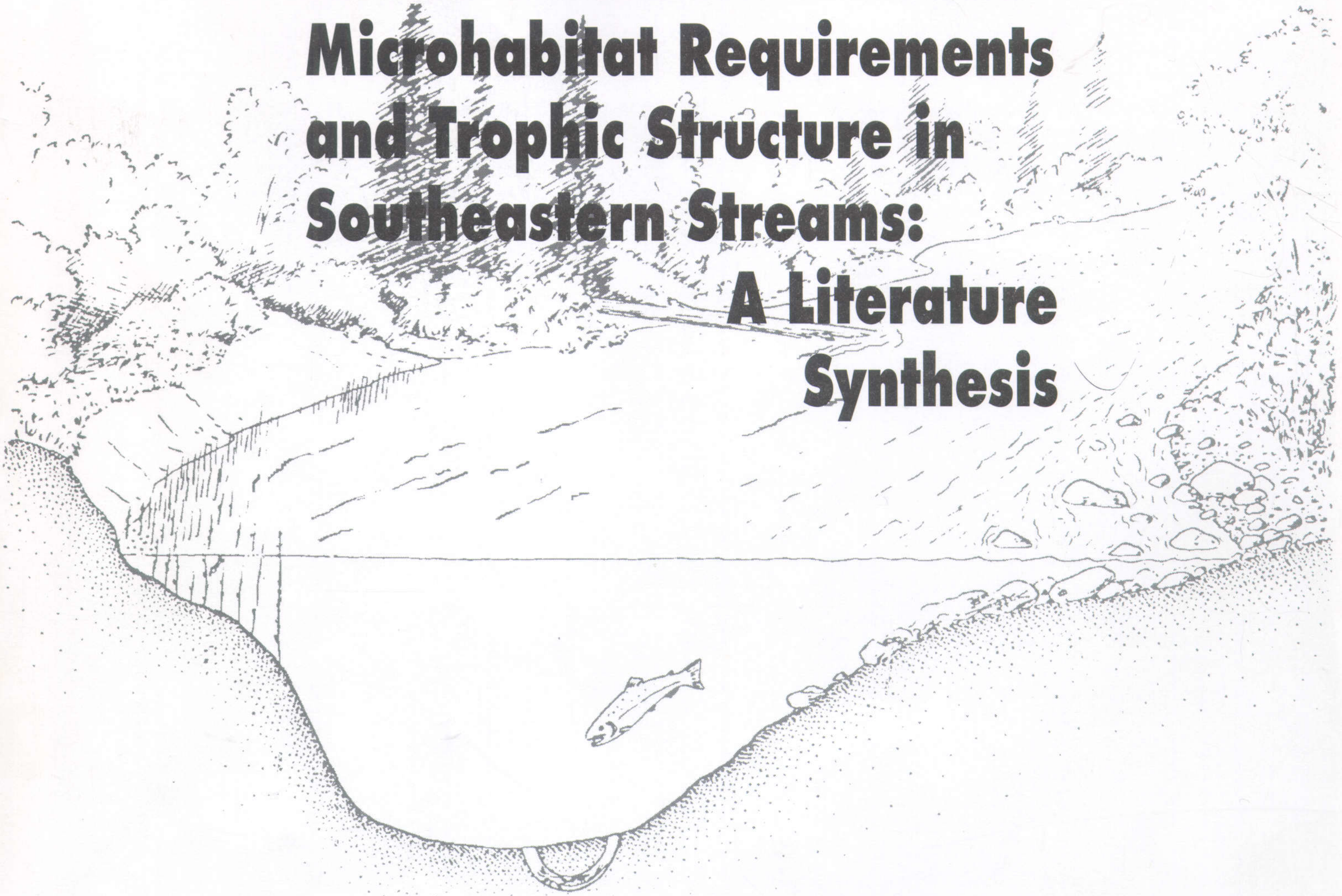
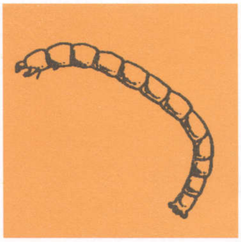
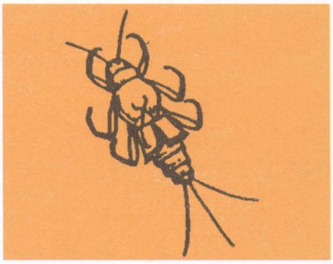
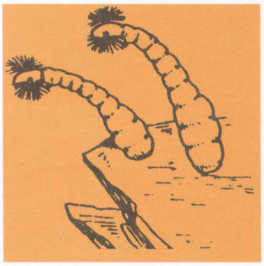
Benthic Macroinvertebrate Microhabitat Requirements and Trophic Structure in Southeastern Streams: A Literature Synthesis









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Lowell T. Frobish, Director
Auburn University
Auburn University, Alabama

Benthic Macroinvertebrate Microhabitat Requirements and Trophic Structure in Southeastern Streams: A Literature Synthesis

E. Cliff Webber

Michael R. Struve

David R. Bayne

Department of Fisheries and Allied Aquacultures

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Alabama Agricultural Experiment Station
Auburn University, Alabama 36849

Lowell T. Frobish
Director

Auburn University
Alabama 36849

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INTRODUCTION

A variety of factors regulates the occurrence and distribution of stream-dwelling invertebrates. The most important of these are current velocity, temperature (including the effects of altitude and season) the substratum and dissolved substances (Hynes 1970). Other important factors include the effects of droughts and floods, food, competition between species, predation, shade, depth, and zoogeography. However, sorting out the relative roles of the biotic and abiotic factors that determine the distribution and abundance of stream macroinvertebrates remains a complicated task.

Recent studies have emphasized the importance of stream hydraulic forces in regulating invertebrate communities. Investigations have included attempts to predict both the distribution and abundance of invertebrates by measuring the heterogeneity of flow characteristics within a stream reach (Statzner and Higler 1985; review by Statzner and Higler 1986; Davis 1986; Smith-Cuffney and Wallace 1987; reviews by Gore 1987, 1989; Statzner et al. 1988; Davis and Barmuta 1989; Heede and Rinne 1990; Gore et al. 1992). Organismic responses have been linked to stream hydraulics, within whole catchments or within reaches of different types of lotic waters (Statzner and Higler 1986). In fact, many of the factors listed above have been incorporated into models designed to predict invertebrate community structure (i.e., distribution, abundance, diversity) in streams and rivers (Gore 1978; Gore and Judy 1981; Peckarsky 1983; Wright et al. 1984; Armitage 1989).

The purpose of this paper is to review, evaluate, and synthesize the scientific literature on the following topics: (1) microhabitat preferences of benthic macroinvertebrates in warmwater streams of the Southeastern United States; (2) use of macroinvertebrates as key indicators for assessing instream flow needs in the Southeast; (3) trophic relationships between fish and macroinvertebrates in Southeastern streams; and, (4) macroinvertebrate responses to stream regulation, particularly in the Southeast. Our intent was to provide an exhaustive coverage of peer-reviewed studies conducted in the Southeast, and a representative and selective examination of the "gray" literature (i.e., technical reports and papers from state and federal agencies).

The term macroinvertebrate, by definition, refers to aquatic invertebrates retained on a U.S. No. 30 sieve (mesh size = 0.595 mm) (Weber 1973). However, the term has also been applied to organisms retained on sieves smaller than the No. 30 (e.g., see Hudson and Nichols 1986). When citing specific findings of researchers, their terminology is used, but with observations of a more general nature, the terms invertebrate and macroinvertebrate are occasionally used interchangeably.

SOUTHEASTERN STREAMS

The Southeastern United States includes six physiographic provinces, figure 1: Coastal Plain, Piedmont, Blue Ridge, Valley and Ridge, Appalachian, and Interior Low Plateaus (Fenneman 1946). In the hills of the Piedmont province, elevations range from about 366 m near the mountains to about 183 m at the Fall Line where the Piedmont merges with the Upper Coastal Plain. Here the valleys and slopes are often steep as streams and rivers descend through the Fall Line.

Stream gradients north of the Fall Line may range as high as 28 percent (Huryn and Wallace 1987a, 1987b), but only in headwater streams at the higher elevations in the Appalachian Mountains. More typical gradients range from just under 1 percent to about 4 percent as found in the Piedmont (Gordon and Wallace 1975; Wallace et al. 1977). The substratum in these streams is generally heterogenous, consisting predominantly of boulder, cobble, and gravel, with occasional outcrops of bedrock (Tebo and Hassler 1961; Malas and Wallace 1977; Huryn and Wallace 1987a, 1987b) and macroinvertebrate diversity may be high (Lenat 1987). Although many streams north of the Fall Line are warmwater streams, coldwater streams are common at the higher elevations, especially in the mountains, and some support trout populations (Tebo and Hassler 1961; Flecker and Allan 1984).

South of the Fall Line lies the Coastal Plain where the topography is such that stream gradients are usually less than 0.1 percent (Smock et al. 1989), although gradients in portions of the Coastal Plain approach 1 percent (Gordon and Wallace 1975). Substrates are predominantly unstable, shifting sand (Benke and Wallace

Figure 1. Locations of the major physiographic provinces in the Southeastern United States.

1990) and streams are mostly warmwater, including some described as subtropical (Cowell and Carew 1976; Benke et al. 1984; Wallace and Benke 1984; Benke and Jacobi 1986).

Distinguishing between coldwater and warmwater streams is a recent practice that resulted from the identification of different management needs for various lotic ecosystems. Winger (1981), in a review of physical and chemical differences between the two stream types, stated that streams with summer temperatures exceeding 20°C generally contain warmwater fish species. He characterized warmwater streams as usually occurring at relatively low elevations and having cool to warm water in summer, quiet flows, high turbidities, more pools and fewer riffles, substratum of smaller particle size, rooted and floating vegetation and sparse shade and cover, table 1.

The River Continuum and Southeastern Streams

Traditionally, streams have been classified based on drainage basin analysis or order (Strahler 1957). Although this classification system has limitations (Hughes and Omernik 1981), it provided the structural basis for one of the most useful conceptual models of stream ecosystems developed in the last decade, the river continuum concept (RCC) (Vannote et al. 1980; Bruns et al. 1984; Minshall et al. 1985). The RCC integrates predictable and observable biological features of lotic systems from headwater streams to large rivers. Biotic and abiotic variables, figure 2, of lotic ecosystems are categorized by stream size into small headwater streams (orders 1-3), medium-sized streams, or midreaches (orders 4-6) and large rivers (orders > 6). Streams are viewed as longitudinally linked systems in which ecosystem-level processes in downstream areas are linked to those in upstream areas.

The RCC describes assemblages of organisms, or functional groups rather than focusing on individual taxa. Functional groups are general categories into which invertebrates can be grouped based on similar feeding mechanisms (e.g. shredders, collectors, grazers, piercers, engulfer-predators, and parasites) (Cummins 1978). The relative abundances of these groups (biomass) are predicted to change from headwaters to large rivers, figure 2, in response to changes in the quantity and quality of particulate organic matter (POM) inputs (Cummins 1980).

Criticisms of several basic assumptions underlying the RCC appear in the literature (Winterbourn et al. 1981; Rounick and Winterbourn 1983; Statzner and Higler 1985). In general, criticism centers on the worldwide application of the concept that macroinvertebrate communities in headwater streams are dominated by large particle detritivores (shredders) and downstream, functional feeding groups change along a continuum as coarse particulate organic matter (CPOM) is reduced in size to fine particulate organic matter (FPOM). Winterbourn et al. (1981) described headwater streams in New Zealand in which shredders were poorly represented, and the dominant invertebrates were browsers that fed on FPOM and stone-surface organic layers. They also noticed little change in functional groups downstream and no temporal continuum of synchronous species replacements as predicted by the RCC. Rounick and Winterbourn (1983) also found no shredders in unstable, poorly retentive headwater streams in disturbed watersheds.

Minshall et al. (1985) pointed out that the original presentation of the RCC clearly accomodated these sorts of deviations. Minshall et al. considered it unreasonable to expect shredders to dominate if the CPOM supply is unreliable or insufficient, thus whenever CPOM enters a stream it is reduced to FPOM and this activity generally is quantitatively most significant in the headwaters of a river system.

Headwater streams in the Southeast are typical of most in that they are generally influenced by riparian vegetation that limits autotrophic production by shading and contributes large amounts of allochthonous detritus as POM. Most of the POM is leaf material, or CPOM, but smaller quantities of FPOM also enter the stream, especially from the surrounding floodplain (Georgian and Wallace 1983; Webster et al. 1983; Smock and Roeding 1986; Roeding and Smock 1989).

Woody debris also plays an important role in low-order streams. Wallace et al. (1982), Wallace and Benke (1984) and Golladay et al. (1989) described several roles of woody debris: dissipation of the stream's energy; retention of allochthonous organic matter, that can influence both trophic and nutrient dynamics; providing

Table 1. General Features of Warmwater and Coldwater Streams[1].

Characteristic	Stream Type Coldwater	 Warmwater
Valley shape	V	U
Temperature	Cold (< 20°C)	Cool - warm (> 20°C)
Discharge	Low	Medium - high
Velocity	Moderate (high turbulence)	Moderate to high (low turbulence)
Depth	Shallow	Medium to moderate
Width	1 - 6 m	> 3 m
Substratum	Rubble - gravel	Rubble - sand - mud
Gradient	High	Low
Elevation	High	Low
Turbidity	Clear	Clear - turbid
Pools (riffles)	Short (Many riffles)	Long (few riffles)
Temporal variability	High	Low
Aquatic flora	Periphyton	Periphyton and macrophytes
Shade and cover	Extensive	Sparse
Organic material	Coarse particulate organic matter	Fine particulate organic matter
Distance from source	< 8 Km	> 16 Km
Stream order	Low (< 3)	Higher (>3)
Competition	Intraspecific	Interspecific
Predatory fish	Few	Many
Fish community	Salmonidae	Centrarchidae Ictaluridae Catostomidae
Fish diversity	Low	High

[1] Modified from Winger (1981).

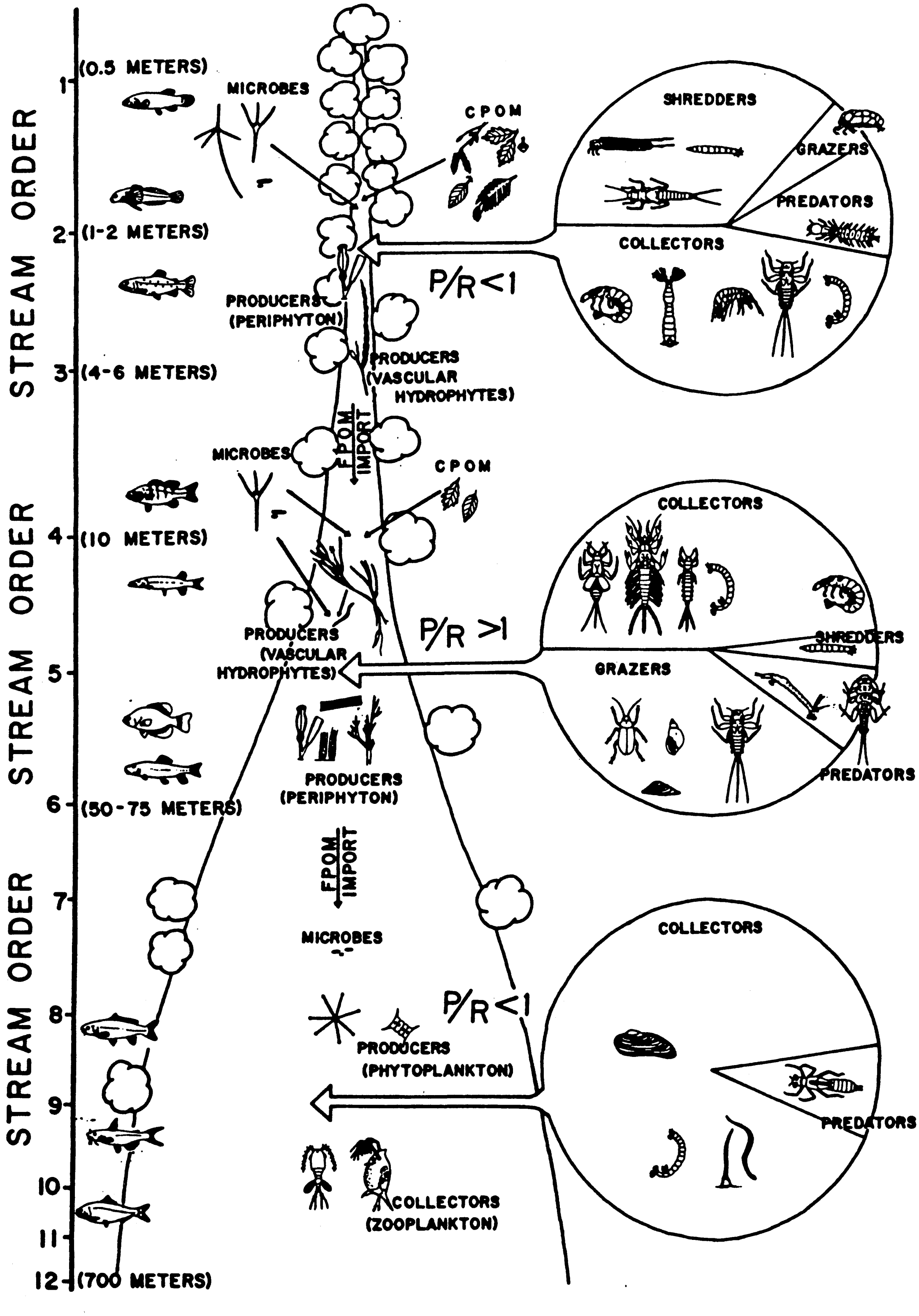

Figure 2. Expected changes in particulate organic matter in parts and functional groups along the river continuum (from Vannote et al. 1980).

habitat (cover) for invertebrates and fish; and, food for some species of aquatic insects.

In response to heavy inputs of CPOM in headwaters, shredders and collectors are predicted to be codominant among invertebrate communities (Vannote et al. 1980). Studies in headwater mountain streams in North Carolina generally support the predictions of the RCC (Woodall and Wallace 1972; Haefner and Wallace 1981; Webster et al. 1983; Huryn and Wallace 1987a, 1987b). Macroinvertebrate communities were dominated by shredders, collectors, and predators, while grazers faired poorly. However, in headwater mountain streams in Virginia, Miller (1985) reported that shredders were only a minor part (<10 percent) of the total macroinvertebrate biomass and that collectors and predators dominated the fauna. In addition, Miller (1985) found similar results in reviewing ten other studies that were conducted in small temperate zone streams between 1978 and 1984.

Huryn and Wallace (1987a), in addition to presenting data that supported RCC predictions, described what they called "mesoscale" habitats. Mesoscale habitats are areas within a stream segment characterized by distinctly different physical environments, and the boundaries between them can be abrupt and well defined (e.g., bedrock-outcrops versus pools formed upstream of woody debris dams). Huyrn and Wallace found that bedrock-outcrops with low substrate roughness and rapid current are generally characterized by entrainment and export of materials entering the habitats' boundaries. Conversely, pools upstream of debris dams are areas of local deposition and can function as sites of organic matter accumulation. Therefore, habitats that are quite different physically within a stream segment may exhibit a quite different functional structure with their respective animal communities (Benke et al. 1984; Huyrn and Wallace 1987a). Thus, a given stream reach may include mesoscale regions that are analogous to various sites along the RCC (Huyrn and Wallace 1987a).

In a headwater Coastal Plain stream in Virginia, Smock et al. (1985) reported that annual production of benthic macroinvertebrates was not dominated by shredders, but by gathering collectors (40-53 percent), followed by filtering collectors (13-34 percent), and then predators (16-30 percent). Production by shredders was negligible (1-5 percent). As part of the same study, Smock and Roeding (1986) found that periphytic algae supported 15-31 percent of annual production, while only 1-3 percent was supported by CPOM. Theoretically, secondary production in fully canopied headwaters should be based primarily on CPOM processing with contributions by algae low (Vannote et al. 1980). Smock and Roeding suggested that only the smallest first-order streams on the Coastal Plain, where CPOM retention was greater because of debris dams, have high abundances of shredders. Smock et al. (1989) showed that macroinvertebrate density was 10 times greater in debris dams than on the sandy sediment and that 85 percent of the CPOM stored on the channel surface was in dams. Obviously, debris dams are a critical habitat for shredders.

In mid-sized streams with a more open canopy, the RCC predicts reduced influence of CPOM and increased importance of autochthonous primary production (e.g. periphyton) and FPOM from upstream. Also, because the effects of riparian vegetation are predicted to be relatively unimportant in medium to larger streams, woody debris (snags) should play a minor role in these streams as well (Wallace and Benke 1984). However, contrary to RCC predictions, research in mid- to large-sized rivers of the Southeastern Coastal Plain has demonstrated that autochthonous production is relatively unimportant and that allochthonous materials are the principal food items along the entire river. Additionally, snags serve as important habitat for macroinvertebrates and sites of high secondary productivity (Cudney and Wallace 1980; Benke et al. 1984). Snags afford a relatively stable habitat compared with the shifting, sandy substrate found in most Coastal Plain streams. In addition, certain game fish apparently forage on macroinvertebrates colonizing these woody substrates (Benke et al. 1985).

Middle order streams usually possess few shredders because of reduced quantities of CPOM, therefore collectors often dominate because of FPOM from upstream. Grazers (scrapers) are also predicted to increase in number because of increased quantities of periphytic algae and vascular plants (Cummins 1977). In a mid-size Piedmont stream, Nelson and Scott (1962) described a trophic structure similar to that predicted by the RCC. In two mid-sized Georgia rivers located in the Coastal Plain, the Satilla and Ogeechee rivers, collectors (gatherers and filterers) comprised the majority of macroinvertebrate production as predicted, however grazers contributed little to either macroinvertebrate production (Benke et al. 1984) or biomass (Benke and Meyer 1988).

Large rivers receive the cumulative inputs of FPOM from upstream and are often dominated by filtering collectors, at least on hard substrates in the river, figure 2. For example, Cudney and Wallace (1980) reported high densities of filter-feeding caddisflies on snag habitats in the Savannah River in Georgia, and Mason (1991) found high-densities of filter-feeding caddisflies on artificial substrates in the Suwanee River in Florida. Bottom muds in the Suwanee River contained primarily mollusks, such as the filter-feeding *Corbicula*, Chironomidae and Oligochaetes. Most of the chironomids and oligochaetes were gathering collectors.

In summary, the RCC offers a good conceptual model regarding the fate, transport and processing of POM in Southeastern streams, even though exceptions exist. However, we want to emphasize a view expressed by James A. Gore (personal communication) during the review of this synthesis: "...that, when considering the evolution and development of lotic systems, hydrologic conditions and within channel hydraulic heterogeneity are the templates upon which the RCC is superimposed. That is, if hydraulic conditions are such that the conflicting forces of pressure and friction drag are compensated for by the shape and behavioral aspects of the benthic organisms, then foraging (on whatever POM happens to be there) with net gains in energy can occur."

Floodplain Dynamics

Another feature typical of low gradient streams, especially in the Coastal Plain, is that the channel usually meanders through heavily forested floodplain wetlands. Floodplain width, which usually is correlated with stream order, has been found to range from about 50 m for first order streams (Smock et al. 1989) to over 1 km for sixth order rivers (Benke and Meyer 1988). Periodic inundation of floodplain forests liberates nutrients and dissolved humic substances. Humic substances leaching from peaty sites may impart a tea-like color to the water resulting in so called "blackwater" rivers (Benke et al. 1984).

Interactions between the stream channel and its floodplain are complex. Recent studies have shown that inundated floodplains are diverse systems, important to both macroinvertebrates and fish (Holder et al. 1970; Welcomme 1979, 1988; Crance 1988; Crance and Ischinger 1989; Junk et al. 1989). The aesthetic and economic value to society of "river swamps" was recognized over 20 years ago when Wharton (1970) described them as "the last environment in the Southeast providing an accessible wilderness experience for rural and urban populations."

Floodplains function in a manner similar to headwater streams of the RCC by serving as an important source of POM (Sniffen 1981; Smock and Roeding 1986; Benke and Meyer 1988; Benke and Wallace 1990). Sniffen (1981) found this to be true in a Coastal Plain stream in North Carolina when he estimated that over 90 percent of the annual aquatic area of the stream-swamp system was floodplain, and only 20 percent of total invertebrate production occurred in the channel proper. Sniffen suggested that the proposed channelization of this stream-swamp system by the U.S. Soil Conservation Service would have eliminated about 80 percent of the benthic production. The importance of floodplain contributions of POM is also illustrated by studies in two mid-size blackwater rivers in Georgia that revealed that allochthonous inputs of bacteria from the floodplain comprised a substantial portion of the microseston available to filter-feeding collectors in the channel (Edwards and Meyer 1986; Edwards 1987).

Stream ecosystems in which productivity is intimately tied to the exchange of nutrients between the channel and floodplain are driven by what Junk et al. (1989) described as the "flood pulse." They referred to a moving littoral boundary as floodwaters spread over the plain liberating nutrients. This boundary facilitates the recycling of organic and inorganic materials between the river and its floodplain and is characterized by high productivity. The water behind this moving front is often alive with rotifers, copepods, algal blooms, and other organisms (Welcomme 1988).

The flood pulse concept appears to be a

logical extension of Odum's (1969) concept of pulse-stabilized communities. According to Odum, a regular, but acute, physical perturbation imposed on the system can maintain the ecosystem at some intermediate point in the developmental sequence. The systems Odum described were relatively fertile and highly productive, and the life histories of many organisms were intimately tied to this periodicity, or pulse (disturbance). Odum cited estuarine and intertidal areas as examples, but applying the analogy to channel-floodplain systems appears appropriate. If changes are not too sudden, communities can adapt to the disturbance (pulse). However, major physical alterations (e.g., highly modified flow regimes below a dam) can devastate the biota (Junk et al. 1989).

MICROHABITAT REQUIREMENTS OF BENTHIC MACROINVERTEBRATES

Because factors such as depth, velocity, and substrate are known to influence the microdistribution of macroinvertebrates, a common view in past studies of stream ecology has been that abiotic factors are far more important than biotic factors (Hart 1983; Teague et al. 1985). However, this view has recently been modified to account for the abiotic regime as either harsh, or benign, to predators (i.e., the "harsh-benign" hypothesis of Connell 1978). In harsher abiotic regimes, predation impacts are predicted to be low, while impacts of predation are predicted to be high in benign abiotic regimes (Peckarsky et al. 1990).

The literature on microhabitat requirements of macroinvertebrates was organized into topic areas suggested in the review by Power et al. (1988) that included: (1) the influence of local abiotic conditions on invertebrates; (2) invertebrate responses to discharge fluctuations; (3) movements of lotic invertebrates; and, (4) life history requirements of invertebrates. Our emphasis was on studies conducted in the Southeastern United States.

Influence of Local Abiotic Factors

Physical variables often mentioned as regulating macroinvertebrate communities in Southeastern streams are temperature, substrate, current velocity, and food availability. Temperature, substrate, and current velocity will be covered separately, but food availability will be discussed within the context of each of these variables.

Temperature. Temperature is related intimately to latitude, altitude, and, in spring-fed or lake-fed (or reservoir-fed) streams, to the distance from the source (Hynes 1970). In addition, although both the seasonal patterns and ranges of temperature for streams vary geographically, the amount of heat accumulated (i.e. degree days) on a yearly basis seems to be predictable when streams of similar size are compared over a range of latitudes (Vannote and Sweeney 1980).

Variations in the size of individuals have been correlated with either temporal or spatial temperature gradients. For example, increased body size has been related to reduced temperatures in aquatic insect species (Cudney and Wallace 1980; Kondratieff and Voshell 1980; Sweeney 1984). In a study of the life history and ecology of *Stenonema modestum*, a multivoltine mayfly, Kondratieff and Voshell (1980) found that adults of winter-spring cohorts were significantly larger than those of summer cohorts. Hauer and Benke (1987) developed predictive equations relating growth of black fly larvae (Simulium spp.) to temperature; one for use during early stages of flooding, the other during late flood and low flow conditions.

Sweeney (1984) summarized the results of studies, primarily conducted in the laboratory, that reported the response of certain life-history characteristics of macroinvertebrates to temperature. However, of the many field studies that have shown correlations between seasonal patterns in life-history characteristics and temperature, Sweeney noted that few have compared populations in two or more habitats differing in temperature. He also pointed out the difficulty in differentiating between the relative importance of temperature and nutrition, because temperature affects not only larval metabolism, but the quantity and quality of food.

In a spring-fed stream in Kentucky, Minshall (1968) identified temperature and substrate as the environmental factors most influencing macroinvertebrate diversity and abundance. Gordon and Wallace (1975), in a study along the length of the Savannah River, found that stream size (drainage area), increased amounts of FPOM and minimum dissolved oxygen (DO) concentration were the most important factors affecting the distribution of net-spinning Trichoptera. However, they found that size and DO were highly correlated with altitude and temperature. Gordon and Wallace reported that the oxygen requirements of certain macroinvertebrates suggested that these species will be restricted to streams where temperatures remain below some maximum level. Apparently the tolerance ranges (i.e., of temperature and dissolved oxygen) of many species in Piedmont and mountainous areas of the Southeast are relatively narrow (Lenat 1983) compared to those for many species found in Coastal Plain streams (Penrose et al. 1982). Gordon and Wallace (1975) indicated that if streams at the higher elevations (i.e., Piedmont and mountainous areas) were exposed to some stress (e.g., warmed surface releases from a flood-control dam) that caused a rise in temperature and/or a lowering of dissolved oxygen, shifts in species could occur, resulting in a fauna similar to that in Coastal Plain streams. However, the effects of a similar disturbance on mid-size or large Coastal Plain streams is unknown because macroinvertebrates in these systems are already acclimated to higher temperatures and lower dissolved oxygen than species upstream (Gordon and Wallace 1975).

The influence of shading on temperature has also been studied in small headwater streams in the southern Appalachian mountains. Following logging and removal of the dense canopy shading the streams, summer water temperatures were several degrees higher than those found in control streams draining adjacent, forested watersheds (Swift and Messer 1971; Webster et al. 1983). However, field studies of this type have yet to separate the effects of elevated temperatures on stream invertebrates from other abiotic changes such as increased streamflow, increased food availability, and increased sedimentation.

Substrate. In high-gradient streams, substratum particle size has been described as a major determinant of the distribution and abundance of benthic macroinvertebrates (Crisp and Crisp 1974; Rabeni and Minshall 1977; Gurtz 1981; Reice 1981; Gurtz and Wallace 1984; Huryn and Wallace 1987a). Each of these studies reported higher densities of macroinvertebrates on larger-sized substrates, such as cobble, than on the smaller particle sizes like sand.

The type of substrate material also influences macroinvertebrate distributions. Gurtz (1981) and Gurtz and Wallace (1984) found substrate types that included moss-covered boulders or bedrock, cobbles, pebbles, sand and associated wood or leaf debris. Gurtz found differing food quantity and quality (measured as FPOM and algae) associated with the various substrate types, plus a current-velocity gradient. Moss-covered rocks trapped more FPOM and had more periphytic algae than other substrates. Highest current velocities were found on the moss-covered bedrock and boulder substrates (erosional zones), while lowest velocities were detected on sand substrates (depositional zones). He found increased macroinvertebrate densities on bedrock and boulders, compared to the other substrates, especially in a stream with extensive logging on the watershed. Gurtz attributed the increased densities to greater food availability, greater protection from scour and less sedimentation because of higher current velocities over the moss-covered substrates.

Recent analyses of stream hydraulics (Statzner et al. 1988) indicate that Gurtz (1981) found variable importance of velocity, depth and substrate because these factors interact simultaneously but "variably," in complex hydraulic equations for Reynolds number, shear stress or boundary sublayer thickness. Statzner et al. (1988) suggested that invertebrates "prefer" a complex hydraulic condition that matches the hydrodynamic character of their body size, shape and behavior. Other studies have also described the importance of hydraulic variables in determining macroinvertebrate distributions (Statzner and Higler 1985; Statzner 1988; Davis and Barmuta 1989; Gore and Bryant 1990; review by Heede and Rinne 1990).

Although current velocity is positively correlated with substratum particle size (Reice 1981), Rabeni and Minshall (1977) demonstrated that particle size has a far greater effect than current velocity on animal distributions in streams. They found that velocity-effects were insignificant compared with substratum-related trapping of detritus, a view that differs from that of Statzner et al. (1988) in which substrate characteristics were less important than mean velocity and complex hydraulics in explaining the distribution of lotic macroinvertebrates.

In low-gradient streams throughout the Coastal Plain, the predominant substrates usually differ greatly from those found in Piedmont and mountainous areas. Smock et al. (1989) identified two types of Coastal Plain headwater streams, differentiated primarily on the basis of channel composition. One type, called "bottomland" streams, has channel substrates composed of clay and silt and often covered by a layer of organic matter. Streams of this type may be characterized by heavy siltation that can degrade bottom habitat, and reduce diversity, abundance, and productivity of benthic invertebrates (Cooper 1987). A second type, called "sandy" bottom streams, is characterized by shifting-sand substrates. The majority of Coastal Plain streams (regardless of size) have relatively homogenous, unstable shifting-sand substrates (Soponis and Russell 1984; Robertson and Piwowar 1985; Scheiring 1985; Keup 1988; Smock 1988; Bain and Boltz 1989), although headwater streams exist that have coarse substrates of boulders, cobble, and gravel (Cowell and Carew 1976). Additionally, outcrops of sandstone bedrock, limestone, and siltstone occasionally occur in Coastal Plain streams.

Wood debris (snags) has been recognized as the most stable substrate for macroinvertebrates inhabiting sandy-bottomed streams in the Southeast (Van Arsdall 1977; Cudney and Wallace 1980; Benke et al. 1984; Wallace and Benke 1984; Smock et al. 1985; Thorp et al. 1985; Roeding and Smock 1989; Smock et al. 1989; Benke and Wallace 1990). Woody debris usually remains in a stream for long periods of time, and the major instability for macroinvertebrates colonizing snag habitat includes periodic exposure to the air as water levels fluctuate (Benke and Wallace 1990) and scouring by floods and sediment.

Coastal Plain streams with snags along the banks typically possess three major microhabitats in which macroinvertebrates can be found: (1) the shifting sandy substratum of the main channel; (2) the muddy, depositional substratum of backwaters; and, (3) submerged wood, or snags (Benke et al. 1985). A fourth benthic habitat exists during flood stage, when the stream inundates all or part of its floodplain for periods up to 3 or more months per year. Benke et al. (1985) found that among the three major habitats, snags had by far the highest animal diversity, standing stock biomass, and secondary production per unit of habitat surface.

Current Velocity. Hydraulic stream ecology is an approach to lotic studies proposed by Statzner et al. (1988) that attempts to relate macroinvertebrate distribution and abundance with various complex characteristics of flow (e.g., kinematic viscosity of water, Froude number, shear velocity), rather than just discharge or mean current velocity. These authors provided an excellent review of how lotic organisms (mainly benthic macroinvertebrates) react to current. Other equally good reviews on benthos and hydraulics occur in Davis (1986) and Heede and Rinne (1990).

Current velocity is considered an essential factor in microhabitat selection by filter-feeding caddisflies. The retreats and nets constructed by these organisms are generally adapted for particular current speed ranges enabling closely related species to partition available food and substrate resources (Edington 1968; Freeman and Wallace 1984; Wallace 1975; Wallace et al. 1977). Cudney and Wallace (1980) found that net-spinning Trichoptera in the Savannah River appear to occupy different microhabitats on the submerged branches and roots. They studied six species at each of three current speed ranges: 10-15 cm per second, 25-50 cm per second, and 50-75 cm per second. Production and biomass estimates for all but one species were highest at the medium current velocity range. Cudney and Wallace stressed that the production estimates were not necessarily on discrete populations found at each velocity range because larvae can drift and change habitats during their life cycle. However, these data suggested that net-spinning hydropsychids are significantly influenced by current velocity.

Cudney and Wallace (1980) also suggested that the spatial heterogeneity of submerged moss-covered snags provided a diversity of microhabitats with respect to current velocity; therefore, the ability of filter-feeders to occupy such microhabitats was possible because of the large differences in catch-net mesh dimensions found among the species. They suggested that these differences in catch-net mesh size were important to the caddisflies because of limited space (microhabitat) availability rather than limited food. Thus, large numbers of filtering species, each feeding in different microhabitats and on different size particles, should result in more efficient utilization of drifting seston.

Cudney and Wallace (1980) reported no evidence of temporal differences in life cycles among the species they studied, although in an Appalachian mountain stream, Benke and Wallace (1980) found distinct temporal differences that probably minimized interspecific competition for space and food. Although the study by Cudney and Wallace (1980) demonstrated that caddisfly species have current velocity preferences, the various instars were generally found over the entire range of current speeds present in the river. However, last instar catchnet mesh dimensions of the six caddisfly species in the Savannah River differed greatly. If these mesh size differences are maintained among species throughout successive larval instars, then temporal similarity in life cycles may reduce overlaps in mesh size between species. Thus, the ability of individual species to occupy different microhabitats could be enhanced by such similarity in life cycles.

Future Needs. Limited experimental data exist from field studies of the effects on biota of modified temperature regimes. Will changes in thermoperiodicity patterns (e.g., below dams or from pollution) disrupt life cycles events, perhaps leading to elimination of some macroinvertebrate species (Ward and Stanford 1987)? Do suboptimal thermal conditions reduce fecundity, thus placing certain species at a competitive disadvantage?

There are also limited data available on the intricacies of flow variables and the controls they exert on biota (Davis 1986; Statzner et al. 1988; Gore et al. 1989), even though mean current velocity and discharge are usually measured in stream studies. Can the hydraulic variables that induce drift in stream macroinvertebrates be identified? Do stream gradient and substrate influences on flow variables result in different drift patterns over coarse substrates compared to other stream substrates (Layzer et al. 1989)?

Although several of the studies cited here reported good correlations between distribution and abiotic factors, there is a strong need for additional experiments that adequately characterize the flow environment preferred by macroinvertebrate communities. For example, Teague et al. (1985) reported that the caddisfly *Dicosmoecus gilvipes* preferred large substrate particles, but in the same geographic region, Lamberti and Resh (1979) reported *that D. gilvipes* preferred the smallest available substrates. However, neither *D. gilvipes* study accounted for substrate heterogeneity, or frequency distributions of the various substrate classes (personal communication, James A. Gore). Several studies have suggested that, even in free-flowing streams, certain hydropsychids may preferentially colonize microhabitats to maximize food delivery rates (i.e., seston transport), and there is considerable evidence that the enhanced levels of secondary production at such sites can be attributed to higher food quality, rather than quantity of the seston (Benke and Wallace 1980; Georgian and Wallace 1981; Parker and Voshell 1983; Ross and Wallace 1983; Voshell and Parker 1985; Smith-Cuffney and Wallace 1987).

Another important consideration when assessing the distributions of macroinvertebrates with respect to physical variables is that, in many cases, distribution is mediated by interactions with other organisms. For example, McAuliffe (1983) found certain midges quickly colonize shallow, recently inundated substrates that lack competitively dominant caddisflies. Caddisflies have also been found to restrict distributions of a grazer population (Hart 1985). Finally, drift rates of benthic insects from pool habitats in logged areas were found to be lower than those from forested pools because of greater light penetration to the stream, thus predation by trout was enhanced in the logged reaches (Wilzbach et al. 1986).

Responses of Benthic Macroinvertebrates to Discharge Fluctuations

Seasonal fluctuations in discharge are critical events in the life histories of most macroinvertebrates. As water levels fluctuate, stream and river habitats expand and contract, resource availabilities shift, certain habitats (e.g., riffles and pools) may become isolated from others and flow regimes may change, thus altering other physical variables (Power et al. 1988). In addition, extreme events (e.g. scouring floods, droughts) can eliminate much of the biota and lead to changes in community composition or succession (Fisher 1983). Thus habitat requirements, especially at the microhabitat level, should include appropriate spatial and temporal components (Minshall 1988; Gore and Bryant 1990).

Natural disturbances, such as floods, are common in lotic systems, yet little is known of the actual response of benthic macroinvertebrates to dynamic flows of varying intensity and duration (Gore 1989). Few studies have focused on the importance of natural physical disturbance to the structure and distribution of stream communities (Hemphill and Cooper 1983), although Fisher et al. (1982) documented changes in stream communities following floods in desert streams. However, successional events caused by seasonal changes were not distinguished from successional events following the disturbance.

Stream ecologists have recently begun emphasizing the role of disturbance as a central theme in community organization (Resh et al. 1988). These authors used a general definition of disturbance from Pickett and White (1985): "a disturbance is any relatively discrete event in time that disrupts ecosystem, community, or population structure, and that changes resources, availability of substratum, or the physical environment." Emphasis has also been directed at examining the role of various ecological theories in predicting recovery from disturbance (Gore et al. 1990).

Historically, the null hypothesis for community structure has been an equilibrium model that assumes a constant environment (Resh et al. 1988). Biotic interactions are also considered the primary determinants of community structure, "all else being equal." These authors interpreted this phrase to mean that the environment remains "constant" or that the communities are adapted to some degree of variability.

The equilibrium model was used by Minshall et al. (1983) to argue that if the time interval between spates in streams was long enough, equilibrium conditions would prevail, and then density-dependent processes should dominate. This rarely disturbed community was contrasted with "opportunistic" species that were associated with frequently disturbed communities.

Another stage in the evolving concepts of disturbance theory was the intermediate disturbance hypothesis developed by Connell (1978) to explain the high species diversity observed in tropical rain forests and coral reefs. The intermediate disturbance hypothesis presumes that a competitive hierarchy of species exists in the absence of frequent disturbances, and superior competitors eliminate inferior ones and species richness is reduced. The superior competitors (resident species) are the more efficient occupiers of habitat. With frequent disturbances, or one of great magnitude, colonizing species (poor competitors) gain a foothold and the resident competitors are displaced. This loss also lowers species richness. At some intermediate level of disturbance, members of both groups coexist and, in this manner, maximum species richness occurs.

A second role for disturbance was proposed with Huston's (1979) "dynamic equilibrium" model. The key to this hypothesis was that the recurrence interval of some disturbance event (e.g., flood, drought, anthropogenic input, etc.) was shorter than the time necessary for competitive, or predator-prey, interactions to result in the elimination of species. Thus, species that are poorer competitors would persist in the system and increase species richness. Huston concluded that diversity is determined not as much by the relative competitive abilities of the competing species as by the impact of the environment (disturbance) on species interactions. Portions of each of these two models have been applied to stream invertebrates (Peckarsky 1983; Ward and Stanford 1983). Resh et al. (1988) felt the dynamic equilibrium model was the most generally applicable hypothesis, although there are limited data available to support it. They also stated that the intermediate disturbance hypothesis has its applicability, but its acceptance in stream ecology will require adequate demonstration of competitive hierarchies and ordered dominance sequences among stream organisms.

Little information exists in the Southeast that defines the role of disturbance and the effects of disturbance frequency, or intensity, on stream communities. We will focus on two classes of natural disturbances common in streams, high water (floods) and low water (drought), then consider research by Reice (1985) in which he tested the species-specific responses of macroinvertebrates to a disturbance (i.e. tumbling patches of cobble) in a North Carolina stream.

Droughts reduce the total available habitat, but the change is gradual. Under natural drought conditions, macroinvertebrates migrate into the wet portions of the channel or down into the hyporheic zone to minimize mortality effects. Benke et al. (1985, 1986) suggested that invertebrates migrate on snag habitats in response to changes in water height as long as the change is slow. This response to drought does, however, concentrate the biota into reduced livable habitat and can increase the impact of competition and/or predation on species. Finally, hydraulic conditions probably become less important as streams become more drought prone. That is, in intermittent streams, hydraulic factors may be secondary to factors that allow retreat to refugia (Matthews 1988).

Floods or spates usually occur suddenly in the Southeast (often in the span of a few hours or days), and little is known about how quickly lotic species can respond to increasing current velocity (Reice 1985) or the rising water level. Benke et al. (1984) observed that simuliids quickly colonized recently inundated snag habitat before other species (e.g. hydropsychids) had a chance to colonize the new substrate. Therefore, most blackfly production apparently occurred as water levels rose, but it was unclear whether this finding was a response to predation pressures, crowding, or microhabitat conditions. Physical changes in the stream channel are often pronounced during floods; while the timing of floods may be quite predictable in snowmelt-fed mountain streams, in runoff and spring-fed streams in the Southeast, floods are unpredictable. The predictability of a disturbance will certainly affect the community's ability to adapt to it (Reice 1985; Resh et al. 1988).

Floods can have a devastating effect on benthic communities confined to the stream channel. Yet, stream organisms seem well adapted to this type of disturbance because populations rebound quickly (often within a few days or weeks after the most severe floods). Recovery may result from the high fecundity of lotic organisms and, in part, from individuals that take refuge in the hyporheic zone. Others escape injury in protected places and backwaters. Recolonization mechanisms are poorly understood, but may include several activities, including swimming, upstream crawling, drifting, or egg laying (Reice 1985).

Reice (1985) also addressed the question of whether the intermediate disturbance hypothesis applies to macroinvertebrate communities and he found no evidence of a competitive hierarchy in the North Carolina stream. Hemphill and Cooper (1983) reported that the caddisfly, *Hydropsyche oslari,* outcompeted the blackfly *Simulium virgatum* under stable flow conditions in their California stream, but *Simulium* was maintained in the system by its ability to recolonize quickly following disturbance. Reice (1985) considered these observations by Hemphill and Cooper (1983) to include species which were always present in the system and not species which had been excluded by the superior competitors. Reice found no increase in rare species on disturbed substrates, relative to undisturbed substrates. Also, species diversity and richness did not change as disturbance frequency increased. He concluded that the intermediate-disturbance hypothesis did not apply to stream communities.

Future Needs. Given the diversity of microhabitats and variation in discharge in streams, the relative importance of different factors that regulate community structure should be expected to vary in both space and time. Efforts to devise research and expand the findings to real-world situations have been hampered by insufficient consideration of the scale of various interspecific interactions. On a single rock, or snag, competition may be important at one point, while predation is critical at another. Studies such as those of Reice (1985) suggest that biotic interactions will be more important at small scales. As scale increases, interspecific interactions should be weaker even though migrations among habitats are common. Research is needed to test these disturbance hypotheses further, especially on a larger scale.

Studies are also needed to assess the availability of refugia for species during vulnerable life history stages. In Coastal Plain streams, floodplains are inundated at high flow, and may persist as lentic, and often isolated habitats, during low flow periods (Welcomme 1988). These inundated 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 larger streams. What are the exact makeups of these communities? What are the roles of these communities in the dynamics of channel-floodplain interactions? With more information on the mobility, ecological tolerance, and habitat requirements of taxa, it should be possible to learn much more from biotic responses to hydrologic "disturbances."

Movements of Benthic Macroinvertebrates

Complex biotic-abiotic interactions regulating benthic macroinvertebrates may be difficult to measure, or interpret, if careful thought is not given to the spatial range of activities of the organisms under study. This applies to enclosure or exclosure experiments, or other density manipulations. This synthesis will concentrate on drift movements because drift is one of the biological processes that describes the population dynamics of invertebrates (Benke et al. 1986). Production, which is closely linked with drift, is another basic process that will be discussed in a later section. Drift dynamics in tailwater habitats will be covered in the section on regulated streams.

Drift can be initiated by biotic interactions as well as by a variety of physical factors (Waters 1961; Bishop 1969; Hynes 1970; Reisen and Prins 1972; Cowell and Carew 1976; Stoneburner and Smock 1979; O'Hop and Wallace 1983; Soponis and Russell 1984; Benke et al. 1986; Obi and Conner 1986; Keup 1988). Several excellent reviews exist that detail many of the results of drift studies (Waters 1972; Müller 1974; Wiley and Kohler 1984).

Drift refers to the downstream transport by the current of benthic animals found on or in bottom substrates, and confusion still exists over the role of behavior in determining periodic drift activity. The terms "active drift" and "passive drift" came to characterize two competing hypotheses about why animals drift (Wiley and Kohler 1984). Waters (1972) described drift activity as catastrophic, behavioral, and constant, although he noted that distinctions are not always clear among these types because of overlap and interactions. According to Wiley and Kohler (1984) these terms actually distinguish temporal characteristics of drift (catastrophic = pulsed; behavioral = periodic; constant = continuous). Furthermore, these authors concluded that drift is neither exclusively active or passive, but a "composite phenomenon" resulting from a variety of causes, some of which are unknown. Pulsed catastrophic drift can be initiated by a variety of abiotic disturbances, including floods, droughts, fluctuating water levels below dams, high temperatures and pollutants. Behavioral drift refers to consistent periodic drift activity occurring often at night, especially with aquatic insects. Waters (1972) defined "the continuous stream of representatives of all species, in low numbers and occurring at all times" as constant drift.

Drift studies in warmwater streams are relatively scarce and few have been conducted in larger streams (> 5th order) of any kind. Drift investigations have also concentrated on the highly predictable diel patterns of night activity found in aquatic invertebrates, especially the insects (see reviews of Waters 1972; Wiley and Kohler 1984; and Keup 1988). Little work has been done on the role that drift plays in population dynamics as a dispersal mechanism, on the habitat origin of drift, on the contribution of drift as a part of total seston transport (e.g., O'Hop and Wallace 1983) or on the contribution of drift to the diet of fish (e.g., Allan 1978).

The processes that maintain upstream populations of benthic insects as downstream losses occur are subject to debate. The exact influence of benthic density on drift density remains unclear, because there is evidence for both a density-independent and a density-dependent relationship (Hildebrand 1974; Walton et al. 1977). While mayflies often dominate stream drift, Hildebrand (1974) demonstrated in artificial streams that drift of four mayfly taxa was not density dependent, but was related to food availability. Hildebrand suggested that increased activity in searching for food at the lower food level contributed to increased drift. Walton et al. (1977) found drift to be density dependent on stones and cobble substrates, but density independent on gravel. The observed density-dependent relationship was attributed to competition for interstitial space which was less prevalent on the gravel substrates.

Macroinvertebrate drift, both the species drifting and the number of individuals, exhibits seasonal fluctuations in addition to predictable diel periodicity. Diel periodicity apparently results from several factors that serve as phase-setting agents (Wiley and Kohler 1984). Waters (1972) and Müller (1974) thoroughly reviewed these environmental factors. Light intensity, however, is apparently the phase-setter usually involved, triggering increased insect activity as incident radiation decreases to some threshold level. This threshold level is about 1 to 5 lux (Waters 1972) although Bishop (1969) recorded levels as low as 0.001 lux in carefully controlled artificial streams. The mechanisms that result in diel drift periodicities remain unclear, although changes in position and activity levels have been proposed by researchers (Elliott 1967; Bishop 1969; Wiley and Kohler 1984). Allan (1978) suggested that fish predation on drift may influence drift patterns. He found that larger nymphs were more prone to drift at night than small nymphs, and considered this an adaptation to avoid predation.

Seasonal periodicity appears closely related to periods of maximum growth, prepupation, and emergence activities (Elliott 1967; Reisen and Prins 1972; Stoneburner and Smock 1979; O'Hop and Wallace 1983). For example, Stoneburner and Smock (1979) observed that seasonal fluctuations in the abundance of exuviae in the drift were correlated with fluctuations in larval drift density. These observations suggest a close relationship between life history stages of macroinvertebrates and their presence in the drift.

The majority of drift studies conducted in more northerly regions of temperate climates indicate that maximum drift density occurs during the summer months (Waters 1972). In contrast, studies conducted in the Piedmont Province of South Carolina reported larval drift densities relatively constant throughout the year, but peaks occurred during the spring and fall (Reisen and Prins 1972; Stoneburner and Smock 1979). A study conducted in subtropical Florida indicated peaks in drift density during the winter and early spring (Cowell and Carew 1976) which generally corresponded to periods of rapid growth, prepupation events, and emergence activities for the given areas.

Benke et al. (1986), studying drift in a sixth-order stream located in the Coastal Plain of Georgia, found high drift rates throughout the year, although drift densities were slightly higher during summer months. They concluded that seasonal abundance patterns for total drift were not evident in Southeastern warmwater streams because of active feeding and growth throughout most of the year.

Understanding temporal variability in Southeastern rivers is a complex issue because of changes in taxonomic composition throughout the year. For example, higher drift densities of certain macroinvertebrates (e.g., Trichoptera) observed during the summer and fall probably reflected seasonal variations in life cycle (Stoneburner and Smock 1979). However, Benke et al. (1986) found certain Diptera (e.g., simuliids), with short generation times, abundant in the drift throughout the year, and their abundance was highest during high discharge. These authors concluded that season and discharge were the important factors that affected both community production and drift dynamics.

Studies have shown that snag habitats, which are small in relation to benthic habitats, contribute significantly to invertebrate production in large warmwater streams (Nilson and Larimore 1973; Cudney and Wallace 1980; Wallace and Benke 1984; Smock et al. 1985; Thorp et al. 1985; Benke et al. 1986). It has been demonstrated in Coastal Plain streams that the high invertebrate biomass and production on snags contributes to the high drift densities observed (Benke et al. 1986). Finally, in larger streams in the Southeast, macroinvertebrates have been reported to drift long distances (Benke et al. 1986; Obi and Conner 1986).

__Future Needs__. Information on the mobility of macroinvertebrates is essential to an understanding of how life history stages of lotic species respond to changes in their environment. Little is known, for example, of the actual response of benthos to dynamic flows of varying intensity and duration. Studies are needed that assess drift as it relates to changing natural flows in a variety of streams and below dams (Gore 1989; Layzer et al. 1989) in tailwater habitats:

(1) What is the habitat origin of most of the invertebrate drift in Piedmont and Coastal Plain streams?

(2) Do the ecological mechanisms that determine behavioral drift differ in mid-sized, and larger, Piedmont and Coastal Plain streams?

(3) Is drift density-dependent or density-independent in mid-sized, and larger, Coastal Plain streams?

(4) Is the nighttime periodicity of drift an adaptation to avoid fish predation?

Little information is available on the role drift plays as a dispersal mechanism, although this area of study will require better techniques of tracking individuals. Another solution to tracking movements of small organisms might be experiments conducted in artificial streams (Kohler 1985), where initial densities from source areas are known and thus, effects of factors such as flow, substratum suitability, crowding, or food availability on movement can be investigated. Finally, newly available habitat could be monitored to determine spatial relations between colonizable habitat and organism sources. These studies would provide information on species mobility and recolonization potential (Gore 1979).

Many of the questions raised in this section can be answered only as we develop and clearly test appropriate hypotheses. Experimental evidence is essential to complete this process. There is a strong need for more experimental work in artificial streams, both in laboratory microcosms and in mesocosm-type channels that allow whole-ecosystem manipulations in a more natural setting.

Life Histories of Benthic Macroinvertebrates

The field of stream ecology still lacks critical life-history knowledge that is essential to current research on the structure and function of aquatic communities and ecosystems (Rosenberg 1979). In addition, microhabitat requirements of benthic macroinvertebrates may change in response to disturbances, depending on the type, magnitude, and frequency of the disturbance. The changes may involve alteration of certain life history traits for selected taxa in the stream. In fact, Wallace (1990) stated that life history traits may influence the rate at which communities recover following disturbances. Butler (1984) described the biological features covered by the term "life history" as, "events that govern the reproduction (and survival) of a species or a population, including fecundity, development, longevity, and behavior."

Several questions raised by Power et al. (1988) illustrate the importance of life history information in attempts to measure the distribution and community structure of lotic species, particularly with respect to understanding how factors such as substrate, depth, current velocity, and temperature influence these organisms. What cues initiate life history events such as oviposition, hatching, larval development, diapause, emergence, and the onset of reproduction? What habitat requirements and resources are necessary for macroinvertebrates to complete their life histories? How have macroinvertebrates adapted various life history characteristics to cope with resource limitations, predation, or disturbance?

Current physical habitat-based models for assessing stream flow needs are utilizing more biological information (Gore and Nestler 1988; Gore et al. 1992). One measure of aquatic invertebrates now being suggested is secondary production (Orth 1987). Adequate life history data are essential in calculating secondary production, whether for individual taxa or the community as a whole (Resh 1977; Benke et al. 1984; Orth 1987). Secondary production, more than density or biomass, is a more direct reflection of utilization of the organic resources in streams by invertebrates. Production of aquatic invertebrates represents a large portion of the food that is available to those fish species that are important for food and recreation. In fact, aquatic insects often comprise the major component of what fishery biologists refer to as "fish food" (Benke 1984).

Resh (1977) and Benke et al. (1984) recommended measuring production by major microhabitat types to derive estimates for the stream, whether for a particular taxon or a functional feeding group. Resh suggested that production estimates that are based on a few replicate samples for one specific microhabitat do not adequately consider either sampling variability or the possibility of differential habitat production. These studies and others conducted in Southeastern streams illustrate the importance of adequate life history data, whether quantifying biomass turnover (Haefner and Wallace 1981; Benke et al. 1984; Huryn and Wallace 1987b), assessing microdistribution preferences (Wallace and Sherberger 1974; Cudney and Wallace 1980) or determining food preferences and life cycles information (Wallace 1975; Manuel and Folsom 1982; Parker and Voshell 1982).

Studies concerning life history cues (e.g., what initiates emergence) have revealed that many lotic species use combinations of light, temperature and flow as stimuli. The importance of temperature as a factor in the life cycle of temperate macroinvertebrates has been extensively reviewed by several authors (e.g., see Ward and Stanford 1982). Much of the evidence for temperature as a critical factor in the life history of benthic invertebrates has come from studies in the altered thermal regimes in regulated rivers (Ward and Stanford 1979). Light (i.e., photoperiod) as a stimulus has seldom been investigated apart from temperature (Power et al. 1988). Bishop (1969) investigated the effects of light on drift activity in an artificial stream and found that a threshold value existed for incident radiation when increased light suppressed drift activity, but, when decreased below the threshold value, higher drift rates occurred. Temperature was held constant in this study.

Future Needs. For most macroinvertebrate species in the Southeast, knowledge of the habitat and resource requirements necessary for various life history stages is generally lacking, especially with respect to filter-feeding macroinvertebrates. The production studies cited earlier in this section include efforts to relate habitat and food preferences to various life stages of macroinvertebrates.

The relative importance of various potentially limiting factors that may occur during different life history stages of an organism is poorly understood, even for salmonid fishes that have been intensely studied (Power et al. 1988). Efforts to identify limiting factors for lotic macroinvertebrates are complicated by the lack of adequate taxonomy for all life stages, species migrations, the relative importance of mortality and growth as limiting factors that constrain population production, and synchrony versus asynchrony of life cycles (Butler 1984).

Innovative experiments are needed to help clarify the intricacies of factors controlling life histories and the consequences such interactions hold for determining distribution and community structure. Larger streams (orders 4-6) have not been widely studied (Webster et al. 1983), particularly in areas such as the Piedmont and Coastal Plain provinces. These studies should consider differences in production statistics among taxa in addition to estimates of abundance and biomass. This approach should allow a more accurate understanding of the ecological roles of coexisting invertebrates (Benke et al. 1984).

A thorough assessment of secondary production in streams also must include appropriate study of the spatial distributions of macroinvertebrates among habitats (Resh 1977). One habitat that merits considerable study is snag habitat (Benke et al. 1984; Webber et al. 1989). Finally, knowledge of the distribution of invertebrate production among functional groups and habitats says much about stream function, however analysis of food consumption by invertebrates is essential before the type and source of food actually supporting the production can be determined (Benke et al. 1984). Food sources and types for invertebrates in Southeastern rivers remain as important unanswered questions.

KEY INDICATORS AND HABITAT GUILDS

Stream ecosystems are complex hydraulic systems containing many species and, as such, efforts at predicting ecological relationships are necessarily based on mechanistic models of a few key processes or species, and their interactions (Power et al. 1988). It is not uncommon to find certain species whose removal from the community or ecosystem will cause measurable changes in structure, distribution, and function (Paine 1980). Standing stock estimates (numbers and biomass), production, and behavior of appropriate species, or "key indicators," [i.e., Minshall's (1988) "keystone species"] can explain much about the structure and function of lotic communities, and thus of the ecosystem as a whole.

Selecting key indicators in a study requires adequate knowledge of the biology of the indicator(s), in addition to knowing the ecological role of the species in the community. Certain "keystone predators" are often used as examples of strong interactors and their importance is obvious in many communities (Power et al. 1988). However, predators should not receive disproportionate attention just because they are bigger, easier to identify or more easily manipulated than less conspicuous species in the system.

Several studies have used sedentary aquatic insects (e.g., case-dwelling hydropsychids) as subjects that can be followed through density manipulations in streams (Hart 1985, 1986;

McAuliffe 1983, 1984). These types of studies set the stage for more thorough investigations of both direct and indirect effects that can impact communities, or food webs, as species-specific densities change in response to external (e.g., rapidly fluctuating water levels) or internal (e.g., altered predation pressure) events. The major use of key indicators, aside from their use in pollution studies, seems to have been in evaluating suitable habitat for instream flow assessments. Bovee (1986) described procedures for selecting key indicators for use in evaluating habitat requirements, although he emphasized fish and not benthic macroinvertebrates. Bovee recognized that it can be impractical to conduct a separate habitat suitability study on each "target" species so he suggested grouping species that behave similarly into guilds. Bovee (1982) defined a guild as "a group of species having similar habitat requirements and exhibiting similar responses to changes in streamflow," and suggested that habitat suitability criteria (e.g., depth, current velocity, substrate) be developed for macroinvertebrates on the basis of factors such as biomass, density, or secondary production. Recently, Orth (1987) also recommended inclusion of secondary production estimates in instream flow assessments. Bovee further suggested a method of circumventing the assumption of equal availability of macroinvertebrates as fish food by dividing the macroinvertebrate community into accessible versus nonaccessible species. Drift samples could be used to determine which species are most common in the drift. Then, criteria would be based on the density or production of only these species. This approach would be valid, of course, only if the fish of interest fed mainly on drift. Bovee also suggested the use of functional feeding groups as a more traditional method of assigning macroinvertebrates to guilds.

Functional feeding groups may not be always the ecologically meaningful ones (Minshall 1988). Minshall referred to a study by Hawkins et al. (1982) that did not find the expected shift from shredders to grazers in unlogged versus logged watersheds. Minshall felt that more information could have been obtained if the 8 to 10 species comprising most of the biomass were evaluated separately rather than combining the entire community into 3 to 6 composite categories (e.g., grazers, collectors, and shredders). Minshall also pointed out that, because one or two taxa often determine the outcome for a particular feeding group, this taxonomic identity should be maintained.

Gore (1977, 1978) described the use of benthic macroinvertebrates as "indicators" of optimum flow conditions in riffle habitats along the Tongue River in Montana. He based the indicator concept on the knowledge that certain organisms have a narrower tolerance than others for changes in the frequency and intensity of discharges. Gore modeled species responses using habitat suitability criteria for the variables of depth, current velocity, and substrate. Gore and Judy (1981) proposed new predictive models for determining optimum conditions for stream macroinvertebrates with respect to maintaining suitable lotic habitat. These authors concluded that the concept of indicator invertebrate species, on a site-specific basis, can be adequately utilized to predict necessary stream flows. Orth and Maughan (1983) also concluded that the derivation of habitat preference criteria should be on a species-specific basis and that a complex of variables should be considered. In recent reviews, Gore addressed many of the criticisms that have been directed toward the use of habitat suitability criteria in assessing instream flow requirements, particularly their use with benthic invertebrates (Gore 1987; Gore and Nestler 1988; Gore 1989).

<u>Future</u> <u>Needs</u>. Except for the work by Gore (1977, 1978) and Gore and Judy (1981), stream ecology studies have not utilized "indicator species" in assessing microhabitat requirements for benthic macroinvertebrates. However, the use of indicator organisms is not new in ecology. Lenhard and Witter (1977) reviewed the use of aquatic insects as indicators of environmental pollution. Other studies have suggested use of communities, rather than species or species complexes (Gaufin and Tarzwell 1956; Harris et al., 1984); habitat guilds (Bovee 1986) including production estimates (Orth 1987); or species diversity (Gore et al. 1992) as "indicators" of flow needs. In the Southeast, macroinvertebrate key indicators and/or habitat guilds, have not been identified in streams and studies are needed to evaluate these approaches for determining optimum habitat for stream invertebrates.

TROPHIC RELATIONSHIPS BETWEEN FISH AND MACROINVERTEBRATES

Understanding the interactions between fish and macroinvertebrate communities in stream ecosystems is fundamental both to the dynamics of natural systems and to the management of aquatic resources for food production and recreation. In lentic waters, there is clear evidence that fish predation can directly alter the composition of macroinvertebrate communities (Brooks and Dodson 1965; Hall et al. 1970). Yet, in lotic waters, trophic linkages to fishes are not well understood. In fact, in a review of predator-prey relationships in streams, Allan (1983) concluded that fish do not commonly play a major role in structuring invertebrate communities.

Several studies in high gradient streams have shown that, in general, invertebrate densities and community structure are unaffected by fish predation (Allan 1982; Reice 1983; Flecker and Allan 1984; Culp 1986; Reice and Edwards 1986). These experiments were conducted in streams having coarse substrates with average to moderate flows. In addition, salmonids were typically the only major vertebrate predator in each case except in studies by Reice (1983) and Flecker and Allan (1984). Differing results were reported, however, by Hemphill and Cooper (1984), in which trout eliminated conspicuous taxa such as amphibian larvae, notonectids, and lestids that live on substrates or in the water column, but taxa that burrowed into the substrate, or were less conspicuous, were generally unaffected. Hemphill and Cooper demonstrated the importance of refugia in determining the effects of predators on specific prey taxa.

In other studies, Flecker (1984) and Koetsier (1989) tested the impact of predation by benthic fish (sculpins) on invertebrates. Koetsier (1989), working in Idaho, found that mottled sculpins significantly reduced the density and biomass of several invertebrate species; and Flecker (1984), working in West Virginia, noticed that a vertebrate predator guild, including sculpins and blacknose dace, significantly depressed the abundance of chironomids and the stonefly *Leuctra*. Because chironomids comprised about 85 percent of the benthic fauna in this study, fish predation played an important role in structuring the macroinvertebrate community.

Schlosser and Ebel (1989) stocked four species of cyprinids in an experimental stream. The cyprinids significantly reduced invertebrate abundance, however, the effect of predation was habitat-related because abundance decreased most in "structurally complex" pools, but showed little response to predation in shallow riffles and raceway habitats. For example, numbers of pool-dwelling chironomids and crustaceans declined more in the presence of fish than riffle-dwelling hydropsychids and simuliids. Schlosser and Ebel concluded that cyprinids probably restrict their habitat to deep stream pools with cover to minimize their exposure to terrestrial wading predators.

Several investigators have suggested that invertebrates are more susceptible to fish predation in streams containing silt-sand substrates than in streams with coarse materials (Angermeier 1985; Gilliam et al. 1989). Juvenile creek chubs (Cyprinidae) in a silty-bottom stream reduced total invertebrate volume and density by 79-90 percent and 55-61 percent, respectively (Gilliam et al. 1989). Chironomids showed no fish effects, but the two dominant taxa, Oligochaeta and Isopoda, were heavily grazed by the chubs thus causing a shift to smaller size classes for both groups. The main differences in the stream used by Gilliam et al. and streams in other studies were soft sediments, higher density of fish, low drift rates, and lower flow rates.

The work by Gilliam et al. (1989) strongly supports the view that stream fish can significantly influence benthic invertebrate communities in warmwater streams. This conclusion contrasts with published work on salmonid fish in streams (Allan 1982; Culp 1986; Reice and Edwards 1986). In fact, in the study by Flecker (1984) in which fish predation played an important role in structuring the macroinvertebrate community, he deemphasized the effect by concluding that strong predation effects (i.e., by fish) are likely only with macroinvertebrates that are not replenished rapidly by drift (e.g., the chironomids and *Leuctra*), or that occur in slow moving waters.

Drift is the major mechanism for dispersal of aquatic stages of stream invertebrates (Williams and Hynes 1976), and several studies have suggested that many fishes obtain a portion of their diet from the drift (Henry 1979; Mancini et al. 1979; Benke et al. 1985, 1986). Benke et al. (1985) found that, although most of the larger fish species consumed invertebrates originating from snag habitats, several smaller species (e.g., minnows and darters) tended to ingest either sand-dwelling midges or terrestrial insects from the water surface. Their work suggested two food chains in this Coastal Plain stream: a sand fauna -> small fish -> piscivore food chain; and a snag fauna -> sunfish food chain. Benke et al. (1985) did not include any analysis of changes in community structure because of fish predation, however they suggested that because of the importance of snag habitat as a source of macroinvertebrates for fish, extensive removal of snags in low-gradient streams could be devastating to the fish community, especially sunfishes.

Future Needs. There is strong evidence that in warmwater streams of the Southeast, higher water temperatures enhance the ability to detect predation effects of fish on macroinvertebrates because the fish have higher metabolic and consumption rates (Flecker 1984). However, to adequately address trophic relationships between fish and macroinvertebrates, it may be necessary to conduct experiments in artificial streams that are large enough to accommodate appropriate predator-prey populations, but in which environmental variables can be controlled.

Field studies also are needed to determine, in a greater range of streams, the importance of snag habitat as a source of food for fishes in low-gradient streams. Would removal of snag habitat actually cause a shift in the fish community from sunfishes to one dominated by suckers and the small fishes that feed on benthic fauna? Would addition of snag material to barren streams enhance the diversity, abundance, and production of both the invertebrates and the fishes that depend on them for food? Because the role of fish predation in streams has considerable practical as well as theoretical interest, a critical need exists to develop improved approaches to answer these questions.

BENTHIC MACROINVERTEBRATES IN REGULATED RIVERS

The mechanisms that macroinvertebrates have evolved to cope with water level fluctuations in unregulated streams may be nonfunctional in regulated streams, especially below hydropower dams where there are rapid changes in flow. In fact, little information is available on functional responses of macroinvertebrates to peaking hydroelectric flows (Gore 1989; Gore et al. 1989; Gore et al. 1990; Troelstrup and Hergenrader 1990). The large and rapid (within minutes) changes in discharge at hydroelectric dams result in corresponding changes in flows in tailwaters. In addition, associated with the change in flow are changes in other variables (e.g., depth, width, velocity, water temperature and quality). The potential impacts of these short-term, recurring disturbances downstream from dams are important considerations for the biota in tailwaters (see review by Armitage 1984).

Observed Effects. Fluctuations in flow resulting from hydroelectric peaking operations have been associated with reductions in river productivity in terms of both the tailwater fishery (Trotzky and Gregory 1974) and benthic macroinvertebrates on which the fish populations depend (Fisher and LaVoy 1972; Trotzky and Gregory 1974; Nestler et al. 1986; Curtis et al. 1987; Nestler et al. 1988).

A number of variables have been used by stream ecologists to document the reduced productivity or carrying capacity of tailwaters affected by rapidly fluctuating flows. These include reduced macroinvertebrate diversity, density, and biomass (Fisher and LaVoy 1972; Kroger 1973; Trotzky and Gregory 1974; Gislason 1985). Studies conducted in the Southeast have found high macroinvertebrate density, but low diversity just downstream from both flood-control and hydropower dams (Webber 1979; Ney and Mauney 1981; Herlong and Mallin 1985; Jackson 1985; Hudson and Nichols 1986; Reed 1989). However, studies in which change in flow was gradual over a period of several days revealed negligible effects on macroinvertebrate communities (Williams and Winget 1979; Gersich and Brusven 1981).

Underlying Mechanisms. As flow is altered below dams, several variables are affected including velocity, depth, width, and wetted perimeter (the distance along the stream bottom from one shoreline to the other). Cross-sectional geometry is the primary determinant of the relationships among these variables, thus, the empirical relationship between discharge and velocity is site-specific. For example, Williams and Winget (1979) reported that, when flow was reduced, mean velocity was reduced more than width or depth.

One direct consequence of increased variability in discharge is that the daily range between minimum and maximum flow, velocity, depth, width, or other hydrologic variables may increase over the corresponding unregulated range, therefore, over short periods of time, the range of physical habitat conditions to which the biota are exposed can be greater in regulated than in unregulated streams (Cushman 1985). This situation could pose a threat to macroinvertebrates, such as various filtering collectors (e.g., net-spinning caddisflies or simuliids) that require specific velocities for food capture (Gordon and Wallace 1975; Cudney and Wallace 1980). The lack of a hydraulic equilibrium in tailwaters also violates a major assumption of the Instream Flow Incremental Methodology developed by the U.S. Fish and Wildlife Service (Bovee 1982) to assess instream flow requirements of aquatic biota; this could confuse the use of such methodologies in assessing instream flows necessary for protecting tailwater fisheries (Cushman 1985). However, Gore et al. (1989) demonstrated that dynamic flow models can correct the problem of lack of equilibrium flows.

Another consequence of dams involves the elimination of high seasonal discharges in downstream reaches. This change promotes sedimentation, which reduces habitat heterogeneity, including the availability of the hyporheic zone (Williams and Winget 1979). Williams and Winget also found enhanced algal growth as a result of this change in discharge. Although the number of macroinvertebrate species changed little in their study, Williams and Winget found marked shifts in community structure.

High flows may still occur downstream from dams, if only during hydroelectric operations. These high flows have often caused extensive armoring (i.e., flushing of fines leaving coarse bed materials) of the stream bed (Matter et al. 1983a; Gislason 1985) and created substrate instability that negatively impacts populations of shelter-building macroinvertebrates and mollusks (Gashignard and Berly 1987).

Rapid flow variations below dams can also be accompanied by rapid changes in water quality and temperature, especially when there is a hypolimnial discharge (Gore 1980). Consequently, spates of discharged water can be quite different from downstream water with respect to temperature, dissolved oxygen (DO), hydrogen sulfide, ammonia, iron, manganese, and other chemicals (Brooker 1981). Temperature changes downstream from reservoirs can be dramatic, changing by several degrees Celsius (Matter et al. 1983a; Walburg et al. 1983); thus causing shifts in community structure (Pfitzer 1954; Gore 1977; Hauer and Stanford 1982) and altering emergence patterns of aquatic insects requiring specific thermal stimuli (Hauer and Stanford 1982; Walberg et al. 1983; Yemelina 1988; review by Ward and Stanford 1979).

Low DO levels in hypolimnetic discharges reduced macroinvertebrate density and diversity in several studies downstream from Tennessee Valley Authority (TVA) reservoirs (Isom 1971; Hill 1980; Yeager et al. 1987) and below Jordan Dam in Alabama (Harris et al. 1989). In general, macroinvertebrate communities in tailwaters with seasonally low DO were dominated by chironomids. Reductions in macroinvertebrate density downstream from reservoirs has also been attributed to poor water quality other than low DO (Petts 1984). For example, oxidation of iron and manganese compounds are known to cause benthic deposits and coatings on substrates that may indirectly influence distribution and structure of benthic communities (Krenkel et al. 1979).

Changes in discharge or water level have been found to stimulate invertebrate drift. Increases in drift rate have been associated with initial discharge surges (Matter et al. 1983b; Irvine 1985), although other investigators (Minshall and Winger 1968; Armitage 1977; Corrarino and Brusven 1983) reported increased drift rates following reductions in stream discharge. Increased drift, particularly if it occurs during daylight hours, could increase feeding activity by fish (Minshall and Winger 1968; Corrarino and Brusven 1983), although if increased drift continued for a long time, the benthos obviously could be depleted (Minshall and Winger 1968; Gore 1977), causing lower fish productivity. Drift losses during peaking operations have been calculated as almost 14 percent of the macroinvertebrate standing crop in 1 month in a 12-km tailwater reach (Matter et al.

1983a). However, it is also clear that inputs of seston (zooplankton and *Chaoborus*) from the reservoir supplements the tailwater food base through drift (Novotny and Faler 1982; Matter et al. 1983a; Jackson 1985). In addition to the changes in discharge, changes in depth, width, and velocity have also been implicated in the stimulation of drift (Gore 1977; Ciborowski et al. 1977).

Invertebrate drift changes, both in quantity and quality, with distance downstream from an impoundment. Zooplankton populations that usually comprise the main component of the drift immediately below the dam decline rapidly with distance downstream (Keefer 1977; Novotny and Faler 1982; Jackson 1985), primarily because of their removal from the water column by filter-feeding macroinvertebrates (Herlong and Mallin 1985). With increasing distance downstream, the drift composition begins to resemble that of an unregulated stream (Keefer 1977; Novotny and Faler 1982). As zooplankton moves downstream, there is a differential removal of organisms with the larger microcrustaceans disappearing from the drift before the smaller rotifers (Herlong and Mallin 1985). They attributed this finding to the larger mesh nets of filter-feeders in the immediate tailwaters and selective removal of the larger microcrustaceans.

Macroinvertebrate Communities. Southeastern tailwaters are usually dominated by small-size collectors, both filterers and gatherers, with few shredders, predators, or grazers (Krenkel et al. 1979; Walburg et al. 1983; Herlong and Mallin 1985; Novotny 1985; Hudson and Nichols 1986; Yeager et al. 1987). Several kilometers downstream from a dam, Herlong and Mallin (1985) and Walburg et al. (1983) found the fauna to resemble that predicted by the RCC for unregulated streams with filtering collectors still dominant, but gathering collectors, predators, and grazers were well represented.

Food is a critical factor determining the composition of macroinvertebrate communities of tailwaters, along with the abiotic variables already described. In regulated streams, the reservoir is the main source of food for downstream macroinvertebrates, although tributaries to tailwaters may contribute significant quantities of food. Reservoirs serve as particle traps and retain much of the POM washed in from the watershed (Matter et al. 1983b) and because reservoirs release POM in the form of limnetic plankton (Webster et al. 1979), tailwaters generally do not receive the same type of allochthonous POM recharge as that found in natural headwater streams.

Higher quality seston (i.e., greater quantities of plankton) is more common from surface-release dams than that found in hypolimnial releases, mainly because the water originates from the epilimnion of the reservoir where plankton occurs in greater densities than in the hypolimnion. Gore (1977, 1980) reported low densities of aquatic insects below a reservoir that he attributed, in part, to the lack of seston in the hypolimnial discharge. However, several tailwater reaches in the Southeast, fed by hypolimnial releases, have high macroinvertebrate densities, apparently supported by entrained plankton (Novotny and Faler 1982).

Species richness reported in Southeastern tailwaters is often low, relative to that above the reservoir (Hill 1980; Novotny 1985). However, Hudson and Nichols (1986) found over 200 invertebrate taxa below Hartwell Dam on the Savannah River and concluded that the high diversity may have been previously overlooked because the fauna consisted mostly of small oligochaetes and chironomids, often not identified beyond the class or family level. Macroinvertebrate diversity commonly increases further downstream as environmental conditions begin to resemble unregulated reaches.

Future Needs. Considerable data exists regarding various responses of benthic macroinvertebrates to stream regulation (Ward and Stanford 1987), although interpretation is often limited by a lack of basic knowledge (e.g., life history data, food habits, microhabitat requirements) for many lotic macroinvertebrates. A critical need exists for studies (i.e., biomass and production) that address how the life cycles of macroinvertebrates in tailwater reaches have adapted to altered thermal patterns, flow regimes, and food supply (i.e., quantity and quality).

The short-term flow fluctuations downstream from hydroelectric dams strand macroinvertebrates along shorelines and induce drift (Brusven 1984). Because drift dynamics in tailwaters differ greatly from that found in unregulated streams, several questions need to be addressed.

(1) What are the recolonization mechanisms in tailwater reaches?

(2) Does catastrophic drift characterize habitats below dams with frequent disturbance (peaking flows), and will recovery by macroinvertebrate communities be faster in these frequently disturbed streams than in rarely disturbed streams because the component species have adapted to the disturbance events?

(3) What type of drift periodicity is exhibited by the principal macroinvertebrates colonizing substrates in tailwaters?

(4) What are the ecological mechanisms that determine behavioral drift in regulated stream?

There is also need for better understanding of how macroinvertebrate communities have adjusted their microhabitat preferences in tailwaters to utilize the seston originating from the reservoir. It is clear that tailwater communities are dominated by collectors that depend heavily on reservoir seston. Finally, there is a strong need for more information on the trophic relationships between the macroinvertebrate communities in tailwaters and the resident fishery. We found one study on this relationship in regulated streams of the Southeast (Odenkirk 1987).

If changes in structural and functional variables occur along the river continuum, then the impact of stream regulation on these variables should be influenced by dam location (Ward and Stanford 1987). The serial discontinuity concept (SDC) was developed in the last decade, to provide a broad conceptual framework with which to address the disruptions (discontinuities) in the river continuum brought on by stream regulation (Ward and Stanford 1983). These authors listed four objectives of the SDC: (1) to recognize the importance of dam position; (2) to propose discontinuity distance as a measure of the upstream or downstream shifts (e.g., in heterotrophy versus autotrophy) that result from impoundment; (3) to promote a watershed approach for research in regulated streams; and (4) to offer a predictive conceptual model to be tested. With the SDC model, Ward and Stanford predicted downstream shifts of thermal regimes and POM dynamics. Stated differently, streams influenced by impoundments tend to mimic lower order areas upstream.

The SDC has had only limited testing to date. Stanford and Ward (1984) examined the limnology of a series of impoundments along the Gunnison River in Colorado and reported results consistent with their predictions of serial discontinuity; that is, shifts in distribution were attributed to resets in hydrologic patterns, temperature changes, and nutrient availability. Gore and Bryant (1986) examined impacts of multiple impoundments on the Arkansas River. Implications of the SDC include a displacement of benthic macroinvertebrate functional groups and fish assemblages downstream, such that mid-order reaches should resemble low-order streams in comparable natural stream systems. In general, Gore and Bryant found SDC predictions valid. However, their work indicated that substrate was the primary factor determining macroinvertebrate distributions; and impacted areas exhibited communities that contained low-order functional groups. However, fish communities did not resemble a low-order community in the RCC; thus the impoundment did not function as a reset mechanism for fish, but as a distributional barrier.

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