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THERMAL REGULATION OF FUNCTIONAL GROUPS IN RUNNING WATER ECOSYSTEMS

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K. W. Cummins and M. J. Klug

Kellogg Biological Station
Michigan State University
East Lansing, Michigan 48824

412 7000

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1.0. ABSTRACT

Thermal Regulation of Functional Groups in Running Water Ecosystems

The research plan encompassed three general objectives: 1) Derivation of generalized models of detrital processing in stream ecosystems with special emphasis on thermal control; 2) Characterization of functional groups of running water organisms, particularly macroinvertebrates (shredders, collectors, scrapers, piercers, predators); 3) Demonstration of the importance of food quality, and the interaction between temperature and food quality, in controlling growth and survivorship of stream functional groups.

2.0. INTRODUCTION

The research effort supported by ERDA, during the period October 1, 1974 through June 30, 1977, has been concentrated on the processing of particulate organic matter (POM or detritus) by stream macro- and microconsumer organisms. A major focus of the work has been on the interaction between temperature and substrate quality in the general control of detritus processing, that is the conversion to CO_2, organism biomass, and dissolved organic matter (DOM). Within temperature-substrate quality interactions, the majority of the effort has been directed at the regulation of growth and survivorship of detrital feeding macroinvertebrate functional groups - shredders and collectors.

For the microconsumers (bacteria and fungi) substrate quality is biochemical; for the macroconsumers it is primarily a function of the presence of microconsumers (microbes). Temperature exerts a major control on microbial colonization and growth and, therefore, on growth and survivorship of detrital feeding macroinvertebrates which depend on microbial biomass for the majority of their nutrition. In addition, temperature also has a direct effect on macroinvertebrate metabolism and growth.

During the period of ERDA support, 1974-1977, a total of 15 papers have been published, are in press, including a book, or are ready to be submitted, and three theses have been completed. Six papers, which have acknowledged ERDA support, deal with general models of stream ecosystem structure and function (Cummins, 1974, 1975a, 1975c, 1977; Cummins et al., 1977a; Barnes et al., 1977), four papers, two theses and a book concerning functional groupings and other aspects of the ecology of macroinvertebrates (Petersen, 1974; Cummins, 1975b, 1976; Merritt and Cummins, 1977; Ward and Cummins, 1977a, 1977b; King, 1977; Ward, 1977), and five papers treat various aspects of detrital processing (Petersen and Cummins, 1974; Boling et al., 1975; Suberkropp et al., 1975; Cummins et al., 1977b; Barnes et al., 1977). (See Section 3.0. for a complete listing of papers which acknowledge ERDA support.)

The progress report, a major portion of which consists of brief summaries of published and in-press papers or prepared manuscripts, covers three general areas: 1) generalized models of detritus processing in stream ecosystems with special emphasis on thermal control; 2) characterization of functional groups of running water organisms, particularly macroinvertebrates (shredders, collectors, scrapers, piercers and predators); and 3) the importance of food quality, and the interaction between temperature and food quality, in controlling growth and survivorship of stream functional groups.

3.0. Publications 1974-1977

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Cummins, K. W. 1974. Structure and function of stream ecosystems. BioScience 24: 631-641.

Petersen, R. C. 1974. Life hisotry and bionomics of *Nigronia serricornis* (Say) (Megaloptera: Corydalidae). Ph.D. Thesis. Mich. State Univ., East Lansing. 210 p.

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Ward, G. M. and K. W. Cummins. 1977a. Ecology and natural history of *Paratendipes albimanus* (Meigen) (Diptera: Chironomidae). Ann. Ent. Soc. Am. Submitted.

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King, R. H. 1977. Natural history and ecology of Stictochironomus annulicrus (Townes) (Diptera: Chironomidae), Augusta Creek, Michigan. Ph.D. Thesis. Mich. State Univ., East Lansing.

Ward, G. M. 1977. The influence of detrital food quality and temperature on the life history and pattern of growth in the stream detritivore Paratendipes albimanus (Meigen) (Diptera: Chironomidae) in a Michigan headwater stream. Ph.D. Thesis. Michigan State Univ. 88 p.

4.0. SUMMARY OF PROGRESS 1974-1977

4.1. Generalized Model of Factors Affecting Detrital Processing in Streams

Major elements of a conceptual model of detritus processing in headwater streams have been treated in three papers in which the principal investigator was a sole or co-author. The general model of stream ecosystems presented in Cummins (1974) proposed basic components of structure and function. Organic matter, primarily of allochthonous origin, was partitioned into coarse (CPOM) and fine (FPOM) particulate and dissolved (DOM) fractions. Microbial colonization and metabolism of particulates was viewed as constituting food quality for shredder and collector detrital feeding functional groups. Physical and biological (microbial) processes convert DOM, of terrestrial and in-stream origin, to particulates. The inorganic carbon fixed by primary producers in a given stream system is the nutritive source for the scraper macroinvertebrate functional group. Shredders reduce CPOM particle size and collectors filter and gather FPOM from the water column and sediments respectively. Macroinvertebrate predators act as partial controls on the other animal functional groups.

The importance of sources of organic matter and the time variant (non-steady state) nature of running water ecosystems was discussed in Cummins et al. (1977a). The unmeasured storage in, and introduction from, the sediments, major debris accumulations (e.g. log jams), and the flood plain of particulate organic matter renders most annual stream organic budgets of little value. That is, budgets based on inputs estimated from litter and bank traps and outputs calculated from collections of export do not account for internal adjustments on a greater than annual time basis.

Changes in running water ecosystem structure and function with increasing stream and river size are the subject of Cummins (1977). Headwater streams, Strahler (1957) orders 1-3, are generally dependent on allochthonous organic inputs as the major energy supply. The ratio of gross primary production (P) to total community respiration (R) is often less than 1, and important interacting system components are: CPOM - aquatic hyphomycete fungi - shredders. In midsized running waters, orders 4-6, the P/R ratio tends to be greater than one and important components include: periphyton - scrapers. Collectors are important in headwater and midsized systems, particularly the latter. Large rivers, orders greater than 6, have a P/R ratio less than one, due to increased depth and turbidity induced light attenuation, and are dominated by FPOM - bacteria - collectors.

4.2. Time-Temperature Leaf Litter Processing

4.2.1. Generalized Model

Using primarily the data gathered on leaf litter processing in Augusta Creek and the KBS experimental stream channels, a generalized model involving both time and temperature was developed (see Appendix 1). The leaf pack method (Cummins, 1972, 1974; Petersen and Cummins, 1974) was used to simulate natural litter accumulations in streams and in the littoral zone of lakes.

The model of leaf processing uses both time (days) and temperature (degree days) as independent variables. By testing for lack of fit, it can be determined if adding degree days to a model with days alone results in a significant reduction of error. In 5 of the 13 cases tested (5 of 10 stream data sets), degree days added significantly to the goodness of fit (Appendix 1). The two variable model isolates the effect of temperature on leaf litter processing, and serves as a valuable tool in assessing the importance of various biological factors in controlling processing rates. Temperature control is mediated primarily through its effect on microbial metabolism.

A detailed test of the importance of temperature in leaf litter processing was performed using the KBS experimental stream channels. After stocking both channels to simulate Augusta Creek, ash (rapidly processed) and aspen (slowly processed) leaf packs were introduced after varying periods of incubation in Augusta Creek. In addition, unconditioned leaf litter of both species was introduced into the channels. The artificial streams were operated at mean temperatures of 5 and 10°C and compared to data gathered over the same six month fall-winter period in Augusta Creek, during which stream temperatures ranged between 0 and 2°C. The temperature effects were quite striking. Processing rates of leaf litter and growth of macroinvertebrates, periphyton and microconsumers (bacteria and fungi) in the warm (10°C) channel were significantly higher as compared to the cold channel (5°C) or the natural stream (0-2°C). The higer temperature apparently allowed for increased nutrient turnover by microorganisms (and attached algae) as well as directly influencing their metabolic rate. The increased microbial biomass in turn resulted in accelerated growth of detrital feeding macroinvertebrate functional groups (shredders and collectors; see Section 4.5 below and Appendix 2).

4.2.2. Microbial Processing

Studies of the relative dominance of various hyphomycete fungal species at different temperatures in Augusta Creek and laboratory culture revealed cool and warm adapted species (Appendix 3). Hickory and oak leaves were cultured in Augusta Creek during three seasons, fall, winter and summer, and total microbial activity measured as respiration (Gilson differential respirometer) at a range of temperatures from 5 to 40°C. Again, cool and warm adapted communities were observed and, in addition, different respiration rates were obtained on the two leaf types at the same temperature (Appendix 3).

When leaves were incubated for periods of 1 day or 1 week in a third order reach of Augusta Creek and then moved to a cold first order feeder spring, the cool adapted forms of the spring were able to displace the initial colonizers from the warmer third order site (Appendix 3), although it took considerably longer in the case of the 1 week set.

4.3. Characterization of Functional Groups of Stream Organisms

The functional groups of stream organisms proposed by Cummins (1973, 1974) have been elaborated and further defined in subsequent publications (Cummins 1975b, 1975c, 1976, 1977). Particular emphasis has been placed on the detrital feeding functional groups - shredders and collectors. The shredders consume coarse particulate organic matter (CPOM), particularly leaf litter, and the collectors fine particulate organic matter (FPOM). Shredders feed selectively on the most conditioned (highest microbial biomass) leaf litter while collectors feed primarily according to size of organic particles, independent of food quality (i.e. microbial biomass).

Scrapers are morphologically and behaviorally adapted to feeding upon attached, non-filamentous algae, primarily diatoms. Piercers, either herbivores or predators, feed by sucking the fluids from filamentous algae (or vascular hydrophytes) or prey respectively. Engulfers are predators which are variously adapted for whole prey capture and ingestion.

The families and genera of North American insects have been placed in at least tentative functional groups by Cummins (in Merritt and Cummins, 1977; see examples in Appendix 4) and other ecological characteristics given. The summaries are designed to permit the classification of aquatic insects into functional groups with minimal taxonomic separations. That is only that level of taxonomic separation required to characterize a functional group need be performed.

In order to rapidly determine the biomass per individual, size-dry weight correlations have been established for various representatives of the different functional groups (Appendix 5). It has been demonstrated that biomass determinations can be made within broad animal categories (e.g. taxonomic families or orders) using the empirically determined coefficients. This provides for the efficient characterization of the benthic macroinvertebrate community: only minimal taxonomic separations need be made in order to categorize animals by functional group and estimate their biomass.

In depth studies of the collectors Paratendipes albimanus (Chironomidae; Ward and Cummins 1977a, 1977b, Appendices 6 and 7) and Stictochironomus annulicrus (Chironomidae; King 1977; Appendix 8) were conducted in Augusta Creek, the KBS experimental channels and various culture facilities (living streams and temperature control cabinets). Both species are collector-gatherers, that is, deposit feeders, dependent upon FPOM. P. albimanus is the smaller of the two and is univoltine, while S. annulicrus has two generations per year in Augusta Creek (except in a few, cold first order springs). In the case of both species of collectors a definite relationship between growth and food quality, that is microbial biomass associated with the particulate detrital food, exists. When compared to shredder (Tipula) feces or ground up, conditioned leaf litter, natural stream detritus is of generally lower quality. At this point it is not clear whether selective feeding and/or increased ingestion rates, account for the growth rates observed in field populations.

Nigronia serricornis was studied in detail as an example of an engulfer (predator), in the field, experimental streams and laboratory culture. This predator, which has a two year life cycle, was shown to consume a wide range of prey species. Growth was confined primarily to late spring, summer and early fall. The remainder of the two year cycle, the animals fed, but exhibited a lower metabolic rate and did not grow (Petersen, 1974).

4.4. Relation Between Macroconsumer Growth and Survivorship and Food Quality

The effect of food quality on growth and survivorship of shredders, collectors and scrapers was investigated during the 1974-1977 contract periods. Food quality for shredders and collectors was defined in terms of microbial colonization as measured by detrital respiration, ATP content, C/N ratio and direct observation by light and scanning electron (SEM) microscopy (Petersen and Cummins, 1974; Cummins, 1975; Suberkropp et al., 1975).

As shown by other investigators (e.g. Barlocher and Kendrick, 1973a, 1973b; Mackay and Kalff, 1973) the presence of microorganisms, equated with conditioning, has a significant effect on the growth of shredders such as Tipula abdominalis (Cummins, 1974). T. abdominalis larvae will not eat sterile leaves unless they are softened with pectinase, suggesting that recognition of food quality has a mechanical basis (Suberkropp and Klug, Kellogg Biological Station, unpublished data).

Detailed studies on two collectors, the midges Paratendipes albimanus and Stictochironomus annulicrus, also showed a significant correlation between food quality (microorganism activity or biomass) and growth. Data on P. albimanus and S. annulicrus, which are representative collector-gatherers, have been summarized in detail in Ward and Cummins (1977a, 1977b and Appendices 6 and 7), Ward (1977) and King (1977; Appendix 8). Detrital respiration by particle size (Cummins et al., 1977 and Appendix 9) or leaf type (Petersen and Cummins, 1974) has been shown to be a useful way to characterize the food quality of particulate organic matter for shredders and collectors. Future research will focus on the use of temperature and particle size specific respiration (μl O_2 mg ash-free dry wt^{-1} $time^{-1}$) to predict shredder and collector growth in both the large, KBS experimental channels and a natural stream (Augusta Creek, Michigan).

The influence of food quality on collector growth and survivorship was also demonstrated in an experiment conducted in the KBS artificial stream channels (1975-1976). Fine particulate organic matter (FPOM), in the size range < 1 mm > 250 μm, was made from conditioned oak and hickory leaves that were ground into particles. Both stream channels were stocked with natural

Augusta Creek fauna and flora and operated at natural stream temperatures. The original hypothesis that FPOM of a given particle size would be of approximately the same food quality regardless of origin was disproven since growth and survivorship of collectors was significantly greater in the channel stocked with hickory FPOM than the one into which oak particles were introduced. Some representative data from the FPOM experiment are summarized in Appendix 10.

4.5. Interaction Between Temperature and Food Quality in Controlling Macroconsumer Functional Group Growth and Survivorship

Two major experiments were conducted in the KBS artificial stream channels (Cummins, 1972) dealing with the effects of thermal regime and food quality.

The first experiment involved a comparison, under normal fall-winter stream temperature regimes, between ash, a rapidly conditioned and processed leaf type, and aspen, which is conditioned and processed slowly. Both channels were stocked with natural fauna and flora to simulate a first order tributary of Augusta Creek. One experimental channel was stocked with ash leaf litter, the other with aspen. Leaf processing and macroinvertebrate growth rates were followed in each stream over a six month period. Growth rates and survivorship of both shredders and collectors were higher in the ash-aspen experiment and are given in Appendix 2.

A second experiment dealt with the effect of temperature on the processing of ash and aspen leaf litter and macroinvertebrate growth and survivorship in the KBS artificial stream channels. The channels were operated at mean temperatures of 5 and 10°C respectively and the results compared to data gathered over the same six month fall-winter period in Augusta Creek, during which stream temperatures ranged between 0 and 2°C. The major finding was a demonstration that macroinvertebrate growth and survivorship are strongly affected by temperature in such a fashion that animal biomass remained comparable under different temperature regimes. That is, although the average weight per individual of shredder, collector, scraper or predator was significantly greater in the warm (10°C) channel, survivorship was significantly less - the result being approximately equal biomass per m^2 in the two channels (or in leaf packs under all three temperature regimes). A more complete description of the results is presented in Appendix 2.

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