Review of Macroinvertebrate Drift in Lotic Ecosystems

By

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Table of Contents

Abstract

1 Stream ecologists have incorporated the landscape perspective for several decades when conducting ecological work in streams. Although macroinvertebrate drift has been studied for more than five decades in lotic systems, it has not sufficiently been incorporated into the modern stream ecology or ecotone ecology and instituted on a landscape level of investigation. An early review of drift of stream insects emphasized that there is not a distinct drift fauna. Rather it is the benthic community that participates in the drift due to many biotic and abiotic factors. Furthermore, spatial and temporal scales of drift vary considerably between stream systems and seasons (Table 1). Other reviews of the literature have been conducted typically with some limitation in time covered or subjects, concentrating on the underlying mechanisms behind drift. In several reviews on the effects of flow on benthic organisms drift was viewed purely as a mechanism of dispersal. Interestingly, they stated that little is known about the biological processes involved in water column entry (besides accidental drift), instream transport, and settlement. In particular, what are the key principles behind settlement of drifting individuals.

In the past half century, most studies on stream drift have concentrated on the underlying biotic and abiotic processes (Fig. 1) involved in drift. It has even been suggested that drift be used as a standard component of bioassessment because it provides complimentary information to traditional benthic sampling. One of the most studied properties of drift is its diel periodicity. Investigations in tropical, subtropical, and temperate regions have shown that drift displays distinct circadian patterns.

2 Several studies have used drift to improve the understanding of life histories of Trichoptera communities in a wide range of biomes to include streams from Oregon, Denmark, Pyrénées, and Laurentia. One study from Scotland used drift as a metric for evaluating colonization

patterns of mayfly nymphs. Also, a study conducted in Minnesota investigated drift in relation

to the biology of selected species within Megaloptera, Ephemeroptera, and Diptera. Several

studies in recent decades have examined the relationship between macroinvertebrate drift and

salmon/trout ecology in temperate and alpine streams.

    3 There is limited information on how landscape disturbances within sub-basin or watersheds

at various temporal and spatial scales influence stream drift. In addition, land use effects on the

terrestrial component of drift have been studied very little. Also, quantifying drift subsidy from

non-fish bearing to fish bearing sections of montane streams has to our knowledge only been

examined once in Southeast Alaska. Generally speaking, drift has rarely been incorporated into

ecological interactions and ecosystem processes in fluvial systems and their adjacent riparian

areas. Especially overlooked is the link between upland ecosystems with habitats downstream in

the catchment area.

    Several studies have explored the importance of downstream export of coarse and fine

particulate organic matter and how it is processed by macroinvertebrates. However, these

studies have generally ignored the downstream export of the macroinvertebrates themselves,

although several studies suggest that more organisms drift over a unit of stream bottom than are

actually present within the benthic community of that area.

    4 The literature in the past four decades has clearly demonstrated that abiotic factors

influence drift. These factors can result in either active drift, which is initiated by the

macroinvertebrate or in passive drift, which is a result of a change in the physical conditions of

the stream. The overall importance of abiotic factors compared to biotic factors depends on the

relative strength of the two groups (Fig. 1). In some cases biotic factors override the abiotic such

as stream discharge, and in other cases abiotic factors such as sediment or spates override the biotic ones.

5 Early on it was recognized that physical disturbances of the bottom substrate, sedimentation, anchor ice, or pollution (Fig. 1) would lead to catastrophic drift. This distinguished this type of drift from behavioral drift. A field manipulation study showed that abiotic factors such as a spate could override the influence of biotic factors such as predation.

Daily activity patterns in insect larvae and instars in streams hold particular interest because of the importance as food for predators. For Trichoptera, it was demonstrated that there was a consistently higher drift rate at night compared to day. In general, it has been concluded that most insect species are nocturnal as well as Gammarus and leeches. The diurnal pattern may have evolved as a predator avoidance with field observations supporting the claim. However, a few species, mostly species of caddisfly larvae, are diurnal with peak activities during the day.

Seasonal differences in drift rates have been observed in all studies conducted over several months. In general, there seems to be agreement between peak drift rates and peaks in the productivity of the ecosystem under study.

6 Different sizes and life cycle stages have been found to drift at greater rates than would be expected when compared to the benthic community. The age classes most likely to drift appear to vary with species and ecosystem under investigation. Furthermore, most field studies are not able to isolate specific biotic factors, but rather measure the cumulative effects of all factors present at a given time. This is likely the reason behind the many seemingly conflicting results.

A literature review of 22 studies revealed that the presence of predatory invertebrates caused an increase in drift in the presence of a predator. The presence of vertebrates had variable effects, but prey decreased their activity. Similarly, a meta-analysis based on existing data sets

from the literature, looked at the impact on stream benthic prey by drift feeding versus benthic

feeding fish predators and concluded that they would have different ecological impacts on drift.

However, studies manipulating these two factors are needed to assess the exact impacts on drift.

From a study on Oregonian Trichoptera it was concluded that drift catches were a result of a

permanent downstream displacement and not due to random activity in the immediate vicinity of

the nets. Others have also concluded that drift is an important ecological factor in recolonization

of large sections of river after catastrophic disturbances such as floods. Information on inter- and

intraspecific competition is very limited. Furthermore, there are conflicting results on the

influence and magnitude of competition for food and space play in drift.

   Macroinvertebrate drift in lotic ecosystems can be assessed on several ecological scales in

time and space. Of the two, time has received the most attention ranging from daily to seasonal

variations. Typically, drift has been assessed on a limited spatial scale such as one river (Table

1). Only one study has determined drift on a landscape level using 52 streams. Drift studies

have primarily focused on information found within a single low-order stream, but often data on

stream order is not even provided (Table 1).

   7 In general, strong seasonal differences in drift rates have been reported by most studies,

with spring to autumn being the most common period under investigation. Rates vary 4 - 10 fold

between season lows and highs (Table 1). Unfortunately, it is not possible to conduct

meaningful comparisons of drift rates between studies due to lack of detail provided on total

discharge patterns and how drift rates are actually quantified and reported (Table 1).

   8 Early on, it was proposed that drift is part of a colonization cycle involving two

unidirectional movements upstream and downstream. At the headwaters, competition for

resources result in active drift downstream causing a depletion of the headwater population.

Upstream movements of adults or imago should close the cycle. There have been several

studies, which have confirmed that insects in fact do move upstream. Of particular interest is a

mark-recapture study of imago showing unidirectional flight upstream to the headwaters.

Moreover, isotope labeled adults of Baetis were found to fly 1.6-1.9 km upstream from where

they emerged. Furthermore, computer modeling has suggested that upstream-biased dispersal

would increase individual fitness, which always drove random dispersers to extinction. It was

argued that the density dependent model solved the stream drift paradox.

   Alternatively, some authors have proposed that drift is a result of a population reaching

carrying capacity, and that drift is a surplus that does not lead to depopulated headwaters. By

quantifying upstream/downstream movements of macroinvertebrates in a Welsh stream it was

found that a net loss due to drift occurred in eight species, however, none of the insects showed a

strong overall upstream flight preference. Similarly, other studies did not find unidirectional

flight of adults, rather random movements. These observations suggest that there would be no

need for a cyclical repopulation mechanism if only a small portion of benthos occur in the drift.

In addition, a computer simulation showed that drift does not need to be deterministic, and

random movements can account for persistence of the headwater population despite drift.

   9 Several studies have quantified CPOM export (Table 2) from stream reaches, but only two

studies included macroinvertebrate drift and CPOM/detritus in the same study to assess the total

downstream transport. This is especially important since the food quality of drifting

macroinvertebrates is much greater than CPOM or detritus and may be an essential food subsidy

to downstream collectors. Despite this early recognition that macroinvertebrate drift is an

important part of downstream export only two studies have included both.

The monthly ratios between macroinvertebrate drift and CPOM (calculated in g day^{-1}) in an Appalachian headwater stream ranged from 0.007 - 0.883 (median 0.043). Daily macroinvertebrate drift ranged from 0.061 – 1.911 g day^{-1} while CPOM ranged from 0.223 – 33.132 g day^{-1}. Within the Southeast Alaska maritime temperate coniferous forest biome it was determined that average export from 52 headwater streams ranged from 50 – 240 mg m^{-3} for aquatic and terrestrial insects combined and 10 – 390 mg m^{-3} for detritus.

10 Drift net design is usually a compromise between filtration efficiency, clogging, and later sorting time using 500 μm mesh size. To avoid clogging in most situations mesh size has been reported to be around 440 μm. Often modifications to a basic square net frame are made to meet sampling challenges under differing field conditions ranging from large rivers to steep headwater streams.

11 From habitats most frequently examined such as temperate regions (Table 1) insect taxa such as Ephemeroptera, Simuliidae, Plecoptera, and Trichoptera dominate the drift composition. However, Megaloptera, Diptera, Crustacea, and Coleoptera may also contribute significantly to drift rates.

12 The greatest need for future research involving macroinvertebrate drift appear to be a need for data concerning landscape level investigations. Total drift measured across landscapes will provide a cumulative measure of all the factors involved (Fig.1), but drift can also be measured in response to landscape changes as a result of human activities, which typically alter many of the abiotic as well as the biotic factors simultaneously. Particularly, drift export from fishless headwater streams into fish-bearing streams need to be investigated in greater detail to examine the significance of macroinvertebrate drift subsidies for fish downstream. In mountainous regions, headwater streams drain the greatest amount of surface area and due to the steepness of

the terrain they are usually fishless or they have very low densities effecting minimal influence on the downstream export of drift. Additionally, other stream dwelling vertebrates such as the harlequin duck *Histriónicus histriónicus* and the dippers *Cínclus sp.* would benefit from a downstream export of macroinvertebrates. Stream drift needs to be evaluated in the context of other ecological processes on the sub-basin or watershed level including their riparian areas. Furthermore, assessment of how management activities in sub-basins may influence stream drift on various spatial and temporal scales.

1 Introduction

The importance of the natural disturbance regime and human impacts within a watershed has long been recognized as paramount to understand the water quality and the biotic makeup of a stream system and stream ecologists have incorporated the landscape perspective for several decades when conducting ecological work in streams (Whitton 1975, MacDonald et al 1991, Naiman et al. 1992, Maybeck et al. 1996, Karr & Chu 1999).

Responses by macroinvertebrates to watershed impacts have been studied extensively and are commonly used as a measure of the intensity of watershed pollution (Maybeck et al. 1996), disturbances (MacDonald et al. 1991), and to evaluating the ecological integrity of stream systems (Karr & Chu 1999). However, none of the authors address the impacts on macroinvertebrate drift, which is critical in downstream recolonization after major disturbances (Minshall & Petersen 1985, Pinay et al. 1990, Hershey & Lamberti 1998) and downstream export of nutrients (Polis et al. 1997, Wipfli & Gregovich 2002).

Allan and Johnson (1997) suggest that the focus of investigation of aquatic systems should be on the landscape level. In the past decades several parameters of stream systems have been investigated at the landscape level such as aquatic-terrestrial ecotones (Naiman & Décamps 1990, Edmunds & Huryn 1996, Naiman et al. 1998), salmonids (Bisson et al. 1992, Willson & Halupka 1995, Wipfli et al. 1998, Cederholm et al. 2000, Montgomery 2003), and large woody debris (Maser & Sedell 1994, Bilby & Bisson 1998) and sediment delivery (Benda et al. 1998). Longitudinal movement of biological materials and their processing by macroinvertebrates in lotic systems have received great attention in Western rivers since the 1980's (Vannote et al. 1990, Polis et al 1997). There is a general consensus that mid-order stream food webs are subsidized by downstream exports from headwater streams (Vannote et al. 1990, Naiman et al.

1992, Minshall et al. 1992, Allen & Johnson 1997). In addition, the upstream movement of nutrients by returning salmon *Onchorynchus sp.* has been shown to be critical for the entire food web support of the otherwise Western oligotrophic rivers draining into the Pacific Ocean (Li et al. 1987, Cederholm et al. 2000).

However, the downstream export of macroinvertebrate drift has received little attention and has not been incorporated into the landscape or watershed level of investigation. The often fishless steep headwater streams of mountainous regions may provide large quantities of nutrient rich exports to downstream fish bearing streams from macroinvertebrate drift. Quantitatively drift may be less than CPOM, but qualitatively it is a superior food source with high protein content (Young & Huryn 1997).

An early review of drift of stream insects (Waters1972) emphasized that there is no distinct drift fauna but rather it is the benthic community that participates in drift due to many complex biotic and abiotic factors. In addition, this review emphasized that drift is quite variable in space and time both within and among stream systems (Table 1). Other reviews have been limited in subject matter or to studies conducted within short time periods (Brittain & Eikeland 1988) (Mackay 1992, Dahl & Greenberg 1996, Palmer et al. 1996), but often concentrate on the underlying biological and ecological mechanisms that cause drift rather than the role that drift plays in the ecology of streams. In a review on the effects of flow on benthic organisms, Hart and Finelli (1999) viewed drift strictly as a mechanism of dispersal, a conclusion supported by Palmer et al. (1996) and Mackay (1992). Interestingly, Hart and Finelli (1999) stated that little is known about the biological processes leading to organisms entering the water column (besides accidental drift), instream transport and settlement back onto the substrate. In particular, they point out that there is little theory related to the settlement of drifting individuals.

Most drift studies have focused on the underlying biotic and abiotic factors regulating stream drift (mini review by Brittain & Eikeland, 1988). One of the most studied properties of drift is its diel periodicity. Investigations in both tropical (Statzner et al. 1984; Benson & Pearson 1987; Ramirez & Pringle 1988; Flecker 1990, 1992; Pringle & Ramirez 1998) and temperate (Brittain & Eikeland, 1988) regions have shown that drift displays distinct circadian patterns.

Several studies have focused on improving the understanding of life histories of Trichoptera communities (can there be a life history of a community?) in a wide range of biomes including Oregon (Anderson 1967), the Pyrénées (Lavandier & Cereghnio 1995), Denmark (Iversen 1980) and in Laurentia (Lauzon & Harper 1988). One study from Scotland used drift as a metric for evaluating colonization patterns of mayfly nymphs (Giller & Cambell 1989). A study conducted in Minnesota investigated drift in relation to the biology of selected species within Megaloptera, Ephemeroptera, and Diptera (Krueger & Cook 1984). Several studies in recent decades have examined the relationship between macroinvertebrate drift and salmon/trout species (Shubina & Martynov 1990, Young et al. 1997, Hetrick et al. 1998, Miyasaka & Nakano 2001). Wilzbach et al (1986) examined prey capture efficiency and growth of cutthroat trout in relation to drift in logged versus unlogged riparian zones. Hubert and Rhodes (1989) looked at drift in relation to food selection by brook *Salvelinus fontinalis* trout similar to Allan (1981) who also measured stream drift as part of a diet study by brook trout. LaVoie and Hubert (1994) determined the use of drift of brown trout. Quantifying drift as food subsidies from non-fish bearing to fish bearing montane streams has, to our knowledge, been examined only once in a study of Southeast Alaska streams (Wipfli & Gregovich 2002).

There is limited information on how disturbances within sub-basin or watersheds at various temporal and spatial scales influence stream drift. In addition, the relationship between upland

land use and drift has received little study (Edwards & Huryn 1996). Generally speaking, drift

has rarely been examined in the context of ecological interactions or ecosystem processes in

fluvial systems and adjacent riparian areas. In particular, the link between upland ecosystems

with downstream habitat for fish has received little attention (Badri et al. 1987, Polis et al. 1997).

Several studies have explored the importance of downstream export of coarse and fine

particulate organic matter and how it is processed by macroinvertebrates (Vannote et al. 1980;

Wallace et al. 1986, 87; Cuffney & Wallace 1989). However, these studies have generally

ignored the downstream export of the macroinvertebrates themselves, despite the fact that more

organisms drift over a unit of stream bottom than are actually present in that area as benthic

community (Bishop & Hynes 1969, Townsend & Hildrew 1976, Benke et al. 1991, Forrester

1994*a*).

A great deal of discussion in the past four decades has sought to explain the lack of

depopulation of upstream reaches by drifting larvae and nymphs (Müller 1954, Waters 1972,

Anholt 1995, Speirs & Gurney 2001). Although few studies have addressed this issue a Danish

study clearly demonstrated that a Plecoptera species drift down stream as nymphs and repopulate

the upper reaches by flying upstream (Madsen 1976, Madsen & Butz 1976).

Unfortunately, it has not been possible to conduct a meta-analysis of published drift rates

because discharge rates, stream order, and land use information is inconsistent, vague, or

unavailable (Table 1).

2 Abiotic Factors

The literature in the past four decades has clearly demonstrated that abiotic factors influence

drift (Brittain & Eikeland 1988). These factors can result in either active drift, which is initiated

by the organism or in passive (or accidental) drift, which is a result of a change in the physical conditions of the stream (Brittain & Eikeland 1988). In addition, catastrophic drift may occur when physio-chemical changes take place from pollution. The overall importance of abiotic versus biotic factors in initiating drift depends on the type and strength of these cues (Fig. 1). In some cases biotic factors override the abiotic such as stream discharge (Lancaster 1992, Fonseca & Hart 1996), and in other cases abiotic factors such as sediment inputs (Walton 1978, O'Hop & Wallace 1983, Culp et al. 1986) or spates dominate the biotic ones (Badri et al. 1987).

Landscape level activities such as timber harvest and grazing within a watershed or sub-basin will determine the drift regimen of a stream, including drift quantity and quality, as a result of the cumulative effects of both the abiotic and biotic factors. The ecological implications of cumulative abiotic and biotic influences on drift in managed and unmanaged landscapes are relatively unknown.

2.1 Current Discharge

In general, most studies have found a positive correlation between discharge and stream drift (Fig. 1) (Elliot 1968, Brooker & Hemsworth 1978, Clifford 1978, Dance & Hynes 1979, O'Hop and Wallace 1983, Cuffney & Wallace 1989). In an apparent exception to this rule, drift density declined with increased discharge on three of four sampling dates during summer months in a northern Alaska stream which was attributed to low benthic densities during peak flows (Miller & Stout 1989). Different species and even different life history stages within species can vary greatly in their susceptibility to passive drift. Differences in susceptibility to changes in discharge, often result in different species composition of drift between spates and low flows (Dance and Hynes 1979).

In a study by Elliot (1968) in a Dartmoore stream in Great Britain, there was clearly a positive correlation between drift of Trichoptera and stream discharge. A study from British Columbia (Lancaster 1992) in a manipulated montane stream evaluated the effects of changes in discharge on drift of mayflies by creating spates simulating rainstorms. Lancaster's (1992) results demonstrated that an increase in discharge of three or four times greatly increased drift. However, the increase in drift rate was apparent only at sunset when the nymphs are more active and presumably more vulnerable to drift. However, the relative importance of passive and active modes of entry into drift could not be determined by the study. The study revealed no apparent effect of spates on the size distribution of nymphs in the drift compared to unmanipulated flows. Another study on Trichoptera drift in a Danish low-gradient woodland stream concluded that high water flows were the main cause of drift (Iversen 1980). Similarly, Flecker (1990, 1992) concluded that Andean streams with unpredictable spate events were responsible for a fourfold increase in drift. Drift in Appalachian streams increased exponentially with discharge (O'Hop & Wallace 1983). A comparative study of a natural versus experimental disturbance in a Swiss stream reported that natural flooding increased drift densities five fold (Matthaei et al. 1997). Similarly, the experimental spate increased drift dramatically (Matthaei et al. 1997). A study from southern England demonstrated that for some stonefly and Chironomidae species there were positive correlations between mean daily discharge and mobility of the insects in the stream measured through colonization rates (Winterbottom et al. 1997). In a two-year study from the middle Rhône River, there was a great increase in taxa richness downstream during spates, which was attributed to accidental (passive drift) drift (Cellot 1989*a*, 1996).

A tank experiment using two species with very different biology (*G. pulex and E. ignita*) simulated lowland streams with fine bottom sediment, demonstrated that drift is highly

influenced by the hydrological environment in the stream (Borchardt 1993). Benthic macroinvertebrates showed increased drift with increase in shear stress caused by increases in discharge. However, woody debris on the stream bottom provided refugia from exposure to hydrological stress. Drift rates are expected to be lower in streams with high complexity created from woody debris. This relationship could have major consequences for stream restoration and riparian zone management in general.

In contrast to spates, dramatic increases in accidental or passive drift (termed catastrophic drift, Fig. 1) as a result of reducing stream flow to half – simulating dam operations – were observed using experimental channels in Oregon (Corrarino & Brusven 1983). Interestingly, drift still peaked at night regardless of time of dewatering. Evidence of stranded insects in the dewatered zone was greatest in fall and least in spring. Similarly, Johansen (1990) showed greatest drift rates in a Norwegian river during a short drought period where dewatered areas appeared. Otherwise, Johansen (1990) found a positive relationship between drift rate and discharge.

2.2 Temperature

In general, stream temperature has not been shown to have a primary influence on stream drift. Rather, it has been inferred that increases in temperature increase insect activity, which may then increase the risk of accidental drift (Williams 1990, Winterbottom et al. 1997). Temperature was positively correlated with drift and a greater regulator of stream drift than discharge in an Ontario stream but this pattern was shown only during moderate flow (Williams 1990). Temperature effects on drift may be more difficult to detect across a range of flow conditions. Dudgeon (1990) found a significantly positive correlation between stream

temperature and number of drifting taxa in a tropical stream. However, there were no significant

relationships between drift densities (across all taxa) and prevailing temperatures or temperatures

on preceding sampling dates.

2.3 Disturbance

Early in the study of drift, it was recognized that physical disturbances of the stream substrate,

sedimentation, anchor ice, or pollution (Fig. 1) could lead to catastrophic drift (Waters 1972).

Lancaster (1990) showed that abiotic factors such as spates could override the influence of biotic

factors such as predation. Large-scale catastrophic drift due to spates was reported from a

Moroccan stream system in the Atlas Mountains (Badri et al. 1987). The upstream regions were

almost depleted of benthos from 4,360 individuals m^{-2} to 95 individuals m^{-2}, and from 26 to 9

taxa groups, while the receiving floodplain had a tremendous increase in numbers as well as

increases in species richness to 2,725 individuals m^{-2} and 25 taxa groups, which dropped to 630

individuals m^{-2} and 10 taxa groups 5 days later (Badri et al., 1987). Although there was a large

downstream movement of biomass during flood events, after one month the density of animals

and taxa returned to levels prior to the spate. Catastrophic flooding in an alpine river in

Switzerland produced a similar, dramatic increase in drift densities due to extensive substratum

movement in the whole channel (Matthaei et al. 1997). Correspondingly, spates in New Zealand

streams (McLay 1968) resulted in heavy disturbances of the benthic community followed by

severe displacement of the benthic community downstream. Similarly, spates and spring run-off

resulting in periods of high water in two Ontario streams showed a positive correlation between

discharge and drift (Dance & Hynes 1979). O'Hop and Wallace (1983) found a positive

relationship between macroinvertebrate drift and drifting detritus and inferred that detritus acted

as a disturbance agent. However, this increase may have been more related to increases in discharge than physical disturbance of the streambed by detritus.

Sediment inputs have been shown to have a direct effect on drift (Brooker & Hemsworth 1978, Walton 1978). In a field experiment using sand, Culp et al. (1986) demonstrated that macroinvertebrates in riffles responded differently to sediment transport as opposed to sediment deposition. Saltating sediment transport across a riffle resulted in catastrophic drift with an immediate increase in drift by some taxa in response to scouring by fine sediments and a delayed diurnal drift response from other certain taxa. This is probably due to the taxas different depth distribution within the benthic environment. There were no significant changes in drift when sand was just deposited within the riffle. These results suggest that sediment transport even at low levels early on in the rise of the hydrograph acts as a disturbance at the entire macroinvertebrate community rather than on individual species. Consequently, increases in sediment input from road surfaces or forest/range activities may greatly influence macroinvertebrate drift.

Drift can be an important recolonization pathway for macroinvertebrates after a disturbance in desert streams experiencing droughts as well as severe spates (Gray & Fisher 1981), although aerial pathways of insect dispersal, which can take place in all directions and from neighboring streams, were believed to be more important downstream for a certain species.

2.4 Photo Period (diel periodicity)

Daily activity patterns in insect larvae and instars in streams hold particular interest because of the importance of macroinvertebrates as food for vertebrate predators (Bailey 1981*a*). For Trichoptera, Elliot (1968, 1971*b*) demonstrated that there was a consistently higher drift rate at

night compared to day. In a controlled tank experiment, Elliot (1973) demonstrated that a leech species was primarily active at night, which corresponded to the highest drift numbers from field sampling. *Baetis* and Chironomidae in mountain streams of Idaho showed a 2-3-fold increase in night drift compared to day (Skinner 1985). Waters (1972) concluded that *Gammarus* as well as most other insect species are nocturnal and the low diurnal activity pattern probably evolved in response to predator avoidance. Diurnal variation in drift persisted through the ice-covered period in northern Russian streams during early spring (Schubina & Martynov 1990). However, a few species, mostly caddisfly larvae, are diurnal with peak activities during the day (Waters 1972). Chironomidae in mountain streams of Idaho primarily displayed diurnal drift (Skinner 1985). Another day-active group is water mites (Hydracarina), which are visual predators that probably require light to find prey (Bishop & Hynes 1969, Waringer 1992, Johansen 2000). On the basis of a comparison of stream drift between two sampling nights in Oregon with and without moonlight, Anderson (1966) suggested that diel periodicity of drift rate appears to be a direct response to lowered light (visible spectrum only) intensity at sunset. In contrast, Statzner et al. (1985) concluded that moonlight did not depress Trichoptera drift in tropical streams at the Ivory Coast. Pringle and Ramirez (1998) also avoided sampling drift during the fourth quarter lunar phase, presumably because higher light levels influenced drift. The trigger is usually light intensity with a threshold value of 1 to 5 lux (Waters 1972) and daily changes in water temperature as a result of sunlight versus dark has been ruled out as influencing diel periodicity (Waters 1972). Further field evidence of light as the driver for the diurnal drift pattern was provided from a temperate Australian stream, where drift increased significantly during a solar eclipse (Cadwallader & Eden 1977). Moreover, variations in light intensity were used in a

19

manipulative field study to demonstrate how light regulates drift patterns on a daily basis (Haney et al. 1983).

In contrast, a Colorado study increased ultraviolet B-radiation to stream sections during the day and observed an increase in macroinvertebrate drift during the day compared to control sections (Kiffney et al. 1997). This suggests that ultraviolet B-radiation may be another regulator of drift. This is an important observation, because streams at high elevation have higher levels of ultraviolet B-radiation than low elevation streams. Although other factors may influence drift there is little field evidence for how important these factors might be (Fig. 1). In a drift study from Nepal, only low elevation samples (1500 m) showed nocturnal drift. In high-elevation samples (4000 m), drift was aperiodic (Brewin & Ormerod 1994). Drift patterns in a high Andean stream (3000 m) had higher drift rates during the day compared to night (Turcotte & Harper 1982). An altitudinal comparison of periodicity of drift in Puerto Rican streams showed that low elevation (30-700m) sites had nocturnal drift, while high-elevation sites (1800-2700m) had diurnal drift (Pringle & Ramirez 1998). This pattern of high-elevation streams showing strong diurnal or aperiodic drift patterns may not be entirely due to elevation differences, because many lowland sites had fish present, while high-elevation sites were fishless. However, a Norwegian drift study north of the Arctic Circle (68°N) showed greater drift rates during night compared to day in August and October, while there were no differences between day and night drift rates in May and June when the sun does not set (Johansen et al 2000). This supports the notion that light is one of the most important regulators of drift.

If the periodicity of drift is examined more finely, there is often a peak just after darkness followed by an exponential decline through the middle of the night and a minor peak at the end of the night (Waters, 1972, Statzner & Mogel 1985, Schreiber 1995). These crepuscular peaks in

activity were also confirmed by a study on *Baetis* from British Columbia (Lancaster 1992) with a four-fold increase in drift just after sunset and, to some extent, before dawn, and for other Trichoptera species in a high-elevation study in the Pyrénées (Lavandier & Cereghnio 1995). Rincon and Lobon-Cervia (1997) found similar daily drift patterns at two times of the year, the January low drift period and the July high in an Iberian stream. The crepuscular nature of drift pattern was also reported from a French study using a known fauna in an artificial stream (Neveu 1980). In tropical Australia stream drift pattern was unmistakably nocturnal with a crepuscular peak during most of the months (Benson & Pearson 1987).

For Oregonian Trichoptera, diel periodicity was not evident using total numbers per hour of a given species. However, when larvae were classified into small (≤ 3 mm) and large (> 3 mm) individuals, there was a highly consistent pattern of large larvae drifting at night (Anderson 1967). O'Hop and Wallace (1983) also reported that larger and older individuals showed stronger diel periodicity in their drift patterns in Appalachian headwater streams, which may be in response to an increase in susceptibility to predation for larger individuals.

Using observations of epibenthic activities of *Baetis* nymphs and simultaneous collection of stream drift, Wilzbach (1990) concluded that *Baetis* does not drift at night because it is hungry and in search of food. Gut fullness data suggested that *Baetis* feed continuously. Similarly, Kohler (1985) found that starved *Baetis* nymphs foraged on top of stones both day and night while well-fed nymphs only foraged at night, but they had similar drift patterns peaking at night. These studies suggest that nymphs are not accidentally dislodged during foraging. In contrast, Statzner and Mogel (1985) found that gut fullness of *Baetis* observed in a German river, peaked just after sunset and were lowest just before sunset. This would suggest that feeding activities were lower during night than during the day and feeding is not continuous. Likewise, Ploskey

and Brown (1980) also confirmed that drifting and non-drifting nymphs had similar gut-content weight and caloric content. However, using regression analysis, they attributed drift as a passive phenomenon resulting from increased forage activity during dark periods, which is in sharp contrast to the previous two studies mentioned. Skinner (1985) also found that the larger the size class involved in drift the greater the night/day drift ratio became. However, we have not found studies that have looked at drift patterns as they relate to body size and foraging ecology, which may help explain the contrasting patterns reported here.

The many studies observing diel drift patterns by macroinvertebrates still give rise to two underlying mechanisms to explain drift. 1) A passive phenomenon due to increased forage activity which typically occurs during crepuscular hours, or 2) an active process where larger individuals seem to drift at a higher rate to avoid predation (see section 3.4). Regardless of the explanation, the consequence of drift is that downstream reaches receive an input of new individuals at varying rates during a 24-hour period.

2.5 Seasonal Patterns

Strong seasonal variations in drift rates have been confirmed by numerous studies across all biogeographic regions, although drift never stops completely in lotic ecosystems. Generally, there is a positive correlation between biomass production and drift rates. In a temperate stream in Great Britain, Elliot (1968) demonstrated that Trichoptera show seasonal variation in their drift patterns. This was mostly linked to developmental differences between species. From a field study on drift of a leech, Elliot (1973) demonstrated that there were seasonal differences in drift activity. A study in Wales evaluated seasonal differences in macroinvertebrate drift in general (Hemsworth & Brooker 1979) and found that drift occurred throughout the year with

22

peaks during summer during the time of highest stream productivity. They reported peak drift numbers of individuals of 34,000-798,000 d^{-1}. This probably lies within the upper range compared to other studies (Table 1).

In a study on *Baetis* from Minnesota, Waters (1966) found that drift rates were markedly different between summer and winter. Summer drift was significantly higher compared to winter, except in late winter and early spring, which had high drift rates corresponding to spring melt, which significantly increased discharge. However, drift occurred throughout the year with significant winter production as well. In temperate Australia, drift varied with season, with peaks of total drift in spring and summer (Schreiber 1995). Other studies from temperate regions have shown similar patterns (Cowell & Carew 1976, Clifford 1978, Lauzon and Harper 1988, Dudgeon 1990, Moser & Minshall 1996, Rincon & Lobon-Cervia, 1997).

Similar to cold/warm seasonal differences at higher latitudes, distinct pulses of macroinvertebrate drift between wet and dry seasons were reported from tropical Australia with the highest rates during the productive wet season (Benson & Pearson 1987). Additionally, they reported that over a 24 h period >12 times the standing biomass of a given area may drift by. Similarly, results from Central America (Ramirez & Pringle 1988) and New Zealand (McLay 1968) streams showed strong seasonal variations with highest drift rates in summer.

In northern Boreal biomes streams and rivers are ice covered for extended periods of time, and very limited information on drift exists. Shubina and Martynov (1990) compared macroinvertebrate drift in two ice-covered salmon streams in March and April in the northern European USSR and found significant drift taking place. In addition, their drift samples contained exuviae of mayfly and stonefly larvae, indicating growth during the ice-covered period. Another winter study of snow-covered streams at high elevation (>3000 m), found that

23

the density of drifting organisms was relative low (Table 1), when compared to summer drift in other high-elevation streams (Pennuto et al. 1998).

In general, there seems to be an agreement between peak drift rates and peaks in the productivity of the ecosystem correlated with phenology - highest standing biomass and productivity by the aquatic and riparian vegetation (Armitage 1977, Clifford, 1978, Shubina & Martynov1 990, Cellot 1996, Moser & Minshall 1996) with maximum drift during summer and minimum during winter (Rincon & Lobon-Cervia 1997). Drift rates were also highest around summer in an Australian temperate stream (Schreiber 1995). Lauzon & Harper (1988) reported that peak drift correlated with peak biomass production of aquatic organisms and seston biomass. In a seasonal tropical stream in Hong Kong, community level trends in drift were lacking, although some species had their highest drift rates during summer when productivity was highest (Dudgeon, 1990). A similar pattern was observed by Cowell and Carew (1976) in a subtropical Florida stream.

3 Biotic Factors

If biological interactions were at least partially responsible for drift, it would be expected that drifting species would have adapted behavioral mechanisms that allow them to enter into active drift and to perform a landing downstream. Personal observations by Skinner (1985) revealed that midge larvae did not appear to be as good drifters as *Baetis sp*. because their ability to exit drift is very poor. Reidelbach and Kiel (1990) used artificial streams and video equipment to demonstrate how blackfly larvae had several behavioral patterns involved in landing at and getting attached at a specific site. Furthermore, their behavior would change and adapt depending on how strong the affinity for a given site was. Blum (1989) investigated drift

24

postures of eight stonefly larvae. He found different postures for passive and active drift events, and each species had its own distinct features of posture regulating drift.

Through experimental investigations, Wiley and Kohler (1980) demonstrated that mayfly nymphs experience increased vulnerability to drift due to behavioral regulation of oxygen consumption. As oxygen content decreases, the nymphs must increase their exposure and thereby increase susceptibility to accidental drift.

A laboratory study investigated the interaction of food, cover, and predators on the drift of *Baetis* nymphs (Instar III) during dark and light hours (Corkum & Pointing 1979). They found that nymphs drifted significantly more during dark than under light. None of the variables nor their interactions significantly influenced nymphal drift during light conditions. However, at night, the presence of stonefly predators was the only factor contributing significantly to an increase in drift rate.

3.1 Endogenous Rhythms

In a controlled tank experiment where light periods and timing were varied, Elliot (1973) was unable to detect an endogenous rhythm for a leech rather activity was determined by light levels. From field sampling the drift numbers of the leech were highest during darkness and virtually absent during daylight. Generally, endogenous rhythms of macroinvertebrates as a regulator of drift have not been reported from other studies.

3.2 Life Stage

Certain size classes and life stages drift at greater rates than the benthic community as a whole. The age classes most likely to drift appear to vary with species and ecosystem under investigation (Brittain & Eikeland 1988).

For the Trichoptera group, Elliot (1968, 1971*b*) established that all aquatic life stages were present in drift. However, primarily uncased individuals were found to be drifting. In another study in southwest England, Elliot (1971*a*) showed that drifting cased Trichoptera had cases made up of plant material rather than stones. Mostly 1-3 instar were in the drift due to their light casing material (Elliot 1971*b*, Otto 1976), which suggests that drift of these organisms was passive in nature. All stages within a two-year life cycle of a leech were reported to drift (Elliot 1973). Waters (1972) recorded that the greatest drift occurs in the younger life cycle stages. In contrast, Iversen (1980) found that instar distribution in drift and benthos of a Trichoptera species was not significantly different in a Danish woodland stream. Lancaster (1992) demonstrated in a manipulative study that all nymph sizes of *Baetis* were equally represented in the drift indicating equal vulnerability to spates. Yet, Madsen and Butz (1976) and O'Hop and Wallace (1983) showed that larger, and consequently older, nymph stages were more likely to drift. In laboratory experiments with *G. pulex* it was demonstrated that larger individuals were primarily drifting at night, which supports the hypothesis that large individuals become nocturnal because of increased predation risk with greater body size (Andersson et al. 1986). Cellot (1989*b*, 1996) concluded that seasonal variations in macroinvertebrate drift in the Rhône River reflected life-cycle characteristics of the aquatic organisms similar to Waters (1972), Müller (1974), and Statzner et al. (1984) rather than the flow regime (Elliot 1968, Lancaster 1992).

Peak drift levels recorded during the wet season in northern Australia appeared to be more closely associated with lifecycles of the drifting taxa than with the disturbance caused by increased current velocities (Benson & Pearson 1987). In Neotropical streams various larval stages of shrimp make up a majority of the drift (Ramirez & Pringle 1988, Pringle & Ramirez 1998), but no adults were reported. Monthly drift samples for a period of one year in a Minnesota stream found that Megaloptera drift may have been mostly associated with pupation (Krueger & Cook 1984). Also, Ephemeroptera were found to increase drift rates at the end of their life cycle. In contrast, a Diptera species was found to exhibit virtually no drift behavior throughout its lifecycle. Drift responses to streamflow fluctuations in a Colorado study showed that, for several mayfly species with poor swimming ability and unfavorable hydrodynamic profiles, drift rates of larger age classes increased with increasing flow due to passive displacement. This was not as pronounced in smaller individuals (Poff et al. 1992).

Predicting which life cycle stage that is most prone to drift is very species specific. It is important to know a species' biology to understand how and why a species engages in drift. Generalizations based on order, family or genus may not be sufficient to predict which life stage drifts the most (Fig. 1). However, Hershey et al. (1993) demonstrated using benthic density and drift samples that the entire *Baetis* population moves downstream during the arctic summer, which indicates that all life stages participate in drift.

Furthermore, most field studies are not able to isolate specific biotic factors, but rather measure cumulative effects of all factors present at a given time (Table 1). This is likely the reason behind the many seemingly conflicting results (Müller 1974, Madsen & Butz 1976, Otto 1976, Statzner et al. 1984, Lancaster 1992).

3.3 Predator Escape

A literature review of 22 studies (Wooster & Sih 1995) revealed that the presence of predatory invertebrates caused an increase in drift. The presence of vertebrates had variable effects on drift rates, but prey significantly decreased their activity such as crawling rate and emergence from refuge habitat in the presence of a predator (Wooster & Sih 1995). Similarly, Dahl and Greenberg (1996) conducted a meta-analysis, based on existing data sets of drift feeding versus benthic feeding fish predators on stream benthic prey and concluded that feeding behavior has had different ecological impacts on drift. However, studies manipulating these two factors are needed to assess the exact ecological impacts on drift.

Using four experimental stream channels Lancaster (1990) demonstrated that the presence of predatory stoneflies increased drift of *Baetis*. Furthermore, larger individuals were more likely to drift than smaller ones when they came in contact with a predator. Rader and McArthur (1995) also observed drift as a result of encounters with predatory stoneflies. Flume experiments examining blackfly (Simuliidae) use of microhabitat demonstrated that they select high current velocities to minimize predation by stoneflies (Plecoptera), and drift was observed as an escape measure from predators (Malmqvist & Sackmann 1996), although it was not significantly more common than being captured. An experimental field study in a southern Swedish stream showed that large-scale introductions of predatory stonefly increased drift significantly of its prey at night but not during the day (Malmqvist & Sjöström 1987).

Peckarsky (1996) demonstrated that different species of mayfly larvae have alternative predator avoidance behaviors in response to predator presence. Tradeoffs in resource acquisition, fecundity, and mobility of a species determines how likely an individual is to enter into drift. In an earlier study Peckarsky (1980) demonstrated that not all mayfly species use drift

28

as an escape mechanism when they encounter a predatory stonefly. Change in posture or crawling was also observed to be escape mechanisms. Kratz (1996) showed that the relationship between total predator impact through consumption and initial Baetid density was curvilinear with greatest predator effects at intermediate prey densities. At low densities, more prey could find refugia and at high densities prey-handling time by the predator influenced the response. This suggests that invertebrate predator impacts can be strongly density dependent illustrating a predator functional response. Through another experimental analysis of a *Baetis* species Kratz (1996) suggested that drift was determined by two factors. Using a gradient of algal biomass and different densities of predatory stoneflies, he demonstrated that baetid per capita emigration declined with increasing algal biomass (a *Baetis* refugia), but generally increased with increasing stonefly numbers (Kratz 1997).

The relationship between invertebrate drift and fish feeding has been well established in the field as well as in the laboratory (Waters 1972; Allan 1981, 1982; Wilzbach et al. 1986, Nakano et al. 1999). In particular, salmonids eat the greatest number of drifting benthos (Allan 1981, Hubert & Rhodes 1989, Lavoie & Hubert 1994), but also seem to be somewhat selective for species (Hubert & Rhodes 1989) and size (Lavoie & Hubert 1994). The important question is whether the presence of fish influences the macroinvertebrate community. Noteworthy is the observations made by Allan (1982) that a 10-25 percent (4.86 g m^{-2} beginning trout biomass) reduction in trout did not affect the drift density of the macroinvertebrate community of the stream. Furthermore, density by species and species composition did not change either. He concluded that the invertebrate community is highly adapted to fish predation. Other fish manipulation studies, which both increased and decreased trout populations (7-186%) in small streams have found no or only slight changes in drift and benthic densities (Zelinka 1974, Macan

1977). In contrast, Wilzback and Cummins (1986) showed that removal of trout increased drift

density significantly during the day, especially in logged sections compared to forested sections.

No drift density differences were observed for night drift. In addition, differences in species

composition of drift from trout removal pools and control pools were observed. However, their

densities of trout appear to be much higher (122 g m^{-3}) than in Allan's (1982) study. In

comparison, Nakano et al. (1999) also had a standing biomass of charr *Salvelinus sp.* in

unmanipulated streams that was much lower with 5.60 g m^{-2} (1 year) to 28.10 g m^{-2} (4 year)

(Data converted from fork length using ln weight = -4.65 + ln length (Power et al. 2002). It has

been shown that feeding activity of coho salmon and brown trout is correlated to peaks in

macroinvertebrate drift (Young et al. 1997). Neotropical fish communities also take advantage

of drifting insect (Flecker 1990, 1992). In another field experiment trout were introduced in

cages into small Scandinavian fishless streams (Friberg et al. 1994). The results showed no

significant difference in diel activity or the rate of drift for most species. In contrast, a tank

experiment (McIntosh & Peckarsky 1996) revealed that mayflies alter their behavior according

to the presence or absence of introduced fish odor. However, the behavioral alterations were

dependent on the previous experience of the mayfly population to trout exposure and time of

day. Mayflies drifted more during the day when risk of predation was low, and mayfly

populations from trout streams showed a stronger diel drift pattern compared to populations from

fishless streams. Similarly, a tank experiment by Miyasaka and Nakano (2001) showed that

Baetis used visual cues to detect day-feeding Masu salmon (*Oncorhynchus masou*), but used

chemical cues to detect night-feeding sculpins (*Cottus sp.*). They suggested that *Baetis* are able

to use unique cues to each predator type they may encounter.

Large *Gammarus* drifted less when they received chemical cues from introduced trout.

Likewise, introductions of sculpins (*Cottus gobio*) into a stream previously devoid of these

predators significantly reduced the drift rate of *G. pulex*, although drift of insect larvae was not

affected (Andersson et al. 1986), which was further confirmed by laboratory experiments. From

these experiments it was also revealed that the largest individuals primarily drifted at night

presumably to avoid predators. From a tank experiment, it was shown that presence of fish, fish

part or their secretions decreased drift of *G. pulex* (Williams & Moore 1985). These conclusions

were confirmed in a Danish field experiment. Brown trout (*Salmo trutta*) were introduced into

the lower half of two normally fishless streams. This resulted in lower drift rates and lower

densities of *G. pulex* (Andersen et al. 1993). Also, if injured Amphipods were added, settling

rate for *G. pulex* was significantly greater suggesting that *G. pulex* use Amphipod secretions as

cues to fish feeding upstream. In contrast, Forrester (1994*a*) concluded from manipulating

densities of brook charr (*Salvelinus fontinalis*) that the propensity to drift was greatly increased

for some mayfly species when charr densities went up, however, other mayfly species showed no

response or decreased drift due to the presence of brook charr.

Observations using video cameras of mayfly movements on the substrate and in the water

column in experimental stream channels revealed that they are able to determine direction and

distance traveled, upstream and downstream, in response to predatory fish, especially at low

current velocity and turbulence (McIntosh & Townsend 1998). This is in contrast to entering

into drift. Exceedingly high nocturnal drift rates from a relatively small Neotropical stream were

attributed to a high number (>30) of diurnally active fish species (Ramirez & Pringle 1988).

Using a combination of natural streams and manipulative field experiments in Venezuelan

Andean streams, Flecker (1990) provided evidence that an increase in drift-feeding fishes

increased nocturnal and decreased diurnal drift. Further evidence for the risk-of-predation

hypothesis is the observation in an Andean stream where trout have been introduced recently.

Mayfly (*Baetis*) displayed nighttime drift peaks, but was aperiodic in neighboring fishless

streams (Flecker 1990). Furthermore, a fish exclusion experiment suggests that the differences

in drift densities are not a consequence of nymph consumption by day-active predatory fish.

Instead, it appears that nocturnal activity evolved as a result of exposure to fish predation

(Flecker 1990).

In conclusion, it appears that the macroinvertebrates increase drift rates in response to

invertebrate predators and decrease drift rates in response to fish presence, especially during the

day (Fig. 1).

3.4 Distributional Dispersal

Spatial distribution of benthic invertebrate populations is primarily by downstream drift

through emigration from and immigration into habitat patches downstream (Minshall & Petersen

1985). They further suggested that, benthic populations at a given habitat unit would exist in a

state of dynamic equilibrium analogous to the colonization of oceanic islands. Anderson (1967)

concluded from a study on Oregonian Trichoptera that drift was a result of a permanent

downstream displacement and not due to random localized movements in the immediate vicinity.

This conclusion was largely based on the observation that benthos counts appeared to be too low

compared to drift counts. From a manipulated field experiment in British Columbia it was shown

that upstream benthic densities were decreased and *Baetis* colonization increases downstream

when a predatory stonefly was introduced upstream (Lancaster 1990). Benson and Pearson

(1987) concluded that drift in a tropical Australian stream during the wet season was dispersive

of the population, rather than depletive, which serves to distribute young larvae and nymphs to areas of suitable habitat downstream. From a manipulative field study in Idaho, Moser and Minshall (1996) concluded that drift was a primary method of colonization during spring, but equal in significance to crawling during summer and autumn. Matthaei et al. (1997) concluded that drift is an important ecological factor in recolonization of large sections of a river after catastrophic disturbances such as floods. Comparatively, in a nine meter blocked section of a stream, Wilzbach and Cummins (1989) showed that recruitment of species to a riffle were sufficient to compensate for short-term loss due to downstream drift. In other words, drift did not deplete the population short-term. Using field observations, Richards and Minshall (1988) demonstrated that emigration and immigration by a mayfly species onto rock surfaces were positively correlated to periphyton abundance. About 50 percent of immigrants arrived via drift and the other half by crawling with immigration rates up to 5.8 individuals/100cm^2/hour. This study suggested that macroinvertebrate drift might be involved in distributional dispersal in response to food abundance. Several studies have confirmed that drift of a *Baetis* population from a habitat patch occur in response to low food quality (Kohler 1985, Richards & Minshall 1988) or as a function of absolute food supply, but reporting that it is not density dependent (Hinterleitner-Anderson 1992).

Downes and Keough (1998) viewed drift strictly as dispersal and colonization processes, although they pointed out that better information was needed to understand dispersal and colonization processes. From their literature review they concluded that we have a reasonable knowledge of transport at the mesoscale (across riffles and pools), but poor on the microscale (across riffle to pool patches such a rock, log or pebbles). Additionally, we have poor

understanding of the behavior involved in drift, mortality, and behavior at the end of dispersal. (Also see section 4.5.)

3.4.1 Intraspecific Competition

The influence of intraspecific resource competition remains unclear despite the availability of both field data and laboratory experiments. Some studies indicate that limitations in space and food increase drift rates, while others report that there is no influence on drift.

From a one-year long study in southwest England, Elliot (1968) concluded that there was very little displacement of one species of Trichoptera at the upper reaches of the stream indicating limited intraspecific competition. In contrast though, he suggests that overcrowding from a rapidly growing population of Hydropsyche resulted in increased stream drift. Waters (1972), postulated that intraspecific competition within cohorts could result in drift when they reach older life cycle stages and have become larger or be a result of greater feeding activity. It has been suggested that downstream distributional changes may be linked to stream productivity (Waters 1966, Hall et al. 1980). Size of a species generally increase downstream, and number of drifting individuals are typically greater than individuals found in the benthic environment (Waters 1966, Hall et al. 1980), further strengthening the argument for the presence of intraspecific competition.

In a study from Minnesota on *Baetis* it was apparent that there were no linear correlation between population densities and drift rates (Waters 1966). Drift/benthos ratios of select mayfly species demonstrated marked differences between species even within the same genus (Lehmkuhl & Anderson 1972) making it difficult to evaluate presence or absence of intraspecific competition. In contrast, Madsen (1976) determined that nymphs are displaced downstream by

34

drift in response to an increase in density, which would infer intraspecific composition. Further, mark-recapture results of adults demonstrated that most females had a unidirectional movement upstream towards the headwater (Madsen & Butz 1976). Using an artificial stream with regulated discharge and artificial bottom, Pegel (1980) was able to demonstrate a significantly positive correlation between drift rate (individuals m^{-3}) and benthic density (individuals $100cm^{-2}$ $12h^{-1}$) for Simuliidae larvae of several species. He also showed that drift intensity was positively correlated with density, and suggested that density alone might help trigger drift, but that competition for food did not trigger drift. In order to evaluate the effect of density on drift rates, Williams & Moore (1985) conducted a laboratory experiment with *G. pseudolimnaeus* by adding 20, 50, 200, or 600 individuals into tanks and observing drift rates. The addition of extra individuals resulted in lower drift rates. William and Moore hypothesized that the decrease in drift was related to feeding congregation behavior. *G. pseudolimnaeus* is an opportunistic feeder and often congregates in large numbers (e.g. 900/0.1 m^2 stream bottom).

From another tank experiment, Palmer (1995) concluded that drift of herbivorous *Baetis* was higher when resources were patchy compared to uniform. From visual observations he also concluded that inter- and intra-specific competition was not a significant factor influencing drift. Conversely, Bailey (1981*a*) concluded from a laboratory study on an Australian mayfly that competition for space increased the insect's tendency to drift.

Under controlled conditions in an artificial stream system, Hildebrand (1974) clearly demonstrated that drift was density independent using representatives of three taxa groups. He concluded that intraspecific competition for space was not a regulator of population levels. However, using two levels of food density, he suggested that intraspecific competition for food

might be a mechanism resulting in increased drift and population regulation as hypothesized early on by Waters (1966).

Fonseca and Hart (1996) provided good evidence of intraspecific competition for food resources from an Arctic river. Using stable isotopes they showed that *Baetis* nymphs drifted less in a fertilized section of the river compared to an unfertilized section. Furthermore, black fly neonates showed that dispersal rates were higher in slow than in fast current velocities. They concluded that accidental dislodgment caused by water currents was generally unimportant for the species under investigation. Rather, they attributed drift to a voluntary response to reduced feeding rates as a result of competition for food.

3.4.2 Interspecific Competition

In general, there is very limited information available from the literature on interspecific competition and what information that is available is mostly anecdotal (Palmer 1995). A South Carolina study showed that predatory stonefly (Perlidae) might enter drift as a result of interference competition for refugia both within and between species (Rader & McArthur 1995). Using a combination of microcosm experiments and stream-caging experiments in different stream sections (fertilized versus unfertilized) Hershey and Hiltner (1988) suggested that caddisfly dislodgment of black flies accounted for a significantly lower density of black flies.

From underwater visual observations and drift net sampling, Statzner and Mogel (1985) demonstrated that surface activity and inter- and intraspecific encounters were highest during the day when drift rates were lower and surface densities higher than night. In addition, drift distances were very short during the day. Inter and intraspecific encounters often resulted in short movements on the same stone (15*15 cm) where the encounter took place. These

observations imply that intraspecific competition for food or intra- and interspecific competition for space did not influence drift.

4 Temporal and Spatial Scales of Drift

Macroinvertebrate drift in lotic ecosystems can be assessed on different scales in time and space. Drift as it relates to time has received the most attention ranging from daily (Elliot 1973, Cowell and Carew, 1976, Bailey 1981a, Lancaster, 1992, Forrester 1994*b*) to seasonal variations (Cowell & Carew 1976, Clifford 1978, Lauzon & Harper 1988, Dudgeon 1990, Moser & Minshall 1996, Rincón & Lobón-Cerviá 1997). Typically, drift has been assessed on very limited spatial scales such as a single stream or river (Table 1). Only one study has determined drift on a landscape level using 52 headwater streams in the Southeast Alaskan archipelago (Wipfli & Gregovich 2002). They viewed drift as biomass export downstream. In contrast, the underlying mechanism behind drift itself on a longitudinal scale has been well studied. Studies have been conducted on as little as short reaches (O'Hop & Wallace 1983, Benson & Pearson 1987, Ramírez & Pringle 1998) to entire systems across the spectrum of several (1-8) stream orders (Slack et al. 1976, Minshall et al 1992, Young & Huryn 1997). Two basic hypotheses have emerged to explain the mechanism behind drift. Müller (1954) hypothesized that macroinvertebrates are displaced downstream through drift in response to interspecific competition and an upstream unidirectional migration is necessary to avoid headwater depletion. Alternatively, Waters (1972) proposed that stream drift only represented excess production, and an upstream migration therefore is not necessary. (Also see Section 4.5.)

Finally, numerous investigators have studied drift using manipulated streams (Brooker & Hemsworth 1978, Culp et al. 1986, Giller and Cambell 1989, Andersen et al. 1993, Kiffney et al.

1997), artificial streams (Corkum & Pointing 1979, Miyasaka & Nakano 2001), or conducted

visual observations (Peckarsky 1980, Statzner & Mogel 1985, Richards & Minshall 1988, Blum

1989).

In general, the majority of investigations have been on really small-scale studies that were

limited on a spatial scale, but have been expansive in time.

4.1 Stream Order

Drift studies have primarily focused on low-order streams (i.e. Waters 1966; Elliot 1968,

1971*a*, 1971*b*; Lancaster 1992; Iversen 1980; Winterbottom et al. 1997; Benson & Pearson 1987;

Pringle & Ramirez 1998; Wipfli & Gregovich 2002), but often information on stream order is

not provided (Table 1). Borchardt (1993) studied drift in a much larger system such as the River

Wye in Wales, while Cellot (1989*a*, 1996) studied a sixth order stream, and Minshall et al (1992)

studied an eighth order stream in Idaho.

A study in Colorado compared a third-order and a sixth-order stream (Kiffney et al. 1997). A

fourth-order black-water stream was used by Ramirez and Pringle (1988) in the tropics. Several

studies (Table 1) have been conducted using third order streams (i.e. Skinner 1985, Tilley 1989,

Moser & Minshall 1996, Johansen 2000).

4.2. Spatial Scales

Most drift field studies have been conducted within individual streams (Elliot 1968, 1973;

Anderson 1967; Ramirez & Pringle 1988; McLay 1968; Cadwallader & Eden 1977; Tilley 1989;

Bergey & Ward 1989; Rader & McArthur 1995; Matthaei et al. 1997). Also, Winterbottom et al.

(1997), Marsh (1980), Gray and Fisher (1981), and Williams (1990) studied the mobility of

benthic invertebrates using a single stream. Likewise, a single stream was used to assess drift in a tropical stream in northern Australia (Benson & Pearson 1987). A few studies have compared two streams from different regions or biomes (Slack et al. 1977, Shubina & Martynov 1990), of different size (Kiffney et al. 1997), or of discharge pattern (Dance & Hynes 1979, O'Hop & Wallace 1983).

In recent decades, the channel side-arm influence on drift was assessed for a large river providing information on how river complexity impacts drift (Eckblad et al. 1984, Sheaffer & Nickum 1986, Cellot 1996). The quantity and quality of drifting organisms from sidearms into the main channel depended on the degree of connectedness, stream flow and other flow characteristics (i.e., lentic versus lotic). Within the archipelago of Southeast Alaska, Wipfli and Gregovich (2002) assessed stream drift, both macroinvertebrates and detritus, on the landscape composed of 52 headwater streams distributed on four islands and the mainland over hundreds of km^2.

One of the important questions regarding drift is the distance traveled by individuals. Waters (1972) reported an average daily distance of about one meter, with extreme values of 10 to 15 meters. In an earlier field experiment Waters (1965) by blocking drift across an entire stream demonstrated that drift was reduced 38 m downstream from blockage across two riffles and a pool indicating that organisms normally drifted through at least this distance. He suggested that daily distances were probably 50-60 m. In a field experiment in a small tributary stream in New Zealand, where benthic invertebrates were introduced into drift through disturbing the substratum, McLay (1970) demonstrated that almost all drift occurred at a distance less than 36 m upstream of the collection sites even as areas farther upstream were disturbed. However, there were great variations among species, which could be related to a species' ability to swim.

Similarly, Hemsworth and Brooker (1979) calculated drift distances on a daily basis, which were

up to 51 m d^{-1}. Early work by McLay (1970) and Elliot (1971a) established that drifting animals

return to the substrate according to an exponential decay function, which was also used by

McIntosh and Townsend (1998).

In a tank experiment it was demonstrated that the average distance traveled was less than 10

m. However, about 1% of the drift traveled between 13-45 m (Waters 1972). Using a benthic

disturbance field experiment, McLay (1970) reported travel distances up to 36 m in 30 minutes.

This is in contrast to the average value of less than 7 m for 50% of the individuals in a controlled

experiment releasing 50 individuals in 72 trials (Elliott 1971a). Travel distance was within a few

hours and measured at low water velocities (<15 cm s^{-1}). Elliot (1971a) also found that poor

swimmers traveled greater distances. Somewhat similar distances were reported from a

Minnesota stream (Waters 1965). Other tank experiments using different instars of Trichoptera

concluded that drift distance was dependent on instar size. Much lower distances (<1 m) were

reported for a mayfly in low current experimental streams (McIntosh & Townsend 1998). In a

study where instars were actually dropped into the stream at specific points, instar I drifted the

longest in the drop-in experiments (30 cm) versus instar V, which only drifted 5 cm (Otto 1976)

suggesting that larger instars are better at exiting the water column and reach the bottom

substrate.

In a mark-recapture study from southern Sweden, Trichoptera larvae with organogenic cases

traveled distances up to 30 m in one day (Otto 1976). Using isotopes in an Arctic river,

minimum drift distances of *Baetis* were estimated to be 2.1 km for one-third to one-half of the

nymph population during the three summer months of June to August (Hershey et al. 1993).

Lancaster et al. (1996) were able to demonstrate that the settling coefficient (negative

exponential function) for drifting insects was directly correlated to stream complexity. Increased complexity resulted in shorter distances traveled by dislodged individuals.

Waters (1965) demonstrated that organisms are distributed relatively evenly in the water column. Cellot (1989*b*, 1996) working in the Rhône River confirmed this for large rivers. However, this was not the case for a large river in Wales, where the majority of the drifting macroinvertebrates were found in the bottom 10 cm (Hemsworth & Brooker 1979). This was also the case for drift samples of the upper Mississippi River (Matter & Hopwood 1980).

4.3 Temporal Scales

In general, strong seasonal differences in drift rates have been reported by most studies, with spring to autumn being the most common period under inquiry. Rates vary 4-10 fold between season lows and highs (Table 1). Unfortunately, it is not possible to conduct meaningful comparisons of drift rates between studies due to lack of detail provided on total discharge patterns and how drift rates are reported (Table 1). The late 1960's marks the period where investigations were initiated into long-term trends in drift patterns.

In southwest England, Elliot (1968) conducted one of the first studies on seasonal patterns in drift by investigating drift of Trichoptera for more than two consecutive years. A study in Wales was evaluating seasonal differences in macroinvertebrate drift (Hemsworth & Brooker 1979) where they found that drift occurred throughout the year with peaks during summer. Strong seasonal changes were also reported from temperate Australian streams (Schreiber 1995), and the Iberian Peninsula (Rincon & Lobon-Cervia 1997) with greatest drift rates during late spring and summer. Spring peaks in drift rates were also reported from a large river in a two-year study on the Rhône River, France (Cellot 1996). Seasonal differences in drift were also reported from

streams within the Boreal forests of northern Sweden (Müller 1954, 1974). During spring the drifting biomass was 4 - 5 times higher ($>$2500 mg/1000cm^2 d) than later in the summer and autumn seasons ($\sim$500 mg/1000cm^2 d). In contrast, the number of individuals was somewhat constant between breaking-up of ice and freeze-up, but with a distinct decline towards autumn (Table 1).

Often the drift rate in streams has been measured against the standing biomass or density of the benthic community. Measured as the number of organisms per unit discharge (m3) drift makes up only a few percent of the benthic community, but measured on a 24 hour period, drift is up to eight times the standing biomass that drifts by (i.e. Waters 1972, Armitage 1977, Schreiber 1995). Monthly samples were taken to obtain seasonal (wet/dry) variation in drift from a tropical (Costa Rica) stream (Ramirez & Pringle 1988). Drift ranged from 2.5-25 m^{-3}, greatest in the wet season, and was not correlated to benthic densities, which ranged from 228-1504 m^{-2}, lowest in the wet season.

4.4 Biogeographic Regions and Land Use Types

Our current knowledge and understanding of macroinvertebrate drift and its ecology has primarily been shaped by the disproportionate investigation of certain biogeographic regions (Table 1). Most studies have been concentrated in the temperate regions of Europe (Hemsworth & Brooker 1979, Cellot 1996, Winterbottom et al. 1997), North America (Skinner 1985, Rader & McArthur 1995), and New Zealand (Edwards & Huryn 1996) with a few in temperate Australia (Schreiber 1995). Very few studies have been conducted in the Ethiopian and Oriental regions in recent decades (Table 1).

Unfortunately, most studies provided limited information on the condition of vegetation in the landscape such as species composition and age of forest or riparian zone, and almost no information on land use patterns, although a few exceptions exist (Table 1). Drift studies conducted within forested regions -- both within deciduous, coniferous, and mixed forests -- seems to dominate the literature (Table 1). A few studies have been carried out in streams within the coastal temperate coniferous forest region of the Pacific Northwest (Anderson 1966, 1967; Hetrick et al. 1998; Wipfli & Gregovich, 2002). Most studies on drift of POM have been conducted in temperate coniferous biomes (Table 2).

4.5 Ecological Interactions

Drift is an important mechanism for macroinvertebrate dispersal downstream. The continuous downstream movement could potentially depopulate the upper reaches long term, which would require upstream movement for recolonization as initially proposed by Müller (1954). On the contrary, opponents argue that downstream drift only represent excess production, which has no long-term effect on the population viability (reviewed by Waters 1972).

Early on, Müller (1954) proposed that drift is part of a colonization cycle involving two unidirectional movements patterns, upstream and downstream. At the headwaters, competition for resources result in active drift downstream causing a depletion of the headwater population and subsequent colonization in downstream reaches. Upstream flights of egg-laying adults or imago complete the cycle. There have been several studies and examples, which have confirmed that adult insects in fact do move upstream (Waters 1972, Madsen & Butz 1976, Hershey et al. 1993). Of particular interest is the mark-recapture study of imago by Madsen and Butz (1976) showing unidirectional flight upstream to the headwaters. Moreover, isotope labeled adults of

Baetis was found to fly 1.6-1.9 km upstream from where they emerged (Hershey et al. 1993). In addition, a number of studies suggest that adult insects not capable of flying do move upstream in sufficient numbers to compensate for drift by crawling upstream along the bottom edges of the stream (Waters 1972, Müller 1982, Williams & Williams 1993). A recent example comes from tropical freshwater shrimp (March et al. 1998) that compensate for downstream drift by crawling upstream in large numbers. Furthermore, computer modeling by Anholt (1995) suggested that upstream-biased dispersal into depopulated areas would increase individual fitness, which otherwise drove random dispersers to extinction, because depopulated upstream reaches would provide more rapid growth to successful colonists. He argued that his density dependent model solved the stream drift paradox because upstream movement alone would not be expected to match drift rates perfectly at all times. This is in clear contrast to the empirical evidence from field studies by Hinterleitner-Anderson et al. (1992) that yielded little evidence for density dependant drift behavior. In contrast, Bird and Hynes (1981) concluded from a field study that upstream and across stream movement were not consistently different from one another therefore arguing that upstream movement is only random movement.

Alternatively, some authors (Bishop & Hynes 1969, Waters 1972, Wilzbach & Cummins 1989) have proposed that drift is a result of a population reaching carrying capacity (i.e., density dependent), and that drift is a surplus not leading to depopulated headwaters. Williams and Williams (1993) who quantified upstream/downstream movements of macroinvertebrates in a Welsh stream, found a net loss due to drift in eight species studied. Furthermore, none of the insects showed a strong overall upstream flight preference. In addition, Bird and Hynes (1981) found that adults moved randomly rather than unidirectionally upstream. Bishop and Hynes (1969) did not observe upstream movements of adults, and suggested that there would be no

need for a cyclical repopulation mechanism if only a small portion of benthos occur in the drift as did in their study. Also, a computer simulation showed that drift does not need to have a deterministic direction (Speirs & Gurney 2001), but random movements of aquatic stages can account for persistence of the headwater population despite drift. In contrast, Bergey and Ward (1989) concluded from their fieldwork that upstream movement was non-random with a distinct upstream movement. However, Waters (1965) demonstrated in a field experiment that there was no correlation between drift and standing biomass suggesting that there was no evidence of competition for resources as confirmed by Hinterleitner-Anderson et al. (1993). Interestingly, Wilzbach and Cummins (1989) showed that drifting animals had a three-fold higher mortality rate within 12 hours after collection compared to benthic animals. However, they did not speculate whether it was due to a difference in handling -- drift net versus benthic sampling -- or due to biological differences. However, drift nets may add substantial stress to trapped animals in the net, which is not the case for benthic individuals (Svendsen Pers. Obs.). In sharp contrast to most studies, Ladle et al. (1980) demonstrated, using an artificial chalk stream in southern England, that aerial introduction of macroinvertebrates was quite adequate to rapidly establish potentially depleted stream benthic faunas.

4.6 Exports Downstream

   The river continuum concept provides a useful framework for the export, and processing of coarse (CPOM) and fine (FPOM) particulate organic matter (Cuffney & Wallace 1989, Vannote et al. 1990), which in turn influences the community composition of macroinvertebrate and abundance of food source for juvenile salmon (Meehan 1996, Hershey & Lamberti 1998). The implication of this is that upstream production and retention capabilities of nutrients subsidize

open downstream communities (Polis et al. 1997). Often, nutrient-subsidized systems exhibit elevated densities of higher-level consumers. Consequently, downstream communities must be considered open systems thereby making them very vulnerable to changes in upstream subsidies (Polis et al. 1997).

The importance of the riparian zone in the delivery of CPOM of forested headwater streams is often underscored. Shredders processing bacteria and fungi infested (Suberkropp 1998) CPOM into FPOM downstream is well known (Hershey & Lamberti 1998). Additionally, the quality and importance of riparian inputs for non-forested rivers such as prairie rivers (Wiley et al. 1990) and alpine streams (Thorp & Delong 1994) is quite different. Often, primary production is the main carbon source in these nonforested ecosystems.

However, all of these studies evaluate the processing of leaves, needles, twigs, and pieces of wood. Several studies have quantified CPOM or detritus export (Table 2) from stream reaches, but only two studies included macroinvertebrate drift and CPOM in the same study to assess the total downstream transport. This is especially important ecologically since the food quality of drifting macroinvertebrates is much greater than CPOM and may be an essential food supplement to downstream collectors (Naiman 1983). Despite the early recognition that macroinvertebrate drift is an important part of downstream export only two studies have included both. Headwater streams in the southern Appalachian Mountains had lower export of (0.134 kg y^{-1}) yearly non-storm aquatic and terrestrial macroinvertebrate biomass (O'Hop & Wallace 1983) compared to other studies (15.6 - 43.4 kg y^{-1}) they reported (Armitage 1977, Neveu 1980, Table 1).

The monthly ratios between macroinvertebrate drift and CPOM (calculated in g day^{-1}) in an Appalachian headwater stream ranged from 0.007 - 0.883 (median 0.043). Macroinvertebrate

46

drift ranged from 0.061 – 1.911 g day^{-1} while CPOM ranged from 0.223 – 33.132 g day^{-1}. Wipfli and Gregowich (2002) determined that average export from 52 headwater streams within the Southeast Alaska maritime temperate coniferous forest biome ranged from 50 – 240 mg m^{-3} for aquatic and terrestrial insects combined and 10 – 390 mg m^{-3} for detritus.

Compared globally, downstream drift of macroinvertebrates ranges dramatically from site to site (Table 1), but drift appears to be an important ecological component of streams within all life zones and biomes. Many smaller streams export about 1 - 10 individuals per m^3, while larger rivers export up to 630 individuals per m^3. This results in thousands of individuals exported per day, adding potential food for fish downstream and increasing the number of consumers at all trophic levels.

The export of terrestrial insects in drift appears to be positively correlated with the structural complexity of the riparian vegetation (Table 3). Streams running through pastures and agricultural lands have the lowest input, while streams in forests receive the largest contributions of terrestrial insects. In particular, oldgrowth coniferous forests provide significant export inputs to headwater streams (Bilby & Bisson 1992). This is a similar pattern to the contributions of CPOM (Table 2), which is highest in oldgrowth forests and lowest in agricultural lands or young forests.

Nutrient subsidies to downstream reaches from headwater streams greatly determine the complexity of the downstream food web. Specifically, consumer densities are directly donor controlled with food from across the trophic spectrum (Polis & Strong 1996). Consequently, macroinvertebrate drift from headwater streams should be viewed as a critical element in downstream subsidies.

5 Statistical Analyses

   The studies from the 1960's and 70's were relatively simple in their statistical analysis limited to evaluate daily and seasonal differences in drift (Waters 1965, Elliot 1970). However, often data reporting did not involve statistical analyses but were simply by number of individuals drifting or weight by taxonomic group by river/stream station or over a time period (McLay 1968, Dance & Hynes 1979, Marsh 1980). Few studies used regression analysis to evaluate drift and discharge (Dance & Hynes 1979) or drift rates, density, and food levels (Hildebrand 1974), or drift and activity (Ploskey & Brown 1980). An Australian study used time series analysis to detect periodicity (Schreiber 1995). Simple linear correlation analysis was employed by O'Hop and Wallace (1983) to evaluate how drift was influenced by discharge, fine and coarse detritus, and inorganic sediments. Regression analysis was also used to assess the influence of water temperature, discharge, and trout odor on drift rates in a recent study (Williams 1990). Stepwise regression analyses were used by Dodgeon (1990) to evaluate the influence of stream temperature on drift rate and number of taxa in the drift. In recent decades ANOVAs have been used due to better experimental designs (Culp et al. 1986, Tilley 1989, Moser & Minshall 1996). As something new, seasonal patterns were investigated using DECORANA ordination techniques. Similarly, Rincon (1997) used cluster analysis and DCA to evaluate temporal variation in drift numbers between season, and day and night. To assess annual and spatial variations in drift Cellot (1996) used Principal Component Analysis. In the past decade, computer modeling has been employed as a new tool (Anholt 1995, Speirs & Gurney 2001). Broadly taken, statistical analyses employed in drift studies have largely reflected the general trend in ecological studies for the past forty years.

6 Methodologies

Drift net design is usually a compromise between filtration efficiency and clogging using 500 μm mesh size (Burton & Flannagan 1976, Slack et al. 1991) avoiding standing waves in front of the nets. For example, Wipfli and Gregovich (2002) used a cylindrical tube with a net attached due to the steep gradients in Southeast Alaska. Another important consideration is sampling efficiency, which is related to mesh size (Elliott 1970). To avoid clogging in most situations mesh size was reported to be around 440 μm (Elliot 1968, 1970; Slack & Tilley 1977; Wefring & Hopwood 1981; Krueger & Cook 1984). Other studies have used similar mesh size (Cowell & Carew 1976, Hemsworth & Brooker 1979, Iversen 1980, Light & Adler 1983), but occasionally other mesh sizes have been used ranging from 50 – 365 μm (Statzner & Mogel 1985, Slack et al. 1991, Young et al. 1997, Pringle & Ramirez 1998, Wipfli & Gregovich 2002). Matthei et al. (1997) used double nets consisting of an inner net of 400 μm and an outer net of 90 μm. However, they only sampled drift for one hour. Slack et al. (1991) concluded that important fractions of early life stages (small) passed through 425 μm and 209 μm nets and mesh size of 106 μm or less were needed. However, serious clogging (< 20% flow left) occurred after just 8 minutes making it impractical in most field studies. Williams (1985) compared net and pump sampling for Chironomidae and concluded that the pump method was superior by proving representative samples of all size classes.

A study in Great Britain suggested that drift net should be raised above the stream bottom to avoid collecting specimens, especially cased Trichoptera, crawling along the bottom (Elliot 1968, 1970). Young et al. (1997) raised their nets 2 cm above the surface and Matthaei et al. (1997) raised their nets 3-4 cm above the substratum and Elliot raised his nets 10 cm above the substrate (Elliot 1973). In contrast, a procedural manual for measuring drift suggests placing

drift nets right at the bottom (Wetzel & Likens 1990). However, they were also interested in

measuring organic debris movements. In small streams, the top of the net is usually above the

surface with the bottom close to the substrate (Elliott 1970, Pegel 1980, Wetzel & Likens 1990)

and the net may span the entire stream (Young et al. 1997). In medium sized streams nets are

also placed just above the substrate, but may not necessarily reach the surface (Elliott 1970), and

seldom do they span the entire width of the stream (Giller & Cambell 1989). Cellot (1989*a*,

1996) placed the drift net in the middle of the water column in a large European river to get a

representative sample.

   However, Johansen (1990) stacked 3 nets on a central metal rod to obtain surface, water

column, and substrate drift samples from a Norwegian river. This was essentially a modification

of the design used by Field-Dodgson (1985). To sample drift in the upper Mississippi River,

Wefring and Hopwood (1981) constructed two new net attachments; a bottom net with a

concrete weight and a surface sampler attached to a boat. However, the nets themselves were

standard. Furthermore, Elliott (1970) stressed that total daily discharge of the stream as well as

the discharge through the net should be known. However, many studies do not provide that

essential information (Table 1). Individual net and tube designs were reviewed by Elliott (1970).

Steffan (1997) described a special drift/emergence net combination. This drift net collects

emerging imago from the uppermost layer of the stream. Mundie (1964) also constructed a

sampling device that combines an emergence trap with a drift net. This design improves the

efficiency of sampling the emerging imago entering into drift. Another combination net was

developed by Hobbs and Butler (1981), which combined drift sampling with upstream

movements of aquatic macroinvertebrates.

Using field experiments combined with computer simulations, the effect of sample duration between 10 and 40 minutes in order to quantify stream drift were investigated in Alberta, Canada (Culp et al. 1994). They found that mean densities were not significantly affected, but the sample variance decreased curvilinearly as sample duration increased. Their results also suggested that in order to obtain a standard error within 10% of mean drift for a given period, at least three samples were needed using sampling times between 10 and 40 minutes. Furthermore, increasing sampling periods also improved precision. Irregular sampling times were used by Young et al. (1997) to improve precision during crepuscular periods by reducing sampling time from 3 to 2 hours. Allan and Russek (1985) suggested 5-6 samples when day and night drift was poorly correlated and if densities were low. They also provided equations to quantify sample drift density, 24 hour drift rate and 24 hour drift density of a stream.

Since the total discharge is related to the number of animals drifting past a sampling point, comparisons of drift numbers should be expressed per unit volume rather than per unit time (Elliot 1968) over a 24-hour period (Waters 1972, Hemsworth & Brooker 1979).

Elliot (1968) sampled drifting Trichoptera over 24 hour periods with nets being emptied every 3 hours. This has been followed by a number of researchers (Anderson 1967, Iversen 1980, Andersson et al. 1986, Brewin & Ormerod 1994, Lavandier & Cereghnio 1995, Pringle & Ramirez 1998). Wetzel and Likens (1990) suggested leaving nets in for 30 to 60 minutes, which was also reported by Young et al. (1997). This short sampling period was also suggested by Elliott (1970) if hourly differences in diel activity were to be measured (Lavandier & Cereghnio 1995). Most studies however, have used sampling periods of 24 hours with net cleaning every 3 to 4 hours (Hemsworth & Brooker 1979, Brewin & Ormerod 1994, Schreiber 1995, Rincon &

Lobon-Cervia 1997, Benson & Pearson 1987). Most studies have sampled drift across riffles in small and medium sized streams (i.e. Waters 1965, 1966; Dudgeon 1990).

Anderson (1967) used only five sampling dates in the southern Cascades to get seasonal information. In a study on Trichoptera species, Iversen (1980) used monthly samples to determine seasonal variations in drift, benthic densities, and energetics. This time schedule was also used to obtain seasonal differences in tropical streams in northern Australia (Benson & Pearson 1987) and in North Carolina (O'Hop & Wallace 1983).

Several studies have used biomass (wet and dry weights) as a response variable for drift (Waters 1965, 1966, Hall et al. 1980, Bergey & Ward 1989, Benke et al. 1991, McIntosh & Peckarsky 1996, Wipfli & Gregovich 2002), but number of individuals (Table 1) have been reported most often (McLay, 1970; Elliot 1971*b*, 1973; Lancaster 1992; Wipfli & Gregovich 2002). (See Table 1.)

7 Taxonomic Groups

From habitats most frequently examined such as temperate regions (Table 1), insect taxa that dominate drift composition include Ephemeroptera, Simuliidae, Plecoptera, and Trichoptera (Bishop & Hynes 1969, Brittain & Eikeland 1988). However, Megaloptera, Diptera, Crustacea, and Coleoptera may also contribute significantly to the drift (i.e. Benke et al. 1991). One study focused on the drift of Trichoptera in a temperate stream in Southwest England (Elliot 1968). Several studies have focused on *Baetis* species or mayflies exclusively (Waters 1966, Corkum & Pointing 1979, Ploskey & Brown, 1980, Skinner, 1985, 1985, Richards & Minshall 1988, Wilzbach, 1990, Forrester 1994, Lancaster 1992, Hershey et al. 1993, Kratz 1996). In a study

from Wales the most common taxonomic groups found in drift were Plecoptera, Ephemeroptera, Diptera, and Trichoptera (Hemsworth & Brooker 1979).

Müller (1954) demonstrated from the Boreal Forest Biome that drift composition was different from the benthic community. Particular groups of animals such as Hydracarina and Coleoptera often form a relatively large portion of the benthos community, but seldom occur in drift. In a French study using a 200 m long artificial stream it was clearly established that not all benthos participate in drift (Neveu 1980). The artificial stream was stocked with 24 different orders of invertebrates at a density close to the nearby river, which served as a source. However, their standing biomass was higher than in the river. Mostly, the drift was made up of Baetidae, Trichoptera, Chironomidae, Simuliidae, Gammaridae and some Coleoptera. Noteworthy is the great differences in drift rates within insect orders. Another French study on drift in the Rhône River demonstrated that the composition of drift in large rivers is different than the composition in low order streams (Cellot 1996). Hydra, Gammarus, Diptera and Chironomidae accounted for over 40% of the drift. Likewise, Chironomidae made up the majority of drift in an Idaho high elevation mountain stream (Tilley 1989). Another study of Boreal streams indicated that Ephemeroptera, Plecoptera, Trichoptera, and Simuliidae dominated (>90%) the drift composition in March and April (Shubina & Martynov 1990). Interestingly, drift in Arctic streams in northern Alaska (Slack et al. 1977) and north of the Arctic Circle in Norway (Johansen et al. 2000) were dominated by the same taxonomic groups (orders and superfamilies). Immature stages of mollusks were observed to be a major portion of drift in a Minnesota stream running through agricultural fields (Marsh 1980). A laboratory investigation of 23 larval species representing Ephemeroptera, Plecoptera, and Trichoptera revealed different drift behaviors. Mayflies seemed to swim often leading to drift, while caddis larvae were reluctant to do so.

Stonefly nymphs were intermediate. Differences among taxa seemed more important in explaining swimming activity compared to habitat preferences (Otto & Sjöström 1986). This may very well explain observed field differences. Mollusks were also well represented in a drift study of a stream running through moorland with no canopy cover in western England (Armitage 1977).

Results from a Neotropical stream demonstrated that shrimp larvae constituted an important component of the drift, which is quite different from temperate streams (Ramirez & Pringle 1988, Pringle & Ramirez 1998), but traditional drifting taxa such as Ephemeroptera, Coleoptera, Tricoptera, and Diptera were also noted as a significant contribution to the drift (Pringle & Ramirez 1998). Results from a forest stream in Hong Kong also showed that the 'traditional' drifting taxa were well represented (Dudgeon 1983, 1990).

8 Conclusion – Future Research Needs

In the past half-century, most studies on stream drift have concentrated on the underlying biotic and abiotic processes that cause drift as outlined in Fig. 1 (Brittain & Eikeland 1988, Speirs & Gurney 2001). Pringle & Ramirez (1998) suggested that drift be used as a standard component of bioassessment because it provides complimentary information to traditional benthic sampling. Other studies have concentrated on macroinvertebrate drift as a food source for fish (Allan 1981, Wilzbach et al. 1986, Shubina & Martynov 1990, LaVoie IV & Hubert 1994). Although stream ecologists have incorporated the landscape perspective for several decades (Vannote et al. 1990, Naiman et al. 1992, Allen & Johnson 1997, Polis et al. 1992 Townsend et al. 1997, Hershey & Lamberti 1998, Cederholm et al. 2000), macroinvertebrate drift has not been consistently incorporated.

However, the greatest need for future research involving macroinvertebrate drift seems to be on the landscape level. Total drift measured across landscapes will provide a cumulative measure of all the factors involved (Fig.1), but drift can be measured in response to landscape changes as a result of human activities, which typically alter many of the abiotic as well as the biotic factors simultaneously. In particular, drift export from fishless headwater streams into fish-bearing streams needs to be investigated in greater detail. In mountainous regions, headwater streams drain the greatest amount of surface area (Naiman & Décamps 1990) and due to the steepness of the terrain they are usually fishless (Wipfli & Gregovich 2002) or they have very low densities (Allan 1982) with minimal influence on the downstream export of drift. Additionally, other stream dwelling vertebrates such as the harlequin duck *Histriónicus histriónicus* (Rodway 1998, Robert & Clutier 2001) and the dippers *Cínclus sp.* (Santamarino 1993, Tyler & Ormerod 1994) would benefit from a downstream export of macroinvertebrates. Stream drift needs to be evaluated in the context of other ecological processes on the sub-basin or watershed level including their riparian areas. In addition, the relationship between forest and agricultural management activities needs to be addressed.

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10 Acknowledgements
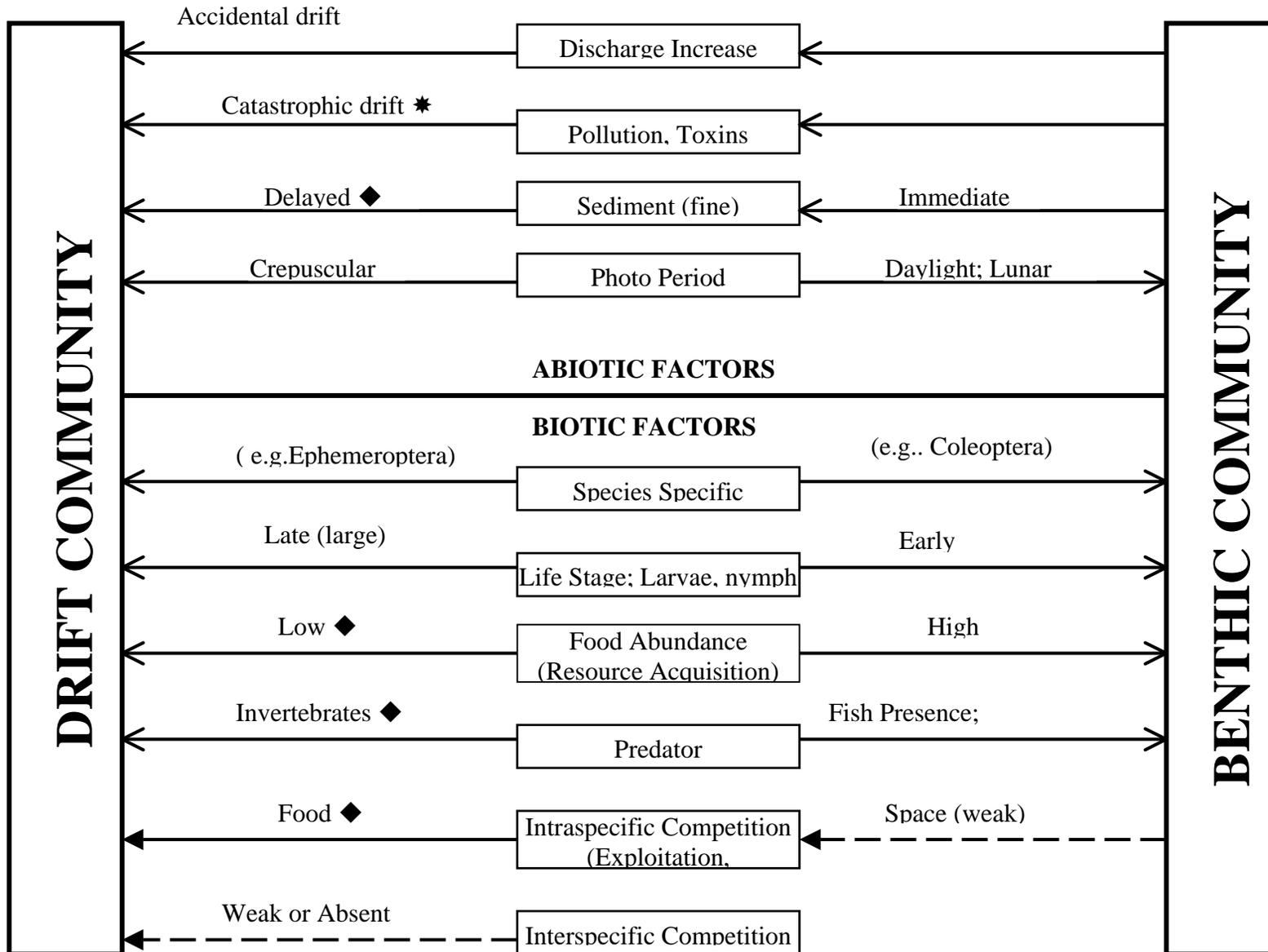
Fig. 1. A conceptual model of abiotic and biotic factors regulating macroinvertebrate drift in lotic ecosystems. The magnitude of drift at a given moment is dependent on the cumulative effect of all factors present at a given time, hence predicting the likelihood of a benthic organism entering into drift. (◆ active drift, ✸ passive drift)

Table 1. Drift rates of aquatic organisms (mean values or ranges) from selected macroinvertebrate field studies by biogeographic (Wallace 1876) and political regions, Holdridge's life zones (Heywood & Watson 1995), and biome (Cox & Moore 1993), number of months, years of study, and actual months sampled by Roman numerals. Stream order, land use and discharge included if available.

	Life Zone	Biomes	Land Use	Stream Order	No. of Months	Year	Months	Discharge (m^3s^{-1}) (mean or range)*	Drift Rate (individuals)	Source
Australian Region										
Australia, ACT	Warm Temp.	Sclerophyll Forest			2	1978	VII-IX		26.8 hour^{-1} †	Bailey, 1981a
Australia, ACT	Warm Temp.	Sclerophyll Forest			4	1978	III-VII	334-1900 $m^{-3} h^{-1}$	982-1071 d^{-1}	Bailey 1981b
Australia, Queensland	Tropical	Mesophyll Vine Forest	Forest	3	14	1983/84	IV-XII II-VI		0.36-3.98 m^{-3}	Benson & Pearson 1987
Australia, Victoria	Warm Temp.	Sclerophyll Forest	Forest	0.1		1976	X	75-87 $m^3 d^{-1}$	267-401 net^{-1}d^{-1}	Cadwallader & Eden 1977
New Zealand	Cool Temp.	Range	Range		5	1964/65	I-VII		1.41-46.30 m^{-3}	McLay, 1968
New Zealand	Cool Temp.	Deciduous Forest	Grassland	1-3	2	1993	I-II		3.9-7.7 m^{-2}d^{-1}	Edwards & Huryn 1996
Ethiopian Region										
Ivory Coast	Tropical	Tropical rain forest	Forest						0-220 h^{-1}m^{-2}	Statzner et al. 1984/85
Nearctic Region										
Alaska	Polar	Arctic Tundra	Range	4	10	1984-90	VI-VIII	0.32 to 3.8	0.05-1.51 m^{-3} †	Hershey et al. 1993
Alaska	Cool Temp.	Coniferous Forest	Forest	2	3	1989	VI-VIII		25-150 mg d^{-1}	Hetrick et al. 1998
Alaska	Polar	Arctic Tundra	Wilderness	1	1	1971	VIII	0.05	240 h^{-1}net^{-1}	Slack et al. 1976

Alaska	Polar	Arctic Tundra	Wilderness	2	1	1971	VIII	0.5	70 h^{-1}net^{-1}	Slack et al. 1976
Alaska	Polar	Arctic Tundra	Wilderness	3	1	1971	VIII	1.4	72 h^{-1}net^{-1}	Slack et al. 1976
Alaska	Subpolar	Boreal Forest	Wilderness	4	1	1971	VIII	2.7	53 h^{-1}net^{-1}	Slack et al. 1976
Alaska	Subpolar	Boreal Forest	Wilderness	5	1	1971	VIII	3.5	30 h^{-1}net^{-1}	Slack et al. 1976
Alaska	Polar	Arctic Tundra	Wilderness	1	2	1981	X-XI	0.02	0.21-13.1 m^{-3}	Miller & Stout 1989
Alaska	Polar	Arctic Tundra	Wilderness	1	2	1982	V-VI	1.03	0.004-0.27 m^{-3}	Miller & Stout 1989
Alaska	Polar	Arctic Tundra	Wilderness	1	2	1982	VII-IX	0.04	0.001-0.034 m^{-3}	Miller & Stout 1989
Alaska	Polar	Arctic Tundra	Wilderness	1	2	1983	VI-VII	0.04	0.011-3.7 m^{-3}	Miller & Stout 1989
Alaska	Subpolar	Taiga	Wilderness	4	2	1981	X-XI	0.86	0.03-1.9 m^{-3}	Miller & Stout 1989
Alaska	Subpolar	Taiga	Wilderness	4	2	1982	V-VI	1.82	0.16-3.8 m^{-3}	Miller & Stout 1989
Alaska	Subpolar	Taiga	Wilderness	4	2	1982	VII-IX	0.66	0.07-0.7 m^{-3}	Miller & Stout 1989
Alaska	Subpolar	Taiga	Wilderness	4	2	1983	VI-VII	1.11	0.01-2.1 m^{-3}	Miller & Stout 1989
Alaska	Cool Temp.	Deciduous Forest	Forest	2	3	1989	VI-VIII		25-150 mg d^{-1}	Hetrick et al. 1998
Alaska	Cool Temp.	Deciduous Forest	Clearcut	2	3	1989	VI-VIII		30-120 mg d^{-1}	Hetrick et al. 1998
Alaska, Southeast	Cool Temp.	Coniferous Rainforest	Forest	1	25	1996 1997 1998	II-XII I-XII I-II	1.2-3.6 Ls^{-1}	5-6000 stream^{-1}d^{-1} 2.4 (1-22) m^{-3}	Wipfli & Gregovich 2002
Arizona	Sub-tropical	Desert			3	1979	VI-VIII		663-3229 m^{-2}d^{-1}	Gray & Fisher 1981

Location	Zone	Vegetation	Habitat	Col5	n	Year	Months	Value1	Value2	Reference
Arizona, Utah, Nevada	Montane	Coniferous Forest	Variable		1 3	1993 1994	IX I-IV	141-566	2.3-5.9 gm^{-3}s^{-1}	Shannon et al. 1996
Arkansas	Warm Temp.	Deciduous Forest	Forest	2	1	1977	VI		0.024-0.125 m^{-3} †	Ploskey & Brown 1980
British Columbia	Cool Temp.	Model		2	2	1990	V, VII	1	0.1-120 hour^{-1} †	Lancaster 1992
British Columbia	Cool Temp.	Coniferous Rainforest	Forest	3	1	1979	VIII		669-2079 d^{-1} ‡	Culp et al. 1986
California	Montane				1	1993	IX	0.7 to 3.4	3-165 d^{-1} †	Kratz 1996
Colorado	Subalpine	Range	Grazing	3	1 5	1979 1980	XII II, IV, VI, VIII, X	0.12-2.73	21595 m^{-1}d^{-1} (stream width)	Bergey & Ward 1989
Colorado	Montane	Deciduous Forest			4	1975/76	VII, VI	0.58-0.68	12.48-22.00 m^{-3}	Allan 1982
Colorado	Alpine	Alpine	Wilderness		6	1975-77	VI-X		0.2-104 hour^{-1}	Allan 1981
Florida	Sub-tropical	Mixed Forest			13	1971/72	XII-XII	2.86 (0.015-32.5)	0.03-0.49 m^{-3} †	Cowell & Carew 1976
Florida	Sub-tropical	Deciduous Forest	Forest	3	11	1979/80	II-I		1-92 d^{-1}	Soponis & Russell 1984
Georgia	Warm Temp.	Floodplain Swamp		6	13	1981/82	XII-XII	50.7	20.426 m^{-3}	Benke et al. 1991/94
Georgia	Warm Temp.	Floodplain Swamp		6	12	1983	I-XII	79.1	22.775 m^{-3}	Benke et al. 1991/94
Idaho	Montane				4	1967	VII-IX, XI	0.01-0.08	2.034-334.0 m^{-3}	Minshall & Winger 1968
Idaho	Montane			3	1	1977	VII	0.43	1.46-22.9 m^{-3}	Tilley 1989
Idaho	Montane	Coniferous Forest	Forest	1	3	1983/85	VI-VIII	0.1	2.31-5.84 100 cm^{-2}hr^{-1}	Richards & Minshall 1988

Location	Climate	Vegetation	Habitat			Year	Month		Density	Reference
Idaho	Montane	Coniferous Forest	Forest	3	1	1983	X		77-1356 m^{-3}	Skinner 1985
Kentucky	Warm Temp.	Deciduous Forest	Forest Reserve	1	2	1977	VII-VIII	0.17	0.082-6.322 m^{-3}	Mancini et al. 1979
Maryland	Warm Temp.	Coniferous Forest	Forest	2	1	1986	VIII	0.1 - 0.5	240-630 m^{-3}	Wilzbach & Cummins 1989
Maryland	Warm Temp.	Deciduous Forest	grazing	2	2	1988	VII-VIII	0.1	12-18 hour^{-1} †	Wilzbach 1990
Michigan	Cool Temp.	Model							45-120 net^{-1}d^{-1} †	Hildebrand 1974
Minnesota	Cool Temp.	Deciduous Forests	Agriculture	2	9	1975 1976 1977	IX-XI I, IV-VI, XI; I	0.015	1-1398 net^{-1}d^{-1}	Marsh 1980
Minnesota	Cool Temp.	Mixed Forests	Forest		13	1971/71	VI-VI	0.7	674 d-1 †	Hall et al. 1980
Minnesota	Warm Temp.	Deciduous Forest			2	1981	VI-VII	main 471-1305 sidearm 32-393	main 1.10-3.30 m^{-3} sidearm 3.33-7.22 m^{-3}	Eckblad et al. 1984
Montana	Cool Temp.	Range		3	12	1980/81	VI-V	4.1-96.3 (peak: 283)	80-700 100m^{-3}	Perry & Perry 1986
New Hampshire	Cool Temp.	Deciduous Forests	Forest		2	1980	III-IV		0.25-2.8 m^{-3} †	Haney et al. 1983
New Hampshire	Cool Temp.			2	3	1989 1990	VIII VI, VIII		301-1546 d^{-1} †	Forrester 1994*a*
North Carolina	Warm Temp.	Deciduous Forest		1	1	1985	XII	0.81 Ls^{-1} (0.05-22.8)	120 d^{-1}	Wallace et al. 1989
North Carolina	Warm Temp.	Deciduous Forest	Forest		12	1977/78	VI-V	485.5-3352.0	859-9507 d^{-1}	O'Hop & Wallace 1983
Ontario	Cool Temp.	Coniferous			1	1981	IX	0.45-0.76	458.3-1603 d^{-1}	Williams 1990

Location	Zone	Forest	Land use		N	Year	Months			Reference
Ontario	Cool Temp.	Mixed Forests	Agriculture		15	1966/67	VII-IX	0.1-20	48,00-257,000 d^{-1}	Bishop & Hynes 1969
Ontario	Cool Temp.	Coniferous Forest	Agriculture		12	1977	I-XII		1.25-5067 $hour^{-1}$	Bird & Hynes 1981
Oregon	Montane				12	1967/68	VII-VI	2.8 (0.03-5.7)	332-1614 d^{-1}	Lehmkuhl & Anderson 1972
Oregon	Warm Temp.	Coniferous Forest	Forest		1	1964	II		100-1200 3 hrs^{-1}	Anderson 1966
Oregon	Warm Temp.	Coniferous Forest			5	1967/68	V, VII-IX, II		377-3046 d^{-1} †	Anderson 1967
Pennsylvania	Cool Temp.	Deciduous Forest	Ruderal	1-2	2	1981	VII, IX	0.082	0.702 m^{-3}	Light & Adler 1983
Pennsylvania	Cool Temp.	Deciduous Forest	Ruderal	1-2	2	1981	VII, IX	0.063	0.998 m^{-3}	Light & Adler 1983
Quebec	Cool Temp.			2	13	1981 1982	VI-VII I-VI		0.003-0.9m^{-3}	Lauzon & Harper 1988
Quebec	Cool Temp.	Boreal Forest	Forest		1	1986	V	600 $m^{3}s^{-1}$ (200-1600)	day: 0.025-3 m^{-3} night: 0.25-2.2 m^{-3}	Hudon 1994
South Carolina	Warm Temp.	Deciduous Forest	Deciduous Forest		2	1990	V-VI	2.15	46 d^{-1} †	Rader & McArthur 1995
Wyoming	Alpine	Alpine/ Subalpine	Wilderness	2	4	1989-92	XI, II, II, II		1-6 m^{-3}	Pennuto et al. 1998
Wyoming	Alpine	Alpine	Wilderness	2	3	1985	VII-IX	0.01 -0.78.	88-249 hr^{-1}	Hubert & Rhodes 1989
Wyoming	Montane	Range	Grazing		2	1992	VII-IX	0.15-3.68	0.50-167 $m^{-3}d^{-1}$	LaVoie IV & Hubert 1994

Neotropical Region

Location	Zone	Forest	Land use		N	Year	Months			Reference
Costa Rica	Tropical	Evergreen Forest		4	2	1993	XI-XII		0.7-11.8m^{-3}	Ramirez & Pringle 1988
					8	1994	I-V, VIII			

Country	Climate	Vegetation	Land use	Order	N	Year	Months	Discharge	Value	Reference
Ecuador	Tropical	Alpine	Shrubland		6	1976/77	VIII-VII	0.013-0.03	0.68-2.82 m^{-3}	Turcotte & Harper 1982
Venezuela	Tropical	Deciduous Forest		3 & 4	2	1987/88	XII-I		0.48-900 m^{-3} †	Flecker 1992
Venezuela	Tropical	Evergreen Forest	Forest	4	2	1987/88	XII-I		80-1700 m^{-3}d^{-1}	Flecker 1990

Oriental Region

Country	Climate	Vegetation	Land use	Order	N	Year	Months	Discharge	Value	Reference
Hong Kong	Tropical	Evergreen Forest			1	1978	XI		775-1050 d^{-1}	Dudgeon 1983
Hong Kong	Tropical	Evergreen Forest	Forest		12	1983/84	VII-VI		2.78 ±0.25 5 (spate)	Dudgeon 1990
Nepal	Montane	Evergreen/ deciduous	Forest	3 & 2	2	1993	VI-VII		1.35 m^{-3} (0.23-3.46)	Brevin & Ormerod 1994

Palearctic Region

Country	Climate	Vegetation	Land use	Order	N	Year	Months	Discharge	Value	Reference
Austria	Montane	Coniferos Forest	Reserve		13	1989/90	IV-VIII IX-III IV-VIII IX-III	8640-475200 m^{3}d^{-1}	2.5 ± 0.32 m^{-3} 2.01 ±0.22 m^{-3} 2.5 ± 48 mg m^{-3} 1.04±0.12 mg m^{-3}	Waringer 1992
Denmark	Warm Temp.	Deciduous Forest	Forest		12	1974/75	X-IX	30 Ls^{-1} m^{-1} (1-142)	0-1672 d^{-1} †	Iversen 1980
England, UK	Warm Temp.				9 12 8	1980 1981 1982	IV-XII I-XII I-VIII		5-400 m^{-3} †	Williams 1985
England, UK	Warm Temp.	Deciduous Forests	Moorland	1-2	6 7	1971 1971/72	IV-IX X-IV	0.45-3.98 (23 spate)	7.34-14.44 m^{-3} 0.24-1.68 m^{-3}	Armitage 1977
France	Warm Temp.	Deciduous Forest	Forest/ agriculture		3	1972/73/ 74	VI	45-150 m^{3}h^{-1}	1.40-5.47 m^{-3}	Neveu & Échaubard 1975
France	Warm Temp.	Deciduous Forest	Forest/ agriculture	7	1	1985	VII	536 ±36	2.14-4.24 m^{-3}	Cellot 1989*a*

Country	Climate	Vegetation	Land use		Sites	Year	Months			Reference
France	Warm Temp.	Deciduous Forest	Forest Wilderness	6	24	1989/90	I-XII	main down 80-1000 main up 80 150 sidearms 0.1 0.2	2.94-3.16 m^{-3} 3.28-3.59 m^{-3} 6.77-7.68 m^{-3}	Cellot 1996
France, Pyrénées	Montane Alpine	Conif. Forest	Forest Wilderness	4	15	1971-73	VII-XI, IV	0.07-0.42	0.02-0.56 m^{-3} †	Lavandier 1992
France, Pyrénées	Montane Alpine	Conif. Forest	Forest	4	15	1971-73	VII-XI, IV		42 hour^{-1} †	Lavandier & Cereghnio 1995
Japan, Northern	Cool Temp.	Mixed Forest	Forest	3	8	1991-94	VI-VIII	0.4-1.5	0.1-1.0 mgs^{-1} (entire stream)	Nakano et al. 1999
Morocco	Sub-tropical	Maki		2-3	1	1985	V	0.1-15	2.59-5.19 m^{-3}	Badri et al. 1987
Norway	Boreal	Coniferous Forest	Forest		5	1988	VI-X	0.9 (0.05-1.9)	1.2-2.7 m^{-3}	Johansen 1990
Norway	Boreal	Coniferous Forest	Forest		5	1988	VI-X	1.34 (0.05-3.3)	2.5-19.2 m^{-3}	Johansen 1990
Norway	Boreal	Boreal Deciduous Forest	Wilderness	3	4	1996	V, VI, VIII, X	0.5	2.42-7.72 m^{-3}	Johansen 2000
Spain	Warm Temp.	Deciduous Forest	Forest & agriculture		6	1986 1987	VII-VIII, X I, III, V		0.03-0.16 m^{-3}	Rincón & Lóban-Cerviá 1997
Sweden, North	Boreal	Boreal Forest	Forest		6	1953	V-X		35-408 10 dm^{-2}d^{-1}	Müller 1954
Sweden, South	Cool Temp.				1	1984	VI		1200-6375d^{-1}	Andersson et al. 1986
Sweeden, Southern	Cool Temp.				2	1985 1986	IX V		0.04-1.08 m^{-3} †	Malmqvist & Sjöström 1987
Switzerland	Montane	Coniferous Forest	Forest	6	2	1993 1994	II VII	3.4 (max 30)	28.78-1041.28 m^{-3}	Matthaei et al. 1997
USSR, European	Boreal	Taiga	Natural		3	1985 1986/87	IV IV, III		0.55-1.94 m^{-3}	Shubina & Martynov 1990
Wales, UK	Warm Temp.			2 & 3	2	1975	V-VI	0.7-5.0	44000-698000 d^{-1}	Brooker & Hemsworth

1978

Wales, UK	Warm Temp.	Range	Grazing	1	12	1983/84	VIII-VII	25-500 over 15 cm substrate d^{-1}	Williams & Williams 1993
Wales, UK	Warm Temp.				8	1975/76	III-V, VII, VIII, XI, XII, II	34,000-798,000 d^{-1}	Hemsworth & Brooker 1979

* If discharge measurements were not given in m^{3}s^{-1} by the source, if possible, values were converted from Ls^{-1} or total discharge over a given time frame.

† Study focused on one or a few species. Total drift not assessed.

‡ Field manipulation study.

Table 2. Drift export of coarse particulate organic matter (CPOM) in lotic ecosystems by political region, Holdridge's life zones (Heywood & Watson 1995), biome (Cox & Moore 1993), number of months, years of study, and actual months sampled by Roman numerals. Land use provided if available.

Political Region	Life Zone	Biome	Land Use	No. of Months	Years	Months	CPOM*	Source
Alaska	Cool Temp.	Temp. Coniferous Forest	Oldgrowth Forest	25	1996 1997 1998	II-XII I-XII I-II	§ 240 mg m^{-3} (10-1360)	Wipfli & Gregowich 2002
Alaska	Polar Subpolar	Tundra Taiga	Wilderness	8	1981/ 82/83	X-XI, V-VI, VII-IX, VI-VII	9.4 mg m^{-3} 393.8 mg m^{-3}	Miller & Stout 1989
Austria	Montane	Coniferous Forest	Reserve	12	1989/90	IV-III	§ 0-27 mg m^{-3}	Waringer 1992
British Columbia	Cool Temp.	Coniferous Forest	Forest	12	1997/98	V-IV	0-0.4 mgL^{-1}	Kiffney et al. 2000
Hawaii	Tropical	Evergreen Tropical Forest	Agriculture & Forest	14	1998/99	II-XII, I-III	1533.7 ± 944.4 g d^{-1}	Larned 2000
Idaho	Montane	Temp. Coniferous Forest/range	Forest & Grazing	5	1977/78	III, VI-VII, IX-X	1-74 mg m^{-3} 8-488 mg m^{-3} 5-360 mg m^{-3} 1-17 mg m^{-3}	Minshall et al. 1992
Model Stream							†2-26(storm) mgL^{-1}	Mulholland et al. 1985
Nepal	Montane	Evergreen/ deciduous	Forest	2	1993	VI-VII	32-40 d^{-1}	Brewin & Ormerod 1994
Nepal	Montane	Evergreen/ deciduous	Agriculture	2	1993	VI-VII	1-53 d^{-1}	Brewin & Ormerod 1994
New Zealand	Cool Temp.	Grassland	Riparian Tussock	4	1995/96	I-IV	0.001-0.630 mgL^{-1}	Young & Huryn 1997
North Carolina	Warm Temp.	Mixed Forest	Forest Reserve	12	1977/78	VI-V	12.046 g day^{-1} (0.223-33.132)	O'Hop & Wallace 1983
North	Montane	Temp.	Forest	12+	1985-93	I-XII	0.106-0.171 mg L^{-1}	Wallace et al. 1995

Carolina		Forest						
North Carolina	Warm Temp.	Mixed Forest	Forest	12	1984/85	I-XII	1096-5301 g str.$^{-1}$y^{-1}	Cuffney et al. 1990
Quebec	Cool Temp.	Boreal Forest	Mixed Forest	1	1986	V	1.5-9.5 mg m^{-3}	Hudon 1994
Quebec	Cool Temp.	Boreal Forest	Mixed Forest	5 6	1979 1980	VI-X IV-VI, IX-XI	1.0-6.7 g m^{-2}year^{-1}	Naiman 1983
South Africa	Maki (Chaparral)	Fynbo Shrubland	Grazing Pre-fire	12	1986/87	II-II	0.002-0.5 g m^{-3}	Britton 1990
South Africa	Maki (Chaparral)	Fynbo Shrubland	Grazing Post-fire	12	1986/87	II-II	0.008-1.0 g m^{-3}	Britton 1990
Sweden	Cool Temp.	Deciduous Forest	Forest & Agriculture	12	1975/76	IX-I, II-V, VII-XII	‡ 10-22,000 g d^{-1} ‡ 10-42,000 g d^{-1} ‡ 1-9,510 g d^{-1}	Malmqvist et al. 1978
Tennessee	Subtropical	Deciduous Forest	Forest	1	1978	VI	5000 mg d^{-1}m^{-1}	Newbold et al. 1983
Washington	Cool Temp.	Coniferous Forest	Oldgrowth 25 Year Old	12	1982-84	VI-V	0.001-0.400 mg L^{-1} 0-0.100 mg L^{-1}	Bilby & Bisson 1992

∗ Defined as >5, >4, or >1 mm depending on study. ‡ Leaf particles only, no wood.
† Reported as seston and may include fine silt particles. § Reported as detritus.

Table 3. Stream drift rates of terrestrially derived invertebrates from selected field studies by political region, Holdridge's life zones (Heywood & Watson 1995), and biome (Cox & Moore 1993), number of months, years of study, and actual months sampled by Roman numerals. Land use provided if available.

Political Region	Life Zone	Biome	Land Use	No. of Months	Years	Months	Terrestrial Drift † (Individuals or mg)	Source
Alaska	Cool Temp.	Deciduous Forest	Forest	7	1988 1989	V-VII, X V, VII-VIII	25-120 mg m^{-2} d^{-1}	Hetrick et al. 1998
Alaska	Cool Temp.	Deciduous Forest	Clearcut	7	1988 1989	V-VII, X V, VII-VIII	39-100 mg m^{-2} d^{-1}	Hetrick et al. 1998
Alaska	Cool Temp.	Coniferous Forest	Forest	25	1996 1997 1998	II-XII I-XII I-II	01-15.5 m^{-3}	Wipfli & Gregowich 2002
Ecuador	Subalpine	Alpine	Shrubland	1	1976	X	476 d^{-1}	Turcotte & Harper 1982
				1	1976	XII	370 d^{-1}	
				1	1977	I	395 d^{-1}	
				1	1977	III	1084 d^{-1}	
				1	1977	V	518 d^{-1}	
				1	1977	VII	481 d^{-1}	
England, UK	Warm Temp.	Deciduous Forest	Moorland	5 7	1971 1971/72	IV-IX X-IV	(summer) 0.20 mg m^{-3} (winter) 0.03-0.07 mg m^{-3}	Armitage 1977
France	Warm Temp.	Deciduous Forest	Forest & agriculture	3	1972/73/ 74	VI	1.29-3.83 m^{-3}	Neveu & Échaubard 1975
Japan, Northern	Cool Temp.	Mixed Forest	Forest	12	1995/96	III-II	0.2-71.8 mg d^{-1} m^{-2}	Kawaguchi & Nakano 2001
Japan, Northern	Cool Temp.	Mixed Forest	Grassland	12	1995/96	III-II	0.07-29.87 mg d^{-1} m^{-2}	Kawaguchi & Nakano 2001
New Zealand	Cool Temp.	Deciduous Forest	Tussock Grassland	12	1992/93	XI-X	0.8-4.9 mg m^{-2} d^{-1}	Edwards & Huryn 1995
New Zealand	Cool Temp.	Deciduous Forest	Pasture	2	1993	I-II	1.32 mg m^{-2} d^{-1}	Edwards & Huryn 1996
New Zealand	Cool Temp.	Deciduous Forest	Tussock Grassland	2	1993	I-II	11.56 mg m^{-2} d^{-1}	Edwards & Huryn 1996

New Zealand	Cool Temp.	Deciduous Forest	Forest	2	1993	I-II	5.67 mg m^{-2} d^{-1}	Edwards & Huryn 1996
Norway	Subpolar	Boreal Forest	Deciduous Forest	4	1996	V, VI, VIII, X	0-1.56 m^{-3}	Johansen et al. 2000
Ontario	Cool Temp.	Coniferous Forest	Forest & agriculture	13	1975/76	VI-VI	0.39 kg y^{-1} 1.63 kg y^{-1} 2.67 kg y^{-1} 6.81 kg y^{-1}	Dance & Hynes 1979
Spain	Warm Temp.	Deciduous Forest	Forest & agriculture	6	1986 1987	VII-VIII, X I, III, V	0.012-0.09 m^{-3}	Rincón & Lóban-Cerviá 1997
Virginia	Warm Temp.	Deciduous Forest	Forest	5	1986	IV-VIII	5-75 net^{-1} per 15 min	Garman 1991

† Lack of weight measure indicates number of individuals.