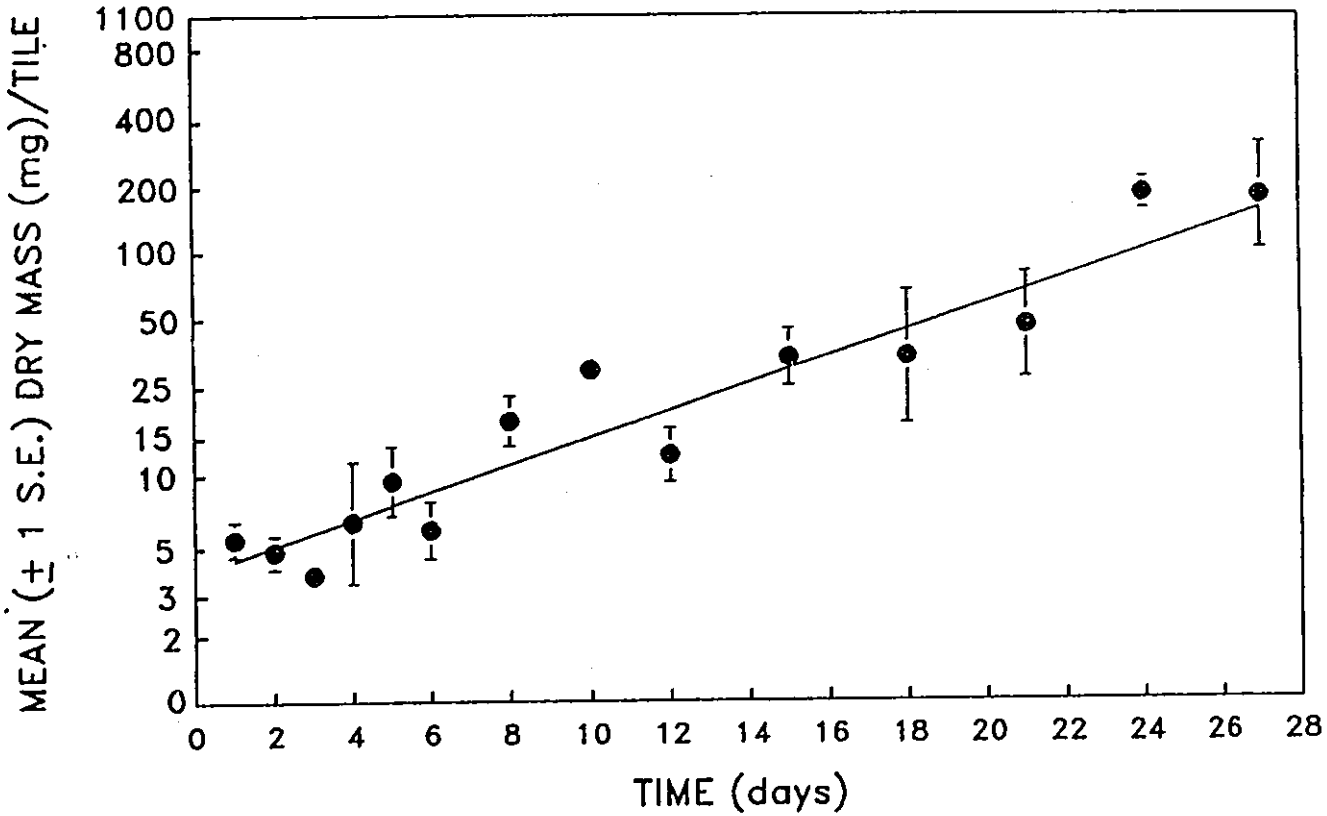


Figure 3.8 Temporal pattern of total detritus (measured as dry mass mg/tile) accumulation (n=68 tiles). Accumulation was exponential. The curve represents least squares regression: (Ln(y+1) = 0.137x + 1.312; R^2=0.65). Note log scale on y-axis.

Table 3.6 Summary of replicated least squares regression for periphyton (AFDM) against time for Treatment 1. A linear relationship between periphyton and time occurred on Ln(x+1) transformed data (n=68 tiles), given by the equation Ln(y+1) = 0.131x + 0.528 (R^2=0.68).

SOURCE OF VARIATION	DF	SUM OF SQUARES	MEAN SQUARE	F	p
Among	13	82.649	6.358	13.08	
Regression	1	74.292	74.292	106.68	p<0.001
Deviation	12	8.357	0.696	1.43	
Within	54	26.245	0.486		
Total	67	108.894	0.697		

Table 3.7 Summary of replicated least squares regression for detritus (dry mass) against time for Treatment 1. A linear relationship between dry mass and time occurred on Ln(x+1) transformed data (n=68 tiles), given by the equation Ln(y+1) = 0.137x + 1.312 (R^2=0.65).

SOURCE OF VARIATION	DF	SUM OF SQUARES	MEAN SQUARE	F	p
Among	13	90.727	6.979	10.57	
Regression	1	82.274	82.274	116.80	p<0.001
Deviation	12	8.453	0.704	1.07	
Within	54	35.654	0.660		
Total	67	126.381	0.813		

Simuliids

Twenty-four h black fly accrual was clearly lower on the oldest tiles (18-27 d) than on younger tiles (1-15 d). The shape of the regression curve (Appendix III.8) for Treatment 3 (Fig. 3.9) was consistent with the hypothesis that tile surface quality declined with tile age. Replicated least squares regression (using data for tiles aged 15-27) showed a significant decrease in the number of black flies arriving to older tiles (Table 3.8, R^2=0.42, $p<0.005$). The tile age over which accrual of black flies declined (12 days and older) corresponded to the age at which greatest periphyton and total detritus accumulation occurred (Fig. 3.10, Fig. 3.11).

Periphyton and Total Detritus

Periphyton biomass (measured as AFDM) and total detritus (dry mass) increased exponentially as a function of tile age for all treatments (Fig. 3.10, Fig. 3.11, respectively). Replicated least squares regression yielded linear functions for periphyton and detritus against tile age for all treatments, on Ln(x+1) transformed data (Table 3.6, Table 3.7, Appendix III.9). Rate of periphyton accrual did not differ significantly among treatments (Fig. 3.10, Table 3.9; ANCOVA, slopes, $p>0.05$). However, periphyton biomass varied significantly among treatments (Table 3.9; ANCOVA, intercepts differ, $p<0.001$; NR > RBF > RALL). Similarly, the rate of detrital accumulation was not significantly different among treatments (Fig. 3.11, Table 3.10; ANCOVA, slopes, $p>0.05$), but biomass was (Table 3.10; ANCOVA, intercepts differ, $p<0.001$; NR > RBF > RALL). In all cases, no removal (Treatment 1) tiles contained more periphyton and detritus than tiles of equivalent age from which black flies (Treatment 2) or all animals (Treatment 3) were removed.

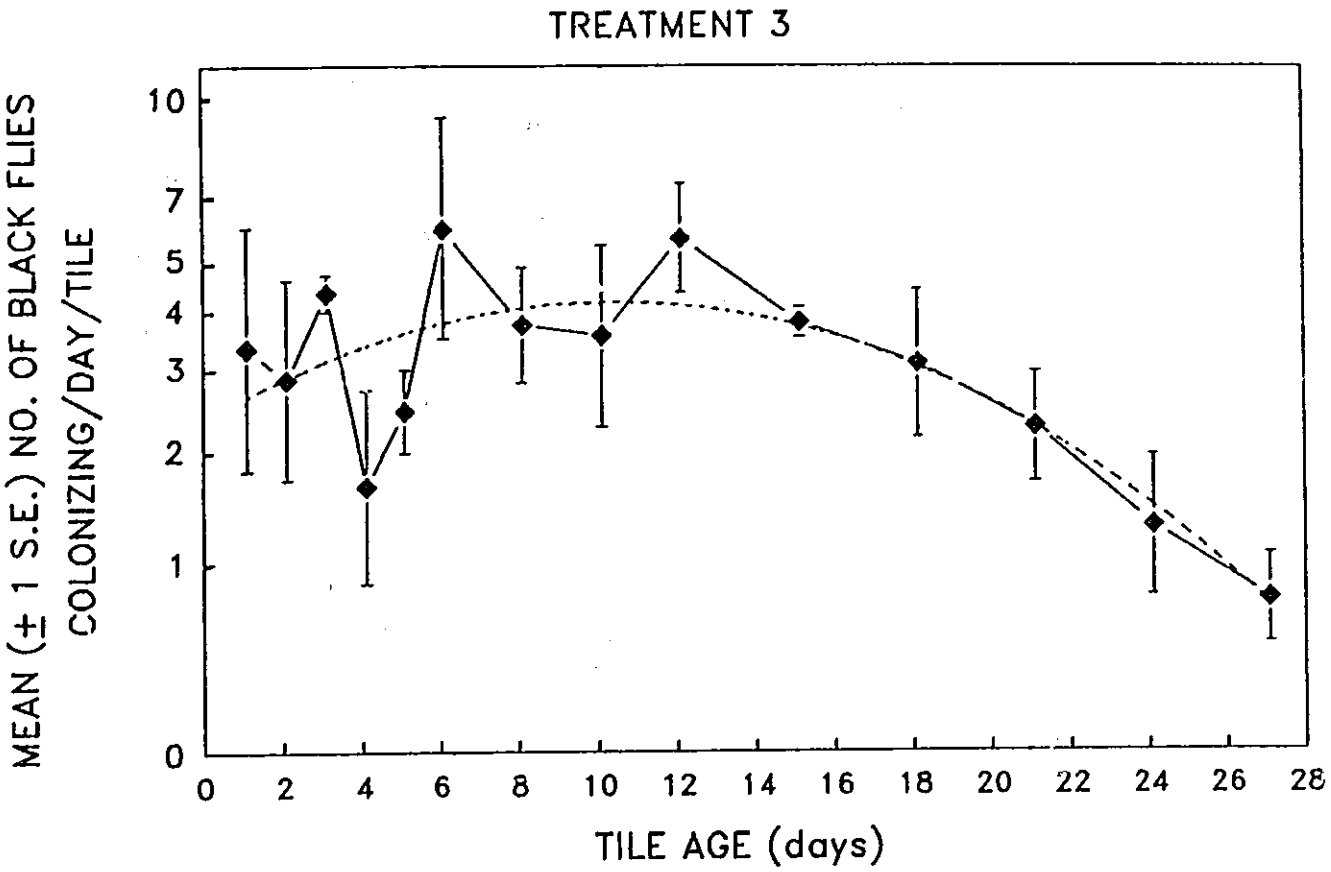


Figure 3.9 Black fly colonization over 24 h on Treatment 3 tiles of different age (n=74 tiles). Equation of the curve is $Ln(y+1) = 1.225 + 0.082x - 0.004x^2$ as determined by forward stepwise multiple linear regression (Appendix III.8).

Table 3.8 Summary of replicated least squares regression for number of black flies colonizing per tile (over 24 h) against tile age for Treatment 3 (n=23 tiles; R^2=0.42). Note that analysis was performed on tiles aged 15-27 days.

SOURCE OF VARIATION	DF	SUM OF SQUARES	MEAN SQUARE	F	P
Among	4	2.807	0.702	3.33	
Regression	1	2.741	2.741	125.30	p<0.005
Deviation	3	0.066	0.022	0.104	
Within	18	3.788	0.210		
Total	22	6.595	0.459		

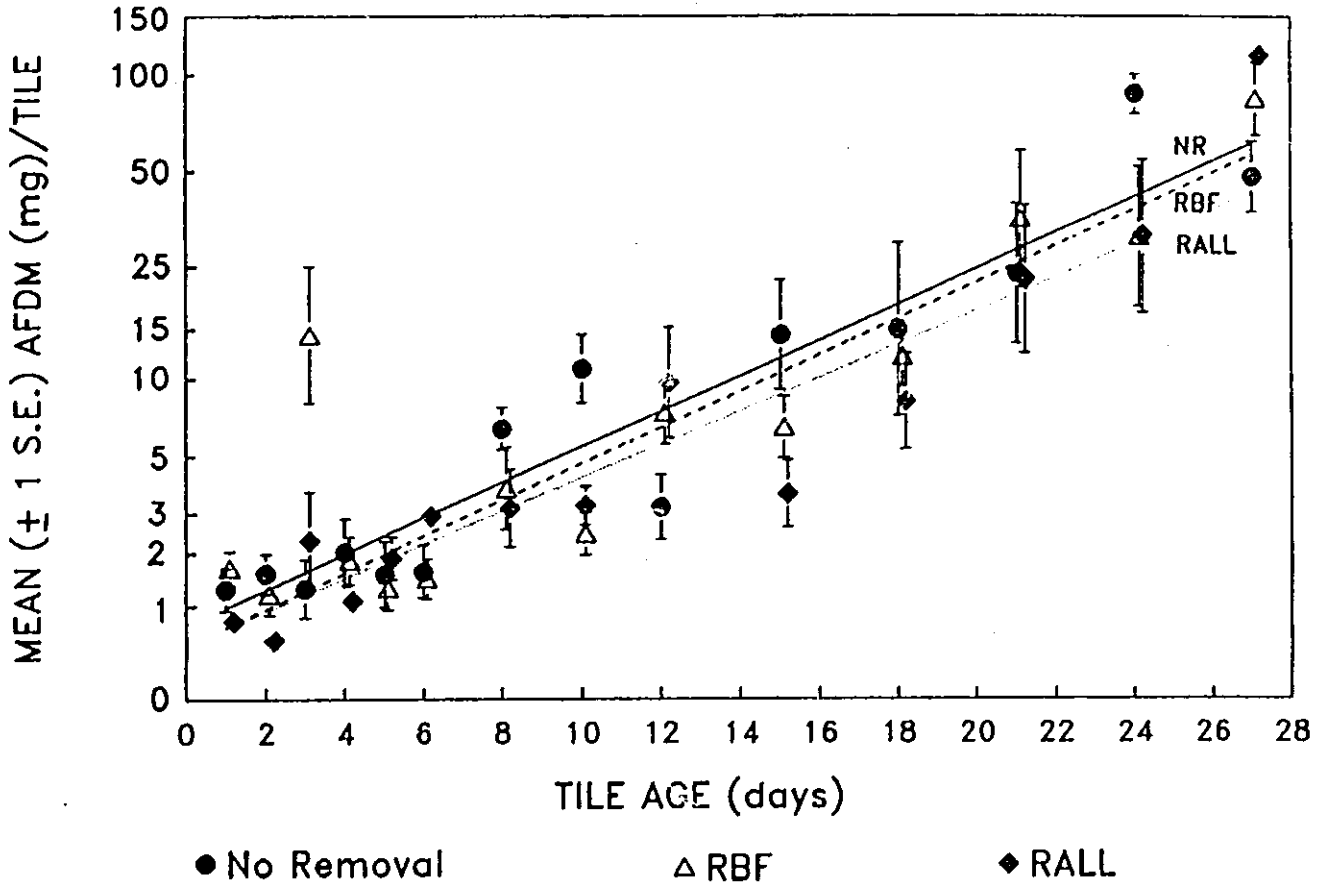


Figure 3.10 Periphyton growth over 28 days for all treatments. Curves represent least squares regression (NR: $Ln(y+1) = 0.131x + 0.528$, $R^2=0.68$, n=68 tiles; RBF: $Ln(y+1) = 0.133x + 0.386$, $R^2=0.74$, n=69 tiles; RALL: $Ln(y+1) = 0.124x + 0.384$, $R^2=0.63$, n=70 tiles). There were no significant differences in rate of growth (Ancova, slopes, $p>0.05$), although differences in biomass occurred among treatments (Ancova, intercepts, $p<0.001$).

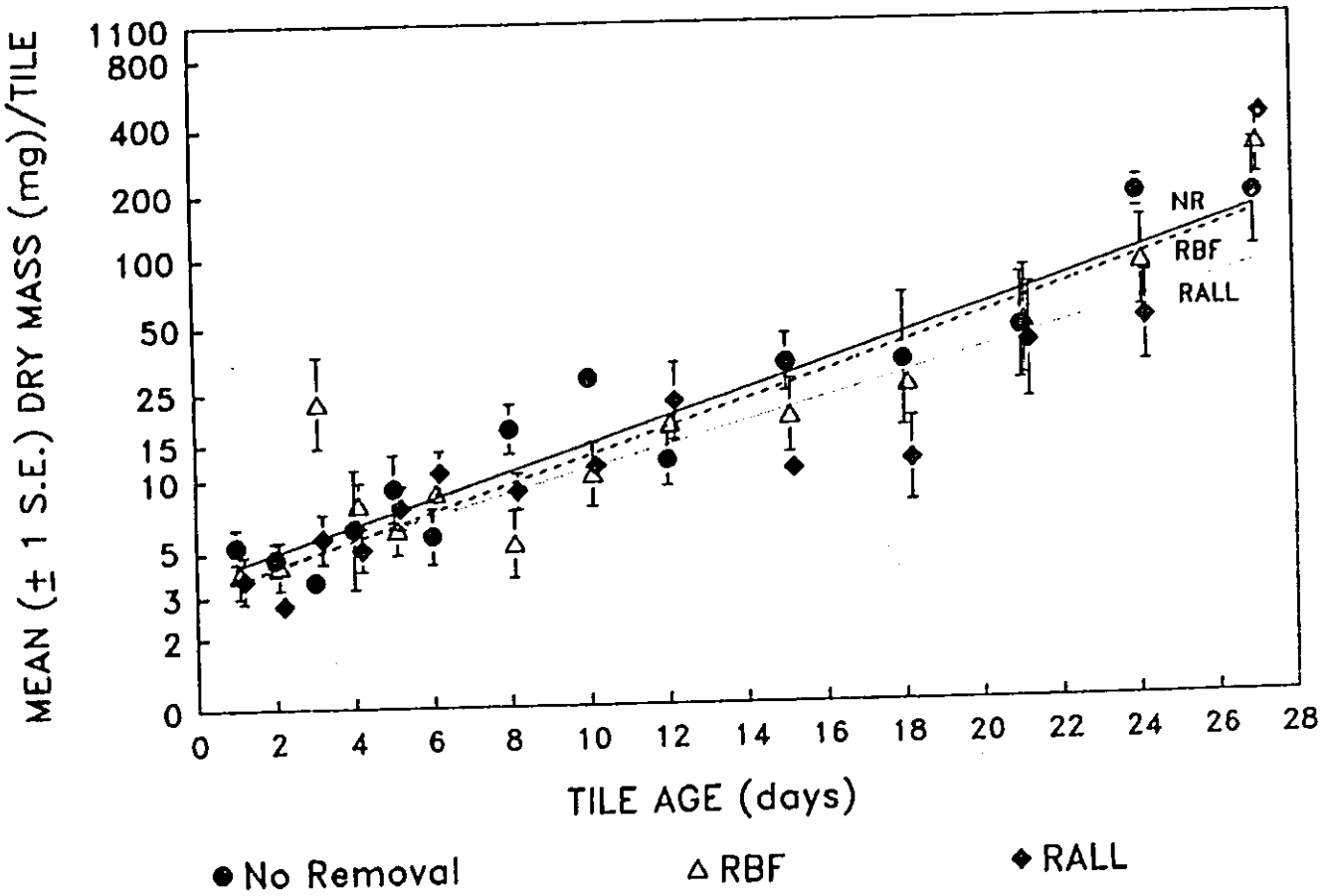


Figure 3.11 Accumulation of total detritus over 28 days for all treatments. Curves represent least squares regression (NR: $Ln(y+1) = 0.137x + 1.312$, $R^2=0.65$, n=68 tiles; RBF: $Ln(y+1) = 0.141x + 1.147$, $R^2=0.74$, n=64 tiles; RALL: $Ln(y+1) = 0.118x + 1.240$, $R^2=0.59$, n=68 tiles). Rate of accumulation did not differ significantly among treatments (Ancova, slopes, $p>0.05$), but biomass did (Ancova, intercepts, $p<0.001$).

Table 3.9 Summary of analysis of covariance (ANCOVA) for periphyton (AFDM) on tiles of different ages for all treatments (n=68, 69, 70 tiles for NR, RBF, RALL, respectively). Growth was not significantly different among treatments, but biomass was.

SOURCE OF VARIATION	DF	SUM OF SQUARES	MEAN SQUARE	F	p
SLOPES					
Among	2	0.247	0.124	0.181	p>0.05
Deviation	36	24.548	0.682		
INTERCEPTS					
Among	2	83.801	41.901	64.214	p<0.001
Deviation	38	24.795	0.652		

Table 3.10 Summary of analysis of covariance (ANCOVA) for detritus (dry mass) on tiles of different ages for all treatments (n=68, 64, 68 tiles for NR, RBF, RALL, respectively). Growth was not significantly different among treatments, but biomass was.

SOURCE OF VARIATION	DF	SUM OF SQUARES	MEAN SQUARE	F	p
SLOPES					
Among	2	1.169	0.585	0.713	p>0.05
Deviation	36	29.529	0.820		
INTERCEPTS					
Among	2	96.759	48.379	59.889	p<0.001
Deviation	38	30.698	0.808		

Objective 3: Potential Effect of Biotic Interactions

I endeavoured to test two hypotheses concerning the potential effects of biotic interactions on black fly colonization. According to the null hypothesis (Fig. 3.3 A; H_0), equal numbers of larvae colonizing over 24 h on Treatment 2 tiles (black fly removal) and Treatment 3 tiles (all animals removed) of all ages were expected if biotic interactions did not hinder black fly colonization. Alternatively, if interspecific competition was important, more black fly larvae were expected to accrue on Treatment 3 tiles, from which all taxa were removed, than on Treatment 2 tiles, from which only black flies were removed (Fig. 3.3 B; H_1).

Simuliids

Twenty-four h accrual of black flies on Treatment 2 tiles was more variable with respect to tile age than on Treatment 3 tiles (Fig. 3.12). Numbers of black flies fluctuated apparently without pattern (neither linear nor curvilinear models explained the observed overall pattern) on Treatment 2 tiles of all ages, and variation was high among replicates. As outlined above, numbers of black flies exhibited a curvilinear decline with increasing tile age on Treatment 3 tiles.

On very young tiles (1-2 days old), densities were equivalent between Treatments 2 and 3. Numbers were relatively constant on Treatment 3 tiles of 4-14 days of age. More black flies generally occurred on these tiles than on Treatment 2 tiles of the same age (Fig. 3.12). However, 24-h accrual of black flies on 15-day-old tiles was equivalent for treatments 2 and 3. There was a reversal of relative abundances of larvae on tiles of different treatments that were older than 12 days. Larval accrual declined significantly on Treatment 3 tiles aged 15 days and older (Table 3.8, $R^2=0.42$, $p<0.005$), and the slopes of regression lines for days 15-27 for treatments 2 and 3 were significantly different (Table 3.11; ANCOVA, slopes, $p<0.05$). In

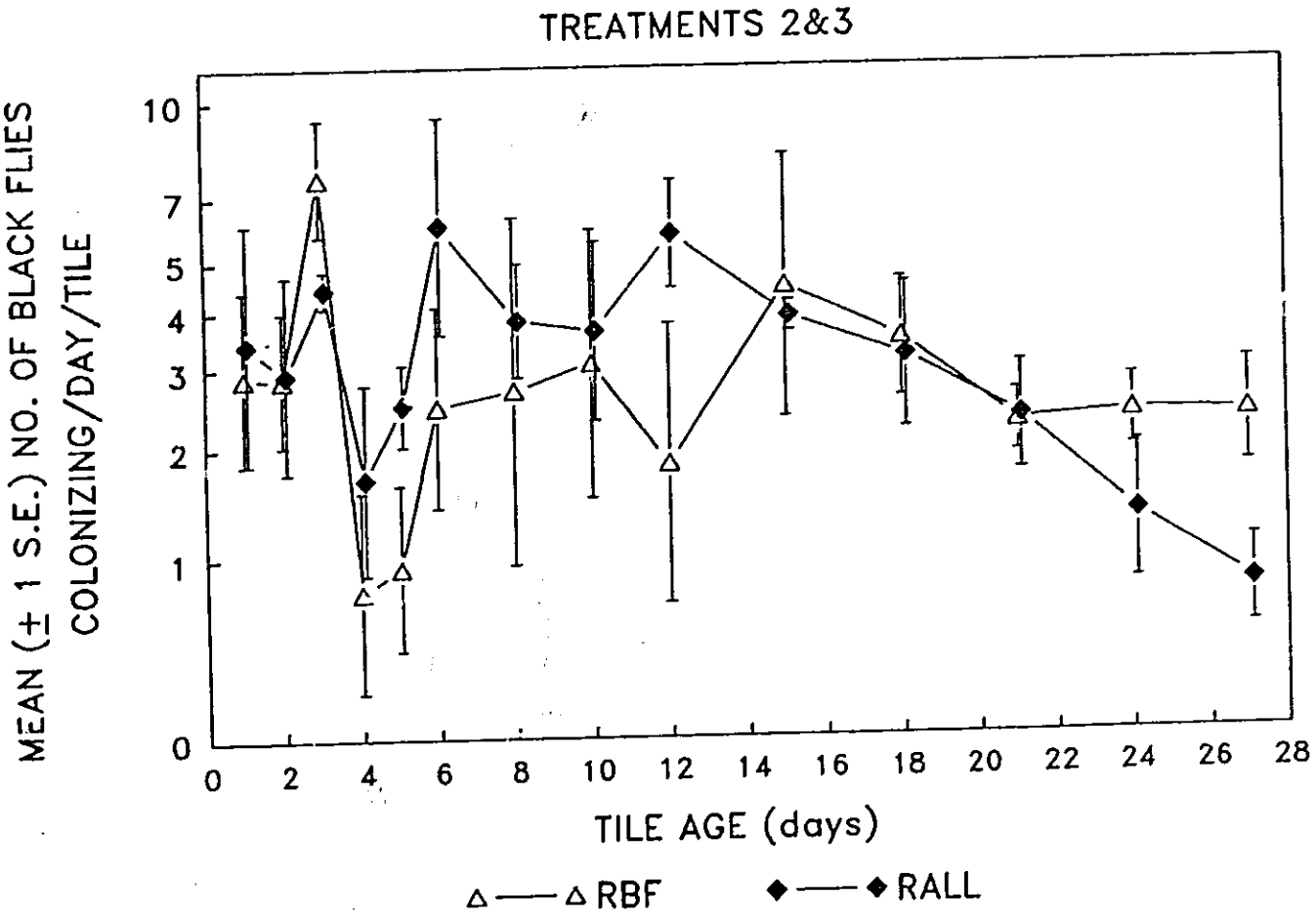


Figure 3.12 One-day immigration of black fly larvae to tiles of different age, in the presence (RBF; n=75 tiles) and absence (RALL; n=74 tiles) of potential competitors. Fewer black flies occurred on 4-12 day old RBF tiles than RALL tiles, consistent with predictions (interference). However, more black flies occurred on RALL tiles aged 24-27 days than RBF tiles, contrary to predictions.

Table 3.11 Summary of analysis of covariance (ANCOVA) for the number of black flies colonizing Treatment 2 (RBF; n=27) and Treatment 3 (RALL; n=23) tiles of different age over 24 h. Note that analysis was performed on tiles aged 15-27 days. On older tiles (24 days or more) of equivalent age, significantly more black flies immigrated to RBF tiles than RALL tiles, contrary to prediction. Rates of accrual (slope) differed significantly between treatments.

SOURCE OF VARIATION	DF	SUM OF SQUARES	MEAN SQUARE	F	p
SLOPES					
Among	1	0.429	0.429	7.422	$p<0.05$
Deviation	6	0.346	0.058		
INTERCEPTS					
Among	1	22.152	22.152	200.098	$p<0.001$
Deviation	7	0.775	0.111		

addition, numbers of black flies were generally lower on Treatment 3 tiles aged 15 days or older (Table 3.11; ANCOVA, intercepts, $p<0.001$).

Until 12 days of tile age, Treatment 2 tiles had fewer larvae than Treatment 3 tiles, as would be expected if interspecific competitors inhibit black fly colonization. Thus, the observed pattern was consistent with my hypothesis of interference for the first half of the study period (1-12 days). On tiles aged 15-21 days, tiles from treatments 2 and 3 supported relatively equal numbers of black flies. However, treatments 2 and 3 diverged at 24 days of age, and numbers reversed. On tiles aged 24 days and older, more larvae occupied Treatment 2 tiles, which supported other taxa (primarily grazer/collectors), than Treatment 3 tiles, on which densities of other taxa had been reduced. This result is inconsistent with both the null and alternative hypotheses: the null hypothesis (Fig. 3.3 A; H_0) predicted equivalent numbers on tiles of both treatments in the absence of interference to black flies by other taxa, whereas the alternative hypothesis (Fig. 3.3 B; H_1) predicted fewer larvae on Treatment 2 tiles relative to Treatment 3 tiles, due to interference. This outcome suggests that on older tiles, larval simuliid immigration to areas already partially colonized by other taxa was not adversely affected by those taxa.

Grazer/collectors

Numbers of individuals of grazer/collectors gradually increased with increasing tile age (Fig. 3.13) in both treatments 2 and 3, and appeared to reach a plateau on 12 day old tiles. On tiles older than 12 days, the relative abundances of grazer/collectors on tiles of different treatments reversed. Since grazer/collectors were not removed from Treatment 2 tiles, one would expect these tiles to have greater abundances of grazer/collectors than Treatment 3 tiles from which

grazer/collectors (as one component of the total taxa) had been removed throughout the study.

Figure 3.13 also illustrates the effectiveness of the removals on non-black fly taxa. Although Treatment 3 tiles involved complete removal of all taxa, and Treatment 2 tiles did not, not all taxa were removed effectively. Treatment 3 tiles had fewer grazer/collectors present than Treatment 2 tiles, but the difference was not as great as anticipated. Complete removal of all individuals was probably not achieved (due to limitations in the visibility of some taxa, largely grazer/collector-gatherers), as also shown by the visual counts, which generally underestimated actual numbers of animals present on tiles. This would contribute to a lack of stronger treatment effects (differences in non-simuliid abundance between treatments 2 and 3).

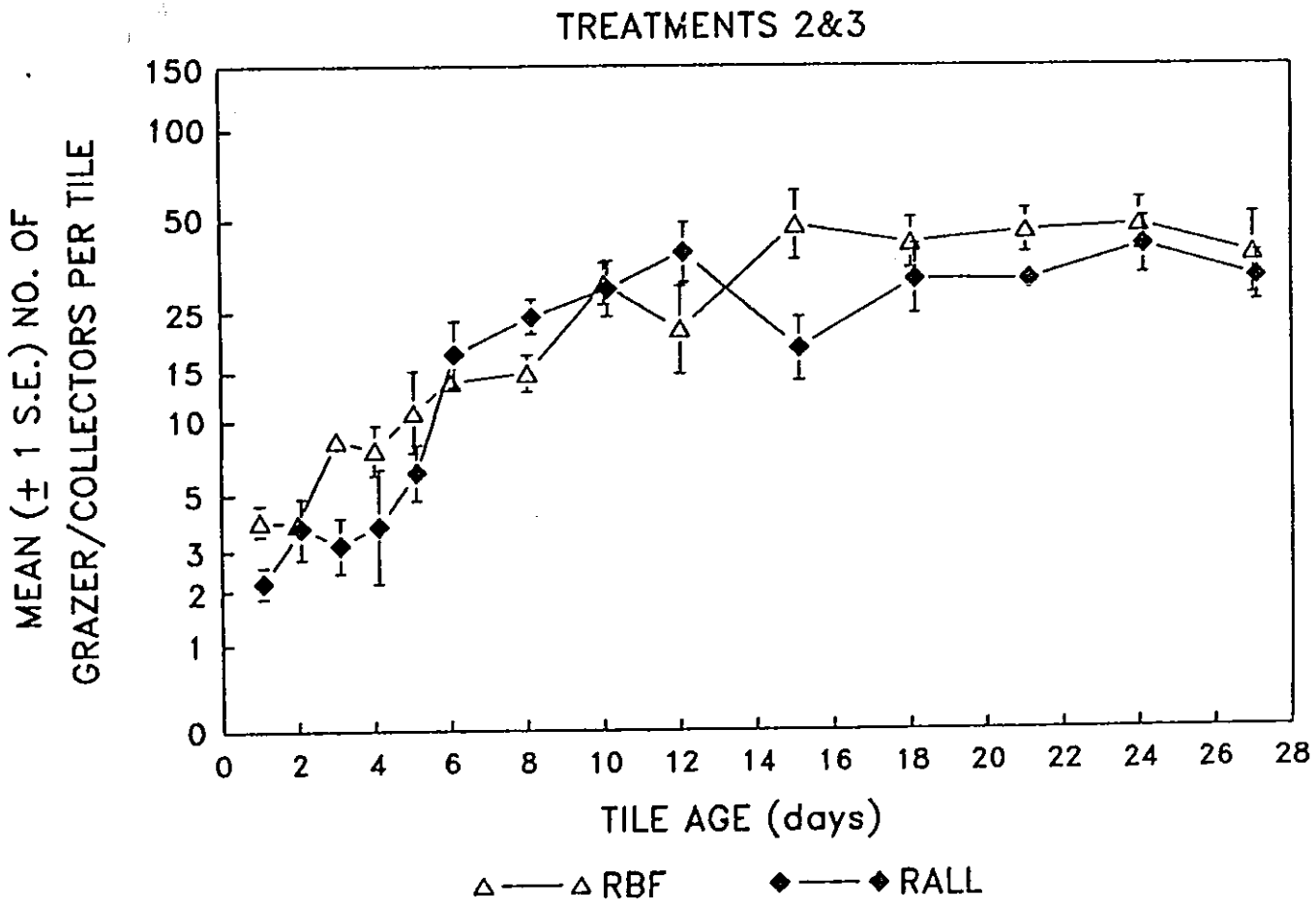


Figure 3.13 Immigration of grazer/collectors to RBF (n=74) and RALL (n=76) tiles of different age. More grazer/collectors occurred on RBF than RALL tiles. Numbers of grazer/collectors were depressed by removals, but effectiveness of removals was lower than anticipated.

DISCUSSION

Comparison of Enumeration Methodologies

Generally, visual counts were found to misrepresent the number of individuals on tiles. However, black fly larvae were relatively sessile and sufficiently visible against tile surfaces for enumeration using this method. Of the taxa enumerated, actual numbers of black flies were best represented by estimates using the viewer box, especially on young (1-12 day old) tiles. As time progressed, it became increasingly difficult to distinguish between early and middle instar larvae and strands of algae. Small larvae were generally difficult to see and tended to release from the substrate upon tile movement as opposed to larger larvae that were less likely to release from the substrate (they tended to curl onto the substrate). There were problems with this method for other taxa as well.

Baetis larvae were highly mobile, and tended to swim from tile surfaces before they could be captured during the manipulation. This taxon was probably underrepresented by the actual counts as a result. In contrast, Asellus was probably overrepresented by actual counts. These animals were highly mobile and showed almost continual movement over tiles during visual enumeration. During manipulation, Asellus, which was primarily located beneath tiles, drifted into the net used for sample collection from the underside of the tiles. Chironomids were often small and difficult to distinguish from algal strands. In addition, as surface material accumulated, they became camouflaged by the substrate, and, as a result, many were undetected through the viewing box. This group was clearly underestimated by visual counts. These problems contributed to the weak correspondence between the viewing box method and the actual count method of assessing the abundances of organisms. Placing the box over tiles did not generally appear to disrupt natural movements of taxa, except occasionally those of Baetis or Simulium. These instances usually had an accompanying

disturbance (e.g., the handler stumbled and disturbed the surrounding cobbles).

Richards and Minshall (1988) also used a clear viewing box to observe the movements of Baetis on natural substrates in the field. Viewing boxes were mounted over areas of low and high periphyton levels to remain stationary. Their counts reflected natural densities, and the viewing boxes did not appreciably affect macroinvertebrate behaviour.

Similar methodology was used in a study investigating the effects of hydropsychid competition and disturbance on simuliid abundance (Hemphill and Cooper 1983, Hemphill 1988). In these studies, abundances of the two groups were estimated by placing a grid over the quadrats and tabulating taxa by presence or absence in cells of the grid. These studies found a high correlation between visual counts based on presence/absence and actual numbers present on boulder surfaces.

Although the usefulness of visual counts is limited for most taxa encountered during this study, for black flies only, this method reasonably estimates the number of individuals, and shows promise for further applications in the field. It provides the advantage of rapid data collection and a simple methodology, compared with the typical methods of sample collection, which also require laboratory sample sorting, identification, and enumeration. Also, data can be gathered without disturbing the substrate or the organisms. Modification of the viewing box (e.g., placing a grid on the bottom) would facilitate counting larvae in the field further.

Field Experiments

This experiment was designed to examine colonization, a basic process in ecological systems. In the natural stream, this process may be viewed at many spatial and temporal scales. I limited the spatial

scale of my experiment to a single, small, [illegible]e stream. This scale was further reduced to an examination of commun[illegible], development on artificial substrates with surface area (tile= 90.25 cm^2) within the range of small cobble (surface areas) found naturally in the stream. Temporally, this study was limited to a single month (June) in the summer season. The analyses were performed on data collected from the final day of study, and therefore, any statistical analyses were done on independent data points.

Like laboratory experiments, field experiments have the advantage of controlling for specific variables through manipulation, but gain the additional benefit of increased realism. Unlike laboratory experiments, those conducted in the natural setting will undoubtedly be marked by greater variation because it is not possible to control all variables equally. I chose to use manipulations in the field because I expected that this approach would provide a more realistic setting regarding physical conditions, the potential colonists, and the development of the community on the substrates.

Taxonomic Richness and Composition

Although artificial substrates were used in this experiment, they were colonized by many different taxa. Among all treatments, 38 taxa were collected, while 35 taxa were collected from the Treatment 1 tiles. Eight of the 35 taxa dominated taxonomic composition of samples. These taxa were composed of filter-feeders, detritivores, and grazer/collectors. Predators were also present on tiles, but generally colonized surfaces toward the end of the study (third week), with the exception of the flatworm Dugesia.

My survey of natural cobbles in the same stream (Chapter I) had similar results. While 31 taxa were collected in that study, only nine

taxa were abundant. Use of tiles in this study reflected the natural fauna occurring in the stream.

Morin (1987) noted that tiles tended to overestimate natural simuliid densities (of some species, and at some sites, but not others) and cautioned against tneir use. Although in my study population densities on natural substrates were not measured concurrently with those on tiles, my results do not support this finding. Results of my survey of natural cobbles (Chapter I), conducted within two weeks of the completion of the colonization study, are similar to tile results in terms of taxonomic composition, dominance of a few taxa, and the large proportion of chironomids.

Dunnigan (1991) collected 11 common (>1% of total abundance) taxa in Hobbs-Mackenzie Creek. However, his collections represented heterogenous natural substrate, and included taxa that inhabited the surfaces of stones in addition to taxa that typically occupy the interstitial areas between stones, and the underlying sediments (such as ostracods and oligochaetes). He treated Chironomidae as a single taxonomic group. Although my study was limited to one specific microhabitat (upper surfaces of substrates), I collected a comparable number of dominant taxa (8), but at lower densities. A large proportion of dominant taxa, including Baetis, Hydropsyche, Asellus, Simulium, and Chironomidae were common to both studies. Differences in abundances between the two studies could be attributed to seasonal and yearly variation due to nutrient levels, algal and faunal succession, environmental conditions, and substrate sampled. My tiles also reflected the most abundant taxa collected during the survey of cobbles (Chapter I). Thus, tiles appear to have adequately reflected the biota occurring on stream cobbles under natural conditions.

Temporal Pattern

In my study, all eight dominant taxa arrived within 24 h. This suggests that tile surfaces were suitable for colonization by a variety of taxa within 24 h of initial placement. Within 24 h, black flies immigrated to tiles, and reached relatively constant numbers. Black flies were expected to arrive quickly because they tend to be opportunists (Downes and Lake 1991). Gradual decline began after 15 days, which coincided with increasing numbers of other taxa, (especially grazer/collectors), and substrate surface changes, notably a rapid (exponential) increase in both periphyton and detritus. This pattern followed prediction for black flies.

Grazer/collectors also colonized tiles immediately, but numbers increased more gradually, reaching a relatively constant level after approximately 10 days, and increasing again near the end of the study. This pattern probably reflected the gradual establishment of periphyton and accrual of detrital material over time. Predatory taxa and shredders would be expected to arrive much later when prey (attracted to resources on the tiles) had accrued (Malmqvist et al. 1991). This pattern was also present in my study. Although the occasional predator was collected early in the study, predatory taxa that had established on tile surfaces (collected consistently through time) had not done so before the third week of the study, with the exception of Dugesia.

Chironomidae abundances (largely grazers and collectors) were anticipated to lag behind those of black flies until a food base on tiles developed. This apparently contradictory pattern also was found by Khalaf and Tachet (1977) for chironomids and for Baetis (Lake and Doeg 1985). Fisher et al. (1982) studied succession in a desert stream following a flash flood. They found that the initial colonizers were those that could utilize algae. Grazer/collector taxa immigrated significantly during the first week. Substrates were colonized by

diatoms immediately, and diatoms dominated surfaces until blue-green and green algae appeared approximately three weeks after the disturbance. Gore (1982) and Boulton and Lake (1992) also found that collector-gatherers and filter-feeders arrived prior to shredders or predators. My study showed a similar pattern. As other detrital material accumulated, the diversity and abundances of taxa that could use this additional food source also increased. Thus, a food source must have been present on the tiles, even after a short period of exposure to natural stream conditions. By the third day, it was evident that at least diatoms were colonizing tiles because they were slippery to the touch, but bare to the naked eye. The curve for black fly colonization from my study corresponds to the pattern found by others (Khalaf and Tachet 1977, Downes and Lake 1991).

In a colonization study by Khalaf and Tachet (1977), black fly numbers increased quickly, became constant, then decreased again after 24 days and continued to decline for the remainder of the study (28 days). They attributed declining numbers partially to pupation and emergence. However, results of their 28-day study also suggest that as debris settled on substrates, macroinvertebrates other than simuliids became more numerous. Black flies comprised 10% of collections initially, but less than 1% at the completion of the study. This pattern has been documented subsequently by Hemphill and Cooper 1983, Ciborowski and Clifford (1984), Lake and Doeg 1985, Downes and Lake 1991, and Malmqvist et al. 1991. Gersabeck and Merritt (1979) found a similar pattern for black flies. Larvae colonized tiles rapidly, and after reaching peak numbers (5-7 days), numbers declined. Periphyton was evident on the substrates after 13 days, suggesting that it was responsible for the decline. Their study and that of Downes and Lake (1991) suggested that the declining phase in simuliids was due to periphyton growth, and possibly intraspecific interactions as larvae attempted to maintain equidistant positions from others.

Another potential reason for decline of black fly numbers on older tiles is interspecific interactions. Hemphill and Cooper (1983) and Hemphill (1988, 1991) have demonstrated that competition occurs between Hydropsyche and Simulium. Hydropsychids appear to be competitive dominants, displacing simuliids, but slower colonizers. As numbers of hydropsychids increase, black flies emigrate to other, vacant habitats. Hydropsychids are known to consume prey captured in nets, including black fly larvae (Peterson and Davies 1960). Thus, decreases in black fly abundance could be due to emigration, from pressures of predation or competition, or reduced habitat suitability. Malmqvist et al. (1991) attributed high black fly larval densities in his study to an absence of predation and competition from hydropsychids. Later, dominance of Hydropsyche may have reduced Simulium abundance by competition for that space. Morin's (1991) study revealed a seasonal component to the co-occurrence of these taxa. Differences in biomasses of simuliids and hydropsychids were attributed to competitive effects. Biomasses of simuliids and hydropsychids were negatively correlated in summer, but not in winter, on individual stones.

Unlike my study, these studies involved serial removal of artificial or natural substrates, or observations through time. Therefore, it is difficult to attribute increases or decreases of any taxon to a specific cause (predation, competition), because cohort effects (i.e., phenological changes in population size) could not be accounted for. My experimental design precluded this complication. Declining black fly numbers were not due to an emerging population, but rather, to declining substrate quality.

Microhabitat Quality

Treatment 3 allowed assessment of substrate quality and the response of black fly larvae to changes in the substrate according to the duration of time that the tile remained in the stream. Although

complete removal of all animals was not achieved during my study, my results suggest that black fly densities declined on older tiles due to declining substrate quality that occurs as the levels of periphyton and detritus accumulate.

Periphyton and total detritus accumulated exponentially with time, and biomass of each variable differed significantly among treatments (Ancova, intercepts differ, $p<0.001$). As material settled onto tiles and periphyton developed, fewer black flies immigrated to older tiles than younger tiles.

Several studies have documented observations implying a negative effect of periphyton to black fly abundance (Zahar 1951, Maitland and Penney 1967, Gersabeck and Merritt 1979, Rühm and Pegel 1986b, Pruess 1989). Hemphill and Cooper (1983) and Hemphill (1988) manipulated field plots of periphyton, Simulium, and Hydropsyche in an investigation of disturbance (algal scouring) and competition. Simulium colonized scoured areas quickly, but numbers declined on control plots in apparent response to higher algal levels. Downes and Lake (1991) showed that Austrosimulium victoriae larvae were more abundant on brick halves with reduced periphyton, but Austrosimulium torrentium occurred here not due to lowered periphyton levels, but due to lowered densities of other taxa. Hershey and Hiltner (1988) found that black flies shifted positions on cobbles to areas with less periphyton. Higher abundances of black flies in shaded than in open reaches, where periphyton was more prevalent, were noted by Towns (1981; cited in Morin and Peters 1988). Morin and Peters (1988) found a negative correlation between black fly abundances and periphyton biomass. In a study investigating responses of macroinvertebrates to periphyton, Dunnigan (1991) reported that simuliids were more abundant on newly-placed streambank stones devoid of periphyton than on stones of other treatments (either removal of macroinvertebrates, periphyton and macroinvertebrates, or controls).

I also found that periphyton, as well as detritus, incurred a negative response from simuliids. My colonization experiment is consistent with these published accounts and my surveys of natural substrates (Chapter I), and my laboratory experiments examining the effect of periphyton on simuliid density (Chapter II) concur.

The most likely reason for such an effect is a potential reduction in the ability of larval silk to adhere securely to the substrate. Chutter (1968), Barr (1982), and Colbo (1974; cited in Colbo and Wotton 1981) suggested that periphyton may interfere with larval attachment, thereby preventing larvae from remaining on surfaces accumulating material over time. Barr (1982) estimeated the half-life of a silk pad to be approximately 3 days. Black flies are primarily suspension-feeders, but can scrape periphyton. Browsing by larvae may be an attempt to maintain a relatively clear space around the silk pad (Chance 1970).

Tiles in my study were colonized largely by diatoms, and green algae became apparent by approximately 13-15 days. Filamentous algal mats did not establish on tiles during this study. However, filaments did drift onto some tiles on occasion from upstream algal mats. Although the algal community was not examined for taxonomic composition, it is most probable that diatoms dominated for the majority of the study, (since tiles were slippery to the touch). Green algae began to colonize tiles of intermediate age, but filamentous forms were not visibly present, even on 28-day old tiles (although small fragments were visible on some tiles). Stock and Ward (1989) found that diatoms tended to be the initial colonizers of bare substrates, and other algal types colonized more slowly. Grazing pressure can cause algal assemblages to be dominated by small adnate diatoms (Lamberti and Resh 1983, Gregory 1983, Hart 1985).

Cattaneo and Amireault (1992) found that diatom assemblages were well-represented on artificial substrates, but green and blue-green algal species composition tended to be underrepresented. They also found that biomass was underestimated approximately 2-fold relative to natural substrates. My biomass estimates may have been underestimated also. Based on observations of stream cobbles, my tiles had much less growth on them than the natural substrates.

In addition to the changes in substrate surface due to periphyton growth, settling of suspended particles, and drift of debris (leaf material, twigs, silt), and organisms could also alter the surface. Exuvia, tubes of chironomids, old silk pads of black flies, hydropsychid cases and nets, could all affect the surface, increasing surface complexity, and potentially attracting additional taxa, by providing additional shelter or food. This accumulation may also hinder black fly attachment.

Biotic Interactions

My results indicated that black fly colonization was hindered on young tiles (4-15 days of age) by the presence of other taxa. Until tiles were 15 days old, fewer black flies occurred on Treatment 2 tiles on which other taxa were present, than Treatment 3 tiles from which they had been removed. This suggests that black flies were affected by the presence of other organisms, and colonized tiles with reduced densities of animals over those with other animals present. This result was consistent with the alternative hypothesis that interspecific interactions negatively affect establishment of black flies.

Among the dominant taxa collected, Hydropsyche is the most probable taxon to suspect as a causal factor to this pattern. This taxon was considerably more abundant than black flies, and tends to occupy similar microhabitats since it also feeds on suspended particles.

Since they will consume black flies, and habitat overlaps with that of black flies, they are potential competitors for feeding sites, attachment sites, and food resources, as well as potential predators. Some studies have noted that competition between the two taxa occurs (Hemphill 1988, 1991).

The temporal pattern of hydropsychid abundance in my study closely resembled the pattern for black flies on Treatment 1 tiles. Both species increased and decreased on the same days (Appendix III.1A, III.1B, III.2A, III.2B). There was no reasonable evidence to suggest that hydropsychids were responsible for the apparent interference incurred by black fly larvae on young tiles. None of the other dominant taxa are likely to produce this effect.

Few predators occurred on tiles, and those that did (e.g., Dugesia flatworms, Thienemannimyia and Ablabesmyia chironomids, Empididae) were limited in number. Other, more highly mobile predators (odonates, stoneflies, megalopterans) may have influenced densities, but were not collected during the study. This may have partially accounted for reduced numbers of black flies on Treatment 2 tiles, but it does not seem reasonable to attribute this result solely to predation. Although the observed pattern follows the prediction, the taxon or taxa underlying this pattern remains in question.

At approximately 15 days of tile age, black fly densities in treatments 2 and 3 converged and subsequently began to diverge on tiles aged over 21 days. Black flies became more abundant on Treatment 2 tiles than Treatment 3 tiles, contrary to predictions. On tiles aged 15-21 days, black flies colonizing over a 24 h period did not appear to be influenced by presence or absence of other taxa on tiles. On tiles aged 24 and 27 days, when periphyton accumulation was the greatest, more black flies immigrated over 24 h to tiles where other taxa (largely

grazers and collector-gatherers) occurred, in direct contrast to both hypotheses. This result suggests that black fly larvae were not adversely affected by the presence of other animals after 15 days' age, and their immigration to tiles appeared to be facilitated by other taxa on 24 and 27 day old tiles.

The majority of taxa colonizing tiles were grazer/collectors (mainly chironomids). These taxa consume algae and other materials from the surface. They also utilize these materials for building shelters, for burrowing, or concealment from predators. This result suggests that black flies may indirectly benefit due to removal of periphyton and detritus by grazer/collector taxa, which might enhance suitability of the substrate for black fly larvae.

Support for this new hypothesis could be obtained from the AFDM and dry mass results. Differences among treatments for biomass of periphyton and detritus occurred, but growth rates for neither variable were significantly different among treatments. For both variables, 27-day-old tiles of Treatment 3 had more material present than either 27-day-old tiles of Treatment 1 (that had the least) or 27-day-old tiles of Treatment 2 (intermediate). If facilitation occurs, one would anticipate similar levels of periphyton and detritus between Treatment 1 and Treatment 2 tiles due to the presence of grazer/collectors, and significantly more biomass on Treatment 3 tiles due to their absence. Although the periphyton data for the final day of study are consistent with the facilitation hypothesis, the overall results for the study do not substantiate this alternative explanation for the pattern observed in black fly numbers near the end of the study.

The lack of clear results for this part of the study may partially be due to inadequate treatment effects (removals). Effectiveness of removals was low, but sufficient to allow differences among treatments

with respect to abundances of black flies and grazer/collectors later in the study to be detected, although not always at a significant level. In practice, complete removal was not achieved on Treatment 3 tiles. In addition, large variation among replicates, especially toward the end of the study also limited my ability to demonstrate this effect conclusively.

As previously mentioned, several field studies and observations imply that increasing levels of periphyton reduce habitat quality for black flies, by preventing secure attachment of the silk pad. Organisms that remove this material could thus have a positive influence on black fly habitat, perhaps extending the time that larvae are able to remain on a substrate which would otherwise become unsuitable more rapidly. Feminella et al. (1989) showed that considerable amounts of periphyton could be removed by grazing taxa. They placed tiles on a stream bottom to allow access to periphyton by grazing taxa. Other tiles were elevated into the water column and colonization by grazers other than swimmers, such as Baetis, was prevented. As predicted, grazers were more abundant on stream bottom tiles, and consumed large quantities of algae. Periphyton accrual was significantly greater on raised tiles. This experiment demonstrated the marked effect that algal consumers could have on periphyton abundance. My tiles were placed on the stream bottom and would have been fully accessible to grazers.

Other studies have also demonstrated that grazers can have a substantial impact on periphyton biomass (Lamberti and Resh 1983, McAuliffe 1984a, 1984b, Hart 1985, 1987b, Hill and Knight 1987, Lamberti et al. 1987) at natural densities. However, their ability to control periphyton levels varies. DeNicola et al. (1990) found that Juga, a snail, could deplete algal resources, but Baetis had virtually no effect. Grazing of periphyton also altered the succession and

composition of the algal community; filamentous forms developed more slowly and diatoms remained prevalent.

Based on the results of this study, the following adjustments to future black fly colonization studies may result in more robust conclusions regarding biotic conditions affecting black fly colonization. Prolonging future black fly colonization studies by even a few days (3-6) would make the temporal pattern of decline for black flies with time stronger, and may result in stable periphyton levels on substrates. Chlorophyll a analyses would also have provided an additional measure of periphyton biomass. My experiment was not designed with the intention of examining the potential facilitative effect of other taxa on simuliid colonization. Rather, this was a hypothesis derived from the results of the study. This indirect effect should be investigated experimentally to test its validity in black fly colonization dynamics, with appropriate study design.

Conclusions

My study revealed a colonization pattern of initial rapid immigration typical of opportunistic species, followed by a period of relatively constant numbers. Midway through the study (15 days), black fly numbers declined on tiles and continued to decline for the duration of the study. This result was as predicted. Coinciding with the decline in simuliid abundance was an increase in periphyton and detritus. Black flies appeared to immigrate to younger tiles due to degradation of the substrate with increasing tile age. This response was also as predicted.

My results revealed that the role and nature of biotic interactions affecting black fly colonization may be more complex than anticipated. Although biotic interactions apparently interfered with black fly colonization, their effect dissipated as the substrate aged.

Black flies may derive a benefit from an interaction with grazer/collectors, as they remove detritus and periphyton from the surface, perhaps enabling black flies to maintain attachment to an otherwise unsuitable substrate, or prolonging the time period of substrate suitability for black fly colonization.

Future Research

The most obvious hypotheses to investigate, based on this colonization study, are those involving biotic interactions. My study has alluded to a more complex role of interspecific interactions than anticipated. Both interference and facilitation may be important to black fly colonization and subsequent establishment and success of populations. My study was not designed to test for facilitative interactions. Therefore, the facilitation hypothesis generated from this work requires direct experimental testing. There are few studies in the literature that have addressed interspecific interactions, and work at the community level is also lacking. Longer-term studies would also allow the potential effects of successional events (other biota) to be investigated.

Video recording of arrivals and departures would provide the necessary documentation for the frequency and intensity of interactions, as well as immigration/emigration rates regarding population maintenance. My study was conducted on a broad scale, such that these parameters could not be measured.

GENERAL CONCLUSIONS

My studies have shown that flow, substrate features, and, possibly, biotic interactions are important components to larval black fly microhabitat selection. My field surveys assessed microhabitat selection by correlating black fly density with a variety of abiotic factors. My approach improved upon past studies by (1) examining specific substrate characteristics (evenness, texture, face, substrate size, amount of periphyton and detritus) at the level of individual cobbles, (2) quantifying abiotic variables (depth, current velocity Froude number) at the location of each cobble rather than selecting replicate sites within the stream reach from which cobble samples were removed to represent the conditions to which cobbles were exposed, and (3) examining the other biota also occupying the cobble sampled, rather than the simuliid population only.

While my surveys demonstrated that flow was of prime importance (Froude number explained more variation in density than any other single variable), they also indicated that the composite effect of substrate (evenness, dry mass, surface area) was also significant. My surveys revealed that, at least at low to moderate densities of simuliids, other taxa, especially Chironomidae, are associated with black flies. The proximity of these co-occurring biota to black flies warrants further attention. Although a limited number of studies suggest that habitat segregation between early and late-instar larvae may occur (Gersabeck and Merritt 1979, Rühm and Pegel 1986a), my surveys, at the scale of investigation employed (top and bottom faces of whole cobbles), produced no evidence of differential habitat selection by larvae of varying size.

I examined further the effect of substrate using tiles modified for the features of texture, evenness, and periphyton. Although Casey and Clifford (1989) and Clifford et al. (1989) examined texture (roughness) quantitatively for macroinvertebrates (particularly

mayflies) on tiles colonized in the field, this appears to be the first attempt to characterize quantitatively, particular surface features, under controlled laboratory conditions, for black flies. My experiments confirmed that texture affected larval substrate selection (by 24 h), at least at low larval density (consistent with habitat selection theory). There was no demonstrated effect of texture at high density, except when modified by periphyton: greater periphytic growth on rough tiles corresponded to fewer black flies; less periphytic growth on smooth tiles corresponded to more black flies. Additional refinement of quantitative assessment of texture and evenness would improve upon the measurement of these variables.

Of particular interest was the formation of consistent banding patterns by simuliids. Regardless of surface type, black flies aggregated, forming distinct rows transverse to the direction of flow, suggesting that, regardless of the available substrate choices, aggregative tendency of larvae predominates. To my knowledge, this study, and that of Colbo (1987), are the only demonstrations of consistent banding patterns in an experimental situation. I have developed an experimental system that consistently produces strong banding patterns, which may be useful in future studies investigating the causes of black fly aggregation.

The colonization pattern demonstrated for black flies in my field experiment (initial rise, subsequent decline) followed prediction, and concurs with the pattern observed by others (Tachet and Khalaf 1977, Doeg and Lake 1985, Downes and Lake 1991, Malmqvist et al. 1991). My study differs from previous studies in eliminating the confounding effect of density differences on substrates due to cohort status, thereby allowing one to clearly distinguish between the influences of substrate quality and biotic interactions on black fly colonization.

Numbers of black fly larvae declined due to deterioration of substrate quality as a result of periphytic growth and accumulation of detritus. Biotic interactions were possibly an important component of larval colonization. Interference was apparently operating on younger tiles, although results concerning the biota involved were inconclusive. The study also implied that facilitation by grazers/collector-gatherers may prolong habitat suitability for black flies by reducing periphyton and detritus levels.

Further studies should test experimentally the facilitation hypothesis arising from this work. More rigorous tests concerning the general role of biotic interactions to simuliid distributions are still necessary. Manipulation of black fly larval density and of the type, density, and proximity of other biota would aid to clarify their associations with black flies. The role of predation could also be investigated. The relative importance of substrate, interspecific interactions (interference or facilitation), and intraspecific interactions (interference or facilitation) requires further attention. In addition, the cues for formation of bands (intraspecific cues versus hydrodynamic cues) and the relative importance of each to these patterns, warrant additional investigation. My laboratory system could be useful for such studies.

APPENDIX I

Appendix I.1A Taxonomic composition of samples from Wigle Creek. Abbreviations of taxonomic names are listed in Appendix I.6A.

SAMPLE NO.	HD	DU	PH	OL	GH	HA	CL	IS	BA	CA	HC	ME	HY	HT	HP	SV	HE
1T	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
1B	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2T	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3T	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
3B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4T	0	0	3	1	0	0	0	0	0	0	0	1	0	0	0	0	0
4B	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
5T	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5B	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
6T	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	2	1
6B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7T	0	0	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0
7B	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8T	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0
9T	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
9B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
10T	0	0	2	1	0	0	0	0	0	1	0	0	0	0	0	0	0
10B	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11T	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0
11B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
12T	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0
12B	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0
13T	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	5	0
13B	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0
14T	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	17	0
14B	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	16	0
15T	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	5	0
15B	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	2	0
16T	0	0	4	1	0	0	0	0	0	0	0	0	0	0	0	0	1
16B	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0
17T	0	1	1	2	0	0	0	0	0	1	0	0	0	0	0	2	0
17B	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0
18T	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0
18B	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0
19T	0	0	5	1	0	0	0	0	0	1	0	0	0	0	0	0	0
19B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20T	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1
20B	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
21T	0	1	0	2	0	0	0	0	0	0	0	0	0	0	3	1	0
21B	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	3	0
21T	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
22B	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0
23T	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23B	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
24T	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
24B	0	0	2	0	0	0	0	0	1	1	0	0	0	0	0	3	0
25T	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25B	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0
26T	0	0	5	0	0	0	0	0	0	0	0	0	1	0	1	304	0
26B	0	0	13	1	0	1	0	0	1	0	0	0	0	0	1	59	0
27T	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	35	0
27B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0
28T	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	12	0
28B	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	25	0
29T	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0
29B	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	4	0

Appendix I.1A (Continued)

SAMPLE NO.	HD	DU	PH	OL	GH	HA	CL	IS	BA	CA	HC	ME	HY	HT	HP	SV	HE
30T	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	40	0
30B	0	1	17	1	0	0	0	0	0	0	0	0	0	0	6	48	0
31T	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31B	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
32T	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	49	0
32B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0
33T	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	3	0
33B	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Dam1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	89	0
Dam2	0	0	19	0	0	0	0	0	0	0	0	0	0	0	0	49	1
Dam3	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	257	1
Dam4	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	247	0

Appendix I.1B Taxonomic composition of samples from Wigle Creek. Abbreviations of taxonomic names are listed in Appendix I.6A.

SAMPLE NO.	EM	EU	TH	CO	DI	PO	CR	CR	NA	PR	CH	TY	RH	PT	IC	CP
1T	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0
1B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
2T	0	1	0	0	0	1	0	0	0	0	9	2	0	0	3	0
2B	0	0	0	0	0	0	0	1	0	0	2	0	0	0	1	0
3T	0	0	0	0	2	0	0	0	0	0	0	0	0	6	2	0
3B	0	0	0	0	0	5	0	0	0	0	0	0	0	2	2	0
4T	0	0	1	0	0	9	0	0	9	0	0	1	0	0	10	0
4B	0	0	0	0	2	1	0	1	0	0	0	0	0	1	0	0
5T	0	0	0	0	0	1	0	0	0	0	0	0	0	1	5	0
5B	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0
6T	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
6B	0	0	0	0	0	3	0	2	0	0	0	0	0	0	0	0
7T	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0
7B	0	0	0	0	0	3	0	4	0	2	0	6	0	0	1	0
8T	0	0	0	0	0	1	0	0	0	0	0	4	0	0	5	0
8B	0	0	3	0	0	3	0	0	0	0	0	0	0	0	4	0
9T	0	0	0	1	0	3	2	11	0	2	1	1	0	0	2	0
9B	0	1	2	0	0	4	0	9	0	0	0	0	0	0	1	0
10T	0	0	0	0	0	0	0	2	0	0	6	1	0	5	6	0
10B	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0
11T	0	0	7	1	0	3	2	12	0	0	0	0	0	0	12	0
11B	0	0	4	1	0	5	0	1	0	0	0	0	0	0	2	0
12T	0	0	0	0	0	2	2	0	3	0	0	0	0	0	14	0
12B	0	0	6	0	0	13	0	21	0	0	0	0	0	0	1	0
13T	0	0	12	1	0	51	0	23	2	0	2	3	0	4	72	0
13B	0	0	0	1	0	2	0	4	0	0	0	0	0	0	1	0
14T	0	0	7	1	0	34	0	49	0	0	0	1	0	0	23	1
14B	0	4	5	1	0	4	0	4	0	0	0	4	0	1	6	1
15T	0	0	1	0	1	4	0	1	0	0	2	0	0	1	0	4
15B	0	0	4	0	0	21	0	12	0	0	3	0	0	0	2	0
16T	0	0	0	0	0	1	0	1	0	2	3	1	0	1	2	0
16B	0	0	0	0	0	0	0	8	0	0	0	2	0	0	1	0
17T	0	0	0	0	0	0	0	4	2	0	5	1	0	0	10	0
17B	0	0	1	0	0	2	0	0	0	0	1	3	0	0	0	0
18T	0	0	0	0	0	1	0	2	1	0	4	2	0	3	2	0
18B	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0
19T	0	0	0	0	0	4	0	2	2	0	8	11	1	6	11	1
19B	0	0	0	0	0	1	0	3	0	0	0	0	0	0	1	0
20T	0	0	0	0	0	14	2	1	1	0	0	3	0	1	12	0
20B	0	0	0	1	1	1	0	1	1	0	5	1	0	0	2	0
21T	0	0	29	0	0	48	0	57	0	0	0	0	0	0	65	1
21B	0	0	6	0	0	17	0	13	0	0	8	3	0	0	6	0
21T	0	0	8	0	0	22	0	25	0	0	10	1	2	0	3	1
22B	0	0	10	1	0	6	3	5	0	0	0	6	0	0	1	1
23T	0	0	5	2	0	25	0	21	0	0	3	9	0	13	35	0
23B	0	0	0	2	0	2	0	10	0	0	1	4	0	0	1	1
24T	0	0	4	0	0	90	10	48	0	0	6	7	0	0	27	1
24B	0	0	1	0	0	14	0	11	0	0	0	3	0	0	4	1
25T	0	0	0	0	3	23	0	72	0	0	6	6	0	6	40	5
25B	0	0	0	0	0	18	0	29	1	17	0	9	0	4	15	0
26T	1	0	16	0	0	73	0	75	0	0	0	2	0	0	73	3
26B	0	0	3	0	0	25	0	15	0	0	0	3	0	5	9	2
27T	0	0	1	0	0	25	0	14	0	0	0	1	5	0	31	2
27B	0	0	0	0	0	5	0	2	0	0	0	1	0	0	0	0
28T	1	0	0	0	0	31	5	0	0	0	0	2	0	0	69	0
28B	0	0	2	0	0	8	0	3	0	0	1	1	0	0	2	0
29T	0	0	0	0	0	1	2	15	0	0	0	0	0	0	10	1

Appendix I.1B (Continued)

SAMPLE NO.	EM	EU	TH	CO	DI	PO	CR	OR	NA	PR	CH	TY	RH	PT	IC	CP
29B	0	0	0	0	0	8	0	1	0	0	0	0	0	0	0	1
30T	0	6	0	0	0	11	6	4	0	0	3	0	0	0	6	0
30B	0	0	1	0	0	59	4	3	0	0	0	3	3	8	5	2
31T	0	0	0	0	14	21	0	0	7	0	0	10	0	0	17	2
31B	0	0	0	0	0	5	0	5	0	0	0	1	0	0	2	1
32T	0	0	31	0	0	56	0	36	0	0	0	0	0	0	95	1
32B	0	0	1	0	0	7	0	3	0	0	0	0	0	0	0	0
33T	0	0	3	1	0	29	0	6	0	0	0	0	0	1	19	0
33B	0	0	3	0	0	3	0	4	0	1	2	2	0	0	2	0
Dam1	0	0	0	0	0	3	0	4	0	0	2	1	0	1	0	2
Dam2	11	0	0	0	0	12	0	0	0	0	0	0	0	0	0	3
Dam3	0	0	0	0	0	47	0	11	0	0	0	1	0	0	0	3
Dam4	2	0	0	0	0	24	3	6	0	0	0	0	0	0	0	1

Appendix I.2 Raw data of abiotic variables measured in Wigle Creek. (DM = dry mass; EVEN = evenness; E = even; U = uneven; PERI = periphyton; A = absent; P = present; H = horizontal; V = vertical; B = bottom; T = top; C.V. = current velocity; SURF = surface area)

SAMPLE NO.	DM (mg/cm^2)	EVEN E=0,U=1	PERI A=0,P=1	ASPECT H=0,V=1	FACE B=0,T=1	C.V. (cm/s)	DEPTH (cm)	SURF (cm^2)	FROUDE NO.
1T	0.264	0	0	0	1	0.0	14.0	76.0	0.000
1B	0.107	0	0	0	0	0.0	14.0	35.6	0.000
2T	0.039	0	0	0	1	0.0	18.5	78.8	0.000
2B	0.041	0	0	0	0	0.0	18.5	53.1	0.000
3T	0.045	0	0	0	1	0.0	28.0	70.9	0.000
3B	0.117	0	0	0	0	0.0	28.0	65.8	0.000
4T	0.087	0	0	0	1	0.0	17.0	77.3	0.000
4B	0.201	0	0	0	0	0.0	17.0	93.6	0.000
5T	0.033	0	0	0	1	0.0	13.0	131.6	0.000
5B	0.001	0	0	0	0	0.0	13.0	102.0	0.000
6T	0.144	0	0	0	1	17.5	3.0	65.1	0.104
6B	0.021	0	0	0	0	17.5	3.0	52.8	0.104
7T	0.017	0	0	0	1	14.1	6.0	106.3	0.034
7B	0.803	0	0	0	0	14.1	6.0	60.9	0.034
8T	0.019	0	0	0	1	17.2	6.5	108.3	0.047
8B	0.130	0	0	0	0	17.2	6.5	54.6	0.047
9T	0.019	0	0	0	1	24.8	5.0	102.2	0.125
9B	0.820	0	0	0	0	24.8	5.0	90.2	0.125
10T	0.013	0	0	0	1	7.1	8.0	79.4	0.006
10B	0.072	0	0	0	0	7.1	8.0	40.1	0.006
11T	1.528	0	0	0	1	21.1	6.0	65.0	0.076
11B	6.861	0	0	0	0	21.1	6.0	50.2	0.076
12T	0.274	0	0	0	1	26.9	7.0	135.6	0.106
12B	0.146	0	0	0	0	26.9	7.0	34.3	0.106
13T	0.107	0	0	0	1	22.0	6.0	120.8	0.082
13B	1.596	0	0	0	0	22.0	6.0	56.4	0.082
14T	0.025	0	0	0	1	50.4	9.0	204.7	0.288
14B	0.273	0	0	0	0	50.4	9.0	79.5	0.288
15T	0.240	0	0	0	1	53.8	8.0	61.8	0.369
15B	11.661	0	0	0	0	53.8	8.0	82.1	0.369
16T	0.288	0	1	0	1	0.0	4.5	90.6	0.000
16B	1.801	0	1	0	0	0.0	4.5	50.5	0.000
17T	0.177	0	1	0	1	0.0	8.5	141.4	0.000
17B	0.258	0	1	0	0	0.0	8.5	103.5	0.000
18T	0.472	0	1	0	1	0.0	7.0	81.6	0.000
18B	0.103	0	1	0	0	0.0	7.0	50.3	0.000
19T	0.391	0	1	0	1	0.0	7.0	90.9	0.000
19B	0.003	0	1	0	0	0.0	7.0	68.2	0.000
20T	0.066	0	1	0	1	0.0	5.0	222.7	0.000
20B	0.150	0	1	0	0	0.0	5.0	61.9	0.000
21T	0.665	0	1	0	1	19.2	5.0	43.4	0.075
21B	1.951	0	1	0	0	19.2	5.0	53.0	0.075
21T	0.898	0	1	0	1	17.0	5.0	75.4	0.059
22B	0.810	0	1	0	0	17.0	5.0	60.4	0.059
23T	1.311	1	1	0	1	4.3	4.0	75.7	0.005
23B	0.171	0	1	0	0	4.3	4.0	62.6	0.005
24T	0.518	1	1	0	1	4.1	6.5	118.9	0.003
24B	0.367	0	1	0	0	4.1	6.5	85.0	0.003
25T	0.766	0	1	0	1	11.5	5.0	133.3	0.027
25B	0.775	0	1	0	0	11.5	5.0	100.9	0.027
26T	0.011	0	1	0	1	27.4	4.5	212.7	0.170
26B	0.070	1	1	0	0	27.4	4.5	160.7	0.170
27T	0.085	0	1	0	1	16.6	3.0	60.1	0.094
27B	0.584	0	1	0	0	16.6	3.0	48.3	0.094
28T	0.654	1	1	0	1	15.7	3.0	61.8	0.084
28B	0.408	1	1	0	0	15.7	3.0	57.6	0.084
29T	0.049	0	1	0	1	17.2	3.5	62.9	0.086
29B	1.269	0	1	0	0	17.2	3.5	45.2	0.086
30T	0.020	0	1	0	1	16.3	4.0	133.2	0.067
30B	0.135	0	1	0	0	16.3	4.0	97.7	0.067
31T	1.087	1	0	0	1	0.0	11.5	106.4	0.000
31B	0.051	1	0	0	0	0.0	11.5	41.0	0.000
32T	0.222	1	0	0	1	28.3	7.0	47.8	0.117

Appendix I.2 (Continued)

SAMPLE NO.	DM (mg/cm^2)	EVEN E=0,U=1	PERI A=0,P=1	ASPECT H=0,V=1	FACE B=0,T=1	C.V. (cm/s)	DEPTH (cm)	SURF (cm^2)	FROUDE NO.
32B	0.316	1	0	0	0	28.3	7.0	19.3	0.117
33T	0.074	1	0	0	1	22.5	9.0	182.0	0.057
33B	1.419	1	0	0	0	22.5	9.0	98.4	0.057
Dam1	0.566	1	1	1	1	31.7	1.0	50.0	1.025
Dam2	0.810	1	1	1	1	31.7	1.0	50.0	1.025
Dam3	1.831	0	1	1	1	35.6	1.0	19.5	1.293
Dam4	0.964	0	1	1	1	35.6	1.0	19..	1.293

Appendix I.3A Taxonomic composition of samples collected from Hobbs-Mackenzie Creek. Abbreviations of taxonomic names are listed in Appendix I.6B.

SAMPLE NO.	HD	DU	SP	PH	OL	HA	AS	IS	BF	ST	EL	HP	HT	CM	SV	AN
1B	0	0	0	0	0	0	30	0	0	1	0	0	0	0	3	0
1T	0	1	0	0	0	0	49	0	0	0	0	7	0	0	0	1
2B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2T	0	4	0	0	3	0	37	0	0	0	1	9	0	0	1	26
3B	0	3	0	0	0	0	23	0	0	0	0	0	0	0	0	4
3T	0	0	0	0	0	0	54	0	1	0	1	0	2	0	1	10
4B	0	1	0	0	0	0	7	0	0	2	0	2	0	0	0	0
4T	0	0	0	0	7	0	47	0	0	0	1	8	2	0	0	16
5B	0	1	0	0	0	0	7	0	0	2	0	2	0	0	0	0
5T	0	0	0	0	0	0	12	0	0	0	0	3	6	0	0	2
6B	0	2	0	0	1	0	15	0	0	0	2	0	0	0	0	0
6T	0	0	0	0	3	0	5	0	0	0	0	5	0	0	0	5
7B	0	3	0	0	0	0	30	0	1	1	1	10	2	3	0	2
7T	0	0	0	0	1	0	29	0	1	0	2	20	0	0	0	2
8B	0	2	0	0	0	0	6	0	0	3	0	5	0	3	1	0
8T	0	0	0	0	0	0	4	0	0	0	0	7	0	1	0	0
9B	0	1	0	0	0	0	10	0	0	7	0	4	0	0	0	0
9T	0	0	0	0	0	0	53	0	1	0	1	8	1	0	1	6
10B	0	1	0	0	0	0	11	0	0	5	0	2	0	0	0	0
10T	0	2	0	0	3	0	76	0	1	0	0	11	5	0	0	15
11B	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
11T	0	1	0	0	0	0	4	0	0	0	0	6	0	0	3	16
12B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12T	0	0	0	0	0	0	2	0	2	0	0	0	1	0	0	0
13B	0	1	0	0	0	0	4	0	2	0	0	7	0	0	0	1
13T	0	0	0	0	1	0	2	0	0	0	0	20	0	0	0	3
14B	0	0	0	0	0	1	2	0	0	1	0	6	2	0	0	0
14T	0	2	0	0	3	1	34	0	1	0	0	19	8	0	0	13
15B	0	3	0	0	0	0	6	0	1	0	1	9	0	0	1	0
15T	0	0	0	0	3	2	4	0	0	0	0	22	8	0	0	25
16B	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
16T	0	0	0	0	0	0	1	0	0	0	0	11	0	0	0	17
17B	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0
17T	0	0	0	0	0	3	29	0	0	1	1	6	8	0	0	4
18B	0	0	0	0	0	0	5	0	0	0	0	1	0	0	0	0
18T	0	0	0	0	0	2	4	0	1	0	0	1	0	0	2	4
19B	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0
19T	0	0	0	0	0	0	2	0	0	0	0	1	0	0	1	0
20B	0	0	0	0	0	0	1	0	0	0	0	4	0	0	0	0
20T	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0
21B	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
21T	0	0	0	0	2	0	46	0	2	0	0	4	1	0	2	3
22B	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
22T	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23B	1	1	0	0	1	0	4	0	0	1	2	22	4	0	1	0
23T	0	0	0	0	2	1	7	0	0	0	1	16	12	0	43	0
24B	0	0	0	0	0	0	7	0	0	0	0	2	0	0	3	0
24T	0	0	0	0	0	0	1	0	0	0	0	3	0	0	2	0
25B	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
25T	0	0	0	0	0	0	5	0	0	0	0	11	0	0	7	2
26B	0	1	0	0	1	0	11	0	0	0	0	3	1	0	1	0
26T	0	0	0	0	2	0	3	0	2	0	0	3	1	0	6	2
27B	0	0	0	0	0	1	0	0	0	0	0	0	0	0	2	0
27T	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
28B	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
28T	0	0	0	0	1	0	0	0	0	0	0	4	0	0	5	0
29B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0

Appendix I.3A (Continued)

SAMPLE NO.	HD	DU	SP	PH	OL	HA	AS	IS	BF	ST	EL	HP	HT	CM	SV	AN
29T	0	0	0	0	1	0	0	0	0	0	1	2	0	0	1	1
30B	0	0	0	0	0	0	0	0	0	0	0	4	1	0	1	0
30T	0	0	0	0	0	0	0	0	1	0	0	1	0	0	5	0
31B	0	0	C	0	0	0	0	0	0	0	0	1	0	0	1	0
31T	0	3	0	0	0	0	2	0	0	0	0	18	5	0	1	4
32B	0	0	0	0	0	0	12	0	7	0	0	32	5	0	0	5
32T	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33B	0	1	0	1	0	0	17	0	3	2	1	25	3	0	2	0
33T	0	0	0	0	0	0	16	0	0	0	0	27	9	0	4	3
34B	0	2	0	0	0	0	2	0	0	0	0	10	0	1	0	0
34T	0	0	0	0	0	0	0	0	1	0	0	15	0	0	4	1
35B	0	0	0	0	0	0	0	0	0	0	0	13	0	0	1	0
35T	0	0	0	0	0	2	4	0	2	0	0	40	2	0	2	2
36B	0	0	0	0	2	0	1	0	2	0	0	13	2	0	2	0
36T	0	0	0	0	1	0	3	0	1	0	0	8	2	0	13	2
37B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
37T	0	0	0	0	1	4	0	0	1	0	0	18	2	0	0	3
38B	0	0	0	0	0	0	0	0	0	0	0	2	0	0	3	0
38T	0	0	0	0	0	0	1	0	1	0	0	2	0	0	15	2
39B	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0
39T	0	0	0	0	0	1	0	0	2	0	2	11	1	0	2	0
40B	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
40T	0	0	0	0	0	0	0	0	3	0	0	0	0	0	5	8
41B	0	0	0	0	0	0	0	0	1	0	0	4	0	0	2	0
41T	0	0	0	0	0	1	0	0	1	0	0	3	0	0	1	0
42B	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
42T	0	0	0	0	1	0	0	0	0	0	0	2	0	0	4	0
43B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
43T	0	0	0	0	0	0	19	0	4	0	0	1	0	0	4	0
44B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
44T	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0
45B	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0
45T	0	0	0	0	0	0	1	0	2	0	0	21	0	0	9	0
46B	0	0	0	0	0	0	0	0	1	0	0	25	0	0	7	0
46T	0	0	0	0	0	0	1	0	6	0	0	106	0	0	16	15
47B	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0
47T	0	0	0	0	3	0	0	0	0	0	0	22	0	0	7	0
48B	0	0	0	0	0	0	0	0	0	0	0	45	0	0	2	0
48T	0	0	0	0	0	0	0	0	0	0	0	45	0	0	15	0
49B	0	0	0	0	0	0	0	0	0	0	0	23	0	0	1	0
49T	0	0	0	0	0	0	0	0	1	0	0	12	0	0	4	1
50B	0	0	0	0	0	1	0	0	0	0	0	13	0	0	0	0
50T	0	0	0	0	0	0	2	0	0	0	0	3	0	0	5	0
51B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
51T	0	0	0	0	0	0	0	0	0	0	0	3	0	0	1	0
52B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52T	0	0	0	0	0	0	0	0	0	0	0	3	0	0	1	0
53B	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0	0
53T	0	0	0	0	0	0	0	0	0	0	0	23	0	0	1	2
54B	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
54T	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	9
55B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
55T	0	0	0	0	1	1	13	0	0	0	1	3	0	0	0	0
56B	1	1	0	0	0	0	8	1	0	0	0	4	0	0	0	0
56T	0	0	0	0	0	0	4	0	1	1	0	2	0	0	8	0
57B	0	0	0	0	0	0	10	0	0	0	0	10	0	0	0	0
57T	0	0	0	0	0	2	13	0	3	0	0	20	0	0	13	6
58B	0	0	0	0	0	0	3	0	3	0	0	12	0	0	0	0
58T	0	0	0	0	2	0	6	0	1	0	0	17	0	0	2	2

Appendix I.3A (Continued)

SAMPLE NO.	HD	DU	SP	PH	OL	HA	AS	IS	BF	ST	EL	HP	HT	CM	SV	AN
59B	0	3	0	0	0	0	1	0	1	0	0	18	0	0	1	0
59T	0	0	1	0	0	0	1	0	0	0	0	75	0	0	5	3
60B	0	0	0	0	0	0	1	0	0	0	0	6	0	0	0	0
60T	0	0	0	0	0	0	0	0	0	0	0	16	0	0	3	1
61B	0	0	0	0	0	0	3	0	0	0	0	3	0	0	0	0
61T	0	0	0	0	0	0	1	0	0	0	0	11	0	0	4	0
62B	0	0	0	0	0	0	0	1	0	0	0	18	0	0	1	0
62T	0	0	0	0	0	0	1	0	0	0	0	18	0	0	5	0
63B	0	0	0	0	0	0	0	0	0	1	0	11	0	0	1	1
63T	0	0	0	0	0	0	1	0	0	0	0	12	0	0	1	0
64B	0	0	0	0	1	0	3	0	0	3	0	5	0	0	0	0
64T	0	0	0	0	0	0	2	0	0	0	0	8	0	0	1	0
65B	0	0	0	0	0	1	1	0	2	1	0	1	0	0	0	0
65T	0	0	0	0	1	0	2	1	0	0	1	2	0	0	0	4
66B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
66T	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
67B	0	1	0	0	0	0	0	0	0	0	0	3	0	0	1	0
67T	0	0	0	0	0	0	1	0	0	0	0	9	0	0	3	0
68B	0	1	0	0	0	0	0	0	0	0	0	25	0	0	3	0
68T	0	0	0	0	0	0	0	0	2	0	0	58	0	0	6	0
69B	0	0	0	0	0	0	3	0	0	0	0	8	0	0	0	0
69T	0	1	0	0	6	0	0	0	1	0	1	15	0	0	6	0
70B	0	0	0	0	0	0	1	0	3	0	0	54	0	0	9	0
70T	0	1	0	0	0	0	0	0	2	0	0	33	0	0	2	0

Appendix I.3B Taxonomic composition of samples collected from Hobbs-Mackenzie Creek. Abbreviations of taxonomic names are listed in Appendix I.6B.

SAMPLE NO.	EM	AR	EU	TV	TH	CO	PO	PT	AB	CR	NA	MT	DI	CH	RC	IC
1B	0	0	6	0	3	1	0	0	0	0	0	0	0	0	0	4
1T	0	0	8	0	0	0	0	0	0	7	0	0	0	0	0	0
2B	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0
2T	0	0	45	0	2	0	0	0	0	39	0	0	0	0	0	52
3B	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
3T	0	0	1	0	0	0	0	0	0	4	0	0	0	0	0	0
4B	0	0	1	0	2	1	0	0	0	0	0	0	0	0	0	0
4T	0	0	19	10	3	0	0	0	0	20	0	6	0	0	0	0
5B	0	0	1	0	0	0	0	0	0	3	0	0	0	0	0	0
5T	0	0	15	0	0	0	0	0	1	12	0	0	0	0	0	0
6B	0	0	1	0	0	1	0	0	2	0	0	0	0	0	0	1
6T	0	0	11	0	4	0	0	0	1	3	0	0	0	0	0	7
7B	0	0	2	0	0	1	2	0	5	0	0	0	0	0	0	0
7T	0	0	13	0	0	0	0	0	1	0	0	0	0	0	0	11
8B	0	0	0	0	0	1	0	0	2	1	0	0	0	0	0	0
8T	0	0	1	0	0	0	0	0	1	5	0	0	0	0	0	0
9B	0	0	5	0	2	2	0	0	1	0	2	0	0	0	0	0
9T	0	0	6	0	2	0	0	0	0	7	0	0	0	0	0	4
10B	0	0	2	0	2	1	0	0	1	0	0	0	0	0	0	2
10T	0	0	23	3	0	0	0	0	2	6	0	0	0	0	2	23
11B	0	0	7	0	1	0	0	0	0	0	0	0	0	0	0	0
11T	0	0	0	0	0	0	0	0	0	74	0	0	0	0	0	0
12B	0	0	3	0	0	3	0	0	0	3	3	0	0	0	0	0
12T	0	0	7	0	0	0	0	0	1	4	0	0	2	0	0	4
13B	0	0	4	0	1	0	0	0	1	2	0	0	0	0	0	0
13T	0	0	53	6	0	0	0	0	0	24	0	0	0	0	0	0
14B	0	0	5	0	3	0	0	0	0	0	0	0	0	0	0	0
14T	0	0	50	5	1	0	0	0	3	89	0	0	0	0	0	0
15B	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	3
15T	0	0	54	1	1	0	0	0	3	0	0	0	0	0	0	35
16B	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
16T	0	0	82	0	0	0	0	0	0	31	0	0	0	0	0	0
17B	0	0	7	0	0	7	1	0	1	3	0	0	0	0	0	0
17T	0	0	16	0	2	2	2	0	2	10	0	0	0	0	0	0
18B	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
18T	0	0	3	1	2	0	0	0	0	0	0	1	0	0	0	0
19B	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0
19T	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0
20B	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
20T	0	0	3	1	0	0	0	0	0	1	0	0	0	0	0	0
21B	0	0	7	0	0	0	0	0	1	0	0	0	0	0	0	0
21T	0	0	17	0	1	0	2	0	2	20	0	0	0	0	0	0
22B	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
22T	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23B	0	0	9	2	3	0	0	0	0	0	0	0	0	0	0	0
23T	0	0	38	0	2	0	0	0	0	0	0	0	0	0	0	0
24B	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0
24T	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0
25B	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0
25T	0	0	33	4	2	0	0	0	0	4	0	2	0	0	0	0
26B	0	0	4	3	0	0	1	0	1	1	0	0	0	0	0	0
26T	0	0	26	1	0	0	2	0	0	2	0	0	0	0	0	0
27B	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
27T	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0
28B	0	0	16	0	2	0	0	0	0	0	0	0	0	0	0	0
28T	0	0	25	0	2	0	0	0	0	0	0	0	0	0	0	0
29B	0	0	3	0	1	0	0	0	0	0	0	0	0	0	0	0

Appendix I.3B (Continued)

SAMPLE NO.	EM	AR	EU	TV	TH	CO	PO	PT	AB	CR	NA	MT	DI	CH	RC	IC
29T	0	0	13	1	0	0	0	0	0	1	0	0	0	0	0	0
30B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30T	0	0	9	1	2	0	0	0	0	0	0	0	0	0	0	0
31B	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0
31T	0	0	61	2	6	0	6	0	0	6	0	0	0	0	0	0
32B	0	0	54	0	6	4	0	5	0	22	0	0	0	0	0	0
32T	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
33B	0	1	8	0	4	2	0	0	3	0	0	1	0	0	0	0
33T	0	0	38	2	8	0	0	0	0	22	0	0	0	0	0	0
34B	0	0	2	0	3	0	0	0	0	0	0	0	0	0	0	0
34T	0	0	6	0	3	0	0	0	0	0	0	0	0	0	0	0
35B	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0
35T	0	0	24	0	6	0	0	0	0	0	0	0	0	0	0	0
36B	0	0	153	0	0	0	0	0	0	33	0	0	0	0	0	0
36T	0	0	201	0	2	0	0	0	0	33	0	0	0	0	0	0
37B	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0
37T	0	0	95	0	5	1	0	0	0	64	0	0	0	0	0	0
38B	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0
38T	0	0	125	0	2	0	0	0	0	8	0	0	0	0	0	0
39B	0	0	6	0	0	0	0	0	0	0	2	1	0	0	0	0
39T	0	0	188	0	2	0	0	0	0	52	0	0	0	0	0	0
40B	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0
40T	0	0	36	0	0	0	0	0	0	0	0	0	0	0	0	2
41B	0	0	25	0	1	0	0	0	0	5	0	0	0	0	0	0
41T	0	0	124	0	0	0	0	0	0	3	0	0	0	0	0	0
42B	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0
42T	0	0	33	0	1	0	1	0	0	0	1	0	0	0	0	0
43B	0	0	18	0	2	0	0	0	0	8	0	0	0	0	0	0
43T	0	0	20	0	2	0	0	0	0	0	0	0	0	0	0	0
44B	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
44T	0	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0
45B	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
45T	0	0	50	0	1	0	0	0	0	0	0	0	0	0	0	0
46B	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0
46T	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
47B	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0
47T	0	0	35	0	1	0	0	0	1	0	0	0	0	0	0	0
48B	0	0	4	0	1	0	0	0	0	0	0	0	0	0	0	0
48T	0	0	65	2	0	0	0	0	0	2	0	0	0	0	0	0
49B	0	0	4	0	3	0	0	0	0	2	0	0	0	0	0	0
49T	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
50B	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
50T	0	0	12	1	0	0	0	0	0	1	0	0	0	0	0	0
51B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
51T	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
52B	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0
52T	0	0	4	1	3	0	0	0	1	0	0	0	0	0	0	1
53B	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
53T	0	0	5	0	1	0	0	0	0	0	0	0	0	0	0	0
54B	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
54T	0	0	15	0	2	0	0	0	0	3	0	0	0	0	0	6
55B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
55T	0	0	3	0	2	0	0	0	0	0	0	0	0	0	0	0
56B	0	0	1	0	1	0	1	0	0	2	0	0	0	1	0	0
56T	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
57B	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
57T	1	0	14	0	1	0	0	0	0	0	0	0	0	0	0	6
58B	0	0	1	0	3	0	0	0	2	0	0	0	0	0	0	0
58T	0	0	4	0	9	0	0	0	0	1	0	0	0	0	1	0

Appendix I.3B (Continued)

SAMPLE NO.	EM	AR	EU	TV	TH	CO	PO	PT	AB	CR	NA	MT	DI	CH	RC	IC
59B	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0
59T	0	0	47	1	11	0	0	0	1	4	0	0	0	0	0	1
60B	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
60T	0	0	16	0	0	0	0	0	0	2	0	0	0	0	0	1
61B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
61T	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0
62B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
62T	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
63B	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	1
63T	0	0	2	0	0	0	0	0	2	0	0	0	0	0	0	1
64B	0	0	0	2	0	1	0	0	2	1	0	0	0	0	0	0
64T	0	0	4	0	1	0	0	0	0	3	0	0	0	0	0	19
65B	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
65T	0	0	4	0	1	0	0	0	0	6	0	0	0	0	0	0
66B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
66T	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
67B	0	0	5	0	1	0	0	0	0	0	0	0	0	0	0	0
67T	0	0	88	1	0	0	0	0	0	4	0	0	0	0	0	0
68B	0	0	7	0	1	0	0	0	0	0	0	0	0	0	0	1
68T	0	0	133	1	0	0	1	0	0	8	0	1	0	0	0	5
69B	0	0	1	1	0	1	0	0	0	2	0	0	0	0	0	0
69T	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
70B	0	0	56	0	0	0	0	0	0	0	5	0	0	0	0	0
70T	0	0	76	0	0	0	0	0	0	9	0	0	0	0	0	3

Appendix I.4 Raw data of abiotic variables measured in Hobbs-Mackenzie Creek. (DM = dry mass; AFDM = ash-free dry mass; EVEN = evenness; E = even; U = uneven; PERI = periphyton; A = absent; P = present; B = bottom; T = top; C.V. = current velocity; SURF = surface area)

SAMPLE NO.	DM (mg/cm^2)	AFDM (mg/cm^2)	SILT (mg/cm^2)	EVEN E=0,U=1	PERI A=0,P=1	FACE B=0,T=1	C.V. (cm/s)	DEPTH (cm)	SURF (cm^2)	FROUDE NO.
1B	0.050	0.037	0.013	0	0	0	10.0	4.5	62.0	0.023
1T	2.771	1.556	1.215	0	1	1	10.0	4.5	53.6	0.068
2B	0.339	0.145	0.194	1	0	0	36.1	5.0	72.3	0.266
2T	5.812	0.633	5.179	1	1	1	36.1	5.0	91.1	0.665
3B	0.647	0.460	0.187	1	0	0	14.4	5.5	102.0	0.038
3T	1.409	0.366	1.044	1	1	1	14.4	5.5	101.1	0.085
4B	0.260	0.036	0.224	0	1	0	19.7	6.0	139.9	0.066
4T	31.406	3.719	27.687	0	1	1	19.7	6.0	43.4	0.132
5B	1.581	0.046	1.535	0	1	0	12.9	8.0	71.4	0.021
5T	2.370	0.700	1.671	0	1	1	12.9	8.0	83.2	0.034
6B	12.758	0.343	12.415	0	1	0	19.3	4.5	193.9	0.085
6T	3.950	0.514	3.436	0	1	1	19.3	4.5	42.4	0.254
7B	1.910	0.348	1.563	0	1	0	19.3	4.5	97.2	0.085
7T	2.392	0.303	2.089	0	1	1	19.3	4.5	184.7	0.254
8B	6.715	0.310	6.405	0	1	0	16.1	4.5	32.6	0.059
8T	2.617	0.233	2.384	0	1	1	16.1	4.5	109.0	0.176
9B	0.204	0.054	0.150	0	1	0	29.0	7.9	64.6	0.109
9T	9.386	3.790	5.597	0	1	1	29.0	7.9	17.6	0.175
10B	0.154	0.029	0.125	0	1	0	25.8	9.0	83.8	0.075
10T	7.256	0.913	6.343	0	1	1	25.8	9.0	93.2	0.113
11B	0.461	0.106	0.356	1	1	0	32.2	9.0	28.4	0.118
11T	8.797	2.506	6.290	1	1	1	32.2	9.0	38.9	0.176
12B	0.177	0.044	0.133	0	0	0	16.1	11.0	27.1	0.024
12T	0.902	0.352	0.550	0	1	1	16.1	11.0	64.5	0.033
13B	0.425	0.234	0.191	0	1	0	29.0	8.0	59.3	0.107
13T	2.686	0.925	1.760	0	1	1	29.0	8.0	92.6	0.172
14B	0.442	0.235	0.208	:	0	0	35.5	6.0	26.0	0.214
14T	6.833	2.757	4.076	1	1	1	35.5	6.0	50.2	0.427
15B	0.377	0.190	0.186	1	1	0	38.7	8.0	46.2	0.191
15T	4.287	1.796	2.491	1	1	1	38.7	8.0	59.9	0.305
16B	0.253	0.083	0.170	1	1	0	25.8	8.0	30.0	0.085
16T	5.444	1.235	4.208	1	1	1	25.8	8.0	40.8	0.136
17B	0.252	0.076	0.176	0	0	0	19.3	4.0	47.2	0.095
17T	4.818	2.008	2.810	0	0	1	19.3	4.0	58.9	0.381
18B	0.072	0.026	0.046	0	0	0	19.3	3.5	65.5	0.109
18T	0.112	0.039	0.072	0	0	1	19.3	3.5	63.5	0.762
19B	3.004	0.080	2.924	1	0	0	19.3	5.0	72.5	0.076
19T	1.137	0.164	0.973	1	0	1	19.3	5.0	14.6	0.191
20B	3.739	0.354	3.385	1	0	0	19.3	5.0	107.2	0.076
20T	0.077	0.024	0.053	1	0	1	19.3	5.0	123.9	0.191
21B	11.959	0.049	11.911	1	0	0	16.1	4.5	137.8	0.059
21T	15.185	0.683	14.502	1	0	1	16.1	4.5	54.6	0.176
22B	0.026	0.100	0.000	0	0	0	35.5	8.0	49.9	0.160
22T	0.089	0.026	0.063	0	0	1	35.5	8.0	71.9	0.256
23B	3.383	0.422	2.961	1	0	0	51.6	5.0	111.6	0.542
23T	1.650	1.025	0.624	1	0	1	51.6	5.0	31.4	1.356
24B	1.777	0.044	1.733	1	0	0	45.1	8.0	90.5	0.259
24T	0.379	0.047	0.332	1	0	1	45.1	8.0	50.9	0.415
25B	0.047	0.019	0.028	1	0	0	19.3	4.0	84.4	0.095
25T	0.692	0.141	0.551	1	0	1	19.3	4.0	37.0	0.381
26B	12.469	0.405	12.064	1	0	0	19.3	4.5	136.9	0.085
26T	1.083	0.183	0.900	1	0	1	19.3	4.5	52.9	0.254
27B	0.248	0.055	0.193	0	0	0	19.3	7.0	75.8	0.054
27T	0.299	0.091	0.207	0	0	1	19.3	7.0	24.1	0.095
28B	0.039	0.018	0.021	0	0	0	19.3	8.0	119.5	0.048
28T	2.483	0.185	2.298	0	0	1	19.3	8.0	64.4	0.076
29B	0.091	0.039	0.051	0	0	0	22.6	7.0	48.6	0.074
29T	0.618	0.090	0.528	0	0	1	22.6	7.0	44.5	0.130
30B	0.207	0.058	0.150	0	0	0	27.7	5.0	69.4	0.157
30T	0.105	0.002	0.103	0	0	1	27.7	5.0	50.5	0.392
31B	0.474	0.019	0.455	0	0	0	29.0	11.0	115.5	0.078
31T	3.523	0.211	3.312	0	0	1	29.0	11.0	57.7	0.107
32B	0.150	0.025	0.125	1	1	0	12.9	3.5	112.8	0.048

Appendix I.4 (Continued)

SAMPLE NO.	DM (mg/cm²)	AFDM (mg/cm²)	SILT (mg/cm²)	EVEN E=0,U=1	PERI A=0,P=1	FACE B=0,T=1	C.V. (cm/s)	DEPTH (cm)	SURF (cm²)	FROUDE NO.
32T	0.155	0.074	0.081	1	1	1	12.9	3.5	180.0	0.339
33B	0.411	0.255	0.156	1	1	0	16.1	4.0	162.4	0.066
33T	0.305	0.153	0.152	1	1	1	16.1	4.0	223.3	0.265
34B	0.376	0.103	0.273	1	1	0	22.6	4.5	74.0	0.115
34T	0.849	0.373	0.476	1	1	1	22.6	4.5	56.9	0.346
35B	1.963	0.558	1.405	1	1	0	12.9	5.0	51.3	0.034
35T	5.677	1.358	4.318	1	0	1	12.9	5.0	37.1	0.085
36B	0.072	0.023	0.049	1	0	0	48.4	4.0	168.8	0.596
36T	0.910	0.086	0.824	1	0	1	48.4	4.0	130.7	2.383
37B	0.058	0.028	0.030	0	1	0	41.9	7.0	90.0	0.256
37T	5.923	0.411	5.512	0	1	1	41.9	7.0	94.6	0.447
38B	0.034	0.009	0.024	1	1	0	41.9	4.5	106.8	0.398
38T	0.079	0.025	0.053	1	0	1	41.9	4.5	106.8	1.193
39B	0.321	0.018	0.303	1	1	0	38.7	6.0	83.6	0.254
39T	0.370	0.093	0.277	1	1	1	38.7	6.0	50.5	0.508
40B	0.412	0.023	0.389	1	0	0	51.6	4.0	87.7	0.678
40T	0.106	0.030	0.076	1	1	1	51.6	4.0	76.6	2.711
41B	0.337	0.042	0.296	0	1	0	38.7	4.5	62.6	0.339
41T	0.228	0.058	0.170	0	1	1	38.7	4.5	118.2	1.017
42B	0.131	0.015	0.116	0	0	0	35.5	5.0	58.7	0.256
42T	0.918	0.180	0.739	0	0	1	35.5	5.0	24.5	0.641
43B	0.197	0.029	0.168	1	0	0	41.9	6.0	101.9	0.298
43T	0.053	0.016	0.037	1	0	1	41.9	6.0	132.7	0.597
44B	1.596	0.504	1.091	0	0	0	41.9	8.5	70.0	0.211
44T	1.299	0.205	1.094	0	0	1	41.9	8.5	68.2	0.325
45B	0.168	0.017	0.151	0	0	0	45.1	8.5	119.9	0.244
45T	1.209	0.128	1.081	0	0	1	45.1	8.5	99.6	0.377
46B	1.244	0.213	1.031	1	1	0	45.1	6.0	164.4	0.346
46T	0.589	0.431	0.158	1	1	1	45.1	6.0	189.9	0.692
47B	0.358	0.050	0.308	1	1	0	38.7	6.5	48.0	0.235
47T	3.599	0.344	3.255	1	1	1	38.7	6.5	45.9	0.436
48B	1.107	0.657	0.450	1	1	0	32.2	4.5	93.6	0.235
49B	0.349	0.151	0.198	0	1	0	32.2	7.0	114.6	0.151
49T	0.077	0.044	0.033	0	1	1	32.2	7.0	121.0	0.265
50B	1.109	0.131	0.978	1	0	0	25.8	6.0	69.7	0.113
50T	0.169	0.062	0.107	1	0	1	25.8	6.0	103.4	0.226
51B	0.111	0.055	0.055	0	0	0	25.8	13.0	19.9	0.052
51T	0.113	0.047	0.066	0	0	1	25.8	13.0	25.6	0.068
52B	0.224	0.027	0.197	0	0	0	19.3	8.0	33.5	0.048
52T	0.083	0.029	0.054	0	0	1	19.3	8.0	52.1	0.076
53B	0.105	0.036	0.069	0	1	0	32.2	4.0	27.5	0.265
53T	0.544	0.288	0.256	0	1	1	32.2	4.0	37.9	1.059
54B	0.093	0.023	0.070	0	1	0	29.0	5.0	68.5	0.172
54T	1.057	0.112	0.945	0	1	1	29.0	5.0	77.7	0.429
55B	0.031	0.025	0.006	0	0	0	19.3	3.5	85.0	0.109
55T	0.237	0.115	0.121	0	0	1	19.3	3.5	126.0	0.762
56B	1.781	1.549	0.232	0	0	0	32.2	3.5	29.7	0.303
56T	0.075	0.041	0.034	0	0	1	32.2	3.5	56.0	2.118
57B	1.275	0.162	1.113	1	1	0	25.8	4.0	78.8	0.169
57T	0.420	0.206	0.214	1	1	1	25.8	4.0	92.8	0.678
58B	0.445	0.078	0.366	1	1	0	22.6	4.0	128.9	0.130
58T	0.139	0.062	0.076	1	1	1	22.6	4.0	149.2	0.519
59B	0.966	0.173	0.794	1	1	0	22.6	4.0	67.8	0.130
59T	0.994	0.573	0.421	1	1	1	22.6	4.0	85.6	0.519
60B	5.450	0.178	5.272	1	1	0	19.3	4.0	30.9	0.095
60T	0.607	0.139	0.467	1	1	1	19.3	4.0	33.8	0.381
61B	0.282	0.019	0.263	0	0	0	22.6	9.0	41.5	0.058
61T	0.652	0.134	0.518	0	0	1	22.6	9.0	56.9	0.086
62B	0.633	0.525	0.108	0	0	0	54.8	7.5	15.8	0.408
62T	0.444	0.185	0.259	0	0	1	54.8	7.5	27.0	0.680
63B	0.786	0.125	0.661	0	0	0	22.6	6.0	54.6	0.086
63T	3.985	0.579	3.406	0	0	1	22.6	6.0	58.4	0.173
64B	7.014	0.297	6.717	1	1	0	35.5	8.5	64.7	0.151
64T	0.143	0.032	0.112	1	1	1	35.5	8.5	82.4	0.233
65B	0.026	0.006	0.020	1	1	0	16.1	7.0	49.6	0.038
65T	0.055	0.020	0.035	1	1	1	16.1	7.0	169.8	0.066

Appendix I.4 (Continued)

SAMPLE NO.	DM (mg/cm²)	AFDM (mg/cm²)	SILT (mg/cm²)	EVEN E=0, U=1	PERI A=0, P=1	FACE B=0, T=1	C.V. (cm/s)	DEPTH (cm)	SURF (cm²)	FROUDE NO.
66B	0.021	0.003	0.018	0	0	0	19.3	7.5	33.0	0.051
66T	0.018	0.009	0.008	0	0	1	19.3	7.5	74.0	0.085
67B	0.064	0.039	0.025	1	1	0	45.1	6.0	125.6	0.346
67T	0.229	0.065	0.163	1	1	1	45.1	6.0	135.2	0.692
68B	2.685	0.289	2.396	1	1	0	41.9	4.5	44.7	0.398
68T	0.686	0.222	0.464	1	1	1	41.9	4.5	109.5	1.193
69B	1.850	0.440	1.410	0	0	0	22.6	3.5	27.3	0.148
69T	1.403	0.659	0.744	0	0	1	22.6	3.5	27.3	1.038
70B	3.625	0.829	2.796	1	0	0	38.7	6.0	53.9	0.254
70T	2.177	0.219	1.958	1	0	1	38.7	6.0	93.8	0.508

Appendix I.5 Black fly size data (head width) from Hobbs-Mackenzie Creek. Number of animals in each size class.

SAMPLE	HEAD WIDTH (mm)														
NO.	0.25	0.51	0.76	1.01	1.26	1.52	1.77	2.02	2.27	2.53	2.78	3.03	3.28	3.54	3.79
1B	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
2T	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
6T	0	1	0	0	1	1	0	0	0	2	0	0	0	0	0
9T	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
11T	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0
15B	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
18T	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
21T	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
22T	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
23T	0	1	1	1	1	1	0	5	1	1	5	6	3	8	4
24B	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0
25T	0	0	0	0	0	0	2	0	1	1	1	1	0	1	0
26B	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
26T	0	0	0	0	0	0	0	0	0	0	0	1	0	2	3
27B	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
28T	0	0	0	0	0	0	2	1	0	0	0	0	0	0	2
29T	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
30T	0	0	0	0	1	0	0	1	0	0	0	0	0	1	1
31B	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
31T	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
33B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
33T	0	1	0	0	0	1	0	0	1	0	0	0	1	0	0
35T	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
36B	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
36T	0	0	5	0	1	0	3	0	1	2	0	1	0	0	0
38B	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
38T	0	0	1	2	0	0	2	0	2	3	1	1	1	0	1
39T	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
40T	0	0	1	1	1	1	0	0	0	0	0	1	0	0	0
41B	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
41T	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
42T	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0
43T	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1
45T	0	1	2	1	0	0	0	2	2	0	1	0	0	0	0
46B	0	0	0	0	0	0	0	1	2	1	1	1	0	1	0
47T	0	0	1	1	0	0	1	0	1	1	2	0	0	0	0
48B	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
48T	0	0	1	2	0	0	2	0	1	6	1	1	0	1	0
49B	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
49T	0	0	0	0	0	0	0	0	0	0	0	1	2	1	0
50T	0	0	0	0	0	2	1	0	0	0	0	1	1	0	0
51B	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
52T	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
53T	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
56T	0	0	0	0	0	0	0	0	0	2	0	1	1	2	0
57T	0	0	1	1	0	1	2	0	1	1	2	1	1	2	0
58T	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0
59B	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
59T	1	0	1	0	0	1	2	0	0	0	0	0	0	0	0
60T	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0
61T	0	0	0	0	1	0	0	2	1	0	0	0	0	0	0
62B	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
63B	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
63T	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
64T	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
67B	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
67T	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0
68B	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1

Appendix I.5 (Continued)

SAMPLE	HEAD WIDTH (mm)														
NO.	0.25	0.51	0.76	1.01	1.26	1.52	1.77	2.02	2.27	2.53	2.78	3.03	3.28	3.54	3.79
68T	0	0	0	2	1	1	0	1	0	0	0	1	0	0	0
69T	0	0	0	1	0	0	1	1	0	1	1	1	0	0	0
70B	0	0	1	1	0	2	1	0	0	0	0	1	0	1	0
70T	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0

Appendix I.6A Taxonomic list of animals collected from Wigle Creek, and abbreviations of taxonomic names.

TAXON	ABBREVIATION
Coelenterata	
Hydra	HD
Platyhelminthes	
Tricladida	
Dugesia	DU
Mollusca	
Gastropoda	
Physa	PH
Annelida	
Oligochaeta	OL
Hirudinea	
Glossophoniidae	
Glossophonia heteroclides	GH
Arthropoda	
Arachnida	
Hydracarina	HA
Hexapoda	
Collembola	
Isotomidae	
Isotomurus	IS
Ephemeroptera	
Baetidae	
Baetis	BA
Caenidae	
Caenis	CA
Odonata	
Zygoptera	
Calopterygidae	
Calopteryx	CL
Coleoptera	
Hydrophilidae	HY
Hemiptera	
Mesoveliidae	
Mesovelia	ME
Corixidae	
Hesperocorixa	HC
Trichoptera	
Hydroptilidae	
Hydroptila	HT
Hydropsychidae	
Hydropsyche	HP
Diptera	
Tipulidae	
Hexatoma	HE
Simuliidae	
Simulium vittatum	SV
Empididae	EM
Chironomidae	
Immatures	IC
Pupae	CP
Chironomus	CH
Corynoneura	CO
Cricotopus	CR
Dicrotendipes	DI
Eukiefferiella	EU
Nanocladius	NA
Orthocladius	OR
Paratanytarsus	PT

Appendix I.6A (Continued)

TAXON	ABBREVIATION
Chironomidae (continued)	
Paratendipes	PR
Polypedilum	PO
Rheotanytarsus	RH
Thienemanniella	TH
Thienemannimyia	TY

Appendix I.6B Taxonomic list of animals collected from Hobbs-Mackenzie Creek, and abbreviations of taxonomic names.

TAXON	ABBREVIATION
Coelenterata	
Hydra	HD
Platyhelminthes	
Tricladida	
Dugesia	DU
Mollusca	
Gastropoda	
Physa	PH
Pelecypoda	
Sphaeriidae	
Sphaerium	SP
Annelida	
Oligochaeta	OL
Arthropoda	
Arachnida	
Hydracarina	HA
Crustacea	
Isopoda	
Asellidae	
Asellus	AS
Hexapoda	
Collembola	
Isotomidae	
Isotomurus	IS
Ephemeroptera	
Baetidae	
Baetis flavistriga	BF
Heptageniidae	
Stenonema	ST
Coleoptera	
Elmidae	EL
Trichoptera	
Hydroptilidae	
Hydroptila	HT
Hydropsychidae	
Hydropsyche	HP
Philopotamidae	
Chimarra	CM
Diptera	
Tipulidae	
Antocha	AN
Simuliidae	
Simulium vittatum	SV
Empididae	EM
Ceratopogonidae	
Atrichopogon	AR
Chironomidae	
Immatures	IC
Ablabesmyia	AB
Chironomus	CH
Corynoneura	CO
Cricotopus	CR
Dicrotendipes	DI
Eukiefferiella	EU
Metriocnemus	MT
Nanocladius	NA
Paratanytarsus	PT
Polypedilum	PO
Rheocricotopus	RC
Thienemanniella	TH
Tvetenia	TV

APPENDIX II

Appendix II.1 Light levels (lux) over experimental tanks.

TANK	POSITION*	REPL.1	REPL.2	REPL.3	MEAN	S.E.
1	U	435.9	452.1	441.3	443.1	4.76
	D	430.6	446.7	446.7	441.3	5.37
2	U	414.4	457.5	473.6	448.5	17.67
	D	419.8	462.9	457.5	446.7	13.56
3	U	425.2	435.9	457.5	439.5	9.50
	D	419.8	425.2	446.7	430.6	8.22

* U: Upstream, D: Downstream

Appendix II.2A Numbers of black flies on smooth even and smooth uneven tiles in the first replicate of the pilot study using low larval density and bare tiles. Note that the last data row represents a 24 h time period.

TIME (min)	NUMBER OF BLACK FLIES	
	UNEVEN	EVEN
0	176	176
20	183	152
40	187	154
60	188	155
80	177	156
100	175	151
120	176	150
140	175	150
160	173	148
180	176	153
200	175	154
220	172	153
240	174	155
24 h	166	136

Appendix II.2B Numbers of black flies on smooth even and smooth uneven tiles in the second replicate of the pilot study using low larval density and bare tiles. Note that the last data row represents a 24 h time period.

TIME (min)	NUMBER OF BLACK FLIES	
	UNEVEN	EVEN
0	175	81
20	189	83
40	185	80
60	191	84
80	191	84
100	194	86
120	194	83
140	194	83
160	196	79
180	196	79
200	192	74
220	198	76
240	205	78
24 h	178	82

Appendix II.3 Detrital biomass on tiles, as measured by dry mass (Experiment 4, high larval density, periphyton covered tiles, 3, 4 August 1990). Tile types are denoted by SE (smooth even), RE (rough even), SU (smooth uneven), and RU (rough uneven).

	DRY MASS (g)				
TREATMENT	REPL.1	REPL.2	REPL.3	MEAN	S.E.
SE	0.0077	0.0279	0.0067	0.0141	0.0069
RE	0.3335	0.2036	0.7040	0.4137	0.1499
SU	0.0109	0.0319	0.0175	0.0201	0.0062
RU	0.5473	0.6702	0.2780	0.4985	0.1158

Appendix II.4 Periphyton biomass on tiles, as measured by ash free dry mass (AFDM) (Experiment 4, high larval density, periphyton covered tiles, 3, 4 August 1990). Tile types are denoted by SE (smooth even), RE (rough even), SU (smooth uneven), and RU (rough uneven).

	AFDM (g)				
TREATMENT	REPL.1	REPL.2	REPL.3	MEAN	S.E.
SE	0.0027	0.0056	0.0030	0.0038	0.0009
RE	0.0840	0.0349	0.0785	0.0658	0.0155
SU	0.0004	0.0052	0.0005	0.0020	0.0016
RU	0.0805	0.1444	0.1302	0.1184	0.0194

Appendix II.5 Raw data for laboratory Experiment 1 (low larval density, and tiles with periphyton absent, 9-10 May 1990). Tile surfaces are denoted by SE (smooth even), RE (rough even), SU (smooth uneven), and RU (rough uneven). Note that the last data row represents a 24 h time period (S.E. = standard error; REPL = replicate).

	SE					RE				
TIME	REPL 1	REPL 2	REPL 3	Mean	S.E.	REPL 1	REPL 2	REPL 3	Mean	S.E.
0	105	85	112	100.67	8.09	150	140	128	139.33	6.36
20	98	53	129	93.33	22.06	180	103	120	134.33	23.35
40	95	60	128	94.33	19.63	201	112	123	145.33	28.01
60	98	61	124	94.33	18.28	194	124	120	146.00	24.03
80	108	68	105	93.67	12.86	183	130	117	143.33	20.19
100	96	66	104	88.67	11.57	181	126	112	139.67	21.06
120	92	66	112	90.00	13.32	191	126	106	141.00	25.66
140	87	70	114	90.33	12.81	180	123	109	137.33	21.71
160	91	71	112	91.33	11.84	192	128	126	148.67	21.67
180	87	69	112	89.33	12.47	193	125	112	143.33	25.12
200	91	68	112	90.33	12.71	196	123	114	144.33	25.96
220	88	68	109	88.33	11.84	202	120	117	146.33	27.85
240	88	64	94	82.00	9.17	213	130	99	147.33	34.03
260	88	54	105	82.33	14.99	209	133	110	150.67	29.91
24h	60	50	80	63.33	8.82	139	103	101	114.33	12.35

Appendix II.5 (Continued)

	SU					RU				
TIME	REPL 1	REPL 2	REPL 3	Mean	S.E.	REPL 1	REPL 2	REPL 3	Mean	S.E.
0	157	157	138	150.67	6.33	140	92	155	129.00	19.00
20	151	119	82	117.33	19.94	131	71	163	121.67	26.96
40	156	116	93	121.67	18.41	95	70	157	107.33	25.86
60	157	122	102	127.00	16.07	133	77	181	130.33	30.05
80	148	125	102	125.00	13.28	131	74	217	140.67	41.56
100	151	129	96	125.33	15.98	119	83	209	137.00	37.47
120	151	121	108	126.67	12.73	128	80	226	144.67	42.96
140	149	126	100	125.00	14.15	127	77	235	146.33	46.62
160	149	130	94	124.33	16.13	126	77	223	142.00	42.90
180	142	119	113	124.67	8.84	125	75	217	139.00	41.59
200	146	122	114	127.33	9.61	128	79	225	144.00	42.90
220	145	130	117	130.67	8.09	129	77	235	147.00	46.49
240	143	145	86	124.67	19.34	134	75	248	152.33	50.78
260	151	138	89	126.00	18.88	132	72	243	149.00	50.09
24h	130	140	128	132.67	3.71	80	79	178	112.33	32.83

Appendix II.6 Raw data for laboratory Experiment 2 (low larval density, and tiles with periphyton absent, 19-20 July 1990). Tile surfaces are denoted by SE (smooth even), RE (rough even), SU (smooth uneven), and RU (rough uneven). Note that the last data row represents a 24 h time period. Missing data are represented by NA (S.E. = standard error; REPL = replicate).

	SE					RE				
TIME	REPL 1	REPL 2	REPL 3	Mean	S.E.	REPL 1	REPL 2	REPL 3	Mean	S.E.
0	92	129	74	98.33	16.19	95	138	112	115.00	12.50
20	91	132	65	96.00	19.50	95	115	118	109.33	7.22
40	77	123	53	84.33	20.54	91	137	138	122.00	15.50
60	86	132	41	86.33	26.27	81	127	129	112.33	15.68
80	88	122	39	83.00	24.09	113	133	121	122.33	5.81
100	88	116	40	81.33	22.19	110	127	127	121.33	5.67
120	76	116	43	78.33	21.11	105	127	129	120.33	7.69
140	74	114	42	76.67	20.83	105	119	122	115.33	5.24
160	74	126	42	80.67	24.48	103	125	128	118.67	7.88
180	72	117	46	78.33	20.74	103	127	126	118.67	7.84
200	72	121	43	78.67	22.76	102	134	134	123.33	10.67
220	65	122	52	79.67	21.50	103	136	134	124.33	10.68
240	64	NA	57	60.50	3.50	103	NA	128	115.50	12.50
24h	23	72	30	41.67	15.30	52	96	112	86.67	17.94

Appendix II.6 (Continued)

	SU					RU				
TIME	REPL 1	REPL 2	REPL 3	Mean	S.E.	REPL 1	REPL 2	REPL 3	Mean	S.E.
0	92	95	68	85.00	8.54	106	119	90	105.00	8.39
20	94	85	84	87.67	3.18	105	121	72	99.33	14.43
40	111	82	68	87.00	12.66	108	134	98	113.33	10.73
60	104	80	79	87.67	8.17	113	130	83	108.67	13.74
80	90	82	72	81.33	5.21	93	125	84	100.67	12.44
100	90	82	71	81.00	5.51	98	128	76	100.67	15.07
120	92	82	80	84.67	3.71	97	128	72	99.00	16.20
140	92	88	73	84.33	5.78	97	127	70	98.00	16.46
160	97	90	69	85.33	8.41	85	123	74	94.00	14.84
180	97	92	67	85.33	9.28	89	129	79	99.00	15.28
200	97	90	63	83.33	10.37	89	130	67	95.33	18.46
220	95	103	69	89.00	10.26	84	126	71	93.67	16.60
240	93	NA	77	85.00	8.00	81	NA	71	76.00	5.00
24h	20	77	45	47.33	16.50	17	70	92	59.67	22.26

Appendix II.7 Raw data for laboratory Experiment 3 (high larval density, and tiles with periphyton absent, 1-2 August 1990). Tile surfaces are denoted by SE (smooth even), RE (rough even), SU (smooth uneven), and RU (rough uneven). Note that the last data row represents a 24 h time period (S.E. = standard error; REPL = replicate).

	SE					RE				
TIME	REPL 1	REPL 2	REPL 3	Mean	S.E.	REPL 1	REPL 2	REPL 3	Mean	S.E.
0	358	803	734	631.67	138.28	404	482	746	544.00	103.48
20	355	599	640	531.33	88.96	403	623	743	589.67	99.55
40	447	539	619	535.00	49.69	420	547	741	569.33	93.34
60	485	593	623	567.00	41.90	447	615	685	582.33	70.62
80	427	659	808	631.33	110.85	385	580	948	637.67	165.06
100	444	672	638	584.67	71.01	491	651	756	599.33	108.49
120	385	578	512	491.67	56.63	388	532	574	498.00	56.32
140	404	479	713	532.00	93.05	389	594	806	596.33	120.38
160	325	531	722	526.00	114.63	293	575	843	570.33	158.79
180	375	606	807	596.00	124.81	422	443	791	552.00	119.65
200	453	403	828	561.33	134.11	502	582	772	618.67	80.07
220	398	671	618	562.33	83.58	405	595	748	582.67	99.21
240	396	569	668	544.33	79.48	390	684	648	574.00	92.59
24h	310	511	582	467.67	81.45	388	433	850	557.00	147.07

Appendix II.7 (Continued)

	SU					RU				
TIME	REPL 1	REPL 2	REPL 3	Mean	S.E.	REPL 1	REPL 2	REPL 3	Mean	S.E.
0	496	558	561	538.33	21.18	422	615	656	564.33	72.14
20	505	595	658	586.00	44.40	553	582	519	551.33	18.21
40	563	650	643	618.67	27.91	560	562	442	521.33	39.67
60	522	675	493	563.33	56.46	537	526	442	501.67	30.00
80	446	566	630	547.33	53.93	481	516	628	541.67	44.33
100	420	562	657	546.33	68.86	388	563	502	484.33	51.28
120	562	571	594	575.67	9.53	491	500	630	540.33	44.91
140	442	542	1008	664.00	174.41	491	348	798	545.67	132.75
160	327	479	657	487.67	95.36	342	396	552	430.00	62.96
180	533	526	717	592.00	62.53	547	596	662	601.67	33.32
200	432	525	539	498.67	33.58	449	300	771	506.67	138.99
220	502	587	558	549.00	24.95	510	472	503	495.00	11.68
240	526	632	841	666.33	92.54	522	446	817	595.00	113.15
24h	360	461	228	349.67	67.46	375	420	215	336.67	62.20

Appendix II.8 Raw data for laboratory Experiment 4 (high larval density, and tiles with periphyton present, 3-4 August 1990). Tile surfaces are denoted by SE (smooth even), RE (rough even), SU (smooth uneven), and RU (rough uneven). Note that the last data row represents a 24 h time period (S.E. = standard error; REPL = replicate).

	SE					RE				
TIME	REPL 1	REPL 2	REPL 3	Mean	S.E.	REPL 1	REPL 2	REPL 3	Mean	S.E.
0	580	750	957	762.33	109.01	709	707	792	736.00	28.01
20	522	857	995	791.33	140.44	497	526	888	637.00	125.78
40	590	718	1039	782.33	133.55	521	862	825	736.00	108.03
60	561	797	1069	809.00	146.77	563	918	844	775.00	108.13
80	528	733	1019	760.00	142.38	575	806	812	731.00	78.02
100	622	729	947	766.00	95.63	612	562	916	696.67	110.61
120	675	674	1026	791.67	117.17	598	956	795	783.00	103.52
140	556	637	976	723.00	128.64	512	577	840	643.00	100.27
160	574	627	890	697.00	97.71	498	707	918	707.67	121.24
180	541	677	686	634.67	46.91	487	544	876	635.67	121.29
200	560	729	800	696.33	71.18	504	488	647	546.33	50.54
220	536	685	786	669.00	72.61	503	490	589	527.33	31.06
240	367	617	825	603.00	132.40	301	541	469	437.00	71.11
24h	633	502	658	597.67	48.37	272	379	381	344.00	36.00

Appendix II.8 (Continued)

	SU					RU				
TIME	REPL 1	REPL 2	REPL 3	Mean	S.E.	REPL 1	REPL 2	REPL 3	Mean	S.E.
0	757	443	876	692.00	129.15	785	624	779	729.33	52.70
20	807	494	722	674.33	93.45	782	609	586	659.00	61.86
40	834	669	901	801.33	68.94	723	470	628	607.00	73.79
60	948	876	906	910.00	20.88	677	494	615	595.33	53.73
80	869	746	803	806.00	35.54	803	535	624	654.00	78.81
100	870	546	843	753.00	103.79	769	484	694	649.00	85.29
120	873	839	704	805.33	51.61	817	509	545	623.67	97.22
140	943	617	370	643.33	165.93	834	477	360	557.00	142.56
160	878	723	459	686.67	122.31	711	369	332	470.67	120.64
180	885	653	652	730.00	77.50	721	414	528	554.33	89.60
200	845	603	619	689.00	78.14	665	467	419	517.00	75.29
220	919	594	622	711.67	103.98	585	415	388	462.67	61.66
240	625	599	354	526.00	86.33	647	438	345	476.67	89.30
24h	629	434	638	567.00	66.55	339	249	248	278.67	30.17

APPENDIX III

Appendix III.1A Taxonomic composition of samples collected during tile manipulations from Hobbs-Mackenzie Creek on June 28, 1990. Taxonomic abbreviations are listed in Appendix III.4. (TRT = Treatment; TRT 1 = No removal, TRT 2 = Removal of black flies, TRT 3 = Removal of all taxa).

TILE NO.	TRT	DAYS IN	HD	DU	PH	OL	HA	AS	IS	BF	ST	EL	VL	HT	HP	SV
253	1	1	0	0	0	0	0	6	0	0	0	0	0	0	4	0
254	1	1	1	0	0	0	0	0	0	2	0	0	0	0	1	0
255	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
256	1	1	0	0	0	0	0	0	0	2	0	0	1	0	0	1
257	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	2
258	1	1	0	0	0	0	0	2	0	1	0	0	0	0	1	0
235	1	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0
236	1	2	0	0	0	0	0	4	0	0	0	0	0	0	1	0
237	1	2	0	0	0	0	0	5	0	7	0	0	0	0	0	0
238	1	2	0	3	0	0	0	2	0	0	0	0	0	0	1	0
239	1	2	0	0	0	0	0	5	0	1	0	0	0	0	3	1
240	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	5
217	1	3	0	0	0	0	0	5	0	0	0	0	0	0	2	1
218	1	3	0	2	0	0	0	9	0	0	0	0	0	0	1	5
219	1	3	0	0	0	0	0	0	0	1	0	0	0	0	4	0
220	1	3	0	0	0	0	0	2	0	0	0	0	0	0	0	1
221	1	3	0	0	0	0	0	1	0	0	0	0	0	0	0	0
222	1	3	0	0	0	0	0	0	0	0	0	0	0	0	1	2
199	1	4	0	0	0	0	0	3	0	1	0	0	0	0	0	1
200	1	4	0	0	0	0	0	0	0	0	0	0	0	0	0	2
202	1	4	0	1	0	0	0	4	0	0	0	0	1	0	1	0
181	1	5	0	0	0	0	0	1	0	0	0	0	0	0	2	3
182	1	5	0	0	0	0	0	1	0	0	0	0	0	0	1	0
183	1	5	0	0	0	0	0	0	0	2	0	1	0	0	3	1
184	1	5	0	1	0	0	0	2	0	0	0	0	0	0	0	0
185	1	5	0	0	0	0	0	1	0	1	0	0	0	0	0	1
186	1	5	0	0	0	0	0	1	0	0	0	0	0	0	3	2
163	1	6	0	0	0	0	0	2	0	0	0	0	0	0	1	1
164	1	6	0	0	0	0	0	1	0	1	0	0	0	0	1	1
165	1	6	0	0	0	0	0	0	0	1	0	0	0	0	2	0
166	1	6	0	0	0	0	0	0	0	1	0	0	0	0	2	1
167	1	6	0	0	0	0	0	1	0	0	0	0	0	0	1	1
168	1	6	0	0	0	0	1	2	0	1	1	0	0	0	1	0
145	1	8	0	0	0	0	0	3	0	1	0	0	0	0	2	0
146	1	8	0	0	0	1	0	10	0	0	0	0	0	0	3	1
147	1	8	0	0	0	0	0	3	0	0	0	0	0	0	5	3
148	1	8	0	0	0	0	0	0	0	2	0	0	0	0	4	1
149	1	8	0	0	0	0	0	1	0	1	0	0	0	0	1	0
150	1	8	0	0	0	0	0	1	0	0	0	0	0	0	3	0
127	1	10	0	0	0	0	0	2	0	5	0	0	0	0	2	2
128	1	10	0	1	0	0	1	9	0	0	0	0	0	0	1	0
130	1	10	0	0	0	0	0	0	0	0	0	0	0	0	15	1
131	1	10	0	0	0	0	0	0	0	3	0	0	0	0	8	4
132	1	10	0	0	0	0	0	4	0	1	0	0	0	0	6	1
109	1	12	0	0	0	0	0	2	0	0	0	0	0	0	0	0
110	1	12	0	0	0	0	0	4	0	5	0	0	0	0	16	4
111	1	12	0	0	0	0	0	2	0	2	0	0	0	0	2	3
113	1	12	0	1	0	0	0	2	0	0	0	0	0	0	3	0
114	1	12	0	0	0	0	0	0	0	1	0	0	0	0	1	0
91	1	15	0	0	0	0	0	2	0	0	0	0	0	0	0	0
92	1	15	0	0	0	0	0	2	0	0	0	0	0	0	0	1
93	1	15	0	0	0	0	0	2	0	2	0	1	0	0	16	3
94	1	15	0	0	0	0	0	7	0	3	0	0	0	0	1	0
95	1	15	0	0	0	0	0	6	0	4	0	1	0	0	8	2
96	1	15	0	0	0	0	0	8	0	1	0	0	0	0	11	2

Appendix III.1A (Continued)

TILE NO.	TRT	DAYS IN	HD	DU	PH	OL	HA	AS	IS	BF	ST	EL	VL	HT	HP	SV
73	1	18	0	0	0	0	0	2	0	3	0	0	0	0	4	0
75	1	18	0	0	0	0	0	0	0	0	0	0	0	0	0	7
76	1	18	0	0	0	0	0	1	0	1	0	0	0	1	3	3
77	1	18	0	0	0	0	0	10	0	2	0	0	0	0	1	0
78	1	18	0	0	0	0	0	2	0	3	0	0	0	3	5	1
55	1	21	0	0	0	0	0	10	0	5	0	0	0	0	2	0
56	1	21	0	0	0	0	0	3	0	3	0	0	0	0	4	2
57	1	21	0	0	0	0	0	5	0	5	0	0	0	0	3	1
58	1	21	0	0	0	0	0	10	0	2	0	0	0	0	1	2
59	1	21	0	0	0	0	0	13	0	3	0	0	0	0	8	0
60	1	21	0	0	0	0	0	3	0	1	0	0	0	0	1	2
38	1	24	0	0	0	0	0	3	0	1	0	0	0	0	0	1
39	1	24	0	2	0	0	0	3	0	1	0	0	0	0	1	0
40	1	24	0	0	0	0	0	2	0	5	0	0	0	0	2	3
41	1	24	0	0	0	0	0	3	0	1	0	0	0	0	0	0
42	1	24	0	0	0	0	0	2	0	2	0	0	0	0	1	0
6	1	27	0	0	0	0	0	6	0	0	0	0	0	0	1	0
19	1	27	0	0	0	0	0	4	0	1	0	0	0	0	1	0
20	1	27	0	0	0	0	0	3	0	4	0	0	0	0	5	0
21	1	27	0	0	0	1	0	2	0	1	0	0	0	0	2	2
259	2	1	0	0	0	0	0	1	0	1	0	0	0	0	3	2
260	2	1	0	0	0	0	0	2	0	3	0	0	0	0	0	3
261	2	1	0	0	0	0	0	1	0	1	0	0	0	0	6	1
262	2	1	0	0	0	0	0	2	0	0	0	0	0	0	1	0
263	2	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0
264	2	1	0	0	0	0	0	1	0	1	0	0	0	0	1	3
241	2	2	0	1	0	0	0	0	0	0	0	0	0	0	1	4
242	2	2	0	0	0	0	0	0	0	2	0	0	0	0	2	2
243	2	2	0	0	0	0	0	2	0	0	0	0	0	0	0	1
244	2	2	0	0	0	0	0	0	0	1	0	0	0	2	0	6
245	2	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0
246	2	2	0	0	0	0	0	1	0	1	0	0	0	0	1	0
223	2	3	0	0	0	0	0	1	0	0	0	0	0	0	0	0
225	2	3	0	0	0	0	0	0	0	1	0	0	0	0	0	3
226	2	3	0	0	0	0	0	1	0	1	0	0	0	0	3	1
227	2	3	0	0	0	0	0	2	0	3	0	0	0	0	3	2
228	2	3	0	0	0	1	0	6	0	5	0	0	0	0	15	12
205	2	4	0	0	0	0	0	4	0	1	0	0	0	0	1	0
206	2	4	0	0	0	0	0	1	0	0	0	0	1	0	2	0
207	2	4	0	0	1	0	0	3	0	2	0	0	0	0	0	0
208	2	4	0	0	0	0	0	1	0	0	0	0	0	0	0	2
209	2	4	0	0	0	0	0	1	0	1	0	0	0	0	1	1
210	2	4	0	0	0	0	0	2	0	0	0	0	0	0	0	0
187	2	5	0	0	0	0	0	3	0	1	0	0	0	1	1	0
188	2	5	0	0	0	0	0	1	0	2	0	0	0	0	2	1
189	2	5	0	0	0	0	0	0	0	0	0	0	0	0	0	1
190	2	5	0	0	0	0	0	3	0	1	0	0	0	0	1	0
191	2	5	0	0	0	0	0	3	0	2	0	0	0	0	0	0
192	2	5	0	0	0	0	0	2	0	0	0	0	0	0	1	0
169	2	6	0	0	0	0	0	0	0	4	0	0	0	0	7	3
170	2	6	0	0	0	0	0	1	0	1	0	0	0	0	1	0
172	2	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
173	2	6	0	0	0	0	1	3	0	0	0	0	0	2	1	0
174	2	6	0	0	0	0	0	3	0	1	0	0	0	0	2	2
151	2	8	0	0	0	0	0	0	0	0	0	0	0	0	2	3
152	2	8	0	1	0	0	0	2	0	0	0	0	0	0	15	30
154	2	8	0	0	0	0	0	2	0	2	0	0	0	0	0	0
155	2	8	0	0	0	0	0	7	0	2	0	0	0	0	0	0
156	2	8	0	0	0	0	0	2	0	1	0	0	0	0	1	2

Appendix III.1A (Continued)

TILE NO.	TRT	DAYS IN	HD	DU	PH	OL	HA	AS	IS	BF	ST	EL	VL	HT	HP	SV
133	2	10	0	0	0	0	0	1	0	0	0	0	0	0	0	1
134	2	10	0	0	0	0	0	3	0	2	0	0	0	0	0	0
136	2	10	0	0	0	0	0	2	0	3	0	0	0	0	4	0
137	2	10	0	0	0	0	0	0	0	0	0	0	0	0	2	12
138	2	10	0	0	0	0	0	1	0	0	0	0	0	0	2	3
115	2	12	0	0	0	0	0	2	0	0	0	0	0	0	0	0
117	2	12	0	0	0	0	0	0	0	0	0	0	0	0	0	1
118	2	12	0	0	0	0	0	4	0	2	0	0	0	0	3	9
119	2	12	0	0	0	0	0	6	0	1	0	0	0	0	5	0
120	2	12	0	0	0	0	0	5	0	1	0	0	0	0	2	5
97	2	15	0	0	0	0	0	1	0	0	0	0	0	0	1	4
99	2	15	0	1	0	0	0	2	0	0	0	0	0	0	1	13
100	2	15	0	0	0	0	0	3	0	5	0	0	0	0	4	2
101	2	15	0	0	0	0	0	3	0	2	0	0	0	0	0	0
102	2	15	0	0	0	0	0	4	0	2	0	0	0	0	3	0
79	2	18	0	0	0	0	0	2	0	3	0	0	0	0	6	0
80	2	18	0	0	0	0	0	2	0	2	0	0	0	0	0	3
81	2	18	0	0	0	2	0	0	0	0	0	0	0	0	0	3
83	2	18	0	0	0	0	0	7	0	2	0	1	0	0	12	2
84	2	18	0	0	0	0	0	2	0	5	0	0	0	0	4	4
61	2	21	0	0	0	0	0	4	0	2	0	0	0	0	0	0
62	2	21	0	0	0	0	0	2	0	0	0	0	0	0	0	0
63	2	21	0	0	0	0	0	3	0	4	0	0	0	0	2	7
64	2	21	0	0	0	0	0	0	0	2	0	0	0	0	0	2
65	2	21	0	0	0	0	0	8	0	1	0	0	0	0	0	0
66	2	21	0	1	0	0	0	3	0	3	0	0	0	0	4	0
43	2	24	0	0	0	0	0	6	0	2	0	0	0	0	2	3
44	2	24	0	0	0	0	0	10	0	3	0	0	0	0	0	0
45	2	24	0	0	0	0	0	6	0	1	0	1	0	0	1	2
47	2	24	0	0	0	0	0	1	0	4	0	0	0	0	1	2
48	2	24	0	0	0	0	0	6	0	2	0	0	0	0	1	1
7	2	27	0	0	0	0	0	6	0	0	0	0	0	0	10	3
8	2	27	0	0	1	0	0	5	0	6	0	0	0	0	5	2
11	2	27	0	0	0	0	0	0	0	3	0	0	0	0	0	0
27	2	27	0	0	0	0	0	2	0	2	0	0	0	0	2	0
28	2	27	0	0	0	0	0	4	0	7	0	0	0	0	1	3
30	2	27	0	0	0	0	0	2	0	1	0	0	0	0	0	0
265	3	1	0	1	0	0	0	1	0	1	0	0	0	0	1	3
266	3	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1
267	3	1	0	0	0	0	0	0	0	0	0	0	0	0	2	26
268	3	1	0	0	0	0	0	2	0	1	0	0	0	0	0	0
269	3	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1
270	3	1	0	0	0	0	0	0	0	0	0	0	0	0	3	1
247	3	2	0	0	0	0	0	0	0	1	0	0	0	0	0	2
248	3	2	0	0	0	0	0	0	0	4	0	0	0	0	0	0
249	3	2	0	0	0	0	0	2	0	1	0	0	0	0	1	2
250	3	2	0	0	0	0	0	1	0	1	0	0	0	0	0	1
251	3	2	0	0	0	0	0	2	0	2	0	0	0	0	1	11
252	3	2	0	0	0	0	1	1	0	1	0	0	0	0	1	6
229	3	3	0	0	0	0	0	2	0	0	0	0	0	0	2	2
230	3	3	0	0	0	0	0	1	0	1	0	0	0	0	0	4
231	3	3	0	0	0	0	0	1	0	0	0	0	0	0	0	1
232	3	3	0	0	0	0	0	0	0	1	0	0	0	0	2	2
233	3	3	0	0	0	0	0	0	0	0	0	0	0	0	1	4
234	3	3	0	0	0	0	0	1	0	1	0	0	0	0	1	2
211	3	4	0	0	0	0	0	2	0	1	0	0	0	0	0	0
212	3	4	0	0	0	0	0	2	0	0	0	0	0	0	2	1
213	3	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
214	3	4	0	0	0	0	0	1	0	0	0	0	0	0	0	1

Appendix III.1A (Continued)

TILE NO.	TRT	DAYS IN	HD	DU	PH	OL	HA	AS	IS	BF	ST	EL	VL	HT	HP	SV
216	3	4	0	3	0	0	0	3	0	2	0	0	0	0	0	3
193	3	5	0	0	0	0	0	2	0	1	0	0	0	0	1	1
194	3	5	0	0	0	0	0	3	0	0	0	0	0	0	3	2
195	3	5	0	0	0	0	0	0	0	0	0	0	0	0	3	1
196	3	5	0	0	0	0	0	4	0	0	0	0	0	0	0	0
197	3	5	0	0	0	0	0	4	0	1	0	0	0	0	1	2
198	3	5	0	0	0	0	0	0	0	0	0	0	0	0	0	6
175	3	6	0	0	0	0	1	4	0	2	0	0	0	0	2	4
176	3	6	0	0	0	0	0	7	0	1	0	0	0	0	0	1
177	3	6	0	0	0	0	0	3	0	2	0	0	0	0	4	3
178	3	6	0	0	0	0	0	0	0	0	0	0	0	0	1	2
179	3	6	0	0	0	0	0	0	0	2	0	0	0	0	1	4
180	3	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
158	3	8	0	0	0	0	0	2	0	0	0	0	0	0	2	2
159	3	8	0	0	0	0	0	0	0	3	0	0	0	0	5	3
160	3	8	0	0	0	0	0	0	0	0	0	0	0	0	2	2
161	3	8	0	0	0	0	1	0	0	1	0	0	0	1	3	1
162	3	8	0	0	0	1	0	1	1	3	0	0	0	0	8	4
139	3	10	0	0	1	0	0	6	0	3	0	0	0	0	5	2
140	3	10	0	0	0	0	0	6	0	4	0	0	0	0	1	0
141	3	10	0	0	0	0	0	2	0	2	0	0	0	0	2	1
142	3	10	0	0	0	0	0	4	0	3	0	0	0	0	0	11
143	3	10	0	0	0	0	0	0	0	0	0	0	0	0	0	1
144	3	10	0	0	0	0	0	0	0	0	0	0	0	1	5	1
121	3	12	0	0	0	0	0	3	0	2	0	0	0	0	4	7
122	3	12	0	0	0	0	0	1	0	2	0	0	0	0	2	6
123	3	12	0	0	0	0	0	10	0	4	0	0	0	0	4	9
124	3	12	0	2	0	0	0	19	0	4	0	0	0	0	0	2
125	3	12	0	0	0	0	0	1	0	3	0	0	0	0	0	4
126	3	12	0	0	0	0	0	1	0	1	0	0	0	0	1	4
103	3	15	0	0	0	0	0	1	0	1	0	0	0	0	12	10
104	3	15	0	0	0	0	0	1	0	2	0	0	0	0	7	5
105	3	15	0	0	0	0	0	2	0	2	0	0	0	0	6	1
106	3	15	0	0	0	0	0	2	0	0	0	0	0	0	3	5
107	3	15	0	0	0	0	0	1	0	0	0	0	0	0	2	1
108	3	15	0	0	0	0	0	0	0	0	0	0	0	0	5	1
85	3	18	0	0	0	0	0	0	0	1	0	0	0	0	0	1
86	3	18	0	0	0	0	0	0	0	4	0	0	0	0	1	4
87	3	18	0	0	0	0	0	2	0	9	0	0	0	0	12	3
88	3	18	0	0	0	0	0	1	0	0	0	0	0	0	0	2
89	3	18	0	0	0	0	0	1	0	0	0	0	0	0	2	0
68	3	21	0	0	0	0	0	1	0	2	0	0	0	3	3	2
69	3	21	0	0	0	0	0	5	0	1	0	0	0	0	1	3
70	3	21	0	0	0	0	0	26	0	2	1	0	0	0	4	0
71	3	21	0	0	0	0	0	1	0	3	0	0	0	0	2	0
72	3	21	0	0	0	0	0	3	0	3	0	0	0	0	1	4
49	3	24	0	0	0	0	1	5	0	1	0	0	0	0	0	0
50	3	24	1	0	0	0	0	0	0	0	0	0	0	0	1	1
51	3	24	0	2	0	0	0	1	0	4	0	0	0	0	0	0
52	3	24	0	0	0	0	0	0	0	0	0	0	0	0	0	0
54	3	24	0	0	0	0	0	9	0	1	0	0	0	0	4	1
33	3	27	0	0	0	0	2	2	0	1	0	0	0	0	1	2
35	3	27	0	0	0	0	0	3	0	6	0	1	0	0	1	1
36	3	27	0	0	0	0	0	8	0	4	1	0	0	0	1	0

Appendix III.1B Taxonomic composition of samples collected during tile manipulations from Hobbs-Mackenzie Creek on June 28, 1990. Taxonomic abbreviations are listed in Appendix III.4.

TILE NO.	AR	AB	CO	CR	DI	EU	NA	PO	RC	TH	TV	IC
253	0	0	0	0	0	0	0	0	0	0	0	0
254	0	0	0	0	0	1	0	0	0	1	0	0
255	0	0	0	0	0	0	0	0	0	0	0	0
256	0	0	0	0	0	1	0	0	0	0	0	0
257	0	0	0	0	0	0	0	0	0	0	0	0
258	0	0	0	0	0	0	0	0	0	0	0	0
235	0	0	0	0	0	0	0	0	0	0	0	0
236	0	0	0	0	0	1	0	0	0	0	0	0
237	0	0	0	0	0	3	0	0	0	0	1	0
238	0	0	0	0	0	0	0	0	0	0	0	0
239	0	0	0	0	0	1	0	0	0	0	0	0
240	0	0	0	0	0	0	0	0	0	0	0	0
217	0	0	1	0	0	1	0	0	0	0	0	0
218	0	0	0	0	0	1	0	0	0	0	0	0
219	0	0	0	0	0	0	0	0	0	0	0	0
220	0	0	0	0	0	0	0	0	0	0	0	0
221	0	0	0	0	0	1	0	0	0	0	0	0
222	0	0	0	0	0	0	0	0	0	1	0	0
199	0	0	0	0	0	0	0	0	0	0	0	0
200	0	0	0	0	0	1	0	0	0	0	0	0
202	0	0	0	0	0	0	0	0	0	0	0	0
181	0	0	0	0	0	0	0	0	0	1	0	0
182	0	0	0	0	0	2	0	0	0	0	0	0
183	0	0	0	0	0	0	0	0	0	0	0	0
184	0	0	0	0	0	2	0	0	0	1	0	0
185	0	0	0	0	0	0	0	0	0	0	0	0
186	0	0	0	0	0	3	0	0	0	1	0	0
163	0	0	0	0	0	0	0	0	0	0	0	0
164	0	0	0	0	0	0	0	0	0	1	0	0
165	0	0	0	0	0	1	0	0	0	0	0	0
166	0	0	0	0	0	0	0	0	0	0	1	0
167	0	0	0	0	0	1	0	0	0	0	0	0
168	0	0	0	0	0	1	0	0	0	0	0	0
145	0	0	0	0	0	1	0	0	0	0	0	0
146	0	0	0	0	0	0	0	0	0	0	0	0
147	0	0	0	0	0	3	0	0	0	0	0	0
148	0	0	0	0	0	0	0	0	0	0	0	0
149	0	0	0	0	0	0	0	0	0	0	0	0
150	0	0	0	0	0	0	0	0	0	0	0	0
127	0	0	0	0	0	2	0	0	0	0	0	0
128	0	0	0	0	0	0	0	0	0	0	0	0
130	0	0	0	0	0	0	0	0	0	2	0	0
131	0	0	0	0	0	0	0	0	0	2	0	0
132	1	0	0	0	0	0	0	0	0	0	0	0
109	0	0	0	0	0	1	0	0	0	0	8	0
110	0	0	0	0	0	3	0	0	0	1	0	0
111	0	0	0	2	0	0	0	0	0	0	1	0
113	0	0	0	1	0	0	1	0	0	0	0	1
114	0	4	0	0	0	0	0	0	0	0	0	0
91	0	0	0	0	0	0	0	0	0	0	0	0
92	0	0	0	3	0	1	0	0	0	0	1	0
93	0	0	0	0	0	2	0	0	0	0	0	0
94	0	0	0	0	0	4	0	0	0	0	0	0
95	0	1	0	1	0	0	0	0	0	0	0	0
96	0	0	0	0	0	0	0	0	0	0	0	0
73	0	0	0	0	0	1	0	0	0	0	0	0
75	0	0	0	0	0	0	0	1	0	0	1	0

Appendix III.1B (Continued)

TILE NO.	AR	AB	CO	CR	DI	EU	NA	PO	RC	TH	TV	IC
76	0	0	0	0	0	0	0	0	0	0	0	0
77	0	0	0	0	0	2	0	0	0	0	0	0
78	0	0	0	0	0	0	0	0	0	1	0	0
55	0	0	0	0	0	0	0	0	0	2	0	0
56	0	0	0	0	0	2	0	0	0	0	0	0
57	0	0	0	0	0	2	0	0	0	2	0	0
58	0	0	1	0	0	0	0	0	0	0	0	0
59	0	0	0	0	0	3	0	0	0	1	0	0
60	0	0	0	0	0	2	0	0	0	0	0	0
38	0	0	0	0	0	0	0	0	0	0	0	0
39	0	0	0	0	0	2	0	0	0	1	0	0
40	0	0	0	0	0	1	0	0	0	0	0	0
41	0	0	0	0	0	3	0	0	0	0	0	0
42	0	0	1	0	0	0	0	0	0	1	0	0
6	0	0	0	0	0	1	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0	1	0	0
20	0	0	0	0	0	5	0	0	0	1	0	0
21	0	0	1	0	0	0	0	0	0	1	0	0
259	0	0	0	0	0	0	0	0	0	0	0	0
260	0	0	0	0	0	0	0	0	0	1	0	0
261	0	0	0	0	0	0	0	0	0	0	0	0
262	0	0	0	0	0	2	0	0	0	0	0	0
263	0	0	0	0	0	1	0	0	0	0	0	0
264	0	0	0	0	0	1	0	0	0	0	0	0
241	0	0	0	0	0	0	0	0	0	0	0	0
242	0	0	0	0	0	1	0	0	0	0	0	0
243	0	0	0	0	0	0	0	0	0	1	0	0
244	0	0	0	0	0	0	0	0	0	0	0	0
245	0	0	0	0	0	0	0	0	0	0	0	0
246	0	0	0	0	0	1	0	0	0	0	0	0
223	0	0	0	0	0	0	0	0	0	1	0	0
225	0	0	0	0	0	0	0	0	0	0	0	0
226	0	0	0	0	0	1	0	0	0	0	0	0
227	0	0	0	0	0	0	0	0	0	0	0	0
228	0	0	0	0	0	2	0	0	0	0	0	0
205	0	0	0	0	0	3	0	0	0	2	0	0
206	0	0	0	0	0	1	0	0	0	0	0	0
207	0	0	0	0	0	0	0	0	0	0	0	0
208	0	0	0	0	0	0	0	0	0	0	0	0
209	0	0	0	0	0	0	0	0	0	0	0	0
210	0	0	0	0	0	1	0	0	0	0	0	0
187	0	0	0	0	0	0	0	0	0	0	0	0
188	0	0	0	2	0	3	0	0	0	1	0	0
189	0	0	0	0	0	2	1	0	0	0	2	0
190	0	0	0	0	0	0	0	0	0	0	0	0
191	0	0	0	0	0	0	0	0	0	0	0	0
192	0	0	0	0	0	0	0	0	0	0	0	0
169	0	0	0	0	0	2	0	0	0	0	0	0
170	0	0	0	0	0	0	0	0	0	0	0	0
172	0	0	0	0	0	1	0	0	0	0	0	0
173	0	0	0	1	0	1	0	0	0	0	0	0
174	0	0	0	0	0	2	0	0	0	0	0	0
151	0	0	0	0	0	1	0	0	0	1	0	0
152	0	0	0	0	0	1	0	0	0	1	0	0
154	0	0	0	0	0	0	0	0	0	0	0	0
155	0	0	0	0	0	0	0	0	0	0	0	0
156	0	0	0	0	0	0	0	0	0	0	0	0
133	0	0	0	0	0	3	0	0	0	0	0	0
134	0	0	0	0	0	0	0	0	0	0	0	0

Appendix III.1B (Continued)

TILE NO.	AR	AB	CO	CR	DI	EU	NA	PO	RC	TH	TV	IC
136	0	0	0	0	0	1	0	0	0	0	0	0
137	0	0	0	0	0	0	0	0	0	0	0	0
138	0	0	0	0	0	2	0	0	0	1	0	0
115	0	0	0	0	0	0	0	0	0	0	0	0
117	0	0	0	0	0	0	0	0	0	0	0	0
118	0	0	0	0	0	2	0	0	0	1	0	0
119	0	0	1	0	0	1	0	0	0	2	2	0
120	0	0	0	0	0	1	0	0	0	0	0	0
97	0	0	0	0	0	1	0	0	0	0	0	0
99	0	0	0	0	0	1	0	0	0	0	0	0
100	0	0	0	0	0	1	0	0	0	0	0	0
101	0	0	0	0	0	0	0	0	0	1	0	0
102	0	0	0	0	0	0	0	0	0	1	0	0
79	0	0	0	0	0	0	0	0	0	1	0	0
80	0	0	0	0	0	0	0	0	0	2	0	0
81	0	0	0	0	0	1	0	0	0	1	0	0
83	0	0	0	0	1	0	0	0	0	1	0	0
84	0	0	0	0	0	0	0	0	0	2	0	0
61	0	0	0	0	0	0	0	0	0	4	0	0
62	0	0	0	0	0	1	0	0	0	0	0	0
63	0	0	0	0	0	3	0	0	0	0	0	0
64	0	0	0	0	0	0	0	0	0	0	0	0
65	0	0	0	0	0	0	0	0	0	0	0	0
66	0	0	1	0	0	2	0	0	0	2	0	0
43	0	0	0	0	0	1	0	0	0	1	0	0
44	0	0	0	0	0	1	0	0	0	0	0	0
45	0	0	0	1	0	1	0	0	0	0	3	0
47	0	0	1	0	0	1	0	0	0	0	0	0
48	0	0	1	0	0	1	0	0	0	1	0	0
7	0	0	1	1	0	3	0	0	0	0	0	0
8	0	0	0	0	0	1	0	0	0	2	0	0
11	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	1	0	0
28	0	0	0	1	1	1	2	0	2	0	0	0
30	0	0	0	3	0	1	0	0	0	0	1	0
265	0	0	0	0	0	0	0	0	0	0	0	0
266	0	0	0	0	0	0	0	0	0	0	0	0
267	0	0	0	0	0	2	0	0	0	0	0	0
268	0	0	0	0	0	0	0	0	0	1	0	0
269	0	0	0	0	0	0	0	0	0	1	0	0
270	0	0	0	0	0	0	0	0	0	0	0	0
247	0	0	0	0	0	0	0	0	0	0	0	0
248	0	0	0	0	0	0	0	0	0	0	0	0
249	0	0	0	0	0	0	0	0	0	0	0	0
250	0	0	0	0	0	0	0	0	0	1	0	0
251	0	0	1	0	0	0	0	0	0	0	0	0
252	0	0	0	0	0	3	0	0	0	0	0	0
229	0	0	0	0	0	0	0	0	0	0	0	0
230	0	0	0	0	0	0	0	0	0	0	0	0
231	0	0	0	0	0	0	0	0	0	0	0	0
232	0	0	0	0	0	0	0	0	0	0	0	0
233	0	0	0	0	0	1	0	0	0	0	0	0
234	0	0	0	0	0	1	0	0	0	0	0	0
211	0	1	0	0	0	0	0	0	0	0	0	0
212	0	0	0	0	0	2	0	0	0	1	0	0
213	0	0	0	0	0	0	0	0	0	0	0	0
214	0	0	0	0	0	0	0	0	0	0	0	0
216	0	0	0	0	0	1	0	0	0	0	0	0
193	0	0	0	0	0	0	0	0	0	0	0	0

Appendix III.1B (Continued)

TILE NO.	AR	AB	CO	CR	DI	EU	NA	PO	RC	TH	TV	IC
194	0	0	0	0	0	0	0	0	0	2	0	0
195	0	0	0	0	0	1	0	0	0	0	0	0
196	0	0	0	0	0	0	0	0	0	1	0	0
197	0	0	0	0	0	1	0	0	0	0	0	0
198	0	0	0	0	0	0	0	0	0	0	0	0
175	0	0	0	0	0	1	0	0	0	1	0	1
176	0	0	0	0	0	0	0	0	0	0	0	0
177	0	0	1	0	0	0	0	0	0	0	0	0
178	0	0	0	0	0	1	0	0	0	0	0	0
179	0	0	0	0	0	2	0	0	0	0	0	0
180	0	0	0	0	0	0	0	0	0	0	0	0
158	0	0	0	0	0	3	0	0	0	0	0	0
159	0	0	1	0	0	3	0	0	0	1	1	0
160	0	0	0	0	0	1	0	0	0	0	0	0
161	0	0	0	0	0	1	0	0	0	0	0	0
162	0	0	0	0	0	0	0	0	0	0	0	0
139	0	0	0	0	0	1	0	0	0	0	0	0
140	0	0	1	1	0	1	0	0	0	0	0	0
141	0	0	0	0	0	0	0	0	0	0	0	0
142	0	0	0	0	0	1	0	0	0	1	0	0
143	0	0	0	0	0	1	0	0	0	2	0	0
144	0	0	0	0	0	3	0	0	0	0	3	0
121	0	0	0	0	0	5	0	0	0	0	0	0
122	0	0	0	0	0	2	0	0	0	0	0	0
123	0	0	0	0	0	5	0	0	0	0	0	0
124	0	0	0	0	0	0	0	0	0	1	0	0
125	0	0	0	0	0	3	0	0	0	0	0	0
126	0	0	0	0	0	1	0	0	0	0	0	0
103	0	0	0	0	0	8	0	0	0	0	0	0
104	0	0	0	0	0	5	0	0	0	0	0	0
105	0	0	0	0	0	4	0	0	0	0	0	0
106	0	0	0	0	0	8	0	0	0	0	0	0
107	0	2	0	1	0	0	0	0	0	0	2	0
108	0	0	0	0	0	3	0	0	0	4	0	0
85	0	0	0	0	0	0	0	0	0	0	0	0
86	0	0	0	0	0	5	0	0	0	0	0	0
87	0	0	0	0	0	7	0	0	0	1	0	0
88	0	0	0	0	0	0	0	0	0	0	0	0
89	0	0	0	0	0	1	0	0	0	0	0	0
68	0	0	0	0	0	2	0	0	0	1	0	0
69	0	0	0	5	0	0	0	0	0	1	0	0
70	0	0	0	0	0	1	0	0	0	2	0	0
71	0	0	0	0	0	1	0	0	0	0	0	0
72	0	0	0	0	0	0	0	0	0	0	0	0
49	0	0	0	0	0	3	0	0	0	0	0	0
50	0	0	0	4	0	2	0	0	0	2	0	0
51	0	0	0	0	0	0	0	0	0	0	0	0
52	0	0	0	0	0	0	0	0	0	0	0	0
54	0	1	0	0	0	0	0	0	0	0	0	0
33	0	0	1	0	0	1	0	0	0	3	0	0
35	0	0	0	0	0	1	0	0	0	0	0	0
36	0	0	0	0	1	2	0	0	0	2	0	0

Appendix III.2A Taxonomic composition of tile samples collected from Hobbs-Mackenzie Creek on June 28, 1990. Taxonomic abbreviations are listed in Appendix III.4. (TRT = Treatment; TRT 1 = No removal, TRT 2 = Removal of black flies, TRT 3 = Removal of all taxa)

TILE NO.	TRT	DAYS IN	HD	DU	PH	OL	GH	HA	AS	IS	BF	CT	ST	EL	HR	VL	HT	HP	AN	SV	EM
253	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	4	0	5	0
254	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	17	0
255	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
256	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
257	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
258	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
235	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	1	0
236	1	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
237	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0
238	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
239	1	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	15	0	3	0
240	1	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	8	0
217	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	12	0
218	1	3	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0
219	1	3	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	5	0	15	0
220	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	5	0
221	1	3	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	4	0
222	1	3	0	1	0	0	0	0	1	0	1	0	0	0	0	1	0	11	2	3	0
199	1	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
200	1	4	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	4	0	0	0
202	1	4	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3	0
181	1	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	0	27	0
182	1	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
183	1	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	4	0
184	1	5	0	0	0	0	0	0	1	0	4	0	0	0	0	0	0	7	0	0	0
185	1	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
186	1	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	4	0
163	1	6	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	5	0	14	0
164	1	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	3	0
165	1	6	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	8	0	3	0
166	1	6	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	2	1	9	0
167	1	6	0	0	0	1	0	0	0	0	5	0	0	0	0	0	0	0	0	1	1
168	1	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
145	1	8	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	11	0	13	0
146	1	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	3	0
147	1	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	19	0
148	1	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	0	40	0
149	1	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	28	0	8	0
150	1	8	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	31	0	1	0
127	1	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	3	0
128	1	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
130	1	10	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	48	0	3	0
131	1	10	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	45	0	22	0
132	1	10	0	0	0	0	0	1	3	0	2	0	0	0	0	0	0	19	0	8	0
109	1	12	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	6	0	7	0
110	1	12	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	25	2	21	0
111	1	12	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	3	0	0	0
113	1	12	1	0	0	0	0	0	2	0	3	0	0	0	0	0	0	6	0	2	0
114	1	12	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
91	1	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	5	0
92	1	15	0	0	0	1	0	0	0	0	3	0	0	0	0	0	0	14	0	2	0
93	1	15	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	56	1	10	0
94	1	15	0	2	0	0	0	0	1	0	2	0	0	0	0	0	0	10	2	3	0
95	1	15	0	0	0	3	0	0	2	0	1	0	0	1	0	0	0	67	0	34	0
96	1	15	0	0	0	1	0	0	3	0	0	0	0	0	0	0	0	18	0	14	0
73	1	18	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	31	0	14	0
75	1	18	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0	16	0	13	0

Appendix III.2A (Continued)

TILE NO.	TRT	DAYS IN	HD	DU	PH	OL	GH	HA	AS	IS	BF	CT	ST	EL	HR	VL	HT	HP	AN	SV	EM
76	1	18	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	2	0	1	0
77	1	18	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	3	0	0	0
78	1	18	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	3	4	2	0
55	1	21	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	2	0	3	0
56	1	21	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	7	0	6	0
57	1	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
58	1	21	0	1	0	0	0	0	2	0	2	0	0	0	0	0	0	1	1	0	0
59	1	21	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0
60	1	21	0	1	0	1	0	0	4	0	0	0	0	0	0	0	0	4	1	1	0
38	1	24	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	2	1	0	0
39	1	24	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	2	1	0	0
40	1	24	0	0	0	1	0	0	3	0	2	0	0	0	0	0	0	29	2	6	0
41	1	24	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	2	0
42	1	24	0	0	0	1	0	0	2	0	1	0	0	0	0	0	0	1	1	18	0
6	1	27	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0	4	0	2	0
19	1	27	0	0	0	7	0	0	7	0	0	0	1	0	0	0	0	0	0	0	0
20	1	27	0	1	0	3	0	1	0	0	3	0	0	0	0	0	0	36	6	8	0
21	1	27	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	4	1	1	0
259	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
260	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
261	2	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	7	0	3	0
262	2	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	4	0	10	0
263	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
264	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
241	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0
242	2	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	1	0
243	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
244	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3	0
245	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
246	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	3	0
223	2	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
225	2	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
226	2	3	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	6	0
227	2	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	3	0
228	2	3	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	8	0	2	0
205	2	4	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
206	2	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
207	2	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
208	2	4	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	18	0	6	0
209	2	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
210	2	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
187	2	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
188	2	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	3	0
189	2	5	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
190	2	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
191	2	5	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	3	0	0	0
192	2	5	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
169	2	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	31	0	2	0
170	2	6	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	2	0
172	2	6	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
173	2	6	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	4	0	1	0
174	2	6	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0	5	0	0	0
151	2	8	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	18	0	0	0
152	2	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23	0	2	0
154	2	8	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
155	2	8	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0
156	2	8	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	10	0	2	0
133	2	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0
134	2	10	0	0	0	0	0	0	3	0	1	0	0	0	0	0	0	2	0	0	0

Appendix III.2A (Continued)

TILE NO.	TRT	DAYS IN	HD	DU	PH	OL	GH	HA	AS	IS	BF	CT	ST	EL	HR	VL	HT	HP	AN	SV	EM
136	2	10	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	7	1	1	0
137	2	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	0	4	0
138	2	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	4	0
115	2	12	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
117	2	12	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
118	2	12	0	0	0	0	0	0	2	0	2	0	0	0	0	0	0	16	0	4	0
119	2	12	0	0	0	0	0	0	4	0	1	0	0	0	0	0	0	[illegible]	0	0	0
120	2	12	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	4		[illegible]	0
97	2	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	7	0
99	2	15	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	6	1	3	0
100	2	15	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	14	0	0	0
101	2	15	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	6	0	1	0
102	2	15	0	1	0	1	0	0	2	0	0	0	0	0	0	0	0	11	6	0	0
79	2	18	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	46	0	1	0
80	2	18	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	10	2	3	0
81	2	18	0	0	0	1	0	0	3	0	0	0	0	0	0	0	0	34	0	0	0
83	2	18	0	0	0	0	0	1	4	0	2	0	0	0	0	0	0	40	2	2	1
84	2	18	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	2	1	0
61	2	21	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	4	2	1	0
62	2	21	0	0	0	0	0	0	3	0	2	0	0	0	0	0	0	5	1	2	0
63	2	21	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	8	0	0	0
64	2	21	0	0	0	4	0	0	4	0	1	0	0	0	0	0	0	35	0	1	0
65	2	21	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	3	0	1	0
66	2	21	0	0	0	0	0	1	12	0	1	0	0	0	0	0	0	4	[illegible]	1	0
43	2	24	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	3	1	1
44	2	24	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0
45	2	24	0	0	0	1	0	0	2	0	1	0	0	0	0	0	0	6	0	8	0
47	2	24	0	0	0	0	0	0	3	0	0	0	1	0	0	0	0	1	0	0	0
48	2	24	0	0	0	3	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
7	2	27	0	0	0	8	0	0	3	0	1	0	0	0	0	0	0	29	12	2	0
8	2	27	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	4	2	0	0
11	2	27	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	1	1	2	0
27	2	27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
28	2	27	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	6	3	0	0
30	2	27	0	0	0	2	0	0	8	0	0	0	0	0	0	0	0	4	0	2	0
265	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0
266	3	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	2	0
267	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
268	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
269	3	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0
270	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0
247	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
248	3	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	4	0	1	0
249	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	1	0
250	3	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
251	3	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	2	0
252	3	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0
229	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	4	0
230	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
231	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	3	0
232	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	2	0
233	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0
234	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0	8	0
211	3	4	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
212	3	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
213	3	4	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3	0
214	3	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
216	3	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	4	0
193	3	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	2	0

Appendix III.2A (Continued)

TILE NO.	TRT	DAYS IN	HD	DU	PH	OL	GH	HA	AS	IS	BF	CT	ST	EL	HR	VL	HT	HP	AN	SV	EM
194	3	5	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	1	0
195	3	5	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0
196	3	5	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	13	0	3	0
197	3	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
198	3	5	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	6	0	2	0
175	3	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	35	0
176	3	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0
177	3	6	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	4	1	1	0
178	3	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	9	0
179	3	6	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	14	0	5	0
180	3	6	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	6	0	1	0
158	3	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
159	3	8	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	54	0	2	0
160	3	8	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	9	0	0	0
161	3	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	1	3	0
162	3	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	4	0
139	3	10	0	0	0	0	0	1	0	0	2	0	0	0	0	0	0	2	0	0	0
140	3	10	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0
141	3	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	4	0
142	3	10	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	24	0	2	0
143	3	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
144	3	10	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	17	1	7	0
121	3	12	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	42	0	0	0
122	3	12	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	2	0
123	3	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	2	0
124	3	12	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0
125	3	12	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	5	0	0	1
126	3	12	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	16	1	1	0
103	3	15	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	18	0	0	0
104	3	15	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	29	0	3	0
105	3	15	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	12	0	2	0
106	3	15	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	10	0	8	0
107	3	15	0	0	0	0	0	0	5	0	0	0	0	0	0	1	0	19	0	2	0
108	3	15	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0	1	0
85	3	18	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0
86	3	18	0	0	0	0	0	0	3	0	2	0	0	0	0	0	0	23	0	5	0
87	3	18	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	31	0	0	0
88	3	18	0	0	0	1	0	0	18	0	2	0	0	0	0	0	0	28	0	0	0
89	3	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17	4	4	0
68	3	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	0	5	0
69	3	21	0	0	0	0	0	0	4	0	1	0	0	0	0	0	0	4	0	0	0
70	3	21	0	0	0	1	0	0	13	0	0	0	0	0	0	0	0	4	0	1	0
71	3	21	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	19	0	1	0
72	3	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	37	0	4	0
49	3	24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	1	3	0
50	3	24	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	15	1	0	0
51	3	24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52	3	24	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	17	0	1	0
54	3	24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
33	3	27	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	3	0	0	0
35	3	27	0	0	0	0	0	0	3	0	2	0	0	0	0	0	0	13	7	0	0
36	3	27	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	3	0	0	0

Appendix III.2B Taxonomic composition of tile samples collected from Hobbs-Mackenzie Creek on June 28, 1990. Taxonomic abbreviations are listed in Appendix III.4.

TILE NO.	AR	CD	MU	AB	CO	CR	DI	EU	MT	MP	NA	PT	PP	PO	PC	RC	TH	TY	TV	IC
253	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	7	0	0	2
254	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0
255	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
256	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
257	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
258	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
235	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
236	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
237	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0
238	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
239	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	1	1	0	0	0
240	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
217	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
218	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
219	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
220	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
221	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0
222	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0	0	0
199	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0
200	0	0	0	0	0	1	0	3	0	0	0	0	0	0	0	0	9	0	0	0
202	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
181	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	2	0	0	0
182	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0
183	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
184	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	3	0	0	3
185	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0
186	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	1	0	0	0
163	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0
164	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0	5	0	0	0
165	0	0	0	0	1	2	0	6	0	0	0	0	0	0	0	0	3	0	0	0
166	0	0	0	1	0	0	0	9	0	0	0	0	0	0	0	0	1	0	0	1
167	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	3	0	0	0
168	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0
145	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
146	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
147	0	0	0	0	0	0	0	44	0	0	0	0	0	0	0	0	2	0	2	10
148	0	0	0	0	1	1	0	17	0	0	2	0	0	0	0	0	8	0	0	0
149	0	0	0	0	2	5	0	19	0	0	0	0	0	0	0	0	2	0	0	0
150	0	0	1	0	0	2	0	21	0	0	0	0	0	0	0	0	0	0	1	0
127	0	0	0	0	1	3	0	12	0	0	0	0	0	0	0	0	0	0	4	0
128	0	0	0	0	0	6	0	13	0	0	0	0	0	0	1	0	5	0	0	0
130	0	0	0	0	0	1	0	16	0	0	0	0	0	0	0	0	3	0	1	0
131	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
132	0	0	0	0	1	0	0	17	0	0	0	0	0	0	0	0	11	0	0	0
109	0	0	0	0	0	0	0	19	0	0	0	0	0	0	0	0	5	0	6	5
110	0	0	0	1	0	1	0	17	0	0	0	0	0	0	0	0	3	0	1	0
111	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	15	1	0	9
113	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	8	0	0	6
114	0	0	0	4	5	0	0	5	0	0	0	0	0	0	0	0	8	4	0	8
91	0	0	0	1	0	1	0	36	0	0	0	0	0	0	0	0	2	0	2	0
92	0	0	0	0	1	3	0	58	0	0	0	0	0	0	0	0	9	0	1	23
93	0	4	0	0	0	1	0	63	0	0	0	0	0	0	0	0	0	0	0	0
94	0	0	0	0	0	0	0	36	0	0	0	0	0	0	0	0	5	0	0	0
95	0	0	0	1	1	0	0	28	0	0	0	0	0	0	0	0	8	1	0	13
96	0	0	0	1	0	1	0	31	0	0	0	0	0	0	0	0	2	0	2	0
73	0	0	0	0	1	0	0	26	0	0	0	0	0	0	0	0	7	0	0	0
75	0	0	0	1	0	1	0	13	0	0	1	0	0	0	0	0	0	0	2	0

Appendix III.2B (Continued)

TILE NO.	AR	CD	MU	AB	CO	CR	DI	EU	MT	MP	NA	PT	PP	PO	PC	RC	TH	TY	TV	IC
76	0	0	0	0	0	2	0	20	0	1	0	1	0	0	0	2	5	0	0	0
77	0	0	0	0	3	0	0	6	0	0	0	0	0	0	0	0	2	1	0	3
78	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0	2	0	0	0
55	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	7	0	0	0
56	0	0	0	0	1	3	0	34	2	0	2	0	0	0	0	0	6	0	0	0
57	0	0	0	0	0	1	0	11	0	0	0	0	0	0	0	0	1	0	0	0
58	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	12	0	0	0
59	0	0	0	1	0	1	0	9	0	0	0	0	0	0	0	0	5	0	0	0
60	0	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0	5	0	0	0
38	0	0	0	1	1	9	0	8	0	0	0	0	0	0	0	0	6	0	0	0
39	0	0	0	0	1	0	0	22	0	0	0	0	0	0	0	0	4	0	0	0
40	0	0	0	0	0	0	0	63	0	0	0	0	0	0	0	0	4	0	0	0
41	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0
42	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	5	0	0	0
6	0	0	0	0	1	1	0	8	0	0	0	0	0	0	6	0	5	6	0	5
19	0	0	0	0	4	27	3	8	0	0	13	4	0	0	0	0	1	0	0	1
20	0	0	0	0	0	14	0	120	0	0	0	0	0	0	0	0	6	0	0	0
21	0	0	0	0	0	0	0	28	0	0	0	0	0	0	0	0	0	0	0	0
259	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
260	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
261	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	3	0	0	0
262	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	1	0	0	0	0
263	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
264	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
241	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
242	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0
243	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0	0	0
244	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
245	0	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
246	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
223	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
225	0	0	0	0	0	0	0	8	1	0	0	0	0	0	0	0	0	0	0	0
226	0	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0	1	0	0	0
227	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	2	0	0	0
228	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0
205	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0	0	0
206	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0
207	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
208	0	0	0	1	1	0	0	4	0	0	0	0	0	0	0	0	8	0	0	0
209	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	4	0	0	2
210	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	4	0	0	15
187	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0
188	0	0	0	0	0	2	0	10	0	0	0	0	0	0	0	0	3	0	0	0
189	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	11	0	1	1
190	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0
191	0	0	0	0	0	1	0	1	0	0	2	0	0	0	0	0	14	0	0	0
192	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	0	1	0	0	1
169	0	0	0	1	1	0	0	4	0	0	0	0	0	0	0	1	2	0	0	0
170	0	0	0	0	6	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0
172	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	11	0	0	0
173	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	6	0	0	3
174	0	0	0	0	0	1	0	11	0	0	0	0	0	0	0	0	1	0	0	0
151	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	10	0	0	0
152	0	0	0	0	0	1	0	9	0	0	0	0	0	0	0	0	1	0	0	0
154	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	4	0	0	0
155	0	0	0	0	0	5	0	3	0	0	0	0	0	0	0	0	0	0	0	5
156	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0	4	0	0	0
133	0	0	0	0	0	1	0	7	0	0	0	1	0	0	0	0	6	0	0	5
134	0	0	0	0	5	0	0	12	0	0	0	0	0	0	0	0	26	0	0	0

Appendix III.2B (Continued)

TILE NO.	AR	CD	MU	AB	CO	CR	DI	EU	MT	MP	NA	PT	PP	PO	PC	RC	TH	TY	TV	IC
136	0	0	0	0	2	0	0	2	0	0	0	0	0	0	0	0	11	0	2	0
137	0	0	0	0	0	0	0	23	0	0	0	0	0	0	0	0	9	0	0	8
138	0	0	0	0	0	0	0	26	0	0	0	0	0	0	0	0	0	0	0	7
115	0	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0	6	0	0	0
117	0	0	0	0	0	0	0	44	0	0	0	0	0	0	0	0	1	0	0	0
118	0	0	0	0	0	0	0	10	0	0	1	0	0	0	0	0	5	0	0	0
119	0	0	0	0	1	0	0	13	0	0	0	0	0	0	0	0	13	0	0	8
120	0	1	0	0	1	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0
97	0	0	0	0	0	0	0	79	0	0	1	0	0	0	0	0	0	0	0	0
99	0	0	0	0	0	0	0	36	0	0	0	0	0	0	0	0	1	0	0	0
100	0	0	0	0	1	0	0	10	0	0	0	0	0	0	0	0	2	0	0	0
101	0	0	0	0	7	3	0	11	0	0	3	0	0	0	0	0	9	0	0	4
102	0	0	0	0	1	16	0	35	0	0	0	0	0	0	0	1	8	0	0	35
79	0	0	0	1	0	7	0	26	0	0	3	0	0	2	0	1	26	0	1	0
80	0	0	0	0	0	0	0	34	0	0	0	0	0	0	0	0	4	0	0	4
81	0	0	0	0	1	3	0	14	0	0	2	0	0	0	0	0	7	0	0	0
83	0	0	0	1	1	1	0	25	0	0	0	0	0	0	0	0	4	0	1	0
84	0	0	0	0	0	1	0	9	0	0	0	0	0	0	0	0	2	0	1	0
61	0	0	0	0	0	4	0	10	0	0	1	0	0	0	0	1	1	0	2	2
62	0	0	0	0	0	1	0	8	0	0	0	0	0	0	0	0	14	0	6	6
63	0	0	0	0	1	0	0	72	0	0	0	0	0	0	0	0	3	0	0	0
64	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0	8	0	6	6
65	0	0	0	0	0	22	0	13	0	0	4	0	0	0	0	0	7	0	5	5
66	0	0	0	0	0	1	0	18	0	0	3	0	1	0	0	0	10	0	0	0
43	0	0	0	0	0	0	0	30	0	0	0	0	0	0	0	0	4	0	0	0
44	0	0	0	1	1	26	0	0	0	0	5	0	0	0	0	0	9	0	0	0
45	0	1	0	0	0	1	0	35	0	0	0	0	0	0	0	0	13	0	3	11
47	0	0	0	5	0	17	0	20	0	0	0	1	0	0	0	0	10	0	4	0
48	0	0	0	0	1	5	0	6	0	0	0	1	0	1	0	0	13	0	0	37
7	0	3	0	0	0	27	0	24	4	0	2	0	0	0	0	0	5	0	0	0
8	0	0	0	0	0	19	1	5	0	0	1	0	0	0	0	0	4	0	0	0
11	0	0	0	0	0	5	0	7	0	0	0	1	0	0	0	0	9	0	0	8
27	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	1	4	0	39	0	0	2	0	0	0	0	4	15	0	2	3
30	0	0	0	0	0	3	0	5	0	0	0	0	0	0	0	0	13	0	1	21
265	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
266	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
267	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
268	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
269	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
270	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
247	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
248	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
249	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
250	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0
251	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
252	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
229	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	2	0	0	0
230	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
231	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
232	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
233	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
234	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
211	0	0	0	1	0	0	0	0	0	0	2	0	0	0	0	0	3	0	0	0
212	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	2	0	0	0
213	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
214	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
216	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
193	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	4	0	0	0

Appendix III.2B (Continued)

TILE NO.	AR	CD	MU	AB	CO	CR	DI	EU	MT	MP	NA	PT	PP	PO	PC	RC	TH	TY	TV	IC
194	0	0	0	0	0	1	0	2	0	0	1	0	0	0	0	0	2	0	0	1
195	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0
196	0	0	0	0	1	0	0	10	0	0	0	0	0	0	0	0	2	0	0	1
197	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0
198	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
175	0	0	0	0	0	0	0	42	0	0	0	0	0	0	0	0	2	0	0	0
176	0	0	0	0	0	1	0	4	0	0	3	0	0	0	0	0	2	0	0	0
177	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	1	1	0	0	0
178	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	5	0	0	0
179	0	0	0	0	1	0	0	12	0	0	0	0	0	0	0	0	7	0	0	4
180	0	0	0	1	0	0	0	9	0	0	0	0	0	0	0	0	2	0	0	4
158	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	12	0	0	0
159	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	8	0	1	10
160	0	0	0	0	1	3	0	2	0	0	1	0	0	0	0	0	3	0	5	0
161	0	0	0	0	0	8	0	8	0	0	0	0	0	0	0	0	15	0	0	0
162	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0	5	0	0	0
139	0	0	0	0	1	4	0	8	0	0	1	0	0	0	0	0	12	0	0	0
140	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	11	0	0	0
141	0	0	0	0	4	3	0	17	0	0	1	0	0	0	0	0	4	0	0	0
142	0	0	0	0	2	5	0	12	0	0	3	0	0	0	0	0	19	0	0	2
143	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	1	0	0	0
144	0	0	0	0	0	0	0	25	0	0	0	0	0	0	0	0	3	0	2	11
121	0	0	0	0	0	0	0	19	0	0	1	0	0	1	0	0	2	0	0	0
122	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0	0	0	0	0
123	0	0	0	0	0	0	0	41	0	0	0	0	0	0	0	0	4	0	2	3
124	0	0	0	0	0	1	0	18	0	0	3	0	0	0	0	0	10	0	0	0
125	0	0	0	1	1	1	0	65	1	0	2	0	0	0	0	0	5	0	0	0
126	0	0	0	0	3	1	0	2	0	0	2	0	0	0	0	0	8	0	2	0
103	0	0	0	0	1	3	0	14	0	0	2	0	0	0	0	0	7	0	0	0
104	0	0	0	0	1	4	0	19	0	0	0	0	0	0	0	0	6	0	0	0
105	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	1	0	0	2
106	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
107	0	0	0	0	0	1	0	8	0	0	0	0	0	0	0	0	2	2	0	9
108	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0
85	0	0	0	0	3	0	0	4	0	0	0	0	0	0	0	0	9	0	0	0
86	0	0	0	3	1	0	0	29	0	0	1	0	0	0	0	0	7	0	2	8
87	0	0	0	0	1	3	0	29	0	0	2	0	0	0	0	1	8	0	0	7
88	0	0	0	0	2	3	0	6	0	0	3	0	0	0	0	0	5	0	0	3
89	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0	3	0	0	0
68	0	1	0	2	0	5	0	9	0	0	2	0	0	0	0	0	3	0	6	6
69	0	0	0	1	0	5	0	8	0	0	0	0	0	0	0	0	3	1	0	14
70	0	0	0	1	5	8	0	9	0	0	1	0	0	0	0	0	2	0	0	0
71	0	0	0	1	0	4	0	10	0	0	1	0	0	0	0	0	1	0	1	0
72	0	0	0	0	0	0	0	23	0	0	0	0	0	0	0	0	2	0	0	1
49	0	0	0	0	0	0	0	35	0	0	0	0	0	0	0	0	3	0	0	16
50	0	0	0	0	0	2	0	23	0	0	0	0	0	0	0	0	3	0	2	3
51	0	0	0	0	0	26	0	24	0	0	13	7	0	0	0	0	5	0	0	51
52	0	0	0	0	0	2	0	23	0	0	0	0	0	0	0	0	3	0	0	0
54	0	0	0	0	0	7	0	3	1	0	0	0	0	0	0	0	2	0	0	0
33	0	0	0	0	0	13	0	1	0	0	0	0	0	0	0	0	0	0	6	0
35	0	0	0	0	0	7	0	13	0	0	0	0	0	1	0	0	0	0	0	14
36	0	0	0	0	1	0	0	4	0	0	0	0	0	0	0	0	13	0	0	0

Appendix III.3 Visual counts of animals on tiles on June 28, 1992. Abbreviations of taxonomic names as in Appendix III.4. (TRT = treatment; TRT 1 = No removal, TRT 2 = Removal of black flies, TRT 3 = Removal of all taxa; TOT CHIR = total chironomids; GRAZ COLL = grazer/collectors)

TILE NO.	TRT	DAYS IN	DU	PH	OL	HA	AS	BF	HP	AN	SV	TOT CHIR	GRAZ COLL
253	1	1	0	0	0	0	0	0	0	0	2	0	0
254	1	1	0	0	0	0	0	0	0	0	19	0	0
255	1	1	0	0	0	0	0	0	0	0	2	3	3
256	1	1	0	0	0	0	0	0	0	0	2	0	0
257	1	1	0	0	0	0	0	0	0	0	0	0	0
258	1	1	0	0	0	0	0	0	0	0	1	0	0
235	1	2	0	0	0	0	0	0	0	0	1	0	0
236	1	2	0	0	0	0	0	0	0	0	0	0	0
237	1	2	0	0	0	0	0	0	0	0	0	0	0
238	1	2	0	0	0	0	2	0	0	0	0	0	0
239	1	2	0	0	0	0	0	0	0	0	2	0	0
240	1	2	0	0	0	0	0	0	0	0	6	0	0
217	1	3	0	0	0	0	0	0	0	0	3	0	0
218	1	3	0	0	0	0	0	0	0	0	0	0	0
219	1	3	0	0	0	0	0	0	0	0	11	0	0
220	1	3	0	0	0	0	0	0	0	0	3	0	0
221	1	3	0	0	0	0	0	1	0	0	4	1	2
222	1	3	0	0	0	0	0	0	0	0	11	1	1
199	1	4	0	0	0	0	0	0	0	0	0	0	0
200	1	4	0	0	0	0	0	0	0	0	0	0	0
202	1	4	0	0	0	0	0	0	0	0	1	0	0
181	1	5	0	0	0	0	0	0	0	0	27	1	1
182	1	5	0	0	0	0	1	0	0	0	0	0	0
183	1	5	0	0	0	0	0	0	0	0	9	3	3
184	1	5	0	0	0	0	1	0	0	0	5	1	1
185	1	5	0	0	0	0	0	1	0	0	0	1	2
186	1	5	0	0	0	0	0	0	0	0	7	3	3
163	1	6	0	0	0	0	0	0	0	0	6	3	3
164	1	6	0	0	0	0	0	0	0	0	1	1	1
165	1	6	0	0	0	0	0	0	0	0	3	2	2
166	1	6	0	0	0	0	0	0	0	0	1	6	6
167	1	6	0	0	0	0	0	0	0	0	0	0	0
168	1	6	0	0	0	0	1	0	0	0	0	0	0
145	1	8	0	0	0	0	0	0	0	0	15	14	14
146	1	8	0	0	0	0	0	0	0	0	21	1	1
147	1	8	0	0	0	0	0	0	0	0	13	11	11
148	1	8	0	0	0	0	0	1	0	0	47	4	5
149	1	8	0	0	0	0	0	0	0	0	5	4	4
150	1	8	0	0	0	0	0	0	0	0	18	9	9
127	1	10	0	0	0	0	0	0	0	0	4	0	0
128	1	10	0	0	0	0	15	3	0	0	0	0	3
130	1	10	0	0	0	0	0	0	0	0	2	4	4
131	1	10	0	0	0	0	0	0	0	0	14	6	6
132	1	10	0	0	0	0	0	0	0	0	1	4	4
109	1	12	0	0	0	0	0	4	0	0	6	3	7
110	1	12	0	0	0	0	0	0	0	0	29	1	1
111	1	12	0	0	0	0	0	0	0	0	10	1	1
113	1	12	0	0	0	0	4	5	0	0	3	4	9
114	1	12	0	0	0	0	0	3	0	0	0	1	4
91	1	15	0	0	0	0	0	2	0	0	23	9	11
92	1	15	0	0	0	0	0	0	0	0	2	11	11
93	1	15	0	0	0	0	0	0	0	0	13	17	17
94	1	15	0	0	0	0	5	6	0	0	4	5	11
95	1	15	0	0	0	0	0	0	0	0	41	3	3
96	1	15	0	0	0	0	0	0	0	0	36	13	13
73	1	18	0	0	0	0	1	4	1	0	13	2	6

Appendix III.3 (Continued)

TILE NO.	TRT	DAYS IN	DU	PH	OL	HA	AS	BF	HP	AN	SV	TOT CHIR	GRAZ COLL
75	1	18	0	0	0	0	0	0	0	0	26	2	2
76	1	18	0	1	0	0	1	1	0	0	58	7	8
77	1	18	0	1	0	0	0	1	0	0	12	0	1
78	1	18	0	0	0	0	0	6	0	0	2	0	6
55	1	21	0	0	0	0	2	1	0	0	0	3	4
56	1	21	0	0	0	0	0	0	0	0	6	5	5
57	1	21	0	0	0	0	0	0	0	0	5	5	5
58	1	21	0	0	0	0	7	0	0	0	0	1	1
59	1	21	0	0	0	0	1	0	0	0	0	1	1
60	1	21	0	0	0	0	0	0	0	0	1	1	1
38	1	24	0	0	0	0	4	6	0	0	0	0	6
39	1	24	0	0	0	0	0	1	0	0	0	1	2
40	1	24	0	0	0	0	0	1	0	0	16	6	7
41	1	24	0	0	0	0	0	2	0	0	0	0	2
42	1	24	0	0	0	0	0	0	0	0	0	0	0
6	1	27	0	0	0	0	2	4	0	0	1	2	6
19	1	27	0	0	0	0	7	0	0	0	0	0	0
20	1	27	0	0	0	0	0	1	0	0	8	1	2
21	1	27	0	0	0	0	0	2	0	0	0	0	2
259	2	1	0	0	0	0	0	0	0	0	1	0	0
260	2	1	0	0	0	0	0	0	0	0	3	1	1
261	2	1	0	0	0	0	0	0	0	0	1	0	0
262	2	1	0	0	0	0	0	0	0	0	12	1	1
263	2	1	0	0	0	0	0	0	0	0	0	0	0
264	2	1	0	0	0	0	0	0	0	0	1	0	0
241	2	2	0	0	0	0	0	1	0	0	2	0	1
242	2	2	0	0	0	0	0	0	0	0	2	0	0
243	2	2	0	0	0	0	0	0	0	0	0	0	0
244	2	2	0	0	0	0	0	0	0	0	0	0	0
245	2	2	0	0	0	0	0	1	0	0	0	0	1
246	2	2	0	0	0	0	0	0	0	0	3	0	0
223	2	3	0	0	0	0	1	0	0	0	1	0	0
225	2	3	0	0	0	0	0	0	0	0	1	2	2
226	2	3	0	0	0	0	0	0	0	0	7	2	2
227	2	3	0	0	0	0	0	0	0	0	0	0	0
228	2	3	0	0	0	0	0	0	0	0	16	0	0
205	2	4	0	0	0	0	0	0	0	0	0	0	0
206	2	4	0	0	0	0	0	0	0	0	0	0	0
207	2	4	0	0	0	0	0	0	0	0	0	0	0
208	2	4	0	1	0	0	1	0	0	0	3	1	1
209	2	4	0	0	0	0	0	0	0	0	0	0	0
210	2	4	0	0	0	0	0	0	0	0	0	0	0
187	2	5	0	0	0	0	0	0	0	0	0	0	0
188	2	5	0	0	0	0	0	0	0	0	3	6	6
89	2	5	0	0	0	0	1	2	0	0	0	0	2
190	2	5	0	0	0	0	0	0	0	0	0	0	0
191	2	5	0	0	0	0	0	2	0	0	0	0	2
192	2	5	0	0	0	0	0	0	0	0	0	0	0
169	2	6	0	0	0	0	0	0	0	0	5	0	0
170	2	6	0	0	0	0	0	0	0	0	0	0	0
172	2	6	0	0	0	0	0	0	0	0	0	0	0
173	2	6	0	0	0	0	0	0	0	0	4	3	3
174	2	6	0	0	0	0	0	0	0	0	0	1	1
151	2	8	0	0	0	0	0	1	0	0	0	1	2
152	2	8	0	0	0	0	0	0	0	0	29	6	6
154	2	8	0	0	0	0	0	0	0	0	8	2	2
155	2	8	0	0	0	0	0	0	0	0	0	0	0
156	2	8	0	0	0	0	0	0	0	0	0	0	0
133	2	10	0	0	0	0	2	1	0	0	0	0	1

Appendix III.3 (Continued)

TILE NO.	TRT	DAYS IN	DU	PH	OL	HA	AS	BF	HP	AN	SV	TOT CHIP	GRAZ COLL
134	2	10	0	0	0	0	0	1	0	0	0	4	5
136	2	10	0	0	0	0	0	0	0	0	4	1	1
137	2	10	0	0	0	0	0	0	0	0	17	6	6
138	2	10	0	0	0	0	0	0	0	0	3	3	3
115	2	12	0	0	0	0	3	1	0	0	0	0	1
117	2	12	0	0	0	0	3	2	0	0	0	0	2
118	2	12	0	0	0	0	0	0	0	0	6	6	6
119	2	12	0	0	0	0	0	0	0	0	1	3	3
120	2	12	0	0	0	0	0	0	0	0	4	1	1
97	2	15	0	0	0	0	0	0	0	0	4	18	18
99	2	15	0	0	0	0	0	0	0	0	14	10	10
100	2	15	0	0	0	0	0	4	0	0	0	3	7
101	2	15	0	0	0	0	0	2	0	0	0	0	2
102	2	15	0	0	0	0	1	4	0	0	0	2	6
79	2	18	0	0	0	0	1	1	0	0	0	3	4
80	2	18	0	0	0	0	0	0	0	0	4	9	9
81	2	18	0	0	0	0	0	0	0	0	14	0	0
83	2	18	0	0	0	0	0	2	0	0	4	4	6
84	2	18	0	0	0	0	1	3	0	0	3	7	10
61	2	21	0	0	0	0	2	0	0	0	0	1	3
62	2	21	0	0	0	0	1	2	0	0	0	0	2
63	2	21	0	0	0	0	0	0	0	0	19	9	9
64	2	21	0	0	0	0	0	3	0	0	3	5	8
65	2	21	0	0	0	0	8	2	0	0	0	0	2
66	2	21	0	0	0	0	2	0	0	0	0	0	0
43	2	24	0	0	0	0	0	3	0	0	3	4	7
44	2	24	0	0	0	0	0	0	0	0	0	0	0
45	2	24	0	0	0	0	1	0	0	0	3	7	7
47	2	24	0	0	0	0	0	0	0	0	3	7	7
48	2	24	0	0	0	0	0	0	0	0	0	0	0
7	2	27	0	0	0	0	0	0	0	0	4	2	2
8	2	27	0	0	0	0	0	5	0	0	0	0	5
11	2	27	0	0	0	0	1	3	0	0	0	0	3
27	2	27	0	0	0	0	0	4	0	0	0	0	4
28	2	27	0	0	0	0	0	4	0	0	3	6	10
30	2	27	0	0	0	0	0	0	0	0	0	0	0
265	3	1	0	0	0	0	0	0	0	0	0	0	0
266	3	1	0	0	0	0	0	0	0	0	1	0	0
267	3	1	0	0	0	0	0	0	0	0	0	0	0
68	3	1	0	0	0	0	0	0	0	0	0	0	0
269	3	1	0	0	0	0	0	0	0	0	0	0	0
270	3	1	0	0	0	0	0	0	0	0	1	0	0
247	3	2	0	0	0	0	0	0	0	0	4	0	0
248	3	2	0	0	0	0	0	0	0	0	1	0	0
249	3	2	0	0	0	0	0	0	0	0	0	0	0
250	3	2	0	0	0	0	0	0	0	0	3	1	1
251	3	2	0	0	0	0	0	0	0	0	11	0	0
252	3	2	0	0	0	0	0	0	0	0	4	0	0
229	3	3	0	0	0	0	0	0	0	0	2	0	0
230	3	3	0	0	0	0	0	0	0	0	3	0	0
231	3	3	0	0	0	0	0	0	0	0	0	0	0
232	3	3	0	0	0	0	0	0	0	0	3	1	1
233	3	3	0	0	0	0	0	0	0	0	7	0	0
234	3	3	0	0	0	0	0	1	0	0	0	1	2
211	3	4	0	0	0	0	0	0	0	0	0	0	0
212	3	4	0	0	0	0	0	0	0	0	0	4	4
213	3	4	0	0	0	0	0	0	0	0	0	0	0
214	3	4	0	0	0	0	7	0	0	0	0	0	0
216	3	4	0	0	0	0	0	0	0	0	0	0	0

Appendix III.3 (Continued)

TILE NO.	TRT	DAYS IN	DU	PH	OL	HA	AS	BF	HP	AN	SV	TOT CHIR	GRAM COLL
193	3	5	0	0	0	0	0	0	0	0	3	1	1
194	3	5	0	0	0	0	0	0	0	0	3	1	1
195	3	5	0	0	0	0	0	0	0	0	0	0	0
196	3	5	0	0	0	0	0	0	0	0	0	2	2
197	3	5	0	0	0	0	0	0	0	0	0	0	0
198	3	5	0	0	0	0	0	1	0	0	5	5	6
175	3	6	0	0	0	0	0	0	0	0	2	0	0
176	3	6	0	0	0	0	0	0	0	0	0	0	0
177	3	6	0	0	0	0	0	0	0	0	5	3	3
178	3	6	0	0	0	0	0	0	0	0	2	2	2
179	3	6	0	0	0	0	0	0	0	0	5	2	2
180	3	6	0	0	0	0	2	0	0	0	3	0	0
158	3	8	0	0	0	0	0	0	0	0	0	0	0
159	3	8	0	0	0	0	0	2	1	0	7	3	5
160	3	8	0	1	0	0	1	2	0	0	0	0	2
161	3	8	0	0	0	0	0	0	0	0	2	1	1
162	3	8	0	0	0	0	0	0	0	0	6	5	5
139	3	10	0	0	0	0	0	0	0	0	1	3	3
140	3	10	0	0	0	0	0	0	0	0	2	1	1
141	3	10	0	0	0	0	0	0	0	0	2	0	0
142	3	10	0	0	0	0	1	1	0	0	12	0	1
143	3	10	0	0	0	0	0	0	0	0	0	1	1
144	3	10	0	0	0	0	0	0	0	0	6	3	3
121	3	12	0	0	0	0	0	0	1	0	11	5	5
122	3	12	0	0	0	0	0	3	0	0	7	2	5
123	3	12	0	0	0	0	3	0	0	0	9	12	12
124	3	12	0	0	0	0	13	3	0	0	1	0	3
125	3	12	0	0	0	0	0	1	0	0	4	7	8
126	3	12	0	0	0	0	0	1	0	0	1	1	2
103	3	15	0	0	0	0	0	2	0	0	8	1	3
104	3	15	0	0	0	0	0	1	0	0	5	3	4
105	3	15	0	0	0	0	0	3	0	0	2	2	5
106	3	15	0	0	0	0	0	0	0	0	2	17	17
107	3	15	0	0	0	0	0	2	0	0	2	2	4
108	3	15	0	0	0	0	0	0	0	0	10	0	0
85	3	18	0	0	0	0	0	2	0	0	0	0	2
86	3	18	0	0	0	0	0	1	0	0	5	11	12
87	3	18	0	0	0	0	1	11	0	0	1	0	11
88	3	18	0	0	0	0	2	2	0	0	0	2	4
89	3	18	0	0	0	0	1	6	0	0	10	8	14
68	3	21	0	0	0	0	0	0	0	0	2	0	0
69	3	21	0	0	0	0	1	8	0	0	0	0	8
70	3	21	0	0	0	0	11	0	0	0	0	0	11
71	3	21	0	0	0	0	0	1	0	0	0	1	2
72	3	21	0	0	0	0	0	4	1	0	6	4	8
49	3	24	0	0	0	0	0	1	0	0	1	4	5
50	3	24	0	0	0	0	0	4	0	0	0	2	6
51	3	24	0	0	0	0	0	4	0	0	1	3	7
52	3	24	0	0	0	0	0	0	0	0	0	0	0
54	3	24	0	0	0	0	0	0	0	0	0	0	0
33	3	27	0	0	0	0	0	0	0	0	0	0	0
35	3	27	0	0	0	0	0	0	0	0	0	0	0
36	3	27	0	0	0	0	1	0	0	0	0	1	1

Appendix III.4 Taxonomic list of animals collected from HMC during the colonization study (during manipulations in bags, on tiles, and visual counts) and abbreviations of taxonomic names. Asterisks designate grazer-collector taxa.

TAXON	ABBREVIATION
Coelenterata	
Hydra	HD
Platyhelminthes	
Tricladida	
Dugesia	DU
Mollusca	
Gastropoda	
*Physa**	PH
Annelida	
Oligochaeta	OL
Hirudinea	
Glossophoniidae	
Glossophonia heteroclides	GH
Arthropoda	
Arachnida	
Hydracarina	HA
Crustacea	
Isopoda	
Asellidae	
Asellus	AS
Hexapoda	
Collembola	
Isotomidae	
Isotomurus	IS
Ephemeroptera	
Baetidae	
*Baetis flavistriga**	BF
*Centroptilum**	CT
Heptageniidae	
*Stenonema**	ST
Coleoptera	
Elmidae	EL
Hydrophilidae	HR
Veliidae	VL
Trichoptera	
Hydroptilidae	
*Hydroptila**	HT
Hydropsychidae	
Hydropsyche	HP
Diptera	
Tipulidae	
*Antocha**	AN
Simuliidae	
Simulium vittatum	SV
Empididae	EM
Ceratopogonidae	
Atrichopogon	AR
Culicoides	CD
Muscidae	MU
Chironomidae	
Immatures	IC
Ablabesmyia	AB
*Corynoneura**	CO
*Cricotopus**	CR
*Dicrotendipes**	DI
*Eukiefferiella**	EU
Metriocnemus	MT

Appendix III.4 (Continued)

TAXON	ABBREVIATION
Chironomidae (continued)	
Nanocladius*	NA
Micropsectra*	MP
Paratanytarsus*	PT
Phaenopsectra*	PP
Polypedilum*	PO
Psectrocladius*	PC
Rheocricotopus	RC
Thienemanniella*	TH
Tvetenia*	TV
Thienemannimyia	TY

Appendix III.5 Physical conditions at tile placement and removal, and dry mass and ash-free dry mass accumulated on tiles. Abbreviations of taxonomic names as in Appendix III.4. (TRT = treatment; TRT 1 = No removal, TRT 2 = Removal of black flies, TRT 3 = Removal of all taxa; C.V. = current velocity; DM = dry mass; AFDM = ash-free dry mass)

			TILE PLACEMENT			TILE REMOVAL			DM	AFDM
TILE NO.	TRT	DAYS IN	DEPTH (cm)	C.V. (cm/s)	FROUDE NO.	DEPTH (cm)	C.V. (cm/s)	FROUDE NO.	(mg/ Tile)	(mg/ Tile)
253	1	1	9.0	58.8	0.391	6.0	56.2	0.536	2.6	0.7
254	1	1	3.0	21.2	0.152	1.0	14.8	0.222	4.7	2.8
255	1	1	4.0	25.4	0.165	2.0	24.8	0.312	9.7	0.6
256	1	1	5.0	28.8	0.169	3.0	20.6	0.144	3.7	2.3
257	1	1	4.0	25.2	0.162	2.5	18.5	0.139	5.6	1.0
258	1	1	9.0	21.7	0.053	7.5	19.0	0.049	2.2	0.7
235	1	2	4.0	41.3	0.434	3.0	43.7	0.649	4.6	1.3
236	1	2	7.0	26.4	0.102	5.0	17.2	0.061	6.0	3.1
237	1	2	4.0	25.9	0.171	3.0	12.6	0.054	1.8	0.6
238	1	2	3.0	18.5	0.116	2.0	11.3	0.065	2.2	1.0
239	1	2	8.0	40.6	0.210	5.0	33.1	0.224	6.4	2.5
240	1	2	9.5	15.7	0.026	8.0	34.9	0.155	2.8	1.2
217	1	3	3.0	32.2	0.351	2.5	27.0	0.297	4.5	2.2
218	1	3	11.0	39.1	0.142	9.0	23.3	0.061	2.5	1.2
219	1	3	10.0	36.9	0.139	6.0	32.5	0.179	1.4	0.4
220	1	3	7.0	40.5	0.238	4.5	15.2	0.052	2.9	0.4
221	1	3	7.0	34.6	0.175	5.0	16.3	0.054	2.7	0.7
222	1	3	4.0	63.0	1.012	3.0	32.4	0.356	10.4	4.2
199	1	4	12.0	31.8	0.086	3.5	8.9	0.023	17.3	3.0
200	1	4	8.0	27.5	0.096	2.0	41.5	0.877	5.0	0.8
202	1	4	5.0	36.8	0.276	1.0	19.3	0.378	1.2	2.4
181	1	5	6.0	16.3	0.045	5.0	25.2	0.130	6.5	0.2
182	1	5	8.0	19.4	0.048	8.0	12.8	0.021	16.4	1.5
183	1	5	9.0	31.2	0.110	6.0	39.3	0.263	4.9	2.8
184	1	5	6.0	24.8	0.104	3.0	31.4	0.335	2.9	0.8
185	1	5	6.0	36.7	0.228	7.0	15.4	0.035	52.4	43.1
186	1	5	6.0	70.7	0.849	6.0	67.9	0.783	23.9	3.4
163	1	6	3.0	26.6	0.240	4.0	60.4	0.931	3.8	1.8
164	1	6	5.0	20.2	0.083	5.0	23.6	0.114	4.4	1.2
165	1	6	4.5	38.2	0.331	5.0	48.8	0.485	16.2	3.9
166	1	6	4.0	37.8	0.364	2.0	48.8	1.212	2.2	1.1
167	1	6	6.0	17.2	0.050	4.0	34.9	0.310	3.4	0.6
168	1	6	7.0	19.9	0.058	8.5	12.2	0.018	248.6	50.4
145	1	8	3.5	26.4	0.204	12.0	42.9	0.157	12.4	3.5
146	1	8	1.5	38.7	1.016	2.0	30.3	0.467	174.4	108.3
147	1	8	3.0	53.7	0.980	9.0	28.9	0.095	7.3	4.7
148	1	8	2.0	38.1	0.740	4.0	26.7	0.181	20.1	8.7
149	1	8	3.0	24.0	0.195	2.0	31.9	0.520	15.9	6.5
150	1	8	9.0	36.7	0.153	10.0	53.3	0.289	36.8	9.5
127	1	10	3.0	60.0	1.223	5.0	35.0	0.249	30.8	5.9
128	1	10	3.0	58.4	1.160	3.0	12.4	0.052	24.9	13.2
130	1	10	8.0	38.5	0.188	7.5	39.6	0.213	25.6	10.1
131	1	10	8.0	36.3	0.168	7.0	35.1	0.179	8.6	5.5
132	1	10	6.0	58.3	0.578	5.0	39.8	0.323	30.9	24.5
109	1	12	5.0	29.8	0.181	3.0	33.4	0.379	5.8	2.3
110	1	12	4.5	42.4	0.407	1.0	14.0	0.199	10.4	5.7
111	1	12	5.0	32.3	0.212	3.0	45.7	0.711	27.3	17.5
113	1	12	4.0	28.1	0.202	3.0	38.7	0.508	6.1	1.3
114	1	12	5.0	19.2	0.075	3.0	34.5	0.405	16.1	4.2
91	1	15	4.0	34.0	0.294	3.0	16.6	0.093	94.9	40.8
92	1	15	4.0	35.9	0.328	10.0	45.7	0.213	21.7	2.3
93	1	15	7.0	89.2	1.158	6.0	101.4	1.746	22.0	10.1
94	1	15	7.0	38.3	0.214	5.0	34.2	0.238	55.6	37.8
95	1	15	7.0	39.5	0.227	3.0	52.7	0.944	32.2	18.0
96	1	15	19.0	59.7	0.191	12.0	65.8	0.368	12.2	6.8

Appendix III.5 (Continued)

TILE NO.	TRT	DAYS IN	TILE PLACEMENT DEPTH (cm)	TILE PLACEMENT C.V. (cm/s)	TILE PLACEMENT FROUDE NO.	TILE REMOVAL DEPTH (cm)	TILE REMOVAL C.V. (cm/s)	TILE REMOVAL FROUDE NO.	DM (mg/ Tile)	AFDM (mg/ Tile)
73	1	18	6.0	60.4	0.621	5.0	48.1	0.472	9.5	6.2
75	1	18	6.0	37.6	0.240	5.0	31.7	0.205	168.4	83.4
76	1	18	2.0	35.9	0.656	1.0	31.2	0.989	113.2	34.2
77	1	18	6.0	20.6	0.072	5.0	28.2	0.163	3.8	1.2
78	1	18	7.5	54.3	0.400	6.5	47.1	0.348	39.4	14.6
55	1	21	4.0	33.7	0.290	4.0	34.0	0.294	10.3	5.4
56	1	21	4.0	17.6	0.079	5.0	21.4	0.093	13.8	300.7
57	1	21	3.0	15.0	0.076	3.0	34.3	0.400	201.1	38.2
58	1	21	3.0	17.1	0.100	2.0	18.1	0.168	46.8	20.4
59	1	21	3.0	33.6	0.384	2.0	9.2	0.043	21.3	8.4
60	1	21	3.5	28.8	0.242	3.0	27.6	0.258	250.1	111.2
38	1	24	10.0	6.4	0.004	10.0	4.8	0.002	207.9	248.8
39	1	24	8.0	8.0	0.008	3.0	18.0	0.110	204.7	85.0
40	1	24	7.0	9.2	0.012	2.0	42.4	0.915	761.3	151.7
41	1	24	6.5	7.5	0.009	2.0	18.3	0.170	421.3	104.8
42	1	24	11.0	7.5	0.005	4.0	37.7	0.361	126.7	62.8
6	1	27	10.0	7.4	0.006	4.0	37.9	0.366	78.7	29.2
19	1	27	8.0	25.4	0.082	10.0	8.3	0.007	55.7	28.2
20	1	27	3.5	15.3	0.068	9.0	44.4	0.223	488.3	58.8
21	1	27	4.0	25.5	0.166	9.0	44.4	0.223	398.9	80.8
259	2	1	2.0	51.4	1.344	2.0	28.5	0.413	3.0	1.8
260	2	1	4.0	25.4	0.165	2.0	31.7	0.513	2.3	1.4
261	2	1	3.0	36.1	0.443	2.0	32.7	0.546	0.9	0.7
262	2	1	4.0	14.2	0.051	3.0	14.9	0.075	3.7	1.8
263	2	1	8.5	17.8	0.038	8.0	17.5	0.039	7.5	2.6
264	2	1	3.5	25.4	0.188	2.5	17.0	0.118	29.0	10.1
241	2	2	4.0	12.9	0.042	2.0	17.5	0.155	6.7	2.1
242	2	2	3.0	37.0	0.465	1.0	24.6	0.619	4.8	1.6
243	2	2	6.0	15.1	0.039	6.0	18.9	0.061	1.3	0.5
244	2	2	4.0	75.3	1.444	4.0	26.0	0.172	4.4	1.0
245	2	2	8.0	29.9	0.114	7.0	23.0	0.077	1.5	0.3
246	2	2	3.0	29.0	0.286	2.0	27.7	0.390	4.9	2.0
223	2	3	4.0	62.5	0.994	2.0	30.5	0.473	83.4	37.3
225	2	3	3.0	38.0	0.491	3.0	26.9	0.246	29.6	25.7
226	2	3	9.0	35.1	0.139	6.0	21.3	0.077	36.5	29.2
227	2	3	4.0	39.0	0.388	2.5	36.3	0.538	11.7	5.8
228	2	3	5.0	66.8	0.910	4.0	48.5	0.601	4.4	2.0
205	2	4	7.0	51.2	0.382	0.5	3.0	0.018	11.8	0.5
206	2	4	5.0	47.1	0.452	0.5	3.0	0.018	4.3	2.1
207	2	4	9.0	34.0	0.131	2.0	21.5	0.236	54.2	16.8
208	2	4	6.0	35.8	0.217	2.0	27.5	0.384	9.7	2.4
209	2	4	5.0	35.1	0.251	3.0	9.4	0.030	3.2	1.4
210	2	4	3.0	32.4	0.356	5.0	13.1	0.035	9.9	3.0
187	2	5	4.0	77.4	1.525	4.0	20.6	0.108	4.1	1.7
188	2	5	8.0	56.1	0.400	9.0	16.6	0.031	4.9	2.1
189	2	5	9.0	34.3	0.133	6.0	14.7	0.037	3.8	0.8
190	2	5	9.0	57.5	0.375	12.0	18.7	0.030	15.6	1.5
191	2	5	5.0	40.1	0.328	5.0	19.8	0.080	2.7	0.1
192	2	5	5.0	26.3	0.141	3.5	19.5	0.111	38.3	2.0
169	2	6	7.0	70.6	0.725	6.0	54.9	0.513	13.3	0.4
170	2	6	9.0	83.5	0.790	3.0	3.0	0.003	7.3	2.0
172	2	6	4.0	28.7	0.210	3.0	17.6	0.105	8.1	1.8
173	2	6	4.0	31.3	0.249	7.0	23.3	0.079	8.4	1.2
174	2	6	2.0	30.7	0.480	8.0	26.0	0.086	4.7	2.0
151	2	8	5.0	26.1	0.139	6.0	16.8	0.048	33.5	11.0
152	2	8	4.5	60.7	0.834	5.0	62.9	0.807	8.3	3.6
154	2	8	2.0	41.5	0.877	5.0	14.8	0.044	7.1	2.4
155	2	8	3.0	30.8	0.323	15.0	12.1	0.010	4.1	0.9

Appendix III.5 (Continued)

TILE NO.	TRT	DAYS IN	TILE PLACEMENT DEPTH (cm)	TILE PLACEMENT C.V. (cm/s)	TILE PLACEMENT FROUDE NO.	TILE REMOVAL DEPTH (cm)	TILE REMOVAL C.V. (cm/s)	TILE REMOVAL FROUDE NO.	DM (mg/ Tile)	AFDM (mg/ Tile)
156	2	8	3.5	37.2	0.403	3.5	38.6	0.433	1.0	5.0
133	2	10	10.0	58.0	0.343	10.0	17.6	0.031	9.5	3.1
134	2	10	8.0	24.9	0.079	8.0	20.0	0.051	15.5	2.1
136	2	10	6.0	45.2	0.347	4.5	38.1	0.329	26.9	4.3
137	2	10	5.0	51.9	0.549	4.0	46.3	0.546	5.4	1.2
138	2	10	7.5	65.9	0.591	3.0	60.8	1.255	3.4	1.7
115	2	12	3.0	16.3	0.091	1.0	9.3	0.088	17.9	3.9
117	2	12	4.0	19.0	0.092	2.0	21.8	0.243	45.6	13.4
118	2	12	4.0	30.4	0.235	2.0	25.0	0.318	16.9	5.2
119	2	12	4.0	50.2	0.643	2.5	48.9	0.974	12.1	4.7
120	2	12	4.0	19.8	0.100	2.5	34.5	0.486	21.6	13.1
97	2	15	10.0	41.5	0.175	10.0	63.1	0.406	6.0	3.1
99	2	15	6.0	55.7	0.528	10.0	41.4	0.174	11.3	6.4
100	2	15	9.0	15.2	0.026	6.0	48.0	0.391	59.4	31.5
101	2	15	2.0	64.7	2.134	12.0	33.6	0.096	31.0	11.8
102	2	15	2.0	22.1	0.248	20.0	27.7	0.039	13.7	6.2
79	2	18	4.5	23.6	0.127	3.0	21.1	0.151	28.4	12.8
80	2	18	7.0	39.1	0.223	4.5	25.2	0.144	35.6	12.2
81	2	18	8.0	42.9	0.235	4.0	15.6	0.062	21.3	9.1
83	2	18	5.0	26.9	0.147	6.0	43.7	0.325	72.9	23.0
84	2	18	3.0	34.3	0.400	4.0	56.7	0.820	17.9	5.3
61	2	21	6.0	25.0	0.106	5.0	28.8	0.169	487.1	109.5
62	2	21	3.0	14.0	0.066	1.0	14.9	0.226	104.0	60.6
63	2	21	3.0	39.5	0.529	3.0	47.5	0.768	182.9	92.3
64	2	21	3.0	32.2	0.351	2.0	26.7	0.362	5.9	3.3
65	2	21	3.0	28.9	0.284	2.0	11.9	0.072	40.0	16.3
66	2	21	4.0	27.5	0.192	9.0	21.6	0.053	48.0	28.3
43	2	24	8.5	9.2	0.010	2.0	22.5	0.258	176.5	64.7
44	2	24	9.8	4.1	0.002	7.0	10.8	0.017	70.0	31.6
45	2	24	5.0	12.5	0.032	1.0	33.3	1.129	18.7	10.4
47	2	24	3.5	8.0	0.019	3.0	34.6	0.407	294.0	115.2
48	2	24	8.5	5.2	0.003	4.5	3.0	0.002	66.2	6.7
7	2	27	10.0	13.9	0.020	6.0	35.9	0.219	298.9	106.7
8	2	27	14.0	25.4	0.047	12.0	36.4	0.113	135.4	56.1
11	2	27	6.0	17.7	0.053	3.0	10.0	0.034	139.1	32.1
27	2	27	6.0	21.7	0.080	5.0	12.2	0.030	552.0	130.9
28	2	27	9.0	23.8	0.064	4.0	25.8	0.169	652.0	126.0
30	2	27	5.5	25.4	0.120	9.0	16.0	0.029	7.7	3.2
265	3	1	9.0	35.1	0.139	6.0	25.7	0.112	6.3	1.0
266	3	1	5.0	20.7	0.088	2.5	36.5	0.544	3.1	2.4
267	3	1	3.0	32.1	0.349	1.0	22.9	0.532	0.6	0.2
268	3	1	2.0	30.3	0.467	1.5	17.4	0.205	4.5	1.1
269	3	1	8.0	23.1	0.068	3.0	23.2	0.183	1.2	0.7
270	3	1	3.0	26.3	0.236	3.0	40.7	0.563	3.8	0.9
247	3	2	3.0	54.3	1.001	2.5	25.3	0.261	1.4	0.5
248	3	2	6.0	31.3	0.166	5.0	41.3	0.347	1.8	0.6
249	3	2	3.0	27.1	0.250	2.0	7.8	0.031	2.4	0.7
250	3	2	10.0	52.0	0.276	7.0	26.7	0.104	9.7	3.9
251	3	2	10.0	71.3	0.518	7.0	52.0	0.394	2.9	0.2
252	3	2	15.0	68.0	0.314	12.0	68.4	0.397	1.2	0.7
229	3	3	10.0	15.7	0.025	7.5	19.9	0.054	2.8	1.3
230	3	3	10.0	21.5	0.047	6.0	25.4	0.110	36.1	24.7
231	3	3	8.0	25.9	0.085	7.0	25.4	0.094	14.0	10.8
232	3	3	8.0	28.9	0.106	5.0	37.1	0.281	3.8	0.8
233	3	3	7.0	30.9	0.139	5.0	5.6	0.006	2.9	0.7
234	3	3	7.0	55.6	0.450	3.0	53.8	0.984	4.4	2.8
211	3	4	7.0	25.7	0.096	2.5	6.8	0.019	36.7	3.8
212	3	4	6.0	30.4	0.157	0.5	12.3	0.309	6.5	1.1

Appendix III.5 (Continued)

TILE NO.	TRT	DAYS IN	TILE PLACEMENT DEPTH (cm)	C.V. (cm/s)	FROUDE NO.	TILE REMOVAL DEPTH (cm)	C.V. (cm/s)	FROUDE NO.	DM (mg/ Tile)	AFDM (mg/ Tile)
213	3	4	5.0	46.9	0.448	0.5	3.00	0.018	3.4	1.0
214	3	4	6.0	47.3	0.380	0.5	3.00	0.018	1.9	0.7
216	3	4	6.0	24.6	0.103	5.0	41.5	0.351	5.7	1.4
193	3	5	3.5	19.2	0.107	4.5	48.0	0.522	2.7	1.8
194	3	5	5.0	27.3	0.152	3.0	33.1	0.371	11.1	4.1
195	3	5	10.0	42.5	0.184	9.0	13.9	0.022	6.2	2.6
196	3	5	6.5	69.4	0.756	10.0	28.6	0.083	42.9	1.1
197	3	5	5.0	24.9	0.126	3.0	14.1	0.068	10.8	1.0
198	3	5	4.0	28.4	0.205	2.5	38.9	0.617	6.0	1.1
175	3	6	9.0	29.8	0.101	9.0	29.8	0.101	15.6	4.4
176	3	6	7.0	22.2	0.072	8.0	22.3	0.063	6.7	1.9
177	3	6	2.0	37.6	0.719	2.0	52.3	1.391	10.2	2.4
178	3	6	6.0	61.0	0.632	10.0	48.9	0.244	3.8	2.0
179	3	6	2.0	24.3	0.301	10.0	33.3	0.113	10.9	3.0
180	3	6	5.0	48.2	0.474	5.0	22.0	0.098	21.7	3.6
158	3	8	7.0	48.3	0.340	15.0	20.2	0.028	10.5	6.5
159	3	8	5.0	29.4	0.176	5.0	49.8	0.505	12.2	4.2
160	3	8	3.0	26.7	0.242	5.0	25.0	0.127	7.9	1.3
161	3	8	6.0	43.3	0.318	5.0	72.0	1.058	8.8	5.4
162	3	8	5.0	60.7	0.750	9.0	35.8	0.145	3.5	0.8
139	3	10	4.0	51.1	0.666	2.0	28.0	0.400	11.9	3.2
140	3	10	7.0	29.8	0.129	6.0	27.6	0.129	12.5	8.8
141	3	10	6.0	52.6	0.470	13.0	30.6	0.073	7.0	4.5
142	3	10	4.0	29.8	0.226	5.0	14.6	0.043	9.5	4.1
143	3	10	3.0	35.4	0.426	16.0	12.3	0.010	10.8	3.0
144	3	10	8.0	80.1	0.817	8.0	30.0	0.115	12.9	1.4
121	3	12	6.0	51.5	0.450	3.0	50.7	0.873	79.3	19.4
122	3	12	4.0	22.9	0.133	4.0	52.3	0.696	11.8	8.7
123	3	12	7.0	39.9	0.232	5.0	13.5	0.037	4.5	2.6
124	3	12	3.0	42.0	0.600	1.0	17.4	0.307	38.6	25.4
125	3	12	5.0	15.0	0.046	10.0	40.2	0.165	38.0	21.2
126	3	12	4.0	22.7	0.132	3.0	21.7	0.160	13.5	1.6
103	3	15	4.0	40.2	0.413	7.0	31.4	0.143	9.5	4.6
104	3	15	7.0	62.5	0.568	6.0	80.1	1.090	8.4	5.3
105	3	15	8.0	19.9	0.051	5.0	26.0	0.138	12.6	6.9
106	3	15	6.0	49.6	0.417	3.0	70.4	1.683	7.3	0.6
107	3	15	7.0	35.4	0.183	8.0	41.6	0.220	34.1	2.0
108	3	15	6.0	26.1	0.116	7.0	32.3	0.152	13.1	4.7
85	3	18	5.0	27.1	0.150	3.5	32.6	0.310	4.5	3.9
86	3	18	3.0	43.5	0.643	2.0	53.8	1.476	4.8	2.5
87	3	18	7.0	50.0	0.364	7.0	71.0	0.734	74.3	23.9
88	3	18	4.0	19.9	0.101	4.5	25.5	0.148	25.1	13.4
89	3	18	6.0	54.5	0.504	10.0	37.0	0.139	22.9	7.6
68	3	21	2.0	18.4	0.172	2.0	35.8	0.651	17.9	7.9
69	3	21	3.5	14.3	0.060	3.0	25.3	0.218	170.5	92.0
70	3	21	6.0	10.5	0.019	5.0	9.7	0.019	71.3	37.9
71	3	21	3.0	13.9	0.065	2.5	31.8	0.413	67.4	30.1
72	3	21	4.5	40.2	0.367	3.0	73.2	1.820	4.8	3.6
49	3	24	10.5	6.9	0.005	3.0	17.2	0.101	76.2	46.2
50	3	24	9.0	7.5	0.006	6.0	22.1	0.083	11.9	2.7
51	3	24	15.0	5.2	0.002	12.0	15.7	0.021	97.0	39.5
52	3	24	10.5	6.9	0.005	3.0	33.1	0.371	59.0	29.5
54	3	24	8.5	5.2	0.003	2.0	29.8	0.453	468.0	103.5
33	3	27	8.0	11.1	0.016	9.5	32.8	0.116	363.3	108.0
35	3	27	12.0	40.8	0.141	6.0	40.6	0.280	423.8	112.3
36	3	27	11.0	20.8	0.040	7.0	11.1	0.018	9.0	2.2

Appendix III.6 Summary of the regression coefficients and coefficients of determination (R^2) for the abiotic factors (Appendix III.5) significantly influencing the distribution of S. vittatum larvae from a forward stepwise multiple linear regression. (CV = current velocity; FR = Froude number. Dash (--) denotes the absence of any significant factors.

DAYS IN STREAM	FACTOR	Y-INTERCEPT	REGRESSION COEFFICIENT	STANDARD ERROR	R^2
1	--				
2	--				
3	--				
4	--				
5	CV	-2.245	1.017	0.456	0.24
6	CV	-0.960	0.741	0.322	0.26
8	--				
10	--				
12	--				
15	FR	1.279	1.754	0.621	0.35
18	--				
21	FR	0.848	1.472	0.462	0.40
24	FR	0.552	2.522	0.747	0.47
27	$(CV)^2$	-1.421	0.384	0.114	0.51

Appendix III.7 Taxa present on Treatment 1 (No Removal) tiles in Hobbs-Mackenzie Creek (0 = absent; 1 = present) on each day of the study. Abbreviations of taxonomic names are listed in Appendix III.4.

	DAYS													
TAXON	1	2	3	4	5	6	8	10	12	15	18	21	24	27
HD	1	0	0	0	0	0	0	0	1	0	0	0	0	0
DU	0	1	1	1	1	0	0	1	1	1	0	1	1	1
PH	0	0	0	0	0	0	0	0	0	0	1	0	0	0
OL	0	1	0	0	0	1	1	1	1	1	0	1	1	1
GH	0	0	0	0	0	0	0	0	0	0	0	0	1	0
HA	0	0	0	1	0	1	0	1	0	0	1	0	1	1
AS	1	1	1	1	1	1	1	1	1	1	1	1	1	1
BF	1	1	1	1	1	1	1	1	1	1	1	1	1	1
ST	0	0	0	0	0	1	0	0	0	0	0	0	1	1
EL	0	0	0	0	1	0	0	0	0	1	0	0	0	0
HR	0	0	1	0	0	0	0	0	0	0	0	0	0	0
VL	1	0	1	1	0	0	0	0	0	0	0	0	0	0
HT	0	0	0	0	0	0	0	0	0	0	1	0	0	0
HP	1	1	1	1	1	1	1	1	1	1	1	1	1	1
AN	1	0	1	0	0	1	0	0	1	1	1	1	1	1
SV	1	1	1	1	1	1	1	1	1	1	1	1	1	1
EM	0	0	0	0	0	1	0	0	0	0	0	0	0	0
AR	0	0	0	0	0	0	0	1	0	0	0	0	0	0
CD	0	0	0	0	0	0	0	0	0	1	0	0	0	0
MU	0	0	0	0	0	0	1	0	0	0	0	0	0	0
AB	0	0	0	0	0	1	0	0	1	1	1	1	1	0
CO	0	0	1	0	0	1	1	1	1	1	1	1	1	1
CR	1	0	0	1	0	1	1	1	1	1	1	1	1	1
DI	0	0	0	0	0	0	0	0	0	0	0	0	0	1
EU	1	1	1	1	1	1	1	1	1	1	1	1	1	1
MT	0	0	0	0	0	0	0	0	0	0	0	1	0	0
NA	1	0	0	0	0	0	1	0	1	0	1	1	0	1
MP	0	0	0	0	0	0	0	0	0	0	1	0	0	0
PT	0	0	0	0	0	0	0	0	0	0	1	0	0	1
PO	0	0	0	0	0	0	0	0	0	0	1	0	0	0
PC	0	0	0	0	0	0	0	1	0	0	0	0	0	1
RC	0	1	0	0	0	0	0	0	0	0	1	0	0	0
TH	1	1	1	1	1	1	1	1	1	1	1	1	1	1
TV	0	1	0	0	0	1	1	1	1	1	1	0	0	0
TY	0	0	0	0	0	0	0	0	1	1	1	0	0	1
IC	1	1	0	0	1	1	1	0	1	1	1	0	0	1
TOTAL	11	10	11	10	8	15	12	14	16	16	20	14	15	18

Appendix III.8 Summary of the regression coefficients and coefficients of determination (R^2) from a forward stepwise multiple linear regression for black flies from Treatment 3 (all taxa removed) assessing the effect of tile age (n=74 tiles).

FACTOR	REGRESSION COEFFICIENT	S.E.	R^2
Intercept	1.225		
$(\text{Tile Age})^2$	-0.004**	0.001	0.09
Tile Age	0.082*	0.038	0.06
Total			0.15

** p<0.01 * p<0.05

Appendix III.5A Summary of replicated least squares regression for periphyton (AFDM) against tile age for Treatment 2. A linear relationship between periphyton and tile age occurred on Ln(x+1) transformed data (n=69 tiles), given by the equation Ln(y+1) = 0.133x + 0.386 (R^2=0.74).

SOURCE OF VARIATION	DF	SUM OF SQUARES	MEAN SQUARE	F	p
Among	13	91.842	7.065	17.40	
Regression	1	84.767	84.767	143.78	0.001
Deviation	12	7.075	0.590	1.45	
Within	55	22.328	0.406		
Total	68	114.170	0.637		

Appendix III.9B Summary of replicated least squares regression for periphyton (AFDM) against tile age for Treatment 3. A linear relationship between periphyton and tile age occurred on Ln(x+1) transformed data (n=70 tiles), given by the equation Ln(y+1) = 0.123x + 0.384 (R^2=0.63).

SOURCE OF VARIATION	DF	SUM OF SQUARES	MEAN SQUARE	F	p
Among	13	69.923	5.379	11.07	
Regression	1	60.806	60.806	80.038	0.001
Deviation	12	9.117	0.760	1.563	
Within	56	27.221	0.486		
Total	69	97.144	0.697		

Appendix III.9C Summary of replicated least squares regression for detritus (dry mass) against tile age for Treatment 2. A linear relationship between periphyton and tile age occurred on Ln(x+1) transformed data (n=64 tiles), given by the equation Ln(y+1) = 0.141x + 1.147 (R^2=0.74).

SOURCE OF VARIATION	DF	SUM OF SQUARES	MEAN SQUARE	F	p
Among	13	97.066	7.467	14.88	
Regression	1	89.728	89.728	146.72	0.001
Deviation	12	7.339	0.612	1.22	
Within	50	25.093	0.502		
Total	63	122.160	0.708		

Appendix III.9D Summary of replicated least squares regression for detritus (dry mass) against tile age for Treatment 3. A linear relationship between periphyton and tile age occurred on Ln(x+1) transformed data (n=68 tiles), given by the equation Ln(y+1) = 0.118x + 1.240 (R^2=0.59).

SOURCE OF VARIATION	DF	SUM OF SQUARES	MEAN SQUARE	F	p
Among	13	67.135	5.164	11.70	
Regression	1	53.391	53.398	46.64	0.001
Deviation	12	13.737	1.145	2.59	0.05
Within	54	23.831	0.441		
Total	67	90.966	0.664		

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