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Invertebrate Drift-Ecology and Significance to Stream Fishes[1]

ABSTRACT

Many species of invertebrates, though not all, exhibit high rates of downstream drift in a diel periodicity. Most are night-active, for whom light intensity is the phase-setting mechanism; but some species are day-active, for whom water temperature may be the phase-setter. Diel patterns consist of one or more peaks, occurring at various times of the 24-hour period depending on species. Magnitude of the drift appears to be a function of water temperature, current velocity, stage of life cycle, and population density and growth rate.

The direct significance of invertebrate drift to stream fish is in an apparent increase in availability as food. Whereas stream salmonids utilize drifting invertebrates as food to varying degrees, a substantial proportion of the diet is also gained by bottom foraging.

INTRODUCTION

It is now well known that many species of stream invertebrates — those we usually consider as members of the bottom fauna — drift downstream as a natural occurrence. Sometimes drift occurs in extremely large quantities, raising questions about the capacity of the stream to sustain such high rates of attrition. Usually these high rates of drift occur within some pattern of diel periodicity[2], with inflections occurring at regular and predictable times of the 24-hour period (Tanaka 1960; Waters 1962a; Müller 1963a,b).

Drift in a diel periodicity appears to be the result of some behavioral characteristic of the animal, but drifting also occurs, at lower rates, continuously or randomly as a normal event in streams (Dendy 1944). In addition, and to an extremely variable degree, drift occurs as the result of some physical disturbance, usually floods, with sometimes catastrophic consequences for the invertebrate populations (Moffett 1936; Minckley

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[2] "Diel periodicity" is used here as synonymous to "diurnal periodicity," used in my previous reports and elsewhere, meaning a recurring pattern with a period of 24 hours. To avoid confusion with the use of "diurnal", referring only to the daylight hours, "diel" is specific and clearly preferable. The term "circadian rhythm" is generally reserved to indicate an endogenous rhythm, the period of which is approximately 24 hours in its free-running state (Pitendrigh 1960).

1964; many others). These three "types" of drift were recognized in a simple classification as *behavioral*, *constant*, and *catastrophic* drift, respectively (Waters 1965). It is true that there may be interactions between two or more types, that it is not always possible to distinguish among the three, and that to the individual organism, suddenly caught in a rush of current, the effect may be the same. Nevertheless, the causes and effects on invertebrate populations, as well as on the rest of the stream community, may be decidedly different among these types. It is the first of these, behavioral drift, that has been a subject of much recent investigation throughout the world.

Three major areas of interest can be identified. First, studies on the descriptive nature and ecology of the periodicity phenomenon: these include the shape of diel patterns; environmental phase-setting mechanisms and their relation to circadian activity rhythms; factors affecting the magnitude of the drift, particularly at maximum times within the 24-hour period; and the taxa that are or are not involved. Second, the function of high drift rates in the production ecology and life histories of the invertebrates themselves: this problem includes the distance of displacement; the effect on emergence periods; phenological and life history factors affecting diel periodicity and magnitude; the relation of drift rate to population density and production; and the effect of attrition and possible upstream return mechanisms. Third, the significance of the drift phenomenon to the invertebrates' main predators, stream fishes: this area includes drift as a means of food transport affecting fish carrying capacities of stream sections downstream from the drift source; the moving organism as a more available food item; and the relative reliance of fish on drift feeding or bottom foraging.

Information in all areas is far from complete, although new problems have been defined. Considerable basic information has been published, though for the most part fragmentary; tentative generalizations reached so far invariably have exceptions and no doubt will be modified or possibly reversed as more data accumulate; general hypotheses remain open to further testing. The investigation of drift has raised questions important to stream fishery management as well as in the ecology of stream invertebrates. It has offered new techniques in the study of streams and raised questions about some old ones. And it has pointed up some fundamental differences between the operation of stream and lake ecosystems.

DIEL PERIODICITY

Most species exhibiting a diel periodicity in drift are night-active — i.e., the drift occurs primarily at night and little during the daytime (*see also* Anderson 1966,1967; Elliott 1965a,b, 1967a,b; Levanidova and Levanidov 1965; Madsen 1966; Müller *et al.* 1963; Schwarz 1967). Changes in drift within a 24-hour period are often precipitous. Darkness appears to be required for high drift; i.e., it does not appear to be a crepuscular phenomenon. However, some species are day-active, and exhibit highest rates of drift during the daytime (Müller 1966a; White 1966; Anderson 1967; Waters 1968).

It seems most likely that diel drift periodicities are the result of circadian activity rhythms entrained by cyclic factors, or *Zeitgeber* (Aschoff 1960), in the external environment. Harker (1953) demonstrated rhythmic activity of mayfly nymphs held in constant darkness, constant light and reversed illumination, the greatest activity occurring during periods of normal night-time. Elliott (1967a) and Schwarz (1967) reported continued rhythmic drift in constant darkness; however, Müller (1966b) reported arhythmic drift after only one normal cycle in continuous darkness over a natural stream. Continuous artificial light, in either laboratory or natural streams, apparently inhibits the activity and eliminates a drift periodicity (Elliott 1965a; Müller 1965a, 1966a; Holt and Waters 1967); Müller (1966a) reported arhythmic drift in the constant light of the

polar summer. Thus, in the case of night-active periodicities, the entraining factor appears clearly from experimental evidence to be light. It appears to act only as an "on-off", or triggering, mechanism; i.e., there is a threshold effect (about 1 lux, or less), and natural light changes above the threshold, such as those due to cloudy weather during the daytime, do not affect the drift (Holt and Waters 1967). However, Anderson (1966) has indicated a depressant effect of moonlight, and Müller (1966a) has observed both higher and lower night-time drift (different species) in a stream section artificially shaded continuously for several days.

In day-active periodicities, water temperature may be the entraining factor. In one reported case, drift of the trichopteran *Oligophlebodes sigma* increased parallel with water temperature as it normally increased during the daytime and decreased in the evening and night. The daily pattern approximated a sine wave, while light intensity did not appear to affect the drift in any way (Waters 1968).

Diel activity rhythms in many groups of animals most commonly include two peaks during the 24-hr period (Aschoff 1966), and this also appears to be the case with invertebrate drift. Müller (1965b, 1966a) has recently emphasized two common types of diel pattern with two peaks in drift: the *bigeminus* pattern with the major peak occurring first (i.e. after sunset) and the *alternans* pattern, in which the lower of the two peaks occur first and the major peak just prior to dawn. Müller further suggests that in the shortest nights of summer the minor peak is eliminated, while three peaks may occur in the longer nights of winter. Müller reported the *bigeminus* pattern for the amphipod *Gammarus pulex* and the *alternans* pattern for two species of *Baetis* mayflies in Germany. In Minnesota, the *bigeminus* type was observed for the amphipods *Gammarus pseudolimnaeus* (Waters 1962a; and Fig. 1) and *Hyalella azteca* (Koslucher and Madson 1966); both patterns were observed for different species in the mayfly genus *Baetis* (Waters 1962a; and Fig. 1). However, some species simply show an unorganized increase at night without definite peaks, particularly at low drift rates.

A major factor affecting the magnitude in diel periodicities is current velocity. It would seem obvious that excessive current velocities would increase drift, up to the point of catastrophic conditions, and many authors report higher drift with higher velocities. However, Elliott (1967a,b) measured drift in density units — i.e., number of organisms per unit volume of water — and observed that daily drift densities remained relatively constant over a short period of time, such as a month, even in abnormal discharge with higher current velocity. Under such conditions, however, the quantity of organisms passing a sampling point per unit time (drift rate) is higher because of the increased discharge. Certain abnormal velocities appear to have a great effect on drift rate if they occur at times of day when the organisms are active and drift is normally high (e.g., at night), but the same velocities may have little or no effect at other times (Waters, unpublished data). On the other hand, I have observed increased drift of rheophilic organisms (*Baetis*) when current velocity was experimentally reduced to very low levels (unpublished data), and Elliott (1967b) also observed *Baetis* (and *Ephemerella*) abundant in the drift at very low current velocities during a drought. Hughes (1966) described a vertical swimming and falling-back reaction of *Baetis harrisoni* nymphs in the absence of current, apparently to create their own current for respiratory facilitation. Such behavior can be easily observed with *Baetis* nymphs in a pan of still water, and may account for increased drift in very slow currents; in a natural stream such drift could function to displace the nymph to a site of more rapid current. Water temperature also may affect the magnitude of the nocturnal drift for some night-active species, though apparently not for all (Müller 1963c, 1966a; and unpublished data).

Five major taxa appear most prominently in exhibiting diel periodicities: amphipods,

the insect orders Emphemeroptera, Plecoptera, and Trichoptera, and the family Simuliidae of the Diptera (*see especially* Müller 1966a; Elliott 1967a,b; Anderson 1967).
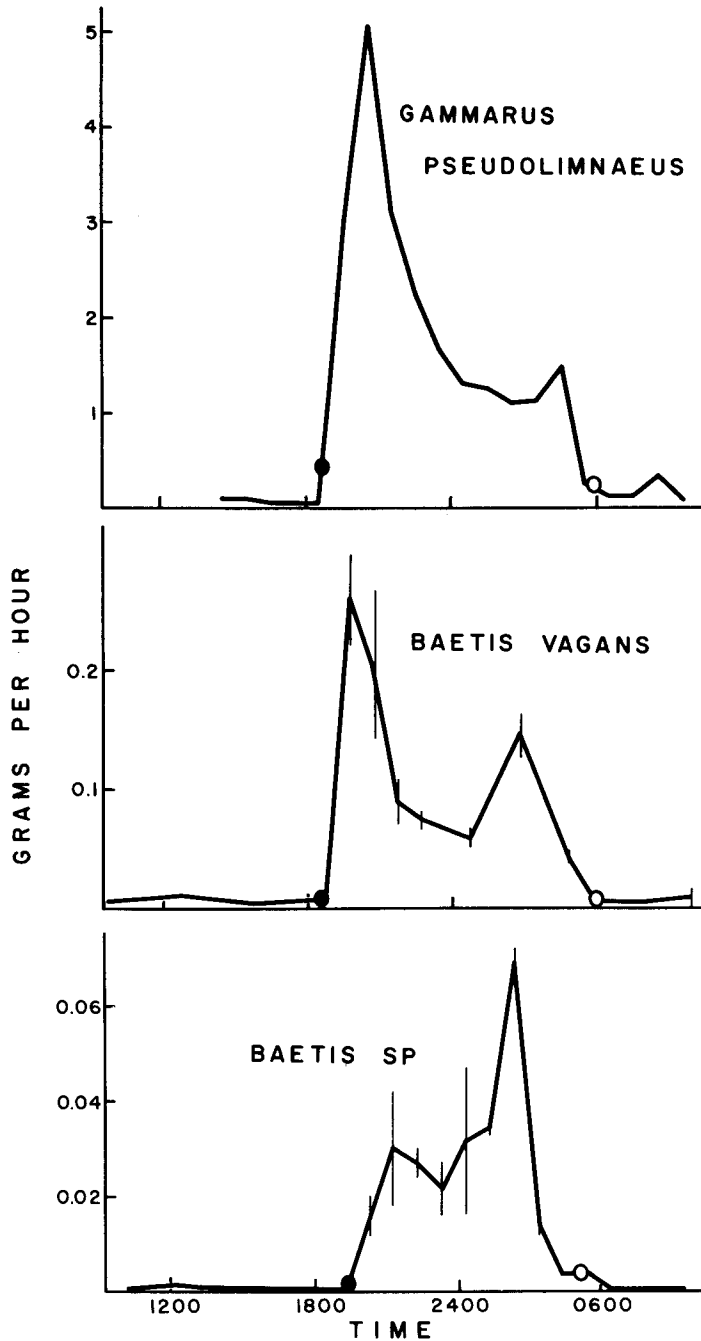

FIGURE 1

DIEL PERIODICITY IN DRIFT, MINNESOTA STREAMS. *GAMMARUS PSEUDOLIMNAEUS*, VALLEY CREEK, SEPT. 7-8, 1966, ONE SAMPLE PER HOUR, *BIGEMINUS*-TYPE; *BAETIS VAGANS*, VALLEY CREEK, SEPT. 11-12, 1962, MEAN OF TWO SAMPLES, *BIGEMINUS*-TYPE; *BAETIS* SP., FAIRHAVEN CREEK, AUG. 9-10, 1966, MEAN OF TWO SAMPLES, *ALTERNANS*-TYPE. CLOSED CIRCLES, SUNSET; OPEN CIRCLES, SUNRISE. VERTICAL LINES REPRESENT RANGE.

In all of these groups, however, there are species exhibiting no apparent behavioral drift, although abundant on the stream bottom. Fewer reports have indicated other groups exhibiting drift to varying degrees: aquatic mites, Isopoda, Coleoptera, Hemiptera, Megaloptera, Odonata, Dixidae (Diptera), and Turbellaria (*see especially* Müller 1966a; Elliott 1967a). Amphipods, Ephemeroptera, and Plecoptera appear to be night-active, while some Trichoptera and simuliids are night-active, some day-active. Anderson (1967) reports one species of Trichoptera (*Amiocentrus aspilus*) that is apparently day-active in early instars, but night-active as large larvae. Müller (1966a) reported *Baetis* nymphs, normally night-active, became day-active at water temperatures near freezing. All reports of the drift of aquatic mites indicate a day-active form (Besch 1966; Müller 1966a; Elliott 1967a). Notably absent in drift periodicities are most burrowing forms, large strong-swimming predators, molluscs, stone-cased Trichoptera, and dipterans other than Simuliidae, particularly Chironomidae, even though sometimes abundant. The entire mayfly genus *Baetis* is apparently universal in exhibiting marked periodicities and has been reported most frequently. *Baetis*, some species of *Gammarus*, and some Simuliidae appear to be the main groups exhibiting extremely high rates of drift.

FUNCTION OF DRIFT IN INVERTEBRATE POPULATIONS

The distance of drift — i.e., downstream displacement — would appear to be a parameter of major importance in evaluating the effect of drift on invertebrate populations. A single attempt to measure the daily mean distance of drift by a blocking technique resulted in estimates of about 50-60 m for *Baetis* and *Gammarus* (Waters 1965). In a somewhat similar experiment, Elliott (1967a) found most of the drift originated in a stream section only 10 m upstream from the sample net. Such a parameter would be likely to vary considerably among invertebrate species, type of stream, and conditions at the time. It seems clear that the organisms do not simply drift passively in the current during the entire period of darkness (or daylight, in day-active forms). Very probably, "The detached animals spend only a short time in the drift and re-attach as soon as possible" (Elliott 1967a). For example, in Madsen's (1966) experiments, most *Baetis* nymphs re-attached to the substrate within 2-3 sec, and *Ephemerella ignita* within 5-6 sec when released into a current velocity of 30 cm/sec. Probably the mean displacement is greatest during times of greatest drift intensity, when perhaps growth and production rates are highest and re-attachment to a suitable but unoccupied site is most difficult. That some displacement does occur, however, seems clear from the blocking experiments and the results of Anderson (1967); that is, the accumulation of organisms in the drift net is not simply the result of activity in the vicinity of the net opening.

A number of authors have reported delayed hatching of insect eggs and a consequent prolonged hatching period (Macan 1957; Illies 1959; Hynes 1961; Elliott 1967b), suggesting variability in incubation time. For a species with a high propensity to drift, the individuals within a cohort may be subjected to significant differences in environmental conditions during their nymphal life because of drifting along the course of a stream, and the time to reach maturity may be variable. Consequently, the emergence period may be broader for those species with a high propensity to drift. A corresponding broader period of hatching for the next generation may result, thus giving the appearance of variable incubation time and delayed hatching. The drift of early instars from upstream areas, where different environmental conditions may result in a different duration of incubation, might present the same effect. *Beatis* is an excellent example of a group which, laying their eggs on a fixed substrate such that all eggs from a single female incubate under similar environmental conditions, have a high propensity to drift, broad emergence periods, and apparent prolonged hatching periods. Conversely, the emergence

periods of species with low drift propensity may be shorter. However, data on drift propensity among the many stream insect species have not been obtained sufficiently to be more than suggestive on this point at present.

There seems little question that in many species behavioral drift is related to the stage of life cycle. Most evidence points to the general conclusion that propensity to drift increases in the later stages (Müller 1966a; Elliott 1967a,b; Anderson 1967). The mean size of invertebrates is frequently larger in drift samples than in bottom samples, even though the smallest sizes may still exhibit a diel drift periodicity. The effect may be gradual throughout the life cycle, or drift may increase sharply at the end of the life cycle, perhaps being related to some pre-emergence or pupation activity. However, there also appear some instances in which drift occurs mostly, or only, in the very young stages (Anderson 1967; Elliott 1967a). Annual or seasonal cycles, when occurring, appear most closely related to life cycle stages. Generally, drift is greatest during the warm months and least in winter, although there are some exceptions to this generalization (Müller 1966a; Anderson 1967; Elliott 1967a), wherein a few species were reported to drift mainly in winter or very early spring. ("Winter", however, is a relative term and may be quite different between continental and oceanic climates.) The highest drift of amphipods appears generally in summer and autumn (Waters 1962a; Müller 1966a), although the timing may vary among different years; the maxima may correspond to the time of maturity for those individuals hatched during the principal periods of reproductive activity reported for some gammarids by Hynes (1955). In the case of insects, highest drift also occurs primarily in the warm months, but in these groups it is more precisely associated with the later life-cycle stages, depending on time of emergence, number of generations per year, etc. (Müller 1966a; Waters 1966; Anderson 1967; Elliott 1967a,b). The function of greater activity and drift during later stages or pre-emergence periods can only be speculated upon at this time, being perhaps a relationship to increasing population pressure at the high growth rates that often occur in later stages, a search for suitable pupation or emergence sites, or a mechanism to distribute reproductive processes as widely as possible.

Frequently considered by several investigators is the role that drift plays in the production ecology of invertebrates. The questions of possible depopulation in the upstream areas and compensatory upstream migration are valid questions significant to understanding of this role. Almost all data presented so far have failed to show a correlation, during a season or though a life cycle, between drift and population density (Waters 1964, 1966; Müller 1966a; Elliott 1967a), although an exception to this generalization is reported by Pearson and Franklin (1968). It appears unlikely that drift rate is characteristically any fixed proportion of the standing crop, in either numbers or biomass. However, drift and standing crop (of similar types of organisms) appear more closely related when compared among different streams; roughly, both appear higher in more productive streams (Waters 1961). My own hypothesis is that behavioral drift is some function of production rate, perhaps after the bottom carrying capacity is filled, and acting as a means of removing excess production during periods of highest nymphal growth. The work of Dimond (1967), following a number of streams in drift and bottom sampling through several years of recovery after forest insecticide treatment, essentially provided an experimental test which supported this hypothesis; his results indicated that high drift rates occurred only after bottom densities returned to stable levels, or carrying capacity. Several authors have suggested that drift acts as a "relief" mechanism for crowded populations (Müller 1954; Elliott 1967a,b). Furthermore, Elliott (1967b) reported strong correlations between drift and growth rates. Periods of highest growth rate would also be the periods of highest production rate, unless mortality were also

correspondingly high. For many species the later stages of the life cycle are times of high growth rates and relatively low mortality rates, so that with increased competition for life requirements as production rates tended to exceed the bottom carrying capacity, higher drift rates might be expected. This scheme cannot work for all species, however, because many species show little propensity to drift; for these species some other mechanism for removal of excess production must suffice.

Müller's (1954) "colonization cycle" has stimulated considerable interest, particularly since the discovery of diel periodicities indicated much higher levels of drift than were known previously. In this hypothesis, the adults fly to the upper reaches of the stream habitat to oviposit, the immatures drift downstream in response to population pressure as they grow, and thereby extend their range, and, upon emergence, the adults fly back upstream. This hypothesis has been interpreted to suggest that the upstream adult flight compensates for depopulation caused by drift from the upper reaches (Roos 1957; Elliott 1967a). While the system might be found to operate for some species in a relatively short stream, there appear no data at the present time to support it for a given species in a given stream. It obviously cannot operate for a crustacean, despite high drift rates (as Müller pointed out), nor does it for all insects. It definitely does not operate for the mayfly *Baetis vagans* in Valley Creek, Minnesota, despite extremely high drift rates (Waters 1966). Elliott (1967a) reported the movement of adults at Walla Brook, England, usually in the same direction as the wind was blowing. However, Roos (1957) reported migration of adult females mainly in an upstream direction, primarily for several trichopterans and *Baetis* sp., and Thomas (1966) reported adult Plecoptera walking upstream. I observed the trichopteran *Oligophlebodes sigma* making definite and regular upstream flights during oviposition (Waters 1968). It therefore seems likely that the adults of some insect species, but not all, characteristically move upstream at least for a certain distance to oviposit. In these cases, some concentration at the uppermost limit of the stream (if such can be defined) should be expected, although in relatively long streams it would seem unlikely that the adults would attempt to reach the upper limit if this were beyond their flight capability. When such movements occur, they may function to compensate for downstream drift of eggs laid on the water surface, for possible mass movements during pupation or emergence, or to ensure re-colonization of temporary streams or streams damaged by floods. There have been no data presented so far indicating that, for a given species exhibiting both high drift rates and upstream flight, the upstream areas definitely are or are not depleted within its life cycle by behavioral drift. Until sufficient such data are obtained, the answer to the question of whether the upstream flight of adults is "necessary" to re-colonize upstream areas must be delayed.

SIGNIFICANCE TO STREAM FISHES

The principal direct importance of drifting invertebrates to their fish predators probably lies in an increase in the availability of food. While this may seem self-evident as a generalization, the specific relationships between drift and fish production, especially the behavior patterns of both the invertebrates and the fish, remain little known.

A probable indirect effect of drift, which may very well be the more important quantitatively, is that the drift phenomenon, having evolved for many species and presumably therefore having some selective value to the invertebrates, may have the effect of optimizing the production of invertebrates and thus maximizing the fish's food supply.

There appear two direct effects of drift upon fish food availability. The first is that drift may transport invertebrates from an area of their production (for example, a shallow productive riffle inaccessible to the fish) to an area where they may be consumed (such as a pool where the fish reside), and to a wider assemblage of fish species with varying

discrete micro-habitats. Significant reductions in drift across pools have been observed (Waters 1962b). The fish are thus provided with a food supply irrespective of whether they take the invertebrates while actually drifting or by foraging on the pool bottom after the invertebrates have settled out. Mason and Chapman (1965) and Peterson (1966) have reported higher fish standing crops in stream sections having the higher incoming drift, suggesting that the level of incoming drift food is a factor in determination of a stream section's carrying capacity for fish. Secondly, a drifting invertebrate is moving and would seem to be more visible and therefore more available, since visual stimulation is an important factor in salmonid feeding (Chapman 1966).

Earlier investigators of invertebrate drift assumed its importance to fish feeding by equating it with fish food supply and studied drift essentially as a measurement of available fish food (Needham 1928; Lennon 1941; Ide 1942; Reimers 1957). Some workers have made direct observations of fish feeding on drift (Müller 1954; Horton 1961; Keenleyside 1962; McCormack 1962; White 1966). Some have compared the distributions of invertebrate forms in fish stomachs to distributions in drift and bottom samples, and have concluded that there is utilization of the drift and found differences in drift utilization among different fish species (Needham 1929; Müller 1954; Nilsson 1957; Peterson 1966; White 1966; Elliott 1967c). White and Elliott, comparing fish stomach contents with drift at different times of day, observed higher proportions of drifting forms in the stomachs at the same times that their drift was high. It might be expected that day-active forms would be of greater significance in fish feeding activity; in one report, brook trout (apparently a daylight feeder) preyed more heavily on day-active drift (White 1966).

On the other hand, some of these same authors report a substantial if not a major portion of the fish diet (i.e., stomach contents) composed of non-drifting bottom forms. Warren *et al.* (1964) reported greatest food consumption in stream sections with the least drift, because of a much greater abundance of bottom forms in these sections. Furthermore, there appear to be some streams in which there is little or virtually no drift and yet contain productive fish populations. It seems clear that there is considerable variation among streams, among fish species, and in the utilization of different species of drifting invertebrates. Salmonids, while being opportunists and taking advantage of drifting foods, also rely heavily on bottom foraging.

A final problem that may be posed — and upon which we have little information — is the effect that a drift-feeding fish population may have on the drift itself; i.e., is there a possible feedback mechanism involved? Chapman (1966) pointed out that such feedback could not occur against drift of an allochthonous source, such as terrestrial insects. But a fish population heavily exploiting its supply of aquatic foods, particularly if the bottom density is kept below carrying capacity by foraging, might be expected to reduce drift rates significantly; Peterson (1966), in his investigations in separated stream sections, concluded that such an event did in fact occur. Conversely, extremely high drift rates may indicate that the food supply is under-utilized and that the fish population might be profitably managed at a higher density.

ADDENDUM — A Critique of Equipment and Procedures

Techniques utilized in drift investigations depend on the objectives of the study. Some of the principal objectives in drift studies have been: (1) Intensity of drift activity; (2) Displacement of the organisms; (3) Comparison of drift among several streams; (4) Propensity to drift for given species; (5) Emergence times of adults; and (6) Contribution of allochthonous organisms.

Most drift nets employed have been of a stationary type affixed in some way to the stream bottom, or to the banks or surface, and left in place for a given period of time.

Nets used in early investigations consisted of a flat mesh or seine-like net stretched across a part or all of the stream's profile (Needham 1928; Lennon 1941; Dendy 1944; Müller 1954), or simply a Surber bottom sampler set on the stream bottom. Knowledge of the precise proportion of the stream's cross-section or total discharge was often lacking in these earlier studies, unless the net filtered the entire stream, although the measurements were valid as relative measures of drift intensity when used in a consistent procedure. Present drift samplers are mainly of two general types: (1) a rectangular net placed from the stream bottom to above the surface which then filters a known proportion, or "slice", of the stream cross-section (Waters 1962a), and (2) nets with a round mouth opening, often with a propeller-driven counting device to measure current velocity through the net, filtering a known area of the stream cross-section and a known volume of water (Müller 1958; Elliott 1967a).

Either the rectangular or circular net provides a relative measure of drift intensity, but they differ in the way that total drift (i.e., of the entire stream) may be calculated. Since the rectangular net collects the organisms moving over a known portion of a width transect, the distribution of drift across an entire width transect must be known so that the ratio of the total drift in the sample portion may be computed and, assuming that this ratio remains constant at least for the experimental period, the total drift may be computed with the sample alone as the product of this ratio and the drift in the sample net (Waters 1962b). With the circular counting net the total drift may be computed by knowing the distribution of drift density in all portions of the stream cross-section, relating the discharge in the counting net to this distribution; usually, the drift density (i.e., quantity of drifting organisms per unit volume of water) is assumed to be constant throughout the cross-section and the total drift is computed as the product of the ratio of total discharge to discharge in the net, and the drift in the net. This latter method, with its necessary assumption, is subject to error because the drift density may not be constant throughout the cross-section; knowledge of the distribution of drift density throughout the cross-section would entail the simultaneous use of many circular counting nets, an expensive proposition. However, this method may be the only one feasible in a large stream, where use of the rectangular net, sampling a "slice" of the cross-section, may be impossible. Large rivers present a difficult problem, for which there seems no ready solution at the present time.

A clear distinction between *drift rate* and *drift density* should be recognized. Drift rate, as used in this paper and my previous reports, is defined as the quantity of organisms passing a width transect, or portion thereof, per unit time; it is a measure of displacement, or the movement of organisms from one place to another (although the distance of displacement is another question). Drift density, in the sense of Elliott (1967a,b), is the quantity of organisms per unit volume of water, in much the same way as plankton density can be defined. Drift rate may be computed from drift density with the additional knowledge of discharge. The use of counting nets to measure drift density may involve an error due to the possible movement of the organisms relative to the ambient water; for example, the organisms may be actively swimming upstream relative to the surrounding water while attempting to re-attach to a stream substrate, although drifting downstream relative to the stream bottom. In this case the drift density measured with a counting net would be an underestimate of the actual density. However, this measure of *drift density*, used in the method indicated in the previous paragraph to estimate total drift, would still provide an unbiased estimate of *drift rate*. On the other hand, a dipper or grab technique, such as the use of a Juday plankton trap (Welch 1948), would provide an accurate measure of density, but if this density measure were used, with discharge, to estimate drift rate, the result (e.g., with the organisms swimming "upstream") would be an overestimate. The significance of this source of error is

129

unknown, because little information is available on the specific behavior of drifting organisms; possibly it is small and may be negligible, but an assessment would be helpful.

In my own studies in small streams, wherein I have been most interested in drift rate and displacement (e.g., from a riffle to a pool, etc.), I have preferred the simple rectangular net because the total drift can be estimated with neither the sampling nor systematic errors indicated above, and because a large number of nets can be employed within a reasonable expense. Cushing (1964) and Mundie (1964) have described rectangular nets with a narrow opening with sharp metal sides that would provide a more precise estimate, probably keeping sampling error to a minimum. Anderson (1967) described another rectangular net with protective shields on the top and bottom surfaces, apparently required in turbulent mountain streams.

Comparison of drift rates among a number of streams present a difficult problem due to the lack of a standard measure. Total drift rate is unsuitable because streams differ in size, and it would be expected that larger streams would have higher total drift rates; mean drift per unit of stream width is difficult because a given stream varies in width in its course (Waters 1961); the mean drift rate per unit stream discharge, obtained with counting nets, would entail a large number of counting nets. Obviously, the mean daily drift per some unit of stream size would provide the best standard. Probably the ideal would be an accurate measure of total daily drift rate divided by the total discharge, to provide a standard of *daily drift rate per unit discharge.* (For reasons discussed in relation to the use of counting nets, a single measurement with this type of net probably would not provide a precise estimate.)

A measure of the propensity to drift for various taxa is of considerable ecological interest; some ratio of drift to bottom density would provide such a measure. I have expressed the ratio of daily drift over a unit of stream bottom area (actually the drift rate across the square dimension) to the standing crop on the same unit area (Waters 1965). However, this technique may be subject to a serious systematic error in that the bottom densities may be distributed quite differently along a width transact than are drift rates because of a concentrating effect of drift in the center of the stream, or where there is the greatest discharge. Elliott (1965b) described a technique, using drift density, to compute the percentage of the standing crop on a unit area that is drifting above that area at any instant of time; this estimate would be subject to the same possible errors discussed above for estimating drift density. Probably the best measure would be an estimate of the total daily drift rate (standardized by dividing by the total discharge) relative to an estimate of bottom fauna density in the area upstream from the drift sampling, obviously a difficult job. Probably present techniques of drift sampling with one or two nets will suffice to approximate ranking of stream invertebrate taxa according to drift propensity until greater precision is required.

The use of drift sampling to collect emerging and ovipositing adults appears useful as an adjunct to stream insect life history investigations, more precisely determining the specific dates and time of day that certain species emerge and/or return to the stream for oviposition (Anderson 1967; Elliott 1967b). The rectangular net, projecting above the surface, would collect adults drifting on the surface; Mundie (1966) and Elliott (1967a) have described floating drift nets which sample the water surface and can be used over any depth of water. The apparatus described by Mundie (1964, 1966) provided an additional compartment for the collection of emerging adults.

Much the same type of equipment is used for the collection of floating terrestrial organisms as a measure of allochthonous contribution to the available fish food supply. By using a stop net upstream, the area constituting the source of terrestrial organisms can be precisely determined, as can the relative contribution of various bank cover types

(Needham 1928).

A common problem confronting drift investigators is that of possible clogging of nets and backwash, resulting in an underestimate of drift rates. One solution appears to be in the design of the drift net in such a way that the width dimension of the net immediately behind the mouth is larger than that of the mouth itself, providing relief of water pressure in the collecting portion of the net (Cushing 1964; Mundie 1964, 1966). The drift trap illustrated by Anderson (1967) also appears to employ the same principle. Another solution has been to lead away a portion of the stream discharge with large-diameter pipe and allow the water to free-fall into the filtering net or seive (Müller 1965b; Kubicek 1966). Müller's method also included an ingenious apparatus involving a series of seives rotating according to a programmed timer, providing an automatic sampling schedule for periodicity studies.

Some years ago, I conducted a series of experiments with rectangular nets in an attempt to solve the problem of clogging and backwash (unpublished); the tests were run in a solid trough in which the presence of backwash could be detected with a current meter. They included empirical analyses of drifting organisms in the natural stream for evaluation, and were conducted in a wide variety of stream conditions. Tests were made on different mesh size, dimension of net mouth opening, length and shape of net, and sampling interval. By varying these factors, backwash could be eliminated in virtually all stream conditions. For example, a net with a mouth width of 15 cm (6 in), a length of 2 m (6 ft), and a mesh opening size of about 0.5 mm, could be sampled for 24 hr without backwash except under the most extreme conditions of debris, such as heavy leaf fall in the autumn. Net shape had a significant effect; e.g., a net cylindrical for most of its length was less liable to clog than one that tapered throughout its length. Consequently, I preferred to have a large number of nets available in a variety of size, shape, and mesh for use in various stream conditions, the simple rectangular net being relatively inexpensive. Requirements will certainly vary with type of stream and conditions and should be determined individually. The mesh size used should be as large as possible and still capable of retaining the smallest organisms desired; when this is critical, of course, the mesh size should be tested empirically with the actual organisms. The degree of turbidity is an important factor, but would usually be less of a problem in salmonid streams than in warm-water streams that are more often in a turbid condition. Certain conditions, such as severe floods, heavy deciduous leaf fall, spring "blooms" of filamentous algae, willow catkins, and "cotton" seeds from cottonwood trees (*Populus* spp.) present special problems that may have no ready solution.

Another practical problem facing the researcher is the sometimes extreme effort and time required in picking the samples, since some drift experiments accumulate samples at an alarming rate. Sorting techniques involving various taxes have been proposed, but the organisms must be sorted alive and often this is not feasible when samples are collected in a frequent schedule. I have found flotation techniques usually to be of little value since the drifting organic debris is often of about the same density as the organisms. Sub-sampling may be employed where samples are extremely large, but great care must be taken to obtain unbiased sub-samples. In general, the best procedure I have found is to use the largest size mesh, the smallest net, and the shortest sampling interval commensurate with the intensity of the drift and the objective of the specific study, and plan on expending sufficient resources to sort the samples manually.

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