

PHYSICAL-BIOLOGICAL COUPLING IN STREAMS: The Pervasive Effects of Flow on Benthic Organisms

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■ **Abstract** Flowing water has profound effects on a diverse array of ecological processes and patterns in streams and rivers. We propose a conceptual framework for investigating the multiple causal pathways by which flow influences benthic biota and focus particular attention on the local scales at which these organisms respond to flow. Flow (especially characteristics linked to the velocity field) can strongly affect habitat characteristics, dispersal, resource acquisition, competition, and predation; creative experiments will be needed to disentangle these complex interactions. Benthic organisms usually reside within the roughness layer, where the unique arrangement of sediment particles produces strongly sheared and highly three-dimensional flow patterns. Thus, accurate characterization of the local flow environments experienced by benthic organisms often requires the use of flow measurement technology with high spatial and temporal resolution. Because flow exhibits variation across a broad range of scales, it is also necessary to examine how organism-flow relationships at one scale are linked to those at others. Interdisciplinary approaches are needed in the study of physical-biological coupling; increased collaboration between ecologists and experts in fluid mechanics and hydraulic engineering is particularly desirable. A greater understanding of physical-biological coupling will not only yield deeper insights into the ecological organization of streams and rivers, it will also improve our ability to predict how flow alterations caused by various human activities affect these vital ecosystems.

INTRODUCTION

Understanding linkages between organisms and their abiotic environment is a critical step in developing predictive models regarding the structure and function of ecosystems. For example, the physical world profoundly shapes a wide array of fundamental ecological processes, including dispersal, resource acquisition, and species interactions. A more complete knowledge of the connections between

biological processes and physical factors is also needed to address such diverse problems as the decline of estuarine fisheries (23), the role of forests in global climate change (63), and the spread of exotic organisms such as zebra mussels (187). In fact, studies of physical-biological coupling have undergone a kind of renaissance in ecology, with new models, measurements, and experiments being used to examine a diverse array of phenomena and systems (*1, 45, 47, 56, 57, 59, 99, 160, 169, 198, 204*) [*italic indicates citations from marine systems*].

In stream ecosystems, the physical world is governed by water in motion. Indeed, the central tenet of our review is that flowing water is often the dominant forcing function (or “master variable” sensu 162) to which other stream processes and patterns can be traced. For example, flow has shaped (both literally and figuratively) almost every feature of these systems, including their channel morphology and disturbance regimes, the distributions of organisms in space and time, as well as rates of energy transfer and material cycling (2, 80). Because of these pervasive effects, we suggest that flow deserves a high priority in the research agendas of stream ecologists. In particular, stream ecology would benefit from a more unified conceptual framework as well as from greater consensus about the utility of particular physical measurements and models relating ecological processes and patterns to flow conditions. Such advances will not only yield deeper insights into the structure and function of stream ecosystems, they will also aid in the development of improved methods for protecting and managing these vital systems. For instance, one of the largest impacts of human activities on streams and rivers stems from the modification of their flow regimes (132, 154, 158). Moreover, the growing demand for fresh water will only intensify the pressures on these systems. Thus, an improved understanding of physical-biological coupling in streams will also enhance our ability to solve pressing environmental problems.

Our review is organized into four parts. First, we examine the direct and indirect mechanisms by which flow can affect bottom-dwelling (or benthic) organisms; we provide a selective review of studies (including some from marine systems, *which are marked with italicized reference numbers*) that illuminate our understanding of these effects. This literature review emphasizes experimental studies that have focused primarily on invertebrates and benthic algae. Second, we consider the sources and scales of spatial and temporal flow variation in streams. Recognizing how flow varies with scale is crucial for understanding the ecological consequences of flow. Third, we evaluate alternative methods for measuring the flow characteristics experienced by benthic organisms, as well as for studying flow effects experimentally. Our understanding of organism-flow interactions will be greatly enhanced by the development and use of more accurate methods for quantifying benthic flow characteristics. Finally, we briefly place these ideas about physical-biological coupling in a broader context by considering their relevance for environmental problem-solving.

A familiarity with fluid mechanic principles is essential for studying organism-flow interactions. Owing to space limitations, we have not attempted to provide

an overview of the relevant fluid mechanics and instead direct the reader to several ecologically oriented introductions to this field (41, 45, 47, 80, 136, 198). In particular, we do not reproduce common equations and formulae because space limitations preclude an adequate discussion of the assumptions needed for their proper application. Nonetheless, we offer a few introductory comments about our use of flow terminology. In general, the flow characteristics of greatest relevance to benthic organisms are linked to time-averaged or time-varying components of the velocity time series. Thus, we focus primarily on flow characteristics related to the velocity of water past a point (measured in units of length per time—e.g., (m/s)) rather than the volumetric flow rate or discharge (measured in units of volume per time—e.g., (m³/s)) (198). Indeed, many of the flow forces and processes affecting benthic organisms (e.g., drag, lift, diffusivity, and mass transfer) vary as a function of velocity (47, 198). Velocity varies across a broad range of space and time scales, so it is also important to define which scales are relevant to particular ecological questions. Our review emphasizes flow mechanisms operating at organismal scales, due to the role of individuals as the fundamental building-blocks of populations, communities, and ecosystems. In particular, the flow conditions experienced by benthic organisms differ from those experienced farther above the stream bed due to the presence of a velocity gradient, which is created by friction between the moving water and the stationary bed (136). Unfortunately, the complex topography of many stream beds often makes it impossible to predict near-bed velocities using simple formulae such as the log-linear relationship between velocity and height above the bed (136). Thus, when the objectives of ecological studies require the accurate estimation of the flow characteristics experienced by benthic organisms, it will often be necessary to make measurements immediately adjacent to the bed (2, 89).

FLOW EFFECTS ON ECOLOGICAL PROCESSES

The mechanisms (*sensu* 55) by which flow affects benthic organisms can operate via either direct or indirect paths. By direct, we mean that various hydrodynamic forces or mass transfer processes act on the organisms in question and alter their “performance.” In terms of causal pathways, there are no intervening variables between flow and the organisms’ response. For example, organisms can be eroded from or deposited on specific regions of the stream bed by flowing water, thus altering local population size. Indirect effects of flow, on the other hand, occur by altering some intermediate abiotic or biotic variable, which in turn affects the study organisms. For example, flow can determine the distribution of sediment particle sizes available in a stream reach, which in turn may affect biota that require specific sediment particles for shelter. This distinction between direct and indirect effects is useful if we wish to identify flow mechanisms, predict how organisms are likely to respond to altered flow fields, and interpret the degree to which the evolutionary history of organisms has entailed adaptation to flow *per se*.

Ecological processes affected by flow

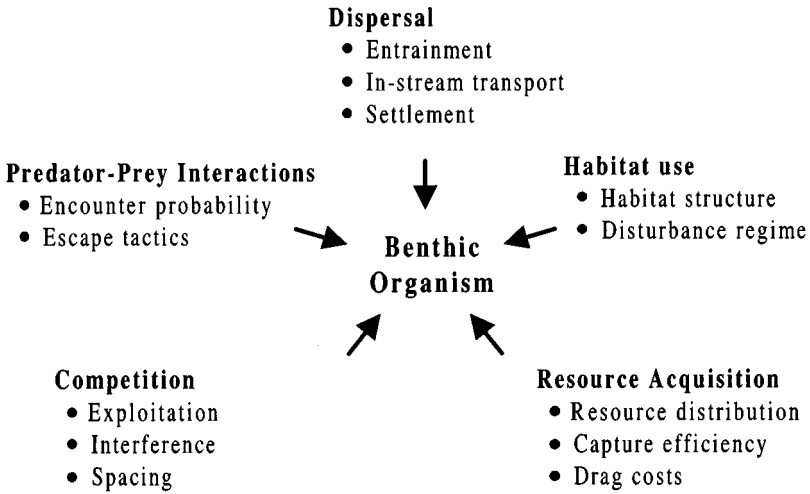


Figure 1 Alternative causal pathways by which flow can affect benthic organisms. Key components of each ecological process can be modified by flow, thereby affecting the performance, distribution, and abundance of organisms. Potential interactions among pathways not shown.

Flow can affect benthic organisms via multiple causal pathways. We illustrate these diverse pathways in a simple diagram (Figure 1) and focus first on dispersal, which can be viewed as an initializing process that delivers organisms to a particular benthic habitat. This ordering reflects the growing belief that local populations of many benthic organisms (e.g. those inhabiting a particular sediment patch) are open, in the sense that they are affected by immigration and emigration processes occurring over much larger spatial scales such as the channel reach or catchment (54, 111, 140, 169). Thus, we begin our discussion by examining how flow influences the dispersal of benthic organisms into and out of local areas. Next, we consider how flow affects various components of the abiotic environment that determine patterns of habitat use. In addition to the effects of flow on these abiotic conditions, it can also modify the acquisition of limiting resources that determine rates of growth and reproduction as well as competitive interactions. Finally, flow can impact benthic organisms by mediating the effects of predators or pathogens. For most benthic organisms, flow characteristics such as average velocity affect patterns of distribution and abundance via multiple (and sometimes countervailing) mechanisms that can operate at different spatial and temporal scales. As a result, ecologists will need considerable ingenuity to disentangle the multifarious causal pathways that link the biology and physics of stream ecosystems.

Dispersal

Stream organisms are often carried downstream via water currents (128). Indeed, these suspended or “drifting” organisms can provide a significant supply of immigrants to newly available substrates (192). Such drifting organisms are rarely adapted to planktonic life, which suggests that they are either accidentally dislodged from the bed or they actively entered the water column in search of more favorable benthic habitats elsewhere in the stream (2). In either case, an explicit focus on the hydrodynamic mechanisms governing water column entry, instream transport, and settlement is critical for understanding how such transport affects the dispersal and dynamics of benthic populations.

Water Column Entry The first step required for flow-mediated transport is entry to the water column. The simplest way in which benthic organisms are removed from the bed and transported in the water column is via the same passive entrainment mechanisms that move sediment particles (80). Specifically, wherever water flows around a solid body, one or more forces (drag, lift, and the acceleration reaction) act on the object (45). The magnitude of such forces generally increases nonlinearly with velocity and body size (47, 198).

Although hydraulic engineers and fluvial geomorphologists have quantified the drag forces or critical erosion velocities required to move sediment particles of different size (80), such information is much less common for benthic stream organisms. One study of benthic meiofauna demonstrated that their critical entrainment velocities were lower than those of the sandy sediments they inhabited (139). Another study found that the shear stress required to dislodge benthic algae varied by more than 25-fold, depending on the taxonomic composition and physiognomy of the assemblage (15). More extensive studies in marine environments have emphasized the importance of peak, as opposed to average, forces in causing the dislodgement of benthic organisms (44, 46, 61, 143). These results reinforce the conclusions of work on sediment transport in turbulent flows, which have found that the majority of transport events are associated with infrequent, high velocity turbulent motions near the bed (133, 168). Such turbulent flow structures are also likely to play an important role in the entrainment of stream benthic organisms.

In contrast to the passive entrainment of sediment particles, many benthic organisms are able to lower their dislodgement risk by various morphological and behavioral traits (96, 99, 198). For example, the streamlined bodies of some stream invertebrates and fish (198) and flexible stems of stream macrophytes (99) reduce the drag forces experienced by these organisms. In addition, microorganisms may be protected from dislodgement by their small size, which allows them to inhabit zones of greatly reduced velocity that often exist within a few hundred micrometers of the surfaces to which they attach (175). Other benthic organisms have specialized structures that reduce the probability of dislodgement, including mucilage (13), hooks (39), and suckers (77). Finally, stream invertebrates and fish exhibit a wide range of behaviors that lessen the flow forces they experience. For

example, when exposed to high flows, both crayfish (118) and fish (201) modify their posture to avoid dislodgement. Other animals such as flatworms reduce the chance of dislodgement by their behavioral avoidance of microhabitats with high flows (84).

In spite of various adaptations to reduce dislodgement, benthic organisms may be unable to avoid entrainment during bed-moving floods (14, 37, 161, 193). Such extreme disturbances can lead to catastrophic drift (2), in which a large fraction of the biota may be transported downstream. On the other hand, the presence of benthic organisms on the stream bed can sometimes reduce the probability of sediment entrainment. For example, the silken shelters created by large aggregations of hydropsychid caddis larvae can dramatically lower the probability of sediment entrainment compared to sediment where such larvae are absent (179).

Rather than avoid flow dislodgement, some benthic organisms seem to actively exploit the flow as an opportunity for dispersal. For example, the rate at which larval black flies enter the water column decreases with increasing water velocity (75), which clearly conflicts with a passive entrainment model. Similarly, grazing mayflies drifted at higher rates when algal abundances were low, even though flow remained constant (101). In both studies, the investigators suggested that water column entry represented an active foraging strategy by which individuals sought to locate better feeding areas. Other species use drift as a predator-avoidance behavior (116, 147). Stream algae also appear to use fluid-mediated dispersal to avoid unfavorable habitats. For instance, Bothwell et al (17) demonstrated that benthic diatoms selectively emigrated from experimentally darkened flumes by altering their buoyancy or form resistance, thereby increasing their entrainment into the flow.

Instream Transport Once an organism enters the water column, several factors can influence its travel distance and transit time. Recent theoretical developments provide a valuable framework for examining the processes governing instream transport. Specifically, advection-diffusion models demonstrate that transport distances and times are controlled by the organism's settling velocity as well as the degree of turbulent mixing (48, 62, 81, 120). These investigations have identified the Rouse number (i.e., a dimensionless ratio of settling velocity to shear velocity) as a critical parameter determining the distribution of organisms in the water column and their potential delivery to the bed (81, 120). Such advection-diffusion models can also provide a basis for constructing null hypotheses regarding the expected settlement patterns of benthic organisms if they behaved as passive particles (177). Furthermore, differences between observed and expected patterns can yield valuable insights into the adaptations used by organisms to modify their settlement rates.

In contrast to these mechanistic transport models, studies of stream drift transport have largely been empirically based. For example, two early field studies observed a characteristic negative exponential relationship between the fraction of organisms remaining in the drift and the distance downstream from their point

of entry to the water column (64, 119). This rate of exponential decay was, in turn, inversely related to average velocity. These earlier models have been extended to investigate variation in drift distances due to channel geomorphology (107) and invertebrate behavior (3). For example, studies comparing the drift of live and dead invertebrates have demonstrated that swimming behavior and related adjustments of posture while in transport can either decrease (3, 32, 139) or increase (3, 28) the distance traveled relative to a passive particle. Thus, organisms may avoid settling in unfavorable habitats by decreasing their settling velocity, whereas they may avoid drift-feeding fish by increasing their settling velocity to rapidly exit the water column.

Settlement The fate of dispersing organisms depends on the location and timing of settlement, which can be loosely defined as a process that includes contact with and reversible attachment to the bed. Although it can be difficult to distinguish between the mechanisms that affect water column transport vs. settlement per se, the latter process necessarily involves direct contact with the substratum. Thus, settlement is much more likely to be affected by local conditions and steep gradients in the interfacial world between the water column and the bed.

Settlement processes have received considerable attention in marine systems (recent reviews in *1, 26*), whereas less is known about these processes in streams (73, 140). Flow affects settlement by altering the hydrodynamic forces that deliver organisms to the bed as well as by providing or mediating various cues related to bed suitability (*1*). Near-bed flow characteristics can strongly affect the location of settlement, particularly for small organisms that are also weak swimmers (26, 73). For example, areas of flow separation and reattachment may enhance deposition of organisms onto the bed (*129, 183*). In marine systems, flow serves as a direct or indirect settlement cue. For instance, the ability of settling organisms to detect waterborne chemical cues that provide information about bed suitability (e.g., the presence of food resources or conspecifics) depends in part upon rates of turbulent mixing (*1, 146*). Although near-bed flow characteristics in marine systems and streams are not always comparable, stream researchers could nonetheless benefit from more careful attention to the approaches and results of their marine colleagues (recent reviews by *1, 26, 146*) as they begin examining the potential importance of such cues.

Valuable insights about the effect of flow on settlement in streams have come from studies of benthic algal immigration (185). Several investigations have demonstrated an inverse relationship between the immigration rate of algal cells and velocity (150, 183). Further mechanistic studies are needed to determine whether the reduced immigration observed at high velocities is caused by lower rates of cell delivery to the bed or higher post-contact rates of cell removal (i.e., entrainment).

If the dispersal of benthic organisms is strongly affected by flow, then benthic distributions may reflect hydrodynamic processes rather than post-settlement habitat preferences. Although these "supply-side" processes can be quite important in marine systems (26, 169, 177), stream ecologists have generally assumed

that the high mobility of benthic invertebrates should override the effects of initial settlement in controlling benthic distributions (but see 54, 140). In one of the few explicit tests of this assumption, Fonseca examined the mechanisms and consequences of flow-mediated dispersal in larval black flies. She found that larvae had difficulty attaching to the bed in all but the slowest flows, which led to a reduced settlement probability in faster flows (i.e., those preferred for feeding) (74). Moreover, related field experiments in which she manipulated larval settlement rates demonstrated that these dispersal constraints caused larval abundances to be lower than expected in their preferred feeding sites (73).

Overall, there are many parallels between the flow processes governing sediment transport and organismal dispersal (168). These similarities strongly suggest that ecologists would benefit from closer interaction with experts in hydraulic engineering and fluvial geomorphology as they seek to understand the ways that flow affects the entrainment, transport, and settlement of stream benthic organisms.

Habitat Use

Upon settlement, a benthic organism will encounter a suite of local abiotic conditions. In turn, these habitat characteristics are often affected by flow, which can lead to flow-dependent patterns of habitat use. Of course, many local habitat features ultimately derive from broad-scale variations in climate and geology that control the hydrology and water quality of streams within a catchment or region (10). Moreover, regional differences in hydrological disturbance regimes can act as a powerful filter that limits the pool of species (and species traits) available to colonize a particular catchment (152). Thus, disturbances associated with floods and droughts are often regarded as a primary determinant of broad-scale variations in the structure and function of stream ecosystems (2, 10, 155, 193, 207).

At more local scales, flow controls the erosional and depositional processes that determine bed form and composition (80, 110). Consequently, flow influences many habitat features of potential importance to benthic organisms, including channel sinuosity, pool-riffle sequences, and the abundances and arrangements of different sizes of sediment particles. The strong covariation between bed characteristics and flow can make it difficult to identify the causal pathways underlying relationships between benthic organisms and habitat structure. Some ecological patterns are probably linked directly to habitat characteristics per se. For example, certain benthic organisms may prefer particular sediment particle sizes for attachment, shelter, or locomotion (40, 96, 122), regardless of local flow conditions.

On the other hand, flow mechanisms probably play an important role in many correlations between benthic organisms and various habitat features (177). For instance, several passive suspension feeders are more abundant on large substrates, in part because these are commonly characterized by higher velocities that are preferred for foraging (38). Similarly, some detritivores are more common in sediments containing high concentrations of fine particulate organic matter (122), which in turn are more likely to be retained in microhabitats with slow flows. Still other organism-sediment associations may stem from the

residual effects of sediment-specific differences in the intensity of past disturbances (76).

Some of the most dramatic effects of flow on physical habitat occur as the result of floods and droughts. In particular, the channel scouring that occurs during large floods often results in extensive displacement and mortality of benthic organisms (8, 9, 79, 172, 174). Relatively little study has focused on the precise mechanisms by which floods affect benthic organisms, however (but see 14). Some benthic organisms are presumably crushed by bed load, whereas others may be abraded by suspended sediment (11, 76). Mortality of organisms that are dislodged from the bed during a flood can occur either during transport or after deposition in unfavorable environments such as deep pools or receding flood plains.

The abundances of benthic organisms sometimes recover relatively quickly after floods (37, 184), which implies the existence of spatial refuges where the negative effects of disturbance are ameliorated. At a microscopic scale, some diatoms can persist within protected crevices on the surface of individual sand grains, whereas they are scoured from the more exposed surfaces of those sediment particles (7, 121). At a larger scale, Lancaster & Hildrew (106) have identified portions of the streambed known as hydrodynamic dead zones (167), in which bed shear stress undergoes little or no increase during a flood. They suggest that these areas of minimal flow change can serve as refugia for organisms that would otherwise be dislodged or harmed by the high shear stress that occurs elsewhere in the channel. Indeed, their studies have demonstrated that some benthic invertebrate taxa are relatively more abundant in flow refugia after a storm than before it (see also 76). It is not always clear whether this increase reflects an active immigration of individuals to flow refugia, a passive deposition of individuals within flow refugia, or a reduction in the abundance of individuals from areas outside those refugia. One recent study has demonstrated active use of flow refuges during floods (90). Specifically, larval black flies moved to more sheltered sites on boulders and artificial substrata within minutes after near-bed velocities began increasing during either natural or experimentally created floods. After flood waters receded, the larvae returned to more exposed sites on those same substrata.

Another potential refuge for stream organisms during floods is the hyporheic zone. Palmer et al (142) conducted one of the few explicit tests of this hypothesis by focusing on the vertical distribution of benthic meiofauna before and after floods. Although these invertebrates are very susceptible to entrainment by flows and thus would benefit from moving into the hyporheos, they showed no tendency to move deeper into stream bed sediments to avoid high flows. Further studies are needed to determine whether other benthic organisms make use of such hyporheic refuges.

Droughts, which are characterized by extremely low flows, impose a very different set of stresses on benthic organisms (19, 206). In comparison to floods, much less study has focused on the ecological responses to such low flows. As flows decline, some benthic organisms may experience greater resource limitation or physiological stress due to reduced rates of mass transfer (see below). Habitat availability also declines during droughts, which can lead to increased intensities of either competition or predation. Experimental studies are needed to disentangle

the flow-related mechanisms by which droughts affect benthic populations and communities.

Resource Acquisition

To grow and reproduce, all organisms must obtain resources such as dissolved nutrients or particulate foods from their environment. Flow can enhance or hinder the rate and efficiency of resource acquisition via its effects on the distribution of resources as well as the ability of organisms to locate and gather those resources. For example, the water column distribution of various dissolved substances used by benthic organisms is affected by the magnitude of turbulent mixing, whereas the vertical concentration profile of suspended particles is determined by both turbulence and particle settling velocities (see Dispersal, above). In general, low settling velocities of suspended material and high levels of turbulent mixing tend to homogenize the concentration of these resources in the water column (120, 130). Therefore, in the absence of local sources or sinks, spatial heterogeneity in flow characteristics will be the primary determinant of any variation in the flux of these limiting resources to organisms. Further studies are needed, however, to validate this assumption of resource homogeneity. For example, tributaries carrying high concentrations of seston can create locally enriched resource plumes that affect the distribution of suspension feeders (67). Similarly, the discharge of nutrient-rich groundwater can produce localized regions of high algal growth (195). Recent studies have even suggested that dissolved organic matter can be converted to particulate organic matter by turbulence-induced flocculation, which can potentially modify the quantity and quality of resources available to passive suspension feeders (34).

In addition to altering the distribution of suspended or dissolved materials, flow can influence the ability of organisms to locate or obtain these resources. The best examples of this effect in streams come from studies of nutrient uptake, growth, and photosynthesis in benthic algae (16, 185 and references therein). For example, the nutrient uptake rates of benthic algae and aquatic plants are sometimes limited by the rates of molecular diffusion of dissolved materials across the laminar (viscous) sublayer (198), which typically surrounds organisms. Because the thickness of this layer is inversely proportional to velocity (47, 198), increases in flow can enhance the rate at which limiting nutrients are exchanged with the water column (82). This stimulatory effect of velocity is reduced for thinner mats (185) and nutrient-replete cells (16).

Several authors have tried to establish a mechanistic relationship between water flow and uptake rates of limiting nutrients through the analysis of dimensionless parameters such as the Sherwood number (145) and the Stanton number (189). These parameters describe the enhancement of diffusion across a surface in terms of flow velocity, surface roughness, and nutrient-specific diffusion coefficients. Although diffusion limitation is often associated with photosynthetic processes, it can also pose a challenge for animals. For example, in microhabitats with low velocities, many benthic invertebrates actively circulate water past respiratory

organs to decrease the thickness of the laminar sublayer, thereby increasing the rate of gas exchange (66, 205).

In addition to their role as nutrients, dissolved chemical compounds can also serve as olfactory cues. In fact, olfaction is the most common sensory system used in communication and directed search (58), and many stream inhabitants use olfaction to avoid predators, find prey, or select mates (see 52 for a recent review). Because odors are usually transported by turbulent water flow, there is a strong link between odor-mediated searching behavior and ambient flow conditions. First, the temporal and spatial distribution of odorant within odor plumes is determined by turbulent mixing and dilution processes (71, 123, 203). Second, many organisms use the direction and strength of flow as ancillary rheotactic cues to navigate successfully in a turbulent odor plume (72, 212). The interaction between these two flow effects often produces a unimodal relationship between search success and velocity (72, 203). For example, when flow is slowest, searching success is low because there is insufficient mechanical stimulation for rheotaxis, even though odor dilution is minimal. At higher velocities, search success increases as the strength of potential rheotactic cues increases. In very fast water, foraging efficiency is again reduced because rates of dilution are so high that the odor is rapidly diluted below detectable levels.

Such unimodal relationships between measures of organismal performance and velocity may be widespread in benthic environments. For example, flow can have countervailing effects on the accrual of benthic algae (12). At the lowest velocities, nutrient uptake by algae is limited by the thickness of the viscous sublayer and by low levels of turbulent flux. In contrast, the greater drag associated with high velocities causes increased algal sloughing. Maximum levels of algal biomass often occur at intermediate velocities as a result of this type of subsidy-stress relationship (12).

Flow has similar effects on the collection of particulate resources by passive suspension feeders (115, 124, 173, 199, 204). For example, ingestion rates of these consumers are often limited by low flux rates of seston when velocities are slow, whereas high drag may impair the performance of the feeding structures in fast flows. These offsetting mechanisms commonly produce a unimodal relationship between ingestion rate and velocity (115, 124, 173, 204). Further support for these conclusions comes from theoretical (31, 114, 170) and experimental (21, 22, 104) studies of the mechanisms by which organisms remove food particles from suspension. Moreover, recent studies have demonstrated flow-dependent phenotypic plasticity in the morphology of feeding appendages, which suggests that the design of these structures represents a balance between maximizing particle encounter rates and minimizing drag costs (210; see also 93).

Competition

When flow controls the supply rate of limiting resources such as nutrients or suspended particles, it can also potentially mediate the intensity and outcome of competitive interactions. One striking feature of such interactions is their unidirectional

nature. For example, upstream organisms can reduce the availability of resources that might otherwise be used by individuals located farther downstream, but not vice versa. The mechanisms by which upstream consumers alter resource availability can involve either exploitation or interference (*sensu* 86). In exploitation competition, resources are directly consumed by upstream individuals, leading to a progressive reduction in resource availability as a water mass passes over an array of organisms. Such exploitation competition has been modeled in marine bivalves by using advection-diffusion equations to describe how the concentration of seston declines in response to resource uptake (27, 204). High levels of resource depletion are most likely to occur where consumer densities and per capita consumption rates are both high, and where bulk mixing due to turbulence is low. There is also evidence that such resource depletion occurs in some streams (108, 125, 208), although few investigations have focused on the flow mechanisms that govern this process.

A second mechanism by which consumers modify resource availability to organisms located farther downstream involves alterations of flow characteristics rather than resource consumption *per se*. Specifically, flow patterns are modified by the shapes and activities of benthic organisms, which can in turn impact downstream patterns of resource flux (60). In the case of suspension-feeding black flies, Clark & Hart (35) demonstrated that flow disruptions caused by upstream larvae reduced the local mean velocity and increased the relative turbulence intensity experienced by downstream neighbors, which in turn can lower their ingestion rates (33). Similarly, Hemphill (94) and Englund (65) reported that velocities were reduced by as much as 50% several body lengths downstream from net-spinning caddis flies.

Whether via exploitation or interference, the reduction in resource availability caused by upstream organisms can alter interactions among consumers. For example, Hart (87) observed that black fly larvae often behaved aggressively toward nearby upstream neighbors in an effort to displace them. Moreover, such aggressive behavior declined in response to an experimental increase in seston concentration, thereby suggesting that food concentration and velocity can be viewed as partially substitutable resources (*sensu* 190) for these passive suspension feeders. Similarly, the aggressive interactions typical of many salmonids stem from competition for preferred feeding sites that are governed by water-borne delivery of invertebrate prey (69).

When flow mediates competitive interactions, it can also affect the spatial distribution of consumers. For example, several authors have shown that passive suspension feeders avoid sites located immediately downstream from other individuals (33, 65, 94). Likewise, Matczak & Mackay (117) demonstrated that nearest-neighbor distances in territorial net-spinning caddisflies declined in response to experimental increases in either velocity or food concentration. Because flow also mediates density-dependent emigration from foraging sites, a heterogeneous flow environment can in turn give rise to spatially patchy distributions of consumers (75). It is not yet clear how such flow-mediated competitive interactions contribute to patterns of resource partitioning (114).

Physical disturbances caused by extremely high or low flows can also alter the outcome of interspecific competition. For example, Hemphill & Cooper (95) demonstrated that winter floods modified the outcome of competition for space between net-spinning caddisflies and black flies. Specifically, scouring during floods created open space that was rapidly colonized by competitively subordinate black flies. In the absence of disturbance, such space was usually monopolized by larval caddisflies. Zhang et al (211) also found that black flies benefited from hydraulic disturbances that occur below dammed sites on rivers, apparently due to the reduced impact of less disturbance-tolerant predators and competitors.

Predator-Prey Interactions

Flow can affect the outcome of predator-prey interactions by altering either predator-prey encounter rates or the predator's ability to successfully capture prey following an encounter. For example, Hansen et al (84) and Hart & Merz (92) performed lab and field experiments, respectively, examining how predator-prey interactions between flatworms and black fly larvae varied as a function of velocity. Flatworms were unable to tolerate the high velocities preferred by black fly larvae, thereby providing larvae with a flow-mediated refuge from these predators. Moreover, even where velocities were slow enough to allow encounters between flatworms and larvae, the probability of successful capture declined markedly with increasing flow owing to difficulties in handling prey at higher velocities. Similar reductions in predator impact with increasing velocities have been observed in stoneflies (115, 148). Hart & Merz (92) suggested that such flow-mediated refuges may be common in many benthic communities because of the tendency for prey to be smaller than their predators, which would expose them to lower drag forces and thereby reduce their risk of dislodgement in high flows.

Interactions between benthic algae and grazers can also be mediated by flow. DeNicola & McIntire (43) conducted studies in a laboratory flume demonstrating that high flows prevented snails from grazing on algae occurring in exposed microhabitats. Poff & Ward (156, 157) found that mobile caddisfly grazers moved more slowly as flow rate increased, and that their negative effect on algal abundance was greater in slow flows. Similarly, Hart (88) showed that grazing crayfish were able to eliminate filamentous green algae from microhabitats characterized by velocities <20 cm/s, whereas the algae flourished at velocities >50 cm/s. Indeed, this latter velocity corresponded closely to the flow threshold at which the crayfish had difficulty maintaining their hold on the stream bed (118).

In summary, the potent and diverse flow effects documented in the preceding sections strongly support the view that flow is the fundamental abiotic factor controlling ecological processes and patterns in streams. Developing a more comprehensive understanding of these important effects depends not only on greater attention to the mechanisms by which organisms respond to flow, but also the range of flow conditions that benthic organisms are likely to experience. Accordingly, we first turn our attention to the nature of flow heterogeneity in benthic environments,

and subsequently examine methods for quantifying flow characteristics in these settings.

SOURCES AND SCALES OF FLOW VARIATION

Flow characteristics in a particular stream vary over a broad range of space and time scales. Velocity exhibits spatial variation from scales as short as the Kolmogorov scale ($\sim 10^{-4}$ m) at which turbulence is completely dissipated to heat, to scales as long as those describing channel forms such as the meander wavelength ($\sim 10^2$ m). Temporal variation in velocity occurs at scales as short as those associated with the smallest turbulent eddies ($\sim 10^{-2}$ s) to scales as large as the recurrence intervals of bankfull floods ($\sim 10^7$ s). One of the central challenges in the study of organism-flow interactions is to determine which of these space and time scales, which span more than six orders of magnitude, are most important for understanding particular ecological processes and patterns. Given our focus on the flow environments experienced by individual benthic organisms, we are particularly interested in the range of flow conditions an organism would encounter over the array of microhabitats it can occupy during its lifespan.

In the last two decades, several different approaches have been followed in applying principles from fluid mechanics and hydraulic engineering to predict benthic flow characteristics and examine their effects on organisms, including: (a) the application of boundary layer theory (41, 45, 136, 175, 198); (b) the classification of near-bed flow fields depending on velocity and depth, as well as the size and spacing of roughness elements (42, 209); and (c) prediction of benthic flow characteristics from coarse-scale hydraulic engineering models (180). Although these approaches are often useful for predicting flow characteristics in simplified settings (e.g., in pipes or on flate plates) or as the spatial average for an entire channel reach, the physical models on which they are based were not designed to predict the local flow environments actually experienced by benthic organisms that inhabit the topographically variable surface of a natural stream bed.

Some of the challenges involved in using physical models to predict flow patterns in benthic environments can be illustrated by examining the vertical gradient in flow characteristics that exists in many streams. Recently, Nikora et al (134) developed a simplified hydraulic model for spatially averaged open channel flow over a rough bed that subdivides the flow into several vertical layers (Figure 2) (see also 163). The model's focus on hydraulically rough flow is particularly relevant because such flows are the norm for most natural streams (29, 80), with turbulent eddies extending to the substratum surface where they disrupt the formation of a viscous sublayer. When the depth of the flow is much greater than the height of the roughness elements, an outer and logarithmic layer will exist. In the logarithmic layer, average velocity exhibits a log-linear relationship with height above the bed. Flow characteristics in this layer can be readily predicted according to the "law of the wall" (136), but this is not the layer inhabited by most

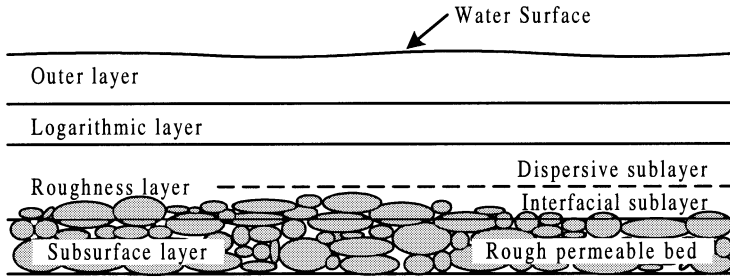


Figure 2 Subdivision of hydraulically rough open-channel flow into horizontal layers (modified from 134). Importantly, flow velocities within the “roughness layer” are unpredictable based solely on knowledge of overlying flow (e.g., logarithmic layer). This figure is not drawn to scale.

benthic organisms. Rather, stream benthic organisms usually live in the roughness layer, which includes a zone that extends above the roughness crests where three-dimensional flows are present (the dispersive sublayer) as well as a zone among the roughness elements per se (the interfacial sublayer). Unfortunately, no models are currently capable of predicting flow characteristics at any specific location within this roughness layer (i.e., in a particular microhabitat where an organism might reside), because local flow patterns are highly three-dimensional and uniquely dependent on the exact shape, size, and arrangement of these roughness elements.

An alternative means of describing near-bed flow patterns was proposed by Davis & Barmuta (42; see also 209), who built on earlier work (126) to develop a classification system based on the height and spacing of roughness elements. Irregularity in the arrangement of these elements on natural stream beds, however, makes the classification of near-bed flow into well-defined categories more challenging. Moreover, a large range of flow microhabitats are likely to occur within each flow category (e.g., wake-interference flow), so these classification systems may lack adequate resolution for describing the flow field experienced within a particular microhabitat.

Of course, spatial flow variation also occurs on scales larger and smaller than those associated with sediment particles in the roughness sublayer. For example, an alternating sequence of riffles and pools creates heterogeneity in both bed slope and roughness on the scale of tens to hundreds of meters. On the other hand, the pitted and grooved surfaces of individual substrata produce heterogeneity on a millimeter scale. Collectively, these complex topographic features cause marked heterogeneity in benthic flow characteristics, which is likely to produce an equally heterogeneous array of ecological processes and patterns.

Temporal flow variation is also a conspicuous feature of stream benthic environments. Considerable attention has focused on the ecological consequences of extreme flow variations associated with floods and droughts that operate on relatively long time scales (36, 97, 153). Paradoxically, ecologists have focused much

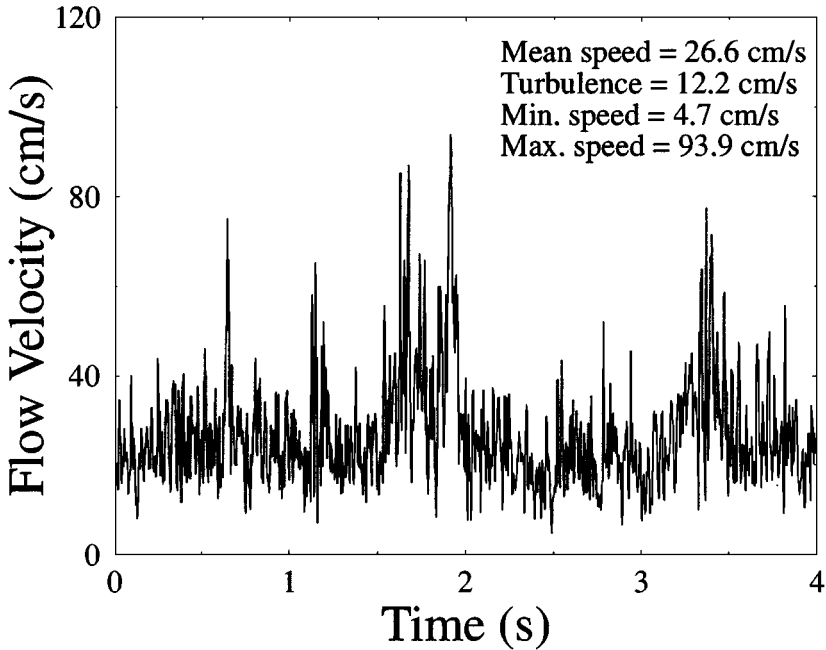


Figure 3 Four-second velocity time series collected using a hot-film velocimeter. Data were collected at 256 Hz from a 2-mm height above the surface of a natural stone inhabited by black fly larvae in Taylor Run (Chester County, PA). Turbulence is measured as the standard deviation of the time series, or the root mean square (RMS) turbulence intensity.

less on the effects of short-term flow variation associated with turbulence (Figure 3), even though it is a more prevalent phenomenon (80). Indeed, except for the smallest benthic organisms living in the slowest flows, turbulence is the rule rather than the exception in streams and rivers (29). Turbulent flows are highly irregular and unpredictable in nature, and they are characterized by large, rotating eddies that produce intense mixing (188). Benthic organisms will often be subjected to shear-induced turbulence and may also experience quasi-periodic oscillations in the flow due to vortex shedding from upstream objects. Turbulent flows can be characterized by several different quantities in three dimensions, including turbulent stresses, kinetic energy flux, and various scales (e.g., Kolmogorov, Taylor, integral) of eddy lengths (20, 166, 176, 188).

It is sometimes incorrectly assumed that turbulent fluctuations are relatively unimportant in near-bed flows due to the general reduction in velocity and corresponding inertial forces immediately above the stream bed. As demonstrated by Figure 3, time series of velocity recorded just 2 mm above the stream bed can reflect a high degree of turbulence, with velocities varying by more than an order of

magnitude (89). Some characteristics of turbulence can be predicted in simplified settings, such as the development of a turbulent boundary layer along a flat plate (136). In the roughness layer where most benthic organisms live, the generation of turbulence involves a more complex array of processes. In particular, high levels of turbulence can arise when flow separation around upstream roughness elements produces vortices that are advected downstream (42, 133, 209). Indeed, such flow disturbances are caused by benthic biota as well as bed features per se (135, 171). Analysis of vertical and horizontal components of turbulent flow fluctuations over coarse gravel beds has also demonstrated bursting phenomena, which include infrequent sweeps of high velocity water toward the bed and associated ejections of low velocity water away from the bed (168). These bursting motions are known to play important roles in sediment entrainment (136) and may be equally important in governing the transport of benthic organisms to and from the bed (45).

Although traditional models from fluid mechanics and hydraulic engineering are useful for describing flow variation in geometrically simple settings or at larger scales, their utility for characterizing flow patterns within the roughness layer is much more limited. Thus, when these models are used to make predictions about benthic flow characteristics, they are likely to produce two kinds of errors that pose problems for the study of organism-flow interactions. First, the flow characteristics predicted at any particular location on the bed will usually differ from the true conditions because the models are unable to account for the complex 3-D flow patterns in the roughness layer. Moreover, the sign and magnitude of difference between predicted and actual flow characteristics is likely to vary dramatically depending on the local setting to which the model is applied. Ultimately, such inaccuracies can greatly distort our estimation of the intensity and importance of organism-flow relationships (*sensu* 202).

A second, and perhaps more serious, consequence of the misapplication of traditional engineering models is that they will usually underestimate the spatial and temporal heterogeneity of flow fields available to benthic organisms. Of course, the tractability of such models is enhanced when they assume a more homogeneous flow setting, but what is the price of such simplification? A growing body of theory suggests that environmental heterogeneity per se is a critical factor governing ecological processes and patterns (85, 98, 144, 191). Indeed, the mosaic of microhabitats created by flow heterogeneity is likely to be an essential property of stream ecosystems, given the role of flow in controlling the availability of refuges (92, 105), affording opportunities for niche diversification (114), mediating dispersal (140), and constraining food web dynamics (162). Thus, although spatial and temporal heterogeneity in flow creates numerous challenges for ecological research, such heterogeneity is too important to be ignored.

Two more recent approaches to flow modeling may enhance our ability to characterize heterogeneous flow environments and examine their effects on benthic organisms. In particular, advances in computational methods have made it possible to develop more realistic models of flow patterns. The first approach toward a more realistic description of flow involves the use of computational fluid dynamic

models. This class of computer models can provide detailed predictions of flow fields in one, two, or (occasionally) three dimensions via numerical solution of the Navier-Stokes equations (the fundamental equations governing mass and momentum transfer in a moving fluid) (4). The power of these models stems from their versatility. For example, predictions of flow patterns can be obtained for flows around relatively simple objects such as cylinders (4, 91), or very complex structures such as a moth wing in flight (113). Thus, such models offer a potentially valuable bridge between the direct, but usually labor-intensive measurement of the benthic flow characteristics at a particular locale, and the ultimate goal of predicting near-bed flows for much larger portions of the stream bed (30). Moreover, such models are likely to provide valuable insights regarding scale-dependent patterns of physical-biological coupling.

A second approach involves the application of advection-diffusion (= dispersion) theory to study the turbulent transport of suspended particles and benthic organisms. For example, a number of research groups have developed hydrodynamically explicit models for predicting the distribution of organisms in the water column under various flow conditions (48, 59, 62, 81, 120, 194). Although these models still require simplifying assumptions, they also increase the level of realism through incorporation of more complex topographic relief (194), organismal behavior (62, 194), and tidal forcing (62, 81, 194).

QUANTIFICATION AND MANIPULATION OF BENTHIC FLOW FIELDS

The direct measurement of benthic flows can play at least two important roles in advancing ecological research in streams. First, there is a critical need for the validation of physical flow models. As indicated above, we need to quantify the accuracy of these models by determining how predicted near-bed flows differ from those actually experienced by benthic organisms. Second, when accurate flow models are unavailable, direct measurements provide the only means of quantifying the benthic flow environments inhabited by stream organisms. Although a diverse array of instruments and techniques are available for quantifying flow, the investigator must carefully consider various trade-offs regarding spatial and temporal resolution, cost, and difficulty of use (Table 1). For example, the existence of complex velocity gradients within the roughness layer places a premium on the use of instruments with fine spatial resolution (29). This challenge was highlighted by Hart et al (89), who used hot-film anemometry to measure velocities in the vicinity of larval black flies inhabiting natural stone surfaces. They found no statistical relationship between velocities measured 2-mm above the stone (i.e., the height at which larvae hold their filtering appendages), and those measured at 10-mm height (see also 12). Moreover, larval abundance was strongly related to the 2-mm height velocities, but unrelated to those at 10-mm height. These results suggest that flow measurements made with coarse spatial resolution may

fail to detect significant organism-flow relationships. The results also emphasize how a knowledge of the study organism's natural history can help guide decisions about flowmeter resolution. Considerations about the temporal resolution of flow measurements are particularly important for assessing the effects of turbulence on benthic organisms. Although turbulence affects many critical processes, including dislodgement (133), settlement (120), resource acquisition (16), and competitive interactions (35), the flowmeters used by stream ecologists often lack adequate temporal resolution for characterizing turbulent flows. Fortunately, flowmeters with sufficiently high spatial resolution for making measurements at scales relevant to benthic organisms also tend to have high sampling frequencies for quantifying turbulence, although there are exceptions to this pattern.

Rather than espouse any one device or technique, we urge investigators to consider carefully the operating principles and limitations of different devices before making a selection (Table 1). As mentioned above, the size of the study organism may dictate the necessary spatial resolution of the flowmeter (hot-film or hot-bead anemometry for very small invertebrates, propeller or electromagnetic flowmeters for large aquatic macrophytes). Moreover, before any new technique is adopted for measuring benthic flows, it should be thoroughly calibrated against a reliable standard in flow fields similar to those where it will be deployed (e.g., strongly sheared, near-wall conditions). For example, acoustic Doppler velocimeters (ADV) have recently been adopted for use by benthic stream ecologists (18, 135). Although the performance of ADV has been carefully validated for use in open water (5), its spatial resolution may be too large to provide accurate flow measurements in the first few mm above the bed where many benthic organisms live (70). It is also important to be clear about the flow parameter being measured. For example, dissolution techniques measure the rate of mass transfer at a given point but may not provide reliable information on average velocity due to the confounding effects of turbulence. Similarly, some methods only measure speed (a scalar) rather than velocity (a vector defined by both speed and direction), although the difference between these two measures in strongly unidirectional flows may be small, given suitable instrument alignment. In sum, we believe that greater attention to the suitability of alternative methods for quantifying benthic flows will markedly enhance our understanding of physical-biological coupling in streams.

Experimental studies are needed to understand the mechanisms underlying organism-flow relationships. It is important to be aware of the many trade-offs inherent in conducting such experiments in the laboratory versus the field (49, 165). The ability to control, manipulate, and quantify flow will almost always be easier when studies are conducted in laboratory flumes (45, 137). For example, the assumptions of uniform and fully developed flow can often be met in the laboratory (136, 137). Moreover, by manipulating substratum geometry, it is possible to create a variety of flow microhabitats (103, 129). It is even possible to decouple average velocity and turbulence characteristics in the laboratory via the use of upstream grids, weirs, and varied levels of bed roughness (109, 136, 137). For instance, Weissburg & Zimmer-Faust (203) were able to distinguish the roles of

TABLE 1 Flow measurement devices/methods.

Device/method ^a	Max. spatial resolution ^b	Max. frequency response ^c	Cost ^d	Lab/Field	Pros	Cons	Suppliers ^e	References ^f
Flow visualization/ Particle image velocimetry	variable	30 Hz. typical NTSC video	\$-\$\$\$\$	both	Non-invasive, can be used in boundary layers. 3-D. Frequency response can be increased with high speed imaging systems.	Boundary layer and high resolution applications may require costly cameras or lights and may be restricted to lab.	24, Dantec, TSI	25, 75, 178
Volumetric flow measurements	variable	0.1 Hz	\$	both	Easy method for estimating average velocity through a known cross sectional area.	Variable precision. No turbulence or boundary layer information. 1-D.	NA	124, 186
Dissolution methods	variable	<0.01 Hz	\$	both	Easy method for measuring average flow or mass transfer rates at a point.	Slow response time. Usually coarse spatial resolution; invasive. Measurement of velocity easily confounded by turbulence. 1-D.	131	53, 100, 151
Fließwasser- stammisch (FST) Hemispheres	30 cm ³	<0.01 Hz	\$-\$\$	both	Direct integrated estimate of shear stress on platform near the bed.	Highly invasive, sensitive to bed roughness, no boundary layer or turbulence information. 1-D.	182	50, 78, 106
Drag deflection, strain	1 cm ³	1 Hz	\$-\$\$	both	Robust method of estimating mean or maximum velocity.	Unsuitable for most boundary layer conditions, invasive. 1-D.	6	65
Bentzel tubes	0.5 cm ²	0.1 Hz	\$	both	Simple measurement of mean velocity.	Not commercially available or commonly used in ecological research, invasive. 1-D.	68	94
Propeller Bucket wheel	0.25 cm ³	1 Hz	\$-\$\$\$\$	both	Easy, sturdy method of measuring mean velocity in free stream.	Unsuitable for most boundary layer conditions, invasive. 1-D.	Nixon, Pygmy, Schlidknecht	88, 92, 156

Thermistors	approx. 0.002 cm ³	100 Hz	\$	both	Sturdy method for measuring fine scale flows in boundary layer and free stream.	Electronic and thermal drift, built-it-yourself technology, limited range of sensitivity, invasive, 1-D.	102	51, 200
Pitot tubes	0.05 cm ³	10 Hz	\$-\$\$\$\$	lab	Can be fine scale, operates by well understood physical principle.	Not commonly used in ecological research, invasive, require steady, non-accelerating flows, 1-D. Insensitive in slow flow.	Midwest instruments, Dwyer instruments, 197	46, 164
Electromagnetic meters	0.5 cm ³	10 Hz	\$\$-\$\$\$\$	both	Sturdy, 2-D, directional, no calibrating.	Invasive. Limited boundary layer applications. Poorly defined sample volume.	Marsh-McBirney, InterOcean Systems	71, 72, 139, 212
Hot film	approx. 0.0004 cm ³	10,000 Hz	\$\$\$\$	both	Suitable for many boundary layer measurements, high spatial and temporal resolution. 1 to 3-D.	Electronic and thermal drift, frequent calibration, fragile sensors, invasive, non-directional.	Dantec, TSI	89, 171
Hot film shear probes	0.1 cm ²	1000 Hz	\$\$\$\$	both	Suitable for many boundary layer measurements, direct measurement of friction velocity and skin friction.	Electronic and thermal drift, frequent calibration, non-directional, not-suited for oscillatory flow. 1-D.	Dantec, TSI	61, 83, 143
Acoustic Doppler	approx. 0.25 cm ³	25 Hz	\$\$\$\$	both	Sturdy, 3-D, non-invasive, no calibrating, direct measurement of Reynolds stresses, directional.	Strong backscatter from solid bed, may be unsuitable for some near-bed measurements.	SonTek, NorTek, Med-systems Inc.	18, 70, 135
Laser Doppler	approx. 0.001 cm ³	1000 Hz	\$\$\$\$	lab	3-D, non-invasive, excellent for boundary layer measurements.	Requires high powered lasers and optics. Unsuitable for field use due to beam alignment and other problems.	Dantec, TSI, Medtronics	181, 209

^aDepending on flow field and deployment method, some techniques measure flow speed rather than velocity.

^bMaximum spatial resolution is defined by the volume occupied by measurement device or area of probe exposed to flow.

^cMaximum frequency responses are for typical deployment.

^dCosts are estimated in US Dollars: \$ = < \$500, \$\$ = \$500 to \$2,500, \$\$\$ = \$2,500 to \$5,000, \$\$\$\$ = \$5,000 to \$15,000, \$\$\$\$\$ = > \$15,000.

^eSuppliers are for commonly used systems in aquatic research. Where citations are given as a supplier, the referenced paper gives details on construction or principles of operation.

^fReferences are for field and lab deployments in ecological research.

mean velocity and turbulence in governing an odor-mediated predator-prey interaction by varying velocity and bed roughness in a laboratory flume.

Although field experiments generally offer greater realism than the laboratory, it can be much more difficult to quantify the benthic flow characteristics produced in such experiments. This is particularly true when field experiments are conducted within the roughness layer. One compromise is to deploy appropriately shaped substrata that project well above the surrounding bed or that are raised off the bed entirely. This technique not only reduces the problems stemming from vortex shedding by upstream roughness elements, it can also take advantage of the relatively predictable flow behavior over simple geometrical shapes (91). Indeed, this approach may offer one of the best opportunities for predicting near-bed flow characteristics from flow measurements made at coarser scales.

Even when flow is not the primary focus of study, the experimentalist may need to be concerned with flow effects. For example, field experiments examining species interactions commonly use barriers (metal cages or mesh fences) to prevent the emigration and immigration of organisms. Unfortunately, these barriers will often change the local flow environment as well (149, 196). Particularly where different kinds of cages are used for different treatments (cages with open sides vs. those with closed sides), it can be difficult to determine whether observed treatment effects are due to species interactions or to the confounding effects of different flows. Thus, investigators need to be aware of flow modifications (even inadvertent ones) to attribute cause and effect correctly in a variety of experimental studies.

ORGANISM-FLOW INTERACTIONS AND ENVIRONMENTAL PROBLEM-SOLVING

Many human activities modify the natural flow regime in streams and rivers (154, 158). For example, flow patterns have been altered by dams, channelization, and urbanization. Given the pervasive effects of flow on the structure and function of stream ecosystems, such activities may have undesirable consequences. Thus, it is imperative that we examine the ways in which human activities alter natural flow patterns, and the consequences of these alterations for the health of stream ecosystems. Two brief examples serve to illustrate the range of environmental problems for which a better understanding of organism-flow interactions is required.

Dams provide many social benefits (e.g., hydropower, flood control, and recreation), but they can also damage streams and their biota (154). In the past, the magnitude and timing of flow releases from hydropower dams has often been dictated primarily by the economics of power generation, with much less concern for the instream flows needed to provide critical ecosystem goods and services (159). Unfortunately, the flow modifications caused by dams can negatively affect sediment transport, resource availability, and species interactions (112, 162). If we had a more complete understanding of the ways that spatial and temporal flow

variations affected the structure and function of stream ecosystems, it might be possible to manage water releases from dams in a manner that would achieve a better balance between economic and environmental benefits.

An improved understanding of flow effects would also enhance efforts to restore streams and rivers (138). Many streams have been degraded as the result of channelization, removal of riparian vegetation, water abstraction, pollutant discharges, and stormwater runoff. Restoration efforts often focus on improving physical habitat within the channel, replanting streamside forests, and building stormwater retention structures. Because one of the goals of these restoration practices is to create flow conditions that improve the health of streams, it is clear that such efforts would benefit from a more complete knowledge of physical-biological coupling (141).

SUMMARY AND FUTURE DIRECTIONS

Flow affects the biota of streams in so many different and powerful ways that it should be viewed as the primary environmental factor determining the essential character of these important ecosystems. Although some areas of stream research have already adopted this view (127, 155), we hope that this explicit statement will encourage more ecologists to identify the critical information about flow effects needed to develop improved models of stream ecosystem behavior. We see these information needs as threefold. First, research must focus on the direct and indirect mechanisms by which flow affects organisms. Indeed, creative experimental designs will be needed to disentangle the multiple causal pathways by which such flow effects are manifested. Second, we must rigorously measure the natural flow fields actually experienced by stream organisms. In spite of the large technical challenges involved in quantifying benthic flow characteristics in streams, we are convinced that this approach will yield substantial rewards. Third, research on physical-biological coupling in streams needs to become more scale-explicit. Our review has emphasized the understudied, but critically important, organismal scales at which many flow effects operate. Yet flow varies across a broad range of interconnected space and time scales. Thus, more attention needs to focus on how physical-biological coupling at coarse scales is linked to fine-scale coupling (160). Given the interdisciplinary nature of this entire field, we believe that collaborations between ecologists and experts in fluid mechanics (e.g., hydraulic engineers, fluvial geomorphologists) are likely to be particularly fruitful.

Finally, an improved understanding of flow effects should produce important societal benefits. Streams and rivers are among the most intensively modified ecosystems on our planet, and many human activities alter natural flow regimes. By developing a better understanding of organism-flow interactions, as well as predictive models of such physical-biological coupling, ecologists can help improve our ability to protect and manage these valuable systems.

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