Chapter 4
Suspension and Filter Feeding in Aquatic Insects

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Abstract Aquatic insect feeding occurs at the nexus of habitat, food source and size, and behavior and relies largely on the complexities of mouthpart morphology. This intersection has important consequences for tropic interactions, nutrient processing, and ecosystem function. In aquatic habitats, immature insects feed in a variety of ways; however, consumption of small suspended particles (seston) in the water column is a common mode for representatives of several insect groups. Ingestion of seston can occur via active or passive removal and broadly encompasses filter and suspension feeding. In this chapter, we explore the ways in which various aquatic insects acquire food particles. We focus on food sources and particle sizes, feeding behavior, morphology of mouthparts, and trophic importance. The major groups explored include Ephemeroptera (mayflies), Diptera (true flies), and Trichoptera (caddisflies), each of which have evolved unique strategies for obtaining particles from the water column. Members of this feeding group are critical as food sources for aquatic and terrestrial organisms, they play large roles in nutrient cycling, and some are vectors of important human and animal diseases.

4.1 Introduction

Insects feed on almost all available food sources, including live and dead plant material, animals, fungi, bacteria, and protozoans. However, within the insects there are some taxa that specialize on feeding on suspended particles of food within the water column. Also known as collector filters or suspension feeders (hereafter, filter feeders), these insects comprise an important group of animals in both flowing (lotic) and stagnant (lentic) waters. In moving waters, filter feeding is often passive,

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inasmuch as insects rely on the current to deliver particles to them. In standing waters, an active filtering behavior is often observed, either using moving mouthparts to filter particles out of the water column or via the use of burrows that take advantage of currents produced in proximity to their tubes. Feeding styles are not mutually exclusive, as some inhabitants of moving water also use burrows to facilitate particle capture (e.g., some mayflies). Regardless of the mode, these animals contribute to energy processing and conversion of dead biomass into living tissue and are also important for the transport of resources across habitats (i.e., resource subsidies). Our objectives in this review are to examine the mechanisms of suspension feeding across aquatic insect taxa, the source and composition of their food sources, their importance within aquatic food webs, and research directions and challenges for the future. Earlier reviews of some of these topics can be found in Cummins and Klug (1979), Wallace and Merritt (1980), and Merritt et al. (2008).

4.2 Mechanisms for Gathering and Ingesting

Insects in the filter-feeding guild have evolved a myriad of modifications for particle capture, some of which do not necessarily involve specialized mouthparts (Wallace and Merritt 1980; Merritt and Wallace 1981; Huryn et al. 2008; Hershey et al. 2010). Contrasting mechanistic strategies that serve the same basic purpose can be seen in the diversity of stream dwelling species across several taxonomic groups that are generally considered to be passive filter feeders or filter collectors (Merritt et al. 2008). These insects take advantage of consistent water flow while primarily in a sedentary mode. Other members of the guild inhabit low flow or stagnant water and are more active filter feeders in that they employ a variety of strategies to move fluid and particles past trapping structures and mouthparts for collection and ingestion.

4.2.1 Passive Filter Feeders

Perhaps the best examples of passive filter feeders with modified mouthparts are black fly larvae (Diptera: Simuliidae). They are widespread in lotic systems, both tropical and temperate, and have evolved elaborate cephalic (labral) fans that are deployed in the current to collect particles; they are then retracted toward the oral cavity where trapped particles are removed by other mouthparts and ingested. Cephalic fans represent a truly specialized feeding adaptation by this group, and the feeding action and hydrodynamic considerations have been extensively reviewed elsewhere (Currie and Craig 1987; Craig and Galloway 1987; Adler and Currie 2008). Particle entrapment efficiency is related to current velocity and density of setae on the fans. Species with large fans and densely packed setae are associated with lower velocity, whereas species with smaller fans and larger spaces between setae are found in faster flowing stream sections (Palmer and Craig 2000). However, there is much variability within this generalization as fan size and setal density change with instar and larval environment (Lucas and Hunter 1999). Spacing between setae and number of setae on labral fan rays is phenotypically plastic: it is affected by current velocity and food concentrations in which the larvae develop (Lucas and Hunter 1999).

Within the same lotic habitats, and often found adjacent to black fly larvae on a substrate, are species of Trichoptera (e.g., Hydropsychidae, Philopotamidae, Polycentropidae, Dipseudopsidae) and Diptera (Chironomidae: *Rheotanytarsus*) that construct nets out of silk to collect particles from the current. These organisms anchor themselves to a substrate and build nets of various mesh sizes and shapes (Wallace and Merritt 1980; Merritt and Wallace 1981). The nets are then periodically cleaned or consumed by the larvae using largely biting and chewing mouthparts (e.g., mandibles and maxillae). Larvae of net builders are otherwise sedentary often living in retreats built with silk and available materials. Similar to black fly larvae, net mesh size varies with species, instar, and current velocity (Plague and McArthur 2003; Wiggins 2005). Philopotamidae larvae construct very fine mesh tubular nets (mesh size in the <1 μm range) and use an extended membranous labrum to harvest trapped material (Wiggins 1996, 2005), often small detrital particles (Shapas and Hilsenhoff 1976). In contrast, some late instars of Hydropsychidae species generally build nets with mesh sizes in the 500 μm range and trap more intact invertebrates and large particles than fine particulate matter (Wallace and Merritt 1980; Wotton 1994). *Rheotanytarsus* (Chironomidae) larvae utilize both silken nets and sticky secretions from salivary glands on filaments at the opening of their tube dwellings to collect particles in flowing water (Merritt and Wallace 1981).

Additional means of collecting suspended particulates in flowing water is accomplished through setaceous limbs in some groups (e.g., prothoracic legs in Isonychia and meso- and meta-thoracic legs in *Brachycentrus*). In these cases, the insects face the current with legs extended laterally to collect passing particles, which are then harvested via setaceous mouthparts directly (*Isonychia*) or manipulated into a bolus by the forelegs and transferred to the mouth (*Brachycentrus*) (Merritt and Wallace 1981, but see Hershey et al. 2010).

4.2.2 Active Filter Feeders

Active filter feeders in non-flowing water utilize brush-like modifications of mouthparts to generate fluid movement on their own (e.g., mosquito larvae) and simultaneously collect and ingest particles brought toward the oral cavity with other mouthparts, or create fluid movements with body undulations and gill movements in constructed tubes or burrows (e.g., Chironomidae, Ephemeridae, Dipseudopsidae) to move water through silken nets and setaceous appendages and mouthparts. Larval mosquito feeding has been extensively studied and currents generated by mouthparts have been detailed (Clements 1999 and references therein). Currents generated by the feeding of this group are generally vertical and lateral, moving particles up and into to the oral cavity and expelling fluid downward and laterally.

Other active filterers include tube- or burrow-dwelling Chironomidae (*Chironomus*) and Ephemeroptera (Ephemeridae, Polymitarcyidae) found in sediments in lentic habitats or in depositional zones of lotic habitats. *Chironomous* species utilize silk for tube lining and to construct nets that capture particulates brought into the tube or burrow by body undulations. Ephemeridae (e.g., *Ephemera*) construct U-shaped burrows in sediment and also use body undulations and gill movements to bring particulates in and collect them on foreleg setae and mouthparts (Wallace and Merritt 1980). Similarly, Dipseudopsidae larvae construct silk lined tubes in sediment and use body undulations to move water through, collecting trapped material from the inner surfaces with setaceous mandibles (Wiggins 1996, 2005).

It is important to note that although filter feeding per se may be the primary mode of food acquisition in the groups discussed here, most species are flexible in modes of obtaining food. Both mosquito and black fly larvae, for example, regularly switch to browsing on surfaces to harvest available biofilms. Thus, the same mouthparts used in filter feeding are used to brush or scrape microorganisms and detritus from surfaces. In the case of mosquito larvae, this feeding mode can predominate in some species or under certain conditions (low suspended organic matter or presence of predators) (Merritt et al. 1992; Yee et al. 2004; Yee and Kehl 2014; Roberts 2014).

4.3 Relationship Among Filter-Feeding Taxa

Recent phylogenetic analyses suggest a long and complicated evolutionary history for insects, dating back approximately 479 million years (Early Ordovician) (Misof et al. 2014). Diversification has continued unabated, producing not only differences in morphology and feeding modes, but also in types of metamorphosis, emergence of flight, behavioral differences, and ecological diversity. Aquatic insects appear within 12 different insect orders, and invasions by terrestrial forms into freshwater have occurred at least 50 times (Klaas-Douwe et al. 2014). Given this, it is also likely that filter feeding evolved independently several times. Specifically, Ephemeroptera (mayflies), Trichoptera (caddisflies), and Diptera (true flies) contain a high number of filter-feeding taxa. However, these three groups are not closely related, with the true flies and caddisflies being the most closely related among the three, although these two groups are likely still separated by tens of millions of years (Misof et al. 2014). Within Diptera, there do seem to be strong relationships in the feeding apparatus of Culicidae, Chaoboridae, and Dixidae (Wagner et al. 2008), and more distantly with Simuliidae (Craig 1974); all these Diptera do appear in the same Infraorder (Culicomorpha, Wagner et al. 2008). We might speculate that given the diversity of filter-feeding modes outlined elsewhere in this review, the evolution of filter feeding likely was due to the availability of various niches within different aquatic systems at different times, and not due to a single instance of the evolution of mouthparts or behavior. However, at present there is no single review on the evolution of filter feeding across aquatic insect groups.

4.4 Suspension Feeding Across Insect Taxa

Of the approximately 1 million species of insects identified, three orders dominate those that use filter feeding to obtain food: Ephemeroptera (mayflies), Diptera (true flies), and Trichoptera (caddisflies). There are other orders that also exhibit filtering, including Coleoptera; however given that perhaps only one-fifth of all insect species have been described (Stork 2018), it is likely that more species that exhibit filter feeding are yet to be found. Also of note is that the vast majority of individuals that exhibit filter feeding are larvae, which likely is explained by the fact that adult forms of these groups are terrestrial and have different modes of obtaining food, or don’t feed at all (e.g., Ephemeroptera). The key distinguishing features among species in this group are the morphology of specialized mouthparts or hairs, and in some instances, the use of silk for capture and sieving of particles. Moreover, filter-feeding insects can be divided into those that filter using their body parts (e.g., mouthparts or legs) or constructed habitats (e.g., burrows, tubes, nets) to collect particles.

4.4.1 Coleoptera

Beetles are the most diverse group of animals on Earth, representing about 40% of all insect species (Stork 2018); however when examining their feeding behavior the vast majority rely on modes other than filter feeding. Nevertheless, at least two aquatic families of beetles are known to use filtering to obtain food particles: Scirtidae and Spercheidae. Although the mechanism and ecology of filter feeding is not well studied in either group, the fact that it exists in some beetles may hint at the use of this feeding mechanism in other less studied families.

Scirtidae (marsh beetles) are a widely distributed family of beetles with short-lived adults occurring in the terrestrial environment (reviewed in Yee and Kehl 2014). Larvae are aquatic, and often can be found in lotic or lentic waters, including marshes, swamps, and ground pools; they also reside in phytotelmata, including tree holes (Kitching 2000). In all habitats, larvae are shredders or detritivores, feeding on fungi, algae, and other organic matter. However, small particles are captured using a complex filtering structure, which is present on the hypopharynx, and various types of microorganisms are filtered by a dense maxillary or mandibular set of bristles (Fig. 4.1), or collected from the detrital or container surface (Lawrence 2016). These particles are subsequently sorted on a complex and greatly modified hypopharynx. Other aspects of feeding in this family can be found in Hannappel and Paulus (1987).

Spercheidae (filter-feeding water scavenger beetles) are represented by a single genus (*Spercheus*) containing about 20 species (Yee and Kehl 2014). Found in shallow lentic waters, these are unique among beetles as both larvae and adults use filter feeding to obtain food. Both life history stages stay on the underside of leaves, where they may sit and filter. In adults, the clypeal bristles rests above the surface of the water, whereas the complex clypeus itself remains below (Rothmeier

Fig. 4.1 Head and mouthpart of larval *Prionocyphon* sp. (Coleoptera: Scirtidiae) noting dense maxillary or mandibular set of bristles. Phase contrast image by R. Ruta, University of Wroclaw, Poland

and Jäch 1986). Adults remove food particles from the bristles by the use of a galea comb. A more comprehensive evaluation of the feeding of adults can be found in Rothmeier and Jäch (1986). For larvae, food is often detritus or small invertebrates, whereas adults feed on algae or decaying plant material (Archangelsky 1997; Hansen 1997). The mouthparts of larvae and adult are both well adapted to filtering and contain several sections of bristles and setae (Fig. 4.2).

4.4.2 Ephemeroptera

Mayflies comprise a well-studied group of filter-feeding insects with about 3200 species (Stork 2018). Most Ephemeroptera juveniles (nymphs) feed, whereas short-lived adults have vestigial mouthparts and do not. Beyond other forms of feeding, including scraping algae and predation, there are at least nine families where filter feeding occurs, including the Baetidae, Coloburiscidae, Ephemeridae, Heptageniidae, Isonychiidae, Leptophlebiidae, Oligoneuriidae, Polymitarcidae, and Siphlonuridae (Brittain 1982; Merritt et al. 2008; Ramírez and Gutiérrez-Fonseca 2014). Among these families, there is wide variation in how filtering ensues, and how it may be classified (e.g., passive versus active filtering). For instance, *Curotenetes*

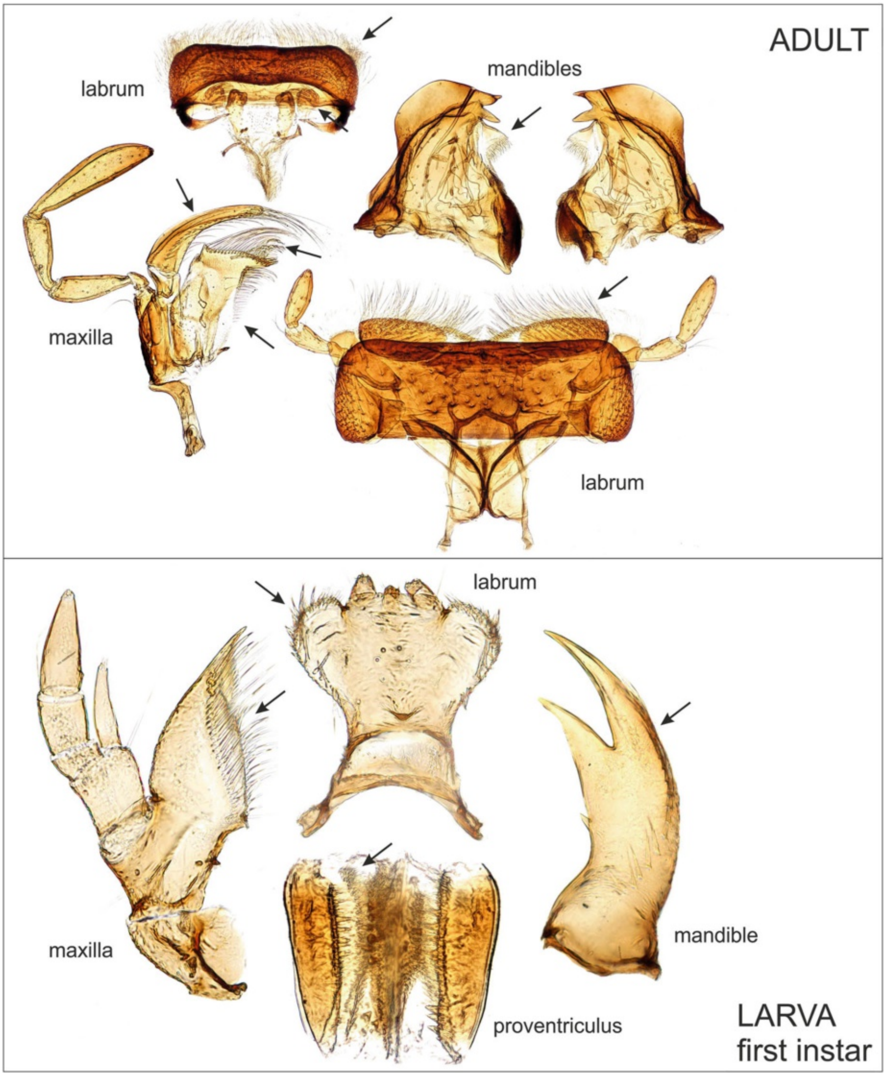

Fig. 4.2 Mouthpart of *Spercheus emarginatus* (Coleoptera: Sphericidae) 1st instar larvae and adult. Arrows indicate setae associated with the mouthparts used in filtering. Images by M. Fikáček, National Museum, Czech Republic

albomanicatus extend their long seti-covered forelegs into the water current to capture particles before bringing them close to their mouthparts for feeding (Clemens 1917), thus filtering via morphological adaptations of the body (e.g., Fig. 4.3). A similar behavior is seen in *Oligoneuriella rhenana*, where labial and maxillary palps remove particles from foreleg setae (Elpers and Tomka 1995). Long fringes of setae on legs do not necessarily indicate a filter-feeding function, as hairs on the hind legs are more

Fig. 4.3 Ventral view of head of mayfly larvae (Ephemeroptera: Isonychiidae) showing interlocking setae on legs. Inset: Close-up of the setae used for filtering on leg segments. Photo by D.A. Yee, University of Southern Mississippi, USA

likely for swimming (Lancaster and Downes 2013). More direct particle collection can be achieved by fringes of setae on the mouthparts, as seen in some genera including *Oligoneuriella* and *Isonychia* (Elpers and Tomka 1995; Wallace and O'Hop 1979). In the Coloburiscidae, Isonychiidae, and Oligoneuriidae, nymphs may also possess coxal gill tufts that can be used to aid filtering (Zhou 2010). Besides morphological adaptations, some mayflies construct burrows, especially among the Polymitarcidae. For instance, *Povilla* sp. dig a burrow, often in submerged wood, which are then lined with silk-like proteinaceous material produced via the anus (Hartland-Rowe 1953). Nymphs use their abdominal gills to increase water flow through their U-shaped burrows, where particles may then land on various portions of their body (Hartland-Rowe 1953, 1958). This effect is further enhanced by the presence of secondary hairs on the filtering setae, which when interlocked with adjacent hairs can capture very small particles (4–8 μm) (Hartland-Rowe 1953, 1958). For *Tortopus* sp. (Polymitarcyidae), nymphs have mandibular tusks that they also use to construct U-shaped burrows, especially in mud along stream banks (Scott et al. 1959), and have filtering setae on several body parts including the tibia and mandibles that are likely for gathering particles (Molineri et al. 2010). These particles are then removed via the palps (Scott et al. 1959). Rhythmic moving of gills in many burrowing mayflies (e.g., *Ephemera*) likely aid in current movement and enhance particle deposition (Eastham 1939).

4.4.3 Diptera

The most speciose order of insects to contain filter-feeding members is the Diptera, or true flies, with about 155,000 species (Storks 2018). However, within the taxon, there are only five out of over 180 families of flies that contain a high proportion of filter-

Fig. 4.4 Ventral view of a black fly larval (Diptera: Simuliidae) head with cephalic fan (right side extended, left side collapsed). Photo by D.A. Yee, University of Southern Mississippi, USA

feeding species: Simuliidae, Culicidae, Dixidae, Chaoboridae, and Chironomidae. However flies do exist with filter-feeding attributes in other families, including Stratiomyiidae, Syrphidae, and Calliphoridae. However, as has been pointed out elsewhere, there is a great need for research into the feeding biology of other fly larvae (Wallace and Merritt 1980).

4.4.3.1 Simuliidae

Black flies are represented by 2300 species worldwide (Adler and Crosskey 2018), and are most often found in lotic waters. Adults are high pestiferous for their biting behavior on humans. Blackfly larvae have a highly adapted filter-feeding structure known as a cephalic fan (Fig. 4.4), which individually are located between their antenna and mouths, and are capable of retracting and folding depending on feeding activity (Craig 1974; Wallace and Merritt 1980). Working in conjunction with current speed, a unique body position, and beating of the fans, black fly larvae are able to collect a variety of particles (summarized by Merritt et al. 1996). The fans trap particles of 0.09 to 350 μm in size, including bacteria, algae, diatoms, other insects, and detritus (reviewed in Wallace and Merritt 1980). However, the considerably smaller particle size found in their guts suggests that another mechanism for capture may be involved. Specifically, Ross and Craig (1980) identified a mucosubstance associated with the cephalic fan of several genera, which when applied to the fans acts in a way to retain particles smaller than the fan alone can capture. Entrapment of particles was initially presumed to be enhanced by this endogenous mucous secretion on the fans, but the source of mucous-like substances on fan setae surfaces appears to be derived from flocculation of dissolved organic matter (Ciborowski et al. 1997). Regardless of the source, this amorphous material may also aid in entrapment of organic matter and serve as a food source for larvae. Particles in general are removed by the larvae via sweeping their mouthparts over the surface of the fan. Finelli et al. (2002) showed that under experimental trials black fly larvae feeding behavior was more related to benthic water velocity than to food concentration. Not all simuliids are equipped with large fans (e.g., species in the genera *Gymnopais* and *Twinnia*, Craig 1974) but instead may scrape or browse on surfaces (Wallace and Merritt 1980). Although simuliids produce silk as a holdfast onto surfaces in fast-moving lotic habitats, they do not appear to use it for particle capture.

4.4.3.2 Culicidae

Mosquitoes contain approximately 3500 species worldwide, and all species have larvae that occur in freshwater to brackish lentic or slow-moving lotic environments (Laird 1988). These habitats also include container systems, including both natural (e.g., phytotelmata like bromeliads, tree holes, bamboo stumps) and artificial (e.g., vehicle tires, cemetery vases) containers (Kitching 2000; Vezzani 2007; Yee 2008). Mosquitoes are insects best known for their association with disease, being responsible for millions of new infections by pathogens and hundreds of thousands of deaths in humans each year. Perhaps because of this, we know a good deal about mosquito feeding, especially among those genera most active in vectoring pathogens. Mosquitoes have an aquatic larval phase followed by a terrestrial adult phase, and although adults may still feed on plant nectar, growth is the sole purview of the larval phase. Outside of a few predatory taxa (e.g., all *Toxorhynchites*, some *Psorphora*) mosquito larvae have specific adaptations for filter feeding and obtain nourishment from heterotrophic microorganisms, algae, and detritus (e.g., Walker et al. 1988). The mouthparts of mosquitoes are adapted for straining particles from the water column and from surfaces. The entire apparatus, referred to as mouth brushes (Fig. 4.5), are primarily composed of well-developed mandibles and maxillae, with lateral palatal brushes located on a reduced labrum (reviewed by Pucat 1965). The action of these brushes, other mouth structures including setae, and pumping action of the pharynx combine to create strong water currents surrounding the mouth, bringing particles within reach (Merritt et al. 2008). In general, actively feeding larvae move suspended particles toward the mouth with modified mouth brushes, creating local currents that can extend into the surrounding water up to several centimeters. These brushes are not necessarily the primary mode of particle capture but serve as fluid movers: acting more like paddles than sieving mechanisms (Clements 1999). The mouth brushes do pick up some particles, but interestingly, they are cleaned not only by other mouthparts, but also by other structures (e.g., comb scales, pecten) located on the penultimate abdominal segment and respiratory siphon. The length of the setae influences the distance that a particle may be retrieved, and currents generated by brushes can move particles as far as from 40 mm away toward the mouth (Merritt et al. 1992; Clements 1999). Among genera, mosquitoes may utilize different feeding behaviors, so there are great differences in food type and performance in different environments. Categorization of mosquito larval feeding behavior has been based on particle size range and the general location of the food item (Merritt et al. 1992). Collector-filtering or filtering is found to be

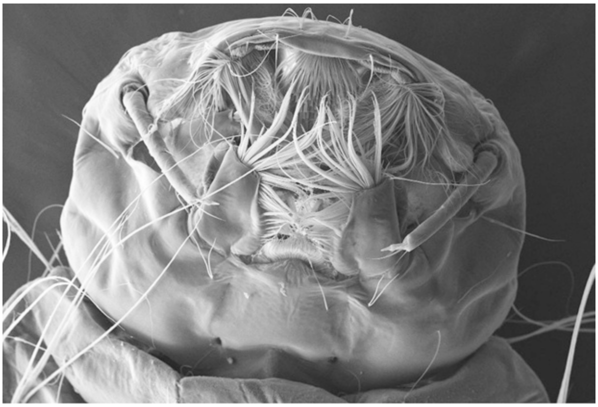

Fig. 4.5 Scanning electron micrograph of a head and mouthparts of *Aedes albopictus* (Diptera: Culicidae) showing the mouth bristles. Photo by J. H. Deerman, University of Southern Mississippi, USA

dominant in the *Culex*, *Anopheles*, and *Culiseta*, wherein larvae remove particles that are suspended in the water column or floating on or at the water surface. Other genera, like *Aedes* and *Wyeomyia*, feed by removing particles on or loosely connected to surfaces like submerged rocks and vegetation ("browsers," Merritt et al. 1992; Clements 1999). Some Culicine larvae (e.g., *Aedes* and *Culex* spp.) filter feed primarily beneath the surface, suspended beneath their respiratory siphon. In contrast, *Anopheles* larvae feed at the air–water interface and primarily collect particles and material in the surface microlayer. This group generates currents that travel mainly parallel to the water surface and any expelled fluid moves downward and away from the head capsule (Clements 1999). Food sources and differences among larval assimilation and acquisition rates may also influence multiple measures of mosquito life history (e.g., Yee et al. 2015; Yee 2016). This can affect pathogen transmission by influencing the body size and nutritional reserves of emerging females, as well as the numbers of emerging females from any particular habitat (Juliano et al. 2014; Alto et al. 2015). The rich literature on mosquito larval nutrition has been reviewed by Clements (1999) and Dadd (1973).

4.4.3.3 Dixidae

With 173 species, dixids are a small group of flies that are found in association with aquatic habitats and are closely related to mosquitoes (Wagner et al. 2008). Also called "meniscus midges," dixids are found in the surface tension around stones and organic substrates in slow-moving lotic or lentic habitats like ponds, lakes, and marshes (Wallace and Merritt 1980). Larvae also share similar morphological adaptations with Culicidae, including the anatomy of the labral brushes, but often consume just algae and detritus. Larvae hang in the water surface of leaves of macrophytes or riparian vegetation, and take on a curled "U-shape"; adults do not feed.

4.4.3.4 Chaoboridae

With only 50 species, phantom midges are also found in similar habitats as both their closest relatives, the mosquitoes and dixids (Wagner et al. 2008). Although most species are predatory, *Australomochlonyx nitidus* filter feeds exclusively, using a large, conspicuous, fan-like set of hairs on the mandibles (Colless 1977). In addition, this species contains a unique morphological adaptation to feeding, the oral bullae. The oral bullae consist of a hair-covered membranous structure that lies on either side of the pharyngeal orifice but below the mandible, which are likely used to transfer food from the mouthparts to the mouth itself (Colless 1977).

4.4.3.5 Chironomidae

Midges, or non-biting midges, are one of the most specious families of flies, with greater than 20,000 species (Merritt et al. 2008). Adults generally do not feed and are poor fliers, but are often more abundant than larvae. Larvae are small and occupy more aquatic and semi-aquatic habitats of any other aquatic insect, including permanent and temporary lotic and lentic habitats, and can be found across a vast range of temperatures, elevations, and environmental conditions. Many filter-feeding larvae employ silk as a means of particle capture. Often, a net is spun across the opening of a small burrow located within the substrate, and larvae move their body in small undulations to facilitate water movement across the net (Berg 1950). This net, along with associated particles, is consumed before the larvae spin another one to replace it. *Rheotanytarus muscicola* constructs small silk cases that are attached to the substrate in lotic environments. In later instars, the larvae add a salivary secretion to two to five small protuberances, which look like small arms, incorporated into the case (Kullberg 1988). These secretions are then periodically consumed along with any particles. Another chironomid, *Odontomesa fulva*, directly filter feeds using setae associated with their mouthparts (reviewed in Pinder 1986), which seems to be a rare condition in filter-feeding Chironomidae.

4.4.4 Trichoptera

With over 14,300 species (Storks 2018), caddisflies are one of the more diverse filter-feeding insect orders. Although there are caddisflies that have evolved morphological adaptations to filter, most species use woven nets of silk for filtering particles from lotic water. This silk is produced via the labial glands of the mouth and is very similar in composition to Lepidopterans (Sehnal and Sutherland 2008). Nets of silk vary in size, pore diameter, and location, but are all produced via the salivary glands (Wallace and Merritt 1980; Merritt et al. 2008). For instance, pore size ranges from $>200,000\ \mu m^2$ in Arctopsuchinae to $<200\ \mu m^2$ in Macronematinae (Wallace and Merritt 1980). Moreover, the type of particles captured can vary with species, habitat, and net morphology, with diatoms, algae, and detritus being the most common types of food. Caddisflies are divided into three broad suborders, the Annulipalpia, Integripalpia, and the Spicipalpia (Holzenthal et al. 2007). The most common filter feeders belong to the family Hydropsychoidea (Annulipalpia), which often dominates freshwater streams in North America (Wallace and Merritt 1980). These caddisflies build shelters, or retreats, of silk nets that may also incorporate material from the surrounding area, including organic particles, detritus, and mineral fragments. Mesh size within this family is often based on environmental conditions, including current speed and temperature. For instance, net mesh size tends to be larger in species that reside in cold fast-moving upstream sites, but smaller mesh sizes are found in downstream sites with slower current speeds (Merritt et al. 2008). Other families that construct silken nets within the Annulipalpia include the Polycentropodidae, Dipseudopsidae, and Philopotamidae. The smallest mesh sizes are found in the Philopotamidae (0.4 μm^2) (Wallace and Malas 1976). Mesh can be produced rapidly with as many as 70 individual strands being excreted at a time, and nets are often found on the underside of rocks in slow-moving currents (Wallace and Malas 1976).

Silk is often used to construct caddisfly cases (caddis), wherein a variety of particles, including pieces of leaves, small rocks, snail shells, wood, or other debris, are adhered together. Construction particles are often specific to certain species, and cases come in a dazzling array of sizes and shapes (Ross 1964; Merritt et al. 2008). When constructing a caddis, a larva starts with an oval frame of silk, to which they attach a larger net in a set of complex behaviors, involving anchoring, resting, and weaving (Ross 1964). Similar to other complex behaviors in insects, the actual type and size of net or caddis is the result of several highly conserved steps, which when added together produce the variety of filter-feeding structures seen in Trichoptera. Besides the protection afforded by the net itself, the caddis can serve as a food-capturing device, wherein particles that enter through the larger upstream opening adhere to the silk lining of the tube. Once prey or particles are passively captured on the nets, they are removed in a number of distinct ways (Merritt and Wallace 1981). Elongated forelimbs are used by some hydropsychoids to remove small living prey that was captured in their nets. Other species that capture organic particles may remove them using specialized, densely arranged bristles, located either on their mouthparts (e.g., *Macronema* sp.) or on their forelegs (e.g., *Phylocentropus* sp.). Others sweep particles into their mouth using setae along the upper labrum (Merritt and Wallace 1981).

Some caddisflies use a combination of approaches for capturing food particles via direct filtering, often via net spinning and tube building. These include *Macronema* sp. mentioned above, which build a short, upward pointing tube in wood on bark in streams that contains a small section laced with a silk net (Wallace and Sherberger 1974). Particles that land on the netting are then removed via the legs or mouthparts. Members of the genus *Phylocentropus* (Dipseudopsidae) first build a long Y-shaped tunnel below the substrate of the stream. One side of the tunnel is longer than the other, and it normally extends upward and protrudes far above the bottom, whereas the other is shorter and often does not protrude as far. The larva also builds a bulge into the shorter tube, where it spins a silken net. By occupying the longer tube and moving its body in an undulating motion, the larva causes a current to be produced passing from the longer tube to the short tube across the net. In this way, the larvae achieves particle capture (Wiggins 2005). Caddisflies in the genus *Neureclipsis* (Polycentropodidae) dispense with a burrow or tube and instead build a large, cornucopia-shaped net, which can be as long as 20 cm, and is often attached to a underwater structure like a branch (Wallace and Merritt 1980).

Other species do not build a caddis, burrow, or use silk to filter feed. Some Brachycentridae use long setae on their middle and hind legs to aid in particle capture, whereas several *Drusus* sp. (Limnephilidae) possess spines or long hairs on the head and body that allow for prey capture (Bohle 1983; Graf et al. 2005).

4.5 Food Sources

Although populations of filter feeders are limited by many factors, the abundance and quality of food items available for capture is certainly a primary constraint. For most filter feeders, where you are (habitat) defines what you eat. Most immature filter feeders are either relatively sessile (attached to substrates directly or via constructed refugia) or restricted to small, defined habitats (e.g., container breeding mosquito larvae). Movement to higher quality habitats after hatching from the egg may be possible (e.g., stream dwelling insects drifting downstream), but such movements can increase predation risks and a new habitat is no guarantee of higher quality food resources. This general lack of choice is further constrained by body size and specific tools for particle capture.

4.5.1 Food Size Range

As might be expected within a phylogenetically and morphologically diverse feeding guild, food items can vary considerably with taxon and size (instar) of the individual. Generally speaking, most filter-feeding insects collect and ingest a mixture of particles ranging from colloidal (nanometer size range) to coarse particulate organic matter (CPOM $>$ 1 mm) and whole macroinvertebrates (sometimes even younger conspecifics). FPOM (fine particulate organic matter, $>$0.45 μm, $<$1 mm) is considered the "sweet spot" in terms of ingestibility and food value (Bundschuh and McKie 2016). Indeed, most studies of insect filter feeders show this size range of particles to be predominant in the guts of filter feeders, with a majority of species or life stages feeding on sources between 1 and 300 μm (Huryn et al. 2008). Although there is evidence that DOM (dissolved organic matter)—defined as material passing through a glass fiber (GF/F) filter in many cases, but more precisely defined as being less than 0.45 μm in diameter (Nebbioso and Piccolo 2013)—is concentrated and assimilated, this reflects natural aggregation, adsorption, and consolidation of dissolved substances (Ciborowski et al. 1997; Kaplan and Cory 2016) more than any targeted mechanism of ingestion by filter feeders. Assimilation of smaller soluble compounds such as amino acids and sugars likely necessitates the presence of particles and colloidal compounds for adequate fluid ingestion and movement through the digestive tract (Merritt et al. 1992). Mosquito larvae, for example, primarily consume particles in the 1–50 μm size range, but this varies with species and instar (Merritt et al. 1992). Larger particles can also be ingested, depending on the shape (e.g., strands of algal filaments or nematodes), but cross-sectional diameter for these particles is usually within the size ranges noted above (Clements 1999). Other examples include black fly larvae, which consume a high percentage of large (>40 μm) particles (Kurtak 1978; Wotton 1994), yet still are capable of ingesting colloidal size material (Wotton 2009).

4.5.2 Types and Selection of Ingested Particles

The particulate components consumed by filter and suspension feeders include a wide range of detritus (animal and plant-based) and fecal material, microorganisms, small metazoans, and live invertebrates, in addition to mineral and inert materials. Gut content analysis of filter feeders has identified bacteria, algae, protozoans, micro-metazoans, fungi, small invertebrates, and often a dominance of amorphous detritus (Wallace and Merritt 1980; Merritt et al. 1992; Clements 1999; Wiggins 2005; Huryn et al. 2008). Detritus itself is an important substrate for microorganisms and ingestion of plant detritus in particular is considered a means of harvesting-associated microbial biomass rather than the generally refractory substrate (Cummins and Klug 1979; Cummins et al. 2008). This may not necessarily be the case for ingestion of animal-derived detritus, in which the substrate itself (soft tissues, small pieces of chitinous exoskeleton) can be digested and assimilated without microbial intervention. The higher relative food value of animal vs. plant detritus has been demonstrated in studies of larval mosquitoes (Yee and Juliano 2006; Yee et al. 2007, 2015; Winters and Yee 2012).

Apart from size range restrictions noted above, many filter feeders show little selection of ingested particles. Particles with no food value (e.g., clay, charcoal, plastic) are readily consumed and passed through the gut, even in the presence of particles or solutes with actual food value (Merritt et al. 1992; Clements 1999). Recent work has shown that not only are inert materials, such as small plastic particles, ingested by mosquito larvae, they may be transferred to the adult stage and presumably to higher trophic levels (Al-Jaibachi et al. 2018). Any "choice" of food source is largely made by females selecting oviposition sites, because larval or nymphal habitat determines the type and quality of ingestible material. Some direct selection of food may occur with large passive filter feeders, such as net spinning caddisflies in the Hydropyschidae subfamily Arctopsychinae, where larvae appear to harvest high-quality food items (e.g., insects) from nets while ignoring or discarding other large detritus particles (Wallace and Merritt 1980; Wiggins 2005; Huryn et al. 2008).

Bacteria For almost all filter-feeding insects bacteria represent a constant and important food source. Their contribution to the growth of many filter-feeding species is well documented, including important indirect roles in nutrition and initiation of development (Strand 2017; Valzania et al. 2018). Bacteria are ubiquitous in aquatic habitats, are in the size range (generally 0.5–5 μm) of particles collected by the majority of filter feeders, and are associated with the surfaces of bigger particles ingested by some larger filter-feeding species as well. Bacterial carbon was estimated to contribute up to 67% to black fly larval growth in some river systems (Meyer and Edwards 1987) and black flies have reportedly been reared to pupation on bacterial suspensions alone (Adler and Currie 2008). However, bacteria appear to be inadequate for complete mosquito development (Valzania et al. 2018), and in many cases, it is not clear how much bacteria contribute to filter feeder production relative to other food sources. Further, bacterial diversity is such that considering the category to be homogenous in food value to each filter feeder is untenable. Digestibility of bacterial species by aquatic insects can vary considerably (e.g., Austin and Baker 1988), and it has been suggested that filter-feeding organisms in non-flowing systems ultimately select for indigestible forms in their immediate environment (e.g., Kaufman et al. 2002). The recent research emphasis on gut bacterial communities in insects, and especially mosquitoes, suggests that many forms of ingested bacteria survive digestion and become residents, even passing transtadially into adults (Strand 2017; Guégan et al. 2018). Nonetheless, bacteria in the mosquito gut originate from and reflect the larval environment (Strand 2017; Guégan et al. 2018). This exploration of gut bacterial communities, therefore, can also give a picture of what types of bacteria are ingested and subsequently digested, providing information about the food value of specific particles harvested by this filter-feeding group. Additionally, studies of bacterial communities with and without filter feeders present can be useful in identifying food sources. For example, *Flavobacterium* was abundant in habitats without *Aedes triseriatus* larvae, but was greatly reduced in their presence (Xu et al. 2008). Subsequent studies showed this bacterium to be readily digested and assimilated, and capable of supporting larval growth (Chen et al. 2014).

Algae Many types of algae (single cells and small colonies across a range of taxa) are also important as food for many filter feeders. This is especially true for *Anopheles* mosquitoes, which feed primarily at the air–water interface in many permanent and semi-permanent aquatic habitats (Kaufman and Walker 2006; Tuno et al. 2018). Black fly larvae, mainly those below lake impoundments, harvest suspended algal cells at high rates in lotic habitats and grow better when they do (Wotton 1994). The same is true for net-spinning caddisflies exploiting lake outlet habitats (Wiggins 2005). It has been shown that black fly larvae can measurably reduce algae particles in stream water, but do not have the same effect on bacteria (Parkes et al. 2004). Like bacterial food sources, algal species vary greatly in their digestibility and food value to filter feeders to the extent that use of certain resistant algal types has been proposed as a means of larval mosquito control (Marten 1987, 2007; Garros et al. 2008a, b), and particular algal species have been identified as keys to mosquito production from larval habitats (Tuno et al. 2018).

Protozoans and Meiofauna Non-photosynthetic protists (e.g., ciliates, flagellates, amoebas) are thought to be important components of the food resources for many filter-feeding diptera, such as mosquitoes. Several studies have shown their decline after larval feeding, presumably reflecting ingestion and digestion (e.g., Kaufman et al. 2002; Walker et al. 2010). However, recent studies suggest that their consistent role as food sources for mosquitoes is questionable and that they may even compete with insect filter feeders for bacteria and micro-eukaryotes (Skiff and Yee 2015; Duguma et al. 2017). Similarly, meiofauna (e.g., rotifers, nematodes) may be nutritious food for many filter feeders, but their relative contribution to growth is unknown.

Fungi Fungi (usually yeasts and other Ascomycota) are generally less recognized as food items for filter feeders than they are for other functional feeding groups such as shredders (Cummins and Klug 1979; Cummins et al. 2008), but their presence in fragmented CPOM derived from leaf material and colonization of FPOM are potentially sources of valuable nutrition in many stream systems (Cummins and Klug 1979; Cummins et al. 2008; Webster et al. 2016). The value of fungi to mosquito nutrition has long been recognized and recent studies identify yeasts as an important food for complete development in larval mosquitoes (Díaz-Nieto et al. 2016; Souza et al. 2016; Steyn et al. 2016; Valzania et al. 2018).

Detritus and Other Material Although microorganisms are key components in the diets of most filter feeders, the bulk of ingested material is in the ill-defined detritus category. Origins of ingested detritus include senescent leaf material, fecal material from other arthropods, and carcasses of insects and arthropods. The relative importance of allochthonous vs. autochthonous detrital food sources in filter feeder diets will vary with habitat, but allochthonous inputs of terrestrial plant material are key to many stream systems and larval mosquito habitats (Cummins and Klug 1979; Cummins et al. 2008). Terrestrial leaf input into headwater stream systems is well documented for its effect on insect communities, and the cascade of FPOM and fecal material made available after initial processing of the leaf inputs is harvested by many groups of filter feeders (Wotton and Malmqvist 2001; Cummins et al. 2008; Bundschuh and McKie 2016). Fecal material produced by filter feeders is also a food source for members of the same functional group and sometimes the same species of filter feeder (Wotton et al. 1998). Even though the food value of fecal material to filter feeders is initially low due to prior digestion, colonization by microorganisms on the high surface area material greatly increases the nutritional content (Wotton and Malmqvist 2001). Other plant-derived allochthonous inputs include flower parts and pollen, which have been shown to contribute to the growth of mosquito larvae (Kaufman et al. 2010; Wondwosen et al. 2018). Pollen from grasses, maize, and sugar cane deposited on the surface of *Anopheles* habitats can be directly consumed and digested by the larvae (Asmare et al. 2017; Wondwosen et al. 2017, 2018), circumventing the usual plant detritus to microbial biomass transformation pathway usually necessitated by more refractory plant parts.

As mentioned above, insect and animal detritus inputs also can significantly increase filter feeder production. Some of these inputs are of terrestrial (allochthonous) origin, but others can be autochthonous (e.g., consumption of arthropod cadavers originating within the system—Tsurim and Silberbush 2016). The filter-feeding caddisfly larvae, *Brachycentrus*, has been observed feeding on moth larvae that had fallen into a stream (Ohkawa and Ito 2001), although the distinction between this being a detritus consuming process or predation event is vague. Aquatic insects in general are thought to benefit from animal carcass inputs (e.g., anadromous salmon—Claeson et al. 2006), but specific effects on filter feeders are not well known.

4.6 Trophic Importance

Filter-feeding insects are often the most abundant functional group within aquatic habitats. Black fly larvae and net-spinning caddisflies, for example, dominate the benthic invertebrate community in many stream and river sections, particularly those below lake outlets or impoundments (Huryn and Wallace 2000). Production estimates for the groups have sometimes approached 1000 g dry weight per m^2 in certain locations (Wotton 1988). In lentic systems, sediment dwelling filter feeders can also dominate the benthos, and large filter-feeding mayfly emergence swarms from parts of the Great Lakes and Mississippi basin (Brittain 1982) are even detectable by weather radar. Mosquito emergence from arctic habitats is also legendary, if not yet completely quantified in terms of biomass (Culler et al. 2018). Some work has been done to estimate production estimates for medically important mosquitoes, like *Aedes aegypti* (Focks and Chadee 1997; Morrison et al. 2006), including work in New Orleans, Louisiana, which found city blocks to produce 362–558 adult females per day (Focks et al. 1981).

Although biomass and production of filter feeders varies greatly within aquatic ecosystems, the group has important roles in transformation, retention, and export of organic matter from systems (Cummins and Klug 1979; Cummins et al. 2008). As discussed above, the filter-feeding group functions as primary and secondary consumers, detritivores, and even predators. They can also be classified as decomposers in that they process decaying organic matter, primarily in the FPOM category. Their consumption of detritus and microorganisms, and production and consumption of fecal material, contributes to nutrient spiraling within stream systems, and via adult emergence, they transfer organic carbon and other nutrients upstream and back to the terrestrial environment (Newbold et al. 1982; Wallace and Hutchens 2000; Cummins et al. 2008; Webster et al. 2016). Perhaps more importantly, filter feeders serve as prey items for a variety of aquatic predators including other aquatic insects and fish, linking microbial biomass, primary production, and detrital dynamics to higher trophic levels in the system (e.g., Curtis et al. 2018). Black fly larvae, for example, are often the dominant prey item for predaceous stoneflies (Malmqvist 1994). In some systems, such as phytotelmata habitats of mosquitoes, filter feeders themselves may represent the highest trophic level (Kitching 2001).

4.7 Future Directions

Like any subject related to our knowledge of insects, filter feeding is an underexplored area with vast gaps in data and understanding. This is particularly true with respect to quantifying the diversity of species that use this feeding mode, and the degree to which those taxa use filter feeding with respect to other forms of feeding. Most, if not all, filter-feeding aquatic insects are capable of obtaining food in other ways. For instance, mosquito larvae can switch between filtering in the water column and browsing surfaces given the concentration of food available in the environment (Merritt et al. 1992; Yee et al. 2004). Thus, although the adaptations for filter feeding, like net building or tunnel building in caddisflies, may appear to limit food choices, this flexibility in food gathering likely means that the contribution of these species to detrital processing and their trophic position are much more complicated than currently known.

Perhaps the two largest future challenges for filter-feeding aquatic taxa (and for those that study them) will be climate change and invasions by non-native species, with the former likely exacerbating the latter. Among filter-feeding taxa, mosquitoes contain the most invasive species, some of which are of immense importance due to their proclivity to spread human and animal disease. *Aedes aegypti* (yellow fever mosquito) and *Aedes albopictus* (Asian tiger mosquito) are the best studied of these invasives, as they are not only found throughout the world due to the actions of human actions but also are important as vectors for several major arboviruses (dengue, chikungunya, Zika) (Lounibos 2002). Other species, like *Culex quinquefasciatus/pipiens*, is also found distributed across the globe, and is a main vector of West Nile virus (Lounibos 2002). When any of these species comes in contact with native fauna, it has the potential to disrupt ecological interactions, detrital processing, and disease dynamics. Invasive species may also affect taxa important as filter feeding in aquatic systems. For example, invasive dreissenid mussels, which have invaded many lentic water ways throughout North America, can negatively affect resident mayfly larvae (*Hexagenia* sp.) via the bioturbation activities of the mussels (Osterling et al. 2007).

Future climate change, especially increasing temperatures, is going to have significant effects on ectotherms, including insects (Deutsch et al. 2008). These effects include modifying distributions and influencing population sizes via alternations in thermal limits and habitat suitability. For instance, Hering et al. (2009) investigated the potential for a changing climate to affect 1134 species and subspecies of Trichoptera and found that many endemic species were likely sensitive to a changing climate; however, this study did not specifically separate species by feeding type. Although investigations of climate change have been conducted for steam insects (Bonada et al. 2007; Durance and Ormerod 2007), there are almost no investigations of filter-feeding insects specifically, or how filter feeders as a group may be affected by increasing temperatures. Understanding how filter-feeding insects will be affected by changes in climate will be important, given their role in processing detritus as well as their importance as prey for many other insect and non-insect predators alike.

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