THE DRIFT OF STREAM INSECTS[1]

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The drift of stream insects and other invertebrates refers to their downstream transport in stream currents. While stream invertebrates are adapted by various means for maintaining their position in running waters, it is to be expected that the occasional individual will lose its attachment or orientation to its substrate and drift downstream. However, it is only within the last 20 years that observations have been made of large numbers of aquatic insects in the drift. The quantities have been large enough to bring into question the stream's productive capacity to withstand such a high rate of attrition and the possible necessity for an upstream return of some kind. Furthermore, it has interested many ecologists that the drift usually occurs in some type of diel periodicity and that probably circadian rhythms are involved.

It should be emphasized at the beginning that a "drift fauna," as distinct from the bottom fauna, does not exist and is, in fact, an inappropriate term. Drifting is merely a temporary event in the life of many members of the bottom fauna or other substrate-oriented populations.

Among the earliest studies on invertebrate drift were those of Needham in 1928 (84), who was primarily concerned with the drift of terrestrial insects that fell onto the stream surface, as a fish food source. But, in capturing these organisms with a net stretched across a small stream, he also collected drifting aquatic forms. Several other investigations on drift were completed in the next two decades, leading to the conclusion that a continuous drift of invertebrates must be considered a natural feature of streams (18, 19, 50, 59). Subsequent investigations, both in the United States and Europe, revealed the presence of large quantities of invertebrates in the drift (5, 42). But the contribution having perhaps the greatest impact in stimulating interest and research into the subject was published in 1954 by Müller on the drift in north Swedish streams (74). In this work, Müller also reported large quantities, even in a very small stream, and made observations on the qualitative relationships among drift, the bottom fauna, and

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food consumed by fish. Müller at this time also proposed his "colonization cycle" hypothesis for population regulation, including the downstream drift of aquatic immatures and upstream flight of winged adults. The discovery of diel periodicities in drift, reported only about one decade ago by Müller (75, 76), Tanaka (96), and Waters (105), provided an important stimulus to research on the nature of the rhythms involved. It has been in the past ten years, then, that the great bulk of detailed research has been done on the subject of stream invertebrate drift.

Distinctions among the causes of drift (or types of drift according to cause) were early recognized, since these have different ecological implications in the organisms' downstream displacement. "Catastrophic" drift (70), for example, results from the physical disturbance of the bottom fauna, usually by flood and consequent bottom scouring, but also by other factors such as drought, high temperature (115), anchor ice (85), pollution, and insecticides (17). The drift occurring at night, or other consistent period of the day, resulting from a behavior pattern characteristic of certain species, was termed "behavioral" drift; and the continuous stream of representatives of all species, in low numbers and occurring at all times, was termed "constant" drift (108). It is, of course, not always possible to distinguish among the three types, for they overlap to some extent and also interact, but the effects may be decidedly different. For example, in respect to the effect on the insects' populations, catastrophic drift may have a decimating effect; behavioral drift, although in large quantities, may be density-dependent and serve only to keep populations at optimal levels; and constant drift probably has no significant effect. It is behavioral drift, involving sometimes large quantities and having the interesting aspect of rhythm involvement, that has received the greatest scientific attention.

Research on the ecology of the drift phenomenon in all its forms is too new to draw firm conclusions as to its full significance. Certainly, as an example of biological cycles occurring in nature it is an exciting subject for study. Information is accumulating rapidly. For example, published papers dealing directly with the subject in the three years between this review (essentially through 1970) and my previous one (through 1967) (111) constitute about 50 percent of the total number available at this writing. There have been other reviews or extensive summaries which have variously emphasized general or specific aspects, and the reader is referred to these for general discussion: Frost & Brown (40), Hynes (48), Müller (79), Ulfstrand (102), and especially Hynes (49) who, in his recent book, considers the subject in the setting of a comprehensive treatment of stream ecology.

There is a rapidly enlarging literature on the methods and equipment employed in the study of drift, but a discussion of these is not included in this review. A critique of methods was included in my previous review (111) and, more recently, a review specifically of sampling methods has been made by Elliott (34). Additionally, Elliott (36) has provided a booklet including methods of statistical treatment of benthic samples.

DIEL PERIODICITY IN DRIFT

A diel periodicity is defined as a recurrent temporal pattern with a period of 24 hr; it is the pattern observed in the field, as opposed to a circadian rhythm or an endogenous element (16). The first observations of a diel periodicity in the drift of stream insects, from three different parts of the world, all included the mayfly genus *Baetis* (75, 96, 105). Early reports also included the crustacean *Gammarus,* another invertebrate that has figured significantly in invertebrate drift investigations (76, 105). *Baetis* and *Gammarus,* as well as most other stream insects exhibiting a periodicity, are night-active, with higher drift occurring in darkness. Other reports of night-active drift periodicities followed shortly afterward (60, 83, 86). Usually there appeared a sharp increase at about the time of full darkness, some pattern of change during the night, and a sharp return to daytime levels at dawn. However, some fewer species, mostly caddisflies, are day-active, showing higher rates of drift during the daytime (2, 8, 79, 81, 87, 110, 114).

It has been postulated that the night-active trait is the result primarily of nocturnal foraging behavior (27). Presumably, this has evolved with the selective value to the insect of being able to forage with the maximum protection against predators in the dark (14, 63). This does not explain why some species are day-acitve; however, day-active periodicities may be the result of a direct metabolism-activity relationship related to water temperature (110). While food gathering may be the principal activity resulting in drift, other behavior may effect a similar result. Those caddisfly larvae, for example, that must leave their cases to build new ones as they grow may do so at night (to avoid predators?) and drift without the case (105). Crowding and subsequent loss of substrate as growth occurs may result in increased activity, dislodgement, and difficulty of reattachment; higher drift has been observed at times of most rapid growth (27). There is also the possibility that some prepupation or pre-emergence activity also results in a drift periodicity. However, from observations that many species exhibit a drift periodicity throughout their life cycle it would seem most likely that foraging is the main factor in periodic behavior.

It is not entirely agreed as to the involvement of circadian rhythms and the degree to which the drift periodicities are the result of external factors in the environment. However, it seems likely that endogenous locomotory rhythms are present to some degree and that these are synchronized, or entrained, by environmental phase-setting agents. The phase-setter most usually involved, of course, is light intensity. It apparently acts in an "on-off" fashion, triggering the insects' increased activity as it falls to some threshold level of intensity, which appears to be about 1 to 5 lux (0.1 to 0.5 ft candles) measured at the water surface (13, 27, 43, 78), although Bishop (6), with more precise control of intensity and wavelength in the laboratory, determined the threshold as low as 0.001 lux. Bishop also concluded that wavelength made little difference in the organisms' response and that it was the total energy level that was effective. There also appear to be differences among species in response and threshold level.

Several investigators have varied light experimentally, using artificial light during the normal night and darkening during the daytime, with essentially similar results: drift virtually ceased with the application of light and increased when darkness was experimentally applied during the day (6, 23, 43, 80). Some authors report continued periodicities for some time, at least for several species, in continuous darkening produced experimentally (25, 28, 78, 79, 93, 94). Continuous light, however, depresses the rhythm entirely through the organisms' negative phototaxis and eliminates a drift periodicity, either artificially (25, 43) or in the natural light of the polar summer (78, 79, 81, 82) or even possibly in moonlight (1, 8). Chaston (11, 14) considered the first peak after sunset due to the loss of light but a subsequent peak later in the night the result of endogenous activity. It appears, therefore, that a relatively weak endogenous rhythm is involved, being labile and easily shifted and entrained (6).

The question of whether water temperature, which sometimes exhibits a striking diel cycle in streams, acts as an entraining mechanism has been considered. Experiments with artificial control of water temperature in a small stream clearly excluded this factor as an entraining agent for species of *Baetis* and *Gammarus* (115). Observations in polar regions, with constant temperatures but cycling light intensity, indicated the same result for some mayflies, stoneflies, and black flies (81). In a single report, water temperature was indicated as the entraining agent for a day-active caddisfly, *Oligophlebodes sigma* (110); however, this has not been confirmed experimentally nor reported for other species.

The type of behavior of aquatic insects involved in diel periodicities has been of frequent interest. Several observations have been made of organisms spending the daylight hours beneath stones on the stream bottom or in interstitial spaces of the substrate, but moving to upper surfaces upon fall of darkness for the purpose of foraging (25, 28). This added exposure apparently increases the probability of dislodgement by water currents. Herbivores seek the algae on tops of stones, while predators follow in response to the exposure of their prey, and thus both may exhibit the observed periodicity in drift (68). Other experiments and observations have indicated that an increased frequency of active swimming or crawling movements occur after dark, which would also expose the organisms to dislodgement by the current (11, 28, 32, 63, 94). A loss of orientation in the absence of an overhead light, observed for *Baetis,* was suggested as contributing to their dislodgement in darkness (44). Organisms have been observed to drift in all strata of water, not just along the bottom (102, 108); Elliott (34) has indicated that at any one time the density of drifting organisms is fairly constant in all portions of the stream flow. Aquatic insects that are characteristic of the swifter portions of streams, when suddenly released into water currents, successfully achieve reattachment to the substrate in only a matter of seconds; this is accomplished, however, not necessarily by actively searching for the substrate, but rather by being thrown into contact with the substrate by the turbulence of the current (63–65). The single downstream movement of an organism probably is relatively short, and the total displacement during a night is achieved in a saltatory fashion (8). In other words, it seems unlikely that the organisms swim freely or drift for long distances.

A method to calculate the percentage of the bottom fauna that is drifting in the water column above a unit area of bottom at any instant of time has been presented by Elliott (24). This percentage has been considered by Elliott (24, 25), Ulfstrand (102), and Bishop & Hynes (8) to be very low: up to only 0.5 percent, and usually less than 0.01 percent, although Kubicek (54) calculated up to about 4 percent in a Czechoslovakian stream. As small as these figures appear, however, they amount to a daily drift over a unit area of stream bottom that is often many times the quantity of organisms existing on the unit area, at usual riffle velocities. For example, at 0.01 percent the ratio of 24-hr drift to the standing crop on 1 m^2, at a current velocity of 1 m/sec, would be over 8. At 4 percent, the ratio would be about 3500, but it seems certain that this was due to some concentrating effect at the sampling location. Pearson & Franklin (88) reported the ratio of 24-hr drift over 1 m^2 to standing crop on the same area to be up to 161 for *Baetis* and 35 for Simuliidae. And Ulfstrand (102) reported daily drift in a Lapland stream that was equivalent to the entire estimated population on the stretch of river from the drift sample point upstream to 30 to 400 m, depending on species (calculated from author's data), or up to over 5 percent of the population in an 8 km stretch of river. With these drift densities providing a colonizing potential of this magnitude, it is perhaps surprising that standing crops on the bottom remain as stable as they do, which argues strongly for the existence of competition for space on the bottom substrate and a rather precisely determined carrying capacity. When small areas are denuded of benthos, such high drift provides the means of rapid recolonization (107).

Perhaps the best measure of drift intensity for comparative purposes among different streams is the total quantity of organisms drifting past a given point per 24 hr, divided by the total discharge of the stream as a measure of stream size. This calculation provides an estimate of the average density of drifting organisms. Some of the highest drift densities reported, in terms of numbers/24 hr per m^3/sec, are: 2.16×10^6, all species, in the Missouri River, United States (5); 3.0×10^6, all species, including 0.88×10^6 *Baetis* sp., in the River Tjulån, Lapland (102); 1.1×10^6 *Baetis vagans* and 0.43×10^6 *Gammarus pseudolimnaeus* in Valley Creek, Minnesota (105); and the highest reported yet for either single or combined species,

14.9×10^6 *Beatis* sp. and 0.96×10^6 Simuliidae in the Green River, Utah (88) (calculated from authors' data). Drift periodicities commonly involve two peaks during the 24-hr period. In most cases, these include a major peak occurring early in the night upon first darkness, a somewhat exponential decrease through the middle of the night, and a minor peak just before dawn; this is termed the "bigeminus" pattern. The converse of this is the "alternans" pattern, wherein a minor peak occurs at first dark, and then the drift builds up to a major peak prior to dawn (Müller 79). The alternans pattern has been observed primarily in the mayfly genus *Baetis* (79, 111, 112), but also in the Turbellaria and Simuliidae (31, 79). Other species of *Baetis* and most other taxa exhibit the bigeminus pattern. Müller (79) has indicated up to two secondary peaks in the long night of winter and only the major peak in the shortest nights of summer, even within the same species. Many species simply show an unorganized increase at night, without a well-defined pattern. More frequent sampling—e.g., at intervals of 30 min—has revealed additional minor peaks that may go unnoticed when sampling intervals of 1 to 3 hr are employed (31). In the case of the day-active caddisfly, *Oligophlebodes sigma* referred to above, the diel curve was approximately a smooth sine wave, parallel to that of water temperature (110).

Other environmental factors, while having no direct effect on the period or phase-setting of the drift periodicity, may affect the amplitude of the drift. These include primarily current velocity, discharge, and water temperature. It would seem that water current velocity would have a direct positive effect. Floods and higher discharges usually have the expected effect of increasing the drift (3, 8, 25, 61, 74, 102) sometimes to the point of catastrophic results (10, 35). On the other hand, unusually low discharges with reduced current velocities have also been observed to increase the drift, under both natural and experimental conditions (10, 72, 88). This result is apparently due to a swimming response of the organism seeking greater currents for respiratory facilitation; certain species have been observed to release from the substrate and undertake swimming activity in experimentally stilled water (25, 44, 64, 72). Furthermore, in a natural stream, unusually low discharges may be accompanied by a partial exposure of the stream bed, resulting in migration and increased densities, and an intensification of factors affecting drift (88).

Natural stream temperatures have been correlated positively with total daily drift in the cases of *Gammarus pulex,* a common European amphipod (77), and the stonefly, *Diura bicaudata* (94). Under experimentally controlled temperatures in a stream, higher temperatures resulted in higher drift for *Baetis vagans* nymphs, but not for *Gammarus pseudolimnaeus* (115). Apparently water temperature affects the amplitude of the drift for some species but not for others; information on the subject is sparse at this time.

Taxa of stream insects that are most important quantitatively in drift are the Ephemeroptera, family Simuliidae of the Diptera, Trichoptera, and

Plecoptera, apparently in that order. Additionally, amphipods of the genus *Gammarus* are frequently reported in marked periodicities and high drift rates, especially in calcareous streams (57, 81, 89, 105); the isopod, *Asellus*, has also been observed to drift in a diel periodicity (98). In most of these groups, there are species exhibiting no apparent behavioral drift, even though sometimes abundant in the bottom fauna (26, 27, 71, 112). On the other hand, the mayfly genus *Baetis* appears universally to exhibit high drift rates and marked periodicities (4, 24, 39, 41, 75, 88, 89, 105, 112, 113). Other insect groups are sometimes reported to drift in minor quantities. Others, more properly considered as part of the lentic benthos and plankton, appear in stream drift below impoundments and may dominate the drift in these areas or occur in a diel periodicity (55, 73, 95).

Chironomidae larvae, while abundant, frequently show little propensity to drift in a diel periodicity (1, 3, 8, 26, 68, 90). Burrowing and casemaking forms, and strong-swimming predators appear less frequently in the drift, except the latter may sometimes follow their herbivorous prey in increased nocturnal activity (2, 68). Almost all drifting mayflies, stoneflies, black flies, and crustaceans are night-active, while some caddisflies are day-active, some night-active. The mayfly *Baetis*, the crustacean *Gammarus*, and the Simuliidae are the taxa usually responsible for the highest reported drift of stream invertebrates.

LIFE HISTORY

The study of invertebrate drift has become an important adjunct to traditional methods of investigating stream insect life histories (2). For several species, it has been observed that the greatest drift occurs in the younger life cycle stages (2, 25, 112). This is an essential ingredient of Müller's "colonization cycle," although it is possible that it is important to many species as a dispersal mechanism, even if the adults do not make an upstream migration, since it may result generally in a more efficient distribution of the young. However, Bishop & Hynes (8) felt the relative lack of larger individuals in the drift was due to selective predation by fish.

The converse of the above has been more frequently observed, i.e., a higher relative propensity to drift during the later and larger life cycle stages (2, 25, 79, 102). High behavioral drift at night also often includes relatively more larger specimens (3). Several reasons for this may be postulated. First, growth in biomass is often greatest during later life cycle stages, which may place the greatest intensity of population pressure upon available living space. The consequent increase in intra-specific competition may result in increased activity and drift. Secondly, the greater activity, and consequent drift, of these later stages may function to distribute adults to all areas of the stream suitable for reproduction. Third, the larger organisms, protruding into the current farther, may be thus more susceptible to dislodgement (94). Finally, increased drift may result from pre-pupation and pre-emergence activity as the mature larvae and nymphs move to stream banks, preferred bottom types, or areas of current velocity more suitable for the actual emergence. For example, the drift measured at different points in the life cycle has indicated lateral migrations at certain stages (2, 27).

The presence of pupae, exuviae, adults, and egg masses are often reported in drift collections (2, 27, 29, 99, 100, 113). These data have assisted in ascertaining the times of day and season that emergence and oviposition take place, as well as the specific behavior involved in emergence and egg-laying.

POPULATION DYNAMICS AND PRODUCTION

Some of the early observations of large quantities in the drift (5, 42, 74) forced some speculation as to its function in population dynamics and the means by which a stream invertebrate community adapts to such an apparent high rate of attrition. In one of the earliest discussions of drift, Denham (19) suggested that overcrowding and competition were contributing factors. Müller, in proposing his "colonization cycle," suggested that as small larvae grew in size and required greater space, they were forced to seek new space, the consequence being downstream drift and therefore colonization of all suitable habitat through the stream's course. Thus, drift acted as a means of keeping population densities down to the carrying capacity of the stream bottom, as well as providing a means by which all of a stream's suitable areas could be colonized. There is little in the literature to suggest that behavioral drift reduces population densities to below carrying capacity; yet the sometimes extreme quantities in the drift have given rise to postulates of some means of upstream return. An alternative explanation is that, while drift may maintain population densities down to carrying capacity levels, it does not further reduce densities to the point of requiring an upstream return, and that the high drift rates observed are the result of high rates of production that tend to exceed the carrying capacity.

Arguments for both positions have been largely hypothetical, for it is extremely difficult to devise the critical experiments necessary for firm conclusions. Nevertheless, recent information has appeared which bears upon the problem.

Müller's "Colonization Cycle."—Müller's originally proposed "colonization cycle" consisted of the upstream flight of adults for oviposition, with a concentration of eggs and young larvae in an upper reach, the downstream drift of immatures to colonize all suitable habitats, and an upstream return of the adults to complete the cycle (74). The main emphasis of Müller's paper appeared to be upon drift as a colonizing mechanism; but subsequent discussion in the literature emphasized the upstream flight of adults and whether such a return was necessary as a compensating factor for drift. It would seem that the two elements of the hypothesis are not mutually required; i.e., drift of immatures could well function as a distribution mechanism even though the adults did not undertake an upstream flight and oviposition occurred randomly along a stream's course.

It is well documented that flying adults of some stream insect species undertake a directed upstream migration, particularly gravid females. One of the most striking examples is that of the caddisfly, *Oligophlebodes sigma,* in a Utah mountain stream, recently described in detail by Pearson (87); the larvae also exhibit high drift rates, in a day-active periodicity. Earlier, the reported collection of adults in directional traps on a Swedish stream indicated a predominance of gravid females, mostly caddisflies, flying in an upstream direction (Roos, 91). Elliott (30, 35) reported the upstream adult flight of several caddisfly species on a small English stream. Another caddisfly, *Philopotamus montanus,* was also reported to make upstream flights during oviposition on a Swedish stream (58). Adults of the stonefly, *Capnia atra,* have been observed walking on the snow-covered stream banks in an upstream direction (97).

On the other hand, mayflies of the genus, *Baetis,* frequently observed to exhibit high drift rates, have rarely been reported to make an upstream flight (exception: 91). In a study of adult flights over an English stream, Elliott (25) observed that the direction of flight for Plecoptera and Ephemeroptera was simply the same as that of existing winds, and Bishop & Hynes (8) observed swarming adults with no persistent upstream movement.

Immature forms of some species appear to have the ability to swim or crawl upstream, which has been suggested by some investigators to serve as a potential compensation for downstream drift (47, 92). Marking experiments with ^{32}P, however, indicated no upstream movement of the tagged insects in a Canadian stream (7). Such movements that do occur appear to involve far fewer individuals than those drifting downstream and probably do not seriously compensate for behavioral drift, as simultaneous data on both drift and upstream movement have indicated (9, 37).

There appear to be few documented examples of a true colonization cycle containing all elements of Müller's original hypothesis. Dorris & Copeland (22) reported the nymphs of *Hexagenia rigida* moved downstream in a Mississippi River channel prior to emergence, while egg-laying was concentrated in the upstream end. But the closest illustration appears to be that of a stonefly, *Isoperla goertzi,* in a European stream, reported by Schwarz (94). In this case, drift reduced upstream populations, there was an upstream flight of adults, and oviposition occurred mostly in the headwaters; numbers only were reported, however, and these were generally low. Another example is the caddisfly, *Oligophlebodes sigma,* in a Utah stream (Pearson, 87). A high drift of the larvae occurred, while the flight of gravid female adults was clearly directed upstream and resulted in a concentration of oviposition in an upstream area. However, it was concluded in this case that, whereas the high drift did not significantly reduce upstream populations, the upstream adult flight functioned to concentrate eggs in a protected headwater reach, rather than in downstream areas that were severely damaged by anchor ice and winter floods. The drift of larvae, then, served to colonize the downstream areas in which benthic populations had been seriously reduced by winter conditions. Pearson suggested that this mechanism has evolved in north temperate regions, where anchor ice often occurs in downstream reaches of small streams but not in the more stenothermic headwaters near spring sources.

The evidence should not be considered conflicting. It suggests, rather, that variation exists among insect species and streams, and that neither a universal confirmation nor general rejection of the "colonization cycle" hypothesis is indicated. The extent to which upstream adult flight and larval swimming compensate for drift remain undetermined, at least on a general basis, and probably is variable also.

Gammarid crustaceans present a somewhat different case. Commonly occurring in the small stream benthos, they are often observed to exhibit high drift rates along with stream insects. While having no flying stage, it has been postulated that they may undertake a return swimming migration to compensate for drift. They have been observed to undertake significant upstream movements after being displaced by floods (70). While moving upstream, they have been trapped into unpopulated flowing experimental devices (46). Hynes (49, p. 154) reported that upon introduction of *Gammarus pulex* to a stream in the Isle of Man, it moved upstream and established itself in numbers as far as 3 km in four years. The amphipod, *Niphargus*, was observed to "drift" out of springs, forage in the stream, and return to rock crevices by upstream migrations (56). In an extensive study of *Gammarus pulex fossarum* in a small German stream, both downstream drift and upstream migration were measured; movements in both directions were related primarily to reproductive activities of males and in a night-active bigeminus pattern (57). Gammarids have been observed in both downstream and upstream movements where the current direction reversed due to tidal influence, although the movement was in the direction of current flow (20). However, experiments on *Gammarus pseudolimnaeus* involving an enclosure open to upstream migrations in a natural stream indicated no significant upstream movements, and, where all drifting gammarids were removed from the steam after capture, there appeared no reduction of standing crops immediately upstream from the collecting nets, even under conditions of high drift, indicating no "need" for upstream return (108). Hughes (45) demonstrated the ability of *Gammarus pulex* to swim upstream in a laboratory stream as a food-seeking activity; he suggested that the drift in a natural stream is the net downstream effect of drifting with the current after accidental dislodgement and partial compensation by upstream movement.

At present it seems most likely that while gammarids have considerable swimming ability and can make upstream migrations to colonize new areas, recolonize after floods, or seek mates or new food resources, a complete or major upstream compensation for downstream drift does not occur.

Drift relation to production.—As an alternative to the requirement of upstream compensation for drift, it has been suggested that the attrition by drift amounts only to that which is produced in excess of the stream bottom carrying capacity, and that the remainder is sufficient as to require no upstream compensation (Waters, 104). For a species adapted to the bottom type of the given section, the drift is often greater leaving the section than that entering it, the difference being equivalent to that quantity produced in the section (less any other removal or mortality), as has been observed for the mayfly, *Baetis vagans*, on a riffle (106, 109). An extension of this hypothesis is that the level of drift is of some function of the rate of production, and that mean drift rate might be used as an index to the productive capacity of a stream's benthos.

This production hypothesis was made originally on the basis of a comparison of drift rates and other production indices among a group of streams of varying productive capacity, over only a summer period, in which the drift was greater in those streams considered to be the more productive (104). A similar relationship was observed in European streams (42, 81), each of these cases involving only two streams, however. Unfortunately, this type of comparison has not been repeated on a broader basis in terms of number of streams and duration of observations. Pearson (87) has made direct comparisons between drift and production rates for the caddisfly, *Oligophlebodes sigma*, and the mayfly, *Baetis bicaudatus*, in a Utah mountain stream; among several stations sampled, he showed a positive correlation between production rate and drift for *O. sigma* but not for *B. bicaudatus*.

There is little evidence that benthic populations are reduced by behavioral drift in upstream reaches to "depopulated" levels, and several observations have been made specifically of the absence of such reductions, even with high drift (25, 29, 74, 87, 92, 102). In one instance where drifting mayfly nymphs (along with gammarids mentioned above) were experimentally removed from a stream, standing crops remained essentially constant (108).

The relationship of drift to bottom population densities has not been clearly determined. With few exceptions (87, 88), there appears to be no direct relation. The probable density-dependent relation between drift and standing crop, therefore, is not linear. Morris et al (73) found the drift in the Missouri River to be composed of insects that were uncommon in the benthos; rather, the drifting species were found as attached populations on submerged brush and similar substrates. The same effect may be present, to varying degrees, in most streams. Observation of drift and bottom standing crop in a group of streams in which the benthos had been decimated by pesticide application indicated significant drift only after the bottom standing crops had completely recovered, i.e., returned to carrying capacity levels (21). Bishop & Hynes (8) concluded that their study stream (Speed River, Ontario) was so affected by spates that the bottom fauna rarely reached carrying capacity, so that the drift was not the result of competition for food and space, but only of current and flow, mediated by light. A correlation of drift and growth rate of insect immatures has been reported by Elliott (27, 29); i.e., the drift of a species is greater at the time and stage of life cycle at which the growth is greater. Since production rate of a population is a function of the individual's growth rate, periods of high growth rate may correspond to the time of highest production rate for the population, with the consequence being greater drift. On the other hand, some species have little or no propensity to drift, even when existing in abundance in the benthos, and in these cases production in excess of the carrying capacity obviously must be brought into equilibrium by other means of removal.

It seems clear that neither upstream compensation nor the excess production hypothesis is universally applicable. It is equally certain that variation exists and that a variety of mechanisms are involved in the ecology of stream invertebrate drift. This is not to suggest that further research on these two hypotheses is useless, but rather that investigations on given taxa or circumstances will be more fruitful than attempts to decide on one mechanism to the exclusion of the other.

Distance of drift.—The distance which stream insects drift is of considerable significance to the populations concerned. Of course, it is the net mean distance of downstream displacement which is the parameter of principal interest, since one individual's movement, while being short, may displace another which consequently moves, and since some upstream migration may compensate partially for drift. Almost all reports of drift measure the number or biomass of organisms passing a given point on a stream, but the displacement effect is unknown unless the mean distance is also known.

Early suggestions of individual movements were up to about 1 m or at most 10 to 15 m (42). Stonefly nymphs (*Diura bicaudata*) were reported to make a daily downstream movement of only 50 to 100 cm, or up to 5 m in extreme current (94). By collecting drift at various distances downstream from a complete block of drift, Waters (108) estimated the maximum distance for which behavioral drift was effective at about 50 to 60 m per night for *Baetis* and *Gammarus*; these estimates were subjected to a more rigorous analysis by McLay (69), using the same data, resulting in a correction to about 100 m for *Baetis* and 130 m for *Gammarus*, with means of 21.6 m for *Baetis* and 28.5 m for *Gammarus*. McLay also proposed a model by which the mean distance traveled could be estimated, using experimental disturbances of the stream bottom to release organisms into the drift; in an example for a group of species from a small New Zealand stream, the mean distance was 10.7 m. More recently, Elliott (38) has also proposed a model for estimation of the drift distance. His studies included both blocking experiments and the release of organisms at varying distances upstream from the samplers. Both McLay and Elliott found an exponential relation in the return of released organisms to the substrate. Elliott reported that the mean drift distance varied with species, current velocity, and type of substrate (e.g., areas of vegetation acted as sieves and filtered out certain organisms more rapidly), but not between day and night, nor month to month. Mean daily distances ranged up to about 20 m in Elliott's experiments. However, *Baetis* and *Gammarus,* two taxa that are often reported in high drift rates, were among those that exhibited the shortest mean daily distances, being about 1 to 5 m.

Data available so far, particularly in view of the large quantities reported in the drift relative to bottom populations discussed in a previous section, do suggest that distances traveled are often long enough to have significant effects on populations existing in a discrete area, such as a riffle reach, and to require either high production rates or upstream compensation to sustain this degree of attrition.

DRIFT AND FISH FEEDING

The relationship between invertebrate drift and fish feeding has been of considerable interest to fisheries managers as well as to other stream ecologists. An obvious hypothesis is that fish constitute a sort of "drift sampler" (69), utilizing drifting invertebrates because they are moving and therefore more accessible as prey (19). The significance of this type of feeding may be a greater efficiency in food transfer from the invertebrate to the carnivorous fish level, and thus higher fish production, than with bottom foraging alone. Early studies on drift had as their objective the determination of available fish food (50, 59, 84). Direct observations of fish feeding on drift in natural streams have been made by a number of investigators (4, 51, 74), in some cases with skin-diving gear (53, 114). Direct observations have also been made in flowing aquaria and artificial streams (52, 66). In one case, significant feeding of brook trout on the day-drifting caddisfly larvae, *Brachycentrus americanus,* was observed during the daylight period (114). Salmonids, particularly, select and defend territories which are best suited for the interception of drift; the size and location of the territory is determined by the drift density and patterns of drift in the water currents (51, 52, 66).

Many investigators have compared fish stomach contents with the composition of drift and benthos and found selective feeding on drift (4, 26, 62). The degree of such selectivity differs among fish species (53, 74, 90), and there appears to be a varying utilization of bottom foods as well as drift (101, 103). Young salmonid fry appear to depend most heavily on drift, and as the fish grow larger there is relatively greater dependence on bottom foraging (33, 40).

Since behavioral drift occurs most often in a diel periodicity, a number of studies have included a comparison of the periodicity of fish feeding with the drift periodicity. It has been observed in some cases that maximum fish feeding occurs at times of highest drift. Juvenile coho salmon, for example, rely chiefly on drift and feed primarily at night (66). Brown trout apparently feed well into the night, utilizing the more accessible drifting foods (26, 33). However, Chaston (12) has suggested that correlations of feeding and drift may be due to the fish foraging, from the tops of rocks, those kinds of organisms that are also in the drift, but not feeding on the drift itself. In some cases, a lack of correlation has been reported (15, 101).

At this time, the most accurate generalization that may be offered is that probably stream fishes are opportunists and frequently utilize drifting invertebrates. It is also clear that full reliance on drift is not usually the case, and bottom foraging, particularly with older fish, is also important in their trophic ecology.

A second type of relationship between fish feeding and drift, in addition to the increased accessibility of the prey, is that drift may function to transport insect foods. Such transport may occur from an area of the stream in which insect production is high, such as a shallow riffle, to an area of high fish density, such as a pool. The abundance of some rheophilic insects is often very high in shallow, swift riffles where fish, having little cover, are scarce; on the other hand, the fish occupy a suitable pool below the riffle where they utilize incoming drifting foods, whether taken as they drift or by bottom foraging after the drift has settled in the reduced current of the pool. The drift of rheophilic insects off a riffle has been observed to be greater than that drifting onto it, and less coming out of a pool than drifting into it (4, 106, 109). Higher carrying capacities of stream fish have been observed in natural and experimental stream sections having the higher incoming drift (67, 90), suggesting that the supply of food to a section of stream in the form of drifting invertebrates assists in setting the carrying capacity and consequently the level of production, for the stream's fish. It may be hypothesized that this drift mechanism facilitates fish utilization of stream insects and also, along with increased accessibility, tends to maximize fish production. Streams with high drift rates might be expected to have the higher fish carrying capacities and fish production. This relationship, however, has yet to be confirmed on a broad basis.

SIGNIFICANCE AND NEEDS

A great deal of information on the drift of stream invertebrates has recently been gained. Perhaps the greatest impact that the additional knowledge has had is related to the measurement of drift as a rate, rather than a static quantity, and it therefore emphasizes the dynamic character of biological communities. We are, for example, more concerned now with the relationship between this rate and other dynamic parameters of stream populations: production, mortality, migrations, predation rates, etc.

An additional effect that drift knowledge has had, especially in respect to the diel periodicities, is the emphasis on cyclic events. No longer should the investigator be content with single-sample assessments taken only at one time of the diel period, not only for drift but probably for other types of behavior and other types of organisms.

Nevertheless, many unsolved problems and gaps in knowledge remain. Additional data on species involvement, shape of diel pattern, and phenology no doubt will be obtained by continued basic sampling in more streams of different types and in new geographic areas. The involvement of phase-setting mechanisms and effects on amplitude by environmental factors such as temperature, current velocity, and water quality, can be further elucidated by experimental means, either in laboratory-controlled artificial streams or in sections and diversions of natural streams devoted to experimental purposes. The more elusive problems of the ecological significance of drift to production biology, population dynamics, life history, and the trophic ecology of fishes are difficult to attack; these will require more imaginative experimental design, creative analysis and, certainly, expense. But these efforts should also contribute increasingly to our knowledge of the function and succession of stream communities, especially in respect to their dynamic character.

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