GEORGIA INSTITUTE OF TECHNOLOGY
OFFICE OF CONTRACT ADMINISTRATION
SPONSORED PROJECT INITIATION

Date: September 13, 1976

Project Title: Computer Analysis of Methods for Measuring Production of Aquatic Animals

Project No: G-32-633 (continuation of C-10-631)

Project Director: Dr. A.C. Benke

Sponsor: National Science Foundation

Agreement Period: From 9/1/76 Until 6/30/77

Type Agreement: Letter dated 9/1/76

Amount:

$3,066.96	NSF	
2,657.00	GIT	(G-32-317)
$5,723.96	Total	

Reports Required:

Final Report

Sponsor Contact Person (s):

Technical Matters

Dr. J. Thomas Callahan
Assistant Program Director
Ecosystem Analysis Program
Ecology and Systematic Biology Section
Division of Biological and Medical Sciences
National Science Foundation
Washington, D.C.

Contractual Matters (thru OCA)

Mr. F. G. Naughten
Grants Manager, Area 4
National Science Foundation
Washington, D.C. 20550
Phone (202) 632-5965

Defense Priority Rating:

Assigned to: Biology (School/Laboratory)

COPIES TO:

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- Other

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GEORGIA INSTITUTE OF TECHNOLOGY
OFFICE OF CONTRACT ADMINISTRATION

SPONSORED PROJECT TERMINATION

Date: OCTOBER 14, 1977

Project Title: COMPUTER ANALYSIS OF METHODS FOR MEASURING PRODUCTION OF AQUATIC ANIMALS

Project No: G-32-633 (CONTINUATION OF C-10-631)

Project Director: DR. A. C. BENKE

Sponsor: NATIONAL SCIENCE FOUNDATION

Effective Termination Date: 6/30/77 (GRANT EXPIRATION)

Clearance of Accounting Charges: BY 6/30/77

Grant/Contract Closeout Actions Remaining:

- _ Final Invoice and Closing Documents
- X Final Fiscal Report DUE BY 9/30/77.
- _ Final Report of Inventions
- _ Govt. Property Inventory & Related Certificate
- _ Classified Material Certificate
- _ Other ____________

Assigned to: BIOLOGY (School/Laboratory)

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- Project Code (GTRI)
- Other ____________

CA—4 (3/76)

GEORGIA INSTITUTE OF TECHNOLOGY
ATLANTA, GEORGIA 30332

OFFICE OF
THE DIRECTOR OF
FINANCIAL AFFAIRS

October 19, 1977

Division of Grants and Contracts
National Science Foundation
Washington, D. C. 20550

Gentlemen:

Enclosed in triplicate is the final fiscal report for Grant Number BMS75-03151.

If you have any questions or desire additional information, please let us know.

Sincerely yours,

per Evan Crosby
Associate Director of
Financial Affairs

EC/bs
Enclosures as stated
cc: Dr. A. C. Benke
Dr. J. W. Crenshaw
Mr. E. E. Renfro
Mr. A. H. Becker✓
File B-10-631, B-10-318
G-32-633

NATIONAL SCIENCE FOUNDATION
Washington, D.C. 20550

RESEARCH GRANT BUDGET & FISCAL REPORT

Form Approved
Budget Bureau No. 99-R0013

Please read instructions on reverse side carefully before completing this form.

INSTITUTION AND ADDRESS: Georgia Inst. of Tech. Atlanta, Georgia	NSF PROGRAM: Ecosystem Studies	GRANT PERIOD from 1/1/75 to 6/30/77 REPORTING PERIOD from 1/1/75 to 10/5/77*
GRANT NUMBER: BMS75-03151 — BUDGET DUR. (MOS.): 24	PRINCIPAL INVESTIGATOR(S): Benke	GRANTEE ACCOUNT NUMBER: B-10-631, G-32-633

	NSF Funded Man Months Cal.	Acad.	Summ.	NSF AWARD BUDGET	CUMULATIVE GRANT EXPENDITURES *Do Not Round*
A. SALARIES AND WAGES					
1. Senior Personnel					
a. 1 (Co)Principal Investigator(s)		1	2	$ 4,700	
b. Faculty Associates					
Sub-Total				$ 4,700	$ 4,700.00
2. Other Personnel (Non-Faculty)					
a. 1 Research Associates—Postdoctoral	2			2,000	
b. Non-Faculty Professionals					
c. 1 Graduate Students				4,400	
d. Pre-Baccalaureate Students					
e. Secretarial—Clerical					
f. 1 Technical, Shop, and Other				325	
TOTAL SALARIES AND WAGES				$ 11,425	$ 11,622.98
B. STAFF BENEFITS IF CHARGED AS DIRECT COST				413	422.76
C. TOTAL SALARIES, WAGES, AND STAFF BENEFITS (A + B)				$ 11,838	$ 12,045.74
D. PERMANENT EQUIPMENT					
As In Revised Proposal Budget				1,100	1,070.00
E. EXPENDABLE EQUIPMENT AND SUPPLIES				500	809.93
F. TRAVEL 1. DOMESTIC (INCLUDING CANADA)				2,100	1,299.18
2. FOREIGN					
G. PUBLICATION COSTS				500	111.40
H. COMPUTER COSTS IF CHARGED AS DIRECT COST				1,500	1,520.00
I. OTHER DIRECT COSTS					201.70
J. TOTAL DIRECT COSTS (C through I)				$ 17,538	$ 17,057.95
K. INDIRECT COSTS 65% of Salaries & Wages — 65% of $2,324.97=$1,511.23; 68% of $9,298.01= 6,322.65; $11,622.98=$7,833.88				7,426	7,833.88
L. TOTAL COSTS (J plus K)				$ 24,964	$ 24,891.83
M. AMOUNT OF THIS AWARD (ROUNDED)				$ 25,000	
N. CUMULATIVE GRANT AMOUNT				$ 25,000	
O. UNEXPENDED BALANCE (N. BUDGET MINUS L. EXPENDITURE)					$ 108.17

REMARKS: Use extra sheet if necessary

*No Obligations were incurred outside the grant period of 1/1/75 to 6/30/77

FOR NSF USE ONLY
Final Fiscal Report Accepted

Grant Closed ______ Remains Open ______
By ______ Date ______
Grants Administration Section, Area ______

SIGNATURE OF PRINCIPAL INVESTIGATOR	TYPED OR PRINTED NAME	DATE
	A. C. Benke	10/17/77

I CERTIFY THAT ALL EXPENDITURES REPORTED ARE FOR APPROPRIATE PURPOSES AND IN ACCORDANCE WITH THE AGREEMENTS SET FORTH IN THE APPLICATION AND AWARD DOCUMENTS

SIGNATURE OF AUTHORIZED OFFICIAL	TYPED OR PRINTED NAME & TITLE	DATE
for	Evan Crosby, Associate Director of Financial Affairs	10/19/77

FOR NSF USE ONLY

Organ. Code	F.Y.	Fund ID	Prog. Code	Ob. Class	O/Dres.	Award No.	Amd.	Inst. Code	Unexpended Balance	Trans.	Lot
									$		

NATIONAL SCIENCE FOUNDATION
Washington, D.C. 20550

SUMMARY OF COMPLETED PROJECT

Form Approved
OMB No. 99R0013

Please read instructions on reverse carefully before completing this form.

1. INSTITUTION AND ADDRESS		2. NSF PROGRAM	3. GRANT PERIOD
Georgia Institute of Technology Atlanta, Georgia 30332		Ecosystem Analysis	1/1/75 to 6/30/77 from to
4. GRANT NUMBER BMS75-03151	5. BUDGET DUR. (MOS) 24	6. PRINCIPAL INVESTIGATOR(S) Arthur C. Benke	7. GRANTEE ACCOUNT NUMBER

8. SUMMARY (Attach list of publications to form)

The objective of this project was to test, with computer simulations, the accuracy of current methods used in measuring production of aquatic invertebrates. It was our thesis that these methods (Instantaneous growth, removal-summation, Allen curves, and Hynes) under certain conditions will greatly underestimate actual production.

A computer program was developed using a compartment model in which discrete size classes (instars) of a population were represented by a set of differential equations. For each simulation, we were able to specify growth and mortality for each instar, as well as degree of synchrony in the recruitment pattern. For any simulation, the actual production value could be directly determined as an accumulation within a separate compartment. The population was sampled at regular intervals during each simulation, so that the sample data could be utilized in each of the current field methods. This estimate could then be compared with actual production.

All methods were reasonably accurate when recruitment occurred over a 7-day interval, mortality was constant among instars, and animals spent the same amount of time in each instar. Each method tended to produce greater underestimates as recruitment time increased (development became less synchronous), as relative mortality among early instars increased, and when animals spent more time in later instars. Actual production values were often twice as much as estimated values. Although each method usually produced underestimates, the removal-summation method seemed to be the most accurate.

The results of the simulations may help explain why these direct methods usually produce much lower estimates than indirect methods based upon the amount of food required to feed their fish predators. Our results suggest that we need to modify our direct methods to account for potential sources of error, and we are currently exploring such possibilities. By increasing our accuracy in estimating animal production, it improves our ability in evaluating the role of consumers in the energy and material balance of natural ecosystems.

9. SIGNATURE OF PRINCIPAL INVESTIGATOR/ PROJECT DIRECTOR	TYPED OR PRINTED NAME	DATE
	Arthur C. Benke	9/30/77

NSF Form 98A (5-76)

PUBLICATIONS:

1. Benke, A.C. and J.B. Waide. 1977. In defence of average cohorts. Freshwater Biology 7:61-63. (copies attached)

2. Waide, J.B., and A.C. Benke. 1977. A discrete instar model for simulating cohort growth, survivorship and production (in preparation).

3. Benke, A.C., and J.B. Waide. 1977. Analysis of Production/Biomass ratios and field methods for estimating secondary production using computer simulations (in preparation).

FINAL TECHNICAL LETTER REPORT

to the

NATIONAL SCIENCE FOUNDATION

ECOSYSTEM ANALYSIS PROGRAM

INSTITUTION: Georgia Institute of Technology

PRINCIPAL INVESTIGATOR: Arthur C. Benke

GRANT NO. BMS75-03151

STARTING DATE: 1-1-75

COMPLETION DATE: 6-30-77

GRANT TITLE: Computer Analysis of Methods for Measuring Production of Aquatic Animals

SCIENTIFIC SUMMARY:

The objective of this project was to test, with computer simulations, the accuracy of current methods used in measuring production of aquatic invertebrates. It was our thesis that these methods (instantaneous growth, removal-summation, Allen curves, and Hynes) under certain conditions will greatly underestimate production.

A computer program was developed using a compartment model in which discrete size classes (instars) of a population were represented by a set of differential equations. For each simulation, we were able to specify growth and mortality for each instar, as well as degree of synchrony in the recruitment pattern. For any simulation, the actual production value could be directly determined as an accumulation within a separate compartment. The population was sampled at regular intervals during each simulation, so that the sample data could be utilized in each of the field methods. These estimates could be compared for accuracy with the actual production.

Most of the simulations were for an 8-instar population. Recruitment into the first instar approximated the positive half of a sine curve, and totaled 10,000 individuals for all simulations. The interval of recruitment was either 7 days, 56 days or 112 days. Three different growth patterns were utilized: one in which individuals spent equal amounts of time in each instar, and others in which the amount of time increased by a factor of 1.2 and 1.4, respectively. Six basic mortality patterns were tried in the simulations, beginning with constant mortality for all instars, and using various combinations of high and low mortality in early or late instars. Finally, percent emergence was set at either 1% or 5%.

All methods were reasonably accurate when recruitment occurred over a 7-day interval, mortality was constant, and animals spent an equal amount of time in each instar. Each method tended to produce greater underestimates as recruitment time increased (i.e., development became less synchronous), as relative mortality among early instars increased, and when animals spent more time in later instars. Underestimates were worse at 1% emergence than at 5%. The poorest estimates were often only half of actual production. Although each method usually produced underestimates, the removal-summation method seemed to be the most consistently accurate. Detailed tables of simulation results are presented in the papers prepared for publication.

The major source of error in the methods appeared to be that the apparent survivorship curve (i.e., a plot of total density against time) was assumed to approximate the actual survivorship curve (probability of an individual surviving to a given instar). Under certain conditions the difference between the two became quite large. Thus, one approach to improving accuracy of the methods would be to correct the survivorship curve. We are currently exploring this and other means of improving the methods.

The results of our simulations suggest that until improved methods are developed, we should recognize that results produced by any of the current methods are probably giving an underestimate, particularly if recruitment is

not well synchronized. Furthermore, our results may help explain why these direct methods usually produce much lower estimates than indirect methods based upon the amount of food required to feed their fish predators, a phenomenon known as the "Allen paradox."

PUBLICATIONS:

1. Benke, A.C. and J.B. Waide. 1977. In defence of average cohorts. Freshwater Biology 7:61-63. (copies attached)

2. Waide, J.B., and A.C. Benke. 1977. A discrete instar model for simulating cohort growth, survivorship and production (in preparation).

3. Benke, A.C., and J.B. Waide. 1977. Analysis of Production/Biomass ratios and field methods for estimating secondary production using computer simulations (in preparation).

THESES (supported in part by NSF funds):

1. Van Arsdall, T.C., Jr. 1977. Production and colonization of the snag habitat in a southeastern blackwater river (M.S. thesis, School of Biology, Georgia Institute of Technology).

2. Hunter, R.J. 1977. Invertebrate drift of the Satilla River (M.S. thesis in preparation, School of Biology, Georgia Institute of Technology).

SCIENTIFIC COLLABORATORS:

1. Jack B. Waide, Assistant Professor, Department of Zoology, Clemson University

2. Robert Hunter, graduate student

3. Thomas Van Arsdall, graduate student

Respectfully submitted,

Date 30 Sept. 1977

Arthur C. Benke
Principal Investigator

Freshwater Biology (1977) 7, 61–63

In defence of average cohorts

ARTHUR C. BENKE and JACK B. WAIDE School of Biology,
Georgia Institute of Technology, and Institute of Ecology, University of Georgia, U.S.A.

SUMMARY. Hynes & Coleman (1968) proposed a method for estimating benthic secondary production for use with populations in which cohorts cannot be distinguished and for use with unidentified benthos. Hamilton (1969) corrected and refined the method, emphasizing the concept of the average cohort. Zwick (1975) recently suggested the method should not be used since: (1) too many conditions need to be filled for use with unidentified material, and (2) it is strongly dependent on growth patterns. This paper shows that Zwick misinterpreted the concept of the average cohort, and his apparent invalidation of the method due to dependence on growth patterns is erroneous.

Introduction

Considerable interest has developed recently in measuring the production of freshwater benthos directly from field data. The most popular methods (instantaneous growth, Allen curve, and removal-summation) can be applied only to populations in which cohorts can be recognized. However, for many benthic species, cohorts are difficult to distinguish and these methods are useless. Therefore, when Hynes & Coleman (1968) proposed a method to be used with populations in which cohorts cannot be distinguished and which can be applied to the entire (unidentified) benthos, it aroused much interest. The basis of the 'Hynes' method is that the size frequency distribution averaged over a year is assumed to be equivalent to an 'average' cohort. Hamilton (1969) was soon to point out two errors in the method, the most important change being that one needs to multiply the production of the average cohort by the number of size classes present to obtain annual production.

Correspondence: Dr A. C. Benke, School of Biology, Georgia Institute of Technology, Atlanta, Georgia 30332, U.S.A.

Hamilton also described how to correct for nonlinear growth and evaluated other sources of error. His paper now serves as the model from which others have used the method.

Much debate has naturally arisen over the reliability of this new method. Fager (1969) was the first to criticize the approach as being strongly dependent on the number of samples and on the pattern of growth and suggested that it should not be used. Hamilton (1969) successfully demonstrated that Fager's resulting discrepancies were due to his modifying the Hynes method rather than any basic errors in logic. Waters & Crawford (1973) compared results obtained using four different methods (Hynes, Allen curve, removal-summation, and instantaneous growth) on the same field data collected for a stream mayfly in which the cohort could be distinguished. They found good agreement among all methods, with the Hynes estimate about 20% higher than the others.

More recently, Zwick (1975) has renewed the attack on the Hynes method. He claims that the method is unsuitable for two major reasons: (1) too many conditions need to be filled for the method to be applicable to unidentified benthos, and (2) it is strongly dependent on growth patterns. Apparently, many freshwater ecologists share Zwick's scepticism over the first reason and have limited their use of the method to single species (e.g., Waters & Crawford, 1973; Winterbourne, 1974; McClure & Stewart, 1976; Martien & Benke, 1977). The most notable exception is the work of Fisher & Likens (1973). It is not the purpose of this note to support or defend the use of the method for mixed species estimates, but rather to defend the concept of the average cohort and its use for single species. We wish to point out an error in Zwick's calculations that makes his apparent invalidation of the Hynes method erroneous.

Discussion

To illustrate how nonlinear growth supposedly results in serious error, Zwick re-examined Hamilton's Table 4A–E, specifically Table 4D, which is reproduced here as Table 1 (Zwick's Table 2). There are three size (i.e. length) classes represented, each class including all organisms falling within 0.5 mm of the median length of the class. Ten samples are taken at

TABLE 1. (Table 2 from Zwick 1975): for explanation see text

Length class (L_i)	Sampling interval											
	6	7	8	9	10	1	2	3	4	5	$\bar{n}$	n_g
1	25	20									4.5	7.49
2			10	9		7	6	4	2		3.8	2.11
3									1	1	0.2	0.33

equal intervals over a year. The average size frequency distribution represented by the $\bar{n}$ column is assumed to represent an *average cohort*, where the number of such average cohorts is equal to 3, the number of size classes. The rationale for determining an average cohort is the same as that used in constructing a time-specific life table (Southwood, 1966), except that instead of determining age (or size) distribution at one point in time, it is an average over an entire generation (assuming univoltinism).

Production is calculated from the formula

$$P = 3\left[(\bar{n}_1 - \bar{n}_2)\left(\frac{L_1 + L_2}{2}\right)^3 + (\bar{n}_2 - \bar{n}_3)\left(\frac{L_2 + L_3}{2}\right)^3 + \bar{n}_3(L_3^*)^3\right],$$

where the $\bar{n}_i$ (i = 1,2,3) are taken from Table 1, the L_i are the median lengths of each length class and L_3^* is the maximum length of length class 3 (or 3.5), since the surviving individuals are assumed to grow to the maximum size. Zwick incorrectly thought that Hamilton made an error using 3.5, believing that it was an average of L_3 and L_4 (which does not exist), but this was not his major source of concern.

From Table 1, the $\bar{n}$ calculations assume linear growth, or an equal amount of time spent in each size class. Hamilton's n_g column is a corrected average cohort derived from $\bar{n}$ and taking into account unequal amounts of time spent in size classes. The values of the $\bar{n}$ and n_g columns of Table 1 are then substituted into the above equation, yielding estimates of the production of the population under consideration. For the case we are considering here, production calculated from $\bar{n}$ is

TABLE 2. (In part from Table 3 of Zwick, 1975). Production of five model populations (Table 4A–E of Hamilton, 1969) calculated in four different ways

Population	Annual production in volume units			
	Calculation from n_g	Calculation from $\bar{n}$	Zwick's calculation	Actual cohort calculation
A	119.94	140.91	339.9	113.3
B	119.10	131.07	317.7	105.9
C	80.07	81.99	239.7	79.9
D	180.66	201.36	484.4	161.3
E	150.75	129.42	446.7	148.9

201.36 volume units, while it is 180.66 using the values of n_g.

Zwick's invalidation of the method is based upon direct calculation of production from the single cohort plotted in Table 1. He noted the losses as five specimens of class 1; ten specimens between classes 1 and 2; eight specimens of class 2; one specimen between classes 2 and 3; and one specimen survives. Converting to volume and summing yields 161.3 volume units. For some unexplained reason, Zwick incorrectly considered this actual cohort to be an average cohort and he multiplied this production value by 3. His results were then displayed with Hamilton's values for the five model populations (Table 2). Since his values were much larger than Hamilton's, he then concluded that nonlinear growth results in large errors. Hamilton clearly did not intend his actual cohort to be the average cohort. The average cohort is represented by the $\bar{n}$ or n_g column in the Table. The correct actual cohort values (not multiplied by 3) are presented in the fourth column of Table 2, and their correspondence to the n_g values is particularly striking. Even the values estimated from $\bar{n}$ are within 25% error. Thus, Zwick's exercise done correctly supports rather than refutes the claim by Hamilton that the results do not strongly depend on growth pattern. This is especially true since Hynes and Coleman (1968) and Hamilton (1969) only intended the method to provide rough approximations.

The Hynes method will continue to remain a controversial method for various reasons, particularly due to the question of generation time and the validity of combining all benthic invertebrate species for one estimate. We suspect the latter will be resolved by combining closely related species rather than all species and then summing the calculations for the separate groups. Another more subtle reason why inaccuracies may occur in the Hynes method, as well as other methods, is that age distributions determined directly from field data may not accurately reflect the true survivorship of a cohort. We are currently investigating the magnitude of errors caused by such subtle reasons using computer simulations of hypothetical populations. However, neither Fager (1969) nor Zwick (1975) have presented a valid reason for rejecting the method based upon non-linear growth.

Acknowledgments

We thank Drs Andrew L. Hamilton and Thomas F. Waters for reading the manuscript and for helpful discussions. Our investigations on this subject are supported by grant BMS75-03151 from the National Science Foundation.

References

Fager E.W. (1969) Production of stream benthos: A critique of the method of assessment proposed by Hynes and Coleman (1968). *Limnol. Oceanogr.*, 14, 766–770.

Fisher S.G. & Likens G.E. (1973) Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. *Ecol. Monogr.*, 43, 421–439.

Hamilton A.L. (1969) On estimating annual production. *Limnol. Oceanogr.*, 14, 771–782.

Hynes H.B.N. & Coleman M.J. (1968) A simple method of assessing the annual production of stream benthos. *Limnol. Oceanogr.*, 13, 569–573.

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McClure R.G. & Stewart K.W. (1976) Life cycle and production of the mayfly *Choroterpes (Neochoroterpes) mexicanus* Allen (Ephemeroptera: Leptophlebiidae). *Ann. Entomol. Soc. Amer.*, 69, 134–144.

Southwood T.R.E. (1966) *Ecological Methods.* Methuen, London.

Waters T.F. & Crawford G.W. (1973) Annual production of a stream mayfly population: a comparison of methods. *Limnol. Oceanogr.*, 18, 286–296.

Winterbourne M.J. (1974) The life histories, trophic relations and production of *Stenoperla prasina* (Plecoptera) and *Deleatidium* sp. (Ephemeroptera) in a New Zealand river. *Freshwat. Biol.*, 4, 507–524.

Zwick P. (1975) Critical notes on a proposed method to estimate production. *Freshwat. Biol.*, 5, 65–70.

(Manuscript accepted 1 September 1976)