ENERGETICS OF NATURAL POPULATIONS
OF FRESHWATER MACROCONSUMERS

Progress Report
(1969-1974)

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Reporting Period: September 1, 1969 - September 30, 1974

PREPARED FOR THE U. S. ATOMIC ENERGY COMMISSION

UNDER CONTRACT NO. AT(11-1)-2002

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ABSTRACT
(Research Support 1969-1974)

The research encompassed two main phases: 1) the determination of energetic parameters for populations of selected macroinvertebrates, particularly Leptodora kindtii (Crustacea : Cladocera) and Glossosoma nigrum (Insects : Trichoptera) and, 2) the assessment of the functional roles played by important macroinvertebrates of stream benthic communities. Respiration energy expenditure was shown to be as high as 90% in predator populations and 70 to 80% in herbivore-detritivore populations. For herbivores with two generations per year production was similar between generations and between years. Based on a large number of caloric determinations of many species of macroinvertebrates, an average value of 5.5 Kcal/ash-free gram was estimated to be suitable for most energy budget determinations. It was shown that the macroinvertebrates of running waters can be usefully partitioned into shredders (large particle detritivores), collectors (fine particle detritivores), scrapers (periphytic algal grazers) and predators. The shredders account for approximately 20 - 24% of the processing of leaf litter to CO₂, animal biomass and fine particles and measured feeding rates of collectors indicate they have a significant effect upon the fine particles (approximately < 4 mm).

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SUMMARY OF PROGRESS

Since 17 publications (4 in press) have resulted from support of AEC Contract No. AT-11-1)-2002 (see listing in next section), it is assumed that these papers and chapters in journals, books and published symposia proceedings constitute the best documentation of the work performed during the period 1969-1974. Therefore, only brief summaries of the research, presented by year, are included in the narrative below.

The research encompassed two main phases during the period. The first was the measurement of the caloric content of various life stages of a number of species of organisms - particularly macroinvertebrates or food items of macroinvertebrates and the determination of energy budgets (ingestion-egestion-assimilation-respiration-growth and reproduction) for selected species. The second phase, which is continued in the present renewal request, entailed the assessment of the functional roles of macroinvertebrates (and their food sources) in stream ecosystems. These rates are summarized in Fig. 1. Special emphasis has been placed on the processing of particulate matter by the stream macroinvertebrates.

1969 - 1970

Energy budget parameters were determined for five macroinvertebrate species populations which cut across ecosystem and trophic lines. Particular emphasis was directed toward the planktonic predator Leptodora kindtii (Crustacea : Cladocera. Cummins et al., 1969; Moshiri et al., 1969; Moshiri and Cummins, 1969; Costa and Cummins, 1969; Costa and Cummins, 1972) and the stream grazing herbivore Glossosoma nigrior (Insecta : Trichoptera. Cummins, 1969). Considerable attention was directed toward development of a "procedural package" for determining energy budget parameters (Cummins et al., 1969). Ingestion and assimilation rates were measured through tracer experiments (^{14}C) in which the tagged material -- food items and macroinvertebrates -- was combusted to CO_2 trapped in ethylamine and counted using liquid scintillation procedures.

Other organisms investigated included the herbivorous zooplankter Daphnia pulex (Crustacea : Cladocera. Cummins et al., 1969) the stream grazing herbivore Neophylax oligius (Insecta : Trichoptera) and the invertebrate stream predator Nigronia serricornis (Insecta : Megaloptera. See Petersen, 1974).

1970 - 1971

In the process of summarizing the methods used in preparing energy budgets (Cummins, 1971) and through the determination of energy equivalents for various life stages of a number of invertebrate species and their food materials, a compendium of energetic data was prepared (Cummins and Wuycheck, 1971). Based on this extensive summary it was proposed that 5.5 Kcal/ash-free gram was an adequate mean value to be used in calculations involving freshwater macroinvertebrates, particularly given the large variances associated with assessing the density (and age structure) of natural populations.

Fig. 1. A conceptual model of functional groups in stream ecosystems (modified from Cummins, 1973) emphasizing the processing of particulate and dissolved organic matter. CPOM is represented by deciduous leaves, coniferous needles, a twig, bark, nut and flowers. Initial colonization of FPOM is exemplified by an aquatic hyphomycete fungal spore and the utilization of DOM by rod-shaped and spheroid bacteria. The plant community is represented by diatoms (microproducers) and moss (macroproducers). The animal examples are: shredders - caddisfly and stonefly larvae and a stonefly nymph; collectors - blackfly and midge larvae and a mayfly nymph; scrapers - a caddisfly larva; predators - fishfly and midge larvae and fish (sculpin and trout).

During this project period, the emphasis shifted to preparing energy budgets for ecosystems. Grounded on the realization that data at the level of populations can be summed only if information is available on the general, overall structural and functional relationships of the ecosystem in question, the research effort was concentrated on a stream ecosystem. The approach that was initiated, and continued to the present, was the establishment of the general structural and functional dimensions of a woodland stream ecosystem (Fig. 1.) and to continually refine the model by detailed study of energy flow through key populations. Thus studies of stream macroinvertebrates representing different functional groups were initiated or continued in the case of Glossosoma, Neophylax and Nigronia. Investigations of the shredders Tipula caloptera (Insecta : Diptera), Pycnopsyche lepida, P. guttifer, Lepidostoma costalis (Insecta : Trichoptera) and Pteronarcys nobilis (Insecta : Plecoptera), the collectors Stenonema spp. (a complex of species including S. fuscum, S. tripunctatum, and S. canadense) were begun.

1971 - 1972

Primary emphasis was directed toward feeding and growth of the shredders and their dependence upon, and processing rate of, leaf litter. Field studies were conducted using leaf packs - accumulations of leaf litter lashed loosely together, fastened to bricks and placed in the stream facing into the current so as to simulate natural aggregations of leaves at the leading edges of obstructions in the stream. The role of the shredders in processing leaf litter in streams was demonstrated and the importance of leaf species in determining rates of processing, mediated through the microbial populations on the leaves, was established.

Field sampling was initiated in which the standing crop of the macroinvertebrates and the standing crop of detritus were measured simultaneously. Detritus collected, using either a 900 cm² or a 300 cm² sampler (Cummins, 1972; Boling et al., 1974), was fractioned into six particle size categories (Boling et al., 1974) representing fractions shown to be of ecological importance -- i.e. either general food or fecal categories.

Experiments on leaf litter utilization were initiated in two large (11 meters long, 1.5 meters wide and 0.3 meters deep) artificial stream channels. The processing capacity of such systems for dissolved organic matter derived from leaf litter and the effects of this leachate on the macroinvertebrates was also investigated (Cummins et al., 1972).

1972 - 1973

Data were gathered and synthesized in two general areas: specific field and laboratory measurements of population parameters such as density (survivorship), feeding, growth and respiration of representative macroconsumers in each functional group (Fig. 1); and, overall aspects of the role played by macroconsumer populations in particulate organic matter processing in streams (Cummins et al., 1973; Cummins, 1973a). Relative growth rates (mg/mg/day) and consumption indices (mg consumed/mg individual/day) were determined for several species (Cummins et al., 1973) and it was shown that the presence of shredders (e.g. Tipula) enhanced the growth of collectors (e.g. Stenonema).

A cooperative effort with members of the Systems Science group at Michigan State was initiated directed at converting the conceptual model of detritus processing to a more formal mathematical model. Particular attention was focused on detrital food quality, quality being defined as degree of conditioning, that is, the density (and activity) of the detrital microbial flora. As a first approximation, conditioning was equated with microbial respiration associated with the detritus (as measured in the Gilson differential respirometer).

As an aid to exchange with other stream ecologists, particularly those engaged in research projects related to detrital processing, a World Wide Directory of Stream Ecologists was prepared and circulated (Cummins, 1973b)

1973 - 1974

The data gathered with AEC support was used to compare freshwater ecosystems, particularly with regard to the processing of detritus (Cummins, 1974a). Also, generalizations relative to stream macroinvertebrates were summarized (Cummins, 1974b). The model of detritus processing, consisting essentially of a two-dimensional array of particle size against conditioning was refined and tested (Boling et al., 1974).

All available data on the macroinvertebrate predator Nigronia serricornis were summarized and integrated (Petersen, 1974). The data support the hypothesis that Nigronia has a three year life cycle with the most dramatic weight increases concentrated during the warm months of the first year.

Initial studies in laboratory culture, the experimental stream channels and Augusta Creek demonstrated that a fruitful approach to further categorizing the functional groups of macroinvertebrates concerns the importance of thermal regimes in controlling growth rates. The period required for the nymphal or larval phase of the life cycle can be described on the basis of cumulated temperature fairly independent of the time interval. Some species exhibit periods of greatly reduced or negligible growth above or below a thermal limit (Stenotherms), but during growth weight increase is closely correlated with cumulated temperature. In a few instances, the data indicate that food quality can moderate or override the basic thermal effect. This opens the possibility that changes in temperature regime can be compensated for by adjustments in food quality (see review in Cummins, 1974c).

TECHNICAL DOCUMENTS AND PUBLICATIONS

Publications

- Cummins, K. W., R. R. Costa, R. E. Rowe, G. A. Moshiri, R. M. Scanlon, and R. K. Zajdel. 1969. Ecological energetics of a natural population of the predaceous zooplankter Leptodora kindtii (Focke) Crustacea:Cladocera). *Oikos*, 20:189-223.
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- Cummins, K. W., M. J. Klug, R. G. Wetzel, R. C. Petersen, K. F. Suberkropp, B. A. Manny, J. C. Wuycheck and F. O. Howard. 1972. Organic enrichment with leaf leachate in experimental lotic ecosystems. BioScience 22:719-722.
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- Cummins, K. W. 1973b. A world wide directory of stream ecologists. Mich. State Univ. Inst. Water Res. Tech. Rept. 28. 67 p.
- Petersen, R. C. and K. W. Cummins. 1974. Leaf processing in a woodland stream. Freshwater Biol., 4, in press.
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Petersen, R. C. 1974. Life history and bionomics of Nigronia serricornis (Say) (Negalloptera:Corydalidae). Ph.D. Dissertation, Michigan State Univ. 210 p.

Technical Documents

<u>Document No.</u>	<u>Date</u>	<u>Document or Publication</u>	<u>Title</u>
COO-2002-1	1969	Progress Report	Energetics of natural populations of the plankton predator <u>Leptodora kindtii</u> (Focke). K. W. Cummins. Progress Report, 136 pp.
COO-2002-2	1970	Publication	Energy budgets. K. W. Cummins. Pp. 31-37 in: An Amer. Assoc. Advancement Science Symposium (Boston, Dec. 29, 1969). Inst. Freshwater Research, Mich. State Univ., Tech. Rept., 7, 42 pp.
COO-2002-3	1970	Manuscript	Energy budgets for the stream caddisfly <u>Glossosoma nigrior</u> (Insecta: Trichoptera: Glossosomatidae). K. W. Cummins, R. C. Peters, J. C. Wuycheck, F. O. Howard and V. I. Holt. 50 pp.
COO-2002-4	1970	Progress Report	Energetics of natural populations of freshwater macroconsumers. K. W. Cummins. Progress Report, 20 pp.
COO-2002-5	1973	Publication	A world wide directory of stream ecologists. K. W. Cummins. Inst. Freshwater Res., Mich. State Univ., Tech. Rept. 28. 67 p.
COO-2002-6	1971	Multilithed paper (distributed from Kellogg Biological Station	An energy budget model for woodland stream ecosystems. K. W. Cummins. 5 pp.
COO-2002-7	1971	Publication	Energy relations in cladoceran populations. K. W. Cummins. Trans. Amer. Micros. Soc. 90:101-102.
COO-2002-8	1971	Publication	Calorific equivalents for studies in ecological energetics. K. W. Cummins and J. C. Wuycheck. Mitt. int. Ver. Limnol. 18:1-158.
COO-2002-9	1972	Publidation	What is a river -- zoological description. pp. 33-52., in: Oglesby, R. T., C. A. Carlson, J. A. McCann (eds.). Ecology and Man. Academic Press, N. Y., 465 pp.

<u>Document No.</u>	<u>Date</u>	<u>Document or Publication</u>	<u>Title</u>
COO-2002-10	1971	Progress Report	Energetics of natural populations of freshwater macroconsumers. K. W. Cummins. Progress Report, 36 pp.
COO-2002-11	1972	Publication	Organic enrichment with leaf leachate in experimental lotic ecosystems. K. W. Cummins, M. J. Klug, R. G. Wetzel, R. C. Petersen, K. F. Suberkropp, B. A. Manny, J. C. Wuycheck, and F. O. Howard. BioScience, 22:719-722.
COO-2002-12	1972	Publication	Trophic relations of aquatic insects. K. W. Cummins, Ann. Rev. Ent., 18:183-206.
COO-2002-13	1973	Publication	The utilization of leaf litter by stream detritivores. K. W. Cummins, R. C. Petersen, F. O. Howard, J. C. Wuycheck and V. I. Holt. Ecology, 54:336-345.
COO-2002-14	1973	Publication	Leaf processing in a woodland stream. R. C. Petersen and K. W. Cummins. Freshwater Biology in press.
COO-2002-15	1973	Manuscript	The influence of leaf litter conditioning time on ingestion and growth rates of the stream detritivore <u>Lepidostoma costalis</u> (Trichoptera). K. W. Cummins, D. K. King, G. L. Spengler, and V. I. Holt.
COO-2002-16	1973	Manuscript	The metabolism of microorganisms associated with leaf litter in streams as determined with hickory leaf discs. K. W. Cummins and R. C. Petersen.
COO-2002-17	1973	Manuscript	Respiratory metabolism of the stream caddisfly <u>Glossosoma nigrum</u> Banks (Trichoptera: Glossosomatidae). K. W. Cummins, R. C. Petersen, V. I. Holt and J. C. Wuycheck.
COO-2002-18	1973	Manuscript	Estimates of field density and production of the stream caddisfly <u>Glossosoma nigrum</u> Banks (Trichoptera: Glossosomatidae). K. W. Cummins, J. C. Wuycheck, R. C. Petersen, F. O. Howard and R. H. King.
COO-2002-19	1973	Manuscript	Laboratory determined growth and feeding rates of the stream caddisfly <u>Glossosoma nigrum</u> Banks (Trichoptera: Glossosomatidae). K. W. Cummins, R. C. Petersen, D. K. King, V. I. Holt and L. M. Ewers.

<u>Document No.</u>	<u>Date</u>	<u>Document or Publication</u>	<u>Title</u>
COO-2002-20	1972	Progress Report	Energetics of natural populations of freshwater macroconsumers. K. W. Cummins.
COO-2002-21	1973	Manuscript	A simple bioassay for detrital consumer activity in streams. K. W. Cummins.
COO-2002-22	1973	Progress Report	Energetics of natural populations of freshwater macroconsumers. K. W. Cummins.
COO-2002-23	1974	Progress Report	Energetics of natural populations of freshwater macroconsumers. K. W. Cummins.