esf STATE UNIVERSITY OF NEW YORK

COLLEGE OF ENVIRONMENTAL SCIENCE AND FORESTRY

SYRACUSE CAMPUS
SYRACUSE, NEW YORK 13210

SYRACUSE CAMPUS
SYRACUSE, N. Y. 13210
Schools of:
- Biology, Chemistry, & Ecology
- Continuing Education
- Environmental and Resource Engineering
- Environmental and Resource Management
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Applied Forestry Research Institute
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Institute of Environmental Program Affairs
State University Polymer Research Center
U.S. Forest Service Cooperative Research Unit

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CRANBERRY LAKE, N. Y. 12927
Charles Lathrop Pack Demonstration Forest
Cranberry Lake Biological Station

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Archer & Anna Huntington Wildlife Forest
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Forest Technician Program

WARRENSBURG CAMPUS
WARRENSBURG, N. Y. 12885
Charles Lathrop Pack Demonstration Forest
Summer Field Program

December 5, 1978

Dr. Robert J. Behnke
Colorado Cooperative Fishery Unit
Colorado State University
Fort Collins, Colorado 80521

Dear Dr. Behnke:

I am writing to inform you that Larry Zuckerman has not yet completed his master's thesis. This has developed into a larger project than either of us had envisioned; it also lagged a bit because of Larry's need to work 40 hr/wk to support himself this term. I have read parts of the thesis and would say it could be a publishable document, certainly of interest beyond upstate New York. As I have explained to Larry, I am willing to have him leave for Colorado as scheduled. However, this might not be an ideal situation either for him or for you. Unless his not entering would disrupt your program, I hope you will consider holding his admission until Fall 1979. I believe he plans to come to Fort Collins by early summer, perhaps to establish some kind of employment. Larry has had several quite original ideas during the preparation of his thesis. He still has some growing up to do, but I will miss his intellectual input to our program--I think he will be worth waiting for.

Enclosed are some items (in press) that may help indicate the direction of our program, particularly for prospective graduate students interested in fish ecology. Surprisingly, Upstate New York possesses a rich fish fauna, and the opportunities for study of stream communities ~~is~~ are excellent. Naturalized population of Pacific salmon and other salmonids provide more ecological material than I can handle; we also have access to centrarchid populations in the Adirondack study lakes, which are ideal in tests of resource partitioning.

If it sounds like I am "pushing" our program--I am! This seemed to be an opportunity to advertise a bit--evidently most students envision NY state (as I did) as a huge city; actually I can think of few places whose aquatic resources surpass those of

ESTABLISHED IN 1911 TO ADVANCE ENVIRONMENTAL SCIENCE AND FORESTRY THROUGH
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upstate New York. So--if you have any solid prospects, please send them along. Also, feel free to call or write if Larry's delay will cause a problem--I can be flexible. My phone number is (315) 473-8619.

Sincerely,

Neil H. Ringler

Neil H. Ringler
Assistant Professor

NHR:rtp

Neil H. Ringler

IMPORTANT: CAREFULLY READ THE INSTRUCTIONS BEFORE COMPLETING THIS FORM.

SUNY / RESEARCH FOUNDATION APPLICATION

FORWARD ORIGINAL AND TWO PHOTOCOPIES
TO UNIVERSITY AWARDS COMMITTEE

F365-478

- FOR COMMITTEE USE ONLY -			
REVIEWER		SUB-COMMITTEE CHAIRMAN	
CONTROL NO.		PROGRAM CYCLE	YEAR

1. ENTER REVIEW DISCIPLINE USING LISTING ON OPPOSITE PAGE

NAME	NUMBER	CHART OF ACCTS.
Zoology	40	

2. PLEASE CHECK ONLY ONE OF THE FOLLOWING TYPES OF AWARDS:

		AMOUNT REQUESTED
☐ PROGRAM 1	FACULTY RESEARCH FELLOWSHIP*	$
☒ PROGRAM 2	GRANT-IN-AID	$ 3783.00
☐ PROGRAM 3	FACULTY RESEARCH FELLOWSHIP* AND GRANT-IN-AID	$

*PROGRAM SUPPORT AND FINAL FORMAT FUNDING LEVELS CONTINGENT ON BUDGETARY APPROPRIATION AND FURTHER SUBJECT TO JOINT AWARDS COUNCIL DETERMINATIONS

3. ☒ DR. ☐ MR. ☐ MISS ☐ MRS. ☐ MS.

4. SOCIAL SECURITY NUMBER 569-60-5194

5. PRINCIPAL INVESTIGATOR (LAST, FIRST, MIDDLE INITIAL)
Ringler, Neil H.

6. ACADEMIC TITLE
Assistant Professor

7. DEPARTMENT
Environmental and Forest Biology

8. CAMPUS NAME AND ADDRESS
S.U.N.Y. College of Environmental Science & Forestry, Syracuse, N.Y. 13210

9. HOME ADDRESS

STREET	CITY & STATE	ZIP CODE
18 Getman Drive	Baldwinsville, New York	13027

10. DEGREES HELD

	INSTITUTION	YEAR
B.A.	California State University at Long Beach	1967
M.S.	Oregon State University	1970
Ph.D.	University of Michigan	1975

11. PROFESSIONAL POSITIONS HELD BY PRINCIPAL INVESTIGATOR

	DATES
Assistant Professor (S.U.N.Y.)	Sept. 1975 - Present

12. IS THIS YOUR FIRST UAC APPLICATION? ☐ YES ☒ NO

13. THIS PROJECT WILL BE CONDUCTED ☒ ON-CAMPUS ☐ OFF-CAMPUS ☐ BOTH

14. DOES THE RESEARCH SET FORTH IN THIS APPLICATION INVOLVE HUMAN SUBJECTS?
☐ YES ☒ NO
IF "YES," OFFICIAL SIGNATURE IS REQUIRED IN ITEM 33 TO INDICATE CAMPUS CERTIFICATION.

15. IF THIS PROJECT IS TO BE EXECUTED IN COOPERATION WITH OTHER INVESTIGATORS, SUBMITTING SEPARATE APPLICATIONS, LIST THEIR NAMES, CAMPUSES, AND SOCIAL SECURITY NUMBERS.
N.A.

16. TITLE OF PROJECT (MUST NOT EXCEED 60 DIGITS, INCLUDING SPACES AND PUNCTUATION):
Prey selection by non-visual fishes

- TO BE COMPLETED BY THE COMMITTEE -			AWARD	CLASS
☐ ONE SET OF ATTACHMENTS	☐ ATTACHMENTS TO BE RETURNED	ATTACHMENTS CONSIST OF		

CUT
CUT
CUT

17. BRIEF SUMMARY OF PROJECT, INCLUDING OBJECTIVES, SIGNIFICANCE, AND GENERAL PROCEDURES (LIMIT TO THIS SPACE).

Optimal foraging theory has provided a framework for predicting responses to prey that should be adaptive. In contrast to other vertebrate groups, however, few kinds of fishes have been examined to test these model predictions. Furthermore, available models are restricted to visual predators, despite the potential role of other sensory modalities (acoustico-lateralis, tactile, gustatory, olfactory). A fundamental knowledge of predation processes, for both visual and non-visual feeders, is essential in predicting the consequences of perturbation of aquatic systems.

This project would examine prey selection by two species of presumed olfactory/gustatory feeders held in a simulated stream. Direct observation of behaviors would be tape-recorded from an electronic organ and decoded by computer. Immediate objectives are to examine the role of prey size, distribution, and abundance in the selection of food by non-visual feeders, and to compare the "rules" of prey selection with those known in sight-feeders. Future work would examine responses of visual and non-visual predators to shifts in environmental complexity and resource availability. The proposed research complements field analyses of predation, resource partitioning, and competition being carried out under natural conditions.

18. PROPOSED BUDGET

IF YOU ARE APPLYING FOR A FACULTY RESEARCH FELLOWSHIP UNDER PROGRAM 1, ENTER STIPEND REQUESTED. IF YOU ARE APPLYING FOR A GRANT-IN-AID UNDER PROGRAM 2, ITEMIZE ALL BUDGET ENTRIES AND EXPLAIN IN DETAIL. IF YOU ARE APPLYING FOR A COMBINATION OF A FACULTY RESEARCH FELLOWSHIP AND A GRANT-IN-AID UNDER PROGRAM 3, ENTER BOTH STIPEND REQUESTED AND ITEMIZE AND EXPLAIN BUDGET IN DETAIL. FOR EXAMPLE, IN THE PAYROLL CATEGORY, EXPLAIN THE ROLE OF EACH INDIVIDUAL (INCLUDING STUDENTS) IN THE PROJECT AND SPECIFY THE PERIOD OF EMPLOYMENT OF EACH; IN SUPPLIES AND EQUIPMENT, JUSTIFY ALL ITEMS EXCEEDING $100.00; AND IN TRAVEL, CLEARLY EXPLAIN THE NECESSITY FOR ANY FUNDS REQUESTED AS WELL AS THE BASIS FOR YOUR CALCULATION OF THE SPECIFIED AMOUNT. **FAILURE TO EXPLAIN BUDGET ENTRIES IN DETAIL FOR A GRANT-IN-AID UNDER EITHER PROGRAM 2 OR PROGRAM 3 MAY RESULT IN THEIR AUTOMATIC DELETION.**

STIPEND (APPLICABLE ONLY UNDER PROGRAMS 1 AND 3) PROGRAM SUPPORT AND FINAL FORMAT FUNDING LEVELS CONTINGENT ON BUDGETARY APPROPRIATION AND FURTHER SUBJECT TO JOINT AWARDS COUNCIL DETERMINATIONS		$
SALARY & WAGES (SPECIFY SALARIES AND FRINGE BENEFITS, THIS CATEGORY NOT TO INCLUDE THOSE FOR APPLICANT.) *Salary for one grad. student training in behavior analysis Fall 1979-Spring 1980*	S & W - GRADUATE STUDENTS INDICATE # OF STUDENTS	$ 400.00
	S & W - UNDERGRADUATE STUDENTS INDICATE # OF STUDENTS	$
	S & W - OTHER	$
	TOTAL SALARIES	$ 400.00
NOTE: Fringe Benefits are to be calculated on all salaries except those for graduate students.	TOTAL FRINGE BENEFITS AT CURRENT COST RATE	$
CONSULTANT SERVICES		$
TRAVEL (ITEMIZE TRAVEL, FOOD, LODGING, ETC.) *(Fish collection trips)* ☐ FOREIGN ☒ DOMESTIC *6 trips x 125 mi x 0.13¢/mi*		$ 98.00
CONSUMABLE SUPPLIES *Motion picture film; video tape; fish food*		$ 450.00
EQUIPMENT *Electronic behavior recorder; computer-recorder interface; plexiglas viewing chamber; immersion cooler; circulation pump*		$ 2,635.00
MISCELLANEOUS *Computer time*		$ 200.00
	GRAND TOTAL REQUESTED	$ 3,783.00

Question 27

Project Description: Prey Selection by Non-Visual Feeders

Introduction

Predator-prey relationships in fish communities have been studied for more than a century, but the details of prey selection are unknown for most of the 20,000 species of fishes (Ringler 1978a). Optimal foraging theory (Schoener 1971; Pyke 1977) has provided a framework for predicting responses to prey that should be adaptive. In contrast to other vertebrate groups, however, only two fish species (bluegill sunfish: Werner and Hall 1974; brown trout: Ringler 1975, 1978b) have been examined to test these model predictions. Furthermore, available models are restricted to visual predators, despite a rich literature on the potential role of other sensory modalities (acoustico-lateralis, tactile, gustatory, and olfactory).

Studies that address the interrelationships of sensory physiology, behavior, and trophic ecology (e.g. Miller 1978) provide a fruitful field of research in basic biology. From a pragmatic standpoint, an understanding of these interrelationships would appear essential in predicting the consequences of perturbation of aquatic systems. For example, the consequences of environmental change depend, in part, on the sensory mode(s) employed in detecting and locating prey. Some kinds of change (e.g. increased turbidity) may be expected to select for non-visual feeders, and prediction of such shifts in community structure would be of real value.

Even for visual predators a lack of information on how spatial and temporal variation in prey abundance affect predation rates has been recognized as a bottleneck in developing models of population and community stability (Murdoch and Oaten 1975). A recent study in a simulated stream (Ringler 1975, 1978b) showed that trout altered the area (depth) searched in response to prey density. Size-selective predation approximately tripled energy intake relative to random feeding, although several days and hundreds of encounters were required to learn the appropriate responses. Disproportionate predation on an abundant prey type ("switching") was a temporary phenomenon,

7. (16) Complete the following table based on your knowledge of life histories.

Species	Spawning time (season)	Nest (redd) type, if any	Time of fry emergence or leaving nest (season)	Feeding habits (adults)	Structure useful in aging	Secondary sex characters of ♂♂
Semotilus atromaculatus						
American eel						
White sucker						
Official N.Y. State Fish						
Lepomis gibbosus						
I. nebulosus						
Cutlips minnow						
Oncorhynchus kisutch						

which was evidently masked by the effect of prey size during most of the experimental period. Brown trout ultimately achieved 54-91% of an hypothetical diet in which prey are ranked in order of energy content. Deviations from an optimal diet were explained in terms of a feeding strategy that deals with heterogeneous distribution of prey, as well as with the behavior capabilities of the predator.

Current work, pursued under a UAC grant, is revealing details of the predation process that had been little recognized by aquatic ecologists. Brown trout apparently have individual "tastes" in their diet selection (Ringler 1978c), so that fish may reject a prey type that is preferred by another individual. Such tastes appear to persist for at least three weeks and can markedly alter energy intake. Furthermore, short-term reversals in diet selection of trout are now evident, suggesting that motivational changes associated with distasteful prey may be comparable to those recently discovered in sticklebacks by Thomas (1977).

Individual differences also have become evident in attempts to measure a (hypothetical) threshold of prey density, below which trout responses are either absent or qualitatively different (Ringler and Bradowski 1978). In fact, if such a threshold exists, it may have meaning only at the individual level. Social facilitation of feeding (e.g. Olla and Samet 1974) evidently occurs in brown trout, since observation of one individual feeding reduces the time required for a second fish to attack prey (Ringler and Santapaga 1978). This phenomenon is still under investigation in the laboratory, and we are a long way from understanding its role in nature.

Methods and Objectives of The Project

As elements of the natural environment (e.g. variation in prey palatability, social interactions) have been added to the investigation of brown trout, their flexibility as aquatic predators has become increasingly clear. We can now explore the way in which factors such as turbidity, substrate complexity, or water temperature influence such a visual predator. For species relying heavily on other sensory modes, such as taste or smell, however, the "rules" governing prey selection are unknown.

The proposed research will employ two presumed olfactory/gustatory predators, both of which are stream dwellers equipped with barbels. These fish are the madtoms (Noturus spp.) and the burbot (Lota lota). Madtoms forage principally from stream substrates utilizing barbels (Scott and Crossman 1973), whereas burbot presumably can employ either gustatory or visual cues depending on environmental conditions, as has been described in a marine relative (Brown 1969). Thus, the work provides a logical link with an analysis of brown trout feeding currently in progress.

The experimental facility will be a plexiglass-enclosed stream channel similar to that used for brown trout, but equipped with a variable-velocity control. (Much of the present facility, e.g., holding tanks and filtration apparatus, can serve both projects simultaneously.) Behaviors associated with foraging on bottom particles (e.g. "probe", "tilt", "eat") and responses to drifting prey (e.g. "fixate", "approach", "drift-back") will be encoded with a modified Dawkins (1971) electronic organ whose output is recorded on tape and later decoded by computer. The data are to be analyzed with the aid of techniques described by Slater (1973) and Hazlett (1977) using APL and SPSS routines.

Question 27 (continued)

The immediate objectives of the project are to examine the role of prey size, distribution, and abundance in the selection of food by non-visual predators, and to compare the "rules" of food selection with those known in sight feeders. Future work in the experimental facility would examine responses of visual and non-visual predators to shifts in environmental complexity and resource availability. This would entail analysis of behavioral interactions, including social facilitation and competition. A long-term goal is the development of a flexible model that is applicable to a variety of feeding types, and which can be used in prediction or assessment of perturbations in fish communities.

Context of the Project in an Overall Aquatic Ecology Program

This project complements and supports a broader program in trophic ecology currently in progress in the Department of Environmental and Forest Biology. The feeding ecology of five species of salmonids in the Salmon River system has recently been examined as part of a master's student program (Johnson 1978). Another student (Zuckerman 1978) is completing analysis of resource availability and life history strategies of white suckers in two Adirondack stream-lake systems. A new student (Baldigo) plans to examine resource partitioning between two naturally-occurring sunfish species. These and future studies are being coordinated with those of Dr. Robert Werner, who is studying feeding ecology of redbreast sunfish, distribution and ecology of fish larvae, and ultimately primary production in these same systems. We have obtained Federal funding (U.S. Fish and Wildlife Service) for related work in the St. Lawrence River (Ringler 1977; Werner 1977) and plan to seek state and federal funding for our Adirondack studies during 1979.

The experimental stream and recording facility complements research under natural conditions, permitting detailed analysis of hypotheses difficult or impossible to test in the field.

References

Brown, J. M. 1969. Feeding behavior of cod (Gadus morhua). J. Fish.Res. Board Can. 26:583-596.

Dawkins, R. 1971. A cheap method of recording behavioural events, for direct computer access. Behavior. 40:162-173.

Hazlett, B. A. (ed.) 1977. Quantitative methods in the study of animal behavior. Academic Press, New York. 222 p.

Question 27 (continued)

Johnson, J. H. 1978. Natural reproduction and juvenile ecology of Pacific salmon and steelhead trout in tributaries of the Salmon River, New York. M.S. Thesis, S.U.N.Y., Syracuse.

Miller, R.J. 1978. Feeding mechanisms in fishes as a function of habitat association. Chapter In: Clepper, H. (ed.). Predator-Prey Systems in Fish Communities. Sport Fishing Inst., Washington, D.C. (c. 600 p., available in December).

Murdoch, W. W. and A. Oaten. 1975. Predation and population stability. In: Advances in Ecological Research. 9:1-131. (A. MacFadyen, ed.)

Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. Quart. Rev. Biol. 201:1-18.

Ringler, N. H. 1977. Feeding ecology of fishes in the St. Lawrence River. pp. 91-109. In: Geis, J. W. (ed.). Preliminary Report: Biological characteristics of the St. Lawrence River. S.U.N.Y. College of Environmental Science and Forestry. Inst. of Envir. Progr. Affairs, Syracuse, NY

Ringler, N. H. 1978a. Prey selection by benthic feeders. Chapter In: Clepper, H. (ed.). Predator and Prey Systems in Fish Communities. Sport Fishing Inst., Washington, D.C. (c. 600 p., available in December).

Ringler, N. H. 1978b. Selective predation by drift-feeding brown trout (Salmo trutta). J. Fish. Res. Board Can. (accepted with revisions 9/19/78).

Ringler, N. H. 1978c. Palatability, individual variation and "switching" in brown trout (Salmo trutta). Animal Behav. (In preparation).

Ringler, N. H. and D. Brodowski. 1978. Response thresholds in a drift-feeder. Envir. Biol. Fishes. (In preparation).

Ringler, N. H. and R. Santapaga. 1978. Social facilitation of feeding in brown trout. (Manuscript in preparation).

Schoener, T. W. 1971. Theory of feeding strategies. Annual Review of Ecology and Systematics. 2:369-404.

Scott, W. B. and E. J. Crossman. 1973. Freshwater fishes of Canada. Bull. 184, Fish. Res. Board of Can. 166 p.

Slater, P. J. B. 1973. Describing sequences of behavior. pp. 131-153. In: Bateson, P.P.G. and P. H. Klopfer (eds.). Plenum Press, N.Y. 336 p.

Thomas, G. 1977. The influence of eating and rejecting prey items upon feeding and food searching behavior in Gasterosteus aculeatus L. Anim. Behavior. 25(1):52-66.

Question 27 (continued)

Werner, R. G. 1977. Ichthyoplankton and inshore larval fishes of the St. Lawrence River. pp. 31-60. *In*: Geis, J. W. (ed.). Preliminary Report: Biological Characteristics of the St. Lawrence River. S.U.N.Y. College of Environmental Science and Forestry. Inst. of Envir. Progr. Affairs, Syracuse, N.Y.

Werner, E. E. and D. J. Hall. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). Ecology. 55:1042-1052.

Zuckerman, L. D. 1978. Resource availability and life history strategies of two populations of white suckers (*Catostomus commersoni*). M.S. Thesis in prep., scheduled for completion in December. S.U.N.Y., Syracuse.

Question 28

Biographical Sketch

I was born and raised in Long Beach, California, where I developed an interest in marine biology through direct contact with the Pacific coast, and in aquatic biology through hiking/camping trips to the Sierra Nevada Mountains. I graduated from Lakewood High School and California State University at Long Beach (Biological Science) and moved to Corvallis, Oregon in 1967 to begin a graduate degree program. Following a year of classes there I married Beatrice Nicolen De Mille, and spent a year in the Oregon Coast Range studying the effects of logging on salmon spawning beds. This led to a Master of Science degree (Fisheries) and ultimately to a publication in Transactions of the American Fisheries Society.

Following two years in the U.S. Army Signal Corps, and a tour of duty in Vietnam, I entered the University of Michigan to pursue the Ph.D. This institution was chosen because of its program in aquatic ecology, and also because of the opportunities in teaching, which I had long regarded as a career goal. As a Teaching Fellow in ichthyology, fishery biology, and aquatic entomology I acquired some basic instructional skills, as well as a genuine commitment to this profession. Prior to undertaking dissertation research I participated in an interdisciplinary study of Michigan's Au Sable River, which resulted in several publications and some recommendations for future use that have been implemented. My thesis research, which entailed analysis of feeding behaviors of brown trout from an ecological point of view, provided a nucleus for both teaching and research endeavors at the College of Environmental Science and Forestry.

My present position is a challenging one. I teach population ecology, fishery biology and (alternate summers, at Cranberry Lake Biological Station) ecology of Adirondack fishes. I have also taught ichthyology during a sabbatical leave and share responsibility with Dr. R. G. Werner for conducting an Aquatic Ecology seminar. These courses relate directly to my research interests in aquatic ecology and fisheries, which have been detailed elsewhere in this proposal. I currently have five graduate students pursuing Master's degrees in aquatic ecology and fisheries under my direction.

Aside from career matters, we have had two children, Justin 2½ yrs and Scott 8 mo., since arriving in New York. We have found both upstate New York and the College of Environmental Science and Forestry a productive place in which to live and work.

Neil H. Ringler

STATE UNIVERSITY COLLEGE OF ENVIRONMENTAL
SCIENCE AND FORESTRY
Department of Environmental and Forest Biology

FBL 522 Course Outline N. Ringler
Spring 1978

POPULATION ECOLOGY

I. Description and Analysis of Populations

Lect. No.	Date	
1	1/18/77	Introduction to population ecology
2	1/23	Life tables (Lab: Discussion of research papers)
3	1/25	Intrinsic rates of natural increase (r)
4	1/30	Euler equation for calculation of r; stable and stationary age distributions; relationship of r to body size (Lab: Life tables and calculation of rates of increase)
5	2/1	Birth rates, death rates, and the population consequences of life history phenomena
6	2/6	Population consequences of life history phenomena (continued); development and use of models in ecology (Lab: Logistic model of population growth)
7	2/8	Time lag and stochastic models of population growth
8	2/13	Stochastic models (continued); projection matrices (Lab: Projection matrices) Proj Matrix CONT'D (Horst)
9	2/15	QUIZ ("Study Encourager": 50 points) Lectures 1-7

II. Population Genetics, Natural Selection, and Evolution

Lect. No.	Date	
10	2/20	Fitness and selection coefficients; rates of evolution (Lab: Research paper - topic evaluation)
11	2/22	Rates of evolution (continued); genetic load; individual, kin, and group selection
12	2/27	Evolution of sexual reproduction and sex ratios (Lab: Estimating the size of animal populations)
13	3/1	Survivorship and senescence; reproductive value; life history strategies and tactics
--	3/6	EXAM (150 points) Lectures 1-13
14	3/9	Reproductive strategies and tactics: models of clutch size
--	3/13	SPRING RECESS
--	3/15	SPRING RECESS

III. Regulation and Interaction in Populations

15	3/20	Processes that limit population growth, and their relation to population density (Lab: Tests of density dependence)
16	3/22	The role of behavior in population regulation
17	3/27	Role of behavior in population regulation (continued); oscillations vs. fluctuations in abundance; role of survival and fertility rates in oscillating populations (Lab: Presentation of research papers)
18	3/29	Oscillations in abundance related to time lags, and to predator-prey interactions
19	4/3	Lotka-Volterra model of predator-prey interactions; examples from experimental and natural populations of protozoans, mites, and snails (Lab: Presentation of research papers)
20	4/5	Leslie-Gower model of predator-prey interactions; some sobering realities and considerations for ecologists

Regulation and Interaction in Populations (continued)

Lect. No.	Date	
21	4/10	Role of learning in predation; functional response to prey density; searching images (Tinbergen); individual variation in feeding behavior (Lab: Presentation of research papers)
22	4/12	Profitability hypothesis (Royama)
23	4/17	Experimental components approach (Holling) (Lab: Presentation of research papers)
24	4/19	Experimental components (continued)
25	4/24	Experimental components (continued); optimization models
26	4/26	Optimal foraging and size-selective predation (Werner and Hall; O'Brien, et al.; Pyke et al.; MacArthur and Pianka)
27	5/1	Predation, switching and population stability (Murdoch and Oaten) (Lab: Predation, switching and population stability continued)
		EXAM (200 points)

Required texts:

Pianka, E.R. 1974. Evolutionary Ecology. Harper & Row, N.Y. 356 pp.

Wilson, E.O. and W.H. Bossert. 1971. A Primer of Population Biology. Sinauer Associates, Inc. Sunderland, Massachusetts.

Recommended for grad. students:

Emlen, J.M. 1973. Ecology: An evolutionary approach. Addison Wesley Publishing Co., Reading, Massachusetts. 493 pp.

Additional reading material in the form of dittos, reserve books, and journals will be assigned throughout the course. One of the following texts may prove useful, but their acquisition is entirely optional:

Emmel, T.C. 1976. Population Biology. Harper & Row, N.Y. 371 pp.

Krebs, C.J. 1972. Ecology: The Experimental Analysis of Distribution and Abundance. Harper & Row, N.Y. 694 pp.

McNaughton, S.J. and L.L. Wolf. 1973. General Ecology. Holt, Rinehart, and Winston, Inc., N.Y. 710 pp.

Ricklefs, R.E. 1973. Ecology. Chiron Press, Portland, Oregon. 861 pp.

Wilson, E.O. 1975. Sociobiology. Belknap Press of Harvard University Press. Cambridge, Massachusetts. 697 pp.

Dobzhansky, T., F.J. Ayala, G.L. Stebbins, and J.W. Valentine. 1977. Evolution. W.H. Freeman & Co., San Francisco. 572 pp.

STATE UNIVERSITY COLLEGE OF ENVIRONMENTAL SCIENCE AND FORESTRY

Fishery Biology - FZO 440
4 cr. hr.

Lec. MWF 8:30 - 9:35
Lab. F 1:55 - 4:55

Required Text: Principles of Fishery Science by
Everhart, Eipper and Youngs
Cornell Univ. Press. 1975
(at Orange Book Store)

COURSE OUTLINE
N. Ringler

Sept. 8 F	Introduction to fishery biology LAB: Discussion of field trips and term project

ASPECTS OF THE ASSESSMENT OF FISH POPULATIONS

Sept. 11 M	Biology of selected North American fishes: characteristics and ecological features
13	Biology of *Salvelinus* spp.
15	Biology of *Salmo* spp.
15-17	LAB: Wolf Lake Field Investigation (1st half of class)
18 M	Biology of *Oncorhynchus* spp.
20	Population identification; introduction to statistical inference
22	Estimation of population density
22-24	LAB: Wolf Lake Field Investigation (2nd half of class)
25 M	Estimation of population density (cont'd)
27	Estimation of population density (cont'd)
29	Analysis of age and growth; Von Bertalanffy growth model LAB: Age determination
Oct. 2 M	NO CLASS (ROSH HASHANAH)
4	Von Bertalanffy (cont'd) and Ricker growth models; introduction to mortality
6	Survivorship and mortality LAB: Tioughnioga River Field Investigation (1st half)
9 M	**EXAM I (100 Points)**
11	NO CLASS (YOM KIPPUR)
13	Return and review exam LAB: Tioughnioga River Field Investigation (2nd half)

Oct.	16 M	Survivorship and mortality (cont'd)
	18	Production
	20	Limits on production LAB: Age and Growth I

DYNAMICS OF EXPLOITATION

	23 M	Behavioral interactions and their role in fish production
	25	Behavioral interactions and their role in fish production
	27	Behavioral interactions; effects of exploitation on a fish population LAB: Salmon River Field Trip
	30 M	Exploitation (cont'd); Optimum breeding density: Spawner-recruitment curves
Nov.	1	Spawner-recruitment curves (cont'd); introduction to models of exploitation
	3	Surplus production model (Schaefer) LAB: Age and Growth II
	6 M	Dynamic pool model (Ricker)
	8	EXAM II (150 POINTS)
	10	Dynamic pool model (Beverton and Holt LAB: Age and Growth II (cont'd)

APPROACHES TO THE MANAGEMENT OF FISHERIES

	13 M	Goals and approaches to fishery management; on the ecology of humans and fishes
	15	Evaluation of restrictions on size, season, bag, and method of capture
	17	Evaluation of restrictions on size, season, bag, and method of capture LAB: Simulation models: SALMON, TUNA, OR PLAICE (Li, Adams, and Kao)
	20 M	Removal of presumed competitors
	22	Basis and evaluation of regulations in N.Y. State (Guest Lecture: Mr. Leslie Wedge, Sr. Aquatic Biologist, NYDEC)
	24	No class, No lab (THANKSGIVING HOLIDAY)

Nov.	27 M	Habitat manipulation Compet. + Coexist. in Stream Fishes (Li)
	29	Utilization of predator-prey studies TERM PROJECT DUE BY 8:30 A.M.
Dec.	1	Diversity, stability, and the assessment of impacts on aquatic communities LAB: Feeding ecology of fishes
	4 M	Making a living from knowledge of fishes: The role of the biological consultant (GuestLecture: Mr. Jeffrey Barnes, President, Terrestrial Environmental Specialists)
	6	The role of hatchery introductions
	8	Fish pathology (Guest Lecture/Lab: Dr. John Schachte, Jr., Associate Fish Pathologist, NYDEC) LAB: Fish Pathology
	11 M	Fish toxicology (Guest Lecture: Dr. Hank Appleton, Research Scientist, Syracuse Research Corporation)
	13	Relationship of watershed management to fishery biology: An example from Oregon streams
	15	Introduction to aquaculture; Review
	19	EXAM III (200 POINTS)

Chapter In: Clepper, H. (ed.). 1978. Predator-Prey Systems in Fish
Communities. Sport Fishing Institute, Washington, D.C. (c. 600p,
available in December 1978)

PREY SELECTION BY BENTHIC FEEDERS

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INTRODUCTION

Biologists have shown a strong inclination toward describing diets of fishes that feed on or near the bottom, and general patterns can often be inferred from these descriptions. The details of the prey selection process, however, have been examined in relatively few species, and much remains to be learned. Predicting variation in feeding patterns of benthic foragers, e.g. with species, life history stage, season, and habitat presents a challenge not only to fishery biologists, but to all ecologists interested in testing the generality of ecological principles. The information currently available suggests one basis for evaluating the effects of perturbations in prey communities. At the same time, additional investigations of feeding behavior, which are required to fulfill this and other goals, provide almost limitless potential for future research.

The goals of this chapter are to review what is known of prey selection in benthic feeders, and to suggest future studies that may contribute to our understanding and use of aquatic resources. The chapter will begin with a brief introduction to modes of detection, acquisition, and handling of benthic prey. Processes that lead to diet selection will then be examined, with a view toward providing general principles.

MODES OF DETECTION, ACQUISITION AND HANDLING OF BENTHIC PREY

Prey selection by fishes is governed, in part, by their abilit detect and locate prey, and these processes may involve different se modalities under varying environmental conditions. Once located, pr must be captured, manipulated, and in some cases sorted (e.g. by siz taste, or texture) prior to entering the alimentary canal.

Sensory Modalities

Vision, smell, taste, and touch are commonly employed in dete of benthic food, and in some species acoustico-lateralis and electr receptors also play a significant role. Rainbow trout (<u>Salmo gaird</u> in shallow streams and lakes (Jenkins 1969a; Ware 1972) and flounde (<u>Platichthys flesus</u>) in estuarine environments (Moore and Moore 196 appear to locate prey visually, and for such predators prey movemen been shown to be a major factor in detection. Considerable variatio ists in retinal sensitivity of fishes (Muntz 1975), but at least in salm food can be located visually at night (Jenkins 1969b; Tanaka 1970). fish (<u>Carassius auratus</u>) can discriminate between different colors brightness cues are eliminated (Muntz and Cronly-Dillon 1966). Oth species that possess visual pigments sensitive to different wavelen probably also have color vision, but this has not been investigated the standpoint of predator-prey interactions. Although visual fie few species have been studied in detail, fields in the shape of spheres, truncated spheres, or hemispheres have been hypothesized (Ware 1973; Werner and Hall 1974; Obrien et. al. 1976).

Olfaction may play an important role in guiding fish to areas of food abundance. Blinded bluntnose minnows (Hyborhynchus (=Pimephales) notatus) can discriminate odors of some aquatic invertebrates (Hasler 1957), and cod (Gadus morhua) appear to be attracted to odors of intact marine invertebrates (Brawn 1969). Exploratory and feeding behavior of juvenile sockeye salmon (Oncorhynchus nerka) can be evoked by aqueous extracts of food (McBride et. al. 1962). Electrical stimulation of the olfactory lobes elicits feeding activity in goldfish indistinguishable from that observed under normal conditions. This response is not evoked by stimulation of the taste centers (Grimm 1960). Habituation to new odors seems to occur within 15 minutes in a variety of benthic fishes including rays (Raja battis), eels (Anguilla anguilla), sturgeon (Acipenser ruthenus), and soles (Solea vulgaris) (Bateson 1890). For most species the ecological significance of olfaction in prey detection has not been assessed. Presumably, odors associated with molting, metamorphosis, and/or emergence of prey organisms could act to stimulate benthic foraging, whether or not such odors permit orientation to the food.

Taste buds in the mouth, pharynx, gill cavity and on the gill arches aid in judging the palatability of food once contact is made. In some fishes, e.g. bullheads (Ictalurus), this contact may occur before food enters the mouth, by means of thousands of taste buds distributed over the body, as well as on tactile barbels. Such fish are capable of using the sense of taste to guide them to chemical clu~~s~~es (Bardach, Todd and Crickmer 1967). Sensory papillae on the lips of suckers (Catostomidae) also permit assessment of food prior to capture, and in hake (*Urophycis chuss*) and searobins (*Prionotus carolinus* and *P. evolans*) taste buds are located on specialized fin rays that serve as feelers (Bardach and Case 1965). In cod small benthic prey can be located in complete darkness with the aid of a barbel and pelvic fins equipped with taste buds, but large or pelagic prey are ordinarily located visually (Brawn 1969). The significance of tactile receptors has been little examined in fishes; presumably these aid in judging texture, which may provide a cue to prey composition.

Water displacement acting on the lateral line receptors permits localization of prey in at least one surface feeding species (*Aplocheilus lineatus*) (Schwartz 1965). Benthic feeders are presumed to use the lateral line in locating active prey (Alexander 1970), but behavioral experiments have not yet provided thresholds in terms of the size, distance, and frequency of stimulating objects (Dijkgraaf 1966). Modified lateral line organs serving as electroreceptors are found in sharks and rays, elephant fishes (Mormyridae), knife fishes (Gymnotidae), electric eels (Electrophoridae), and some catfish (*Amiurus*; *Kryptopterus*) and possibly certain other fishes (Bennett 1971). These receptors are capable of detecting prey movement, and may act in concert with ordinary lateral line receptors, particularly in turbid water or when prey are buried in bottom sediments. The gnashing sounds of feeding should be within hearing range of many fishes, and individuals detecting the sounds of other fish feeding may learn to orient to the source (Tavolga 1971).

Adaptations for Prey Capture and Handling

Feeding behavior and ecology are closely related to morphological adaptations for capturing and handling prey. These processes are facilitated by various modifications, particularly of the jaws, teeth, gill arches, and fins. A modified dorsal fin in goosefish (Lophiidae) is used to attract prospective prey near the mouth, which is rapidly opened to engulf the prey. Pacific electric rays (Torpedo californica) utilize an electric charge to immobilize prey, which may be moved toward the mouth by undulatory movements of the pectoral fins, or by a suction created by lifting the body from the substrate (Bray and Hixon 1978). In most fishes food acquisition involves a sucking action, in which prey are engulfed whole. Suction may be increased in teleosts through the action of motile maxillary bones that close off the sides of the mouth (Alexander 1970). Additionally, protractile premaxillary bones in the upper jaw of minnows and suckers (Cypriniformes) and in a different form in perch relatives (Perciformes), permit the mouth opening to be extended into crevices; this adaptation probably also facilitates foraging while holding the body nearly horizontal (Alexander 1970).

Variously modified teeth in the jaws, "tongue", palate, and inner surface of the gill arches aid in securing the prey, and their rearward orientation directs food toward the throat. Certain cichlid fishes of African lakes have highly specialized jaw teeth that permit scraping of benthic organisms, including algae, from rocky substrates (Fryer 1959). In suckers and minnows jaw teeth are replaced by pharyngeal teeth borne on the last gill arch, which operate against each other or against a bony pad at the base of the skull. In most fishes the gill arches are equipped with taste and touch receptors, as well as gill rakers that vary from short and blunt to long and fine. Thus, the gill arches and associated musculature create a branchial sieve that can manipulate and sort food from inorganic bottom materials. Specializations of the remainder of the gut will not be considered here, except to point out that variation in diameter, length, and structural details of the gut can often be correlated with diet composition.

PREY SELECTION

Patterns of benthic prey selection are the outcome of characteristics of fishes, characteristics of their prey, and the interaction of both with their environment. Such features are all clearly interdependent, but are discussed separately here for the sake of convenience.

Characteristics of Fishes

One determinant of prey selection is the spatial distribution of the predator, although to some extent morphological and behavioral adaptations for prey handling govern the kinds of habitats searched. Mendelson (1975) found broad similarities between the diets of two species of shiners (<u>Notropis</u>) observed to feed in midwater and the invertebrate drift fauna, whereas the diet of a largely bottom feeding species was closely correlated with benthos composition. The considerable overlap in diet (69-84%) among four species was explained in terms of relatively indiscriminate feeding in particular habitats rather than predation on certain kinds of prey. In small lakes, pumpkinseeds (Lepomis gibbosus) and longear sunfish (Lepomis megalotis) both searched bottom sediments methodically, but pumpkinseeds tended to feed nearest to shore, and relied heavily on molluscs. There seemed little doubt that the crushing, molariform pharyngeal teeth of pumpkinseeds played a role in their diet selection (Werner et. al 1977).

Distributions of fish may shift seasonally, e.g. as water level drops or vegetative cover expands, and diets may be expected to reflect such shifts. Zaret and Rand (1971) found little diet overlap among four bottom dwelling species (Aequidens coeruleopunctatus, Eleotris picta, Rhamdia wagneri, Synbranchus mormoratus) in a Panama stream during the dry season, when prey were scarce. Overlap between four (of five possible) pairs of these species increased during the wet season, when prey were abundant. Yet where significant overlap occurred, foraging patterns were separated by day vs. night feeding. Thus we can expect temporal, as well as spatial, variation in foraging to influence patterns of prey selection.

Turning to patterns of prey selection within a single species, or population, fish size has been shown to markedly influence the diet. Werner et al (1977) found that small size classes of sunfish and shiners were restricted to shallow, vegetated areas of a lake, probaby by predation pressure. Jenkins (1969a) and others have demonstrated the importance of size in gaining a feeding station within salmonid hierarchies, although resulting differences in diet could not be detected. In channel catfish (Ictalurus punctatus) "swimways" to and from a feeding station are related to fish size, and small fish must wait until large individuals complete feeding (Randolf and Clemens 1976b). Large fish tend to take larger prey (Keast 1965; Cadwallader 1975a; Kislalioglu and Gibson 1976a), and this broadens the size range and usually the diversity of items consumed. Such differences have been explained on the basis of mouth (gape) size, but swimming speed and/or manuverability may sometimes be important (e.g. in flounders, Moore and Moore 1976a). The age of fishes seems to have little effect on diet patterns (apart from its correlation with size). Diets have also been shown not to differ appreciably between sexes of the same species (Atmar and Stewart 1972; Cadwallader 1975a; Ringler 1975; Randolf and Clemens 1976a), although differences might be expected to develop under some circumstances, such as prior to spawning activity or when males and females select different habitats.

Prey selection by individuals is highly dependent on hunger level and experience, both of which have been analyzed in detailed laboratory studies. Although stomach fullness appears to be only one component of hunger (Rozin and Mayer 1964), bulk of food in the stomach has often been used to define hunger state (Brett 1971; Ware 1972). Rates of stomach evacuation may prove useful in describing hunger in these terms (e.g. Elliott 1972). Where feasible a better approach may be an operational definition of hunger in terms of the quantity of food that would be eaten if a fish were fed _ad libitum_. Thus, a schedule of food deprivation time (Beukema 1968) can be developed to define hunger state. The effects of hunger on predation rates are well documented in some species. In rainbow trout predation rates declined at low hunger levels, apparently because the fish took progressively longer to manipulate food (Ware 1972). Handling time in sticklebacks (_Spinachia spinachia_) also increased with declining hunger (Kislalioglu and Gibson 1976a). Beukema (1968) found that hungry sticklebacks (_Gasterosteus aculeatus_) captured the most prey because 1) they grasped and ate a greater proportion of discovered prey and 2) they swam more actively than satiated fish and thus had more prey encounters. One is tempted to suggest that this latter phenomenon might regulate the rate of movement among microhabitats.

Much remains to be learned of the effects of hunger on diet selection. Ivlev (1961) concluded that satiation was the controlling mechanism behind increased prey selection by carp (_Cyprinus carpio_) among chironomids, amphipods, and molluscs. In a detailed model of vertebrate predation Holling (1965) proposed that when a palatable prey species was eaten the predator "learned a lesson", which was gradually extinguished in the absence of reinforcement. Hunger was considered of critical importance to this learning process, in the sense that capture of palatable food operated to lower the level of hunger required before a subsequent attack would occur. The model predicted that reaction distance to a prey item would increase ("improve") with experience. Yet Beukema (1968) found that food deprivation did not alter reactive distance in sticklebacks. Ware (1971) discovered this same phenomenon in rainbow trout; he therefore suggested that experience can modify reactive distance directly, rather than indirectly through hunger as proposed by Holling. Ringler (1975) found that considerable changes in hunger (stomach fullness) were not reflected in changes in prey selection by brown trout (Salmo trutta). Thomas (1977) proposed that, in addition to satiation effects, short-term positive and negative motivational after-effects occurred following "eat" and "reject" encounters, respectively. In sticklebacks these effects appeared to change both the subsequent search path and the probability of eating a particular item.

Experience has been dealt with in terms of familiarity with particular kinds of prey. However, there is almost no information on learning to forage in particular regions of prey abundance, or on the mastery of specific kinds of foraging behaviors. Surprisingly little is known of the rates at which various fishes learn to respond to prey, but one finding seems clear: learning is not instantaneous. Failure to attack prey upon first encounter appears to be a general phenomenon (Ivlev 1961; Springer and Smith-Vaniz 1972; Curio 1976). Yet mosquitofish (Gambusia affinis) and goldfish apparently had to taste highly unpalatable food items before rejecting them

(Russell 1966). Rainbow trout averaged 24 exposures to artificial prey (chicken liver) over a 4-day period ("latent phase") before approaches were observed, and some fish required up to 11 days (Ware 1971). Brown trout required 50-150 exposures to crickets and mealworms during 15 minutes before significant numbers of attacks occurred. These fish required 1200-1800 exposures during 4-6 days before responses stabilized (Ringler 1975).

Repeated successful encounters with a prey species may result in a "searching image" (Tinbergen 1960) for a particular species, a phenomenon in which the ability to respond, and probably to detect (Krebs 1973), other kinds of prey is markedly reduced. A major criterion in the establishment of a search image in rainbow trout is an increase in the reactive distance to prey with successive encounters; the time delay between prey recognition and approach to prey, as well as the development of a complete feeding sequence, is also involved. The effects of this kind of learning apparently last more than 2 weeks but less than 3 months in rainbow trout (Ware 1971). Although comparative data are few, these results seem to parallel those obtained for sticklebacks by Beukema (1968). Exactly how, or whether, search images are formed in other benthic feeders is difficult to say, particularly in those species that search other than visually.

Social facilitation of feeding may also be important. Olla and Samet (1974) found that mullet (Mugil cephalus) are more likely to feed when within sight of another feeding individual, and cod appear to recognize and respond to actions of other individuals associated with feeding (Brawn 1969). Presumably many fishes have the ability to respond to feeding behaviors; if so, this could reduce the time required for habituation to novel prey, and for development of a search image. A related phenomenon has been described by Frick (1970) and Hobson (1968), in which members of at least eight marine families follow the foraging activities of goatfish (Mulloidichthys dentatus). The follower species apparently associate the sand cloud raised by the foraging goatfish with prospective meals flushed from cover.

There is some indication that considerable variation in prey selection may occur among individuals. Bryan and Larkin (1972) found that individual trout in a small stream and in experimental ponds exhibited small but significant differences in their selected diet, and that these differences persisted to result in "food specialization". The results evidently were not attributable to heterogeneous distribution of prey. Their explanation for specilization was that individuals differ in the probability of detecting a particular kind of prey, because of differences in searching technique, capturing technique, and feeding rhythm. From the search image point of view, these behavioral differences could result from initial learning by individuals of different prey species encountered by chance. Interactions among individuals may also have promoted specialization, as the authors did observe frequent agonistic encounters. In a laboratory stream where visual communication was eliminated, brown trout exhibited little individual variation in prey selection (Ringler 1978).

Characteristics of Prey

Prey characteristics influencing diet selection include those that govern prey recognition (e.g. form, contrast, and movement), and those that determine encounter frequency (e.g. size, distribution, and abundance). Prey movement appears to be an important, and particularly for young fishes an essential, criterion of prey recognition by visual predators. In benthic communities this may involve movement of the prey over the substrate (Ware 1972; Moore and Moore 1976a; Rimmer and Power 1978) and/or subtle motions of structures such as gill lamellae in an otherwise stationary mayfly (Stuart 1953). Motion provided by downstream drift may elicit attacks even on inedible debris (Kalleberg 1958), and many fishes are known to prey on benthic organisms brought into suspension through disturbance of the substrate by foraging (Mundie 1969; Hobson 1968). A modelincorporating the visual mechanics of teleosts has been developed by Ware (1973). The model showed that prey activity accounted for the greatest fraction (19%) of the variation in diets of rainbow trout, the remainder being accounted for by degree of exposure (16%), density (11%), and size (1%). Experimental evidence also points to the importance of prey movement in increasing predation rates in rainbow trout (Ware 1973) and sticklebacks (Kislalioglu and Gibson 1976b), although this effect was not important for cod (Brawn 1969). Analyses of the effect of prey behaviors on risk of predation have been performed on few species. Stein and Magnuson (1976) showed that crayfish may successfully "threaten" smallmouth bass (<u>Micropterus dolomieui</u>) with their chelae. Nyberg (1971) found that attack velocity in largemouth bass was adjusted to the location (substrate vs. water column), kind (worm, fish, or crayfish), and mobility of prey to be captured. One might anticipate that behaviors peculiar to certain classes of prey, such as respiratory, or preemergence movements, may become a part of the search image of benthic fishes.

Form and contrast have proved significant determinants of prey risk in avian predators (Curio 1976), but much less is known of their significance in fishes. Hester (1968) demonstrated a positive relationship between visual acuity and target contrast in goldfish. Ware (1971) found that reaction distance of rainbow trout was related to contrast of artificial prey (colored chicken liver) with a dark background. Furthermore, trout that were trained on white food and then provided with black food responded as if they had never experienced this kind of prey, whereas the fish did exhibit "transfer of learning" to light grey and dark grey food. Presumably, prey of very different shape or form would also require a latent period before attacks were initiated. Sticklebacks, for example, appeared to respond to stimuli associated with mysids in the order movement ≥ length > color > shape. Attacks on the head region were attributed to its greater thickness, presence of appendages, and darker color. Limited data suggested that color and shape stimuli were additive in their effect on fish predation (Kislalioglu and Gibson 1976b).

Prey selection based on palatability has been little studied in an ecological context. We do know that rainbow trout, trained to operate a trigger to obtain food in the laboratory, can discriminate among prey (food pellets) on the basis of taste (Adron et al. 1973). Cod attack but reject formalin-treated mussels (Brawn 1969), and bluegills reject or fail to attack fire ants in the laboratory (Prather 1960). Yet the role, or even the frequency, of truly distasteful prey in natural aquatic systems has not been assessed. Moderately distasteful prey may be accepted when alternate prey are unavailable, or early in a feeding period when hunger levels are high (Holling 1965).

The role of prey size, distribution, and abundance in diet selection has been investigated intensively in fishes. This is in part because these parameters are easiest to measure, but also because of their potential contribution to an understanding of changes in prey communities associated with fish predation (Murdoch and Oaten 1975; Vince et al. 1976). The aquarium experiments of Ivlev (1961) with benthic feeding carp and bream (Abramis brama) showed how feeding preference was related to total and relative prey abundance and to spatial distribution of prey. He employed an "electivity" index, E, which describes whether a prey item is eaten in proportion to its abundance in the environment ($E=0$), in numbers exceeding this abundance ($1 \geq E > 0$), or in numbers fewer than this abundance ($-1 \leq E < 0$). Many recent investigators have used this descriptive index to summarize their results. Yet, useful information about ration size is thereby obscured, and variation in electivity may result from differences in prey exposure (availability), a characteristic that varies seasonally, daily, or even from hour to hour. Although electivity indices may prove useful in describing deviations from random feeding, such indices seem destined to play a minor role in genuine understanding of prey selection.

A growing literature on optimal foraging theory (Emlen 1966, MacArthur and Pianka 1966; Pyke et al. 1977) provides us with general predictions of how fish should feed, assuming that individuals with the most efficient feeding strategies will tend, over the long term, to contribute most to future generations. One prediction of optimal foraging theory is that a fish should add new species to its diet as long as the reduction in energy (or time) expenditure per prey item is greater than the increased energy (or time) required to pursue, attack, and eat the new prey species. A second prediction is that fish should have the capacity to "rank" prey species by energy content or search time, i.e. they should be able to respond differentially to different kinds of prey. A third prediction is that when prey are scarce, they should be consumed as encountered (feeding should not be selective), but as prey abundance increases the lowest ranked (most costly) prey should be the first to be dropped from the diet. Optimal diets may not represent a maximum possible food intake, because fish must not only feed but must avoid predators, find mates, build nests, etc. Griffiths (1975) suggested that strategies employed by larval and adult vertebrates may be different, because of the time required for a complex neural apparatus to develop. One might also expect strategies to differ because of differences in the size and distribution of prey available to larvae and adults, but available data for fishes seem too few to test this hypothesis.

Predictions based on optimal foraging theory are proving increasingly valuable in framing hypotheses for the proximate, or short term, basis of prey selection. Studies of how fish actually discriminate among prey, can, in turn, contribute to future theoretical formulations. Two major hypotheses for proximate prey selection can be identified, although they need not be considered mutually exclusive. The first is that the selected diet results from a differential response to stimuli characteristic of the prey. Shifts in diet are explained in several ways, including the development of a searching image (Tinbergen 1960), and the development of a preference for certain kinds of prey through an active choice process (Krebs 1973). The second hypothesis is that the selected diet results from variation in prey distribution. Shifts in diet are brought about largely by changes in the area searched, so that fish move toward regions of maximum "profitability" in terms of number of prey encountered (Royama 1970; See also Charnov 1976). Predation by brown trout has been examined in the context of these ideas (Ringler 1975, 1978). Although capable of foraging directly from the substrate, the fish in these experiments were subjected to three species of drifting prey, which simulated aquatic invertebrates dislodged or emerging from the substrate. The trout diets changed daily and during 5-minute intervals; responses to the prey species tended to stabilize after 4-6 days and 800-1200 prey captures. Selection (electivity) was greatest at high total prey densities, yet no prey species was completely excluded from the diet. Although the fish tended to move into regions (depths) of high prey density, the diet was not explicable solely on the basis of this movement. Size-selective predation was a dominant characteristic of the response. This seemed to involve development of a preference for large prey, rather than a change in the ability to detect the prey. Some evidence suggested that high relative abundance could result in selection of prey species;

this effect was evidently masked by that of size during most of the experimental period. Similarly, the differential response based on size obscured any influence of prey shape or palatability during these experiments. Prey selection resulted in as much as a 3-fold increase in caloric intake relative to a random diet (prey taken as encountered). Brown trout ultimately achieved 54-91% of an hypothetical optimum diet in which prey were ranked in order of size (caloric content). It was suggested that deviations from the hypothetical optimum may be explained in terms of a feeding strategy that deals with variation of prey abundance in time and space, as well as the behavioral capabilities of brown trout.

The significance of prey size does not seem to be limited to laboratory systems, as Metz (1974) demonstrated a close correlation between body length of drifting insects and their electivity in a natural trout stream. Ware (1972) found a strong correlation (r = 0.98) between prey size and reaction distance in rainbow trout, and concluded that this property of foraging behavior contributes to, and may explain, size selective predation. He also discovered that for prey of a given size predation rate increased linearly with density, but that substrate-oriented search waned when the trout captured fewer than 3.5 prey items/minute. Ware suggests that foraging behavior may be controlled by a critical rate of food capture, thus providing a mechanism by which Royama's (1970) "profitability" hypothesis may operate.

Size-selective predation has been reported for a number of other fishes capable of bottom foraging, e.g. bluegill (Werner and Hall 1974), sticklebacks (Kislalioglu and Gibson 1976a), and black bullhead (Repsys et al. 1976), and it appears to be a very general phenomenon. Obrien et al. (1976) have shown that in bluegill selective predation is based on a judgement of "apparent size" (prey length/distance to predator) rather than absolute size. This mechanism has yet to be examined in other species; for predators foraging at a fixed distance above the substrate, apparent and absolute prey sizes may be identical. Large size classes of prey are sometimes excluded from the diet, because of difficulty in successfully attacking them. Thus large crayfish appear able to defend themselves from smallmouth bass, so that small individuals are most vulnerable (Stein and Magnuson 1976). Large decapods and mysids exhibit a rapid escape that prevents their capture by sprats (Sprattus sprattus) (Moore and Moore 1976b). Mouth gape and/or the size of the buccal cavity probably limit ingestion of large sizes of prey in many benthic foragers. Presumably, handling time and energy ultimately exceed the gain for large prey, although this tradeoff can depend on hunger level (Werner 1974; Kislalioglü and Gibson 1976a), and thus indirectly on prey density.

Environmental Influences on Prey Selection

Environmental factors such as temperature, dissolved oxygen concentration, turbidity, and substrate composition can be expected to influence the behavior of both fish and their prey. Such influences will be treated elsewhere in this Symposium, but a few pertinent results should be presented here. Rising temperatures may stimulate activity and emergence of benthic invertebrates, thereby promoting foraging activity of fishes. Warm temperatures also increase rates of gastric evacuation in fishes (e.g. Elliot 1972). Although this could reduce the extent of feeding selectivity, concurrent increases in prey availability probably act to ameliorate this effect. Randolf and Clemens (1976a) have shown that individual channel catfish become acclimated to feed within a relatively narrow range of temperature (±2°C) and dissolved oxygen (±4 mg/l), but that the population as a whole fed within much broader limits. One result of acclimation to different ranges of these environmental factors was that small fish did not feed when large fish fed, and vice versa. The degree to which individual acclimation schedules explain "specialization" (Bryan and Larkin 1972) in feeding remains to be examined for other fishes.

Increasing turbidity under laboratory conditions from 2-3 JTU to 85-90 JTU cut the reaction distance of flounders in [illegible] half, and doubled the time required in prey capture. For highly mobile decapods the fraction of successful escapes increased from 55% in clear water to 100% in turbid water (Moore and Moore 1976a). Deposition of sediment is known to markedly alter benthic communities.
Less well studied, however, are the effects of changes in substrate composition on foraging efficiency. Brawn (1969) carefully documented the foraging behavior of cod, which utilized olfactory and taste cues in

locating bits of mussel buried up to 3 cm in gravel. These fish were incapable of detecting prey buried under sand, even in layers as thin as 1.5 mm, presumably because odors could not penetrate the fine spaces between sand particles.

Habitat complexity has been shown to influence predation rates and diet selection. Vince et. al. (1976) compared killifish (Fundulus heteroitis) predation on amphipods in aquaria simulating low marsh habitats (where Spartina stalks are spread out) with predation in simulated high marsh habitats (where Spartina stalks are close together). They found that killifish exhibited size-selective predation only in the low marsh, apparently because of the greater ease of detecting prey there. Field experiments showed further that killifish predation could regulate the abundance and size distribution of amphipods and snails, through differential predation in habitats of varying complexity.

On a finer scale, Ware (1972) found that, in rainbow trout, both the feeding rate and total prey consumption were inversely related to substrate (litter) complexity. These effects were attributed to increased cover within which prey (amphipods) could escape predation, as there were no conspicuous changes in fish behavior in response to different substrates. Field and laboratory data have suggested major increases in the proportion of amphipods exposed as temperature increases (Ware 1973), and presumably this effect interacts with that of substrate complexity in governing prey selection. Future analyses of environmental interactions are almost certain to contribute to our knowledge of prey selection in benthic feeders; these analyses should be of considerable utility in assessment of perturbations of prey communities.

SUMMARY

Predicting variation in feeding patterns requires an understanding of the processes of prey selection, but relatively few detailed studies of benthic feeders have been made. Available knowledge of morphological and behavioral adaptations reveals varied modes of prey detection, acquisition, and handling among benthic fishes. Much remains to be learned of fishes that locate food using taste, smell, or electric receptors, particularly in those that manipulate bottom sediments.

Patterns of benthic prey selection are the outcome of characteristics of fish and their prey, and the interaction of both with their environment. Spatial and temporal variation in habitats searched lead to major differences in diets among benthic fishes. Such differences are related, in part, to fish size, but this factor also influences prey selection within specific habitats, and it appears to be of far greater importance than age or sex. Hunger levels influence prey handling time and may regulate the rate of movement among microhabitats; the extent of selectivity is not a simple function of hunger. Surprisingly little is known of the rates at which fishes learn to respond to prey. In visual feeders learning appears to involve an increased distance of reaction, a reduced time delay between recognition and approach, and an increased proportion of completed feeding sequences. Both social facilitation and individual variation in feeding behavior merit attention in future studies.

Prey characteristics influencing diet selection include those that govern prey recognition and encounter frequency. Movement is an important

criterion for prey recognition in visual feeders, but the significance of specific prey behaviors remains to be examined. Distance of reaction is directly related to target contrast, and limited data suggest that the effects of prey color and shape stimuli may be additive. The ecological significance of taste in benthic feeders cannot presently be assessed.

Prey size, distribution, and abundance play a central role in diet selection. Optimal foraging theory provides general predictions of prey suitability in terms of time or energy, and such predictions provide guidance in studies of proximate mechanisms of prey selection. Considerable evidence suggests that benthic feeders are size-selective. They also appear capable of locating areas of prey abundance, and foraging behavior may be controlled by a critical rate of food capture. Selective predation has been shown to increase food intake relative to random feeding, although several days may be required to learn the appropriate responses.

Environmental factors influence prey selection by benthic feeders. Rates of gastric evacuation and foraging activity increase with temperature in fishes, as does the degree of exposure of aquatic invertebrates. Individual fish may become acclimated to feed within narrow limits of temperature and dissolved oxygen, which acts to partition their feeding in time and space. By altering rates of prey discovery, the complexity of benthic environments has been shown to influence both predation intensity and the extent of size selectivity. Analyses of interactions among environmental factors seem destined to contribute importantly to our understanding of prey selection.

LITERATURE CITED

Adron, J.W., P.T. Grant, and C.B. Cowey. 1973. A system for the quantitative study of the learning capacity of rainbow trout and its application to the study of food preferences and behavior. J. Fish. Biol. 5(5): 625-636.

Alexander, R. McN. 1970. Functional design in fishes. Hutchinson University Library, London. 160 p.

Atmar, G.L. and K.W. Stewart. 1972. Food, feeding selectivity and ecological efficiencies of <u>Fundulus notatus</u> (Cyprinodontidae). Amer. Midl. Nat. 88: 76-89.

Bardach, J.E. and J. Case. 1965. Sensory capabilities of the modified fins of the squirrel hake (<u>Urophycis chuss</u>) and searobins (<u>Prionotus carolinus</u> and <u>P. evolans</u>). Copeia 1965(2): 194-206.

Bardach, J.E., J.H. Todd and R. Crickmer. 1967. Orientation by taste in fish of the genus <u>Ictalurus</u>. Science 155: 1276-1278.

Bateson, W. 1890. The sense organs and perceptions of fishes, with remarks on the supply of bait. J. Marine Biol. Assoc. London 1: 225-256.

Bennett, M.V.L. 1971. Electroreception. pp. 493-574 <u>In</u>: Fish Physiology, Vol 5 (W.S. Hoar and D.J. Randall, eds.). Academic Press, New York.

Beukema, J.J. 1968. Predation by the threespine stickleback (<u>Gasterosteus aculeatus</u> L.): The influence of hunger and experience. Behavior 31: 1-126.

Brawn, J.M. 1969. Feeding behavior of cod (<u>Gadus morhua</u>). J. Fish. Res. Bd. Canada 26: 583-596.

Bray, R.N. and M.A. Hixon. 1978. Night-shocker: Predatory behavior of the Pacific electric ray (<u>Torpedo californica</u>). Science 200: 333-334.

Bryan, J.E. and P.A. Larkin. 1972. Food specialization by individual trout. J. Fish Res. Bd. Canada 29: 1615-1624.

Cadwallader, P.L. 1975. The food of the New Zealand common river galaxias, *Galaxius vulgares* Stokel (Pisces: Salmoniformes). Austr. J. Mar. Freshwat. Res. 26(1): 15-30.

Charnov, E. 1976. Optimal foraging, the marginal value theorem. Theor. Pop. Biol. 9(2): 129-136.

Curio, E. 1976. The ethology of predation. Springer-Verlag, New York. 250 p.

Dijkgraaf, S. 1966. Biological significance of the lateral line organs, pp. 83-95 *In:* Lateral Line Detectors (P. Cahn, ed.)

Elliott, J.M. 1972. Rates of gastric evacuation in brown trout, *Salmo trutta* L. Freshwater Biol. 2: 1-18.

Emlen, J.M. 1966. The role of time and energy in food preference. Amer. Natur. 100: 611-617.

Fricke, H.W. 1970. Zwischenartliche Beziehungen der tropischen Meerlarsche *Pseudupeneus barberinus* und *Pseudupeneus macronema* mit einigen anderen marinen Fischen. Natur. Museum 100: 71-80.

Fryer, G. 1959. The trophic interrelationships and ecology of some littoral communities of Lake Nyasa with especial reference to the fishes, and a discussion of the evolution of a group of rock-frequenting cichlidae. Proc. Zool. Soc. Lond. 132 (1959): 153-281.

Griffiths, D. 1975. Prey availability and the food of predators. Ecology 56: 1209-1214.

Grimm, R.J. 1960. Feeding behavior and electrical stimulation of the brain of *Carassius auratus*. Science 131: 162-163.

Hasler, A.D. 1957. Oflactory and gustatory senses of fishes. pp. 187-209 *In:* The physiology of fishes (M.E. Brown, ed.). Academic Press, New York.

Hester, F.J. 1968. Visual contrast thresholds of the goldfish (Carassius auratus). Vision Res. 8: 1315-1336.

Hobson, E.S. 1968. Predatory behavior of some shore fishes in Gulf of California. U.S. Fish and Wildl. Serv. Res. Rep. 73: 1-92.

Holling, C.S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. Mem. Entomol. Soc. Canada No. 45. 60 p.

Ivlev, V.S. 1961. Experimental ecology of the feeding of fishes (English Transl. into Russian by D. Scott). Yale Univ. Press, New Haven, 302 p.

Jenkins, T.M. 1969a. Social structure, position choice and microdistribution of two trout species (Salmo trutta and Salmo gairdneri) resident in mountain streams. Anim. Behav. Monogr. 2 (part 2): 57-123.

Jenkins, T.M. 1969b. Night feeding of brown and rainbow trout in an experimental stream channel. J. Fish. Res. Bd. Canada 26: 3275-3278.

Kalleberg, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (Salmo salar L. and S. trutta L.). Rep. Inst. Freshwater Res. Drottningholm 30: 55-98.

Kislalioglu, M. and R.N. Gibson. 1976a. Prey 'handling time' and its importance in food selection by the 15-spined stickleback, Spinachia spinachia (L.) J. Exp. Mar. Biol. Ecol. 25(2): 151-158.

Kislalioglu, M. and R.N. Gibson. 1976b. Some factors governing prey selection by the 15-spined stickleback, Spinachia spinachia (L.) J. Exp. Mar. Biol. Ecol. 25(2): 159-169.

Keast, A. 1965. Resource subdivisions amongst cohabiting fish species in a bay, Lake Opinicon, Ontario. Proc. 8th Conf. Great Lakes Res. Div. Univ. Mich. pp.106-132.

Krebs, J.R. 1973. Behavioral aspects of predation. pp. 72-111 *In:* Perspectives in ethology. P.P.G. Bateson and P.H. Klopfer (eds.) New York, Plenum Press. 336 p.

MacArthur, R.H. and E.R. Pianka. 1966. On optimal use of a patchy environment. Amer. Natur. 100: 603-609.

McBride, J.R., D.R. Adler, R.E.E. Jonas and N. Tomlinson. 1962. Olfactory perception in juvenile salmon I. Observations on response of juvenile sockeye to extracts of foods. J. Fisheries Res. Bd. Canada 19: 327-334.

Mendelson, J. 1975. Feeding relationships among species of *Notropis* (Pisces: Cyprinidae) in a Wisconsin stream. Ecological Monographs (1975) 45: 199-230.

Metz, J-P. 1974. The invertebrate drift on the surface of a prealpine stream and its selective exploitation by rainbow trout (*Salmo gairdneri*). Oecologia 14(3): 247-267.

Moore, J.W. and J.A. Moore. 1976a. The basis of food selection in flounders, *Platichthys flesus* (L.) in the Severn estuary. J. Fish. Biol. 9(2): 139-156.

Moore, J.W. and T.A. Moore. 1976b. The basis of food selection in some estuarine fishes. Eels, *Anguilla anguilla* (L.), whiting *Merlangius merlangus* (L.), sprat, *Sprattus sprattus* (L.), and stickleback, *Gasterosteus aculeatus* L. J. Fish Biol. 9(5): 375-390.

Mundie, J.H. 1969. Ecological implications of the diet of juvenile coho in streams. pp. 135-152 *In:* Symposium on salmon and trout in streams, J.G. Northcote (ed.). H.R. MacMillon Lectures in Fisheries Univ. British Columbia, Vancouver, B.C.

Muntz, W.R.A. 1975. Visual pigments and the environment. pp. 565-578 In: Ali, M.H. (ed.) Vision in Fishes, New approaches in research. Plenum Press, NY 386 p.

Muntz, W.R.A., and J.R. Cronly-Dillon. 1966. Color discrimination in goldfish. Anim. Behav. 14: 351-355.

Murdoch, W.W. and A. Oaten. 1975. Predation and population stability. In: Advances in ecological research 9: 1-131 (A. MacFadyen, ed.).

Nyberg, D.W. 1971. Prey-capture in the largemouth bass. Amer. Midl. Naturalist. 86: 128-144.

O'brien, W.J., N.A. Slade, and G.L. Vinyard. 1976. Apparent size as the determinant of prey selection by bluegill sunfish (Lepomis macrochirus), Ecology 57: 1304-1310.

Olla, B.L. and C. Samet. 1974. Fish-to-fish attraction and the facilitation of feeding behavior as mediated by visual stimuli in striped mullet Mugil cephalus. J. Fish. Res. Bd. Canada 31: 1621-1630.

Prather, E.E. 1960. A note on the results of feeding fire ants to bluegill and redear sunfish. Proc. 14th Ann. Conf. Southeastern Assoc. of Game and Fish Commissioners. p. 124.

Pyke, G.H., H.R. Pulliam, and E.L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. Quart. Rev. Biol. 201: 1-18.

Randolph, K.N. and H.P. Clemens. 1976a. Some factors influencing the feeding behavior of channel catfish in culture ponds. Trans. Amer. Fish. Soc. 105(6): 718-724.

Randolph, K.N. and H.P. Clemens. 1976b. Home areas and swimmways in channel catfish culture ponds. Trans. Amer. Fish. Soc. 105 (6): 725-730.

Repsys, A.J., R.L. Applegate and D.C. Hales. 1976. Food and food selectivity of the black bullhead, *Ictalurus melas*, in Lake Poinsett, South Dakota. J. Fish. Res. Bd. Canada 33: 768-775.

Rimmer, D.M. and G. Power. 1978. Feeding response of Atlantic salmon (*Salmo salar*) alevins in flowing and still water. J. Fish. Res. Bd. Canada. 35:329-332.

Ringler, N.H. 1975. The mechanism of selective predation in drift-feeding brown trout (*Salmo trutta*). Ph.D. dissertation, University of Michigan, Ann Arbor. 198 p.

Ringler, N.H. 1978. Selective predation by drift-feeding brown trout (*Salmo trutta*). J. Fish. Res. Bd. Canada (in review).

Royama, T. 1970. Factors governing the hunting behavior and selection of food by the great tit (*Parus major* L.). J. Anim. Ecol. 39: 619-669.

Rozin, P. and J. Mayer. 1961. Regulation of food intake in the goldfish. Amer. J. Physiol. 206: ~~968-974.~~ 1430-1436

Russell, E. 1966. An investigation of the palatability of some marine invertebrates to four species of fish. Pacific Sci. 20: 452-460.

Schwartz, E. 1965. Bau und funktion der Seitenlinie des Streifenhechtlings (*Apolocheilus lineatus* Cuv. u. Val) Z. Vergleich Physiol. 50: 55-87.

Springer, C.G. and W.F. Smith-Vaniz. 1972. Mimetic relationships involving fishes of the family Blenniidae. Smithson. Contrib. Zool. 112: 1-36.

Stein, R.A. and J.J. Magnuson. 1976. Behavioral response of crayfish to a fish predator. Ecology 57(4): 751-761.

Stuart, T.A. 1953. Spawning migration, reproduction and young stages of loch trout (*Salmo trutta* L.). Freshwater Salmon Fish Res. 5: 39 p.

Tanaka, H. 1970. On the nocturnal feeding activity of rainbow trout (*Salmo gairdneri*) in streams. Bull. Freshwat. Fish. Res. Lab (Tokyo) 20: 73-82.

Tavolga, W.N. 1971. Sound production and detection. pp. 135-205 *In:* Fish Physiology, Vol V. W.S. Hoar and D.J. Randall (eds.) Academic Press, NY 600 p.

Thomas, G. 1977. The influence of eating and rejecting prey items upon feeding and food searching behavior in *Gasterosteus aculeatus* L. Anim. Behav. 25(1): 52-66.

Tinbergen, L. 1960. The natural control of insects in pine woods. Arch. Neerl. Zool. 13: 265-343.

Vince, S., I. Valiela, N. Backus, and J.M. Teal. 1976. Predation by the salt marsh killifish, *Fundulus heteroclitus* (L.) in relation to prey size and habitat structure. Consequences for prey distribution and abundance. J. Exp. Mar. Biol. Ecol. 23(3): 255-266.

Ware, D.M. 1971. Predation by rainbow trout (*Salmo gairdneri*): the effect of experience. J. Fish. Res. Bd. Canada 28: 1847-1852.

Ware, D.M. 1972. Predation by rainbow trout (*Salmo gairdneri*): the influence of hunger, prey density and prey size. J. Fish. Res. Bd. Canada 29: 1193-1201.

Ware, D.M. 1973. Risk of epibenthic prey to predation by rainbow trout (*Salmo gairdneri*). J. Fish. Res. Bd. Canada 30(6): 787-797.

Werner, E.E. 1974. The fish size, prey size, handling time relation in several sunfishes and some implications. J. Fish. Res. Bd. Canada 31: 1531-1536.

Werner, E.E. and D.J. Hall. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (Lepomis macrochirus). Ecology 55: 1042-1052.

Werner, E.E., D.J. Hall, D.R. Laughlin, D.J. Wagner, L.A. Wilsmann, and F.C. Funk. 1977. Habitat partioning in a freshwater fish community. J. Fish. Res. Bd. Canada 34: 360-370.

Zaret, T.M. and A.S. Rand. 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. Ecology 52(2): 336-342.

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Selective Predation by Drift-Feeding Brown Trout (<u>Salmo</u> <u>trutta</u>)

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Consumption of three species of prey by brown trout (<u>Salmo</u> <u>trutta</u>) in a laboratory stream was studied during 7-d experiments. Two drift rates (5 and 10 organisms/min) and three ratios (1:1, 2:1, 5:1) of small:large alternate prey were employed. [Prey selection changed daily and during 5-min intervals.] Responses [among] to prey species stabilized after 4-6 d and 800-1200 prey captures, but no prey was completely excluded from the diet. Size-selective predation was a dominant characteristic of the response. The fish appeared to alter the area (depth) searched in response to prey density; electivity was greatest when prey densities were high. Disproportionate predation on abundant prey ("switching") was a temporary phenomenon, which may have been masked by [that of] prey size, ~~during most of the experimental period~~. Brown trout ultimately achieved 54-91% of an hypothetical diet in which prey are ranked in order of size (energy content). Deviations from an optimal diet may be explained in terms of a feeding strategy that deals with heterogeneous distribution of prey, as well as with the behavioral capabilities of the predator.

<u>Key words</u>: Behavior; fish; invertebrate drift; optimal foraging; predation; prey size and abundance; Salmonidae; search image; streams.

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INTRODUCTION

A voluminous literature on diets in fishes demonstrates the kinds and abundances of food items captured under natural conditions. Many, and perhaps most, fishes forage selectively at least part of the time. Yet the details of the prey selection process are largely unknown, except in a few species that have been studied under simulated lentic conditions (e.g. Beukema 1968; Ivlev 1961; Ware 1971, 1972; Thomas 1977). Available data also provide little understanding of the consequences of prey selection in terms of optimal foraging theory. A notable exception (Werner and Hall 1974) has been the demonstration that predatory behavior of bluegill sunfish sc. name (*Lepomis macrochirus*) tends to maximize return with respect to time spent foraging.

Investigations of predation by drift-feeders have lagged behind those of littoral-or pelagic-feeders. This seems surprising in view of a continuing interest in invertebrate "drift" and its role in community stability (e.g. Waters 1972; Allen 1975). Field studies have detected selective predation by stream-dwelling fishes (Reimers 1957; Metz 1974; Griffith 1974), but these do not provide a means of evaluating the pattern of prey selection. Controlled studies of predation by stream-dwelling fishes should broaden our understanding of predation processes in aquatic systems, and may prove of value in evaluating perturbations of prey communities in streams.

The objectives of the present study were to describe predation by brown trout sc. name (*Salmo trutta*) in a laboratory stream; to evaluate the effects of prey size, relative and total abundance, and spatial distribution on the fish's diet during a realistic interval of time; and to determine the extent to which the diet maximizes energy intake. I hypothesized that changes in the diet would be brought about through the formation of a searching image (Tinbergen 1960), the development of a preference for specific kinds of prey (Krebs 1973), and/or by altering the area searched (Beukema; Royama 1970). It was anticipated that the feeding behavior of brown trout might lead to the selection of an optimal diet (MacArthur and Pianka 1966; Schoener 1971).

Materials ~~M~~ETHODS

Study Animals ~~and the Experimental Facility~~

Wild brown trout (Salmo trutta) were electrofished from Big Creek, a tributary of the North Branch of the AuSable River, Crawford County, Michigan. Individuals were removed from the same 1.2-km stream section at 4-to 7-wk intervals between 4 April 1974 and 7 January 1975. The fish were transported in oxygenated stream water to the laboratory, where they were placed in holding tanks adjusted to the stream temperature. Based on a scale analysis, all but 3 of 50 fish studied were 24-33 mo old; the others were 39-42 mo old. The length and weight of the experimental fish were as follows:

	Mean ± SE (Range)
Total Length (mm)	244 ± 11.6 (229-269)
Weight (g)	122.12 ± 21.73 (103.54-162.59)

There were 22 females (3 mature) and 28 males (3 mature).

The prey species were adult brine shrimp (Artemia salina), subadult house crickets (Acheta domestica), and mealworm larvae (Tenebrio molitor). All prey were preserved by freezing but were thawed before use. Samples were drawn from a single large batch of brine shrimp. Crickets and mealworms were sorted to obtain two size categories (Table 1). Samples of each category were dried for 48 h at 65°C, weighed, and burned in a muffle furnace at 600°C. Ash-free dry weights were used to convert wet weight to caloric content, based on published data (Table 2).

Table 1
near here

Table 2
near here

Following transport from the stream, the fish were placed in 800-L tanks and acclimated by 1° daily increments to 15°C (±1.0°). A 15-h photoperiod, representative of midsummer light conditions, was maintained throughout the study. While in these tanks, the fish were provided 1.25 brine shrimp/L twice daily. The fish began eating brine shrimp within 4 to 7 d, but detailed observations were not made for a period of at least 3 wk.

A "holding stream" (3.0 x 0.45 x 0.30 m) was used to condition the trout to feeding on drifting brine shrimp. About 15% of the individuals showed little or no feeding response after 3 d and were returned to the holding tanks for a later trial. Fish that fed actively were transferred to an "experimental stream" 2 to 3 d prior to an experiment. The stream was an essentially square 1350-L fiberglass trough, 50 cm wide, 12 m in circumference, and filled to a depth of 25 cm (Fig. 1). Continuous circulation of the water was provided by means of an electric pump. The bottom of the stream was covered with gravel 1.5 - 2.5 cm in diameter. The straight sections of the tank were provided with windows, and each section was bounded by two 20 x 20-mm-mesh screens. One fish was placed in each section; the arrangement of screens prevented visual contact between individuals. A 20 x 35-cm piece of styrofoam suspended above the lower end of each stream section provided overhead cover, and refuge from the current was supplied beneath the cover in the form of a rectangular (10 x 12 x 20 cm) rock. The water surface was smooth, and eddies were eliminated by placement of fine

Fig. 1
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mesh screens above and/or below each section. Mean current velocity, 13.5 cm/s, did not vary significantly among sections. Light intensity was maintained at 18 ± 2 lx incident to the stream surface.

All experiments were run at 17±0.5°C, because feeding was most active at this temperature. Water quality was maintained by filtration with activated charcoal and glass wool, and by periodic addition of aged tap water. Dissolved oxygen levels remained near saturation, pH varied between 7.8 and 8.0, and total alkalinity ranged from 46 to 68 mg/L.

Methods

The fish were fed once a day while in the experimental stream; the time of day of feeding varied from 1000 to 1800 h but was always the same (± 15 min) for a given individual. Automatic feeders, similar in design to the conveyor belt described by MacPhee (1961), were used to introduce the prey. Crickets and mealworms floated (mealworms were injected with a small quantity of air), whereas brine shrimp were distributed throughout the water column, including the surface. Nylon nets downstream from the fish ensured that each prey item was encountered only once.

The hunger states of the fish were maintained at a similar level by allowing 24 h between trials. Elliott (1972) showed that brown trout evacuated about 95% of the digestible organic matter in a meal of _Tenebrio molitor_ in 24 h at 17°C. Examination of the gut contents of four fish fed 25 large mealworms, and four fish fed 50 small crickets, confirmed that Elliott's results were applicable to the present study.

Feeding sequences were recorded by means of a hand-keyed, 20-channel Esterline-Angus events recorder. As each prey item drifted by, I recorded the prey species, and whether the fish approached, attacked, missed, or rejected the item. In certain of the experiments, the vertical distribution of prey and the position of the fish during each attack ~~was~~ were recorded with respect to a grid marked on the back wall of the stream channel.

Although some fish rejected prey, this was a rare event. Similarly, approaches not followed by attack were relatively rare, and it was often difficult to distinguish approaches to two items in close proximity. Therefore, the analysis in this paper is based on the number of prey actually eaten.

In the preliminary phase of the study, several drift rates, prey sizes, and exposure times were used to establish realistic conditions for the major experimental phase. The major phase of the study, which employed 27 fish, was carried out from 14 October to 9 February 1975. Following transfer to the experimental stream, the trout were exposed to brine shrimp for 2-3 d prior to the recording of their behavior ("Day 1"). During Days 2-7 each fish were exposed to one of two drift rates (5/min and 10/min) and three ratios (1:1, 2:1, 5:1) of small:large ~~m~~novel prey. Responses were analyzed during short (5 min) intervals and daily. This design permitted analysis of the role of total and relative prey abundance, as well as prey size, in diet selection. Responses to small crickets:large mealworms vs small mealworms:large crickets were also examined to evaluate the role of species of prey as opposed to its size. This effect was examined only at the high drift rate. Three fish, randomly assigned with respect to time (date), were used in each treatment.

RESULTS

Prey Selection

Brown trout appeared to detect prey visually. Prey were approached from downstream and briefly fixated before being sucked into the mouth. An account of the feeding behavior is given in Ringler (1975).

Differences were evident among individuals in level of feeding activity, as measured by the number of brine shrimp eaten on Day 1. I found no correlation of Day 1 feeding activity with the length, weight, or sex of the fish. At the high drift rate individual variation in timing of the response to novel prey was surprisingly small. Brine shrimp consumption declined abruptly when alternate prey were introduced on Day 2; 5-25 min were required before many novel prey were attacked. The numbers of prey eaten on Days 6-7 were ranked in order of prey size by all three trout, and all maintained some response to brine shrimp throughout the experiment.

Variation in the response attributable to temporal variation in prey availability was removed by calculating the percentage of available prey eaten during each 5-min interval (Fig. 2A). Experiments at the same drift rate but at Ratios 2:1 and 5:1 revealed a similar pattern. Except for Day 5 at Ratio ~~4~~5:1, there was little indication that selection of crickets over mealworms increased within a given feeding period. In contrast, the response to brine shrimp generally decreased within each period. These features were also evident from examination of data from individuals and were not an

Fig. 2A-2B
near here

artifact produced by pooling the results from three fish.

When the species combination was changed to large mealworms, small crickets and brine shrimp, the general pattern was retained (Fig. 2B), although the fish seemed slightly more selective. At the 5:1 ratio the response to large mealworms continued to increase during Days 5 and 6, while that to small crickets decreased. The only major deviation from parallel for the first series of experiments also occurred at Ratio 5:1 (Day 5). These departures from the general pattern evidently were not the result of limitations on prey handling time or stomach capacity, since one would expect that once these began to exert an effect, it would be evident throughout the remainder of the experiment. The pattern on Day 5 also did not suggest development of a search image, since the probability of encounter of large prey was least at Ratio 5:1.

At the low drift rate (5 alternate prey/min), individual variation in the feeding response appeared to be more marked than at the high drift rate, particularly at ratio 1:1. One fish, XC-2, never attacked the alternate prey, and another, XB-2, consumed none until Day 4 ~~(Fig. 4)~~. The rate of encounter, rather than initial differences in the fish, evidently influenced individual variation, since no significant difference was found between experiments in feeding activity on Day 1 (Student's t, 8 df, = 0.71; P > 0.50).

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Prey Selection dependence on ~~Effects of~~ Prey Size, Relative Abundance, ~~and~~ Drift Rate, and Distribution ~~on the Daily Response~~

The experimental design permitted two layouts of the data. Layout 1 tested the effect on the selected diet of 1) the species combination (i.e., small mealworms:large crickets versus small crickets:large mealworms), 2) the ratio of small:large alternate prey, and 3) time (day). Three-way analysis of variance provided the basis for the following conclusions ~~(Table 3)~~.

~~Table 3 near here~~

The mean percentage of brine shrimp eaten decreased significantly over time ($F_{5,60} = 30.32$; ~~(~~$P < 0.001$), reaching a minimum by Day 6 (Fig. ~~5~~ 3). The shift away from brine shrimp was evidently not affected by any differences in stimuli from different combinations or relative abundances of alternate prey. The daily decrease in brine shrimp consumption was virtually identical for both species combinations. The prey ratio also had no significant effect on the mean response to brine shrimp. The response to crickets and mealworms increased significantly with time and appeared to reach a plateau by Day 6. Differences in

Fig. ~~5~~ 3 near here

response to large mealworms compared to large crickets were not statistically significant. Similarly, comparison of the mean response to small crickets and small mealworms revealed no significant differences between species. Although ~~cases were found in which~~ a few fish seemed to show greater selection for large ~~prey when they were mealworms (page 10)~~ mealworms, this effect was evidently overridden by that of size and/or abundance ~~in these experiments~~.

Prey ratios appeared to affect the response to large prey. Multiple pairwise comparisons (Tukey's T) showed that the mean response at Ratio 1:1 was significantly lower than the others ($P < 0.01$). The response to small prey was also lowest at Ratio 1:1, although the difference was not statistically significant in the ANOVA model. The biological significance of differences in response among ratios will be considered in a subsequent section.

Of major interest was the comparison of responses among available prey types. The daily response to brine shrimp (Fig. ~~5~~ 3, dashed curve) clearly differed from the response to the alternate prey. Because brine shrimp were superabundant (about 20% could be captured; ~~see also page 18~~), analysis of the percentage eaten exaggerates the difference in response to brine shrimp and alternate prey. This effect was eliminated by assuming that the mean number of brine shrimp eaten on Day 1, when no alternate prey are present, is one estimate of "effective availability". When the response is calculated on this basis (Fig. ~~5~~ 3, solid curve) brine shrimp appear to be selected on Day 2, but by Day 3 or 4 the alternate prey receive the greatest response.

The percentage of large alternate prey eaten averaged higher than that of small alternate prey. Considerable variability was evident among individuals in the extent of the difference, particularly early in the experiments when the fish were first exposed to the novel food. A profile analysis (Morrison 1967) indicated that the difference between mean response levels was significant ($F_{1,34} = 11.69$; $P < 0.01$); the profile segments did not diverge significantly from parallel lines ($P > 0.54$). The results of profile analyses for each ratio were substantially the same as those for the lumped data; in each case the percentage of large prey eaten was greater than that of small prey (Ratio 1:1, $F_{1,10} = 3.50$; $P < 0.05$, Ratio 2:1, $F_{1,10} = 4.52$; $P < 0.05$, Ratio 5:1, $F_{1,10} = 10.48$, $P < 0.01$)

Separate analyses for Days 2-4 and 5-7 showed no evidence that the profile segments diverged from parallel lines. Thus, although the trout became increasingly selective of the alternate prey relative to brine shrimp, their response to crickets and mealworms tended to increase together. This suggests that the fish were not forming a searching image for large prey to the gradual or complete exclusion of small, but simply exhibited a preference for large prey. As they became increasingly familiar with the new and larger prey, the number eaten gradually increased at the expense of brine shrimp captures. Some of the fish during Days 6-7 approached but did not attack brine shrimp; such behavior occurred only rarely prior to experience with alternate prey. This points to an active selection process rather than the "visual filtering" (Tinbergen 1960) characteristic of the formation of a searching image. Whatever its internal basis, the selection process permitted the capture of at least some brine shrimp throughout the experimental period.

Layout 2 tested the effect on the diet of two drift rates of alternate prey (5 and 10/min), as well as the Ratio and Time effects. A 3-way ANOVA provided the basis for the following interpretation of the results, ~~(Table 4).~~ Brine shrimp consumption decreased significantly ($F_{5,60}=9.27$; $P<0.001$) during the experiment at both drift rates of alternate prey (Fig. 4~~6~~). At the high rate the response to brine shrimp seemed to decline more rapidly and to a lower level than at the low rate, but this effect was not statistically significant ($P > 0.10$).

FIG 4 near here

The percentage of large mealworms eaten increased significantly over time at both drift rates, reaching a plateau by Day 5 or 6. The mean response (61.9%) at the high drift rate was greater than the response (53.2%) at the low drift rate, but the difference was not statistically significant ($P > 0.25$). The mean percentage of small crickets eaten also increased significantly with time; the response averaged over 6 d was virtually identical at both drift rates.

~~Table 4 near here~~

As the ratio of small crickets:large mealworms was increased at the low drift rate from 1:1 to 2:1 to 5:1, consumption of small crickets increased from 24.5% to 54.5% to 61.8%, respectively. The number of alternate prey eaten averaged 42.72, 84.28 and 94.07 at the respective ratios. I found a similar ranking in the response to large mealworms. Evidently the fish did not simply respond to the combined stimulus from the crickets and mealworms. For example, ~~summing~~ the visible surface area (Table 1) for crickets and mealworms ~~gives daily values of~~ totaled 2820, 2406, and 1991 mm^2 for the respective ratios; the number of alternate prey eaten was ranked in opposite order. Possibly the trout respond initially to the most abundant novel prey, because of the greater probability of encountering them. The response, however, is soon generalized to the preferable large prey, and these are ultimately selected. This conjecture is supported by the finding that on Day 2 at Ratio 5:1 (low drift rate) small crickets were selected over large mealworms for the first 20 min. Initial selection of small prey at Ratio 5:1 also occurred at the high drift rate (Fig. ~~3~~2B); this phenomen lasted about 10 min.

When data from each drift rate were treated separately the difference in mean response to crickets and mealworms approached statistical significance at the high drift rate ($F_{1,16} = 3.44$; $P < 0.10$); this was due to the significantly greater ($p < 0.05$) response to mealworms during Days 5-7. Since profiles were parallel ($P > 0.50$), the trout evidently did not increase their response to large mealworms at the expense of small crickets. Use of an electivity index (Ivlev 1961) suggested that the trout were most selective when alternate prey were most abundant (Fig. ~~7~~ 5). This pattern agrees qualitatively with the mathematical predictions of Emlen (1966), and the empirical results of Ivlev (1961). A 3-way ANOVA demonstrated that the mean difference in electivity between drift rates was significant for brine shrimp ($F_{1,12} = 11.88$; $P < 0.01$), though not for mealworms ($F_{1,12} = 1.83$; $P > 0.15$).

Fig. ~~7~~ 5
near here

It appeared that the inflection point in the percentage of prey eaten (Fig. ~~6~~ 4) occurred later at the low drift rate for both large and small prey. This result may be explained in terms of a cumulative learning process (Holling 1965): each time a prey item is captured the fish "learns a lesson", which is gradually extinguished in the absence of reinforcement. At the low drift rate the time between encounters provides longer intervals during which extinction can occur, as well as fewer opportunities for learning. The limits to the response (asymptotes) during the later days of the experiments may also have been influenced by the learning process. Consumption of alternate prey species reached an asymptote, for both drift rates, at about the same percentage level (70-75% for large mealworms; 51-57% for small crickets). If limits were related only to physical constraints (e.g., minimum prey handling time or stomach capacity), one would expect the fish to capture similar absolute numbers (not percentages) of prey at the two drift rates.

Response limits were also determined by the time required to approach, attack, and swallow a prey item. Thus, some prey invariably were missed as others were captured. Since prey consumption declined markedly within certain feeding periods (Fig~~s~~. 3 ~~and 4~~), satiation effects were also evidently involved. One may infer that by Day 4 (high drift rate) or Day 5 (low drift rate) a substantial reduction in hunger level occurred within the feeding period. Contrary to Ivlev's (1961) predictions, the trout did not become increasingly selective as they approached satiation, at least in terms of their response to crickets versus mealworms.

~~The Role of Prey Size and Distribution~~

integrate with previous section

Unlike the other prey types, brine shrimp were distributed throughout the water column. Analysis of variance showed that significant differences ($F_{4,510}$ = 321; $P < 0.01$) existed in brine shrimp availability among the five depths studied. More than 40% of the brine shrimp were found at the surface, and 70% were in the upper half of the water column. A difference in brine shrimp abundance also existed between the first two time intervals ($F_{5,510}$ = 32.4; $P < 0.01$). The Time X Depth interaction term was significant ($F_{20,510}$ = 5.81; $P < 0.01$), ~~because~~ and the increase in available brine shrimp was greatest in the surface layer. This change in availability, however, probably had little influence on the pattern of prey selection previously described. Even during the first 5 min brine shrimp were 2 to 4 times as abundant as both alternate prey species combined; thereafter, the number of brine shrimp remained nearly constant.

Condense

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Analysis of the trout's response to brine shrimp on Day 1 showed that the main effects of time ($F_{5,510}$ = 10.23; $P < 0.01$) and of depth ($F_{4,510} = 8.13$; $P < 0.01$) accounted for most of the variation in number of brine shrimp eaten. Availability evidently influenced consumption rate. For example, at Depth 5 (19-25 cm) a relatively small but constant number of brine shrimp was eaten, but this represented a large and increasing fraction of those available at this depth. The percentage of brine shrimp eaten was ranked in approximately reverse order of the number available at each depth, a result suggesting that brine shrimp were superabundant.

A more satisfactory measure of changing responses among depths was the fraction of all brine shrimp in the diet captured at each depth. The mean contribution of brine shrimp to the diet varied significantly among depths ($F_{4,510} = 30.33$; $P < 0.01$), but a more important finding was the significant interaction of depth with time ($F_{20,510} = 1.88$; $P < 0.05$). At the surface and at Depths 2 and 3 an increase occurred in the contribution of brine shrimp, whereas in the lower depths (4 and 5) a decrease occurred. These data document a tendency of the fish to move from lower to higher depths; an upstream movement toward the point of prey delivery was also documented (Ringler 1975). These results suggest that within relatively short (30-min) periods brown trout can concentrate their attacks in areas of highest prey density.

The upward movement of the fish continued when alternate prey were introduced on Days 2-7. Data on the vertical distribution of feeding were available from experiments in which brine shrimp and one species of alternate prey were presented on Days 2-7. The number of brine shrimp eaten decreased, but the fraction attributable to surface captures greatly increased. This effect was demonstrated by all five fish presented 150 small crickets for 15 min, along with 500 brine shrimp. The experiment also showed that more than 6 times as many crickets as brine shrimp were attacked at the water surface, where brine shrimp were 1.33 times as abundant as crickets. A difference existed, therefore, in trout responses to prey species, apart from that resulting from different spatial distributions. Differential predation rates appeared to be largely attributable to the size discrepancy among species.

I tested this hypothesis by employing tiny crickets (mean length = 2.4 mm; wt = 0.0043 g) with approximately 80% of the visable surface area of brine shrimp. The crickets were introduced (5/min) with brine shrimp (33-min) during 6-d experiments. The mean response of five brown trout to brine shrimp remained nearly constant. Attacks on crickets increased gradually over time, but when the superabundance of brine shrimp was taken into account, predation on brine shrimp (the larger prey) was 2.1 times that on crickets after 6 d.

Selective Predation and Energy Content

The trout in the experimental system fed selectively. As long as 4-6 d and 800-1200 successful attacks were required before responses to prey seemed to stabilize. The abundance and spatial distribution of prey affected the outcome, but prey size appeared to be the overriding factor in the selection. Based on the caloric differences among prey species (Table ~~8~~3), size selective predation should lead to increased energy intake. I calculated, for an observed daily ration, the energy content of a diet obtained by feeding at random (prey consumption in proportion to abundance in the drift). The energy content of an hypothetical diet was also calculated, where the largest prey is taken first; if the total number of captures exceeds the number of large prey, the fish takes the next largest item, and so on. This method assumes that the time taken to attack and eat different species was identical. Because the total number of prey eaten was very similar during Day 1 (brine shrimp only) and Days 2-7 (brine shrimp, crickets, and mealworms), this assumption appears valid here. ~~for the prey sizes used in this study~~.

Table ~~5~~3
near here

Comparison of the observed energy intake with the "random" and "optimal" values provided one measure of the consequences of selective predation (Fig. ~~8~~6). Variation in random and optimum values resulted from changes in the number of prey eaten, and to a small extent from daily fluctuation in mean prey weight. Initially, the observed energy gain differed little from that predicted by random feeding. By Day 7, however, selective predation had more than tripled average energy intake relative to a random diet. The "optimum" was approached but never reached, the peak response averaging 87% of optimum by the end of the experiment.

Fig. ~~8~~ 6
near here

Considering the prey ratios separately, there was no mean difference between observed and random on Day 2 for Ratio 1:1. In fact, in some individuals the energy content of the diet on Day 2 was considerably below the random value. These instances correspond to a continued consumption of large numbers of brine shrimp. A positive departure from random almost always occurred by Day 3, however, and all of the trout tended to increase their energy intake toward the hypothetical optimum value.

Comparisons among ratios, as well as other analyses can be made by expressing the data in the form of an "optimization index": $\text{O I} = \frac{\text{Observed Energy Intake}}{\text{Optimum Energy Intake}} \times 100$. The peak value ranged from 54.30 to 91.20, depending on drift rate and prey ratio. At the high drift rate (Fig. ~~9A~~ 7A), significant differences occurred among the ratios ($F_{2,12} = 8.98$; $P < 0.01$). Pairwise multiple comparisons (Tukey's T) showed that the O I at Ratio 1:1 was significantly less than at Ratios 2:1 and 5:1, but these latter were not significantly different from each other. The time effect was significant ($F_{5,60} = 67.12$; $P < 0.01$), but the Ratio X Time interaction was not. The outcome at the low drift rate (Fig. ~~9B~~ 7B) showed a similar pattern, with the O I averaging significantly lower at Ratio 1:1 than at Ratios 2:1 or 5:1.

Fig. ~~9A-9B~~ 7A-7B
near here

When averaged over all ratios, the extent of optimization at the high drift rate (73.80) was considerably greater than at the low drift rate (57.38). This overall difference was significant at the 10% level ($F_{1,12} = 3.23$). Drift rate appeared to have its greatest effect at Ratio 1:1 (cf. Figs. ~~9A~~ 7A and ~~9B~~ 7B). The optimization index appeared to reflect the combined patterns of predation on the three prey species (Fig. ~~6~~ 4), particularly the greater mean response to large mealworms, earlier peak response to small crickets, and smaller contribution of brine shrimp at the high drift rate.

DISCUSSION

Selective predation in brown trout appeared most directly related to prey size, distribution, and total abundance. Bisson (1978) found that prey size was the most important factor affecting prey vulnerability in drift-feeding rainbow trout. A simulation by O'Brien et al. (1976) suggests that, given more than one visable prey item, active selection by "apparent size" (prey length/distance to fish) provides the best explanation for predation by sunfish on Daphnia. This model would appear to require modification where significant opportunities for learning exist. For example, ~~Ware (1972) has shown that~~ the distance from which rainbow trout attack prey increases not only ~~is correlated~~ with prey size, but also ~~that it increases~~ as~~ymptotically~~ with experience (Ware 1972). I was unable to record reaction distances for brown trout ~~to prey~~, but it seemed clear that these were not constant. Initially ~~Early in the experiments~~ the fish ~~trout~~ moved several cm to capture brine shrimp; later I observed instances in which actual contact of brine shrimp with the snout failed to elicit a response.

Differential responses among prey species required several days to stabilize, and no prey were excluded from the diet. The learning processes considered in analyzing shifts in diet were 1) formation of a searching image ("learning to see", Tinbergen.1960), 2) development of a preference for specific kinds of prey (active "choice" among species, Krebs 1973), and 3) alteration of the area searched (movement into areas of "profitability" in terms of prey consumed/time (Royama 1970). The evidence did not suggest that sudden changes occurred in the predator's ability to detect the prey, i.e., search images were not apparent. Yet the experimental conditions probably minimized the role of detection. The three prey species were readily visible, edible, and necessarily passed through the fish's visual field. In natural streams where cryptic prey, turbid water and constantly changing light conditions present a more demanding feeding situation, prey detection might become a significant, or even dominant, factor. My results do not refute the search-image idea; they simply show that prey selection in trout can also result from an active, differential response to the characteristics of the prey.

Variation in diets among individual trout was small, although differences in foraging behavior (e.g., feeding activity, body position) were sometimes evident. Bryan and Larkin (1972) have shown that individual trout may exhibit differences in their diet, evidently because of differences in searching technique, capturing technique, and feeding rhythm. Interaction among individuals may have played a role in bringing about specialization, as the authors observed frequent agonistic displays among fish. In my study little specialization was evident, perhaps ~~where~~ because interactions with conspecifics were eliminated.

Brown trout apparently altered the area searched in response to prey density, which seems to support Royama's (1970) "profitability" hypothesis. Their continued capture of at least a few brine shrimp at all depths also supported the prediction of periodic sampling of all "niches". Ware (1972) suggests that rate of capture serves as an internal signal to control foraging behavior~~, and that this provides a sufficient condition for Royama's hypothesis to operate~~. My data do not provide a test of this idea in the context of drift feeding, but one might postulate that discrete rates of capture exist, beyond which ~~trout movement~~ foraging would be largely restricted to specific depths (prey concentrations).

Murdoch and Oaten (1975) have considered the stabilizing effect on community structure of "switching", which is defined as disproportionate predation on the most abundant prey species. Although brown trout were not actually subjected to changing prey ratios over time, comparison of their responses at Ratios 1:1, 2:1, and 5:1 suggested that switching did not generally occur.

· why introduce these here?

no ?

The relationship between the proportion prey types consumed ~~(N_1/N_2)~~ and the proportion available ~~(H_1/H_2)~~ was roughly linear, i.e., preference (c) remained constant. Murdoch et al. (1975) examined data from a number of studies in terms of three generalizations about switching. The present study seems to support their second generalization, which is that if preference when prey are equally common is weak, but consistent among predators, then the predator should not switch. Of significance here is that, in brown trout, the preference "at equality" (Ratio 1:1) was evidently based on prey size differences, rather than on differences in palatability or catchability.

An apparent exception to the general failure to switch was the initial (Day 2) disproportionate response to small crickets when these were five times as abundant as large mealworms. This phenomenon was most pronounced at the low drift rate, perhaps because preference was weaker at reduced levels of prey abundance (Murdoch et al. 1975). For most of the experimental period, large size discrepancies may have minimized the effect of prey abundance. While the available data do not rule out the significance of switching by brown trout, they do suggest that within a given area prey size may be more important than abundance in prey selection. If trout predation stabilizes prey communities, this may result mainly from movement into areas containing disproportionately high numbers of a prey species. In fact, the clearest documentation of switching in fishes (Murdoch et al. 1975) has involved predation by guppies (Poecilia reticulata) on two spatially separated species. As yet nothing is known of the ability of fishes to "anticipate" predictable patterns of prey availability (emergences), and the role of temporal heterogeneity in switching has not been investigated.

I did not attempt to quantify hunger within feeding periods, although this could be done in terms of gut capactiy (e.g., Ware 1971). My observation of parallel shifts in response to the two larger prey types suggests that considerable change in stomach fullness may fail to be reflected in greater selectivity. The results seem to contrast with those of Ivlev (1961), who concluded that satiation was the mechanism that increased selectivity of carp (Cyprinus carpio). The apparent lack of effect of hunger on prey selectivity of brown trout, however, could have been caused both by an absence of differences in palatability between the prey types, and by the short duration of the daily sessions.

That experience can modify reaction distance (and thus prey selection) directly has been proposed by Ware (1971) to explain feeding behavior in rainbow trout. Similarly, Thomas (1977) proposed that, in addition to satiation effects, short-term positive and negative changes in motivation occur following "eat" and "reject" episodes, respectively. In sticklebacks these motivational effects appear to change both the search path and the probability of eating a particular item. Recent (unpublished) data suggest that short-term effects may also characterize brown trout feeding, particularly when prey species differ in palatability.

Ware (1972), Hansen (1972) and others have shown that predation rates can be stimulated by depriving fish of food for varying lengths of time. In systems where prey distributions are spatially discontinuous, a major role of hunger might be to regulate the rate of movement among microhabitats. Thus, Beukema (1968) found that, in addition to increasing the number of complete responses to prey, higher hunger levels increased the swimming activity of sticklebacks. Presumably, nearly satiated trout would be least likely to move within the water column, and this could contribute indi~~cate~~rectly to selective predation in drift feeders.

Brown Trout as Optimal Foragers

A basic hypothesis in most studies of optimal foraging is that net rate of energy intake will be maximized (Pyke et al. 1977). I assumed, provisionally, that equal energy expenditure was required in capturing the three prey species, and therefore, that total energy intake was an appropriate "currency" (Schoener 1971) to be maximized. Brown trout ultimately achieved as much as 91% of an hypothetical optimum diet in the laboratory. This required a relatively long period, during which familiarity was gained with new food types. The period was probably exaggerated by the short duration (30 min) of the feeding sessions. Although such brief periods of availability do occur in natural streams, this is the lower end of a spectrum extending to at least 5 h. Another factor that may have prolonged the approach to an optimum diet was the 3-wk exposure to brine shrimp prior to the sudden introduction of (energetically) more desirable prey. Nevertheless, the results suggest that models of prey selection need to incorporate the behavioral capabilities of predators, since the time to acquire an appropriate response can be appreciable.

Even after 800-1200 prey captures during 6 d the trout periodically sampled areas of low density, as well as species of low energy content. Such sampling appears to represent a "cost". Yet, leaving areas of high density permits sampling of areas where density may have recently become even higher. Within a given area, periodic sampling of even the least desirable prey (e.g., brine shrimp) may function to maintain the ability to respond rapidly to subsequent changes in abundance. Because of constraints imposed by the distribution of the prey and the behavioral capabilities of the predator, therefore, an optimal feeding strategy need not be directly reflected in a maximum energy intake. This generalization seems to complement the theoretical treatment by Pulliam (1974).

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LITERATURE CITED

Allen, J. D. 1975. The distributional ecology and diversity of benthic insects in Cement Creek, Colorado. Ecology 56:1040-1053.

Beukema, J. J. 1968. Predation by the three-spined stickleback (*Gasterosteus aculeatus* L.): The influence of hunger and experience. Behavior 31:1-126.

Bisson, P. A. 1978. Diel food selection by two sizes of rainbow trout (*Salmo gairdneri*) in an experimental stream. J. Fish. Res. Board Can 35:971-975.

Bryan, J. E. and P. A. Larkin. 1972. Food specialization by individual trout. J. Fish. Res. Board Can. 29:1615-1624.

Cummins, K. W. and J. C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Int. Verein. Theor. Angew. Limnol. Mitt. No. 18. 158 pp.

Elliott, J. M. 1972. Rates of gastric evacuation in brown trout, *Salmo trutta* L. Freshwater Biol. 2:1-18.

Emlen, R. M. 1966. The role of time and energy in food preference. Amer. Nat. 100:611-617.

Englemann, M. D. 1961. The role of soil arthropods in the energetics of an old field community. Ecol. Monogr. 31:221-238.

Griffith, J. S. 1974. Utilization of invertebrate drift by brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Salmo clarki*) in small streams in Idaho. Trans. Amer. Fish. Soc. 103(3):440-447.

Hansen, A. S. 1972. The role of prior feeding and temperature in the regulation of food uptake by brook trout. Ph.D. dissertation, University of Michigan, Ann Arbor. 167 p.

Holling, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation.

Mem. Entomol. Soc. Canada No. 45. 60 pp.

Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. (Transl. from Russian by D. Scott.) New Haven: Yale University Press, 302 pp.

Kitchell, J. F. and J. T. Windell. 1970. Nutritional value of algae to bluegill sunfish, *Lepomis macrochirus*. Copeia 1970: 186-190.

Krebs, J. R. 1973. Behavioral aspects of predation. Pages 72-111 in Perspectives in ethology, P.P.G. Bateson and P.H. Klopfer (eds). New York: Plenum Press. 336 pp.

MacArthur, R. H. and E. R. Pianka. 1966. On optimal use of a patchy environment. Amer. Natur. 100:603-609.

MacPhee, C. 1961. An experimental study of competition for food in fish. Ecology 42:666-681.

Metz, J. P. 1974. Die invertebratendrift an der Oberflache eines Voralpenflusses und ihre selektive Ausnutzung durch die Regenbogenforellen (*Salmo gairdneri*). Oecologia 14:247-267.

Morrison, D. F. 1967. Multivariate statistical methods. New York: McGraw-Hill Book Co. 338 pp.

Murdoch, W. W. 1969. Switching in general predators: Experiments on predator specificity and stability of prey populations. Ecol. Monogr. 39:335-354.

Murdoch, W. W. and A. Oaten. 1975. Predation and population stability. Advances in Ecological Research 9:1-131.

Murdoch, W. W., S. Avery, and M. E. B. Smyth. 1975. Switching in predatory fish. Ecology 56:1094-1105.

O'Brien, J. W., N. A. Slade, and G. L. Vinyard. 1976. Apparent size as the determinant of prey selection by bluegill sunfish (*Lepomis macrochirus*). Ecology 57:1304-1310.

Pulliam, H. R. 1974. On the theory of optimal diet. Amer. Natur. 108:59-74.

Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. Quart. Rev. Biol. 201:1-18.

Reimers, N. 1957. Some aspects of the relation between stream foods and trout survival. Calif. Fish and Game. 43:43-69.

Ringler, N. H. 1975. The mechanism of selective predation in drift-feeding brown trout (*Salmo trutta*). Ph.D. dissertation. The University of Michigan, Ann Arbor. 198 p.

Royama, T. 1970. Factors governing the hunting behavior and selection of food by the great tit (*Parus major* L.). J. Anim. Ecol. 39:619-669.

Schoener, T. W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 11:369-404.

Slobodkin, L. B. and S. Richman. 1961. Calories/gm in species of animals. Nature 191:299.

Thomas, G. 1977. The influence of eating and rejecting prey items upon feeding and food searching behavior in *Gasterosteus aculeatus* L. Anim. Behav. 25(1):52-66.

Tinbergen, L. 1960. The natural control of insects in pine woods. Arch. Neerl. Zool. 13:265-343.

Von Hentig, R. 1971. Einfluss von salzgehalt und temperature auf entwicklung, wachstum, fortpflanzung und energiebilanz von *Artemia salina*. Marine Biol. (Berlin) 9:145-182.

Ware, D. M. 1971. Predation by rainbow trout (*Salmo gairdneri*): The effect of experience. J. Fish. Res. Board Can. 28:1847-1852.

Ware, D. M. 1972. Predation by rainbow trout (*Salmo gairdneri*): The influence of hunger, prey density, and prey size. J. Fish. Res. Board Can. 29:1193-1201.

Waters, T. F. 1972. The drift of stream insects. Ann. Rev. Entomol. 17:253-272.

Werner. E. E. and D. J. Hall. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*) Ecology 55:1042-1052.

TABLE 1

Mean Weight and Linear Dimensions of Prey Species

	Weight (g)	Length (mm)	Width (mm)	Visible surface area (length x width) (mm^2)
Brine Shrimp	0.0070	2.69	--	--
Small Crickets	0.0127	5.71	1.84	10.51
Small Mealworms	0.0128	7.74	1.21	9.37
Large Crickets	0.0296	9.30	2.98	27.71
Large Mealworms	0.0282	13.48	2.01	27.09

TABLE 2

Estimates of Energy Equivalents of the Prey

	Joules/g Ash-Free Dry Weight	Source	Best Estimate Derived from Available Data	Ash-Free Dry Weight/ Wet Weight[1] mean ± 2 SE (N)	Calculated Joules/g Wet Weight
Brine Shrimp	23218	Von Hentig 1971	22862	0.09159 ± 0.00053 (18)	2093.9
	22510	Calculated from chemical composition of commercial product			
Mealworms	26418	Slobodkin and Richmann 1961			
	27799[2]	Englemann 1961	27816	0.29442 ± 0.00129 (29)	8189.5
	29234	Kitchell and Windell 1970			

TABLE 2 (continued)

	Joules/g Ash-Free Dry Weight	Source	Best Estimate Derived from Available Data	Ash-Free Dry Weight/ Wet Weight[1] mean ± 2 SE (N)	Calculated Joules/g Wet Weight
Crickets	24669	Cummins and Wuycheck 1971	24669	0.32840 ± 0.00345 (28)	8101.4

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[1] No significant differences ($P < 0.05$) were detected in moisture content of small as compared to large prey of a given species.

[2] The published value was 6579 calories/g (= 27527 J)dry weight; the figure here is corrected for ash weight.

Table ~~5~~ 3

Estimated Energy Content Per Prey Item

	Mean Weight (g) ± 2 SE	Estimated Joules/g Wet Weight (From Table 2)	Joules Per Prey Item
Brine Shrimp	0.0070 ± 0.00000	2093.9	14.64
Small Crickets	0.01276 ± 0.00002	8101.4	103.39
Small Mealworms	0.01284 ± 0.00003	8189.5	105.14
Large Crickets	0.02957 ± 0.00006	8101.4	239.53
Large Mealworms	0.02813 ± 0.00005	8189.5	230.37

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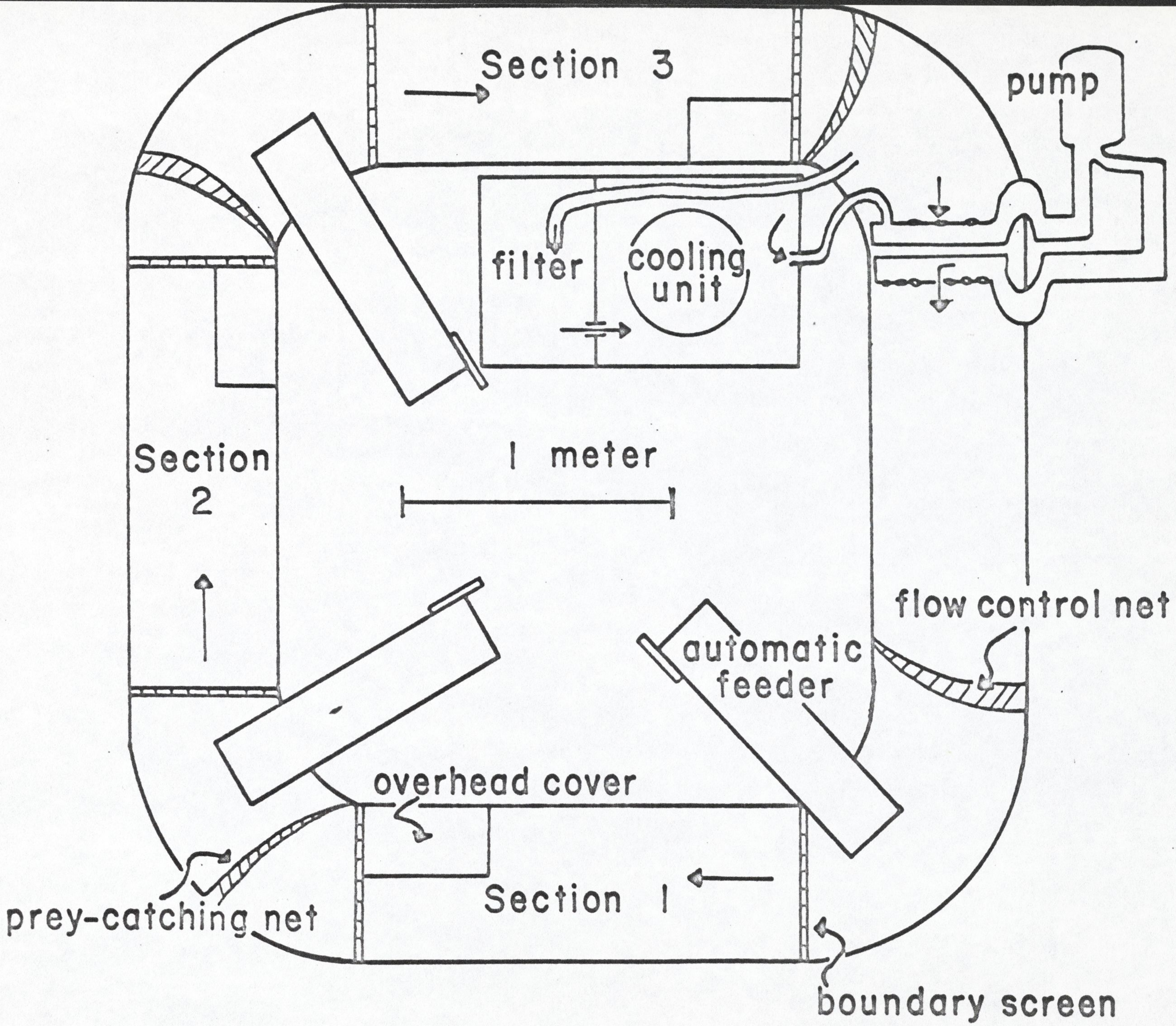
Figure 1	Diagram of the experimental stream, as seen from above with lighting canopy and covering screen removed. Arrows indicate direction of water circulation.
Figure 2	delete Number of prey eaten as a function of time at prey size Ratio (small:large) 1:1. Each point represents the response to a prey species during a 5-min interval of the daily feeding period. As in all experiments, only brine shrimp (34/min) were available on Day 1. Prey on Days 2-7 were brine shrimp (34/min), small mealworms (5/min) and large crickets (5/min).
Figure ~~3~~ 2	Mean percentage of prey eaten as a function of time (n = 3 fish at each prey ratio of small:large). Drift rate of brine shrimp = 34/min; drift rate of mealworms + crickets = 10/min. Species combinations were A. brine shrimp, small mealworms and large crickets; B. brine shrimp, small crickets and large mealworms.
Figure 4	delete Percentage of each prey species eaten as a function of time at prey Ratio 1:1. Drift rate of brine shrimp = 34/min; drift rate of mealworms + crickets = 5/min.
Figure ~~5~~ 3	Comparison of the mean daily response to three prey types. Data are averaged over three prey ratios and two species combinations (n = 18 fish). Drift rate of mealworms + crickets = 10/min. Dashed brine shrimp curve was calculated on the basis of 1021 available brine shrimp; solid curve was calculated by assuming an "effective availability" of 200 brine shrimp.

Figure ~~6~~ 4 Comparison of the mean daily response among all prey species. Data are averaged over three prey ratios (n = 9 for each drift rate). Brine shrimp curve was calculated by assuming an "effective availability" of 200 brine shrimp. H = high drift rate; L = low drift rate.

Figure ~~7~~ 5 Comparison of "electivity" (Ivlev 1961) at high and low drift rates (n = 9 fish at each drift rate). Solid lines indicate electivity for large mealworms; dashed lines show electivity for brine shrimp.

Figure ~~8~~ 6 Daily changes in the mean energy content of an hypothetical optimum diet (OPT) based on a ranking of prey in order of size, the observed diet (OBS), and a random diet (RND) obtained by feeding on prey in proportion to their abundance in the drift. Mealworms + crickets = 10/min; brine shrimp = 34/min. Data are averaged over both species combinations (n = 6 fish for each ratio).

Figure ~~9~~ 7 Comparison among prey ratios of the daily optimization index. Data are averaged over both species combinations (n = 6 fish for each ratio). A. High drift rate (brine shrimp = 34/min; mealworms + crickets = 10/min). B. Low drift rate (brine shrimp = 34/min; mealworms + crickets = 5/min).


Section 3
pump
filter
cooling unit
Section 2
1 meter
flow control net
automatic feeder
overhead cover
prey-catching net
Section 1
boundary screen

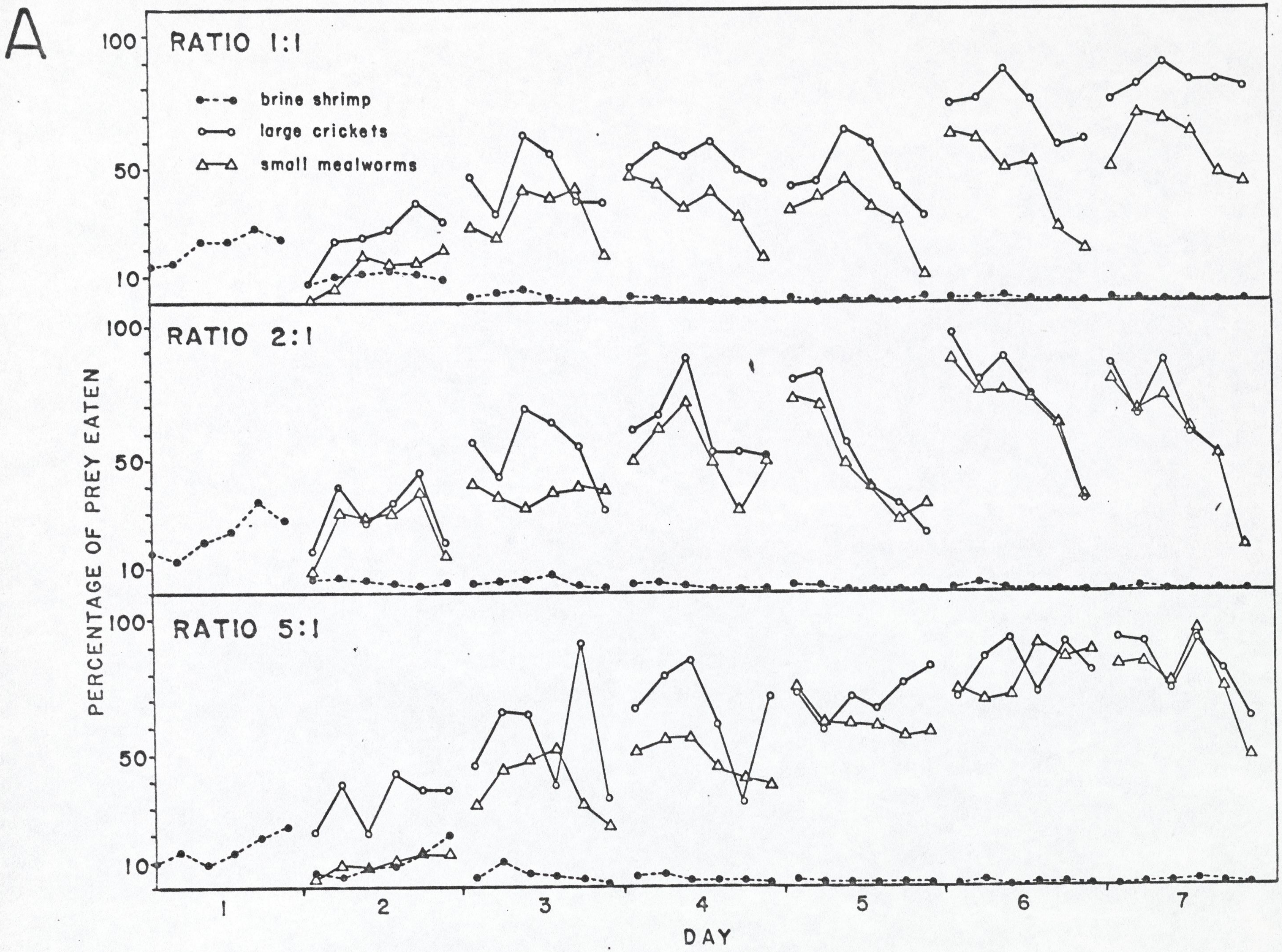

A
RATIO 1:1
brine shrimp
large crickets
small mealworms
RATIO 2:1
RATIO 5:1
100
50
10
PERCENTAGE OF PREY EATEN
1
2
3
4
5
6
7
DAY

FIG 3A

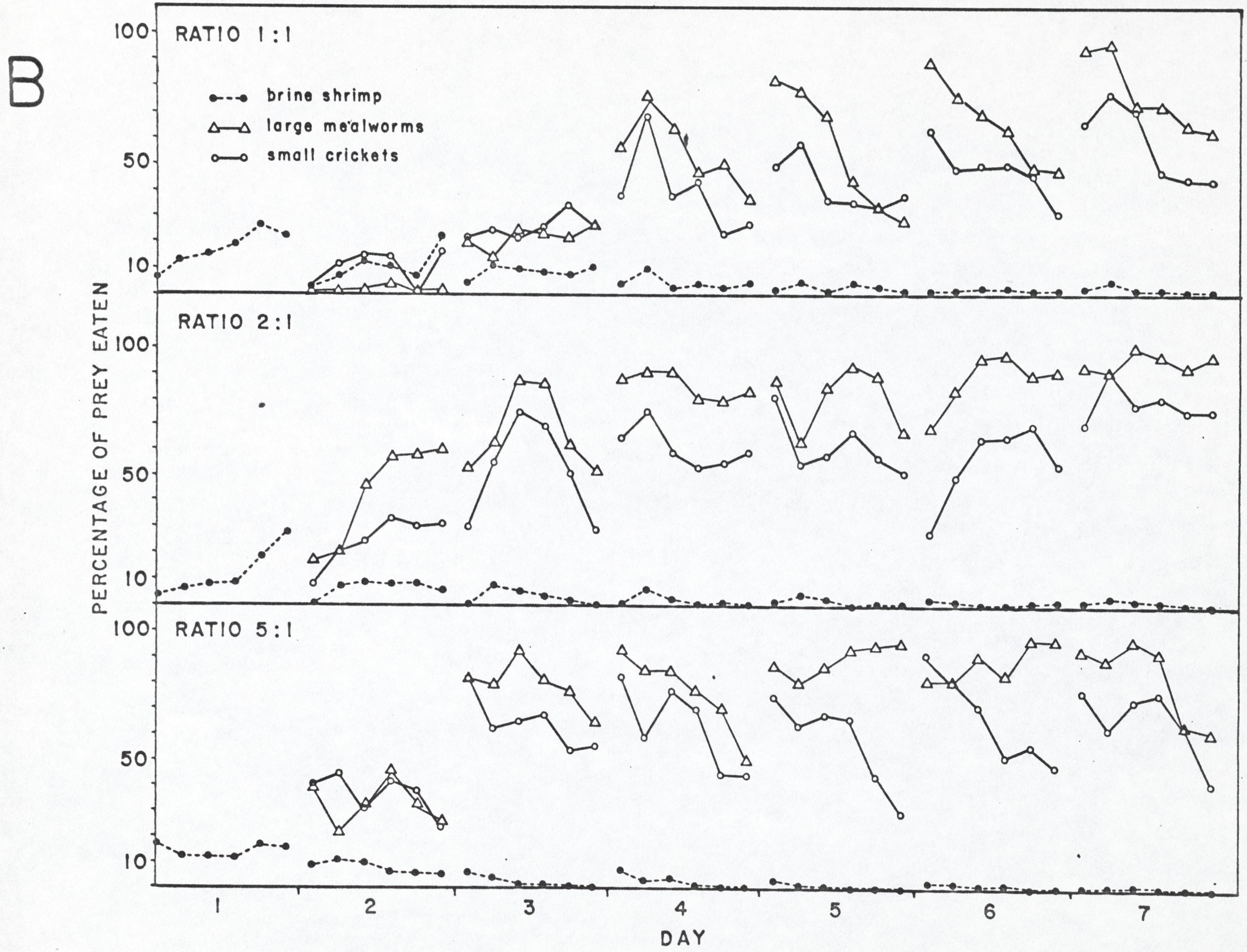

B
RATIO 1:1
brine shrimp
large mealworms
small crickets
RATIO 2:1
RATIO 5:1
100
50
10
PERCENTAGE OF PREY EATEN
1
2
3
4
5
6
7
DAY

Fig 2B

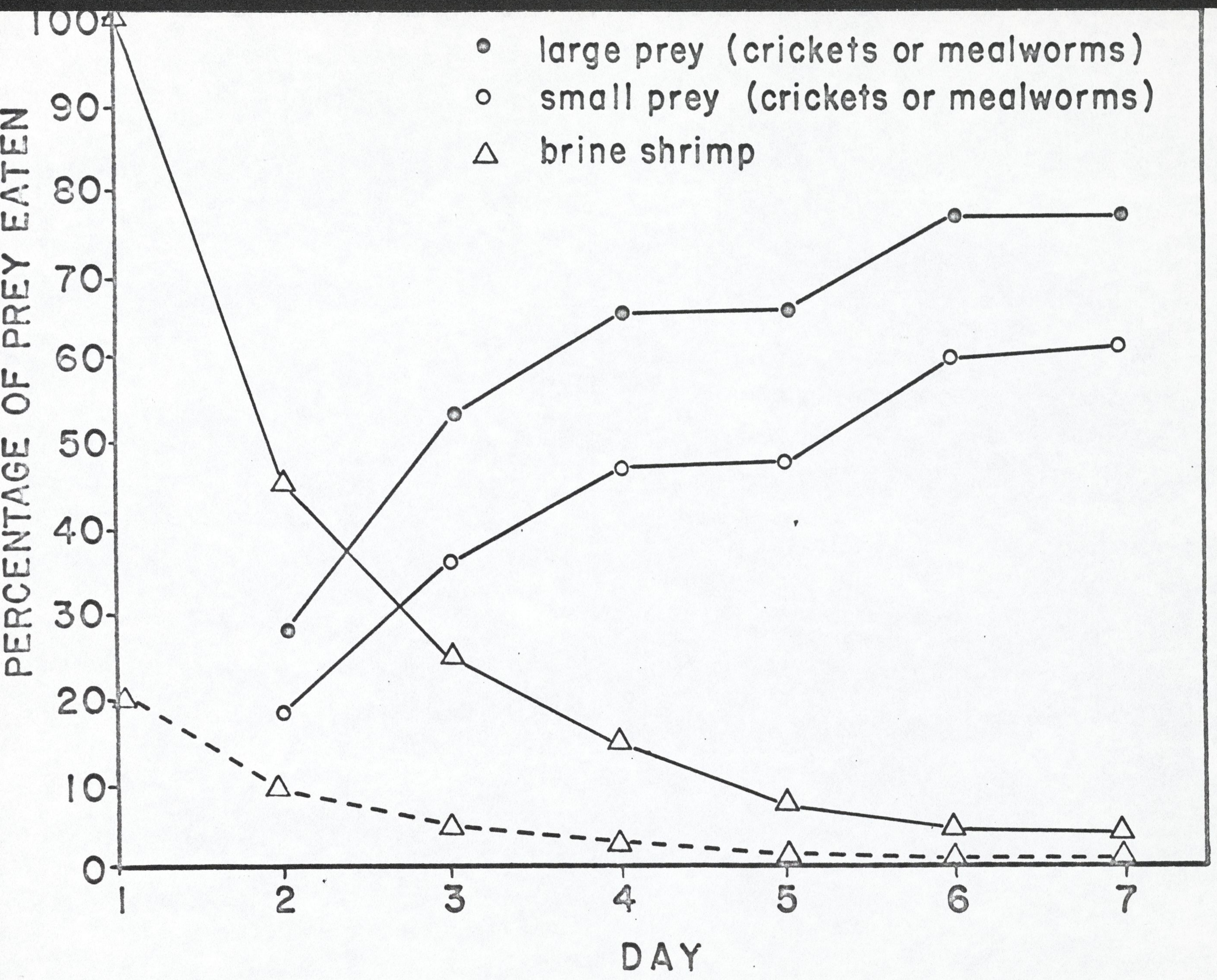

large prey (crickets or mealworms)
small prey (crickets or mealworms)
brine shrimp
PERCENTAGE OF PREY EATEN
100
90
80
70
60
50
40
30
20
10
0
1
2
3
4
5
6
7
DAY

FIG ~~2~~3

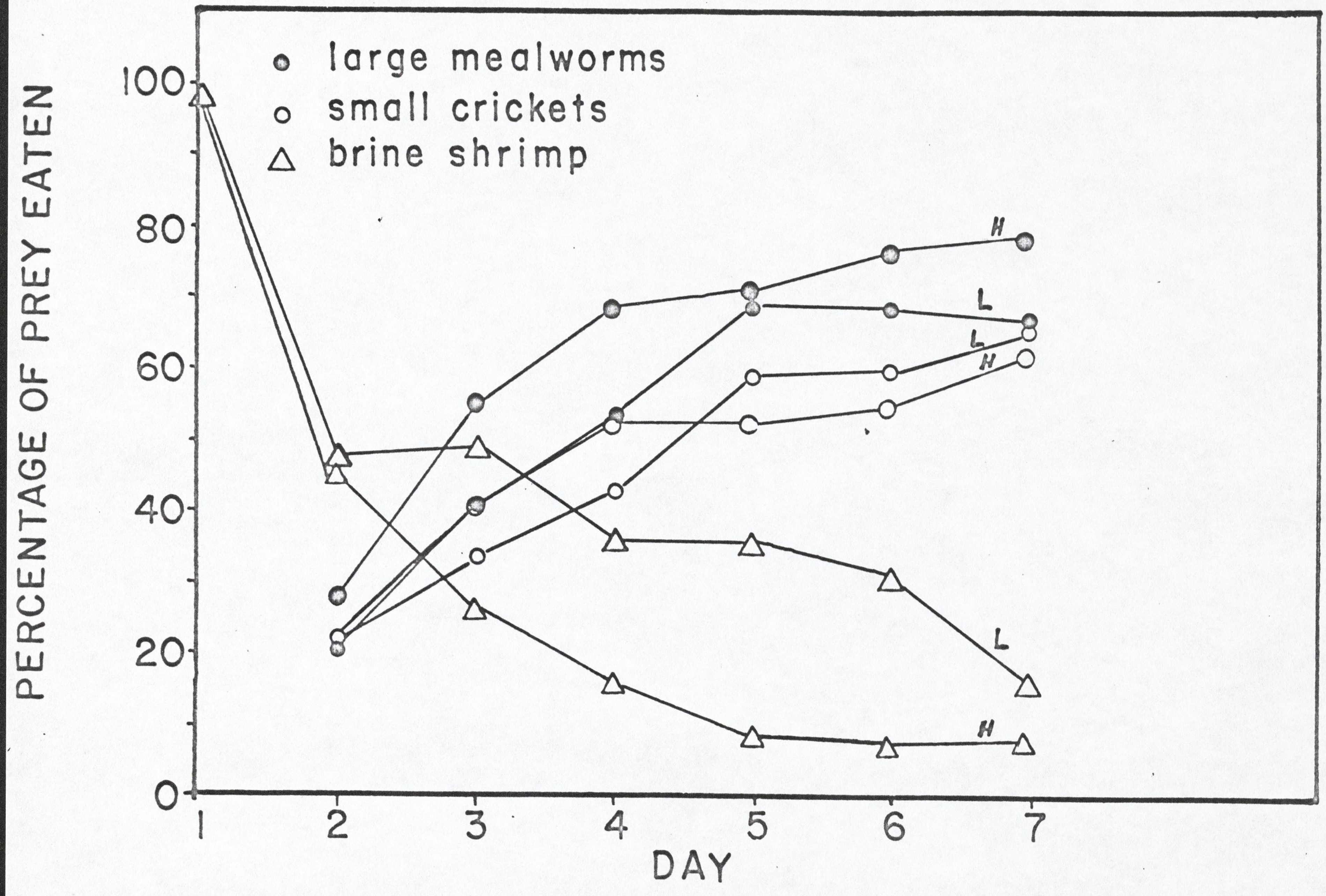
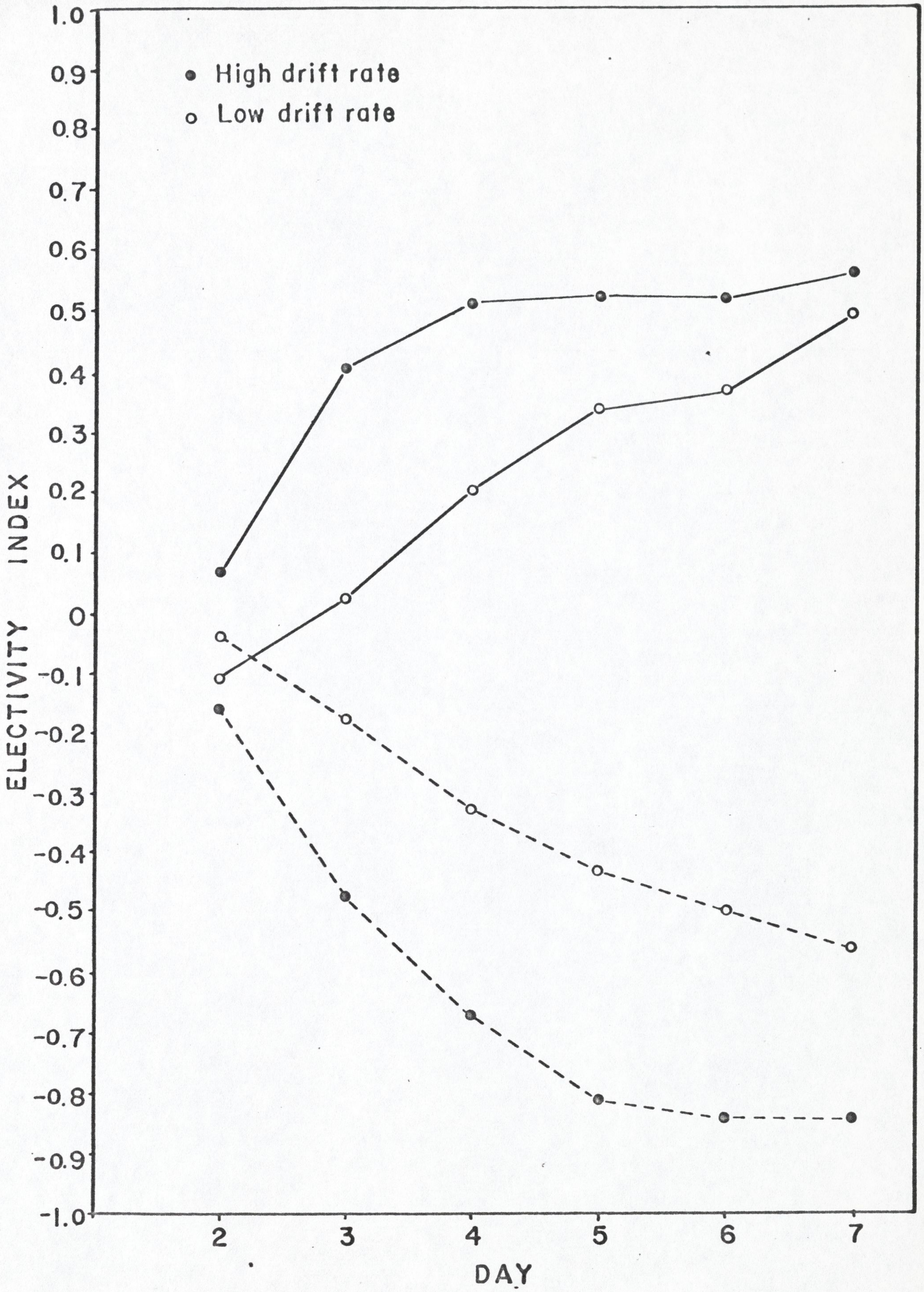

large mealworms
small crickets
brine shrimp
PERCENTAGE OF PREY EATEN
100
80
60
40
20
0
1
2
3
4
5
6
7
DAY
H
L
L
H
L
H

FIG 4



● High drift rate
○ Low drift rate
ELECTIVITY INDEX
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
-0.5
-0.6
-0.7
-0.8
-0.9
-1.0
2
3
4
5
6
7
DAY

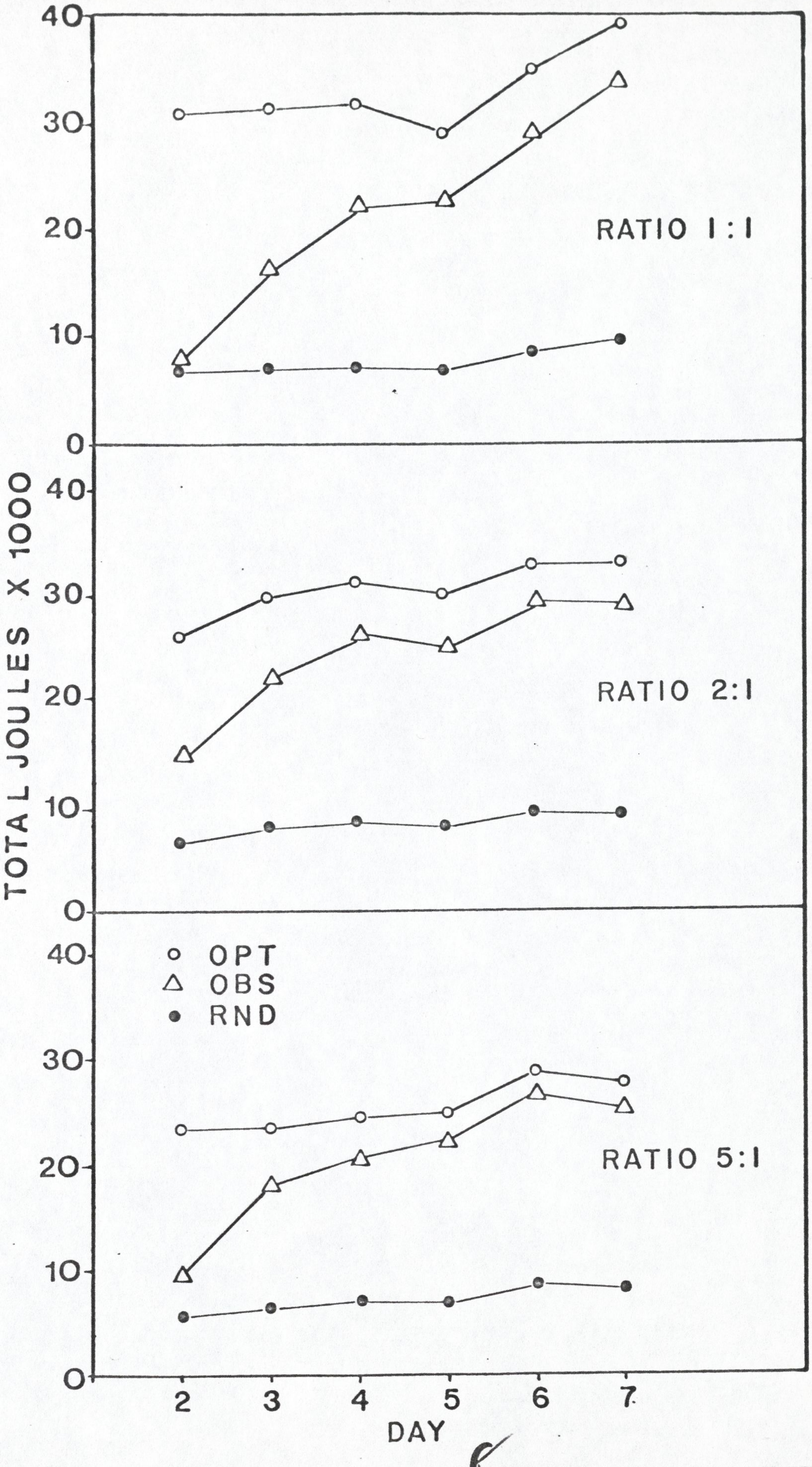
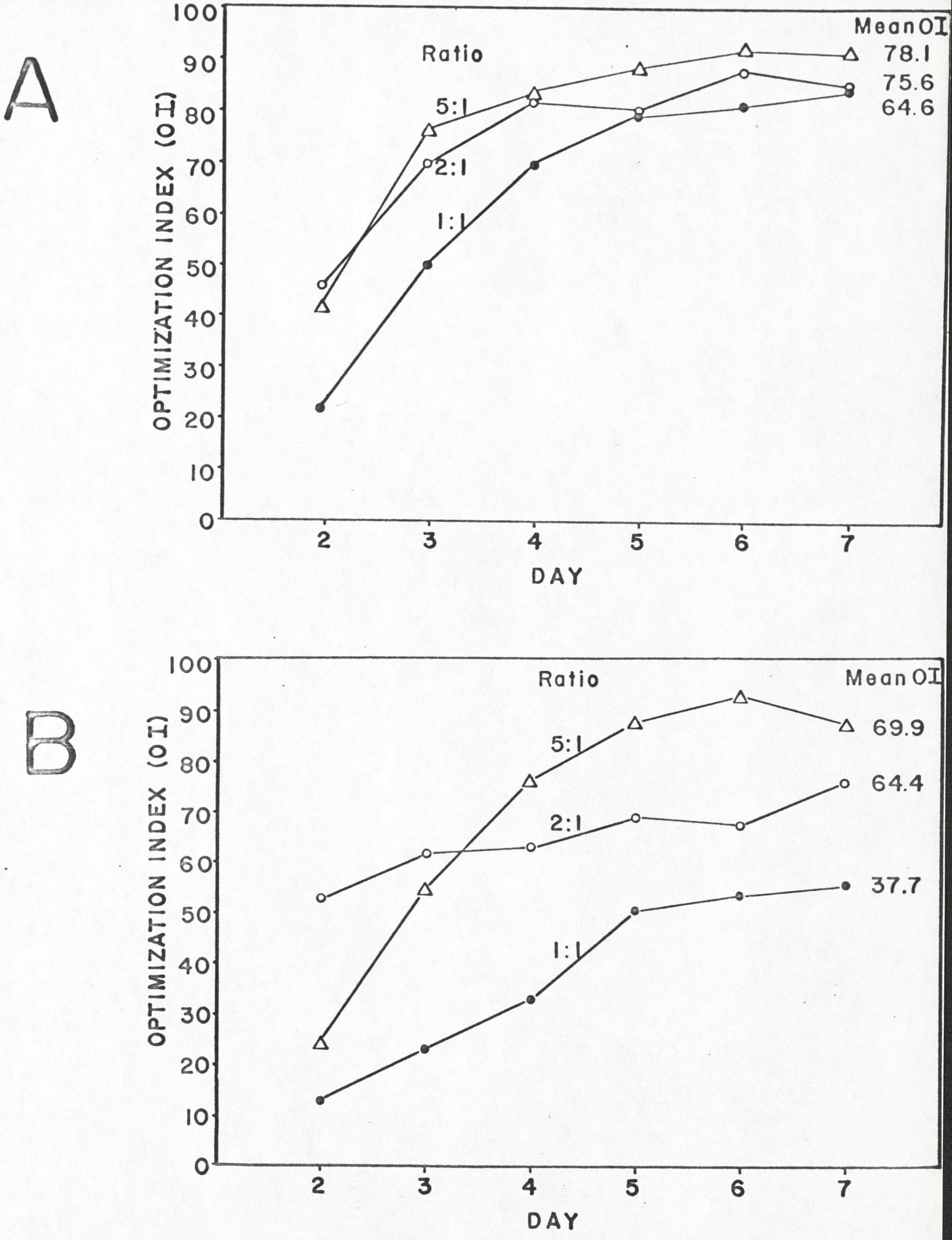

TOTAL JOULES X 1000
40
30
20
10
0
RATIO 1:1
RATIO 2:1
RATIO 5:1
○ OPT
△ OBS
● RND
2
3
4
5
6
7
DAY

FIG ~~8~~ 6


A
Ratio
Mean OI
5:1
2:1
1:1
78.1
75.6
64.6
OPTIMIZATION INDEX (OI)
0
10
20
30
40
50
60
70
80
90
100
2
3
4
5
6
7
DAY
B
Ratio
Mean OI
5:1
2:1
1:1
69.9
64.4
37.7
OPTIMIZATION INDEX (OI)
0
10
20
30
40
50
60
70
80
90
100
2
3
4
5
6
7
DAY

7