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FILTER-FEEDING ECOLOGY OF AQUATIC INSECTS

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INTRODUCTION

Filter feeders are organisms that have evolved various sieving mechanisms for removing particulate matter from suspension (100). Several groups of aquatic insects, with habitats ranging from high elevation streams to saltwater estuaries, use this feeding method and consume significant quantities of suspended material (seston), including living organisms and both organic and inorganic detritus. Filter-feeding insects constitute important pathways for energy flow and are very important in the productivity of aquatic environments. Yet, some of these animals epitomize the complex relationship between man and insects since biting adults of certain groups are among man's oldest adversaries. The major objectives of this article are to review the means by which filter-feeding insects obtain their food and to assess the role of these animals in aquatic ecosystems. Filter-feeding strategies by other invertebrates in both marine and freshwater habitats have been partially reviewed elsewhere (82, 100, 101).

SOURCES OF FOOD

Lotic ecosystems in forested regions receive large inputs of allochthonous organic matter (4, 36-38, 98, 137). Anderson & Sedell (4) recently reviewed the role of macroinvertebrates in detritus processing. There is ample evidence from lotic studies that the concentration of particulate organic seston

is skewed toward the smallest size fractions (<50 μm) (119, 148, 191). Since most filter feeders ingest fine particulate organic matter (FPOM) well below 1 mm, most of the coarse particulate organic matter (CPOM) cannot be utilized. Therefore, CPOM must be converted to FPOM and made available to filter-feeding insects by the following pathways: (*a*) physical abrasion, (*b*) microbial activity, (*c*) egestion and comminution by invertebrates, (*d*) direct inputs of FPOM from terrestrial runoff, and (*e*) flocculation of dissolved organic matter (DOM) (4). DOM concentration is generally higher than particulate organic matter (POM) in both lotic (63, 226) and lentic waters (73); however, DOM is not a static endpoint of processing since it may be utilized by microorganisms or flocculate in alkaline waters (118, 119, 128). It has been suggested that the lower productivity of softwater streams (96) may be partially associated with their lower ability to trap dissolved organic compounds (117).

Minshall (141) recently suggested that the role of allochthonous organic matter in streams has been overemphasized. He attributes this to the following factors: (*a*) concentration of most studies on small streams located in deciduous forest biomes, (*b*) failure to consider rapid turnover of low-standing crop periphyton biomass, (*c*) misinterpretation of photosynthesis-respiration ratios, and (*d*) failure to consider autotrophic production which enters the detrital food chain. Conversely, lentic environments have historically been considered as having grazer (or autotrophic) based food chains. However, recent studies indicate the detritus-microbial complex has been underestimated in these systems (73, 171, 229). Rich & Wetzel (171) suggest that nonpredatory losses (i.e. aerobic and anaerobic decomposition) or carbon from a plant-herbivore transfer, e.g. DOM and egestion, may be more than the amount of material and energy transmitted up the grazer food chain. These nonpredatory losses may be subjected to anaerobic metabolism. The resultant products undergo deferred respiration and may form energy-rich intermediate products which then subsidize other processes. Thus, ecosystem efficiencies of detritus processing in lakes are considerably higher than efficiencies indicated by conventional food chain efficiencies (171).

The complexities of the grazer and detrital pathways are beyond the scope of this article; indeed, Goldman & Kimmel (73) suggest that trying to separate allochthony from autochthony may be fruitless because of extensive intermeshing of the two pathways and our inability to separate the two analytically. Thus, in both lotic and lentic waters, a mixture of organic material of both known (e.g. algae, animals) and unknown origin (i.e. detritus) will be in suspension; the microbial flora associated with the latter can be extremely important in the nutrition of filter-feeding animals (6, 14). Cummins & Klug (39) have recently reviewed the current status of microbial-animal interactions in stream invertebrates.

MORPHO-BEHAVIORAL ADAPTATIONS AND ASSOCIATED HABITATS

Filter-feeding is well documented in the following insect orders: Ephemeroptera, Trichoptera and Diptera. Within each of these orders there is considerable evidence, based on existing phylogenies (e.g. 169), that filter-feeding has evolved independently several times. However, in all known examples, adaptations for filter-feeding center around specialized anatomical structures (e.g. setae, mouth brushes, or fans) and silk secretions which act as sieves. The following examples are not inclusive and the reader is referred to Hynes (96), Merritt & Cummins (136), and Wesenberg-Lund (228) for additional references.

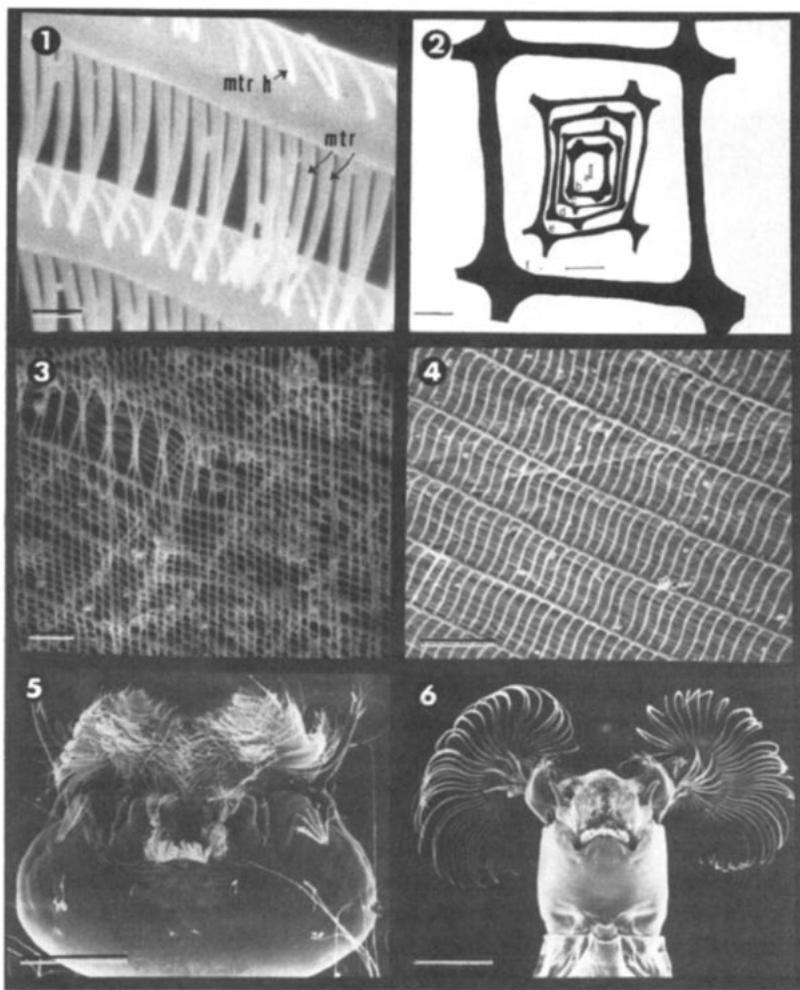
Ephemeroptera

Although most mayflies feed by methods other than filtering (58), a number of diverse groups have evolved filter-feeding mechanisms. Most morphological adaptations for filter feeding in mayflies involve the use of setae on the mouth parts or forelegs which act as filters, although silk-like secretions have been documented (84, 184).

Siphlonurids have several filter-feeding groups, which include *Isonychia*, found primarily in the Holarctic and Oriental Realms, and several members of the Coloburiscinae in the southern hemisphere (57). The latter are very similar to *Isonychia* (57) which have a well-developed fringe of elongate setae on their forelegs (26). *Isonychia* nymphs orient facing into the current with their setiferous forelegs extended in front of the body (Figure 71). As *Isonychia* sieves seston, the forelegs are periodically brought within reach of the setiferous labial and maxillary palps (26). The long filtering setae on the forelegs of *Isonychia* are latched to adjacent setae by two types of microtrichia and this coupling mechanism results in minute pore sizes, possibly with colloidal retention capabilities (Figure 1). It is not known to what extent nymphs rely on this coupling device for feeding (214). Nymphal gut analyses indicate that *Isonychia* are primarily omnivores (26, 29) or detritivores (194, 214).

The oligoneurids (12, 58) and leptophlebiids (58, 159, 160) have several genera that are probably filter feeders. Filter feeding in these groups has been suggested by deduction from the elongate setae found on specialized mouth parts or forelegs. Similar specialized mouth parts are also known in some baetids (106) and ephemerellids (96).

Nymphs of ephemerids are found in a wide variety of lotic and lentic habitats (58, 125). They are regarded as deposit feeders or "mud-eaters" (95), and it has been suggested that much of their feeding, especially in *Hexagenia*, may be filter feeding (58). Bioenergetic data support some filter feeding since the caloric and organic matter of *Hexagenia* gut contents are



Figures 1–6 Examples of structures used for food capture by filter-feeding insects. 1. SEM photomicrograph of a portion of two filtering setae of an *Isonychia* foreleg. Note two types of microtrichial arrangement, microtrichia (*mtr*) and hook-like microtrichia (*mtr h*). Scale = 1 μm . 2. Individual net meshes of several species of last instar hydropsychid larvae, all drawn to the same scale. The innermost mesh (*a*) is that of *Macronema zebrafatum*, and the outermost mesh (*f*) is that of *Arctopsyche irrorata*. Scale = ca 100 μm . 3. A section of the capture net of *Wormaldia* (SEM). The net is composed of double layers of rectangular mesh arranged diagonally. Scale = 2.4 μm . 4. A section of the catchnet of *Macronema zebrafatum* (SEM). Scale = ca 40 μm . 5. Head of *Culex*, ventral view; note mouthbrushes used in feeding (SEM). Scale = 350 μm . 6. Head of *Simulium*, ventral view, showing extended cephalic fans used for filter feeding (SEM). Scale = 400 μm .

higher than those of surface sediments inhabited by the nymphs (246). Nymphal burrowing and gill movements produce turbidity in the surrounding water (67) which possibly generate water currents that carry seston into the characteristic U-shaped burrow (Figure 7f) (245). Gill movements, at least in *Ephemera*, are remarkably rhythmic and establish symmetrical currents through the burrow along the body axis (52).

Polymitarcid nymphs construct burrows in a variety of substrates in lentic and lotic habitats. African *Povilla* and Neotropical *Asthenopus* are generally associated with submerged wood, although they may be found with other substrates (13, 32, 84, 85, 184). In fact, *Povilla* can cause serious damage to wooden boats and pilings below the waterline (32, 105). Using their large mandibular tusks, the nymphs construct U-shaped burrows which are lined with proteinaceous material apparently originating in the Malpighian tubules and secreted via the anus. The nymphs mold the material with their forelegs and mouthparts into a silk-like lining along the inner wall of the burrow (84, 85, 184). As in ephemerids, nymphs utilize their abdominal gills to pass water through their burrows where it is filtered through dense setae on the forelegs, mandibles, palps, and forehead (84, 85, 184). The filtering setae possess a double row of secondary hairs which, with spacing between hairs as small as 4–8 µm, interlock with those of adjacent setae (84, 85, 184). Both genera primarily filter feed on minute particles (84, 184); however, larger nymphs of *Povilla* have been observed leaving their burrows at night to feed on periphytic algae (162).

Another polymitarcid, *Tortopus*, also has well-developed mandibular tusks and first instars have a preference for burrowing in mud substrates (205). Later instars construct deep U-shaped burrows which honeycomb submerged clay banks of large rivers, such as the Savannah, where they comprise over 90% of the invertebrate biomass of clay substrate (189). Although details on feeding are lacking, it has been inferred that they are filter feeders based on their morphological similarity to *Povilla* and the scarcity of organic matter found in substrates occupied by the nymphs (189).

Trichoptera

Caddisflies are one of the most diverse insect orders in lotic waters and much of this diversity has been attributed to the many ways they use silk (122, 232). Most filter-feeding trichopterans belong to the Hydropsychoidea (232) and use silken nets as passive filters. There are significant differences in net structure within the Hydropsychoidea (Figures 2–4) which often coincide with differences in the anatomical structures used in feeding.

Philopotamid larvae construct elongate, sac-like nets (Figure 7a) which have the smallest mesh openings known for any trichopteran larvae [as

small as $0.4 \times 0.4 \mu\text{m}$ for *Wormaldia* (Figure 3) and $0.5 \times 5.5 \mu\text{m}$ for final instar *Dolophilodes* and some *Chimarra* (213)]. A philopotamid net may be composed of millions of individual meshes and each larva possesses the ability to secrete ca 70 silk strands simultaneously (213). Larval food, primarily fine detritus and diatoms (124, 194, 234), is swept from the net's surface with a flexible, brush-like labrum (232).

The African polycentropodid, *Protodipseudopsis* (70), and Nearctic *Phylocentropus* (217) construct branched tubes adapted to depositional areas of streams (Figure 7k). These genera are probably unique among filter-feeding trichopterans with regard to their depositional habitat and apparent ability to actively filter water (70). Their food consists primarily of fine detritus and some algae. Holarctic *Neureclipsis* feed primarily on small animals (194, 232) and erect large cornucopia-shaped nets (up to 20 cm in length) that are composed of irregular meshwork (Figure 7g) (16). European *Plectrocnemia* occur in regions of low current velocities ($<10 \text{ cm/sec}$) and construct large nets lacking organized meshes (55). The latter nets are apparently used more as snares for trapping benthic prey than as sieves for drifting organisms (88, 89).

Numerically, net-spinning hydropsychid caddisflies are a predominant group of lotic insects throughout the world and comprise ca 80% of all trichopterans in larger North American streams (172). The larvae occasionally clog water intakes of electrical generating plants (179, 206) and exuviae have clogged the filters of municipal water works (116). Most hydropsychid larvae construct fixed silken nets, perpendicular to the current, that are used to capture food (Figure 7b) (102, 181–183). *Macronema* larvae may construct rather complex structures (183, 215) (Figure 7h); in fact, they may be considered pioneer "physicists" having perfected the Pitot Tube long before Henri himself. The nets are spun in a figure-eight motion with smaller meshes near the substrate and larger meshes in distal areas (181, 182). Mesh sizes are determined by dimensions of larval mouth parts (102), and differences in capture net mesh size are associated with anatomical structures used in feeding, particularly in *Macronema* (183, 210).

There are large differences in mesh size among genera and species of hydropsychids (Figure 2) and an increase in net and mesh size with each successive larval instar (1, 102, 124, 216, 234). Studies have shown that there is a change in food type and an increase in mean foregut particle size with subsequent instars and mesh sizes (124, 210, 211, 244), although there is considerable overlap in particle sizes (216). Mesh sizes range from $>200,000 \mu\text{m}^2$ in the Arctopsychinae (1, 210, 212) to $<200 \mu\text{m}^2$ in *Macronema* (Figure 4) (183, 211, 215, 244). Mesh shapes of *Macronema* are elongate and more similar to the philopotamids than other hydropsychids. The elongate mesh has several advantages in that it allows for a reduction

in silk expenditure by the larva with fewer spinning movements required to construct a net that captures fine particles (212).

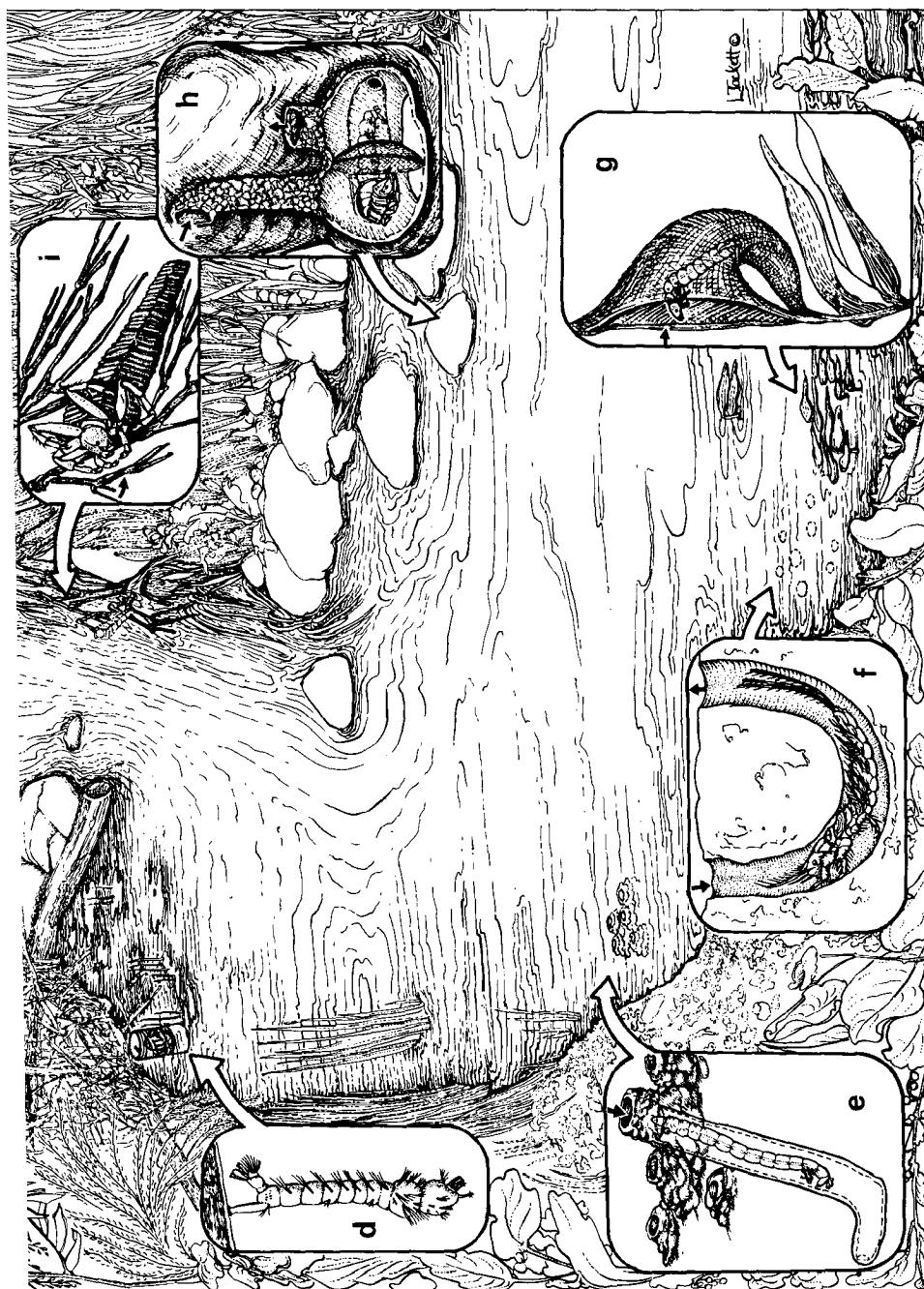
Hydropsychid larvae respond readily to changes in velocities (53, 55) and the proportion of larvae that spin nets decreases with reduction in current velocity or temperature (163, 164). Apparently, specialized head setae are current-sensing devices (102), and laboratory and field studies indicate that some species may have preferences for different current velocity ranges (15, 66, 102, 124, 188, 216) or microhabitats (124, 156, 188, 243). Studies have also shown that larger meshed catchnets are often associated with increased current velocities (1, 102, 124, 216). The general pattern suggests that increased filtration rates offset lower seston-capture efficiencies (larger meshes at faster flows); whereas smaller meshes, although more efficient at seston-capture, filter less water per time interval due to velocity-resistance limitations imposed by their small meshes.

Studies of larval hydropsychid feeding habits indicate they are primarily omnivores; however, late instars of Arctopsychinae and some other hydropsychids ingest significant amounts of animal food (10, 102, 107, 124, 134, 158, 170, 186, 216). *Macronema* larvae feed primarily on microseston (183, 211, 244).

Numerous changes occur in streams between headwaters and rivers (R. L. Vannote, unpublished manuscript; 37, 38), and hydropsychid species composition often shows sequential longitudinal changes (1, 5, 56, 74). Edington & Hildrew (56) were able to relate the longitudinal distribution of species to different temperature regimes for maximizing net growth efficiencies. However, feeding strategies may also be important (74, 233); Alstad (1) has shown that catchnet mesh dimensions of Utah hydropsychids are correlated with distribution along stream gradients.

Figure 7a-l Lotic habitat showing some representative filter-feeding insects. (a) Tube-like nets of philopotamid caddisfly larvae on the lower surface of a stone. (b) A hydropsychid caddisfly larva grazing on materials trapped on its capture net. (c) A larva and tube case of *Rheotanytarsus* (Chironomidae). Note the anterior arms which support the strands of the "catchnet." (d) A culicine mosquito larva in a discarded container. (e) A larva and J-shaped tube of *Chironomus*. This type of tube is associated with deposit-feeding midges, (see 130). (f) A nymph of *Hexagenia* (Ephemeridae) in its U-shaped burrow. (g) The caddisfly larva and cornucopia-shaped net of *Neureclipsis* (Polycentropodidae) (see 16). (h) The larva and filtering apparatus of *Macronema* (Hydropsychidae) consisting of a "Pitot tube" device which serves as a water intake opening (see 183, 215). (i) A *Brachycentrus* caddisfly larva in its filtering position with the legs arranged radially around the opening of the case. (j) Simuliid larvae in a filtering position with their cephalic fans extended while attached to trailing vegetation. (k) *Phylocentropus* (Polycentropodidae) caddisfly larva in its branched dwelling tube. These inhabit depositional areas and most of the structure is below the stream bed (see 70, 217). (l) An *Isonychia* (Siphlonuridae) mayfly nymph in filtering position with its setiferous forelegs extended into the current.





Notwithstanding the wealth of published information on hydropsychids, many aspects of their biology deserve additional attention. Larval catchnets in some streams may be covered with debris, but the extent to which this alters net porosity and filtration rates is unknown. Existing data on net mesh size vs current velocity suggest that large meshes exchange reduced seston-capture efficiencies for larger volumes of water filtered per unit of time. The latter may result in more selective feeding for higher quality food items (i.e. animal prey). Additionally, in colder climates many hydropsychids do not maintain nets in winter (121, 133, 186, 234) and little information is available on larval feeding modes and food demands during this period.

Two genera of brachycentrids, *Oligoplectrum* and *Brachycentrus* (152, 230), and several Asian limnocentropids (*Limnocentropus* spp.) (231) have specialized anatomical adaptations for filter feeding. Brachycentrids are the only Nearctic larvae belonging to the Limnephiloidea (tube-case makers) known to possess filter-feeding habits (232). Both genera differ from other brachycentrids by their elongated meso- and metathoracic legs and their dense combs of short, stout setae and spines along the ventral leg margins, which aid in filtering (69, 152, 230). While filtering, larvae attach the anterior end of the case to the substrate with silk, and face into the current with legs extended radially around the case opening (Figure 7*i*). The forelegs are used for sweeping food from the last two pairs of legs and forming a food bolus (152). Both *Brachycentrus* (134, 135) and *Oligoplectrum* (152, 232) have omnivorous feeding habits; however, carnivory is more prevalent in the final instars (134, 152). *Brachycentrus* feed by filtering and grazing (68), but it is assumed that filtering is the primary mode (69). A distinct diel periodicity associated with the filtering posture may coincide with maximum food drift (68). Although all instars assume similar postures when filtering, size differences among instars probably change filter porosity (69).

Diptera

SIMULIIDAE Black fly larvae are adapted for life in lotic waters by their size and streamlined shape, method and sites of attachment, and feeding behavior (96, 97). Over 150 years ago, Verdat (209) accurately described the basic structure and function of larval mouthparts, stating that "the organs (cephalic fans) are used by the larva as nets, a weight or a hand to catch the animalcules on which it feeds." He also correctly interpreted their feeding behavior as passive in nature. They feed by filtering water with specialized structures termed cephalic fans (Figure 6), normally relying on water flow to transport seston (21, 22, 64, 80, 204, 242). Material is removed from the closed fans by intermittent sweeping of the mandibles over the fans' surfaces (21, 35, 64, 108) and is then passed to the cibarium and into the foregut. Although filtering is usually the primary feeding mode, larvae

are also capable of scraping organic material from the substratum with their mandibular teeth (3, 18, 21, 108, 161, 166). Other comprehensive treatments have also added to the knowledge of cephalic fan structure, function, and evolution (64, 80, 166, 178, 236). Not all simuliids possess well-developed fans, and in some genera (e.g. *Gymnopais* and *Twinnia*) they are absent in most instars (21, 34, 49, 50, 236). These atypical larvae possess either reduced fans or modified labral and mandibular structures that serve as efficient raking or scraping organs (34, 35, 50).

Simuliids have a characteristic feeding position that allows them to minimize energy expenditure. They attach to the substrate with the posterior circlet of hooks and twist their bodies longitudinally, from 90–180°, so that the ventral surface of the head and fans face the current (Figure 7j) (21, 64, 192). Chance (22) has shown that they select areas of substratum where current flow is rapid and the boundary layer is thinnest. Thus, larvae avoid the potential problem of insufficient mixing of particulate material and ensure that their fans are exposed to water flow fast enough to provide an adequate food supply.

Simuliid larvae ingest, irrespective of quality, particles of food ranging in size from 0.091 μm (colloidal) to 350 μm , with the majority of studies reporting sizes <100 μm (3, 21, 65, 108, 139, 200, 235, 238, 239, 242). These foods include: bacteria (6, 65, 72), algae and diatoms (18, 19, 120), other insects (192), and detritus (3, 20, 120, 200). Larvae can be reared successfully on a suspension of bacteria alone (65), and may ingest algal filaments up to 1 mm or more in length (18). Some of the above studies suggest that different ranges of particle size exist for different species and instars; however, in most instances it appears that the range of particle sizes ingested reflects that of the seston at the time of sampling.

CULICIDAE, DIXIDAE, AND CHAOBORIDAE Mosquito larvae occur in a wide variety of habitats, including stream margins, brackish water, forest pools, tree and crab holes, plant axils, and even pit latrines (7, 62, 71, 202). Their mouth parts consist of well-developed mandibles and maxillae, a reduced labium, and a modified labrum with attached brushes (Figure 5). The labral brushes of culicid and dixid larvae are similar in structure, musculature, and function to the cephalic fans of simuliid larvae, and are possibly homologous (31, 236). The anatomy of larval culicid mouth parts was reviewed by Shalaby (193) and Pao & Knight (157), and Pucat (165) conducted a comprehensive study of functional mouth-part morphology.

Surtees' (202) classification of culicine larvae as filter feeders, browsers, or predators is probably the most widely accepted (165). A reduction in the length of the labral brushes, maxillary and mandibular setae, with an increase in the sclerotization, size, and serration of the mandibular teeth,

generally occurs in a progression from filter feeders to predators (83, 165, 202). Filter-feeding genera (e.g. *Anopheles*, some *Culex*, and *Mansonia*) produce currents with their labral brushes. This type of feeding has been termed “free” or “eddy” feeding (168). Anophelines and culicines tend to feed in different microhabitats, with anophelines feeding primarily in the surface film whereas culicines feed below the surface (83). Most filter feeders tend to feed immediately below the surface, maintaining contact at the air-water interface with their siphons (Figure 7d), whereas browsers (e.g. *Aedes*, *Culiseta*) are generally bottom feeders (202). Browsers abrade solid material to obtain particles that require further manipulation by the mouth parts before ingestion (165). Harbach (83), who has questioned the classification system of Surtees (202), instead uses four categories of nonpredatory feeding: plankton feeders, surface feeders, bottom feeders, and scavengers. The latter two categories include the “browsers” of Surtees’ classification, and Harbach suggests that bottom feeding may be a specialized type of filter feeding.

Most filter-feeding culicid larvae ingest particulate matter from colloidal to 50 μm in size (27, 43, 46, 90, 139, 165). Dadd (43) found that all instars of *Culex pipiens* optimally ingested particles with mean diameters between 0.5 and 2 μm . Merritt et al (139) showed a proportional increase in coarser material (2–50 μm) ingested by later instars of *Aedes triseriatus*, whereas early instars preferentially ingested smaller particles (<2 μm). Other studies have revealed particle size limits ingested by mosquito larvae (7, 27, 43, 165), and these limitations are related to particle shape and texture (41, 43).

Microorganisms and particulate organic detritus generally constitute a major part of larval culicid diets (2, 23, 27, 165). Several species can develop through all larval stages in sterile synthetic media with most of the essential nutrients in solution (113, 197). Nutritional requirements of mosquito larvae have been the subject of intensive investigations and are reviewed elsewhere (27, 45, 93).

Two related families of nematoceran Diptera, the Dixidae and Chaoboridae, are either filter feeders or have filter-feeding representatives. Dixid larvae are typically found in the meniscus zone around stones and organic substrates in lotic and lentic habitats. Most larvae assume an inverted “U” position while feeding on algae and detritus which they sieve from water with their mouth brushes (153, 185). In addition to relying on stream currents for food transport, dixid larvae can generate elliptical flows by rotating their labial brushes (153). Although first instars of all species are usually found in pool areas or sheltered locations, later instars of some groups move into faster flow areas and readily change locations during the day (153). Stream drift data suggest that a diel periodicity is associated with their activity (60).

Unique among chaoborid larvae, which are primarily predaceous, is the Australian genus *Australomochlonyx* which has mouth parts equipped with enlarged fans of long hairs used to strain small particles from surrounding water (31). The larvae possess a novel pair of structures called the oral bullae for transferring food from the mouthbrushes to the mouth (31).

CHIRONOMIDAE Chironomids may be the most diverse family of insects in their selection of habitats (150, 154), and from the standpoint of their numbers and productivity they compose an important part of the aquatic fauna. Larval food and feeding habits are varied (28, 145) and filter feeding is primarily known within the Chironominae. The ability to spin silk has great adaptive importance (114) and plays a major role in filter-feeding species. Berg (11) and Walshe (220) have described habits of certain filtering species in detail, and these generally involve the use of a silken tube, which houses the larva, with a conical catchnet spun across the lumen of the tube. The location of the catchnets and feeding behavior may vary among genera and species (11, 220). Many larvae are active filterers and create water currents through their burrows with rhythmic undulations of their bodies. Periodically, the larva devours its catchnet with adhering debris that has been swept into the burrow by the water currents. Defecation occurs after eating the old net and prior to spinning a new one (11, 220). The time interval required for spinning a food net, producing currents through it, and eating the net is about three to four minutes (11). Differences in food type and size may be important aspects of chironomid biology (130, 132); however, factors such as particle retention capabilities and ultrastructure of catchnets have not been investigated using modern techniques (e.g. SEM).

Chironomus plumosus, one of several chironomids inhabiting soft substrates in lotic and lentic habitats, constructs a U-shaped burrow and is typically regarded as a filter feeder (218). However, *C. plumosus* constructs two additional tube types, a blind J-shaped and an open-ended horizontal tube, which are associated with different habitats and population densities (Figure 7 e) (131). Furthermore, differences in tube shapes impose characteristic types of feeding, whereby the U-shaped tubes are more suited to suspension feeding and the horizontal and J-shaped tubes to deposit feeding. Since U- and J-tubes occur in the same microhabitat, this arrangement may avoid direct food competition by allowing individual species to alter their feeding mode (130).

Rheotanytarsus, a passive filter feeder, constructs small silt cases that are attached to the substratum in flowing waters (Figure 7c). Later instars add extended ribs or arms to the anterior end of the case. These arms support a sheet-like mass of "salivary secretion" (219). Periodically, the larva re-

moves and eats sections of this "mass," including adhering seston, before secreting a new one (190, 219). The size, shape, and number of arms of *Rheotanytarsus* tubes are quite variable but structural differences may relate to differences in microcurrents and food supply (190).

Physical factors such as currents and wind may be important factors in chironomid dispersal in lake sediments (47, 48), but larvae may also select particular habitats. For example, the preference of one species for a sheltered shore was attributed to the availability of microorganisms and minute particles (132). A second species in the same lake preferred a specific substrate particle size and the wave action of an exposed shore (129).

Most studies on chironomid ecology have concentrated on numerical abundance, species composition, or life histories (123), and many basic questions on coexistence mechanisms of species remain unanswered. The majority of chironomid species in a New Brunswick bog lake appeared to be ecologically isolated by habitat type, microdistribution, food resource, or other niche parameters (167). Earlier studies by Berg (11) and Walshe (220) have also suggested some habitat and microhabitat partitioning.

OTHER DIPTERA Certain brachyceran and cyclorrhaphan dipteran larvae have evolved filter-feeding mechanisms (51, 173–175). Some species within the Stratiomyidae, Syrphidae, and Calliphoridae possess a cibarial filter which concentrates food, particularly bacteria and small detrital particles (173–175). Pharyngeal ridges found in some cyclorrhaphous Diptera larvae also act as sieves which concentrate food while reducing the amount of liquid ingested (51). Other dipteran families may possess similar feeding mechanisms; however, little research has been conducted on their feeding habits.

FEEDING RATES, BIOENERGETICS, AND PRODUCTION

Few energy budgets are available for filter-feeding insects; however, there is considerable information on gut loading and passage time. Burrowing *Hexagenia* nymphs turn over digestive tract contents in ca 4.4 to 5.5 h (245), and this is affected by nymphal size and temperature, with maximum gut loading time at about 20°C (245). Gut retention times of *Hydropsyche* range between 1.54 and 2.63 h (127). Simuliid retention times range from 20 min to 2 h, with most values falling between 20 and 30 min (65, 109, 111, 127, 147, 240, 242). Feeding rates and gut retention times of simuliids are dependent on the following factors: species, larval age, filtering efficiency, water temperature and velocity, and seston quality, size, and con-

centration (22, 61, 109, 111, 147, 242). *Culex* gut retention times are proportional to the time spent filtering and are in the range of 20–40 min (42). However, nutritive particulates (e.g. dried yeast powder, *Chlorella*) are ingested faster and have shorter gut retention times than those lacking nutritive properties (e.g. silica gel, diatomaceous earth), and the rate of ingestion of the latter is greater in water containing soluble material such as yeast extract (41). These results indicate that ingestion can be externally influenced by chemical regulatory factors or phagostimulants which speed ingestion and accelerate growth by increasing the proportion of time spent filtering (41, 42, 44). The ultimate effect of autophagostimulation would be to accelerate the buildup of high population densities, which would counteract growth-retarding factors (99) produced by highly crowded larvae of some mosquito species (44).

Calculated assimilation efficiencies for filter feeders are few and include: 68% for *Hexagenia* (246); 49% for *Cheumatopsyche analis* (= *pettiti*), a hydropsychid feeding on diatoms (126); 1.8% for simuliids feeding on detritus (240) and ca 57.1% for those feeding on diatoms (127). Net growth efficiencies reported for filter feeders are as follows: 44.1% for *Isonychia* (203); 88% for *Hexagenia* (245); 69.6% for *Hydropsyche* feeding on algae (127); ca 52% for *Hydropsyche* and *Diplectrona* feeding on *Tubifex* and algae (56); ca 40% for simuliids feeding on detritus (240) and 49.5% for those feeding on diatoms (127). The above results are variable and reflect differences in food material and methods (direct and indirect) used to obtain values, as well as species differences at various temperature regimes. In addition, laboratory-derived assimilation efficiencies may be misleading when transposed to field situations since it is often assumed that filter feeders feed continuously, which is not always true as has been shown for some simuliid larvae (22, 143). To our knowledge, no detailed bioenergetic studies have been conducted on larval mosquitoes. This is rather surprising, considering that self-perpetuating colonies have been established for several species and that these medically important arthropods have probably received more research efforts than any other group of insects known to man. This area of filter-feeding biology deserves much more attention than it has received to date.

As noted by Waters (225), it is production, or elaboration of biomass that is important from the ecosystem standpoint since this biomass is available to higher trophic levels. Few production studies are available for filter-feeding insects, yet they suggest that filter feeders play a very significant role in the productivity of fresh waters. Nelson & Scott (149) measured the production of filter feeders (primarily hydropsychids, simuliids, *Rheotanytarsus*, and *Isonychia*) as 20.2 g ash-free dry wt/m²/yr on a rock-outcrop

community in the Oconee River, Georgia. Production of filter feeders surpassed that of all other combined animal feeding categories (149).

Annual production of the burrowing mayfly *Hexagenia* in midwestern reservoirs ranges between 0.447 and 2.407 g wet wt/m² (92, 94). Wood (237) has estimated that the decline in *Hexagenia* populations in Lake Erie due to man's activities has resulted in a loss of 70 million lbs (wet wt) of an important source of fish food. Furthermore, he suggested this loss was correlated with the concurrent loss of 15 million lbs of fish production (237). Conversely, in Lake Oneida, New York, only slight changes in growth rates of yellow perch occurred following *Hexagenia* extinction within the lake (25).

There are few production studies involving only hydropsychids. *Diplec-trona* annual production was ca 0.097 g dry wt/m² in a small Tennessee stream (40), and combined annual production of 6 net-spinning caddisfly species in a southern Appalachian stream was 1 g ash-free dry wt/m², with that of individual species ranging from 0.027 to 0.605 g (10). Production estimates of hydropsychids from enriched streams or large rivers are higher. Hopkins (91) found hydropsychid production approached 15 g dry wt/m²/yr in an enriched New Zealand stream. Annual production of net-spinning caddisflies on submerged woody substrates (snags) in the Satilla River, Georgia, ranges from 11 to 27 g dry wt/m² of snag surface area (208) and is higher for the same filter-feeding group in the Savannah River, Georgia and South Carolina (M. Cudney, personal communication).

Simuliid production estimates range from 0.044 g dry wt/m²/yr (241) to about 20 g dry wt/m² in one month (207) [Using Waters' (225) wet-dry wt conversion values]. Approximately 0.2 g dry wt/m²/yr were obtained for four simuliid species in a Pyrenean stream (151) and ca 5.9 g dry wt/m²/yr for two species in an English chalk stream (111). However, a number of simuliid species studied have multivoltine life cycles and actual production estimates may be higher, based on Benke's (9) modification which considers the cohort production interval (CPI). Using this latter procedure, annual simuliid production in the Satilla River, Georgia, is 13–43 g dry wt/m² of snag surface area (Benke, personal communication). There are many production estimates available for chironomids (e.g. 123, 225), but they are not included since precise feeding habits of many species are not known at this time.

Production, integrated with precise feeding habits and bioenergetic data, can yield a better understanding of the functional role of individual species in ecosystems (10); however, it is not always feasible to obtain all of the above parameters which would contribute to a much better understanding of the structure and function of aquatic communities.

MAJOR FACTORS AFFECTING ABUNDANCE AND SEASONAL CYCLES

Food

Studies suggest that filter-feeder abundance in lotic waters is strongly influenced by both quality and quantity of seston. High abundance of filter-feeding simuliids and hydropsychids in lake outlets and below impoundments, followed by a precipitous downstream decrease, may be associated with declining seston quality (20, 24, 107, 140, 156, 207, 242). Carlsson et al (20) and Wotton (242) attributed huge larval simuliid aggregations immediately below a Swedish lake outlet to minute particles of $<2\text{ }\mu\text{m}$ in size, produced on the lake bottom and presumably rich in microflora (171). Large particles, such as phytoplankton and coarse detritus did not seem to regulate black fly larval abundance (20). Progressive downstream decrease in hydropsychid populations in lake outflows have also been associated with declining phytoplankton (24, 156) and zooplankton (107). As a group, six species of net-spinning caddisflies in a southern Appalachian stream are net producers of detritus. They egest more detritus than they consume, filtering algae, animals, and detritus from the seston and egesting a lower quality detritus (including undigested algae and animal materials) as feces. These results suggest a system in which animal populations influence their own densities by affecting seston quality and quantity through their feeding activities. However, this is questionable in larger rivers where some filter-feeder populations are probably limited by substrate availability at suitable current velocities (66, 208).

Temperature

The fauna of most temperate zone waters are exposed to distinct seasonal changes in temperature regime. The magnitude of diel and seasonal temperature changes in lotic habitats is affected by the following: (a) latitude and altitude (96), (b) ground water influence (54, 96), (c) stream size (54, 96, 198, 203), and (d) forest cover (79).

Seasonal temperature cycles exert major influences on life cycles of many invertebrates, affecting both developmental rates and the number of annual generations. Sweeney (203) found *Isonychia bicolor* to be bivoltine, with a summer generation completing egg to adult development in ca three months and the overwintering generation requiring about nine months. Nymphs of the latter generation failed to grow at winter temperatures below 15°C (203). In temperate zones, hydropsychids may have either univoltine (59, 121, 187) or bivoltine life cycles (66, 121, 170, 208). Mackay (121) has shown that individual species of *Hydropsyche* may be bivoltine in the lower,

warmer reaches of a stream and univoltine in the colder headwaters. Three different annual life cycle patterns of a Japanese stenopsychid have been related to differences in accumulated degree days (77). *Stenopsyche* feeding rates are directly related to water temperature, and below 4°C larvae stop eating (77). The number of simuliid generations may also vary with longitudinal distribution within a river system and this is presumably temperature or food related (112). Hatching time and development rates of some black flies are also intimately related to accumulated temperature regimes (degree days) (144, 176).

Two European hydropsychid species, one adapted to "summer cool" and another to "summer warm" conditions, had lower net growth efficiencies when reared under temperature regimes other than those normally inhabited by them (56). This may be partially related to increased energy expenditure on the larval ventilatory respiration movements (164). Edington & Hildrew's (56) study may have far-ranging implications on the distribution of lotic insects; however, there is little comparable data for other filter-feeding species and localities. Sweeney (203) has shown development in *Isonychia* is positively correlated with increased diel temperature pulses. These latter observations may be very important for filter-feeding insects since energy flow through a number of species may conceivably increase and decrease at different times of the day and distribute their optima over a 24 hour period. The above results assume that food quality was not altered with temperature changes, and the possibility of diel fluctuations affecting the microbial flora associated with detritus was apparently not considered. Colbo & Porter (30) recently demonstrated that low food supply caused marked changes in development time, survival, terminal adult size, and fecundity in simuliids. However, the combined effects of temperature and food quality on filter-feeding insects have not been adequately assessed.

Temperature also influences the ultimate size of immature insects, as the overwintering generation of multivoltine species attains higher individual weights than those of the summer generation(s). This phenomenon is known from filter-feeding *Isonychia* (203), hydropsychids (M. Cudney, personal communication) and simuliids (112). Tropical *Povilla* are exposed to small annual temperature fluctuations and life cycles may be under lunar influence (32, 33). However, mature *Povilla adusta* from cooler Lake Victoria are larger than those from warmer Lake Barombi Mbo, and development rates are faster in the latter (33). Laboratory-reared mosquitoes display similar tendencies (81, 86). Thus, the phenomenon of larger terminal body size at cooler temperatures is not limited to lotic habitats of temperate zones. Other factors (e.g. substrate, current velocity, dissolved oxygen, etc.) may affect the abundance and distribution of filter-feeding insects and are reviewed by Hynes (96).

IMPORTANCE OF TEMPORAL DIVERSITY IN LIFE CYCLES

Temporal variability in life cycles may be very important at both the species and ecosystem levels. Different instars within species may consume different sizes or classes of foods and lessen intraspecific food demands during any one period. Likewise, interspecific variability may result in ecological segregation between species since food demands may be temporally separated (78, 155). Even within the simuliids, where any differences among instars with respect to either type or size of food particles are at best tenuous, studies report a seasonal succession of species (e.g. 20, 112, 140, 199). Many hydropsychids often have a range of larval instars present throughout much of the year (10, 59, 121, 208, 234), and evidence indicates that different hydropsychid instars and species may consume different types or sizes (124, 216) of foods. However, there may be considerable overlap in the range of particle sizes ingested (211, 216). Thus temporal variability, resulting in a broader range of seston utilization, should increase the processing efficiency of energy inputs within a given section of stream (216). Several studies have been concerned with seston utilization by individual species or species groups, yet there is little information on this subject for all filter feeders at a given locality throughout a year.

ROLE OF FILTER FEEDERS IN LOTIC WATERS

Leopold (115) addressed the question of dominant downhill motion of materials and attributed the continuity and stability of inland communities to the retardation and storage functions performed by living organisms. The unidirectional flow of lotic waters imposes special problems on retardation and storage of materials. The evolutionary diversity of filter feeders, whereby different species consume a wide range of sizes and types of materials, probably aids in this retardation and storage, and increases the efficiency of a given reach of stream in utilizing its organic inputs (216). These organisms are an integral component of aquatic ecosystems since they feed upon a very dilute food resource and convert previously dispersed, minute materials to larger animal biomass, i.e. their own bodies. Filter feeders also assist in the further processing of materials produced by the feeding activities of other functional groups, such as shredders (39, 195). The continual use and reuse of materials in downstream passage has been termed "spiraling" (227).

The efficiency of filter feeders in removing and processing seston appears to vary greatly among localities. Only a minute fraction of the organic matter entering a 1700 m section of the Fort River, Massachusetts, is

converted to CO₂ by *all* of the benthic insects (63). In contrast, simuliid larvae removed ca 60% of the cellular algae within a 0.4 km section of a California lake outlet stream (120). Theoretically, black flies may filter out all the particles in a 0.6 km section of an English chalk stream at high densities and low seston concentrations (111). Laboratory energetics data, combined with field data from Deep Creek, Idaho, indicate that hydropsychids and simuliids remove 1% of the seston flowing over them each day during the summer and suggest that complete removal of seston would occur in 9.21 km of stream (127). However, both studies (111, 127) assume declining seston concentrations, uniform densities of filter feeders, constant feeding rates, and no seston renewal—conditions which do not actually exist in stream environments. Nevertheless, these studies indicate that filter feeders possess the ability to collect significant quantities of seston.

PROBLEMS, PERSPECTIVES, AND GENERAL CONCLUSIONS

Impoundment of streams is a growing feature of our landscape. Ward & Short (224) have stated that “the number of streams regulated by dams is increasing more rapidly than our understanding of the ecological consequences.” The extent to which impoundments modify filter-feeder populations is beyond the scope of this review, although we have mentioned some of these effects on food. Baxter (8) has reviewed environmental effects of impoundments, but several important aspects deserve mention. Hypolimnia discharge can alter downstream temperature regimes to such an extent that some filter-feeding species are reduced or absent (75, 221, 224). The magnitude of changes varies with individual species since some species downstream of hypolimnia discharges are favored, presumably due to increased particulate matter (201). Other species are adversely affected, probably because of altered temperature regimes (201, 221, 223). Seasonal temperature trends downstream of deep release dams are usually “winter warm” and “summer cool” compared to those of surrounding unimpounded streams, but many other factors may also affect organisms (223).

Several studies suggest that surface discharges often result in increased filter-feeder populations below impoundments (196, 224). Surface discharges may positively influence downstream filter feeders by: (a) allowing limnetic plankton production to enter the discharge stream, (b) sustaining seston input and prevent scouring through regulated release, and (c) allowing thermal regimes that maintain synchrony of insect life cycles (196). However, massive seasonal flow alterations, common to many irrigation projects of the western US, can have devastating effects on the fauna (75, 76, 142, 222). Other physical (e.g. dissolved oxygen) and chemical parame-

ters also vary with the source of discharge. The possible interactions between the source and quantity of discharge, and temperature regimes are further confounded by seston quantity, quality, and size (196, 201, 224).

The construction of large dams and impoundments in Africa has led to an increase in breeding sites for certain pestiferous species of filter-feeding insects (e.g. mosquitoes, black flies) and the subsequent spread of infectious diseases, such as malaria and onchocerciasis (17, 87, 138). In addition, organic detritus settling to the bottom of impoundments has produced mass outbreaks of chironomid midges that cause severe annoyance and allergy problems (17, 180).

A better understanding of filter-feeding ecology, including the particle sizes ingested, has aided in the development of more selective particulate black fly larvicides (103, 104), and recent studies have discussed the effects of velocity and particle concentration on larvicide formulation and application (22, 109).

Rubenstein & Koehl (177) suggest that many biological filters can use methods other than sieving for particle capture. Thus, filter feeders need not be restricted to sieving and may use other capture methods, such as direct particle interception, electrostatic attraction, and deposition of particles—the latter being important only at low velocities (177). Materials accumulating on sieving devices increase the particle-capturing ability of the filter while simultaneously increasing the filter's resistance to flow. Thus, animals may alter the rate at which they clean off their filter and thereby change the filter porosity (177). A number of noninsect, invertebrate filter feeders are known to use mucus secretions to retain small particles (100, 110). Other than direct sieving, there is sparse information concerning any of the above mechanisms and how they possibly relate to particle retention by filter-feeding insects. Few studies have dealt with factors affecting filtering efficiency in insects. Kurtak's (109) study of black flies suggests that an individual larva has a seston-capture efficiency of less than 10% and this efficiency varies with species, particle size, concentration, and current velocity.

Selection by food quality appears to be important in some hydropsychids such as *Parapsyche* larvae, which may reject leaf fragments placed in their nets. Conversely, small insects are readily consumed under the same conditions (J. B. Wallace, personal observation). Simuliid larvae are also known to reject certain large particles (21). Most of our knowledge of food ingested is based on gut content analysis; however, methods are variable and Moore (146) has provided a critical review. Accurate measurement of gut contents can also be misleading because of differential assimilation efficiencies of various food types, and the paucity of bioenergetic studies involving filter-feeding insects confounds this problem.

In summary, there are many unanswered questions relating to modes of particle capture, seston-capture efficiencies as influenced by velocity and food concentration, selectivity of particles, and assimilation of various food types as influenced by food quality. These latter questions, when coupled with meager production data and problems relating to temporal abundance of species and instars, suggest that our comprehension of aquatic insect filter-feeding biology at present is very marginal.

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Literature Cited

1. Alstad, D. N. 1979. Comparative biology of the common Utah Hydropsychidae. *Am. Mid. Nat.* In press.
2. Ameen, M., Iversen, T. M. 1978. Food of *Aedes* larvae in a temporary forest pool. *Arch. Hydrobiol.* 83:552-64.
3. Anderson, J. R., Dicke, R. J. 1960. Ecology of the immature stages of some Wisconsin black flies. *Ann. Entomol. Soc. Am.* 53:386-404.
4. Anderson, N. H., Sedell, J. R. 1979. Detritus processing by macroinvertebrates in stream ecosystems. *Ann. Rev. Entomol.* 24:351-77.
5. Badcock, R. M. 1976. The distribution of Hydropsychidae in Great Britain. *Proc. Int. Symp. Trichop.* 1st, pp. 49-58.
6. Baker, J. H., Bradnam, L. A. 1976. The role of bacteria in the nutrition of aquatic detritivores. *Oecologia Berlin* 24:95-104.
7. Bates, M. 1949. *The Natural History of Mosquitoes*. New York: MacMillan. 379 pp.
8. Baxter, R. M. 1977. Environmental effects of dams and impoundments. *Ann. Rev. Ecol. Syst.* 8:255-83.
9. Benke, A. C. 1979. A modification of the Hynes method for estimating secondary production with particular significance for multivoltine populations. *Limnol. Oceanog.* 24:168-71.
10. Benke, A. C., Wallace, J. B. 1979. Trophic basis of production among net-spinning caddisflies in a southern Appalachian stream. *Ecology*. In press.
11. Berg, C. O. 1950. Biology of certain Chironomidae reared from *Potamogeton*. *Ecol. Monogr.* 20:83-101.
12. Berner, L. 1954. Phoretic association between a species of *Simulium* and a mayfly nymph, with a description of the nymph. *Ann. Mag. Nat. Hist. Ser. 12* 7:116-21.
13. Berner, L. 1978. The Status of *Asstenopus curtus* (Hagen). *Acta Amazonica* 8:103-5.
14. Berrie, A. D. 1976. Detritus, microorganisms and animals in fresh water. In *The Role of Terrestrial and Aquatic Organisms in Decomposition Processes*, ed. J. M. Anderson, A. Macfayden, pp. 323-38. Oxford: Blackwell.

15. Boon, P. J. 1978. The pre-impoundment distribution of certain Trichoptera larvae in the North Tyne river system (Northern England), with particular reference to current speed. *Hydrobiologia* 57:167-74.
16. Brickenstein, C. 1955. Über den Netzbau der Larve von *Neureclipsis bimaculata* L. *Abh. Bayer. Akad. Wiss. Math. Naturwiss. Kl., N. F. H.* 69:1-44.
17. Brown, A. W. A., Deom, J. O. 1973. Summary: Health aspects of man-made lakes. In *Man-made Lakes: Their Problems and Environmental Effects*, Geophys. Monogr. Ser. 17, ed. W. C. Ackermann, G. F. White, E. B. Worthington, pp. 755-68. Washington DC: Am. Geophys. Union.
18. Burton, G. J. 1973. Feeding of *Simulium hargreavesi* Gibbins larvae on *Oedogonium* algal filaments in Ghana. *J. Med. Entomol.* 10:101-6.
19. Carlsson, G. 1962. Studies on Scandinavian black flies. *Opusc. Entomol. Suppl.* 21:1-280.
20. Carlsson, M., Nilsson, L. M., Svensson, Bj., Ulfstrand, S., Wotton, R. S. 1977. Lacustrine seston and other factors influencing the blackflies inhabiting lake outlets in Swedish Lapland. *Oikos* 29:229-38.
21. Chance, M. M. 1970. The functional morphology of the mouthparts of black fly larvae. *Quaest. Entomol.* 6:245-84.
22. Chance, M. M. 1977. *Feeding biology of black fly larvae*. PhD thesis. Univ. Alberta, Edmonton. 236 pp.
23. Christophers, S. R. 1960. *Aedes aegypti* (L.). *The Yellow Fever Mosquito. Its Life History, Bionomics and Structure*. Cambridge: Univ. Press. 739 pp.
24. Chutter, F. M. 1963. Hydrobiological studies on the Vaal River in the Vereeniging area. Part I. Introduction, water chemistry and biological studies of the fauna of habitats other than muddy bottom sediments. *Hydrobiologia* 21:1-65.
25. Clady, M., Hutchinson, B. 1976. Food of the yellow perch *Perca flavescens* following a decline of the burrowing mayfly, *Hexagenia limbata*. *Ohio J. Sci.* 76:133-38.
26. Clemens, W. A. 1917. An ecological study of the mayfly *Chironetes*. *Univ. Toronto Biol. Ser.* 17:1-43.
27. Clements, A. N. 1963. *The Physiology of Mosquitoes*. Oxford: Pergamon. 393 pp.
28. Coffman, W. P. 1978. Chironomidae. See Ref 136, pp. 345-76.
29. Coffman, W. P., Cummins, K. W., Wuycheck, J. C. 1971. Energy flow in a woodland stream ecosystem: I. Tissue support trophic structure of the autumnal community. *Arch. Hydrobiol.* 63: 232-76.
30. Colbo, M. H., Porter, G. N. 1979. Effects of the food supply on the life history of Simuliidae. *Can. J. Zool.* 57:301-6.
31. Colless, D. H. 1977. A possibly unique feeding mechanism in a dipterous larva. *J. Aust. Entomol. Soc.* 16:335-39.
32. Corbet, P. S. 1957. Duration of the aquatic stages of *Povilla adusta* Navas. *Bull. Entomol. Res.* 48:243-50.
33. Corbet, S. A., Sellick, R. D., Wiloughby, N. E. 1974. Notes on the biology of the mayfly *Povilla adusta* in West Africa. *J. Zool. London* 172:491-502.
34. Craig, D. A. 1974. The labrum and cephalic fans of larval Simuliidae. *Can. J. Zool.* 52:133-59.
35. Craig, D. A. 1977. Mouthparts and feeding behavior of Tahitian larval Simuliidae. *Quaest. Entomol.* 13:195-281.
36. Cummins, K. W. 1974. Structure and function of stream ecosystems. *Bio-Science* 24:631-41.
37. Cummins, K. W. 1975. The ecology of running waters; theory and practice. *Proc. Sandusky River Basin Symp., Tiffin, Ohio*, pp. 277-93.
38. Cummins, K. W. 1977. From headwater streams to rivers. *Am. Biol. Teacher* 39:305-12.
39. Cummins, K. W., Klug, M. J. 1979. Feeding ecology of stream invertebrates. *Ann. Rev. Ecol. Syst.* 10. In press.
40. Cushman, R. M., Elwood, J. W., Hildebrand, S. G. 1977. Life history and production dynamics of *Alloperla mediana* and *Diplectrona modesta* in Walker Branch Tennessee. *Am. Midl. Nat.* 98:354-64.
41. Dadd, R. H. 1970. Comparison of rates of ingestion of particulate solids by *Culex pipiens* larvae: Phagostimulant effect of water-soluble yeast extract. *Entomol. Exp. Appl.* 13:407-19.
42. Dadd, R. H. 1970. Relationship between filtering activity and ingestion of solids by larvae of the mosquito *Culex pipiens*: A method for assessing phagostimulant factors. *J. Med. Entomol.* 7:708-12.
43. Dadd, R. H. 1971. Effects of size and concentration of particles on rates of ingestion of latex particulates by mosquito larvae. *Ann. Entomol. Soc. Am.* 64:687-92.
44. Dadd, R. H. 1973. Autophagostimula-

- tion by mosquito larvae. *Entomol. Exp. Appl.* 16:295-300
45. Dadd, R. H. 1973. Insect nutrition: Current developments and metabolic implications. *Ann. Rev. Entomol.* 18: 381-420
46. Dadd, R. H. 1975. Ingestion of colloid solutions by filter-feeding mosquito larvae: Relationship to viscosity. *J. Exp. Zool.* 191:395-406
47. Davies, B. R. 1976. Wind distribution of the egg masses of *Chironomus anthracinus* (Zetterstedt) in a shallow, wind-exposed lake (Loch Leven, Kinross). *Freshwater Biol.* 6:421-24
48. Davies, B. R. 1976. The dispersal of Chironomidae larvae: A review. *J. Entomol. Soc. South Afr.* 39:39-62
49. Davies, L. 1960. The first instar larva of a species of *Prosimulium*. *Can. Entomol.* 92:81-84
50. Davies, L. 1974. Evolution of larval head-fans in Simuliidae as inferred from the structure and biology of *Crozetia crozettensis* (Womersley) compared with other genera. *Zool. J. Linn. Soc.* 55: 193-224
51. Dowding, V. M. 1967. The function and ecological significance of the pharyngeal ridges occurring in the larvae of some cyclorrhaphous Diptera. *Parasitology* 57:371-88
52. Eastham, L. E. S. 1939. Gill movements of nymphal *Ephemera danica* and the water currents caused by them. *J. Exp. Biol.* 16:18-33
53. Edington, J. M. 1965. The effect of water flow on populations of net-spinning Trichoptera. *Mitt. Int. Ver. Theor. An-gew. Limnol.* 13:40-48
54. Edington, J. M. 1966. Some observations on stream temperature. *Oikos* 15:265-73
55. Edington, J. M. 1968. Habitat preferences in net-spinning caddis larvae with special reference to the influence of water velocity. *J. Anim. Ecol.* 37:675-92
56. Edington, J. M., Hildrew, A. G. 1973. Experimental observations relating to the distribution of net-spinning Trichoptera in streams. *Verh. Int. Ver. Limnol.* 18:1549-58
57. Edmunds, G. F. 1975. Phylogenetic biogeography of mayflies. *Ann. Mo. Bot. Gard.* 62:251-63
58. Edmunds, G. F., Jensen, S. L., Berner, L. 1976. *The Mayflies of North and Central America*. Minneapolis: Univ. Minn. Press. 330 pp.
59. Elliott, J. M. 1968. The life histories and drifting of Trichoptera in a Dartmoor stream. *J. Anim. Ecol.* 37:615-25
60. Elliott, J. M., Tullett, P. A. 1977. The downstream drifting of larvae of *Dixa* in two stoney streams. *Freshwater Biol.* 7:403-7
61. Elouard, J. M., Elsen, P. 1977. Variations de l'absorption des particules alimentaires et de la vitesse du transit digestif au cours d'un nycthémère chez les larves de *Simulium damnosum* Theobald, 1903. *Cah. ORSTOM Ser. Entomol. Med. Parasitol.* 15:29-39
62. Fish, D., Hall, D. W. 1978. Succession and stratification of aquatic insects inhabiting the leaves of the insectivorous pitcher plant, *Sarracenia purpurea*. *Am. Midl. Nat.* 99:172-83
63. Fisher, S. G. 1977. Organic matter processing by a stream-segment ecosystem: Fort River, Massachusetts, USA. *Int. Rev. Gesamten Hydrobiol.* 62:701-27
64. Fortner, G. 1937. Zur Ernährungsfrage der *Simulium* Larve. *Z. Morphol. Okol. Tiere* 32:360-83
65. Fredeen, F. J. H. 1964. Bacteria as a source of food for black-fly larvae in laboratory cultures and in natural streams. *Can. J. Zool.* 42:527-48
66. Fremling, C. R. 1960. Biology and possible control of nuisance caddisflies of the upper Mississippi River. *Agric. Home Econ. Exp. Sta., Iowa State Univ. Res. Bull.* 483:856-79
67. Fremling, C. R. 1967. Methods for mass rearing *Hexagenia* mayflies. *Trans. Am. Fish. Soc.* 96:407-10
68. Gallopp, G. W. 1974. Diel periodicity in the behavior of the caddisfly, *Brachycentrus americanus* (Banks). *Freshwater Biol.* 4:193-204
69. Gallopp, G. W. 1977. Responses of caddisfly larvae (*Brachycentrus* spp.) to temperature, food availability and current velocity. *Am. Midl. Nat.* 98:59-84
70. Gibbs, D. G. 1968. The larva, dwelling-tube and feeding of a species of *Protodipseudopsis*. *Proc. R. Entomol. Soc. London A* 43:73-79
71. Gillett, J. D. 1972. *The Mosquito: Its Life, Activities, and Impact on Human Affairs*. New York: Doubleday. 358 pp.
72. Glötzel, V. R. 1973. Populationsdynamik und Ernährungsbiologie von Simuliidenlarven in einem mit organischen Abwässern verunreinigten Gebirgsbach. *Arch. Hydrobiol. Suppl.* 42: 406-51
73. Goldman, C. R., Kimmel, B. L. 1978. Biological processes associated with suspended sediment and detritus in lakes and reservoirs. In *Current Perspectives on River-Reservoir Ecosystems*. *Proc. N. Am. Benthol. Soc. Symp.*, ed. J.

- Cairns, E. F., Benfield, J. R., Webster, pp. 19–44. Blacksburg, Va.
74. Gordon, A. E., Wallace, J. B. 1975. Distribution of the Family Hydropsychidae in the Savannah River Basin of North Carolina, South Carolina and Georgia. *Hydrobiologia* 46:405–23
75. Gore, J. A. 1977. Reservoir manipulations and benthic macroinvertebrates in a prairie river. *Hydrobiologia* 55:113–23
76. Gore, J. A. 1978. A technique for predicting instream flow requirements of benthic invertebrates. *Freshwater Biol.* 8:141–52
77. Gose, K. 1970. Life history and instar analysis of *Stenopsyche griseipennis*. *Jpn. J. Limnol.* 31:96–106
78. Grant, P. R., Mackay, R. J. 1969. Ecological segregation of systematically related stream insects. *Can. J. Zool.* 47:691–94
79. Gray, J. R. A., Edington, J. M. 1969. Effect of woodland clearance on stream temperature. *J. Fish. Res. Board. Can.* 26:399–403
80. Grenier, P. 1949. Contribution à l'étude biologique des simuliides de France. *Physiol. Comp. Oecol.* 1:165–330
81. Hagstrum, D. W., Workman, E. B. 1971. Interaction of temperature and feeding rate in determining the rate of development of larval *Culex tarsalis*. *Ann. Entomol. Soc. Am.* 64:668–71
82. Hall, D. J., Threlkeld, S. T., Burns, C. W., Crowley, P. H. 1976. The size-efficiency hypothesis and the size structure of zooplankton communities. *Ann. Rev. Ecol. Syst.* 7:177–208
83. Harbach, R. E. 1977. Comparative and functional morphology of the mandibles of some fourth stage mosquito larvae. *Zoomorphologie* 87:217–36
84. Hartland-Rowe, R. 1953. Feeding mechanism of an ephemeropteran nymph. *Nature* 172:1109–10
85. Hartland-Rowe, R. 1958. The biology of a tropical mayfly *Povilla adusta* Navas with special reference to the Julian rhythm of emergence. *Rev. Zool. Bot. Afr.* 58:185–202
86. Heuvel, M. J. van den. 1963. The effect of rearing temperature on the wing length, thorax length, leg length and ovariole number of the adult mosquito, *Aedes aegypti* (L.). *Trans. R. Entomol. Soc. London* 115:197–216
87. Heyneman, D. 1971. Mis-aid to the third world: Disease repercussions caused by ecological ignorance. *Can. J. Public Health* 62:303–13
88. Hildrew, A. G., Townsend, C. R. 1976. The distribution of two predators and their prey in an iron-rich stream. *J. Anim. Ecol.* 45:41–57
89. Hildrew, A. G., Townsend, C. R. 1977. The influence of substrate on the functional response of *Plectrocnemia conspersa* (Curtis) larvae. *Oecologia Berlin* 31:21–26
90. Hinman, E. H. 1932. The role of solutes and colloids in the nutrition of anopheline larvae. *Am. J. Trop. Med.* 12:263–71
91. Hopkins, C. L. 1976. Estimate of biological production in some stream invertebrates. *N. Z. J. Mar. Freshwater Res.* 10:629–40
92. Horst, T. J., Marzolf, G. R. 1975. Production ecology of burrowing mayflies in a Kansas reservoir. *Verh. Int. Ver. Limnol.* 19:3029–38
93. House, H. L. 1974. Nutrition. In *The Physiology of Insecta*, ed. M. Rockstein, 5:1–62. New York: Academic
94. Hudson, P. L., Swanson, G. A. 1972. Production and standing crop of *Hexagenia* in a large reservoir. *Stud. Natl. Sci., Eastern N. M. Univ.* 1(4):1–42
95. Hunt, B. P. 1953. The life history and economic importance of a burrowing mayfly, *Hexagenia limbata*, in Southern Michigan lakes. *Bull. Inst. Fish. Res.* vol. 4. 151 pp.
96. Hynes, H. B. N. 1970. *The Ecology of Running Waters*. Toronto: Univ. Toronto Press. 555 pp.
97. Hynes, H. B. N. 1970. The ecology of stream insects. *Ann. Rev. Entomol.* 15:25–42
98. Hynes, H. B. N. 1975. The stream and its valley. *Verh. Int. Ver. Limnol.* 19:1–15
99. Ikeshoji, T., Mulla, M. S. 1970. Overcrowding factors of mosquito larvae. *J. Econ. Entomol.* 63:90–96
100. Jørgensen, C. B. 1966. *Biology of Suspension Feeding*. Oxford: Pergamon. 357 pp.
101. Jørgensen, C. B. 1975. Comparative physiology of suspension feeding. *Ann. Rev. Physiol.* 37:57–79
102. Kaiser, P. 1965. Über Netzbau und Strömungssinn bei den Larven der Gattung *Hydropsyche* Pict. *Int. Revue Gesamten Hydrobiol.* 50:169–224
103. Kershaw, W. E., Williams, T. R., Frost, S., Hynes, H. B. N. 1965. Selective effect of particulate insecticides on *Simulium* among stream fauna. *Nature* 208:199
104. Kershaw, W. E., Williams, T. R., Frost, S., Matchett, R. E., Mills, M. L., Johnson, R. D. 1968. The selective control of *Simulium* larvae by particulate insecti-

- cides and its significance in river management. *Trans. R. Soc. Trop. Med. Hyg.* 62:35-40
105. Kimmins, D. E. 1948. Ephemeroptera from Nyasaland with descriptions of new species. *Ann. Mag. Nat. Hist. Ser. 12* 1:825-36
106. Kimmins, D. E. 1955. Ephemeroptera from Nyasaland, with descriptions of three new species and some interesting nymphal forms. *Ann. Mag. Nat. Hist. Ser. 12* 8:859-80
107. Kubíček, F. 1970. On the drift of a brook running through a pond. *Vestn. Česk. Spol. Zool.* 34:219-26
108. Kurtak, D. C. 1973. *Observations on filter feeding by the larvae of black flies*. PhD thesis. Cornell Univ., Ithaca. 157 pp.
109. Kurtak, D. C. 1978. Efficiency of filter feeding of black fly larvae. *Can. J. Zool.* 56:1608-23
110. LaBarbera, M. 1978. Particle capture by a Pacific brittle star: Experimental test of the aerosol suspension feeding model. *Science* 201:1147-49
111. Ladle, M., Bass, J. A. B., Jenkins, W. R. 1972. Studies on production and food consumption by the larval Simuliidae of a chalk stream. *Hydrobiologia* 39: 429-48
112. Ladle, M., Bass, J. A. B., Philpott, F. R., Jeffery, A. 1977. Observations on the ecology of Simuliidae from the River Frome, Dorset. *Ecol. Entomol.* 2:197-204
113. Lea, A. O., Dimond, J. B., Delong, D. M. 1956. A chemically defined medium for rearing *Aedes aegypti* larvae. *J. Econ. Entomol.* 49:313-15
114. Leathers, A. L. 1922. Ecological study of aquatic midges and some related insects with special reference to feeding habits. *Bull. US Bur. Fish.* 38:1-61
115. Leopold, A. 1941. Lakes in relation to terrestrial life patterns. In *A Symposium on Hydrobiology* pp. 17-22. Madison: Univ. Wis. Press
116. Lepneva, S. G. 1964. *Larvae and pupae of Annulipalpia, Trichoptera. Fauna of the USSR. Vol. 2, No. 1. Engl. Transl.* Israel: Israel Program for Sci. Transl., 1970
117. Lock, M. A., Hynes, H. B. N. 1975. The disappearance of four leaf leachates in a hard and soft water stream in south western Ontario, Canada. *Int. Revue Gesamten Hydrobiol.* 60:847-55
118. Lush, D. L., Hynes, H. B. N. 1973. The formation of particles in freshwater leachates of dead leaves. *Limnol. Oceanogr.* 18:968-77
119. Lush, D. L., Hynes, H. B. N. 1978. Particulate and dissolved organic matter in a small partly forested Ontario stream. *Hydrobiologia* 60:177-85
120. Maciolek, J. A., Tunzi, M. G. 1968. Microeston dynamics in a simple Sierra Nevada lake-stream system. *Ecology* 49:60-75
121. Mackay, R. J. 1979. Life history patterns of some species of *Hydropsyche* in southern Ontario. *Can. J. Zool.* In press
122. Mackay, R. J., Wiggins, G. B. 1979. Ecological diversity in Trichoptera. *Ann. Rev. Entomol.* 24:185-208
123. Mackey, A. P. 1977. Quantitative studies on the Chironomidae of the River Thames and Kennet, Part 4, Production. *Arch. Hydrobiol.* 80:327-48
124. Malas, D., Wallace, J. B. 1977. Strategies for coexistence in three species of net-spinning caddisflies in second-order southern Appalachian streams. *Can. J. Zool.* 55:1829-40
125. McCafferty, W. P. 1975. The burrowing mayflies of the United States. *Trans. Am. Entomol. Soc. Philadelphia* 101: 447-504
126. McCullough, D. A. 1975. The bioenergetics of three aquatic insects determined by radioisotopic analyses. *BNWL (Batelle Pac. Northwest Lab., Richland, Wash.)* 1928: 219 pp.
127. McCullough, D. A., Minshall, G. W., Cushing, C. E. 1979. Bioenergetics of lotic filter-feeding insects *Simulium* spp. and *Hydropsyche occidentalis* and their function in controlling organic transport in streams. *Ecology*. In press
128. McDowell, W. H., Fisher, S. G. 1976. Autumnal processing of dissolved organic matter in a small woodland stream ecosystem. *Ecology* 57:561-69
129. McLachlan, A. J. 1976. Factors restricting the range of *Glyptotendipes paripes* Edwards in a bog lake. *J. Anim. Ecol.* 45:105-13
130. McLachlan, A. J. 1977. Some effects of tube shape on the feeding of *Chironomus plumosus* L. *J. Anim. Ecol.* 46:139-46
131. McLachlan, A. J., Cantrell, M. A. 1976. Sediment development and its influence on the distribution and tube structure of *Chironomus plumosus* L. in a new impoundment. *Freshwater Biol.* 6:437-43
132. McLachlan, A. J., Dickinson, C. H. 1977. Micro-organisms as a factor in the distribution of *Chironomus lugubris* Zetterstedt in a bog lake. *Arch. Hydrobiol.* 80:133-46
133. Mecom, J. O. 1970. Unusual case build-

- ing behavior of *Hydropsyche occidentalis* larvae. *Entomol. News* 81:33–35
134. Mecom, J. O. 1972. Feeding habits of Trichoptera in a mountain stream. *Oikos* 23:401–7
135. Mecom, J. O., Cummins, K. W. 1964. A preliminary study of the trophic relationships of the larvae of *Brachycentrus americanus* (Banks). *Trans. Am. Microsc. Soc.* 83:233–43
136. Merritt, R. W., Cummins, K. W., eds. 1978. *An Introduction to the Aquatic Insects of North America*. Dubuque, Iowa: Kendall-Hunt. 441 pp.
137. Merritt, R. W., Lawson, D. L. 1979. Leaf litter processing in floodplain and stream communities. In *Strategies for Protection and Management of Floodplain Wetlands and Other Riparian Ecosystems. Proc. Symp. Dec. 1–13, 1978, Callaway Gardens, Ga. Gen. Tech. Rep. WO-12. For Serv. USDA*, ed. R. R. Johnson, J. F. McCormick, pp. 93–105. Washington DC. 410 pp.
138. Merritt, R. W., Newson, H. D. 1978. Ecology and management of arthropod populations in recreational lands. In *Perspectives in Urban Entomology*, ed. G. W. Frankie, C. S. Koehler, pp. 125–62. New York: Academic.
139. Merritt, R. W., Mortland, M. M., Gersabeck, E. R., Ross, D. H. 1978. X-ray diffraction analysis of particles ingested by filter-feeding animals. *Entomol. Exp. Appl.* 24:27–34
140. Merritt, R. W., Ross, D. H., Peterson, B. V. 1978. Larval ecology of some lower Michigan black flies with keys to the immature stages. *Great Lakes Entomol.* 11:177–208
141. Minshall, G. W. 1978. Autotrophy in stream ecosystems. *BioScience* 28: 767–71
142. Minshall, G. W., Andrews, D. A. 1973. An ecological investigation of the Portneuf River, Idaho: a semiarid-land stream subjected to pollution. *Freshwater Biol.* 3:1–30
143. Mokry, J. E. 1975. Studies on the ecology and biology of black fly larvae utilizing an in situ benthosurvey. *Verh. Int. Ver. Limnol.* 19:1546–49
144. Mokry, J. E. 1976. Laboratory studies on the larval biology of *Simulium venustum*. *Can. J. Zool.* 54:1657–63
145. Monakov, A. V. 1972. Review of studies on feeding of aquatic invertebrates conducted at the Institute of Biology of Inland Waters, Academy of Science, USSR. *J. Fish. Res. Board. Can.* 29:363–83
146. Moore, J. W. 1977. Some aspects of the feeding biology of benthic herbivores. *Hydrobiologia* 53:139–46
147. Mulla, M. S., Lacey, L. A. 1976. Feeding rates of *Simulium* larvae on particulates in natural streams. *Environ. Entomol.* 5:283–87
148. Naiman, R. J., Sedell, J. R. 1979. Characterization of particulate organic matter transported by some Cascade Mountain streams. *J. Fish. Res. Board. Can.* 36:17–31
149. Nelson, D. J., Scott, D. C. 1962. Role of detritus in the productivity of a rock-outcrop community in a Piedmont stream. *Limnol. Oceanogr.* 7:396–413
150. Neumann, D. 1976. Adaptations of chironomids to intertidal environments. *Ann. Rev. Entomol.* 21:387–414
151. Neveu, A. 1973. Estimation de la production de populations larvaires du genre *Simulium*. *Ann. Hydrobiol.* 4: 183–99
152. Nielsen, A. 1943. Postembryonale Entwicklung und Biologie der rheophilien Köcherfliege *Oligoplectrum maculatum* Fourcroy. *K. Dan. Vidensk. Selsk. Biol. Skr.* 19:1–87
153. Nowell, W. R. 1951. The dipterous family Dixidae in western North America. *Microentomology* 16:187–270
154. Oliver, D. R. 1971. Life history of the Chironomidae. *Ann. Rev. Entomol.* 16:211–30
155. Oswood, M. W. 1976. Comparative life histories of the Hydropsychidae in a Montana lake outlet. *Am. Midl. Nat.* 96:493–97
156. Oswood, M. W. 1979. Abundance patterns of filter-feeding caddisflies and sisson in a Montana (USA) lake outlet. *Hydrobiologia*. In press
157. Pao, B., Knight, K. L. 1970. Morphology of the fourth stage larval mouthparts of *Aedes* (*Aedimorphus*) *vexans*. *J. Ga. Entomol. Soc.* 5:115–37
158. Pavlichenko, V. I. 1977. Role of larvae of *Hydropsyche angustipennis* in the destruction of blackflies in flowing reservoirs of the Zaporozhye Oblast USSR. *Sov. J. Ecol.* 8:84–85
159. Peters, W. L. 1971. A revision of the Leptophlebiidae of the West Indies. *Smithson. Contrib. Zool.* 62:1–48
160. Peters, W. L., Edmunds, G. F. Jr. 1970. Revision of the generic classification of the eastern hemisphere Leptophlebiidae. *Pac. Insects* 12:157–240
161. Peterson, B. V. 1956. Observations on the biology of Utah blackflies. *Can. Entomol.* 88:496–507

162. Petr, T. 1973. Some factors limiting the distribution of *Povilla adusta* Navas in African lakes. *Proc. Int. Conf. Ephemeroptera, Ist.* 1970:223-30
163. Philipson, G. N. 1969. Some factors affecting the net-spinning of the caddisfly *Hydropsyche instabilis* Curtis. *Hydrobiologia* 34:369-77
164. Philipson, G. N., Moorhouse, B. H. S. 1974. Observations on ventilatory and net-spinning activities of larvae of the genus *Hydropsyche* Pictet under experimental conditions. *Freshwater Biol.* 4:525-33
165. Pucat, A. M. 1965. The functional morphology of the mouthparts of some mosquito larvae. *Quaest. Entomol.* 1:41-86
166. Puri, I. M. 1925. On the life history and structure of the early stages of Simuliidae. *Parasitology* 17:295-334
167. Ramcharan, V., Patterson, C. G. 1978. A partial analysis of ecological segregation in the chironomid community of a bog lake. *Hydrobiologia* 58:129-35
168. Renn, C. E. 1941. The food economy of *Anopheles quadrimaculatus* and *A. crucians* larvae. See Ref. 115, pp. 329-42
169. Resh, V. H., Solem, J. O. 1978. Phylogenetic relationships and evolutionary adaptations of aquatic insects. See Ref. 136, pp. 33-42
170. Rhame, R. E., Stewart, K. W. 1976. Life cycles and food habits of three Hydropsychidae species in the Brazos River, Texas. *Trans. Am. Entomol. Soc. Philadelphia* 102:65-99
171. Rich, P. H., Wetzel, R. G. 1978. Detritus in the lake ecosystem. *Am. Nat.* 112:57-71
172. Roback, S. S. 1962. Environmental requirements of Trichoptera. In *Seminar in Biological Problems in Water Pollution*, 3rd. USPHS Pub. No. 990-WP-25, ed C. M. Tarzwell, pp. 118-26
173. Roberts, M. J. 1969. Structure of the mouthparts of the larvae of the flies *Rhagio* and *Sargus* in relation to feeding habits. *J. Zool. London* 159:381-98
174. Roberts, M. J. 1970. The structure of the mouthparts of syrphid larvae (Diptera) in relation to feeding habits. *Acta Zool. Stockholm* 51:43-65
175. Roberts, M. J. 1971. The structure of the mouthparts of some calypterate dipteran larvae in relation to their feeding habits. *Acta Zool. Stockholm* 52:171-88
176. Ross, D. H., Merritt, R. W. 1978. The larval instars and population dynamics of five species of black flies and their responses to selected environmental factors. *Can. J. Zool.* 56:1633-42
177. Rubenstein, D. I., Koehl, M. A. 1977. The mechanisms of filter-feeding: some theoretical considerations. *Am. Nat.* 111:981-94
178. Rubtsov, I. A. 1964. Simuliidae. Part 14. In *Die Fliegen der Palaearktischen Region*, ed. E. Lindner, pp. 1-48. Stuttgart: Schweizerbart
179. Ruff, J. W. 1961. Caddis flies, fish and power plant condensers. *Public Works* March 1961:115-16
180. Rzoska, J. 1964. Mass outbreaks of insects in the Sudanese Nile basin. *Verh. Int. Ver. Limnol.* 15:194-200
181. Sattler, W. 1955. Über den Netzbau der Larve von *Hydropsyche angustipennis* Curt. *Naturwissenschaften* 42:186-87
182. Sattler, W. 1958. Beiträge zur Kenntnis von Lebensweise und Körperbau der Larve und Puppe von *Hydropsyche* Pict. mit besonderer Berücksichtigung des Netzbaues. *Z. Morphol. Ökol. Tiere* 47:115-92
183. Sattler, W. 1963. Über den Körperbau, die Ökologie und Ethologie der Larve und Puppe von *Macronema* Pict., ein als Larve sich von "Mikro-Drift" ernährendes Trichoptera aus dem Amazonasgebiet. *Arch. Hydrobiol.* 59: 26-60
184. Sattler, W. 1967. Über die Lebensweise, insbesondere das Bauverhalten, neotropischer Eintagsfliegen-Larven. *Beitr. Neotrop. Fauna* 5:89-110
185. Schremmer, F. 1950. Bau und Funktion der Larvenmundteile der Dipterengattung *Dixa* Meigen. *Oesterr. Zool. Z.* 2:379-413
186. Schröder, P. 1976. Zur Nahrung der Larvenstadien der Köcherfliege *Hydropsyche instabilis*. *Entomol. Ger.* 3:260-64
187. Schröder, P. 1976. Zur Phänologie von *Hydropsyche instabilis* in Föhrenbach/Schwarzwald, unter besonderer Berücksichtigung der Larvenstadien. *Beitr. Naturkd. Forsch. Suedwestdeutschl.* 35:137-48
188. Schwartz, A. 1972. *Net-spinning and habitat partitioning in hydropsychid caddis larvae*. PhD thesis. Univ. Penn., Pa. 87 pp.
189. Scott, D. C., Berner, L., Hirsch, A. 1959. The nymph of the mayfly genus *Tortopus*. *Ann. Entomol. Soc. Am.* 52:205-13
190. Scott, K. M. F. 1967. The larval and pupal stages of the midge *Tanytarsus (Rheotanytarsus) fuscus* Freeman. *J. Entomol. Soc. South Afr.* 30:174-84

191. Sedell, J. R., Naiman, R. J., Cummins, K. W., Minshall, G. W., Vannote, R. L. 1978. Transport of particulate organic material in streams as a function of physical processes. *Verh. Int. Ver. Limnol.* 20:1366-75
192. Serra-Tosio, B. 1967. La prise de nourriture chez la larve de *Prosimulium inflatum* Davies, 1957. *Trav. Lab. Hydrobiol. Piscic. Univ. Grenoble* 57:58-97-103
193. Shalaby, A. M. 1956. On the mouth-parts of the larval instars of *Anopheles quadrimaculatus* (Say). *Bull. Soc. Entomol. Egypte* 40:137-74
194. Shapas, T. J., Hilsenhoff, W. L. 1976. Feeding habits of Wisconsin's predominant lotic Plecoptera, Ephemeroptera and Trichoptera. *Great Lakes Entomol.* 9:175-88
195. Short, R. A., Maslin, P. E. 1977. Processing of leaf litter by a stream detritivore: Effect on nutrient availability to collectors. *Ecology* 58:935-38
196. Simmons, G. M., Voshell, J. R. Jr. 1978. Pre- and post-impoundment benthic macroinvertebrate communities of the North Anna River. See Ref. 73, pp. 45-61
197. Singh, K. R. P., Brown, A. W. A. 1957. Nutritional requirements of *Aedes aegypti* L. *J. Insect Physiol.* 1:199-220
198. Smith, K. 1972. River water temperatures—an environmental review. *Scott. Geogr. Mag.* 88:211-20
199. Sommerman, K. M., Sailer, R. I., Esselbaugh, C. O. 1955. Biology of Alaskan black flies. *Ecol. Monogr.* 25:345-85
200. Speir, J. A. 1976. *The ecology and production dynamics of four species of black flies in western Oregon streams.* PhD thesis. Oregon State Univ., Corvallis. 297 pp.
201. Spence, J. A., Hynes, H. B. N. 1971. Differences in benthos upstream and downstream of an impoundment. *J. Fish. Res. Board Can.* 28:35-43
202. Surtees, G. 1959. Functional and morphological adaptations of the larval mouthparts in the sub-family Culicinae with a review of some related studies by Montschadsky. *Proc. R. Entomol. Soc. London* 34:7-16
203. Sweeney, B. W. 1978. Bioenergetic and developmental response of a mayfly to thermal variation. *Limnol. Oceanogr.* 23:461-77
204. Tonnoir, A. 1925. Australasian Simuliidae. *Bull. Entomol. Res.* 15:213-55
205. Tsui, P. T. P., Peters, W. L. 1974. Embryonic development, early instar morphology, and behavior of *Tortopus incertus*. *Fla. Entomol.* 57:349-56
206. Uéno, M. 1952. Caddis fly larvae interfering with the flow in the water way tunnels of a hydraulic power plant. *Kontyû* 19:73-80
207. Ulfstrand, S. 1968. Benthic animal communities in Lapland streams. A field study with particular reference to Ephemeroptera, Plecoptera, Trichoptera and Diptera: Simuliidae. *Oikos Suppl.* 10:1-116
208. Van Arsdall, T. C. 1977. *Production and colonization of the snag habitat in a southeastern blackwater river.* MS thesis. Ga. Inst. Technol., Atlanta. 45 pp.
209. Verdat, F. J. 1823. Mémoire pour servir à l'histoire des *Simulies*, genre d'insectes de l'ordre des diptères. *Naturwiss. Anz.* 9:65-70
210. Wallace, J. B. 1975. The larval retreat and food of *Arctopsyche*; with phylogenetic notes on feeding adaptations in Hydropsychidae larvae. *Ann. Entomol. Soc. Am.* 68:167-73
211. Wallace, J. B. 1975. Food partitioning in net-spinning Trichoptera larvae: *Hydropsyche venularis*, *Cheumatopsyche etrona*, and *Macronema zebratum*. *Ann. Entomol. Soc. Am.* 68:463-72
212. Wallace, J. B., Malas, D. 1976. The significance of the elongate, rectangular mesh found in capture nets of fine particle filter feeding Trichoptera larvae. *Arch. Hydrobiol.* 77:205-12
213. Wallace, J. B., Malas, D. 1976. The fine structure of capture nets of larval Philopotamidae, with special emphasis on *Dolophilodes distinctus*. *Can. J. Zool.* 54:1788-1802
214. Wallace, J. B., O'Hop, J. 1979. Fine particle suspension-feeding capabilities of *Isonychia* spp. *Ann. Entomol. Soc. Am.* 72:353-57
215. Wallace, J. B., Sherberger, F. F. 1975. The larval dwelling and feeding structure of *Macronema transversum*. *Anim. Behav.* 23:592-96
216. Wallace, J. B., Webster, J. R., Woodall, W. R. 1977. The role of filter feeders in flowing waters. *Arch. Hydrobiol.* 79: 506-32
217. Wallace, J. B., Woodall, W. R., Staats, A. A. 1976. The larval dwelling-tube, capture net and food of *Phycocentropus placidus*. *Ann. Entomol. Soc. Am.* 69:149-54
218. Walshe, B. M. 1947. Feeding mechanisms of *Chironomus* larvae. *Nature* 160:474
219. Walshe, B. M. 1950. Observations on the biology and behaviour of larvae of

- the midge *Rheotanytarsus*. *J. Queckett Microsc. Club* 3:171–78
220. Walshe, B. M. 1951. The feeding habits of certain chironomid larvae. *Proc. Zool. Soc. London* 121:63–79
221. Ward, J. V. 1974. A temperature-stressed stream ecosystem below a hypolimnial release mountain reservoir. *Arch. Hydrobiol.* 74:247–75
222. Ward, J. V. 1976. Effects of flow patterns below large dams on stream benthos: a review. In *Instream Flow Needs Symposium, Vol. II. Am. Fish. Soc. Symp.*, ed. J. F. Orsborn, C. H. Allman, pp. 235–53
223. Ward, J. V. 1976. Effects of thermal constancy and seasonal temperature displacement on community structure of stream macroinvertebrates. In *Thermal Ecology II, ERDA Symp. Ser.* 40, ed. G. W. Esch, R. W. McFarland, pp. 302–7
224. Ward, J. V., Short, R. A. 1978. Macroinvertebrate community structure of four special lotic habitats in Colorado, USA. *Verh. Int. Ver. Limnol.* 20: 1382–87
225. Waters, T. F. 1977. Secondary production in Inland waters. *Adv. Ecol. Res.* 10:91–164
226. Weber, C. I., Moore, D. R. 1967. Phytoplankton, seston, and dissolved organic carbon in the Little Miami River at Cincinnati, Ohio. *Limnol. Oceanogr.* 12:311–18
227. Webster, J. R. 1975. *Analysis of potassium and calcium dynamics in stream ecosystems on three southern Appalachian watersheds of contrasting vegetation*. PhD thesis. Univ. Georgia, Athens. 232 pp.
228. Wesenberg-Lund, C. 1943. *Biologie der Süßwasserinsekten*. Berlin: Springer, 682 pp.
229. Wetzel, R. G., Rich, P. H. 1973. Carbon in freshwater systems. In *Carbon and the Biosphere, USAEC CONF-720510*, ed. G. M. Woodwell, E.V. Pe-
can, pp. 241–63
230. Wiggins, G. B. 1965. Additions and revisions to the genera of North American caddisflies of the family Brachyceridae with special reference to the larval stages. *Can. Entomol.* 97:1089–106
231. Wiggins, G. B. 1969. Contributions to the biology of the Asian caddisfly family Limnocentropodidae. *R. Ont. Mus. Life Sci. Contrib.* 74:29 pp.
232. Wiggins, G. B. 1977. *Larvae of the North American Caddisfly Genera*. Toronto: Univ. Toronto Press. 401 pp.
233. Wiggins, G. B., MacKay, R. J. 1978. Some relationships between systematics and trophic ecology in Nearctic aquatic insects, with special reference to Trichoptera. *Ecology* 59:1211–20
234. Williams, N. E., Hynes, H. B. N. 1973. Microdistribution and feeding of the net-spinning caddisflies of a Canadian stream. *Oikos* 24:73–84
235. Williams, T. R., Connolly, R., Hynes, H. B. N., Kershaw, W. E. 1961. Size of particles ingested by *Simulium* larvae. *Nature* 189:78
236. Wood, D. M. 1978. Taxonomy of the Nearctic species of *Twinnia* and *Gymnopais* and a discussion of the ancestry of the Simuliidae. *Can. Entomol.* 110: 1297–1337
237. Wood, K. G. 1973. Decline of *Hexagenia* nymphs in western Lake Erie. *Proc. Int. Conf. Ephemeroptera*, 1st 1970:26–32
238. Wotton, R. S. 1976. Evidence that blackfly larvae can feed on particles of colloidal size. *Nature* 261:697
239. Wotton, R. S. 1977. The size of particles ingested by moorland stream blackfly larvae. *Oikos* 29:332–35
240. Wotton, R. S. 1978. Growth, respiration, and assimilation of blackfly larvae in a lake-outlet in Finland. *Oecologia Berlin* 33:279–90
241. Wotton, R. S. 1978. Life-histories and production of blackflies in moorland streams in Upper Teesdale, Northern England. *Arch. Hydrobiol.* 83:232–50
242. Wotton, R. S. 1978. The feeding-rate of *Metacnephia tredecimatum* larvae in a Swedish lake-outlet. *Oikos* 30:121–25
243. Wu, Y. F. 1931. A contribution to the biology of *Simulium*. *Pap. Mich. Acad. Sci. Arts Lett.* 13:543–99
244. Yamauchi, H. 1977. Some observations of the capture nets of hydropsychid larvae. *Biol. J. Nara Women's Univ.* 27:7–8 (In Japanese with English summary)
245. Zimmerman, M. C., Wissing, T. E. 1978. Effects of temperature on gut-loading and gut-clearing times of the burrowing mayfly, *Hexagenia limbata*. *Freshwater Biol.* 8:269–77
246. Zimmerman, M. C., Wissing, T. E., Rutter, R. P. 1975. Bioenergetics of the burrowing mayfly, *Hexagenia limbata*, in a pond ecosystem. *Verh. Int. Ver. Limnol.* 19:3039–49