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19. Aquatic Invertebrate Research

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)ointed out by the editors of several recent books (Barnes and Minshall 1983, Resh
Rosenberg 1984; Merritt and Cummins 1984), the freshwater biology literature,
;cially that concerned with stream ecology and aquatic invertebrates, has expanded
:mously in the last 15 years. Research at Coweeta follows this worldwide trend. The
)ose of this chapter is to review the aquatic invertebrate work at Coweeta during the
and present and to address future prospects, particularly as they relate to long-term
ogical research at Coweeta.

1ere are approximately 73.4 km of streams within the confines of the Coweeta
rologic Laboratory. This distance is composed primarily of small, low-order
1ms: first, 41.7 km (57%); second, 15.8 km (21.5%); third, 11.1 km (15.1%);
th 4.3 km (5.8%); and, fifth, 0.6 km (0.9%) (Table 19.1). These estimates were
e from digitized stream lengths on a 1:7200 map, so a number of small first-order
hes were not measured; They are thus conservative for first-order streams. More
ι three-quarters of the total stream length at Coweeta is composed of smaller first-
second-order streams.

`ost small streams draining undisturbed catchments are heavily shaded by the sur-
ιding forest. Rhododendron is especially dense along most stream margins. On
.sturbed catchments, litter fall and lateral inputs of coarse particulate organic mat-
CPOM) into Coweeta streams range from ca. 350 to 568 g DM m^{-2} yr^{-1} (Webster
Patten 1979; Webster and Waide 1982; Webster et al. 1983; Webster 1983). The
available measurements of primary production in Coweeta streams indicate a low

Table 19.1. Stream Lengths in Various Orders Within the Confines of the Coweeta Experimental Forest

Drainage Basin	Total Stream Length (km)	Length (km) in Various Orders				
		1st	2nd	3rd	4th	5th
Dryman Fork	15.2	8.5	2.4	2.6	1.8	—
Ball Creek	27.7	15.6	6.4	4.8	1.0	—
Shope Fork	27.9	16.3	6.4	3.7	1.5	—
Coweeta Creek	2.7	1.4	0.6	—	—	0.6
Coweeta Creek Basin[a]	58.2	33.2	13.4	8.5	2.5	0.6
Sum of all[b]	73.4	41.7	15.8	11.1	4.3	0.6

Based on digitized stream lengths by J. O'Hop from 1:7200 U.S. Forest Service Coweeta Map.
[a] Includes Ball Creek, Shope Fork, and Coweeta Creek.
[b] Includes Dryman Fork, Ball Creek, Shope Fork, and Coweeta Creek.

level of net primary production in an undisturbed second-order stream, i.e., 2.6 g ash free dry mass (AFDM) m^{-2} yr^{-1} (Hains 1981; Webster et al. 1983). This represents < 1% of the allochthonous inputs (Webster et al. 1983; Webster 1983). Thus, the small streams that represent > 78% of stream length at Coweeta can be characterized as primarily heterotrophic systems.

Response of Invertebrates to Ecosystem Disturbance

Aquatic invertebrate studies at Coweeta have traditionally focused on the effects of forest disturbance on stream ecosystems. Tebo (1955) studied the influence of sediments discharged from a logged catchment [Watershed (WS) 10] on the downstream fauna in Shope Fork. Invertebrate densities in Shope Fork were reduced significantly by accumulated sediment which altered the streambed. The sedimentation problem was ameliorated to some extent by high water during the spring months, which reworked the streambed and exposed the original substrate. Tebo's study was among the first in North America to document the influence of sediments on invertebrates, and it additionally demonstrated the importance of physical factors (i.e., current velocity and discharge) on invertebrate fauna.

Gurtz (1981) and Gurtz and Wallace (1984) studied the response of aquatic macroinvertebrates to a major catchment disturbance, the clearcutting of WS 7, and found that substrate type was an important factor in determining the direction and magnitude of the aquatic invertebrate response. Following road building and logging in WS 7, inorganic and organic seston increased in Big Hurricane Branch (BHB), which drains WS 7 (Gurtz et al. 1980), and silt deposition caused a redistribution of stream fauna among substrate types. In BHB, more taxa increased in the moss covered rock face habitat followed by the cobble riffle, pebble riffle, and sand substrates; whereas, more taxa decreased in abundance in sand followed by pebble riffle, cobble riffle and rock face (boulder) substrates. Larger substrates require more stream power to move them, occur where current velocity is high, and are less susceptible to deposition of fine particles

rtz and Wallace 1984). The response of various invertebrate taxa to disturbance
gests that biological stability is closely associated with physical stability of the
itat. Moss associated with large substrates apparently facilitates the colonization by
ertebrates of these otherwise exposed surfaces.

ieorgian (1982) showed that several species of grazers in Shope Fork were
ociated with different substrate particle sizes and current velocities. Haefner and
llace (1981a,b) found that certain benthic taxa displayed different distributions
h regard to substrate preference. Malas and Wallace (1977), Wallace et al. (1977),
Ross and Wallace (1982) also found that the distribution of some species of net-
ining caddisflies were closely associated with larger substrate sizes and hence
ier velocities.

/oodall and Wallace (1972) investigated the benthic fauna in four Coweeta streams
ining catchments with different treatment histories: initial stages of old field succes-
1 (WS 6), undisturbed hardwood forest (WS 18), coppice hardwood forest (WS 13),
a catchment converted to white pine forest (WS 17). Significant differences in
ertebrate densities and biomass existed among streams. The old field catchment
am had the highest faunal densities. The coppice catchment stream supported the
nest biomass. The pine plantation catchment had significantly lower densities and
mass than the other three streams. The old field catchment stream also had higher
sities of taxa belonging to the scraper functional group, while the streams in hard-
od and coppice hardwood catchments had higher densities of leaf-shredding organ-
s (e.g., Merritt and Cummins 1984).

laefner and Wallace (1981a) found that there were significant changes in inver-
·ate densities in the stream draining WS 6 between 1968 and 1969 (Woodall and
llace 1972) and 1978 to 1979. The major changes in invertebrate fauna were a
rease in insect scrapers and an increase in shredder densities. However, stream
edder taxa densities in WS 6 remained lower than those of the hardwood forest
am (WS 18). The shift in functional feeding group densities coincided with 10 years
errestrial secondary succession which had resulted in more shading of the old field
am, which, coupled with increases in allochthonous detritus inputs, altered the
rgy base of the stream. Changes in taxa and functional groups can occur in fairly
rt time periods following catchment disturbance. Gurtz (1981) and Gurtz and
llace (1984) found stream collector-gatherers and scraper taxa increased while
dominant shredder species declined during the first year of logging of the BHB
chment.

/ebster and Patten (1979) studied three of the streams investigated by Woodall and
llace (1972) (WS 6, WS 17, and WS 18). Webster and Patten found that although the
·s of organic matter processing differed among streams, the pathways were similar
ll streams. They concluded that stream ecosystems have low resistance to perturba-
1, but high resilience following disturbance. A major aspect of stream resilience in
dwater streams is replacement of organic matter by allochthonous inputs (Webster
Patten 1979; Gurtz et al. 1980). Consequently, recovery of streams from catchment
ircutting is closely linked to restoration of surrounding terrestrial vegetation and
refore recovery of allochthonous inputs (Gurtz et al. 1980; Haefner and Wallace
1a; Webster et al. 1983).

There is another aspect of stream recovery that extends beyond the simple restoration of allochthonous leaf litter inputs. This concerns woody litter, which has a very slow rate of decomposition in streams (Triska and Cromack 1980). Most (> 77%) leaf litter inputs occur in the 3 month autumn season (Webster and Patten 1979). Stream flow at Coweeta is generally highest in winter and early spring (Chapter 3). Thus, there must be some mechanism for retention of CPOM inputs within stream reaches if the organic matter is to be fully utilized by microbial flora and animal fauna within these streams. Low stream power (Leopold et al. 1964), high roughness (Chow 1959), and shallow narrow channels which are readily subject to obstruction by woody debris, enhance debris dam formation and consequently CPOM and FPOM retention (Sedell et al. 1978; Naiman and Sedell 1979; Bilby and Likens 1980; Bilby 1981; Wallace et al. 1982a; Cuffney et al. 1984).

Recent measurements of wood in various Coweeta streams indicate that Sawmill Branch (WS 6) has < 10% the volume of wood per meter squared measured for any other Coweeta stream considered to date (Wallace and Huryn, unpublished data). All woody debris was removed or burned on WS 6 prior to its conversion to grass in 1958. In Sawmill Branch (WS 6), early successional species such as black locust have not yet entered the stream channel in quantities sufficient to restore significant woody debris structure. As retention of both coarse particulate organic matter (CPOM) and fine particulate organic matter (FPOM) is enhanced by woody debris (Bilby and Likens 1980), this suggests that simple restoration of leaf litter inputs alone will not restore the stream to its previous state. Interestingly, Webster and Golladay (1984) recently reported that both organic and inorganic seston in Sawmill Branch still remains extremely high 27 years since disturbance. Likens and Biley (1982) and Swanson et al. (1982) suggested that recovery of streams may actually lag behind, or be out of phase with that of the terrestrial forest, since large stable debris dams will be reestablished only after mature trees die and fall into the stream channel. Thus, while total allochthonous inputs of leaf fall may be restored to stream channels quite early in succession, retention of CPOM in the stream channels having little woody debris may be much lower than that of streams with extensive woody debris. Molles (1982) found that for New Mexico streams, differences in woody debris may influence the relative abundance of both shredder and grazer functional groups. Although there was no difference in taxa present, Molles found relative abundance of shredders and benthic organic matter were much higher in streams with abundant debris dams.

Influence of Invertebrates on Stream Ecosystem Processes

Most, but not all, of the aquatic research at Coweeta has focused on the effect of watershed disturbance on stream biota and stream ecosystem function. These studies have involved changes in energy inputs to streams including alteration of the surrounding forest and changes in physical characteristics of streams such as increased sediment loads during and after catchment disturbance. With several exceptions, studies have not focused on examining what role macroinvertebrates have in ecosystems. If physical characteristics of Coweeta headwater streams favor retention of organic matter, what

he influence of the invertebrate fauna on ecosystem processes? Benthic invertebrates small and represent an insignificant portion of total catchment biomass; therefore, suggestion that they influence ecosystem function would seem remote at first nce. The suggestion that insect shredders can generate considerable quantities of OM and DOC by their feeding is supported by indirect evidence such as high inges-n rates, low assimilation efficiencies, and their ability to comminute CPOM to OM (McDiffit 1970; Grafius and Anderson 1979; Golladay et al. 1983; Meyer and top 1983). However, little direct evidence has been obtained to substantiate the stence, magnitude, and importance of macroinvertebrates in producing FPOM from OM in streams. Indeed, Winterbourn et al. (1981) suggested for New Zealand eams that macrobenthos, especially insect shredders, are of minor importance in the duction of FPOM.

Vallace et al. (1982b) devised an experiment to examine the role of insects in cessing CPOM in two small headwater streams at Coweeta. We applied a pesticide one of two adjacent streams, which resulted in massive invertebrate drift (primarily atic insects) from the treated stream. Aquatic insect densities were reduced to < % of those in the adjacent reference stream by applications of pesticide. Benthic nmunity structure shifted from a system dominated by insect shredders to one domi-ed by noninsects such as Oligochaetes, Turbellaria, and various other noninsect ups. Chironomids and a few predaceous dragonfly nymphs were the only insects naining in this stream in any abundance (Wallace et al. 1982b; Cuffney et al. 1984). _eaf species breakdown rates were studied concurrently with the pesticide treatment l exhibited the same relative sequence of breakdown in both the treated and the erence stream (i.e., dogwood > red maple > white oak > rhododendron). wever, reduction of densities of shredders and other insect fauna in leaf bags in the atment stream significantly reduced leaf breakdown rates well below those of the erence stream. The more refractory the leaf species, the greater the effect insect lusion had on breakdown rates (Wallace et al. 1982b). Furthermore, suspended M concentrations in streamwater and transport to downstream areas were signifi-ntly lower following treatment, whereas no significant difference existed prior to atment. Nonstorm FPOM export to downstream reaches in the post-treatment iod was 3.9 times higher in the reference stream than that of the treatment stream allace et al. 1982b). Average particle size of transported organic matter was also aller in the treated stream than in the reference stream (Cuffney et al. 1984).

he above studies (Wallace et al. 1982b; Cuffney et al. 1984) indicated that benthic ertebrates play an active and substantial role in the processing of CPOM to FPOM headwater streams. Therefore, the conclusion of Winterbourn et al. (1981) that ects have little influence on the generation of FPOM in streams seems unwarranted, east in the small headwater streams of Coweeta. Through comparison of the physical racteristics of Coweeta and New Zealand streams, a contrast in the amount of ody litter and therefore retentiveness of the streams becomes apparent. The weeta streams had more woody litter allowing for the development of high shredder sities; whereas in the New Zealand streams, the paucity of wood reduced the poten- for instream processing of litter by shredders and the resulting comminution vailable CPOM to FPOM. This conclusion is supported by another study of a New land stream in which the quantity of wood was similar to that of Coweeta streams

(Rounick and Winterbourn 1983). Here these authors acknowledge that in the retentive, wood dominated stream, the general pattern of the invertebrate community did agree with the generalization of the continuum concept of Vannote et al. (1980).

Physical Characteristics of Streams vs. Food Exploitation by the Biota

Undisturbed Coweeta streams tend to retain a large portion of their CPOM inputs. The biota, dominated by shredder biomass, exploit these retentive characteristics by feeding on the retained CPOM and in doing so comminute CPOM to FPOM, which is more easily entrained and transported downstream (Table 19.2). Conversely, in larger downstream reaches which are less easily subjected to channel obstruction, the physical characteristics favor entrainment. The biota of these larger streams are dominated by collector-gatherers (especially filtering collectors) and favor retention. The biota are exploiting the physical characteristics of these systems. In the unidirectional, harsh physical environments of streams, it is difficult to visualize how the biota could function otherwise, i.e., shredders in downstream reaches where there is little retention and passive filter feeders in environments with high retention and little entrainment. In small headwater streams, the biota may exert considerable influence by comminution of CPOM to FPOM, thereby promoting downstream transport of POM. The downstream fauna probably has a progressively smaller role in offsetting stream physical characteristics as a result of higher downstream discharge and large cross sectional areas in proportion to the substrate available. Entrainment and physical transport probably overwhelm the retention capacity of the biota (e.g., Haefner and Wallace 1981b; Ross and Wallace 1983). This suggestion is supported to some extent by Webster's

Table 19.2. Some Characteristics of Streams vs. that of the Accompanying Fauna

Characteristic	Headwater Streams of Forested Regions	Large Rivers
Stream length	ca. 74% of total stream length in North America[a]	Much less
Interface with terrestrial environment	Maximal	Less(?)[b]
Inputs of terrestrial litter	Maximal	Less(?)[b]
Retention devices	Abundant[c]	Few
Organic matter inputs	Retained	Entrained
Invertebrate community structure[d]	Favor entrainment (i.e., shredders)	Favor retention (i.e., filter-feeders)

[a] First- and second-order streams represent ca. 74% of the total stream length in North America (Leopold et al. 1964).
[b] These characteristics are probably not true of large, lowland rivers with extensive flood plains subject to seasonal flooding, which may result in large inputs of allochthonous organic matter.
[c] Influenced by low stream power, high bed roughness, and narrow, shallow channels which are easily obstructed.
[d] Microhabitats with high entrainment, e.g., steep-gradient, rock face substrates, exist within headwater reaches and influence invertebrate community structure over relatively short mesospatial scales (see text).

83) computer simulation, which suggested that the importance of macroinver-
ates in overall organic matter processing decreases downstream.

hese retention and entrainment characteristics don't necessarily relate to an entire
am or a given stream reach. Even Coweeta headwater streams have localized areas
ch may favor deposition or transport. For example, excluding filter-feeding
onomid larvae, the average densities of insect filter feeders in Sawmill Branch,
dy Branch, Hugh White Creek, and BHB are about $2200/m^2$ of rock face substrate
ca. 320, 260, and $205/m^2$ for cobble, pebble, and sand substrates, respectively
sed on data from Haefner 1980 and Gurtz 1981). Conversely, debris dams retain
;e amounts of CPOM and FPOM and may harbor high densities of shredders such
epidostoma and _Tipula_. These microhabitats have fauna which reflect local physical
racteristics.

iologists often fail to recognize that very localized physical conditions may exert
)ng influences on stream biota and microhabitat preferences and even influence
d availability to the organism. Rock face substrates are shallow, high velocity habi-
; (Haefner and Wallace 1981a,b; Gurtz and Wallace 1984). Here, filter feeders such
arapsyche cardis occupy shallow depths, where a great proportion of potential food
ses within the height (<1 cm) of their catchnets (Smith-Cuffney and Wallace,
)ress). Higher stream velocities above these rock face substrates also enhance the
ɛ at which food is delivered to these passive filterers. Furthermore, moss growing on
; substrate may facilitate the presence of invertebrates by providing heterogen-
us microhabitats with respect to velocity gradients as well as attachment sites for
ertebrates.

√loss-covered rock face substrates also provide habitat for some of the fauna found
debris dams, e.g., *Peltoperla*. Moss both traps and retains particulate organic and
rganic material. Francie Smith-Cuffney has been using different densities of "artifi-
l moss" on rock outcrop substrates in Big Hurricane Branch and Hugh White Creek,
l has found up to 100 g $AFDM/m^2$ of organics may be retained in this "moss" within
0-day sampling period. About 40% of the trapped organic materials are particles
250 μm diameter. Mosses also serve as major sites of primary production and pro-
le attachment sites for algae in these streams (Hains 1981). Thus, very localized
as of streams possess physical characteristics which are exploited on a mesospatial
lle by the biota.

Secondary Production in Coweeta Streams

veral studies have addressed secondary production of aquatic invertebrates in
weeta streams. The production studies to date are biased toward Trichoptera (Table
.3). In an adjacent drainage system, Benke and Wallace (1980) estimated net-
nning caddisfly production as 1 g AFDM m^{-2} yr^{-1}. Similar results were obtained by
ss and Wallace (1983) in Coweeta streams. Haefner and Wallace (1981b) found that
)duction of two species of net-spinning caddisflies in Sawmill Branch (WS 6) was 4.9
AFDM m^{-2} yr^{-1}, or about 3.4 times higher than that of an undisturbed reference
eam (Grady Branch, WS 18). All of the above studies, as well as that of Georgian and
ıllace (1981) and Ross and Wallace (1982), attempted to quantify the influence of

Table 19.3. Secondary Production of Aquatic Invertebrates in Coweeta and Nearby Streams

Organism	Reference	Production mg AFDM m^{-2} yr^{-1}	Location
Copepoda			
Bryocamptus zschokkei	1	ca. 360	WS 14
Ephemeroptera			
Baetis spp.	2	63–1,112[a]	WS 14, WS 7
Plecoptera			
Peltoperla maria	3	414–560	WS 6, WS 18
Trichoptera			
Rhyacophila spp.	4	2–115[b]	Dryman Fork
Wormaldia moesta	5	67	Dryman Fork
Diplectrona modesta	5–7	31–647	Several locations
Parapsyche apicalis	5	180–188	Dryman Fork
Parapsyche cardis	5–7	161–4,274	Several locations
Arctopsyche irrorata	6	604	Tallulah Headwaters
Hydropsyche spp.	5,6	27–175[c]	Several locations
Cheumatopsyche h. enigma	5	26–151	Dryman Fork
Glossosoma nigrior	8	612	Shope Fork
Agapetus spp.	8	21	Shope Fork
Neophylax consimilis	8	150–176	Shope Fork
Goera fuscula	8	9–16	Shope Fork
Goerita semata	10	238	Rock Face, Ball Ck.
Brachycentrus spinae	9	261	Dryman Fork
Diptera			
Chironomidae	11	224[d]	litterbags WS 54
Chironomidae	12	1,608[e]	Ball Ck. (WS 27)
Blepharicera spp.	8	307–325[f]	Shope Fork
Prosimulium spp.	4	32–167	Dryman Fork
Simulium spp.	4	54–348	Dryman Fork

References 1–11 as follows: 1, O'Doherty (1985); 2, Wallace and Gurtz (1986); 3, O'Hop et al. (1984); 4, D. H. Ross and J. B. Wallace (unpublished data); 5, Ross and Wallace (1983); 6, Benke and Wallace (1980); 7, Haefner and Wallace (1981b); 8, Georgian and Wallace (1983); 9, Ross and Wallace (1981); 10, Huryn and Wallace (1985); 11, Huryn and Wallace (1986); and, 12, Huryn, (unpubl.). In addition to the above, production estimates for several other taxa of Ephemeroptera, Plecoptera, Trichoptera, Diptera, and crayfish are completed (Huryn, Wallace, Gurtz, unpublished data).
[a] Weighted stream production for all substrates for 21-month period.
[b] Range for individual species (n = six species).
[c] Range for individual species (n = four species).
[d] Average per litterbag; yearly P/B = 42.
[e] Weighted stream production (WS 27) for all substrates.
[f] Total production for three species.

filter feeders on particulate organic seston, and results suggested that filter feeders ingest only a minute portion of the total transported organic matter.

In a study conducted in Shope Fork, the secondary production of a grazer guild was estimated to be about 1.2 g AFDM m^{-2} yr^{-1} (Georgian and Wallace 1983). Overlap between six grazer species was calculated on the basis of density, biomass, and production. (Overlaps based on production should most closely reflect patterns of resource consumption.) Production of each species was concentrated in short, <6 week to 3 month, time periods, and mean overlap based on production was significantly lower

ı that based on either biomass or densities. This lends support to Vannote's (1978)
othesis that various species within a functional group are organized to minimize
iods of similar resource use by two or more species. While the assumption underly-
the cause of the temporal separation of production (the avoidance of interspecific
ıpetition) was not tested, the various species do tend to occupy different micro-
itats as well (Georgian 1982).

econdary production estimates require a knowledge of life cycles or specific growth
:s, the standing stock densities, and biomass. Thus, they are very labor intensive.
tinism and length of immature development have been identified as the two most
ıortant factors influencing production (Benke 1979; Waters 1979), yet life history
lies are often considered unfashionable. Ecosystem studies are often oriented
ard the processing of organic matter and nutrient cycling by various groups of
anisms. The integration of production, feeding habits, and bioenergetic data can
d a much better understanding of the role of animal populations in ecosystems (e.g.,
ıke and Wallace 1980; Fisher and Gray 1983; Benke 1984). O'Hop et al. (1984)
wed that, although the average benthic density in one stream was more than twice
t of the other, *Peltoperla* production was similar. Standing stock densities alone did
 detect differences in growth rates and survivorship between the two streams. In
ımary, numerical abundances and biomass may lead to erroneous interpretations
ıut the role organisms play in ecosystems.

ɔ date, most Coweeta secondary production studies have focused on bivoltine,
voltine, or semivoltine species with clearly discernible life cycles. However, there
 exceptions. O'Doherty (1985) estimated production of an harpacticoid copepod as
 360 mg AFDM m^{-2} y^{-1}, and Wallace and Gurtz (1986) estimated *Baetis* production
 :xcess of 2 g AFDM m^{-2} y^{-1} for rock face substrates in Big Hurricane Branch for the
 ıt year following logging of WS 7. Based on gut analyses, literature-derived assimila-
 ı efficiencies, and production, Wallace and Gurtz (1986) estimated that *Baetis* used
 ıut the same proportion (7.4 to 9%) of net primary production in both Big Hurricane
 ınch and a reference stream, Hugh White Creek. Total diatom consumption by *Bae-*
 was about 25 times higher in Big Hurricane Branch than in Hugh White Creek, and
 ıduction of both *Baetis* and diatoms was much higher in the former stream (Hains
 ₹1; Webster et al. 1983; Wallace and Gurtz 1986).

f we are going to understand responses of many species to disturbance and their role
 ₂nergy flow and nutrient cycling, we must have more data on life cycles and species-
 :cific growth rates, feeding habits, and bioenergetic efficiencies. It is rather appall-
 . that the most abundant insects in Coweeta streams are the chironomids, and that
 y recently have any data on growth rates been obtained for this group in Coweeta
 ₂ams (Huryn and Wallace 1986). Sixty-six taxa of chironomids were identified from
 gh White Creek and Big Hurricane Branch from three collections spanning a
 ·month period (Gurtz 1981; Gurtz and Wallace 1984). Annual estimates of P/B
 oduction/$\bar{x}$ (= mean) biomass) ratios of chironomids range from <1 in arctic tun-
 ı ponds to over several hundred in warm streams. Benke (1984) suggested that annual
 ₹'s may exceed 500 under favorable conditions. Some recently initiated field growth
 dies for chironomid larvae in Coweeta streams indicate daily growth rates of 7 to
 % of larval AFDM/day at temperatures of about 14°C, with highest growth rates in
 ·ly instars (Huryn and Wallace 1986). Annual P/B's for chironomids may approach

20 to 50 at Coweeta. Based on a pretreatment chironomid biomass of 86 mg AFDM/m^2 for the pesticide treated stream (Cuffney et al. 1984) and a daily growth rate of ca. 0.125 mg mg AFDM body wt d^{-1}, chironomid production alone may approach 4 g AFDM m^2 yr^{-1} in some Coweeta streams. Chironomids are just one of several groups in need of research if we are going to address to role of invertebrates in energy flow and nutrient cycling in streams.

We have little knowledge of the meiofauna composition of Coweeta streams, and less is known about their feeding habits and potential P/B ratios. In published studies to date, the only attempt to address meiofauna is the work of O'Dougherty (1985), who estimated secondary production of the copepod, *Bryocamptus zschokkei*, at ca. 360 mg AFDM m^{-2} yr^{-1}. This production value is slightly less than production of a dominant shredder in Coweeta streams, but greater than several other species (cf. Table 19.3).

Based on existing studies, Table 19.3 shows that secondary production of invertebrates does not appear to be very high in Coweeta streams. Several factors probably attribute to this rather low level of secondary productivity. These include rather cool annual temperature regimes, generally low stream nutrient concentrations, and shading of most streams (which limits autochthonous production and food quality available to invertebrates). Food quality and temperature are important factors influencing growth and life cycles of invertebrates (see Merritt and Cummins 1984; Resh and Rosenberg 1984).

There is little direct evidence that insect predators exert much impact on other invertebrate populations at Coweeta. Pesticide treatment of a headwater stream reduced large insect predators to less than 8% of the population levels for the adjacent reference stream during an 8-month period following treatment (Wallace et al. 1982; Cuffney et al. 1984) and within this same 8-month period, noninsect populations increased in the treated stream. Dragonfly larvae, primarily *Lanthus vernalis* Carle, were the only significant insect predators remaining in the treated stream. In the reference stream, insects represented the most frequent items in *Lanthus* guts (73% of prey). The food of *Lanthus* in the treated stream reflected the shift in invertebrate community structure, with noninsects constituting 87% of all prey items (Wallace et al., unpublished data). Within two years, insect biomass had recovered in the treated stream. This shift in community structure was reflected in *Lanthus* diets, as insects represented 82% of their prey in the treatment stream vs. 78% in the reference stream during the second year of recovery. These data suggest that generalist predators such as *Lanthus* can shift to alternative prey when confronted by massive changes in community structure. However, more research is needed on prey and predator production and turnover, availability of prey production to predators, and the energetic requirements of predators in order to adequately assess the influence of predation on benthic community structure at Coweeta.

Future Prospects

Coweeta offers unique opportunities for assessing both short- and long-term consequences of ecosystem disturbance on invertebrates, and for addressing long-term recovery of lotic ecosystems. Pesticide treatment of a small headwater stream at Coweeta resulted in massive invertebrate drift, subsequent changes in benthic com-

1ity structure, lower leaf litter breakdown rates, and significant reductions in amount of fine organic matter transported to downstream reaches. Can restora- ι of these functional characteristics occur before full structural (i.e., taxonomic))very of various insect species? During 1982 to 83, leaf breakdown rates in the nerly treated stream were not significantly different from those of the reference am. Although populations of the predominant pretreatment shredder *Peltoperla* 1ained extremely low in treatment stream, *Lepidostoma* and tipulids were present arge numbers. *Lepidostoma* and *Tipula* were actually much more abundant in :r bags from the treated stream than in the reference stream during 1982 to 1983 gel 1984). Particulate organic seston concentrations had increased several fold in treated stream compared to the 1980 levels. These results suggest that functional)very may occur before full structural recovery of the shredder group. This work 1eing continued, and offers an approach to investigate changes in ecosystem pro- 3es caused by benthic organisms without altering energy inputs or the physical struc- ? of the stream.

Vebster (1983) developed a series of models to evaluate the role of macroinver- rates in streams. Overall, the simulations suggested that macroinvertebrates were 3onsible for only a small portion of the respiration of detritus, and that the major ? of macroinvertebrates is in the conversion of benthic detritus to organic seston. s model suggested that although macroinvertebrates were responsible for only 27% he annual POM transport, their activities may contribute as much as 83% of the M transported during low flow (late summer). Although stochastic processes, i.e., rm flows, may dominate annual export budgets, there may be long periods of base ν in which biological processes predominate. Webster's efforts in this regard resent an excellent contribution, and such models are highly useful in showing us ere problems exist in research efforts.

'urther knowledge of a number of important aspects of streams are mandatory for litional refinement of Webster's model. These include aspects such as: (1) What more accurate secondary production estimates for both macroinvertebrates and iofauna? (2) What are the rates of microbial respiration in Coweeta streams? (3) w do macroinvertebrates influence community metabolism? (4) What are the rela- ? rates of microbial respiration on detritus in streams in which macroinvertebrate 1sities have been manipulated vs. unmanipulated streams? (5) How comparable patterns and quantity of particulate organic matter export during storm flows in croinvertebrate manipulated and unmanipulated streams? (6) Does macroinver- rate manipulation influence annual output budgets for particulate and dissolved ;anic export to downstream areas? (7) How does manipulation influence the timing 1 magnitude of organic matter export to downstream areas during storm and non- rm periods?

\nother area where Coweeta offers excellent possibilities for long-term study con- ns the potential influence of acidic precipitation on stream ecosystems. Streams 1ining high elevation catchments with shallow soils underlain by granitic bedrock are 1ught to represent areas most sensitive to acidic precipitation (Record et al. 1982). weeta has many catchments with these characteristics, e.g., WS 27. Acidification of 2am water reduces diversity of aquatic fauna, but the exact mechanisms and conse- 2nces for ecosystem level processes remain unclear (Wiederholm 1984). Other than

brief experimental acidification studies at Norris Brook (Hall et al. 1980), the sequence of changes during acidification are uncertain. Especially lacking is the documentation of long-term changes in a single stream. Recent efforts have focused on studies of the invertebrates and some system processes on WS 27. This project should result in the best invertebrate documentation available for a single stream at Coweeta.

While there is currently no evidence to demonstrate any acidification effects on WS 27 stream fauna, this does not imply that there need be no long-term concern. One reported effect of acidification that may be especially relevant for Coweeta in the future is its influence on decomposer organisms. Leaf litter decomposition proceeds much slower in acidified (pH 4.3 to 5.6) than in more neutral waters (pH 6.0 to 6.5) (Traaen 1980). Hendrey et al. (1976) attributed an abnormal accumulation of coarse organic detritus on the bottom of acidified Swedish lakes to this phenomenon. This reduction in decomposition rates is probably related to a reduction in heterotrophic microorganism activity on detritus and to reduced invertebrate abundances in acidified waters. Based on the studies of Wallace et al. (1982b) and Cuffney et al. (1984), we know that reduction in densities of insects can drastically alter detritus processing and potentially influence energy and nutrient flow to downstream areas. In acidified waters where both invertebrate and microbial activities are reduced, the potential influence of acidification on stream energy and nutrient flow may equal or exceed the effect of reducing invertebrates alone as in the experiments of Wallace et al. (1982) and Cuffney et al. (1984). While there is no strong current evidence to support acidification of Coweeta streams, the potential for impact certainly exists and requires long term vigil. The availability of baseline data on invertebrate abundance, biomass, and production; combined with heterotrophic respiration, leaf litter processing rates, and long-term data on stream chemistry, place this Laboratory in a unique position for assessing any long-term changes in stream ecosystems.