A functional classification of the drift: traits that influence invertebrate availability to salmonids

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Abstract: Twelve categories/traits were used to classify and rank aquatic invertebrates based on their propensity to drift and importance as a food resource for salmonids. Invertebrate availability was based on their (*i*) propensity to intentionally drift, (*ii*) likelihood of being accidentally dislodged by the current, (*iii*) drift distance, (*iv*) adult drift, (*v*) benthic exposure, (*vi*) body size, and (*vii*) abundance. This study represents the first attempt to characterize the intentional drift propensity of stream invertebrates. A ranking procedure separated invertebrates into *Baetis* and three groups decreasing in availability. Predicted ranks were significantly correlated with the actual rank of invertebrates in trout guts taken in three separate studies conducted in the central Rocky Mountains, suggesting that this procedure can effectively rank invertebrates based on their availability as a food resource for salmonids. A cluster analysis separated the 95 taxa into four drift guilds and six availability groups. This study provides criteria for determining when alterations in invertebrate community composition will affect food resources for higher trophic levels by causing a decline in the most available taxa. This research also supports previous findings that floods are important in maintaining invertebrates that represent an important food resource for salmonids.

Résumé : Douze catégories ou traits ont été utilisés pour classer les invertébrés aquatiques et leur attribuer un rang d'après leur tendance à dériver et leur importance comme ressource alimentaire pour les salmonidés. La disponibilité des invertébrés a été établie en fonction (*i*) de leur tendance à dériver intentionnellement, (*ii*) de la probabilité qu'ils soient emportés accidentellement par le courant, (*iii*) de la distance de dérive, (*iv*) de la dérive des adultes, (*v*) de l'exposition benthique, (*vi*) de leur visant à caractériser la tendance à dériver intentionnellement des invertébrés de cours d'eau. Une méthode d'attribution de rangs a servi à séparer les invertébrés en *Beatis* et trois groupes de disponibilité décroissante. Les rangs prévus étaient corrélés de manière statistiquement significative avec les rangs réels occupés par les invertébrés dans les estomacs de truite dans trois études distinctes réalisées dans la région centrale des montagnes Rocheuses, ce qui indiquerait que cette méthode peut effectivement servir à hiérarchiser les invertébrés en fonction de leur disponibilité comme ressource alimentaire pour les salmonidés. Une analyse par grappe a séparé les 95 taxons observés en quatre groupes de dérive et six groupes de disponibilité. Cette étude fournit des critères permettant de déterminer quand les modifications de la composition de la communauté des invertébrés influeront sur les ressources alimentaires des niveaux trophiques plus élevés en entraînant une réduction des taxons offrant la plus grande disponibilité. Ces travaux viennent également appuyer les constatations antérieures voulant que les inondations soient importantes pour maintenir les populations d'invertébrés qui représentent une ressource alimentaire importante pour les salmonidés.
[Traduit par la Rédaction]

Introduction

Invertebrates play an important role in lotic ecosystems by influencing functional processes (e.g., decomposition, primary production, nutrient spiraling) and by forming the major link between primary producers and higher trophic levels (fish). As a food resource, not all invertebrates are equally important. Differences in predator (e.g., trout versus sculpin) and prey (mayflies versus clams) traits (morphology, behavior, life history) create differences in availability. For example, most trout (the focus of this study) feed primarily in the drift, and some aquatic insects are only available in the drift as adults since immature stages occur in the hyporheic zone (DeWalt and Stewart 1995), are inactive during the summer (diapause), or are concealed within the epibenthic habitat (Ward 1992). The ecotrophic coefficient is the proportion of the total benthic invertebrate production that is consumed by the entire fish assemblage (Ricker 1946). In trout streams, this proportion likely ranges between 0.30 and 0.50 (Waters 1988). Such low ecotrophic coefficients (Waters 1988) can, in part, be explained by differences in availability among invertebrates. For salmonids, availability is primarily defined by the propensity to drift (both immature nymphs and adults). I propose a conceptual model and procedure for ranking invertebrates based on their availability to drift-feeding salmonids. Ranking aquatic invertebrates according to their importance in maintaining food supplies for higher trophic levels may be an important step in predicting the effects of disturbances (floods, dams, diversions, pollutants) on trout populations. If the impact of disturbances on highly ranked invertebrates is determined, changes in salmonid food resources can be predicted.

Classifying organisms into ecological aggregates that are functionally similar and transcend taxonomic boundaries (functional groups or guilds) is a valuable approach applied to a wide range of organisms for a variety of purposes (Southwood

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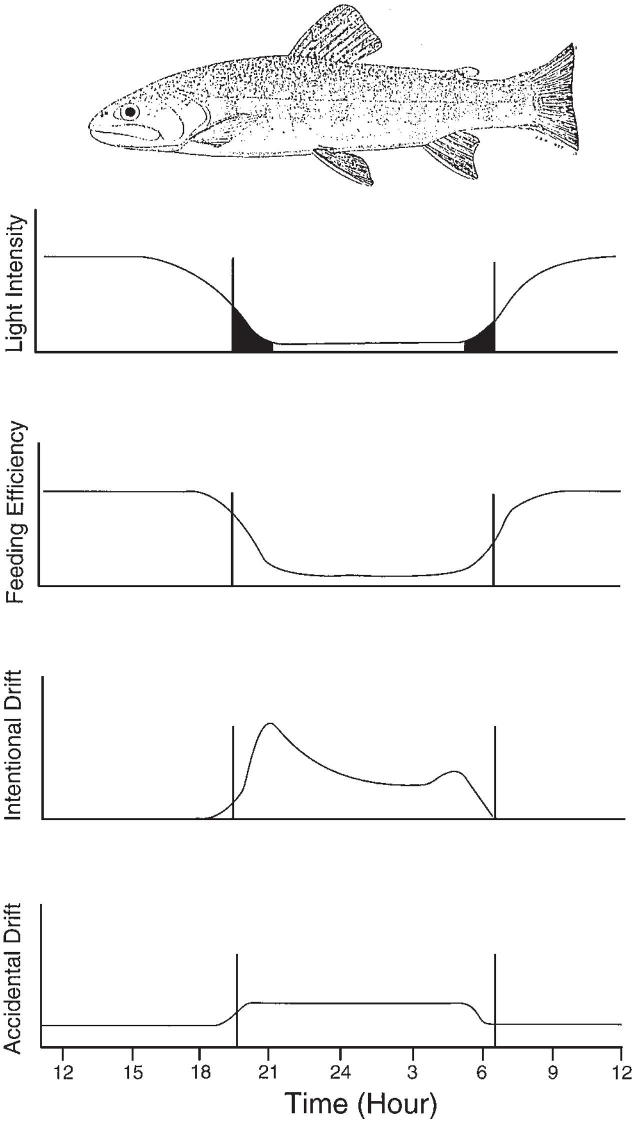
Fig. 1. Conceptual model showing the diel relationships between light intensity, trout feeding efficiency, and intentional and accidental drift of aquatic macroinvertebrates. Note that intentional drift is confined to periods of darkness (twilight and night). See text for a complete explanation.



1988; Keddy 1994). In streams, the guild or functional group concept has been successfully applied to invertebrates (Cummins 1973; Growns and Davis 1994; Merritt and Cummins 1995), fish (Karr et al. 1986; Poff and Allan 1995), and most of the plants and animals of an entire river ecosystem (Resh et al. 1994). One of the most appealing aspects of the guild concept is its ability to condense a large amount of species-specific information into a few categories that have generalized attributes, thus reducing the complexity associated with a large number of species (Hawkins and MacMahon 1989; Townsend and Hildrew 1994).

The objective of this paper is to provide criteria for classifying stream invertebrates into guilds based on their propensity to drift and to rank invertebrates based on their importance as a food resource for trout. I have estimated the dietary importance of various taxa in small to midsized snowmelt run-off streams of the subalpine, montane, and foothill zones of the central Rocky Mountains. The taxonomic categories used in this study were primarily taken from Ward and Kondratieff (1992). Taxa found in trout streams of the central Rocky Mountains were classified at the order, family, or genus level and ranked with respect to criteria that determine availability: (*i*) adult and immature drift propensity, (*ii*) exposure of taxa inhabiting the surface benthos, (*iii*) general patterns of relative abundance, and (*iv*) invertebrate body size.

Methods

Conceptual model

Figure 1 represents the conceptual basis for this paper and summarizes the following information. Trout are visual, size-selective, opportunistic generalists that primarily feed on the drift (e.g., Newman 1987; Allan 1995). Although benthic feeding is prevalent in turbid rivers (Tippets and Moyle 1978), among young-of-the-year (YOY) (Grant and Noakes 1987; Hubert and Rhodes 1992) and apparently among salmonids with a subterminal mouth (Nakano and Furukawa-Tanaka 1994), drift-feeding is the primary means of energy acquisition for most juvenile and adult salmonids in the Rocky Mountains and remains an important part of the diet for larger (>30 cm) piscivores (e.g., Griffith 1974; Angradi and Griffith 1990; Nakano et al. 1992). Prey detection and foraging efficiency are reduced with decreasing levels of light (Jenkins 1969; Ginetz and Larkin 1976; Hyatt 1979; Wilzbach et al. 1986). Invertebrates entrained in the drift during daylight hours and at twilight periods (dawn and dusk) are most easily detected and therefore most available to salmonids. Except for bright moonlit nights, night drift (before morning and after evening twilight) is primarily unavailable. Recent research provides convincing evidence that invertebrate nocturnal drift is an effective predator avoidance adaptation to minimize the risks of predation by drift-feeding fish (Allan 1978; Dill 1987; Flecker 1992; Douglas et al. 1994; McIntosh and Peckarsky 1996).

Stream invertebrates can be accidentally dislodged (passive drift) or, for various reasons, intentionally enter the drift (e.g., Peckarsky 1980; Kohler 1985; Malmqvist and Sjöström 1987; Forrester 1994; Scrimgeour et al. 1994). The term “intentional” implies an active process resulting from the decisions made by individuals (Dill 1987). Except for catastrophic drift induced by stressful conditions (stranding, oxygen deficiency), it appears that most intentional/active drift is primarily confined to hours of darkness when fish prey detection is reduced (Walton 1980; Ciborowski 1983; Kohler 1985; Rader and McArthur 1995; Wooster and Sih 1995), whereas most daytime drift is accidental or associated with changes in life cycle events (Waters 1965, 1972; Ciborowski 1983). Recent research has shown that trout can suppress daytime drift (e.g., Flecker 1992; Douglas et al. 1994; McIntosh and Peckarsky 1996) and that invertebrates will often delay drifting until night in response to unfavorable conditions initiated during the day (e.g., Poff and Ward 1991; Rader and McArthur 1995). Although the prevalence of intentional versus accidental drift during the night night versus the day requires further investigation, several studies suggest that most intentional drift is confined to the safer periods of darkness and the amount of intentional drift during the day is probably small compared with accidental dislodgment and drift associated with changes in life cycle events.

If there were no twilight periods (dusk and dawn), there would be no need to classify invertebrates based on their propensity to intentionally drift because invertebrates that intentionally leave the substrate probably confine their drifting activity to periods of darkness and are therefore relatively unavailable as food for salmonids. Even though salmonid feeding efficiency declines with decreasing irradiance (e.g., Wilzbach et al. 1986), several studies indicate that salmonids can actively feed at twilight (McCormack 1962; Ringler

Table 1. Traits or categories and scores used to classify stream invertebrates based on their availability to drift-feeding salmonids.

Categories/scores	0	1	3	6	9
Intentional drift	No drift/catastrophic	Rare	Occasional	—	Frequent
Accidental drift					
Habitat	Hyporheic	Depositional	—	—	Erosional
Flow exposure	Avoiders/NA	Obligates	—	Facultatives	—
Mobility	Sessile/NA	Attached	Crawlers	—	Swimmers
Drag index	NA	<6.0	6.0–12.0	>12.0	—
Drift distance	Passive sinkers/NA	Active swimmers	Active settlers	Passive floaters	—
Adult drift					
Emergence behavior	Winter/NA	—	Crawl to bank	Drift/swim to surface	—
Ovipositing behavior	Overhanging vegetation/NA	—	Crawl underwater/dropped	Run across/land on surface	—
Diel activity	NA	Nocturnal	—	Diurnal	—
Benthic exposure	Buried/hyporheic	Concealed	Exposed	—	—
Size (mm)	—	<1.0	1.0–5.0/>20.0	—	5.1–20.0

Note: NA indicates subcategory scores for taxa when categories were not applicable. For example, the Flow Exposure category would not apply to taxa that spend most of their life cycle in the hyporheic zone. A dash indicates that no subcategory was assigned to that particular score.

1979; Bachman 1984; Clapp et al. 1990). Invertebrates that intentionally drift or are accidentally dislodged during twilight periods are exposed to predation and likely make a significant contribution to salmonid energy intake. Therefore, invertebrates were classified based on their propensity toward both accidental dislodgment (during the day and at twilight) and intentional drift (twilight).

Why would stream invertebrates intentionally drift at twilight if they are exposed to trout predation? Invertebrates that intentionally drift at twilight probably leave the safety of the substrate because of their inability to accurately detect levels of light in the water column. At twilight, invertebrates that inhabit substrate crevices are undoubtedly exposed to a darker microenvironment than the level of light surrounding salmonids. Holt and Waters (1967) suggested that the gradual increase in drift at dusk, rather than a sudden and synchronized rise, may be caused by the exposure of invertebrates to varying levels of light and amounts of shadow in the benthos. On a larger scale, invertebrates from dark, shaded stream sections may drift at twilight into brighter reaches with an open canopy. At twilight, many invertebrates may intentionally but prematurely drift from dark habitats into a dimly lit water column with a bright background sky, exposing themselves to predation by trout. Hence, understanding invertebrate availability to trout requires characterizing both accidental dislodgment and intentional drift propensity.

Ranking procedure

In addition to categories defining benthic exposure and size, nine categories (“Intentional Drift”, “Habitat”, “Flow Exposure”, “Mobility”, “Drag Index”, “Drift Distance”, “Emergence Behavior”, “Ovipositing Behavior”, and “Diel Activity”) were used to classify stream invertebrates based on their propensity to intentionally drift, accidental dislodgment by the current, and the drift characteristics of adults (Table 1). All categories were divided into subcategories/species traits. Each invertebrate taxon was assigned to a single subcategory and received the corresponding score. The higher the score the greater the availability as a food resource for trout. Invertebrates were ranked based on their total score summed across all categories. The procedure used to assign invertebrates to specific subcategories had an ordered, hierarchical arrangement. Invertebrates were classified starting with the top category and proceeding down the table (Table 1). Habitat had an important influence on a taxon’s total score or rank. For example, Flow Exposure, Mobility, Drag Index, and Drift Distance did not apply (NA) to taxa inhabiting the hyporheic zone or depositional areas. (I assumed that accidental dislodgment and drift entry from hyporheic and depositional areas was rare.) Similarly, Emergence Behavior and Oviposition Behavior did not apply to noninsect taxa.

Numerous publications (>50) on aquatic invertebrate biology were used to classify taxa (i.e., Claassen 1931; Needham et al. 1935; Ross 1944; Jensen 1966; Harper and Hynes 1972; Harper 1973; Wiggins 1973, 1996; Edmunds et al. 1976; Baumann et al. 1977; McAlpine et al. 1981; McCafferty 1981; Stewart and Stark 1984, 1988; Swisher and Richards 1991; Ward and Kondratieff 1992; DeWalt and Stewart 1995; Merritt and Cummins 1995). Information on some traits was often not known for all species in a taxonomic group. The traits used to characterize some genera were often based on information from a single “Type” or “Exemplar” species (as in Merritt and Cummins 1995). Also, some taxa were difficult to assign to a single subcategory. For example, most species in the families Nemouridae and Leuctridae are winter stoneflies but some species emerge in the summer (Harper 1973). When a genus contained species that could fit into more than one subcategory, the most prevalent subcategory was chosen. The taxonomic resolution (order, family, or genus) used in the classification process was determined by the redundancy of traits within a group. For example, all genera in the family Heptageniidae in trout streams of the Central Rocky Mountain region had the same traits and were classified in the same subcategories. I used two criteria to determine the level of taxonomic resolution. When one or more genera in a family occupied different habitats (hyporheic, depositional, or erosional) or occupied the same habitat but differed by two or more of the other 11 categories, the family was separated at the generic level. Habitat was important because it would determine the applicability (NA) of subsequent categories which could have a important influence on the magnitude of the final score.

Category descriptions

Intentional drift

Most stream invertebrates can *intentionally* enter the drift in an attempt to avoid extreme conditions that fluctuate beyond the normal range of variation (disturbance/catastrophic drift). For example, numerous invertebrate taxa intentionally drifted in response to oxygen stress when flow was reduced in a small (50 cm wide) cold-water spring in Idaho (Minshall and Winger 1968). I have attempted to identify invertebrates that under normal, nondisturbance conditions intentionally drift and are therefore consistently available for salmonid consumption (primarily at twilight). Under nondisturbance conditions, stream invertebrates probably range from frequent intentional drifters to taxa that rarely intentionally enter the drift. I make the assumption that there is a relationship between intentional drift propensity and the ability to exit the drift. The ability to efficiently exit the drift will determine the magnitude of the risks associated with drifting (e.g., time of exposure to salmonid predation) and, therefore, the intentional drift frequency. Data on drift distances of various taxa (Elliott 1971; Otto and Sjöström 1986; Allan and Feifarek 1989) and the behavioral responses of mayfly prey to stonefly predators support this assertion (Corkum 1978; Peckarsky 1980; Molles and Pietruszka 1983; Williams 1987; Peckarsky and Penton 1989). The ability to exit the drift depends on settling efficiency, and settling efficiency depends on three factors: (*i*) swimming ability, (*ii*) agility in regaining a foothold on the substrate (e.g., trailing a silk thread), and (*iii*) sinking postures. Stream invertebrates were classified according to these three criteria using information derived from a variety of sources on settling efficiency, drift distances, and behavioral observations (e.g., Elliott 1971; Ciborowski and Corkum 1980; Otto and Sjöström 1986; Williams 1987; Peckarsky and Penton 1989). I also reviewed the literature on intentional drift to gather empirical data on the intentional drift frequency of various taxa (Table 2). Based on this review, four nondisturbance mechanisms can elicit an intentional drift response: (*i*) avoidance of predators, (*ii*) avoidance of nonpredatory, aggressive interactions, (*iii*) searching for a patchily distributed food resource, and (*iv*) oxygen regulation. The intentional drift frequency (rare, occasional, and frequent) of specific taxa has only been determined for confrontations with predators and aggressors (Table 3). Taxa were classified as "Rare", "Occasional", and "Frequent" based on the percentage of encounters (predation or aggression) producing an intentional drift response (Frequent ≥ 50%; 50% < Occasional > 10%; Rare ≤ 10%). Taxa with apparently no propensity to intentionally drift except when stranded or otherwise physiologically stressed were placed in the "No Drift/Catastrophic" category. Since this review included only a small proportion of the invertebrate assemblage, a procedure that maximized empirical information from Table 3 was used for classifying most taxa without empirical data. Taxa with known settling traits but absent in the review (no empirical data) were given the same classification as taxa in Table 3 with the same settling traits (e.g., swimming ability, stone cases, drift posture, etc.). Taxa absent from the review with unknown settling traits were classified based on the intentional drift frequency or settling efficiency (e.g., Elliott 1971; Ciborowski and Corkum 1980; Otto and Sjöström 1986) of taxa present in Table 3 with the same mobility characteristics (sessile, attached, crawlers, swimmers).

An abundance of information indicated that *Baetis* were frequent intentional drifters (Table 3). Amphipods, like baetids, were placed in the Frequent category because they are good swimmers with rapid settling capabilities (Elliott 1971). The Ephemerellidae are weak swimmers with a thick exoskeleton. However, *Ephemerella ignita*, *E. subvaria*, and *E. invaria* were placed in groups that always returned to the bottom faster than dead individuals (Elliott 1971) or were intermediate with respect to settling efficiency (Ciborowski and Corkum 1980; Otto and Sjöström 1986). However, based on their intentional drift response to predators and aggressors (Table 3), I placed *Ephemerella* and all Ephemerellidae in the Rare group. Although Heptageniidae (classified as Occasional in Table 3) are also weak swimmers with an intermediate settling efficiency, they drift more frequently during confrontations, tend to swim more often than Ephemerellidae (Otto and Sjöström 1986), and are agile at regaining a foothold when brought in contact with the substrate (Elliott 1971). Even though Isonychiidae, Siphlonuridae, and Leptophlebiidae (except *Choroterpes* and *Traverella*) are swimmers/clingers (Merritt and Cummins 1995), they were classified as Occasional intentional drifters based on the response of *Leptophlebia*, *Paraleptophlebia*, and *Nesameletus* to predators or aggressors (Table 3). I found no information on the intentional drift propensity of burrowing mayflies (Ephemeridae, Polymitarcyidae) or on mayflies that bury themselves in soft sediments (Caenidae and most Tricorythidae). However, *Ephemera danica* is a weak swimmer and has difficulty in regaining a "foothold" on the substrate (Otto and Sjöström 1986). Burrowing mayflies were therefore classified with other weak swimmers in the Rare subcategory. With no information to indicate otherwise, mayflies that bury themselves in the sediment were classified with burrowers. Except for Perlidae and Taeniopterygidae, all Plecoptera were classified as Rare intentional drifters. Most are poor swimmers (weak side-to-side movements) with an intermediate to low settling efficiency. They often curl into a "U" or "J" shape, increasing their settling rate but decreasing their ability to regain a foothold on the substrate (Otto and Sjöström 1986). Unlike other Plecoptera, Perlidae were assigned to the Occasional category because they use their legs as oars and are strong, agile swimmers (Stewart and Szczytko 1983; Otto and Sjöström 1986; Rader and McArthur 1995). *Taeniopteryx* and *Brachyptera* (Taeniopterygidae) are poor swimmers but because of their drifting posture can readily regain a foothold on the substrate (Madsen 1969; Otto and Sjöström 1986). Both families have an Occasional tendency to intentionally drift during confrontations (Table 3). Trichoptera were separated into case-makers (especially rock cases) with no intentional drift propensity (see *Glossosoma*, Table 3) and net-spinners. Net-spinning caddisflies will occasionally drift during confrontation (see Hydropsychidae and Polycentropidae, Table 3) and will often trail a silk thread to enhance their settling efficiency (Elliott 1971; Otto and Sjöström 1986). Net-spinning Lepidoptera were classified with net-spinning Trichoptera in the Occasional category. Free-living (*Rhyacophila*) and case-making caddis larvae (No Drift) are nonswimmers with poor reattachment abilities (Otto and Sjöström 1986). Except for the Simuliidae, all Diptera (Rare category) were considered nonswimmers with a poor settling efficiency that do not drift during predator–prey or aggressive confrontation (see Blephariceridae and Chironomidae, Table 3). Simuliidae frequently drifted when confronted by predators and they trail a silk thread to increase their settling rate (Hynes 1970; Hemphill 1988; Reidelbach and Kiel 1990). Odonates were placed in the Occasional category based solely on swimming ability. The remaining groups (Elmidae, Oligochaeta, Turbellaria, Gastropoda, and Pelecypoda) were nonswimmers that were placed in the No Drift category.

For a few taxa, empirical evidence (behavioral observations) differed from theoretical predictions based on the presumed relationship between intentional drift frequency and settling efficiency. For example, Perlidae were classified as swimmers but only occasionally drifted during confrontation. Perlid stoneflies are also proficient at crawling (e.g., Corkum 1978) and may drift/swim as a secondary option to avoid confrontation. The ability to predict intentional drift frequency based on traits that determine settling efficiency may be limited if other nondrifting tactics are an equally efficient means of avoiding confrontation. For most taxa, however, settling efficiency and intentional drift frequency should be related because agile crawlers are usually poor swimmers. For example, morphological traits that enhance crawling agility (e.g. dorsoventral flattening) should also diminish swimming ability (e.g., absence of streamlining) and settling efficiency.

Some taxa in Table 3 responded to the same mechanism (e.g., predation) in different studies with different propensities to intentionally drift. Empirical observations could vary because of differences among studies. My estimates of intentional drift frequency will, to some degree, depend on the magnitude of risk associated with each study. For example, different species of predators may represent different levels of risk and therefore invoke different intentional drift frequencies. I was unable to assess the comparative level of risk experienced by individuals in different studies. The most prevalent response (rare, occasional, or frequent) was used to classify each taxa.

Habitat

The next five categories (Habitat, Flow Exposure, Mobility, Drag Index, Drift Distance) were used to classify stream invertebrates with respect to their propensity toward accidental dislodgment by the current. Habitat predicts the frequency of accidental dislodgment based on general habitat differences (Table 1). Habitat is divided into three types: "Hyporheic" (White 1993), "Depositional", and "Erosional" (Ward 1992; Merritt and Cummins 1995). Depositional habitats (e.g.,

Table 2. Intentional/active drift propensity is shown for 61 invertebrate taxa based on 44 studies.

Taxon	Stimulus	Propensity	Evidence	Reference
Ephemeroptera				
Baetidae				
Baetis bicaudatus	Predators	Frequent	Observations	Peckarsky 1980
Baetis bicaudatus	Predators	Frequent	Observations	Peckarsky and Penton 1989
Baetis buceratus	Aggression	—	Observations	Statzner and Mogel 1985
Baetis phoebus	Predators	Frequent	Observations	Peckarsky 1980
Baetis rhodani	Predators	Frequent	Observations	Williams 1987
Baetis rhodani	Predators	Frequent	Observations	Malmqvist 1986
Baetis rhodani	Predators	Frequent	Observations	Malmqvist and Sjöström 1987
Baetis rhodani	Aggression	Occasional	Observations	Williams 1987
Baetis tricaudatus	Predators	Frequent	Observations	Scrimgeour et al. 1994
Baetis tricaudatus	Predators	Frequent	Drift samples	Corkum and Clifford 1980
Baetis tricaudatus	Predators	Frequent	Observations	Molles and Pietruszka 1983
Baetis tricaudatus	Predators	Frequent	Observations	Soluk and Collins 1988
Baetis tricaudatus	Predators	Frequent	Observations	Walde and Davies 1984
Baetis tricaudatus	Predators	Occasional	Observations	Kohler and McPeek 1989
Baetis tricaudatus	Predators	—	Observations	Scrimgeour and Culp 1994
Baetis tricaudatus	Low food	—	Observations	Kohler 1985
*Baetis tricaudatus**	Flow reduction	—	Drift samples	Corrarino and Brusven 1983
Baetis tricaudatus	—	Frequent	Drift samples	Ciborowski 1983
Baetis vagans	Predators	Frequent	Observations	Williams 1987
Baetis vagans	Predators	—	Drift samples	Corkum and Pointing 1979
Baetis vagans	Aggression	Occasional	Observations	Williams 1987
Baetis vagans	—	Frequent	Observations	Corkum 1978
Baetis sp.	Predators	Frequent	Drift samples	Lancaster 1990
Baetis sp.*	Flow reduction	—	Both	Minshall and Winger 1968
Baetis spp.	Predators	Frequent	Drift samples	Forrester 1994
Baetis spp.	Flow reduction	—	Drift samples	Poff and Ward 1991
Psuedocloeon sp.	Low oxygen	—	Observations	Wiley and Kohler 1980
*Drunella grandis**	Flow reduction	—	Both	Minshall and Winger 1968
Ephemerella altana	Predators	Rare	Observations	Molles and Pietruszka 1983
Ephemerella aurivillii	Predators	Occasional	Observations	Scrimgeour et al. 1994
Ephemerella inermis	—	Occasional	Drift samples	Ciborowski 1983
Ephemerella infrequens	Predators	Rare	Observations	Peckarsky 1980
Ephemerella infrequens	Predators	Rare	Observations	Peckarsky and Penton 1989
*Ephemerella lata**	Oxygen stress	—	Observations	Wiley and Kohler 1980
Ephemerella subvaria	Predators	Occasional	Observations	Williams 1987
Ephemerella subvaria	Predators	Rare	Observations	Peckarsky 1980
Ephemerella subvaria	Predators	Rare	Observations	Soluk and Collins 1988
Ephemerella subvaria	Aggression	Rare	Observations	Williams 1987
Ephemerella sp.	Predators	No Drift	Drift samples	Forrester 1994
Ephemerella sp.*	Flow reduction	—	Both	Minshall and Winger 1968
Eurylophella sp.	Predators	No Drift	Drift samples	Forrester 1994
Heptageniidae				
Cinygmula mimus	Predators	Occasional	Observations	Peckarsky and Penton 1989
Cinygmula sp.	Predators	Occasional	Observations	Peckarsky 1980
Cinygmula sp.*	Flow reduction	—	Both	Minshall and Winger 1968
Epeorus deceptivus	Predators	Occasional	Observations	Peckarsky and Penton 1989
Epeorus longimanus	Flow reduction	—	Drift samples	Poff and Ward 1991
Heptagenia hebe	Predators	—	Observations	Peckarsky 1980
Rhithrogena semicolorata	Predators	Rare	Observations	Williams 1987
Rhithrogena semicolorata	Aggression	Rare	Observations	Williams 1987
Stenacron interpunctatum	Predators	Rare	Drift samples	Walton 1980
*Stenacron interpunctatum**	Oxygen stress	—	Observations	Wiley and Kohler 1980
Stenonema fuscum	Predators	Occasional	Observations	Peckarsky 1980
*Stenonema pulchellum**	Oxygen stress	—	Observations	Wiley and Kohler 1980
Stenonema vicarium	Predators	Occasional	Observations	Williams 1987
Stenonema vicarium	Aggression	Rare	Observations	Williams 1987

Table 2 (*continued*).

Taxon	Stimulus	Propensity	Evidence	Reference
Stenonema sp.	Predators	No Drift	Drift samples	Forrester 1994
Leptophlebiidae				
Leptophlebia cupida	Predators	Occasional	Drift samples	Corkum and Clifford 1980
Paraleptophlebia adoptiva	Predators	Occasional	Observations	Ode and Wissinger 1993
Paraleptophlebia heteronea	Predators	Frequent	Both	Culp et al. 1991
Paraleptophlebia heteronea	Predators	Occasional	Observations	Scrimgeour et al. 1994
Paraleptophlebia mollis	Aggression	Occasional	Observations	Corkum 1978
Paraleptophlebia spp.	Predators	Occasional	Drift samples	Forrester 1994
Siphlonuridae				
Nesameletus ornatus	Predators	Occasional	Observations	McIntosh and Townsend 1994
Plecoptera				
Leuctridae				
Leuctra fusca	Predators	—	Drift samples	Malmqvist and Sjöström 1987
Nemouridae				
*Nemoura cinctipes**	Flow reduction	—	Both	Minshall and Winger 1968
Perlidae				
Acroneuria abnormis	Aggression (?)	Frequent (?)	Observations	Walton et al. 1977
Acroneuria abnormis	Aggression	Occasional	Observations	Rader and McArthur 1995
Taeniopterygidae				
*Brachypteri risi**	Oxygen stress (?)	—	Observations	Madsen 1969
Taeniopteryx burksi	Predators	Frequent	Drift samples	Walton 1980
Taeniopteryx metequi	Predators	Frequent	Drift samples	Walton 1980
Trichoptera				
Glossosomatidae				
Glossosoma nigrior	Predators	No Drift	Observations	Kohler and McPeek 1989
Hydropsychidae				
Cheumatopsyche sp.	Aggression	Rare	Observations	Glass and Bovbjerg 1969
Hydropsyche bronta	Predators	Occasional	Drift samples	Michael and Culver 1987
Hydropsyche instabilis	Flow reduction	—	Observations	Edington 1965
Polycentropodidae				
Plectrocnemia conspersa	Aggression	Occasional	Observations	Hildrew and Townsend 1980
Rhyacophilidae				
Rhyacophila sp.*	Flow reduction	—	Both	Minshall and Winger 1968
Uenoidae				
Neothremma sp.*	Flow reduction	—	Both	Minshall and Winger 1968
Diptera				
Blephariceridae				
Blephariceri micheneri	Aggression	No Drift	Observations	Dudley et al. 1990
Chironomidae	Predators	—	Drift samples	Malmqvist and Sjöström 1987
Chironomidae	Predators	No Drift	Drift samples	Lancaster 1990
Chironomidae*	Flow reduction	—	Both	Minshall and Winger 1968
Simuliidae	Aggression	—	Observations	Chance 1970
Simuliidae	Aggression	—	Observations	Tonnoir 1925
Simuliidae	Flow reduction	—	Drift samples	Poff and Ward 1991
Cnephia dacotensis	Aggression	—	Observations	Gersabeck and Merritt 1979
Cnephia dacotensis	Flow alteration	—	Observations	Gersabeck and Merritt 1979
Prosimulium fuscum	Predators	Frequent	Observations	Wiley and Kohler 1981
Prosimulium fuscum	Aggression	Rare	Observations	Wiley and Kohler 1981
Prosimulium mixtum	Aggression	—	Observations	Harding and Colbo 1981
Prosimulium mixtum	Aggression	—	Observations	Gersabeck and Merritt 1979
Prosimulium mixtum	Flow alteration	—	Observations	Gersabeck and Merritt 1979
Simulium noelleri	Predators	—	Observations	Wooton and Merritt 1988
Simulium piperi	Aggression	Rare	Observations	Hart 1986
Simulium tuberosum	Predators	Frequent	Observations	Wiley and Kohler 1981
Simulium tuberosum	Aggression	Rare	Observations	Wiley and Kohler 1981
Simulium virgatum	Predators	Frequent	Observations	Hemphill 1988

Table 2 (*concluded*).

Taxon	Stimulus	Propensity	Evidence	Reference
Simulium vittatum	Predators	Frequent	Observations	Hansen et al. 1991
Simulium sp.	Predators	—	Observations	Fuller and DeStaffan 1988
Simulium sp.*	Flow reduction	—	Drift samples	Corrarino and Brusven 1983
Simulium sp.*	Flow reduction	—	Both	Minshall and Winger 1968
Simulium spp.	Aggression	—	Observations	Disney 1972
Tricladida				
Planariidae				
Dugesia sp.*	Flow reduction	—	Both	Minshall and Winger 1968
Amphipoda				
Gammaridae				
Gammarus pulex	Predators	—	Drift samples	Malmqvist and Sjöström 1987

Note: "Stimulus" indicates the mechanisms ("Predators", "Aggression", "Food", and "Oxygen") producing an intentional drift response. The mechanisms producing drift are not known for studies manipulating flow. "Frequent", "Occasional", and "Rare" indicated intentional drift propensity and was only determined where (1) the percentage drifting of the total number of nymphs was known, (2) the percentage of drift behavior was compared with other responses (e.g., crawling, remaining stationary), or (3) the authors made explicit statements regarding drift frequency. "No Drift" indicates the absence of intentional drift to a specific stimulus. "Evidence" describes the methods used to determine an intentional drift response. Studies using drift samples without behavioral observations were used only when authors explicitly stated that drift was intentional. A dash indicates that information was not sufficient to make a decision on the appropriate classification. An asterisk indicates studies where the stimulus fluctuated beyond the normal range of variation (i.e., disturbance/catastrophic drift).

pools and margins) form under baseflow conditions but do not include small pockets of slow water and redeposited materials in erosional reaches (e.g., riffles). I assume that organisms residing within the hyporheos are not accidentally dislodged and that macroinvertebrates inhabiting depositional areas contribute less to the drift than invertebrates from erosional habitats. Macroinvertebrates in depositional habitats are less likely to be dislodged and can rapidly return to the benthos (Waters 1962; Bailey 1966; Campbell 1985). Therefore, I assigned a greater score for taxa that primarily reside in erosional (9) compared with depositional (1) habitats. In the Rocky Mountains, nymphs in the families Capniidae, Leuctridae, Taeniopterygidae, and Chloroperlidae spend most of their aquatic existence as part of the hyporheic fauna (e.g., Ward and Kondratieff 1992; DeWalt et al. 1994; DeWalt and Stewart 1995). Large taxa (e.g. *Sweltsa* spp.) are probably an exception. Such taxa should be assigned to erosional habitats because they appear in the surface benthos long before emergence (Mackay 1969; Harper et al. 1991).

Flow exposure

Flow Exposure group classification was recently proposed to provide insight into the response of macroinvertebrates to small-scale flow conditions (Growns and Davis 1994). Whereas Habitat was used to classify invertebrates on a larger scale according to preferred units within stream reaches, Flow Exposure is an indication of flow preferences within habitat units. Growns and Davis (1994) partitioned invertebrates from streams in Australia into groups experiencing differing degrees of exposure to near-bed flows. "Avoiders" spent most of their life cycle within the substratum out of direct contact with the flow. Avoiders included taxa that dug burrows or buried themselves in fine sediment. "Facultatives" were invertebrates that often occurred in exposed areas (e.g., upper surfaces), but had the ability to move into protected crevices. "Obligates" (Hydroptilidae, Blephariceridae, Tanytarsini, Psephenidae, net-spinning Trichoptera) were fully exposed to the water column for most of their life cycle and had behavioral (e.g., fixed retreats) or morphological (e.g., hydraulic suckers) adaptations for attachment. Simuliidae were placed in the Facultative category, but were difficult to classify because they can move from one fixed location to another and yet are fully exposed to the current. In this paper, Chironomidae were separated into free-living taxa (Avoiders) and those that were primarily tube-dwellers (Tanytarsini, *Cardiocladius*, *Cricotopus*) of the Obligate group. Both Hynes (1970) and Growns and Davis (1994) provide several examples of each Flow Exposure group. I propose that Flow Exposure groups can help to estimate the likelihood of dislodgment. Adaptations that prevent dislodgment are usually less efficient in Facultatives than in Obligates because Facultatives are more mobile. I assume an evolutionary tradeoff between mobility and attachment; adaptations that enhance attachment efficiency reduce mobility and dislodgment. Therefore, Facultatives should be accidentally dislodged more frequently than Obligates. For example, the more mobile *Stenacron interpunctatum* was accidentally dislodged more frequently at high current velocities (25.0 $cm \cdot s^{-1}$) than the slower, less agile *Taeniopteryx* spp. (Walton 1980). Also, Ciborowski (1987) surveyed the literature which included numerous taxa representing a wide range of mobility and found that drift frequency was positively correlated with benthic locomotory ability.

Mobility

Because of the probable tradeoff between mobility and attachment, the propensity to drift should also be affected by various levels of mobility (Corkum 1978; Ciborowski 1987). I make the general assumption that greater mobility increases the likelihood of dislodgment. Therefore, the likelihood of dislodgment descends from swimming > crawling > attached > sessile. Mobility subcategories are based only on mobility/attachment traits and differ from other similar categories (e.g., skaters, clingers, sprawlers from Merritt and Cummins 1995) in that they do not include a description of invertebrate habits or modes of existence. "Sessile" macroinvertebrates (e.g. late-instar Hydroptilidae) remain fixed in one position for most of their aquatic existence or as long as they are part of the epibenthic habitat. "Attached" taxa (e.g., Brachycentridae, Simuliidae, net-spinning caddisflies) are typically fastened in one position for days or weeks but can move, if necessary, to new locations in response to changing conditions. "Crawlers" include a wide range of taxa (e.g., Heptageniidae, Gastropoda, Glossosomatidae) that move with varying degrees of speed and agility. Crawlers have various morphological adaptations that also enhance attachment (sharp tarsal crawls, sucker-like ventral gills, a setal disk), but they rarely remain in the same place for more than a day and they must move in order to feed. Blephariceridae and Psephenidae were placed in the Attached category because of their slow mobility and exceptionally efficient adaptations to the current. "Swimmers" (Baetidae, Siphlonuridae,

Table 3. Invertebrate intentional drift propensity based on their response to mechanisms (predation and aggression) that influence drift frequency.

Taxon	Predators	Aggression
Ephemeroptera		
Baetidae		
Baetis	Frequent (91%); Occasional (9%)	Frequent (100%)
Ephemerellidae		
Ephemerella	Occasional (25%); Rare (63%); No Drift (12%)	Rare (100%)
Eurylophella	No Drift (100%)	—
Heptageniidae		
Cinygmula	Occasional (100%)	—
Epeorus	Occasional (100%)	—
Rhithrogena	Rare (100%)	Rare (100%)
Stenocron	Rare (100%)	—
Stenonema	Occasional (67%); No Drift (33%)	Rare (100%)
Leptophlebiidae		
Leptophlebia	Occasional (100%)	—
Paraleptophlebia	Frequent (25%); Occasional (75%)	Occasional (100%)
Sipholnuridae		
Nesameletus	Occasional (100%)	—
Plecoptera		
Perlidae		
Acroneuria	—	Frequent ? (50%); Occasional (50%)
Taenopterygidae		
Taeniopteryx	Occasional (100%)	—
Trichoptera		
Glossomatidae		
Glossosoma	No Drift (100%)	—
Hydropsychidae		
Cheumatopsyche	—	Rare (100%)
Hydropsyche	Occasional (100%)	—
Polycentropidae		
Plectrocnemia	—	Occasional (100%)
Diptera		
Blephariceridae		
Blepharicera	—	No Drift (100%)
Chironomidae	No Drift (100%)	—
Simulidae		
Prosimulium	Frequent (100%)	Rare (100%)
Simulium	Frequent (100%)	Rare (100%)

Note: Only studies indicating the intentional drift frequency were used (Table 2). A dash indicates categories where no information was available. Numbers in parentheses are the percentage of studies indicating the designated response. See Table 2 for the sample size of studies and species comprising each taxon.

Leptophlebiidae) are streamlined taxa that are capable of directional "porpoise-like" swimming undulations (Hynes 1970; Wilzbach et al. 1988). Taxa with side-to-side thrashing movements (e.g., Rhyacophilidae, Tipulidae, most Chironomidae) produce very weak directional locomotion and were not classified with Swimmers. No attempt was made to relate various types of crawling locomotion or various degrees of crawling and swimming agility (e.g., Baetidae versus Siphlonuridae) to increasing or decreasing propensity toward accidental dislodgment. Mobility characteristics were only determined for taxa that reside in the epibenthic habitat. Taxa from depositional or hyporheic habitats were not classified (NA).

Drag index

Almost all invertebrates that venture from low-flow microhabitats will experience drag caused by a turbulent, three-dimensional microflow environment (Nowell and Jumars 1984). Very few, if any, invertebrates large enough to be eaten by trout (>1.0 or 2.0 mm) can reside within the boundary layer of a stream, especially in high-gradient streams typical of the Rocky Mountains. The Drag Index relates invertebrate size and shape to the probability of dislodgment. The force necessary to dislodge individual organisms is equivalent to the current velocity passing though its frontal projection area. The amount of drag experienced by stream organisms subjected to identical microflow conditions is a function of both body size and shape which will determine the difference in the amount of pressure impending on the front (upstream, high pressure zone) compared with the rear (downstream, low-pressure turbulent zone) of an invertebrate (Vogel 1994). Because habitat selection, flow exposure, and morphological adaptations related to attachment and mobility will also determine the propensity toward accidental dislodgment, some measure of drag by itself is not an adequate estimation of the likelihood to accidentally drift. For this reason the preceding three categories (Habitat, Flow Exposure, and Mobility) were included (Table 1). Wilzbach et al. (1988) suggested that body shape, expressed as the ratio of height to width, was a reasonable index of drag and the propensity to become dislodged. They found that as the height to width ratio increased, drag increased and the current velocity required to dislodge killed individuals decreased. Stream invertebrates can be classified into four morphological types based on their general body shape: (*i*) streamlined, (*ii*) cylindrical, (*iii*) dorsoventrally flattened, and (*iv*) spherical/globular. Some cylindrical invertebrates are more round in cross section (Tipulidae), whereas others are somewhat compressed in the dorsoventral direction (Perlidae). All invertebrate taxa were assigned to one of the four morphological types and the height to width ratio was measured for each (Table 4). The height to width ratio was then combined with body size to calculate the Drag Index (see below). Body size (length of invertebrate in the direction of the flow) will also influence the amount of drag experienced by stream invertebrates (Vogel 1994). For example, large (45 mm) Tipulidae (height/width ≈ 1.0) will experience greater drag under similar microflow conditions than small Tipulidae (15 mm). Streamlined taxa (e.g., Baetidae) were a special case because their bodies were designed to reduce drag (Vogel 1994). They were automatically assigned to the subcategory with the lowest score (1) regardless of the magnitude of their Drag Index. For stream invertebrates inhabiting the epibenthic habitat, I propose combining both shape and size in one index. The Drag Index (D) can be calculated as follows:

$$D = (H/W)\cdot L$$

where L is body length (cerci excluded) and H and W are the maximum body height and width. H and W were measured using calipers accurate to 0.02 mm whereas L was determined by calculating the midmost length of the size ranges for each taxon (see Table 4). Trichoptera were measured in their cases or tubes. Under similar microflow conditions, very small (length <5.0 mm) or dorsoventrally flattened taxa ($D < 6.0$) should experience less drag than taxa with a large height/width. Index values <6.0 included invertebrates (*Psephenus*, *Rhithrogena*) known to experience reduced drag (Wilzbach et al. 1988). However, intermediate-sized (5.0–20.0 mm) cylindrical/spherical taxa ($6.0 > D < 12.0$) and large (>20.0 mm) cylindrical/spherical taxa ($D > 12.0$) should experience intermediate and high levels of drag, respectively. Cutoff points defining high, intermediate, and low levels of drag were not empirically determined.

Table 4. Calculations used to determine the Drag Index (*D*) of various taxa.

Taxon	Type	Ratio	*L*	*D*	*n*
Ephemeroptera					
Baetidae	1	0.79	6.0	4.7	6
Ephemerellidae					
Drunella grandis	2	0.68	14.0	9.5	6
Drunella doddsi	2	0.57	14.0	8.0	7
Attenella	2	0.70	7.0	4.9	4
Ephemerella	2	0.74	10.0	7.4	8
Serratella	2	0.60	7.0	4.2	5
Heptageniidae	3	0.47	12.5	5.9	10
Leptophlebiidae					
Chloroterpes	1	0.51	6.5	3.3	3
Paraleptophlebia	1	0.65	8.0	5.2	6
Traverella	1	0.55	8.5	4.7	3
Isonychiidae					
Isonychia	1	0.80	14.0	11.2	5
Siphlonuridae					
Ameletus		0.71	10.0	7.1	8
Plecoptera					
Chloroperlidae	2	0.65	15.0	9.8	10
Nemouridae	2	0.72	7.5	5.4	8
Perlidae	2	0.07	22.5	1.5	10
Perlodidae	2	0.69	14.0	9.7	10
Pteronarcydae	2	0.71	35.0	24.9	6
Trichoptera					
Brachycentridae	2	1.00	9.0	9.0	6
Glossosomatidae	2	0.81	5.5	4.5	10
Helicopsychidae	2	0.67	5.0	3.4	8
Muscidae	2	1.00	8.0	8.0	0
Psychodidae					
Maruina	2	0.70	4.5	3.2	5
Simuliidae	2	1.65	3.3	5.4	10
Stratiomyidae	2	0.58	10.0	5.8	6
Tabanidae	2	1.14	30.0	34.2	2
Tanyderidae	2	1.00	11.0	11.0	0
Tipulidae					
Antocha	2	0.93	18.0	16.7	3
Dicranota	2	1.00	18.0	18.0	5
Hexatoma	2	1.00	45.0	45.0	3
Limnophila	2	1.00	30.0	30.0	0
Limonia	2	1.00	16.0	16.0	6
Pedicia	2	1.00	16.0	16.0	6
Rhabdomastix	2	1.00	18.0	18.0	0
Tipula	2	1.10	45.0	49.5	2
Hydropsychidae	2	0.99	19.0	18.8	10
Hydroptilidae	2	0.27	2.5	0.7	8
Lepidostomatidae	2	1.00	9.0	9.0	6
Leptoceridae	2	1.00	12.5	12.5	3
Uenoidae	2	0.94	12.0	11.3	10
Limnephilidae					
Allomyia	2	1.00	22.0	22.0	2
Dicosmoecus	2	1.00	19.5	19.5	6
Ecclisomyia	2	1.00	12.0	12.0	0
Glyphopsyche	2	1.00	19.5	19.5	0
Hesperophylax	2	1.00	20.5	20.5	6
Limnephilus	2	1.00	17.0	17.0	0
Onocosmoecus	2	1.00	16.0	16.0	0
Psychoglypha	2	1.00	19.5	19.5	2
Psychoronia	2	1.00	19.5	19.5	0
Pycnopsyche	2	1.00	18.5	18.5	0
Philopotamidae	2	1.00	12.0	12.0	3
Polycentropodidae	2	1.00	24.0	24.0	5
Psychomyiidae	2	1.00	6.0	6.0	0
Rhyacophilidae	2	0.73	13.5	9.9	10
Diptera					
Athericidae	2	1.03	15.0	15.5	8
Blephariceridae	2	0.59	7.5	4.4	6
Chironomidae	2	1.00	5.0	5.0	10
Deuterophlebiidae	3	0.46	3.0	1.4	5
Empididae	2	1.00	4.5	4.5	8
Coleoptera					
Dryopidae adult	4	0.64	7.0	4.5	5
Elmidae larva	2	0.84	6.0	5.0	6
Elmidae adult	4	0.77	5.0	3.9	6
Psephenidae	3	0.37	4.5	1.7	6
Odonata	2	0.63	25.0	15.8	6
Lepidoptera					
Petrophila	2	0.80	18.0	14.4	3
Megaloptera					
Corydalidae	2	0.65	16.0	10.4	5
Sialidae	2	0.60	21.0	12.6	5
Turbellaria	2	0.40	7.5	3.0	6
Amphipoda	2	1.95	8.5	16.6	10
Gastropoda	4	0.83	8.0	6.6	8
Hydracarina	4	0.46	2.0	0.9	6

Note: Type refers to one of four general morphological types for stream invertebrates (1 = streamlined, 2 = cylindrical, 3 = dorsaventrally flattened, and 4 = spherical/globular). Ratio and *L* are the average height/width and the size range midpoint based on body length (mm), respectively. *n* is the number of individuals measured to determine the height/width. A "0" indicates where the height/width was inferred from other closely related taxa. Taxa that spend most of their life cycle in the hyporheic zone are not included (e.g., Capniidae and Leuctridae).

In the absence of data to indicate otherwise, cutoff points (6 and 12) were determined by visual inspection of the exponential relationship between the drag of morphologically different taxa and current velocity (Wilzbach et al. 1988). If current velocity can be measured at the scale of an individual organism, then the Drag Index (*D*) can be combined with Reynolds number (Re). Reynolds number is based on body size and has been used to estimate pressure drag and the force of microcurrent conditions (Vogel 1994):

$$\mathrm{Re} = (U{\cdot}D)/v$$

where U is the average velocity of the fluid and v is the kinematic viscosity. Because both shape (height/width) and body size are important, substituting the Drag Index for body size in calculating Reynolds number should provide a more accurate estimate of the drag exerted on stream invertebrates.

Drift distance

Availability depends on both accidental drift frequency and the distance traveled during a drift event. Dislodged invertebrates that quickly return to the benthos should be less available than those that remain in the water column. Habitat (e.g., riffle versus pool) will influence both frequency and distance, whereas Flow Exposure, Mobility, and the Drag Index primarily influence only drift frequency. Drift Distance was determined by settling efficiency which also provided part of the criteria used to classify invertebrates based on their intentional drift propensity. However, the effects of settling efficiency are reversed when considering accidental versus intentional drift. For intentional drifters, the ability to efficiently exit the drift should increase availability by increasing the propensity to intentionally drift at twilight. With respect to accidental drift, however, settling efficiency will decrease the time in the drift and, therefore, availability. For example, *Baetis* is an active swimmer that frequently deliberately drifts (a score of 9 in the Intentional Drift category) but can quickly return to the substrate when dislodged (a score of 1 in the Drift Distance category). Traits that determine drift distance and settling efficiency were included as components of availability with respect to both intentional and accidental drift.

Elliott (1971) separated invertebrates into three groups: (*i*) passive drifters that travel as far as dead individuals at slow and fast current velocities, (*ii*) typically passive drifters that could return to the bottom faster than dead individuals at slow, but not fast current velocities, and (*iii*) active settlers that return to the bottom faster than dead individuals at all current velocities. The ability to actively return to the bottom depends on three traits: (*i*) swimming ability, (*ii*) agility in regaining a foothold, and (*iii*) sinking postures. Because taxa that actively settle differ in settling efficiency (Elliott 1971) and because taxa that passively settle can either float or sink, the active–passive dichotomy was not sufficient to predict differences in drift distance and availability. Based on the literature (McLay 1970; Elliott 1971; Ciborowski and Corkum 1980; Otto and Sjöström 1986; Allan and Feifarek 1989), I divided taxa that actively returned to the substrate into two groups: “Active Swimmers” (Baetidae, Amphipoda, Perlidae) and “Active Settlers” that were weaker swimmers and (or) used various sinking postures (Ephemerellidae and most Plecoptera) and efficient ways of regaining a foothold (claws and silk) on the substrate (e.g., Heptageniidae, Ephemerellidae, Simuliidae, Rhyacophilidae, net-spinning Trichoptera). Passive settlers were also divided into two groups based on buoyancy characteristics. “Sinkers” (Trichoptera with rock cases, clams, and snails) were negatively buoyant taxa that readily settle out of the drift (e.g., Otto 1976). Other taxa (“Floaters”) that slowly floated to the bottom (no ballast) and lacked reattachment capabilities (claws, silk) were assigned to the farthest drifting category (a score of 6). Turbellaria, Diptera (except Simuliidae), and some Trichoptera with cases constructed of plant materials (e.g., Brachycentridae) were classified as Floaters.

Adult Drift

Ovipositing and emergence behavior and diel activity were used to classify emerging nymphs and aerial adults with respect to their occurrence in the drift and exposure to fish predation. Many taxa that are largely unavailable as immatures can become an important food resource during relatively brief periods of transition between the aquatic and terrestrial environment. Emerging adults that drift or swim to the surface are more available than those that crawl to the bank or emerge in winter. Similarly, adults that run across the water or land on the surface are more susceptible than adults that crawl into the water or drop their eggs from the air. Adults that avoid the water and lay their eggs on overhanging vegetation or recently exposed rock surfaces are least available to fish. Plus, adults that are active (ovipositing, mating, dispersal/flying) during the day, including morning and evening twilight periods (crepuscular activity), were deemed more available than primarily nocturnal taxa (e.g., most Trichoptera). Although many adult Trichoptera may begin activity during the evening hours, most taxa do not reach peak activity until well after sunset and twilight.

Benthic exposure

The “Benthic Exposure” category was similar to the “Flow Exposure” category except it does not refer to dislodgment by the current and the propensity to drift, but to the location of macroinvertebrates in or on the substrate with respect to trout detection and benthic feeding behavior. Despite conceptual differences, these two traits were correlated and somewhat redundant. For many taxa, flow exposure and benthic exposure were based on the same microspatial traits (e.g., flow avoiders were almost always concealed within the substrate). I adopted the rationale that if two categories were redundant for most taxa, but can help resolve differences in availability for a few, they both were included. For example, taxa classified as Obligates in the Flow Exposure category (e.g., net-spinning caddisflies) were fully exposed to the current, but may have been concealed between substrate crevices (i.e., classified as “Concealed” in the Benthic Exposure category). Benthic Exposure separated taxa that dig burrows, were buried in fine sediment, or occurred in the hyporheic zone from those that spent the majority of their aquatic existence in the epibenthic habitats (concealed or exposed). Concealed invertebrates typically occurred in crevices or on substrate undersurfaces whereas “Exposed” taxa resided on upper sunlit surfaces. Although many taxa can use both concealed and exposed surfaces (Heptageniidae), most predominantly occurred in one or the other during the day. I make the assumption that salmonids do not have the low-light visual acuity necessary to feed on the bottom substrate at night. Therefore, the movement of invertebrates from concealed surfaces during the day to exposed at night (Rader and Ward 1990; Culp et al. 1991) was not relevant behavior that might influence availability. However, if such benthic movements take place at twilight and increase the probability of accidental dislodgment, then this behavior might increase availability depending on the invertebrate’s propensity towards accidental dislodgment. The propensity to become accidentally dislodged has already been estimated by classifying taxa based on previously defined traits. Macroinvertebrates that occur within moss or thick filamentous algae were classified as Concealed. Based on quantitative observations of salmonid foraging behavior during the day in the field, Bachman (1984) found that adult brown trout (*Salmo trutta*) consumed nearly 87% of their prey from the drift and removed less than 15% directly from the bottom substrate. Gowan (1995) found that only 5% of brook trout (*Salvelinus fontinalis*) daytime feeding forays were benthic (95% were in the drift). (There are no data, that I am aware of, pertaining to the proportion of benthic versus drift forays by salmonids at night.) Therefore, the lower subcategory scores for Benthic Exposure (Concealed = 1 and Exposed = 3) reflect salmonid preferences for feeding in the drift. All drift categories have at least one subcategory with a score of 6 or 9.

Size

The “Size” category was based on the body length (cerci excluded) of late-instar larvae. Early-instar larvae are often buried in the hyporheic zone or too small to be available as food for juvenile and adult trout (Wilzbach et al. 1986). Species descriptions in taxonomic keys provided size ranges for each taxa. Invertebrates were assigned to Size subcategories based on their size range midpoint. Separate size ranges for adult aquatic insects were not used because late-instar and adult size ranges were almost always identical. As trout grow, they select larger invertebrates that provide a greater energy return but never completely ignore smaller prey (Ringler 1979; Allan 1981). Wankowski and Thorpe (1979) suggested that prey profitability would increase with prey size up to some optimum and then decline with larger prey because of increased “handling” costs. The optimum prey size would be 10.0–20.0 mm long for a 20.0- to 30.0-cm trout. Prey <1.0 mm rarely constitute a substantial portion of salmonid diets (e.g., Skinner 1985; Hubert and Rhodes 1992; Bozek et al. 1994). However, if sufficiently abundant, some taxa <1.0 mm can be occasionally consumed (Young et al. 1997). Therefore, taxa <1.0 mm were given a score of 1 instead of 0. All else being equal (e.g., abundance), invertebrates between 1.0 and 5.0 mm are small but commonly consumed (Skinner 1985; Bozek et al. 1994). Taxa in the 5.1- to 20.0-mm range are often disproportionately selected by feeding salmonids (Allan 1981; Skinner 1985). Taxa >20.0 mm are exceptionally large and presumably difficult to handle. Size subcategory scores reflect this hump-shaped relationship between profitability and prey size (Wankowski and Thorpe 1979). Therefore, small (1.0–5.0 mm) and very large (>20.0 mm) taxa are assigned a score of 3 and taxa between 5.1 and 20.0 mm are given a score of 9. Size rankings are based on the selectivity of juvenile and adult trout with body lengths between 6.0 and 30 cm. YOY trout are usually <6 cm and often feed directly from the bottom (e.g., Hubert and Rhodes 1992).

Abundance

Because salmonids tend to specialize on the most frequently consumed prey in its recent feeding history, availability is, in large part, defined by abundance (Allan 1981). “Abundance” will interact with the propensity to drift (intentional or accidental), adult drift, benthic exposure, and size to determine availability. For example, abundant taxa of adequate size with a strong propensity to drift (intentional and accidental) should be most available as food for trout. Rare taxa, however, will have a low availability regardless of their size and propensity to drift, and taxa that seldom drift or are small (<1.0 mm) will have a low availability regardless of their abundance. Therefore, the subtotal scores for each taxon based on intentional drift, dislodgment, adult drift, benthic exposure, and size (traits of Table 1) were multiplied by a factor expressing the differing affects of abundance on availability. The subtotal from Table 1 for rare taxa was reduced by one half (multiplied by 0.5) to produce the final availability score. The availability of rare taxa is low regardless of other traits (drift propensity and size). However, the availability of abundant and common taxa will be influenced by all three (drift propensity, size, and abundance). Therefore, abundant taxa with subtotal scores (based on drift propensity and size; Table 1) equal to or greater than the average (mean subtotal score = 36) were increased by 50% (multiplied by 1.5). Abundant taxa with subtotals less than the average did not occur. If they did, however, they should be multiplied by 1.0 (i.e., the effect of a high abundance should be offset by a less than average score on drift propensity and size). Similarly, common taxa with a subtotal score greater than the average or equal to and less than the average were increased by a factor of 1.2 or 1.0, respectively.

Invertebrates were assigned to specific abundance categories based primarily on notes found in regional keys. “Rare” taxa were relatively easy to recognize because they were consistently among the least collected taxa throughout their range. Only three taxa (*Baetis*, Simuliidae, and Chironomidae) were designated as “Abundant”. All other macroinvertebrates were classified as “Common”. Abundant and Common designations were difficult because some invertebrates may be abundant in one location and common in another depending on changing environmental conditions. Abundance designations based on quantitative samples would increase accuracy and the model’s ability to predict availability.

Data analysis

Spearman’s rank correlation was used to determine the significance of the association between the predicted rankings and the relative abundance (percent by numbers) based on actual fish gut data. A priori rankings were compared to three data sets that quantified the number of both immature and adult macroinvertebrates. Allan (1978) examined the gut contents of 18 adult brook trout from Cement Creek, a third-order tributary of the East River in Colorado. Bozek et al. (1994) and Young et al. (1997) examined gut contents from 20 and 37 adult Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*), respectively, taken from the same drainage in the headwaters of the North Fork of the Little Snake River. Cement Creek and the North Fork of the Little Snake River are located at similar elevations within the montane zone of the central Rocky Mountains (Colorado and Wyoming).

Because of difficulties associated with catching trout, the primary deficiency of most gut analyses is their failure to detect the importance of taxa that contribute to energy consumption but are absent from guts during sampling. Gut samples will characterize invertebrate availability for the previous 12–24 h at a spatial scale determined by fish movements. For example, gut samples from resident trout that forage from a single location will characterize invertebrate availability for a relatively small stream section. Most trout gut analyses are based on relatively small sample sizes (20–25 gut samples). Studies of trout diets at large spatial scales and over the course of a complete growing season are time intensive and therefore rare. The relative importance of different invertebrate taxa in salmonid diets based on gut analysis may exclude important taxa. Gut analyses should, however, reflect the rank order of availability for the taxa that do occur in the guts and they should not include relatively unavailable taxa. Therefore, if this index is efficient at ranking taxa based on their availability to drift-feeding salmonids, then (*i*) the rank abundance of taxa in guts should be correlated with rankings based on the index, (*ii*) gut samples should not include the least available taxa as identified by this index, and (*iii*) some taxa, present in the benthos and known to be important in salmonid diets, might be absent because of sampling deficiencies. These three studies were chosen because of their location in the Rocky Mountains and because both immature and adult insects were counted and benthic samples collected (Allan 1978; Bozek et al. 1994; Young et al. 1997). Benthic samples helped to identified taxa present in the stream but, because of possible sampling deficiencies, were absent from gut analyses. These analyses are preliminary tests. They do not validate the accuracy of this index in determining invertebrate availability to drift-feeding salmonids. Validation may require field studies relating the presence of highly ranked invertebrate taxa with drift abundance and numerous trout gut samples.

One objective of this research was to identify similar taxa (guilds) based on traits that determine availability. Initially, taxa were separated into groups based on the ranking procedure described previously. Groups were identified by gaps of seven or more points between consecutively ranked taxa (see Results). For comparison, a hierarchical cluster analysis (Gauch 1982) was also used to group taxa with similar availability traits. In this analysis, taxa were assigned to groups based on the minimum Euclidean distance between an individual taxon and the center of the most similar cluster. The final result was a dendrogram. Nonhierarchical cluster analyses classify taxa based on an optimization routine: minimization of the pooled within-cluster variance (O’Muircheartaigh and Payne 1977). This nonhierarchical technique was run using ISODATA software (Ball and Hall 1967) and differed from the hierarchical procedure in that it does not produce a dendrogram, but did calculate an R^2 correlation coefficient for each variable/category and the total amount of variation explained by the analysis. Both cluster analyses used data from Table 5: 95 rows (taxa) and 12 columns (categories). Data in the body of the table consisted of subcategory scores assigned to taxa from Table 1. Subcategories that did not apply to some taxa (NA in Table 5) were treated as zeros. None of the data (subcategory scores) were standardized. Therefore, categories with wide-ranging values were weighted heavier than categories with scores of smaller magnitude. This was a convenient way of emphasizing categories (e.g., Habitat) that are known to have an important impact on availability. Since “Abundance” was treated as a multiplier (category subtotal scores were multiplied by a value (0.5, 1.0, 1.2, 1.5) reflecting the importance of abundance on availability), it had an important impact on the assignment of taxa into availability groups. However, “Abundance” is the most likely invertebrate attribute to vary across space and time. For comparison (to analyze the effects of “Abundance”), each analysis (the ranking procedure and both cluster analyses) was rerun excluding “Abundance” as a multiplier and only using the traits of

Table 5. Subcategory scores are shown for each taxon found in mid- to small-sized streams of the Rocky Mountains.

Taxon	Active drift	Habitat	Flow exposure	Mobility	Drag index	Drift distance	Emergence behavior	Ovipositing behavior	Diel activity	Benthic exposure	Size (mm)	Size scores	Abundance	Total	Rank
Ephemeroptera															
Baetidae															
Acentrella	9?	9	6	9	1	1	6	3	6	3	4–8	9	C	74.4	3.0
Baetis	9	9	6	9	1	1	6	3	6	3	4–8	9	A	93.0	1.0
Callibaetis	9?	1	NA	NA	NA	NA	6	6?	6	3	6–10	9	R	20.0	(57.5)
Diphetor	9?	9	6	9	1	1	6	3	6	3	4–8	9	R	31.0	42.0
Caenidae	1?	1	NA	NA	NA	NA	6	6	6	0	2–6	3	R	11.5	(82.0)
Ephemerellidae															
Attenella	1?	9	6	3	1	3	6?	6	6	1	5–9	9	R	25.5	(46.5)
Drunella	1?	9	6	3	3	3	6	6/3	6	1	8–20	9	C	63.6	(6.5)
Ephemerella	1	9	6	3	3	3	6	6/3	6	1	6–14	9	C	63.6	(6.5)
Serratella	1?	9	6	3	1	3	6?	6	6	1	5–9	9	C	61.2	(11.0)
Timpanoga	1?	1	NA	NA	NA	NA	6	6	6?	0	12–15	9	R	14.5	(72.0)
Ephemeridae	1?	1	NA	NA	NA	NA	6	6	1/6	0	12–24	9	R	12.0	(79.5)
Heptageniidae	3	9	6	3	1	3	6	6	6	1	7–18	9	C	63.6	(6.5)
Isonychiidae	3?	9	6	3/9	3	3	3/6	6	6	1	10–18	9	R	26.0	45.0
Leptophlebiidae															
Choroterpes	3?	9	6	3	1	3	6	6?	6	1	5–8	9	R	26.5	44.0
Leptophlebia	3	1	NA	NA	NA	NA	6	6	6	1	7–15	9	R	16.0	(68.5)
Paraleptophlebia	3	9	6	3/9	1	3	6	6	6	1	6–10	9	C	63.6	(6.5)
Traverella	1?	9	6	3	1	3	6	6?	6	1	7–10	9	R	25.5	(46.5)
Polymitarcyidae	1?	1	NA	NA	NA	NA	6	6	1/6	0	12–17	9	R	12.0	(79.5)
Siphlonuridae															
Ameletus	3?	9	6	3/9	3	3	3	6	6	1	6–14	9	C	62.4	(9.5)
Parameletus	3?	1	NA	NA	NA	NA	3	6?	6	1	10–13	9	R	14.5	(72.0)
Siphlonurus	3?	1	NA	NA	NA	NA	3	6	6	1	10–20	9	R	14.5	(72.0)
Tricorythidae	1?	1	NA	NA	NA	NA	6	6	6	0	4–8	9	C	23.0	49.0
Plecoptera															
Capniidae	1?	0	NA	NA	NA	NA	0	6?	6	0	5–10	9	C	16.0	(68.5)
Chloroperlidae															
Alloperla	1?	0	NA	NA	NA	NA	3	6	6?	0	8–13	9	C	19.0	(61.0)
Paraperla	1?	0	NA	NA	NA	NA	3	6	6?	0	18–20	9	R	12.5	(77.0)
Plumiperla	1?	0	NA	NA	NA	NA	3	6	6?	0	6–8	9	C	19.0	(61.0)
Suwallia	1?	0	NA	NA	NA	NA	3	6	6?	0	8–10	9	R	12.5	(77.0)
Sweltza	1?	9	6	3	3	3	3	6	6	1	12–18	9	C	60.4	12.0
Triznaka	1?	0	NA	NA	NA	NA	3	6	6?	0	6–8	9	R	12.5	(77.0)
Leuctridae	1?	0	NA	NA	NA	NA	3/0	6	6	0	6–10	9	C	19.0	61.0
Nemouridae	1?	9	6	3	1	3	3/0	6	6	1	5–10	9	C	57.6	14.0
Perlidae	3	9	6	3	6	1	3	6	1	1	20–40	3	C	50.4	23.0
Perlodidae	1?	9	6	3	3	3	3	6	1	1	8–20	9	C	54.0	(15.5)
Pteronarcyidae	1?	9	6	3	6	3	3	3	1/6	1	25–50	3	C	46.8	34.0
Taeniopterygidae	3	0	NA	NA	NA	NA	0/3	0	6?	0	6–10	9	R	9.0	(86.5)

Table 5 (*continued*).

Taxon	Active drift	Habitat	Flow exposure	Mobility	Drag index	Drift distance	Emergence behavior	Ovipositing behavior	Diel activity	Benthic exposure	Size (mm)	Size scores	Abundance	Total	Rank
Trichoptera															
Brachycentridae	0?	9	1	1	3	6	6	6	1	3	6–12	9	C	54.0	(15.5)
Glossosomatidae	0	9	6	3	1	0	6	3	1	3	3–8	9	C	49.2	(26.5)
Helicopsychidae	0?	9	6	3	1	0	6	3?	1	3	4–6	9	C	49.2	(26.5)
Hydropsychidae	3	9	1	1	6	3	6	3	1	1	10–28	9	C	51.6	(20.0)
Hydroptilidae	0?	9	1	0	1	NA	6	3	1	3	1–5	3	C	29.0	43
Lepidostomatidae	0?	9	6	3	3	0	6	3	1	1	7–11	9	C	49.2	(26.5)
Leptoceridae	0?	9	6	3	6	0	6	6	1	1	10–15	9	R	23.5	(48.0)
Limnephilidae															
Allomyia	0?	9	6	3	6	0	6	0	1	1	18–26	3	R	17.5	(65.0)
Dicosmoecus	0?	9	6	3	6	0	6	3	1	1	6–23	3	C	45.6	(35.5)
Ecclisomyia	0?	9	6	3	6	0	6	3?	1	1	10–14	9	R	22.0	50.0
Glyphopsyche	0?	1	NA	NA	NA	NA	6	0?	1	1	16–23	3	R	6.0	94.0
Hesperophylax	0?	9	6	3	6	0	6	0	1	1	18–23	3	C	42.0	(38.5)
Limnephilus	0?	9	6	3	6	0	6	0	1	1	10–24	9	C	49.2	(26.5)
Onocosmoecus	0?	1	NA	NA	NA	NA	6	0	1	1	10–22	9	R	9.0	(86.5)
Psychoglypha	0?	9	6	3	6	0	6	0	1	1	16–23	3	R	17.5	(65.0)
Psychoronia	0?	9	6	3	6	0	6	0	1	1	16–23	3	R	17.5	(65.0)
Pycnopsyche	0?	9	6	3	6	0	6	0	1	1	16–23	3	R	17.5	(65.0)
Philopotamidae	3?	9	1	1	3	3	6	3	1	1	10–14	9	C	48.0	(31.5)
Polycentropodidae	3	9	1	1	6	3	6	3	1	1	20–28	3	C	44.4	37
Psychomyiidae	3?	9	1	1	3	3	6	3	1	1	4–8	9	R	20.0	(57.5)
Rhyacophilidae	0?	9	6	3	3	3	6	3	1	1	11–18	9	C	52.8	17.0
Uenoidae	0?	9	6	3	3	0	6	3/0	1	1	10–14	9	C	49.2	(26.5)
Diptera															
Athericidae	0?	9	6	3	6	6	3	0	6?	1	12–18	9	C	58.8	13.0
Blephariceridae	0?	9	1	1	1	6	6	0	6	3	5–10	9	R	21.0	54
Ceratopogonidae	0?	1	NA	NA	NA	NA	6	6?	6	1	1–5	3	R	11.5	(82.0)
Chironomidae (free-living)	0?	9/1	0	3	1	6	6	6/3	6/1	1	2–8	9	A	70.5	4
Orthocadiinae															
Cardiocladius	0?	9	1	1	1	6	6	6/3	6	1	2–5	3	C	48.0	(31.5)
Cricotopus	0?	9/1	1	1	1	6	6	6/3	6	1	2–5	3	C	48.0	(31.5)
Tanytarsini	0?	9/1	1	1	1	6	6	6/3	6	1	2–5	3	C	48.0	(31.5)
Deuterophlebiidae	0?	9	1	3	1	6	6	3?	6	3	3	3	R	20.5	55.0
Dixidae	0?	1	NA	NA	NA	NA	3	0	6	1	2–5	3	R	7.0	(91.5)
Empididae	0?	9/1	0	3	1	6	6?	6?	6?	1	2–7	3	C	49.2	(26.5)
Muscidae	0?	9	0	3	3	6	3?	3?	6	1	6–10	9	R	21.5	(52.0)
Psychodidae															
Maruina	0?	9	1	3	1	6	3?	3?	6	3	2–5	3	C	45.6	(35.5)
Pericoma	0?	1	NA	NA	NA	NA	6?	6?	6	1	2–5	3	R	11.5	(82.0)
Simuliidae	9	9	6	1	1	3	6	6/0/3	6	3	1–5.5	3	A	79.5	2.0

Table 5. (*concluded*).

Taxon	Active drift	Habitat	Flow exposure	Mobility	Drag index	Drift distance	Emergence behavior	Ovipositing behavior	Diel activity	Benthic exposure	Size (mm)	Size scores	Abundance	Total	Rank
Stratiomyidae	0?	9	0	3	1	6	6	0	6?	1	2–18	3	R	17.5	(65.0)
Tabanidae	0?	1	NA	NA	NA	NA	3?	0	6	1	10–50	3	R	7.0	(91.5)
Tanyderidae	0?	9?	0	3	3	6	3?	3?	6	1	8–14	9	R	21.5	(52.0)
Tipulidae															
Antocha	0?	9	0	3	6	6	3?	0	6	1	12–24	9	C	51.6	(20.0)
Dicranota	0?	9	0	3	6	6	3?	0	6	1	12–24	9	C	51.6	(20.0)
Hexatoma	0?	1?	NA	NA	NA	NA	3	0	6	1	30–60	3	R	7.0	(91.5)
Limnophila	0?	1?	NA	NA	NA	NA	3	0	6	1	20–40	3	C	10.0	(85.0)
Limonia	0?	9?	0	3	6	6	3	0	6	1	10–22	9	C	51.6	(20.0)
Pedicia	0?	9	0	3	6	6	3	0	6	1	10–22	9	C	51.6	(20.0)
Rhabdomastix	0?	1	NA	NA	NA	NA	3	0	6	1	12–24	9	R	10.0	(85.0)
Tipula	0?	1	NA	NA	NA	NA	3	0	6	1	30–60	3	R	7.0	(91.5)
Coleoptera															
Dryopidae	0?	9	6	3	1	3	NA	NA	NA	1	4–10	9	C	34.0	(40.5)
Elmidae	0?	9	6	3	1	3	3	3	NA	1	2–8	3	C	34.0	(40.5)
Psephenidae	0?	9	1	1	1	6	3	3	1?	1	3–6	3	R	14.5	(72.0)
Odonata	3?	1	NA	NA	NA	NA	3	6	6	1	>10	9	R	14.5	(72.0)
Lepidoptera															
Petrophila	3?	9	1	1	6	3	6	3	1	1	11–25	9	R	21.5	(52.0)
Megaloptera															
Corydalidae	0?	9	6	3	6	3	3	0	6?	1	40–80	3	R	20.0	(57.5)
Sialidae	0?	9	6	3	6	3	3	0	6?	1	16–26	3	R	20.0	(57.5)
Collembola	0?	1	NA	NA	NA	6	NA	NA	NA	NA	<1.0	1	C	8.0	(89.0)
Oligochaeta	0?	1	NA	NA	NA	NA	NA	NA	NA	0	2–20	9	C	10.0	(85.0)
Turbellaria	0?	9	6	3	1	6	NA	NA	NA	1	5–10	9	C	42.0	(38.5)
Amphipoda	9?	9	6	9	6	1	NA	NA	NA	3	5–12	9	C	62.4	(9.5)
Gastropoda															
Snails	0?	1	NA	NA	NA	NA	NA	NA	NA	1	4–12	9	C	13.0	75.0
Pelecypoda	0?	1	NA	NA	NA	NA	NA	NA	NA	0	2–8	3	R	2.0	95.0

Note: A question mark and NA indicate uncertain designations based on closely related taxa and categories that were not applicable. A solidus separates scores where multiple designations apply. The first score was used to calculate the total and rank. A, C, or R indicate Abundant, Common, or Rare taxa, respectively. Parentheses indicate shared ranks.

Fig. 2. Association between the predicted ranks versus the actual percent abundance (average number of individuals per gut) of macroinvertebrates from (*a*) brook trout and (*b* and *c*) cutthroat populations using data from Allan (1978), Bozek et al. (1994), and Young et al. (1997).

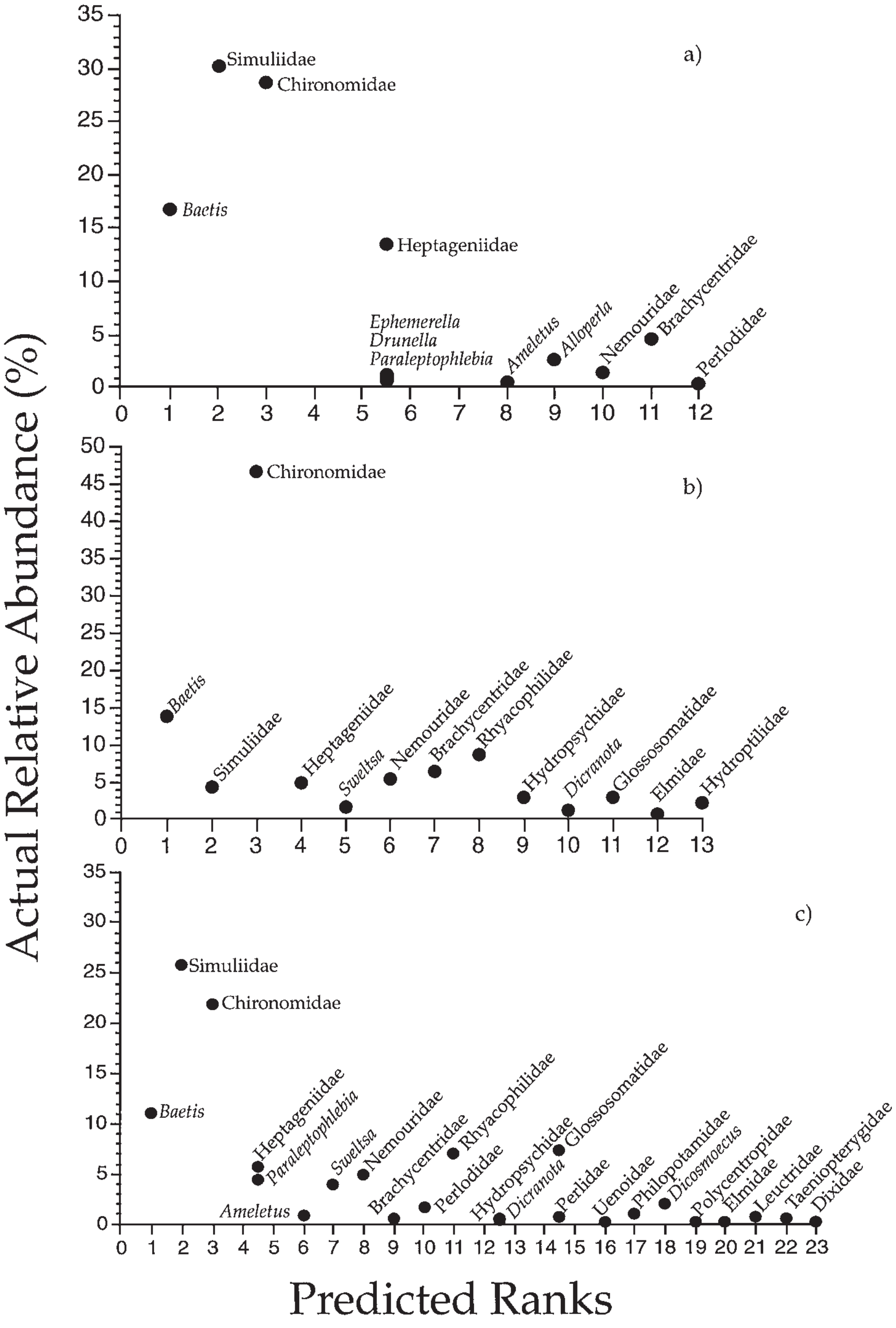
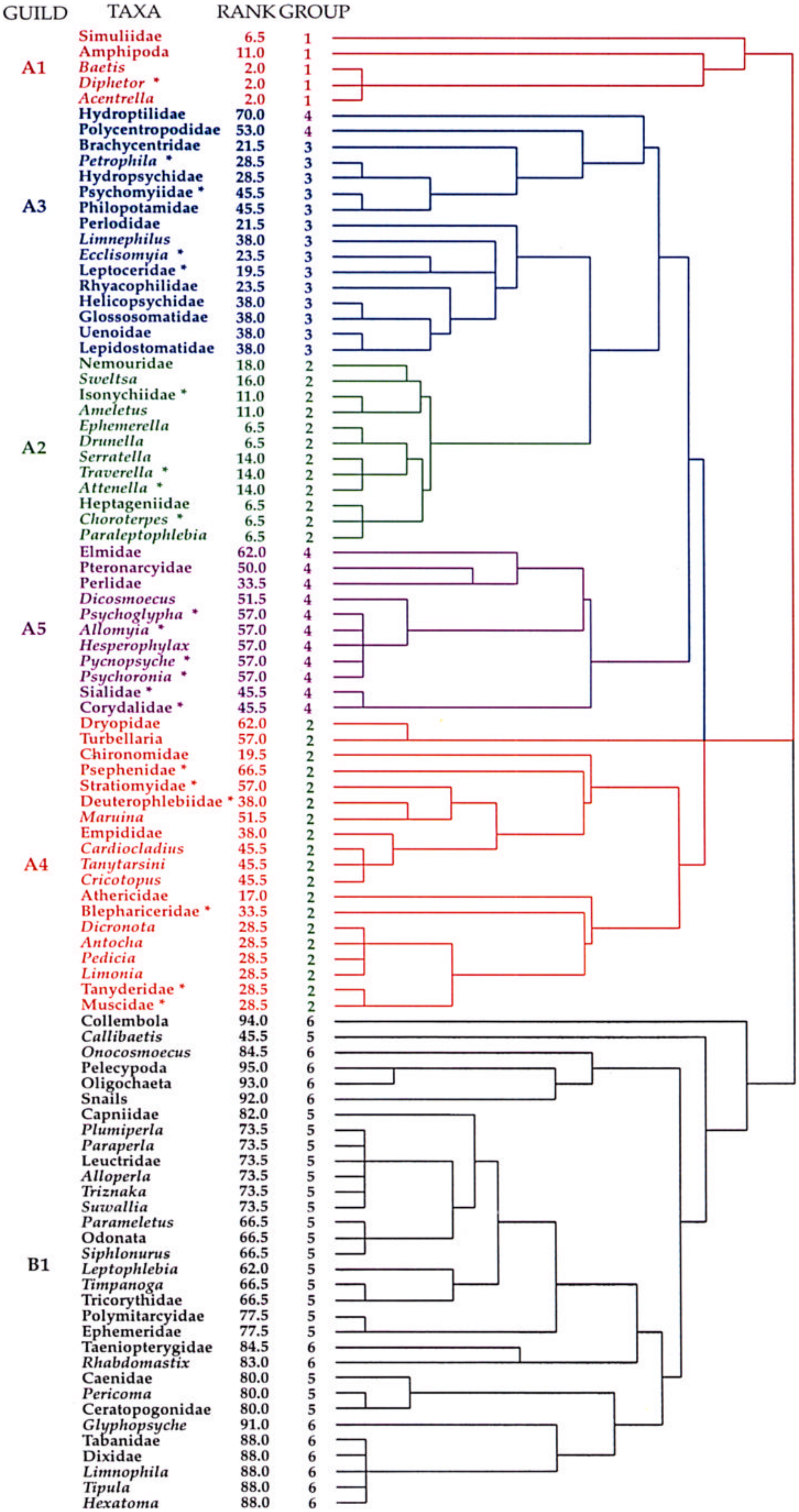


Table 1. Both the cluster analysis and ranking procedure were also used to classify taxa into drift groups based only on the first six categories of Table 1 (Intentional Drift, Habitat, Flow Exposure, Mobility, Drag Index, and Drift Distance).

Results

When stream invertebrates were ranked according to their availability based on the total of category scores (including Abundance as a multiplier), they separated into *Baetis* and three groups (Table 5). *Baetis* was the highest ranked taxon with a score 13.5 points higher than the next highest ranked taxa, Simuliidae. The Simuliidae, *Acentrella*, and free-living Chironomidae were separated by 4 or fewer points and comprised the first group. The second availability group started with the Heptageniidae, *Paraleptophlebia*, *Ephemerella*, and *Drunella* (tied ranks) and gradually decreased (consecutive taxa were separated by 1 point or less) through an additional



GUILD	TAXA	RANK	GROUP
A1	**Simuliidae**	6.5	1
	Amphipoda	11.0	1
	Baetis	2.0	1
	Diphetor *	2.0	1
	Acentrella	2.0	1
A3	**Hydroptilidae**	70.0	4
	Polycentropodidae	53.0	4
	Brachycentridae	21.5	3
	Petrophila *	28.5	3
	Hydropsychidae	28.5	3
	Psychomyiidae *	45.5	3
	Philopotamidae	45.5	3
	Perlodidae	21.5	3
	Limnephilus	38.0	3
	Ecclisomyia *	23.5	3
	Leptoceridae *	19.5	3
	Rhyacophilidae	23.5	3
	Helicopsychidae	38.0	3
	Glossosomatidae	38.0	3
	Uenoidae	38.0	3
	Lepidostomatidae	38.0	3
A2	**Nemouridae**	18.0	2
	Sweltsa	16.0	2
	Isonychiidae *	11.0	2
	Ameletus	11.0	2
	Ephemerella	6.5	2
	Drunella	6.5	2
	Serratella	14.0	2
	Traverella *	14.0	2
	Attenella *	14.0	2
	Heptageniidae	6.5	2
	Choroterpes *	6.5	2
	Paraleptophlebia	6.5	2
A5	**Elmidae**	62.0	4
	Pteronarcyidae	50.0	4
	Perlidae	33.5	4
	Dicosmoecus	51.5	4
	Psychoglypha *	57.0	4
	Allomyia *	57.0	4
	Hesperophylax	57.0	4
	Pycnopsyche *	57.0	4
	Psychoronia *	57.0	4
	Sialidae *	45.5	4
	Corydalidae *	45.5	4
A4	**Dryopidae**	62.0	2
	Turbellaria	57.0	2
	Chironomidae	19.5	2
	Psephenidae *	66.5	2
	Stratiomyidae *	57.0	2
	Deuterophlebiidae *	38.0	2
	Maruina	51.5	2
	Empididae	38.0	2
	Cardiocladius	45.5	2
	Tanytarsini	45.5	2
	Cricotopus	45.5	2
	Athericidae	17.0	2
	Blephariceridae *	33.5	2
	Dicronota	28.5	2
	Antocha	28.5	2
	Pedicia	28.5	2
	Limonia	28.5	2
	Tanyderidae *	28.5	2
	Muscidae *	28.5	2
B1	**Collembola**	94.0	6
	Callibaetis	45.5	5
	Onocosmoecus	84.5	6
	Pelecypoda	95.0	6
	Oligochaeta	93.0	6
	Snails	92.0	6
	Capniidae	82.0	5
	Plumiperla	73.5	5
	Paraperla	73.5	5
	Leuctridae	73.5	5
	Alloperla	73.5	5
	Triznaka	73.5	5
	Suwallia	73.5	5
	Parameletus	66.5	5
	Odonata	66.5	5
	Siphlonurus	66.5	5
	Leptophlebia	62.0	5
	Timpanoga	66.5	5
	Tricorythidae	66.5	5
	Polymitarcyidae	77.5	5
	Ephemeridae	77.5	5
	Taeniopterygidae	84.5	6
	Rhabdomastix	83.0	6
	Caenidae	80.0	5
	Pericoma	80.0	5
	Ceratopogonidae	80.0	5
	Glyphopsyche	91.0	6
	Tabanidae	88.0	6
	Dixidae	88.0	6
	Limnophila	88.0	6
	Tipula	88.0	6
	Hexatoma	88.0	6

Fig. 3. Cluster dendrogram (hierarchical technique) showing the classification of 95 taxa into five availability groups (A1–A5) and one relatively unavailable group (B1). Values in the rank column identified the rank availability of each taxa as a food resource for salmonids (see text for a complete description). The ranking procedure and cluster analysis were based on the traits in Table 1 excluding abundance. When abundance was included as a multiplier used to modify availability scores, taxa with an asterisk were given a Rare designation for streams in the subalpine and montane zones of the central Rocky Mountains and comprised a second unavailable group.

32 taxa. The third and least available group started with the beetles (Elmidae and Dryopidae) and declined in score (1 point or less separated consecutively ranked taxa) through 56 taxa until reaching the Pelecypoda. Gaps of 7 and 8 points separated group 1 from 2 and group 2 from 3, respectively. Sixty-one percent of the taxa occurred in the least available group (group 3). The most highly ranked taxa (in descending order) of the most diverse orders were (*i*) *Baetis*, *Acentrella*, Heptageniidae, *Paraleptophlebia*, *Ephemerella*, and *Drunella* (Ephemeroptera), (*ii*) Simuliidae and free-living Chironomidae (Diptera), (*iii*) *Sweltsa*, Nemouridae, Perlodidae, and Perlidae (Plecoptera), and (*iv*) Brachycentridae, Rhyacophilidae, and Hydropsychidae (Trichoptera).

Predicted ranks were significantly correlated with the actual rank of macroinvertebrates in trout guts from each of the three studies examined (Fig. 2). Spearman's correlation coefficient (r) was 0.61 ($P = 0.018$), 0.66 ($P = 0.008$), and 0.70 ($P = 0.0001$) for data from Allan (1978), Bozek et al. (1994), and Young et al. (1996), respectively. These results suggested that this index was proficient at predicting the rank of macroinvertebrates occurring in gut samples from specific streams. All taxa, except Hydroptilidae (Bozek et al. 1994), Leuctridae, Dixidae, and Taeniopterygidae (Young et al. 1997), occurred in the top two highest ranked availability groups. Out of a total of 48 taxa (gut samples from all three studies), these four taxa were represented by a single individual and were ranked in the lowest availability group. The most abundant taxa in guts from each study (Fig. 2) always occurred in the highest ranked group. The ranking procedure predicted which taxa would occur in trout stomachs and their rank order of abundance.

Based on benthic samples collected from each site, several taxa with predicted high availability were absent from trout guts. In particular, *Rhithrogena* spp. (Heptageniidae), *Pteronarcella badia* (Pteronarcyidae), and *Rhyacophila* spp. (Rhycophilidae) were common in the benthos but absent from brook trout guts in Cement Creek, Colorado (Allan 1978). Similarly, Perlodidae, Perlidae, *Ephemerella* spp., and *Drunella* spp. were common in the benthos but absent from cutthroat gut samples in the North Fork of the Little Snake River (Bozek et al. 1994; Young et al. 1997). Either the index has exaggerated the importance of these taxa as a food resource for trout or their absence from these gut examinations was a result of sampling deficiency. Since these taxa were commonly consumed by trout in other studies (e.g., Tusa 1968; Griffith 1974; Skinner 1985), their absence was probably due to sampling deficiencies.

The cluster analysis (abundance excluded) accounted for 65% of the variation (n-dimensional space) in the assignment of taxa into groups. Both hierarchical and nonhierarchical techniques assigned taxa to similar clusters. Therefore, only results from the hierarchical technique (dendrogram) are shown (Fig. 3) and the nonhierarchical technique is used to provide R^2 values. The cluster analysis separated stream invertebrates into six groups or proposed guilds based on their availability to salmonids in the Rocky Mountain Region (Fig. 3). Results from the rankings procedure corresponded to results from the cluster analysis. Similarly ranked taxa clustered into the same groups (Fig. 3). The rankings of individual taxa were used to determine the relative availability of each guild (A1 > A2 > A3 > A4 > A5 > B1).

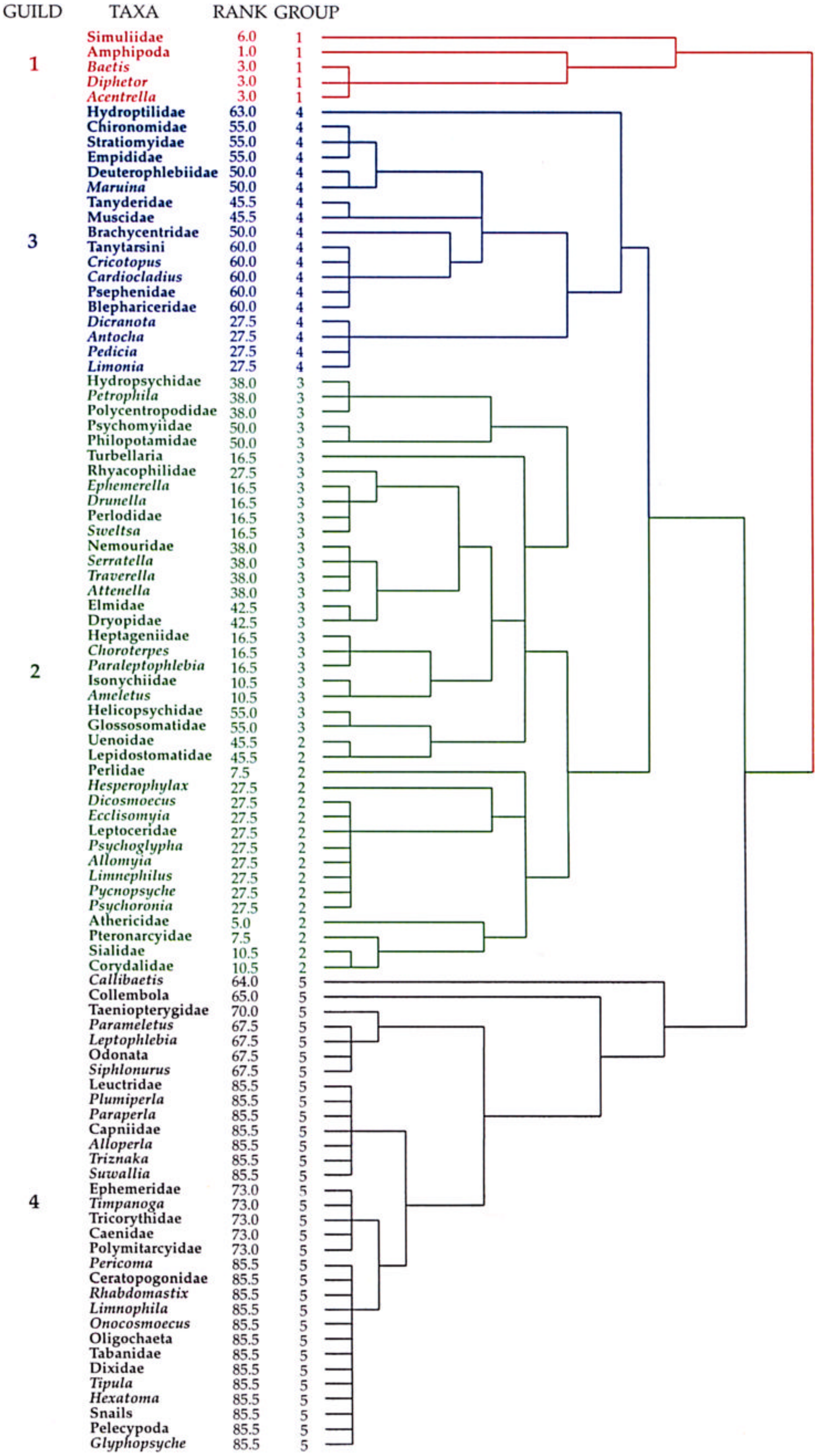
Habitat ($R^2 = 0.996$) separated taxa into two groups (A and B). Taxa in the A group inhabited riffles whereas taxa in the least available group (B) inhabited either the hyporheic zone or depositional areas. Mobility ($R^2 = 0.758$), Intentional Drift ($R^2 = 0.681$), Drift Distance ($R^2 = 0.663$), Drag Index ($R^2 = 0.574$), Flow Exposure ($R^2 = 0.554$), Adult Diel Activity ($R^2 = 0.562$), and Ovipositing Behavior ($R^2 = 0.553$) were all important in separating taxa of the A group into five clusters (Fig. 3). Benthic Exposure ($R^2 = 0.432$) and Size ($R^2 = 0.428$) were somewhat less important because they were only influential in separating a few taxa into their respective clusters. Emergence Behavior ($R^2 = 0.183$) was the only category that appeared to have little influence on the separation of taxa into guilds.

In addition to inhabiting the hyporheos and depositional areas, taxa in B1 dig burrows and bury themselves in fine sediment. All taxa in the most available guild (A1) were swimmers (except Simuliidae) and frequent intentional drifters in the facultative Flow Exposure category. Other swimmers (e.g., *Callibaetis*, *Parameletus*, *Siphlonurus*, *Leptophlebia*) inhabited depositional areas or clustered into the A2 guild (Isonychiidae, *Paraleptophlebia*, *Ameletus*). Guilds A3 and A5 were primarily composed of the most and least available Trichoptera, respectively. Size was the primary difference. Trichoptera in the A3 guild were closer to the more available intermediate size class whereas A5 Trichoptera were either too small or too large. Riffle dwelling stoneflies (Perlodidae, Nemouridae, *Sweltsa*, Pteronarcyidae, Perlidae) were dispersed among three guilds (A2, A3, and A5). Size was again important, as Pteronarcyidae and Perlidae (A5) were large and considered difficult to handle. Nemouridae and *Sweltsa* (A2) had day-active adults whereas Perlodidae (A3) were nocturnal. Taxa in the A4 guild were composed of the most available, riffle-dwelling dipterans that were crawlers with a high drag index and would passively float once dislodged. Most dipterans in A4 also had day-active adults.

The primary affect of including abundance as a factor in the cluster analysis was to create a second relatively unavailable guild (B2). Twenty-one riffle-dwelling taxa from the A group were assigned a Rare designation which added them to the less available B group. These taxa are identified with an asterisk in Fig. 3. All total, 56% or 53 taxa (B1 + B2) comprised the relatively unavailable B group; rare riffle-dwelling taxa and taxa that inhabit depositional areas or the hyporheos. Including abundance also added the Chironomidae to the most available guild (A1) because it clustered with *Baetis* and the Simuliidae which were also given an Abundant designation.

The final objective was to propose a functional classification of the drift based on the first six categories in Table 1. For amphibiotic aquatic insects, this is a functional classification of immature stages since adult traits were excluded. When

Fig. 4. Cluster dendrogram (hierarchical) showing the classification of 95 taxa into four guilds with similar propensities to drift based on six traits (Intentional Drift, Habitat, Flow Exposure, Mobility, Drag Index, and Drift Distance). Values in the rank column identify the drift rank of each taxon based on its total score using the first six traits of Table 1 (see text for complete descriptions).



stream invertebrates were ranked using the sum of category scores, which was a measure of their propensity to drift (intentional and accidental), they separated into Amphipoda and three groups. Amphipods were the highest ranked taxa with a score 5.0 points higher than group 1. Group 1 was composed of three taxa (*Baetis*, *Acentrella*, *Diphetor*) with tied ranks and was 5.0 points greater than the much larger group 2. Group 2 started with the Simuliidae and gradually decreased (consecutive taxa were separated by no more than 2 points) through an additional 57 taxa. The third and least likely group to drift started with *Callibaetis* and declined in score (1 point or less separated consecutively ranked taxa) through 33 taxa. A gap of 7 points separated group 2 from group 3. Taxa in group 3 should have a low propensity to drift.

The cluster analysis assigned taxa into four guilds based their propensity to drift (Fig. 4). The cluster analysis accounted for 86% of the variation in the assignment of taxa into guilds. As in the availability cluster analysis, invertebrate rankings corresponded to the results from the cluster analyses (i.e., similarly ranked taxa clustered into the same groups). Based on this analysis, the propensity to drift was greatest in guild 1 and decreased through guilds 2 and 3 to the least likely group of taxa to drift, guild 4 (Fig. 4).

Three variables (Habitat, $R^2 = 0.996$; Flow Exposure, $R^2 = 0.993$; Mobility, $R^2 = 0.800$) were most important in controlling the clustering of taxa into drift guilds. All members of guild 4 inhabited depositional or hyporheic habitats whereas all taxa in guilds 1, 2, and 3 were classified in the Riffle subcategory. Except for the Simuliidae, all taxa in guild 1 were swimmers with a frequent propensity to intentionally drift and were classified as Facultative in the Flow Exposure category. Simuliidae shared the same traits with the rest of the taxa in guild 1 except they were assigned to the Attached mobility subcategory. All six variables, including Intentional Drift ($R^2 = 0.661$), Drag Index ($R^2 = 0.691$), and Drift Distance ($R^2 = 0.670$), were important in assigning and clustering taxa into guilds 2 and 3. Guild 2 was composed of riffle-dwelling mayflies, stoneflies, and caddisflies (free-living, net-spinning, case-making, tube-dwelling). Except for Psephenidae, Brachycentridae, and Hydroptilidae, taxa in guild 3 were primarily riffle-dwelling dipterans.

A comparison of drift and availability revealed that the guild with the greatest propensity to drift (*i*) was identical to the guild with the greatest availability to salmonids (A1) (Figs. 3 and 4). Similarly, the guild with the least propensity to drift (4) was identical to the group with the lowest availability (B1). Except for Hydroptilidae and Brachycentridae (A3), drift guild 2 included availability guilds A2, A3, and A5 and three difficult taxa to classify (Athericidae, Dryopidae, Turbellaria) from A4. Except for these three taxa, A4 was identical to drift guild 3. The A5 group was one of the least available groups to salmonids because of size and adult characteristics, not because of their drift propensity because they were part of the second most likely group to drift (2).

Discussion

The ability of this model to predict differences in drift and availability among groups of taxa with different traits depends on (*i*) identifying the important traits, (*ii*) understanding their relationship to drift and availability, and (*iii*) gathering sufficient trait information on taxa for accurate classification. The traits chosen for this analysis and invertebrate classification fall into five groups: intentional, accidental and adult drift propensity, exposure on the stream bottom, and body size. Intentional drift propensity is a behavioral trait whereas accidental drift, adult drift, benthic exposure, and body size incorporate both behavioral and morphological characteristics. Many more traits were considered than were included in this analysis. Some traits (e.g., functional feeding groups) were excluded in favor of morphological and behavioral attributes that could better define the propensity to drift. For example, Hydroptilidae and *Baetis* are both grazers but they have very different drift propensities. Differences in drift are likely determined by different morphological and behavioral traits (facultative flow exposure, streamlined, swimmers versus obligate flow exposure, attached, case-makers) and is only indirectly related to mouth part morphology and the consumption of algae. Other potentially important traits were considered but could not be included because of a lack of information (e.g., ability of adults to quickly break the surface tension of the water and fly away, adult tendency to swarm, life cycle synchrony). Waters (1968) found that the drift of a rock-cased caddisfly (*Oligophlebodes sigma*) in a trout stream in Utah peaked during the day when temperatures were highest. This day-active pattern is opposite from many species whose drift peak occurs at night. To the extent that future research reveals this behavior to be typical of other caddisflies, day-active, temperature-dependent drift might be an important trait that will influence availability and should be included in future classification efforts. More information is also needed for some traits included in this analysis. This study represents the first attempt to characterize the intentional drift propensity of stream invertebrates. Although stream ecologists have long recognized that stream invertebrates could, for a variety of reasons, intentionally release their hold on the substrate and drift downstream (Waters 1972), it was not until the recent emphasis on behavioral observations (e.g., Peckarsky 1980) that such empirical data were available. However, adequate information on intentional drift frequencies has only been determined for five genera (*Baetis*, *Ephemerella*, *Paraleptophlebia*, *Prosimulium*, and *Simulium*). Further research on the intentional drift frequency of other taxa is required. A better understanding of how each trait influences invertebrate drift and availability will also increase predictability. Differences between subcategory scores should be determined by the relationship (linear, quadratic, etc.) between a particular trait and availability. Although the general direction of the relationship (positive or negative) was known for all traits or categories, the specific shape (a straight line was assumed for most traits) was only known for a few categories (e.g., Drift Distance). For example, "Passive Floaters" are known to drift five or six times farther than invertebrates that actively swim to exit the drift (Elliott 1971). For most categories, however, there were no data to indicate appropriate differences between subcategory scores. In the absence of data relating flow exposure groups to dislodgment, "Facultatives" were arbitrarily assigned a three times greater score than "Obligates." Future research should clarify relationships between each category/trait and drift/availability to provide more accurate information on differences among subcategory scores.

Predicting differences in availability among groups of aquatic taxa with different traits is the first step in predicting the actual food or energy available for salmonid growth and reproduction. Actual available energy depends on: (*i*) abundance and species composition of the aquatic invertebrate community, (*ii*) abundance and species composition of the terrestrial invertebrate community, (*iii*) abundance of vertebrate prey (e.g., amphibians, mice, and small fish), and (*iv*) the environmental attributes that influence the availability of the first three factors (e.g., density of riparian vegetation). This study has investigated the relationship between food availability and the species composition of the benthic community by exploring traits that influence drift and availability of specific taxa. Future research should include the terrestrial invertebrate component and the environmental factors that influence the amount of both aquatic and terrestrial inputs as part of a model to estimate total energy available for salmonid production.

A simple equation can be used to express the aquatic species component of a larger model for predicting actual food availability for salmonids. The contribution of the aquatic species composition (ASC) can be calculated as

$$\mathrm{ASC} = \sum_{i=1}^{n} (\mathrm{St}_i \cdot A_i)$$

where n is the number of taxa in availability guilds A1–A5 (Fig. 3). St is an availability factor based on classifying each taxon according to the traits found in Table 1 and is the subtotal score (sum the subcategory scores for each taxa) from Table 5 (abundance excluded). A is an abundance factor. How it is calculated depends, in part, on the spatial scale. Patterns at large scales (comparisons in food availability across regions, basins, and watersheds) may be best detected with coarse-grained data (Margalef 1968). Therefore, at larger scales, presence–absence data based on qualitative sampling techniques could be used to identify the taxa in guilds A1–A5 and A becomes a multiplier (0.5, 1.0, 1.2, 1.5) used to modify St. Also, information on large-scale patterns of relative abundance could be gathered from the literature (e.g., regional keys), in addition to qualitative samples, and used to separate taxa into abundance categories (rare, common, and abundant). The choice of a multiplier depends on the abundance category and if the taxa have an availability score greater than or less than the mean St (see Methods for a complete description). At smaller scales (stream reaches and habitat units), pattern detection may require fine-grained data (quantitative estimates of population density). For small-scaled predictions, St for each taxon could be multiplied by density estimates based on quantitative benthic samples. This equation used at large or small scales (using coarse-grained or fine-grained data) provides a single value expressing relative food availability of aquatic invertebrates for salmonids based on a relatively simple level of taxonomic resolution (primarily family with some genus identifications).

This investigation and invertebrate classification has a variety of potential uses related to the transfer of energy from lower to higher trophic levels. Both natural and anthropic disturbances can alter macroinvertebrate community structure, causing some taxa to decrease whereas the abundance of others might remain unchanged or even increased (e.g., effects of eutrophication). This study provides specific criteria for determining when alterations in invertebrate community structure will affect food resources for higher trophic levels by causing a decline in the most available taxa. The relationship between total invertebrate production and salmonid production is not a positive, linear function. Increased production of unavailable taxa may have little or no impact on salmonid production. Similarly, if species were deleted from the community, the function of transporting energy from lower to higher trophic levels may or may not be altered. The relationship between community diversity and ecosystem function (transfer of energy to higher trophic levels; Lawton 1994) may depend on the availability of the deleted taxa. That is, ecosystem function will decline as available taxa are deleted. This research also supports previous findings that floods are important in maintaining invertebrates that represent an important food resource for salmonids (Power et al. 1996). Taxa that were efficient at exploiting recently disturbed habitats (Power et al. 1996) were identified in this study as being the same taxa that are most available to salmonids (e.g., mayflies in guilds A1 and A2). The least resilient taxon (*Dicosmoecus*), which when abundant can suppress algal resources and mayfly populations, was assigned to one of the guilds with the lowest availability (A5). Hemphill and Cooper (1983) also found an increase in the abundance of *Simulium virgatum* (Simuliidae) and a decrease in *Hydropsyche oslari* (Hydropsychidae) as disturbance frequency increased. Hart (1987) suggested that disturbances might prevent the competitively superior species (*H. oslari*) from excluding the “fugative” species (*S. virgatum*). My results indicate that Simuliidae (group A1) possess traits that make them more available to salmonids than Hydropsychidae (group A3). Both studies (Hemphill and Cooper 1983; Power et al. 1996) suggest that traits that enhance recovery from disturbances may also increase availability to salmonids. Combining the availability traits of this research with life history traits that determine resilience to physical disturbance (growth rate, generation time, dispersal capability) may help to define the role of disturbances in maintaining invertebrates that are important in maintaining salmonid populations. In addition to being an important fish food, invertebrates can also be used as a biomonitoring tool to assess the health of stream ecosystems (Rosenberg and Resh 1993). However, drift can carry invertebrates from unimpacted upstream areas into downstream impacted sites creating the false perception of a healthy environment. Knowledge of the drift propensity of specific taxa (drift guilds 1 and 2 versus 3 and 4) can be valuable in separating taxa that seldom drift from frequent drifters that might temporarily occur in the benthos but are not indicative of localized impacted conditions.

This study was specific to trout streams of the subalpine, montane, and foothills zones of the central Rocky Mountains. Invertebrate classification was based on traits specific to taxa that reside within this ecoregion. Although taxa in other ecoregions may be classified differently from taxa in the Rocky Mountains, the traits/categories/criteria found in Table 1 can be used to rank and classify taxa in trout streams from all ecoregions. Similarly, the ranking and classification of taxa in this study was based on their importance as a food resource for juvenile and adult trout. Gape-limited YOY trout that forage in side channels, backwaters, and stream margins primarily rely upon smaller aquatic insects and microcrustaceans as a food resource (Shiozawa 1986; Hubert and Rhodes 1992). A separate set of criteria is necessary to rank and classify invertebrates based on their importance to YOY trout.

This study is an investigator-defined, a priori classification of stream invertebrate taxa into both drift and availability guilds using specifically defined criteria (traits or categories of Table 1) and objective clustering techniques. The predictive power of this model depends on the degree that these guilds represent real ecological units. Although a preliminary analysis comparing the predicted with the actual rank of taxa in salmonid guts suggests that these guilds may represent real ecological units, future research should expand upon this test and compare the predicted rankings to a larger data set including both drift and trout gut analyses in the Rocky Mountains.

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References

Allan, J.D. 1978. Trout predation and the size composition of stream drift. Limnol. Oceanogr. **23**: 1231–1237.

Allan, J.D. 1981. Determinants of diet of brook trout (*Salvelinus fontinalis*) in a mountain stream. Can. J. Fish. Aquat. Sci. **38**: 184–192.

Allan, J.D. 1995. Stream ecology: structure and function of running waters. Chapman and Hall, Inc., New York.

Allan, J.D., and Feifarek, B.P. 1989. Distances travelled by drifting mayfly nymphs: factors influencing return to the substrate. J. N. Am. Benthol. Soc. **8**: 322–330.

Angradi, T.R., and Griffith, J.S. 1990. Diel feeding chronology and diet selection of rainbow trout (*Oncorhynchus mykiss*) in the Henry's Fork of the Snake River, Idaho. Can. J. Fish. Aquat. Sci. **47**: 199–209.

Bachman, R.A. 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. Trans. Am. Fish. Soc. **113**: 1–32.

Bailey, R.G. 1966. Observations on the nature and importance of organic drift in a Devon river. Hydrobiologia, **27**: 353–367.

Ball, G.H., and Hall, D.J. 1967. A clustering technique for summarizing multivariate data. Behav. Sci. **12**: 153–155.

Baumann, R.W., Gaufin, A.R., and Surdick, R.F. 1977. The stoneflies (Plecoptera) of the Rocky Mountains. Mem. Am. Entomol. Soc. **31**: 1–208.

Bozek, M.A., DeBrey, L.D., and Lockwood, J.A. 1994. Diet overlap among size classes of Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*) in a high-elevation mountain stream. Hydrobiologia, **273**: 9–17.

Campbell, R.N.B. 1985. Comparison of the drift of live and dead *Baetis* nymphs in a weakening water current. Hydrobiologia, **126**: 229–236.

Chance, M.M. 1970. The functional morphology of the mouthparts of black fly larvae (Diptera: Simuliidae). Quaest. Entomol. **6**: 245–284.

Ciborowski, J.J.H. 1983. Influence of current velocity, density, and detritus on drift of two mayfly species (Ephemeroptera). Can. J. Zool. **61**: 119–125.

Ciborowski, J.J.H. 1987. Dynamics of drift and microdistribution of two mayfly populations: a predictive model. Can. J. Fish. Aquat. Sci. **44**: 832–845.

Ciborowski, J.J.H., and Corkum, L.D. 1980. Importance of behaviour to the re-establishment of drifting Ephemeroptera. *In* Advances in ephemeroteran biology. *Edited by* J.F. Flanagan and K.E. Marshall. Plenum Press, New York. pp. 321–330.

Claassen, P.W. 1931. Plecoptera nymphs of America (north of Mexico). Thomas Say Found. Ent. Soc. Am. **3**: 1–199.

Clapp, D.F., Clark, R.D. Jr., and Diana, J.S. 1990. Range, activity, and habitat of large, free-ranging brown trout in a Michigan stream. Trans. Am. Fish. Soc. **119**: 1022–1034.

Corkum, L.D. 1978. The influence of density and behavioural type on the active entry of two mayfly species (Ephemeroptera) into the water column. Can. J. Zool. **56**: 1201–1206.

Corkum, L.D., and Clifford, H.F. 1980. The importance of species associations and substrate types to behavioural drift. *In* Advances in ephemeroteran biology. *Edited by* J.F. Flanagan and K.E. Marshall. Plenum Press, New York. pp. 331–341.

Corkum, L.D., and Pointing, P.J. 1979. Nymphal development of *Baetis vagans* McDunnough (Ephemeroptera: Baetidae) and drift habits of large nymphs. Can. J. Zool. **57**: 2348–2354.

Corrarino, C.A., and Brusven, M.A. 1983. The effects of reduced stream discharge on insect drift and stranding of near shore insects. Freshwater Invertebr. Biol. **2**: 88–98.

Culp, J.M., Glozier, N.E., and Scrimgeour, G.J. 1991. Reduction of predation risk under the cover of darkness: avoidance responses of mayfly larvae to a benthic fish. Oecologia, **86**: 163–169.

Cummins, K.W. 1973. Trophic relations of aquatic insects. Annu. Rev. Entomol. **18**: 183–206.

DeWalt, R.E., and Stewart, K.W. 1995. Life histories of stoneflies (Plecoptera) in the Rio Conejos of southern Colorado. Great Basin Nat. **55**: 1–18.

DeWalt, R.E., Stewart, K.W., Moulton, S.R. II, and Kennedy, J.H. 1994. Summer emergence of mayflies, stoneflies, and caddisflies from a Colorado mountain stream. Southwest. Nat. **39**: 249–256.

Dill, L.M. 1987. Animal decision making and its ecologcal consequences: the future of aquatic ecology and behaviour. Can. J. Zool. **65**: 803–811.

Disney, R.H.L. 1972. Observations on sampling pre-imaginal populations of blackflies (Dipt., Simuliidae) in West Cameroon. Bull. Entomol. Res. **61**: 485–503.

Douglas, P.L., Forrester, G.E., and Cooper, S.D. 1994. Effects of trout on diel periodicity of drifting in baetid mayflies. Oecologia, **98**: 48–56.

Dudley, T.L., D'Antonio, C.M., and Cooper, S.D. 1990. Mechanisms and consequences of interspecific competition between two stream insects. J. Anim. Ecol. **59**: 849–866.

Edington, J.M. 1965. The effect of water flow on populations of net-spinning Trichoptera. Mitt. Int. Ver. Theor. Angew. Limnol. **13**: 40–48.

Edmunds, G.F., Jensen, S.L., and Berner, L. 1976. The mayflies of North and Central America. University of Minnesota Press, Minneapolis, Minn.

Elliott, J.M. 1971. The distances travelled by drifting invertebrates in a Lake District stream. Oecologia, **6**: 191–220.

Flecker, A.S. 1992. Fish predation and the evolution of invertebrate drift periodicity: evidence from neotropical streams. Ecology, **73**: 438–448.

Forrester, G. 1994. Influences of predatory fish on the drift dispersal and local density of stream insects. Ecology, **75**: 1208–1218.

Fuller, R.L., and DeStaffan, P.A. 1988. A laboratory study of the vulnerability of prey to predation by three aquatic insects. Can. J. Zool. **66**: 875–878.

Gauch, H.G. Jr. 1982. Multivariate analysis in community ecology. Cambridge University Press, Cambridge, Mass.

Gersabeck, E.F. Jr., and Merritt, R.W. 1979. The effect of physical factors on the colonization and relocation behavior of immature black flies (Dipteria: Simuliidae). Environ. Entomol. **8**: 34–39.

Ginetz, R.M., and Larkin, P.A. 1976. Factors affecting rainbow trout

(*Salmo gairdneri*) predation of migrant fry of sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. **33**: 19–24.

Glass, L.W., and Bovbjerg, R.V. 1969. Density and dispersion of laboratory populations of caddisfly larvae (Cheumatopsyche, Hydropsychidae). Ecology, **50**: 1082–1084.

Gowan, C. 1995. Trout responses to habitat manipulation in streams at individual and population scales. Doctoral dissertation, Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, Co.

Grant, J.W.A., and Noakes, D.L.G. 1987. Movers and stayers: foraging tactics of young-of-the-year brook char, *Salvelinus fontinalis*. J. Anim. Ecol. **56**: 1001–1013.

Griffith, J.S. Jr. 1974. Utilization of invertebrate drift by brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Salmo clarki*) in a small stream in Idaho. Trans. Am. Fish. Soc. **103**: 440–447.

Growns, I.O., and Davis, J.A. 1994. Longitudinal changes in near-bed flows and macroinvertebrate communities in a Western Australian stream. J. N. Am. Benthol. Soc. **13**: 417–438.

Hansen, R.A., Hart, D.D., and Merz, R.A. 1991. Flow mediates predator–prey interactions between triclad flatworms and larval black flies. Oikos, **61**: 187–196.

Harding J., and Colbo, M.H. 1981. Competition for attachment sites between larvae of Simuliidae (Diptera). Can. Entomol. **113**: 761–763.

Harper, P.P. 1973. Life histories of Nemouridae and Leuctridae in southern Ontario (Plecoptera). Hydrobiologia, **41**: 309–356.

Harper, P.P., and Hynes, H.B.N. 1972. Life-histories of Capniidae and Taeniopterygidae (Plecoptera) in southern Ontario. Arch. Hydrobiol. Suppl. **40**: 274–314.

Harper, P.P., Lauzon, M., and Harper, F. 1991. Life cycles of sundry stoneflies (Plecoptera) from Quebec. Rev. Entomol. Qué. **36**: 28–42.

Hart, D.D. 1986. The adaptive significance of territoriality in filter-feeding larval black flies (Diptera: Simuliidae). Oikos, **46**: 88–92.

Hart, D.D. 1987. Processes and patterns of competition in larval black flies. *In* Black flies: ecology, population management and annotated world list. *Edited by* K.C. Kim and R.W. Merritt. Pennsylvania State University, University Park and London. pp. 109–128.

Hawkins, C.P., and MacMahon, J.A. 1989. Guilds: the multiple meanings of a concept. Annu. Rev. Entomol. **34**: 423–451.

Hemphill, N. 1988. Competition between two stream dwelling filter-feeders, *Hydropspyche oslari* and *Simulium virgatum*. Oecologia, **77**: 73–80.

Hemphill, N., and Cooper, S.D. 1983. The effect of physical disturbance on the relative abundances of two filter-feeding insects in a small stream. Oecologia, **58**: 378–382.

Hildrew, A.G., and Townsend, C.R. 1980. Aggregation, interference and foraging by larvae of *Plectrocnema conspersa* (Trichoptera: Polycentropidae). Anim. Behav. **28**: 553–560.

Holt, C.S., and Waters, T.F. 1967. Effect of light intensity on the drift of stream invertebrates. Ecology, **48**: 225–234.

Hubert, W.A., and Rhodes, H.A. 1992. Sizes of prey consumed by age-0 brown trout in Douglas Creek, Wyoming. J. Freshwater Ecol. **7**: 277–282.

Hyatt, K.D. 1979. Feeding strategy. *In* Fish physiology. *Edited by* W.S. Hoar, D.G. Randall, and J.R. Brett. Academic Press, New York. pp. 71–119.

Hynes, H.B.N. 1970. The ecology of running waters. Liverpool University Press, Liverpool, U.K.

Jenkins, T.M. 1969. Night feeding of brown and rainbow trout in an experimental stream channel. J. Fish. Res. Board Can. **26**: 3275–3278.

Jensen, S.L. 1966. The mayflies of Idaho. M.S. thesis, University of Utah, Salt Lake City, Utah.

Karr, J.R., Fausch, K.D., Angermeier, P.L., Yant, P.R., and Schlosser, I.J. 1986. Assessing biological integrity in running waters. Ill. Nat. Hist. Surv. Spec. Publ. No. 5.

Keddy, P.A. 1994. Applications of the Hertzsprung–Russell star chart to ecology: reflections on the 21st birthday of *Geographical Ecology*. Trends Ecol. Evol. **9**: 231–234.

Kohler, S.L. 1985. Identification of stream drift mechanisms: an experimental and observational approach. Ecology, **66**: 1749–1761.

Kohler, S.L., and McPeek, M.A. 1989. Predation risk and the foraging behavior of competing stream insects. Ecology, **70**: 1811–1825.

Lancaster, J. 1990. Predation and drift of lotic macroinvertebrates during colonization. Oecologia, **85**: 48–56.

Lawton, J.H. 1994. What do species do in ecosystems? Oikos, **71**: 367–374.

Mackay, R.J. 1969. Aquatic insect communities of a small stream on Mont St. Hilaire, Quebec. J. Fish. Res. Board Can. **26**: 1157–1183.

Madsen, B.L. 1969. Reactions of *Brachyptera risi* (Morton) nymphs to water current. Oikos, **20**: 95–100.

Malmqvist, B. 1986. Drift of mayflies in response to disturbance by predacious stonefly nymphs. *In* Proceeding of the 3rd European Congress of Entomology. Nederlandse Entomologishe Vereiniging, Amsterdam, The Netherlands. pp. 107–110.

Malmqvist, B., and Sjöström, P. 1987. Stream drift as a consequence of disturbance by invertebrate predators. Oecologia, **74**: 396–403.

Margalef, R. 1968. Perspectives in ecological theory. University of Chicago Press, Chicago, Ill.

McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R., and Wood, D.M. 1981. Manual of nearctic Diptera. Vol. 1. Agric. Can. Res. Branch Monogr. No. 27.

McCafferty, W.P. 1981. Aquatic entomology: the fishermen's and ecologists' illustrated guide to insects and their relatives. Science Books International, Boston, Mass.

McCormack, J.C. 1962. The food of young trout (*Salmo trutta*) in two different becks. J. Anim. Ecol. **31**: 305–316.

McIntosh, A.R., and Peckarsky, B.L. 1996. Differential behavioural response of mayflies from streams with and without fish to trout odour. Freshwater Biol. **35**: 141–148.

McIntosh, A.R., and Townsend, C.R. 1994. Interpopulation variation in mayfly antipredator tactics: differential effects of contrasting predatory fish. Ecology, **75**: 2078–2090.

McLay, C.L. 1970. A theory concerning the distance travelled by animals entering the drift of a stream. J. Fish. Res. Board Can. **27**: 359–370.

Merritt, R.W., and Cummins, K.W. 1995. An introduction to the aquatic insects of North America. 3rd ed. Kendall and Hunt, Dubuque, Iowa.

Michael, D.I., and Culver, D.A. 1987. Influence of plecopteran and meglaopteran predators on *Hydropsyche* (Trichoptera: Hydropsychidae) microdistribution and behavior. J. N. Am. Benthol. Soc. **6**: 46–55.

Minshall, G.W., and Winger, P.V. 1968. The effect of reduction in stream flow on invertebrate drift. Ecology, **49**: 580–582.

Molles, M. Jr., and Pietruszka, R.D. 1983. Mechanisms of prey selection by predaceous stoneflies: roles of prey morphology, behavior and predator hunger. Oecologia, **57**: 25–31.

Nakano, S., and Furukawa-Tanaka, T. 1994. Intra- and interspecific dominance hierarchies and variation in foraging tactics of two species of stream-dwelling chars. Ecol. Res. **9**: 9–20.

Nakano, S., Fausch, K.D., Furukawa-Tanaka, T., Maekawa, K., and Kawanabe, H. 1992. Resource ultilization by bull char and cutthroat trout in a mountain stream in Montana, U.S.A. Jpn. J. Ichthyol. **39**: 211–217.

Needham, J.G., Traver, J.R., and Hsu, Y. 1935. The biology of mayflies. Comstock Publishing Co., Ithaca, N.Y.

Newman, R.M. 1987. Comparison of encounter model predictions with observed size-selectivity by stream trout. J. N. Am. Benthol. Soc. **6**: 56–64.

Nowell, A.R.M., and Jumars, P.A. 1984. Flow environments of aquatic benthos. Annu. Rev. Ecol. Syst. **15**: 303–328.

Ode, P.R., and Wissinger, S.A. 1993. Interaction between chemical and tactile cues in mayfly detection of stoneflies. Freshwater Biol. **30**: 351–357.

O'Muircheartaigh, C.A., and Payne, C. 1977. The analysis of survey data. Vol. I. Exploring data structures. John Wiley & Sons, Inc., New York.

Otto, C. 1976. Factors affecting the drift of *Potamophylax cingulatus* (Trichoptera) larva. Oikos, **27**: 93–100.

Otto, C., and Sjöström, P. 1986. Behavior of drifting insect larvae. Hydrobiologia, **131**: 77–86.

Peckarsky, B.L. 1980. Predator–prey interactions between stoneflies and mayflies: behavioral observations. Ecology, **61**: 932–943.

Peckarsky, B.L., and Penton, M.A. 1989. Mechanisms of prey selection by stream-dwelling stoneflies. Ecology, **70**: 1203–1218.

Poff, N.L., and Allan, J.D. 1995. Functional organization of stream fish assemblages in relation to hydrological variability. Ecology, **76**: 606–627.

Poff, N.L., and Ward, J.V. 1991. Drift responses of benthic invertebrates to experimental streamflow variation in a hydrologically stable stream. Can. J. Fish. Aquat. Sci. **48**: 1926–1936.

Power, M.E., Parker, M.S., and Wootton, J.T. 1996. Disturbance and food chain length in rivers. *In* Food webs: integration of patterns and dynamics. *Edited by* G.A. Polis and K.O. Winemiller. Chapman and Hall, Inc. New York. pp. 286–297.

Rader, R.B., and McArthur, J.V. 1995. The effects of refugia on the drift and habitat selection of predaceous stoneflies in a sandy-bottomed stream. Oecologia, **103**: 1–9.

Rader, R.B., and Ward, J.V. 1990. Diel migration and microhabitat distribution of a benthic stream assemblage. Can. J. Fish. Aquat. Sci. **47**: 711–718.

Reidelbach, J., and Kiel, E. 1990. Observations on the behavioural sequences of looping and drifting by blackfly larvae (Dipteria: Simuliidae). Aquat. Insects, **12**: 49–60.

Resh, V.H., Hildrew, A.G., Statzner, B., and Townsend, C.R. 1994. Theoretical habitat templets, species traits, and species richness: a synthesis of long-term ecological research on the Upper Rhône River in the context of concurrently developed ecological theory. Freshwater Biol. **31**: 539–554.

Ricker, W.E. 1946. Production and utilization of fish populations. Ecol. Monogr. **16**: 373–391.

Ringler, N.H. 1979. Prey selection by drift-feeding brown trout (*Salmo trutta*). J. Fish. Res. Board Can. **36**: 392–403.

Rosenberg, D.M., and Resh, V.H. 1993. Freshwater biomonitoring and benthic macroinvertebrates. Chapman and Hall, Inc., New York.

Ross, H.H. 1944. Caddisflies or Trichoptera of Illinois. Ill. Nat. Hist. Surv. Bull. No. 23.

Scrimgeour, G.J., and Culp, J.M. 1994. Foraging and evading predators: the effect of predator species on a behavioural trade-off by a lotic mayfly. Oikos, **69**: 71–79.

Scrimgeour, G.J., Culp, J.M., and Cash, K.J. 1994. Anti-predator responses of mayfly larvae to conspecific and predator stimuli. J. N. Am. Benthol. Soc. **13**: 299–309.

Shiozawa, D.K. 1986. The seasonal community structure and drift of microcrustaceans in Valley Creek, Minnesota. Can. J. Zool. **64**: 1655–1654.

Skinner, W.D. 1985. The importance of behavioral, morphological and size aspects to the capture and ingestion of invertebrates by drift feeding trout. M.S. thesis, Idaho State University, Pocatello, Idaho.

Soluk, D.A., and Collins, N.C. 1988. Balancing risks? Responses and non-responses of mayfly larvae to fish and stonefly predators. Oecologia, **77**: 370–374.

Southwood, T.R.E. 1988. Tactics, strategies and templets. Oikos, **52**: 3–18.

Statzner, B., and Mogel, R. 1985. An example showing that drift net catches of stream mayflies (*Baetis* spp., Ephemeroptera, Insecta) do not increase during periods of higher substrate surface densities of the larvae. Verh. Int. Ver. Limnol. **22**: 3238–3243.

Stewart, K.W., and Stark, B.P. 1984. Nymphs of North American Perlodinae genera (Plecoptera: Perlodidae). Great Basin Nat. **44**: 373–415.

Stewart, K.W., and Stark, B.P. 1988. Nymphs of North American stonefly genera (Plecoptera). Thomas Say Found. Monogr. No. 12.

Stewart, K.W., and Szczytko, S.W. 1983. Drift of Ephemeroptera and Plecoptera in two Colorado rivers. Freshwater Invertebr. Biol. **2**: 117–131.

Swisher, D., and Richards, C. 1991. Emergers. Lyons and Burford, New York.

Tippets, W.E., and Moyle, P.B. 1978. Epibenthic feeding by rainbow trout (*Salmo gairdneri*) in the McCloud River, California. J. Anim. Ecol. **47**: 549–559.

Tonnoir, A.L. 1925. Australasian Simuliidae. Bull. Entomol. Res. **15**: 213–255.

Townsend, C.R., and Hildrew, A.G. 1994. Species traits in relation to a habitat templet for river systems. Freshwater Biol. **31**: 265–275.

Tusa, I. 1968. On the feeding biology of the brown trout (*Salmo trutta*) in the Loucka Creek. Zool. Listy, **17**: 379–395.

Vogel, S. 1994. Life in moving fluids. 2nd ed. Princeton University Press, Princeton, N. J.

Walde, S.J., and Davies, R.W. 1984. The effect of intraspecific interference on *Kogotus nonus* (Plecoptera) foraging behaviour. Can. J. Zool. **62**: 2221–2226.

Walton, O.E. 1980. Active entry of stream benthic macroinvertebrates into the water column. Hydrobiologia, **74**: 129–139.

Walton, O.E., Reice, S.R., and Andrews, R.W. 1977. The effects of density, sediment particle size and velocity on drift of *Acroneuria abnormis* (Plecotera). Oikos, **28**: 291–298.

Wankowski, J.W.J., and Thorpe, J.E. 1979. The role of food particle size in the growth of juvenile Atlantic salmon (*Salmo salar* L.). J. Fish Biol. **14**: 351–370.

Ward, J.V. 1992. Aquatic insect ecology. 1. Biology and habitat. John Wiley & Sons, Inc., New York.

Ward, J.V., and Kondratieff, B.C. 1992. An illustrated guide to the mountain stream insects of Colorado. University of Colorado Press, Niwot, Co.

Waters, T.F. 1962. A method to estimate the production rate of a stream bottom invertebrate. Trans. Am. Fish. Soc. **91**: 243–250.

Waters, T.F. 1965. Interpretation of invertebrate drift in streams. Ecology, **46**: 327–334.

Waters, T.F. 1968. Diurnal periodicity in the drift of a day-active stream invertebrate. Ecology, **49**: 152–153.

Waters, T.F. 1972. The drift of stream insects. Annu. Rev. Entomol. **17**: 253–272.

Waters, T.F. 1988. Fish production – benthos production relationships in trout streams. Pol. Arch. Hydrobiol. **35**: 545–561.

White, D.S. 1993. Perspectives on defining and delineating hyporheic zones. J. N. Am. Benthol. Soc. **12**: 61–69.

Wiggins, G.B. 1973. A contribution to the biology of caddisflies (Trichoptera) in temporary pools. Life Sci. Contrib. Ont. Mus. No. 88.

Wiggins, G.B. 1996. Larvae of the North American caddisfly genera (Trichoptera). 2nd ed. University of Toronto Press, Toronto, Ont.

Wiley, M.J., and Kohler, S.L. 1980. Positioning changes of mayfly nymphs due to behavioural regulation of oxygen consumption. Can. J. Zool. **58**: 618–622.

Wiley, M.J., and Kohler, S.L. 1981. An assessment of biological interactions in an epilithic stream community using time-lapse cinematography. Hydrobiologia, **78**: 183–188.

Williams, D.D. 1987. A laboratory study of predator–prey interactions of stoneflies and mayflies. Freshwater Biol. **17**: 471–490.

Wilzbach, M.A., Cummins, K.W., and Hall, J.D. 1986. Influence of habitat manipulations on interactions between cutthroat trout and invertebrate drift. Ecology, **67**: 898–911.

Wilzbach, M.A., Cummins, K.W., and Knapp, R.A. 1988. Towards a functional classification of stream invertebrate drift. Verh. Int. Ver. Limnol. **23**: 1244–1254.

Wooster, D., and Sih, A. 1995. A review of the drift and activity responses of stream prey to predator presence. Oikos, **73**: 3–8.

Wooton, R.S., and Merritt, R.W. 1988. Experiments on predation and substratum choice by larvae of the muscid fly, *Limnophora riparia*. Holarct. Ecol. **11**: 151–159.

Young, M.K., Rader, R.B., and Belish, T.A. 1997. Influence of macroinvertebrate drift and light on the activity and movement of Colorado River cutthroat trout *Oncorhynchus clarki pleuriticus*. Trans. Am. Fish. Soc. **126**: 428–437.