Biotic and abiotic controls in river and stream communities*

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Abstract. Lotic ecologists share a major goal of explaining the distribution and abundance of biota in the world's rivers and streams, and of predicting how this biota will respond to change in fluvial ecosystems. We discuss five areas of research that would contribute to our pursuit of this goal. For mechanistic understanding of lotic community dynamics, we need more information on:

1. Physical conditions impinging on lotic biota, measured on temporal and spatial scales relevant to the organisms.

2. Responses of lotic biota to discharge fluctuations, including the processes that mediate community recovery following resets caused by spates or droughts.

3. Movements of lotic organisms that mediate gene flow, resource tracking, and multilevel species interactions.

4. Life history patterns, with special emphasis on ontogenetic bottlenecks that determine the vulnerability of populations confronting environmental perturbation.

5. Consequences of species interactions for community- and ecosystem-level processes in rivers and streams.

Without attempting to be comprehensive in our review, we discuss limits and limitations of our knowledge in these areas. We also suggest types of data and technological development that would advance our understanding. While we appreciate the value and need for empirical and comparative information, we advocate search for key mechanisms underlying community interactions as the crucial step toward developing general predictions of responses to environmental change. These mechanisms are likely to be complex, and elucidation of interacting bilateral, or multilateral, biotic and abiotic controls will progress only with the continuing synthesis of community- and ecosystem-level approaches in lotic ecology.

Key words: streams, rivers, communities, life histories, algae, zoobenthos, fish, discharge, disturbance.

Lotic ecology is increasingly becoming an ecosystem-oriented or holistic science (sensu Benke et al. 1984, Cummins 1973, Cummins et al. 1983, Minshall et al. 1983). During the past

two decades, the study of stream ecology has progressed rapidly (cf. Barnes and Minshall 1983, Fontaine and Bartell 1983) and a pervasive theme has emerged: that biotic dynamics and interactions are intimately and inextricably linked to variation in abiotic factors.

Few ecosystems possess either the frequency or intensity of environmental changes observed among lotic ecosystems (e.g., Fisher et al. 1982, Power and Stewart 1987, Webster et al. 1983).

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Moreover, processes that structure communities in flowing waters often occur on spatial and temporal scales that permit direct observation and manipulation. For example, many lotic species complete their life histories, or significant portions of their life histories, within the confines of channels, where the opportunities, risks, and stresses that they encounter can be ascertained. In contrast, it is much more difficult to assess the range of conditions experienced by organisms in more open terrestrial, marine, or lake environments. In clear water, movements, foraging, and social behavior of animals may be observed directly by underwater snorkeling or bankside observations (Hart 1983, Matthews et al. 1986, Peckarsky 1983, Power 1984a). Many lotic vertebrates and invertebrates seem unperturbed by quiet, close-range observation. Observations that might be difficult or dangerous in other habitats, such as forests or the marine intertidal, are feasible in streams and should be encouraged.

Streams offer field ecologists the distinct advantage of geomorphic repetition on various spatial scales. Variously-sized particles (boulders, cobbles, logs, leaves) are replicated habitat patches for small organisms; sequences of alternating pool and riffle habitats are repeated along long reaches of meandering rivers; various lateral habitats (oxbows, stranded pools, scroll lakes, marginal swamps) develop in floodplains; drainage networks are made up of numerous tributaries; local landscapes are often dissected by a number of drainage basins. In addition, some physical aspects of channels (width, depth, substratum texture) are broadly predictable from their position in drainage networks (Leopold et al. 1964). Thus, lotic ecologists can choose, on various spatial scales, sites that are comparable in many respects for structured comparisons or for manipulative field experiments.

A fundamental goal of ecology is to synthesize information about the natural world and then to predict how the structure and function of species, populations, communities, and/or ecosystems may respond to change. There is a particular urgency among lotic ecologists to find ways of predicting the effects of change, not only because streams are naturally variable, but also because streams and rivers are vulnerable to anthropogenic disturbances. Many of the world's great river systems have been subjected to extensive dam building, diking, channelization, and the clearing of woody debris for navigation (e.g., Craig and Kemper 1987, Davies and Walker 1986, Lillehammer and Saltveit 1984, Sedell et al. 1978, Ward and Stanford 1979). These alterations often significantly alter the basic physical character of the lotic ecosystem. In both temperate and tropical regions, land use and deforestation have greatly increased the transport of terrestrially-derived sediment, which often greatly alters both chemical and physical variables. Throughout human civilization rivers have been the repository of domestic waste, but more recently this problem has become even more acute as industrialized nations produce, use, and dispose of agricultural and industrial chemicals and pollutants. Many of these new compounds have destructive effects on aquatic organisms. In addition to these physical and chemical changes, introductions of exotic species of fish and invertebrates is common (Moyle et al. 1986). Such introductions may result in significant changes in population dynamics, community structure, and genetic integrity of native species (Marnell et al. 1987, Stanford and Ward 1986).

The purpose of this paper is to summarize and discuss, with specific examples, the complexity of biotic-abiotic interactions in lotic ecosystems. We organize these thoughts within several topic areas that seem to us to be especially important: (1) influence of local physical conditions on organisms; (2) responses to discharge fluctuations; (3) movements of lotic organisms; (4) life histories; and (5) effects of species interactions on lotic communities and ecosystems. These topics are highly interrelated so that information acquired on one topic will be useful, or essential, in solving problems in other areas. Filling gaps in our knowledge of these topics will help to answer broader questions, such as the relative importance of local and contemporary versus biogeographic or historical factors in determining species distributions, or how to predict the response of lotic communities to major environmental change. In particular, information from these five areas will help us to assess the scales over which these larger questions must be investigated.

In the following discussion we will raise major unresolved issues pertinent to each research area, discuss limitations of our current information and ability to investigate these issues,

and suggest specific directions for future research, including types of data that would be useful and new technologies that might be applied or developed in order to acquire these data.

Influence of local abiotic conditions

Abiotic conditions of the local environment often determine whether lotic organisms can either colonize or persist in new or changing habitats. Many different abiotic variables or interactive processes may be involved. In spite of the myriad of correlative studies on the influences of abiotic variables on the distribution and abundance of stream biota, we still have much to learn about physicochemical controls. Some areas of investigation may be more important than others.

In general, stream ecologists have not effectively considered surface and viscous forces and small-scale physicochemical gradients, mainly because of inability to measure them. It is only recently, for example, that oxygen microelectrodes have been used in environmental research. Beforehand, oxygen gradients over benthic assemblages such as periphyton communities were measured too far above the organisms to ascertain actual environmental conditions experienced by attached cells or the processes that created these conditions (Carlton and Wetzel 1987, Revsbech and Jorgensen 1983). Similarly, only limited quantitative information exists on the intricacies of flow variables and the controls they exert on biota living in streams (Statzner et al. 1988—see this issue), even though discharge is nearly always measured in stream studies. For example, velocity gradients within the water column can be steep in fast flowing waters. Using laser doppler anemometry, Statzner and Holm (1982) have documented flows as high as 15–25 cm/s within a few mm from the bottom of experimental flumes, and as high as 35 cm/s only 10 μm above surfaces of mayflies and limpets tested in these flumes. Such observations challenge older ideas that torrent-dwelling fauna may live in relatively still water because their small, flattened bodies do not project above the "no-slip" region of boundary layers (Ambuhl 1959).

Velocity gradients produce shearing forces that resist the organism's ability to cling to the available substratum (Koehl 1984). They also determine how "well-stirred" an organism's environment is with respect to delivery of nutrients and food particles, and removal of wastes or allelochemicals (Vogel 1981). In addition, velocity gradients determine thickness of laminar sublayers and how frequently these are penetrated by turbulent eddies. By observing diatoms flowing under a microscope set over an artificial stream, Stevenson (1983) showed that small roughness elements (in this case, threads 0.1 mm in diameter) increased the rate at which cells within turbulent eddies penetrated laminar sublayers and contacted the substratum. If the diatoms remained in contact with the bed long enough to secrete cement, they were able to colonize. Techniques of flow visualization in the laboratory are also yielding detailed information on how near-boundary flow affects feeding by certain aquatic insect taxa, especially black fly larvae (Craig and Chance 1982). However, similar measurements to assess flow environments in natural lotic habitats are still impeded by the lack of robust, or inexpensive, current-measuring devices with fine-scale vertical resolution.

Sampling temporal variation in flow over scales meaningful to lotic organisms will also require thought and empirical experience. For example, the flow that dislodges insects is unlikely to be characterized accurately by the mean shear velocity; rather, drift may be induced by a high velocity burst of flow that comes over the substratum only periodically. Conceivably, a very short, sudden burst would dislodge insects whereas a gradual increase to the same final velocity would not. For understanding of certain flow–organism relationships, time courses of flow variation, organism response, and the response time of the current measuring device must all be properly coordinated.

Adequate sampling of natural flow environments (see Statzner et al. 1988—this issue) will set the stage for experimental studies of biotic responses to flow. Do algae grow faster in higher flow because of higher rates of nutrient delivery (Whitford and Schumaker 1964)? Or do the algae accrue more rapidly because grazers and epiphytes are impeded by the shear stress of localized flow patterns? Experimental studies are required to assess the relative importance of various mechanisms that may mediate correlations of biota with environmental factors like flow.

Experimental investigation of the causes for distributions of lotic biota with respect to physical variables is also needed on a larger scale. Correlative surveys are essential first steps in documenting broad geographic patterns of association of lotic biota with physical factors such as stream depth, substratum, flow, canopy, or temperature. However, without experimental supporting evidence, correlative data may be misleading or wrongly interpreted. If standing crops of algae growing on different areas of the stream bottom are similar despite variation in light reaching the streambed, algae may not be light-limited (Hynes 1970); or, algae may be light-limited, but differential harvesting by grazers dampens between-site variation and thereby masks light effects (Hawkins et al. 1982, Power 1984a). Another example is the case history of a trichomycterid catfish in a central Panamanian stream. During intense field work from 1978 to 1980, including many diurnal and nocturnal snorkeling censuses of fishes in a 3-km reach, Power (personal observations) always found *Pygidium striatum* in the coarse gravel of riffles. The catfish was fossorial, and pursued insects through the interstices of cobble-bedded riffles. In 1985 *Pygidium* did not occur in these habitats, but instead rested on beds of deep stream pools, where it had never been seen previously. In 1984 heavy winds had blown many trees into the channel upstream where, during spates, they moved and scraped fine sediments from channel walls. The channel had become wider and deeper, and formerly clean gravel riffles were paved with fine, clay sediments, eliminating this habitat for *Pygidium*. If the fish had been censused only after these events, it might have been considered a species with affinity for deep stream pools, when pools were likely less preferred as habitat than clean riffles.

In many cases the distributions of lotic organisms with respect to physical variables are mediated by interactions with other organisms. Water striders remain near stream margins in the presence of trout, but forage over central areas of channels where trout are absent, or have been removed (Cooper 1984a). Cased midges colonize shallow, recently inundated substrata that are devoid of competitively dominant sedentary caddisflies (McAuliffe 1983, 1984). These caddisflies also restrict distributions of grazing mayflies (Hart 1985). Brown trout introduced into streams aggressively dis-

place brook trout from their habitats (Fausch and White 1981). Drift rates of benthic insects from stream pools in logged areas are lower than those from forested pools because of enhanced predation by trout in logged reaches (Wilzbach et al. 1986).

Despite many documented cases in which physical or biotic factors force biota to reside in sub-optimal or non-preferred areas of stream segments, habitat in lotic environments has been designated as "available," "usable," or even "optimal" on the basis of occupancy alone (Bovee 1982). Evaluations of habitat quality should be supported by experimental and process-oriented studies. Comparisons of habitat use by species at different densities and food levels, or in the presence or absence of other species suspected to influence their distributions or behavior, will likely reveal constraints resulting in the occupation of habitats that are less preferred, and possibly inadequate in the long term (Baltz et al. 1987, Moyle and Baltz 1985). Measurements of demographic rates (growth, reproduction, and survivorship) and energetics (Benke et al. 1988—see this issue) of organisms in these various settings are required for an understanding of the requirements of taxa at various stages of their life histories. "Habitat suitability index models" (Raleigh et al. 1984, Stier 1985, Stuber et al. 1982), which incorporate detailed information on requirements for all life history stages of target species, seem a particularly useful approach to quantifying local abiotic controls.

Responses of lotic biota to discharge fluctuation

Seasonal fluctuations in discharge are crucial in the life histories of many fluvial species (e.g., Welcomme 1985). As water levels rise and fall, river and stream habitats expand and contract, resource availabilities shift, certain habitats become more or less isolated from others, and flow regimes change, altering other physical gradients. Yet extreme events (scouring spates, episodes of de-watering) can eliminate much of the biota, and set the stage for periods of biotic recovery, or succession (Fisher 1983), between these disturbances. Species assemblages that develop between "resets" may exhibit recurrent or divergent patterns.

In few other natural ecosystems can ecolo-

gists quantify so precisely the seasonal changes in habitat and resource availabilities as in rivers and streams. As water levels rise, the availability of food increases for lotic frugivores, grazers, insectivores, and detritivores that forage over inundated floodplains (Goulding 1981, Welcomme 1985). Black flies in the Ogeechee River on the southeastern coastal plain of the USA increase rapidly in numbers and in body size when the river rises onto its floodplain and bacterial food in the seston increases (Hauer and Benke 1987). Conversely, Harper (1978) reported that increased secondary production was related to lower discharges in a second-order stream in Quebec when compared with production during an exceptionally wet summer the previous year. Certain predatory species, however, may experience decreasing food availability with rising water as prey concentrations are diluted or prey species find more effective refuges on the floodplain (Lowe-McConnell 1975, 1987). The ratio of maximal area flooded to minimal wetted area remaining in rivers in the dry season closely predicts the catch of fish in African floodplain rivers (Welcomme and Hagborg 1977). These relationships may well characterize floodplain rivers worldwide (Welcomme 1985, 1988—see this issue).

Water levels affect not only the area and availability of lotic habitat, but also the degree of habitat isolation, and therefore the availability of refugia for species during vulnerable stages. On floodplains, a variety of lateral habitats are inundated at high flow, and may persist as lentic, and often isolated, habitats during low flow periods (Welcomme 1979, 1985). These lateral habitats are nurseries and refugia for many species. They provide opportunities for comparative studies and manipulative field experiments of temporarily isolated components of the biota of large rivers, during periods that may be critical in their life histories (Bayley 1982; M. Rodriguez, University of Colorado, work in progress).

In smaller channels, riffles are complete or partial barriers between pool habitats (and vice versa) at low flow, but become corridors during periods of high flow. Riffles or pools may serve as temporary refuges from predators and competitors. The duration of these refuges depends on the hydrograph, channel morphology, and on the tolerance of various species and size classes for crossing barriers under particular hy-

drologic conditions. Theoretical models have predicted relative dispersal rates or frequencies which permit predators and prey to co-exist in patchy environments (e.g., Hastings 1977, Murdoch and Oaten 1975). Streams with pool-riffle differentiation offer excellent natural habitats in which to test these models (Power et al. 1985).

For more precise predictions concerning the influence of discharge fluctuation on availability of habitat and resources for lotic taxa, and therefore on production of their populations, more detailed knowledge of their ecology may be required. In a Panamanian stream, the densities of armored catfish tripled with a modest 20-cm drop in baseflow level from the rainy to the dry season. Because much of the channel was U-shaped, this drop in water level reduced the total (plan view) area of submerged streambed in a 3-km reach by only 18%; habitat contraction appeared insignificant. But armored catfish avoided areas less than 20 cm deep, where herons and kingfishers fished frequently and effectively. The area of deeper habitat changed 2–4-fold with 20-cm seasonal baseflow changes. Catfish densities tracked increases and decreases in habitat availability so rapidly (within days) that behavioral habitat selection, rather than recruitment or mortality, must have accounted for fluctuations in their density. Armored catfish with seasonally constant depth distributions showed pronounced seasonal trends in somatic growth, but not in mortality (Power 1984b, 1987). Similar depth distributions of lotic fishes subject to predation by wading and diving birds were observed in temperate streams (Matthews et al. 1986).

Scouring floods and spates may enhance co-existence of lotic species by maintaining an intermediate level of disturbance (Connell 1978, Lubchenko 1978, Ward and Stanford 1983). On boulders in southern Californian streams, spates open up areas that are subsequently colonized by black fly larvae. Between high-water disturbances, substrata are increasingly dominated by competitively superior hydropsychid caddisflies (Hemphill and Cooper 1983). Interspecific co-existence in lotic environments, as mediated by hydrographic disturbances, also occurs on much larger spatial scales. Introduced mosquitofish (*Gambusia*) have extirpated native Sonoran topminnows (*Poeciliopsis*) from southwestern streams, mainly by predation. In mountainous streams subject to spates, however, the topmin-

nows can persist because they are better able to seek out areas of reduced current during high water, while populations of the less spate-adapted mosquitofish are periodically washed away (Meffe 1984). This study illustrates heuristic coupling of detailed behavioral observations with large scale surveys to explain regional distribution patterns.

Whether changes in discharge have benign or catastrophic effects on lotic biota depends on schedules of precipitation and properties of catchments. Well-vegetated catchments, as well as those with lakes or swamps, act as hydrologic capacitors, storing water to release it slowly over prolonged periods (Hynes 1975, Welcomme 1979). Where climatic, geologic, or anthropogenic factors decrease permeability of catchment soils and eliminate intermediate storage compartments for water, discharge fluctuates more abruptly and extremely, and scouring spates or drought can destroy biota (Cross et al. 1987, Matthews 1987, Tett et al. 1978). The severity, duration, and areal extent of the disturbance, as well as its frequency and timing, determines how completely the community is "reset" (sensu Fisher 1983). One component of recovery between floods or droughts is recolonization, and another is regeneration from residual survivors capable of enduring the disturbance.

For most lotic species, too little information is available to evaluate the relative importance of resistance versus recolonization during recovery from discharge-related disturbance. Abilities of local biota to resist flood or drought depend on the physicochemical tolerances of individual taxa (Matthews 1987, Peckarsky 1980), and on the availability of "safe sites" or refugia within or accessible from channels. In general, we know very little about the abilities of various lotic taxa to resist flood or drought. Microbes produce resistant resting stages that may endure unfavorable conditions for many years. Algae that have dried to white dust along stream margins may be perfectly capable of regenerating when inundated. Nostoc (a cyanobacteria) that had been dried 107 years on a herbarium sheet began to grow when it was immersed in water (Scherer et al. 1984). Other algae may persist even on severely scoured rock substrata. In Oklahoma streams, basal pads of Rhizoclonium (a green alga) are amazingly resistant to natural and experimental scour, and some

blue-greens have partially endolithic growth habits that protect them from abrasion (Power and Stewart 1987). Some invertebrates also have extraordinary physicochemical tolerance. The African midge Polypedilum vanderplanki can survive years in sunbaked mud, yet grow rapidly when ephemeral pool habitats re-water (McLachlan and Cantrell 1980).

In general, however, invertebrates and vertebrates are vulnerable to desiccation, crushing, or washout (Harvey 1986, Minshall et al. 1983). Nonetheless, local populations may persist during spates or droughts in refugia lateral to or underneath the channel. The appearance of invertebrates in wells several km from surface waters indicates that hyporheic and groundwater channels may be important as refugia for some zoobenthos and permanent habitat for others (Stanford and Gaufin 1974, Stanford and Ward 1988). Pore space, oxygen gradients, substratum stability, and organic flux through the hyporheic habitat determine its suitability for organisms. While these factors have received considerable attention with regard to streambed suitability for salmonid spawning (e.g., Allen 1969), they have just begun to be investigated as determinants of the quality of hyporheic habitat for other lotic organisms (Stanford and Ward 1988, Williams 1984).

Indeed, streams seem to exhibit a myriad of habitats that may serve as temporal refugia from spates. Burrows of animals like catfish or crocodilians may provide critical refugia for smaller animals below water tables when channels are dry. In a drying pool of a western Ecuador stream, where only one endemic poeciliid remained in the hot shallow surface water, 192 specimens comprising 8 families, 12 genera, and 13 species were recovered from the subterranean burrow of a catfish (Rhamdia wagneri) (Glodek 1978). The opening to this burrow in the streambed was only several cm in diameter. Such refugia, while inconspicuous to ecologists, may be critical to the persistence of fauna over periods of dewatering. Small tributaries that backflood from water entering their mouths from the spate-swollen main channel may function as refugia (cf. Stout 1981). Fishes took cover in the dead water of undercut stream banks as floodwaters rose in a Panamanian stream (Power, personal observations). Lotic insects in endorheic spring-streams in southcentral Washington (USA) recover rapidly after floods despite

the absence of an upstream community, the lack (in winter) of ovipositing adults, and limited hyporheic refuge in shifting sand beds; larvae that survived in debris or along the flood edge, or eggs in "microrefugia," are the most likely recolonists (Cushing, unpublished data). Knowledge of channel features that provide refugia during changes in discharge is of obvious importance when studying processes that maintain diversity or influence productivity of lotic biota (Lowe-McConnell 1987, Sullivan 1986).

Resistance to drought or spate also depends on the timing of these disturbances relative to life histories of lotic biota. Larval fish are swept away or crushed in spates that have minimal, or beneficial effects on older conspecifics (Harvey 1987). Entire year classes may be lost if multiple spawnings cannot compensate for the loss of fry to particular flood events (Starrett 1951). Traits of life history stages also influence recolonization potential. The sculpin Cottus asper occurs in low elevation and coastal streams of western North America. These streams are subject to periodic dewatering. Cottus asper has pelagic larvae, and these and juveniles can live in estuaries. Consequently, this sculpin can quickly recolonize streams wiped out by drought by migrating upstream from estuarine refugia. In contrast, Cottus gulosus lives predominantly in trout streams, which are normally permanent, and it has benthic larvae. It has taken over a decade for C. gulosus to recolonize only a few kilometers of a native stream that dried during an unusual drought year (Smith 1982).

In Sonoran desert streams, spates eliminate 99% of the insect fauna from reaches with fine gravel substratum, but an "air force reserve" of winged adults, in addition to larvae drifting down from undisturbed habitats upstream, recolonize habitats soon after the waters subside (Fisher et al. 1982, Gray 1981). In contrast, cold, desert springbrooks in Washington (USA) do not have upstream sources of colonists; and, theses streams often flood during winter, when aerial adults are not ovipositing (Cushing, unpublished data). More geographical comparisons of this type would be useful in assessing general controls on the rates and types of processes mediating recovery of lotic communities between drought or high discharge.

Discharge fluctuations in rivers and streams provide repeated opportunities to study responses of biota to variability in physical factors, resource availabilities, and biotic interactions. Rapid and intense changes in discharge appear to act as disturbance events that, if severe enough, will likely alter community structure in streams. But spates and floods are in fact essential to the life histories of organisms and the function of their communities (Welcomme 1988). With more information on mobilities and ecological tolerances and requirements of taxa, it should be possible to interpret biotic responses to hydrographic "disturbances" in a more insightful manner (see also Resh et al. 1988 in this issue).

Movements of lotic organisms

Inadequate knowledge of the rates and pathways of movements of stream organisms still confounds attempts to measure processes and interactions in lotic communities, and underlies much of the confusion over appropriate spatial scales of investigation (see also Minshall 1988 in this issue). For example, cage experiments intended to assess effects of predators can be difficult to interpret if the design is incommensurate with scales of movement of organisms. If an insectivorous fish is enclosed in a cage, predation by the fish (if it can respond normally when confined) could be swamped by migration of benthos to the new structure. A fish exclosure, on the other hand, may not develop higher densities of benthos even if predation in the external environment is an important control. Insects that have to migrate through a gauntlet of predators to reach the exclosure may never arrive. Careful thought must be given to the spatial range of activities of organisms under study before enclosure or exclosure studies, or other density manipulations, are designed or interpreted. When possible, it is desirable to use whole habitats, separated by natural barriers to movement as experimental units (pools separated by riffles or vice-versa, cobbles separated by sandy substratum, reaches above and below water falls, channels separated by drainage divides) (Bayley 1982, Cooper 1984b, Endler 1980, Hart 1983, Hemphill and Cooper 1984, Kohler 1984, 1985, McAuliffe 1983, 1984, Power 1984a, 1987, Power et al. 1985, Seghers 1974a, 1974b).

Inadequate observation may distort the importance of particular pathways of movement. For example, drift nets intended to sample insects moving downstream also collected (un-

intentionally) organisms that crawled upstream along the nets (Statzner, personal observation). Sampling of any process, including rates of movement along various pathways by organisms, should, whenever possible, be attended by direct observations of sampling gear to make sure it is collecting the intended type of information (Greene 1979). Such direct observations are often feasible in flowing waters.

Movements of lotic organisms, whether over distances of microns or thousands of kilometers, are controlling processes in any stream system. Such processes may: mediate gene flow; affect coexistence of competitors, predators and prey, mutualists, hosts and parasites; translocate energy and nutrients; and determine the potential of biota for colonizing new or emptied habitats. The fact that many biota are more or less confined to the stream channel also facilitates studies of movement-mediated interactions. Rivers and streams, for example, are good arenas for studies of rates and patterns of gene flow in populations (Zimmerman 1984).

Genes may, in fact, "flow" independently of organisms, as has been demonstrated with movements of extracellular DNA among microbes in laboratory settings. The extent to which genetic material in viruses, plasmids, or as free DNA is exchanged laterally among organisms in natural environments like rivers and streams is as yet unknown, but is obviously of great interest both to population geneticists and evolutionary biologists, and to people with general concerns about the release of genetically engineered organisms. In Florida rivers, free DNA, presumably released from dying bacteria, is present in easily measurable concentrations, yet is rapidly cycled. Labeled DNA is taken up by living cells rapidly enough to produce turnover times of 12–24 hours (J. Paul, University of South Florida, personal communication). Bacterial transformation (uptake of free DNA by living cells) may therefore occur in lotic environments, and allow genes to be transmitted laterally through, or among, populations. Exchange of plasmids by conjugating bacteria is another process that could promote such exchange (Levin 1986).

The possibility and type of lateral genetic exchange depends on distributions and movements of microbes in lotic environments, about which little is known. Bacterial distributions on substratum are often patchy. For example, high densities of bacteria have been observed at the junctures of branches of filamentous algae (A. K. Ward, University of Alabama, personal communication). Bacteria also aggregate around heterocysts of cyanobacteria. Do bacteria move to these sites directed by chemotaxis along gradients of substances released by algae? Or do cells simply grow or adhere better in these microenvironments? How far do bacteria travel in lotic water columns? What determines their deposition, and ability to adhere to substrata? Little is known about the relative importance of colonization versus local growth in determining bacterial densities in flowing waters. Nearly nothing is known about the effects of near boundary flow on growth-promoting or growth-inhibiting factors on spatial scales that affect bacteria in natural lotic habitats.

Movements of larger components of the microbial flora in streams (fungi, algae) are also largely uninvestigated. But, as an example, studies of colonization of allochthonous leaves by aquatic hyphomycetes and selective feeding on these by aquatic invertebrates have provided insightful, mechanistic results (Arsuffi and Suberkropp 1984, Suberkropp and Arsuffi 1984, Suberkropp et al. 1983). This system could be studied from an island biogeographic perspective to derive predictions about colonization potential from species-specific rates of spore production and dissemination, and growth once new leaf islands were colonized (T. L. Arsuffi, University of Georgia, personal communication).

Attached algae in many streams undergo dramatic cycles of growth, senescence, decay, and export. Although little is known about processes that regulate algal biomass at a site (Round 1984), even less is understood about the fate of cells that are detached and exported by scouring spates, by decay and abscission, or by grazing. At what rate do they continue to divide, or produce reproductive bodies? Can they re-attach? Filamentous green algae egested from grazing fishes may continue to photosynthesize (M. E. Power, W. J. Matthews, A. J. Stewart, University of Oklahoma, unpublished data), suggesting that certain benthic algae resist digestion, as has been found for certain phytoplankters (e.g., Porter 1973). Therefore, although grazing can deplete attached algae at a site (Hart 1985, Lamberti and Resh 1983, Power et al. 1985). it may also produce unexpected streamwide effects on algal

abundance, productivity, and taxonomic composition. To understand impacts of grazing on algae over large regions of lotic habitats, we must develop methods for tracking movements and fates of egested or exported algae. New techniques, such as DNA probes or immunofluorescence, could be applied to the challenging problems of tracking small organisms and their progeny in natural waters.

Larger scale movements of lotic organisms include the long migrations of tropical and temperate fishes (Welcomme 1985). Among the most spectacular of these migrations are the "piracema" or "subienda" of the great South American rivers, in which adult fishes travel thousands of kilometers to place their eggs and young in upstream spawning sites on the rise of the rainy season floods (Goulding 1980, 1981, Lowe-McConnell 1987, 1988—see this issue, Welcomme 1985, 1988). An extensive marking program (Bonetto and Pignalberi 1964, Bonetto et al. 1971) suggests that separate upriver and downriver populations exist for some of the migratory fish stocks, such as *Prochilodus platensis*, a characin of great ecological and commercial importance in the Parana and Paraguai Rivers (Lowe-McConnell 1987). Knowledge of the timing, distance, and controls on fish migrations is necessary to assess the amount of habitat required to maintain their populations. Such information is urgently needed, as large dams have been or are being built across migration routes of fishes in most of the world's large rivers (Bonetto and Wais 1985, Bonetto et al. 1987, Hynes 1986).

In contrast to the piracema fishes, certain fishes in smaller temperate (Hill and Grossman 1987) and tropical (Power 1984a) streams have rather restricted movements. Sculpins in the Flathead River, Montana, show genetic differentiation between groups sampled from riffles separated by as little as one kilometer (Zimmerman and Wooton 1981). Mexican goodeids (Turner et al. 1983), Mexican guppies (Vrijenhoek 1978, 1979), and Trinidadian guppies (Endler 1980, Seghers 1974a, 1974b) show genetic differentiation over relatively short reaches (tens of kilometers). Where such microgeographic variation in gene frequencies occurs in streams, the stage is set for an array of population and evolutionary studies. Headwater populations in many streams are periodically exterminated or drastically reduced as their habitats dry up, and recolonists

must come from downstream populations. Such cycles offer repeated opportunities to study evolutionary processes like natural and sexual selection, genetic drift, and gene flow in populations of different sizes (Turner et al. 1983). Numbers of predators often tend to increase downstream (Endler 1978, Seghers 1974b, Shelford 1911, Vannote et al. 1980). Predators apparently induce genetic changes in coloration (Endler 1983), behavior (Seghers 1974a, 1974b), body size (Liley and Seghers 1975), and life history (Reznick and Endler 1982) in Trinidadian guppies. These studies exemplify the suitability of some lotic organisms for studies of evolutionary ecology.

Movements of fishes and other organisms affect not only gene flow but also outcomes of species interactions and the potential of various taxa to colonize or recolonize habitats. An unresolved question in stream fish ecology is the relative importance of habitat diversity versus immigration and extinction rates in producing the common patter of downstream addition of species (e.g., Horwitz 1978, Schlosser 1982, Sheldon 1968, 1987). Studies of movements are necessary to evaluate these factors (Matthews 1987, Sheldon 1984).

Of all types of movements of lotic organisms, drift by lotic insects is perhaps the best studied. Drift can be initiated by biotic interactions as well as by a variety of physical factors (Allan 1987, Cadwaller and Eden 1977, Kohler 1985, Waters 1972, Wiley and Kohler 1984, Wilzbach et al. 1986). However, the processes that maintain upstream populations of benthic insects in the face of downstream losses are subject to debate. The relative importance of surplus upstream production (Waters 1966) versus upstream crawling (Brown and Brown 1984) or upstream flight of ovipositing females (Muller 1974, 1982) has not to our knowledge been evaluated for any taxa. Sampling programs that do not take into account the local and long-distance movements of species can become highly biased (Lauzon and Harper 1986). Clearly, information on all pathways of movement by organisms is necessary for management programs intended to promote or reduce the abundance of particular populations.

Despite the advantages of studying movements of organisms that are confined within channels, tracking individuals, particularly small individuals, in flowing waters can be like

searching for moving needles in complex haystacks. One solution is to make the needles more detectable (using telemetry, improved marks, and applications of genetic markers, DNA probes, or immunofluorescence to track individuals and their progeny). We need both simple and technically advanced innovations to devise marks and tracking methods that have minimal effect on the behavior or fitness of organisms, yet are easy to detect. Another challenge is to develop tracers that do not impose environmental hazards. For example, fingerprint ratios of stable isotopes (Peterson and Fry 1988, Peterson et al. 1985) may be useful alternatives to introduced radioactive isotopes as ecological tracers.

A second solution is to reduce the size of the haystack. Movements of small organisms (microbes, meiofauna, insects) can be initially investigated in flumes (e.g., Kohler 1985, Palmer and Molloy 1986, Stevenson 1983). In these settings, where initial densities from source areas are known, effects of factors like flow, substratum suitability, crowding, or food availability on movement can be well-defined.

A third approach is to monitor newly available habitat rather than individuals, to learn how quickly and by whom it is colonized. Careful observation of spatial relations between colonizable habitat and potential sources, marking studies, and frequent sampling that reveals the arrival times of various colonizing species, will provide valuable information on species mobility and recolonization potential (Gore 1979, Matthews 1987, Sheldon 1984). Diffusion equation modeling could be applied, as it has been for terrestrial insect movements (Kareira 1983), in cases where the time course of spread and the spatial relationships of point sources or point sinks are sufficiently well specified (Okubo 1980). Such models could generate useful quantitative comparisons of movement by various taxa, or by single taxa under various conditions.

Information on mobility will be crucial to our understanding of how various life history stages of lotic species can respond to opportunities, stresses, and hazards in their hydrologically dynamic environments.

Life histories of lotic organisms

To understand and predict the response of organisms to variation and change within and between lotic ecosystems, we need information about their life histories. A number of key questions immediately arise. What are the cues that initiate life history events like oviposition, hatching, larval metamorphosis, diapause, emergence, the onset of reproduction? What habitats and resources are necessary for particular stream taxa to complete their life histories? Where are "ontogenetic bottlenecks" (cf. Werner and Gilliam 1984) that regulate population size? What happens to populations when these are relaxed or constricted? How variable are allocations of resources by lotic species to growth versus reproduction?

Lotic species are often regionally different in age and size at first reproduction, in numbers of generations per year, and in the degree of synchrony of life history stages (e.g., Newell and Minshall 1978), all of which suggest another set of related questions. How much of this variation is due to environmental plasticity, and how much to genetic differences? What are the consequences of particular suites of life history traits for populations confronting resource limitation, predation, or disturbance of their environments?

Of all these questions, we have the most information on the first, regarding life history cues. Many lotic insects, fishes, and plants use combinations of light, temperature, and flow level as cues for life history events. The importance of temperature in the life histories of temperate benthic insects has been extensively studied (cf. Newell and Minshall 1978, Sweeney and Vannote 1981) and reviewed (cf. Sweeney 1984, Ward and Stanford 1982). Evidence for the importance of temperature in the life histories of benthic insects comes from study of their disruption by altered thermal regimes in regulated rivers (Ward and Stanford 1979). Spawning migrations of riverine fish are often initiated when rains or rising water levels stimulate reproductive readiness and upstream swimming in adults. Young spawned as floodwaters begin to rise have access to rich, newly inundated habitat, and escape exposure to predators in the main channel (Lowe-McConnell 1987, Welcomme 1979). Downstream from impoundments, fish stocks may in some cases be maintained, despite truncation of their natural habitat, if flow releases mimic natural hydrologic regimes that trigger hormonal readiness and upstream movements of adult fishes, and

if lateral floodplain habitat is maintained for nursery areas (Davies 1979). All too often, however, specific habitats that species require to complete critical life history stages disappear when rivers are channelized or impounded. For example, the Truman Dam on the Osage River inundated the only known spawning grounds for the largest remaining population of the paddlefish (Polyodon) in North America (Pflieger 1975). At one time ranked as the most important commercial fish in the Mississippi Valley (Pflieger 1975), paddlefish have declined drastically owing to loss of spawning habitat and overfishing. At this point, the species is maintained in the Upper Osage River only by a laboratory breeding program (W. L. Pflieger, Missouri Department of Conservation, personal communication).

Because many large rivers were not studied before being massively altered, we shall never know the ecological roles of species that have been lost (cf. Davies and Walker 1986). However, we know enough about life history requirements of many river species to anticipate consequences of impoundment and channelization on their life history characteristics and to plan regulation projects accordingly. Moreover, implementation of conservation-minded mitigation procedures would in many cases not only help preserve species diversity but also give ecologists the opportunity to test, on a large scale, ideas about physical and hydrologic controls on life histories of lotic species (Ward and Stanford 1979, 1984).

Catastrophes unrelated to impoundments and channelization can befall lotic populations (cf. Resh et al. 1988—see this issue), and their vulnerability increases with the synchrony of their life histories. During recent piracema migrations of characins (Prochilodus) in the Parana River, Argentina, rains that triggered the migration also washed agrotoxins into the river from soybean fields in the catchment, with the reported result of "100s of kms of dead fish" (R. Welcomme, Food and Agriculture Organization, personal communication). Yet migratory fish stocks may be resilient in the face of catastrophe. Some African species have made a strong comeback after being undetected for 4–5 yr during the Sahelian drought (R. Welcomme, personal communication). This resilience comes from high per capita fecundity; but during bottleneck periods, genetic diversity may

be lost. We know too little about life histories of most lotic taxa to predict their responses to crashes in population size, or changes in its age structure.

In contrast to "white fish" of tropical rivers, which migrate along main channel and thereby avoid the severe conditions that develop in headwaters or floodplains during periods of low water, "black fish" remain resident in standing waters when these are stranded, and resist stresses such as de-oxygenation with adaptations like air-breathing or aquatic surface respiration (Kramer 1983, Lewis 1970, Welcomme 1979). Reproduction of these resident fishes, as well as fishes in less seasonal environments, can show wide ranges of synchrony (Kramer 1978) and other life history features (Lowe-McConnell 1975). Increased physiological tolerance of such species, parental care preventing predation, siltation, or oxygen stress of eggs and young, and risk-spreading for those that reproduce asynchronously all contribute to the resistance of the population to potential bottlenecks for particular life history stages.

Some tropical and subtropical lotic insects also have asynchronous or little synthesized life histories. In a stream in Zaire, emergence of caddisflies occurred at any time of the year (Statzner 1986). Aquatic Diptera in a warmwater river of the southeastern USA are also asynchronous (Benke et al. 1984). Because different life history stages are often in different types of habitat, the vulnerability of the whole population to localized disturbance is reduced (Statzner 1987). Not all tropical insect populations have asynchronous life histories, however (McElravy et al. 1982, Turcotte and Harper 1982a, 1982b), and cues such as fluctuations in rainfall or water level may influence life cycle rhythms in these species.

Insect faunas in desert streams are vulnerable to unpredictable spates and dry periods. For example, in the southwestern USA selection has favored mayflies, small diptera, and other taxa with shortened aquatic stages of development; in general they have no diapause or dormancy, and winged adults are almost continually present, ready to recolonize habitats depauperated by catastrophic spates (Gray 1981, Gray and Fisher 1981). In colder, more mesic areas, however, insect life histories are usually more sharply synchronized as seasonal temperature regimes restrict periods of potential activity (e.g.,

Clifford et al. 1978, Hauer and Stanford 1982). Canalized responses to temperature regimes as cues for diapause, emergence, and other crucial life history events may render temperate species particularly vulnerable to thermal alterations of their environment (Stanford and Hauer 1988, Ward and Stanford 1979, 1984).

Photoperiod as a life history cue has seldom been investigated independently from temperature. Khoo (1964) showed that whereas growth was largely controlled by temperature among winter Plecoptera, maturation was affected by photoperiod. Photoperiod is the only environmental stimulus to vary consistently with latitude. Research is needed on how lotic animals perceive photoperiod, what parameters (e.g., day length, rate of change in day length) affect them, and whether the effect is direct or mediated ecologically (e.g., predators may have more time to feed when days are longer, Sweeney 1984).

For most lotic species, adequate ecological information to assess the needs and vulnerabilities of various life history stages is generally lacking. One basic problem is that different life history stages of many species are not described taxonomically. For example, the larvae of many temperate and most tropical fish species cannot be identified to species or genus until they have grown beyond stages that may be critical bottlenecks for populations. The same is true for many lotic insects. Some algae may be incorrectly split into separate taxa instead of being recognized as plastic phenotypic variants or heteromorphic life history stages. In addition to further application of traditional techniques of association (transplants and common gardens for algae, rearing and examination of pupae for insects), biochemical techniques (immunofluorescence, DNA probes) should be applied to support morphologically-based solutions to taxonomic problems.

The relative importance of various potentially limiting factors during various life history stages are not well understood, even for salmonid fishes which have been intensely studied. Limiting factors appear to vary geographically (Baltz and Moyle 1982, Leggett and Carscadden 1978). Species that migrate, or have winged adult stages, present further challenges for "key factor analyses" (Morris 1963) of the relative importance of mortality and growth limiting factors that constrain population production. To our knowledge, a complete key factor analysis over the complete ontogeny of any lotic species has never been carried out. Lotic taxa that complete their life cycles within restricted regions (mollusks, crustacea, apterous insects, some plants, sedentary fishes) are tractable subjects for complete life history studies.

While it is difficult to recognize life history bottlenecks for lotic populations, we have even less information about the consequences of relaxing or constricting them. Yet certain lotic taxa have life histories that would be particularly amenable to experimental manipulation of potentially limiting factors or resources. For example, armored catfish (Loricariidae) in Panamanian streams begin their lives as eggs and fry in nests in hollow logs. Parental males, effectively using their armor, completely block the entrance to the nest, thereby limiting predation on the young by characin fishes and freshwater crabs. Nest logs appear to be in short supply, as male loricariids will tenaciously occupy artificial structures with suitable attributes for spawning (Moodie and Power 1982). After leaving the nest, young armored catfish remain in riffle nursery areas where they graze on algae. Predation and other unknown factors apparently maintain populations at levels below those required to deplete food resources. At lengths of 4–5 cm, they outgrow cover available in riffles and become more vulnerable to predation. They enter pools at this size, and are food-limited for much of the rest of their lives (Power 1984a, 1984b, 1987).

What would happen to these armored catfish if more nest logs were provided? Would increased recruitment of young fish to riffle habitats attract and feed more predators? Or would the density, size, or age structure of catfish populations change? How would these changes affect population dynamics of other fish species or the entire community? Similar questions arise for many other important stream species. Indeed, we know too little about the life cycle of any lotic species to predict population and community consequences of altering ontogenetic bottlenecks. We may anticipate that these effects will be complex, as most species have very different, even opposite, ecological relationships with each other depending on their relative size or age (Werner and Gilliam 1984).

Thus, the questions posed at the beginning of this section remain largely unanswered. Innovative experiments are needed to elucidate

the intricacies of factors controlling life histories and the consequences such interrelations hold for maintenance of stream communities. In many streams, especially in unstudied tropical and high latitude areas, a direct observational approach may yield important new understanding of life history strategies.

Species interactions and their consequences

Rivers and streams contain many species. Functional relationships of lotic species may change with density. They nearly always change with ontogeny. Omnivory is common, if not the rule, at least during a portion of the life history; indeed, most lotic organisms derive their energy and elemental constituents from several trophic levels. Webs of direct and indirect interactions link disparate taxa within channels and radiate through the riparian zone (Cummins et al. 1983) to the divides between catchments (Hynes 1975), and in some considerations, beyond the catchment into adjacent drainages, e.g., as for flying insects, migrating decapods, and waterfowl.

Given the mathematical intractability of such complexity, predictive ecology is necessarily based on mechanistic models of a few key processes, or species, and their interactions. Inferences based on quantitative knowledge of natural history can identify "strong interactors" in many communities. These are species whose removal from the community or ecosystem will cause pronounced changes in structure and function (MacArthur 1972, Paine 1980). Biomass dynamics, production, and behavior of well-chosen species may provide powerful insights into community structure and function within ecosystems.

How do we decide which species matter? "Keystone predators" are often held as examples of strong interactors, and their importance is undeniable in many communities. However, predators may receive disproportionate attention, because they are often bigger, easily identified, and more easily manipulated than are less conspicuous species in food webs. Yet, the latter may also exert critical influences on the community as a whole. In many streams, large organisms such as amphibians, fish, or crayfish (Bovbjerg 1970, Cooper et al. 1986, Hairston 1981, Power et al. 1985), and sedentary lotic insects

(Hart 1985, 1986, McAuliffe 1983a, 1983b) are tractable subjects for density manipulations. These studies have set the stage for more thorough investigations of direct and indirect effects that cascade through communities or food webs, as species-specific densities change in response to external (e.g., enhanced nutrient loading) or internal (e.g., altered predation rates) events. Techniques are needed that will allow densities or activities of key members of lotic communities to be experimentally manipulated. Cages (Peckarsky 1980), longitudinal divisions of channels (Rader and Ward 1988), elevated tiles (King and Ball 1966, Lamberti and Resh 1983, Power 1984a), tethered predators (Power and Matthews 1983), use of antibiotics or specific toxins (Wallace et al. 1986), and manipulations of light (Towns 1981) or nutrients (Peterson et al. 1985) have all proven useful. But these techniques, unfortunately, suffer in varying degrees from the constraint that in ecology it is virtually impossible to manipulate one or a few key variables and maintain "real world" conditions. Innovative field manipulations that minimize or control artificial effects, coupled with clear documentation of processes before, during, and after experimental treatments, would advance understanding of community ecology in streams.

Need for predictions about consequences of changes in density or composition of microbial communities in flowing waters becomes even more urgent as more and more microbes are genetically altered and designed for use in environmental engineering. For example, natural or engineered bacteria with ability to metabolize and mineralize organic toxins are being studied in the laboratory for possible use in cleansing polluted surface- and groundwaters. To be effective such microbes would have to be released into the environment, where they could dominate or replace native populations.

Cooper and Stout (1982) studied the ability of bacteria to use p-cresol (a phenolic by-product of coal gasification) as a carbon substrate. They carried out their studies in flasks, microcosms, and large outdoor experimental stream channels. Bacteria were able to use p-cresol as a carbon source in all three experimental settings, but only in the outdoor stream channel did an indirect effect of p-cresol on stream biota appear. Increased respiration and decreased photosynthesis by the alga *Spirogyra* sp., which

was stressed by p-cresol, reduced dissolved oxygen in the channel to less than 1 ppm, severely affecting fish and aquatic invertebrates (Stout and Kilham 1983). This effect was not seen in microcosms which had fewer photoautotrophs, or in flasks, which were oxygenated. Overlooking factors in simulations of natural environments can lead to serious environmental consequences, especially when densities of organisms at base levels in food chains are manipulated.

Clearly, ecological effects of organisms change with their density, often qualitatively (cf. Allee 1951). Sparse floating macrophytes in the Parana River, Argentina, may provide essential cover for larval fish; but, decomposing macrophytes can deprive these same fish of oxygen (I. Wais, personal observations). When armored catfish are sparse, they may enhance the growth of attached algae (and food availability for each other) by clearing substrata of sediment. When catfish are dense, they compete exploitatively for this food, and diminish algal productivity by overgrazing (Power 1984c, 1987). Interactions of species at low densities are seldom studied because data are not easily obtained. Low intensity interactions could be of critical importance, however, in determining the geographic range of particular species, in determining their success in colonizing new habitats, or in affecting ability of stressed populations to resist the event or recover after stress abates.

It has been argued that streams are abiotically controlled, because physical disturbance and stress maintain populations at such low densities that biotic interactions are not important (cf. Huston 1979). However, biotic interactions per se may be important in allowing populations to endure abiotic stresses. In the example mentioned above, catfish burrows appear to be vital refugia for other species during droughts in an Ecuadorian stream (Glodek 1978). The thought that populations at low densities are "pre-interactive" or not functionally important may derive from a past tendency by researchers to equate "biotic interactions" with competition. Biotic interactions may be less frequently observed at low population densities, but from the point of view of the individual organism, those that do occur are critically important. In many cases the distributions of lotic organisms with respect to physical variables are mediated by interactions with other organisms. Net-spinning caddisflies may compete for sites of retreat

attachment and are known to attempt "take overs" of retreats of other individuals apparently occupying better sites (Haddock 1977). Black fly larvae are also known to attack individuals that are within reach and case-bearing midges colonize shallow, recently inundated substrata that are devoid of competitively dominant, sedentary caddisflies (McAuliffe 1983, 1984). Despite these apparent instances of interspecific competition, both black fly and net-spinning caddisfly populations are known to occur in exceptionally high densities in which individuals are living virtually on top of each other. Thus, competitive interactions for space may be greatly mediated by the concentration of energy resources (Stanford and Hauer 1988). More studies of species over ranges of relative densities are needed to assess how the density-driven changes may directly or indirectly affect other populations and, hence, community structure and function, particularly if some sort of competition is inferred a priori.

Species interactions usually change with ontogeny. Large perlid stoneflies, generally considered predators, are primarily detritivorous during their early stages and become predatory only when they grow larger (Stanford 1975, Stewart and Stark 1988). Adult bass in Oklahoma streams prey upon and displace juvenile centrarchids, which are major predators on centrarchid eggs and larvae. Therefore, in pool habitats with large bass, centrarchid eggs and larvae enjoy improved survivorship, juvenile centrarchids are killed or driven out, and adult centrarchids enjoy higher reproductive success (Harvey 1987). Aquatic macrophytes and filamentous algae can potentially escape from invertebrate grazers, owing to their comparatively large girth; grazers may use such plants as substratum rather than food. Grazers that ingest or export young plants may benefit older, more robust plants of the same species by grooming off harmful epiphytes or stimulating local nutrient regeneration (Bronmark 1985, Dudley et al. 1986).

Ontogenetic changes in species interactions are likely to be driven in large part by morphological constraints. Size-related mechanical constraints on mouths and defensive structures, as well as locomotory performance, will in many cases determine whether a particular life stage of an organism is a predator, prey, competitor, host, or indirect mutualist of another. Func-

tional morphology and associated inter- and in-
traspecific interactions have been widely stud-
ied in fishes (cf. Gatz 1979, Werner and Hall
1979); but less is known about this topic in in-
vertebrates (Hershey and Dodson 1987), and al-
most nothing is known for attached algae or
microbial colonies (but see Power et al. 1988,
Steinman et al. 1987).

Also as noted above, many lotic animals
undergo ontogenetic shifts in their diets, and
many are omnivorous during a given life his-
tory phase. To quantify the importance of var-
ious food sources for a given consumer species,
careful analyses not only of the gut contents
but also of the efficiencies with which con-
sumers can assimilate various foods must be car-
ried out (Benke and Wallace 1980, Mayer and
Likens 1987). To quantify the roles of particular
consumers in determining mortality within prey
populations, data on other mortality factors
("key factor analyses") as well as population
productivities, measured over adequate tem-
poral and spatial scales, are required. Food web
analyses of lotic communities are clearly daunt-
ing in their complexity. However, new and
improved techniques, such as multiple stable
isotopes (Peterson et al. 1985) and track auto-
radiography (Burkholder 1986, Knoechel and
Kalff 1976) are now available for sorting out
sources of energy and nutrients for lotic organ-
isms. Unidirectional flow and containment
within channels make streams and rivers ideal
environments to better understand how the dy-
namics of food availability and renewal, and of
consumer responses, influence communities and
ecosystems.

Indeed, much has been learned recently about
the trophic dynamics of small, temperate
streams, particularly for aquatic insect com-
munities (Benke and Wallace 1980, Cummins
1973, Lamberti and Resh 1983). However, ex-
cept for a few studies (e.g., Cummins et al. 1983,
Cushing and Wolf 1982, Fisher and Likens 1972,
Mulholland 1981), relatively little is known
about carbon budgets in lotic systems. This is
especially true for large rivers, particularly those
in the tropics.

The importance of terrestrial sources of or-
ganic matter to small streams has been recog-
nized for several decades (Boling et al. 1975,
Hynes 1963, Merritt and Lawson 1979, Petersen
and Cummins 1974, Suberkropp et al. 1975) and
is a central theme in the development of hy-

potheses on structure of stream and river com-
munities (Minshall et al. 1983, Vannote et al.
1980). Studies of the importance of allochtho-
nous inputs have concentrated on secondary
production of aquatic insects that shred leaves
(Merritt and Cummins 1984). The importance
of allochthonous POM goes beyond the nour-
ishment of invertebrates; however, trophic
linkages to fishes are much less understood. De-
tritivory among fishes appears to be more com-
mon in tropical streams than temperate streams,
although most detritivorous fishes may in fact
be obtaining their nutrition from the associated
microbes (Bowen 1983, 1984) and invertebrates.

Lake ecologists are presently debating the im-
portance of top-down versus bottom-up control
(predation and herbivory versus resource lim-
itation) (Carpenter et al. 1987, McQueen et al.
1986). McQueen et al. have associated positive
correlations between consumer and resource
densities with bottom-up control, and negative
correlations with top-down control. In rivers
and streams, patterns seem more dynamic than
in lakes; but the perspective of directional con-
trol may offer some new insights, although many
believe that in streams controls are "multilat-
eral" and operate simultaneously from above
and below.

Top-down and bottom-up controls may not
act independently, and lotic organisms provide
opportunities to study their interactions. For
example, grazing on cyanobacteria in the family
Rivulariacea removes attenuated distal hairs
(Power et al. 1988, Wickstrom and Castenholz
1985) that may function in phosphorus uptake
(Livingstone and Whitton 1983, Sinclair and
Whitton 1977). Nutrient availability, in turn,
may influence growth forms of algae in ways
that render them more or less susceptible to
grazers. Ecologists need to scrutinize the me-
chanics of growth, grazing, and predation (what
individuals or tissues are taken? At what rate?
What happens to the residue?). These detailed
studies, coupled with knowledge of the influ-
ence of factors like flow, temperature, light, nu-
trient availability, or population densities, will
form a more solid basis for predicting responses
of lotic communities to environmental change.

How far out on the web of direct and indirect
effects do we need to look to explain and predict
the distribution and abundance of lotic organ-
isms? This depends on "what is going on in the
environment" (Elton 1927). For example, stream

channels in deforested southeastern Brazil are choked with fine clay sediment, and contain very low densities and diversities of fish and invertebrates. In these streams, the "strong interactor" who (next to man) most profoundly affects distributions and abundances of lotic organisms may be the terrestrial leaf cutter ant, *Atta* spp. *Atta* densities increase where forests have been cut in South America, and their chambers and tunnels honeycomb the soil to depths several meters below the surface. These tunnels and holes greatly increase infiltration of rain into the ground, which could reduce erosion of soils and slow the movement of water to channels, stabilizing the hydrograph. However, in intense rainstorms, water accumulates in ant chambers so rapidly that they may burst downslope, spewing mud and water. Therefore, the net effect of *Atta* on how water sediment travels to stream channels is complex, and may depend on their densities, the size and configuration of their tunnels, soil properties, slope, and rainstorm intensities and durations (Ana Coelho-Netto, Universidade Federal de Rio de Janeiro, personal communication).

The scope of any study of river or stream communities may determine the interpretation of the results. As mentioned earlier, local processes may produce unexpected community or ecosystem level effects. For example, dense groups of anadromous salmon digging redds in tributaries of North American Great Lakes locally reduce aquatic insect populations. Yet their decaying carcasses supplement nutrients, and may increase future insect production (Richey et al. 1975). Extrapolations from observations or experimental studies on local scales to inferences about their significance in communities and ecosystems must be made with eyes wide open to "what goes on in the environment" on larger spatiotemporal scales (Minshall 1988).

Conclusions

The term "versus" seems to pervade much of community and ecosystem ecology today: biotic versus abiotic factors, direct versus indirect effects, top-down versus bottom-up controls. Alternative hypotheses are the roots of scientific method. But clearly the relative importance and effect of such factors or "controls" shift with dynamic changes in density of organisms and environmental conditions. Perhaps what is really needed is more appreciation for bilateral, or multilateral, controls on communities. For example, an interesting controversy over what controls the longitudinal distribution of hydropsychid species remains unresolved (see Alstad 1986, Thorp et al. 1986). Is it the availability of food resources between habitats along the stream continuum (Alstad's view) or is it the species-specific mesh size of the filtering net (view of Thorp et al.)? It may be instructive in instances like this to exclude the singular "versus" approach and devise testable predictions of the problems that incorporate multiple and dynamic controls.

Mechanistic models that allow formulation of testable hypotheses are useful for comprehending such controls and their interactions. When applied to incongruous problems, like the caddisfly example, good models tend to formalize the magnitude of ecological understanding (Hall and Day 1977); testing that understanding then resides in the realm of experimentation.

Will models derived from study of small, tractable lotic systems predict aspects of the behavior of larger systems? By studying invertebrate dispersal in floating algal mats in streams, could we learn anything about fish dispersal in floating meadows of the Amazon? Will studies of microbial communities in laboratory microcosms yield predictions useful in natural rivers or streams?

Certain local processes scale up to produce effects of overwhelming importance on environments or ecosystems. These may be exemplified by the construction of tunnels and chambers by ants in the catchment, the growth of algae and macrophytes over the water surface, the physiological response of aquatic insects to temperature, or the use of refugia by prey to escape predators. Lotic ecologists must quantify the importance of local processes, determine their community- and/or ecosystem-wide consequences, and compare results across latitudes if we are to understand and predict responses of river and stream communities to biotic and abiotic controls.

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