Chapter 21

Macroinvertebrate Drift, Adult Insect Emergence and Oviposition

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21.1 INTRODUCTION

Aquatic invertebrates exhibit movements and behaviors that are ecologically important, not only because these processes are critical to the life cycles and population dynamics of individual species, but because they mediate key roles played by such invertebrates in the intricate web of life associated with streams, rivers, and their surrounding watersheds. For instance, although most stream invertebrates are benthic, they can also be found drifting with the current. This process of drift is essential to dispersal and colonization that help maintain populations of these animals (Brittain and Eikeland, 1988; Hart and Finelli, 1999; Downes and Lancaster, 2010). Similarly, of the many stream invertebrates that are insects, nearly all transition to becoming winged, air-breathing adults via emergence and, after a period in this form, oviposit (i.e., lay their eggs) back in streams. These are key stages in their life cycle (Huryn and Wallace, 2000; Merritt et al., 2008), but also processes by which they become vulnerable to aquatic predators like fishes and are linked to terrestrial food webs, often serving as prey for animals like birds, bats, spiders and lizards (Baxter et al., 2005; Sabo and Hoekman, 2015). Therefore, stream ecologists study these processes of drift, emergence, and oviposition to address questions at scales from individual invertebrates and populations of a species, to food webs and ecosystem processes in streams, rivers and their surrounding landscapes. Increasingly, conditions necessary to support insects not just at the larval stage, but throughout their life cycles (e.g., egg, larvae, pupae, adult), are understood to be important to species’ management and recovery efforts (Peckarsky et al., 2000). These other life stages are traditionally understudied in stream ecology, but are nonetheless critical to the persistence of aquatic invertebrate populations.

This chapter introduces key concepts and sampling methods concerning drift of benthic stream invertebrates, and the emergence, and oviposition behavior of lotic insects. In the previous edition of this text, Smock (2006) outlined methods associated with drift and emergence as a means of dispersal, and with an emphasis on techniques traditionally used in the context of invertebrate life history and population studies. Naturally, these methods, and the overarching topic of dispersal, continue to be of importance to the practicing stream ecologist. Here, however, we focus on these processes to include description of the growing array of methods for their quantification being applied in food web and ecosystem studies. Finally, we extend our treatment to encompass oviposition, a phenomenon closely linked to both emergence and drift, the details of which are receiving fresh attention as new studies (e.g., Lancaster et al., 2010a; Encalada and Peckarsky, 2012) have raised awareness of its importance to the ecology of stream insects and, with its potential consequence for the communities of organisms to whom they are linked (Kennedy et al., 2016).

21.1.1 Drift of Stream Invertebrates

Although most invertebrates that occur in streams and rivers are benthic, a net placed in the water column often will collect many individuals. These organisms are drifting, an activity whereby they enter the water column and are transported...
downstream by the current. Entry into the water column by invertebrates can be broadly classified as accidental (passive) or behavioral (active). Drift is one of the most important mechanisms for the dispersal to and colonization of downstream habitats by lotic invertebrates, and is also a stage at which invertebrates are particularly vulnerable as prey to fish. Because drift is such a fundamental process in streams and rivers, it is the most widely studied movement of benthic invertebrates (see reviews and syntheses by Waters, 1972; Müller, 1974; Brittain and Eikeland, 1988; Rader, 1997; Allan and Castillo, 2007; Naman et al., 2016).

Early observations of diel periodicity in drift concentrations (r m⁻³; sometimes called drift density) motivated decades of research by stream ecologists into drift dynamics. These studies demonstrated that the majority of species actively drift in maximum numbers sometime during the night. Changes in ambient light intensity, although not the ultimate cause for active drift, serve as the trigger or proximate cause for this behavioral drift (Naman et al., 2016). Factors that can influence active drift include dispersal to more favorable habitats (Walton et al., 1977; Hershey et al., 1993; Koetsier et al., 1996; Siler et al., 2001), escape from predators and competitive interactions (Flecker, 1992; McIntosh et al., 2002), and movements associated with key life-history events such as egg-hatching, pupation, and emergence (Otto, 1976; Krueger and Cook, 1981; Ernst and Stewart, 1985).

Passive drift occurs when invertebrates are accidentally dislodged from the benthos. Changes in discharge are an important variable that can influence the rate of passive drift (Gibbins et al., 2007a; Miller and Judson, 2014; Kennedy et al., 2014). Catastrophic drift represents an extreme case of passive drift and occurs when large numbers of invertebrates are physically removed from the channel bed and a high proportion of the available invertebrates become entrained in the drift. If the conditions for initiating catastrophic drift persist for prolonged periods of time, benthic populations can be depleted, reducing benthic invertebrate populations over long time-scales (i.e., months). The lowest threshold for catastrophic drift occurs when shear stress is sufficient to entrain sand and “sand blast” invertebrates off the bed. At higher levels of shear stress, large numbers of invertebrates may be physically removed from the bed, and at even higher shear stress the cobble substrates on which invertebrates live will be mobilized. Thus, catastrophic invertebrate drift can be initiated at discharges that may or may not drive major changes in streambed or channel form (Gibbins, 2007a,b; Naman et al., 2016). Chemical pollution and abrupt changes in water quality have also been shown to precipitate catastrophic drift (Brittain and Eikeland, 1988; Wallace et al., 1989).

While invertebrates stand to benefit from actively drifting, this movement also poses significant costs, particularly increased risk of predation by drift-feeding fish. Minimizing predation risk by drift-feeding fish underlies the diel periodicity in active drift exhibited by invertebrates (Flecker, 1992). For instance, the propensity of invertebrates to exhibit nocturnal drift increases as the risk of predation by the visual-feeding fish increases, whereas drift is usually aperiodic in fishless streams (Flecker, 1992; Forrester, 1994; March et al., 1998). Because drift-feeding fish are visual feeders, their ability to detect and capture prey increases with the size of invertebrates. Thus, predation risk also can affect the size distribution of drifting invertebrates, with larger individuals that are more vulnerable to predation being more prone to drift at night (Allan, 1978, 1984).

Invertebrate drift can constitute the primary prey source for a diverse guild of fishes (Grossman, 2014). Thus, in many contexts, drift availability is a primary determinant of the capacity of streams and habitats to support fish populations (Rosenfeld et al., 2014). For instance, field studies have directly linked the magnitude of drift flux to fish abundance, growth, and survival (Fausch et al., 1991; Keeley, 2001; Rosenfeld et al., 2005; Naman et al., 2016). Linked drift-foraging bioenergetics models explicitly consider river hydraulics, invertebrate drift biomass, and the mechanics of drift-feeding to describe foraging dynamics and how food availability translates into fish growth (Hughes and Dill, 1990; Hayes et al., 2000). These models are increasingly being used to estimate the capacity for streams to support drift-feeding fishes (Rosenfeld et al., 2014). These models can also be used to evaluate how fish growth rates will be influenced by alternative prey and temperature scenarios that would be difficult to test in a field setting (Dodrill et al., 2016). Accurate estimates of drift biomass are a critical input parameter of these models.

Methods are provided in this chapter (Fig. 21.1) to: (1) quantify the rate of net clogging, which informs the design of drift studies; (2) quantify variation in drift among habitat types in wadeable streams; (3) quantify variation in drift between day and night; and (4) quantify the vertical distribution of drift in large rivers.

### 21.1.2 Emergence of Adult Stream Insects

Sampling of stream insects has historically focused on their immature stages (e.g., see Chapter 20); however, nearly all of these insects metamorphose into adults that emerge, mate, and oviposit, so methods for quantifying emergence and occurrence of adults in terrestrial habitats are important. Studies of insect emergence provide not only an understanding of insect life cycles, dispersal, colonization, and population ecology, but also food web and ecosystem processes that link water and land. Further, measures of emergence may reveal responses of insects to stressors (e.g., pollutants) or community interactions.
interactions different from those detected through measures of benthic larvae alone (e.g., Walters et al., 2008; Schmidt et al., 2013; Wesner, 2016). In addition, regardless of the ecological questions under investigation, collection of adults can be necessary to obtain species-level identifications, owing to the incomplete taxonomy of immature forms for many groups of aquatic insects.

Emergence is a process that can be highly heterogeneous in time, which presents challenges to its measurement. In temperate zones, emergence of individual taxa is typically seasonal and may be highly synchronous over a few days to a few months (Sweeney and Vannote, 1982), whereas it can be more continuous in tropical regions (Corbet, 1964) or may exhibit variation with wetdry seasons (Suhaila et al., 2012). Emergence by the overall assemblage of insects in temperate streams often peaks in early summer and declines sharply by late summer (Sweeney and Vannote, 1982; Malison and Baxter, 2010), but can also provide a low level of flux to riparian zones during autumn through early spring (Jackson and

**FIGURE 21.1** Approaches to sampling macroinvertebrate drift. (A) Traditional rectangular drift net equipped with recording flow meter. The second flow meter outside the net is used to record ambient stream water velocity, needed for estimating filtration efficiency of drift nets (see Basic Method 1). (B) Large river invertebrate drift-sampling equipment. The whole apparatus is raised and lowered through the water column using a hand-power winch and chain attached to the end of the cable, and a lead weight attached to the bottom of the chain keeps the circular plankton net from moving downstream. This setup is from filtration-efficiency experiments, and the black cord running from the flow meters to the boat transmits velocity readings to on-board computers for visualization; during routine drift sampling, stand-alone flow meters are used. (C) Preparing for drift sampling in the Colorado River, Grand Canyon, AZ, USA. The hand-powered winch (A-reel) is mounted to a chest-height platform, the winch cable is extended out beyond the bow of the boat by means of a crane and pulley and net is lowered to desired depth using the depth gauge on the left side of the winch. (D) Quantifying invertebrate drift on the Green River downstream of Flaming Gorge Dam, Uth, USA.
Fisher, 1986; Nakano and Murakami, 2001), or may depart from these patterns altogether as has been observed in some Mediterranean climate streams (Rundio and Lindley, 2012). Moreover, diel patterns in emergence and flight behavior of adults occur (e.g., Jackson, 1988), which can influence effectiveness of the trapping methods. Large pulses of emergence can be easily missed, so estimating total emergence flux, which is often needed for food web or ecosystem studies (e.g., as index of secondary production; see Chapter 25), requires frequent and prolonged sampling (e.g., Jackson and Fisher, 1986; Nakano and Murakami, 2001; Malison and Baxter, 2010; Rundio and Lindley, 2012; Kennedy et al., 2016).

The flux of emergent insects also varies spatially, with attendant implications for sampling. Spatial patterns in emergence may be related to river and riparian habitat characteristics, as well as distribution of larval stages and behavior during metamorphosis. For instance, emergence flux may be greater from habitats that retain aquatic insects emerging through the water column (e.g., pools; Iwata, 2007), or provide insects predation refuge (e.g., floating algal mats; Power et al., 2004), and could be amplified by habitat complexity such as sinuosity (Iwata et al., 2003), thermal heterogeneity (Uno, 2016) or increased surface area of the land—water interface (Sabo and Hagen, 2012). Emergence flux can even vary in relation to the availability and quality of oviposition substrates available during the egg-laying in the prior generation (Encalada and Peckarsky, 2012; Kennedy et al., 2016). Another source of spatial variation in emergence arises from the different approaches that taxa use in their transition to land. For instance, most Diptera and Trichoptera actually emerge through the water column, while taxa such as Plecoptera and some Ephemeroptera typically emerge from stream banks (Merritt et al., 2008). Thus, different methods of sampling may capture adults of different groups with varying efficiency (Malison et al., 2010).

The total flux of emergence from a given habitat or stream in turn influences the magnitude of flux into adjacent terrestrial habitats. Following emergence, the number of adult insects penetrating riparian zones typically declines with distance from the stream edge (Jackson and Resh, 1989; Sanzone et al., 2003; Power et al., 2004; Briers et al., 2005). A recent meta-analysis (Muehlbauer et al., 2014) showed this pattern followed a negative power function, though the relationship was mediated by stream size and 10% of flux was predicted to occur >500 m from the water’s edge, suggesting dispersal of some adults may extend the ecological “signature” of streams throughout watersheds, particularly when the complexity and extent of stream networks are considered (Sabo and Hagen, 2012).

Insect traits such as dispersal behavior or preferences for oviposition sites, along with riparian conditions, may also influence the distribution of postemergent adults, with additional implications for sampling methods. Many adult insects undertake dispersal flights that can result in mating and/or laying of eggs far from the site of emergence, facilitating colonization of new habitats, genetically linking populations (e.g., Kovats et al., 1996; Turner and Williams, 2000; Winterbourn and Crowe, 2001; Macneale et al., 2005), and connecting food webs in mainstem rivers and tributaries (Uno and Power, 2015). Indeed, a “colonization cycle” has been hypothesized, the central component of which is that the flight of females prior to ovipositing should be primarily directed upstream, thereby compensating for the predominately downstream drift of the immature individuals living in the water (Müller, 1982). The results from field studies designed to test this colonization cycle, however, are equivocal (Hershey et al., 1993; Jones and Resh, 1988; Winterbourn and Crowe, 2001; Macneale et al., 2004), with theoretical studies having resolved this “drift paradox” by demonstrating that random benthic dispersal (i.e., upstream crawling), high benthic production, and density-dependent survival are sufficient to compensate for downstream drift and allow for benthic population persistence in lotic environments (Anholt, 1995; Humphries and Ruxton, 2002). Dispersal distances may also be taxon-specific: Ephemeroptera tend to remain very near streams whereas Trichoptera and Chironomidae often travel farther inland, for example (Muehlbauer et al., 2014). Moreover, adult insect behavior and distribution may be mediated by riparian habitat characteristics (e.g., vegetation, microclimate; Collier and Smith, 2000; Briers et al., 2003; Petersen et al., 2004) and differences between the sexes (e.g., Petersen et al., 1999). Any of these factors may require consideration when choosing the type of trap or net, in sampling design, and in interpretation of study findings.

Methods are provided in this chapter to introduce methodology for sampling emerging adults and estimating emergence flux (Fig. 21.2) to (1) examine the differences in emergence that occur both spatially and temporally within a stream, (2) quantify dispersal distances of adult insects laterally from a stream, and (3) quantify emergence or postemergent adults in order to compare different habitats in terms of insect prey availability to terrestrial insectivores.

### 21.1.3 Oviposition by Stream Insects

Much like emergence, oviposition by stream insects is understudied relative to larval life stages. This is likely due predominately to practical considerations: insect oviposition often occurs only during specific, narrow windows of time within a day and within a year, and the time insects spend in the egg stage is commonly short compared to other life stages (Jackson and Sweeney, 1995). However, the egg-life stage is just as important to the survival of insects as any other stage,
and consideration of oviposition and egg development can reveal important life history bottlenecks that influence the presence and persistence of insect groups within a habitat or ecosystem (Kennedy et al., 2016).

Insect oviposition is necessarily tied to the presence of emergent adults, which, as noted earlier, are often present only for short periods of time (Sweeney and Vannote, 1982). Because the egg-laying stage occupies just a portion of this already limited amount of time available to observe emergent adults, studying the oviposition can be challenging. For taxa such as many Ephemeroptera and Chironomidae that can be particularly short-lived, mating swarms of adults can be a visual cue that oviposition is about to commence (Sweeney and Vannote, 1982; Gray, 1993). Additionally, emergent adults tend to be most active in crepuscular periods when the visual contrast between water and land surfaces is greatest (Bernáth et al., 2004). For a given taxon, the presence of eggs or spent adults in or around the water surface provides another line of evidence that oviposition is ongoing or recently concluded, which allows inference about the timing, seasonality, and duration of egg-laying.

Stream insects exhibit a range of oviposition behaviors, from generalized behaviors such as broad-cast spawning on the water surface, to more specialized behaviors such as cementing eggs on emergent rocks or even females ovipositing fertilized eggs onto the back of the male with whom they recently copulated (Vieira et al., 2006). However, little is known about oviposition for most stream insect species, with a recent synoptic database of traits for >14,000 North American aquatic invertebrates only yielding a description of oviposition behaviors for 957 taxa (Vieira et al., 2006). Among mayflies, for instance, Encalada and Peckarsky (2007) identified five distinctive behaviors for 17 mayfly species in a single Rocky Mountain watershed, ranging from dropping eggs into the water from midair, to crawling down

![FIGURE 21.2 Approaches to measuring emergence of adult stream insects, including a floating trap (A), a trap for capturing taxa that emerge along stream banks (B), and methods for sampling postemergent insects in the terrestrial environment, including a sticky trap (C) and a light trap (D). Photo credits: (A & B) C.V. Baxter; (C) E. Kortenhoeven; (D) D. Herasimtschuk.]

emergent rocks and depositing eggs under the water surface. At another extreme, at least one mayfly species has been observed to release parthenogenic eggs via bursting of the abdomen while still in the subimaginal stage (Funk et al., 2008). In some cases, eggs are not even laid in water: many blackflies (Simuliidae), dragonflies (Odonata), and other taxa lay eggs either on or within vegetation along the shoreline (Adler et al., 2004; Corbet, 1999), whereas the males of many giant water bug (Belostomatidae) species rear eggs on their backs (Smith, 1976). In general, however, results from past studies indicate that egg masses are disproportionately found near the stream margins and are laid on emergent mineral or wood substrates in moderate water velocities (Peckarsky et al., 2000; Hoffmann and Resh, 2003; Lancaster et al., 2010a,b). Rock size and flow velocity were the only consistently important physical variables affecting the distribution of egg masses for 17 taxa considered in one study, for instance (Reich and Downes, 2003), and population densities of both Baetis mayflies and Ecnomus caddisflies have been affected by experimental manipulations of emergent rock and log substrates (Encalada and Peckarsky, 2012; Macqueen and Downes, 2015). Indeed, a synthesis of oviposition behaviors for those species where behavior is known indicates that most cement eggs to underwater substrates (Statzner and Beche, 2010).

As with oviposition behaviors, the characteristics of insect eggs are generally not well-described for most lotic insect species (Vieira et al., 2006). Nonetheless, for those taxa that have been studied, there is impressive variability in egg characteristics (Fig. 21.3). Egg fecundity, for instance, can vary across orders of magnitude, from eggs distributed by broadcast spawners as singlets, to egg masses in the thousands that may represent contributions from several females (e.g., Hoffman and Resh, 2003). Similarly, some species diapause for months while in the egg stage, whereas others hatch instantly upon being laid or are even ovoviviparous (e.g., some Baetidae and Capniidae, Lancaster and Downes, 2013). In general, egg masses tend to be on the scale of a few millimeters in size, and may be gelatinous and bulbous, or arranged in a flat mat or a stringy line (Fig. 21.3). This dimorphism may confer fitness benefits to species adapted for certain habitats and oviposition sites; the flat arrangement of Hydropsyche caddisfly eggs may allow them to persist in fast-water habitats, for example, whereas the thickly gelatinous egg masses laid by Ethochorema caddisflies may render them less vulnerable to predation (Bovill et al., 2015). The shape and other characteristics of these egg masses vary within insect families or even genera (Lancaster and Downes, 2013); however, making species-specific egg mass identification possible.

Methods are provided in this chapter to: (1) observe insect oviposition and search for insect eggs; (2) quantify egg densities and oviposition-site selection; and (3) rear insect eggs and quantify hatch success.

21.2 GENERAL DESIGN

21.2.1 Site Selection

Naturally, the selection of sites for conducting studies of drift, emergence, or oviposition will depend upon the questions under investigation, and the choice of site can have important consequences for the types of methods that are most appropriate or the adaptations to techniques that may be required. Below we provide some guidance along these lines, but there is no single recipe for selecting the study sites. With respect to drift, for instance, investigations into its diel periodicity might focus on collecting replicate samples in habitat types where drift concentrations are high (e.g., downstream of riffles), investigations into invertebrate population dynamics or habitat use by fishes might require drift measurements from a range of habitats within a stream reach, whereas investigations into the role of benthic density in controlling drift might be done across habitats and among streams. However, there are limits to the types of habitats where drift can be sampled. Specifically, drift nets become difficult to maintain or inefficient for measuring drift accurately under conditions of very fast (>1–2 m/s) or very slow water velocity (<0.1 m/s). Nets can be positioned at any location within the channel, but placement in midstream at the downstream end of a riffle usually is most productive in terms of the number of species and individuals captured. Drift-sampling methods for wadeable streams are well established, and the vast majority of drift studies have been conducted in these settings. Drift can also easily be sampled from a boat in large rivers by adapting plankton sampling techniques originally developed by oceanographers (Kennedy et al., 2014). Drift sampling in large rivers is often easier and safer than traditional benthic invertebrate sampling, which are both important considerations in any study design. Further, because drift samples are spatially integrated, the variance in individual drift samples tends to be much lower than for benthic samples (Allan and Russek, 1985). Thus, regular measurement of invertebrate drift can be a useful and low-cost alternative or complement to traditional benthic sampling, such as in long-term invertebrate monitoring programs whose purpose is to inform fish population trends.

The best tools to measure adult insect emergence and oviposition also depend upon study questions and context. For instance, the choice of emergence trap style, positioning (e.g., pools, riffles, bankside) within a stream reach (or reaches),
FIGURE 21.3  Morphological diversity of aquatic macroinvertebrate egg masses. Included are photos of (A) *Baetis* spp., (B) *Simulium vittatum*, (C) *Brachycentrus occidentalis*, (D) *Hydropsyche occidentalis*, and (E & F) Chironomidae. Photos credit: M. Schroer.
Drift: Drift is easily sampled in most streams by using drift nets set in the water for short amounts of time (Fig. 21.1). Various factors must be considered when sampling drift, including the mesh size and length of the net, length of the sampling period, the number of nets needed for adequate replication, sampling location, and the manner of data analysis and presentation (Brittain and Eikeland, 1988).

The mesh size of the nets will depend on the objectives of the study, but the typical mesh size used is 200–300 μm. Nets with a larger mesh size will not retain small individuals that are abundant in drift such as Chironomidae, resulting in inaccurate conclusions regarding the species composition and magnitude of drift. Nets with a smaller mesh size can be used, for example with a 40–60-μm mesh to capture meiofauna in the samples, but these nets clog rapidly and can only be deployed for short amounts of time during quantitative investigations of the drift.

Comparisons of the species composition, drift concentrations, drift biomass (mg/m³), and mean size of drifting individuals can be made between habitat units within a stream, across a range of discharges in a stream, across different streams, or across time periods (e.g., day vs. night, seasonally). Most investigations of invertebrate drift revolve around computing drift concentration (# m⁻³), which requires knowing the number of invertebrates captured by the nets per unit volume of water filtered by the nets (Naman et al., 2016). Because drift concentrations are often small (i.e., <1 m⁻³), this quantity is often expressed as numbers of invertebrates drifting per 100 m³ of water:

\[
\text{Drift Concentration} = \frac{[(N)(100)]}{[(t)(A)(V)]}
\]

where \(N\) represents number of invertebrates in a sample; \(t\), time that the net was in the stream (s); \(A\), the area of the net mouth that is submerged (m²); and \(V\), mean water velocity at the net mouth (m/s).

As drift nets become clogged with debris, the velocity of water entering the net decreases. Many investigators attempt to account for this by measuring the water velocity in the net at the start and end of the deployment and then estimating the average water velocity over the duration of the deployment. However, decreases in velocity associated with clogging are nonlinear and typically follow a logistic pattern, where velocity is high and constant at the start of the deployment until nets become appreciably clogged and then velocity drops rapidly and approaches zero (Muehlbauer et al., 2016). Thus, spot measurements of velocity at the start and end of the deployment are insufficient, because they do not account for the nonlinear decreases in velocity. Although sophisticated procedures have been developed for estimating the volume sampled by clogged nets (e.g., Faulkner and Copp, 2001), we recommend instead that drift-sampling regimens be designed to avoid net clogging altogether because clogged nets and long deployment times introduce several other sources of sampling error into drift-concentration estimates.

A major source of sampling error arises from clogged drift nets because they do not actually sample a representative parcel of water (Smith et al., 1968; McQueen and Yan, 1993). A clogged drift net actually blocks the flow of the stream and forces water to flow around this barrier. However, suspended particles may not flow around the net to the same degree...
as the water if their density is greater than water. That is, the inertia of suspended particles such as invertebrates may carry them into a clogged net to a greater degree than the water that is flowing around the net (Sabol and Topping, 2013). Similarly, if the density of a suspended particle is less than water, these particles may avoid the net to a greater degree than the water. Back pressure in a clogged net can also cause particles that have been captured by the net to be flushed out over the course of the deployment (Muehlbauer et al., 2016).

Filtration efficiency, or the ratio of velocity into the net relative to ambient stream water velocity, is a metric of net performance (Tranter and Smith, 1968; McQueen and Yan, 1993). Ideally, filtration efficiency of drift nets should be ~1, indicating that the sampler is isokinetic and flow conditions inside the net are representative of ambient conditions outside the net. At a minimum, filtration efficiency should not be allowed to drop below 0.85 during drift sampling (Smith et al., 1968; Muehlbauer et al., 2016). In our studies of invertebrate drift in rivers of the Western United States, we have found that 250-μm nets will only maintain high filtration efficiency for a maximum of 10 min (Kennedy et al., 2014). Thus, our drift-sampling collections are limited to 5 min, and by using a net with a large opening (i.e., 50 cm diameter) we are still able to collect reasonably large samples (i.e., >30 m³). If short-duration drift samples do not adequately capture large taxa at a given site, we recommend that multiple short duration samples that maintain high efficiency be aggregated in the field, rather than extending the duration of individual drift samples beyond acceptable levels of filtration efficiency (i.e., <0.85). Below, we describe an exercise that demonstrates how filtration efficiency of nets declines over time that can be used to identify maximum deployment times for drift studies (Basic Method 1).

Another source of sampling error that can be introduced when drift nets are deployed for a long period of time occurs during laboratory processing of samples. Specifically, long drift net collections will collect large numbers of invertebrates, which often necessitates subsampling or sample splitting procedures. Although numerous tools and statistical approaches exist for minimizing the error that is introduced with sample splitting in the laboratory (see Chapter 15), these approaches necessarily introduce another source of sampling error that does not exist when an entire drift sample is processed for invertebrates.

The length of the net is an important consideration in drift studies, because long nets have a greater surface area for filtering water and will clog at a slower rate than a short net. The length of nets that are used for sampling drift in rivers is often reported as the ratio of length:opening (e.g., a 5:1 net is five times as long as the net opening). Most nets are 3:1 but custom lengths are also available. As the net length increases, however, deploying, retrieving, and washing nets down becomes more difficult. In our experience a 5:1 net strikes a good balance and allows for reasonably long deployment times under most conditions while not being overly cumbersome to retrieve.

Accurate estimates of the volume of water sampled by nets are critical in quantitative studies of the drift. The best approach for estimating water volume sampled by a drift net involves mounting a small, inexpensive flow meter in the mouth of each net (e.g., General Oceanics model 2030R; Fig. 21.1A,B). We also recommend that ambient velocity be measured during each drift net deployment so filtration efficiency of the net can be estimated on-site. This allows samples to be discarded and new, shorter duration samples to be immediately collected if filtration efficiency is observed to have dropped below acceptable levels (i.e., <0.85). Alternatively, if nets are deployed for short amounts of time, and prior investigations have demonstrated deployment times are sufficiently short so as to avoid net clogging (Basic Method 1), then spot measurements of water velocity using a portable meter (e.g., Marsh-McBirney, Son-Tek) at the start and end of drift sampling will suffice. Identifying maximum deployment times for drift nets in a particular stream is best done using portable flow meters that will continuously record and log water velocity readings, so filtration efficiency curves can be developed.

Early studies of diel periodicity in invertebrate drift often involved continuous drift sampling over an entire 24-h cycle, and numerous drift studies continue to use this sampling design. Although this type of exhaustive sampling design is required for investigations into diel drift periodicity, there are many applications where this approach may not be necessary. For instance, drift-feeding fish are visual feeders, and their ability to capture prey declines at night. Thus, daytime drift may accurately represent prey availability to drift-feeding fish, and including night-time samples that have elevated drift concentrations owing to behavioral drift may actually inflate estimates of prey availability (Allan and Russek, 1985). Further, Allan and Russek (1985) demonstrated that in some settings a single night-time drift collection shortly after dark was representative of total night-time drift. Moreover, even the most dedicated stream ecologist is prone to errors when sleep deprived, and in our experience this type of nonstop night work inevitably leads to poor quality samples (i.e., filtration efficiency <0.85, errors on field notes, etc.) that have to be discarded. Thus, we recommend that practicing stream ecologists first identify whether 24-h drift sampling is critical to their specific research question before embarking on a continuous 24-h sampling design. In many cases, drift research questions can be addressed with short duration, high quality samples collected during daytime hours that are complemented by more limited and strategic collections of night-time drift samples.
21.2.3 General Procedures—Emergence and Postemergent Insects

Traps and nets: There are several techniques that may be used to collect and quantify adult insects as they emerge from a stream, or insects that have already emerged and are occupying nearby riparian or terrestrial habitats. With respect to the former, a number of different types of emergence traps have been developed; their designs, applicability for use under different sampling conditions, and the factors affecting their performance are discussed in detail elsewhere (e.g., Davies, 1984; Malison et al., 2010). A common type of emergence trap is pictured in Fig. 21.2 (see Malison et al., 2010 for details of trap construction). Measurement of emergence as a part of food web and ecosystem studies has placed new demands on the techniques used. For example, trap designs have been adjusted (e.g., made more lightweight and inexpensive) to facilitate studies in which large numbers of measurements must be made simultaneously. Traps typically consist of a triangle- or pyramid-shaped wooden or plastic frame, enclosing an area of 0.5 m², for instance constructed with sheets of acetate coated with sticky resin (e.g., pools vs. riffles) may differ in rates of emergence, and composition of insects emerging from the water column is likely to differ from that emerging from the stream bank. Owing to the latter, investigators have adapted the floating trap design to capture bank-emerging taxa (Fig. 21.2B)—for instance, by including overhanging netting on three sides that can be buried into the bank substrate to prevent insects from escaping and potential predators from entering the trap (Paetzold et al., 2006; Malison et al., 2010). In the case of large-bodied stoneflies that emerge from riverbanks, estimates of emergence flux may even be obtained via visual counts of their exuviae (D. Walters, personal communication). The deployment duration for traps prior to sample collection will depend upon the questions but is typically not longer than 4–5 days to avoid loss of insects via mortality. In addition to the use of a bottle, insects may be removed from a trap using an aspirator or small vacuum (e.g., BioQuip Hand-Held Vac/Aspirator, BioQuip Products, Rancho Domingues, CA, USA). Below we describe an exercise (Basic Method 3) to quantify and compare emergence flux and composition from different habitats within a stream (i.e., pool, riffle, mid-channel, and bank).

Postemergent adult aquatic insects found in riparian or nearby terrestrial habitats are commonly sampled using sticky traps, light traps, funnel nets or a variety of other terrestrial arthropod sampling tools (pitfall, Malaise traps, beating nets, etc.). Sticky traps or light traps (Fig. 21.2C,D) seem best to determine the abundance and species composition of active adults or the dispersal distances traveled laterally from the stream channel by individuals (Collier and Smith, 1995; Kovats et al., 1996), whereas funnel nets (Turner and Williams, 2000) and flat-design sticky traps (Bird and Hynes, 1981; Smith et al., 2014) may be used to quantify the direction of adult flights, such as up- and downstreams (but see Macneale et al., 2004). Sticky traps collect in a more passive fashion than do light traps, which in some cases may be advantageous. They can also be left unattended for several weeks, allowing time-integrated estimates of aerial insect abundance. Sticky traps are often cylindrical (typically 0.1–0.2 m²), for instance constructed with sheets of acetate coated with sticky resin (e.g., Tanglefoot, The Tanglefoot Company, Grand Rapids, MI, USA) and suspended (from poles or sometimes vegetation) 1–2 m above the ground. However, height above the ground may influence the composition of aerial insects captured (Jackson and Resh, 1989; Smith et al., 2016), and, indeed, there are likely important patterns in insect distribution within the “airscape,” which have yet to be investigated (Gurnell et al., 2016). Another sticky trap design, described by Smith et al. (2014), uses 150-mm Petri dishes coated with resin, suspended on poles. This trap, which may be used to quantify flight direction, can be coated with resin prior to transport to the field with the lid on, which also facilitates efficient retrieval of the trap (cylindrical traps must be covered upon retrieval, often with a sheet of acetate or cellophane).
Disadvantages to using sticky traps include the negative effect of the resin on insect specimens (identification is typically done with the trap under magnification, rather than by removing insects from the trap), the potential for accumulation of insects to influence trap efficiency (Muirhead-Thompson, 2012), and the exposure of trapped insects to weather and even predators (e.g., birds, bears) that may cause specimen deterioration.

Light traps are an active-sampling tool used to collect and characterize postemergent adult insects; they range from towers with automated collection mechanisms to simple, battery-operated lamps set in close proximity to a killing agent (e.g., a bottle or tray of ethanol; Fig. 21.2D). Benefits to their use include rapid collection of a “snapshot” of insect occurrence, often of a large number of individuals, good specimen preservation and the fact that, owing to insect attraction to the light, a single trap provides a sample integrated across a large area. On the other hand, the latter may be a disadvantage if more absolute estimates of insect occurrence are desired. Light traps capture species that are nocturnally active, and differences in light attraction among taxa also introduce bias (Basset et al., 1997; Yi et al., 2012; Muirhead-Thompson, 2012). Investigations of stream-riparian food webs linked by emergent aquatic insects frequently employ sticky traps or light traps to estimate indices of emergence flux and/or availability of prey for terrestrial insectivores. However, the various forms of bias described above require consideration in such studies, and more direct measurements of emergence may be required if the aim is to generate absolute estimates of this flux from particular habitats. Below we describe an exercise (Basic Method 4) employing sticky traps to quantify dispersal distances of adult aquatic insects laterally from a stream. We also outline procedures (Advanced Method 3) by which measures of emergence or postemergent insects may be used to compare the availability of emergent insects as potential prey for terrestrial insectivores among streams.

### 21.2.4 General Procedures—Oviposition by Stream Insects

Aquatic insect oviposition methods can be generally categorized in four groups: (1) methods for quantifying the presence of egg-laying females; (2) methods for quantifying the contribution of egg-laying females to predator and detrital food webs; (3) observations of insect oviposition behaviors, and (4) methods for recording the distribution of eggs. Studies focused on the presence of food web contributions of gravid females generally utilize very similar procedures to the emergent adult and drift methods, often with modifications for capturing adults entering the water from the air (e.g., air-facing sticky traps, Encalada and Peckarsky, 2007). With some modification, sticky traps such as those described earlier in this chapter (e.g., Smith et al., 2014), stream exclosures (e.g., Nakano et al., 1999), or drift nets deployed during specific times (e.g., Encalada and Peckarsky, 2007) could all conceivably be used toward these purposes (see Basic Methods 2–3).

Approaches for understanding the site selection process, behaviors, and related environmental cues for oviposition can range from relatively simple field observations to rigorous protocols. A great deal can be learned about insect oviposition by observing the behaviors of adult insects and such approaches are highly recommended, especially as a pilot for more involved field studies. Field observations do not require much sampling gear beyond a pair of binoculars and some sample vials to collect oviposited eggs in the event larvae or adults are needed for identification (see Basic Method 5).

Beyond field observations, the methods for studying oviposition behaviors or the distribution of eggs are similar to other procedures designed to quantify habitat site selection (Garshelis, 2000). Common approaches quantify both the available and utilized habitat to determine the environmental factors associated with the presence or absence of a species. This often requires consideration of species-specific habitat needs in the context of the hierarchical arrangement of stream and river systems: river segments, reaches, channel units, and microhabitats (see Chapter 2). Additionally, given the patchy distribution of egg masses on substrates that are not present in equal proportions from segment-to-segment or reach-to-reach, structured, nonrandom sampling of commonly preferred microhabitats (e.g., emergent rocks or vegetation) may be required for adequate egg detection (e.g., Encalada and Peckarsky, 2006). Alternatively, a two-stage sampling procedure that characterizes both habitat availability and utilization can be employed in order to quantify egg mass densities throughout a reach (Reich and Downes, 2003). Regardless, these methods are predicated on the ability to identify egg masses as belonging to a given species. Because this information is not readily available for many aquatic insects, the rearing of eggs to larvae or adults may be necessary to permit identification (see Basic Method 6).

### 21.3 SPECIFIC METHODS

#### 21.3.1 Basic Method 1: Filtration Efficiency of Drift Nets

**Objective:** Determine maximum deployment times for drift nets in a stream.

1. Place a single drift net in a stream at a location with moderate- to fast-water velocity for that stream (Fig. 21.1A.D).

Alternatively, if sufficient flow meters are available, drift nets can be placed in both slow and fast velocity habitats to
demonstrate how the rate of clogging varies with water velocity. Prior to actually deploying the drift net, dunk the net in the stream repeatedly as air bubbles on a dry net can temporarily reduce filtration efficiency at the start of a deployment. Orient the net so that the mouth is perpendicular to the direction of flow and anchor it in place with rods driven into the substrate.

2. Use a recording flow meter (e.g., model 2030R, General Oceanics, Miami, Florida) affixed at the mouth of each net using string, zip ties, or cable to record the velocity of water entering the net during the deployment at 1-min intervals (see Chapter 3). Position a second recording flow meter 0.5–1 m to the side of the net to continuously record ambient stream water velocity at 1-min intervals. Periodically, compare the ambient stream velocity with the velocity estimates at the net to identify when the velocity into the net has slowed appreciably. Remove the net when the velocity into the net is <20% of ambient.

3. Discard the contents of the net. Thoroughly clean the net and repeat steps one to two to obtain multiple estimates of filtration efficiency over time.

4. Make a plot showing the filtration efficiency (y-axis) over the duration of the deployment (x-axis), where filtration efficiency = net velocity/ambient velocity. Identify how long it took for the filtration efficiency to drop below 0.85; this represents the maximum amount of time that drift nets should be deployed during future drift studies that have similar flow and suspended solid conditions. Use statistical software to fit linear, negative exponential, and logistic curves to the filtration efficiency graph. Conduct analyses to identify which of these functional relationships best describes how water velocity changes over time and as the net becomes clogged.

### 21.3.2 Basic Method 2: Drift Concentrations Among Habitats

**Objective:** Quantify variation in drift concentration and biomass among habitats in a stream.

1. Place a single drift net in each of several different habitat units (e.g., riffle, glide, pool) in a stream reach (Fig. 21.1A). Orient the net so that the mouth is perpendicular to the direction of flow and anchor it in place with rods driven into the substrate. The net should be positioned at mid-depth in the water column or, if the stream is shallow, the bottoms of the net should be 2–3 cm above the sediment to reduce the possibility of invertebrates crawling into the net.

2. Prior to actually deploying the drift net, dunk the net in the stream repeatedly as air bubbles on a dry net can temporarily reduce filtration efficiency at the start of a deployment. After wetting down the net, attach the sampling bucket to the end of the net. As above, use the flow meter to record the velocity of water entering the net during the deployment. Record the starting value displayed on the flow meter before putting the net into the stream. At the same time the drift net is put into the stream, place the second flow meter 0.5–1 m to the side of the net to record ambient stream water velocity.

3. Record the width of the drift net and the height of water passing into the drift net. Measure height at three different places if the drift net is not fully submerged.

4. Remove the drift nets from the stream after 15 min or when a filtration efficiency of 0.85 is estimated to occur (see Basic Method 1), whichever is shorter. Simultaneously, remove the ambient flow meter. Record the ending value displayed on both flow meters. Wash the contents of the net into a bucket partly filled with water. Use forceps to remove any invertebrates that remain clinging to the inside of the nets. Wash the contents of the bucket through a sieve with a mesh size equal to or smaller than that of the net. Preserve the material from each net separately in bottles or sealable bags with 70% ethanol (final concentration). Label the samples with location, date of collection, habitat unit, time period of sampling, and investigator.

5. Repeat steps one to four for a minimum of three consecutive samples in each habitat unit. Nets should be placed in the same location during each sampling interval.

6. In the laboratory, separate all organisms from the debris in the samples. This is best accomplished using a stereo-microscope at low power. Count the number of invertebrates in each sample. To determine the species' composition, identify and enumerate the taxa of invertebrates in the samples (see Chapters 20 and 25). Conduct analyses to determine if there are differences in the species composition and relative abundance of drifting organisms among habitats.

7. Determine the size of each individual collected in the samples. This can be accomplished by various methods: (1) Measure the length of all invertebrates in each sample using an ocular micrometer fitted in a stereo-microscope. Calculate the mass of each individual using published regression equations relating the organism length to mass for a wide variety of aquatic invertebrates (Benke et al., 1999). Note that this approach is required for drift-foraging bioenergetics models that require as inputs the biomass of prey discretized into 1-mm size bins of length, because prey selection by fish is
related to the length of prey (Hayes et al., 2000; Dodrill and Yackulic, 2016); or (2) place all invertebrates collected in a sample together in an aluminum weighing pan and dry them in a drying oven for 24 h at 60°C. Weigh the pooled invertebrates on an electronic balance.

9. Calculate the mean individual dry mass of the drifting organisms (=pooled dry mass/number of individuals in the sample) and the mean drift concentration of invertebrates in each sample. Conduct comparisons to determine whether there are differences in drift concentration among habitat units.

### 21.3.3 Advanced Method 1: Quantifying Active Drift of Stream Invertebrates

**Objective:** Compare the drift concentration of invertebrates in a stream between day and night.

1. Place drift nets across the stream channel (Fig. 21.1D). Nets are placed in the stream with the net face perpendicular to the direction of flow and anchored with rods driven into the substrate. Nets should be positioned at mid-depth in the water column or, if the stream is shallow, the bottoms of the nets should be 2–3 cm above the sediment to reduce the possibility of invertebrates crawling into the nets. Presuming channel width permits, use at least three nets positioned along a cross-section to gather samples to encompass spatial variation in the drift estimate for a site.

2. Record the width of the drift net and the height of water passing into the drift net. Measure height at three different places if the drift net is not fully submerged.

3. Remove the drift nets from the stream after 15 min or when a filtration efficiency of 0.85 is estimated to occur (see Basic Method 1), whichever is shorter. Simultaneously, remove the ambient flow meter. Record the ending value displayed on both flow meters. Wash the contents of the net into a bucket partly filled with water. Use forceps to remove any invertebrates that remain clinging to the inside of the nets. Wash the contents of the bucket through a sieve with a mesh size equal to or smaller than that of the net. Preserve the material from each net separately in bottles or sealable bags with 70% ethanol (final concentration). Label the samples with location, date of collection, habitat unit, time period of sampling, and investigator.

4. Repeat steps one to three for a minimum for three consecutive daytime samples and then repeat again after dark to obtain night-time samples. Nets should be placed in the same location during each sampling interval.

5. In the laboratory, separate all organisms from the debris in the samples. This is best accomplished using a stereomicroscope at low power. Count the number of invertebrates in each sample.

6. Calculate the mean drift concentration of invertebrates in the stream during each time interval. Construct a curve showing the change in drift concentration over time. Conduct analysis to evaluate any difference between day and night drift concentrations.

### 21.3.4 Advanced Method 2: Quantifying Drift in Unwadeable Rivers

**Objective:** Compare the vertical distribution of drift in deep rivers.

1. Prior to starting any boat-based drift-sampling program, familiarize yourself with safety procedures for working from boats, read manuals describing the operation and maintenance of the equipment that will be used, and be cognizant of the hazards and risks that water quality sampling entails.

2. Collecting drift in large rivers from a boat requires different types of equipment than sampling drift in wadeable streams. Plankton nets with a circular opening and bridle are used, because nets are raised and lowered through the water column to collect drift samples rather than being staked into the benthos. Flow strength is high in large rivers, so large weights (e.g., 75-lb US Geological Survey Columbus-Type sounding weights; Rickly Hydrological) are needed to keep nets from being pushed downstream. A hand powered winch (A-reel) that is mounted to a frame at chest height is used to raise and lower drift nets through the water column. A boom or crane that extends over the bow of the boat allows the winch cable to be raised and lowered smoothly over a pulley. Even with large weights, drift nets are often pushed downstream such that the winch cable may rub on the bow of the boat; a roller can be mounted to the front of the boat to prevent wear and friction on the boat and cable. Connectors (Type B; Rickly Hydrological) are used to attach a 1-m length of chain to the end of the cable, and then the sounding weight is attached to the bottom of the chain (Fig. 21.1C). The circular drift net with bridle is then clipped halfway down the chain using a carabiner (see Fig. 21.1B). It is important to keep heavy-duty wire cutters nearby in case the drift net becomes caught at the bottom and the winch cable needs to be cut. Also consider the type of boat available (i.e., propeller vs. jet drive) when procuring nets, as long nets are easily destroyed in propellers.
3. Position the boat facing the upstream in moderate current and hold position by motoring or tying the boat off to a buoy or similar. Lift the sounding weight off the boat and slowly lower it without dropping it; the standard 0.25-cm diameter cable that comes on A-reels is rated for static loads >500 lbs, but dropping a heavy weight, even from a short height, creates a dynamic load that can easily break the winch cable. Use the winch to lower the weight so that it is just touching the water surface. Adjust the depth gage on the winch so it reads zero. Lower the weight to the river bottom to determine depth and record this value and then raise weight back to the surface. Record the starting value of the flow meter that is positioned in the net mouth and clip the net into the drop chain. Affix the ambient flow meter to the sounding weight and record its starting value.

4. Slowly raise and lower the drift net using the A-reel for the duration of the 5—10 min sample. Never lower the drift net to closer than 0.5 m from the bottom to prevent benthic material from being dislodged and captured by the net, and never allow the net to break the surface of the water. Each round trip vertical sample represents a “transit”; strive for a minimum of two transits for each drift sample (Topping et al., 2011). Maintain a constant rate of movement both up and down the water column so that each transit samples all depths equally. After 5—10 min, pull the net out of the water and record the ending time of the deployment and the values displayed on both the net and ambient flow meter. Estimate the filtration efficiency of the net by comparing flow meter readings to ensure it was above 0.85. Discard samples and shorten deployment times if filtration efficiency is less than 0.85. Use an on-board washdown sprayer to hose the sides of the net off and into the collecting bucket. Alternatively, dunk the net in the river several times to flush the contents of the net into the collecting bucket.

5. Follow procedures in the Basic Methods for preserving and laboratory processing of samples.

6. Repeat steps one to four and collect multiple depth integrated samples and also samples where the net is parked near bottom, at mid-depth, and near-surface. The ordering of different types of samples should be randomized over the course of the collection (i.e., do not collect all depth integrated first, then all near-bottom next).

7. Calculate the mean drift concentration and biomass of invertebrates for each type of sample (i.e., depth integrated and different fixed depths).

21.3.5 Basic Method 3: Quantifying Emergence of Adult Stream Insects

Objective: Measure and compare the numbers, fluxes, and composition of adult insects that emerge from different habitats within a stream. Optionally, determine if emergence differs between day and night.

1. Construct (e.g., as per description above and, for instance, Malison et al., 2010; Cadmus et al., 2016) and deploy floating emergence traps (Fig. 21.2A) over the primary habitats (e.g., pools, riffles, glides) in a stream. For instance, some investigators (e.g., Iwata, 2007) have reported greater emergence from pools compared to riffles; is this what you observe? In a paired fashion, deploy modified traps encompassing the stream bank adjacent to each of those within a habitat unit. It is common to deploy six to eight traps per habitat unit (three to four floating, three to four bankside) within a stream reach. However, determining the number of traps to deploy per-habitat type should depend upon the anticipated variability of emergence and magnitude of difference, and a more sophisticated way of addressing the question of sample size is to conduct a power analysis (e.g., see Aho, 2014). This requires use of an existing emergence data set, which ideally is generated via pilot measurements, but often draws upon published data from a site that may have similar characteristics to those being studied.

2. After 24—48 h, remove all insects from the trap using an aspirator (or from the collection bottle), and preserve them in 70% ethanol. Label the sample with location, trap number, date, sampling time period, and investigator. As described above, emergence can be highly heterogeneous in time, so many time periods may need to be sampled if a comparison is to be representative of the habitats or the temporal scope of inference is intended to be seasonal or annual.

3. Optional: Divide sampling into day and night periods, recording the number of hours the traps were in place during both periods.

4. In the laboratory, identify (using keys such as those found in Merritt et al., 2008) and count the number of insects collected in each trap. In addition, measure the lengths of individuals.

5. Calculate the flux, or emergence flux, or production [g dry mass (DM) m⁻² d⁻¹] using direct weighing or published lengthmass regressions (e.g., Rogers et al., 1977; Sample et al., 1993; Stagliano et al., 1998; Sabo et al., 2002). If regressions do not exist for a particular taxon, then use one from a related taxon that has a similar morphology or weigh directly.

6. Express the results as the mean number of taxa, individuals and/or total dry biomass emerging per square meter per hour from each habitat or during the day and night. Conduct analyses describing differences in the number of taxa, individuals or total biomass emerging from the different habitats or during the day and night.
21.3.6 Basic Method 4: Investigating Lateral Dispersion of Emergent Stream Insects

Objective: Quantify the extent to which adult aquatic insects disperse laterally from a stream. Optionally, determine directionality of adult insect flight.

1. Construct (e.g., as per description above and, for instance, Smith et al., 2014) sticky traps (Fig. 21.2C) and deploy them at sampling locations at a minimum of five locations, such as 0, 25, 50, 100, and 200 m on a transect away from the stream. Other spacing regimes may be used depending on the size of the drainage basin and its geography.

2. Set up sticky traps at each sampling point along the transect, noting the time of their deployment.

3. Optional: Evaluate directionality of flight by aerial insects. Use a flat-trap design and deploy traps at each point along the transect to capture insects flying in each cardinal direction. For instance, if using the Smith et al. (2014) trap design, position four traps on each pole, mounted at right angles.

4. Allow sticky traps to collect for at least 24 h (ideally a few days, as temporal heterogeneity of emergence can be high, and comparisons may be more representative if integrated over more time). Collect traps (noting time) and label them as above.

5. In the laboratory, identify, count, and measure the number of insects of aquatic taxa collected on each trap. Depending upon the size of the trap, this may require use of a stereomicroscope mounted on a movable arm, or, in cases where detailed taxonomic resolution is not required, a magnifying lens mounted on an arm (such as are sometimes used for reading) may also be used.

6. Calculate the emergence biomass intercepted by each trap [g dry mass (DM) m⁻² d⁻¹] using published lengthmass regressions, as described in Basic Method 3.

7. Express the results as the number of taxa, individuals, or total emergence flux captured at each trap. If traps were operated for different time periods, express the results per a standard time period. Develop a graph showing the change in number of taxa, individuals, and/or flux with distance from the stream and/or compare directionality of insect dispersal at each location.

21.3.7 Advanced Method 3: Investigating Availability of Emergent Insects as Potential Prey for Terrestrial Insectivores

Objective: Compare the availability of emergent adult insects as potential prey for terrestrial insectivores among stream-riparian ecosystems.

1. Deploy emergence traps (as per Basic Method 3) in reaches of the same or different streams across which you intend to make comparison. If the goal is to represent what may be available to terrestrial insectivores, then it is important that traps sample emergence from the suite of habitats that contribute the most to this availability (a pilot comparison using Basic Method 3 may be conducted to determine this). Construct a map that will allow you to estimate the area of each habitat type in each reach (see Chapter 3) stratify the habitats within the site you wish to represent, and install at least six to eight traps per habitat unit throughout each reach (e.g., three to four floating, three to four bank side; or conduct power analysis to determine trap number using data from Basic Method 3).

2. Optional: Use sticky traps to make comparison among reaches of an index of postemergent insect availability as prey for terrestrial insectivores. This may be advantageous if it is not possible to visit sites on the short time interval required for emergence traps, or if study questions pertain to distribution of potential insect prey extending beyond habitats immediately adjacent to the stream. Install at least four transects of sticky traps (as per Basic Method 4), alternating the side of the stream from which each extends. Alternatively, in settings where traps cannot be left unattended for longer periods and where a rapid “snapshot” is required, light traps may be used in a similar fashion (but see caveats regarding biases associated with both trap types above).

3. Collect insects from emergence traps for at least three sample periods, with each deployment encompassing at least 24 h, but ideally 2–3 days. If the temporal scope of inference is intended to be seasonal or annual (as would typically be necessary to gauge prey availability and possible responses by insectivore populations), more sampling periods will likely be needed.

4. Follow procedures in the Basic Methods for preserving and laboratory processing of samples, and estimate the total biomass flux for each sample, as well as for different taxa [g dry mass (DM) m⁻² d⁻¹].

5. Calculate the average emergence flux from different habitats within each reach, the average for each reach-sample period combination, and the average for each reach across all sampling periods. To obtain the most representative estimates of these, calculate them as averages weighted by the occurrence of each habitat type sampled within each
reach. In addition, riparian insectivores may respond to the total flux of emerging prey that crosses the stream-riparian boundary (i.e., the total food available), rather than the mean flux per unit area across the stream surface (Gratton and Vander Zanden, 2009). Therefore, estimate total emergence flux at the reach scale (Benjamin et al., 2013) as average flux associated with each habitat type times the surface area of each habitat occurring within the reach (as derived from the map for each reach).

6. Compare estimates of mean and total emergence flux among reaches. Also, assess whether reaches differed in the timing of emergence among the sample periods. Finally, compare the composition of emergence flux among reaches. Different terrestrial insectivores may exhibit preference for or avoidance of different adult aquatic insects as prey (Marczak et al., 2007) and may respond to heterogeneity in prey availability at different scales (Power and Rainey, 2000). For instance, most web-building spiders are unlikely to capture large-bodied taxa such as dragonflies or large stoneflies and may make more use of aerial, smaller taxa such as midges or mayflies (e.g., Kato et al., 2003), whereas ground-dwelling predators (e.g., many spiders, beetles, reptiles and amphibians) may be responsive to availability of prey that spend more time crawling than flying (e.g., Paetzold et al., 2006). Similarly, predators that capture insects via aerial, hawking behavior (like many birds and bats) are likely to be more responsive to flying insects, whereas those that mainly glean from vegetation or other surfaces may exhibit other preferences (e.g., Hagen and Sabo, 2011). With these possibilities in mind, estimate emergence flux that may represent availability of prey for different types of predators and compare among reaches.

21.3.8 Basic Method 5: Observing Oviposition by Stream Insects

**Objective:** Record the timing and behavior of insect egg-laying.

1. Consult fly-fishing “hatch” charts, species descriptions in taxonomic journals, or other local or species-specific sources to anticipate likely emergence times. In the absence of such information, dusk in late spring or early summer is a peak egg-laying time for many insects.
2. Find a reach of stream that allows observation of multiple habitats such as riffles, rocky shores, littoral vegetation, and backwaters.
3. Watch for insects flying around the stream. Record any behaviors of these insects, such as mating swarms, mate pairs flying together, or females dipping their abdomens in the water, along with the timing of these activities. Pay special attention to any adult insects that appear to be flying toward the water or crawling on rocks or other emergent substrate.
4. After adults leave a habitat (e.g., a boulder), check the spot for any eggs. Special attention should be paid to large emergent substrates, which may need to be partially removed from the water to locate eggs. If possible, collect any eggs along with their corresponding adults, as this makes identification much simpler (compare with Basic Method 6). Standard insect nets or sticky traps (see Basic Method 4) may be useful for this purpose.
5. If any gravid females are captured, pay special attention to any eggs that may be laid in the net or on the sticky trap during capture to assist in the identification of unknown egg masses.
6. Record the habitats used or avoided by adults, both for mating and for egg-laying. If possible, also record the characteristics, locations, and densities of the egg masses.

21.3.9 Basic Method 6: Rearing Stream Insect Eggs

**Objective:** Hatch insect eggs to larvae for the purposes of identifying egg masses to species, or establishing an experimental laboratory stock.

1. Search for eggs in stream habitats. If specific taxa are of interest, descriptions in taxonomic journals may include pictures of the species’ egg masses for reference. For many species, check specifically for eggs in stream margin habitats, and on the sides or undersides of rocks, wood, or other large or emergent substrates.
2. Scrape eggs as delicately as possible from substrates, using a scalpel or similar tool. Place eggs in vials containing river water for transport to lab. If you seek to minimize egg-hatching outside of the lab, maintain water temperatures at or below that of the studied system.
3. Egg-rearing in the lab is relatively easy for taxa with short gestation times, such as many Diptera, Ephemeroptera, and Trichoptera. In these cases, simply replace the water in the vial every 2—3 days to minimize fungal or bacterial growth. For all lab-rearing scenarios, the water should be river water (which, in some cases, may need to be filtered) or dechlorinated water, kept at or below room temperature.
4. For taxa with longer gestation times or sensitivities to high temperatures (e.g., Pteronarcyidae), care needs to be taken to regulate temperature (∼20°C), ensure sufficient oxygenation, and mimic natural diurnal light patterns. In such instances, eggs can be reared in containers with an air stone in a climate controlled room.

5. Count the eggs and record physical characteristics of the eggs as they mature, and check on the vials at least daily to look for hatched larvae. Counting the eggs can be made easier by first photographing the eggs under a dissecting microscope and performing the counts on the image.

6. Once hatched, more care is required to rear individuals to late instars or adults for identification. Rearing containers such as small plastic food storage containers can be fitted with an air stone and situated in a climate controlled room to rear larvae. Water should still be changed regularly, and basic habitat for larvae such as small gravel or sticks should be provided. Small pipettes are very helpful for manipulating larvae.

7. Depending on the feeding ecology of the aquatic taxa, biofilm covered stream rocks, leaves conditioned in stream water for approximately one week, small midges, or store-bought fish food need to be supplied regularly. In many instances, mortality rates are minimized by providing more than one food supply.

8. Record proportional hatch success, the growth of instars, the feeding regimen, and identify larvae once they reach sufficient size.

21.3.10 Advanced Method 4: Characterizing Habitat Availability and Site Selection for Oviposition

Objective: Quantify differences in oviposition site selection as a function of environmental factors such as channel unit types, location within channel units, and substrate types.

1. Identify and delineate the stream segments to be sampled using maps, imagery, or field-based methods presented in Chapter 2.

2. Randomly choose reaches for sampling within each segment. The number of replicate reaches will depend on the magnitude of differences to be detected among segments and the variance within each reach.

3. Within each reach, two types of points will be sampled: Systematic points to quantify both habitat availability and oviposition-site selection and stratified points for oviposition-site selection for underrepresented habitats.

4. Distribute five transects, oriented perpendicular to the flow, equally throughout the reach. Transects will span the extent of wetted channel or from the wetted edge to the channel thalweg.

5. Sample 10 points along each transect to characterize the channel unit type; water depth and velocity; substrate size, type and emergent area; distance from bankfull; other desired physical characteristics of the stream or river for a total of 50 systematics points per reach. Equally space the points across the entire channel, or out to the extent to which wading is safe.

6. Supplement the 50 systematic points per reach with up to 15 additional random points per strata (i.e., stratified points), where strata can include microhabitats such as submerged mineral substrate, emergent mineral substrate, submerged wood, emergent wood, or emergent vegetation.

7. At each of the systematic and stratified sample points, examine a single substrate particle for egg masses, enumerating the number of egg masses by egg type.

8. Measure and record values for the physical variables described in step five at each of the systematic and stratified sample points.

9. Conduct analyses to investigate differences in egg density (response variable) as a function of reach type, channel unit types, substrate types, egg location within a channel unit, and velocity.

21.4 QUESTIONS

1. What aspects of drift nets influence the time at which clogging occurs? What aspects of the deployment site influence the time to net clogging?

2. What factors might be responsible for observed differences in drift among habitat types? Which habitats afford the highest prey delivery rates for drift-feeding fishes?

3. What factors might be responsible for observed differences in the vertical distribution of drift in a large river? What type of sampling approach (i.e., vertically integrated or fixed depth) is most appropriate for estimating total drift loads for a reach (# s⁻¹) versus estimating the amount of drift biomass that is available to drift-feeding fish in a deep river?
4. What differences might occur in drift concentrations and the species drifting as stream size (order) increases? Would you expect seasonal differences in drift concentrations? Why?

5. What factors might be responsible for differences in the numbers or fluxes of emerging insects among different habitats? What factors might cause day-to-day, day versus night variation, or differences in emergence timing among different streams?

6. If composition of emergence differed among habitats, stream reaches, or samples collected using different traps, why might this be?

7. Benthic sampling devices (e.g., Chapter 15) and emergence traps often provide very different estimates of the species composition of stream invertebrate communities. What are some of the reasons for these differences?

8. Do the numbers of adult taxa collected laterally from the channel (via sticky traps) show an exponential decrease with distance from the channel? Why or why not?

9. What ecological advantages might the specific timing of oviposition confer on population success? Consider this both in terms of time-of-day and any synchronous timing of egg-laying within a population.

10. Where are insect eggs being laid? How might egg morphology vary depending on habitat conditions?

21.5 MATERIALS AND SUPPLIES

Field Materials
- Rectangular drift nets and metal holding rods (wadeable streams)
- Circular drift (plankton) nets, sounding weights, and winch (deep rivers)
- Emergence traps (floating, and bank-side)
- Sticky traps (including covers or cellophane for retrieval)
- Current velocity meter
- Meter sticks or tapes
- Buckets (5 gallon)
- Sieves (series of mesh sizes)
- Forceps
- Aspirator
- Ethanol (70%)
- Bottles or vials or sealable bags
- Labeling paper and pencils
- Hip boots or waders
- Jeweler’s loupe or magnifying glass
- Binoculars
- Scalpel

Laboratory Materials
- Stereomicroscopes
- Ocular micrometer (optional)
- Digital camera mounted on microscope (optional)
- Drying oven (optional)
- Electronic balance (optional)
- Rose Bengal
- Aluminum weighing pans
- Acrylate adhesive
- Soft forceps
- Clear, multiwell plates or dishes with lids
- Ethanol
- Dechlorinated water
- Vials
- Subsampling device
- Air stone
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