Chapter 6. Sampling Aquatic Insect Emergence

I.J. DAVIES

1 Why Sample Insect Emergence?

In the last stage of their life cycle, aquatic insects undergo both a metamorphosis to the adult form and a transition from the aquatic to the terrestrial environment. This transition, or emergence, of adults is a prerequisite for reproduction and dispersal of each species. As a quantity, emergence represents the final component of insect production, a measure of the cumulative effects of growth, natural mortality and predation throughout the life cycle, and a potential net export of insect material from an aquatic system. Because the taxonomy of larval forms is so often poorly developed, the adults also provide the only means of identifying some insects.

After they have emerged, insects may be sampled by hand collecting, pitfall traps, sticky traps, sweep nets or light traps. Although each of these methods can yield a large number of specimens, catches often contain a high proportion of terrestrial species and give little information about the point of origin or absolute numbers of emerging insects.

Alternatively, aquatic insects can be intercepted on their way to the water surface or contained, once there, by a wide variety of funnel, tent, or box shaped devices known as emergence traps. These traps are passive samplers used to provide continuous or periodic records of emergence from fixed locations. Because traps are generally inexpensive to construct, easy to use, and yield specimens that do not have to be sorted from the sediment, many stations can be monitored with the minimum of effort. Emergence traps are often the only practical way of sampling habitats where boulders, gravel, bedrock or dense vegetation preclude the use of corers and grabs for sampling larval insects. In addition, the temporal sequence of emergence provides important information on insect life history and may be used in monitoring programs to document the effects of sudden environmental change.

The first published account on the use of emergence traps was given by Needham (1908): 'Quite as an experiment, and without expecting any large results, we made a tent of cheese cloth . . . and set it directly in the bed of Beaver Meadowbrook, just above the fish ponds, to capture and retain such winged insects as might upon transformation arise from the surface of the water

beneath it.... Our first peep into it on the morning of the 16th was revelation. Insects of five orders in astonishing numbers had transformed beneath it, and were assembled under the ridge cord, waiting to be picked off. There were several square feet of Chironomidae in the top, and stone flies and crane flies and caddis flies and May flies were scattered all over the sides.'

Following this initial application, emergence traps have become widely used in the study of aquatic insect communities. Many of the common designs and trapping techniques have been previously summarized by Kajak (1957), Morgan (1971), and Mundie (1956, 1971a). The goals of this chapter are to update this information, review what is known about trap performance and the factors that affect it, discuss patterns of insect emergence, and examine some of the practical aspects of using emergence traps as sampling devices.

2 Some General Comments on Emergence Traps

Ideally, emergence traps should sample without bias, capture and retain both adults and exuviae, and allow subimagoes to continue their transformation into the full adult stage. Traps should protect individual specimens from damage by wind, waves, extremes of temperature and deterioration after death. Specimens inside a trap should be safe from predation by fish, invertebrates, and birds. Traps should also be easy to construct, install, and operate; they must be rugged, portable, relatively free of maintenance problems such as algal build-up and deterioration due to sunlight or rust; and, finally, they should be inexpensive. In practice, few traps approach this ideal standard. Problems arise because the spectrum of insect habitat is so diverse that no single trap design is adequate for all applications. To cope with local conditions of wind, waves, water depth, or emergent vegetation, design compromises must be made, with the result that a large number of specialized trap designs have evolved.

The process of choosing or designing a trap involves four distinct phases. First, the sampling requirements of an experiment or monitoring program must be defined. Considerations of sample size, adequate coverage of all habitats and ease of trap use may be of primary importance when emergence sampling is used to establish a species list, but is of little concern in an experimental program where traps of high sampling efficiency are needed to provide an accurate estimate of emergence. Second, trap choice is further restricted by the emergence habits of the taxa under study. For instance, many hemimetabolous species leave the water before eclosion—nymphs climb emergent vegetation and stones, or crawl shoreward onto the bank. Included in this group are the Odonata, most species of Plecoptera, and some Ephemeroptera. Among holometabolous insects, the Megaloptera and some species of Diptera and Trichoptera, also emerge from shore. Traps designed to

monitor shore-emerging taxa must span the region between terrestrial and aquatic habitats without acting as a bridge or impeding the migrations of larvae or nymphs. Third, physical constraints of the habitat, such as water depth, current speed, wave action, and the occasional presence of large amounts of vegetation, play a role in the choice of a trap. As a general rule, traps should alter the sampling environment as little as possible. Final considerations include cost, portability, ease of trap use, and the required frequency of servicing. A number of published trap designs are outlined below. Details of their construction and operation are given in the Appendices, Sections 9.1, 9.2 and 9.3.

3 Trap Designs

3.1 Open water traps

Floating traps, illustrated in Fig. 6.1, enclose an area of lake surface (usually 0·25–0·5 m^2) inside a tent or cage supported by a framework of wood or metal. Designs are kept light-weight and transparent by employing as much clear plastic or mesh in their construction as possible. Except for two models that operate in the semi-submerged mode (Fig. 6.1c, d), surface traps float with their open bases just below the water surface. Plastic coverings such as celluloid, acrylic sheet or polyethylene film (see Table 6.1) protect the catch from damage by wind or rain, but some screen covering is always necessary to reduce condensation build-up. Mesh with a 250 μm opening will retain even the smallest insects. To remove the catch, traps are generally lifted out of the water with their bases covered and insects are collected by hand or with the aid of an entomological aspirator. Although some models lessen this work by including a removable sample bottle (Fig. 6.1c, d, e), insects often remain in the body of the trap and must still be recovered by lifting the trap. Floating traps offer the advantage of being able to collect large numbers of insects because they can be built to almost any dimension. Disadvantages are that surface traps are somewhat cumbersome to use, are susceptible to damage by wind, waves and vandals, and, except for Mundie's pyramidal design (Fig. 6.1c), do not retain pupae or floating insect exuviae. Details on the design and use of floating traps are given in Appendix 9.1.

Traps suspended in the water column are free of the influences of wind, rain, and the condensation problems associated with surface models. Submerged traps can also be made relatively immune to damage by wave action, depending on how they are suspended. Because the emergence of pupae or nymphs is restricted to an air space inside a removable bottle, collections of insects and exuvia can be made by simply removing and capping the sample bottle while holding it inverted under the water surface.

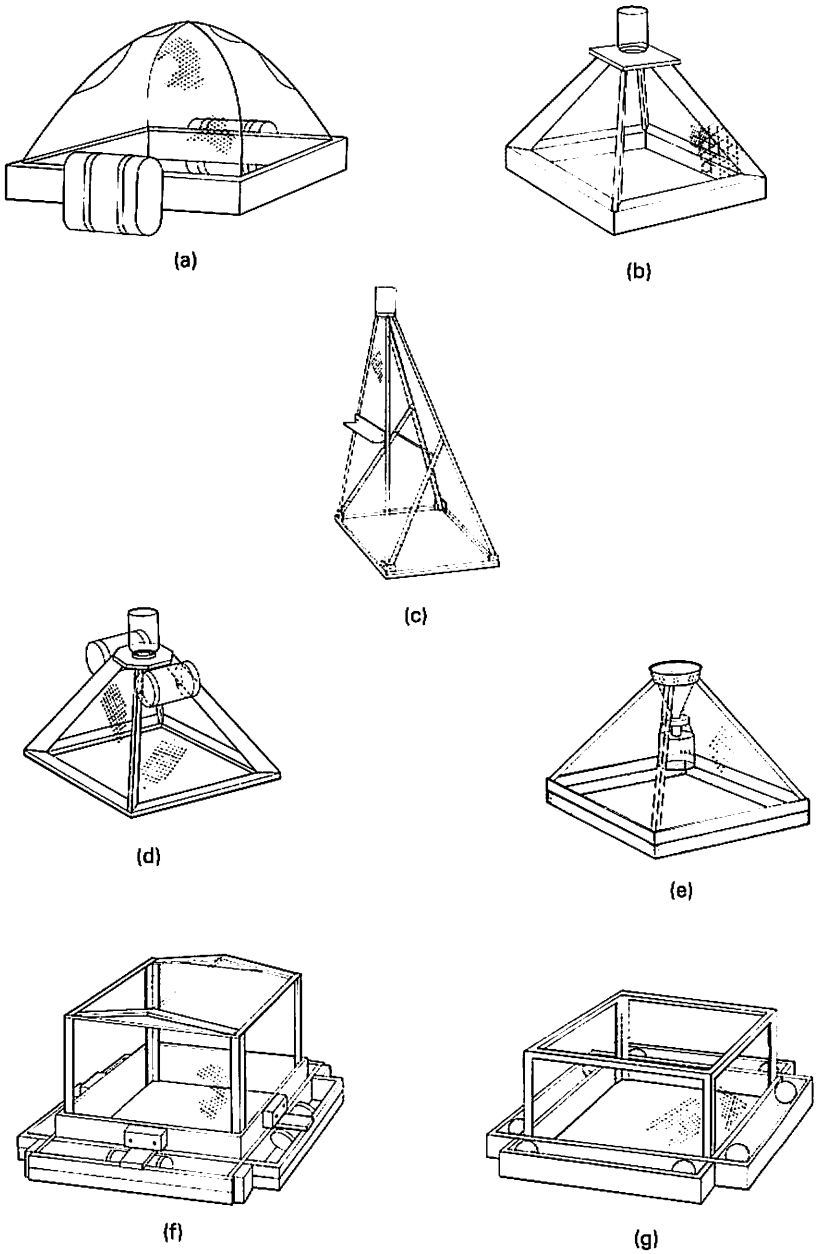


Fig. 6.1 Floating traps for open water. Designs originally described by: (a) Miller (1941), (b) Scott & Opdyke (1941), (c) Mundie (1971a), (d) Wohlschlag (1950), (e) Boyle (1979), (f) Macan (1949), (g) Morgan (1958).

Table 6.1 Properties of common plastics used to make emergence traps.

Type	Relative cost	Properties	Solvent or bonding technique
Acrylic (sheet)	High	Colourless, transparent, strong, degrades very slowly in sunlight, brittle, good resistance to oil and gasoline, S.G.[1] = 1·2, R.I.[2] = 1·5.	Methylene chloride*, Methyl-ethyl-ketone.
Cellulose acetate (sheet)	Medium	Colourless, good transparency, flexible, quickly discolours and becomes brittle in sunlight, good resistance to oil and gasoline, thermoforming[3], S.G. = 1·3, R.I. = 1·5.	Acetone*, Chloroform, Ethyl acetate, Methyl-ethyl-ketone.
Cellulose acetate butyrate (sheet)	Medium	Colourless, good transparency, flexible, degrades slowly in sunlight (embrittles, discolours), good resistance to oil and gasoline, thermoforming, S.G. = 1·2, R.I. = 1·5.	Acetone*, Ethyl acetate, Methyl-ethyl-ketone, Methyl cellosolve.
Cellulose acetate propionate (sheet)	Medium	Colourless, good transparency, flexible, degrades at a moderate rate in sunlight (embrittles, discolours), thermoforming, S.G. = > 1.	Ethyl acetate, Methyl-ethyl-ketone, Methyl cellosolve.
Polycarbonate (sheet)	High	Colourless, good transparency, flexible, high impact strength, high temperature resistance, degrades slowly in sunlight, S.G. = 1·2, R.I. = 1·6.	Methylene chloride*.
Polyethylene (film)	Low	Colourless, slight opacity, flexible, chemically inert degrades at a moderate rate in sunlight, S.G. = 0·91–0·94, R.I. = 1·5.	Not soluble, Glues ineffective, Heat sealing*.
Polystyrene	Medium	Colourless, good transparency, light-weight, brittle, degrades quickly in sunlight, poor resistance to oil and gasoline, S.G. = 1·1, R.I. = 1·6.	Toluol, Xylol, 'Model Cement'.
Vinyl (sheet)	Medium	Colourless, good transparency, flexible, thermoforming, S.G. = 1·2 (see Flannagan & Lawler (1972) for light transmission characteristics).	Tetrahydrofuran, Methylene chloride, Cyclohexanone, Ethyl acetate, Heat sealing.

[1] S.G. = Specific gravity
[2] R.I. = Refractive index
[3] will soften and can be easily worked at temperatures < 100 °C
* indicates best solvent or method of bonding

Disadvantages of the submerged design include the rapid build-up of algae and detritus on the trap, which reduces its transparency, the tendency of the sample bottle to become clogged with blue-green algae or tree pollen, the limited volume of air inside to house insects and keep them alive once they have emerged, and the fact that Ephemeroptera or other hemimetabolous insects seldom complete the transition from subimagoe to adult inside the trap. Further, restrictions on the size of the trap, imposed by the capacity of the sample bottle, structural strength of materials and manageability, usually limit sampling area to between 0·10 and 0·25 m^2.

Early versions of the submerged funnel (Fig. 6.2 and Fig. 6.3a) were constructed from metal mesh supported and strengthened by a stiff wire frame. These traps were heavy, expensive, time consuming to build, and rather opaque. Plastics dominate the list of construction materials in more recent

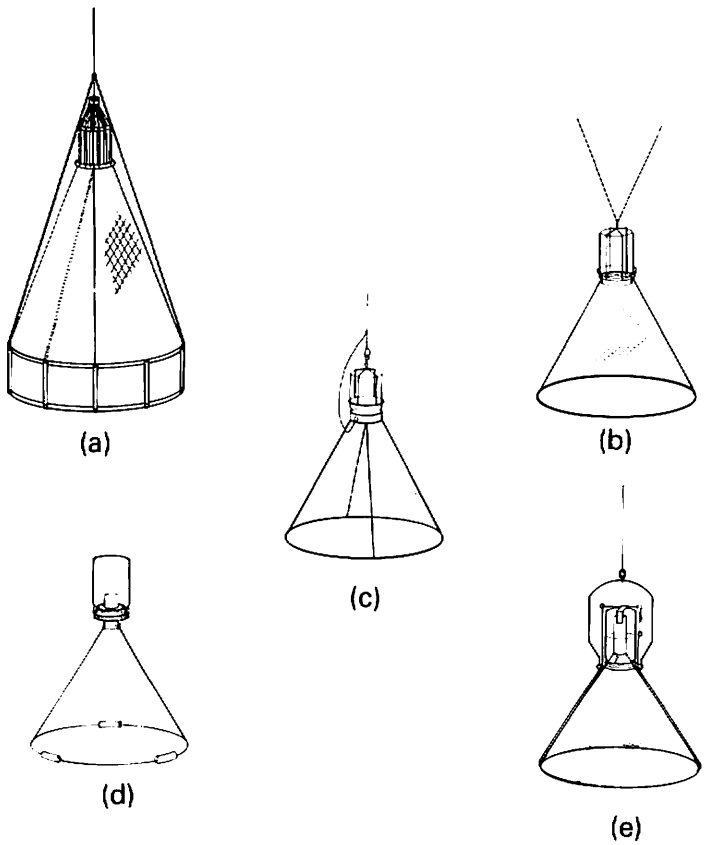


Fig. 6.2 Submerged traps for open water. (I) Designs originally described by: (a) Grandilewskaja-Decksbach (1935), (b) Brundin (1949), (c) Mundie (1955), (d) Palmén (1955), (e) Jónasson (1954).

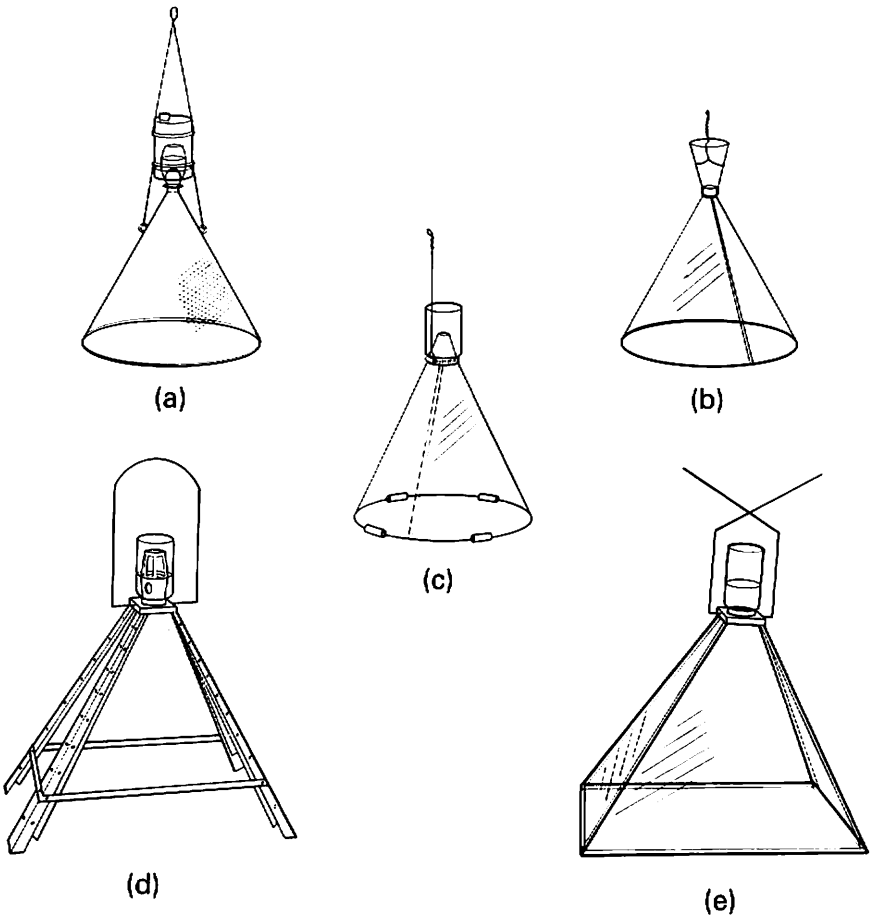


Fig. 6.3 Submerged traps for open water. (II) Designs originally described by: (a) Borutsky (1955), (b) Sublette & Dendy (1959), (c) Hamilton (1965), (d) Fast (1972), (e) Welch (1973).

models (Fig. 6.3b, c, d, e); the properties of common plastics are given in Table 6.1, as an aid to designers. Details of several models of submerged funnel traps are summarized in Appendix 9.1.

To illustrate some practical aspects of trap construction, installation and use, I have chosen as an example an inexpensive and versatile version of Hamilton's (1965) design for further description.

3.1.1 Construction of a submerged funnel trap

Referring to Fig. 6.4a, the two parameters which define sampling area (A) and shape of a submerged funnel trap are: its basal diameter (2R'); and height (h)

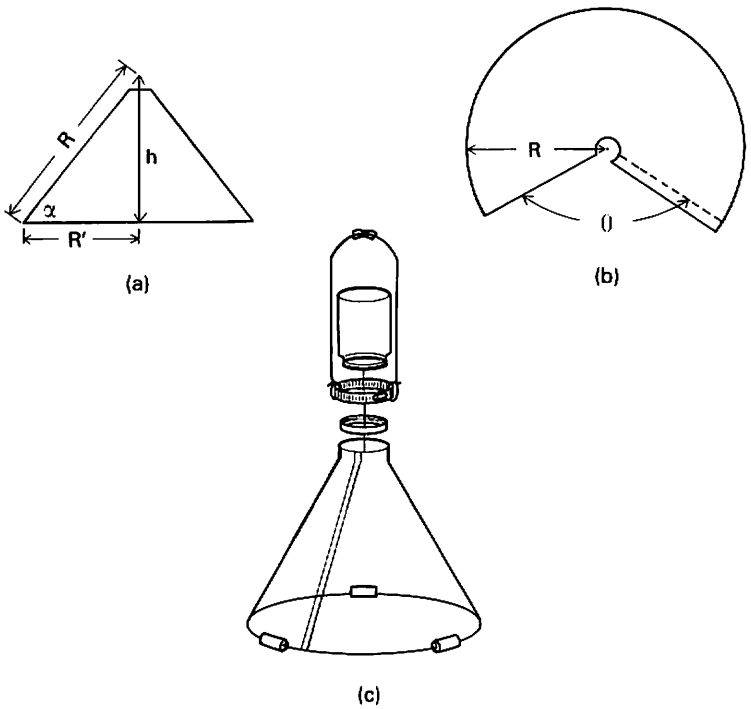


Fig. 6.4 Construction details of a submerged funnel trap. (a) Basic specifications, (b) pattern design, (c) exploded view of the final trap.

or pitch angle (α) of the cone [where $R' = +\sqrt{A/\pi}$ and $\alpha = \tan^{-1}(h/R')$]. Once these specifications have been finalized, a pattern for forming the cone from sheet plastic (Fig. 6.4b) can be drawn. The radius (R) of the circular pattern equals $R'/\cos\alpha$ and the angle of the pie shaped cut-out (θ) is $360 - (360 \times \cos\alpha)$ degrees. Note than an extra 1 cm of material is left to allow for seam overlap.

Although a variety of clear plastics may be used to form the cone, cellulose acetate butyrate (0·75–1·00 mm thickness) offers some advantages over other materials listed in Table 6.1. It has good mechanical, chemical and optical properties, can be easily shaped when heated (i.e. is a thermoforming plastic), is quite resistant to degradation by sunlight, and is widely available at moderate cost.

Trap blanks cut according to the pattern (Fig. 6.4b) are made into cones by bringing the two straight sides together and clamping them between wood strips to form an overlapping seam. A small amount of acetone dispensed from a hypodermic syringe along the edge of the overlap will be drawn in between the two layers of plastic by capillary action to create a solvent weld.

Clamps may be removed after five minutes, but the seam should be left to harden overnight before proceeding.

Once the seam has set, the apex of the cone is softened, either in boiling water or with a 'heat gun', and formed into a cylindrical collar by pushing a glass jar or other object of the correct diameter through the hole in the top of the cone from the inside. A Bakelite jar lid, with its center portion removed to within 6 mm of the rim, is fitted into the collar (Fig. 6.4c) and held in place by a gear-type stainless hose clamp, set over the outside of the collar and tightened. The lid reinforces the cone and serves as a threaded attachment point for a glass sample bottle. Reheating the neck of the trap shrinks the acetate plastic tightly around the lid. Excess material can now be cut away. Split lead weights (gill net leads) in 2–3 cm lengths are crimped over the basal edge of the cone to provide trap stability. These weights grip well if the surface of the plastic has been roughened at the attachment points by burning in shallow grooves or holes with a soldering iron.

A loop of 45 kg breaking strength, nylon monofilament (marine fishing line) tied around the hose clamp forms a suspension bridle. Wear on the bridle can be reduced by wrapping the clamp with vinyl tape and by stringing a short length of stiff vinyl or rubber tube onto the monofilament to prevent the bridle from kinking when the trap is hung from a surface float by a piece of strong fishing line. An alternate suspension scheme, employed for its shock absorbing characteristics, uses a bridle made of surgical rubber tubing attached either to the neck of the trap (Dr. H.E.Welch, Freshwater Institute, personal communication), or directly to the cone (Rosenberg *et al.* 1980).

3.1.2 Anchoring techniques

The choice of an anchoring system can greatly influence trap performance. While a trap that sits directly on the bottom requires only a single line to raise and lower it or attach it to a marker float, suspended traps require a more complex mooring.

The simplest technique uses a single rock anchor attached to a float (Fig. 6.5a) to hold the trap in position. Unfortunately, this method does not stabilize traps against wind and wave action. Float movements may tangle the trap in the anchor line or confound the interpretation of spatial patterns of emergence in areas where the substrate is not uniform. During periods of calm, the trap may hang directly over the portion of the bottom disturbed by the anchor, or the mooring line may interfere by tilting the trap.

The advantage gained by adding a second anchor (Fig. 6.5d) usually outweighs the additional cost and effort involved. Anchors should be placed parallel to the prevailing wind and far enough apart so the ropes rise to the surface at an angle of 50–60 degrees. By keeping the lines tight, a trap can be

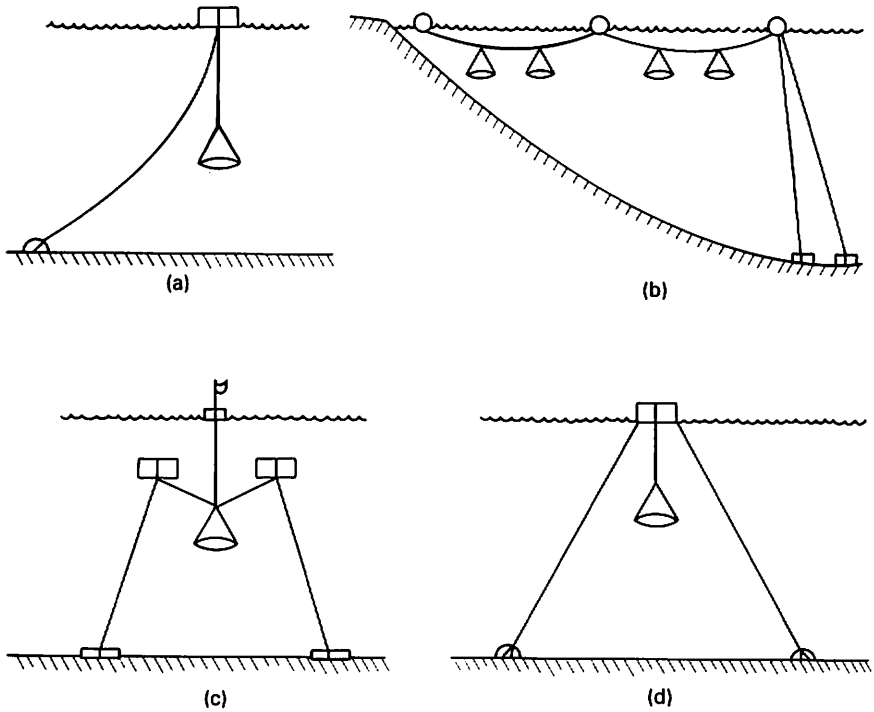


Fig. 6.5 Anchoring techniques. (a) Single anchor, (b) cable suspension with floats, (c) a submerged suspension scheme (d) double anchored surface float.

held on station, free of interference from anchors or mooring ropes. The effect of wave action is also reduced as waves tend to break over the float rather than lift it. To lessen strain on the mooring ropes, small floats should be used at the most exposed stations.

Submerged buoys (Fig. 6.5c), described by Welch (1973), are a practical alternative to surface floats. Although somewhat more costly and time consuming to install they allow traps to be hung beneath ice. Submerged floats can also be used to keep traps secure from wave action or to make stations less conspicuous and therefore less susceptible to unwanted inspections or vandalism.

Mundie (1971a) described a method for suspending traps from a taut cable (Fig. 6.5b) held at one end by a large anchor in deep water, supported by floats along its length, and fastened to shore. Although the method allows an investigator access to traps simply by pulling a small boat along the cable from station to station, it is cumbersome to install, may present a hazard to navigation, and does not protect traps from damage by wave action that causes vertical oscillations in the cable.

3.1.3 Floats

Foam plastics dominate the list of flotation materials because they are convenient to use and widely available. Polyethylene and polypropylene foams are extremely durable but most expensive; closed cell urethane foam is less costly but has poor abrasion resistance. Expanded polystyrene, sold either in closed cell form (Styrofoam®) or as beads bonded into sheets or blocks, is the most commonly used material even though it has low resistance to abrasion and may become rapidly colonized by burrowing insect larvae (see Section 4.4). These disadvantages may be partially overcome by sealing floats in polyethylene bags (Fig. 6.6a). Plastic strapping (industrial banding) clamped around the float makes a convenient attachment point for ropes. Flotation materials can also be sandwiched between two pieces of plywood which are then bolted together (Fig. 6.6b). Foams can easily be cut with a knife, saw, or hot wire, although some plastics give off toxic gases when heated. Air-filled floats made from sealed plastic pipe or empty containers provide useful alternatives to foam in many situations.

Ice cover in northern latitudes poses a special problem where emergence must be monitored at the same location over several years. Ropes and floats left to freeze in place will be dragged off station during spring break-up. If floats are removed and lines sunk below the maximum depth of ice cover it is often impossible to find them again.

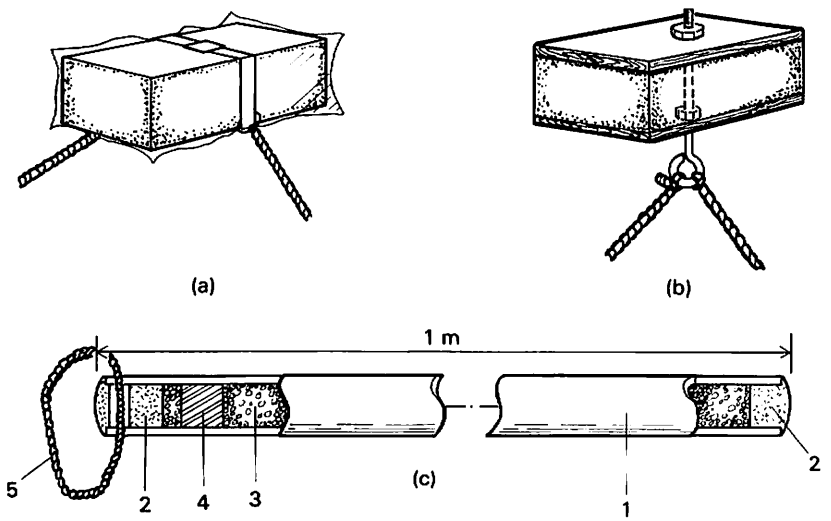


Fig. 6.6 Float designs. (a) Expanded polystyrene sealed in polyethylene film, (b) expanded polystyrene/plywood construction, (c) 'winter' marker float (shown in partial section view with components as follows; (1) aluminum tube, (2) silicone sealant, (3) foam polyethylene, (4) lead weight, (5) attachment rope).

To solve this problem I have developed an inexpensive 'winter float' (Fig. 6.6c) which marks stations in the autumn and allows anchor lines to be retrieved without damage the following spring. The float is a one meter length of seamless aluminium tube (22 mm o.d. × 1 mm wall), sealed at either end with a plug of silicone adhesive to make it air tight. Closed cell polyethylene foam rod (used in the concrete construction industry) provides back-up flotation, should any air leaks occur, and holds a lead weight (85–90 g) firmly against one end of the tube. The weight keeps the tube floating upright in the water with 80% of its length submerged. Lines attached to the float are held beneath the ice when the top part freezes in place. In the spring, heat from sunlight, warm air or meltwater is rapidly distributed to all parts of the ice in contact with the aluminium, and the tube melts free along its entire length. As ice breaks away from shore and begins to move, tension on the anchor ropes pulls the tube through the hole melted around it, allowing it to float safely under the ice.

3.2 Traps for shallow standing water

Many of the previously mentioned open water traps can be used or adapted to sample shallow ponds or inshore areas; however, a number of traps have been made specifically for this purpose. Unlike their open water counterparts, built to withstand wind and waves, these shallow water traps have been designed to accommodate emergent vegetation, prevent condensation or anaerobic conditions from developing inside the trap, and allow insects to move freely into the shallows prior to emergence.

Staked or floating traps for heavily vegetated areas, illustrated in Fig. 6.7 and described in detail in Appendix 9.2, are tall form structures with basal areas between 0·1 to 0·7 m^2, built to stand over emergent plants. These traps are either installed with their bases above the substrate or moved frequently to accommodate the migrations of larvae or nymphs in this habitat. Some designs are equipped with removable sample bottles, but, because the efficiency of these collecting devices is variable, the entire trap should be emptied at frequent intervals to prevent catch loss.

Traps shown in Fig. 6.8 and described in Appendix 9.2 are intended for surface or semi-submerged use in shallow areas without emergent vegetation. With the exception of a floating silk cone (Frank 1965; Fig. 6.8d), none of these traps was designed to collect insect exuviae.

Figures 6.9 and 6.10 illustrate traps which are set directly on the substrate in the shallows. Details of their construction and operation are given in Appendix 9.2. Fully submerged models in this category retain both insects and exuviae in an apical sample bottle and are set or emptied in the same manner as open water funnel traps. One notable exception is the design of

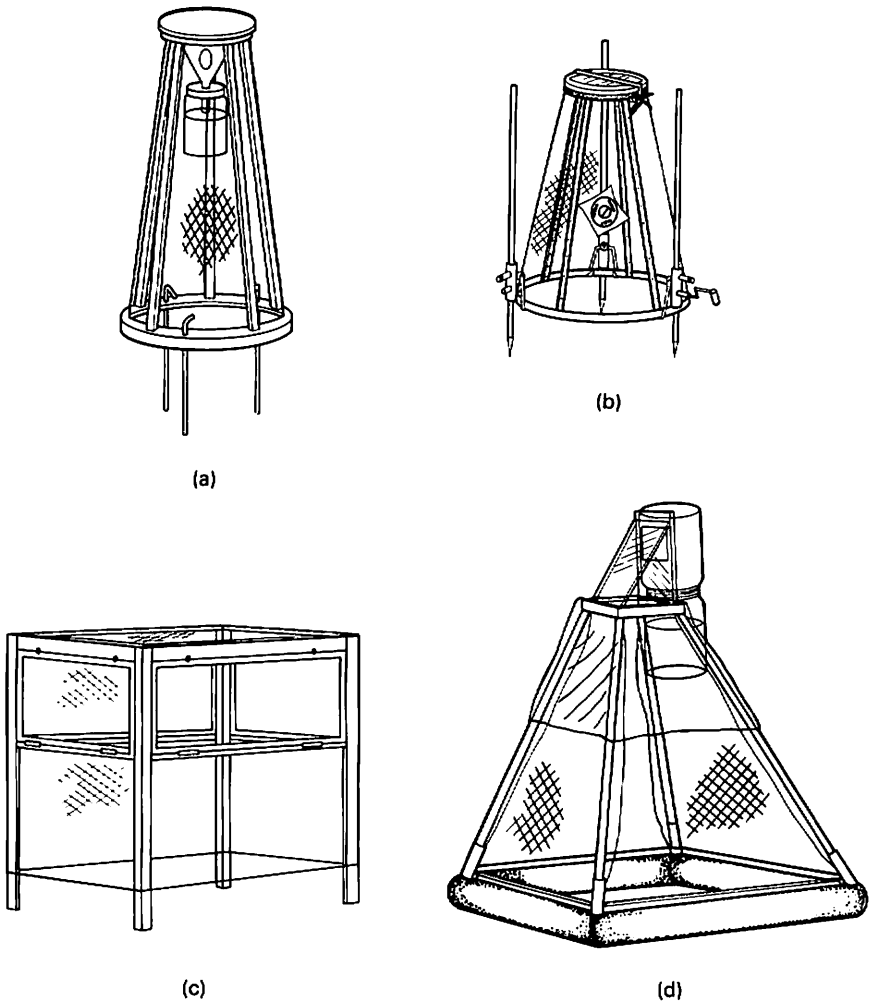


Fig. 6.7 Traps for shallow vegetated habitats. Traps originally described by: (a) Lammers (1977), (b) Corbet (1965), (c) Judd (1949), (d) LeSage & Harrison (1979).

Lindeberg (1958; Fig. 6.9c) which functions as a fully submerged funnel in shallow rockpools containing only a few centimetres of water. Exuviae may be collected from semi-submerged traps if the bottom of the trap is closed off with a screen prior to lifting it from the water (Butler 1980; Fig. 6.10c). Alternatively, exuviae can be contained within a cylinder at the surface (Kajak 1957; Fig. 6.9a) and collected after the upper trap portion has been removed. Traps set directly on the bottom should be well vented to prevent anaerobic conditions from developing inside. Sampling locations should also be changed periodically to avoid containment effects.

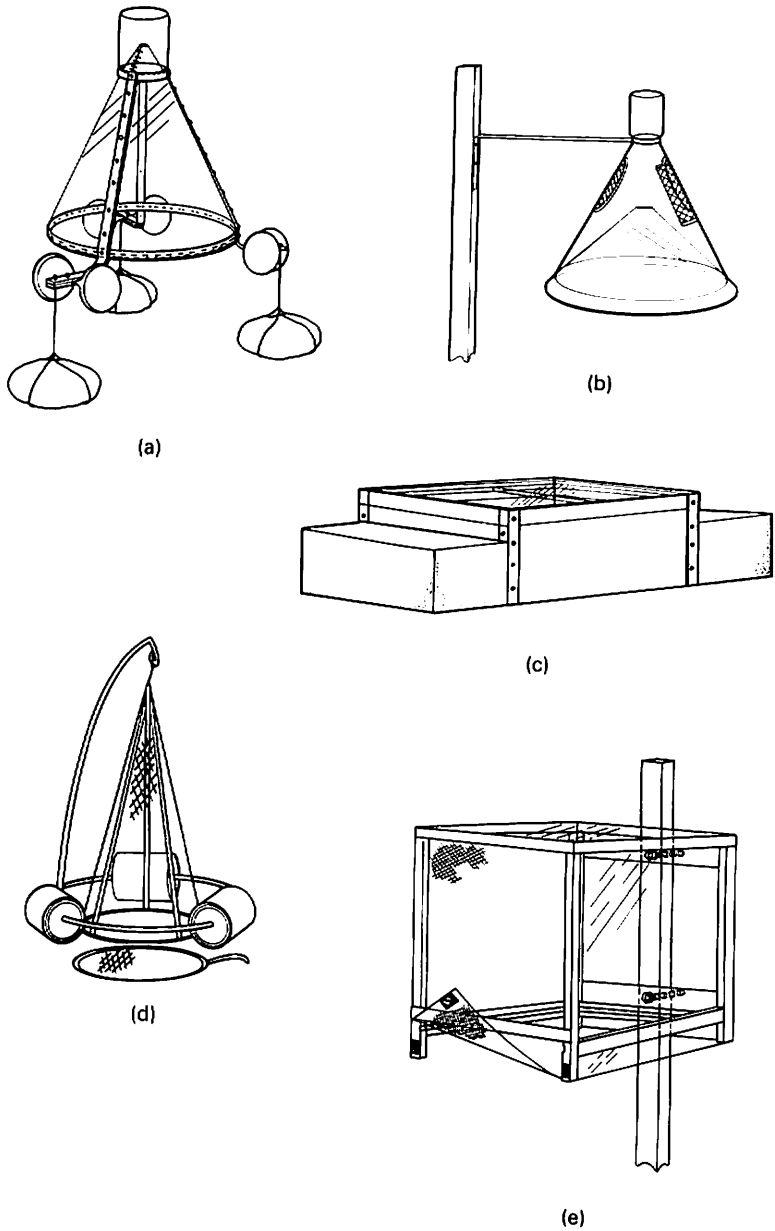


Fig. 6.8 Traps for shallow protected areas with little or no emergent vegetation. Designs originally described by: (a) Mundie (1956), (b) McCauley (1976), (c) Street & Titmus (1979), (d) Frank (1965), (e) Kimerle & Anderson (1967).

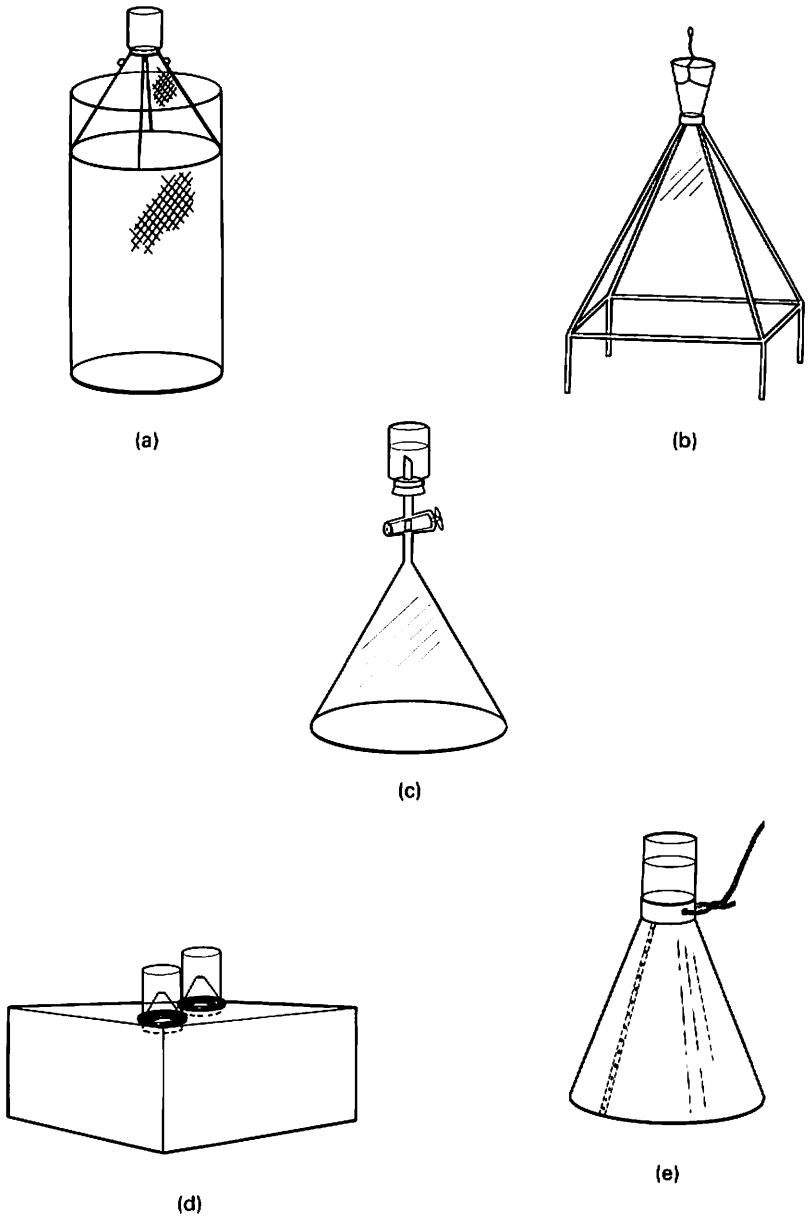


Fig. 6.9 Traps which are set directly on the bottom in standing water. (I) Designs originally described by: (a) Kajak (1957), (b) Sublette & Dendy (1959), (c) Lindeberg (1958), (d) Cheng (1974), (e) Mulla *et al.* (1974).

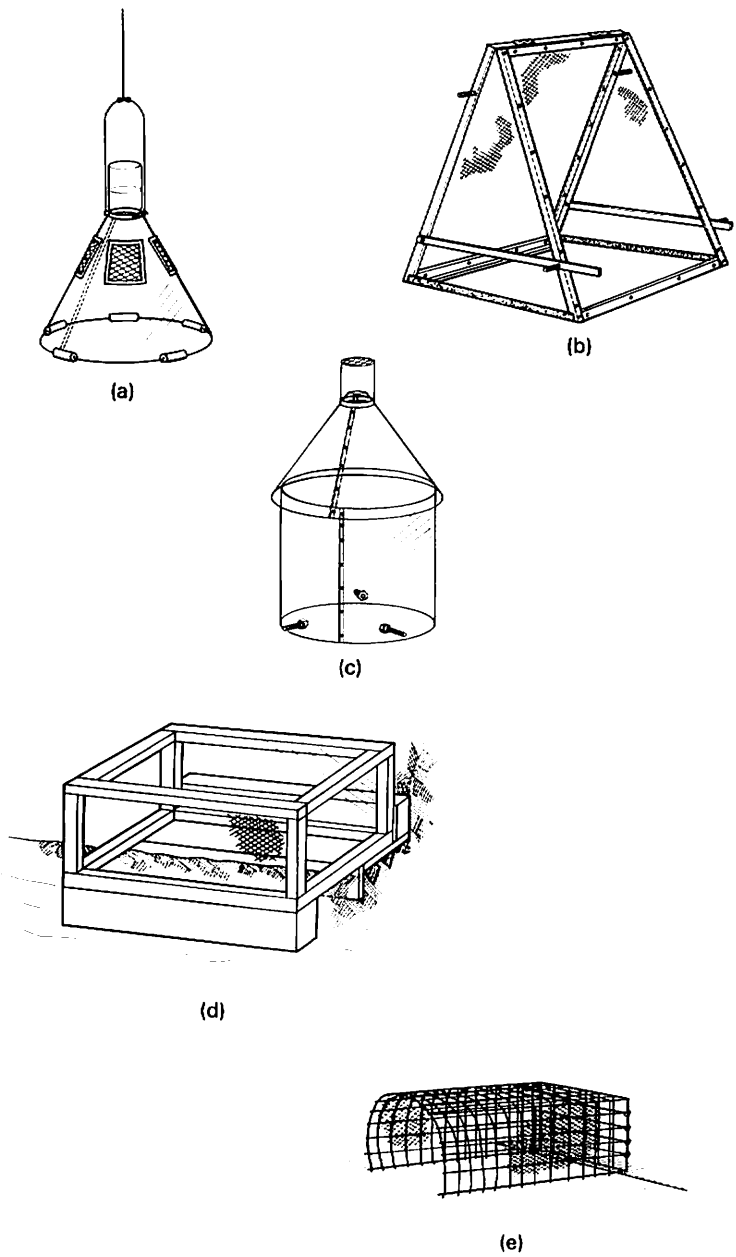


Fig. 6.10 Traps which are set directly on the bottom in standing water. (II) Designs originally described by: (a) Davies (1980), (b) Ettinger (1979), (c) Butler (1980), (d) Morgan (1971), (e) Cook & Horn (1968).

The water's edge is, perhaps, the most difficult of all shallow habitats to sample. Traps must not obstruct the movement of larvae or nymphs as they crawl shoreward to emerge, yet they must capture and retain adults. Two models illustrated here are a modified box (Morgan 1971; Fig. 6.10d) set with half its open base on land and the other half floating on the water, and a wire cage, lined with screen, built by Cook & Horn (1968) to monitor damselfly emergence from a pond (Fig. 6.10e). On rock shorelines with irregular shapes, a tent rather than a cage may make a more useful type of trap.

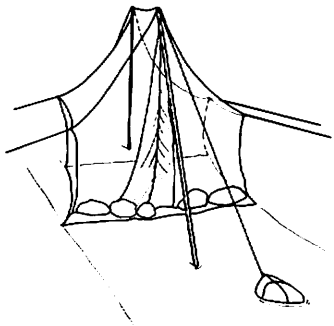
3.3 Traps for running water

Techniques for sampling insect emergence from flowing water differ somewhat from those employed in standing or open water habitats. Trap construction must be sufficiently robust to withstand 'worst-case' conditions, even though these may occur infrequently. Without some mechanism to compensate for fluctuating water levels, traps can become stranded during periods of low flow or inundated by a spate. In addition, a number of different trap designs may be needed to adequately sample the bank, pool, and riffle habitats present in a small section of stream.

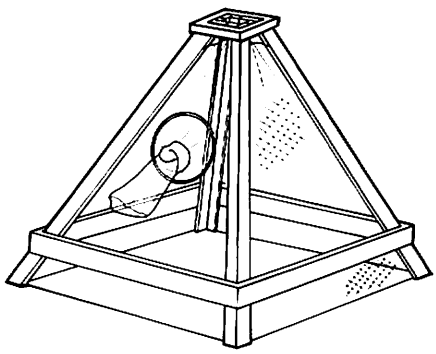
A popular technique for monitoring emergence from small streams uses a tent or screen covered cage (0·5–1·0 m^2 basal area) set directly on the stream bottom with the edge of its open base below the water surface (Fig. 6.11a, b; Appendix 9.3). Drifting insects are excluded from these samplers, but, because the base is not sealed against the substrate, crawling larvae and nymphs are free to enter or leave. Debris accumulations on the upstream side of the cage can be minimized if the stream is allowed to flow through the trap under flaps along its base (Fig. 6.11c). With this technique, however, surface drift is also included in the estimate of emergence. As with floating traps used in open or standing water, the maximum mesh opening of the tent or cage covering should be 250 μm to retain the smallest insects. Except for the pyramid design shown in Fig. 6.11b, which is emptied from the outside via a sleeve in the wall, investigators must enter tents or cages to make collections. Care must be taken during this operation to avoid disturbing the substrate inside the trap.

A greenhouse (Fig. 6.11d), built to completely enclose an 11·1 m^2 area of a small brook and its banks, is an expanded version of the cage concept. While several workers have successfully used the design (Appendix 9.3), it is an expensive and relatively permanent structure that is poorly suited to most applications.

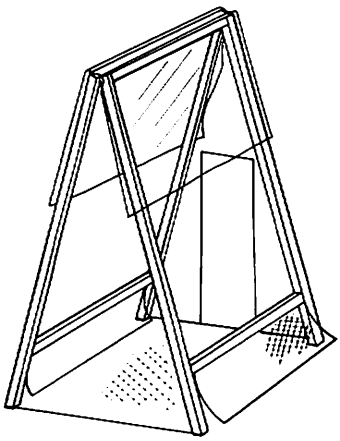
Whenever stream depth exceeds more than a few centimeters, floating or suspended traps become a practical alternative to stationary cages. Under conditions of low to moderate flow, many of the floating traps used to sample standing water can be adapted for this purpose. Surface drift can be excluded



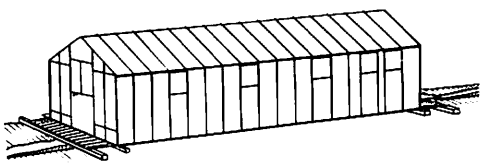
(a)



(b)



(c)



(d)

Fig. 6.11 Traps for shallow running water. Designs originally described by: (a) Needham (1908), (b) Harper & Magnin (1971), (c) Anderson & Wold (1972), (d) Illies (1971).

if the trap sides extend several centimetres into the water around the entrance. This modification also helps create a still pool inside, which reduces the number of insects that are washed away by current. Adding an entrance baffle similar to those illustrated in Fig. 6.12c and d further protects against catch loss. Where flows are more extreme, traps may be protected from upset by currents or floating debris by trailing them in the lee of a floating boom (Fig. 6.12b) or by enclosing the sampler in a rugged, boat-like float (Fig. 6.12a, but see also Section 4.4 on float colonization). Further details on the construction and use of floating traps are given in Appendix 9.3.

The problem with using surface traps to estimate emergence from running water is that effective sampling area and origin of the specimens cannot be easily discerned. Samples are a composite made up of insects from the substrate beneath the trap, those from the subsurface drift, and, in the case of some large species of Ephemeroptera and Trichoptera, those that arrive with the surface drift and simply crawl into the trap to use it for refuge or as a convenient place to oviposit.

Several traps have been built to selectively sample each of these catch components. A triangular pyramid (Fig. 6.13a), set with its base just above the substrate, and an open-bottom box with screened ends (Fig. 6.13b) placed directly on the stream bed, each sample insects from an area directly beneath and exclude drifting insects. The trap shown in Fig. 6.13c samples only the drift component. Surface or subsurface flow enters the trap through a narrow slit and exits from a large, partially screened opening at the rear and insects emerge into a pyramid-shaped air chamber located over the exit screen. Similarly, a plankton net attached to a wedge-shaped headpiece with a slit entrance (Mundie 1971b) can be used to collect drifting insects and exuviae from streams. A composite sample of drifting and emerging insects originating from a known area of stream bed can be obtained by constructing an experimental channel (Fig. 6.13d) which has a collecting net over its outlet and a fine mesh (200 μm) screen attached to the upstream end to exclude stream drift from the outside. Finally, tent or cage traps similar to those previously mentioned for use in standing water can be set along the edge of the stream to monitor bank-emerging species, although, as Williams (1982) estimated, this component of emergence may represent less than 10% of the total for a small, north-temperate stream.

As an alternative to sampling insects directly, Thienemann (1910) suggested that pupal exuviae, which are distinctive for most species, could be collected and used to monitor emergence. This method has been used by Humphries (1938) and Carrillo (1974) for lakes and by Coffman (1973) to study emergence phenology in a stream. While the sampler shown in Fig. 6.13c or the modified drift net of Mundie (1971b) (Appendix 9.3) can be used to collect exuviae from the surface drift, experiments by Wilson & Bright (1973) suggest

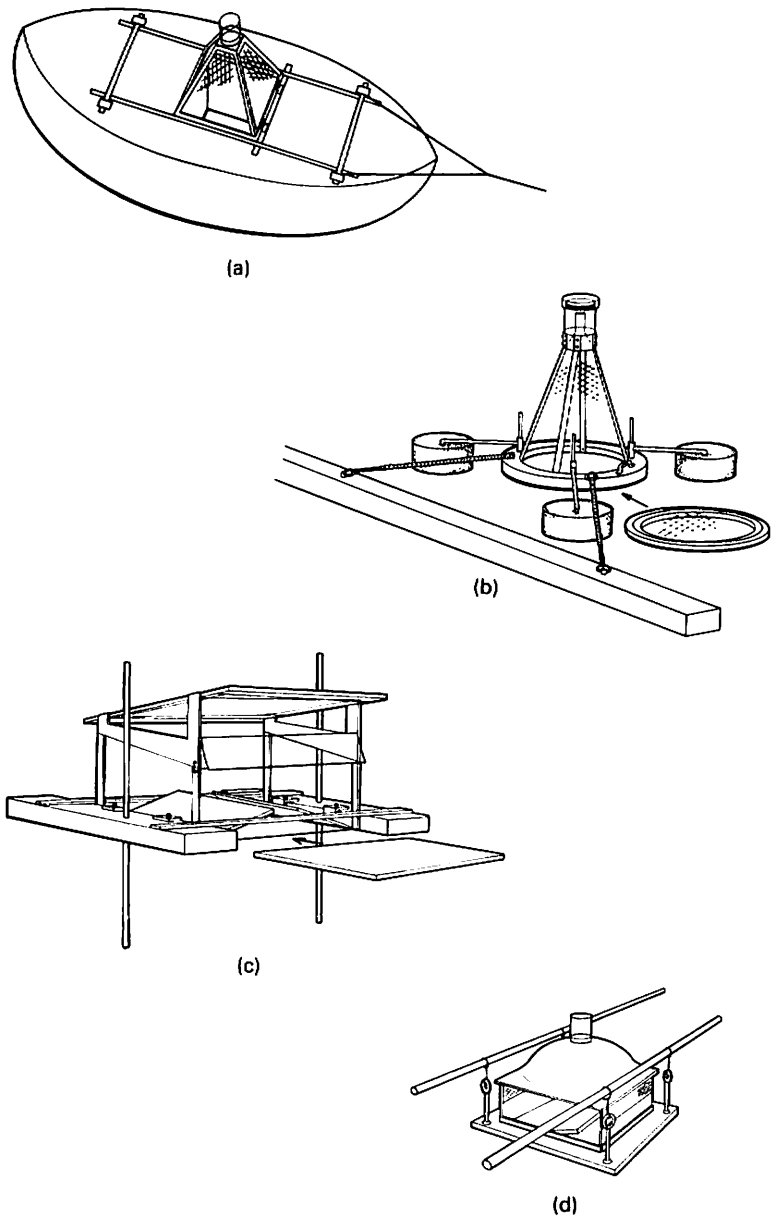


Fig. 6.12 Floating and suspended traps for streams and rivers. Designs originally described by: (a) Langford & Daffern (1975), (b) Corbet (1966), (c) Boerger (1981), (d) Nordlie & Arthur (1981).

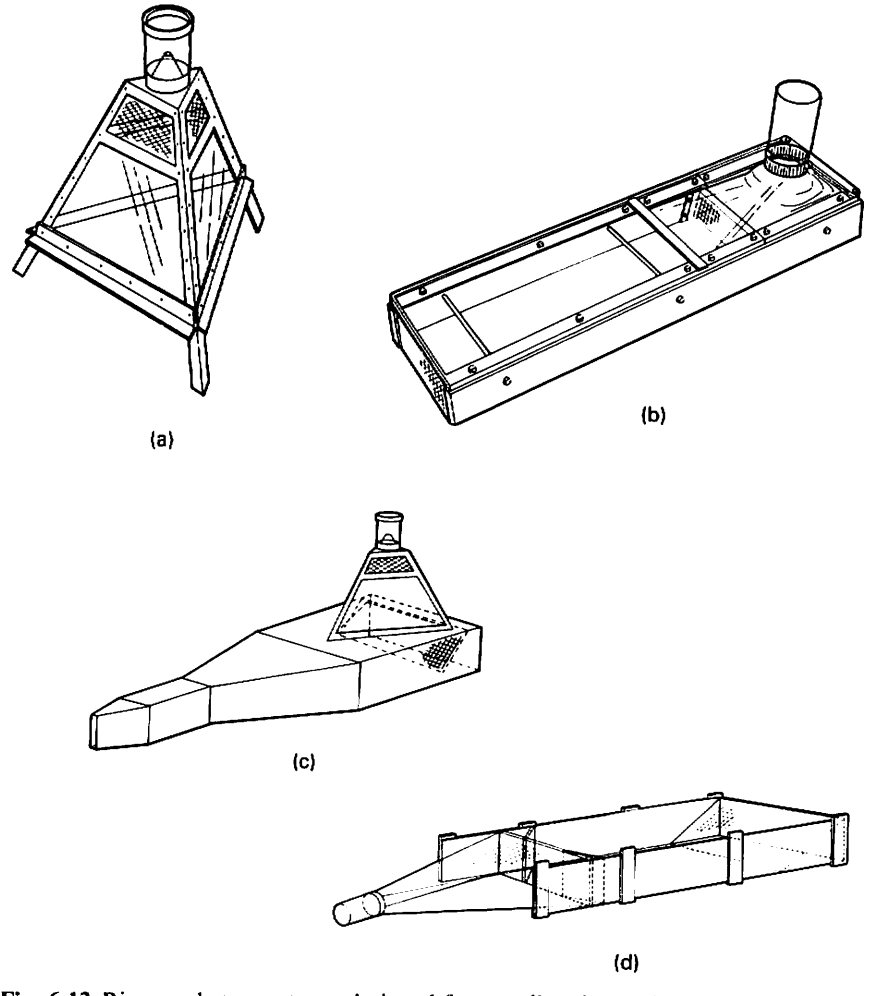


Fig. 6.13 River and stream traps designed for use directly on the substrate by: (a) Mundie (1956), (b) Hamilton (1969), (c) an enclosed bottom, drift sampler (Mundie 1964), (d) an experimental channel (Wartinbee & Coffman 1976).

that, at best, this method yields a qualitative sample of local populations. They concluded that exuviae only remain afloat in a stream for about 2 h and that many of these were washed up onto the bank or became entangled in weeds.

4 Factors Which Influence the Performance of Emergence Traps

Although much effort has been devoted to the design of emergence traps, few attempts have been made to understand the basic principles that govern their

performance. Evidence to support claims that a particular design attribute improves trap performance or that one design is superior to another is often anecdotal, qualitative, or based on single experimental trials with little or no replication. It should not be assumed that these data are misleading or suspect, but rather that testing has been inadequate and that the list of variables which control trap sampling efficiency is incomplete.

4.1 Transparency

Light plays an important modifying role in insect emergence. For most species, patterns of emergence show a diel periodicity that is closely correlated with ambient light levels. Many species exhibit strong positive phototaxis, a behavior which Scott & Opdyke (1941) tried unsuccessfully to use to attract insects toward a clear glass sample bottle at the top of a darkened cage trap. Over a seven day test period the total number of insects accumulated in daily collections from a darkened trap was only 12 % of the emergence measured by an adjacent unshaded trap (Fig. 6.14), suggesting that pupae and nymphs actively avoided the darker one. This avoidance reaction was particularly noteworthy because most emergence occurred during low light conditions at dusk, with a second minor peak at dawn. Mundie (1957), Sublette & Dendy (1959) and Morgan *et al.* (1963) also mentioned that insects tended to avoid opaque traps.

A field experiment by Kimerle & Anderson (1967) compared the catch performance of clear and opaque versions of three trap types: a submerged pyramid, a floating pyramid and their staked box design, and showed consistent catch reductions of 80 % for opaque traps of each model (Fig. 6.14). Similar results were obtained when they used clear and blackened funnel traps to monitor emergence from a tank in two sets of well replicated laboratory experiments. Fast (1972) also noted catch reductions when he covered his traps with black plastic instead of the usual clear polyethylene.

Boerger (1981) used floating box traps to empirically define the relationship between trap opacity and relative sampling efficiency over a range of transparencies from 0 % to 80 %, in increments of 20 %. Within the limits of experimental error, results (Fig. 6.14) showed a threshold effect for chironomid emergence. No significant differences in efficiency were noted among traps that transmitted more than 60 % of ambient light, but below this level, catches were abruptly halved.

In the first of a set of three experiments in which I examined the effect of trap transparency on the catch performance of submerged funnels, a straight line relationship existed (Fig. 6.14, 1978 data) between these two variables when traps set 0·5–1·0 m above the bottom were used to sample chironomid emergence from a shallow (2 m) bay. Below 50 % transparency, submerged

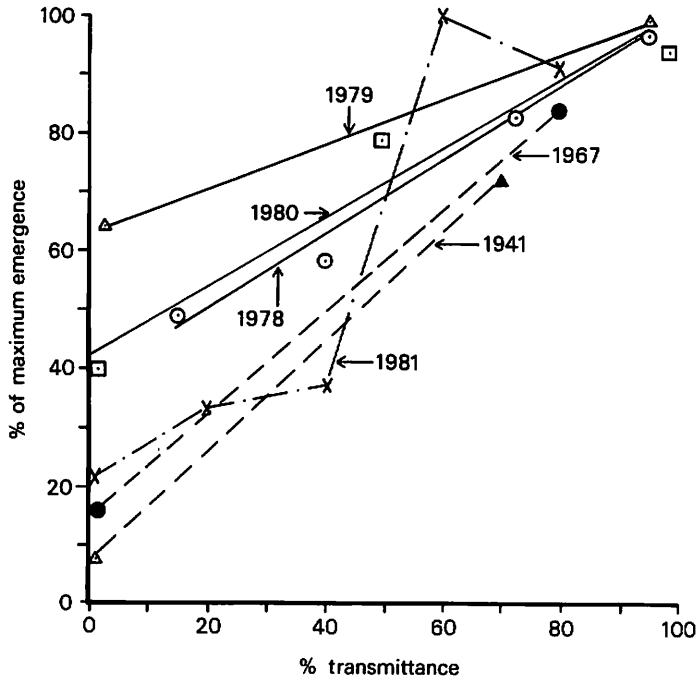


Fig. 6.14 Emergence trap transparency as a percent of surface light and its effect on trap capture efficiency. A linear decrease was assumed for all data except that of Boerger (1981) who proposed a threshold effect. Scott & Opdyke (1941), ▲, floating pyramid; Kimerle & Anderson (1967), ●, staked box; I.J.Davies (1978 ⊙, 1979 △, 1980 ⊡ unpublished data), submerged funnel; Boerger (1981), ×, floating box.

traps always sampled with a higher relative efficiency than the surface designs tested by Scott & Opdyke (1941), Kimerle & Anderson (1967) and Boerger (1981). In this and subsequent experiments a minimum of three traps of the Hamilton (1965) type, modified as shown in Fig. 6.4c, were used for each transparency. Funnels were sprayed on the outside surface with grey paint to achieve the required opacity and transparency was measured *in situ* with an underwater light meter. Sample bottles were not painted. Traps were sampled for one 24 h period each week throughout the ice free season and emergence rates for the periods between samplings were estimated by linear extrapolation in order to calculate season totals, which formed the basis of comparison among traps (see Section 8 for calculation details).

In order to determine whether the reduction measured in the first experiment applied when the distance between trap and substrate was increased, I hung clear and opaque traps 1 m below the lake surface over a deeper (5 m) location. Although individual estimates of emergence (Fig. 6.14,

1979 data) were quite variable, the mean value for opaque traps was 60% of that for clear traps, suggesting that part of the observed reduction at shallow stations could be attributed to a bottom shading effect.

In a third experiment, traps set within 1 m of the bottom at a 2 m deep location, were removed between sampling periods to minimize their influence on periphyton growth or larval activity prior to emergence. Results (Fig. 6.14, 1980 data) were identical to those of the first experiment; thus either shading effects were established very rapidly or they did not cause pupae to migrate away from the area prior to emergence.

Regardless of whether the relationship is a linear or a threshold phenomenon, traps made from opaque materials catch fewer insects than clear traps of the same type. In practice, most standard traps transmit between 70% and 95% of ambient light. Unless design changes produce a major increase in transparency, improvements in catch performance will probably be obscured by normal sampling variance. However, algae and detritus build-ups, which prevent the traps from operating at maximum efficiency, and larval insects that colonize the trap surface and may eventually contaminate the catch should be periodically removed by brushing.

4.2 Effect of trap size on catch

The catch performance of an emergence trap can be influenced by size in two ways. First, effectiveness and reproducibility of a trap are related to the area which it samples. Large traps are best suited to collecting a few rare species along with numerous common insects, while small traps catch fewer specimens but generally show less sampling variability. Second, the efficiency of a trap may change with size; if the entire trap is enlarged or reduced characteristics such as internal temperature, shading, pupal avoidance or catch retention may change disproportionately. For example, in the arctic, where insect flight is often impaired by low temperatures, the percentage of the total catch entering the apical sample bottle of a floating pyramid trap will diminish as the trap is enlarged if height changes in proportion to basal area. Problems can also arise when some trap dimensions are scaled disproportionately. If the basal area of a submerged funnel trap is enlarged without increasing the size of the sample bottle, the air space inside may be too small to accommodate all of the specimens during periods of peak emergence. Many insects may then die due to overcrowding and fall back onto the water surface where they, along with the exuviae that remain, decay and sink or block the entrance of pupae into the sample bottle. I shall refer to this temporary decrease of capture efficiency as 'trap saturation'.

Although size and area are important variables in trap design, little has been done to quantify their relationship to catch performance. Scott &

Opdyke (1941) suggested that, on the basis of catch per unit area, floating pyramid traps with a basal opening of 0·25 m^2 were more efficient than 1·0 m^2 versions of the same design, used the previous year. Morgan *et al.* (1963) compared the catches of three adjacent box traps of basal areas 0·37, 0·46 and 0·70 m^2 and concluded that the mid-size trap was the most efficient. No optimum size should have been assigned in either case. Experimental designs were incomplete, unreplicated and ignored either spatial or temporal variations in emergence patterns.

Mundie (1956) suggested that ascending pupae might find it difficult to avoid large traps; capture efficiency should, therefore, be directly related to trap area. Palmén (1962), however, reported that submerged funnel traps with basal areas of 0·25, 0·50 and 1·0 m^2 sampled with equal efficiency, but no data were presented. In a well replicated experiment, Rosenberg & Wiens (1983) showed that submerged funnel traps with basal areas of 0·10 and 0·28 m^2 gave equal mean estimates of chironomid emergence from a reservoir over a 93 day experimental period. Although the means were equal, samples with the highest variability were consistently obtained from large traps.

The results of a short experiment which I conducted to determine relative capture efficiency of submerged funnel traps, each with the same size sample bottle but different basal areas, are shown in Table 6.2. All traps caught chironomids with equal efficiency and showed no evidence of saturation at an average emergence rate of 49 individuals $m^{-2} d^{-1}$. Coefficients of variation indicate the relative uniformity of emergence throughout the test location.

Table 6.2 Chironomid emergence measured at a 2 m deep location in Lake 226 NE, Experimental Lakes Area (ELA), with submerged funnel traps of four different basal areas. All types were equipped with 375 ml (58 mm cap diameter) glass sample bottles. Tabulated values are estimates of total emergence (number m^{-2}) for each trap over a 37 day experimental period, calculated as the integral of 8 separate 24 h collections (see Section 8). Mean and coefficient of variation (C.V. = standard deviation as a percentage of the mean) are also listed for traps of each size.

	Trap area (m^2)			
Replicate No.	0·05	0·10	0·15	0·25
1.	1631	700	2641	1995
2.	2161	1707	2164	1330
3.	2874	1597	1021	—
Mean =	2222	1335	1942	1663
C.V.	28·1%	41·3%	42·9%	28·3%

4.3 Tilting of the trap

Jónasson (1954) and Morgan *et al.* (1963) speculated that submerged funnels may have underestimated emergence because the effective sampling area decreased each time the traps were tilted by wave action. The size of this reduction can be calculated by simplifying trap movements and expressing them as simple harmonic motion.

Consider a funnel with a cone pitch of 50°, driven by wave action so that it swings like a bell through an angle of 45° in each direction. Further angular displacement would cause air loss from the bottle and identify samples as invalid. At the maximum height of each swing, a projected view of the trap base becomes an elipse covering 71% of the maximum sampling area. An analytical solution to the equation of extreme trap motion shows that a time-averaged reduction of basal area is only 13% (F.A.J.Armstrong personal communication). In a real system, where such motion is rare, differences should routinely be less than 5%; an insignificant level of error.

4.4 Float colonization

A serious source of sample bias comes from the use of foam plastic floats around the basal entrance of surface traps. These plastics are rapidly colonized by insect larvae or nymphs that eventually mature and emerge into the trap. Langford & Daffern (1975) showed that, over the course of one season, foam polystyrene which surrounded the underwater entrance to their trap became heavily colonized by Ephemeroptera nymphs. Wrubleski & Rosenberg (in press) noted abnormally high catches of two species of *Glyptotendipes* (Chironomidae) in a version of the LeSage & Harrison (1979) trap. The source of these adults was a large colony of *Glyptotendipes* larvae that had established itself in the foam polystyrene floats around the base of the trap.

Minor modifications to trap design can usually eliminate or reduce sample bias caused by float colonization. Hollow plastic floats, available from commercial fishing supply outlets, empty plastic containers, or lengths of plastic pipe and standard plumbing fittings (of PVC or ABS plastic) can be used to construct air-filled floats in a variety of shapes and sizes. These floats can easily be kept free of larvae by periodically cleaning them, but because they can develop leaks, they lack the inherent reliability of foam materials. Alternatively, foam floats can be sealed in polyethylene bags or simply placed away from the trap entrance. Where water depth and current permit, the latter solution can be achieved by using submerged traps or by extending the entrance of a surface model considerably below the floats, a modification

which also prevents catch loss when wave action breaks float contact with the water surface.

4.5 Trap depth

The interpretation of catch data from emergence traps used to sample standing or open water habitats depends on the premise that trap catch accurately reflects the distribution and abundance of larvae or nymphs in the substrate beneath. Implicit in this assumption is the understanding that insects rise vertically through the water column without being displaced horizontally and that fish predation is minimal as larvae or nymphs swim to the surface.

At shallow stations there is reasonable evidence to support this view. Borutsky (1939a) observed only a 4% difference in the catches from traps set near the bottom and those hung just below the water surface. Palmén (1955) reported that a pair of funnel traps placed directly on the substrate and two traps suspended 0·5 m above the bottom at a 1·5 m deep station caught similar numbers of chironomids. In a separate study, Palmén (1962) found that pairs of traps set on the bottom, and at 1 m and 2 m above the bottom all gave the same estimate of emergence.

The extent to which fish prey on insects emerging from the profundal is also unknown. Predation can be eliminated by placing traps directly on the bottom, but, apart from the inconvenience of raising and lowering submerged traps over any distance, the method suffers from a technical problem related to the effect of pressure on gas volume and solubility. For each 10 m increment of depth, pressure increases by one atmosphere. Gas solubility is directly proportional to pressure, while gas volume varies as the reciprocal of pressure. Consequently, the air space inside a submerged trap is first compressed to some fraction of its original volume as the sampler is lowered into position, and continues to shrink as the air dissolves in the surrounding water; thus placing a practical lower limit of about 6–10 m depth on this technique. Jónasson (1954) noted an additional problem: traps set near the bottom at deeper stations caught chironomid pupae, most of which died or failed to emerge. An air bubble, which forms in the thoracic region under the pupal skin just prior to emergence, expands as pupae rise through the water column. It is possible that expansion of this gas bubble aids in the eclosion process. Pressure change may, therefore, be a necessary prerequisite for successful emergence.

Bretschko (1974) designed a funnel trap which sampled directly from the bottom, but, unlike previous designs, did not have to be lifted to be emptied. A long hose (25 mm diameter) connected the trap apex to a detachable sample bottle at the water surface. Preliminary results indicated that the hose

did not inhibit emergence, as the number of adults in the trap corresponded roughly to the decrease in developing larval populations beneath.

4.6 Design of the sample chamber

Once insects are inside, the utility of an emergence trap is largely determined by the design of the sample chamber. In its simplest form, the chamber is an open-bottomed, air-filled cavity into which insects emerge. Commonly, no provisions are made to retain dead insects, keep specimens in good condition, or to prevent fish from feeding on the catch. Specimen removal is also difficult if the chamber is large. Several modifications have been introduced to improve on this basic design.

To facilitate sample removal, the entire catch of a submerged trap is contained within an emergence chamber formed by an air space inside a sample bottle. If a funnel (Fig. 6.3c) or 'stand pipe' (Fig. 6.2d, e) entrance is added at the mouth of the bottle, catch retention is improved, but the condition of the specimens remains a function of the number of insects in the chamber and the length of time which they are left there. Although sample retention is improved by this technique, overall sampling efficiency may be decreased if the modification blocks or discourages insects from entering the sample bottle, or if the presence of additional specimens damages other insects in the catch (Rosenberg & Wiens 1983).

A sloping baffle, added to some designs of surface trap (Figs. 6.1c, 6.8b, 6.12c, d), forms a one-way entrance that prevents catch loss. Baffles placed below the water surface inside a trap retain imagoes, pupae and exuviae but may do little to prevent fish predation; when placed above the water line (e.g. Fig. 6.12c, d) they keep adults dry in the upper portion of the trap and away from fish. Disadvantages of the latter arrangement are that pupae, exuviae and adults that fail to fly past the baffle are not included in the sample.

To simplify the job of removing insects from tent or cage traps, several models have been fitted with a removable sample bottle, usually located at the highest point of the funnel or pyramid-shaped emergence chamber, where flying insects tend to congregate. A funnel-shaped entrance (Fig. 6.7a) or an auxillary cone in the sample bottle (Fig. 6.8a) ensures that specimens which enter are retained. The efficiency of this sample collector will depend on the amount of light at the top of trap, the strength of the phototactic response and flight activity of the specimens. Each of these variables is related to time of day and air temperature, so the effectiveness of the collector will vary accordingly.

The use of preservatives (usually alcohol or formalin based) in the sample bottle of submerged (Fig. 6.3a) or surface traps (Figs. 6.1e, 6.7a, d, 6.12b) is not recommended. Although such preservatives may keep the catch from deteriorating, insects may not be saved in optimum condition. For example,

Mundie (1964) stated that chironimid wings do not inflate properly if the adults die immediately after emerging. Long periods of record may also be lost if preserving traps are left to sample for an extended time and become damaged or upset. Furthermore, Potter & Learner (1974) showed that some preservatives can adversely affect catch performance. Traps with 70 % alcohol or 4 % formalin (1·5 % aqueous formaldehyde) caught fewer insects than those containing a saline-detergent-copper sulfate solution.

4.7 Temperature and frequency of emptying

While the thermal tolerance limits of many insect species differ, their lifespans and decomposition rates after death are temperature dependent processes. High temperature inside a trap can cause significant mortality, such as that reported by Sandrock (1978) for the greenhouse design of Illies (1971). Although traps set over water tend to moderate daily extremes, mean temperature plays an important role in determining how frequently traps should be emptied.

For lake temperatures below 5 °C, Welch (1973) found no evidence of chironomid mortality when submerged traps were emptied at three day intervals. Laville (1971a) concluded that weekly collections were sufficient for traps at a cold alpine study site, whereas Mundie (1956) recommended that submerged traps with funnel entrances be emptied at least twice a week in temperate summer climates, and Palmén (1962) advised daily servicing.

Trap design also plays an important role in determining the frequency of sample collections. Experiments by Morgan & Waddell (1961) and Morgan *et al.* (1963) showed that open-bottom box traps emptied several times a day gave the same total estimate of emergence as those emptied once daily. No mortality occurred in the box traps, but several dead insects were found in a submerged funnel after only one day. Boerger (1981) found that over a four day sampling period, floating box traps with entrance baffles (Fig. 6.12c) retained specimens in good condition. Traps without baffles yielded the same total number of insects if sampled daily, but considerably fewer if left for the full four days. Tests by McCauley (1976) showed that catch loss from surface funnel traps (Fig. 6.8b), which were stocked with known numbers of one-day-old chironomid adults, remained fairly constant at 5 % of the catch per day over a 10 day experiment. In addition, loss rate was independent of stocking density up to a simulated emergence rate of 100 individuals $m^{-2} d^{-1}$.

4.8 Predation

Several studies have shown that predation is a problem in emergence traps. Reported instances of insect predators include: Empididae (Sprules 1947;

Morgan *et al.* 1963); Trichoptera larvae (Jónasson 1954); halipid and gyrinid beetles (Morgan *et al.* 1963); spiders (Morgan *et al.* 1963); mites (Mundie 1956); dragonflies and damselflies (LeSage & Harrison 1979). In addition, Palmén (1962) reported losses of pupal exuvia to amphipods.

The narrow, upper portions of surface traps, where insects tend to congregate, is a favourite hunting place for the spiders and dragonflies which are frequently caught when traps are set over vegetation. Even if traps are equipped with a sample bottle containing preservative, predators will usually avoid it and continue to capture insects as they emerge into the trap. The only practical solution is to inspect traps frequently and remove predators at least once a day.

Fish are rarely mentioned as predators in emergence traps, even though insects are one of their major dietary items. Mundie (1956) found larval minnows <8 mm long in submerged traps, but concluded that they were probably too small to eat insects. An examination of the adult:exuviae ratio in the catch of submerged funnel traps, used at the Experimental Lakes Area (ELA) suggested that fish predation was a problem at some stations (Davies, unpublished data). Dipteran adults and exuviae generally occurred in equal numbers in the catch, except when water temperatures exceeded 22 °C and exuviae deteriorated rapidly (i.e. $A:E > 1$). Occasionally ratios $\ll 1$ were recorded for some stations. A small cone placed in the sample bottle of traps at these locations retained cyprinids and larval fish that entered the trap, thus confirming the predation problem. Attempts to exclude these fish by redesigning the entrance to the sample bottle have failed; the only sure solution has been to set traps directly on the bottom, a method that sometimes creates more problems than it solves.

5 Tests of Sampling Efficiency

Emergence traps have been in use for more than 75 years, yet there is surprisingly little data to indicate whether the samples that they provide are accurate or simply qualitative. Initially, traps were used as qualitative samplers to make taxonomic collections, study emergence phenology (temporal sequence) as an aid to understanding life histories, and to investigate phenomena such as the diel periodicity of emergence. More recently, traps have been used to make quantitative collections for estimating total emergence, but evidence to support their use in this role is far from conclusive.

5.1 Absolute accuracy

Three lines of investigation have been used to determine the accuracy of emergence traps:

(1) Field observations.
(2) Analysis of catch data.
(3) Comparison of total measured emergence with an expected value, calculated either as the difference in larval abundance before and after the emergence period, or as the number of mature larvae in the sediment just prior to emergence.

Using the first two methods, several authors have shown that traps were inappropriate samplers or gave biased estimates of emergence for some species. Wohlschlag (1950) noted that large species of caddisflies, mayflies and dragonflies were able to crawl out of his partially submerged pyramid trap. Corbet (1964) suggested that during periods of windy weather dragonflies may preferentially seek out surface traps for shelter. A sex ratio that differed greatly from the expected value of one, led Illies (1971) to conclude that female Simuliidae (*Odagmia ormata*) used his greenhouse trap as a refuge. The data of Flannagan & Lawler (1972) show that, for several species of Trichoptera, submerged funnel traps caught large numbers of females but few males, indicating a possible trap bias.

Table 6.3 summarizes the results of several attempts to measure trap sampling efficiency by the third, or experimental, approach. In each case, submerged funnels were used to sample chironomid emergence. Overall, the results are inconclusive and highly variable, but it may be unreasonable to expect otherwise, given the number of species and methods involved in these tests. It is instructive, however, to consider the errors associated with such experimental estimates. First, the technique ignores mortality and predation losses that occur between the time that the larvae are sampled and the onset of emergence. Welch (1976) showed that these losses could amount to more than half of the standing crop of fourth instar larvae present just prior to emergence, and corrected his estimates accordingly. Real sampling efficiency of traps may, therefore, be considerably higher than values reported in Table 6.3. A second source of error which causes an underestimate of trap efficiency was reported by Potter & Learner (1974) who found that blue-green algae accumulated in the top of their traps and blocked pupal access to the sample bottle. Under the same conditions, floating box traps were 2–3 times more efficient, presumably because they did not concentrate the algae and allowed more surface area for emergence. A third source of error, an underestimate of larval abundance, may give rise to an inflated value of trap efficiency. Except where calculated efficiencies exceed 100 %, this type of error can easily go undetected. If larvae are sampled after the onset of emergence or if they continually migrate into a habitat, an underestimate of their abundance will result. While the latter hypothesis is convenient, there is little published evidence to support the claim that chironomid larvae in lakes undergo purposeful migrations just prior to emerging (see Section 6.1).

Table 6.3 Sampling efficiency of submerged funnel traps, calculated by expressing numbers of captured Chironomidae as a percentage of the decrease in larval standing stock. Larval abundances were not corrected for mortality or predation losses except by Welch (1976). Potter & Learner's (1974) results are given only for species ≥5% of the total trap catch.

Study	Chironomid	Trap efficiency
Borutsky (1939a)	*Chironomus plumosus*	13%–17%
Borutsky (1939b)	Tanypodinae	55%–76%
Jónasson (1954)	*Chironomus anthracinus*	54%
Mundie (1956)	Tanypodinae	79%
	Chironomus plumosus	15%
	Tanytarus sp.	2%–6%
Hamilton (1965)	Overall	~36%
Sandberg (1969)	Overall (mud bottom)	12%–16%
	Overall (*Cladophora*)	74%
Laville (1971a)	Overall (deep stations)	30%–63%
	Overall (shallow stations)	24%–83%
Bretschko (1974)	*Lauterbornia coracina*	93%
	Micropsectra contracta	>43%
	Heterotrissocladius marcidus	220%
	Heterotrissocladius grimshawi	97%
	Paratanytarsus austriacus	190%
	Protanypus forcipatus	>31%
	Estimated overall	~50%
Potter & Learner (1974)	*Procladius choreus*	15% and 7%
	Psilotanypus rufovittatus	18%
	Glyptotendipes paripes	3% and 2%
	Microtendipes sp.	12% and 16%
	Tanytarsus inopertus	8% and 3%
	Tanytarsus lugens	10% and 6%
Welch (1976)	*Pseudodiamesa arctica*	343%
	Lauterbornia sp. nov.	26%
	Trissocladius sp. nov.	31%
	Orthocladius spp.	125%
	Overall	46%

The results of two experiments suggest that some traps provide accurate estimates of emergence under laboratory conditions. Kimerle & Anderson (1967) and McCauley (1976) measured total emergence from a screen-covered tank or pool stocked with sediment and chironomid larvae. In each case, these totals were compared on an areal basis to simultaneous estimates of emergence from traps set inside the experimental enclosure. Kimerle &

Anderson found that surface traps made from plastic funnels gave a 10% overestimate of total emergence, while McCauley, using clear vinyl funnels set as surface traps, found that actual and estimated totals of emergence were not significantly different.

5.2 *Comparative efficiency*

5.2.1 Submerged versus surface traps

Most tests of trap efficiency compare the relative catch performance of two different designs and comparisons are usually undertaken to select traps that give the highest catch per unit effort, to calibrate a new model against some standard trap, or to demonstrate that two designs sample with the same efficiency. Tests therefore reflect the relative merit of each trap as a sampler in a particular application; under other circumstances, the sampling efficiency of each design can be considerably different.

To illustrate this variability, consider a popular test in which the catch performance of submerged funnels is compared with that of floating or staked box traps. Guyer & Hutson (1955) claimed that funnel traps made of sheet metal and floating box design of Macan (1949) sampled with equal efficiency. Morgan *et al.* (1963) showed that a pair of floating box traps (Morgan & Waddell 1961) each caught three times the number of insects and 60% more species than a single submerged funnel (Jónasson 1954) of the same basal area. Kimerle & Anderson (1967) compared their staked box design with a submerged pyramid of equal sampling area. Over a 33 day experiment, the sum of daily collections from the box totalled 20 times the number of insects sampled by the submerged trap. A repeat of the Kimerle & Anderson experiment (Davies, unpublished data) based on a full season comparison between three staked box traps and three submerged funnels (Fig. 6.4c), basal area of all traps = 0·2 m^2) in a shallow, well-sheltered bay of Lake 239 (ELA), showed that annual estimates of chironomid emergence from box traps were twice that of the funnels.

These differences are difficult to interpret because critical pieces of evidence are missing. Laboratory studies (Kimerle & Anderson 1967, McCauley 1976) have shown that, under controlled conditions, surface traps sample with 100% efficiency; however, no comparable experiments have been performed with submerged traps. Absolute sampling efficiency of submerged funnel traps has been measured in several field experiments, but the results are quite variable and inconclusive (Table 6.3). Similarly, an attempt by Potter & Learner (1974) to estimate the accuracy of floating box traps showed that for species making up more than 5% of the total catch, trap efficiency varied between 14% and 65% of the potential emergence yield.

Kajak (1958) proposed a mechanism to explain why surface traps catch more than submerged models. He noted in an experiment that funnel traps caught the same number of insects when placed directly on the bottom as they did at the surface when they were mounted inside a close fitting mesh cylinder that extended down to the sediment. Traps floated on the surface without cylinders caught between three and six times more than those with cylinders, implying that the floating traps caught more because they attracted pupae or adults. Kajak speculated that insects with nocturnal or crepuscular habits were attracted by the reduced light regimen inside the muslin covered traps, but this mechanism contradicts the usual inverse relationship between transparency and catch performance and fails to explain the results of Morgan *et al.* (1963) and Kimerle & Anderson (1967), who each used highly transparent traps. It is possible, however, that pupae were attracted to the calm water inside the floating traps. Although it is not clear whether pupae can distinguish sheltered areas, it would be a selective advantage for the eclosion process if they could. This attraction hypothesis is consistent with the observation that catches are always highest in surface traps. It also explains why in the Lake 239 experiment, where the water was usually calm and there was little to distinguish between the inside and outside of a surface trap, the differences in catch between surface and submerged traps were smaller than those observed in the open water comparisons done by others.

Regardless of whether insects are attracted to surface traps or avoid submerged ones, the source of the consistent catch difference observed between the two types must be resolved by further testing before emergence traps can be used with confidence to obtain accurate estimates of insect emergence for standing water habitats.

5.2.2 Stream traps

Floating box traps with open bottoms perform poorly in streams. A test by Gledhill (1960) showed that a benthic pyramid trap (Mundie 1956) retained its catch, while a floating box (Macan 1949) did not. Macan (1964) repeated the experiment and included an additional comparison between his box trap and a floating cone (Mundie 1956). Boxes trapped more Ephemeroptera, but fewer Trichoptera per unit area than the cones, and only 64% of the trichopteran species found in the cones. The pyramid trap consistently gave the highest estimate of total emergence and caught more species of Ephemeroptera, Plecoptera and Trichoptera than the other traps. Macan suggested that catch loss, particularly from the box trap, was the major reason for the observed differences. Boerger (1981) showed that chironomid losses from floating box traps could be drastically reduced or eliminated if traps were equipped with entrance baffles.

Catch loss can also be reduced by placing traps on the stream bottom. To test whether the sampling efficiency of these 'containment' traps was a function of size or design type, Flannagan (1978) used large cage traps (1·0 m^2 base) and small (0·1 m^2 base) low-profile samplers (Hamilton 1969) to sample a stream. Both models were set directly on the bottom and each gave similar estimates of trichopteran emergence on an areal basis. The data of Sandrock (1978) suggested that greenhouse traps collected fewer insects per unit area than smaller tent traps; insect mortality due to high temperature inside the greenhouse seemed to be the principle reason for this difference. Apart from these few studies, there is little other evidence to evaluate the efficiency of stream traps.

6 Patterns of Emergence

During their brief period of sexual maturity, adult insects must survive predation and the rigors of the terrestrial environment until they can reproduce successfully. Many aquatic insect species accomplish this by emerging in a highly synchronized fashion at a distinct time each season. This mass emergence of a few species at a time maximizes the chances of mating success, prevents interference from other insects and helps to keep losses to a minimum by briefly 'saturating' the predation mechanisms. Other aquatic insects choose asynchronous emergence as a reproductive strategy. The net result is a temporal series of species emerging in pulses throughout the season, superimposed on a lower, more continuous background rate of emergence.

In addition to separations in time, the emergence of some species is further localized by habitat. These spatial patterns, such as the general decline of total emergence with depth in a lake, or the close association between leaf-mining Chironomidae and specific types of vegetation, may reflect the food habits of the larvae. A second type of habitat association comes from specific emergence requirements, such as the need for Odonata nymphs to crawl to shore, or climb onto rocks or vegetation before eclosion can take place.

Corbet (1964) identified four basic temporal patterns: continuous, sporadic, seasonal, and rhythmic. Continuous emergence shows no seasonal trends and occurs mainly in the tropics. Elsewhere, a few species of stream insects and some members of the genus *Cricotopus* exhibit this behaviour in temperate systems that do not freeze. Sporadic emergence is exemplified by *Hexagenia* sp., which emerges along a 960 km reach of the Mississippi River at intervals of 6–11 days (Fremling 1960). Progressions of peak emergence along the river give the illusion of adult migrations. Seasonal emergence is common at temperate and polar latitudes. The length of the season, which shortens as one moves northward, is defined by the period of open water, except in arctic lakes, where ice cover occasionally remains all year round,

forcing insects to emerge through cracks in the ice and from open areas around the shore (Welch 1973, 1976). The timing of emergence within each of the previous categories may be strongly rhythmic. In rare cases, as with the marine chironomid *Clunio marinus*, timing is derived from lunar cycles (Caspers 1951); however, emergence in most species shows a distinct diel periodicity.

Temperature and photoperiod are the variables most likely to control and synchronize emergence, but the relationships are complex and poorly understood. Weather also exerts a modifying influence; insect emergence measured in floating or submerged traps is lowest on stormy or windy days and reaches its highest value during clear, calm periods (Vallentyne 1952; Davies unpublished data).

The onset of chironomid emergence in the spring appears to require a minimum threshold temperature, which ranges from 6·5 °C (Carrillo 1974) to 8 °C (Morgan 1958) for temperate latitudes, 7 °C in alpine climates (Laville 1971a), between 4 °C and 5 °C for high-arctic tundra ponds (Danks & Oliver 1972), and as low as 2 °C for high-arctic lakes (Welch 1973). As water temperature rises, overall emergence increases to a peak value in the first half of the season, then tapers off, sometimes with a minor pulse in the latter half of the season, and ceases before freezeup. Among individual species, though, the timing of emergence and the length of the emergence period is quite variable.

For species that exhibit synchronous habits, the emergence period may extend from a few days to a month or more, but lasts on average about two weeks (Palmén 1955; Flannagan & Lawler 1972). Within a population, protandry (the tendency for the onset of male emergence to precede that of the females) is frequently observed (Palmén 1962; Sandberg 1969; Harper & Magnin 1971; Danks & Oliver 1972; Flannagan & Lawler 1972; Welch 1973; Sandrock 1978).

Distribution of emergence throughout the day is also characteristic for each species. Trichoptera and Chironomidae (particularly the Chironomini and Tanypodinae) emerge primarily around dusk or shortly thereafter, with a second minor peak at dawn (Scott & Opdyke 1941; Sprules 1947; Potter & Learner 1974; Friesen *et al.* 1980; Ali 1980), although Miller (1941) found that maximum chironomid emergence occurred between 04:00 h and 07:00 h daily. The diel pattern may be somewhat more variable for members of other chironomid subfamilies. For example, Potter & Learner (1974) reported that peak emergence of Orthocladiinae occurred at dawn, followed by a lower continuous rate throughout the day with a mid-afternoon minimum, but LeSage & Harrison (1980) found that *Cricotopus* spp. adhered to the common dusk-dawn pattern described above. Simuliidae emerge during daylight hours (Sprules 1947), or from noon until dusk, but seldom after dark (Davies 1950). Ephemeroptera are primarily evening emergers (Sprules 1947; Friesen *et al.*

1980), although seasonal differences may occur (Friesen *et al.* 1980). Flannagan (1978) noted a strong seasonal modification of diel periodicity in trichopteran emergence: in the spring, Trichoptera emerged during the day; by mid-summer, full darkness was preferred; in the fall, peak emergence had reverted to the early evening. Flannagan hypothesized that caddisflies were able to optimize conditions for flight and minimize the risk of desiccation by shifting the timing of emergence according to seasonal conditions. Overall, the emergence of most species is minimum between 09:00 h and 11:00 h (solar time) daily, making this an ideal time to clear or set emergence traps.

6.1 Larval migrations prior to emergence

Spatial and temporal patterns of emergence can sometimes be interpreted in more than one way, giving radically different explanations for a set of observations. For example, it has been noted in several studies that standing crops of larvae in the littoral areas of lakes, measured prior to emergence, seemed insufficient to account for the total number of insects trapped from that area (Borutsky 1939b; Wohlschlag 1950; Bretschko 1974; Bagge *et al.* 1980). The reverse seemed true for the profundal. For each study it was proposed that larvae migrated shoreward just prior to emergence. While such a redistribution may be possible with the highly mobile larvae of *Chaoborus*, and has been shown to occur for one species of chironomid colonizing a newly flooded reservoir (Cantrell & McLachlan 1977), data presented by Borutsky and the others could not rule out the possibility that the apparent migrations may have been an artefact caused by underestimates of larval standing crop (Scott & Opdyke 1941). Alternatively, emergence may be an estimate of production, not standing crop (Illies 1971; Speir & Anderson 1974; Davies 1980), and the apparent disparity between larval abundance and number of adults may simply reflect differences in generation times between warm littoral and cold profundal regions. The issue of larval migrations raised here deserves close attention in future studies because it is fundamental to our understanding of emergence mechanisms.

7 Sampling Strategies and Analytical Techniques

The design of an emergence study follows a simple hierarchical structure. First, a clear definition of a central study purpose is required. Spatial and temporal patterns of emergence, physical restrictions on sampling, habitat diversity and an estimate of the precision needed to answer the question are examined, in turn, to determine where, when and how to sample. Considerations of cost, time and available manpower will further modify the strategy and determine trap type, number of traps and a sampling schedule.

Qualitative studies, aimed at characterizing the insect fauna of a habitat or documenting changes in species composition that result from environmental disruptions, require extensive collections from all parts of the habitat. Except where a single species or group is being monitored, characterization studies usually require a minimum of one full season's data. Where long-term changes are being measured, annual variation in species composition must also be considered. Emergence collections are often made in conjunction with larval sampling programs. Larval material can be used to derive life history information, while examination of emergent adults is often the only way of establishing the taxonomic identity of larvae. To obtain adequate samples from all habitats, a variety of trap designs may be needed. Although it is important that these traps collect all species of interest, estimates of abundance may not be required, so accuracy can sometimes be sacrificed in favour of other criteria. As a result, large, inexpensive traps that are simple to construct and easy to use are often chosen to give the maximum number of specimens for the least cost and sampling effort.

By comparison, quantitative studies are primarily concerned with accuracy and minimizing sample variance. To achieve these goals, the scope of investigations is often narrowed to include only single groups of insects or habitats. Traps are chosen for their ability to sample accurately or with the same relative efficiency at all locations. Trap design should be standardized, whenever possible, to permit comparisons within and between studies. Finally, the emphasis in sampling must be shifted towards replication to allow statistical analysis of the data.

For control versus treatment comparisons involving one variable, such as a test of the relative catch efficiency of two trap designs, simple random sampling with replication is adequate. Where possible, a uniform location should be selected for the tests to minimize random errors. If the abundance of an insect group is measured in several different habitats, estimates of overall variance calculated from a simple random sample will usually be too high. Stratified random sampling (Elliott 1971) can often reduce overall variance, but choice of the stratification criteria is critical (see Chapter 8). In cases where a variable that controls the abundance of insects, such as vegetation density or bottom type, varies along a well defined gradient (e.g. depth), transect sampling approximates the stratified random approach, particularly if the position of the transect is randomized in a direction perpendicular to the gradient. In addition, transect sampling offers two practical advantages over other techniques. First, positional effects, such as orientation to the sun or prevailing wind direction, are held constant along the transect. Second, the orderly arrangement of stations makes them easy to find and minimizes travel time between traps.

To illustrate some of the practical aspects of a quantitative study, consider

the problem of designing a sampling program to give an estimate of total chironomid emergence from a lake. Chironomid abundance is usually a function of habitat type and lake depth at a given location. Because the distribution of emergence is not uniform, a simple random sampling scheme is inappropriate. For shallow lakes with several distinct habitats, stratified random sampling is recommended, with sampling effort distributed among habitats in proportion to their size. Where habitat seems relatively uniform around the lake, a depth-stratified sampling scheme is more appropriate. Trap placement at equal intervals of depth, however, tends to overemphasize the importance of deep stations.

Sampling effort can be equalized by dividing the lake into several intervals of depth and distributing a number of traps among the intervals in proportion to the area that each occupies. If a fixed number of stations is required, however, the lake can be divided into equal intervals of area on a hypsographic plot (area *versus* depth) and the corresponding depth intervals read from the curve.

The choice of a trap will be largely determined by its sampling efficiency, ease of use, cost, and the wind and wave conditions of the lake. Traps should be large enough to ensure that zero counts are rare during periods of emergence. Beyond this minimum, size has no apparent effect (Table 6.2) or a detrimental effect (Rosenberg & Wiens 1983) on sample variance. The number of traps required at each sample location will depend on the aims of the study. While there is some evidence to suggest that a single trap may catch between 80% and 90% of the maximum numbers of insects at any location (Laville 1971a) and approximately 60% of the species (Sandberg 1969; Rosenberg *et al.* 1980), the practice is not recommended. For some specified level of error, it is possible to calculate the number of traps that are required from a preliminary estimate of mean and variance (see Chapter 8). However, an understanding of how the variance of emergence estimates is distributed in lakes may help to assign a reasonable level of expectation of accuracy.

Estimates of the spatial variability of chironomid emergence at a shallow location are given in Table 6.2. Coefficients of variation (C.V.) ranged between 28·1% and 42·9%, and appeared to be independent of trap size. Similarly, five submerged funnels (0·1 m^2), suspended 1 m above the bottom at a 2 m depth location in Lake 239 (ELA), gave estimates of 11 496, 12 324, 8401, 10 997 and 9228 chironomids $m^{-2} yr^{-1}$, a mean of 10 501, and a C.V. of 15·4% (Davies, unpublished data). Considering that trap locations in each experiment were chosen for apparent uniformity of the substrate, these estimates probably represent minimum expected variability among 2 m deep stations in each lake.

Rosenberg *et al.* (1980) measured spatial variability of chironomid emergence in a newly flooded northern reservoir. Clay shorelines were particularly unstable and drowned forest and sunken debris were common in

most areas. Table 6.4 summarizes their results. Variability was highest in the shallows and declined sharply with depth. Although species composition differed at each location, mean emergence at a given depth was similar among shoreline types.

These examples suggest that, beyond a 2 m depth, estimates of emergence can be obtained with a $\pm 30\%$ level of precision from a minimum of two or three replicates at each location. Many more replicates are needed at shallow

Table 6.4 Spatial variability of chironomid emergence and its dependence on depth (from Rosenberg *et al.* 1980, Table 1). Reported values are mean emergence, X (number $m^{-2}\ yr^{-1}$), and coefficient of variation, C.V. (%), for 4 submerged funnel traps ($0{\cdot}1\ m^2$), monitored continuously at each of 4 depths and 3 shoreline types.

Depth (m)	Clay		Bedrock		Marsh	
	X	C.V.	X	C.V.	X	C.V.
1·0	1867	128·9	1765	61·1	769	107·8
2·0	2985	44·9	2509	45·3	2161	20·1
3·5	1356	22·8	1561	15·8	1818	38·9
4·5	764	27·0	1012	19·7	1081	16·7

stations to give the same estimate of precision. Because most areas of the lake do not require extra traps, a decision must be made to either abandon the concept of equal sampling effort, or to accept higher levels of variability in the shallows and minimize the contribution that these stations make to an overall estimate of emergence by increasing the number of sampling strata, thus isolating areas of high variability. The latter solution is usually preferred because it uses fewer traps.

An estimate of long-term fluctuations in insect abundance must be considered whenever systems are compared over several years or when current conditions are referred to previous baseline data, to test for differences. The results of a long-term study to determine temporal variation of emergence at a fixed location are shown in Table 6.5. Single traps, at each of four depths, were used to measure annual emergence of Diptera ($>90\%$ Chronomidae) over 9 consecutive years (Davies, unpublished data). Annual catch differences were highest in the shallows, but variability, expressed as a percentage of the long-term mean for each location, was lowest at the 1 m station and increased with depth. Lake averages were less variable than the results for any individual station. While additional stations were used in the calculation of lake averages, the major reason for the discrepancy is that stations did not respond proportionately to, or even in the same direction, as the overall trend for a

Table 6.5 Long-term variability of dipteran emergence in Lake 226 SW (Experimental Lakes Area). Entries are estimates of emergence (number m^{-2} yr^{-1}) from a single location at each of 4 depths over 9 years, with means ($\bar{X}$) and coefficients of variation (C.V.). Lake-average emergence is corrected for lake morphometry (number m^{-2} yr^{-1}). Bold type indicates years in which emergence increased.

Depth (m)	Year										
	1973	1974	1975	1976	1977	1978	1979	1980	1981	$\bar{X}$	C.V.
1	4403	**11 134**	8138	**11 901**	**14 112**	11 332	6227	**10 228**	10 186	9740	30·8
3	4711	**9 616**	4151	**4 322**	3 477	1 399	**3054**	2 212	**6 259**	4356	55·8
5	2486	2 473	280	**1 591**	1 111	679	**982**	769	**3 969**	1593	73·8
7	19	**697**	70	**140**	**406**	65	**224**	**435**	237	248	92·0
Lake-average	1855	**2 984**	1825	**2 709**	**3 024**	1 921	1675	1 563	**2 992**	2283	27·4

given year, so that individual deviations tended to cancel each other out. Lake-average (or total) emergence appears, therefore, to be the most useful indicator of long-term change. In the absence of whole-lake data, littoral collections made from the same locations each year (a technique used to reduce the spatial component of variability), provide a potentially stable alternative, while the small size and relatively high variability of profundal estimates make them unsuitable as indicators of long-term change.

Emergence trapping programs may be operated on a continuous or periodic basis. Continuous trapping yields more rare species than periodic sampling, but is a time-consuming, labour-intensive practice, so fewer stations, in total, can be monitored. For studies concerned with estimating overall emergence and examining major species, returns can be maximized for a given amount of work by using a large number of traps and operating them discontinuously. Rosenberg *et al.* (1980) showed that, compared to continuous records, information loss was minimal when traps were operated for one 48 h period each week.

A seasonal record of emergence for stations which have been sampled discontinuously may be constructed by plotting daily rates of emergence and extrapolating between the points with straight lines. Total emergence is then equal to the area under the curve between the first and last sampling days (i.e. the integral of daily emergence m^{-2} over the season) and may be calculated as:

$$\text{Integral Emergence} = \sum_{i=1}^{d-1} \frac{X_i + X_{i+1}}{2} \cdot (T_{i-1} - T_i) \qquad (6.1)$$

where: d is the total number of sampling periods in a season. X_i is emergence unit-area^{-1} day^{-1} in the ith sampling period, T_i is the mid-point time of the ith sampling period [i.e. (the day that traps were set – the day they were cleared)/2], and $(T_{i+1} - T_i)$ is the number of days between sampling periods.

Lake total emergence for the season is therefore:

$$\text{Lake total emergence} = \sum_{j=1}^{n} E_j \cdot A_j \qquad (6.2)$$

where: n is the number of sample strata, E_j is the mean seasonal emergence unit area^{-1} (average of sample replicates) in the jth sample stratum, A_j is the area of the jth sample stratum.

Short term comparisons between trap replicates, habitats, or whole systems may yield spurious differences, caused solely by variations in the timing of emergence. Without data for a full season, even species differences should be interpreted with caution. Seasonal data provide the only logical basis for comparing systems, particularly if the total periods of emergence are dissimilar due to latitude or climatic effects. Except where differences in emergence distribution are considered, comparisons between lakes should be

made with annual, lake-average data (seasonal total emergence/lake surface area), a figure which reflects the relative productivity of each system, independent of its size or morphometry.

8 Predicting Insect Emergence

A generalized relationship between the standing crop of benthic organisms and lake trophic status has been recognized for some time (Johnson 1974), but is poorly understood. Vallentyne (1952) showed that the concept could be extended to insect emergence by calculating that total chironomid emergence equalled 0·3 % of annual sedimentation in a lake, a process that was presumed to be a covariate of productivity. Similarly, the relationship between chironomid emergence and the C:N ratio of sediments (Laville 1971b) suggested a link between primary production and emergence, because the C:N ratio of sediments increases as lakes become more eutrophic (Welch 1973). More direct connections with productivity were established by Teal (1957), who estimated that total insect emergence was equal to 4·6 % of gross photosynthesis in a cold, temperate spring, and by Welch (1967), who found that total dipteran emergence amounted to approximately 1 % of gross primary production in a small eutrophic pond. Other studies (summarized in Davies 1980, Table 2) have shown that dipteran emergence accounts for 0·1 %–2·2 % of gross phytoplankton production in a wide variety of lakes.

A number of empirical relationships between dipteran emergence and phytoplankton production (Davies 1980) are summarized in Table 6.6. These relationships were derived from long-term data sets on a number of small shield lakes in the Experimental Lakes Area, ranging in terms of phytoplankton production from oligotrophic (21·0 gC m^{-2} yr^{-1}) to eutrophic (116·7 gC m^{-2} yr^{-1}) (Fee 1980).

Lake-average emergence, as biomass or numbers of Diptera, was strongly correlated with phytoplankton production (equations 1 and 2 of Table 6.6) when data averaged over several years were compared. The depth distribution of emergence was also a function of lake trophic status. Emergence tended to be concentrated in the shallow littoral areas of eutrophic lakes, but spread over a much wider range of depth in oligotrophic systems according to a pattern which paralleled the depth distribution of phytoplankton production in the water column. Thus, equation 3 of Table 6.6 could be used to predict the biomass of emergence at each depth from an estimate of phytoplankton production at that depth, for all lakes, regardless of their overall trophic state. Insect size, however, was related to lake productivity. The average size of an individual adult was largest in eutrophic systems (equation 4, Table 6.6), but within each lake, size was also a function of depth. The number of insects emerging from a given depth, therefore, could not be calculated by dividing

Table 6.6 Empirical relationships between dipteran emergence in lakes and phytoplankton production.

Equation No.	Relationship[1]		Definition of symbols and units
1	$\bar{B} = -0{\cdot}0111 + 0{\cdot}00867\overline{PP}$	$\bar{B}$	Lake-average dry biomass of emergent Diptera, corrected for morphometry ($g\ m^{-2}\ yr^{-1}$).
2	$\bar{E} = 1147{\cdot}5 + 40{\cdot}815\overline{PP}$	B_{zi}	Average integral dry biomass of Diptera emerging per unit area from the ith depth interval ($g\ m^{-2}\ yr^{-1}$).
3	$B_{zi} = 0{\cdot}160 + 0{\cdot}050PP_{zi}$	B_{95}	The depth above which 95 % of the lake-total biomass of Diptera emerges (m).
4	$\bar{W} = -0{\cdot}138 + 0{\cdot}069 \ln \overline{PP}$	$\bar{E}$	Lake-average number of emergent Diptera, corrected for morphometry (Number $m^{-2}\ yr^{-1}$).
5	$\bar{N} = 72\,432(\overline{PP})^{-1{\cdot}202}$	E_{zi}	Average integral number of Diptera emerging per unit area from the ith depth interval (Number $m^{-2}\ yr^{-1}$).
6	$E_{zi} = \bar{N} \times PP_{zi}$	E_{95}	The depth above which 95 % of the lake-total number of Diptera emerge (m).
7	$B_{95} = -1{\cdot}154 + 0{\cdot}972\bar{Z}_c$	$\bar{N}$	Average number of Diptera emerging per gC of PP_{zi}. Units of number $m\ gC^{-1}$ results when estimates of E_{zi} are divided by B_{zi} for each interval of depth.
8	$E_{95} = -0{\cdot}106 + 0{\cdot}819\bar{Z}_c$	$\overline{PP}$	Lake-average phytoplankton production corrected for morphometry ($gC\ m^{-2}\ yr^{-1}$).
		PP_{zi}	Average integral phytoplankton production per unit volume in ith depth interval ($gC\ m^{-3}\ yr^{-1}$).
		$\bar{W}$	Mean dry weight of an individual dipteran adult (mg).
		$\bar{Z}_c$	Mean depth of 1 % of surface irradiance during the ice free season (m).

[1] from Davies (1980).

biomass (B_{zi}, equation 3) by the average weight of an adult ($\overline{W}$, equation 4). Instead, an empirical factor $\overline{N}$ was derived (equation 5) which could be used in equation 6 to calculate numbers of Diptera emerging at each depth from a water column distribution of annual phytoplankton production. Because emergence and phytoplankton production were so closely related, and primary production, in turn, was light-dependent, the mean depth of the euphotic zone was closely correlated with the lower depth limit of emergence (equations 7 and 8).

Although these relationships seem to be powerful tools, they have important limitations. They were derived for lakes in a single geographic and climatic region, from long-term data in systems where phytoplankton were the major primary producers. The relationships might be obscured in individual years by annual variability, or may break down in systems where macrophytes or allochthonous carbon inputs dominate the energy supply. While initial tests suggest that these equations do work in a much broader context, their real value is a conceptual one. They demonstrate a new potential use of emergence studies and emphasize the need for more quantitative work in the field.

9 Appendices

9.1 Emergence traps for open water habitats

Reference and illustration	Description	Comments
Floating traps		
Adamstone & Harkness (1923)	Wood frame base supporting wire hoops covered with a muslin tent.	Trap must be lifted to permit catch removal. Exuviae are not retained.
Miller (1941) Fig. 6.1a	Wood frame base supporting wire hoops covered with a muslin tent. Hollow metal floats are attached to the outside of the frame. Sampling area: 0·37 m^2.	Trap must be lifted to permit catch removal. Exuviae are not retained.
Scott & Opdyke (1941) Fig. 6.1b	A wood frame pyramid covered with coarse mesh over a muslin tent. Sampling area: 0·25 m^2.	Use of an apical sample bottle abandoned in favour of emptying as above. Wire mesh covering protects the trap from animals. Exuviae are not retained.

(*continued*)

Section 9.1 (contd)

Reference and illustration	Description	Comments
Macan (1949) Fig. 6.1f	A wood frame box, covered on the top and three sides with cellulose acetate sheet and on fourth side with fine nylon mesh. A wooden raft with hollow metal floats fits around the trap such that the open base of the box is held just below the water surface. Sampling area: 0·3 m^2.	To retrieve the catch, the box is lifted free of the raft and closed off at its base. Insects are then collected by hand or with the aid of an entomological aspirator. Exuviae are not retained.
Wohlschlag (1950) Fig. 6.1d	A wood frame pyramid covered inside with plastic screen and equipped with a removable glass sample bottle at its apex. Hollow metal floats are attached near the top of the frame. Sampling area: 0·25 m^2.	In use, only the sample bottle floats above the water surface. Exuviae not easily sampled.
Morgan & Waddell (1961) Fig. 6.1g	Similar to Macan's (1949) floating box trap except that the top is a flat piece of acrylic sheet and all four sides are mesh-covered. Sampling area: 0·46 m^2.	Exuviae are not retained. See also: Morgan (1958), Morgan *et al.* (1963), Edwards *et al.* (1964) and Morgan (1971).
Mundie (1971a) Fig. 6.1c	An aluminum (duralumin) frame pyramid with one vertical, mesh-covered side (250 μm opening), three sides and an internal baffle covered with polyethylene film, and a removable glass sample bottle at the apex. All coverings are held in place by aluminum strips bolted to the frame. Sampling area: 0·25 m^2.	The trap can be operated as a surface, semi-submerged or fully submerged unit. The angled internal baffle prevents catch loss.
Boyle (1979) Fig. 6.1e	A wood frame pyramid covered with nylon mesh and supported by foam plastic floatation at its base. A funnel, with holes around the top and the lid of the sample bottle glued to its stem, is set in the apex of the	Although the reported efficiency of the sample collector is high, some insects may remain in the body of the trap. Exuviae are not retained.

Section 9.1 (contd)

Reference and illustration	Description	Comments
	trap and covered with a glass plate. Insects entering the funnel fall into the sample bottle where they are retained. Sampling area: 0·5 m^2.	
Submerged traps		
Grandilewskaja-Decksbach (1935) Fig. 6.2a	A metal frame funnel covered with screen or mesh.	Further details not available.
Borutsky (1939a)	A metal frame covered with screen or mesh.	Further details not available.
Brundin (1949) Fig. 6.2b	A cone of brass screen with its base reinforced with copper wire and a sample bottle bound to the apex with twine. All metal seams are welded. Sampling area: 0·25 m^2.	The trap is suspended by a cord from a surface float attached to a wire yoke, wrapped around a glass sample bottle. Exuviae float on the water surface inside the sample bottle.
Jónasson (1954) Fig. 6.2e	A conical frame of galvanized wire, covered with galvanized mesh and attached to an apical tube. Wire and sheet metal form a hinged bracket to hold a glass sample bottle over the tube with its rim sealed against the outside of the mesh cone. Sampling area: 0·25 m^2.	Apical tube prevents insects from escaping from the sample bottle.
Borutsky (1955) Fig. 6.3a	A conical metal frame covered with metal mesh, and equipped with a dual chambered collecting vessel.	Emergence occurs in the inner chamber of the sample collector. Insects fly vertically into the surrounding outer chamber which contains preservative.
Guyer & Hutson (1955)	A sheet metal cone with a removable glass sample bottle. Sampling area: 0·42–0·84 m^2.	Exuviae float on the water surface inside the sample bottle.

(continued)

Section 9.1 (contd)

Reference and illustration	Description	Comments
Mundie (1955) Fig. 6.2c	A conical brass-wire frame, covered with copper gauze, and equipped with a threaded copper collar at its apex which holds a removable glass sample bottle. Sampling area: 0·25 m^2.	A wire yoke around the sample bottle serves to attach the trap to a cable support from the surface. A safety chain prevents trap loss when the bottle is changed. Both adults and exuviae are retained.
Palmén (1955) Fig. 6.2d	A cone of stainless steel gauze with a tube welded to its apex. A weighted wire circle is attached to the base for strength and ballast. Sampling area: 1·0 m^2.	The sample bottle is friction-fitted onto a rubber stopper which encircles the tube at the top of the trap. Both adults and exuviae are retained.
Kajak (1957)	A conical wire frame covered with cotton ('Miller gauze'). Sampling area: 0·2 m^2.	Various configurations and sample containers were tested.
Sublette & Dendy (1959) Fig. 6.3b	A galvanized wire frame covered with polyethylene film that is heat bonded to form a cone. An inverted Erlenmeyer flask, attached to the top of the cone by elastic bands, acts as a sample collector. Sampling area: 0·09 m^2.	Wire tied around the flask serves to attach the trap to a surface float. Both insects and exuviae are collected.
Hamilton (1965) Fig. 6.3c	A removable glass sample bottle, containing an auxiliary plastic cone to prevent catch loss, is attached to the top of a cellulose-acetate-butyrate funnel by a plastic jar lid with its center portion removed, A stiff wire, fixed to a hose clamp at the apex, forms an attachment point for suspending the trap. Split lead weights are clamped to the basal rim of the funnel. Sampling area: 0·1 m^2.	The trap, which was primarily intended for sampling chironomids, has also been used to capture Trichoptera and Ephemeroptera by Flannagan & Lawler (1972). Also see Davies (1980) and Fig. 6.4 for modifications and construction details. Adults and exuviae are retained within the sample bottle.

Section 9.1 (contd)

Reference and illustration	Description	Comments
Fast (1972) Fig. 6.3d	A pyramidal frame of welded angle iron with sides covered by polyethylene film, held in place by redwood lath strips. A removable glass sample bottle is attached to the top of the frame by the rim of a metal jar lid. Extensions of the frame hold the trap base above the substrate. Sampling area: $0{\cdot}5\,m^2$.	A perforated styrofoam cup inside the sample jar prevents catch loss.
Welch (1973) Fig. 6.3e	A square pyramid of clear acrylic with a removable glass sample bottle at its apex. The trap is suspended from a submerged float via a wire bridle (see Fig. 6.5c). Sampling area: $0{\cdot}25\,m^2$.	Divers can be used to tend the traps during periods of ice cover. Exuviae float on the water surface inside the sample bottle.
Bretschko (1974)	Large funnels ($1\,m^2$) set directly on the lake bottom have a 2·5 cm diameter hose leading from the top of the trap to a sample bottle floating on the lake surface.	Maximum hose length 10 m. Deeper stations must be tended by divers. Both adults and exuviae retained in the sample bottle.
Davies (1980) Fig. 6.4	A slightly modified version of Hamilton's (1965) trap. Sampling area: $0{\cdot}1\,m^2$.	See Section 3.1.1 for construction details.

9.2 Emergence traps for shallow water habitats

Reference and illustration	Description	Comments
Traps for Areas with Emergent Vegetation		
Judd (1949) Fig. 6.7c	An open-bottomed, wood frame cage covered on the top and sides with copper screen. The upper portion of each side is a hinged door to allow access to the trap interior for specimen	Exuviae are not retained.

(continued)

Section 9.2 (contd)

Reference and illustration	Description	Comments
	removal. A cage is set over vegetation and supported, with its base below the water surface, on four stakes driven into the sediment. Sampling area: 0·7 m^2.	
Edwards *et al.* (1964)	The floating box trap of Morgan & Waddell (1961), Fig. 6.1g, modified slightly by adding stoppered holes to the roof. Sampling area: 0·18 m^2.	Catch removed by inserting an insect aspirator through the holes in the trap roof. Exuviae are not retained.
Corbet (1965) Fig. 6.7b	A truncated cone frame made of aluminum with a glass plate top, covered on the sides by fine plastic screen, held in place by aluminum strips bolted to the frame. Metal rod legs slip through sleeves on the frame and are secured in place by set screws. A rubber sampling port is fixed to one side. Sampling area: 0·1 m^2.	This lightweight, stackable design can be set over vegetation and emptied with the aid of an aspirator while viewing through the glass plate. Exuviae are not easily collected.
Lammers (1977) Fig. 6.7a	A tall form trap made from pine struts on a plywood ring base and covered on the inside with nylon mesh. A funnel-and-sample-bottle collector hangs from a plastic cover plate at the top of the trap. Steel rods through the base of the trap can be driven into the substrate to provide stability. Sampling area: 0·5 m^2.	Insects enter the sample bottle, which contains preservative, through holes in the side of the funnel. Exuviae are not retained.
LeSage & Harrison (1979) Fig. 6.7d	As one of several versions described, this trap consists of a nylon mesh tent supported externally by a wooden pyramidal frame attached at its base to a sealed, plastic pipe float. An acrylic headpiece with an opening near the top funnels	Suggested preservative: 70% ethanol mixed with glycerine or ethylene glycol. Exuviae are not retained.

Section 9.2 (contd)

Reference and illustration	Description	Comments
	insects toward a removable sample bottle, partially filled with preservative. A polyethylene skirt around the top of the trap protects the catch from rain. Sampling area: 0·37 m^2.	
Floating and staked designs[1]		
Mundie (1956) Fig. 6.8a	An internal aluminum frame supporting a nylon mesh or cellulose acetate cone. The mesh or plastic is held by aluminum strips bolted to the frame and by copper staples around the base. A removable glass sample bottle containing an auxiliary acetate cone threads into a collar at the trap apex. Hollow metal floats are fixed to extensions of the trap frame at its base. Sampling area: 0·25 m^2.	The trap is intended for partially submerged operation, but can be set as a surface sampler. The cone in the sample bottle prevents catch loss. Exuviae are not retained.
Frank (1965) Fig. 6.8d	A cone of silk or fine nylon is suspended upside down from an arm attached to a ring float made of wire and empty tin cans. Fabric tape and stiff wire strengthen the cone and hold its base open. Sampling area: 0·06 m^2.	A cloth disc stretched over a wire frame attached to a long wood handle is used to seal the base and lift the trap out of the water without loss of exuviae or adults.
Kimerle & Anderson (1967) Fig. 6.8e	A wood frame cube, covered on the top and 3 sides with polyethylene film and on the front with nylon mesh. Coverings are held on with wooden lath strips, stapled or nailed to the frame. The trap bottom can be closed off by raising a flap of the mesh front and sliding a square of plastic	The trap, with its base extending a few cm below the water surface, is held in position by bolting it to a stake that has been driven into the sediment. The bottom of the trap is open during sampling, but closed off prior to removal to prevent loss of

1. Also see Appendix 9.1, Floating Traps.

(*continued*)

Section 9.2 (contd)

Reference and illustration	Description	Comments
	or masonite hardboard along a groove cut in the inside edge of the bottom portion of the frame. Velcro® strips can be used to secure the lower edges of the mesh to the frame. Sampling area: 0·23 m^2.	specimens. Exuviae are not retained.
McCauley (1976) Fig. 6.8b	Two clear vinyl cones pitched at different angles are stacked and glued together at their bases to form a chambered trap. A screw cap with a hole in it is clamped to the apex of the outer cone to serve as an attachment for a removable sample vial. Nylon mesh vents cover holes in the outer cone. Sampling area: 0·1 m^2.	The trap is attached to a stake via a bracket so that its base rests just below the water surface. The catch is removed by inverting the trap and washing insects into the vial with preservative, sprayed through the vent windows. Exuviae are not easily sampled.
Street & Titmus (1979) Fig. 6.8c	A metal frame box with plastic or metal sides and a removable glass plate top, painted on its underside with a film of fruit tree grease-band (Boltac® or Tanglefoot®). Foam polystyrene blocks on two sides provide floatation. Trap adapted from Green (1970). Sampling area: 0·1 m^2.	Emerging insects rise to the top of the trap and become stuck to the glass plate. The grease can be dissolved with acetone to remove insects. Exposed plates should be kept in sealed containers to avoid catching other insects. Exuviae are not retained.
Traps Set Directly on the Bottom		
Kajak (1957) Fig. 6.9a	A conical surface trap (see Appendix 9.1: Kajak), adapted as a free-standing model by attaching it to the inside of a close-fitting cylinder made of wire and covered with 'Miller gauze'. The bottom of the cylinder is pressed into the sediment. Sampling area: 0·20 m^2.	The whole assembly should periodically be cleaned and moved to a different location to overcome colonization or containment effects. Exuviae remain on the water surface inside the cylinder.

Section 9.2 (contd)

Reference and illustration	Description	Comments
Lindeberg (1958) Fig. 6.9c	An inverted glass funnel with a stopcock in the stem, topped with a removable sample bottle, press-fitted onto a rubber stopper surrounding the stem. Use: (1) invert funnel over a shallow pool, (2) open stopcock and fill the funnel with water by suction, (3) close the stopcock, (4) quickly invert a sample bottle $\frac{2}{3}$ full of water over the stopper and seal in position, (5) open the stopcock. Sampling area: 0·07 m^2.	External air pressure keeps the trap full of water, thus giving the sampling convenience of a submerged trap in extremely shallow habitats. Emergence of large insects may be inhibited by the small diameter of the funnel stem.
Sublette & Dendy (1959) Fig. 6.9b	A polyethylene covered wire-frame pyramid which stands above the substrate on leg-like extensions of the frame to allow water circulation within the trap. Wire tied around the detachable sample flask at the apex of the pyramid provides an attachment point for a rope to raise or lower the trap from the surface. Sampling area: 0·09 m^2.	The trap may be operated either partially or fully submerged, although in the latter mode, it is easier to empty. Adults and exuviae are contained within the sample flask.
Paasivirta (1972)	Stainless mesh cone (see Appendix 9.1: Palmén), set directly on the bottom at shallow stations. Sampling area: 0·5 m^2.	Also see Paasivirta (1975).
Cheng (1974) Fig. 6.9d	An open-sided metal box with vials fitted into holes in the top. Sample vials contain auxiliary cones to prevent catch loss. Sampling area: 0·25 m^2.	In the fully submerged mode both adults and exuviae are retained.
Ali & Mulla (1979) Fig. 6.9e	A submerged funnel trap made of galvanized sheet metal with a removable glass sample bottle. Sampling area: 0·3 m^2.	Trap does not permit water circulation. Consequently, anoxia may develop inside.

(continued)

Section 9.2 (contd)

Reference and illustration	Description	Comments
Ettinger (1979) Fig. 6.10b	A folding tent of nylon mesh with two sides stretched over rectangular aluminum frames, hinged together at the top. Triangular mesh sides supported by rubber bands at the base are held taut during sampling by hinged metal stays which slip over pins in the frame to keep the trap open. Side panels are tucked inwards when the trap is folded flat for removal. Sampling area: 0·1 m^2.	By closing the trap with its base held under the water surface, both adults and exuviae are retained. Because traps are lightweight and fold flat, they are extremely portable.
Butler (1980) Fig. 6.10c	A free-standing semi-submerged trap made from polycarbonate sheet. Side seams are held together with bolts. The cone and cylinder are joined and sealed with silicone adhesive. The rim of a jar lid, glued to the outside of the cone at its apex, serves to attach a sample bottle with a screen-covered end. Brass bolts extending outward from the base of the cylinder support weights and help to stabilize the trap in soft sediment. Sampling area: 0·05 m^2.	Insects and exuviae are removed by lifting the trap out of the water with its base covered, inverting the unit, and washing specimens into the sample bottle with a spray of preservative.
Davies (1980) Fig. 6.10a	A modification of the trap illustrated in Fig. 6.4. Vents, cut in the body of the trap, to allow water circulation are covered with nylon mesh (250 μm) which is held in place by acetate plastic strips, glued around the perimeter of each vent. Extra weights around the base assure trap stability under mild wave action. Sampling area: 0·1 m^2.	Traps operate in the fully submerged mode. Adults and exuviae are contained within the sample bottle.

Section 9.2 (contd)

Reference and illustration	Description	Comments
Traps for Shore		
Cook & Horn (1968) Fig. 6.10e	A sturdy box, open along the bottom and at one end, made from heavy fence wire, and lined inside with fibreglass screen. Sampling area: 0·28 m^2.	A qualitative trap for sampling Odonata that is set with its open end sloping downward toward the water.
Morgan (1971) Fig. 6.10d	A wood frame box with an open bottom, nylon mesh front, and acrylic sheet covering the top, back and sides. Bank material is cut away and replaced by a wooden board with a vertical front lip that is sunk into the bank at the water's edge to stop burrowing insects from crawling underneath the board. The trap front is supported just beneath the water surface by a float. Sampling area: unspecified.	This trap requires calm waters and sand or soil-covered banks. On rocky shorelines a tent may make a more useful trap.

9.3 Emergence traps for running water

Reference and illustration	Description	Comments
Cages and Tents		
Needham (1908) Fig. 6.11a	A muslin tent with a flap entrance. The trap base is sealed against the stream bed with stones. Sampling area: 0·56 m^2.	First recorded use of an emergence trap. Investigator must enter the trap to make collections.
Ide (1940)	A wood frame cube covered on the top and four sides with copper screen ($\sim$ 1000 μm mesh). Base extends below the water surface, but does not seal against the substrate. Access to the trap interior is through a door in one side. Sampling area: 0·83 m^2.	Investigator must enter the trap to make collections.

(continued)

Section 9.3 (contd)

Reference and illustration	Description	Comments
Sprules (1947)	Trap style: see Ide (1940). A corner seat minimizes the time the investigator spends standing on the substrate inside the trap. Sampling area: 0·83 m^2.	Investigator must enter the trap to make collections.
Davies (1950)	Trap style: see Ide (1940). A finer mesh covering is used to retain Simuliidae. Sampling area: 0·83 m^2.	Investigator must enter the trap to make collections.
Harper & Magnin (1971) Fig. 6.11b	A pyramid shaped tent of nylon mesh supported by an external wood frame. A mesh sleeve, sewn to a hole in the tent wall, is tied off close to the tent to prevent insects from becoming caught in the folds of material. Sampling area: 0·5 m^2.	Specimens can be collected without lifting the trap, by reaching inside through the sleeve. Also see Harper & Cloutier (1979).
Illies (1971) Fig. 6.11d	A commercial greenhouse built to cover the complete cross section of a stream and its banks. Dimensions (L, W, H): 12·2 × 2·8 × 2·3 m, coverage: 11·1 m^2 of stream. See Böttger (1975) and Lehman (1979) for less expensive polyethylene-film-on-wooden-frame versions. Also see Malicky (1976), Zwick (1977), Sandrock (1978), Malicky (1980).	Investigators must enter the greenhouse to make collections. Advantages: (1) stream flow not restricted, (2) no substrate disruption during sampling, (3) large sample area, all habitats sampled. Disadvantages: (1) relatively permanent, (2) expensive to construct, (3) time consuming to sample, (4) thermal effects and intensive sampling may alter the habitat.
Anderson & Wold (1972) Fig. 6.11c	An 'A' frame of wood covered with fiberglass screen. Polyethylene film, secured to the upper third of the sloped sides, protects the catch from rain. A door in one end provides access to the trap. Screen flaps along the base of each angled side allow peak flows and debris to pass	Investigator must enter the trap to make collections.

Section 9.3 (contd)

Reference and illustration	Description	Comments
	through the trap. Dimensions: base = 1 m^2, height = 2 m.	
Masteller (1977)	A plastic mesh (500 μm) tent which covers the entire width of a stream and its banks. Dimensions: base = 15·8 m^2, L = 5·2 m, W = 3·1 m. The trap is similar in concept to the greenhouse of Illies (1971), but inexpensive by comparison.	Investigator must enter the trap to make collections. Apart from permanence and cost, the advantages and disadvantages listed for Illies' (1971) greenhouse apply.
Flannagan (1978)	A wood frame cube similar to that of Ide (1940) with 400 μm Nitex® cloth covering 3 sides, a Nitex covered door on the fourth side, a vinyl sheet roof, and a metal cross-bar to stand on while inside. Sampling area: 1·0 m^2.	Investigator must enter the trap to make collections. Vinyl roof protects specimens from rain.
Floating and Suspended Traps		
Judd (1957)	A slightly modified version of Miller's (1941) floating tent trap. Sampling area: 0·37 m^2.	Useful only during conditions of low flow.
Macan (1964) Fig. 6.1f and Fig. 6.8a	The box trap of Macan (1949) and Mundie's (1956) cone trap. Traps float on the water surface, held in place by a rope bridle attached to opposite banks of a small stream. Sampling area: Box = 0·33 m^2, cone = 0·25 m^2.	Useful only during conditions of low flow.
Corbet (1966) Fig. 6.12b	A partially submerged trap for use in rivers. A saran mesh cone, supported by a plywood ring base and aluminum struts, is attached to an apical aluminum collar. A machined sample container with a removable top and inverted funnel entrance fits into the collar. The position of foam floats attached to the trap base	Stability of the trap in strong currents or waves is improved by tethering it to the lee side of a wood boom. Prior to lifting the trap for sample removal, the base is sealed with a mesh-covered ring to retain both insects and exuviae.

(*continued*)

Section 9.3 (contd)

Reference and illustration	Description	Comments
	via metal rods and adjustable sleeves sets the height of the trap in the water. Sampling area: not reported, but $\sim 0{\cdot}5\,m^2$.	
Langford & Daffern (1975) Fig. 6.12a	An aluminum frame pyramid, covered with nylon mesh and hinged at its base over a rectangular hole in a boat-shaped foam polystyrene float. Intended for use in rivers that are subject to wide fluctuations in level and may carry heavy loads of debris, the trap is trailed by a rope bridle from anchor points on opposite shores. Sampling area: $0{\cdot}25\,m^2$.	The apical sample bottle used in initial experimental trails was omitted in subsequent models. Float material was colonized by Ephemeroptera nymphs.
LeSage & Harrison (1979) Fig. 6.7d	The previously discussed floating tent design or a truncated version, for improved stability at windy locations, can be used to sample streams. Further modifications include a sleeve on the side of the tent [see Appendix 9.3, Cages and Tents, Harper & Magnin (1971)], to allow easy access to the trap interior. Sampling area: $0{\cdot}37\,m^2$.	Not suited to conditions of high flow.
Boerger (1981) Fig. 6.12c	A wood frame box trap with a hinged lid, mesh-covered sides and a sloping polyethylene covered roof. Two acrylic baffles in the base angle inward to prevent catch loss. A sliding panel, which fits into grooves cut in the frame, is used to close off the trap. The box rests on a float made of foam polystyrene blocks. Aluminum rods placed through holes in	Trap can move vertically as water levels change in the stream. A flexible, polyethylene skirt at the front of the hinged top permits access to the trap interior without risking catch loss. Exuviae are not retained.

Section 9.3 (contd)

Reference and illustration	Description	Comments
	each float are driven into the stream bed to hold the trap in place. Sampling area: 0·1 m^2.	
Nordlie & Arthur (1981) Fig. 6.12d	An acrylic plastic box with an open bottom, an angled baffle inside to prevent loss of insects, screen-covered windows for ventilation, and a commercially available domed acrylic skylight top. A removable sample bottle with a mesh bottom is attached to a hole in the centre of the dome by the rim of a jar lid. Plastic strips, glued to the outside of the box, support it on a square acrylic collar, which is suspended above the water surface from pipes laid across an experimental stream channel. Sampling area: 0·18 m^2.	Trap height must be adjusted frequently to cope with fluctuating water levels. The base of the box can be closed off with a sliding panel prior to lifting the trap free of the collar for emptying.
Traps Set Directly on the Bottom		
Mundie (1956) Fig. 6.13a	A triangular pyramid frame made of heavy metal, covered on two sides with acrylic sheet and on the third side and around the top by copper mesh (250 μm opening). A removable sample jar containing a small cone to prevent insects from returning to the body of the trap is threaded into a collar at the top of the pyramid. Ropes or wires anchor the trap to the streambed or shore. Sampling area: 0·16 m^2.	Trap can be operated either partially or fully submerged and is designed to allow water to flow over the substrate. See also: Gledhill (1960), Macan (1964), and Mundie (1971a).
Hamilton (1969) Fig. 6.13b	An open-bottomed low profile box with stainless steel sides, a clear plastic top, and removable entrance and exit screens which allow water to flow through the	The trap functions in the fully submerged mode in streams as little as 12 cm deep. Also see a modified design by Williams (1982).

(continued)

Section 9.3 (contd)

Reference and illustration	Description	Comments
	trap but prevent drifting organisms from entering. Above the rear screen, which is angled upward, a shallow vinyl pyramid supports a removable glass sample bottle attached to a threaded collar. Sampling area: 0·1 m^2.	Exuviae float on the water surface inside the sample bottle.
Drift Samplers and Miscellaneous Designs		
Mundie (1964) Fig. 6.13c	A long sheet metal box, tapering in two stages from a narrow vertical slit, which is the trap's only entrance, to a large exit at the rear. An oblique exit screen slopes upward from a narrow gap at its base, directing drift organisms towards an air-filled chamber where insects emerge and become trapped. The upper third of this triangular pyramid chamber is screened to prevent condensation build-up inside and is topped with a removable sample bottle containing a small cone to prevent insects from falling back into the water. Entrance slit = 2·5 cm × 20 cm.	This trap can be set directly on the bottom in shallow streams or supported by lateral floats where water depth exceeds the height of the entrance. In place of the vertical slit entrance, a short length of pipe can be used as a subsurface intake to exclude surface drift. Sample volume is a function of intake size, stream depth and water velocity. Also see Mundie (1966) and Williams (1982).
Mundie (1971b)	A wedge-shaped metal box, with a slit entrance, used as a headpiece for a plankton net. The sampler collects insect drift from a stream.	The wedge-shaped design protects the net from debris and eliminates any bow wave (back-pressure) at the front of the sampler by allowing through only a small fraction of the net's straining capacity.
Carrillo (1974)	Plywood box trap, used on lakes to collect only the floating exuviae of emerging insects. These boxes are open on the top and bottom and covered on	Collections of exuviae are made by periodically skimming the water surface inside the box with a fine mesh dip net.

Section 9.3 (contd)

Reference and illustration	Description	Comments
	the outside with foam polystyrene floatation. Sampling area: 1–2 m^2 depending on box dimensions.	
Wartinbee & Coffman (1976) Fig. 6.13d	Experimental channels with wooden sides, set several cm into the stream bed, and high enough to contain the entire depth of flow. Fine mesh nets (200 μm opening), attached to the upstream and downstream ends of the channel, stop drift from entering the channel and collect both drift and emerging insects originating from within the channel. Sampling area: 0·6–3·5 m^2 depending on dimensions.	Advantages: (1) A large but closely defined sampling area. Disadvantages: (1) large sample size, (2) labour intensive sampling, (3) installation and servicing disrupt the surrounding stream bed. Also see Wartinbee (1979).

10 References

Adamstone F.B. & Harkness W.J.K. (1923) The bottom organisms of Lake Nipigon. *Univ. Toronto Stud., Biol.*, **22**, 121–170.

Ali A. (1980) Diel adult eclosion periodicity of nuisance chironomid midges of central Florida U.S.A. *Environ. Ent.*, **9**, 365–370.

Ali A. & Mulla M.S. (1979) Diel periodicity of eclosion of adult chironomid midges in a residental recreational lake. *Mosq. News*, **39**, 360–364.

Anderson N.H. & Wold J.L. (1972) Emergence trap collections of Trichoptera from an Oregon stream. *Can. Ent.*, **104**, 189–201.

Bagge P., Ilus E. & Paasivirta L. (1980) Emergence of insects (esp. Diptera, Chironomidae) at different depths in the archipelago of Lovisa (Gulf of Finland) in 1971. *Ann. Ent. Fenn.*, **46**, 89–100.

Boerger H. (1981) Species composition, abundance and emergence phenology of midges (Deiptera:[SIC] Chironomidae) in a brown-water stream of west-central Alberta, Canada. *Hydrobiologia*, **80**, 7–30.

Borutsky E.V. (1939a) Dynamics of the biomass of *Chironomus plumosus* in the profundal of Lake Beloie. *Arb. Limnol. Sta. Kossino*, **22**, 156–195.

Borutsky E.V. (1939b) Dynamics of the total benthic biomass in the profundal of Lake Beloie. *Proc. Kossino Limnol. Stn.*, **22**, 196–218. (English translation by M. Ovchynnyk, Mich. State Univ., Mich. Dep. Conserv. 26 pp. + 9 Figs.).

Borutsky E.V. (1955) A new trap for the quantitative estimation of emerging chironomids. (In Russian). *Trud. Vsesoyuz. Gidrobiol. Obschch*, **6**, 223–226.

Böttger K. (1975) Produktionsbiologische studien an dem zentralafrikanischen. Bergbach Kalengo. (Studies on the productivity of the Kalengo-stream in Central Africa). *Arch. Hydrobiol.*, **75**, 1–31. (German with English abstract and summary).

Boyle T.P. (1979) New floating trap for capturing and preserving emerging aquatic insects. *Prog. Fish-Cult.*, **41**, 108–109.

Bretschko G. (1974) The chironomid fauna of a high-mountain lake (Vorderer Finstertaler See, Tyrol, Austria 2237m asl). *Ent. Tidskr.*, **95**, *Suppl.*, 22–33.

Brundin L. (1949) Chironomiden und andere Bodentiere der Südschwedischen Urgebirgsseen. *Rep. Inst. Freshw. Res. Drottning.*, **30**, 1–914.

Butler M.G. (1980) *The Population Ecology Of Some Arctic Alaskan Chironomidae (Diptera)*. Dissertation. Univ. of Michigan, Ann Arbor, 170 pp.

Cantrell M.A. & McLachlan A.J. (1977) Competition and chironomid distribution patterns in a newly flooded lake. *Oikos*, **29**, 429–433.

Carrillo R.J. (1974) *Emergence Dynamics Of A Lentic Chironomidae (Diptera) Community In Northwestern Pennsylvania*. Dissertation. Univ. of Pittsburgh, 316 pp.

Caspers H. (1951) Rhythmische Erscheinungen in der Fortpflanzung von *Clunio marinus* (Dipt. Chiron.) und das Problem der lunaren Periodizität bei Organismen. *Arch. Hydrobiol. Suppl.*, **18**, 415–594.

Cheng L. (1974) A simple emergence trap for small insects. *Pan-Pacific Ent.*, **50**, 305–307.

Coffman W.P. (1973) Energy flow in woodland stream ecosystem: II The taxonomic composition and phenology of the Chironomidae as determined by the collection of pupal exuviae. *Arch. Hydrobiol.*, **71**, 281–322.

Cook P.P. Jr. & Horn H.S. (1968) A sturdy trap for sampling emergent Odonata. *Ann. Ent. Soc. Am.*, **61**, 1506–1507.

Corbet P.S. (1964) Temporal patterns of emergence in aquatic insects. *Can. Ent.*, **96**, 264–279.

Corbet P.S. (1965) An insect emergence trap for quantitative studies in shallow ponds. *Can. Ent.*, **97**, 845–848.

Corbet P.S. (1966) Diel periodicities of emergence and oviposition in riverine Trichoptera. *Can. Ent.*, **98**, 1025–1034.

Danks H.V. & Oliver D.R. (1972) Seasonal emergence of some high arctic Chironomidae (Diptera). *Can. Ent.*, **104**, 661–686.

Davies D.M. (1950) A study of the blackfly populations of a stream in Algonquin Park, Ontario. *Trans. R. Can. Inst.*, **59**, 121–160.

Davies I.J. (1980) Relationships between dipteran emergence and phytoplankton production in the Experimental Lakes Area, northwestern Ontario. *Can. J. Fish. Aquat. Sci.*, **37**, 523–533.

Edwards R.W., Egan H., Learner M.A. & Maris P.J. (1964) The control of chironomid larvae in ponds using TDE (DDD). *J. Appl. Ecol.*, **1**, 97–117.

Elliott J.M. (1971 reprinted 1973) *Some Methods for the Statistical Analysis of samples of Benthic Invertebrates. Freshw. Biol. Assoc. Sci. Publ.*, **25**, 148 pp.

Ettinger W.S. (1979) A collapsible insect emergence trap for use in shallow standing water. *Entomol. News*, **90**, 114–117.

Fast A.W. (1972) A new aquatic insect trap. *Mich. Acad.*, **5**, 115–124.

Fee E.J. (1980) Important factors for estimating annual phytoplankton production in the Experimental Lakes Area. *Can. J. Fish. Aquat. Sci.*, **37**, 513–522.

Flannagan J.F. (1978) Emergence of caddisflies from the Roseau River, Manitoba. In: *Proc. of the 2nd. Int. Symp. on Trichoptera.* M.I.Crichton (ed.), The Hague: W.Junk, p. 183–197.

Flannagan J.F. & Lawler G.H. (1972) Emergence of caddisflies (Trichoptera) and mayflies (Ephemeroptera) from Heming Lake, Manitoba. *Can. Ent.*, **104**, 173–183.

Frank G.H. (1965) The hatching pattern of five species of chironomid from a small reservoir in the eastern Transvaal Lowveld as revealed by a new type of trap. *Hydrobiologia*, **25**, 52–68.

Fremling C.R. (1960) Biology of a large mayfly, *Hexagenia bilineata* (Say), of the Upper Mississippi River. *Iowa Agric. Home Econ. Exp. Stn. Res. Bull.*, **482**, 842–852.

Friesen M.K., Flannagan J.F. & Laufersweiler P.M. (1980) Diel emergence patterns of some mayflies (Ephemeroptera) of the Rouseau River (Manitoba, Canada). In: *Advances in Ephemeroptera Biology.* J.F.Flannagan & K.E.Marshall (eds.), New York: Plenum, p. 287–296.

Gledhill T. (1960) The Ephemeroptera, Plecoptera and Trichoptera caught by emergence traps in two streams during 1959. *Hydrobiol.*, **15**, 179–188.

Grandilewskaja-Decksbach M.L. (1935) Materialien zur Chironomidenbiologie verschiedener Becken. Zur Frage über die Schwankungen der Anzahl und der Biomasse der Chironomidenlarven. *Proc. Kossino Limnol. Sta.*, **19**, 145–182.

Green M.B. (1970) Insect populations of sludge drying beds. *Wat. Pollut. Contr.*, **69**, 399–408.

Guyer G. & Hutson R. (1955) A comparison of sampling techniques utilized in an ecological study of aquatic insects. *J. Econ. Ent.*, **48**, 662–665.

Hamilton A.L. (1965) *An Analysis Of A Freshwater Benthic Community With Special Reference To The Chironomidae.* Dissertation. Univ. British Columbia, Vancouver, B.C. 92 + 216 pp.

Hamilton A.L. (1969) A new type of emergence trap for collecting stream insects. *J. Fish. Res. Board Can.*, **26**, 1685–1689.

Harper F. & Magnin E. (1971) Émergence saisonière de quelques éphéméroptères d'un ruisseau des Laurentides. *Can. J. Zool.*, **49**, 1209–1221.

Harper P.P. & Cloutier L. (1979) Chironomini and Pseudochironomini of a Quebec highland stream (Diptera: Chironomidae). *Ent. Scand. Suppl.*, **10**, 81–94.

Humphries C.F. (1938) The chironomid fauna of the Grossen Plöner See, the relative density of its members and their emergence period. *Arch. Hydrobiol.*, **33**, 535–584.

Ide F.P. (1940) Quantitative determination of the insect fauna of rapid water. *Univ. Toronto Stud., Biol. Ser.*, **47**, 1–13.

Illies J. (1971) Emergenz 1969 in Breitenbach, Schlitzer produktionsbiologische Studien (1). (Emergence 1969 on Breitenbach (Schlitz studies on productivity, No. 1). *Arch. Hydrobiol.*, **69**, 14–59. (German with English Abstract and Summary.)

Johnson M.G. (1974) Production and productivity. In: *The Benthos of Lakes.* R.O. Brinkhurst (ed.), London: Macmillan, p. 46–64.

Jónasson P.M. (1954) An improved funnel trap for capturing emerging aquatic insects, with some preliminary results. *Oikos*, **5**, 179–188.

Judd W.W. (1949) Insects collected in the Dundas Marsh, with observations on their period of emergence. *Can. Ent.*, **81**, 1–10.

Judd W.W. (1957) A study of the population of emerging and littoral insects trapped as adults from tributary waters of the Thames River at London, Ontario. *Amer. Midl. Nat.*, **58**, 394–412.

Kajak Z. (1957) Metody ilościowego połowa imagines Tendipedidae. (Methods of the Quantitative capture of emerging imagines and pupae of the Tendipedidae). *Ekol. Pol. (B)*, **3**, 49–61. (Polish with English Summary).

Kajak Z. (1958) Próba interpretacji dynamiki liczebności fauny bentonicznej w wybranym środowisku lachy wiślanej 'Konfederatka'. *Ekol. Pol*, **6**, 205–291. (Preliminary interpretation of the dynamics of benthic fauna abundance in a chosen environment of the Konfederatka Pool (Old River Bed) adjoining the Vistula River) English Trans., 1965, from Office of Technical Services, U.S. Dept. of Commerce, Washington, D.C., No. OTS 63-11396. 77 pp.

Kimerle R.A. & Anderson N.H. (1967) Evaluation of aquatic insect emergence traps. *J. Econ. Ent.*, **60**, 1255–1259.

Lammers R. (1977) Sampling insects with a wetland emergence trap: design and evaluation of the trap with preliminary results. *Amer. Midl. Nat.*, **97**, 381–389.

Langford, T.E. & Daffern J.R. (1975) The emergence of insects from a British river warmed by power station cooling-water. Part I—The use and performance of insect emergence traps in a large, spate-river and the effects of various factors on total catches, upstream and downstream of the cooling-water outfalls. *Hydrobiologia*, **46**, 71–114.

Laville H. (1971a) Recherches sur les chironomides (Diptera) lacustres du Massif de Néouvielle (Hautes-Pyrénées). Première partie: systématique, écologie, phénologie. *Ann. Limnol.*, **7**, 173–332. (In French).

Laville H. (1971b) Recherches sur les chironomides (Diptera) lacustres du Massif de Néouvielle (Hautes-Pyrénées). Deuxieme partie: communautés et production. *Ann. Limnol.*, **7**, 335–414. (In French).

Lehman J. (1979) Chironomidae (Diptera) aus Fliessgewässen Zentralafrikas (Systematik, Ökologie, Verbreitung und Produktionsbiologie. Teil I: Kivu-Gebiet, Ostzaire. (Chironomids from running waters of Central Africa (Diptera) (Systematic, Ecology, distribution and production biology). Part I: Region of Kivu, east-Zaire). *Spixiana Suppl.*, **3**, 1–144. (In German).

LeSage L. & Harrison A.D. (1979) Improved traps and techniques for the study of emerging aquatic insects. *Ent. News*, **90**, 65–78.

LeSage L. & Harrison A.D. (1980) The biology of *Cricotopus* (Chironomidae: Orthocladinae) in an algal-enriched stream. Part I: Normal biology. *Arch. Hydrobiol. Suppl.*, **57**, 375–418.

Lindeberg B. (1958) A new trap for collecting emerging insects from small rockpools with some examples of the results obtained. *Ann. Ent. Fenn.*, **24**, 186–191.

Macan T.T. (1949) Survey of a moorland fishpond. *J. Anim. Ecol.*, **18**, 160–186.

Macan T.T. (1964) Emergence traps and the investigation of stream faunas. *Rivista di Idrobiologia*, **3**, 75–92.

Malicky H. (1976) Trichoptera—Emergezn in zwei Lunzer Bächen, 1972–74. (Emergence of Trichoptera in 1972–74 from two streams near Lunz (Austria)). Schlitzer Produktionsbiologische Studien Nr. 14. *Arch. Hydrobiol.*, **77**, 51–65. (German with English abstract and summary).

Malicky H. (1980) Evidence for seasonal migrations of larvae of two species of philopotomid caddisflies (Trichoptera) in a mountain stream in lower Austria. *Aquat. Insects.*, **2**, 153–160.

Masteller E.C. (1977) An aquatic emergence trap on a shale stream in western Pennsylvania, U.S.A. *Melsheimer Ent. Ser.*, **23**, 10–15.

McCauley V.J.E. (1976) Efficiency of a trap for catching and retaining insects emerging from standing water. *Oikos*, **27**, 339–345.

Miller R.B. (1941) A contribution to the biology of the Chironomidae of Costello Lake, Algonquin Park, Ontario. *Univ. Toronto. Stud. Biol.*, **49**, 1–63.

Morgan N.C. (1958) Insect emergence from a small Scottish loch. *Int. Ver. Theor. Angew. Limnol. Verh.*, **13**, 823–825.

Morgan N.C. (1971) Factors in the design and selection of insect emergence traps. In: IBP Handbook No. 17, *A Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters*. W.T.Edmondson and G.G.Winberg (eds.). Oxford: Blackwell, p. 93–108.

Morgan N.C. & Waddell A.B. (1961) Insect emergence from a small trout loch, and its bearing on the food supply of fish. *Sci. Invest. Freshwat. Fish. Scot.*, **25**, 1–39.

Morgan N.C., Waddell A.B. & Hall W.B. (1963) A comparison of the catches of emerging aquatic insects in floating box and submerged funnel traps. *J. Anim. Ecol.*, **32**, 203–219.

Mulla M.S., Norland R.L., Ikershoji T. & Kramer W.L. (1974) Insect growth factors for the control of aquatic midges. *J. Econ. Ent.*, **67**, 165–170.

Mundie J.H. (1955) On the distribution of Chironomidae in a storage reservoir. *Int. Ver. Theor. Angew. Limnol. Verh.*, **12**, 577–581.

Mundie J.H. (1956) Emergence traps for aquatic insects. *Int. Ver. Theor. Angew. Limnol. Mitt.*, **7**, 1–13.

Mundie J.H. (1957) The ecology of Chironomidae in storage reservoirs. *Trans. R. Ent. Soc. Lond.*, **109**, 149–232.

Mundie J.H. (1964) A sampler for catching emerging insects and drifting materials in streams. *Limnol. Oceanogr.*, **9**, 456–459.

Mundie J.H. (1966) Sampling emerging insects and drifting materials in deep flowing water. *Gewässer*, **41/42**, 159–162.

Mundie J.H. (1971a) Techniques for sampling emerging aquatic insects. In: *IBP Handbook No. 17, A Manual for Methods for the Assessment of Secondary Productivity in Fresh Waters*. W.T.Edmondson & G.G.Winberg (eds.), Oxford: Blackwell, p. 80–93.

Mundie J.H. (1971b) The diel drift of Chironomidae in an artificial stream and its relation to the diet of Coho Salmon Fry, *Oncorhynchus kisutch* (Waulbaum [SIC]). *Can. Ent.*, **103**, 289–297.

Needham J.G. (1908) Report of the entomological field station conducted at Old Forge, N.Y. in the summer of 1905. *Bull. N.Y. St. Mus.*, **124**, 167–172.

Nordlie K.J. & Arthur J.W. (1981) Effects of elevated water temperature on insect emergence in outdoor experimental channels. *Environ. Pollut. Ser. A.*, **25**, 53–65.

Paasivirta L. (1972) Taxonomy, ecology and swarming behaviour of *Tanytarsus gracilentus* Holmgr. (Diptera, Chironomidae) in Valassaaret, Gulf of Bothnia, Finland. *Ann. Zool. Fenn.*, **9**, 255–264.

Paasivirta L. (1975) Insect emergence and output of incorporated energy and nutrients from the oligotrophic lake Pääjärvi, southern Finland. *Ann. Zool. Fenn.*, **12**, 126–140.

Palmén E. (1955) Diel periodicity of pupal emergence in natural populations of some chironomids (Diptera). *Ann. Zool. Soc. Vanamo.*, **17**, 1–30.

Palmén E. (1962) Studies on the ecology and phenology of the Chironomids (Dipt.) of the Northern Baltic. 1. *Allochironomus crassiforceps* K. *Ann. Ent. Fenn.*, **28**, 137–168.

Potter D.W.B. & Learner M.A. (1974) A study of the benthic macro-invertebrates of a shallow eutrophic reservoir in South Wales with emphasis on the Chironomidae (Diptera); their life histories and production. *Arch. Hydrobiol.*, **74**, 186–226.

Rosenberg D.M. & Wiens A.P. (1983) Efficiency of modifications in the design and use of submerged funnel traps for sampling Chironomidae (Diptera). *Hydrobiologia*, **98**, 113–118.

Rosenberg D.M., Wiens A.P. & Bilyj B. (1980) Sampling emerging Chironomidae (Diptera) with submerged funnel traps in a new northern Canadian reservoir, Southern Indian Lake, Manitoba. *Can. J. Fish. Aquat. Sci.*, **37**, 927–936.

Sandberg G. (1969) A quantitative study of Chironomid distribution and emergence in Lake Erken. *Arch. Hydrobiol. Suppl.*, **35**, 119–201.

Sandrock F. (1978) Vergleichende Emergenzmessung an zwei Bächen des Schliterzerlandes (Breitenbach und Rohrwiesenbach 1970–1971). Schlitzer Produktionsbiologische Studien (24). (A comparison of the insects emerging from two brooks in the region of Schlitz (Breitenbach and Rohrwiesenbach 1970–1971)). (Schlitz studies on productivity, no. 24). *Arch. Hydrobiol. Suppl.*, **54**, 328–408.

Scott W. & Opdyke D.F. (1941) The emergence of insects from Winona Lake. *Invest. Ind. Lakes*, **2**, 3–14.

Speir J.A. & Anderson N.H. (1974) Use of emergence data for estimating annual production of aquatic insects. *Limnol. Oceanogr.*, **19**, 154–156.

Sprules W.M. (1947) An ecological investigation of stream insects in Algonquin Park, Ontario. *Univ. Toronto. Stud., Biol. Ser.*, **56**, 1–81.

Street M. and Titmus G. (1979) The colonisation of experimental ponds by Chironomidae (Diptera). *Aquat. Insects*, **1**, 233–244.

Sublette J.E. & Dendy J.S. (1959) Plastic material for simplified tent and funnel traps. *Southwestern Nat.*, **3**, 220–223.

Teal J.M. (1957) Community metabolism in a temperate cold spring. *Ecol. Monogr.*, **27**, 283–302.

Thienemann A. (1910) Das Sammeln von Puppenhäuten de Chironomiden. Eine Bitte um Mitarbeit. *Arch. Hydrobiol.*, **6**, 213–214.

Vallentyne J.R. (1952) Insect removal of nitrogen and phosphorus compounds from lakes. *Ecol.*, **33**, 573–577.

Wartinbee D.C. (1979) Diel emergence patterns of lotic Chironomidae. *Freshwat. Biol.*, **9**, 147–156.

Wartinbee D.C. & Coffman W.P. (1976) Quantitative determination of Chironomid emergence from enclosed channels in a small lotic ecosystem. *Am. Midl. Nat.*, **95**, 479–485.

Welch H.E. (1967) *Energy Flow Through The Major Macroscopic Components Of An Aquatic Ecosystem.* Dissertation. Univ. Georgia, Athens, Ga. 97 pp.

Welch H.E. (1973) Emergence of Chironomidae (Diptera) from Char Lake, Resolute, Northwest Territories. *Can. J. Zool.*, **51**, 1113–1123.

Welch H.E. (1976) Ecology of Chironomidae (Diptera) in a polar lake. *J. Fish. Res. Board Can.*, **33**, 227–247.

Williams D.D. (1982) Emergence pathways of adult insects in the upper reaches of a stream. *Int. Revue ges. Hydrobiol.*, **67**, 223–234.

Wilson R.S. & Bright P.L. (1973) The use of chironomid pupal exuviae for characterizing streams. *Freshwat. Biol.*, **3**, 283–302.

Wohlschlag D. (1950) Vegetation and invertebrate life in a marl lake. *Invest. Ind. Lakes*, **3**, 321–372.

Wrubleski D.W. & Rosenberg D.M. (in press) Overestimates of Chironomidae (Diptera) abundance from emergence traps with polystyrene floats. *Am. Midl. Nat.*

Zwick P. (1977) Plecopteren-Emergenzweier Lunzer Bäche, 1972–1974, Schlitzer Produktionsbiologische studien Nr. 30. (Plecoptera emerging from two streams at Lunz, 1972–1974). *Arch. Hydrobiol.*, **80**, 458–505 (German with English abstract and summary).

Chapter 7. The Estimation of the Abundance and Biomass of Zooplankton in Samples

EDWARD McCAULEY

1 Introduction

Techniques of enumeration are essential for generating observations that can be used to test predictions derived from theories or to provoke questions leading to new areas of investigation. The ability to distinguish between estimates of important ecological variables, such as the abundance and biomass of species, directly influences our ability to test predictions and, therefore, to conduct our science. These estimates also form the basis of empirical theories or relationships that can make quantitative predictions about the distribution and abundance of organisms in nature. It is important, therefore, for ecologists to assess their techniques for producing estimates of these basic ecological variables routinely and critically.

The scope of this review is restricted to discussing techniques for determining the number of individuals of a particular size class or cohort present in a sample of zooplankton and the average mass of these individuals. These are the two essential quantities required to calculate the production of a population since multiplying the number of individuals by their average mass yields an estimate of the biomass of the size class or set of individuals in the population being considered and the rate of production is defined as the biomass accumulated by a population per unit time (Chapter 2).

My goals are simple:

(1) To describe techniques, including their assumptions, commonly used to estimate the biomass of individuals and populations in samples.
(2) To evaluate the accuracy and precision of these techniques by presenting estimates of these quantities gathered from actual studies.
(3) To illustrate how the information concerning assumptions, accuracy and precision can be used to make decisions about the utility of the various techniques.

The limitations, in achieving these goals, are not in the descriptive aspects, but in the availability of data to evaluate both the accuracy and the precision of estimates from the various techniques. When empirical estimates are not