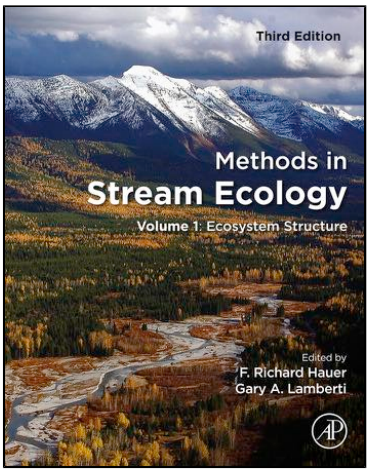

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Chapter 18

Invertebrate Consumer–Resource Interactions

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18.1 INTRODUCTION

Historically the biota of streams were viewed as being influenced strongly by abiotic factors such as disturbance, current velocity, substrate, water temperature, and light levels (Stevenson et al., 1996; Allan and Castillo, 2007). However, benthic environments in streams are zones of high biological activity in which species interactions such as herbivory and predation are important processes (Lamberti and Resh, 1983; Peckarsky, 1982). Streams are open, nonequilibrium systems having multiple patches connected by migration (Cooper et al., 1990; Palmer et al., 1996; Forrester et al., 1999; see also Chapter 21), while classic theory describing species interactions was developed for closed, equilibrium systems (e.g., Slobodkin, 1961). Nonetheless considerable evidence and theory has accumulated suggesting that species interactions can be important determinants of the distribution and abundance of stream biota (e.g., Caswell, 1978; Nisbet et al., 1997; Diehl et al., 2000). For this reason, stream ecologists have developed methods for studying interactions among species comprising food webs, which are designed to answer questions related to the influence of those interactions on observed patterns of distribution and abundance of consumers and resources.

Because streams are highly heterogeneous, open systems defined by flow dynamics, such methods are often challenging to design and implement. While relationships among species can sometimes be inferred from observations of distribution and abundance of species (see Chapter 22), experimentally testing mechanisms or processes explaining those relationships often require simplifying complex systems and/or closing them to immigration or emigration, both of which are often critical to explanations of patterns. Consequently innovative methods to address those challenges are essential to a full understanding of the role of species interactions in stream ecosystems.

Species interactions in stream ecosystems are often complex involving multiple trophic levels and pathways (Lamberti, 1996). However, subsets of food webs, termed "interaction modules" are often studied to break down complex food webs into simpler components (Estes et al., 2013). While some complexity is undoubtedly lost using such simplification, it is also possible to reassemble component interactions to ask questions involving multiple food web levels. For example, the dynamics of interactions between predators and grazers and between grazers and algae must both be understood to test questions involving cascading trophic interactions from predators on algae-mediated by grazers (Pace et al., 1999).

Furthermore food web interactions between consumers and resources can be examined from the perspectives of bottom-up effects of resources on consumers and top-down effects of consumers on resources (Power, 1992; Rosemond et al., 2000). In this chapter, we will focus on methods to answer questions about the top-down effects of invertebrate herbivores on plant resources and invertebrate predators on prey. However, experiments can also be conducted to assess "bottom-up" effects of plants (e.g., Lamberti et al., 1987b, 1989) and for investigating herbivorous fish effects on plants (Power and Matthews, 1983; Power et al., 1985; see also Chapter 19).

While unique aspects exist for each of herbivore–plant and predator–prey interactions, questions can be addressed about both trophic links using similar methods. For example, both predators and grazers can affect the biomass (abundance), distribution (heterogeneity), and species composition of prey and algae in streams (Steinman et al., 1987, 1989).

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Moreover, the contrast between accessibility of habitats to consumers and resources can be exploited to exclude consumers from treatments in experiments designed to test effects of consumers on resources. Therefore, fundamentals of methods to test those types of questions are often similar. Also, effects of both predators on prey assemblages and grazers on algal assemblages depend not only on consumer preferences but also on prey or plant defenses (Carpenter et al., 1987). Therefore these interactions have similar conceptual underpinnings and potential consequences for stream ecosystems.

In this chapter, we also include some innovative methods unique to one or the other of those two food web links. For example, raised platforms are an effective means to restrict the accessibility of some invertebrate grazers while allowing algae to colonize (Lamberti and Resh, 1983). Similarly, methods have been developed by stream ecologists to examine the nonconsumptive effects (NCEs) of predators on prey behavior and life histories recognizing that such NCEs may have stronger consequences for prey fitness than mortality due to consumption by predators (McPeek and Peckarsky, 1998). While there are corollaries in the study of herbivore−plant interactions [e.g., herbivores can change the productivity of some species of algae either positively by cropping competitors (Steinman et al., 1989) or negatively by causing nonconsumptive scouring of algae (Scrimgeour et al., 1991)], those areas of inquiry are not as well developed as are NCEs of predators on prey. However, measuring alternate response variables in experiments designed to test consumptive effects of herbivores on algae provides avenues for investigating those alternative questions. Furthermore while electivity indices have been devised to test for predator preferences of prey species, those same methods can be applied to ask questions about grazer preferences for specific algal taxa.

18.1.1 Top-Down Interactions Between Invertebrate Grazers and Primary Consumers

Primary producers and their consumers interact in benthic environments—producers become established, grow, and reproduce while primary consumers (hereafter termed "grazers," largely animals) ingest producer biomass to likewise grow and reproduce. Primary producers in streams consist of algae, bryophytes (i.e., mosses and liverworts), vascular plants, and some autotrophic bacteria. In most small streams, however, benthic algae are the dominant primary producers (Bott, 1983; Wehr and Sheath, 2003) and will grow on virtually any submerged surface, inorganic or organic, living or dead (Lamberti, 1996). Benthic algae commonly found in streams include diatoms, filamentous and nonfilamentous green algae, blue-green algae (Cyanobacteria), and sometimes red algae, and other algal groups (see Chapter 11). The entire attached microbial community is considered to be *periphyton* (historically called "aufwuchs" or more recently "biofilm"), of which algae are usually the main living component. The benthic surface on which periphyton grows also is sometimes used to describe the growth, such as *epilithon* (literally, "on the surface of rocks"), *epipsammon* ("on sand"), or *epidendron* ("on submerged wood"). Some algae, *epizoon*, can even grow on the bodies, shells, or cases of animals (see also Chapter 11).

Grazing is the consumption of living producers or their parts by primary consumers. Many aquatic animals consume periphyton, either for most of their energy intake (as with invertebrate *scrapers*; see Chapter 20) or as a variable portion of their diet (as with *omnivores*). Arguably most aquatic invertebrates probably consume periphyton during at least some part of their lives (Lamberti, 1996). The diversity of invertebrate grazers in streams spans a broad range of taxonomic groups, but insects, mollusks, and crustaceans are particularly important (Lamberti and Moore, 1984). Among the more conspicuous benthic grazers in streams are caddisflies (Trichoptera), mayflies (Ephemeroptera), and snails (Gastropoda), and much work has been done on their grazing ecology (reviewed by Feminella and Hawkins, 1995; Steinman, 1996). Regardless of the specific organisms, it is clear that many aquatic grazers consume benthic producers (Gregory, 1983) and that, for some, their growth and development is linked directly to algal production (e.g., Feminella and Resh, 1990, 1991; Hill, 1992).

Given the energetic value, lack of mobility, and nutritional quality of benthic producers and their consumption by a diverse array of grazers, it is reasonable to postulate that grazers have strong impacts on plant assemblages in many streams. Indeed, grazers do alter many structural and functional attributes of benthic algae, but their effects are not consistent in direction or magnitude across streams, time, algal assemblages, or grazer type (Gregory, 1983; Feminella and Hawkins, 1995; Steinman, 1996). For example, biotic factors such as grazer species, abundance, or size (Lamberti et al., 1987a; Steinman, 1991) and algal successional state (Dudley et al., 1986; DeNicola et al., 1990; McCormick and Stevenson, 1991) can each influence producer responses to consumption. However, the strength and outcome of the producer−consumer interaction also is dependent on many abiotic factors such as light (Steinman, 1992; Wellnitz and Ward, 2000), ambient nutrients (Rosemond, 1993), substratum (Dudley and D'Antonio, 1991), flow (DeNicola and McIntire, 1991; Opsahl et al., 2003; Poff et al., 2003), season (Rosemond, 1994; Rosemond et al., 2000), and disturbance (Feminella and Resh, 1990; Pringle and Hamazaki, 1997). For example, a low standing crop of algae can result from heavy grazing pressure, low light or nutrient concentrations (poor growing conditions), recent disturbance such as a flood, or some combination of these and other factors.

18.1.2 Top-Down Interactions Between Invertebrate Predators and Prey

In many streams, fish are the top predators feeding on invertebrates on the stream bottom or drifting in the water column (Hyatt, 1979; see also Chapters 19 and 22); and predatory fish often suppress predation by invertebrates (Peckarsky and McIntosh, 1998). However, in streams without fish, invertebrates are often the top predators and most commonly include representatives of many orders of stream insects including dragonflies and damselflies (Odonata), stoneflies (Plecoptera), hellgrammites (Megaloptera), caddisflies (Trichoptera), and true flies (Diptera) (Peckarsky, 1982; Allan and Castillo, 2007; see also Chapters 15 and 20). Common prey taxa for invertebrate predators include mayflies (Ephemeroptera) and Diptera (Chironomidae, Simuliidae). Most studies of invertebrate predation in streams have been conducted with benthic-feeding stoneflies (e.g., Malmqvist and Sjostrom, 1980; Allan, 1982; Molles and Pietruszka, 1983, 1987; Peckarsky, 1985; Walde and Davies, 1987). In contrast, less is known about the effects of other invertebrate predators in streams.

Predators can affect prey populations and communities by direct predator-induced mortality, or by direct and indirect effects on prey behaviors and life histories (Sih, 1987; Strauss, 1991). For example, predators can have indirect community-level effects ("top-down" cascading trophic effects) if reducing prey abundance increases resources used by prey (Carpenter et al., 1987; Power, 1990). Alternatively predators can have direct, but NCEs on prey populations through predator-induced changes in prey behavior or life history (Peckarsky et al., 1993, 2002). In this case, interactions between predators and prey that do not result in prey death can still have negative consequences on prey population growth (McPeek and Peckarsky, 1998). This outcome may occur if predator-avoidance behavior is costly to prey in terms of lost feeding time, shifting to unfavorable food patches, or changing to less-favorable feeding times (Peckarsky, 1996). Alternatively, prey may alter their development to reduce exposure to dangerous predators (Crowl and Covich, 1990; Peckarsky et al., 2001). Thus the impacts of predators in streams can be studied from two general perspectives: (1) effects of predator-induced mortality on prey populations and communities and (2) consequences of antipredatory behavior and life histories on prey fitness and prey population growth.

The impact of consumers on different algal taxa or prey species depends on relative vulnerability, immigration rates, and tendency to emigrate from patches where consumers are foraging (Peckarsky, 1985; Kohler, 1983; Kohler and McPeek, 1989; Lancaster et al., 1991; Forrester, 1994). Thus it is important to know the prey *exchange rate*, the rate at which resources move in and out of areas where consumers are feeding. For example, in streams with fast-flowing riffles and high invertebrate drift rates (see Chapter 21), predation may be swamped by prey immigration (Cooper et al., 1990; Englund, 1997). In contrast, benthic algae in general are a more stationary resource (more easily depressible, but also high turnover rates) than invertebrate prey, suggesting that in open systems with high levels of invertebrate movement, grazers should have greater effects on algae than predators on prey (Peckarsky et al., 2015). In streams with low rates of prey immigration, or where predators induce high rates of prey emigration (Sih and Wooster, 1994), predators may have more substantial impacts (Cooper et al., 1990), similar to those of grazers on algae. Thus the influence of consumers on organisms living in open systems with extensive dispersal needs to be assessed relative to other influences on resource population dynamics (Palmer et al., 1996).

Causal factors responsible for algal or prey abundance patterns are impossible to identify using descriptive or observational approaches alone, which are limited to providing strong inference and generating hypotheses (Power et al., 1998). Only controlled experiments, those done under field (in situ) conditions being best, can be used to evaluate the separate and combined effects of consumers and other possible causal factors on resources (Peckarsky, 1998). In this chapter, we describe field approaches, both observational and experimental, to assess the effects of consumers on resources in streams. All experiments involve the manipulation of consumer abundances over time, using either consumer exclusions or cage enclosures.

These experiments are designed to be conducted in low- to middle-order streams (orders 2–5) where benthic consumers often predominate, but they can be modified for use along the margins of large rivers and even in the littoral zones of lakes. Similar experiments can also be conducted within laboratory artificial streams, where a high level of control is possible (reviewed by Lamberti, 1993). However, field experiments typically provide more realistic conditions and responses (i.e., higher accuracy) than laboratory experiments. Unfortunately although more accurate, experiments in natural streams often are prone to more variable responses (i.e., lower precision) than those in the laboratory, and so may require larger numbers of replicates to achieve the same level of precision. Logistical constraints and the possibility of unanticipated events (e.g., floods, drought, vandalism, etc.) also should be considered when designing field experiments. Naturally, in both public and private waterways, permission from appropriate officials or landowners should be obtained before conducting field experiments.

The specific objectives of this chapter are to introduce methods to (1) provide an introduction to the consumers and resources involved in lotic herbivory and predation; (2) compare field measurements of predator consumption

(gut contents) to estimates of prey availability to generate hypotheses on selective predation at the community level (*Basic Method 1*); (3) quantify top-down effects of consumers on the distribution, abundance, and taxonomic composition of resources in streams (*Basic Methods 2* and *3*); (4) measure effects of predators on prey behavior and life histories (*Advanced Method 1*); and (5) illustrate the advantages and limitations of field experiments for measuring consumer impacts on resources in streams.

18.2 GENERAL DESIGN

18.2.1 Site and Species Selection

Small- to moderate-sized (order 2−5) wadeable rocky-bottom streams with riffle habitats are preferable for the methods described in this chapter because they typically contain benthic grazers, invertebrate predators, and productive algal assemblages, and often have the high water clarity necessary to allow visual estimates of invertebrate abundance. If comparisons among streams are of interest, replicate streams or reaches should be selected for similarities in as many attributes as possible, except for one factor suspected as important to explaining differences in grazing or invertebrate predation [e.g., riparian canopy (shading)], channel form, current velocity (e.g., low- and high-flow classes), stream water nutrient levels, substrate type or presence of fish). Less desirable than using stream reaches (or different streams) as true replicates are experimental designs comparing two reaches that differ in some environmental feature and sampling multiple nonindependent habitat units within each reach as spatial replicates, which is considered pseudoreplication (*sensu* Hurlbert, 1984). A single stream reach can be used if the study question only concerns description of grazing or predation, in which case environmental factors can be measured and used as statistical covariates. These latter two experimental designs may be the only practical approach in some studies of species interactions, although they have limited extrapolational power to other streams or stream reaches (Hurlbert, 1984).

The feasibility and specifics of methods described in this chapter will also depend on access to streams containing abundant populations of grazing invertebrates (e.g., Trichoptera, Ephemeroptera, Gastropods), or large predatory stoneflies (Plecoptera: families Perlidae or Perlodidae) and potential mayfly prey species (Ephemeroptera: families Baetidae, Leptophlebiidae, Heptageniidae, Ephemerellidae). While it is possible to substitute other predatory taxa (e.g., dragonflies or hellgrammites), these methods were designed specifically for stonefly−mayfly interactions and, thus, have the highest probability of succeeding if those taxa are used. Many methods involve field collection of grazers, predators, and prey, and will work best if desired taxonomic groups are abundant. For enclosure experiments (*Basic Method 3* and *Advanced Method 1*) researchers should use the most abundant grazer or predator species; prey species most abundant in predator diets should be used for *Advanced Method 1*.

Exclosure and enclosure experiments in *Basic Methods 2* and *3* should be carried out in high clarity, moderately shallow (<50 cm), moderately flowing (10−25 cm/s) runs or riffles in the field, if such habitats are available and will not be disturbed overnight. Alternatively *Basic Method 3* and *Advanced Method 1* can be carried out in the laboratory if the researchers have access to dechlorinated water (e.g., well water or stream water) that can be distributed to replicate enclosures. However, best results will be obtained using circular enclosures setup streamside and using natural stream water.

18.2.2 Field-Derived Electivity Indices—Generating Hypotheses for Community-Level Effects

A simple method of estimating selective predation in the field involves comparing the proportion of prey in predator guts to relative prey abundance in the habitat (Chesson, 1978). Although these methods have been developed specifically for predator−prey interactions, they may also be adapted to test preferences of grazers for different algal taxa or morphological groups. Although gut content data may provide an accurate record of undigested prey parts, there are many potential limitations to this method (see also Chapter 22). Variation in gut clearance time of different prey species (Hildrew and Townsend, 1982) may lead to overestimation of prey with heavily sclerotized parts compared to soft-bodied prey. Partial consumption of prey may leave heavily sclerotized parts uneaten (Martin and Mackay, 1982; Peckarsky and Penton, 1985). Furthermore ingestion of prey fragments, prey maceration, regurgitation during preservation, or alteration of gut contents by preservatives may also constrain our ability to quantify predator diets accurately from gut contents. Thus gut contents show only part of what has been eaten, and could result in misinterpretation of the relative consumption rates of different prey species. Similarly, silica valves of diatoms are readily identified in grazer guts, but soft algae may not be possible to distinguish (see Chapter 11).

Field estimates of prey or algae preferences also depend on the accuracy of estimates of resource abundance. While quantifying proportions of algal taxa in the biofilm is relatively straightforward (see Chapter 11), a large literature describes

potential problems with the accuracy of benthic samples (Resh, 1979; see also Chapter 20). Using samples of prey abundance to estimate their availability to predators assumes that (1) samples accurately reflect relative prey densities, (2) predators encounter prey at rates commensurate with measured prey density, and (3) the predator perception of available prey is the same as that of the investigator. Little is known about natural predator–prey encounter rates (Peckarsky et al., 1994) or predator perception of available prey in streams (O'Brien and Showalter, 1993), since it is difficult to observe stream predators in their natural habitat. Consequently hypotheses of differential predation based on data obtained by this field approach should be tested using experiments (e.g., Peckarsky and Penton, 1989).

To estimate selectivity from field data, investigators compare the proportions of each prey item in consumer gut contents to its relative abundance in the habitat. The simplest approach (correlation) involves comparing the ranks of prey types in the predator guts and in the habitat using Spearman's rank correlation analysis (Zar, 2010). A significant positive correlation indicates no selectivity (similar ranks of prey items in the diet and in the environment); no correlation or significant negative correlations suggest selective predation (feeding is weakly or strongly disproportionate to availability of prey in the environment). A second approach involves calculations of electivity indices (Ivlev, 1961; Jacobs, 1974; Chesson, 1978; see also situation-specific modifications in Johnson, 1980; Lechowicz, 1982), which compare the proportion of each prey item in the predator's gut (r_i) to its proportion in the habitat (p_i). For preferred prey, $r_i > p_i$; whereas $r_i < p_i$ suggests avoidance or prey unavailability; and if $r_i \sim p_i$, that prey item is being consumed in proportion its abundance in the environment. This method generally provides no significance tests (but see Lechowicz, 1982), but can be used to compare the strengths of selection or avoidance among alternative prey. Finally remember that this approach can only be used to hypothesize positive or negative selection for certain prey species, and that further tests are necessary to determine the reasons why specific patterns were observed.

18.2.3 Field Experiments

18.2.3.1 Relatively Sedentary Herbivore Platform Exclusions

Benthic grazers that do not swim or exhibit low drift rates (e.g., cased caddisflies, snails, etc.) can be excluded by elevating artificial substrata above the stream bottom, which are then mostly inaccessible to those grazers over short periods (Lamberti and Resh, 1983; Feminella et al., 1989). A "platform" supporting algal substrata (stream rocks or unglazed clay tiles) is erected in each replicate habitat unit and a control plot is placed directly on the streambed adjacent to each platform. Sampling of grazers and periphyton on the treatment and control plots is conducted over time extending to ≥30 day. This design enables comparison of an "ambient" level of grazing (periphyton in control plot) with a "reduced" level of grazing depending on which grazer species are excluded (periphyton in platform plot). Artifacts of caging (see Peckarsky and Penton, 1990; *Basic Method 3*) are minimized with this design, but uncontrolled differences in depth, light, current velocity, or other factors may exist between each control and platform pair, which may affect experimental results. Such bias may be minimized by selecting plots with minimal environmental variation in all but the variables of interest (Feminella et al., 1989). It is also important to note that this design *rarely* excludes all grazers. Some swimming or drifting nontarget species (e.g., mayflies, chironomids, some fishes), as well as occasional target grazers, may accumulate on platforms, possibly occurring at higher densities than on the streambed (e.g., Lamberti et al., 1992). These animals will require manual removal periodically during the experiment. If that is not feasible, it may be necessary to estimate the abundance of grazers on platforms during the experiment and consider it as a covariate in statistical analyses.

18.2.3.2 Herbivore and Predator Cage Enclosures

Alternatively mobile grazer or predator species composition and density can be manipulated directly within stream enclosures or "cages." These enclosures can be made from simple materials, stocked with known densities of consumers, and can be submersed (e.g., Peckarsky, 1984; Feminella and Hawkins, 1994; Stelzer and Lamberti, 1999) or floated in the stream (e.g., Lamberti et al., 1987b). One set of cages containing a replicate of each treatment may be deployed in each stream reach (as blocks) and sampling of all treatments is conducted over time extending to ≥30 days. This design allows comparisons among known levels of grazing or predation, which can range from zero to high, and exerts more control over grazing pressure than provided by the platform design. It is also possible to measure consumption by particular species and/or size classes of grazers or predators, which may exert very different impacts on periphyton (Feminella and Resh, 1991; Steinman, 1991) or prey species (Allan and Flecker, 1988; Peckarsky and Penton, 1989). However, some consideration must be given to potential cage effects that result from altered (usually reduced) flow, increased sedimentation (Peckarsky and Penton, 1990), and colonization by unwanted consumers (see Walde and Davies, 1984; Cooper et al., 1990); each of these potential artifacts may alter the effectiveness of consumer manipulations and confound interpretation of results.

In addition, more maintenance generally will be required for cages than for platforms. In some instances, however, such as when conducting intraspecific consumer experiments or when quantifying effects of individual consumers on resources, cages may be the only suitable design.

18.2.3.3 Nonconsumptive Effects of Predators on Prey Behavior and Life History

Experimental protocols similar to ones described in Section 18.2.3.2 can be used to test the effects of nonfeeding predators on prey behavior or life history by introducing cues from foraging predators into arenas without allowing predators to consume prey. Mouthparts of stoneflies can be glued with Barge Cement if they forage naturally in chambers with mayflies (Peckarsky et al., 1993). Using these protocols in shallow streams where observations of predator and prey behavior are feasible enables feeding behavior (foraging on rock surfaces, drift among different rocks) and life history parameters (growth rates, development times, size at maturity) to be compared statistically with and without predator cues.

18.3 SPECIFIC METHODS

18.3.1 Basic Method 1: Electivity Indices for Invertebrate Predators

18.3.1.1 Field Protocols

Researchers should collect invertebrates using a sampler designed for sampling in stream riffles (D-frame net, Surber sampler, Hess sampler; see Chapter 15). Methods can be standardized either by sampling the same microhabitat or by using the same effort for each sample (or both). If available to the researcher, an electrofishing machine may be equipped with a smaller anode and placed inside a Hess Sampler to take samples of benthic invertebrates (Taylor et al., 2001). (Note: These methods can be modified to calculate electivity indices for grazer species on different algal taxa. See Steinman, 1996).

1. Using methods described in Chapter 15, or in Taylor et al. (2001), collect macroinvertebrates from a prescribed area of substrate (including large cobbles) in a shallow (<30 cm) riffle with moderate flow (20–30 cm/s). The size of the area disturbed, and the number of samples taken depends on the productivity of the stream with a goal of collecting at least 100 individuals. Samples may be combined for analysis or kept separate to preserve replication and estimate variation.
2. Place each sample in a shallow pan, and use forceps to remove and preserve all large predatory stoneflies in a jar or Whirl-pak containing 70% ethanol. If no predatory stoneflies are collected, discard the sample (no useful information will be obtained). Preserve the rest of the sample after removing large bits of detritus and inorganic sediment. One of the major advantages of the "electrobugging" method is that samples contain much less debris and can be sorted more efficiently than standard "kick" samples (Taylor et al., 2001).

18.3.1.2 Laboratory Sorting, Counting, and Reference Protocols

1. Sort each sample and record the numbers of individuals collected of each predatory stonefly and prey taxon on Table 18.1. Since stoneflies primarily eat midges, blackflies, and mayflies (Peckarsky, 1985), or sometimes caseless caddisflies (Stewart and Stark, 2002), other taxa need to be identified only to order (see Chapter 15). However, blackflies (Simuliidae), midges (Chironomidae), and mayflies should be identified at least to family (especially Baetidae, Leptophlebiidae, Heptageniidae, and Ephemerellidae).
2. Prepare a reference collection of the invertebrates found at the stream to facilitate this process and minimize errors in identification.
3. Calculate the total numbers of each prey taxon and the proportion of the total individuals in all samples combined (p_i) and record data on Table 18.1. Alternatively proportions of prey taxa may be calculated for each sample to estimate variability of relative prey abundance.

18.3.1.3 Protocol for Gut Content Analyses

1. Use two pairs of forceps to pull the head from the prothorax of each individual of the most abundant predatory stonefly taxon. The foregut, which should remain intact and attached to the head, can then be dissected and examined for recognizable prey parts. If the foregut does not remain attached to the head, dissect the thorax (through the ventrum) and

TABLE 18.1 Data sheet for recording benthic prey data and predator gut contents to calculate Spearman rank correlation coefficients or Ivlev's electivity index for selective predation (see *Basic Method 1*). *Note*: gray cells are not applicable.

	Number in Benthic Samples						Rank	Number in Predator Guts						Rank	(Eq. 18.1)
Samples	1	2	3	...*n*	**total**	p_i	**Habitat**	1	2	3	...*n*	**total**	r_i	**Diet**	**Ivlev's E_i**
Predator taxon															
Prey taxa															
Baetidae															
Ephemerellidae															
Heptageniidae															
Leptophlebiidae															
Other Ephemeroptera															
Plecoptera															
Trichoptera															
Chironomidae															
Simuliidae															
Other Diptera															
Total Prey															

anterior abdomen to extract the foregut. Since large predatory stoneflies swallow their prey whole, prey should be identifiable, provided a short time has elapsed since the predator's last meal.[1]

2. Use the reference collection of potential prey taxa or taxonomic references to identify prey in the predator's foregut. Prey fragments (claws, mandibles, head capsules, etc.) can be identified by comparison to whole specimens.
3. Record numbers of each prey taxon found in each predator gut on Table 18.1; calculate totals for each taxon, and the proportion of the total prey individuals for all predators combined (r_i). Alternatively, stoneflies may be analyzed separately to estimate variation in predator diets.

18.3.2 Basic Method 2: Relatively Sedentary Herbivore Exclusion Using Platforms

18.3.2.1 Platform Construction

1. Construct 5–10 grazer-exclusion platforms, the exact number depending on the experimental design (see following paragraphs). Platforms are made of J-shaped aluminum or steel-supporting rods and square 1/4″ Plexiglas plates, the latter of which are used to hold tiles or rocks as a periphyton substratum. The resulting platform should look similar to the ones shown in a stream in Fig. 18.1. It is also possible to make platform supports from polyvinylchloride (PVC) pipe and elbow joints, depending on how rigorous the stream environment may be.
2. Cut Plexiglas into ~400 cm^2 plates (approximate dimensions = 20 × 20 × 0.4 cm). Drill a 3/8″ hole midway through one of the four sides, about 1 cm from the edge, which allows the plate to be attached to the supporting rod. Cut a second set of plates for use in the control plots; these do not require a hole.
3. Using a drill press or metal lathe to secure the supporting rod, drill a 5/16″ hole (ca. 1″ long) into one end of the rod. Next, using a 3/8″ tap, thread the drilled hole to accept a 3/8″ hex bolt. Bend the threaded rods into the necessary J-shape with a metal jig in a bench vise, with the threaded end on the shorter end of the bend. (This step is most easily

1. For best results, samples should be taken in the morning because most predatory stoneflies are nocturnal feeders (Peckarsky, 1982) and food items in the gut will be less digested.

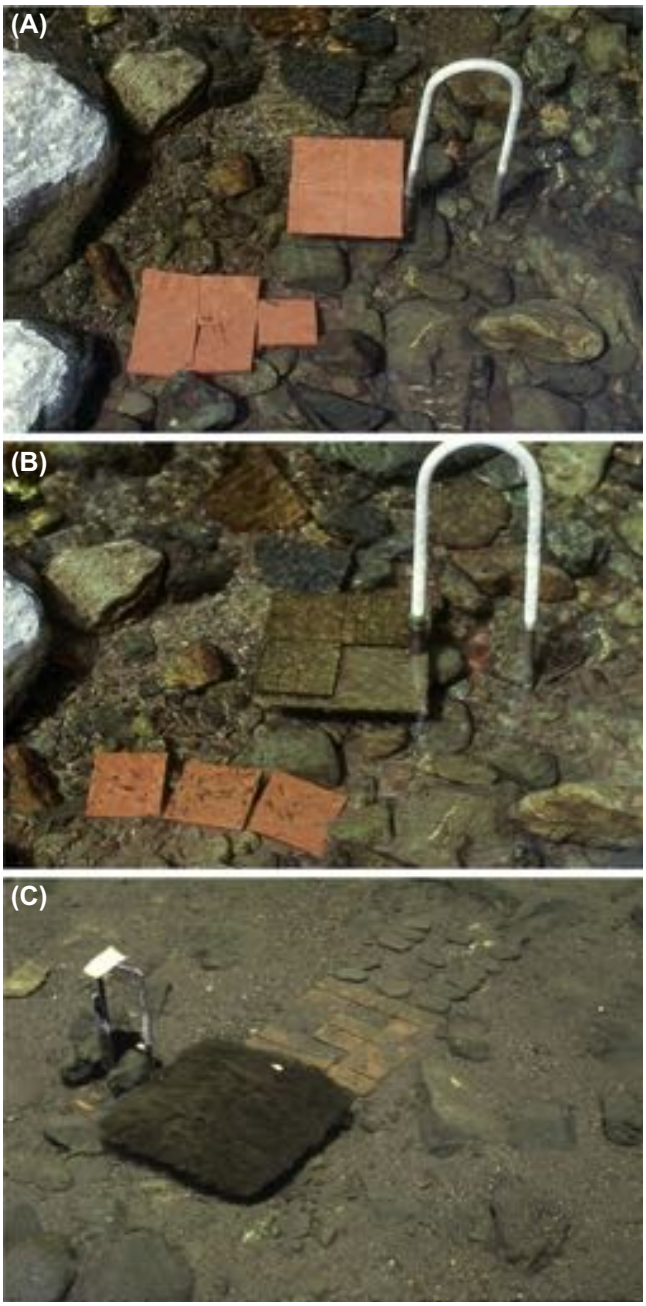

FIGURE 18.1 Grazer exclusion using platform design. Aluminum platform design showing quarry tiles (7.5 × 7.5 cm) on raised Plexiglas plates (ungrazed platforms) and on the streambed (grazed controls) at the beginning (A) and end (B) of the experiment. Tiles missing from platform and control plots in (B) were sampled before photograph was taken and objects on control tiles are grazing caddisflies. (C) Metal platform design showing periphyton growth at the end of a 90-day grazer exclusion in a California, USA, stream. Note luxuriant algal growth on the platform; rocks at upper right were used to calibrate quarry tiles (see also Lamberti and Resh, 1983). *(A and B) From Feminella et al. (1989). (C) Photo: Gary Lamberti.*

done with aluminum rods; steel rods are more durable but require heating before bending, which should be done by a qualified machinist.) Screw a hex bolt into the hole to ensure that it is seated properly.

18.3.2.2 Initial Fieldwork

1. Before embarking on a field study, give thought to the scale of the grazing question you are asking and then design your experiment appropriately. Regardless of whether you are working with platforms, or cages (see later), you should consider

that one unit (platform or cage) is equal to one experimental replicate (*sensu* Hurlbert, 1984). Therefore to achieve a treatment $n = 3$, for example, you will need three platforms or cages and an equivalent number of control units for comparison. Any sample taken from one of those units at a particular time contributes only one replicate; additional samples from that same unit constitute only "subsamples" or pseudoreplicates. Samples taken over time from the same experimental unit are not true replicates but rather are "repeated measures" (Zar, 2010). Decide at what spatial scale you wish to ask the grazing question—within a channel unit (e.g., pool), along a stream reach, or over a valley segment (see Chapter 2). Match the distribution of your replicates to this "inference space." Place your replicates (typically a paired treatment and control plot) at random within the channel unit of interest, along the study reach, or dispersed over a segment. Measure other environmental covariables that might influence the outcome of the experiment, such as canopy cover, current velocity, and water depth. Analyze the results using an appropriate statistical test (see *Analyses*).

2. Incubate unglazed clay tiles on the streambed for at least 2 weeks (and preferably for one month) to allow algal colonization; the number of tiles incubated should be enough to supply all plots plus an additional 10% to allow for loss. Sterilized rocks, such as those obtained from a quarry, can be substituted for tiles to provide more realism in any study that we describe. From here forward, however, we will describe methods for the use of tiles. A tile size of 7.5 × 7.5 cm is appropriate, four of which can be cut from one standard 6″ × 6″ tile using a tile cutter or masonry saw. Tiles should be incubated in a single microhabitat (similar depth, flow, and shading) so that similar periphyton assemblages are present on all tiles across all treatments at the beginning of experiments.

18.3.2.3 Installation of Platforms

1. Install supporting rods for platform plates in the selected sites within the stream. We recommend use of reinforcement bar (of similar diameter to that of supporting rods) and a small sledgehammer to make a pilot hole in the substratum. Once embedded into the streambed about 30 cm, carefully remove the pilot bar and in its place insert the supporting rod; the rod is then tapped in place with the sledge. Next, secure four precolonized tiles to each platform and control plate with dabs of silicon sealant on the undersides or with two heavy-duty rubber bands; use of silicon will prevent accidental dislodgement of tiles during the experiment. If rubber bands are used, be sure to subtract the area covered by rubber bands on each tile when estimating periphyton abundance later, as tile areas underneath rubber bands will not accrue algae. Attach the platform plate to the supporting rod with a washer and hex bolt; use a wrench to tighten firmly but do not overtighten or the plate may break. Place the control plot (plate with secured tiles accessible to grazers) on the streambed near the platform but not shaded by it.
2. At each location, install one replicate platform and one control plot, while matching current velocities, shading, and, if possible, depth. The latter may be achieved by using natural streambed contours to minimize the platform distance above the substratum, while maintaining sufficient elevation to prevent colonization by crawling grazers. Alternatively in more homogenous-bottomed streams, bricks or cinder blocks may be used underneath control plates, which serve to match elevation (depth) with paired platforms, yet still permit grazer access to tiles (Feminella et al., 1989). It is best to place each platform and control plot side by side (rather than upstream–downstream) so they will have minimal flow influences on each other.
3. Measure physical parameters for each platform and control plot including water depth, current velocity, and irradiance (see Chapters 3–7), and dissolved nutrients if feasible (see Chapters 31–33). Current velocity over the substrata can be measured with a current meter or by releasing inert dye (e.g., fluorescein) with a pipette and measuring time of travel (see Chapter 4). Irradiance can be measured with a portable light meter held close to the water surface (or with an underwater probe; see Chapter 7), or estimated indirectly by measuring overhead canopy with a fish-eye camera lens or spherical densiometer (Lemmon, 1957; Feminella et al., 1989). One set of four canopy measurements (i.e., facing upstream, downstream, and right and left banks) can be taken for both platform and control plot at each site; the four readings are then averaged for a single estimate for that site.

18.3.2.4 Sampling Platform Substrates

1. Decide on how many tiles to sample from each plot (platform or control) at the end of the experiment (≥30 days). Because each plot represents one replicate, it is necessary to sample only one tile per platform and control couplet. However, to reduce variability, you may want to sample two or more tiles per plot and then pool the sampled material before analysis. The same tiles can be used to sample both macroinvertebrates and periphyton. However, extra tiles may be needed for additional analyses such as algal taxonomic composition, primary production, or elemental composition (see later). Sampling over time (e.g., 1-week intervals) also can be employed to examine how patterns develop over time (e.g., Lamberti and Resh, 1983).

2. Sample macroinvertebrates from tiles at the end of the experiment. Dislodge macroinvertebrates from a tile into a downstream net (mesh size ≤250 μm) and then empty the net contents into a labeled heavy-duty plastic sample bag (e.g., Ziplock or Whirl-pak) or jar and preserve with 80% ethanol. Be sure to sample undersides of tiles for mobile invertebrates (e.g., mayflies, stoneflies, etc.). Manually remove any sessile invertebrates such as blackflies, chironomid midges, and caddisflies. The latter two groups often attach their organic (algal-rich) cases to tiles, which may remain after larvae are removed. Thus investigators should indicate whether they removed cases prior to sampling or left them in place as part of the periphyton sample.
3. Sample periphyton from tiles after invertebrates have been removed (see Chapter 12 for specific protocols). In the field, periphyton can be scraped or brushed from the tile into water and placed in a darkened container on ice. Alternatively the entire tile can be placed in a plastic container, stored on ice in the dark, and scraped in the laboratory later the same day.

18.3.2.5 Laboratory and Data Analyses

1. Analyze periphyton for biomass (as ash-free dry mass, AFDM) and chlorophyll *a* content and also compute the biomass/chlorophyll *a* ratio (see Chapter 12), although many other variables also can be measured if desired.
2. If researchers are interested in comparing compositions of the diets of grazers to the proportions of algal taxa in the habitat (e.g., to calculate electivity indices), they may also wish to determine taxonomic structure (see Chapter 11) of algae in the periphyton.
3. Researchers can also ask questions about the impact of grazing on primary production (see Chapter 34) or elemental composition (e.g., Stelzer and Lamberti, 2002; Aberle et al., 2005; see also Chapter 36), which are conceptually comparable to analyses of NCEs of predators on prey.
4. Macroinvertebrate community structure and density also can be compared for control (grazed) and platform (ungrazed) plots to evaluate shifts in consumer populations.

18.3.3 Basic Method 3: Herbivore or Predator Manipulation Using Enclosures

18.3.3.1 Enclosure Construction

1. In-stream enclosures can be constructed from various materials, or prefabricated containers can be modified for use. All designs should be fitted with mesh on at least the upstream and downstream sides, and optimally on all sides to allow for water exchange. Enclosure (and mesh) size should be scaled to the size and density of consumers used in the study. Animals vary greatly in their ability to behave "normally" within an enclosure, so there is no steadfast rule governing the size of the cage relative to the size of the animal used. However, the best choice in a cage size is one that collectively (1) provides the best possible control of the variable of interest; (2) is economically and logistically feasible to build, deploy, and maintain; and (3) has the lowest potential for cage-related artifacts. It is important to note, however, that use of galvanized metal hardware cloth for enclosures, even when used in situ, may have toxic effects on caged grazers; thus use of inert plastic or fiberglass mesh rather than metal for enclosures is strongly advised.
2. Construct cages ($n = 20-30$) suitable for the consumer of interest. For small consumers (e.g., small caddisflies, snails, or small stoneflies), plastic food containers with two or more sides replaced by window screening may be suitable (Fig. 18.2A). Cut window screening (1-mm mesh for grazing experiments, and 2- to 3-mm mesh for predation experiments to enclose/exclude large predators but allow colonization of smaller prey species) to size and secure to containers with silicone aquarium sealant or chemically inert hot glue. Lightly roughen container edges with sandpaper prior to attaching the screen to maintain the adhesive bond for a longer period. Allow at least 24 h for the adhesive to cure before immersing the enclosure. For large consumers (e.g., limnephilid caddisflies, crayfish, large stoneflies), larger enclosures can be made of hardware cloth, porous plastic containers, plastic gutters, or PVC pipe cut longitudinally (e.g., Feminella and Hawkins, 1994).
3. If the budget allows, cages can be constructed with stainless steel mesh on all six sides for maximum durability and exchange of flow (Peckarsky, 1984). These larger, more durable materials also allow experiments to be performed in fast-flowing stream sections, such as in riffles or runs, where rheophilic consumers (e.g., heptageniid and baetid mayflies, glossosomatid caddisflies, perlid, and perlodid stoneflies) predominate. Alternatively rectangular open-topped enclosures with upstream and downstream ends covered with mesh (~800 μm openings: small enough to retain prey but large enough to minimize clogging) can be used to observe consumer behavior in very shallow water (<10 cm). A simple design is a fabricated plexiglas box (Fig. 18.3), but cheaper materials may be used, such as Rubbermaid shoe boxes, with openings cut in the sides and screened with Nitex attached to walls with hot-melt glue. The floor

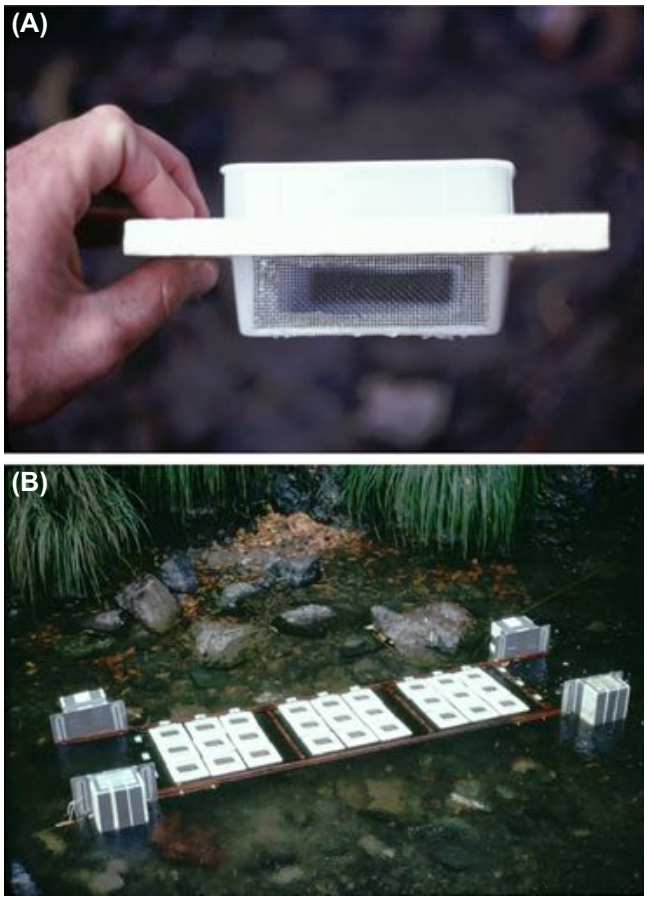

FIGURE 18.2 Grazer enclosures used to manipulate densities of small benthic grazers. (A) Each enclosure is ~500 cm^3 with sides screened with 1-mm^2 mesh and fitted with a styrofoam collar for flotation. (B) Floating rack holding 27 enclosures tethered in a stream run of Big Sulfur Creek, California, USA. *Photos: Gary Lamberti (see also Lamberti et al., 1987b).*

of each enclosure should be covered with a standardized number of cobbles ranging from 5 to 15 cm in diameter with the same size distribution in each enclosure. To observe predator–prey interactions with grazing prey, it is best to use natural algal-covered stream substrata from which all invertebrates have been carefully removed. Such cobbles also provide food for prey, refuges for predators and prey, and anchor enclosures to the streambed.

4. Enclosures may float or be submersed and integrated into the substrate. To float small enclosures at the stream surface, cut "collars" from 1/2″- to 3/4″-thick styrofoam panels (Fig. 18.2A). Leave enough of a styrofoam border around the complete enclosure so that it remains buoyant and stable when placed in the stream. Coarse mesh covers can be placed on floating enclosures (or those protruding above the water surface) to exclude falling debris or reduce disturbance by terrestrial animals, although take care to minimize changes to irradiance. In addition to the consumers under investigation, the enclosures may contain substratum tiles and additional materials, such as sand for caddisfly case-building material. Sets of enclosures may be held in place within rectangular wooden racks, which are predrilled and strung tennis racquet-style with monofilament line (30–60 lb test) to secure individual enclosures and collars (Fig. 18.2B). Racks can be floated by attaching styrofoam blocks to each of the corners and held in place by tethering to rebar stakes or trees on the bank. Some slack in the tethers is desirable in case water level changes. Alternatively individual enclosures can be tethered to stakes or bricks in the channel with monofilament and allowed to "free float" in the stream. The ideal location for racks is generally in a stream "run," which provides both flow and flotation room.
5. Submersed enclosures are placed directly on the streambed and integrated into the substrate by placing natural substrate around them to facilitate colonization by benthos other than the consumer being manipulated. In swift current, it may be necessary to attach them with hose clamps, zip ties, or other materials to reinforcement bar pounded into the streambed or to concrete cinder blocks (Fig. 18.4). For larger enclosures, stream cobbles lining enclosure bottoms may be used as ballasts as well as habitat for colonization of periphyton or prey. Unless enclosure walls are considerably higher than

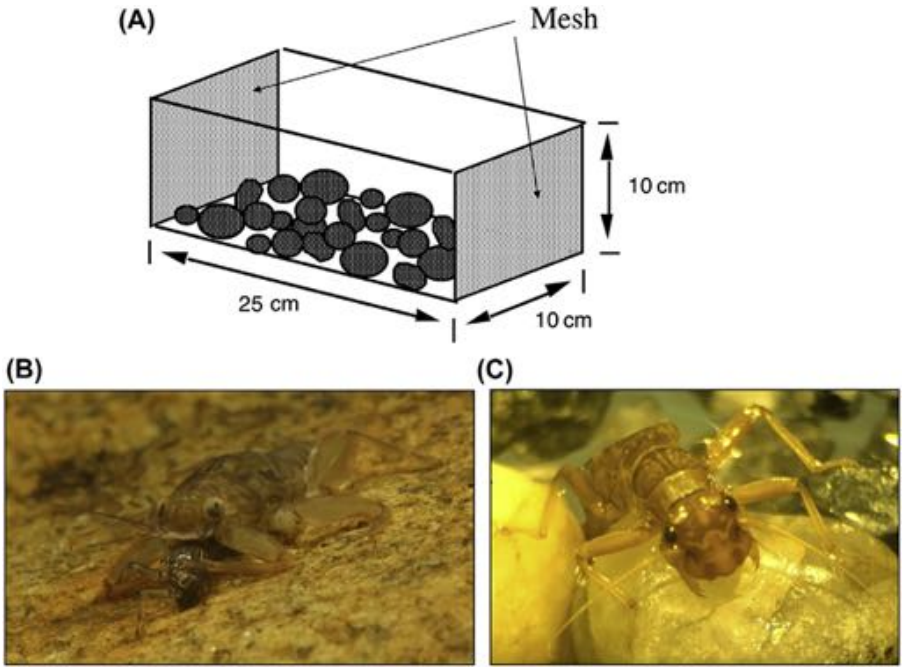

FIGURE 18.3 In situ enclosures. (A) Drawing of rectangular chambers for *Basic Method 3* that can be used in the field. *Shaded areas* represent screen mesh or Nitex. Photographs of (B) *Drunella doddsi* consuming *Baetis bicaudatus*, and (C) *Megarcys signata* foraging. *(A) From Peckarsky and Penton (1989). (B) Photo: Angus McIntosh. (C) Photo: Michael Benton.*

that of the stream surface, enclosures must be completely covered with mesh so that consumers are effectively isolated and experimental treatments can be maintained.

18.3.3.2 Enclosure Installation

1. Locate a study site that will receive enclosures. Unless the questions involve comparisons among different stream types, it is less critical to replicate the experiment over several sites (cf. platform design), because a full range of experimental treatments and replicates can be interspersed within a single site and inference across a larger space is less important. In enclosure studies, the main effect is consumer species or density and the response consists of various resource variables.
2. Incubate unglazed clay tiles or other chosen substrates on the streambed, as described previously (*Basic Method 2—Initial Fieldwork*).

FIGURE 18.4 Photograph of 12 large, partially submersed polyvinylchloride enclosures (dimensions: 103 cm L × 32.5 cm D) used to study herbivorous tadpoles in high-gradient streams near Mount St. Helens, Washington, USA. Enclosures contain algal-covered stream cobbles that are used both as grazing substrata for tadpoles and as ballasts for enclosures in fast riffles. Coarse mesh covers used to isolate and protect animals are shown in the six enclosures in the upper part of photograph. Direction of flow is from upper left to lower right of photograph (see also Feminella and Hawkins, 1994). *Photo: Jack Feminella.*

3. Survey the stream reach to identify the numerically dominant large, benthic grazer(s) (e.g., snails, mayflies, caddisflies, crayfish, etc.) or predators (e.g., stoneflies, dobsonflies) in the stream. Measure the ambient density of these consumers on the streambed either by making visual counts from replicate quadrats ($N = 15–30$) placed randomly in all habitat types (e.g., riffles and pools) throughout the study reach, or by taking preliminary samples of specific microhabitats where more cryptic consumers are most common (e.g., cobbles, boulders). These estimates will yield a full range of consumer densities from low (across all habitat units) to high (within preferred habitat) to yield a large operational range of consumer abundances in which to bracket experimental treatments, and will provide greater extrapolational power for experimental results.
4. Choose treatments and number of replicates for each treatment. Use ambient consumer density and no consumers, with at least three replicates of each treatment. Optionally, include treatments of one-half ambient density and double ambient density, or add replicates to increase statistical power. In a more complex design, habitat (e.g., shading or current velocity) contrasts can be added to some replicates to achieve a two-factor experimental manipulation (i.e., effects of consumers and irradiance/current). Shading can be achieved by placing neutral-density shade-screen over the top of some enclosures, whereas velocity contrasts can be achieved by placing the full complement of density treatments within replicated stream sections with the desired velocity classes [e.g., 0–4 cm/s (low), 10–15 cm/s (moderate), and/or ≥30 cm/s (high velocity)].
5. Select a relatively uniform site in the study reach in which to install enclosures. Place precolonized tiles in enclosures and suspend in the rack or anchor to the stream bottom (see earlier). Collect individuals of the selected consumers (grazers or predators) from the stream. Randomize the collected consumers and place the appropriate number of animals into each replicate enclosure.[2] Establish a block in each identified microhabitat (velocity range, depth, rows of enclosures, etc.) and place one replicate of each treatment in each block. Ideally the number of blocks should be equal to or greater than the number of treatments and treatments are equally represented across blocks.

18.3.3.3 Sampling Enclosures

1. At the end of the experiment, sample all enclosures; the same tiles can be used to quantify both macroinvertebrates and periphyton abundance. However, extra replicate enclosures may be needed for additional analyses such as algal taxonomic composition, primary production, stable isotopes, or elemental composition.
2. Manually remove all macroinvertebrates from enclosures at the end of the experiment (≥30 days) and preserve in 70% ethanol or 5% formalin.[3] Count the remaining target grazers or predators; identify and count other macroinvertebrates that have colonized the enclosures. Quantify the difference between starting and ending consumer abundance to determine mortality. Optionally measure consumer growth rates in enclosures by weighing a subsample of consumers collected at the beginning of the experiment and used for stocking cages, and at the end of the experimental period (e.g., Lamberti et al., 1987b).
3. Sample periphyton chlorophyll *a* and biomass from tiles at the end of the experiment, as described previously and in more detail in Chapter 12. If desired, set aside some biomass for other analyses (e.g., elemental composition, stable isotopes).

18.3.4 Advanced Method 1—Experiments to Test Nonconsumptive Predator Effects on Prey Behavior and Life History

18.3.4.1 Experimental Design

1. The best design for experimental units to test these questions is circular (10–15 cm diameter), which reduces edge effects, and flow-through, rather than recirculating, to prevent contamination by waste products (e.g., Fig. 18.5). Artificial stream channels can be made of Plexiglas or modified cylindrical food containers, and powered by water (Walde and Davies, 1984; Peckarsky and Cowan, 1991) or air pressure (Wiley and Kohler, 1980; Mackay, 1981). Air pressure necessitates recirculation of water and some type of refrigeration; water-powered chambers can use cold running water and central mesh-covered standpipes to regulate water levels. These designs can be modified depending on facilities

2. Minimize position effects (e.g., velocity or depth gradients) by using a randomized complete block design (see Zar, 2010).
3. Formalin is preferable to ethanol for preserving biomass because less tissue is lost to leaching. However, formalin is a known carcinogen and therefore extreme caution should be exercised in its use, including the use of PPE.

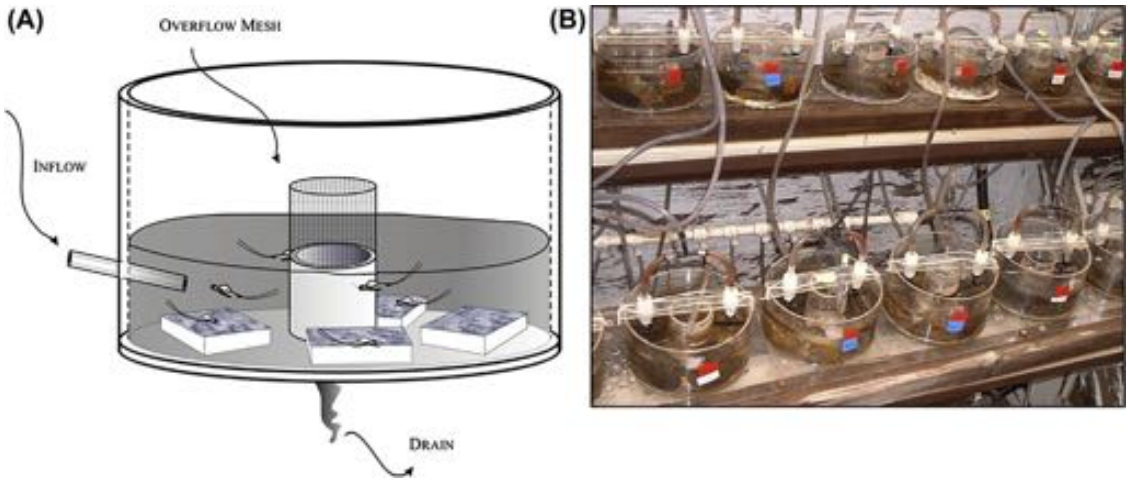

FIGURE 18.5 Small flow-through streams for predation experiments. (A) Drawing (by Peter Ode) and (B) photograph of two different designs of circular chambers for *Advanced Method 1* that could be used in the laboratory or streamside to contain small animals. *(B) Photo: Joanne Peckarsky.*

available, but cool temperatures (10°−15°C) and good oxygenation are essential conditions to facilitate natural predator and prey foraging behavior, growth, and development.

2. Set up replicate circular arenas supplied with dechlorinated water (well water or stream water) in the laboratory or preferably by diverting natural stream water into streamside artificial streams (Peckarsky and Cowan, 1991), which enables natural light and temperature regimes to be maintained. Natural algal-covered substrata can be collected from the stream and used for food and refuges for prey and predators, or algae can be colonized on tiles as in *Basic Method 2* and placed in experimental channels.
3. Add 5−10 prey of a selected species to channels with algal-covered natural rocks, or unglazed tiles for ease of viewing. For behavioral trials, arenas should be left uncovered to facilitate observation. If rearing prey to maturity, channels should be covered with mesh emergence nets that allow light to penetrate.
4. To measure effects of stonefly predators on prey behavior/life history, use a toothpick to place a small drop of Barge Cement on the mouthparts of a stonefly while it is anesthetized in a weak suspension of Alka-Seltzer and water (club soda can also be used; Peckarsky et al., 1993). Allow glued stoneflies to recover in a holding chamber before using them in experiments. To start the experiment, place one stonefly in each chamber randomly allocated to the predator treatment, and a small piece of gravel with Barge Cement in chambers allocated to controls.
5. Observe and record feeding behavior (instantaneous scan of numbers of individuals foraging on the surface of substrates) or drift behavior (number drifting per unit time) of prey several times during a 24-h period in chambers with and without glued stoneflies. Nighttime observations should be made using dim red light. Numbers of stoneflies visible foraging should also be recorded and compared to known natural feeding periodicity of the predators (determined in preliminary observations with nonglued stoneflies).
6. To measure the effects of glued stoneflies on prey life histories, prey should be reared to maturity (black wing pad—Stage IV) under these same treatments, and then preserved for analysis of size and fecundity (numbers of eggs per female).
7. Using a similar experimental design, chemical cues from trout (e.g., brook trout, *Salvelinus fontinalis*) feeding in separate chambers can be dripped into experimental arenas to test the effects of those cues on prey behavior and life history. Small chambers (Fig. 18.5) allow greater replication, but larger chambers (Fig. 18.6) provide a more realistic environment in which to measure prey life histories and behavior (McIntosh and Peckarsky, 1996; Peckarsky and McIntosh, 1998).

18.3.5 Data Analysis

18.3.5.1 Electivity Indices

Using the combined samples (Table 18.1) compare the fractional composition of each item (1) in the guts of the stoneflies (r_i) to its fractional composition in the available food supply (p_i) using Ivlev's electivity index (1961):

$$E_i = (r_i - p_i)/(r_i + p_i) \tag{18.1}$$

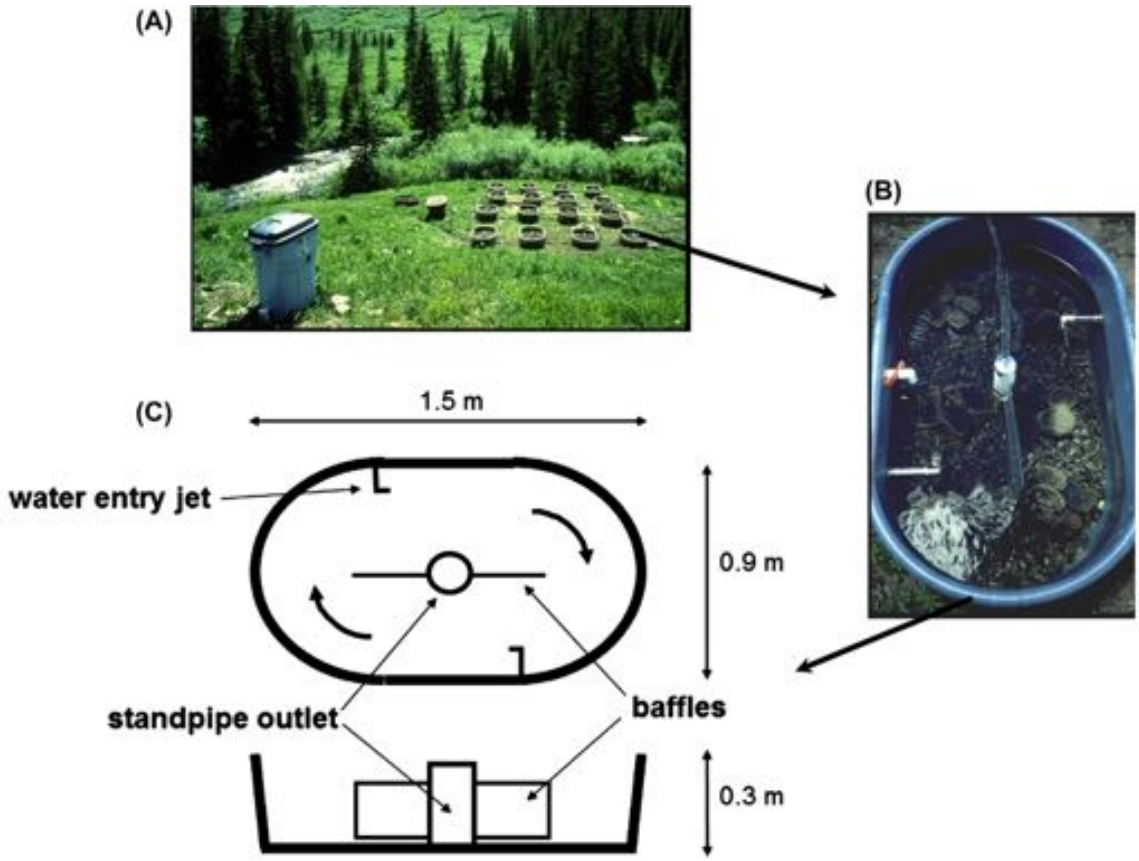

FIGURE 18.6 Large artificial streams useful for *Advanced Method 1*. (A) Artificial streams at Rocky Mountain Biological Laboratory, Colorado, USA, are gravity-fed with water from a nearby fishless stream, which provides a source of fishless water for controls. Fishless water can also be gravity fed to a 110-L holding tank (shown at left) containing two brook trout, and then dripped into tanks allocated to a fish-cue treatment. Alternatively, fish can be added directly to streams. (B) Single artificial stream; fish water drips in through spout with orange ribbon. (C) Schematic diagram of an artificial stream in top and side views. *(A) and (B) Photos: Barbara Peckarsky. (C) From McIntosh and Peckarsky (1996).*

Values of E_i can range from −1 to +1 indicating avoidance to preference, with values near zero indicating that the prey item is eaten in a similar proportion that it was collected in the environment. Record the electivities for each prey taxon on Table 18.1. Use these combined data to prepare a bar graph illustrating the electivities of each prey taxon placing prey taxa on the horizontal axis in order of decreasing electivity. Alternatively electivities may be calculated for predators in each benthic sample separately, in which case mean and variation around the mean can be plotted for each prey taxon. Electivities may also be compared among different species of predators within streams, or the same species of predators among different streams. Also using data from the combined samples, calculate a nonparametric Spearman Rank Correlation Coefficient (Zar, 2010) to test for significant correlation ($p < .05$) between the ranks of potential prey taxa in the diets and in the habitat of the stoneflies (see Table 18.1).

18.3.5.2 Exclosure Experiments (Platforms)

Parametric statistics can be used to analyze data provided that assumptions of normality, homogeneity of variance, and sample unit independence are met (Zar, 2010). For the platform studies in which there are two grazing levels (i.e., platform vs. control plots), an independent *t*-test (or one-way ANOVA with two groups) can be used to compare the treatments. An even better approach may be a paired *t*-test (parametric test) or Wilcoxon signed-rank test (nonparametric test). Those tests examine the *difference* between the paired control and platform plots for a specific response variable and will statistically remove the variation associated with unaccountable differences among the paired plots. Differences between paired platform and control plots can then be compared for each variable (both treatment and response) measured (e.g., periphyton AFDM, chlorophyll *a*, grazer density). If samples are taken over time, then a repeated-measures ANOVA can be used to compare treatment and control responses over the experiment (Zar, 2010). The latter analysis will allow a simultaneous

assessment of (1) treatment effects (e.g., effects of grazers on periphyton measures), (2) time effects (e.g., periphyton measures varying over the experiment), and (3) the treatment × time interaction (e.g., effects of grazers on periphyton measures varying over time). Add covariables (e.g., velocity, irradiance) to the statistical model as needed.

18.3.5.3 Enclosure Experiments

If only consumers (≥2 levels) were manipulated, then a one-way ANOVA or its nonparametric equivalent (Kruskal–Wallis test) is appropriate (Zar, 2010). If, in addition to consumers, a second factor (e.g., irradiance) is manipulated, then a two-factor ANOVA should be used or a nonparametric equivalent (Friedman test). If ANOVA reveals significant differences among treatments, *a posteriori* multiple contrasts (e.g., Tukey HSD test) can be used to identify where specific differences reside (Zar, 2010).

18.3.5.4 Nonconsumptive Effects

Numbers of prey individuals foraging on rock surfaces and prey drift rates can be compared between predator treatments and controls graphically and statistically using MANOVA on multiple, interdependent response variables, and subsequent ANOVAs on individual response variables if the MANOVA is significant (Peckarsky and McIntosh, 1998). Data should be transformed to meet the assumptions of parametric statistical tests. Similarly life history parameters (i.e., growth rates, development times, size at emergence) can be compared graphically and by MANOVA (see Peckarsky et al., 1993) to test whether prey life histories respond to predator cues.

18.4 QUESTIONS

1. What are the strengths and limitations of field-generated electivity indices? What hypotheses were suggested by the electivity indices or by correlations between gut contents and benthic data? Did these two types of analyses generate the same hypotheses? How would you test those hypotheses experimentally?
2. Were the exclosures (platforms) effective at eliminating some or all consumers? Did you notice any colonization by invertebrates other than the ones you were trying to exclude? Were there any confounding effects of the exclosure?
3. Were there significant effects of consumers on resource abundance (or other measured response variables)? If tested, were there significant effects of canopy or current velocity on periphyton within or among grazed treatments (i.e., grazer × canopy/current interactions)? What can you conclude about the relative importance of light, current, and grazing on periphyton abundance in your stream(s)?
4. If the consumer exclusion resulted in significant periphyton or prey accrual, what does this indicate about the overall importance of grazing or predation in your stream(s)? Would you expect this same result during all seasons or in all other streams within or outside the watershed/region? What are the implications of your findings for the potential of consumers to regulate resource populations in nature?
5. If multiple consumer treatments were used in enclosures, what was the relationship between consumer density (grazers or predators) and resource (periphyton or prey) abundance? If consumer growth was measured, how did this vary with density, and what can you conclude about the importance of intraspecific and/or interspecific interactions among consumers?
6. Did the biomass/chlorophyll *a* ratio differ among grazing treatments? Among stream reaches? Why might this pattern occur and what does it indicate?
7. Is periphyton or are prey a limiting resource for grazers or predators in your stream? Why? Is it possible for the biomass of benthic grazers or predators to exceed that of their resources? How might this occur? If resources were indeed limiting and consumers were competing for those resources, how might you test for the specific competitive mechanism (i.e., exploitation vs. interference)?
8. Why should investigators include controls and replication when designing experiments?
9. What are the potential fitness costs of lower growth rates, longer development times, and/or smaller size at maturity associated with avoiding predators? Alternatively how might prey increase their fitness by accelerating their development, even if they emerge at smaller sizes in streams with dangerous predators? (Consider the probability of surviving the larval stage).
10. What did behavioral observations tell you about the possible mechanisms of observed effects of predator cues on prey life history?

18.5 MATERIALS AND SUPPLIES

Field and Laboratory Materials (see Chapter 12 for materials to conduct periphyton analyses)
- 80% ethanol
- Net or sieve (≤250-μm mesh)
- Paper labels
- Squirt bottles
- Collecting jars, Whirl-pak, or Ziplock sample bags
- Collecting devices (D-nets, Surber sampler, Hess sampler, "electrobugging" machine)
- Shallow sorting pans
- Plastic eyedroppers and soft forceps

Field Equipment
- Current velocity meter (optional)
- Light meter or spherical densiometer (optional)

Platform Materials
- 1/4″ Plexiglas squares (20 × 20 cm)
- 1/2″ aluminum bar
- 3/8″ drill bit, drill, and drill press (or metal lathe)
- 3/8″ hex bolts (1/2″ long), washers, and nuts
- 3/8″ tap for hex bolt
- Form or jig used to bend aluminum bar into J-shape
- Heavy gauge rubber bands
- Reinforcement bar (used for pilot hole)
- Sledgehammer
- Unglazed clay tiles (7.5 × 7.5 cm)

Cage Enclosure Materials
- Aquarium (silicone) sealant
- Duct tape
- Fiberglass mosquito netting (≈1-mm mesh size)
- Monofilament nylon (30–60-pound test)
- Plastic food containers (pint size or larger) or similar enclosure
- Queen bee tags
- Reinforcement bar
- Rope for rack tethers
- Styrofoam blocks for rack flotation (∼1 ft^3 or 0.03 m^3); four blocks per rack
- Styrofoam sheets to make collars to float enclosures within rack; one per enclosure
- Utility knife
- Wood frame and hardware (for floating rack), large enough to fit all enclosures

Materials for Nonconsumptive Predator Experiments
- Enclosures/rearing chambers/observation chambers
- Flashlights with red acetate to produce dim red light for nighttime observations
- Various plumbing supplies and a first-name basis with the local hardware store
- Water or air source (for circulating flow in chambers if trials are done in the laboratory)

Laboratory Equipment
- Desiccator
- Dissecting microscope
- Drying and ashing ovens
- Electronic balance (±0.1 mg)
- Filtration apparatus (vacuum pump, filter funnel, Erlenmeyer filter flask, tubing)
- High-speed centrifuge
- Spectrophotometer or fluorometer
- Petri dishes for sorting samples
- Dissecting microscope
- Dissecting forceps
- Invertebrate identification guide (see Appendix 15.1)

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